

REVIEW



Review and Meta-Analysis of the Environmental Biology and Potential Invasiveness of a Poorly-Studied Cyprinid, the Ide *Leuciscus idus*

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ABSTRACT

The ide *Leuciscus idus* is a large-bodied cyprinid native to freshwaters around the Baltic, Black, Caspian, White, Barents, Kara, Laptev and North seas as well as the Aral Sea region. Historically an important commercial species, the ide is used in recreational fisheries and as an ornamental fish, and is subject to translocation and stocking events. The ide is less well-studied than many European cyprinids and relatively little is known of the risks it poses to native species and ecosystems where introduced. The present review and meta-analysis examine available data on the ide's environmental biology to provide an assessment of its potential invasiveness. A long-lived, omnivorous species, the ide is a habitat generalist that inhabits lowland rivers and nutrient-rich lakes, but also some brackish waters where it is facultatively anadromous. The ide displays variable age and length at maturity and asymptotic growth in body length, can be highly productive and migratory, and can withstand variable environmental conditions. Despite several attributes that should facilitate acclimation to novel environments, the ide has established relatively few self-sustaining populations outside its native range, and is therefore not currently considered to be invasive. However, as introductions are likely to continue, increased propagule pressure could lead to the development of invasive non-native populations in some locations.

KEYWORDS

Morphology; distribution; diet; habitat use; growth; reproduction; parasites; non-native species; environmental impact

1. Introduction

Translocations and introductions of freshwater fish species have a long history in Europe (Copp et al. 2005). Some of these species, such as the ide *Leuciscus idus*, have received relatively little scientific study in both their native and introduced ranges (e.g., Brabrand 1985; Kulíšková et al. 2009; Rohtla et al. 2015a). This is despite the ide's domestication and increased use in restoration aquaculture (e.g., Krejszeff et al. 2009; Kupren et al. 2010). Historically a species of economic importance (e.g., Järvalt et al. 2003;

Ståhlberg and Svanberg 2011), commercial fisheries for ide have existed in the rivers Ob and Irtysh of East Siberia (Berg 1949; Zhuravlev and Solovov 1984), as well as in some parts of the Baltic Sea, where angling for anadromous populations is still common (Järvalt et al. 2003; Skovrind et al. 2016). The current economic importance of ide in North America (e.g., Mandrak et al. 2014; Howeth et al. 2016) and in some European countries relates to the species' use as a garden pond fish (Vooren 1972; Lever 1977; Copp et al. 2005; Hanel et al. 2011; Harzevili et al. 2012) and as a

sport fish for recreational angling (Järvalt et al. 2003), including the ornamental varieties (Hickley and Chare 2004) known as blue orfe and golden orfe (Smith 1995). The name “ide” is from Swedish *id*, originally referring to its bright color. According to “Svensk ordbok” (<http://svenska.se>), it is old Swedish/old Norse and can be dated to 1459–1460 (medieval accountancy documents from Stockholm). Its likely original meaning was *glödande* (glowing) or *strålande* (radiant).

Although the ide has been introduced to several parts of the world (e.g., North America, New Zealand, UK, and non-native parts of continental Europe), making it a potentially invasive species, there remains a paucity of information regarding the ide’s potential threat to native species and ecosystems. In fact, with such poorly-studied species, non-native species risk assessments tend to be characterized by elevated uncertainty (Hill 2009; Humair et al. 2014). To mitigate this, extensive reviews of available past and current literature, from both peer-reviewed and “gray” sources, have proved useful to inform the risk analysis process with regard to less well-studied species (e.g., Copp, Britton et al. 2009; Copp et al. 2016). Following this approach, the aim of the present study was to carry out a review and meta-analysis of available data and information on the environmental biology of ide, encompassing the species’ morphology, distribution, habitat use, ontogeny and growth, reproduction, diet, predators, and parasites and pathogens under natural conditions. The present study therefore excludes all literature that covers the use of ide in aquaculture, except for those documents that have a direct bearing on its environmental biology. The present review concludes with a general discussion on the species’ potential invasiveness and consequential threat to native species and ecosystems.

2. Review

2.1. Morphology

The genus *Leuciscus* is one of several genera of the family Cyprinidae in Eurasia. The ide has a streamlined body, with a wide head, blunt snout, and terminal mouth. The dimensions and position of the fins indicate that ide is mainly a still-water species, though this preference for lentic waters appears to hold for juvenile individuals, as sub-adults show a preference for water velocities up to 0.8 m s^{-1} , with no such preference demonstrated by adults (Scholten et al. 2003). Dorsal and ventral fins are almost opposite to each other, with the anal fin having a straight or slightly concave hind edge. The dorsal fin usually has

three unbranched and eight branched rays, though specimens from the rivers Ob, Kama and Yenisei (Siberia) and from Lake Võrtsjärv (Estonia) have been reported to have 7–9 branched rays (Berg 1949; Järvalt et al. 2003). The pectoral fins have one unbranched and 16–17 branched rays, whereas the respective numbers in the ventral and anal fins are two and eight, and three and 8–12, respectively (Järvalt et al. 2003). In male ide, the first unbranched ray of the pectoral fin is much thicker than in females (Järvalt et al. 2003) and all fins are olive-gray or reddish in color (Tadajewska 2000; Järvalt et al. 2003). Pharyngeal teeth are in two rows (3.5–5.3, rarely 2.5–5.2) and hooked at the top (Järvalt et al. 2003). Eyes are slightly yellow, the back is green to blackish gray, sides are silvery, and the belly is white. During the spawning period, nuptial tubercles are present on the head and body of both sexes, but to a lesser extent on females (Järvalt et al. 2003). The number of scales of the lateral line varies moderately between populations, ranging from 51 to 65 (Veld 1969; Järvalt et al. 2003). The number of gill rakers and vertebrae is usually 10–15 and 45–48, respectively (Järvalt et al. 2003).

There has been little study of the geographical variability in ide morphology. Xantoric varieties (*L. idus* aberr. *orfus*) have been reared in Europe since the 18th century, perhaps resulting from intentional selection of mutated individuals (Berg 1949). Currently, the ornamental varieties of ide, golden and blue orfe, are reared in Belgium, the Netherlands, New Zealand, Germany, Italy, and the USA (Koopmans and Van Emmerik 2006), with imports to the UK in 2000–2004 coming from the latter three countries (Copp et al. 2007). Specimens of golden and blue orfe tend not to differ from the wild form in terms of life-history traits, but may exhibit some variation in the proportions of their body shape (Witkowski et al. 1997).

2.2. Distribution

The native distribution of ide encompasses river basins that drain into the Baltic, Black, Caspian, White, Barents, Kara, and Laptev seas, extending from the River Rhine basin (North Sea) in the west to Sweden and Finland in the north, to the River Lena basin and the Aral Sea region in the east, and to the Alps and the northern parts of the Black and Caspian seas basins in the south (Figure 1). The ide is also a common species in the brackish Baltic, Caspian, and Azov seas (Järvalt et al. 2003; Bogutskaya and Naseka 2006). Genetic research on ide is limited to few studies of population structure and demographic history,



Figure 1. Native (gray) and introduced (red) distributional ranges of ide *Leuciscus idus* in Europe. Adapted from Freyhof and Kottelat (2008) and updated with information from Cala (1970), Järvalt et al. (2003) and Bogutskaya and Naseka (2006).

which have demonstrated higher levels of differentiation amongst freshwater relative to anadromous populations (Wolter et al. 2003; Barinova et al. 2004; Zhigileva et al. 2010; Skovrind et al. 2016).

The ide has been introduced into some European countries outside its native Eurasian range (Figure 1), however its native status in some countries remains contentious. For example, in France, Spain, the Netherlands and Great Britain, the ide is listed as having been introduced with successfully established self-sustaining populations (Holčík 1991; Elvira 2001). In the case of France (Keith et al. 2011), the ide may be native to eastern waters that drain into the Rhine basin, whereas the ornamental variety “ide rouge” has been introduced elsewhere (Spillmann 1961). At least two Dutch sources refer to the ide as being native to the Netherlands (i.e., Koopmans and Van Emmerik 2006; Schiphouwer et al. 2014), which includes the River Rhine (Leuven et al. 2011). Undated specimens of ide in the collection of the Muséum National d’Histoire Naturelle de Paris are attributed to the Rhine and two of its tributaries in France, the rivers Moselle and Ill (Pascal et al. 2003). A similar uncertainty exists for the Iberian Peninsula, where the ide was previously listed amongst fish species introduced to France but not found in Iberia (Clavero and García-Berthou 2006). A subsequent review (Leunda 2010) reported ide to have been introduced to Iberia in the 2000s, presumably via the ornamental trade, which is a

well-known vector for non-native fish introductions to open waters (Chan et al. 2019). Although previously reported as present in Italy (Copp et al. 2005), a recent re-evaluation found this not to be the case (P. Bianco, personal communication). Greater certainty exists for the UK, where an initial introduction in 1874 to lakes at Woburn Abbey (Bedfordshire, England) and reports in 1879 of the species in the wild are well documented (Wheeler and Maitland 1973; Lever 1977). During this era of “acclimation societies” (mid-19th to early 20th centuries), introductions of fishes for ornamental purposes, such as pumpkinseed *Lepomis gibbosus*, golden orfe and bitterling *Rhodeus amarus*, occurred both in England (Copp et al. 2007) and elsewhere (Copp et al. 2005), including ponds of aristocratic estates of the Russian Empire beginning in 1902 (Virbickas 2000). Subsequent introductions of the ide, especially golden and blue orfe, for angling have occurred into water bodies throughout most of England and Wales (Wheeler and Maitland 1973; Hickley and Chare 2004), where the ide is now present in ponds and water courses (Copp et al. 2006, 2007).

Translocations of the ide to non-native locations have also occurred within its native range. For example, golden orfe was introduced to a natural alpine lake (Štrbské Pleso), which is located at 1346 m a.s.l. in the High Tatra mountains of Slovakia (Balon and Žitňan 1964). This introduction occurred in the 1930s or early 1940s, and the population still thrives

in this lake despite unfavorable conditions of cold water and ice cover lasting for almost six months a year. Introductions outside of Europe include North America and New Zealand. The ide was initially introduced to the USA in 1877 and has since been recorded in at least 22 states, including golden orfe into garden ponds and aquaculture facilities of California (Dill and Cordone 1997). Despite a long history of introductions in the USA, a paucity of confirmed, recent records of established populations in the USA suggests that most of these introductions have been unsuccessful. With the records being poor and contradictory (Nico et al. 2020), there is high uncertainty about the current status and distribution of ide in the USA. In Canada, there are currently no reported wild populations. Furthermore, the ide is not currently known to occur in the Great Lakes region, though occurrence records for the species do exist from all of the Great Lakes states except Michigan and Wisconsin (Nico et al. 2020). Further, in the mid-1980s, golden orfe was introduced to several ponds north of Auckland in New Zealand, and earlier reports indicate that the species may have established self-sustaining populations in these small ponds or lakes (Chadderton 2003), though its range was believed to be highly localized (McDowall 2000). Despite extensive surveys (B. David, personal communication), there have been no recent confirmed reports on the continued presence of ide in New Zealand (Collier and Grainger 2015).

2.3. Habitat use

The ide is a benthopelagic, rheophilic, and potamodromous species that can occupy a wide range of habitats, encompassing various types of fresh and brackish water bodies. The ide's habitat is described as a general preference for deep, clean, and cool water of rivers and lakes (Wheeler 1978; Witeska et al. 2014), including large, flow-through, nutrient-rich lakes (Cala 1970; Virbickas 2000; Järvalt et al. 2003; Winter and Fredrich 2003; Kulíšková et al. 2009). In the rivers Eg and Uur (Mongolia), ide habitat was described as consisting of slow water velocities in the water column over gravel substratum (Mercado-Silva et al. 2008). The ide is also known to inhabit and feed in brackish estuaries as well as in the Baltic and Caspian seas, where it is commonly found at salinities < 8 (Müller and Berg 1982; Järvalt et al. 2003; Bogutskaya and Naseka 2006). Brackish water ide can usually withstand salinities up to 15 (Van Beek 1999), with extreme examples of populations from the

Öresund Strait (Sweden) and Zuiderzee (Netherlands), where salinities can temporarily reach even 20 psu (Veld 1969; Cala 1970). Finally, sudden influxes of saline waters into these habitats are often responsible for mass ide mortalities (Carl 2012).

The ide uses a variety of habitats during different seasons and life-history stages, tending to inhabit rivers and flood plains in the early spring to spawn, and shallower littoral or shoreline habitats as larvae and juveniles (e.g., Grift et al. 2003). During the winter, the ide typically retreats to deep depressions or refuges in lakes or in the lower stretches of rivers (McDowall 2000). When feeding, the ide seeks out “deep quiet embayments and oxbows, especially where the bottom is overgrown with soft submerged macrophytes” (Dulmaa 1999). In rehabilitated sections of the River Rhine flood plain, juvenile ide were found to be restricted to shallow areas (< 1 m deep) of various water velocities ($0\text{--}0.40$ m s⁻¹) with little (1–5%) submerged terrestrial vegetation cover (Grift et al. 2003). Disappearance of these habitats, caused by river regulation, canalization, and embankments, is thought to be the limiting factor for growth and survival during the early ontogeny of rheophilic cyprinids (Grift et al. 2003).

Given the broad native range of the ide (cf. Section 2.2: *Distribution*), the species tolerates a wide range of temperatures, though the preferred temperature range is 4–20 °C, with minimum and maximum tolerated temperatures of near 0 °C and 35 °C, respectively (Leuven et al. 2011). Laboratory studies of upper lethal temperatures for ide under controlled conditions have revealed an ability of embryos, larvae, and juveniles to acclimatize to, and tolerate, increasing water temperatures (Florez 1972a; Kupren et al. 2010). A general lethal/stress range of 24–27 °C has been reported for this species (Lehtonen 1996).

Despite having broad temperature and salinity tolerances, the ide is intolerant of low dissolved oxygen concentrations, such as in heavily-polluted or eutrophic and turbid waters, with significant mortality of larvae and juveniles at oxygen concentrations < 2 mg L⁻¹ (Florez 1972b). Elevated turbidity can result in larger-scale ide movements, possibly due to reduced foraging efficiency of this visually-oriented predator (Kulíšková et al. 2009), and this could be a contributing factor to declines or reduced abundance in ide populations at heavily-polluted or eutrophic sites in various regions across the species' European range (e.g., Anttila 1973; Penczak and Koszalinska 1993; Kulíšková et al. 2009; Skovrind et al. 2016). The sensitivity and intolerance of ide to pollution has led to

suggestions of the species being used as a bioindicator with regard to water quality (reviewed in Witeska et al. 2014).

The ide is a migratory (potamodromous) species, undergoing annual upstream spawning migrations in early spring (Ciolac 2004), although in the Baltic Sea and nearshore river basins, it is facultatively anadromous, mostly spawning in fresh (Cala 1970; Eriksson and Müller 1982; Rohtla et al. 2015a) and possibly brackish waters (Erm et al. 1970). After spawning, the adults return to their feeding grounds and later to overwintering habitats in deeper waters from where they move very little (e.g., Kulíšková et al. 2009). Early larval stages are subject to downstream drift (e.g., Zitek et al. 2004a, 2004b), and can represent a major proportion of the larvae found in freshwater tidal estuaries (Scheffel and Schirmer 1991) – a relatively common phenomenon of many European riverine fish species (Pavlov 1994). There are few studies that have examined the habitat use and migratory behavior of wild ide inhabiting fresh (Winter and Fredrich 2003; Kulíšková et al. 2009) and brackish waters (Cala 1970; Eriksson and Müller 1982; Rohtla et al. 2015a).

Although the ide is often considered to have a limited home range, it can undertake moderately long migrations (Järvalt et al. 2003), with movements up to 278 km and a mean linear home range of 53.5 km, as reported in the Netherlands (de Leeuw and Winter 2006, 2008). For example, upstream migrations have been documented through fish ladders (Lelek and Libosvářský 1960), though in the cited case, the ide represented only 1% of the observed fishes. Genetic analyses have suggested that, in a 120 km stretch of the River Elbe, the resident ide stock could be considered as a single panmictic unit; this emphasizes the high migration capacity of the species' populations that inhabit the large lowland rivers of central Europe, especially during the spawning period (Wolter et al. 2003). Indeed, great variability in home-range area and spawning migration distance, with co-existing highly-mobile and mainly sedentary individuals, have been reported for individual adult ide in the middle reaches of the rivers Elbe (Germany) and Vecht (Netherlands) (Winter and Fredrich 2003). Spawning-site fidelity has been detected in all tagged ide in the River Vecht, whereas individuals in the River Elbe moved between 60 and 90 km downstream for spawning and tended to use new spawning sites each year (Winter and Fredrich 2003). Variability in spawning migration patterns observed in different regions across the native range of ide reflect differences in river conditions and may indicate a degree of spawning site

plasticity (Kulíšková et al. 2009). In the rivers Elbe and Vecht, differences were also observed in the autumnal upstream migrations to wintering habitats (Winter and Fredrich 2003). A similar study carried out on the upper reaches of the River Elbe found that turbidity significantly increased diurnal movements and home range area, with spawning migrations of 3–100 km always followed by return migrations to the initial tagging location (Kulíšková et al. 2009) – a pattern that is uncommon for most other migratory cyprinids (Smith 1991).

In fresh waters, water retention structures appear to act as barriers to ide dispersal and migratory movements. For example, movement distances of ide in the weir-regulated River Meuse in the Netherlands were shorter than those in free-flowing rivers, and few individuals were observed to migrate further upstream in rivers with fishways at the weirs and hydropower stations (de Leeuw and Winter 2008). The impediment that these structures exert on spawning migrations is one of the mechanisms attributed to population declines of ide and other rheophilic cyprinids in northern Europe (Peñáz and Jurajda 1996; Povž 1996; Schiemer et al. 2004).

Spawning runs of anadromous ide in the vicinity of the Öresund Strait (Baltic Sea) may extend up to 50 km inland within the River Kävlinge, Sweden (Cala 1970). Also, the few Baltic Sea re-captures of ide tagged in a small river near Umeå (Sweden) were all widely distributed along the coast, suggesting that individuals can cover considerable distances in brackish waters (Johnson 1982). Furthermore, an analysis of the genomic structure of ide populations in the western Baltic Sea region suggests that ide can migrate not only along the coastline, but that they may also cover significant distances (e.g., up to 55 km) across deeper waters of the Baltic Sea (Skovrind et al. 2016). On the Estonian coast of the brackish eastern part of the Baltic Sea (salinity \approx 4–7 psu), 72% of the sampled ide had hatched in semi-enclosed, brackish bays that are flushed with fresh water during spring spawning, with only 28% of the individuals hatched in truly lotic environments (Rohtla et al. 2015a). The young-of-year (YoY) of anadromous Baltic ide migrate to the sea during the first two months of life (Rohtla et al. 2015a) or after one year in fresh water (Cala 1970). This difference in age at emigration most likely reflects acclimation to different adult rearing salinities, as migration to higher salinities requires larger body sizes in order to withstand increases in osmotic pressure. Following their migration to the sea, juvenile ide

subsequently perform annual, non-spawning, freshwater migrations together with the spawning adults in the spring (Rohtla et al. 2015a).

2.4. Ontogeny and growth

2.4.1. Early development and growth

The eggs of ide are quite sensitive to environmental perturbations during their initial days of development, with survival as low as 15% in lotic conditions, which drops even further to 1% in lentic conditions with abundant vegetation (Pliszka 1953). Growth rates of ide larvae are amongst the highest in cyprinids, with relative weight gain being rapid during the first year of life and then decreasing with age (Zhukov 1965; Rohtla et al. 2015b). A laboratory study on early ontogeny suggested the presence of eleven different stages in the post-hatch embryonic, larval, and juvenile periods (Kupren et al. 2015). Standard lengths (SL) of ide free embryos at hatching, and at two and six months post-hatch, are 5–6 mm, 16–24 mm, and 45–57 mm, respectively (Cala 1970; Koblickaya 1981; Järvalt et al. 2003). In earthen aquaculture ponds in Flanders (Belgium), mean SL of YoY fish reared on natural foods at the end of the growth season was 88 mm at densities between 200 and 500 kg ha⁻¹. In low density ponds (i.e., 6.9–12.5 kg ha⁻¹), SL after the first growth season was up to 187 mm (Verreycken 1998). Further, in the River Kävlinge (Sweden), growth of YoY ide has been recorded to end in November (Cala 1970).

Somatic growth rates are relatively fast until sexual maturation after which they decrease, with annual growth increments becoming minimal after age 10 years (Rohtla et al. 2015b). This makes the body length/weight relationship a poor predictor of age in larger individuals (Cala 1970; Rohtla et al. 2015b), with otolith weight being a more robust (indirect) parameter (Rohtla et al. 2015b). There are no reported differences in growth rate between male and female ide (Cala 1970; Erm and Kangur 1985). The largest recorded SL is 665 mm (Witkowski et al. 1997) and total body mass 5.2 kg (Finnish Fishing Journal 1973). Total body mass for ide rarely exceeds 3.0 kg in the Baltic Sea and its tributary basins (Cala 1970; Järvalt et al. 2003; M. Rohtla, unpublished data).

2.4.2. Age and growth

Age of ide has historically been estimated from scale annuli (Cala 1970; Järvalt et al. 2003), though otolith thin sections have recently been used (Rohtla et al. 2015b). The formation of scales commences at

18–21 mm SL when ide is 40 to 50 days old (Ristkok 1970; Cala 1971a). If accurate (annulus-based) age estimates are desired, then stained otolith thin sections have been recommended over scales, especially when ageing older individuals, with the only disadvantage being represented by the destructiveness of the method (i.e., otolith extraction requires sacrifice of the fish: Rohtla et al. 2015b; see also Vilizzi 2018). The maximum recorded age for ide is 29 years (Rohtla et al. 2015b), with mean age of (anadromous) spawning stocks usually ranging 6–11 years (Cala 1970; Erm and Kangur 1985; Rohtla et al. 2015b). The oldest specimens of ide from the River Danube and its tributaries in Slovakia were nine years old, although 1–3 year-old juveniles dominated in populations from various habitats, including the main channel, side arms and tributaries, backwaters, and/or small isolated oxbows (Balon 1962). The oldest golden orfe in the introduced population of Slovakia's Štrbské Pleso Lake was 11 years old (Balon and Žitňan 1964).

Based on length-at-age data from the native and introduced ranges of ide (Tables A1 and A2; see also Appendix: *Age and growth modeling*), global growth in body length is asymptotic with an estimated $SL_{\infty} = 422.4$ mm (Table 1); and it is characterized by large variation within year classes (Figure 2a) – noting that only recently have ide individuals been aged over 15 years (i.e., up to 29: Nicolaisen 1996; Rohtla et al. 2015b). Lotic populations achieve a larger size relative to lentic ones (Figure 2b), and the same occurs in arid relative to continental and temperate climates (Figure 2c), whereas under cold climates asymptotic size decreases progressively in areas with warm, temperate and cold summers (Figure 2d). Condition factor for ide has been reported to vary from 0.46 to 3.51 (Table 2). The parameters for body length-to-weight relationships in ide are available for both TL and SL (Table 3).

2.5. Reproduction

2.5.1. Sexual maturation, gonad development, and fecundity

In Europe, age at maturity varies with increasing latitude from one to ten years (Table 4). Males usually mature one year earlier than females (Cala 1971b; Balon 1962; Koopmans and Van Emmerik 2006), though no differences in age at maturity have been observed among sexes in Estonia (Oolu 1970; Haberman et al. 1973). Also, gonads of older and larger ide tend to ripen earlier in the season than

Table 1. Growth of ide *Leuciscus idus* as modeled by the von Bertalanffy growth function (VBGF).

Parameter	Estimate	SE	LCI	UCI	<i>t</i>	<i>P</i>
Global (<i>n</i> = 733, <i>N</i> = 87)						
SL_{∞}	422.4	9.2	405.0	442.6	45.66	< 0.001
<i>K</i>	0.17	0.01	0.15	0.18	17.68	< 0.001
t_0	0.06	0.10	-0.15	0.24	0.53	0.571
Habitat (Lentic: <i>n</i> = 263, <i>N</i> = 29; Lotic: <i>n</i> = 470, <i>N</i> = 58)						
SL_{∞} Lentic	399.1	9.3	382.1	419.5	42.89	< 0.001
SL_{∞} Lotic	495.1	24.3	454.7	543.6	20.36	< 0.001
<i>K</i> Lentic	0.19	0.01	0.16	0.21	15.42	< 0.001
<i>K</i> Lotic	0.12	0.01	0.10	0.14	10.69	< 0.001
t_0	-0.07	0.11	-0.29	0.12	-0.64	0.522
Climate class (B: <i>n</i> = 11, <i>N</i> = 2; C: <i>n</i> = 298, <i>N</i> = 42; D: <i>n</i> = 339, <i>N</i> = 33)						
SL_{∞} B	524.1	34.2	458.8	592.4	15.32	< 0.001
SL_{∞} C	390.0	10.2	371.6	410.5	38.06	< 0.001
SL_{∞} D	420.9	9.0	404.8	438.9	47.76	< 0.001
<i>K</i>	0.17	0.01	0.15	0.19	16.83	< 0.001
t_0	0.06	0.10	-0.14	0.25	0.62	0.534
Climate type D (Dfa: <i>n</i> = 7, <i>N</i> = 1; Dfb: <i>n</i> = 222, <i>N</i> = 23; Dfc: <i>n</i> = 110, <i>N</i> = 9)						
SL_{∞} Dfa	497.9	29.2	442.0	555.9	17.07	< 0.001
SL_{∞} Dfb	439.8	8.3	424.9	455.9	52.96	< 0.001
SL_{∞} Dfc	383.4	7.9	368.9	399.0	48.31	< 0.001
<i>K</i>	0.18	0.01	0.16	0.20	18.86	< 0.001
t_0	0.25	0.10	0.04	0.43	2.44	0.015

For each "best-fit" model, parameter estimates are provided including SE (standard errors) and 95% lower and upper confidence intervals (LCI and UCI, respectively). SL_{∞} = asymptotic standard length (mm); *K* = Brody's growth coefficient (years⁻¹); t_0 = age of fish at 0 mm SL. *n* = number of mean LAA values (see Table A2); *N* = number of populations. Statistically significant parameters in bold. Climate classes and types as defined in Appendix Table A1. See also Figure 2a–d.

gonads of smaller fish or first-time spawners (Cala 1971b). The cycle of male gonad development in Lake Võrtsjärv (Estonia) commences in July and reaches its final stage by October/November, when the gonadosomatic index (GSI) is between 1.2% and 1.8%, increasing with body size. Males can render milt prior to spawning and continue to produce milt for relatively long periods (Cala 1971b; Järvalt et al. 2003). In females, ovaries are located only in the dorsal area of the body cavity, apparently associated with the swim bladder by connective tissue. In juveniles, immature ovaries are cylindrical, but with age become dorsoventrally slightly flattened. When sexual maturity is reached, the ovaries extend into the proximal direction of the abdominal cavity. The entire body cavity of spawning ide, except for the space occupied by internal organs, is then filled by the ovaries (Cala 1971c).

Ovary development in the ide commences in July of the year prior to spawning and reaches its final level by October/November when GSI can be between 15% and 30%, increasing with body size (Cala 1971b; Järvalt et al. 2003). In female ide from the River Danube (at Paks, Szödliget, and Dunakiliti in Hungary), GSI in March was 7%, increasing to 15.6% in early May, decreasing to 10% in late May, and then to < 1% in July and August, and increased again to about 6% in September–November (Lefler et al. 2008). Two weeks before the onset of spawning, the ovaries of ripening females contain three types of developing eggs (Cala 1971c): unripe (diameter = 0.1–0.5 mm, to

be spawned in subsequent years), ripening (0.5–1.3 mm), and ripe (1.3–1.85 mm). In the River Danube, the transition of oocytes from the stage of primary growth to cortical alveoli in ide was observed in July–August, with vitellogenesis initiated already in August–September (Lefler et al. 2008). In March, the ovaries of ide from the River Danube contained oocytes in the stage of vitellogenesis only, whereas in July no vitellogenic oocytes were present, and oocytes in the stage of primary growth were much more numerous than those at the stage of cortical alveoli. In September, only a few oocytes in the stage of cortical alveoli were present, with those in primary growth and vitellogenesis being almost equal. In October, oocytes in the stage of cortical alveoli remained low, with vitellogenic oocytes being predominant (Lefler et al. 2008).

The diameter of mature eggs varies from 1.4–2.3 mm (Table 5), and egg size does not appear to depend on female size (Järvalt et al. 2003). Four-year-old ide from Lake Mosąg (Poland) produced smaller eggs (1.28 mm) than 5–9 year-old conspecifics (1.44–1.57 mm) (Targońska et al. 2012). The oldest individuals in the population either produced the highest percentage of both dead embryos during incubation and morphological abnormalities in recently-hatched fish, or they failed to produce eggs at all (Targońska et al. 2012).

Absolute fecundity of female ide is highly variable (Table 5) and most likely depends on growth rate, size at maturity, life-history type, and/or

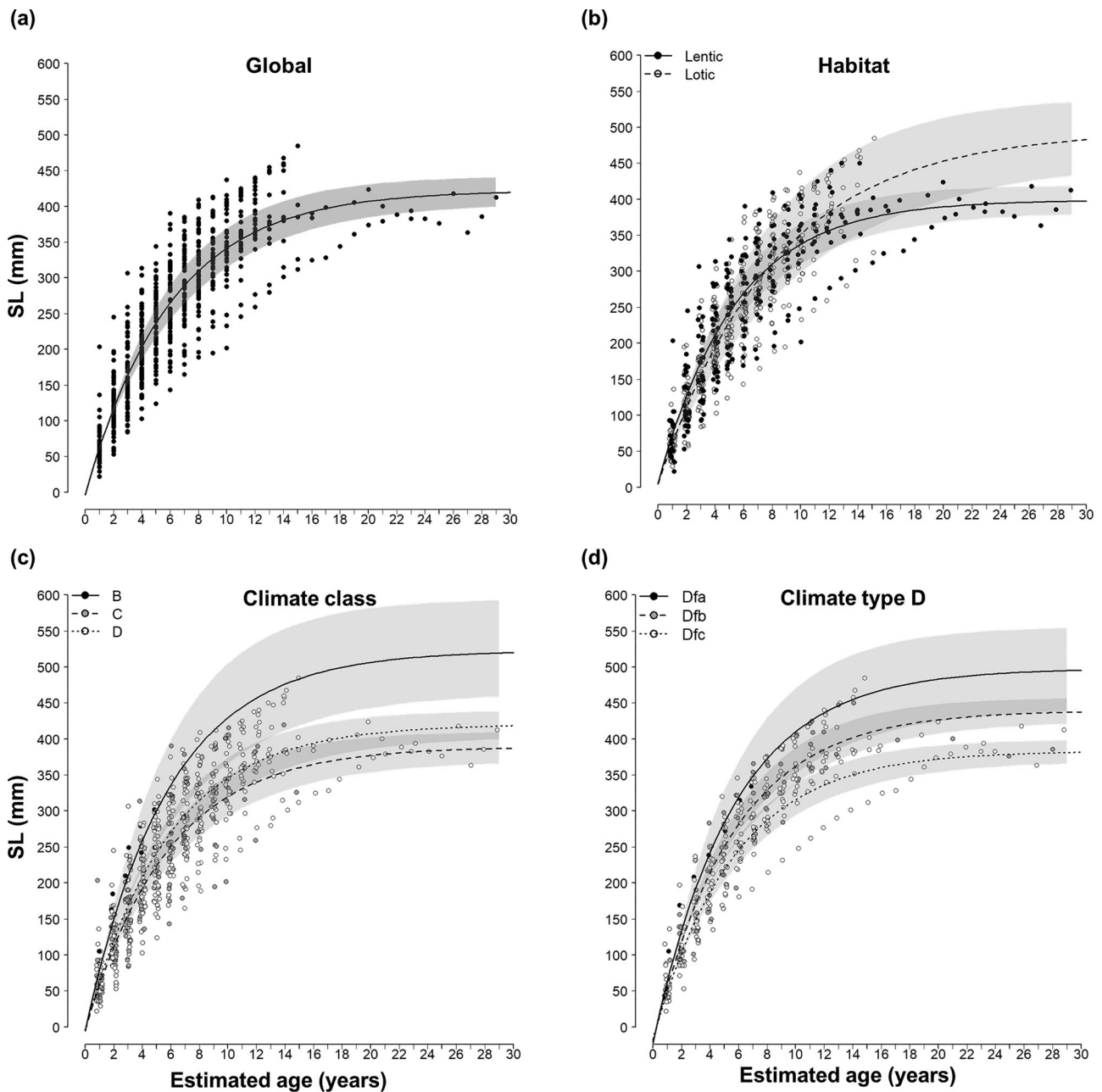


Figure 2. Growth in length of ide at the global scale as described by the von Bertalanffy growth function (VBGF) fitted to: (a) global dataset, (b) habitat, (c) Köppen-Geiger climate class and (d) climate type D. In the scatterplots, each point represents a single mean length-at-age value (see Table A2) 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 1.

geographic origin. The most distinct increase in absolute fecundity is observed between the fourth and seventh year of life (Targońska et al. 2012). In the River Kävlinge (Sweden), absolute fecundity was better correlated with body mass rather than body length, ovary weight or age (Cala 1971b). Relative fecundity (per gram of eviscerated weight) was 65–124 eggs in Lake Võrtsjärv, Estonia (Pihu 1960), and 153–182 eggs in the rivers Nasva and Kasari (Erm and Kangur 1985).

2.5.2. Reproductive behavior

Ide spawning occurs during one clear seasonal peak per year in the early spring (Lefler et al. 2008). Depending on location, this can occur anytime between February through June (Vriese et al. 1994; Dulmaa 1999; de Leeuw and Winter 2008; Witeska et al. 2014) and is triggered by increasing water temperatures. A similar time frame has been reported for locations of the River Danube in Hungary (Lefler et al. 2008). In the Ural and west and central Siberia

Table 2. Condition factor K for ide at various locations. Decimal places as per original source.

Water body	Country	Mean	Min	Max	Reference
River Nasva	Estonia	1.50	1.29	1.65	Kangur (1963)
River Dvina	Belarus	2.38	2.00	2.75	Zhukov (1965)
River Dnieper	Belarus	2.18	1.71	2.47	Zhukov (1965)
River Nemunas	Belarus	2.09	1.76	2.50	Zhukov (1965)
Various locations	Estonia	2.1	1.57	3.51	Ristkok (1974)
Various locations	Estonia	–	1.6	2.2	Järvalt (1981)
River Ob	Russia	2.04	1.79	2.36	Zhuravlev and Solovov (1984)
Lake Barselwann (1994)	Norway	1.16	–	–	Simonsen (2000)
Lake Barselwann (2000)	Norway	1.18	0.79	1.47	Simonsen (2000)
(Several)	Croatia	1.060	1.050	1.070	Treer et al. (2009)
Kopački Rit Nature Park	Croatia	1.211	0.888	1.44	Jelčić et al. (2010)
Yser, Meuse and Scheldt river basins	Belgium	1.08	0.46	1.85	H. Verreycken (unpublished data)

Decimal points as per source study.

Table 3. Total length-weight relationship ($W = aTL^b$) parameters for ide at various locations. Decimal places as per original source.

Water body	Country	Length	Measurement	a	b	Reference
Lake Chany	Russia	SL	cm	0.0054	3.396	Tyurin (1927) <i>vide</i> Froese and Pauly (2019)
River Volkhov	Russia	SL	cm	0.0071	3.259	Tyurin (1927) <i>vide</i> Froese and Pauly (2019)
River Volga	Russia	SL	cm	0.01574	2.444	Gundrizer (1958) <i>vide</i> Froese and Pauly (2019)
Western Siberia	Russia	TL	cm	0.01760	3.066	Gundrizer (1958) <i>vide</i> Froese and Pauly (2019)
Western Siberia	Russia	TL	cm	0.0040	3.468	Gundrizer (1958) <i>vide</i> Froese and Pauly (2019)
River Enisey	Russia	TL	cm	0.02940	2.878	Podlesnyi (1958) <i>vide</i> Froese and Pauly (2019)
River Kävlinge	Sweden	TL	mm	0.0037	3.339	Cala 1970
River Danube (Žofin sidearm)	Slovakia	SL	mm	0.0004	2.864	Naiksatam (1976) <i>vide</i> Hensel (2015)
Rivulet Bystrice	Czechia	SL	mm	0.0112	3.1422	Hanel (1984)
Unspecified locations	Finland	TL	cm	0.01185	2.878	Koli (1990) <i>vide</i> Froese and Pauly (2019)
Several locations	Netherlands	TL	cm	0.003489	3.3630	Klein Breteler and de Laak (2003)
Lake Sailimu	China	SL	mm	0.0087	3.3999	Fan and Quan (2008)
Several locations	Croatia	TL	cm	0.0092	3.048	Treer et al. (2008)
River Ergis	China	TL	cm	0.017	3.099	Huo et al. (2011)
Inland waters of Flanders	Belgium	TL	cm	0.0054	3.256	Verreycken et al. (2011)
Lower River Irtysh	Russia	SL	cm	0.0212	3.0269	Liberman and Chemagin (2017)

Table 4. Age (years) and SL (mm) at maturity for ide at various locations.

Water body	Country	Age	SL	Reference
Baltic Sea, Lake Sarvalaxträsket, River Porvoonjoki	Finland	8–10	–	Segerstråle (1933)
River Volga (delta area)	Russia	3	–	Berg (1949)
River Volga (middle reaches)	Russia	4–8	–	Lukin and Shteynfeld (1949)
Unspecified locations in France	France	3	–	Dottrens (1952) <i>vide</i> Spillmann (1961)
Rivers Turgai and Irgiz	Kazakhstan	2–4	–	Sidorova (1959)
River Danube	Slovakia	1	–	Balon (1962)
River Kama	Russia	4–5	–	Zhukov (1965)
Baltic Sea	Estonia	6–7	300–350	Oolu (1970)
River Kävlinge	Sweden	6–8	271–373	Cala (1971b)
Lake Vörtjärvä	Estonia	5–7	260–300	Haberman et al. (1973)
Lokka Reservoir	Finland	6–7	–	Mutenia (1978) <i>vide</i> Siriwardena (2008)
Lake Ugij	Mongolia	5–6	267–283	Dulmaa (1999)
River Nemunas	Lithuania, Belarus	4–5	≈250	Vechkanov (2000); Virbickas (2000)
Reared from hatchery eggs, brood stock of unspecified origin	Poland	3–4	–	Witeska et al. (2014)

regions (Russia), Estonia, Kazakhstan, Lithuania, and Sweden, spawning takes place between the beginning of March and the beginning of June at water temperatures of 4–13 °C (Ereshchenko 1956; Zhukov 1965; Cala 1970; Zhuravlev and Solovov 1984; Virbickas 2000; Järvalt et al. 2003; Petlina and Romanov 2004).

Spawning usually commences a few days after ice break-up and generally lasts only 3–9 days under stable temperatures (Cala 1970; Zhuravlev and Solovov 1984; Järvalt et al. 2003). Males reach the spawning grounds earlier and depart later than females (Cala 1970). Sex ratio during spawning can be slightly in favor of either females or males, but usually does not

significantly deviate from a 1:1 ratio as in the Baltic Sea (Cala 1970; Oolu 1970; Erm and Kangur 1985). A ratio of 1:3.67 (F:M) has been documented in fresh waters of Serbia (Lujić et al. 2013). Larger individuals usually spawn first (Cala 1970), with spawning occurring in the vegetated and marshy zones of lakes (Popov et al. 2005) or in river backwaters and flood plains (Zhukov 1965; Petlina and Romanov 2004). Spawning habitat requirements include water velocities of 0–60 cm s⁻¹ at depths of 0–100 cm over substrata that can contain stones, coarse gravel, fine and coarse sand (Vriese et al. 1994), but also pebbles covered with algae, flooded grass, and plants associated

Table 5. Reported mature egg size (mm) and absolute fecundity (AF) for ide at various native and introduced (UK) locations.

Water body	Country	Egg size	AF	Reference
Unspecified locations	France	2.5	–	Dottrens (1952) <i>vide</i> Spillmann (1961)
Lake Võrtsjärv	Estonia	1.4–1.8	16,820–108,300	Pihu (1960)
(Unspecified)	Romania	–	15,000–125,000	Bănărescu (1964)
River Kävlinge	Sweden	1.4–2.1	42,279–263,412	Cala (1971b, 1971c)
River Ob (upper reaches)	Russia	1.5–1.8	36,722–167,772	Zhuravlev and Solovov (1984)
River Kasari, River Nasva	Estonia	–	213,700–247,200	Erm and Kangur (1985)
Unspecified locations	United Kingdom	–	39,000–114,000	Maitland and Campbell (1992)
River Orhon	Mongolia	–	70,300–173,600	Dulmaa (1999)
River Nemunas	Lithuania	1.9–2.3	35,000–150,000	Virbickas (2000)
Unspecified locations	France	2.5	60,000–160,000	Keith and Allardi (2001)
River Dnieper	Russia	–	39,000–114,000	Berg (1964)
Unspecified locations	France	1.9–2.3	–	Keith et al. (2011)

with sand (Mann 1996). Spawning in the flooded shallow regions of lakes and rivers usually occurs at depths of 0.5–1.0 m, mainly on dead vegetation (Haberman et al. 1973; Zhuravlev and Solovov 1984; Erm and Kangur 1985). In the brackish coastal waters of Estonia, spawning occurs on algae (e.g., *Chara* sp.) or sandy/stony bottom (Oolu 1970; Erm and Kangur 1985). Spawning occurs during both day and night (Cala 1970; Petlina and Romanov 2004). Adhesive eggs attach to vegetation, gravel or other substrata (Cowx and Welcomme 1998). Ide do not guard their eggs once laid, and the duration of the embryonic development depends on ambient water temperatures and lasts about two weeks at 10–12 °C (Järvalt et al. 2003). The hatched embryos stick to macrophytes and start active swimming shortly before absorption of the yolk sac at 6.1–6.9 mm SL (Järvalt et al. 2003). The nursery habitat of ide has been described as having velocities of 0–10 cm s⁻¹ at depths of 0–100 cm (Vriese et al. 1994).

Ide reproductive success depends on water temperature and level during spring spawning. Springs without steep drops in water temperature, accompanied by high and stable water levels throughout the season, usually result in successful spawning events (Cala 1970; Florez 1972a; Järvalt et al. 2003). Preferred temperatures for spawning are variable depending on location, though ide typically require cooler waters. For example, although a preferred temperature range of 15.7–19.0 °C for spawning has been reported (Kupren et al. 2010), temperatures above 16 °C may result in reduced ovulation success (Targońska et al. 2011). Variability in preferred spawning temperatures indicates that ide is highly plastic in spawning requirements (Winter and Fredrich 2003; Kucharczyk et al. 2008). Deficiency in oxygen levels (e.g., due to pollution) during early development (cf. eggs and larvae), along with predation, can also affect spawning success (Cala 1970, Florez 1972b).

Where it coexists with other cyprinid species, the ide can occasionally hybridize with common bream *Abramis brama*, asp *Leuciscus aspius*, common carp *Cyprinus carpio*, dace *Leuciscus leuciscus*, roach *Rutilus rutilus*, and rudd *Scardinius erythrophthalmus* (Schwartz 1972, 1981; Kopiejewska et al. 2003; Yadrenkina 2003; Witkowski et al. 2015). It is not clear whether these hybridizations have had negative impacts on parental species in the wild.

2.6. Diet

The ide is generally described as omnivorous (Cala 1970; Brabrand 1985; Järvalt et al. 2003), though occasionally as herbivorous (Winfield and Nelson 1991), with a stable isotope study conducted in Lake Baikal (Siberia) suggesting that in the littoral zone the species is both detritivorous and planktivorous (Katzenberg and Weber 1999). The range of food items encompasses molluscs, crustaceans, bryozoans, insects, fish eggs and larvae, as well as age 0+ and 1+ juveniles of cyprinids, higher plants (macrophytes), seeds, detritus, rotifers, algae, and insect larvae (Cala 1970; Brabrand 1985; Rask 1989). These studies all suggest a broad and opportunistic diet that includes both animal and plant taxa (Table A3) and varies according to ontogeny and season (Cala 1970), with the shift to plants apparently influenced strongly by the intensity of inter- and intra-specific interactions and by the availability of animal prey (Brabrand 1985).

The onset of exogenous feeding in ide larvae is at 6.1–6.9 mm SL in the wild (Petlina and Romanov 2004) and at 6.5–7.2 mm SL under controlled (laboratory) conditions (Kupren et al. 2015). Larvae of 8.9–16.2 mm SL were found to feed on zooplankton and benthic invertebrates, whereas juveniles (20.3–28.4 mm SL) fed on insects and plant material (Zygmunt 1999; Petlina and Romanov 2004). In Lake Võrtsjärv (Estonia), YoY ide mainly consumed Trichoptera, Ephemeroptera, and Chironomidae

(Järvalt et al. 2003). Sub-adults and adults feed on plant material and benthic invertebrates, with larger individuals also preying on fishes (Cala 1970; Brabrand 1985; Rask 1989; Järvalt et al. 2003), including juveniles of bighead carp *Hypophthalmichthys nobilis*, roach, and common bleak *Alburnus alburnus* (Sanft 2015). In the River Kasari (Estonia), the diet of adult ide comprised *Asellus* sp., Trichoptera, Diptera, Coleoptera, and Chironomidae larvae (Järvalt et al. 2003). In the River Yenisei (Siberia), molluscs were the main prey item of adults (Dolgin 2009), whereas in the upper River Ob (Siberia), prey items included Coleoptera, Trichoptera, Odonata, and Chironomidae (Zhuravlev and Solovov 1984). In the upper River Volga basin, dreissenid mussels were important food items for benthophagous fish species, including ide, the latter having been found to consume the largest-sized mussels amongst fishes in the region (Shcherbina and Buckler 2006). In the brackish coastal waters of Estonia, smaller ide fed mainly on Ostracoda, Amphipoda, and small snails, whereas larger specimens fed mostly on clams and the crustacean *Saduria entomon*. Occasionally, small fishes such as ninespine stickleback *Pungitius pungitius* and eggs and young of whitefish *Coregonus lavaretus* have also been consumed (Oolu 1970; Järvalt et al. 2003).

Seasonal changes in the diet of ide vary according to prey availability (Tyutenkov 1956; Cala 1970; Brabrand 1985). For example, in Lake Kurgaldzhin (Kazakhstan), sub-adults and adults preyed mainly on *Gammarus* sp. (53%) in spring, when macrophytes represented only 5% of the biomass intake, increasing to 95% in summer, with Chironomidae becoming important in autumn (Tyutenkov 1956). In the River Kävlinge (Sweden), plant material (such as *Lemna minor* and *Potamogeton* sp.) and seeds were also eaten mainly in summer and early autumn (Cala 1970; Brabrand 1985). Fish eggs were present in the diet in May only, and YoY fishes in October and November (Brabrand 1985). In winter, the ide does not stop feeding (Järvalt et al. 2003), with Oligochaeta representing a major hibernical dietary item in the River Kävlinge (Cala 1970). In mesotrophic lakes of southeast Norway, ide consumption of macrophytes increased when animal food supply was scarce (Brabrand 1985). In that study, the ide was observed to feed upon various marsh plants (e.g., water horsetail *Equisetum fluviatile*) as well as upon clasping pondweed *Potamogeton perfoliatus* in shallow littoral areas of the lakes. Also, diet shift to plants appeared to be strongly influenced by the supply of animal food items and the intensity of interspecific competition with roach.

The ide is a visually-oriented feeder and consequently experiences reduced foraging success where turbidity is high (i.e., visibility is low) (Kulíšková et al. 2009). In addition, the ide is considered to be a hearing specialist (cf. ostariophysian fishes), such that hearing may also play a role in prey localization (Schuijff et al. 1977).

2.7. Predators

All ontogenetic stages of ide are susceptible to some level of predation. The eggs and larvae of ide are heavily predated by threespine stickleback *Gasterosteus aculeatus*, even driving the local extinction of ide populations in Norway (Nicolaisen 1996). Juvenile ide are susceptible to predation by piscivorous fishes, including pikeperch *Sander lucioperca* and northern pike *Esox lucius* (Cieśla and Kaczkowski 2004), including both juvenile and adult stages (www.cabi.org/isc/datasheet/77315). The Amur catfish *Silurus asotus* has also been listed as a predator of ide (*ibid.*). In the River Lena (Siberia), the absence of ide in some stretches was postulated to be the result of a high density of predators, dominated by the taimen *Hucho taimen* – a large salmonid native to that region (Holčík 1984). It has also been suggested that predation by brown trout *Salmo trutta* was likely responsible for decreases of ide abundance following stream water quality improvement (Eklöv et al. 1998). The ide is most likely to be predated at small size (i.e., as juveniles), whereas larger individuals reach a size refuge from gape-limited predators (Diekmann et al. 2005).

The ide is also susceptible to predation by piscivorous birds such as great cormorant *Phalacrocorax carbo sinensis* and osprey *Pandion haliaetus*. In Norway, the ide is vulnerable to predation by ospreys, as evidenced by the significant proportion (i.e., 32%) of ide in the diet of these birds in some locations (Swenson 1979). Cormorant predation of the ide has been observed in Estonia (Vetemaa et al. 2010), the Netherlands (Veldkamp 1995), and Czechia (Kortan et al. 2008). In the latter country, fishpond losses of ide were attributed to cormorant predation. Maximum prey size of cormorants is approximately 1 kg and, since most adult ide typically weigh >1 kg, adult ide might escape predation by cormorants in Estonian coastal waters (Vetemaa et al. 2010).

2.8. Pathogens and parasites

Spring Viraemia of Carp (SVC) is the most serious viral disease to which ide are susceptible (Dixon et al.

1994), and this is regarded as a notifiable disease by the Office International des Epizooties (OIE). Transmission of SVC is usually through introduction of fishes infected with the virus. In recent years, the emerging disease koi herpesvirus CyHV-3 (KHV) has spread worldwide, causing significant mortalities amongst common carp and its ornamental varieties, and has also been designated as notifiable by the OIE. Whilst ide do not appear to be susceptible to infection with KHV, Bergmann et al. (2009) isolated the virus from healthy individuals, suggesting that ide may develop carrier status if exposed to this virus. Also, mortalities of cyprinid species caused by a virus with a close serological relationship to pike fry rhabdovirus (PFR) have been reported (Way et al. 2003). Although the ide was not amongst the affected species, it is likely that it is susceptible to this virus, as suggested by experimentally-infected ornamental varieties of ide with PFR-80560 (Haenen and Davidse 1993). Bacterial diseases of ide are considered to be non-species specific; and these include *Flexibacter columnaris* and *Aeromonas punctata* (De Charleroy et al. 1993), even though little information exists on mortalities of wild ide caused by bacteria.

The ide can be infected by a wide range of mainly generalist parasites that infect cyprinids and other freshwater fish species (Table A4). The taxonomic diversity of the parasitofauna is high, partly because ide acts as a host to marine parasites, e.g. *Hysterothylacium aduncum* and *Pseudoterranova decipiens* (Palm et al. 1999), due to its tolerance of brackish water environments (Järvalt et al. 2003). In addition, the diversity of indirectly transmitted parasites that use intermediate hosts such as molluscs and fishes reflects the broad dietary spectrum of ide (Järvalt et al. 2003). The species richness of certain groups, particularly protists, platyhelminths and nematode larvae, may not be accurate; this is because the records of many ide parasites have been by morphological identification, which can be unreliable without molecular confirmation. The ide has the potential to act as a source of parasitic infection, but no more than other cyprinid species. The ide can harbor high numbers of directly transmitted parasites, such as the crustacean *Ergasilus sieboldi*, which can cause pathology in wild fish populations (Alston and Lewis 1994). The ide also acts as an intermediate host for parasites of veterinary and medical importance, such as the liver fluke *Opisthorchis felineus* (Izyumova 1987) and the highly pathogenic, eel-swimbladder nematode *Anguillicoloides crassus* (Thomas and Ollevier 1992). Most notably, wild ide in Norway were

reported to be infected with *Spironucleus vortens* (Sterud and Poynton 2002), suggesting that ide could potentially constitute a threat as a reservoir for spiro-nucleosis, which is highly pathogenic to cultured fishes. The common ectoparasites *Argulus foliaceus* and *Piscicola geometra* can act as mechanical vectors of SVC (Ahne 1985), which has been isolated from ide (Dixon et al. 1994).

2.9. Threats, conservation, and commercial importance

In rivers across Europe, the ide and other rheophilic cyprinids have experienced declines, and in several cases the ide is considered vulnerable or endangered (review in Grift 2001; see also Winter and Fredrich 2003). Within its native range, the ide continues to be threatened by human-mediated impacts such as pollution and eutrophication (Müller 1982; Kulíšková et al. 2009), water retention structures and habitat destruction in rivers (Peňáz and Jurajda 1996; Scholten et al. 2003; Bukelskis and Kesminas 2016), habitat modifications in brackish waters (Veld 1969), non-native species introductions (Zhuravlev and Solovov 1984; Petlina and Romanov 2004), and overfishing (Erm and Kangur 1985). Changes in future climate might also pose a threat, with the species being predicted to suffer from reduced temperature compatibility in its introduced range of England and Wales (Britton et al. 2010). As a result of all these pressures, there is a growing interest in ide aquaculture, particularly in Poland, for the purpose of restocking to supplement declining natural populations (Kucharczyk et al. 2008; Kupren et al. 2010). This interest in ide aquaculture is, at least partly, economical as it is derived from current fisheries regulations that force angling associations to stock ide to all water bodies. Interestingly, following the impoundment of the River Warta (Poland), ide was one of the most abundant fish species in the most degraded section of this river, probably due to the absence of large rheophilic fishes (Kruk 2007) – this demonstrates that in some locations the ide can prevail under conditions of environmental perturbation and weak competition. Counter-intuitively, long-term, stream water-quality improvement in southern Sweden has coincided with a considerable decline in ide abundance but concurrent increases in brown trout *Salmo trutta* abundance (Eklöv et al. 1998). This contrasts no change in ide presence in the River Rhine despite water-quality and habitat improvements between 1980–1990 and 2000–2010 (Fedorenkova et al. 2013).

Relatively fast growth rates and large body size make the ide a desirable target for commercial and especially recreational fisheries, and as a consequence it is a popular sport fish across Europe (Järvalt et al. 2003; Hickley and Chare 2004; Harzevili et al. 2012). The peak of the ide's commercial importance dates to the 1920–30s in countries such as Estonia and the Netherlands, whereas little is known about the current importance, stock status, and conservation of this species in most other countries. Notably, the ide is currently marked as of “Least Concern” in the IUCN Red List of Threatened Species (www.iucnredlist.org/species/11884/3312021), although it is classified as being “Vulnerable” to “Endangered” in a number of countries across Europe.

In Belgium, the ide is considered an important fish for recreational angling, with continuous re-stocking programmes in Flemish rivers since the 1990s (1–5 tons yr^{-1} since 2000). However, these have not (yet) resulted in increased abundances (Flemish Freshwater Fish Monitoring Network: H. Verreycken, unpublished data). In Flanders, where the species is currently marked as “Vulnerable” according to the Flemish IUCN Red List (Verreycken et al. 2014), there is a closed angling season for ide from April 16 through May 31. Additionally, a minimum angling size of 25 cm (total length: TL) remains in force in Wallonia, but no longer in Flanders.

In Estonia, the ide has historically been an important commercial species, with catches of freshwater resident (mainly lakes Peipsi and Võrtsjärv) and anadromous individuals peaking in the 1920–30s and in the 1980s at 54 and 177 tons yr^{-1} , respectively (Järvalt et al. 2003). Currently, catches of 3–5 tons yr^{-1} are reported from coastal waters (www.agri.ee). Overfishing during the spawning runs has been the main factor responsible for the collapse of anadromous ide stocks in the country (Erm and Kangur 1985). To protect ide stocks in the sea and in coastal rivers, a legal minimum size of 38 cm (TL) and several no-fishing zones have been established. Despite these measures, and an almost complete cessation of commercial fishing for ide, most stocks in the coastal sea have not yet recovered from the collapse (Eschbaum et al. 2016). A relatively steep increase in the numbers of juvenile ide has been recorded in recent years (Eschbaum et al. 2016), suggesting that successful spawning seasons, albeit irregular, can result in high densities of sub-adults. The ide is a popular sport fish in Estonia, and recreational anglers from all over the country travel to West Estonia to target anadromous ide from the Baltic Sea during its spawning migration

into rivers and semi-closed bays. The number of different anadromous spawning stocks is unknown, but the most abundant runs occur in Hiiumaa Island (Käina Bay and Kõrgessaare region) and in Matsalu and Saunja bays. No re-stocking of ide is currently conducted in Estonia. In the Estonian Red List of Threatened Species, the ide is currently marked as “Data deficient” (<http://elurikkus.ut.ee>).

In Finland, the ide was previously a popular species for household use, but it has fallen into disfavor along with the general decrease in appreciation of cyprinids for human consumption. The capture of ide for market sale still takes place in the Archipelago Sea and the Gulf of Finland as well as in estuaries of the northern Gulf of Bothnia. However, ide stocks have been declining locally owing to eutrophication, dam building, and water level regulation, and some stocks have even vanished as a result of water acidification. In the Finnish Red List of Threatened Species, the ide is currently classified as “Least concern.”

In Latvia, the ide is a common species in coastal waters, but populations are small and the number of rivers inhabited by the species has declined from ≈ 76 to ≈ 40 (Birzaks et al. 2011). Landings of ide have decreased in the traditional fishing areas of the coastal waters of the Gulf of Riga (western Latvia), where a minimum legal size of 30 cm (TL) has been established. In the Latvian Red List of Threatened Species, the ide is currently not listed (J. Birzaks, personal communication).

Albeit rare in coastal waters of Lithuania, the ide is still common and relatively abundant in the Curonian Lagoon and in the largest rivers of the country, namely the Nemunas and Neris (Virbickas 2000; Bukelskis and Kesminas 2016). Similar to Estonia, a substantial increase in the numbers of juvenile ide has been recorded in recent years in some rivers, e.g. the Nemunas and in Curonian Lagoon, although in other rivers ide abundance has remained unchanged or has decreased (Bukelskis and Kesminas 2016). In the River Nemunas, the relative abundance of ide juveniles ranged from 1.1% to 2.9% in 2015 (Bukelskis and Kesminas 2016), and in the Curonian Lagoon juveniles comprised 3.1–6.7% of the entire juvenile fish community of the shore area in 2012 (Repečka et al. 2012). The ide has never been commercially important in Lithuania, and until the 1980s annual landings rarely exceeded 4 tons yr^{-1} (mean 2.5 tons). Landings of ide dramatically decreased in the 1990s to 0.2–0.3 tons yr^{-1} and even further at the beginning of the 21st century, with mean landings being at just 33 kg yr^{-1} (Bukelskis and Kesminas 2016). Some signs of

recovery were observed in 2015, when commercial catches suddenly increased to 419 kg (Bukelskis and Kesminas 2016), possibly as a consequence of a recently-documented recovery in juvenile ide abundance. Similar to Latvia, a minimum legal size of 30 cm (TL) has been enforced in Lithuania, even though the ide is not present in the Lithuanian Red List of Threatened Species. In 2016, a study that proposed an ide re-stocking programme for inland water bodies, where ide populations were extinct or nearly extinct, was accepted by the Fisheries Department of The Ministry of Agriculture of the Republic of Lithuania (Bukelskis and Kesminas 2016), and state-supported ide re-stocking started in 2017 with 516,000 YoY individuals released in 2020.

In the Netherlands, considerable quantities of ide were once caught in the brackish water zones of the former Zuiderzee (Veld 1969). But, following construction of the Afsluitdijk (or Enclosure Dam), the gradual transition from fresh to salt water of the IJssel estuary (northwestern Netherland) coincided with a decrease in ide catches in Lake IJssel from 6.7 tons in 1935 to 2 tons in 1940 (Veld 1969). The ide is included in the Fisheries Act, which specifies the permitted landing sizes and quantities for all listed species. A closed season for angling exists from April 1 through May 31, but with no minimum size limit. As in Flanders, the ide is listed as “Vulnerable” in the IUCN Red List for the Netherlands (De Leeuw et al. 2003), but is no longer included in the new Red List (Spikmans and Kranenbarg 2016). Also, the ide is not included in the Annexes of the Habitats Directive or the Dutch Flora and Fauna Law.

In Poland, the ide is considered an important angling species (Witkowski et al. 1997), with a minimum legal size of 25 cm (TL). The maximum permitted daily catch is 5 kg in fresh waters and 10 kg in the Baltic Sea. Levels of total allowable commercial catches in rivers, reservoirs and lakes are established individually for each water body (or river stretch). In 2018, commercial catches of ide reached almost 1.56 tons, amounting to 0.7% of total inland fishery landings of all fish species. Recreational catches are much higher and amounted to 31.36 tons in 2017 (Wołos et al. 2020). The only restriction applied to marine commercial fisheries dealt with a minimum legal size of 25 cm (TL) in the “western internal waters” (the Szczecin and Kamiński Lagoons). According to the Fishing Monitoring Center in Gdynia, the ide was not recorded in official commercial fishery statistics from Poland’s Baltic coastal waters between 2004 and 2019 (including the Szczecin and Vistula Lagoons). This

might be explained by low numbers of fish in the environment as well as not reporting ide in the catches by fishers, although some specimens might have been classified as “other freshwater fishes” or as roach. Additionally, between 2015 and 2017, the catches from fishers’ boats shorter than 8 m were no longer required to report catches, and there is no obligation to report individual recreational fishery catches from Poland’s Baltic coastal waters. The Poland Inland Fishery Act imposes an obligation to re-stock rivers with fish, including the ide, but the origin of fish is not taken into consideration by inspection authorities. In 2018, 6,135,000 ‘hatched eggs’ (*a source translata*) and 14,482 kg of autumn juveniles (1,266 kg age 1+ and 37,232 kg age 2+) and 140 kg of mature fish were released to rivers and open lakes (Mickiewicz and Wołos 2020). In the Gulf of Gdansk, where anglers caught ide in the vicinity of Gdynia in the 1960s (M. Skóra, unpublished data), the ide must have been more abundant in the past but is now a rare species (Skóra 1996). Between 2005 and 2007, the share of ide numbers and mass in the catches at the mouth of the coastal River Reda amounted to < 0.01% and 0.04%, respectively (Skóra 2015). The ide is also very rare free-embryos in the Vistula Lagoon, where in 2001 and 2012 the proportion in fyke nets and nordic gill nets was 0.05% and < 0.01%, respectively (Nermer et al. 2012). A similar situation was observed in the Szczecin Lagoon, where the percent of ide in fyke-net and gill-net catches amounted to ≈0.12% and ≈0.04%, respectively (Wawrzyniak et al. 2017). In the Międzyodrze waters (the 28 km stretch of the most downstream part of the lower River Odra), the ide is considered a common species. Between 1952 and 2002, mean catches of the ide reached 915 kg annually and amounted to 0.62% of the total catch in that area (Neja 2011). For some inland rivers, a considerable increase in both ide abundance and biomass has been observed in recent decades (Kruk et al. 2017; Penczak et al. 2017). According to the Polish Red List of Fishes (Witkowski et al. 2009), the ide is of “Least concern” in inland waters, but “Vulnerable” in the coastal rivers of the Baltic Sea.

In Slovakia, the ide used to be a relatively important fish species for freshwater commercial fisheries in the 1950s, representing 7.9% (≈22 tons) of the total catch of the State Fishery in 1955–1958 (Balon 1962). In that period, the ide was considered the most popular cyprinid species after common carp, and it also contributed considerably to overall catches of recreational anglers. Nevertheless, large-scale monitoring data for 2011 and 2020 suggest that ide populations

have declined in most Slovak rivers (V. Kováč, unpublished data), except for the River Danube, where it is still relatively abundant (Bammer et al. 2015).

In Sweden, the ide is rarely captured at various monitoring sites across the country, but there does not seem to have been any overall decline since 2001. Therefore, the ide is currently not included in the Swedish Red List of Threatened Species. In the commercial coastal fishery, the species' catches are very low and without any identifiable trend since 1999.

3. Potential invasiveness and ecological impacts in non-native regions

Owing to its relatively high growth rate and large body size (Rohtla et al. 2015b), the ide is an attractive species for introductions outside its native range, being a popular ornamental fish and a target species for anglers in many countries (e.g., Järvalt et al. 2003; Hickley and Chare 2004). Once introduced, the ide has so far not demonstrated itself to be invasive (e.g., in the USA, New Zealand, England). That is, despite repeated introductions outside of its native range, there is little evidence that the species has established self-sustaining populations or spread elsewhere. Indeed, the ide has been described as “local and rare” (Maitland 1972), though present in seven of the nine regions of England (Copp et al. 2007). A lack of demonstrated invasive nature and the importance of ide as an ornamental species are the reasons why it was not included in legislation for regulating non-native fishes in England & Wales, namely the Import of Live Fish Act 1980 and related orders (Copp et al. 2007). Nonetheless, the ide possesses many attributes associated with species that can acclimate to novel environments, specifically omnivory, longevity, and habitat plasticity (e.g., Cala 1970; Rohtla et al. 2015a; Rohtla et al. 2015b). Furthermore, the scientific literature is devoid of studies, and even claims, of adverse impacts of ide on native species and ecosystems in locations where it has been introduced (www.cabi.org/isc/datasheet/77315).

The potential impacts of ide in its introduced range include competition and disease transmission, though of these impacts the most difficult to demonstrate is likely to be competition. The most likely potential competitors would presumably be other bottom-feeding species, especially other cyprinids with functional similarity (e.g., dace and chub *Squalius cephalus*). The ide can host infectious agents (SVC) or act as carrier (KHV) of viral diseases and parasites (see Section 2.8: *Pathogens and parasites*), and therefore stocked ide

can act as a vector for the infection of local fish populations. For example, *Ergasilus sieboldi* is a common parasite of ide in the ide's native range (Sobecka et al. 2004; Rusinek 2007), but *E. sieboldi* is usually non-native to the locations where the ide has been introduced, such as England (Kennedy 1975). Furthermore, the ide can be the paratenic host for *Anguillicoloides crassus* (Thomas and Ollevier 1992), which means that careless translocations of infected ide can potentially introduce this swim-bladder parasite to regions where it was previously not present. The ide is generally an omnivorous feeder of most abundant food items, and its diet shifts largely with ontogeny, seasonality and food availability (see Section 2.6: *Diet*). Recent outdoor experimental studies, to test for non-native fish competition with native fishes, found limited and potentially unimportant changes in the diet and trophic position in native fishes following the introduction of omnivorous introduced fishes, specifically pumpkinseed (Copp et al. 2017) and sunbleak *Leucaspis delineatus* (Bašić et al. 2019). Similar studies are needed to determine whether non-native ide exerts competitive pressure on native fishes under natural or near-natural conditions.

There is contrasting information on the sensitivity of ide to environmental perturbations. Habitat improvements that have been conducted following environmental perturbation have had positive (Kruk et al. 2017), neutral (Fedorenkova et al. 2013), or even negative (Eklöv et al. 1998) effects on ide abundance. For example, in the River Warta (Poland), the ide responded rather positively to perturbations, prevailing even when other large rheophilic species were absent (Kruk 2007). The latter should be considered as a rare example, as ide populations mostly suffer under environmental perturbations (e.g., Müller 1982; Scholten et al. 2003; Bukelskis and Kesminas 2016; M. Rohtla, personal observation), which would potentially limit population growth and subsequent invasiveness. Under controlled laboratory conditions, early-life stages of ide have demonstrated good acclimatization and tolerance to increasing water temperatures (Florez 1972a; Kupren et al. 2010). The latter suggests that the ide may be adaptable to climate change-driven increases in temperature, but this does probably not give an advantage to ide compared to other cyprinids since they have similar temperature tolerances. For example, the abundance of vimba *Vimba vimba* has increased tremendously in the Baltic Sea of late, whereas the numbers of ide have increased only slightly.

Once a localized breeding population of ide has successfully established itself in a novel environment, the species' demonstrated long-distance movements in its native range indicate that it could potentially disperse to a wide geographical area (Winter and Fredrich 2003; Kulíšková et al. 2009; Rohtla et al. 2015a). This means that un-invaded parts of a given water course could be colonized relatively rapidly, but evidence for this is lacking. Furthermore, as the salinity tolerance of ide is relatively high (Van Beek 1999; Skovrind et al. 2016), there is also some potential for colonizing new, closely-located water courses through marine and brackish water pathways when suitable conditions are present (e.g., during large riverine runoff). Although the possibility of such events is largely unknown, it may be most plausible in regions where salinity levels are projected to decrease due to climate change (e.g., Durack et al. 2012). As the ide can also be relatively long-lived (Rohtla et al. 2015b), introduced populations could potentially withstand the occasional environmental perturbations that hinder successful reproduction in a given year, as in the case of tench *Tinca tinca* introduced to Ireland (O'Maoileidigh and Bracken 1989) and of native tench populations in England (Copp 1997). The potential risks of ide hybridizing with native species is likely to be restricted to closely-related native cyprinids (Kopiejewska et al. 2003; Yadrenkina 2003; Witkowski et al. 2015).

In summary, virtually all aspects of the environmental biology of introduced ide require further study, though some initial information is available for native populations on migratory behaviors, diet, diseases, growth, and potential hybridization with native species. Existing evidence suggests that the ide does not appear to pose an elevated risk of being invasive where introduced outside its native range in Europe. Further afield, the ide may become invasive, such as been observed with another European cyprinid, namely the rudd in North America (e.g., Guinan et al. 2015). In an initial invasiveness risk screening for England & Wales, the ide attracted an intermediate mean risk score of 20, which placed it at the lowest extent of the "high risk" score range for that region (Copp, Vilizzi et al. 2009; Britton et al. 2010). A similar mean score (20.2) and risk ranking was reported for Iberia (Almeida et al. 2013), and a lower score (14.0), albeit still considered as high risk, for Scotland (Vilizzi et al. 2019). Very early on, some North American sources (see Nico et al. 2020) recommended against introductions of the ide to California. Despite these concerns, there has been little study of the ide

in North America (Nico et al. 2020). There have been, however, reports that consignments of ide imported to the USA from Germany carried benign diseases (McAllister et al. 1985). The lack of evidence for demonstrated impacts may appear to corroborate the extant risk-screening outcomes, but this lack of evidence is due to a general lack of study of the ide impacts rather than from the absence of impacts. As introductions of ide are likely to continue, given its angling popularity and use as an ornamental species, this propagule pressure could lead to the development of invasive populations in some non-native locations. The fact that the species is not considered likely to be affected by climate warming (Lehtonen 1996; Britton et al. 2010) could be viewed as either advantageous or disadvantageous, depending upon whether or not the risk assessment area is likely to experience a warmer climate in future decades.

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Appendix

Age and growth modeling

Data on ide 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 this study), LAA data originally given as total length (TL, mm) were converted to standard length (SL, mm) using the formula $SL = -0.36 + 0.863TL$ (M. Rohrla, unpublished data).

The latitude and longitude of the water body where each ide 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. ide populations). The distributional range of ide was then categorized as either "native" or "non-native" (Figure 1). For each water body, the corresponding habitat was labeled as either "lentic" (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).

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

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

where SL_{∞} is the asymptotic SL, K the instantaneous growth rate or Brody's growth coefficient (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 A1) 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 x64 v3.6.3 (R Development Core Team 2020) using packages FSA and nlstools (Ogle 2016) with 1000 bootstrap confidence interval estimates of the parameters (and with additional code written by LV).

Table A1. Water bodies for which length-at-age data for ide were retrieved.

ID	Water body	Country	Lat	Lon	Range	Habitat	Climate	
							Class	Type
1	Baltic Sea (Orregrund)	Finland	60°16'N	26°26'E	Native	Lentic	D	Dfb
2	Baltic Sea (Pellinki)	Finland	60°13'N	25°52'E	Native	Lentic	D	Dfb
3	Baltic Sea (Väinameri)	Estonia	58°87'N	23°28'E	Native	Lentic	D	Dfb
4	Kamskoe Reservoir	Russia	55°12'N	49°16'E	Native	Lentic	D	Dfb
5	Kráľová Reservoir	Slovakia	48°12'N	17°48'E	Native	Lentic	C	Cfb
6	Kremenchuk Reservoir	Ukraine	49°16'N	32°38'E	Native	Lentic	D	Dfb
7	Kuybyshev Reservoir	Russia	53°46'N	48°55'E	Native	Lentic	D	Dfb
8	Lake Arresø	Denmark	56°00'N	12°04'E	Native	Lentic	C	Cfb
9	Lake Barselvann	Norway	58°10'N	08°08'E	Non-native	Lentic	C	Cfb
10	Lake Chany	Russia	54°50'N	77°40'E	Native	Lentic	D	Dfb
11	Lake Dzhalangash	Kazakhstan	48°83'N	62°01'E	Native	Lentic	B	BSk
12	Lake Ilmen	Russia	58°16'N	31°17'E	Native	Lentic	D	Dfb
13	Lake Kamyś-Samarské	Kazakhstan	51°14'N	51°22'E	Native	Lentic	D	Dfa
14	Lake Längelmävesi	Finland	61°34'N	24°25'E	Native	Lentic	D	Dfc
15	Lake Peipus	Estonia	58°41'N	27°29'E	Native	Lentic	D	Dfb
16	Lake Sarvalaxträsket	Finland	60°44'N	26°12'E	Native	Lentic	D	Dfb
17	Lake Sayram	China	44°36'N	81°12'E	Non-native	Lentic	D	Dfb
18	Lake Skårsvatnet	Norway	60°24'N	06°13'E	Native	Lentic	D	Dfc
19	Lake Štrbské Pleso	Slovakia	49°07'N	20°03'E	Native	Lentic	D	Dfc
20	Lake Suzhargan	Kazakhstan	49°46'N	63°38'E	Native	Lentic	B	BSk
21	Lake Tarankol	Kazakhstan	53°71'N	67°79'E	Native	Lentic	D	Dfb
22	Lake Võrtsjärv	Estonia	58°17'N	26°02'E	Native	Lentic	D	Dfb
23	Laytham Park ponds	United Kingdom	53°86'N	00°87'W	Non-native	Lentic	C	Cfb
24	Mietkowski Lake	Poland	50°57'N	16°37'E	Native	Lentic	C	Cfb
25	Pond near Rusovce (Bratislava)	Slovakia	48°08'N	17°06'E	Native	Lentic	C	Cfb
26	Pond near Vlčie hrdlo (Bratislava)	Slovakia	48°08'N	17°06'E	Native	Lentic	C	Cfb
27	River Barbarka	Poland	51°13'N	20°02'E	Native	Lotic	C	Cfb
28	River Czarna Konecka	Poland	51°18'N	19°54'E	Native	Lotic	C	Cfb
29	River Czarna Taraska	Poland	51°06'N	20°21'E	Native	Lotic	C	Cfb
30	River Danube	Slovakia	–	–	Native	Lotic	–	–
31	River Danube (Břeclav)	Czechia	48°45'N	16°52'E	Native	Lotic	C	Cfb
32	River Danube (Koviljsko-Petrovaradinski Rit)	Serbia	45°14'N	20°01'E	Native	Lotic	C	Cfa
33	River Danube (Kravany)	Slovakia	48°59'N	20°12'E	Native	Lotic	D	Dfb
34	River Danube (Lake Lion)	Slovakia	47°46'N	17°43'E	Native	Lotic	C	Cfb
35	River Danube (Little Danube near Bratislava)	Slovakia	48°08'N	17°06'E	Native	Lotic	C	Cfb
36	River Danube (Little Danube near Kolárovo)	Slovakia	47°55'N	17°59'E	Native	Lotic	C	Cfb
37	River Danube (Little Danube, Kanál Asód)	Slovakia	47°53'N	18°00'E	Native	Lotic	C	Cfb
38	River Danube (Medved'ov)	Slovakia	47°47'N	17°39'E	Native	Lotic	C	Cfb
39	River Danube (Stúrovo)	Slovakia	47°47'N	18°43'E	Native	Lotic	C	Cfb
40	River Danube (Žitava)	Slovakia	47°50'N	18°07'E	Native	Lotic	C	Cfb
41	River Danube (Žofín branch)	Czechia	50°04'N	14°24'E	Native	Lotic	C	Cfb
42	River Daugava	Belarus	–	–	Native	Lotic	–	–
43	River Dnieper	Belarus	–	–	Native	Lotic	–	–
44	River Drzewiczka	Poland	51°35'N	20°34'E	Native	Lotic	C	Cfb
45	River Hron	Slovakia	47°49'N	18°45'E	Native	Lotic	C	Cfb
46	River Hron (Kalná, Želiezovce, Vozokany)	Slovakia	48°19'N	18°24'E	Native	Lotic	C	Cfb
47	River Hron (Pohronský)	Slovakia	47°58'N	18°39'E	Native	Lotic	C	Cfb
48	River Hron (Revištské Podzámčie and Žiar)	Slovakia	48°31'N	18°43'E	Native	Lotic	C	Cfb
49	River Ilych (Sar'yudin)	Russia	62°40'N	57°46'E	Native	Lotic	D	Dfc
50	River Irtysh (lower reaches)	Russia	58°11'N	68°15'E	Native	Lotic	D	Dfc
51	River Kama	Russia	–	–	Native	Lotic	–	–
52	River Karakol	Kyrgyzstan	42°48'N	78°39'E	Native	Lotic	D	Dfb
53	River Kasari	Estonia	58°43'N	23°59'E	Native	Lotic	D	Dfb
54	River Kävlinge	Sweden	55°43'N	12°59'E	Native	Lotic	C	Cfb
55	River Luciąża	Poland	51°22'N	19°51'E	Native	Lotic	C	Cfb
56	River Nasva	Estonia	58°12'N	22°23'E	Native	Lotic	D	Dfb
57	River Nemunas (BY)	Belarus	–	–	Native	Lotic	–	–
58	River Nemunas (LT)	Lithuania	–	–	Native	Lotic	–	–
59	River Numedalslågen	Norway	59°29'N	09°55'E	Native	Lotic	D	Dfb
60	River Ob	Russia	–	–	Native	Lotic	–	–
61	River Ob (upper reaches)	Russia	–	–	Native	Lotic	–	–
62	River Pilica	Poland	51°51'N	21°16'E	Native	Lotic	C	Cfb
63	River Porvoonjoki	Finland	60°23'N	25°40'E	Native	Lotic	D	Dfb
64	River Thaya	Czechia	48°37'N	16°56'E	Native	Lotic	C	Cfb
65	River Vakh	Russia	60°48'N	76°42'E	Native	Lotic	D	Dfc
66	River Volga (Kamskoe)	Russia	53°46'N	48°55'E	Native	Lotic	D	Dfb
67	River Volga (middle reaches)	Russia	–	–	Native	Lotic	–	–
68	River Volga (mouth of River Sviyaga)	Russia	53°46'N	48°55'E	Native	Lotic	D	Dfb
69	River Volga (Nizhny)	Russia	56°19'N	44°00'E	Native	Lotic	D	Dfb
70	River Wąglanka	Poland	51°22'N	20°17'E	Native	Lotic	C	Cfb

(Continued)

Table A1. Continued.

								Climate	
71	River Wolbórka	Poland	51°32'N	20°03'E	Native	Lotic	C	Cfb	
72	River Žitava	Slovakia	47°51'N	18°08'E	Native	Lotic	C	Cfb	
73	Rivers in Łódź region	Poland	51°40'N	19°26'E	Native	Lotic	C	Cfb	
74	Rivulet Bystřice	Czechia	49°38'N	18°43'E	Native	Lotic	D	Dfb	

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). Class: B = Arid; C = Temperate; D = Continental. Type: BSk = (Arid) Steppe – Cold; Cfa = (Temperate) Without dry season – Hot summer; Cfb = (Temperate) Without dry season – Warm summer; Dfa = (Continental) Without dry season – Hot summer; Dfb = (Continental) Without dry season – Warm summer; Dfc = (Continental) Without dry season – Cold summer.

Table A3. List of taxa encountered in the natural diet of ide.

Kingdom/Phylum	Class	Scientific name or lowest taxon	Reference(s)			
Protista						
Euglenozoa	Kinetoplastea	<i>Bodo edax</i>	(17)			
		<i>Polyoecta dumosa</i>	(17)			
Ciliata	Oligotrichida	<i>Tintinnidium fluviatile</i>	(17)			
	Peritrichia	<i>Carchesium polypinum</i>	(17)			
		<i>Zoothamnium</i> sp.	(17)			
	Prostomatida	<i>Prorodon ovum</i>	(17)			
	Nassulida	<i>Nassula elegans</i>	(17)			
	Cyrtophorida	<i>Chilodonella cucullulus</i>	(17)			
	Hymenostomata	<i>Colpidium colpoda</i>	(17)			
		<i>Colpidium cucullus</i>	(17)			
	Protozoa <i>incertae sedis</i>	<i>Cercobodo cometa</i>	(17)			
	Animalia					
Rotifera	ns	ns	(1)			
	Bdeloidea	<i>Rotaria neptunia</i>	(17)			
	Monogononta	<i>Anuraeopsis fissa</i>	(17)			
		<i>Asplanchna priodonta</i>	(17)			
		<i>Brachionus calyciflorus</i>	(17)			
		<i>Brachionus diversicornis</i>	(17)			
		<i>Keratella cochlearis</i>	(17)			
		<i>Keratella quadrata</i>	(17)			
		<i>Lecane bulla</i>	(17)			
		<i>Lecane luna</i>	(17)			
		<i>Trichocerca rousseleti</i>	(17)			
		<i>Trichocerca pygocera</i>	(17)			
		<i>Polyarthra major</i>	(17)			
		<i>Polyarthra minor</i>	(17)			
		Annelida	Clitellata	ns	(1, 6)	
				Lumbricidae	(2, 8)	
		Arthropoda	Branchiopoda	ns	(1, 8)	
				<i>Bosmina coregoni</i>	(17)	
				<i>Bosmina longirostris</i>	(17)	
				<i>Chydorus sphaericus</i>	(17)	
				<i>Daphnia cucullata</i>	(17)	
				<i>Pleuroxus uncinatus</i>	(17)	
<i>Polyphemus pediculus</i>	(17)					
Ostracoda	ns			(1, 17)		
Maxillopoda	<i>Canthocampus</i> sp.			(17)		
	<i>Cyclops strenuus</i>			(17)		
	<i>Cyclops</i> sp. (one species?)			(1, 2, 8)		
	<i>Diaptomus</i> sp. (one species?)			(2)		
	<i>Mesocyclops</i> sp.			(17)		
	Malacostraca			<i>Asellus</i> spp. (<i>aquaticus</i>)	(1, 4, 9)	
				<i>Gammarus</i> spp.	(1, 4, 11)	
				<i>Saduria entomon</i>	(4, 11)	
	Arachnida			Hydrachnidia	(1)	
				Insecta	<i>Corixa</i> spp.	(1, 8)
	<i>Dysticus</i> spp.				(9)	
	Ephemeroptera (nymph)				(1, 6)	
<i>Ephemera vulgata</i> (nymph)	(5)					
<i>Naucoris cimicoides</i>	(8)					
<i>Pentatoma rufipes</i>	(5)					
<i>Plea minutissima</i>	(8)					
<i>Tabanus</i> spp.	(9)					
Trichoptera (larva)	(1, 5, 12)					
Coleoptera (larva, imago)	(1, 8, 12)					
Lepidoptera (larva)	(8)					
Odonata (nymph)	(1, 12)					
<i>Phryganea</i> spp.	(9)					
Ceratopogonidae (larva)	(1)					
Chironomidae (larva, pupa, imago)	(1, 2, 5, 8, 9, 11, 12, 17)					
Simuliidae (larva, pupa)	(1)					
Mollusc	Gastropoda				<i>Acroloxus lacustris</i>	(1)
					<i>Anisus vortex</i>	(1)
					<i>Bathyomphalus contortus</i>	(1)
					<i>Bithynia leachii</i>	(1)
					<i>Bithynia tentaculata</i>	(1, 11)
					<i>Bithynia</i> spp.	(4)
					<i>Gyraulus</i> spp.	(1)
		<i>Hydrobia</i> spp.	(1, 2, 10, 11)			
		<i>Lymnaea</i> spp.	(1, 4, 8)			

(Continued)

Table A3. Continued.

Kingdom/Phylum	Class	Scientific name or lowest taxon	Reference(s)
		<i>Physa fontinalis</i>	(1)
		<i>Planorbis carinatus</i>	(1)
		<i>Radix baltica</i>	(10)
		<i>Theodoxus fluviatilis</i>	(10, 11)
		<i>Viviparus fasciatus</i>	(1)
		<i>Valvata macrostoma</i>	(1)
		<i>Valvata piscinalis</i>	(1)
	Bivalvia	<i>Cardium</i> sp. (one species?)	(4)
		<i>Cerastoderma glaucum</i>	(11)
		<i>Dreissena polymorpha</i>	(12)
		<i>Dreissena bugensis</i>	(12)
		<i>Macoma baltica</i>	(10)
		<i>Mya arenaria</i>	(11)
		<i>Mytilus edulis</i>	(1, 4, 7, 10)
		<i>Tellina</i> sp. (one species?)	(4)
Chordata	Actinopterygii	<i>Alburnus alburnus</i>	(13)
		<i>Coregonus albula</i>	(3)
		<i>Coregonus lavaretus</i> (egg, juvenile)	(10)
		<i>Hypophthalmichthys nobilis</i> (juvenile)	(14)
		<i>Leuciscus idus</i> (egg, juvenile)	(1)
		<i>Osmerus eperlanus</i>	(3)
		<i>Perca fluviatilis</i> (juvenile)	(1)
		<i>Pungitius platygaster</i>	(8)
		<i>Pungitius pungitius</i>	(10)
		<i>Rutilus rutilus</i> (juvenile)	(1)
Plantae			
Chlorophyta	Chlorophyceae	Cladophora	(1)
Charophyta	Charophyceae	Characeae	(3)
Equisetophyta	Equisetopsida	<i>Equisetum fluviatile</i>	(15)
Magnoliophyta	Monocots	<i>Carex</i> spp. (seeds)	(1)
		<i>Lemna minor</i>	(1)
		<i>Potamogeton perfoliatus</i>	(15)
		<i>Potamogeton</i> spp.	(1)
	Nymphaeales	<i>Nymphaea alba</i> (seeds)	(1)

ns = taxa not specified. Source references in footnote.

References: ¹Cala (1970); ²Collett (1905) *vide* Cala (1970); ³Huitfeldt-Kaas (1917) *vide* Cala (1970); ⁴Jääskeläinen (1917, 1921) *vide* Cala (1970); ⁵Mühlen von Zur and Schneider (1920) *vide* Järvalt et al. (2003); ⁶Berg (1949); ⁷Seegerstråle (1933); ⁸Popescu et al. (1960) *vide* Cala (1970); ⁹Martinson (1980) *vide* Järvalt et al. (2003); ¹⁰Oolu (1970); ¹¹Erm and Kangur (1985); ¹²Shcherbina and Buckler (2006); ¹³Froese and Pauly (2019); ¹⁴Sanft (2015); ¹⁵Braband (1985); ¹⁶Zhuravlev and Solovov (1984); ¹⁷Zygmunt (1999).

Table A4. Eukaryotic parasites of ide.

Taxonomic groups/species	Family	Geographical distribution	Reference(s)
Protists			
Phylum: Ciliophora			
Class: Oligohymenophorea			
<i>Apiosoma baninae</i>	Epistylididae	Eurasia	(1)
<i>Apiosoma olae</i>	Epistylididae	Rare specialist	(1)
<i>Apiosoma piscicola</i>	Epistylididae	Widespread	(1, 17)
<i>Ichthyophthirius multifiliis</i>	Ichthyophthiriidae	Widespread	(1, 17, 37)
<i>Paratrichodina incissa</i>	Trichodinidae	Eurasia	(1, 17)
<i>Trichodina domerguei</i>	Trichodinidae	Eurasia	(17)
<i>Trichodina esocis</i>	Trichodinidae	Widespread	(1)
<i>Trichodina mutabilis</i>	Trichodinidae	Widespread	(1)
<i>Trichodina nemachili</i>	Trichodinidae	Eurasia	(1)
<i>Trichodina nigra</i>	Trichodinidae	Widespread	(1)
<i>Trichodina pediculus</i>	Trichodinidae	Widespread	(1)
<i>Trichodina rectangli</i>	Trichodinidae	Eurasia	(1, 18)
<i>Trichodina reticulata</i>	Trichodinidae	Widespread	(1)
<i>Trichodina rostrata</i>	Trichodinidae	Eurasia	(1)
<i>Trichodinella subtilis</i>	Trichodinidae	Eurasia	(17)
<i>Tripartiella copiosa</i>	Trichodinidae	Widespread	(1, 5, 35)
Class: Phyllopharyngea			
<i>Chilodonella hexasticha</i> and <i>Chilodonella piscicola</i> (require molecular analysis for discrimination)	Chilodonellidae	Widespread	(1, 5)
Phylum: Euglenozoa			
Molecular data does not support currently recognized families.			
Class: Kinetoplastea			
<i>Cryptobia branchialis</i>	Cryptobidae	Widespread	(1, 5)
<i>Ichthyobodo necator</i> species complex	Bodonidae	Widespread	(1)
<i>Trypanosoma carassii</i>	Trypanosomatidae	Widespread	(1)
<i>Trypanosoma inexpectata</i>	Trypanosomatidae	Specialist, Volga River basin	(1)
<i>Trypanosoma schulmani</i>	Trypanosomatidae	Eurasia	(1)
Phylum: Metamonada			
Class: Trepomonadea			
<i>Spironucleus vortens</i>	Hexamitidae	Widespread	(38)
Phylum: Oomycota			
Class: Peronosporae			
<i>Saprolegnia</i> sp.	Saprolegniaceae	Widespread	(5)
Fungi			
Phylum: Microsporidia			
Class: Microsporea			
<i>Ichthyosporidium hertwigi</i>	Ichthyosporidiidae	Widespread	(5)
<i>Ichthyosporidium hoferi</i>	Ichthyosporidiidae	Widespread	(5)
Animalia			
Phylum: Cnidaria			
Class: Myxozoa			
<i>Chloromyxum cristatum</i>	Chloromyxidae	Eurasia	(1, 17, 18)
<i>Chloromyxum fluviatile</i>	Chloromyxidae	Eurasia	(1, 17, 37)
<i>Chloromyxum legeri</i>	Chloromyxidae	Eurasia	(17)
<i>Henneguya cutanea</i>	Myxobolidae	Eurasia	(1)
<i>Henneguya zschokkei</i>	Myxobolidae	Widespread	(18)
<i>Myxidium macrocapsulare</i>	Myxidiidae	Widespread	(1, 17)
<i>Myxidium rhodei</i>	Myxidiidae	Eurasia	(1, 17, 35)
<i>Myxobilatus legeri</i>	Myxobolidae	Eurasia	(1, 17)
<i>Myxobolus albovae</i>	Myxobolidae	Eurasia	(1)
<i>Myxobolus alvarezae</i>	Myxobolidae	Eurasia	(4)
<i>Myxobolus bramae</i>	Myxobolidae	Eurasia	(1, 17)
<i>Myxobolus carassii</i>	Myxobolidae	Eurasia	(1, 17, 35)
<i>Myxobolus cycloides</i>	Myxobolidae	Eurasia	(1)
<i>Myxobolus dispar</i>	Myxobolidae	Eurasia	(1, 17, 37)
<i>Myxobolus dogieli</i>	Myxobolidae	Eurasia	(1)
<i>Myxobolus donecae</i>	Myxobolidae	Eurasia	(1, 17)
<i>Myxobolus dujardini</i>	Myxobolidae	Widespread	(1, 13, 17, 18)
<i>Myxobolus elegans</i>	Myxobolidae	Eurasia	(1, 11)
<i>Myxobolus ellipsoides</i>	Myxobolidae	Eurasia	(1)
<i>Myxobolus exiguus</i>	Myxobolidae	Eurasia	(1, 20)
<i>Myxobolus gigas</i>	Myxobolidae	Eurasia	(1, 17)
<i>Myxobolus improvisus</i>	Myxobolidae	Eurasia	(1)
<i>Myxobolus intimus</i>	Myxobolidae	Eurasia	(4)
<i>Myxobolus kubanicus</i>	Myxobolidae	Eurasia	(5)
<i>Myxobolus kuleminae</i>	Myxobolidae	Eurasia	(1)

(Continued)

Table A4. Continued.

Taxonomic groups/species	Family	Geographical distribution	Reference(s)
<i>Myxobolus macrocapsularis</i>	Myxobolidae	Eurasia	(1, 17)
<i>Myxobolus muelleri</i>	Myxobolidae	Widespread	(1, 17, 20, 35, 37)
<i>Myxobolus muelleriformis</i>	Myxobolidae	Eurasia	(1)
<i>Myxobolus multiplicatus</i>	Myxobolidae	Eurasia	(1, 17, 18)
<i>Myxobolus musculi</i>	Myxobolidae	Widespread	(1)
<i>Myxobolus nemetzeki</i>	Myxobolidae	Eurasia	(1, 17, 20)
<i>Myxobolus obesus</i>	Myxobolidae	Eurasia	(1, 17)
<i>Myxobolus oviformis</i>	Myxobolidae	Eurasia	(1)
<i>Myxobolus permagnus</i>	Myxobolidae	Eurasia	(1)
<i>Myxobolus pseudodispar</i>	Myxobolidae	Eurasia	(1)
<i>Myxobolus strelkovi</i>	Myxobolidae	Eurasia	(1)
<i>Thelohanellus fuhrmanni</i>	Myxobolidae	Eurasia	(1)
<i>Thelohanellus oculileucisci</i>	Myxobolidae	Eurasia	(1, 19, 37)
<i>Thelohanellus pyriformis</i>	Myxobolidae	Eurasia	(1, 17)
<i>Zschokkella nova</i>	Myxidiidae	Eurasia	(1, 17, 35, 37)
<i>Zschokkella striata</i>	Myxidiidae	Eurasia	(5)
Phylum: Platyhelminthes			
Class: Cestoda			
<i>Caryophyllaeides fennica</i>	Lytocestidae	Eurasia	(3, 6, 17, 20, 24, 28, 40)
<i>Caryophyllaeus brachycollis</i>	Caryophyllaeidae	Eurasia	(3, 6, 12, 28)
<i>Caryophyllaeus laticeps</i>	Caryophyllaeidae	Eurasia	(3, 6, 17, 24, 28, 37)
<i>Ligula intestinalis</i>	Diphylobothriidae	Widespread	(3, 17)
<i>Proteocephalus torulosus</i>	Proteocephalidae	Widespread	(3, 14, 17, 18, 40)
<i>Schistocephalus solidus</i>	Diphylobothriidae	Widespread	(13)
<i>Schizocotyle acheilognathi</i>	Bothriocephalidae	Widespread	(3)
<i>Triaenophorus nodulosus</i> (l)	Triaenophoridae	Widespread	(3, 6, 17, 18)
Class: Monogenea			
<i>Dactylogyrus alatus</i>	Dactylogyridae	Eurasia	(2, 7, 16, 26, 30)
<i>Dactylogyrus crucifer</i>	Dactylogyridae	Eurasia	(12, 24)
<i>Dactylogyrus fallax</i>	Dactylogyridae	Eurasia	(2, 20, 30)
<i>Dactylogyrus haplogonoides</i>	Dactylogyridae	Eurasia	(6)
<i>Dactylogyrus micracanthus</i>	Dactylogyridae	Eurasia	(2, 7, 16, 30)
<i>Dactylogyrus nasalis</i>	Dactylogyridae	Eurasia	(2)
<i>Dactylogyrus ramulosus</i>	Dactylogyridae	Eurasia	(2, 6, 7, 17, 20, 26, 30)
<i>Dactylogyrus robustus</i>	Dactylogyridae	Eurasia	(2, 6, 7, 17, 30)
<i>Dactylogyrus similis</i>	Dactylogyridae	Eurasia	(2, 20, 24)
<i>Dactylogyrus sphyrna</i>	Dactylogyridae	Eurasia	(12, 24)
<i>Dactylogyrus tuba</i>	Dactylogyridae	Eurasia	(2, 6, 7, 12, 14, 16, 17, 20, 24, 30, 35, 37)
<i>Dactylogyrus vistulae</i>	Dactylogyridae	Eurasia	(26)
<i>Dactylogyrus yinwenyingae</i>	Dactylogyridae	Eurasia	(2, 20, 30)
<i>Diplozoon paradoxum</i>	Diplozoidae	Eurasia	(9, 17, 24)
<i>Gyrodactylus carassii</i>	Gyrodactylidae	Eurasia	(6, 10, 30)
<i>Gyrodactylus decorus</i>	Gyrodactylidae	Eurasia	(36)
<i>Gyrodactylus laevis</i>	Gyrodactylidae	Eurasia	(30)
<i>Gyrodactylus leucisci</i>	Gyrodactylidae	Eurasia	(31)
<i>Gyrodactylus medius</i>	Gyrodactylidae	Widespread	(17)
<i>Gyrodactylus prostae</i>	Gyrodactylidae	Eurasia	(2, 6, 7, 9, 12, 17, 18, 20, 24, 30, 35, 37)
<i>Gyrodactylus scardiniensis</i>	Gyrodactylidae	Eurasia	(7)
<i>Gyrodactylus tulensis</i>	Gyrodactylidae	Eurasia	(10, 30)
<i>Gyrodactylus vimbi</i>	Gyrodactylidae	Eurasia	(30, 31)
<i>Paradiplozoon alburni</i>	Diplozoidae	Eurasia	(2, 20, 30)
<i>Paradiplozoon bliccae</i>	Diplozoidae	Eurasia	(9, 35)
<i>Paradiplozoon homoion</i>	Diplozoidae	Eurasia	(2, 17, 30)
<i>Paradiplozoon leucisci</i>	Diplozoidae	Eurasia	(7)
<i>Paradiplozoon megan</i>	Diplozoidae	Eurasia	(2, 6, 7, 14, 17, 30, 35)
Class: Trematoda			
<i>Allocreadium dogieli</i>	Allocreadiidae	Eurasia	(3)
<i>Allocreadium isoporum</i>	Allocreadiidae	Eurasia	(17, 20, 25, 33, 34, 37, 40)
<i>Allocreadium transversale</i>	Allocreadiidae	Eurasia	(3)
<i>Apharyngostrigea cornu</i> (m)	Strigeidae	Widespread	(3*)
<i>Apophallus muehlingi</i> (m)	Heterophyidae	Eurasia	(6, 14, 24)
<i>Aspidogaster limacoides</i>	Aspidogastridae	Widespread	(17, 40)
<i>Asymphylogora imitans</i>	Lissorchiidae	Eurasia	(3, 25)
<i>Asymphylogora kubanica</i>	Lissorchiidae	Eurasia	(25, 35)
<i>Asymphylogora markewitschi</i>	Lissorchiidae	Eurasia	(3, 13, 17, 22, 35, 40)
<i>Asymphylogora parasquamosa</i>	Lissorchiidae	Eurasia	(3, 25, 32)
<i>Asymphylogora tincae</i>	Lissorchiidae	Eurasia	(17, 25)
<i>Bolbophorus confusus</i> (m)	Diplostomidae	Eurasia	(3*)
<i>Bucephalus polymorphus</i>	Bucephalidae	Eurasia	(3*, 17, 22)
<i>Bunocotyle cingulata</i>	Hemiuridae	Eurasia	(17)

(Continued)

Table A4. Continued.

Taxonomic groups/species	Family	Geographical distribution	Reference(s)
<i>Bunodera luciopercae</i>	Allocreadiidae	Widespread	(40)
<i>Diplostomum chromatophorum</i> (m)	Diplostomidae	Eurasia	(21)
<i>Diplostomum commutatum</i> (m)	Diplostomidae	Eurasia	(3*)
<i>Diplostomum helveticum</i> (m)	Diplostomidae	Eurasia	(3*)
<i>Diplostomum mergi</i> (m)	Diplostomidae	Widespread	(3*)
<i>Diplostomum spathaceum</i> (m) Some records may be <i>Diplostomum pseudospathaceum</i> which is morphologically similar	Diplostomidae	Widespread	(3, 17, 18, 20, 24)
<i>Hysteromorpha triloba</i> (m)	Diplostomidae	Widespread	(3, 17)
<i>Ichthyocotylurus erraticus</i> (m)	Strigeidae	Widespread	(3)
<i>Ichthyocotylurus pileatus</i> (m)	Strigeidae	Widespread	(3, 17, 21, 24)
<i>Ichthyocotylurus platycephalus</i> (m)	Strigeidae	Widespread	(3, 17, 20, 21, 33, 35)
<i>Ichthyocotylurus variegatus</i> (m)	Strigeidae	Eurasia	(3, 37)
<i>Mesostephanus appendiculatoides</i> (m)	Cyathocotylidae	Widespread	(3*)
<i>Metorchis bilis</i> (m)	Opisthorchiidae	Eurasia	(3*)
<i>Metorchis xanthosomus</i> (m)	Opisthorchiidae	Eurasia	(3*)
<i>Metagonimus yokogawai</i> (m)	Heterophyidae	Eurasia	(3, 17, 22, 24)
<i>Nicolla skrjabini</i>	Opecoelidae	Eurasia	(24,25)
<i>Opisthorchis felineus</i> (m)	Opisthorchiidae	Eurasia	(3, 17, 21)
<i>Palaeorchis incognitus</i>	Lissorchiidae	Eurasia	(3, 24)
<i>Paracoenogonimus ovatus</i> (m)	Cyathocotylidae	Eurasia	(3*, 14, 17, 20, 21, 24, 35)
<i>Phyllodistomum folium</i>	Gorgoderidae	Eurasia	(3, 17, 21, 22)
<i>Phyllodistomum macrocotyle</i>	Gorgoderidae	Eurasia	(17)
<i>Plagioporus angusticolle</i>	Opecoelidae	Eurasia	(20)
<i>Posthodiplostomum cuticola</i> (m)	Diplostomidae	Widespread	(3, 17, 20, 22, 24, 35)
<i>Pseudamphistomum truncatum</i> (m)	Opisthorchidae	Eurasia	(3*)
<i>Rhipidocotyle campanula</i> (m)	Bucephalidae	Eurasia	(3, 6, 21, 22, 24, 37)
<i>Rhipidocotyle fennica</i> (m)	Bucephalidae	Eurasia	(37)
<i>Sanguinicola armatus</i>	Aporocotylidae	Eurasia (one record in USA)	(22)
<i>Sanguinicola volgensis</i>	Aporocotylidae	Eurasia	(3, 14, 17, 35)
<i>Sphaerostoma bramae</i>	Opecoelidae	Eurasia	(3, 17, 18, 20, 27)
<i>Sphaerostoma globiporum</i>	Opecoelidae	Eurasia	(3*, 21, 22, 24, 40)
<i>Sphaerostoma minus</i>	Opecoelidae	Rare specialist, Curonian Lagoon	(3)
<i>Tylodelphys clavata</i> (m)	Diplostomidae	Widespread	(3*, 14, 18, 20, 22, 24, 33, 35)
Phylum: Nematoda			
Class: Chromadorea			
<i>Anguillicoloides crassus</i> (l)	Anguillicolidae	Adult is eel specialist, widespread	(39)
<i>Anisakis simplex</i> (l)	Anisakidae	Widespread	(35)
<i>Camallanus lacustris</i>	Camallanidae	Widespread	(3, 40)
<i>Camallanus truncatus</i>	Camallanidae	Widespread	(40)
<i>Cucullanus dogieli</i>	Cucullanidae	Eurasia	(3, 23)
<i>Cucullanus heterochrous</i>	Cucullanidae	Eurasia	(20)
<i>Desmidocercella numidica</i> (l)	Desmidocercidae	Widespread	(3*)
<i>Gnathostoma hispidum</i> (l)	Gnathostomatidae	Eurasia	(3*)
<i>Hysterothylacium aduncum</i> (l)	Raphidascarididae	Widespread	(27)
<i>Kalmanmolnaria intestinalis</i>	Skrjabinidae	Eurasia	(23)
<i>Philometra ovata</i>	Philometridae	Eurasia	(3, 17)
<i>Philometra rischta</i>	Philometridae	Eurasia	(6, 17, 24, 35)
<i>Pseudoterranova decipiens</i> (l)	Anisakidae	Widespread	(27)
<i>Raphidascaris acus</i> (l)	Raphidascarididae	Widespread	(8, 17, 20, 23, 37, 40)
<i>Rhabdochona denudata</i>	Rhabdochonidae	Eurasia	(3, 8, 17)
<i>Spiroxys contorta</i> (l)	Gnathostomatidae	Widespread	(23, 24)
<i>Streptocara crassicauda</i>	Acuariidae	Widespread	(35)
Phylum: Acanthocephala			
Class: Eoacanthocephala			
<i>Neoechinorhynchus rutili</i>	Neoechinorhynchidae	Widespread	(3, 6, 8, 17, 18, 35)
Class: Palaeacanthocephala			
<i>Diectophyme renale</i> (l)	Diectophymidae	Widespread	(23)
<i>Eustrongylides excisus</i> (l)	Diectophymidae	Eurasia	(23)
<i>Pseudocapillaria tomentosa</i>	Capillariidae	Widespread	(20, 23, 40)
<i>Schulmanella petruschewskii</i>	Capillariidae	Eurasia	(23)
Phylum: Acanthocephala			
Class: Eoacanthocephala			
<i>Neoechinorhynchus rutili</i>	Neoechinorhynchidae	Widespread	(3, 6, 8, 17, 18, 35)
Class: Palaeacanthocephala			
<i>Acanthocephalus anguillae</i>	Echinorhynchidae	Eurasia	(8, 12, 14, 17, 18, 20, 35, 37, 40)
<i>Acanthocephalus clavula</i>	Echinorhynchidae	Eurasia	(17, 18)

(Continued)

Table A4. Continued.

Taxonomic groups/species	Family	Geographical distribution	Reference(s)
<i>Acanthocephalus gracilacanthus</i>	Echinorhynchidae	Eurasia	(29, 33)
<i>Acanthocephalus lucii</i>	Echinorhynchidae	Eurasia	(6, 8, 35)
<i>Corynosoma semerme</i> (l)	Polymorphidae	Widespread	(20)
<i>Echinorhynchus salmonis</i>	Echinorhynchidae	Widespread	(18)
<i>Pomphorhynchus laevis</i> (Some records may be <i>Pomphorhynchus tereticollis</i> which is morphologically similar)	Pomphorhynchidae	Eurasia	(3, 6, 12, 17, 20)
Phylum: Annelida			
Class: Clitellata			
<i>Hemiclepsis marginata</i>	Glossiphoniidae	Eurasia	(3, 17, 35)
<i>Piscicola geometra</i>	Piscicolidae	Widespread	(3, 17, 18, 24, 35)
Phylum: Mollusc			
Class: Bivalvia			
Glochidia larvae	Margaritiferidae Unionidae	Widespread	(14, 17, 24, 35, 37)
Phylum: Arthropoda (Crustacea)			
Class: Hexanauplia			
<i>Caligus lacustris</i>	Caligidae	Eurasia	(5)
<i>Ergasilus briani</i>	Ergasilidae	Eurasia	(3, 5, 17, 20)
<i>Ergasilus sieboldi</i>	Ergasilidae	Eurasia	(5, 14, 17, 20, 24, 33, 35, 37)
<i>Lamproglana pulchella</i>	Lernaeidae	Eurasia	(3, 5, 17, 20, 24)
<i>Lernaea cyprinacea</i>	Lernaeidae	Widespread	(5)
<i>Tracheliastes polycolpus</i>	Lernaeopodidae	Palaeartic	(5, 14, 17, 18, 20, 24, 35, 37)
Class: Ichthyostraca			
<i>Argulus coregoni</i>	Argulidae	Widespread	(5, 24)
<i>Argulus foliaceus</i>	Argulidae	Eurasia	(3, 5, 17, 24, 35, 37)

Taxonomy follows the World Register of Marine Species (WoRMS) database, except for Crustacea taxonomy, which follows the World of Copepods database (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. Data on host specificity and geographical distribution is sourced from the Host-Parasite Database of the Natural History Museum, London (www.nhm.ac.uk/research-curation/scientific-resources/taxonomy-systematics/host-parasites/database/searchjsp), recent literature in Web of Science (www.apps.webofknowledge.com/) and the World of Copepods database. The listed metazoan parasites (except Cnidaria) occur as adults, trematode metacercariae (m) and nematode larvae (l). Most records are based on morphology, which is not a reliable method of identification for some species, particularly where parasites occur as metacercariae and larvae. Parasites are generalists in the fish host unless described as specialist. Some records are specified for Cyprinidae (*). Distribution data refers to any stage of the specified parasite in any of its hosts. Geographical data is subject to reporting bias. Source references in footnote.

¹Bauer (1984); ²Bauer (1985); ³Bauer (1987); ⁴Cech et al. (2012); ⁵de Charleroy et al. (1993); ⁶Djikanovic et al. (2012); ⁷Dorovskikh (1997); ⁸Dorovskikh (1999); ⁹Dzika (2008); ¹⁰Ergens (1988); ¹¹Eszterbauer (2002); ¹²Gelnar et al. (1994); ¹³Grabda (1971); ¹⁴Grabda-Kazubska and Pilecka-Rapacz (1987); ¹⁵Grabda-Kazubska and Okulewicz (2005); ¹⁶Hao et al. (2014); ¹⁷Izyumova (1987); ¹⁸Järvalt et al. (2003); ¹⁹Jeżewski and Kamara (1999); ²⁰Kirjušina and Vismanis (2007); ²¹Liberman (2020); ²²Molnar (1969); ²³Moravec (1994); ²⁴Moravec (2001); ²⁵Niewiadomska (2003); ²⁶Ondračková et al. (2004); ²⁷Palm et al. (1999); ²⁸Pojmańska (1991); ²⁹Popiołek (2016); ³⁰Pugachev et al. (2010); ³¹Rautskis (1988); ³²Rokicki (2004); ³³Rolbiecki (2003); ³⁴Rusinek (2007); ³⁵Sobecka et al. (2004); ³⁶Sterud (1999); ³⁷Sterud and Appleby (1997); ³⁸Sterud and Poynton (2002); ³⁹Thomas and Ollevier (1992); ⁴⁰Zhokhov (2003).