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A Stranger in Our Midst – 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 and North seas. Historically an important commercial species, the ide is exploited 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 the ide's acclimation to novel environments, the species has established relatively few self-sustaining populations outside its native range, and is therefore not considered to be invasive. However, as introductions are likely to continue, this 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). However, 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).

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 characterised 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 'grey' sources, have proved useful to inform the risk analysis process of less well-studied species (e.g. Copp et al. 2009a, 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 thus 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

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 of 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-grey or reddish in colour (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 grey, 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 the river basins that drain into the Baltic, Black, Caspian, White, Barents, Kara and Laptev seas, extending from the River Rhine basin in the west to Sweden and Finland in the north, to the River Lena basin in the east, and to the Alps and the northern parts of the Black and Caspian seas basins in the south (Fig. 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, 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 (Fig. 1), however its native status in some countries remains contentious. For example, in France, Spain, the Netherlands and 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, while 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 incertitude 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). Here, the ide was however subsequently reported to have been introduced in the 2000s (Leunda 2010) and 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), followed by reports in 1879 of the species in the wild, is well documented (Wheeler and Maitland 1973; Lever 1977). During this era of 'acclimation societies' (mid-19th to early 20th centuries), introductions of fish 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), and the ide is now present in ponds and water courses across most of England and Wales (Copp et al. 2006, 2007).

Introductions of the ide to non-native locations have also occurred within its native range (cf. translocations). For example, in Slovakia 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 (Balon and Žitňan 1964). This introduction occurred in the 1930s or early 1940s, and the population still thrives in this lake despite unfavourable conditions of cold water and ice cover lasting for almost six months a year. Introductions outside of Europe include North America and New Zealand. Ide was initially introduced to the USA in 1877 and has since been recorded in at least 22 states, including golden orfe in 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 that country suggests that most of these introductions have been unsuccessful. With the record 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 for 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 indicated 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 localised (McDowall 2000). However, there have been no recent confirmed reports on the continued presence of ide in New Zealand (Collier and Grainger 2015), despite extensive surveys (B. David, personal communication).

2.3 Habitat use

The ide is a benthopelagic, rheophilic and potamodromous species that can occupy a wide range of habitats from various freshwater body types to brackish waters. 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 psu (Müller and Berg 1982; Järvalt et al. 2003; Bogutskaya and Naseka 2006). Brackish water ide can usually withstand salinities up to 15 psu (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). However, sudden influxes of saline waters into these habitats are often responsible for mass kills (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 holes 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 the rehabilitated sections of the River Rhine flood plain, juvenile ide were restricted to shallow areas (< 1 m deep) of various water velocities (0–0.40 m s^{-1}) with little (1–5%) inundated terrestrial vegetation cover (Grift et al. 2003). Disappearance of these habitats, caused by river regulation, canalisation 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 temperature of near 0 °C and 35 °C, respectively (Leuven et al. 2011). Laboratory studies of upper lethal temperatures for ide under controlled conditions revealed an ability of embryos, larvae and juveniles to acclimatise 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 ide (Lehtonen 1996).

Despite having broad temperature and salinity tolerance, 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). Increasing turbidity can result in larger-scale ide movements, possibly due to reduced foraging efficiency of this visually-oriented predator (Kulíšková et al. 2009), and 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 ide's sensitivity and intolerance 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 freshwater 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). However, few studies have examined the habitat use and migratory behaviour 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 ide is often considered to have a limited home range, undertaking relatively short migrations (Järvalt et al. 2003), with long-distance movements up to 278 km and a mean linear home range of 53.5 km, has been reported in the Netherlands (de Leeuw and Winter 2006, 2008). For example, upstream migrations have been documented through fish ladders (Lelek and Libosvárský 1960), though in the cited case the ide represented only 1% of the fish observed. Additionally, 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, emphasising 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, has 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 ide's native range 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 movement 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, ide movement and dispersal appear to be limited by water retention structures. For example, movement distances of ide in the weir-regulated Meuse River 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 (Peňáz and Jurajda 1996; Povž 1996; Schiemer et al. 2004).

Spawning runs of anadromous ide in the vicinity of Øresund 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 suggested 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 ≈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 up to sexual maturation, after which they decrease, with annual growth increments becoming minimal after age 10 years (Rohtla et al. 2015b). This makes body length/weight 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). However, 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 are 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 dealing with 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 Štrbské Pleso Lake was 11 years old (Balon and Žitňan 1964).

Based on length-at-age data from the ide's native and introduced ranges (Tables A1 and A2; see also Appendix: *Age and growth modelling*), global growth in body length is asymptotic with an estimated $SL_\infty = 422.4$ mm (Table 1), and is characterised by large variation within year classes (Fig. 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 (Fig. 2b), and the same occurs in arid relative to continental and temperate climates (Fig. 2c), whereas under cold climates asymptotic size decreases progressively in areas with warm, temperate and cold summers (Fig. 2d). Condition factor for ide has been reported to vary from 0.46 to 3.51 (Table 2). The reported total length-weight relationship parameters for ide are provided in Table 3.

2.5 Reproduction

2.5.1 Sexual maturation, gonad development, and fecundity

In Europe, age at maturity varies with increasing latitude from 1 to 10 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 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 gonado-somatic 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 dorso-ventrally 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, Sződliget 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, with GSI increasing 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 Danube ide 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 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). However, ide of age 4 years 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 produce the highest percentage of both dead embryos during incubation and morphological abnormalities in hatched larvae, or they fail 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 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 behaviour

Spawning in ide 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 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 to 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 favour 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). However, 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 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 ide's nursery habitat has been described as having velocities of 0–10 cm s^{-1} at depths of 0–100 cm (Vriese et al. 1994).

Reproductive success in ide 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 °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 (Kucharczyk et al. 2008; Winter and Fredrich 2003). 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 they co-occur, ide can occasionally hybridise with common bream *Abramis brama*, asp *Leuciscus aspius*, common carp *Cyprinus carpio*, dace *Leuciscus leuciscus*, roach *Rutilus rutilus* and rudd *Scardinius erythropthalmus* (Schwartz 1972, 1981; Kopiejewska et al. 2003; Yadrenkina 2003; Witkowski et al. 2015). It is not clear whether these hybridisations 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 ide is both detritivorous and planktivorous (Katzenberg and Weber 1999). The range of food items encompasses molluscs, crustaceans, bryzoans, 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, encompassing both animal and plant taxa (Table A3) and varying 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 in 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 (Petlina and Romanov 2004; Zygmunt 1999), and 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 juvenile 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), the main prey item of adults was represented by Mollusca (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 are important food items for benthophagus fish species, including ide, the latter having been found to consume the largest-sized mussels among fish in the region (Shcherbina and Buckler 2006). In the brackish coastal waters of Estonia, smaller ide mainly feed on Ostracoda, Amphipoda and small snails, whereas larger specimens feed 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* are also consumed (Oolu 1970; Järvalt et al. 2003).

Seasonal changes in ide diet vary according to prey availability (Tyutenkov 1956; Cala 1970; Brabrand 1985). For example, in Lake Kurgaldzhin (Kazakhstan), sub-adults and adults mainly preyed upon *Gammarus* sp. (53%) in spring, whereas macrophytes represented only 5% of the biomass intake in spring, which increased to 95% in summer, and 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 mainly eaten 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, ide do not stop feeding (Järvalt et al. 2003), with Oligochaeta representing a main winter dietary item in the River Kävlinge (Cala 1970). In mesotrophic lakes in southeast Norway, the ide's consumption of macrophytes increased when animal food supply was scarce (Braband 1985). In that study, 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. The authors noted that the 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 localisation (Schuijf 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 species of fish including pikeperch *Sander lucioperca* and northern pike *Esox lucius* (Ciesla and Kaczkowski 2004), and the Amur catfish *Silurus asotus* also has been listed as a predator of ide (www.cabi.org/isc/datasheet/77315). 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 the region (Holčík 1984). It has also been suggested that predation by brown trout *Salmo trutta* was likely responsible for the 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). However, northern pike can reportedly prey on both juvenile and adult stages of ide (www.cabi.org/isc/datasheet/77315).

The ide is also susceptible to predation by piscivorous birds such as great cormorant *Phalacrocorax carbo sinensis* and osprey *Pandion haliaetus*. In Norway, ide are 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 on ide has been observed in Estonia (Vetemaa et al. 2010), the Netherlands (Veldkamp 1995) and the Czech Republic (Kortan et al. 2008), where fishpond losses of ide were attributed to cormorant predators. Maximum prey size of cormorants is ≈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 fish 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 include *Flexibacter columnaris* and *Aeromonas punctata* (De Charleroy et al. 1993). However, 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 fish reflects the broad dietary spectrum of ide (Järvalt et al. 2003). However, the species richness of certain groups, particularly protists, platyhelminths and nematode larvae, may not be accurate since the records of many ide parasites are by morphological identification which can be unreliable without molecular confirmation. Ide have the potential to act as a source of parasitic infection, but no more than other cyprinid species. The ide can harbour 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 spironucleosis, which is highly pathogenic to cultured fish. 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 are 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 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). However, 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 the river, probably due to the absence of large rheophilic fishes (Kruk 2007), hence demonstrating that in some locations ide can prevail under conditions of environmental perturbation and weak competition. Counter-intuitively, long-term stream water quality improvement in southern Sweden has resulted in considerable decline of ide abundance whilst facilitating increases in brown trout *Salmo trutta* abundance (Eklöv et al. 1998). Whereas, no difference in ide presence has been reported for 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 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 angling, with ongoing re-stocking programmes in Flemish rivers since the 1990s (1–5 tons yr^{-1} since 2000), which however 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. Also, a minimum angling size of 25 cm (total length: TL) is in force in Wallonia, but not anymore 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 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 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). However, 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. 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, ide is currently marked as 'Data deficient' (http://elurikkus.ut.ee).

In Finland, ide used to be a popular species for household use, but it has fallen into disfavour along with the general decrease in appreciation of cyprinids for human consumption. Some ide are still caught for the market in the Archipelago Sea and the Gulf of Finland as well as in estuaries of the northern Gulf of Bothnia. 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, ide is currently marked as 'Least concern'.

In Latvia, 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, ide is currently not listed (J. Birzaks, personal communication).

Albeit rare in coastal waters of Lithuania, ide is still common and relatively abundant in the Curonian Lagoon and in the country's largest rivers 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 the Nemunas River and Curonian Lagoon in recent years, 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 varied 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). Ide has never been commercially important in Lithuania, and until the 1980s annual landings rarely exceeded 4 tons yr^{-1} (mean 2.5 tons). However, ide landings 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 ide is not enlisted in the Lithuanian Red List of Threatened Species. In 2016, a study proposing an ide re-stocking programme for inland water bodies with extinct or nearly extinct ide populations 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 resulting 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). 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 angling size. As in Flanders, ide was listed as ‘Vulnerable’ in the IUCN Red List for the Netherlands (de Leeuw et al. 2005), but is not included in the new Red List anymore (Spikmans and Kranenbarg 2016). Also, 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 marine waters. Levels of total allowable commercial catches in rivers, reservoirs and lakes are established individually for each water body (or river stretch). In 2018, the 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 Kamieński Lagoons). According to the Fishing Monitoring Centre in Gdynia, no ide was recorded in official commercial fishery statistics from marine areas of Poland 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 have been exempted from the obligation of reporting, and individual recreational fishery in Polish marine waters does not have to report catches at all. Poland's Inland Fishery Act imposes an obligation to re-stock rivers with fish including the ide, but for inspection authorities the origin of fish is not taken into consideration. In 2018, 6,135,000 yolk-sac larvae with 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 et al. 2020). In the Gulf of Gdansk, where the ide was caught by anglers 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 less than 0.01% and 0.04%, respectively (Skóra 2015). The ide is very rare also 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). However, in the Międzyodrze wetlands (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 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, 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 Danube, where it still represents a relatively abundant fish species (Bammer et al. 2015).

In Sweden, the ide is rarely captured in different monitoring areas 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 England’s nine regions (Copp et al. 2007). A lack of demonstrated invasive nature and the ide’s importance as an ornamental species are the reasons why the species was not included in legislation for regulating non-native fishes in England & Wales, 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, b). However, 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 probable 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: *Parasites and pathogens*), 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 its 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 in England (Kennedy 1975). Furthermore, 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 this species 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 (e.g. Cala 1970; Brabrand 1985; Järvalt et al. 2003). 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 *Leucaspius delineatus* (Bašić et al. 2018). As such, further study is 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), ide responded rather positively to perturbations, prevailing even when other large rheophilic species were absent (Kruk 2007). However, 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 observations), which would potentially limit population growth and subsequent invasiveness. Under controlled laboratory conditions, early life-stages of ide have demonstrated good acclimatisation and tolerance to increasing water temperatures (Florez 1972a; Kupren et al. 2010). The latter suggests that 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, or are even more thermophilic than some other species. 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 localised 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 can potentially disperse to a wide geographical area (Winter and Fredrich 2003; Kulíšková et al. 2009; Rohtla et al. 2015a). This means that new regions can be colonised relatively rapidly in a given water course, 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 colonising 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 populations in England (Copp 1997). The potential risks of ide hybridising 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 behaviours, diet, diseases, growth and potential hybridisation 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. However, further afield, the ide may become invasive, such has been observed with another European cyprinid, 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 et al. 2009b; 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). However, 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 ide in North America (Nico et al. 2020). There have been, however, reports of benign diseases being imported to the USA from Germany (McAllister et al. 1985). The lack of evidence for demonstrated impacts may appear to corroborate these risk screening outcomes, but this lack of evidence is due to a general lack of study of the ide’s impacts rather than from the absence of impacts. As introductions of the 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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Tables

Table 1. Growth of ide *Leuciscus idus* as modelled by the VBGF. 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 A3); N = number of populations. Statistically significant parameters in bold. Climate classes and types as defined in Appendix Table S1 in Electronic Supplementary Material. See also Fig. 3a–d.

Parameter	Estimate	SE	LCI	UCI	t	P
Global (n = 733, N = 87)						
SL_{∞}	422.4	9.2	405.0	442.6	45.66	**< 0.001**
K	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: n = 283, N = 31; Lotic: n = 450, N = 56)						
$SL_{\infty\text{Lentic}}$	398.5	9.2	381.3	417.5	43.07	**< 0.001**
$SL_{\infty\text{Lotic}}$	503.2	25.7	459.2	563.1	19.58	**< 0.001**
K_{Lentic}	0.18	0.01	0.16	0.22	15.59	**< 0.001**
K_{Lotic}	0.12	0.01	0.10	0.14	10.43	**< 0.001**
t_0	−0.08	0.11	−0.32	0.12	−0.75	0.451
Climate class (B: n = 11, N = 2; C: n = 298, N = 42; D: n = 339, N = 33)						
$SL_{\infty\text{B}}$	524.1	34.2	458.8	592.4	15.32	**< 0.001**
$SL_{\infty\text{C}}$	390.0	10.2	371.6	410.5	38.06	**< 0.001**
$SL_{\infty\text{D}}$	420.9	9.0	404.8	438.9	47.76	**< 0.001**
K	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: n = 7, N = 1; Dfb: n = 222, N = 23; Dfc: n = 110, N = 9)						
$SL_{\infty\text{Dfa}}$	497.9	29.2	442.0	555.9	17.07	**< 0.001**
$SL_{\infty\text{Dfb}}$	439.8	8.3	424.9	455.9	52.96	**< 0.001**
$SL_{\infty\text{Dfc}}$	383.4	7.9	368.9	399.0	48.31	**< 0.001**
K	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**

Table 2. Condition factor *K* for ide at various native range locations. Decimal points as per source study.

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 Neman	Belarus	2.09	1.76	2.50	Zhukov (1965)
(Several)	Estonia	2.1	1.57	3.51	Ristkok (1974)
(Several)	Estonia	–	1.6	2.2	Järvalt (1981)
River Ob	Russia	2.04	1.79	2.36	Zhuravlev and Solovov (1984)
Lake Barselvann (1994)	Norway	1.16	–	–	Simonsen (2000)
Lake Barselvann (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	Jelkić et al. (2010)
Yser, Meuse and Scheldt basins	Belgium	1.08	0.46	1.85	*Hoc opus*

Table 3. Total length-weight relationship ($W = a\mathrm{TL}^{b}$) parameters for ide at various native range locations.

Water body	Country	Length		a	b	Reference
Lake Chany	Russia	SL	cm	0.0054	3.396	Tyurin (1927) *fide* Froese and Pauly (2019)
River Volkhov	Russia	SL	cm	0.0071	3.259	Tyurin (1927) *fide* Froese and Pauly (2019)
River Volga	Russia	SL	cm	0.01574	2.444	Gundrizer (1958) *fide* Froese and Pauly (2019)
Western Siberia	Russia	TL	cm	0.01760	3.066	Gundrizer (1958) *fide* Froese and Pauly (2019)
Western Siberia	Russia	TL	cm	0.0040	3.468	Gundrizer (1958) *fide* Froese and Pauly (2019)
River Enisey	Russia	TL	cm	0.02940	2.878	Podlesnyi (1958) *fide* Froese and Pauly (2019)
River Kävlinge	Sweden	TL	mm	0.0037	3.339	Cala 1970
River Danube sidearm Žofín	Slovakia	SL	mm	0.0004	2.864	Naiksatam (1976) *fide* Hensel (2015)
Rivulet Bystřice	Czechia	SL	mm	0.0112	3.1422	Hanel (1984)
(Unspecified)	Finland	TL	cm	0.01185	2.878	Koli (1990) *fide* Froese and Pauly (2019)
(Several)	Netherlands	na	na	0.003489	3.3630	Klein Breteler and de Laak (2003)
Lake Sailimu	China	SL	mm	0.0087	3.3999	Fan and Quan (2008)
(Several)	Croatia	TL	cm	0.0092	3.048	Treer et al. (2008)
River Ergis	China	TL	cm	0.017	3.099	Huo et al. (2011)
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)

1653 **Table 4**. Age (years) and SL (mm) at maturity for ide at various native range 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 Shteynfel'd (1949)
(Unspecified)	France	3	–	Dottrens (1952) *fide* Spillmann (1961)
River Turgai, River 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 Võrtsjärv	Estonia	5–7	260–300	Haberman et al. (1973)
Lokka Reservoir	Finland	6–7	–	Mutenia (1978) *fide* Siriwardena (2008)
Lake Ugiy	Mongolia	5–6	267–283	Dulmaa (1999)
River Neman	Lithuania, Belarus	4–5	≈250	Vechkanov (2000); Virbickas (2000)
(Unspecified)	Poland	3–4	–	Witeska et al. (2014)

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)	France	2.5	–	Dottrens (1952) *fide* 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, c)
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)	UK	–	39,000–114,000	Maitland and Campbell (1992)
River Orhon	Mongolia	–	70,300–173,600	Dulmaa (1999)
River Neman	Lithuania	1.9–2.3	35,000–150,000	Virbickas (2000)
(Unspecified)	France	2.5	60,000–160,000	Keith and Allardi (2001)
River Dnieper	Russia	–	39,000–114,000	Berg (1964)
(Unspecified)	France	1.9–2.3	–	Keith et al. (2011)

Figure legends

Fig. 1 Native (grey) 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).

Fig. 2 Growth in length of ide at the global scale as described by the von Bertalanffy growth fuction (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 S3) 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.

1666 **Figures**

1667 **Fig. 1**

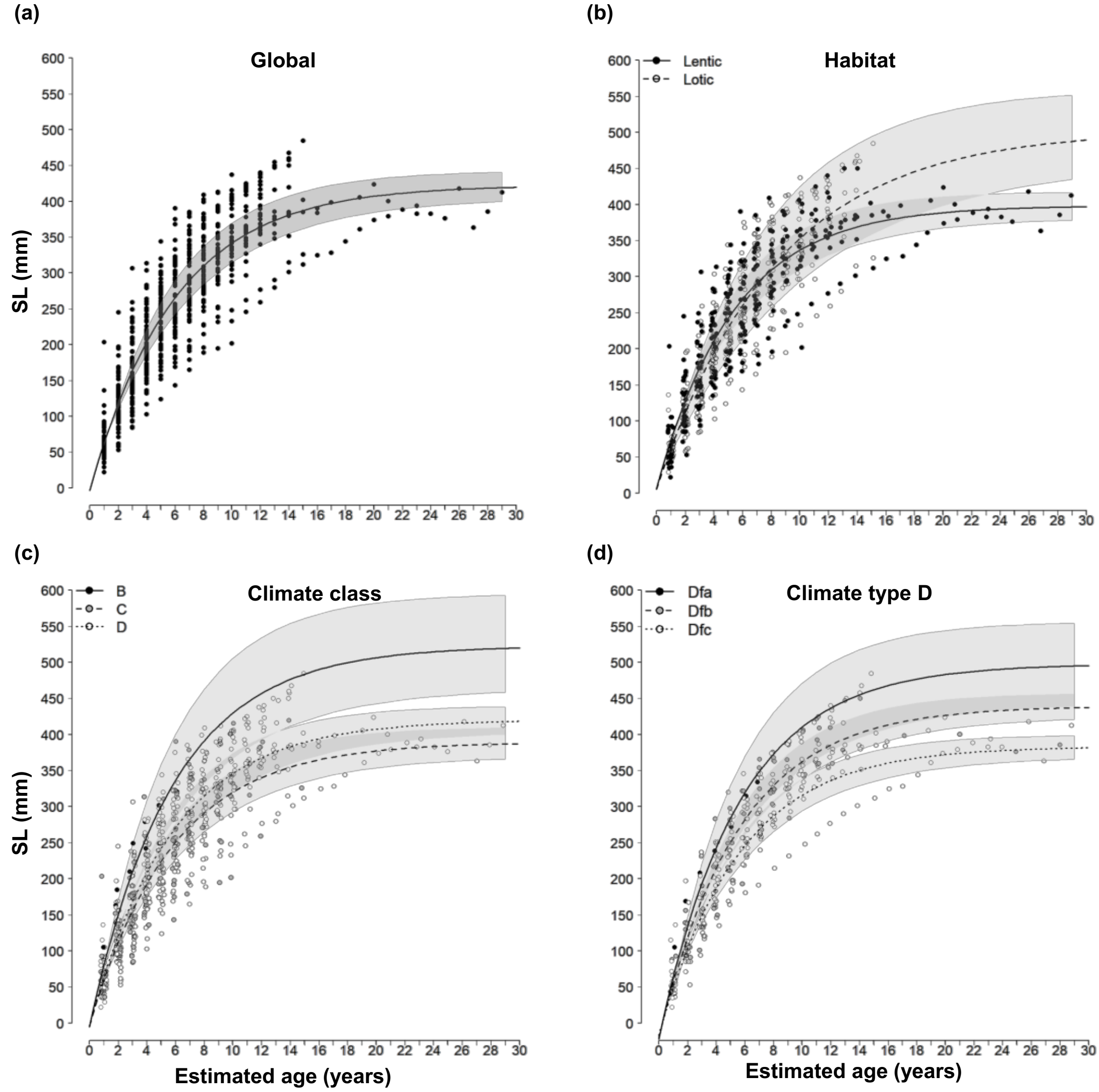
(a)
Global
SL (mm)
0 50 100 150 200 250 300 350 400 450 500 550 600
0 2 4 6 8 10 12 14 16 18 20 22 24 26 28 30
(b)
Habitat
Lentic
Lotic
0 50 100 150 200 250 300 350 400 450 500 550 600
0 2 4 6 8 10 12 14 16 18 20 22 24 26 28 30
(c)
Climate class
B
C
D
SL (mm)
0 50 100 150 200 250 300 350 400 450 500 550 600
0 2 4 6 8 10 12 14 16 18 20 22 24 26 28 30
Estimated age (years)
(d)
Climate type D
Dfa
Dfb
Dfc
0 50 100 150 200 250 300 350 400 450 500 550 600
0 2 4 6 8 10 12 14 16 18 20 22 24 26 28 30
Estimated age (years)

Fig. 2

Appendix

Age and growth modelling

Data on ide growth were retrieved from both primary and secondary (cf. *fide*) literature sources. A necessary condition for inclusion of a literature source was that it provided mean length-at-age (LAA) values for the population under study. Whenever mean LAA values were provided for only one or a few age classes (e.g. as representative of the population from which fish were sampled), these were still included into the global database for the sake of completeness (cf. Vilizzi and Copp 2017). For these analyses (and in other relevant parts of the present study), LAA data originally given as total length (TL, mm) were converted to standard length (SL, mm) using the formula SL = −0.36 + 0.863TL (M. Rohtla, 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 categorised as either 'native' or 'non-native' (Fig. 1). For each water body, the corresponding habitat was labelled as either 'lentic' (natural lakes and man-made reservoirs) or 'lotic' (water courses). Based on the water body's latitude and longitude, the corresponding Köppen-Geiger climate class and type (Peel et al. 2007) were identified with reference to a regular 0.5 degree latitude/longitude grid for the period 1951–2000 (Kottek et al. 2006: http://koeppen-geiger.vu-wien.ac.at/data/Koeppen-Geiger-ASCII.zip).

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

$$\mathrm{SL} = \mathrm{SL}_\infty \left(1 - e^{(-K(\mathrm{age} - t0))}\right)$$

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 & 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).

Appendix Tables

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

							Climate	
ID	Water body	Country	Lat	Lon	Range	Habitat	Class	Type
1	Baltic Sea (Orrengrund)	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 Kamyš-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

							Climate	
ID	Water body	Country	Lat	Lon	Range	Habitat	Class	Type
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	Lotic	C	Cfb
26	Pond near Vlčie hrdlo (Bratislava)	Slovakia	48°08'N	17°06'E	Native	Lotic	C	Cfb
27	River Barbarka	Poland	51°13'N	20°02'E	Native	Lentic	C	Cfb
28	River Czarna Konecka	Poland	51°18'N	19°54'E	Native	Lentic	C	Cfb
29	River Czarna Taraska	Poland	51°06'N	20°21'E	Native	Lentic	C	Cfb
30	River Danube	Slovakia	–	–	Native	Lentic	–	–
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 (Medveďov)	Slovakia	47°47'N	17°39'E	Native	Lotic	C	Cfb
39	River Danube (Štúrovo)	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

							Climate	
ID	Water body	Country	Lat	Lon	Range	Habitat	Class	Type
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	Dfc
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 Neman (BY)	Belarus	–	–	Native	Lotic	–	–
58	River Neman (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
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

							Climate	
ID	Water body	Country	Lat	Lon	Range	Habitat	Class	Type
74	Rivulet Bystřice	Czechia	49°38'N	18°43'E	Native	Lotic	D	Dfb

Table A2 Mean length-at-age (standard length: SL, mm) values for ide. Source references in footnote.

	Estimated age (years)																													
ID	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	Reference
1	36	71	101	135	169	193	240	272																						(45)
2	43	85	117	150	185	220	262	286	325																					(45)
3	53	106	147		292	322	340	345	365	390	387	410			402	384	399		405	424	400		383	383	376	418	364	386	412	(39)
4	86	130	174	221	249	268	294	321	348	366	393	417	450	450																(54)
5	84	160	224	282	344																									(22)
6			191	234	277	322	345	364	386	406																				(5)
7	35	114	137	226																										(1)
7			237	251	282	300	346	363	391	401	425	440																		(40)
8	51	85	119	153	178	210	235	253																						(34)
9*	204	245	306	314	310																									(48)
10		156	204	233	276	283	290																							(37)
11	92	163	210	242	249																									(47)
12	88	139	180	217	256	292	325																							(9)
13	105	169	208	239	272	315	334																							(46)
14	22	53	94	160	183	219	258	282	316	327	341	354	368																	(4)
15	72	140	190	232	265																									(38)
16	43	85	121	159	194	230	268	302	326	342	356	369	379	383																(45)
17		138	174	249	298																									(13)
18**	41	94	120	146	164	181	191	215	232	248	262	277	290	302	312	325	328	344	361	374	379	389	394							(32)
18	44	93	154	202	240	257	273	291	305	323	338	356	375	385	385	391														(32)
19	50	104	149	202	240	283	314	336	351	363	378	380																		(3)
19	66	100	134	164	198	233	262	279	293	311	327	340	348	352																(31)
20	105	185	249	279	302	321																								(47)
21	93	167	233	283	320	346	366																							(20)
22		105			277	290	310	332	340	357	366	360		380																(15)

23					174	169	179	196	239	202			(55)
24	50	96	148	208	275	391	385	409					(21)
25	51	77	93										(24)
26	62	84											(24)
27	91	122				236	232						(55)
28	93	107	155	169	196	225	255	276	295	315	345	364	(55)
29						198							(55)
30		136	182	215	256	268	316	328	356				(43)
31	51	94	145	184	214	248	285						(35)
32		120	145	181		253							(26)
33	56	132	173	193									(2)
34	50												(2)
35	64	95	111	172	261	319	338						(31)
36	70	136	177	233	279	323	340						(2)
36	57	142	218	257	300	323	340						(2)
37	59	97	134				248	259		297			(43)
37	49	85	120	166	200	218	240	247	302				(49)
37	69	105	148	179	208	235	256	271	289	297			(49)
38	80	127	173	187	186								(2)
38	72	152	238	280	311								(2)
38	51	119	161	174	217	250							(2)
39	57	138	201	233	253	270	288	305	327				(2)
40	60	135	181	218	250								(2)
41	60	82	105	132	157	192	198	227	251	305			(30)
42	53	104	153	200	245	286	338	378	413				(52)
43	59	118	169	211	255	293	355	383					(52)
44		105		167	201		275	279			316	405	(55)
45	71		134	167	193	220			293				(43)
46	36	62	107	136	175	183	195						(6)
46	78	113	145	168	197	216							(41)

47	71	103	134	167	193	220	249	271	293							(44)
48	29	58	85	117	152	175	206	228	253	288	297					(6)
48	68	95	126	158	174	214	242	262	290	314						(41)
49	41	85	125	169	212	252	292	326	355							(33)
50	136	197	231	251	287	310	291	324	324							(25)
51	58	102	141	174	207	238	268									(28)
52	52	95	134	180	222	242	255									(10)
53			148	191		298	354	374	387	404	417	438	447	468	485	(12)
54	69	142	204	260	299	333	359	377	394	401	414					(7)
54	55	127	180	247		375	378	399	412	416						(8)
55		143	176	173	195	235	257	298	315	337	360	390	355			(55)
56						312	346	368	388	405	422	434		458		(11)
57	52	104	153	198	244	270										(51)
58	65	100	150	200	270	315	360	365	390	410	420	428	455	460		(38)
59		114	158	199	230	250	265	275	284	334						(17)
60		195	259	304	344	368	383	403		437						(50)
60		160	190	195	207											(50)
61	73	138	177	209	257	298	320	349	368							(53)
62		103	142	190	196	220	255	283	306	327	349	382				(55)
63	46	91	132	174	211	243	277	304	332	350	363	375	386			(45)
64	58	99	153	201	249	282	330	338	352							(18)
65	50	99	133	163	198	234	260									(29)
66	58	108	156	220	250	303	340	376	390	396	409	423				(36)
67	61	112	157	200	223	253	289	309	328	346	378	394				(50)
68	48	94	142	183	223	257	276	288	313	345						(27)
69	115	139	179	213	232	257	278	319	331	344	359	383	416			(14)
70				186		210										(55)
71														420		(55)
72	36	60	84	103	124	143	165	189	195	233	246	259	280	315	326	(23)
72	63	117	153	193	224	245	265	295	321	332						(42)

73		156	223	264	265	318	327	351	331	380				460	(19)
74	60	103	138	172	216	256	296	324	335	345	360				(16)

References: [1]Autko (1958) *fide* Sayfullin and Shakirova (2014); [2]Balon (1962); [3]Balon and Žitňan (1964); [4]Brofeldt (1917) *fide* Segestråle (1933); [5]Brujenko et al. (1974); [6]Čajka (1975) *fide* Hensel (2015); [7]Cala (1970); [8]Cala (1971b); [9]Domrachev and Pravdin (1926); [10]Dukravets et al. (2001); [11]Erm and Kangur (1985); [12]Erm et al. (2002); [13]Fan and Quan (2008); [14]Golovko (1973) *fide* Sayfullin and Shakirova (2014); [15]Haberman et al. (1973); [16]Hanel (1984); [17]Heggenes (1983); [18]Hochman (1956); [19]Jakubowski and Penczak (1970); [20]Jereščenko (1959) *fide* Balon (1962); [21]Kleszcz (2008); [22]Kovrižnych et al. (1986) *fide* Hensel (2015); [23]Krišofík (1961) *fide* Hensel (2015); [24]Krupka (1972) *fide* Hensel (2015); [25]Liberman and Chemagin (2017); [26]Lujić et al. (2013); [27]Lukin (1934) *fide* Sayfullin and Shakirova (2014); [28]Menshikov and Bukiriev (1934) *fide* Balon (1962); [29]Muromova (1930) *fide* Balon (1962); [30]Naiksatam (1976) *fide* Hensel (2015); [31]Nevický (1992) *fide* Hensel (2015); [32]Nicolaisen (1996); [33]Nikolsky et al. (1947); [34]Otterstrøm (1930) *fide* Segestråle (1933); [35]Peňáz (1961); [36]Platonova (1958) *fide* Sayfullin and Shakirova (2014); [37]Popov et al. (2005); [38]Probatov (1929) *fide* Balon (1962); [39]Rohtla et al. (2015b); [40]Sayfullin and Shakirova (2014); [42]Sedlár (1966) *fide* Hensel (2015); [43]Sedlár (1989) *fide* Hensel (2015); [44]Sedlár et al. (1985) *fide* Hensel (2015); [45]Segestråle (1933); [46]Serov (1959); [47]Sidorova (1959); [48]Simonsen (2000); [49]Šindléryová (1965) *fide* Hensel (2015); [50]Svetovidova (1949) *fide* Balon (1962); [51]Zhukov (1958) *fide* Balon (1962); [52]Zhukov (1965); [53]Zhuravlev and Solovov (1984); [54]Zinov'ev (1965) *fide* Sayfullin and Shakirova (2014); [55]*Hoc opus*.

* Golden orfe escaped or translocated from a nearby amusement park pond.

** Golden orfe sympatric with wild ide.

Table A3 List of taxa encountered in the natural diet of ide. ns = taxa not specified. Source references in footonote.

Kingdom/Phylum	Class	Scientific name or lowest taxon	Reference(s)
Protista			
Euglenozoa	Kinetoplastea	*Bodo edax*	(17)
		Polyoecta dumosa	(17)
Ciliata	Oligotrichida	*Tintinnidum fluviatile*	(17)
	Peritrichia	*Carchesium polypinum*	(17)
		Zoothamnium sp.	(17)
	Prostomatida	*Prorodon ovum*	(17)
	Nassulida	*Nassula elegans*	(17)
	Cyrtophorida	*Chilodonella cucullulus*	(17)
	Hymenostomata	*Colpidium colpoda*	(17)
		Colpidium cucullus	(17)
Protozoa *incertae sedis*	Protozoa *incertae sedis*	*Cercobodo cometa*	(17)
Animalia			
Rotifera	ns	ns	(1)
	Bdeloida	*Rotaria neptunia*	(17)
	Monogononta	*Anuraeopsis fissa*	(17)
		Asplanchna priodonta	(17)
		Brachionus calyciflorus	(17)
		Brachionus diversicornis	(17)
		Keratella cochlearis	(17)
		Keratella quadrata	(17)
		Lecane bulla	(17)
		Lecane luna	(17)
		Trichocerca rousseleti	(17)
		Trichocerca pygocera	(17)
		Polyarthra major	(17)
		Polyarthra minor	(17)
Annelida	Clitellata	ns	(1, 6)
		Lumbricidae	(2, 8)
Arthropoda	Branchiopoda	ns	(1, 8)
		Bosmina coregoni	(17)
		Bosmina longirostris	(17)
		Chydorus sphaericus	(17)
		Daphnia cucullata	(17)
		Pleuroxus uncinatus	(17)
		Polyphemus pediculus	(17)
	Ostracoda	ns	(1, 17)
	Maxillopoda	*Canthocampus* sp.	(17)
		Cyclops strenuus	(17)
		Cyclops sp. (one species?)	(1, 2, 8)
		Diaptomus sp. (one species?)	(2)
		Mesocyclops sp.	(17)

Kingdom/Phylum	Class	Scientific name or lowest taxon	Reference(s)
	Malacostraca	*Asellus* spp. (*aquaticus*)	(1, 4, 9)
		Gammarus spp.	(1, 4, 11)
		Saduria entomon	(4, 11)
	Arachnida	*Hydrachndiae*	(1)
	Insecta	*Corixa* spp.	(1, 8)
		Dysticus	(9)
		Ephemeroptera (nymph)	(1, 6)
		Ephemera vulgata (nymph)	(5)
		Naucoris cimicoides	(8)
		Pentatoma rufipes	(5)
		Plea minutissima	(8)
		Tabanus	(9)
		Trichoptera (larva)	(1, 5, 12)
		Coleoptera (larva, imago)	(1, 8, 12)
		Lepidoptera (larva)	(8)
		Odonata (nymph)	(1, 12)
		Phryganea	(9)
		Ceratopogonidae (larva)	(1)
		Chiromidae (larva, pupa, imago)	(1, 2, 5, 8, 9, 11, 12, 17)
		Simuliidae (larva, pupa)	(1)
Mollusca	Gastropoda	*Acroloxus lacustris*	(1)
		Anisus vortex	(1)
		Bathyomphalus contortus	(1)
		Bithynia leachii	(1)
		Bithynia tentaculata	(1, 11)
		Bithynia spp.	(4)
		Gyraulus spp.	(1)
		Hydrobia spp.	(1, 2, 10, 11)
		Lymnaea spp.	(1, 4, 8)
		Physa fontinalis	(1)
		Planorbis carinatus	(1)
		Radix baltica	(10)
		Theodoxus fluviatilis	(10, 11)
		Viviparus fasciatus	(1)
		Valvata macrostoma	(1)
		Valvata piscinalis	(1)
	Bivalvia	*Cardium* sp. (one species?)	(4)
		Cerastoderma glaucum	(11)
		Dreissena polymorpha	(12)
		Dreissena bugensis	(12)
		Macoma baltica	(10)
		Mya arenaria	(11)
		Mytilus edulis	(1, 4, 7, 10)
		Tellina sp. (one species?)	(4)
Chordata	Actinopterygii	*Alburnus alburnus*	(13)

Kingdom/Phylum	Class	Scientific name or lowest taxon	Reference(s)
		Coregonus albula	(3)
		Coregonus lavaretus (egg, juvenile)	(10)
		Hypophtalmichthys nobilis (juvenile)	(14)
		Leuciscus idus (egg, juvenile)	(1)
		Osmerus eperlanus	(3)
		Perca fluviatilis (juvenile)	(1)
		Pungitus platygaster	(8)
		Pungitius pungitius	(10)
		Rutilus rutilus (juvenile)	(1)
Plantae			
Chlorophyta	Chlorophyceae	Cladophora	(1)
Charophyta	Charophyceae	Characeae	(3)
Equisetophyta	Equisetopsida	*Equisetum fluviatile*	(15)
Magnoliophyta	Monocots	*Carex* spp. (seeds)	(1)
		Lemma minor	(1)
		Potamogeton perfoliatus	(15)
		Potamogeton spp.	(1)
	Nymphaeales	*Nymphaea alba* (seeds)	(1)

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

Table A4 Eukaryotic parasites of ide. 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 which 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/search.jsp), 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.

Taxonomic groups/species	Family	Geographical distribution	Reference(s)
Protists			
Phylum: Ciliophora			
Class: Oligohymenophorea			
Apiosoma baninae	Epistylididae	Eurasia	(1)
Apiosoma olae	Epistylididae	Rare specialist	(1)
Apiosoma piscicola	Epistylididae	Widespread	(1, 17)
Ichthyophthirius multifiliis	Ichthyophthiriidae	Widespread	(1. 17, 37)
Paratrichodina incissa	Trichodinidae	Eurasia	(1, 17)
Trichodina domerguei	Trichodinidae	Eurasia	(17)
Trichodina esocis	Trichodinidae	Widespread	(1)
Trichodina mutabilis	Trichodinidae	Widespread	(1)
Trichodina nemachili	Trichodinidae	Eurasia	(1)
Trichodina nigra	Trichodinidae	Widespread	(1)
Trichodina pediculus	Trichodinidae	Widespread	(1)
Trichodina rectangli	Trichodinidae	Eurasia	(1, 18)
Trichodina reticulata	Trichodinidae	Widespread	(1)
Trichodina rostrata	Trichodinidae	Eurasia	(1)

Taxonomic groups/species	Family	Geographical distribution	Reference(s)
Trichodinella subtilis	Trichodinidae	Eurasia	(17)
Tripartiella copiosa	Trichodinidae	Widespread	(1, 5, 35)
Class: Phyllopharyngea			
Chilodonella hexasticha and *Chilodonella piscicola* (require molecular analysis for discrimination)	Chilodonellidae	Widespread	(1, 5)
Phylum: Euglenozoa	Molecular data does not support currently recognised families.		
Class: Kinetoplastea			
Cryptobia branchialis	Cryptobidae	Widespread	(1, 5)
Ichthyobodo necator species complex	Bodonidae	Widespread	(1)
Trypanosoma carassii	Trypanosomatidae	Widespread	(1)
Trypanosoma inexpectata	Trypanosomatidae	Specialist, Volga River basin	(1)
Trypanosoma schulmani	Trypanosomatidae	Eurasia	(1)
Phylum: Metamonada			
Class: Trepomonadea			
Spironucleus vortens	Hexamitidae	Widespread	(38)
Phylum: Oomycota			
Class: Peronosporea			
Saprolegnia sp.	Saprolegniaceae	Widespread	(5)
Fungi			
Phylum: Microsporidia			
Class: Microsporea			
Ichthyosporidium hertwigi	Ichthyosporidiidae	Widespread	(5)
Ichthyosporidium hoferi	Ichthyosporidiidae	Widespread	(5)
Animalia			
Phylum: Cnidaria			

Taxonomic groups/species	Family	Geographical distribution	Reference(s)
Class: Myxozoa			
Chloromyxum cristatum	Chloromyxidae	Eurasia	(1, 17, 18)
Chloromyxum fluviatile	Chloromyxidae	Eurasia	(1, 17, 37)
Chloromyxum legeri	Chloromyxidae	Eurasia	(17)
Henneguya cutanea	Myxobolidae	Eurasia	(1)
Henneguya zschokkei	Myxobolidae	Widespread	(18)
Myxidium macrocapsulare	Myxidiidae	Widespread	(1, 17)
Myxidium rhodei	Myxidiidae	Eurasia	(1, 17, 35)
Myxobilatus legeri	Myxobilatidae	Eurasia	(1, 17)
Myxobolus albovae	Myxobolidae	Eurasia	(1)
Myxobolus alvarezae	Myxobolidae	Eurasia	(4)
Myxobolus bramae	Myxobolidae	Eurasia	(1, 17)
Myxobolus carassii	Myxobolidae	Eurasia	(1, 17, 35)
Myxobolus cycloides	Myxobolidae	Eurasia	(1)
Myxobolus dispar	Myxobolidae	Eurasia	(1, 17, 37)
Myxobolus dogieli	Myxobolidae	Eurasia	(1)
Myxobolus donecae	Myxobolidae	Eurasia	(1, 17)
Myxobolus dujardini	Myxobolidae	Widespread	(1, 13, 17, 18)
Myxobolus elegans	Myxobolidae	Eurasia	(1, 11)
Myxobolus ellipsoides	Myxobolidae	Eurasia	(1)
Myxobolus exiguus	Myxobolidae	Eurasia	(1, 20)
Myxobolus gigas	Myxobolidae	Eurasia	(1, 17)
Myxobolus improvisus	Myxobolidae	Eurasia	(1)
Myxobolus intimus	Myxobolidae	Eurasia	(4)
Myxobolus kubanicus	Myxobolidae	Eurasia	(5)
Myxobolus kuleminae	Myxobolidae	Eurasia	(1)
Myxobolus macrocapsularis	Myxobolidae	Eurasia	(1, 17)
Myxobolus muelleri	Myxobolidae	Widespread	(1, 17, 20, 35, 37)

Taxonomic groups/species	Family	Geographical distribution	Reference(s)
Myxobolus muelleriformis	Myxobolidae	Eurasia	(1)
Myxobolus multiplicatus	Myxobolidae	Eurasia	(1, 17, 18)
Myxobolus musculi	Myxobolidae	Widespread	(1)
Myxobolus nemetzeki	Myxobolidae	Eurasia	(1, 17, 20)
Myxobolus obesus	Myxobolidae	Eurasia	(1, 17)
Myxobolus oviformis	Myxobolidae	Eurasia	(1)
Myxobolus permagnus	Myxobolidae	Eurasia	(1)
Myxobolus pseudodispar	Myxobolidae	Eurasia	(1)
Myxobolus strelkovi	Myxobolidae	Eurasia	(1)
Thelohanellus fuhrmanni	Myxobolidae	Eurasia	(1)
Thelohanellus oculileucisci	Myxobolidae	Eurasia	(1, 19, 37)
Thelohanellus pyriformis	Myxobolidae	Eurasia	(1, 17)
Zschokkella nova	Myxidiidae	Eurasia	(1, 17, 35, 37)
Zschokkella striata	Myxidiidae	Eurasia	(5)
Phylum: Platyhelminthes			
Class: Cestoda			
Caryophyllaeides fennica	Lytocestidae	Eurasia	(3, 6, 17, 20, 24, 28, 40)
Caryophyllaeus brachycollis	Caryophyllaeidae	Eurasia	(3, 6, 12, 28)
Caryophyllaeus laticeps	Caryophyllaeidae	Eurasia	(3, 6, 17, 24, 28, 37)
Ligula intestinalis	Diphyllobothriidae	Widespread	(3, 17)
Proteocephalus torulosus	Proteocephalidae	Widespread	(3, 14, 17, 18, 40)
Schistocephalus solidus	Diphyllobothriidae	Widespread	(13)
Schizocotyle acheilognathi	Bothriocephalidae	Widespread	(3)
Triaenophorus nodulosus (l)	Triaenophoridae	Widespread	(3, 6, 17, 18)
Class: Monogenea			
Dactylogyrus alatus	Dactylogyridae	Eurasia	(2, 7, 16, 26, 30)
Dactylogyrus crucifer	Dactylogyridae	Eurasia	(12, 24)
Dactylogyrus fallax	Dactylogyridae	Eurasia	(2, 20, 30)

Taxonomic groups/species	Family	Geographical distribution	Reference(s)
Dactylogyrus haplogonoides	Dactylogyridae	Eurasia	(6)
Dactylogyrus micracanthus	Dactylogyridae	Eurasia	(2, 7, 16, 30)
Dactylogyrus nasalis	Dactylogyridae	Eurasia	(2)
Dactylogyrus ramulosus	Dactylogyridae	Eurasia	(2, 6, 7, 17, 20, 26, 30)
Dactylogyrus robustus	Dactylogyridae	Eurasia	(2, 6, 7, 17, 30)
Dactylogyrus similis	Dactylogyridae	Eurasia	(2, 20, 24)
Dactylogyrus sphyrna	Dactylogyridae	Eurasia	(12, 24)
Dactylogyrus tuba	Dactylogyridae	Eurasia	(2, 6, 7, 12, 14, 16, 17, 20, 24, 30, 35, 37)
Dactylogyrus vistulae	Dactylogyridae	Eurasia	(26)
Dactylogyrus yinwenyingae	Dactylogyridae	Eurasia	(2, 20, 30)
Diplozoon paradoxum	Diplozoidae	Eurasia	(9, 17, 24)
Gyrodactylus carassii	Gyrodactylidae	Eurasia	(6, 10, 30)
Gyrodactylus decorus	Gyrodactylidae	Eurasia	(36)
Gyrodactylus laevis	Gyrodactylidae	Eurasia	(30)
Gyrodactylus leucisci	Gyrodactylidae	Eurasia	(31)
Gyrodactylus medius	Gyrodactylidae	Widespread	(17)
Gyrodactylus prostae	Gyrodactylidae	Eurasia	(2, 6, 7, 9, 12, 17, 18, 20, 24, 30, 35, 37)
Gyrodactylus scardiniensis	Gyrodactylidae	Eurasia	(7)
Gyrodactylus tulensis	Gyrodactylidae	Eurasia	(10, 30)
Gyrodactylus vimbi	Gyrodactylidae	Eurasia	(30, 31)
Paradiplozoon alburni	Diplozoidae	Eurasia	(2, 20, 30)
Paradiplozoon bliccae	Diplozoidae	Eurasia	(9, 35)
Paradiplozoon homoion	Diplozoidae	Eurasia	(2, 17, 30)
Paradiplozoon leucisci	Diplozoidae	Eurasia	(7)
Paradiplozoon megan	Diplozoidae	Eurasia	(2, 6, 7, 14, 17, 30, 35)
Class: Trematoda			
Allocreadium dogieli	Allocreadiidae	Eurasia	(3)
Allocreadium isoporum	Allocreadiidae	Eurasia	(17, 20, 25, 33, 34, 37, 40)

Taxonomic groups/species	Family	Geographical distribution	Reference(s)
Allocreadium transversale	Allocreadiidae	Eurasia	(3)
Apharyngostrigea cornu (m)	Strigeidae	Widespread	(3*)
Apophallus muehlingi (m)	Heterophyidae	Eurasia	(6, 14, 24)
Aspidogaster limacoides	Aspidogastridae	Widespread	(17, 40)
Asymphylodora imitans	Lissorchiidae	Eurasia	(3, 25)
Asymphylodora kubanica	Lissorchiidae	Eurasia	(25, 35)
Asymphylodora markewitschi	Lissorchiidae	Eurasia	(3, 13, 17, 22, 35, 40)
Asymphylodora parasquamosa	Lissorchiidae	Eurasia	(3, 25, 32)
Asymphylodora tincae	Lissorchiidae	Eurasia	(17, 25)
Bolbophorus confusus (m)	Diplostomidae	Eurasia	(3*)
Bucephalus polymorphus	Bucephalidae	Eurasia	(3*, 17, 22)
Bunocotyle cingulata	Hemiuridae	Eurasia	(17)
Bunodera luciopercae	Allocreadiidae	Widespread	(40)
Diplostomum chromatophorum (m)	Diplostomidae	Eurasia	(21)
Diplostomum commutatum (m)	Diplostomidae	Eurasia	(3*)
Diplostomum helveticum (m)	Diplostomidae	Eurasia	(3*)
Diplostomum mergi (m)	Diplostomidae	Widespread	(3*)
Diplostomum spathaceum (m) (Some records may be *Diplostomum pseudospathaceum* which is morphologically similar)	Diplostomidae	Widespread	(3, 17, 18, 20, 24)
Hysteromorpha triloba (m)	Diplostomidae	Widespread	(3, 17)
Ichthyocotylurus erraticus (m)	Strigeidae	Widespread	(3)
Ichthyocotylurus pileatus (m)	Strigeidae	Widespread	(3, 17, 21, 24)
Ichthyocotylurus platycephalus (m)	Strigeidae	Widespread	(3, 17, 20, 21, 33, 35)
Icthyocotylurus variegatus (m)	Strigeidae	Eurasia	(3, 37)
Mesostephanus appendiculatoides (m)	Cyathocotylidae	Widespread	(3*)
Metorchis bilis (m)	Opisthorchiidae	Eurasia	(3*)
Metorchis xanthosomus (m)	Opisthorchiidae	Eurasia	(3*)

Taxonomic groups/species	Family	Geographical distribution	Reference(s)
Metagonimus yokogawai (m)	Heterophyidae	Eurasia	(3, 17, 22, 24)
Nicolla skrjabini	Opecoelidae	Eurasia	(24,25)
Opisthorchis felineus (m)	Opisthorchiidae	Eurasia	(3, 17, 21)
Palaeorchis incognitus	Lissorchiidae	Eurasia	(3, 24)
Paracoenogonimus ovatus (m)	Cyathocotylidae	Eurasia	(3*, 14, 17, 20, 21, 24, 35)
Phyllodistomum folium	Gorgoderidae	Eurasia	(3, 17, 21, 22)
Phyllodistomum macrocotyle	Gorgoderidae	Eurasia	(17)
Plagioporus angusticolle	Opecoelidae	Eurasia	(20)
Posthodiplostomum cuticola (m)	Diplostomidae	Widespread	(3, 17, 20, 22, 24, 35)
Pseudamphistomum truncatum (m)	Opisthorchidae	Eurasia	(3*)
Rhipidocotyle campanula (m)	Bucephalidae	Eurasia	(3, 6, 21, 22, 24, 37)
Rhipidocotyle fennica (m)	Bucephalidae	Eurasia	(37)
Sanguinicola armatus	Aporocotylidae	Eurasia (one record in USA)	(22)
Sanguinicola volgensis	Aporocotylidae	Eurasia	(3, 14, 17, 35)
Sphaerostoma bramae	Opecoelidae	Eurasia	(3, 17, 18, 20, 27)
Sphaerostoma globiporum	Opecoelidae	Eurasia	(3*, 21, 22, 24, 40)
Sphaerostoma minus	Opecoelidae	Rare specialist, Curonian Lagoon	(3)
Tylodelphys clavata (m)	Diplostomidae	Widespread	(3*, 14, 18, 20, 22, 24, 33, 35)
Phylum: Nematoda			
Class: Chromadorea			
Anguillicoloides crassus (l)	Anguillicolidae	Adult is eel specialist, widespread	(39)
Anisakis simplex (l)	Anisakidae	Widespread	(35)
Camallanus lacustris	Camallanidae	Widespread	(3, 40)
Camallanus truncatus	Camallanidae	Widespread	(40)
Cucullanus dogieli	Cucullanidae	Eurasia	(3, 23)
Cucullanus heterochrous	Cucullanidae	Eurasia	(20)
Desmidocercella numidica (l)	Desmidocercidae	Widespread	(3*)
Gnathostoma hispidum (l)	Gnathostomatidae	Eurasia	(3*)

Taxonomic groups/species	Family	Geographical distribution	Reference(s)
Hysterothylacium aduncum (l)	Raphidascarididae	Widespread	(27)
Molnaria intestinalis	Skrjabillanidae	Eurasia	(23)
Philometra ovata	Philometridae	Eurasia	(3, 17)
Philometra rischta	Philometridae	Eurasia	(6, 17, 24, 35)
Pseudoterranova decipiens (l)	Anisakidae	Widespread	(27)
Raphidascaris acus (l)	Raphidascarididae	Widespread	(8, 17, 20, 23, 37, 40)
Rhabdochona denudata	Rhabdochonidae	Eurasia	(3, 8, 17)
Spiroxys contorta (l)	Gnathostomatidae	Widespread	(23, 24)
Streptocara crassicauda	Acuariidae	Widespread	(35)
Class: Enoplea			
Dioctophyme renale (l)	Dioctophymidae	Widespread	(23)
Eustrongylides excisus (l)	Dioctophymidae	Eurasia	(23)
Pseudocapillaria tomentosa	Capillariidae	Widespread	(20, 23, 40)
Schulmanela petruschewskii	Capillariidae	Eurasia	(23)
Phylum: Acanthocephala			
Class: Palaecanthocephala			
Acanthocephalus anguillae	Echinorhynchidae	Eurasia	(8, 12, 14, 17, 18, 20, 35, 37, 40)
Acanthocephalus clavula	Echinorhynchidae	Eurasia	(17, 18)
Acanthocephalus gracilacanthus	Echinorhynchidae	Eurasia	(29, 33)
Acanthocephalus lucii	Echinorhynchidae	Eurasia	(6, 8, 35)
Corynosoma semerme (l)	Polymorphidae	Widespread	(20)
Echinorhynchus salmonis	Echinorhynchidae	Widespread	(18)
Neoechinorhynchus rutili	Neoechinorhynchidae	Widespread	(3, 6, 8, 17, 18, 35)
Pomphorhynchus laevis (Some records may be *Pomphorhynchus tereticollis* which is morphologically similar)	Pomphorhynchidae	Eurasia	(3, 6, 12, 17, 20)
Phylum: Annelida			
Class: Clitellata			

Taxonomic groups/species	Family	Geographical distribution	Reference(s)
Hemiclepsis marginata	Glossophoniidae	Eurasia	(3, 17, 35)
Piscicola geometra	Piscicolidae	Widespread	(3, 17, 18, 24, 35)
Phylum: Mollusca			
Class: Bivalvia			
Glochidia larvae	Margaritiferidae Unionidae	Widespread	(14, 17, 24, 35, 37)
Phylum: Arthropoda (Crustacea)			
Class: Hexanauplia			
Caligus lacustris	Caligidae	Eurasia	(5)
Ergasilus briani	Ergasilidae	Eurasia	(3, 5, 17, 20)
Ergasilus sieboldi	Ergasilidae	Eurasia	(5, 14, 17, 20, 24, 33, 35, 37)
Lamproglena pulchella	Lernaeidae	Eurasia	(3, 5, 17, 20, 24)
Lernaea cyprinacea	Lernaeidae	Widespread	(5)
Tracheliastes polycolpus	Lernaeopodidae	Palaearctic	(5, 14, 17, 18, 20, 24, 35, 37)
Class: Ichthyostraca			
Argulus coregoni	Argulidae	Widespread	(5, 24)
Argulus foliaceus	Argulidae	Eurasia	(3, 5, 17, 24, 35, 37)

[1]Bauer (1984); [2]Bauer (1985); [3]Bauer (1987); [4]Cech et al. (2012); [5]de Charleroy et al. (1993); [6]Djikanovic et al. (2012); [7]Dorovskikh (1997); [8]Dorovskikh (1999); [9]Dzika (2008); [10]Ergens (1988); [11]Eszterbauer (2002); [12]Gelnar et al. (1994); [13]Grabda (1971); [14]Grabda-Kazubska and Pilecka-Rapacz (1987); [15]Grabda-Kazubska and Okulewicz (2005); [16]Hao et al. (2014); [17]Izyumova (1987); [18]Järvalt et al. (2003); [19]Jeżewski and Kamara (1999); [20]Kirjušina and Vismanis (2007); [21]Liberman (2020); [22]Molnar (1969); [23]Moravec (1994); [24]Moravec (2001); [25]Niewiadomska (2003); [26]Ondračkova et al. (2004); [27]Palm et al. (1999); [28]Pojmańska (1991); [29]Popiołek (2016); [30]Pugachev et al. (2009); [31]Rautskis (1988); [32]Rokicki (2004); [33]Rolbiecki (2003); [34]Rusinek (2007); [35]Sobecka et al. (2004); [36]Sterud (1999); [37]Sterud and Appleby (1997); [38]Sterud and Poynton (2002); [39]Thomas and Ollevier (1992); [40]Zhokhov (2003).