Contemporary perspectives on the ecological impacts of invasive freshwater fishes

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Abstract

Introductions of non-native freshwater fish continue to increase globally, although only a small proportion of these introductions will result in an invasion. These invasive populations can cause ecological impacts in the receiving ecosystem through processes including increased competition and predation pressure, genetic introgression and the transmission of non-native pathogens. Definitions of ecological impact emphasise that shifts in the strength of these processes are insufficient for characterising impact alone and, instead, must be associated with a quantifiable decline of biological and/or genetic diversity and lead to a measurable loss of diversity or change in ecosystem functioning. Assessments of ecological impact should thus consider the multiple processes and effects that potentially occur from invasive fish populations where, for example, impacts of invasive common carp *Cyprinus carpio* populations are through a combination of bottom-up and top-down processes that, in entirety, cause shifts in lake stable states and decreased species richness and/or abundances in the biotic communities. Such far-reaching ecological impacts also align to contemporary definitions of ecosystem collapse, given they involve substantial and persistent declines in biodiversity and ecosystem functions that cannot be recovered unaided. Thus, while not all introduced freshwater fishes will become invasive, those species that do develop invasive populations can cause substantial ecological impacts, where some of the impacts on biodiversity and ecosystem functioning might be sufficiently harmful to be considered as contributing to ecosystem collapse.

Key words: Biological invasion, ecosystem functioning, alien fish, non-native fish, *Cyprinus carpio*.

1. Introduction

In recent decades, human activities have resulted in substantial declines in biodiversity, especially in freshwater fishes (Tickner *et al*., 2020). The causal factors in freshwater fish diversity decline include flow alteration, pollution, habitat degradation, overexploitation and invasive species (Dudgeon *et al*., 2006; Tickner *et al*., 2020). Non-native fishes continue to be introduced around the world (Perrin et al., 2021) and freshwaters are recognised as highly susceptible to the invasion of introduced species (Moorhouse & MacDonald 2015). However, only a relatively small proportion of these introduced fishes will develop invasive populations (e.g., the 'tens' rule; Williamson & Fitter, 1996), with ecosystems that are already disturbed being particularly vulnerable to invasion (Johnson *et al*., 2008). As these invasive populations have the potential to cause substantial ecological impacts in the receiving ecosystem (Cucherousset & Olden, 2011), it is important to understand the processes that determine the strength of these impacts (Gallardo *et al*., 2016).

Multiple factors determine whether an introduced freshwater fish will establish a sustainable population that then disperses and causes ecological impact (i.e. becomes invasive). Establishment probability varies according to the traits of the introduced species (e.g. life-history traits, thermal preferences), and the characteristics of the introduction event(s) (e.g. number of individuals introduced) and the receiving environment (e.g. abiotic/ biotic characteristics) (Ruesink, 2005; Garcia-Berthou, 2007). Should an invasive population develop then these intrinsic and extrinsic factors can also affect the population abundance of the invader, where abundance is then another important influence on the strength of ecological impact (Yokomizo *et al*., 2009; Jackson *et al*., 2015).

Invasive freshwater fishes can impact native communities and habitats through a variety of processes, including increased predation pressure and competitive interactions, genetic introgression with taxonomically similar species, and disease transmission (Gozlan *et al*., 2010a; Cucherousset & Olden, 2011). The foraging behaviours of invasive fish can also alter the structure of their physical environment, such as macrophyte extirpation (Weber & Brown, 2009). While an invasive fish population might only cause impacts from one of these processes, some invaders will cause a range of impacts caused by multiple processes (Vilizzi *et al*., 2015). Thus, it is important to not just understand how these processes act in isolation but also how they can act additively and/ or synergistically in an invading freshwater fish population (Britton *et al*., 2015; Jackson *et al*., 2015). When assessing impact severity, however, it is also important to define what constitutes the ecological impact of invasive fish so that appropriate assessments are made. Where impacts are particularly severe and unable to be resolved without management interventions then there is potential that they have contributed to ecosystem collapse (Newton *et al*., 2021).

The aim of this review is to thus provide a contemporary perspective on the ecological impacts of invasive freshwater fish by synthesising the factors influencing their initial establishment and invasion, before discussing the processes by which ecological impacts can develop and the factors that determine impact strength. Examples of how populations of invasive fish can cause multiple ecological impacts in invaded freshwaters are then provided to highlight how definitions of both ecological impact and ecosystem collapse are important for informing impact assessment and risk management.

2. Establishment and invasion probabilities

The probability of an introduced species establishing a sustainable population that then disperses and impacts native species will vary according to the characteristics of the introduced species and the introduction itself, and the receiving environment (Fig. 1).

2.1 The introduced species

For a species to develop an invasive population requires their survival of being introduced, and an ability to adapt to the new conditions and then establish a sustainable population (Kolar & Lodge, 2002). A species moved between biogeographic regions of similar climate characteristics and that is then introduced into an environment of comparable abiotic properties has a higher probability of establishing and invading than the converse scenario (Bomford *et al*., 2010; Howeth *et al*., 2016). Indeed, introduced species that can express their traits in the new range in a similar manner to their native range have been suggested as generally having higher invasion probabilities through complying with the adaptation hypothesis (Ricciardi & Mottiar, 2006). It should be noted, however, that there is a contrasting hypothesis to this: that for an introduced species to establish in a new range, it should modify it traits in order to gain advantage over a different set of competitors and/or predators (Ludsin *et al*., 2001).

By focusing on the intrinsic characteristics of the invader, the adaptation hypothesis thus predicts that a non-native species pre-adapted to the conditions of the new ecosystem will have a relatively high establishment and invasion probability through its specialisations and competitive abilities that do not require modification in the new range (Catford *et al*., 2009). For example, non-indigenous European barbel *Barbus barbus* (L.) expressed the same traits (e.g. prolonged reproductive period) and behaviours (high individual variability in home ranges) in the River Severn basin, Western England, as populations in their indigenous range (Gutmann Roberts *et al*., 2018), which enabled their relatively rapid establishment and dispersal (Antognazza *et al*., 2016).

Introduced fishes are also often released into new environments without their usual parasite fauna due to factors including only a sub-set of the population being moved that lacks the parasite richness of the donor population and with some of the parasites that are transported having complex lifecycles for which the intermediate hosts are missing in the new range (Colautti *et al*., 2004; Heger & Jeschke, 2014). This 'enemy release' of an introduced species from its natural parasites (and/or natural predators) thus provides greater energy allocation for somatic growth and reproduction (Sheath *et al*., 2015). However, this might be counter-acted by 'parasite acquisition', where native parasites infect the introduced species (Sheath *et al*., 2015). Plasticity in how behavioural, physiological and/ or life-history traits are expressed is also important following establishment, as individuals that are dispersing at invasion front are predicted to have a suite of traits more suited to population expansion (e.g. boldness, high activity and exploratory behaviours, high resource acquisition) than those in the core range (Brownscombe *et al*., 2012; Tarkan *et al*., 2021).

2.2 Introduction characteristics

Colonisation pressure refers to the number of species introduced or released into a single location, with a generally positive relationship between the number of introductions and the number of established species in that location (Catford *et al*., 2009). It can thus serve as a null model for predicting the number of invasive species in specific regions and for understanding temporal or spatial differences in non-native species richness (Catford *et al*., 2009). An important component of colonisation pressure is propagule pressure, which generally refers to the number of individuals of a species introduced into a specific location (propagule size) and their frequency of introduction (propagule number) (Britton & Gozlan, 2013). Propagule pressure is important for both determining establishment probability and positively influencing subsequent invader abundances (Lockwood *et al*., 2005; Simberloff, 2009; Britton & Gozlan, 2013). Although the shape of the establishment curve (the probability of invasion as a function of the number of founders) is likely to vary according to factors including the carrying capacity of the receiving habitat (Drake & Lodge, 2006), empirical evidence suggests a non-linear relationship, with thresholds of propagule size above which establishment and relatively abundant invasive populations are highly probable to develop (Britton & Gozlan, 2013). Where populations do establish from a small number of founders, low genetic diversity (at least compared with the native range) is likely to result (e.g. Hardouin *et al*., 2018), potentially leading to genetic bottlenecks and low adaptive capacity (Hanfling, 2007).

2.3 Receiving environment

The species richness and species-specific abundances of the receiving environment is an important determinant for establishment probability and invader impact, with the biotic resistance hypothesis predicting communities with higher richness will resist establishment, invasion and impact (Britton *et al*., 2012). Establishment and invasion of a non-native fish can thus be impeded by strong competitive pressure from trophically analogous native species, strong predation pressure from species at higher trophic positions, and/ or from native pathogens that host-switch to infect the introduced propagules - although predation tends to be the strongest resistor to invasion in freshwaters (Alofs & Jackson, 2014). Biotic resistance through predation was measured from both common carp *Cyprinus carpio* L. (hereafter 'carp') and perch *Perca fluviatilis* (L.) on topmouth gudgeon *Pseudorasbora parva* (Temminck & Schlegel 1846) establishment (Britton, 2011) and population abundance (Davies & Britton, 2015a). Biotic resistance from carp was only overcome when angler trophic subsidies were available (Britton *et al*., 2015). Lake ecosystems with food webs of greater biodiversity have also been measured as providing higher resistance and resilience to alien largemouth bass *Micropterus salmoides* (Lacepède, 1802) (Calizza *et al*., 2021). For non-native fish introduced into England and Wales, infections by native parasites are common, although the extent to which these native parasites inhibit the ability of the non-native fishes to establish and invade is unclear (Sheath *et al*., 2015).

Biotic resistance to invasion and impact can, however, be relatively weak in freshwaters that have been disturbed through other anthropogenic activities, where the Disturbance hypothesis predicts that where anthropogenic activities have increased resource availability and modified the physical structure of the ecosystem then introduced species have an equal chance of succeeding in the new environment as native species (Catford *et al*., 2009). Riverine disturbances, such as impoundment, generally leads to shifts towards lentic species and functional guilds from specialist to generalist species (Noble *et al.,* 2007), which often favour non-native over native species (Johnson *et al*., 2008). In Australia, impoundments tend to favour carp invasion over the persistence of native fishes such as Murray cod *Maccullochella peelii* (Mitchell 1838) (Britton *et al*., 2011a). The creation of multiple reservoirs by hydroelectric dams in Southern Brazil has provided opportunities to create sport fisheries based on non-native species such as peacock basses (*Cichla* spp.) (Espínola *et al*., 2010), where high predation rates from their invasive populations further decrease native fish species richness and abundance (Pelicice & Agostinho, 2009; Britton & Orsi, 2012; Tarkan et al., 2012). The likelihood of finding non-indigenous species in impounded rivers is up to 300 times higher than in natural lakes, with reservoirs frequently supporting multiple invaders (Johnson *et al.,* 2008). A further anthropogenic disturbance is the presence of other non-native species, where the Invasion meltdown hypothesis predicts that the presence of one or more established invasive species can cause an 'invasion domino effect' through making the habitat or community more amenable for other introduced species (Simberloff & Von Holle, 1999; Catford *et al*., 2009). For example, the transformation of Lake Naivasha, Kenya, from an oligotrophic, macrophyte dominated system to a eutrophic, algal dominated system by the invasion of Louisiana Red Swamp crayfish *Procambarus clarkii* (Girard, 1852) in the 1970s (Smart *et al*., 2002; Jackson *et al*., 2012) meant that when carp were accidentally introduced in 1999, the lake conditions were already highly suitable for their establishment (Hickley *et al*., 2004a,b). The rapid establishment of an abundant carp population meant that within seven years of their introduction, they were main species being exploited in the artisanal fishery by 2006 (Britton *et al*., 2007).

3. Ecological processes

Ecological impacts from invasive freshwater fishes can include decreased native species richness and abundance, altered habitat structure, and decreased genetic integrity of native fishes (Gozlan *et al*., 2010a). These impacts manifest from a range of processes that develop according to the interactions of the invader with the native communities, including their competitive, predation, reproductive and foraging interactions, as well as their host-parasite relationships (Fig. 1).

3.1 *Competition*

Where the invasive and native species share prey resources, and where these resources are limiting, then strong inter-specific competitive interactions can develop (Gozlan *et al*., 2010a). Where these competitive interactions are particularly intense and the invader is a strong competitor then the native fishes can be competitively excluded from their original niche (Bøhn *et al*., 2008; Tran *et al*., 2015). Competitive pressure from invasive fishes can also directly impact non-fish taxa, with the reciprocal nature of freshwater and riparian food-webs meaning that dietary overlaps can occur between invasive fishes and native spiders and birds (Epanchin *et al*., 2010; Jackson *et al*., 2016), potentially leading to strong cascading effects (e.g. Eby *et al*., 2006).

Although competition can be considered an important process that contributes to the strength of ecological impact, studies based on the ecological application of stable isotope analysis tend to suggest that rather than sharing resources and potentially competing, even functionally analogous native and non-native species often show strong patterns of trophic niche (as the isotopic niche) divergence (Jackson *et al*., 2015). Where the non-native and native species diverge in their trophic niches then this has been posited as facilitating their co-existence, with the non-native fish integrating into the native food web through their consumption of largely unexploited prey resources (e.g. Tran *et al*., 2015; Britton *et al*., 2019).

3.2 *Predation*

Predation is a mechanism that frequently drives changes in native communities, especially in relation to the composition and functional diversity of the native communities (Sharpe *et al*., 2017). Severe predation impacts from non-native freshwater fishes on native communities tend to be through piscivory with, for example, largemouth bass in Zimbabwe reducing the abundance of stream-dwelling *Barbus* fishes by 99 % (Gratwicke & Marshall, 2001). Predation by Nile perch *Lates niloticus* L. in Lake Victoria, East Africa, was a principal driver of severe reductions in the species richness of endemic fishes (Cucherousset & Olden, 2011).

Predation by non-native fishes can also deplete invertebrate prey populations, with the relative strength of these impacts having been explored in the last decade through comparative functional response experiments (Dickey *et al*., 2020). These experiments explore the relationships of prey resource use and its availability between the invader and tropically analogous native species (Dick *et al*., 2014). Metrics, including prey attack rate and handling time (Dick *et al*., 2014, 2017a,b), enable impacts at the population level to be predicted through incorporation of invader population abundances (Dickey *et al*., 2020). Thus, a highly abundant species with a low maximum consumption rate could be predicted as causing high impacts on prey populations (Laverty *et al*., 2017). While these experiments provide a rapid impact assessment tool (e.g. Alexander *et al*., 2014; Penk *et al*., 2017), they can lack ecological complexity, with both non-native and native fishes likely to switch to alternative prey resources when their extant prey become depleted in the wild (Dominguez-Almela *et al*., 2021).

3.3 *Genetic introgression*

The release of non-native species into a community where taxonomically similar species are present can result in genetic introgression (Harrison & Larson, 2014; Blackwell *et al*., 2020). This is strongly evident in the *Carassius* genus, where hybrid forms of naturalised crucian carp *Carassius carassius* (L.) and non-native goldfish *Carassius auratus* (L.) develop; as these hybrids are reproductively viable then they lead to further introgression with both pure strains and other hybrids (Hänfling *et al*., 2005). Introgression between crucian carp and gibel carp *Carassius gibelio* (Bloch, 1782) can also occur (Papoušek *et al*., 2008). The movement of genetically distinct native fish populations between discrete river basins for fishery enhancement purposes can also result in intra-specific genetic effects, where European barbel reared in hatcheries using broodstock from a specific river basin and released into other basins have resulted in a loss of basin-specific genetic integrity (Antognazza *et al*., 2016).

3.4 *Foraging behaviours affecting habitat structure*

The negative consequences of the foraging behaviours of invasive fish for habitat structure arise when the invader acts as an ecological engineer (Cucherousset & Olden, 2011). Non-native fishes, such as carp and goldfish, are recognized as having the potential to alter their invaded habitats through transforming the structure of the aquatic vegetation, primarily though the loss of submerged macrophytes, mainly through these being uprooted during benthic foraging (Weber & Brown, 2009; Vilizzi *et al*., 2015; Section 5.1). Invasive salmonid fishes can also act as strong ecological engineers that transform their physical environment (Moore, 2006), where the redd construction in spawning gravels by invasive Chinook salmon

Oncorhynchus tshawytscha (Walbaum 1792) in New Zealand, ultimately modified the geomorphology of the river by disrupting its pool-riffle sequences, where the disruptions developed from the cumulative effects of decreases in fine sediments, detritus, mosses, algae, and macrophytes (Field-Dodgson, 1987).

3.5 *Host-parasite relationships*

Although the enemy release hypothesis suggests non-native fishes often bring few of their native parasites from their natural range, those parasites that are co-introduced can then host-switch to native species (Britton, 2013; Spikmans *et al.,* 2020). For example, the Asian tapeworm *Schyzocotyle acheilognathi* has achieved a global distribution, mainly due to cyprinid fishes being moved around the world for aquaculture (Britton *et al*., 2011b). This tapeworm has been recorded in over 200 fish species (across 10 orders and 19 families) (Scholz *et al*., 2012; de León *et al*., 2018). Host impacts include damage to the intestinal tract, loss of condition and reduced growth rates, and impacts on foraging behaviours and mortality (Britton *et al.,* 2011b; Pegg *et al*., 2015).

Where native fishes have low immune-suppression responses to infection by a novel parasite (e.g. due to lacking co-evolution) then the consequences of infection can sometimes be severe. The nematode parasite *Anguillicola crassus* infected the European eel *Anguilla anguilla* (L.) following its introduction into Europe through movements of the Japanese eel *Anguilla japonica* (Temminck & Schlegel 1846). in the aquaculture industry. In European eel, infections are concentrated in the swim-bladder, where heavy and repeated infections can cause considerable pathology, potentially impacting the ability of adult eels to migrate back to their spawning grounds in the South Atlantic (Kirk, 2003; Currie *et al*., 2020). Non-native fishes can also act as parasites, such as invasive sea lamprey *Petromyzon marinus* (L.) in the North

American Great Lakes, where its direct parasitism of native fish species was implicated in declining catches and values of their associated fisheries (Guo *et al*., 2017).

4. Factors affecting the strength of ecological impact of invasive freshwater fishes

The ecological impacts from an invasive freshwater fish population are unlikely to be static over time and space, with multiple abiotic and biotic factors influencing the extent of their ecological impacts. Although factors such as propagule pressure, native species richness and the extent of anthropogenic influences how ecological impacts can develop (Section 2), invader abundance, time since introduction, their status (as native or non-native invaders) and context-dependency can then influence the actual strength of their impact (Fig. 1).

4.1 *Invader population abundance*

Population abundance can strongly influence the ecological impacts of invasive fishes, with the relationship between abundance and impact often assumed to be positive and proportional (Yokomizo *et al*., 2009, Elgersma & Ehrenfeld, 2011). However, empirical evidence supporting this assumption is weak due to most abundance-impact studies only testing invader absence versus high invader density (e.g. Britton *et al*., 2010a). Yet the population abundances of an invasive fish can vary considerably across their range due to being affected by a wide range of abiotic and biotic characteristics (e.g. Kurtul *et al*., 2022). Testing of invader abundance versus ecological impact often indicates these relationships are non-linear (Elgersma & Ehrenfeld, 2011; Kornis *et al*., 2014), with Yokomizo *et al*. (2009) suggesting four relationships potentially exist: linear, S-shaped, low-threshold and high-threshold. In topmouth gudgeon, both linear and non-linear density-impact relationships were recorded, where the relationship with zooplankton body mass was low-threshold, but was high-threshold for zooplankton biomass and abundance (Jackson *et al*., 2015). Non-linear relationships between invader abundance and impact have also been detected in carp (Vilizzi *et al*., 2015), where despite high consistency in the detection of ecological impacts from their invasive populations (Weber & Brown, 2009), the strength of these impacts have a strong relationship with carp biomass, with tipping points often evident (Vilizzi *et al*., 2015; Section 5).

4.2 ***Time since introduction***

Temporal variation in ecological impact can occur through invader population abundances often varying with time since the introduction (Vilizzi *et al*., 2015). The relationship between time since introduction and ecological impact for New Zealand mud snail *Potamopyrgus antipodarum* in Europe revealed that over 41 years, changes in their spatial distribution and population abundances closely mapped on to their ecological impacts on native species (Haubrock *et al*., 2022). The ecological impacts of invasive fishes have similarly been demonstrated as not being static temporally. For example, the impacts of the globally invasive brown trout *Salmo trutta* (L.) over 170 years was highest immediately after their introduction and decreased thereafter, with impacts being non-significant after 100 years (Závorka *et al*., 2018). As these impact declines were considered to be due to local adaptation and/ or extinction of native species then it was argued, however, that these results should not be considered as accepting that the long-term effects of invasive fishes will be weak (Závorka *et al*., 2018). In addition, some introductions can result in populations that remain at low abundance for prolonged periods and that have low ecological impacts, but with an environmental trigger then resulting in the sudden development of a highly abundant and disruptive population (Spear et al., 2021).

4.3 ***Native versus non-native invaders***

Ecological impacts can also develop where the introduction involves native species being released into a native population of wild conspecifics that results in modified patterns of intraspecific diversity, such as where hatchery reared fishes are used to enhance wild populations for angling (Antognazza *et al*., 2016; Cucherousset *et al*., 2016). Comparisons of invasion-induced impacts from intra- versus inter-specific diversity from salmonid fishes indicated that the global impacts of 'native introductions' exceeded those from non-native invaders, where the impacts were mainly detected at the individual level (Buoro *et al*., 2016). The reasons for this potentially relate to the Adaptation hypothesis (Section 2), where the 'native invaders' have enhanced local abundances as they are pre-adapted to establishing and invading in their new environment, with their high ecological similarity with native conspecifics then resulting in their greater ecological impact (Buoro *et al*., 2016).

4.4 *Context dependencies*

Context dependent ecological impacts arise when the strength of the impact of an invasive fish species differs with changes in the biotic, abiotic, spatio-temporal and/ or observational circumstances (Catford *et al*., 2022). Context dependency can be mechanistic (the impact differs under different ecological and spatiotemporal conditions) or apparent (the impact appears to vary under different conditions but are instead driven by confounding factors, methodological issues and/ or statistical inference) (Catford *et al*., 2022). Mechanistic context dependency was apparent in experimental studies that paired bluegill *Lepomis macrochirus* (Rafinesque 1819) with carp and mosquitofish *Gambusia affinis* Baird & Girard 1853), with bluegill only having significant effects on prey abundances when the other fishes were absent, with non-significant effects in their presence (Nowlin & Drenner, 2000). While carp generally has highly deleterious impacts on aquatic macrophytes at global levels through their benthic foraging (Weber & Brown, 2009; Section 5), in the initial years following their introduction into Lake Naivasha, Kenya, previously suppressed native macrophytes increased in coverage due to the predation by carp on an invasive crayfish population that had been the key driver of macrophyte depletion (Britton *et al*., 2007). Apparent context dependencies could occur in field based studies assessing life history traits of invasive fish over latitudinal gradients that fail to account for confounding issues of factors such as population abundances that can influence density-dependent processes (Davies & Britton, 2015b).

5. Ecological impacts from populations of invasive freshwater fishes

The ability of an introduced fish to establish and invade, the processes by which an invader can cause impact, and the factors influence impact strength are all important considerations in ecological impact. When an invasive fish population develops, however, multiple processes and impacts can manifest that must now be considered at population, community and ecosystem levels (Fig. 2). The consideration of these impacts at these higher levels of biological organisation is important for two main reasons. Firstly, the management of invasive fishes is usually focused at populations of specific species, where the aim is usually to reduce the strength of the population impacts by reducing (or eliminating) their abundance (Britton *et al*., 2011; Rytwinski *et al*., 2019). The commensurate management responses are usually based on risk assessment processes (Britton *et al*., 2011; Vilizzi *et al*., 2019, 2021), where the compilation of population level case studies is of high value to managers and policy-makers (e.g. Copp *et al*., 2009; Cucherousset *et al*., 2018; Rohtla *et al*., 2021). Secondly, invasive populations of specific freshwater fishes often impact several components of the native ecosystem, with the impacts of juvenile stages often differing from those of adults (e.g. through differences in body sizes and ontogenetic dietary shifts) (Gozlan *et al*., 2010a,b). Correspondingly, species-specific case studies provide different perspectives on the ecological impacts of invasive fishes by revealing how population level impacts can involve multiple processes and impact types.

5.1 *Common carp*

Analysis on the global application of the risk assessment tool Freshwater Fish Invasiveness Screening Kit (FISK) revealed carp was the most widely screened species, where it was assessed as having a high risk of invasiveness in all regions (Vilizzi *et al*., 2019). Carp is also one of only eight fishes list on the list of '100 of the World's Worst Invasive Species' (Lowe *et al*., 2000), being invasive in countries and regions as diverse as Australia (Koehn, 2004), North America (Weber *et al*., 2011), East Africa (Britton *et al*., 2007; Oyugi *et al*., 2011) and India (Singh *et al*., 2010). Carp ecological impacts in lakes develop from their simultaneous alteration of bottom-up and top-down processes that result in 'middle-out' effects (Weber & Brown, 2009). Carp benthic foraging activities results in the resuspension of sediments that increase turbidity, nutrient levels and phytoplankton production, and reduces benthic invertebrate abundance, diversity, and richness (also affected by direct predation) (Vilizzi *et al*., 2015; Vilizzi & Tarkan, 2015). This foraging also uproots aquatic macrophytes that also increases turbidity, nutrients and phytoplankton, which then negatively impacts macrophyte regeneration via shading and smothering (Vilizzi *et al*., 2015). These direct and indirect effects can act in concert to shift lake stable states from oligotrophic to eutrophic, which negatively impacts the abundance and richness of native fishes (mainly of piscivores and sight predators), and severely compromises amenity values (e.g., sport fishing) (Vilizzi *et al*., 2015).

The meta-analysis of carp experimental studies by Vilizzi *et al*. (2015) revealed that in up to 87 % of assessed studies, carp increased turbidity, nitrogen, phosphorus and phytoplankton, with up to 90 % of studies detecting decreases in aquatic macrophytes, benthic invertebrates, amphibians, waterfowl and fish. The strongest evidence was for impacts on nutrients and aquatic macrophytes, with impact also a function of carp biomass. Vilizzi *et al*. (2015) suggested the critical biomass value (± SE) for impact was 476 ± 38 kg ha^{-1}, reducing to 198 ± 40 kg ha^{-1} when only critical biomass values from experiments on 'free-ranging' carp were assessed. However, carp impacts on lake ecosystems can be apparent at lower biomass, with Zambrano & Hinojosa (1999) suggesting that significantly increased turbidity can occur at 50 to 75 kg ha^{-1}. The relationship of carp biomass-impact is also non-linear, often involving sudden shifts from clear- to turbid-water state in shallow water bodies at carp densities between 174 and 300 kg ha^{-1} (e.g. Williams *et al*., 2002; Parkos *et al*., 2003; Matsuzaki *et al*., 2009). Bajer *et al*. (2009) suggested a threshold biomass of 100 kg ha^{-1} can cause dramatic declines in vegetation cover and waterfowl abundance.

5.2 *Topmouth gudgeon*

The introduction of cyprinid topmouth gudgeon from its native range in Southeast Asia into Europe first occurred in the 1960s and the species has since spread to at least 32 countries, with its invasion success related to its traits of fast growth, early maturity and reproductive behaviours (Gozlan *et al*., 2010b). A small-bodied species (generally <100 mm), its ecological impacts relate to their trophic interactions with native fishes and transmission of a novel pathogen to native fishes.

The small body size, functional similarity with native cyprinid fishes, and propensity for forming highly abundant populations have raised concern over the potential of topmouth gudgeon to out-compete native species (Tran *et al*., 2015). This was emphasised by experimental work by Laverty *et al*. (2017) where, despite native bitterling *Rhodeus amarus* (Bloch 1782) having higher consumption rates than invasive topmouth gudgeon, the invader was predicted as having higher deleterious effects on prey communities due to its considerably higher population abundances. Some studies based on stomach contents analyses have suggested high dietary similarity between invasive topmouth gudgeon and native fishes (e.g. Declerck *et al*., 2002), with chironomid larvae a common prey item (Wolfram-Wais *et al*., 1999). However, in the Dniprodzerzhynsk Reservoir, Ukraine, dietary overlap was low between topmouth gudgeon and co-occurring cyprinids that included roach *Rutilus rutilus* (L.) and rudd *Scardinius erythrophthalmus* (L.) (Didenko & Kruzhylina 2015). When assessed using stable isotope analysis (as bulk $\delta^{13}C$ and $\delta^{15}N$), the trophic niches of topmouth gudgeon and functionally analogous native fishes overlapped when the invader was in very high abundance, leading to decreased growth rates in the native species (Britton *et al*., 2010a), but were highly divergent at lower population abundances (Jackson & Britton, 2014; Tran *et al*., 2015).

Invasive topmouth gudgeon can also co-introduce the pathogen Rosette Agent *Sphaerothecum destruens* into the native fish community, where the invader is the healthy, reservoir host but where naïve fishes are highly susceptible to infection that can result in high mortality rates (Gozlan *et al*., 2005; Andreou *et al*., 2011). Moreover, following transmission to native species, the pathogen can persist in the fish community even if the reservoir topmouth gudgeon host has been removed through eradication (Al-Shorbaji *et al*., 2016). Given that this disease transmission is largely independent of topmouth gudgeon density (at least in contrast to the consequences of trophic interactions) then the long-term consequences of this topmouth gudgeon impact are potentially more severe than those relating to trophic interactions, with Spikmans *et al*. (2020) associating the presence of both the fish and parasite with decreased native fish diversity and abundance in the Netherlands.

5.3 *European barbel*

When compared with carp and topmouth gudgeon, the invasive range of European barbel is spatially limited, being constrained to western England (where it has been introduced from eastern England; Wheeler & Jordan, 1990) and some river basins in Southern Europe (Carosi *et al*., 2017). In Italy, their riverine introduction has resulted in invasive populations being in sympatry with a number of native *Barbus* species, including endemic *Barbus plebejus* (Bonaparte, 1839) and *Barbus tyberinus* (Bonaparte, 1839). In the Tiber River basin, invasive populations of European barbel are now widespread; in their presence, the endemic barbels have significantly reduced relative weight (Carosi *et al*., 2017). European barbel have also genetically introgressed with the endemic *Barbus* spp., with some endemic populations now comprising of only 4 % pure *B. tyberinus* and 23 % pure *B. plebejus* (Zaccara *et al*., 2021). Moreover, the hybrid forms have larger lengths for age than the pure endemic forms, with the population with the largest trophic niche (but of lower trophic position) being the endemic population with the highest number of introgressed European barbel alleles (de Santis *et al*., 2021).

European barbel were deliberately introduced into the River Severn, Western England, in 1956 as an angling enhancement (Wheeler & Jordan 1990), with a population establishing rapidly that spread throughout the basin (Antognazza *et al*., 2016). With no native *Barbus* fishes present, there have been no genetic introgression issues. While their initial ecological consequences for native fish communities were not quantified, recent dietary studies indicated patterns of trophic niche divergence between barbel and three other cyprinid species formed in the initial weeks after larval emergence (Gutmann Roberts & Britton 2018). These results were supported by stable isotope analyses, which indicated that the trophic niche of barbel and chub *Squalius cephalus* (L.) only converged when the fish were relatively large (> 300 mm), with this convergence driven by some individuals of both species having diets comprising of large proportions of isotopically-distinct angling baits (Gutmann Roberts *et al*., 2017). While these fish were initially assumed to be a sink for these marine derived nutrients, subsequent work indicated that these had been trophically transferred to larger individual Northern pike *Esox* *lucius* (Nolan *et al*., 2019). Thus, these non-indigenous European barbel have modified angling styles, resulting in substantial allochthonous nutrient inputs that are integrated into the riverine food web.

6. Defining ecological impact and considering ecosystem collapse

Increased competition and predation, and genetic introgression and pathogen transfer, can thus all result from the invasion of non-native freshwater fishes. However, Gozlan *et al*. (2010a) argued that these processes were not sufficient to characterize the ecological impact of an introduced fish. Instead, they argued there is a requirement for these processes to be associated with a quantifiable and significant decline of biological or genetic diversity threatening the long-term integrity of native species, and these changes must lead to a measurable loss of diversity or change in ecosystem functioning if the species is to be considered harmful (Gozlan *et al*., 2010a). Thus, an invasion that results in increased inter-specific competition would only be considered harmful if this results in, for example, a shift in diversity and/or functioning (e.g. through species displacement).

The species-specific case studies of Section 5 demonstrated how freshwater fish invasions can lead to measurable changes in biological and genetic diversity, and ecosystem functioning. Through the transmission of *S. destruens*, introduced topmouth gudgeon can severely impact native fish diversity through population extirpations (Gozlan *et al*., 2005; Andreou *et al*., 2011). Invasive European barbel in Italy have resulted in some pure-strain endemic barbel populations now being close to extirpation (Zaccara *et al*., 2021). Invasive carp populations can affect both diversity (e.g. of macroinvertebrates and macrophytes) and ecosystem functioning (e.g. shifts from clear water, macrophyte dominated to highly turbid, algal dominated) (Weber & Brown, 2009; Vilizzi *et al*., 2015). Importantly, with carp being an ecosystem engineering species, their impacts can manifest in freshwaters that are relatively undisturbed and thus do not have to align to the Disturbance or Invasion meltdown hypothesis (although both anthropogenic disturbances and extant invaders can accelerate their invasion; Britton *et al*., 2010b). This ability of carp to create substantial ecological impacts in pristine environments is in contrast to many other invasive freshwater fishes that whilst being highly impacting, tend to be associated with systems that are already modified. For example, invasive peacock basses severely reduce native fish diversity in southern Brazil and thus have a strong ecological impact according to the definition of Gozlan *et al*. (2010a). However, their presence in these waters is primarily due to disturbance, with the introduction usually to create sport angling opportunities in reservoirs that were created for hydropower generation (Britton & Orsi 2012).

In recent years, the concept of ecosystem collapse has increased in attention, where it was recently defined by Newton *et al*. (2021) as "a degraded ecosystem state that results from the abrupt decline and loss of biodiversity, ecosystem functions and/or services, where these losses are both substantial and persistent, such that they cannot fully recover unaided within decadal timescales". There are examples of where invasive fishes have contributed to the collapse of freshwater ecosystems, such as at Lake Naivasha, Kenya, where recovery to its pre-invaded state would require substantial interventions (Newton *et al*., 2021). However, the altered ecosystem functioning of this lake also involves a number of invasive non-fish taxa (e.g. *P. clarkii*) and substantial anthropogenic disturbances from industrial scale horticulture (Hickley *et al*., 2004b; Hickley *et al*., 2015). Nevertheless, carp are a species whose invasion has the potential to lead to ecosystem collapse without any other factor being involved in the loss of biodiversity, ecosystem functions and/or services (Weber & Brown, 2009; Vilizzi *et al*., 2015). Indeed, that the relationship between carp biomass and impacts tends to be non-linear, with rapid changes occurring at certain tipping points, further supports this evidence of carp-driven ecosystem collapse through their middle out effects resulting in abrupt changes in ecosystem functioning (Weber & Brown, 2009).

7. Conclusions

The impacts of invasive freshwater fishes remain of high conservation concern due to their negative consequences for freshwater biodiversity (Tickner *et al*., 2020). Nevertheless, it is apparent that the severity of ecological harm that results from these invasive fishes varies considerably, with differences apparent between species (e.g. due to differences in traits) and within species (e.g. due to context dependencies). The definition of ecological impact by Gozlan *et al*. (2010a) emphasises that impact assessment must consider measurable losses of diversity or changes in ecosystem functioning if harm is to be quantified, providing a framework appropriate for impact assessment. However, the definition of ecosystem collapse of Newton *et al*. (2021) is also potentially helpful as it focuses on the extent of ecosystem degradation more generally, rather than just on the invading population, enabling assessment of the extent of the role invasion played in degradation (e.g. whether the invasive fish are drivers or symptoms of ecosystem degradation).

The ecosystem collapse definition of Newton *et al*. (2021) also provides context around ecosystem recovery ("…cannot fully recover unaided within decadal timescales"), suggesting that where ecological harm is particularly severe then management interventions should be used to reduce these. Indeed, the management of non-native fish in freshwater ecosystems is common, where removals are used to reduce impacts and improve fishery performance (Britton *et al*., 2011c; Rytwinski *et al*., 2019), with eradication using chemical treatments often being highly effective (Britton & Brazier, 2006). The eradication of carp from a South African reservoir by rotenone application resulted in relatively rapid improvements in water clarity, with the phytoplankton community shifting from one typical of eutrophic waters to one more typical of a lower nutrient state (Dalu *et al*., 2020). Notwithstanding, managing non-native freshwater fish in large open systems can be highly challenging due to methods such as chemical treatments being non-species specific and difficult to apply over large spatial areas (Britton *et al*., 2011a,c). Correspondingly, risk-based approaches to managing invasive freshwater fishes remain important, where understanding the drivers and consequences of their ecological impacts should be a fundamental component of the risk assessment process.

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Figure captions

Figure 1. Summary of how the interactions of the invasive fish population and the abiotic and biotic components of the receiving environment influence the invader's ecological impact.

Figure 2. The ecological impacts of invasive fish that can develop from individual to ecosystem levels.