



Controlling common carp (*Cyprinus carpio*): barriers, biological traits, and selective fragmentation

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Received: 12 May 2022 / Accepted: 13 December 2022 / Published online: 23 December 2022
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Abstract The common carp (*Cyprinus carpio*) is a non-native fish species in many parts of the world which has negative impacts on freshwater environments including plant loss, re-suspended sediment, and altered nutrient flux. Eradication of common carp can be extremely difficult and conventional management efforts have focused on control or containment, achieved with barriers that decrease or eliminate access to specific habitats. Here, we examined

biological traits of common carp that can be exploited with barriers to control populations and minimize ecological impacts; however, an important consideration during barrier design and implementation are impacts on non-target, native species (i.e., selective fragmentation). Phenology, such as differences in reproductive timing, could be used to operate barriers to minimize impacts on some native species. Sensory ability could also be exploited in cases where common carp is more sensitive to electrical, acoustic, visual and/or chemical stimuli. Differences in morphology of common carp compared to native species could contribute to barrier design (e.g., 5.0 cm spacing in vertical bars screens), whereby larger common carp are excluded but many native species can pass. Behaviour, such as common carp jumping, can also be exploited to separate carp from native species with modified barriers. We explore cases of each trait being used through diverse case studies: phenology (Sea Lamprey Control Program); sensory capability (carbon-dioxide deterrents); morphology (vertical bar screens); and behaviour (the Williams' cage). The approach taken here with common carp can be applied to other aquatic non-native species to assess the potential for barriers to reduce associated negative impacts on native fish species with selective fragmentation.

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Keywords Aquatic invasive species · Management · Control · Fish migration · Habitat protection

Introduction

Non-native species in aquatic environments can have direct or indirect biological impacts on native species through predation, competition, hybridization, habitat modification, and transmission of novel pathogens/diseases (Gozlan et al. 2010). Once established, these species can expand their geographic range (Lorenzoni et al. 2010) and rapidly colonize new habitats (Penne and Pierce 2008). Eradication of established populations can be difficult (Rytwinski et al. 2019; Yick et al. 2021) and understanding their ecology is key to informing and guiding effective management strategies (Lennox et al. 2016; Green and Grosholz 2021; Smith et al. 2022).

The common carp (*Cyprinus carpio*), a cyprinid native to Eurasia, is among the most ecologically damaging, non-native species on the planet (Lowe et al., 2004). Introduced throughout the world for food, aquaculture, and recreational fisheries purposes, common carp can become a dominant species in a variety of freshwater ecosystems (Weber and Brown 2009; Bajer and Sorensen 2010). Common carp often use shallow, vegetated wetlands, deltas and river backwaters for spawning and littoral habitat for feeding (Penne and Pierce 2008). Once established, common carp populations can reach high abundances, drastically altering ecosystems by causing increased turbidity and nutrient mobilization, decreased density of macrophytes, homogenization of habitats and, ultimately, lower community diversity of macroinvertebrates, fishes, and waterfowl (Miller and Crowl 2006; Matsuzaki et al. 2009; Maceda-Veiga et al. 2017). Life-history strategies of common carp enable populations to expand rapidly and attain high biomasses (Britton et al. 2011). These strategies include adult longevity (up to 64 years; Koch 2014), long breeding seasons (between water temperatures of 17 and 28 °C; Panek, 1987), and repeated spawning events in a single year (Smith and Walker 2004). Recent research has shown that many populations of common carp exhibit source-sink dynamics in which adults home to specific shallow spawning locales that lack egg predators (Dauphinais et al. 2018; Sorensen and Bajer 2021).

Depending on invasion stage, management options for non-native fish species include no action, control/containment, and eradication (Rytwinski et al. 2019). Rytwinski et al. (2019) identified five categories of

intervention strategies that can be integrated to control or eradicate populations of non-native fishes: chemical (e.g., application of piscicides); physical (e.g., passive netting); biological (e.g., introduction of sterile predators; see Koenig et al. 2015); environmental (e.g., drawdown of water); and harvest regimes (e.g., intentional over-fishing). Control or containment can be implemented with techniques such as physical barriers or non-physical deterrents, often combined with other targeted measures, with the goal of halting or decreasing spread and impacts (Fausch et al. 2009; Sorensen and Bajer 2020). For common carp control, the main goal of these deterrents and barriers is often to eliminate or reduce access to spawning habitats, thereby decreasing recruitment and, ultimately, common carp populations. Eradication can be implemented to limit the initial spread of non-native species and to eliminate specific populations or species within distinct habitats or waterbodies (Green and Grosholz 2021; Yick et al. 2021). The more established that a non-native population becomes, the more difficult complete eradication will be and, in these cases, control techniques are used to manage populations with the aim of alleviating adverse ecological impacts (Britton and Brazier 2006).

Physical barriers (e.g., weirs, culverts, or vertical bar screens) have been used in invaded waterbodies to control common carp (Jones et al. 2021). Barriers can be active (e.g., trap-and-sort), whereby trapped fish have to be manually sorted and removed, resulting in a substantial investment in labour (e.g., the Cootes Paradise Marsh Fishway of Hamilton Harbour, see Chow-Fraser 1998). Alternatively, passive barriers (e.g., vertical bar screens) do not require manual sorting and removal, therefore requiring less human intervention. Additionally, there are other types of non-physical deterrents that use acoustic, chemical, electrical, or visual cues to deter non-native species, rather than physically blocking passage (Jones et al. 2021). However, barriers can also limit the movement of native or desirable species, leading to increased interest in selective fragmentation (Rahel and McLaughlin 2018). Selective fragmentation permits certain species to pass while minimizing access to non-native species by using variation in biological traits, such as morphology, sensory capability, behaviour or phenology (Rahel and McLaughlin 2018; Zielinski et al. 2020). Despite noted success of some

barriers including over 50% reduction in common carp biomass in Hamilton Harbour, Lake Ontario following barrier installation (Boston et al. 2016) and 90% reduction in some Minnesota lakes (Sorensen and Bajer 2020), concerns remain regarding the unintended consequences on native fish populations (Escobar et al. 2018).

Herein, we review the use and efficacy of barriers as a means to achieve selective fragmentation that controls common carp populations while minimizing effects on native fishes. To determine use and efficacy of barriers for achieving selective fragmentation, we first explore primary and grey literature. Next, we refine a conceptual model based on biological traits and selective fragmentation (from Rahel and McLaughlin, 2018) in support of refinement of management strategies and conventional control techniques for undesirable non-native species, such as common carp. Then, we examine the application of each biological trait in case studies. Finally, based on the findings, conceptual model, and case studies, we propose recommendations for the application and implementation of barriers targeting movement of common carp and identify knowledge gaps regarding science-based modifications and refinements to barrier use.

Approach

To compile primary and grey literature addressing the use of barriers as a fisheries management tool to control common carp, we conducted a search on Google Scholar. We used the following search string with Boolean operators: aquatic invasive species OR introduced OR non-native OR exotic OR introduced AND aquatic OR freshwater OR lake OR wetland, AND exclusion structure OR control OR barrier OR screen OR vertical bar screens, AND common carp OR *Cyprinus carpio*. English search terms and strings were used exclusively. All references returned from the search terms were systematically checked by the lead author, first with a review of the abstract to confirm relevance, followed by full text screening of relevant literature. We placed no restrictions on publication date or journal and also included grey literature. We also went through the references of peer-reviewed journal and review articles to compile additional

sources (“snowballing”), which decreased the risk of missing relevant studies and materials.

During review, studies were assigned into one of three groups: (1) relevant empirical studies that examined the efficacy of barriers for controlling common carp movements; (2) non-relevant empirical studies that contained search words but did not examine barrier efficacy and, (3) review papers that contained search words, but did not report new results. Neither of the latter two groups were used in the main analysis, but were retained as potential sources for discussion. All relevant empirical studies (group 1) were categorized based on the biological trait used to achieve selective fragmentation with barriers for common carp including: phenology (e.g., differences in timing of seasonal migrations); sensory capability (e.g., reaction to stimuli such as sound); morphology (e.g., total length; TL); and, behaviour (e.g., common carp jumping behaviours). Measures of barrier efficacy were extracted from each study (e.g., percentage of common carp excluded beyond the barrier or subsequent decreases in population abundance). Results from the literature search were aggregated into sections that focused on: barriers in general; biological traits (phenology, sensory capability, morphology and behaviour); case studies; an integration of biological traits; and additional considerations for design, implementation and assessment. A key part of the integration section was the creation of a conceptual model based on the framework for biological traits and selective fragmentation presented by Rahel and McLaughlin (2018). This conceptual model demonstrates how the biological traits can be used to decrease access to specific habitats by common carp (e.g., spawning sites), while minimizing negative consequences for native species.

Findings

Trends in Barrier Research on Common Carp

Through our literature search, we found a total of 68 relevant studies: 26 relevant empirical studies that examined the efficacy of barriers on controlling common carp (group 1), 17 empirical studies that contained search words but did not examine barrier efficacy (group 2), and 22 review papers (group 3). Of the 26 relevant empirical studies, the majority were

peer-reviewed (19; 73%), while seven were grey literature (27%). The 26 empirical studies that examined barrier efficacy for common carp were then further divided based on their focal biological trait: phenology (0); sensory capability (11); morphology (10); and behaviour (11) (see Table 1). The majority of studies occurred in North America (17; 65%) with many from the Laurentian Great Lakes area and inland lakes in Minnesota, followed by Oceania (8; 38%) mostly in Australia, and finally one study in Asia (Japan). Further, we found no studies in Africa or Europe. Most studies were published after 2011, with the earliest dating from 1995 (Table 1). Across all relevant empirical studies, only five studies reported using active barriers (19%), while the majority (19; 73%) focused on passive barriers (Table 1).

Barriers: a brief introduction

Barriers, including culverts, fishways, screens, traps, or other exclusion structures, can be designed to decrease access to specific areas by non-native species (Jones et al. 2021). Specifically, for this study, we consider barriers used to minimize access of non-native species to spawning or foraging habitat, thereby decreasing recruitment and improving habitat conditions. Usage of barriers can mitigate harmful impacts on native ecosystems and fauna by limiting their dispersal (Rahel 2013), reducing recruitment and, ultimately, decreasing abundance/biomass (van der Burg et al. 2021). In a global review, Jones et al. (2021) found that barriers targeting aquatic non-native species have been largely successful at limiting passage; however, considerable prior knowledge and planning are required before implementation and operation. Information regarding the biological traits of the targeted species including phenology, sensory capability, morphology, and behaviour (Rahel and McLaughlin 2018), can be used to implement selective fragmentation to minimize negative, unintended impacts on native species. In the following sections, we review each of these biological traits, which may be exploited to limit passage of non-native species using barriers and support the implementation of a selective fragmentation approach for common carp exclusion.

Biological Traits

Phenology

Variation in movement phenology, the timing of recurring biological events, is a biological trait that can be used to implement selective fragmentation for controlling non-native fishes (Rahel and McLaughlin 2018). Broadly, phenological differences among species can manifest in diel movement patterns, such as nocturnal versus diurnal species (e.g., Johnson et al. 2016), or seasonal migration patterns, such as spring (e.g. walleye, *Sander vitreus*) versus fall spawning (e.g. salmonids, *Salmonidae*) (Chuine and Régnière 2017; see Fig. 1a; Table 2). In general, fewer studies have examined diel activities of common carp relative to those studying seasonal movements. Previous studies found no consistent patterns of diel activity in common carp, with similar activity across day and night (Banet 2016), selection of shallower depths during the day relative to night (Larocque et al. 2020), and a lack of movement through locks at night (Whitty et al. 2022). These mixed results related to common carp diel activity suggest that additional studies are needed to evaluate the potential use of diel activity patterns to achieve selective fragmentation.

Seasonal migration patterns are driven primarily by environmental factors that result in variation of resources across space and time (Dingle and Drake 2007). It has been widely documented that common carp undertake movements from littoral habitats to shallow, vegetated marshes, deltas, and floodplains during the spring to spawn (Penne and Pierce 2008; Banet et al. 2021). In many cases, common carp in lotic systems migrate considerable distances (e.g., hundreds of km in Australia) to access spawning habitats (Stuart and Jones 2006b). Such migrations may make common carp vulnerable to control, whereby barriers can be placed to limit movements (Stuart and Conallin 2018), especially to spawning habitat (Banet et al. 2021). Prior to spawning, sexually mature common carp often form aggregations in specific areas (Diggle et al. 2012), which could also contribute to effective control with barriers if placed in the correct location, such as wetland entrances (Conallin et al. 2012). In temperate regions, common carp start migrating to spawning habitat when water temperatures rise above 10 °C (Chizinski et al. 2016) and subsequent spawning activities occur at

Table 1 Barriers used to exclude non-native common carp from specific habitats. Active barriers require manual sorting and separating of fish (i.e., native fishes vs. common carp), whereas passive barriers do not. The Williams' cage separates jumping common carp from non-jumping native species, while push traps incorporate weighted, hanging finger style elements to separate common carp. Note that not all studies report passage rates of common carp, therefore alternate measures are included in assessment of efficacy (e.g., reductions in biomass). Grey shading is to aid in visualization

Location	Active or passive	Design	Biological trait	Spacing (cm)	In situ or laboratory	Notes on efficacy	References
Mississippi River Lock, Wisconsin, USA	Passive	Acoustic	Sensory Capability	N/A	In situ	Did not eliminate passage of common carp, some individuals were deterred.	Zielinski and Sorensen (2015); Zielinski et al. (2014)
Cootes Paradise Marsh, Lake Ontario, Ontario, Canada	Passive	Strobe & acoustic	Sensory Capability	N/A	In situ	Weak avoidance response in common carp	Bzonek et al. (2020)
North and South Heron Lakes, Minnesota, USA	Passive	Electric	Sensory Capability	N/A	In situ	No marked common carp were captured beyond the barrier, as well as a decrease in abundance	Verrill and Berry (1995)
Cootes Paradise Marsh, Lake Ontario, Ontario, Canada	Passive	Acoustic	Sensory Capability	N/A	In situ	Moderate decrease in catch rate (#/hour) in common carp, reflective of weak avoidance response	Bzonek et al. (2021a)
Hamilton Harbour, Ontario, Canada	Passive	Strobe & acoustic	Sensory Capability	N/A	In situ	Avoidance response to stroboscopic and acoustic stimuli	Bzonek et al. (2021b)
Kohlman Creek, Minnesota	Passive	Bubble curtain	Sensory Capability	N/A	In situ	Common carp passage was decreased (although not statistically significant)	Riesgraf et al. (2022)
Hamilton Harbour, Ontario, Canada	Passive	Strobe	Sensory Capability	N/A	Laboratory	No significant impact of stroboscopic stimuli on juvenile common carp	Kim et al. (2019)
Hamilton Harbour, Ontario, Canada	Passive	Strobe	Sensory Capability	N/A	Laboratory	Significant avoidance response to stroboscopic stimuli	Kim and Mandrak (2017b)
Hamilton Harbour, Ontario, Canada	Passive	Electric	Sensory Capability	N/A	Laboratory	Significantly reduced passage beyond electric barrier, with a low voltage	Kim and Mandrak (2017a)

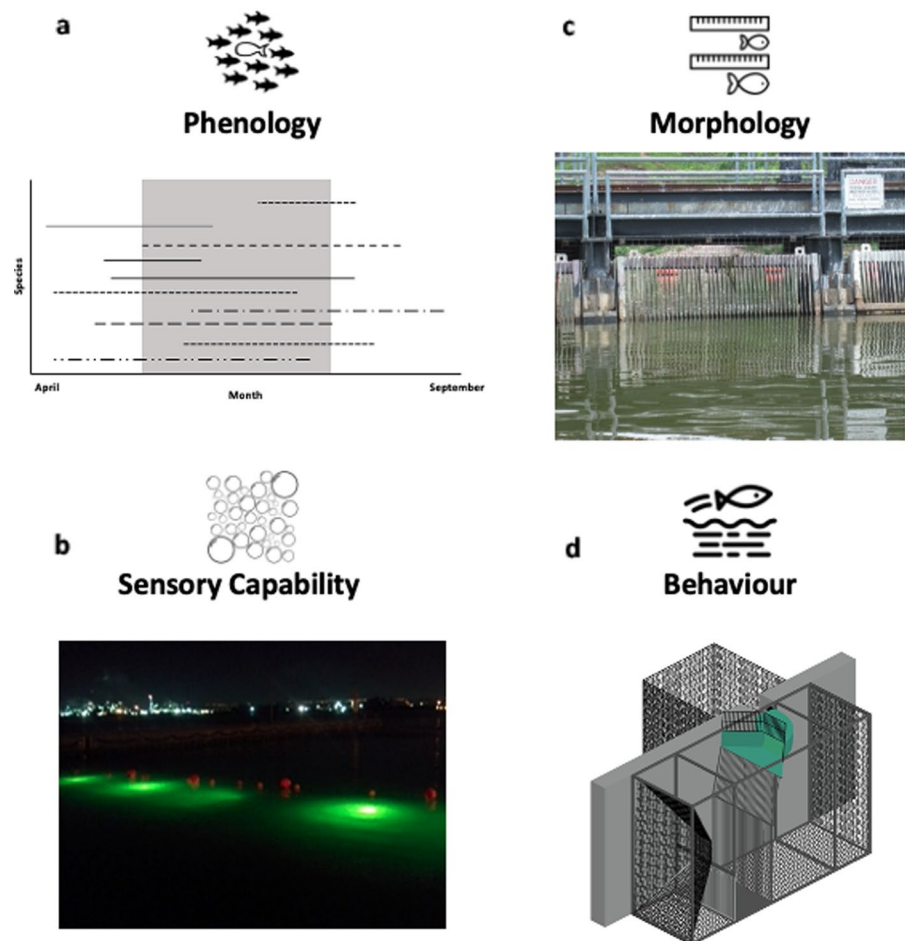
Table 1 (continued)

Location	Active or passive	Design	Biological trait	Spacing (cm)	In situ or laboratory	Notes on efficacy	References
Nikko, Tochigi, Japan	Passive	Acoustic	Sensory Capability	N/A	Laboratory	Moderate avoidance response to acoustic stimuli (30 Hz)	Matsuda (2021)
Cootes Paradise Fishway, Lake Ontario, Ontario, Canada	Active	Vertical bar screens	Morphology	5.0	In situ	Prevents passage to 95% of common carp. Decrease in biomass, reduction in turbidity and improvement in habitat conditions	Lougheed et al. (2004)
Delta Marsh, Lake Winnipeg, Manitoba, Canada	Passive	Vertical bar screens	Morphology	9.0	In situ	Partial exclusion of common carp improved habitat conditions, resulting in increased recruitment	Parks (2006); Caskenette et al. (2018)
Tommy Thompson Park, Lake Ontario, Ontario, Canada	Passive	Vertical bar screens	Morphology	9.0	In situ	Efficacy will be evaluated in the future	Barnes et al. (2020)
Metzger Marsh, Lake Erie, Ohio, USA	Passive	Vertical bar screens	Morphology	7.0	Laboratory	Excluded 100% of common carp longer than 34 cm, and permitted passage to northern pike (native species) smaller than 70 cm	French et al. (1999)
Murray-Darling Basin, New South Wales, Australia	Passive	Mesh & vertical bar screens	Morphology	4.4 3.14	In situ	92% of adult common carp excluded, but could also exclude up to 65% of native species	Hillyard et al. (2010)
Lakes Crescent and Sorell, Tasmania, Australia	Passive	Mesh	Morphology	0.5	In situ	Barriers trapped common carp, where they were physically removed, leading to eradication	Diggle et al. (2012); Taylor et al. 2012; Yick et al. (2021)

Table 1 (continued)

Location	Active or passive	Design	Biological trait	Spacing (cm)	In situ or laboratory	Notes on efficacy	References
Lake Ohinewai, Waikato, New Zealand	Passive	Vertical and horizontal bar screens	Morphology	3.0	In situ	Successful exclusion resulting in initial decrease in common carp (koi) biomass, followed by increase (physical removal is required)	Tempero et al. (2019)
Purgatory Creek, Minnesota, USA	Passive, with active capabilities	Vertical bar screens	Morphology	Not noted	In situ	Decreased biomass (below 100 kg/ha), improvement in water quality, young-of-year carp were able to pass through	Sorensen et al. (2015)
Murray River, New South Wales, Australia	Passive	Mesh	Morphology	0.1	In situ	No significant decrease in abundance within wetlands with barriers	Nichols and Gilligan (2003)
Lake Bonney, South Australia, Australia	Active	Finger style	Behaviour	3.1	Laboratory	91% of common carp were successfully trapped, with zero escaping	Thwaites et al. (2010); Thwaites et al. (2011)
Torrumberry Weir, Murray River, New South Wales, Australia	Passive	Williams' cage	Behaviour	2.5	In situ	Prevented 88% of common carp from accessing upstream habitats, while permitting 99.9% of native species passage	Stuart et al. (2006)
Valentine National Wildlife Refuge, Nebraska, USA	Passive	Finger style	Behaviour	0.3	In situ	In combination with physical removal, decrease in common carp abundance	Wanner et al. (2009)
Lock 1, Murray River, South Australia, Australia	Active	Williams' cage	Behaviour	5.0	In situ	Effective separation of common carp resulting in a reduction of common carp abundance and bycatch of native species was very low (0.03%)	Stuart and Conallin (2018)

Fig. 1 Examples of biological traits that could be considered when implementing selective fragmentation with barriers for non-native common carp. **a** Overlap of arrival and departure dates for non-native common carp (grey) compared to native species (black lines) in efforts to compare phenologies. (modified from Vélez-Espino et al. 2011). **b** Strobe light deterrent in Hamilton Harbour, Canada to exploit the sensory capability of common carp **c** Vertical bar screen spacing (5.0 cm) at the fishway of Cootes Paradise Marsh, Canada designed to exclude common carp **d** Diagram of the Williams' cage, which is designed to exploit the jumping behaviours of common carp



water temperatures between 17 and 28 °C (Panek 1987). For example, in Lake Susan, Minnesota, at 10 °C common carp migrated *en masse* to spawning habitat after 83% of northern pike (*Esox lucius*; a native species) had already completed migration (initiated at 4 °C) and returned to non-spawning habitat (Chizinski et al. 2016). Therefore, seasonal barriers activated based on environmental parameters such as water temperatures could be used to impose selective fragmentation, whereby barriers (Sorensen and Bajer 2020) are opened and closed when waters reach specific temperatures.

While we found few examples of differences in phenology being used to achieve selective fragmentation for common carp control, operation of barriers based on migration timing information, including arrival, duration, and departures for both native and targeted non-native species hold promise (Table 2). For example, the fishway at Cootes Paradise Marsh is

operated seasonally (i.e., open during the winter and closed during the spring), although the opening and closing is based more on calendar dates rather than fish migration timing (Table 1). Barriers based on phenology (i.e., time-based) are akin to timing windows or reduced activity periods that are frequently used in fish habitat management to reduce harm from in-water works during periods when a species or life process is particularly sensitive (Tunney et al. 2022). These windows are generally defined based on species phenology, but adjustments to their start or end dates can be made based on what is deemed an acceptable level of risk. For the operation of barriers based on phenologies, it is important to consider all native species that could be blocked or have reduced access when the barriers are closed. Further, native fishes may migrate at similar times as common carp, so perfect separation could be challenging (Chizinski et al. 2016). In addition to timing or water

Table 2 Biological traits in native *and* non-native species (i.e., common carp) that should be examined prior to design, implementation, and operation of barriers. Grey shading is to aid in visualization

Biological trait		Description	Tool or technology	Reference
<i>Phenology</i>				
Phenology	Spawning period	Seasonal differences in spawning migration timing	Barrier operated seasonally	Vélez-Espino et al. 2011
	Diel pattern	Nocturnal or diurnal activity	Barrier operated daily/nightly	Mallen-Cooper 1999
Motivation	Obligate or facultative migrator	Some species require access to specific habitats for successful spawning	Enhanced passage of obligate migrants	Klinger et al. 2003
Spawning frequency	Single or multiple spawning events	Some species can spawn multiple times over a broader suite of conditions	Enhanced passage of single event spawners	Chuine and Régnière 2017
	Semelparous or iteroparous	Some species only spawn once before death	Enhanced passage of semelparous species	Rahel and McLaughlin 2018
<i>Sensory capability</i>				
Acoustic	Auditory system, lateral line	Species disparities in reactions to sound and pressure	Use of sound as a deterrent	Bzonek et al. 2020
Chemical	Olfactory system	Attractants or repellents could guide or discourage movement	Application of natural or synthetic compounds	Fredricks et al. 2021
Vision		Fish avoid noxious stimuli	Application of CO ₂	Suski 2020
	Visual acuity	Difference in responses to varying light wavelengths	Use of different light frequencies and strobing	Bzonek et al. 2022
Electroreception	Number of electroreceptors	Differential response to electric stimuli	Electrical current to guide or deter	USFWS 2021
<i>Morphology</i>				
Shape	Girth, width, depth	Differences in body shape can allow differential access	Use of vertical bar screens or mesh	Taylor et al. 2012
		Image recognition to identify species	Identification software to allow selective passage	Zielinski et al. 2020
<i>Behaviour</i>				
Locomotion	Jumping ability	Height of barrier can promote differential access	Use of low-head barriers	Stuart and Conallin 2018
		Jumping behaviour to separate species	Instillation of selective traps (e.g., Williams' cage)	
	Swimming ability	Velocity barriers to promote differential access	Use of velocity flumes	Rahel and McLaughlin 2018
		Flow field manipulation to differentially guide species	Use of flow fields to guide or deter	

temperature, other environmental drivers of migration or life-history processes (e.g., spawning or overwintering movements) that could be used to enhance the efficacy of selective fragmentation approach include photoperiod (i.e., light-dark cycles), hydrology, meteorology, or water quality (Lucas and Baras 2008). Finally, interannual variation in movement phenology and environmental drivers (e.g., water temperature) should also be considered, with the implementation plan for barriers formulated based on multiple years of data.

Sensory capability

Barriers based on sensory capability exploit varying responses to sensory stimuli across different fish species; however, responses to sensory cues can be complex (determined by sensory acuity and perception; Elmer et al. 2021) and altered by fish cognitive function (e.g., habituation). In general, innate behavioral responses to sensory stimuli are poorly understood, although this is currently an area of active study and development (Rahel and McLaughlin 2018). Barriers based on sensory capability can be advantageous in that they do not necessarily physically restrict navigation or water flow within the waterway (Noatch and Suski 2012).

Various sensory capabilities of fishes can be exploited to implement selective fragmentation using electrical, visual, acoustic, or chemical cues (Table 2). For example, electrical barriers can be used to induce behavioural avoidance and block passage of fish species; however, they are more commonly used to stun fish and arrest upstream movement. The use of an electrical barrier decreased common carp passage within a laboratory setting (Table 1; Kim and Mandrak 2017a). In Minnesota and other areas in the central USA, electrical barriers have been effective at eliminating the upstream movement of common carp in streams into lakes, where no common carp were recorded moving past the barrier (Table 1; Verrill and Berry 1995).

By targeting visual sensory capabilities, strobe lights can be used as non-physical barriers, resulting in behavioural avoidance. There are several important considerations including type, intensity, and or/colour of lights (Sullivan et al. 2016). Relative to other barrier types, there are fewer studies examining the effectiveness of light-based barriers (Kim and Mandrak

2017b), with the existing studies presenting mixed results of efficacy with common carp. For example, in a laboratory setting, strobe lights were an effective deterrent for common carp; however, the lights also impacted non-target native fishes (Kim and Mandrak 2017b). In combination with acoustic stimulus, strobe deterrents resulted in avoidance by common carp (Bzonek et al. 2022). However, some caveats associated with strobe lights include decreased efficacy in turbid waters, biofouling (Bzonek et al. 2020), and lack of species specificity (although they are safe and easy to install; Dennis and Sorensen 2020).

Barriers based on acoustic deterrents are of special interest because they are safe for humans and generally easy to deploy (Vetter et al. 2018). In Hamilton Harbour, an in situ experiment using acoustic deterrents found that movements of native buffalo fishes (*Ictiobus* spp.) and common carp, which have similar auditory capabilities, were affected as the fishes exhibited avoidance responses (Table 1; Bzonek et al. 2021b). In another study, acoustic deterrents elicited a weak avoidance response from common carp undertaking upstream movements within the Mississippi River, USA (Riesgraf et al. 2022). Bubble curtains that produce complex sound, visual stimuli, and hydrodynamic fields were more effective at decreasing (but not entirely eliminating) downstream passage of common carp relative to upstream in a Minnesota stream (Fig. 1b; Zielinski and Sorensen 2015). In laboratory studies, acoustic bubble curtains have proven successful at reducing common carp passage by 75–85% (Zielinski et al. 2014).

Barriers based on chemical stimuli, such as high concentrations of carbon dioxide (CO₂), can produce an avoidance response in fishes (Rahel and McLaughlin 2018). Common carp repeatedly avoided high concentrations of CO₂ within a laboratory setting (Table 1; Bzonek et al. 2022); however, CO₂ deterrents are likely not to be species selective, as CO₂ can induce equilibrium loss in all fish species and reduce environmental quality by lowering water pH (Suski 2020). Additional research is needed to explore the applications of CO₂ deterrents (See Case Study #2 below).

Multi-modal deterrent systems that employ several types of sensory cues have been shown to strongly enhance barrier efficacy and reduce habituation, including for common carp (Dennis et al. 2019). Among the most promising of these are ensonified

bubble curtains, or bioacoustic fish fences (BAFF), which combine sound, air curtains, lights, and, potentially, CO₂ (Dennis and Sorensen 2020). These systems have been shown to be over 95% effective in the laboratory at deterring common carp that did not habituate (Dennis et al. 2019). Further, BAFF are also proving effective in the field for deterring other non-native carp species (bighead *Hypophthalmichthys nobilis* and silver *Hypophthalmichthys molitrix*; USFWS 2021) and for diverting out-migrating juvenile salmonids from a low-survival migration route (Perry et al. 2014). In summary, exploiting sensory capabilities of common carp to implement selective fragmentation is a relatively new concept, and there is more work to be done to examine efficacy in terms of passage rates.

Morphology

Selective fragmentation can be achieved by designing barriers to minimize access to undesirable species, while permitting passage to desirable species. Vertical bars or mesh screens have been used to restrict the movement of large-bodied fishes, such as adult and subadult common carp, while allowing smaller or laterally compressed species to pass through (Fig. 1c; Table 1 Rahel and McLaughlin 2018). Vertical bar screens with spacing ranging from 3.1 to 9.0 cm and meshes with spacing ranging 0.3 to 5.0 cm have been used (Table 2). While the majority of barriers used to exclude common carp have yielded positive results, such as decreased abundance and reduced passage into wetlands or other target habitats (Table 1), there are important features to be considered during the design phase. Shortcomings of morphological barriers include clogging (e.g., from debris, ice, or vegetation; Sorensen et al. 2015) and inhibition of navigation.

Prior to designing selective physical barriers, knowledge of the morphology of both targeted non-native species and native species that use the habitat is required (Table 1). There is a trade-off between screen spacing within the barrier and the size of both common carp and native species attempting to gain passage. For example, while planning barriers for Metzger Marsh in Lake Erie, experimental barriers were used to identify optimal designs across varying shapes and sizes to decrease access to common carp and allow access for native northern pike (French

et al. 1999). Vertical bar screens with 5.0 cm spacing limited common carp greater than 34 cm TL and northern pike larger than 70 cm TL, but smaller individuals of both species could still access the wetland (Fig. 1c; French et al. 1999). As such, exclusion of common carp using this type of bar spacing may also exclude larger (potentially more fecund) individuals of native fishes; however, the majority of native species would be able to pass through.

As decreasing the reproductive activity and ensuing recruitment by common carp is one of the main goals of exclusion, minimizing access for sexually mature common carp (i.e., > 30 cm TL; Brown et al. 2005) is an important success criterion for barriers. Physical barriers with vertical bar screens with 7.0 cm spacing were installed in Delta Marsh in Lake Winnipeg; however, this spacing was only able to partially exclude sexually mature common carp from wetland areas (i.e., smaller adults still gained access), resulting in common carp accessing and spawning within high-quality habitats, which was opposite to the intended management outcome (Caskenette et al. 2018). Therefore, an important consideration for designing spacing of bar screens is common carp morphology and the TL at which they reach sexual maturity, which is influenced by climate (Schmidt 2015). Further, smaller individuals that gain access to the spawning habitat through the barrier may mature and remain on that side, thereby circumventing the original management goal of the barrier.

Based on previous examples of physical barriers for common carp (see Table 1), body morphology can be an effective biological trait to control passage of common carp; however, in some cases where exclusion barriers were deemed effective, they were used in combination with other management strategies (e.g., Taylor et al. 2012). This is consistent with Rytwinski et al. (2019), where the use of multiple (integrated) intervention strategies to control non-native fishes has been most effective. For example, in New Zealand and Minnesota, temporary exclusion barriers were used in combination with active physical removal by commercial netting and boat electrofishing to control common carp (Table 1; Tempero et al. 2019; Sorensen and Bajer 2021). Similarly, in Tasmania, mesh exclusion barriers were paired with radio-tagged “Judas” common carp (Patil et al. 2014). The Judas fish were then tracked to identify their spatial distribution during aggregation periods (discussed

further in next section) and subsequently targeted for physical removal using gill nets and electrofishing (Table 1; Yick et al. 2021).

Behaviour

Fish behaviour can be exploited to implement effective selective fragmentation based on variability in specific behaviours among native and non-native species (Table 1; Williams et al. 2012; Lennox et al. 2016). For example, common carp exhibit a unique jumping behaviour not shown by most native fishes in Australia and can be used as a mechanism to escape entrapment (Fig. 1d; Table 1; Stuart et al. 2006). This jumping behaviour has been exploited in southern Australia using a modified barrier, the Williams' cage, where common carp are separated from non-jumping native species (Stuart and Conallin 2018). The Williams' cage is a structure designed to permit selective removal whereby the first stage confines both native fishes and common carp. Native fish passage is permitted via a false floor (Stuart et al. 2006), but common carp are captured in a second stage by jumping a low barrier (i.e., 30 cm above water surface) into a separate cage (Fig. 1d; Table 2). Common carp remain in holding cages until manually removed for commercial disposal (Stuart and Conallin 2018). The cage is constructed from vertical bar screens (4.2 cm spacing) to facilitate unobstructed passage of small-bodied and laterally compressed fishes. The Williams' cage effectively separated 88% of common carp, while permitting 99.9% passage of Australian native species (Stuart et al. 2006). Application of the Williams' cage assumes limited jumping by native species (i.e., most fishes cannot jump more than 30 cm), which should be confirmed prior to its application in other systems (Morán-López and Uceda Tolosa 2017).

In addition to jumping, common carp also exhibit a pushing behaviour when confronted with barriers (Thwaites et al. 2010). Similar to the Williams' cage and jumping, exploiting the common carp's pushing behaviour (i.e., fish exerting force to pass through a barrier) assumes that native species do not exhibit the behaviour as well. Barriers that take advantage of this pushing behaviour include one-way steel "fingers" (spaced 3.1 cm apart) designed to be pushed through by sexually mature common carp (> 30 cm TL) to entrap them in a holding cage (Table 1; Thwaites

2011). In Australia, the push trap has effectively separated over 90% of adult common carp in a laboratory trial, and its effectiveness was confirmed in a field trial on the Murray River (Conallin et al. 2016). However, both Thwaites et al. (2010) and Conallin et al. (2016) called for additional studies to assess native fish pushing ability. In contrast to other types of barriers, these jumping and pushing traps require ongoing removal of entrapped common carp (i.e., active barrier rather than passive; Hillyard et al. 2010). These are just two examples of behaviours that common carp exhibit that have been explored in field and laboratory studies and provided focal native species also do not exhibit these behaviours, they can be exploited to achieve selective fragmentation. However, considerable work remains to assess these behaviours in other native fish species and also to determine if common carp exhibit other potentially exploitable behaviours.

Case Studies

We have identified cases where each of four biological traits has been used to prevent access to a target species, while aiming to permit passage of native species. The intent of these case studies is to explore the utility of exploiting phenology, sensory capability, morphology, and behaviour to implement selective fragmentation.

Phenology: Sea Lamprey Barriers

As we did not find any published studies that used and evaluated differences in phenology of common carp versus native species to implement selective fragmentation using barriers, we use an example based on sea lamprey (*Petromyzon marinus*). The Sea Lamprey Control Program in the Laurentian Great Lakes has made use of differing phenologies among invasive and native fishes to operate barriers on a seasonal basis (Fig. 2a). This program has been operating for decades, with important lessons that can be learned relevant to the implementation of seasonal barriers. Invasive sea lamprey use the Great Lakes proper during their adult parasitic feeding phase, but require seasonal access to tributaries for spawning and larval habitat (Applegate 1950). Barriers to prevent access of migratory adults to these tributaries

Fig. 2 Examples of each biological trait that could be used to implement selective fragmentation to exclude common carp from certain habitats. **a** The Sea Lamprey Control Program within the Laurentian Great Lakes exploits the phenology of non-native sea lamprey. Specifically, 12 seasonal barriers are closed to eliminate access to non-native sea lamprey, and opened before and after the migration to allow passage to native species. **b** CO₂ barriers were experimentally tested within Cootes Paradise Marsh at the fishway. The CO₂ barriers resulted in significant avoidance by common carp at a relatively low concentration of 70 mg/L. **c** The fishway at Cootes Paradise Marsh (installed in 1996) is an active physical barrier that uses 5 cm vertical bar screen aimed at exploiting the morphology of common carp relative to native species. The fishway has successfully decreased common carp biomass and populations. **d** The Williams' cage is an active physical barrier that has been used in the Murray River, Australia and is based on the jumping behaviour of common carp. The Williams' cage is designed to separate non-jumping native species



remain a critical component of an integrated control strategy (Siefkes et al. 2013); however, there is increasing pressure to permit passage for native fishes while maintaining sea lamprey control through selective fragmentation (Zielinski et al. 2020; Walter et al. 2021). As sea lamprey only need to be blocked when adults are migrating into tributaries to spawn, one way to mitigate impacts to native fishes is to operate barriers (often low-head barriers; Fig. 2a) seasonally to allow passage of native fishes (Klingler et al.

2003). Although sea lamprey differ greatly from common carp, some lessons can be taken from this successful program that may help with common carp control.

Seasonal barriers provide benefits to desirable fishes only if the spawning phenologies of the invasive and desirable fishes differ. Sea lamprey have a prolonged spring/summer spawning run that can last up to four months (Applegate 1950). As most obligate migratory fishes native to the Great Lakes share

a similar spring migration phenology, the benefits for desired fishes of a seasonal versus permanent barrier are low. For example, an average of only 5% and 7% of longnose sucker (*Catostomus catostomus*) and white sucker (*C. commersoni*), respectively, passed outside of the operation window of electrical barriers operated on eight Lake Superior tributaries over a 25-year period (Klinger et al. 2003). Similarly, Velez-Espino et al. (2011) found that a seasonal barrier operating for a duration of 75 days would block 99% of the sea lamprey run, but result in <10% passage for most other common Great Lakes spring migratory species. Despite these challenges, seasonal barriers allow fishes with migratory phenologies that fall outside of the sea lamprey spawning window, including fall spawners and summer resident species, unimpeded access (Vélez-Espino et al. 2011; Miehl et al. 2020). The Sea Lamprey Control Program provides an example for how to identify situations where a common carp barrier based on phenology could be used to allow access for native species. Further, it reinforces that a review of migration timing and duration for common carp and target native fishes at a site of a proposed barrier is essential prior to operation.

Sensory Capabilities: Carbon Dioxide

Cootes Paradise Marsh, Lake Ontario, Canada is a 250 ha river-mouth coastal marsh that supports aquatic biodiversity by providing habitat for many native fish species. Increasing common carp populations were first identified as a conservation issue in the 1930s, with many management strategies undertaken in the following decades. The Cootes Paradise fishway (a physical barrier, described in detail in Case 3) was installed in 1996 to exclude common carp from moving between Hamilton Harbour and Cootes Paradise Marsh (Fig. 2b). A temporary CO₂ barrier was added to the fishway in 2019 to evaluate the feasibility of using chemical barriers in wetland locations to control common carp movement. CO₂ was used in a previous laboratory study, where it was observed to be a more effective common carp deterrent than the concurrently tested acoustic or stroboscopic stimuli (Bzonek et al. 2022).

Elevated CO₂ at the barrier (70 mg/L compared to 40 mg/L ambient conditions; Bzonek and Mandrak, 2022) was sufficient to produce behavioural avoidance in common carp, with a 10-fold decrease

in catch rates from 2.56 individuals per hour during control trials to 0.26 individuals per hour during deterrent trials. The concentration of the CO₂ plume is a key feature of this type of barrier, and common carp displayed significant avoidance at a concentration of 70 mg/L. However, this proof-of-concept barrier benefited from low water-flow, high ambient CO₂ concentrations, and a small target area. Permanent, management-oriented CO₂ barriers will require more effective delivery systems with specialized equipment and access to large volumes of CO₂ (Zolper et al. 2019). Management-oriented CO₂ barriers will also need to be balanced against the considerations of altering ecosystem conditions and the broad-scale halting of native fish dispersal.

Morphology: the Fishway at Cootes Paradise Marsh

The Cootes Paradise Marsh fishway is an example of a barrier exploiting differences in the morphology of common carp and native species. The fishway is a 40 m wide physical barrier with 5.0 cm vertical bar screen spacing designed to exclude common carp greater than 35 cm fork length (Fig. 2c). The goals of the structure were to eliminate access of common carp large enough to physically damage marsh habitat (i.e., uprooting of macrophytes and increased turbidity; Loughheed et al. 1998) and to reduce recruitment. In addition to eliminating passage of common carp, the fishway was also designed to permit passage to native species. Specifically, the fishway has six cages, where fish that enter become entrapped and are subsequently sorted manually (i.e., native species permitted to access the marsh and common carp are returned to Hamilton Harbour). Initially, the goal was to reduce the density of large common carp to <50 kg/ha, but this goal has been progressively reduced to <20 kg/ha due to continued success. Further, the barrier has been extremely effective at eliminating common carp in Cootes Paradise Marsh, with population reductions of >95% (formerly approximately 800 kg/ha; Theysmeijer 1999) and has also led to a steady decline in the overall common carp population in the adjacent harbour (Boston et al. 2016).

Important considerations for the implementation and operation of the fishway include dynamic water levels, which have resulted in several floods over the 25+ years since installation. The fishway has been outfitted with spillways to accommodate extreme

flows; however, there have been occasions when water levels have overtopped the fishway (e.g., 2019) resulting in fishes, including common carp, circumventing the structure. Despite periodic flooding, the fishway at Cootes Paradise Marsh has been effective at decreasing access to common carp, permitting access to native species, and improving habitat conditions. As it is an active physical barrier, the success of the fishway at reducing common carp populations has only been possible due to the extensive labour-intensive efforts of the fishway staff.

Behaviour: Williams' Carp Cage

Since its release in the late 1960s, common carp have invaded much of continental Australia where it has had serious detrimental impacts on native fishes and aquatic habitats (Koehn 2004; Stuart et al. 2021). While investigating the potential efficacy of biocontrol continues (McCull et al. 2018), there is an ongoing commercial application of the Williams' carp cage (Stuart and Jones 2006a; Stuart and Conallin 2018). Over the past 15 years, the Williams' cage has been applied at Lock 1 in the lower Murray River, southern Australia, where there is a continuous series of slow-flowing weir pools with very high common carp abundances that have caused severe ecological impacts (Fig. 2d; Koehn et al. 2018; Stuart and Conallin 2018).

Each Austral spring and summer (September–December), as fishes migrate upstream through the Lock 1 vertical-slot fishway, the Williams' cage automatically separates common carp by exploiting its jumping behaviour, which preliminary work revealed local native fishes did not display (Stuart et al. 2006). Actively migrating common carp enter the Williams' cage, then jump over a low (30 cm) inclined floating barrier made from vertical-bar mesh with 4.2 cm bar spacing, which allows unimpeded passage of small-bodied and laterally compressed native fishes, such as the abundant bony herring (*Nematalosa erebi*). Jumping common carp are then confined into two separate buoyant holding cages stationed within the weir pool. These are serviced by an on-site gantry and emptied daily by a commercial fisher with catches stored in on-site freezer facilities. Meanwhile, native fishes are released via a manually raised false floor and crowder, which also raises and lowers the vertical-bar jumping barrier.

Between 2008 and 2022, a total of 932 metric tonnes (~372,000 fish at 2.5 kg each) of common carp were removed from the Williams' cage in Lock 1 fishway. These common carp are mostly sold for garden fertilizer, marine crayfish bait, or domestic human consumption. There has been virtually no (0.03%) bycatch of the 7,874 large- and medium-bodied native fishes which were also counted migrating through the fishway over the 15-year sampling period. Several lessons are highlighted by the long-term commercial application of the Williams' cage. First, common carp jumping and separation efficiencies are highest in spring (pre-spawning) and then decline in summer (post-spawning) with the cage entirely removed in autumn/winter when few fish migrate. Second, while some aspects of the Williams' cage can be automated (i.e., common carp separation, small-bodied and laterally compressed fish passage, and native fish release), the actual removal and disposal of common carp requires considerable daily effort by on-site weir operations staff and a commercial fisher. Third, common carp remain a low-value market fish so there is marginal economic/ecological return at low/medium biomass sites and this has strongly restricted broader adoption of the technology. Finally, demonstration of ecological benefits from commercial common carp removal remains unquantified, but population modelling suggests this may be most favourable during sequential years of low flows when common carp recruitment is poor (Koehn et al. 2018).

Integration of Biological Traits

Although most examples of how barriers are used to implement selective fragmentation for common carp have exploited one biological trait (e.g., sensory capability or behaviour), there remains potential to integrate multiple traits to maximize effectiveness and minimize negative impacts on native species. In our conceptual model which could be applied to other aquatic non-native species, from left to right, the order of biological traits can be thought of as 'order of defence' in terms of proximity to habitat that is being protected (Fig. 3). First, the phenology of non-native and native species, including arrival and departure or water temperature associated with spawning initiation (see Table 2), should dictate when barriers are opened or closed. Selective fragmentation could

also be implemented if the non-native species has different spawning phenologies relative to native species (e.g., spring-migrating versus fall) or have varying migratory strategies (e.g., migratory or resident; Table 2). In addition to arrival and departure dates, environmental drivers of migration (such as cumulative growing degree days; see Chezik et al. 2014; Swanson et al. 2021; Table 2) could also be used to determine timing of opening or closing of barriers. Alternatively, the barriers could be opened and closed daily according to diel movements (although this would require considerable maintenance unless automated; Table 2).

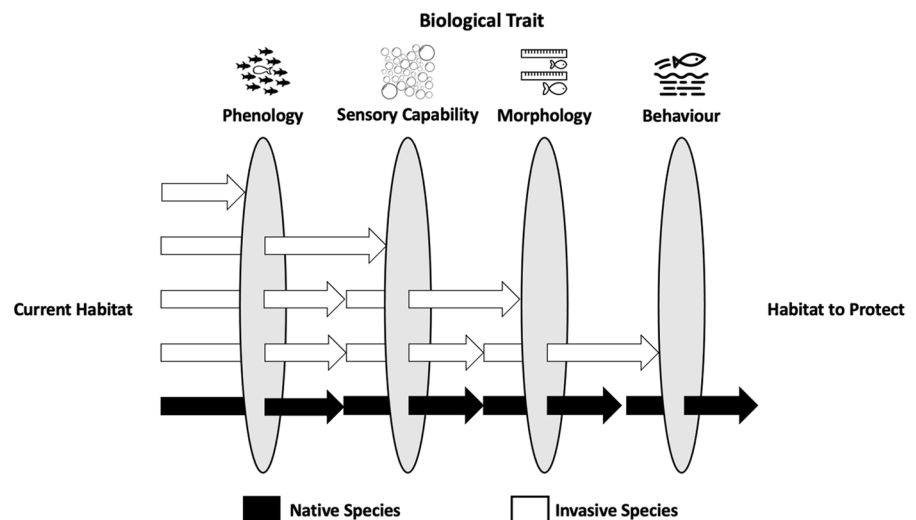
Second in the conceptual model, barriers based on sensory capability could be used in combination with any of the other biological traits (Fig. 3). These non-physical barriers based on acoustic, auditory, chemical, or visual stimuli, are more novel with substantial knowledge gaps remaining in their development and in situ application with a need for additional assessments of efficacy (Bzonek et al. 2021a). Examples of data that could be collected to contribute to the design, implementation, and operation of these barriers are largely dependent on the sensory type, but could include sensitivity of the gustatory and olfactory systems, inner ear (acoustic pressure and particle acceleration), lateral line, or visual spectral sensitivity (wavelengths detected; Table 2). Barriers based on sensory capability could be operated during the arrival and migration of the target non-native species (phenology) and turned off after departure to

minimize impacts on native species. Alternatively, sensory capability barriers could supplement additional physical barriers based on morphology or behaviour.

Next, barriers based on fish morphology could be operated according to the phenologies of non-native versus native species, and even supplemented with non-physical barriers based on sensory capabilities. Effective design would require knowledge of native vs. non-native fish species morphologies, such as girth, depth, TL, or cross-sectional shape (Table 2) to maximize passage for native species while minimizing access to non-native species. These design aspects of barriers based on fish morphology are often transferable to other barrier types. Further, morphological traits were considered during the design of the Williams' cage and push trap (i.e., vertical bar screen spacing), therefore having application in combination with other biological traits.

Finally, barriers based on fish behavior, similar to morphology, could also be operated according to phenologies (e.g., migration or diel shifts), or supplemented with barriers based on sensory capabilities (Fig. 3). It is necessary to understand the behaviour of the non-native species to determine which species could be exploited for selective fragmentation. In the case of common carp, it is necessary to explore its propensity to jump or push at barriers, relative to the abilities of native species (Table 2). Other types of potential behaviours that could be exploited include separation (vertical and horizontal), schooling/

Fig. 3 Conceptual model of biological traits (grey ovals) that could be exploited to implement selective fragmentation of non-native common carp from desired habitat with barriers. This figure has been modified from Rahel and McLaughlin (2018)



shoaling, or additional responses to barriers (e.g., swimming over; Table 2). Broadly, more research is necessary to determine the efficacy of using multiple biological traits to implement selective fragmentation with barriers for common carp, while minimizing impacts on native species.

Additional considerations for design, implementation, and Assessment

Overall, barriers can be used to decrease passage of non-native species (Jones et al. 2021); however, there are some important considerations for design to optimize efficacy and promote passage for native species. The common carp has become established across the globe in a wide variety of ecosystems and every site is different, with varying morphometry (e.g., water depth or waterbody dimensions) and diversity of native species present (including other biota such as herpetofauna). Impacts on local and native aquatic fauna should be considered during the design phase, with careful consideration of the biological traits of native species. Notably, many of the temperate ecosystems in which common carp thrive contain native species with similar migratory attributes, including spring spawning.

There are a variety of factors that may influence the choice and implementation of carp barriers that extend beyond the biology of the animals or efficacy of the barrier. For example, cost of exclusion methods both in terms of capital expenditures and ongoing staffing and maintenance (e.g., the Cootes Paradise fishway; see Galbraith and Theysmeyer 2018) will, in most instances, play a significant role in decision making (including the decision to do nothing). Site characteristics (e.g., spatial scale, water depth, currents), potential conflicts with other water users (e.g., kayakers, anglers, commercial vessel traffic), and social and cultural acceptance of a given method also need to be considered. Additionally, species that possess considerable phenotypic plasticity for life-history traits can respond quickly to altered selection regimes (Hendry et al. 2017). Therefore, an important consideration is whether the installation of poorly designed barriers might promote selection of fish with alternate life histories capable of circumventing barriers. Considerations will vary within the context of a given site, region, issue, and approach; therefore, it is not

possible to generalize about what will work in every scenario.

Although the use of barriers to exclude common carp has generally yielded positive results (see Table 2), there has been a general lack of rigorous assessment for efficacy. Specifically, a Before-After-Control-Impact (BACI) design should be used as a robust analytical tool to examine barrier effectiveness (see Smokorowski and Randall 2017). It is crucial to monitor both before and after the impact (ideally equal time periods) and with multiple suitable controls specified. Further, any assessment should examine the efficacy of both excluding common carp and allowing the passage of native species.

Summary and conclusion

The common carp has strong negative impacts on many aquatic ecosystems where it is established, especially shallow lakes and wetlands. Although barriers are reasonably effective in terms of population control and exclusion (often in combination with other management strategies such as physical removal or fish toxicants), they can have maintenance burdens that require significant resources. Additionally, there remains much work to be done to increase efficacy and limit off-target impacts on native species.

We explored biological traits of common carp including phenology, sensory capability, morphology, and behaviour to identify and consider the implementation of selective fragmentation using barriers, thereby alleviating associated negative ecological consequences and, ultimately, reducing common carp recruitment and populations. Differences in phenologies (i.e., spawning migration timing or diel shifts) across native species and common carp could be exploited to operate barriers to maximize access for native species and minimize access to common carp. Sensory capabilities, including reactions to acoustic, electric, chemical or visual stimuli of common carp can be exploited when they differ from those of native species. Differences in fish morphology (e.g., girth or body size) can contribute to barrier spacing (i.e., vertical bar screens) to reduce access to adult common carp, which tend to be larger and broader than many native species. Finally, variations in behaviour, such as jumping or pushing abilities, can be exploited during the barrier design phase, where native species that

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