



Biocontrol in Australia: Can a carp herpesvirus (CyHV-3) deliver safe and effective ecological restoration?

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Abstract The Australian Government is considering Cyprinid herpesvirus 3 (CyHV-3) for biocontrol of invasive common carp (*Cyprinus carpio* L.). We review the evidence-base for its potential ecological risks, benefits and effectiveness. Lower carp abundance may boost native fish biomass and improve water clarity, but there is little evidence available to suggest that the virus, alone or used in combination with other methods, can deliver effective or safe biocontrol. Further, the virus may already be present in

Australia. Overseas, the virus has caused sporadic and localized mortalities of carp in lakes and rivers, but has generally had no long-term measurable effect on wild carp or native fish populations. The temperature range of disease (18–28 °C), unknown co-factors causing outbreaks, and predictable re-colonization and recruitment boom of immune and virus-resistant carp, following a biocontrol release, remain formidable and unmitigated barriers to success. CyHV-3 infection trials on Australian biota have unexplained high mortality rates of recreationally-important and threatened fishes, and the role of asymptomatic carriers remains uncertain. Finally, Australia has national and international obligations to ensure that there are no

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perverse outcomes from biocontrol actions. Despite political pressure, there is no environmental justification to rush the release of this virus. To achieve the Government goals of restoring native biodiversity we advocate that key uncertainties, risks and efficacy barriers first need to be addressed. It is only then that viral biocontrol could be considered a viable tool to complement broader ecological restoration strategies for Australia's waterways.

Keywords Biological control · Cyprinid herpesvirus 3 (CyHV-3) · Risks · Invasive alien species · River restoration · Ramsar · Murray–Darling Basin

Introduction

Biocontrol is one of few environmental management actions that can transform ecosystems. Australia has a long history of biocontrol successes, such as the reduction of previously super-abundant prickly pear (*Opuntia* spp.) by releasing a cactus moth (*Cactoblastis cactorum*) during the 1930's (Dodd 1936), or the decline of European rabbit (*Oryctolagus cuniculus*), caused by releases of myxoma virus in the 1950's and rabbit haemorrhagic disease virus in 1996 (Pedler et al. 2016). However, Australia's biodiversity has also been damaged following what with hindsight were reckless biocontrol releases. For example, the introduction of cane toads (*Rhinella marina*) to control cane beetles (*Dermolepida albohirtum* and *Lepidiota frenchi*) and eastern gambusia (*Gambusia holbrooki*) to control mosquitos, not only failed to reduce pest populations but the biocontrol agents subsequently became environmentally destructive invasive species themselves (Shine 2010; Hinchliffe et al. 2017). These releases were driven in large part by a zealous focus on anecdotal benefits and political expediency, without rigorous testing of their likely effectiveness or risks (Pyke 2008; Turvey 2013). Perverse outcomes often arise from well-intentioned environmental management interventions (Hobbs et al. 2011), and therefore invasive species control decisions should not be assumed safe without a substantial evidence-base (Simberloff and Stiling 1996; Doherty and Ritchie 2017; Kopf et al. 2017).

Cyprinid herpesvirus 3 (CyHV-3), previously referred to as Koi herpesvirus, is being considered as

Australia's next major biocontrol agent. The virus has never been applied as a biocontrol but it is being evaluated as a potential tool to control invasive common carp (*Cyprinus carpio* L.), hereafter 'carp' (McColl et al. 2016a, b; McColl et al. 2017). The potential release of CyHV-3 is a key focus of Australia's National Carp Control Plan (NCCP 2017) which is a project intended to help restore native biodiversity. As far as we are aware, the potential release of CyHV-3 would represent the first large-scale attempt at viral biocontrol in an aquatic ecosystem. CyHV-3 was first detected in aquaculture operations in Germany, Israel and the United States in the 1990's, subsequently spread to over 33 countries, and caused widespread mortality events of carp in fish farms, and to a much lesser extent in lakes and rivers (Boutier et al. 2015).

Although carp is one of the most widely cultured fish produced for food world-wide, it is also one of the most prolific invasive species (Lowe et al. 2000), often causing ecological changes that adversely affect biodiversity and ecosystem functioning (Koehn 2004; Weber and Brown 2009; Kulhanek et al. 2011; Vilizzi et al. 2015). Originally from the Black, Caspian and Aral Sea basins (Balon 1995), carp was first introduced into Australia for aquaculture in the mid-1800s, but only became abundant and widespread in the wild following floods in the 1970's (Koehn 2004). In 1964 a new genetic strain spread from fish farms, and had expanded to most of the Murray-Darling Basin (MDB) by 1977 (Shearer and Mulley 1978). Carp are now widely distributed in Queensland, New South Wales, Victoria, and South Australia and are also found in two lakes in Tasmania. Carp is currently one of the most prolific freshwater fishes in Australia, and where it occurs it makes-up approximately 60–90% of all fish biomass (Harris and Gehrke 1997; Koehn 2004; Kopf et al. 2018). In Australia, the effects of carp are ecosystem-dependent, but high densities have been associated with elevated turbidity and pelagic algae (King et al. 1997; Robertson et al. 1997) and declines in macrophytes (Fletcher et al. 1985) and native fish biomass (Kopf et al. 2018).

Here, we provide an independent perspective on the risks, benefits and effectiveness of CyHV-3 as a biocontrol agent for carp in Australian waterways. We address four questions relevant to scientists, managers and policy-makers: (1) Can native species be infected

by or transmit CyHV-3?; (2) What are the broad ecological risks of unintended and perverse outcomes from biocontrol with CyHV-3?; (3) Is there evidence of CyHV-3 delivering effective control of wild carp populations? and (4) What are the potential ecological restoration benefits of carp control? This is not an exhaustive list of potential benefits, efficacy or safety issues, but provides a synthesis of the epidemiological and ecological evidence-base for considering CyHV-3 as a biocontrol agent. The viability of carp biocontrol, like any natural resource management initiative, ultimately depends on social acceptability and whether benefits exceed costs. Socio-economic and human health issues, such as the cost of a clean-up, effects on drinking water, tourism, infrastructure, food security and aquaculture industries, although important, are not considered here.

1. Can native species be infected by or transmit CyHV-3?

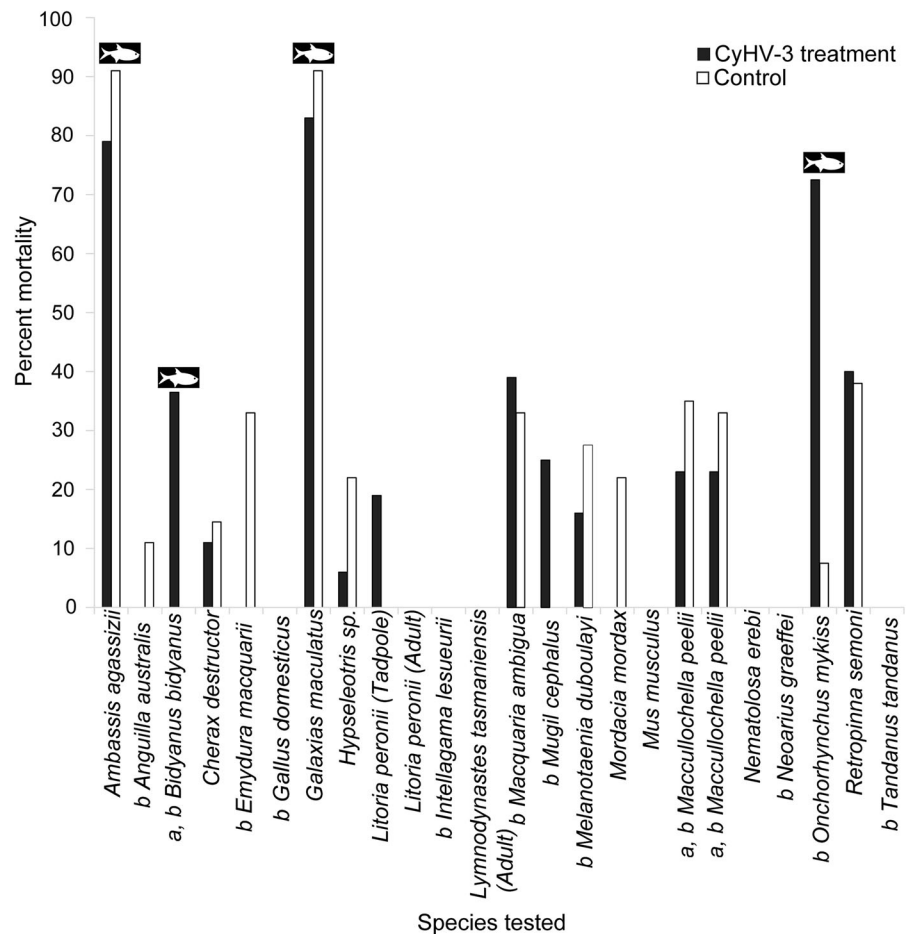
Knowledge of the species-specificity of a potential biocontrol agent is fundamental to avoid perverse outcomes for non-target species. Herpesviruses are generally host-specific and host-stable and CyHV-3 is not reported to have caused disease in any species other than carp, koi and related hybrids (Boutier et al. 2015). McColl et al. (2016b) reported on the susceptibility of 22 Australian non-target species to CyHV-3 and concluded there were no clinical signs of disease or molecular evidence of viral infection. However, Australian non-target fish species suffered high rates of mortality in both virus treatments and controls (Fig. 1). Species with unusually high mortality rates in the virus treatments included, but were not limited to, non-native but recreationally important rainbow trout (*Oncorhynchus mykiss*; 45–100% mortality) and a native fish, silver perch (*Bidyanus bidyanus*; 27–46% mortality). Silver perch are listed as threatened by the Australian Environmental Protection and Biodiversity Conservation Act 1999 (EPBC 1999). For both species, the percent mortality in the controls (no virus present) was less than 10%. High mortalities (up to 91% in Common Galaxias *Galaxias maculatus* and Olive perchlet *Ambassis agassizii*) in the controls of other Australian species tested indicated that laboratory conditions were inadequate for reliable experimentation. Given the unexplained mortalities, we

recommend additional susceptibility and transmission trials for non-target fish species (Table 1), focusing especially on taxa that suffered high (e.g. > 20%) rates of mortality in controls or treatments (Fig. 1).

Based on existing evidence of herpes virus epidemiology (Boutier et al. 2015) and absence of clinical disease symptoms (McColl et al. 2016b), it is highly unlikely that the CyHV-3 can cause disease in native species. Although CyHV-3 exposure adversely affecting native species is highly improbable, these potentially catastrophic risks and unquestionably high rates of mortality in experiments should not be ignored. Native species may have never been in contact with the virus, and the large geographic area of carp in Australia represents a novel opportunity for virus evolution (Lighten and van Oosterhout 2017).

A related issue of uncertainty in the literature is which species act as asymptomatic carriers or vectors that could carry and transmit a viral infection. Piscivorous waterbirds are potential vectors via physically transporting water or infected fish (Ilouze et al. 2010). Over 29 potential asymptomatic carrier species of fish in nine families, and two species of invertebrates have tested positive for CyHV-3 DNA (Kempter et al. 2012; Boutier et al. 2015; Fabian et al. 2013, 2016; Gaede et al. 2017). Importantly, some of the non-target species which tested positive also effectively transmitted the virus to naïve cohabitant carp (Kempter et al. 2012; Fabian et al. 2013, 2016). Despite claims by McColl et al. (2016b), effective transmissions by non-target species in several independent studies suggests that some non-target species carry and transmit the virus. However, several of these previous trials were performed using highly sensitive 'nested PCR', prone to lab contaminations (OIE 2012), which may have falsely detected viral DNA. McColl et al. (2016b) found no molecular evidence of any non-target Australian species replicating CyHV-3, but did not conduct studies to determine whether non-target species could effectively transmit the virus. McColl et al. (2016b) used RT-PCR and a qPCR method initially designed by Gilad et al. (2004), which is considered to be one of the international reference methods for testing CyHV-3 (OIE 2012). Research is needed to identify non-target species that may effectively transmit the virus, or act as potential asymptomatic carriers (Table 1). Furthermore, no previous research has evaluated the potential for sub-lethal effects (e.g. compromised immune function, stress,

Fig. 1 Median percent mortality of non-target species in Australia exposed to CyHV-3 (black-virus treatments), compared to controls (white-no virus present) by McColl et al. (2016b). Values represent the median of both immersion and injection procedures by McColl et al. (2016b; Table 1). Species denoted (a) are listed as threatened by the Australian Environmental Protection and Biodiversity Conservation Act 1999 (EPBC 1999) and by the International Union for the Conservation of Nature (IUCN) Red List and species denoted (b) are considered recreationally or commercially important. Statistical comparisons and error bars could not be calculated because replicate exposure trials were either not conducted or not reported for all but one non-target species (*M. peelii*). Fish silhouettes highlight species discussed in the text



growth, reproduction) of low-level viral infections on potential carriers. Better knowledge of the species-specificity of CyHV-3 asymptomatic carriers and transmission is likely to serve the dual purpose of mitigating risks and improving the accuracy of epidemiological models needed to predict the spread of disease.

2. What are the broad ecological risks of unintended and perverse outcomes from biocontrol with CyHV-3?

The removal of invasive species requires a whole-ecosystem perspective (Zavaleta et al. 2001; Simberloff et al. 2013), with rigorous assessment of the risks of removing widespread and established species from environments (Kopf et al. 2017). Unlike the low-likelihood lethal or sub-lethal risks of CyHV-3

infection of non-target species (Question 1), other ecological risks following mortality events of dense carp populations are highly likely and include changes in water quality, food webs, consumer populations and the spread of other diseases (Lighten and van Oosterhout 2017; McColl et al. 2017; Paton and McGinness 2018). The severity and duration of these impacts will depend heavily on highly uncertain CyHV-3 disease efficacy, timing, and the mortality rates of carp in a range of environments.

Even a carp mortality rate of only 10–20%, with compounding effects at the landscape scale in warm months, is likely to result in high concentrations of dead carp. Carp carcass decomposition and associated increases in biological oxygen demand from the organic matter and nutrients released in these environments are likely to cause localized hypoxia or anoxia and increases in the prevalence of toxic cyanobacteria blooms. The likelihood and severity of

Table 1 Ecological safety and efficacy research recommendations to address before releasing CyHV-3 in comparison to research underway by Australia's National Carp Control Plan (NCCP 2017)

Research recommendations	Addressed by NCCP
Non-target disease and mortality experiments, including additional experiments on taxa that suffered high (e.g. > 20%) rates of mortality in controls or treatments (Fig. 1).	Partially (see text)
Cross-reactivity of CyHV-3 with other viruses and salinities	Yes
Sub-lethal effects of non-target CyHV-3 exposure and additional transmission studies to confirm species-specificity of asymptomatic carriers and vectors	No
Test whether CyHV-3 is present in Australian waterways	Proposed
Experimental field trials of CyHV-3-induced common carp mortality rates	No
Experimental field and laboratory trials of common carp removal and complementary restoration actions required for the ecological recovery of Australian biodiversity	No
Quantify common carp biomass density in Australian waterways	Yes
Determine the distribution of genetic CyHV-3 disease resistance in wild common carp	Proposed
Epidemiological modelling of disease efficacy and long-term carp population responses	Yes
Quantitative food web modelling of the short and long-term impacts of common carp removal	Partially (see text)
Nutrient, cyanobacteria and hypoxia field experiments and modelling of carp decay	Yes
Plan for complementary carp biocontrol and restoration activities	No
Design fish-kill clean-up and management strategy	Yes

these problems increases with warm water temperatures (Kerr et al. 2013, Whitworth and Baldwin, 2016, Whitworth et al. 2012), which are required for CyHV-3 disease activity. Eutrophication, deoxygenation, and fish carcasses may promote outbreaks of other diseases (Paton and McGinness 2018). Botulism (*Clostridium botulinum*) in particular is widespread in wetlands of the MDB (WHA 2013). Warm temperatures, high organic matter concentrations, eutrophication, hypoxia and carcasses promote outbreaks of toxins that can cause botulism (Evelsizer et al. 2010). This disease has led to the deaths of hundreds to thousands of birds and is a risk to other vertebrates (Paton and McGinness 2018), potentially including humans, domestic live-stock and native species. Effects of botulism on fish species in Australia are not well understood, but hypoxia is an increasingly common cause of native fish kills in the MDB (King et al. 2012; Small et al. 2014). Native fishes generally suffer high mortality rates when dissolved oxygen concentrations drop below 2–3 mg/L (Small et al. 2014) and susceptibility is likely to increase with other toxic compounds released from dead carp and high temperatures.

Wetlands, dry-land river waterholes and shallow lake ecosystems will be particularly vulnerable to hypoxia, poor water quality and the ensuing ecological risks resulting from mass, or minor, carp mortality events. These environments with slow or no water current, higher water temperatures and often high densities of carp are likely hot-spots for unwanted ecological change. Physical removal of carp carcasses, following a potential biocontrol release, could mitigate these risks, but we are skeptical that this can be achieved quickly at large spatial scales in complex river-floodplain networks. In the MDB alone, there are approximately 5.7 million hectares of wetlands and 16 Ramsar wetlands of international importance (Pitcock and Finlayson 2011) protected under the Australian Environmental Protection and Biodiversity Conservation Act 1999 (EPBC 1999). Warm temperatures, shallow wetlands and high carp densities often coincide with the breeding seasons and sites of a range of fauna (Paton and McGinness 2018). These fauna include threatened waterbirds, fishes, frogs, turtles and mammals protected under the EPBC Act 1999 and are the subjects of significant investments in environmental flows and other conservation management actions.

Several potential environmental risk modelling approaches are useful to explore the plausible ecological outcomes and uncertainties of releasing CyHV-3 to control carp. First, computational extensions of qualitative modelling based on expert elicitation workshop assessments may be used to translate uncertain interactions of carp removal into quantitative predictive ecosystem ensemble models (Baker et al. 2017). Conceptual ecosystem and food web models are being developed by Australia's National Carp Control Plan and we recommend that these be developed into quantitative assessment tools (Table 1). This approach has offered valuable insight into the unexpected consequences of past non-native species interventions (Raymond et al. 2011) and could be a useful forecasting tool to predict the plausible ecological consequences of carp removal. Lastly, decision theory may be used to distinguish between critical and irrelevant sources of uncertainty and therefore risk, allowing managers to prioritize mitigation activities, and ensure that the chosen actions are robust to limited information (McDonald-Madden et al. 2010).

3. Is there evidence of CyHV-3 delivering effective control of wild carp populations?

CyHV-3 has decimated carp farming operations globally (Boutier et al. 2015) but, despite spreading to over 33 countries world-wide, there is little evidence that the virus has suppressed wild populations in lakes, rivers or wetlands. The 50–100% rates of CyHV-3-induced carp mortality, observed in high-density aquaculture ponds (Haenen et al. 2004) and optimal laboratory conditions (McColl et al. 2016b), cannot be used to infer biocontrol efficacy in open ecosystems such as rivers, wetlands or lakes. In natural aquatic ecosystems, fish are mobile, have a higher genetic diversity, patchier density, and the environment is more dynamic and heterogeneous (e.g., water temperature) than aquaculture ponds or laboratory conditions. The realized mortality rate of carp, following CyHV-3 biocontrol application in the wild, is likely to be much lower and more variable than in laboratory trials and aquaculture ponds.

Of the few CyHV-3 confirmed carp fish-kills in rivers or lakes world-wide, most have had little or no long-term detectable effect on carp abundance.

Thresher et al. (2018) synthesized and reviewed the available information on CyHV-3-induced carp mortalities in North American lakes. The available information, though coarse grained, suggested that even large and very conspicuous CyHV-3-induced carp mortality events generally had little or no detectable effect on carp abundance (Fig. 2). In fact, carp relative abundance was on average 11.5% higher after the CyHV-3-induced carp mortality events reviewed by Thresher et al. (2018). Data in Fig. 2 spans as much as 16 years prior to the mortality event (median 6 years), and 7 years afterwards (median 5 years).

There have been only two confirmed instances where CyHV-3-induced mortality rates were high and population suppression may have occurred: Lake Biwa, Japan (Uchii et al. 2013) and Blue Springs Lake in the United States (Thresher et al. 2018). In Lake Biwa, CyHV-3 disproportionately infected and killed approximately 60–80% of a Japanese strain of common carp (Uchii et al. 2013), while the Eurasian genetic lineages, from which most invasive carp in Australia have descended (Haynes et al. 2009), were

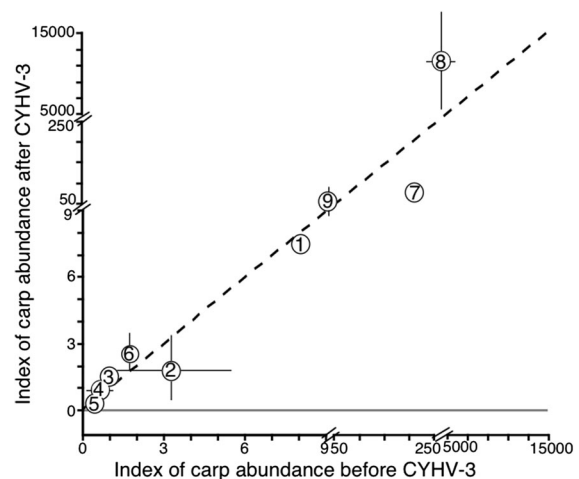


Fig. 2 Indices of common carp relative abundance for individual North American lakes (Thresher et al. 2018) before and after CyHV-3 mortality events. Sampling methods vary among lakes, and include gill netting, trapping, electrofishing and seine netting. Numbers indicate lakes: 1. Twin Buttes Reservoir, Texas; 2. Lake Scugong, Ontario; 3. Rice Lake, Ontario; 4. Buckhorn Lake, Ontario; 5. Balsam Lake, Ontario; 6. Lake Mohave, Nevada; 7. Blue Springs Lake, Missouri; 8. Lake Sinnissippi, Wisconsin; 9. Cheyenne Pond, Nebraska. The dashed line (slope of 1 and an intercept of 0) illustrates no change in carp relative abundance. Error bars were calculated as $2 \times \text{SE}$ for lakes where pre- and post-event carp data were available

largely unaffected. Data on the long-term impacts of mortality on carp abundance in Lake Biwa following the disease outbreak were not available for analysis. In Blue Springs Lake, however, adult abundance and recruitment of carp in the lake has remained low up for up to five years after the 2012 fish-kill event (Thresher et al. 2018). There have been no reports of recurrent CyHV-3 mortality events following the initial outbreak in either lake. We suspect that the high mortality rate of carp in Blue Springs Lake reflects the very small size of the lake, close connectivity of fish and hence the rapid dissemination of the virus throughout the water body, whereas long-term population suppression appears to be maintained by egg predators and piscivorous fish that increased in abundance following the disease out-break (Thresher et al. 2018).

Lake Biwa and Blue Springs Lake are not good models for Australian conditions if the virus was released. Although Lake Biwa is Japan's largest lake, at 670 km², both it and Blue Springs Lake (3 km²) are dwarfed by the 1 million km² area of the MDB, let alone the entire continent. Furthermore, the vast network of river channels, warm dry-land floodplains, wetlands and in- and off-channel storages, that comprise the Australian carp distribution, contrasts starkly with the single-lake ecosystems in Japan and the United States. In contrast to lakes, we are aware of no published pre-and-post outbreak evaluation of how CyHV-3 affected carp densities in river ecosystems. CyHV-3 is now present in most rivers in Japan and, despite significant declines in Japanese genetic strains, invasive Eurasian genetic strains have remained widespread and likely carry latent infections (Uchii et al. 2014; Minamoto et al. 2012). Gibson-Reinemer et al. (2017) speculated that a long-term decline in carp abundance throughout the Mississippi River Basin could have been from CyHV-3 disease-induced recruitment failure. They speculate that CyHV-3 was the causative agent, but present no data to establish a causal link. Most of the carp decline reported by Gibson-Reinemer et al. (2017) pre-dates by decades the discovery of CyHV-3 in North America, or the onset of mortality events attributable to the virus. Further research testing whether CyHV-3 is limiting carp recruitment or adult populations in North America is needed.

Mortality events in wild carp populations have been sporadic in time and space, and appear infrequently, or never, after the initial disease outbreak (Uchii et al.

2013; Thresher et al. 2018). Low rates of mortality and once-off outbreaks of disease in wild populations contrast with assumptions made to model potential CyHV-3 impacts on Australian carp. Brown and Gilligan (2014) used a meta-population model of the MDB to predict impacts of CyHV-3 on resident carp populations. They reported that substantial reductions in carp required a minimum of 30% mortality of the total population every 2–3 years. These assumed parameter values greatly exceed the mortality rates, spatial extent and the frequency of fish-kills, observed in the wild outside of Australia, potentially yielding overly optimistic estimates of the impacts of a carp biocontrol, based on CyHV-3.

Given the high uncertainty in CyHV-3-induced carp mortality rates and frequency of outbreaks in rivers, lakes and wetlands, we recommend that carefully contained field experimental trials be conducted to help refine the wide-ranging estimates (Table 1). Because of the difficulty of containing the virus in natural environments, experiments should first be conducted in quarantined mesocosms or overseas in countries already affected by the virus. Pending the results of experimental field trials, experiments could be scaled up to progressively larger (e.g. 20 km²) and more complex natural ecosystems whereby carp and virus density, temperature and interactions with native species could be examined.

Temperature is a key factor influencing carp mortality from CyHV-3 (Minamoto et al. 2012; Marshall et al. 2018). CyHV-3 can cause disease (i.e. clinical signs and mortalities) between the 'permissive' water temperatures of 18–28 °C. Above 30 °C the virus ceases to replicate and is innocuous to carp. This property has been used to immunize carp against the virus, with temperatures above 30 °C effectively inhibiting viral replication and allowing the development of a protective adaptive immune response in fish (Ronen et al. 2003). Furthermore, CyHV-3-infected carp can express 'behavioural fever', when they actively seek warm water (Rakus et al. 2017) to stimulate both healing and immunization. In the northern MDB, surface water temperatures in summer can be above 30 °C for 3–4 months per year, whereas permissive temperatures occur for short periods during spring and autumn (Queensland Government, unpublished data). The thermal profile of river-floodplain ecosystems is also spatially heterogeneous (Li et al. 2017), such that the water

temperature of shallow lakes and wetlands can be over 10 °C warmer than the connected river channel environment. It seems unlikely that the virus will be an effective biocontrol agent in warm months during the Australian summer, particularly in shallow floodplain environments where carp aggregate in waterholes and wetlands. Virus release during certain seasons or in warm floodplain ecosystems could cause population-level immunization, rather than mass mortality. Given the dispersal capability and behavioural fever expressed by carp, individuals may seek out warm floodplain environments, and we expect immunized individuals to re-colonize regions where the virus was previously effective. Epidemiological modelling currently underway by Australia's National Carp Control Program (Table 1) will address some aspects of these knowledge gaps, but critical uncertainties may remain regarding virus ecology and its interaction with carp behaviour, movement, river-floodplain flows and temperature.

In other Australian settings, cold-water pollution, downstream of major dams, is likely to provide CyHV-3 disease refuge habitat for carp. Water temperatures downstream of large dams in the MDB are often lower than 15 °C (Lugg and Copeland 2014), outside the permissive temperature range for CyHV-3 disease (Marshall et al. 2018). Infection with CyHV-3 at low temperature (< 15 °C) is incompatible with efficient virus replication and is usually associated with no detectable clinical signs (Sunarto et al. 2014). Compared to warm water temperatures, active immunization at temperatures below 15 °C is less likely, since the immune response of fish is reduced (Abram et al. 2017). In addition, CyHV-3-infected fish, maintained at low temperatures, frequently develop disease when returned to permissive temperatures (Sunarto et al. 2014). Management options do exist for reducing cold-water pollution (Lugg and Copeland 2014) and should be considered in modelling and pre-release mitigation measures (Table 1) to improve disease efficacy.

In addition to the temperature limitations on biocontrol efficacy, innate genetic resistance of carp to CyHV-3 disease occurs (Rakus et al. 2009; Ito et al. 2014; Piackova et al. 2013). Genetic resistance will be strongly selected for following CyHV-3 release, thereby further reducing the efficacy of biocontrol. Ancestors of CyHV-3 may have infected carp populations, long before the initial outbreaks of the disease

were first reported in the late 1990s (Gao et al. 2018). Assuming that the evolutionary rate of CyHV-3 is constant and similar to mammalian alphaherpesviruses, genetic analyses suggest that the virus has co-evolved with carp for tens of thousands of years (Gao et al. 2018). This co-evolution occurred before carp was introduced to Australia in the mid-1800's (Koehn 2004) and even before the species was first cultured by humans (Balon 1995). The exact causes of the recent disease re-emergence are unclear. However, implications of the long co-evolutionary history of CyHV-3 and carp suggests that the virus could already be present in wild Australian populations (Marshall et al. 2018). Japan conducted a nation-wide survey in 2008, which revealed that CyHV-3 had unexpectedly spread to 90% of rivers tested, without disease outbreaks reported in most rivers (Minamoto et al. 2012). Similar surveys should be conducted in Australia to test for the assumed absence of the virus (Table 1).

Wild carp in Australia are susceptible to CyHV-3 disease (McColl et al. 2016b), but the extent to which genetic variability and resistance-conferring genes (Rakus et al. 2009) will facilitate resistance to the disease remain unknown (Table 1). Reproductively viable hybrids between carp and goldfish (*Carassius auratus*) occur in Australian wild carp populations (Haynes et al. 2012). Goldfish are resistant to disease caused by CyHV-3 and experimental infections of goldfish x carp hybrids have revealed moderate-high resistance to CyHV-3 (Hedrick et al. 2006; Bergmann et al. 2010). Hybridization may introduce resistance alleles into carp populations (McColl et al. 2016b), conferring a strong selective advantage to individuals carrying these genes if the virus was introduced. More research is needed to understand the prevalence and spatial distribution of goldfish x carp hybridization in Australia and resultant resistance to the CyHV-3 (Table 1).

In addition to temperature and genetic constraints on biocontrol efficacy, the extremely high fecundity and short generation time of carp increases the speed at which wild populations are expected to recover. Recovery is likely to occur following large-scale flooding events, which are known to enhance carp recruitment in Australian river-floodplain ecosystems (King et al. 2003; Stuart and Jones 2006; MacDonald and Crook 2014). Effective population control would therefore require the implementation of an effective

mitigation strategy (Table 1) to limit a recruitment boom of virus-resistant carp in years following release of CyHV-3. This constraint has previously been recognized (McColl et al. 2016a, b), but there is currently no technology or plan in Australia to effectively prevent a recruitment boom of virus-resistant carp following a biocontrol release. Other than aligning a potential biocontrol release to coincide with a long-term drought, there is currently no feasible method of preventing or minimising carp recruitment at large spatial scales. Spawning site sabotage, barriers that exclude carp from spawning sites (Weber and Brown 2009; Koehn et al. 2018) and ‘Judas-male’ approaches (Bajer et al. 2011), though useful in small-scale applications, are unlikely to be effective over large scales in Australia. Similarly, the logistics of increasing the abundance of predatory fish or other taxa that consume carp eggs to the level required for effective population control (Bajer et al. 2012) are daunting.

Thresher et al. (2012, 2014) suggested that CyHV-3 release, followed by stocking large numbers of carp that are both immune to CyHV-3 and produce male-only offspring (‘daughterless technology’), constituted a theoretically feasible option for recruitment suppression. Options for producing daughterless offspring include a Mendelian system (Thresher et al. 2014), chromosomal manipulation (Trojan Y; Teem et al. 2014; Schill et al. 2017), or gene drives (e.g. Beaghton et al. 2016). None of these approaches has been tested in the field. Their genetic feasibility when applied to carp is uncertain and most methods would require substantial lead-in time and logistical effort, even if CyHV-3 was used first to depress carp populations. Gene drives potentially avoid logistical challenges. In theory, even the release of a small number of gene-drive-altered daughterless carp could permanently alter or suppress a targeted population (Esvelt et al. 2014). However, this desirable feature of gene drives also significantly increases the risk to non-target species (Webber et al. 2015). The ethics and uncertainty associated with gene drives and other genetic biocontrol approaches are currently being debated, with a recommendation that use be highly restricted and not yet applied in widespread biocontrol (National Academies Press 2016; Esvelt and Gemmell 2017).

4. What are the potential ecological restoration benefits of carp control?

The goal of Australia’s National Carp Control Plan is to “restore native biodiversity”. We suggest that this goal is not achievable by carp control alone, and advocate strongly for the implementation of broader ecological restoration principles (Palmer et al. 2005; McDonald et al. 2016). Ecological restoration includes assisting the recovery of a degraded, damaged or destroyed ecosystem. Successful programs include: (1) setting a target for native biodiversity recovery, based on a clearly defined reference site or model of a dynamic and healthy ecosystem; (2) publically available assessments of pre- and post-ecological condition; (3) improvement in ecological condition and resilience with minimal follow-up maintenance; and (4) causing no lasting harm to the ecosystem (Palmer et al. 2005; McDonald et al. 2016).

There is strong evidence of benefits to biodiversity in freshwater ecosystems, following effective reductions of carp from lakes (Kulhanek et al. 2011; Vilizzi et al. 2015). However, unexpected results are common, and ecological recovery is highly context-dependent, with little data available from river ecosystems (Weber and Brown 2009). There is also little evidence available to evaluate whether CyHV-3 application can facilitate ecological restoration, since the virus has never been intentionally applied as a biocontrol and no field experiments have tested ecological responses (Table 1). With the exceptions of Blue Springs Lake and Lake Biwa (Uchii et al. 2013; Thresher et al. 2018), long-term ecological changes following disease out-breaks have not been documented and remain poorly studied. Carp may increase water turbidity and algal densities (King et al. 1997), decrease benthic algae and macrophyte densities (Robertson et al. 1997; Zambrano and Hinojosa 1999) and negatively affect native fish and benthic invertebrate abundance (Zambrano et al. 2001; Kulhanek et al. 2011; Vilizzi et al. 2015; Kopf et al. 2018). Nevertheless, uncertainty remains about the generality of the impacts of carp across habitats, and especially whether these impacts in river-floodplain ecosystems can be reversed if carp abundance is reduced.

Historical estimates of native species abundance and biomass in Australia are unavailable, but conceptual historical food webs and modelling of biomass can help set recovery baselines for native fish

communities (Kopf et al. 2018). To help inform native fish restoration targets, an expert panel suggested that native fish abundance in the MDB may have declined by $\sim 90\%$ since Europeans colonized Australia (Koehn et al. 2014). Effective control of carp and environmental flows in the MDB could more than double native fish biomass, via bottom-up release and production of basal food resources (Kopf et al. 2018). It remains unknown whether there is a threshold density of carp which could promote the recovery of river ecosystems, if this varies among habitats, or if other invasive species (e.g. tench *Tinca tinca*) would fill the ecological role of carp. We therefore recommend the development of quantitative food web models to better understand the likely responses of native and invasive species (Table 1). Where experimental removal has reduced carp densities to less than 100–450 kg/ha, lakes have been more likely to shift from a turbid eutrophic state to a clearer macrophyte-dominated state, sometimes with benefits for nutrient cycling and food webs linking plankton, macroinvertebrates and native fish (Zambrano et al. 2001; Weber and Brown 2009). Turbidity, phytoplankton biomass and benthic biofilm development have been significantly altered in Australian floodplain wetlands by manipulating densities of carp ranging from 101 to 1180 kg/ha (King et al. 1997; Robertson et al. 1997).

The biomass density of carp in rivers, lakes and wetlands is heterogeneous and dynamic, commonly ranging from 5 kg/ha to over 1000 kg/ha (Weber and Brown 2009). Assessments of the density of carp in Australian systems are poor, with current work by Australia's National Carp Control Plan expected to yield more precise estimates (Table 1). Previous estimates from lakes and billabongs range from 150 to 690 kg/ha (Fletcher et al. 1985), and 176 kg/ha was estimated for the Lachlan River (Brown and Gilligan 2014).

Given the uncertainties in carp reduction necessary to achieve goals of biodiversity recovery in diverse habitats in Australia, we emphasize the need for field experiments and mesocosm studies, which manipulate carp biomass densities, to understand ecosystem responses (Table 1). The estimated carp biomass threshold densities could then serve as quantitative reference targets for comparison with pre-release mortality experiments to determine whether CyHV-3 has the potential to achieve the desired goals.

Complementary restoration and management actions would be essential to achieve ecological restoration targets, including: improving land-use practices to reduce sediment run-off; restoring natural patterns of connectivity; mitigating cold-water pollution from dams; managing environmental flows; complementary carp biocontrol technology to prevent a recruitment boom; and the development of re-introduction and rehabilitation programs for key functional groups (e.g. macrophytes; mussels; predatory fish) (Table 1).

Conclusion

There is currently insufficient evidence regarding the efficacy, benefits and ecological safety of CyHV-3, to responsibly engage in a continental-scale biocontrol release. Greater understanding of the effectiveness of the virus in Australian rivers and wetlands and the potential ecosystem-level outcomes of suddenly reducing carp biomass densities will be required, even after the completion of Australia's National Carp Control Plan research (Table 1).

The release of a novel virus may unpredictably and irreversibly change ecosystems. Though unexpected outcomes may be unavoidable, rigorously addressing the research gaps and undertaking complementary restoration measures (Table 1) will help reduce uncertainty and maximize potential ecological benefits. Despite the powerful potential of contemporary modelling approaches, our limited knowledge of both CyHV-3 disease efficacy and the response of Australian ecosystems to sudden reductions in carp densities severely restricts our current confidence in assessing ecological responses to biocontrol. Wide-ranging mortality rates in the wild, poorly described ecological and biological co-factors contributing to CyHV-3 disease out-breaks and the lack of information regarding the biomass density and genetic resistance of carp in Australian waterways (Table 1) contribute to extremely high uncertainty. The current range of plausible ecological risks therefore ranges from little-to-no adverse effects on native species, to catastrophic reductions in water quality that cause severe and widespread fish-kills, potentially with lasting effects on biodiversity. Similarly, the high uncertainty in CyHV-3 efficacy in the wild limits our ability to estimate the likely range of potential benefits

for native species, which is necessary to rationally justify this biocontrol.

Despite political pressure, there is no environmental justification to rush the release of this viral biocontrol without the necessary evidence. It is important to recognize that the impacts of carp on Australian native biodiversity are relatively static. Carp expanded to their major current range and relative abundance decades ago (Shearer and Mulley 1978; Koehn 2004). Likewise, the potential of CyHV-3 to provide a biocontrol solution would not diminish if the research and decision time-frames were extended to reduce key uncertainties and to ensure maximum biocontrol effectiveness.

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