Introductory section common to all papers

The National Carp Control Plan (NCCP) is being developed to examine and make recommendations about the feasibility of using a virus to assist in controlling common carp in Australia. The plan is to be developed by December 2019. Although focussed primarily on viral biocontrol, the NCCP will also make recommendations about the investigation and potential future use of other carp control methods.

This issues paper is one of seven prepared to summarise topics central to the NCCP's development, provide updates on emerging research results, and, where relevant, situate NCCP research within the broader context of scientific literature. Some papers within the series are intended primarily to provide background information or updates, whereas others seek stakeholder input to help shape development of the National Carp Control Plan document. An NCCP engagement report will be completed and published summarising stakeholder input.

The papers draw on results from the NCCP research program, the broader scientific literature, and stakeholder knowledge. Paper topics are:

i. Why and how did the National Carp Control Plan originate?
ii. What is science telling us about the potential use of the carp virus as a biological control agent for carp?
iii. Non-target species susceptibility testing and host-switching risk in carp biocontrol
iv. Water quality and carp biocontrol using Cyprinid herpesvirus 3 (CyHV-3)
v. Managing water quality impacts by carcass management/clean up.
vi. Understanding potential social and economic impacts of carp control
vii. Genetic biocontrol and common carp (provided as final report)

Each of the papers can be read in sequence or singly. Many of the important questions and challenges associated with carp control are multidisciplinary and multifaceted, so cross-referencing between papers is used to direct readers towards more detailed discussions of a particular topic, or to Frequently Asked Questions (FAQs) on the NCCP website (http://www.carp.gov.au/FAQ), when necessary.

Common or European carp (*Cyprinus carpio*, referred to simply as 'carp' in these papers) are an introduced pest fish common throughout a large area of Australia. When carp are abundant, they can damage aquatic ecosystems in several ways, generating environmental, economic and social costs. Carp control initiatives in Australia are therefore based on the general premise that reducing carp numbers below the densities at which they cause environmental damage could result in improved environmental, social, and economic outcomes. While there is evidence for environmental improvements following carp control, these may not eventuate in all ecosystems, follow uniform transition pathways from the 'pre-control' to 'carp controlled' states, or be achieved without activities to address other, non-carp impacts.

.

Issues Paper 1. Why and how did the National Carp Control Plan originate?

Table of Contents

1.0. About this paper

This paper provides background information about the NCCP’s origins and rationale, including

(i) the carp problem: introduction to Australia, establishment, expansion, and ecological impacts;
(ii) carp control measures attempted or proposed in Australia; and
(iii) why the carp virus might be suitable as a biological control agent for carp in Australia.

This information provides the context for subsequent papers, and illustrates some of the fundamental 'value propositions' that biological control could potentially deliver, if research indicates that that virus release can be managed safely and has the capacity to substantially reduce carp numbers. Importantly, none of these considerations preclude the use of other control methods; in fact, optimal carp suppression would most likely result from combining biocontrol with other methods, such as physical removal. Briefly, key reasons for considering biocontrol as a carp control option include:

(i) The potential for carp suppression over broad geographic areas;
(ii) The potential for other control measures, such as physical removal, to work more effectively if deployed on a carp population already suppressed by viral disease; and
(iii) The potential to obtain a period of reduced carp populations during which new approaches to carp control, or more coordinated options for deployment of existing approaches, can be developed.

2.0. Carp in Australia: history and impacts

2.1. Introduction to Australia, establishment, and expansion

Australia's first carp introductions occurred during the mid-19th century at several locations in Victoria, Tasmania, and New South Wales (Koehn et al., 2000). Most of these early releases, along with subsequent introductions through the early 20th century, either failed to become established, or persisted as small, geographically-restricted populations (Koehn et al., 2000). However, introductions around Sydney during the early 1900s gave rise to a genetic variant (strain) of carp called the 'Prospect strain', which has become widespread through the Murray-Darling Basin (MDB) and coastal streams (Haynes et al., 2009).

During the early 1960s carp, probably imported illegally from Germany, escaped from Boolarra Fish Farms Pty Ltd into a reservoir at Morwell, Victoria (Haynes et al., 2009). These fish were from a genetic strain new to Australia, subsequently labelled the 'Boolarra Strain'. The Boolarra Strain's escape heralded approximately three decades of carp range expansion (Koehn et al., 2000; Koehn, 2004). Early eradication attempts failed, and by the mid-late 1960s, these fish had entered the Murray River (Koehn et al., 2000). By the mid-late 1990s, carp geographic range in Australia was similar to the present, although carp numbers and distribution are inherently dynamic and variable through time (Koehn, 2004; Koehn et al., 2018).

Reasons for the rapid population growth and geographic spread of the Boolarra strain are varied. Carp possess biological traits that make them particularly successful at invading new habitats (Koehn, 2004). These include natural dispersal capacity (ability to travel, either as swimming adults or drifting larvae), rapid growth, early maturity, and the ability to produce numerous eggs (Koehn, 2004). Additionally, extensive flooding during the mid-1970s, and again during the mid-1990s, created favourable conditions for carp dispersal and reproduction, increasing population growth and spread across regions (Koehn, 2004). Genetic evidence also indicates that Boolarra strain carp interbred with carp from previous introductions, especially the Prospect strain, creating hardy, vigorous crossbreeds (Haynes et al., 2009). The interplay of these variables has seen carp become the most abundant large-bodied fish in the Murray-Darling Basin, and prevalent in numerous coastal catchments (Koehn, 2004).

Modelling based on carp climatic tolerances indicates that carp could, theoretically, occupy all Australian freshwaters (Koehn, 2004). Intermittent water availability prevents carp establishment in many parts of central Australia, but the reasons why carp are not found in tropical Australia is unclear. High species diversity, with consequent intense competition for resources, and predation pressure have been proposed to explain carp's absence from far northern Australia, yet the species has successfully colonised ecologically-similar rivers in Papua New Guinea following deliberate introduction by humans (Koehn, 2004). Thus, the likelihood that carp will further expand their Australian range is difficult to assess.

2.2. How do carp affect Australian ecosystems?

European colonisation dramatically altered land and water management in Australia. River flows have been blocked or changed, water diverted within and between catchments, and vegetation cleared. Changes to Australian freshwater habitats following European colonisation have tended to benefit invasive plant and animal species, which are often more successful than native species at using degraded environments (e.g. Catford et al., 2011; Stuart and Jones, 2006). Carp have been particularly successful in colonising altered river systems. Changes ranging from regulation of river flow regimes (e.g. construction of dams with water released downstream via human operation) to reductions in water quality (e.g. resulting from increased erosion and pollutants entering rivers) have increased spawning, growth, and feeding opportunities for carp, while reducing native fish habitat (Stuart and Jones, 2006; Bice and Zampatti, 2011; Koehn et al., 2018). High carp abundances are therefore partly symptomatic of broader ecological degradation.

Nonetheless, carp can also drive ecological degradation in their own right (Weber and Brown, 2009; Vilizzi et al., 2015). Research on the ecological impacts of carp is characterised by many North American studies, but has occurred in numerous countries, including Australia (Pinto et al., 2005; Vilizzi et al., 2014, 2015; Akhurst et al., 2017). Systematic reviews and meta-analyses, which combine and analyse results from multiple studies, have been important in understanding the environmental impacts of carp, and have included Australian data (Weber and Brown, 2009; Vilizzi et al., 2015). For example, Vilizzi et al. (2015) reviewed 119 studies, 14 of which were Australian. Experimental studies conducted in natural ecosystems, and covering time periods and geographic extents sufficient to detect carp impacts, have been similarly useful (Vilizzi et al., 2015). In this context, experimental studies are those in which variables, such as carp density, and carp access to particular habitat types, are subject to controlled manipulation so their effects can be disentangled from other factors occurring alongside them (e.g. Vilizzi et al., 2014).

In combination, systematic reviews and experimental studies have produced a strong, but still incomplete, evidence base demonstrating that carp can degrade aquatic ecosystems. These studies show that carp can muddy waters, increase nutrient levels, and reduce abundance of large aquatic plants rooted in the riverbed (macrophytes), invertebrates (e.g. aquatic insects and crustaceans), and some fish species (Weber and Brown, 2009; Vilizzi *et al.*, 2014, 2015). For example, in a review of 37 experimental studies, four of which were Australian, carp increased water turbidity (muddiness) in 91% of studies, reduced invertebrates in 94%, and reduced macrophytes in 96% of surveyed studies (Weber and Brown, 2009). A more recent analysis supported these results, finding strong evidence for carp impacts on the same ecosystem components (Vilizzi et al., 2015). These conclusions do not imply that carp are always the most important stressor affecting aquatic ecosystems. Rather, they identify pathways by which carp can impact ecosystems, and document instances in which these pathways appear to be either present or absent in particular ecosystems (in addition to other stressors affecting those ecosystems).

Riverbed (benthic) feeding by adult carp is one of the most commonly-identified pathways for carp impacts (Weber and Brown, 2009). Adult carp feed by syphoning sediment from the riverbed using their vacuum-like mouths, filtering out food items and ejecting the remaining material into the water around them. This feeding style reduces water clarity, liberates nutrients from sediments into the water column where they can fuel algal growth, and limits sunlight availability for macrophytes (Weber and Brown, 2009; Vilizzi et al., 2014, 2015). Suspended sediment also smothers macrophytes. Cumulatively, these impacts reduce macrophyte abundance (Weber and Brown, 2009; Vilizzi et al., 2014, 2015). These benthic feeding effects are termed ‘bottom-up’ effects, because they influence the most basic levels of the food web: aquatic plants, nutrients, and, by extension, water clarity (Kaemingk et al., 2016).

A second carp impact pathway involves feeding, or ‘trophic’ effects. Both adult and young (juvenile) carp contribute to these impacts (Sheldon and Walker, 1993; Kaemingk et al., 2016). Juvenile carp, up to approximately 10 cm in length, feed predominantly on zooplankton (microscopic animals living in the water column) (Sierp et al., 2009; Weber and Brown, 2009). When small carp are abundant, their feeding activity may alter zooplankton communities, resulting in reduced grazing by zooplankton on microscopic plants, called phytoplankton, living in the water column (Weber and Brown, 2009; Akhurst et al., 2017). Phytoplankton include the harmful species responsible for blue-green algal blooms, so reduced zooplankton grazing pressure (in response to carp predation on zooplankton) can translate to increased prevalence of harmful algae (Sierp et al., 2009; Weber and Brown, 2009; Akhurst et al., 2017). Evidence for carp impacts on both zooplankton and phytoplankton, is, however, complex and varies between ecosystems (see Sierp et al., 2009 for a summary). Juvenile carp may also compete for food with small native fish, especially during dry conditions (Mazumder et al., 2012). Adult carp generally do not feed directly on zooplankton, but do feed directly on small invertebrates like molluscs, crustaceans, and insect larvae, and can reduce their abundance (Sheldon and Walker, 1993). These direct impacts of carp feeding are often termed ‘top-down’ effects, because they involve carp acting as a predator on smaller organisms further down in the food web (Kaemingk et al., 2016).

The bottom-up and top-down impacts of carp may reinforce each other. For example, zooplankton consumption by juveniles can reduce grazing pressure on phytoplankton, while nutrient enrichment by adults can further fuel phytoplankton growth (e.g. Sierp et al., 2009; Akhurst et al., 2017). The potential for carp to affect ecosystems through multiple pathways is summarised by an ecological idea called the ‘middle-out’ framework (Weber and Brown, 2009). The middle-out framework acknowledges that a complete understanding of carp impacts requires consideration of both bottom-up and top-down impacts, as well as potential interactions between these two sets of impacts (Kaemingk et al., 2016).

A third class of carp impacts has received much less research attention than those described above, but is potentially important in Australian ecosystems. Carp are large-bodied, often abundant, and tend to eat more plant material, zooplankton, and small-bodied invertebrates than native fish of comparable size (Kopf et al., 2018). Consequently, carp may have access to a large store of energy before it is exploited by native fishes. Once this energy is consumed by carp and 'locked up' in their bodies, it cannot flow through the ecosystem to fuel native fish growth and reproduction (Kopf et al., 2018). Reduced energy availability to native fishes may cause substantial population reductions (Kopf et al., 2018).

Carp impacts are often considered in terms of 'threshold' densities, typically expressed as total carp mass per unit area, above which ecological damage occurs. Historically, a threshold density of 450 kilograms per hectare (kg $ha^{-1)}$ has been widely cited both in Australia and internationally, based mainly on the impacts that carp held in enclosures have on macrophytes (Vilizzi et al., 2014). However, enclosure experiments may not accurately recreate the effects of 'free-ranging' carp (Vilizzi et al., 2015). More recent evidence from both Australia and overseas indicates that thresholds for carp impacts vary between ecosystems, and in some cases may be as low as 50 to 75 kg ha^{-1} (Vilizzi et al., 2014). The middle-out framework also suggests that the impacts resulting from a given carp density will depend upon the age structure of the carp population. For example, a carp biomass of, say, 300 kg ha^{-1} that consists primarily of juveniles in their first year of life will have different ecological impacts compared to the same biomass of mature adult carp.

2.2.1. Carp impacts: understanding complexity

Understanding carp impacts can be complex, because carp occur in many different habitat types, and their impacts differ both between ecosystems, and within a given ecosystem through time. In Australia, carp use habitats ranging from tidal upper estuaries in subtropical southeast Queensland to temperate dryland regulated rivers in the southern MDB. This diverse range of habitats will not experience the same set of impacts from a given carp density. Additionally, each of these habitats is subject to other, non-carp, environmental impacts, some of which may outweigh those related to carp. Nonetheless, the carp impacts summarised above are well-reported in the scientific literature, and have occurred with sufficient frequency and intensity to be identified in meta-analyses and systematic reviews. Enough evidence has thus accumulated to conclude that carp cause environmental damage in addition to being symptomatic of broader ecological degradation.

Even strong evidence that carp can negatively affect ecosystems does not, however, mean that removing carp or reducing their abundance will result in ecosystem recovery to the previous, carp-free state. Although there is both peer-reviewed and anecdotal evidence for ecosystem recovery following carp removal in some locations (e.g. Pinto et al., 2005), some degraded ecosystems may shift to an alternative 'stable state', centred around a new set of organising processes, following carp removal (Kaemingk et al., 2016).

3.0. Carp control measures in Australia

3.1. Early approaches

Carp's invasive potential was recognised quickly following the Boolarra strain's escape from captivity, and in 1962 the Victorian Government recommended that carp be eradicated (Koehn et al., 2000). Since that time, numerous techniques or approaches to carp control have been attempted or suggested. Early attempts tended to involve techniques that kill all or most aquatic animals inhabiting a waterbody, such as application of the fish poison (piscicide) rotenone. While these techniques may be justifiable if eradication of a geographically-isolated invasive species seems achievable, they are clearly inappropriate for managing an established pest over large geographic areas. More recent approaches to carp control have largely focussed on various forms of physical removal. Some basic population biology helps to contextualise the opportunities and challenges associated with carp control via physical removal.

3.2. Pest population dynamics

A proportion of the deaths occurring in most wild animal populations can be attributed to 'density-dependent' effects. Density dependence occurs when population size exceeds availability of a limiting resource (e.g. food, shelter, space), and 'pulls' populations back towards their habitat's 'carrying capacity' (i.e. the state in which the population is using the full amount of a key limiting resource available to it) (Thresher, 1997). Carp control programs, regardless of the methods they use, that only remove the portion of the population that would have died anyway through density dependent processes will not drive sustained population declines; they only 'skim off the surplus' (Nuñez et al., 2012). Rather, effective carp control must kill individuals that would otherwise have survived density-dependent regulation. Population biologists refer to this type of mortality as 'additive', because deaths from the control method add to the natural mortality already experienced by the pest population (Nuñez et al., 2012).

Unfortunately, removing carp (and indeed most pest species) at a rate sufficient to induce additive mortality is challenging once they have attained high abundance across large geographic areas (Nuñez et al., 2012). Figure one explains this challenge graphically. The 'S'-shaped curve in Figure one is called a logistic growth curve, and provides a simplified representation of population growth in many fish species. The logistic curve illustrates a population's progression from the 'founder' stage, when it has just colonised a new habitat, through to carrying capacity, when the population is using the full amount of the limiting resource(s) available to it.

The bottom left end of the logistic curve shows the founder stage. Here, the population grows slowly because there are too few reproductively-capable adults to ensure consistently-successful spawning. Founder populations are prone to extinction through unpredictable events, such as cold snaps, that are unrelated to the relationship between population size and resource availability (i.e. these events are 'density independent'). A population at the founder stage generally provides good prospects for control through physical removal. Carp in the Tasmanian lakes (see case study at section 3.3.4) were probably at the founder stage when control operations began (Thresher, 1997).

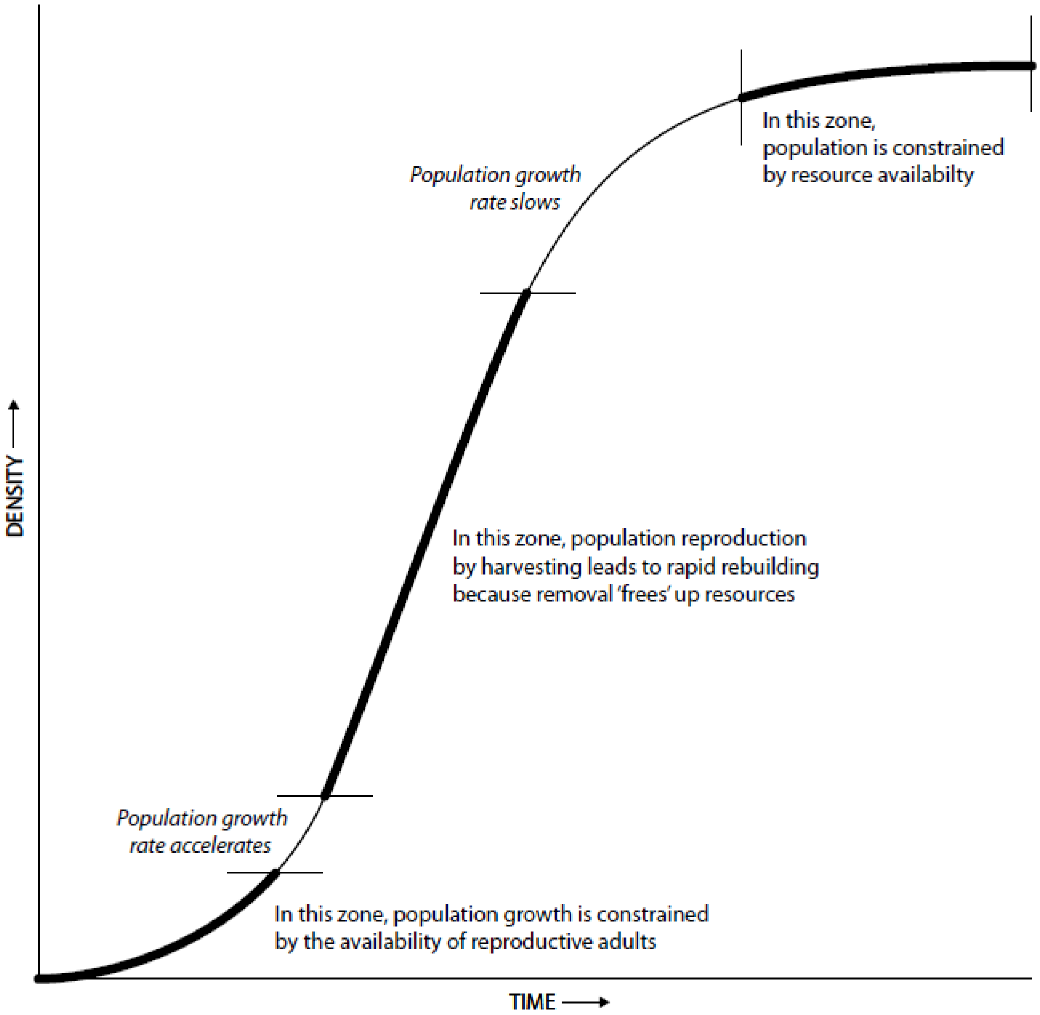

Figure 1: This 's'-shaped curve, called the logistic growth curve, approximates the growth trajectory of many fish populations through time. The bottom left portion of the curve shows slow growth as a 'founder' population becomes established in a new habitat. At this stage, population growth is limited by the abundance of reproductively-competent adults. Founder populations are susceptible to extinction through unpredictable events such as extreme weather or disease. At the top right portion of the curve, the population is at 'carrying capacity' (i.e. the habitat cannot support any more individuals). Therefore, population growth is limited by resource availability rather than reproduction. When a population is at carrying capacity, removing individuals often stimulates rapid population growth, because the removals 'free up' resources for reproduction and growth. In the middle portion of the curve, growth is limited by neither resource availability nor reproduction, and the population has a strong tendency to grow. To control a pest species at carrying capacity (top right of the curve), management actions would ideally push abundance all the way back down the curve to the bottom left 'founder' stage, where control, and even eradication, is more achievable. Depleting a population at carrying capacity back to the founder stage is, however, challenging, because it requires inflicting sufficient mortalities to overcome the population's natural tendency to grow as removals free up resources.

The top right end of the logistic curve shows a population at carrying capacity. Here, the population has grown so that it is using limiting resources to the full extent possible. At carrying capacity, competition for resources among members of the same species reduces reproductive success and creates high mortality rates in both juveniles and adults (Thresher, 1997). During periods of high resource abundance, populations can exceed their environment's usual carry capacity, but are almost always fated to crash when resource availability sinks back to 'normal' levels.

The middle section of the logistic curve is most important for understanding the effects of physical removal on a population at carrying capacity. During this phase of population growth, reproductively-capable individuals have become sufficiently abundant that reproductive success no longer constrains population growth, yet the overall number of individuals is low relative to resource availability (Thresher, 1997). Consequently, the population can grow rapidly. The 'steepness' of the curve in this area shows that a short time interval sees a substantial increase in density. Most importantly, harvesting individuals from a population at carrying capacity tends to fuel rapid growth by 'freeing up' resources, shifting the population back into the middle, 'high growth' section of the curve (Thresher, 1997; Weber et al., 2016). Population growth that occurs when a population is released from density-dependence by harvesting is called 'compensatory growth' and has been demonstrated for North American carp populations (Weber et al., 2016). Carp removal, regardless of whether by fishing or a virus, needs to occur with sufficient intensity to move the population all the way back to the founder stage if long-term control is to be achieved.

Successfully reducing carp abundance also requires that removal occurs over all areas of carp's Australian distribution, and across all size classes (Brown et al., 2019). Failure in either area protects a portion of the population, facilitating compensatory reproduction and population rebuilding (Brown et al., 2019). These basic considerations apply to all forms of physical removal.

3.3. Approaches to physical removal

3.3.1. Deliberate overfishing

Deliberate overfishing has frequently been suggested as a control option for pest fish, given that (i) globally, overfishing has often occurred, even when the primary goal was sustainable management, and (ii) many pest fish, including carp, are edible or otherwise usable as a resource. While intuitively appealing, attempts to control pests by harvesting are often ineffective, and in some instances have increased pest abundance or distribution as communities begin to value pests as an income source (Nuñez et al., 2012; Pasko and Goldberg, 2014). Although carp are commercially fished in New South Wales, Victoria, and South Australia, there have been no coordinated, sustained attempts to reduce carp numbers using commercial fishing. However, the economic viability and impact on carp populations of commercial harvesting has been modelled for the Lachlan River (GHD, 2011). This modelling indicated that an annual commercial catch of 300 tonnes per year would be commercially viable, but would have little impact on carp abundance (GHD, 2011). During consultation with the NCCP, commercial fishers who target carp have indicated that realistic evaluation of the potential for harvest to reduce carp numbers has been hampered by regulatory barriers (i.e.

fishers are not allowed to fish to their full potential, thereby artificially limiting their capacity to reduce carp numbers).

The challenges and opportunities associated with harvest-based management differ depending upon whether harvesting is commercial (i.e. supply to markets), incentivised (operators paid, usually by a government agency, to remove the pest species), or on a recreational or volunteer basis (Nuñez et al., 2012; Pasko and Goldberg, 2014). Commercial fishers aim to make economic profits, and must therefore consider the cost of catching fish relative to market prices. Catching carp in remote and/or inaccessible locations will generally be expensive and time-consuming relative to more accessible locations, reducing expected returns. Yet fishing effort in these areas would be essential for population reduction (Brown et al., 2019. The profitability of commercial fishing also typically declines as the target species reduces in abundance, because catching rare or sparsely-distributed individuals is more time-consuming, and therefore more costly, than catching abundant fish.

For these reasons, it seems likely that carp harvesting to achieve population reduction would need to be incentivised rather than operating on a purely commercial basis. Incentive schemes have achieved localised success for some pest species, but need to be carefully structured to achieve management goals (Gosling and Baker, 1989). Incentives need to encourage increased fishing effort and continued catches as numbers decline, and, for carp, would need to ensure application of fishing effort in locations and size classes that might otherwise be economically unattractive.

Regardless of whether harvesting is conducted on a commercial or incentivised basis, creation of economic opportunities based on pest species can be problematic. Operators may be reluctant to eliminate the species upon which their income depends (Gosling and Baker, 1989; Nuñez et al., 2012; Pasko and Goldberg, 2014). In the United Kingdom (U.K.), innovative incentive structures facilitated eradication of coypu (a large, semi-aquatic rodent indigenous to South America) (Gosling and Baker, 1989). Funding for coypu trapping was made available for only ten years, and trappers were offered a bonus of up to three times their annual salaries if eradication was achieved. This bonus amount also reduced annually after six years had elapsed, encouraging trappers to strive for eradication (Gosling and Baker, 1989).

Commercial carp removal for control may not be effective as the sole control method. However, manual removal of carp using commercial fishing techniques could be applied as part of an integrated carp control program of control.

3.3.2. Community ‘carp buster’ events

Community-based carp fishing events provide opportunities to increase awareness of pest fish, but have little capacity to provide meaningful carp reductions (Norris et al., 2013). Research in the Queensland portion of the MDB found that carp buster events catch only a small proportion of the carp in a given location, occur over short time periods and restricted geographical areas, and tend not to capture juvenile carp (Norris et al., 2013). Collectively, these factors mean that carp buster events do not exert sustained pressure on all portions of the carp population, and allow ample opportunity for population rebuilding between events (Norris et al., 2013). Nonetheless, carp buster events play a useful role in carp control by increasing community awareness and raising funds that could contribute to more efficient forms of localised carp removal and to native fish habitat restoration (Norris et al., 2013). Carp buster events should therefore form part of an integrated carp control strategy.

3.3.3. Trapping

Several trap designs, of varying sophistication, durability, and intended permanence, have been developed and/or trialled for carp removal. Portable or temporary trap designs can be easily moved between locations in response to reports of high carp abundance, or perceived likely environmental benefits of localised carp reductions. Such designs are typically constructed from netting attached to a structural framework, and include traditional fishing gear types such a fyke nets, as well as purpose-built mesh carp traps incorporating a food dispenser and a mesh 'wing' that respectively attract and direct carp into the trap. The latter trap type is currently deployed by teams of Aboriginal rangers in the Balonne district of southern Queensland. The traps are designed to be set in low-flow, off-channel wetlands, and can be set for up to 10 days. The trapping program aims to temporarily reduce carp abundance in the habitat types used by small-bodied native fish, thereby improving spawning and recruitment opportunities for these species. The carp traps can capture 300 – 400 carp per set, with the largest recorded capture consisting of 900 carp. The effectiveness of these traps in meeting management objectives has not yet been formally evaluated.

Other, more permanent trap designs are usually installed along carp migration pathways, and are designed to exploit carp's migratory instincts and behavioural propensity to jump over and/or push through in-stream obstacles. The Williams carp separation cage, arguably the most successful carp trap design, has been trialled and refined over a ten-year period through a permanent installation at Lock 1 in the Murray River (Stuart and Conallin, 2018). Over the trial, the cage captured 723 tonnes of carp, and only two individual native fish (Stuart and Conallin, 2018). Catches are largest when carp are migrating to spawn, as they are strongly motivated to traverse in-stream obstacles at these times (Stuart and Conallin, 2018). In 2004, the Williams cage's inventors were awarded a Eureka Prize for excellence in research and innovation. A 'fleet' of Williams cages could potentially be installed on strategic fishways as part of an integrated carp control program (Stuart and Conallin, 2018).

3.3.4. Physical removal of carp from Tasmanian lakes: a carp control case study

The Tasmanian Government's campaign to eradicate carp from Lakes Crescent and Sorell illustrates features of an effective physical removal program. Carp were introduced into the two lakes during the early 1990s, possibly by anglers using small carp as live bait (Koehn et al., 2000). When carp were detected in the lakes, the Tasmanian Government decided to attempt eradication to protect the lakes' recreational and conservation values, and to prevent further spread of carp in the state.

Lakes Crescent and Sorell, and the carp populations inhabiting them, possessed features favourable to control by physical removal. Both lakes had water release structures in place, enabling isolation from downstream waterways. The lakes' carp populations were also almost certainly in the 'founder' stage, where population growth is limited by spawner biomass (i.e. the number of reproductively-capable adults) (Thresher, 1997). Founder populations are inherently susceptible to extinction through random events such as weather extremes, or through deliberate increases in mortality, such as through fishing (Thresher, 1997). The two lakes are also in regions that are climatically sub-optimal for carp (having temperatures lower than the optimum range in which carp spawn effectively), which means that populations are unlikely to rebuild rapidly following depletion (Koehn et al., 2000). These features indicated that physical removal had potential to successfully control carp.

Physical removal of carp from the Tasmanian lakes has been aided by some innovative technologies, including the 'Judas carp' approach, which uses sterile, radio-tagged male carp to locate spawning aggregations (Diggle et al., 2004). The Judas approach originated for control of terrestrial vertebrate pests that exhibit social behaviour, but are difficult to locate (for example, due to rugged or remote terrain) (Wilcox et al., 2004; Campbell and Donlans, 2005). A Judas animal, fitted with a radio collar or other locating device, is released into the wild, and, following its social instincts, seeks out other members of its species. The locating device 'betrays' the group's location, enabling destruction or capture. The Judas animal is usually allowed to escape to find more members of its species, repeating the cycle (Wilcox et al., 2004). The approach has been used on a range of terrestrial vertebrate pests including feral goats (Campbell and Donlans, 2005), pigs (Wilcox et al., 2004), donkeys (Woolnough et al., 2012), and starlings (Woolnough, et al., 2006). While generally useful, the degree of success achieved with the Judas approach depends upon various facets of the target species' behaviour (Woolnough et al., 2006). The Judas approach is not a stand-alone control method, but a means of improving the efficiency of physical removal.

The Judas carp approach proved useful in the Tasmanian lakes, enabling managers to find carp aggregations which could then be targeted with a variety of fishing gear types (Diggle et al., 2004). Sterilising the Judas carp with the fish equivalent of a vasectomy prevented them from spawning successfully, while leaving their reproductive instincts (and hence their desire to join spawning aggregations) intact. In the Tasmanian lakes, managers found that identifying three radio-tagged carp in a location signified an aggregation (Diggle et al., 2004).

Carp sex pheromones have also been used in the Tasmanian lakes to lure carp into traps (Centre for Invasive Species Solutions, 2014). A pheromone is a 'signalling chemical' that an animal produces and releases into the environment to communicate with others of its species. Sex pheromones indicate reproductive availability. Pheromone deployment involves surgical implantation of pheromone-releasing devices, called 'slow osmotic pumps' in carp. Implanted fish then become the 'bait' in a trap (GHD, 2011). Relatively little peer-reviewed information is available on the use of pheromone traps in carp control. However, pheromone trapping has formed part of the Tasmanian carp control strategy (Centre for Invasive Species Solutions, 2014). Pheromone trapping is only effective during spawning seasons, when male carp are actively searching for reproductively-ready females (Centre for Invasive Species Solutions, 2014). Perhaps surprisingly, a pheromone trapping trial at Lake Cargelligo (NSW) found that the use of pheromone-implanted carp in traps did not significantly increase trapping success (Centre for Invasive Species Solutions, 2014). Reasons underlying differences in pheromone-trapping success between Tasmania and NSW are unclear.

Carp were eradicated from Lake Crescent in 2007, but are still present at low densities in Lake Sorell. The Tasmanian Inland Fisheries Service continues to pursue carp eradication in Lake Sorell, and is confident that this objective will be achieved. The intense fishing effort to which carp in the lakes have been subjected is also reducing the population's genetic diversity and viability, aiding control efforts (Inland Fisheries Service, 2018). Carp management in the two lakes has cost approximately $10 million over 22 years.

3.3.5. Physical removal: key issues summary

Controlling an established pest fish with a complex population structure and demographic traits conferring high resilience is challenging, regardless of the method used. However, the pest population traits outlined in Section 3.2 above pose particular challenges to control by physical removal, because operators must access all parts of the species' range, exert constant pressure on the population, and remove individuals at a rate sufficient to overcome compensatory processes and induce additive mortality. For these reasons, physical removal has worked most successfully in closed carp populations, such as those in the Tasmanian Lakes. Many of these challenges also apply either wholly or partly to biocontrol; for example, virus-induced mortalities must be additive rather than compensatory if they are to induce long-term declines. Furthermore, none of these challenges preclude use of various physical removal methods as part of an integrated carp control strategy. Indeed, the challenges inherent in controlling an established pest mean that deploying a diverse suite of control approaches will be necessary to drive and maintain sustained carp suppression.

3.4. Biological control

3.4.1 Previous biocontrol approaches

Viral biocontrol of carp using Spring Viraemia of Carp Virus (SVCV), a single-stranded RNA virus of the family Rhabdoviridae, was considered as a control option during the 1990s (Crane and Eaton, 1997). Concerns over the virus's species-specificity and efficacy prevented ongoing investigation of SVCV as a carp control option for Australia (Crane and Eaton, 1997; Thresher et al., 2013).

3.4.2 Genetic biocontrol

In contrast to 'classical' biological control that uses parasites or pathogens (disease-causing organisms) to control pests, genetic biocontrol works by changing the target species' genetic material to reduce reproductive success or survival. Several genetic biocontrol technologies are potentially applicable to carp, most likely in combination with other control methods. These techniques require research investment, probably over timescales approaching a decade, to confirm their applicability to carp in Australia and prepare for deployment. Potential genetic biocontrol options for carp in Australia are discussed in issues paper seven.

4.0. The carp virus as a potential biocontrol agent

4.1. Carp virus background

The carp virus emerged as a virulent pathogen of aquacultured carp in Germany and Israel during the mid-1990s, and has since caused major, but usually non-recurring, mortalities among wild carp in Japan, North America, and South Africa (Boutier et al., 2015; Thresher et al., 2018). The carp virus is a double-stranded DNA virus of the family Alloherpesviridae. Mechanisms underpinning CyHV-3 emergence are unclear, but the virus may have circulated innocuously among wild carp for many centuries, before conditions in intensive aquaculture increased virulence through an unidentified evolutionary change (Uchii, et al., 2013). Evolution of the carp virus, in the context of potential host switching, is addressed in issues paper three.

Although currently occurring in 33 countries globally, the carp virus has never been deliberately used a biological control agent. Rather, disease outbreaks have resulted from the virus's unwanted entry to valued populations of carp (including koi), or its unintended and unplanned introduction to invasive populations that are viewed as pests (Gibson-Reinemer et al. 2017).

International outbreaks prompted interest in CyHV-3 as a potential biological control agent for carp in Australia. The Invasive Animals Cooperative Research Centre (IACRC) funded CSIRO researchers to investigate the virus in relation to two prerequisites for a biocontrol agent; host specificity and capacity to kill the target organism (McColl and Crane, 2013; McColl et al., 2016).

4.2. Is the virus species-specific?

The first key question about the carp virus was whether it has potential to infect any species other than carp. Australian experiments testing the susceptibility of non-target species (NTS) to CyHV-3 infection exposed 22 species, comprising 13 native fish species, introduced rainbow trout, a lamprey, a crustacean (freshwater yabbies), two frog species, two native reptiles (a freshwater turtle and a water dragon), chickens (a representative bird), and mice (a representative mammal) to the virus (McColl et al., 2016). Wherever possible, both adults and juveniles of each species were tested, with exposure occurring through injection of virus into the body cavity, and/or by addition of virus to the test animals' tank water ('bath') (McColl et al., 2016). Some species, such as Australian smelt (a small native fish), were unable to survive the physical stress associated with direct injection, and therefore only underwent bath exposure.

The standard for identifying infection was the presence of carp virus mRNA in the cells of non-target species (McColl et al., 2016). Viruses are essentially sequences of DNA enclosed in a protein coat, and lack any means of reproducing themselves (replicating) unless they can invade a host cell, and use the 'cellular machinery' (organelles) contained therein to make copies of viral DNA. However, DNA cannot be copied directly, but must first be transcribed into mRNA. The essential role of mRNA as an intermediary in viral replication means that detection of viral mRNA strongly indicates that the virus has invaded host cells and is replicating (i.e. has infected the host). Thus, evidence of replication was the definition of infection used in the CSIRO non-target susceptibility trials (McColl et al., 2016). In contrast, detecting a virus's DNA in a potential host's tissues only proves that the virus is present, not that it is replicating.

The Reverse Transcription Polymerase Chain Reaction (RT-PCR) of Yuasa et al. (2012), which was designed to detect carp virus mRNA, was used to search for evidence of replicating carp virus in NTS as part of the CSIRO trials (McColl et al., 2016). Various molecular techniques used to detect the carp virus and diagnose infection, including the Yuasa et al. (2012) RT-PCR, are discussed in more detail in issues paper three. The RT-PCR did not detect carp virus mRNA in any of the non-target test animals, although some individuals tested positive for carp virus

DNA (McColl et al., 2016). Some native fishes exposed to the virus showed unexpectedly high mortalities (McColl et al., 2016). RT-PCR did not detect carp virus mRNA in any of these fishes, indicating that they were not infected by the virus, but the mortalities remain unexplained.

While the initial work by McColl et al. (2016) was promising and formed part of the argument for investing in the NCCP, it also identified some important areas requiring more detailed investigation. The NCCP consequently commissioned a review of best-practice methods in trials designed to test the susceptibility of animals to infection by viruses ('viral challenge trials'). Although the review is still in progress, preliminary conclusions indicate that further testing is likely to be recommended. Issues paper three discusses species specificity and host-switching risk in more detail.

4.3. Does the virus kill carp effectively?

The CSIRO research described above (McColl et al., 2016) also investigated the virus's capacity to effectively kill carp. Carp were exposed to the virus at various concentrations using the same techniques as employed in the non-target susceptibility trials (injection and bath). The experiment indicated that exposing carp to the highest possible virus concentration was important to maximise mortality (from McColl and Crane, 2013). Carp mortalities varied with virus delivery method (injection or bath) and virus concentration (McColl and Crane, 2013).

An additional trial was also conducted to determine whether virus-induced mortality varies with carp size/age. Over four separate experiments, carp of 2.6, 12.1, 18.5, and 30 cm in length were exposed to the virus by injection, bath, and/or contact with infected individuals (two carp exposed via the latter pathway) (McColl and Crane, 2013). Although carp numbers in each of the four experiments were low (ranging from 6 – 20 individuals), results indicated that mortality rates are likely to be highest in smaller, younger carp (McColl and Crane, 2013).

4.4. Emergence of the NCCP

The CSIRO non-target susceptibility and carp lethality research indicated that the carp virus is specific to carp, and can kill carp (particularly young individuals) effectively. Thus, the virus seemed to satisfy the base prerequisites for a biological control agent. Information requirements for implementing a biocontrol program, however, greatly exceed knowledge of host-specificity and laboratory-measured efficacy. Transmission patterns and lethality under field conditions must be understood, systems for virus production and dissemination developed, and potential ecological, social, and economic risks, including risks to water quality following carp kills, assessed. These considerations then need to be incorporated into a cost-benefit analysis (discussed in more detail in issues paper six) to inform an evidence-based decision on the viability of virus release.

Biological control of a pest fish species has never been attempted globally, so numerous knowledge gaps prevented an immediate assessment of whether the virus's apparent potential, as indicated by the CSIRO trials, equate to safe and effective deployment in Australian ecosystems. To further investigate the feasibility and effectiveness of the carp virus as a biocontrol agent the Australian Government therefore invested $15 million in the development of the NCCP, including a program of research, planning, and community consultation.

4.5. Potential for integrated measures to control carp

If virus release is viable, CyHV-3 may drive an initial reduction in carp numbers over approximately 8 – 10 years. Other control measures (e.g. physical removal) could then capitalise on this reduction to sustain long-term suppression. Bringing an integrated suite of control measures to bear on a carp population already reduced by viral disease could potentially achieve greater reductions than would have been possible had the same set of measures been deployed on a larger pre-virus population. Virus-induced population suppression may also initiate ecological recovery in some systems. However, improvements in river health will often be reliant upon ecological restoration measures that extend beyond carp control.

5.0 Conclusions

Although carp have been present in Australia since the mid-19th century, they were not recognised as serious pests until the mid-1960s, as the Boolarra Strain carp began expanding their geographic range and abundance (Koehn et al., 2000; Koehn, 2004). Carp now occupy most of the MDB, and many coastal catchments (Koehn, 2004). Because carp inhabit many different habitat types, occur alongside numerous other environmental stressors, and fluctuate in abundance through time both within and between locations, their ecological impacts vary between ecosystems (Weber and Brown, 2009; Kaemingk et al., 2016; Vilizzi et al, 2014. 2015). However, there is now strong evidence that carp negatively affect ecosystems (Weber and Brown, 2009; Vilizzi et al., 2015).

Potential ecological impacts of carp in Australia include increased turbidity, and decreased abundance of macrophytes, invertebrates, and native fishes (Sheldon and Walker, 1993; Vilizzi et al., 2014; Kopf et al., 2018). These impacts may result from carp's interaction with the fundamental ecological processes of nutrient cycling and primary production (bottom-up impacts), or occur as a direct result of carp predation on invertebrates and zooplankton (top-down impacts) (Weber and Brown, 2009; Vilizzi et al., 2015; Akhurst et al., 2017). Bottom-up and top-down impacts may also interact. The ecological concept called the middle-out framework encapsulates the idea that carp impacts can result from multiple, and sometimes interacting pathways (Weber and Brown, 2009; Kaemingk et al., 2016) Some recent research has also identified that carp may monopolise energy low in the food chain, thereby reducing opportunities for Australian native fish to grow and reproduce (Kopf et al., 2018). There is relatively little research on this class of impacts, but it may be one of the most important pressures carp exert on Australian aquatic ecosystems.

Numerous control methods have been proposed or trialled for carp in Australia since the 1960s (Koehn et al., 2000). None have delivered widespread or lasting carp suppression. Some methods, like indiscriminate poisoning, are inappropriate for broadscale control, while others, like sustained harvesting, have not been implemented in a coordinated, strategic manner. Regardless of the method used, controlling a pest species that has attained high densities over broad areas is challenging because the population dynamics of most pest species (including carp) allow rapid rebuilding in response to losses (Thresher, 1997; Nuñez et al., 2012; Pasko and Goldberg, 2014; Weber et al., 2016). These population dynamics are one of the reasons pests are effective at invading and colonising new habitats (e.g. Koehn, 2004). Control must remove enough individuals to induce additive mortality and overcome compensatory responses (Nuñez et al., 2012; Weber et al., 2016). The Tasmanian experience of carp control through physical removal illustrates features of a successful physical removal program, while also highlighting the challenges inherent in implementing such an approach in much larger, and more complex mainland carp populations. Nonetheless, coordinated use of various physical removal approaches will undoubtedly have an ongoing role in a coordinated carp control program.

The carp virus emerged as a potential biocontrol agent for carp in Australia after causing mortalities in both farmed and wild carp internationally. CSIRO research provided preliminary indications that the virus infects only carp, and can kill carp effectively (McColl and Crane, 2013; McColl et al., 2016). Further work was, however, to undertake additional research, planning, and community consultation to inform decision-making on carp control in Australia, and the NCCP was formed on this basis.

6.0 References

Akhurst, D.J., Jones, G.B., Clark, M. & Reichelt-Brushett, A. (2017) Effects of fish and macrophytes on phytoplankton and zooplankton community structure in a subtropical freshwater reservoir. *Limnologica* 62, 5 – 18. http://dx.doi.org/10.1016/j.limno.2016.09.009

Bice, C.M. & Zampatti, B.P. (2011) Engineered water level management facilitates recruitment of non-native common carp, *Cyprinus carpio*, in a regulated lowland river. *Ecological Engineering* 37, 1901 – 1904. http://dx.doi.org/10.1016/j.ecoleng.2011.06.046

Boutier, M., Ronsmans, M., Rakus, K., Jazowiecka-Rakus, J., Vancsok, C., Morvan, L., Peñaranda, M.M.D., Stone, D.M., Way, K., van Beurden, S., Davison, A.J. & Vanderplasschen, A. (2015). Chapter four – Cyprinid herpesvirus 3: an archetype of fish alloherpesviruses. *Advances in Virus Research* 93, 161 – 256.

Brown, P., Wisniewski, C. & Gilligan, D. (2019). *The role of commercial fishing in control of invasive freshwater fish species*. Draft final report to the National Carp Control Plan.

Campbell, K. & Donlan, C.J. (2005). Feral goat eradication of islands. *Conservation Biology* 19, 1362 – 1374. DOI: 10.1111/j.1523-1739.2005.00228.x

Catford, J.A., Downes, B.J., Gippel, C.J. & Vesk, P.A. (2011) Flow regulation reduces native plant cover and facilitates exotic invasion in riparian wetlands. *Journal of Applied Ecology* 48, 432 – 442. doi: 10.1111/j.1365-2664.2010.01945.x

Centre for Invasive Species Solutions (2014). *Case study: carp pheromone attractant trials*. Web page. https://www.pestsmart.org.au/carp-pheromone-attractant-trials/. Accessed 24/03/2019

Crane, M.S. & Eaton, B.T. (1997). Immuno-contraceptive control for carp. In: J. Roberts & R. Tilzey (eds) *Controlling carp exploring the options for Australia.* Proceedings of a workshop 22 – 24 October 1996, Albury. CSIRO Land and Water, Griffith NSW.

Diggle, J., Day, J., Bax, N. (2004). *Eradicating European carp from Tasmania and implications for national European carp eradication*. Inland Fisheries Service, Hobart. Last accessed 24/03/2019 at http://www.frdc.com.au/Archived-Reports/FRDC%20Projects/2000-182-DLD.pdf

GHD (2011). *Feasibility of commercial carp harvesting in the Lachlan River Catchment*. Final Report, October 2011. Report to the Lachlan Catchment Management Authority.

Gibson-Reinemer, D.K., Chick, J.H., VanMiddlesworth, T.D., VanMiddlesworth, M. & Casper, A.F. (2017) Widespread and enduring demographic collapse of invasive common carp (*Cyprinus carpio*) in the upper Mississippi River system. *Biological Invasions* DOI 10.1007/s10530-017-1405-5.

Gosling, L.M. & Baker, S.J. (1989). The eradication of muskrats and coypus from Britain. *Biological Journal of the Linnean Society* 38, 39 – 51.

Haynes, G.D., Gilligan, D.M., Grewe, P. & Nicholas, F.W. (2009). Population genetics and management units of invasive common carp *Cyprinus carpio* in the Murray-Darling Basin, Australia. *Journal of Fish Biology* 75, 295 – 320. doi:10.1111/j.1095-8649.2009.02276.x

Inland Fisheries Service (2018). *Carp management program quarterly report October to December 2018*. Accessed at https://www.ifs.tas.gov.au/media/publications/CMP_OCTOBER-DECEMBER_2018.pdf 24/03/2019.

Kaemingk, M.A., Jolley, J.C., Paukert, C.P., Willis, D.W., Henderson, K., Holland, R.S., Wanner, G.A. & Lindvall, M.L. (2016) Common carp disrupt ecosystem structure and function through middle-out effects. *Marine and Freshwater Research*. http://dx.doi.org/10.1071/MF15068

Koehn, J.D. (2004) Carp (*Cyprinus carpio*) as a powerful invader in Australian waterways. *Freshwater Biology* 49, 882 – 894. http://dx.doi.org/10.1111/j.1365-2427.2004.01232.x

Koehn, J., Brumley, A. & Gehrke, P. (2000) *Managing the Impacts of Carp*. Kingston, Australian Capital Territory: Bureau of Rural Sciences.

Koehn, J.D., Todd, C.R., Zampatti, B.P., Stuart, I.G., Conallin, A., Thwaites, L. & Ye, Q. (2018) Using a population model to inform the management of river flows and invasive carp (*Cyprinus carpio*). *Environmental Management* 61, 432 – 442. DOI 10.1007/s00267-017-0855-y

Kopf, R.K., Humphries, P., Bond, N.R., Sims, N.C., Watts, R.J., Thompson, R.M., Hladyz, S., Koehn, J.D., King, A.J., McCasker, N. & McDonald, S. (2018). Macroecology of fish community biomass – size structure: effects of invasive species and river regulation. *Canadian Journal of Fisheries and Aquatic Sciences* 76, 109 – 122. https://doi.org/10.1139/cjfas-2017-0544

Mazumder, D., Johansen, M., Saintilan, N., Iles, J., Kobayashi, T., Knowles, L. & Wen, L. (2012) Trophic shifts involving native and exotic fish during hydrologic recession in floodplain wetlands. *Wetlands* 32, 267 – 275. DOI 10.1007/s13157-011-0262-8

McColl, K.A. & Crane, MStJ. (2013). *Cyprinid herpesvirus 3, CyHV-3: its potential as a biological control agent for carp in Australia.* PestSmart Toolkit publication, Invasive Animals Cooperative Research Centre, Canberra, Australia.

McColl, K.A., Sunarto, A., Slater, J., Bell, K., Asmus, M., Fulton, W., Hall, K., Brown, P., Gilligan, D., Hoad, J., Williams, L.M. & Crane, M. St J. (2016) Cyprinid herpesvirus 3 as a potential biological control agent for carp (*Cyprinid carpio*) in Australia: susceptibility of non-target species. *Journal of Fish Diseases*, doi:10.1111/jfd.12591.

Norris, A., Chilcott, K. & Hutchison, M. (2013) *The role of fishing competitions in pest fish management.* PestSmart Toolkit publication, Invasive Animals Cooperative Research Centre, Canberra, Australia.

Nuñez, M.A., Kuebbing, S., Dimarco, R.D. & Simberloff, D. (2012). Invasive species: to eat or not to eat, that is the question. *Conservation Letters* 5, 334 – 341.

Pasko, S. & Goldberg, J. (2014). Review of harvest incentives to control invasive species. *Management of Biological Invasions* 5, 263 – 277. doi: http://dx.doi.org/10.3391/mbi.2014.5.3.10

Pinto, L., Chandrasena, N., Pera, J., Hawkins, P., Eccles, D. & Sim, M. (2005) Managing invasive carp (*Cyprinus carpio* L.) for habitat enhancement at Botany Wetlands, Australia. *Aquatic Conservation: Marine and Freshwater Ecosystems* 15, 447 – 462. DOI: 10.1002/aqc.684

Sheldon, F. & Walker, K.F. (1993) Pipelines as a refuge for freshwater snails. *Regulated Rivers: Research and Management* 8, 295 – 299.

Sierp, M.T., Qin, J.G. & Recknagel, F. (2009) Biomanipulation: a review of biological control measures in eutrophic waters and the potential for Murray cod *Maccullochella peelii peelii* to promote water quality in temperate Australia. *Reviews in Fish Biology and Fisheries* 19, 143 – 165. DOI 10.1007/s11160-008-9094-x

Stuart, I.G. & Conallin, A.J. (2018) Control of globally invasive common carp: an 11-year commercial trial of the Williams' cage. *North American Journal of Fisheries Management DOI: 10.1002/nafm.10221*

Stuart, I.G. & Jones, M. (2006) Large, regulated forest floodplain is an ideal recruitment zone for non-native common carp (*Cyprinus carpio* L.). *Marine and Freshwater Research* 57, 333 – 347.

Thresher, R.E. (1997). Physical removal as an option for the control of feral carp populations. In: J. Roberts & R. Tilzey (eds) *Controlling carp exploring the options for Australia.* Proceedings of a workshop 22 – 24 October 1996, Albury. CSIRO Land and Water, Griffith NSW.

Thresher, R.E., Allman, J. & Stremick-Thompson, L. (2018) Impacts of an invasive virus (CyHV-3) on established invasive populations of common carp (*Cyprinus carpio*) in North America. *Biological Invasions*, DOI: https://doi.org/10.1007/s10530-017-1655-2

Thresher, R.E., Hayes, K., Bax, N.J., Teem, J., Benfey, T.J. & Gould, F. (2018). Genetic control of invasive fish: technological options and its role in integrated pest management. *Biological Invasions* DOI 10.1007/s10530-013-0477-0

Uchii, K., Minamoto, T., Honjo, M.N. & Kawabata, Z. (2004). Seasonal reactivation enables *Cyprinid herpesvirus 3* to persist in a wild host population. *FEMS Microbiology and Ecology* 87, 536 – 542.

Yuasa, K., Kurita, J., Kawana, M., Kiryu, I., Oseko, N. & Sano, M., (2012). Development of mRNA-specific RT-PCR for the detection of koi herpesvirus (KHV) replication stage. *Diseases of Aquatic Organisms* 100, 11 – 18. doi: 10.3354/dao02499

Vilizzi, L., Tarkan, A.S. & Copp, G.H. (2015) Experimental evidence from Causal Criteria Analysis for the effects of common carp *Cyprinus carpio* on freshwater ecosystems: a global perspective. *Reviews in Fisheries Science and Aquaculture* 23, 253 – 290. DOI: 10.1080/23308249.2015.1051214

Vilizzi, L., Thwaites, L.A., Smith, B.B., Nicol, J.M. & Madden, C.P. (2014) Ecological effect of common carp (*Cyprinus carpio*) in a semi-arid floodplain wetland. *Marine and Freshwater Research* 65, 802 – 817. http://dx.doi.org/10.1071/MF13163

Weber, M.J. & Brown, M.L. (2009) Effects of common carp on aquatic ecosystems 80 years after "Carp as a Dominant": ecological insights for fisheries management. *Reviews in Fisheries Science* 17, 524 – 537. 10.1080/10641260903189243

Weber, M.J., Hennen, M.J., Brown, M.L., Lucchesi, D.O. & St. Sauver, T.R. (2016). Compensatory response of invasive common carp *Cyprinus carpio* to harvest. *Fisheries Research* 179, 168 – 178. http://dx.doi.org/10.1016/j.fishres.2016.02.024

Wilcox, J.T., Aschehoug, E.T. & Scott, C.A. (2004). A test of the Judas technique as a method for eradicating feral pigs. *Transactions of the Western Section of the Wildlife Society* 40, 120 – 126.

Woolnough, A.P., Hampton, J.O., Campbell, S., Lethbridge, M.R., Boardman, W.S.J., Sharp, T. & Rose, K. (2012). Field immobilization of feral 'Judas' donkeys (*Equus asinus*) by remote injection of medetomidine and ketamine and antagonism with atipamezole. *Journal of Wildlife Diseases* 48, 435 – 443.

Woolnough, A.P., Lowe, T.J. & Rose, K. (2006). Can the Judas technique be applied to pest birds? *Wildlife Research* 33, 449 – 455. https://doi.org/10.1071/WR06009

Figure captions

Figure 1: This 's'-shaped curve, called the logistic growth curve, approximates the growth trajectory of many fish populations through time. The bottom left portion of the curve shows slow growth as a 'founder' population becomes established in a new habitat. At this stage, population growth is limited by the abundance of reproductively-competent adults. Founder populations are susceptible to extinction through unpredictable events such as extreme weather or disease. At the top right portion of the curve, the population is at 'carrying capacity' (i.e. the habitat cannot support any more individuals). Therefore, population growth is limited by resource availability rather than reproduction. When a population is at carrying capacity, removing individuals often stimulates rapid population growth, because the removals 'free up' resources for reproduction and growth. In the middle portion of the curve, growth is limited by neither resource availability nor reproduction, and the population has a strong tendency to grow. To control a pest species at carrying capacity (top right of the curve), management actions would ideally push abundance all the way back down the curve to the bottom left 'founder' stage, where control, and even eradication, is more achievable. Depleting a population at carrying capacity back to the founder stage is, however, challenging, because it requires inflicting sufficient mortalities to overcome the population's natural tendency to grow as removals free up resources.