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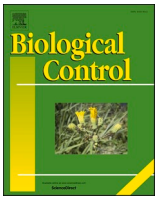

Bioprospecting for biological control agents for invasive tilapia in Australia

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HIGHLIGHTS

- Mozambique tilapia is listed in the top 100 of the world's worst invasive species.
- We used a robust framework to assess the safety and efficacy of viral biocontrol.
- Tilapia lake virus has been considered as the most promising biocontrol agent.
- We have identified the essential information required for biocontrol of tilapia.

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ABSTRACT

Originating in Africa, tilapia (Pisces, *Cichlidae*) now have a worldwide distribution and are both a prime model system for evolutionary biology and an important aquaculture species in over 135 countries. In contrast, Mozambique tilapia (*Oreochromis mossambicus*) is also listed in the top 100 of the world's worst invasive alien species and has been documented to have severe impacts on freshwater ecosystems primarily through displacement of native species and habitat alteration. In Australia, both *O. mossambicus* and the lesser-known spotted tilapia (*Tilapia mariae*) have established significant populations within Queensland waters, and recent incursions into northern New South Wales are of great concern. Eradication attempts using a combination of electrofishing and piscicide (poison) are rarely successful in open waterways, and given their invasive nature, there is a lack of demonstrated broad-scale effective control mechanisms for tilapia. Biological control (biocontrol), where it is feasible can be a cost-effective, a safe (species specific) and practical solution to managing invasive species because it does not require reapplication of chemicals or poisons, and once established should be self-sustaining. Based on the development of previous viral biocontrol strategies for rabbits and carp, we used a robust assessment framework for bioprospecting of biocontrol agents and found that tilapia lake virus (TiLV), and possibly tilapia parvovirus (TiPV), may offer the potential for biocontrol for invasive tilapia in Australia. TiLV causes high mortality in wild and cultured tilapia, but not in other species, and spreads through a waterborne route - an important transmission pathway for a successful viral biocontrol of fish. However, safety and efficacy, two major concerns for a successful biocontrol virus, need to be taken into consideration before the use of any exotic biocontrol virus is considered. Herein, we describe a systematic approach to assess known pathogens for their suitability as potential agents for biological control of tilapia and outline the possible next steps to further investigate the top candidates.

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1. Introduction

Tilapia refers to a group of subtropical to tropical tilapiine fish of the family *Cichlidae*, one of the most species-rich families of vertebrates (Kocher, 2004). Tilapia are grouped into three genera according to parental care patterns: *Oreochromis* (maternal mouthbrooders), *Sarotherodon* (paternal or biparental mouthbrooders), and *Tilapia* (substrate-spawners) (Trewavas, 1982a, Trewavas, 1982b). The rapid radiation of cichlid fish in their origin, the East Africa Great Lakes, resulted in the evolution of almost 2000 unique species in the past 10 million years, making the African cichlids an ideal model system for studying the mechanism of vertebrate evolution and speciation (Kocher, 2004, Seehausen, 2006, Trewavas, 1947). The adaptive nature of cichlids also contributed to the successful spread of tilapia worldwide. They have been introduced into five continents (Asia, North and South America, Europe and Australia) for reasons including biological control of aquatic weeds and insects, as ornamental species, to augment capture fisheries, and as an aquaculture commodity (Canonico et al., 2005, De Silva et al., 2004). They are now the second most important aquaculture commodity after carp (FAO, 2019), despite also being listed in the Global Invasive Species Database among the top 100 of the world's worst invasive alien species (GISD, 2006, Lowe et al., 2000).

Tilapia culture has expanded worldwide, initially with Mozambique tilapia, *Oreochromis mossambicus*, and then the more productive Nile tilapia, *O. niloticus*. Currently, tilapia are farmed in over 135 countries with global production estimated at 4.5 Mt and valued at US$7.5 billion (FAO, 2019). Tilapia, also known as the 'aquatic chicken' because they offer affordable and high-yield source of protein, exhibit high value aquaculture traits including high fecundity, rapid growth rate, tolerance to adverse water quality, and relative resistance to disease and other stressors (De Silva et al., 2004). Because they can be raised in a wide range of production systems – from subsistence backyard ponds to high intensity farms - they have made a significant contribution to food production, poverty alleviation and livelihood support in Asia and the Pacific nations (De Silva et al., 2004).

Mozambique tilapia are maternal mouthbrooders (Trewavas, 1982a, Trewavas, 1982b). They can grow up to 40 cm long and 1.1 kg, and are considered a "model invader" because they are aggressive, have extraordinary environmental adaptability, phenotypic plasticity, high hybridization capacity and rapid reproduction (Pérez et al., 2006). They are considered an invasive species in Australia, and also in the Bahamas, Dominican Republic, Mexico and the United States of America (USA) (GISD, 2006). In Australia, tilapia have caused severe damage to the natural environment primarily through displacement of native species, habitat alteration, predation, and as a vector of diseases and non-native parasite transmission (Hutchison et al., 2011, IA-CRC, 2012a, Russell et al., 2012b, Russell et al., 2010, Wilson et al., 2019). A study conducted in Queensland (Greiner and Gregg, 2008) suggested that the current economic impact costs of tilapia may lie between A$1.2 million and A $13.6 million per annum (2020/21 dollar terms). If targeted efforts to control tilapia are not undertaken, the economic costs of tilapia in Queensland could increase to over A$35.4 million per annum (Hardaker and Chudleigh, 2021). Further, it is likely that, on a national scale, the impact costs could be significantly higher if tilapia are allowed to spread into other key Australian waterways, in particular to the Murray-Darling Basin (MDB).

Despite the importation of live tilapia into Australia being prohibited since 1963, the ornamental *O. mossambicus* from either Singapore or Indonesia were released by a Brisbane aquarist in 1977 (Bluhdorn and Arthington, 1989, McKay, 1977, McKay, 1978). Since then, the species has been reported to establish in many eastern catchments in Queensland, from Brisbane to Cairns (Fig. 1). The population in the Burnett catchment is of particular concern since this catchment is only two kilometres from the MDB watershed. Another area at high risk of invasion is the Gulf of Carpentaria (GoC) (IA-CRC, 2012b), in which both *T. mariae* and *O. mossambicus* recently established in the Walsh River catchment in 2017 and 2019, respectively (B. Holmes, *unpubl. data*). In addition, the species has also been established in Western Australia in Geraldton in 1978 and later in the Gascoyne, Chapman, Minilya and Lyndon Rivers, all of which constitute part of the Pilbara Drainage (Morgan et al., 2004).

T. mariae is a freshwater and estuarine cichlid native to West Africa and has become established in Australia, the United States and Russia (Courtenay and Robins, 1973, Ivoylov, 1986, Cadwallader et al., 1980). In contrast to *O. mossambicus*, which is a maternal mouthbrooder, *T. mariae* is a substrate-spawner – the females lay their eggs on hard substrate where they are fertilised by males (Russell et al., 2012a). Owing to its relatively low growth rate and fecundity, high natural mortality and

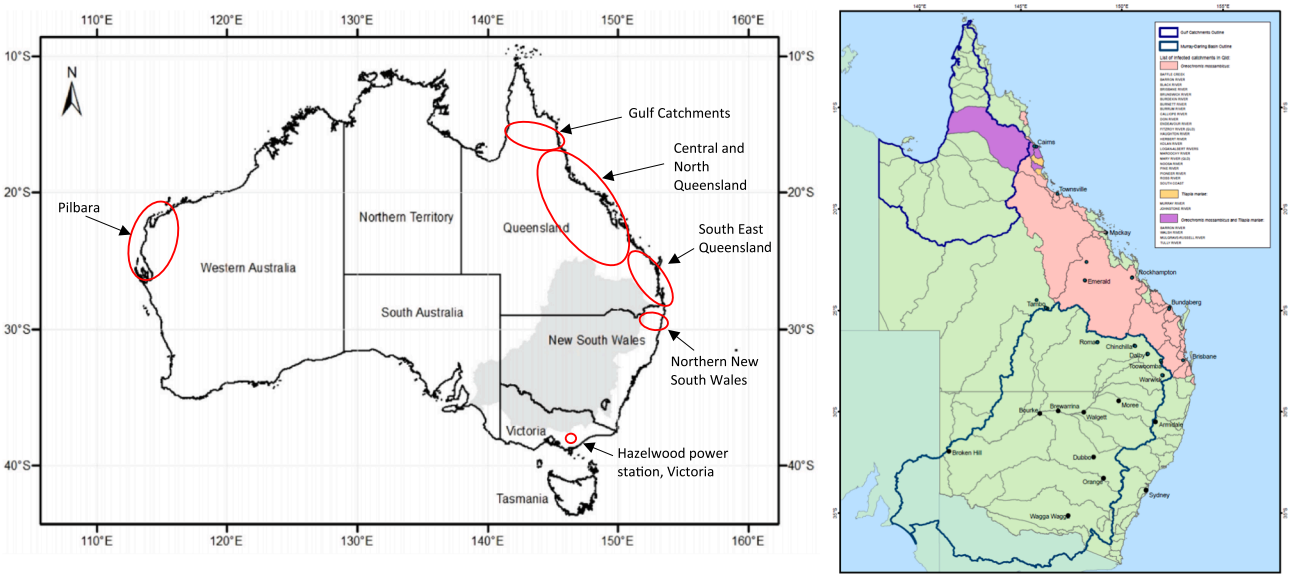

Fig. 1. Geographical distribution of tilapia in Australia. Left panel: red circles indicate approximate spread of tilapia across Australia (adapted from (Jha et al., 2013)). Right panel: *Oreochromis mossambicus* and *Tilapia mariae* distribution in Queensland (Source: Queensland Department of Agriculture and Fisheries). Blue borders indicate the Murray Darling Basin (in the south), and the Gulf of Carpentaria (in the north). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

small maximum size (32 cm long and 550 g) compared to other tilapia species, it is not extensively cultured (Bradford et al., 2011). Nevertheless, the attractively coloured *T. mariae* is a desirable ornamental fish and is most likely present in aquaria in many countries outside its natural range. When *T. mariae* was introduced to Australia is unclear (Bradford et al., 2011). The species was first found in a cooling pond of the Hazelwood power station in temperate Victoria in 1978 (Cadwallader et al., 1980). During the 1980s, the species was also detected near Cairns, North Queensland, and has since become established in surrounding river catchments and estuaries between Innisfail and Cairns (Webb, 2007). Recent spread of the species to the western-flowing Walsh River in North Queensland in 2017 has increased the risk of invasion across the GoC catchments and across to the Northern Territory in northern Australia (Fig. 1).

Nile tilapia is a highly invasive fish in more than 100 countries but is not yet established in Australia (De Silva et al., 2004, GISD, 2021, Valdez-Moreno et al., 2019, Welch, 2020). However, because of its mouthbrooding reproductive strategy and environmental adaptability, *O. niloticus* presents the same significant risk as *O. mossambicus* if found in Australia. Nile tilapia have been reported to cause severe harm to native biodiversity and ecosystems into which they are introduced (Canonico et al., 2005). These include alteration of water quality, eutrophication, and predation of eggs and young of other fish species which may lead to extinction of native fish species.

2. Management of invasive tilapia in Australia

While there is now an effective environmental DNA (eDNA) surveillance tool (Noble et al., 2015) for early detection and mapping of the distribution of tilapia, current management mechanisms are inadequate to control tilapia once establishment has occurred. Indeed, it is now clear that current education programs are failing to stop tilapia spread, and options for management post-incursion are extremely limited. Eradication is routinely attempted by using a combination of electrofishing and piscicide, but is rarely successful in open waterways because of the invasive nature of tilapia. Eradication was thought to be achieved for one incursion of *T. mariae* in a restricted length of Eureka Creek (Mitchell River Catchment) (Pearce et al., 2009). However, the detection of *T. mariae* in the same section of Eureka Creek again in 2019 cast doubt over the success of the original attempts. Eradication of infestations in other systems (e.g., Fitzroy River Catchment) has not been possible. Indeed, there is a lack of demonstrated effective control mechanisms for tilapia and thus there is a critical need to develop and evaluate other potential tilapia control agents.

Where feasible, biocontrol can be a cost-effective, safe and practical solution to manage invasive species at the landscape scale because it does not require reapplication of chemicals or poisons, and once established may be self-sustaining. Excellent examples of this methods are the use of myxoma virus (MYXV) and rabbit haemorrhagic disease virus (RHDV), which were released in 1950 and 1995, respectively, as biological control agents (BCAs) for rabbits in Australia. The sustained reductions of ~ 90 % of rabbit populations and the impacts of the two rabbit BCAs resulted in an estimated benefit of A$70 billion to Australia's agricultural industries in the 60 years between 1950 and 2010 (Cooke et al., 2013). Based on the success with the use of MYXV and RHDV, spring viremia of carp virus (SVCV; Rhabdovirus) was proposed as a potential BCA for common carp (*Cyprinus carpio*) (Stevenson, 1978), which are regarded as the most devastating invasive fish in Australia. However, subsequent research found that SVCV was not specific for carp (Family *Cyprinidae*). The virus not only infected other fish species within the Family *Cyprinidae* (for example, goldfish, tench), but also those of other families including sheatfish (*Siluridae*), guppy (*Poecilliidae*) and Northern pike (*Esocidae*) (Crane, 1995). Therefore, SVCV was inappropriate as a BCA and its investigation as a potential BCA for carp was terminated.

By 2000, Australia's *National Management Strategy for Carp Control* was adopted by the Carp Control Coordinating Group (CCCG, 2000). It recognised that the existing techniques to control carp, such as poisoning and physical removal, are often effective on a small scale but failed on a broad scale. A strategic research plan identified possible techniques for controlling carp including habitat manipulation, genetic control, and carp-specific pathogens. In the mid-2000 s, an investigation of koi herpesvirus (KHV) (Hedrick et al., 2000), taxonomically known as cyprinid herpesvirus 3 (CyHV-3) (Waltzek et al., 2005), as a potential BCA was proposed as part of an integrated carp control program (Fulton, 2006, McColl et al., 2007).

CyHV-3 was first reported in Israel and Germany in 1998 (Hedrick et al., 2000) and subsequently spread to at least 28 countries across Europe, America, Africa, and Asia (OIE, 2021b), including Indonesia, from which an isolate was transferred to Australia's high-containment laboratory, the CSIRO Australian Centre for Disease Preparedness (CSIRO ACDP). Subsequent research showed that an Indonesian isolate was highly virulent in carp sourced from Australian waters (Sunarto et al., 2011) and the virus was specific to carp (McColl et al., 2017). The results encouraged further investigations of CyHV-3 as a potential BCA as part of the National Carp Control Plan (NCCP, 2019).

Recently it has been suggested that combined viral biocontrol and genetic technologies would be a better approach for effective carp control and possible long-term eradication of carp (Thresher et al., 2014a, Thresher et al., 2014b). Based on our experience with viral biocontrol in rabbits and carp (McColl et al., 2014, McColl and Sunarto, 2020, Kerr et al., 2021, Strive and Cox, 2019), here we describe a systematic approach to assess known pathogens for their suitability as potential BCAs for tilapia, and outline the possible next steps to further investigate the top candidates.

3. Biological control agent assessment criteria

Initially, BCA assessment criteria adapted from Henzell et al. (2008) and Peacock (2015) for rabbit biocontrol in Australia were used to assess

Table 1
Biocontrol agent assessment criteria.

1.	**Appropriateness**
	Safety – the BCA should be species-specific, not infecting, let alone affecting, any non-target species in Australia (including humans). Socially acceptable – the nature and biological action of the BCA needs to be acceptable to the community. Humane – the BCA should not cause undue pain or suffering.
2.	**Effectiveness**
	Virulence – the BCA needs to cause high mortality in tilapia. Survivors are likely to seroconvert, become more resistant and may confer the resistance to their offspring through maternal immunity. This would likely lead to recovery of the tilapia populations. Impacts on all ages – ideally the BCA needs to have high impacts on both juvenile and adult tilapia. Effectiveness in wild fisheries – the BCA needs to cause high enough mortality to exceed productivity in wild tilapia populations. No unfavourable interaction with other pathogens – endemic pathogen(s) should not provide cross-protection against the BCA.
3.	**Efficiency**
	Transmission – the BCA should have the ability to transmit efficiently among tilapia and have the capacity to spread through the local, regional, and national tilapia populations (self-disseminating). Persists in the environment – the BCA should persist despite death of a high proportion of hosts and, once established, should causes repeated outbreaks. Cost for research and development – benefits should exceed the cost of testing the safety and efficacy of the BCA, risk assessment, and cost-benefit analysis. Cost for manufacture and distribution – preferably, the organism(s) could be cultured, prepared, and stored in large quantities to allow effective distribution. Public and government approval requirements – expected delay due to public and government approval processes.

Adapted from Henzell et al. (2008) and Peacock (2015)

the appropriateness, effectiveness, and efficiency of potential BCAs for tilapia in Australia (Table 1). The BCA assessment using the criteria summarised in Table 1 is a complex process and the selection criteria used in this review may not cover all aspects of the assessment. Another limitation of the assessment is that it involves subjective scoring, which affects the consistency of the results. For example, how many studies would have to be done to justify inclusion of a criterion, and then assessment of each criterion as "positive", "minor concerns", or "major concerns"?

In assessing potential BCAs for tilapia, the most important initial screening criteria were reduced to 'safety' and 'efficacy', just as had been done when assessing the potential of different viruses as potential BCAs for rabbits and carp. Species-specificity is an important determinant of the safety of a potential BCA, not only of the released BCA but also of any future generations of the agent that may arise following mutations in the field. On the other hand, it is virulence and transmission that are important in determining the efficacy of the BCA (Di Giallonardo and Holmes, 2015). Therefore, to be considered as a potential BCA candidate, an agent should, initially at least, satisfy-three key determinants – species-specificity (Table 1 criteria 1.1), high levels of virulence (criteria 2.1), and effective transmission (criteria 3.1).

3.1. Safety of the BCA

The BCA should have a narrow host range, affecting tilapia only. No other species sharing, or using, tilapia-infested waterways – be they other fish species, aquatic or terrestrial animals, or humans – should be affected (Peacock, 2015). The absence of disease in any species anywhere in the world, other than tilapia, would be the most compelling evidence for the specificity of the selected BCA. Nevertheless, given the unique nature of Australia's fauna (including its fish), it will be critical to assess the susceptibility to infection of various Australian species in a non-target species (NTS) testing program (McColl et al, 2017). OIE recommends a three-stage approach to assess susceptibility of a species to infection with a specific pathogen: 1) the route of transmission is consistent with natural pathways for the infection; 2) the pathogenic agent has been adequately identified; and 3) the presence of the pathogenic agent constitutes an infection (OIE, 2021a).

3.2. Efficacy of the BCA

The suitability of potential exotic BCAs will inevitably be based on published scientific evidence collected from overseas work, and further work may be required for assessments at a local level (Henzell et al., 2008). Most uncertainty relates to the likely virulence, transmissibility, and persistence of a BCA in wild fisheries. To be effective as a BCA, the agent needs to cause high mortality in tilapia of all ages. Ideally the BCA would be a self-disseminating agent that has the ability to transmit efficiently. For this reason, spread primarily by waterborne routes would be advantageous, as would persistence of the agent in the environment following the death of a high proportion of hosts.

Ideally, the BCA would have no unfavourable interaction with other pathogens. Endemic pathogen(s) should not provide cross-protection against the BCA such as occurred in Australia where previous exposure to non-pathogenic Australian rabbit calicivirus RCV-A1 increased survival of the rabbits during outbreaks of RHDV (Strive et al., 2013, Cooke et al., 2018). Clearly, research would be required to systematically assess the possibility of interfering endemic agents and viral mutants and reassortants arising if a virus was the chosen BCA (Chaput et al., 2020). This would involve, for example, *meta*-transcriptomic analyses (Turnbull et al., 2020) of Australian tilapia populations to identify the presence of other viruses.

3.3. Other factors affecting selection of a BCA

Having assessed the safety and efficacy of the selected BCA, consideration can then be given to other criteria listed in Tables 1. A naturally occurring agent in wild and farmed tilapia would likely be more socially acceptable than a genetically modified organism (GMO). The use of a GMO would also require additional time for approval and processing. In addition, a BCA that killed tilapia relatively humanely and not causing undue pain or suffering would be preferable (Sharp and Saunders, 2011).

Lethal pathogens have never been used or approved as controls for invasive fish, so a delay would be expected due to the need for public and government approval processes for the pathogenic biocontrol of tilapia. The requirements for, and consequences of, an aquatic BCA are quite different from those of a terrestrial BCA. For example, the impacts of fish kills on water quality and food webs need to be managed (Brookes and Hipsey, 2019, Beckett et al., 2019). Applying hydrological, ecological, and epidemiological modelling to test different scenarios and to predict the outcomes of the introduction of a BCA into a new environment will help inform the BCA release strategy for the biocontrol of tilapia in Australia (Joehnk et al., 2020, Durr et al., 2019).

3.4. The essential information required for the potential biocontrol of tilapia

Recently, selection criteria for a potential BCA were developed for another invasive pest fish in Australia, the common carp. McColl and Sunarto (2020) emphasized that, in developing a viral biocontrol program for carp, two basic criteria had to be met: an understanding of the biology of the targeted pest species and the potential BCA. For tilapia in Australia, there is a lack of understanding of the biology of the species in Australian conditions, and much also remains to be learned about potential BCAs, be they viral or some other infectious agent. Table 2 summarizes the essential information required for a potential biocontrol program on tilapia. The table identifies information already acquired about the targeted pest ('Knowns'), but, more importantly, summarizes the essential additional information that will be necessary not only to understand tilapia biology in Australia, but also to select an appropriate BCA ('Unknowns').

4. Biocontrol agent candidate assessment findings

Tilapia pathogens fall into the general categories of viruses, bacteria, fungi, and parasites. Overall, this bioprospecting review found that a large number of bacteria, fungi, and parasites have been associated with natural disease outbreaks in tilapia worldwide. However, none were specific for tilapia and therefore were rejected as BCA candidates. More promisingly, a number of viruses have been reported in tilapia.

4.1. Viruses

At least nine viruses have been detected in tilapia (Machimbirike et al., 2019), the first DNA virus being Lymphocystis disease virus (LCDV) (Paperna, 1973, Weissenberg, 1965), while infectious pancreatic necrosis virus (IPNV) was the first RNA virus (Hedrick et al., 1983). Neither has been associated with high natural mortality in tilapia, excluding them from consideration as BCAs. Seven viruses have been associated with disease outbreaks in tilapia. These are TiLV (Eyngor et al., 2014), TiPV (Liu et al., 2020), Tilapia larvae encephalitis virus (TLEV) (Shlapobersky et al., 2010), Bohle iridovirus (BIV) (Ariel and Owens, 1997), nervous necrosis virus (NNV) (Bigarré et al., 2009), infectious spleen and kidney necrosis virus (ISKNV) (Subramaniam et al., 2016, Suebsing et al., 2016), and iridovirus-like agents (McGrogan et al., 1998, Smith et al., 1997). Subramaniam et al. (2016) suggested that the irido-like viruses reported by Smith et al. (1997) and McGrogan et al. (1998) could actually be ISKNV isolates which would reduce the list to

Table 2
The essential information required for the potential biocontrol of tilapia.

Information required	Knowns	Unknowns
Tilapia biology in Australia	• Tilapia biomass across Australia	• Future estimates of tilapia biomass • Genomic and transcriptomic study of tilapia in Australia
Epidemiology of the BCA	• Global epidemiology	• Laboratory epidemiology • BCA epidemiology under Australian conditions • Genome of the BCA
Safety of the BCA (species specificity)	• Overseas field outbreaks	• Susceptibility of Australian native fish to the BCA • Human safety
Efficacy of the BCA	• Overseas field outbreaks	• BCA-host interactions: o Virus transmission (R_0) o Virulence of different BCA isolates in different strains of tilapia including tilapia hybrids • Survey of Australian tilapia for endemic pathogen(s)
Epidemiological modelling of the release and spread of the BCA	• TiLV as a model for the tilapia BCA	• Extensive studies required
Evolution of the BCA	• Rabbit and carp biocontrol viruses	• Increasing virulence or innocuity?
Broad-scale control measure(s) to complement the BCA	• Regional measures available	• Could other BCAs complement the selected BCA? • Genetic biocontrol
Social risks		• Views of local affected populations versus the Australian-wide population
Ecological concerns	• Ecological risk assessment	• Environmental clean-up procedures after fish kill events • Prey switching
Economic drivers	• Cost-benefit analysis of proposed investment in tilapia biocontrol • Business case for tilapia biocontrol	• Current and future impact and control costs associated with tilapia in Australia • Potential effectiveness and feasibility of the release of a BCA
Restoration benefits from tilapia control		• Expert elicitation study on the ecological consequences of reduced tilapia

Adapted from McColl and Sunarto (2020)

six candidates. None of the Iridoviruses (LCDV, BIV, ISKNV and Iridolike viruses) nor NNV are specific to tilapia, and therefore, were not considered as suitable candidates for BCAs. On the other hand, TiLV, TiPV, and TLEV are believed to be species-specific to tilapia (Table 3).

4.1.1. *Tilapia lake virus (TiLV)*

TiLV, taxonomically assigned as *Tilapinevirus tilapiae* under the genus *Tilapinevirus* and the family *Amnoonviridae* (Adams et al., 2017, Bacharach et al., 2016a, Kuhn et al., 2019; ICTV, 2021), is an enveloped and negative-sense ssRNA virus (Bacharach et al., 2016b, Eyngor et al., 2014). No other viruses within the family *Amnoonviridae* have been reported in tilapia (ICTV, 2021). The 10-segmented 10 kb genome contains 14 functional genes encoding 14 proteins (Acharya et al., 2019). Alignment analyses of segment 1 (Taengphu et al., 2020) and segment 3 (Skornik et al., 2020) as well as whole-genome sequences (Jansen et al., 2018) from geographically different isolates revealed high nucleotide identity, suggesting that a new recently-evolved virus has emerged. A relatively recent reassortment event, particularly those of segments 5 and 6, complicates phylogenetic analysis by individual segments and illustrates the need to exercise caution when using the analysis to infer geographical origin and the movement of the virus (Chaput et al., 2020). TiLV was first reported to cause mass die-offs in farmed and wild tilapia in Israel as early as summer 2009 (Eyngor et al., 2014). Around the same time, similar disease outbreaks called syncytial hepatitis of tilapia (SHT) were reported from farmed tilapia (*O. niloticus*) in Ecuador (Ferguson et al., 2014). The samples which were collected in 2011–2012 tested positive for TiLV (Del-Pozo et al., 2016). Since then TiLV has been reported from 16 countries across four continents (Surachetpong et al., 2020), suggesting that the virus is able to survive in different ecological niches and climates.

Natural morbidity and mortality due to TiLV are restricted to tilapia and tilapia hybrids (Surachetpong et al., 2017, Eyngor et al., 2014). Affected farmed species includes Nile tilapia (*O. niloticus*) in Ecuador (Ferguson et al., 2014), Egypt (Fathi et al., 2017), India (Behera et al., 2018), Indonesia (Koesharyani et al., 2018), Thailand (Dong et al., 2017b, Surachetpong et al., 2017) and Uganda (Mugimba et al., 2018); grey tilapia hybrid (*O. niloticus* × *O. aureus*) in Israel (Eyngor et al., 2014); red tilapia (*Oreochromis spp*.) in Thailand (Dong et al., 2017b, Surachetpong et al., 2017) and red tilapia hybrid (*O. niloticus* × *O. mossambicus*) in Malaysia (Amal et al., 2018). A wide range of wild tilapiines including *Tilapia zilli, O. aureus, Sarotherodon (Tilapia) galilaeus* and *Tristamella simonis intermedia* from the Kinneret Lake in Israel (Eyngor et al., 2014), wild black tilapia (*Oreochromis* spp.) in Malaysia (Abdullah et al., 2018), wild Nile tilapia in Lake Victoria (Tanzania and Uganda) (Mugimba et al., 2018) and in Peru (OIE, 2018) have been affected by TiLV.

Other fish species co-cultured with tilapia have not been affected by TiLV. These include grey mullet (*Mugil cephalus*) and common carp (*C. carpio*) in Israel (Eyngor et al., 2014); grey mullet and thin-lipped mullet (*Liza ramada*) in Egypt (Fathi et al., 2017); rohu (*Labeo rohita*), catla (*Catla catla*), mrigal (*Cirrhinus mrigala*), milk fish (*Chanos chanos*) and pearl spot (*Etroplus suratensis*) in India (Behera et al., 2018). However, wild river barb (*Barbonymus schwanenfeldii*) was found to be TiLV-positive by RT-PCR in Malaysia (Abdullah et al., 2018). Clearly, there is a need to differentiate TiLV genomic RNA (gRNA) from mRNA, the latter indicating viral replication in the host, particularly in non-target species such as river barb that was gRNA-positive by RT-PCR.

Experimental infection of 10 warm-water fish species including giant gourami (*Osphronemus goramy*), snakeskin gourami (*Trichogaster pectoralis*), iridescent shark (*Pangasianodon hypophtthalmus*), walking catfish (*Clarias macrocephalus*), striped snakehead fish (*Channa striata*), climbing perch (*Anabas testudineus*), common carp (*C. carpio*), silver barb (*Barbodes gonionotus*), Asian sea bass (*Lates calcarifer*), and red hybrid tilapia (*Oreochromis* spp.) revealed that only red hybrid tilapia and giant gourami were affected by TiLV (Jaemwimol et al., 2018). The mortality of red hybrid tilapia infected with TiLV by intraperitoneal (IP) injection was 63–85 % and that of giant gourami was 100 %. Despite the cumulative mortality of giant gourami being significantly higher than that of tilapia, only 53.55 % (8/15) of giant gourami samples were TiLV-positive by RT-qPCR compared to 100 % (15/15) of those of tilapia, suggesting that not all dead giant gourami may have been infected with the virus. African cichlid (*Aulonocara* spp.) is susceptible to TiLV infection (Yamkasem et al., 2021a). However, cichlids endemic to India, *viz* pearlspot (*Etroplus suratensis*), orange chromide (*Pseudetroplus maculatus*), and canara pearlspot (*E. canarensis*), are not susceptible to TiLV infection (Thangaraj et al., 2022). Zebrafish are susceptible to TiLV infection via intraperitoneal injection but not cohabitation (Widziolek et al., 2020, Rakus et al., 2020).

Wide variations in mortality associated with TiLV have been reported in wild and farmed tilapia. For example, 0.71 % mortality in wild black tilapia (*O. niloticus*) and 15–25 % in farmed red hybrid tilapia (*O. niloticus* × *O. mossambicus*) have been reported in Malaysia (OIE, 2017b, Abdullah et al., 2018, Amal et al., 2018). Similarly, low mortality

Table 3
Summary of information for the candidate biocontrol agents worthy for further investigation.

Candidate biocontrol agents	Appropriateness			Effectiveness				Efficiency				
	Species specificity	Socially acceptable	Humane	Virulence in tilapia	Impacts on all ages of tilapia	Effectiveness in wild fisheries	Interactions with other pathogens	Transmission	Persists in the environment	Cost for research & development	Cost for manufacture & distribution	Public and government approval requirements
Tilapia lake virus (TiLV)	TiLV causes disease outbreaks and mortalities in farmed and wild tilapia, but not in other fish species co-cultured or sharing waterways with tilapia. Wild river barb was found to be TiLV-positive by RT-PCR and giant gourami was affected by TiLV via IP injection and co-habitation challenges.	TiLV is a naturally occurring virus in wild and farmed tilapia (not a GMO). Prototype vaccines are available to protect farmed and ornamental tilapia.	Acute mortality occurs within a few days post infection. Chronic up to 24 days and sub-clinical infection have also been observed.	Experimental infection of tilapia with TiLV conducted in geographically different regions resulted in consistently high levels of mortality. Wide variations in mortality associated with TiLV have been reported in wild and farmed tilapia, ranging from0.71% to 90%.	TiLV has been reported to cause mortality in all age groups of tilapia.	TiLV causes mortality of wild tilapia in Israel, Malaysia, Tanzania, Uganda, and Peru. The virus causes significant decline in tilapia populations in Kinneret Lake, Israel.	No antagonistic interactions have been observed during co-infections with other pathogens in tilapia. No other viruses within the family *Amnoonviridae* have been reported in tilapia.	Epidemiological findings and cohabitation mode of horizontal transmission demonstrates the ability of TiLV to spread by waterborne routes. Vertical transmission has also been observed.	Most likely but need to determine how long TiLV survives in the water and in dead fish. TiLV RNA has been detected in mucus, feces and water tanks containing TiLV-infected fish.	Medium-sized project to test the efficacy (virulence and transmission). Large project to test the safety (susceptibility of non-target species).	TiLV grows in cell cultures and could be transported in freeze dried formor cold at 4°C.	Expected delay due to public and government approval processes. Australia has very strong legislative mechanisms for approval of biocontrol agent (Biological Control Act 1984), which may facilitate the processes.
Tilapia parvovirus (TiPV)	It has only been reported in tilapia in China and Thailand.	Vaccine is not available.	TiPV causes acute mortality in tilapia within 11 days.	TiPV causes 60-70% mortality in cage-farmed tilapia.	TiPV has been reported in all size of adult tilapia.	Unknown	No other parvovirus has been reported in tilapia or any other fish species.	TiPV is contagious, spreading to six cities in three provinces in China.	Unknown	Little is known about the characteristics of the virus.	TiPV grows in cell culture.	Ditto above.
Tilapia larvae encephalitis virus (TLEV)	It has only been reported in tilapia in Israel.	Vaccine is not available.	The virus affects brain with clinical signs of a whirling syndrome.	High mortality rates of up to 96% and 80% in blue and red tilapia larvae, respectively.	TLEV has only been reported in larvae of tilapia.	Unknown	No other herpesvirus has been reported in tilapia.	TLEV is capable of both vertical and horizontal transmission.	Unknown	Little is known about the characteristics of the virus.	TLEV has not been isolated or cultured in cell lines.	Ditto above.

Key: Positive | Minor concerns | Major concerns

of 6.4 % and 9.2 % in farmed tilapia have been reported in Chinese Taipei (OIE, 2017a) and Egypt (Fathi et al., 2017), respectively, the latter experiencing "summer mortality" in which TiLV was detected but the causal link was inconclusive (Nicholson et al., 2017). Subclinical infections have been reported in farmed tilapia in Thailand (Senapin et al., 2018) as well as in wild and farmed tilapia in Lake Victoria (Tanzania and Uganda) (Mugimba et al., 2018). In contrast, TiLV has caused disease outbreaks in wild tilapia populations in Israel and decreased the annual yield of *Tilapia galilaeus* from the Kinneret Lake from 316 t in 2005 to 52, 8, and 45 tons in 2007, 2009, and 2010, respectively (Eyngor et al., 2014). Interestingly, although the lake hosts 27 species of fish encompassing members of the families *Cichlidae*, *Cyprinidae*, *Mugillidae*, and *Claridae*, only tilapia (*Cichlidae*) were affected. In farmed tilapia, the disease resulted in massive mortality in Israel (Eyngor et al., 2014), 10–80 % mortality in Ecuador depending on the tilapia strain (Ferguson et al., 2014), 20–90 % mortality in Thailand (Dong et al., 2017b, Surachetpong et al., 2017) and 80–90 % in India (Behera et al., 2018).

Experimental infection of tilapia with TiLV by intragastric, intra-coelemic, and IP routes, and by cohabitation conducted in geographically different regions resulted in consistently high levels of mortality. The mortality of Nile tilapia infected with TiLV via intragastric and intra-coelemic routes was 40–45 % and 70 %, respectively, which occurred from 6 to 15 days post infection (dpi) (Pierezan et al., 2020, Pierezan et al., 2019). The mortality of cohabitating tilapia was 55.71 % from 3 to 15 dpi (Liamnimitr et al., 2018) and 80 % from 4 to 9 dpi (Eyngor et al., 2014). Virus challenge by IP injection resulted in high mortality, ranging from 75 to 85 % which occurred from 2 to 10 dpi (Eyngor et al 2014), 66–88 % from 1 to 12 dpi (Tattiyapong et al., 2017), 63–85 % from 4 to 24 dpi (Jaemwimol et al., 2018) and 100 % from 3 to 7 dpi (Behera et al 2018).

The causes of the variation in mortality are not known, but they may be attributed to different species, strain or family of tilapia, culture systems or other environmental factors. For example, 80 % mortality in the Chitralada strain compared to 10–20 % mortality in all male Genetically Improved Farmed Tilapia (GIFT) have been reported in Ecuadorian farms, despite both being *O. niloticus* (Ferguson et al., 2014). Furthermore, host resistance to TiLV is highly heritable in families of the GIFT strain, suggesting that selective breeding to increase the resistance of farmed tilapia to TiLV is feasible (Barría et al., 2020). Clinical outbreaks of TiLV have been reported in summer at water temperature of 22 to 32 °C in Israel (Eyngor et al., 2014), ≥25 °C in Egypt (Fathi et al., 2017) and 25 to 27 °C in Ecuador (Ferguson et al., 2014), suggesting that temperature plays an important role in TiLV outbreaks. Co-infection of TiLV with other pathogens including *Aeromonas spp*., particularly *A. veronii*, may also affect the severity and outcome of the disease (Amal et al., 2018, Nicholson et al., 2017, Rao et al., 2021). Although stocking density, dissolved oxygen levels and pond production cycles have been considered as risk factors of TiLV disease in aquaculture settings, no single factor has been attributed to TiLV outbreaks (Ali et al., 2020, Kabuusu et al., 2017). In controlled laboratory conditions, mortality is also dose-dependent, in which mortalities of 48.89 % and 77.78 % were observed in *O. mossambicus* IP-injected with low (10^3 $TCID_{50}$/mL) and high (10^5 $TCID_{50}$/mL) doses of TiLV, respectively (Waiyamitra et al., 2021). It is estimated that the LD_{50} of TiLV by IP injection was 5.7×10^4 $TCID_{50}$ (Yang et al., 2018).

Although small fish are more susceptible to TiLV infection than larger fish (Roy et al., 2021), all age groups of tilapias appear to be susceptible to TiLV. Fertilized eggs, larvae, fry, fingerlings, juveniles, adults and broodstocks of tilapia have tested positive for, or been affected by, TiLV (OIE, 2017c, OIE, 2018, Dong et al., 2017a, Behera et al., 2018, Eyngor et al., 2014, Ferguson et al., 2014, Pulido et al., 2019, Surachetpong et al., 2017, Yamkasem et al., 2019). Cumulative mortality of broodstock was 5–10 % while that of fry was 90–100 % (Yamkasem et al., 2019), suggesting that the maturity of the host's immune system may play a role in the outcome of the disease. TILV has also been detected in reproductive organs including ovary and testis, suggesting that TiLV can be vertically transmitted. The detection of TiLV RNA in mucus (Liamnimitr et al., 2018), feces and water tanks containing TiLV-infected fish (Pierezan et al., 2019) and cohabitation mode of horizontal transmission (Eyngor et al., 2014, Liamnimitr et al., 2018) demonstrates the ability of TiLV to spread by waterborne routes, an important pathway for a successful biocontrol agent of aquatic invasive fish.

Natural co-infections of TiLV and other pathogens including parasites, bacteria (*Aeromonas hydrophila, A. veronii, A. isthiosmia, A.*

enteropelogenes, Streptococcus agalactiae) and virus (*Tilapia parvovirus*, TiPV) have been reported in farmed tilapia (Yamkasem et al., 2021b, Amal et al., 2018, Basri et al., 2020, Nicholson et al., 2017, Nicholson et al., 2020, Rao et al., 2021, Surachetpong et al., 2017). Mortality rates due to TiLV outbreaks among tilapia farms in Thailand were 20 %-90 %, in which higher rates were associated with secondary bacterial and parasitic infections (Surachetpong et al., 2017). Co-infections of TiLV and *A. veronii* in farmed red hybrid tilapia in Malaysia resulted in 25 % mortality (Amal et al., 2018) while that of *TiLV, A. hydrophila* and *S. agalactiae* was 70 % (Basri et al., 2020). An experimental challenge in tilapia, in which co-infection of TiLV and *A. hydrophila* resulted in 93 % mortality while those of either TiLV or *A. hydrophila* alone was 34 % and 6.7 %, respectively (Nicholson et al., 2020) supported the reported high rate of mortality during co-infections in farmed tilapia. These results are also consistent with those of other bacterial and viral co-infections in tilapia, in which multiple infections have a synergistic effect that resulted in increased severity of the disease and higher rate of mortality in tilapia (Dong et al., 2015, Abdel-Latif et al., 2020).

Mathematical modelling estimated the reproductive number (R_0) for Nile tilapia infected with TiLV at 2.6×10^5 $TCID_{50}$/fish via cohabitation was 2.59, indicating that the virus was spreading within a tilapia population and the incidence of the disease was increasing under the test conditions (Yang et al., 2018). Furthermore, the authors estimated that the population of Nile tilapia decreased to 12 % of the initial population size after 16 dpi. These epidemiological findings suggest that TiLV is contagious and once established has the ability to persist in the environment and causes repeated outbreaks in tilapia populations.

TiLV causes disease outbreaks and mortalities in farmed and wild tilapia populations, but not in other fish species co-cultured or sharing waterways with tilapia (Eyngor et al., 2014, Surachetpong et al., 2017, Behera et al., 2018, Fathi et al., 2017), suggesting that TiLV is specific to tilapia. Though tilapia and its hybrids are the only species known naturally to be affected by TiLV, viral genomic RNA has also been detected by RT-PCR in healthy wild river barb (Abdullah et al., 2018) and mortality in giant gourami experimentally infected with TiLV has been reported (Jaemwimol et al., 2018). However, only 53.55 % (8/15) of giant gourami samples were TiLV-positive by RT-qPCR compared to 100 % (15/15) of those of tilapia, suggesting that not all dead giant gourami may have been infected with the virus. The huge difference of mortality rate of giant gourami infected with TiLV by IP injection (100 %) and co-habitation (5 %) further raises questions if the giant gourami is a true alternative host for TiLV. Although TiLV appears to be specific for tilapia, and although there are no native Australian fish belonging to the families *Cichlidae* (tilapia), *Osphronemidae* (gourami) or *Cyprinidae* (carp and barb), rigorous non-target species testing would be required before the use of any viral biocontrol could be considered. This has been the case with the proposed viral biocontrol agents for carp (McColl et al., 2017) and would be equally applicable for tilapia biocontrol to overcome concerns about the specificity of TiLV.

4.1.2. Tilapia parvovirus virus (TiPV)

Recently, a novel virus tentatively named TiPV has emerged in cage-cultured tilapia in China (Liu et al., 2020). TiPV is a spherical, 30 nm in diameter, non-enveloped virus with a linear, non-segmented, ssDNA genome (4269 bp) which consists of two major ORFs encoding NS1 and VP1 proteins. The virus is tentatively classified into a newly proposed genus of Chapparvovirus within the family *Parvoviridae* (ICTV, 2021). The first outbreaks of the disease were reported in farmed Nile tilapia from August to September 2015 in Hubei, China. Since then, it has been reported from six cities across three provinces in China. The disease affected adult tilapia resulting in 60–70 % mortality. Clinical signs of diseased fish include anorexia, lethargy, darting or corkscrew movements, haemorrhages on the body surface, lower jaw, anterior abdomen and fin bases, exophthalmia and pronounced ocular lesions. Most outbreaks occurred at water temperatures of 28–30 °C, but samples collected at water temperature from 22 to 32 °C have also been reported positive for TiPV, suggesting that temperature may play a role in disease outbreaks. The virus has been isolated on tilapia brain cells allowing further studies including experimental infection, in which the virus caused 90 % mortality within 11 days at 28 °C, similar to those naturally observed in cage culture systems. In November 2020, TiPV was detected in juvenile red tilapia during a disease outbreak associated with TiLV in Thailand (Yamkasem et al., 2021b). Owing to the nature of the outbreak (co-infection with TiLV), the role of TiPV in this outbreak is unknown.

4.1.3. Tilapia larvae encephalitis virus (TLEV)

Based on morphological, biophysical and very limited phylogenetic analyses, TLEV resembles a herpes-like virus (Shlapobersky et al., 2010). The virus has been associated with a high mortality rate in tilapia larvae including laboratory-reared blue tilapia (*O. aureus*), *O. niloticus* and *S. galilaeus*, in Israel. The disease is characterised by a whirling syndrome (a spiral swimming behaviour), darkened skin in blue tilapia and pale skin in red tilapia followed by high mortality rates of up to 96 % and 80 % in blue and red tilapia larvae, respectively. The virus was capable of both vertical transmission and horizontal transmission through water from infected fish (Sinyakov et al., 2011). After the first outbreaks of TLEV in tilapia larvae in Israel a decade ago (Shlapobersky et al., 2010, Sinyakov et al., 2011), the virus was never reported again either in Israel or in other countries, raising a question of whether the virus still persists in the environment. The virus has only been associated with mortalities in tilapia larvae in hatcheries, suggesting that the impact of TLEV in adult tilapia and its effectiveness in wild fisheries may be insignificant. TLEV has not been isolated in cell cultures, hindering further characterisation of the virus, and therefore, the cost for research and development as well as manufacture and distribution are major concerns.

4.1.4. Nervous necrosis virus (NNV)

NNV is the causative agent of viral nervous necrosis (VNN) otherwise known as viral encephalopathy and retinopathy (VER), a lethal disease of many marine and freshwater fish species associated with vacuolation of the central nervous system and the retina (Yoshikoshi and Inoue, 1990, OIE, 2019b). NNV is a small non-enveloped virus with positive sense ssRNA molecules. It belongs to the genus *Betanodavirus* within the family *Nodaviridae* (Mori et al., 1992). Following the first report of VNN outbreaks in Nile tilapia larvae in France (Bigarré et al., 2009), the disease has also been associated with mortality of tilapia larvae in Thailand (Keawcharoen et al., 2015), Indonesia (Yanuhar et al., 2018), and Egypt (Taha et al., 2020). The disease has been reported in more than 50 species belonging to 32 families from 12 different orders (OIE, 2019b). Furthermore, 177 marine species are susceptible to the virus and natural disease outbreaks of VNN have been reported in 62 marine and 12 freshwater fish species (Bandin and Souto, 2020).

4.1.5. Iridoviruses

Family *Iridoviridae* consists of two sub-families: *Alphairidovirinae* (*Lymphocystivirus, Ranavirus* and *Megalocytivirus*) which infect ectothermic vertebrates (bony fish, amphibian, and reptiles) and *Betairidovirinae* (*Iridovirus* and *Chloriridovirus*) which infect insects and crustaceans (Chinchar et al., 2017). Four iridoviruses including LCDV (*Lymphocystivirus)*, Bohle iridovirus (*Ranavirus*), ISKNV (*Megalocytivirus*) and Irido-like viruses, which are possibly ISKNV isolates, have been reported in tilapia. LCDV infection was first reported in South American cichlid in Guatemala (Weissenberg, 1965) and in African tilapia in East Africa (Paperna, 1973). The virus has been associated with the formation of wart-like growths, but mortalities have not been recorded in tilapia. Lymphocystiviruses infect more than 100 species of marine and freshwater fish (Chinchar et al., 2017).

Bohle iridovirus was first isolated from metamorphs of the ornate burrowing frog (*Limnodynastes ornatus* Gray,1842) in Bohle, North Queensland, Australia (Speare and Smith, 1992). Since then, the virus has been shown to infect amphibians, reptiles, and fish including tilapia (*O. mossambicus*) (Ariel and Owens, 1997), suggesting that BIV are

capable of infecting hosts from different classes (Chinchar et al., 2009, Chinchar et al., 2017). Natural disease outbreaks in tilapia associated with ISKNV infections have been reported in Canada, the USA and Thailand (McGrogan et al., 1998, Subramaniam et al., 2016, Dong et al., 2015, Suebsing et al., 2016, Smith et al., 1997). Mortalities of 50–75 % among Nile tilapia fry (Subramaniam et al., 2016) and up to 50 % in adults (Dong et al., 2015) were much lower than those in one of the main host, mandarin fish (*Siniperca chuatsi*), where mortality was up to 100 % (He et al., 2000). ISKNV is not only highly pathogenic in mandarin fish, but also able to infect 13 cultured and 39 wild marine fish species in the South China Sea (Wang et al., 2007) as well as freshwater fish (Chinchar et al., 2017).

4.2. Bacteria

Bacteria are potentially deadly pathogens for both wild and cultured fish and are responsible for mass mortality events in aquaculture facilities across the globe (Ibrahim, 2020). However there are no bacteria specific for tilapia (Plumb and Hanson, 2011). Six major bacterial pathogens associated with mortality events in tilapia have been documented and include the following genera: *Streptococcus, Aeromonas, Flavobacterium, Francisella*, *Edwardsiella* and *Pseudomonas* (Bromage et al., 1999, Anshary et al., 2014, Raj et al., 2019, Tartor et al., 2021, Plumb and Hanson, 2011, Ibrahim, 2020). These bacteria have not only caused natural outbreaks in other freshwater fish (Pękala-Safińska, 2018), but also in marine fish species (Toranzo et al., 2005). Therefore, all are inappropriate as BCA candidates.

4.3. Fungi

The most common fungal infection in freshwater fish is Saprolegniosis (El-Deen et al., 2018, Torto-Alalibo et al., 2005), while the fungal disease considered the most detrimental to freshwater, brackish water, wild and farmed fish throughout the world appears to be *Aphanomyces invadans* (Afzali et al., 2015). Interestingly, *O. niloticus* (Afzali et al., 2015) and *O. mossambicus* (Lilley et al., 1998) appear to be resistant to this deadly fungus while other tilapia species including *O. andersoni, O. machrochir, T. rendalli* and *T. sparrmanii* (OIE, 2019a) and at least 94 other fish species have been identified as susceptible to *A. invadans*. Likewise, none of the Saprolegnia and Branchiomyces detected in mass mortalities of tilapia are species-specific to tilapia.

4.4. Parasites

Numerous fish parasites exist which cause mass mortality in cultured tilapia, particularly in young ages. In addition to the damage caused by *O. mossambicus* in Australia, it appears that some of their exotic parasites have likely been co-introduced from African rivers and tributaries as four species of parasites - three monogeneans (*Cichlidogyrus tilapiae, C. sclerosus, C. halli)* and one trichodinid (*Trichodinia sp*) - have been reported on both African native and introduced Australian tilapia (Wilson et al., 2019). The most serious monogenean parasites in tilapia, *Gyrodactylus* sp., and the most numerous protozoans, *Trichodina* sp., are not species-specific to tilapia. A novel Myxosporean parasite, *Myxobolus bejeranoi,* has only been reported in tilapia hybrid (*O. aureus* male × *O. niloticus* female), which is an important aquaculture species in Israel (Lövy et al., 2018). However, the effectiveness of *Myxobolus* spp. in wild fisheries is unknown. In fact, every parasite found in aquaculture facilities are present in wild fish populations but most of them are not associated with disease outbreaks (Valladao et al., 2018) and therefore the species specificity of *Myxobolus* spp. is a major concern.

5. Discussion

A wide range of pathogens associated with disease outbreaks and mortalities in tilapia were assessed for their potential as BCAs for tilapia in Australia. No bacteria, fungi or parasites are considered as being host specific to tilapia. Although many bacteria (e.g. *Salmonella* spp. for rodents), fungi (chytrid fungus for frogs) and parasites (protozoa for rats) have been proposed and tested as potential BCAs for vertebrates pests, only viruses have demonstrated efficacy and been successfully released (Saunders et al., 2010). To date, there have only been three successful viral biocontrols of vertebrate pests: FPLV (parvovirus) contributing to the elimination of cats on Marion Island, and MYXV (myxoma virus) and RHDV (calicivirus) to control the feral rabbit population in Australia and New Zealand (Saunders et al., 2010, McColl et al., 2014). The remarkable success of MYXV and RHDV in the biological control of rabbits in Australia has led to ongoing research into similar solutions for other vertebrate aquatic pests including carp and recently tilapia.

Out of nine viruses detected in tilapia, six viruses (LCDV, IPNV, BIV, VNN, ISKNV and Irido-like viruses which are possibly ISKNV isolates) were first reported in species other than tilapia and therefore are not suitable as BCA candidates. However, three viruses originally reported in tilapia (TLEV, TiPV and TiLV) are apparently specific to tilapia, and therefore are categorised in this review as being tentatively worthwhile biocontrol candidates for further investigation. TLEV was categorised under a 'watching brief'. This means that TLEV was not currently selected for further investigation but will be watched as a possible future BCA through the international literature and scientific networks. TiPV is the first and only parvovirus known to infect fish and information on the virus is limited. However, it has been reported in two countries. Therefore, TiPV was categorised as 'tentatively worthwhile' for further investigation. TiLV was considered the most promising potential BCA candidate and was categorised as 'worthwhile for active further investigation'. These findings have been used to inform the cost-benefit analysis and business case for tilapia biocontrol in Australia. The successful identification of TiLV as the most promising BCA candidate and the positive cost-benefit ratio of 1 to 2.81 from this project suggest that the investment in tilapia biocontrol research is likely to be worthwhile (Hardaker and Chudleigh, 2021).

CSIRO has already imported TiLV isolates into Australia's high-containment laboratory (CSIRO ACDP) and developed the capability to work with this exotic virus in a laboratory setting. To demonstrate the efficacy of TiLV as a potential BCA for tilapia in Australia, the susceptibility of two tilapia species present in Australian waterways (*O. mossambicus* and *T. mariae*) to TiLV is being tested. If the two tilapia species are susceptible to TiLV, work would progress following a process similar to approved rabbit biocontrol (IA-CRC, 2014) and currently underway for carp biocontrol (NCCP, 2019). This process broadly consists of the following components: safety and efficacy testing, initially, followed by hydrological, ecological, epidemiological and economic modelling, and development of optimised release strategies. Social and ecological risk assessments, bioethical issues and public acceptance will be needed to support an application to release a new BCA against tilapia in Australia. If a new tilapia BCA is approved for release in Australia, a structured collaborative program of release strategies, clean-up, and post-release monitoring and evaluation will be developed similar to the program for carp control (McColl and Sunarto, 2020).

Further work including the identification of other broad-scale control measure(s) such as genetic control to complement the virus would need to be considered (Wedekind, 2019). Australia is currently investing in research to investigate these broadly applicable technologies for managing invasive fish species. A prerequisite for genetic biocontrol approaches is a thorough assessment of the genetic diversity of Australian tilapia (population genomics analyses). This is important as there is already significant evidence of hybridisation occurring among wild tilapia populations (Ovenden et al., 2014). The simultaneous use of two or more classical control methods could also provide a more effective means of controlling invasive tilapia. Such methods could include electrofishing, trapping, the use of chemical attractants, and habitat restoration.

6. Conclusions

Nine viruses have been reported in tilapia, but only three (TLEV, TiPV and TiLV) are considered to be specific for tilapia. TiLV is considered as the most promising potential BCA candidate and its susceptibility testing in two tilapia species present in Australian waterways is underway.

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Author contribution and agreement

AS: Conception and design of the project, acquisition of data, contribution of knowledge, analysis of data, and drafting and revising of the manuscript. JG, KAM, KKN, SC, TH, EA, MT, and BH: Acquisition of data, contribution of knowledge, analysis of data, and drafting of the manuscript. TS: Conception and design of the project, contribution of knowledge, and drafting and revising of the manuscript. All authors have seen and approved the final version of the manuscript being submitted.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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