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Research Article

Parasites of the invasive tilapia *Oreochromis mossambicus*: evidence for co-introduction

Julian R. Wilson[1], Richard J. Saunders[1,2] and Kate S. Hutson[1,3,*]

[1]Centre for Sustainable Tropical Fisheries and Aquaculture and the College of Science and Engineering, James Cook University, 4811, Queensland, Australia

[2]Animal Science, Queensland Department of Agriculture and Fisheries

[3]Current address: Cawthron Institute, Private Bag 2, Nelson, 7042, New Zealand

Author e-mails: julian.wilson@my.jcu.edu.au (JRW), richard.saunders@jcu.edu.au (RJS), kate.hutson@cawthron.org.nz (KSH)

*Corresponding author

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Abstract

Reduced parasite species diversity and infection intensity on invasive populations can facilitate establishment and spread of invasive species. We investigated the parasite diversity of invasive populations of tilapia *Oreochromis mossambicus* from published literature and necropsies conducted on 72 fish captured in the Ross River, north Queensland, Australia. The parasite diversity of invasive *O. mossambicus* from 13 countries was compared to published reports on endemic populations in African river systems and tributaries to determine parasite species that had likely been co-introduced. In total, four parasite species were shared between native and invasive tilapia. We propose that these parasites (three monogeneans, *Cichlidogyrus tilapiae* Paperna, 1960, *Cichlidogyrus sclerosus* Paperna and Thurston, 1969, *Cichlidogyrus halli* (Price and Kirk, 1967) and one trichodinid *Trichodina heterodentata* Duncan, 1977) have likely been co-introduced with invasive *Oreochromis mossambicus* populations. Invasive Australian *O. mossambicus* had substantially reduced parasite diversity (five species) compared to cumulative parasite species diversity documented from the native region (23 species). Australian *O. mossambicus* were infected by two co-introduced parasites and three additional parasite species that have not been recorded previously on this species in Africa indicating possible parasite "spillback" from Australian natives or alternatively, acquisition from other introduced fauna. The substantially reduced parasite diversity on invasive Australian *O. mossambicus* could contribute to the ability of this species to become a serious fish pest.

Key words: co-invasive, Cichlidae, aquatic animal health, enemy release hypothesis, spillback, ornamental fish trade

Introduction

The enemy release hypothesis proposes that invaders lose their co-evolved parasites in the process of invasion, which might give them a competitive advantage over native species (Torchin et al. 2003). Empirical support for this hypothesis comes from observations across a range of taxa, which confirm that invader populations typically harbour less than half the parasite diversity found in native populations (Torchin et al. 2003; Tuttle et al. 2017). Various mechanisms lead to this pattern, such as the low probability of parasitised hosts being translocated, early parasite extinction following host establishment and absence of susceptible hosts in the new location (MacLeod et al. 2010). However, the competitive advantage conferred by the enemy release hypothesis may be reduced over time as more parasite species are co-introduced with repeat incursions or as parasite species from the invaded habitat/location infect the invader population (Colautti et al. 2004; Goedknegt et al. 2016).

Those parasite species that survive the invasion period tend to exhibit direct life cycles and/or low host-specificity and are thus more likely to establish populations in the new location, either on the invasive host or new native hosts (= co-invasion; Bauer 1991; Lymbery et al. 2014). Co-invasion can have severe ramifications on native fish populations (Britton 2013). This is exemplified in Europe where the introduction of the Asian cyprinid *Pseudorasbora parva* (Temminck and Schlegel, 1846) and its associated protozoan parasite, *Sphaerothecum destruens* (Arkush, Mendoza, Adkison and Hedrick, 2003) has caused mass population declines for the endangered European cyprinid *Leucaspius delineates* (Heckel, 1843) (see Gozlan et al. 2005). Some native parasite species may also transfer to the invasive fish (Poulin and Mouillot 2003; Sheath et al. 2015). A potential consequence of this interaction is "parasite spillback", whereby the invasive fish species can act as a reservoir of infectious native parasites that can negatively impact native fish populations already pressured from other factors, such as competition (Kelly et al. 2009a). Alternatively, "parasite dilution" may occur where native hosts have reduced parasitic loads when other invasive fish species are present (Kelly et al. 2009b). The complex interaction between the invasive host, parasites and the environment has the potential to modify population regulatory processes and have consequent flow-on effects to ecosystem dynamics.

Mozambique tilapia, *Oreochromis mossambicus* (Peters, 1852), is a major pest fish species worldwide and can dominate waterways where it has been introduced. The native range of *O. mossambicus* includes Malawi, Mozambique, South Africa (Eastern Cape Province, KwaZulu-Natal), Swaziland, Zambia and Zimbabwe (Cambray and Swartz 2007). *Oreochromis mossambicus* has been introduced into rivers beyond its native range in Africa and all continents except Antarctica (Global Invasive Species Database 2006). The spread of this species has occurred through escapes from aquaculture expansion and the ornamental aquarium trade (Pullin 1988). In Australia, *O. mossambicus* has invaded the Pilbara Drainage of Western Australia and extensive locations in Queensland including the Burnett River, Burdekin River, Endeavour River and notably the Ross River and its associated tributaries in Townsville (Arthington 1989; Veitch et al. 2006; Russell et al. 2012). The source of many incursions can generally be traced back to escapees from illegal stocks in farm dams, ornamental ponds or to the aquarium industry (see Russell et al. 2012). The species' successful invasion of foreign river systems can be attributed to its flexible life history traits, which include a wide thermal (12 °C–32 °C) and salinity tolerance (0–36 ppt), an omnivorous diet and aggressive territorial behaviours (Oliveira and Almada 1998; Uchida et al. 2000; Schnell and Seebacher 2008; Zaragoza et al. 2008).

It is plausible that a reduced parasite faunal assemblage has facilitated the success of invasive *O. mossambicus* populations. Recent research showed that invasive populations of *O. mossambicus* in New Caledonia had entirely lost their gill parasites (Firmat et al. 2016). Furthermore, Roche et al. (2010) found introduced Nile tilapia, *Oreochromis niloticus* (Linnaeus, 1758), was infected by a single parasite species from its native range, but shared eight native parasite species (although at lower abundance) with the native *Vieja maculicauda* (Regan, 1905). The parasite diversity of *O. mossambicus* in its native range has been well documented (e.g., Madanire-Moyo et al. 2011, 2012; Sara et al. 2014), which provides an opportunity to examine the potential for the co-introduction of parasitic organisms associated with the invasion of tilapia. The first aim of this study was to identify parasite species that may have been co-introduced with *O. mossambicus* worldwide. This was determined by comparing parasite species that were shared between the native distribution and invasive populations by generating a comprehensive host-parasite list from published records. The second aim was to examine parasite species diversity on invasive *O. mossambicus* populations in the Ross River northern Queensland, Australia, to identify co-introduced parasite species and the potential for parasite spillback.

Materials and methods

Global comparison of parasite fauna of Oreochromis mossambicus

An exhaustive list of known protozoan and metazoan parasite fauna of *O. mossambicus* in native and invasive populations was assimilated from published resources. The major search engines used included the bibliographic database Web of Science (http://apps.webofknowledge.com) and the library catalogue of James Cook University (https://www.jcu.edu.au/library) using topic search terms "parasit*", "*Oreochromis mossambicus*" and the 26 synonyms listed in FishBase (Froese and Pauly 2018). The host-parasite database of the Natural History Museum (Gibson et al. 2005; http://www.nhm.ac.uk/; accessed on 09/05/2017) was also consulted for records of helminths known to infect *O. mossambicus*. Farmed, aquarium, research or experimental populations of *O. mossambicus* or hybrid hosts were not considered as "native" or "invasive" populations; thus, parasite records in these scenarios were excluded for this study. Some records were omitted because the specific host fish location was not clarified or data were not presented in primary literature (i.e., books, book chapters, or conference abstracts).

Comparisons of parasite faunal assemblages between native and invasive populations should be made cautiously, as they are dependent on robust and sensitive necropsies and accurate host and parasite species identifications. Identifications can be verified if representative material is deposited in curated museum collections, but unfortunately this is not common practice. It is important to note that there are limitations to the taxonomic resolution of existing studies and several studies that identify parasite species do not necessarily aim to determine complete parasite assemblages. Furthermore, sampling bias may occur through multiple mechanisms including, but not limited to, seasonal sampling, sample gear and fish size. Many systems, including the Ross River in Australia, are inundated with numerous other invasive freshwater fish species (Webb 2007) and it is plausible that some parasite species could alternate origins such as other native or invasive hosts, or have broad distributions. For the purpose of this study, parasites identified to the taxonomic rank of species that were shared between the native range and invasive *O. mossambicus* populations were considered as evidence of co-introduction into non-native aquatic systems.

Parasite species diversity on invasive O. mossambicus *populations in the Ross River*

Oreochromis mossambicus is believed to have invaded the Ross River, north Queensland, Australia and surrounding tributaries *c.* 1978 (Russell et al. 2012). Fish in this system (n = 10) have been previously genotyped by Ovenden et al. (2015) and confirmed as the "*mossambicus*" haplotype. For this study, 72 *O. mossambicus* were sampled between June to October 2016 from four locations within the Ross River catchment, Townsville, north Queensland (Figure 1) including three freshwater localities Black Weir (19.318°S; 146.737°E), James Cook University or "Campus Creek" (19.329°S; 146.761°E), Aplins Weir (19.303°S; 146.781°E) and one brackish locality in Annandale or "Annandale Creek" (19.307°S; 146.791°E). Black Weir and Aplins Weir were river localities whereas Campus Creek and Annandale Creek were associated small ponds or tributaries. At the time of sampling there was no connectivity between locations due to lack of rainfall. All fish were caught using a monofilament cast net (2.7 m drop, 19 mm mesh) or a dab net (0.4 × 0.4 m with a 10 mm stretched mesh). Fish were placed immediately into individual buckets of dechlorinated freshwater with strong aeration from a battery powered aerator and transported to the laboratory for dissection. Sampling was conducted under General Fisheries Permit Number 186281.

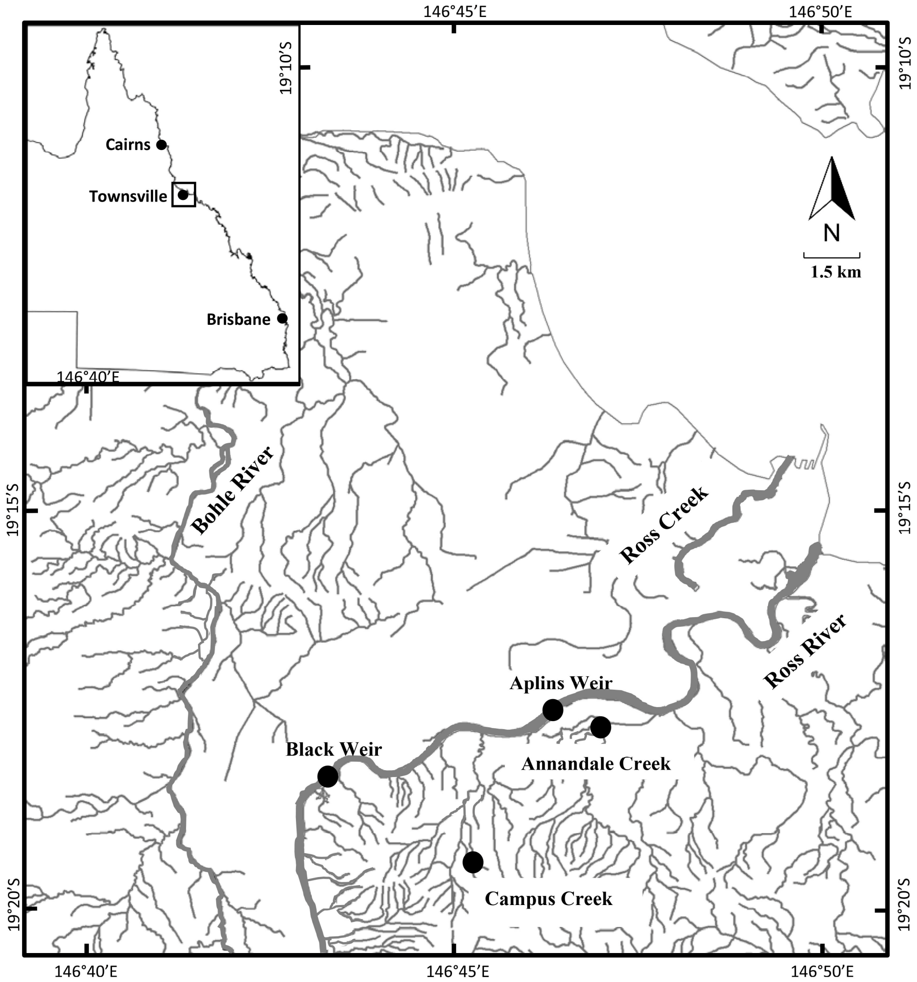

Figure 1. Map of Ross River (lower) Catchment, Townsville, north Queensland, Australia including the sample sites of Mozambique tilapia, *Oreochromis mossambicus,* from the Townsville region: Black Weir, Campus Creek (James Cook University), Aplins Weir, and Annandale Creek.

Table 1. Size and site data of sampled Mozambique tilapia, *Oreochromis mossambicus* in the Ross River, n = 72 (± SE).

	Campus Creek	Annandale Creek	Black Weir	Aplins Weir
n	30	8	28	6
Length (mm)				
$\bar{X}$	76 ± 3	63 ± 4	229 ± 3	248 ± 56
Max	121	87	396	430
Min	34	54	100	102
Weight (g)				
$\bar{X}$	8 ± 1	4 ± 1	389 ± 76	608 ± 341
Max	30	10	1046	1959
Min	1	2	16.4	17

Thorough necropsies were conducted to recover protozoan and metazoan parasites from *O. mossambicus*. Prior to dissection each fish was overdosed with the anaesthetic AQUI-S (as per the manufacturer's instructions) in accordance with animal ethics approval (James Cook University Ethics Approval A2065). Each fish was designated a unique code. Weight (in grams) and total length (L_T in mm) was recorded to the nearest millimetre for each individual. External examinations for parasites

Table 2. Prevalence (%) and mean intensity of parasite fauna of *Oreochromis mossambicus* in the Ross River, Queensland, Australia (based on the definitions by Bush et al. 1997). Representative specimens were accessioned to curated museum collections including the Natural History Museum, London (NHMUK), Queensland Museum (QM) and the South Australian Museum (SAMA).

Parasite	Total number of parasites	Prevalence (%)	Mean Intensity	Average fish size (mm)	Museum accession numbers
Argulus sp.	25	13	3	323 ± 31	NHMUK 2018.189–190; QM W29421
Cichlidogyrus tilapiae	24	13	2	79 ± 6	SAMA 36295–36303
Unidentified bivalve	45	18	3	278 ± 28	QM MO85831
Transversotrema patialense	1	1	1	87	QM G237842
Echinostome sp.	150	7	30	143 ± 72	Not accessioned
Piscinoodinium sp.	2	3	1	383 ± 14	Not accessioned
Ichthyophthirius multifiliis	1	1	1	350	Not accessioned
Unidentified encysted parasite larva	1	1	1	75	Not accessioned

were made by placing whole fish under a Leica M60 stereomicroscope. Individual fish were submerged in physiological saline baths followed by skin scrapes of the entire body surface to capture ectoparasites on the skin, but the scales were not removed (Cribb and Bray 2010). The gill basket was removed and each gill arch and associated gill filaments were examined for gill parasites. All holding water and physiological saline baths were poured through a 60 µm sieve to capture macro-parasites that may have fallen off during holding or transport. Endoparasites were sought by examining the stomach, caecum and large intestine using a “gut washing” technique (see Cribb and Bray 2010) and internal tissue squashes of liver, kidney, gall bladder, spleen, brain, heart and muscle were made on glass slides and viewed using an Olympus BX53 light phase contrast compound microscope. Digital images were made of discovered parasite specimens using an Olympus UC50 camera attached to the Olympus BX53 microscope. Parasites were fixed in 70% EtOH, labeled and stored for future reference.

Parasites were identified to the lowest possible taxonomic rank using comparative morphology techniques from published literature sources. Monogenean parasites were identified using proteolytic digestion techniques (Vaughan et al. 2008). Crustacean ectoparasites were mounted on a concave slide, cleared in lactophenol, and examined at 40x magnification under a Leica M60 stereomicroscope. Trematodes were mounted, unstained, on a glass slide and examined under a Leica M60 stereomicroscope. Representative parasite specimens were deposited into curated museum collections (see Table 2).

Results

A total of 38 putative parasite types have been reported from the native range of *Oreochromis mossambicus* of which 23 have been identified to species (Table 3). Records from invasive populations in Australia had notably reduced documented parasite species diversity (13 putative parasite types, of which five have been identified to species; Figure 2; Table 3). A cumulative maximum of four parasite species were shared between native

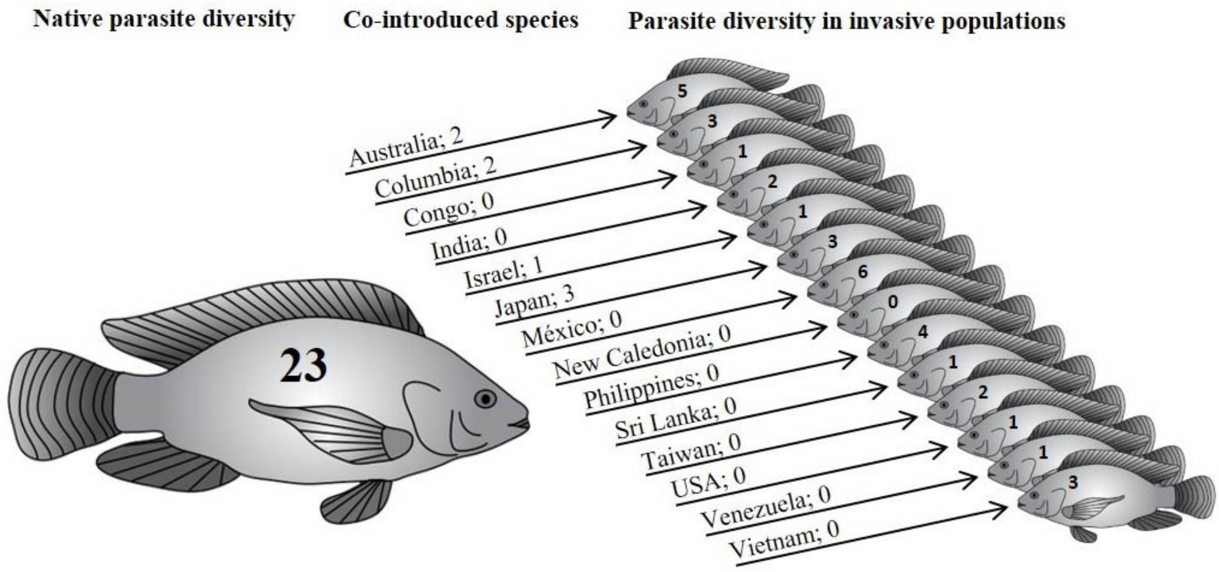

Figure 2. Schematic indicating the native parasite species diversity of *Oreochromis mossambicus* and the number of likely parasite species co-introduced with other established invasive populations worldwide. The native range of *O. mossambicus* was considered to comprise Malawi, Mozambique, South Africa (Eastern Cape Province, KwaZulu-Natal), Swaziland, Zambia and Zimbabwe (IUCN). Numbers shown on the fish (LHS) indicate the total number of recorded parasite species in the native range (i.e., 23 parasite species) and the country where the fish is invasive (RHS). Numbers between the fish indicate the total number of shared parasite species between the native parasite assemblage and invasive populations in the specified country. Note that sampling sensitivity varies between countries.

Table 3. Protozoan and metazoan parasite fauna of *Oreochromis mossambicus* in native and invasive populations.

Taxon	Location	Population	Microhabitat	Distribution	References
Dinoflagellata					
Piscinoodinium sp. Lom, 1981	Australia	Invasive	Gills		Present study
	Philippines	Invasive	NR		Arthur and Lumanlan-Mayo (1997) as Oodinidae gen. sp.
Oligohymenophorea					
Apiosoma piscicola Blanchard, 1855	Native range[a]	Native	Skin	Worldwide (Smit et al. 2017)	Viljoen and Van As (1985)
Apiosoma viridis	Native range	Native	Skin	Africa	Viljoen and Van As (1985)
Chilodonella hexasticha (Kiernik, 1909)	Native range[a]	Native	NR	Worldwide (Bastos Gomes et al. 2017)	Oldewage and Van As (1987)
[a]***Chilodonella piscicola* ((Zacharias 1894; syn. *C. cyprini* (see Moroff 1902)	Vietnam	Invasive	NR	Worldwide (Bastos Gomes et al. 2017)	Arthur and Te (2006)
Epistylis sp.	Philippines	Invasive	Skin		Arthur and Lumanlan-Mayo (1997)
Ichthyophthirius multifiliis Fouquet, 1876	Philippines	Invasive	Skin	Worldwide (Trujillo-González et al. 2018)	Arthur and Lumanlan-Mayo (1997)
	Australia	Invasive	Skin and fins		Webb (2003); Present study
	Vietnam	Invasive	NR		Arthur and Te (2006)
Paratrichodina africana Kazubski and El-Tantawy, 1986	India	Invasive	Gills	Americas, Africa and Asia	Mitra and Bandyopadhyay (2005)
Scopulata constricta	Native range	Native	Skin	Africa	Viljoen and Van As (1985)
Scopulata dermata	Native range	Native	Skin	Africa	Viljoen and Van As (1985)
Scopulata epibranchialis	Native range	Native	Gills, skin	Africa	Viljoen and Van As (1985)
Trichidinella sp.	Philippines	Invasive	Gills		Arthur and Lumanlan-Mayo (1997)
Trichodina sp.	Native range	Native	NR		Oldewage and Van As (1987)
	Philippines	Invasive	Gills		Arthur and Lumanlan-Mayo (1997)

Table 3. *(continued)*

Trichodina canton Basson and Van As 1994	Taiwan	Invasive	Gills	Oceania	Basson and Van As (1994)
Trichodina centrostrigeata Basson, Van As and Paperna, 1983	Taiwan	Invasive	Gills	Americas, Europe, Asia, Oceania	Basson and Van As (1994)
	India	Invasive	Gills		Mitra and Bandyopadhyay (2005)
Trichodina compacta van As and Basson, 1989	Philippines	Invasive	Skin and gills	Americas, Africa, Oceania	Arthur and Lumanlan-Mayo (1997)
Trichodina heterodentata Duncan, 1977	Native range	Native[a]	Gills	Worldwide	Basson et al. (1983)
	Israel	Invasive	Gills		Basson et al. (1983)
	Australia	Invasive	Gills		Dove and O'Donoghue (2005)
**Trichodina pediculus* Müller, 1786	Vietnam	Invasive	NR	Europe, Asia, Oceania	Arthur and Te (2006)
Trichodina minuta Basson, Van As and Paperna 1983	Native range	Native	Skin, fin and gills	Africa	Basson et al. (1983)
Bivalvia					
Unidentified bivalve larva (glochidium)	Australia	Invasive	Gills		Present Study
Chromadorea					
Contracaecum sp. Raillet and Henry, 1912 (larvae)	Native range	Native	NR		Boomker (1994a); Barson et al. (2008a); Madanire-Moyo et al. (2012); Sara et al. (2014); Tavakol et al. (2015)
	Mexico	Invasive	Free or encapsulated in abdominal cavity, mesentery, liver, stomach wall		Pérez-Ponce de León et al. (1996); Moravec (1998)
Gnathostoma binucleatum Almeyda-Artigas, 1991 (larvae)	Mexico	Invasive	Musculature	Americas	Moravec (1998)
Gnathostoma sp. (larvae)	Mexico	Invasive	Musculature		Moravec (1998); Vidal-Martínez (2001): not sighted: in Gibson et al. (2005)
Goezia nonipapillata Osorio-Sarabia, 1982	Mexico	Invasive	Lumen of digestive tract	Americas	Pérez-Ponce de León et al. (1996); Moravec (1998); Vidal-Martínez (2001): not sighted: in Gibson et al. (2005)
Paracamallanus cyathopharynx (Baylis, 1923)	Native range	Native	NR	Africa, Asia	Madanire-Moyo et al. (2012); Sara et al. (2014)
Procamallanus laevionchus (Wedl, 1862)	Native range	Native	NR	Africa, Asia	Madanire-Moyo et al. (2012)
Rhabdochona sp.	Native range	Native			Boomker 1994a
Rhabdochona kidderi texensis Moravec and Huffman, 1988	United States	Invasive	NR	Americas	Moravec (1998)
Un-identified nematode larva	Native range	Native	NR		Boomker (1994a, b); Madanire-Moyo et al. (2012)
Palaeacanthocephala					
Telosentis sp.	Australia	Invasive	Intestine		Webb (2003)
Secernenta					
Eustrongylid sp.	Australia	Invasive	Operculum		Webb (2003)
Trematoda					
Clinostomum sp. Leidy, 1856	Native range	Native	NR		Madanire-Moyo et al. (2012)
	Australia	Invasive	Body cavity		Webb (2003)
Clinostomum complanatum (Rudolphi, 1814)	Native range	Native	Encysted in muscles	**Worldwide (Sereno-Uribe et al. 2013)	Barson et al. (2008a)
Diplostomum sp. Nordmann, 1842	Native range	Native	NR		Madanire-Moyo et al. (2012)
	Mexico	Invasive	NR		Pérez-Ponce de León et al. (1996)
Diplostomum compactum (Lutz, 1928)	Mexico	Invasive	NR	Americas	Pérez-Ponce de León et al. (1996); Lamothe-Argumedo et al. (1997)
	Venezuela	Invasive	NR		Aragort et al. (1997): not sighted: in Gibson et al. (2005)

Table 3. *(continued)*

Drepanocephalus olivaceus Nasir and Marval 1968	Mexico	Invasive	NR	Americas	Pérez-Ponce de León et al. (1996)
Echinostome sp.	Australia	Invasive	Gills		Webb (2003); Present study
Metacercarial cysts	Australia	Invasive	Body cavity		Webb (2003)
Neascus sp. Von Nordmann, 1832	Native range	Native	NR		Madanire-Moyo et al. (2012)
Neutraclinostomum intermedialis (larvae) Lamont 1920	Native range	Native			Sara et al. (2014)
Posthodiplostomum minimum (MacCallum, 1921)	Mexico	Invasive	NR	Americas, Europe, Africa	Lamothe-Argumedo et al. (1997);
Ribeiroia ondatrae (Price, 1931)	Mexico	Invasive	NR	Americas	Pérez-Ponce de León et al. (1996)
Saccocoeliioides sp.	Mexico	Invasive	NR		Vidal-Martínez (2001): not sighted: in Gibson et al. (2005)
Tetracotyle sp. Diesing, 1858	Native range	Native	NR		Madanire-Moyo et al. (2012)
Transversotrema patialense (Soparkar, 1924) Cruz and Sathananthan 1960 (syn. *Transversotrema laruei* Velasquez, 1958)	Philippines	Invasive	Skin	Worldwide (Womble et al. 2015)	Arthur and Lumanlan-Mayo (1997)
	Australia	Invasive	Skin		Present Study
Tylodelphys sp. Diesing, 1850	Native range	Native	NR		Madanire-Moyo et al. (2012)
Cestoda					
Gryporynchid cestode larvae	Native range	Native	Intestines		Barson et al. (2008a); Madanire-Moyo et al. (2012); Sara et al. (2014)
Schyzocotyle acheilognathi (Yamaguti, 1934)	Australia	Invasive	Intestine	Worldwide (Kuchta et al. 2018)	Webb (2003)
Monogenea					
Monogenea gen. sp.	Phillipines	Invasive	NR		Arthur and Lumanlan-Mayo (1997)
Anacanthorus colombianus Kritsky and Thatcher, 1974	Colombia	Invasive	NR	Americas	Kritsky and Thatcher 1974; Kohn and Pinto-Paiva (2000)
[b]*Cichlidogyrus* spp.	Native range	Native	Gills		Olivier et al. (2009)
Cichlidogyrus sp.	Venezuela	Invasive	Gills		Aragort et al. (1997) not sighted: in Gibson et al. (2005)
Cichlidogyrus dossoui Douëllou, 1993	Native range	Native	Gills	Americas, Africa	Madanire-Moyo et al. (2011; 2012)
Cichlidogyrus halli (Price and Kirk, 1967)	Native range	Native	Gills	Africa, Asia	Olivier et al. (2009); Madanire-Moyo et al. (2011; 2012); Sara et al. (2014); Firmat et al. (2016)
	Japan	Invasive	Gills		Maneepitaksanti and Nagasawa (2012)
Cichlidogyrus sclerosus Paperna and Thurston, 1969	Native range	Native	Gills	Americas, Africa, Asia	Paperna and Thurston (1969); Olivier et al. (2009); Madanire-Moyo et al. (2011; 2012); Firmat et al. (2016)
	Colombia	Invasive	Gills		Kritsky and Thatcher 1974; Kohn and Pinto-Paiva (2000)
	Japan	Invasive	Gills		Maneepitaksanti and Nagasawa (2012)
Cichlidogyrus tilapiae Paperna, 1960	Native range	Native	Gills	Americas, Africa, Asia, Oceania	Olivier et al. (2009) Madanire-Moyo et al. (2011; 2012); Firmat et al. (2016; as *Cichlidogyrus* cf. *tilapiae*)
	Australia	Invasive	Gills		Webb (2003); Present study
	Colombia	Invasive	Gills		Kohn and Pinto-Paiva (2000); Kritsky and Thatcher (1974)
	Japan	Invasive	Gills		Maneepitaksanti and Nagasawa (2012)
Dactylogyrus sp.	Philippines	Invasive	NR		Arthur and Lumanlan-Mayo (1997)
[c]*Enterogyrus* spp. Paperna, 1963	Native range	Native	NR		Madanire-Moyo et al. (2012)
Enterogyrus cichlidarum Paperna 1963	Native range	Native	Stomach mucosa		Olivier et al. (2009)

Table 3. *(continued)*

Scutogyrus sp. Pariselle and Euzet 1995	Native range	Native	Gills		Firmat et al. 2016
Scutogyrus chikhii Pariselle and Euzet, 1995	Congo	Invasive	Gills		Pariselle and Euzet (1995)
Scutogyrus gravivaginus (Paperna and Thurston, 1969)	Native range	Native	Gills		Olivier et al. (2009)
Scutogyrus longicornis (Paperna and Thurston, 1969)	Native range	Native	Gills		Madanire-Moyo et al. (2011; 2012)
Arthropoda					
Argulus sp.	Australia	Invasive	Body, Fins		Webb (2003, 2008); Present Study
Argulus indicus Weber, 1892	Philippines	Invasive	NR	Europe, Oceania	Arthur and Lumanlan-Mayo (1997)
Argulus japonicus Thiele 1900	Native range[a]	Native	Skin	Worldwide (Trujillo-González et al. 2018)	Avenant-Oldewage (2001); Sara et al. (2014)
Dolops ranarum (Stuhlmann, 1891)	Native range	Native	NR	Africa	Madanire-Moyo et al. (2012)
Ergasilus sp. von Nordmann, 1832	Native range	Native	NR		Madanire-Moyo et al. (2012)
Lernaea sp.	Native range	Native	NR		Oldewage and Van As (1987)
Lernaea cyprinacea	Native range[a]	Native	Body	Worldwide (Welicky et al. 2017)	Robinson and Avenant-Oldewage (1996); Barson et al. (2008b); Dalu et al. (2012); Welicky et al. (2017)
Subtriquetra rileyi Junker, Boomker and Booyse, 1998	Native range	Native	NR	Africa	Luus-Powell et al. (2008)
Clitellata					
Zeylanicobdella arugamensis De Silva, 1963	Sri Lanka	Invasive	Skin	Asia, Oceania	De Silva (1963)

[a]Indicates parasites documented from the native range in southern Africa but are considered to have been introduced (i.e., exotic) in that region as per Smit et al. (2017). [b]Includes two proposed species. [c]Includes three proposed species. NR = not recorded. *See Van As and Basson (1989) for discussion regarding the validity of the identification of this species from various freshwater fishes. **See Bastos Gomes et al. 2017 for possible synonymy with *C. hexasticha*; see Sereno-Uribe et al. 2013 for account of taxonomic instability. Identifications made by other authors were not authenticated because of the lack of accessioned specimens in curated collections. Information on parasite species' distributions was determined from records by FAO global regions (i.e., Africa, Americas, Asia, Europe, Oceania). Where a parasite species can be found in all five regions the distribution was termed 'worldwide' and a key reference or review is indicated.

and invasive populations (Table 3) including three monogeneans (*Cichlidogyrus tilapiae* Paperna, 1960; *Cichlidogyrus sclerosus* Paperna and Thurston, 1969 and *Cichlidogyrus halli* (Price and Kirk 1967)), and one trichodinid (*Trichodina heterodentata* Duncan, 1977).

A total of 72 *Oreochromis mossambicus* were sampled from the Ross River and surrounding tributaries. Campus Creek (76 ± 3 mm; mean ± SE) and Annandale Creek (63 ± 4 mm) had smaller average fish sizes in comparison to Black Weir (229 ± 3 mm) and Aplins Weir (248 ± 56 mm; Table 1). External necropsy of the skin and gills revealed that 35 of the 72 *O. mossambicus* examined were infected with parasites. Seven different types or species were identified, comprising a monogenean (*Cichlidogyrus tilapiae* Paperna, 1960), a branchiurid crustacean (*Argulus* Müller, 1785 sp.), a parasitic larval stage of a freshwater mussel species (i.e., glochidium, unidentified bivalve sp.), two digeneans (Echinostome sp. and *Transversotrema patialense* Soparkar, 1924), one dinoflagellate (*Piscinoodinium* sp. Lom, 1981) and one hymenostomatian (*Ichthyophthirius multifiliis* Fouquet, 1876) (Table 2). We also found a single case of an unidentified encysted parasite larva on the skin (Table 2). No endoparasite fauna were detected. This study provides the first record of *O. mossambicus* as a host for parasitic bivalve larva.

Australian *O. mossambicus* shared two parasites with the native range in Africa including *Cichlidogyrus tilapiae* and *Trichodina heterodentata* (see Dove and O'Donoghue 2005; Webb 2003, 2008; present study). Australian *O. mossambicus* were infected by three additional parasite species (*Ichthyophthirius multifiliis*, *Schyzocotyle acheilognathi* (Yamaguti, 1934) Brabec, Waeschenbach, Scholz, Littlewood and Kuchta, 2015 and *Transversotrema patialense*) that have not been recorded on this species in the native range (Table 3; Figure 2).

Discussion

Oreochromis mossambicus in Australia exhibited relatively low parasite diversity (five species; 13 putative types) compared to the cumulative species richness in native host populations (23 species; 38 putative types; Figure 2, Table 3) and only two parasite species were proposed to be co-introduced in Australia, with a total of four species considered co-introduced elsewhere (Figure 2). Various parasite-host and environmental interactions following incursion can account for this loss of parasite diversity on invasive fish populations (Goedknegt et al. 2016). First, it is plausible that some *O. mossambicus* were introduced into these new localities without parasites. Second, parasites present on the infected hosts might have died or been compromised during the transportation process, decreasing the potential to establish in the new environment. Third, co-introduced parasites could lack suitable intermediate hosts during developmental stages to close life cycles and thus are unable to propagate (Torchin et al. 2003). Finally, parasite loss can occur because of environmental changes in the new locality (i.e., outside the tolerance limits of the parasite species, but within the tolerance limits of the host fish) or through predator interactions (Grutter 1999). These pressures contribute to reduced parasite abundance on invasive fish species where low densities inhibit the parasite species' ability to establish populations in the non-native environment.

Release from parasites, pathogens and predators or the "enemy release" hypothesis has been cited extensively for invaders that have become widespread. Torchin et al. (2003) found an average reduction of 50% in parasite species richness of invasive populations compared to their native counterparts. For example, invasive peacock grouper, *Cephalopholis argus* (Bloch and Schneider, 1801), are host to ten parasite species in their native range in the Indian Ocean compared to three species in invasive populations in the Pacific Ocean (Vignon et al. 2009). Similarly, we found invasive *O. mossambicus* in Australia were host to 13 compared to 38 putative parasite types in their native range (Table 3). It is important to consider that subsampling of hosts could result in an overestimation of enemy release and that appropriate biogeographical sampling is needed to eliminate bias (Colautti et al. 2005). Our sample size (n = 72) gave 95% confidence of detecting parasites in the Ross River tributaries at a prevalence of ≥ 5% (Sergeant 2018). Furthermore, prior examination of *O. mossambicus* in this system (i.e., Webb 2003) gives further confidence in the temporal distribution of parasite species. Nevertheless, more species may be found with an increase in the temporal and spatial scale of the sampling within the Ross River.

Global comparisons of the parasite diversity of *O. mossambicus* showed that the majority of parasites reported on invasive populations were not shared with the native populations in Africa. Although parasite diversity may be initially reduced on invasive hosts, exposure to new native parasites in the new environment can potentially result in the addition of new parasite species. Hence parasite loss for invasive fish is theorised to decrease with increased residency in the new system (Colautti et al. 2004; Goedknegt et al. 2016). The Ross River *O. mossambicus* population, believed to have established nearly 40 years ago, was infected with 13 parasite types (Webb 2003; present study), of which only two species are proposed to have been co-introduced (Figure 2). This indicates that the Ross River population has limited original parasite diversity, but has acquired up to eleven new parasites since its invasion.

One of the parasites recovered, the unidentified bivalve glochidium, is believed to be indigenous to the Ross River system (Widarto 2007). However, the remaining ten putative types have unknown origins. The *Argulus* sp. collected in this study could not be compared with Webb's *Argulus* sp. A, which was also collected in the Ross River, because Webb (2008) did not accession parasite specimens. Our *Argulus* sp. specimens were clearly morphologically distinct from *A. indicus* Weber, 1892 (reported from *O. mossambicus* in the Phillipines; Table 3) and *Argulus japonicus* Thiele, 1900 (reported from *O. mossambicus* in South Africa; Table 3) and represent a new species. Thus, there was no evidence that the *Argulus* sp. collected in this study was shared with the native range in Africa.

The four parasite species we propose that have successfully been co-introduced with invasive *O. mossambicus* elsewhere exhibit direct life cycles (i.e., *Cichlidogyrus tilapiae*, *C. sclerosus, C. halli* and *Trichodina heterodentata*). Parasite species that exhibit direct life cycles only require a single host species to reproduce and it can be expected that parasites that exhibit this life history will be able to establish and reproduce in optimal conditions. Parasites that exhibit complex life cycles require multiple susceptible host species (either new native hosts and/or suitable invasive hosts) and specific host interactions to successfully colonise new environments. *Trichodina heterodentata* has been described from *O. mossambicus* in its native range (Basson et al. 1983) and also from *O. mossambicus* in introduced populations (Australia, Dove and O'Donoghue 2005; Israel, Basson et al. 1983). However, it is possible that *T. heterodentata* is not a native parasite of *O. mossambicus* and has host-switched from other commonly introduced fishes on which it has also been recorded, such as *O. niloticus* or *Carassius auratus* (see Basson and Van As 1994; Table 3). Dove and O'Donoghue (2005) found that *T. heterodentata* infected 17 species of fishes in Australia and suggested the most plausible origin was that it has been introduced to Australia with *O. mossambicus*. Nevertheless, the authors note that there are multiple possible fish hosts that could co-introduce *T. heterodentata* (see Dove and O'Donoghue 2005 for a list of known host fishes) and the possibility that *T. heterodentata* is a native Australian species cannot be discounted.

The monogenean gill parasite *Cichlidogyrus tilapiae*, a native parasite of *O. mossambicus* (see Madanire-Moyo et al. 2011, 2012) was recorded in the invasive Ross River population (Table 2), but the co-invasion of *C. tilapiae* on native fish species in Australia has not been investigated. However, other cichlid parasites (including monogeneans, trematodes and cestodes) can transfer from introduced African tilapias to native and non-native fauna (Vanhove et al. 2016). For example, *Cichlidogyrus* spp. and *Enterogyrus malmbergi* are believed to have transferred from exotic African *Oreochromis* spp. to native American cichlid fish (Jiménez-García et al. 2001). It is plausible that *Cichlidogyrus* spp. could host-switch when translocated to new environments given that Messu Mandeng et al. (2015) showed that *Cichlidogyrus* spp. have host-switched from a cichlid host to *Aphyosemion* spp. (Cyprinodontiformes, Nothobranchiidae) under natural conditions. This is a concern because hosts that have not co-evolved with parasites have little to no adaptive immunity against infection (Lymbery et al. 2014).

Parasite reduction on invasive fish hosts can lead to increased vigour within the new environment. The absence of parasites and loss of parasite diversity is likely to increase the fitness of the invasive hosts conferring competitive advantages over most native fish (Colautti et al. 2004). Furthermore, the loss of parasites may lead to a "compensatory release" whereby energy invested in immunological responses are not needed and are utilised for other growth mechanisms instead (Colautti et al. 2004). This could result in increased invasive fish condition and fecundity, thus further contribute to the invasive success of *O. mossambicus* in non-native rivers. However, parasite interactions are intrinsically complex and it is evident from this study that *O. mossambicus* parasite fauna in the Ross River, Australia, is in flux: they have lost many species from their native range and acquired several species from their non-native range (see also

Roche et al. 2010). Hypothetically, the loss of parasites has likely conferred a competitive advantage to *O. mossambicus* (as per the enemy-release hypothesis) and the gain of other parasites over time has probably altered this competitive advantage. Further, that *O. mossambicus* have gained other parasites suggests there is considerable potential for parasite “spillback” to native species. However, the role of other invasive species in this ecosystem should not be discounted. Importantly, while we have observed changes in the parasite fauna of *O. mossambicus*, relative “fitness” and spillback has not been measured. Furthermore, in comparing the parasite fauna of Ross River *O. mossambicus* to other invasive populations, it is clear that there are parasite species that have the potential to co-invade that do not yet appear to infect *O. mossambicus* in the Ross River. Thus, prevention of further incursions into already invaded systems remains important to keep new parasitic diseases from becoming established.

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