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Distribution, diet and potential ecological impacts of the introduced Mozambique mouthbrooder *Oreochromis mossambicus* Peters (Pisces: Cichlidae) in Western Australia

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Abstract

Oreochromis mossambicus is a highly successful invader of aquatic ecosystems due to its adaptable life history, trophic flexibility, ability to tolerate extreme and often unfavourable environmental conditions and maternal care of offspring. Upon introduction to areas outside of its natural range, these characteristics often give *O. mossambicus* a competitive advantage over indigenous fishes. Accordingly, *O. mossambicus* may have deleterious impacts on aquatic communities. Since nonindigenous *O. mossambicus* populations were first observed in Western Australia in the Gascoyne/Lyons River system (*ca* 25°S) in 1981, the species has spread north to the Lyndon and Minilya Rivers (*ca* 23°S), and south to the Chapman River (*ca* 28°S). There is a high probability of further range expansions of this cichlid in Western Australia due to natural dispersal and human-mediated translocation. Adult and juvenile *O. mossambicus* consumed primarily detritus and vegetal matter, though juveniles collected from the Gascoyne River were carnivorous. There was no demonstrable dietary overlap between *O. mossambicus* and the carnivorous and omnivorous sympatric species in the Chapman and Gascoyne Rivers. However, a statistically significant dietary overlap was noted between *O. mossambicus* and the native species *Craterocephalus cuneiceps* and *Hypseleotris aurea* in the Lyons River. Anecdotal observations of agonistic behaviour by breeding male *O. mossambicus* indicated that such behaviour was mainly directed towards other breeding males. The semi-arid climate of the Indian Ocean (Pilbara) Drainage Division results in the reduction of riverine habitats to small isolated pools during extended dry periods. Thus, in these restricted environments resource competition may occur between *O. mossambicus* and indigenous species.

Keywords: *Oreochromis mossambicus*, agonistic behaviour; cichlid; dietary overlap; freshwater fish; introduced species; tilapia; translocation

Introduction

The Mozambique mouthbrooder or tilapia, *Oreochromis mossambicus* (Fig. 1), is one of the most translocated freshwater teleosts worldwide (Arthington 1986; Blühdorn & Arthington 1990; Costa-Pierce 2003; Canonico *et al*. 2005). *Oreochromis mossambicus* is indigenous to fresh and brackish waters of southeastern Africa (Trewavas 1983; Skelton 2001) and has been cultured in many countries, most notably in Africa and Asia, for human consumption (Cadwaller *et al*. 1980). Their introduction into Australia was, however, as an ornamental species (Arthington 1986; Allen *et al*. 2002). Introduced *O. mossambicus* populations occur in tropical and subtropical areas of Australia including northeastern Australia (Queensland) and Western Australia (Arthington & Blühdorn 1994; Morgan *et al*. 2004). While the distribution and biology of the species has been well documented in Queensland (*e.g.* Arthington 1986; Arthington & Milton 1986; Blühdorn & Arthington 1990; Mather & Arthington 1991; Arthington & Blühdorn 1994; Blühdorn & Arthington 1994; Mackenzie *et al*. 2001; Russell *et al*. 2003; Canonico *et al*. 2005), little is known of its biology and potential impacts in Western Australia. This is of particular concern as the arid rivers in the Indian Ocean Drainage Division of Western Australia support five endemic freshwater teleosts with restricted distributions within this region (Morgan & Gill 2004).

Unfortunately, the characteristics that make *O. mossambicus* desirable as an aquaculture species also predispose it for success as an invasive species (Canonico *et al*. 2005). For example, the species is euryhaline and may reproduce in salinities from fresh to seawater (Laundau 1992; Skelton 2001), tolerates high concentrations of ammonia and nitrite (Popma & Masser 1999), tolerates wide temperature regimes and low

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Figure 1. Male *Oreochromis mossambicus* collected from the Gascoyne River in Western Australia (198 mm standard length). (Photo: Mark Allen).

dissolved oxygen levels (Lovell 1998; Mackenzie *et al.* 2001), and is omnivorous, commonly consuming macrophytes, filamentous algae, phytoplankton, detritus and benthic organisms (Bruton & Boltt 1975; De Silva *et al.* 1984; Merrick & Schmida 1984; Arthington 1986; Laundau 1992). Furthermore, mouthbrooding (*i.e.* the maternal care of the fertilised eggs and newly hatched offspring) and protracted reproductive periods reduce the risk of offspring predation (Merrick & Schmida 1984).

There is a paucity of research on the precise environmental impacts of *O. mossambicus*, or the extent of competition, if any, between this introduced species and sympatric native fish in Australian waters and worldwide (Arthington 1986; Arthington & Blühdorn 1994; Mackenzie *et al.* 2001; Russell *et al.* 2003; Canonico *et al.* 2005). The high reproductive effort, growth rate, maternal care of offspring, and trophic and physiological flexibility enable the rapid establishment of *O. mossambicus*, often to the detriment of native species (Cadwaller *et al.* 1980; Canonico *et al.* 2005). *Oreochromis mossambicus* will also consume macrophytes (Arthington *et al.* 1994), which has led to their deliberate introduction, particularly in America, as a biocontrol agent (McCann *et al.* 1996, Helfman *et al.* 1997). This may lead to the disappearance of native aquatic plants when the species reaches high densities (Fuller *et al.* 1999). In Australia, *O. mossambicus* is a declared noxious species in Queensland and its importation into this country has been prohibited since 1963 (Arthington 1986; Blühdorn & Arthington 1990).

The occurrence of *O. mossambicus* in the Pilbara region provides the opportunity to examine the distribution, biology and potential ecological impacts of *O. mossambicus* in Western Australia, which are currently unknown. The persistence of the species in these often arid and unpredictable environments is most likely influenced by the ability to occupy unexploited niches, or to displace less competitive or smaller species. The successful colonisation of rivers (such as the Gascoyne River), which are exposed to irregular rainfall events and may remain as a series of small, disconnected pools for extended periods, may be to the detriment of native sympatric species. Thus, the objectives of this study were to document distribution and potential range expansions, provide baseline dietary data and discuss possible impacts of *O. mossambicus* in Western Australia.

Methods

Distribution and study sites

During part of a larger study by the Murdoch University Centre for Fish and Fisheries Research, sampling was undertaken in all rivers in the Indian Ocean (Pilbara) Drainage Division of Western Australia between December 2000 and November 2002 (see Morgan *et al.* 2003; Morgan & Gill 2004; Morgan *et al.* 2004). *Oreochromis mossambicus* was collected from the Chapman, Gascoyne, Lyons, Lyndon and Minilya rivers (Fig. 2). The Chapman River, at *ca* 28°S, is the most southerly location where this species occurs in Western Australia. *Oreochromis mossambicus* has been present in the Gascoyne River since 1981 (Allan *et al.* 2002), and rapidly spread throughout the main tributary, the Lyons River (Blühdorn & Arthington 1990). The Minilya and Lyndon rivers, just north of the Gascoyne River, represent the most recent range expansion of the species in Western Australia.

Sampling regime

Oreochromis mossambicus and sympatric species

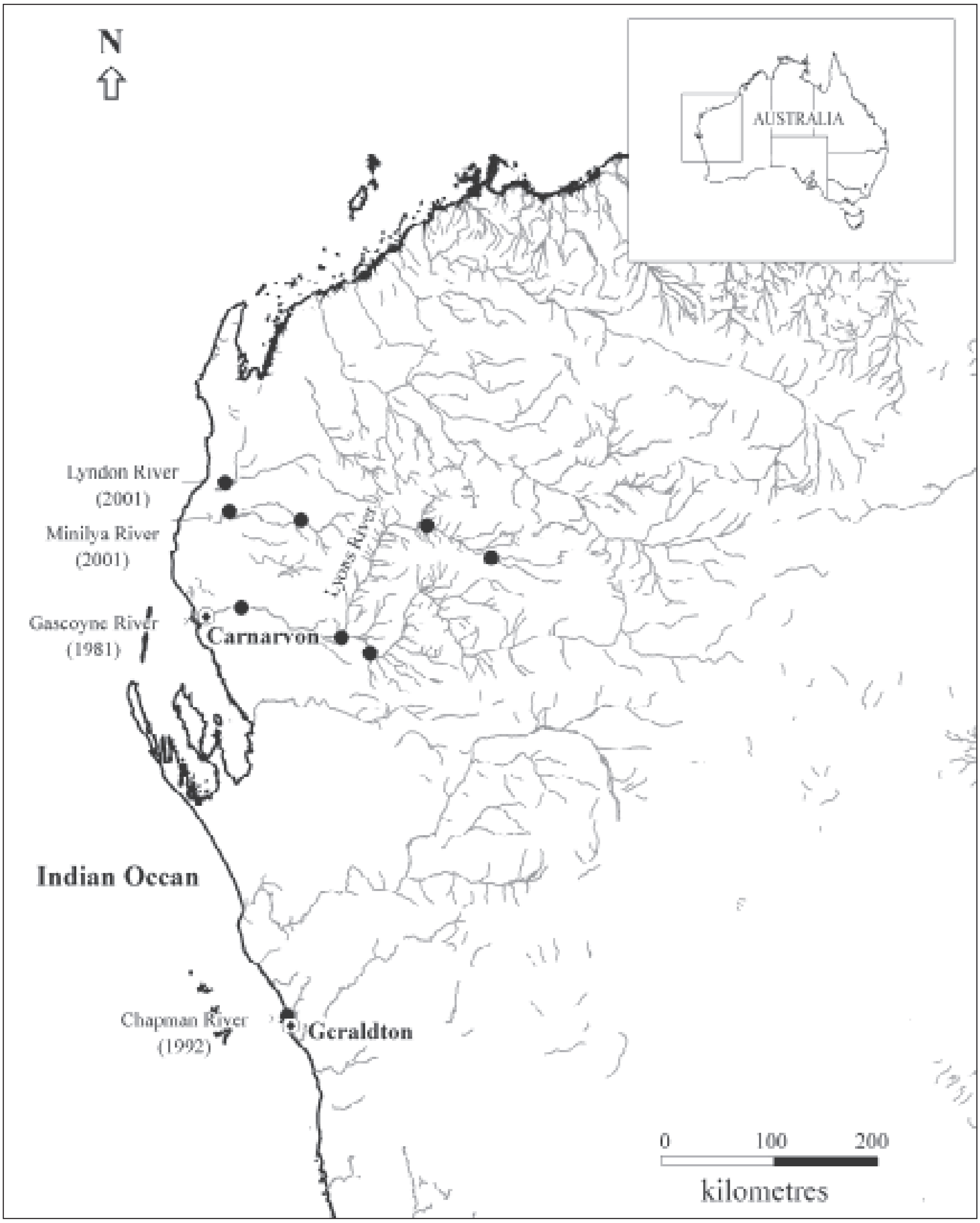

Figure 2. Sample sites (●) where *Oreochromis mossambicus* was collected in the Indian Ocean (Pilbara) Drainage Division of Western Australia. The year *O. mossambicus* was discovered in each river is included in parenthesis.

(where present) were collected with a seine net (either 21, 10 or 5 m seine net, with 3 mm mesh and 1.5 m drop). Seine samples were collected along banks adjacent to littoral and emergent vegetation (Chapman River, Lyons River), and across small pools (Gascoyne River). A small number of male *O. mossambicus* were collected utilising fishing lures in the Gascoyne River. A sub-sample of co-occurring species was retained for dietary analyses. After collection, specimens were anaesthetised and placed in 70% ethanol. Temperature, pH and conductivity were recorded from just below the water surface at each site when sampling.

Dietary analysis

The standard length (SL) of each fish was measured to the nearest 1 mm and the stomach, or in species that do not possess a well-defined stomach, the wide anterior section of the intestine was removed and inspected initially under a dissecting microscope. As *O. mossambicus* and other species collected were often detritivorous, the intestinal contents were inspected under a compound microscope (100–400 x magnification) and the small particulate matter identified to the lowest possible taxon. The diets of each species were analysed using the percentage frequency of occurrence and the percentage volumetric contribution of each dietary taxon (Hynes 1950; Hyslop 1980). The percentage frequency of occurrence is the percentage of all fish in a sample that have ingested a particular dietary item. The percentage volumetric contribution is the contribution of each taxon to the total gut contents of each fish, and was determined using the points method and estimates of stomach fullness (Hynes 1950; Hyslop 1980).

Volumetric data allow the best estimation of the relative importance of each dietary item (Hyslop 1980), therefore the percentage volumetric data for each individual dietary sample analysed were used to create similarity matrices for each species based on the Bray-Curtis similarity measure in the PRIMER v5.0 statistical package (Clarke & Gorley 2001). A one-way analysis of similarity (ANOSIM) was performed on the Bray-Curtis similarity matrices to provide a measure of dietary overlap between species, and between *a priori* designated size groups within the same species. ANOSIM is a non-parametric test that uses a permutation procedure applied to a ranked similarity matrix, based on, in this case, a Bray-Curtis similarity matrix. The test statistic R is a measure of the discrimination between groups, with a value of 0 indicating no differences between groups, and a value of 1 indicating that each member within an *a priori* designated group is more similar to other members of the group than it is to members of any other group. The significance value of each pairwise comparison (one-way ANOSIM) is used to indicate dissimilarity, with percentages below 5% (*i.e.* $p < 0.05$) usually considered statistically significant. Where possible, a more conservative significance level of $p < 0.01$ or $p < 0.001$ was highlighted in the results obtained. To graphically display differences and similarities in diets of the Chapman River fish samples, the Bray-Curtis similarity matrix was then classified using hierarchical agglomerative cluster analysis with group-average linking (Clarke & Gorley 2001).

Results

Chapman River study site

Oreochromis mossambicus was collected in the Chapman River estuary (114.631°E, 28.728°S) (Fig. 2). A small weir prevents the species' ingress upstream, thus, *O. mossambicus* is presently restricted to the lower reaches of this system. *Paspalum distichum* dominated the riparian vegetation creating a sheltered habitat at the waters edge, a characteristic that also makes this species a major weed of drainage channels in parts of Australia (Sainty & Jacobs 1994). Dietary analysis was conducted on three seasonal samples (*i.e.* spring, summer, autumn) of *O. mossambicus* and sympatric native species collected at this location (Tables 1, 2). No large *O. mossambicus* (*i.e.* greater than 112 mm) were collected.

A total of 4940 fishes comprising seven species was captured from the Chapman River study site in spring (24/10/02), summer (05/02/03), autumn (13/04/03) and winter (9/07/03) samples (Table 1), including two introduced fishes, *i.e. O. mossambicus* and *Gambusia holbrooki* (Poeciliidae), and five estuarine fishes, *i.e. Mugil cephalus* (Mugilidae), *Acanthopagrus butcheri* (Sparidae), *Amniataba caudavittata* (Terapontidae), *Hypseleotris compressa* (Eleotridae), and *Pseudogobius olorum* (Gobiidae). The prevalence of *O. mossambicus* and sympatric species varied greatly over four seasonal samples (Table 1). In spring, *O. mossambicus* comprised 12.7 % of collected specimens, and occurred at a density of 0.34 m^{-2} in the Chapman River. It was the fourth most prevalent species after *G. holbrooki* and two native fishes. In summer, the mean density of *O. mossambicus* increased markedly to 3.23 m^{-2}, and it was the most prevalent species (48.4 % of fish collected). This pattern continued in autumn with the mean density of *O. mossambicus* increasing to 8.47 m^{-2}. This cichlid was still the most prevalent species and comprised 64.1 % of fish collected. In winter the density of *O. mossambicus* decreased to 1.1 m^{-2} (34.3 % contribution), and was the second most abundant species after the indigene *P. olorum*. Over the year, the only native species captured in appreciable quantities were *H. compressa*, *P. olorum* and *A. butcheri* (Table 1).

Twenty-three prey items were identified from the intestinal tracts of *O. mossambicus* and six co-occurring species collected from the Chapman River in spring (Table 2). The bulk of the diet of small *O. mossambicus* was algae (60.9 %), with vegetal matter (10.9 %) and silt/biofilm (12.0 %) also important. In summer and autumn, the diet of *O. mossambicus* was also dominated by these three dietary items in varying quantities (dietary data for remaining seasons not shown). The diet of sympatric native species was predominantly carnivorous, except for *M. cephalus* which consumed vegetal matter and unidentified organic matter (Table 2). The bulk of the diet of *G. holbrooki* was terrestrial insects; a dietary item unutilised by other species except *A. butcheri*. Some dietary variation was displayed by each species between seasons, and importantly, ANOSIM demonstrated a highly significant ($p<0.001$) difference between the diet of *O. mossambicus* and all sympatric species in each season (spring global R = 0.44, summer global R = 0.695, autumn global R = 0.736), except for *M. cephalus* in spring ($p<0.01$). Classification of the mean volumetric contributions of the different dietary taxa revealed three distinct groups (Fig. 3). The first group consisted of the three seasonal *G. holbrooki* samples, in which diets consisted principally of terrestrial insects. The second grouping included the three *O. mossambicus* samples and the one spring *M. cephalus* sample. This group primarily ingested vegetal matter, algae, silt/biofilm and sand. The third group included all other samples from species that were primarily carnivorous. The diets of this group (including *H. compressa*, *A. butcheri*, *P. olorum* and *A. caudavittata*) included insect larvae (dipteran larvae and ephemeropteran nymphs) and Crustacea.

The mean temperature in the Chapman River increased from 23.1 °C (± 0.00 SE) in spring to 27.5 °C (± 0.11 SE) in summer, and decreased in autumn to 22.9 °C (± 0.06 SE), and decreased again in winter to

Table 1

Total number, percentage contribution, density and length range of *Oreochromis mossambicus* and six co-occurring species collected from the Chapman River in (a) spring, (b) summer, (c) autumn and (d) winter 2002/2003. NB: Dietary analysis was restricted to samples equal to or larger than five specimens.

	O. mossambicus	***G. holbrooki***	***A. butcheri***	***A. caudavittata***	***M. cephalus***	***H. compressa***	***P. olorum***
(a)							
Total specimens collected	76	220	16	7	5	134	140
Percentage contribution	12.7 %	36.8%	2.7 %	1.2 %	0.8%	22.4%	23.4%
Density (m^{-2} ± SE)	0.34 (± 0.022)	0.88 (± 0.169)	0.06 (± 0.013)	0.02 (± 0.006)	0.02 (± 0.006)	0.52 (± 0.125)	0.56 (± 0.121)
Length Range (SL)	32–44 mm	25–36 mm	31–134 mm	45–69 mm	28–56 mm	30–59 mm	24–44 mm
(b)							
Total specimens collected	1344	1333	1	18	1	65	14
Percentage contribution	48.4 %	48.0 %	~0 %	0.6 %	~0 %	2.3 %	0.5 %
Density (m^{-2} ± SE)	3.23 (± 0.292)	3.86 (± 1.828)	0.01 (± 0.003)	0.05 (± 0.007)	0.01 (± 0.002)	0.13 (± 0.058)	0.04 (± 0.020)
Length Range (SL)	30–40 mm	22–29 mm	137 mm	20–73 mm	101 mm	43–55 mm	15–25 mm
(c)							
Total specimens collected	847	428	–	1	–	44	1
Percentage contribution	64.1 %	32.4 %	–	0.1 %	–	3.3 %	0.1 %
Density (m^{-2} ± SE)	8.47 (± 3.530)	4.28 (± 0.680)	–	0.01 (± 0.010)	–	0.44 (± 0.080)	0.01 (± 0.010)
Length Range (SL)	9–63 mm	17–27mm	–	30 mm	–	28–57mm	28 mm
(d)							
Total specimens collected	84	23	16	–	9	25	88
Percentage contribution	34.3 %	9.4 %	6.5 %	–	3.7 %	10.2 %	35.9 %
Density (m^{-2} ± SE)	1.05	0.29	0.20	–	0.11	0.31	1.10
Length Range (SL)	18–112 mm	22–31 mm	19–139 mm	–	26–149 mm	28–69 mm	11–41 mm

Table 2

Number of dietary samples, mean stomach fullness and percentage dietary contribution by volume (and percentage occurrence in parenthesis) of *Oreochromis mossambicus* and six co-occurring species collected from the Chapman River in spring (October 2002).

	O. mossambicus	***G. holbrooki***	***A. butcheri***	***A. caudavittata***	***M. cephalus***	***H. compressa***	***P. olorum***
Dietary sample	*n* = 12	*n* = 12	*n* = 12	*n* = 7	*n* = 5	*n* = 12	*n* = 12
Mean stomach fullness (± SE)	5.4 (± 0.61)	4.6 (± 0.58)	5.5 (± 0.45)	5 (± 0.76)	5.4 (± 0.40)	4.8 (± 0.53)	5.1 (± 0.6)
Prey type							
Algae (Unicell/Filament)	60.9 (100)	17.6 (50.0)	0.8 (25.0)	–	14 (100)	37.8 (91.7)	25.2 (75.0)
Bacillariophyceae	3.7 (100)	1.0 (25.0)	–	–	6.6 (100)	1.9 (83.3)	0.6 (41.7)
Vegetal matter	10.9 (91.7)	1.4 (25.0)	5.5 (75.0)	0.1 (14.3)	18.1 (100)	1.3 (33.3)	5.6 (75.0)
Seeds	–	–	0.2 (8.3)	–	–	–	–
Porifera gemmules/spicules	–	–	–	–	0.8 (80.0)	–	–
Protozoa	–	–	–	–	1.9 (80.0)	–	–
Arachnida	–	5.7 (25.0)	–	–	–	–	–
Terrestrial insects	–	54.3 (83.3)	2.5 (33.3)	–	–	–	–
Coleoptera (larvae)	–	–	1.4 (8.3)	–	–	–	5.7 (8.3)
Diptera (larvae)	–	9.2 (41.7)	36.5 (83.3)	69.6 (85.7)	–	22.7 (66.7)	54.4 (75.0)
Diptera (pupae)	–	1.1 (8.3)	5.6 (33.3)	3.1 (42.9)	–	4.1 (16.7)	0.7 (8.3)
Trichoptera (larvae)	–	–	7.3 (33.3)	–	–	–	–
Ephemeroptera (nymphs)	–	–	9.7 (41.7)	0.9 (14.3)	–	4.1 (8.3)	–
Anisoptera (larvae)	–	–	–	11.4 (14.3)	–	–	–
Zygoptera (larvae)	–	–	–	–	–	6.9 (8.3)	–
Amphipoda	–	–	–	1.4 (14.3)	–	12.8 (16.7)	–
Ostracoda	0.8 (16.7)	–	1.0 (33.3)	0.2 (14.3)	–	–	–
Gastropoda	–	8.6 (8.3)	14.7 (33.3)	–	–	0.9 (16.7)	–
Teleost	–	–	–	6.9 (14.3)	–	–	–
Organic matter (not identified)	5.8 (100)	–	6.8 (75.0)	2.4 (57.1)	16.5 (100)	2.5 (50.0)	3.9 (83.3)
Silt/biofilm	12.0 (83.3)	0.5 (8.3)	–	–	15.4 (100)	2.2 (33.3)	1.6 (66.7)
Sand	4.0 (100)	–	4.0 (83.3)	1.6 (28.6)	16.3 (100)	0.5 (8.3)	0.7 (25.0)
Unidentified	2.0 (41.7)	0.7 (16.7)	4.2 (66.7)	2.4 (57.1)	10.6 (100)	2.2 (50.0)	1.5 (33.3)

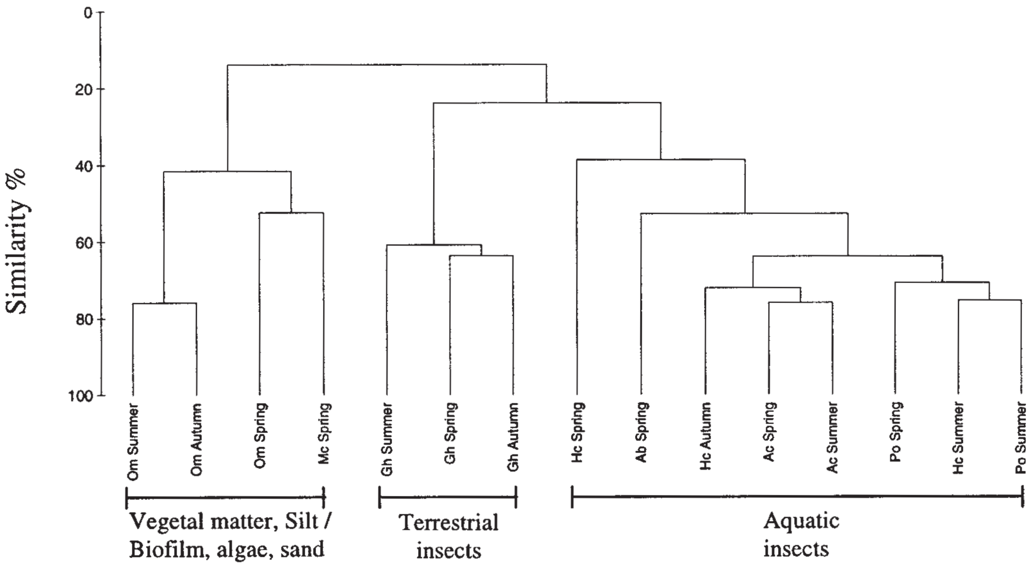

Figure 3. Classification of the mean volumetric contributions of the different dietary taxa of *O. mossambicus* and co-occurring species in the Chapman River in spring, summer and autumn 2002/2003. Species abbreviations are: Om = *O. mossambicus,* Ab = *A. butcheri,* Ac = *A. caudavittata,* Mc = *M. cephalus,* Hc = *H. compressa,* Gh = *G. holbrooki,* Po = *P. olorum.*

11.9 °C (± 0.01 SE) The mean pH in the Chapman River displayed little variation between spring (8.2 ± 0.00 SE), summer (8.5 ± 0.01 SE) autumn (8.6 ± 0.01 SE) and winter (8.6 ± 0.01 SE). Mean conductivity increased from spring (6.03 $mScm^{-1}$ ± 0.023 SE) to summer (10.73 $mScm^{-1}$ ± 0.031 SE), and again in autumn (11.90 $mScm^{-1}$ ± 0.003 SE) before declining in winter (6.80 $mScm^{-1}$ ± 0.005 SE).

Gascoyne River study site

Oreochromis mossambicus was collected from large tracts of the Gascoyne river system (Fig. 2). The dietary study site, Rocky Pool (114.138°E, 24.756°S), is a small riverine pool with a maximum depth of approximately 1.2 m situated 50 km east of the river mouth and the coastal town of Carnarvon. The benthic environment was dominated by the native macrophyte *Najas marina*. Netting was undertaken in standing pools downstream from Rocky Pool, approximately 3 km from the coast (113.671°E, 24.861°S), though *O. mossambicus* was not collected. *Oreochromis mossambicus* was found in permanent pools and artificial farm wells as far inland as Mt Augustus.

A total of 2404 fishes was collected from the Gascoyne River study site in one spring sample (22/10/2002). Four species were collected (Table 3), *i.e. O. mossambicus, M. cephalus, H. compressa* and *Leiopotherapon unicolor* (Terapontidae). *Oreochromis mossambicus* was the third most common species (though only marginally more abundant than *L. unicolor*) with a density of 0.03 m^{-2} (2.7 % of fish collected). Two distinct *O. mossambicus* size classes were present, *i.e.* specimens 165–198 mm, and 23–53 mm (Table 3). The most abundant species collected was, by far, *H. compressa* (1.2 m^{-2}, 89.4 % contribution). *Mugil cephalus* was the second most abundant species (0.08 m^{-2}, 6.2 % contribution). The terapontid *L. unicolor* comprised 1.7 % of fish collected, at a density of 0.02 m^{-2}.

Twenty prey items were identified from the intestinal tracts of *O. mossambicus* and three co-occurring species (Table 3). The primary food items consumed differed between *O. mossambicus* size classes. In contrast to small fish in the Chapman River, small fish from the Gascoyne River were insectivorous consuming ephemeropteran nymphs (43.6 %) and dipteran larvae (19.5 %) (Table 3). Large fish (165–198 mm) consumed primarily vegetal matter (54.2 %) and silt (12.4 %). Two of the native species were mostly insectivorous, with *L. unicolor* consuming primarily dipteran larvae (36.2 %) and terrestrial insects (27.5 %), while *H. compressa* consumed dipteran larvae (35.4 %) and ephemeropteran nymphs (14.9 %). *Mugil cephalus* consumed sand (58.9 %) and vegetal matter (17.2 %). ANOSIM between species' diets revealed a highly significant (Global R = 0.736; p<0.001) difference between the diets of all species including the two *O. mossambicus* size classes. In the Gascoyne River, the recorded mean temperature was 28.7 °C (± 0.01 SE), pH 8.5 (± 0.01 SE) and conductivity 3.37 $mScm^{-1}$ (± 0.003 SE).

Lyons River study site

Oreochromis mossambicus was collected from two sites on the Lyons River (Fig. 2). The study site, Cattle Pool (116.817°E, 24.278°S), is a small riverine pool near Mt Augustus. One hundred and twenty six fish were collected from the Lyons River study site in one autumn sample (02/05/02). Four species were captured (Table 4), *i.e. O. mossambicus, L. unicolor, Craterocephalus cuneiceps* (Atherinidae) and *Hypseleotris aurea* (Eleotridae). *Oreochromis mossambicus* and *C. cuneiceps* both comprised *ca* 40 % of collected specimens and occurred at a density of 6.25 m^{-2}. *Hypseleotris aurea* occurred at a density of 3.12 m^{-2} and contributed 19.8 % of the total catch. *Leiopotherapon unicolor* was the least common species with only one specimen collected.

Small *O. mossambicus* (12–27 mm) collected in the Lyons River consumed predominantly algae (13.3 %),

Table 3

Total number, percentage contribution, density, length range, number of dietary samples, mean stomach fullness and percentage dietary contribution by volume (and percentage occurrence in parenthesis) of *Oreochromis mossambicus* and three co-occurring species collected from the Gascoyne River in spring (October 2002).

	O. mossambicus	***O. mossambicus***	***L. unicolor***	***M. cephalus***	***H. compressa***
Total specimens collected	43	21	40	150	2150
Percentage contribution	1.8 %	0.9 %	1.7 %	6.2 %	89.4 %
Density (m^{-2} ± SE)	0.02 (± 0.006)	0.01 (± 0.001)	0.02 (± 0.009)	0.08 (± 0.085)	1.18 (± 0.410)
Length Range (SL)	23–53 mm	165–198 mm	69–105 mm	94–110 mm	24–49 mm
Dietary sample	*n* = 14	*n* = 13	*n* = 11	*n* = 9	*n* = 11
Mean stomach fullness (± SE)	5.5 (± 0.75)	5.2 (± 0.63)	6.5 (± 0.62)	4.1 (± 0.77)	5.1 (± 0.41)
Prey type					
Algae (Unicell/Filament)	5.1 (92.9)	7.4 (100)	–	6.7 (100)	7.7 (90.9)
Vegetal matter	3.8 (71.4)	54.2 (100)	2.1 (42.9)	17.2 (100)	0.9 (54.5)
Bacillariophyceae	1.0 (28.6)	1.1 (92.3)	–	1.2 (33.3)	0.2 (9.1)
Seeds	–	1.9 (7.7)	4.6 (35.7)	–	–
Nematoda	–	–	0.1 (7.1)	0.5 (33.3)	–
Terrestrial insects	2.3 (28.6)	4.5 (61.5)	27.5 (57.1)	–	1.0 (27.3)
Coleoptera (larvae)	1.3 (7.1)	–	–	–	–
Diptera (larvae)	19.5 (57.1)	–	36.2 (64.3)	–	35.4 (90.9)
Diptera (pupae)	0.1 (0.0)	–	5.1 (21.4)	–	1.1 (9.1)
Trichoptera (larvae)	–	–	1.3 (21.4)	–	11.0 (54.5)
Ephemeroptera (nymphs)	43.6 (92.9)	–	–	–	14.9 (27.3)
Copepoda	–	–	–	–	–
Ostracoda	1.5 (21.4)	0.2 (15.4)	12.5 (64.3)	1.3 (66.7)	11.2 (72.7)
Gastropoda	–	–	0.3 (7.1)	–	2.5 (18.2)
Teleost/invertebrate eggs	–	–	–	–	–
Teleost	–	–	7.0 (7.1)	–	–
Organic matter (not identified)	2.7 (57.1)	5.2 (100)	–	–	7.3 (81.8)
Silt / biofilm	12.4 (100)	21.5 (100)	–	13.3 (100)	2.9 (45.5)
Sand	4.4 (92.9)	1.2 (84.6)	0.6 (14.3)	58.9 (100)	0.8 (18.2)
Unidentified	2.4 (50.0)	2.8 (61.5)	2.8 (57.1)	1.0 (55.6)	3.2 (54.5)

vegetal matter (17.1 %) and silt/biofilm (42.5 %) (Table 4). A concordant diet was recorded for both sympatric, native species. *Craterocephalus cuneiceps* consumed primarily algae (14.8 %), vegetal matter (19.7 %) and silt/biofilm (42.0 %). Similarly, *H. aurea* consumed algae (14.7 %), vegetal matter (17.8 %) and silt/biofilm (41.8 %). Thus, all species predominantly consumed the same dietary items, *i.e.* most likely the same detrital matter. ANOSIM confirmed that no statistical difference existed between the dietary composition of all species (Global R = 0.018, p>0.05). In the Lyons River, the recorded mean temperature was 31.3 °C, pH 8.5 and conductivity 2.477 $mScm^{-1}$.

Lyndon and Minilya rivers study sites

Oreochromis mossambicus was collected from one site in the Lyndon River and two sites in the Minilya River (Fig. 2). The Minilya River (114.778°E, 23.908°S, sampled 2km east of Middalya Homestead) and the Lyndon River (113.964°E, 23.539°S, Learmonth Minilya Road) are intermittent rivers that drain into Lake McCleod during flood events. In the Minilya River, 132 *O. mossambicus* were collected with a length range of 43–117 mm, and a mean density of $0.72m^{-2}$. The only native species recorded was *L. unicolor* (132 specimens with a mean density of 0.90 m^{-2}). Forty-five *O. mossambicus* were collected from the Lyndon River (77–120 mm), with a mean density of 0.34 m^{-2}. No other species were collected. The salinity in the small drying pools in the Lyndon River was *ca* 149 $mScm^{-1}$, *i.e.* between two and three times the salinity of seawater.

Discussion

Distribution

The distribution of *O. mossambicus* is increasing in Western Australia, a pattern that has been observed in nonindigenous populations on the east coast of Australia as well as in many other countries (Arthington & Blühdorn 1994; Canonico *et al.* 2005). After the initial discovery of *O. mossambicus* in the Gascoyne River in 1981, the species quickly spread throughout this river and a major tributary, the Lyons River (Blühdorn & Arthington 1990). It is likely that this population originated from ornamental stock, though the affiliation of this group with the more recently discovered populations in Western Australia is unknown. The occurrence of *O. mossambicus* in the Chapman River was recorded in the Western Australian Museum records in 1992, though the species was originally noted from a farm dam in the Chapman River region in 1978. It is possible that this may be the source of the Chapman River population, through flooding or human intervention. It is likely that the absence of a barrier in the Chapman River (*i.e.* weir/gauging station) would have allowed the species to spread further upstream, as observed in the Gascoyne and Lyons Rivers.

Human intervention was cited by Blühdorn *et al.* (1990) as most likely responsible for multiple, isolated *O. mossambicus* populations in Queensland. Accordingly, nonindigenous populations of ornamental fishes are often found adjacent to populated areas (Lintermans 2004). It is therefore no surprise that *O. mossambicus* has

Table 4

Total number, percentage contribution, density, length range, number of dietary samples, mean stomach fullness and percentage dietary contribution by volume (and percentage occurrence in parenthesis) of *Oreochromis mossambicus* and three co-occurring native species collected from the Lyons River in Autumn (May 2002).

	O. mossambicus	***H. aurea***	***C. cuneiceps***	***L. unicolor***
Total specimens collected	50	25	50	1
Percentage contribution	39.7 %	19.8 %	39.7 %	0.01 %
Density (m^{-2})	6.25	3.12	6.25	0.12
Length Range (SL)	12–27 mm	20–33 mm	14–33 mm	60 mm
Dietary sample	*n* = 12	*n* = 12	*n* = 12	–
Mean stomach fullness (± SE)	4.8 (± 0.32)	6.1 (± 0.29)	5.25 (± 0.28)	–
Prey type				
Algae (Unicell/Filament)	13.3 (100)	14.7 (100)	14.8 (100)	–
Bacillariophyceae	8.3 (100)	9.3 (100)	8.1 (100)	–
Vegetal matter	17.1 (100)	17.8 (100)	19.7 (100)	–
Terrestrial insects/parts	0.6 (58.3)	0.4 (41.7)	0.5 (50)	–
Copepoda (larvae)	0.1 (8.3)	–	0.1 (8.3)	–
Organic matter (not identified)	10.1 (100)	9.1 (100)	8.6 (100)	–
Silt/biofilm	42.5 (100)	41.8 (100)	42.0 (100)	–
Sand	1.2 (100)	0.8 (83.3)	1.3 (83.3)	–
Unidentified	7.0 (100)	6.2 (100)	4.9 (91.7)	–

been found in the Chapman and Gascoyne Rivers which are both located adjacent to the large regional centres of Geraldton and Carnarvon, respectively. Flooding may also result in rapid range expansions, particularly as northwestern Australia experiences highly seasonal precipitation that results in intermittent watercourses and frequent localised flooding (Unmack 2001). Fish from the Gascoyne River are likely to have seeded populations in the Minilya and Lyndon rivers nearby, either through flooding and/or deliberate release. Although the Minilya and Lyndon rivers are not directly connected, these rivers are in close proximity and both drain into the same intermittent flood pan, Lake McCleod. During a flood event, Lake McCleod may have allowed individuals to colonise rivers that are not connected during dry periods.

Temperature is one of the most important environmental factors affecting the distribution of *O. mossambicus*. At 27°17' S, the *O. mossambicus* population in North Pine Dam in Queensland may be close to the southern limit of the potential range of this species because of low winter water temperatures (Arthington 1986; Blühdorn & Arthington 1990). The most southerly *O. mossambicus* population in Western Australia is located at a similar latitude (*ca* 28°45′ S). However, *O. mossambicus* may be able to populate habitats at considerably higher latitudes due to the ability to tolerate lower temperatures at higher salinities (Arthington 1986; Skelton 2001). In the freshwater North Pine Dam in southeastern Queensland, Blühdorn & Arthington (1990) noted fish kills when the temperature dropped below 14 °C. Juvenile (*i.e. ca* 50 mm) *O. mossambicus* were collected from the Chapman River in autumn and kept in large outside tanks (in freshwater) at Murdoch University until the following winter. At the onset of winter in Perth, a large proportion of these fish perished at between approximately 14 °C and 15 °C. However, *O. mossambicus* was collected, in good condition (*i.e.* not emaciated, and with full intestines), from the estuarine Chapman River in winter at temperatures of between 11.5°C and 12°C. It is also interesting to note that the natural range of the species in eastern Africa extends southwards from Mozambique to the Pongola River in freshwater (*ca* 27°S), and in brackish water further south to Algoa Bay at a latitude of *ca* 35°S (Loiselle 1996). Thus, the spread of *O. mossambicus* southwards, as speculated by Arthington (1986), may occur through the colonisation of estuarine environments.

Dietary analysis

Detritus dominated the diet of large *O. mossambicus* in the Gascoyne River, and smaller fish in the Chapman River. The detritus included algae, vegetal matter, Bacillariophyceae and quantities of inorganic matter including silt. De Silva (1985) noted that *O. mossambicus* was omnivorous, though a detritivorous diet was adequate for reproduction and normal growth in Sri Lankan reservoirs. Juvenile *O. mossambicus* often display a more carnivorous diet than mature fish (Bruton & Boltt 1975). The differing diets of small fish from the Gascoyne (insectivorous) and Chapman (detritivorous) Rivers is indicative of trophic plasticity that allows *O. mossambicus* to utilise various food sources (Arthington *et al.* 1994). Furthermore, although detritus typically has a low nutritional value, it is not usually resource limited and therefore allows *O. mossambicus* to utilise a common food source that many co-occurring native species, often carnivorous or omnivorous, will not consume.

ANOSIM demonstrated that the diets of *O. mossambicus* and co-occurring species in the Chapman and Gascoyne rivers were significantly different. Most native species in the Chapman River are carnivorous or omnivorous, and typically feed on or near the substrate. These species include *Acanthopagrus butcheri* (Sarre *et al.* 2000), *A. caudavittata* (Wise *et al.* 1994; Potter *et al.* 1994), *P. olorum* (Gill & Potter 1993) and *H. compressa* (Merrick & Schmida 1984), and similarly, in the Gascoyne River, the carnivorous *L. unicolor* and omnivorous *H. compressa* (Merrick & Schmida 1984). Thus, while no statistically significant dietary overlap exists, these native species and *O. mossambicus* inhabit and feed in similar areas. Blühdorn *et al.* (1990) also noted that in an artificial reservoir in Queensland, food resources were partitioned between *O. mossambicus* and two other species of comparable size; *i.e. Tandanus tandanus* (Plotosidae) and *L. unicolor*. *Oreochromis mossambicus* will often exploit an unrealised dietary niche, and as invasive species, detritivores are least likely to impact upon the colonised ecosystem (Moyle & Light 1996). Dietary analysis alone does not indicate that *O. mossambicus* competes with and disadvantages co-occurring native carnivorous and omnivorous fishes in these rivers.

Although the diets of all species captured in the Chapman and Gascoyne rivers were significantly different, the diets of *O. mossambicus* and the native species *C. cuneiceps* and *H. aurea* were very similar – in fact the dietary composition (Table 4) implies that all species were consuming the same detritus. *Craterocephalus cuneiceps* is a detritivore (Allen *et al.* 2005), however no data are available on the natural dietary preferences of *H. aurea*, though it is reasonable to assume a diet similar to that of the closely related omnivorous *H. compressa* (Merrick & Schmida 1984). It is very likely that in the restricted habitat of a small intermittent pool, the three species will utilise the same feeding areas and food resources, and if these are in short supply, they may compete for one or other resource, of both.

Potential ecological impacts

Although *O. mossambicus* has been declared a noxious species in some countries and parts of Australia, there is a paucity of research on its impacts on native fish (Arthington *et al.* 1994; Canonico *et al.* 2005). There is evidence that recruitment has declined in some co-occurring native species in Australia, and in areas where *O. mossambicus* thrives, few native species may be found (Mackenzie *et al.* 2001). Against this background, some generalisations can be made regarding the impact of the species in a Western Australian context. While breeding, male *O. mossambicus* become territorial and aggressive to their own species and others. At Rocky Pool in the Gascoyne River, males were observed guarding nests (*ca* 60–80 cm diameter) in the littoral zone, that had been cleared of macrophytes. The different antagonistic behaviours described by Turner (1986) were all observed. Most aggressive behaviour was directed towards other breeding males and to a lesser extent other fish. This territorial behaviour may not have a serious impact in areas with low densities of the introduced cichlid, however in the small residual pools of the Gascoyne River large areas of the substrate may be occupied by nests, restricting the movements of native species.

The variable seasonal densities of *O. mossambicus* in the Chapman River may influence the prevalence and distribution of native species within this system. At peak densities in autumn, *O. mossambicus* occurred at *ca* 8.5 fish per m^{-2} and contributed 64.1 % of fish collected. Native species were almost non-existent except for *H. compressa*. This phenomenon may be due to the displacement of indigenes by *O. mossambicus*, though it may also be influenced by the native species' biology. The size classes of the two rarest species, *A. butcheri* and *M. cephalus*, indicate that only juveniles were collected. Juveniles of these species may have increased in size and migrated to different estuarine habitats in subsequent sampling seasons and thus were not represented in our samples. Similarly, during reduced winter temperatures, *O. mossambicus* may occupy different habitats thus explaining the reduced densities of this species. Also, colder temperatures may increase the mortality of juveniles from the previous reproductive period, as observed in *O. mossambicus* populations in South Africa (Cochrane 1986). It is unknown how large *O. mossambicus* grows in the Chapman River, as the largest specimen collected (112 mm) was considerably smaller than fish collected in the Gascoyne River, and the species maximum size of *ca* 350 mm (Arthington & Blühdorn 1994). Larger fish may occupy different sections of the estuary, or the species may grow no larger when exposed to low temperatures at this high latitude. Under unfavourable environmental conditions, *O. mossambicus* populations may become stunted, with small maximum sizes and precocious reproduction (Fryer & Iles 1972; Blühdorn & Arthington 1990; James & Bruton 1992). Longer-term research is needed to determine if these variations in diversity and prevalence of introduced and indigenous fishes are a regular seasonal phenomenon, or whether native species are decreasing in diversity and abundance over longer periods.

The potential impacts of *O. mossambicus* are likely to be of greater severity in more northern rivers for two reasons. Firstly, milder winter temperatures may reduce the cold-induced mortality of juveniles from the previous reproductive season (Cochrane 1986). Indeed, it is possible that mild winter temperatures in northern populations may allow breeding year round. Secondly, the variable hydrological regime of intermittent rivers (such as the Gascoyne) in northern areas, concentrates fishes in small residual ponds where resource competition is more likely. The negative effects in these circumstances may be greater than in a perennial water body such as the Chapman River. Blühdorn *et al.* (1990) described the *O. mossambicus* population in the Gascoyne River as having a "low population density", though the species now appears abundant in the Gascoyne and Lyons rivers, and has become the dominant species.

The native species under greatest threat from *O. mossambicus* identified in this study are *C. cuneiceps* and *H. aurea*. Not only are these species likely to be competing for food and space in small intermittent pools, but both natives are endemic to Western Australia and have limited distributions. *Craterocephalus cuneiceps* is also found in the Gascoyne River but rarely co-occurs with *O. mossambicus* (Morgan *et al.* 2004, Allen *et al.* 2005). This may explain why *C. cuneiceps* is the most abundant and widespread species in the nearby Murchison River (which is free of introduced fishes), and why it occurs in such low densities in the majority of sites sampled in the Gascoyne River (Allen *et al.* 2005). The gudgeon *H. aurea* is found only in the Gascoyne/Lyons and Murchison Rivers, and is listed as 'conservation dependent' by the Australian Society for Fish Biology.

This study represents the first research on the dietary composition and possible ecological impacts of *O. mossambicus* in Western Australia. The results infer that, to varying degrees, *O. mossambicus* may negatively impact on native species through resource competition and agonistic behaviour. Furthermore, there is evidence of dietary overlap between *O. mossambicus* and endemic Western Australian species *C. cuneiceps* and *H. aurea*, both of which have restricted distributions. Considering the expanding range of *O. mossambicus* in Western Australia, it is likely that this trend will continue and a greater number of native fish communities and species will be exposed to this invasive cichlid.

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