

The biology and management of *Tilapia mariae* (Pisces : Cichlidae) as a native and invasive species: a review

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Abstract. *Tilapia mariae* (Cichlidae) is a tropical teleost, native to West African coastal drainages in the Gulf of Guinea and naturalised in the USA, Australia and possibly Russia. This paper reviews published information on the species from its native and introduced range to improve the effective management of fisheries as well as manage current infestations, reduce further spread and promote research on control measures outside its natural range. Within its natural range, the species is abundant and contributes to the local subsistence and artisanal fisheries; however, it is not extensively utilised for aquaculture. Outside its native range, it has proliferated, particularly in disturbed aquatic ecosystems. *Tilapia mariae* has several characteristics that make it successful in both its natural and introduced range. These include plasticity in reproductive behaviour (particularly parental care of the brood), a variety of feeding behaviours and dietary components, tolerance of a wide range of environmental conditions and aggressive behaviour to other fish species. Although tilapiine species are considered to be amongst the world's worst invasive alien species, surprisingly little information is available on potential impacts of *T. mariae* on native species and aquatic ecosystems outside its native range.

Additional keywords: aquaculture, artisanal fisheries, biology, invasion, management.

Introduction

Tilapia mariae Boulenger, 1899 (Pisces:Cichlidae) is a freshwater and estuarine teleost that occurs naturally in West Africa, from Côte d'Ivoire to Cameroon, and has been introduced to at least three other continents (Welcomme 1988). In its native range, it can be the dominant fish species in streams, rivers, lakes and estuaries (e.g. Akpaniteaku and Aguigwo 2003), and supports local subsistence and artisanal fisheries in some catchments (e.g. Nwadiaro 1987). Unlike other tilapiine species (Lim and Webster 2006), *T. mariae* has yet to be extensively cultured locally or globally (King and Etim 2004), but appears to have some potential for aquaculture (Ajuzie 1996; Vassallo *et al.* 2007). Around the world, it has become a desirable aquarium species, owing to its attractive appearance, hardiness and ability to readily reproduce. Combined with introductions for the purpose of aquaculture, this has resulted in the species becoming naturalised in the United States, Australia and possibly Russia (Welcomme 1988; Holcik 1991; Robins *et al.* 1991). Unlike other introduced tilapiine species (Canonico *et al.* 2005), only three published studies have documented potential detrimental impacts of *T. mariae* on native ichthyofauna (Courtenay and Deacon 1983; Brooks and Jordan 2010; Kroon *et al.* 2011).

In this paper, we review all biological aspects of *T. mariae* from available literature sources, obtained from studies in its native and introduced ranges, and from field and laboratory studies. Most work in the species' natural range has been done in

Nigeria, with a small number of key works contributing much of the life history information (Whitehead 1962; Schwanck 1987a; Ikomi and Jessa 2003; King and Etim 2004). The review follows Pyke (2001, 2005), and includes the species' introductions, impact and options for management. We envisage that this review will contribute to improved management and culture of the species' stocks in its native range, and effective management of current infestations, reduction of further spread, and promotion of research on control measures outside its natural range.

Biology at the species level

Species taxonomy and nomenclature

The name tilapia is derived from the African Bushman word meaning 'fish' and is commonly applied to species in the genera *Tilapia*, *Oreochromis* and *Sarotherodon* within the Cichlidae. The tilapiines have gone through extensive re-arrangements of their taxonomy (e.g. Apfelbach 1967; Trewavas 1973, 1982, 1983). The generic division of *Tilapia*, *Sarotherodon* and *Oreochromis* is based on meristic, morphometric and ethological characteristics (Trewavas 1982). For example, *Tilapia* species are substrate spawners, whereas *Sarotherodon* are paternal or bi-parental mouthbrooders, and *Oreochromis* are maternal mouthbrooders. This classification has been confirmed phylogenetically (Pouyaud and Agnese 1995).

The specific name of *Tilapia mariae* has been retained since first described, and was taken from Miss Mary Kingsly, who collected the type specimen (Van den Audenaerde 1966). Various synonyms have been applied to the species: *T. microcephala* Lonnberg, 1903, *T. dubia* Lonnberg, 1904, *T. meeki* Pellegrin, 1911, *T. heudeloti* Boulenger, 1915, and *T. mariae dubia* (excl. syn. *T. haugi*) Trewavas, 1962. Based on different-sized individuals and colour patterns, *T. meeki* was originally described as a separate species, but is now recognised as being the same species as *T. mariae* (Whitehead 1962; Hanel and Novak 1981). Trewavas (1962) adopted the subspecific designation *T. mariae dubia* and suggested that *T. mariae* has affinities with *T. haugi*. However, the subspecies *dubia* has been abandoned and *T. haugi* is recognised to occur further south. The most accepted common name for *T. mariae* is spotted tilapia, owing to the 2–6 large spots posterior to the gills in adult specimens. Other common names, more generally used in Australia, include black mangrove cichlid and Niger cichlid.

Appearance and morphology

In its native range, the maximum recorded sizes are 323-mm total length (TL) (King 1996a) and 550-g fresh weight (Whitehead 1962), although total lengths of 190–220 mm are more common (Table 1). In Florida (USA), the maximum documented size is slightly larger (350-mm TL) but up to almost three times heavier (1350 g) (Shafland 1996), and in Queensland (Australia) the maximum recorded size is 333-mm TL at 952 g (D. Russell, unpubl. data). The body of *T. mariae* is laterally compressed with a depth 42–54% of standard length (SL) in natural conditions (Whitehead 1962; Van den Audenaerde 1966; Ivoylov 1986) and a blunt head comprising 30–35% the SL (Van den Audenaerde 1966). Detailed accounts of morphological and meristic measurements and counts are presented by Whitehead (1962), Van den Audenaerde (1966), Anene (1999) and Ivoylov (1986). Dorsal, anal and caudal fins in juveniles and adults differ, with (i) the posterior extremities of the dorsal and anal fins rounded in juveniles and pointed and elongated to almost the end of the caudal fin in adults, and (ii) the posterior edge of the truncate caudal fin slightly rounded in juveniles but completely rounded in adults (Whitehead 1962; Van den Audenaerde 1966; Anene 1999). The mean fin ray counts differ between localities (Table 2), reflecting an effect of local environmental conditions (Whitehead 1962; Anene 1999), and possibly the existence of subspecies (Anene 1999).

Tilapia mariae is a polyphyodont species; that is, a species that produces several sets of teeth successively throughout its life. Tooth germs and replacement teeth in various stages of development are in the cavity of the dentary bone (Holje *et al.* 1986), with both immature and mature parts of the dentition innervated (Tuisku and Hildebrand 1995). The species is suitable for the study of tooth–nerve interactions in other polyphyodont species (Holje *et al.* 1986), with several studies conducted for application in higher animals (Hildebrand *et al.* 1988; Tuisku and Hildebrand 1992, 1994, 1995, 1996, 1997).

Tilapia mariae has internal and external morphology that reflects a cellulose diet, and foraging behaviour that includes plankton-filtering and grazing. The mouth is small, with jaws that have 4–6 series of slender-shafted external teeth, the outer row

Table 1. Maximum total lengths (TL), standard lengths (SL), weights, and estimated parameters of the length–weight relationship for *Tilapia mariae* (Cichlidae)

Location	Habitat	Sample size	Max. TL (mm)	Max. SL (mm)	Max. fresh weight (g)	Parameters of the length–weight relationship $W = aTL^b$	Source
Nigeria	Stream	–	225	–	284	–	Ajuzie (1996)
Nigeria	Lake	–	191	148	–	–	Anene (1999)
Nigeria	River	46	210	–	–	0.0300	Bongonyinge (1984) in King (1996a)
Nigeria	River	750	197	175	148	–1.6320	Ikomi and Jessa (2003)
Nigeria	River	375	250	–	–	0.7412	King (1996a)
Nigeria	Stream	51	323	–	–	0.0336	King (1996a)
Nigeria	River	211	117	–	–	0.0145	King (1996a)
Benin	River	68	207	–	–	0.2180	Laleye (2006)
Nigeria	Stream	45	171	–	–	–3.9800	Olurin and Sotubo (1989)
Florida (USA)	Canal	–	350	–	1350	–	Shafland (1996)
Nigeria	Lagoon	70	171	15	86.5	–0.8088	Soyinka and Ayo-Olalus (2009)
Nigeria	Lagoon	77	181	13.5	105.4	–1.4391	Soyinka and Ayo-Olalus (2009)
Nigeria	Stream	75	303	–	550	–	Whitehead (1962)
Queensland (Australia)	River	2283	333	–	952	–	D. Russell, unpubl. data

Table 2. Meristic counts of spines and soft rays of *Tilapia mariae* (Cichlidae) showing considerable variation between populations

Fin rays	Count	Frequency			
		Nigeria	Cameroon	Nigeria	West African museum specimens
Dorsal	XV	33	12	2	7
	XVI	92	13	51	3
	XVII	2	1	0	0
Mean ± s.d.		15.75 ± 0.47	15.58 ± 0.58	15.96 ± 0.19	15.30 ± 0.48
	10	23	0	0	0
	11	18	0	1	0
	12	60	0	13	1
	13	24	5	36	0
	14	1	9	2	2
	15	0	15	1	7
Mean ± s.d.		11.70 ± 1.0	14.34 ± 0.77	12.74 ± 0.69	14.5 ± 0.97
Pectoral	10	23	0	0	0
	11	18	0	1	0
	12	60	0	13	1
	13	24	1	36	0
	14	1	8	2	2
	15	0	7	1	7
Mean ± s.d.		11.70 ± 1.0	14.38 ± 0.62	12.74 ± 0.69	14.5 ± 0.97
Anal	9	23	0		
	10	31	10		
	11	67	6		
	12	3	0		
Mean ± s.d.		10.40 ± 0.82	10.38 ± 0.5		
Number of specimens		127	16	53	10
Range of TL (mm)		109–191	37–195	165–303	101–157
Source		Anene (1999)	Van den Audenaerde (1966)	Whitehead (1962)	Whitehead (1962)

with one notch and the inner tricuspid (Whitehead 1962). Adults have ~76 external teeth in the upper row (Van den Audenaerde 1966) and 60–65 functional teeth in the lower jaw (Holje *et al.* 1986), whereas juveniles have far fewer external teeth (Van den Audenaerde 1966). The fine and flattened teeth are suited to filtering plankton (Anibeze 2001), whereas spoon-shaped crowns on the outermost teeth indicate grazing behaviour (Trewavas 1974). The lower part of the first gill arch contains 8–17 gill-rakers or spines (Whitehead 1962; Van den Audenaerde 1966; Teugels *et al.* 1992). Plankton filtering is aided by the ~1180 primary gill lamellae and 152 secondary gill lamellae, with primary lamellae length in adults being up to 12–16% of TL (Shephard 1992). The numerous slender, serrated pharyngeal teeth (Whitehead 1962; Teugels *et al.* 1992), with the anterior set bent backwards and minutely bicuspid, and the posterior set larger, straight and bicuspid (Van den Audenaerde 1966), further contribute to the breakdown of plant material. Moreover, the species has a relatively large intestine length-to-SL ratio of 9.27:1 (Anibeze 2001), and examples of gut length-to-SL ratios of 3.5:1 (Edema *et al.* 2007a) and 2.89:1 (Edema *et al.* 2007b).

Like all Cichlidae, *T. mariae* are physoclistous; that is, there is no connection between the swim bladder and the gut, as the connection closes and becomes reduced early in the larval stage. The volume of the swim bladder at the onset of the late juvenile stage is 3.06–3.91 cm³, which is 8.5% the volume of the fish (Reyer 1977). The density of the fish is 1.002× that of water (Reyer 1977).

The colour pattern of *T. mariae* is distinctive; however, it changes upon the fish reaching sexual maturity and shows variation among adults. Late juveniles are olive-green to creamy-white and have up to nine sharply delineated, dark vertical bands running from the dorsal fin to the under surface (Whitehead 1962). Upon reaching the adult phase, the colour changes to a milky colour with two to six dark blotches on the middle of the flanks, and light green to yellow head and dorsal fringes (Baldaccini 1973). Several other colour and pattern combinations are seen (Whitehead 1962; Baldaccini 1973; Trewavas 1974), which are generally related to stages of gonad development and behaviour (see reproduction section), but can also be associated with changes in environment. For example, dark bands change to blotches upon removal from water, dark bands re-develop when returning to the water, and blotching appears to be more intense against a light background (Whitehead 1962).

Age–sex categories

Four age–sex categories can be distinguished in free-swimming *T. mariae*: early juvenile, late juvenile, adult males, and adult females. The early-juvenile stage has no colour development and is effectively transparent (Whitehead 1962). The colour pattern develops from striped in the late-juvenile stage to the spotted pattern upon reaching maturity (Whitehead 1962). In adults, sexual dimorphism in colour is not evident (Whitehead 1962; Van den Audenaerde 1966; Apfelbach 1969; King and Etim 2004), but differences in morphology exist within

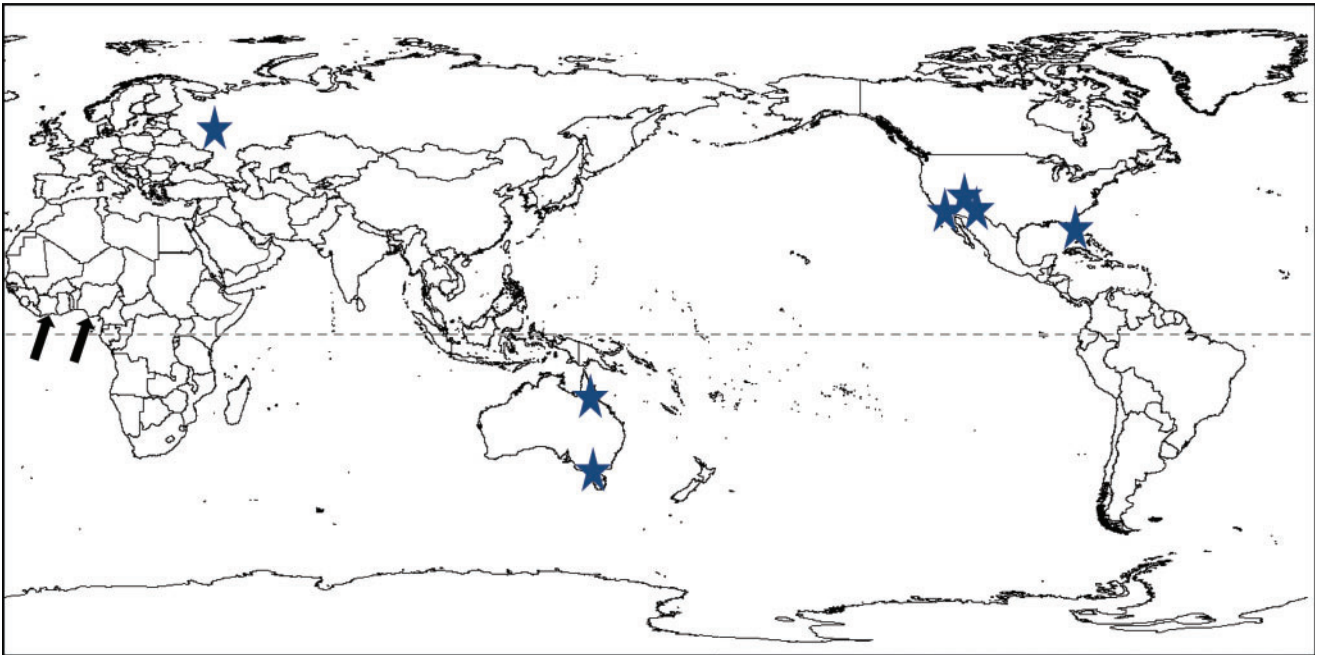


Fig. 1. The natural range of *Tilapia mariae* (Cichlidae) from Côte d'Ivoire to Ghana and Benin to Cameroon in the coastal drainages of the Gulf of Guinea, western Africa (arrows), and locations of introductions or establishment of *Tilapia mariae* (Cichlidae) in Queensland and Victoria (Australia), California, Nevada, Arizona and Florida (USA), and Russia (stars). Note that the actual location and range in Russia is unknown.

breeding pairs. Males are approximately one-third larger than females (Schwanck 1989; Annett *et al.* 1999), and generally have longer pelvic fins extending to the first soft ray of the anal fin (Whitehead 1962; Van den Audenaerde 1966). Moreover, males and females exhibit different behaviours during agonistic, sexual and parental activities (Apfelbach 1970; Baldaccini 1973; Schwanck 1989).

Male-to-female sex ratios in adult *T. mariae* are generally biased towards females, and range from 1 : 1.6 to 1 : 3.1 in its native range (Olurin and Sotubo 1989; Ikomi and Jessa 2003; King and Etim 2004; Anene and Okorie 2008). Soyinka and Ayo-Olalusi (2009) report an overall male-biased population (1 : 0.7), although with high monthly variability. In adult fish, the sex ratio is female-biased in the smaller and larger sizes classes but male-biased in the middle size classes (King and Etim 2004; Anene and Okorie 2008). Changes in sex ratio with size, time and location are likely to be a product of differences in natural mortality or longevity between sexes (King and Etim 2004), differential exploitation by humans, and more aggressive behaviour of females than males during brood care, resulting in higher catches by hooks and nets (Anene and Okorie 2008). Clear evidence of sex reversal is not reported in the literature, but is suggested by Anene and Okorie (2008).

Hybridisation and genetics

Many tilapiine species are able to hybridise both naturally and with human intervention (Wohlfarth and Hulata 1983; and references therein). Taylor *et al.* (1986) reports hybridisation for *T. mariae* in Florida based on three phenotypes intermediate between *T. mariae* and *T. zilli*. These show: (i) variation in shape and meristics, (ii) intermediacy in jaw and pharyngeal dentitions,

and (iii) markings that combine features of both species. In Australia, electrophoretic examination of introduced tilapiines demonstrated that *T. mariae* is a non-hybridised species (Mather and Arthington 1991).

Tilapia mariae has $2n = 40$ chromosomes with 1 double-length chromosome pair that includes four metacentric chromosomes (Vervoort 1980; Thompson 1981). The report by Wohlfarth and Hulata (1983) of a chromosome number of $2n = 42$ is most likely derived from an apparent misprint in Vervoort (1980). The sex-determining locus is on the linkage group LG(3) and the female is heterogametic (WZ-ZZ system) (Cnaani *et al.* 2008).

Specific primers were developed for tilapiine species using *Oreochromis niloticus* (Bardakci and Skibinski 1999). Using the SCAR-RAPD marker technique, variation in primer length was found between *Tilapia mariae* and four *Oreochromis* species, but no variation was found within species tested.

Distribution, habitat and abundance

Tilapia mariae occurs naturally in West African coastal drainages of the Gulf of Guinea, from Tabou River in Côte d'Ivoire (4.3°N, 7.2°W) to south-west Ghana (5.0°N, 2.0°W) and then from south-east Benin (6.3°N, 2.0°E) to the Kribi River in Cameroon (2.7°N, 10.0°E) (Fig. 1). In Nigeria, where the majority of research has been conducted, the climate generally consists of a single wet season in the middle of the calendar year and a single dry season at the end and start of the calendar year. Wet- and dry-season water levels can be markedly different in both the lower and upper reaches of watercourses.

Tilapia mariae has been introduced to and become naturalised in three states of the USA, in two states of Australia, and possibly Russia (Welcomme 1988; Holcik 1991; Robins *et al.* 1991)

(Fig. 1). In the USA, the species is well established in Florida (25.0–28.0°N), Arizona (32.40°N, 111.75°W) and Nevada (36.7°N, 114.7°W), with additional populations in California (33.0°N, 115.5°W) (Courtenay and Hensley 1979; Courtenay and Deacon 1982, 1983; Nico 2009; USGS 2009). In Australia, the species is found in fresh and estuarine waters of eastern flowing rivers in North Queensland from Innisfail (17.58°S) to Cairns (16.83°S) (Webb 2007), with recent reports from a western-flowing catchment (M. Pearce, pers. comm.). An outlying population exists in the cooling waters of a power station in Victoria, Australia (38.3°S, 146.4°E) (Cadwallader *et al.* 1980). No information is available on its range or habitat in Russia.

Tilapia mariae has been classified as an estuarine species of freshwater origin (Ecoutin *et al.* 2005; after Albaret 1999). In its natural range, *T. mariae* occurs in fresh and brackish water (Odum 1995; Olukolajo and Oluwaseun 2008; Kone *et al.* 2003). In the Ethiopie River (Nigeria), *T. mariae* is generally abundant in wider sections of watercourses with a silty and sandy substratum, with adults found in swift-flowing and deep water (>5-m depth) and juveniles in shallow littoral waters (<2-m depth) around submerged macrophytes (Ikomi and Jessa 2003). Its distribution changes seasonally, with it occurring in large rivers during the dry season but moving into clearer streams and small rivers with increasing water levels during the wet season (Whitehead 1962). Generally, it does not occur in the upper reaches of watercourses owing to its inability to cross natural barriers such as falls and rapids (Trewavas 1974; Odum 1995). In the constructed canals of Florida, juveniles occur in the shallow water along banks, with adults inhabiting the deeper mid portions (Loftus and Kushlan 1987). In Queensland (Australia), *T. mariae* is a microhabitat generalist in lowland freshwater rivers (Rayner *et al.* 2008).

Tilapia mariae is a common species in both its natural and introduced ranges. In its natural range, it is abundant by number and weight in both fisheries-dependent (Adite and Van Thielen 1995;) and independent studies (Olurin and Sotubo 1989; Odum 1995; Anene 1999; Akpaniteaku and Aguigwo 2003; Ikomi and Jessa 2003; Oti 2003). In the upper Ethiopie River, >1200 mature individuals were counted in a 1-km stretch (Schwanck 1987b). In its introduced range, *T. mariae* is the most abundant exotic fish species in Florida (USA) (Loftus and Kushlan 1987), and is locally abundant in Queensland (Russell *et al.* 2003; Rayner *et al.* 2008). In southern Florida, *T. mariae* commonly makes up >20% by number and weight in fisheries-independent surveys (Metzger and Shafland 1985), contributing >50% of the total biomass (Courtenay and Hensley 1979). Population density can reach up to one breeding pair per metre along shorelines of canals (Annett *et al.* 1999). In Queensland, fisheries-independent surveys generally consist of <10% *T. mariae* by number, but can reach up to 19% of the total catch (Russell *et al.* 2003). In Victoria, the species is now the dominant fish species in a constructed lake with elevated water temperatures (Osborne 1980).

Biology

Physiology

Physiological studies specific to *T. mariae* are scarce and are generally undertaken with the intention of applying the results of

these studies to investigations of higher vertebrate function. The early development of the nervous and visual systems of *T. mariae* has been investigated by testing for nicotinamide adenine dinucleotide phosphate (NADPH)-diaphorase activity in the embryonic and larval stages. In the embryo, NADPH-diaphorase activity is first present in the brain 20 h after fertilisation (Villani 1999a), followed by the olfactory organ, otic vesicles, superficial neuromasts, and intestinal tract (48 h) and the cervical spinal cord (3.5 days) (Villani 1999a). Upon hatching, NADPH-diaphorase activity is detected around the digestive tract (Villani 1999b), and in the retina and optic tectum, but not in the optic nerve (Villani *et al.* 2001), with further activity occurring in the gill arches and adrenomedullar tissue (4.5 days after fertilisation) (Villani 1999b).

Fish that exhibit parental care are sensitive to administrations of the hormone prolactin, which overstimulates sensory receptors in the forebrain. Intramuscular injections of mammalian prolactin into *T. mariae* induce phasic reactions of neuron populations in the area dorsalis of the telencephalon 10–90 min post-injection that last for 15 min (Blüm and Fiedler 1974). Similar injections result in maximum prolactin concentrations in serum and organs after 1–3 h, before disappearing after 28–30 h (Blum 1968).

Growth, development and morphological relationships

In this review, we recognise four life cycle stages in *T. mariae*: embryonic, larval, juvenile (both early and late), and adult (after Balon 1975). Eggs develop in the female ovaries before they are deposited onto substrata to be externally fertilised by the male. Ovarian development has been reported in either four or five stages, namely immature, ripening, ripe, ripe-running and partly spent (Ikomi and Jessa 2003; after Bagenal and Braun 1978), and immature, mature, ripe, and spent (King and Etim 2004; after Lagler 1978). Immature eggs are 0.8 mm in diameter (Ikomi and Jessa 2003), whereas ripe eggs range from 1.4 to 3.0 mm in diameter (Table 3) and weigh 2–8 mg (King 1996a). Ripe eggs are pale yellow and ripe-running eggs are deep yellow or olive-green (Ikomi and Jessa 2003).

The eggs hatch to become larvae at between one to three days (Whitehead 1962) and five to seven days (Annett *et al.* 1999) post-fertilisation. The larvae have specialised head glands by which they anchor themselves to the substrate; these disappear as the larvae become strong enough to swim independently (Arnold *et al.* 1968). This transformation to a free-swimming, early-juvenile stage occurs 4–10 days after hatching (Baldaccini 1973; Schwanck 1986, 1987a; Annett *et al.* 1999), at which time they rise from the substrate to form schools. At 40–60 days after hatching (15–40-mm TL), parental care decreases, the early-juvenile stage finishes and the late-juvenile stage commences (Baldaccini 1973; Osborne 1980; Schwanck 1989; Annett *et al.* 1999). The late-juvenile stage is characterised by a lack of parental care and the dark vertical stripes that appear ~110 days after hatching (Whitehead 1962).

In the field, females can reach maturity (i.e. carry ripe eggs) around 100-mm TL (Table 3), with the median length at sexual maturity being 177-mm TL, or 58% of its asymptotic length (King and Etim 2004). In captivity, the species matures and starts breeding at smaller sizes than in the field (Schwanck 1980; Turner *et al.* 1989). In aquaria, males can reach sexual maturity

Table 3. Reproductive characteristics of *Tilapia mariae* (Cichlidae) showing considerable variation between studies

Minimum female TL at maturity (mm)	Number of eggs	Ripe egg size (mm)	Gonadosomatic index % (range)	Fecundity-TL relationship ($F = a \cdot TL^b$)		Relative fecundity (eggs kg^{-1})	Fecundity-bodyweight relationship ($F = a \cdot W^b$)		Source
				a	b		a	b	
116	285-554	1.4	2.53	-	-	9270	-	-	Adebisi (1987)
110	424-2781	-	2.25 (1.4-3.4)	0.006	2.490	-	18,499	1.020	Anene and Okorie (2008)
122	339-1881	-	-	1.048	2.393	-	-	-	Camara (1984) in King (1997a)
85 (SL)	484-1191	-	-	-	0.301	9000	-	-	Ezemonye and Osietzaghe (2005)
	280-560	2	(0.69-4.73)	1.716	0.999	-	1,897	0.588	Ikomi and Jessa (2003)
	900-2000	-	3.37 (1.10-6.38)	-	-	8000	-	-	King (1996b)
110	953-3200	-	-	8.759	2.012	-	-	-	King (1997a)
100	1500-1150	1.5-30	-	9.240	1.820	-	-	-	King and Etim (2004)
100	700-1800	2.5	-	-	-	-	-	-	Schwanck (1986, 1987a, 1989)
									Whitehead (1962)

at 12 months (Slovin and Rowland 1978) and at sizes as small as 5 g at 66-mm TL (Schwanck 1980).

Tilapia mariae generally shows an isometric length-weight growth relationship ($W = aTL^b$), with values of the *b* parameter close to three (Table 1). Some populations, however, trend towards allometric growth, with *b* values deviating below three (Olurin and Sotubo 1989; King 1996a; Soyinka and Ayo-Olalusi 2009). Values of *b* do not differ between females and males (Ikomi and Jessa 2003; Olurin and Sotubo 1989). In its native range, the relationship between TL and SL ($TL = 0.4387 + 1.2331 \times SL$) is linear (Laleye 2006). In Victoria, the relationship between age and TL is $Age = 1.761 \times TL + 0.55$, determined using measured growth of juvenile and immature specimens (Osborne 1980).

The length-frequency distribution of *T. mariae* in its native range shows either a bimodal or uni-modal pattern. In the Ethiopie River (Nigeria), *T. mariae* shows a bi-modal length-frequency distribution, with a major mode at 80-89-mm TL (>20% individuals) and a minor mode at 120-129-mm TL (Ikomi and Jessa 2003). In the Ologe lagoon (Nigeria), the major mode is at 130-160-mm TL, with a minor mode at 90-110-mm TL (Soyinka and Ayo-Olalusi 2009). Populations showing uni-modal distribution have a mode at 140-150-mm TL (Olurin and Sotubo 1989) and 110-160-mm TL (Soyinka and Ayo-Olalusi 2009). These results exclude early juvenile fish,

In its native range, *T. mariae* shows considerable variation in condition factor ($k = 100 W/TL^3$) with location, season and growth stage, and some variation with sex. In the Ethiopie River (Nigeria), condition factors range from 2.8 to 4.2, with values above 3.8 for eight months of the year and below 3.0 in December and July (Ikomi and Jessa 2003). Peak values are associated with high food availability at the start and end of the wet season and females running ripe, whereas lower values occur immediately after spawning. In a Nigerian seasonal rain-forest stream, the condition factor of fish caught from late dry season to early wet season ranged from 4.1 to 5.9 (Olurin and Sotubo 1989). Higher *k* values are reported from Nigerian lakes (Elliott 1986; Anene 2005), suggesting higher and more diverse food availability and lower predation pressure in these systems. Soyinka and Ayo-Olalusi (2009) reported higher *k* values in adult males; however, differences between male and female fish are generally minimal (Olurin and Sotubo 1989; Anene 2005; Soyinka and Ayo-Olalusi 2009). Condition factors decrease as individuals attain their maximum length (Anene 2005).

Tilapia mariae's growth rate, as measured by the growth performance index ($\Phi' = \log_{10}K + 2 \log_{10} L_{\infty}$), is relatively high for fish species (King and Etim 2004) but was the lowest for the five African cichlid fish examined in Nigeria (King 1997b). King (1997b) reported an index of $\Phi' = 2.50$, with L_{∞} (asymptotic length, TL) = 221 mm and *K* (growth co-efficient, year⁻¹) = 0.461. A similar growth index value of 2.57 was obtained by King and Etim (2004) using 12 months of length-frequency data, with $L_{\infty} = 304$ mm and $K(\text{year}^{-1}) = 0.40$. Overall, the species shows minor seasonal variation in growth, with the lowest growth corresponding with peaks in breeding.

The pattern of growth in *T. mariae* has been examined using the deposition of calcareous concretions onto fish otoliths. In juveniles, the formation of daily micro-growth increments are the

result of endogenous daily rhythms of rest and activity, and are not influenced by external factors such as photoperiod, feeding frequency or the water temperature cycle (Rosa and Re 1985).

Reproduction

In their native range, female *T. mariae* can breed year-round, as shown by the presence of ripe eggs in ovaries throughout the year (Ikomi and Jessa 2003; King and Etim 2004). Breeding intensity, however, implied by the proportion of individuals with various ovarian development stages (King and Etim 2004), is not the same for all months. For example, the gonadosomatic index (GSI) peaks in alternate months throughout the year (Anene and Okorie 2008), suggesting a cycle of parental care, ovarian maturation and spawning of ~60 days. Across these cycles, there are two or three large peaks in the GSI during the year (Ikomi and Jessa 2003; King and Etim 2004). Although some spawning takes place every month, most occurs 0–6 days before the full moon (Schwanck 1987b). Hence, the lunar phase may be used as a cue for synchronised breeding, but also corresponds to maximum light conditions for parental care during critical stages of the development of the young (Schwanck 1987b).

The seasonal timing of egg production and spawning varies with the flow conditions of a watercourse. In African rivers and streams, spawning peaks during the wet season (Ikomi and Jessa 2003; King and Etim 2004; Anene and Okorie 2008), with King and Etim (2004) also reporting a peak at the start of the dry season. Fewer and larger peaks exist in egg production in more seasonal watercourses (Ikomi and Jessa 2003; King and Etim 2004). In contrast, a year-round cycle of spawning occurs in a constructed lake, with a series of slightly lower GSI values during the dry season (Anene and Okorie 2008).

Based on the time periods for ovarian development, spawning, and parental care, *T. mariae* could potentially raise six successful broods in a year. In aquaria, ovaries take on average 34 days to fully develop after premature brood loss at the larval stage (Baldaccini 1973). Moreover, in the field, parental care is afforded to a brood for 40–60 days, and the natural cycle of spawning can be ~60 days (Anene and Okorie 2008). Hence, ovary maturation is occurring in at least the later part of parental care. In addition, most of adult females (72%: King and Etim 2004; 82%: Ikomi and Jessa 2003) have ovaries in a mature to ripe stage of development. However, owing to high brood mortality, it is likely that the number of successful broods is lower and the number of spawning attempts higher.

The fecundity of *T. mariae* is high compared with other cichlid species, but low compared with other substrate-spawning *Tilapia* spp. (King 1996b; King and Etim 2004). Egg numbers range from 200 to 3200 per ovary (Table 3), and increase both linearly and non-linearly with body length (Ikomi and Jessa 2003; King and Etim 2004; Anene and Okorie 2008) and weight (Ikomi and Jessa 2003; Anene and Okorie 2008). The rate of increase (b) of fecundity (F) with body length (TL) ($F = aTL^b$) (1.82: King and Etim 2004; 2.49: Anene and Okorie 2008) is similar to that of mouth-brooding tilapias. This suggests that the reproductive characteristics of *T. mariae*, as first postulated by Whitehead (1962), are intermediate between those of substrate and mouth brooders. However, the b value is not consistent across habitats, with a value of 1.0 (Ikomi and Jessa

2003), suggesting fecundity increases approximately linearly with body length (Ezemonye and Osiezaghe 2005) (Table 3).

Courtship and mating

Courtship and mating by *T. mariae* has been described both in the field (Schwanck 1987a; Annett *et al.* 1999) and in aquaria (Apfelbach 1969; Baldaccini 1973; Turner *et al.* 1989; Schwanck 1987a). Moreover, Baldaccini (1973) described in detail the behaviour and colouration exhibited during courtship, mating and parenting. The courtship and mating process initially involves agonistic intra- and intersexual interactions for dominance and territories, and a short, aggressive pre-courtship phase between the male and female. This is followed by a courtship phase where mostly monogamous breeding pairs are established, and a mating phase with the deposition of ripe eggs by the female and fertilisation by the male. In aquaria, the pair will stay together during successive reproductive cycles (Apfelbach 1969; Baldaccini 1973), but we found no evidence of this for wild fish.

Generally, *T. mariae* moves in small groups or schools comprising of juveniles and adults of both sexes during non-reproductive phases. At the onset of courtship and mating, both males and females will establish separate territories, with the males' territory being the focus of reproductive activities (Apfelbach 1969; Annett *et al.* 1999). When space is limited, the males must establish dominance over conspecific individuals to establish a territory (Schwanck 1980). In aquaria, male dominance is related to androgenic hormone state, measured by the size of the genital papilla; larger fish are more dominant when hormone states are similar (Schwanck 1980). In dominance encounters between females, the larger individual will always gain access to males (Turner *et al.* 1989).

At the start of the pre-courtship phase, both sexes will adopt breeding colours and the male will aggressively defend his territory from conspecific individuals and other species (Schwanck 1987a; Annett *et al.* 1999). When the female has ripe ovaries, she will leave her territory and visit the territories of several males. Initially, both females and males show very similar levels of aggression towards each other, with a series of chases and butts and the female repeatedly fleeing the males' territories (Apfelbach 1969; Baldaccini 1973; Annett *et al.* 1999). Eventually, the female is increasingly tolerated by a single male and a courtship is entered into (Baldaccini 1973).

Male courting is initially aimed at larger females but males will redirect their courting attention to females that show the most interest (Schwanck 1987a). Female choice is not clearly understood; however, it seems to be most influenced by the male's behaviour, but can change over time as courtship may last for days. Some evidence exists for female choice based on male size (Schwanck 1987a). During the actual courtship, the aggressive behaviour displayed by the male and female during pre-courtship is rare or absent (Lamprecht 1973; Turner *et al.* 1989). When the pair is established, both members become aggressive to intruders and they defend their shared territory (Annett *et al.* 1999). This pair bond is only evident before spawning, with the parents avoiding each other (Lamprecht 1973) or even becoming aggressive towards each other (Lamprecht 1972) while sharing brood care responsibilities. Pairs are likely to be broken when the eggs or larvae are

disrupted, owing to the male being ready to spawn but the female not able to respond (Baldaccini 1973).

Tilapia mariae adopt colour patterns associated with courtship, mating and parenting that are variations of the typical barred or spotted colouration (Baldaccini 1973; Trewavas 1974; Slovin and Rowland 1978). No sexual differences exist in the colour patterns and the way they correlate to behaviour. Baldaccini (1973) describes nine colour patterns of both reproductive and non-reproductive fish in aquaria, which incorporate variations in background colour, spots and bars. During reproduction, the background colour varies from white-grey through to black, whereas the spots and bars go through various stages of development depending on the reproductive phase or activity. A reddish colour appears on the body adjacent to the operculum and on the throat of both sexes, whereas the upper margins of the dorsal and caudal fins are also often tipped red-pink, sometimes underlined with a yellow-white colour (Ajuzie 1996; Anene 1999). Few of the behaviours of *T. mariae* are exclusively associated with a single colour pattern, with the exceptions of (i) schooling juveniles always having the typical barred pattern, and (ii) parents that are moulting eggs and larvae always have a false barred pattern. However, frequently observed colour patterns shown in encounters between adults are often associated with particular behaviours (Baldaccini 1973). For example, territorial individuals that are courting and showing aggressive behaviour are generally spotted, and those escaping are generally barred (Baldaccini 1973; Slovin and Rowland 1978; Annett *et al.* 1999).

Egg deposition generally takes place on a stone or rocky substrate (Annett *et al.* 1999), pieces of wood, and macrophyte leaves (Whitehead 1962). Apfelbach (1969) noted a preference for the under-surface of stones, with the female turning upside down during deposition. Egg depositions have been recorded at depths of 15 cm to >4.0 m (Whitehead 1962; Schwanck 1989), with larger females laying eggs in deeper water (Schwanck 1989). Variation in depth may also be related to availability of substrate and water temperature. The deposition site is prepared by clearing away debris (Annett *et al.* 1999), and egg deposition generally occurs within one day of territory establishment and courtship (Schwanck 1987a). In some cases, egg deposition can be delayed for six days, with a large proportion of breeding pairs even failing to lay eggs (Schwanck 1987a). The female will deposit the adhesive eggs in rows of six to seven eggs, with the male immediately fertilising the eggs in alternate runs to the spawning female (Baldaccini 1973).

Parental care

Tilapia mariae is primarily a monogamous breeding species, but with reported cases of bigamy (Schwanck 1989) and polygamy (Lamprecht 1973; Annett *et al.* 1999), shown by group-rearing of broods, adoption of broods, and non-breeders sharing and defending territory with breeders. Parental care of the brood extends until the end of the early juvenile stage, with males and females having differentiated parental roles (Apfelbach 1970) and showing a high degree of intra-pair coordination (Schwanck 1989). In its native range, three role types of brood-guarding during the embryonic and larval stages have been observed: (1) female at the brood, male in surroundings; (2) parents take turns, and (3) parents stay together at the brood (Schwanck 1989). In all cases, the female makes more attacks towards conspecific

individuals and other predators. The female is assumed to make the choice of roles, with type (1) chosen when male motivation is low, type (2) when the female is smaller, and type (3) when brood vulnerability increases. In Florida, the parental care closely resembles type (1) (Annett *et al.* 1999). In aquaria, parental roles are more indistinct and more intra-pair aggression is shown (Schwanck 1989; Baldaccini 1973).

In its native range, both parents are involved in nest preparation before the eggs are laid. In Florida, females do nearly all nest preparation (Annett *et al.* 1999), whereas in aquaria males perform the role (Baldaccini 1973). During the egg guarding stage, the female will fan or aerate the eggs if oxygen levels are low (Schwanck 1989). Newly hatched larvae are transferred by mouth by both sexes to a previously dug pit (Apfelbach 1969; Baldaccini 1973; Annett *et al.* 1999). Occasionally, after disturbances, the young are transferred to new pits, with the female taking on the additional pit preparation and transfer (Baldaccini 1973).

Male desertion during the embryonic and larval stages is common, with up to 33% of nests guarded by only one parent, usually the female, but sometimes the male (Schwanck 1989; Annett *et al.* 1999). Male desertion may be related to: (i) low return on investment for early stage broods; (ii) strongly female-biased sex ratios leading to high female availability; (iii) poor feeding conditions, or (iv) a low requirement for effort put towards defence (Schwanck 1989). However, more than 20% of male deserters return to their brood, most within two days but some up to 15 days after desertion (Schwanck 1989). Male return may be related to: (i) higher return on investment with older brood, or (ii) lost opportunity to re-mate since egg production in females is generally synchronised.

Guarding times become more (Schwanck 1989) or less (Annett *et al.* 1999) equitable between the female and male during the early-juvenile stage, with the female continuing to make more attacks on intruders (Schwanck 1989; Annett *et al.* 1999). Broods can be left unguarded up to 5% of the total guarding time when both parents are attacking intruders simultaneously (Schwanck 1989). In Florida, the male guards the early juvenile stage, with the female patrolling the school and attacking and defending against conspecific individuals and predators (Annett *et al.* 1999). When the brood reaches the late-juvenile stage, parental care decreases rapidly until the brood is abandoned and a new reproductive cycle may start.

Brood mortality of *T. mariae* is high, up to 30% after the first day after egg deposition and 80% within a week (Schwanck 1989), but decreases as the young become more developed. Conspecific individuals are most likely to attack all brood stages (Schwanck 1989), with up to 41% of (mostly male) parental cannibalism of eggs and larvae in aquaria (Schwanck 1986). Uni-parental broods are more prone to mortality than bi-parental broods (Schwanck 1989), and when both parents are removed, large numbers of predators will converge on the brood (Whitehead 1962).

Foraging, diet and nutrition

Tilapia mariae is primarily herbivorous, feeding on phytoplankton and macrophytes, with small amounts of animal sources in its diet. Its dental anatomy reflects grazing of algae and plants from the substrate, whereas its gill morphology

allows consumption of large proportions of phytoplankton where it is abundant. As *T. mariae* has a diet that includes coarse plant material, it is considered to be ecologically intermediate between the macrophagous and microphagous trophic guilds of tilapiines (Teugels *et al.* 1992). *Tilapia mariae* exhibits variation in body length with different diets, but, unlike some other cichlid species, does not exhibit phenotypic plasticity in morphology when forced to adapt to different feeding modes (Stauffer and Van Snik Gray 2004).

Components of *T. mariae*'s diet in its native range were listed in Fagade (1971), Anibeze (2001), Ikomi and Jessa (2003), Olurin and Awolesi (1991), Olurin and Fagade (1994), Anene (2004a) and Soyinka and Ayo-Olalusi (2009). Phytoplankton, consisting of various algae taxa, contributed to most of the diet in each of these studies. In the present study, phytoplankton is grouped into diatoms (Bacillariophyceae), desmids (Desmidiaceae), euglenids (Euglenaceae), and colonial, unicellular and filamentous algae (Chlorophyceae, Xanthophyceae, Cyanophyceae). Except euglenids (<1% of stomach contents in all studies), all of the above algae groups have been well represented by at least one study, although their relative contribution varied strongly with location. Colonial, unicellular and filamentous algae were the most common components of diets by number and proportion, with no particular genus or species being dominant across studies. Diatoms, predominantly *Conscinodiscus* spp. and *Navicula* spp. (Fagade 1971; Olurin and Awolesi 1991; Soyinka and Ayo-Olalusi 2009), and desmids, predominantly *Cosmarium* sp. (Olurin and Awolesi 1991; Olurin and Fagade 1994), were also well represented in the diet. In these studies, macrophyte components (plant fragments, seeds) were present in all stomachs, whereas animal sources, including allochthonous invertebrates, free-swimming invertebrates, benthic invertebrates, Protozoa, Rotifera, fish eggs, invertebrate larvae, and fish remains, were generally present in low proportions. However, Fagade (1978) reported a diet consisting of mainly *Dipterus* larvae in Lekki Lagoon, Nigeria. Detritus and sand were commonly found in the stomach in amounts less than 10%. Overall, *T. mariae*'s diet varies with age, with smaller fish (<70-mm SL) consuming more unicellular algae and benthic larvae, and larger fish consuming more detritus, macrophytes and allochthonous insects (Ikomi and Jessa 2003).

The herbivorous nature of *T. mariae* has been confirmed in the USA and Australia. In Florida, a breeding pair spent 6.4% of the time feeding on the surface of aquatic vegetation and other substrate (Annett *et al.* 1999), with no further information from stomach examinations available. In the Mulgrave River, northern Queensland, the proportional contributions of diet categories were: macrophytes (31–54%), filamentous algae (17–25%), and detritus (21–26%) (Rayner *et al.* 2009). In Victoria, both diatoms and filamentous green algae were present in almost 100% of stomachs, followed by macrophytes (67%), desmids (32%), blue green algae (18%), and crustaceans (8%) (Osborne 1980). Stomach contents differed with size, with juveniles containing more desmids and blue-green algae than adults, and crustaceans being absent from adult stomachs (Osborne 1980).

The low proportion of empty stomachs reported throughout the year suggests that *T. mariae* is more or less a continuous feeder. However, Ikomi and Jessa (2003) found a higher

diversity of diet and more individuals with stomach contents during the wet season in the Ethiopie River, Niger. The proportion of individuals with empty stomachs ranges from 0% (Fagade 1971) and 3.6% (dry season: Olurin and Awolesi 1991) to 13% (Anibeze 2001; Anene 2004a). Stomach analysis in one study revealed that the contents consisted of 37.8% crude protein, 4.7% fat, 14.3% moisture, with a crude ash content of 16.9% and nitrogen free extract of 26.3% (Anibeze 2001).

Tolerances and toxicities

Only a few tolerance and toxicity studies have been conducted on *T. mariae*, including responses to changes in temperature, dissolved oxygen, copper, glyphosate and benzocaine. In Florida, preferred temperatures of introduced brood-stock were assessed after acclimation to various temperatures (Siemien and Stauffer 1989). After an acclimation temperature of 15°C, the preferred temperature was 25.2°C, and after acclimation at 20°C the preferred temperature was 31.3°C. The preferred temperature after acclimation at 25–35°C was 33.0°C. In Roger Springs, Nevada, the species is established at temperatures of 28–29°C (Courtenay and Deacon 1983).

The potential range of *T. mariae*, like other non-native tropical invasive fish, is most likely restricted by their lack of tolerance to low temperatures (Shafland and Pestrak 1982). When exposed to decreasing temperatures from 25°C, the following morphological and physiological changes were observed in adult *T. mariae*: (i) increased agitation when disturbed; (ii) darkening of body and fin colouration, with dramatic intensification of red abdominal chromatophores; (iii) gradual decline in activity; (iv) relatively abrupt loss of equilibrium; (v) resting near the bottom; (vi) swimming and/or surface bobbing at an angle of 45–90°, and (vii) haemorrhaging at the base of some fins (Shafland and Pestrak 1982). Associated sub-lethal and lethal temperatures were: reduced feeding at 15–18°C, loss of equilibrium at 13.9°C, no feeding at 13.1°C, and death at 11.2°C. Using thermal bioassays, Siemien and Stauffer (1989) found lower and upper lethal temperatures of 11°C and 37°C respectively, with no effect of acclimation temperature on lethal temperatures.

Although *T. mariae* occurs in both freshwater and saline habitats in its native and introduced range, no published salinity preferences or tolerances are available. In Nevada, the species is established in Rogers Spring where salt levels are high (specific conductance $3.72 \times 10^3 \mu\text{mhos cm}^{-1}$ at 25°C) (Courtenay and Deacon 1983). *Tilapia mariae* appears to be tolerant of very low dissolved oxygen levels, showing an absolute minimum oxygen saturation tolerance of 7.3% at 28°C in laboratory experiments, with a mean minimum of 10.1% (Webb 2008).

Exposure of adult *T. mariae* to four days of copper (Cu^{2+}) at concentrations of 20–100 $\mu\text{g L}^{-1}$ caused olfactory neuron damage at all concentrations, with damage less severe and confined to receptor cells at lower concentrations (Bettini *et al.* 2006). Recovery of olfactory neuron damage from copper levels of 20 $\mu\text{g L}^{-1}$ was complete after 10 days (Bettini *et al.* 2006). Glyphosate has a concentration lethal to 50% of exposed *T. mariae* individuals (LC_{50}) of 45.1 mg active ingredient (a.i.) L^{-1} after 96 h of exposure, with no effects recorded at concentrations <15.6 mg a.i. L^{-1} (Jahl and Larsson 1998). Surprisingly, fish showed 90% survival at 1000 mg a.i. L^{-1} , owing to toxicity being reduced by an acidifying effect.

Benzocaine (ethyl-*p*-amino-benzoate) has been recommended as a sedative for *T. mariae* (Ross and Geddes 1979). A dosage of 1 : 15 000 is used for fish weighing 0–1 g, 1:10 000 for 1–50 g and 1:5000 for 50–100 g, with sedation and recovery times varying with temperature.

Predators, parasites and threats

Tilapia mariae suffers from heavy predation, especially during the embryonic, larval and juvenile stages. In addition to high levels of parental cannibalism, brood attacks by non-breeding conspecific individuals are very common and comprise the majority of attacks by large predatory fish (Schwanck 1989). Moreover, several smaller predatory fish species hide in vegetation and snatch embryos and juveniles (Schwanck 1989). In its native range, 11 species are known to prey on non-adult *T. mariae* (Adebisi 1981; Schwanck 1989; King and Etim 2004), whereas only three species (*Mormyrops deliciosus*, *Hepsetus odoe*, and *Parachana obscura*) are reported to prey on adults (Adebisi 1981; King and Etim 2004).

In Florida, the native largemouth bass (*Micropterus salmoides floridana*) and Florida gar (*Lepisosteus platyrhincus*) prey on *T. mariae* (Courtenay and Deacon 1983; Annett 1998; Hill *et al.* 2004). Between 1984 and 1987, the peacock cichlid (*Cichla ocellaris*), a native of tropical South America, was introduced to prey on *T. mariae*. *Cichla ocellaris* became naturalised in less than five years and was considered a successful predator (Shafland 1996), with *T. mariae* contributing up to 75% of the inspected stomach contents (Shafland 1995).

In its native range, *T. mariae* carries heavy parasite loads (Nmor *et al.* 2003; King and Etim 2004; Olurin and Somorin 2006). However, no information is available on associated mortality or detrimental effects. In Nigeria, the percentage of individuals infected by intestinal helminths was 64% (Nmor *et al.* 2003) and 62% (Olurin and Somorin 2006), with the number of parasites significantly higher compared with other fish species (Nmor *et al.* 2003). Parasite load increased with both bodyweight and length, but did not differ between males and females (Nmor *et al.* 2003; Olurin and Somorin 2006). Although *T. mariae* is not listed as a known host of any Myxosporea protozoa in a study by Fomena and Bouix (1997), the myxosporean parasite, *Myxobolus noumensis* sp. nov., was subsequently described in the kidney and spleen of *T. mariae* (Fomena and Bouix 2000). Reported gill parasites on *T. mariae* include *Cichlidogyrus cubitus*, *C. dossoui*, *C. testificatus* and *C. yanni* (Ancyrocephalidae) (Pouyaud *et al.* 2006).

In Nigeria and Cameroon, fish populations, including *T. mariae*, are drastically reduced during the dry season when rainforest streams dry up (Teugels *et al.* 1992). Similarly, when watercourses in Nigeria seasonally flood, many fish are left stranded in temporary waterholes and will perish when the water disappears. King and Etim (2004) estimate that 10% of these stranded fish are *T. mariae*.

In its native range *T. mariae* is an important component of subsistence and artisanal fisheries (Nwadiaro 1987; King and Etim 2004; Anene and Okorie 2008; Soyinka and Ayo-Olalusi 2009), with resulting fishing pressures on stocks. Depending on the habitat and fishery, the species is regarded as both highly exploited (Anene 2004b) and under-exploited (King and Etim

2004) with exploitation ratios (fishing mortality:total mortality) of 0.57 and 0.43, respectively.

Waterway pollution from human waste and industries, including petrochemicals, sawmills and rubber processing, poses a threat to *T. mariae* in its natural range (Isamah *et al.* 2000; Achuba 2002). Indicators of environmental stress, such as lipid peroxidation and anti-oxidant enzyme levels, are significantly higher in individuals where higher pollution loads are present (Isamah *et al.* 2000; Achuba 2002). However, *T. mariae* may avoid severe effects of pollution and excess accumulation of heavy metals, owing to its primarily herbivorous and lotic feeding nature. For example, anti-oxidant enzyme levels in *T. mariae* were significantly lower than *Malapterurus electricus* captured in the lentic region of the same watercourse (Achuba 2002). Heavy metals, such as mercury (Lewis and Chancy 2008), lead (Daka *et al.* 2008) and cadmium (James and Okolo 2003) accumulate in *T. mariae* in low concentrations compared with other fish species, whereas iron accumulates in higher concentrations, and levels of lead and zinc are not significantly different (James and Okolo 2003).

Occurrences outside the species' natural range

Introductions

Tilapia mariae is a desirable and versatile aquarium fish, and a species with potential for aquaculture (Ajuzie 1996). Although the species is most likely present in aquariums in many countries, it is naturalised only in the USA, Australia and possibly Russia (Welcomme 1988; Holcik 1991; Robins *et al.* 1991). No available information exists on the introduction to Russia, except that it was for the purpose of aquaculture (Ivoylov 1986).

In the USA, *T. mariae* was introduced between 1972 and 1974 to southern Florida (Courtenay and Hensley 1979) most probably as a result of escapes from tropical fish farms (Shafland 1976). It quickly established in highly modified fresh and brackish canal systems (Hogg 1976; Shafland 1976; Clark 1981), and more recently in natural watercourses (USGS 2009). In 1980, an established population was discovered at Rogers Spring in Nevada, a release point for aquarium fish (Courtenay and Deacon 1982, 1983). The species is now considered naturalised in Florida, Arizona and Nevada, and present in California (Nico 2009; USGS 2009).

The dates and reasons for the introductions of *T. mariae* to Australia remain speculative. It was detected near Cairns, North Queensland, around 1980 (Webb 2007), and has since become naturalised in some eastern-flowing rivers and estuaries between Innisfail and Cairns (Mather and Arthington 1991; Russell *et al.* 2003; Rayner *et al.* 2008). In 1978, it was naturalised in the cooling waters of a power station in temperate south-eastern Australia (Cadwallader *et al.* 1980), where it still occurs. Recent records in a tributary of the western-flowing Walsh River in North Queensland (M. Pearce, pers. comm.) have substantiated predictions that the species has the potential to spread into the Gulf of Carpentaria and large areas of northern Australia (Bradshaw *et al.* 2007).

Impacts

Southern Florida has the highest number of naturalised freshwater fish in the world (Brooks and Jordan 2010), with *T. mariae*

being the most common of these (Loftus and Kushlan 1987). The species has been highly successful in invading waterways with poor water quality and competing with native fishes (Annett *et al.* 1999). For example, 30% of sunfish (*Lepomis* spp.), a species with similar territorial and spawning behaviour, are ejected from territories through competition with *T. mariae* (Brooks and Jordan 2010). In Nevada, the species competes with smaller native fish and invertebrates for green algae in the desert springs (Courtenay and Deacon 1983). In North Queensland, the species is locally abundant (Russell *et al.* 2003; Rayner *et al.* 2008), with only one publication documenting potential impact on relative abundance of native and endemic species (Kroon *et al.* 2011). Kroon *et al.* (2011) documented that the presence of the invasive fish species *T. mariae*, *Poecilia reticulata*, and *Xiphophorus maculatus* significantly changed the composition of species abundance assemblages in a Far North Queensland catchment. Five native fish species were more abundant at sites without these invasives, including the endemics *Cairnsichthys rhombosomoides* and *Glossogobius* sp.4.

Management

In southern Florida, possession of *T. mariae* has been banned since 1974 (Clark 1981). The intentional release of the exotic peacock cichlid (*C. ocellaris*) has proven to be partly successful as a biological control agent (Shaffland 1995). However, the long-term prospects of this control are uncertain as *T. mariae* has continued its range expansion (USGS 2009). In Australia, *T. mariae* is a declared noxious fish under the relevant State Fisheries Acts in all states and territories, except Western Australia, and is listed on the National Noxious Fish List (Bureau of Rural Sciences 2007). In Queensland, the species must not be kept or released, and must be disposed of if caught (DEEDI 1994). Current control measures for all tilapiine species in Queensland focus on education and awareness, spot eradication and prevention of further spread. In 2008, an unsuccessful eradication was attempted using rotenone in a 5-km section of the Walsh River, a tributary of the western-flowing Mitchell River (M. Pearce, pers. comm.). Electro-fishing has been investigated as a method to control a similarly invasive tilapiine (*Oreochromis mossambicus*) in North Queensland (Thuesen *et al.* 2011). Adult numbers were significantly reduced over three years, but this caused an increase in juvenile recruitment (Thuesen *et al.* 2011).

Conclusions and recommendations

The biology of *T. mariae*, unlike other tilapiine species, has not been extensively studied, with a total of 101 published works identified and included in this review. Of these, ~50% are field studies conducted in its native environment, and 17% are studies and reports from its introduced range. These studies highlight several characteristics of the species' biology. First, *T. mariae* shows great variation in morphological attributes, including condition factor, size distributions and length–weight relationships, in response to the hugely varied habitats where the species occurs. Second, these studies reveal some plasticity in reproductive behaviour, particularly in the manner in which parental care is exhibited. Specifically, whereas *T. mariae* is generally described as a monogamous breeding species, both laboratory

and field studies have demonstrated that both bigamy (Schwanck 1989) and polygamy (Lamprecht 1973; Annett *et al.* 1999) occur. Third, *T. mariae* demonstrates a variety of feeding behaviours and dietary components, which are reflected in the species' dental anatomy and gill morphology. We propose that, relative to species with specialised reproductive and feeding behaviours, such plasticity may contribute to the competitive advantage of *T. mariae* in both native and introduced regions. Moreover, the species' documented tolerance of a wide range of temperatures, salinity and dissolved oxygen concentrations, and its aggressive behaviour to other piscine species, is likely to further consolidate this advantage. In contrast, the inferred high fecundity of *T. mariae* does not appear to be supported by the relative low number of eggs produced per female (Table 3), the high brood mortality, and the high predation pressure suffered by embryonic, larval and juvenile stages (Schwanck 1989).

Tilapia mariae is common in its native range, and supports local subsistence and artisanal fisheries in some catchments (Nwadiaro 1987; King and Etim 2004; Anene and Okorie 2008; Soyinka and Ayo-Olalusi 2009). However, pressures from over-exploitation (Anene 2004b) and pollution (Achuba 2002; Isamah *et al.* 2000) are evident in other catchments. To inform management of the wild populations and fisheries of *T. mariae* in its native range, more detailed information is required on the stock structure of the species. Moreover, we suggest that comparative research on morphology, meristics and genetics will reduce the uncertainty around the potential existence of *T. mariae* subspecies and tilapiine hybrids. Further research on the species' behavioural and physiological tolerances of pollutants could inform the management of both point and diffuse sources of waterway pollution in its native range.

Unlike other tilapiine species (Lim and Webster 2006), *T. mariae* has yet to be extensively cultured locally or globally (King and Etim 2004). We only found one reference to the culture of *T. mariae* outside its native range (Vassallo *et al.* 2007). This disparity is most likely owing to its relatively low growth rate and fecundity, high natural mortality and small maximum size compared with other tilapiine species that are extensively cultured. Nevertheless, the species appears to have some potential for aquaculture (Ajuzie 1996). We propose that more research on reproductive and developmental biology of *T. mariae* may further clarify its potential for aquaculture. Furthermore, quantifying its function in aquatic food-webs could aid in the development of diets for aquaculture, as well as target the maintenance and rehabilitation of native habitats. These research areas may also elucidate innovative control strategies outside its native range.

Tilapiine species, specifically *Oreochromis mossambicus*, are amongst the world's worst invasive alien species (International Union for the Conservation of Nature 2010), with *T. mariae* a declared noxious fish in most of Australia (Bureau of Rural Sciences 2007) and its possession banned in Florida (Clark 1981). Despite its status, the documented impact of *T. mariae* in the USA is restricted to territorial competition with *Lepomis* spp. during the breeding season (Brooks and Jordan 2010), and food competition with smaller native fish and sportfish (Courtenay and Deacon 1983). It is unclear whether such competition has resulted in an associated decline in abundance or distribution of native species. Only one published

record exists on the potential impact of *T. mariae* on native species and ecosystems in Australia (Kroon *et al.* 2011), but none exist from Russia. In Australia, territorial and food competition is likely to exist, given the presence of species with similar reproductive behaviour (e.g. various catfish species, *Arius* spp., *Neosilurus* spp., *Porochilus* spp., and *Tandanus* spp.) and dietary preferences (e.g. various garfish species, *Arrhamphus* spp.; small-headed grunter, *Scortum parviceps*, and bony bream, *Nematolosa erebi*) within the current range of *T. mariae*. Whether *T. mariae* directly prey on native fauna, including different life history stages of macro-invertebrates, frogs and fish, is currently unknown. To improve our understanding of *T. mariae*'s potential impact of on native species and ecosystems, we propose that: (i) abundance and distribution of native organisms should be compared in invaded and non-invaded areas, and (ii) the species' function in aquatic food-webs should be quantified. Such understanding could also elucidate potential biological and economic impacts on commercial and recreational fisheries resources.

The long-term efficacy of *T. mariae* management strategies, including the banning of its possession (Clark 1981; DEEDI 1994), the introduction of the peacock cichlid (*C. ocellaris*) in Florida (USA) (Shafland 1995), public awareness and education in Australia (DEEDI 2000), and electro-fishing are uncertain and have not been quantified. In North Queensland, *T. mariae*'s distribution continues to expand both within and across river systems after its first detection in Cairns around 1980 (Webb 2007), at least partly through human-assisted spread. We found no studies at all on the use of native predators, parasites and diseases as biological control agents, and these may be fruitful areas of further research to inform management. Overall, greater effort in prevention of its release may be required to arrest the spread of *T. mariae* outside its native range. We suggest that more detailed information on *T. mariae*'s life history characteristics, including critical invasion patterns and processes, is required to inform such prevention. Once the species is established, complete removal through the application of piscicides or exhaustive fishing effort is likely only possible at smaller scales. At larger scales, management strategies that focus on those biological aspects that give *T. mariae* a competitive advantage over native species may provide the best chance to reduce its abundance and distribution. These could include the reduction of: (i) the availability of herbivorous and planktivorous food sources; (ii) the availability of substrates suitable for egg deposition, and (iii) large fluctuations in water temperature, salinity and dissolved oxygen. Given that in the USA and Australia, *T. mariae* predominantly occurs in disturbed aquatic environments, particular attention should be paid to achieving such reductions in abundance and distribution, in the context of rehabilitating the integrity and resilience of native aquatic ecosystems.

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