Sonic Cichlids

Phillip S. Lobel, James G. Garner, Ingrid M. Kaatz, and Aaron N. Rice

Abstract Bioacoustics has become a key feature of cichlid behavioral studies over the last 20 years, due in large part to new technologies and software. The hypothesis that some cichlid species produce species-specific sounds is gaining support with data from several studies. Sounds are specific to behavioral context for many species. Cichlids are advanced teleost fishes possessing a complex pharyngeal jaw. This morphological feature has been proposed as the key functional innovation responsible for the evolutionary success and explosive adaptive radiation of the group. This evolutionary success has been mostly attributed to their expanded adaptability to process a wide variety of food types due to the capability of thoroughly grinding food in the pharyngeal apparatus, an ability that most other fishes lack. The evidence regarding the role of the pharyngeal jaw complex in sound production is evaluated, and suggests that this same morphology enables cichlids to produce a complex and varied acoustic repertoire. Although, the sonic mechanism may be more complex morphologically than just the pharyngeals clacking. More studies are needed to carefully document the sounds correlated to specific behaviors of cichlids and to statistically examine the species specificity of sympatric species sounds. Future research is needed that experimentally tests the response of female fish to acoustic playback combined with visual and chemical cues in order to determine how critical sound communication is to the sympatric evolution of cichlid species.

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1 Introduction

It has been almost 60 years since the first reports on the sonic behavior of cichlids. Fryer and Iles (1972) reviewed the discoveries by Bauer (1963), Myrberg et al. (1965), and Rodman (1966) and suggested that the use of sounds by cichlids may be important as a means of species recognition and mate location. However, research on cichlid bioacoustics progressed slowly until about the year 2000 (Fig. 1, earlier reviews of cichlid sounds include Lobel 2001; Amorim et al. 2004 and Longrie et al. 2013).

Historically, research was hindered by the expense and difficulty of using hydrophones and the technology for acoustic analyses, but these former obstacles have been eliminated by modern video camcorders, personal computers, and especially new software for acoustic analysis. The first underwater study of the sonic behavior by cichlids in the wild showed that cichlids were indeed quite acoustically active in Lake Malawi and sounds differed among neighboring species (Lobel 1998). Since then, cichlid bioacoustics has become an active topic for research. Another field study, also in Lake Malawi, documented possible population variation in cichlids calls over a geographic range (Danley et al. 2012). The nature/nurture question was examined in *Oreochromis niloticus,* and suggested that the ontogeny of sound production in juveniles was innate and not learned (Longrie et al. 2008). Acoustic features that could provide signature differences were examined by Bertucci et al. (2012a, b). The Tanganyikan cichlid, *Neolamprologus pulcher*, has been proposed

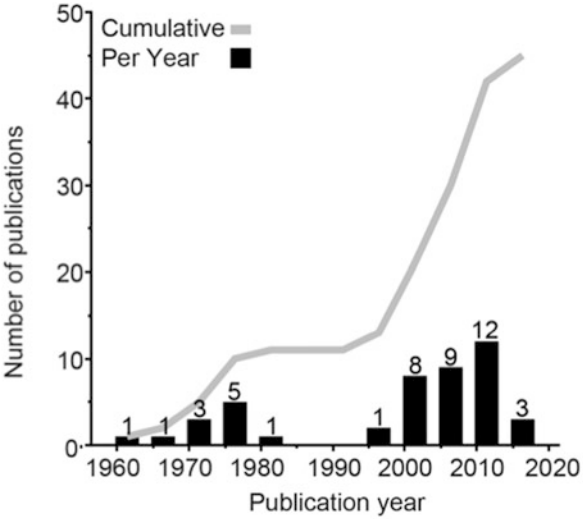

Fig. 1 Summary of scientific papers describing sound production in cichlids per year (black columns) and cumulatively (gray line). Citations for papers that describe the production of sounds or behavioral use of sounds ($N = 51$) were discovered through literature searches using the Web of Science database (with coverage from 1864-present), and the literature cited list of relevant papers (e.g., Baerends and Baerends-van Roon 1950 in the case of Raj 1916)

as a silent species based on the lack of sounds recorded under laboratory conditions (Pisanski et al. 2015), prompting a need for closer investigation of acoustic activity in other species. Laboratory experiments have shown using acoustic playback experiments that increases in noise can impact behavior by reducing behavioral activity levels that normally coincide with sound production (Slabbekoorn et al. 2012).

It has been well known for a long time that cichlids display complex behaviors during the behavior of mate selection (Baerends and Baerends-van Roon 1950; Keenleyside 1991; Barlow 2000). Cichlids are clearly multi-modal in their communication (Rosenthal and Lobel 2006; Amorim et al. 2008; Verzijden et al. 2010). Vision and coloration are key in the mate selection process for the *Pseudotropheus zebra* species complex of Lake Malawi (Couldridge and Alexander 2002). But visual cues are not necessarily the sole communication modality, nonvisual cues are implicated in experimental studies (Blais et al. 2009). Recent reviews have focused on the importance of visual cues and color patterns in the evolution of cichlid and other fishes (Rowland 1999; Seehausen et al. 1999). While visual cues are undoubtedly important, olfactory and acoustics cues also play significant roles. For example, Chien (1973) determined that the combination of visual and olfactory cues presented together increased spawning rates in the cichlid, *Pterophyllum* spp., above the rates observed when only one cue was presented; i.e., the effects of the various stimuli are additive (Rowland 1999). Visual cues are apparently not the primary cue in all species examined. Furthermore, chemical cues have received attention as being important in cichlid communication (Maruska and Fernald 2012). The exact role of acoustics in this mate selection process by cichlids is an ongoing hot topic today. During courtship, females prefer acoustic over silent males but the visual presence of the male is required (Estramil et al. 2014). Sounds and visual cues are synchronous during agonistic encounters (Bertucci et al. 2010). Blais et al. (2009) determined experimentally that visual signals alone cannot explain mate choice and that other signals must also be involved as a factor in female choice. However, they did not assess other cues such as olfaction or acoustics.

Cichlid fishes are widely studied with regard to understanding the processes of speciation (e.g., Sturmbauer 1998; Kornfield and Smith 2000; Salzburger and Meyer 2004; Kocher 2004; Salzburger 2009). The rapid and extensive species radiation (“species flocks”) seen in cichlids is unrivaled in other vertebrate groups (Liem 1973; Echelle and Kornfield 1984; Barlow 2000; Kornfield and Smith 2000; Salzburger and Meyer 2004; Turner 1999; Turner et al. 2001). One underlying mechanism for this evolutionary success is the cichlid’s complex pharyngeal jaw, a highly adaptable morphological feature (Liem 1973, 1991) coupled with the cichlid’s complex mating behavior, short generation time with numerous offspring. Cichlids provide an opportunity to observe speciation at different stages of progression, allowing investigation of the process and mechanisms of evolution (Kornfield and Smith 2000; Kocher 2004). Species divergence in closely related sympatric cichlids, especially in the Great Lakes of Africa has been hypothesized to have occurred, in part, due to assortative mating. Cichlid mate choice studies confirm that assortative mating does occur in several species in the field and in captivity

(Blais et al. 2009; Egger et al. 2008; Knight and Turner 2004; Salzburger et al. 2006). The key to understanding this process is to decipher the factors involved in cichlid mate selection. The influences of visual and chemical cues as prezygotic isolating mechanisms have been examined (Couldridge and Alexander 2002; Blais et al. 2009; Kidd et al. 2006; Maan et al. 2004; Plenderleith et al. 2005). Acoustic signals have not yet been similarly investigated.

This review will highlight the possible morphological mechanisms and biological significance for the occurrence and variability of sounds produced by cichlid species during aggression and courtship. Sounds are also associated with other behaviors, particularly feeding and swimming, which are not necessarily intentionally produced. The essential scientific question is whether certain sound patterns produced by cichlids are ethologically meaningful. For reviews of fish bioacoustics and communication including terminology (see Moulton 1960; Demski et al. 1973; Ladich 1997; Kasumyan 2009; Ladich 2015; Blaxter 1981; Fine et al. 1977; Hawkins 1986; Hawkins and Myrberg 1983; Myrberg 1980, 1981; Myrberg et al. 1978; Popper and Fay 1973, 1993; Schwarz 1985) for cichlid communication (see Nelissen 1991; Lobel 2001; Amorim et al. 2004; and Longrie et al. 2013) and for animal communication in general (see Bradbury and Vehrencamp 1998). Sound production is widespread throughout the phylogeny of fishes with evidence of sound production from 72 families (Rice et al. 2020).

2 Checklist of Sound Producing Cichlid Species

There are now a total of 39 cichlid species identified as sound producers (Table 1), and this represents an increase of an additional 19 species since Lobel (2001). One of the most conspicuous results is that all the recent studies have been on African species. Surprisingly, the last acoustic study of a Central/South American cichlid species was by Schwarz in 1980! The primary literature for cichlid acoustic biology numbers 55 publications (as of 2019). Table 1 lists the documented sound producing cichlids using the scientific name as published; and it cross-references to the most recent scientific name in current usage in FishBase (http://www.Fishbase.org), which is cross-linked to the definitive reference for current fish taxonomy, the Eschmeyer Catalog of Fishes (http://www.calacademy.org/scientists/projects/catalog-of-fishes). Cichlid species nomenclature is frequently changing and is the subject of a great deal of scientific discussion. In this review, we will try to use the most referenced names or the name cited in the original literature. Our purpose is not to update the taxonomy but only to clearly specify which species is being referenced.

The six specific questions regarding cichlid bioacoustics include:

1. Are specific sounds associated with specific behaviors?
2. What are the temporal patterns of calling activity?
3. What morphological structures produce the sounds?
4. What are the key characteristics of sound patterns that distinguish species?

Table 1 Sound producing cichlids list of synonymies

Species ($n = 39$)[a] Name in publication	Current name	Literature cited ($n = 54$)
Cichlasoma nigrofasciatum	*Amatitlania nigrofasciata* (Günther, 1867)	(1) Myrberg et al. (1965)
Cichlasoma citrinellum	*Amphilophus citrinellus* (Günther, 1864)	(1) Schwartz (1974a)
Cichlasom centrarchus	*Archocentrus centrarchus* (Gill, 1877)	(3) Schwartz (1974a, b, 1980)
Haplochromis burtoni	*Astatotilapia burtoni* (Günther, 1894)	(5) Fernald (1975), Hirata and Fernald (1975), Nelissen (1977, 1978), Maruska and Fernald (2010, 2012), Nelissen (1977, 1978)
Pseudotropheus elongatus	*Chindongo elongatus* (Fryer, 1956)	(1) Lobel (2001)
Aequidens portalegrensis	*Cichlasoma portalegrense* (Hensel, 1870)	(1) Brown and Marshall (1978)
Cynotilapia afra (Günther, 1894)		(1) Danley et al. (2012)
Pundamilia nyererei	*Haplochromis nyererei* (Witte-Maas & Witte, 1985)	(3) Verzijden et al. (2010), Slabbekoorn et al. (2012), Estramil et al. (2014)
Pundamilia pundamilia	*Haplochromis pundamilia* (Seehausen & Bouton, 1998)	(1) Verzijden et al. (2010)
Hemichromis bimaculatus (Gill, 1862)		(2) Myrberg et al. (1965), Rowland (1978)
Herotilapia multispinosa (Günther, 1867)		(2) Baylis (1974), Brown and Marshall (1978)
Labeotropheus fuelleborni (Ahl, 1926)		(1) Danley et al. (2012)
Labidochromis caeruleus (Fryer, 1956)		(1) Higgs et al. (2011)
Maylandia aurora (Burgess 1976)		(1) Danley et al. (2012)
Metriaclima callainos, Pseudotropheus callainos	*Maylandia callainos* (Stauffer & Hert, 1992)	(7) Amorim et al. (2004, 2008), Simoes et al. (2006), Smith (2007), Smith and Van Staaden (2009), Van Staaden and Smith (2011), Danley et al. (2012)
Pseudotropheus emmiltos (MCP Amorim pers. com. 2018 *M. emmiltos)*	*Maylandia emmiltos* (Stauffer, Bowers, Kellogg & McKaye, 1997)	(2) Amorim et al. (2008), Simoes et al. (2008a)
Pseudotropheus fainzilberi	*Maylandia fainzilberi* (Staeck, 1976)	(2) Amorim et al. (2008), Simoes et al. (2008a)
Metriaclima lombardoi	*Maylandia lombardoi* (Burgess, 1977)	(3) Smith (2007), Smith and Van Staaden (2009), Van Staaden and Smith (2011)

(continued)

Table 1 (continued)

Species (n = 39)[a] Name in publication	Current name	Literature cited (n = 54)
Metriaclima zebra, Pseudotropheus zebra	*Maylandia zebra* (Boulenger, 1899)	(11) Amorim et al. (2004, 2008), Simoes et al. (2006); Simoes et al. (2008a, b), Bertucci et al. (2010), Van Staaden and Smith (2011), Danley et al. (2012), Bertucci et al. (2012a, b), Bertucci et al. (2013)
Copadichromis conophorus	*Mchenga conophoros* (Stauffer, LoVullo and McKaye, 1993)	(2) Lobel (1998, 2001)
Melanochromis auratus (Boulenger, 1897)		(3) Smith (2007), Smith and Van Staaden (2009), Van Staaden and Smith (2011)
Neochromis omnicaeruleus (Seehausen and Bouton, 1998)		(1) Verzijden et al. (2010)
Neolamprologus pulcher (Trewavas and Poll, 1952)		(2) Spinks et al. (2017); Pisanski et al. (2015)
Tilapia mossambicus	*Oreochromis mossambicus* (Peters, 1852)	(9) Rodman (1966), Konstantinova et al. (1979), Amorim et al. (2003), Amorim and Almada (2005), McPherson (2012), Pujiyati et al. (2016), Lanzing (1974), Marshall (1971, 1972)
Tilapia nilotica	*Oreochromis niloticus* (Linnaeus, 1758)	(4) Bauer (1963), Longrie et al. (2008, 2009, 2013)
Tilapia nilotica × *Tilapia macrocephala*	Hybrid	(1) Bauer (1963)
Tilapia mariae	*Pelmatolapia mariae* Boulenger, 1899	(2) Kottege et al. (2015), Albrecht (1966)
Petrotilapia nigra (Marsh, 1983)	–	(1) Danley et al. (2012)
Simochromis babaulti	*Pseudosimochromis babaulti* (Pellegrin, 1927)	(1) Nelissen (1978)
Melanochromis cyaneorhabdos	*Pseudotropheus cyaneorhabdos* (Bowers & Stauffer, 1997)	(3) Smith (2007), Smith and Van Staaden (2009), Van Staaden and Smith (2011)
Melanochromis johannii	*Pseudotropheus johannii* (Eccles, 1973)	(3) Smith (2007), Smith and Van Staaden (2009), Van Staaden and Smith (2011)
Pseudotropheus "zebra gold"	Species undescribed	(3) Amorim et al. (2004, 2008), Simoes et al. (2006)
Pseudotropheus "zebra gold" x Maylandia zebra	Hybrid	(1) Simoes et al. (2008a)
Pterophyllum sp. (probably *scalare*) (Schultze, 1823)		(1) Myrberg et al. (1965)
Psuedetroplus maculatus (Bloch 1795)	*Etroplus maculatus*	(2) Raj 1916 cited in Baerends and Baerends-van Roon (1950)

(continued)

Table 1 (continued)

Species ($n = 39$)[a] Name in publication	Current name	Literature cited ($n = 54$)
Tilapia galilaea	*Sarotherodon galilaeus* (Linnaeus, 1758)	(1) Brown and Marshall (1978)
Simochromis diagramma (Günther, 1894)		(2) Nelissen (1975, 1978)
Tramitichromis intermedius (Trewavas, 1935)		(7) Lobel (1998, 2001), Rice et al. (2001), Rice and Lobel (2002, 2003); Ripley et al. (2002), Ripley and Lobel (2004)
Tropheus brichardi (Nelissen & Thys van den Audenaerde, 1975)		(1) Nelissen (1978)
Tropheus duboisi (Marlier, 1959)		(1) Nelissen (1978)
Tropheus moorii (Boulenger, 1898)		(2) Nelissen (1977, 1978)

[a] Fishbase https://www.fishbase.de/

5. Is there any relationship between body size and call characteristics?
6. How might an increase in ambient noise confound acoustic communication?

2.1 Calling Activity and Caller Sex

The behavioral processes of courtship and spawning are similar across cichlid species, often involving approach, leading, circling, and quivering (Baerends and Baerends-van Roon 1950; Barlow 2000; Ripley and Lobel 2004, 2005). Although the specifics of circling behavior may differ between genera (Stauffer et al. 1993), "quivering" is associated with circling and courtship in many cichlids as they swim around each other and ripple their abdominal muscles. Sound production correlates with quivering in *Tramitichromis intermedius, Copidichromis conophoros* (Lobel 1998; Ripley and Lobel 2004), *Simochromis diagramma* (Nelissen 1975), and in *Pseudotropheus* species (Amorim et al. 2004, 2008). It is likely that many cichlids that share this quiver behavior will also produce sounds. One known exception, *Oreochromis mossambicus*, does not produce sound during the specific quiver behavior but it does produce sounds during other courtship behavior (Amorim et al. 2003). Whether a fish produces sound during quivering or other behaviors, sound production appears to be regularly associated with cichlid courtship (Lobel 1998; Amorim et al. 2003, 2004, 2008). The hypothesis is that female fish could use these courtship-associated sounds as one cue to assess a potential mate's identity and quality. Actual spawning associated sounds are hypothesized to coordinate reproductive timing synchronizing gamete release.

Diel patterns of sound production in cichlids have been suggested for two cichlid species, both exhibiting a diurnal peak (Brown and Marshall 1978; Longrie et al. 2013). For *Herotilapia multispinosa*, sounds were enumerated during reproductive and agonistic behaviors during different stages of the reproductive period. Spawning is reported to be restricted to daylight hours (Brown and Marshall 1978), but no monitoring of sounds was done nocturnally. In *Oreochromis niloticus*, direct acoustic sampling of fishes over a 24-h period found peak diurnal calling activity (Longrie et al. 2013). This is an aspect of future research well worth examining in more detail. Early pre-dawn calling by males could be a stimulus for spawning. The courtship sound produced by male *Oreochromis mossambicus* was reported to facilitate oviposition in females (Marshall 1972). It is possible that some cichlids may be sonically active before daylight. Smith (2007) recorded cichlid-like sounds in the field in areas where cichlid species were present and found nocturnal peaks in the production of these sounds. On coral reefs, damselfishes (Pomacentridae) were once thought to be only acoustically active during daytime until 24-h recordings revealed pre-dawn peaks in chorus activity (Mann and Lobel 1995). It makes sense that acoustic signals would be used in low light periods, possibly as an early cue to stimulate females to initiate egg hydration prior to spawning. The technology and software for underwater acoustics have greatly advanced in recent years and allows for documenting the natural cycle of sound production for sonic fishes in the wild as well as assessing the impacts from noise pollution (Lindseth and Lobel 2018).

For species whose social behavioral context for sound production are known ($N = 39$; Table 2) as of the year 2019, 20 species produced sounds during agonistic intraspecific encounters and 30 spp. in reproductive display context (Table 2). For studies of reproductive behaviors, in all species the callers were male when sex was identified in all except *Pelmatolapia mariae* where the caller was female. Acoustic male courtship displays are known or proposed in 21 (55%) of these (Table 2). For reproduction-associated contexts monitored with a hydrophone, 30 species (79%) produce sounds in reproductive context during various aspects of nest visiting male calling in association with nest, or male courtship display to female ($n = 20$, 53%) or courtship encounters with unspecified sex ($n = 5$, 13%). Female calling in *Pelmatolapia mariae* was recorded in the vicinity of the nest area ($n = 1$, 3%). Of these, the males of four species (11%) were observed to engage in courtship with a visiting female but no sounds were observed before the recordings began which were limited to passive recording of sounds (no video) from the focal male's nest after the field observations. Both male and female cichlids have been observed to produce sounds in some species (see Table 2) although sound production by both sexes may not be universal. It should be noted that acoustic studies in fishes have largely focused on male behaviors even though in many fishes a mechanism of known sound production is present in males and females of the species (Ladich 2015). Among those cichlids where males and females have been noted to produce sounds in the context of aggression: 50% of species with specifically identified sex of caller in agonism were female and 70% were male ($N = 20$ species).

Table 2 Behavioral context of sound production in cichlids

Species[a,b] (Total = 39)	Agonism[c,d] (sex of sound producer)	Reproduction[b,d]	Literature
SOUTH AMERICAN CICHLIDS (n = 6):			
Amatitlania nigrofasciata	A (female)	–	Myrberg et al. (1965)
Amphilophus citrinellus	A (male)	–	Schwartz (1974a)
Archocentrus centrarchus	A (male & female)	–	Schwartz (1980)
Cichlasoma portalegrense	A (unknown)	–	Brown and Marshall (1978)
Herotilapia multispinosa	A (male and female)	Cd, Cf	Brown and Marshall (1978)
	A	Cd	Baylis (1974)
Pterophyllum sp. (possibly *scalare*)	A (adult pair, sex unknown)	–	Myrberg et al. (1965)
AFRICAN CICHLIDS (n = 32 species):			
Astatotilapia burtoni	A (male and female)	Cc “sexual quiver”	Nelissen (1977, 1978)
	–	Cd	Maruska et al. (2012)
Chindongo elongatus	No context	No context	Lobel (2001)
Cynotilapia afra	–	Cd hypothesized	Danley et al. (2012)
Haplochromis nyererei	A (male)	Cd	Verzijden et al. (2010)
Haplochromis pundamilia	–	Cd	Verzijden et al. (2010)
Hemichromis bimaculatus	A (male and female)	–	Myrberg et al. (1965)
	No context	No context	Lobel (2001)
Labeotropheus fuelleborni	–	Cd hypothesized	Danley et al. (2012)
Labidochromis caeruleus		Cd male “quiver” paired with female	Higgs et al. (2011)
Maylandia aurora	–	Cd hypothesized	Danley et al. (2012)
Maylandia callainos	–	Cd	Amorim et al. (2008)
	–	Cd hypothesized	Danley et al. (2012)
Maylandia emmiltos	–	Cd	Amorim et al. (2008)
Maylandia fainzilberi	–	Cd	Amorim et al. (2008)
Maylandia lombardoi	–	Cd	van Staaden and Smith (2011)
Maylandia zebra	A (male)	–	Bertucci et al. (2012a, b)
	A (male and female)	–	Simoes et al. (2008b)
	–	Cd	Amorim et al. (2008)
	–	Cd hypothesized	Danley et al. (2012)
Mchenga conophoros	A (male) irregular noisy pulses	Cd	Lobel (2001, 1998)
Melanochromis auratus	–	Cd	van Staaden and Smith (2011)

(continued)

Table 2 (continued)

Species[a,b] (Total = 39)	Agonism[c,d] (sex of sound producer)	Reproduction[b,d]	Literature
Neochromis omnicaeruleus	–	Cd	Verzijden et al. (2010)
Neolamprologus pulcher	A (male and female)	–	Spinks et al. (2017)
Oreochromis mossambicus	A (male-male, male-female groups male caller)	Cd, Cs	Amorim et al. (2003)
Oreochromis niloticus	A (male and female)		Longrie et al. (2013)
		Cd	Bauer (1963)
Tilapia nilotica x Tilapia macrocephala	–	Cd	Bauer (1963)
Pelmatolapia mariae	A (male)	–	Albrecht (1966)
		Female sound producer nest area	Kottege et al. (2015)
Petrotilapia nigra	–	Cd hypothesized	Danley et al. (2012)
Pseudosimochromis babaulti	A	Cc "sexual quiver"	Nelissen (1978)
Pseudotropheus cyaneorhabdos	–	Cd	van Staaden and Smith (2011)
Pseudotropheus johannii		Cd	van Staaden and Smith (2011)
Pseudotropheus 'zebra gold'	–	Cd	Amorim et al. (2008)
Sarotherodon galilaeus	–	Cd, Cf	Brown and Marshall (1978)
Simochromis diagramma	A (male and female)	Cc "sexual quiver"	Nelissen (1975, 1978)
Tramitichromis intermedius	–	Cd	Lobel (1998), Ripley and Lobel (2004, 2005)
Tropheus brichardi	A	Cc "sexual quiver"	Nelissen (1978)
Tropheus duboisi	A	Cc "sexual quiver"	Nelissen (1978)
Tropheus moorii	A (male and female)	Cc "sexual quiver"	Nelissen (1977, 1978)

[a] Lake Malawi *Pseudotropheus* "zebra gold" (Amorim et al. 2008)

[b] No Context: Undetermined context either agonism or courtship *Chindongo elongatus* ($n = 1$); No social contexts, agonistic-like and courtship-like displays to model *Hemichromis bimacultus* ($n = 1$); No social context, jaw clicking sounds produced in distress on land *Pseudetroplus maculatus* ($n = 1$)

[c] Agonism total ($n = 20$), female caller specified ($n = 10$), male caller specified ($n = 14$), sex could not be verified ($n = 5$)

[d] Reproductive sounds $n = 31$; Cf = female in courtship display ($n = 2$); Cd = courtship call to female by male detected with a hydrophone ($n = 20$); Cd = proposed as male display human audition no data analysis Bauer (1963) (1); Cc = male courtship call inferred from reproductive display "sexual quiver" ($n = 6$); Cs = spawning ($n = 1$); Cd hypothesized ($n = 6$) hydrophone recording of a male courting a female at his breeding cave by means of passive acoustics ($n = 6$); Female calling in the vicinity of nest paired with a male *Pelmatolapia mariae* ($n = 1$)

The pattern of sound production with reproductive behavior has not always been clear and more research is needed to define if such sounds are meaningful to the fishes. For example, in *Oreochromis niloticus* females and males produced agonistic sounds but no sounds were detected during courtship from either sex (Longrie et al. 2013). Males of *H. multispinosa* produced abundant sounds in both agonistic and reproductive contexts (Brown and Marshall 1978). In this species, males and females produced sounds throughout the egg, larval, and free-swimming young stages of offspring development during agonistic encounters with intruders. There are only five studies that statistically describe the temporal characteristics of female sounds and associated behavior in detail. These include pulsed sounds while mouthbrooding embryos for *Oreochromis niloticus* (Longrie et al. 2013); broadband frequency 2-pulsed sound in agonism for *Neolamprologus pulcher* (Spinks et al. 2017), interpulsed sounds in agonism for *Maylandia zebra* (Simoes et al. 2008b); and single-pulse sounds in the vicinity of nest with males for *Pelmatolapia mariae* (Kottege et al. 2015). Myrberg et al. (1965) described the pulse rate for *Hemichromis bimaculatus* female agonistic sounds during the parental care period.

Agonistic sounds between females were also described for *Maylandia zebra* (Simoes et al. 2008b). Female sounds were shorter in duration and consisted of fewer pulses than males (Simoes et al. 2008b). Males produce sounds during courtship-associated displays to females, and females seem to be silent in this context for video documented studies (e.g., Ripley and Lobel 2004). *M. zebra* juveniles are active sound producers during agonistic interactions, producing isolated pulses early in development (Bertucci et al. 2012a, b). There were two species (6%) where the callers also included a female although their sounds were observed anecdotally and not digitally recorded ($n = 22$ species; sex of caller specifically examined). Females of *Tramitichromis intermedius*, *Archocentrus centrarchus, Oreochromi mossambicus*, and *Astatotilapia burtoni* were observed as silent (Lanzing 1974; Ripley and Lobel 2004; Maruska et al. 2012). It is important to note that the sex of the caller is often difficult to determine exactly when recording fishes in groups and with omnidirectional hydrophones. Thus, this aspect deserves closer study.

Sounds of Juvenile Cichlids The ontogeny of sound production in cichlids has only received limited study to date. The Malawi cichlid, *M. zebra* juveniles are active sound producers during agonistic interactions, producing isolated pulses early in development (Bertucci et al. 2012a, b). Young *Oreochromis niloticus*, also produce sounds, supporting the hypothesis that sound production is not learned in cichlids (Longrie et al. 2008). The onset of vocal ability in young males of *Tramitochromis intermedius* was detected at about 7 months of age (Ripley and Lobel 2004).

3 Sound Producing Mechanism

Definitive experiments have not yet demonstrated which muscles and bones are used for sound production by cichlid fishes. The pharyngeal bones of some fishes have been implicated as the sound-producing instrument (Darwin 1874; Marshall 1962) and the same has been proposed for cichlids (Lanzing 1974; Rice et al. 2001; Rice and Lobel 2002, 2003; Marshall 1962; Nelissen 1977). Sounds produced by the pharyngeal apparatus are presumably amplified by the swimbladder (Rowland 1978; Marshall 1962). Cichlids produce a clear and distinct sound while feeding and grinding food in the pharyngeal mill, as well as during courtship and agonistic behavior (Lobel 2001; Lanzing 1974; Nelissen 1977; Rodman 1966). However, an alternative mechanism called the "buckling method" (an indirect swimbladder associated muscle mechanism) has been proposed by Longrie et al. (2009), and is discussed below. Not all sounds may be volitional, and any behavioral significance has not yet been demonstrated. For example, the agonistic "thump" described for *Herotilapia multispinosa* by Brown and Marshall (1978) coincides with a head jerking upward and downward but also coincided with well-established agonistic frontal displaying suggesting a possible volitional nature to the sounds. Sounds were also produced during jaw snapping during agonistic behaviors (Baylis 1974; Brown and Marshall 1978). Brown and Marshall (1978) described non-pulsed "thump" sounds as most likely incidental to behaviors and not communicative. Jaw snapping is proposed as a mechanism for the reproductive season of sound production in females for *Tilapia mariae* (Kottege et al. 2015). These sounds could be incidental to body movements or intentional acoustic components of displays. The specific context for these sounds was less ritualized and less tightly linked to a specific body posture or behavioral display than is typically found in other cichlids.

If cichlid pharyngeal jaws are involved in sound production, as preliminary evidence indicates, then perhaps it is possible that different pharyngeal tooth morphologies may produce different types of sounds (i.e., sounds with different individual pulse waveforms, e.g., Lobel 2001). Of course, the key experiment would be to determine if such different pulse waveforms produce different sound qualities that are directly detectable by a fish. It is possible that the simplest type of acoustic signal produced is the specific sound of individual pulses, which are then frequently repeated (Fig. 2). It may be the perceived sound of the pulse in combination with pulse rate timing that may contribute to species recognition. Prior studies in other fishes, especially the damselfishes (Pomacentridae), show that pulse number and/or repetition rate is closely correlated with the behavioral context of sounds (Hawkins 1986; Myrberg 1981, 1997; Olivier et al. 2015; Spanier 1979). Pomacentrids that produce similar sounds to cichlids have had their sound production mechanism described as including jaw element movements similar to the feeding process (Olivier et al. 2015; Parmentier and Fine 2016).

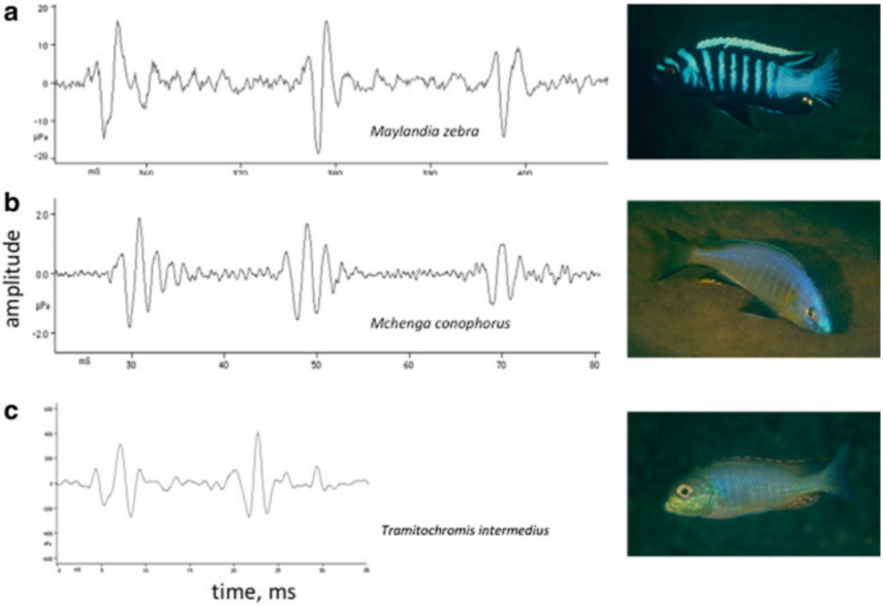

Fig. 2 Example of the waveform patterns from three cichlids in Lake Malawi. (**a**) *Maylandia zebra*, (**b**) *Mchenga conophorus*, and (**c**) *Tramitochromis intermedius.* The simplest type of acoustic signal produced is the specific sound of individual pulses, which are then frequently repeated. Field recordings made underwater of free-living fishes in their natural habitat (depth 3–8 m) at Cape McClear, Lake Malawi National Park offshore of the World Wildlife Fund Education Center and at Otter Point, August 5–27, 1990 (Lobel 1998)

Pharyngeal jaws in cichlids are well known for their advanced capability for complex muscle modulation and bone movement (Liem 1973, 1991). Four cichlid species (Tables 3 and 4) produce sounds that exhibit more complex amplitude modulation patterns and pulse repetition rates than ones produced by many other fish families with simpler and probably less manipulatable pharyngeal apparatuses. For example, the morphology of the pharyngeal jaw complex suggested a close relationship between pomacentrids (damselfishes) and cichlids within Labroidei (Wainwright et al. 2012; Lauder and Liem 1983), although this close relationship has been overturned in recent molecular phylogenies (e.g., Betancur-R et al. 2017). Cichlids differ significantly from other fishes in the muscle and bone architecture of their pharyngeal apparatus (Liem and Greenwood 1981; Kaufman and Liem 1982; Seehausen et al. 1999; Stiassny and Jensen 1987).

If this difference in pharyngeal morphology is a basis for sound production, then presumably pomacentrids may not be able to forcibly occlude or grind the pharyngeal jaws in the way that the cichlids do. The pomacentrid sound production mechanism has been described as resulting from jaw element movements similar to the feeding process (Parmentier et al. 2007; Parmentier and Fine 2016; Olivier et al. 2017). Sound production in pomacentrids has been extensively described

Table 3 Acoustic traits of cichlid species sounds associated with agonistic and reproductive behavior. Frequency range was reported if no other frequency data were available

Species (n = 35) (current name)	Behavioral Context	Sound pattern	Bioacoustic traits: Sound duration (ms)	Pulse #; pulse rate	Pulse duration	Intra-call interval PP = pulse period; IPI = Interpulse interval	Frequency (Hz): “PEAK” = dominant or peak; “Main, Principle, Maximum intensity, Primary” = peak; Instantaneous; “MIDDLE” = middle “FUND” = fundamental “RANGE” = minimum to maximum	Literature cited
South America (n = 5):								
Amatitlania nigrofasciata	A	Pulsed	ND	20 pulses/sec pulse rate (no sample size)	ND	ND	480 MIDDLE (no sample size)	Myrberg et al. (1965)
Archocentrus centrarchus	A	Pulsed	500–4000 (no sample size)	ND	ND	ND	100–700 maximum energy, 100–1300 RANGE (no samples size)	Schwartz (1974a)
Cichlasoma portalegrens	A	Single pulse “thump”	ND	ND	ND	ND	80–300 principle (no sample size); 80–600 RANGE	Brown and Marshall (1978)
Herotilapia multispinosa	A	Single pulse “thump”	93 (27–225)	Non-pulsed	ND	ND	85–1250 RANGE, 100–300 principle	Brown and Marshall (1978)
	A	Single pulse “woof”	211 (87–348)	Non-pulsed	ND	ND	85–1400 RANGE, 105–300 principle	Brown and Marshall (1978)

	A	Pulsed “volley”	359 (99–1056)	ND	37 (17–65)	82 (5–205) IPI	85–1400 RANGE, 150–450 principle	Brown and Marshall (1978)
	A, Cd and Cf	Pulsed “growl”	200 (108–1600)	ND	5 (3–10)	121 (76–316) IPI	100–600 RANGE, 150–350 principles	Brown and Marshall (1978)
Pterophyllum sp. (probably *scalare*)	A	Pulsed “broad-band high Hz pulse & low Hz pulse”	ND	6 pulses/sec pulse rate (no samples size)	ND	ND	Maximum Intensity 3300 Hz, Frequency components >10 kHz, low frequency pulse ~300 Hz (no sample size)	Myrberg et al. (1965)
Africa ($n = 30$):								
Astatotilapia burtoni	Type2 feeding & shortly after” aggression “chewing”	Pulsed	1500 (300–3500)	4 (2–8)	50 (30–90)	ND	7000 (2500 - 16,000) Main, 1250–10,000 lower & >20,000 upper frequency	Nelissen (1978)
	A & Cc Type1	Pulsed	370 (230–1410)	13 (5–37)	ND	ND	320 (120–630) Main 80–1000 RANGE	Nelissen (1978)
	Cd	Pulsed	240 ± 137 (51–695)	9 ± 4 (2–19)	10 ± 3 (5–26)	18 ± 13 (5–98) IPI	499 (129–904) PEAK; <50–1500 RANGE	Maruska et al. (2012)
Cynotilapia afra	PAM	Pulsed	446 ± 190	13 ± 6	9 ± 1.2	35 ± 6.6 PP	ND	Danley et al. (2012)
Haplochromis nyererei	A, Cd	Pulsed	In data analysis	6 ± 0.4 S.E.M.	ND	PP (in data analysis)	PEAK in figure	Verzijden et al. (2010)
Haplochromis pundamilia	Cd	Pulsed	In data analysis	7 ± 0.4 S.E.M.	ND	PP (in data analysis)	PEAK in figure	Verzijden et al. (2010)

(continued)

Table 3 (continued)

Species ($n = 35$) (current name)	Behavioral Context	Sound pattern	Bioacoustic traits: Sound duration (ms)	Pulse #; pulse rate	Pulse duration	Intra-call interval PP = pulse period; IPI = Interpulse interval	Frequency (Hz): "PEAK" = dominant or peak; "Main, Principle, Maximum intensity, Primary" = peak; Instantaneous; "MIDDLE" = middle "FUND" = fundamental "RANGE" = minimum to maximum	Literature cited
Hemichromis bimaculatus	DISPLAY TO MODEL: A "thump", A "purr" (display at model)	Pulsed "purr"; Undetermined "thumps"/burst	ND	43 ± 8 pulses/sec "purr" RATE; 11 ± 4 "thumps"/sec	ND	ND	500 maximum intensity; 500 maximum energy	Rowland (1978)
	A	Pulsed "brrr," 3–5 single pulse "thumps" 1) female "brrr" parental care 2) male "brrr" 3) male "thump"	ND	(1) 35 pulses/sec (2) 35 pulses/sec (3) 12 "thump" sounds/sec (no sample size)	ND	ND	250–350, 400–450, 500–700 ($n = 3$ individual fish) PEAK	Myrberg et al. (1965)
	DISPLAY TO MODEL: male "quiver"	Pulsed	ND	10–15 pulses/sec	ND	ND	<100 (no sample size)	Rowland (1978)

Labeotropheus fuelleborni	PAM	Pulsed	364 ± 148	12 ± 4	9 ± 1	35 ± 6 PP	ND	Danley et al. (2012)
Labidochromis caeruleus	Cd	ND	ND	ND	ND	ND	300 PEAK (no samples size)	Higgs et al. (2011)
Maylandia aurora	PAM	Pulsed	376 ± 125	12 ± 4	12 ± 2	35 ± 9 PP	ND	Danley et al. (2012)
Maylandia callainos	Cd	Pulsed	476 (349–652)	8 (6–11)	12 (10–13)	67 (50–79) PP	517 (425–620) PEAK	Amorim et al. (2004)
	Cd	Pulsed	660 ± 409	9 ± 5	ND	ND	ND	Smith (2007)
	Cd	Pulsed	ND	ND	ND	(IPI long no data)	~180–500 PEAK, ~20–1200 RANGE (multiple species pooled data, no sample size)	Smith and van Staaden (2009)
	Cd	Pulsed	618 (349–1033)	10 (6–15)	ND	73 (61–83) PP	150 (132–182) Peak1 FUND PEAK; 520 (474–567) Peak2	Amorim et al. (2008)
	PAM	Pulsed	205 ± 108	11 ± 2	5 ± 1	17 ± 4 PP	None	Danley et al. (2012)
Maylandia emmiltos	Cd	Pulsed	760 (302–987)	16 (10–22)	ND	48 (31–62) PP	134 (112–145) Peak1 FUND PEAK, 448 (418–485) Peak2	Amorim et al. (2008)
Pooled data: *Maylandia emmiltos, Maylandia fainzilberi and Pseudotropheus “zebra gold” x M. zebra*	Cd	Tonal sound; **COMPLEX** frequency modulated tonal and pulsed	514 ± 131 (282–833); 550 ± 119 (334–796)	ND	ND	ND	44 ± 20 (23–86); 34 ± 8 (22–54) PEAK	Simoes et al. (2008a)
Maylandia fainzilberi	Cd	Pulsed	723 (398–1118)	9 (7–11)	ND	87 (64–108) PP	138 (124–151) Peak1 FUND PEAK; 473 (438–549) Peak2	Amorim et al. (2008)
Maylandia lombardoi	Cd	“Grunting”	220 ± 117	8 ± 4	ND	ND	226 ± 42 primary	Smith (2007)

(continued)

Table 3 (continued)

Species ($n = 35$) (current name)	Behavioral Context	Sound pattern	Bioacoustic traits: Sound duration (ms)	Pulse #; pulse rate	Pulse duration	Intra-call interval PP = pulse period; IPI = Interpulse interval	Frequency (Hz): "PEAK" = dominant or peak; "Main, Principle, Maximum intensity, Primary" = peak; Instantaneous; "MIDDLE" = middle "FUND" = fundamental "RANGE" = minimum to maximum	Literature cited
	Cd	Pulsed hypothesized "grunting" (no waveform)	Duration in analysis	ND	ND	(PP difficult to measure, no IPI data, recording noise)	Primary in analysis	van Staaden and Smith (2011)
	Cd	Pulsed	ND	ND	ND	(IPI short no data)	~180–500 PEAK, ~20–1200 RANGE (six species pooled)	Smith and van Staaden (2009)
Maylandia zebra	A	Pulsed	961 ± 295 (549–1430) male–male	9 ± 3 (5–14)	ND	126 ± 24 (90–161)	138 ± 15 (117–164) Peak1 (higher energy PEAK and FUND); 463 ± 35 (434–551) Peak2;	Simoes et al. (2008b)
	A	Pulsed	524 ± 153 (358–733) female–female	5 ± 1 (4–6)	ND	124 ± 27 (93–165) PP	143 ± 7 (134–152) Peak1 (higher energy PEAK and FUND; 480 ± 29 (445–525) Peak2	Simoes et al. (2008b)
	A (juvenile)	Single pulse	5 ± 0.25 SE	Non-pulsed	Non-pulsed	Non-pulsed	1611 ± 78 SE instantaneous frequency	Bertucci et al. (2012b)
	PAM	Pulsed	764 ± 407	17 ± 2	16 ± 5	55 ± 13 PP	ND	Danley et al. (2012)

	Cd	Pulsed	532 (384–786)	9 (7–14)	10 (8–11)	66 (60–74) PP	460 (399–509) PEAK	Amorim et al. (2004)
	Cd	Pulsed	672 (421–857)	9 (7–12)	ND	87 (68–113) PP	156 (129–221) Peak1 FUND PEAK, 489 (424–558) Peak2	Amorim et al. (2008)
Maylandia zebra	Cd	Pulsed: 1) Lead swim; 2) quiver display; 3) no display; 4) circle swim	567 ± 247 (214–1210); 1199 ± 647 (298–2622); 481 ± 381 (201–1276); 562 ± 157 (343–853)	7 ± 2 (4–12); 15 ± 8 (5–33); 5 ± 3 (3–12); 7 ± 1 (6–9)	ND	92 ± 20 57–120); 87 ± 19 (60–133); 100 ± 13 (79–116); 83 ± 21 (53–135) PP	Peak1 (higher energy PEAK and FUND) and 2: 133 ± 15 (117–164), 459 ± 52 (375–539) Peak1(higher energy PEAK and FUND and 2; 150 ± 31 (109–258), 489 ± 62 (398–586) Peak1 (higher energy PEAK and FUND) and 2; 129 ± 18 (117–164), 454 ± 48 (375–539) Peak1 (higher energy PEAK and FUND) and 2; 141 ± 0 (141–141), 471 ± 30 (422–492)	Simoes et al. (2008b)
Maylandia "zebra katale"	Cd	Pulsed	ND	ND	ND	(IPI long no data)	~180–500 PEAK, ~20–1200 RANGE (six species pooled)	Smith and van Staaden (2009)
Mchenga conophoros	A	Irregular interpulses and pulse clarity	ND	ND	ND	ND	ND	Lobel (2001)
	Cd	Pulsed	181 ± 59 (78–654)	10 ± 3 (5–30) 18 ± 2 (14–22) call duration/ pulse# **pulse rate**	7 ± 2 (3–10)	16 ± 6 (8–35) IPI	471 ± 50 (372–594) PEAK	Lobel (1998)

(continued)

Table 3 (continued)

Species (n = 35) (current name)	Behavioral Context	Sound pattern	Bioacoustic traits: Sound duration (ms)	Pulse #; pulse rate	Pulse duration	Intra-call interval PP = pulse period; IPI = Interpulse interval	Frequency (Hz): "PEAK" = dominant or peak; "Main, Principle, Maximum intensity, Primary" = peak; Instantaneous; "MIDDLE" = middle "FUND" = fundamental "RANGE" = minimum to maximum	Literature cited
Melanochromis auratus	Cd	"Grunting"	311 ± 179	ND	ND	ND	268 ± 158 primary	Smith (2007)
	Cd	Pulsed hypothesized "grunting" (no waveform)	Duration in analysis	ND	ND	(PP difficult to measure, no IPI data, recording noise)	Primary in analysis	van Staaden and Smith (2011)
	Cd	Pulsed	ND	ND	ND	(IPI short no data)	~180–500 PEAK, ~20–1200 RANGE (six species pooled)	Smith and van Staaden (2009)
Neochromis omnicaeruleus	Cd	Pulsed	In data analysis	8 ± 0.4 S.E.M.	ND	(PP in data analysis)	PEAK in figure	Verzijden et al. (2010)
Neolamprologus pulcher	A (with social behavior)	Pulsed (two-pulse)	896 ± 804 (with behavior)	2 ± 0.7	12 ± 4	(IPI <400 data in figure)	12,281 ± 3740 PEAK	Spinks et al. (2017)
	A	Pulsed (two-pulse)	918 ± 770 (male sounds)	2 ± 0.1	14 ± 2	ND	12,710 + 4304 PEAK	Spinks et al. (2017)
	A	Pulsed (two-pulse)	670 + 910 (female sounds)	2 ± 1	9 ± 1	ND	13,396 + 2202 PEAK	Spinks et al. (2017)
	A	Pulsed (two-pulse)	ND	ND	ND	ND	Often first pulse ~7000 – ~15,000, second pulse ~7000–>17,000 PEAK (no sample size)	Spinks et al. (2017)

Oreochromis mossambicus	A	Continuous pulse series and/or pulsed	246 (112–775)	Non-pulsed	Non-pulsed	Non-pulsed	Mean 40–60 (range < 300) ND	McPherson (2012)
	A	ND	50–500 (no sample size)	ND	ND	ND	120–1400 RANGE (no sample size)	Konstantinova et al. (1979) (as cited in Amorim et al. 2003)
	Cd, Cs	Pulsed	712 ± 458 (100–2834)	17 ± 9 (4–60)	12 ± 1 (9–15)	44 + 14 (22–137) PP	354 (207–524) PEAK; 38–1262 RANGE	Amorim et al. (2003)
	Cd	Pulsed hypothesized (no waveform) three sound types	ND	7–18 “double pulses”; 2–12; 4–6; (no sample sizes)	7–10; 6–12; 25–30; (no sample sizes)	35–100 PP; 7–95 PP; 100–250 PP; (no samples sizes)	200–259 FUND; 200–250 RANGE; 185–250 RANGE (no sample sizes)	Konstantinova et al. (1979) (as cited in Amorim et al. 2003)
Oreochromis niloticus	A (control group juveniles)	Continuous pulse series (double or triple pulses)	314 ± 79	2 ± 0.4	143 ± 24	No interpulse present	68 ± 33 Main PEAK: 35 ± 11 Peak1 FUND, 72 ± 13 Peak2, 121 ± 22 Peak3	Longrie et al. (2008)
	A (isolated juveniles)	Continuous pulse series (double or triple pulses)	285 ± 80	2 + 0.5	109 ± 13	No interpulse present	46 ± 13 Main PEAK; 45 ± 7 Peak1 FUND, 109 ± 17 Peak2, 173 ± 30 Peak3	Longrie et al. (2008)
	A	Pulsed	127 ± 20	2–4 range	114 ± 7	ND	57 ± 14 Peak1 Main peak	Longrie et al. (2009)
	A (female nest territoriality)	Pulsed	321 ± 101 SE	3 ± 1 SE	105 + 23 SE	ND	50 ± 14 SE PEAK	Longrie et al. (2013)
	A (female oral incubation of eggs vs intruders)	Pulsed	265 ± 84 SE	3 + 1 SE	107 ± 21 SE	ND	48 ± 16 SE PEAK	Longrie et al. (2013)

(continued)

Table 3 (continued)

Species ($n = 35$) (current name)	Behavioral Context	Sound pattern	Bioacoustic traits: Sound duration (ms)	Pulse #; pulse rate	Pulse duration	Intra-call interval PP = pulse period; IPI = Interpulse interval	Frequency (Hz): "PEAK" = dominant or peak; "Main, Principle, Maximum intensity, Primary" = peak; Instantaneous; "MIDDLE" = middle "FUND" = fundamental "RANGE" = minimum to maximum	Literature cited
Pelmatolapia mariae	Context not determined	Single pulse	~10 ms	Non-pulsed	Non-pulsed	Non-pulsed	~3000–8000 "most energy" with higher harmonics <20,000, <8000 PEAK	Kottege et al. (2015)
Petrotilapia nigra	PAM	Pulsed	422 ± 217	18 ± 9	10 ± 3	28 ± 5 PP	ND	Danley et al. (2012)
Pseudosimochromis babaulti	A and Cc Type1	Pulsed	590 (240–1470)	26 (8–40)	20 (10–20)	ND	193 (125–500) Main, 50–800 RANGE	Nelissen (1978)
Pseudotropheus cyaneorhabdos	Cd	"Grunting"	220 ± 62	8 ± 3	ND	ND	212 ± 49 primary	Smith (2007)
	Cd	Pulsed hypothesized "grunting" (no waveform)	Duration in analysis	ND	ND	(PP difficult to measure, no IPI data, recording noise)	Primary in analysis	van Staaden and Smith (2011)
	Cd	Pulsed	ND	ND	ND	(IPI short no data)	~180–500 PEAK, ~20–1200 RANGE (six species pooled)	Smith and van Staaden (2009)
Pseudotropheus johannii	Cd	"Grunting"	287 ± 172	10 ± 5	ND	ND	228 ± 56 primary	Smith (2007)

	Cd	Pulsed hypothesized "grunting" (no waveform)	Duration in analysis	ND	ND	(PP difficult to measure, no IPI data, recording noise)	Primary in analysis	van Staaden and Smith (2011)
	Cd	Pulsed	ND	ND	ND	(IPI short no data)	~180–500 PEAK, ~20–1200 RANGE (six species pooled)	Smith and van Staaden (2009)
Pseudotropheus "zebra gold"	Cd	Pulsed	668 (310–1022)	11 (4–20)	10 (9–11)	63 (52–77)	436 (389–480) PEAK;	Amorim et al. (2004)
	Cd	Pulsed	774 (558–1122)	13 (8–20)	ND	66 (53–78) PP	152 (135–202) Peak1 FUND PEAK, 477 (432–545) Peak2	Amorim et al. (2008)
Simochromis diagramma	Feeding and A "chew" sounds	Pulsed	2000–3000 (no sample size)	3 pulses/sec RATE (no sample size)	100 (no sample size)	ND	6000–10,000 PEAK, ~4000–20,000 (no sample size)	Nelissen (1975) (preliminary study to Nelissen 1978)
	A and Cc "brrr" sound	Pulsed	500–2000 (no sample size)	ND	ND	ND	70–300 RANGE (no sample size)	Nelissen (1975) (preliminary study to Nelissen 1978)
	Type2 "chewing"	Pulsed	2450 (1060–3800)	7 (3–11)	100 (50–150)	ND	8000 (6000–10,000) Main, 3000–6000 Lower and ~20,000 Upper Frequency	Nelissen (1978)
	A & Cc Type1	Pulsed	1110 (600–1700)	26 (16–37)	10 (10–10)	ND	200 (100–200) Main, 50–500 RANGE	Nelissen (1978)

(continued)

Table 3 (continued)

Species ($n = 35$) (current name)	Behavioral Context	Sound pattern	Bioacoustic traits: Sound duration (ms)	Pulse #; pulse rate	Pulse duration	Intra-call interval PP = pulse period; IPI = Interpulse interval	Frequency (Hz): "PEAK" = dominant or peak; "Main, Principle, Maximum intensity, Primary" = peak; Instantaneous; "MIDDLE" = middle "FUND" = fundamental "RANGE" = minimum to maximum	Literature cited
Tramitichromis cf. *intermedius*	Cd	Pulsed	199 ± 44 (120–304)	9 ± 2 (6–12); 21 ± 2 (17–33) call duration/ pulse# **pulse rate**	6 ± 1 (3–11)	15 ± 5 (8–34) IPI	388 (305–480) PEAK	Lobel (1998)
	Cd	Pulsed wild caught (captive born)	Nested mean 171	Nested mean 10	ND	ND	Nested mean 323 PEAK	Ripley and Lobel (2004)
Tropheus brichardi	Type2 "chewing"	Pulsed	2200 (80–5000)	4 (1–8)	90 (50–170)	ND	7850 (250–>20,000) Main, 1000–6300 Lower and 6300—>20,000 Upper Frequency	Nelissen (1978)
	A and Cc Type1	Pulsed	830 (250–2350)	32 (9–92)	20 (10–30)	ND	620 (800–900) Main, 200–2000 RANGE	Nelissen (1978)
Tropheus duboisi	Type2 "chewing"	Pulsed	1370 (110–3900)	5 (1–10)	80 (40–130)	ND	6606 (2500–12,500) Main, 630–3150 lower and 2150 - >20,000 upper frequency	Nelissen (1978)

	A & Cc Type1	Pulsed	460 (70–1470)	19 (3–33)	10 (10–10)	ND	470 (125–1250) Main, 63–5000 RANGE	Nelissen (1978)
Tropheus moorii	Type2 "chewing"	Pulsed	1060 (300–2100)	4 (2–10)	50 (40–80)	ND	5500 (800 – Above 20,000) Main, 630–8000 lower and 4000 - >20,000 upper frequency	Nelissen (1978)
	A & Cc Type1	Pulsed	400 (150–900)	20 (5–35)	20 (6–70)	ND	840 (50–1250) Main, 25–3150 RANGE	Nelissen (1978)

Statistics reported as mean ± SD (range) unless otherwise noted. *ND* no data

Table 4 Bioacoustic research topics

Research topic species	Results	Literature cited
HEARING CONSPECIFIC CALLS		
Astatotilapia burtoni	Females have hearing sensitive to male call frequency range	Maruska et al. (2012)
Labidochromis caeruleus	Hearing sensitive to tone bursts 100–1000 Hz and conspecific male call	Higgs et al. (2011)
Haplochromis nyererei	Males and females discriminate conspecific sounds from white noise bursts by change in activity level when responding to playback	Estramil et al. (2014)
Tramitichromis intermedius	Hearing peak matches the call dominant frequency	Ripley et al. (2002)
SOUND PROPAGATION DISTANCE		
Maylandia zebra	Courtship sound waveform pulse pattern barely discernable at 40 cm	Simoes et al. (2008b)
Maylandia fainzilberi, Pseudotropheus "zebra gold" × *M. zebra, P. emmiltos*	Sounds were recordable within one body length of fish (12 + 0.8 SD, 11–15 cm)	Simoes et al. (2008a)
Maylandia callainos, M. fainzilberi, M. zebra, M. emmiltos, Pseudotropheus "zebra gold"	Sounds with clear structure detectable at 1–2 body lengths (8.7–13.9 cm range for all species)	Amorim et al. (2008)
CALL ONTOGENY		
Maylandia zebra	Development of agonistic sound patterns in juveniles: Single to double pulsed; sound production first detected at >43 days	Bertucci et al. (2012b)
Oreochromis niloticus	First sounds in nest construction 210 days of age	Longrie et al. (2008)
Tramitichromis intermedius	Number of days of age to first courtship sound production 211 ± 3 SD	Ripley and Lobel (2004)
CALLING ACTIVITY PATTERNS		
Archocentrus centrarchus	Acoustic agonistic activity level varies through the reproductive cycle (mean sounds toward mate/day)	Schwartz (1980)
Herotilapia multispinosa	Calling activity rates (mean # agonistic "volley" sounds/15 min): Prespawning (highest # of calls), egg, larval, and free-swimming stages Relative # sounds/14 min; mean # growling reproductive and agonistic sounds/day	Brown and Marshall (1978)
Oreochromis niloticus	Diurnal calling peak, 24-hr acoustic monitoring	Longrie et al. (2013)
Tramitichromis intermedius	Calling peaks leading up to and just before spawning	Ripley and Lobel (2004)

(continued)

Table 4 (continued)

Research topic species	Results	Literature cited
CONTEXT SPECIFIC CALLS		
Maylandia zebra	Male courtship early calls longer duration, more pulses, shorter pulse period, higher frequency from later circle, and lead swim courtship calls	Simoes et al. (2006)
	Male–male agonistic sounds longer duration and pulse period than male courtship sounds	Simoes et al. (2008b)
Haplochromis nyererei	No difference between agonism and courtship call	
Tramitichromis intermedius	Difference between agonism and courtship calls: Courtship sound regular and distinct pulses	Lobel (2001)
FEMALE SOUND PRODUCTION		
Archocentrus centrarchus	Female 5–30 sounds/day; mean sounds and attacks/day over time	Schwarz (1980)
Hemichromis bimaculatus	Female agonistic sounds	Myrberg et al. (1965)
Maylandia zebra	Female agonistic sounds shorter duration with fewer pulses than male agonistic and courtship sounds	Simoes et al. (2006), Simoes et al. (2008b)
Neolamprologus pulcher	Female agonistic sounds	Spinks et al. (2017)
Oreochromis niloticus	Female agonistic sounds	Longrie et al. (2013)
Pelmatolapia mariae	Female sounds near in nest area evaluated with vector analysis	Kottege et al. (2015)
CONTESTS INFLUENCE CALLING		
Oreochromis mossambicus	Male–male contest winners produced more calls that were longer in pulse duration and lower in peak frequency	Amorim and Almada (2005)
Haplochromis nyererei	Dyadic contests elicit sounds	Verzijden et al. (2010)
COMPLEX CALL		
Hemichromis bimaculatus	Pulsed and “thump” sounds overlap	Rowland (1978)
Maylandia fainzilberi, Pseudotropheus “zebra gold” × *M. zebra, M. emmiltos*	Continuous waveform tonal “moan” with or without frequency modulation produced alone or precedes interpulsed sound (species data pooled)	Simoes et al. (2008a)
NON-PULSED WAVEFORM PATTERNS		
Cichlasoma portalegrense	Single pulse	Brown and Marshall (1978)
Hemichromis bimaculatus	Single pulse “thump” in bursts of 3–5	Myrberg et al. (1965)

(continued)

Table 4 (continued)

Research topic species	Results	Literature cited
Herotilapia multispinosa	Single pulse "thump" and "volley" in established contexts; "woof" unestablished	Brown and Marshall (1978)
Maylandia fainzilberi, Pseudotropheus "zebra gold" × *M. zebra* hybrid, *M. emmiltos*	Continuous waveform low amplitude, tonal, sometimes frequency modulated	Simoes et al. (2008a)
Maylandia zebra	Single pulse in juveniles	Bertucci et al. (2012b)
Neolamprologus pulcher	Single pulse broadband frequency	Spinks et al. (2017)
Oreochromis mossambicus	Continuous pulse series and/or Interpulsed (variable interpulses)	McPherson (2012)
Oreochromis niloticus	Continuous pulse series (double and triple pulsed)	Longrie et al. (2008)
Pelmatolapia mariae	Single pulse broadband frequency	Kottege et al. (2015)
PLAYBACK OF CONSPECIFIC SOUNDS or NOISE		
Archocentrus centrarchus	Sounds playback inhibited higher aggression in receivers toward conspecifics but this data was not confirmed in a later study	Schwartz (1974b, 1980)
Astatotilapia burtoni	Females prefer male calls to white noise	Maruska et al. (2012)
Hemichromis bimaculatus	Fishes respond significantly more to conspecific sound model playbacks over silent models	Rowland (1978)
Maylandia zebra	Territorial males respond to conspecific sounds but not temporal coding modifications	Bertucci et al. (2013)
Oreochromis mossambicus	Male agonistic sounds silence other males in a preliminary study	McPherson (2012)
Haplochromis nyererei	Females prefer males producing sounds versus silent males	Verzijden et al. (2010)
	Females were not attracted to male sounds alone requiring the visual presence of a male	Estramil et al. (2014)
CALL VARIATION and BODY SIZE		
Astatotilapia burtoni	Mean peak frequency of male calls inversely related to body size	Maruska et al. (2012)
Haplochromis nyereri	Noise playback reduced the intensity of courtship behavior	Slabbekoorn et al. (2012)
Maylandia callainos	Mean peak frequency of male calls inversely related to body size	Amorim et al. (2004)
Maylandia callaino, M. fainzilberi, M. zebra, M. emmiltos, and Pseudotropheus "zebra gold"	Peak frequency inversely correlated with body size	Amorim et al. (2008)

(continued)

Table 4 (continued)

Research topic species	Results	Literature cited
Maylandia zebra	Larger males produce lower frequency courtship sounds	Simoes et al. (2008b)
	Amplitude, temporal, and frequency call features correlated with body size	Bertucci et al. (2012a, b)
Haplochromis nyererei and H. pundamilia, Neochromis omnicaeruleus	Peak frequency correlates inversely with standard length	Verzijden et al. (2010)
INDIVIDUAL ACOUSTIC SIGNATURES		
Maylandia zebra	Instantaneous frequency, frequency modulation rate and pulse amplitude modulation rate that could serve as acoustic signatures for individuals	Bertucci et al. (2012a, b)
POPULATION CALL VARIATION		
Maylandia callainos and M. zebra	Variation in call parameters within Lake Malawi based on call means	Danley et al. (2012)
MULTIMODAL SIGNALING		
Maylandia callainos, M. lombardoi, Pseudotropheus cyaneorhabdos, P. johannii	Species combined audio and visual display	Smith and van Staaden (2009)
Maylandia zebra	Sound and visual signals reduce aggression	Bertucci et al. (2010)
Maylandia fainzilberi and *Pseudotropheus emmiltos*	Calls differed most between two sympatric species similar in color	Amorim et al. (2008)
Pundamilia nyererei	Phonotaxis alone insufficient for female attraction to male, visual cues also required	Estramil et al. (2014)
Tramitichromis intermedius	Wild born and captive cichlids hypothesized to use similar multi-modal signaling	Ripley and Lobel (2004)
REDUCED ACOUSTIC ACTIVITY DURING VISUAL DISPLAYS		
Melanochromis auratus	Sound production without visual displays	Smith and van Staaden (2009)
Maylandia zebra "katale"	Calling without "quiver" visual display	Smith and van Staaden (2009)
Oreochromus mossambicus	Calling activity intensified when territory was established	Amorim et al. (2003)
SILENT SPECIES?		
Astatoreochromis alluaudi	Lack of higher frequency register sounds in a monitored aquarium (>5000 Hz)	Spinks et al. (2017)
Cyphotilapia frontosa	Electric stimulation studies correlated with a vocal mechanism in another cichlid found no sound response from the muscles in this species	Longrie et al. (2009)

(continued)

Table 4 (continued)

Research topic species	Results	Literature cited
HYDRODYNAMIC SOUNDS		
Astatotilapia burtoni	Non-intentional sound production due to body motions proposed	Fernald (1975), Hirata and Fernald (1975)
Pseudotropheus emmiltos	Single pulse "dart" sounds are produced by sudden 180° swimming turns (spectrogram, sounds not described)	Simoes et al. (2008a)
ENVIRONMENTAL IMPACT ON SOUND PRODUCTION		
Oreochromis mossambicus	Hypothesized salinity effects on sound production influencing the swimbladder	Pujiyati et al. (2016)

(Lobel and Kerr 1999; Lobel and Mann 1995; Myrberg et al. 1978, 1986; Myrberg and Riggio 1985; Mann and Lobel 1995, 1997, 1998; Spanier 1979). However, the mechanism of sound production still needs to be studied across species.

3.1 Functional Morphology of the Cichlid Sound Mechanisms

Despite the recent research describing cichlid sounds and behavior, the morphological mechanism(s) responsible for these sounds still requires detailed study. In many sonic fish species, there are clear morphological adaptations and specializations dedicated to sound production (e.g., Bass and Ladich 2008; Kasumyan 2008). These sonic mechanisms involve the swimbladder (e.g., Alexander 1966; Fange 1966; Parmentier and Diogo 2006), different bones or fins (Fine et al. 1996; Parmentier et al. 2010), connective tissues (Parmentier et al. 2007), or in some cases multiple mechanisms (Kaatz 2002; Kaatz et al. 2017; Sörensen 1894–1895). In some species of fish, such as the rockfishes (Family Scorpaenidae), their sonic ability was initially hypothesized or inferred based on the identification of well-developed sonic muscles (Hallacher 1974), and later confirmed through acoustic recordings (Širović and Demer 2009). Even though it is now recognized that the occurrence of sounds in cichlids is widespread, the exact identity of the sonic mechanism is elusive with a few different hypotheses proposed or initially tested in the literature (Rice and Lobel 2003; Parmentier and Fine 2016).

The acoustic properties of fish sounds can be suggestive of the sonic mechanism: muscle-driven sounds typically have harmonic frequency structure, and variable call durations, while stridulatory sounds (produced by the grinding of hard surfaces) are broadband and shorter duration (Demski et al. 1973). However, these spectral and temporal properties of sounds are likely endpoints along a continuum, as there are many examples of muscle driven sounds that produce short duration pulses with little spectral structure, such as in red drum (Family Sciaenidae) (Guest and Lasswell 1978). Since most fishes are ectothermic, the frequency in sounds produced by muscles has a temperature-dependent response: warmer water temperatures increase the contraction speed of sonic muscles, which increases the frequency of the call (Connaughton et al. 2002; McKibben and Bass 1998). In the case of toadfishes (Family Batrachoididae), the contraction rate of the sonic muscle sets the fundamental frequency of the call (McKibben and Bass 1998).

The cichlid sonic mechanism is difficult to identify based only upon the acoustic properties of the cichlid sounds. The majority of cichlid sounds are relatively short duration (duration <1 s) and low frequency (dominant frequencies <1000 Hz). Based on the conceptual framework of Demski et al. (1973), these types of sound could be produced by either muscular or osteological mechanisms. Furthermore, there are aspects of the sounds, such as harmonic content (reviewed in Rice and Lobel 2003) and stereotypic acoustic features (Lobel 1998; Rice and Lobel 2003) that make the case even more ambiguous. Despite the number of publications documenting sounds produced by different cichlid species, comparatively few have examined the functional morphology. To date, two morphological systems have been hypothesized to be the source of cichlid sounds: pharyngeal teeth with associated musculature, which is then amplified by the swimbladder, and the buckling method involving abdominal musculature impinging directly on the swimbladder (Longrie et al. 2009).

3.2 Pharyngeal Teeth

The earliest hypothesis for the sonic mechanism in cichlids focused on the pharyngeal teeth (Lanzing 1974; Lanzing and Higginbotham 1976). The cichlid pharyngeal jaws have been suggested as a critical evolutionary innovation responsible for driving the ecological success and diversification of the family (Liem 1973, 1978, 1979; Liem and Greenwood 1981; Liem and Osse 1975). Early observations of cichlid noted that sounds associated with feeding behavior showed similar acoustic properties to communicative sounds (Lanzing 1974); however, some species show differences in the acoustic properties between these sound types (Longrie et al. 2009).

The shapes of cichlid pharyngeal teeth are intricate and elaborate (Casciotta and Arratia 1993; Lanzing and Higginbotham 1976), and show a diet-dependent phenotypic plasticity (Huysseune 1995; Smits et al. 1996a; Smits et al. 1996b; Trapani 2003). Many of the upper pharyngeal jaw teeth have “hooks,” whereas the bottom teeth are more of flat surface (Lanzing and Higginbotham 1976); for example, see Fig. 3. Lanzing and Higginbotham (1976) suggested that the divergent morphology of upper and lower pharyngeal jaw teeth form a “hook and anvil arrangement” and could be involved in the production of sounds. Sounds created by occluding teeth would presumably produce short duration, broadband sounds, with relatively higher

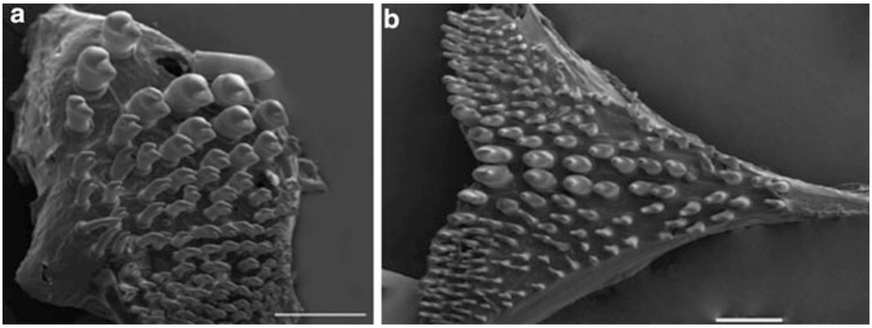

Fig. 3 Detail of the pharyngeal teeth from a *Tramitochromis intermedius* male. The upper and lower pharyngeal jaw teeth form a "hook and anvil arrangement." The magnification on the lower PJ is 15x and the magnification on the upper PJ is 19x. SEMs taken by A. Rice using a JEOL JSM-840 SEM

frequencies. A similar sonic mechanism has been suggested in jacks (Carangidae; Taylor and Mansueti 1960).

3.3 Pharyngeal Jaw Complex

One of the hypothesized evolutionary innovations and keys to the cichlid adaptive radiations in both the African Rift Lakes and the Neotropics is their highly developed pharyngeal jaw apparatus (e.g., Burress 2016; Liem 1973; Wainwright et al. 2012). The jaws are suspended and controlled by a suite of pharyngeal jaw muscles that are responsible for jaw occlusion, lateral, and anterior-posterior movement (Claes and De Vree 1991; Liem 1973). Intriguingly, the pharyngeal jaw muscles of cichlid fish have different physiological properties (Rice et al. 2001), which are also sexually dimorphic (Rice and Lobel 2002). This finding suggests the hypothesis that one sex is more morphologically adapted to produce sounds than is the other sex. Other sonic species of fish, where primarily the males produce the sounds, show a sexual dimorphism in sonic muscle morphology or physiology (Brantley et al. 1993; Walsh et al. 1987; Walsh et al. 1989) or brain regions controlling sound production (e.g., Bass and Andersen 1991; Bass and Baker 1990; Knapp et al. 1999). Thus, the corroborating evidence of physiological difference in pharyngeal jaw muscle performance, sexual dimorphisms in muscle physiology, along with the intricate movements of pharyngeal jaws sets the stage for in vivo physiological experiments to demonstrate the degree to which the pharyngeal jaw complex is involved in cichlid sound production (Rice and Lobel 2003).

Examples of sounds from one male *Tramitichromis intermedius* support the notion that the pharyngeal jaws are involved in sound production and that such sounds are amplified by the swimbladder. A typical courtship sound is illustrated in Fig. 4a showing both the series of pulses in a single call (Fig. 4a) and the detailed

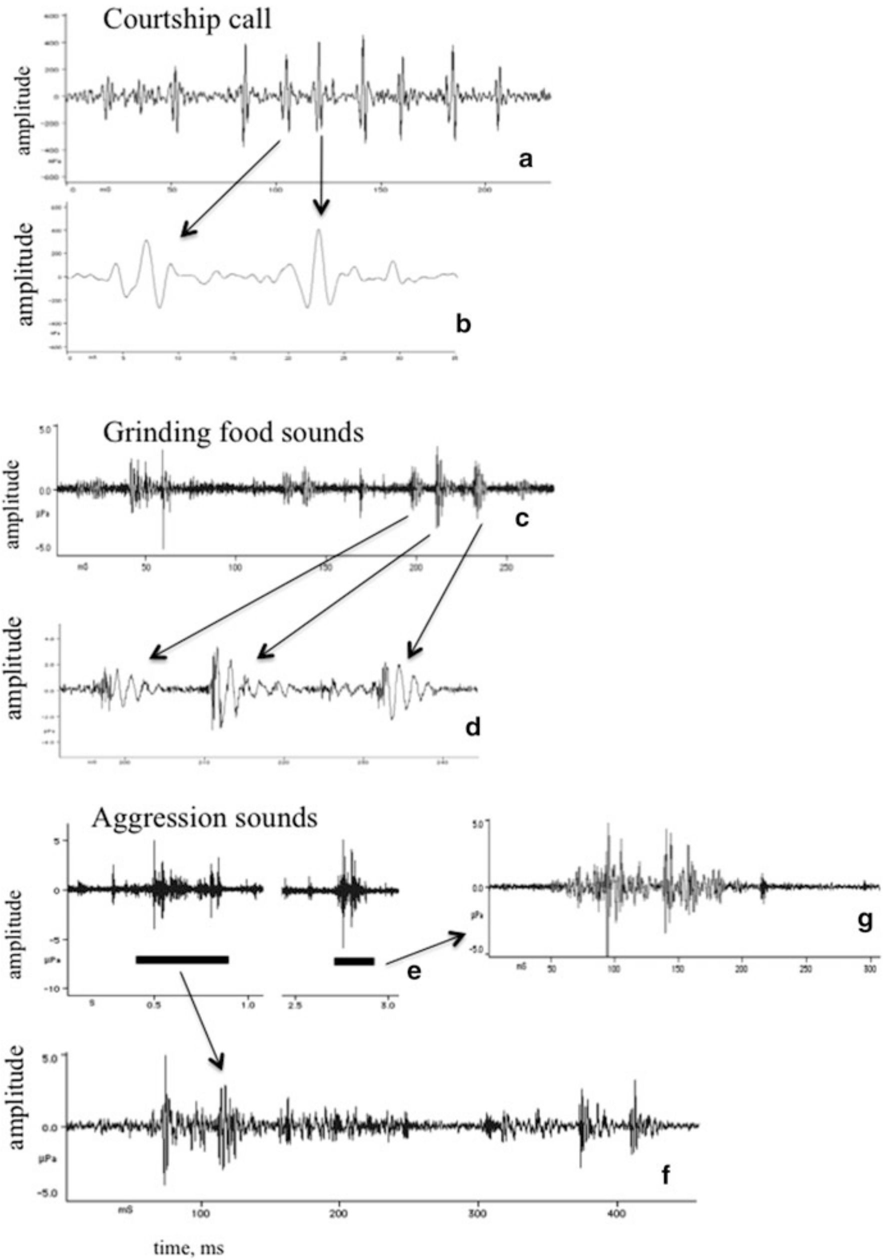

Fig. 4 Examples of courtship and grinding food sounds from one male *Tramitichromis intermedius* and aggressive sounds from *Copadichromis conophorus*. A typical courtship sound showing both the series of pulses in a single call composed of 10 pulses and overall duration of about 195.5 ms (**a**) and the detailed waveform structure of two pulses (**b**), pulse durations 6.69 and 7.33 ms separated by an interpulse interval of 8.54 ms. The same fish grinding consumed small sand-dwelling prey (**c**, **d**). In the audio–video recording, it was easily observable that the fish was

waveform structure of two pulses (Fig. 4b). A similar analysis involved sounds recorded while the same fish consumed small sand-dwelling prey. In the audio–video recording, it was easily observable that the fish was manipulating and grinding a hard-bodied prey in its buccal cavity. The series of food grinding sounds are shown with corresponding oscillographic patterns (Fig. 4c). Detailed waveform structure of two grinding sound pulses is shown in Fig. 4d. Courtship sounds are distinguished by distinct and consistently repetitive pulsed patterns with defined temporal meristics and repeatable pulse waveforms. Grinding sounds are highly irregular with inconsistent properties and appear much like simple noise type signals. Significantly, the two types of sounds from the same individual fish displayed the identical dominant frequency at 517 Hz indicating that amplification and resonance by the swimbladder were involved.

3.4 Fin-Girdle Muscles (Buckling Mechanism)

Research on *Oreochromis niloticus* raises the possibility of another sonic mechanism in cichlids termed “buckling” (Longrie et al. 2009). *O. niloticus* produces short duration, pulsed sounds in agonistic contexts (Longrie et al. 2009). This sound production coincided with posterior movement of the pectoral and pelvic girdles (Longrie et al. 2009). Electrical stimulation of the lateral body in anesthetized fish also resulted in sound production, with a decreased amplitude in fish with a deflated swimbladder (Longrie et al. 2009). Using the kinematic and electrostimulation data combined with morphological inspection, Longrie et al. (2009) suggest that the *vesica longitudinalis* muscle, which originates on the post-cleithrum, runs ventral to the swimbladder and inserts on the second anal fin pterygiophore is the candidate sonic mechanism (Longrie et al. 2009). This work raises interesting questions as to whether the *vesica longitudinalis* is involved in sound production more broadly across cichlid species, or whether it is an independent evolutionary innovation in tilapiine fish. It also raises the question of whether silent cichlids would represent a secondary loss of a vocal mechanism or independent origins of different vocal mechanisms.

Fig. 4 (continued) manipulating and grinding a hard-bodied prey in its buccal cavity. Oscillographic of the entire food grinding sequence of 227 ms duration. Courtship call and food grinding produce the same dominant frequency at 517 Hz. (**d**) Detail of the individual grinding sounds waveform, indicated by arrows. The first pulse is 8.17 ms duration; interpulse interval 5.74 ms, second pulse is 10.32 ms followed by 10.75 ms interpulse interval and third pulse is 7.17 ms. (e, f, g) Two bursts of an “aggressive sound” for comparison that was made by *Mchenga (Copadichromis) conophorus*: The first (left) is 351.2 ms duration and the second (right) is 168.7 ms

3.5 Evolutionary Implications

If cichlid pharyngeal jaws are involved in sound production, as preliminary evidence indicates, then we can expect that different pharyngeal jaw morphologies may produce different types of sounds. It remains to be determined if such different pulse waveforms reflect different types of sounds that are directly detectable by a fish. It is possible that the simplest type of acoustic signal produced is the specific sound of individual pulses, which are then frequently repeated. It may be the perceived sound of the pulse in combination with pulse rate timing that may contribute to species recognition. It is clear from prior studies that pulse number and/or repetition rate is closely correlated with the behavioral context of sounds.

Cichlids have attracted a great deal of attention as an adaptive radiation, particularly within the African rift lakes, with a spectacular diversity of behavior, ecology, and morphology (Albertson et al. 1999; Galis and Metz 1998; Kornfield and Smith 2000). It is no surprise then, that this lineage would show a widespread variety in sound production, and potentially sonic mechanisms. It is fascinating to investigate what is the cichlid sound producing mechanism(s). It has the potential to illustrate the evolution of acoustic diversity, especially among sympatric species. This research could potentially reveal the genetic mechanisms that are foundational to morphological specializations (Streelman et al. 2007), and has been proposed for the diversity of cichlid head and jaw morphologies (Albertson and Kocher 2006; Albertson et al. 2003).

4 Sound Characteristics

Many, but not all, cichlids produce a soft “purr” or “drumming” sound while performing courtship behavior, often accompanying the “quiver” display (Rowland 1978; Lobel 1998; Ripley and Lobel 2004; Brown and Marshall 1978). Fish sounds can be broadly categorized along a spectrum from continuous “long” sound to a series of short pulses or notes (Lobel et al. 2010). For cichlid species whose temporal patterns have been analyzed to date, most species consist of a series of regular pulses or notes with regular interpulse intervals (Table 3). Exceptions include in *H. multispinosa*, agonistic sounds are continuous, whereas in *M. conophoros* agonistic sounds are comprised of pulses with irregular interpulse intervals. Grunting and clicking species distinguished by Van Staaden and Smith (2011), varied in interpulse interval suggesting some species may have more continuous call patterns than others but the noise level of the recording environment precludes this conclusion. In the genus *Maylandia*, males have been documented to produce low amplitude, frequency-modulated sounds in addition to higher amplitude pulsed sounds (Simoes et al. 2008b). *Hemichromis bimaculatus* produced two different sound types in the same display (Rowland 1978). Single-pulse sound types were additionally produced by *Hemichromis bimaculatus*, *Herotilapia multispinosa*, *Maylandia zebra*

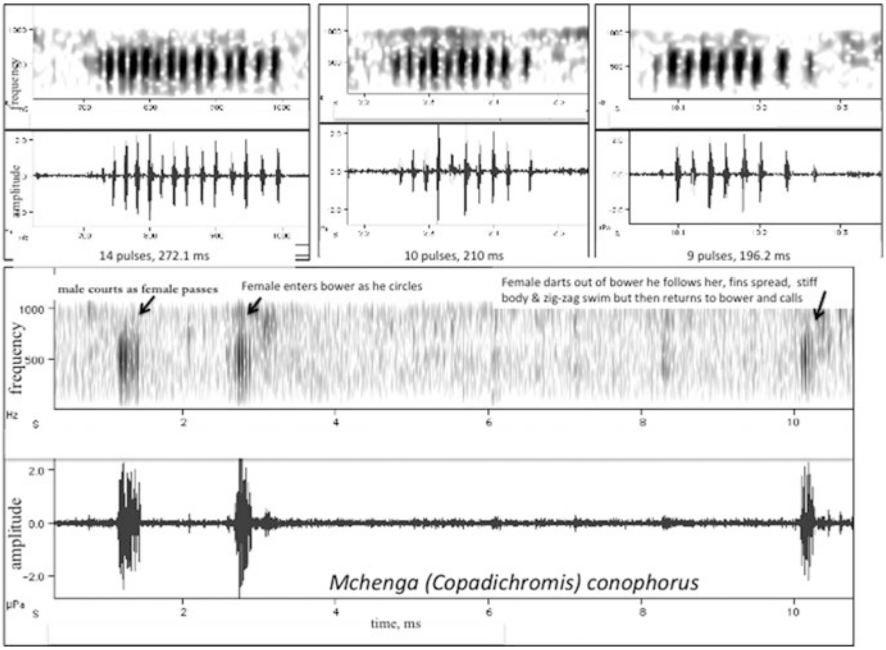

Fig. 5 Courtship sequence shown for *Mchenga (Copadichromis) conophorus* (Aug 23, 1990; 08:18:48–08:19:05 Hrs). Female enters bower and spawns then leaves the arena. See Fig. 7 for the fish recorded

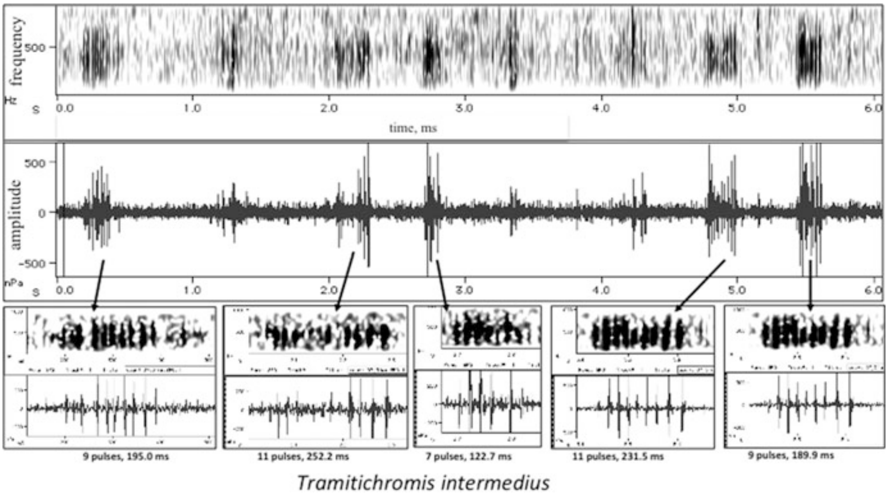

Fig. 6 Courtship sequence shown for *Tramitichromis intermedius* (Aug 22, 1990; 07:51–07:51:30 Hrs). A single male courting a single female as she swims casually passing-by, but she does not stop. See Fig. 8 for the fish recorded

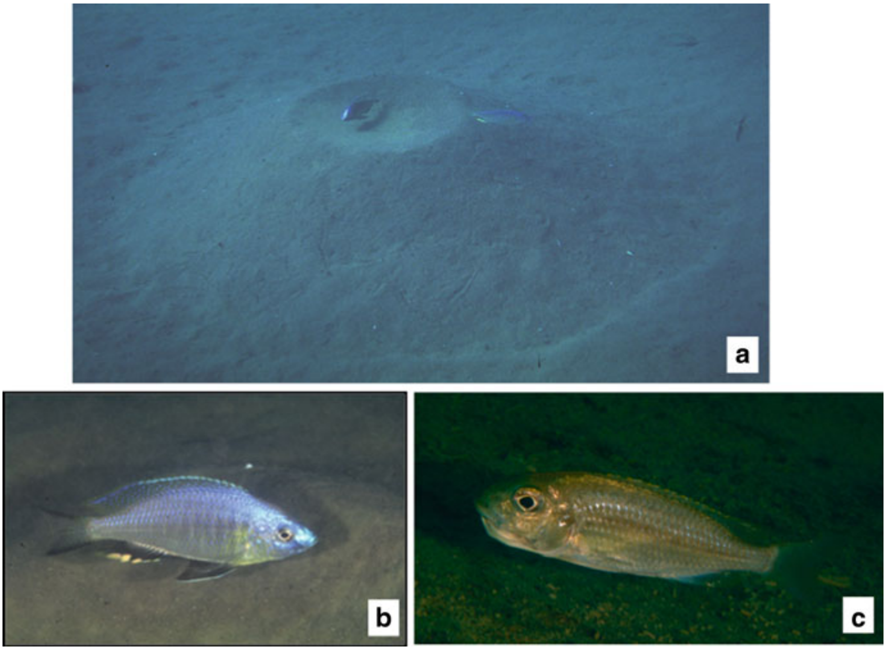

Fig. 7 (**a**), A male *Mchenga (Copadichromis) conophorus* defending his bower from an intruder male. (**b**) Male *M. conophorus* and (**c**) Female *M. conophorus* shown holding embryos in her mouth. Photographed at Cape McClear, Lake Malawi National Park offshore (depth 3–8 m) of the World Wildlife Fund Education Center and at Otter Point, August 5–27, 1990 (photos by P. S. Lobel)

juveniles, and *Oreochromis mossambicus.* However, some examples of sounds from these fishes appear to include occasional pulsed sections. An acoustic repertoire of a cichlid can range from one to four sound types per species. Typically, a male will display and produce sounds in the presence of a female pre-reproductively as a female approaches the spawning site. Examples of such sonic behavior while courting are shown for *Mchenga (Copadichromis) conophorus* (Fig. 5) and *T. intermedius* (Fig. 6). These same fish are shown in their natural habitat (Figs. 7 and 8).

4.1 Acoustic Patterns

The spectral and temporal sound measurements for cichlids are summarized in Table 3. Of the 39 cichlid species whose sounds have been acoustically detected with a hydrophone or analyzed to some extent, the three cichlids with few data are: *Amphilophus citrinellus*, *Chindongo elongatus*, and *Sarotherodon galilaeus.* Among the other 35 cichlid species whose sounds have been analyzed to some extent, six species have had pulse rate described and seven species have had call rate

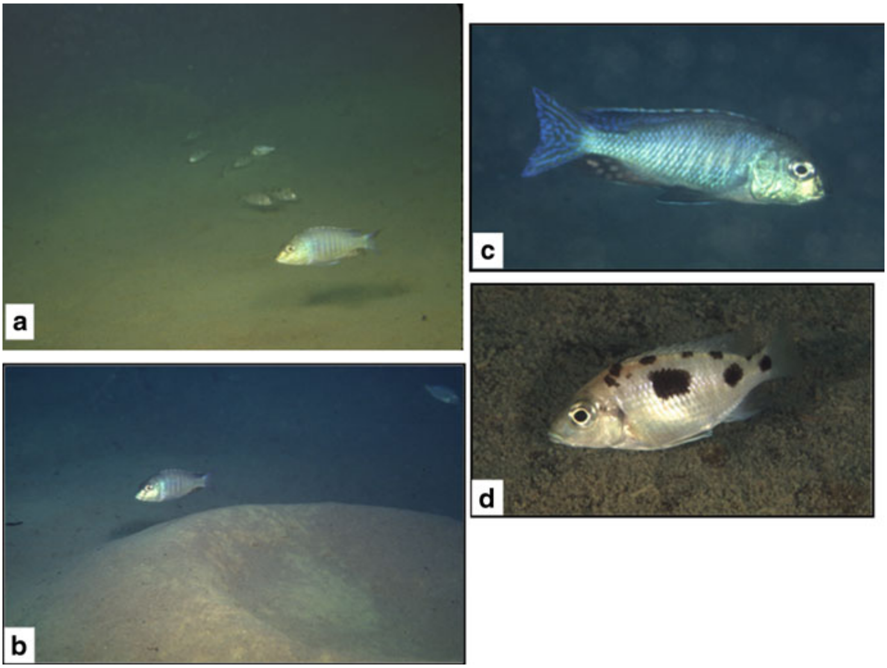

Fig. 8 (**a**) A male *Tramitichromis intermedius* with several females in background. (**b**) A male patrolling the rim of his bower. (**c**) A male in courtship colors. (**d**) A female. Photographed at Cape McClear, Lake Malawi National Park offshore (depth 3–8 m) of the World Wildlife Fund Education Center and at Otter Point, August 5–27, 1990 (photos by P. S. Lobel)

described. Additional acoustic traits have been reported for 30 species (Table 3) but not every species had all characteristics measured. *Pterophyllum* sp. has only had pulse rate (6 pulses/sec) and frequency described; *Amatitlania nigrofasciata* has only had rate (20 pulses/sec) and frequency described; two species, *Labidochromis caeruleus* and *Cichlasoma portalegrense*, have only had frequency described. *Pelmatolapia mariae* had sounds described in general but without temporal or frequency data listed (Table 3).

4.2 Typical Sound Characteristics

Pulsed sound types best characterize cichlid sounds and it is intriguing to contemplate whether this temporal information is meaningful in communication (e.g., Kihslinger and Klimley 2002). The number of species for which pulsed sounds (excluding chewing sounds) were statistically described were: duration ($n = 26$); pulse number ($n = 26$); pulse duration ($n = 19$); pulse period ($n = 10$); and interpulse interval ($n = 4$). Temporal sound traits for these sounds produced during agonism or courtship with statistical descriptions available for species including ranges (that exclude species with high frequency chewing sound types and single pulse sounds) for minimum to maximum range values are: call duration (ms) 277 ± 160 SD to 1319 ± 789 SD (51–4000; $n = 28$; 16 species; pulse number 6 ± 3 SD to 24 ± 19 SD (2–92, $n = 28$, 15 species); pulse duration (ms) 9 ± 5 SD to 21 ± 19 SD (3–70, $n = 17$, 13 species); pulse period (ms) 57 ± 24 SD to 118 ± 45 SD (7–250); $n = 17$; 6 species); and interpulse interval (ms) 21± 31 SD to 138 ± 122 SD (5–316, $n = 5$, four species). These values characterize the described sounds of cichlids that are produced in pulse series at a lower frequency range.

Most cichlids produce one sound type per call, which consists of a series of short pulses (Table 3). Not all contexts have been acoustically surveyed in all known acoustic cichlids therefore a statistic for call repertoire would be hypothetical. However, for the species with data, the reported maximum repertoire size for social contexts the conservative estimate for sounds of a certain origin or numerically described ranges from 1 to 4; $n = 35$ species. *Herotilapia multispinosa* had the largest repertoire (Brown and Marshall 1978). Non-Pulsed (single or continuous) are known from ten species (Tables 3 and 4) but have only been quantitatively described for three species for natural sounds with comparable range data for *H. multispinosa*, *O. mossambicus*, and *O. tilapia*. These sounds appear to be shorter in duration than pulsed calls. Their temporal duration ranges of minimum to maximum are 119 ± 94 SD ($n = 4$, three species) to 437 ± 237 SD ($n = 4$, three species).

A recent review has provided a lexicon for what could constitute different types of complex acoustic behaviors including variation across populations, across or within individuals, across or within contexts (Bolgan et al. 2018). Complex patterning within a call has been documented in two species of cichlids (Table 4). *H. bimaculatus* agonistic sounds include two sounds that overlapped on spectrograms, a pulsed sound and “thump” which is not sufficiently expanded to determine the pattern, although it lacks pulses on the spectrograms available (Rowland 1978). Male courtship sounds in three other species (*Maylandia emmiltos*, *M. fainzilberi* and a hybrid of *Pseudotropheus* “zebra gold’ × *M. zebra*) consisted of a continuous waveform sometimes frequency-modulated sound followed by a pulsed sound. Increased complexity in vertebrate calls is well established to play a range of significant roles in both intra- and interspecific communication in frogs (Zelick et al. 1999).

Call rate per minute (aka calling rate) has been described for ten species: *Archocentrus centrarchus* (*Hemichromis bimaculatus* (Myrberg et al. 1965; Rowland 1978); *Herotilapia multispinosa* (Brown and Marshall 1978); *Maylandia callainos*, *Pseudotropheus* “zebra gold,” *Pseudotropheus emmiltos*, *Maylandia fainzilberi*, and *Maylandia zebra* (Amorim et al. 2008); *Oreochromis mossambicus* (Amorim et al. 2003) and *Oreochromis niloticus* (Longrie et al. 2013). Sounds per minute is a readily comparable sound characteristic that can be compared across species and has been calculated for male courtship calls in six species. Among *Maylandia callainos*; *M. emmiltos*; *M. fainzilberi*; and *M. zebra*; *Pseudotropheus* “zebra gold” (Amorim et al. 2008); *M. emmiltos* had the highest call rate with 1.4 sounds/min and was statistically higher than the other species (Table 5). *Oreochromis mossambicus* call rate in courtship was 1.1 ± 07 sounds/min.

Table 5 Acoustic comparisons between sympatric cichlid species

Species call type	Temporal (ms) Traits that differed (no differences)	Frequency (Hz) Traits that differed (no differences)	Literature cited
Mchenga conophoros and Tramitichromis intermedius			
Male courtship	Pulse duration, pulse rate	Not tested	Lobel (1998)
	(call duration, pulse number, interpulse)		
Maylandia zebra, Maylandia callainos, and Pseudotropheus “zebra gold”			
Male courtship	Pulse number, pulse duration differed between some but not all species	Peak higher in *M. callainos*	Amorim et al. (2004)
	(call duration, pulse period)	(peak)	
M. zebra, M. callainos, and P. “zebra gold”			
Male courtship	Call duration, pulse number, pulse period differed between some but not all species	Peak differed between contexts	Simoes et al. (2006)
Maylanida faizilberi, M. zebra, M. callainos, and M. emmiltos and P. “zebra gold”			
Male courtship	Call rate, pulse number, pulse period differed between some but not all species	(peak)	Amorim et al. (2008)
	(call duration)		
Maylandia aurora, M. callainos, and M. zebra			
Nest associated (trill call)	Call duration, pulse duration, pulse period (pulse number)	Not tested	Danley et al. (2012)
Haplochromis pundamilia, and Haplochromis nyererei, Neochromis omnicaeruleus			
Male courtship	Pulse period	(peak)	Verzijden et al. (2010)
	Call duration, pulse number differed between some but not all species		
Maylandia callainos, M. lombardoi, Pseudotropheus johanii, and *P. cyaneorhabdos*			
Male courtship	Call duration, pulse number/call, number of calls/display	Primary	Van Staaden and Smith (2011)
	Pulse period distinguishes interpulsed “click” sounds of *M. callainos* from other species’ “grunting”		
	M. callainos differs from other species (discriminant function analysis)		
NO CALL DIFFERENCES:			
Petrotilapia nigra, Cyanotilapia afra, and *Labreotropheus fuellborni*			
Nest associated (trill call)	(described but not tested for differences: Call duration, pulse number, pulse duration, pulse period were similar)	Not tested	Danley et al. (2012)
Maylandia lombardoi and *Pseudotropheus cyaneorhabdos* (discriminant function analysis)			
Male courtship	(call duration)	(primary)	Van Staaden and Smith (2011)

Temporal Data The number of species for which temporal data was reported from reproductive and agonistic calls are: call duration $n = 26$; pulse number $n = 26$; pulse duration $n = 19$; pulse period $n = 10$; and between pulse interval $n = 4$. For these sounds minimum and maximum values for temporal traits (all data pooled) are: sound duration (ms) 255 ± 165 SD to 1226 ± 803 SD (27–4000; $n = 31$; 16 species); pulse number 6 ± 3SD to 23 ± 19SD (2–92; $n = 28$; 15 species); pulse duration (ms) 9 ± 5SD to 21 ± 19 SD (3–70; $n = 17$; 13 species); pulse period (ms) 57 ± 24 SD to 118 ± 45 SD (7–250; $n = 17$; 6 species); and interpulse interval (ms) 21 ± 31 SD to 138 ± 122 SD (5–316; $n = 5$; four species). The details are given in Table 3.

Frequency Data Frequency measurements describing cichlid sounds differ across publications with range, fundamental, maximum, center, or dominant (dominant synonyms are peak, principle, primary, and main) frequency values (Table 3). Frequency range measurements are subject to different methods, vary as a function of FFT used in the spectrogram, and these details are not always reported in cichlids. But, since many cichlids sounds are pulsed and broadband, frequency may not be the best way to describe these sounds. The number of species for which social context reproductive or agonistic sound frequency data was reported are: peak frequency $n = 29$ and frequency range $n = 18$. Frequency measurements describing cichlid sounds differ across publications with range, maximum, middle, or dominant (peak, principle, main) frequency values published for 31 species (Table 3). Frequency range measurements are subject to different methods and are not widely reported. Some examples for social contexts for minimum and maximum range values are: 95 Hz ±55 to 1385 Hz ± 1202 (25–5000 Hz; $n = 16$; 10 species). The minimum to maximum dominant frequency was: 493 Hz ± 1095 and the maximum was 1487 Hz ± 3555 (50–16,000, $n = 36$; 18, species).

Frequency range is low in *Oreochromis nilotucus* and *O. mossambicus* compared to some other cichlids. The sounds produced were described as very low, with most of the energy below 200 Hz (Longrie et al. 2008, 2009, 2013; McPherson 2012) and a mean dominant frequency below 68 Hz (46–68 Hz;) compared to other cichlids (Amorim et al. 2003; Longrie et al. 2013). The tonal sounds of several additional species, *Maylandia emmiltos*, *M. fainzilberi*, and *Pseudotropheus "zebra gold"* × *M. zebra*, are also very low among cichlids (Range 22–86 Hz Peak frequency), which have been recorded to date.

Frequency range is high with peak or main frequency well above 1000 Hz, for *Neolamprologus pulcher* (agonistic sounds, Spinks et al. 2017), *Pterophyllum (scalare?)* (Myrberg et al. 1965), and *O. mossambicus* (Lanzing 1974). High frequency (greater than 1000 Hz) sounds have also been reported from *Tropheus moorii, T. duboisi, T. brichardi, Simochromis diagramma, and Astatotilapia burtoni* (Nelissen 1978). These pulsed high-frequency range sounds seem to be different sound types from the typical pulsed lower frequency sounds of cichlids. Six of these species had sound ranges described for several sound characteristics and these are summarized by (mean ± SD): sound duration (ms) 370 ± 399 to 3660 ± 1141

(80–5000; $n = 5$; five species); pulse number 2 ± 1 to 8 ± 3 (1–11; $n = 6$; six species); pulse duration (ms) 42 ± 8 to 124 + 38 (30–170; $n = 5$; five species); and dominant frequency (Hz) 3667± 2021 to 12,833 ± 1768 (2500–16,000; $n = 3$; three species). We excluded the higher frequency chewing call types from our final characterization of cichlid sound call parameters analysis below. It is important to note that while understudied feeding sounds even if incidental can have a significant impact on social behavior suggesting their use as foraging cues as observed in a group foraging cyprinid (Scholz and Ladich 2006).

Fish Size and Dominant Frequency In general, among teleosts with simple swimbladders, larger fish produce lower frequency sounds than do smaller fish (Demski et al. 1973; Fine et al. 1977; Myrberg and Riggio 1985). This applies to cichlids (Myrberg et al. 1965; Rowland 1978) and also to pomacentrids, which have similar swimbladder structure (Myrberg et al. 1993; Lobel and Mann 1995). The hypothesis is that sound quality in terms of amplitude and frequency is in large part a morphologically determined signal related to swimbladder and body size. It is a basic principle of underwater physics that larger swimbladders resonate at lower frequencies than smaller ones (Clay and Medwin 1977; Urick 1983). This association could provide a reliable indicator of male size to the listening female fish that is selecting among potential mates.

Body size is an important variable affecting ultimate reproductive success of male cichlids and many other fishes (Bisazza and Marin 1991; Hert 1990; Magnhagen and Kvarnema 1989; Myrberg et al. 1986; Noonan 1983). Two studies have demonstrated that, in fact, the dominant frequency of the courtship sound from two pomacentrid species does decrease with increasing male size (Myrberg et al. 1993; Mann and Lobel 1995). A preference for females to mate with larger males, producing lower frequency courtship calls, has been demonstrated experimentally for the bicolor damselfish, *Stegastes partitus*. Female choice in this pomacentrid is also strongly influenced by the vigorousness of male courtship activity (Myrberg et al. 1986; Knapp and Warner 1991). Vigor is defined by the rate at which males display courtship-swimming motions and simultaneously produce courtship sounds although Knapp and Warner (1991) did not include bioacoustics. An individual cichlid's sounds differ in call parameters relating to body size (Amorim et al. 2004; Simoes et al. 2008b; Bertucci et al. 2012a, b; Verzijden et al. 2010; Maruska et al. 2012). Frequency patterns could contribute to individual sound differences (Bertucci et al. 2012a, b). However, the frequency may not vary significantly between species (Amorim et al. 2008). It is still an open question as to whether the specific acoustic structure conveys specific information or whether it is merely the occurrence and rapidity of sound production, but not details, that matter for fish mate selection. The simplest information that might be communicated by a fish's sonic behavior may be an individual male's location, readiness to spawn, and or his overall vigor (Lobel 2001).

4.3 Aggression and Courtship

The typical sound produced by a cichlid during aggressive and courting behavior is a series of rapid low frequency (typically 200–600 Hz) pulses. The "grunting" and "clicking" cichlid sound types described by Van Staaden and Smith (2011) were distinguished by discernibility of the duration of the interpulse interval. These acoustic traits could provide signature differences among individuals (Bertucci et al. 2012a, b). The territorial cichlid males responded to conspecific sounds but not temporal coding modifications (Bertucci et al. 2013). These preliminary data support the hypothesis that cichlid sounds are temporally structured in a way that contains information that could be used in the mate selection process. This type of acoustic coding has long been documented and is common in insects and amphibians and marine mammals, and has been proposed for fishes as well (Myrberg et al. 1978; Kihslinger and Klimley 2002; Spanier 1979). For example, pulse coding of species-specific sounds is a well-known feature of the mating behavior of *Drosophila* and other arthropods (Ewing 1989). Male field crickets with longer calling-bout durations are preferred by females (Hedrick 1986). Acoustic communication is a demonstrated feature in amphibian sexual selection (Ryan 1985; Zelick et al. 1999). It seems reasonable to consider that if insects and amphibians are using pulsed sounds in mate selection then the same is possible, even likely, for some fishes.

The following example illustrates typical courtship associated sounds for three cichlid species and emphasizes the comparative details of interspecific variation in single pulse patterns. It is possible that specific waveform structure of single pulses is a product of the sound producing mechanism. Waveforms of courtship sounds for *Maylandia zebra* (formerly *Pseudotropheus zebra*, Stauffer et al. 1997), *Mchenga (Copadichromis) conophoros,* and *Tramitochromis intermedius* are shown in Fig. 2.

Individual fish can vary the type of sound produced in different behavioral contexts. Courtship and aggressive sounds are hard to distinguish acoustically by listening when played to humans through a loudspeaker. Sounds differ between agonistic and courtship contexts for *Maylandia* species (Simoes et al. 2008b). However, in one other cichlid, *Pundamilia nyererei*, sounds produced in different contexts were the same (Verzijden et al. 2010). Acoustic contests in a laboratory setting between males did not show a correlation between male size, increased fighting intensity, and call number (Amorim and Almada 2005). Studies of *O. niloticus* demonstrated that in male–male contests winners were quick to court, courtship duration was extended and their calls were greater in number with longer pulse durations and lower peak frequencies than previous contest losers (Amorim and Almada 2005), traits that correlate with increased fitness in other vertebrate species. Dyadic contests elicited agonistic sound production in *P. nyererei* (Verzijden et al. 2010). These sounds are associated with aggressive behavior between males.

Mchenga (*Copadichromis*) *conophoros* aggressive sounds (Fig. 4e, f and g) are composed of irregular and longer duration pulses, which are clearly distinguishable from the regular and distinct pulses that are seen in typical courtship sound patterns.

5 Playback Experiments

Early evidence demonstrated the ability for individual male recognition by female *H. bimaculatus* (Nobel and Curtis 1939). For future research, playback of sounds will be crucial to discern if sounds elicit a behavioral response, which would support the notion that the sounds have specific temporal encoding information. There have been, so far, a limited number of experimental studies on cichlids, which are summarized in Table 4. Playback experiments have demonstrated that a cichlid will respond to conspecific sounds (Rowland 1978). Rowland (1978) conducted behavioral studies to observe the reaction of cichlids to physical models and to the playback of those sound recordings during repeat model experiments. He presented dummy fish with and without playback of the fish's courtship-display-like and aggressive-display-like sounds as well as presentations with white noise and silence. There was no difference to fish response between white noise and silent dummies, but fish showed a significant response to dummies playing back conspecific sounds over silent dummies. Cichlid sound playback in another study resulted in listeners becoming less aggressive (Schwarz 1974b). Schwartz (1974a, b) found that male *Archocentrus centrarchus* responded to conspecific sounds and that in this species acoustic cues inhibited aggression. This species does not apparently produce a courtship-associated sound (Schwarz 1980). A preliminary study of neighboring *O. mossambicus* nest territory holding males were found to produce agonistic "thump" sounds which are not the typically multi-pulsed call (McPherson 2012) and observations of playback suggest a possible chorusing interaction by the lead caller of played-back sound. Bertucci et al. (2013) found that male cichlids during agonistic encounters responded to sounds in general, but not to modification of variation in temporal patterns. Auditory plasticity influences female cichlid hearing and there is overlap between female hearing in reproductive condition and male courtship songs indicating the importance of sound in reproductive communication (Maruska et al. 2012). Two studies found that females preferred males with natural calls compared to males with (a) noise with male (Maruska et al. 2012) and (b) silent with male in playback experiments (Verzijden et al. 2010). Estramil et al. (2014) experimentally demonstrated the multimodal nature of cichlid sounds with females only responding to sounds if live males are present.

6 Species-Specific Sounds

Simple comparison of the pulse rate in the courtship calls of two sympatric species (but different genera) that live close together in Lake Malawi, *Mchenga (Copadichromis) conophoros*, and *Tramitichromis intermedius*, revealed statistically significant differences in pulse rate and pulse duration but not pulse number, call duration or inter-pulse duration (Lobel 1998). Lake Victoria cichlids (Verzijden et al. 2010) produce species-specific sounds. *Maylandia* spp. male courtship sounds differ in temporal acoustic traits (Amorim et al. 2008; Danley et al. 2012) and peak frequency (Amorim et al. 2004). Male courtship sounds of Lake Malawi cichlids differed among four congeneric and heterogeneric species with a more significant difference between congeners (Van Staaden and Smith 2011) and similar sounds for one pair of heterogeneric species. Male courtship calls of Lake Victoria cichlids, congeners, and heterogeneric species, are species specific (Verzijden et al. 2010). The importance of male calls to female listeners was shown experimentally to the female cichlid ear, with peak sensitivity occurring when females are in reproductive condition prior to the mouthbrooding phase (Maruska et al. 2012) in response to changing hormones demonstrating a peak in call sensitivity during reproductive conditioning. Yet, to date, no playback studies have examined the role of specific temporal or frequency trait differences among different species calls to the female listener. Studies examining contrasting differences in sound characteristics between the males of cichlid species are summarized in Table 5.

6.1 Sonic Diversity and Color Patterns

Nelissen (1975, 1977, 1978) provided a detailed analysis of the sounds of some Lake Tanganyika cichlids and found that several species displayed different acoustic repertoires. The number of sonic displays produced by a species was negatively correlated with the number of color patterns that species displayed with its behavior (Nelissen 1978). Species could be substituting between visual acoustic diversity and sonic diversity. The most sonically diverse species (*Tropheus* spp.) displayed the fewest color changes. The sonically least active species, *Simochromis* spp. maybe using color pattern displays to communicate. Another species, *Astatotilapia burtoni,* was intermediate. Increased sound activity with behavior was found for *Tropheus* spp., which is mainly nocturnal, compared to the diurnally active *Simochromis* (Nelissen 1978). A similar pattern is well known in coral reef fish communities where many nocturnal species (e.g., holocentrids, pempherids, and sciaenids) are also among the most sonically active. More recently, Amorim et al. (2008) found that among five Lake Malawi cichlid fish species of the *Maylandia (Pseudotropheus) zebra* complex, that the male courtship acoustic signals differed significantly in the number of pulses and in pulse period. They reported that the largest differences in acoustic variables were found between the two sympatric Mphanga Rocks species *P. emmiltos* and *P. fainzilberi*, that, in contrast to the other three species, look (to us at least) very similar to each other in color and pattern.

6.2 Silent Behavior and/or Non-acoustic Cichlids

Although many cichlids appear to make sounds with specific behavior, there have been several reported as being silent during certain behavioral interactions. This is an intriguing phenomenon and further study will be interesting. Ladich and Popper

(2001) refer to fish species that are not known to produce volitional sound as non-vocal. “Silent” is applied to fishes that have been examined for acoustic ability and found to lack it (Kaatz et al. 2010). Although many cichlids appear to make sounds with specific behavior, there have been 11 species reported as being silent during certain behavioral interactions (Table 6). *Neolamprologus pulcher* did not produce sounds during acoustically monitored social interactions (Pisanski et al. 2015, but see Spinks et al. 2017) although it did produce sounds when males were exposed to their image in a mirror (Spinks et al. 2017). The only evidence for possibly silent cichlid species is an anecdotal report found in Spinks et al. (2017) for *Astatoreochromis allaudi*, based on aquarium studies. *Cyphotilapia frontosa* lacked an acoustic response to electrical stimulation that did stimulate sounds in one other tested cichlid known to be a sound producer (Longrie et al. 2009). However, it should be emphasized that no behavioral studies of living social groups have yet been conducted for these species. The occurrence of these silent cichlid species raises the question as to whether this represents a secondary loss of this ability, or whether sounds in cichlids are independently derived. This exciting research is in its beginning phase of discovering which fish species may be making behaviorally relevant sounds. This is an intriguing phenomenon for further study.

Contexts that were well monitored and found to lack sound for all individuals tested in a species with other acoustic contexts included are listed in Table 6. Some examples are: *Hemichromis bimaculatus* courtship and spawning, brood care (Myrberg et al. 1965); *A. nigrofasciata* reproduction and male fighting (Myrberg et al. 1965); courtship, spawning, and guarding of fry in *O. niloticus* (Longrie et al. 2009); juveniles schooling and female during agonism, spawning, brooding, and fry release for *Tramitichromis cf. intermedius* (Ripley and Lobel 2004)*; Pterophyllum (scalare sp?) for* schooling adults and parents on nest or with eggs, larvae, or fry without intruders (Myrberg et al. 1965) courtship associated *A. centrarchus* during spawning for *H. multispinosa* (Brown and Marshall 1978). *Neolamprologus pulcher* did not produce sounds during acoustically monitored social interactions including male–male agonism and courtship (Pisanski et al. 2015, but see Spinks et al. 2017). Female *Tilapia mariae* did not produce sounds during male–female and male–male agonistic interactions (Kottege et al. 2015). Courted males of *Oreochromis mossambicus* were silent when displayed by vocalizing males (Amorim et al. 2003). Individuals of the subpopulation *Maylandia zebra* "katale" only produced incidental patterned sounds on the territory while clearing gravel, not during visual courtship displays (Smith and Van Staaden 2009; Van Staaden and Smith 2011). There are additional unpublished data reported by Spinks et al. (2017) supporting silence in another cichlid species, *Astatoreochromis allaudi*, based on aquarium studies. It is possible that there is individual variation in vocal activity (Van Staaden and Smith 2011); therefore, a statistically adequate number of individuals should be investigated before concluding the sonic status of a species or a specific behavioral context.Relatively low-intensity acoustic activity has, so far, been observed in three cichlid species (Table 4). Calling with visual courtship displays was rare or absent in some individuals of two tested species (*Maylandia zebra* “katale” and *Melanochromis auratus*) compared to other sympatric species (Van Staaden and

Table 6 Cichlids displaying behaviors unaccompanied by sounds

Species (current name, catalogue of fishes)	Behavioral context[a]: Silent, no sounds detected	Acoustic	Literature cited
Contexts with no sounds detected ($n = 11$ species)			
Amatitlania nigrofasciata	Prespawning, courtship, A (male–male fighting)	A (female caller and male), A (Nest defense female caller brooding)	Myrberg et al. (1965)
Archocentrus centrarchus	Reproductive (male and female): Cs, quiver, jerk, dig, nip substratem pseudoskim, aerate, jolt; Fin-flick, yawn	A	Schwartz (1980)
Hemichromis bimaculatus	Non-aggressive courtship; Cs; egg fanning; mate exchange over eggs or young; fin flicking over young	A (male and female); A (nest defense female caller parental period egg incubation, larvae, and free-swimming young); A (female returned to aquarium male caller), A (male–male conflict)	Myrberg et al. (1965)
Herotilapia multispinosa	Cs	Cd, A	Brown and Marshall (1978)
Maylandia zebra “katale”	Cd (visual courtship display without sound)	Male calls on territory while gravel clearing	Smith and Van Staaden (2009)
Oreochromis mossambicus	A (nearly always silent); males which could be acting as sneakers were silent while courted by vocal courting male	A (territorial male groups); Cd; Cs; Nest associated (male call in nest)	Amorim et al. (2003)
Oreochromis niloticus	Cd, Cs, and A Free alevins protection (female)	A, Nest associated (fin display, dig, hover), A mouth egg incubation (female)	Longrie et al. (2013)
Neolamprologus pulcher	Cd, A (male–male aggressive and submissive; female submissive) lower frequency sounds	None	Pisanski et al. (2015) (but see Spinks et al. (2017))
Pelmatolapia mariae	A (male–male, male–female)	Nest associated female caller paired male in area	Kottege et al. (2015)
Pterophyllum sp. (probably *scalare*)	School (adult group swimming); mated pair alone on nest with eggs, larvae, or free-swimming fry	A (nest defense egg and larvae, parent with free-swimming fry, parent–intruder aggression)	Myrberg et al. (1965)
Tramitichromis intermedius	Schooling (juveniles); A (female), Cf (female courtship), Cs (female), brooding, and fry release (females)	Cd	Ripley and Lobel (2004)

[a] *A* agonism, *Cd* male courtship display to female, *Cs* spawning

Female silence in courtship (“Cd”) is implied by the presence of a male calling during courtship but was only scored as a silent context when specifically examined

Smith 2011). However, reproductive behaviors were also uncommon in the small aquarium population tested (Smith and Van Staaden 2009). Intraspecific agonistic interactions of non-territorial males and females in *O. mossambicus* were rarely associated with inter-pulsed sound production (Amorim et al. 2003) while territoriality was the condition under which males began calling in greater abundance. In another study, territorial *O. mossambicus* males were found to produce distinct agonistic "thump" and pulsed courtship sounds on nest territories in the field (McPherson 2012). More studies are required to explore this aspect of cichlid bioacoustics.

7 Sound Detection and Hearing

The hearing abilities have not been measured in many cichlid species, compared to other taxa, and most of the work on the auditory system has examined ear or otolith morphology. The cichlid *Sarotherodon macrocephala* responds to underwater sound stimulation from 50 to 900 Hz with maximum sensitivity at 100 Hz (Fay and Popper 1975). This range of hearing sensitivity is typical for percoid type fishes without special morphological adaptations for hearing (e.g., ostariophysians, clupeids, Fay 1988; Popper and Fay 1973, 1993). The ears in both Old World *Sarotherodon macrocephala* and New World *Aequidens pulcher* are very similar to one another (Popper 1977). The otoliths of Cichlidae are diagnostic for the family (Gaemers 1984; Gaemers and Crapon de Crapona 1986). Sexual dimorphism in otoliths occurs in those haplochromine species that have a maximum male size greater than maximum female size (Gaemers and Crapon de Crapona 1986). The auditory sensitivity of the Malawi cichlid, *Tramitichromis intermedius* is correlated with the frequency range of sounds it produces during aggression and courtship (Ripley et al. 2002). The acoustic cichlid *Astatotilapia burtoni*'s hearing is sensitive to its own call acoustic traits (Maruska et al. 2012) as is the hearing in *Labidochromis caeruleus* (Higgs et al. 2011). The peak hearing sensitivity of *Tramitochromis intermedius* corresponds with the dominant frequency of its courtship calls (Ripley et al. 2002).

Auditory psychophysiological data support the notion that fishes, in general, have peak auditory sensitivity below 1000 Hz (Fay 1988; Popper and Fay 1993). The fish's central (brain) and peripheral (ear) auditory systems are fully capable of processing: 1) sound amplitude fluctuation with respect to both sensitivity and pattern discrimination and 2) sound source localization in azimuth and elevation (Fay 1988; Popper and Fay 1993). The response by females to pulsed courtship calls for mate selection has been demonstrated experimentally for a pomacentrid and is implicated in other fishes (Gerald 1971; Fine et al. 1977; Myrberg et al. 1978, 1986; Myrberg and Spires 1980; Schwarz 1985; Spanier 1979). That a cichlid can detect and learn response to sound has been demonstrated in *Oreochromis aureus*, which was behaviorally conditioned to associate a buzzer sound to being fed. Acoustic interaction between sexes is also suggested by results, which indicated that the courtship sound produced by male *Oreochromis mossambicus* (syn. *Sarotherodon*, *Tilapia mossambica*) facilitated oviposition in females (Marshall 1972). Auditory plasticity in male and female *Astatotilapia burtoni* has been examined and could influence how social sounds are detected through the reproductive cycle (Maruska and Fernald 2010).

Lateral line systems of fishes are sensitive to water displacement as well as near field and likely low-frequency sound. Both the lateral line and the ear are innervated by the VIIIth cranial nerve (see Webb et al. 2021). Various cichlid genera possess at least eight trunk canal patterns (Webb 1990). Another potential sensory adaptation, which is very poorly understood, may involve enlarged sensory pores in the mandible. These pores are apparently linked to the lateral line and presumably, may have a role associated with enhanced sound detection (Konings 1995). This feature has been identified in the genera *Aulonocara, Tramitichromis*, and related species (Konings 1995; Turner 1996). How these lateral line and sensory pore patterns may be related to a cichlid's response to sounds is not known. The suggestion is that these mandibular pores function to detect sounds or vibrations produced by invertebrate prey moving beneath the sand (Janssen 1990; Konings 1995). The role of lateral line cues in fish communication is an emerging topic of study (Butler and Maruska 2015, 2016; Weeg and Bass 2000; Weeg et al. 2005).

7.1 Background Noise Interference

Background noises due to pumps, filters, lights, and echoes in aquarium settings make it difficult to conduct critical experiments in small aquaria on how cichlid fishes produce and respond to sounds (Nelissen 1991). Acoustic recordings and playbacks made in an aquarium may be potentially misleading when interpreting specific acoustic characteristics of fish sounds because of reflections and reverberations against the walls (Akamatsu et al. 2002; Hawkins 1973). The type of aquarium wall materials may also have an impact on sound recordings (Parmentier et al. 2014).

Background noises (e.g., aquarium pumps and filters) sometimes appear as dark horizontal bands in sonograms (Nelissen 1978) and can mask part or all of a fish’s sound, making analysis difficult (Rowland 1978). The effects of constant aquarium noise on a cichlid’s development and behavior may also be a concern. Damage to fishes’ hearing can result from excessive noise (Banner and Hyatt 1973; Cox et al. 1987; Ha 1985; Popper and Clarke 1976). Experiments have shown that environmental noise reduces behavioral activity levels in a cichlid and could therefore also impact its acoustic display activity (Slabbekoorn et al. 2012).

The influence of aquarium noises on fish hearing and communication is important to determine from three perspectives. First, how such noise affects acoustic recordings is an analytical issue. Second, it is a potential problem when interpreting behavior in an aquarium because we do not know how this noise may directly interfere by masking fish communication. Third, the direct effect on hearing and the development of hearing as fish are raised in captivity is an obvious concern. It is possible that fishes housed in high noise aquaculture and aquarium systems may have their hearing adversely impacted.

8 Future Directions

Two alternative (but mutually compatible) hypotheses have been proposed to explain rapid and extensive speciation of cichlids, one based on morphological plasticity and the other on sexual selection by female mate choice (Greenwood 1991). Morphological plasticity is inherent in cichlids and enables rapid anatomical changes, especially in the feeding mechanism of which the pharyngeal jaws are a key component (Liem 1973, 1991; Greenwood 1973, 1991). Alternatively, sexual selection is based upon female choice between variants in male features, most notably coloration (Dominey 1984; Seehausen et al. 1999) and bower (nest) height and shape (Stauffer and Kellogg 1996). The hypothesis debate is based, in part, upon the premise that anatomical changes in the pharyngeal jaws are not affected by sexual selection (Greenwood 1991). If, however, the pharyngeal apparatus is important for sound production as well as feeding, then some features of the morphology may be linked to sexual selection (as related to sound production) as well as trophic specialization. For female choice to function on this basis, different pharyngeal morphologies would be expected to produce sounds with different qualities. Preliminary observations of individual pulse waveforms among cichlids and pomacentrids reveal such differences. The evidence available to date indicates that sound production is an integral part of cichlid behavior, including courtship. However, before its role in the speciation process can be evaluated, the role of sound communication in mate selection needs to be determined. Darwin (1874; pp. 366–367) argued, “It is almost certain that in [fishes] sound producing instruments have, at least in some cases, been developed through sexual selection as a means for bringing the sexes together.” This hypothesis remains to be rigorously tested and although data is accumulating that suggests sounds do play an essential role in mate selection among cichlids, however, acoustics may not be the prime driver alone. Coincident signals of colors, fins and swimming, and odors may also be required to reinforce a female’s choice of a mate. Most simply, sound with behavior could serve to be an initial attention attracting display without any deeper content to the acoustic signal. These hypotheses are ready for experimental testing.

Acoustic signals are involved in much of the social and reproductive behavior of many animals, and the behavioral influence of sounds has been extensively studied in these terrestrial groups. In contrast, research, to date, on the acoustic communication of fishes has primarily focused on the description of sounds, sonic morphology, and definition of the contexts in which sounds are produced. Progress in the field of fish bioacoustics has lagged behind that of terrestrial systems mainly due to limitations of technology and the logistical difficulty of research in the underwater environment. Recent advancements have provided better tools to successfully conduct such studies and the number of fishes discovered making sounds has grown enormously in the last few decades (Rosenthal and Lobel 2006; Webb et al. 2008). Although it is now known that many fishes make sounds, only a limited number of studies have experimentally examined the behavioral significance of these sounds by using audio playback (Ladich 1997; Luczkovich and Keusenkothen 2007; Lugli 1997; Lugli et al. 2004; McKibben and Bass 1998; Myrberg et al. 1986; Myrberg and Riggio 1985; Rollo and Higgs 2008; Winn 1972; Yan and Popper 1991).

There is now ample evidence that cichlids, like many fishes, make distinct sounds associated with specific behaviors. The field of fish bioacoustics is making progress. However, to advance closer to the level of understanding that has been achieved in the studies of terrestrial animals, the next phase of research for fishes needs to focus on experiments using playback trials to determine on how sounds combined with visual and chemical cues are behaviorally relevant.

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