

Acoustic communication in fishes: Temperature plays a role

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Abstract

Temperature affects peripheral and central mechanisms of signal production and detection in ectothermic animals. This study reviews for the first time the effects of temperature on acoustic communication in fishes and analyses whether changes in sound properties are coupled to changes in auditory sensitivities. Effects of temperature on sound production have been studied in approximately one dozen families of teleosts. Calling activity increased or was unaffected by temperature, in the latter case probably because seasonal, daily and lunar rhythms also influence mating behaviour and calling. Sound characteristics (pulse repetition rate, fundamental frequency) are positively correlated with temperature if pulses are directly based on sonic muscle contractions. In fishes possessing other sonic mechanisms, the dominant frequency of their pulsatile pectoral sounds may increase as well. Auditory sensitivities were mainly determined in otophysines, which possess enhanced hearing abilities. Studies revealed that hearing increased with temperature, in particular at higher frequencies. We know close to nothing about whether temperature-dependent changes in sound characteristics are coupled to changes in auditory sensitivity or mate choice. Female midshipman toadfish appear to choose males based on call frequency, which varies with temperature. Future studies need to address several topics: (i) temperature effects on sound production have to be separated from other sources of variation; (ii) effects on hearing need to be studied in many more taxa; (iii) potential negative effects of global warming on acoustic communication (because of temperature coupling) need to be investigated because fish constitute a major source of protein for humans.

KEYWORDS

calling activity, fundamental frequency, hearing, pulse repetition rate, sound characteristics, temperature coupling

1 | INTRODUCTION

Sound detection and acoustic communication are affected by temperature in ectothermic animals such as fishes, in which body temperature depends on air or water temperature. Temperature affects physiological and metabolic processes including neuromuscular and sensory systems as well as behaviour (Brenowitz, Rose, & Capranica, 1985; Carey & Zelick, 1993; Fay & Ream, 1992; Fonseca & Correia, 2007; Oldfield, 1988). Among ectothermic vertebrates, temperature effects on calling and hearing are well known in anurans. Acoustic properties of sounds may depend highly (pulse rate) or moderately (call length, carrier frequency) on body temperature (Zweifel, 1968; Gerhardt, 1978; Gerhardt & Huber, 2002). Furthermore, the central nervous system of frogs includes auditory neurons which respond to particular rates of amplitude modulations depending on temperature. This selective sensitivity parallels the temperature-dependent shifts in pulse rates of mating calls and, subsequently, female choice (Brenowitz et al., 1985; Gerhardt, 1978; Hubl, Mohnke, & Schneider, 1977).

Fishes possess a large diversity of sound-generating mechanisms and produce a large array of vocalizations important in conflict resolution, territory and nest advertisement, mate choice and most likely predator defence (Amorim, 2006; Amorim, Vasconcelos, & Fonseca, 2015; Fine & Parmentier, 2015; Ladich & Fine, 2006; Ladich & Myrberg, 2006). Furthermore, fishes evolved a variety of sound-detecting mechanisms enabling them to hear conspecifics and heterospecifics including predators and prey (Ladich, 2014; Ladich & Schulz-Mirbach, 2016).

This study is the first review on our knowledge on the effects of temperature on calling activity, sound characteristics and auditory sensitivity in fishes. It also analyses whether temperature coupling exists in fishes between acoustic properties of sounds and hearing abilities, similar to frogs. The review draws attention to the importance of temperature effects on acoustic communication in fishes. Fishes are key elements in aquatic ecosystems and the major source of protein for many people. A rise in water temperatures due to global warming affects acoustic communication and thus potentially impacts reproduction and fish stocks in the long run. Topics for future research in this field are suggested and discussed.

2 | CALLING ACTIVITY

Calling activity at different temperatures has been investigated in representatives of several fish families (Table 1). This has either been done in the laboratory, in outdoor tanks or in the field. The various experimental set-ups and their outcomes are described and discussed below. The measured variability illustrates that differences between species, families and recording conditions need to be interpreted cautiously. In the laboratory, for example, experimental changes in temperature were accompanied by seasonal light cycles or by a constant 12 hour to 12 hour (12 hr: 12 hr) light cycle, with the latter being close to the natural photoperiod in tropical species but not to temperate zone species. Calling activity may additionally vary

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seasonally between different months, times of the day (day, dawn and dusk, night), lunar cycle or perhaps acclimation time in laboratory studies. This makes the description of temperature effects and comparisons between available studies even more challenging.

In general, the calling activity—defined here as the number of sounds produced per unit of time—increased in the majority of studies with rising temperature (Table 1). A lack of a temperature effect on calling activity does not exclude effects on sound characteristics (Table 2).

2.1 | Laboratory studies

Studies carried out in the laboratory can control parameters including the light cycle and isolate the effect of temperature on sound production. The Amazonian Striped Raphael catfish (*Platydoras armatulus*, Doradidae) produce more distress sounds at 30°C than at 22°C when hand-held during the day (Papes & Ladich, 2011). Photoperiods may affect calling activity in addition to temperature. The gudgeon (*Gobio gobio*, Cyprinidae), a small shoaling Eurasian cyprinid, emits creaking sounds during various behaviours such as digging, foraging, when disturbed or hindered, or during pursuit behaviour. The number of 10-min time periods during which a shoal of four fish produce creaking sounds is highest at 17°C (temperature range: 8–17°C) and during low-light hours (night) (Ladich, 1988).

Juvenile grey gurnards (*Eutrigla gurnardus*, Triglidae) produce grunts and knocks during competitive feeding. In contrast to the gudgeon, the sound production rate in juvenile grey gurnards is not associated with experimental temperatures but to light hours

TABLE 1 List of families and species in which calling activity has been investigated at different temperatures including a short description of correlations of calling activity to temperature and other factors. Seasonal light cycle indicates seasonal changes either in the laboratory or in the field. Systematics following Nelson, Grande, and Wilson (2016)

Species	Reference	Location: Temp. Range	Temperature and Calling activity	Light	Other factors and Calling activity
Gudgeon (<i>Gobio gobio</i> , Cyprinidae)	Ladich (1988)	Lab: 8–17°C	Creaks: increase	Seasonal	Calling: higher at night
Lined Raphael (<i>Platydoras armatulus</i> , Doradidae)	Papes and Ladich (2011)	Lab: 22, 30°C	drum. s.: increase	12:12 hr 1)	–
Atlantic cod (<i>Gadus morhua</i> , Gadidae)	Brawn (1961)	Lab: 4–17°C	Grunts: not corr.	Seasonal	Months: max. February–March: daily: increase with spawning after sunset
Oyster toadfish (<i>Opsanus tau</i> , Batrachoididae)	Maruska and Mensinger (2009)	Outdoor concrete tank: 14–25°C	Grunts: increase	Seasonal	pos. corr. with day length; pos. corr. with tidal amplitude difference
	Montie et al. (2015)	May River: 21–26°C	Boatwhistle: increase	Seasonal	Not corr. to salinity or depth
<i>Opsanus</i> sp.	Rice et al. (2016)	GA, NC: 13–30°C	Chorusing duration corr. to temp. below 20 and above 24°C	Seasonal	–
<i>Opsanus tau</i>	Ricci et al. (2017)	Harris Creek; 20–28°C	Boatwhistle: not corr.	Seasonal	Increase before sunrise and after sunset
	Monczak et al. (2017)	May River, 11–33°C	Boatwhistle: not corr.	Seasonal	Calling influenced by lunar phase: max. full moon; more frequent April/May
Lusitanian toadfish (<i>Halobatrachus didactylus</i> , Batrachoididae)	Amorim et al. (2006)	Tagus River: 10–23°C	Sound prod: pos. corr.	Seasonal	Sound prod. dropped end of July at high temperature
Painted goby (<i>Pomatoschistus pictus</i> , Gobiidae)	Vicente et al., 2015	Lab: 14–22°C	Drum rate: not affected	seas. 2)	
Jarboa terapon (<i>Terapon jarbua</i> , Terapontidae)	Schneider (1964)	Lab: 20, 25, 30, 33°C	drum. s, threat. s.: increase	6 hr light 3)	Increase when light turned on
Croaking gourami (<i>Trichopsis vittata</i> , Osphronemidae)	Ladich and Schleinzner (2015)	Lab: 25, 30, 35°C	Croak interval: decrease	12:12 hr 4)	–
Grey gurnard (<i>Eutrigla gurnardus</i> , Triglidae)	Amorim (2005)	Juveniles, lab: 5–12°C	s. prod. rate: not corr.	Seasonal	s. prod. rate highest at light hours when fish more active
Bullhead (<i>Cottus gobio</i> , Cottidae)	Ladich (1989)	Lab: 8, 13°C	Higher at 13°C	12:12 hr	s. prod. higher at night
Spotted weakfish (<i>Cynoscion nebulosus</i> , Sciaenidae)	Montie et al. (2015)	May River: 22–30°C	Knocks, clucks: increase	Seasonal	More calling in deeper water
	Montie et al. (2017)	Lab: 15–30°C 5)	Calling: pos. corr.	Seasonal	Calling incr. when light cycle shifted from 13.5 to 14.5 hr daily rhythm: start once light turned off, max. after 3 hr
	Monczak et al. (2017)	May River; 16–33°C	Calling: pos. corr.	Seasonal	Months: highest June–August incr. with day length. lunar phase: max. first quarter
Black drum (<i>Pogonias cromis</i> , Sciaenidae)	Rice et al. (2016)	GA, NC: 13–20°C	Chorusing assoc. with temp. below 20°C	Seasonal	Chorusing primarily at night
	Monczak et al., 2017	May River: 13–24°C	Calling: pos. corr.	Seasonal	

(Continues)

TABLE 1 (Continued)

Species	Reference	Location: Temp. Range	Temperature and Calling activity	Light	Other factors and Calling activity
Silver perch (<i>Bairdiella chrysoura</i> , Sciaenidae)	Monczak et al., 2017	May River: 12–28°C	Chorusing; pos. corr.	Seasonal	Months: peak calling in April
Red drum (<i>Sciaenops ocellatus</i> , Sciaenidae)	Montie et al. (2016)	Lab: 15–30°C 5)	Calling; pos. corr.	Seasonal	Daily pattern: max. in the evenings

12: 12 hr, 12 hour light to 12 hour dark cycle; drum., drumming; GA, Georgia; Lab, laboratory; NC, North Carolina; pos. corr., Positively correlated to temperature; prod., Production; s., sound; temp., Temperature; seas., Seasonal; threat., threatening.

1) Acclimation time (A.t.): 3 weeks. 2) A. t.: 24 hr. 3) A. t.: 18 hr. 4) A. t.: 2 d. 5) Reproductive season simulated.

when fish were more active (Amorim, 2005). The Atlantic cod (*Gadus morhua*, Gadidae) produces grunting sounds during aggressive and courtship behaviour as well as when frightened and chased. Analysis of calling activity from 4 to 17°C reveals no temperature effect but a seasonal and daily pattern (Table 1) (Brawn, 1961). The painted goby (*Pomatoschistus pictus*, Gobiidae) emits drum sounds during courtship. Again, the drum emission rate is not related to temperature (14–22°C) according to Vicente, Fonseca, and Amorim (2015). These studies in non-related taxa—namely the gurnard, cod and goby—reveal that the lack of a correlation does not depend on a particular behavioural context but likely on seasonal and daily patterns of foraging or reproductive behaviour.

In contrast, Schneider (1964) mentions that juvenile Indo-Pacific Jarbua terapon (*Terapon jarbua*, Terapontidae) emits many more agonistic sounds at 30°C than at lower temperatures (25 and 20°C), with an increase when light was turned on. Similarly, the territorial bullhead (*Cottus gobio*, Cottidae) produces more sounds at 13°C than at 8°C (Ladich, 1989). The increase in calling activity is based on a higher number of agonistic encounters and a higher number of calls per interaction (Figure 1a). In the croaking gouramis (*Trichopsis vittata*, Osphronemidae), sound intervals decrease with increasing temperature (Ladich & Schleinzner, 2015). Studies on sciaenids reveal an increase in calling with temperature and a seasonal and daily rhythm (Montie et al., 2017; Montie et al., 2016). The spotted weakfish (*Cynoscion nebulosus*, Sciaenidae) increases calling when the light cycle shifted to 14.5 hr and when light is turned off (Montie et al., 2017).

The periods during which fish were allowed to acclimate to experimental temperatures varied widely, ranging from a few hours (18 hr, Schneider, 1964) up to 3 weeks (Papes & Ladich, 2011) or have not been mentioned (Table 1). No study tested and compared different acclimation periods in the same species at the same temperatures. Thus, we do not know whether those fish acclimated for a longer period would emit more or fewer calls. Such a study was carried out only with regard to hearing and will be dealt with later (Wysocki, Montey, & Popper, 2009).

Several studies investigated sound production in the oyster toadfish (*Opsanus tau*, Batrachoididae) and reported conflicting results. Grunts, which are typically uttered during agonistic interactions (Maruska & Mensinger, 2009), increased in number with rising temperature as well as with day length and maximum tidal amplitude in an outdoor concrete tank (Table 1). Montie, Vega, and Powell (2015) note an increase in the number of boatwhistles—the advertising calls of the oyster toadfish—in the May River, South Carolina, whereas Rice, Morano, Hodge and Muirhead (2016) observe that chorusing is related to temperatures below 20°C and above 24°C. No such correlations to temperature are described at other locations. Instead, Monczak, Berry, Kehrner, and Montie (2017) and Ricci, Bohnenstiehl, Eggleston, Kellogg, and Lyon (2017) mention seasonal, lunar and daily calling rhythms as well as differences between recording locations (Montie et al., 2015) (Table 1). Amorim, Vasconcellos, Marques, and Almada (2006) observe seasonal patterns of emission of different sound types (croaks, grunt trains, boatwhistles) in Lusitanian toadfish (*Halobatrachus didactylus*, Batrachoididae); these patterns are significantly correlated to the temperature in the Tagus estuary, Portugal. The temperature dependency is, however, lacking at the end of the breeding season (Figure 1b).

Sound recordings were carried out in several species of sciaenids in the field, and they typically yield a positive correlation to temperature (Monczak et al., 2017; Montie et al., 2015) along with dependencies on water depth, seasonal, daily and lunar rhythm. Rice et al. (2016) found that chorusing occurs at night and at temperatures below 20°C (2016).

In summary, an unambiguous temperature dependency can be shown only when all other parameters (ecological, behavioural) are kept constant. Otherwise daily, seasonal (or lunar) factors related to mating and spawning behaviour may influence or obscure possible effects of temperature on calling activity.

3 | SOUND CHARACTERISTICS

Physical properties of sounds are typically affected by ambient temperature in ectothermic animals such as fishes and frogs, but to different degrees. This dependency is most often found in the temporal patterns of sounds. In sound duration, opposite effects were observed in different species or even within a species producing

2.2 | Sound recordings in the field

Sound recordings in the field lack certain limitations of laboratory studies but also have disadvantages. For example, it is unknown which and how many individuals are calling at the same time and how many have left a particular area in the meantime.

TABLE 2 Fish species in which temporal patterns of sounds have been investigated at different temperatures, including a short description of changes at higher temperatures. Note that the striped Raphael produces two different sound types by two different sound-generating mechanisms. Systematics according to Nelson et al. (2016)

Species	Reference	Temperatures	PRR/FF	PP	Duration
Speckled piranha (<i>Serrasalmus spilopleura</i> , Serrasalminae)	Kastberger (1981)	Lab: 22–32°C	PRR: increase		Decrease
Striped Raphael (<i>Platydoras armatulus</i> Doradidae)	Papes and Ladich (2011)	Lab: 22, 30°C	drum. s.: FF increase	Decrease	No change
				Min AB: decr.	Shorter
<i>Pollimyrus adspersus</i> (Mormyridae)	Crawford, Cook, and Heberlein (1997)	Field: 26–29°C	Moan: PF increase ^{a)} Grunt: PRR increase		
Oyster toadfish (<i>Opsanus tau</i> , Batrachoididae)	Fine (1978)	Field: 17.6–25°C	FF: increase		Not correlated ind. var.
	Edds-Walton et al. (2002)	Field: 16–17, 22–22°C	Boatwhistle.: PRR increase, ind. var.		
	Maruska and Mensinger (2009)	Field: 14–25°C	Grunts: FF increase		
	Rice et al. (2016)	GA, NC: 13–30°C	Boatwhistle: FF increase		
	Ricci et al. (2017)	Harris Creek; 20–28°C	Boatwhistle: FF increase		
Lusitanian toadfish (<i>Halobatrachus didactylus</i> , Batrachoididae)	Amorim et al. (2006)	Field: 10–23°C	Boatwhistle: FF increase	Decrease	Increase
			Grunt train: FF increase	gr. period: decrease	Not correlated.
				Croak: PP incr.	Croak: decr.
Plainfin midshipman (<i>Porichthys notatus</i> , Batrachoididae)	Brantley and Bass (1994)	Lab: 14–26°C (hums)	Hums: FF increase		
		Lab: 10–19°C (grunts)	Grunts: FF increase		
Padanian goby (<i>Padogobius bonelli</i> , Gobiidae)	Torricelli, Lugli, and Pavan (1990)	Lab: 15–12°C	FF: increase		Increase
Arno goby (<i>Padogobius nigricans</i> , Gobiidae)	Lugli, Torricelli, Pavan, and Miller (1996)	Lab: 16–18, 19–21, 22–24°C	FF: increase	Seasonal	Decrease
Painted goby (<i>Pomatoschistus pictus</i> , Gobiidae)	Vicente et al. (2015)	Lab: 14–22	PRR: increase	PP decrease	Decrease
Croaking gourami (<i>Trichopsis vittata</i> , Osphronemidae)	Ladich and Schleizer (2015)	Lab: 25, 30, 35°C		BP/PP decrease	Decrease
Jarbua terapon (<i>Terapon jarbua</i> , Terapontidae)	Schneider (1964)	Lab: 20, 25, 30, 33°C	freq. deeper at lower temperature	Decrease	
Northern searobin (<i>Prionotus carolinus</i> , Triglidae)	Connaughton (2004)	Lab: 15–17.5°C	FF: increase		Not correlated
Grey gurnard (<i>Eutrigla gurnardus</i> , Triglidae)	Amorim (2005)	Lab: 5–12°C		Grunt: decrease	Increase
				Knock: decr.	Decrease
Squeteague (<i>Cynoscion regalis</i> , Sciaenidae)	Connaughton et al. (2000, 2002)	Lab: 12, 18, 24°C	drum. s. PRR incr.		

Min AB, min PP in stridulatory sounds produced during abduction of pectoral spine; BP, burst period; decr., decrease; drum. s., drumming sounds; FF, fundamental frequency; freq., frequency; gr., grunt; ind. var., individual variation; PF, peak frequency; PP, pulse period; PRR, pulse repetition rate; strid. s., stridulatory sounds.

^a Defined as contraction rate of sonic muscles. For acclimation periods, see Table 1.

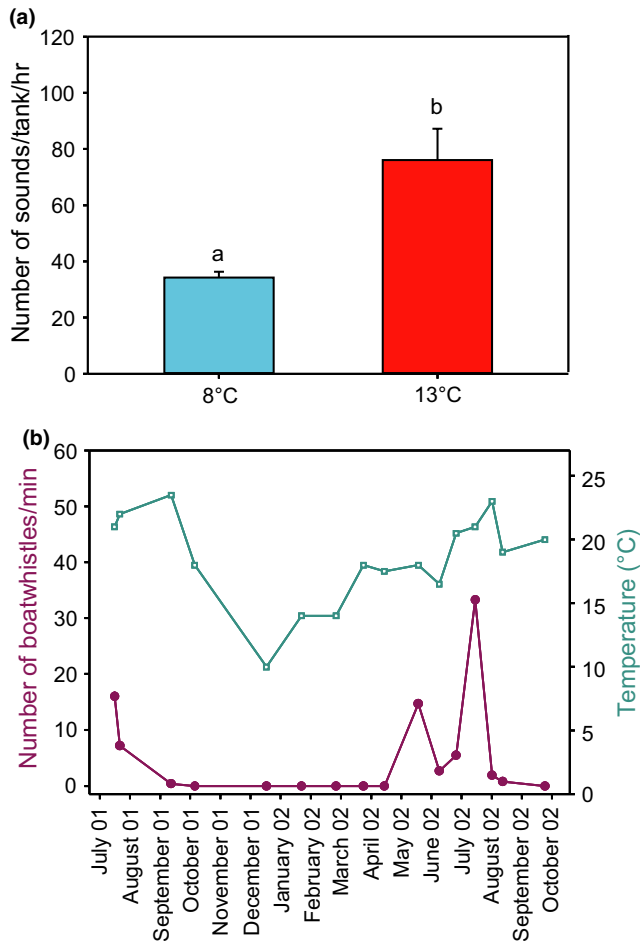


FIGURE 1 (a) Mean number of sounds produced per hour by three bullheads during agonistic interactions at two temperatures ($N = 12$). (b) Mean number of boatwhistles (filled circles) emitted by the Lusitanian toadfish from July 2001 to September 2002 in Tagus estuary, Portugal. Squares show temperature during recordings. Drawings based on Ladich (1989) and Amorim et al. (2006) [Colour figure can be viewed at wileyonlinelibrary.com]

different sound types. The relationship between dominant frequencies (frequency with greatest amplitude) or sound pressure levels and temperature is less clear, mainly because these two sound characteristics have rarely been investigated.

3.1 | Temporal patterns of sounds

Fishes evolved a variety of sound-generating mechanisms which may be classified according to the organs involved into swim bladder, pectoral and head mechanisms (Fine & Parmentier, 2015; Ladich, 2014; Ladich & Fine, 2006; Ladich & Winkler, 2017). Swim bladder mechanisms are the most widespread type among fishes and consist of fast-contracting muscles, called drumming (sonic or vocal) muscles, which vibrate the swim bladder. This can occur directly when drumming muscles are either entirely or partly attached to the bladder, or indirectly when muscles are entirely detached and vibrate the bladder via tendons or bones (Ladich & Bass, 2011). Pectoral sounds are produced by the pectoral fins or the pectoral girdle in

fishes that possess either well-developed, tiny or even no swim bladders, such as adult sculpins (Ladich, 1989). Head mechanisms are based on friction of bones such as in the seahorse (*Hippocampus* sp., Syngnathidae) (Colson, Patek, Brainerd, & Lewis, 1998). No clear pattern in the occurrence of sonic mechanisms exists among different taxa; some species such as several catfishes or seahorses may exhibit two different types of mechanisms, other species none at all (Fine & Ladich, 2003; Oliveira, Ladich, Abed-Navandi, Souto, & Rosa, 2014).

Independent of the sound-producing mechanism, all fish sounds are built up of pulses produced either singly (seahorse), continuously over some time (even up to 1 hr in the plainfin midshipman *Porichthys notatus*, Batrachoididae), or in different regular or irregular patterns (Amorim, 2006). In drumming sounds, each cycle typically reflects one muscle contraction. Muscle contractions can be amalgamated into individual pulses, trains of pulses or continuous long duration tonal sounds. Temporal patterns of pulses within sounds are almost always correlated to the temperature if they are based directly on contractions of sonic muscles. The pulse repetition rate (PRR) and fundamental frequency (FF) will increase, and the pulse period (PP, time between the onset of two successive pulses following one another) decreases when the temperature rises (Table 2). Large individual variation, however, was described in the PRR and sound duration of the oyster toadfish's mating calls at the same temperature (Edds-Walton, Mangiamale, & Rome, 2002; Fine, 1978).

The striped Raphael as well as representatives of several other catfish families possesses two fundamentally different sound-generating mechanisms (Fine & Ladich, 2003; Ladich & Fine, 2006): a swimbladder mechanism in which a bony plate vibrates the swim bladder when a drumming muscle contracts and moves this plate rapidly (elastic spring mechanism), and a pectoral stridulatory mechanism consisting of an enhanced first fin ray (pectoral spine) which is rubbed in a groove of the shoulder girdle and produces a series of short pulses. Swimbladder vibrations result in the emission of low-frequency drumming sounds with fundamental frequencies (muscle contraction rate) of 70 to approximately 300 Hz (Figure 2a). The FF is highly temperature-dependent, ranging from approx. 70 Hz at 22°C to 100 Hz at 30°C in the striped Raphael (Figure 2b).

Representatives of numerous families show a strong dependency of muscle contractions rates (PRR, FF, PP) on temperature (Table 2). This is because muscle contraction is controlled by the discharge rate of the sonic motoneurons (Bass & Baker, 1991) located in the brainstem and spinal cord (Bass, Chagnaud, & Feng, 2015; Ladich & Bass, 2005, 2011). The sonic motoneuron discharge rate is highly temperature-dependent as demonstrated in the midshipman, oyster toadfish, the non-related Pacific staghorn sculpin (*Leptocottus armatus*, Cottidae) and the northern searobin (*Prionotus carolinus*, Triglidae) (Bass & Baker, 1991), and most likely in all species possessing sonic muscles in which one muscle contraction results in a single cycle of a sound. In addition, the Ca^{2+} uptake rate of the sarcoplasmic reticulum of the sonic muscle correlates with temperature, which helps to drive a higher FF (Feher, Waybright, & Fine, 1998).

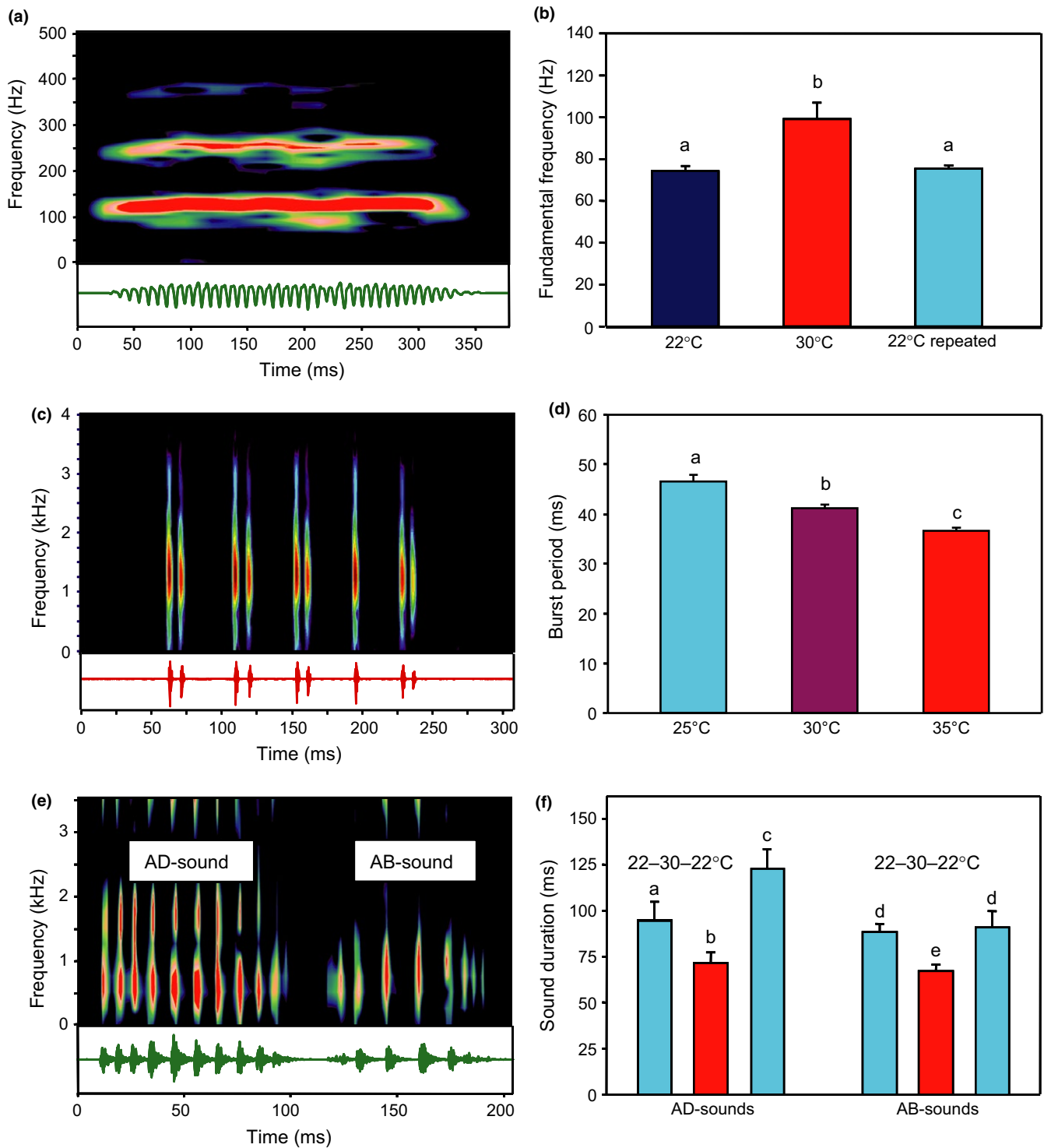


FIGURE 2 Sonograms and oscillograms of sounds (left column) of stenothermal fish species possessing different sound-generating mechanisms. Right column: effects of temperature on sound characteristics. (a) Drumming sound of a striped Raphael recorded at 30°C. The main energy is concentrated in a fundamental frequency (FF) at ~100 Hz. (b) Mean (+SE) FF of drumming sounds recorded at 22°C, 30°C and again at 22°C: FF increases significantly with temperature ($N = 8$ at 30°C and $N = 5$ at 22°C). Modified from Papes and Ladich (2011). (c) Croaking sound produced by croaking gouramis during agonistic interactions consisting of four double-pulsed and one single-pulsed burst, each one produced by one pectoral fin. (d) The mean (+SE) burst periods at different temperatures decreased significantly ($N = 11$). Modified from Ladich and Schleinzner (2015). (e) Stridulatory sounds in a striped Raphael produced during adduction and abduction of one pectoral spine. Note the large variability in pulse periods within and between sounds. (f) Mean (+SE) duration of AD- and AB-sounds illustrating that stridulatory sounds become shorter at the higher temperature and that duration may differ at the same temperature (AD-sounds at 22°C) ($N = 8$). Modified after Papes and Ladich (2011) [Colour figure can be viewed at wileyonlinelibrary.com]

In the croaking gourami, croaking sounds are produced when enhanced pectoral fin tendons are stretched and plucked similar to guitar strings. Typically two tendons per fin are plucked, yielding series of double-pulsed (seldom single-pulsed) bursts when pectoral fins are beaten alternately (Figure 2c). Burst periods (and PPs within bursts) decrease with increasing temperature, and as the discharge rate of sonic motoneurons strongly depends on temperature (Bass & Baker, 1991), the two effects are likely correlated (Figure 2d) (Ladich & Fine, 1992; Ladich & Schleizer, 2015).

In contrast to the mechanisms described above, the relationship between pulse patterns and temperature is less straightforward in pectoral stridulatory mechanisms in catfishes. The sweep of one pectoral spine, and thus one pectoral muscle contraction, results in a series of pulses of different PP (Figure 2e) (Fine & Ladich, 2003; Knight & Ladich, 2014; Parmentier et al., 2010). Analyses of minimum and maximum PPs of sounds produced during abduction (AB-sound) and adduction (AD-sound) of pectoral spines in the striped Raphael reveal that only one of four PP-measures shows a temperature dependency (Papes & Ladich, 2011).

The total duration of acoustic signals is expected to become shorter at higher temperatures because pulses and PPs become shorter due to the higher muscle contraction rates. Most studies seem to fit this assumption (Table 2). For example, stridulatory sounds in the striped Raphael are shorter at 30°C than 22°C (Figure 2f) (Papes & Ladich, 2011). Nevertheless, such a relationship may be lacking or may be reversed or may even show different trends within one species. In the striped Raphael, sound duration may differ even at the same temperature when experiments are repeated (Figure 2f, AD-sound) or may not be affected at all (drumming sounds). In the grey gurnard grunt, duration increases and knock duration decreases with temperature (Table 2) (Amorim,

2005). Among toadfishes, an increase, decrease and lack of a correlation were reported depending on species and sound types (Table 2).

3.2 | Dominant frequency and sound pressure level

In drumming sounds, the main energy occurs in the FF (the muscle contraction rate) (Figure 2a) or a multiple of the FF (e.g. the second or the third harmonic). In short pulsatile sounds such as pectoral sounds of catfishes or croaking gouramis or chirp sounds of the bicolor damselfish (*Stegastes partitus*, Pomacentridae), the main energies do not reflect sonic muscle contraction rate but rather size and thus resonance properties of structures within fish (e.g. the swim bladder in bicolor damselfish according to Myrberg, Ha, & Shablott, 1993). More recently, Colleye, Nakamura, Frédérick, and Parmentier (2012) suggested that resonant sounds result from vibration of the rib cage in the yellowtail clownfish (*Amphiprion clarkii*, Pomacentridae). In species generating pulsatile sounds, the main energies are often concentrated at frequencies above 500 Hz or even 1 kHz (Figure 2c,e) (Table 3). In the croaking gourami, the dominant (peak) frequencies increases with temperature (Figure 3), but no such effect was observed in the painted goby (Vicente et al., 2015).

The sound pressure level of sounds has seldom been measured at different temperature (Table 3). Studies on the speckled piranha (*Serrasalmus spilopleura*, Serrasalminidae) and squeteague (*Cynoscion regalis*, Sciaenidae) revealed that sound levels increase with temperature (Connaughton, Taylor, & Fine, 2000; Kastberger, 1981). No such increase was reported in other studies in which sound levels were determined (Table 3). Higher sound levels are most likely due to larger muscles and faster muscle contraction rates and thus an increase in volume velocity at higher temperatures (Fine & Waybright, 2015).

TABLE 3 Fish species in which dominant frequency and sound pressure levels have been investigated at different temperatures including a brief description of changes at higher temperatures. Systematics according to Nelson et al. (2016)

Species	Reference	Temperatures	Dominant frequency	Sound pressure level
Speckled piranha (<i>Serrasalmus spilopleura</i> , Serrasalminidae)	Kastberger (1981)	22–32°C		Increase
Striped Raphael (<i>Platydoras armatulus</i> , Doradidae)	Papes and Ladich (2011)	Lab: 22, 30°C	stridulatory s.: increase	Not affected
Painted goby (<i>Pomatoschistus pictus</i> , Gobiidae)	Vicente et al. (2015)	Lab: 14–22	Not affected	Not affected
Croaking gourami (<i>Trichopsis vittata</i> , Osphronemidae)	Ladich and Schleizer (2015)	Lab: 25, 30, 35°C	Increase	
Northern searobin (<i>Prionotus carolinus</i> , Triglidae)	Connaughton (2004)	15–17.5°C		No correlation
Grey gurnard (<i>Eutrigla gurnardus</i> , Triglidae)	Amorim (2005)	Lab: 5–12°C	Grunt: peak freq. increase Knocks: peak freq. increase	
Squeteague (<i>Cynoscion regalis</i> , Sciaenidae)	Connaughton et al. (2000, 2002)	12, 18, 24°C	Increase	Increase

freq., frequency; s., sound.

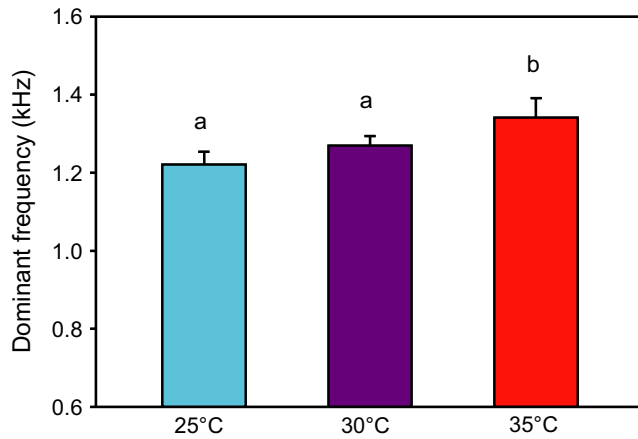


FIGURE 3 Mean (+SE) dominant frequencies of croaking sounds in croaking gouramis showing a significant increase between 25 and 35°C ($N = 11$). Modified from Ladich and Schleizer (2015) [Colour figure can be viewed at wileyonlinelibrary.com]

3.3 | Temperature-independent (seasonal) changes in sound production

While many studies revealed a relationship between calling activity/sound characteristics and temperature, several studies failed to report such a relationship (cod—Brawn, 1961; oyster toadfish—Monczak et al., 2017; Ricci et al., 2017; Lusitanian toadfish—Amorim et al., 2006). A drop in the calling activity of the Lusitanian toadfish in late July despite high temperatures (Figure 1b) most likely reflects seasonal androgen changes according to the authors (the effects of sex steroids on fish acoustic communication are reviewed in Maruska & Sisneros, 2015). A correlation between calling activity and temperature is furthermore lacking in representatives of gobiids and triglids (Amorim, 2005; Vicente et al., 2015). In the painted goby, temperature does not affect the drum emission rate, but there is a clear decrease in sound duration and PP at higher temperatures (Vicente et al., 2015).

Sound characteristics may vary significantly between individuals at the same temperature. Fine (1978) and Edds-Walton et al. (2002) describe large variation in the PRR and sound duration of the oyster toadfish's mating calls, assuming that these may help to distinguish individuals when multiple males are present during mate choice.

In tropical regions where the photoperiod is constant and temperature fluctuates minimally throughout the year, fish vocalizations may also reveal seasonal changes in sound features. Borie, Mok, Chao, and Fine (2014) characterize sounds in the South American silver croaker (*Plagioscion squamosissimus*, Sciaenidae) in the Central Amazon and find clear differences in advertisement calls emitted in the mating and outside the mating season (where bursts are shorter and consist of fewer pulses). Thus, equatorial fishes must rely on seasonal cues that differ from those experienced by species in temperate zones, such as water depth (wet and dry season). They can then adapt their mating activity and calling behaviour accordingly.

4 | AUDITORY SENSITIVITIES

4.1 | Auditory thresholds

Temperature-dependent changes in hearing have (with one exception) been determined only in otophysines, a fish taxon characterized by auditory (Weberian) ossicles (Weber, 1819, 1820). The Weberian ossicles increase their auditory sensitivity and detectable frequency range compared with taxa lacking any accessory hearing structures (Ladich & Schulz-Mirbach, 2016). Dudok van Heel (1956) observes a broadening of the range of pitch detection at higher temperatures in the Eurasian minnow (*Phoxinus phoxinus*, Cyprinidae). The upper limit of pitch discrimination rise from 1,260 Hz at 16°C to 1,420 Hz at 25°C. Changes in thresholds were not analysed.

In the goldfish (*Carassius auratus*, Cyprinidae), Fay and Ream (1992) observe an increased responsiveness and lower thresholds of saccular nerve fibres, along with an upshift of the fibre's best frequency, with increasing temperature. This finding of lower thresholds with increasing temperature matches with subsequent studies in otophysines using the auditory evoked potential (AEP) recording technique. The AEP technique allows non-invasive electrophysiological measurements of auditory sensitivities in which entire audiograms can be determined (Ladich & Fay, 2013).

Recently, auditory thresholds were determined in representatives of three eurythermal (temperate zone) and two stenothermal (tropical zone) freshwater families and one marine species (Table 4). All species reveal an increase in auditory sensitivity with increasing temperature. The stenothermal striped Raphael shows an increase in sensitivity in the mid-to-high frequency range of up to 8 dB after 3 weeks of acclimation to 22 and 30°C (Figure 4a) (Papes & Ladich, 2011). Wysocki et al. (2009) observe a similar change in sensitivity in the stenothermal pictus cat (*Pimelodus pictus*, Pimelodidae). The authors find that sensitivity increases with increasing frequency by up to 5 dB at 4 kHz (Table 4).

While the changes in sensitivity were rather similar among the stenothermal catfish families (Doradidae, Pimelodidae), the differences were astonishing among eurythermal catfish families. Wysocki et al. (2009) describe a change in sensitivity of up to 20 dB in the eurythermal channel catfish (*Ictalurus punctatus*, Ictaluridae) when temperature is raised from 18 to 26°C (Figure 4b). In contrast, a much smaller increase (maximally 10 dB) is observed in the eurythermal Wels catfish (*Silurus glanis*, Siluridae) in a comparable temperature range (Figure 4c, Table 4) (Maiditsch & Ladich, 2014). In the channel catfish, a total increase of 36 dB is described between 10 and 26°C at 4 kHz (Wysocki et al., 2009).

In summary, raising the temperature by 8–10°C results in a sensitivity increase in maximally 10 dB in representatives of the silurid and cyprinid families belonging to two different orders of Otophysines (Table 4). Interestingly, in the ictalurid the increase was twice as high under comparable conditions. This major difference between the three eurythermal species (families) contradicts the assumption by Wysocki et al. (2009) that large sensitivity differences are expected in species physiologically adapted to tolerate a wide temperature

TABLE 4 Overview of bony fishes for which hearing thresholds were determined at different temperatures. Maximum increase in sensitivity (dB) between the lowest and highest temperature is shown, and frequency at which the highest increase was observed. Systematics according to Nelson et al. (2016)

Species	Reference	Temperature	Max increase	Remarks
Common carp (<i>Cyprinus carpio</i> , Cyprinidae) ^a	Maiditsch and Ladich (2014)	15, 25°C	7.1 dB (0.5 kHz)	Accl, 1st mes.
Wels catfish (<i>Silurus glanis</i> , Siluridae) ^a	Maiditsch and Ladich (2014)	15, 25°C	10.4 dB (0.5 kHz)	Accl, 1st mes.
Striped Raphael (<i>Platydoras armatulus</i> , Doradidae) ^b	Papes and Ladich (2011)	22, 30°C	7.5 dB (4 kHz)	Accl, 1st mes.
Channel catfish (<i>Ictalurus punctatus</i> , Ictaluridae) ^a	Wysocki et al. (2009)	10, 18, 26°C	36.4 dB (4 kHz)	Accl
Pictus cat (<i>Pimelodus pictus</i> , Pimelodidae) ^b	Wysocki et al. (2009)	22, 26, 30°C	5.2 dB (4 kHz)	Accl
Alaska pollock (<i>Gadus chalcogrammus</i> , Gadidae)	Mann et al. (2009)	5, 8, 10°C	21 dB (0.3 kHz)	Not accl., ^c

Accl, acclimation for 3 weeks; 1st mes., differences based on first measurement if thresholds were determined twice at a particular temperature,

^a Eurythermal, ^b Stenothermal. ^c One specimen measured at three temperatures during one trial.

range (eurythermal species in temperate zones) but not in species adapted to a narrow range (stenothermal species of tropical zone). Additional investigations in species living in different temperature regimes are required to clarify whether the change in sensitivity is larger in eurythermal vs. stenothermal species.

The study by Wysocki et al. (2009) is the first one showing that acclimation may affect auditory sensitivity in fish. Channel catfish acclimated for 3 weeks have higher auditory sensitivities than unacclimated ones after an increase in water temperature.

The only non-otophysine species investigated so far is the Alaska pollock (*Gadus chalcogrammus*, Gadidae). Mann, Wilson, Song, and Popper (2009) show in this gadid species an increase in sensitivity of 21 dB when the temperature raises from 5 to 10°C (Table 4). This value needs to be compared cautiously to the results in otophysines because it is based on a single specimen measured without acclimation to the temperature. Nevertheless, it indicates that a hearing improvement can be expected for otophysine and non-otophysine species independent of accessory hearing structures (Ladich & Schulz-Mirbach, 2016).

4.2 | Latencies

The latency, namely the time between the onset of a sound stimulus and the onset of the AEP, depends on temperature. Latencies in response to single clicks are significantly shorter at 25°C than at 15°C in common carp (*Cyprinus carpio*, Cyprinidae) and the Wels catfish (Maiditsch & Ladich, 2014). A similar trend towards shorter latencies at higher temperatures is reported in the stenothermal striped Raphael. Papes and Ladich (2011) show that the latency decreases in three of four AEP peaks at the higher temperature.

4.3 | Temperature-independent (seasonal) changes in auditory sensitivity

Auditory sensitivity can change during the course of the breeding season. Bhandiwad, Whitchurch, Colley, Zeddies, & Sisneros (2017)

and Sisneros (2009) show that the saccular sensitivity of different morphs of the plainfin midshipman was 8–13 dB higher in summer reproductive than in winter non-reproductive specimens. Such seasonal plasticity may enhance detection of males' mating calls by females during the breeding season. This change in auditory sensitivity seems to be oestrogen-dependent and independent of temperature because all experiments were carried out at constant temperature (14–16°C) in the laboratory.

Females of the social cichlid *Astatotilapia burtoni* (Cichlidae) are 10–13 dB more sensitive to low-frequency sounds (100–200 Hz) in the spectral range of male courtship sounds when they are sexually receptive compared to during the mouth-brooding parental (non-receptive) phase. These differences in thresholds are clearly independent of temperature (28°C) and depend primarily on circulating sex-steroid levels in females (Maruska, Ung, & Fernald, 2012).

5 | TEMPERATURE COUPLING BETWEEN SOUND CHARACTERISTICS AND FEMALE CHOICE

Optimization of acoustic communication requires that temperature-dependent changes in sound characteristics are paralleled by appropriate changes in auditory sensitivity. Gerhardt (1978) investigates which synthetic calls female gray treefrogs (*Hyla versicolor*, Hylidae) prefer at particular temperatures. He observes that gravid females choose call pulse rates of 15 per second at 16°C and of 24 per second at 24°C. Their choice corresponds to the properties of males' mating calls produced at the same temperature. Gerhardt (1978) terms this phenomenon "temperature coupling" and hypothesizes that the pattern-generating system and the pattern-recognition system share the same or similar neural networks. Brenowitz et al. (1985) demonstrate that the temporal tuning of auditory neurons in the midbrain shifts to higher rates when body temperature increases in the gray treefrog. This shift parallels the shift in the pulse rate of males' mating calls.

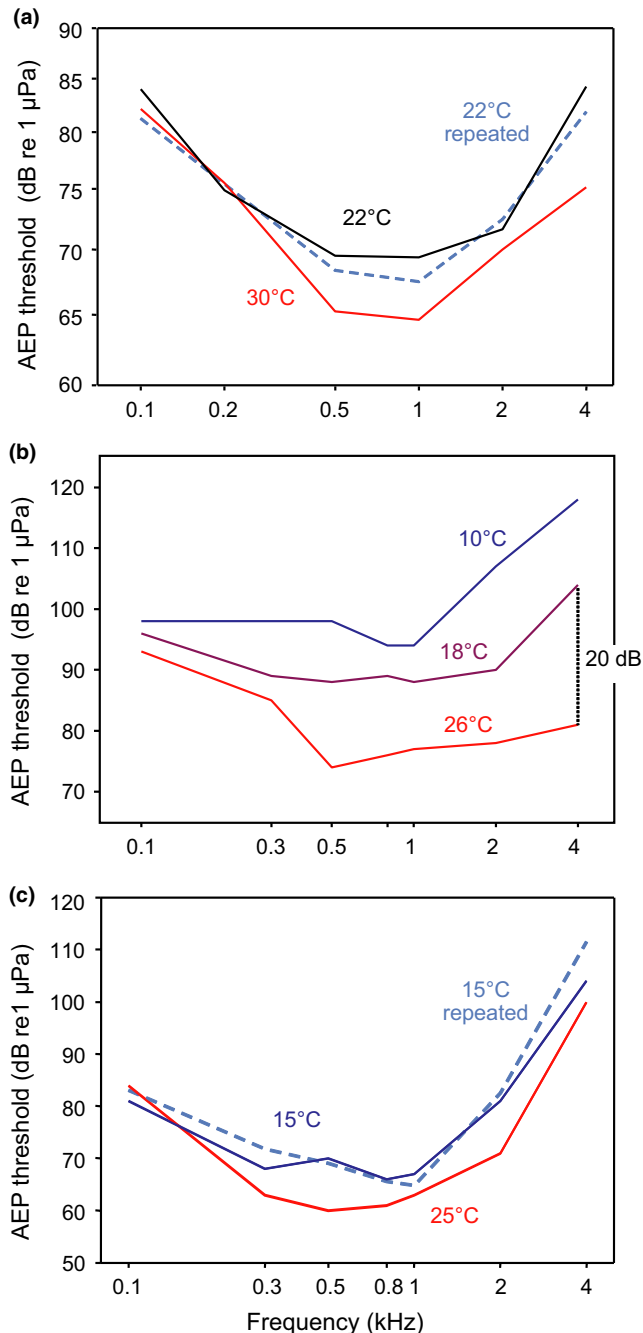


FIGURE 4 Mean auditory thresholds of stenothermal (a) and eurythermal (b, c) fishes after acclimation to different temperatures. (a) Striped Raphael after acclimation to 22, 30 and again 22°C (dashed line) for 3 weeks each ($N = 8$). Modified after Papes and Ladich (2011). (b) Channel catfish after acclimation to 10, 18 and 26°C ($N = 8-9$). Modified after Wysocki et al. (2009). (c) Wels catfish after acclimation to 15, 25 and again to 15°C (dashed line) ($N = 8$). Modified after Maiditsch and Ladich (2014) [Colour figure can be viewed at wileyonlinelibrary.com]

Does such temperature coupling exist in fishes? Temperature coupling between sound characteristics and female choice, indicating changes in auditory sensitivity, has so far only been demonstrated in one fish species. McKibben and Bass (1998) show in outdoor concrete tanks that gravid female plainfin midshipman prefer pure

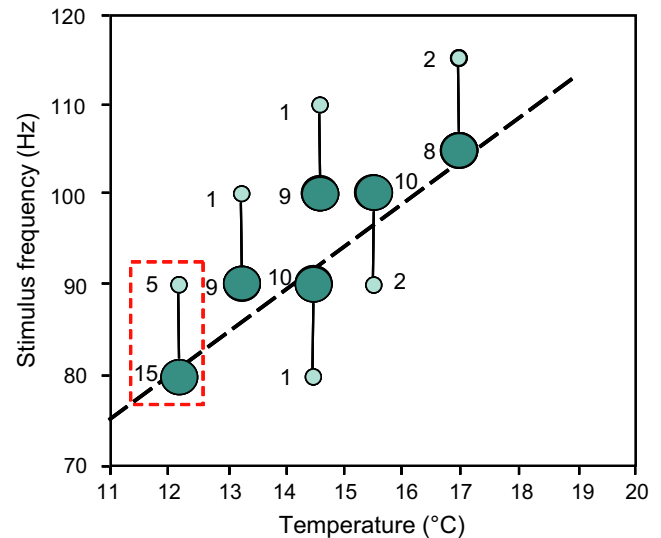


FIGURE 5 Number of female plainfin midshipman choosing a speaker playing back a particular stimulus frequency at different temperatures. Fifteen females preferred the 80 Hz tone at 12°C but only five chose the 90 Hz tone (dashed rectangle). At 14.5°C, females showed an opposite preference. Modified after McKibben and Bass (1998) [Colour figure can be viewed at wileyonlinelibrary.com]

tone stimuli which are similar to fundamental frequencies of males' mating calls (hums) at particular temperatures (Figure 5). When 80 and 90 Hz tones are played back simultaneously via two underwater speakers, females prefer the 80 Hz tone at 12°C and the 90 Hz tone at 14.5°C (Figure 5). The authors mention, however, that females will not encounter males whose sound frequencies differ by 10 Hz but signals will differ by less than 10 Hz at any one temperature in the field. This leaves the question open whether females choose according to frequency differences. Experimental data indicate that the most sensitive frequency of auditory neurons shifts upward with temperature in midshipman, similar to the situation in goldfish (Fay & Ream, 1992).

Crawford (1997) shows that midbrain auditory neurons in the weakly electric *Pollimyrus adspersus* (Mormyridae) are most sensitive to synthetic click trains with interclick intervals similar to that of natural sounds. This indicates that auditory temporal computation occurs in regions that are apparently homologous in fish, frogs and terrestrial vertebrates.

Wysocki and Ladich (2002) show that the minimum PP resolvable by the auditory system in various species possessing hearing specializations was below 1.5 ms. This enables otophysines and osphronemids (labyrinth fishes or gouramis) to process each pulse within a pulse series of intraspecific sounds. Papes and Ladich (2011) examine whether the temporal resolution increases with temperature. They analyse AEPs in response to double-click stimuli with varying click period (0.3–5 ms) in the striped Raphael at 22 and 30°C. Temporal resolution was determined by analysing the minimum resolvable click period at the two temperatures. The data show that the minimum resolvable click period in response to double-clicks is 0.8 ms and does not change with temperature (Figure 6).

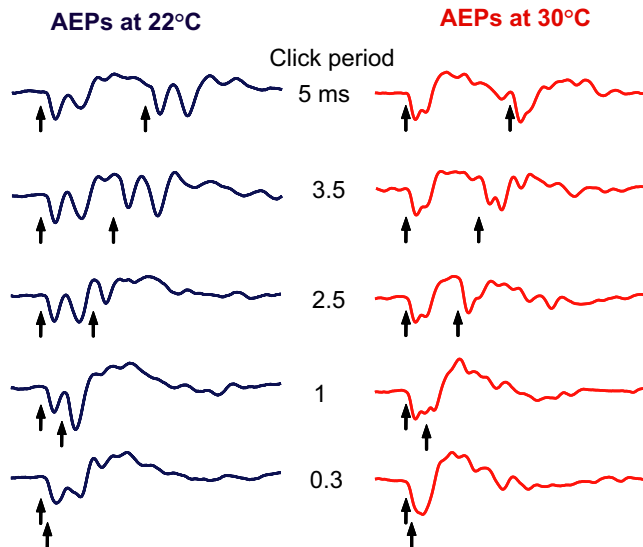


FIGURE 6 AEPs in response to double-click stimuli at 22 and 30°C of one striped Raphael. Arrows indicate the onset of each click within double-clicks of different click periods. Modified from Papes and Ladich (2011) [Colour figure can be viewed at wileyonlinelibrary.com]

6 | SUMMARY AND FUTURE RESEARCH

Our knowledge on the effects of ambient temperature on sound production, hearing sensitivity and on the coupling between both processes for optimization of acoustic communication is quite uneven in fishes.

The effects on calling activity have been described in approximately one dozen families and range from an increase with rising temperature up to no changes. Investigating the effect of temperature on calling activity unambiguously calls for laboratory experiments that keep all other ecological factors including photoperiod constant. Such studies are only possible when recording fish sounds in the field at the same time of the day at different temperatures. Temperature effects may be separated from other factors by measuring calling activity at constant temperatures and varying other factors such as light accordingly.

Temporal and spectral sound characteristics are typically affected by temperature, particularly when pulse rates (FF) are directly based on the contraction rate of sonic muscles. Sonic muscles are directly controlled by the discharge rates of sonic/vocal motoneurons and pacemaker neurons in the brainstem. Despite temperature-dependent physiological processes, considerable variability has been reported in PRR and sound duration at the same temperature, for example in the oyster toadfish (Edds-Walton et al., 2002). Factors behind this temperature independency in call features are an important topic for future research. Other sound characteristics such as dominant frequencies and sound pressure levels need to be measured more often to determine whether or why they do not depend on temperature.

Temperature effects on hearing were almost exclusively described in otophysines (cyprinids, catfishes). It is necessary to

investigate hearing in many more taxa, in particular in species lacking accessory hearing structures, to determine whether an increase in auditory sensitivity is a common feature in fishes. In addition, clarification is required as to whether stenothermal (tropical) species differ from eurythermal (temperate zone) species in their ability to adapt to different temperature regimes. Such studies should not be limited to audiograms but need to include temporal resolution in parallel to temporal patterns of sounds.

Acclimating fish for a particular period of time (hours, days) to particular temperatures may affect communication. While acclimation time does affect auditory sensitivity (Wysocki et al., 2009), it is not known whether it affects sound production. Such a study can be carried out only in the laboratory because it is impossible to control certain conditions in the field, such as identifying the number of individuals that are calling.

We know close to nothing about whether the numerous changes in sound characteristics are linked (coupled) to temperature-dependent changes in auditory sensitivities. Based on studies of other ectothermic taxa (frogs, insects), the assumption is that such a coupling exists to make sound communication more meaningful. If sound characteristics are used to assess a conspecifics' fitness, then animals must be able to separate changes in physical properties of sounds due to temperature from those due to fitness, for example size. So far, only one study is available, indicating that such a phenomenon exists in fishes (McKibben & Bass, 1998). In order to prove that temperature coupling exists, female choice needs to be tested at different temperatures in several non-related species.

Finally, are sound production and hearing in general—and temperature coupling in particular—affected by global warming in fishes? Munday, Hernaman, Dixon, and Thorrold (2011) and Bignami, Enochs, Manzello, Sponaugle, and Cowen (2013) argue that elevated CO₂ may affect otolith (calcareous structures within the inner ear) development in orange clownfish (*Amphiprion percula*, Pomacentridae) and cobia (*Rachycentron canadum*, Rachycentridae). Bignami et al. (2013) conclude that otoliths may increase in size, resulting in an increase in hearing range, but potential effects on temporal resolution and acoustic communication are not discussed. Narins and Meenderink (2014) argue that communication relies on the presence of both vocalizations and frequency-matched auditory receptors. They predict that the expected temperature change at the end of the century will effectively uncouple the sound production and detection systems in frogs if the most sensitive inner ear frequency in females does not track the male call frequencies. Based on these considerations, I suggest that fish taxa in which temperature coupling is an essential element of acoustic communication, temperature uncoupling may have deleterious effects on mating success. This may negatively affect their population biomass, potentially the entire food web and subsequently fisheries.

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