

Agonistic Behavior and Acoustic Communication

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ABSTRACT

Sounds are uttered in agonistic contexts by representatives of 30+ families of fishes but this number mainly reflects the scientific expenditure and less so the actual distribution of sound-producing families. Sounds are emitted in numerous contexts: distressful or disturbance-situations, e.g. being attacked or grabbed by predators, competitive feeding, and competition for space and sometimes mates. During dyadic contests, acoustical displays are part of a complex, signaling system, which includes visual and acoustical displays as well as physical fighting (biting, mouth-wrestling, ramming). Sounds are primarily uttered by the attacking animal during brief, intraspecific encounters or by both opponents during long contests and seldom by fleeing or submissive individuals.

A small number of experimental studies on the functional significance of sound production has shown that sound production can influence the course of the agonistic interactions, although the observations and interpretation are sometimes contradictory. The most likely explanation is that the acoustic signals help to assess the fighting ability of opponents and thus decide contests before they escalate to more costly phases (damaging combat). The ontogenetic development of sound production and agonistic behavior has been studied thus far in only a single species, the labyrinth fish *T. vittata*. Results showed changes in sound characteristics as well as the sequence of behavioral patterns.

Key Words: Distress calls; Competitive feeding; Agonistic sounds; Appeasement; Acoustic displays; Sound characteristics; Fighting ability assessment; Ontogeny; Evolution.

1. INTRODUCTION

Defending oneself or resources such as food, mates, and space (e.g. territories) is a widespread behavior with a clear survival value for the lives of animals. Defense and offense often begin with signals from different modalities, such as visual, acoustical or olfactory signals, before physical interactions occur. Producing signals represents an economic way for solving disputes over resources which are otherwise decided at much higher costs (injury, death). Numerous species of fishes emit sounds in these agonistic contexts.

Fishes often produce sounds also in distress or disturbance situations, e.g. when being caught, prodded or hand held. Distress sounds are not only uttered in an anthropogenic context, but toward piscine predators. Besides these interspecific, agonistic situations, numerous fishes produce sounds during aggressive, intraspecific encounters during competition. Low levels of aggression are observed during competitive feeding. Higher levels of aggression are shown while competing for mates and space. The current review is based on two reviews on this topic by Myrberg (1981) and Ladich (1997a). We provide here an overview of this field, describing agonistic behavior in more detail and adding new data on ontogenetic development and functional significance.

2. BEHAVIORAL CONTEXTS

2.1 Distress Situations

A large diversity of fish sounds was described up through the 1970s, when fish were handled, prodded, or netted. Fish and her coworkers used manual (e.g. holding their tails) and electric stimulation to determine the sound-producing abilities of a large number of Pacific and North Atlantic fishes (Fish et al., 1952; Fish and Mowbray, 1970). While Fish and Mowbray (1970) were unsuccessful in recording sounds in 11 cartilaginous species (seven families) from the North Atlantic and the Caribbean coasts, they were successful in recording sounds from numerous bony fishes. More than 200 species, from 48 families, emitted sounds. Although some of the sounds described were of questionable biological significance, particularly swimming sounds, air-release sounds, and those elicited under electric stimulation, the majority of sound recordings revealed that distress sounds are widespread among fishes.

Myrberg (1981) using additional sources, listed 37 families of marine fishes (and characins) whose members produce “startle” sounds in disturbing contexts, such as toward divers. Such sounds are similarly widespread among freshwater fishes. In fact, several investigations used the propensity of characids and catfishes of all sizes and sexes to produce sounds when hand held, to study sound generation, sound characteristics, and sonic mechanisms

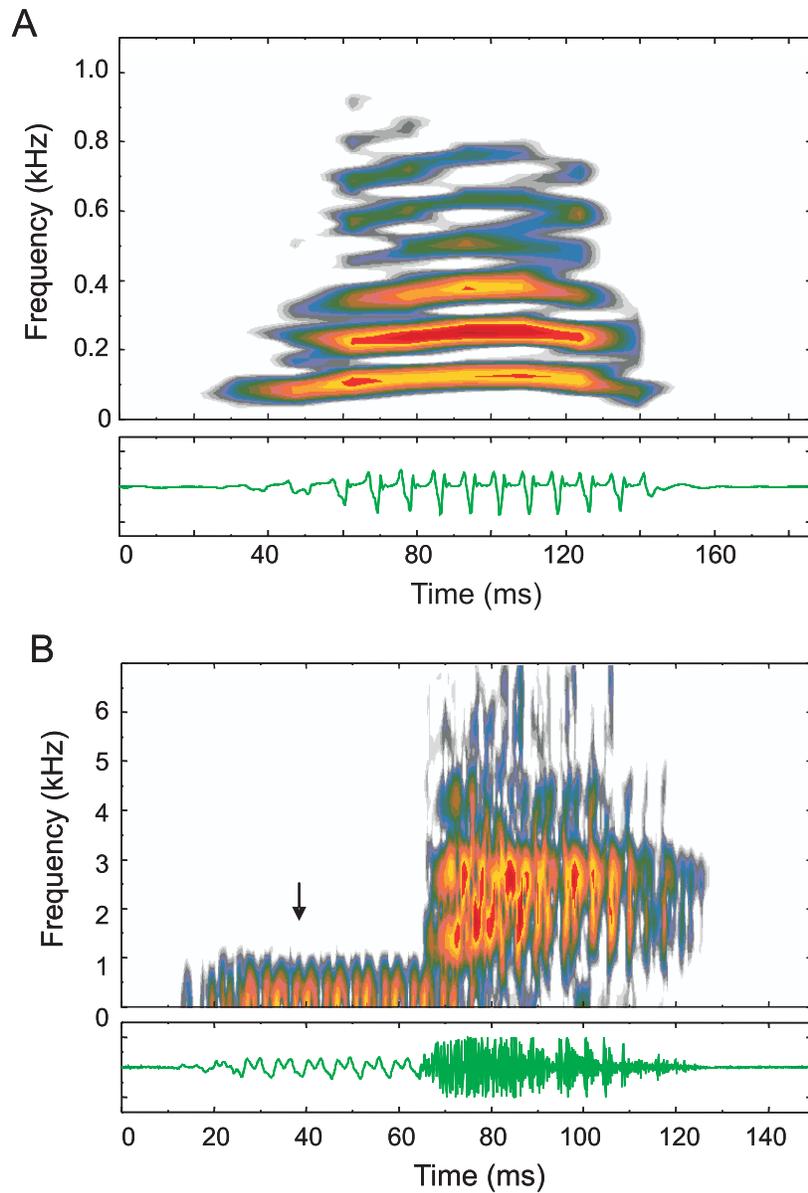


Fig. 5.1: Sonograms and oscillograms of sounds uttered in distress situations when hand held: A) drumming sound of a red-bellied piranha *Pygocentrus nattereri* (sampling frequency 16 kHz, filter bandwidth 30 Hz, overlap 50%), and B) drumming (arrow) and pectoral stridulation sound in the long-whiskered catfish *Pimelodus blochii*. (Sampling frequency 16 kHz, filter bandwidth 450 Hz, overlap 75%) both species from Amazonia. Note that the harmonic structure of the drumming sounds can be seen in the piranha but not in the catfish due to the large filter bandwidth in the latter.

(Pfeiffer and Eisenberg, 1965; Markl, 1971; Kastberger, 1981; Ladich, 1997b, 1999; Heyd and Pfeiffer, 2000) (Fig. 5.1A, B). Such comparative studies revealed interesting interfamilial as well as contextual differences in the production of distress sounds. Several tropical catfish families such as doradids, pimelodids, mochokids, ariids, and auchenipterids possess two sound-generating mechanisms: drumming muscles, which vibrate the swimbladder in various ways, and a pectoral stridulatory apparatus. The former mechanism induced the emission of low-frequency harmonic sound with main energies below 500 Hz, while rubbing of the pectoral spine in the grooves of the shoulder girdle leads to emission of a series of short, broadband pulses with main energies between 800 and 4000 Hz (Fig. 5.1B) (Fine and Ladich, 2003). In disturbance situations, both types of sounds are uttered to a different extent. Drumming sounds are of similar intensity as stridulatory sounds in pimelodids. The latter are much lower in intensity than the former in doradids and are lacking in mochokids (Ladich, 1997b). These differences are likely due to morphological constraints, e.g. relatively larger drumming muscles and smaller pectoral spines in pimelodids than doradids or mochokids. Intensity of stridulatory sounds was higher than that of drumming sounds in three of four species in air compared to water. The doradid *Platydoras costatus* and the pimelodid *Pimelodus blochii* produced significantly more stridulatory sound than drumming sounds in air. The high frequency content of pectoral sounds is mainly above the hearing abilities of many fish predators, e.g. cichlids, and can only be perceived by hearing specialists. Two different types of acoustic signals—low-frequency sounds and high-frequency sounds—might be an adaptation to the hearing abilities of predators (Ladich, 1997b).

Distress sounds have not only been registered by humans but in a few cases, against potential heterospecific predators as well. The long-spine squirrelfish *Holocentrus rufus* and the related soldierfish *Myripristis berndti* emitted grunts and staccato sounds against moray eels introduced into their territories (Winn et al., 1964; Salmon, 1967). Cods *Gadus morhua* were also observed to produce grunts toward a conger eel and click sounds in the presence of seals or human divers (Brawn, 1961; Vester et al., 2004). Myrberg (1981) noted that serranids produced drumbeats when sharks approached.

The functional significance of sound production against heterospecifics, in particular predators, can be derived from our knowledge of other taxa or from intuition. Fishes might try to deter or attract predators or alarm conspecifics. However, in no case have investigators observed predators that were startled or retreated when distress calls were emitted. This could be an effect of the somewhat artificial experimental situation encountered in the case cods and holocentrids or the fact that the sounds simply had no effect. Markl (1968) observed that stridulating sounds did not keep a doradid catfish from being eaten by a piranha. Distress calls could have an alarm function by warning conspecifics and thus helping them to seek protection and survive. This could increase the inclusive fitness of the sender, if protected conspecifics

are closely related to the sender or could represent altruistic behavior. A further explanation could be that distress calls function to attract additional predators that disrupt the predation event, allowing the prey an opportunity to escape. There exists evidence that this is the case with alarm substances in fishes and with distress calls in birds (Högstedt, 1983; Matthis et al., 1995; Chivers et al., 1996). Alarming conspecifics and heterospecifics has been shown in birds and mammals (Bradbury and Vehrencamp, 1998). Winn and colleagues (1964) observed that long-spine squirrelfish retreated in 7 of 11 experiments into crevices or remained there when staccato sounds were played back via underwater speakers. This reaction was nonspecific because holocentrids also responded to toadfish boat whistles. In summary, the functional significance of distress calls is still widely unproven and needs to be explored in more careful experimental setups.

2.2 Competitive Feeding

Foraging and competition for food most likely result in agonistic interactions among numerous fishes. Intraspecific encounters usually occur at a moderate level of aggression which means that disputes end quickly after a few behavioral acts. Sound production during competitive feeding was noted in the squirrelfish *Holocentrus ascensionis* and several serranids, such as by the Nassau grouper *Epinephelus striatus* (Fish and Mowbray, 1970). More detailed observations were performed on further nonrelated groups—cyprinids and gurnards—indicating that vocalization is widespread among fishes under these circumstances.

The European gudgeon *Gobio gobio* is a nonterritorial, shoaling cyprinid, which produces creaking sounds during various foraging contexts (Ladich, 1988). Sounds are emitted either singly or in a series of rapidly repeated pulses (Fig. 5.2A). Vocalization increases with the general level of activity at higher temperatures and shows no diurnal pattern. Gudgeons “called” in response to digging of other members of the group and a variety of disturbances such as being touched and hindered by conspecifics. In some cases, the disturbed individual swam aggressively around another individual, beating with its tail fin and emitting loud creaking sounds over a longer period. Neither fleeing nor chasing was observed after a gudgeon call (Ladich, 1988).

Gurnards regularly emitted knocks, grunts and growls during competitive feeding. The streaked gurnard *Trigloporus lastoviza* produces growling sounds during foraging (Amorim and Hawkins, 2000). Growls are trains of sound pulses lasting up to 3 s. Foraging fish usually circle the feeding area, often aggressively displaying to competitors, including vocalizations and grasping food items. Individuals that growl while circling are more likely to grasp food items than silent individuals. Gray gurnards produce a series of knocks of 6–12 ms duration while grasping food and fleeing. Grunts, approximately 70 ms in duration, are produced during approaching and chasing conspecifics and

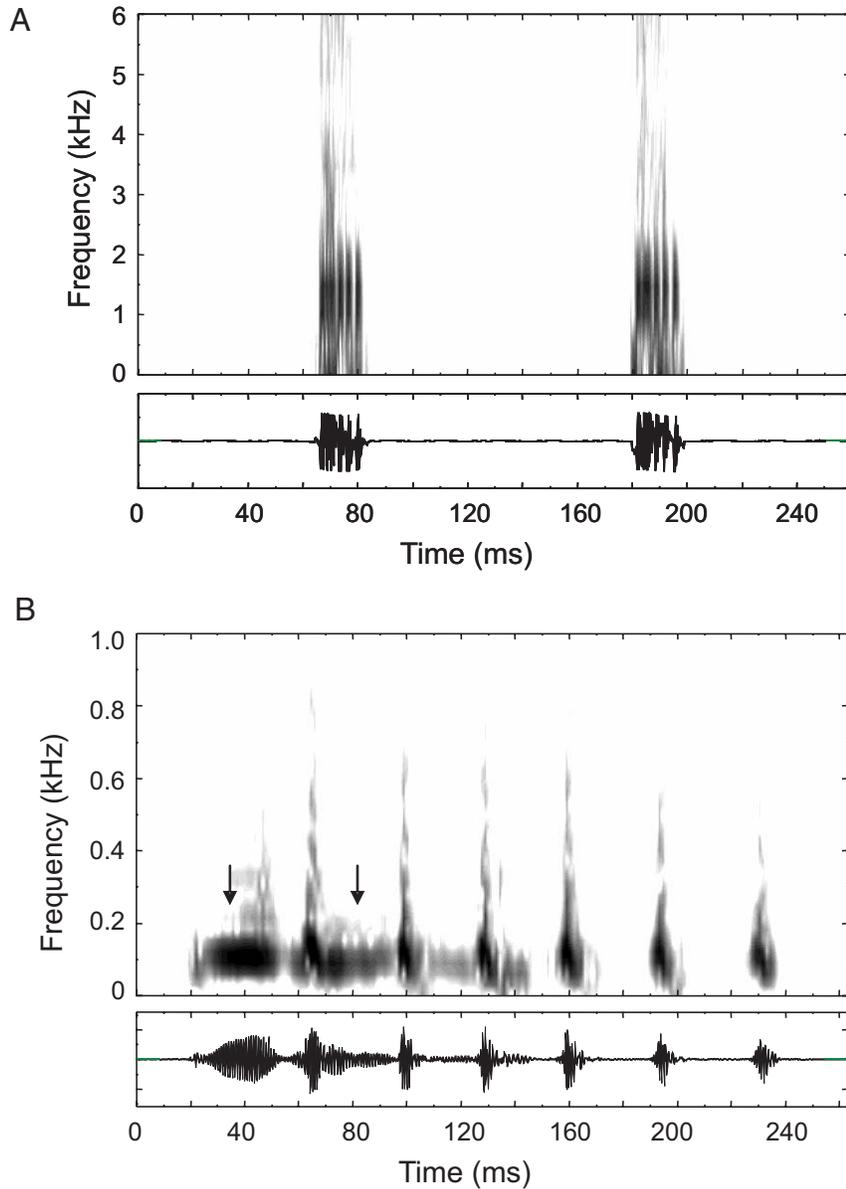


Fig. 5.2: Sonograms and oscillograms of sounds uttered during various agonistic contexts in fishes: (A) creaking sounds uttered by the European gudgeon *Gobio gobio* during competitive feeding (sampling frequency 32 kHz, filter bandwidth 500 Hz, overlap 75%) and (B) series of six short thumps and two longer moans (arrows) emitted by two bichir *Polypterus retropinnis*. The first two moans were produced by a submissive fish during retreat, while the series of thumps originate from the attacking fish. The first thump and the second moan overlap in time (sampling frequency 16 kHz, filter bandwidth 40 Hz, overlap 45%).

during frontal display (Fig. 5.3). The functional significance of these sounds remains unknown. Sound playbacks did not appear to have a significant effect on the frequency of any behavioral category (Amorim, 1996).

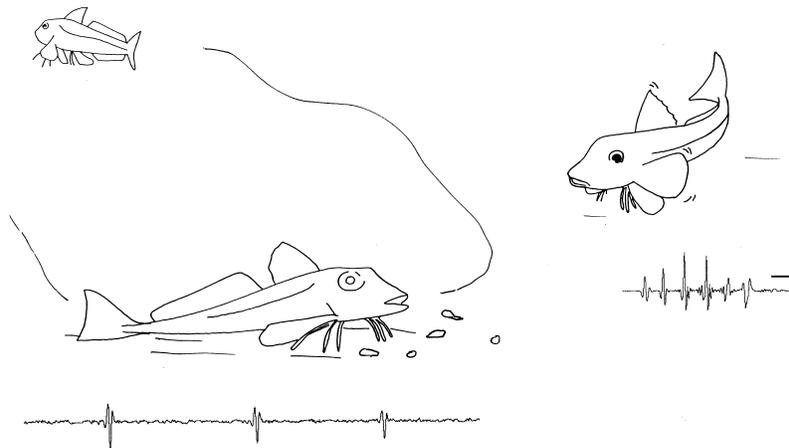


Fig. 5.3: Typical interaction between two gray gurnard *Eutrigla gurnardus* during competitive feeding. The left gurnard is producing knocks while grasping a food item and fleeing whereas the right fish emits a grunt during a frontal display. Note oscillogram of three single knocks produced by the left gurnard and a grunt "call" emitted by the right fish (from Amorim, 1996). Scale bar 10 ms.

2.3 Competition for Space

Fishes aggressively display toward conspecifics while establishing and maintaining territories. Such behavioral acts are often accompanied by sound production in numerous species. Aggressive interactions are not always associated with the monopolization of particular areas (territories); they can also serve to maintain distances between individuals within an aggregation. Salmon (1967) observed in the nonterritorial soldierfish *Myripristis berndti*, that smaller individuals are frequently chased by larger individuals emitting a series of knocks. The author hypothesized that maintaining distances decreased the likelihood of more than one individual being caught by predators.

High levels of aggression were usually displayed during competition over territories (Myrberg, 1972a). These aggressive encounters consisted either of simply chasing away an intruder or complex contests involving a series of different behavioral elements (displays) often following a predictable sequence. Contests can readily be staged in the laboratory and usually begin with the less costly displays, such as visual threats or sounds, followed by more costly bites and rams, likely incurring injury or death. Animals try to gain information about fighting abilities through assessing signals and solving conflicts without

escalated fighting (Krebs and Davies, 1993). Acoustic displays are frequently part of the first (low cost) phase of contests and have been observed in representatives of 30+ families of bony fishes (Table 5.1). The number of families is probably much higher because our list does not include uncountable reports in the aquarium literature.

Fighting behavior is described below in detail from laboratory observations in two nonrelated species to illustrate the differences in agonistic behavior and the sequences of displays. Agonistic interactions begin, in most cases, after an intruder comes into the range of vision of a territory owner. In a few cases, acoustic stimuli suffice to trigger threat displays. The European river bullhead *Cottus gobio* (family Cottidae) responds to the sight of an intruding conspecific by approaching to a distance of a few centimeters, raising its gill covers and branchial rays/membrane, spreading one or both pectoral fins, opening and protruding the mouth, darkening and lowering the head, and starting to nod (Fig. 5.4). A single nodding movement or a series thereof is always accompanied by the production of a single knock or a train of them, resembling a growl (Ladich, 1989). This sound is produced by contraction of the cephaloclavicular muscle (according to Barber and Mowbray, 1956), resulting in rapid adduction of the pectoral girdle relative to the skull. In this way, enlarging the ventral and lateral portions of the head stops abruptly at the moment of sound emission due to contraction of the *musculus cephaloclavicularis*, causing reduction in volume of the pharynx and deformation of the gill arches (Ladich, 1989). The intruder usually answers the threat by erecting its ventral fins (Fig. 5.4) and rapidly swimming away. If the intruder does not respond, both might start to threaten each other by visual and acoustic displays. Then, either one or both fish retreat or the territory owner lunges forward, bites the intruder, chases it for sometime in the tank and vocalizes. No difference was evident in the ability to emit sounds in the two sexes.

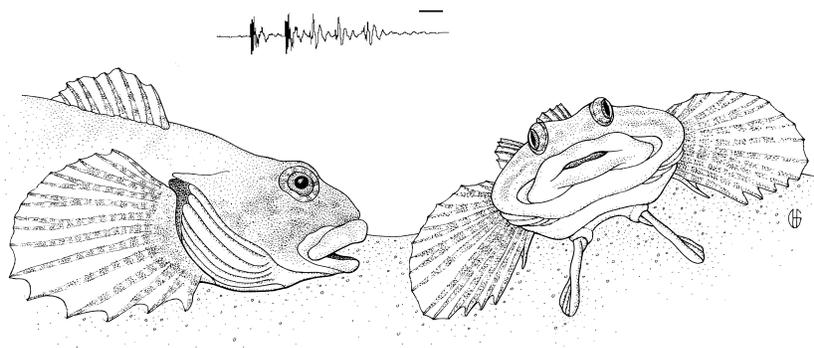


Fig. 5.4: Typical threatening posture in the river bullhead *Cottus gobio*. The left male is attacking an intruder, while spreading the opercular covers and darkening and vocalizing. Insert shows an oscillogram of a 5-pulsed growling sound (drawing by H.C. Grillitsch). Scale bar 50 ms.

Table 5.1: Systematic listing of families whose members produce sounds during intraspecific agonistic interactions. Distress or disturbance sounds emitted during handling or other manipulations are not included. Species, sound types and behavioral context according to authors. Table modified from Myrberg (1981) and Ladich (1997a). Taxonomy according to Nelson (1994).

Polypteridae, bichirs	<i>Polypterus retropinnis</i>	thumps by the attacker	Ladich and Tadler (1988)
Notopteridae, knife fishes	<i>Xenomystus nigri</i>	moans by the submissive fish	Benl (1957)
Mormyridae, elephant fishes	<i>Gnathonemus petersii</i>	grunting or barking sound	Rigley and Marshall (1973)
	<i>Pollimyrus adspersus</i>	click sounds, singly or in series	Crawford et al. (1986)
Cyprinidae, carps, minnows	<i>Notropis anostanus</i>	hoots and pops	Stout (1975)
		single or series of knocks during chasing, lateral display, mirror image	
	<i>Gobio gobio</i>	creaking sounds during foraging	Ladich (1988)
	<i>Pimephales notatus</i>	various bursts during aggressive encounters	Johnston and Johnson (2000)
Cobitidae, loaches	<i>Botia horae</i>	clicks against intruders	Valinsky and Rigley (1981)
	<i>Botia hymenophysa</i>	defense	Klausewitz (1958)
Ictaluridae	<i>Ameiurus nebulosus</i>	ratchet sound emitted by intruder and when being attacked	Rigley and Muir (1979)
Mochokidae, squeakers	<i>Synodontis schall</i>	deep grunt by the attacked fish	Abu-Gideiri and Nasr (1973)
Doradidae, thorny catfishes	<i>Platydoras</i> , <i>Agamyxis</i>	during cover site defense	Kaatz (1999)
Auchenipteridae	<i>Tatia</i> , <i>Trachelichthys</i>	during cover site defense	Kaatz (1999)
Pimelodidae,	<i>Rhamdia quelen</i>	drumming as threatening signal,	Schachner and Schaller (1981)
long-whiskered catfishes		stridulations as defense signal	
Callichthyidae	<i>Hoplosternum thoracatum</i>	aggressive sounds in fighting males, threat sounds in females	Mayr (1987)
	<i>Corydoras</i> spp.	high-pitched creaks during chases, low-pitched claps during pre-chase grunts during threatening and fleeing, both sexes	Kaatz and Lobel (1999)
Gadidae, cods	<i>Gadus callarias</i>		Brawn (1961)

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Table 5.1: (Contd.)

Batrachoididae, toadfishes	<i>Melanogrammus aeglefinus</i> <i>Gaidropsaurus mediterraneus</i> <i>Opsanus tau</i>	grunts during aggressive and defensive behavior, both sexes thumps—disputes over shelter sites	Hawkins and Rassmussen (1978) Almada et al. (1996)
	<i>Porichthys notatus</i>	grunt and growl—aggressive and threatening behaviour aggressive encounters	Tavolga (1960); Gray and Winn (1961); Winn (1967) Cohen and Winn (1967); Brantley and Bass (1994)
Cyprinodontidae, pupfishes	<i>Cyprinodon bifasciatus</i>	pursuits calls against territory intruders	Johnson (2000)
Holocentridae, squirrelfishes	<i>Holocentrus rufus</i> <i>Myripristis berndti</i>	grunts and staccatos in territorial defense, mobbing knocks when chasing smaller fish, growls during more aggressive interactions	Winn et al. (1964) Salmon (1967)
	<i>Myripristis violaceus</i>	thumps and grunts while tail beating and chasing conspecifics	Horch and Salmon (1973)
Scorpaenidae, rockfishes	<i>Sebastiscus marmoratus</i>	knock by invaders and defenders	Miyagawa and Takemura (1986)
Triglidae, searobins	<i>Trigloporus lastoviza</i> <i>Eutrigla gurnardus</i>	growling during competitive feeding knocks, grunts and growls during competitive feeding	Amorim and Hawkins (2000) Amorim (1996)
Cottidae, sculpins	<i>Cottus gobio</i>	knocks and growls to threaten away conspecifics, both sexes	Ladich (1989, 1990)
Serranidae	<i>Epinephelus striatus</i>	distinctive boom sounds during antagonistic encounters	Lobel (1993)
Sciaenidae, drums	<i>Corvina nigra</i>	knocks when male drives away males during courtship	Dijkgraaf (1947)

Terapontidae, grunters	<i>Therapon jarbua</i>	short aggressive drumming sounds and longer threatening sounds	Schneider (1964b)
Centrarchidae, sunfishes	<i>Lepomis</i> spp.	rasping sounds during aggressive interactions	Ballantyne and Colgan (1978)
Percidae, perches	<i>Etheostoma</i> spp.	drums, knocks and purrs during aggressive encounters, produced by males	Johnston and Johnson (2000)
Sparidae, porgies	<i>Lagodon rhomboides</i>	clicks produced in defense of territory	Caldwell and Caldwell (1967)
Oplegnathidae, knifejaws	<i>Oplegnathus fasciatus</i>	single or complex pop calls emitted against intruder	Nakazato and Takemura (1987)
Cichlidae, cichlids	<i>Hemichromis bimaculatus</i>	br-r sound before attacking an intruder, both sexes	Myrberg et al. (1965)
	<i>Pterophyllum</i> sp.	tzz-tzz sounds produced during ritualized fighting and prior to attacking	Myrberg et al. (1965)
	<i>Cichlasoma nigrofasciatum</i>	br-r sounds during frontal displays	Myrberg et al. (1965)
	<i>Cichlasoma centrarchus</i>	growling during aggressive encounters, both sexes	Schwarz (1974)
Pomacentridae, damselfishes	<i>Stegastes partitus</i>	pop during hostile encounters, chirp as keep-out signal	Myrberg (1972)
	<i>Stegastes planifrons</i>	pop sounds during hostile encounters	Thresher (1976)
	<i>Stegastes dorsopunicans</i>	pop sounds during hostile encounters	Burke and Bright (1972)
	<i>Stegastes xanthurus</i>	threatening and fighting sounds, shaking sound during submission	Schneider (1964a)

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Table 5.1: (Contd.)

	<i>Amphiprion clarkii</i>	aggressive staccato rattling by resident females	Moyer (1980)
	<i>Dascyllus albisella</i>	pops and multiple-pulse chirps during chasing	Mann and Lobel (1998)
Labridae, wrasses	<i>Symphodus cinereus</i>	same, during threatening	Protasov and Romanenko (1962)
Blenniidae, blennies	<i>Parablennius pilicornis</i>	knocks emitted during chasing	Amorim (1996)
Gobiidae, gobies	<i>Padogobius martensi</i>	agonistic sound during territorial defense, before fighting	Toricelli and Romani (1986), Torricelli et al. (1990)
	<i>Odontobutis obscura</i>	calls to threaten invaders	Takemura (1984)
	<i>Proterorhinus marmoratus</i>	during agonistic interactions, both sexes	Ladich and Kratochvil (1989)
Osphronemidae, gouramis	<i>Trichopsis vittata</i>	croaking sounds in fighting males	Ladich et al. (1992a); Ladich (1998)
	<i>Colisa lalia</i>	tone bursts and chirps in fighting males	Schuster (1986)
Ostraciidea, boxfishes	<i>Ostracion meleagris</i>	buzz sound—males attacking spawning pairs	Lobel (1996)

Males of the croaking gourami *Trichopsis vittata*, a southeast Asian air-breathing labyrinth species (Anabantoidei), defend their breeding sites via complex behavioral actions. Staged, dyadic contests begin when one or both fish approach one another with spread, unpaired fins (= lateral displaying) and circling. As soon as individuals are close to each other in an antiparallel position, they rapidly beat their pectoral fins. This is generally accompanied by the production of pulsed, croaking sounds (Fig. 5.5). Croaking sounds consist of a series of double pulses generated when two enhanced pectoral tendons are stretched and plucked by bony elevations of a fin ray (see Fig. 5.8) (also see Chapter 1). Opponents always generate sound alternately (Ladich et al., 1992a; Ladich, 1998). Contests are organized in bouts (mean 15 s), after which individuals usually swim to the surface for air breathing. If contests are not decided during the lateral display and the vocalizing phase, gouramis switch to the frontal display phase, in which opponents typically protrude their mouths toward each other and usually pivot approx. 45° around the longitudinal axis. The tails of both gouramis are usually bent to one side, with the tail of one fish extending in the opposite direction from the tail of the other (Henglmüller and Ladich, 1999). Sounds are not produced during this second, escalating phase. Frontal displaying is frequently interrupted by bites to the mouth of the opponent, causing injury. After each bite, individuals surface for air breathing. Agonistic bouts during both lateral and frontal display phases, are highly synchronized so that no difference in duration of behavioral acts occurs between opponents. The lateral display time takes about half the total

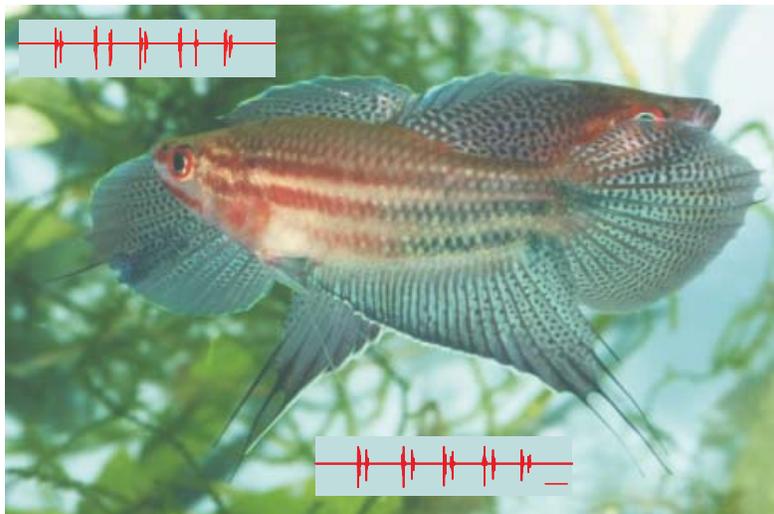


Fig. 5.5: Fighting display of two vocalizing males of the croaking gourami *Trichopsis vittata*. Rivals produce acoustic signals alternately while beating pectoral fins rapidly, spreading unpaired fins, and circling in a head-to-tail position. Inserts show oscillograms of croaking sounds emitted by the opponents. Note the difference in pulse periods between opponents. Scale bar 25 ms.

time in escalated contests (570 s versus 1370 s). A few cases end with mouth biting, followed by mouth wrestling during which gouramis grip the opponent's mouth for several minutes (Ladich, 1998). Giving up, i.e. the end of the fight, is signaled by the loser moving toward the surface and away from the opponent, folding its fins and exhibiting three or four dark horizontal bars.

As demonstrated above, acoustic displays are always part of a complex signaling system during agonistic interactions. Contests always include visual displays in which individuals try to increase their body size/contour by erecting fins, opercular covers and gill membranes, as in the case of *C. gobio*. Some movements, such as nodding, could be part of the visual displays or just a side effect of sound generation. It should be added that additional stimuli, such as vibratory or electric signals, may be part of agonistic displaying. Although neither has been proven to play a role in fighting by vocalizing fish, it can be presumed that fin or tail beating pushes a stream of water toward the opponent that will be sensed by the lateral line.

Acoustic displays consist of one type of sound, such as croaking in gouramis or several types, indicating different levels of aggression or different meanings. Single knocks and, at higher levels of aggression, a series of rapidly repeated knocks were recorded in *C. gobio* and the satinfin shiner *Cyprinella analostana* (= *Notropis analostanus*) (Stout, 1975; Ladich, 1989). Schneider (1964b) observed short drumming sounds during aggressive attacks and much longer sounds of higher intensity, which he termed "threatening" (drohlaute) in tigerperches *Terapon jarbua*. Similar agonistic vocalization were noted in several other species (see Table 5.1).

The majority of observations showed that in the course of territorial contests the attacker (usually the territory holder) or, in cases of long interactions, both contestants (i.e. the territory holder and the challenger) produce sounds. Only occasionally has sound production been reported in the submissive or fleeing individual. For instance, in the bichir *Polypterus retropinnis* threatening behavior consists of erecting all dorsal fins and emitting a series of thumps. If the smaller individual does not flee, biting results (Ladich and Tadler, 1988). The fleeing fish usually produces moans, a flight or submissive sound (Fig. 5.2B). The anemone fishes *Amphiprion xanthurus* and *A. polymnus* produce shaking sounds as a reaction to attacks by opponents. These sounds, together with a special horizontal swimming behavior, probably indicate a nonaggressive state (Schneider, 1964a). Ratchet sounds, emitted by brown bullheads *Ameiurus* (= *Ictalurus*) *nebulosus*, when being attacked, may be an appeasement display (Rigley and Muir, 1979). Similar stridulatory sounds were also heard from pimelodid catfish *Pimelodus blochii* when the defeated individuals were bitten (F.L., pers. obs.). These vocalizations might also be regarded as distress sounds.

3. FUNCTIONAL SIGNIFICANCE OF SOUNDS

Sounds uttered during intraspecific agonistic interactions termed aggressive, threatening, submissive or appeasement by various authors are often thought to possess a deterrent function. However, this function is widely unproven and alternative interpretations are possible. Agonistic sounds always occur together with visual stimuli and that is why the functional effect of the acoustical modality is difficult to establish. Carefully designed experiments are necessary to separate the acoustical component from the visual one. Experimental approaches include sound playbacks, separate tanks, mirrors, muting individuals, and correlative analyses.

Playbacks are the most successful tools for studying the functional significance of acoustic signals (McGregor, 1992; Myrberg, 1997a). Playbacks of agonistic, short distance-sounds are often unsuccessful to elicit a (biological meaningful) response because visual stimuli are lacking (but see Lugli, 1997). Therefore, visual stimuli are added in many experiments.

3.1 Playback Experiments

Playing back fighting sounds (= rapid series of knocks) to two fighting male satinfish shiners *C. analostana* resulted in an increase in occurrence and duration of aggressive behavior (Stout, 1963). In a subsequent paper, Stout (1975) showed that the response of males depends on the rank within a dominance hierarchy. Sound playback stimulated aggressive behavior in isolated, dominant males in front of a mirror but decreased aggressive behavior in submissive males. Such a dual function of the same sound type has otherwise not been demonstrated. An increase in agonistic displays was also observed in the skunk loach *Botia horae* (Valinsky and Rigley, 1981). Residents exhibited lateral displays at a significantly higher-rate when click sounds were played back. An opposite effect was observed in the following investigations although the experiments are not wholly comparable. Schwarz (1974) played back low growling sounds to pairs of the cichlid *Archocentrus* (= *Cichlasoma*) *centrarchus* that were acoustically, but not visually, separated from each other. Playbacks markedly lowered the number of highly aggressive encounters males directed at either male or female partners. Similar observations were described in the catfish *Ameiurus nebulosus* (Rigley and Muir, 1979). Playbacks of ratchet sounds decreased the number of attacks at intruders by residents (Rigley and Muir, 1979). Thus in the latter two species, agonistic sounds appeared to inhibit aggression by the receiver. Laboratory playbacks of pops, the sound of aggression in damselfishes (*Stegastes*), resulted in deterring significant intrusion into residential nest pots by conspecifics, if the sounds were transmitted from within the pots. The smaller the intruder, the greater the deterrent effect (Riggio, 1981).

Using sound production to deter intruders from entering territories has long been known in the bird world (Krebs, 1976; Krebs et al., 1978). But the

same function has also become known in the world of fishes. Bicolor damselfishes *Stegastes* (= *Pomacentrus*) *partitus*, residents of western Atlantic coral reefs, also use one of their five known sounds, the so-called chirp, as a “keep-out” signal in territorial maintenance (Myrberg, 1997b). This sound, known to be a courtship-sound in this and related species, was also found to have an important, second function through experimental sound-playbacks directly in the field (Fig. 5.6). Conspecific intruders rapidly entered neighboring territories within a few minutes after the residents had been removed. Such “empty” territories, from which the resident’s chirp sounds were repeatedly transmitted, remained intruder free however, for extended periods before eventual intrusion. The same result occurred in laboratory colonies but the deterrent effect was briefer.

3.2 Muting Experiments

Muting fish and comparing their behavior with intact fish is another approach to investigating the influence of sound production during agonistic encounters. This approach circumvents the artificial presentation and combination of acoustical and visual stimuli in playback tests. To our knowledge, this has only been done twice, most likely due to difficulties in deactivating the sonic mechanism without affecting movements or behavior. Valinsky and Rigley

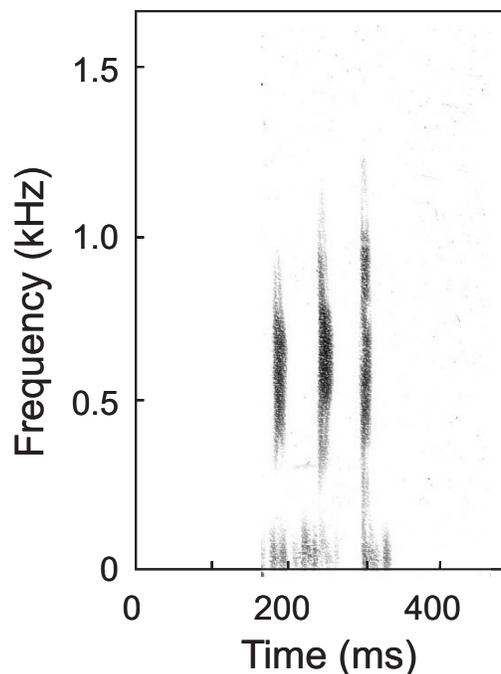


Fig. 5.6: Sonogram of a chirp sound of *Stegastes partitus*. Filter bandwidth 20 Hz.

(1981) muted skunk loaches by blocking the opercular cover movements with a steel wire, thus inhibiting production of click-sounds. Muted fish were unable to chase intruders away from their shelters despite exhibiting a larger number of lateral displays. The croaking gourami *T. vittata* produces sounds by plucking two enhanced pectoral fin tendons. Cutting these two tendons (out of 11) did not inhibit swimming movement or rapid pectoral fin beating but eliminated sound generation (Ladich et al., 1992b). In pairings in which size asymmetry of opponents was pronounced, larger fish won significantly more contests regardless of ability to vocalize. When the size difference was small, intact males had a statistically higher chance to win contests (Ladich et al., 1992b). These two muting studies signify the importance of sound production during agonistic interactions.

3.3 Correlative Experiments

Another tool, correlative analysis, was used by Ladich (1998) in pair-wise contests of male croaking gouramis, to determine whether sound characteristics influenced winning and if relative fighting ability was assessed by acoustic signals. Winners were usually larger than their opponents and this effect was more pronounced in contests decided during the lateral display phase than in contests escalated to the frontal display phase. Sounds of winners had a higher sound pressure level and also a lower dominant frequency. Neither the number of acoustic signals nor durations of lateral and frontal displays were predictors of contest outcome. Acoustical measures correlated highly with body weight. These results indicated that traits correlated with the resource holding power (RHP) (such as dominant frequency and sound pressure level) could be used as predictors of the outcome, while traits not correlated with size (such as number and duration of displays) did not influence winning. This indicates that morphological and sound characteristics influence winning in male gouramis. Moreover, the results showed that croaking gouramis settle conflicts without damaging combats by assessing asymmetries in different components of RHP such as body weight and length, which may reliably be signaled by both acoustic and visual signals (Ladich, 1998).

Amorim and Almada (2005) showed an interesting relationship between the outcome of male contests and subsequent courtship behavior in the cichlid *Oreochromis mossambicus*. Courtship sounds emitted by winners were characterized by longer pulse durations and lower peak frequencies compared with those produced by losers. Winners also showed significantly shorter courtship latencies and longer courtship durations than losers.

4. EVOLUTION OF ACOUSTICAL DISPLAYS

We do not know when acoustic displays evolved in fishes. It is rather safe to assume that cartilaginous fishes do not produce voluntary sounds (no reliable

report exists) and we have no reports on sound production in sarcopterygian bony fishes, such as lungfishes. The “oldest” group in which sound production has been described are representatives of the genus *Polypterus* or bichirs (Ladich and Tadler, 1988), a group that is thought to be an early line of actinopterygians (ray-finned fishes), comprising the majority of modern fishes (Nelson, 1994). Fossil remains of *Polypterus* are known back to the middle Cretaceous and, thus, one might speculate that acoustic communication in fishes arose some 100 million years ago among members of this taxon (Ladich and Popper, 2004). However, the sonic mechanism in *Polypterus* is not known and hence sound production cannot be derived from morphological structures. In general, sound-producing mechanisms (see Chapter 1), such as drumming muscles or tendons, do not fossilize except perhaps for the pectoral spines of catfishes. Fossil remains from representatives of well-known, sound-producing catfish families, such as doradids and mochokids, are known from the late Mesozoic or early Pleistocene (Gayet and Meunier, 2003) some 70 million years ago. Sound production in catfishes might have evolved as a byproduct of pectoral spine-locking, during which the spine can be locked in an abducted, right angle position, forming a formidable defensive weapon (Fine and Ladich, 2003). Ridged processes may rub in the pectoral girdle during abduction and adduction of the spine, producing stridulatory sounds.

It may be assumed that acoustic displays evolved in addition to or as a substitute for other signals, e.g. visual or electrical. Environmental constraints such as light limitation during dusk and dawn, night or in turbid waters might have decreased the usefulness of visual signals and increased the efficiency of the acoustical communication channel. Marshall (1967) demonstrated that several deep-sea fishes possess sound-producing mechanisms. There exist some indications that use of visual and acoustic displays is inversely related in some taxa.

Labyrinth fishes or gouramis (suborder Anabantoidei) represent an interesting group of fishes because only representatives of genus *Trichopsis* possess a well-developed, pectoral sound-producing mechanism and regularly vocalize during agonistic interactions (Kratochvil, 1985). Representatives of other genera, such as *Colisa*, *Macropodus*, *Betta*, and *Trichogaster*, vocalize only occasionally or are not known to produce sounds (Kratochvil, 1985; Schuster, 1986). Comparative analysis of agonistic behavioral elements, utilized during contests, showed that visual signals appear to be more elaborate in representatives of genera *Macropodus*, *Betta*, and *Trichogaster* than in *Trichopsis*. While all species exhibit lateral displays (spreading of unpaired fins) during contests, the former genera also spread opercula and gill membranes, while frontal displaying. Biting is common in the dwarf gourami *Colisa lalia* and mouth-wrestling in the paradise fish *Macropodus opercularis*, the Siamese fighting fish *Betta splendens*, and in bite sessions and fin tuggings in the blue gourami *Trichogaster trichopterus* (Simpson, 1968; Frey and Miller, 1977; Bischof, 1996). Therefore, it is assumed that *Trichopsis* gains information about an

opponent's fighting ability by acoustical and a few visual displays and less so by a large number of escalating, physical, and damaging combats. The distribution of visual and acoustical displays, as well as physical fighting behavior among labyrinth fishes, suggests that acoustical displays evolved instead of or as an alternative means of assessing the fighting ability of opponents.

Similar development may have taken place in cichlids with regard to color patterns since visual communication is well developed in cichlid fishes. Actually, individuals communicate with each other by changing their body coloration in many species. Body colors can change quite quickly by contraction and expansion of chromatophores. Nelissen (1978) investigated the distribution of the number of color patterns and number of sound types in six species of cichlids from Lake Tanganyika. Distribution ranged from *Tropheus brichardi*, which has seven sounds and four color patterns, to *Simochromis babaulti* with one sound and ten color patterns. This resulted in an inverse relationship, which could be due to different life histories. *Simochromis* is more active during the day and *Tropheus* is night active. Insufficient data cannot assess the aforesaid notion but the interesting idea is that environmental constraints, such as light levels or visibility, might have prompted selection of acoustical displays in fishes.

5. SOUND CHARACTERISTICS

Do fish use a particular type of sound during agonistic interactions? Are aggressive sounds characterized by particular physical features? Morton (1977) found in his classical work a relationship between motivation and the structure of sound in birds and mammals. Sounds used in a hostile context are harsh and/or relatively low in frequency, while sounds uttered in an appeasing or friendly, approachable manner are higher in frequency and more pure in tone. Fish possess much smaller vocal repertoires than birds and mammals and major changes in the frequency content of sound are physically not possible. Nevertheless, some structural differences are found between aggressive sounds and advertisement or courtship sounds. Aggressive sounds are brief and broadband (harsh) whereas sounds uttered in other contexts (submission, courtship) are frequently of longer duration and occasionally tonal. Physiologically, these differences are mainly based on differences in the contraction rate of sonic muscles. The male midshipman *Porichthys notatus* produces tonal hums of long duration that serve as advertisement calls to attract gravid females to a nest and short broadband grunts as aggressive calls that drive potential intruders from the nest (Bass and McKibben, 2001). The chondrosteian *Polypterus retropinnis* produces a series of broadband thumps while threatening and attacking conspecifics whereas the attacked fish utters longer tonal moans while fleeing (Ladich and Tadler, 1989) (Fig. 5.2B).

Territorial males of the electric fish *Pollimyrus adspersus* (formerly *P. isidori*) produce moans, growls and grunts during courtship with moans and growls more tonal than grunts (Crawford et al., 1986). Of the two sounds heard during aggression (pop, hoot), the pop correlated most closely with lunges and chases. Pops are more click-like with a sharp onset, very short duration and a broad power spectrum. Croaking gouramis *Trichopsis vittata* produce pulsed croaking sounds with their pectoral fins during agonistic encounters (Marshall, 1966; Kratochvil, 1978; Ladich et al., 1992a). During spawning, females emit similar pectoral sounds of much lower intensity (Brittinger 1991, pers. obs.). Thus differences in motivation may be encoded in sound intensity and less so in sound structure in some species.

Bicolor damselfish and their closely related congeners of genus *Stegastes* produce extremely brief and intense single pulses of sound, the pop, during aggressive interactions. And accordingly the longer the aggressive contest, the more pops heard from both contestants; but each pop is invariably a single pulse of 10–20 ms. Pops are produced by both sexes. Several acoustical characters of pops stand in contrast to other sounds produced by these fishes during courtship. Although the latter also possess pulses of 10–20 ms, each sound invariably has more numerous pulses (chirp: 3 pulses, long chirp: 4–7 pulses, growl: 8–12, grunt: highly variable, minimally 16) and all are produced exclusively by males. The chirp and long chirp are comparable to the pop in intensity but the growl and grunt far lower. Intensity differences are likely due to the former two being used to attract distant females and the latter two produced while prospective spawning partners are at or in the nest (Myrberg, 1972b). Experimental evidence indicates that low intensity characterizes those sounds produced at or in the nest to preclude acoustical interception of such sounds by neighboring, competitive males during spawning activity (Kenyon, 1994). Motivation obviously plays a role in damselfishes (*Stegastes*), regarding their pop sounds, produced during aggression. Riggio (1981) found that the frequency of pops by a territorial resident was relatively low at the territorial border, but as intruders approached the residence, frequency rapidly increased, peaking at the entrance of the residence.

Some species, in particular catfishes, possess two sound-generating mechanisms (see above): swimbladder drumming and pectoral spine stridulation. While drumming sounds are usually harmonic and of low frequency, stridulatory sounds consist of a series of sharply increasing broadband pulses (Ladich, 1997b). Kaatz (1999) after investigating 83 species from 14 families concluded that catfishes produce more stridulatory sounds in disturbance situations and more swimbladder sounds in intraspecific conflicts. Heyd and Pfeiffer (2000), studying 19 species from 8 families of catfishes, concluded that stridulatory sounds have a warning or defense function, while drumming sounds serve intraspecific communication. Thus we can assume a motivation-dependent difference in sound types uttered in various contexts.

6. ONTOGENETIC DEVELOPMENT OF AGONISTIC BEHAVIOR AND VOCALIZATION

Agonistic behavior begins early in development, often when the fish is just a few days old. Therefore, it is expected that sound production is widespread in juvenile fish given the competition for food and space, independent of reproductive behavior. Immature skunk loaches *Botia horae* emit clicking sounds when defending their territories (Valinsky and Rigley, 1981). Juvenile tigerperches *Terapon jarbua* utter drumming sounds and juvenile mormyrids *Gnathonemus petersii*, clicking sounds (Schneider, 1964b; Rigley and Marshall, 1973). Unfortunately, neither ontogenetic development of vocalizations nor agonistic behavior were investigated in these species. It has been shown in birds and mammals, however, that sound characteristics change with growth and the sound repertoire often increases until maturation.

Development of agonistic behavior and vocalization has only been shown in the croaking gourami *T. vittata* from hatching to sexual maturity (Henglmüller and Ladich, 1999; Wysocki and Ladich, 2001). Initial interactions started when fry were 11 days old and consisted of approach and flight in a feeding context. Lateral displays first occurred during the third week, circling shortly afterwards, and pectoral fin beating when fish were seven weeks old. Rapid pectoral fin beating was first accompanied by sound-emission at eight weeks (Fig. 5.7). Initially, croaking sounds were formed mainly of a series of single pulses, each pulse produced by one pectoral fin. Later, single pulses gave way to double pulses (Fig. 5.8). Furthermore, pulse period and number of pulses increased. The dominant frequency of croaks decreased and sound intensity significantly increased (Figs. 5.8, 5.9). Following vocalization, frontal display and mouth-biting occurred at the age of 10 weeks. Initially, young exhibited vertical bars which gave way to dots and horizontal bars at eight weeks when fish started to vocalize. The order of appearance of behavioral patterns during ontogeny corresponded to the order of appearance in fights between adults (Ladich, 1998; Henglmüller and Ladich, 1999; Wysocki and Ladich, 2001). The character of sounds changed widely during ontogeny, probably due to development of sound-generating structures and to larger body size. Croaks consisted initially of single pulses, which suggested that only one pectoral tendon was enlarged, while subsequent production of a series of double pulses signified that the tendons of both pectoral fins were fully developed. Increase in the number of double pulses per croak likely reflected more intense aggressive encounters, which was reflected in longer lateral display sequences associated with longer fight duration. Decrease in dominant sound frequencies with increase in body size is a general phenomenon in animals, based largely on resonance. Such a correlation is known in several adult fishes, such as all three species of croaking gouramis (Ladich et al., 1992a), damselfishes (Myrberg et al., 1993) and mormyrids

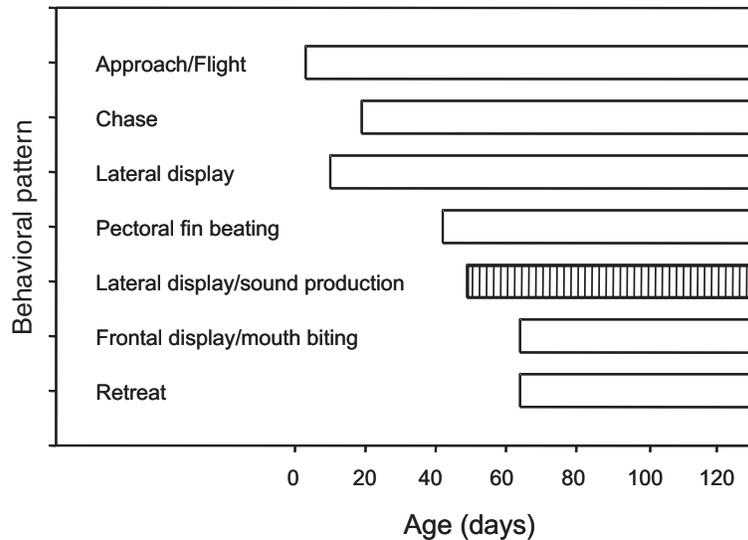


Fig. 5.7: Chronological development of the agonistic behavioral patterns in *Trichopsis vittata* posthatching. The first occurrence of behavioral patterns is indicated. Note the first appearance of sound production (after Henglmüller and Ladich, 1999).

(Crawford et al., 1997). Size dependency of call frequency has been mentioned for other groups such as searobins, tigerperches, and cichlids (Schneider, 1964b; Myrberg et al., 1965; Bayoumi, 1970). The frequency change in gouramis during ontogeny is probably based on growth of the suprabranchial chamber, an air-breathing cavity dorsal to the gills, suggested to be the main resonating structure in gouramis. Wysocki and Ladich (2001) further showed that changes in sound production are accompanied by changes in auditory sensitivity. The most sensitive frequency within this range shifted from 2.5 kHz to 1.5 kHz and thresholds decreased by 14 dB. Comparison between audiograms and sound-power spectra revealed that juveniles are not able initially to detect conspecific sounds. Results indicated that auditory sensitivity develops prior to the ability to vocalize and that vocalizations occur prior to the ability to communicate. Early settlement young of the bicolor damselfish are essentially deaf but hearing sensitivity rapidly increases up to the adult sensitivity level during the late juvenile stage (Kenyon, 1996).

Acknowledgments

We thank Heidemarie Grillitsch for the drawings in Figures 5.4 and 5.5. FL's research was supported by the Austrian Science Fund (FWF no 15873). AAM's research was supported by the US National Science Foundation and the US Office of Naval Research.

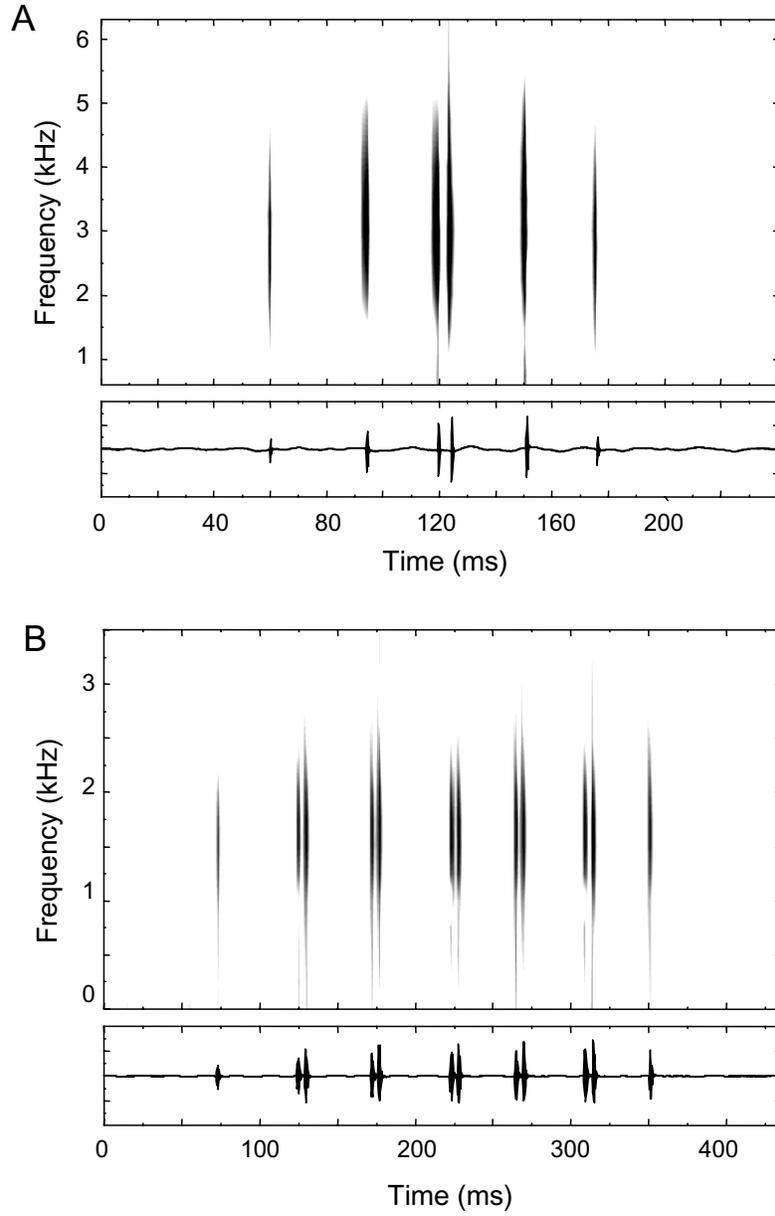


Fig. 5.8: Sonograms and oscillograms of croaking sounds of A) a 0.11 g and B) a 0.78 g juvenile of *Trichopsis vittata* (sampling frequency 16 kHz, filter bandwidth 250 Hz and 300 Hz, respectively, overlap 50%). Note the differences in axis ranges and in number of double pulse in relation to number of single pulses (after Wysocki and Ladich, 2001).

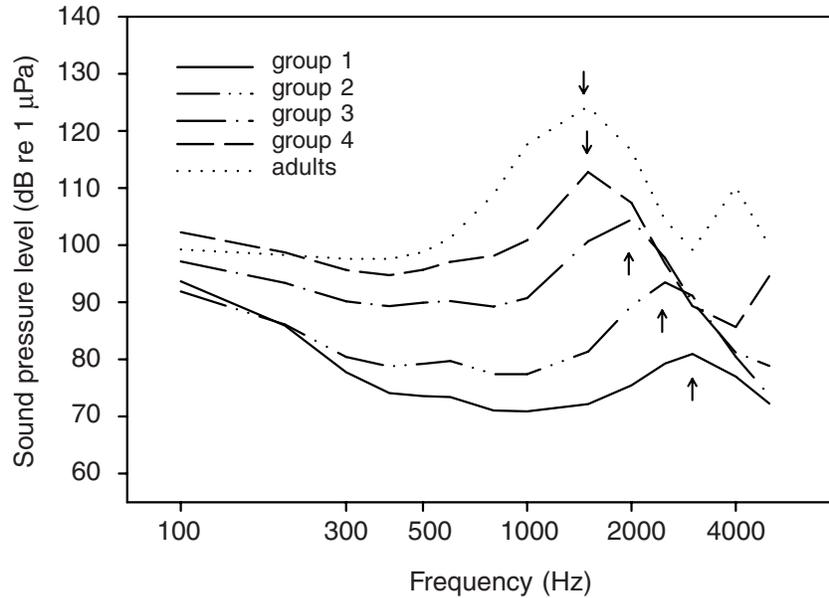


Fig. 5.9: Sound power spectra (means) of juvenile of *Trichopsis vittata* (group 1: 0.1–0.17 g; group 2: 0.18–0.3 g; group 3: 0.31–0.65 g; group 4: 0.66–1 g). Note the decrease in peak frequency of sounds as well as increase in sound intensity with growth (arrows) (after Wysocki and Ladich, 2001).

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