

Sound Production and Associated Behavior in Triggerfishes¹

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TWO ATLANTIC and five Pacific species of triggerfish produce sounds by movements of the pectoral fins against the side of the body. The behavior associated with sound production was observed in the field and in populations established in the laboratory. The sounds produced by all species when held by the hand underwater were analyzed and the pectoral fin-air bladder mechanism used to produce the sounds was studied principally by a series of ablation experiments.

It has been known for many years that triggerfishes are capable of producing sounds (Sørensen, 1884; Möbius, 1889). At least three possible mechanisms of sound production have been suggested: stridulatory mechanisms, consisting either of movements of the front teeth against one another in *Balistes carolinensis*, *B. capricornis*, *B. vetula*, and *Melichthys piceus* (Fish, Kelsey, and Mowbray, 1952; Moulton, 1958; Vincent, 1963) or of the first dorsal fin spine against underlying bones in *B. erythrodon* (Schneider, 1961); movements of the pectoral girdle bones against one another and the air bladder in *B. aculeatus* (Möbius, 1889); and "fluttering" or "drumming" of the pectoral fins against the side of the body in *M. piceus*, *M. buniva*, *B. vetula*, and *B. carolinensis* (Sørensen, 1884; Cunningham, 1910; Fish et al., 1952; Moulton, 1958). At the area of contact between the fin and body wall, the air bladder evaginated to form two bilateral lobes covered by a thin layer of integument and some en-

larged scales, called the "tympanum" by Gregory (1933). A better term, the "drumming membrane," was used and illustrated by Moulton (1958). None of these proposed mechanisms of sound production have been verified experimentally.

Sounds produced by tooth stridulation in triggerfishes have been recorded underwater in the laboratory, and from fish feeding in the field (Moulton, 1958). Sounds produced by pectoral fin movements have most commonly been elicited from specimens held in the air, although Moulton (personal communication) has since recorded them from specimens underwater. Schneider (1961) and Tavalga (1965) concluded that pectoral fin sounds were not normally produced by triggerfishes under natural conditions in the field.

As a result of the above studies, there is considerable confusion as to the nature and operation of sound-producing organs in triggerfishes, as well as to the significance of the sounds themselves. This paper attempts to demonstrate that the pectoral fin-drumming membrane mechanism is used by several species, and that the sounds themselves are correlated with agonistic behavior in the field and the laboratory.

MATERIALS AND METHODS

Hawaiian triggerfish (*Rhinecanthus rectangulus*, *Melichthys buniva*, *M. vidua*, *Balistes bursa*, and *B. capistratus*) were captured by hook and line, in fish traps, or by removing individuals from holes and ledges in the reef. All fish were captured from shallow waters (3–20 m) off the coast of Waikiki and Waiānae, Oahu, from November to July, 1964–65. The fish ranged from 15 to 38 cm in total length. Individuals of the same species were hand-held underwater in fiberglass aquaria about 7.5 cm from an Atlantic Research Corp. hydrophone (LC-57) connected to a Uher 4000-S Report tape recorder. Tape speed during all

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recordings was 18.75 cm/sec (7.5 in/sec). The tanks were 1.2 m \times 0.6 m \times 0.6 m deep, with a capacity of 758 liters. Water temperatures ranged from 21° to 23°C. Individual fish of the same species usually differed in size by no more than 7.5 cm.

All Bimini observations and experiments were carried out in November 1965 and January 1966. Specimens of *B. vetula* and *M. piceus* were captured at depths of 2–7 m by hook and line and recorded hand-held under water in concrete tanks, 1.8 \times 0.9 \times 0.6 m deep, using an Ampex (601) or Uher tape recorder. Specimens ranged from 18 to 26 cm in total length. The record level was adjusted so that sounds of normal fish peaked at no more than -1 on the VU meter of the Ampex, and at about the same level on the Uher (VU meter not calibrated).

A series of operations were carried out on *R. rectangulus*, *B. vetula*, and *M. piceus*. Sounds from fish were recorded before and after removal of part or all of the pectoral fin on one or both sides of the body. The role of the air bladder was determined by piercing the drumming membrane with a syringe and replacing most of the gas with water. The record level remained constant during all recordings (after an initial adjustment for each normal fish), so that relative changes in intensity of sounds produced by normal and operated fish could be measured. Only one recording system was used in any set of experiments. All fish were given at least 10 minutes to recover from handling and operations. No anaesthetic was used. The first five pectoral fin sounds produced by normal and operated fish were usually chosen for analyses. However, a few sounds of the fish were always masked by louder noises caused by tooth stridulation or violent contractions of the body. These could be recognized easily and were not included. Therefore, only the first five pectoral fin sounds free of these disturbances were analyzed.

Sound durations were measured from oscillographs made with a Fairchild oscilloscope (701) and Grass Kymograph camera (C-4) at film speeds of 250 mm/sec. The effect of operations on the overall intensity of fish sounds recorded on tape was determined. A General Radio Co. Impact-Noise Analyzer (Type 1556-

B) was connected to the output of the tape recorder and a peak sound pressure value was determined for the loudest of the first five pectoral fin sounds of a normal fish. The peak sound pressure of the same fish after the operation was also obtained. The peak value for the normal fish was considered as 0 decibel, while the value for the operated fish was considered as positive db (if the value exceeded that of the normal fish) or negative db (if the value was less than the normal fish). These changes in relative sound pressures (and all others mentioned below) were measured in db relative to 0.0002 microbar, but are not related to the original underwater sound pressures. Comparisons between pressure levels of normal and operated fish could be made because recordings were carried out at the same record level and with equal distances between the sound source and the hydrophone.

Relative sound pressures at various octave band frequencies were also measured from tape recordings. The output of a General Radio Co. Octave Band Noise Analyzer (Type 1558-A) was connected to the input of the Impact Analyzer. Sine wave signals of either 400 or 1000 Hz were applied to the input of the Octave Band Analyzer when in the "all pass" filter position, and with the preamplifier set to the 20 kHz weighting (essentially flat response from 20 Hz to 20 kHz). The Impact Analyzer was then calibrated to give a peak sound pressure value 3 db higher than the root mean square value shown by the Octave Band Analyzer for the sine wave. After calibration, the tape recorder output was connected to the input of the Octave Band Analyzer and readings for the fish sounds determined from the Impact Analyzer at various filter positions on the Octave Band Analyzer. The loudest of the first five sounds produced by each of ten normal fish in each species was measured, and considered as 0 db. Then, the sound pressures of the same sound in each octave band were compared to the level obtained for the unfiltered signal. The sound pressures of the filtered signal were always less than the total sound pressure, and this decrease was measured and expressed as negative db relative to the total sound energy.

The behavior of fish in the field was studied using SCUBA gear or, in clear waters, from

the surface. Observations were noted on submersible writing slates and behavior of fish was photographed with a Nikonos underwater camera. It was usually possible to sit on the bottom 1–2 m from individual fish, observe apparently normal behavior, and clearly detect by ear sounds correlated with pectoral fin movements.

Observations on two groups of 11 *B. vetula* were carried out in Bimini after establishing the fish in large, circular, concrete tanks 4 m in diameter and 0.6 m deep. Six shelters, constructed from building blocks, were placed around the tank periphery. A hydrophone was placed in the center of the tank. Color changes, sound production, and associated behavior were noted during a total of 6 hours of recordings on each group of fish, from 0900 to 1400 hours. Further observations and recordings were made in a fish pen 10 m \times 6 m \times 2–3 m deep (depending upon tidal conditions) in which 40–50 *B. vetula* and *M. piceus* were maintained.

RESULTS

The Pectoral Fin-Drumming Membrane Mechanism

The anatomy of the pectoral fin and drumming membrane in *R. rectangulus* is shown in Figure 1. The fin was composed of a single stout spine and the rays which supported most of the effective surface of the fin. The fin was

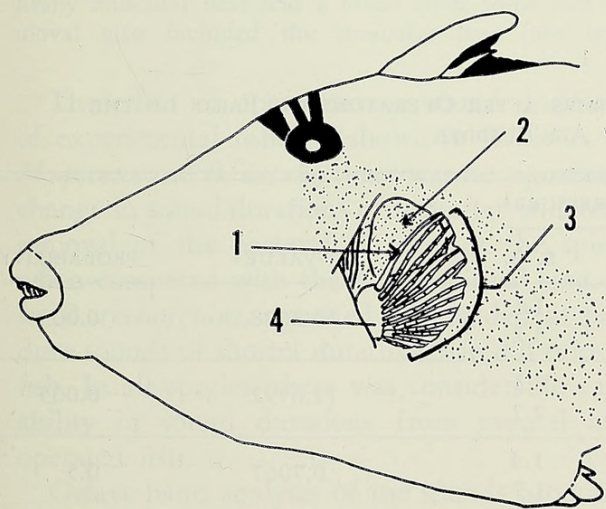


FIG. 1. External anatomy of the sound-producing apparatus in *Rhinecanthus rectangulus*. 1, Pectoral fin spine; 2, drumming membrane; 3, pectoral fin rays; 4, fleshy muscular lobe of pectoral fin.

supported at the base by a fleshy, muscular lobe. The drumming membrane was located just behind and partly above the fin, and was covered with thin scales. The anatomy of the area was essentially identical in all other species examined, differing slightly in the number and length of the rays and the surface area of the tympanum.

Movements of the pectoral fins during sound production by fish held underwater were also similar in all species. In *R. rectangulus*, the spine of the fin was pressed against the drumming membrane and moved back and forth across its surface when a sound was produced. As the spine was moved posteriorly, the rays were folded, then stretched taut as the spine was moved anteriorly. In *B. vetula* and *M. piceus*, the whole fin was moved across the drumming membrane, without folding of the rays. The number of back-and-forth sweeps of the fin across the drumming membrane varied from sound to sound within each fish, and ranged from one to seven movements in a series. Both pectoral fins appeared to complete these movements synchronously. Oscillographs of these sounds are shown in Figure 2.

No sounds resembling those of pectoral fin drumming could be detected from any fish when the fins were held immobile against the side of the body. Similarly, bilateral removal of the entire fin (rays, spine, and fleshy basal lobe) in eight fish of three species resulted in no further production of sounds.

The change in peak sound pressure of sounds produced by other operated fish, when compared with their own normal sounds, is shown in Figure 3 and analyzed statistically in Table 1. Removal of both the spine and rays of one pectoral fin (leaving the basal lobe intact) resulted in only slight reductions in sound pressure in three fish, and no change in two other specimens of *R. rectangulus*. When the same operation was performed bilaterally, sound pressures averaged about 16 db below those of normal fish. Removal of the spine from one pectoral fin in five specimens of *R. rectangulus*, *B. vetula*, and *M. piceus* had little effect on sound pressures; but, with the spines removed bilaterally, sound pressures averaged 13 db below those of normal fish. Unilateral or bilateral removal of the rays from the pectoral fin did

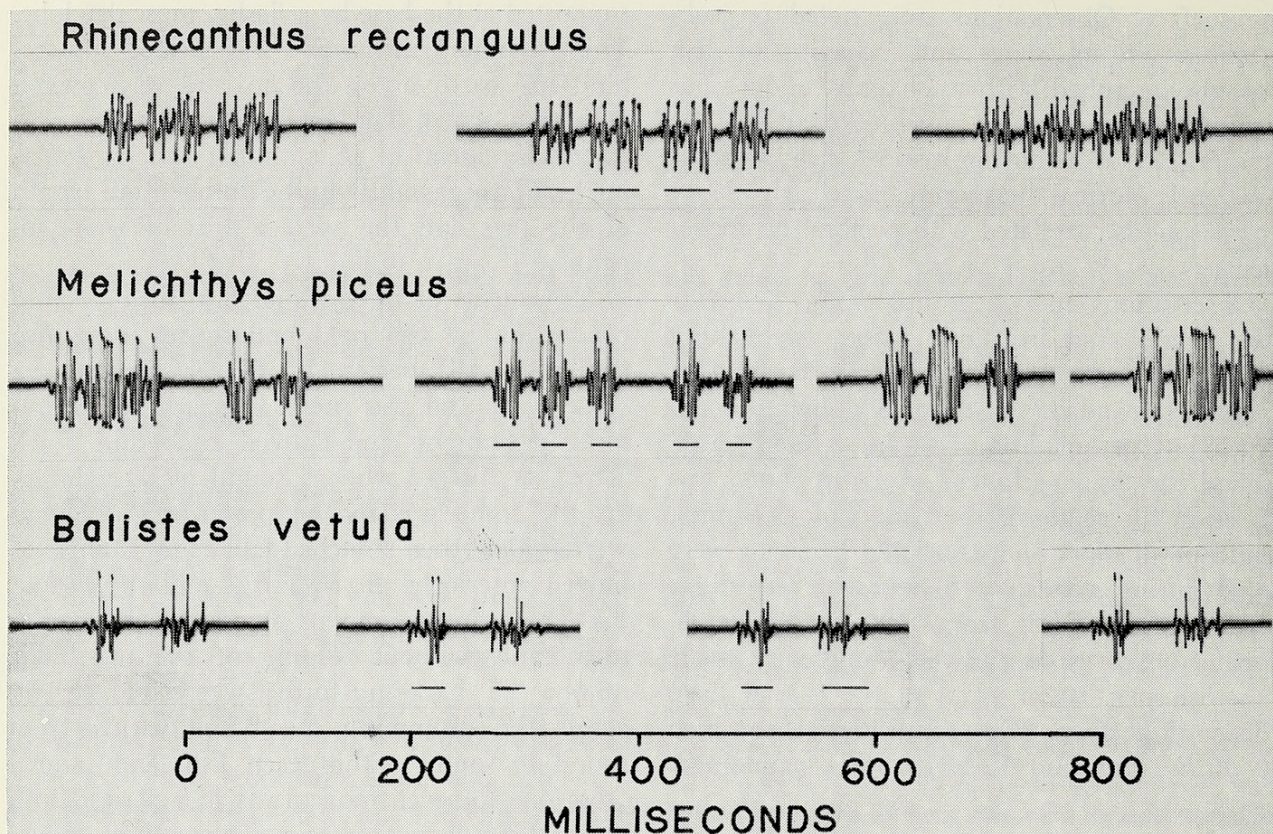


FIG. 2. Pectoral fin sounds of three species of triggerfishes. Note that most of the sounds can be resolved into groups of two or more pulses (each pulse is indicated by a solid line under recording). Each pulse corresponds to one sweep of the pectoral fins across the drumming membrane.

not result in significant changes in sound pressure. When a small hole was made in the drumming membrane (but only a few bubbles of gas were allowed to escape from the airbladder), again there was no significant change in sound

pressures. However, when the hole was held open with the syringe, allowing most of the gas to escape, sound pressures averaged 13.7 db below those of fish with only a small hole in the drumming membrane.

TABLE 1

PEAK SOUND PRESSURES PRODUCED BY TRIGGERFISHES AFTER OPERATIONS ON PARTS OF THE PECTORAL FINS AND AIR BLADDER

CONDITION	PEAK SOUND PRESSURE ¹		T-VALUE	PROBABILITY
	\bar{X}	S. D.		
One fin removed ²	-2.2	1.1	15.2688	0.005
Both fins removed ²	-16.4	3.2		
One spine removed	-1.8	3.3	11.6792	0.005
Both spines removed	-13.0	2.7		
Unilateral removal of rays	0.73	1.4	0.7067	0.5
Bilateral removal of rays	-0.33	1.7		
Small hole in air bladder	-0.4	1.4	9.4785	0.005
Gas removed from air bladder	-13.7	5.3		

¹ Sound pressures are expressed as positive db (above) or negative db (below) peak sound pressures of normal fish.

² Experiments performed on *Rhinecanthus rectangulus* only.

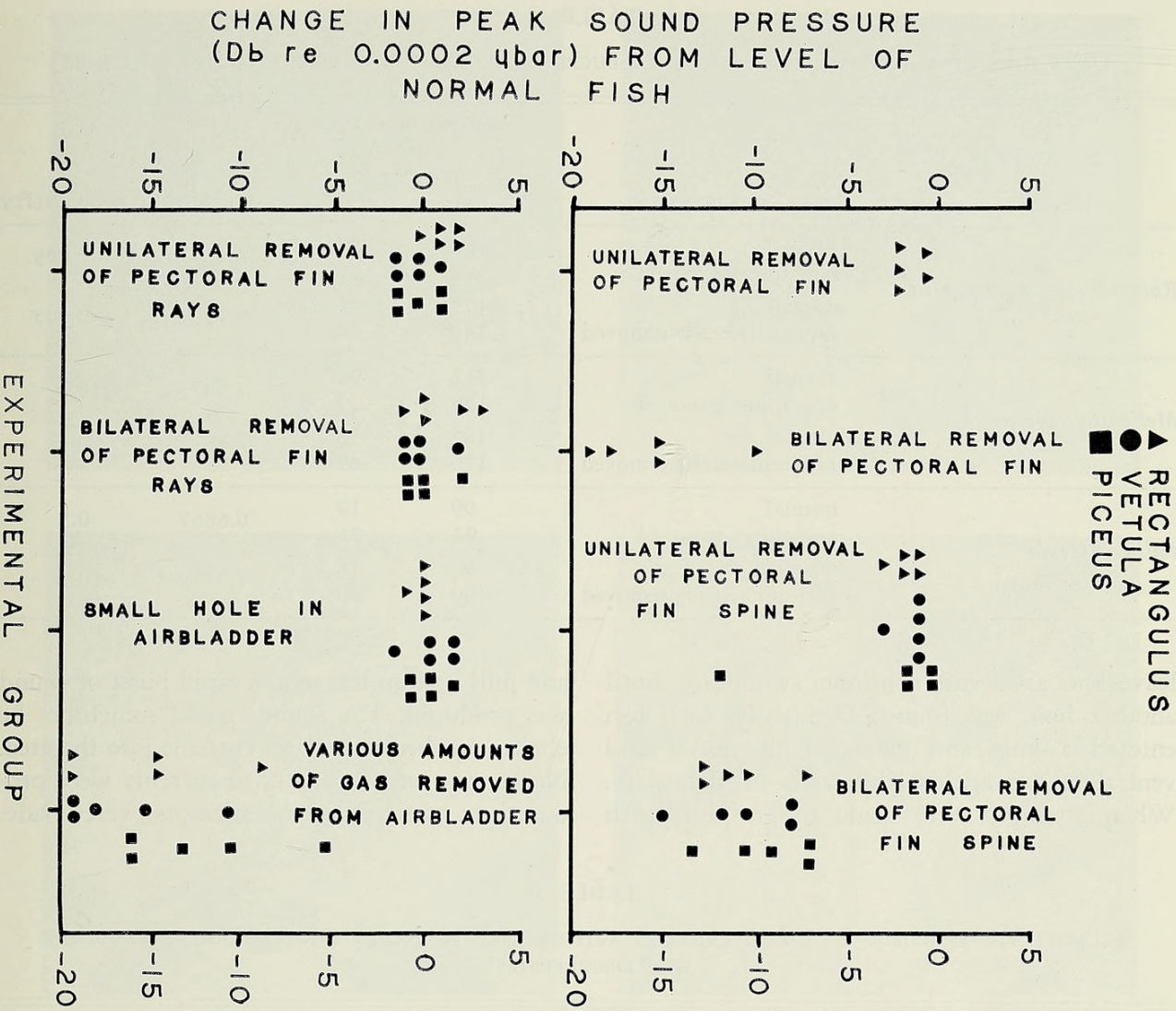


FIG. 3. The change in peak sound pressures of operated fish from those of normal animals after various operations on parts of the sound-producing mechanisms. The pectoral fin consisted of a proximal fleshy muscular base and a distal stout spine and some rays. No sounds were detected when bilateral removal also included the muscular base (see text).

The effect of operations on sound durations of experimental fishes is shown in Table 2. In *M. piceus* and *B. vetula*, there was no significant change in sound durations of fish after unilateral removal of the pectoral fin rays or the spine, when compared with their own normal sounds. In *R. rectangulus*, operated fish tended to produce sounds of shorter duration than did normal fish. In all species, there was considerable variability in sound durations from normal and operated fish.

Octave band analyses of the sounds produced by all species are shown in Table 3. Sounds produced by pectoral fin movements ranged from below 75 Hz to below 9600 Hz in all species except *B. bursa*. This species, which was

smaller than all others (total length under 20 cm), produced some sounds with measurable pressures above 9600 Hz. Most of the acoustic energy in other species was found between 150 and 1200 Hz, but there was considerable intra-specific variation not only between fish but also in consecutive sounds produced by the same fish.

Behavior Associated with Sound Production

All species but *B. capistratus* were observed in the field. When approached by a diver, about half the fish swam away rapidly. Other fish showed quite different behavior (Fig. 4). They swam in irregular paths, sometimes in wide circles, and then stopped by a hole or ledge in the reef. When again approached, the fish might

TABLE 2
DURATIONS OF THE FIRST FIVE SOUNDS PRODUCED BY NORMAL AND OPERATED TRIGGERFISHES

SPECIES	CONDITION	SOUND DURATION (MSEC)		T-VALUE	PROBABILITY
		X	S. D.		
<i>Rhinecanthus rectangulus</i>	normal	180	84	6.6667	0.005
	one spine removed	128	69		
	normal	179	53	7.1154	0.005
	rays unilaterally removed	149	46		
<i>Melichthys piceus</i>	normal	212	92	1.5473	0.1
	one spine removed	175	79		
	normal	185	76	0.7716	0.2
	rays unilaterally removed	170	62		
<i>Balistes vetula</i>	normal	99	19	0.6867	0.5
	one spine removed	93	21		
	normal	92	18	1.5472	0.1
	rays unilaterally removed	100	20		

leave the area and continue swimming until another hole was found. Eventually, each fish entered a hole and extended its dorsal and ventral spines against the walls of the space. When attempts were made to grasp the fish

and pull it from the area, a rapid burst of sound was produced. The sounds could sometimes be elicited by directing water currents into the area. No sounds were heard until currents were produced or until grasping attempts were made.

TABLE 3
RELATIVE DISTRIBUTION OF SOUND PRESSURE WITHIN OCTAVE BANDS (Hz) IN SOUND PRODUCED BY TRIGGERFISHES¹

SPECIES	SOUND PRESSURE (DB) IN OCTAVE BANDS ²							
	75- 150	150- 300	300- 600	600- 1200	1200- 2400	2400- 4800	4800- 9600	9600- 19200
<i>Melichthys buniva</i>	-20.6	-13.8	-8.2	-5.8	-8.2	-16.1	-31.8	—
	7-21	3-18	4-11	1-10	4-12	9-21	26-37	—
<i>Melichthys vidua</i>	-8.3	-4.4	-6.8	-9.9	-11.7	-18.6	-23.6	—
	4-11	1-6	2-12	3-14	7-23	10-27	13-38	—
<i>Melichthys piceus</i>	-12.3	-4.9	-4.1	-8.7	-13.7	-20.5	-29.9	—
	9-17	2-11	2-7	6-13	10-18	17-25	27-35	—
<i>Balistes bursa</i>	-16.8	-9.7	-6.4	-8.0	-5.1	-10.1	-22.1	-24.1
	11-27	4-18	3-10	2-11	2-17	2-21	15-31	22-40
<i>Balistes capistratus</i>	-8.4	-3.8	-4.5	-8.9	-11.7	-18.0	-25.4	—
	5-14	2-7	2-10	2-14	2-18	10-28	11-33	—
<i>Balistes vetula</i>	-16.3	-10.1	-5.9	-3.0	-8.5	-12.8	-24.1	—
	11-21	2-14	3-10	1-8	6-11	9-19	15-30	—
<i>Rhinecanthus rectangulus</i>	-4.8	-4.8	-5.1	-11.2	-15.6	-23.0	-26.3	—
	3-8	1-8	3-10	8-16	2-17	13-31	24-34	—

¹ Data show mean and range of pressures at each octave band.
² Numbers represent db below total sound energy, so that smallest reductions represent octave bands of greatest amplitude.

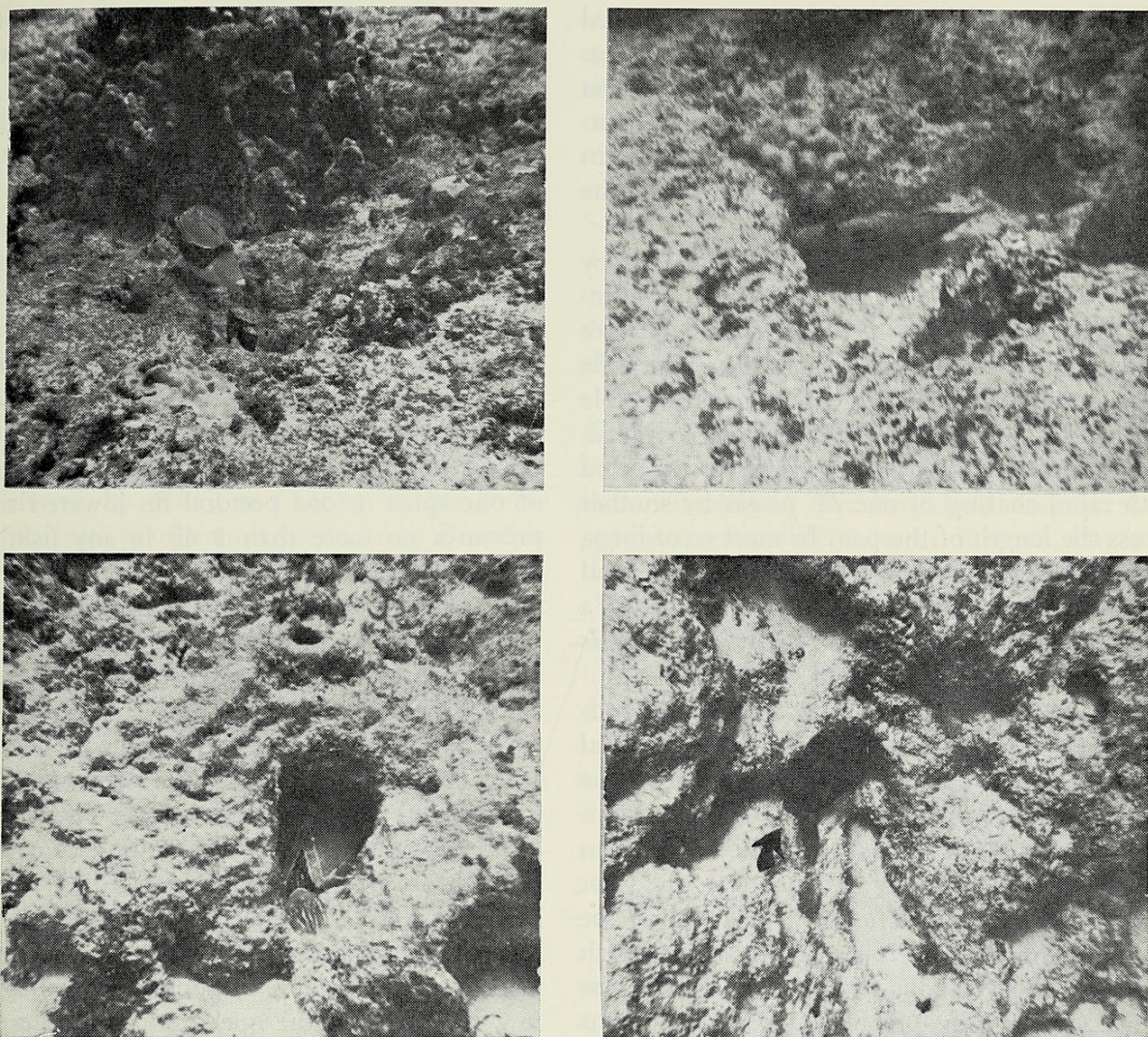


FIG. 4. Escape behavior of *Rhinecanthus rectangulus* when chased by a diver. *Upper left*: A fish circles toward the diver and then enters a hole in the reef (*upper right*). *Below*: Each photograph shows a fish which has entered a hole and locked its spines in place. The tails protrude from the holes.

All fish stopped producing sounds a few seconds after attempts to dislodge them ceased. If pulled from the area, the fish continued to produce sounds until released. These observations are based upon the behavior of over 60 *R. rectangulus*, and at least 15 fish in the remaining species (excluding *B. capistratus*).

Most fish in the field were widely spaced, although in *Melichthys* sp. occasionally some were seen swimming in groups. In *Balistes* and *Rhinecanthus*, individual fish swam alone near the bottom, with only 5–10% of the fishes remaining near a hole or ledge in the coral for brief periods (5–30 minutes). On one occasion, 17 *B. bursa* were seen feeding on a small area of coral. Several large fish briefly chased smaller conspecifics away from the area, then

returned to feed. The chasing was accompanied by a slight opening of the mouth and rapid, continuous volleys of pectoral fin drumming sounds. In two other cases, quite different behavior was observed during sound production. One fish approached another which had been hovering near a hole for several minutes. The "resident" and the "intruder" then slowly circled, simultaneously rising about 1–2 m off the bottom. Brief volleys of pectoral fin sounds were produced by both fish as they circled. In addition, the body coloration of both changed from the usual tan to a bright yellow. The intruding fish then swam away from the area. Brief chasing between conspecific *R. rectangulus* was also observed, but no sounds were detected.

On two separate occasions, individual *B.*

vetula near coral ledges in Bimini were observed to chase approaching conspecifics from the area. The aggressive fish changed in body coloration from a light to a dark brown, while the opercular area became bright yellow. Pectoral fin drumming sounds were produced by one of the aggressive fish during chasing.

Many pectoral fin sounds were produced by *B. vetula* and *M. piceus* in the fish pen at Bimini. In three hours of recordings, sounds were produced at least once a minute. However, the large number of fish present made impossible the identification of the individuals involved. On four occasions, loud sounds were correlated with rapid chasing of one *M. piceus* by another across the length of the pen. In most recordings, presumably of sounds from both species, several sounds were produced in a series for up to a 9-second period. In a few cases, the sounds consisted of a single, loud burst.

Individuals of *M. piceus* in the circular concrete tank remained in the shelters for several days and only occasionally ventured into the open central area. This behavior was not comparable with that of conspecific fish in the pen or the field, and so only *B. vetula* was used for further observations. These fish adapted to the tank very quickly, i.e., they accepted food (fresh conch), produced sounds, and swam about the whole area within one hour after populations were established.

The most intense aggressive behavior occurred within the first 2–3 hours after the fish were placed in the tank. One fish in each of the two groups was dominant over all others. Chasing, sometimes accompanied by pectoral fin sounds, characterized the behavior of all aggressive fish. Submissive fish, usually smaller individuals, were dark or light brown in color. Most aggressive fish usually had bright yellow opercula.

A total of 134 aggressive interactions were observed, consisting of chasing of a conspecific by an aggressive fish. In 44 observations, the aggressive fish produced sounds by pectoral fin drumming just before or during the chase. Sounds were also produced during other less frequent interactions, i.e., when two fish circled slowly around one another for a few seconds (sounds produced by both fish in three observations); when one fish, after producing sounds, displaced a second fish from a shelter (12 ob-

servations); and when resident fish inside their shelters produced sounds in response to intruding fish (12 observations).

DISCUSSION

Pectoral fin movements against the drumming membrane appear to be responsible for production of sounds in three species of triggerfishes, representing three different genera. The data indicate that movements of the stiff pectoral fin spine across the drumming membrane contribute to most of the resultant sound pressure. The system must be extremely efficient, as removal of one spine or one pectoral fin lowered sound pressures no more than 2 db in any fish. The sounds of most normal fish peaked 22–25 db above background levels in the recording tanks, but we did not measure the absolute level of sound pressure in the water. Removal of both spines or most of the gas from the air bladder reduced intensities about 15–20 db. A very low level of sound remained when only the basal lobe of the fins was left intact. The acoustic energy released may represent muscle contraction sounds, or the sound of the base striking the side of the body.

Removing the gas from the air bladder resulted in a reduction in sound intensities, but it was noted that the operation had little effect on the frequencies contained in the sounds. In all species, the air bladder did not appear to emphasize any particular frequencies, and hence it probably does not function as a resonator. It may be that the air bladder acts chiefly as an efficient sound coupler to the water medium.

When the fleshy muscular lobe was held against the side of the body, or was removed, no detectable sounds were produced. Although no control was carried out for this specific operation, the data indicate that an intrinsic mechanism is not involved in sound production when fish of these species are hand-held underwater. It is possible, of course, that sounds may be produced by means of intrinsic mechanisms under other conditions.

Unilateral removal of the spine or rays did not affect duration of sounds in *M. piceus* or *B. vetula*. The results support the conclusion that the pectoral fins move synchronously on either side of the body during sound production.

In *R. rectangulus*, sounds produced after the operations were significantly shorter in duration than were those of normal fish. However, when hand-held underwater for over a minute, even unoperated fish of this species gradually produced more abbreviated sounds. We believe that the effect after operations reflected this species-specific response to prolonged handling, and was not causally related to the operations themselves.

The octave band analyses of the sounds produced by seven species showed similarities in frequency spectra. Most of the acoustic energy was concentrated in the lower frequencies, as was shown by Moulton (1958) in his sonographic displays of sounds produced by *B. vetula* and *M. piceus*.

Triggerfishes produced sounds in the field under conditions involving agonistic interactions. These sounds were quite loud and, when produced by a fish chased into a narrow hole in the reef, could function to startle a predator. Sound production under these circumstances is probably a behavior adaptation which, in addition to the bony plates and trigger mechanism, serves to promote survival of these relatively slow-moving fish.

Intraspecific aggressive behavior, with sound production, was infrequently observed in the field and only in two species (*B. bursa* and *B. vetula*). Triggerfish were usually observed swimming alone, and when they did meet conspecifics they were quite aggressive. Wide spacing between individuals seemed to be the normal social organization of each species at the time studied. Individual fish, observed from the surface, were seen swimming near the bottom, stopping occasionally to feed and inspect a ledge or hole in the reef. Sometimes a suitable hiding place was defended for a brief period. It may be that a fish which has found a suitable vacant hiding place nearby would be better able to escape from a predator. Several *R. rectangulus* consistently returned to the same hole when approached several times during a 2-hour period. It would be interesting to mark fish and determine if they swam regularly over a definite home range, returning at dusk to the same hole which would be defended as are territories by other vertebrates.

When placed in groups in the fish pen and

in the circular concrete tank, Bimini species frequently produced sounds and, in *B. vetula*, showed color changes associated with aggressiveness by fish in the field. Under these conditions, interactions were more common due to the crowding of several fish within a small area. Sounds with correlated color changes were produced by individual fish when chasing one another, when defending their shelters, and when displacing other fish from the inside of the shelter.

Triggerfish sounds may function in other situations, particularly in reproductive behavior, but at present no information is available about these situations. The hand-held sounds show species-specific differences in duration, but little difference in frequency content. It is quite probable that temporal variation in the rate and intervals at which pulses are produced could carry information to distinguish between signals of different species, especially when the sounds are used in conjunction with changes in body coloration. Further study of these fish is certainly indicated.

SUMMARY

Triggerfishes produce sounds correlated with movements of the pectoral fins against the side of the body. The air bladder evaginates to form two bilateral lobes covered by thin scales at the area of contact between the fins and body wall. A series of operations were performed on these structures in *Balistes vetula*, *Melichthys piceus*, and *Rhinecanthus rectangulus* in order to analyze their contribution to the sounds. The single stout pectoral fin spine contributed to production of most of the sound energy, but some was contributed by the fleshy muscular lobe of the fin. Removing the gas from the air bladder resulted in markedly reduced sound intensities. The sounds of these fish, and those of *B. capistratus*, *B. bursa*, *M. vidua*, and *M. buniva* were found to be quite similar in frequency spectra, with most of the acoustic energy below 1200 Hz.

Field and laboratory observations also were made on all species. The production of pectoral fin sounds during escape and aggressive behavior was described. In some species, these interactions were accompanied by color changes as well, usually in the aggressive or dominant fish.



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