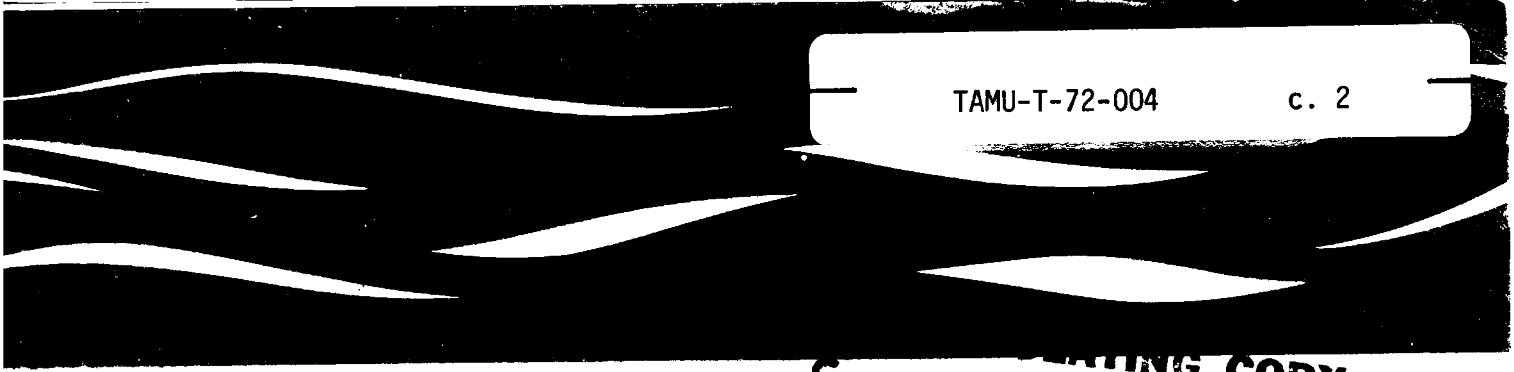


A HYDROPHONIC STUDY OF THE FEEDING ACTIVITIES OF WESTERN ATLANTIC PARROTFISHES

Prepared by

JOHN D. SARTORI and THOMAS J. BRIGHT
Department of Oceanography
Texas A&M University

TAMU-SG-72-203

August 1972

A HYDROPHONIC STUDY OF THE FEEDING ACTIVITIES OF WESTERN ATLANTIC PARROTFISHES

By
John D. Sartori and Thomas J. Bright
Department of Oceanography
Texas A&M University

August 1972

TAMU-SG-72-203

Supported by the National Sea Grant Program
Institutional Grant 2-35213
Under the United States Department of Commerce
National Oceanic & Atmospheric Administration

ABSTRACT

A Hydrophonic Study of the Feeding Activities of Western Atlantic Parrotfishes. (August 1972)

John D. Sartori and Thomas J. Bright

A passive acoustic technique for monitoring feeding and related activities in parrotfishes has been developed and is herein described.

Recordings of feeding sounds and visual observations made in the field have verified the existence of a cyclical diel grazing behavior in the parrotfishes studied.

Spectrographic analyses of parrotfish feeding sounds have revealed the existence of a behavioral change in feeding habit with age among the species studied. Juveniles and small adults of 127-254 mm in length feed rather superficially by rasping algae from hard substrates. Individuals of 305 mm or greater in length characteristically bite such hard substrates while feeding. These behavioral differences are reflected in the production of two characteristic and readily distinguishable feeding sounds. The CRUNCH is the feeding sound characteristic of fishes in the larger size category. The feeding sound characteristically produced by small size category fishes is termed the SCRAPE. The CRUNCH and the SCRAPE differ in their basic temporal and frequency structures.

In the laboratory the amount of calcareous material removed from a coral substrate during a fish's grazing activities was related to the number of feeding sounds heard during the interval of grazing. A relationship of 1/6 g of calcareous material removed per CRUNCH feeding sound was thereby derived. By relating this value to the average number of feeding sounds recorded per day over a known area in the field it was calculated that 1050 kg/ha/yr of calcareous material would be removed by grazing parrotfishes in the study area. This value compares favorably with the 600 kg/ha/yr figure calculated by Bardach (1961) who obtained his value by examining gut contents for calcareous material and estimating the standing crop of parrotfishes on a "typical Bermuda reef". The general agreement of these results is interpreted as a verification of the correctness of the basic assumptions upon which the passive acoustic method is based.

ACKNOWLEDGMENTS

I would like to thank Dr. Thomas Bright for his able assistance, advice, and especially for his personal friendship throughtout my research. I am also grateful to Dr. Richard Rezak and Dr. Jack Anderson for their helpful criticism after reviewing this report.

Field studies were made possible through the generosity of the Bahamas Underway Explorers Society and the Perry Foundation who donated support and habitat time. The assistance of my fellow aquanauts Dr. Thomas Bright and Dan Taylor, support divers Tom Burke and Ray Mathewes, and Hydro-Lab staff members Bob Wicklund and Gary Myers is also gratefully acknowledged.

I am further indebted to the directors and staff of Sea-Arama Marineworld in Galveston, Texas, for the use of aquaria and working space. The hospitality, concern, and assistance of Dr. Ken Gray, Jim Ketcham, and Paula Trost are particularly appreciated.

The excellent jobs of typing and drafting were performed by Judy McMillan, Gail Langley, and Gerda Merkel.

Support for this project was provided by the Texas A&M University Sea Grant Program under the Department of Commerce's National Oceanic & Atmospheric Administration's Institutional Grant 2-35213.

TABLE OF CONTENTS

Page

ABSTRACT. ii

ACKNOWLEDGMENTS iv

LIST OF TABLES. vi

INTRODUCTION 1

LITERARY HISTORY. 5

EQUIPMENT AND METHODS 9

RESULTS AND DISCUSSION. 13

- Feeding Sound Analyses 13
- Diurnal Grazing Cycle. 27
- A Technique for Assessing the Effect of Grazing on Coral Substrates 35

CONCLUSIONS 41

REFERENCES. 45

APPENDIX A. 49

APPENDIX B. 63

APPENDIX C. 71

LIST OF TABLES

Table Page

1 The spectral analyses of the feeding sounds of large parrotfishes (305-356 mm in length and larger). 15

2 The spectral analyses of the feeding sounds of small parrotfishes (127-254 mm in length). 18

3 The spectral characteristics of the CRUNCH and the SCRAPE (M = mean value). 21

4 Calculations of the removal of calcareous material from several species of corals by a 457 mm *Scarus quacamaia* in relation to the number of feeding sounds recorded 37

INTRODUCTION

The family Scaridae (commonly known as parrotfishes) is a typically tropical group characteristic of Pacific as well as Atlantic coral reefs. The coalescence of their jaw teeth to form strong beak-like dental plates and the striking coloration of at least some male species account for their common name.

Species of _Sparisoma_ and _Scarus_ are the most common family representatives throughout the Atlantic and West Indies, however, two small somewhat atypical genera, _Cryptotomus_ and _Nicholsina_, occur within the same range.

Parrotfishes are prominent citizens of the reef community, and their importance is manifest in several ways. A great ecological impact stems from their ability to directly utilize such primary producers as benthic algae, algal stubble, and interstitial or permeating algal growth, coupled with the fact that, on a weight basis, they are often dominant among West Indian coral reef fishes (Randall 1963a, Bardach 1959). The importance of scarids in food web relationships is further emphasized by Randall (1963a). Through stomach content analysis, he found that the scarids, as a family, are the principal prey for predacious fishes on large Caribbean reefs.

From a behavioral standpoint parrotfishes are important as well. Probably the most significant aspect of parrotfish behavior concerns their feeding activities; they are grazers, rasping and biting the coral substrate to obtain their food.

The earliest recorded observations of the coral rasping habits of Pacific parrotfishes may be those of Darwin (1909), made during his voyage aboard the H. M. S. Beagle. Atlantic species, unlike their Pacific counterparts, do not browse living coral polyps. Their food supply consists almost entirely of the filamentous algal material which grows in mats over dead sections of the reef (Randall 1967). It is not likely, therefore, that Atlantic parrotfishes would have a direct destructional effect on living hermatipic corals, however they remain important as sediment producers and agents of reef attrition as they ingest considerable amounts of calcareous coralline material in the process of feeding.

It was with the realization that the most significant aspects of parrotfish behavior are feeding-related that the various phases of this investigation were chosen. The objectives of primary interest were: 1) to acoustically characterize different sizes and possibly species of feeding fishes; 2) to determine the daily intervals of most active grazing; and 3) to investigate the potential of a technique designed to assess the effect of grazing on a given substrate.

While some of these subjects have been previously researched to varying extents, the present approach is essentially unique in that it relies almost entirely upon an acoustic means of monitoring. As would be expected, the characteristic biting and rasping activities of feeding parrotfishes are accompanied by a relatively high level of sonic output. The monitoring technique employed here was consequently designed to utilize this type of raw acoustic data as the basic source of behavioral information. Thus, the technique is similar to the actographic studies discussed by Busnel (1963) and simply involves the passive recording of sounds which, upon appropriate analysis, can be related to some characteristic activity of the organism generating the monitored sound.

The results obtained here were, as a whole, quite satisfactory, and in all cases at least a broad generalization concerning the activity in question was possible. This is encouraging especially in consideration of the limited extent to which the system was employed during this initial trial run.

The main advantage of the system is its ability to effectively monitor bio-acoustic events which occur remote from the observer.

LITERARY HISTORY

Studies concerning the feeding habits of herbivorous marine fishes are fairly numerous. While the majority of publications on the Scaridae have been taxonomic in nature (Winn and Bardach 1957, Schultz 1958, Randall 1963b, Schultz 1969), several papers dealing with feeding and ecology in shallow tropical waters provide valuable sources of reference on the feeding of scarids. The most notable of these are: Odum and Odum (1955), Hiatt and Strasburg (1960), Stephenson and Searles (1960), Stephenson (1961), Randall (1961, 1963a, 1965, 1967), Talbot (1965), and Bakus (1964, 1966, 1969). Additional information concerning feeding behavior in parrotfishes and other reef herbivores is offered incidentally through several studies of reef erosion and processes of sediment production and transport (Grabau 1913; Cloud 1952, 1959; Emery 1956; Newell 1956; and Bardach 1961).

The use of electro-acoustic techniques for studying animal activities and behavior patterns has become recognized as a valid and accurate observational approach and is now applied to the study of several types of organisms. A general review of bio-acoustics in the marine environment has been prepared by Travolga (1965). Several papers describing marine bio-acoustic techniques, applications, and results of bio-acoustic experiments have been compiled in two symposia volumes (edited by Travolga 1964, 1967).

In several instances direct relationships have been identified between audible sound production and the feeding activity of marine fishes. The sounds most often involved are those generated by the stridulation of pharyngeal teeth. Moulton (1958) described such stridulatory feeding sounds of triggerfishes and puffers, and Steinberg, et al. (1965) described similar sounds produced by the Queen Triggerfish and Slippery Dick. Brawn (1961) describes how the presence of food will cause excitement and increased aggressive behavior in cod, and as a result an increase in the frequency of sound production. Croakers and other sciaenids also increase their drumming behavior during feeding (Marshall 1962). Moulton (1960) was able to initiate a characteristic feeding reaction in jacks (*Caranx* sp.) by playing back thumps and tooth stridulation sounds recorded during earlier feeding sessions. This suggests the possibility of using recorded sounds to monitor feeding activities as mentioned by Cummings, et al. (1966). A nondescriptive acoustical study of fish feeding behavior was actually conducted by Rekubratskii (1969). He used passive recording procedures, similar to those discussed by Busnel (1963), to characterize the feeding responses of predacious fishes in relation to different types of food. The technique used in the present study is essentially the same, differing only in its application (i.e. to study the grazing mode of feeding in parrotfishes).

Information on the technical aspects of underwater acoustics and recording techniques in general is offered by: Steinberg, et al.

(1962), Boughton (1963), Andrieu (1963), Brandt (1963), Davis (1964), Haslett (1967), and Holt (1967).

EQUIPMENT AND METHODS

Field observations were achieved primarily through the use of the Hydro-Lab underwater habitat, a facility which was located in 14.7 m of water approximately 2000 m off Lucaya, Grand Bahama Island. The sand bottom immediately landward to the outer reef was selected as the permanent site for the manned undersea habitat. Hydro-Lab is essentially a horizontally aligned cylinder 4.9 m long and 2.4 m in diameter. It is capable of accommodating two to three persons for a period of up to one week. Two bunks, a shower head, tables, a-c and d-c lighting, and a Citizens Band radio for shore communications comprise the interior accessories. Surface support is supplied by a tender buoy which is moored to the top of the habitat. The support buoy has a 7 m T-Craft hull and houses a 16.5 hp Lister diesel generator, 300 psi air compressor, and 300-gallon fuel and water tanks. Fresh water, breathing air, and 120 V a-c and 12 V d-c electrical power are transferred from the buoy to the habitat via an umbilical, thereby eliminating the need for constant manned surface support. Compressed air and oxygen bottles and 12 V batteries are stored within the habitat as emergency sources of electrical power and breathing gases. Hydro-Lab served as our base of operations during a seven-day saturation dive lasting from July 20 through July 27, 1971.

Recordings to be used in the determination of a grazing activity cycle were made from within the habitat using a Sony 630 D tape deck and two 24 V d-c amplifiers coupled with Atlantic Research LC-10 hydrophones through the habitat's entry hatch. Twenty-two 90-min tapes of scarid feeding sounds at three permanently chosen stations were made in this way. Recordings were made over full 24-hr time intervals on five successive days. A nearly continuous daytime recording was obtained for the three stations collectively by monitoring them alternately throughout the daylight hours. At night, however, an automatic timer, which allowed a 5-min recording once each hour, was coupled with the recorder.

In order to insure the reliable identification of scarid feeding sounds during tape playback it was necessary to make numerous visual correlations between these sounds and the feeding activities which generated them. The habitat, with its large viewing port, offered an excellent means for doing this. Supplemental recordings were made with a Sony TC 124 portable cassette recorder rigged with an Inter-Ocean R-130 hydrophone and a Radioear Bone receiver as a listening device. The main unit was housed in a plexiglas case that could be carried by a diver. This arrangement also permitted simultaneous recording and observation and further allowed the diver to record in areas outside the immediate field of view provided by the underwater facility. The use of double SCUBA rigs allowed excursions from the habitat base which averaged approximately two hours in duration. Two to three such excursions were made each day during the saturation dive by each of the three resident aquanauts.

A Kay 7030A Vibralyzer was used to obtain the spectral analyses which were essential in attempting to acoustically characterize the feeding sounds of various sizes and species of parrotfishes. Sounds to be analyzed were selected from among those appearing on the twenty-two 90-min tapes used to determine the grazing activity cycle. The feeding sounds of several species and sizes of parrotfishes were analyzed in order to insure an adequate comparison of their acoustic characteristics.

The final phase of the study was intended to evaluate a technique for measuring the effect a grazing parrotfish has on various coral substrates. Very generally, the technique involved a series of experiments in which a 457 mm Rainbow Parrotfish, *Scarus guacamaia* was isolated in a 500-gal aquarium with several preweighed pieces of oven dried coral. The dry weight differential recorded after a timed feeding session was then related to the number of feeding sounds heard and an assessment of the fish's effect on the particular coral substrate could be made. To minimize disturbance of the fish during periods of observation the observer remained concealed and observed and recorded events of interest with a closed circuit Sony Videocorder video TV system. The technique and the preliminary results of its first employment are discussed in greater detail in the final section of this paper.

RESULTS AND DISCUSSION

Feeding Sound Analyses

The stated objective of this phase of the study was to attempt an acoustic characterization among different sizes and species of parrotfishes based upon the spectrographic analyses of their feeding sounds as recorded in the field. In the case of species differentiation, the present level of analysis has allowed the identification of only a few apparent patterns. On the other hand, a much more conclusive relationship has been revealed between size categories of feeding parrotfishes and types of feeding sounds.

The two basic types of feeding sounds recognized have been defined as the CRUNCH and the SCRAPE. The CRUNCH is a relatively low frequency, long duration feeding sound generated by the more leisurely biting activities of parrotfishes of 305-356 mm in length or larger, while the SCRAPE is a higher frequency, short duration sound which is characteristically repeated in rhythmic sequence and characterizes the rasping-type feeding activities of parrotfishes in the 127-254 mm size category.

Other acoustic properties important in differentiating the CRUNCH and SCRAPE include the number of component pulses making up the entire sound. Pulse, as used here, refers to the smallest unitary homogeneous parcel of sound waves that can be defined through oscillographic or sound spectrum analysis. The temporal spacing of repeated sounds, total frequency range spanned, and the frequency range of maximum concentration of acoustical energy (commonly called the predominant frequency range) are also important. Table 1 is a compilation of the spectral analyses of field-recorded sounds produced by several different species of feeding parrotfishes. All individuals represented are within the 305-356-mm-and-above size range. As stated, this category is represented by fishes that characteristically feed by biting at hard substrates and includes adult (305-356 mm) male and female *Sparisoma viride*, and adult (usually larger than 457 mm) *Scarus guacamaia*, *Scarus coelestinus*, and *Scarus coeruleus*.

Although the temporal and frequency characteristics of feeding sounds of parrotfishes within either of the separate size groupings differ only slightly, there are several instances in which a loosely defined pattern seems to be present (Table 1, p. 12). For example, a predominant frequency level of 2,000 hz for the female *Sparisoma viride* and a 1,000-4,000 hz level for the slightly larger male may represent a degree of frequency discrimination based on differences of sex or more likely size. In addition, a slightly higher frequency range of 0-8,000 hz is exhibited by *Scarus coelestinus* as compared to the 0-6,000 hz range of most other species, and a predominant frequency level of 2,000-3,000 hz appears to be peculiar for *Scarus guacamaia*.

Table 2 is a similar compilation of the spectral analyses of feeding sounds of fishes in the 127-254 mm size range. Fishes in this size category are typical raspers and included here are the

Table 1. The spectral analyses of the feeding sounds of large parrotfishes (305-356 mm in length and larger)

Figure Number	Sound Producer (Size & Species)	Description of Sound	Sound Duration (sec)	Number of Component Pulses	Frequency Range (khz)	Predominant Frequency (khz)	Comments
	305 mm ♀ *Sparisoma viride*	CRUNCH	0.21	27	0-6	4-5	Higher than expected predominant frequency
10	305 mm ♀ *Sparisoma viride*	"	0.36	21	0-4	0-2	Evidence of a trailing SCRAPE-like sound (audible)
1	305 mm ♀ *Sparisoma viride*	"	0.40	12	0-6	0-2	Typical for the species
	305 mm ♀ *Sparisoma viride*	"	0.45	26	0-2.5	0-2	Possibility of upper range obscurance by background level
	305 mm ♀ *Sparisoma viride*	"	0.45	16	0-4	0-1	
11	305 mm ♀ *Sparisoma viride*	"	0.30	15	0-6	0-2	Short SCRAPE-like component with undifferentiated frequency structure
	305 mm ♀ *Sparisoma viride*	"	0.65	12	0-6.5	0-2	

Table 1 (continued)

Figure Number	Sound Producer (Size & Species)	Description of Sound	Sound Duration (sec)	Number of Component Pulses	Frequency Range (khz)	Predominant Frequency (khz)	Comments
	305 mm ♀ *Sparisoma viride*	CRUNCH	0.36	20	0-6	0-4	
	356 mm ♂ *Sparisoma viride*	"	0.25	15	0-6	1-4	
2	356 mm ♂ *Sparisoma viride*	"	0.28	18	0-5.5	1-4	
	305 mm ♂ *Sparisoma viride*	"	0.15	8	0-6	0-2	
	356 mm *Scarus coeruleus*	"	0.09	8	0-6	4	
3	457 mm *Scarus coeruleus*	"	0.45	32	0-6	0-2.5	
	762 mm *Scarus coelestinus*	"	0.30	9	0-7	4-6	
4	610 mm *Scarus coelestinus*	"	0.19	20	0-8	0-3	
	610 mm *Scarus guacamaia*	"	0.35	12	0-5.6	0-3	

Table 1 (continued)

Figure Number	Sound Producer (Size & Species)	Description of Sound	Sound Duration (sec)	Number of Component Pulses	Frequency Range (khz)	Predominant Frequency (khz)	Comments
	610 mm _Scarus_ _guacamaia_	CRUNCH	0.40	15	0-5.6	2-2.6	
5	610 mm _Scarus_ _guacamaia_	"	0.23	21	0-4.5	2-3	
	610 mm _Scarus_ _guacamaia_	"	0.12	18	0-6	0-2	High level of background noise

Table 2. The spectral analyses of the feeding sounds of small parrotfishes (127-254 mm in length)

Figure Number	Sound Producer (Size & Species)	Description* and Number of Sounds	Individual Sound Duration (sec)	Spacing of Sound Units (sec)	Frequency Range (khz)	Predominant Frequency (khz)
12	254 mm ♂ *Scarus vetula*	CRUNCH (1)	0.18 (23 pulses)	—	0-3	2
6	229 mm ♀ *Scarus vetula*	SCRAPES (3)	0.05- 0.06	0.53- 0.90	0-7	1.2-2.8
13	254 mm ♂ *Scarus taeniopterus*	CRUNCH (1)	0.20 (13 pulses)	—	0-3.2	0-1
		SCRAPE (1)	0.04	—	0-7	6-7
7	254 mm ♂ *Scarus taeniopterus*	SCRAPES (5)	0.04- 0.05	0.50	0-12	Spread over entire range
8	127 mm Striped juvenile	SCRAPES (6)	0.03- 0.04	0.50	0-11	Spread over entire range
9	152 mm Juvenile parrotfish (species unknown)	SCRAPES (5)	0.04- 0.07	0.40- 0.60	0-8	Spread over entire range

*Number of sounds recorded appears in parenthesis male and female *Scarus vetula*, male *Scarus taeniopterus* and two unidentified juvenile species. Small female *Sparisoma viride* and several other species of unidentified juvenile parrotfishes all within the range of 152-203 mm have also been observed to rasp while grazing and characteristically produce SCRAPE sounds. Unfortunately, no recordings of the SCRAPES produced by these latter two types of fishes were made. Also, whereas the smaller adult male parrotfishes encountered (*Scarus vetula* and *Scarus taeniopterus* of about 254 mm) generally rasp while feeding they occasionally produce a nearly typical CRUNCH-like sound (Table 2, p. 18). Spectrographic analyses have revealed that the frequency structure of this sound is basically similar to the frequency structure typical of CRUNCHES produced by fishes in the larger size category. Figure 12 (Appendix A) is a sonogram of a CRUNCH produced by a 254 mm male *Scarus vetula*, and Fig. 13 (Appendix A) portrays both a CRUNCH and a SCRAPE produced by a single 254 mm male *Scarus taeniopterus* during feeding. The CRUNCH can not be considered a characteristic feeding sound for fishes of this size due to its very infrequent production, however, its occasional occurrence may indicate the transition from the rasping to the biting mode of feeding in a fish which is at the upper limit of the smaller size category. A behavioral change in feeding habit with age is thus implied—juvenile and small adult parrotfishes are characteristic raspers; larger adult parrotfishes are characteristic biters.

The possibility of some degree of species separation based on feeding sound characteristics is also indicated in Table 2 (p. 15). However, to what extent these relatively fine distinctions are coincidental is uncertain. In both cases, it can be seen that there is a moderate amount of variation among the sonic characteristics of analyzed sounds even among fishes of the same species and size.

This is expected, however, in consideration of the essentially mechanical nature in which parrotfishes generate adventitious feeding sounds. For example, as the fused jaw teeth move across the irregularities of a coral substrate only certain parts of the biting surface will be in contact with the substrate at any point in time. The velocity at which the teeth travel as they skip across the coral surface also must vary instantaneously. As a result the components of each feeding sound are irregularly spaced and a certain degree of variation is inherent in the frequency structure. Nonetheless, a sufficient degree of distinction can be consistently made between the CRUNCH and the SCRAPE to justify their definition as the two fundamental feeding sounds. Shown in Table 3 are the spectral characteristics of the CRUNCH and the SCRAPE.

The CRUNCH is a long duration sound composed of a variable number of pulses, and it has a mean duration time of 0.31 sec for the sounds analyzed. Most acoustical energy is contained in the range of 0-6,000 hz, and a predominant mode in the frequencies of maximum energy expenditure generally exists in the 0-4,000 hz range. When this sound is repeated several times in succession it

Table 3. The spectral characteristics of the CRUNCH and the SCRAPE (*M* = mean value)

Description of Sound	Sound Duration (sec)	Sound Spacing (sec)	Number of Pulses	Pulse Duration (sec)	Frequency Range (khz)	Predominant Frequency (khz)
CRUNCH	0.09-0.65 (M = 0.31)	Highly variable (M ≧ 1.0)	8-32 (M = 17)	0.003-0.013 (M = 0.007)	0-8 (Most in the range of 0-6)	0-4
SCRAPE	0.04-0.07 (M = 0.05)	0.40-0.90 (M = 0.50)	1-4 (M = 2)	0.003-0.013 (M = 0.007)	0-12	Acoustical energy typically well distributed over the entire range of frequencies

is usually at irregular intervals but with a temporal spacing of generally not less than 1.0 sec. As mentioned previously, this fact relates directly to the more leisurely feeding behavior of the larger parrotfishes which produce the CRUNCH sound. Their preference is to feed by taking rather large deliberate bites from a coral surface and its algal mat while hovering in the water just above. Each forward biting action is followed by a brief "recovery" maneuver of variable duration in which the fish draws back a short distance from the substrate before making another feeding lunge. The result is a series of CRUNCH sounds which occur irregularly spaced in time but are typically separated by no less than 1.0 sec.

The SCRAPE is a high frequency sound (up to 12,000 hz) composed of from 1-4 pulses, and it is characteristically repeated in quick rhythmic sequence. Each individual SCRAPE in such a sequence has a mean duration of 0.05 sec and is quite regularly spaced at a mean value of 0.5 sec from each preceding and following sound in the sequence. The temporal spacing here again is directly related to a behavioral phenomenon since small parrotfishes feed by rhythmically rasping an algal covered substrate and thereby produce a series of regularly spaced SCRAPE sounds. The methodical and almost stereotyped manner of feeding of small parrotfishes as compared to the variable and essentially irregular feeding approaches of larger parrotfishes is a basic behavioral difference that accounts for what may well be the most distinctive criterion for differentiating the two types of feeding sounds. The SCRAPE occasionally exhibits a predominant mode of maximum expenditure of acoustic energy in the 3,000-5,000 hz frequency range. However, more commonly the expenditure of acoustic energy is spread rather uniformly over the total range of frequencies spanned. This property of the SCRAPE is readily identifiable in the sonograms appearing in Figs. 6 through 9 which are among those representing the feeding sounds of each of the species studied (Fig. 1-13; Appendix A). All sonograms are of the contour display type and amplitude is contoured at six decibel (db) increments over a total range of 42 db, with the darkest shaded level representing the highest amplitude. Frequency is represented along the vertical axis, and time is represented along the horizontal axis.

The sonograms of CRUNCHES in Figs. 10 and 11 are also quite interesting. In Fig. 10 there is evidence of a trailing SCRAPE-like sound component probably produced when the fish's teeth superficially nicked the substrate at the end of a typical biting action. In this case, as in a typical SCRAPE, the frequencies are well spread over the entire range covered by the sound and the trailing component can be heard in the form of a light, momentary crescendo rather than as a discrete sound. In Fig. 11 a similar short trailing component is present, however, in this case the basic frequency structures of the main CRUNCH sound and the trailing component do not differ and no terminating crescendo effect or other indication of its presence can be discerned aurally. This implies that the SCRAPE appears higher pitched to a listener not only because it reaches into higher frequency levels, but also because its acoustical energy is spread more uniformly over these levels. The low frequency sound components of the SCRAPE thus become isolated and de-emphasized in favor of the higher frequencies giving the sound a relatively higher pitch. The CRUNCH, which lacks pronounced high frequency components, is biased toward the lower frequencies and therefore appears lower in pitch.

Finally, it was necessary to investigate the possibility that the observed differences in feeding sounds were the result of inherent physical properties of different coral substrates being rasped or bitten rather than the result of the species or sizes of the feeding fishes themselves. This was accomplished by isolating a 457 mm Scarus guacamaia in a tank with several known species of corals. The feeding sounds that later resulted were recorded and analyzed with a Kay Vibralyzer in the same manner as were the previously studied sounds. Basically, it was found that, except for the expected amount of seemingly inevitable variation, the type of substrate had no effect on the frequency characteristics of the feeding sounds generated. Figures 14 through 18 (Appendix B) are sonograms of the sounds produced by the captive 457 mm S. guacamaia while feeding on species of Diploria strigosa, Porites astreoides, Montastrea annularis, Colpophyllia natans, and Acropora palmata, respectively. From these figures it is evident that sonic variations occurring from one coral to the next are mainly temporal in nature—resulting from chance contact between the fish's teeth and the coral surfaces and variations in the intensities and sizes of bites attempted by the fish. The important fact is that the frequency structures of feeding-generated sounds are generally consistent, and in some cases surprisingly so, regardless of the species of coral. A 0-3,000 hz concentration of acoustical energy exists in all cases with, generally, another lesser concentration up to 6,000 hz. Energy expenditure in frequencies above 6,000 hz exists, but at a much less intense level. These values are very similar to those obtained from tape recordings of the feeding sounds of the same species of fish in the Bahamas (Table 1, p. 15). The importance of similarity of frequency structures in making feeding sound comparisons among fishes within the same size category must be emphasized, as temporal characteristics of mechanically generated sounds are at the mercy of too many uncontrollable variables. This type of variation should not be confused with the temporal considerations which help to distinguish the feeding sounds of small and large fishes, however. Such temporal variations are the result of behavioral differences in feeding habit and are not chance variations as those mentioned above. The final conclusion must, therefore, be that the species of coral itself is not significant when considering the cause of frequency structure variations among parrotfish feeding sounds. Whatever significant distinctions do exist must be due to different species or sizes of feeding fishes or to other conditions which affect the fishes' feeding behavior.

In summary, the most important fact revealed by the sonic analyses is the indication of a behavioral change in feeding habit with age among the parrotfishes studied. Small parrotfishes (juveniles and small adults) of from 127-254 mm in length feed rather superficially by rasping the algal growth covering hard substrates. Parrotfishes of 305 mm or greater in length characteristically bite or gnaw at such hard substrates during their feeding endeavors. These differences in feeding behavior ultimately account for the production of two basic types of feeding sounds—the SCRAPE and the CRUNCH—which are believed to be characteristic of the small and large parrotfish feeding categories respectively.

The CRUNCH and the SCRAPE differ in their basic sonic characteristics including, most importantly, their temporal properties and frequency structures. The temporal spacing of repeated sounds, in particular, defines a basic difference between the CRUNCH and the SCRAPE and directly reflects the differences in feeding behavior which exist between large and small size categories of fishes. Analyses have also suggested that the SCRAPE sounds higher pitched than the CRUNCH because of a tendency to distribute its acoustical energy into higher frequency ranges. The CRUNCH, with only low frequency components naturally appears lower in pitch.

Finally, tests using several different species of corals as feeding substrates have shown that, except for a small degree of inherent variation, the type of substrate is negligible in affecting the frequency characteristics of feeding-generated sounds.

Diurnal Grazing Cycle

The daily occurrence of sounds at four stations along the reef is represented graphically (Figs. 19-31; Appendix C) and forms the basis for determining the cycle of grazing activity. Each graph shows the time of occurrence and relative numbers of both the SCRAPE and CRUNCH sounds at the designated stations. Bars above the zero line represent the number of CRUNCHES heard per 5-min intervals and those below represent the number of SCRAPES, also with a resolution time of 5 min. Local time is shown along the bottom edge of each graph.

In cases where several shaded bars occur adjacent to one another the graphs should not necessarily be interpreted to mean that sounds were heard continuously over the time intervals spanned. What is actually indicated is that a number of sounds was recorded within each of the shaded 5-min intervals and considerable gaps where no sounds were heard occur within these intervals. The appearance of a sequence of adjacently placed bars does indicate a high level of feeding activity in the immediate area, however, because the presence of a large number of feeding fishes will increase the likelihood of detecting feeding sounds within each interval of recording time.

Station I was a small solitary coral head surrounded by an expanse of bare sand that separated it from the main reef by a distance of approximately 15 m. Unfortunately, as in several other instances, data are quite incomplete for this station, however, it can be seen that parrotfish sound production is definitely a daytime phenomenon. A certain level of sound production is indicated in practically all cases of daytime monitoring. There is also an indication that the sonic activity associated with parrotfishes at this station is sporadic in nature, which may be due to the station's isolated location. The two types of feeding sounds generally occur together, but either may also occur independently. In such cases, the occurrence of solitary SCRAPES was more frequent than the occurrence of solitary CRUNCHES. The earliest definite identification of sounds was for CRUNCHES at 0815 hr on July 23 (Fig. 19). The latest recording of definite feeding sounds was at 1935 hr on July 25 (Fig. 21).

Station I-A was located on one of a series of patch heads that ran slightly landward and to the rear of the habitat. The station was found to be generally active during the midafternoon (1300 to 1600 hr) on July 23 (Fig. 23), the only occasion on which it was monitored. There was a slightly greater proportion of CRUNCHES recorded, however a high degree of correlation between CRUNCHES and SCRAPES is evident.

Station II, a large patch head adjacent to the habitat on its seaward side, presented a relatively high level of sustained acoustic output throughout daylight monitoring, thereby indicating a high level of daytime feeding activity. This fact was easily verified by visual observations as Station II was clearly within the field of the habitat's viewing port. Feeding sounds were detected during almost all daytime listening periods, and again concurrence exists between SCRAPES and CRUNCHES. Here, as at Station I, feeding, with its accompanying sound production, is exclusively a daytime activity. On the two occasions when recordings were made during the early morning and late evening hours at Station II (i.e. the evening of July 23 and the morning of July 24) there were no feeding sounds detected earlier than 0835 hr, on July 24 (Fig. 26), or later than 1935 hr, on July 23 (Fig. 25).

Station III-A was located 200 m seaward of the habitat site abreast a large cave in the reef. Recordings from this station relayed a relative predominance of the SCRAPE sound. Again we find a generally high level of acoustic activity associated with parrotfish grazing throughout most of the afternoon hours and a total absence of such sound production during the early morning and late evening. SCRAPES and CRUNCHES occurred concurrently as a rule, but when concurrence did not exist, SCRAPES were more likely to appear independently. The earliest definite feeding sounds were heard at 0810 hr on July 24 (Fig. 29), and the latest were heard at 1920 hr on July 25 (Fig. 30).

The graph appearing in Fig. 32 (Appendix C) represents the average of parrotfish feeding sounds for all four stations computed over the entire five days of monitoring. Although this is a gross overall representation, the averaging helps to present a more uninterrupted picture of the most outstanding aspects of the local parrotfish grazing behavior. As in the individual graphs

(Figs. 19-31), the generally high level of sustained acoustic output of parrotfish origin throughout daylight hours, the absence of early morning (before 0810 hr) and late evening (after 1935 hr) sound production, and the generally concurrent occurrence of SCRAPES and CRUNCHES are quite evident in this figure.

The approximate locations of the stations and the relative position of Hydro-Lab are shown in Fig. 33.

An erratic appearance has been imparted upon the plots of feeding sounds largely as a result of brief interruptions that occurred sporadically throughout daytime monitoring. Bursts in the frequency of sound production during continuous monitoring are evident also. Visual observations have shown that such activity bursts occur when a group of feeding fishes swims within range of a hydrophone. These groups were somewhat heterogeneously composed and usually contained two or three brightly colored adult parrotfishes and a number of smaller drably colored individuals. A few surgeon fishes and butterflyfishes were sometimes included but these fishes proved to be unimportant as sound producers. The aggregations were generally made up of from five to six to as many as 15 individuals and in some cases more than one species of parrotfish was throught to be present. Identification of juvenile fishes was very difficult, however, and such aggregations may represent the schooling of large adult males and smaller females and juveniles in the type of "cow-bull" relationship described by Winn and Bardach (1960). The most important fact, from the standpoint of sound production,

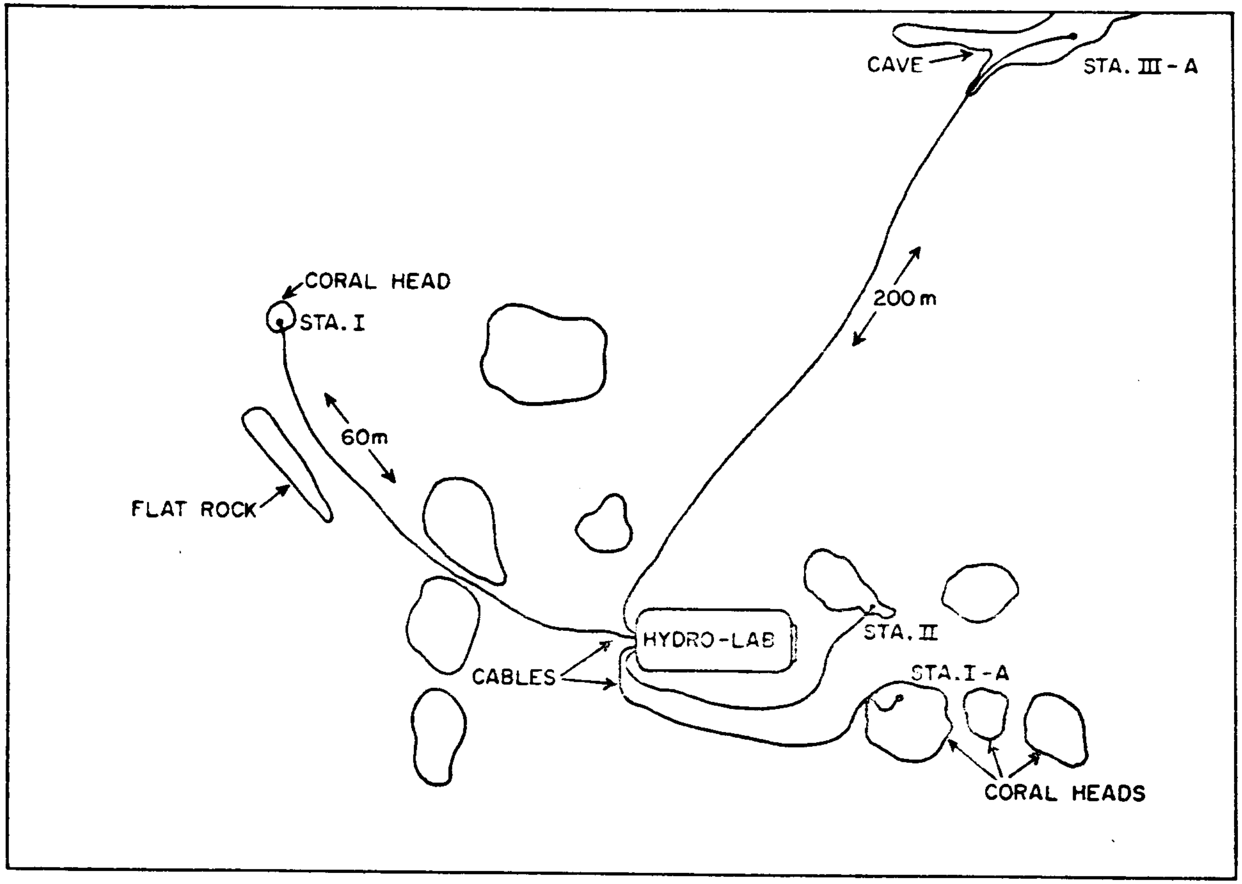


Fig. 33. The approximate locations of the stations and the relative position of Hydro-Lab.

is that the fishes within any single feeding aggregation fell into two broad size categories—juveniles and smaller adults of 127-254 mm in length and larger adults of 305-356 mm. This accounts for the general concurrence of the two types of feeding sounds (CRUNCH and SCRAPE) especially during the most active feeding sessions.

These groups wander about the reef as a nomadic entourage stopping here and there to feed before moving off again in a fairly well defined unit. Feeding stops were quite variable in duration and were observed to range from 30 sec to 10 min or more. When such a group comes within range of a hydrophonic station the system registers an abrupt increase in feeding activity. The temporal spacing of activity bursts is determined by chance passings of the feeding groups; activity bursts being more frequent during afternoon hours when the fish are more actively feeding and are therefore likely to pass a station more often. In instances where extremely high levels of sonic activity appear such as at Station II on July 26 (Fig. 28) or at Station I on July 24 (Fig. 20) the presence of an unusually large feeding group or the convergence of two or more feeding groups is likely since the level of acoustical activity is directly related to the number of feeding individuals. If a coordinated network or a triangulating array of hydrophonic recording stations were used instead of a few isolated sensors the impression of several wandering groups of fishes would probably be gained.

The largest parrotfishes (Blue, Scarus coeruleus, Midnight, Scarus coelestinus, and Rainbow, Scarus guacamaia) which reached a length of 610-914 mm swam solitarily or in groups of two or three. Their periodic stops to bite off pieces of coral are primarily responsible where isolated CRUNCH sounds are recorded. Where a low level of sustained scraping activity occurs (e.g. at Station II on July 24, Fig. 26) the feeding of small relatively nonmobile parrotfishes is probably indicated.

The possibility of confusing extraneous sounds, such as those that may be generated by invertebrates (hermit crabs, gastropods, urchins), with fish sounds exists especially for the SCRAPE. At Station III-A the chance of error was especially great due to its proximity to the cave which undoubtedly offered many territories for invertebrate habitation. Several SCRAPE-like sounds were detected there during night recordings; some gave the impression of a shell being dragged across the substrate, others appeared to be crawling or movement sounds (possibly spiny lobsters), and some resembled the sound of a marble being dropped into a cup (see Bright 1971). As a result, all scraping sounds, especially isolated ones or those not repeated in the characteristic fish-like rhythmic succession, were considered very critically. Cummings, et al. (1964) describe a rhythmic rasping sound that they attribute to the action of the radula of feeding conchs. However, this sound has a much lower frequency range and closer temporal spacing than the rasping sounds of a small parrotfish. Faint mechanical sounds—metallic sounds from the habitat, divers, boats, etc.—can be confused with weak CRUNCHES and again one must be suspicious of a few isolated CRUNCHES especially when they occur at unlikely times of the day. The early morning CRUNCH recorded at 0520 hr at Station I on July 25 (Fig. 21) is an example and probably should not appear on the graph.

The earliest detection of definite feeding sounds for all stations occurred at 0810 hr at Station III-A on July 24 (Fig. 29) and the latest detection of sounds was at 1935 hr at both Station I on July 25 (Fig. 21) and Station II on July 23 (Fig. 25). Our earliest visual observation of active parrotfishes was at 0635 hr on July 25, and the latest sighting of active individuals was at 1955 hr on July 24. Collette and Talbot (1971) observed that parrotfishes in the Virgin Islands first appeared on the reef from 0555 hr to 0635 hr.

In summary, passive acoustic recordings and visual observations indicate a diel grazing behavior in the parrotfishes studied. The fishes feed actively throughout most or all daylight hours (approximately 0810 hr to 1935 hr), however, they move in groups from place to place and this gives the impression of sporadic bursts of feeding activity when a few hydrophones are used for monitoring.

Fishes within feeding aggregations can be grouped into two broad size categories and this accounts for the concurrent production of the SCRAPE and CRUNCH sounds, since these sounds are characteristic of small (127-254 mm) and large (305-356 mm and larger) feeding fishes respectively.

No feeding sounds are heard during early morning or late evening observations, periods when the fishes become inactive.

The feeding of surgeonfishes (Acanthuridae) and other small grazers seen in the area was not accompanied by audible sound production.

A Technique for Assessing the Effect of Grazing on Coral Substrates

The original intent of this part of the study was to assess the effect a parrotfish might have on a particular substrate upon which it was grazing.

To accomplish this a simple experiment was devised in which a single 457 mm *Scarus guacamaia* was placed in a 500-gal aquarium with several preweighed pieces of oven dried coral. Each piece of coral was dried for a period of 8 hr before being placed into the aquarium. In order to persuade the fish to feed upon an oven dried coral it was necessary to apply a thin paste prepared from raw shrimp meat to its surface, thereby simulating the algal growth that would have naturally constituted its nutritive material. After a timed interval of grazing the coral sample was removed, washed, and its dry weight was again determined. In this way the dry weight differential caused by the removal of calcareous material during the fish's grazing activities could be related to the number of feeding sounds heard over the interval. The relationship between the number of feeding sounds and the differential coral weight then served as the basis for determining the fish's effect upon the substrate.

Utilizing this procedure an attempt was made to compare the effect of the fish's grazing activities on four species of corals. The results are presented in Table 4. It is not felt that the present amount of data allows any reliable quantitative generalizations regarding the effects of parrotfish grazing among particular species of corals. A great amount of variability in grazing impact is likely to result from variations in the intensities of the fish's individual feeding rasps, and, therefore, in the amount of calcareous material taken per bite. Also, the use of a substituted food material in the form of the shrimp paste altered feeding behavior by causing the fish to become much more cautious and scrutinizing in its feeding approaches than is normal for fishes grazing in the natural habitat. Such variations naturally become magnified when only a few observations are made. It is felt, however, that this type of passive acoustical technique is potentially useful in assessing the effects of grazing parrotfishes on different types of substrates provided an adequate number of observations are made under carefully controlled conditions.

By analyzing gut contents and estimating the standing crop of parrotfishes on a "typical Bermuda reef" Bardach (1961) calculated that these fishes ingest and redeposit 600 kg of calcareous material per hectare (ha) per year. Conceivably, an analogous calculation could be made using passive acoustical techniques provided a

Table 4. *Calculations of the removal of calcareous material from several species of corals by a 457 mm* Scarus quacamaia *in relation to the number of feeding sounds recorded*

Coral Species	Length of Observation (min)	Water Temperature (°C)	Salinity (o/oo)	pH	Preweight of Coral (g)	Postweight of Coral (g)	Weight Differential (g)	Number Feeding Sounds
Diploria strigosa	75	24.4	22.2	7.89	608	601	7	18
Diploria strigosa	75	24.4	22.2	7.89	1338	1321	17	67
Montastrea annularis	115	24.4	22.2	7.90	1548	1542	6	36
Colpophyllia natans	115	24.4	22.2	7.90	350	343	7	49
Diploria strigosa	154	25.6	24.3	7.75	1305	1299	6	32
Porites astreoides	150	25.6	24.1	7.77	961	960	1	63
Colpophyllia natans	150	25.6	24.1	7.77	338	335	3	7
						TOTAL	47	272

sufficiently reliable calculation of the amount of calcareous material removed per feeding sound could be made. Although the data compiled in Table 4 are probably insufficient for this purpose, a tentative value of 1/6 g of calcareous material removed per CRUNCH sound was calculated.

This was done by relating the total weight differential of corals and the total number of feeding sounds from Table 4 which includes the observations from the entire series of laboratory experiments. An average number of 21 CRUNCH feeding sounds occurring per 11 hr day (the observed interval during which parrotfishes actively fed per 24 hr) was then calculated from the daily occurrence of feeding sounds on July 22 through July 25 at Station II (Figs. 24-27). The occurrence of sounds at Station II on July 26 (Fig. 28) was excluded because the unusually great number of sounds heard over a few intervals of recording time was considered to be anomalous. Using the relationship of 1/6 g of calcareous material removed per CRUNCH, an average figure of 3.5 g (.0035 kg) of calcareous material removed per day was obtained (21 CRUNCHES/day X 1/6 g/CRUNCH).

Bardach (1961) considered the fishes at his study site to be actively feeding for 240 days/yr. The grazeable area of Station II is estimated to be 8 m^2. Utilizing these figures it was calculated that the fishes in the vicinity of Hydro-Lab remove 1050 kg/ha/yr (.0035 kg/day/8 m^2 X 240 days/yr X 10,000 m^2/ha). This value does not differ greatly from that presented by Bardach (1961) particularly in consideration of the limited amount of data upon which the calculations were based and the localized nature of the acoustical observations. The fact that Randall (1963) considered Bardach's (1961) estimate of the standing crop of fishes to be low suggests that his calculation of the amount of calcareous material removed should be adjusted upward to comply even more closely with the value obtained through the passive acoustical method. A second set of calculations using the feeding sounds recorded at Station I on July 23 through July 26 (Figs. 19-22) gave a value for the removal of calcareous material of 520 kg/ha/yr which is also not an extreme departure from Bardach's (1961) results. It would seem that the general agreement of results obtained by either method of calculation verifies the correctness of the basic assumptions upon which the passive acoustical system is based. One additional potential use of this type of system for monitoring the feeding-related activities of parrotfishes is thereby suggested.

CONCLUSIONS

Spectrographic analyses of parrotfish feeding sounds have revealed the existence of a behavioral change in feeding habit with age among those species studied. It was found that juvenile and small adult parrotfishes of 127-254 mm in length feed rather superficially by rasping the algal growth covering hard substrates while parrotfishes of 305 mm or greater in length characteristically bite such hard substrates during their feeding activities. These behavioral differences in feeding habit ultimately account for the production of two basic types of feeding sounds--the SCRAPE and the CRUNCH--which are characteristic of the small and large parrotfish feeding categories respectively.

The CRUNCH and the SCRAPE differ in several of their sonic characteristics including, most importantly, their temporal and frequency structures. The temporal spacing of successively repeated sounds is of particular importance as it is probably the most distinctive feature differentiating the CRUNCH and the SCRAPE. The regular and generally consistent temporal spacing of successively repeated SCRAPES and the highly variable temporal spacing of repeated CRUNCHES also reflects the basic differences in feeding behavior which exist between the small and large size categories of fishes. Analyses have also indicated that the SCRAPE aurally appears higher pitched than the CRUNCH because the SCRAPE exhibits a tendency to distribute its acoustical energy into the higher frequency ranges while the CRUNCH has only low range frequency components.

The spectral analyses of sounds generated by an individual parrotfish grazing on several species of corals have shown that the type of coral substrate is essentially a negligible factor in affecting the frequency structure of feeding-generated sounds.

Passive acoustic recordings and visual observations made from within and around the Hydro-Lab underwater habitat in the Bahamas have verified the existence of cyclical diel grazing behavior in West Indian parrotfishes as suggested by Randall (1967), Collette and Talbot (1971) and others. The fishes feed actively throughout most or all daylight hours (approximately 0810 hr to 1935 hr). However, they move in groups from place to place and this gives the impression of sporadic bursts of feeding activity when a few hydrophones are used for monitoring.

No feeding sounds are heard during early morning or late evening observations indicating periods when the fishes become inactive.

Fishes within any single feeding aggregation can be grouped into two broad size categories and this accounts for the concurrent production of the SCRAPE and CRUNCH sounds.

The feeding of surgeonfishes (Acanthuridae) and other small grazers seen in the area was not accompanied by audible sound production.

Finally, a passive acoustical technique for assessing the effect of grazing fishes on various coral substrates has been devised and tested. Basically, the technique involves relating the amount of calcareous material removed during a fish's grazing activities to the number of feeding sounds heard during the interval of grazing. A great deal of inherent variability in parrotfish rasping behavior combined with a limited amount of data have precluded the possibility of making any reliable quantitative generalizations regarding the effects of parrotfish grazing on particular species of corals. It was possible, however, to determine a tentative relationship of 1/6 g of calcareous material removed per CRUNCH sound from the laboratory experiments. By relating this value to the average number of feeding sounds recorded per day over a known area in the field, it was calculated that 1050 kg/ha/yr of calcareous material would be removed by grazing parrotfishes in the study area. Bardach (1961) calculated a similar value of 600 kg/ha/yr by examining gut contents for calcareous material and estimating the standing crop of parrotfishes on a "typical Bermuda reef". The general agreement of these results seems to verify the correctness of the basic assumptions upon which the passive acoustical system is based, and suggests an additional potential use of this type of system for monitoring the feeding-related activities of parrotfishes.

REFERENCES

ANDRIEU, A. J. 1963. Techniques used for the physical study of acoustic signals of animal origin, p. 25-47. In R. G. Busnel (ed.), Acoustic behavior of animals. Elsevier, Amsterdam.

BAKUS, G. J. 1964. The effects of fish grazing on invertebrate evolution in shallow tropical waters. Allan Hancock Found. Publ. Occasional Paper No. 27: 1-29.

__________. 1966. Some relationships of fishes to benthic organisms on coral reefs. Nature 210: 280-284.

__________. 1969. Energetics and feeding in shallow marine waters. J. Exptl. Zool. 4: 275-369.

BARDACH, J. E. 1959. The summer standing crop of fish on a shallow Bermuda reef. Limnol. Oceanog. 4: 77-85.

__________. 1961. Transport of calcareous fragments by reef fishes. Science 133: 98-99.

BOUGHTON, W. B. 1963. Method in bio-acoustic terminology, p. 3-24. In R. G. Busnel (ed.), Acoustic behavior of animals. Elsevier, Amsterdam.

BRANDT, O. 1963. Principles of underwater acoustics, p. 48-53. In R. G. Busnel (ed.), Acoustic behavior of animals. Elsevier, Amsterdam.

BRAWN, V. M. 1961. Sound production by the cod (*Gadus callarias* L.). Behaviour 18: 239-255.

BRIGHT, T. J. 1971. Bio-acoustic studies on reef organisms. Tektite II Symposium Volume, Science Bulletin. Los Angeles County Museum of Natural History, in press.

BUSNEL, R. G. 1963. Examples of the application of electro-acoustic techniques to the measurement of certain behaviour patterns, p. 54-65. In R. G. Busnel (ed.), Acoustic behaviour of animals. Elsevier, Amsterdam.

CLOUD, P. E., Jr. 1952. Preliminary report on the geology and marine environments of Onota Atoll, Gilbert Islands. Natl. Res. Council, Atoll Res. Bull. No. 12. 73 p.

CLOUD, P. E. jr. 1959. Geology of Sipan, Mariana Islands, U. S. Geol. Surv. Prof. Paper 280-K. 415 p.

COLLETTE, B. B. and F. H. TALBOT. 1971. Nocturnal-diurnal change-over in activity patterns of coral reef fishes observed during the Tektite II program in the Virgin Islands. Tektite II Symposium Volume, Science Bulletin. Los Angeles County Museum of Natural History, in press.

CUMMINGS, W. C., B. D. BRAHY, and W. F. HERRNKIND. 1964. The occurrence of underwater sounds of biological origin off the west coast of Bimini, Bahamas, p. 27-43. In W. N. Travolga (ed.), Marine Bio-acoustics. Pergamon Press, New York.

__________, __________, and J. Y. SPIRES. 1966. Sound production, schooling, and feeding habits of the Margate, Haemulon album Cuvier, off North Bimini, Bahamas. Bull. Marine Sci. 16(3): 626-640.

DARWIN, C. 1909. The voyage of the Beagle. P. F. Collier and Son, New York. 547 p.

DAVIS, L. I. 1964. Biological acoustics and the use of the sound spectrograph. Southwestern Natur. 9(3): 118-145.

EMERY, K. O. 1956. Marine geology of Johnston Island and its surrounding shallows, central Pacific. Ocean. Bull. Geol. Soc. Amer. 67: 1505-1520.

GRABAU, A. W. 1913. Principles of stratigraphy. A. G. Seiler and Co., New York. 1185 p.

HASLETT, R. W. G. 1967. Underwater acoustics. J. Sci. Instrum. 44(9): 709-719.

HIATT, R. W. and D. W. STRASBURG. 1960. Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. Ecol. Monographs 30: 65-127.

HOLT, D. 1967. Opportunities for research utilizing underwater TV and acoustic systems. Bioscience 17(9): 635-636.

MARSHALL, N. B. 1962. The biology of sound producing fishes, p. 45-60. In P. T. Haskell and F. C. Fraser (eds.), Biological acoustics. Symp. Zool. Soc. London No. 7.

MOULTON, J. M. 1958. The acoustic behavior of some fishes in the Bimini area. Biol. Bull. 114: 357-374.

MOULTON, J. M. 1960. Swimming sounds and the schooling of fishes. Biol. Bull. 119: 210-223.

NEWELL, N. D. 1956. Geological reconnaissance of Raroia Atoll, Tuamotu Archipelago. Bull. Am. Mus. Nat. Hist. 109(3): 360.

ODUM, H. T. and E. P. ODUM. 1955. Trophic structure and productivity of a windward coral reef community on Eniwetok Atoll. Ecol. Monographs 25: 291-320.

RANDALL, J. E. 1961. Overgrazing of algae by herbivorous marine fishes. Ecology 42: 812.

__________. 1963a. An analysis of the fish populations of artificial and natural reefs in the Virgin Islands. Caribbean J. Sci. 3(1): 1-16.

__________. 1963b. Notes on the systematics of parrotfishes (Scaridae), with emphasis on sexual dichromatism. Copeia 1963(2): 225-237.

__________. 1965. Grazing effects on sea grasses by herbivorous reef fishes in the West Indies. Ecology 46: 225-260.

__________. 1967. Food habits of reef fishes of the West Indies. Univ. Miami Inst. Marine Sci., Stud. Trop. Oceanog. No. 5: 665-847.

REKUBRATSKII, V. A. 1969. Study of the ecology of fish feeding by recording their sounds. Gibrobiol. Zh. 5(6): 109-113.

SCHULTZ, L. P. 1958. Review of the parrotfishes family Scaridae. U. S. Natl. Mus., Bull. 214: 1-143.

__________. 1969. The taxonomic status of the controversial genera and species of parrotfishes with a descriptive list (family Scaridae). Smithson. Contr. Zool. No. 17: 1-49.

STEINBERG, J. C., M. KRONENGOLD, and W. C. CUMMINGS. 1962. Hydrophone installation for the study of soniferous marine animals. J. Acoust. Soc. Amer. 34(8): 1090-1095.

__________, W. C. CUMMINGS, B. D. BRAHY, and J. Y. MacBAIN (SPIRES). 1965. Further bio-acoustic studies off the west coast of North Bimini, Bahamas. Bull. Marine Sci. Gulf Caribbean 15: 942-963.

STEPHENSON, W. and R. B. SEARLES. 1960. Experimental studies on the ecology of intertidal environments at Heron Island. Australian J. Marine Freshwater Res. 11: 241-267.

STEPHENSON, W. 1961. Experimental studies on the ecology of intertidal environments at Heron Island. Australian J. Marine Freshwater Res. 12: 164-176.

TALBOT, F. H. 1965. The coral structure of Tutia Reef and its fish fauna. Proc. Zool. Soc. London 145: 431-461.

TRAVOLCA, W. N. [ed.] 1964. Marine bio-acoustics, v. 1. Pergamon Press, New York. 413 p.

__________. 1965. Review of marine bio-acoustics, state of the art: 1964. Tech. Report, NAVTRADEVCEN 1212-1. 100 p.

__________ [ed.] 1967. Marine bio-acoustics, v. 2. Pergamon Press, New York. 353 p.

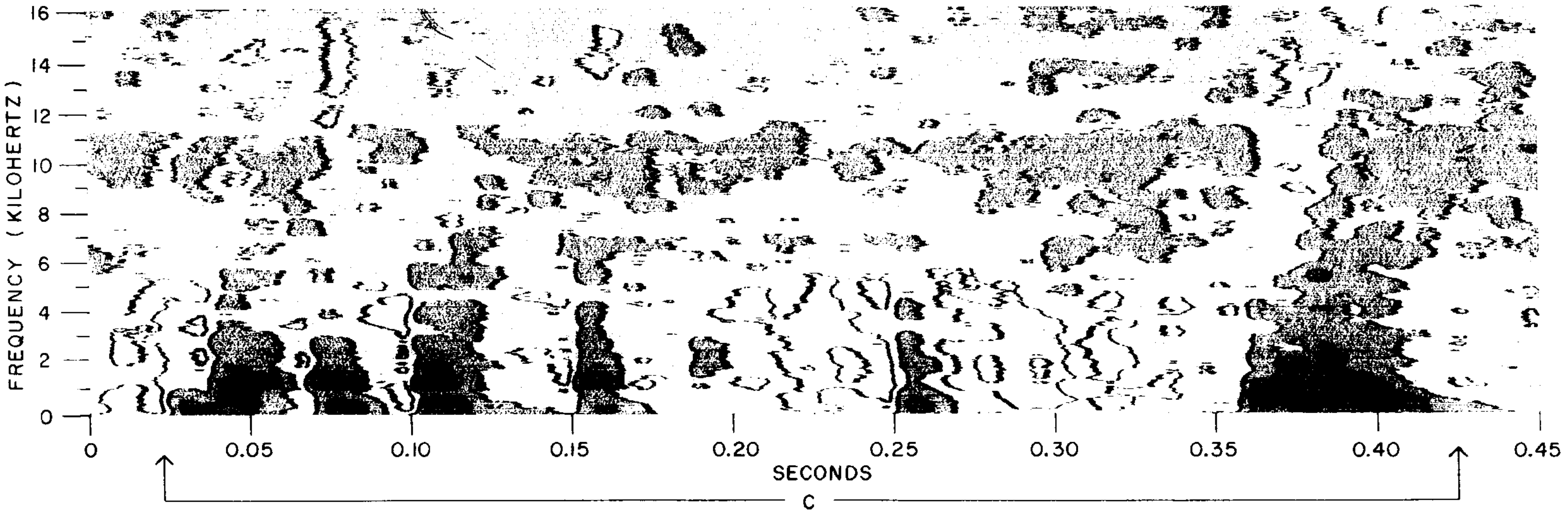
WINN, H. E. and J. E. BARDACH. 1957. Behavior, sexual dichromatism, and species of parrotfishes. Science 125(3253): 885-886.

__________ and __________. 1960. Some aspects of the comparative biology of parrotfishes at Bermuda. Zoologica 45(3): 29-34.

APPENDIX A

Fig. 1. Contour sonogram of a CRUNCH produced by a 305 mm female *Sparisoma viride*. C = CRUNCH.

Fig. 2. Contour sonogram of a CRUNCH produced by a 356 mm male *Sparisoma viride*. C = CRUNCH.


FREQUENCY (KILOHERTZ)
16
14
12
10
8
6
4
2
0
0
0.05
0.10
0.15
0.20
0.25
0.30
0.35
0.40
0.45
SECONDS
C

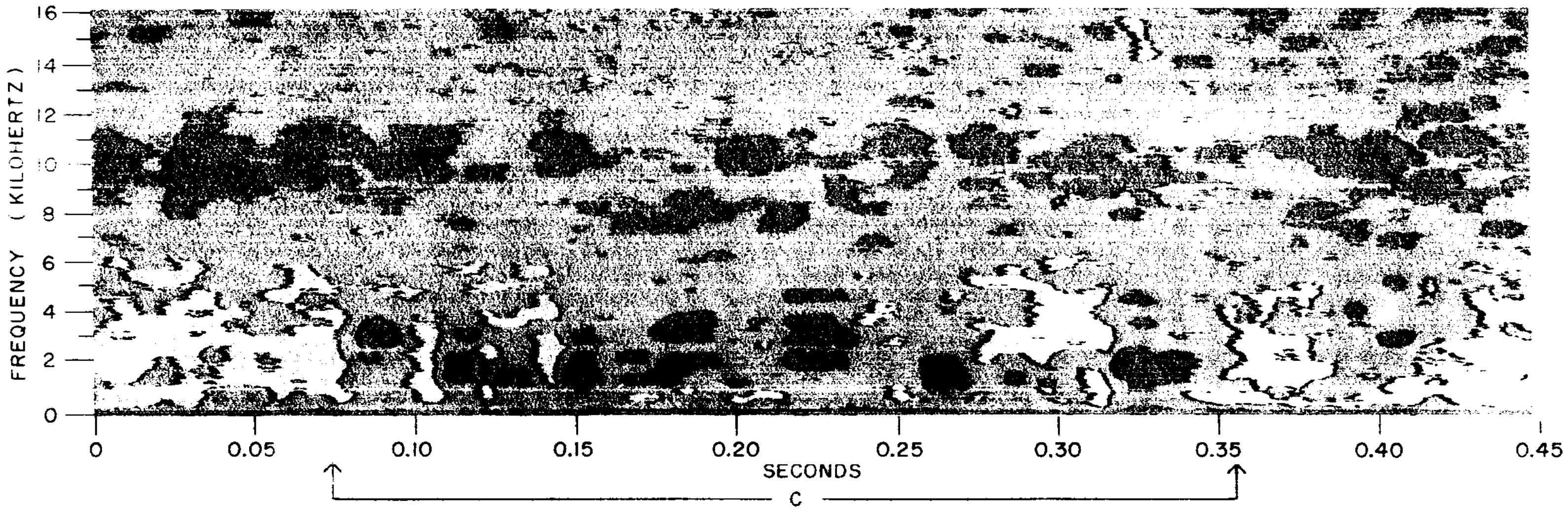
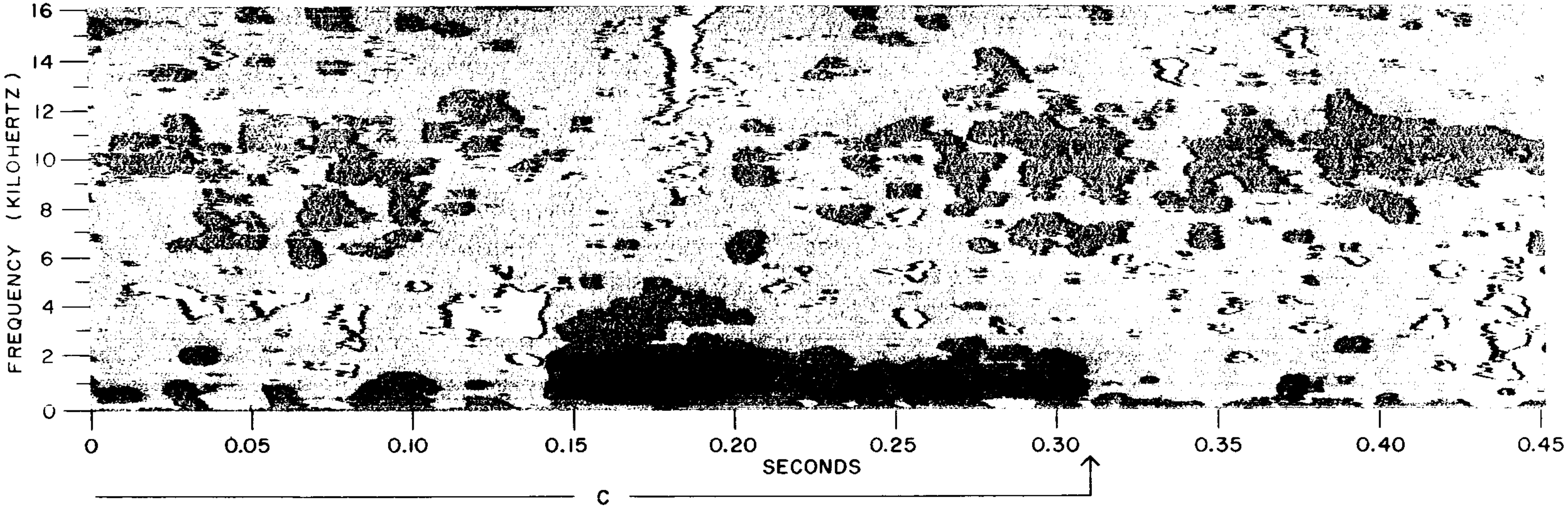

FREQUENCY (KILOHERTZ)
16
14
12
10
8
6
4
2
0
0
0.05
0.10
0.15
0.20
0.25
0.30
0.35
0.40
0.45
SECONDS
C

Fig. 3. Contour sonogram of a portion of a CRUNCH produced by a 457 mm *Scarus coeruleus*. C = CRUNCH.

Fig. 4. Contour sonogram of a CRUNCH produced by a 610 mm *Scarus coelestinus*. C = CRUNCH.


FREQUENCY (KILOHERTZ)
16
14
12
10
8
6
4
2
0
0
0.05
0.10
0.15
0.20
0.25
0.30
0.35
0.40
0.45
SECONDS
C

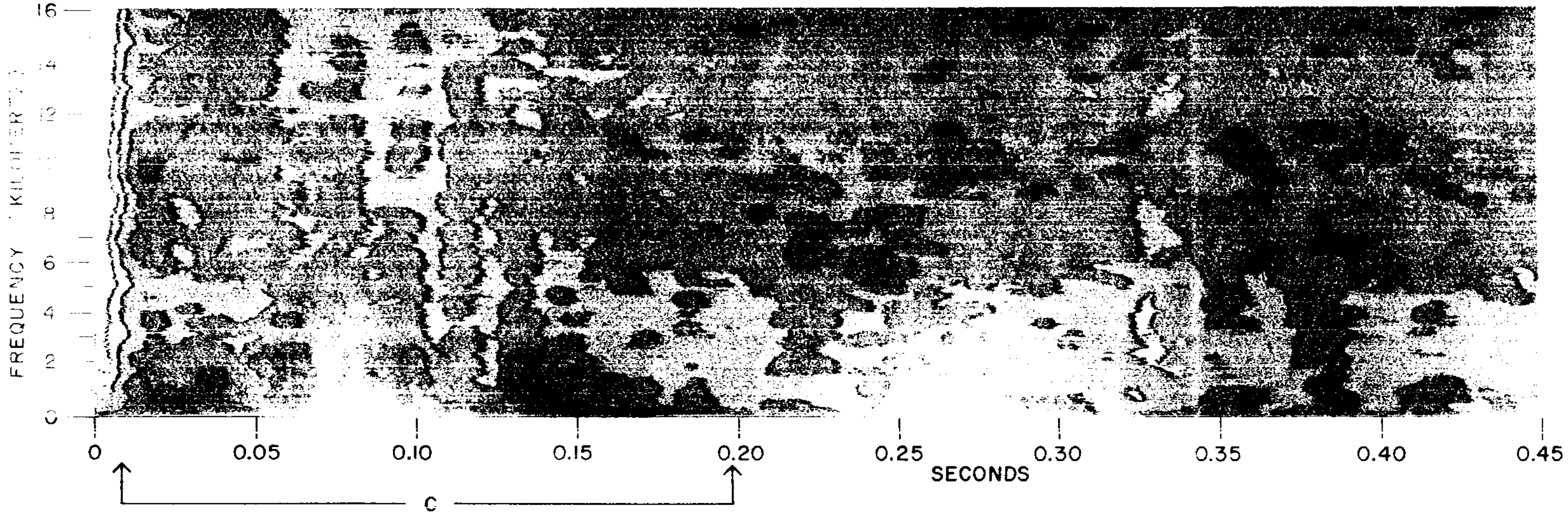
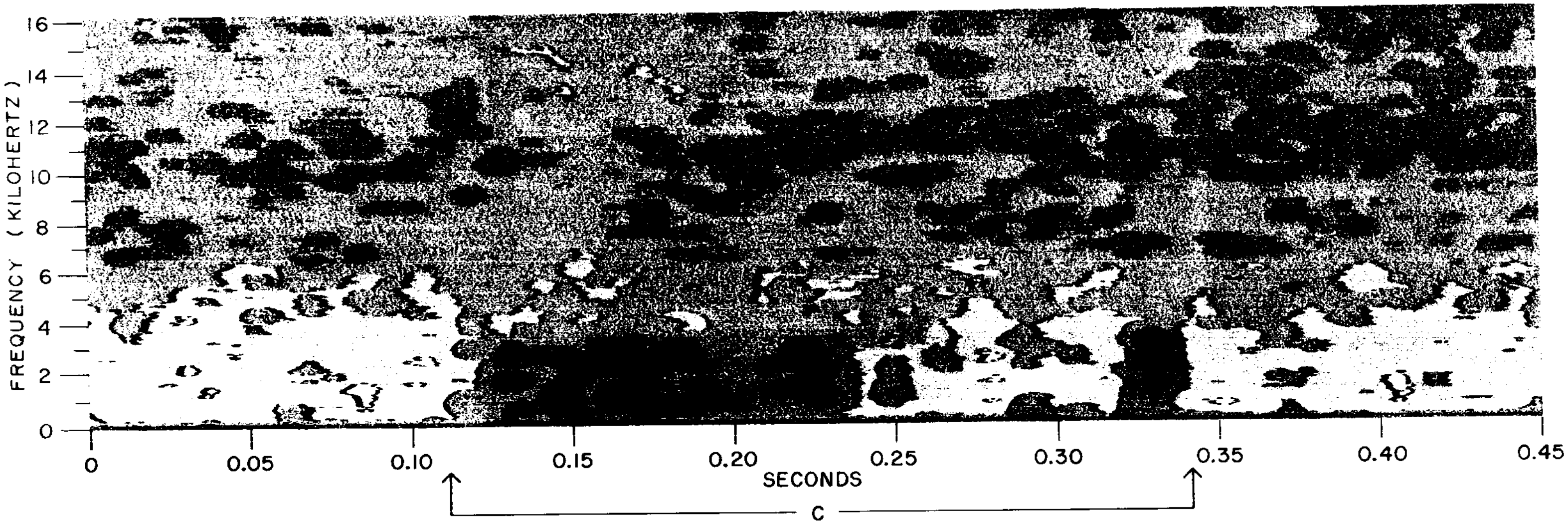

FREQUENCY (KILOHERTZ)
16
14
12
8
6
4
2
0
0
0.05
0.10
0.15
0.20
0.25
0.30
0.35
0.40
0.45
SECONDS
C

Fig. 5. Contour sonogram of a CRUNCH produced by a 610 mm *Scarus guacamaia*. C = CRUNCH.

Fig. 6. Contour sonogram of three SCRAPES produced by a 229 mm female *Scarus vetula*. S = SCRAPE. [The SCRAPES presented here range to 7 khz; the portion of the frequency scale above 4 khz is not shown.]


16
14
12
10
8
6
4
2
0
FREQUENCY (KILOHERTZ)
0
0.05
0.10
0.15
0.20
0.25
0.30
0.35
0.40
0.45
SECONDS
C

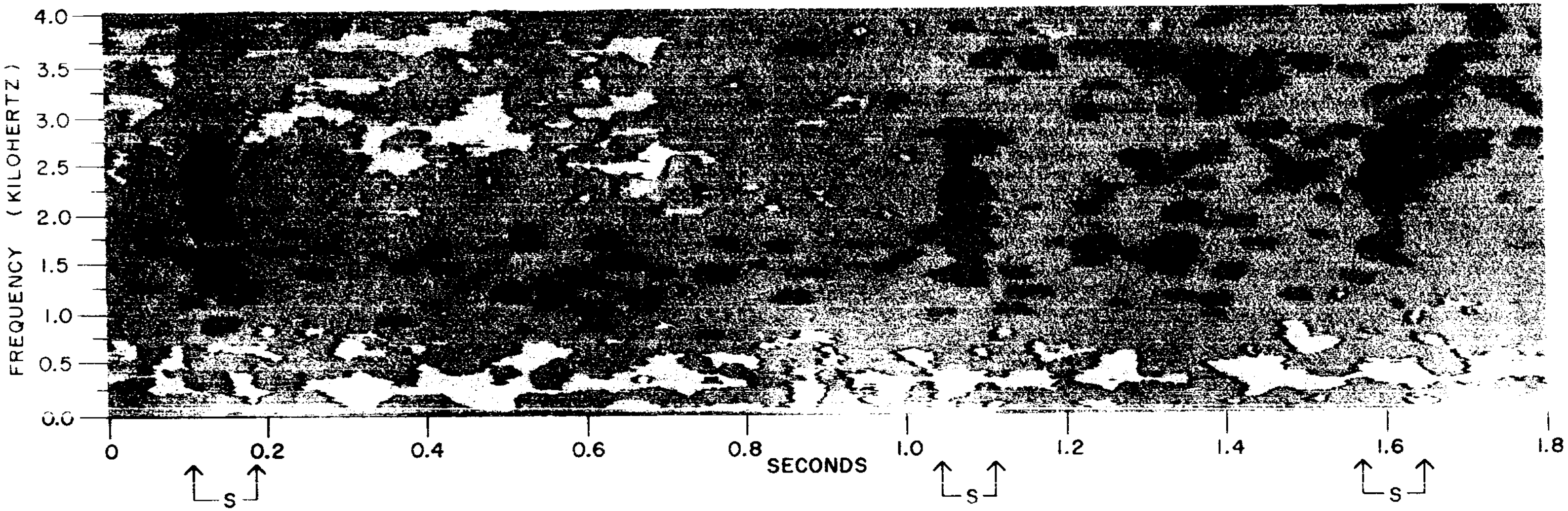
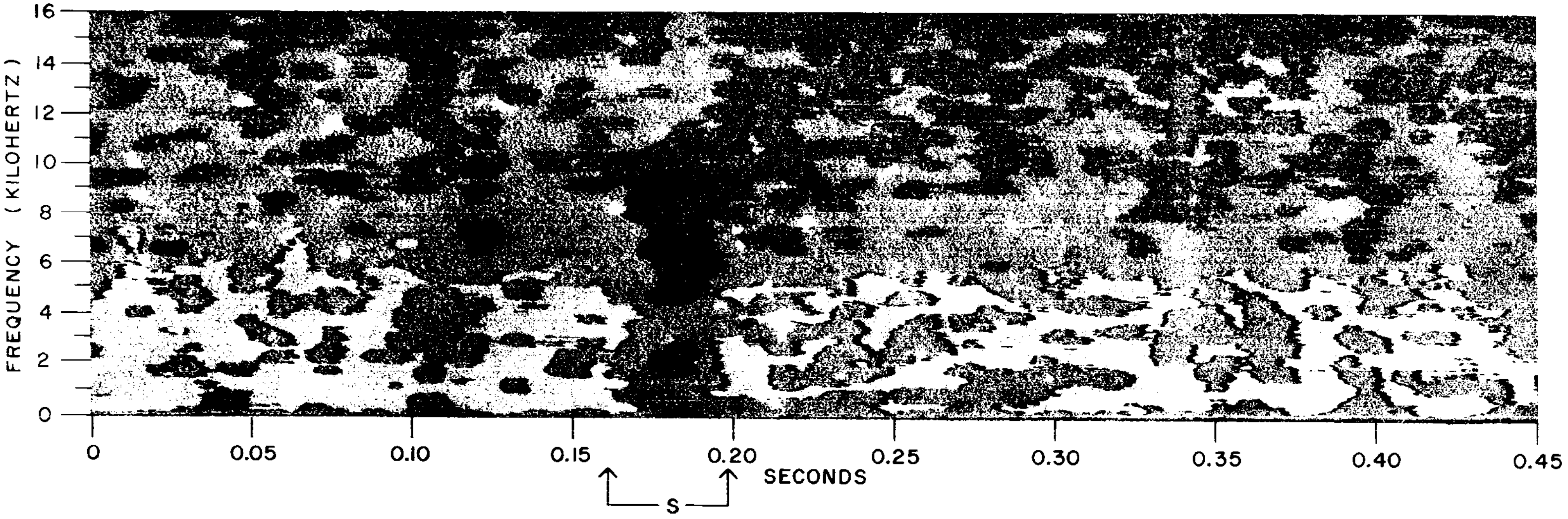

4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
FREQUENCY (KILOHERTZ)
0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
1.8
SECONDS
S
S
S

Fig. 7. Contour sonogram of one of five SCRAPES produced by a 254 mm male *Scarus taeniopterus*. S = SCRAPE.

Fig. 8. Contour sonogram of one of six SCRAPES produced by a 127 mm striped juvenile parrotfish. S = SCRAPE.


FREQUENCY (KILOHERTZ)
16
14
12
10
8
6
4
2
0
0
0.05
0.10
0.15
0.20
0.25
0.30
0.35
0.40
0.45
SECONDS
S

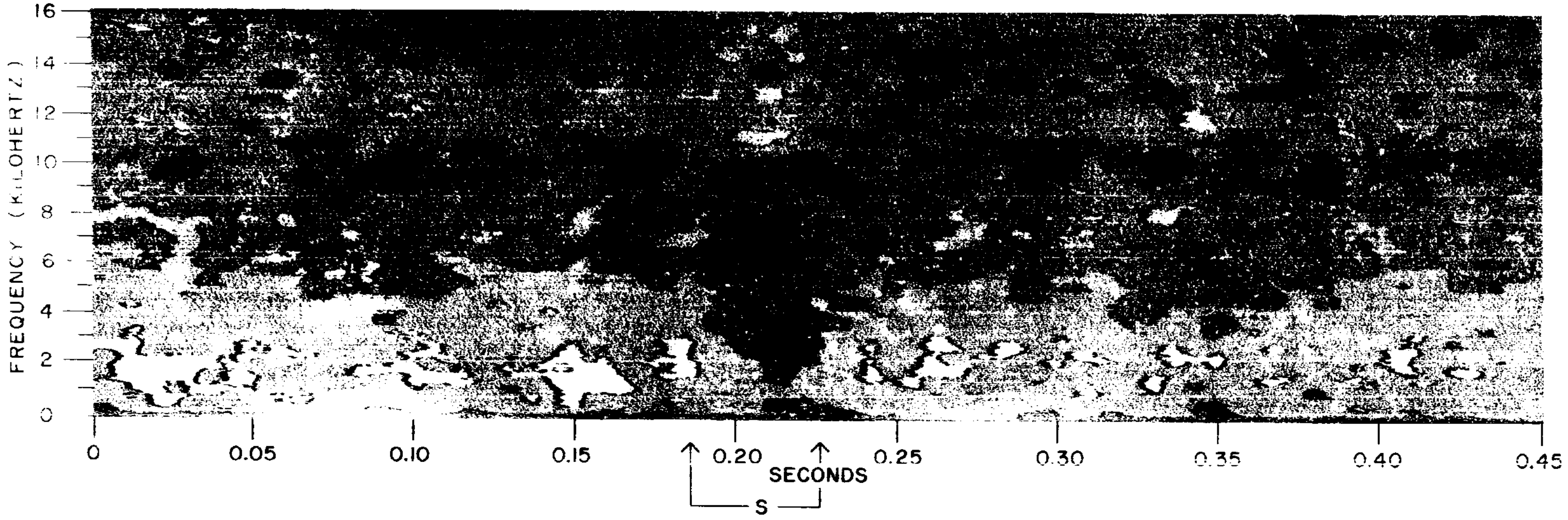

FREQUENCY (KILOHERTZ)
16
14
12
10
8
6
4
2
0
0
0.05
0.10
0.15
0.20
0.25
0.30
0.35
0.40
0.45
SECONDS
S

Fig. 9. Contour sonogram of three of five SCRAPES produced by a 152 mm juvenile parrotfish (species unknown). S = SCRAPE.

Fig. 10. Contour sonogram of a CRUNCH and terminal SCRAPE-like component produced by a 305 mm female *Sparisoma viride*. C = CRUNCH; S' = SCRAPE-like component.

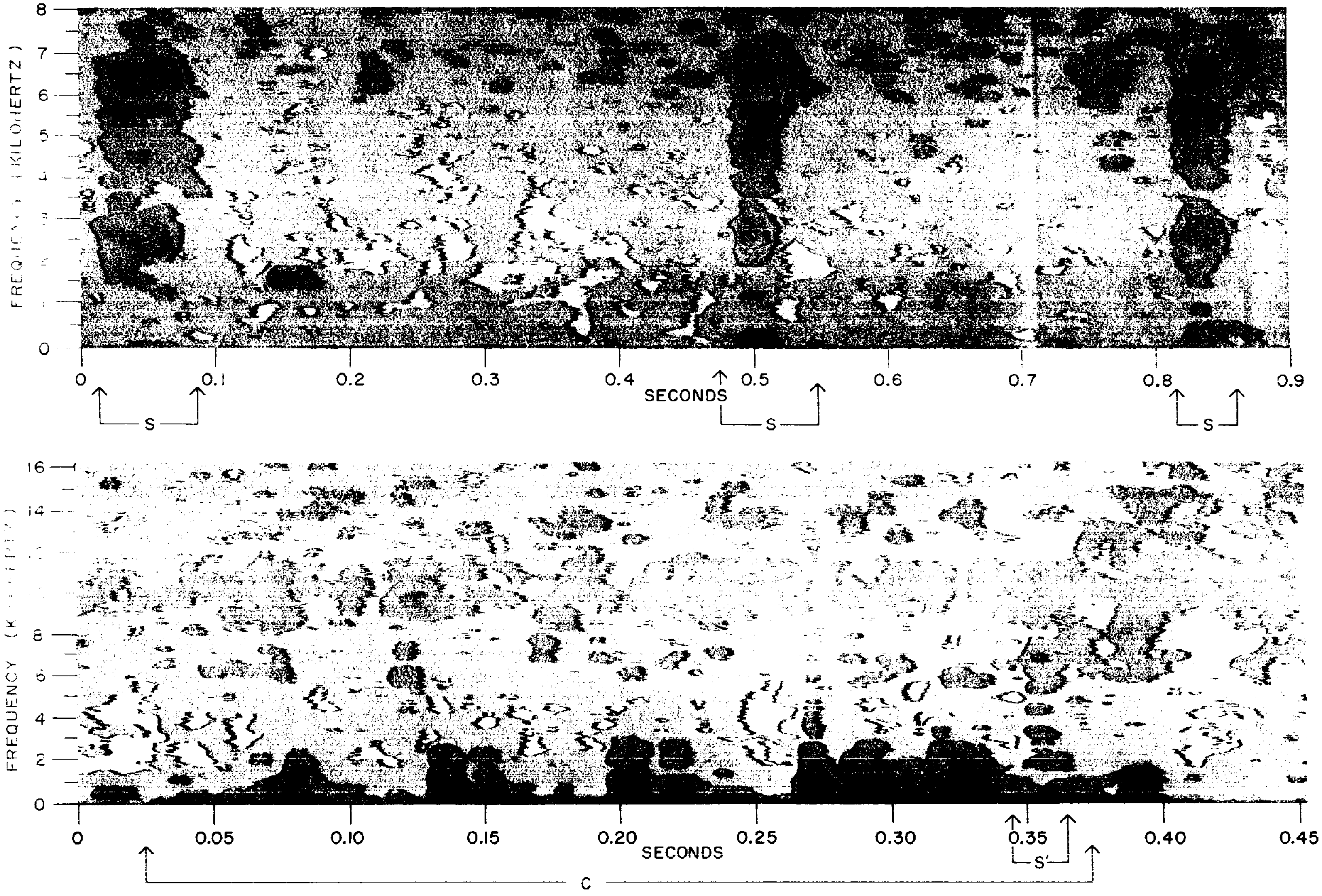
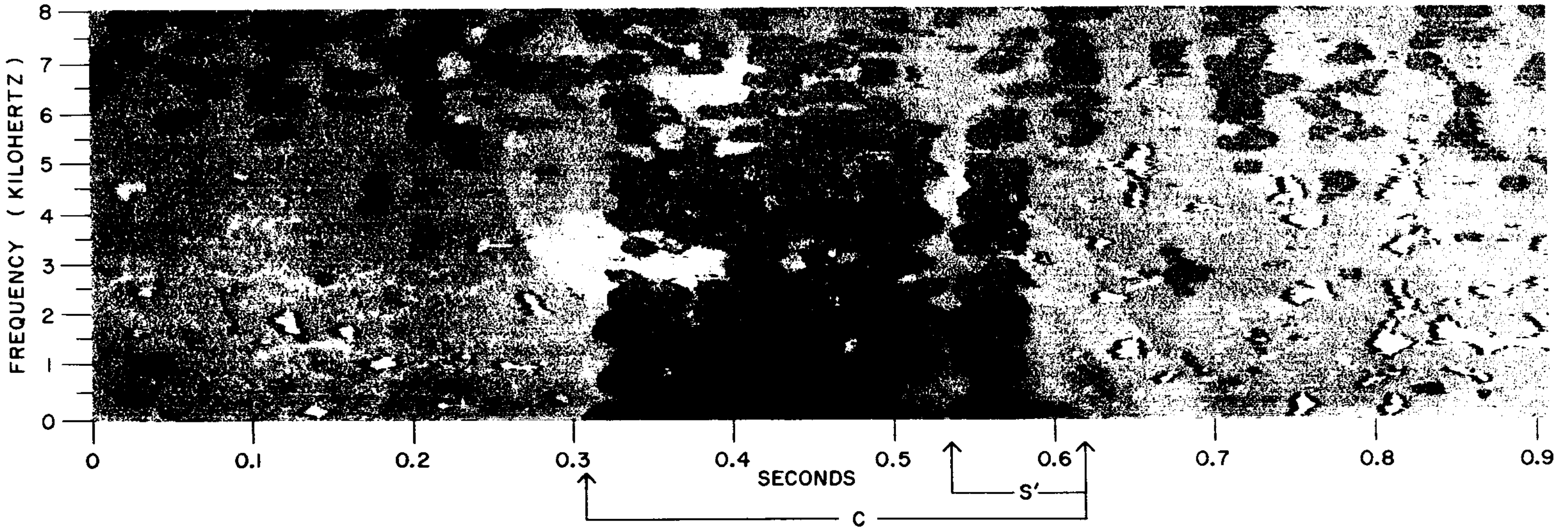
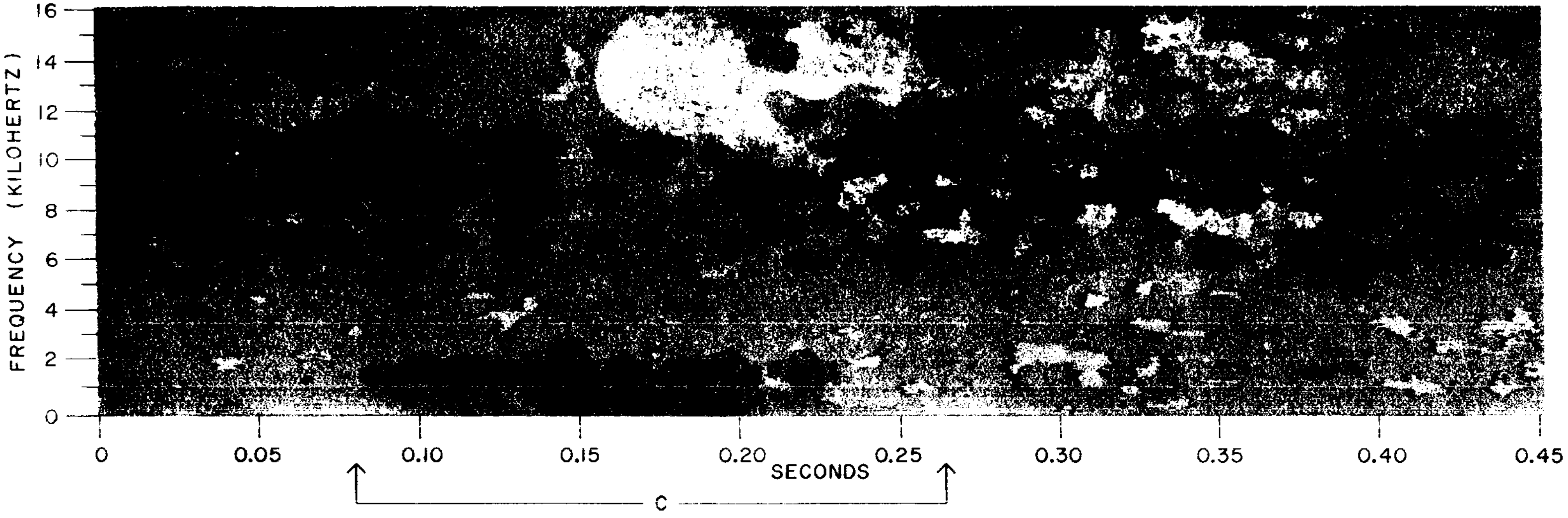

8
7
6
5
4
3
2
1
0
FREQUENCY (KILOHERTZ)
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
SECONDS
S
S
S
16
14
12
10
8
6
4
2
0
FREQUENCY (KILOHERTZ)
0
0.05
0.10
0.15
0.20
0.25
0.30
0.35
0.40
0.45
SECONDS
S'
C

Fig. 11. Contour sonogram of a CRUNCH and terminal SCRAPE-like component produced by a 305 mm female *Sparisoma viride*. C = CRUNCH; S' = SCRAPE-like component.

Fig. 12. Contour sonogram of a CRUNCH produced by a 254 mm male *Scarus vetula*. C = CRUNCH.


FREQUENCY (KILOHERTZ)
8
7
6
5
4
3
2
1
0
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
SECONDS
S′
C


FREQUENCY (KILOHERTZ)
16
14
12
10
8
6
4
2
0
0
0.05
0.10
0.15
0.20
0.25
0.30
0.35
0.40
0.45
SECONDS
C

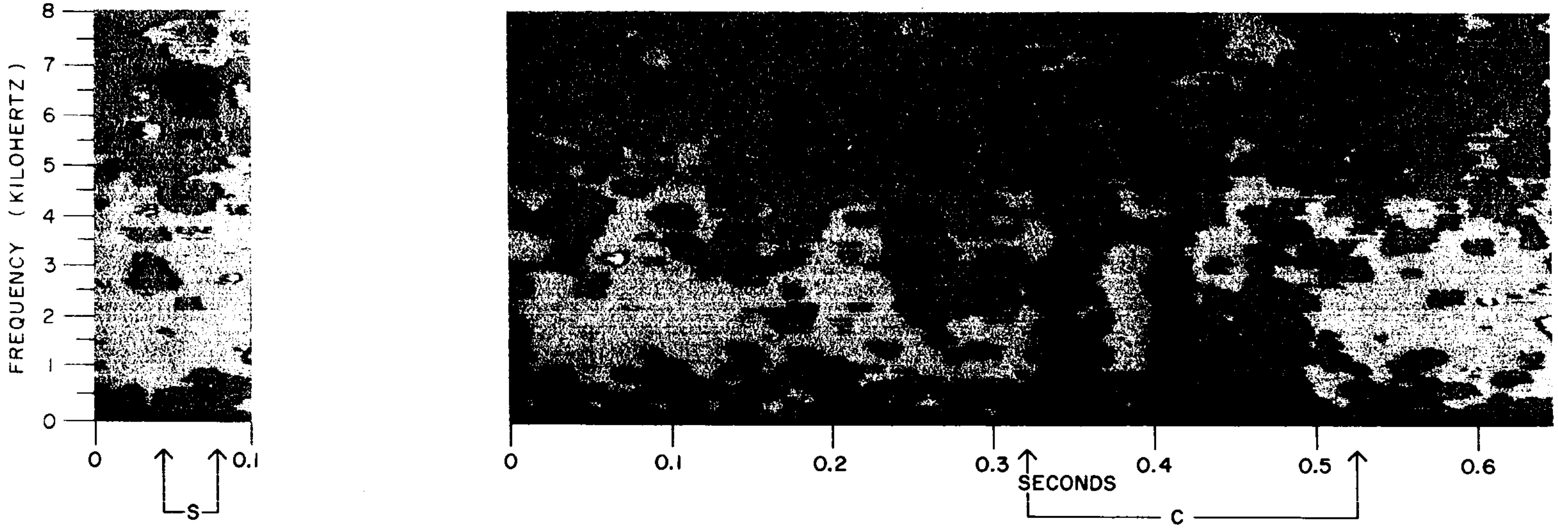


Fig. 13. Contour sonograms of a SCRAPE and a CRUNCH produced by a single 254 mm male *Scarus taeniopterus*. S = SCRAPE; C = CRUNCH.

APPENDIX B

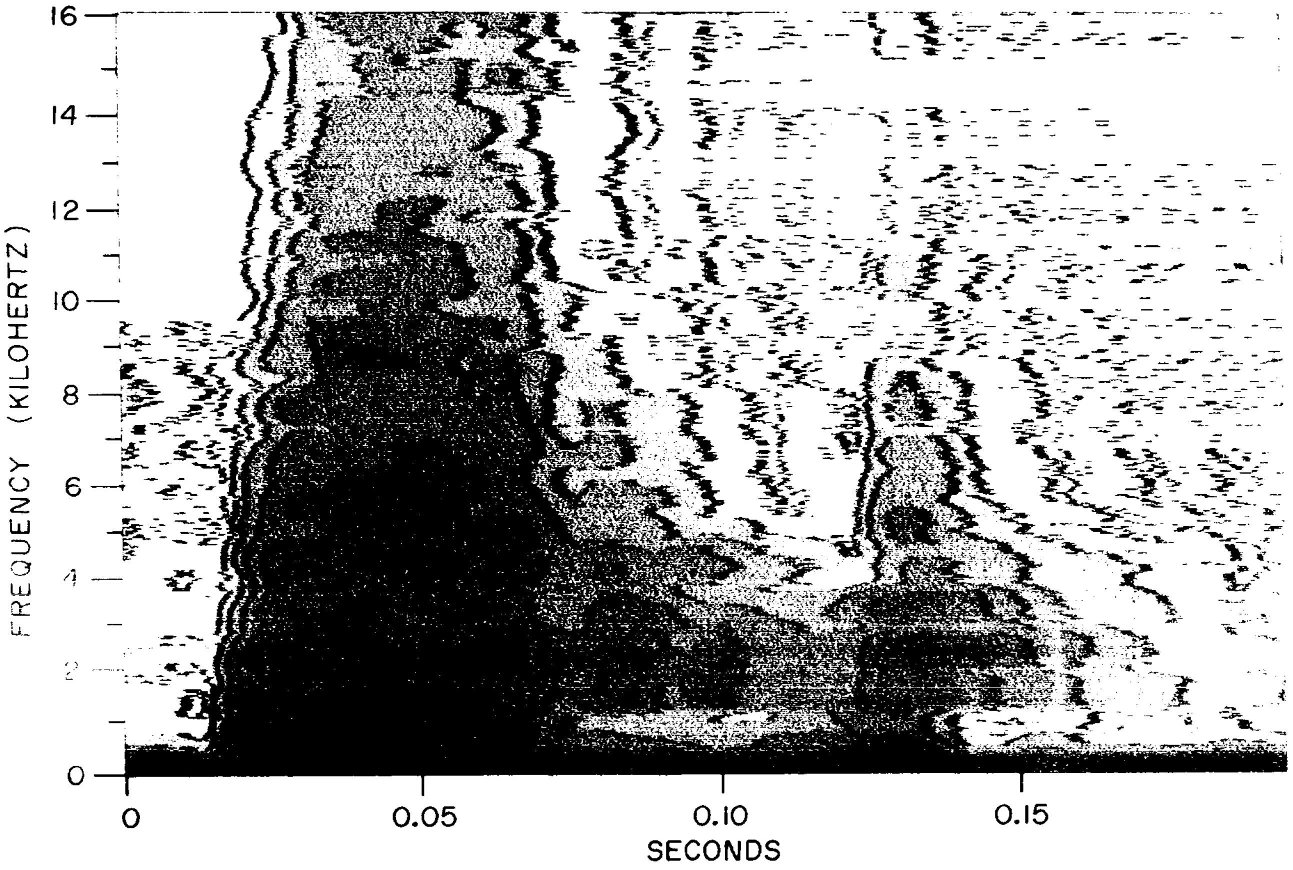


Fig. 14. Contour sonogram of a CRUNCH produced by the captive 457 mm Scarus guacamaia while feeding on Diploria strigosa.

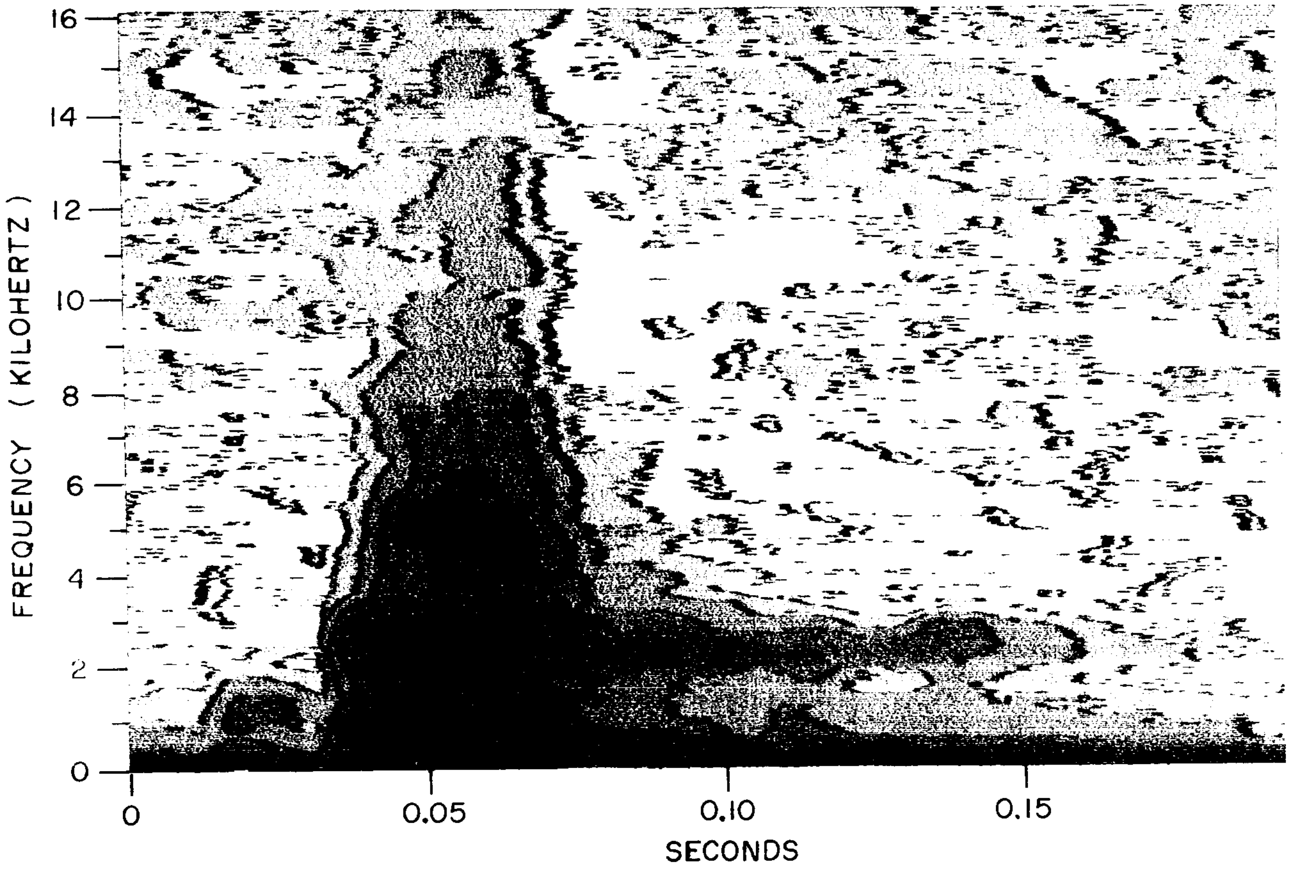


Fig. 15. Contour sonogram of a CRUNCH produced by the captive 457 mm Scarus guacamaia while feeding on Porites astreoides.

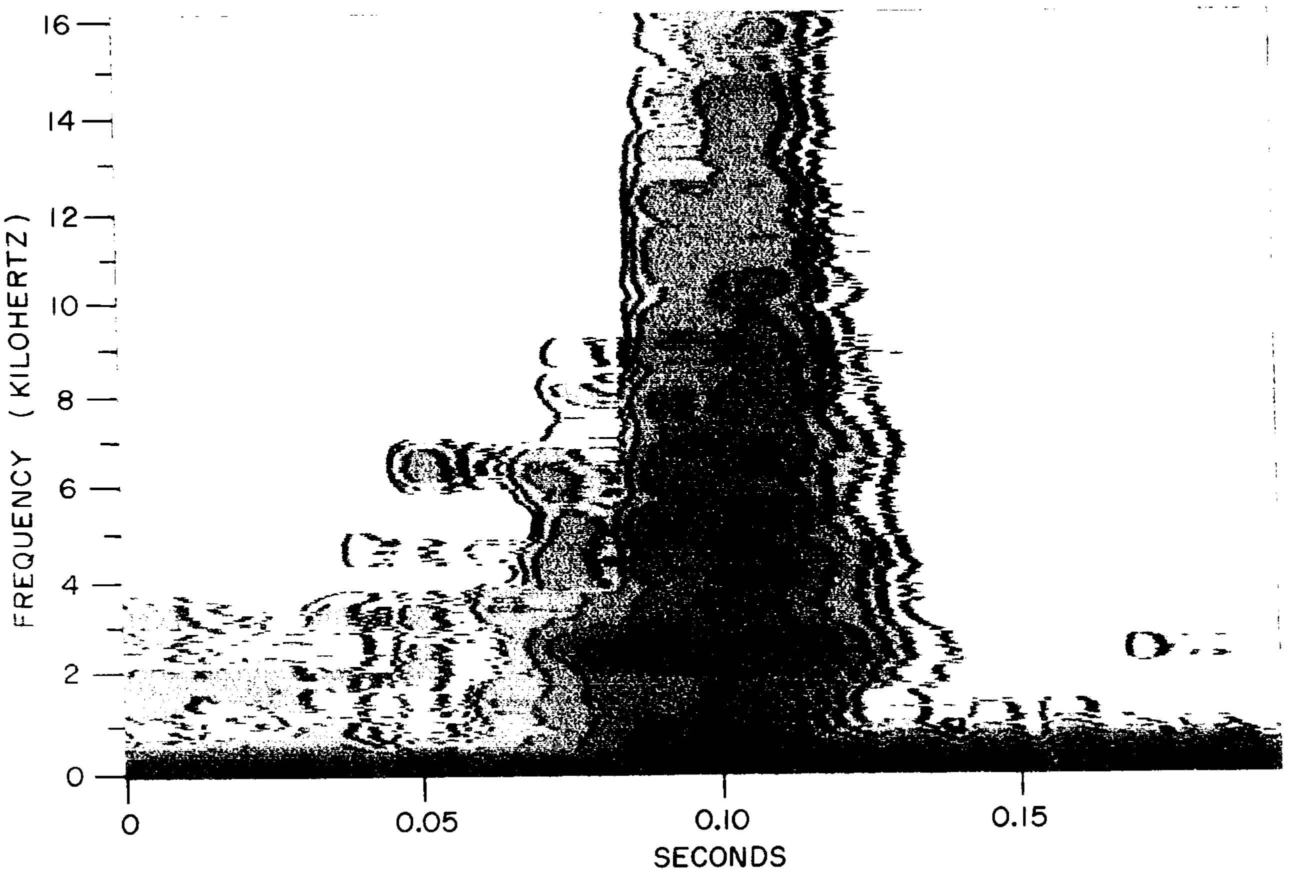


Fig. 16. Contour sonogram of a CRUNCH produced by the captive 457 mm Scarus guacamaia while feeding on Montastrea annularis.

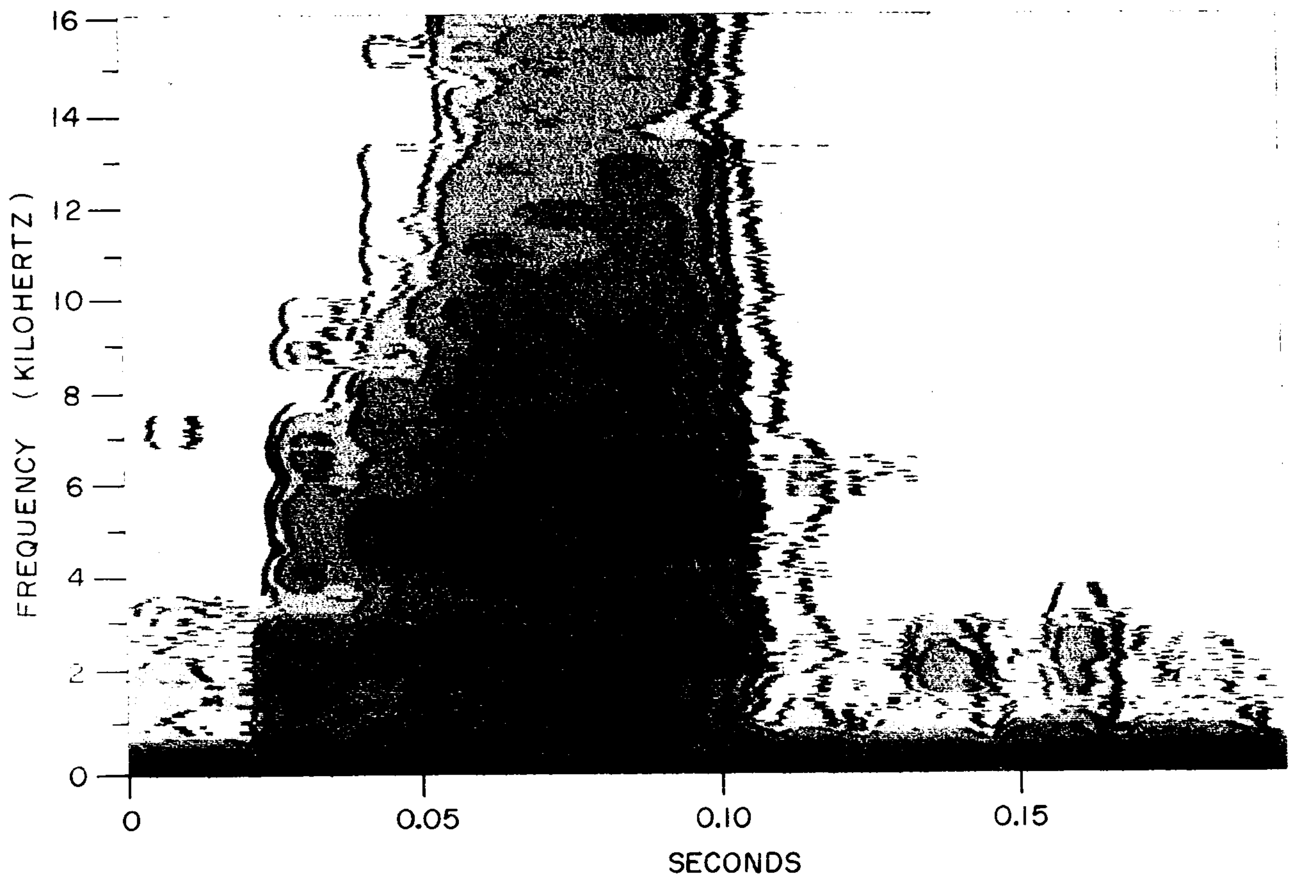


Fig. 17. Contour sonogram of a CRUNCH produced by the captive 457 mm *Scarus guacamaia* while feeding on *Colpophyllia natans*.

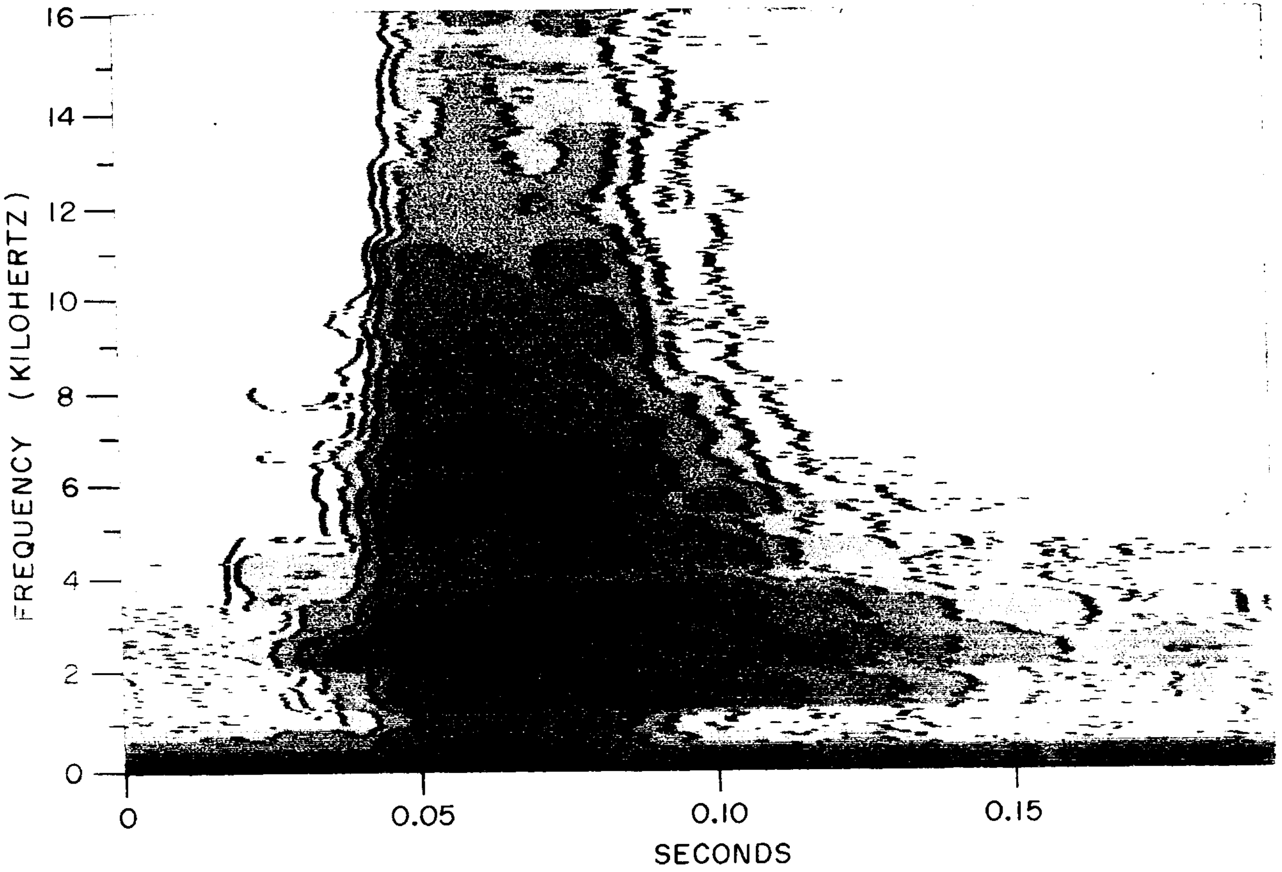


Fig. 18. Contour sonogram of a CRUNCH produced by the captive 457 mm *Scarus guacamaia* while feeding on *Acropora palmata*.

APPENDIX C

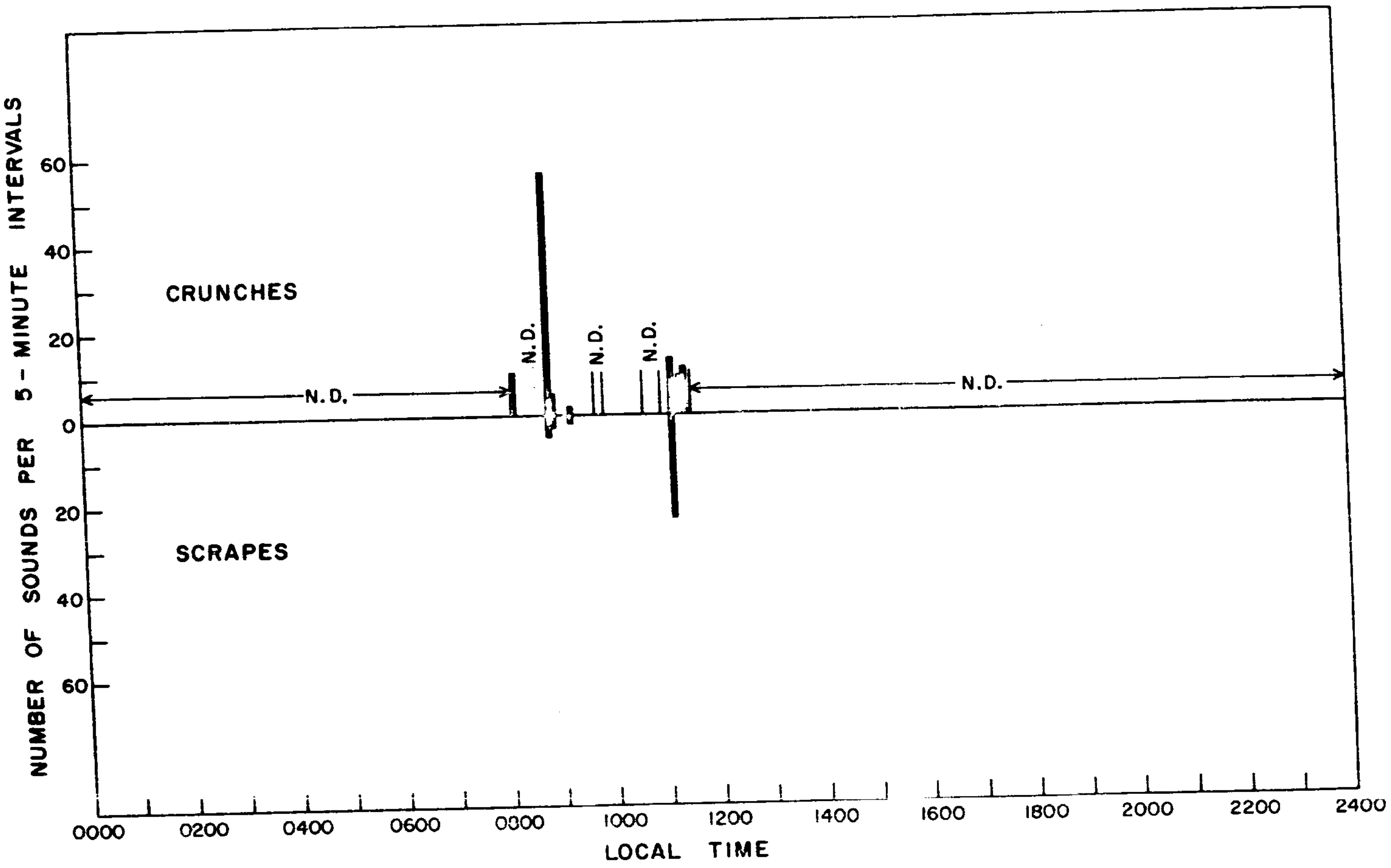


Fig. 19. The occurrence of parrotfish feeding sounds at Station I, July 23, 1971. N.D. = no data.

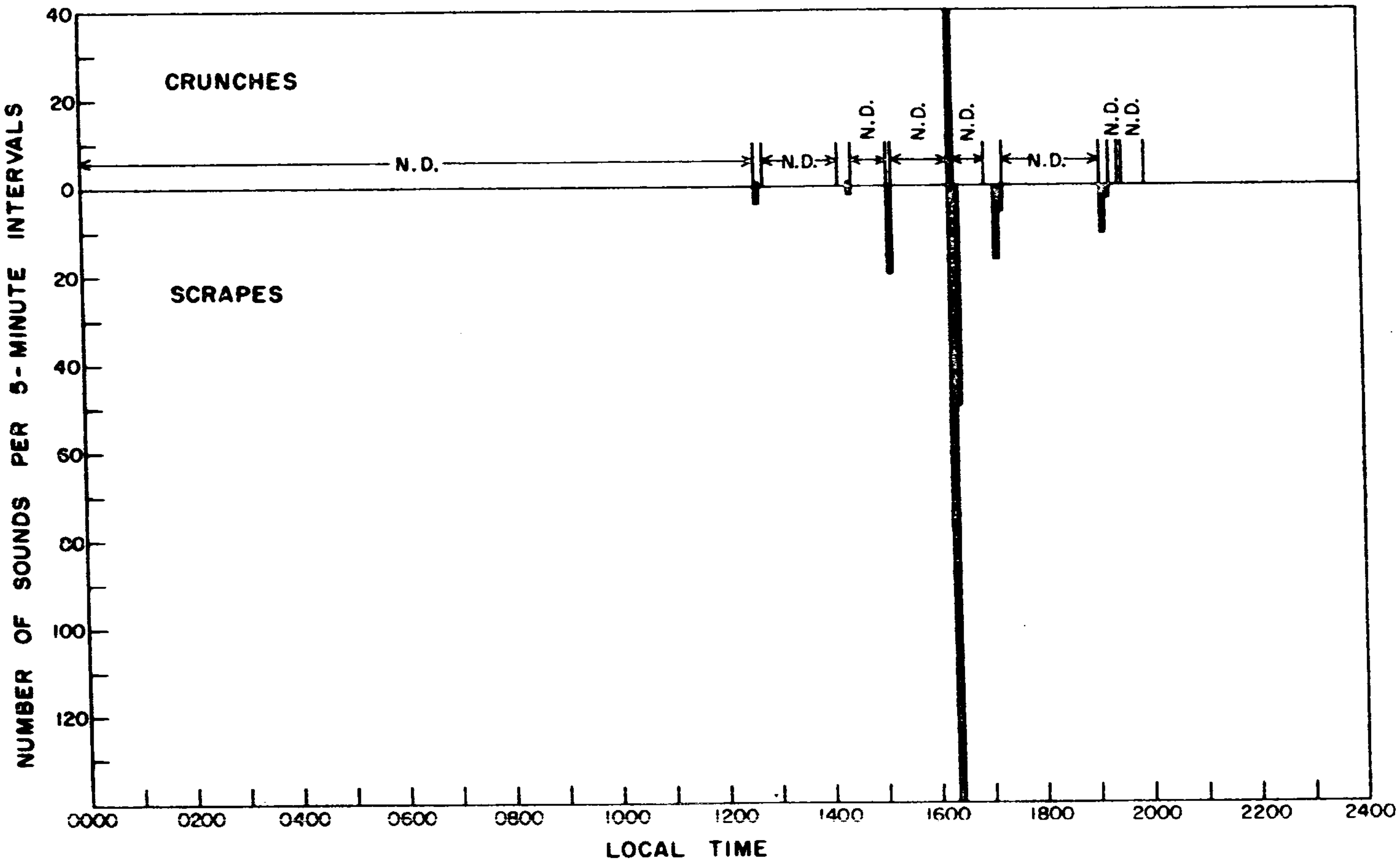


Fig. 20. The occurrence of parrotfish feeding sounds at Station 1, July 24, 1971. N.D. = no data.

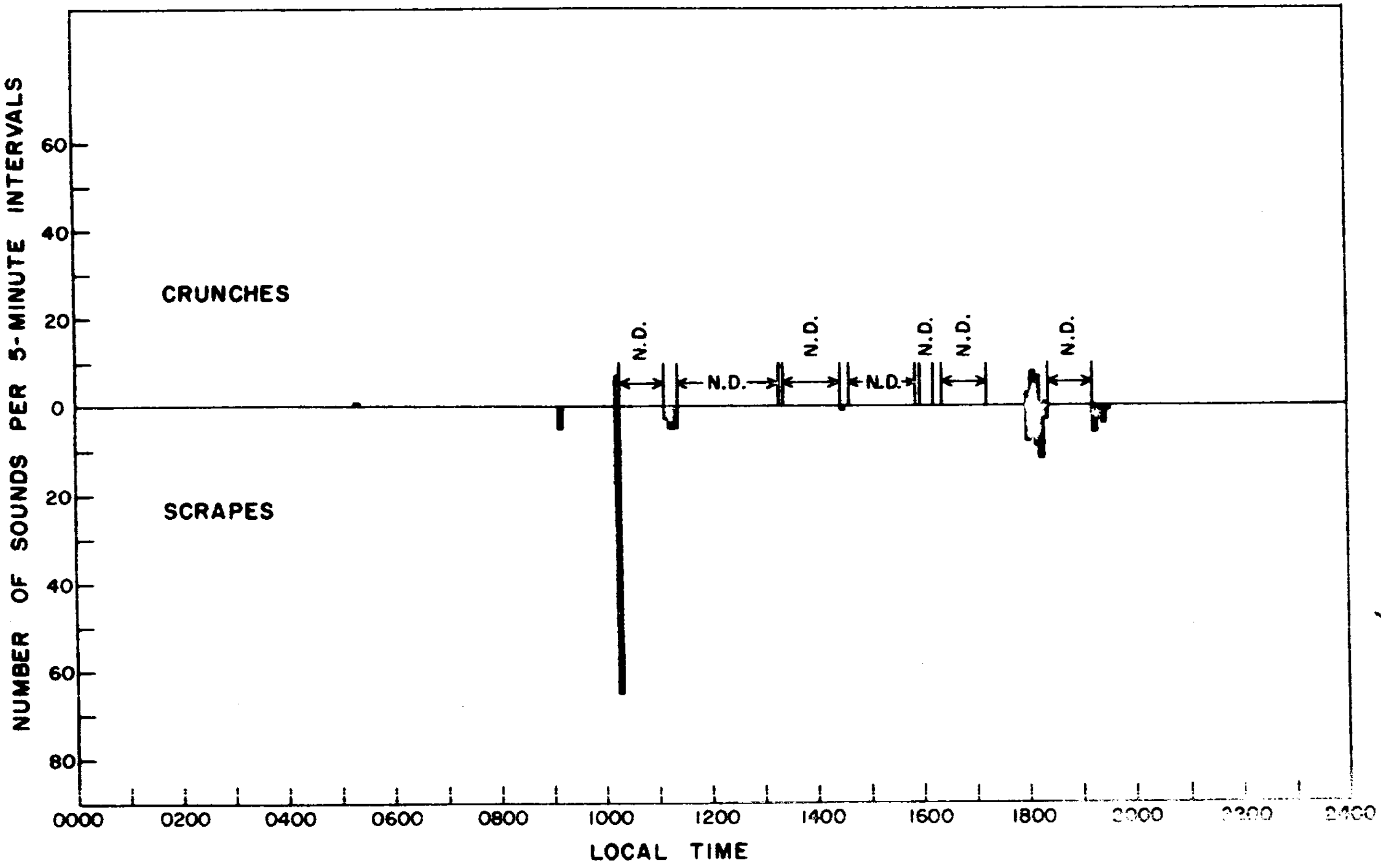


Fig. 21. The occurrence of parrotfish feeding sounds at Station I, July 25, 1971. N.D. = no data.

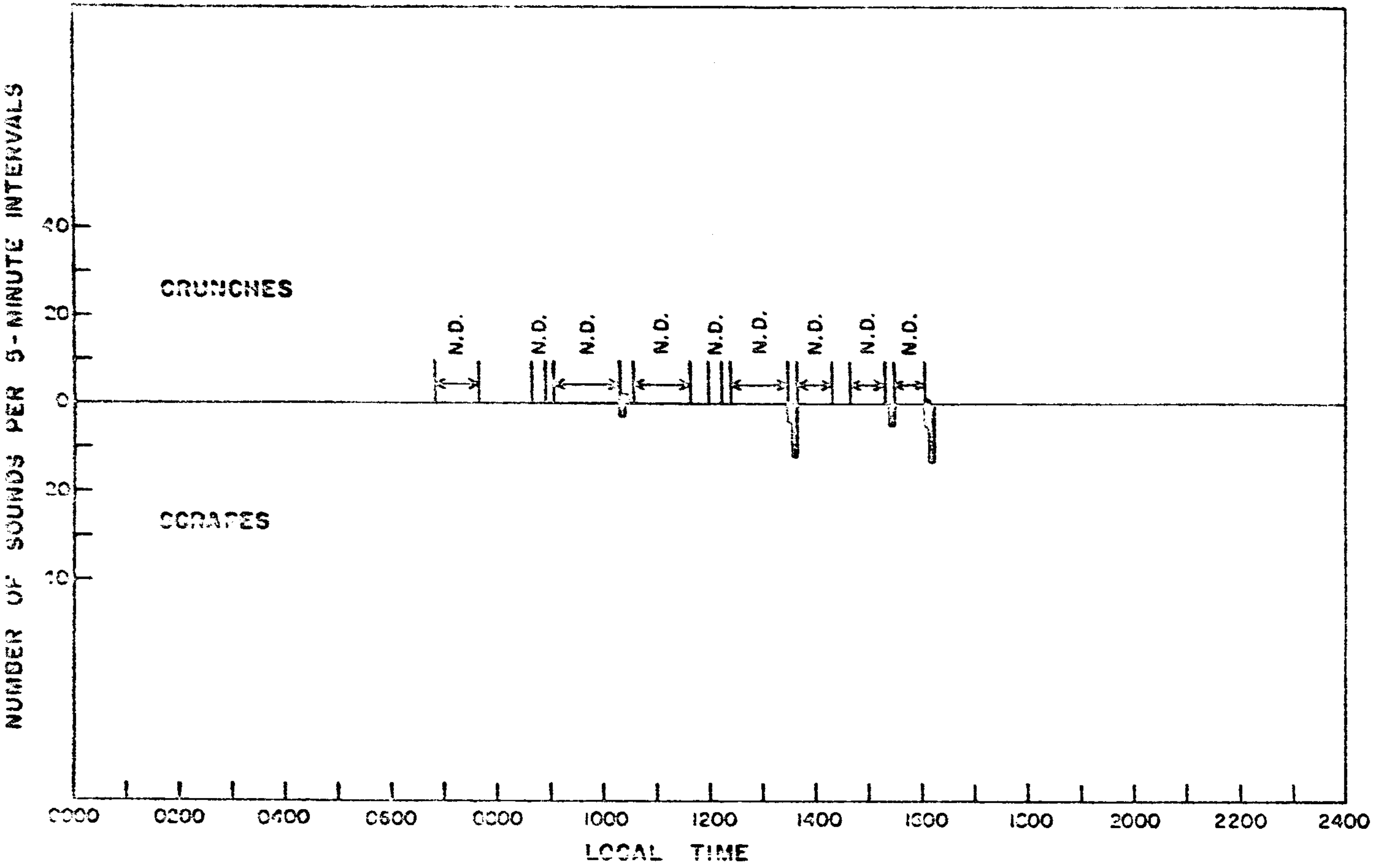


Fig. 22 The occurrence of parrotfish feeding sounds at Station I, July 26, 1971. N.D. = no data.

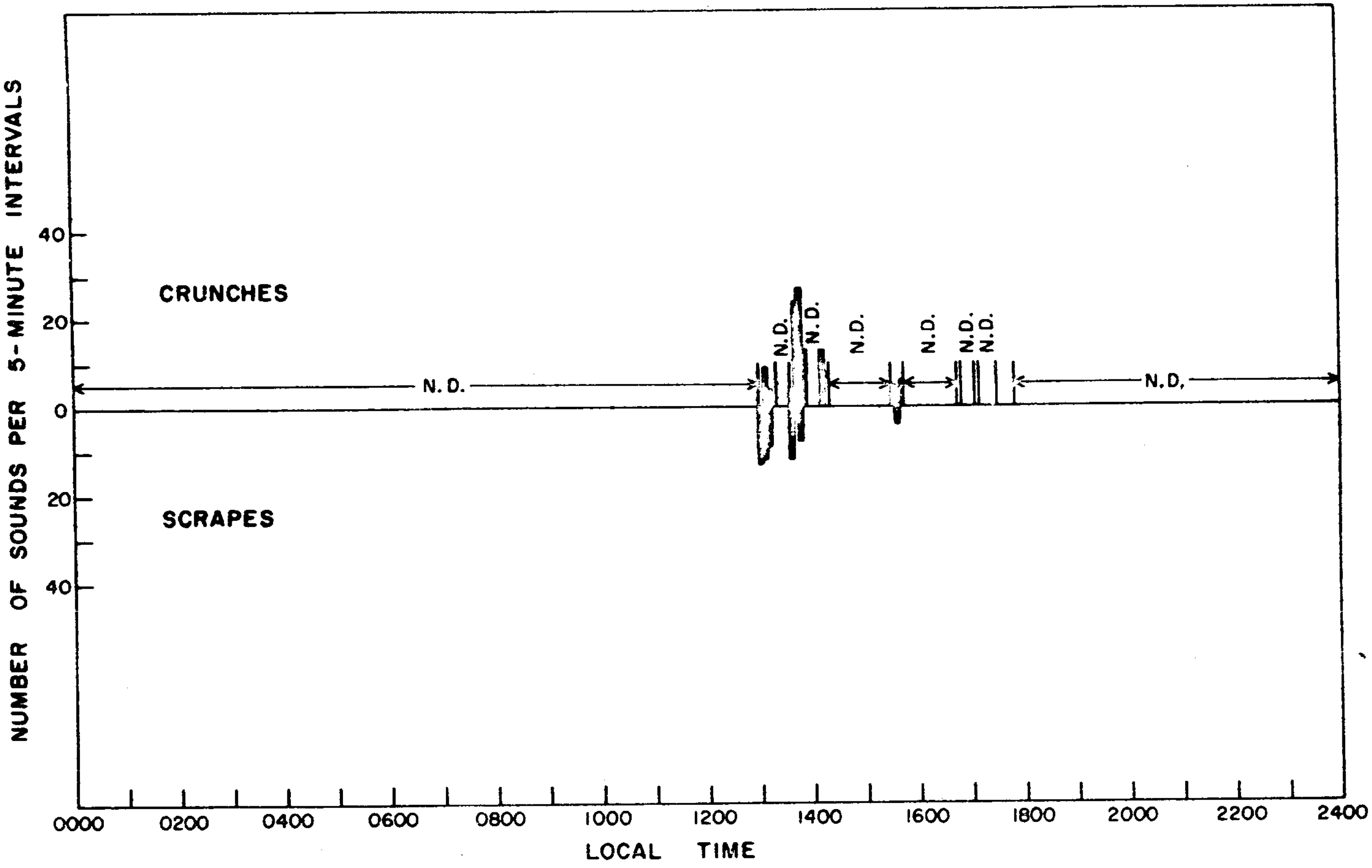


Fig. 23. The occurrence of parrotfish feeding sounds at Station I-A, July 23, 1971. N.D. = no data.

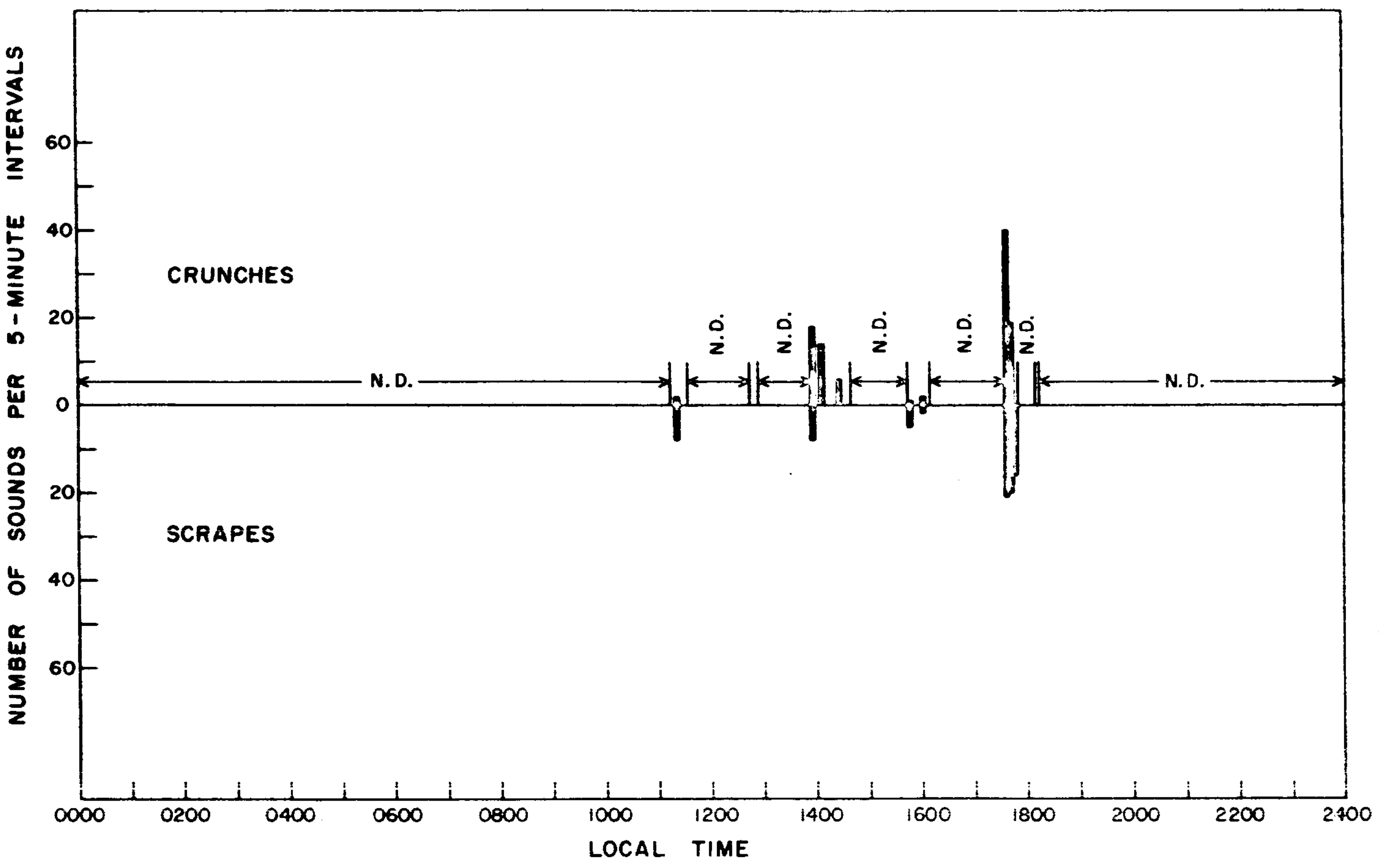


Fig. 24. The occurrence of parrotfish feeding sounds at Station II, July 22, 1971
N.D. = no data.

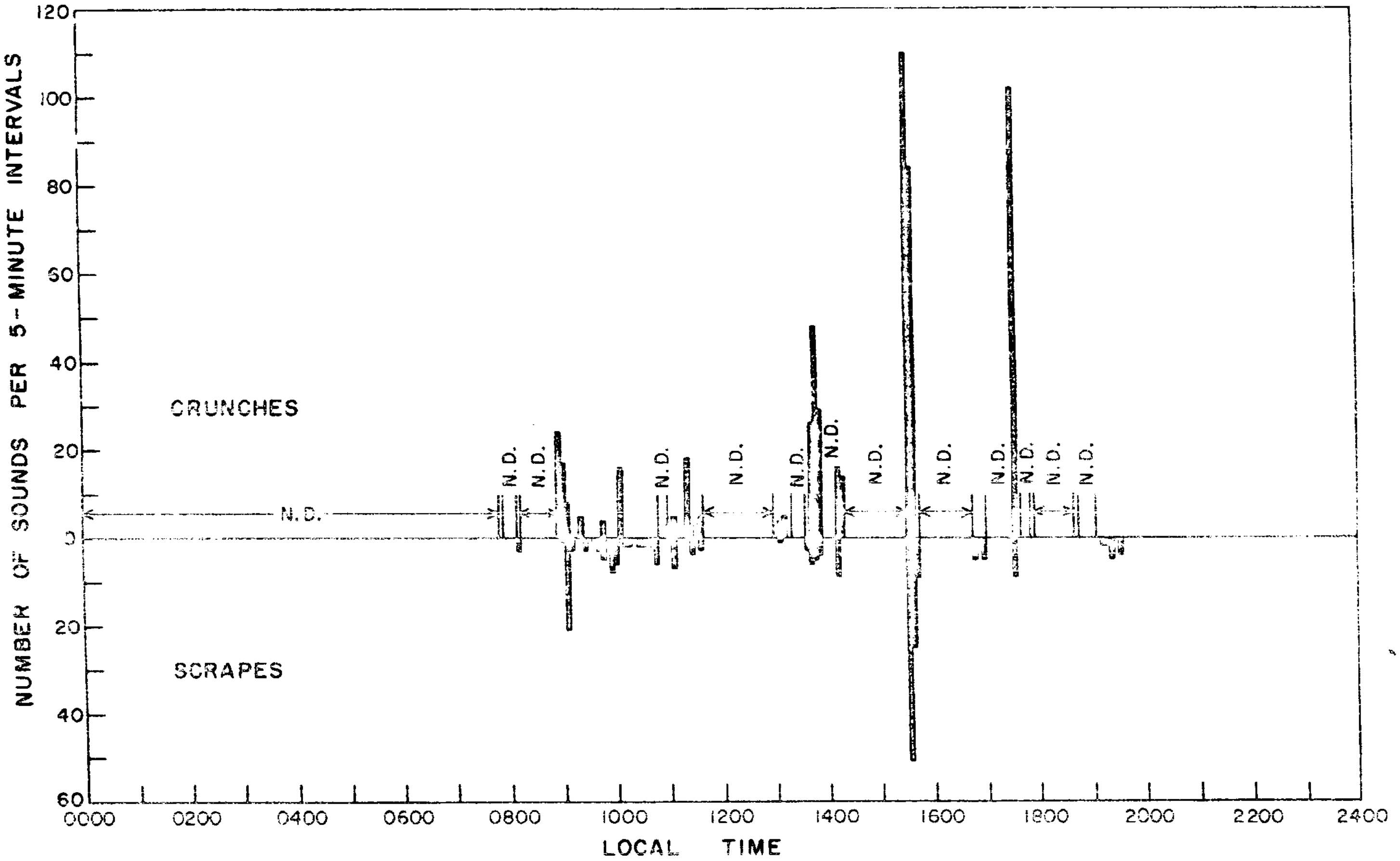


Fig. 25. The occurrence of parrotfish feeding sounds at Station II, July 23, 1971. N.D. = no data.

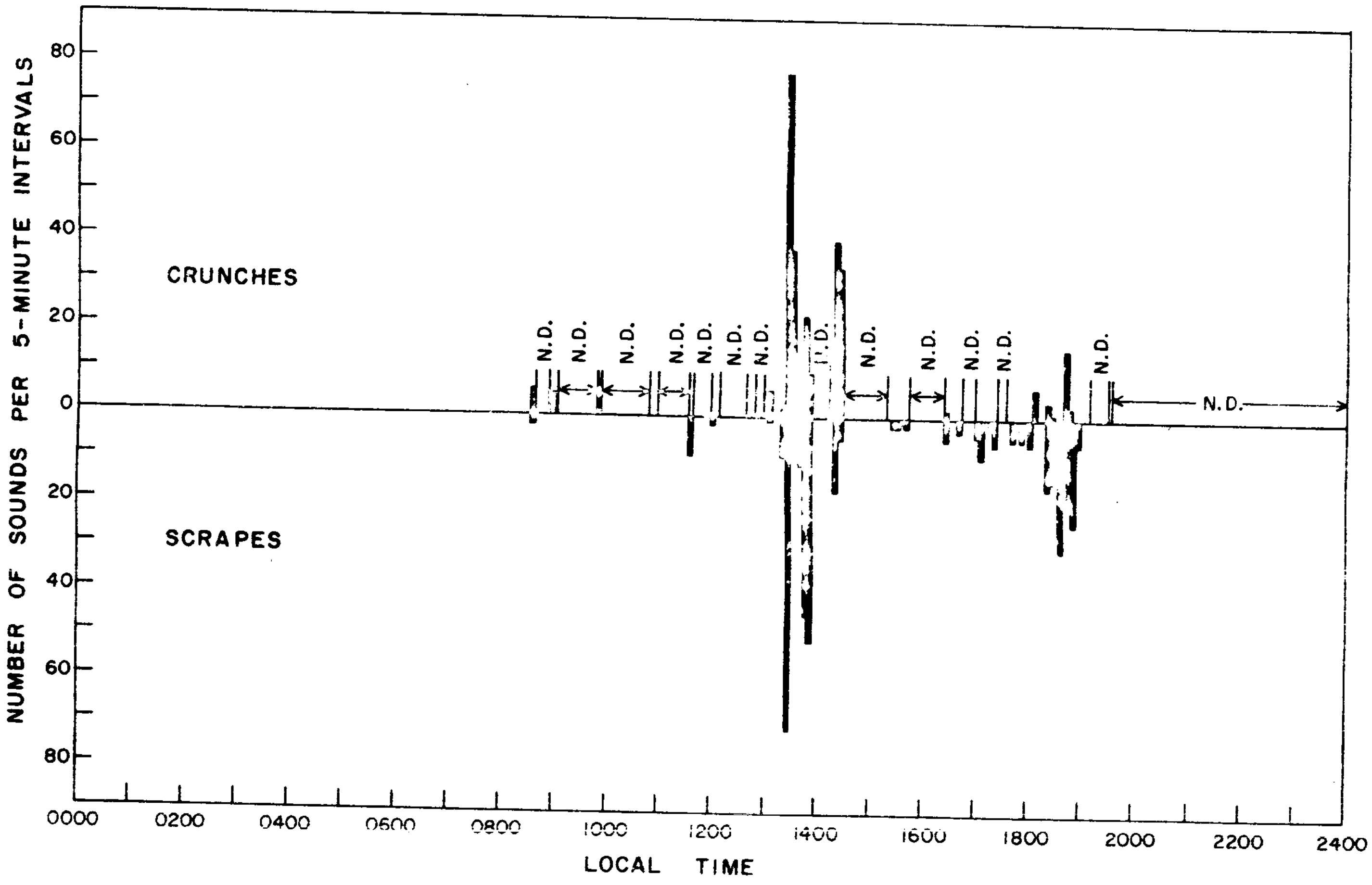


Fig. 26. The occurrence of parrotfish feeding sounds at Station II, July 24, 1971. N.D = no data.

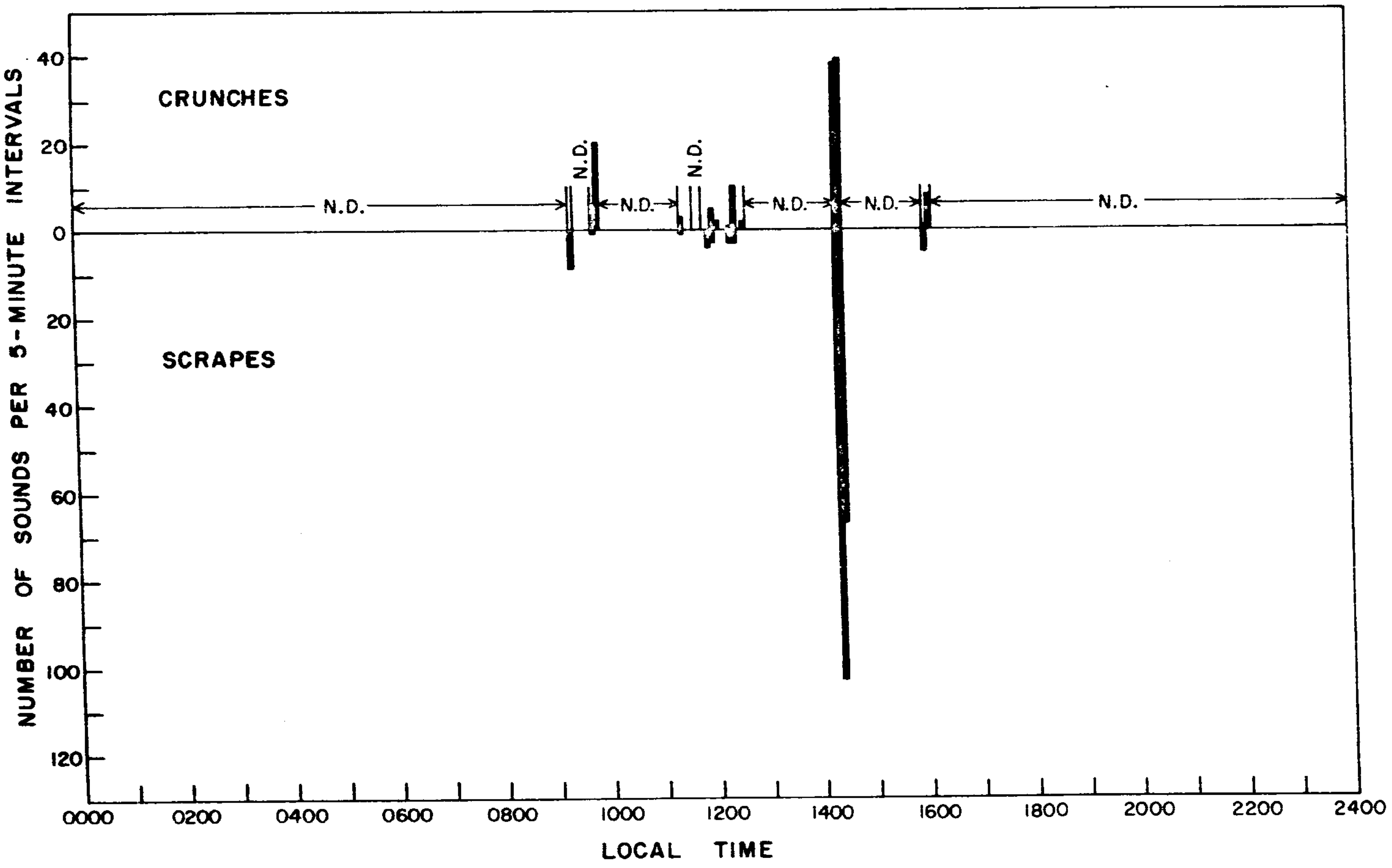


Fig. 27. The occurrence of parrotfish feeding sounds at Station II, July 25, 1971. N.D. = no data.

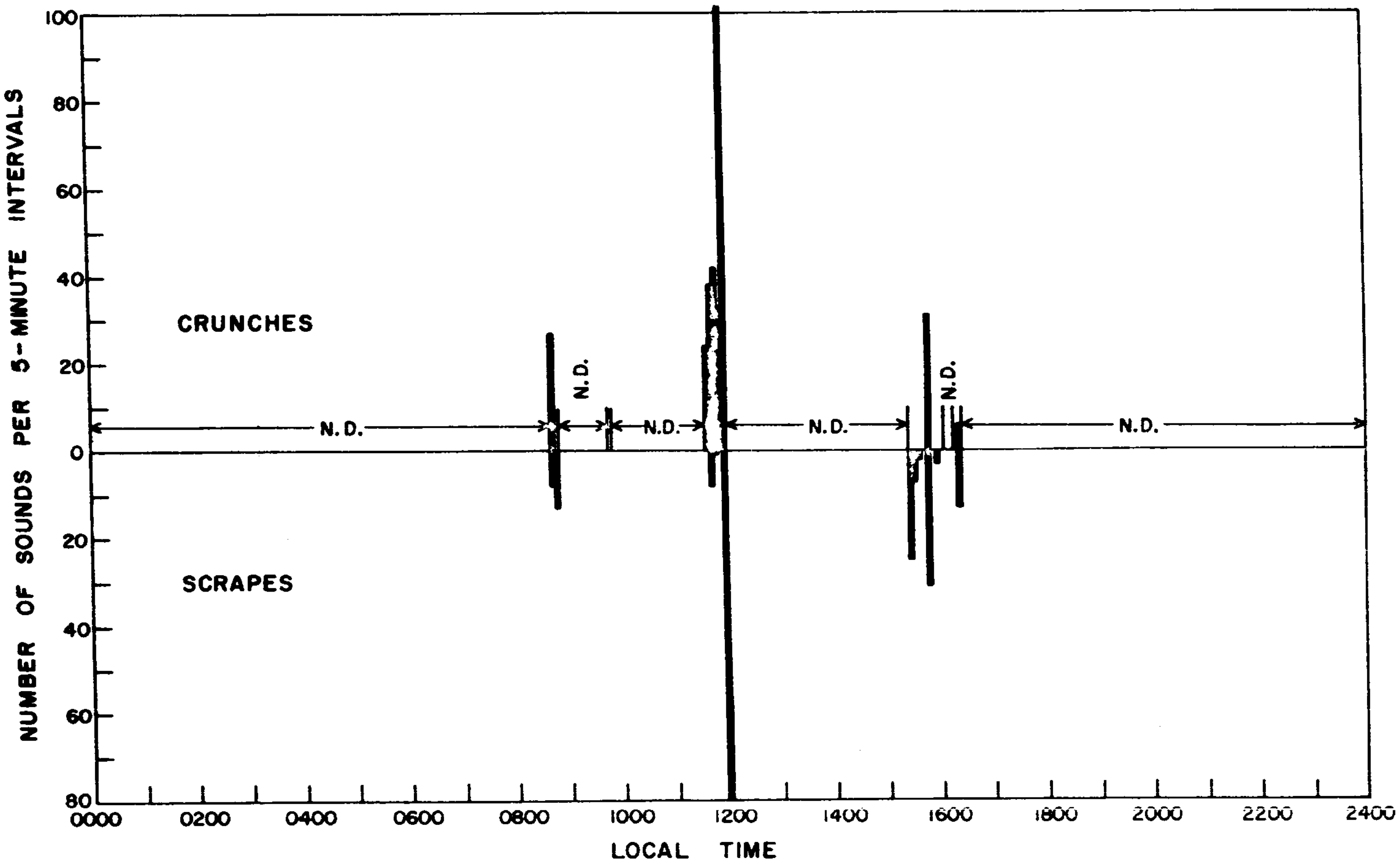


Fig. 28. The occurrence of parrotfish feeding sounds at Station II, July 26, 1971. N.D. = no data.

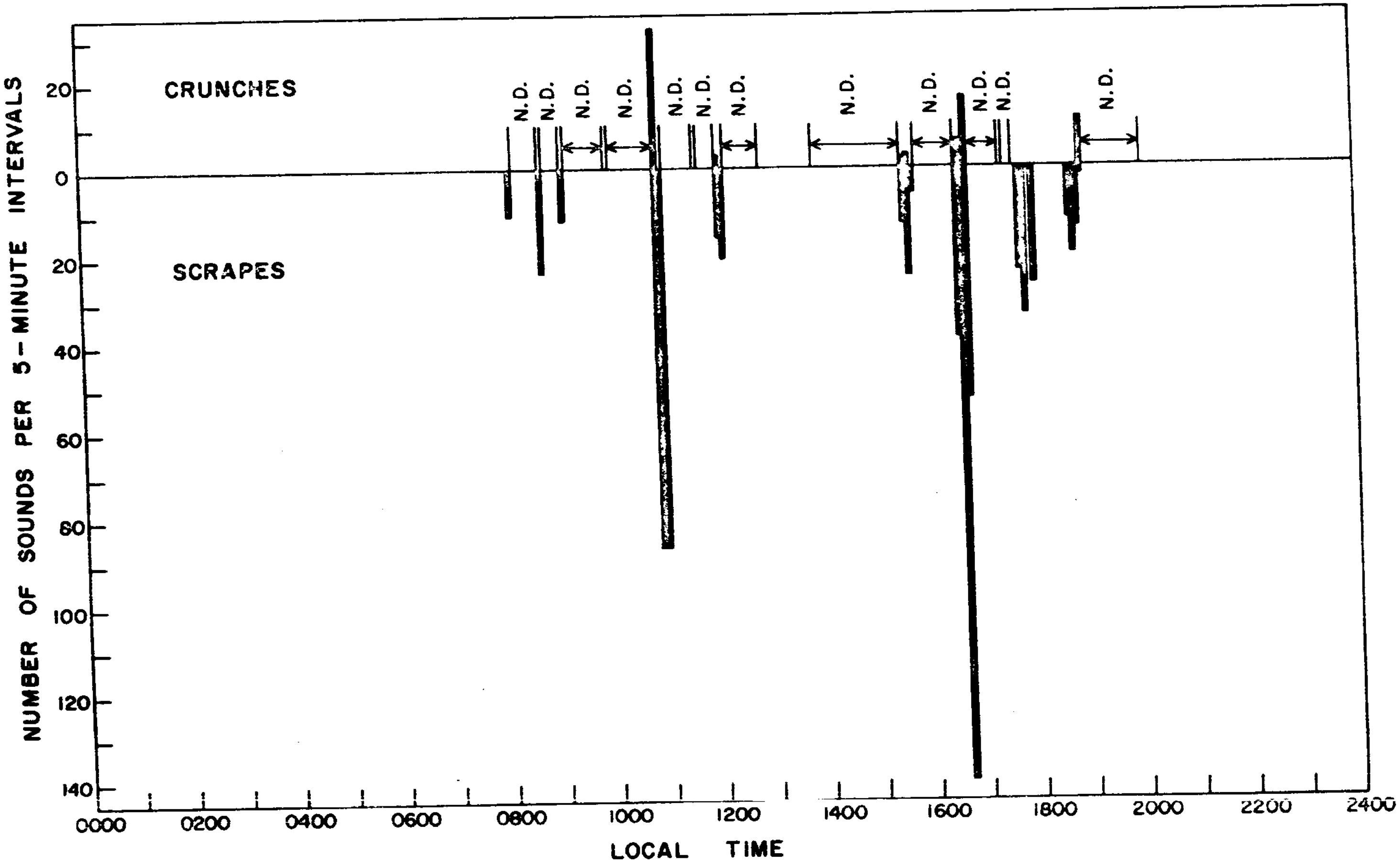


Fig. 29. The occurrence of parrotfish feeding sounds at Station III-A, July 24, 1971. N.D. = no data.

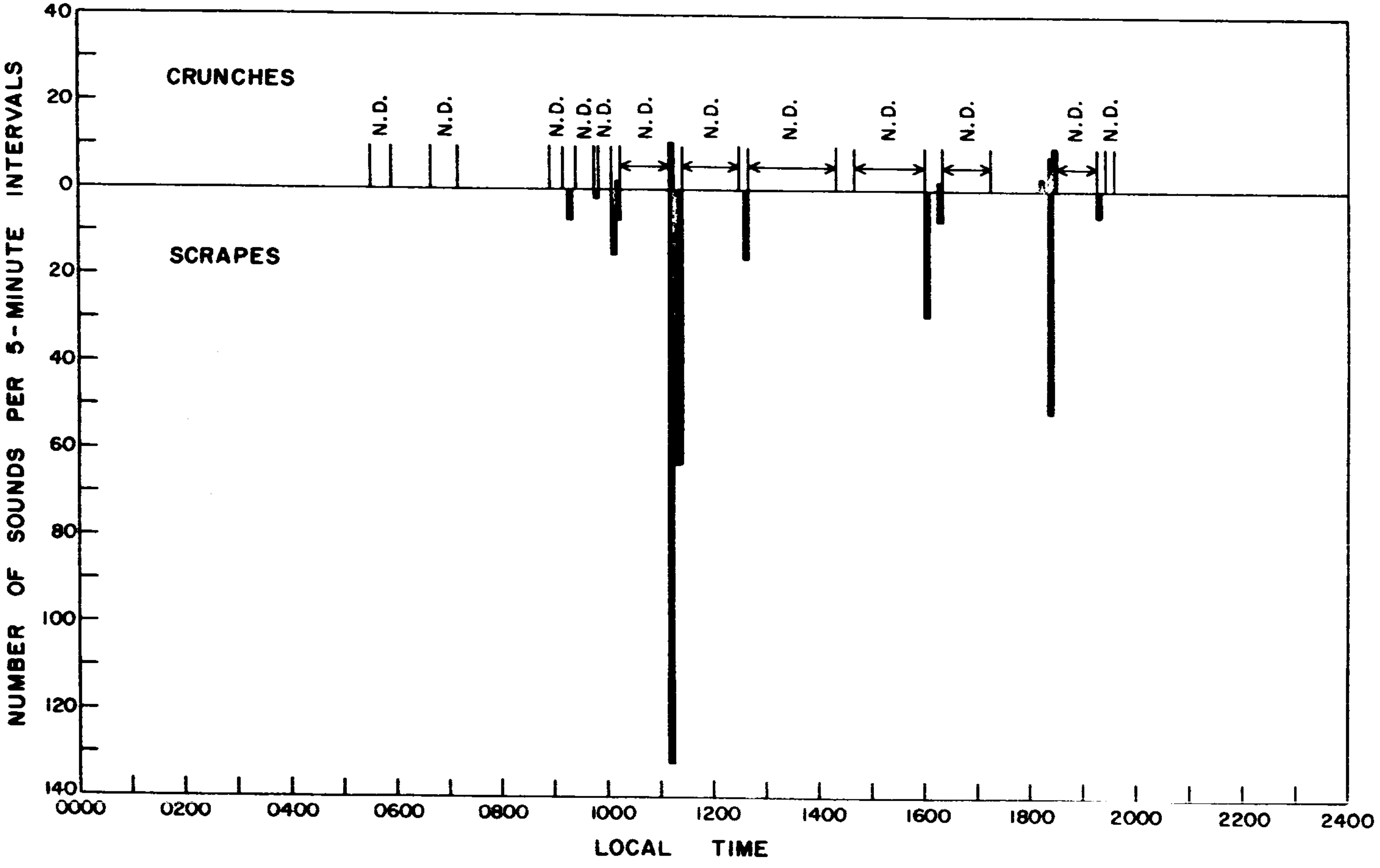


Fig. 30. The occurrence of parrotfish feeding sounds at Station III-A, July 25, 1971. N.D. = no data.

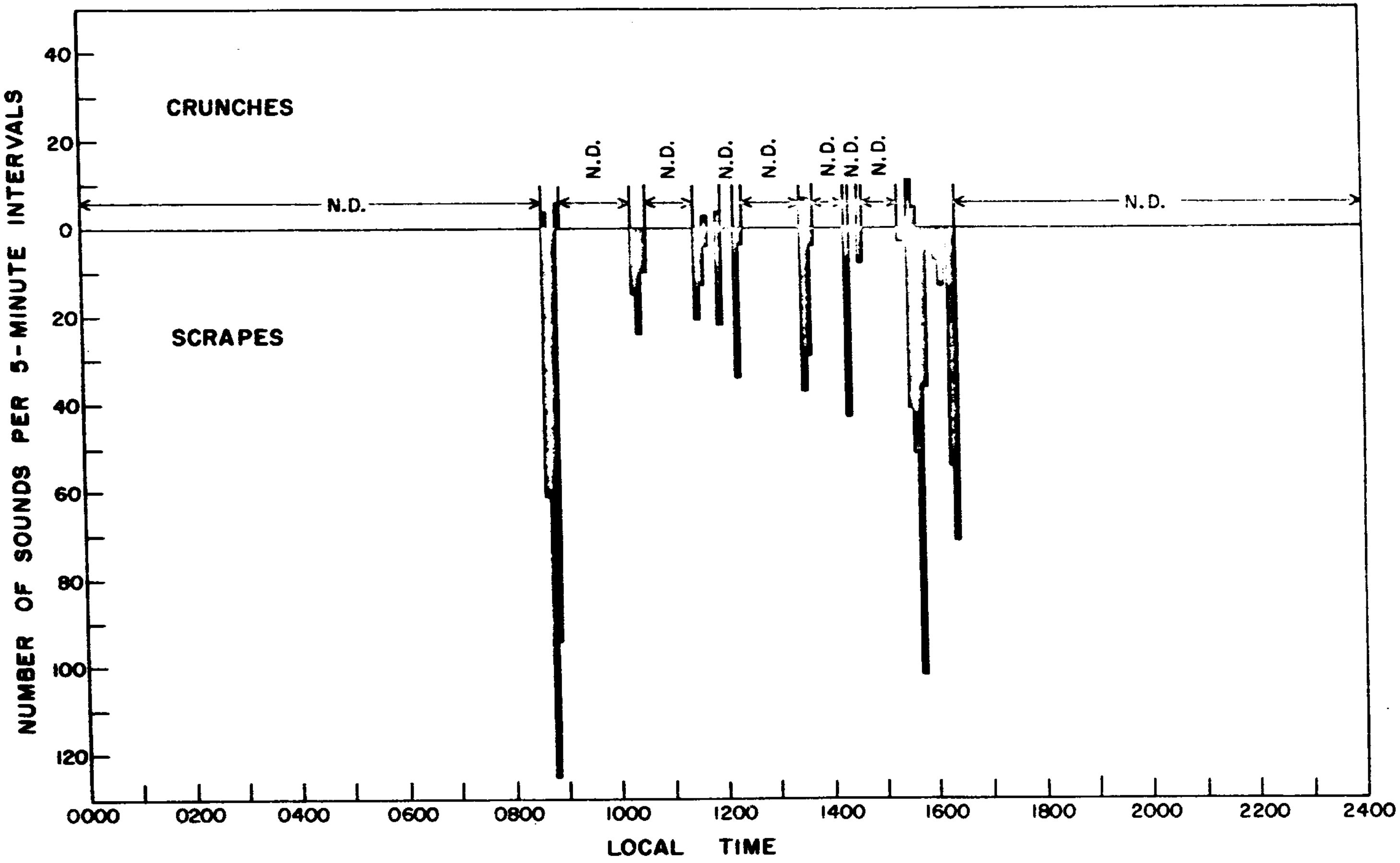


Fig. 31. The occurrence of parrotfish feeding sounds at Station III-A, July 26, 1971. N.D. = no data.

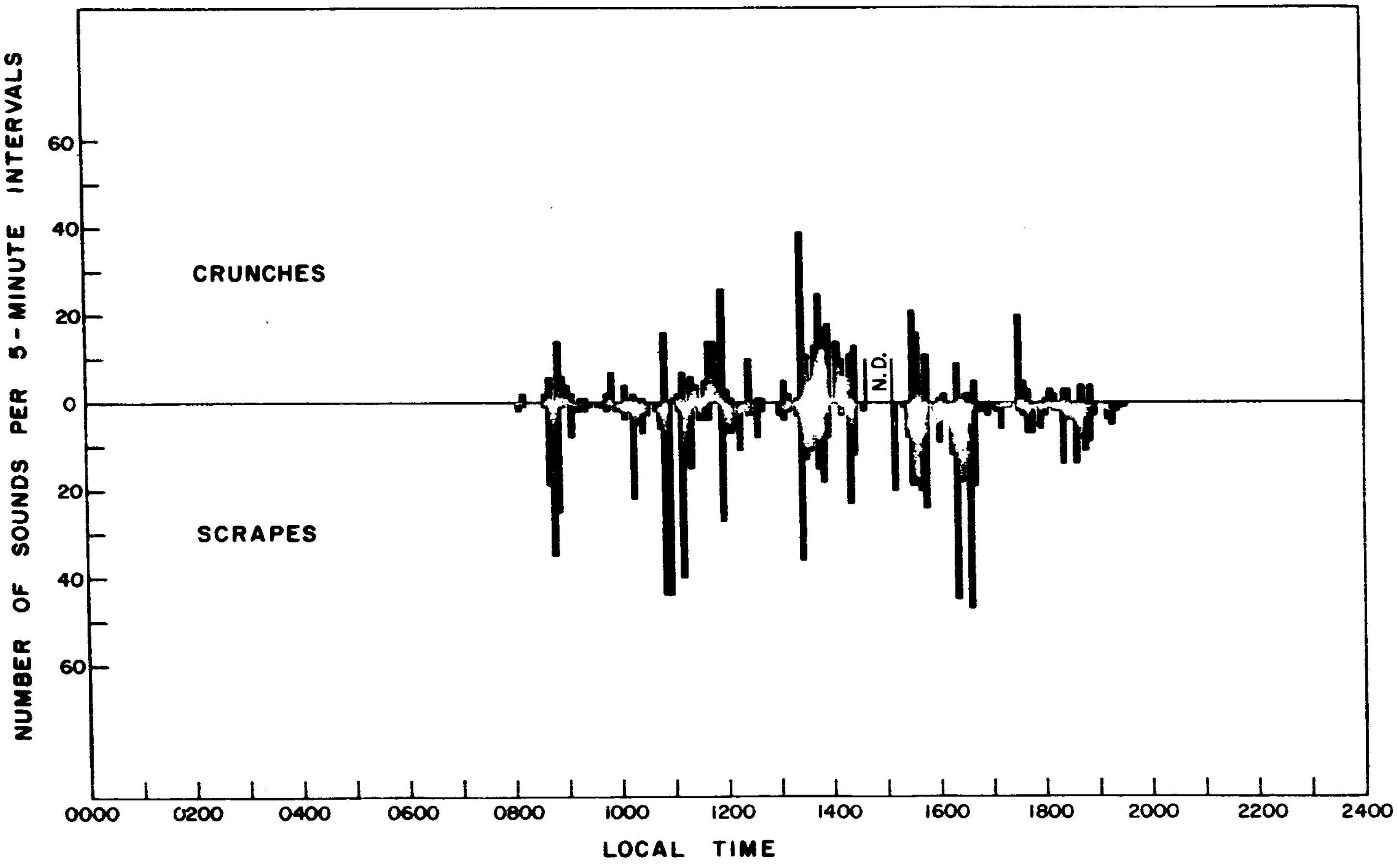


Fig. 32. The average of parrotfish feeding sounds for all stations over five days of monitoring. N.D. = no data.