

## SOUND DISCRIMINATION BY THE BICOLOR DAMSELFISH, *EUPOMACENTRUS PARTITUS*

By ARTHUR A. MYRBERG JR. AND JUANITA Y. SPIRES

*Division of Functional Biology, Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, Florida*

(Received 23 March 1972)

### INTRODUCTION

Although sound production characterizes the reproductive periods of many fishes (Freytag, 1968; Moulton, 1964*a, b*; Protasov & Romanenko, 1962; Tavalga, 1965, 1968; Winn, 1964), its functional significance is largely speculative. Until recently few studies had, indeed, demonstrated clear responsiveness by fishes to playback of their own sounds, and data pertaining to the specificity of acoustic interactions (e.g., pattern discrimination) were for the most part non-existent (Tavalga, 1965, 1968; Wodinsky, 1964). These data are now being obtained on a few species and present evidence points to the importance of such discrimination in intraspecific communication (Fish, 1969; Myrberg, 1972*a*; Spanier, 1970; Stout, 1966; Winn, 1967). One such study, dealing with sounds and their facilitation of courtship in the bicolor damselfish, *Eupomacentrus partitus* (Poey) (fam. Pomacentridae), established that males of various colonies selectively respond to different natural sounds used during playback sequences (Myrberg, 1972*b*). Many of these sounds were, however, quite different structurally and so a logical question arose: would such fish discriminate between their own courtship sounds and those structurally similar sounds of courtship produced by congenetics?

All species of *Eupomacentrus* monitored thus far (*E. fuscus*, *E. leucostictus*, *E. partitus*, *E. planifrons* and *E. variabilis*) produce a number of different sound types during courtship. One of these, the three-pulse chirp, is produced by adult males of all these sympatric species while performing a specific courtship pattern termed the Dip (Fig. 1 and Appendix). Oscillographic and spectrographic analyses of such chirps from among at least three of these congenetics have revealed remarkable similarities in structure (Table 1). This provided, therefore, an excellent opportunity to test for possible response differentials among members of one species during playback of two or more fully analogous and structurally similar sounds.

### MATERIALS AND METHODS

The species selected for testing was the bicolor damsel, *E. partitus*, a ubiquitous reef fish of the Bahamas and southern Florida. A field colony was, at the time, being monitored by underwater television (UTV) at a site where playback tests could easily be undertaken. The colony, consisting of three adult males, six adult females and four juveniles, resided on a small rocky outcrop (Subject Rock, 1.5 × 0.5 × 0.6 m), 1.5 km off the west coast of North Bimini, Bahamas, and at a depth of 20 m (Fig. 2). During

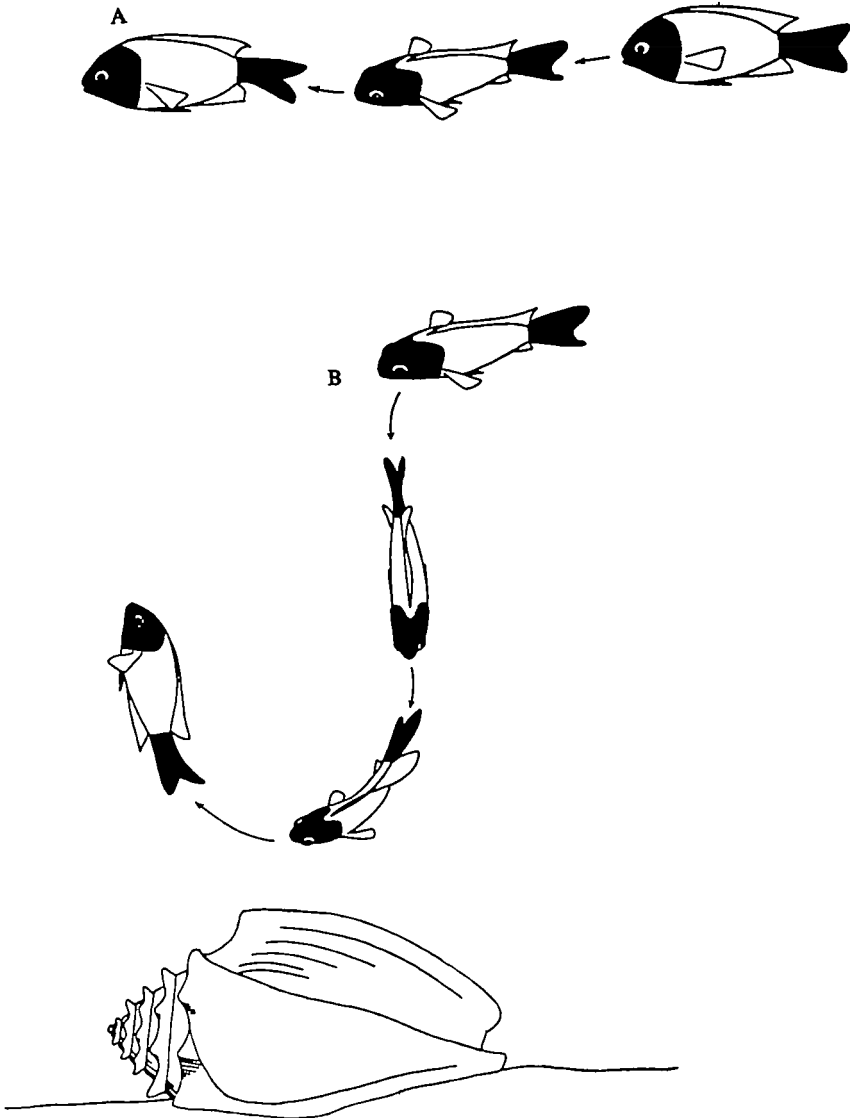


Fig. 1. The two most prevalent motor patterns of courtship in the male bicolor, *Eupomacentrus partitus*. A, Tilt, male showing courtship coloration; B, Dip, male showing courtship coloration (a brief tail flip, noted at the initiation of the 'dive', is not illustrated).

the period of testing, water temperature was approximately 26.5 °C, salinity 36‰. The UTV camera (Kintel 20/20, housing and pan/tilt mechanism designed and fabricated by University of Miami personnel) and its associated acoustical array were cable-connected to a land-based read-out installation on the grounds of the Lerner Marine Laboratory, North Bimini. The video scene was viewed on a monitor (35 cm) and documentation was provided through a video-tape recorder (Ampex, VR 660). Two audio channels of the video recorder provided audio pickup from the surveillance site, as well as from the observers at the monitor. A calibrated pressure hydrophone (Hudson Laboratories, 2 ZP 10, with pre-amplifier) was located on the substrate about

Table 1. Summary of measurements characterizing the three-pulse chirps of those species of *Eupomacentrus* used in the study

(Data opposite each of the species' names were obtained from oscillographic and spectrographic analyses of approximately 30 sounds. Additionally, measurements are provided for each of the chirp sounds used for playback.)

| Species                | Pulse interval (msec) | Pulse duration (msec) | Frequency range to (Hz) | Frequencies of greatest intensity |
|------------------------|-----------------------|-----------------------|-------------------------|-----------------------------------|
| <i>E. partitus</i>     | 40-60                 | 8-15                  | 2400                    | 250-1000                          |
| Lab. chirp             | 50                    | 13-15                 | 2100                    | 250-750                           |
| Field chirp            | 44                    | 9-10                  | 2200                    | 500-900                           |
| <i>E. planifrons</i>   | 45-55                 | 7-12                  | 1200                    | 250-750                           |
| Lab. chirp             | 52                    | 7-8                   | 1200                    | 250-700                           |
| <i>E. leucostictus</i> | 35-40                 | 7-10                  | 2000                    | 250-700                           |
| Lab. chirp             | 38                    | 7-10                  | 2000                    | 250-500                           |

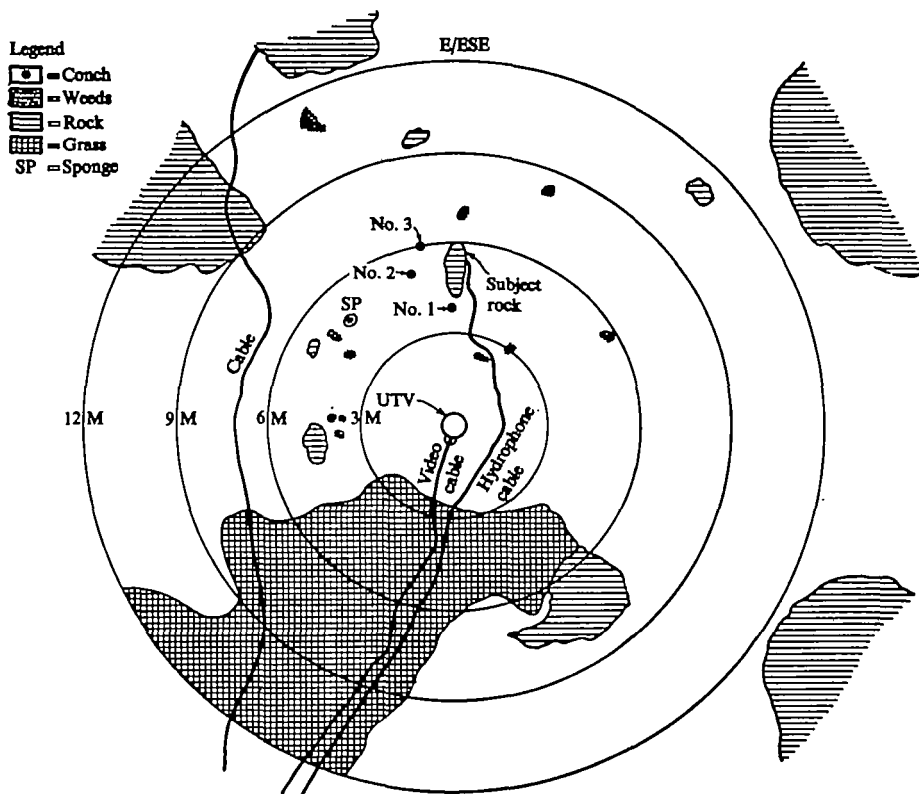


Fig. 2. Bottom topography of the UTV site. Field colony of bicolors was located on, or near, the Subject Rock. Vegetation consisted primarily of *Thalassia testudinum* (some *Syringodium filiforme* present). M = metres distant from UTV housing; E/ESE = east/east-south-east; nos. 1, 2, 3 = conch shell residences of the test males.

1 m from the Subject Rock and a sound projector (Chesapeake Instrument, J-9) rested nearby on a large piece of 'rubberized horsehair'. Associated transformer and armoured cable completed the array. Sounds were recorded and played back on the same Uher 4000L recorder, connected to an audio amplifier (Allen Organ, 750). SCUBA was used to place equipment, as well as to measure distances and obtain supplementary behavioural data. Further details concerning specific hardware and operations of the UTV can be obtained from the following sources: Gordon & Loewenstein (1969), Kronengold *et al.* (1964), Myrberg (1972*b*), Myrberg *et al.* (1969) and Stevenson (1967).

A laboratory colony (three adult males and five adult females), captured near the field colony some ten weeks prior to the present study, resided in an 800 l aquarium (2.5 × 0.6 × 0.6 m) at the Rosenstiel School of Marine and Atmospheric Science. The size of the aquarium used for the colony was dictated largely by the amount of substrate controlled by a similar-sized colony in the field (Myrberg, 1972*b*). During the period of this study the aquarium was supplied by salt water (temperature approximately 27 °C, and salinity 34 ‰) from a continuous flowing, non-recirculating system. Artificial lighting (two 75 W, cool white fluorescent) was controlled by a time switch, sensitive to ambient light entering the window of the laboratory. Lights were extinguished 15 min before sunset and came on 15 min after sunrise. Food, consisting of frozen brine shrimp, chopped penaeid shrimp, and dry food was provided twice a day (morning and late afternoon).

The same audio recorder, amplifier and sound projector used for the field study were also used for the laboratory tests. Substitution was, however, made in the case of the hydrophone (Chesapeake Instrument, SB 154B) and pre-amplifier (Ithaco, 144L). The investigation was begun by recording numerous chirp sounds from the above colonies, as well as chirps produced by laboratory males of two of the congeners, *E. planifrons* and *E. leucostictus*. Sound levels, to be used during subsequent playback periods, were also determined during these recording sessions by a voltmeter and/or oscilloscope. A single chirp was then selected from these recordings as the representative from each colony. This selection was based on clarity and structure, as well as on a low level of ambient noise associated with a given sound. The four resulting sounds were, in turn, recorded separately on tape loops so that each repeated itself every 2.4–2.6 sec. This repetition rate (22–25 chirps/min) was very similar to that heard while dipping activity was occurring frequently among males of the respective bicolor colonies. Subsequent playback studies by Ha (1972) have since demonstrated that this rate was, indeed, optimum for eliciting courtship activity in the species. The particular chirps selected for playback from the *E. partitus* and *E. planifrons* colonies were produced by the dominant male in each case. The social rank of the individual producing the *E. leucostictus* sound was, however, unknown.

The experimental phase of this study was begun by playing back these various loops to each bicolor colony. Tests were carried out during early spring to reduce the probability of high levels of courtship occurring during control periods (i.e., silent periods bracketing all test trials). Each period of playback and control was 5 min in duration with a minimum 'rest' of  $\frac{1}{2}$  hr between sessions (a session consisted of a single playback of each sound included in the experiment, along with the respective control periods). Only two or three sessions were carried out on a given day since

Table 2. *Differential responsiveness of laboratory males of E. partitus to laboratory chirps recorded from a conspecific and from congeners*

| Sound source           | Recorded from | Trial situation | No. of trials | Frequency of specific motor patterns |     |       |      |
|------------------------|---------------|-----------------|---------------|--------------------------------------|-----|-------|------|
|                        |               |                 |               | Tilt                                 | Dip | Nudge | Lead |
| <i>E. partitus</i>     | Laboratory    | Test            | 28            | 445                                  | 438 | 87    | 57   |
|                        |               | Control         | 28            | 154                                  | 172 | 6     | 4    |
| <i>E. planifrons</i>   | Laboratory    | Test            | 28            | 390                                  | 374 | 39    | 35   |
|                        |               | Control         | 28            | 160                                  | 160 | 6     | 4    |
| <i>E. leucostictus</i> | Laboratory    | Test            | 28            | 252                                  | 272 | 47    | 19   |
|                        |               | Control         | 28            | 169                                  | 164 | 13    | 3    |

previous work had shown that a slight decrement in response often occurred after that number of sessions (Myrberg, 1972*b*).

Two observers were present during all experiments. They recorded the frequency of four motor patterns of male courtship (Tilt, Dip, Nudge, Lead – see Appendix) and, except for the first experiment, also the frequency of chirps produced by the males of each colony. Lack of consistent reaction by females and juveniles during previous playback experiments resulted in their activity not being followed during this study.

Statistical analysis of the data obtained during all experiments was carried out by the  $\chi^2$  method ( $\alpha = 0.05$ ). The frequencies of two patterns, Tilt and chirp, were not used in analysis, since both were closely associated with the occurrence of a third pattern, the Dip.

## RESULTS

### *Initial playback to the laboratory colony*

Initial experiments compared the responsiveness of the males of the laboratory colony to the three different three-pulse chirps – one recorded from the colony itself and the other two recorded from laboratory colonies of *E. planifrons* and *E. leucostictus*. Results showed that significantly more courtship patterns were observed during test trials (including those involving sounds from the congeners) than during associated control periods (Table 2). Thus, chirps from any of the three species apparently facilitated courtship to some extent in the test males. The degree of facilitation differed markedly, however. Significantly more courtship occurred during playback of the sound from their own species than that recorded during playback of the sound from either congeneric. Additionally, the level of responsiveness shown to the latter two sounds also differed, i.e., significantly more courtship accompanied the playback of the chirp of *E. planifrons* than the playback of the chirp of *E. leucostictus*.

### *Playback to the field colony*

A few days later the males of the field colony were tested with the same laboratory sounds. Results again showed that members of the species could discriminate between chirps of conspecifics and those of the congeners (Table 3). In this case, the level of responsiveness attained during playback of sounds from the congeners did not differ.

The third experiment, carried out 24 hr later with the field colony, included the previously used sounds, as well as the three-pulse chirp recorded directly from the

Table 3. *Differential responsiveness of field males of E. partitus to laboratory chirps recorded from a conspecific and from congeners*

| Sound source           | Recorded from | Trial situation | No. of trials | Frequency of            |     |       |      |                               |
|------------------------|---------------|-----------------|---------------|-------------------------|-----|-------|------|-------------------------------|
|                        |               |                 |               | Specific motor patterns |     |       |      | Specific sonic pattern: Chirp |
|                        |               |                 |               | Tilt                    | Dip | Nudge | Lead |                               |
| <i>E. partitus</i>     | Laboratory    | Test            | 18            | 107                     | 95  | 15    | 6    | 53                            |
|                        |               | Control         | 18            | 19                      | 19  | 2     | 1    | 14                            |
| <i>E. planifrons</i>   | Laboratory    | Test            | 18            | 63                      | 61  | 3     | 2    | 36                            |
|                        |               | Control         | 18            | 30                      | 30  | 0     | 1    | 21                            |
| <i>E. leucostictus</i> | Laboratory    | Test            | 18            | 75                      | 75  | 4     | 3    | 33                            |
|                        |               | Control         | 18            | 34                      | 34  | 0     | 0    | 24                            |

Table 4. *Differential responsiveness of field males of E. partitus to field and laboratory chirps recorded from conspecifics and also to laboratory chirps recorded from congeners*

| Sound source           | Recorded from | Trial situation | No. of trials | Frequency of            |     |       |      |                               |
|------------------------|---------------|-----------------|---------------|-------------------------|-----|-------|------|-------------------------------|
|                        |               |                 |               | Specific motor patterns |     |       |      | Specific sonic pattern: Chirp |
|                        |               |                 |               | Tilt                    | Dip | Nudge | Lead |                               |
| <i>E. partitus</i>     | Field         | Test            | 10            | 137                     | 134 | 17    | 10   | 57                            |
|                        |               | Control         | 10            | 26                      | 26  | 4     | 1    | 13                            |
| <i>E. partitus</i>     | Laboratory    | Test            | 10            | 38                      | 38  | 6     | 0    | 23                            |
|                        |               | Control         | 10            | 24                      | 24  | 0     | 0    | 14                            |
| <i>E. planifrons</i>   | Laboratory    | Test            | 10            | 22                      | 21  | 5     | 1    | 14                            |
|                        |               | Control         | 10            | 16                      | 16  | 1     | 0    | 12                            |
| <i>E. leucostictus</i> | Laboratory    | Test            | 10            | 42                      | 42  | 5     | 3    | 33                            |
|                        |               | Control         | 10            | 28                      | 28  | 8     | 1    | 20                            |

field colony. This latter sound was found to facilitate courtship to a significantly greater extent than any of the other sounds (Table 4). Responsiveness to the laboratory chirp of *E. partitus* had, indeed, fallen almost to the low level shown during playback of the sounds from the congeners (i.e., not significantly different from control periods). This surprising result was probably due to the test males having the opportunity, during successive playbacks, to compare the two different chirp sequences of *E. partitus* and to respond accordingly. There was, in any case, little doubt that these fish possessed good discriminative ability within the acoustic modality.

#### *Final playback to laboratory colony*

The basis for increased responsiveness to the field chirp could have been either recognition of a familiar sound signature by the field males or that the field sounds possessed an acoustic quality in some way different and no doubt superior to that of the laboratory sounds. To determine which possibility was most likely, a final experiment was carried out with the laboratory colony. The chirp sounds recorded from the two colonies of *E. partitus* were played back in alternation, with a 10 min silent period between test trials. Subsequent results again provided a significant difference in male responsiveness accompanying the playback of these two sounds; and as was shown previously in the field, the laboratory males showed greater response to the unfamiliar

Table 5. *Differential responsiveness of laboratory males of E. partitus to field chirps and laboratory chirps recorded from conspecifics*

| Sound source       | Recorded from | Trial situation | No. of trials | Frequency of            |     |       |      |                                  |
|--------------------|---------------|-----------------|---------------|-------------------------|-----|-------|------|----------------------------------|
|                    |               |                 |               | Specific motor patterns |     |       |      | Specific sonic pattern:<br>Chirp |
|                    |               |                 |               | Tilt                    | Dip | Nudge | Lead |                                  |
| <i>E. partitus</i> | Laboratory    | Test            | 15            | 252                     | 249 | 14    | 9    | 91                               |
|                    |               | Control         | 15            | 231                     | 226 | 2     | 0    | 75                               |
| <i>E. partitus</i> | Field         | Test            | 15            | 330                     | 320 | 13    | 8    | 78                               |
|                    |               | Control         | 15            | 223                     | 220 | 8     | 3    | 50                               |

field sound than to the chirp from their own colony (Table 5). This indicated, indeed, that the colonial males were selecting a sound not for its familiarity but rather on its acoustic nature. Apparently the laboratory sound carried some artifact whose importance remained unrevealed until the sound was tested against one from the field.

#### DISCUSSION

This intriguing problem was subsequently examined by Ha (1972), who recorded and analyzed numerous sounds from both colonies. Only one consistent difference appeared – the pulse intervals (time between onset of one pulse to onset of next pulse) of field chirps were generally 6–8 msec shorter than those of laboratory chirps. This was probably related in some way to resonance achieved in the large laboratory tank. This difference, though slight, nevertheless gained importance when Ha, then, found that laboratory males showed a difference in responsiveness to synthetic chirps that were alike in all respects except for the length of their intervals. That is, significantly more courtship patterns were recorded during playback of chirps having pulse intervals of either 40 or 50 msec than during playback of chirps whose intervals were 35 msec or less. This, therefore, strongly indicated that the entire interval, or some portion thereof, was indeed an important source of information relating to species specificity. This conclusion parallels those of other workers who have previously examined this particular parameter in the sounds of other animals (Bennet-Clark & Ewing, 1970; Busnel, 1964; Falls, 1969; Loftus-Hills & Littlejohn, 1971; Schneider, 1968; Waldron, 1964). Additionally, Ha also varied systematically one component of the interval during playback tests, i.e., pulse duration. Broad variation of this parameter (from 5 to 20 msec) did not, however, bring forth any significant difference in responsiveness. Thus, some other parameter of the interval (e.g., 'off-time') or a combination of parameters carried the essential information to provide the consistent response differentials.

Further work on differences in the level of responsiveness of fishes to changes in the temporal patterning of their sounds will certainly provide ever-increasing insight into the importance of the acoustic modality to species recognition as well as the adaptiveness and evolution of sound-receptor and sound-producing mechanisms.

#### SUMMARY

1. Males of laboratory and field colonies of the bicolor damselfish, *Eupomacentrus partitus*, showed significantly greater response to playback of courtship sounds of

conspecifics than to playback of structurally similar and fully analogous sounds of two closely related and sympatric congeners, *E. leucostictus* and *E. planifrons*.

2. Relative levels of responsiveness by these colonies differed, however, in that laboratory males showed a significant difference in courtship during playback periods of congeneric sounds (recorded in the laboratory) whereas field males showed no such difference.

3. Field males, though responding well to typical laboratory sounds from conspecifics during tests which did not include playback of field sounds from conspecifics, failed to respond well when playback periods did include such field sounds.

4. Present evidence demonstrates that male bicolors possess an excellent discriminative ability within the acoustic modality and that such discrimination is based on some factor of the structural patterning, in time, of the experimental sounds.

5. Present evidence also indicates that the observed response differentials noted during experiments were the result of a slight, but important, difference in at least one typical parameter, i.e., the pulse interval.

This study was supported by contract N00014-67-A-0201-0004, Oceanic Biology Programs, Office of Naval Research and grant GB 31000x, National Science Foundation. We thank Samuel J. Ha for assistance and the privilege to cite various unpublished findings. Karen Munro, Stanley Walewski, Arnold Banner and Joseph Richard also provided either assistance or most helpful criticism of test design and acoustical details. The field portion of the study was carried out through the kind support of the Lerner Marine Laboratory, Bimini, Bahamas – Robert F. Mathewson, Director. This is contribution No. 1523 from the Rosenstiel School of Marine and Atmospheric Science, University of Miami.

#### REFERENCES

- BENNET-CLARK, H. C. & EWING, A. W. (1970). The love song of the fruit fly. *Sci. Am.* **223** (1), 85–92.
- BUSNEL, R. G. (1964). Examples of the application of electro-acoustic techniques to the measurement of certain behaviour patterns. In *Acoustic Behaviour of Animals* (ed. R. G. Busnel), pp. 54–65. New York: Elsevier Publ. Co.
- FALLS, J. B. (1969). Functions of territorial song in the white-throated sparrow. In *Bird Vocalisations* (ed. R. A. Hinde), pp. 207–32. Cambridge University Press.
- FISH, J. F. (1969). The effect of sound playback on the toadfish (*Opsanus tau*). Dissertation Abstract, University of Michigan, Microfilm no. 70-14, 148, 3 pp.
- FRKYTAG, G. (1968). Ergebnisse zur marinen Bioakustik. *Protokolle zur Fischereitechnik* **11**, 252–352.
- GORDON, C. R. & LOEWENSTEIN, J. M. (1969). A system for investigations on the behavior and sonic activity of fishes. *Final Rep., Office Nav. Res., Contract Nonr 840* (13), 15 pp.
- HA, S. J. (1972). Aspects of sound communication in the damselfish, *Eupomacentrus partitus*. Doctoral Dissertation, University of Miami, 68 pp.
- KRONENGOLD, M., DANN, R., GREEN, W. C. & LOEWENSTEIN, J. M. (1964). An acoustic-video system for marine biological research. Description of the system. In *Marine Bio-acoustics* (ed. W. N. Tavolga), pp. 11–25. New York: Pergamon Press.
- LOFTUS-HILLS, J. J. & LITTLEJOHN, M. J. (1971). Pulse repetition rate as the basis for mating call discrimination by two sympatric species of *Hyla*. *Copeia* (1), 154–5.
- MOULTON, J. M. (1964a). Acoustic behaviour of fishes. In *Acoustic Behaviour of Animals* (ed. R. G. Busnel), pp. 655–93. New York: Elsevier Publ. Co.
- MOULTON, J. M. (1964b). Underwater sound: biological aspects. *Oceanogr. Mar. Biol. Ann. Rev.* **2**, 425–54.
- MYRBERG, A. A. JR. (1972a). Using sound to influence the behavior of free-ranging marine animals. In *Behavior of Marine Animals: Current Perspectives in Research*, vol. 2 (ed. H. E. Winn and B. L. Olla), pp. 435–468. New York: Plenum Press.
- MYRBERG, A. A. JR. (1972b). Ethology of the bicolor damselfish, *Eupomacentrus partitus* (Pisces: Pomacentridae). A comparative analysis of laboratory and field behavior. *Anim. Behav. Monogr.* (In the Press).



- MYRBERG, A. A. JR., BANNER, A. & RICHARD, J. D. (1969). Shark attraction using a video-acoustic system. *Mar. Biol.* **2** (3), 264-76.
- PROTASOV, V. R. & ROMANENKO, Y. V. (1962). Significance of certain fish sounds. *Zool. Zhr.* **41**, 1516-28.
- SCHNEIDER, H. (1968). Bio-akustische Untersuchungen am Mittelmeerlaubfrosch. *Z. vergl. Physiol.* **61**, 369-85.
- SPANIER, E. (1970). Analysis of sounds and associated behavior of the domino damselfish, *Dascyllus trimaculatus* (Rüppell, 1828) (Pomacentridae). Master's Thesis, Tel-Aviv University. (Abstract, 2 pp.)
- STEVENSON, R. A. (1967). Underwater television. *Oceanol. Intl.* **2**, 30-5.
- STOUT, J. F. (1966). Sound communication in fishes with special reference to *Notropis analostanus*. *Proc. 3rd Ann. Conf. Biol. Sonar and Diving Mammals*, pp. 159-77.
- TAVOLGA, W. N. (1965). Review of marine bio-acoustics. State of the art: *Tech. Rep. NAVTRADEV-CEN*, no. 1212-1. Port Washington, 100 pp.
- TAVOLGA, W. N. (1968). Fishes. In *Animal Communication* (ed. T. S. Sebeok), pp. 271-88. Bloomington: Indiana University Press.
- WALDRON, I. (1964). Courtship sound production in two sympatric sibling *Drosophila* species. *Science*, N. Y. **144** (3615), 191-3.
- WINN, H. E. (1964). The biological significance of fish sounds. In *Marine Bio-acoustics* (ed. W. N. Tavolga), pp. 213-31. New York: Pergamon Press.
- WINN, H. E. (1967). Vocal facilitation and the biological significance of toad-fish sounds. In *Marine Bio-acoustics*, vol. 2 (ed. W. N. Tavolga), pp. 283-304. New York: Pergamon Press.
- WODINSKY, J. (1964). [General Discussion.] In *Marine Bio-acoustics* (ed. W. N. Tavolga), pp. 249-50. New York: Pergamon Press.

## APPENDIX

A brief description follows of those motor patterns of male courtship in *E. partitus* mentioned in the present study.

The Tilt (Fig. 1 A) is a lateral rolling of the body, 20-45°, that is performed either from a moving or hovering position. It is followed either by a rapid return of the body to the normal upright position or by a smooth transition into the next, most probable pattern of the courtship sequence, the Dip. The latter (Fig. 1 B) is a vertical or near-vertical dive by the actor toward the substrate from a position that is 0.5 to 1 m above the substrate. After tilting and dipping a number of times, the male pitches his body slightly, head down (pelvics expanded), and then, holding that posture, rapidly swims toward a female. This pattern, the Nudge, is directed toward the ventral aspect of the caudal peduncle of the female (often contact is not made, however, since the unique swimming posture of the male prevents him from overtaking a rapidly moving female). Following the Nudge, and especially if contact is made, the male performs the Lead. This rapid movement to the nest area occurs with exaggerated tail movements and slight upward travel followed by long glides close to the substrate (length of glides depends on distance from nest). Often under aquarium conditions the female is already so close to the actor's territory, the Lead is omitted and a rapidly repeating series of Tlts and Dips occur even up to the nest.

The above description constitutes approximately the first half of the total courtship sequence, leading to spawning in the species. The second half relies heavily upon the female nearing the nest area, and this rarely occurred during playback experiments. An inventory of the recognizably species-typical motor patterns of *E. partitus* has been completed (Myrberg, 1972*b*) and the reader is referred there for more information regarding the sequential nature of courtship and other activities, as performed by the subject species in the laboratory, as well as in the field.

