The Behavior of Fish and Other Aquatic Animals

EDITED BY
DAVID I. MOSTOFSKY

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Preface

The revitalized interest in marine life and aquatic animals has brought with it special opportunities for the added participation by the specialties of comparative and experimental psychology. The historical union of the biological sciences and the behavioral sciences was once restricted to matters of abstruse theory or isolated ethological phenomena. Now, advances in both disciplines have created interdependencies in a variety of research settings. Research in aquatic life provides the most recent development for extending this joint partnership. While the level of expertise in this area resides mostly in biology, at least three categories of considerations warrant a critical and careful examination of the argument for a more aggressive and informed involvement by psychology at this time. They provide the guiding spirit for this book.

The first category relates to the value which would be realized as a result of enabling essential contributions to basic science. Much of what classical biology of a century ago defined as its mandate is currently a daily preoccupation of many psychological laboratories. The fine-grain analysis of an organism's behavior, in both its natural and contrived environments, has been increasingly the focus of psychological inquiry. While biologists have refined and adapted much of chemistry and physics for their methodology and analysis, the basic scientific inquiry relating to the behavior of living organisms has been supported by psychologists concerned with learning, perception, biophysical conditioning, social behavior, emotionality, and related "psychological" aspects of the total descriptive profile. These questions take on even greater importance when the issues are raised in the context of comparisons with other species. A disproportionate emphasis by behavioral scientists in studying only selected organisms has resulted in a seriously deficient understanding of aquatic life. For the growth of psychology as a science, and for the necessary complement of the efforts of biologists, such a "knowledgeability gap" needs to be drastically and rapidly reduced.

A second concern relates to the need for supporting the emergence and development of hybrid specialties. The collaborative union among the sciences has had several noticeable effects. First, it has produced a number of disciplines or fields which are identified by their hyphenated or concatonated labels, symbolic of autonymous and viable enterprises which represent an integrated and deliberate program of codisciplinary activity. The behavioral sciences have had their share of such hyphenated unions (witness psychophysics, neuropsychology, and psychopharmacology). Other specialized interests appear on the threshold of gaining such independence and recognition (e.g., behavioral neurophysiology). Whether "behavioral biology," "behavioral ecology," or some comparable endeavor can emerge and survive in the scientific community remains to be seen. More important is the recognition of the *need to explore* joint codisciplinary research for specialized bodies of inquiry. Marine biology, marine ecology, etc., seem to be the sponsoring agents of specialization in which behavioral techniques and theory comprise a meaningful component of the system.

Finally, there is the category of application and practical utilization. One pressing concern in assessing conditions relevant to conditions of marine ecology (and ultimately relevant to any proposed innovations for management of that environment) relates to reliable measurements and to the derivation of predictive equations for the behavior of marine life under specified conditions. Some of these questions are answerable for cellular and molecular levels only. Some are solvable by techniques of chemical assay and biophysical determinations. And not least, a large measure of the final information sought will depend upon understanding the observable (albeit grosser) perceptuomotor activity of these organisms—the daily preoccupation of experimental psychology. There are two realizations of such a behavioral program. First, it enables the derivation of a systematic and programmatic determination of relevant behavior, i.e., it provides a stable set of dependent variables against which to measure a variety of "treatment effects" (akin to the objective in psychopharmacology). Second, it sets the stage for intervention and modification of the environment to assure necessary behavioral control. One can consider the specific instance of toxicity or pollutants. The hope would be that a program of behavior research would ultimately provide an assessment of the effects of such stimuli on a variety of behaviors and functioning of the organism. Also, it is reasonable to plan for a program that would ensure avoidance or compensation by the organism to offset the threat that has invaded his ecological world.

The *Zeitgeist* of such activity has brought with it the need for published materials that can responsibly depict the status quo of existing knowledge, and that can serve to educate the scientist who is desirous of an organized presentation focused on biobehavioral issues and techniques. The appearance of this volume represents the first attempt to organize the original writings of specialists concerned with a variety of these issues and techniques. It is hardly the last work; hopefully it will rather serve to provide the necessary impetus for vitalizing a most important area of inquiry.

David I. Mostofsky

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The Symbiotic Behavior of Fishes

GEORGE S. LOSEY, JR.

I. INTRODUCTION—MODERN VIEWS OF SYMBIOSES

The term "symbiosis" has been variously defined in the last century since its introduction by deBary (1879). I retain the original usage of the term as meaning "living together." This forces the symbiologist to consider virtually any interspecific relationship in which the species have at least some effect on one another. Symbioses have been subdivided in a variety of ways into familiar categories such as mutualism, parasitism, commensalism, etc. (Table I). The degree of harm as opposed to benefit that is realized by the symbionts due to their association was the basis of the earliest subdivision (e.g., Allee *et al.*, 1949). Many subsequent workers have shunned the subjective criteria of "harm" and "benefit" and used more objective indicators such as population growth rate (Odum, 1959), physiological dependency (Cheng, 1967), or survival value

TABLE I
Some Methods of Categorizing Symbioses

	Commensalism	Parasitism	Mutualism	Competition
Classic	Benefit to one No effect to other	Benefit to one Harm to other	Benefit to both	Harm to both
Population growth	Increase to one No effect to other	Increase to one Decrease to other	Increase to both	Decrease to both
Physiological	Facultative metabolic Dependency of one	Obligate metabolic Dependency of one	Obligate metabolic Dependency of both	Undefined

(Losey, 1972a). All of these measures prove to be valuable at one time or another as indicators of the status of the relationship between the species and the individuals of the species.

The form and the consequences of the relationships between symbionts may be highly variable in many cases. Keys (1928) indicated that the effect of ectoparasitic isopods on fish might become important only under adverse conditions. Lincicome (1971) with endoparasites and Losey (1972a, 1974a) with cleaning symbiosis in fish have indicated how some symbioses might exist as a mutualism, commensalism, or parasitism depending upon environmental factors. The status of any symbiosis as a mutualism or parasitism results from the balance of many factors. Our understanding of symbiotic relationships can be greatly increased through study of changes in the status of the symbiosis in response to changes in environmental factors.

This chapter explores a series of symbiotic relationships in fishes that range from broad multispecific types that have little or no intimacy between symbionts to intimate mutualistic relationships. Symbioses that have only limited interest in the study of behavior are avoided. The reviews are intended to aid nonsymbiologists in the understanding of the interspecific behavior of their animals and to encourage research on fish symbioses.

II. FIELD METHODS OF THE MARINE ETHOLOGIST

Although many behavioral problems can be approached by an observer restricted to the surface of the water, compressed gas diving has greatly extended the range of problems that can be approached. The observer may remain under water for many minutes or even hours with SCUBA or rebreather gear or remain for days to weeks in a saturation diving habitat. However, aside from the increased logistic difficulty of such methods, the marine ethologist is faced with

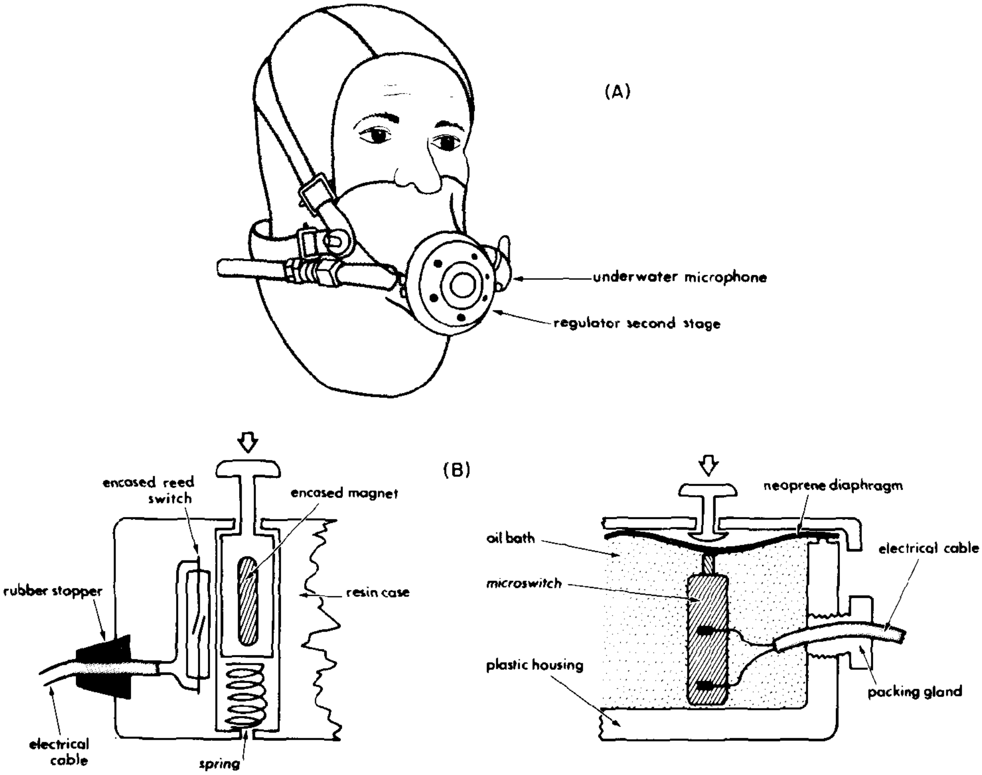

Fig. 1. "A" illustrates one type of underwater microphone for use with a tape recorder. (Drawn from advertisements by Hydro Products, a Tetratech Company, San Diego, California.) "B" gives a stylized drawing of two types of underwater keyboard switches for use with event recorders. Several such switches would be placed in each housing.

additional problems. A free swimming diver generates a variety of acoustic and visual stimuli. Exhaled air and swimming motions of a large and not entirely graceful biped appear to have a strong influence on many fishes. The use of underwater visual and acoustic blinds (Losey, 1971) or nearly bubble-free rebreather gear can help to solve these problems, but cost and logistic difficulty usually prevent their use. Underwater television can solve many of these problems (Myrberg, 1973), but it imposes similar cost and logistic problems. However, in many cases the use of television is demanded for at least some parts of the study. I have found dramatic changes in the types and numbers of fish observed on a Hawaiian reef when a diver was in the water as opposed to when only a television camera was present, and Myrberg (1973) has reviewed the value of television for the marine ethologist.

Those scientists fortunate enough to have access to an underwater television system also eliminate the problem of underwater recording of observations since standard laboratory equipment can be used during playback of video tapes. The diver is less fortunate. Most divers resort to writing slates with underwater paper or plastic. Some waterproof papers can even be used in common duplicating machines to produce standard data formats, maps, etc. (R. Nolan, University of Hawaii, personal communication). Underwater tape recorders can be used by placing a microphone inside of a full-face mask or by using a special mouthpiece that leaves the lips and teeth free to move and incorporates an underwater microphone (Fig. 1a). The tape recorder is probably the single most valuable piece of equipment for the marine ethologist. Underwater event recorders allow an even finer level of quantification in the field (Losey, 1971, 1972a, 1974a), but at present, they are not commercially available. However, a moderate amount of tooling skill can produce a waterproof switch box of reed switches, actuated by magnets, or a diaphram type of switch box (Fig. 1b). This may then be connected to a four- or eight-channel miniature event recorder in an underwater housing to form a powerful data recording tool for the diver. Miniature digital recorders may also be used but they require an interface to a computer or some mechanical data retrieval device.

Regardless of the methods and hardware employed and the handicap of operating in the foreign aquatic medium, recent years have testified to the feasibility of observational and experimental field studies of marine animals. They have proved to be of extreme value in the guidance and interpretation of more highly controlled laboratory studies. In studies of symbioses involving many species, such field observations are extremely important adjuncts to laboratory studies.

III. SYMBIOSES INVOLVING MANY SPECIES

Perhaps the broadest level of analysis of symbiotic interaction involves the temporal and spatial organization of marine reef fishes. Review of the complex predatory interactions and changeover patterns from the diurnal to nocturnal faunal elements is beyond the scope of this chapter. Hobson (1965, 1968, 1972, 1973) provides an in-depth study of these relationships. Instead this chapter will focus upon interactions within feeding guilds which have received a recent surge of attention from fish behaviorists, and upon a few more specialized relationships that cross the boundaries between feeding guilds.

A. Interaction within Feeding Guilds

1. The Guild of Benthic Herbivores

The relationships between species of herbivorous reef fishes have only recently received detailed attention and now promise to be one of the most fascinating symbioses in the reef environment. This section will outline how the social behaviors and feeding habits of many herbivorous fishes are interdependent on other sympatric members of their feeding guild.

Several types of social organizations are found among the benthic herbivorous fishes. They may be solitary home ranging, paired or in small roaming groups, form large uni- or multispecific schools, or show temporary to permanent territorial defense. Jones (1968) and Helfrich *et al.* (1968) were first to mention that the social organization of one species might result from the presence of others. They indicated that the frequent group feeding behavior of the manini (*Acanthurus triostegus*) enabled them to violate the territories of other species that were vigorously defended against individual intruders. Lorenz (1966) hypothesized that the bright colorations of many coral reef fishes served to avoid interspecific aggression. This contributed to the belief of earlier workers that cases of interspecific aggression resulted from "mistaken identity" of another species as a conspecific. Rasa (1969) indicated that the most frequent interspecific attacks of the territorial damsel fish, *Pomacentrus jenkinsi,* were directed toward the morphologically similar surgeon fish, *Ctenochaetus strigosus.*

Recent work, however, tends to refute or at least greatly modify these results. Albrecht (1969), Low (1971), Myrberg (1972), MacDonald (1973), Syrop (1974), Itzkowitz (1974), and Thresher (1974) have shown that several pomacentrid fishes which defend benthic territories and feed on benthic algae defend these territories at least somewhat selectively, usually against other benthic herbivores. In several cases the most frequent attacks were directed toward competitors with little or no morphological similarity to the territory holder. Myrberg and Thresher (1974) have suggested the concept of the serial territory wherein the boundary at

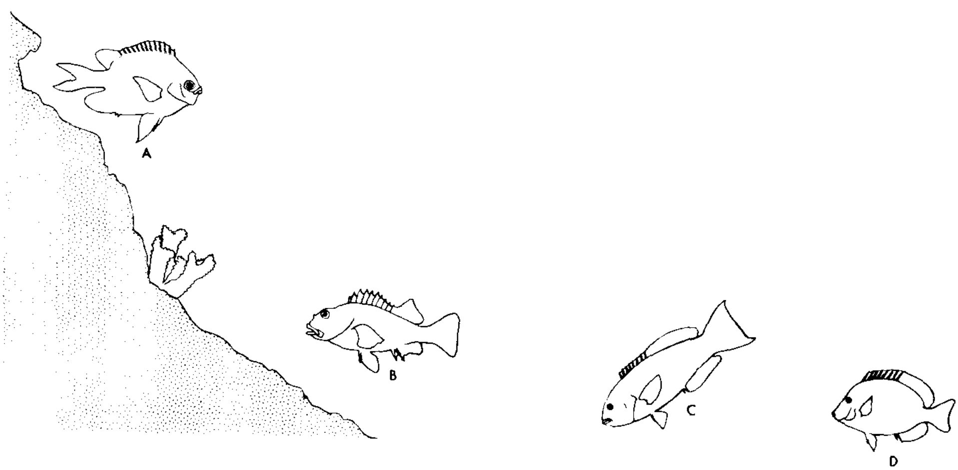

Fig. 2. The distance at which some territorial *Pomacentrus* spp. (A) might be expected to attack a carnivore, (B), an omnivore, (C), and a competitive herbivorous fish (D). The herbivore which probably competes with the territory holder is attacked at the greatest distance. See text.

which an intruder is attacked varies for different species and depends, at least partially, on the intruder's feeding habits (Fig. 2). Jones (1968) indicated the possible existence of a generic pecking order in terms of the species' relative ability to exploit and defend a food supply. This same type of interspecific hierarchy also appears to exist between certain cichlid fishes (G. W. Barlow, University of California, Berkeley, personal communication).

These studies have suggested a variety of problems in the interspecific or symbiotic behavioral ecology and ethology of fishes. I will list some of these problems below, usually with little more than superficial evidence to support their existence. Several of these relationships have also been suggested by Barlow (1974a,b) along with valuable comparisons to the cichlid fishes.

a. Aggression and Interspecific Territorial Defense. The most thoroughly documented form of interaction between herbivorous fishes is territorial defense. Species of acanthurid and pomacentrid fishes have been found to defend territories against other herbivorous fishes (e.g., Low, 1971; Barlow, 1974a). *Eupomacentrus planifrons* (Myrberg and Thresher, 1974) and probably many others express this territory by attacking other species at varying distances from the center of their feeding area: herbivores are attacked at a distant perimeter, whereas species such as carnivores may be tolerated until quite close to the center of the territory, or not attacked at all. The obvious interpretation of this territory as a protected feeding space in *Eupomacentrus jenkinsi* was supported by Syrop (1974). He found that the standing crop of filamentous algae was greater within territories of *E. jenkinsi* as opposed to surrounding unprotected areas, and that they defended larger territories on a reef that had a greater number of herbivorous competitors. He also indicated that the territory holder may maintain the standing crop of algae within the territory at the level of maximum sustainable yield.

Sale (1974) has drawn attention to the importance of interaction between herbivores that all defend territories in the same habitat. In some areas, he found that interactions between species of territorial pomacentrids may be more common than intraspecific interactions. He also found that many of these species coexist in the same microhabitat despite broad overlap in feeding habits and territorial behavior. He has suggested that the relative abundance of these species in any one area is largely determined by chance: i.e., all of the species are nearly equal in their ability to defend a space and that successful recruitment results from the "random creation of vacant living space, and . . . the uncontrolled dispersal of the pelagic larvae of all guild species" (Sale, 1974, p. 1). Coexistence of several competitive species in the same area might also be explained as an "edge effect" such that the habitat studied is intermediate between the habitats to which each species has specialized. There might as well be a ceiling effect on the degree of territoriality that is possible: All of these pomacentrids are