AMER. ZOOL., 14:9-34 (1974).

Contrasts in Social Behavior between Central American Cichlid Fishes and Coral-reef Surgeon Fishes

GEORGE W. BARLOW

Department of Zoology and *Museum of Vertebrate Zoology, University of California, Berkeley, California 94720*

SYNOPSIS. The social systems and related behavior of cichlid and surgeon fishes are compared in terms of (i) physical spacing, (ii) theoretical spacing (communication), (iii) castes, (iv) group composition, (v) open versus closed groups, and (vi) reproductive behavior.

Cichlids only recently invaded Central America. Despite the occurrence of about 100 species there, most are in one genus, *Cichlasoma*. Yet, they express a spectrum of feeding behavior, ranging from grazing herbivore through omnivore to predator, each of varying degrees of specialization. In contrast, their social behavior is remarkably conservative. There is a tendency for the generally found division of labor, with the female doing more of the direct caretaking of the eggs or fry and the male more of the defense, to lead toward polygyny. This is counterbalanced by the need for both parents to defend the fry. Communication is most accessible through a study of color patterns. While seemingly diverse, there is a common plan that entails the use of some or all of the same vertical bars and their central spots, and the appearance of yellow orange, red, or black ventrally.

The coral-reef community is one of the oldest in existence. Surgeon fishes are pantropical, especially in the Pacific Ocean, and have developed distinct generic groupings within a compact family of about 75 species. Most are herbivorous, with some more specialized than others. The species fall into guilds, within which there is broad overlap in diets. The social systems differ radically, both when breeding and when not, and can be understood as consequences of their strategies of obtaining food.

Wickler's classification of reproductive types within the Cichlidae is shown to be no advance over the previous dichotomy of substrate and mouthbreeding species. Poster coloration in surgeon fishes is apparently as important, or more, in extraspecific than intraspecific aggression, and poster-colored surgeon fishes show pronounced rapid color changes when fighting intraspecifically.

INTRODUCTION

An important service rendered by symposia is the identification of areas where work is needed. This paper will have made a contribution if it does nothing beyond creating an awareness of the relatively primitive understanding we have of fish social systems in relation to their environment. This stands in stark contrast to the progress made in recent years in studies of the social systems of birds and mammals (e.g., Crook on weaver birds, 1964, and primates, 1970; Estes, 1969, on wildebeest; Pitelka et al., 1973, on shorebirds; and Tinbergen, 1959, and his colleagues on gulls).

While there has been no shortage of behavioral studies on fishes, most of it either has been fragmented within groups, or has concentrated on certain species. Thus, the comparative studies on cichlid fishes by Wickler (e.g., 1966) and in the field by Lowe-McConnell (e.g., 1969) have been opportunistic rather than programmatic. Apfelbach (1969) concentrated on the genus

So many individuals have helped in ways large and small over the years that they are too numerous to list, but my thanks go to all of them. The manuscript was kindly reviewed by J. R. Baylis and K. R. McKaye. The cichlid work has been generously supported by the National Science Foundation, most recently through grants GB 13426 and GB 32192X.

N.S.F. also funded in part the research on the surgeon fishes. I am pleased to acknowledge substantial support from the Oceanic Institute of Hawaii, through its then Director K. S. Norris. The field trip to Eniwetok was arranged by P. Helfrich, Director of the Eniwetok Marine Biology Laboratory, with funds provided by the Atomic Energy Commission.

Tilapia although he studied but 4 of 11 species intensively. The emphasis has been on reproductive behavior, mostly as seen in the laboratory. (To date, the book by Fryer and Illes [1972] has not been available to me.) Obviously, the study of social systems in fishes calls for observing all types of social behavior, ideally in nature. Programmatic studies of this type are now being pursued by Myrberg (e.g., 1972) on pomacentrids and by Ernest Reese on chaetodontids. Okuno (1963) has attempted a synthetic overview.

Being terrestrial, man is ill equipped and reluctant to invade the aquatic realm to observe fishes there. This attitude has even carried over to easily observed stream and lakeshore species. With the advent of SCUBA it has become possible to watch fishes underwater, even at moderate depths. Unfortunately, the observer is usually limited to 1 to 2 hr per dive, and generally to not more than two dives per day. Water temperatures are such that even with good diving suits a human being experiences a serious heat loss when lying still. And preparation for a dive often consumes considerable time. This, plus the basically hostile environment, makes underwater observations unlikely, though not at all impossible, between about 5:00 PM and 9:00 AM, when much of the most interesting behavior is occurring. Finally, even those who have become good divers have been trained mostly by ichthyologists who have never been underwater. Consequently, the problems inherited by students have usually been formulated by a terrestrially bound professor with more conventional views of fish biology.

Students embarking on a study of fish behavior would be best advised to read beyond the fish literature, studying particularly the recent work done on birds and mammals that lies at the interface of behavior and ecology. These ideas can be tested on fishes and reformulated. Fishes, after all, are the oldest, most diverse, most species-rich, and, in some instances, the most observable of all vertebrates. The ability of the observer literally to fly about in their environment creates possibilities unheard of in the terrestrial realm.

In what follows I attempt to bring together some of my thoughts on the social systems of freshwater cichlid fishes (Cichlidae) and marine surgeon fishes (Acanthuridae). I have been working on cichlids for about 14 years, but mostly in the laboratory. During the last 7 years I have made a number of field trips to Central America where my students and I have observed cichlid fishes underwater, primarily in Nicaragua. We have also watched these fishes in Panama, Costa Rica, El Salvador, and British Honduras.

The involvement with surgeon fishes is more recent but more intense and overtly comparative. I spent 7 weeks at Kealakekua Bay, Hawaii, in 1971, and then 3 weeks at Eniwetok Atoll with Ken McKaye in 1972. Prior to my interest in this group I made incidental underwater observations on their behavior in places ranging from the Gulf of California through the Galápagos Islands and numerous Pacific Islands from Oahu to the Philippines.

Two important points need to be made about the work that follows. It is a premature summary with relatively little documentation. Often there will be noncontrasting information on the two families of fishes, and there will be gaping holes in the story. This summary should be regarded as much a proposal of hypotheses as a declaration of a state of affairs. I anticipate that many of the conclusions here will be replaced as our knowledge grows.

BACKGROUND INFORMATION

Cichlidae

Cichlids are the most successful percoid fishes in fresh water. They are especially species-rich in Africa and South America, and also occur in tropical Asia. In those areas they are a well-established component of the mature fauna and have reasonably well defined genera; often there are many locally sympatric species.

Apparently the cichlid fishes invaded Central America recently from South Amer-

ica as the Panamanian Isthmus emerged, probably during the late Pliocene (Myers, 1966; Miller, 1966). At the time of their entry, Central America had a depauperate fish fauna dominated by poeciliids, that is, the mollies, swordtails, and their allies (Myers, 1966). The advancing cichlids radiated into the different water systems giving rise to nearly 100 species. Reflecting their recency, almost all the species have been placed in *Cichlasoma,* although several different lines obviously exist within that genus. Three other distinct genera, with but six nominal species, have been described.

Geographical isolation has been a decisive factor. Each water system is separated from the next by a land barrier, restricting the movements of both young and adults. One consequence is the apparent re-evolution of similar types in separate drainage systems. While some species are widely distributed, there is a high degree of endemism. In no water system is there an excessive number of sympatric species; the modal number of species appears to be around 10. The extensive Rio Asumacinto system contains 44 known species, but there is endemism within its boundaries (Miller, 1966). Thus, each faunal assemblage in each river system may be thought of as a replicate experiment with some endemic and a few ubiquitous species.

One of the most well-studied aspects of cichlid biology is reproductive behavior, probably because of the ease with which they breed in aquaria and their well-developed parental care. Generally, the male and female form a pair, prepare a nest site, and spawn. The eggs are then tended and fanned, as are the larvae that are kept in prepared places. Protective care continues for some weeks after the fry have become free swimming.

A major variation on this theme is the development of mouthbreeding in at least four different lines; these are represented by a number of genera that can be grouped with *Tilapia* and with *Haplochromis* in Africa, and by *Geophagus* and by *Aequidens* in South America. The other variation is polygyny, a harem society with one male and several substrate breeding, parental females, shown in the genus *Lamprologus* (Wickler, 1965) in Africa and *Apistogramma* (Burchard, 1965) in South America. Both mouthbreeding and polygynous species were derived from species that had joint parental care. Furthermore, mouthbreeding in the New World genera is less well developed than in the African forms.

Fundamental to understanding the adaptiveness of the social system of any animal is a knowledge of its feeding behavior. Unfortunately, there is little precise information available from the cichlid fishes in Central America. Mostly, it is based on watching the fish feed in nature, often under circumstances that preclude a confident knowledge of what is being eaten. Nonetheless, some differences are obvious, such as those between the herbivores and piscivores. Feeding adaptations, moreover, are correlated with morphological differences and with the habitat in which the species occurs. Hence the feeding habits can also be judged from morphology and occurrence.

The fry of all cichlid fishes start as carnivores. Most feed on plankton at first but soon take benthic microfauna as well. The young of many species in the New World nibble mucus from the parents' body. Virtually nothing is known about this type of feeding behavior in nature, however, except for the observations made by us in Nicaragua (Noakes and Barlow, 1973).

Within the juvenile and adult cichlids of Central America one finds almost all general feeding types. The most commonly occurring type is the omnivore. These fishes may eat Aufwuchs, plants, invertebrates, and fishes. Within this category there will doubtless prove to be varying degrees of specialization on different kinds of invertebrates, for example, snails, as well as cichlids that take more of one kind of material than of another. Most species in this group are middle sized, relatively deep-bodied fishes with small to modest gapes such as *Cichlasoma citrinellum, C. beani, C. maculicauda, C. octofasciatum,* and *C. cyano-*

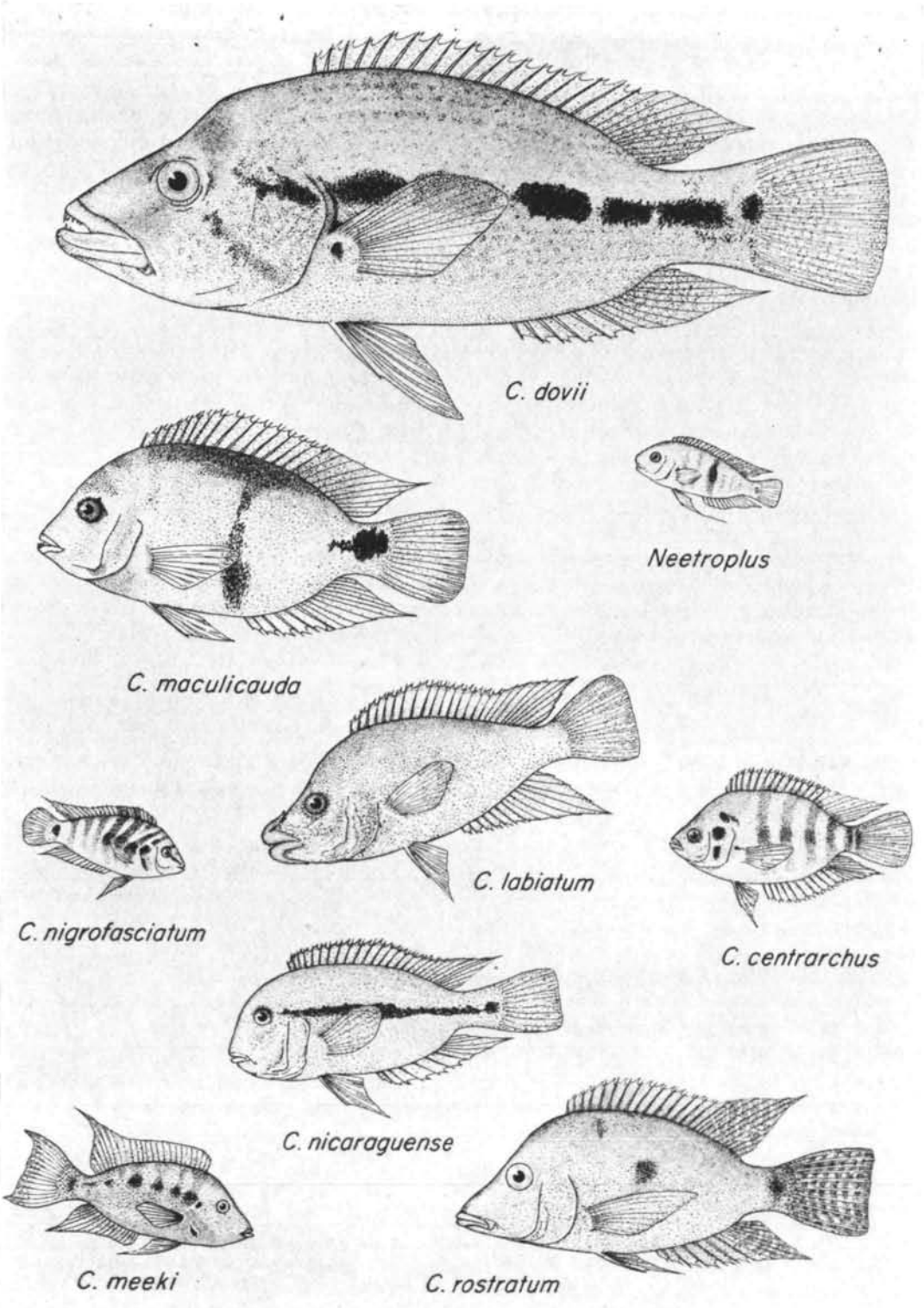

FIG. 1. Eight species of *Cichlasoma* plus *Neetroplus nematopus*. The relative sizes have been estimated. Color patterns are from live specimens; the *C. labiatum* was totally red.

guttatus (see Fig. 1 for some of the species mentioned here).

Many species are largely herbivorous, such as the small monotypic *Herotilapia multispinosa,* the middle sized *Cichlasoma synspilum,* and the large *C. tuba.* These species, nonetheless, can be omnivorous.

A much smaller group is represented by the piscivorous large bass-like species such as *Cichlasoma dovii, C. managuense, C. motaguense, C. friedrichsthalii,* and *Petenia splendida.* These species take a variety of fishes, including other members of their own family, but prefer unarmored fishes such as atherinids.

Another group, perhaps more numerous than the piscivores, are the substrate sifters. Many omnivores sometimes sift the substrate for food, as does *C. citrinellum,* but some species are specialized in this regard. Included here are members of the subgenus *Thorichthys* (the firemouth group, e.g., *C. meeki*) and *C. longimanus.* These are small- to medium-sized species with relatively elongate faces. The most extreme development is seen in *C. longirostris;* this medium-sized fish has a long pointed snout that it plunges into the bottom; it bears an uncanny resemblance to South America cichlids of the genus *Geophagus.*

Close to the sand sifters is the distinctive *Cichlasoma nicaraguense* (usually labelled as its junior synonym *C. spilotum* by aquarists). It occurs in mixed rock and sand habitats. Its feeding behavior is unknown, although it probably takes algae, detritus, and invertebrates while engaging in sand sifting or scraping Aufwuchs. It is a moderate-sized species with a distinctively rounded shape to its head. In many ways, its morphology is intermediate to the next cichlid, *Neetroplus.*

One of the most highly specialized feeding types is that of the Aufwuchs scraper *Nectroplus* (three nominal species). This small, slender species has a down-turned mouth and can be seen rasping the Aufwuchs from rocks. On occasion, however, they can be carnivorous. For instance, they follow under schools of spawning atherines eating the falling eggs. They also prey on the fry of other cichlids.

The next feeding type is one largely inferred from morphology. *Cichlasoma labiatum* is a slender species of medium size that has enormous puffy lips. These evidently act as a gasket when the mouth is pushed into crannies (Baylis, personal communication), facilitating the extraction of detritus and small invertebrates.

The cichlids of Central America thus present a broad spectrum of feeding adaptations. But these adaptations are not profound, for the herbivores will feed as carnivores when suitable prey are presented to them. Even the most carnivorous species will readily take inanimate laboratory food. Nonetheless, the different feeding adaptations are reflected in the size and body shapes of the fishes. And while the most common feeding type is the omnivore, specializations exist. The most highly specialized of these have given rise to the three genera, other than *Cichlasoma,* with but five species.

Acanthuridae

Surgeon fishes occur throughout the tropical seas where coral or rocky reefs provide the appropriate shallow-water habitats. To an ichthyologist they are a refreshingly compact family, consisting of about 75 species in six well-defined genera. While they are an advanced group of percoid fishes, they are members of the oldest continually existing community, that of the coral reef (Newall, 1971). They must, therefore, interact and compete with large numbers of other types of fishes.

There is some element of instability, however, since they have pelagic eggs and larvae that are variously vagile. The more widely distributed species must, in particular, be sufficiently adaptable to cope with the complex of species where they find themselves, for once the specialized Acronurus larva has descended to the reef, it is tied to that habitat. Open water forms a barrier to the adults.

Little is known about the spawning behavior of surgeon fishes. I will return to this later.

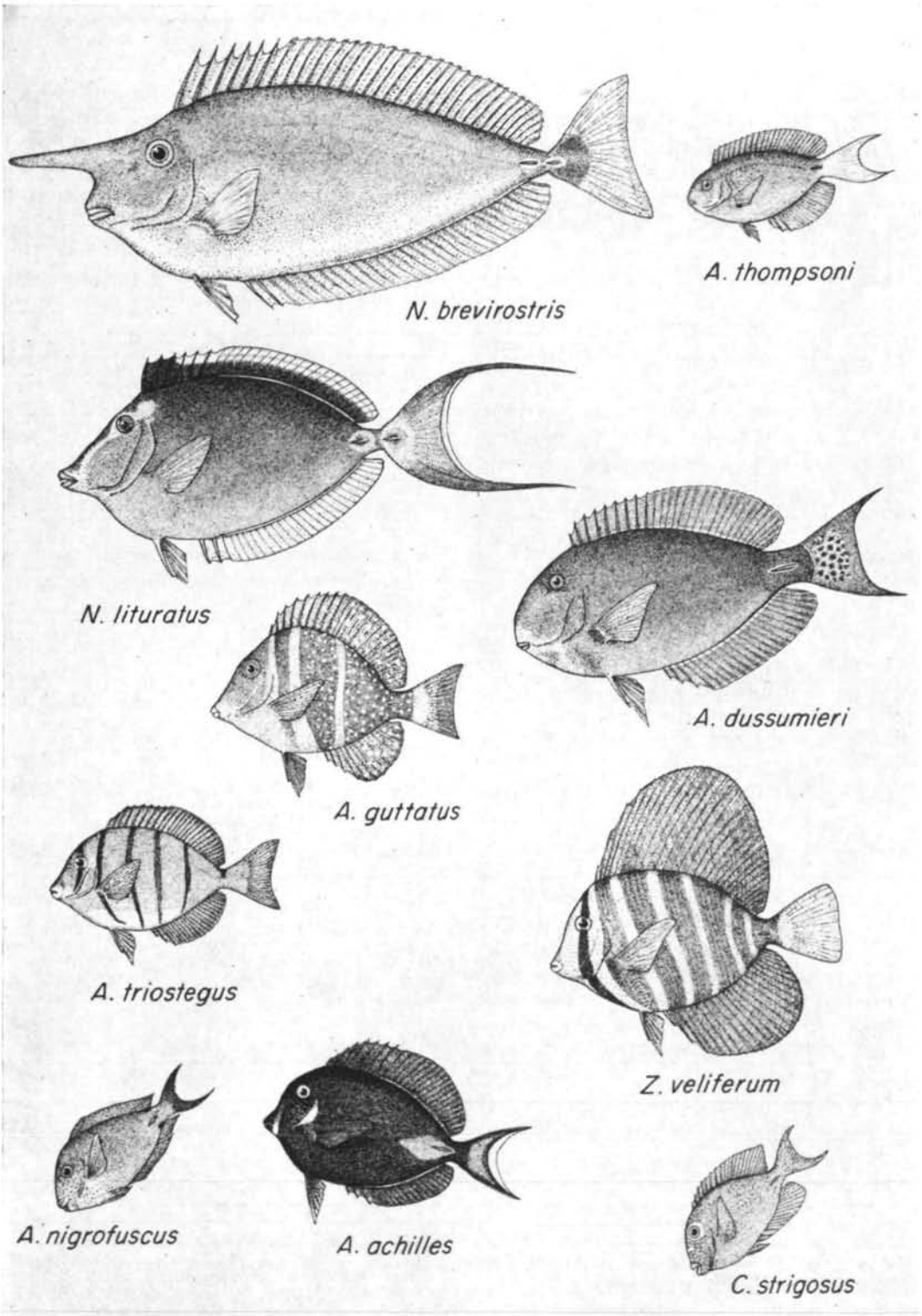

FIG. 2. Ten surgeon fishes, illustrating representatives of the feeding guilds (see text). The relative sizes have been estimated. Color patterns are from a combination of preserved and live specimens and may not be complete or correct in all details.

In contrast to the cichlids, the feeding biology of adult surgeon fishes is relatively well known, at least for the species that occur in Hawaii (Jones, 1968). The planktonic larvae are presumably carnivorous. But as soon as they settle to the reef and metamorphose, most become herbivorous. As they mature, they can be assigned to one of the feeding guilds. (Some representative species are shown in Fig. 2.)

Among the species tied to the hard reefs are the detritus feeders, all of the genus *Ctenochaetus*. Mostly these are small to medium in size. One species, however, the Hawaiian endemic *C. hawaiiensis*, is moderately large.

Perhaps the largest guild, in number of species, is the reef grazers (Jones considered the reef and sand grazers collectively, but they are better treated as separate groups). Most of the reef grazers are in the genus *Acanthurus*. These species are small to medium in size and seem to feed almost continuously by scraping at the reef with their mouths. There is broad overlap in the species of algae they consume (Jones, 1968).

Some division of resources is effected among the reef grazers by some of the species exploiting certain parts of the environment more than others. For example, atop the reef flat *A. guttatus* advances and recedes with the tide, as does *A. triostegus*. Being a smaller species, *A. triostegus* is often further shoreward and less in the surf line. At the edge of the reef flat and where the water surges a great deal one is more apt to encounter *A. achilles, A. glaucopareius,* and *A. lineatus*. Just off the reef flat, but still in the surgy area, are schools of *A. lucopareius*. Just below the rough water, and more intimately associated with the substrate, one finds *A. nigrofuscus* and *A. nigroris*. Here, and moving deeper, the detritus feeders become more abundant. At Eniwetok one species, *A. pyroferus*, is generally not seen until depths of at least 10 m have been reached; it is not clear what it is feeding on, however. None of these species is restricted to one place in the environment; it is common to find them feeding together, and in different areas.

Jones placed the two species of *Zebrasoma* within the grazing guild because of the species of algae found in their guts. But their long snouts suggest access to other types of food. The high rate of feeding, small size, and lack of mobility of *Z. flavescens* suggest that it is indeed a reef grazer. But the larger *Z. veliferum* spends less time feeding and it ranges over wide distances on the reef, suggesting that it is a browser (see below) not a grazer.

The next important guild is the sand grazers. All are in *Acanthurus*. They tend to be large mobile species, such as *A. dussumieri* and *A. mata,* who refuge (Hamilton and Watt, 1970) at selected places on the reef, or range widely among patch reefs. Their strategy is to take refuge on the reef when danger threatens and, when not, to move to nearby sandy areas where they ingest sand. They have a large muscular gizzard in which they remove diatoms and algae from the sand grains (Jones, 1968). These fishes regularly move in schools of mixed species, and each species strongly resembles the others. While often busy with feeding, they seem to have much time available for other kinds of behavior.

Some species are intermediate between reef and sand grazers. *Acanthurus olivaceus* fits this category since it both grazes on the reef and ingests sand. It is intermediate in size, trophic anatomy, color pattern, and behavior. *Acanthurus gahm* may also be of this type.

Browsers are surgeon fishes who feed on relatively leafy algae that is apparently patchy in occurrence but quickly and easily ingested. All spend relatively little time feeding and have much free time. Most browsers are in the genus *Naso* and are large, highly mobile species. They are frequent where reefs drop to depths, such as off headlands, or at pinnacles in atoll lagoons. Two species favor shallow water. One is a typical gray *Naso, N. unicornis*. The other is the atypical *N. lituratus*. *Acanthurus bleekeri* shares many features with these *Nasos,* and may be a browser. *Zebrasoma veliferum,* as noted, may also belong here.

The most exceptional feeding guild within the surgeon fishes is that of the plankton feeders. This type of behavior has appeared in at least two different genera. *Acanthurus thompsoni* is a small typical *Acanthurus* except for its more terete shape. It feeds in schools in deeper water, say 10 to 20 m, off the face of cliffs and pinnacles. *Naso hexacanthus* is a large *Naso* that is said to feed on plankton (Jones, 1968). As is typical of this genus, it is a large highly mobile species. It has, however, a more streamlined shape, and the pair of knives on each side of its caudal peduncle have been reduced to rounded scutes.

These herbivores, then, may be split into guilds within which there is broad overlap in diet. The chief consequences of membership in a guild are size and mobility, time free from feeding, and extent to which competition exists.

The detritus feeders and reef grazers are mostly small busy feeders with time for little else. The reef grazers also compete with many species. All these fishes tend to remain in a relatively small area, although some of them, such as the reef-flat invaders, roam considerably.

At the other extreme are the browsers, large mobile species who feed quickly and have much open time. Competition between the species seems minimal.

The sand grazers are in many ways intermediate between the reef grazers and the browsers. They are large, but generally not as large as the browsers, and they are mobile. They seem to have an intermediate amount of free time, and they often travel and feed in mixed species groups. There is probably no competition for sand since it is available in boundless amounts *if* the fish dare range far enough from the protective reef. To do this, they join company with other species feeding in the same way.

SOCIAL SYSTEMS

Anyone having experience with the recent literature in social systems will be aware that the term means different things to different investigators. For that reason, I will briefly outline what I consider the essential dimensions. Some will not be applicable to certain species, and some are better treated together than separately, as occurs when discussing patterns of spacing and group composition below.

1) *Physical spacing:* A convenient and unambiguous method of describing social systems is to measure the spacing between its units. On the one hand, this will consist of measuring the spacing between solitary animals or groups that can be considered the social units. On the other hand, distance between individuals within a group constitutes a direct description of the social structure of that group. Home range and territoriality are included here.

2) *Theoretical spacing (communication):* Two approaches are conventionally used, the more common being dominance-subordinance relationships. The other measure of theoretical spacing or distance can be the rate of exchange and the consequences of communication between individuals. If these are signals communicating dominance and subordinance relationships, then the approach is identical to the conventional dominance-subordinance hierarchy. However, communication networks extend beyond that into the exchange of signals bearing other types of information. In what follows I will be considering theoretical spacing primarily in the context of approaching and withdrawing.

3) *Castes:* Social systems may consist of groups in which all individuals are basically the same, that is, of one caste, as in certain schooling fishes. Often, however, individuals differ. The two principle differences are age and sex. But caste can be distinguished even within these, particularly in reference to the phase of reproductive cycles, such as courting, parental, and so on. Taken together, age, sex, and reproductive state define an individual's caste (*sensu* McBride, 1971).

4) *Group composition:* Social systems can be defined by the number of individuals, by caste, of which they are composed. For example, one social system in cichlid fishes is the harem (one-male) group, as in *Lam-*

prologus. Another social system, as in *Tilapia,* consists of territorial males in a group receiving females who come individually, thus a lek society.

5) *Open versus closed groups:* If animals may join and leave a group with relatively little disturbance to that group, it is said to be open. If animals in a group resist the joining of that group by another individual, and if the individuals in that group tend to stay together, the group is said to be closed.

6) *Special attributes of reproduction:* To round out or make intelligible the description of a social system, and in particular to appreciate its adaptiveness, it is often necessary to take into consideration the special attributes of reproductive behavior. In some species of cichlid fishes, for instance, there would be no difference in social system as defined in the foregoing. Yet one species might be a substrate breeder, and the other a mouthbreeder. Sometimes, too, it is more convenient to consider attributes such as open versus closed (pair bonding) and communication in the context of reproducing individuals as opposed to those who are not.

Cichlidae

Physical spacing. In all species so far investigated, the fry form a dense school of closely spaced individuals which stays close to the parents. As juveniles, they tend to form aggregations, but information is scanty here. The nonbreeding adults of all species are also inclined to congregate, but there are detectable differences in this behavior.

The small species living in well-articulated environments, such as among rock slides or submerged branches, congregate where such environments exist, then space themselves there. They rely on the environment for protection and do not form conspicuous groups, although they do sometimes move about in groups. *Cichlasoma nigrofasciatum,* as one example, can sometimes be observed moving in groups while feeding. Individual *Neetroplus,* as another, are generally well spaced while associated with the bottom. However, I have seen them in dense schools, numbering perhaps 10,000 individuals, hovering over rocky outcrops at depths of 10 to 15 m in Lake Jiloá, Nicaragua. McKaye (personal communication) has observed them moving in groups over the bottom while feeding.

The medium-sized species that live within an articulated environment are more mobile and more apt to travel in schools. But when not moving, they generally spread out in weakly defined groups or as individuals.

Medium-sized species found in sandy or open areas, such as over beds of *Chara,* are apt to maintain group cohesion both while moving and feeding (e.g., *C. longimanus, C. nicaraguense,* and *C. maculicauda*). However, some of these species also tend either to be isolated (*C. rostratum*), or to move in the company of other species. Occurring over open bottom, therefore, tends to promote continual cohesion, even to the extent of interspecific associations.

The large piscivorous species are inclined to live well spaced, solitarily or in pairs, as seen particularly in *C. dovii* and *C. managuense.* Even these may form small schools or groups as adults (*Petenia splendida,* personal observation; *C. dovii* in rivers of Costa Rica, Meral, personal communication; and *C. dovii* in Lake Jiloá, Baylis, personal communication).

In no case is there adequate information to make conclusive statements about home range. Incidental observations suggest, nonetheless, that some individuals remain in the same general area for a period of at least some days or weeks.

Territoriality in nonbreeding adults is generally transitory and difficult to recognize. It is most commonly seen in one fish feeding on the bottom who, through aggression, maintains space around it free of other individuals. At least one species may have a cave or crevice which has been dug out and in which an individual may seek refuge when threatened with danger (*C. citrinellum*); however, no defense of this retreat has been seen, nor obvious avoidance by another potential occupant.

Large predators such as *C. managuense*

and *C. dovii* may hold territories as pairs the year around. It is not clear whether they actually do, and whether they are going through one breeding cycle after another (Bleick, 1970). Adult *C. dovii* are said not to hold territories in the nonbreeding season in Lake Jiloá (Baylis, personal communication).

Theoretical spacing. Dominance-subordinance *hierarchies* are easy to demonstrate in the laboratory for a variety of Central American cichlids. This problem has not been explored in nature, however, since no fishes were marked so they could be recognized as individuals. However, I doubt the occurrence of stable dominance hierarchies in nature because groups change their composition so readily; they appear to be open groups, not closed. Dominance-subordinance *interactions,* in contrast, are obvious in the field.

It is more profitable to treat these approach-withdrawal relationships in the context of communication. In so doing, it is necessary to consider the three plausible sensory modalities.

It is now known that some communicate acoustically (Myrberg et al., 1965; Schwarz, unpublished). These signals consist of pulsed low-frequency sounds, emitted mostly during aggression, whether between rivals or within pairs. While it is too early to assert with confidence, acoustical signals seem to show little differentiation between species or between the sexes within the species after size differences have been taken into account.

There is even less information about the use of chemical signals. It is known, nonetheless, that some cichlid fishes can recognize not only larvae or fry of their own species, but that they can discriminate between the odor of their own young and that of other young of their own species and of the same age (Kühme, 1963; McKaye and Barlow, unpublished). Since in so many species there is virtually no sexual dimorphism, other than the size relationship *after* pairing, it is likely that sexual discrimination is chemical. I also suspect that chemicals may be the most important signal for species recognition in reproductive behavior.

When considering visual signals it is convenient to divide them into three types: (i) the movements performed, (ii) the shape of the individuals, and (iii) their color patterns. Considering first the relatively stereotyped movements, called here Modal Action Patterns or MAP's (Barlow, 1968), the similarity between the different species is striking. It is possible to use the descriptions in Baerends and Baerends-van Roon's (1950) monograph to deal with most of the species. There are clearly some statistical differences, however, in the frequency of occurrence and sequencing of the various MAP's. And there are some patent but small differences in the MAP's used by different species. For instance, *Neetroplus* sometimes lies on its side in frontal display. And *C. meeki* threatens frontally with greatly extended opercles and branchiostegal membrane. There are also small differences between the species in the degree to which the median fins are raised or closed, and when. Nonetheless, the general conclusion holds that there is no trenchant differentiation among the MAP's in the Central American cichlids. In fact, they differ little from their African substrate-breeding counterparts.

There are obvious differences in shapes between the different species (Fig. 1). However, the general plan of the omnivore is so widely distributed that there is consequently much similarity between many of the species. Several show sexual dimorphism in shape and size with increasing age, or just during the breeding season: Males may develop a large nuchal hump, sometimes together with swelling of the throat (e.g., *C. citrinellum, C. parma,* and *C. dovii*). In some species, the nuchal hump is schematized into an almost wart-like protuberance, as in *C. nicaraguense* and in *Neetroplus*. In some species, such as *C. macracanthum* and *C. nigrofasciatum,* the trailing edges of the dorsal and anal fins are more protracted in the male than in the female. And in freely mated pairs, the male is invariably larger than the female; the difference may

be appreciable (e.g., *C. maculicauda*) or slight (e.g., *Petenia*).

It is when considering coloration that the richest material is found. There is appreciable divergence among the species, but it is not as profound as the initial impression might convey. In particular, the black markings on the body are conservative. These start on the fry as a series of blotches along the top and sides of the body. With development, the blotches break up into a series of eight vertical bars. As they are being elaborated, a distinct black spot develops in the middle of each bar. With further development, the now juvenile fish demonstrate the ability to turn on either the bars or the spots, and to combine the spots into a median stripe running the length of the body (see Fig. 25 in Baerends and Baerends-van Roon, 1950).

The adult thus has available to it a selection of spots, bars, and a stripe of varying length. For convenience, each bar and its spot can be enumerated (Fig. 3).

In a large number of species, the adults have a "neutral" color pattern dominated by a few spots. Two are usually especially well developed, a small black spot at the base of the tail, and another (often number five) just posterior to the center of the body (Fig. 4).

Within a given species the pattern of spots or bars varies (Fig. 4) according to the behavior and environment. In general, the more the fish finds itself in open water, often schooling, the greater the tendency to develop the row of spots into a stripe. While up in the water but over rocks, particularly hovering in groups, the general pattern is for the appearance of the mid-body and base-of-tail spots. When the fish move closer to the bottom, often passing in and out among holes or submerged tree branches, one sees a combination of spots and bars with softly developed edges.

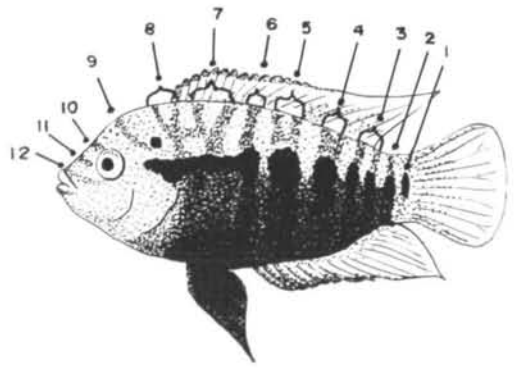

FIG. 3. *Herotilapia multispinosa* in breeding coloration (from Baylis, 1974). The major bars, with visible central spots, are numbered one to eight from rear to front; the head bars are also numbered. Note, too, the black ventral region.

Of more interest to the theme being developed here is the considerable variation in deployment and number of bars and/or spots among the different species. *Cichlasoma citrinellum* is typical of those species that develop the characteristic pattern of one spot at the base of the tail and one spot just to the rear of the middle of the body, plus a few others, while moving about in groups. In contrast, *C. maculicauda* has a pattern in which the mid-body spot is combined with the ventral half of its black bar, giving the fish a vertical slash in the middle of its body; there has also been a fusion of the tail spot with the one or two ahead of it to create a horizontal slash at the base of the tail (Fig. 1). As an extreme example, *Neetroplus* sometimes shows weakly developed barring, but the fish generally have a slaty gray body with but one vertical black bar, number 5 (Fig. 1).

The various species seem consequently to be utilizing an essentially digital code of black spots and/or bars. Not all combinations are seen, and some combinations are favored. No analysis has yet been done on the degree to which sympatric species use different patterns, and allopatric species the same. One of the difficulties is that interspecific communication may be important. For instance, the simple two-spot pattern, or longitudinal stripe, may facilitate interspecific schooling. More critical to species isolation are the color patterns manifested during breeding (see below).

There is similarly a certain conservatism in the use of colors on the body as a whole. The first general conclusion is that when yellow, orange, or red are present, it is commonly found on the ventral surface of the

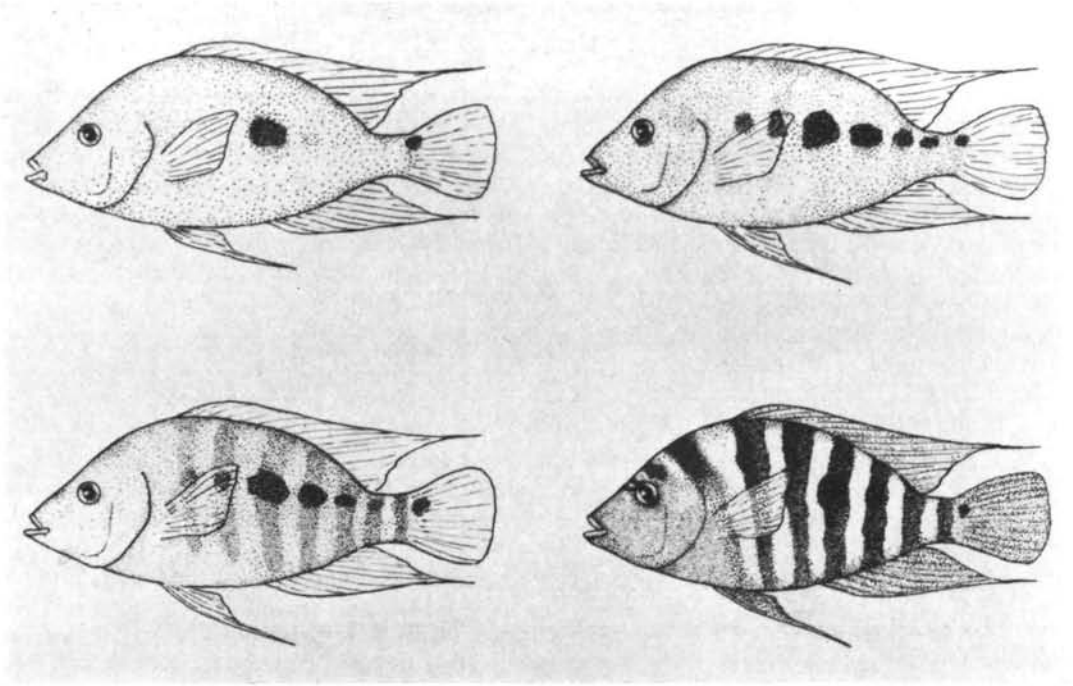

FIG. 4. Four color patterns seen in *Cichlasoma citrinellum* (explained in text).

body. Red is especially characteristic of eyes. Those species that have an appreciable area colored yellow, orange, or red are generally found in more turbid waters. Hues of these longer wave lengths penetrate murky water better than do blue or green. An excellent example of a yellow fish in murky water is *Herotilapia,* which occurs in swamps (Baylis, 1974). Another is the appearance of totally yellow, orange, or red morphs in *C. citrinellum* and *C. labiatum* in the perpetually murky Great Lakes of Nicaragua. On the other hand, *C. salvini* is brilliantly yellow when breeding yet occurs in clear waters in British Honduras; it is also an extremely aggressive species. Other brilliantly colored species occur in those clear waters, such as *C. synspilum* which is a gaudy and variable combination of orange, yellow, and red with black markings. Likewise, *Petenia* occasionally has brilliant yellow or orange morphs in the clear waters of British Honduras. Such correlations between coloration and the spectral properties of the water are difficult to make because of the diverse waters occupied by many species.

The use of blue or green tones in the body seem to characterize those species that generally occur in clearer waters (e.g., *C. urophthalmus*). These species also often have brilliant blue vermiculations on the face, as seen in *C. dovii, C. octofasciatum,* and *Aequidens coeruleopunctatus.* In Nicaragua, the large *C. dovii* tends to occur in the clearer bodies of water and has a decidedly blue and green cast, whereas its counterpart *C. managuense* resides in the murkier areas and has a yellowish tone to its body.

Some species have blue or green on their tops and sides but are orange or red ventrally. Good examples are *C. longimanus,* which occurs in relatively turbid waters, and *C. maculicauda,* which appears both in clear and murky waters.

Many cichlids have pearl-like flecks on their body or fins. This occurs in fishes that dwell in open areas, particularly out over the sand or in midwater. Doubtless they are showing a partial "mirroring" (Denton and Nicol, 1966) to facilitate camouflage. Examples are *C. rostratum* and *C. macracanthum,* and the species of *Geo-*

phagus.

Finally, I need mention the recurring development of black areas on the ventral surface of some species. It appears during breeding (see below) in a variety of species (*C. spilurum, C. macracanthum, C. maculicauda, C. centrarchus, Herotilapia*). This is inverse countershading, which makes the parental fish more conspicuous (Albrecht, 1962; Baylis, 1974).

Breeding colors. One of the most commonly recurring changes during breeding behavior is the intensification of the normal pattern of vertical bars. Contrast is enhanced by making the bars very dark with sharp edges while the interspaces between bars become pale (Fig. 4). There are interesting species differences. One species drops the barring on the head and the first one on the body (*C. macracanthum*). Other species display the bar that connects the eyes dorsally (*C. beani; Herotilapia*) (Fig. 3). Yet another species emphasizes the horizontal body stripe (*C. longimanus*). Other strategies may also be involved. For instance, *C. citrinellum* and *C. nigrofasciatum* show similar black barring when breeding and they are sympatric; however, *C. citrinellum* is a much larger species than *C. nigrofasciatum,* and the female of *C. nigrofasciatum* develops a large orange blotch on her side. Yet another tactic is shown in *Neetroplus:* When the fish breed they merely reverse the color pattern from a gray body with one black bar to a black body but now with the bar white.

It is again early to say with confidence, but there seems to be a correlation between the use of bars versus the stripe and the physical environment. Those species breeding among rocks generally wear bars. Those breeding more in the open favor the stripe, or some combination of spots plus part of the stripe.

There is also a general intensification and spreading of colors, especially yellow, orange, or red, or black, from the ventral surface up the sides (Fig. 3). Many species, moreover, make the eye more conspicuous, particularly by producing a pale eye against a dark face (e.g., *Neetroplus, C. macracanthum*).

Thus, despite the diversity of color patterns in the cichlid fishes of Central America there is a common theme. Mostly it consists of a simple recombining of the spots and/or bars on the body, together with the manipulation of colors yellow to red, or black, ventrally, and blue or green dorsally. There are, of course, also some remarkable exceptions. For instance, *C. tuba* displays a large patch of white when breeding (G. H. Meral, personal communication). And many species show interesting details such as red margins on the fins (*C. alfaroi*).

Castes. There is no noteworthy differentiation into castes. One can distinguish age castes, such as larvae, fry, juveniles, and adults. However, the juveniles are little more than small nonbreeding adults. And there is not much to distinguish between adult males and females when not breeding. Even in breeding pairs, dimorphism is often expressed only as the male being somewhat larger than the female (see below).

Group composition. Group composition in nonbreeding fishes has been described in the section on spacing. Generally, groups are open and highly variable in numbers. Males and females in nonbreeding groups are indistinguishable in their behavior.

Reproductive behavior. In contrast to the diversity of feeding habits, habitats occupied, and morphological differences, the reproductive behavior of these cichlids is noticeably uniform. The typical pattern starts with pair formation. We are least certain as to how pairs form in relation to the holding of a territory. We now suspect that either the female attracts the male to a territory which they then defend (as in *C. nigrofasciatum;* Meral, personal communication), or that the pair forms away from the territory and then captures one for themselves (*C. citrinellum;* McKaye, personal communication). The two fish alternately court in the territory, which is for reproduction, not feeding. The eggs are placed in a chamber. The larvae are similarly hidden away in cavities or pits.

In most species the female is clearly smaller than the male, being about 80 to 90% of his weight, and of a similar color pattern. Females develop full breeding coloration faster than do males, and once having developed it, are less apt to reverse it.

There is also appreciable differentiation of roles. The female does most of the direct care of the eggs and larvae, though not all of it in most species, and is more persistent in remaining near the offspring when danger threatens. The male spends more time patrolling the territory and driving off conspecifics.

When the fry become free swimming they form a large, coherent and ball-shaped school. Both parents vigorously defend these against predation; if the parents are chased away, the fry are eaten within minutes by other fishes which are constantly in attendance.

Not only do the parents defend the fry, but in many species they also help provide food. In some species the parents turn over leaves for the offspring (*C. nigrofasciatum;* G. H. Meral, personal communication), as do the Asian cichlid *Etroplus suratensis* (personal observation) and the African cichlid *Pelmatochromis guentheri* (Myrberg, 1965). When the fry are extremely hungry in almost any Central American species they will begin to graze on the mucus on the sides of their parents (*C. nigrofasciatum, C. spilurum, C. macracanthum, C. friedrichstahlii, C. beani, C. longimanus*). In *C. citrinellum* the response is apparent even when the fry are only modestly hungry (Noakes and Barlow, 1973), as is also true of *C. labiatum.*

The most noteworthy differences in breeding behavior between the different species are consequences of the physical environment. *Aequidens coeruleopunctatus* breeds in streams in Panama where there is little hard substrate on which they can deposit their eggs. The female selects a relatively rare rubbery leaf from among the litter on

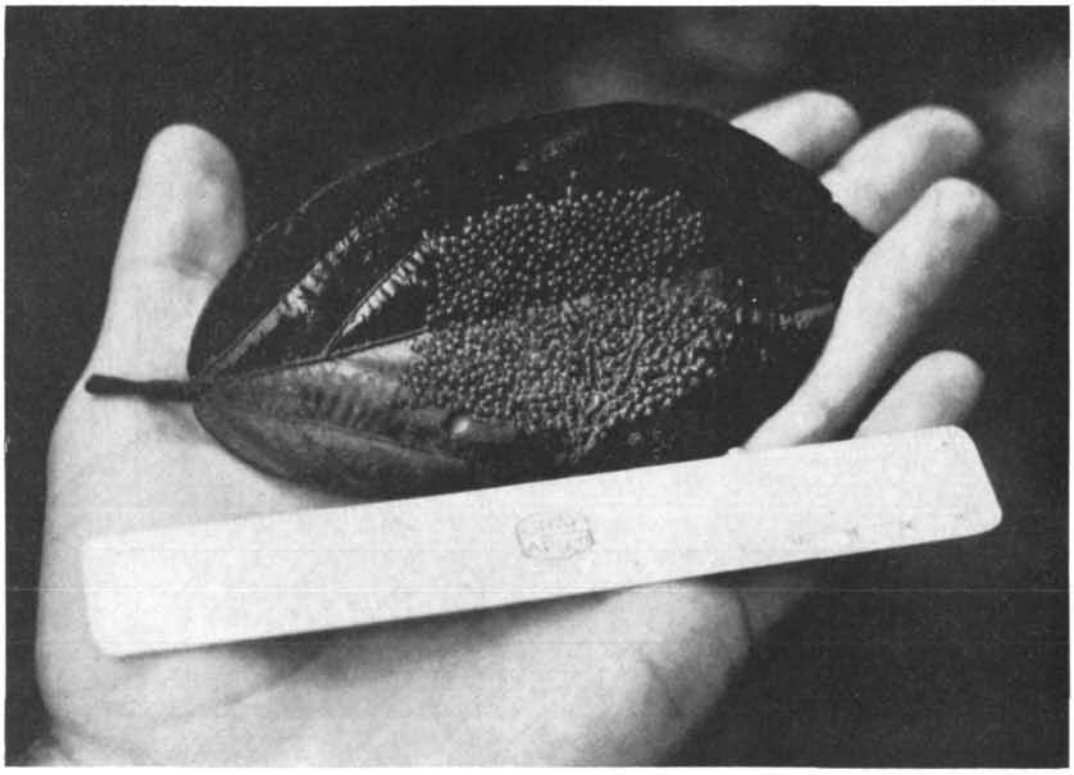

FIG. 5. A clutch of eggs of *Aequidens caeruleopunctata* laid on a particularly rubbery leaf in the Agua Salud, Panama.

the bottom and carries it past the male during courtship. Later she spawns on the leaf (Fig. 5). When danger threatens she grasps the leaf in her mouth and pulls it back under the bank of the stream or into shallow water. If the leaf is turned upside down, she attempts to right it. This is obviously an adaptation both to the shortage of spawning sites and to the fact that they spawn in streams that are subject to periodical torrential flooding. Were the water to suddenly become fast and high, the female could simply back into the quieter waters on the side of the stream, and return to the main stream as the water subsided.

The species *C. centrarchus* and *Herotilapia* both live in habitats where there is considerable vegetation. Both of these small species plaster their adhesive larvae on the plants, well off the bottom. *Petenia* and *C. synspilum* breed over sand bottom in dense vegetation in British Honduras. They expose the roots of these plants, upon which they spawn. The larvae are deposited in sand pits nearby.

Cichlasoma maculicauda breeds in Lake Gatun in Panama in areas where much of the bottom is either clay or covered with dense beds of *Chara*. The one nest John Mertz and I found in clay bottom was almost a perfect cylinder with a diameter equal to the body length of the female, and the depth about equal to twice her body length. The bottom was an enlarged chamber with many rootlets on one wall, presumably where the eggs had been laid. About half way up the hole was a small antechamber in which the larvae had been placed (such a construction would simply never have been seen in the standard aquarium setting).

Cichlasoma nicaraguense is one species that is reasonably sexually dichromatic when breeding. Living in a mixed rock and sand habitat, it digs a remarkably deep hole in the sand by a rock. It lays extremely large but few eggs that lack adhesive threads (I thank the hobbyist Dick Stratton for calling this to my attention). The eggs are not only large but rather buoyant, bouncing around in the bottom of the nest. The absence of adhesive threads, large size, and buoyancy are adaptations to prevent loss of the eggs in the sand. While the female does some fanning of the eggs, she also does an inordinate amount of taking the eggs into her mouth and spitting them out (Stratton, 1968). Apparently this species is but one step away from becoming a mouthbreeder. When the fry swim, the male helps in their defense (personal observation).

There is also a trend toward polygyny in these cichlids. *Aequidens coeruleopunctatus* females are often found alone, caring for their eggs, larvae, or fry. I observed a male and female defending free-swimming fry in which the male ranged up to a meter away from the female, encountered another female, and began courting with her. Meral (personal communication) has made similar observations from one population of *C. nigrofasciatum* in Costa Rica. The often confirmed clearly stronger parental response in the female of most of the Central American cichlids suggests that the potential for polygyny is wide spread.

The general pattern of reproductive behavior within the cichlid fishes, in conclusion, is one of conservatism. Irrespective of other aspects of their biology, particularly their feeding behavior, they tend to have remarkably similar reproductive behavior. The most pronounced divergence in behavior is related to differences in the physical environment in which they breed. There is also a trend toward division of labor. This has meant size dimorphism with the larger male more apt to defend at the boundary of the territory and the female to stay with the offspring. This seems to have laid the ground work for the development of polygyny. The major pressure preventing the development of polygyny is doubtless the necessity of two adult fish to defend the fry against the many predators that lurk around them.

Acanthuridae

Physical spacing. Juvenile fishes have been observed in only a few species, so information about them is fragmentary. The pattern, insofar as known, is to establish solitary feeding territories after meta-

morphosis, as in *Acanthurus chrysosoma* (Okuno, 1963). Juveniles are sometimes differently colored than their adults, and this may be associated with their territorial way of life. However, the juveniles of some species look much like the adults and are also highly territorial: Randall (1961*a*) described well the early behavior of *A. triostegus,* and I have observed them in some detail. Evidently unique among the surgeon fishes, these juveniles occupy intertidal pools, and often at relatively high densities; individual territories are fiercely defended.

Among the adults there is a spectrum of patterns of spacing. In some species feeding territories are held by individuals or by pairs, and range from small to exceedingly large. Within these same species at another time, schooling behavior may prevail and territoriality be lacking.

It seems more appropriate to these fishes to discuss spacing from the point of view of territoriality than from the degree of schooling. Territoriality in these fishes is the securing of a feeding area. (Similarly, much of the grouping behavior can be explained as feeding strategy.) A difficulty in discussing territoriality here, as among nonbreeding cichlids, is that feeding territories are often small and only briefly held, being given up for a new territory. This is not, therefore, the type of territoriality that students of bird and mammal behavior generally refer to when they use the term territoriality. But this behavior grades smoothly into well-defined, apparently persistent territoriality. In what follows, I will proceed from the species that are highly territorial to those that are less so, and on to those that seem to be nonterritorial.

There are many highly territorial small reef grazers, such as *A. nigrofuscus, A. achilles,* and *A. glaucopareius.* These fishes hold territories ranging from roughly 5-20 m^2. Whether these territories change in size, shape, or location through time is unknown.

More widely seen is the pattern found in many of the small reef grazers. This is one of holding territories briefly while feeding, driving away intruders, but then moving on. Frequently these species form schools while traveling from one place to another. Sometimes they feed together, but they are usually alone, as typified by *A. nigroris.* Included here also are *Zebrasoma flavescens* and possibly *Naso lituratus* (this is the smallest of the genus *Naso* and differs from the other *Naso* in many ways).

Many species are weakly, or not at all, territorial. These include a number of small to moderately large species adapted to invading the reef flats at high tide. Since they have to leave these areas as the tide ebbs, persisting territoriality would be disrupted by the tidal cycle. Included here is *A. guttatus,* a schooling medium-sized species. *Acanthurus triostegus* is a smaller species that moves into the yet shallower areas on the reef flat, also in large schools. *Acanthurus lineatus* moves with the tide, but tends to frequent surge channels. *Acanthurus leucopareius* forms groups that move along the edge of the reef front and shows only sporadic if any territoriality. Interestingly, *A. achilles* and *A. glaucopareius* both hold territories on the tops of the reef flat near the front of the reef, yet individuals must forsake their territories at times; then they form schools adjacent to their uncovered territories.

The detritus feeders present some problems in classification, problems that could probably be resolved quickly by marking individuals. The smaller species are evidently territorial and may be living in groups in some species. They are closely bound to the reef and show a fair amount of aggression among themselves, as well as a considerable amount of toleration for members of their own species in close proximity. The large species, *Ctenochaetus hawaiiensis* appears to be a special case. Apparently it lives in groups which gather in numbers of, say, 3 to 20 at what appear to be refuges. Individuals or subgroups may leave and return from time to time. It remains to be determined whether these groups have exclusive use of territories.

Most of the weakly or nonterritorial species are highly mobile, moving about to more patchily distributed food. These are the larger species (plus the smaller reef-flat vagrants mentioned above). A transitional

species is the large *Naso unicornis,* the only gray unicorn fish that feeds in the intertidal and just subtidal areas. Most of the gray *Naso* are large species that move in schools within a given area but show no territoriality. Possibly, however, the males in some *Naso* may be defending stations, off the pinnacles and cliffs where they occur, to serve a reproductive function (see below).

The sand grazers, as already described, refuge in mixed species groups on the reef and move out over the sand to feed in interspecific schools. The sand is essentially a limitless and indefensible resource, and not surprisingly these fishes show no territoriality. They do have a preferred refuge in many cases, and one can properly speak of home range.

One species, *Zebrasoma veliferum* seems exceptional. Unlike the territorial reef grazers, it roams considerable distances along the reef. Yet it also appears to be territorial in that it avoids the area occupied by other *Z. veliferum.* I have seen some displays occur when the fish meet at what might be the boundaries, but no overt aggression. I have also seen this species aggregate in as many as six to eight individuals, but at low tide in patch-reef situations where the animals may have been forced out of their territories.

Finally, it seems likely that the planktivorous *A. thompsoni* is not territorial. These animals live in schools and take refuge in the reef when danger threatens; conceivably, they could have individual holes to which they flee and defend, as does another planktivore, the black trigger fish *Melichthys buniva.*

Theoretical spacing. Dominance hierarchies have not been studied in the field, again because of the failure to mark individuals. They may exist, however, particularly if the species form closed groups. The most likely candidates would be those that most seem to live in groups, such as *Ctenochaetus hawaiiensis* and *C. strigosus.* Dominance hierarchies may also exist in the adult *Naso lituratus* one sometimes finds in groups and in which considerable fighting is seen. Much aggression is also expressed even by apparently nonterritorial reef grazers and by some browsers.

There are rather well-defined dominance-subordinance relationships *between* species. In some instances, the amount of aggression between certain species pairs is more than that seen within them. Thus, interspecific dominance relationships are an important factor in the social life of reef-dwelling surgeon fishes.

An appreciation of aggression interactions is the key to understanding the communication network of the social behavior of surgeon fishes. Almost all the obvious signals seem to be related to aggressive behavior.

The only sensory modality that will be considered in detail is the visual system. I have no knowledge of whether chemicals are used in communication. As for acoustical signals, the twitch-like displays of some of the species may be associated with the production of sound, but little more can be said.

All the surgeon fishes so far observed seem capable at some age of performing MAP's common to aggressive encounters as seen in most teleost fishes. For example, these fishes regularly show lateral display and tail beating. Also seen are vertical postures such as standing on the head or tail, and such overtly aggressive behavior as pursuit, ramming, and cutting with the caudal knife.

There are, nonetheless, some clear divergences in the MAP's employed in communication in the different species. *Acanthurus achilles* can often be observed in displaying pairs, swimming in parallel or in tight circles; one or the other fish may twitch all of the median and paired fins synchronously and repeatedly. *Naso lituratus* occasionally performs what looks like a tail waggle while standing in the parallel position with another of its species; this is obviously restrained tail beating, and often results in the two fish beating more at one another with their heads than with their tails; it is commonly terminated in one deep tail beat (an attempt to cut with the pair of knives) immediately followed by a chase. Another divergence is the pronounced "zooming" seen in *C. hawaii-*

ensis: These fish, particularly when one returns to the group, swim at high speed at one another as though to attack. Suddenly one fish turns off and glides through the water. *Acanthurus olivaceus* shows a similar behavior.

Although I was able to detect species-typical differences in behavior, all the species showed much the same kind of behavior when interacting interspecifically. That is, the species-typical behaviors appear to be restricted largely to intraspecific communication.

There is little differentiation in body shape within each of the various species. However, in the genus *Naso* sexual dimorphism in body shape and size seems more the rule. Several species have a median horn-like protuberance that extends straight ahead from the space above the eyes, which gave rise to the common name of unicorn fishes; only the males have this feature (Fig. 2). Some species lack a horn and have merely a pronounced hump where the horn would otherwise be (*N. vlamingi*). *Naso lituratus* lacks even this nuchal hump, but the male has conspicuous streamers trailing out from the top and bottom margins of its caudal fin (Fig. 2). In all of the *Naso* that are sexually dimorphic (*N. hexacanthus* appears to be isomorphic), the male is usually larger than the female as well.

As with the cichlids, the most workable differences appear in the color patterns. But unlike the cichlids there is no obvious pattern for the group as a whole, with one exception: There is a pronounced tendency for either the caudal peduncle or the tail itself, or both, to bear a contrast-rich marking. Doubtless this is a consequence of the caudal peduncle being armored with a sharp, and perhaps poisonous knife (Randall, 1959; Yasumoto et al., 1971). In most species the knife is carried in a sheathed groove, one on each side of the fish. In *Naso* there are two knives on each side, and these are fixed out and thornlike.

Much of the differentiation in color patterns can be related to the feeding guild and thus to the environment. The planktivores and certain of the browsers spend much of their time out off the reef; all are principally gray through blue and protectively counter-shaded. The large *Naso* in this group commonly form interspecific associations when in open water (*N. brevirostris, N. hexacanthus, N. vlamingi*).

The sand-grazers are also a uniform group. When up over the reef these large fishes are generally black with conspicuous tail markings, such as a white band on the caudal peduncle. They also tend to have subtle markings, particularly yellow on the face, but also elsewhere, such as on the median, pectoral, or tail fin. They are thus much alike in the general pattern of a black fish with a pale tail mark. When out over the pale sand bottom their body coloration fades to gray. They so regularly school and feed together, that I am tempted to suggest that they are engaging in interspecific mimicry. To the observer underwater, these fishes are often difficult to distinguish at a distance because the resemblance is so great. The more subtle color markings are apparent only at close range and probably facilitate species identification.

Acanthurus olivaceus once again reveals its intermediate nature between that of a sand and a reef grazer: Its body color varies between being all black or bicolor. The patch of orange color across its pectoral girdle is bright but relatively small, and it has subtle purple facial markings that are apparent only when up close.

Another form of intermediacy is seen in *N. lituratus*. It is basically black, like the sand grazers. It shares this characteristic not only with the sand grazers but with a goodly number of moderately large fishes that regularly hover up over the reef and take refuge in it, as does the highly mobile *N. lituratus*. But *N. lituratus* also has considerable ornamentation on the face and median fins; its caudal peduncle is brilliant orange, announcing the pair of formidable knives on each side. Thus, it is intermediate in color pattern between the sand grazers and the more colorful reef grazers that will be considered below.

The detritus feeders are usually drab. Most are dull brown with muted thin lines or blue dots on the body and inconspicuous

orange dots on the face. Commonly only one species is found in a given place on the reef. In Hawaii, however, *C. strigosus* and *C. hawaiiensis* occur together. The smaller *C. strigosus* has a conspicuous orange ring around its eye. It sometimes chases the much larger *C. hawaiiensis*. The larger species is black with blue highlights. Interestingly, it spends much time well up from the reef. Thus, *C. hawaiiensis* resembles the sand grazers both in color and in this aspect of its behavior.

Among the reef grazers there has been a flowering of diversity in color patterns. Still, one can detect the tendency for tail markings that advertise the dangerous knife (although not always), as well as special and in some cases subtle facial markings. The types of coloration range from having the body a solid conspicuous color, such as yellow or blue, to marking the body with a variable number of vertical bars or with thin stripes. Some species have patches of color on the body, or polka dots. A common theme also is bright coloration on the pectoral fins or around the eyes.

In spite of this diversity and conspicuousness, there is evidence of protective coloration. For instance, *A. guttatus* is often found where the water is full of tiny bubbles from the surf, and it has numerous white spots. Further, the most common basic colors are inconspicuous, and most species are countershaded.

Many of these species conform to the concept of poster-colored fishes as advanced by Lorenz (1966), and since they range from highly aggressive to highly pacific, this seemed a good opportunity to test his hypothesis. It states that the color patterns associated with aggression are permanently turned on; no further change is necessary or possible. Further, the hypothesis predicts that poster-colored coral-reef fishes will direct their aggression only to members of their own species. A substantiating piece of evidence cited by Lorenz is that many damsel fishes (Pomacentridae) are drab and nonterritorial as adults (my observations on this correlation are to the contrary), whereas their poster-colored juveniles are strongly territorial.

The surgeon fishes have proved capable of extremely rapid and profound color changes, especially in connection with aggressive behavior. The basically black *C. hawaiiensis* sometimes develops a brilliant blue face while chasing. The extremely aggressive lavender tang, *A. nigrofuscus,* produces a dark profile around its head and body, leaving its center pale; *C. strigosus* and *C. striatus* show a similar change when fighting. The most remarkable color changes are shown by the most brilliantly colored species, *Naso lituratus*: When fighting, the forehead becomes brilliant canary yellow as do the pectoral fins. Sometimes during a fight the entire body becomes sky blue, only to change rapidly back to black. Extraordinary and rapid color changes are also seen in the nonposter colored, open-water *Nasos*. Depending on the species, these fishes turn on a brilliant blue-white vest, bib, or wedge just behind the head, with similar color changes on the tail (see *N. tapeinosoma* in Fig. 6*b* of Eibl-Eibesfeldt, 1962).

The remarkable fact in common to all these observations is that the color changes occur in intraspecific encounters. I have seen some changes in extraspecific threats, but only when a well-developed fight occurred (which is infrequent extraspecifically).

The one surgeonfish that was never observed to change colors when aggressive as an adult was *A. triostegus*. This is the least aggressive surgeonfish I have observed. Also, its caudal knife is greatly reduced and "unadvertised." However, the juveniles are aggressive and do show accompanying color changes. Thus, this is an example that is exactly contrary to the poster-color hypothesis: The least aggressive adult is characterized by the lack of change in coloration.

I observed what I believe to be prespawning behavior in *A. triostegus, C. striatus,* and *N. brevirostris*. In each instance the color changes were similar to those seen in aggressive behavior. In the case of *A. triostegus,* the color changes paralleled those noted for aggressive juveniles.

Surgeon fishes can also change their darkness to improve background matching and, thus, protection. The gray *Nasos* are pale

up in the water but darken as they approach the reef to feed. Many of the reef dwelling *Acanthurus* and *Ctenochaetus* darken or fade as appropriate to their surroundings.

There are several conclusions that can be drawn from the analysis of color patterns in surgeon fishes. First, there is considerable species differentiation by color, but where the fish are constrained from dramatic coloration, as in the open-water species, some of this differentiation has been transferred to body shape. Also, there has been either convergence or mimicry in those species that move about together in a habitat that places constraints on the color patterns, i.e., off-reef *Nasos* and the sand grazers.

Diversification of color pattern can occur when the species are intimately associated with the reef that affords protection from predators (a similar view has been expressed by Hamilton, 1969). The diversification of color patterns here is probably a consequence of the abundance of species, since the communication involved in aggression is important in extraspecific encounters as well as in intraspecific hostile behavior. Recall that the reef-dwelling detritus feeders are drab in color when they usually face no competition from other acanthurid detritus feeders. This suggests that the diversity of colors among reef grazers serves to facilitate recognition of intra- versus extra-specific competitors for food. Their existence in the reef affords a measure of escape from predation. Thus, their relationship to predation is seen as permissive of the conspicuousness rather than causative.

There appears to have been selection for extremely rapid color change to communicate aggressive intent within species, even in the poster-colored ones.

Castes. The biology of juvenile surgeon fishes is poorly known. In a few cases, however, the young are clearly different from the adult, usually being solitary and territorial. In at least three widely unrelated species this is associated with the elaboration of bright yellow color. Nonetheless, in *A. triostegus,* in which the young are extremely territorial, the young show marked color changes in association with aggression.

Sex is difficult to distinguish externally in most species, especially in the genera *Acanthurus* and *Ctenochaetus.* Some species, however, live in pairs, suggesting a differentiation into sexual roles. Included here are the very similar *A. achilles* and *A. glaucopareius. Zebrasoma veliferum* lives in groups of one male and two females as well as in pairs; in each instance, the male is larger than the female. Randall (1961*a*) reported that *A. triostegus* may live in schools in which all individuals are male or all female.

In the *Naso* group, sexual dimorphism is often pronounced in shape and in color; the details have already been reported. In *N. lituratus,* while the unicorn is wanting its signal function appears to be served by the canary-yellow patch that is set off against a black background on the forehead during fights.

Group composition will not be discussed separately here, since all of the necessary information has been touched upon in the foregoing, or will be treated under reproduction.

Reproductive behavior. The reproductive behavior of surgeon fishes is poorly known. This is in large part because spawning probably usually takes place about dusk. The reef inhabitants count among their numbers many small planktivorous species that would devour the eggs if they were around much of the day. Releasing the eggs just before dark reduces to a brief period the time the eggs are exposed to predation from those planktivores, and it is also a time when many fish species are taking refuge in the reef (Hobson, 1972).

The reported cases of spawning (Randall, 1961*b*) involve *A. triostegus, C. striatus,* and *Z. scopas (=Z. flavescens).* All of those species were noted to aggregate toward sunset, and to move up in the water to spawn in small groups. The nonbreeding behavior in these species probably facilitates group spawning since each tends to live in groups, although *A. triostegus* is more apt to form large schools, and *C. striatus* to live in small aggregations. *Zebrasoma scopas* may sometimes live in pairs.

In spite of this lack of information, there

is much suggestive evidence about the reproductive behavior of some of the species. For instance, those species that regularly move about in pairs probably also spawn in pairs, although this is not certain. *Zebrasoma veliferum* is a relatively uncommon species that is thinly distributed in its environment; it could profit by living in pairs. Its congener, *Z. flavescens,* lives in large loose aggregations where it is abundant, such as in Hawaii, but is sometimes seen in distinct pairs at Eniwetok where it is much less abundant. *Acanthurus achilles* and *A. glaucopareius* are clearly paired on the reef. *Acanthurus achilles* appears to form pairs as juveniles that may persist through life. In contrast to *Z. veliferum,* these two *Acanthurus* are often locally numerous and have small territories with several neighboring pairs visible to them. Furthermore, when disturbed they swim up from their territories and form schools. It is thus an open question as to whether they might spawn as pairs or within these larger groups.

One of the most interesting of all the surgeon fishes is *N. lituratus.* In some places, such as at Eniwetok, they exist as distinct pairs in the lagoon, but they form dense schools at low tide off the seaward reef. In Hawaii I have often observed one male with one, two, or three females. Occasionally, these animals tarry in nonfeeding groups in shallow water where the females appear to fight over the male.

The shallow-water unicorn fish, *N. unicornis,* seems to have a harem society. In Hawaii I have seen one male drive other males away from groups of presumably females that consisted of about 20 fish.

The other large *Naso* that live off the pinnacles and cliffs may have yet another reproductive strategy. *Naso brevirostris,* for example, is a highly dimorphic species in which one could anticipate sexual competition. While inconclusive, observations by McKaye and me suggest that males hold stations along the cliffs or pinnacles, much as do individuals in a lek society. *Naso vlamingi,* on the other hand is less dimorphic, having only a nuchal hump, which would suggest reduced sexual competition; nothing is known of its breeding behavior. *Naso hexacanthus* is not obviously dimorphic and is strongly schooling, probably in relation to its planktivorous way of life. The implication is that there is no sexual competition as a consequence, ultimately, of its feeding strategy, and that the fish therefore spawn in groups. Nonetheless, this is pure speculation since no information is available.

The evidence suggests a range of reproductive behavior from group spawning through harem formation and leks, and even enduring pairs. There are some suggestions of ecological correlations with breeding strategy, but the relationships are not clear.

DISCUSSION

To recapitulate, the cichlid fishes in Central America are products of a geologically recent radiation in the near absence of competition from other types of fishes. They have occupied almost the entire gamut of trophic types, but this division has not been profound. Interestingly, the least frequently encountered feeding specialization is that of the algal or Aufwuchs scraper. Only *Neetroplus* relies primarily on this food source. This may be because the poeciliid fishes preceded the cichlids into Central America (Myers, 1966), and many of these are specialized as Aufwuchs or algae feeders.

The surgeon fishes, in contrast, are a well-established family, having about the same number of species as do the cichlids in Central America. They exist in a complex, mature community with much trophic competition within and without the family. Other reef grazers include the parrot fishes (Scaridae), the damsel fishes (Pomacentridae), the siganids, and the kyphosids. Within their specialization of algal feeding there is a further division into guilds with narrow feeding habits. But within each guild there is considerable overlap in diet, and this is reflected in the social extraspecific interactions, the type depending on the guild. Thus, in the reef-grazing guild there is much aggressive

interaction between species. But among the sand grazers and among the large *Naso* that live off the reef in open water, the fishes normally move together with little aggressive interaction between species.

I will quickly review the highlights of some, but not all, of the parameters of social systems as they apply to cichlid fishes and surgeon fishes.

The cichlid fishes space themselves either solitarily, in loose groups, or in well-defined schools. The more predatory they are, the more they tend to be solitary, while the more omnivorous, the more they tend to aggregate. But within any species, individuals may at some time be solitary and at others may move in close proximity to members of its species.

Within the surgeon fishes there is also a spectrum of patterns of spacing. Some species maintain relatively persistent feeding territories, others have only transient territories, and others appear never to be territorial.

Both in the cichlids and the surgeon fishes the smaller species that are more bound to the substrate are in general more inclined to be persistently territorial and spaced out. Thus, the small species that are territorial are the most aggressive members of the family.

Turning to the large species, in the Cichlidae these tend to be predators. They are generally well spaced and often territorial. In the laboratory they are exceedingly aggressive, especially *C. dovii.*

In contrast, the large surgeon fishes are generally highly mobile and gregarious species. While aggression is not common, it is seen among station-holding males, and regularly in the reef-dwelling *N. lituratus.*

Living in the open, as most of these large surgeon fishes do, has favored schooling as a maneuver to avoid predation. And when the species so engaged are not in competition for food, extraspecific schooling becomes a simple extension of that protective maneuver. Such behavior is facilitated by a close resemblance among the different species and by reduced aggression.

Something similar may be going on among the cichlid fishes that occur together and that feed over open bottom. In Nicaragua, the three species *C. longimanus, C. nicaraguense,* and *C. rostratum* bear a striking resemblance to one another when not breeding. They commonly school together. However, when feeding there is extraspecific aggression, with *C. longimanus* dominating.

The two families differ emphatically in the use of color in communication. Within the New World cichlids there is a common theme, almost a digital code, in the development of dark vertical bars and their contained black spots. There is also a recurrent pattern in the application ventrally of the colors yellow through orange and red, sometimes black, and blues or greens dorsally.

The only common theme in the coloration of surgeon fishes is the warning coloration associated with the dangerous knife at the base of the tail. Additionally, species that live away from the reef, and thus more exposed to predation, are colored for concealment. In the shelter of the reef, however, the color patterns tend to proliferate, especially among the reef grazers. The detritus feeders that live in the same environment are exceptional in that they are relatively conservative and cryptic in their coloration. This may simply reflect the fact that there are generally few sympatric species of *Ctenochaetus.*

Color changes in the surgeon fishes are more highly developed than in the cichlids of Central America in that they are so much more rapid. These conspicuous, contrast-rich, color changes emerge in the context of hostile encounters, predominantly intraspecifically, when even the most brilliant species change their signals. The drab surgeon fishes can also adopt striking color patterns.

Lorenz (1966) was extremely perceptive when he recognized the nexus between color patterns as signals, aggression, and the intense trophic competition on the coral reef. (It is not clear to me, however, how he decided which species to consider as being poster colored; to me they lie on a continuum of conspicuousness.) Lacking adequate information, Lorenz presumed

perfect habitat partitioning among the poster-colored fishes, with no significant extraspecific competition.

In the reef-grazing surgeon fishes, extraspecific and even extrafamilial competition is an important reality. The conspicuous color patterns probably serve as broadcast signals, loosely addressed both to intra- and to extraspecific competitors. Color changes usually occur only during actual fighting where they are addressed to the object of the aggression. Since the more intense combats are largely reserved to intraspecific encounters, the signals emerging during such fights are primarily for intraspecific communication.

There is little worth commenting on with regard to the castes among cichlids and surgeon fishes. The cichlids are little differentiated when not breeding. Among the surgeon fishes a distinct juvenile caste is present in many species, and within *Naso* the sexes are usually recognizably different.

The problem of group composition has already been touched upon under the category of spacing. It bears repeating that the groups are variable and relatively nondifferentiated in the nonbreeding cichlid fishes. Furthermore, the groups seem to be open since their members leave and other join. Within the surgeon fishes the same situation prevails in many species. However, some species exist as pairs and even as threesomes, which are thus small closed groups. They may live in even larger groups that are closed, in other species, but this remains to be determined.

Generally the most interesting aspect of social organization is the reproductive behavior. Indeed, many writers equate it with social organization. It is here that it is most difficult to make contrasting comments because so little is known about the surgeon fishes. Fragmentary observations suggest that when their behavior is known we will have found a diversity ranging from group spawning through continuously maintained pairs, lek societies, and harems.

In contrast, more is known about reproduction in cichlids than about any other aspect of their social behavior. In Central America they have proved conservative in this regard. They follow the pattern of prolonged courtship with pair bonding, followed by parental care. The female does most of the direct parental care while the male guards the territory or remains nearby until the fry begin swimming. Then both sexes guard them. There is evidence of an inclination toward polygyny, but this is counteracted by selective pressure from predators, requiring both parents for protection of the fry. The greatest differences in reproductive behavior result from adaptations to differences in physical environment, particularly the suitability of the substrate as a spawning platform.

The only recent attempt to put the comparative study of reproductive behavior of cichlid fishes on a more solid footing has been that by Wickler (1962, 1966). He did an excellent job of analyzing the changes in behavior and egg morphology associated with increasing adaptation to spawning in holes. He attempted to relate the method of spawning and parental care to whether the species is monogamous or polygamous, and to whether it is sexually dimorphic or isomorphic. The previous classification divided the various species into substrate breeders versus mouthbreeders. Wickler, however, detected similarities between mouthbreeders and those substrate breeders that hide their eggs and larvae; these were called, collectively, "concealment breeders." The other cichlid fishes were termed "open breeders."

A number of difficulties arise when trying to use his more definitive statement (Wickler, 1966). First, he gave no criteria for clearly distinguishing when a fish should be classified as an open or a concealment breeder. His student Apfelbach (1969) later reclassified *Tilapia mariae* as a concealment breeder, whereas Wickler had considered it an open breeder, although both made the same basic observations. Likewise, we have found that *C. nigrofasciatum* is a hole (concealment) breeder, not an open breeder. In fact, my observations lead me to suspect that virtually all of the Central American cichlids are concealment breeders, which is not to be confused with breeding in the open, away from cover.

The second difficulty is that Wickler (1966) gave no workable criterion for deciding when a species is dimorphic as opposed to isomorphic. His definition was postulational: a species is dimorphic when the species itself can immediately recognize the sex of a conspecific. Evidently in practice he relied on the degree to which he could distinguish the sexes by color pattern. In so doing, he appeared to recognize small differences in the genus *Tilapia,* with which he is familiar. He overlooked pronounced differences in *Cichlasoma:* he tallied as isomorphic the obviously dimorphic and dichromatic *C. nigrofasciatum.*

I have taken the liberty of rearranging, simplifying, and summarizing Wickler's data (Table 1). The old classification is adjacent to the new. If the classification is an improvement, it should reduce the intracategory diversity present in the original classification. As can be seen, there was little if any gain. This is especially true when one considers that the category "open" may be nonexistent, that errors exist in the assignment to the categories, and that the criteria employed are almost impossible for another person to apply.

For analytical purposes the degree of dimorphism should be regarded as continuous rather than discrete. The same applies to the degree to which each species is adapted to a particular set of environmental conditions. In my experience Central American cichlids are all at least size dimorphic to some degree.

Wickler (1966, p. 137) has also commented on the direction of evolution in the reproductive behavior of cichlid fishes: "Evolution within this family leads away from the highly developed monogamy, and thus runs, to a degree, backward." This is a misreading of the evidence. In all known fishes that are parental, outside of the Cichlidae, the male is the parent. The evolutionary progression has been from (i) an exclusively parental male, to (ii) shared parental care by the male and female, to (iii) a division of roles with the female as the direct parent and the male as guardian, to (iv) polygyny (Barlow, 1964). This is clearly a forward progression resulting in a more efficient division of labor between the male and female.

Probably the main hurdle to the develment of polygyny within the Cichlidae is that the school of fry requires the protection afforded by both parents. Polygyny would probably appear more often if predation on the fry were alleviated. This could be done in a number of ways, such as the fry behaving differently. Wickler (1966) has shown one way in which this might proceed with the development of fewer larger eggs leading to larger, and more independent fry. Another adaptation would be for the fry to hug the bottom, thus avoiding many predators. Finally, the cichlids could breed in areas either ecologically or geographically distant from

TABLE 1. *Species of cichlid fishes in each category of reproductive behavior, contrasting two systems of classification.*[a]

	Type of breeding							
	Original classification				Revised classification			
	Substrate		Mouth		Open		Concealment	
Monogamous, Monomorphic	22	63%	2	20%	20	100%	4	16%
Monogamous, Dimorphic	9	26%	1	10%	0	0%	10	40%
Polygamous, Dimorphic	4	11%	6	60%	0	0%	10	40%
Polygamous, Monomorphic	0	0%	1	10%	0	0%	1	4%
Total species	35		10		20		25	
H (Diversity)[b]	1.14		1.13		0		1.42	
	1.84				1.71			

[a] Data from Wickler (1966).

[b] $H = \frac{1}{N}(\log_2 N! - \Sigma \log_2 n!)$.

predators. It would be profitable in this respect to study the behavior in the field of the polygynous *Apistogramma* and *Lamprologus*. Of course it would also be necessary to take into consideration the problem of energetics. Polygyny would necessitate that many animals in the population be ready to breed at the same time. Often this is not the case in the tropics.

It is worthwhile to compare the reproductive strategies of the surgeon and cichlid fishes. The acanthurids require no special surface for spawning. However, those species that live as pairs are territorial reef dwellers. Apparently a physical center of activity promotes a continued association; it also enables a pair to exclude intruders.

Most likely all the surgeon fishes release vast numbers of eggs that become part of the plankton and are widely dispersed. Equally likely, they spawn repetitively, so that the number of gametes produced annually by each fish must be prodigious. With this simple and relatively primitive mode of reproduction, and a long time span, they seem to have produced a diversity of social systems.

The substrate-breeding cichlids, in contrast, require a particular surface on which to leave their eggs, and subsequently a place where they can put their helpless larvae in order to defend them. They then keep the few thousand or hundred vulnerable fry (a relatively small number) close to them, which makes their protection easier. One reproductive cycle takes about six to eight weeks; it is doubtless so energetically costly that it is not immediately repeated in nature. Such a mode of reproduction, however, must be advantageous or it would not have evolved. Yet it has been evolved at a cost. It ties the species, especially the smaller ones, to certain habitats and thus to a limited number of trophic situations. Remarkably, most substrate-breeding cichlids the world over have much the same social system. (One might have expected them to evolve closed groups from an extended family relationship.)

By evolving mouthbreeding some African genera appear to have broken away from previous constraints. The habitat requirements for spawning are minimal, and the fry are more advanced when released. Perhaps as a consequence, there has been a greater trophic radiation, as in the evolution of plankton filtering species.

In both the cichlids and surgeon fishes, nonetheless, the social systems are seen ultimately as consequences of their feeding behavior, but other factors have a profound and sometimes more proximate influence. In this paper, the physical environment and the effect of predation were seen as the most important proximate modulators of the reproductive behavior in the Cichlidae. In the Acanthuridae, timing of spawning was viewed as an adaptation to avoiding egg predators. But the basic social organization of surgeon fishes most clearly reflects their food habits and the physical environment in which they engage in feeding. Here the physical environment means essentially the degree to which they are exposed to predation. Another important variable should prove to be amount of open time, which is also a consequence of feeding behavior.

The social organization of these fishes is not, therefore, some happy accident of a capricious evolutionary machination, but rather it reflects an ultimate fundamental adaptation to the bioenergetics of the species.

REFERENCES

Albrecht, H. 1962. Die Mitschattierung. Experientia 18:284-286.

Apfelbach, R. 1969. Vergleichend quantative Untersuchungen des Fortpflanzungsverhaltens brutplegemono- und -dimorpher Tilapien (Pisces, Cichlidae). Z. Tierpsychol. 26:692-725.

Baerends, G. P., and J. M. Baerends-van Roon. 1950. An introduction to the study of the ethology of cichlid fishes. Behaviour Suppl. 1:1-243.

Barlow, G. W. 1964. Ethology of the Asian teleost *Badis badis*. V. Dynamics of fanning and other parental activities, with comments on the behavior of the larvae and postlarvae. Z. Tierpsychol. 21: 99-123.

Barlow, G. W. 1968. Ethological units of behavior, p. 217-232. *In* D. Ingle [ed.], The central nervous system and fish behavior. Univ. Chicago Press, Chicago.

Baylis, J. R. 1974. The behavior and ecology of *Herotilapia multispinosa* (Pisces, Cichlidae). Z. Tierpsychol. (In press)

Bleick, C. R. 1970. The behavior of the Central American fish, *Cichlasoma managuense*, and the functions of its color patterns: a laboratory and field study. Masters Thesis, Univ. of California, Berkeley.

Burchard, J. E. 1965. Family structure in the dwarf cichlid *Apistogramma trifasciatum* Eigenmann and Kennedy. Z. Tierpsychol. 22:150-162.

Crook, J. H. 1964. The evolution of social organisation and visual communication in weaver birds. (Ploceinae). Behaviour Suppl. 10:1-178.

Crook, J. H. 1970. The socio-ecology of primates, p. 103-166. *In* J. H. Crook [ed.], Social behaviour in birds and mammals. Academic Press, New York.

Denton, E. J., and J. A. C. Nicol. 1966. A survey of reflectivity in silvery teleosts. J. Mar. Biol. Ass. U. K. 46:685-722.

Eibl-Eibesfeldt, I. 1962. Freiwasserbeobachtungen zur Deutung des Schwarmverhaltens verschiedener Fische. Z. Tierpsychol. 19:165-182.

Estes, R. D. 1969. Territorial behavior of the wildebeest (*Connochaetes taurinus* Burchell, 1823). Z. Tierpsychol. 26:284-370.

Fryer, G., and T. D. Iles. 1972. Cichlid fishes of the Great Lakes of Africa. Oliver and Boyd, Edinburgh.

Hamilton, W. J. 1969. Coral fish coloration. 91 p. (Unpublished manuscript)

Hamilton, W. J., and R. E. F. Watt. 1970. Refuging. Ann. Rev. Ecol. Syst. 1:263-287.

Hobson, E. S. 1972. Activity of Hawaiian reef fishes during the evening and morning transitions between daylight and darkness. Fish. Bull. 70:715-740.

Jones, R. S. 1968. Ecological relationships in Hawaiian and Johnston Island Acanthuridae (surgeonfishes). Micronesica 4:309-361.

Kühme, W. 1963. Chemisch ausgelöste Brutpflege- und Schwarmreaktionen bei *Hemichromis bimaculatus* (Pisces). Z. Tierpsychol. 20:688-704.

Lorenz, K. 1966. On aggression. Harcourt, Brace, and World, New York.

Lowe-McConnell, R. H. 1969. The cichlid fishes of Guyana, South America, with notes on their ecology and breeding behaviour. Zool. J. Linnean Soc. 48:255-302.

McBride, G. 1971. Theories of animal spacing: the role of flight, fright, and social distance, p. 53-68. *In* A. H. Esser [ed.], Behavior and environment. Plenum, New York.

Miller, R. R. 1966. Geographical distribution of Central American freshwater fishes. Copeia 1966: 773-802.

Myers, G. S. 1966. Derivation of the freshwater fish fauna of Central America. Copeia 1966:766-773.

Myrberg, A. A. 1965. A descriptive analysis of the behaviour of the African cichlid fish, *Pelmatochromis guentheri* (Sauvage). Anim. Behav. 13: 312-329.

Myrberg, A. A. 1972. Social dominance and territoriality in the bicolor damselfish, *Eupomacentrus partitus* (Poey) (Pisces: Pomacentridae). Behaviour 41:207-231.

Myrberg, A. A., E. Kramer, and P. Heinecke. 1965. Sound production by cichlid fishes. Science 149: 555-558.

Newall, N. D. 1971. An outline history of tropical organic reefs. Amer. Mus. Novitates (2465):1-37.

Noakes, D. L. G., and G. W. Barlow. 1973. Ontogeny of parent-contacting behavior in young *Cichlasoma citrinellum* (Pisces, Cichlidae). Behaviour 46:221-255.

Okuno, R. 1963. Observations and discussions on the social behavior of marine fishes. Publ. Seto Mar. Biol. Lab. 11:111-166.

Pitelka, F. A., R. T. Holmes, and S. F. MacLean, Jr. 1974. Ecology and evolution of social organization in arctic sandpipers. Amer. Zool. 14:185-205.

Randall, J. E. 1959. Report of a caudal-spine wound from the surgeonfish *Acanthurus lineatus* in the Society Islands. Wasmann J. Biol. 17:245-248.

Randall, J. E. 1961*a*. A contribution to the biology of the convict surgeon fish of the Hawaiian Islands, *Acanthurus triostegus sandvicensis*. Pac. Sci. 15:215-272.

Randall, J. E. 1961*b*. Observations on the spawning of surgeonfishes (Acanthuridae) in the Society Islands. Copeia 1961:237-238.

Stratton, E. S. 1968. An ethogram of *Cichlasoma spilotum* (Pisces: Cichlidae). Masters Thesis, Univ. of California, Berkeley.

Tinbergen, N. 1959. Comparative studies of the behaviour of gulls (Laridae): a progress report. Behaviour 15:1-70.

Wickler, W. 1962. Zur Stammesgeschichte funktionell korrelierter Organ- und Verhaltensmerkmale: Ei-Attrappen und Maulbrüten bei afrikanischen Cichliden. Z. Tierpsychol. 19:129-164.

Wickler, W. 1965. Neue Varianten des Fortpflanzungsverhaltens afrikanischer Cichliden (Pisces, Perciformes). Naturwissenschaften 52:219.

Wickler, W. 1966. Sexualdimorphismus, Paarbildung und Versteckbrüten bei Cichliden (Pisces: Perciformes). Zool. Jahrb. Syst. 93:127-138.

Yasumoto, T., Y. Hashimoto, R. Bagnis, J. E. Randall, and A. H. Banner. 1971. Toxicity of the surgeon fishes. Bull. Jap. Soc. Sci. Fish. 37:724-734.