The Population Biology of Coral Reef Fishes

Paul R. Ehrlich

Annual Review of Ecology and Systematics, Volume 6 (1975), 211-247.

Your use of the JSTOR database indicates your acceptance of JSTOR's Terms and Conditions of Use. A copy of JSTOR's Terms and Conditions of Use is available at http://www.jstor.org/about/terms.html, by contacting JSTOR at jstor-info@umich.edu, or by calling JSTOR at (888)388-3574, (734)998-9101 or (FAX) (734)998-9113. No part of a JSTOR transmission may be copied, downloaded, stored, further transmitted, transferred, distributed, altered, or otherwise used, in any form or by any means, except: (1) one stored electronic and one paper copy of any article solely for your personal, non-commercial use, or (2) with prior written permission of JSTOR and the publisher of the article or other text.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

Annual Review of Ecology and Systematics is published by Annual Reviews, Inc.. Please contact the publisher for further permissions regarding the use of this work. Publisher contact information may be obtained at http://www.jstor.org/journals/annrevs.html.

Annual Review of Ecology and Systematics
©1975 Annual Reviews, Inc.

JSTOR and the JSTOR logo are trademarks of JSTOR, and are Registered in the U.S. Patent and Trademark Office. For more information on JSTOR contact jstor-info@umich.edu.

©2001 JSTOR

http://www.jstor.org/
Tue Jun 12 14:33:02 2001

Copyright 1975. All rights reserved

THE POPULATION BIOLOGY OF CORAL REEF FISHES

❖4093

Paul R. Ehrlich
Department of Biological Sciences, Stanford University, Stanford, California 94305

INTRODUCTION

The development of self-contained underwater breathing apparatus (scuba) has, in the past few decades, provided population biologists with access to the shallow waters of the sea. The availability of scuba has also created an enormous sportdiving industry, with much attention paid to tropical areas.

A popular interest in the spectacular fish faunas of coral reefs, analogous to that shown in birds and butterflies, seems to be developing. This interest will have advantages for the professional scientist. Many observations and photographs will be made in field and aquarium by amateurs, and large markets will permit publication of what otherwise would have been unprofitable literature. For instance, an excellent guide to the common fishes of Caribbean reefs, designed for underwater use, has recently appeared (51).

Coral reefs provide diving biologists with a stunning diversity of organisms accessible in three dimensions; a diver is, in a sense, able to do the rough equivalent of flying over, through, and along the edge of a tropical rain forest. Most of the hermatypic (reef-building) corals live in less than 45 m of water (311), a depth that, coincidentally, is almost exactly the maximum recommended by the U.S. Navy for scuba diving with compressed air. Because their symbiotic zooxanthellae require light, no hermatypic corals live below 90 m (311), and even that depth is occasionally approached by scuba divers with more courage than good sense.

Coral reefs occur through the warm waters of the Indo-Pacific and the western Atlantic (primarily Caribbean) seas. Associated with them to one degree or another are the perhaps 6000–8000 species of fishes that are the subject of this review (41, 59).

Scientific work on the biology of reef fishes began relatively recently. Before World War II, pioneering work was done by a few biologists, especially William H. Longley, who used a diving helmet, took pictures of fishes with a camera enclosed in a watertight glass box with front and rear windows of plate glass, and took notes

on a wax-covered slate. The high quality of his work can be appreciated by examining the text and plates of Longley's "Systematic Catalogue of the Fishes of Tortugas, Florida," posthumously completed and edited by Samuel T. Hildebrand of the U.S. Fish and Wildlife Service (153).

After the war, a relatively small but dedicated group of marine biologists using scuba apparatus began to make the observations upon which this review is based. The bibliography indicates the rapid expansion of this field in the 1960s. I would like to single out one man, however, whose taxonomic and ecological work still forms a substantial portion of the significant literature, namely, John E. Randall of the Bernice P. Bishop Museum of Honolulu. Among diving biologists, Jack Randall is a legend in his own time, and the others will understand why I have chosen to dedicate this review to him.

SOME NOTES ON TAXONOMY AND DIVERSITY

The teleostean fishes of coral reefs are sometimes compared with butterflies; indeed many of the most common and beautiful chaetodontids are called butterflyfishes. There are certain similarities between butterflies and reef fishes, but there are striking differences as well. One of these differences lies in the taxonomic structure of the two groups. In general, reef fishes tend to show much more phenetic, ecological, and behavioral diversity than do butterflies, but within any type they show much less differentiation into arrays of closely related genera and species. While these differences to some degree may be due to divergent views of taxonomists working with invertebrates and vertebrates, in general they are reflections of the different patterns of phenetic similarities within the groups. The teleostean fishes comprise perhaps 20,000 species (59), while the butterflies are a somewhat smaller group with 12,000–15,000 (82). The butterflies, a superfamily of the order Lepidoptera, are divided into five families (78), or an average of almost 3000 species per family. A recent work (120) divided the teleosts into 30 orders and 413 families (some 50 species per family).

The taxonomic structure of the teleosts shows up clearly in the diversity of reef fish faunas. For instance, in a study of the fishes of small section of Tague Bay Reef in the Virgin Islands, Ogden (177) found 125 species belonging to 84 genera and 44 families (1.5 species per genus, 1.9 genera per family). The genus most heavily represented was *Haemulon,* the grunts (Pomadasyidae), with six species; the wrasse genus *Halichoeres,* parrotfishes of the genus *Sparisoma,* and pomacentrids of the genus *Eupomacentrus* had five species each. Five other genera were represented by three species, and all the remaining by two or one.

In the Capricorn group at the southern end of the Great Barrier Reef (by no means the richest faunistic area of that reef) the diversity of fishes is much greater (116; B. C. Russell and F. H. Talbot, personal communication). Some 850 species are present, representing about 297 genera and 84 families (2.4 species per genus; 3.5 genera per family). Several genera contain a dozen or more species; *Chaetodon,* 25; *Scarus,* ±24; *Apogon,* ±23; *Pomacentrus,* 19; *Acanthurus* 13; *Halichoeres,* 12.

In contrast, a sample from a rich butterfly fauna in northwest India (260) contained 87 species belonging to 46 genera and four families (1.9 species per genus, 11.5 genera per family). One genus was represented by five species, four genera by four species, and seven genera by three species. Thus, while the numbers of congeneric species in the three faunas are not strikingly disparate, the butterflies have many more phenetically similar groups living sympatrically than do the fishes. The probable reasons for this difference are discussed below.

Reef fishes, like most organisms, include groups considered taxonomically difficult. Considerable confusion in the past has been caused by the dramatic changes in form and color that occur during the development of many of them. For instance, individuals of the bluehead wrasse, *Thalassoma bifasciatum,* are among the most common reef fishes of the Caribbean. The vast majority of individuals are small (<5 cm), with yellow backs and white bellies divided by a black lateral stripe. A second phase of development is comprised of larger individuals that have the black stripe lightened and broadened into a series of rectangular blotches; many in this phase reach 12 cm in length. A third phase is totally different. It consists of large males, generally 10 cm or longer, that have blue heads followed by two vertical black bands and separated by a narrow white or pale blue band just behind the pectorals. The rear half of the body varies in color from yellow-green to blue, and the tail develops dorsal and ventral lobes not seen in the other phases. All fishes of this bluehead phase are males, and they make up only a few percent of individuals seen on reefs. Although the relationship of these forms was long suspected (150, 151) it was not confirmed until Stoll (281) showed that injection with methyl testosterone converted yellowphases to blueheads.

Fishes of all three phases may be sexually mature; individuals less than 4 cm long may spawn. The yellowphase spawns communally; bluehead males spawn with single females (208, 216). The unwary scientist, accustomed to the less varied sexual habits of terrestrial organisms, could well be misled into believing that he or she was dealing with populations of two quite distinct species. Indeed, complex color changes in the parrotfishes has led to the terminal phase ("termphase") male being described as a species distinct from the "midphase" fishes—smaller adult females and males that are very similar in appearance (204, 227, 248, 249, 306, 308). Different phases have been repeatedly given different specific names in other reef fish groups, for example in the wrasse genus *Halichoeres* (210).

While careful taxonomic work has removed much of the confusion caused by phase change in the scarids and labrids, other groups remain taxonomically refractory. One such group is the genus of the hamlets, *Hypoplectrus* (Serranidae), in which the species are "poorly defined" [(29); G. W. Barlow, manuscript]. These small relatives of the groupers are frequently found on reefs and usually occur singly; many individuals are encountered that do not "fit" descriptions in the literature. Whether this is a reflection of complex relationships among the populations with a lack of phenetically distinct species (as it appears to be in certain butterflies such as the *machaon* group of the genus *Papilio*) or whether it simply reflects inadequate taxonomic work cannot currently be determined.

POPULATION ECOLOGY

Despite some taxonomic confusion and occasional difficulty in making accurate specific identifications without killing individuals, reef fishes, in general, make excellent material for ecological investigations. After they have reached maturity, most species are easily distinguished visually from their nearest relatives; the young of many can also be identified (although usually with greater difficulty). Visual censusing and close observation is possible by day or night to a degree seldom possible in investigations of terrestrial organisms, and tagging can be done with relative ease, although wounds from tags may cause heavy mortality in some groups and impede growth in others (198). Promising new techniques for marking individuals with "dayglo" paints are now under development (J. C. Ogden, personal communication). It is even possible to use sonic tags to follow the movements of individuals, but at present this technique is satisfactory only for the largest reef fishes.

Population Structure

In spite of these advantages, there have been relatively few studies that throw light on the structure of reef fish populations. Extensive tagging programs have been carried out with diverse species on reefs off Bermuda (16), the Virgin Islands (198, 203), and Florida (270), leading to the general conclusion that most reef species are sedentary. These and other (220) results coincide with the impressions of divers who visit the same area repeatedly and learn to expect to see a certain bigeye (*Priacanthus cruentatus*) under the same staghorn coral, a familiar butterflyfish in the vicinity of certain holes in the reef (104), or the same group of cleaner wrasse (*Labroides phthirophagus*) at the same station day after day. Stories of pet groupers (Serranidae) living in certain holes on the reef are legion in popular diving magazines.

This conclusion is hardly surpising. Reef fishes are normally utterly dependent upon the reef for food and shelter from predators, and thus selection against wandering must be great. Many strongly territorial species, such as various members of the damselfish genera *Pomacentrus* and *Eupomacentrus,* defend very restricted areas of the reef (219). This close attachment to defended substrate, often casually observed, has been studied in detail in the Great Barrier Reef species *Pomacentrus flavicauda* (160). Individuals were observed to remain in areas roughly 2 m^2 over a five month study period. These home ranges were defended in their entirety not just against conspecifics, but against a wide variety of herbivorous and ominivorous species. Low was able to adduce considerable evidence that this interspecific territoriality functions to assure individuals of *P. flavicauda* an ample supply of their algal food. In *Eupomacentrus planifrons,* the size of the defended territory varied with the *species* of the intruder, but not with the size of the intruding individual (172); this led to the suspicion that different sizes of territories secure different resources.

In contrast, the interspecific territoriality of *Pomacentrus jenkinsi* in Hawaiian waters is reportedly applied indiscriminately to all other fish species (218), and *Eupomacentrus* spp. about 10 cm in length have vigorously attacked me in the shallow waters off St. Croix, Virgin Islands. The bicolor damselfish, *Eupomacentrus partitus,* also defends its territory against selected species, but the basis of its

discriminations is less clear (169). The territorial behavior of these, and presumably other interspecifically territorial fishes, would appear to have a considerable influence on the home ranges of other reef fishes.

In some pomacentrids, such as *Eupomacentrus leucostictus* (46), the young are highly territorial. In others, such as *Abudefduf zonatus,* they are not, and adult territoriality may periodically be abandoned for clustering behavior (144). Pomacentrid fishes of the genus *Amphiprion* (7) live in an intimate mutualistic relationship with sea anemones and show territoriality in aquaria (97, 163, 183). In nature, however, territoriality may be either present or absent (7, 88, 164). In either case, the home range of these fishes, which appear to spend their entire lives associated with a sessile anemone, is extremely restricted. Allen (7) reported *Amphiprion* living more than 30 months with the same anemone. Spawning takes place in a substrate nest immediately adjacent to the anemone (7).

Other pomacentrids that are not territorial nonetheless have highly restricted home ranges on the reef. Sale's careful studies of the wide-ranging Indo-Pacific "banded humbug" *Dascyllus aruanus* (236, 237, 239, 240) showed that in less than 5% of observations were these fish found more than 1 m from an original capture site. Although these fishes are not territorial, agonistic behavior occurs within groups taking shelter in branched corals. The intensity of this behavior varies both with group size and the amount of shelter (and there is a significant interaction between them). This behavior influences patterns of movement among suitable areas of coral and tends to space individuals efficiently where suitable coral colonies are in short supply.

In contrast to the relatively straightforward home range and territorial arrangements of certain pomacentrids (e.g. *Pomacentrus jenkinsi* defending a fixed feeding territory both as juveniles and adults), other reef fishes show a bewildering variety of behavior in their utilization of space. Some Acanthuridae and Pomacentridae establish fixed feeding territories as young, but abandon them as they mature, sometimes forming pairs that defend temporary feeding territories (218). Other groups, such as the chaetodontids, do not normally appear to hold feeding territories (83, contrary to 218).

Surgeonfishes (23) may either hold small permanent or semipermanent territories (5–20 m^2), hold temporary grazing territories, or be nonterritorial and school. Adults of the same species may show territorial behavior at one time or place and not at another. Juvenile acanthurids generally appear to be territorial (23, 183), with the possible exception of *Acanthurus triostegus* where the juveniles are reported both to be territorial (22) and nonterritorial (199, 234). In Hawaii, juveniles of this species are also unique in that they occupy intertidal pools (119).

The significance of different patterns of territoriality and schooling in acanthurids has been discussed (23, 24). The Acanthuridae are, along with the parrotfishes (Scaridae), some pomacentrids, balistids, kyphosids, and blenniids (129, 208), the major grazers on the reef. For instance, one guild grazes on the sand adjacent to the reef and is made up of relatively large, mobile species (*Acanthurus dussumieri, A. xanthopterus, A. mata*). They exploit an almost unlimited food resource, sifting diatoms and algae from the sand (142). Individuals of the sand grazer's guild are

not territorial, but feed in heterotypic schools, quite likely as a predator defense mechanism (80). In contrast, the guild of small reef browsers, such as the spectacular *Acanthurus achilles* of the surge zone, has some highly territorial members. Presumably the reef browsers are defending an area necessary to provide them with an adequate supply of the multicellular algae that grow on the rock or coral substrate (142).

Most interesting is Barlow's (24) interpretation of solitary and schooling behavior in the manini (*Acanthurus triostegus*), the most common surgeonfish in the shallow waters of Hawaii. The "scalpel" at the base of the caudal fin that gives the surgeonfishes their name is very weakly developed in *A. triostegus,* presumably putting it at a disadvantage in social encounters (32). While in some situations manini schooling is an antipredator defense, in others it is a mechanism for gaining access to feeding surfaces defended by the dominant lavender tang, *Acanthurus nigrofuscus.* In essence, a schooling stream of manini swamps the tang's defenses. Barlow showed that schooling reduced the number of attacks on each manini by at least 30% per unit time spent grazing on the substrate. At Lizard Island on the Great Barrier Reef, *A. triostegus* has been observed using this technique to swamp the defenses of territorial pomacentrids (G. Anderson, P. Ehrlich, F. Talbot, and B. Russell, unpublished). Similarly, *Pomacentrus lividus,* defending its feeding territory in the Red Sea, can have its defenses swamped by invading schools of *Acanthurus sohal* (295).

The other prominent group of reef grazers, the parrotfishes (Scaridae), also show a spectrum of spatial behavior that varies between and within species. G. W. Barlow (manuscript) found two species of the genus *Sparisoma* more solitary than two species of *Scarus,* confirming earlier observations of generic difference in social behavior (308). Ogden & Buckman (180), working on the Caribbean coast of Panama, found stationary-territorial, stationary-nonterritorial, and moving flock fishes of *Scarus croicensis* in shallow water (<3 m). While midphase fishes may be territorial in shallow water, they are not in deeper water (at least not at Barlow's Puerto Rico study site in 15–30 m of water).

In shallow water, Ogden & Buckman (180) recorded *Scarus croicensis* foraging in heterospecific schools with one or two species of *Acanthurus,* the barred hamlet (*Hypoplectrus puella*), and, less frequently, the spotted goatfish (*Pseudupeneus maculatus*); I observed similar assemblages in the Grenadines and Virgin Islands. The scarids and acanthurids presumably gain predator protection from increased school size. The hamlets apparently benefit by enhanced feeding opportunities; they snap up small invertebrates stirred up by the milling herd. The goatfishes may gain some protection from predators, but probably do not gain a feeding benefit since they probe the substrate for invertebrates with their barbels and are often themselves followed by small fishes feeding on what they stir up.

In Panama, *Scarus croicensis* spends the days in the shallow waters of the reef and nights in deeper waters (180). Morning and evening migrations occur over narrowly defined routes and thus provide an excellent opportunity to census the population. This behavior is strikingly complementary to that of various nocturnally feeding grunts (primarily *Haemulon flavolineatum* and *H. plumieri*), goatfishes (*Mulloidichthys martinicus*), and snappers (*Lutjanus*), which spend their days rest-

ing in heterotypic schools on Caribbean reefs. These fishes leave the reef in a ritualistic series of movements along narrow routes just at last light. They reverse the process at dawn (J. C. Ogden and P. R. Ehrlich, unpublished). There is some evidence that the same fishes rest in the same schools day after day, and may feed together over sand flats at night. Fishes in these schools are of medium size; nothing is known of the distribution and movements of larger fishes that have outgrown the schools. Studies of the margate, *Haemulon album* (65), indicate similar behavior, with tagged fishes returning to the same daytime positions. Again, parrotfishes that spend their nights in offshore caves at Bermuda migrate daily to feeding grounds along the shore, using sun-compass orientation (309).

Although various aspects of the population structure of a few groups of reef fishes are being gradually elucidated, a great deal remains to be learned. Attempts should be made to tag and follow individuals over major portions of their lives on the reef, and spatial patterns in more groups should be carefully investigated. For instance, final interpretation of the spectacular patterns of butterflyfishes, so abundant on reefs in the Indo-Pacific, will probably have to await more detailed knowledge of their population structure.

Essentially nothing is known about the population structure of such prominent predators on other reef fishes as the carangids (jacks), aulostomids (trumpetfish), synodontids (lizardfish), and lutjanids (snappers). We are similarly ignorant of the activities of the predaceous fishes, such as the holocentrids (squirrelfishes), apogonids (cardinalfishes), and moray eels (Muraenidae), which spend their days sequestered in cavities in the reef (132), or of the abundant bottom-dwelling blennies (Blenniidae) and gobies (Gobiidae) that observations (264, 275) seem to indicate are quite sedentary. We also lack information on the often strangely shaped fishes of the order Tetraodontiformes (Plectognathi), so familiar to divers on reefs. These include the trigger and filefishes (Balistidae), trunkfishes (Ostraciontidae), puffers (Tetraodontidae), and porcupinefishes (Diodontidae), which are predators on invertebrates and, with the exception of the balistids, are relatively slow swimmers and presumably quite amenable to capture-recapture experiments.

Population Dynamics and Genetics

Results of tagging studies have not been used as the basis for estimates of population size, probably wisely so because of the small fraction of the populations marked and the probable violation of basic Lincoln Index assumptions (randomization, no trap-happiness). Other methods of population estimation have been proposed (44), but none seem to have been employed systematically. Indeed, even anecdotal observations of changes in population size are infrequent. Ogden & Buckman (180), with the benefit of unusually accurate census data, recorded a decline in the population of *Scarus croicensis* coincident with the onset of the dry season. They hypothesized that this was related to a reduction in food supply resulting from a lowered level of sedimentation.

In any event, without more knowledge of the population structure of reef fishes, any observed change in numbers is difficult to interpret. From the point of view of the factors controlling both the size of populations and their genetic composition,

it is essential that population units be recognized (83). If, for instance, in every generation, pelagic larvae of a species are widely dispersed over hundreds of miles of reef by currents, then essentially panmictic populations may extend over enormous areas (71). Whether this occurs frequently is questionable, for in many reef areas prevailing currents would at least tend to make movements of larvae more or less unidirectional. Thus the Hawaiian Islands populations of reef fishes with pelagic eggs and larvae must suffer enormous losses as their propagules are swept from the relatively localized coastal current system into the major western current set up by the trade winds (142).

One would expect, furthermore, that populations of such fishes around small oceanic islands would have difficulty maintaining themselves in the face of this attrition. Could, for instance, the acanthurid populations of isolated Johnston Island, "downstream" from the Hawaiian groups (117, 119), be maintained by a steady input of larvae from Hawaiian populations to balance the losses? The evidence seems to be against this (199). The Johnston population of manini, the most common Hawaiian acanthurid, is differentiated from that of Hawaii (194), and so is that of *Ctenochaetus strigosus,* the kole, another common Hawaiian tang (193).

Probably other factors conserve the Johnston fauna. Jones (142) suggested that, as Boden (28) found in Bermuda, there may be temperature and density factors that interact to create patterns of circulation tending to keep planktonic larvae from being carried out to sea. There is some evidence that local gyrals may trap small larvae that, when they are partially grown, may be able to escape and return to islands (235). In addition, "coast countercurrents, long back swirls and eddies" keep many California lobster larvae in the area of the adult distribution (141). Having pelagic larvae does not necessarily mean having huge, virtually panmictic, populations.

Many, if not most, dynamic units in reef fish populations are probably quite large, with a large pool of very young fishes available to reoccupy any segment of reef where larger fishes have suffered a catastrophic decline from storms, predation, or temporary exhaustion of food supply. On undisturbed large reefs these populations are likely to show the kind of stability of size often predicted and occasionally demonstrated (81) for tropical forest animal populations. And, indeed, Smith & Tyler (264) claimed there is no evidence of large fluctuations in abundance of reef fishes throughout the year. As discussed below, however, Australian biologists have observed dramatic fluctuations in species composition (and thus, of course, in the populations of different species) in small areas of reef.

Very recently, the work of M. Soulé (personal communication) and his collaborators has begun to give us a glimpse of the population genetics of reef fishes. Using the techniques of starch gel electrophoresis, he has examined 21–25 loci in populations of five pomacentrids—*Dascyllus aruanus, D. melanurus, Pomacentrus wardi, P. flavicauda,* and *Acanthrochromis polyacanthus*—in the southwest Pacific. *A. polyacanthus* is unusual in that it has no pelagic larval stage (D. R. Robertson, manuscript) and demonstrates parental care of its young on the reef. It shows a high degree of geographic phenetic differentiation, and Soulé has shown that this is accompanied by a high degree of genetic differentiation. Not only are gene frequen-

cies different from population to population, but many alleles are also unique to one or a few populations.

In contrast, Soulé found that the widespread *D. aruanus,* which has pelagic larvae, shows virtually idential allele frequencies over a 3000 km transect from the southern part of the Great Barrier Reef of Australia to Madang, Papua New Guinea. In addition, a single sample of *D. melanurus* from Madang showed at most only one fixed allele difference from *D. aruanus. Pomacentrus wardi,* which also has pelagic larvae, appears to show a pattern similar to *D. aruanus,* with no fixed allelic differences among populations. Between the two species of *Pomacentrus* there is just one fixed allelic difference.

Soulé's data also indicate that geographically and ecologically marginal populations at the southern end of the Great Barrier Reef tend to be less polymorphic than the equatorial populations, a pattern consistent with what little is known for other vertebrates (268).

Soulé (268) and others are in the process of studying allozyme variation in the sergeant major, *Abudefduf saxatilis* (*sensu lato*) a circumtropical reef fish. With the exception of one or two esterase loci, Bermuda and Panama Atlantic populations seem virtually identical at about 28 loci. The eastern Pacific form, *A. troischelii,* virtually indistinguishable morphologically from *A. saxatilis,* differs from it by six fixed alleles. Like *A. saxatilis,* however, *A. troischelii* shows almost no genetic differentiation between the two sampled populations in the Revillagigedo Islands and the Pacific coast of Panama, more than three thousand kilometers apart. *A. "saxatilis"* from Madang, New Guinea is almost a perfect intermediate between *A. troischelii* from the Pacific and *A. saxatilis* from the Atlantic.

These data raise many questions about the role of gene flow in preventing the differentiation of populations. The following comments have arisen from discussions with Soulé. Except for *Acanthochromis,* which apparently lacks a between-reef dispersal stage, the pattern in the pomacentrids is consistent; unless there is complete isolation by emergent land, very little allelic differentiation appears in populations separated by as much as 3000–5000 km.

In sharp contrast, *Acanthochromis* populations on different parts of the Great Barrier Reef and the islands to the north show striking phenetic and genetic differentiation. In fact, there are much greater genetic differences among the *Acanthochromis* populations than between sympatric congeners in the genera *Dascyllus* and *Pomacentrus* and among populations of many terrestrial animals (83). Soulé contended that the relatively low rate of migration and gene flow in *Acanthochromis* probably facilitates geographic differentiation, although without a thorough ecological analysis we cannot rule out the possibility that selection pressures unique to *Acanthochromis* are causing its striking diversification.

Not only should patterns of differentiation among other reef fish populations prove of great interest, but so should comparisons of the level of genetic variability in these ancient (174) "climatically" stable communities with those of other communities—especially the tropical rain forest. Somero & Soulé (267) predicted that populations on reefs, in deep seas, and in rain forests should show more heterozygosity than those in less climactically stable regions, and they have pre-

sented some data to support this hypothesis in a comparison of the genetic variation in samples of fishes, including three reef species, *Dascyllus reticularus, Amphiprion clarkii* (both pomacentrids), and *Halichoeres* sp. (Labridae). These species seem to be more variable than those from areas (Antarctic, temperate estuarine) where one might expect strong directional selection. That hypothesis should be thoroughly tested in the future.

Understanding the genetics of reef fishes will require more, however, than assaying samples for allozyme variation. As indicated above, knowledge of levels of gene flow will be essential, and this means evaluating both the movements of individuals and the probabilities of migrant individuals successfully reproducing (83). Studies relating the frequency with which larvae are found in the oceanic plankton between populations to the differentiation of those populations (244) would be most useful. And, of course, thorough knowledge of gene flow levels will also involve understanding of the genetic systems of various reef species. Fundamental to both of these is spawning behavior and the fate of the eggs and newly hatched young. We have some information about both for a small proportion of reef fishes.

Pomacentrid fishes, both benthic feeders and those that forage in the water column, spawn in pairs on the substrate (3, 6, 43, 57, 72, 97, 99, 110, 111, 126, 144, 148, 170, 232, 238, 279, 285, 292; D. R. Robertson, manuscript). Their spawning behavior is quite similar to that of the closely related freshwater cichlids (301), familiar to home aquarists. The males of some species (e.g. *Abudefduf saxatilis, Chromis multilineata*) spawn consecutively with several females (98, 170), often in a lek system similar to that of certain birds (146). Curiously, this system has not led to the evolution of visually prominent males in many pomacentrid species, or to a terminal phase male as it apparently has in many scarids and labrids.

While the known larval pomacentrids, except *Acanthochromis polyacanthus,* are all pelagic, in some species, at least, they remain closer to the reef than do the young of reef species that are not substrate spawners. The hatchlings of *Abudefduf saxatilis* are reported to assemble in depressions on the reef, and juvenile fishes are found along the outer reef wall (98), an observation that needs confirmation since the morphology of pomacentrid larvae indicates they would be incapable of avoiding being carried by currents (P. F. Sale, personal communication).

The spawning behavior of blennies and gobies seems to be quite similar to that of pomacentrids (38, 219), although most of our information is based on observations of species that do not occur on coral reefs (e.g. 77, 290, 296).

At the opposite end of a behavioral spectrum from the pomacentrids, blennies, and gobies are the acanthurids, scarids, labrids, and at least one goatfish (*Pseudupeneus maculatus*) (216). These fishes do not anchor their eggs to the substrate and then attempt to defend them from numerous substrate predators. Instead they spawn in a frantic dash towards the surface, launching the fertilized eggs into the relatively egg-predator-free upper waters (G. W. Barlow, manuscript; 48, 94, 199, 200, 308). The reproductive behavior of these fishes is extremely varied. Spawning has been observed in only three species of acanthurids, all Indo-Pacific (199, 200). In all three cases, small groups of fishes left a much larger school for the upward spawning rush.

Randall, who made these pioneering observations, at first thought that the upward movement served to confuse possible predators, but eventually decided that its main function was to aid the ejection of the sperm and eggs. The rapid dash to the surface expands the swimbladder and increases pressure on the gonads; a quick flexing of the body as the fish rapidly changes direction and turns back downward may help to release sperm and eggs and mix them. As Jones (142) suggests, however, Randall's first reason may be more important. Fishes that lay demersal eggs must expend a large amount of energy defending them from the abundant predators of the reef substrate—wrasses, butterflyfishes, many pomacentrids, and plectognaths. In contrast, the waters near the surface are relatively free of potential egg predators, many of which are tied to the reef for shelter. As many fishes in both salt and fresh water are able to spawn successfully without such an upward dash, I am tempted to speculate that the ultimate selective value of "gamete-launching" is that relative freedom from predation more than compensates for the loss of pelagic eggs and larvae from currents. The dash also minimizes the exposure of the spawning fishes to predators such as carangids, lutjanids, and serranids.

In scarids and labrids (227), the situation is more complex. Many species have two adult phases. In the midphase, males and females are similar in appearance and spawning is communal, in much the manner of acanthurids (93, 227). The other phase consists of large, brightly colored primary or terminal phase (termphase) males that spawn singly with midphase females in a dash to the surface.

In spawning aggregations of the yellowtail parrotfish, *Sparisoma rubripinne,* over 75% of the fishes were males and each spawning group seemed to consist of a single female and 3–12 males (216). This species also spawns in termphase-midphase pairs, although much more rarely. The abundant striped parrotfish of the Caribbean, *Scarus croicensis,* shows, similar patterns in deep waters (216; G. W. Barlow, manuscript), as does the princess parrotfish, *Scarus taeniopterus* (Barlow, manuscript), and the redband parrotfish, *Sparisoma viride* (216, 308). In shallow waters, *S. croicensis* shows a different social system in which females are the prime territory holders (48).

Barlow (manuscript) speculated that the lek society evolved as males contested for the best spawning locations (which are in short supply). He argued logically that this system could, through sexual selection, explain the evolution of the conspicuous termphase males. The evolution of the shallow water *S. croicensis* system remains unexplained. Barlow also addressed the problem of the retention of midphase group spawning and concluded that in different ecological situations (e.g. different population densities) one or the other system would be favored and that overall selection would favor males that can breed both as midphase and termphase.

In scarids and labrids there is another interesting reproductive phenomenon in addition to two-stage spawning. In many of these fishes, there is protogynous hermaphroditism—functional females changing into males (223–225). The best known case is that of the famous cleaner wrasse *Labroides dimidiatus,* in which Robertson (224, 225) was able to show social control of sex reversal. Social groups of these fishes (in which the sexes are similar in appearance and there is no male termphase) consist of a single male and a harem of females. The tendency of females

to turn into males is suppressed by the presence of the dominant male. The death or removal of that male ordinarily permits the dominant individual in the female pecking order to change rapidly into a male. These fishes are territorial, however, and the death of a male may result in a neighboring male occupying the dead fish's territory and incorporating the dead fish's females into its own harem.

A very similar situation was reported (99) in a serranid (anthiid) fish, *Anthias squamipinnis*, that inhabits reefs in the Indo-Pacific. The system was considered highly adaptive because males are only produced if there is need for them, that is if their density in the population decreases. The breeding ecology of this species is complex and may involve simultaneous group spawning of territorial and nonterritorial males (187).

In *Labroides dimidiatus* there are only secondary males—those derived from females. In other labrids, such as *Thalassoma lunare,* there are both secondary males and primary males, that is, those born male (226). The complexities of the selective systems leading to these patterns in labroids are discussed in detail by Robertson & Choat (226) and expanded upon by them in a discussion of the extremely flexible ontogeny of the parrotfishes (J. H. Choat and D. R. Robertson, unpublished). In the latter work, the sexual ontogeny and ecology of nine Great Barrier Reef scarids are described in detail. One species has only secondary males, others have varying mixtures of primary and secondary males.

Other serranid fishes are synchronous hermaphrodites (can produce eggs and sperm simultaneously), and still others have completely separate sexes (53, 54, 262). Some porgies (Sparidae) are also hermaphroditic (53, 221). Part of the selective value of hermaphroditism may well be increased fecundity, but, other factors must be considered (224, 225), in particular the degree of inbreeding produced by these genetic systems [interestingly, synchronous hermaphrodites have been observed spawning in pairs (53)].

There is a scattering of information on reproduction of other groups of reef fishes, albeit often garnered from nonreef species of the same family (38). Most families appear to have pelagic eggs: Carangidae (jacks), Chaetodontidae (butterfly and angelfishes), Kyphosidae (chubs), Lutjanidae (snappers), Mullidae (goatfishes), Muraenidae (morays), Pomadasyidae (grunts), and Sparidae (porgies). Many cardinalfishes (Apogonidae), often the prominent nocturnal group on a reef, are mouthbrooders (184). Many of the plectognath fishes, including various Tetraodontidae (puffers), Diodontidae (porcupinefishes), and perhaps many Balistidae (triggerfishes) have demersal eggs. The Serranidae (groupers, hamlets, basslets, etc) seem to have species with both demersal and pelagic eggs. A few groups, such as some cliniids and brotulids, are viviparous (29). In these small fishes, populations are highly differentiated, perhaps because the livebearing habit keeps the young close to home (229; J. E. McCosker, personal communication).

Before a reasonably coherent picture of the population genetics of reef fishes can be assembled, several kinds of knowledge are necessary. Further data on allozyme variation must be gathered and evaluated as to the nature of the sample of loci obtained. Enough crossing work should be done to give reasonable assurance that the variation investigated has a genetic basis. In some cases, it should be possible to do this with more readily bred freshwater fishes closely related to reef fishes, e.g.

cichlids instead of pomacentrids. More information needs to be gathered on population structure, especially on the potential for long range gene flow. This is probably the most challenging task. It is one that might be tackled by careful observations of the spread of transplanted fishes into areas where they did not occur before. Transfers have been done and can "take" without causing disruption in the local fauna, as has been demonstrated by the importation of reef game fishes (groupers and snappers) into the Hawaiian Islands (197, 214). Such transplants should only be attempted under very special circumstances, if ever, but when they are carried out or occur naturally they provide an excellent opportunity to gather information on the movement of propagules. Finally, the role of the diverse genetic systems on the reef, involving such phenomena as the "pseudo-lek" systems and hermaphroditism, must be entered into the equation.

COEVOLUTION

Considering the ancient, relatively stable conditions on coral reefs, it is not surprising that the organisms of the reef community show a bewildering variety of tightly coevolved relationships. Some of these, such as the anemonefish-anemone and cleaner-cleanee relationships have been studied in considerable detail. Others, such as plant-herbivore and predator-prey coevolution are just beginning to be investigated, and studies of food utilization and growth in reef fishes are few and far between (e.g. 19, 167, 168).

Plant-Herbivore Coevolution

Of the impressive diversity of reef fishes, only a few groups are primarily herbivorous (10, 129, 207). By far the most prominent are the parrotfishes and the surgeonfishes, which often graze and browse on the reef in herds, reminiscent of large terrestrial herbivores. The chubs, Kyphosidae, are also all herbivorous, but do not usually form large schools. Other herbivorous species are found scattered through families such as the Pomacanthidae (94), Pomacentridae, Siganidae (295), Blenniidae, and various plectognaths. In spite of the presence of these abundant herbivores, however, benthic algae usually do not form prominent stands on reefs as do plants in most terrestrial areas (14, 70, 201).

That reef herbivores have a large impact on benthic algae is obvious from the results of exclosure experiments (76, 201, 277). In Hawaii two months after an exclosure was set up, the dominant alga inside *(Ectocarpus indicus)* attained a height up to 15 mm, and other species averaged 4–30 mm (201). The algal mat in the area outside of the exclosure averaged 1–2 mm in depth. Randall obtained similar results in the Virgin Islands, where algae grew profusely within a one square yard exclosure despite the presence of 16 individuals of the herbivorous *Diadema* sea urchin, which, on the average, tripled in size during the 11 week period of the experiment. When the exclosure was removed, acanthurids and scarids moved in and immediately began grazing.

Reef fishes have also been shown to be important in producing bare "halos" (Randall zones) around reefs; these are areas devoid of the sea grasses (primarily *Thalassia testudinum* and *Cymodocea manatorum*) that cover large areas of the sea

bottom in shallow waters of the Caribbean (206). Apparently, the fishes will only venture a short distance from the shelter of the reef to feed and this produces the Randall zone, an area of cleared sand that fringes the reefs, and is roughly 10 m wide. The phenomenon is quite similar to the production of cropped areas in grassland adjacent to chaparral in California (25). Small herbivores appear to be wary of exposing themselves to predation both above and below water!

However, it is difficult to generalize about the impact of grazing fishes and of grazing invertebrates on the reef flora. For instance, at St. Croix, and possibly in other areas of the Caribbean, the sea urchin *Diadema antillarum* seems to be a more important grazer on algae and sea grasses than are reef fishes, and may be primarily responsible for the reef-edge Randall zone (178, 179). Indeed, on Caribbean reefs where it is abundant, *Diadema* may also add its impact to that of browsing fishes on populations of sessile benthic macro-invertebrates (242). When a reef is cleared of *Diadema* there is an increase in the biomass both of herbivorous fishes and of carnivores, especially labrids that prey on invertebrates associated with the benthic flora (181).

Recent work on the coevolution of terrestrial herbivores and their food plants indicates that the selective impact of the herbivores is great, that major elements of the plants' defenses tend to be biochemical (39, 82, 102), that among closely related plants some are more subject to attack than others (40), and that differential susceptibility is related to biochemical defense strategy (73). Considering the heavy level of grazing on reef algae, one would expect that this flora, too, would show differential susceptibility to grazing; and this expectation is met. On a heavily *Diadema*-grazed patch reef some reef algae did attain leafy growth—*Laurencia obtusa, Caulerpa* spp., and *Dictyota* spp. (178). Experimental exposure of these and "control" algae to fish predation showed that the former three were not eaten as readily as the controls (J. C. Ogden, unpublished).

These algae, as well as blue-green algae that are often avoided by fishes (202) probably have some sort of chemical defense, although low caloric value or structural defenses cannot be eliminated (185). *Caulerpa* contains caulerpin and caulepicin (75, 243), which presumably have a defensive function.

Further effort to isolate possible defensive compounds from algae would seem highly worthwhile. Not only will knowledge of the evolution of algal defenses help in our understanding of the evolution of reef ecosystems, but it may also have highly practical applications in mariculture and elsewhere. There is, for instance, a powerful toxin in some large individuals of tropical marine fishes that frequently causes human poisoning. The disease, known as *ciguatera* or tropical fish poisoning, is sometimes fatal (202). The source of this poison may be an algal toxin that concentrates as it moves up marine food chains (195), perhaps originating in pioneer blue-green algae. If so, there should be a correlation of the poisoning with cyclonic disturbances (276), heavy anchoring activity by boats, or other disturbances likely to provide virgin surfaces on the reef.

On the other hand, ciguatera toxin may have its source in toxic invertebrates, which are much more abundant in the tropics than temperate waters (15), or in small poisonous fishes. Or indeed, the disease may be a compound entity with several distinct sources.

Plankton-Planktivore Coevolution

A common feeding niche of reef fishes is that of fishes that forage for plankton in the water column. Various herring-like fishes, small wrasses, occasional lutjanids, and, especially, a wide array of pomacentrids, make their living eating phytoplankton and zooplankton. Although lagoon plankton appear to be largely resident, the feeding by fishes on oceanic plankton as it is swept over the reef seems to represent a substantial import of energy into the reef (91). Relatively little is known of the devices evolved by plankton in response to predation pressures from fishes, although there are signs of plankton schooling in caves and crevices that provide shelter from predators (91).

Predator-Prey Coevolution

PREDATION ON INVERTEBRATES Marine ecosystems differ from terrestrial ones in having what might be considered a "pseudoflora" of sessile invertebrates potentially subject to grazing by fishes and other mobile predators. Hermatypic corals are consumed by "herbivores," such as scarids, especially in the Pacific where coral cover is more extensive and marine phanerogams are rare in comparison with Caribbean reefs (12, 114, 284). Grazing pressure from fishes seems to account for the relative paucity of sessile invertebrates on the exposed surfaces of the reef (70, 92, 175). Although the upper surfaces of coral slabs at Fanning Island (10) were nearly devoid of benthic organisms, sponges and algae grew on the bottoms. These were immediately attacked by acanthurids, wrasses, scarids, and goatfishes when slabs were turned over. These observations should be repeated since wrasses and goatfishes have not been reported to feed on sponges elsewhere, nor are there records of scarids intentionally feeding on them. In addition, while grazers such as acanthurids and scarids may limit the distribution of some invertebrates, they encourage others by creating suitable settlement surfaces by removing green filamentous algae (295).

Bakus (10, 11) has suggested that grazing constitutes a major selective pressure on benthic marine invertebrates. This view has been supported by the demonstration that many species of sponges and holothurians are toxic, and that toxicity may occur in 100% of coral reef holothurian species. In addition, the bright colors of many unarmored nudibranch molluscs strongly indicate aposematic coloration, and the stinging ability of sea anemones and their relatives is obviously a deterrent to many potential piscine predators. It also seems a logical evolutionary parallel to terrestrial systems where, as mentioned above, plants defend themselves with noxious chemicals and arthropods also commonly have chemical defenses (e.g. 89, 90, 230).

Some fishes, most especially Caribbean grunts (Pomadasyidae), rest on the reef during the day and at night forage off the reef on a wide variety of invertebrates (68). Nothing is known of their coevolution with their prey, but as grunts are eaten by reef piscivores, which deposit much of their feces on the reef, they constitute a channel for energy flow into the reef system.

Sessile or relatively sessile invertebrates are not, of course, limited to chemical defenses. Many have developed mechanical defenses against predation—the shells

of many molluscs and the spines of sea urchins are obvious examples. To overcome the latter, the triggerfishes have evolved appropriate teeth, setback eyes, and behavior that permits them to make fast work of urchins as well as other armored invertebrates (107, 129, 207, 208), while other fishes adopt other successful modes of attack, including the smashing of urchins against rocks by labrids of the genus *Cheilinus* (107). Some small clingfishes and gobies appear to behave as ectoparasites on the urchins with which they are associated, feeding on the urchin's tube feet (289).

CO-OPTION OF INVERTEBRATE DEFENSES All of the fishes of the reef, except the larger sharks and rays, must contend with predators that hunt them. The protective devices they have evolved in coevolutionary races with their predators are extremely varied. Some, for instance, co-opt the defenses of invertebrates. Small apogonids (cardinalfishes) cluster among the spines of sea urchins and crown-of-thorns starfish, presumably gaining protection there when they are not feeding (1, 2, 145, 161, 217, 282). Many of these fishes have longitudinal stripes that help them blend in with the urchin. Fishes of other families also shelter in sea urchins (279, 282), including shrimpfishes (Centriscidae), relatives of the seahorse that hang head downward among the spines (127). The degree of camouflage varies among urchin inquilines; apparently the ability of some predators to hunt among the spines has, in some cases, produced selection for close color resemblance of the fish to the urchin.

Pomacentrid fishes of the genus *Amphiprion* take advantage of the stinging tentacles of sea anemones, much as the apogonids take advantage of sea urchin spines (7). But this is a more perilous symbiosis since sea anemones often use their nematocysts to capture fishes (122). The anemonefish-anemone relationship has thus attracted more attention from biologists (64, 110, 163, 164, 166, 294) than has the fish-urchin relationship. The anemonefishes are not born with immunity to the stings of the anemones, but acquire it gradually by acclimation (67, 162, 165, 245). The fishes are territorial when associated with an anemone. They capture food and bring it to their anemone (86, 115, 163, 166)—although more readily in the aquarium than in nature (7)—so that the relationship is truly mutualistic. Other reef pomacentrids are also sometimes associated with anemones (86, 278, 279), as is at least one wrasse, *Thalassoma amblycephalus* (246), and an apogonid, *Apogon quadrisquamatus* (61). These species, however, do not seem to form as "tight" a relationship with anemones as do the *Amphiprion.*

CHEMICAL DEFENSES Many reef fishes have acquired toxins of their own. Best known of these are the Scorpaenidae (scorpionfishes, stonefishes, lionfishes), which have poisonous defensive spines (35, 208) capable in some species of killing a man. The fish may use these spines to strike out in active defense (130). Siganids have toxic spines, and toadfishes (Batrachoididae) have "the most highly developed venom apparatus in the fish world" (208). Soapfishes (Grammistidae) produce a protein skin toxin, grammistin (209), which has been known to kill other fishes confined with them and is lethal to mammals, producing in cats symptoms similar to ciguatera (212). Trunkfishes (*Ostracion*) and puffers (*Canthigaster*) also have skin toxins

repellent to large predators (J. E. Randall, personal communication). At least one species of flatfish (Pleuronectiformes) produces a toxin lethal to other fishes (56). Some parrotfishes form a mucous envelope in which they pass the night on the reef surface (305), and there is some evidence that this helps to protect them from the nocturnal depredations of moray eels (307). Since these eels use their sense of smell to locate prey (20), the mucous envelope, rather than being distasteful, may simply serve to limit the release of odorant molecules from the resting scarids.

SCHOOLING Another predator-defense strategy utilized by reef fishes, schooling, is seen in diverse groups: tiny fry, herring-like fishes, reef grazers, daytime resting groups of grunts and snappers, and patrolling groups of large predators such as jacks. Eibl-Eibesfeldt (87) differentiated pelagic schooling prey fish, pelagic schooling predators, semipelagic schoolers, schooling substrate grazers, schooling fishes with a fixed refuge on the reef, and facultative schoolers. In agreement with most biologists before and since who have studied fish schooling (e.g. 37, 45, 80, 124, 131, 132, 173, 188, 189, 192, 250, 269), Eibl-Eibesfeldt considered the school "primarily a protective association," citing, among other things, the behavior of schools in the presence of predators, especially the zig-zag streaming of fleeing fishes and the formation of "vacuoles" around the predator. He also suggested that predatory fishes hunting in schools were able to surround schools of food fishes, split off individuals, and corner them.

The principal means by which schooling seems to benefit the prey is through what might be called the "confusion-effect," or the moving swarm (132)—an effect familiar to those who have attempted to spear a fish in a school or net a single butterfly from a swarm. Schools also may serve to lessen the frequency of predator-prey encounters—the larger the school, the greater the advantage (45). Some fishes have coevolved patterns of heterotypic schooling to permit increase in school size (80). In addition, a tightly packed school may frighten a predator by resembling a very large fish (269).

The development, physiology, dynamics, and adaptive value of schooling have been extensively studied by behaviorists (33, 34, 36, 50, 253–259, 303, 304), but definitive experiments on the question of greatest importance to the population biologist—the adaptive value of schooling—remain to be done. It has not been possible to show unequivocally, for instance, that a solitary grunt resting during the day on a patch reef would be less likely to be eaten if it were in a school. Besides the intrinsic difficulty of doing appropriate experiments in nature, an additional complication is the apparently differential response of schooling fishes to different predators. Jack mackerel (*Trachurus symmetricus*) attacked by scorpionfish or rockfish only reacted individually (58). When they were attacked by a bonito or sea lion, however, the mackerel formed schools and rushed off together. The sea lions and bonitos more commonly attack jack mackerel than do rockfish or scorpionfish, and the former make prolonged high speed attacks from above while the latter lunge from below. Shaw (258) also observed individuals from silversides schools being consumed by a fish attacking from below "without ruffling the school." The final complication is, of course, that schooling undoubtedly serves other functions in addition to predator protection (24, 258).

COLORATION One of the most interesting unanswered questions about reef fishes is to what extent color plays a role in predator-prey relationships. In some cases, the concealing function of color in predator and prey species is obvious—flounders, synodontids, groupers, and rockfishes that resemble the substrate, countershaded snappers, and so on. The principles involved are discussed in detail by Cott (63) with numerous examples taken from reef fishes. In some otherwise conspicuous reef fishes, countershading may serve not to conceal the fish but to conceal a conspicuous social signal (123), and it has been suggested that such signals help coordinate interspecific movements such as schooling (186). Many reef fishes also resemble other objects or organisms (212, 215, 302) or have patterns that make it difficult for a predator to fix on the fish when moving rapidly (22). Similarly convergent color patterns (mimicry) in heterotypic diurnal resting schools clearly seem a result of selection by predators (80).

Beyond such observations, however, there is considerable dispute over the significance of coloration in reef fishes. The dispute goes at least as far back as the early years of the century when Reighard (221) concluded that conspicuous colors were without biological significance, and Longley (150–152) argued that most reef fish color patterns served for concealment. More recently, Lorenz (154, 155) claimed that the bright, contrasting "poster colors" of many marine fishes are species-specific sign stimuli that release intraspecific aggression and result in intraspecific territoriality. Lorenz also claimed that these fishes do not change color under various circumstances as do many other fishes (300). This poster coloration is also supposed to provide for species recognition, at least over long range, in the Chaetodontidae (313).

Lorenz appears to have been misled by studying behavior in aquaria where it is often dramatically different from that in nature (e.g. 182, 183). His hypothesis is falsified by a variety of observations. One is that among the most aggressive territorial reef fishes are dull-colored pomacentrids of such genera as *Pomacentrus* and *Eupomacentrus.* Similarly, hamlets (*Hypoplectrus*) fit Lorenz's model in that some of them are brightly colored but some of them are relatively dull-colored and, like many pomacentrids, show interspecific as well as intraspecific territoriality (G. W. Barlow, manuscript).

In contrast, many fishes with spectacular poster colors are not territorial. Many chaetodontids and moorish idols (*Zanclus*)—classic examples of poster coloration —often form feeding assemblages of up to a dozen individuals, (P. Ehrlich, F. Talbot, B. Russell, and G. Anderson, unpublished). These fishes only show interspecific aggression under limited circumstances, especially at close range (<1 m) during crepuscular periods. Their response in nature to both conspecific and heterospecific models is also generally one of curious attraction rather than aggression, and field observations seem to indicate that a major function of their striking colors is to permit pairs or larger groups to assemble when appropriate (P. Ehrlich, F. Talbot, B. Russell, and G. Anderson, unpublished).

Fricke (105, 109) suggested that these colors were species recognition signals in the chaetodontids. This seems unlikely to be the only function, however, when one considers the sympatry of such similar species as *Chaetodon auriga* and *C. vagibundus.* Poster coloration probably does not have a single function (22, 87).

Several other explanations for poster coloration are possible. Cott (63) interpreted the striking dark-light pattern of fishes such as *Dascyllus aruanus* and *Heniochus* sp. as disruptive coloration. In *D. aruanus,* this striking pattern is attractive to conspecifics (103), but whether or not the "disruptive pattern" is functional is in some doubt. My personal observations are that it is not very functional, at least not during most of the day. In the high risk crepuscular period (or to the visual systems of some predators) it may be very effective, and P. F. Sale (personal communication) says that it makes individuals very difficult to see when they are sheltering in coral heads.

There remains the possibility that much poster coloration is aposematic. For instance, I have observed rather large (±10 cm) young french angelfish (*Pomacanthus paru*), which are strikingly colored in black and gold, repeatedly dally unattacked within 1 m or less of large synodontids. Their immunity, however, may be a result of the cleaning behavior of the smaller young with the same pattern. If poster colors were warning colors, one might expect that chaetodontids would be relatively rare in the stomachs of most predators. A check of major works containing stomach content analysis (52, 129, 207, 211, 274) revealed that chaetodontids and the closely related pomacanthids (angelfishes) were virtually absent from the array of prey fishes.

If chaetodontid-pomacanthid coloring is, at least in part, aposematic, one might also expect to find other nonchaetodontid flat-bodied fishes mimicking them. Only one such case has been reported in the literature. Randall & Randall (215) discovered an *Acanthurus* that closely resembled a chrome-yellow *Centropyge* (Pomacanthidae) with a blue eye-ring, a blue line under the mouth, a blue margin on the opercle, and an orange patch just above the base of the tail. They made several attempts to test the *Centropyge* for distastefulness by exposing individuals on lines to predators, with negative results. Although their field experiments were not conclusive, they do indicate that the *Centropyge* was not in a class of distastefulness with grammistids. Direct distastefulness, however, is not the only possible basis for warning coloration. Flattened and armed with spines, pomacanthids and chaetodontids may be difficult targets for many predators to catch or engulf and not generally worth the effort and risk of an attack. J. E. Randall (personal communication) pointed out that the *Acanthurus (A. pyroferus)* which mimics *C. flavissimus,* mimics a *Centropyge, C. vrolikii,* of entirely different appearance at Palau where *C. flavissimus* does not occur. Furthermore, *A. pyroferus* loses the resemblance when it gets larger than *C. vrolikii.* The key element in this system may be the extreme familiarity of the Centropyges with every nook and cranny of their home range. This gives them an advantage over predators not shared by the widely ranging (but equally spiny) *Acanthurus,* and roaming predators, mistaking the latter for *Centropyge,* may decide an attack is not worth the effort.

A point in the argument against aposematic coloring in butterflyfishes and angelfishes is, however, the apparent absence of close Mullerian complexes among them, although many Indo-Pacific species have the same general gestalt, and juveniles of the Atlantic *Pomacanthus paru* and *P. arcuatus* are very similar.

The difficulty predators have in attacking chaetodonids may be enhanced by the frequent presence of eye stripes that tend to conceal the eye, accompanied by false

eyes on the posterior part of the body. With the squarish shape of the fishes and their general slow movements, it may be quite difficult for some predators to decide which end is forward, especially in dim light. These patterns may also serve to protect against hit-and-run predatory attacks of blennies (*Plagiotremus* sp.), which often tear chunks of flesh from the vicinity of the eye (84, 154, 298). Russell worked extensively with the blennies in the field, and believes that chaetodontids are not normally threatened by *Plagiotremus* (B. C. Russell, personal communication). These blennies tend to attack large fishes such as lethrinids and siganids, and bite them on the hind end.

Finally, the spectacular colors of chaetodontids may be a form of "flash coloration." The fishes display a broad, flat "poster" to a predator that disappears when they turn to flee, showing only their narrow posterior aspect or, in some circumstances, a narrow dorsal aspect (123). Interestingly, butterflies display difficult-to-explain poster colors also, but in butterflies we can be sure that these colors rarely, if ever, serve an aggressive purpose, and frequently function as flash colors to deceive predators. Under different conditions, poster patterns on reef fishes may be social signals at one moment and serve as a predator defense at the next.

MIMICRY Mimicry itself is a frequent phenomenon on reefs, often described but sometimes difficult to explain (8, 215). Various hamlets (*Hypoplectrus* spp.) appear to mimic pomacentrids, and I have been momentarily fooled at a distance by the resemblance between the yellowtail hamlet *H. chlorurus* and the yellowtail damselfish, *Microspathodon chrysurus.* (The dark-body, light-tail pattern of these fishes is quite common among reef species, as is the accentuated dark front-half, light rear-half pattern typified by the Caribbean bicolor damselfish, *Eupomacentrus partitus,* the Pacific *Chromis margaritifer,* and some populations of *Acanthochromis polyacanthus.*) It is unlikely that predators willing to attack the largely herbivorous *Microspathodon* would be reluctant to tackle the hamlet—most likely the hamlet more readily approaches its prey disguised as a pomacentrid. Other mimetic pairs include the Pacific saddled puffer, *Canthigaster valenti,* and the saddled filefish, *Paraluteres prionurus;* presumably the latter gains protection when it is mistaken for the poisonous puffer (8). The resemblance of a young *Bodianus* (probably *perdito*) to *Chaetodon ephippum* (49) is more difficult to explain.

The use of eye spots to deflect predator attack has already been mentioned, and such eye spots are frequently found near the base of the caudal fin of many reef fishes or on the dorsal fin. When they are spectacularly developed on the dorsal fin, as in various wrasses (e.g. *Coris aygula, Halichoeres centriquadratus, Anampses twisti*) and juvenile *Bolbometopon bicolor* (Scaridae), the eyespot may, in some situations, be suddenly erected and used to startle predators in much the same way as moths use suddenly exposed eye spots to startle birds (27).

J. E. McCosker (personal communication) recently discovered the use to which at least one reef fish puts its rear eyespot. The Indo-Australian *Calloplesiops altivelis* has a spotted pattern closely resembling that of a sympatric moray eel, *Gymnothorax meleagris.* When alarmed, the fish dashes into a hole in the reef, leaving the rear part of its body exposed. It holds its fins in a manner that exposes the eyespot near

the base of the rear of the dorsal fin. The eye spot, and the attitude of the fins, produces a remarkable simulation of the head of a predaceous moray! Other moray-patterned fishes with rear eye spots, such as *Anampses meleagrides,* may also mimic morays, but appropriate behavior has not been observed.

ATTACK STRATEGIES Against this array of defenses, reef predators mount a variety of attacks (139) ranging from the use of lures (251) and the slow herding of prey into corners by lionfishes (*Pterois*) (108) to the headlong dash of synodontids, groupers, and *Priacanthus* (108, 132). A trumpetfish (*Aulostomus*) will often swim along close to another large fish, using it as cover from which to dash out at prey (87), and groupers follow foraging morays apparently in hope of catching fishes forced into the open by the eel (108). And, of course, predator color patterns have evolved in ways that lessen the chance of detection by prey (e.g. Barlow, 21). Giant Queensland groupers (*Promicrops lanceolatus*) that attain a length of 3 m and a weight of more than a quarter ton sometimes hide in caves and suck fishes weighing several pounds into their mouths (190). Much of the predator activity on many reefs seems to take place in the crepuscular periods as the changeover between day-active and night-active faunas occurs (131, 132, 137, 138, 272).

Cleaning

A very specialized form of predation—the eating of ectoparasites of fishes by small cleaner fishes—forms the center of a most interesting coevolutionary complex on the reef (95). Fishes attacked by ectoparasites have evolved special cleaning postures and color changes when they are solicited by cleaners (84, 95, 148, 156, 203). These serve to make the parasites more obvious and accessible. On reefs, there are two general classes of cleaner fishes. One class is the young of species that are rarely cleaners as adults. Cleaning behavior is frequent in young butterflyfishes, angelfishes, pomacentrids, and wrasses, and is probably always facultative (148, 213). Occasionally, adult chaetodontids (213) and adult wrasses (62) are observed cleaning; and adult pipefishes (Syngnathidae) are now also known to be cleaners (128).

In contrast, two groups of fishes invariably clean as adults and are almost certainly obligatory cleaners. One is the cleaner gobies of the Atlantic (30, 31). Five of twelve species of the subgenus *Elacatinus* of *Gobiosoma* are known to be cleaners and "feed mainly, if not exclusively, on gnathiid isopods that are removed from the bodies, fins, gill chambers and mouths of a wide variety of reef species and fishes that visit reef areas" (30). These small gobies (<3 cm), brightly marked with yellow and black stripes, often set up "cleaning stations" on large sponges, brain, or palmate corals, and are visited by the cleanees. They clean a wide range of fishes, including large piscivores, while the sympatric *Thalassoma bifasciatum,* cleaning while juveniles, is largely restricted to nonpiscivores (66). The *Thalassoma* were devoured by predators in tank experiments, while the gobies were generally spared.

In the Indo-Pacific, wrasses of the genus *Labroides* wear a similar livery and play a similar role (196, 312). The Hawaiian species *Labroides phthirophagus* is an obligate cleaner (312), and all other *Labroides* probably are as well. These cleaner wrasses consume mucus, scales, and dermal and epidermal tissues in addition to

ectoparasites, and they may supplement this cleaning diet with zooplankton (312). Unlike the gobies, however, at least *Labroides dimidiatus* and especially *L. bicolor* do not remain confined to small cleaning stations but move over the reef. At Bora Bora, they were often observed to travel in pairs or small groups, visiting especially the pomacentrids that hold territories (P. Ehrlich and J. P. Holdren, unpublished) in a manner reminiscent of tropical butterflies that "trap-line" from flower to flower gathering pollen (81, 112).

Various authors (105, 106, 156, 297–299, 302) have studied the nexus of signals that mediate the cleaner-cleanee relationship. This interest has been, in part, stimulated by an additional member of the parasite-host-cleaner coevolutionary complex, the cleaner mimic. This mimic, a saber-toothed blenny, *Aspidontus taeniatus,* imitates the appearance and behavior signals of *Labroides* (85, 298, 299, 302) but instead of cleaning the prospective cleanee, *Aspidontus* bites a chunk out of a fin and eats it (interestingly it does not use the saber-teeth in attacking—they are reserved for intraspecific battling). Apparently, the mimetic resemblance is only good enough to fool young or naive fishes; those with more experience learn to avoid the *Aspidontus* (215). The distinction between the behavior of the cleaner and the mimic is blurred, however. On occasion, cleaners will chase and bite fishes without inspecting for parasites (159; B. C. Russell, personal communication).

Many blennies make their living by snatching chunks off larger fishes in hit and run attacks, and are involved in cases of both aggressive and Batesian mimicry (8, 134, 157, 271). These blennies sometimes school with wrasses, which they resemble, dashing at prey from the cover of the school (134). There are also less specialized cleaners than *Labroides* among adult wrasses (213), and the young of many wrasses are cleaners even though the adults are not. Russell (personal communication) thinks that, evolutionarily, cleaning in the wrasses was a natural extension of foraging, the larger fishes simply being treated as additional substrate. This has been followed by more aggressive behavior on the part of *Labroides,* the *Aspidontus* pattern of mimicry, and, finally, the rapid "dash-from-a-hole, take-a-bite, and retreat-to-the-hole" behavior seen in some members of the blenniid genus *Plagiotremus.*

Many questions remain, however, about the present evolutionary state of the *Labroides-Aspidontus* complex, just as they do about all terrestrial mimetic associations (79). Is the mimic putting any selective pressure on the model by increasing the frequency with which *Labroides* are eaten, or by driving away prospective cleanees? If the former were occurring, one might find that where *Aspidontus* is common, *L. dimidiatus* looks slightly more different from *Aspidontus* than it does where *Aspidontus* is rare. To enhance cleanee discrimination the *Labroides* should evolve away from the *Aspidontus* pattern as rapidly as possible without losing its basic cleaner livery.

There should be plenty of flexibility in the system, since the general appearance of the *L. dimidiatus* (as opposed to its detailed appearance) would seem to be enough to announce "cleaner." A Caribbean grouper in an aquarium recognized *L. dimidiatus* as a cleaner even though it had never seen one (125) and naive Pacific fishes recognize *Gobiosoma* (30). Presumably prior experience with the cleaners in

the grouper's home waters was sufficient—indeed recognition of the highly specialized pattern of the cleaners is probably part of the genetic repertoire of piscivores (66). In theory, *Labroides* might be able to evolve a sufficiently different garb to permit cleanees to discriminate between relatively painless cleaners (*L. dimidiatus*) and painful ones (*Aspidontus*), but there is considerable anecdotal evidence that *Aspidontus* can evolve rapidly enough to "stay even" in the evolutionary race.

COMMUNITY ECOLOGY

One question that remains partly open concerns the effects of cleaning symbioses, both those involving cleaner fishes and those involving cleaner shrimp (121, 228), on the diversity of the fish community. Limbaugh claimed (148) that cleaning symbioses were more common in tropical than in temperate waters, and that removing cleaners led to a rapid decline in the diversity of fishes present on the reef. Hobson (135), however, strongly questioned the assumption that tropical communities have a higher proportion of cleaners, and, indeed, numerous cases of cleaning in temperate marine (136, 148) and freshwater (4) fishes are coming to light.

Limbaugh's experiment of removing the cleaners from a reef has been repeated several times (158, 312) without resulting in a decline in diversity. Partial removal of cleaners did, however, lead to an increase in the cleaning behavior of those remaining, as well as changes in the behavior of the cleanees and the behavior and distribution of the remaining cleaners (158, 159). Interestingly, Losey found no increase in the number of ectoparasites (compared with a control reef) after cleaner removal. Further cleaner removal experiments certainly should be carried out in a variety of reef situations.

Whatever their effect on total reef diversity, the presence of cleaners leads to high "point diversity." Slobodkin & Fishelson (261) found that the larger nonterritorial diurnal fish species of the reef tended to aggregate at cleaning stations. These fish species make up about one fourth of the species found on the reef. Thus cleaners form a biological focus of diversity analogous to physical foci such as deep holes and areas of great geometric complexity.

More general studies of reef fish communities using a wide variety of collecting and observational techniques are numerous (5, 13, 17, 55, 61, 62, 69, 116, 118, 143, 176, 191, 263–265, 284, 291) and have painted a reasonably complete picture of the structure of these communities. Carnivores are much more diverse than herbivores or omnivores, but on large reefs the latter two may dominate both by numbers and weight (17, 129, 176). In contrast, carnivores made up more than 50% of the fauna (by weight) in the Virgin Islands (205) and Tanganyika (284). The problem of partitioning the reef fish fauna into carnivores, omnivores, and herbivores is difficult because of sampling problems (284), and compounded because many fishes take refuge on the reef but feed on adjacent sand flats or in the water column (69, 205, 280).

Perhaps the best general description of the way the reef fish fauna is fitted to the reef is "crammed." One interesting bit of evidence for this is the one-way migration of fish species from the crowded reefs of the Red Sea through the Suez Canal.

Mediterranean fishes have been notably unsuccessful at penetrating the reef fauna (9). There are essentially two shifts of fishes on the reefs, day and night, with a time of great activity in the dawn and dusk turnover period (26, 62, 101, 131–133, 149, 247, 272, 273), as the fishes respond to changing light levels (62) in a species-specific sequence (74, 83). Detailed studies of the sharing of resources by reef fish species (264–266, 293) have led to the conclusion that space itself "may play a major, if not decisive role in maintaining numerical stability in coral reef fish communities" (264). An excellent example of this is the severe limitation of populations of saber-toothed blennies, *Plagiotremus* (*Runula*), by the availability of suitable holes for shelter and nest sites. (B. C. Russell, personal communication). These slender predators have highly specific requirements for the size and shape of holes they occupy. By providing suitable artificial nest blocks, Russell has been able to produce an approximate doubling in the populations of two species (*P. rhynorhynchos, P. tapeinosoma*).

The limitations of space are increased by the inter- and intraspecific territorial behavior of so many species, discussed earlier, and seem fundamental to the evolution of many major features of the reef fish fauna. For example, the guilds of grazers (23, 142, 295) might be thought of as largely a function of the finite area available for the growth of algae.

It is difficult to imagine how more species could enter many reef faunas, especially in the "day shift," which is relatively crowded compared to the night (62). The Shannon-Weaver diversity index for the fish community at the Virgin Islands Tektite site was 3.3154 based on individuals and 3.0056 based on biomass; the lower biomass figure reflects the great size of individuals of a few species (264). If, for instance, the large *Scarus vetula* could be replaced by several smaller herbivores, then the reef fish diversity could be increased.

It is, however, impossible to determine whether or not a reef fish fauna is saturated with species without doing field experiments. Similarly the conjecture that reef transients are generally r-selected and residents k-selected (264) will have to await further studies, especially of reproductive biology, for confirmation.

Workers in Australia have recently been making rapid progress toward elucidating both the structure of coral reef fish communities and the causes of their extraordinary species diversity. Extensive work on One Tree Island at the southern end of the Great Barrier Reefs (116, 286, 287) has shown striking differences in fish fauna and fish biomass in ecologically different regions of the reef (e.g. windward and leeward slopes, reef crest, transition to inter-reef ocean bottom, etc). In spite of this general site specificity, however, the precise fauna on a given site within a habitat seems governed largely by chance factors (233, 241; P. Sale, manuscript). On artificial reefs (233), for instance, at least at the southern end of the barrier where breeding is highly seasonal, the physical structure of the reef is relatively unimportant in determining at least the initial species composition of the community.

Sale's work (241; manuscript) on a guild of pomacentrids similarly indicated that random processes involved in removal and recruitment tend to determine which of several highly territorial species occupy a given rubble patch on the reef. Indeed, the growing consensus of the "Australian school" seems that the prevalent notion that high diversity on reefs is possible because of the narrow niches of the species

is false, and that many reef fish species are generalists. Apparently diversity is maintained in the face of limited space by a pattern of steady high mortality and random recruitment (the latter mostly from pelagic young). Talbot (285) and Russell and Talbot (manuscript) suggested along these lines that high tropical diversity in fish faunas exists largely because there has been a great deal of time during which reefs have remained much the same. Presumably this has permitted the allopatric evolution of numerous species to fill broad niches; species that have been able to become and remain sympatric on high productivity reefs because of the patchwork nature of the environment and the stochastic recruitment-loss processes. This pattern agrees with the theoretical conclusion of Levin (147) that heterogeneity may be introduced in homogeneous environments by random colonization events.

An area of considerable importance to the community ecology of reefs that needs much more investigation is the mode of communication among reef species. Visual communication is common (60) but sound and smell may play an important role in the lives of reef fishes (42, 171, 288, 309). Indeed, considering the chemoreceptive abilities of sharks, it seems likely that the reef community is bound together by a web of pheromones and other chemical cues that have not yet even begun to be unravelled.

Reef fishes have virtually been omitted as sources of data to test mathematical theory of community ecology. The only study that has come to my attention is that of Roughgarden (231), who used Randall's (207, 208) data on food habits of Caribbean fishes to illustrate his models of "species packing."

Not only does the structure of the reef influence the structure of the fish community, but the reverse is also true. Fishes, especially scarids, plectognaths, and some pomacentrids (114), destroy coral during their feeding, and are important in bioerosive processes on the reef. They retard coral growth and open corals to invasion by algae (113). In fact, these fishes are a major factor in converting coral reefs into coral sand (18). Ogden and Gerhard (manuscript), for example, estimated that, in Panama, parrotfishes generated an estimated 0.5 kg m^{-2} yr^{-1} carbonate sediment. Overfishing may dramatically change the flora and benthic fauna of the reef (242; J. Ogden, personal communication). This is just one example of the diverse human activities that threaten these fascinating and productive ecosystems (100, 140).

CONCLUSION—REEF FISHES AND BUTTERFLIES

At this point, the major reason for the dramatically different taxonomic structure of reef fishes and butterflies is clear. The reef fishes are a sample of all teleostean fishes, organisms that play a vast array of ecological roles. Even a cursory survey of their morphology reveals a diversity to match these roles. In contrast, the butterflies are a sample of a huge (±200,000 species) order of insects that is almost entirely herbivorous. They are the major group to penetrate the daytime aerial niche as adults; unlike reef fishes, butterflies have no "night shift." Interesting questions remain, however. Why, for instance, can one find more than two dozen species of chaetodontids sympatrically on the Great Barrier Reef, with more than a dozen

mingling together in small areas, when such concentrations of congeners seem very rare in the much smaller butterflies?

Population structure and dynamics are better understood in the butterflies (83) than in the reef fishes, but both groups appear to have relatively sedentary adults and populations subject to rather frequent extinction. In the fishes, however, lack of information on gene flow makes it difficult to state whether disappearance of a species from a section of reef means the end of a mendelian population or merely of a local subunit of such a population. Similarly, although it is now clear that many butterfly populations remain genetically similar because they are under similar selection pressures (83), we do not have enough information to make such statements about the fishes.

Butterflies are known to sequester poisons from their plant food that help protect them from vertebrate predators (47). Little is known about the origins of fish poisons. Although most appear to be endogenous, the ciguatera situation suggests that at least some of the toxins may be derived from the fish's food.

Both groups tend to have bright "poster colors" that have not been entirely explained. Both also have numerous members involved in mimicry—the butterflies apparently more so than the fishes. This may be explained by the frequent use of highly poisonous food plants (82) and the likelihood that, to one degree or another, all butterflies are distasteful (C. L. Remington, personal communication).

At the community level, much more has been done with the fishes than with the butterflies, and the progress made in explaining reef fish diversity suggests that more efforts should be made toward uncovering the determinants of butterfly community composition. The work that has been done on butterflies (252) indicates that, at least in temperate zones, they show much less habitat selection than do the fishes. How can this observation be related to the different phenetic patterns of the two groups? It seems likely that the availability of a diverse array of food plants has presented the butterflies with the evolutionary opportunity to radiate into numerous large complexes of closely related species. But, where any given food plant is widely distributed, adult butterflies can move about their business with few restrictions, since predation pressure on them is generally light. In contrast, much of the behavior of reef fishes seems substrate-oriented because of strong predation pressure. Habitat selection then becomes critical since food and other requisites of life must be found in close proximity to suitable shelter.

Acknowledgments

I wish to thank Gordon Anderson, George W. Barlow, Anne H. Ehrlich, Richard W. Holm, John E. McCosker, John C. Ogden, John E. Randall, Jonathan Roughgarden, Barry C. Russell, Peter F. Sale, Michael E. Soulé, Frank H. Talbot, J. C. Tyler, and Evelyn Shaw-Wertheim, all of whom have reviewed the manuscript, made most helpful comments, and, in many cases, given me access to their unpublished results. J. Howard Choat was kind enough to supply me with two of his unpublished manuscripts. Margaret Craig and her staff at the Stanford Biology Library were extremely helpful in running down sources, and Darryl Wheye showed great patience in helping me prepare the manuscript.

Literature Cited

1. Abel, E. 1960. Fische zwischen Seeigel-Stacheln. *Natur Volk* 90:33–37
2. Abel, E. 1960. Zur Kenntnis des Verhaltens und der Ökologie von Fischen on Korallenriffen bei Ghardaga (Rotes Meer). *Z. Morph. Oekol. Tiere* 48:430–503
3. Abel, E. 1961. Freiwasserstudien über das Fortpflanzungsverhalten des Mönchfisches *Chromis chromis* Linné, einem Vertreter der Pomacentriden im Mittelmeer. *Z. Tierpsychol.* 18:441–9
4. Abel, E. 1971. Zur Ethologie von Putzsymbiosen unheimischer Süsswasserfische im natürlichen Biotop. *Oecologia* 6:133–51
5. Abel, E. 1972. Problem der Ökologischen definition des "Korallenfisches." *Proc. Symp. Corals Coral Reefs, 1969, Mar. Biol. Assoc. India* 449–56
6. Albrecht, H. 1969. Behaviour of four species of Atlantic damselfishes from Colombia, South America (*Abudefduf saxatilis, A. taurus, Chromis multilineata, C. cyanea;* Pisces, Pomacentridae). *Z. Tierpsychol.* 26:662–76
7. Allen, G. R. 1972. *The Anemonefishes: Their Classification and Biology.* Neptune City, NJ: TFH Publ. 288 pp.
8. Allen, G. R., Russell, B. C., Carlson, B. A., Starck, W. H. 1975. Mimicry in marine fishes. *Trop. Fish Hobbyist.* In press
9. Aron, W. I., Smith, S. H. 1971. Ship canals and aquatic ecosystems. *Science* 174:13–20
10. Bakus, G. J. 1964. The effects of fish grazing on invertebrate evolution in shallow tropical waters. *Allan Hancord Found. Publ. Occas. Pap. No. 27.* 22 pp.
11. Bakus, G. J. 1966. Some relationships of fishes to benthic organisms on coral reefs. *Nature* 210:280–84
12. Bakus, G. J. 1967. The feeding habits of fishes and primary production at Eniwetok, Marshall Islands. *Micronesica* 3:135–49
13. Bakus, G. J. 1969. Energetics and feeding in shallow marine waters. *Int. Rev. Gen. Exp. Zool.* 4:275–369
14. Bakus, G. J. 1972. Effects of the feeding habits of coral reef fishes on the benthic biota. *Proc. Symp. Corals Coral Reefs, 1964, Mar. Biol. Assoc. India* 445–48
15. Bakus, G. J., Green, G. 1974. Toxicity in sponges and holothurians: a geographic pattern. *Science* 185:951–53
16. Bardach, J. E. 1958. On the movements of certain Bermuda reef fishes. *Ecology* 39:139–46
17. Bardach, J. E. 1959. The summer standing crop of fish on a shallow Bermuda reef. *Limnol. Oceonogr.* 4:77–85
18. Bardach, J. E. 1961. Transport of calcareous fragments by reef fishes. *Science* 133:98–99
19. Bardach, J. E., Menzel, D. W. 1956. Field and laboratory observations on the growth of some Bermuda reef fisheries. *Proc. Gulf Carib. Fish. Inst., 9th Ses.* 106–13
20. Bardach, J. E., Winn, H. E., Menzel, D. W. 1959. The role of the senses in the feeding of the nocturnal reef predators *Gymnothorax moringa* and *G. vicinus. Copeia* 1959:133–39
21. Barlow, G. W. 1967. The functional significance of the split-head color pattern as exemplified in a leaf fish, *Polycentrus schomburgkii. Ichthyol./Aquar. J.* April–June: 57–70
22. Barlow, G. W. 1972. The attitude of fish eye-lines in relation to body shape and to stripes and bars. *Copeia* 1972: 4–12
23. Barlow, G. W. 1974. Contrasts in social behavior between Central American cichlid fishes and coral-reef surgeon fishes. *Am. Zool.* 14:9–34
24. Barlow, G. W. 1975. Extraspecific imposition of social grouping among surgeon fishes. *J. Zool.* 174:In press
25. Bartholomew, B. 1970. Bare zone between California shrub and grassland communities: the role of animals. *Science* 170:1210–12
26. Bertram, B. C. R. 1965. The behaviour of Maltese fishes by day and night. *Rep. Underwater Assoc. Malta* 1:39–41
27. Blest, A. D. 1957. The function of eyespot patterns in the Lepidoptera. *Behaviour* 11:209–56
28. Boden, B. P. 1952. Natural conservation of insular plankton. *Nature* 169:697–99
29. Böhlke, J. E., Chaplin, C. C. G. 1968. *Fishes of the Bahamas and Adjacent Tropical Waters.* Wynnewood: Livingston. 771 pp.
30. Böhlke, J. E., McCosker, J. E. 1973. Two additional West Atlantic gobies (genus *Gobiosoma*) that remove ectoparasites from other fishes. *Copeia* 1973:609–10
31. Böhlke, J. E., Robins, C. R. 1968. Western Atlantic seven-spined gobies, with descriptions of two new species and a new genus, and comments on Pacific

relatives. *Proc. Acad. Nat. Sci. Philadelphia* 120:45–175
32. Breder, C. M. 1948. Observation on coloration in reference to behavior in tide pool and other marine shore fishes. *Bull. Am. Mus. Natur. Hist.* 92:285–311
33. Breder, C. M. 1954. Equations descriptive of fish schools and other animal aggregations. *Ecology* 35:361–70
34. Breder, C. M. 1959. Studies of social groupings in fishes. *Bull. Am. Mus. Natur. Hist.* 117:397–481
35. Breder, C. M. 1963. Defensive behavior venom in *Scorpaena* and *Dactylopterus. Copeia* 1963:698–700
36. Breder, C. M. 1965. Vortices and fish schools. *Zoologica* 50:97–114
37. Breder, C. M. 1967. On the survival value of fish schools. *Zoologica* 52: 25–40
38. Breder, C. M., Rosen, D. E. 1966. *Modes of Reproduction in Fishes.* New York: Natural History Press. 941 pp.
39. Breedlove, D. E., Ehrlich, P. R. 1968. Plant-herbivore coevolution: lupines and lycaenids. *Science* 162:671–72
40. Breedlove, D. E., Ehrlich, P. R. 1972. Coevolution: patterns of legume predation by a lycaenid butterfly. *Oecologia* 10:99–104
41. Briggs, J. C. 1967. Relationships of the tropical shelf regions. *Stud. Trop. Oceanogr.* 5:569–92
42. Bright, T. J. 1972. Bio-acoustic studies on reef organisms. *Results of the Tektite Program: Ecology of Coral Reef Fishes, Bull. Natur. Hist. Mus. L. A.* 14:45–69
43. Brinley, F. J. 1939. Spawning habits and development of beau-gregory (*Pomacentrus leucostictus*). *Copeia* 1939:185–88
44. Brock, V. E. 1954. A preliminary report on a method of estimating reef fish populations. *J. Wildl. Manage.* 18:297–308
45. Brock, V. E., Riffenburgh, R. H. 1960. Fish schooling: a possible factor in reducing predation. *J. Cons. Perm. Int. Explor. Mer.* 25:307–17
46. Brockmann, H. J. 1973. The function of poster-coloration in the beaugregory, *Eupomacentrus leucostictus* (Pomacentridae, Pisces). *Z. Tierpsychol.* 33:13–34
47. Brower, L. P. 1970. Plant poisons in a terrestrial food chain and implications for mimicry theory. In *Biochemical Coevolution,* ed. K. L. Chambers, 69–82. Corvallis: Univ. Oregon
48. Buckman, N. S., Ogden, J. C. 1973. Territorial behavior of the striped parrotfish *Scarus croicensis* Block (Scaridae) *Ecology* 54:1377–82
49. Burgess, W., Axelrod, H. R. 1971. *Pacific Marine Fishes, Book 2.* Neptune City, NJ: TFH Publ.
50. Cahn, P. H., Shaw, E. 1963. Schooling fishes: the role of sensory factors. *Anim. Behav.* 11:405–6
51. Chaplin, C. G., Scott, P. 1972. *Fishwatchers Guide to West Atlantic Coral Reefs.* Wynnewood: Livingston. 65 pp.
52. Choat, J. H. 1968. Feeding habits and distribution of *Plectropomus maculatus. Proc. R. Soc. Queensl.* 80:13–17
53. Clark, E. 1959. Functional hermaphroditism and self-fertilization in a serranid fish. *Science* 129:215–16
54. Clark, E. 1965. Mating of groupers. *Natur. Hist.* 74:22–25
55. Clark, E., Ben-Tuvia, A., Steinitz, H. 1968. Observations on a coastal fish community, Dahlak Archipelago, Red Sea. *Sea Fish. Res. Sta. Haifa Bull.* 49:15–31
56. Clark, E., Chao, S. 1972. A toxic secretion from the Red Sea flatfish *Pardachirus marmoratus* (Lacépède). *Hebr. Univ. Jerusalem, Steinitz Mar. Lab. Sci. Newslett. No. 2,* p. 14
57. Clarke, T. A. 1970. Territorial behavior and population dynamics of a pomacentrid fish, the Garibaldi, *Hypsypops rubicunda. Ecol. Monogr.* 40:189–212
58. Clarke, T. A., Flechsig, A. O., Grigg, R. W. 1967. Ecological studies during Project Sealab II. *Science* 157:1381–39
59. Cohen, D. 1970. How many recent fishes are there? *Proc. Calif. Acad. Sci.* 38:341–46
60. Colin, P. L. 1971. Interspecific relationships of the yellowhead jawfish, *Opistognathus aurifrons* (Pisces, Opistognathidae). *Copeia* 1971:469–73
61. Colin, P. L. 1974. Mini-prowlers of the night reef. *Sea Frontiers* 20:139–45
62. Collette, B. B., Talbot, F. H. 1972. Activity patterns of coral reef fishes with emphasis on nocturnal-diurnal changeover. *Results of the Tektite Program: Ecology of Coral Reef Fishes, Bull. Natur. Hist. Mus. L.A.* 14:98–124
63. Cott, H. B. 1940. *Adaptive Coloration in Animals.* London: Methuen. 508 pp.
64. Crespigny, C. C. de 1869. Notes on the friendship existing between the malacopterygian fish *Premnas biaculeatus* and the *Actinia crassicornis. Proc. Zool. Soc. London* 1869:248–49
65. Cummings, W. C., Brahy, B. D., Spires, J. Y. 1966. Sound production, schooling, and feeding habits of the margate, *Haemulon album* Cuvier, off North

Bimini, Bahamas. *Bull. Mar. Sci.* 16:626–40
66. Darcy, G. H., Maisel, E., Ogden, J. C. 1974. Cleaning preferences of the gobies *Gobiosoma evelynae* and *G. prochilos* and the juvenile wrasse *Thalassoma bifasciatum. Copeia* 1974:375–79
67. Davenport, D., Norris, K. S. 1958. Observations on the symbiosis of the sea anemone *Stoichactes* and the pomacentrid fish *Amphiprion percula. Biol. Bull.* 115:397–410
68. Davis, W. P. 1967. *Ecological interactions, comparative biology and evolutionary trends of thirteen pomadasyid fishes at Alligator Reef, Florida Keys.* PhD dissertation. Univ. Miami, Miami, Fla. 94 pp.
69. Davis, W. P., Birdsong, R. S. 1973. Coral reef fishes which forage in the water column. *Helgol. Wiss. Meeresunter.* 24:292–306
70. Dawson, E. Y., Aleem, A. A., Halstead, B. W. 1955. Marine algae from Palmyra Island with special reference to the feeding habits and toxicology of reef fishes. *Allan Hancock Found. Occas. Pap. No. 17.* 39 pp.
71. Day, J. H. 1963. Complexity in the biotic environment. *Speciation in the Sea, Syst. Assoc. Publ. No. 5,* 31–49
72. Delsman, H. C. 1930. Fish eggs and larvae from the Java Sea, 16. *Amphiprion percula. Treubia* 12:367–70
73. Dolinger, P. M., Ehrlich, P. R., Fitch, W. L., Breedlove, D. E. 1973. Alkaloid and predation patterns in Colorado lupine populations. *Oecologie* 13:141–204
74. Domm, S. B., Domm, A. J. 1973. The sequence of appearance at dawn and disappearance at dusk of some coral reef fishes. *Pac. Sci.* 27:128–35
75. Doty, M. S., Santos, G. A. 1966. Caulerpicin, a toxic constituent of *Caulerpa. Nature* 211–440
76. Earle, S. A. 1972. The influence of herbivores on the marine plants of Great Lameshur Bay, with an annotated list of plants. *Results of the Tektite Program: Ecology of Coral Reef Fishes, Bull. Natur. Hist. Mus. L.A.* 14:17–44
77. Ebert, E. E., Turner, C. H. 1962. The nesting behavior, eggs and larvae of the bluespot goby. *Calif. Fish Game* 48:249–52
78. Ehrlich, P. R. 1958. The comparative morphology, phylogeny and higher classification of the butterflies (Lepidoptera: Papilionoidea). *Univ. Kansas Sci. Bull.* 39:305–70
79. Ehrlich, P. R. 1970. Coevolution and the biology of communities. *Biochemical Coevolution,* ed. K. L. Chambers, 1–11. Corvallis: Oregon State Univ. Press
80. Ehrlich, P. R., Ehrlich, A. H. 1973. Coevolution: heterotypic schooling in Caribbean reef fishes. *Am. Natur.* 107:157–60
81. Ehrlich, P. R., Gilbert, L. E. 1973. Population structure and dynamics of the tropical butterfly *Heliconius ethilla. Biotropica* 5:69–82
82. Ehrlich, P. R., Raven, P. H. 1965. Butterflies and plants: a study in coevolution. *Evolution* 18:586–608
83. Ehrlich, P. R., White, R. R., Singer, M. C. Gilbert, L. E., McKechnie, S. W. 1975. Checkerspot butterflies: a historical perspective. *Science.* 188:221–28
84. Eibl-Eibesfeldt, I. 1955. Über Symbiosen, Parasitismus und andere besondere zwischenartliche Beziehungen tropischer Meeresfische. *Z. Tierpsychol.* 12:203–19
85. Eibl-Eibesfeldt, I. 1959. Der Fisch *Aspidontus taeniatus* als Nachahmer des Putzers *Labroides dimidiatus. Z. Tierpsychol.* 16:19–25
86. Eibl-Eibesfeldt, I. 1960. Beobachtungen und Versuche on Anemonenfischen (Amphiprion) der Malediven und der Nicobaren. *Z. Tierpsychol.* 17:1–10
87. Eibl-Eibesfeldt, I. 1962. Freiwasserbeobachtungen zur Deutung des Schwarmverhaltens verschiedener Fische. *Z. Tierpsychol.* 19:165–82
88. Eibl-Eibesfeldt, I. 1965. *Land of a Thousand Atolls.* London: Macgibbon & Kee. 195 pp.
89. Eisner, T. 1970. Chemical defense against predation in arthropods. *Chemical Ecology,* ed. E. Sondheimer, J. B. Simeone, 157–217. New York: Academic
90. Eisner, T., Meinwald, J. 1966. Defensive secretions of arthropods. *Science* 153:1341–50
91. Emery, A. R. 1968. Preliminary observations on coral reef plankton. *Limnol. Oceanogr.* 13:293–303
92. Endean, R., Stephenson, W., Kenny, R. 1956. The ecology and distribution of intertidal organisms on certain islands off the Queensland coast. *Austr. J. Mar. Freshwater Res.* 7:317–42
93. Feddern, H. A. 1965. The spawning, growth, and general behavior of the bluehead wrasse, *Thalassoma bifasciatum* (Pisces: Labridae). *Bull. Mar. Sci.* 15:896–941

94. Feddern, H. A. 1968. *Systematics and ecology of western Atlantic angelfishes, family Chaetodontidae, with an analysis of hybridization in Holacanthus.* PhD dissertation. Univ. Miami, Miami, Fla. 117 pp.
95. Feder, H. M. 1966. Cleaning symbiosis in the marine environment. In *Symbiosis, Vol. 1,* ed. S. M. Henry, 327–80. New York: Academic
96. Fishelson, L. 1963. Observations on the biology and behaviour of Red Sea coral fishes. *Sea Fish. Res. Sta. Haifa Bull.* 37:11–26
97. Fishelson, L. 1965. Observations and experiments on the Red Sea anemones and their symbiotic fish *Amphiprion bicinctus. Bull. Sea Fish. Res. Sta. Haifa. Bull.* 39:1–14
98. Fishelson, L. 1970. Behavior and ecology of a population of *Abudefduf saxatilis* (Pomacentridae, Teleostei) at Eliat (Red Sea). *Anim. Behav.* 18: 225–37
99. Fishelson, L. 1970. Protogynous sex reversal in the fish *Anthias squamipinnis* (Teleostei, Anthiidae) regulated by the presence or absence of a male fish. *Nature* 227:40–41
100. Fishelson, L. 1973. Ecology of coral reefs in the Gulf of Aqaba (Red Sea) influenced by pollution. *Oecologia* 12:55–67
101. Fishelson, L., Popper, D., Ganderman, N. 1971. Diurnal cyclic behaviour of *Pempheris oualensis* Cuv. and Val. (Pempheridae, Teleostei). *J. Natur. Hist.* 5:503–6
102. Fraenkel, G. 1959. The raison d'etre of secondary plant substances. *Science* 129:1466–70
103. Franzisket, L. 1959. Experimentelle Untersuchung über die optische Wirkung der Streifung beim Preussenfisch (*Dascyllus aruanus*). *Behaviour* 15: 77–81
104. Fraser-Brunner, A. 1950. *Holacanthus xanthotis* sp. n. and other chaetodont fishes from the Gulf of Aden. *Proc. Zool. Soc. London* 120:43–48
105. Fricke, H. 1966. Attrappenversuche mit einigen plakatfarbigen Korallenfischen im Roten Meer. *Z. Tierpsychol.* 23:4–7
106. Fricke, H. 1966. Zum Verhalten des Putzerfisches, *Labroides dimidiatus. Z. Tierpsychol.* 23:1–3
107. Fricke, H. 1971. Fische als Feinde tropischer Seeigel. *Mar. Biol.* 9:328–38
108. Fricke, H. 1972. *The Coral Seas.* New York: Putnam. 224 pp.
109. Fricke, H. 1973. Behaviour as part of ecological adaptation—in situ studies in the coral reef. *Helgol. Wiss. Meeresunter.* 24:120–44
110. Garnaud, J. 1951. Nouvelles données sur l'éthologie d'un pomacentride: *Amphiprion percula Lacépède. Bull. Inst. Oceanogr. (Monaco).* 48:1–11
111. Garnaud, J. 1957. Ethologie de *Dascyllus trimaculatus* (Ruppell). *Bull. Inst. Oceanogr. Monaco* 54:1–10
112. Gilbert, L. E. 1972. Pollen feeding and reproductive biology of *Heliconius* butterflies. *Proc. Nat. Acad. Sci. USA* 69:1403–7
113. Glynn, P. W., Stewart, R. H., McCosker, J. E. 1972. Pacific coral reefs of Panama: structure, distribution and predators. *Geol. Rundsch.* 61:483–519
114. Glynn, P. W. 1973. Aspects of the ecology of coral reefs in the western Atlantic region. In *Biology and Geology of Coral Reefs,* ed. O. A. Freedman, R. Endean, 271–324. New York: Academic
115. Gohar, H. A. F. 1934. Partnership between fish and anemone. *Nature* 134:291
116. Goldman, B. 1973. *Aspects of the ecology of the coral reef fishes of One Tree Island.* PhD dissertation. Macquarie Univ., Sydney, Australia. 193 pp.
117. Gosline, W. A. 1953. The nature and evolution of the Hawaiian inshore fish fauna. *Proc. Pac. Sci. Cong., 8th Philippines,* 3:347–58
118. Gosline, W. A. 1965. Vertical zonation of inshore fishes in the upper water layers of the Hawaiian Islands. *Ecology* 46:823–31
119. Gosline, W. A., Brock, V. E. 1960. *A Handbook of Hawaiian Fishes.* Honolulu: Univ. Hawaii Press. 377 pp.
120. Greenwood, P. H., Rosen, D. E., Weitzman, S. H., Myers, G. S. 1966. Phyletic studies of the teleostean fishes, with a provisional classification of living forms. *Bull. Am. Mus. Natur. Hist.* 131:341–455
121. Grobe, J. 1960. Putz-Symbiosen zwischen Fischen und Garnelen. *Natur Volk* 90:152–57
122. Gudger, E. W. 1941. Coelenterates as enemies of fishes. IV. Sea anemones and corals as fish eaters. *New England Natur.* 10:1–8
123. Hamilton, W. J. III., Peterman, R. M. 1971. Countershading in the colourful reef fish *Chaetodon lunula*: concealment, communication or both? *Anim. Behav.* 19:357–64

124. Hartline, A. C., Hartline, P. H., Szmant, A. M., Flechsig, A. O. 1972. Escape response in a pomacentrid reef fish, *Chromis cyaneus. Results of the Tektite Program: Ecology of Coral Reef Fishes, Bull. Nat. Hist. Mus. L.A.* 14:93–97
125. Hediger, H. 1968. Putzer-fische in Aquarium. *Natur. Mus.* 98:89–96
126. Helfrich, P. 1958. *The early life history and reproductive behavior of the mao-mao, Abudefduf abdominalis (Quoy and Gaimard).* PhD dissertation. Univ. Hawaii, Honolulu. 207 pp.
127. Herald, E. S. 1961. *Living Fishes of the World.* Garden City, NY: Doubleday. 304 pp.
128. Herald, E. S., Randall, J. E. 1972. Five new Indo-Pacific pipefishes. *Proc. Calif. Acad. Sci.* 39:121–40
129. Hiatt, R. W., Strasburg, D. W. 1960. Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. *Ecol. Monogr.* 30:65–127
130. Hinton, S. 1962. Unusual defense movements in *Scorpaena plumieri mystes. Copeia* 1962:842
131. Hobson, E. S. 1965. Diurnal-nocturnal activity of some inshore fishes in the Gulf of California. *Copeia* 1965:291–302
132. Hobson, E. S. 1968. Predatory behavior of some shore fishes in the Gulf of California. *Res. Rep. 73 Bur. Sport Fish. Wildl.,* 1–92
133. Hobson, E. S. 1968. Coloration and activity of fishes, day and night. *Underwater Natur.* Winter:6–11
134. Hobson, E. S. 1969. Possible advantages to the blenny *Runula azalea* in aggregating with the wrasse *Thalassoma lucasanum* in the tropical Western Pacific. *Copeia* 1969:191–93
135. Hobson, E. S. 1969. Comments on certain recent generalizations regarding cleaning symbiosis in fishes. *Pac. Sci.* 23:35–39
136. Hobson, E. S. 1971. Cleaning symbiosis among California inshore fishes. *Fish. Bull.* 69:491–523
137. Hobson, E. S. 1972. Activity of Hawaiian reef fishes during the evening and morning transitions between daylight and darkness. *Fish. Bull.* 70:715–40
138. Hobson, E. S. 1973. Diel feeding migrations in tropical reef fishes. *Helgo. Wiss. Meeresunter.* 24:361–70
139. Hobson, E. S. 1974. Feeding relationships of teleostean fishes on coral reefs in Kona, Hawaii. *Fish. Bull.* 72:915–1031
140. Johannes, R. E. 1972. Coral reefs and pollution. In *Marine Pollution and Sea Life,* ed. M. Ruivo. London: Fishing News Books
141. Johnson, M. W. 1959. The offshore drift of larvae of the California spiny lobster *Panulirus interruptus. Calif. Coop. Oceanic Fish. Invest. Rep.* 7:147–61
142. Jones, R. S. 1968. Ecological relationships in Hawaiian and Johnston Island Acanthuridae (surgeonfishes). *Micronesica* 4:309–61
143. Jones, R. S., Randall, R. H., Cheng, Y., Kami, H. T., Mak, S. 1972. A marine biological survey of southern Taiwan with emphasis on corals and fishes. *Inst. Oceanogr. Nat. Taiwan Univ. Spec. Publ. No. 1*
144. Keenleyside, M. H. A. 1972. The behaviour of *Abudefduf zonatus* (Pisces, Pomacentridae) at Heron Island, Great Barrier Reef. *Anim. Behav.* 20:763–74
145. Lachner, E. A. 1955. Inquilinism and a new record for *Paramia bipunctata,* a cardinal fish from the Red Sea. *Copeia* 1955:53–54
146. Lack, D. 1968. *Ecological Adaptations for Breeding in Birds.* London: Methuen. 409 pp.
147. Levin, S. 1974. Dispersion and population interactions. *Am. Natur.* 108: 207–28
148. Limbaugh, C. 1964. Notes on the life history of two California pomacentrids: garibaldis, *Hypsypops rubicunda* (Gerard), and blacksmiths, *Chromis punctipinnis* (Copper). *Pac. Sci.* 18:41–50
149. Livingston, R. T. 1971. Circadian rhythms in the respiration of eight species of cardinal fishes (Pisces: Apogonidae); comparative analysis and adaptive significance. *Mar. Biol.* 9:253–66
150. Longley, W. H. 1914. Report upon color of fishes of the Tortugas reefs. *Carnegie Inst. Washington, Yearb.* 13:207–8
151. Longley, W. H. 1915. Coloration of tropical reef fishes. *Carnegie Inst. Washington Yearb.* 14:208–9
152. Longley, W. H. 1916. The significance of the colors of tropical reef fishes. *Carnegie Inst. Washington Yearb.* 15:209–12
153. Longley, W. H., Hildebrand, S. F. 1941. Systematic catalogue of the fishes of Tortugas, Florida with observations in color, habits, and local distribution. *Carnegie Inst. Washington Publ. 535. Pap. Tortugas Lab. 34.* 331 pp.
154. Lorenz, K. 1962. The function of colour

in coral reef fishes. *Proc. R. Inst. G. B.* 39:282–96
155. Lorenz, K. 1963. *Das Sogenannte Böse, Zur Naturgeschichte der Aggression.* Vienna: Barotha-Schoeler. 306 pp.
156. Losey, G. S. 1971. Communication between fishes in cleaning symbiosis. In *Aspects of the Biology of Symbiosis,* ed. T. C. Ching, 45–76. Baltimore: Univ. Park Press
157. Losey, G. S. 1972. Predation protection in the poison-fang blenny, *Meiacanthus atrodorsalis,* and its mimics, *Escenius bicolor* and *Runula laudadus* (Blenniidae). *Pac. Sci.* 26:129–39
158. Losey, G. S. 1972. The ecological importance of cleaning symbiosis. *Copeia* 1972:820–33
159. Losey, G. S. 1972. Behavioural ecology of the "cleaning fish." *Aust. Natur. Hist.* 17:232–38
160. Low, R. M. 1971. Interspecific territoriality in a pomacentrid reef fish *Pomacentrus flavicauda* Whitley. *Ecology* 52:648–54
161. Magus, D. B. 1967. Ecological and ethological studies on echinoderms of the Red Sea. *Stud. Trop. Oceanogr. Miami* 5:635–64
162. Mariscal, R. N. 1969. The protection of the anemone fish, *Amphiprion xanthurus* from the sea anemone, *Stoichactis kenti. Experientia* 25:1114
163. Mariscal, R. N. 1970. A field and laboratory study of the symbiotic behavior of fishes and sea anemones from the tropical Indo-Pacific. *Univ. Calif. Berkeley Publ. Zool.* 91:1–33
164. Mariscal, R. N. 1970. The nature of the symbiosis between Indo-Pacific anemone fishes and sea anemone. *Mar. Biol.* 6:58–65
165. Mariscal, R. N. 1970. An experimental analysis of the protection of *Amphiprion xanthurus* Cuvier and Valenciennes and some other anemone fishes from sea anemones. *J. Exp. Mar. Biol. Ecol.* 4:134–49
166. Mariscal, R. N. 1972. Behavior of symbiotic fishes and sea anemones. In *Behavior of Marine Animals,* ed. H. E. Winns, B. L. Olla, 2:2327–60. New York: Plenum
167. Menzel, D. W. 1959. Utilization of algae for growth by the angelfish, *Holacanthus bermudensis. J. Cons. Perm. Int. Explor. Mer.* 24:308–13
168. Menzel, D. W. 1960. Utilization of food by a Bermuda reef fish, *Epinephelus guttatus. J. Cons. Perm. Int. Explor. Mer.* 25:216–22
169. Myrberg, A. A. Jr. 1972. Social dominance and territoriality in the bicolor damselfish, *Eupomacentrus partitus* (Poey) (Pisces: Pomacentridae). *Behaviour* 41:207–31
170. Myrberg, A. A. Jr., Brahy, B. D., Emery, A. R. 1967. Field observations on reproduction of the damselfish *Chromis multilineata* (Pomacentridae), with additional notes on general behavior. *Copeia* 1967:819–27
171. Myrberg, A. A. Jr., Spites, J. Y. 1972. Sound discrimination by the bicolor damselfish, *Eupomacentrus partitus. J. Exp. Biol.* 57:727–35
172. Myrberg, A. A. Jr., Thresher, R. E. 1974. Interspecific aggression and its relevance to the concept of territoriality in reef fishes. *Am. Zool.* 14:81–96
173. Neill, S. R. S. J., Cullen, J. M. 1974. Experiments on whether schooling by their prey affects the hunting behavior of cephalopods and fish predators. *J. Zool. London* 172:549–69
174. Newell, N. D. 1971. An outline history of tropical organic reefs. *Am. Mus. Novi.* 265:1–37
175. Newman, W. A. 1960. On the paucity of intertidal barnacles in the tropical western Pacific. *Veliger* 2:89–94
176. Odum, H. T., Odum, E. P. 1955. Trophic structure and productivity of a windward coral reef community on Eniwetok Atoll. *Ecol. Monogr.* 25:291–320
177. Ogden, J. C. 1972. An ecological study of Tague Bay Reef, St. Croix, U.S.V.I. *Spec. Publ. Mar. Biol. West Indies Lab. Fairleigh Dickenson Univ. No. 1*
178. Ogden, J. C., Abbott, D. P., Abbott, I. 1973. Studies on the activity and food of the echinoid *Diadema antillarum* Philippi on a West Indian patch reef. *Spec. Publ. Mar. Biol. West Indies Lab. Fairleigh Dickenson Univ. No. 2*
179. Ogden, J. C., Brown, R. A., Salesky, N. 1974. Grazing by the echinoid *Diadema antillarum* Philippi: formation of halos around West Indian patch reefs. *Science* 182:715–17
180. Ogden, J. C., Buckman, N. S. 1973. Movements, foraging groups, and diurnal migrations of the striped parrotfish *Scarus croicensis* Block (Scaridae). *Ecology* 54:589–96
181. Ogden, J. C., Sammarco, P. W., Abbott, D. P. 1973. *Diadema antillarum* and plants: a study of shallow water marine

food chain. *Proc. Assoc. Isl. Mar. Labs. Caribb. Mayaguey* (Abstr.)
182. Okuno, R. 1962. Intra- and interspecific relations of saltwater fishes in aquarium. I. Butterfly fishes. *Jpn. J. Ecol.* 12:129–33
183. Okuno, R. 1963. Observations and discussion on the social behavior of marine fishes. *Publ. Seto Mar. Biol. Lab.* 11:281–336
184. Oppenheimer, J. R. 1970. Mouthbreeding in fishes. *Anim. Behav.* 18:493–503
185. Paine, R. T., Vadas, R. L. 1969. The effects of grazing by sea urchins, *Strongylocentrotus* spp. on benthic algal populations. *Limnol. Oceanogr.* 14:710–19
186. Peterman, R. M. 1971. A possible function of coloration in coral reef fishes. *Copeia* 1971:330–31
187. Popper, D., Fishelson, L. 1973. Ecology and behavior and *Anthias squamipinnis* (Peters, 1855) (Anthiidae, Teleostei) in the coral habitat of Eilat (Red Sea). *J. Exp. Zool.* 184:409–24
188. Potts, G. W. 1969. Behaviour of the snapper, *Lutjanus monostigma* around Aldabra. *Underwater Assoc. Rep.* 1969:96–99
189. Potts, G. W. 1970. The schooling ethology of *Lutjanus monostigma* (Pisces) in the shallow reef environments of Aldabra. *J. Zool. London* 161:223–35
190. Power, A. 1969. *The Great Barrier Reef.* London: Hamlyn. 115 pp.
191. Quiguer, J. 1969. Quelques données sur la repartition des poissons des récifs coralliens. *Cah. Pac.* 13:181–85
192. Radakov, D. V. 1973. *Schooling in the Ecology of Fish.* New York: Wiley. 173 pp.
193. Randall, J. E. 1955. A revision of the surgeon fish genus *Ctenochaetus,* family Acanthuridae, with descriptions of five new species. *Zoologica* 40:149–66
194. Randall, J. E. 1956. A revision of the surgeon fish genus *Acanthurus. Pac. Sci.* 10:154–235
195. Randall, J. E. 1958. A review of ciguatera, tropical fish poisoning, with a tentative explanation of its cause. *Bull. Mar. Sci. Gulf Caribb.* 8:236–67
196. Randall, J. E. 1958. A review of the labrid fish genus *Labroides,* with description of two new species and notes on ecology. *Pac. Sci.* 12:327–47
197. Randall, J. E. 1960. New fishes for Hawaii. *Sea Frontiers* 6:31–43
198. Randall, J. E. 1961. Tagging reef fishes in the Virgin Islands. *Proc. Gulf Caribb. Fish. Inst.* 14:201–41
199. Randall, J. E. 1961. A contribution to the biology of the convict surgeonfish of the Hawaiian Islands, *Acanthurus triostegus sandvicensis. Pac. Sci.* 15:215–72
200. Randall, J. E. 1961. Observations on the spawning of surgeonfishes (Acanthuridae) in the Society Islands. *Copeia* 1961:237–38
201. Randall, J. E. 1961. Overgrazing of algae by herbivorous marine fishes. *Ecology* 42:812
202. Randall, J. E. 1961. Ciguatera: tropical fish poisoning. *Sea Frontiers* 7:130–39
203. Randall, J. E. 1962. Fish service stations. *Sea Frontiers* 8:40–47
204. Randall, J. E. 1963. Notes on the systematics of the parrotfishes (Scaridae), with emphasis on sexual dichromatism. *Copeia* 1963:225–37
205. Randall, J. E. 1963. An analysis of the fish populations of artificial and natural reefs in the Virgin Islands. *Caribb. J. Sci.* 3:31–47
206. Randall, J. E. 1965. Grazing effect on sea grasses by herbivorous reef fishes in the West Indies. *Ecology* 46:255–60
207. Randall, J. E. 1967. Food habits of reef fishes of the West Indies. *Stud. Trop. Oceanogr.* 5:665–847
208. Randall, J. E. 1968. *Caribbean Reef Fishes.* Jersey City, NJ: TFH Publ. 318 pp.
209. Randall, J. E. et al 1971. Grammistin, the skin toxin of soapfishes, and its significance in the classification of the Grammistidae. *Publ. Seto Mar. Biol. Lab.* 19:157–90
210. Randall, J. E., Böhlke, J. E. 1965. Review of the Atlantic labrid fishes of the genus *Halichoeres. Proc. Acad. Nat. Sci. Philadelphia* 117:235–59
211. Randall, J. E., Brock, V. E. 1960. Observations on the ecology of epinepheline and lutjanid fishes of the Society Islands, with emphasis on food habits. *Trans. Am. Fish. Soc.* 89:9–16
212. Randall, J. E., Emery, A. R. 1971. On the resemblance of the young of the fishes *Platax pinnatus* and *Plectorhynchus chaetodontoides* to flat worms and nudibranchs. *Zoologica* 56:115–19
213. Randall, J. E., Helfman, G. 1972. *Diproctacanthus xanthurus,* a cleaner wrasse from the Palau Islands, with notes on other cleaning fishes. *Trop. Fish Hobbyist* 20:87–95
214. Randall, J. E., Kanayama, R. K. 1972. Hawaiian fish immigrants. *Sea Frontiers* 18:144–53
215. Randall, J. E., Randall, H. A. 1960. Examples of mimicry and protective re-

semblance in tropical marine fishes. *Bull. Mar. Sci. Gulf Caribb.* 10:444–80
216. Randall, J. E., Randall, H. A. 1963. The spawning and early development of the Atlantic parrotfish, *Sparisoma rubripinne,* with notes on other scarid and labrid fishes. *Zoologica* 48:49–60
217. Randall, J. E., Schroeder, R. E., Starck, W. A. 1964. Notes on the biology of *Diadema antillarum. Caribb. J. Sci.* 4:421–33
218. Rasa, O. A. E. 1969. Territoriality and the establishment of dominance by means of visual cues in *Pomacentrus jenkinsi* (Pisces: Pomacentridae). *Z. Tierpsychol.* 26:825–45
219. Reese, E. S. 1964. Ethology and marine zoology. *Ann. Rev. Oceanogr. Mar. Biol.* 1964:455–88
220. Reese, E. S. 1973. Duration of residence by coral reef fishes on "home" reefs. *Copeia* 1973:145–49
221. Reighard, J. 1908. An experimental field study of warning coloration in coral-reef fishes. *Carnegie Inst. Washington Pap. Tortugas Lab.* 1:257–325
222. Reinboth, R. 1962. Morphologische und funktionelle Zweigeschlechtlichkeit bei marinen Teleostien (Serranidae, Sparidae, Centracanthidae, Labridae). *Zool. Jahrb. Physiol.* 69:405–80
223. Reinboth, R. 1968. Protogynie bei Papageifischen (Scaridae). *Z. Naturforsch. Teil B.* 23:852–55
224. Robertson, D. R. 1972. Social control of sex reversal in coral-reef fish. *Science* 177:1007–9
225. Robertson, D. R. 1973. Sex changes under the waves. *New Sci.* 31 May: 538–39
226. Robertson, D. R., Choat, J. H. 1974. Protogynous hermaphroditism and social systems in labrid fish. *Proc. Int. Symp. Coral Reefs, 2nd.* 1:217–25
227. Roede, M. J. 1972. *Color as related to size, sex, and behavior in seven Caribbean labrid fish species (genera Thalassoma, Halichoeres and Hemipteronotus).* The Hague: Nykoff
228. Roessler, C., Post, J. 1972. Prophylactic services of the cleaning shrimp. *Natur. Hist.* May:30–37
229. Rosenblatt, R. H. 1963. Some aspects of speciation in marine shore fishes. *Speciation in the Sea, Syst. Assoc. Publ. No. 5,* 171–80
230. Roth, L. M., Eisner, T. 1962. Chemical defenses of arthropods. *Ann. Rev.* Entomol. 7:107–36
231. Roughgarden, J. 1974. Species packing and the competition function with illustrations from coral reef fish. *Theor. Popul. Biol.* 5:163–86
232. Russell, B. C. 1971. Underwater observations on the reproductive activity of the demoiselle *Chromis dispilus* (Pisces: Pomacentridae). *Mar. Biol.* 10:22–24
233. Russell, B. C., Talbot, F. H., Domm, S. B. 1974. Patterns of colonization of artificial reefs by coral reef fishes. *Proc. Int. Symp. Coral Reefs, 2nd.* 1:207–15
234. Sale, P. F. 1969. Pertinent stimuli for habitat selection by the juvenile manini, *Acanthurus triostigus sandvicenses. Ecology* 50:616–23
235. Sale, P. F. 1970. Distribution of larval Acanthuridae off Hawaii. *Copeia* 1970:765–66
236. Sale, P. F. 1971. Extremely limited home range in a coral reef fish, *Dascyllus aruanus* (Pisces: Pomacentridae) *Copeia* 1971:324–27
237. Sale, P. F. 1971. Apparent effect of prior experience on a habitat preference exhibited by the reef fish, *Dascyllus aruanus* (Pisces:Pomacentridae). *Anim. Behav.* 19:251–56
238. Sale, P. F. 1971. The reproductive behavior of the pomacentrid fish, *Chromis caeruleus. Z. Tierpsychol.* 29:156–64
239. Sale, P. F. 1972. Influence of corals in the dispersion of the pomacentrid fish, *Dascyllus aruanus. Ecology* 53:741–44
240. Sale, P. F. 1972. Effect of cover on agonistic behavior of a reef fish: a possible spacing mechanism. *Ecology* 53:753–58
241. Sale, P. F. 1974. Mechanisms of coexistence in a guild of territorial fishes at Heron Island. *Proc. Int. Symp. Corals and Coral Reefs, 2nd.* 1:193–206
242. Sammarco, P. W., Levinton, J. S., Ogden, J. C. 1974. Grazing and control of coral reef community structure by *Diadema antillarum* Phillipi (Echinodermata: Echinoidae): a preliminary study. *J. Mar. Res.* 32:47–53
243. Santos, G. A., Doty, M. S. 1968. Chemical studies on three species of the marine algal genus *Caulerpa.* In *Drugs From the Sea,* ed. H. D. Frendenthal, Washington: Mar. Tech. Soc.
244. Scheltema, R. S. 1971. Larval dispersal as a means of genetic exchange between geographically separated populations of shallow-water benthic marine gastropods. *Biol. Bull.* 140:284–322
245. Schlichter, D. 1968. Das Zusammenleben von Riffanemonen und Anemonenfischen. *Z. Tierpsychol.* 25:933–54
246. Schlichter, D. 1970. *Thalassoma amblycephalus* ein neuer Anemonefisch. *Typ. Mar. Biol.* 7:269–72

247. Schroeder, R. E., Starck, W. A. II 1964. Photographing the night creatures of Alligator Reef. *Nat. Geogr.* 125:128–54
248. Schultz, L. P. 1958. Review of the parrotfishes, family Scaridae. *Bull. US Nat. Mus.* 214:1–143
249. Schultz, L. P. 1969. The taxonomic status of the controversial genera and species of parrotfishes with a descriptive list (Family Scaridae). *Smithsonian Contrib. Zool.* 17:1–49
250. Seghers, B. H. 1974. Schooling behavior in the guppy (*Poecilia reticulata*): an evolutionary response to predation. *Evolution* 28:486–89
251. Shallenberger, R. J., Madden, W. D. 1973. Luring behavior in the scorpionfish, *Iracundus signifer. Behaviour* 47:33–47
252. Sharp, M. A., Parks, D. R., Ehrlich, P. R. 1974. Plant resources and butterfly habitat selection. *Ecology* 55: 870–75
253. Shaw, E. 1960. The development of schooling behavior in fishes. *Physiol. Zool.* 33:263–72
254. Shaw, E. 1961. The development of schooling in fishes. II. *Physiol. Zool.* 34:263–72
255. Shaw, E. 1962. The schooling of fishes. *Sci. Am.* 206:128–38
256. Shaw, E. 1965. The optomotor response and the schooling of fish *Int. Comm. Northwest Atl. Fish. Spec. Publ. No. 6*
257. Shaw, E. 1969. The duration of schooling among fish separated and those not separated by barriers. *Am. Mus. Novit.* 2373:1–13
258. Shaw, E. 1970. Schooling in fishes: critique and review. In *Development and Evolution of Behavior,* ed. R. Aronson et al, 453–80. San Francisco: Freeman
259. Shaw, E., Tucker, A. 1965. The optomotor reaction of schooling carangid fishes. *Anim. Behav.* 13:330–36
260. Shull, E. M. 1962. Over one hundred butterfly species caught in a single day (3rd June 1961) at Mussoorie, India. *J. Lepid. Soc.* 16:143–45
261. Slobodkin, L. B., Fishelson, L. 1974. The effect of the cleaner fish *Labroides dimidiatus* on the point diversity of fishes on the reef front at Eliat. *Am. Natur.* 108:369–76
262. Smith, C. L. 1965. The patterns of sexuality and the classification of serranid fishes. *Am. Mus. Novit.* 2207:1–20
263. Smith, C. L. 1973. Small rotenone stations: a tool for studying coral reef fish communities. *Am. Mus. Novit.* 2512:1–21
264. Smith, C. L., Tyler, J. C. 1972. Space resource sharing in a coral reef fish community. *Results of the Tektite Program: Ecology of Coral Reef Fishes, Bull. Natur. Hist. Mus. L.A.* 14:125–70
265. Smith, C. L., Tyler, J. C. 1973. Population ecology of a Bahamian suprabenthic shore fish assemblage. *Am. Mus. Novit.* 2528:1–38
266. Smith, C. L., Tyler, J. C. 1973. Direct observations of resource sharing in coral reef fish. *Helgol. Wiss. Meeresunter.* 24:264–75
267. Somero, G., Soulé, M. 1974. Genetic variation in marine fishes as a test of the niche-variation hypothesis. *Nature* 249:670–72
268. Soulé, M. 1973. The epistasis cycle: a theory of marginal populations. *Ann. Rev. Ecol. Syst.* 4:165–87
269. Springer, S. 1957. Some observations on the behavior of schools of fishes in the Gulf of Mexico and adjacent waters. *Ecology* 38:166–71
270. Springer, V. G., McErlean, A. J. 1962. A study of the behavior of some tagged south Florida coral reef fishes. *Am. Med. Natur.* 67:386–97
271. Springer, V. G., Smith-Vaniz, W. F. 1972. Mimetic relationships involving fishes of the family Blenniidae. *Smithsonian Contrib. Zool.* 112:1–36
272. Starck, W. A. II, Davis, W. P. 1966. Night habits of fishes of Alligator Reef, Florida. *Ichthyologica* 38:313–56
273. Starck, W. A. II, Schroeder, R. E. 1965. A coral reef at night. *Sea Frontiers* 11:66–74
274. Starck, W. A. II, Schroeder, R. E. 1971. Investigations on the gray snapper, *Lutjanus griseus. Stud. Trop. Oceanogr. Miami* 10:1–224
275. Stephens, J. S., Johnson, R. K., Key, G. S., McCosker, J. E. 1970. The comparative ecology of three sympatric species of California blennies of the genus *Hypsoblennius* Gill (Teleostomi, Blenniidae). *Ecol. Monogr.* 40:213–33
276. Stephenson, W., Endean, R., Bennett, I. 1958. An ecological survey of the marine fauna of Low Isles, Queensland. *Austr. J. Mar. Freshwater Res.* 9:262–318
277. Stephenson, W., Searle, R. B. 1960. Experimental studies on the ecology of intertidal environments at Heron Island. I. Exclusion of fish from beach rock. *Austr. J. Mar. Freshwater Res.* 11: 241–67
278. Stevenson, R. A. 1963. Behavior of the pomacentrid reef fish *Dascyllus albisella*

Gill in relation to the anemone *Marcanthia cookei. Copeia* 1963:612–14
279. Stevenson, R. A. 1963. *Life history and behavior of Dascyllus albisella Gill, a pomacentrid reef fish.* PhD dissertation. Univ. Hawaii, Honolulu, Hawaii. 221 pp.
280. Stevenson, R. A. 1972. Regulation of feeding behavior of the bicolor damselfish (*Eupomacentrus partitus* Poey) by environmental factors. In *Behavior of Marine Animals,* 2: *Vertebrates,* ed. H. E. Winn, B. L. Olla. New York: Plenum
281. Stoll, L. M. 1955. Hormonal control of sexually dimorphic pigmentation of *Thalassoma bifasciatum. Zoologica* 40:125–31
282. Strasburg, D. W. 1966. Observations on the ecology of four apogonid fishes. *Pac. Sci.* 20:338–41
283. Swerdloff, S. N. 1970. *The comparative biology of two Hawaiian species of the damselfish genus Chromis (Pomacentridae).* PhD dissertation. Univ. Hawaii, Honolulu, Hawaii. 183 pp.
284. Talbot, F. H. 1965. A description of the coral structure of Tutia Reef (Tanganyika Territory, East Africa) and its fish fauna. *Proc. Zool. Soc. London* 145:431–70
285. Talbot, F. H. 1970. The south east Asian area as a centre of marine speciation: an ecological analysis of causes. *Rep. Austr. Acad. Sci.* 12:43–50
286. Talbot, F. H., Goldman, B. 1972. A preliminary report on the diversity and feeding relationships of the reef fishes of One Tree Island, Great Barrier Reef system. *Proc. Symp. Corals Coral Reefs, 1969, Mar. Biol. Assoc. India* 425–44
287. Talbot, F. H., Goldman, B. 1974. The ecology of coral reef fishes. In *The Biology and Geology of Coral Reefs,* ed. O. A. Jones, R. Endean. NY: Academic
288. Tavolga, W. N. 1956. Visual, chemical and sound stimuli as cues in the sex discriminatory behavior of the gobiid fish *Bathygobius soporator. Zoologica* 41:49–64
289. Teytaud, A. R. 1971. Food habits of the goby, *Ginsburgellus novemlineatus,* and the clingfish, *Arcos rubiginosus,* associated with echinoids in the Virgin Islands. *Caribb. J. Sci.* 11:41–45
290. Thomson, J. M., Bennett, A. E. 1953. The oyster blenny, *Omobranchius anolus* (Valenciennes) (Blenniidae). *Austr. J. Mar. Freshwater Res* 4:227–33
291. Thresher, R. E. 1974. Small predators on the reef. *Sea Frontiers* 20:219–27
292. Turner, C. H., Ebert, E. E. 1962. The nesting of *Chromis punctipinnis* (Cooper) and a description of their eggs and larvae. *Calif. Fish Game* 48:243–48
293. Tyler, J. C. 1971. Habitat preferences of the fishes that dwell in shrub corals on the Great Barrier Reef. *Proc. Acad. Nat. Sci. Philadelphia* 123:1–26
294. Verivey, D. J. 1930. Coral reef studies. I. The symbiosis between damselfishes and sea anemones in Batavia Bay. *Treubia* 12:305–53
295. Vine, P. J. 1974. Effects of algal grazing and aggressive behaviour of the fishes *Pomacentrus lividus* and *Acanthurus sohol* on coral-reef ecology. *Mar. Biol.* 24:131–36
296. Wickler, W. 1957. Vergleichende Verhaltensstudien an Grundfischen. I. Beitrage zur Biologie, besonders zur Ethologie von *Blennius fluviatilis* Asso im Vergleich zu einigen anderen Bodenfischen. *Z. Tierpsychol.* 14:393–428
297. Wickler, W. 1960. Aquarienbeobachtungen an *Aspidontus* einem ektoparasitischen Fisch. *Z. Tierpsychol.* 17:277–92
298. Wickler, W. 1961. Uber des Verhalten der Blenniiden *Runula* und *Aspidontus* (Pisces: Blenniidae). *Z. Tierpsychol.* 18:421–40
299. Wickler, W. 1963. Zum Problem der Signalbildung, am Beispiel der Vehaltsenmimikry zwischen *Aspidontus* und *Labroides* (Pisces, Acanthopterygii) *Z. Tierpsychol.* 20:657–79
300. Wickler, W. 1967. Specialization of organs having a signal function in some marine fish. *Stud. Trop. Oceonogr. Miami* 5:539–48
301. Wickler, W. 1967. Vergleich des Ablaichverhaltens einiger paarbildender sowie nicht-paarbildender Pomocentriden und Cichliden (Pisces: Perciformes). *Z. Tierpsychol.* 24:457–70
302. Wickler, W. 1968. *Mimicry in Plants and Animals.* New York: World Univ. Library. 249 pp.
303. Williams, G. C. 1964. Measurement of consociation among fishes and comments on the evolution of schooling. *Publ. Mus. Mich. State Univ.* 2:351–83
304. Williams, M. M., Shaw, E. 1971. Modifiability of schooling behavior in fishes: the role of early experience. *Am. Mus. Novit.* 2448:1–19
305. Winn, H. E. 1955. Formation of a mucous envelope at night by parrot fishes. *Zoologica* 40:145–47
306. Winn, H. E., Bardach, J. E. 1957. Behavior, sexual dichromatism and

species of parrotfishes. *Science* 125: 885–69
307. Winn, H. E., Bardach, J. E. 1959. Differential food selection by moray eels and a possible role of the mucous envelope of parrotfishes in reduction of predation. *Ecology* 40:296–98
308. Winn, H. E., Bardach, J. E. 1960. Some aspects of the comparative biology of parrotfishes at Bermuda. *Zoologica* 45:24–34
309. Winn, H. E., Marshall, J. A., Hazlett, B. 1964. Behavior, diel activities, and stimuli that elicit sound production and reactions to sounds in the longspine squirrelfish. *Copeia* 1964:413–25
310. Winn, H. E., Salmon, M., Roberts, N. 1964. Sun-compass orientation by parrot fishes. *Z. Tierpsychol.* 21:798–812
311. Yonge, C. M. 1968. Living corals. *Proc. R. Soc. B* 169:329–44
312. Youngbluth, M. J. 1968. Aspects of the ecology and ethology of the cleaning fish, *Labroides phthirophagus* Randall. *Z. Tierpsychol.* 25:915–32
313. Zumpe, D. 1965. Laboratory observations on the aggressive behaviour of some butterfly fishes (Chaetodontidae). *Z. Tierpsychol.* 22:226–36