

Predation Protection in the Poison-Fang Blenny, *Meiacanthus atrodorsalis*, and Its Mimics, *Ecsenius bicolor* and *Runula laudandus* (Blenniidae)<sup>1</sup>

GEORGE S. LOSEY<sup>2</sup>

**ABSTRACT:** The large canine teeth in *Meiacanthus atrodorsalis* impart a toxic bite which causes this animal to be rejected as a prey item by several piscivorous fishes. Two morphologically and behaviorally similar species, *Runula laudandus* and *Ecsenius bicolor*, may enjoy predator protection through Batesian mimicry and, for the former species, greater feeding efficiency through aggressive mimicry. A limited number of experiments indicate that the predator, *Epinephelus merra*, may learn to avoid *Meiacanthus atrodorsalis* and its mimics.

AS POINTED OUT BY WICKLER (1968), mimicry must be considered in terms of three parties. The "mimic" resembles some "model" in terms of one or several characteristics such as coloration, shape, odor, etc., but utmost importance must be attached to the "third party" which is frequently a predator or prey organism. Usually the third party must encounter both model and mimic and must fail to differentiate perfectly between them. For purposes of clarity, the three types of mimicry discussed in this paper are defined briefly below. But it should be clear that, as with many biological phenomena, it is difficult to provide precise definitions (see Wickler, 1968).

Batesian mimicry is generally the resemblance of a harmless or palatable species to a harmful or unpalatable one. This provides the mimic with some selective advantage similar to that enjoyed by the model, usually predator protection. Müllerian mimicry involves a similar relationship except that both species possess some undesirable qualities. Their resemblance increases the probability that the third party will encounter one of their "type" and learn to avoid all others. Aggressive, or Peckhamian, mimicry

is the resemblance of a "predatory" species to a harmless or nonpredatory form. This relationship facilitates the mimic's "predation" through deception of the third party, which in this case is its "prey" organism.

Mimicry in the form of camouflage is known for many species of fish. Cases of Batesian, Müllerian, and aggressive mimicry are comparatively rare. *Aspidontus taeniatus* Quoy & Gaimard, the aggressive mimic of the cleaning wrasse, *Labroides dimidiatus* (Cuvier & Valenciennes), is the only well-known example of morphological and behavioral mimicry in fishes (Randall, 1955, 1958; Randall and Randall, 1960; Eibl-Eibesfeldt, 1955, 1959; Wickler, 1960, 1961, 1963, 1965a, 1968). *Runula azalea* Jordan & Bollman resembles *Thalassoma lucasanum* (Gill), another cleaning wrasse, but Hobson (1969) concluded that its coloration functions primarily to conceal the blenny within groups of the wrasses in order to facilitate the mimic's attacks on larger fishes. Some other species of *Runula* have at least superficial resemblance to young labrids. Starck (1969) described *Ecsenius midas* which joins large schools of *Anthias squamipinnis*. It is suspected that its resemblance to these numerous anthiids serves as a protection against predation and allows it to exploit planktonic food sources. Other cases of mimicry have been hypothesized such as baits and lures of antennariid fishes, but there is little evidence to support the inclusion of these fishes as examples of true mimicry according to the criteria suggested by Wickler (1965a, 1968).

<sup>1</sup> Supported by a National Institutes of Health Postdoctoral Fellowship and Atomic Energy Commission contract no. AT(29-2)-226. Hawaii Institute of Marine Biology contribution no. 380. Manuscript received 19 July 1971.

<sup>2</sup> University of Hawaii: Department of Zoology, Honolulu, Hawaii 96822; and Hawaii Institute of Marine Biology, P.O. Box 1067, Kaneohe, Oahu, Hawaii 96744.

The large canine teeth in the lower jaw of *Meiacanthus atrodorsalis* (Gunther) have an anterior groove which ends in a depression that is filled with glandularlike tissue (Tomiya, 1956; Springer, 1968). Springer mentioned a lack of information on the possible venomosity of this canine teeth and gland structure. Springer (1971; personal communication, 1969) independently recognized the similarity between two species of *Meiacanthus* and members of the genus *Ecsenius* as an indication of possible mimicry. Four other species of *Meiacanthus* resemble species of the blenniid genera, *Petroscirtes* and *Runula* (V. G. Springer and W. F. Smith-Vaniz, personal communication, 1971).

The present study was begun to investigate the function of the unique canines of *Meiacanthus atrodorsalis* and the possibility of both aggressive and Batesian mimicry among *M. atrodorsalis*, *Ecsenius bicolor* (Day), and a third blenny *Runula laudandus* Whitley.

I thank Dr. Ralph L. Bowers and Mr. Peter Rosti for their help in collecting specimens, and Dr. Victor G. Springer and Mr. William F. Smith-Vaniz for their discussions regarding this project.

#### MATERIALS AND METHODS

Field observations on the distribution and behavior of the three species were made during approximately 250 hours of diving at Eniwetok Atoll. A few hours of correlative observations were made on *Meiacanthus atrodorsalis* in Guam. The number of individuals was censused by swimming around roughly circular areas (about 500 square meters) and counting all individuals within the circles. Recounting of individuals was probably minimal due to the extreme clarity of the water. Behavioral observations were recorded on an underwater tape recorder. Particular note was made of the feeding behavior of the fish and their response when approached. Specimens were speared for gut-content analysis and morphological comparison. Living specimens were captured with quinaldine and hand nets for various laboratory studies. *Runula laudandus* proved to be particularly difficult to capture and was thus excluded from the laboratory studies.

The toxicity of the bite of *Meiacanthus atrodorsalis* was assayed by force-biting the tails of two white laboratory mice and my hand. Subsequent observations were inadvertently provided by bites in the more tender area of my hip.

Predator reactions to *Ecsenius bicolor* and *Meiacanthus atrodorsalis* were observed in a 3-m-diameter, 3/4-m-deep, plastic pool at the Eniwetok Marine Biological Laboratory. Various predators were caught in 1 to 2-m-deep water where they should not have encountered *M. atrodorsalis* (see below). These predators were placed in a "community tank" and fed living *M. atrodorsalis*, *Ecsenius bicolor*, and *Istiblennius paulus*, a tide pool blenny; the latter served as a control. I partially crippled all prey fishes just prior to their introduction by squeezing the caudal musculature. This facilitated their capture by the predators and caused the swimming movements of *I. paulus* to be more similar to that of the other species than they are in intact animals.

The lack of a large number of living specimens prevented a detailed investigation of the possible advantages gained by mimicry, so a small scale study was attempted. Four groupers (members of the "*Epinephalus merra* complex," 100 to 175 mm standard length) were placed in individual, 1-m-diameter wire pens submerged in a pool similar to the one mentioned above. All were fed once at about 0800 and again at 1900 hours daily. *Istiblennius paulus* was again used as a control food. The grouper's feeding reaction to living *Ecsenius bicolor* was checked both before and after they were fed several *Meiacanthus atrodorsalis*. Two of the groupers were fed intact *M. atrodorsalis* and two were fed prey with their canines surgically removed.

#### DEPTH DISTRIBUTION

The census counts made on eight different reefs show that, while all three species occur in the same depth range, their centers of distribution show a slight difference (see Table 1). *Ecsenius bicolor* also differs from the other species in that it is commonly found in rubble

TABLE 1  
MEAN NUMBERS OF FISH OBSERVED ON DIFFERENT REEFS IN ENIWETOK ATOLL LAGOON

DEPTH	REEF TYPE	<i>Meiacanthus atrodorsalis</i>	<i>Ecsenius bicolor</i>	<i>Runula laudandus</i>	NUMBER OF COUNTS
0 to 3 m	fringing reef and small coral heads	0	0	0	many
3 to 5 m	large coral heads	4.75	2.25	0.5	8
5 to 7 m	large coral heads and rubble piles	20.75	12.25	1.25	8
7 to 20 m	lagoon pinnacles	92.8	1.7	0.6	7
> 20 m	lagoon pinnacles	1.2	0	0	5

NOTE: The 0–3 m depth range was not included in the statistical analyses. The center of distribution for *M. atrodorsalis* differs from the other species ( $p < 0.01$ , Kolmogorov-Smirnov method, Tate and Clelland, 1959) but the distributions of *E. bicolor* and *R. laudandus* do not differ from each other ( $p > 0.2$ ).

areas or on eroded rock faces whereas *Meiacanthus atrodorsalis* and *Runula laudandus* are usually found in areas of the reef covered with living coral.

The relative densities also show that *Meiacanthus atrodorsalis* is the most plentiful species over the entire depth range and that *Runula laudandus* is the least plentiful ( $p < 0.005$  by Kruskal-Wallis, nonparametric analysis of variance, Tate and Clelland, 1959).

#### COMPARATIVE MORPHOLOGY

The three species have striking similarities in both morphology and coloration (Figs. 1, 2).

*Meiacanthus atrodorsalis* differs markedly from most other blennies. The prolonged snout and the dark pigmentation which crosses the eye and proceeds posteriorly to near the top of the head give it a distinctive appearance. The sexually dimorphic prolongation of two to five outer caudal rays forms a lobate tail which is enhanced by the yellow pigmentation of the lobate portions and the hyaline membrane between the shorter, more central rays. Its body coloration—the anterior 51 to 71 percent blue-gray and the remainder a bright yellow—further enhances its unique appearance. When it goes into hiding, it adopts a fright coloration with numerous white spots, but its background coloration remains the same. The lack of complete coloration change during behavioral observations and during topical applications of eserine sug-

gests that most of the yellow portion is incapable of significant darkening.

*Runula laudandus* is strikingly similar to *Meiacanthus atrodorsalis*. It is difficult for the inexperienced observer to separate them at more than about 2 m distance in the field, and I still find it difficult to differentiate between them at a distance greater than 5 m. The pigmentation is nearly identical (Figs. 1, 2) and the lesser body depth of *Runula laudandus* (Table 2) is visually compensated by the dorsal fin which this species usually holds erect. It also has a fright coloration that is similar to *Meiacanthus atrodorsalis*, but it may be capable of darkening most of its body.

*Ecsenius bicolor* is less similar to *Meiacanthus atrodorsalis*. Its slightly larger mean size, blunt head, and more robust body make it easy to separate in the field. (But on several occasions, inexperienced personnel who were collecting *M. atrodorsalis* picked up *Ecsenius bicolor* by mistake.) The prolongation of the outer caudal rays is similar but less pronounced and also appears to be sexually dimorphic. Its general coloration is similar except that the head is slightly browner and the yellow portions are more orange. Its fright coloration (Wickler, 1965b) is similar to *Meiacanthus atrodorsalis*. Unlike the other species, it may darken its entire body to a dark brown to black coloration during some behavioral threat displays. One specimen was captured in an entirely light brown coloration, and only after 18 days in

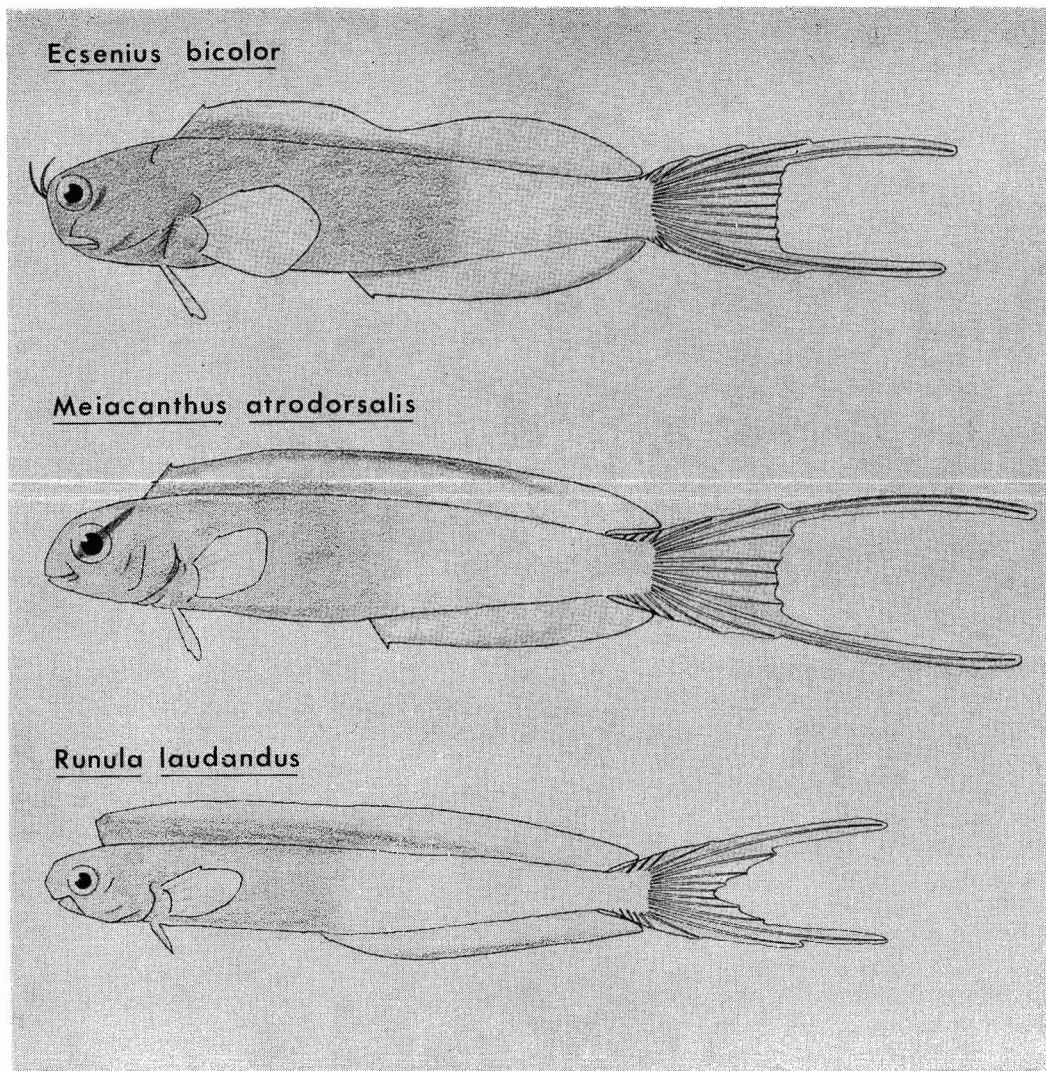


FIG. 1. *Meiacanthus atrodorsalis* (center) and its mimics, *Ecsenius bicolor* (top) and *Runula laudandus* (bottom).

an aquarium did it show a slight trace of yellow in its tail. This color form has been described by Springer (1971).

#### BEHAVIOR

In Eniwetok, *M. atrodorsalis* is commonly found hovering less than 1 m above the coral. Loose aggregations of up to 50 individuals are

frequently formed.<sup>3</sup> They are usually located on the up-current side or over the top of the coral formation and are mixed with diurnal plankton feeders such as *Chromis* and *Dascyllus*. *Runula laudandus* is found in the same areas of the reef and frequently joins groups of *Meiacanthus*

<sup>3</sup> No aggregations were seen in Guam, and there was some indication of territorial defense that was never seen in Eniwetok.

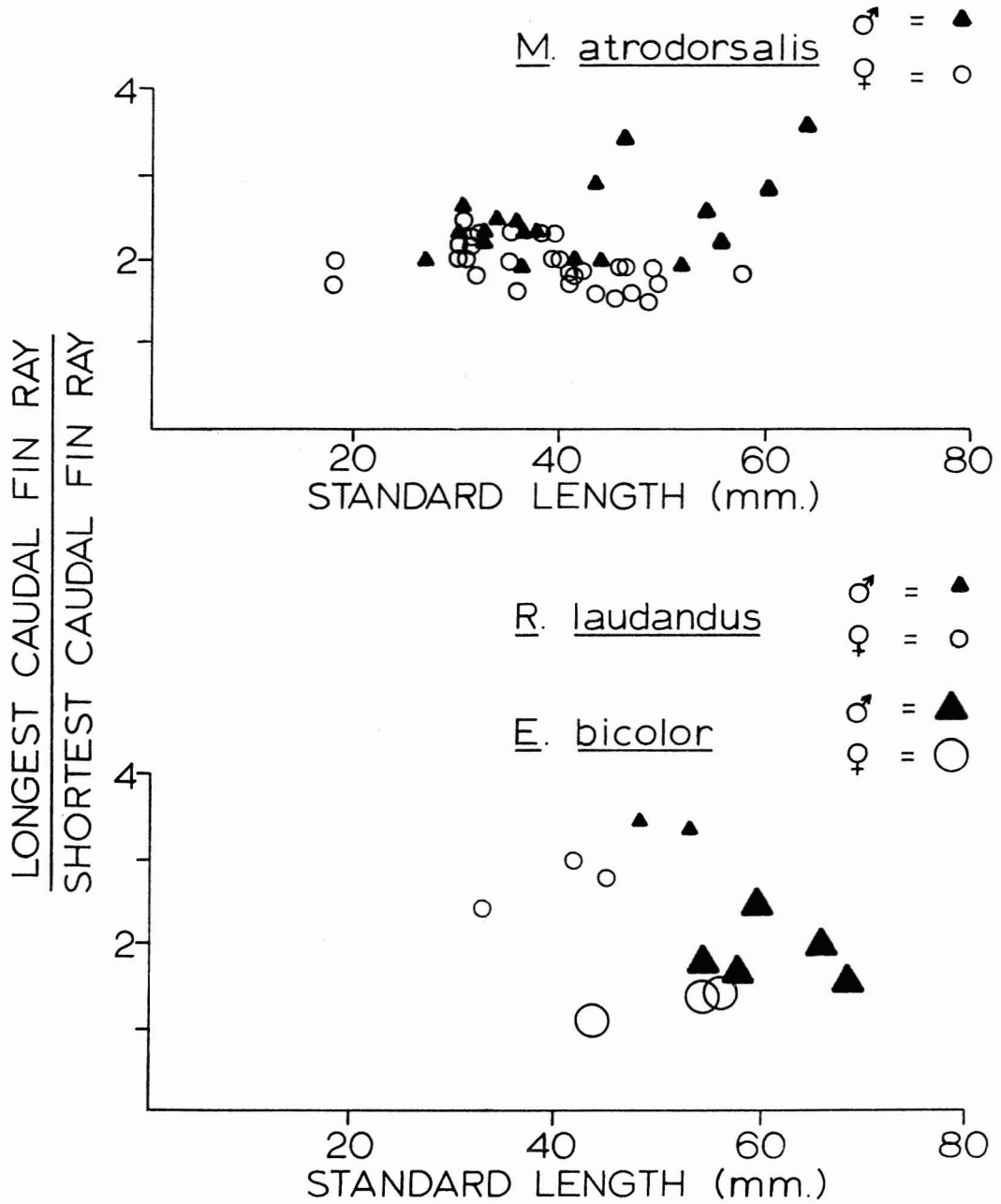


FIG. 2. Comparison of the lobate condition of the caudal fin expressed as the length of the longest ray in the caudal fin divided by the length of the shortest, central ray.

*atrodorsalis*. The *M. atrodorsalis* shows no overt reaction to its presence. *Runula laudandus* does not form intraspecific aggregations, and there is

some indication that it may be territorial. (Fighting behavior was observed on each of the three occasions when more than one *R. laudandus* was

TABLE 2  
MEAN VALUES AND RANGES FOR SELECTED MORPHOLOGICAL MEASUREMENTS AND COUNTS

ITEM	<i>Meiacanthus atrodorsalis</i>	<i>Ecsenius bicolor</i>	<i>Runula laudandus</i>
Number of specimens	50	9	5
Standard Length	39.5, 18-63	56, 53-68	44, 33-53
Greatest Depth			
Standard Length	0.23, 0.19-0.28	0.21, 0.19-0.23	0.16, 0.15-0.18 0.21, 0.18-0.23 (when erect dorsal fin is included)
Length of Darkly Pigmented Area			
Standard Length	0.62, 0.51-0.71	0.74, 0.60-0.82	0.63, 0.59-0.67
Number of Prolonged Outer Caudal Rays	4, 2-5	2 only	4 only
Number of Shorter Central Caudal Rays	5, 4-5	7 only	7 only

observed in the same location.) *Ecsenius bicolor* is usually found on algae-covered rocks and only occasionally on living coral. It is solitary and territorial (Wickler, 1965b) and remains comparatively close to the substratum. It differs from other salariine reef blennies in that it is far more visible and differs from *Meiacanthus atrodorsalis* in that it remains comparatively close to the surface of the rocks. Wickler (1965b) reported that *Ecsenius bicolor* spends far less time out of its refuge than does *Aspidontus taeniatus* which swims free in the water. But my observations in Eniwetok indicate that, although *Ecsenius bicolor* does not stray as far into the water as does *Aspidontus taeniatus*, it spends much of its time outside its refuge. It frequently swims free in the water between rocks and, as noted by Wickler, remains above the substratum while feeding rather than swimming next to the rocks. I have never seen it mix with either *Meiacanthus atrodorsalis* or *Runula laudandus*, or show any reaction to their presence.

The swimming pattern shown by *Meiacanthus atrodorsalis* (and *Runula laudandus*, see below) is unique among Eniwetok fishes and is similar to that seen during threat behavior in *Petroscirtes temminckii* (Wickler, 1965c). Fast swimming is accomplished by attenuated anguilliform movements of the trunk in the normal blenniid fashion. During its normally slow movements,

it is propelled in short darts by caudal beats and constant undulation of its pectoral fins. At the end of each dart, it comes to an abrupt halt and remains still in the water. The body is held motionless by the movements of the pectoral fins. *Runula laudandus* shows similar swimming movements and proceeds in short darts, whereas most other *Runula* species show normal anguilliform swimming. When swimming quickly, its trunk shows anguilliform movements which are typical for *Runula* but are more exaggerated than in *Meiacanthus atrodorsalis*. *Ecsenius bicolor* shows only smooth anguilliform swimming with a collapsed dorsal fin except for certain display swimming described for many blennies (Wickler, 1963, 1965b).

*Meiacanthus atrodorsalis* appears to be a diurnal plankton feeder but may also feed on benthic organisms (Victor G. Springer, personal communication, 1969). It faces into the current during the day and can be seen to dart and take in food items; but in the aquarium it feeds primarily on benthic invertebrates. *M. atrodorsalis* gut contents include some red and brown algal filaments, pelagic fish eggs, a few bryozoan stalks, and a large amount of the amorphous material which is usually abundant in the lagoon water and may be coral mucus. *Runula laudandus* is a diurnal predator (or parasite) and attacks larger fishes, scraping off scales and possibly mucus (see Hobson, 1968) from their bodies.

Its gut contents consist almost entirely of fish scales and a few fish eggs. In my observations it fed primarily on *Holocentrus* spp. and some lutjanids such as *Pterocaesio* spp. It may attack its prey by darting out of a group of *Meiacanthus atrodorsalis* or while swimming alone. *Ecsenius bicolor* feeds entirely on algal material which it scrapes from rocks but will readily accept plankton in an aquarium. One individual was observed feeding repeatedly on the surface of living coral (*Acropora* spp.), but I was unable to capture it for gut content analysis.

When approached by a diver, *M. atrodorsalis* initially swims slowly away but, when the diver stops, it comes back toward him in short jumps and hovers in the water facing the diver. A few large males were found in bore-holes in the rocks, but left their holes as soon as the diver approached and either swam slowly away or toward the diver. At dusk in the aquarium it retired into tubes and crevices and adopted a mottled coloration. I have never observed its behavior at night on the reef. *Runula laudandus* shows similar behavior except that I have never found it in holes. *Ecsenius bicolor* adults almost always dart directly into their tubular refuges in the normal blenniid manner when approached. The juveniles usually dart about the surface of the rocks.

When captured by spear or hand net, *Meiacanthus atrodorsalis* usually bites the net, plastic bag, or spear tines. Its jaws are fully opened in order to bring its large canines to bear.

#### BITE TOXICITY OF *Meiacanthus atrodorsalis*

The force-bitten laboratory mice showed little overt reaction aside from bleeding and licking of their tail for up to 1 hour. The human reaction is best illustrated by the two bites which I received on the hip when two speared *M. atrodorsalis* were placed in a small bag in my bathing suit. The bites were immediately painful, not unlike a mild bee sting. The puncture wounds bled freely for about 10 minutes. Within 2 minutes, each bite was surrounded by an inflamed area about 3 mm in diameter. Within 15 minutes, the inflamed areas increased in size to a maximum diameter of 10 cm. A raised white ring about 2 cm in diameter then formed around each of the wounds and per-

sisted for about 2 hours. The general inflammation disappeared in about 4 hours but the immediate area of the puncture wounds remained inflamed for about 12 hours and the tissues were somewhat hardened for several days. Springer and Smith-Vaniz (unpublished) reported similar experiences with *M. nigrolineatus* but report little or no pain.

The later feeding experiments provided numerous examples of the reactions of fish to the bites. The typical reaction after taking a *M. atrodorsalis* into the mouth was violent quivering of the head with distension of the jaws and operculi. The fish frequently remained in this distended posture for several seconds until the *M. atrodorsalis* emerged from their mouth. Frequently, the *M. atrodorsalis* were little harmed by the experience.

#### PREDATION EXPERIMENTS

The predators in the "community tank" took all of the prey organisms into their mouth at least once (Table 3). All *Istiblennius paulus* were immediately taken and ingested. All fish accepted *I. paulus* as food but the *Rhinecanthus aculeatus* was the most successful at capturing prey quickly. By contrast, only *Hemipteronotus taeniourus* showed much success at eating *Meiacanthus atrodorsalis* without quivering and distending its jaws. After the first few encounters, the *Rhinecanthus aculeatus* avoided *Meiacanthus atrodorsalis* entirely. Even after a *M. atrodorsalis* individual had been taken by one or two predators and rejected, it was still likely to be rejected by the next predator.

The learning experiments were hampered by the fact that two of the groupers refused to take any food. For this reason, after grouper no. 1 was tested with specimens of *M. atrodorsalis* which had had their canines removed, it was tested again with intact *M. atrodorsalis*. The intact specimens of *M. atrodorsalis* were rejected as food items but the specimens of *M. atrodorsalis* without canines were taken readily (Table 4). *Ecsenius bicolor* was accepted as food before the groupers were fed *M. atrodorsalis* and after being fed *M. atrodorsalis* without canines. But after eating only one intact *M. atrodorsalis*, the same grouper refused *Ecsenius bicolor*. After it had attempted to eat intact

TABLE 3  
FEEDING RESPONSES OF FISH IN THE "COMMUNITY TANK"

FOOD OFFERED	PREDATOR SPECIES				
	<i>Epinephalus merra</i> N = 4	<i>Holocentrus opercularis</i> N = 1	<i>Myripristis argyromus</i> N = 7	<i>Rhinecanthus aculeatus</i> N = 3	<i>Hemipteronotus taeniourus</i> N = 1
<i>Part A</i>					
<i>Istiblennius paulus</i> (N <sup>1</sup> = 16)	4	2	1	7	2
<i>Meiacanthus atrodorsalis</i>					
When First to Eat (N <sup>1</sup> = 7)	0	0	0	0	2
When Second to Eat (N <sup>1</sup> = 7)	0	0	0	0	1
When Third to Eat (N <sup>1</sup> = 3)	1	0	0	0	0
<i>Part B</i>					
<i>Istiblennius paulus</i> (N <sup>1</sup> = 16)	4	2	1	7	2
<i>Meiacanthus atrodorsalis</i>					
When First to Eat (N <sup>1</sup> = 11)	1	1	0	0	4
When Second to Eat (N <sup>1</sup> = 7)	0	0	1	0	1
When Third to Eat (N <sup>1</sup> = 3)	1	0	0	0	0

NOTE: Part A presents the number of "normal" feeding responses that were not followed by quivering or distension of the orobranchial chamber. Part B presents the number of actual ingestions of food regardless of behavior. The encounters with *Meiacanthus atrodorsalis* are subdivided as to the number of times that the prey had been taken into the mouth of another fish and rejected previous to the encounter in question. N = the number of fish in the tank. N<sup>1</sup> = the number of prey offered.

*Meiacanthus atrodorsalis* twice, grouper no. 2 took *Ecsenius bicolor* only after it had been in his pen for over 12 hours. Both fish fed readily on *Istiblennius paulus* regardless of treatment except when they were fed immediately after rejecting a *Meiacanthus atrodorsalis*.

When all of the data are considered together (Table 5) it can be seen that intact *M. atrodorsalis* was accepted as food far less than was *Istiblennius paulus* ( $p < 0.01$  by  $\chi^2$ ).

#### DISCUSSION

The results of the predation experiments show that intact *Meiacanthus atrodorsalis* individuals are eaten less frequently than *Istiblennius paulus* and suggest that *Meiacanthus atrodorsalis* is unsuitable as a food item for several reef predators. Springer and Smith-Vaniz (unpublished) have obtained similar results for *M. nigrolineatus* in Israel. It is known from other studies that the diurnal plankton-feeding fishes such as those with which *M. atrodorsalis* are found are subject to predation from predators similar to

those used here (Hobson, 1968; Starck and Davis, 1966). Although the laboratory experiments do not prove that *M. atrodorsalis* is protected from predation in the field, they do show that predators suffer some aversive effects after attempting to eat them. These aversive effects should lend some predator protection because many other prey species are present. The protection observed in the laboratory should be a conservative estimate of what might happen in the field inasmuch as the predators in the laboratory were definitely being trained to feed upon objects which were added to the tanks. As mentioned, some predators such as *Hemipteronotus taeniourus* seem to be capable of eating *Meiacanthus atrodorsalis*, perhaps because *Hemipteronotus taeniourus* bites and frequently incapacitates its prey before taking it completely into its mouth. The other predators take the entire prey organism into their mouths immediately. But absolute protection from predation is, of course, not necessary for the species to enjoy a selective advantage.

It is almost certain that the bite of the ven-



TABLE 4

FEEDING RESPONSES OF TWO *Epinephalus merra* IN THE LEARNING EXPERIMENT

FOOD OFFERED	FISH FED		
	FANGS REMOVED FROM FOOD	FANGS INTACT	
	GROUPER NO. 1	GROUPER NO. 2	GROUPER NO. 1
Control			
<i>Istiblennius paulus</i>	++	++	++
<i>I. paulus</i>	++	++	
Test			
<i>Ecsenius bicolor</i>	++	++	+
Experience			
<i>Meiacanthus atrodorsalis</i>	++	++	-
<i>M. atrodorsalis</i>	++	-	-
<i>M. atrodorsalis</i>	++	-	
<i>M. atrodorsalis</i>	++	-	
Control			
<i>I. paulus</i>	++	+	++
<i>I. paulus</i>	++	++	
Test			
<i>E. bicolor</i>	++	+	-

NOTE: Feeding responses are presented in chronological order. Symbols: ++, eat and retain immediately; +, eat more than 2 hours after introduction of food; -, eat and immediately reject with quivering and distension of the orobranchial chamber; —, show no feeding reaction. Blank spaces indicate that no food was offered.

omous canines of *Meiacanthus atrodorsalis* is responsible for its rejection by predators. Although only a small number of *M. atrodorsalis* without canines were fed to one predator, the fact that all defanged animals were eaten normally, and that the same animal later rejected fish with intact canines, is highly suggestive. The fact that only three out of 20 intact animals were eaten normally by all of the predators also supports this conclusion. The long canines could serve little function in the capture of planktonic prey, but might have some use in feeding on benthic organisms (see Hiatt and Strasburg, 1960) or might be used in intraspecific fighting as in some other blennies (Wickler, 1960). But none of these functions for the canines have

TABLE 5

ALL FEEDING RESPONSES IN LEARNING EXPERIMENT AND IN "COMMUNITY TANK"

FOOD OFFERED	NUM-		CHI SQUARE	PROB-ABILITY
	BER EATEN	BER NOT EATEN		
<i>Part A</i>				
<i>Istiblennius paulus</i>	20	1		
<i>Meiacanthus atrodorsalis</i>	3	11	22.3	<.01
<i>Part B</i>				
<i>Istiblennius paulus</i>	20	1		
<i>Meiacanthus atrodorsalis</i>	7	10	14.3	<.01

NOTE: Part A presents the number of "normal" feeding responses that were not followed by quivering or distension of the orobranchial chamber. Part B presents the number of actual ingestions of food regardless of behavior.

ever been suggested by observations on *Meiacanthus* spp.

The morphology and coloration of *M. atrodorsalis* make it highly visible as it hovers over the reef. Unique and bright visual stimuli are common in noxious or venomous animals and provide warning signals that are easily perceived by potential predators (see Wickler, 1968). Their habit of turning and swimming toward a prospective predator is again a unique behavior that could easily serve a warning function. Their habit of abandoning their "refuge" when approached suggests a maximal display of warning signals to potential predators and again differs from most other blenniid fishes.

*Ecsenius bicolor* shows similarities to *Meiacanthus atrodorsalis* which differ from non-mimetic *Ecsenius* spp. Their behavior differs from other *Ecsenius* in that they remain away from hiding places and swim free in the water much more than do most salariine blennies. But, their swimming pattern and predator reaction differ from *Meiacanthus atrodorsalis*. The few learning experiments which were completed indicate that naive groupers will accept *Ecsenius bicolor* as food until they have experienced *Meiacanthus atrodorsalis* with intact canines. Although this example serves as a strong in-

dication of Batesian mimicry, more experimentation is necessary. These laboratory experiments present a major difficulty in that the species of prey that are presented to the predators may actually appear more similar to the predators in the laboratory since they are presented in the same manner and in the same location. The depth distribution of *Ecsenius bicolor* overlaps that of *Meiacanthus atrodorsalis*, and, although its microhabitat is somewhat different, reef predators should have ample opportunity to encounter both species. On the reef, however, these blennies would be encountered in slightly different locations and engaging in dissimilar activities.

The similar morphology, coloration, and behavior of *Runula laudandus* are strongly suggestive of mimicry. The cooccurrence of *R. laudandus* and *Meiacanthus atrodorsalis* over depth, within the same specific areas of the reefs and even within the same aggregations, is additional evidence of the possibility of mimicry. The joining of *M. atrodorsalis* groups by *Runula laudandus* does not seem to occur because of a lack of specific discrimination by *R. laudandus* because that species appears to be territorial.

Both *Ecsenius bicolor* and *Runula laudandus* might enjoy predator protection through Batesian mimicry of *Meiacanthus atrodorsalis*. Their lesser relative abundances agree with other cases of Batesian mimicry which have been studied (e.g., Carpenter, 1949; Brower, 1958). Some artificially constructed mimicry experiments indicate that, if the experience with the model is sufficiently noxious, the number of mimics may exceed that of the model species without negating the protective value of the association (Duncan and Sheppard, 1965; Brower, 1960). Thus, the slightly subequal numbers of models and mimics in shallow water need not negate the possibility of Batesian mimicry.

The feeding habits of *Runula laudandus* suggest that it may also benefit by aggressive mimicry of *Meiacanthus atrodorsalis*, similar to *Runula azalea* (Hobson, 1969). The mimic may be concealed within the groups of *Meiacanthus atrodorsalis* and ignored by reef fishes which are then attacked by the mimic. In such cases of aggressive mimicry, the importance of

the relative abundance of mimics and models is theoretically different from that for Batesian mimicry (Wickler, 1965a, 1968). In aggressive mimicry, the aversive stimulus is received from the mimic rather than from the model. The aggressive mimic uses a relatively innocuous model. If the abundance of the mimic, *Runula laudandus*, approached that of the model, their prey might quickly learn to give a wide berth to any blue and yellow fish with a lobate caudal (as shown for *Aspidontus taeniatus* by Wickler, 1963). If the numbers of the innocuous *Meiacanthus atrodorsalis* are far greater than that of the mimic, however, the prey should learn to avoid *Runula laudandus* less readily. Limited behavioral observations suggest that the relative densities of model and mimic in 3 to 5 m of water (4.75:0.5) may be marginal for the *R. laudandus* to enjoy the advantages of aggressive mimicry. All the attacks by *R. laudandus* that were witnessed in this depth range were accomplished from behind and only after considerable maneuvering by both the mimic and its prey. On the deeper pinnacles where the mimics have a much lower relative density, however, they were frequently successful at attacking several members of a group before they were avoided.

Springer and Smith-Vaniz (unpublished) found that *Runula townsendi* is rejected as food by some predators. The reason for its rejection is unknown. This raises the possibility that *R. laudandus* might also have some noxious qualities that affect its acceptability as a prey item. If so, the mimetic complex might include elements of Müllerian mimicry as well. It is doubtful, however, that its feeding habits alone would decrease its acceptability as a prey species.

The light brown color form of *Ecsenius bicolor* is of considerable interest to mimetic considerations. V. G. Springer (personal communication) found this brown coloration to be far more common in some areas, and Mr. Peter Rosti (personal communication, 1971) found them to be common in Fiji. Since *Meiacanthus atrodorsalis* appears to be unusually common in the Eniwetok lagoon, the mimetic form of *Ecsenius bicolor* may have a higher selective value for the species and thus exist in greater proportions than the brown form.

## LITERATURE CITED

- BROWER, J. V. Z. 1958. Experimental studies of mimicry in some North American butterflies. Part II. *Battus philenor* and *Papilio troilus*, *P. polyxenes*, and *P. glaucus*. *Evolution* 12: 123-136.
- . 1960. Experimental studies of mimicry. IV. The reactions of starlings to different proportions of models and mimics. *Amer. Nat.* 94:271-282.
- CARPENTER, G. D. H. 1949. *Pseudacraea eurytus* (L.) (Lep. Nymphalidae): a study of a polymorphic mimic in various degrees of speciation. *Trans. R. Ent. Soc. Lond.* 100:71-133.
- DUNCAN, G. J., and P. M. SHEPPARD. 1965. Sensory discrimination and its role in the evolution of Batesian mimicry. *Behaviour* 27: 269-282.
- EIBL-EIBESFELDT, V. I. 1955. Über Symbiosen, Parasitismus, und andere besondere zwischenartliche Beziehungen tropischer Meeresfische. *Z. Tierpsychol.* 12: 203-219.
- . 1959. Der Fisch *Aspidontus taeniatus* als Nachahmer des Putzers *Labroides dimidiatus*. *Z. Tierpsychol.* 16: 19-25.
- HIATT, R. W., and D. W. STRASBURG. 1960. Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. *Ecol. Monogr.* 30:65-127.
- HOBSON, E. S. 1968. Predatory behavior of some shore fishes in the Gulf of Calif. *Res. Rep. U.S. Fish Serv.* 73:1-92.
- . 1969. Comments on certain recent generalizations regarding cleaning symbiosis in fishes. *Pacif. Sci.* 23:35-39.
- RANDALL, J. E. 1955. Fishes of the Gilbert Islands. *Atoll Res. Bull.* 47:1-243.
- . 1958. A review of the labrid fish genus *Labroides*, with descriptions of two new species and notes on ecology. *Pacif. Sci.* 12: 327-347.
- RANDALL, J. E., and H. A. RANDALL. 1960. Examples of mimicry and protective resemblance in tropical marine fishes. *Bull. Mar. Sci. Gulf Caribbean* 10:444-480.
- SPRINGER, V. G. 1968. Osteology and classification of the fishes of the family Blenniidae. *Bull. U.S. Nat. Mus.* 284:1-85.
- . 1971. Revision of the fish genus *Ecsenius* (Blenniidae, Blenniinae, Salariaiini). *Smithson. Contr. Zool.* 72:1-74.
- STARCK, W. H. II. 1969. *Ecsenius (Anthiiblenius) midas* a new subgenus and species of mimic blenny from the Western Indian Ocean. *Notul. Nat. Acad. Philad.* 419:1-9.
- STARCK, W. H. II, and W. P. DAVIS. 1966. Night habits of fishes of Alligator Reef, Florida. *Ichthyologica* 38:313-356.
- TATE, M. W., and R. C. CLELLAND. 1959. Non-parametric and shortcut statistics. Interstate Printers & Publishers, Danville, Illinois. 171 p.
- TOMIYAMI, I. 1956. *Meiacanthus kamoharai* new species (Blenniidae) p. 1083-1086. In Tomiyami and Abe, Figures and descriptions of the fishes of Japan 53.
- WICKLER, W. 1960. Aquarienbeobachtungen an *Aspidontus*, einer ektoparasitischen Fisch. *Z. Tierpsychol.* 17:277-292.
- . 1961. Über das Verhalten der Blenniiden *Rumula* und *Aspidontus* (Pisces, Blenniidae). *Z. Tierpsychol.* 18:421-440.
- . 1963. Zum Problem der Signalbildung, am Beispiel der Verhaltens-Mimikry zwischen *Aspidontus* und *Labroides* (Pisces, Acanthopterygii) *Z. Tierpsychol.* 20:657-679.
- . 1965a. Mimicry and the evolution of animal communication. *Nature* 208:519-521.
- . 1965b. Zur Biologie und Ethologie von *Ecsenius bicolor* (Pisces, Teleostei, Blenniidae) *Z. Tierpsychol.* 22:36-49.
- . 1965c. *Petrosirtes temminckii* (Blenniidae) Drohen, p. 413-416. In G. Wolf [ed.] *Ency. Cinematographica. Inst. Wiss. Film, Göttingen* E519.
- . 1968. *Mimicry*. McGraw-Hill Book Co., New York. 255 p.