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Review Article

A Review of Mimicry in Marine Fishes

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John E. Randall (2005) A review of mimicry in marine fishes. *Zoological Studies* **44**(3): 299-328. The terms protective resemblance, Batesian mimicry, Müllerian mimicry, aggressive mimicry, and social mimicry are defined. Color illustrations are given for 20 examples of protective resemblance in marine fishes. Ninety-eight cases of mimicry in marine fishes are discussed, and 104 color illustrations are presented in support of 56 of these. The explanation for the mimicry of the juvenile surgeonfish *Acanthurus pyroferus* by the angelfish *Centropyge vrolikii*, based on different food habits of the mimic, model, and the territorial damselfish *Plectroglyphidodon lacrymatus*, is questioned. http://www.sinica.edu.tw/Journals/44.3/299.pdf

Key words: Protective resemblance, Mimicry, Marine fishes.

When the subject of mimicry is raised, the first examples that come to mind are in the insect world. However, a surprising number of mimics have been discovered among marine fishes, the subject of this pictorial review.

There is a need to provide a distinction between protective resemblance and mimicry. Poulton (1898, quoted from Cott, 1957: 397) defined them as follows: "In the former an animal resembles some object which is of no interest to its enemy, and in so doing is concealed; in the latter an animal resembles an object which is well known and avoided by its enemy, and in so doing becomes conspicuous." From observations of the Cleaner Wrasse *Labroides dimidiatus* and the Mimic Blenny *Aspidontus taeniatus*, Randall and Randall (1960 : 445) revised Poulton's definition of mimicry to" ... an animal resembles an object which is well known and is avoided or not preyed upon by its enemy, and in so doing becomes conspicuous." Far from being avoided, the Cleaner Wrasse is sought by other fishes of the reef community for its removal of ectoparasites. It serves as the model for the mimicking blenny, enabling the latter to get close enough to nip the fins of reef fishes.

However, there is still some confusion with respect to these 2 terms, as noted by Vane-Wright (1980), who used crypsis for protective resemblance. He explained that it is "probably impossible to provide a "perfect" definition (i.e., mutually exclusive) for either term." For the purpose of this report, protective resemblance is used for an animal that closely resembles a part of a substratum, a plant, or a sedentary animal such as a sponge or soft coral. Mimicry applies only to animals that resemble active animals. In addition to resemblance in color and morphology, the mimic may adopt a pattern of behavior to enhance the deception.

Examples of protective resemblance among fishes are legion. We immediately think of flatfishes that match the surrounding substratum and quickly change their pattern as they move over a

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different colored area or the many frogfishes and scorpionfishes that are wonderfully camouflaged. In addition to protective coloration, these fishes may have fleshy cutaneous flaps and tentacles that augment their concealment. Among the best-known masters of camouflage is the Sargassumfish *Histrio histrio*, typically found in floating masses of *Sargassum* in the open sea, hence far more difficult to detect than one photographed in the Waikiki Aquarium (Fig. 1). Another frogfish, *Antennarius commerson* in the Hawaiian Is. (Figs. 2, 3), was first overlooked as just another small

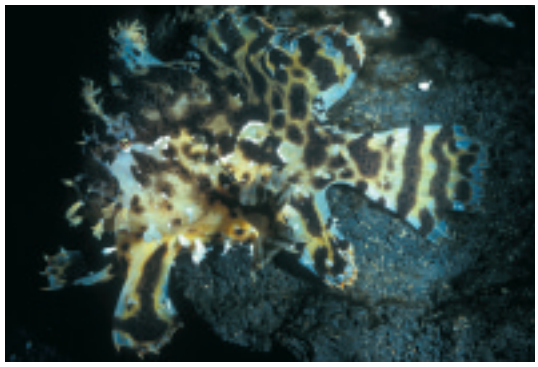


Fig. 1. *Histrio histrio*, Hawaiian Is. (aquarium photo).

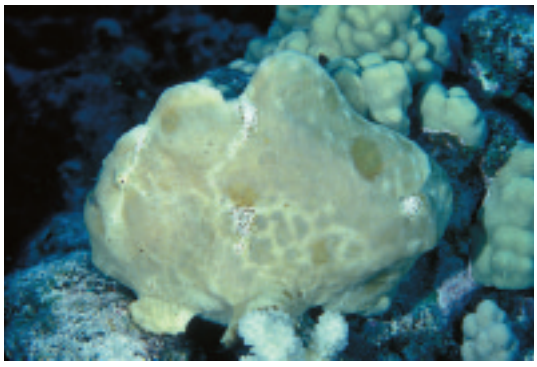


Fig. 2. *Antennarius commerson* and *Porites lobata*, Hawai'i.

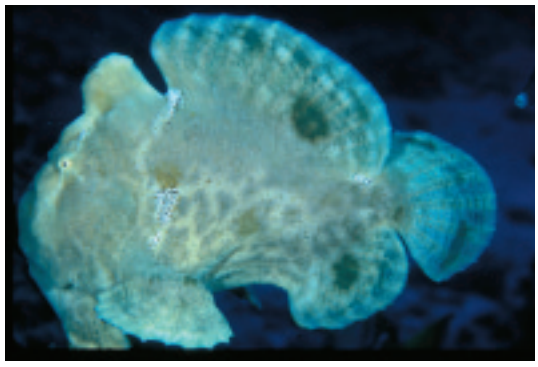


Fig. 3. Same fish as in Fig. 2, but lifted off the bottom.

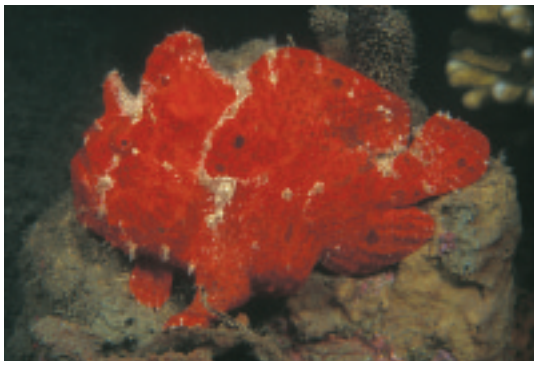


Fig. 4. *Antennarius commerson*, Papua New Guinea.

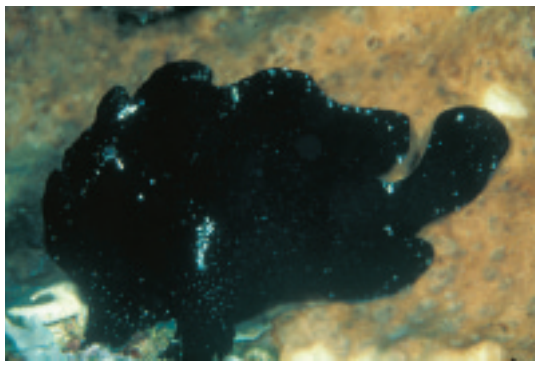


Fig. 5. *Antennarius commerson*, Komodo, Indonesia.

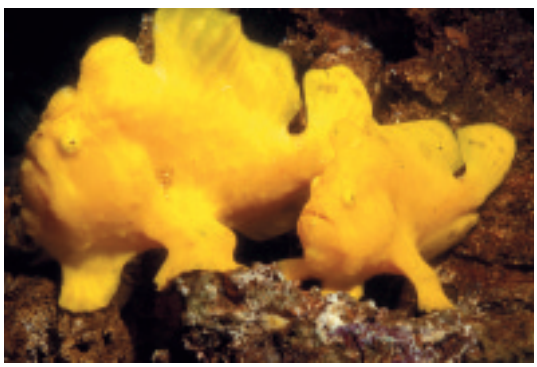


Fig. 6. *Antennarius commerson*, juveniles, Hawaiian Is.

Fig. 7. *Antennarius commerson*, Hawaiian Is.

coral head (*Porites lobata*). Photographs of the same species (Figs. 4-7) depict the range of color it can exhibit. Frogfishes cannot change their color pattern quickly, so they may be found over a substratum unlike that of their color pattern. One in the Waikiki Aquarium in Honolulu changed from orange to dark reddish brown in about 2 weeks after being moved to a different tank.

Breder (1946) reviewed those species of fishes that bear a deceptive resemblance to plants. Randall and Randall (1960) reported 12 examples of fishes that resemble plant material, among them the juvenile labrid *Novaculichthys taeniourus* (Fig. 8), which looks like drifting algae (the deception enhanced by its seemingly disoriented movement); *Iniistius pavo* (Fig. 9), which behaves like a dead leaf on the bottom, moving with the surge; and juvenile *Platax orbicularis* (Fig. 10), which resembles a drifting leaf, often near the surface (the author has observed the same behavior in the Tripletail *Lobotes surinamensis*). Other protectively colored fishes include the seahorse *Hippocampus bargibanti* (Fig. 11), which matches the seafan (*Muricella* sp.) on which it lives; the astounding Leafy Seadragon *Phycodurus eques* of South Australia (Fig. 12); another pipefish *Syngnathoides biaculeatus* (Fig. 13), the wrasse *Novaculoides macrolepidotus* (Fig. 14), and the filefish *Acreichthys tomentosus* (Fig. 15), all of which blend with seagrass; the ghost pipefish *Solenostomus cyanopterus* (Fig. 16), which looks like a drifting piece of seagrass or like the green alga *Caulerpa taxifolia* (Fig. 17); *S. paradoxus* (Fig. 18), which resembles the soft coral *Dendronephthya* sp. in which it is hiding or in a crinoid of the genus *Comanthus* (Fig. 19); and an undescribed clingfish of the genus *Discotrema* (Fig. 20), which is nestled in its host crinoid.

The best-known category of mimicry is Batesian. It was discovered by Henry Walter Bates, who at the age of 23 y explored the Brazilian forest and observed some butterflies of 2 different families that were remarkably alike. The common heliconiine butterflies, although fragile and slow flying, exude noxious secretions and are not preyed upon by birds. Resembling them are the less-common pierids that lack such repellent substances. Bates read his paper to the Linnean Society in London in 1861.

Müllerian mimicry is named for Fritz Müller who also studied butterflies in Brazil. Bates found examples of pairs of inedible butterflies that were

Fig. 8. *Novaculichthys taeniourus*, juvenile, Batu Ata, Indonesia.

Fig. 9. *Iniistius pavo*, juvenile, Hawaiian Is.

Fig. 10. *Platax orbicularis*, juvenile, Sulawesi, Indonesia.

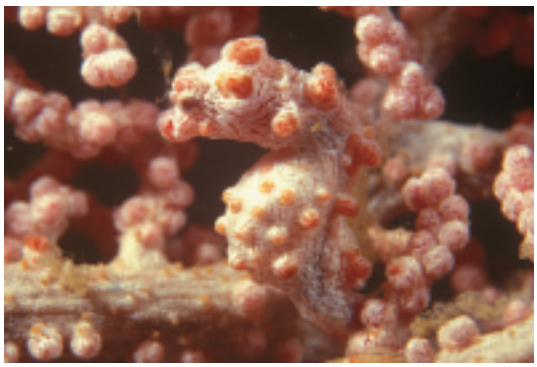


Fig. 11. *Hippocampus bargibanti*, Sulawesi, Indonesia.

not related but looked much alike. Müller (1878) stated that species with inedible properties may evolve to look alike. Fewer individuals of each are sacrificed before predators learn to avoid them (although a predator's aversion may also be innate).

Cott (1957: 398) differentiated Batesian and Müllerian mimicry as follows: "In Batesian mimicry a relatively scarce, palatable, and unprotected species resembles an abundant, relatively unpalatable, or well-protected species, and so becomes disguised. In Müllerian mimicry, on the other hand, a number of different species, all possessing aposematic attributes and appearance, resemble one another, and so become more easily recognized."

The concept that Batesian mimics must be less abundant than their models has been repeated so frequently in the literature that it would seem obligatory. However, Fisher (1930) stated that a Batesian mimic may be more numerous if the model is extremely noxious or if the mimic is a relatively unimportant item of prey. Springer and Smith-Vaniz (1972) discussed 7 possible cases where the mimic may be more abundant. Two of these were shown experimentally to apply when the model was a species of *Meiacanthus*, all of which are believed to have a venomous bite.

Longley (1917) warned that the similarity of 1 fish to an unrelated species does not necessarily mean that mimicry is involved. Mere resemblance might be the case of the cardinalfish *Fowleria* sp., suggested as being a mimic of scorpionfishes by Siegel and Adamson (1983), or the similar example of *Fowleria abocellata* (= *F. vaiuli*) advocated as mimicking *Scorpaenodes guamensis* by Goren and Karplus (1983). More convincing is the apparent mimicry of a scorpionfish by the percoid fish *Centrogenys vaigiensis*, as discussed by Whitley (1935). This fish was first described by Quoy and Gaimard (1824) as a species of *Scorpaena*. Cuvier in Cuvier and Valenciennes (1829) realized it was not a scorpionfish and renamed it *Centropristes scorpenoides*, but Quoy and Gaimard's species name prevails. The similarity may be seen in figure 21 of *C. vaigiensis* and fig-

Fig. 12. *Phycodurus eques*, South Australia (aquarium photo).

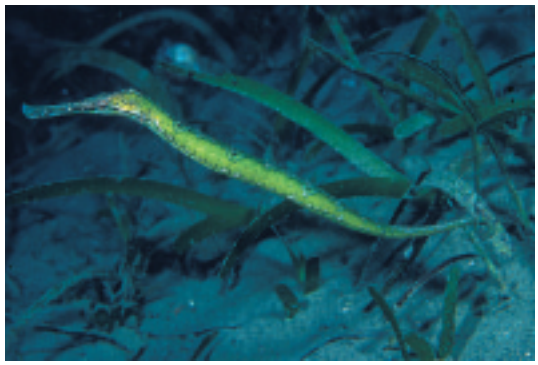
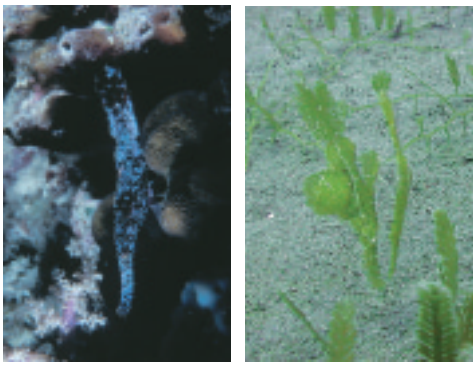


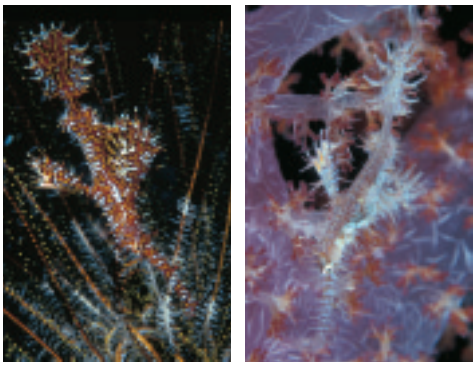
Fig. 13. *Syngnathoides biaculeatus*, Papua New Guinea.

Fig. 14. *Novaculoides macrolepidotus*, Cebu, Philippines.

Fig. 15. *Acreichthys tomentosus*, Papua New Guinea.



Figs. 16-17. *Solenostomus cyanopterus*, Mai I., Indonesia (left); Sulawesi, Indonesia (right; John L. Earle).



Figs. 18-19. *Solenostomus paradoxus*, Alor, Indonesia (left); Papua New Guinea (right).

Fig. 20. *Discotrema* sp., New Britain.

Fig. 21. *Centrogenys vaigiensis*, Sulawesi, Indonesia.

Fig. 22. *Scorpaenodes guamensis*, Mauritius.

Fig. 23. *Myrichthys colubrinus*, Bali, Indonesia.

Fig. 24. *Myrichthys colubrinus*, Tuamotu Archipelago (Yves Lefevre).

Fig. 25. *Laticauda colubrina*, Banda Sea (Ron and Valerie Taylor).

ure 22 of the scorpionfish *Scorpaenodes guamensis*.

An early example of Batesian mimicry in fishes is the resemblance of the harmless Ringed Snake Eel *Myrichthys colubrinus* (Figs. 23, 24) to the venomous sea snake *Laticauda colubrina* (Fig. 25) and other dark-ringed sea snakes (discussed by McCosker and Rosenblatt 1993). Unlike other Indo-Pacific snake eels, in general, this one roams freely in the open by day. The width of the dark bars on the snake eel varies, as shown by the extreme examples of figures 23 and 24. A photograph of a snake eel was recently sent to the author from Tahiti to determine if it was a sea snake. It proved to be another snake eel, *Leiuranus semicinctus*, a less-likely mimic of a sea snake because the dark bars are broader than the pale interspaces and do not completely encircle the body.

Mahadevan and Nagappan Nayar (1965) observed the yellow and black-barred juvenile carangid fish *Gnathanodon speciosus* closely associated with a sea snake of the same color pattern in southeastern India. When approached, the fish "moved closer to the body of the snake, literally hugging the body." They added that it was difficult to see the fish at first sight because its color pattern blended with that of the snake. It should be noted, however, that juveniles of *G. speciosus* often swim at the flank of large bony fishes or ride the bow wave of sharks.

Masterman (1908) reported the similarity of the black-marked pectoral fin of the Common Sole *Solea vulgaris* in Europe to the black 1st dorsal fin of the venomous weeverfishes *Echiichthys vipera* and *Trachinus draco*.

The juvenile of the carangid fish *Alectis ciliaris* (Fig. 26) has long been presumed to be a mimic of venomous jellyfishes. The very long anterior soft dorsal and anal rays of *Alectis* resemble the long thread-like tentacles of virulent cubomedusae. It is not known to associate closely with jellyfishes as do juveniles of some other carangid fishes, stromateoids, etc. (Mansueti 1963).

Schooling juveniles of the Convictfish *Pholidichthys leucotaenia* (Fig. 27) look very much like schools of the juvenile venomous catfish *Plotosus lineatus* (Fig. 28). The catfish aggregate closely for the mutual protection provided by their spines, and Convictfish juveniles may also form dense schools, although they tend to be more dispersed.

Longley and Hildebrand (1940) described *Hemiemblemaria simulus* as a new genus and species of the pike blenny family Chaenopsidae from Tortugas, Florida. They regarded the chaenopsid as a Batesian mimic of the wrasse *Thalassoma bifasciatum*. It was observed to leave the bottom and swim freely with the model, using its pectoral fins like a labrid. *Thalassoma bifasciatum* is well known to feed in part on the ectoparasites of other fishes, therefore enjoying protection from predation (though not complete, because a few have been found in the stomachs of predaceous fishes). This behavior provides the opportunity for the chaenopsid to safely feed on zooplank-

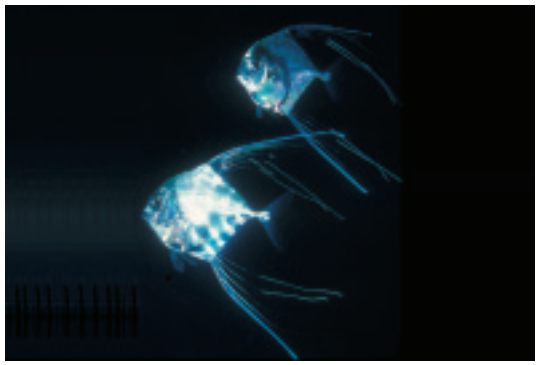


Fig. 26. *Alectis ciliaris*, juveniles, Hawaiian Is.

Fig. 27. *Pholidichthys leucotaenia*, Papua New Guinea.

Fig. 28. *Plotosus lineatus*, Cebu, the Philippines.

ton as it mingles with the labrid. Randall and Randall (1960) reported on the food habits of the chaenopsid (free-living copepods, mysids, and a few small fishes) from specimens collected in the Florida Keys, and they illustrated a juvenile and an adult of both the mimic and the model (the initial-phase adult of the model, not the larger and very differently colored terminal male).

Randall and Emery (1971) were completely deceived by a juvenile of the ephippid fish *Platax pinnatus* (Fig. 29) that they observed and collected in Palau in 1970. They thought it was a turbellarian flatworm because of its coloration and behavior. When on the bottom, its locomotion was like that of a flatworm, and when above the bottom, it oriented horizontally and swam slowly with an undulating motion. Several polyclad flatworms are dark with an orange margin or submarginal band. An example is given here of a possible model, *Pseudoceros periaurantus* (Fig. 30). Some polyclad flatworms are known to be strongly toxic and advertise this with bright warning coloration. Fishes either avoid them, or if they ingest them, they quickly spit them out. Exceptions are puffers, many of which are well known to be toxic themselves (Newman and Cannon 2003).

A small sole (Fig. 31) from Papua New Guinea, estimated to be 12 mm in length by the photographer, appears to be a juvenile of an undetermined species of *Soleichthys*. It moves slowly over the bottom like a flatworm and is believed to be a mimic of an undescribed polyclad of the genus *Pseudoceros* (Fig. 32). Kuiter (1991) first illustrated this juvenile sole and noted its movement like a flatworm. Newman and Cannon (2003) also figured it, as well as its polyclad model.

Heck and Weinstein (1978) observed the striking resemblance of the juvenile of the burrfish *Chilomycterus antennatus* to the sea hare *Aplysia dactylomedia* in seagrass meadows of the Caribbean Sea. They concluded that the burrfish is a Batesian mimic of the unpalatable sea hare.

Kuiter (1991: 116) illustrated "a small anglerfish clinging to rocks like a nudibranch which as a predator can surprise prey and has little fear of being preyed upon as nudibranchs are reported to be of bad taste." His photograph appears to be a juvenile of the frogfish *Antennarius pictus*.

Remarkable examples of Batesian mimicry are those blennies of the genera *Ecsenius*, *Petroscirtes*, and *Plagiotremus* that mimic fang-blennies of the genus *Meiacanthus* (Springer and

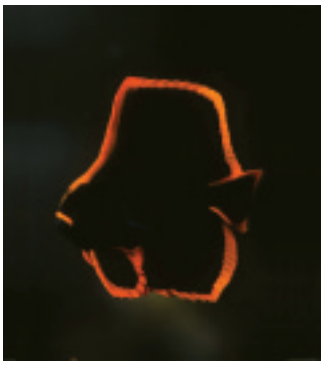


Fig. 29. *Platax pinnatus*, Sulawesi, Indonesia (Mike Severns).

Fig. 30. *Pseudoceros periaurantias* (Leslie Newman and A. Flowers).

Fig. 31. *Soleichthys* sp., Papua New Guinea (David Hall).

Fig. 32. *Pseudoceros* sp., Guam (Gustav Paulay).

Smith-Vaniz 1972, Losey 1972, Russell 1975, Allen et al. 1975, Smith-Vaniz 1976 1987, Russell et al. 1976, Smith-Vaniz et al. 2001). Species of *Meiacanthus* have venomous glands associated with the pair of very large grooved canine teeth in the lower jaw. Species of other genera of fang-blennies, such as *Aspidontus*, *Petroscirtes*, and *Plagiotremus*, also have a pair of large canines in the lower jaw, but they are not venomous. The canines are used in defense and infraspecific aggression, not for feeding (Russell 1977: fig. 2).

Springer and Smith-Vaniz (1972) performed experiments by feeding the Red Sea blennies *Meiacanthus nigrolineatus*, *Ecsenius gravieri*, and *Plagiotremus townsendi* to scorpionfishes and groupers in laboratory tanks in the Gulf of Aqaba. They concluded that "live *Meiacanthus nigrolineatus* is a generally unacceptable prey species, whose unacceptability lies in its bite." *Ecsenius gravieri* and *P. townsendi* are generally acceptable prey species, but they are often not eaten when the predator has previously ingested and rejected *M. nigrolineatus*.

Three cardinalfishes of the genus *Cheilodipterus* and juveniles of the breams *Scolopsis bilineatus* and *S. margaritifera* are also mimics of species of *Meiacanthus*. Russell (1975) wrote of the *Scolopsis*, "Although deeper bodied than the blenny, the belly is white, in pale contrast to the colours above, so that at first sight, especially when viewed from above, the small coral bream appears to be a blenny." He pointed out that the mimicry is further enhanced by the juvenile bream's swimming in the same distinctive way as species of *Meiacanthus*. The blennies swim a short straight distance, pause, then make another linear swim, often in a different direction. The mimicking cardinalfishes of the genus *Cheilodipterus* swim the same way. This is remarkable because species of the family Apogonidae are generally nocturnal. The bream mimicry is most convincing because juveniles of the same species exhibit a different color pattern to correspond to that of species of *Meiacanthus* in the area. The following figures show model species of *Meiacanthus* and their mimics.

In figure 33, *Meiacanthus nigrolineatus* and its mimic, *Ecsenius gravieri*, were photographed together in the Gulf of Aqaba, Red Sea. *Meiacanthus nigrolineatus* is darker in the southern part of the Red Sea; *E. gravieri* closely matches its color there. Unlike other species of *Ecsenius*,

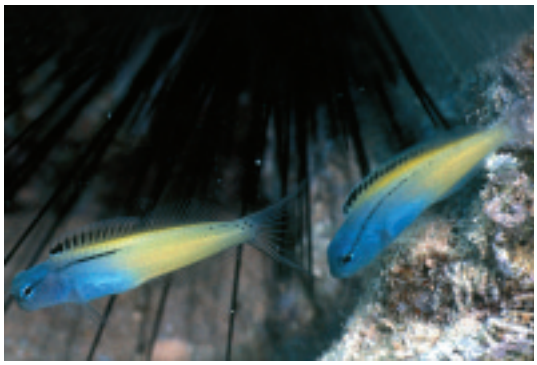


Fig. 33. *Meiacanthus nigrolineatus* (left) and *Ecsenius gravieri*, Red Sea (Victor G. Springer).

Fig. 34. *Plagiotremus townsendi* (Robert F. Myers).

Fig. 35. *Meiacanthus atrodorsalis*, Banda, Indonesia.

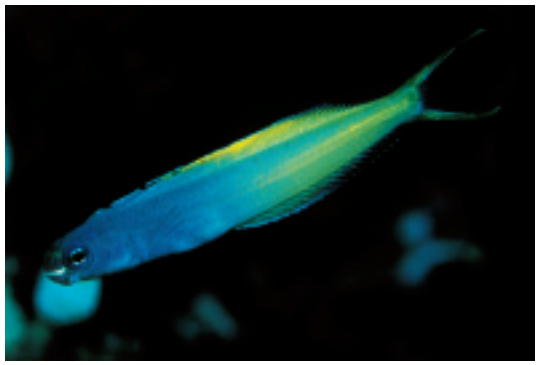


Fig. 36. *Plagiotremus laudandus*, Wetar, Indonesia.

which rest upon the substratum except when moving to a new location or feeding, *E. gravieri* swims freely above the bottom like *M. nigrolineatus*.

Figure 34 of *Plagiotremus townsendi* in the Gulf of Aqaba also shows that it mimics *M. nigrolineatus*. To offset its more-slender body, it tends to hold its dorsal and anal fins erect. The same is true of other mimic species of *Plagiotremus*.

In figure 35, *Meiacanthus atrodorsalis*, wide-ranging in the Pacific from Japan to Australia and east to the islands of Samoa, is mimicked by *Plagiotremus laudandus* (Fig. 36). The bluish

Fig. 37. *Meiacanthus oualanensis*, Fiji.

Fig. 38. *Plagiotremus laudandus flavus*, Fiji.

Fig. 39. *Scolopsis bilineatus*, juvenile, Fiji.

Fig. 40. *Scolopsis bilineatus*, adult, Luzon, the Philippines.

Fig. 41. *Meiacanthus smithi*, Maldive Is.

Fig. 42. *Plagiotremus phenax*, Sumatra, Indonesia.

Fig. 43. *Scolopsis bilineatus*, juvenile, Sumatra, Indonesia.

brown and orange color phase of *Ecsenius bicolor* has been regarded by some authors as a mimic of *M. atrodorsalis*, but it is a marginal example at best (Springer 1988).

The yellow *Meiacanthus oualanensis* (Fig. 37) found in Fiji serves as the model for the yellow *Plagiotremus laudandus flavus* (Fig. 38) (William F. Smith-Vaniz, pers. comm., now prefers to regard *flavus* as a species) and the yellow-phase juvenile of the Bridled Bream *Scolopsis bilineatus* (Fig. 39). Four different color forms of the bream mimic different species of *Meiacanthus*, but the color of the adult bream (Fig. 40) is essentially the same throughout its broad range.

In figure 41, *Meiacanthus smithi* in the Indian Ocean is mimicked by *Plagiotremus phenax* (Fig. 42), and a different-colored juvenile of *Scolopsis bilineatus* (Fig. 43). The species name, *phenax*, is from the Greek for imposter, hence well chosen for the mimicking *Plagiotremus*.

Meiacanthus grammistes from southern Japan to Australia and the Solomon Is. (Fig. 44) is the model for the fangblenny *Petroscirtes breviceps* (Fig. 45), the cardinalfish *Cheilodipterus nigrotaeniatus* (Fig. 46), and a third color form of juvenile *Scolopsis bilineatus* (Fig. 47).

Smith-Vaniz et al. (2001: fig. 15) illustrated a similar mimic-model group, *Meiacanthus lineatus*, *Petroscirtes fallax*, and juvenile *Scolopsis bilineatus*, but their illustration of *P. fallax* shows 2 white instead of bright yellow stripes. However, *Smith-Vaniz* (pers. comm.) has seen photographs of *P. fallax* in which the stripes are bright yellow). Smith-Vaniz et al. cited Yatsu et al. (1983), who mentioned the similarity of *Petroscirtes breviceps* to *Meiacanthus kamoharai* as a possible mimetic pair. Smith-Vaniz et al. also suggested that the young of the nemipterid fish *Pentapodus trivittatus* is a mimic of *Meiacanthus crinitus*. Lacking a photograph of the juvenile *Pentapodus*, they presented one of a subadult, and the resemblance is clear.

Meiacanthus geminatus from Sabah and the Philippines (Fig. 48) is the model for *Cheilodipterus zonatus* (Fig. 49) and the young of *Scolopsis margaritifera* (Fig. 50). An adult of *Scolopsis* is shown in figure 51.

Meiacanthus vittatus from Papua New Guinea (Fig. 52) is mimicked by *Petroscirtes breviceps* (Fig. 53; note the difference from *P. breviceps* of Fig. 45), by *Cheilodipterus parazonatus* (Fig. 54), and by another color form of the juvenile of

Fig. 44. *Meiacanthus grammistes*, Alor, Indonesia.

Fig. 45. *Petroscirtes breviceps*, Sulawesi, Indonesia.

Fig. 46. *Cheilodipterus nigrotaeniatus*, Sulawesi, Indonesia (Gerald R. Allen).

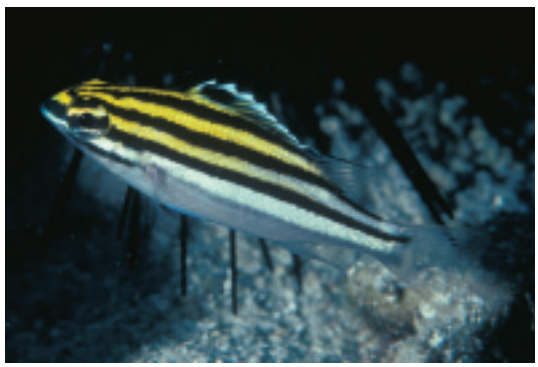


Fig. 47. *Scolopsis bilineatus*, juvenile, Luzon, the Philippines.

Fig. 48. *Meiacanthus geminatus*, Papua New Guinea (Gerald R. Allen).

Fig. 49. *Cheilodipterus zonatus*, Papua New Guinea (Gerald R. Allen).

Fig. 50. *Scolopsis margaritifera*, juvenile, Palau.

Fig. 51. *Scolopsis margaritifera*, adult, Sulawesi, Indonesia.

Fig. 52. *Meiacanthus vittatus*, Papua New Guinea.

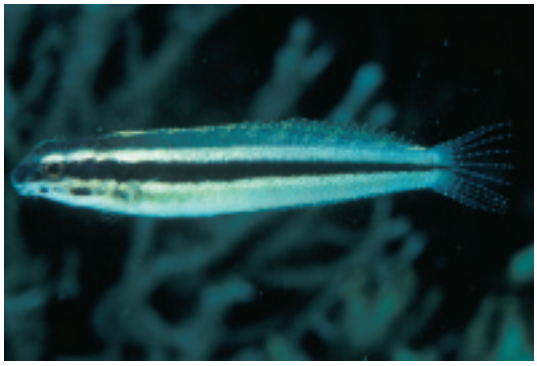


Fig. 53. *Petroscirtes breviceps*, Papua New Guinea.

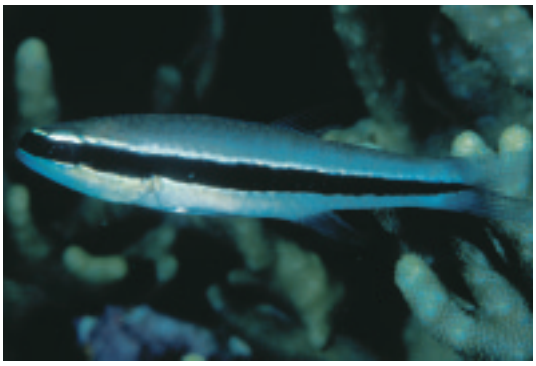


Fig. 54. *Cheilodipterus parazonatus*, Papua New Guinea.

Fig. 55. *Scolopsis margaritifera*, Solomon Is. (Gerald R. Allen).

Fig. 56. *Meiacanthus anema*, Ambon, Indonesia.

Fig. 57. *Amblygobius linki*, Ambon, Indonesia.

Scolopsis margaritifera (Fig. 55).

Springer and Smith-Vaniz (1972) found a museum jar containing a mixture of *Meiacanthus anema* (Bleeker) and the goby *Amblygobius linki* Herre from Buru, Indonesia that had been sorted as 1 species. Both the blenny and the goby have a similar black-striped color pattern in preservative. They wrote, "these two similar species could possibly be involved in a mimetic relationship." The venomous fangblenny would therefore be the model for the mimicking goby. However, they added that the color illustration of *M. anema* by Bleeker from the type locality of Ambon, Indonesia showed the pale spaces between the black stripes as yellow, whereas Herre described the color of *A. linki* from the type locality of Bungau, Sulu Province, Philippines as blue with black stripes. The author collected both species from a brackish area in Ambon Bay, and his photographs (shown here as Figs. 56 and 57) support the suggestion of Batesian mimicry. If *Amblygobius linki* is blue and black in the Philippines, it would be of interest to know if *Meiacanthus anema* occurs in the same area and has the same color. Also it would be more convincing as an example of mimicry if the goby were known to adopt a mode of swimming like the blenny.

Sazima (2002a) presented convincing evidence with color illustrations to show that the juvenile of the haemulid *Pomadasys ramosus* in southeastern Brazil mimics the juvenile of the carangid *Oligoplites palometa*, a species with venom glands in its dorsal and anal spines. He also summarized 24 examples of Batesian mimicry in marine fishes (his table 1).

Springer and Smith-Vaniz (1972) pointed out that the model-mimic pairs of species of *Meiacanthus* and *Plagiotremus* are also Müllerian mimics. Fishes do not prey upon species of *Meiacanthus* because of the venomous bite they can expect, and they try to prevent the species of *Plagiotremus* from approaching within striking range. Both species of fangblennies of a mimic-model pair are avoided by predators; therefore their protection is enhanced by their similarity.

Aggressive mimicry (Wickler 1965 1968), sometimes known as Peckhamian mimicry (after E.G. Peckham, who discovered it while studying spiders), is used to depict an animal or a part thereof that enables a predator to get closer to its prey or to attract its prey to within striking range. Therefore, the Batesian blenny mimic *Aspidontus taeniatus* is also an aggressive mimic (Batesian in resembling the protected Cleaner Wrasse *Labroides dimidiatus*, and aggressive when it bites pieces from the fins of other fishes). The same is true of the mimic species of fangblennies (also called sabertooth blennies) of the genus *Plagiotremus*. Most of the other aggressive mimics operate as mimics only in the juvenile phase. They change to the different adult coloration when they become larger than their models.

Hobson (1969) reported that *Plagiotremus azaleus*, the only fangblenny from the eastern Pacific, aggregates with the labrid *Thalassoma lucasanum*. Although not closely resembling the wrasse, this deceptive behavior improves the success of its attacks on reef fishes for mucus and epidermal tissue. Russell et al. (1976) observed *Plagiotremus tapeinosoma* schooling with the labrid fish *Thalassoma amblycephalum*, the plesiopid *Trachinops taeniatus* (Fig. 58), and the tripterygiid *Forsterygion* sp. for the same advantage. They also reported individuals of an unusual orange color morph of *Plagiotremus rhinorhynchos* swimming with an aggregation of orange *Anthias mortoni* (now *Pseudanthias huchtii*) and actively feeding on zooplankton in the passing current.

Fig. 58. *Plagiotremus tapeinosoma* in school of *Trachinops taeniatus*, New South Wales (Barry C. Russell).

Fig. 59. *Iracundus signifer*, Hawaiian Is.

They wrote: "From amongst the group of anthiines *P. rhynorhynchos* launched a series of attacks against passing fishes, ..." William F. Smith-Vaniz (pers. comm.) made a similar observation in Fiji. While watching a feeding aggregation of yellow *Pseudanthias squamipinnis*, with about 6 *Ecsenius midas* swimming with them (discussed below as an example of social mimicry), he was surprised to see 2 *Plagiotremus rhinorhynchos* in the group, 1 entirely yellow and the other with only a trace of the usual blue stripes.

Perhaps the best-known examples of aggressive mimicry are found in the frogfish family Antennariidae (and other ceratioids) that use a modified 1st dorsal ray as a lure called the illicium. The esca (bait) at the tip of the illicium can look very much like a small fish, worm, shrimp, or octopus and serves to attract prey to within striking distance of the mouth of the frogfish (Pietsch and Grobecker 1978 1987). Similarly, the slender lure from tissue inside the lower jaw of some of the stargazers (*Uranoscopus*) is enticingly wriggled like a worm from the mouth of an otherwise hidden stargazer. One snake eel, *Glenoglossa wassi* McCosker, 1982, has adopted a comparable oral lure. Also, the elongate frilled 1st dorsal ray of the flatfish *Asterorhombus fijiensis* has been shown to serve as a lure (Amaoka et al. 1994), as has that of *A. intermedius*, reported by Manabe and Shinomiya (1998).

An unusual example of luring behavior was discovered in the Indo-Pacific scorpionfish, *Iracundus signifer* (Fig. 59), by Shallenberger and Madden (1973). The dorsal fin looks very much like a small fish. The black spot on the 2nd fin membrane is the eye (which enlarges during luring), the gap between the 1st and 2nd spines is the mouth, and the long 4th dorsal spine is the 1st dorsal spine of the lure. They wrote: "Typically, the lure was snapped from side to side. The first two spines of the spinous dorsal initiated this movement and the rest of the fin followed in a sinuous wave down the back." The 1st and 2nd dorsal spines are alternately closed together then separated, giving the effect of respiration. The resemblance to a small moving fish is remarkable (the authors showed me a motion picture film of the behavior). The prey included apogonid and other scorpaenid fishes up to 1/2 the body length of the predator.

Fig. 60. *Antennarius striatus* and *Astropyga radiata*, Mindoro, the Philippines (Frank Schneidewind).

Schneidewind (2004) provided an example of the frogfish *Antennarius striatus* as a Batesian mimic of the very venomous sea urchin *Astropyga radiata* (Fig. 60). Sea urchins of the genus *Diadema* would be a closer model in color. The esca ("bait") of the frogfish looks like a succulent white or pink worm, so this frogfish is also an aggressive mimic. Sazima (2002b), however, preferred not to regard lures from part of the body of predatory fishes as true examples of aggressive mimicry.

Three of the western Atlantic butter hamlets

Fig. 61. *Chromis cyanea*, Bahamas.

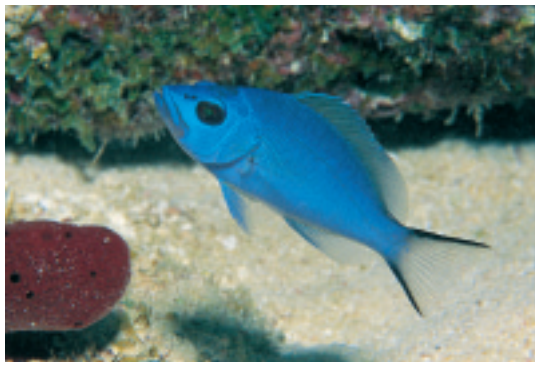


Fig. 62. *Hypoplectrus gemma*, Florida, USA (Paul Humann).

Fig. 63. *Microspathodon chrysurus*, Belize.

Fig. 64. *Hypoplectrus chlorurus*, Puerto Rico.

Fig. 65. *Stegastes diencaeus*, Belize.

Fig. 66. *Hypoplectrus nigricans*, Bahamas.

(*Hypoplectrus* spp.) are regarded as aggressive mimics of harmless damselfishes and thereby get closer to their prey (Randall and Randall 1960). *Chromis cyanea* (Fig. 61) is the model for *H. gemma* (Fig. 62); *Microspathodon chrysurus* (Fig. 63) is the model for *H. chlorurus* (Fig. 64); and uniformly dark brown species of *Stegastes* such as *S. diencaeus* (Fig. 65) are the models for *H. nigricans* (Fig. 66). Thresher (1978) added 3 other mimetic pairs involving *Hypoplectus*, including the young of the angelfish *Holacanthus tricolor* which serves as the model for *Hypoplectrus guttavarius*. Domeier (1994) suggested that these are just chance resemblances, noting that the hamlets do not appear to mimic the behavior of any of the models. However, he added: "It is possible that the recent evolutionary history of *Hypoplectrus* has not allowed for the complete development of typical mimic characteristics." Species of *Hypoplectrus* feed more on crustaceans than on fishes (Randall 1967). Thresher pointed out that the crustacean compound eye, while very sensitive to movement and overall color, does not permit good form vision. Except for the final attack, hamlets move

Fig. 67. *Lutjanus bohar,* juvenile, Sulawesi, Indonesia.

Fig. 68. *Chromis ternatensis*, Sangihe Is., Indonesia.

Fig. 69. *Lutjanus bohar,* juvenile, Fiji (Gerald R. Allen).

Fig. 70. *Chromis margaritifer*, Indonesia.

Fig. 71. *Lutjanus bohar,* large juvenile, Tuamotu Archipelago.

Fig. 72. *Chromis iomelas*, Tuamotu Archipelago.

slowly toward their prey. A general resemblance in color and general shape to a harmless damselfish model would be expected to result in greater success for a predator of crustaceans.

Russell et al. (1976) reported the juvenile of the piscivorous snapper *Lutjanus bohar* (Fig. 67) to be an aggressive mimic of the damselfish *Chromis ternatensis* (Fig. 68), both wide-ranging in the Indo-Pacific. They found a different color form of *L. bohar* (Fig. 69) in Samoa, with *Chromis margaritifer* serving as the model (Fig. 70). *Lutjanus bohar* of figure 71 is mimicking still another white-tailed *Chromis*, *C. iomelas* (Fig. 72), from the South Pacific. The snapper of figure 72 has reached a size larger than its model, so it is starting to assume the adult color pattern. Moyer (1977) wrote that juveniles of *L. bohar* seem to mimic the following species of *Chromis* in Japan: *C. flavomaculata*, *C. weberi*, *C. lepidolepis*, and *C. miyakeensis* (a synonym of *C. notata*).

Russell et al. (1976) were also the first to publish the amazing similarity of the juvenile grouper *Anyperodon leucogrammicus* (Fig. 73) to female wrasses of the genus *Halichoeres*. Their choice of

Fig. 73. *Anyperodon leucogrammicus*, juvenile, Sulawesi, Indonesia.

Fig. 74. *Halichoeres leucurus*, female, Palau.

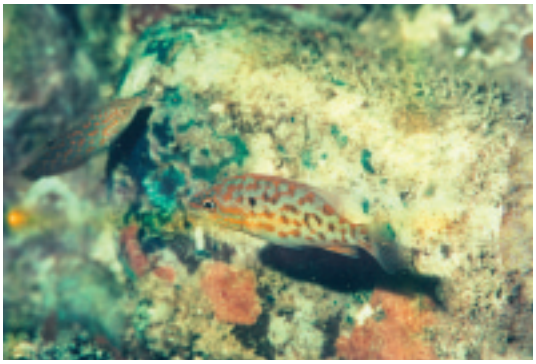


Fig. 75. *Anyperodon leucogrammicus*, juvenile, Sri Lanka (R. Charles Anderson).

Fig. 76. *Halichoeres timorensis*, female, Sri Lanka.

Fig. 77. *Epinephelus multinotatus*, juvenile, Kuwait.

Fig. 78. *Neopomacentrus sindensis*, Bahrain.

Fig. 79. *Oxycheilinus mentalis*, Red Sea.

Fig. 80. *Oxycheilinus mentalis* and *Parupeneus macronemus*, Red Sea (Richard Field).

Fig. 81. *Epibulus insidiator*, female, Red Sea.

Fig. 82. *Pomacentrus sulfureus*, Red Sea.

the model, *H. biocellatus*, is not as close a match as the females of *H. leucurus* (*H. purpurescens* is a synonym) (Fig. 74), *H. melanurus*, *H. richmondi*, and *H. vrolickii*, as shown by Randall and Kuiter (1989).

The documentation of mimicry is enhanced when the mimic exhibits a color pattern to resemble a different model. Such is the case of juvenile *Anyperodon leucogrammicus* in Sri Lanka (Fig. 75), where it mimics the female of *Halichoeres timorensis* (Fig. 76), very different in color from species of the *H. leucurus* complex.

Randall (1995) proposed that the juvenile of the grouper *Epinephelus multinotatus* (Fig. 77) is a mimic of the damselfish *Neopomacentrus sindensis* (Fig. 78) of the Persian Gulf and Arabian Gulf, as first suggested by Nigel Downing (pers. comm.).

Kuiter (1995) regarded the juvenile of the grouper *Plectropomus oligacanthus* as a mimic of the wrasse *Cheilinus celebicus* (now classified in *Oxycheilinus*) from underwater observation in the Seribu Is. north of Jakarta. However, his model is also a predator with "a similar diet." He noted that the grouper of the same size as the wrasse has a larger mouth, hence would take larger prey than *Oxycheilinus*. His figure of the *Plectropomus* is not very convincing as being similar in color or shape to *Oxycheilinus celebicus*. I regard this as a questionable example of aggressive mimicry.

Oxycheilinus mentalis of the Red Sea and western Indian Ocean, a close relative of *O. celebicus*, is a mimic (not a model for an aggressive mimic), as shown by Ormond (1980), who misidentified it as *Oxycheilinus digrammus*. He wrote that it is "able to rapidly change its color to match that of the fish close to which it is swimming" and gave examples of nonpredatory parrotfishes and surgeonfishes with which it swims. Figure 79 shows its non-mimetic color pattern. When *O. mentalis* is close to the goatfish *Parupeneus macronemus* (Fig. 80), it quickly becomes pale with a midlateral dark stripe. Ormond added, "It appears to feed on small fish, fish larvae and perhaps crustaceans."

Ormond provided another example of a labrid fish as an aggressive mimic, the Indo-Pacific Slingjaw Wrasse *Epibulus insidiator*. Resident herbivorous fishes of inshore Red Sea reefs, such as *Acanthurus sohal*, *Plectroglyphidodon lacrymatus*, and *Stegastes nigricans*, vigorously defend the algal substratum of their territory. The surgeonfish *Zebrasoma desjardinii* forms feeding aggregations in order to invade this territory. Ormond wrote, "An adult *E. insidiator*, on seeing such a school of *Z. veliferum* [the Red Sea/western Indian Ocean species of Sailfin Tang is now *Z. desjardinii*], will typically swim over to join it, at the same time changing colouration to an overall dark brown-black, similar to that of the *Zebrasoma*. Within the middle of a *Zebrasoma* school, *Epibulus* is thus difficult to distinguish from the other fish (see Plate II); its hunting approaches to the substrate appear much the same as the grazing movements of *Zebrasoma*. Possibly *Epibulus* may even take some of the smaller pomacentrids that are attempting to defend their territories."

One female color form of *Epibulus insidiator* is entirely bright yellow or yellow with a narrow black bar on each scale of the body (Fig. 81). It is regarded as a probable mimic of the yellow damselfish *Pomacentrus sulfureus* (Fig. 82) of the Red Sea and western Indian Ocean (Field, 1997). Perhaps the same strategy is used to approach other yellow damselfishes of the genus *Pomacentrus*, such as *P. pikei* of the Mascarene Is., *P. moluccensis* of the eastern Indian Ocean and western Pacific, or *Stegastes aureus* of the

Fig. 83. *Mycteroperca tigris*, juvenile, Anguilla (Paul Humann).

Fig. 84. *Thalassoma bifasciatum*, initial phase, Virgin Is.

Fig. 85. *Aethaloperca rogaa*, juvenile, Bali, Indonesia.

Fig. 86. *Centropyge fisheri*, Papua New Guinea.

South Pacific. Just comparing photos of *Epibulus* and damselfishes, one might be skeptical that mimicry is involved. However, in aggressive mimicry, the mimic does not have to precisely duplicate the color and shape of the model to gain the advantage of getting closer to its prey (Roberts 1990). A Batesian mimic generally needs to be a more-exact replica of its model because the mimetic role is to avoid predation.

Sikkel and Hardison (1992) concluded from quantitative observations that the Yellowtail Snapper *Ocyurus chrysurus* is an aggressive mimic of the Yellow Goatfish *Mulloidichthys martinicus*, both wide-ranging in the tropical and subtropical western Atlantic. Both are primarily white with yellow fins and a yellow stripe from the eye to the caudal fin. The snapper, a predator on a variety of fishes and benthic invertebrates (chiefly crustaceans), has greater foraging success when it accompanies the goatfish. Not only does it approach its prey more readily in its guise of the goatfish, but it feeds on fishes and crustaceans flushed by the rooting of the goatfish in the substratum.

Snyder (1999) discovered that the juvenile of the grouper *Mycteroperca tigris* (Fig. 83) is a mimic of the juvenile and initial phase of the abundant *Thalassoma bifasciatum* (Fig. 84) in coloration, size, and swimming mode. Both species are widely distributed in the western Atlantic. He wrote, "By imitating a non-predatory cleaner fish, the mimic appears to enjoy a twofold advantage – it both facilitates prey capture and avoids predation."

Sazima (2002b) found 2 other groupers of the genus *Mycteroperca* that are aggressive mimics of wrasses from his observations in southeastern Brazil. *Halichoeres maculipinna* (whose name was changed to *H. penrosei* by Rocha 2004 for this Brazilian sister species) is the model for *Mycteroperca interstitialis*, and *H. poeyi* is the model for *M. acutirostris*.

Snyder et al. (2001) reported the aggressive mimetic relationship of the juvenile of the Indo-Pacific grouper *Aethaloperca rogaa* (Fig. 85) with dark species of angelfishes of the genus *Centropyge*, such as *C. fisheri* (*C. flavicauda* is a synonym) (Fig. 86) and dark damselfishes of the genera *Pomacentrus* and *Stegastes*.

Still another grouper mimic is the juvenile of the Indo-Pacific *Plectropomus laevis* (Fig. 87), which closely resembles the small toxic toby *Canthigaster valentini* (Fig. 88) (Randall 2005).

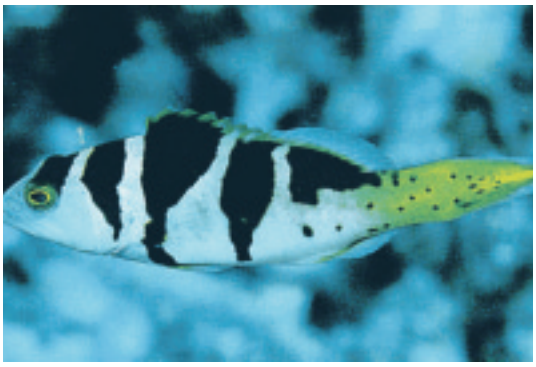


Fig. 87. *Plectropomus laevis*, juvenile, Ogasawara Is. (Hajime Masuda).

Fig. 88. *Canthigaster valentini*, Great Barrier Reef.

Fig. 89. *Paraluteres prionurus*, Tonga.

Fig. 90. *Paraluteres arqat*, Red Sea (Richard Field).

Fig. 91. *Canthigaster margaritata*, Red Sea.

Again, there is a dual basis for the mimicry. Predators do not target species of *Canthigaster* and may therefore overlook the small grouper. Furthermore, by resembling the toby, the grouper can approach its prey more closely.

The Indo-Pacific filefish *Paraluteres prionurus* (Fig. 89) also mimics *Canthigaster valentini*, as shown by Clark and Gohar (1953), Tyler (1966), and Caley and Schluter (2003). The Red Sea *Paraluteres arqat* (Fig. 90) is a mimic of *Canthigaster margaritata* (Fig. 91), as first suspected by Clark and Gohar (1953). The filefishes of the genus *Paraluteres* are usually seen with the 1st dorsal fin fully depressed; once this fin is erect, the effect of mimicry is reduced. The 2nd dorsal fin of *Paraluteres* is broader than that of *Canthigaster*, but it is nearly transparent. Males of *Paraluteres* have 2 pairs of spines on each side of the caudal peduncle; however, these are less apt to betray their deception than an erect 1st dorsal fin.

Sazima (2002b) reported the juvenile of the snook *Centropomus mexicanus* to be an aggressive mimic of the mojarra *Eucinostomus melanopterus* from observations in southeastern Brazil. By resembling the mojarra in shape and color pattern, especially the black-tipped spinous dorsal fin, the snook is able to closely approach otherwise wary prey. It often joins foraging mojarras in order to take advantage of prey dislodged from the substrate by the feeding mojarras. Within an aggregation of mojarras, a snook may also enjoy the protection from predators by schooling. Sazima also found *Centropomus parallelus* in aggregations of the mojarras *Eucinostomus melanopterus* and *E. argenteus* and suggested that this snook may also be an aggressive mimic. He added that *Centropomus unionensis* and

Fig. 92. *Pseudochromis fuscus*, Flores, Indonesia.

Fig. 93. *Pomacentrus chrysurus*, Sumatra, Indonesia.

Fig. 94. *Pseudochromis fuscus*, Bali, Indonesia.

Fig. 95. *Pomacentrus moluccensis*, Gulf of Thailand.

Eucinostomus currani of the Pacific coast of South America may be a mimetic pair as well, judging from their similarities in color pattern and distribution. He provided in tabular form a review of 39 examples of aggressive mimicry in fishes. He divided aggressive mimicry into 3 categories: "(1) fish species that feed on smaller prey than themselves tend to mimic and join fish species harmless to their prospective prey; (2) fish species that feed on larger prey than themselves tend to mimic mostly beneficial fish species (cleaners) or, less frequently, join species harmless to their prospective prey; (3) fish species that feed on prey about their own size tend to mimic their prospective prey species, the "wolf in a sheep's clothes" disguise type."

One of Sazima's 39 examples is from the 3rd category, the carangid *Oligoplites saurus* that mimics the atherinid *Atherinella brasiliensis* (Sazima and Uieda 1980). The carangid joins aggregations of its model and feeds by removing scales from its prey. This is the only known marine example of his type 3 aggressive mimicry.

One would not think that the dottyback *Pseudochromis fuscus* could be an aggressive mimic of damselfishes of the genus *Pomacentrus*, but Munday et al. (2003) demonstrated this from their field research on the Great Barrier Reef. *Pseudochromis fuscus* occurs in 2 distinctly different color morphs: brown (Fig. 92), which is colored like *Pomacentrus chrysurus* (Fig. 93); and yellow (Fig. 94), which most resembles either *P. amboinensis* or *P. moluccensis* (Fig. 95). They noted in the field that the brown dottyback associates with *P. chrysurus*, and the yellow one with the yellow damselfishes. Multiple-choice experiments in the laboratory revealed that the dottyback preferentially selects habitat patches occupied by damselfishes of the same coloration. *Pseudochromis fuscus* is a predator of small fishes, including newly recruited damselfishes.

The example by McCosker (1977), who depicted the fright posture of the Indo-Pacific plesiopid fish *Calloplesiops altivelis*, commonly known as the Comet, is unique. It hides in the reef by day and emerges at dusk. When threatened, it moves headfirst into a hole but leaves the posterior part of its body exposed and expands its fins. It then resembles the head of the moray eel *Gymnothorax meleagris*, with an ocellated black spot at the rear base of the dorsal fin which looks like the moray's eye. This might seem disputable as an example of

Fig. 96. *Novaculoides macrolepidotus*, subadult, Kenya (Andrew Spreinat).

Fig. 97. *Ablabys taenianotus*, Mindoro, the Philippines (Andrew Spreinat).

mimicry until one witnesses the behavior. Photographs of the mimic and model made the cover of *Science* (vol. 97).

Randall and Spreinat (2004) reported the subadult of the Seagrass Wrasse *Novaculoides macrolepidotus* (Fig. 96) to be a mimic of venomous waspfishes of the genus *Ablabys*. Their illustration of the model is the Cockatoo Waspfish (*A. taenianotus*) (Fig. 97). The wrasse (adult shown above as Fig. 14) is usually very cryptic, but the individual of figure 96 was exposed and very sedentary, rocking to and fro like a species of *Ablabys*, and holding its dorsal fin fully erect. It was easily photographed at close range because of its reluctance to move. The fish is also an example of protective coloration in that it resembles a fragment of plant material as well as a waspfish.

Angelfishes of the genus *Centropyge* are mimicked by young of the surgeonfish *Acanthurus pyroferus* (Fig. 98). When first observed and collected in Tahiti in 1956, the author thought it was a

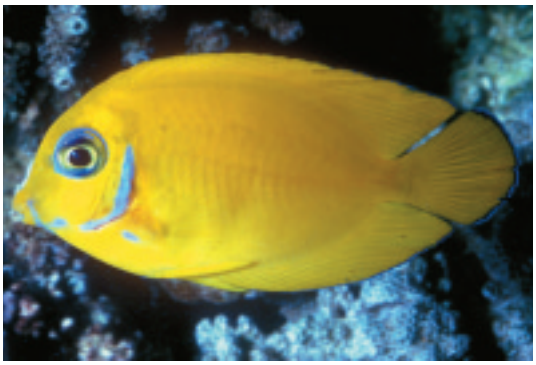


Fig. 98. *Acanthurus pyroferus*, juvenile, Line Is.

Fig. 99. *Centropyge flavissima*, Society Is.

Fig. 100. *Acanthurus pyroferus*, large juvenile, Tahiti.

Fig. 101. *Acanthurus pyroferus*, adult, Marshall Is.

Fig. 102. *Acanthurus pyroferus*, juvenile, Scott Reef, Western Australia.

Fig. 103. *Centropyge vrolikii*, Ambon, Indonesia.

Fig. 104. *Acanthurus tristis*, Bali, Indonesia.

Fig. 105. *Acanthurus tristis*, juvenile, Sumatra.

Fig. 106. *Centropyge eibli*, Bali, Indonesia.

new species of acanthurid. Its striking resemblance to the common small angelfish *Centropyge flavissima* (Fig. 99) immediately suggested mimicry, but it was not clear which was the mimic and which was the model until individuals of the surgeonfish were seen that were beginning to turn brown (Fig. 100), and eventually became the typical *A. pyroferus* adult (Fig. 101). Knowing that juvenile angelfishes of some species of the genera *Holacanthus* and *Pomacanthus* opportunistically clean reef fishes, the little *C. flavissima* was suspected of being a part-time cleaner and therefore protected from predation. Underwater observation and analysis of gut contents of 50 specimens soon disproved that, as no ectoparasites were found. Most of the food material was algal, with some sponge. Then the possibility that the angelfish might have some quality which repels predators was tested, but the fish were readily eaten when speared specimens were offered to jacks and groupers. In writing of the results of that study, Randall and Randall (1960) admitted to not knowing the biological basis of the mimicry. Years later, after experiencing the difficulty of taking underwater photographs of species of *Centropyge*, the author determined that these small angelfishes are extremely wary and quickly take cover in the reef when approached. Predators presumably learn the same and target easier prey.

In the more western part of the Pacific, the young of *Acanthurus pyroferus* (Fig. 102) usually mimic *Centropyge vrolikii* (Fig. 103), the most common species of the genus in Australia and New Guinea (Allen et al. 1998), ranging north to Japan and west to Sumatra. *Acanthurus tristis* (Fig. 104), a close relative of *A. pyroferus*, occurs in the eastern Indian Ocean, including the Andaman Sea and islands of southwestern Indonesia. There the

juvenile (Fig. 105) mimics *Centropyge eibli* (Fig. 106).

Another explanation for the benefit of the mimicry of *Centropyge vrolikii* by the young of *Acanthurus pyroferus* was offered by Eagle and Jones (2004) from observations of these 2 species and the territorial damselfish *Plectroglyphidodon lacrymatus* in Papua New Guinea. They found that the mimic surgeonfish occurs within 1~2 m of similar-sized individuals of the angelfish. The surgeonfish was attacked less frequently by the aggressive damselfish than were other surgeonfishes. The most abundant food category of the angelfish was reported to be sponge material, whereas the diet of the mimic surgeonfish was predominately detrital material and sediment, with small amounts of algae. This was more similar to the food of *P. lacrymatus*, so Eagle and Jones hypothesized, "Mimics may be deceiving the damselfish as to their true diet, which more closely matches the diet of the damselfish than the diet of the angelfish." Sponges dominate the food habits of angelfishes of the genera *Holacanthus* and *Pomacanthus* (Randall and Hartman 1968), but reports of the food habits of species of *Centropyge* have not shown that sponges are an important food source. Hiatt and Strasburg (1960) examined the gut contents of 4 *C. flavissima* from the Marshall Is. and reported it to be entirely herbivorous. Randall (1967) found only algae and detritus in 5 specimens of *C. argi* from the West Indies. Hobson (1974) examined the gut contents of 5 specimens of the endemic Hawaiian *C. potteri*. Filamentous algae were the major food source, but there was much unidentified debris, including sand and foraminiferans; sponges were found in small amounts (with a ranking index of 2.3, compared to 41.7 for algae and 42.3 for the unidentified debris). I examined the stomach contents of 3 specimens of *C. potteri* after collecting them in 1971 and 1972. I found mainly filamentous algae, some detritus, a little fine sediment, and no sponge material. I examined the stomach contents of 8 Bishop Museum specimens of *C. vrolikii* for this report. Only 1 from Ishigaki, Ryukyu Is. had more than 50% of the food composition as sponge material. The others from the Great Barrier Reef, Indonesia, Palau, and Okinawa had eaten mainly algae and detritus (probably mostly diatoms); the stomachs of only 3 of these specimens contained a trace of sponge. It is suggested that the sample size for the food-habit study by Eagle and Jones (2004) was small, and unusual in containing so much sponge material. The reason for the fewer attacks by the damselfish on juvenile *Acanthurus pyroferus* is more likely a benefit of less aggression towards the model angelfish because of the wary behavior of the latter, which darts to the shelter of the reef when threatened. Food habits, however, are an important consideration. Becsuse the surgeonfish is more restricted in its diet to filamentous algae, it probably requires a broader feeding area than the angelfish and is therefore more exposed to predation.

Fig. 107. *Acanthurus pyroferus*, juvenile, Vanuatu (Larry Sharron).

Fig. 108. *Centropyge flavissima* x *C. vrolickii*, Marshall Is.

There is a question as to whether *Acanthurus pyroferus*, which mimics *Centropyge flavissima* in the central and eastern islands of the South Pacific, is the same species as the one in the western Pacific where its young usually resemble *C. vrolikii*. In an area where both species of *Centropyge* occur, and there is only 1 adult form of *Acanthurus pyroferus*, it would seem that the juvenile surgeonfish has the capability of mimicking either species of *Centropyge*, perhaps depending on which one is most common in the area of its settlement on the reef. Evidence for this came from Vanuatu where both species of *Centropyge* occur, as well as hybrids of the two. Juveniles of *Acanthurus pyroferus* have been collected by Larry Sharron at Vanuatu that are mimics (Fig. 107) of

Fig. 109. *Labroides dimidiatus*, Papua New Guinea (Gerald R. Allen).

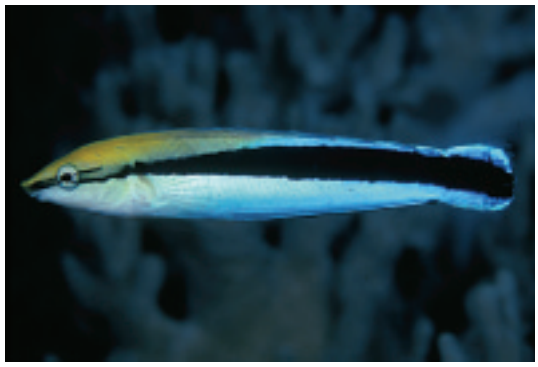


Fig. 110. *Aspidontus taeniatus*, Alor, Indonesia.

Fig. 111. *Labroides dimidiatus*, Tuamotu Archipelago.

the hybrid (Fig. 108).

Barnard (1927) was the first to report the amazing resemblance of the wrasse *Labroides dimidiatus* to the fangblenny *Aspidontus taeniatus* from observations in South Africa. He noted that there are 2 varieties of each species, one with a dark band across the base of the pectoral fin and one without. He wrote, "It would be premature to claim this as a case of mimicry until observations have been made on the habits of these two species and on the possible poisonous qualities of one or the other."

Randall (1955) also observed the close similarity of *Labroides dimidiatus* (Fig. 109) and *Aspidontus taeniatus* (Fig. 110) from fieldwork in the Gilbert Is. (Kiribati) in 1951. He described the unusual mode of swimming of the wrasse, which oscillates the posterior part of its body up and down as if to attract attention, and he saw it picking at the bodies of other fishes. He found calagoid copepods and small isopods in the stomachs of the wrasse and suggested that the blenny is mimicking it because of protection from predation gained by the wrasse due to its parasite-feeding habit.

As a result of field research in Moorea, Society Is. in 1956, Randall and Randall (1960) reported that *Aspidontus taeniatus* feeds in part on the fins of reef fishes. In its guise of the Cleaner Wrasse, and by remaining in the vicinity of a cleaning station, it is able to more closely approach its prey (often juvenile or subadult reef fishes, rather than adults that have learned to avoid it). Juveniles of *Labroides dimidiatus* are black except for a bright blue dorsal stripe, and they gradually change to the adult pattern with growth. The Mimic Blenny matches the color the Cleaner Wrasse of the same size as it grows.

Fig. 112. *Labroides dimidiatus*, Fiji (Gerald R. Allen).

Fig. 113. *Aspidontus taeniatus*, Fiji (Gerald R. Allen).

There is a common 2nd color form of *Labroides dimidiatus* in the Society Is. and the Tuamotu Archipelago that has a salmon pink area near the middle of the body beneath the black stripe (Fig. 111). *Aspidontus taeniatus* lurking in the vicinity of a Cleaner Wrasse of this color pattern on the fringing reef of Moorea was observed to exhibit the same color variation. Does the Mimic Blenny adopt a permanent color pattern to match the *Labroides* model in the area where it is resident, or is it able to alter its pattern if it finds itself in the area with a model of a different color? Catching the Mimic Blenny and switching it to an area with a normal-colored individual, and vice versa, was considered to see if the 2 blennies would change their color to match the new models of *Labroides*. This was not attempted because there was too much opportunity for the displaced blennies to relocate along the linear reef. Ideally, such a transplantation should be made in a lagoon with well-isolated patch reefs, or in large aquaria.

The author collected a specimen of a blenny of the genus *Aspidontus* at Ua Pou in the Marquesas Is. in 1971 that was whitish, becoming yellow posteriorly and on the caudal fin; its dark stripe was not as black as that of *A. taeniatus*, and it had a series of white dots along the upper margin. Typical *Aspidontus taeniatus* and its usual model, *Labroides dimidiatus*, are present in the Marquesas. Because the specimen seemed to represent a new species, it was sent to William F. Smith-Vaniz. He identified it as *A. taeniatus* and illustrated it in an update of his review of sabertooth blennies (Smith-Vaniz 1987: fig. 1C). It is now realized that the fish that served as the blenny's model was the female of the wrasse *Coris hewetti*, at that time undescribed (see Randall 1999: pl. 20, fig. C).

A color variant of *Labroides dimidiatus* with a posterior section of the black stripe replaced by bright yellow (Fig. 112) occurs in the South Pacific from the Samoa Is. to the Coral Sea. No morphological differences could be found to separate it from typically colored specimens of *L. dimidiatus* with which it coexists; however a DNA analysis is suggested to ascertain whether these are merely color variants. Individuals of *Aspidontus taeniatus* near the yellow-marked Cleaner Wrasse have the same color pattern (Fig. 113).

A short-term change in color pattern was demonstrated for the juvenile of the fangblenny *Plagiotremus rhinorhinchos*. Like *Aspidontus taeniatus*, this species is regarded as a mimic of *Labroides dimidiatus*, although as an adult (Fig. 114), it is not as precise a mimic as *A. taeniatus*. Nevertheless, it enjoys a higher striking rate in its attempts to feed on the skin of reef fishes when in the proximity of a Cleaner Wrasse (Côte and Cheney 2004). The juvenile of *A. taeniatus* (Fig. 115) more closely matches the color of juvenile *L. dimidiatus* (Fig. 113) (Kuwamura 1981). In an impressive field experiment in Kimbe Bay, New Britain, Moland and Jones (2004) found 92% of mimetic *P. rhinorhinchos* closely associated with juvenile *L. dimidiatus*. When the Cleaner Wrasse

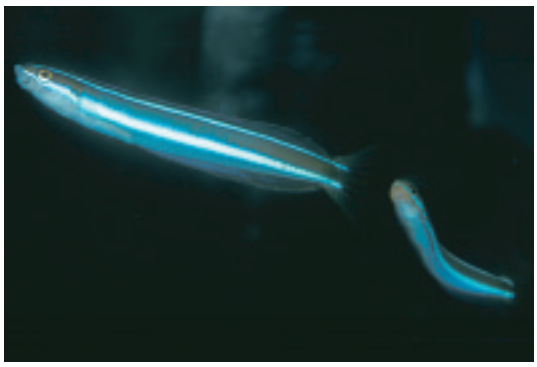


Fig. 114. *Plagiotremus rhinorhynchos*, Wetar, Indonesia.

Fig. 115. *Plagiotremus rhinorhynchos*, juvenile, Flores, Indonesia.

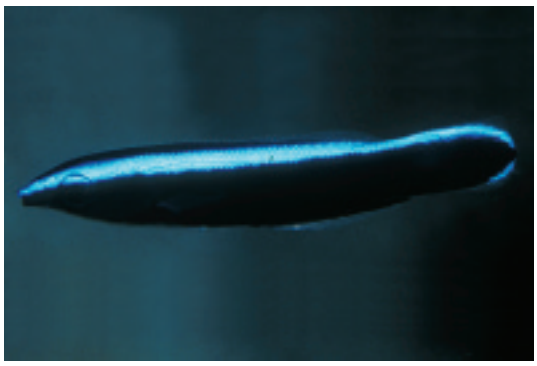


Fig. 116. *Labroides dimidiatus*, juvenile, Moyo I., Indonesia.

Fig. 117. *Ecsenius midas*, Flores, Indonesia.

Fig. 118. *Pseudanthias squamipinnis*, Red Sea.

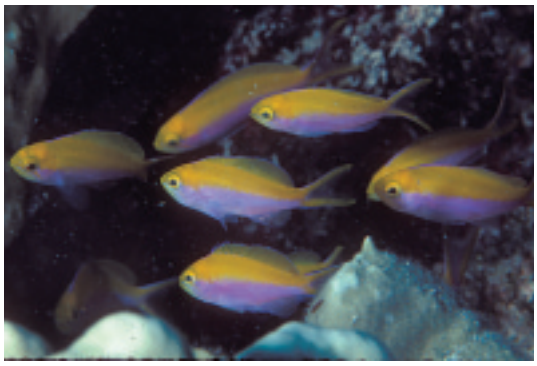


Fig. 119. *Pseudanthias bartlettorum*, Line Is.

Fig. 120. *Pseudanthias dispar* (above) and *Luzonichthys whitleyi*, Line Is.

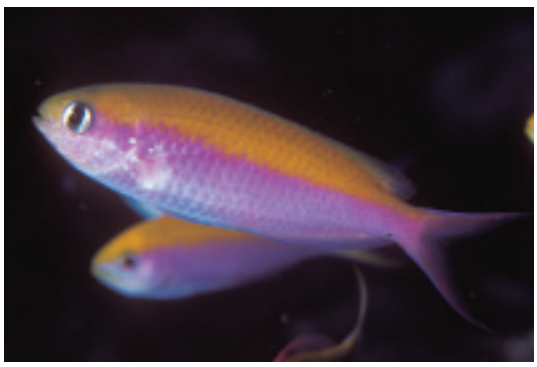


Fig. 121. *Lepidozygus tapeinosoma*, Line Is.

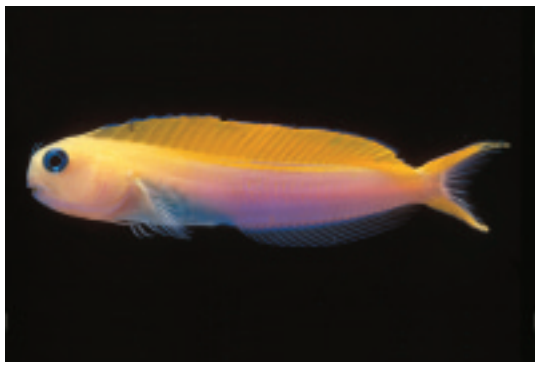


Fig. 122. *Ecsenius midas*, Line Is.

was present, 80% of the fangblenny attacks on prey fishes were successful. When they removed the Cleaner Wrasse, the fangblenny began to change color the 1st day, and by the 7th day it had reverted to its non-mimetic pattern. The success rate of its attacks dropped by 10% the 1st day, and to 20% by the 7th day.

Plagiotremus rhinorhinchos relies heavily on removing mucus and epidermal tissue of prey fishes for its food. *Aspidontus taeniatus* feeds much less frequently by biting pieces from the fins of other fishes, in spite of its closer resemblance to *Labroides dimidiatus* in color, morphology, and mode of swimming. It also feeds on demersal eggs of fishes, and sabellid worm tentacles (Randall and Randall 1960, Kuwamura 1983).

Dafni and Diamant (1984) proposed the term school-oriented mimicry when a normally solitary fish species mingles with a similar aggregating species for the advantage of schooling. Their example was the juvenile of the fangblenny *Meiacanthus nigrolineatus*, which is colored like dark-striped apogonid fishes with a basal caudal spot, and joins their aggregations. Other examples are the blenny *Ecsenius midas* (Fig. 116) which schools with *Pseudanthias* (Fig. 117) (Starck

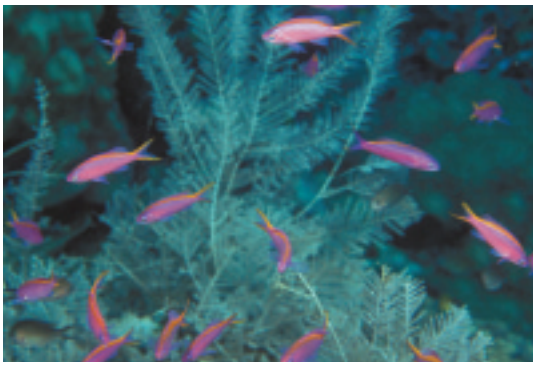


Fig. 123. *Pseudanthias tuka* and *Luzonichthys waitei*, Sulawesi.

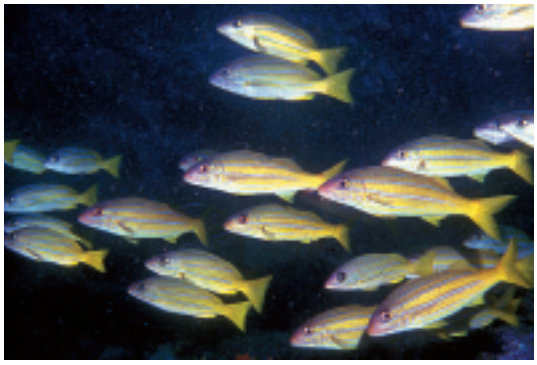


Fig. 124. *Lutjanus kasmira* and *Mulloidichthys mimicus*, Marquesas Is. (John L. Earle).

1969), and the apogonid *Ostorhinchus compressus*, which closely resembles juvenile cardinalfish of the species *Cheilodipterus quinquelineatus* and may aggregate with it (Randall et al. 1990, Kuiter 1991, Allen et al. 2003).

Randall and McCosker (1993) adopted the term social mimicry for fishes, to replace school-oriented mimicry, because the former is in use for mixed flocks of birds. Their example in fishes consisted of the 3 anthiine fishes *Pseudanthias bartlettorum* (Fig. 118), *P. dispar* (Fig. 119), and *Luzonichthys whitleyi* (Fig. 120), the damselfish *Lepidozygus tapeinosoma* (Fig. 121), and the blenniid *Ecsenius midas* (Fig. 122), all with a common yellow and pink color pattern, and which occur in variously mixed schools in the Line Is. and Phoenix Is. These species feed on zooplankton in aggregations above the substratum. The bicolored pattern is the normal coloration only for *P. bartlettorum* and *L. whitleyi*. Randall and McCosker also illustrated *Pseudanthias tuka* and *Luzonichthys waitei* in a mixed aggregation (Fig. 123) as social mimics (in their female color pattern).

Randall and Guézé (1980) described the goatfish *Mulloidichthys mimicus* from the Marquesas Is. and Line Is.; its species name is in reference to its close resemblance to the snapper *Lutjanus kasmira* with which it often schools (Fig. 124). The snapper is mainly nocturnal and tends to form semi-stationary aggregations by day.

Krajewski et al. (2004) presented evidence, including color photos, to show that the western Atlantic Yellow Goatfish *Mulloidichthys martinicus* may be seen in schools with the Smallmouth Grunt *Haemulon chrysargerum*, and is therefore a similar example of social mimicry. One of their photographs shows a previously inactive aggregation of the goatfish joining a school of the grunt when frightened by an approaching diver.

Randall (1998) wrote that herbivorous surgeonfishes of the genus *Acanthurus* may form feeding aggregations of more than 1 species in order to overcome territorial damselfishes trying to protect their private pastures of benthic algae. He provided an illustration of a mixed school of *A. coeruleus* and *A. chirurgus* off the Caribbean coast of Honduras.

Another example of social mimicry was published by Bunkley-Williams and Williams (2000). They observed the juvenile of the Black Snapper *Apsilus dentatus* swimming with a feeding aggregation of Blue Chromis *Chromis cyanea* in 12~27 m on the outer-reef slope in the Cayman Is. Unlike the adult snapper, the juveniles were colored like the damselfish, i.e., blue with a broad black upper and lower margin of the caudal fin. Although slightly larger than the chromis, the snapper were difficult to distinguish. Both the chromis and juvenile snapper feed on zooplankton.

Smith-Vaniz et al. (2001) regarded the fangblenny *Meiacanthus urostigma* as a social mimic of the cardinalfish *Cheilodipterus quinquelineatus*. Both have black stripes and a broad yellow area around a black spot near the base of the caudal fin. The 2nd author of that study, Ukkrit Satapoomin, observed young *M. urostigma* aggregating with juveniles of *C. quinquelineatus*.

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