tached, noncycling cross-bridge might be termed a "latch-bridge," capable of maintaining force but acting as an internal load on the remaining cross-bridges to produce the decrease in velocity (*10*). Attached, noncycling cross-bridges have been postulated in resting smooth muscle (*24*), and their existence is fairly well established for invertebrate smooth muscles of the catch type (*25*).

The basis for the decrease in phosphorylated LC 20 with time cannot be inferred from our data, but must reflect a decrease in the relative activity of kinase to phosphatase. This could come about by enzymatic alteration [see (*26*) for one hypothesis] or different reaction rates for these enzymes when acting on free or attached cross-bridges.

Our results have important functional implications for vascular smooth muscle. On stimulation, there is a fairly rapid initiation of the actin-myosin interaction which has been shown to require phosphorylation of the LC 20. The subsequent decline in phosphorylation and in cycling rates, with maintained numbers of cross-bridges, would produce a high holding economy already demonstrated in this tissue (*27*). This is consistent with the physiological role of arterial smooth muscle, which normally functions tonically, resisting increases in arterial diameter due to blood pressure.

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Chemical Defense Mechanisms on the Great Barrier Reef, Australia

Abstract. *Seventy-three percent of all exposed common coral reef invertebrates, from four phyla (42 species) tested, are toxic to fish. This represents the first evidence of the high incidence of toxicity in the marine tropics among several phyletic groups comprising dominant species. Most of the remaining exposed species have structural defense mechanisms against predation by fish. Of cryptic invertebrates, 25 percent are toxic to fish. The relation between toxicity, fish feeding behavior, community structure, and evolutionary theory is discussed.*

On a visit to the Lizard Island Research Station, north Great Barrier Reef, Queensland, Australia, between 18 May and 5 June 1979, I extended previous research (*1-4*) by conducting studies on common species from several phyla. The results of the laboratory toxicity tests are presented in Table 1 (*5*).

Sponges showed patterns similar to those reported (*4, 6*), that is, there is a relatively high percentage of toxic exposed species although some cryptic species are also toxic. Of the 10 exposed species, four were nontoxic. Of the nontoxic species, *Carteriospongia foliascens* and *Carteriospongia*? sp. are packed with sand grains and are very tough. *Pericharax heteroraphis* has large spicules that are very densely packed, and ? *Hemimycale* sp. is difficult to tear. These characteristics probably serve as physical deterrents to predators; certain of these species may contain mildly noxious compounds not detected by current methods (*4*).

The most toxic sponge was *Haliclona* sp., a cryptic species; toxicity is characteristic of the family Haliclonidae (*4, 6*). The other toxic cryptic sponge (*Chondrilla* sp.) was mildly toxic. Both *Haliclona* sp. and *Chondrilla* sp. may occur as either exposed (subject to fish predation) or cryptic forms since certain species of *Haliclona* show both distributional modes, as does the mildly toxic Caribbean sponge *Chondrilla nucula* Schmidt (*4*).

All but a single species of soft coral studied were toxic. Vermeij (*7*) proposed that those zoanthids and octocorals (*Xenia, Clavularia*) that lack stinging nematocysts may have chemical defenses against grazers since they appear to be eaten by very few fish. The toxicity of *Xenia* sp. in my study supports this contention. Both gorgonian species tested

Table 1. Bioassays of the toxicity to fish of common coral reef animals from Lizard Island, Great Barrier Reef, Australia. A total of 42 frozen species were tested in Sydney; 73 percent of all exposed organisms tested were toxic to goldfish. By exposed is meant that part of the body is exposed to fish or that the animal is exposed to fish during part of the day.

Taxonomic group	Tested	Number of species			
		Exposed		Cryptic	
		Toxic	Non-toxic	Toxic	Non-toxic
Sponges	16	6 (60)*	4	2	4
Soft corals	8	7 (88)	1		
Gorgonians	2	2 (100)			
Asteroids	1		1		
Crinoids	1	1 (100)			
Holothurians	12	6 (100)			6
Ascidians	2		2		

*Numbers in parentheses represent the percent of the total exposed.

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were toxic, as predicted, since gorgonians almost never display evidence of bites from fish and many are toxic to fish, as judged from experiments conducted at Veracruz, Mexico (*2*). The cobalt blue starfish *Linckia laevigata*, the commonest exposed asteroid at Lizard Island, has a very hard skeleton and is well protected from most fish predators by its armor. As predicted, it was nontoxic.

The crinoid *Comatula parvicirrus timorensis* is buried within corals most of the day. It begins to emerge from corals about 2 hours before sunset and is subject to potential fish predation at that time. However, this crinoid is generally avoided by fish since it is toxic, according to my field observations and bioassays. Rideout *et al.* (*8*) reported that a number of comatulids (including *C. parvicirrus timorensis*) contain sulfate esters of polyketides and showed by feeding experiments that these substances provide a chemical defense mechanism against fish.

All of the exposed holothurians tested were toxic to fish; *Bohadschia argus* tested both lethal and mildly toxic, suggesting individual variation in the concentration of toxic steroid saponins. All of the cryptic species were nontoxic. *Holothuria impatiens* was nontoxic to fish on the basis of three tests, whereas two specimens from Mexico (*2*) were toxic to fish. Whether this represents a genetic or seasonal difference is unknown. Two common exposed ascidians were nontoxic to fish. The delicate *Didemnum molle* secretes copious amounts of mucus that perhaps causes it to be avoided by fish (*9*). *Polycarpa aurata* is well protected from many predacious fish by its very tough tunic.

Several simple experiments were designed to observe how a marine fish may detect and reject a toxic food source in the field (*10*). In the first test series, bait was rapidly consumed by pomacentrids and labrids whereas white muscle alone and black epidermis–white muscle of a common toxic holothurian (*Holothuria atra*) was mouthed by several to many fish but rejected. In the second test series, bait was once again rapidly consumed by pomacentrids and labrids whereas black epidermis, plastic-coated black epidermis, and plastic-coated black epidermis with white muscle from the body wall of *H. atra* was mouthed frequently by fish but rejected. One *Paraglyphidodon melas* took a piece of plastic-coated black epidermis–white muscle five times and spat it out each time. The fact that fish bait was rapidly consumed, whereas holothurian white muscle alone and black epidermis–white muscle were mouthed but rejected, suggests that color may be unimportant and that chemoreception is important. Results from the second series of feeding experiments support the interpretation that color may be unimportant. The fact that black epidermis was mouthed in both experiments may indicate that toxin from small pieces of epidermis of *H. atra* is not a deterrent to attempted fish feeding. Previous observations have demonstrated that toxin is secreted in copious amounts but only when living *H. atra* is irritated (*11, 12*). These results (Lizard Island) along with those of Rideout *et al.* (*8*) and Lucas *et al.* (*13*) suggest that marine fish may learn to avoid toxic organisms by trial and error feeding.

Evidence for relatively intense predatory pressures on hard substrates in the tropics in comparison with higher latitudes, as well as evidence of defense mechanisms against fish predation, is continuing to mount (*6, 7, 11, 14–26*). Among the more interesting problems awaiting research include: (i) how certain invertebrate predators, commonly gastropods, can consume highly toxic sponges, gorgonians, and holothurians with no apparent ill effect; (ii) the possible role of toxins in deterring larval settling on sessile invertebrates; and (iii) the role of invertebrate toxins in controlling community structure or in the formation of competitive networks as envisioned by Jackson and Buss (*27*).

Bakus (*2*) and Cameron (*28*) hypothesized that toxicity is correlated with a sessile or slow-moving habit in coral reef organisms. The evidence presented here, in contrast to that of Maiorana (*29*) for terrestrial organisms, indicates that the commonest species of exposed sessile or slow-moving benthic invertebrates are subject to little or no fish predation and that these dominant species are more likely to use defenses such as toxicity which deliver no energy to the predator. Moreover, numerous tropical marine animals are capable of varying degrees of autotomy in contrast to many terrestrial animals. Birch (*30*) suggested that the high frequency of toxicity found in tropical environments might play a major role in allowing some species to become very abundant.

If chemically toxic metabolic by-products have arisen by chance over evolutionary time, we would expect to find examples in which both cryptic and exposed species have toxic representatives, with a higher incidence of toxicity occurring in exposed species where fish predation and grazing, and hence selection pressures, are more intense. This has been demonstrated. The ultimate causal mechanism of toxicity in tropical organisms is most frequently considered to be natural selection under high intensity fish predation (*1, 2, 6, 11, 15, 31*). Such an assumption probably is not testable under natural conditions. Alternative, testable hypotheses that would account for the evolution of toxicity, in part or in whole for a species, would be the canalization and genetic assimilation of ecochemotypes, an analog of ecophenotypes (*32, 33*), and the displacement of small groups of about 800 nucleotides (transposons or "jumping genes") (*34*).

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bacon); black epidermis and white muscle, and white muscle from the body wall of the holothurian *Holothuria atra*. Each of the foods was placed in a separate glass jar and carried to a species-rich fringing reef near Leong Creek where they were separately hand-fed to approximately 20 fish each time (30 May 1979), principally damselfish [*Abudefduf coelestinus* (Cuvier, 1830)], *Paraglyphidodon* [*Abudefduf*] *melas* (Cuvier, 1830), and a few wrasses (*Halichoeres* sp.). A second series of similar foods was prepared, consisting of bait (uncooked, unsmoked bacon), black epidermis, and plastic-coated (Varathane exterior liquid plastic) items. Small pieces of black epidermis and of epidermis with white muscle of *H. atra* were dipped in liquid plastic and air-dried, carried to the same reef, and fed to fish (2 June 1979).

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Extinctions and Introductions in the New Zealand Avifauna: Cause and Effect?

Abstract. *New Zealand, like many other islands, has suffered extinctions of native species and successful introductions of exotic species. It has been uncertain whether the introductions caused the extinctions or whether the extinctions permitted the introductions. On New Zealand's Hauraki Gulf islands, which are unusual in their near lack of introduced mammalian predators and complete lack of mammalian browsers, exotic bird species abundant in mainland New Zealand forest and reaching these islands are virtually absent from unmodified forest. Exotic bird species disappeared from Cuvier Island's forest after elimination of mammalian predators and browsers. Hence extinctions of native species were not due to competition from introduced species but to other factors (such as mammalian predators and habitat alteration). Only after decimation of native species and forest alteration by browsing mammals could exotic birds invade forest.*

On many oceanic islands, native plant and animal species have become extinct since discovery by Europeans, while species introduced from elsewhere ("exotic species") have become established. In fact, island populations account for most modern extinctions and many currently endangered species (*1*). A familiar example is the Hawaiian avifauna, which lost native species and gained exotic species introduced from Asia and North America, such that in most of Hawaii one sees mainly introduced birds (*2*). The causes of these extinctions, and their relation to the introductions, are much debated. Did competition from exotics contribute to extinctions of natives? Were the extinctions instead due to factors such as predation, disease, and habitat changes? Are island communities ecologically saturated, such that exotics can become established only at the expense of natives (*3*)? These questions are of practical importance for conservation, as well as theoretically interesting.

We explored these problems in nonmarine bird communities of Pacific islands. Especially instructive are distributions of native and exotic species on islands of New Zealand's Hauraki Gulf, islands that are unusual in their almost complete lack of introduced European mammals (*4-7*).

Avifaunas of tropical Pacific islands illustrate the difficulties in understanding how introductions of exotics relate to extinctions of natives. On seven archipelagoes (New Guinea, Bismarcks, Solomons, New Hebrides, Figi, Samoa, and Cooks) no exotic bird species occurs in closed forest, and the native avifauna is nearly intact (no extinctions among forest passerines). Interpretation of these facts is equivocal, because all the introduced species are ones confined to open habitats in their land of origin and do not penetrate closed forest even when native forest passerines are few and rare (for example, Rarotonga of the Cook Islands). Thus, these archipelagoes yield no clue whether competition from exotics affects natives, or whether natives can exclude exotic invaders. In Hawaii numerous introduced bird species are ones that do occur in forest in their land of origin and have become common inside native Hawaiian forest (*2*). However, the native Hawaiian forest avifauna has been decimated (13 species are extinct, and 12 are nearly so), and introduced mammalian predators and browsers are widespread. Hence, without further information it cannot be decided whether extinctions of native Hawaiian birds were the cause or result of exotic species penetrating the forest. Similarly, in Tahiti the introduced *Zosterops lateralis* is common in forest, but native forest passerines are extinct or rare, so that the causative relations remain unclear.

Comparison of mainland and island bird communities in the New Zealand archipelago permits us to distinguish cause and effect. New Zealand's biota evolved in the absence of nonmarine mammals except bats. Since man and his associated mammals arrived, New Zealand's avifauna has suffered heavy losses. Subfossil remains show that at least 34 native nonmarine bird species became extinct during the Maori occupation before Europeans arrived (*8*, *9*). Of the approximately 77 native nonmarine species present when European settlement began in the early 19th century, about 8 have become extinct and 13 have become rare or local. At least 143 exotic species, many of them forest birds in their land of origin, were introduced in the 19th century, and about 34 remain established (*8-10*). The causes of the native extinctions are debated (*8*, *11*). Suggestions include (i) predation by introduced mustelids, cats, and rats, as is illustrated dramatically by rapid extinctions of populations of five species on Big South Cape Island after ship rats (*Rattus rattus*) arrived in 1962 (*12*), (ii) reduction in forest area by clearing, (iii) changes in forest structure, and depletion of native food plants important for birds, by introduced browsers (deer and other cervids, goats, pigs, and Australian possums), (iv) competition from introduced bird species, and (v) diseases.

The situation on the New Zealand mainland (North and South Islands) is as