

Induction of Swimming in *Stomphia* (Anthozoa: Actiniaria) by Imbricatine, a Metabolite of the Asteroid *Dermasterias imbricata*

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Abstract. Imbricatine, a benzyltetrahydroisoquinoline alkaloid released by *Dermasterias imbricata*, has been tested for its ability to elicit escape responses in prey of the asteroid. Bioassays demonstrated that imbricatine is very effective at causing the detachment and swimming response in *Stomphia coccinea*, but is less effective at eliciting the same response in *S. didemon*. Two fragments of imbricatine, the benzyltetrahydroisoquinoline and 3-methyl histidine portions, were relatively inactive. Imbricatine did not elicit detachment behavior in either *Urticina* (= *Tealia*) *piscivora* or *Epiactis lisbethae*. The lack of comparable biochemical data for other escape and avoidance behaviors precludes any firm explanations of general patterns of chemical recognition of predators and non-predators by marine invertebrates.

Introduction

Many marine organisms exhibit escape and avoidance responses to chemicals released by their predators. The best documented of these behaviors are the responses of

a wide variety of invertebrate prey species to chemicals secreted by predatory asteroids and mollusks (Feder, 1967; Edmunds, 1974; Mackie and Grant, 1974; Mayo and Mackie, 1976; Phillips, 1975, 1977, 1978; Sloan, 1980; Watanabe, 1983; Harvey *et al.*, 1987). Despite the large number of studies that have demonstrated chemical recognition of predators by their prey, "relatively little information is available concerning the nature of the substances responsible" (Mackie and Grant, 1974). To understand the chemical basis for these behaviors both qualitative and quantitative information is needed. However, the chemical structure of the active substances and the quantities required to elicit the behaviors have been elucidated in only a few cases (Turner *et al.*, 1971; Harvey, 1985; Harvey *et al.*, 1987). This makes it difficult to answer many general questions about the nature of chemical recognition in these interactions.

One of the best studied and most dramatic escape responses of a marine invertebrate is the detachment and swimming behavior of *Stomphia* (*S. coccinea* and *S. didemon*) in response to certain species of asteroids and the nudibranch *Aeolidia papillosa*. This escape response has interested scientists since it was first described by Yentsch and Pierce (1955) and has resulted in a wide variety of studies on different aspects of the interaction: behavioral (Robson, 1961a; Ross, 1965a, b, 1967a, b, 1979; Ross and Sutton, 1964a, 1967a, b), neurophysiological (Hoyle, 1960; Robson, 1961b; Ross and Sutton, 1964b; Lawn, 1976, 1980), morphological (Sund, 1958; Rob-

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† Deceased. D. M. Ross initiated this project and sustained interest in the work for over 15 years. This paper is dedicated to him.

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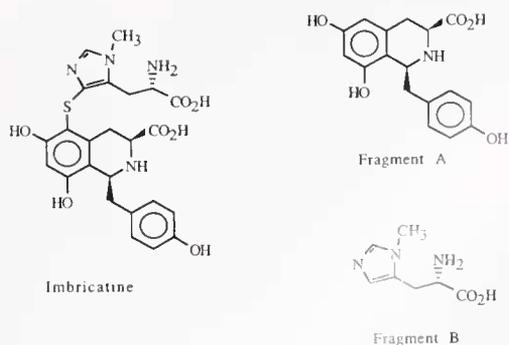


Figure 1. Chemical structures of imbricatine, Fragment A and Fragment B.

son, 1963; Peteya, 1976), ecological (Mauzey *et al.*, 1968; Dalby *et al.*, 1988), and chemical. The first work towards identifying the chemical(s) that elicits the response in *S. coccinea* was by Ward (1965), whose quantitative analyses of the partially purified substance isolated from the asteroid *Dermasterias imbricata* seemed to indicate that the active compound was an amino polysaccharide. However, most of the chemicals previously isolated from asteroids that had been found to elicit escape behaviors were saponins, and Mackie (1970) emphasized that Ward's material was not pure and may have contained asterosaponins.

Several years ago we set out to determine the complete chemical structure of the swimming substance present in the coelomic fluid of *D. imbricata* that elicits swimming in *S. coccinea* (Ayer *et al.*, 1973; Singer, 1975). A bioassay-guided fractionation of the methanol extracts of cut up specimens of *D. imbricata* yielded a single pure substance, which we named imbricatine, that was capable of eliciting pedal disk detachment and swimming in *S. coccinea*. Further structural studies (Pathirana and Andersen, 1986) showed that imbricatine was not an amino polysaccharide or an asterosaponin, but a benzyltetrahydroisoquinoline alkaloid (Fig. 1). Tetrahydroisoquinoline alkaloids are well known from terrestrial plants, however, imbricatine represents the first example of this family of alkaloids to be isolated from an animal source. The 3-methylthiohistidine substituent, the C3 carboxyl substituent, and the C6/C8 hydroxylation pattern on the tetrahydroisoquinoline ring represent structural features not previously encountered in this family of alkaloids. The function and metabolic origin of imbricatine is unknown.

Our work on the chemical structure of imbricatine provided pure samples of this chemical as well as pure samples of the benzyltetrahydroisoquinoline (Fragment A) and the 3-methyl histidine (Fragment B) portions of imbricatine (Fig. 1). Fragments A and B were obtained by Raney Nickel catalyzed hydrogenation (Pathirana

and Andersen, 1986). The major objectives of this paper are: (1) to demonstrate that imbricatine does elicit the swimming response in *Stomphia coccinea* and *S. didemon*, and is effective at very low concentrations, and (2) to examine some of the implications of our bioassays with this chemical and two of its fragments to some general questions concerning chemical recognition in marine invertebrates.

Materials and Methods

Biological assays of imbricatine and Fragments A and B were done with specimens of *S. coccinea* collected by dredging in San Juan Channel, Washington. The animals were held at the Bamfield Marine Station, Bamfield, British Columbia, in running seawater (11°C) trays. Of 10 sea anemones collected, only 7 showed consistent pedal disk detachment and swimming responses to contact with the asteroid *D. imbricata*. These seven anemones were allowed to attach in small glass petri dishes. Tests for the effectiveness of the chemicals (in comparison to a seawater control) and the concentrations needed to elicit the response were conducted as follows. A petri dish with an attached sea anemone was taken out of the water, the remaining water was poured out of the dish, and then 50 μ l of test solution was placed onto the oral disk of the sea anemone. The following behaviors of the sea anemone in response to the chemical were recorded: (1) retraction of the tentacles and closure of the oral disk, (2) elongation of the column, (3) opening of the oral disk and inflation of the tentacles, (4) flexions of the column, and (5) detachment of the pedal disk from the substratum and flexions of the column (swimming). If the anemone did not detach its pedal disk in response to the test solution, 50 μ l of a crude extract of the aboral surface of *D. imbricata* (10 g aboral surface tissue in 100 ml filtered seawater) was then added to be certain that the animal was responsive. Trials in which animals did not respond to the crude extract were not used in the final data analysis. Tests with different chemicals at various concentrations were done in random order at approximately 48-hour intervals. The sea anemones were fed pieces of shrimp muscle after each third trial. Further trials were also done with the sea anemones *Stomphia didemon*, *Urticina piscivora*, and *Epiactis lisbethae* (Ross and Sutton, 1967; Elliott *et al.*, 1985) which are also known to detach in response to *D. imbricata*.

The chemicals tested were imbricatine, Fragments A and B, and a 1:1 combination of Fragments A and B. Solutions were prepared by dissolving solid forms of the chemicals in filtered seawater. Serial dilutions of imbricatine were done starting with a 2×10^{-3} M solution (1 mg/ml), resulting in a series of 7 solutions ranging in con-

Table I

Behavioral responses of *Stomphia coccinea* to imbricatine, benzyltetrahydroisoquinoline (Fragment A), 3-methylhistidine (Fragment B), and a combination of Fragments A and B.

Solution	Molarity	Number of trials	Behaviors elicited*				
			1	2	3	4	5
Imbricatine	2×10^{-3}	14	+	+	+	+	+
Imbricatine	2×10^{-4}	14	+	+	+	+	+
Imbricatine	2×10^{-5}	12	+	+	+	+	+
Imbricatine	2×10^{-6}	19	+	+	+	+	+
Imbricatine	2×10^{-7}	15	14	14	14	1	1
Imbricatine	2×10^{-8}	15	3	—	—	—	—
Imbricatine	2×10^{-9}	14	—	—	—	—	—
Imbricatine	2×10^{-10}	14	—	—	—	—	—
Fragment A	3×10^{-2}	6	+	+	+	+	1
Fragment A	3×10^{-3}	8	5	5	5	—	—
Fragment A	3×10^{-4}	10	—	—	—	—	—
Fragment B	3×10^{-3}	10	—	—	—	—	—
Fragments A + B	3×10^{-3}	9	4	4	4	—	—

* Refer to table caption for explanation of behaviors. (+) indicates that responses occurred in 100 percent of the trials, and (—) indicates no response. Number indicates how many successful responses out of the total number of trials.

The behaviors numbered in table as: (1) retraction of tentacles, (2) elongation of the column, (3) opening of the oral disk and inflation of the tentacles, (4) flexions of the column, and (5) detachment of the pedal disk and flexions of the column (swimming).

centration from 2×10^{-3} M to 2×10^{-10} M. Fragment A was initially assayed using a 3×10^{-2} M solution (1 mg/ml) and was then serially diluted to concentrations of 3×10^{-3} M and 3×10^{-4} M. Small amounts of Fragment B only allowed testing at a molarity of 3×10^{-3} M. A solution that was 3×10^{-3} M in both Fragment A and Fragment B was also tested.

Results

When a solution of imbricatine was placed onto the tentacles of a sea anemone it usually responded by going through the five stages of the swimming response outlined above (greater than 95% of trials). None of the sea anemones responded to filtered seawater control. During trials with high concentrations of imbricatine, all of the sea anemones detached and swam (Table I). Consistent responses were obtained with solutions down to a molarity of 2×10^{-6} M. The chemical was less effective at 2×10^{-7} M and there were no responses to solutions less than 2×10^{-8} M.

Fragments A and B were not as effective as the parent chemical (Table I). The anemones were less responsive, taking a longer time to react and not showing the complete behavioral response. At a high molarity, Fragment A elicited most of the behavioral response except detachment of the pedal disk and swimming. Of six trials with a 3×10^{-2} solution of Fragment A, only one of the sea anemones detached and swam. Five of the sea anemones

retracted quickly in response to the chemical, elongated the column, and opened the oral disk but did not detach. The sea anemones did not respond to the chemical at lower molarities. Fragment B did not elicit a strong response from the anemones and most individuals did not react to the chemical. When Fragments A and B were combined, a response similar to that of Fragment A alone was elicited in some of the anemones.

Stomphia didemon also detached and swam in response to imbricatine. However, numerous trials revealed that some individuals would not consistently detach to even high concentrations of the chemical (2×10^{-3}), and it appears as if this species is not as sensitive to imbricatine as *S. coccinea*. The sea anemones *Urticina piscivora* and *Epiactis lisbethae* did not respond during trials (5 trials for each species) with imbricatine (2×10^{-3}). These sea anemones required physical contact with the seastar to elicit the detachment response.

Discussion

Studies examining the chemical basis of escape and avoidance behaviors of marine invertebrates to seastars have generally found that saponins are the reactive substances (Mackie and Grant, 1974; Harvey *et al.*, 1987). These results, in combination with the widespread occurrence of saponins in seastars (Burnell and ApSimon, 1983), have fostered the common perception that most of these behavioral responses are elicited by saponins

(Mackie and Grant, 1974; Burnell and ApSimon, 1983). However, Burnell and ApSimon (1983) and Mayo and Mackie (1976) reported that the active materials in some asteroids are not saponins. Our results also demonstrate that chemicals other than saponins are used by prey organisms to identify their predators. Thus, quantitative bioassays conducted with pure samples may reveal that other novel chemicals are responsible for eliciting particular escape and avoidance responses in other species.

The results of this study demonstrate that the *D. imbricata* metabolite, imbricatine, is extremely effective at eliciting the detachment and swimming behavior of *S. coccinea*. As little as 50 nanograms of the chemical (50 μL of a 2×10^{-6} M solution) was sufficient to induce the full behavioral response in 100% of the trials. Few other studies have measured the concentrations of the chemicals used in bioassays, but imbricatine is effective at least an order of magnitude lower than that reported for saponins isolated from seastars which elicit escape behaviors in the gastropod *Buccinum undatum* (Mackie et al., 1968; Harvey et al., 1987). The benzyltetrahydroisoquinoline portion of imbricatine (Fragment A) was at least four orders of magnitude less effective at eliciting the response than the whole chemical. This fragment appears to be the more reactive part of the chemical, since the 3-methylhistidine portion (Fragment B) was not effective at the relatively high concentrations tested. Previous studies have demonstrated that two or three chemicals may act synergistically to elicit escape behaviors (Mayo and Mackie, 1976), but a 1:1 mixture of imbricatine Fragments A and B was relatively inactive, ruling out any synergistic interaction of these two unattached fragments. The very low concentrations of imbricatine needed to elicit the response and the stringent structural requirements for biological activity suggest the presence of a selective chemoreceptor in *S. coccinea*.

Prey escape and avoidance behaviors are usually specific to only natural predators, but they may also be elicited by non-predators (Sloan, 1980). It is generally assumed that non-predators cause reactions because they are biochemically similar to the predators, either through taxonomic relatedness or similarity in diet (Mauzey et al., 1968; Margolin, 1976; Dalby et al., 1988). For example, *S. coccinea* and *S. didemon* have strong reactions to three species of asteroids in the order Valvatida but display weak or no reactions to at least 14 other species of asteroids (Ward, 1965; Dalby et al., 1988). Only two of the asteroids that cause the response (*D. imbricata* and *Hippasteria spinosa*) are known to feed on these anemones, and the third species *Asterina* (= *Patiria*) *miniata* does not feed on cnidarians. This indirect evidence suggests that the three closely related asteroids contain similar quantities of the same chemical, and other asteroids that cause weak responses have either smaller quantities

of this chemical or similar chemicals that are less reactive. However, as in most studies, there is no direct evidence to confirm these inferences. It is unknown if asteroids that elicit a particular response contain the same chemicals or if the prey use the same chemicals, or quantities of them, to recognize each asteroid species (Mackie and Grant, 1974).

Some studies have shown that prey discriminate among asteroids by detecting different chemicals released by each species. Mackie and Grant (1974) report that the major steroid glycoside present in the seastar *Marthasterias glacialis* is not present in other asteroid species that cause the same behavioral responses in some marine invertebrates. Also, preliminary structural analyses in our laboratory suggest that the active chemical in the asteroid *Hippasteria spinosa* that causes *Stomphia* spp. to swim is not similar to imbricatine (Andersen, unpub. obs.). Thus, some prey appear to have different receptors for different species of asteroids, and may possess more finely tuned recognition systems than has been previously assumed. We are presently trying to isolate and identify the chemicals from other asteroids which elicit swimming in *Stomphia* spp. to better answer this question.

To increase the ability to discriminate among predators and non-predators, it is likely that many marine invertebrates cue on more than one particular chemical or other type of stimuli. Harvey et al. (1987) found that purified saponins were not as effective at eliciting an escape behavior in *Buccinum undatum* as natural seastar "scented" water, which suggested that the prey may also be responding to other substances released by the asteroid. Our bioassays of the different isolated fractions from *D. imbricata* indicate that imbricatine is the only chemical required to elicit a complete response in *S. coccinea*. But, *S. didemon* was relatively less sensitive to imbricatine. The variation in the responses of different prey organisms to the same species of asteroid is likely due to differences in the type or sensitivity of the chemoreceptors of the prey (Mackie and Grant, 1974). Mackie and Grant (1974) have reported that the same saponins (steroid glycosides) from *M. glacialis* induce behaviors in many different species of prey. Similarly, the reaction of *S. didemon* to imbricatine demonstrates that it has the same or similar type of receptor found in *S. coccinea*, but *S. didemon* may require either greater quantities of this stimulus or different types of cues. *Stomphia didemon* detaches and swims most consistently when it is touched by asteroids. The anemone may also recognize particular cell surface properties of the asteroid. Imbricatine did not elicit escape responses in *Tealia piscivora* or *Epiactis lisbethae*, and these sea anemones also appear to require physical contact cues from *D. imbricata*. Thus, various

prey species may cue on the same or different chemicals, or other characteristics of the same predator.

There is no chemical evidence to support the hypothesis that prey differentiate among seastars on the basis of the quantity of the substance released. Phillips (1978) has presented indirect evidence that the sea urchin *S. droebachiensis* may recognize the difference between foraging and non-foraging *Pycnopodia helianthoides* by cueing on the concentration of chemical(s) released from the asteroid when it is moving compared to when it is stationary. But, it is clear that direct evidence, through chemical studies of the substances involved, is needed to obtain a satisfactory answer to this question.

Our study has demonstrated that *S. coccinea* and *S. didemon* react to a specific chemical released from the asteroid *D. imbricata*. This has confirmed some early inferences by Ross (1966) and others that even though sea anemones are relatively simple animals they have highly evolved sensory systems and complex behavioral responses to very specific stimuli. Structural studies of imbricatine showed that it was not a saponin, which suggests that further studies of the substances that elicit escape behaviors in a wide variety of prey species may reveal that other novel chemicals are used for recognition. We have attempted to address some general questions concerning chemical recognition in marine invertebrates, but the lack of similar biochemical data for comparison precludes any firm explanations of the chemical basis for observed patterns of responses among prey to different species or physiological states of predators and non-predators. Research in this area has not advanced much in the last decade, and we re-emphasize the statement of Mauzey *et al.* (1968) that "the whole subject of avoidance responses of invertebrate animals can only be clarified finally by further, detailed biochemical studies."

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