Defensive Responses of Marine Gastropods (Prosobranchia, Trochidae) to Certain Predatory Seastars and the Dire Whelk, *Searlesia dira* (Reeve)[1]

DANIEL L. HOFFMAN[2]

ABSTRACT: Qualitative comparisons of the predator-induced defensive behaviors of four species of trochid gastropod, *Margarites pupillus*, *M. salmoneus*, *M. rhodia*, and *Calliostoma ligatum*, under controlled laboratory conditions indicate that the degree and strength of the response varies according to the sensory information received from a predator and according to the species of predatory seastar or gastropod inducing the response. Generally, all four species of gastropod demonstrate a weak to moderate avoidance response to the scent of such predatory seastars as *Leptasterias hexactis* and *Pisaster ochraceus*; whereas direct contact with their soft parts elicits strong and often violent defensive behaviors characterized by shell twisting, propodial rearing which often leads to a loss of contact with the substrate, and somersaulting by metapodial thrusting. It is hypothesized that the inversion of the shell induced by direct contact with a predator sets up the metapodial thrusting behavior and also part of the righting repertoire, which facilitates more rapid flight from the predator. *Margarites* spp. respond to the scent and contact with the dire whelk, *Searlesia dira*; whereas *Calliostoma* is unresponsive to the snail, but more responsive to the scent and contact of the sunstar *Pycnopodia helianthoides* than are the other species of gastropods studied.

THE ABILITY OF AN ANIMAL to interpret various sensory cues within its environment concerning the proximity of a predator has major survival value. Phillips (1978) has pointed out that certain marine animals, such as the purple sea urchin *Strongylocentrotus purpuratus*, are able to distinguish between inactive and actively foraging predatory seastars. Also of significance from a cost basis, is the intensity of the response by the animal to the actual or potential threat of predation. An example of such a cost involved in a defensive response would be the loss of purchase with the substrate, increasing the likelihood for an intertidal animal to be dislodged by wave action and killed. Defensive responses of closely related species of trochid gastropods differ in the sensory cues used to elicit the response and the complexity of the response; even the age and size of the snail affect the response (Hoffman and Weldon 1978, Phillips 1978). Presently, there is a wealth of information attesting to the role of chemicals from various seastars which trigger a wide range of defensive responses in a number of marine invertebrates (Feder and Christensen 1966, Feder 1972). Certain other sensory modalities might also be involved; for example, Dayton et al. (1977) have suggested that some marine animals may respond to vibrations caused by the osscles of seastars rubbing together as the animals move.

While in residence at the Friday Harbor Laboratories during the spring of 1978, I had the opportunity to study the defensive behaviors of several species of intertidal and subtidal gastropods (superfamily: Trochacea): *Margarites pupillus* (Gould, 1849), the puppet margarite; *M. salmoneus*

(Carpenter, 1864), the salmon margarite; *M. rhodia* (Dall, 1920), the rosey margarite; and *Calliostoma ligatum* (Gould, 1849), the western ribbed topshell. Schroeter (1972) has shown that *M. pupillus* responds defensively to a wide range of invertebrate predators. Also, Weldon (1977) has demonstrated an avoidance response of *C. ligatum* to predatory seastars. Moreover, for comparative purposes, defensive responses have been documented in many trochid genera, such as *Tegula* (Bullock 1953, Feder 1963, Yarnell 1964, Weldon 1977, Hoffman and Weldon 1978), *Calliostoma* (Feder 1967, Ansell 1969, Weldon 1977, Weldon and Hoffman 1979), *Gibbula* (Feder 1967), *Cittarium* (Hoffman and Weldon 1978), *Monodonta* (Clark 1958), *Norrisia* (Bullock 1953), and *Trochus* (Clark 1958, Kohn and Waters 1966).

The present paper reports on observations of the defensive responses of four species of trochid gastropods when presented with different species of predatory seastars and the dire whelk, *Searlesia dira* (Reeve, 1946). It is hoped that these observations may help characterize trophic relationships that exist within this particular low intertidal–subtidal community, as well as present more information on the variety of predator-induced responses of trochid gastropods.

NATURAL HISTORY

The populations of two species of *Margarites*, *M. pupillus* and *M. salmoneus*, along with populations of *Calliostoma ligatum*, appear to be sympatric in their distribution. The *M. salmoneus* has a type locality of Monterey and is usually considered to be a southern subspecies of *pupillus*. Abbott (1974) records *M. pupillus* as having a distribution from the Bering Sea to San Diego, California, and he describes it as being a common littoral species in the northern half of its range. *Margarites salmoneus* ranges from Washington to southern California and is uncommonly found in 12–80 m of water. According to Abbott (1974), *C. ligatum* ranges from Alaska to San Diego, California, and is also a very common littoral

species from northern California north. *Margarites rhodia* (*M. inflata* Carpenter, 1864) is a subtidal species that ranges from Prince William Sound, Alaska, to Crescent City, California. Although it would be difficult to determine whether Schroeter (1972) was studying both *M. pupillus* and *M. salmoneus*, he found populations of *Margarites* at Cantilever Point to be primarily subtidal. The distribution of the population, size, and recruitment were found to be closely related to the abundance of the algal canopy (*Laminaria* spp., primarily). Diatoms appear to be their primary food source, and Schroeter notes that the algal canopy may increase diatom concentration and thus influence population growth. Sexually mature snails live for at least 2 years, and may live for as many as 4 years.

Leptasterias hexactis and *Pisaster ochraceus* are common forciculate seastars in the rocky intertidal region of the west coast of North America (Ricketts and Calvin 1962). In the San Juan Islands of Washington State the vertical range of these two species is +1.5 to −0.9 m; the foraging activities of both species are characteristically highest in the summer and lowest in the winter (Mauzey 1966, Paine 1966, Menge 1972b). They are food generalists, eating barnacles, mussels, chitons, limpets, and snails (Mauzey 1966, Paine 1966, Mauzey, Birkeland, and Dayton 1968, Menge 1972b). There is strong evidence that in certain intertidal areas of San Juan Island they are also important predators of species of *Margarites* (Menge 1972a). *Pycnopodia helianthoides*, one of the largest of seastars, reaching diameters in excess of 1.3 m, occurs subtidally on mud, sand, shell, gravel, and rocky bottoms as well as the lower rocky intertidal, but in protected waters it seldom occurs in the intertidal (Mauzey et al. 1968). In the San Juan Islands the diet of *Pycnopodia* consists primarily of clams, especially *Saxidomus*; and there is evidence that it will feed on urchins, and to some extent crabs, holothurians and snails (Mauzey et al. 1968). The buccinid gastropod *Searlesia dira* is typically found on major combinations of all substrates, with the exception of sand, and

has a vertical range within the intertidal from $+1.7$ to -1.8 m (Louda 1979). *Searlesia* was long thought to be a scavenger but is now described as an active carnivore that preys on barnacles, limpets, chitons, and snails (Louda 1979). *Pisaster ochraceus* and *Leptasterias hexactis*, along with *Searlesia dira*, were all collected a few decimeters below mean low water at Cantilever Point. Small specimens of *Pycnopodia helianthoides* (average diameter 30 cm) were collected either by dredging or scuba diving.

MATERIALS AND METHODS

The gastropods and echinoderms used in this study were collected in the intertidal and subtidal waters of San Juan Island, Washington, during the months of March and April 1978. With the exception of *Margarites rhodia*, which was dredged off a shell–soft mud substratum in approximately 10 m of water off the main dock of the Friday Harbor Laboratories, the remaining three species of trochid gastropods were collected a few decimeters below mean low water of the rocky intertidal off Cantilever Point (40°30′29″N, 123°0′3″W).

All animals were maintained in 110–185-liter Plexiglas aquariums that were supplied with running seawater (temperature approximately 8–11°C). The seastars and predatory gastropods were maintained in aquariums separate from the trochid gastropods used in this study. Generally, the animals were allowed to acclimate to the laboratory conditions for 3 days before studies were undertaken. Every 2 weeks new snails were collected to prevent the habituation that might result from snails being tested repeatedly.

Behavioral observations were made under two different experimental conditions: still water in a glass bowl and flowing water within a Y-shaped olfactometer. The experiments were designed to test the ability of various predators to elicit defensive behaviors from certain species of trochid gastropods either through contact or distance chemoreception and to characterize the responses elicited by the prey species. To determine the effect of predators on prey species in a still-water environment (a tidal pool situation), 9–12 specimens of the same trochid species were placed in a glass bowl (top diameter either 11.5 or 20 cm) that was half filled with seawater. After an acclimation period of 10 min, either a predator or a 20-ml aliquot of seawater that contained the predator's "scent" was slowly added to the bowl. The aliquots were taken from a beaker that had held one predator per given volume of seawater (100 ml per *Leptasterias* and *Searlesia*, 750 ml per *Pisaster* and *Pycnopodia*). The control for this experiment entailed adding a similar volume of seawater taken from an intake valve. All bowl experiments were run between 08:00 and 11:00 PST under the subdued lighting conditions of the laboratory.

A Plexiglas Y-shaped olfactometer (approximately $90 \times 20 \times 14$ cm) was used to test the ability of the gastropods to detect the waterborne scent of a potential predator. Presumably, if the scent is detected, the gastropods will increase the rate of locomotion and distribute themselves in the device at a distance from the source of the stimulus. This experiment is based on those undertaken by Phillips (1975, 1976). The Y-shaped olfactometer was positioned on a seawater table with the branched arms facing a window with a northern exposure. Reservoirs at both ends of the olfactometer were supplied with running seawater from the intake seawater system; the water was then allowed to run down the main chamber. Predators were placed within one of the reservoirs so that the water would flow over them before passing through the perforated partition and down the side branch. The number of predators placed in each reservoir was a function of their size, since a large predator produces more scent than a much smaller predator and the snail would then respond much more to the larger specimen than to the smaller one (Phillips 1976). To compensate for a possible size effect, six *Leptasterias* (average diameter 5.5 cm) and one *Pisaster* (diameter 12.7 cm) were considered to be of equivalent volume in this series of experiments. The other reservoir of

TABLE 1

Scent- and Contact-Induced Responses in Three Species of *Margarites* and *Calliostoma ligatum* within the Confines of Water-filled Glass Bowls

	PREDATOR			
PREY SPECIES	*Leptasterias hexactis* ($n = 12$)	*Pisaster ochraceus* ($n = 8$)	*Pycnopodia helianthoides* ($n = 4$)	*Searlesia dira* ($n = 8$)
M. pupillus ($n = 128$) ⎫ *M. salmoneus* ($n = 114$) ⎬	Scent: A, B Contact: C, D, E, F, G	Scent: A Contact: C, D, E, F, G	Scent: little or no response Contact: C, D	Scent: A, B, E Contact: C, D, E, H
M. rhodia ($n = 54$)	Scent: A Contact: C, D, E, F, G	Scent: A Contact: C, D, E, F, G	Scent: little or no response Contact: C, D	Not tested Not tested
C. ligatum ($n = 120$)	Scent: A, B Contact: C, D, E, F, G, H	Scent: little or no response Contact: C, D, E, F, G, H	Scent: A, B, E Contact: C, D, F, G	Scent: no response Contact: no response

NOTE: A, extension and waving of cephalic and epipodial tentacles; B, heightened crawling movements; C, contraction of head and tentacles; D, rearing and rapid retreat; E, shell twisting; F, loss of purchase with substrate (especially with prolonged contact); G, leaping and somersaulting with the metapodium; H, movement upward and out of the water; n, total number of snails and seastars observed.

the olfactometer held no predator and served as a control. Twenty-five to seventy-eight specimens of trochid gastropods (depending on the species tested) were closely grouped in the main chamber of the Y-shaped olfactometer. After 2–4 h, the positions of the snails within the two side branches and the main chamber of the olfactometer were recorded. Controls were made in total darkness (with the device enveloped in an opaque plastic tarp) and also in the light with the absence of any predators. These latter experiments tested whether light would affect the distribution of the gastropods within the olfactometer.

RESULTS

Descriptive data of the predator-induced responses of three species of *Margarites* and *Calliostoma ligatum* are summarized in Table 1. For the most part, the responses of these snails are consistent and quite similar. The basic differences between the two genera relate to the degree of responsiveness to different predatory species. For instance, *Margarites* spp. show little or no response to the scent of *Pycnopodia helianthoides*; whereas a moderate flight response is elicited in *Calliostoma* by the seastar. Also, two species of *Margarites* respond moderately to the scent of *Searlesia dira* and very strongly to contact with the soft parts of the snail; however, *Searlesia* elicits no avoidance response from *Calliostoma*.

The difference in stimulation between waterborne scents and contact with the predator is one of intensity. The scent of predators increases the activity of the snails, eliciting an extension and vigorous waving of the cephalic and epipodial tentacles and an increase in the ditaxic locomotory gait. The contact stimulus always surpasses the threshold intensity of distance chemoreception, with the rearing of the anterior end of the foot or propodium and an abrupt change in the direction of movement, often by as much as 120°. The shell is often twisted through an arc of 180°, especially if prolonged contact is made with the predator,

for instance, the adherence of podia to the shell. This shell-twisting behavior, which has been reported in many trochid genera (Ansell 1969), may have adaptive value in extricating the snail from the grasp of the predator (Hoffman and Weldon 1978). Similar shell twisting has been observed in *Margarites pupillus* when conspecifics attempt to graze on algae growing on another's shell (Schroeter 1972); however, in this case, the grazing-induced response is not followed by any rapid flight movement.

Prolonged or repeated contact with a predator sets up a propodial rearing response that usually results in loss of purchase with the substrate and an overturned shell. Under normal circumstances, in the absence of predators, inverted snails invariably right themselves with a propodial pull. However, in *Margarites* and *Calliostoma*, if the propodium cannot make contact with the substrate, the elongated posterior end of the foot or metapodium folds along its long axis and thrusts its pointed tip into the substrate. The foot thrust causes the shell to rotate, facilitating propodial contact with the substrate and thus righting. However, predator-induced overturnings greatly exaggerate the metapodial thrusting behavior, especially with repeated contact stimulation by a predator (Weldon and Hoffman 1979). The snails relinquish their foothold and roll the shell over repeatedly by swinging their foot against the substrate (Figure 1). This leaping or somersaulting response has been described in several species of *Calliostoma* (Feder 1967, Ansell 1969, Weldon 1977, Weldon and Hoffman 1979). The thrusting escape maneuvers on a smooth hard substrate such as a flat rock or glass aquarium tend to be somewhat exaggerated in that the smooth top-shaped shell has more of a tendency to roll; in fact, such surfaces make righting more difficult. But, on irregular or rough surfaces, such as gravel or algal mats, inverted shells have less tendency to roll, facilitating not only escape but also righting.

Predator-activated snails show an increased negative geotaxis (movement upward) on submerged vertical surfaces. Generally, *Margarites* stop at the air–water
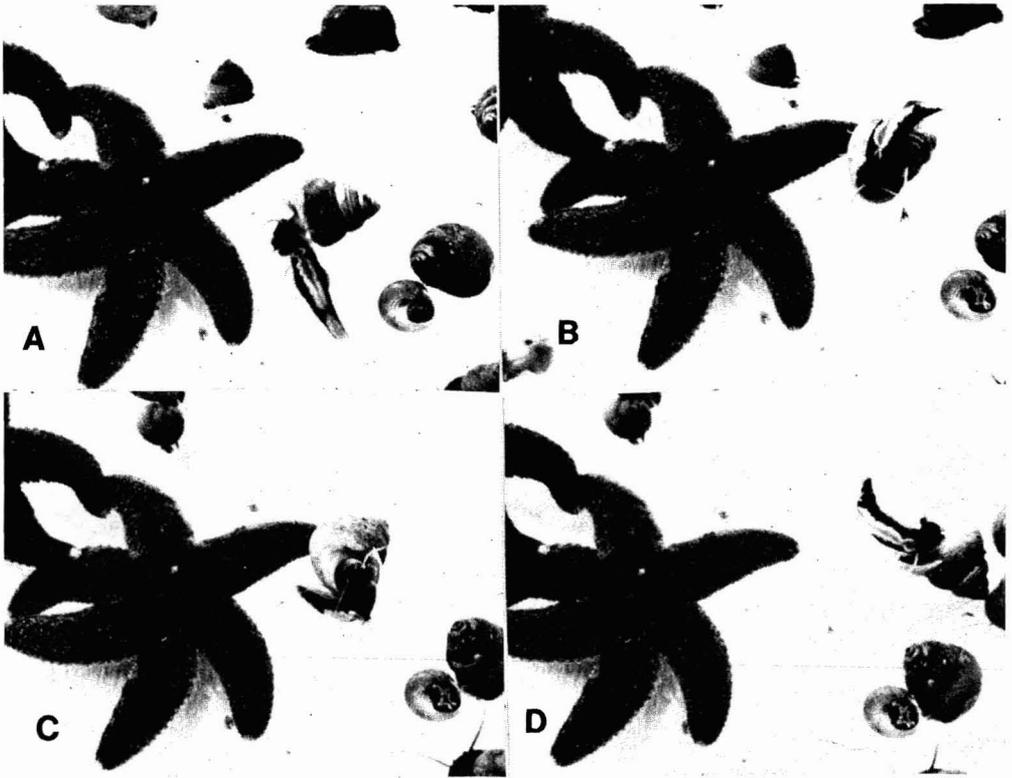
FIGURE 1. Sequence of two metapodial thrusts by *Margarites pupillus* to contact with *Leptasterias hexactis* over a period of 5 sec. *A*, metapodium fully extended in a thrust position; *B*, shell flips, making contact with starfish, metapodium upward at end of thrust; *C*, initiation of second thrust movement with metapodium in contact with substrate; *D*, fully extended metapodium flips snail away from the starfish.

interface, often protruding the head out of water. Once they initiate movement, they may crawl just beneath the surface, often with the edge of the shell out of water. *Searlesia* is able to elicit a response from *Margarites* strong enough to stimulate movement completely out of the water. *Calliostoma*, on the other hand, usually crawls completely from the water when direct contact has been made with either *Leptasterias* or *Pisaster*. Water evacuation induced by predators has been observed in the trochid *Tegula funebralis* (Feder 1963). Such limpet species as *Acmaea limatula* and *A. scutum* also show a negative geotaxis on submerged vertical surfaces to predator scent; this tends to move them out of the foraging range of predators (Phillips 1976).

Data on the ability of a snail to detect the scent of a predator borne in flowing water is presented in Table 2. In the absence of a predator, and under both lighted and dark conditions, *Margarites pupillus* tends to distribute itself randomly within the confines of a Y-shaped olfactometer after 2–4 hr. However, with the introduction of a predator to the system, the movements of the snails result in a distribution that is significantly nonrandom, i.e., significantly greater than expected from a 50:50 distribution ($\chi^2 > 3.8$, $p < 0.05$). It appears that *M. salmoneus* and *Calliostoma ligatum* are more able to differentiate the scent of *Pisaster* than is *M. pupillus*.

Although *Pisaster* and *Pycnopodia* captured and initiated feeding responses on *Margarites* and *Calliostoma* within glass bowls, neither *Leptasterias* nor *Searlesia*

TABLE 2

RESPONSES OF *Margarites* AND *Calliostoma* TO THE SCENT OF PREDATORS IN FLOWING WATERS OF AN
OLFACTOMETER

| | | | | | NUMBER OF SNAILS TO | | |
PREY SPECIES	n	PREDATOR	n	EXPERIMENTAL CONDITIONS	MIGRATE TO CHAMBER WITH PREDATOR	MIGRATE TO CHAMBER WITHOUT PREDATOR	REMAIN IN ORIGINAL CHAMBER
M. pupillus	148	—	—	Light	33	36	79
	150	—	—	Dark	31	37	82
	185	Leptasterias	18	Light	21	75	89
	105	Leptasterias	12	Dark	11	29	65
	119	Pisaster	2	Light	31	34	54
	112	Searlesia	11	Light	28	36	48
M. salmoneus	58	Leptasterias	12	Light	7	34	17
	61	Pisaster	2	Light	3	32	26
C. ligatum	40	Leptasterias	6	Light	4	18	17
	40	Pisaster	1	Light	5	18	19

NOTE: The test criterion for a positive response was an unequal distribution of snails within the two branches. Chi-square values resulted from comparing numbers in the two branches by means of a 2×2 contingency table ($X^2 > 3.8$, $p < 0.05$).

demonstrated any feeding behavior under similar circumstances. Additional feeding-preference experiments were performed in the laboratory using a covered 8-liter plastic aquarium supplied with running seawater. In one experiment, 4 *Leptasterias* (average diameter 6.0 cm) were placed in the aquarium with 24 *M. pupillus* and 24 *C. ligatum*. After 36 hr, 4 *Margarites* had been eaten. Under similar conditions, 6 *Searlesia* were placed in the aquarium with 24 *M. pupillus* and 24 *Trichotropis cancellata*, a subtidal mesogastropod. No snails were attacked or eaten after 36 hr. However, I was able to observe two *Searlesia* actively feeding on *M. pupillus* below the zero tide mark of Cantilever Point during the low tide period, 24 April 1978.

DISCUSSION

The predator-induced defensive responses of *Margarites* and *Calliostoma* observed in the laboratory are similar to those described for other genera of trochids studied both under artificial and field conditions (Bullock 1953, Clark 1958, Feder 1963, Yarnell 1964, Feder 1967, Ansell 1969, Weldon 1977, Hoffman and Weldon 1978). Not surpris-

ingly, the complexity of responsiveness appears to be related to the strength of the stimuli eliciting the responses. Also, the defensive responses of these two genera for the most part are quite similar to each other. The differences between them primarily are in their responsiveness to different predatory seastars or gastropods. Unlike the strong scent-induced avoidance responses of *Tegula funebralis* (Feder 1963) and juvenile *Cittarium pica* (Hoffman and Weldon 1978), for the most part *Margarites* and *Calliostoma* show fairly weak to moderate avoidance responses to such waterborne scents. It is only through direct contact with the soft parts of these predators that strong, and often violent, defenses are evidenced.

If the scent or odor alone elicits an avoidance response, as it does in certain trochid genera, does the resultant response direct the snail away from the grasp of the predator? From the experiments with waterborne scents in an olfactometer, the question appears to be answered in the affirmative. Although these data do appear to be significant, it would be difficult to extrapolate these laboratory conditions with those of the marine benthos, especially in such microhabitats as the undersurfaces of marine kelp

where the hydrodynamics are considerably more complex. The fact that *Margarites* and *Calliostoma* are able to show some, albeit at times a weak, response to the scents of various predators is of significance to their survival. Perhaps, as Phillips (1978) clearly demonstrates, these gastropods may be able to differentiate more readily between foraging and nonforaging predators. During the course of the experiments within the olfactometers, only *Leptasterias* of those predators tested showed any activity by moving about the chamber, and all three species of snails tested did respond positively to the scent of this seastar. It also may be difficult for snails to determine the direction from which the predator's scent is emanating, especially in still waters. Kohn and Waters (1966) observed that *Trochus pyramis* would actually crawl toward *Conus textile*, turning quickly before directly encountering them. *Margarites* also crawls over the shell of *Searlesia*, only to react strongly after contacting the soft parts of the predator.

Margarites and *Calliostoma* have evolved a series of interrelated behavioral responses that are initiated by direct contact with a predator; these are (1) propodial rearing that often results in a loss of purchase with the substrate, with the snail being overturned, and (2) thrusting with the metapodium that results in somersaulting. Propodial rearing is of special significance, as Feder (1963:508) described for a predator-induced reaction in *Tegula brunnea*, "the heavier turban shell tends to throw the animal off balance whenever the foot is raised, and the gastropod falls off its rocky substrate." Similarly in *Calliostoma* and *Margarites*, propodial rearing sets up the conditions that make a more rapid egress possible. In the inverted state the metapodium is able to function as a muscular lever that, by repeated thrusts against the substrate, flips the shell from the immediate vicinity of the predator through a series of violent somersaults. Such predator-induced foot thrust movements have been well documented in *Nassarius* (Weber 1924, 1926, Gore 1966), and should not be confused with the predator-induced kick responses of *Fasciolaria* (Wells 1970, Snyder and Snyder 1971) and *Strombus* (Berg 1974, Field 1977), where the operculum digs into the substrate and flips the shell from the predator.

The similarity of foot movements involved in the righting and defensive behaviors of some gastropods has been well documented (for a review of the literature, see Weldon and Hoffman 1979). Gore (1966) and Gonor (1966) suggest that gastropods that have developed a kick or thrust mode of righting have coupled these movements secondarily with defense. Given the similarity of these movements, the hypothesis that kick and thrust righting historically precede these movements is quite reasonable. An alternative hypothesis has been proposed by Weldon and Hoffman (1979) that kick and thrust movements evolved primarily in escape and appear secondarily in righting. If one assumes that the propodial pull was the primitive mode employed by gastropods in righting—and all modern species of gastropods with the exception of such limpetlike genera as *Acmaea*, *Crepidula*, and *Fissurella* are able to demonstrate this ability (Weldon 1977, Weldon and Hoffman 1979)—then a modification of a predator-induced thrusting and somersaulting behavior of such genera as *Margarites* and *Calliostoma* may have served to orient the shell when the propodium had difficulty in contacting a surface to right upon. Perron (1978) presents evidence on this ontogeny of the escape response in the primitive strombid *Aporrhais occidentalis*; that is, the foot leap used in locomotion may have first appeared as part of an escape response to slow-moving predators.

It is possible to speculate that the kick and thrust foot movements are often, but not always, triggered by contact with a predator. Gore (1966) observes the kicking and shell-twisting response in *Nassarius* when direct contact is made with the seastar *Luidia*. Also, Field (1977:2) reports that the kicking escape response in *Strombus macultatus* is "triggered usually either by some movement of the *Conus* or by direct contact." In ad-

dition, the mushrooming response of limpets is elicited by contact with echinoderms (Bullock 1953). In those species of gastropods that demonstrate strong avoidance responses to predators through distance chemoreception, such as *Tegula funebralis* (Feder 1963, Yarnell 1964) and *Cittarium pica* (Hoffman and Weldon 1978), there is no evidence of any complex kicking or thrusting behavior. For both these species there is no evidence of predator-induced loss of contact with the substrate, because the basic strategy is accelerated locomotion away from the source of stimulation. Of interest is the brown turban snail, *Tegula brunnea*, of which Feder (1963) notes a tendency to be easily overturned when stimulated by a predator. Although no foot thrusting or kicking has ever been described, Weldon (1977) has observed that unlike its congener, *T. funebralis*, the inverted *T. brunnea* will not only probe with its propodium but can probe and right itself with the metapodium as well. But in this case the tip of the metapodium functions more as an organ of prehension, and not, as in the case of *Calliostoma*, as a lever.

The negative geotactic response on vertical surfaces of *Calliostoma ligatum* may be an adaptation to their environment. McLean (1962) has found this species to be most abundant on submerged walls near the kelp beds off the central California coast. Encountering a predator would tend to move the snails upward, or in the case of direct or prolonged contact, would result in a loss of contact with the vertical surface and an all or nothing escape to the bottom; whether such an action would ultimately be conducive to survival has yet to be determined.

Finally, there is good field evidence that the predators that elicit defensive responses in *Margarites* and *Calliostoma* do feed on them under natural conditions, even though they may not comprise a major part of their diet (Mauzey et al. 1968, Menge 1972b, Louda 1979). The behavioral defenses of these gastropods may reduce predatory pressures on their populations and in doing so effectively serve to reduce their role as major components of the diets of these predatory seastars and snails.

LITERATURE CITED

ABBOTT, R. T. 1974. American seashells. 2d ed. Van Nostrand Reinhold, New York.

ANSELL, A. D. 1969. Defensive adaptations to predation in the Mollusca. Symp. Mar. Biol. Assoc. India, II. 487–512.

BERG, C. J., JR. 1974. A comparative ethological study of strombid gastropods. Behaviour 51:274–322.

BULLOCK, T. H. 1953. Predator recognition and escape responses of some intertidal gastropods in the presence of starfish. Behaviour 5:130–140.

CLARK, W. C. 1958. Escape responses of herbivorous gastropods when stimulated by carnivorous gastropods. Nature, London 181:137–138.

DAYTON, P. K., R. J. ROSENTHAL, L. C. MAHEN, and T. ANTEZANA. 1977. Population structure and foraging biology of the predaceous Chilean asteroid *Meyenaster gelatinosus* and the escape biology of its prey. Mar. Biol. 39:361–370.

FEDER, H. M. 1963. Gastropod defense responses and their effect in reducing predation by starfishes. Ecology 44:505–512.

————. 1967. Organisms responsive to pred-
atory seastars. Sarsia 29:371–394.

————. 1972. Escape responses in marine
invertebrates. Sci. Amer. 227:92–100.

FEDER, H. M., and A. CHRISTENSEN. 1966.
Aspects of asteroid biology. Pages 87–127
in R. Boolootian, ed. Physiology of
Echinodermata. Wiley, New York.

FIELD, L. H. 1977. An experimental analysis
of the escape response of the gastropod
Strombus maculatus. Pac. Sci. 31:1–11.

GONOR, J. J. 1966. Escape responses of
North Borneo strombid gastropods elic-
ited by the predatory prosobranchs Aulica
verpertillo and Conus marmoreus. Veliger
8:226–230.

GORE, R. H. 1966. Observations on the
escape responses in Nassarius vibex (Say)
(Mollusca: Gastropoda). Bull. Mar. Sci.
16:423–434.

HOFFMAN, D. L., and P. J. WELDON. 1978.
Flight responses of two species of inter-
tidal gastropods (Prosobranchia: Tro-
chidae) to sympatric predatory gastropods
from Barbados. Veliger 20:361–366.

KOHN, A. J., and V. WATERS. 1966. Escape
responses of three herbivorous gastropods
to the predatory gastropod Conus textile.
Anim. Behav. 14:340–345.

LOUDA, S. M. 1979. Distribution, movement
of diet of the snail, Searlesia dira in the
intertidal community of San Juan Island,
Puget Sound, Washington. Mar. Biol.
51:119–131.

MCLEAN, J. H. 1962. Sublittoral ecology of
kelp beds of the open coast area near
Carmel, California. Biol. Bull. 122:
95–114.

MAUZEY, K. P. 1966. Feeding behavior and
reproductive cycles in Pisaster ochraceus.
Biol. Bull. 131:127–144.

MAUZEY, K. P., C. E. BIRKELAND, and P. K.
DAYTON. 1968. Feeding behavior of as-
teroids and escape responses of their prey
in the Puget Sound region. Ecology 49:
103–119.

MENGE, B. A. 1972a. Competition for food
between two intertidal starfish species and
its effect on body size and feeding.
Ecology 53:635–644.

————. 1972b. Foraging strategy of a star-

fish in relation to actual prey availability
and environmental predictability. Ecol.
Monogr. 42:25–50.

PAINE, R. T. 1966. Food web complexity and
species diversity. Amer. Nat. 100:65–75.

PERRON, F. E. 1978. Locomotion and shell-
righting behaviour in adult and juvenile
Aporrhais occidentalis (Gastropoda: Strom-
baccea). Anim. Behav. 26:1023–1028.

PHILLIPS,   D.   W.   1975.   Distance
chemoreception-triggered avoidance of the
limpets Acmaea (Colisella) limatula and
Acmaea (Notoacmaea) scutum to the pred-
atory starfish Pisaster ochraceus. J. Exp.
Zool. 191:199–210.

————. 1976. The effect of a species-specific
avoidance response to predatory starfish
on the intertidal distribution of two gas-
tropods. Oecologia (Berlin) 23:83–94.

————. 1978. Chemical mediation of inver-
tebrate defensive behaviors and the ability
to distinguish between foraging and in-
active predators. Mar. Biol. 49:237–243.

RICKETTS, E. F., and J. CALVIN. 1962.
Between Pacific tides. 4th ed. Rev. by Joel
Hedgpeth. Stanford University Press, Stan-
ford, Ca.

SCHROETER, S. C. 1972. Characterization of
field populations of Margarites pupillus
(Gould) (Gastropoda, Prosobranchia).
M.S. Thesis, Brigham Young University.

SNYDER, N. F. R., and H. SNYDER. 1971.
Pheromone-mediated   behaviour   of
Fasciolaria   tulipa.   Anim.   Behav.
19:257–269.

WEBER, H. 1924. Ein Umdreh- und ein
Fluchtreflex bei Nassa mutabilis. Zool.
Anz. 60:261–269.

————. 1926. Uber die Umderhreflexe eini-
ger Prosobranchier des Golf von Neapel.
Ein Beigrage zur Bewegungsphysiologie
und Reflexbiologie der Gastripoden. Z.
Vergl. Physiol. 3:389–474.

WELDON, P. J. 1977. Comparative aspects of
gastropod righting and escape behavior.
M.S. Thesis, Bucknell University.

WELDON, P. J., and D. L. HOFFMAN. 1979.
Kick and thrust foot movements in the
righting and escape behaviour of marine
prosobranch   gastropods   (Mollusca:
Gastropoda). Z. Tierpsychol. 50:387–398.

WELLS, F. E. 1970. An ecological study of two sympatric species of *Fasciolaria* (Mollusca: Gastropoda) in Alligator Harbor, Florida. Veliger 13:95–108.

YARNELL, J. L. 1964. The responses of *Tegula funebralis* to starfishes and predatory snails (Mollusca: Gastropoda). Veliger (Suppl.) 56–58.