Pacific Science (1982), vol. 36, no. 4

Responses of Five Holothurian Species to Attacks by a Predatory Gastropod, *Tonna perdix*[1]

ROY K. KROPP[2]

ABSTRACT: In the laboratory *Tonna perdix* attacked and often engulfed individuals of five holothurian species. Two species, *Stichopus chloronotus* and *S. horrens*, sometimes escaped attacks by shedding a piece of body wall and bounding away from the predator. Bounding employed an exaggerated, direct arching peristalsis and was much faster than ordinary crawling. The general response of each of the other three species, *Holothuria atra*, *H. cinerascens*, and *H. hilla*, was a shortening of the body lengthwise accompanied by a swelling of the body into a spherelike shape. This response was not usually effective as an escape maneuver. Only *H. hilla* eviscerated during attacks and this was a direct result of penetration of the visceral cavity by the tonnid radula.

MANY HOLOTHURIANS, particularly tropical species, are known to be toxic. This toxicity is given as the primary reason for the paucity of predators on tropical holothurians (Bakus 1968, 1973, 1974, 1981). The toxin involved is holothurin, which is a saponin (Yamanouchi 1955), and which is found in several orders of holothurians (Nigrelli and Jakowska 1960). Holothurin is very toxic to marine fish (Yamanouchi 1955, Bakus 1968) and has been used by Pacific islanders to catch fish (Frey 1951). However, holothurin has little effect on crustaceans (Yamanouchi 1955).

Toxicity in holothurians is believed to have evolved in response to fish predation (Bakus 1968, 1974, 1981), the intensity of which increases with decreasing latitude (Vermeij 1978). However, fish rarely feed on holothurians (Bonham and Held 1963, Bakus 1973). Invertebrates do feed on sea cucumbers. In temperate regions, asteroid predation on holothurians is well documented (Mauzey et al. 1968, Birkeland, Dayton, and Engstrom 1982). A cymatiid gastropod, *Charonia variegata*, may be a significant predator on holothurians in Jamaica (Parrish 1972). Tonnid gastropods are also reported to eat sea cucumbers (Bakus 1973, Kay 1979). Crustaceans may also prey on holothurians. In Guam I saw a hermit crab, *Dardanus megistos*, and a xanthid crab, *Atergatis floridus*, eating holothurians. A stomatopod, *Gonodactylus oerstedii*, may occasionally feed on small holothurians (Dominguez 1982).

Do holothurians have methods by which predation by invertebrate predators, in particular gastropods, can be avoided? Most information concerning predation on sea cucumbers by gastropods is anecdotal (Edwards 1971, Thorpe 1972). In the present study I examined the responses of five holothurian species to predatory attacks by the tonnid gastropod, *Tonna perdix*.

STUDY ANIMALS

Tonna perdix Linnaeus, a moderately large tonnid found both intertidally and subtidally at Guam, was used as the predator. This species has been seen to feed on holothurians on reef flats at Guam (B. D. Smith, personal communication). Tonnids are equipped with a partially invaginable proboscis (Hyman 1967) which is used to engulf prey. The main buccal gland of tonnids is large and secretes free sulphuric acid, which constitutes 3–5% of the "saliva" (Hyman 1967). The evolutionary

---

[1] Contribution No. 176 from the University of Guam Marine Laboratory. Manuscript accepted 30 May 1982.

[2] Present address: University of Maryland, Department of Zoology, College Park, Maryland 20742.

origin of this solution is uncertain, but it may assist in feeding, especially on soft-bodied prey (Hughes and Hughes 1981).

Three specimens of *T. perdix* were used in this study. When collected they measured 43.6 mm, 84.5 mm, and 88.7 mm in shell length. They were collected from either Shark's Hole or Cetti Bay, Guam.

Five species of holothurians were used as prey. All of these were collected from Piti Bay or Pago Bay, Guam. None of the five has cuvierian tubules.

Stichopus chloronotus Brandt occurs exposed on sand-covered reef pavement during both day and night. This species is very toxic to fish (Yamanouchi 1955, Bakus 1981).

Stichopus horrens Selenka is cryptic by day, dwelling wedged into concavities on the underside of boulders or rubble. Because the species is cryptic it would be predicted to have low toxicity (Bakus 1981).

Holothuria atra Jaeger is exposed both day and night in almost every reef habitat. This species is very toxic to fish (Yamanouchi 1955, Bakus 1968, 1974, 1981).

Holothuria cinerascens (Brandt) is one of the few tropical filter-feeding holothurians (Rowe and Doty 1977). It is cryptic, living wedged into crevices in rocks and dead coral, usually having only the oral tentacles visible. Because of the species' cryptic habits, the toxicity of *H. cinerascens* would be predicted to be low (Bakus 1981).

Holothuria hilla Lesson is usually considered cryptic because it is found under boulders or entwined in pieces of rubble during the day. However, at night it can be found with its anterior end extended a short distance from refuge. Occasionally, a few specimens may be seen fully exposed at night. Bakus (1968) reported the body wall of *H. hilla* to be toxic to fish but did not mention this holothurian in any of his later papers.

METHODS

The tonnids were maintained in the laboratory in 50 l flow-through plexiglass tanks, the bottoms of which were covered by coral sand. The holothurians were held in large flow-through flats (700 l) which were also sand-covered.

All feeding trials and locomotion measurements were made at night using either unfiltered or red-filtered incandescent light. Some initial feeding trials were held in the 50 l tanks but most took place in one of the large flats. Field observations were made at night on the Piti Bay reef flat. Feeding trials were attempted in the field.

During the feeding trials the reaction of the prey to attack by the tonnid and prey behavior during the attack were noted. Any locomotion subsequent to the attack was noted and measured. On occasion the predator made contact with but did not attack the prey. Prey behavior during and immediately after this contact was noted. Locomotion of the two *Stichopus* species was observed and the locomotion rates estimated for normal conditions and after contact with or escape from the predator.

No attempt was made to determine prey preference by *Tonna perdix*, but some measurements of crawling speeds and general observations of prey detection and attack patterns by the tonnid were made.

RESULTS

Tonna perdix

Most of the time a feeding trial was started while the tonnid was buried in the sand with only its siphon exposed. After detecting a prey holothurian placed nearby, the tonnid emerged from the sand and probed the surrounding water with its partially everted proboscis. Upon contact with the prey, the end of the proboscis flared and rapidly moved along the length of the prey until one end of the prey was reached. There were no predictable patterns to the direction of proboscis movement. Once an end of the prey was reached, the proboscis extended lengthwise and engulfed the prey. The prey was considered totally engulfed when the proboscis opening closed around the opposite end of the prey. After engulfment, the tun was usually quiescent for a brief time before crawling away or burying.

TABLE 1

SUMMARY OF ATTACKS BY *Tonna perdix* ON HOLOTHURIANS

PREY	NO. OF ATTACKS	NO. ENGULFED	NO. ESCAPES	NO. SURVIVING ESCAPES
Stichopus chloronotus	7	4	3	3
S. horrens	6	4	2	2
Holothuria atra	4	3	1	1
H. cinerascens	4	3	1	1
H. hilla	7	6	1	0

When actively hunting, the tun crawled upstream sweeping its siphon from side to side. This pattern was occasionally interrupted by vertical siphon probes into the water column and was accompanied by alternate taps of the cephalic tentacles onto the substratum ahead of the tun.

Estimates of locomotion rates by the largest tonnid were 43 ± 2.8 cm/min (tun fed, crawling on sand); 58 ± 1.4 cm/min (tun unfed, crawling on sand); and 183 ± 4.2 cm/min (tun unfed, hunting on the side of the plexiglass tank; $n = 2$ for each estimate).

On several occasions the tonnids came into foot and/or siphon contact with a holothurian but did not attack it. *Stichopus chloronotus*, *S. horrens*, and *Holothuria atra* were contacted on several instances without attack. *H. hilla* was contacted only once without being attacked and *H. cinerascens* was attacked every time it was touched. The largest tun was taken to the field, but it failed to attack any prey despite contact with at least 12 holothurians.

Stichopus chloronotus

Feeding trials on this and the other holothurian species are summarized in Table 1. The initial response of *S. chloronotus* to attack by *T. perdix* was a general contraction of the body that was accompanied by a slight bulging of the body at the point of attack. If engulfment occurred at the posterior end, the anterior end was lifted off the substratum and slowly waved from side to side. When large prey were attacked, the proboscis of the tun remained at the point of attack.

The second stage of the response, if there was not total engulfment, involved the shedding of a piece of the attacked individual's body wall. This shedding occurred as a result of a sudden contraction of the prey body into a "U" shape. As the piece of body wall tore free, the prey rolled away from the predator and, once oriented upright, began to bound away from the attack site using an exaggerated direct arching peristalsis (Heffernan and Wainwright 1974). During this movement the posterior end of the prey was lifted off the substratum and moved anteriorly about 7 to 8 cm. This action caused the body to arch up off the substratum and initiated the peristaltic wave which quickly passed forward. A second peristaltic wave began well before the first had reached the anterior end of the prey body. When bounding after an escape from attack the prey always traveled downcurrent. During this prey movement the tun ingested the cast-off piece of body wall and then moved off upcurrent.

After such an escape the resulting wound was examined and measured (Table 2). The wounds appeared to involve only loss of body wall. The mesentary surrounding the viscera was not punctured. When body wall was lost from the ventrum, the tube feet were left intact. Any body wall lost from the posterior end did not include a small strip of body wall surrounding the anus. Similarly, at the anterior end the oral tentacles were undamaged by attacks there. No attacked prey eviscerated. All wounded prey survived. The body wall wounds healed by growth from the wound edges (new growth) or by the growing together of two sides of the wound brought together by a contraction of the body.

TABLE 2

WOUND TYPE, WOUND SIZE, AND FATE OF PREY AFTER ATTACK BY *Tonna perdix*

PREY	PREY LENGTH (cm)	WOUND TYPE	WOUND SIZE (mm^2)	FATE*
Stichopus chloronotus	26	Body wall loss	42	S
S. chloronotus	17	Body wall loss	17	S
S. horrens	27	Body wall loss	135	S
Holothuria cinerascens†	17	Deep abrasion	104	S
		Abrasion	165	
		Abrasion	57	
		Abrasion	47	
H. hilla	?	Massive tissue loss	Large	D

*S = survived; D = died.

† This individual had four wounds.

The largest *S. chloronotus* totally engulfed was 17 cm (crawling length). It was swallowed within two minutes by the largest tun. The two prey that escaped were 17 cm and 26 cm long.

In response to contact by the predator in the absence of an attack, the prey ceased moving and became rigid but did little else until after the period of contact ended. At this time the prey bounded away in a manner similar to but less intense than bounding after body wall shedding.

During "normal" crawling in the lab *S. chloronotus* moved at about 8.2 ± 3.9 cm/min and the ventrum lifted only about 1.0–1.5 cm off the substratum. This rate of speed increased to about 28 cm/min after contact without attack and to about 39.2 ± 4.6 cm/min after an escape. During escape bounding the ventrum lifted about 7–8 cm off the substratum.

Stichopus horrens

Response to tonnid attack was very similar in this species to that of *S. chloronotus*. The response involved a sudden contraction of the body into a "U" shape and the shedding of a piece of body wall (which was consumed by the tun), followed by downcurrent bounding locomotion. Damage to the prey was only loss of body wall (Table 2). No mesentary surrounding the viscera was punctured and no prey eviscerated. The largest prey engulfed was 16 cm long and was consumed within four minutes. All prey escaping attacks survived and body wall repair was similar to that of *S. chloronotus*.

The response of *S. horrens* to contact with the tun without attack was similar to that of *S. chloronotus*, although on one occasion it was extremely exaggerated. In the field two prey did not respond to contact by the tun, although others began to move by direct arching peristalsis. This response did not last more than two minutes for any individual. One individual, after tun contact ended, raised both ends of its body off the substratum and was swept a short distance downstream by the current.

In the lab locomotion rates were about 13.7 ± 5.7 cm/min for "normal" crawling. In the field very few *S. horrens* moved noticeably—out of 33 individuals observed during a random ten-minute swim, none was moving to any extent. Locomotion after contact without attack varied from about 30 cm/min to about 69 cm/min during one response in the lab. After attack and escape the locomotion rate was about 40 cm/min.

S. horrens, when observed in the field, seemed to orient into the prevailing current. Of the 33 individuals counted during the ten-minute random swim, 25 were oriented with long axis of the body parallel to the direction of the current. Of the eight oriented perpendicular to the current, most were downstream of a boulder or other obstruction.

Holothuria atra

A slight contraction of the body was the initial response of this species to tonnid attack. This was accompanied by slight body swelling. As the attack progressed, the degree of swelling increased. One 16 cm long individual, with a girth of 12 cm, was removed during an attack and measured. The body had contracted to 11 cm in length but had swollen to 19 cm in girth. This particular prey was placed back in the tank with the tun and was attacked again. The prey began to swell, but was released by the tun which then crawled away. Later the cephalic tentacles of the tun touched the prey but quickly recoiled from it. During this latter attack sequence a reddish fluid was seen immediately adjacent to the prey. This prey was not attacked again. On other occasions smaller *H. atra* were quickly engulfed.

In the field several specimens of *H. atra* were observed with 2–3 cm circular, abrasion-like wounds on their bodies. Locomotion rates were not measured for this species.

Holothuria cinerascens

The first response of this species to an attack was a moderate contraction of the body accompanied by slight body swelling. Eventually the body of the prey assumed sphere-like proportions. The tun appeared to be trying to get a "radula-hold" on the prey, but had difficulty doing so. After about 18 minutes the predator seemed to have a grip on the prey. Several times the tun released and reattacked the holothurian, but the only prey response was to maintain its body in a spherelike shape. This episode continued for more than 70 minutes. This 16 cm long prey was never eaten but sustained four wounds. The wounds were abrasionlike and in only one was there penetration to the mesentary surrounding the viscera.

Three smaller *H. cinerascens* (12–14 cm) were engulfed by the largest tun. One of these was attached to the two walls forming one corner of the tank. Its response to the attack was body contraction and swelling. The tun worked its proboscis between the prey and the tank walls until the prey was dislodged and engulfed. This process took five minutes. Many tube feet remained attached to the tank wall after the attack.

Holothuria hilla

As with each of the previous species, the initial response to attack was body contraction. This was accompanied by some twisting of both ends of the body. Body swelling began quickly but was generally limited at this stage to the portion of the body under attack. Upon engulfment of one end of the body, the other end started to swell. Later in the attack the prey usually eviscerated either through the anus or possibly through a body-wall puncture caused by the tun. Only one *H. hilla* escaped from an attack, but it was badly damaged and died two days later.

In the field one *H. hilla*, which was contacted by the foot of the tun, quickly retracted its anterior end back into the hole from which it had been projecting.

Artificial Stimulation of Observed Responses

Several attempts were made in the laboratory and in the field to stimulate some of the observed responses of the holothurians to attacks by the tonnid. Any contact with a holothurian resulted in a slight contraction of the holothurian's body. An attempt was made to stimulate the quick retraction of the anterior portion of the body of *H. hilla* by touching the prey gently and by pinching the midbody region. The only result was a slight body contraction by the prey. However, touching the prey's snout caused quick retraction of the anterior third of its body.

Stichopus horrens was stimulated by firm pinching of the body, by gentle pinching, by touching the posterior region of the body with a rock, and by picking the prey completely off the bottom, squeezing it firmly, and placing it back on the bottom. No response other than body contraction occurred after any of these stimuli.

Rough handling underwater in the laboratory tanks stimulated *Holothuria atra*, *H. hilla*, and *H. cinerascens* to contract and swell similarly to the responses described for each species. Also this handling caused a reddish fluid to be given off by *H. atra*.

DISCUSSION

Margolin (1976) cautions against assuming that prey behavior in response to contact with another animal is actually an escape response without evidence that the animal eliciting the response is a predator on the responding animal. In this study *Tonna perdix* did successfully prey on all of the holothurian species tested. Therefore prey response to contact by *T. perdix* can be called defensive, and actions that enabled prey to get away from the tun can be called escape responses.

Tonnids may be among the fastest of the carnivorous gastropods. The crawling speeds reported here for *T. perdix* are faster than those reported for other tonnaceans. *Cassis tuberosa* and *Cypraecassis testiculus* were reported by Hughes and Hughes (1981) to crawl at about 18 cm/min and 30 cm/min, respectively. Taylor (1974) recorded a speed of about 42 cm/min for *Fasciolaria tulipa*. *T. perdix* traveled much faster on plexiglass than any of the snails studied by Taylor (1974).

The body wall shedding response of *Stichopus* to tonnid attack has not been previously reported. This response, followed by the exaggerated bounding locomotion, was very successful. The success of this response seems to be related to prey size because it cannot be used by relatively smaller prey that can be quickly engulfed. Larger prey also have larger papillae on the margins of the body that may impede movement of the tonnid proboscis along the body of the prey, thus preventing the predator from engulfing one end of the prey.

The tendency for downcurrent bounding shown by *Stichopus* after escape is advantageous because the predator hunts upcurrent. Similarly the orientation of the long axis of the body parallel to the direction of the current may lessen the amount of body area that would be presented to a predator approaching from downstream. However, this orientation may merely give *Stichopus* hydrodynamic stability in the current.

The principal defense of *Holothuria atra* to tonnid attack is probably its large size coupled with its secretion of holothurin. When handled roughly this species gives off holothurin (Bakus 1973). Large prey cannot be engulfed easily, which means that a prey item must be "handled" more. This could cause the secretion of holothurin, causing the predator to retreat from the attack.

The swelling response of *H. cinerascens* seems to be effective, especially when the predator is small. This holothurian lives wedged into crevices, and its swelling would make it difficult for the tun to get a grip on the prey. However, one feeding trial mentioned here showed that the tun can work its proboscis between the prey and the substratum to which the prey was attached and thus can engulf a relatively small individual.

Holothuria hilla seems to have little defense against tonnid attacks; every attack resulted in the death of the prey. Quick retraction of the body back into a hole or crevice may be a successful way to avoid an attack.

The escape responses reported here parallel those of other animals. Many animals obtain refuge from predation by attaining large size (Paine 1976, Vermeij 1978). This protection occurs by rapid early growth and is strengthened by spines (Vermeij 1978) or papillae as in the case of *Stichopus*.

Evidence for increased locomotion in reacting to a predator exists for gastropods in response to sea stars (Feder 1963) or to other gastropods (Kohn and Waters 1966). Temperate holothurians react to contact with certain sea stars by swimming (Mauzey, Birkeland, and Dayton 1968, Margolin 1976). Glynn (1965) reported bounding locomotion by *Astichopus* similar to that reported here for *Stichopus*. In his study the bounding could be stimulated by environmental factors. Glynn also reported bounding speeds much greater than those reported here.

Body wall shedding by *Stichopus* is comparable to tail autotomy by salamanders (Maiorana 1977) or leg autotomy by crustaceans (Robinson, Abele, and Robinson 1970). This shedding, in which cast-off tissue is eaten by the predator, contradicts Bakus' (1981) hypothesis that benthic invertebrates employ defenses against predators that do not supply energy to the predator. This energy sacrifice is advantageous to the holothurian because it gives the prey time to bound away from the predator. Salamander autotomy does depress the reproductive output of the individual involved (Maiorana 1977). Similar depressed reproduction may occur in *Stichopus*, but this has not been investigated.

Many organisms in addition to holothurians produce toxins or noxious fluids to thwart predation; examples include sponges (Bakus and Green 1974), gastropods (Thompson 1960), and plants (Feeny 1977). These secretions are often most effective against general predators, but they are not usually effective against specialists (e.g., Feeny 1977). As shown in this study, holothurian anti-predator mechanisms, which have purportedly evolved in response to a high intensity of fish predation, are not effective against a specialist, *Tonna perdix*, against which holothurians have evolved distinct responses to predatory attacks. Certainly future studies will reveal other examples of this phenomenon in the seas.

ACKNOWLEDGMENTS

I appreciated the considerable assistance of Barry D. Smith during the early portions of this study and am grateful for his comments throughout the study. Thanks to Gerry Davis for help with the night field work. I also thank Geerat Vermeij, Lu Eldredge, Jane Dominguez, and Elizabeth Dudley for their encouragement and helpful comments on the manuscript. Facilities for this study were made available by the University of Guam Marine Laboratory.

LITERATURE CITED

Bakus, G. J. 1968. Defensive mechanisms and ecology of some tropical holothurians. Mar. Biol. 2:23–32.

———. 1973. The biology and ecology of tropical holothurians. Pages 326–367 *in* O. A. Jones and R. Endean, eds. Biology and geology of coral reefs, vol. 2, Biol. 1. Academic Press, New York.

———. 1974. Toxicity in holothurians: a geographical review. Biotropica 6:229–236.

———. 1981. Chemical defense mechanisms on the Great Barrier Reef, Australia. Science 211:497–499.

Bakus, G. J., and G. Green. 1974. Toxicity in sponges and tropical holothurians: a geographical review. Science 185:951–953.

Birkeland, C., P. K. Dayton, and N. A. Engstrom. 1982. A stable system of predation on a holothurian by four asteroids and their top predator. Austr. Mus. Mem. 16:175–189.

Bonham, K., and E. E. Held. 1963. Ecological observations on the sea cucumbers *Holothuria atra* and *H. leucospilota* at Rongelap Atoll, Marshall Islands. Pac. Sci. 17:305–314.

Dominguez, J. H. 1982. Temporal activity patterns of reef-dwelling stomatopods. M.S. Thesis, University of Maryland, College Park. 34 pp.

Edwards, C. E. 1971. A lively *Tonna maculosa* (Dillwyn, 1817). Miami Malac. Soc. Quart. 5:12–13.

Feder, H. M. 1963. Gastropod defensive responses and their effectiveness in reducing predation by starfishes. Ecology 44:505–512.

Feeny, P. 1977. Defensive ecology of the Cruciferae. Ann. Missouri Bot. Gard. 64: 221–234.

Frey, D. G. 1951. The use of sea cucumbers in poisoning fishes. Copeia 1951 (2):175–176.

Glynn, P. W. 1965. Active movements and other aspects of the biology of *Astichopus* and *Leptosynapta* (Holothuroidea). Biol. Bull. 129:106–127.

Heffernan, J. M., and S. A. Wainwright. 1974. Locomotion of the holothurian *Euapta lappa* and a redefinition of peristalsis. Biol. Bull. 147:95–104.

Hughes, R. N., and H. P. I. Hughes. 1981. Morphological and behavioural aspects of feeding in the Cassidae (Tonnacea, Mesogastropoda). Malacologica 20:385–402.

Hyman, L. H. 1967. The invertebrates.

volume 6, Mollusca I. McGraw-Hill, New York. 792 pp.

KAY, E. A. 1979. Hawaiian marine shells. *In* Reef and shore fauna of Hawaii. Sec. 4: Mollusca. B. P. Bishop Mus. Spec. Publ. 64(4): 1–653.

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

MAIORANA, V. C. 1977. Tail autotomy, factual conflicts and their resolution by a salamander. Nature 265: 533–535.

MARGOLIN, A. S. 1976. Swimming of the sea cucumber *Parastichopus californicus* (Stimpson) in response to sea stars. Ophelia 15(2): 105–114.

MAUZEY, K. P., C. BIRKELAND, and P. K. DAYTON. 1968. Feeding behavior of asteroids and escape responses of their prey in the Puget Sound region. Ecology 49: 603–619.

NIGRELLI, R. F., and S. JAKOWSKA. 1960. Effects of holothurin, a steroid saponin from the Bahamian sea cucumber (*Actinopyga agassizi*), on various biological systems. Ann. N. Y. Acad. Sci. 90: 884–892.

PAINE, R. T. 1976. Size-limited predation: an observational and experimental approach with the *Mytilus-Pisaster* interaction. Ecology 57: 858–873.

PARRISH, J. D. 1972. A study of predation on tropical holothurians at Discovery Bay, Jamaica. Page 6 *in* G. J. Bakus, ed. Marine studies on the north coast of Jamaica. Atoll Res. Bull. 152.

ROBINSON, M. H., L. G. ABELE, and B. ROBINSON, 1970. Attack autotomy: a defense against predators. Science 169: 300–301.

ROWE, F. W. E., and J. E. DOTY. 1977. The shallow-water holothurians of Guam. Micronesica 13: 217–250.

TAYLOR, S. L. 1974. Adaptive design of locomotion and foot form in prosobranch gastropods. J. Exp. Mar. Biol. Ecol. 14: 99–156.

THOMPSON, T. E. 1960. Defensive adaptations of opisthobranchs. J. Mar. Biol. Assoc. U. K. 39: 123–134.

THORPE, F. H. 1972. Our tun feeds on sea-cucumbers. *Tonna galea* Linne or "giant tun." Mollusk Chase, April 1972: 4–6.

VERMEIJ, G. J. 1978. Biogeography and adaptation: patterns of marine life. Harvard Univ. Press, Cambridge, Mass. 332 pp.

YAMANOUCHI, T. 1955. On the poisonous substance contained in holothurians. Publ. Seto Mar. Biol. Lab. 4(2–3): 25–45.