

THE MOTILE ESCAPE RESPONSE OF A SESSILE PREY: A SPONGE-SCALLOP MUTUALISM

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Abstract: The association of the sponges *Myxilla incrustans* (Esper) and *Mycale adhaerens* (Lambe) with the scallops *Chlamys hastata hericia* Gould and *C. rubida* (Hines) is shown to be a mutualism, which protects the sponges from predatory sponge-rasping dorid nudibranchs and the scallops from predatory starfish. The sponge is protected by scallop motility (also shown for the *Suberites ficus*-hermit crab association). The sponge helps to protect the scallops by altering the surface texture of the shell so increasing the efficacy of the swimming escape response by decreasing the adhesive abilities of asteroid tube-feet. The sponge also provides tactile camouflage against certain predatory starfish. There was no evidence that either component chemically deceived or repelled the predators of the other component. Predation pressure on both components of the association appears to be the major force leading to the mutualism.

INTRODUCTION

Certain species of scallops are characteristically associated with sponges which cover one or both valves (Bakus, 1966), an association raising questions concerning its type - commensalism, mutualism or parasitism - and the force, or forces, which structure the association.

Sponges can have destructive effects on bivalve hosts by boring (*Cliona*) or by smothering (*Halichondria panicea*) (Korringa, 1951). Beu (1965), who linked shell sculpturing to the presence of a sponge, suggested mutualistic effects of increased food supply and a favorable substratum for the sponge and "almost complete protection" for the scallop. He did not give any evidence and did not name potential predators nor suggest how the protection was attained.

One force which can be experimentally investigated and which is known to favor mutualistic associations is predation (Janzen, 1966). In this study of a scallop-sponge association, I have determined the most likely major predators on the sponges and scallops, estimated the relative survival of the prey as a function of the presence or absence of the other component of the association, and advanced and supported hypotheses which may serve to explain the observed results.

This investigation was made on the sponges *Myxilla incrustans* (Esper) and *Mycale adhaerens* (Lambe), which are commonly found on the scallops *Chlamys hastata hericia* Gould and *C. rubida* (Hines). The doridacean nudibranchs *Archidoris*

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montereyensis (Cooper) and *Anisodoris nobilis* (MacFarland) are among the chief predators of these sponges in the San Juan Archipelago, Washington, the site of this study. Both dorids will eat *Myxilla incrustans* but only *Anisodoris nobilis* will eat *Mycale adhaerens* (Bloom, 1974). Sea anemones, crabs, octopods, and starfish will eat scallops in nature. Starfish, however, predominate numerically in the habitats studied and probably have a greater effect on scallop populations. *Pycnopodia helianthoides* (Brandt), *Pisaster ochraceus* (Brandt), *Orthasterias koehlerii* (de Loria), and *Evasterias troschelii* (Stimpson) eat scallops in the laboratory. The last two starfish have also been observed to prey on scallops in nature (Mauzey, Birkeland & Dayton, 1968).

Two potential mechanisms by which a scallop might reduce predation by dorids on its sponge-cover are by its locomotor activity and by chemically repelling the dorids; sponges might protect scallops from starfish predation by chemical effects (camouflage or repellent), tactile camouflage or hindrance of tube-foot adhesion.

DORID-SPONGE-SCALLOP INTERACTIONS

In order to determine whether predation pressure could account for the association, relative measures of survival of the components when associated and when separated are necessary. Survival curves were determined by placing sponges and scallops in enclosures with flowing sea water with the appropriate predators and monitoring for deaths due to predation. Sponge 'death' was defined as being consumed completely; scallop 'death' due to predation was defined when the shell was devoid of tissue. Since all experiments were monitored daily, death due to causes other than predation was detectable by the presence of rotting tissue. The survival of sponges as a function of the motility of the substratum was determined as follows. Sponges were presented to the dorid predators *Archidoris montereyensis* and *Anisodoris nobilis* in three forms, namely, attached to motile scallops; attached to living scallops rendered non-motile by a rubber band placed around the valves, with the valves held agape by a small block of polyethylene; and attached to shells from which the scallop tissue had been removed. These forms are referred to as 'sponge-covered motile', 'sponge-covered non-motile', and 'sponge-covered empty' scallops, respectively.

The ratio of *Chlamys hastata hericia* to *C. rubida* in the field populations sampled was $\approx 9 : 1$ and was preserved in all experiments using scallops. Both species of sponge were found in approximately equal frequencies on both species of scallops.

Two types of enclosures were used in the dorid-sponge experiments, a) one-liter plastic boxes with screened sides, and b) a shallow aquarium of $1.5 \times 0.5 \times 0.2$ m. The small enclosures contained one dorid and one sponge-scallop combination while the aquarium held 10 dorids and 30 sponge-scallop combinations.

In one aquarium experiment the chemical repellent effect of scallop tissue on dorid nudibranchs was examined. Ten sponge-covered non-motile (but living) scallops and 10 sponge-covered empty shells were presented to 2 individuals each of the above

dorid species. After two days, all scallop shells had been cleaned of their sponge-cover regardless of the presence of living scallop tissue in one half of the shells. From this, I conclude that scallops do not chemically repel or mislead dorid predators and that an empty shell is experimentally equivalent to a non-motile but living scallop.

In a second aquarium experiment the effect of motility of the sponge substratum on sponge survival was examined in a 'semi-natural' setting, *i.e.*, with densities of scallops equivalent to those found in nature and with sufficient room to utilize effectively their swimming escape response. Nine motile scallops and 9 empty scallops covered with *Myxilla incrustans* and 6 motile scallops and 6 empty shells covered with *Mycale adhaerens* were presented to 5 individuals each of the above dorid species. After seven days, the sponges on motile scallops had not been cropped while those on non-motile substrata had been completely eaten (Table I).

TABLE I

Survival of sponge as a function of the motility of the sponge substrata.

	Small enclosures (33 days)			Large enclosures (7 days)		
	Number of sponges			Number of sponges		
	Alive	Eaten	<i>P</i>	Alive	Eaten	<i>P</i>
<i>Myxilla incrustans</i>						
on motile <i>Chlamys</i>	2	6	> 0.05	9	0	< 0.005
on non-motile <i>Chlamys</i>	1	18		0	9	
<i>Mycale adhaerens</i>						
on motile <i>Chlamys</i>	14	10	< 0.005	6	0	< 0.005
on non-motile <i>Chlamys</i>	0	11		0	6	
Both sponges						
on motile <i>Chlamys</i>	16	16	< 0.005	15	0	< 0.005
on non-motile <i>Chlamys</i>	1	29		0	15	

All *Mycale adhaerens* with *Anisodoris nobilis*; all *Myxilla incrustans* with *Anisodoris nobilis* and *Archidoris montereyensis*: non-motile *Chlamys*, shells devoid of scallop tissue: Fisher Exact Probability. Test was used for 2×2 contingency tables with row totals equal to or less than 15: χ^2 test used for all others: *P*, probability of the observed or greater difference occurring by chance.

A further experiment was made to ascertain how effective scallop motility was in reducing predation by dorids on its sponge-cover. Using the small enclosures the chances of dorid predation on the sponge-cover were maximized by severely restricting the ability of the scallop to move away from the dorid while not preventing the scallop from using the escape response. Eight motile scallops and 19 empty shells covered with *M. incrustans*, and 24 motile scallops and 11 empty shells covered with *M. adhaerens* were placed in the individual plastic containers. Into one half of the containers with *M. incrustans*, one *Archidoris montereyensis* was placed. One *Anisodoris*

nobilis was added to each of the remaining containers. After 33 days of an experiment which heavily favored sponge cropping, only 50 % of the sponge-covered motile scallops showed cropping of their sponge-covers while the sponge-covers of the empty shells were almost totally (99 %) eaten in five days (Table I).

Dorids do not appear to be able to consume sponges on unconfined motile scallops and do not discriminate between sponges attached to empty shells and those attached to non-motile shells with a living scallop. In all observations, dorids attempting to feed on sponges attached to motile scallops elicited the escape response of the scallop before the sponge was cropped. Scallops are known to be generally sensitive to disturbance. The swimming escape response can be elicited by shadows falling on the scallop, by the turbulence of a passing diver, by the presence of predatory starfish and by almost any movement. The lack of evidence of chemical effects and the strong evidence that scallop motility is directly related to the survival of sponge-cover supports the hypothesis that scallop motility is the chief means by which sponges derive protection from their molluscan substrata.

To confirm this an experiment was made using the sponge *Suberites ficus* (Johnston) which serves as a home for many species of hermit crabs. Two *Archidoris montereyensis* and two *Suberites ficus* were placed separately in two enclosures (30 × 30 × 15 cm) with flowing sea water. A *Pagurus capillatus* (Benedict) and a *P. dalli* (Benedict) occupied the sponges in one enclosure while the *Suberites ficus* in the other enclosure were not occupied by hermit crabs. The sponge was examined daily for signs of cropping for 30 days. The non-motile *Suberites ficus* were promptly consumed (in 10 days) while the others escaped predation over a period of 30 days.

THE STARFISH-SCALLOP-SPONGE INTERACTIONS

The association of sponges and scallops is, then, beneficial to the sponge and any effect on the scallop must be determined; the effect of sponge-cover on scallop survival to starfish predation has been examined.

Survival curves for *Chlamys* were obtained by exposing the scallops to starfish in large tanks (4.5 m³) (*Pycnopodia helianthoides*, *Orthasterias koehleri*, and *Evasterias troschelii* were chosen because they occur naturally on the scallop beds). A known scallop predator, the cushion star, *Pteraster tessulatus* Ives, was not used because of its rarity and the experimental difficulties of working with this species (Rodenhouse & Guberlett, 1946). *Pisaster ochraceus*, a well-known and quite common predatory starfish, was included even though it does not normally occur in the scallop beds. Scallops were presented in four forms, namely; motile scallops with sponge covering one or both valves; non-motile scallops with sponge-cover; motile scallops without sponge-cover; and non-motile scallops without sponge-cover. These types will be referred to as 'motile-sponge-covered', 'non-motile-sponge-covered', 'motile-clean', and 'non-motile-clean' scallops, respectively.

In one series of experiments, all four types of scallops were offered to separate the

effects of motility and sponge-cover. Five to 19 scallops of each type (20 to 76 scallops in all) were offered together to approximately equal biomasses of *P. ochraceus*, *Evasterias troschelii*, and *Orthasterias koehleri* in separate tanks. The number of scallops consumed per day was determined and the experiment terminated when only one scallop type remained. For the Fisher Exact Probability Test or the χ^2 test (Siegel, 1956), 2×2 contingency tables were used for the number of scallops alive and dead for each cohort at the closest sampling point when 50% of all prey items in the categories to be compared remained. Starfish predation shows species-specific patterns. Since equal numbers of scallops were offered to approximately an equal biomass of starfish, there appears to be a distinct difference in efficiency of predation

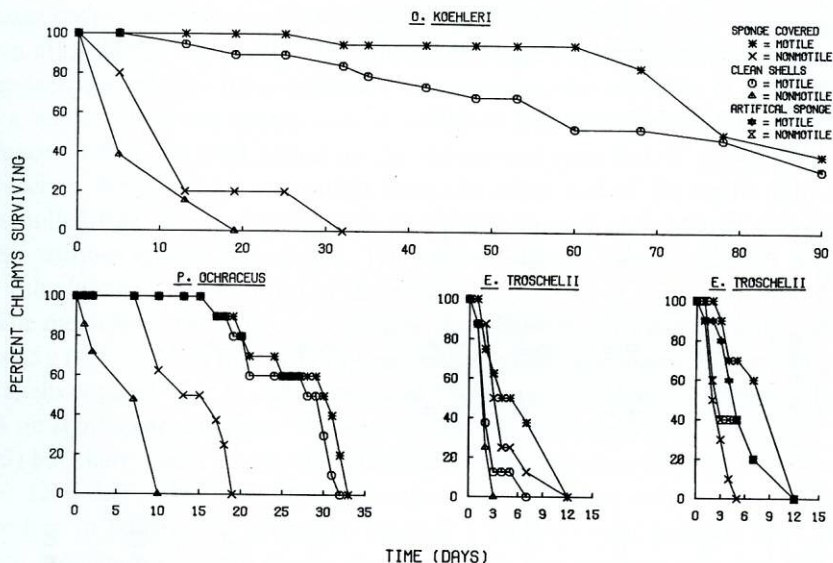


Fig. 1. Survival curves for *Chlamys* in the presence of predatory starfish: see Table II for the number of scallops in each class: lower right plot compares artificial sponge-cover with real sponge-cover, others compare real sponge-cover with no sponge-cover.

(Fig. 1). In a second series of experiments designed to mimic reality, *i.e.*, all scallops were motile, 10 to 15 motile-clean and motile-sponge-covered scallops were offered to *Pisaster ochraceus*, *Evasterias troschelii*, and *Pycnopodia helianthoides*. Experiments were terminated and analyzed as described above. This experiment was done four times for both *Evasterias troschelii* and *Pycnopodia helianthoides* and twice for *Pisaster ochraceus*. *Orthasterias koehleri* was not used because of its lethargic predatory habits (Fig. 1).

As regards differential survival of the scallops (Table II), *Pycnopodia helianthoides* and *Pisaster ochraceus* are equally effective in catching motile sponge-covered or clean scallops, while *Evasterias troschelii* and *Orthasterias koehleri* can capture significantly more clean-motile than sponge-covered-motile scallops. Conversely,

TABLE II
Survival of scallops as a function of motility, sponge-cover and predator: * indicates difference between categories not significant.

	<i>E. troschelii</i>		<i>P. ochraceus</i>		<i>O. koehleri</i>		<i>P. helianthoides</i>	
	Number of scallops Alive Eaten	<i>P</i>	Number of scallops Alive Eaten	<i>P</i>	Number of scallops Alive Eaten	<i>P</i>	Number of scallops Alive Eaten	<i>P</i>
Motile <i>Chlamys</i> with sponge	6	2	6	4	9	9	9	1
without sponge	3	5	5	5	9	10	1	< 0.005
		> 0.05*		> 0.05*		> 0.05*		> 0.05*
Non-motile <i>Chlamys</i> with sponge	7	1	8	0	4	1	6	4
without sponge	2	6	3	4	5	8	6	4
		< 0.025		< 0.05		> 0.05*		> 0.05*
Motile & non-motile <i>Chlamys</i> with sponge	13	3	9	9	17	6	6	4
without sponge	5	11	8	9	10	22	5	5
		< 0.020		> 0.05*		< 0.01		< 0.01
With & without sponge motile <i>Chlamys</i>	9	7	17	3	27	10	6	4
non-motile <i>Chlamys</i>	9	7	0	15	0	18	6	4
		> 0.05*		< 0.001		< 0.001		> 0.05*
Motile <i>Chlamys</i> only								
Experiment 1 with sponge	9	1	9	6	9	6	9	1
without sponge	1	9	7	8	7	8	1	< 0.005
		< 0.05		> 0.05*		> 0.05*		> 0.05*
Experiment 2 with sponge	19	1	6	4	6	4	6	4
without sponge	4	16	6	4	6	4	3	7
		< 0.01		> 0.05*		> 0.05*		> 0.05*
Experiment 3 with sponge	13	2	8	0	13	0	6	4
without sponge	1	14	6	4	6	4	6	4
		< 0.01		> 0.05*		> 0.05*		> 0.05*
Experiment 4 with sponge	15	0	15	0	15	0	6	4
without sponge	0	15	0	15	0	15	5	5
		< 0.01		> 0.05*		> 0.05*		> 0.05*
Total sample size for motile <i>Chlamys</i>	136		70		37		80	

Evasterias troschelii shows no differential predation on motile and non-motile scallops while *Pisaster ochraceus* and *Orthasterias koehleri* can capture significantly more non-motile than motile scallops in the same time (Table II). In general, sponge-covered motile and non-motile animals had equal or higher survival than did clean scallops of the same motility type (Fig. 1, Table II). Clearly scallops benefit from the association, by deriving protection from predatory starfish.

MECHANISMS BY WHICH THE SPONGE-COVER INTERFERES WITH PREDATORY STARFISH

Of the three possible ways by which a scallop could derive protection from its sponge-cover, interference with adhesion and attachment of the tube-foot would seem most likely. To quantify the effects of sponge on attachment and adhesion of tube-feet, the relative force necessary to overcome the adhesion of tube-feet acting on a scallop shell was determined. A shell was suspended from one end of a beam balance so that the shell rested on the submerged tube-feet of an inverted *Pisaster ochraceus*. Weights were suspended from the other end of the beam until the shell was pulled free. Shells covered with *Myxilla incrustans* and *Mycale adhaerens* and shells without sponge were tested. Ten seconds elapsed between putting the shell on the tube-feet and the addition of the weights.

The mean force necessary to overcome the adhesion of *Pisaster ochraceus* tube-feet was 85 g (s.d., ± 53.5) for shells covered with *Myxilla incrustans*, 56.7 g (s.d., ± 23.4) for shells covered with *M. adhaerens*, and 1700 g (s.d., ± 400) for clean shells. There was no significant difference between sponge-covered shells ($t = 1.6$, d.f. = 10, $P > 0.05$) but there was a significant difference between sponge-covered and clean shells ($t = 12.4$, d.f. = 16, $P < 0.001$); sponge-cover markedly reduces the ability of the tube-feet to adhere. To determine whether a scallop could generate even the small force indicated above to escape from a starfish, ten scallops with and five without sponge were placed on an inverted *Pycnopodia helianthoides*. They were held against the tube feet for 15 sec and then were allowed to attempt to escape. All ten sponge-covered scallops were able to break free while three of the five clean scallops were unable to escape ($P < 0.05$, Fisher Exact Probability Test). To ascertain whether the times arbitrarily used in these experiments (10 and 15 sec, respectively) were realistic, the response time between contact by a *P. helianthoides* with an attached *Chlamys* and the initiation of the escape response was noted. 33 scallops (16 sponge-covered and 17 clean) were allowed to remain undisturbed until all the scallops had secreted byssus threads and so were attached to the aquarium. An arm of a *Pycnopodia helianthoides* was touched to each scallop and the time between contact and the initiation of the response was noted. There was no significant difference between mean response times of clean *Chlamys* (6.9 sec, s.d., ± 3.6) and sponge-covered scallops (4.8 sec, s.d., ± 3.6) to *P. helianthoides* ($t = 1.9$, d.f. = 31, $P > 0.05$). The overall mean response time was 5.7 seconds (s.d., ± 3.7). Response to other species of starfish was

slower and the probability of triggering the response in the laboratory was lower.

It is seen that while the predation patterns of three of the four starfish may be explained by the effect of sponge decreasing tube-foot adhesion, one pattern cannot. In the more natural conditions of comparing sponge-covered and clean motile scallops, *Pisaster ochraceus*, *Pycnopodia helianthoides*, and *Orthasterias koehleri* do not distinguish between these two types of scallops. A sponge seems to confer some

TABLE III

Comparison of survival of *Chlamys* covered by *Myxilla incrustans* and artificial (cellulose) sponges under *Evasterias troschelii* predation: * nonsignificant difference between the categories compared.

	Number of scallops		P
	Alive	Eaten	
Motile <i>Chlamys</i>			
With real sponge	7	3	> 0.05*
With artificial sponge	4	6	
Non-motile <i>Chlamys</i>			
With real sponge	5	5	> 0.05*
With artificial sponge	6	4	
Motile & non-motile <i>Chlamys</i>			
With real sponge	8	12	> 0.05*
With artificial sponge	10	10	
Real & artificial sponge on:			
Motile <i>Chlamys</i>	13	7	< 0.01
Non-motile <i>Chlamys</i>	5	20	

advantage to non-motile scallops subject to *Pisaster ochraceus* predation ($P < 0.05$, Table II) and may be seen to confer some advantage to motile and non-motile scallops against predation by this starfish and *Orthasterias koehleri* (Fig. 1), though the difference is not significant for these samples (Table II). For these starfish, scallop motility seems to be a major factor in their failure successfully to capture scallops, and a change in tube-foot adhesion would be expected to play a part in predation failure.

The pattern of predation for *Evasterias troschelii* diverges greatly from those of the other three species, since it consistently exhibits differential predation on sponge-covered and clean scallops but does not distinguish between motile and non-motile scallops (Fig. 1, Table II). Since the escape response does not appear to play a part in scallop survival against *E. troschelii* predation, some other mechanism of interference with starfish predation besides altering tube-foot adhesion must be present. The following experiment was made to try to distinguish between tactile camouflage and chemical effects on the predator. Survival differences between scallops with a sponge-cover (*Myxilla incrustans*) and those with an artificial cover (cellulose sponge)

were determined. Artificial sponge was attached to clean *Chlamys* by rubber bands, rendering the animals non-motile as described above, and by quick-drying epoxy cement to the motile animals. The procedures described above for survival curves against *Evasterias troschelii* for four classes were then followed. The data are given in Fig. 1 and Table III. There is no significant differential predation on artificially covered or naturally-covered scallops, so any chemical effect of the sponge, either by repelling or simply camouflaging the scallop, is unlikely to be effective: the effect appears to be tactile. Chemical effects may be demonstrable under different conditions but they were not evident in this experiment.

DISCUSSION AND CONCLUSIONS

Sponges have been shown to derive protection from dorid predators by virtue of the motility of their substrata. No evidence was found to indicate the presence of any chemical repellent. The general sensitivity of scallops to any form of physical jostling, results in any dorid attempting to crop the sponge-cover of a scallop eliciting the swimming escape response of the scallop. A similar result was found when the *Suberites*-hermit crab association was examined. Dorids were unable to take sponge if the sponge was occupied by a hermit crab but could easily take unoccupied sponge.

Sponge-cover was found significantly to reduce starfish predation on scallops by altering the surface textural properties of scallop shells. 24 times more force is required to pull a clean shell away from the tube-feet of a starfish than to free a sponge-covered shell. Scallops were shown to be able to generate sufficient 'lift' to overcome the adhesion of tube-feet on sponge but were unable to overcome the adhesion of tube-feet on clean shells. The response time of a scallop to contact by a starfish is in the range of 6 sec, a time sufficiently long enough to allow a starfish to attach some tube-feet but not to allow the starfish to crawl over the scallop. Since the probability of capture is a function of the number of tube-feet in contact with the scallop and the adhesive ability of the tube-feet, and since sponge-cover drastically reduces the adhesive ability of tube-feet by altering the surface texture of the shell, sponge-cover can significantly reduce the probability of capture of the scallop.

Tactile camouflage is also indicated as a mechanism by which a sponge serves to protect scallops from predatory starfish. *Evasterias troschelii* does not distinguish between either real and artificial sponge-covers or motile and non-motile scallops but it does show a distinctly greater ability to take scallops with clean shells relative to scallops with sponge-covered shells. These observations are consistent with the hypothesis of tactile camouflage. No evidence was found to indicate any chemical mechanism but such cannot be entirely dismissed.

Beu (1965) also suggested that sponge conferred "almost complete protection" on the scallop but did not elaborate. Certain rarer predators such as the anemone, *Cribrinopsis* sp., and the giant octopus *Octopus dofleini* Wulker have been observed to eat sponge-covered scallops in nature (pers. observ.). Whether there is

differential predation with regard to sponge-cover by these predators is unknown.

Many well-established mutualisms arise from increased food supply for at least one member of the association. Examples abound in the insect pollination literature (Proctor & Yeo, 1973). Predation may also help to structure mutualism in terrestrial environments. Janzen's (1966) work on the bull-horn acacia and its protective ants is a classic example in which ants derive nourishment and the plants derive protection from herbivores.

In the marine environment, these factors also influence mutualisms. Zooxanthellae in coral tissue are protected in a stable milieu while the coral is able to deposit calcium more efficiently (Goreau & Goreau, 1959). The cleaning-shrimp symbiosis in which food is provided to the shrimp while the fishes are 'deloused' is well known (Feder, 1966). Anemone fishes and their cnidarian substrata are also regarded as a mutualism (Mariscal, 1971); the fish derive protection and food while the anemone may derive an occasional meal from an incautious fish predator as well as other benefits (Mariscal, 1970). Similarly, the association of certain anemones with hermit and calappid crabs seems to provide protection to the crab while allowing the anemone to experience a more 'cosmopolitan' life due to its motile substratum (Dales, 1966). There appear, however, to be few examples in terrestrial or marine environments in which mutualism arises from predation on both components of the association and in which predation has structured the mutualism: the association described above minimizes predation by dorid nudibranchs on the sponges and predation by starfish on the scallops.

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