Race Rocks Ecological Reserve

A Comparative Study Of The Escape Responses Of Limpets

Extended Essay
(Biology)

By Jason M. Berg

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General:

Limpets are small, intertidal marine gastropods which are characterized by their conical shells. Limpets range in habitat from the high levels to the lower limits of the intertidal zone depending upon species. The habitable range of some species of limpets can extend below the intertidal zone as well. There is little interspecific competition between various species of limpets because each species occupies its own niche in the series of vertical zones on the shoreline. Limpets can survive on rocky, exposed shorelines because of their specialized foot which allows them to anchor themselves firmly to solid rock. The ability to anchor is needed to keep from being swept away by the currents, waves, and rough water which are common along such exposed shorelines. Some experimental work has been performed on limpets concerning physical structure, behaviour, habitat, reproduction, and adaptability. In order to study the limpet, it is important to review the previous work which has been done. There are five species which will be examined in this report: Diodora aspera, Acmaea mitra, Collisella digitalis, Notoacmaea scutum, and Notoacmaea pelta (refer to Diagrams 1)a) - 1)e) on the next page). These five species are made up of two families: Fissurellidae and Acmaeidae. Since these are the two families which are to be studied, the review of past research will be restricted to these two families.

Diagrams Of Limpet Species

Diagram 1)a): Plate Limpet (<u>Notoacmaea scutum</u>)

Side view:

Vertical:

Diagram 1)b): Shield Limpet (<u>Notoacmaea pelta</u>)

Side view:

Vertical:

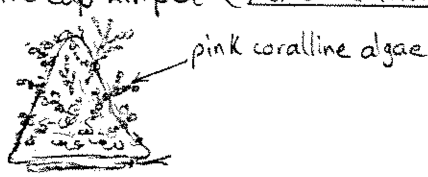
Diagram 1)c): Finger Limpet (<u>Collisella Digitalis</u>)

Side view:

Vertical:

Diagram 1)d): White cap Limpet (<u>Acmaea mitra</u>)

Side view:



Vertical:

Diagram 1)e): Keyhole Limpet (<u>Diodora aspera</u>)

Side view:

Vertical:

An important aspect of the physiology of limpets is the shell formation of the limpet Acmaea. An absence of light inhibits shell growth in some species of limpets, but does not affect growth in other species. The reason why some species continue shell formation regardless of light conditions and why others are inhibited by the absence of light is uncertain. It is speculated that the growth patterns of some species of limpets may depend on a circadian rhythm (Florkin, 1972).

The adaptability of certain limpets to varying environmental conditions is a point of interest. One adaptation of the limpet is its adaptability to varying salinity. Since some limpets are found high in the intertidal zone, they are exposed to rain which reduces the salinity of their environment. The limpet Acmaea scutum is very flexible in its tolerance levels. Acmaea scutum is able to adapt to 50% sea water concentration without any sign of stress, unlike other molluscs. From this, one can discern that certain species of limpets are very well adapted to this form of stress, and that they may encounter it very often in their natural habitat.

Diodora has an interesting aspect to its physical structure. It possesses a type of endocrine gland. This suggests that Diodora is a more complex organism than its nearest relatives - namely Acmaea, which does not possess such a complex structure. A certain tissue near Diodora's cerebral ganglia is present in young limpets. It secretes substances, and appears to diminish after the limpet is involved in sexual activity, suggesting that the gland could influence and control to some extent sexual reproduction in Diodora.

In Acmaea, torsion occurs in the larval stage, and is a ninety degree rotation of the body within its shell. The process only takes a few hours, and subsequent uneven growth of the foot results in further torsion. This adaptation is thought to have developed because of its usefulness in protecting against predators, since it protects sensitive organs like the limpet's head from damage by the extrusion of the foot (Florkin, 1972).

The methods of egg dispersal of Diodora and Acmaea reveal an aspect of their relative evolutionary complexity. Acmaea disperses its eggs in planktonic form. Diodora, on the other hand, coats its eggs with a gelatinous substance which binds the eggs together, and they are deposited in layers. This method of egg dispersal is slightly more advanced than that of Acmaea, affording greater protection against predators with a protective coating, and limiting their dispersal in a favourable environment (since the parent was successful in surviving in that locale).

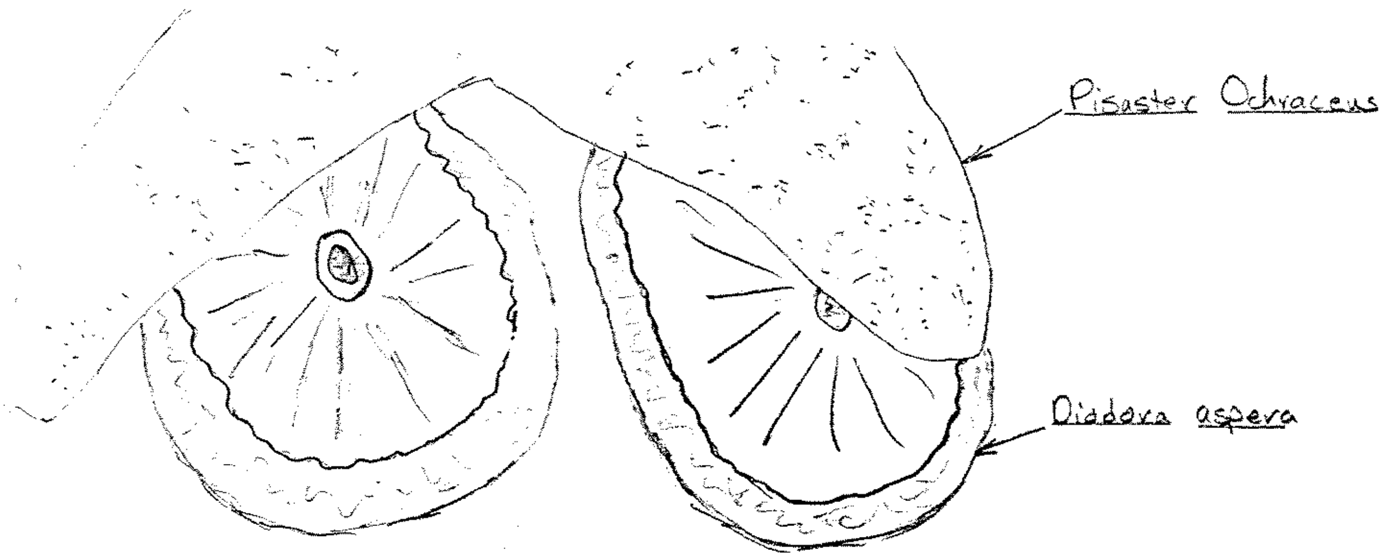
Some important findings have occurred within the area of escape responses of limpets, with which this report is most concerned. The escape responses of limpets are considered to be a result of chemoreception, which applies to many other species of mollusks as well. Bullock (1953) found that limpets gave an escape response only to predatory species, and that this response was allicited by a specific chemical indicator given off or exuded by the predator. An escape response could be produced as well by placing a crushed sample of the same species being tested in the same area. This escape response was classified as a species-specific response. Conversely, when non-predatory species were placed with the mollusks, no escape response occurred. Even when another species was crushed nearby, no response was allicited. Thus, two types of escape response were found: a predator-specific and a species-specific response. Chemoreception, which is an essential adaptation for detection of predators, is also equally important in determining the location of food sources.

Introduction:

The escape responses of marine invertebrates in general has been studied extensively by numerous biologists. Swimming scallops, abalone, various shellfish and snails, sea urchins, anemones, and even species of starfish have been experimentally tested for their response to specific predatory starfish. Various types of responses have been observed. The snail *Nassarius*, for example, somersaults away from certain predators. Swimming scallops swim upward and away by clapping their shells together violently, and abalone move rapidly away, twisting and lifting their shell violently. Much of the work in this field has been done by Bullock, Clark, Feder, Field, Kohn and Waters, Mackie, and Montgomery in a period from 1953 to 1977. In 1970, Mackie analyzed the chemicals involved in these escape reactions and found that steroid glycosides were the chemicals exuded by predatory starfish which ellicit escape responses in their prey. Mackie found that these chemicals were surface active agents, that irritated epidermal parts of prey. In 1972, Feder found that steroid glycosides were present in all species of starfish, even non-predatory starfish, but the chemicals were more concentrated in predatory species. Feder raised the question that perhaps starfish had originally evolved such chemical secretions as an effective prey - catching device. Since most gastropods loosen their hold on the substrate initially in response to the starfish, this may have allowed a starfish to pluck the prey from its foothold more easily. Further escape responses of organisms may have been evolved by prey organisms to counteract the predator's advantage. Returning to the subject of limpets, work regarding their escape responses began many years ago.

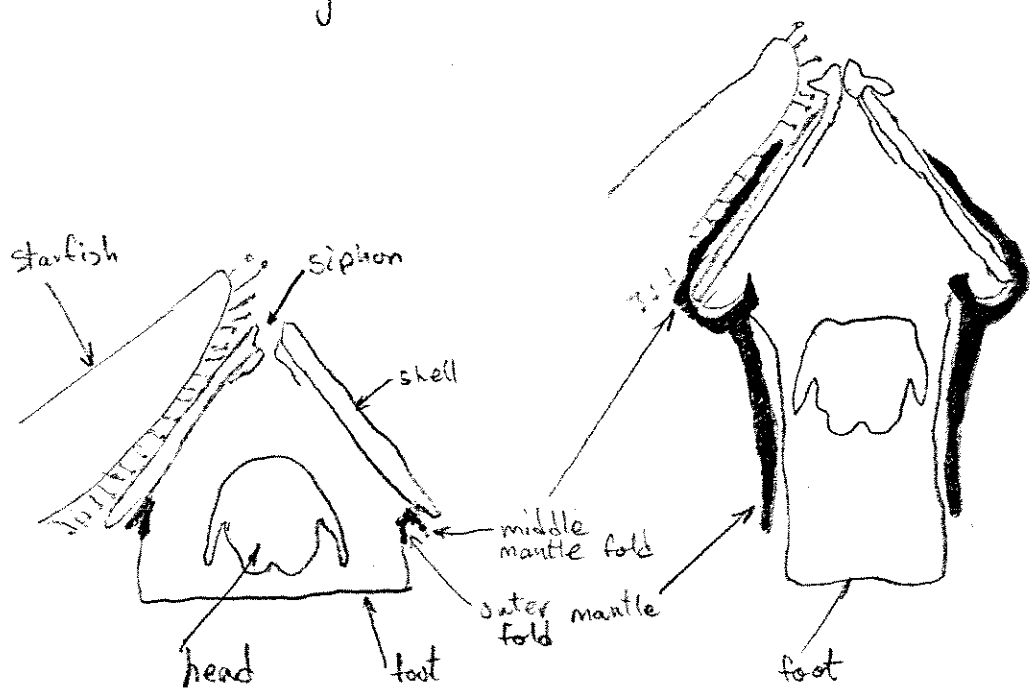
The first recorded observations of limpet escape responses was when E.C. Haderlie (1947) found that "running behaviour" of limpets was ellicited as a result of contact with starfish. T.H. Bullock (1953) concluded that "...escape behaviour of marine invertebrates must represent a phenomenon of considerable ecological importance...these were specialized and apparently effective responses each species had evolved to cope with it's predators." Feder (1972) conducted experiments with _Diodora_ and _Acmaea_, and found that their escape responses differed. Feder found that _Diodora_ remained stationary when contacted by a starfish, raised it shell ("mushrooming" by Bullock) and extended its mantle outside of its shell (refer to Diagrams 2)a) and 2)b) on the next page). This mantle extension removed the starfishes feet from its shell, and prevented it from grasping hold of the limpet. _Acmaea_, on the other hand, escaped by running away (in accordance with Haderlie's results). Some limpet species of _Acmaea_ sensed the presence of the starfish before being touched. _Acmaea_ raised its shell and fled rapidly, its flight lasting for several minutes until it was clear of the starfish. Limpets which exhibited escape responses were very successful in avoiding capture by starfish. Limpets which did not have escape responses or defense mechanisms were readily preyed upon by starfish, an example being the ribbed limpet of the _Acmaea_ genera (Feder 1972). Observations of _Acmaea scabra_ and _Acmaea digitalis_, which are high intertidal limpets, have shown that they do not respond to the presence of _Pisaster ochraceus_ or to contact. As a result, they are preyed upon, and their habitat is limited to the high levels

Diagram 2)a): The Mantle Response of Diodora



* from Feder (1972)

Diagram 2)b): Mantle Response – Side View



* From Feder (1972)

of the intertidal zone, where they are out of reach of starfish.

The research conducted in the past on limpet escape responses form a basis upon which the experiment in this report can proceed. The escape responses of five species of limpets of _Diodora_ and _Acmaea_ genera will be compared and analyzed in relation to the predatory Sunflower Star and Painted Star (_Pycnopodia helianthoides_ and _Orthasterias koehleri_). This will be done in order to probe deeper into some basic questions. Do the escape responses of limpets vary from one species to another according to their intertidal distribution and exposure to predators, have they developed various types of responses to cope with their predators, is the habitat of different species of limpets restricted by their differing escape responses to predators, and does a predator in some part determines the range of habitat of certain limpet species?

Objectives:

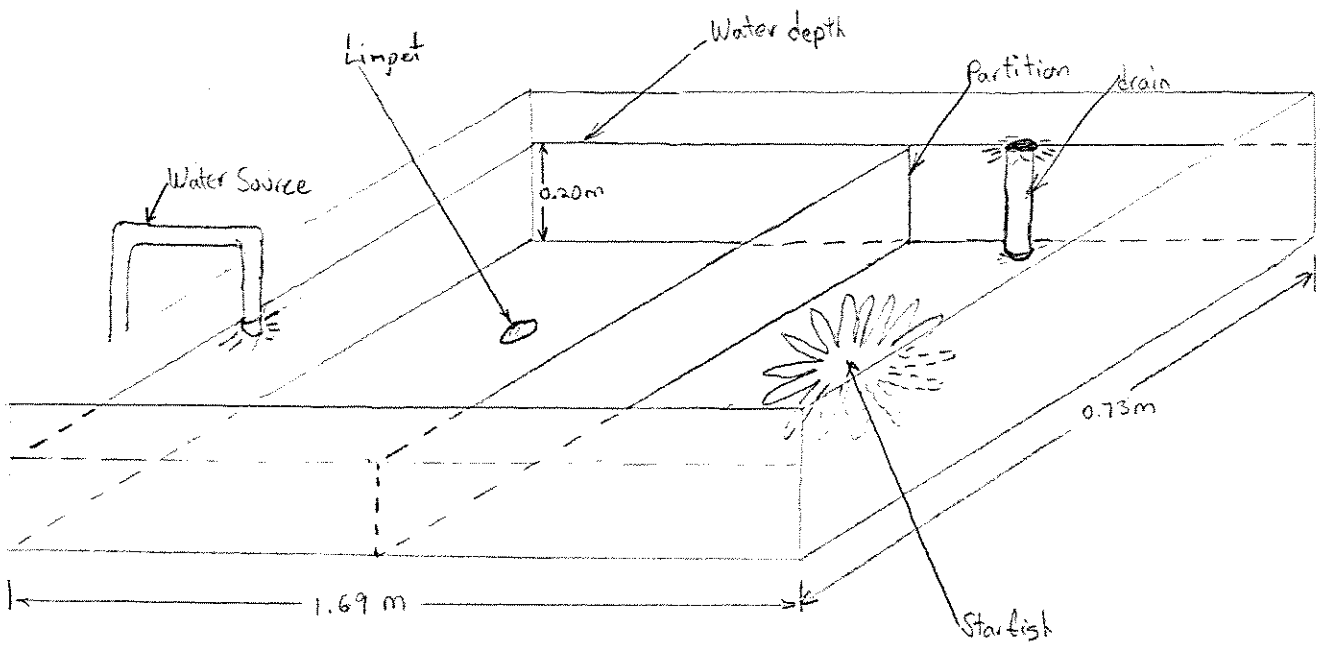
To examine the ideas that the escape responses of limpets vary according to their species, intertidal distribution, and exposure to predators, that limpets have developed various types of responses to cope with predators, and that the habitat of different species of limpets is restricted to some extent by their escape responses to a predator, thus demonstrating that a predator in some ways determines the habitat of some limpet species. To compare and contrast the escape responses of five species of limpet to two species of predatory starfish, and to gain a clearer understanding of the predator - prey relationships concerning limpets and starfish.

Procedure:

Ten specimens of each limpet species (Diodora aspera, Acmaea mitra, Acmaea scutum, Acmaea/Collisella digitalis, and Acmaea pelta) were collected from the marine ecological reserve of Race Rocks on the southern tip of Vancouver Island. The specimens were collected and identified using Light's Manual (Smith, 1975). The limpet populations tested were randomnly chosen from their environment so that they might be a representation of the total population of limpets. This factor also applies to the starfish species. SCUBA was used to collect sublittoral specimens, and others were collected at low tide. The starfish Pycnopodia and Orthasterias were taken from the same location. These animals were maintained in salt water aquariums with sea water supplied from the ocean in the Marine Biology Laboratory at Lester B. Pearson College of the Pacific, Victoria, BC. The temperatures of the water in the aquariums were monitored and varied from 10 degrees to 12 degrees centigrade. The aquariums used were 1.83M long, 0.73M wide, and 0.20M deep (see diagram #3 on next page for experimental apparatus).

The experiment involved introducing a test limpet into the test aquarium and allowing it to adjust to its environment. The starfish had been previously introduced into the test aquarium. The two animals were prevented from contact by a partition. The state of the limpet was determined by its initial clamping down reaction as compared to a slow, relaxed browsing movement in the aquarium. Once the limpet was fairly adjusted and relaxed, the partition was removed and the two subjects were allowed to contact each other. The effect of their contact was observed and noted. This trial was repeated ten times for each limpet species using a different limpet each time, and was performed using both starfish. The maximum velocities of the limpets during their response, and the maximum distance away from the original contact point before the limpet resumed its previous behaviour were measured and recorded for each trial. Other observations pertaining to the nature of the response were noted during the experiment as well. Also, the range of depth at which the specimens were found in relation to zero tide level were noted. The instruments used to determine this were scuba depth gauge and tape measure above the water level, as well as a tide meter to measure tidal height.

Diagram 3): Apparatus Used / Test Aquarium



Data/Observations:

Plate Limpet And Pycnopodia: Table 1)a)

#	Vel.(cm/min)	Dist.(cm)	Initial Response	Comments
1	13.1	94.0	Upon contact, escape response is to twist shell and move away rapidly.	*The response if overtaken by starfish is to stop movement and clamp down firmly.
2	12.0	106.5		
3	14.5	90.2		
4	15.5	101.0		
5	13.0	36.5*		
6	16.4	99.0		
7	15.9	110.5		
8	16.8	112.5		
9	14.0	25.0*		
10	14.6	69.5		

Shield Limpet And Pycnopodia: Table 1)b)

#	Vel.(cm/min)	Dist.(cm)	Initial Response	Comments
1	12.2	79.2	To twist around and move away.	*Clamps down if overtaken.
2	16.5	85.4		
3	15.3	27.5*		
4	15.8	92.1		
5	13.2	83.6		
6	17.9	75.5		
7	14.8	89.3		
8	13.9	12.4*		
9	14.6	22.1*		
10	13.2	85.1		

Finger Limpet And Pycnopodia: Table 1)c)

#	Vel.(cm/min)	Dist.(cm)	Initial Response
1	0.0	0.0	No escape response. Clamped down firmly when contacted.
2	0.0	0.0	
3	0.0	0.0	
4	0.0	0.0	
5	0.0	0.0	
6	0.0	0.0	
7	0.0	0.0	
8	0.0	0.0	
9	0.0	0.0	
10	0.0	0.0	

Whitecap Limpet And Pycnopodia: Table 1)d)

#	Vel.(cm/min)	Dist.(cm)	Initial Response
1	0.0	0.0	In all cases, clamped down tightly when starfish was a few centimetres away.
2	0.0	0.0	
3	0.0	0.0	
4	0.0	0.0	
5	0.0	0.0	
6	0.0	0.0	
7	0.0	0.0	
8	0.0	0.0	
9	0.0	0.0	
10	0.0	0.0	

Keyhole Limpet And Pycnopodia: Table 1)e)

#	Vel.(cm/min)	Dist.(cm)	Initial Response & Comments
1	5.6	35.6	When contacted, moved away and extended mantle outside shell.
2	3.5	42.9	
3	9.9	85.6	
4	6.3	54.1	
5	8.8	38.7	
6	10.2	26.5	*Clamps down when overtaken.
7	12.3	93.2	
8	4.2	12.0*	
9	7.4	67.4	
10	3.8	8.4*	

Data/Observations:

Plate Limpet And Painted Star: Table 2)a)

#	Vel.(cm/min)	Dist.(cm)	Initial Response
1	9.2	15.6	To move away at a speed quick enough to outrun the starfish.
2	8.7	17.9	
3	10.4	16.3	
4	11.3	21.5	
5	7.7	20.3	
6	8.5	19.7	
7	9.0	22.8	
8	9.7	18.1	
9	10.8	16.5	
10	10.3	23.2	

Shield Limpet And Painted Star: Table 2)b)

#	Vel.(cm/min)	Dist.(cm)	Initial Response
1	9.2	22.3	Moved away to get clear of the starfish.
2	6.8	16.3	
3	7.4	18.9	
4	8.5	16.8	
5	11.3	21.2	
6	12.6	28.3	
7	9.7	21.8	
8	11.1	24.6	
9	10.4	14.8	
10	9.3	17.1	

Finger Limpet And Painted Star: Table 2)c)

#	Vel.(cm/min)	Dist.(cm)	Initial Response
1	0.0	0.0	No escape response. Clamps down when contacted.
2	0.0	0.0	
3	0.0	0.0	
4	0.0	0.0	
5	0.0	0.0	
6	0.0	0.0	
7	0.0	0.0	
8	0.0	0.0	
9	0.0	0.0	
10	0.0	0.0	

Whitecap Limpet And Painted Star: Table 2)d)

#	Vel.(cm/min)	Dist.(cm)	Initial Response
1	0.0	0.0	Clamps down shell on contact with starfish.
2	0.0	0.0	
3	0.0	0.0	
4	0.0	0.0	
5	0.0	0.0	
6	0.0	0.0	
7	0.0	0.0	
8	0.0	0.0	
9	0.0	0.0	
10	0.0	0.0	

Keyhole Limpet And Painted Star: Table 2)e)

#	Vel.(cm/min)	Dist.(cm)	Initial Response
1	2.6	10.8	When contacted, limpet extended mantle and moved away.
2	3.9	16.3	
3	2.9	12.9	
4	4.5	18.1	
5	4.3	26.6	
6	4.9	34.0	
7	3.3	17.3	
8	2.4	14.2	
9	3.6	12.7	
10	4.5	19.2	

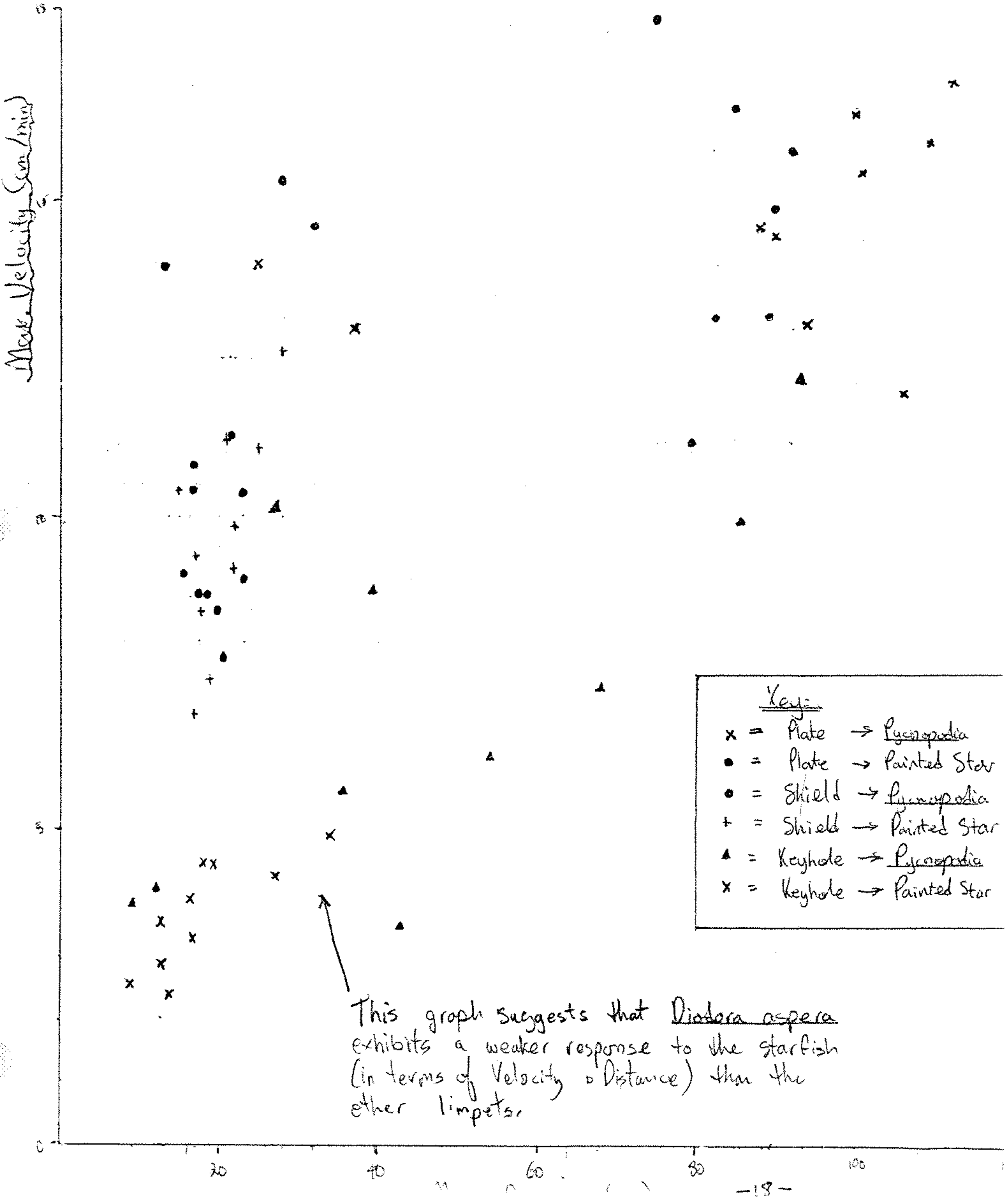
Data/Observations: Table #3

Depths At Which Limpets And Starfish Were Taken/Observed:

Species	Depth Range-->"0" Tide Level
Acmaea scutum	0.0M to +1.5M
Acmaea pelta	0.0M to +1.5M
Acmaea digitalis	+1.5M to +2.3M
Acmaea mitra	-5.0M to +0.5M
Diodora aspera	-6.0M to +0.1M
Pycnopodia	-5.0M to -1.0M
Orthasterias	-4.0M to -1.0M

Graphic Analysis: Velocity (cm/min) Versus Distance (cm) While Comparing Responsive Limpets With *Pycnopodia* And *Orthasterias*

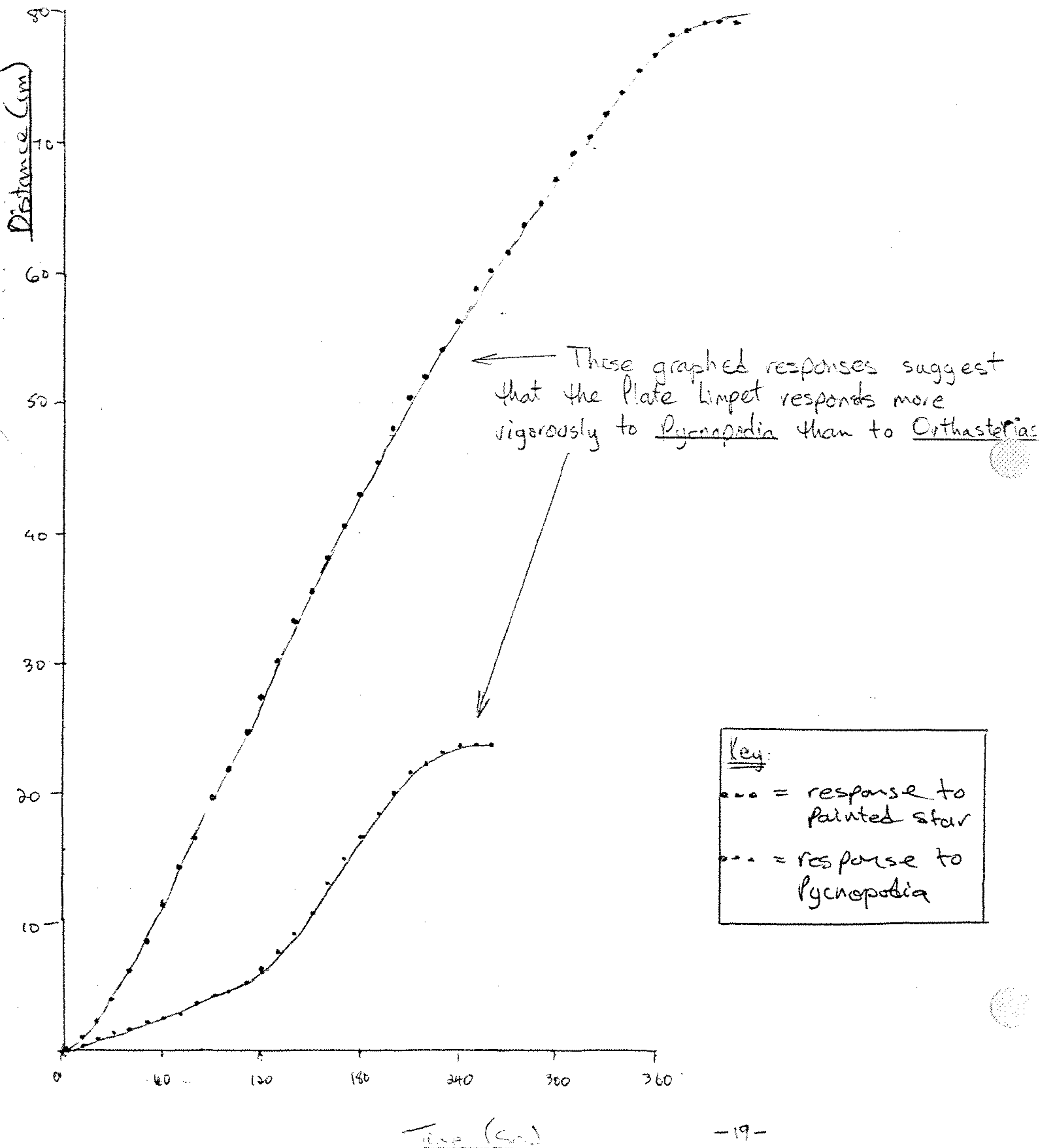
Graph #1:



Graphic - Analysis:

Distance (cm) Versus Time (s) While Plate Limpet Escapes From Pycnopodia (Taken From Exp. Results) And Plate Limpet Escapes From Painted Star

Graph #2



Diagrams Of Directions Of Limpet Responses
From Various Approaches Of Predator

Diagram 4)a): Approach From Behind -

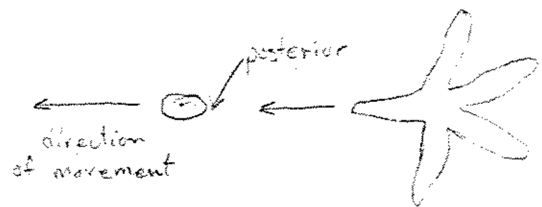


Diagram 4)b): Approach From Front:

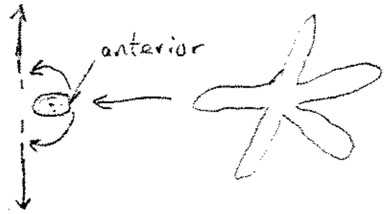
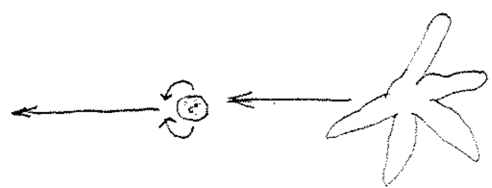


Diagram 4)c): Approach From Side:



Statistical Analysis*:

Calculation Of Mean Velocity Response Of Limpets And Standard Deviation: Table 4)a)

SPECIES INVOLVED	#	MEAN VELOCITY	S.D.
Pycnopodia-->Plate	10	14.53	1.58
Pycnopodia-->Shield	10	14.74	1.71
Pycnopodia-->Finger	10	0.00	0.00
Pycnopodia-->Whitecap	10	0.00	0.00
Pycnopodia-->Keyhole	10	7.20	3.03
Orthasterias-->Plate	10	9.46	1.17
Orthasterias-->Shield	10	9.63	1.79
Orthasterias-->Finger	10	0.00	0.00
Orthasterias-->Whitecap	10	0.00	0.00
Orthasterias-->Keyhole	10	3.63	0.88

Calculation Of Mean Distance Response Of Limpets And Standard Deviation: Table 4)b)

SPECIES INVOLVED	#	MEAN DIST.	S.D.
Pycnopodia-->Plate	10	86.47	20.51
Pycnopodia-->Shield	10	65.22	29.90
Pycnopodia-->Finger	10	0.00	0.00
Pycnopodia-->Whitecap	10	0.00	0.00
Pycnopodia-->Keyhole	10	46.44	29.75
Orthasterias-->Plate	10	19.19	2.74
Orthasterias-->Shield	10	20.21	4.22
Orthasterias-->Finger	10	0.00	0.00
Orthasterias-->Whitecap	10	0.00	0.00
Orthasterias-->Keyhole	10	19.21	7.11

* All statistical calculations have been performed using Stats Plus Human Systems Dynamics Computer Program (1982).

Statistical Analysis:

SECTION A Table 5)a)

ANOVA OF VELOCITY RESPONSE OF FIVE LIMPETS TO TWO STARFISH*

SOURCE	SS	DF	MS	F
STARFISH	189.06	1	189.06	94.73
LIMPETS	2935.66	4	733.92	367.73
STARFISH LIMPETS	134.52	4	33.63	16.85
ERROR	179.62	90	2.00	
TOTAL	3438.87	99		

H'_0: There is no significant difference in the velocity response of the limpets to the two starfish.
H''_0: There is no significant difference in velocity response to the two starfish between the five limpets.
H'''_0: There is no significant difference in velocity response due to interaction between starfish & limpet species.

$F'_{0.05\{1,90\}} = 3.96 \rightarrow 3.96 < 94.73$

$F''_{0.05\{4,90\}} = 2.49 \rightarrow 2.49 < 367.73$

$F'''_{0.05\{4,90\}} = 2.49 \rightarrow 2.49 < 16.85$

Conclusion: Reject all three null hypotheses with 95% confidence.

* ANOVA is the abbreviated form for analysis of variance.

SECTION B Table 5)b)

ANOVA OF DISTANCE RESPONSE OF FIVE LIMPETS TO TWO STARFISH

SOURCE	SS	DF	MS	F
STARFISH	20030.74	1	20030.74	73.45
LIMPET	48148.16	4	12037.04	44.14
STARFISH LIMPET	17178.24	4	4294.56	15.75
ERROR	24544.27	90	273.71	
TOTAL	109901.42	99		

H'_0: There is no significant difference in distance response of the limpets to the two starfish.
H''_0: There is no significant difference in distance response to the two starfish between the five limpets.
H'''_0: There is no significant difference in distance response due to interaction between starfish and limpet species.

$F'_{0.05\{1,90\}}=3.96 \rightarrow 3.96 < 73.45$

$F''_{0.05\{4,90\}}=2.49 \rightarrow 2.49 < 44.14$

$F'''_{0.05\{4,90\}}=2.49 \rightarrow 2.49 < 15.75$

Conclusion: Reject all three null hypotheses with 95% certainty.

SECTION C <u>Table 5)c)</u>

ANOVA OF VELOCITY RESPONSE IN RESPONSIVE LIMPETS TO STARFISH

SOURCE	SS	DF	MS	F
STARFISH	315.10	1	315.10	94.73
LIMPET	592.12	2	296.06	89.00
STARFISH LIMPET	8.48	2	4.24	1.27
ERROR	179.62	54	3.33	
TOTAL	1095.32	59		

H'_0: There is no significant difference in velocity response of responsive limpets to the two starfish.
H''_0: There is no significant difference in velocity response of responsive limpets to the starfish between the limpets.
H'''_0: There is no significant difference in velocity response of responsive limpets due to interaction between starfish and limpet species.

$F'_{0.05\{1,54\}}=4.03 \rightarrow 4.03 < 94.73$

$F''_{0.05\{2,54\}}=3.18 \rightarrow 3.18 < 89.00$

$F'''_{0.05\{2,54\}}=3.18 \rightarrow 3.18 > 1.27$ ($P\ H'''_0 = 0.2875$)

Conclusion: Reject H'_0 and H''_0 with 95% certainty, but accept

H'''_0 has 28.75% probability.

SECTION C <u>Table 5)c)</u>

ANOVA OF VELOCITY RESPONSE IN RESPONSIVE LIMPETS TO STARFISH

SOURCE	SS	DF	MS	F
STARFISH	315.10	1	315.10	94.73
LIMPET	592.12	2	296.06	89.00
STARFISH LIMPET	8.48	2	4.24	1.27
ERROR	179.62	54	3.33	
TOTAL	1095.32	59		

H'_0: There is no significant difference in velocity response of responsive limpets to the two starfish.
H''_0: There is no significant difference in velocity response of responsive limpets to the starfish between the limpets.
H'''_0: There is no significant difference in velocity response of responsive limpets due to interaction between starfish and limpet species.

$F'_{0.05\{1,54\}}=4.03 \rightarrow 4.03 < 94.73$

$F''_{0.05\{2,54\}}=3.18 \rightarrow 3.18 < 89.00$

$F'''_{0.05\{2,54\}}=3.18 \rightarrow 3.18 > 1.27$ (P H'''_0 = 0.2875)

Conclusion: Reject H'_0 and H''_0 with 95% certainty, but accept H'''_0 has 28.75% probability.

SECTION D <u>Table 5)d)</u>

ANOVA OF DISTANCE RESPONSE OF RESPONSIVE LIMPETS TO STARFISH

SOURCE	SS	DF	MS	F
STARFISH	33384.57	1	33384.57	73.45
LIMPET	4207.96	2	2103.99	4.63
STARFISH LIMPET	3824.42	2	1912.21	4.21
ERROR	24544.27	54	454.52	
TOTAL	65961.22	59		

H'_0: There is no significant difference in distance response of responsive limpets to the two starfish.
H''_0: There is no significant difference in distance response to the two starfish between the responsive limpets.
H'''_0: There is no significant difference in distance response of responsive limpets due to interaction between starfish and limpet species.

$F'_{0.05\{1,54\}}=4.03 \rightarrow 4.03 < 73.45$

$F''_{0.05\{2,54\}}=3.18 \rightarrow 3.18 < 4.63$

$F'''_{0.05\{2,54\}}=3.18 \rightarrow 3.18 < 4.21$

Conclusion: Reject all three null hypotheses with 95% certainty.

SECTION E

ANOVA OF VELOCITY/DISTANCE RESPONSE IN NONRESPONSIVE LIMPETS

TOTAL ERROR = 0

H'_0: There is no significant difference in velocity/distance response in nonresponsive limpets to the two starfish.
H''_0: There is no significant difference in velocity/distance response to the starfish between the limpets.
H'''_0: There is no significant difference in velocity/distance response in nonresponsive limpets due to interaction between starfish and limpet species.

Conclusion: Accept all three null hypotheses with 100% certainty.

Discussion:

In the analysis of mean response of limpets in terms of velocity and distance, some important observations can be made. Firstly, that plate limpets and shield limpets seem to exhibit the greatest responses with averages of 14.58cm/min, 86.47cm; and 14.74cm/min,66.22cm respectively in their response to P. helianthoides. The Keyhole limpet appears to exhibit a lesser response which is most evident in terms of its velocity response to the starfish. No evident escape response was ellicited from either the Whitecap limpet or the Finger limpet to any of the sea stars.

The degree of the responses of the Plate, Shield, and Keyhole limpets was graphically shown and suggested the above as well (see Graphs #1 and #2 in Graphic Analysis section). Also, the graphs seemed to indicate that the limpets in general tended to respond most vigorously to P. helianthoides as compared with O. koehleri. Diagrams 4)a), 4)b), and 4)c) show that the direction of limpet escape response when approached by the starfish was always either running ahead or off to one side.

The analysis of variance statistics are used to confirm with a quantitative degree of certainty whether or not the above observations and suggestions are statistically acceptable. In sections A & B of the analysis, it was found with 95% confidence that there was a significant difference in velocity and distance response to the starfish between the five limpets, in relation to the two starfish, and due to interaction between the limpets and starfish. Sections C & D determined with 95% certainty that there was between Keyhole, Shield, and Plate limpets a significant difference in their responses relative to each other, as well as to the two species of starfish. There is 95% certainty that interaction occurred between limpet and starfish species in their distance response, but this was not the case in the velocity response, with only 71.25% certainty of interaction.

Sections E & F determined with 100% certainty that there was no difference in response between Whitecap and Finger limpet species regardless of the starfish that they contacted or limpet species. There was no interaction between limpets and starfish which caused a difference in response. These limpets - A. mitra and A. digitalis - responded identically in every case by clamping down.

How are these confirmed observations relevant to this report? They allow the basic questions put forward in this report to be discussed and analyzed. One may look at each limpet species individually.

First, looking at the Finger limpet (A. digitalis), it is found to have no apparent escape response. As a result, it is vulnerable to predatory starfish (Feder, 1972). It is found only in the high levels of the intertidal zone (refer to table #3), thus having little exposure to P. helianthoides and *O. koehleri* as predators. The fact that it is rarely exposed to such predators shows perhaps that there is not enough selective pressure on the limpet to evolve escape responses. On the other hand, since it is readily preyed upon, the Finger limpet's intertidal distribution is limited to the high levels only, where it is not exposed to these starfish.

Secondly, in the cases of *A. scutum* and *A. pelta*, both of these species exhibit escape responses of a very similar nature - namely a flight response to get away. They are found in the intermediate levels of the intertidal zone, and would be more exposed to predators like *P. helianthoides* and *O. koehleri*. They are able to cope with this predator quite successfully with their escape response. However, their success may be lessened in deeper levels by bigger and faster predators, or other undetermined factors. Why they are not found in the high levels of the intertidal zone cannot be determined from this study.

Thirdly, the Keyhole limpet (*D. aspera*) exhibits a variation of the escape responses of *A. scutum* and *A. pelta* which involves the extension of the mantle to prevent predators from getting a grip on their shell while moving away at the same time (refer to Diagrams #2)a) and #2)b)). *D. aspera* is found in the lowest levels of the intertidal zone as well as sublittorally (Table #3). It is perhaps even more successful at avoiding predation than all the limpets discussed above, since it can cope successfully with the more dangerous predators in deeper waters.

Lastly, the Whitecap limpet (A. mitra) is an interesting exception. It exhibits no detectable escape response except clamping down. Therefore, since this response is similar to A. digitalis, it might be expected that this limpet is readily preyed upon by starfish, and that it's intertidal distribution may be affected by predation. This is not the case. A. mitra is found in the lower levels of the intertidal zone at a wide range of depths (Table #3). How does it avoid predation without an escape response? Perhaps the pink coralline algae often found growing on its shell acts as camouflage, and allows the limpet to avoid being identified as prey. Or, perhaps this limpet is not a preferrable prey item because of some substances contained in its body. If this is so, this limpet may have some very important implications requiring further study.

Suggestions For Further Study:

In the area of limpet escape responses, there are several possible avenues for pursuing the topic further. One could perform large scale population counts over a large area to find with greater accuracy the distribution of limpet species in terms of their escape responses. Also, some study might be conducted to determine if there were different existing escape responses in other parts of the world. From that, one would be able to see if independent evolution had allowed limpets to avoid predation in different ways.

For limpets in general, much work could be done in trying to isolate and determine other specific biotic and abiotic factors which could determine limpet intertidal distribution and zonation. For example, does Gausse's principle of competitive exclusion apply to limpet zonation and niche? What are the relative importances of food resources, land predators, exposure on land, and other factors in determining the intertidal distribution of limpet species?

Further research could be performed to determine why the limpet A. mitra is not readily preyed upon. If it is because it is not a preferred prey item because of certain substances it possesses, then perhaps these substances could be chemically determined. This could have great commercial value for harvested animals like oysters or mussels, for which starfish predation is a great problem. If commercially harvested species could be treated in some way with this chemical(s) or be made to produce it themselves, it could be an effective biological control of starfish predation. However, the reason why the Whitecap limpet is not preyed upon must be determined for certain before anything can be done.

By studying the escape responses of marine invertebrates in general, one can gain further insight into how to control predation upon commercial species.

Sources Of Error:

There were several sources of error in this comparative study of limpet escape responses. Perhaps the most technical in nature is the fact that in the experiment, a few limpets were overtaken by P. helianthoides, forcing them to stop moving and clamp down in defense. Thus, a misrepresentation of distance response occurred, because the normal distance travelled before the limpet stopped or slowed down might not be the same. Therefore, in any further experiments of this nature, these types of values recieved should be omitted from calculations.

The second main source of error is that the experiment was performed in a laboratory under artificial light and in an artificial environment (aquarium). Could these factors and the fact that the experiment was not performed in a natural environment affect the behaviour of both the limpets and starfish, thus ultimately affecting the results of the experiment? In order to ensure that this is not the case, the experiment would have to be performed in the animals natural environment, by using SCUBA and noting observations on a slate. This method would be superior perhaps to the laboratory experiment performed.

Lastly, there is a certain degree of uncertainty due to the fact that the total populations of limpet and starfish species are being represented by random samples. Are these samples truly representative of the species? Are they truly random? One cannot proceed to test the entire population of limpets, because there is simply too much work involved. However, the error implied by this can be reduced by experimenting with larger samples within reasonable limits.

Conclusion:

In this investigation, some basic questions that were posed have now been explored to an extent. To some degree limpet escape responses to certain predators may vary because of their intertidal distribution and exposure to predators. This was demonstrated in the variety of escape responses that occurred: the mantle response of D. aspera, the running responses of A. scutum and A. pelta (refer to Tables 1)a), 1)b), 1)e), 2)a), 2)b), and 2)e)). Species which had differing escape responses tended to be distributed differently in relation to each other (Table #3). However, this does not state that there are no other factors involved in limpet distribution, for certainly there are. It is true that limpets have developed different escape responses to cope with their predators. Some limpets exhibit no escape response. This could make the limpet vulnerable to starfish predation, as in the case of A. digitalis, or perhaps the limpet has some other means of avoiding predation, which may occur in the case of A. mitra. Distribution of A. digitalis is limited by predatory starfish (Feder, 1963), and so it can only thrive in the high levels of the intertidal zone out of reach of starfish. A. mitra, on the other hand may avoid predation by some other means than escape response. Determining exactly how it avoids predation could be of commercial importance if it is a chemical device which it possesses, and this is an excellent subject for further study in this field. In performing a comparative study of this nature, one can gain a greater insight into predator - prey relationships and the limiting effect a predator may have upon its prey, as well as the effectiveness of certain species of limpets at avoiding predation by starfish. In conclusion, one must emphasize that this is only a preliminary study and that much further, detailed work must be done before one can draw definite conclusions to the questions posed in this report. However, some definite insights have been gained in this area of study in doing this report.

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