

MECHANICAL STIMULATION OF ELEVEN SPECIES OF  
OPISTHOBRANCHS FROM THE GULF OF CALIFORNIA

by

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# TABLE OF CONTENTS

	Page
INTRODUCTION . . . . .	1
MATERIALS AND METHODS . . . . .	6
Field Stimulation . . . . .	6
Laboratory Observations . . . . .	7
Laboratory Stimulation . . . . .	9
Potential Predators . . . . .	12
RESULTS . . . . .	14
Areas of Sensitivity . . . . .	14
Responses to a Single Stimulus . . . . .	15
Weak Stimulus . . . . .	16
Strong Stimulus . . . . .	20
Responses to Change in Intensity of a Single Stimulus . . . . .	25
Duration of Response . . . . .	26
Responses to Multiple Strong Stimuli . . . . .	30
Responses to Potential Predators . . . . .	33
DISCUSSION . . . . .	37
SUMMARY . . . . .	43
LITERATURE CITED . . . . .	46

# LIST OF TABLES

Table		Page
1.	Habitat, Sample Size, and Collection Dates of Eleven Species of Opisthobranchs from Puerto Peñasco, Sonora, Mexico . . . . .	8
2.	Responses to a Single Weak Stimulus . . . . .	17-18
3.	Responses to a Single Hard Stimulus . . . . .	21-22
4.	Intensities of a Single Stimulus of 20 msec Duration Necessary for Just Eliciting the Maximum Response of Opisthobranch Species. . . .	27
5.	Frequencies of Stimuli Triggering Shock Reactions and the Duration of These Responses . . . . .	32
6.	Defensive Postures Elicited by Direct Contact with Potential Predators . . . . .	36

## LIST OF ILLUSTRATIONS

Figure	Page
1. Forward motion of the prodger as a function of the voltage used to drive the prodger . . .	11
2. Duration of the response with increased intensity of a single stimulus in eleven species of opisthobranchs . . . . .	29

## ABSTRACT

Responses to mechanical stimuli of various intensities have been recorded in eleven species of opisthobranchs that exhibit a variety of habitat preferences and patterns of coloration. Areas of greatest sensitivity in all species are the head region, extremities, and parts of the mantle or parapodia that cover the gill. Although many responses follow taxonomic lines and a few may be correlated with color patterns, some convergence has occurred in the reactive systems of opisthobranchs from similar intertidal habitats. Species found in the same habitat respond maximally to comparable stimulus intensities and frequencies and for a similar length of time. This is most apparent in species found in an exposed habitat during high and low tides. The responses elicited in opisthobranchs by direct contact with potential predators appear to be defensive in nature and are identical to those evoked by mechanical stimulation with a glass prod.

## INTRODUCTION

Opisthobranchs are gastropod molluscs which differ from other snails in showing some degree of detorsion and a reduction or loss of the shell. With few exceptions they are referred to as marine slugs and exhibit a wide variety of color and form. Two groups of opisthobranchs occur on the rocky shores of the Gulf of California at Puerto Peñasco, Sonora, Mexico. The first consists of species found in exposed habitats in tide pools during low tides and crawling about on rocks and algae during high tides. These organisms are usually small and blend cryptically with their environment, although a few brightly colored forms are also found. Other species occur under rocks or hang from ledges during low tides. This second group may be subdivided further into those which remain on the rocks during high tides, and those which leave the rocks to feed. The former are usually cryptically colored and blend with the rock or a particular species of algae or sponge that grows on the rock, and the latter are generally distinguished by their bright coloration and markings. Representatives from widely diverse taxonomic groups are found in both habitats.

Adult opisthobranchs probably contribute to the energy flow of an ecosystem largely through the production of vast



numbers of eggs and larval stages, and through short life cycles which lead to normal death and eventual consumption by scavengers and decomposition by micro-organisms. Very few adults are preyed upon by other organisms. Wounded specimens are rare (Winkler, 1956; Paine, 1965; Crozier, 1916; and personal observation), and opisthobranchs are only occasionally reported from the stomachs of associated intertidal fish (Garstang, 1889; Thompson, 1960a). Some predation on the californian sea hare, Aplysia californica, by the sea anemone, Anthopleura xanthogrammica, has been reported by Winkler and Tilton (1962), and Thompson (1960) has reported that anemones in aquaria will ingest opisthobranchs presented to them but with a low degree of predictability. McMillan (1941) found that several species of the opisthobranch Facelina would be engulfed by the tentacles of associated anemones, but after a few seconds were released and they moved away unharmed. Generally predation by anemones is believed to play only a small role in the destruction of adult opisthobranchs. Anemones probably play a larger role in the consumption of larval stages along with other plankton and filter-feeders. Some predation of adult opisthobranchs is accomplished by the cephalaspidian Navanax inermis (Paine, 1963, 1965). However, at Puerto Peñasco Navanax are generally small in size and few in number, so probably only a few opisthobranchs fall prey to them.

Some line of defense must, therefore, be operating in adult opisthobranchs. In some the defense is obvious. Many eolids are reported to retain in the tips of their ceratae unexploded nematocysts, obtained from ingested coelenterates, which are discharged upon physical contact (MacGinitie and MacGinitie, 1949; and Ricketts and Calvin, 1964). A strong acid secretion from at least three species of opisthobranchs found off the British Isles has been reported by Thompson and Slinn (1959) and Thompson (1960a,b). Paine (1963) reported a similar acid secretion by three species found on the west coast of North America. A cholinergic agent which may play some defensive role has been extracted from the digestive gland of Aplysia californica (Winkler, Tilton and Hardinge, 1962).

Other defense mechanisms are obscure and are in great need of further elucidation. Thompson (1960a) has reported glands of an unknown function in the epithelium of several species of opisthobranchs which he feels secrete a poison. Crozier (1917) discovered white conical bodies on the posterior ventral surface of the mantle of Chromodoris zebra that produced a white creamy secretion which was extremely distasteful to fish. Mucus itself, which is secreted in large quantities by all opisthobranchs, may serve as a deterrent to potential predation; and protective coloration and texture of many species of genera such as Doto and Aplysia must have

some defensive attributes.

Mechanoreception must play an important role in the defense and food-finding abilities of soft-bodied animals. It has been found through histological studies that a tremendous amount of nervous tissue is involved in the sense of touch in Aplysia californica (Winkler, 1956), and this is concentrated in the lips, anterior tentacles and rhinophores, all of which are connected directly with the cerebral ganglia by many small individual and branching nerves. Excluding this type of anatomical description which is frequent in the taxonomic literature of the Subclass Opisthobranchiata (see especially Hoffman, 1939 and Bullock, 1965), little work has been done with mechanoreception of sea slugs.

The rhinophores, long thought to be chemoreceptors, are reported by Arey (1919), Crozier and Arey (1919), and Argersborg (1922) to have a tactile function. This tactile function is shown quite conclusively for Aplysia juliana by Frings and Frings (1965), who found that stimulation of the rhinophores by a current of water brought about turning of the head toward the current if it was gentle, and away from the current if it was strong. The only extensive accounts of sensory responses to tactile stimulation are those of Crozier (1917) and Crozier and Arey (1919) on the reactions of Chromodoris zebra to manually applied tactile stimuli, and Argersborg's (1923, 1925) reports of reactions to tactile

stimuli in the nudibranch Hermisenda crassicornis.

Opisthobranchs are soft-bodied animals that must be continually receiving and sorting out stimuli from their environment. Under natural conditions, low frequency mechanical stimuli produced by direct contact with plants and animals may play an important part in eliciting defensive responses and postures in these organisms. This study was undertaken to investigate the nature of responses elicited by mechanical stimuli, and to determine areas of greatest sensitivity in eleven species of opisthobranchs collected from the Gulf of California at Puerto Peñasco. The ecological and taxonomic condition of each species has been considered in some detail. Certain responses are universal for a given taxonomic group. However, in this study some evidence for convergence with regard to duration of response, frequency of stimuli which triggers catalepsy or other extreme responses, and degree of response to increased intensity of a single stimulus has been noted among species of different taxonomic levels exhibiting similar coloration patterns and habitat preferences.

## MATERIALS AND METHODS

Opisthobranchs were collected monthly over a one year period beginning August 1, 1965 from Puerto Peñasco. Members of each of the eleven species studied were found in equal abundance at a particular tide level and time of year in three different rocky intertidal habitats. Samples ranged from five to one hundred individuals, although for most species twenty to thirty members were collected. In this area seasonal fluctuation of the opisthobranch populations is extremely marked and few species may be found in the intertidal throughout the year. For this reason collections were made only during specific months of the year for a given species, and these tended to correspond with times of greatest abundance of that species. (List of species, sample size, and collection dates are presented in Table 1).

Organisms were observed in the field and collections of each species were taken to The University of Arizona for more critical work.

### Field Stimulation

A narrow glass rod drawn to a fine point with a small glass bead at the tip ( $11\ \mu$  diameter) was used to stimulate organisms in the field. Stimuli were applied manually and were divided only into light and hard taps. The pressure

exerted varied somewhat from organism to organism.

All species were stimulated while covered with a few inches of water. Casella sp. and Chromodoris banksi are often found out of the water hanging from ledges in the low inter-tidal. When stimulated in this situation, these species do not exhibit the typical rhinophore-branchial plume withdrawal response (Tables 2 and 3), nor do manually applied repetitive stimuli cause the foot to lose contact with the substratum, as is the case when the organism is stimulated under water.

#### Laboratory Observations

Most of the experiments were carried out within three days after collection of the organisms. All were held for a short time in well-oxygenated aquaria to allow for recovery from any stress that might have been imposed during collection or transportation. When studied the organism was placed in a preparation dish ten inches in diameter and covered with one or two inches of sea water taken from the collection area. Air was bubbled in at a slow rate through an air stone. This caused vibrations and slight currents, but had no affect on the responses that were observed. The organism was left in the preparation dish covered with a cardboard box for at least five minutes between stimuli. This allowed exposure only to dim light and minimized external disturbance. Stimuli were applied during both evening and daylight hours, and no appreciable differences in response

Table 1. Habitat, Sample Size, and Collection Dates of Eleven Species of Opisthobranchs from Puerto Penasco, Sonora, Mexico.

Location of Species	Average Size of Organisms in Centimeters	Sample Size	Order 5	Collection Dates
A. Species found in exposed habitats at all times.				
<u>Tridachiella diomedea</u> (Bergh)	3.5	25	Ascoglossa	all year
<u>Stylocheilus longicauda</u> (Quoy & Gaimard)	1.3	70	Anaspidea	June, July, Aug.
<u>Chromodoris norrisi</u> (Farmer)	1.8	10	Nudibranchiata	June, July
<u>Hypselodoris californiensis</u> (Bergh)	4.4	20	Nudibranchiata	Feb., Mar., April
B. Species found in exposed habitats only during high tides.				
<u>Berthellina engeli</u> <sup>1</sup>	8.5	30	Notaspidea	Feb., Mar., April, May
<u>Casella</u> sp. <sup>2</sup>	2.6	100	Nudibranchiata	June, July, Aug.
<u>Chromodoris banksi</u> <sup>1</sup>	4.0	60	Nudibranchiata	June, July, Aug.
<u>Hermisenda crassicornis</u> (Eschscholtz)	1.5	50	Nudibranchiata <sup>4</sup>	Jan., Feb.
C. Species found under rocks at all times.				
<u>Doris</u> sp. <sup>2</sup>	2.5	5	Nudibranchiata	Jan., Feb., Mar.
tan and cream speckled dorid <sup>3</sup>	2.8	5	Nudibranchiata	Jan., Feb.
<u>Dendrodoris krebsii</u> (Morch)	8.0	15	Nudibranchiata	Feb., Mar., April
<p>1. New subspecies currently being described by E. Marcus (in manuscript, Miami)</p> <p>2. New species currently being described by E. Marcus (in manuscript, Miami)</p> <p>3. New genus currently being described by E. Marcus (in manuscript, Miami)</p> <p>4. This species belongs to suborder Eolidacea. All other nudibranchs in this study belong to suborder Doridacea.</p> <p>5. Following the classification of Marcus (1961).</p>				

were found that might be correlated with tidal fluctuations or dark/light activity.

### Laboratory Stimulation

Initial laboratory stimuli were applied as in the field and gross response was recorded. In addition, mucus secretion was observed visually, and change in pH was recorded with pH paper that was placed as close as possible to the area being stimulated. In order to check for nematocyst release a small cotton swab was placed on the tip of the glass rod and after stimulation streaked across a glass slide. The slide was stained with 1% acid fuchsin and 1% methylene blue as prescribed by Stephenson (1928).

In order to observe the response to increased stimulus intensity and to more than a single stimulus, a modification of the methods used by Josephson (1961), to apply controlled stimuli to polyps of the hydroid Syncoryne, and Passano and Pantin (1955), to apply mechanical stimuli to the sea anemone Calliactis parasitica, was employed. A prodder which consisted of a glass rod with a fine bead tip (diameter 11  $\mu$ ) was attached to the center cone of a speaker which was driven electrically by pulses from a Grass SD5 stimulator. It was necessary to run the prodder through a medicine dropper with an internal diameter only slightly larger than the glass rod. The medicine dropper was held firmly in the center of a stiff plastic sheet which was fixed to the metal speaker rim with



several clamps. This eliminated most of the extraneous vibrations that could be observed under a microscope. The forward and backward motion of the prodder became well-defined and all other vibrations negligible. The speaker was mounted in a micro-manipulator, the prodder positioned over the desired point of stimulation and slowly lowered. Upon contact with the stimulation point, the stimulator was turned on at a known frequency, duration, and voltage for a desired length of time. In most cases the reactions were fast and the animal pulled away from the prodder within thirty seconds. In these experiments Passano and Pantin's (1955) procedure of lowering the prodder into contact with the surface of the tissue just before a mechanical stimulus was given and raising it immediately afterwards was followed.

The prodder was calibrated under a compound microscope by measuring its forward movement with an ocular micrometer. Movement of the prodder was a linear function of the voltage applied between thirty and eighty volts (Fig. 1). Some of the difficulties involved in applying mechanical stimuli to soft tissues are discussed in Passano and Pantin (1955). They note the relative nature of strength of mechanical stimuli which is inherent in the experimental design and type of tissue stimulated, and express relative stimulus intensities as a percentage of the maximum current used in any one experiment. These same units are used in

Figure 1. Forward motion of the prodder as a function of the voltage used to drive the prodder.

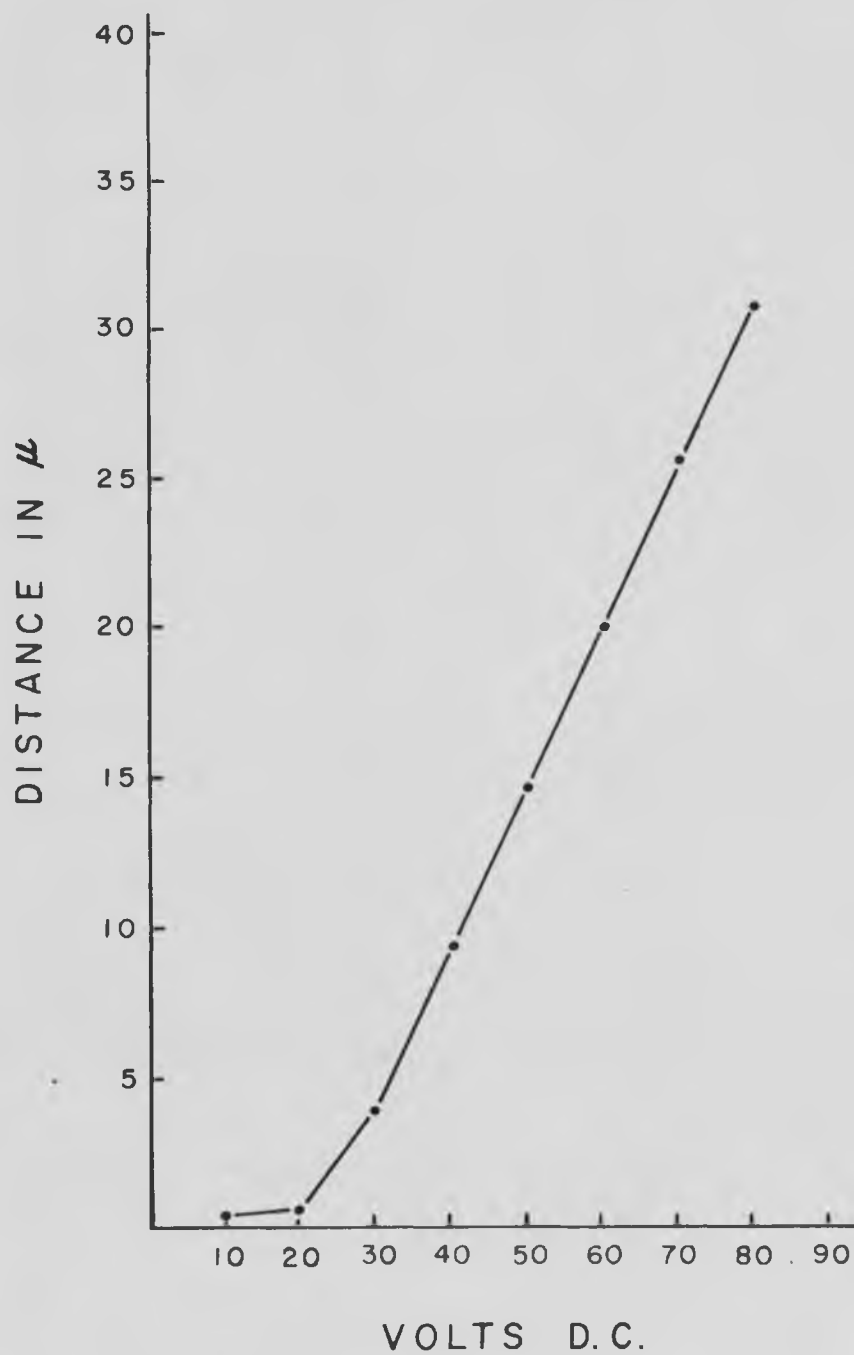


Fig. 1. Forward motion of the prodger as a function of the voltage used to drive the prodger.

the experiments reported below.

### Potential Predators

Since no cases of predation were observed in the field during low or high tides, potential predators were selected from among the larger carnivorous or omnivorous organisms which occupied the same general habitat. Samples of each species of opisthobranchs were subjected to these organisms both in the natural habitat and in aquaria.

The two largest anemones found in the tide pools or drainage channels of the rocky shores at Puerto Peñasco are Phyllactis concinnata and Bunodosoma californica. Several members of each species of opisthobranch were dropped on the oral disc of ten Phyllactis and ten Bunodosoma held in aquaria.

The only large rock crab found at Puerto Peñasco is Eriphia squamata which is primarily a nocturnal scavenger and carnivore. Three groups of ten Eriphia each were held in aquaria containing five individuals of each opisthobranch species. Eriphia were initially fed on clams, but later starved for a period of two weeks prior to the experiments.

The two most common larger tidepool fish at Puerto Peñasco are the Sargeant-Major, Abudefduf saxatilis and the opaleye Girella sp. Groups of ten members of most species of opisthobranchs were dropped individually into several aquaria containing five members of each of these fish species. Individuals of a few species of opisthobranchs that are

abundant in summer months were dropped from the surface of the water in the presence of several species of shore fish.

One of the few known predators of adult opisthobranchs is the cephalaspidian Navanax inermis. Unfortunately only five individuals of this species were collected from the Puerto Peñasco area during the course of a year and none was observed to feed in the field. Specimens of only a few species of opisthobranchs were placed in small well-aerated preparation dishes with Navanax and defensive behavior recorded.

## RESULTS

### Areas of Sensitivity

Each organism was stimulated at several points on the dorsal surface. A few differences in sensitivity to mechanical stimuli between adjacent areas may be noted in all opisthobranch species studied. Sensitivity is a difficult thing to measure, but it can be judged by the intensity of stimulus necessary to elicit a given portion of the maximum response (Bullock, 1965). Maximum responses to a single weak stimulus (stimulus intensity of 12 in arbitrary units; or 12% of maximum voltage used in these experiments) applied to any part of the organism are presented in Table 2. A very weak stimulus (intensity of 0.5 to 3) applied to certain areas of the dorsal surface will elicit no response or a much smaller response. For example, the characteristic maximum response of the dorids to a light stimulus applied anteriorly is complete withdrawal of the rhinophores. A very light stimulus applied to the rhinophore itself will produce a slight inward motion of that rhinophore, while a very light stimulus applied to the midpoint of the dorsal surface will produce no movement at all.

In all species of opisthobranchs studied the head is more sensitive than most other regions of the dorsal surface.

Other structures which display marked sensitivity are the rhinophores, branchial plumes, the edges of the mantle or parapodia and the right posterior dorsal part of the mantle that covers the gill in Berthellina engeli.

When a series of two or three weak stimuli are applied to less sensitive areas they would sometimes evoke a facilitated response. The results, however, were variable and often repetitive light stimulation did not produce any response.

#### Responses to a Single Stimulus

All organisms were stimulated with a glass prodder under natural conditions and under laboratory conditions as a check against reaction shifts imposed by stress or artificial conditions. In all cases responses to field stimulation were indistinguishable from responses produced in the laboratory, although excitability began to diminish five days after collection. Responses to a single stimulus tended to fall into taxonomic groupings (Tables 2 and 3), indicating that reactions must be partly dictated and limited by morphology. However, a certain amount of variability does exist within the order Nudibranchiata and some responses cross taxonomic lines and appear to be correlated with habitat preferences or color patterns.

### Weak Stimulus

All of the responses described in this section and listed in Table 2 could be induced by a stimulus of an intensity of 12 units when applied to some portion of the dorsal surface. Standard tests for acid secretion, nematocyst release, and increased mucus secretion were run, but these showed that the only response evoked by a light mechanical stimulus was the release of a few nematocysts from the ceratae of the eolid Hermisenda crassicornis. In no case was acid secretion elicited by a single mechanical stimulus of any intensity. Some responses are universal no matter what area of the dorsal surface is stimulated, and others vary depending on whether the anterior or posterior portion of the organism is stimulated (Table 2).

A universal response to a light stimulus in the dorid nudibranchs is the rapid withdrawal of either rhinophores or branchial plumes or both simultaneously. With a light stimulus anteriorly only the rhinophores retract. Whereas with a light stimulus posteriorly the branchial plumes retract. In some species a point is reached in the midline between the branchial plumes and the rhinophores where a single light stimulus results in both responses simultaneously or one following the other almost immediately. The four brightly colored species of dorids Casella sedna, Doris sp., Hypselodoris californiensis, and Chromodoris norissi all exhibit this response pattern.



Table 2. Responses to a Single Weak Stimulus

	Maximum Response	Anterior Stimulation	Posterior Stimulation
Order Ascoglossa			
<u>Tridachiella diomedea</u>	The posterior portion of the foot remains attached to the substratum and the anterior part of the organism moves toward the stimulus. There is slight local contraction at the point of stimulation and the parapodia rise and cover part of the dorsal surface. The rhinophores pull back slightly.	The rhinophores pull back and the anterior portions of the parapodia rise over part of the dorsal surface.	The posterior portions of the parapodia rise over part of the dorsal surface.
Order Anaspidea			
<u>Stylocheilus longicauda</u>	The posterior portion of the foot remains attached to the substratum and the anterior part of the organism rises vertically, then turns toward the stimulus. There is slight local contraction at the point of stimulation, and the parapodia close tightly over the gill.	Same as the maximum response.	Same as the maximum response.
Order Nostaspidea			
<u>Berthellina engeli</u>	There is slight local contraction at the point of stimulation and the head and rhinophores withdraw under the mantle.	The head and rhinophores withdraw under the mantle and local contraction is evoked.	Only local contraction is evoked.
Order Nudibranchiata			
Suborder Doridacea			
<u>Dendrodothis krebsii</u> <u>Chromodoris banksi</u> tan & cream speckled dorid	These three species exhibit withdrawal of either the rhinophores or branchial plumes, but never both together. Slight local contraction away from the stimulus is present. In addition, the tan dorid retracts the minute papillae in the immediate area of stimulation.	Only the rhinophores withdraw and slight local contraction is evoked.	Only the branchial plumes withdraw and slight local contraction is evoked.

Table 2. Responses to a Single Weak Stimulus (Cont.)

Maximum Response		Anterior Stimulation	Posterior Stimulation
Order Nudibranchiata			
Suborder Doridacea			
<u>Casella sp.</u>			
<u>Hypselodoris californiensis</u>			
<u>Chromodoris norrisi</u>		Only the rhinophores withdraw and slight local contraction away from the stimulus is evoked.	Only the branchial plumes withdraw and slight local contraction away from the stimulus is evoked.
<p>These three species withdraw either the rhinophores or the branchial plumes. Both retract together if a small area around the midpoint of the dorsal surface is stimulated. There is a slight local contraction at the point of stimulation.</p>			
<u>Doris sp.</u>		The rhinophores withdraw and slight local contraction is present. Forward movement is initiated if the organism is at rest when stimulated.	The branchial plumes withdraw and slight local contraction is present. Forward movement is initiated in resting individuals.
<p>The rhinophores or branchial plumes retract, and both withdraw simultaneously if a small area around the midpoint of the dorsal surface is stimulated. Forward movement is initiated if the organism is at rest when stimulated. Slight local contraction is evoked at the point of stimulation.</p>			
Suborder Eolidacea			
<u>Hermisenda crassicornis</u>		The anterior ceratae rise over the anterior portion of the dorsal surface. Slight local contraction is evoked.	The posterior ceratae rise over the posterior portion of the dorsal surface, and slight local contraction is evoked.
<p>The ceratae rise over part of the dorsal surface, and a few nematocysts are released if the ceratae themselves are stimulated. There is local contraction away from the stimulus.</p>			

These species exhibit the greatest speed of forward movement of the seven dorid species studied, and the most rapid withdrawal of rhinophores and branchial plumes.

In other species of dorids the two responses never occur together or in sequence as a result of a single weak stimulus applied to any part of the organism, although a strong stimulus elicits both responses simultaneously. In this second group are the more cryptic dorid species: Chromodoris banksi, Dendrodoris krebsii, and the tan and cream speckled dorid. These species are all dark in color, blend with their background, and are the slowest moving of the dorids studied.

Doris sp. is unique among the dorids in that a weak stimulus initiates forward movement of the organism if it is not moving at the time of stimulation. It will continue in the same direction, if it is stimulated when moving. This continued movement is true of all other nudibranchs with the possible exception of the very sluggish tan and cream speckled dorid which was never stimulated while moving. This behavior is also true of the notaspidian B. engeli.

Forward movement is initiated by a light mechanical stimulus applied to resting individuals of the two cryptically colored species, Tridachiella diomedea and Stylocheilus longicauda. However, unlike Doris sp. these species respond by turning toward the prodder. This response is reversed with increased stimulus strength which at a strong intensity

results in a movement away from the point of stimulation. It is interesting to note that Frings and Frings (1964) found this same reversal of response to increased water current intensity applied to the rhinophores of Apysia juliana.

T. diomedea, S. longicauda, and H. crassicornis cover that part of the dorsal surface being stimulated. T. diomedea raises the parapodia until they come together in a vertical position over the dorsal surface, H. crassicornis responds by raising the ceratae so they join vertically over the dorsal surface, and S. longicauda pulls the parapodia together over the gill. It must be noted that the dorid nudibranchs, with the exception of the tan and cream speckled dorid, display this same tendency toward protection of the dorsal surface by a flaring of the mantle laterally and then dorsally. However, in order to elicit this response the dorids require a strong single stimulus or a series of rapidly applied strong stimuli.

#### Strong Stimulus

The responses described in this section and listed in Table 3 were elicited by the highest intensity stimulus used (100 in arbitrary units). In only one species is the response elicited by a single strong stimulus identical, except in duration, to that elicited by a single weak stimulus.

Table 3. Responses to a Single Hard Stimulus

Order Ascoglossa	Response
<u>Tridachiella diomedea</u>	There is generally increased local contraction, a flaring of the parapodia up and over the dorsal surface, and movement away from the side stimulated at a 90 degree angle to the axis of the body prior to stimulation.
Order Anaspidea	
<u>Stylocheilus longicauda</u>	The response consists of extreme local contraction and closure of the parapodia over the gill followed by movement away from the side stimulated at a 90 degree angle to the axis of the body prior to stimulation.
Order Notaspidea	
<u>Berthellina engeli</u>	There are extreme contractions at the point of stimulation and a pulling back of the rhinophores which is followed immediately by a loss of contact with the substratum. The organism will float freely in the water for several seconds.
Order Nudibranchiata	
Suborder Doridacea	
<u>Casella sp.</u> <u>Hypselodoris californiensis</u> <u>Chromodoris norrisi</u> <u>Chromodoris banksi</u>	These four species show rapid contraction of the rhinophores & branchial plumes, & extreme contraction at the point of stimulation. Mantle edges flare to some extent in all species, & the body tends to flatten dorso-ventrally. There is a movement away from the side stimulated at a 90 degree angle to the axis of the body prior to stimulation.

Table 3. Responses to a Single Hard Stimulus (Cont.)

Order Nudibranchiata	Response
Suborder Doridacea	
<u>Dendrodoris krebsii</u>	The body flattens dorso-ventrally and the mantle raises rapidly & flips over the entire dorsal surface. Rhinophores & branchial plumes retract for a few seconds, & then extend but are covered by the flared mantle. There is extreme local contraction at the point of stimulation, & movement away from the side stimulated at a 90 degree angle to the axis of the body prior to stimulation.
<u>Doris sp.</u>	This species exhibits only a slight flaring of the mantle edge & local contraction away from the stimulus. The rhinophores & branchial plumes retract, & forward movement is initiated if the organism is at rest when stimulated. Slight local contraction away from the stimulus is present.
tan & cream speckled doris	For a prolonged period of time there is retraction of the branchial plumes, rhinophores, & minute papillae which cover the dorsal surface.
Suborder Eolidacea	
<u>Hermisenda crassicornis</u>	The ceratae rise & cover the entire dorsal surface. There is extreme contraction from the stimulus, & the organism moves away from the side stimulated at a 90 degree angle to the axis of the body prior to stimulation. Many nematocysts are released from the ceratae if they are stimulated.

This response appears in the tan and cream speckled dorid, which is an extensively spiculated species and during high and low tides remains clinging to boulders with which it blends cryptically. The organism withdraws the rhinophores, branchial plumes, and minute papillae which project from the dorsal mantle surface. No general body contraction is observed. The change in the duration of the response from 5 to 30 seconds is the only change elicited by an increased stimulus intensity. This species probably relies largely on its spiculated condition as a means of defense. The spicules give it a more definite shape and size than that of many opisthobranchs, and they also provide a texture which enhances its cryptic appearance. Paine (1963) has proposed that this spiculated condition is an effective defense against predation by Navanax inermis, and Risbec (1928) lists the possession of spicules among the various defensive devices of opisthobranchs.

In all other species a single strong mechanical stimulus evokes a response in a larger portion of the organism than that produced by a weak stimulus (Table 3). Increased local contraction away from the stimulus is a universal response in all these species.

In all species of dorids studied, with the exception of the tan and cream speckled dorid, a flaring of the mantle edge is a common response triggered by a strong stimulus.

The degree of this response varies with the species from the slight flaring exhibited by Doris sp. to the complete covering of the dorsal surface within seconds exhibited by D. krebsii.

The four species of dorids that are found in exposed habitats during high tides, C. norrisi, C. banksi, C. sedna, and H. californiensis show a common response to a single hard stimulus applied to the posterior dorsal surface of the foot. The foot contracts anteriorly and flips up so that the ventral surface projects posteriorly. Often this surface is pointed to the right or left toward the side of the foot that is stimulated. The posterior mantle contracts anteriorly, flares up, and a small stream of mucus with white globules is ejected from the ventral surface of the foot or mantle in this region. This response is similar to that described for Chromodoris zebra by Crozier and Arey (1919).

An interesting response to a single hard stimulus found in most of the species studied is movement away from the side stimulated at a 90 degree angle to the axis of the body prior to stimulation. The three species which do not exhibit this response are Doris sp., B. engeli, and the tan and cream speckled dorid. Occasionally individuals will turn 90 degrees to the side away from the point of stimulation and then swing back to the original position and turn 90



degrees to the other side, prescribing an arc of 180 degrees. This is more frequently seen in S. longicauda and T. diomedea, although most individuals in these two species will only move 90 degrees away from the point of stimulation. This is interesting in light of Clark's (1958) description of herbivorous snails swinging their shells through an arc of 180 degrees, sometimes violently enough to dislodge larger carnivorous snails with which contact had just been established. However, it is doubtful that this response (which is triggered chemically in Clark's herbivorous snails) could serve a similar function in opisthobranchs. It probably serves simply to reorient the slugs in a new direction.

Standard tests for acid secretion, nematocyst release, and increased mucus secretion were run for all species. Mucus secretion can be seen to increase in those dorids which exhibit the tail raising response, and H. crassicornis releases many nematocysts when the ceratae are given a hard stimulus. No cases of acid secretion were found.

#### Responses to Change in Intensity of a Single Stimulus

With increase in intensity of mechanical stimuli there is an increase in the degree of response in all organisms, until at some intensity a maximum response is reached which is not modified by any further increase in stimulus strength. The response itself, as pointed out in the

preceding section, varies with different species; but the intensity which triggers the maximum response is of the same order of magnitude among species that are grouped according to coloration and habitat selection (Table 4). Those organisms which are found under the rocks at all time or move only to the sides of a particular rock at high tides react maximally at the lowest intensities, whereas for organisms which are found exposed at all times a much stronger stimulus is required to elicit a maximum response. The organisms in this last group are subject to a considerable amount of mechanical stimulation imposed on them by currents and swaying algae, and to respond maximally to some low intensity tactile stimulation would appear to be disadvantageous. The two cryptically colored species, T. diomedea and S. longicauda, subject to the greatest amount of mechanical stimulation as a result of their herbivorous habits and concealment in algal beds, require the strongest mechanical stimulus to evoke a maximal response. These data indicate that some degree of convergence has occurred in the reaction systems of opisthobranchs from widely diverse taxonomic groups.

#### Duration of Response

It appears that not only is a very strong mechanical stimulus needed to evoke a maximum response from opisthobranchs living in an exposed habitat at all times, but their

Table 4. Intensities of a Single Stimulus of 20 msec Duration Necessary for Just Eliciting the Maximum Response in Opisthobranch Species.

	Coloration	Mean Threshold Intensity (Units are percentages of maximum vol- tage used)
A. Species always exposed:		
<u>Tridachiella diomedea</u>	cryptic	100
<u>Stylocheilus longicauda</u>	cryptic	100
<u>Chromodoris norrisi</u>	bright	90
<u>Hypselodoris californiensis</u>	bright	90
B. Species exposed only during high tides:		
<u>Berthellina engeli</u>	bright	75
<u>Casella sp.</u>	bright	75
<u>Chromodoris banksi</u>	cryptic	90
<u>Hermisenda crassicornis</u>	bright	67
C. Species always under rocks:		
<u>Doris sp.</u>	bright	33
tan & cream speckled dorid	cryptic	27
<u>Dendrodoris krebsii</u>	cryptic	33

rate of recovery after stimulation is much faster. This was determined by recording with a stopwatch the duration of the response at varying stimulus intensities from 21 to 100. In most cases the response involves more than one area, and to give some degree of consistency to the recordings the response was timed from the initial stimulus contact until the animal had returned to its "normal" state. This presented some problems in those organisms in which a 90 degree turn was evoked by mechanical stimulation. However, usually by the time the 90 degree swing is completed other responses are completed and this point was arbitrarily considered to be the end of the evoked response. Results are presented in Fig. 2. In those organisms which are always in exposed habitats, (T. diomedea, S. Longicauda, C. norrisi, and H. californiensis), the duration of the response reaches a maximum at a stimulus strength of 52, and does not increase with increased stimulus strength even though the maximum response described in Table 3 is not evoked until the stimulus is 90 or 100. (Table 4).

The duration of the response in S. longicauda and T. diomedea that are found on algae with which they blend cryptically is the lowest of any of the species studied.

The duration of the response of organisms that are found under rocks during low tides but that emerge from the rocks during high tides, (B. engeli, Casella sp. and H. crassicornis), levels off when the stimulus intensity reaches

Figure 2. Duration of the response with increased intensity of a single stimulus in eleven species of opisthobranchs.

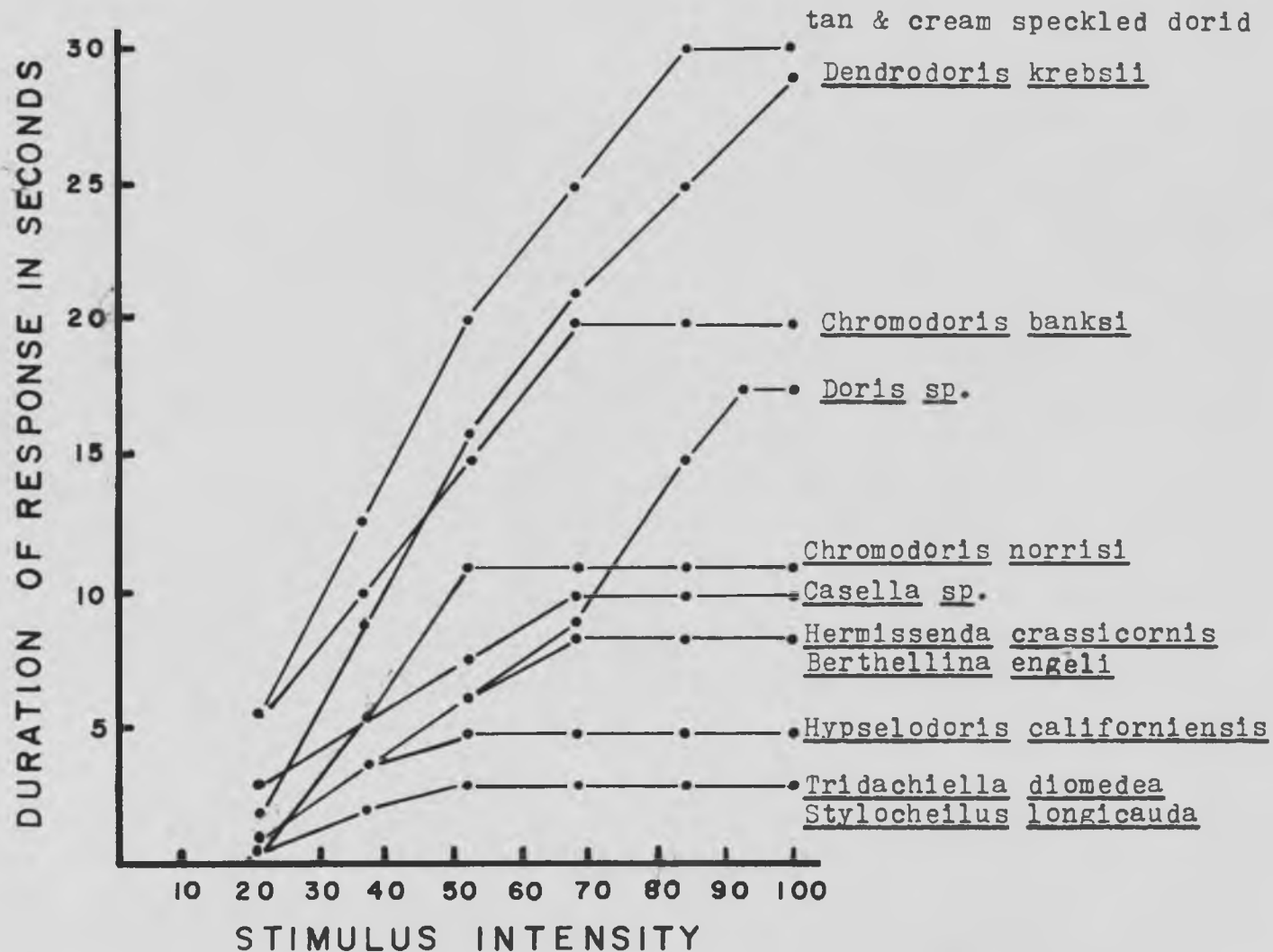


Fig. 2. Duration of the response with increased intensity of a single stimulus in eleven species of opisthobranchs.

68, which is about the same intensity at which three of these species show a maximum response to a strong stimulus. A fourth species, the more cryptically colored C. banksi, has a much longer response duration and requires a strong stimulus to evoke a maximum response (Table 4). It is generally more sluggish in movement than the other species selecting this general habitat.

In those species which are found under or on the sides of rocks during both low and high tides, (Doris sp. D. krebsii, and the tan and cream speckled dorid), the duration of the response is dependent, for the most part, on the intensity of the stimulus, even though a maximum response is evoked at low intensities (Table 4). The most mobile of these species, Doris, recovers from a mechanically evoked response more rapidly than the others.

#### Responses to Multiple Strong Stimuli

It is evident from the previous experiments that as the strength of the stimulus is increased, there is a change in the response from one involving a localized area around the prodder to one involving the whole organism, until a maximum response is reached at some stimulus intensity. However, if a stimulus that is strong enough to evoke a maximum response is repeated several times, an even greater reaction occurs, which appears to be similar to the "shock" reaction

seen in species when exposed to certain potential predators. In order to determine the responses of the various opisthobranch species to repetitive stimulation, multiple strong stimuli with a 20 millisecond duration and an intensity of 100 were applied to each organism at frequencies that varied between 2 and 40 pulses per second. Since H. crassicornis, T. diomedea, and S. longicauda were able to avoid the stimulator by extreme local contraction and rapid movement away from the prodger within ten seconds, stimuli were applied to all organisms for three seconds only. (Table 5).

Apart from the more rapid movements and extreme contraction, the three species mentioned above reacted as they would to a single strong stimulus. In most dorids the response produced is an extreme flaring of the mantle over the dorsal surface, retraction of the rhinophores and branchial plumes, and gradual entrance into a cataleptic state in which the edges of the foot come together, the organism bends dorsally and locks in this position, floating loosely in the water. The notaspidian B. engeli exhibits this response to a single strong stimulus as well as to multiple strong stimuli. Multiple stimuli at a higher frequency produced by bubbling air into the aquarium at a fast rate or by swirling a glass stirring rod in the vicinity of dorids can evoke this same response in these organisms. Two dorids which do not exhibit this response are Doris sp. and the tan and cream



Table 5. Frequencies of Stimuli Triggering Shock Reactions and the Duration of These Responses

	Frequency in Pulses Per Second	Coloration	Mean Response Duration (secs.)
<hr/>			
A. Organisms in exposed habitats all times.			
<u>Tridachiella diomedea</u>	24	cryptic	10
<u>Stylocheilus longicauda</u>	26	cryptic	10
<u>Chromodoris norrisi</u>	22	bright	60
<u>Hypselodoris californiensis</u>	20	bright	30
 B. Organisms in exposed habitats during high tides only.			
<u>Berthellina engeli</u>	16	bright	65
<u>Casella sp.</u>	18	bright	84
<u>Chromodoris banksi</u>	16	cryptic	60
<u>Hermisenda crassicornis</u>	14	bright	50
 C. Organisms found under rocks at all times.			
<u>Doris sp.</u>	10	bright	95
tan and cream speckled dorid	8	cryptic	120
<u>Dendrodoris krebsii</u>	6	cryptic	90

speckled dorid which react as they do to a single hard stimulus.

Those species which are normally found exposed at all times require the highest frequency to trigger extreme responses (Table 5), and those which are found under rocks at all times require the lowest frequency. The durations of the responses are longer than those evoked by a single hard stimulus but fall into groupings that can be correlated with habits and habitat. (Table 5).

#### Responses to Potential Predators

No cases of predation were observed in the field and only an occasional anemone and the cephalaspidian Navanax inermis were observed to prey on opisthobranchs in the laboratory. Other laboratory studies show, however, that no opisthobranch species was avoided and no responses were evoked in opisthobranchs until after contact had been established with the potential predator. The responses of opisthobranch species to this direct contact with various omnivorous and carnivorous organisms are identical to those evoked by various intensities of mechanical stimulation with a glass prodder. (Table 6).

The two species of anemones, Bunodosoma californica and Phyllactis concinnata, fold their tentacles over all opisthobranch species placed on their oral disc, but seldom take them into the digestive cavity, and, if they do so, will

normally reject the partly digested opisthobranch within a few hours. In only a few cases would the opisthobranch die as a result of this stress; most exhibited tremendous powers of regeneration. In one instance an extensively digested Casella sp. was rejected after 24 hours. It was in the form of a ball with a strong protective coating around it. The organism emerged from this "cocoon" within 16 hours, weak, but externally undamaged. The anemones elicit cataleptic or extreme "shock" responses in all species except B. engeli and H. crassicornis, which prey on anemones and appear to have some immunity to nematocysts. This response is probably produced by the chemical-mechanical stimulation of nematocysts rather than by the light tap of tentacles, since it is evoked the instant a few tentacles touch the dorsal surface of the opisthobranch. The response evoked in the dorids is identical to that produced by multiple strong stimuli, except that the cataleptic state lasts for up to five minutes after rejection by the anemone and for a much shorter period of time after multiple mechanical stimulation. Risbec (1928) discusses the defensive attributes of a cataleptic state, but its advantages in dissuading digestion by anemones remains uncertain.

Starved Eriphia squamata will scavenge on dead and injured opisthobranchs of all species, but will seldom eat the entire organism, often touching only the epidermal area.

Healthy crabs of this species will not avoid any of the opisthobranch species until after contact has been established. Normally the crab will approach an opisthobranch and lightly touch some part of it with its chelipeds and then back away. (Table 6).

The two species of shore fish Abudefduf saxatilis and Girella sp. will taste all opisthobranch species that are dropped in an aquarium. All opisthobranchs without exception are rejected and responses evoked by encounter with the fish are similar to those evoked by mechanical stimulation with a glass rod. (Table 6). Defensive responses are not dependent upon attachment of the foot to the substratum. This is in agreement with Thompson's (1960) study on several opisthobranch species found off Britain and Crozier's (1916) study of Chromodoris zebra. Coloration of the species does not deter fish when opisthobranchs are floating in the water. Fish will taste both brightly and cryptically colored species with no indication of learning to associate form and color with distastefulness. During the course of this study no fish was observed to taste opisthobranch species whether brightly or cryptically colored if they were crawling on rocks and algae in the field or on the sides and bottom of aquaria. Crozier (1916) found this to be true of Chromodoris zebra also.

Table 6. Defensive Postures Elicited by Direct Contact With Three Potential Predators.

Opisthobranch Species	<u>Eriphia squamata</u>	<u>Abudefduf</u> and <u>Girella</u>
<u>Tridachiella diomedea</u>	There is local contraction and a slight raising of the parapodia.	There is marked local contraction and flaring of the parapodia over the entire dorsal surface.
<u>Stylocheilus longicauda</u>	There is extreme local contraction away from the stimulus and pulling the parapodia together.	Exhibits the same response as it does to <u>Eriphia</u> .
<u>Berthellina engeli</u>	There is local contraction away from the stimulus.	Exhibits the same response that it does to <u>Eriphia</u> .
<u>Casella</u> sp. <u>Hypselodoris californiensis</u> <u>Chromodoris norrisi</u> <u>Chromodoris banksi</u> <u>Dendrodois krebsii</u>	These five species exhibit retraction of the rhinophores and branchial plumes and a slight flaring of the mantle edges. Some local contraction away from the stimulus is manifested.	Exhibit the same response as they do to <u>Eriphia</u> .
<u>Doris</u> sp.	The rhinophores and branchial plumes withdraw and forward movement is initiated in resting organisms. There is a slight flaring of the mantle edges.	The rhinophores and branchial plumes withdraw and slight local contraction is manifested.
tan and cream speckled dorid	The rhinophores and branchial plumes withdraw.	Exhibits the same response as it does to <u>Eriphia</u> .
<u>Hermisenda crassicornis</u>	The ceratae rise over the dorsal surface and local contraction is present.	Exhibits the same response as it does to <u>Eriphia</u> .

## DISCUSSION

The responses elicited by mechanical stimulation in several species of opisthobranchs from a variety of habitats have been investigated. The significance of some of these responses in the life of the animal is still to be determined. However, a few responses such as retraction of the rhinophores and branchial plumes, raising of various structures to protect the dorsal surface, and local contraction away from the stimulus are similar to the responses evoked by potential predators and may serve to protect the extremities or other sensitive areas from accidental or purposeful damage from these predators. Adult opisthobranchs are generally rejected as a food source by larger predatory organisms. Whether some of the innumerable smaller animals regularly prey on opisthobranchs is not known. Nevertheless it has been shown in these studies that opisthobranchs were not avoided by larger potential predators until after contact had been made, so presumably the responses which were elicited, and which were identical to those produced in the laboratory by a glass prod, serve to protect the organism. These responses appear to be defensive in nature, but whether they are the primary factor in deterring the predator is not known, and in most instances the reason for predator rejection remains

obscure. Since contact is necessary prior to rejection in all eleven species, serious doubt is placed on the warning nature of bright color patterns found in many members of this subclass. This also suggests that chemical stimuli do not prevent some predators from touching the animal. However, cryptic appearance of certain species may well serve as a first line of defense.

Responses produced by mechanical stimulation are generally limited by morphology and tend to follow taxonomic lines. T. diomedea will raise the parapodia when a hard stimulus is applied, S. longicauda will shut the parapodia tightly over the gill, and B. engeli will exhibit extreme local contraction. The dorid nudibranchs all exhibit retraction of the rhinophores and branchial plumes, and, with the exception of the tan and cream speckled dorid, flare the mantle when a strong stimulus is applied. The foot of most dorid species will lose contact with the substratum when multiple hard stimuli are applied. This response is also elicited by swirling water in the vicinity of the organism. An organism disturbed by repetitive mechanical stimuli in the field drops from the side of a rock or algae on which it is crawling and is picked up by the current and carried several feet away. The defensive attributes of this response seem apparent, although it was never evoked by contact with potential predators. Casella sp. and C. banksi are often

found during low tides under ledges out of the water, and in this situation no amount of hard repetitive stimulation can evoke this response.

Although different structures are involved, many types of responses cut across a variety of taxa. There is a tendency to protect the dorsal surface with parapodia, mantle edges, or ceratae. This is exhibited by the cryptically colored T. diomedea as well as the brightly colored Casella sp. Local contraction at the point of stimulation is exhibited by all but one species, and a strong stimulus results in movement away from the stimulus at a 90 degree angle to the axis of the body prior to stimulation in most species.

A few species are unique in their responses to mechanical stimulation. The tan and cream dorid exhibits the same response to both a strong and weak stimulus, varying only the duration of the response. This species probably relies largely on its spiculated condition and cryptic appearance for defense. In S. longicauda, T. diomedea, and Doris sp., movement is elicited by a weak stimulus when applied to resting organisms. In the first two species it results in movement toward the stimulus, whereas Doris sp. moves forward regardless of the area stimulated.

The most sensitive areas in all organisms are the head, and vital external structures or areas that afford limited protection to vital structures.



Whatever the significance of the behavior, it has been shown in this study that responses of opisthobranchs have tended to converge. Responses of species found in exposed habitats at all times generally last for the shortest period of time, and above a certain low stimulus intensity do not increase in duration even though it takes a very strong stimulus to evoke a maximum response in these organisms. A strong stimulus applied to all species found in this group (T. diomedea, S. longicauda, H. californiensis, and C. norrisi) evokes a response which lasts for a short period of time and results in a 90 degree turn away from the stimulus and movement in this new direction. T. diomedea and S. longicauda, which both live and graze on algae and are cryptic in appearance, turn toward the stimulus if it is weak and will often spiral up the prodder if it is left close to the organism after stimulation. They may be observed spiraling on algae in a similar manner during high tides. "Shock" reactions are triggered in these species only at high frequencies, but these responses also have a short duration.

At all times maximum responses of species found under rocks are obtained at low stimulus intensities and the duration of the response increases with increasing stimulus intensity. Extreme or shock responses are evoked in these species by low frequencies of mechanical stimuli, but the response lasts for a relatively long period of time. Species

found in exposed habitats during high tides, when they emerge from under the rocks or ledges, are intermediate in response durations, and intensity of stimulus and frequency of stimuli necessary to trigger maximum responses.

Responses can be correlated with coloration in two instances. The branchial plumes and rhinophores withdraw simultaneously when a single light stimulus is applied to brightly colored dorids regardless of their habitat preference; and intensities of a single stimulus that elicit a maximum response are of the same order of magnitude for all brightly colored species that show a similar habitat preference (Table 4). However, the data are somewhat inconsistent particularly with respect to cryptically colored species.

This study indicates that although some convergence in patterns of behavior exists among opisthobranchs living in the same habitat, an even greater similarity is seen in the strength and frequency of stimuli needed to evoke maximal responses and in the duration of these responses. This is most noticeable in species which are found in an exposed environment at all times. Representatives of three different orders from the primitive Anaspiidea to the more advanced Nudibranchiata show similarities in the length of their reactions and intensities and frequencies of stimuli to which they respond maximally. However, it is necessary to question on what plane this convergence actually exists. In

order to do this a detailed study of the neuro-anatomical features of all these species is needed and electrical recording of nervous activity is vital.

Thompson (1960a) classifies opisthobranchs behaviorally into two broad groups: those which have a preference for concealment which is achieved by coloration, texture, or habitat selection, and those whose behavior is characterized by a disregard for concealment. In light of the data derived from the present study this broad behavioral classification should be re-examined.

### SUMMARY

1. Responses to mechanical stimuli of various intensities have been recorded in eleven species of opisthobranchs that exhibit a variety of habitat preferences and patterns of coloration.
2. Areas of greatest sensitivity in all species are the head region, extremities, and parts of the mantle or parapodia that cover the gill.
3. The strength of a single stimulus necessary to elicit a maximum response and the duration of that response may be correlated with the habits and habitat preference of the opisthobranch species studied.
4. Species found in an exposed habitat during high and low tides, respond maximally only to a strong stimulus, and recover rapidly (i.e. the response has a short duration). However, the duration of the response is relatively independent of the strength of the stimulus and tends to remain the same at high stimulus intensities.
5. Repetitive strong stimuli trigger an extreme or "shock" response. The frequency of stimuli which elicits this response can also be correlated with habitat preference. Opisthobranchs found exposed during both high and low tides exhibit a shock response only at high frequencies.

This type of response lasts for a relatively short time.

6. Species found in more protective situations respond maximally at lower stimulus intensities, are slower to recover, and show an increase in the duration of the response as the stimulus strength is increased. Furthermore, the shock reaction is evoked at lower frequencies of repetitive stimulation.
7. Although responses do not generally appear to be correlated with coloration, two cryptically colored species found in exposed habitats much of the time, Stylocheilus longicauda and Tridachiella diomedea, show a response reversal with increased stimulus strength. These organisms turn toward a light stimulus and away from a strong stimulus. This same response evoked in species from two separate orders may be common among others that live on algae. Cryptically colored species investigated in this study that do not live on algae fail to exhibit this response.
8. No cases of predation on adult opisthobranchs were observed in the field, and only an occasional individual was digested by anemones or predatory opisthobranchs in the laboratory. Potential predators do not avoid opisthobranchs until contact has been established; and responses elicited in opisthobranchs are identical to those produced by a glass prodder and appear to be defensive in nature.

9. These experiments indicate that although many responses follow taxonomic lines, some convergence has occurred in opisthobranchs found in similar habitats.

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