The Swimming Escape Response of the Intertidal Nudibranch *Dendronotus frondosus*

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Introduction—Organisms living in marine environments must deal with a wide variety of potential predators. Many organisms have chemical defense mechanisms as well as behavioral mechanisms to escape predation. Several species of nudibranchs are known swim through the water in what is thought to be an escape response to predators such as sea stars. *Dendronotus frondosus* is a sea slug which is quite abundant in the Northern hemisphere and is common both in the rocky intertidal and also in subtidal areas of the Northeastern Pacific coast, both living and feeding on a variety of hydroid colonies (Morris *et al.* 1980). Previous studies have shown that *D. frondosus* exhibits a swimming behavior (Farmer 1970, Willows 2001). No studies, however, have been found to link the onset of swimming in *D. frondosus* to any specific stimuli, such as that of a predator.

The knowledge that *D. frondosus* does indeed exhibit a swimming behavior led to the question of whether this is indeed a response initiated in order to escape predation. Despite lacking a shell for protection as well as being quite slow moving, nudibranchs have few known predators (Penney 2002). It is also known that contact with the sea star *Pycnopodia helianthoides* commonly initiates an escape response in a wide variety of intertidal invertebrates, as it is a very opportunistic feeder (Morris *et al.* 1980). This study was aimed at determining if the swimming response initiated in *D. frondosus* by *P. helianthoides* would be larger than that initiated by the six-rayed star, *Leptasterias hexactis*. As it is currently unknown if either species actually preys on nudibranchs (Fishlyn *et al.* 1980, Morris *et al.* 1980, Menge 1972), the magnitude of the response from *D. frondosus* to these sea stars could potentially indicate if either might indeed be a predator of *D. frondosus*.

Materials and Methods—Seven *D. frondosus* individuals (with an average length of about 3cm) were collected off of the colonies of hydroid, *Obelia* sp. on the docks of the small boat basin located off of Boat Basin Road in Charleston, OR. The nudibranchs were kept in a saltwater table in the lab, and were fed on the hydroid from which they were collected. Four *L. hexactis* (average diameter of about 4cm) were collected from the rocky intertidal at the South Cove of Cape Arago, also in Charleston, and two small *P. helianthoides* (approximately 7cm in diameter) were collected from the North Cove of Cape Arago. These sea stars were also kept in a saltwater table in the lab.

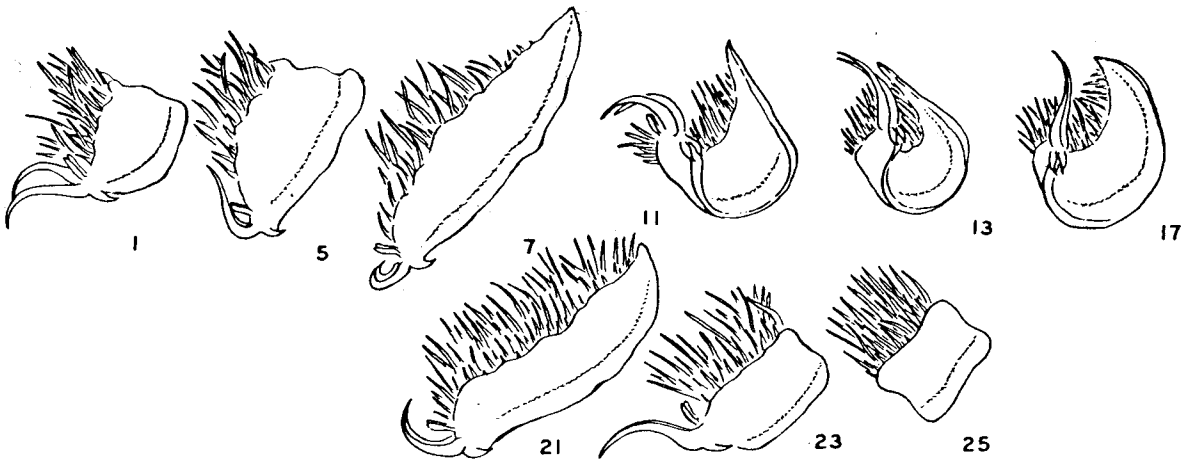
For each trial, one nudibranch and one sea star were placed in a large finger bowl. For the trials with *L. hexactis*, these sea stars were extremely inactive and so the sea stars were placed in contact with the nudibranch repeatedly until swimming behavior was initiated. The response to each consecutive touch was recorded, and the nudibranch was placed back on the hydroid to rest while another individual was used for the next trial. This was done because the behavior appeared to expend a fair amount of energy, and preliminary trials showed the response to diminish when repeated several times in a row, even with a five minute break in between trials. For trials with *P. helianthoides*, these sea stars were extremely active, and so the sea star was simply placed in the finger bowl and allowed to move around the bowl until it came into contact with the *D. frondosus* present in the bowl. Again, the stage of the response was recorded at each consecutive touch from the sea star.

A total of thirty trials were completed with each species of sea star, for a total of sixty trials. In order to characterize the responses more quantitatively, a scale of graded responses was also established. For this scale, the number of muscle contractions observed on each side of the body was used to evaluate the strength of the swimming response.

Figure 1: System of graded responses for quantifying the observed response of *D. frondosus* to touch by the sea stars. Further description of responses is provided below.

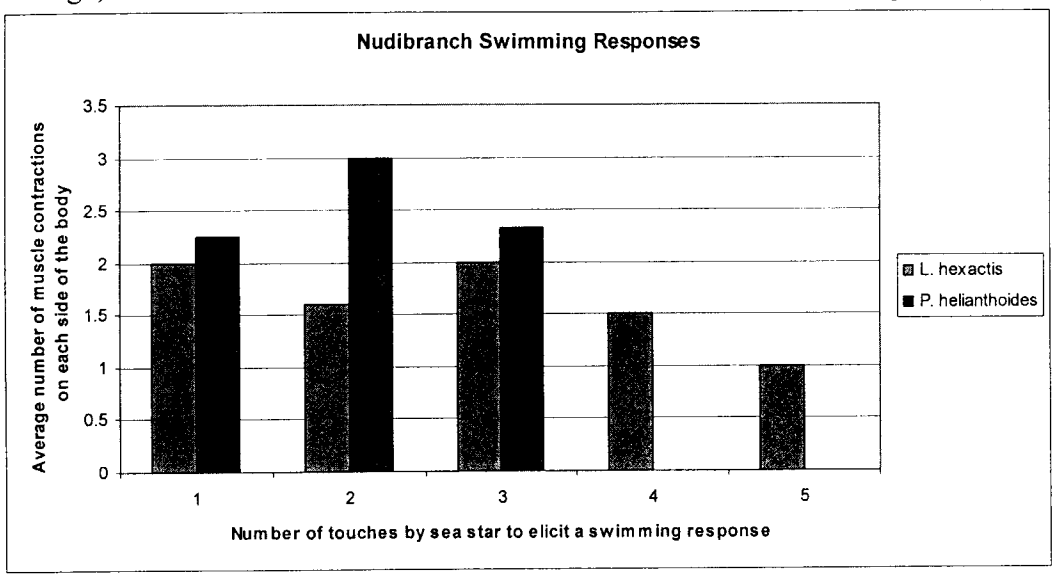
Gradation	Characterization of Response
0	No escape response observed
1	Touch results in *D. frondosus* swinging tail or head away from sea star
2	Touch results in contraction of body forward to move more quickly
3	Touch→slight swimming response (1 muscle contraction on each side of body)
4	Touch results in strong swimming response (2-3 contractions on each side)
5	Touch results in robust swimming response (>3 contractions on each side)

Results—Observation throughout this study led to a characterization of the stages of the escape response of *D. frondosus*. Direct tactile stimulus by the ray or tube feet of the sea stars was always required to elicit a response in *D. frondosus*. Generally, the first stage of the response was for *D. frondosus* to swing the end of its body that had been touched away from the stimulus and to speed up its movement away from the sea star. Further contact generally resulted in a response where *D. frondosus* would move its rostral end forward and then contract the caudal end of its body forward quickly, thereby reducing its total length to less than half its usual length. This allowed much faster movement away from the sea star. Upon further contact, a swimming response was normally elicited. The swimming response consisted of contraction of the muscles on one side of the body, thereby bringing its head into contact (or nearly so) with its tail and forming a circle with its body, followed by contraction of the muscle on the other side of the body to complete the same movement in the other direction. The total number of contractions on each side of the body was extremely variable, but one contraction on each side of the body was sufficient to lift the nudibranch off of the glass finger bowl. Once lifted from the substrate, the foot of *D. frondosus* folded down the center along the length of the body, coming together so that the base of the foot was no longer exposed and thereby making the body more streamlined for movement through the water.
Figure 2: This figure, from Farmer 1970, shows the swimming behavior of *Coryphella iodinea*, which swims using the same method as *D. frondosus*. The bending of the body from side to side can be clearly seen, as well as the folding of the foot, bringing its sides together to make a somewhat pointed edge. This figure shows one contraction on each side of the body.



The number of touches required to elicit a response from the sea stars showed some variation, and most nudibranchs responded to *P. helianthoides* after fewer touches. It generally took more touches from *L. hexactis* to generate a swimming response.

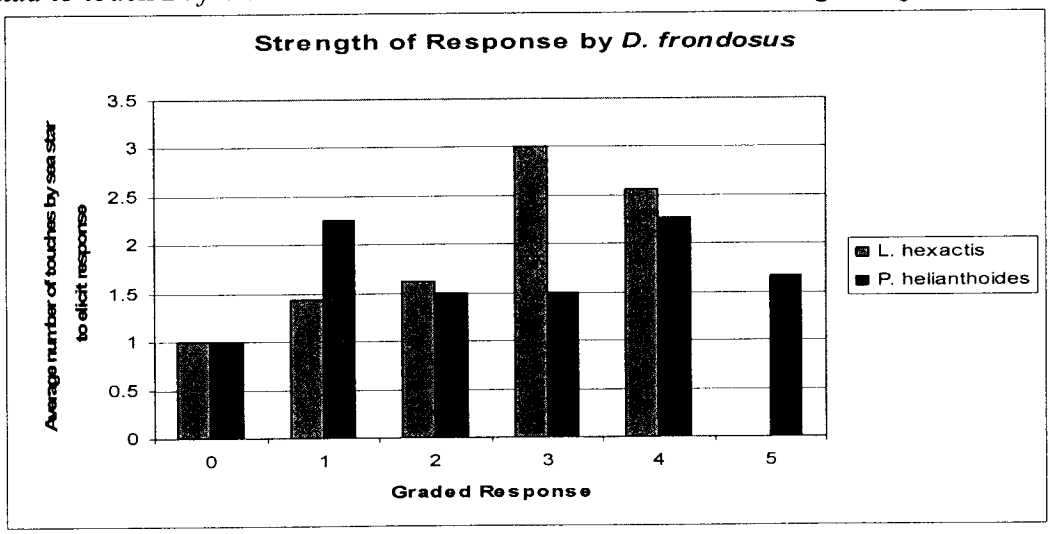
Figure 3: Fewer touches were generally required to elicit a response to *P. helianthoides*. On average, more contact was needed from *L. hexactis* to elicit swimming in *D. frondosus*.



The direction of the swimming movement was highly random, and both slight and strong swimming responses rarely moved the nudibranch more than a centimeter or two away from its starting position. This, however, was often enough to no longer be in the direct path of the sea star, and the nudibranch would then move quickly away from the sea star. The robust swimming behaviors seen moved the nudibranch up to about four centimeters from its starting position, moving it quite clear of the sea stars. Three such robust swimming behaviors were observed, each time from a different nudibranch. Thus, this robust response was not simply due to the fact that the response strength also varied between individuals.

Although the responses to *P. helianthoides* were somewhat stronger, the difference may not be significant. The only robust responses seen (graded response of 5) were elicited by *P. helianthoides*, but the rest of the responses to both sea stars were quite similar.

Figure 4: The graded response, as described above, was used in conjunction with the average number of touches required to elicit a response in order to examine response strength. In general, the responses to *P. helianthoides* rated higher on the graded scale, while *L. hexactis* had to touch *D. frondosus* more times in order to elicit the stronger responses.



Discussion—The results of this study indicate that, although the only extremely strong responses were seen from contact with *P. helianthoides*, the general trend is that responses of *D. frondosus* are quite similar for both sea stars. The main difference is that it generally took fewer touches from *P. helianthoides* for *D. frondosus* to initiate swimming. Thus, there is slight, but not extremely significant, support for the hypothesis that *P. helianthoides* would elicit a stronger escape response from *D. frondosus*. Therefore, this study provides no conclusive proof that either sea star feeds upon this nudibranch, and so it is still speculation that this is indeed an escape response. Other studies have also been inconclusive in determining whether this is indeed an escape response, although that is the common assumption (Farmer 1970, Willows 2001). It is possible that neither prey on D. frondosus, which may use only touch to detect the presence of sea stars and might therefore be unable to detect the difference between them. Further study would be required to determine this.

The swimming response described above is consistent with that described for the majority of nudibranch species, including *D. frondosus*, as lateral bending of the body (Farmer 1970). Although it was observed that this behavior did not result in movement over much distance by the nudibranch, it is believed that the nudibranchs normally use currents to transport them away from predators once they have lifted off of the substrate (Willows 2001).

As described above, swimming by *D. frondosus* seemed to be a last resort for escape, and other methods were attempted first. Swimming is therefore likely much more energetically costly than the other mechanisms first attempted. It has also been suggested that swimming away from predators is a somewhat risky method, as they are transported by currents which may carry them far away from their preferred habitat and food source as well as potentially exposing them to predators (Willows 2001).

Further study is needed to determine what preys upon *D. frondosus* in an effort to concretely determine whether this swimming response is indeed an escape response, as it is believed to be. Interestingly, P. helianthoides actually tended to recoil and alter the direction of its movement when it came into contact with *D. frondosis*, indicating that it might not commonly prey preys upon *D. frondosus*. This study did not investigate other potential predators such as intertidal fishes, nor were the nudibranchs left with the sea stars to see if they would be consumed. Further observation in the field could potentially provide information about other stimuli that might induce the swimming response in *D. frondosus*, as its exact purpose is still under speculation.

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