

Prolonged Withdrawal: A Possible Predator Evasion Behavior in *Balanus glandula* (Crustacea: Cirripedia)

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Abstract

The duration of cirral withdrawal in *Balanus glandula* (Darwin) varies by a factor of three depending on the type of stimulus applied. Contact with potential predators including thaidid gastropods (*Thais emarginata*, *T. lamellosa*), and forcipulate asteroids (*Leptasterias hexactis*, *Pycnopodia helianthoides*) elicits significantly longer withdrawal durations than contact with an herbivorous gastropod (*Tegula pulligo*), a grazing, spinulosid asteroid (*Henricia leviuscula*) or a neutral, brown algal stimulus (*Fucus distichus*). By substantially attenuating the release of metabolites, prolonged withdrawal probably increases the likelihood of being bypassed by nonvisual predators relying on chemical cues to verify that barnacles are alive. The reduced response to the non-predatory species indicates that this is not a generalized response to gastropods or asteroids, but rather that it appears to be specific to potential predatory species.

Introduction

Numerous studies have documented escape responses in mobile invertebrates following exposure to or contact with potential predators (Bullock, 1953; Snyder and Snyder, 1971; Hoffman *et al.*, 1978; Phillips, 1978; Moitza and Phillips, 1979; Fishlyn and Phillips, 1980; see also Ansell, 1969; Mauzey *et al.*, 1968; and Feder, 1972; for reviews). Sessile invertebrates, however, are more limited in how they may respond. Withdrawal of feeding appendages by many sessile organisms (e.g. feeding crowns of sabellid and serpulid polychaetes, hydroid hydranths, bryozoan and phoronid lophophores) involves little more than physical retraction to reduce the likelihood of losing extremities to a predator. The occurrence of sponges on swimming pectinid bivalves (Bloom, 1975; Forester, 1979) constitutes another form of escape by sessile prey from mobile predators.

We report here an apparent escape response in *Balanus glandula*, a common, intertidal acorn barnacle on temperate shores of the west coast of North America (Ricketts *et al.*, 1968). This response involves a prolonged cirral withdrawal and tight closing of the opercular plates following contact with potential predators. Contact with related but non-predatory invertebrates or with an algal stimulus elicits a less prolonged withdrawal. Such a response is very likely important for a species whose predators rely on chemical cues to verify that shelled prey are alive and to initiate attack (Pratt, 1974). A very similar response (tight clamping to the substratum) has been described for the limpet *Notoacmea paleacea* in response to contact with *Leptasterias hexactis*, a predatory, forcipulate asteroid (Fishlyn and Phillips, 1980).

Methods

Individuals of *Balanus glandula* (Darwin) were collected during low water on small stones from the upper intertidal of Grappler Inlet, a shallow (<10 m), meandering inlet immediately adjacent to the Bamfield Marine Station on the west coast of Vancouver Island, British Columbia, Canada (Lat. 48°45'N, Long. 125°10'W). Stones were returned to the laboratory and held out of water for a minimum of 4 h in a cool damp environment prior to each experiment. Organisms used as stimuli were collected from various sites in the vicinity of Bamfield Marine Station and maintained in running seawater throughout. The stimulus organisms and sizes used included: the predatory, intertidal neogastropods *Thais emarginata* (shell length 15–20 mm) and *T. lamellosa* (shell length 35–40 mm), and an herbivorous, subtidal archeogastropod *Tegula pulligo* (shell length 17–20 mm); two predatory starfish, *Leptasterias hexactis* (maximum armspan 70 mm) and *Pycnopodia helianthoides* (maximum armspan 100 mm), and a grazing starfish, *Henricia leviuscula* (maximum armspan 80 mm); and individual thalli of the intertidal brown alga *Fucus distichus*.

Experiments were initiated by submerging freshly collected barnacles in laboratory sea tables in approximately 10 cm of continuously replenished seawater at a temperature of 10° to 12°C. A moderate water current was maintained in the aquaria throughout the experiments to reduce the variance in withdrawal times. Barnacles were left undisturbed for a minimum of 10 min after immersion to permit thermal acclimation; testing commenced when a regular feeding rhythm had been established. The size of *Balanus glandula* tested ranged from 3 to 5 mm opercular diameter, as measured across the inside of the aperture from the rostral to the carinal plates. A maximum of two barnacles were examined on any one stone; individual barnacles were tested only once. To minimize variation due to unrelated factors, only barnacles exhibiting a steady, rhythmic cirral beating for 60 s were tested.

Variation among test individuals was further minimized by monitoring withdrawal times following the brief application of a shadow, created by passing a hand over the stones immediately above the water's surface. Shadow responses were measured twice for each individual, the second test being performed as soon as the barnacle had resumed rhythmic cirral beating following the first test. The mean shadow responses of experimental individuals were (\pm one standard deviation):

3 mm opercular diameter 10.5 s (\pm 8.86), $n = 35$
 4 mm opercular diameter 11.0 s (\pm 8.67), $n = 45$
 5 mm opercular diameter 11.5 s (\pm 8.63), $n = 5$

Individual exhibiting shadow responses in excess of 60 s were not included in the analyses. Less than 25% (22/85) of the barnacles exhibited shadow responses of longer than 15 s.

Experimental stimuli were applied for 60 s in the following manner:

Algae- individual fronds were brushed gently over the opercular plates to simulate wave-induced contact.
 Gastropods- an individual gastropod was detached from the bottom and held immersed until its foot extended. The

anterior portion of the foot was then placed in contact with the test barnacle's opercular plates.

Asteroids- an individual starfish was placed directly on the test subject with its oral disc centered over the barnacle's opercular plates.

Withdrawal duration was measured from the time the stimulus was removed until the barnacle resumed a rhythmic beating with fully extended cirri. When a second barnacle was to be tested on the same stone, the stone was left undisturbed for at least 5 min before applying the second stimulus.

All experiments were performed in August 1980 at the Bamfield Marine Station. The data were analyzed using Duncan's New Multiple Range Test (Steel and Torrie, 1960), where the standard error was computed as the square root of: the error mean square divided by the harmonic mean of the treatment sample sizes. All individuals exhibiting unusually long withdrawal durations (greater than 15 min, twice the mean maximum withdrawal time) were eliminated from the analysis regardless of the experimental stimulus.

Results

The overall mean shadow response time of 10.8 s was less than 10% of the shortest, experimentally-induced mean withdrawal time (Table 1). Thus, although the application of experimental stimuli also involved creating a shadow, the withdrawal in response to an experimental stimulus was substantially longer than would be expected following exposure to a shadow.

Differences in the withdrawal response durations among experimental stimuli were striking in their consistency (Fig. 1). There were no significant differences in withdrawal times among the three non-predatory stimulus treatments (*Fucus distichus*, *Henricia leviuscula*, and *Tegula pulligo*, Fig. 1). Of six possible pairwise combinations among the predatory stimuli, only one was significantly

Table 1. *Balanus glandula*. Sample sizes, barnacle sizes, normal activity levels, and shadow and stimulus response durations for treatment groups. Barnacles sizes are opercular diameters. Values in parentheses are standard errors

Stimulus	N	Mean barnacle size (mm)	Mean cirral beats per min.	Mean shadow response (sec.)		Mean withdrawal duration (sec.)
				Trial 1	Trial 2	
Algae						
<i>Fucus distichus</i>	12	3.7 (0.18)	27.8 (4.08)	9.4 (2.81)	10.1 (3.24)	131 (18.6)
Gastropoda						
<i>Tegula pulligo</i>	11	3.7 (0.20)	25.2 (3.70)	16.6 (3.59)	10.4 (1.34)	169 (24.4)
<i>Thais emarginata</i>	15	3.5 (0.13)	19.6 (2.08)	11.4 (2.51)	11.3 (2.56)	359 (46.8)
<i>Thais lamellosa</i>	10	3.7 (0.21)	25.0 (4.47)	9.0 (1.66)	13.2 (2.94)	418 (64.6)
Asteroidea						
<i>Henricia leviuscula</i>	15	3.4 (0.13)	40.2 (5.35)	6.6 (0.83)	5.2 (0.65)	139 (18.4)
<i>Leptasterias hexactis</i>	15	3.8 (0.18)	21.1 (2.61)	11.9 (1.38)	13.3 (3.17)	349 (47.6)
<i>Pycnopodia helianthoides</i>	7	3.7 (0.19)	22.3 (6.30)	13.4 (3.56)	12.3 (3.03)	281 (30.2)

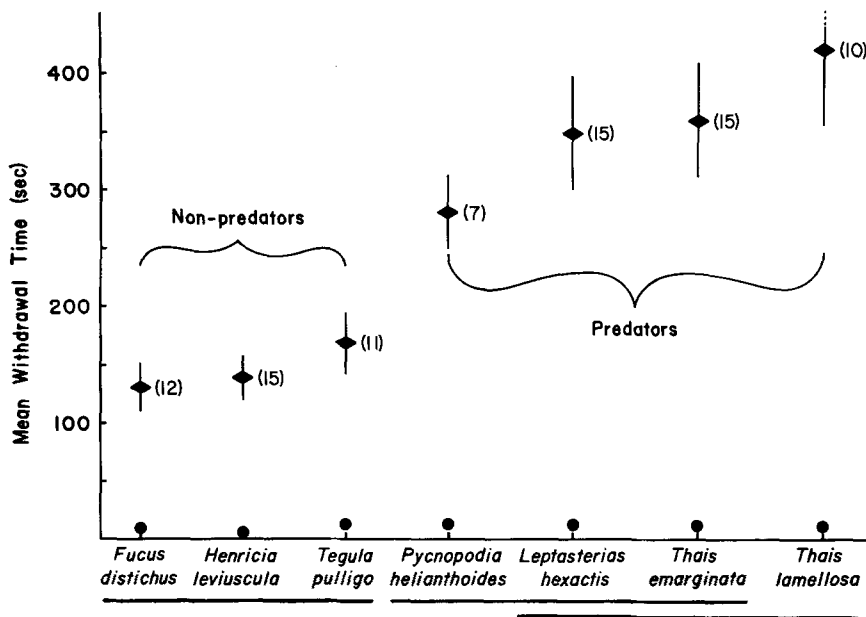


Fig. 1. *Balanus glandula*. Mean shadow response (circles) and stimulus response (diamonds) times. Error bars correspond to \pm one standard error. Sample sizes were the same for both treatments and are indicated in parentheses. Shadow response standard errors are less than the diameters of the symbols. The horizontal lines indicate stimulus response means among which there were no significant differences at a 5% experimentwise level, where the significance levels were determined from Duncan's New Multiple Range Test (Steel and Torrie, 1960, see text). The mean withdrawal response was 145.3 s for non-predatory stimuli and 356.5 s for predatory stimuli

different at a 5% experimentwise level (*Pycnopodia helianthoides* versus *Thais lamellosa*). This difference is not surprising since *P. helianthoides*, although a predator on *Balanus crenatus*, rarely feeds on *B. glandula* (Mauzey *et al.*, 1968). *T. lamellosa*, on the other hand, is a common and significant *B. glandula* predator (Connell, 1970; Dayton, 1971; Spight, 1974; Palmer, 1982). Of particular interest was the existence of significant differences between all pairwise comparisons of predatory and non-predatory stimuli (Fig. 1). The phylogenetic relatedness of stimuli was of less consequence than their status as potential predators. Withdrawal times in response to predatory stimuli were from 93% to 187% longer than the mean response time to non-predatory stimuli.

Discussion

The evidence presented above strongly supports the hypothesis that the nature of the stimulus organism as a potential predator determines the length of the withdrawal response in *Balanus glandula*; contact with potential predators elicits significantly longer withdrawal times. The alternative hypothesis, that prolonged withdrawal is a generalized response following contact with any mobile gastropod or asteroid is rejected because exposure to non-barnacle consuming members of these invertebrate classes elicited withdrawal durations no different from those elicited by the brown algal control (Fig. 1).

Although we did not perform any experiments to determine actual cues used by the barnacles, we strongly suspect they are chemical (e.g. see Blake, 1960; Feder and Lasker, 1964; Wood, 1968; Gurin and Carr, 1971; Fishlyn and Phillips, 1980). Support for this interpretation derives from a distinctive observation made on one barnacle following the application of *Leptasterias hexactis*. In this

instance, on removal of the starfish, three tube feet remained attached to the barnacle's opercular plates. The individual remained withdrawn for more than 45 min, far longer than any other barnacle monitored. Eight minutes after removal of the tube feet with a scalpel, the barnacle began rhythmic cirral beating. It appears that residual chemical stimulants released by the adherent tube feet were sufficient to inhibit reopening. Sensory hairs described on the occludent edges of the mantle (Foster and Nott, 1969) are the probable detectors of such cues while a barnacle is retracted, although the initial withdrawal may be triggered by physical contact with the actively beating cirri.

The adaptive value of this response in *Balanus glandula* probably lies in the dependence of its major predators on olfactory cues. Since most predators of barnacles are capable of consuming them whether they are closed or not (Menge, 1972; Barnett, 1979), physical withdrawal is not likely to protect barnacles from attack unless it increases the handling time sufficiently that a predator would be exposed to physical stresses at low tide. Asteroids and gastropods, however, are nonvisual predators and thus rely on chemical cues both to locate and to identify potential prey (Blake, 1960; Kohn, 1961; Wood, 1968; Castilla and Crisp, 1970; Castilla, 1972; Morgan, 1972). Pratt (1974), in an elegant experiment with the oyster drill *Urosalpinx cinerea*, demonstrated convincingly that *Crepidula fornicata* metabolites were required to initiate attack. Living *C. fornicata* were not attacked when metabolite flow was blocked even though their shell had been contacted by *U. cinerea*. Similar observations have been made by Carriker and van Zandt (1972) who noted that living oysters (*Crassostrea virginica*) were not attacked by *U. cinerea* when their valves were clamped tightly closed. Therefore, reducing or eliminating the release of metabolic byproducts appears to render sessile prey effec-

tively invisible to predators dependent on olfactory information, even after contact with a predator.

The longest mean withdrawal time observed above was less than 7 min. If prolonged withdrawal is an effective evasive tactic against non-visual predators, why are the withdrawal times not longer? Two explanations seem likely. First, predators were not allowed continuous contact with *Balanus glandula* in the above experiments. The very extended withdrawal time noted for a barnacle with tube feet attached to its opercular plates indicates that continuous predator contact will elicit continuous retraction. If a searching predator encounters a barnacle and then leaves without attacking, 5 to 7 min may be sufficient time for the predator to move out of olfactory range, particularly in the intertidal environment of *B. glandula* where water movement is erratic and largely non-directional.

A second factor that may favor such apparently short withdrawal times is that barnacles cannot feed when retracted. More time spent withdrawn is less time spent feeding. Thus the advantage of extending the withdrawal time must be weighed against the cost of reduced feeding time. If reduced feeding time is an important cost, we would predict that starved barnacles or barnacles with less total feeding time per tidal cycle (e.g. barnacles higher in the intertidal) would remain retracted for a shorter time than those barnacles for which there is less of a premium on feeding time. The same prediction would apply to intertidal versus subtidal barnacle species, and possibly also to small versus large barnacles of a single species since growth may be more important in small than in large individuals (Vermeij, 1978).

A final consideration regarding the significance of our results is whether withdrawal after contact with a predator would reduce the probability that a barnacle is eaten. In other words, would a predatory gastropod or starfish not consume a barnacle after having made physical contact with it? The answer would seem to be yes. Emlen (1966) described the movement of *Thais emarginata* across patches of barnacles using time-lapse, underwater movies. Individual *T. emarginata* were observed to feed, then crawl across numerous living barnacles before feeding again. Whether the bypassed barnacles were not recognized as being alive or were bypassed for other reasons, however, is not certain.

Nonvisual predators appear to require olfactory confirmation that the skeletons of shelled prey are still inhabited (as indicated above for *Urosalpinx cinerea* preying on *Crepidula fornicata* (Pratt, 1974) and *Crassostrea virginica* (Carriker and van Zandt, 1972). Because of the long handling times involved (e.g. 12–48 h for a *Thais* spp. to drill and consume an individual, adult *Balanus glandula*, Carefoot, 1977; Palmer, 1980), the attack of unoccupied barnacles would result in a substantial commitment of time by the predator for which it would receive no gain. That initial contact may not be sufficient for a nonvisual predator to recognize whether a potential prey is living has been demonstrated for *Leptasterias*

hexactis (Fishlyn and Phillips, 1980). The limpet *Notoacmea paleacea* possesses a shell that appears to provide a chemical camouflage against its substratum, *Phyllospadix scouleri*. Living limpets exhibited no response to *Leptasterias hexactis*-conditioned seawater, however they did clamp tightly to the *Phyllospadix scouleri* blades following physical contact with *L. hexactis* (Fishlyn and Phillips, 1980, p 40). This tight clamping after contact appeared to reduce substantially the probability that *L. hexactis* would attack. We did not test whether predator metabolites alone would elicit prolonged withdrawal, although the observation with the attached tube feet of *L. hexactis* indicates that they could. We do suggest, however, that such withdrawal would be adaptive even following contact since nonvisual predators appear to require olfactory confirmation that their shelled prey are alive.

We believe that the prolonged withdrawal response in *Balanus glandula* has evolved as a means of reducing the likelihood of attack by chemosensory-dependent predators. The evidence presented above demonstrates clearly that this is not a generalized gastropod- or asteroid-induced response. Thus *B. glandula* appears to be able to distinguish predatory from non-predatory stimuli based on chemical cues even though the cues may derive from phylogenetically closely related organisms.

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