

THE ECOLOGICAL ROLE OF DEFENSIVE SECRETIONS IN THE INTERTIDAL PULMONATE *ONCHIDELLA BOREALIS*

CRAIG M. YOUNG¹, PAUL G. GREENWOOD², AND CYNTHIA J. POWELL³

*Friday Harbor Laboratories, 620 University Rd., Friday Harbor, Washington 98250
and Bamfield Marine Station, Bamfield, British Columbia V0R 1B0, Canada*

ABSTRACT

Repugnatorial glands located in the marginal papillae of the intertidal ochidiid pulmonate *Onchidella borealis* secrete a viscous fluid in response to mechanical or chemical stimulation. In laboratory encounters, this fluid repels intertidal predatory asteroids, particularly *Leptasterias hexactis*, but not predatory gastropods, polyclad turbellarians, nemerteans, or fishes. Intertidal crabs consume dead *O. borealis* readily, but seldom consume living individuals capable of firing their glands. The vertical range of *O. borealis* overlaps that of *L. hexactis*, whereas limpets that are vulnerable to predation by the sea stars generally live higher on the shore. On a small scale, *O. borealis* and *L. hexactis* occupy similar microhabitats (*e.g.*, crevices, algal holdfasts), but are seldom found together. Field and laboratory experiments suggest that this negative spatial correlation may result from expulsion of the sea stars by onchidiids.

INTRODUCTION

Many marine gastropods lacking protective shells have evolved alternative defenses such as incorporation of cnidarian nematocysts, distasteful chemicals, and aposematic or cryptic coloration. Shelled gastropods often exhibit flight behaviors and other evasive tactics (Bullock, 1953; Feder, 1963; Margolin, 1964; Mauzey *et al.*, 1968; Phillips, 1976). The ecological consequences of molluscan chemical defenses have been tested in relatively few cases (*c.f.* Rice, 1985). In many cases, organisms containing protective chemicals are probably not consumed; the ecological significance of the defense is complete protection from most predators. In other cases, defenses may be effective against some predators and not others.

Stylomatophoran pulmonates in the family Onchidiidae occupy the middle and high intertidal zones of rocky shores throughout many areas of the world. The species that have been studied breathe air and are most active at low tide on overcast days (Arey and Crozier, 1921; Pepe and Pepe, 1985). Many species return to home sites during high tide (Pepe and Pepe, 1985; McFarlane, 1980). The margins of the snails are endowed with a row of multicellular glands that secrete a white, viscous fluid. These glands were named repugnatorial glands in *Onchidium floridana* because they were thought to repel fishes and crabs (Arey, 1937; Arey and Crozier, 1921). A unique organic molecule isolated from the glands of *Onchidella binneyi* has been described

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¹ Present Address: Department of Larval Ecology, Harbor Branch Oceanographic Institution, RR 1, Box 196, Ft. Pierce, Florida 33450.

² Present Address: Department of Biological Science, Florida State University, Tallahassee, Florida 32306 (author to whom reprint requests should be addressed).

³ Present Address: 6012 Cambie St., Vancouver, B. C. V5Z 3B1, Canada.

recently (Ireland and Faulkner, 1978), and is thought to be responsible for the observed repulsion.

Studies dealing with the effectiveness of molluscan defenses have mostly dealt with escape responses of shelled gastropods (Clark, 1958; Feder, 1963; Engstrom, 1982; McKillup, 1982; Schmidt, 1982; Garrity and Levings, 1983). The chemical defenses of molluscs have been less studied (Thompson, 1960; Edmunds, 1966; Ambrose *et al.*, 1979; Rice, 1985). Compounds isolated from molluscs have been tested for a repugnatorial effect in a few cases (Ireland and Faulkner, 1978; Thompson *et al.*, 1982). However, the effects of molluscan defenses on the ecology of potential predators has never been investigated.

In this study we document the distribution of *Onchidella borealis* in the intertidal zones of Washington and British Columbia, describe the outcomes of encounters between *O. borealis* and various potential predators, and present preliminary evidence that the defensive secretions can modify the distributions of predatory asteroids. Aside from earlier anecdotal work, there have been no studies of predator-prey interactions involving onchidiids, and to our knowledge, repellent defensive secretions do not influence predator distributions in any other animal species.

MATERIALS AND METHODS

Onchidella borealis were studied on San Juan Island, Washington, and in Barkley Sound, Vancouver Island, British Columbia, from 1973 to 1985. Distributions were documented quantitatively at several sites on the west side of San Juan Island (Marvista Resort, Cattle Point, Eagle Cove, Pile Point) and on Seppings Island in Barkley Sound. Animals for laboratory and field experiments were collected from all of these sites and also from a high density population occupying a cobble field in the intertidal zone of Grappler Inlet, British Columbia.

Onchidella borealis were maintained in the laboratory in glass bowls, beakers, or plastic refrigerator containers covered loosely with plastic lids or cheesecloth. Snails quickly crawled out of containers without covers. Most snails died if they were submerged for more than a day; we obtained highest survival by maintaining snails with damp algae (*Ulva* sp.) or moist paper towels, not submerged in seawater.

Distribution of Onchidella borealis and associates

Vertical zonation was documented at several sites with transects of 50 by 50 cm quadrats. The profile of the shore was measured with a meter stick and line level. At one site, Eagle Cove, the large quadrats were subdivided into 10 cm plots to investigate the small-scale spatial distributions of *O. borealis* and one of its potential predators, *Leptasterias hexactis*.

Encounters between Onchidella borealis and potential predators

We documented responses of potential predators to *O. borealis* by observing individual encounters staged in glass bowls of seawater. Predators used included polyclad flatworms (*Notoplana atomata*), nemerteans (*Paranemertes peregrina*), gastropods (*Searlesia dira*, *Thais lamellosa*), anomuran (*Petrolisthes cinctipes*) and brachyuran (*Hemigrapsus nudus*) crabs, fishes (*Gobiesox meandricus*, *Apodichthys flavidus*), and asteroids (*Leptasterias hexactis*, *Henricia leviuscula*, *Pisaster ochraceus*, *Solaster stimpsoni*). All predators were collected from intertidal areas where *O. borealis* occurred. In instances where the predators showed distinct avoidance of *O. borealis*, the experiments were repeated with freshly killed (by drowning) *O. borealis* to determine

whether the predators responded to the presence of the snail body *per se*, or if repugnatorial gland secretions produced by living snails were necessary to initiate the response.

After observing several encounters between an *O. borealis* and a potential predator, we determined the best way to qualitatively score the encounter. For the worms and the snails, we scored any obvious changes in direction of movement after touching *O. borealis* as a response. The data were thus of a binary (response/no response) nature. Asteroids demonstrated both directional and postural changes, so their responses were divided into four easily recognized categories that could be ranked according to the degree of response. Responses of all potential predators to *O. borealis* were cast in 2-factor or 3-factor contingency tables and analyzed by log-likelihood statistics (Sokal and Rohlf, 1981).

In some experiments, we noted responses of predators to small amounts of repugnatorial gland secretion rather than to the predator itself. Repugnatorial gland secretion was obtained by placing a Pasteur pipette over a repugnatorial gland and probing the animal gently with the pipette until the gland discharged. The secretion was expelled by the snail into the pipette where it remained until use. Because the secretion is more viscous than seawater, it was easily visible when discharged from the pipette. Once used, individual specimens of *O. borealis* were returned to a common container and drawn haphazardly for each set of experiments; thus, individual specimens of *O. borealis* were used in more than one trial. At least 15 minutes elapsed between trials. A given set of animals was never used for more than 2–3 consecutive days before being returned to the field.

Individual behavioral interactions between *O. borealis* and crabs or fishes were difficult to document because of the rapid movements of the predators and the large size disparity between predator and prey. Where these large motile predators were involved, we exposed *O. borealis* to predators in cheesecloth-covered bowls for 5 hours, then noted the number of prey consumed or damaged. Three *O. borealis* and one predator were used in each bowl. Predators were acclimated to laboratory conditions for 3–3.5 hours before the experiments.

Experiments on the Leptasterias/Onchidella interaction

Additional work was undertaken with the asteroid predator *Leptasterias hexactis*, because it regularly occurs in the same tidal zone as *O. borealis* and shows a dramatic response to repugnatorial gland secretions. Laboratory and field feeding experiments were done to determine which common intertidal gastropods were consumed by the starfishes. In the laboratory, 10 each of *O. borealis* and the limpets *Collisella digitalis* and *Notoacmaea scutum* were placed in a bowl with a single starfish. We noted the prey species eaten and replaced individuals as they were consumed, thus the relative proportions of potential prey were constant throughout the experiment. The experiment was repeated twice. A similar experiment was run in the field. The experimental containers used in the field consisted of plastic jars glued to bricks and placed in the mid intertidal zone. Each jar had a cover of nitex screen and was positioned with the lid down so the jar would drain at low tide. Because of the small sizes of the jars (500 ml), only two of each prey item were placed in each jar. The experiments were monitored daily during the spring tidal sequence, but were not monitored during neap tides, when they were exposed for only short periods. Only 2 of 12 jars survived the entire experiment; the rest were damaged or removed by the surf.

Onchidella borealis and *L. hexactis* commonly occupy holdfasts of the brown alga *Hedophyllum sessile* in the mid-intertidal zone. We investigated the possibility

that the repugnatorial glands of *O. borealis* can repel starfish and thereby modify the distributional patterns of the latter. Starfish and snails were seeded into previously defaunated holdfasts (in the lab and field), then emigrations were noted. *Hedophyllum sessile* plants containing neither *L. hexactis* nor *O. borealis* were collected from Pile Pt., San Juan Island. The blades of the plants were removed and the holdfasts were rinsed in fresh water for at least 12 hours to remove all macroscopic organisms. Holdfasts were then transferred to running seawater aquaria, where they showed no signs of decomposition for several days. Holdfasts were divided into two separate aquarium compartments. Small *L. hexactis* were added to each compartment and allowed to enter the holdfasts. After the starfish had colonized both holdfasts, the holdfasts were carefully removed from the water and 20 to 25 *O. borealis* were added to one of them, the other serving as a control. The holdfasts were then placed in separate compartments of empty aquaria and seawater was trickled around them to keep them moist. After two hours, the number of *L. hexactis* that had left each holdfast was recorded. The experiment was repeated six times.

The holdfast experiment was repeated under field conditions. Individual *L. hexactis* were added (during low tide) to small clumps of *H. sessile* holdfasts located between 0.0 m and +1.0 m above MLLW. Five clumps without *O. borealis* served as controls and seven clumps containing *O. borealis* served as treatments. The holdfasts were censused after 24 hours (two tidal sequences) and the number of *L. hexactis* present at each holdfast was recorded. The holdfasts were then removed and examined once again for *O. borealis*.

RESULTS

General observations

In *Onchidella borealis*, the number of repugnatorial glands varies as a function of animal size; large individuals may have more than 20 glands (Fig. 1). Internally, each gland consists of many flask-shaped or columnar secretory cells surrounding a lumen, covered by a thick muscle sheath, and embedded in connective tissue. The lumen of each gland opens to the outside on a distinct, individual marginal papilla (Fig. 1). The ultrastructure of the glands and surrounding structures will be described in a second paper (Greenwood and Young, in prep.). When stimulated mechanically (e.g., with a glass probe) on the dorsum, *O. borealis* may direct its papillae toward the stimulus, but it does not fire until the tip of a papilla is stimulated directly. Upon direct stimulation, the contacted gland releases a milky translucent, viscous substance that is clearly visible; the repugnatorial secretion may extend several millimeters from the animal. Each gland seems to function as an independent effector. When stimulated lightly, a gland does not always discharge the entire contents of its lumen, but can fire repeatedly. However, in other cases, particularly when responding to stimulation by starfish, each gland fires only once, then requires a "recycling period" before it is capable of firing again. The glands appear to require less mechanical stimulation to elicit their firing when probes are coated with starfish mucus, but this was not quantified.

Distribution of Onchidella borealis and associates

Populations of *O. borealis* were found on the west side of San Juan Island where rocky shores are exposed to the moderate wind-generated surf of the Straits of Juan de Fuca and the Rosario Straits. Individuals were only rarely found on the east side of the island where tidal currents are strong and waves are generally

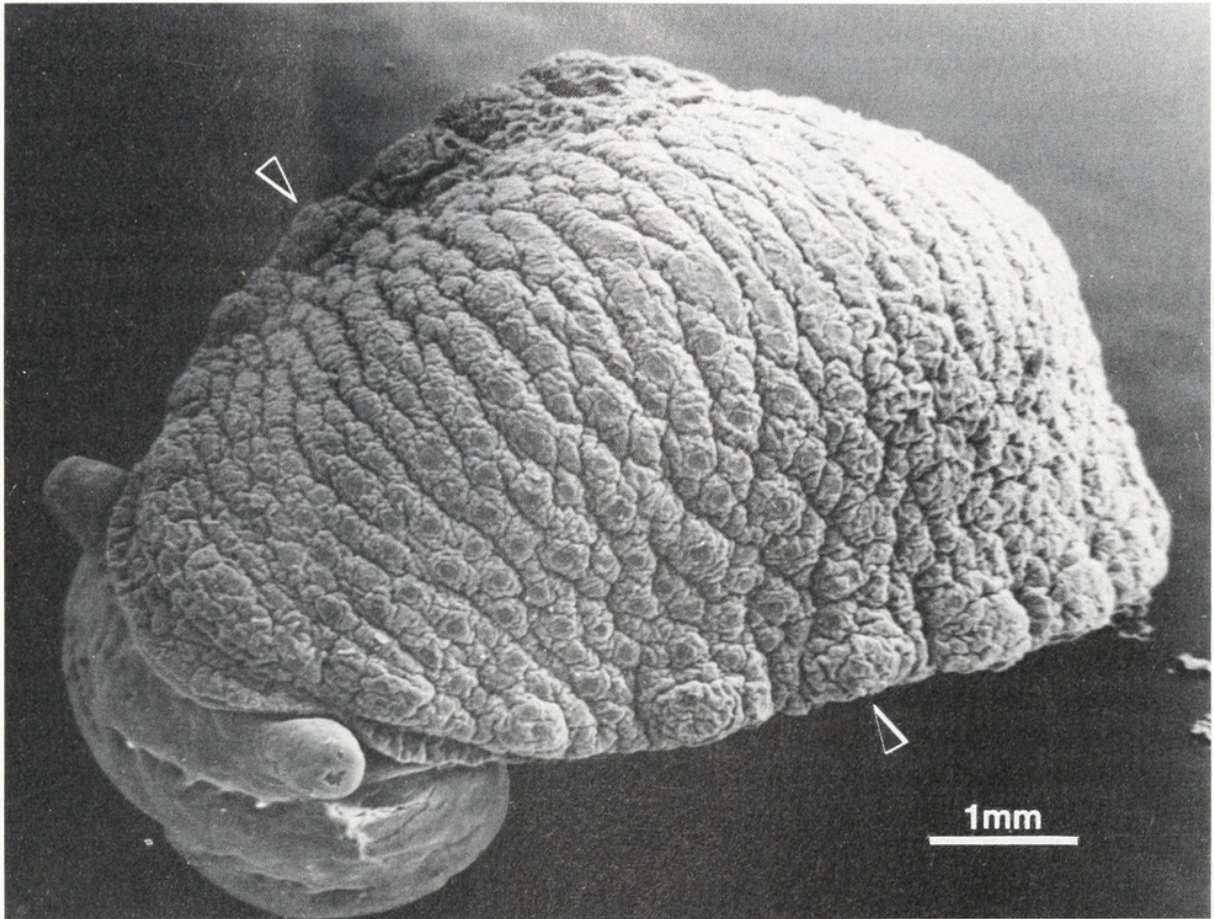


FIGURE 1. Scanning electron micrograph of *Onchidella borealis*, showing marginal papillae (arrow) where repugnatorial glands are located.

small. In Barkley Sound, populations were found on most coasts with moderate exposure. Surprisingly, the highest population density we have encountered is in a very protected cove of Grappler Inlet. There, *O. borealis* occurred abundantly on rocks in the middle intertidal zone, but also on *Ulva* sp. and cobbles overlying mud in the lower intertidal. Comparable habitats in the San Juan Islands never supported populations of *O. borealis*.

On rocky shores at low tide, *O. borealis* primarily occupy crevices, empty barnacle shells, and holdfasts of *Hedophyllum sessile* and *Laminaria* spp. On rainy or foggy days, many individuals leave their shelters and wander over the rock. Figure 2 shows the vertical distribution of *O. borealis*, several co-occurring limpets, and the predatory starfish *Leptasterias hexactis*. The precise tide level occupied by *O. borealis* varies from site to site, but is always between about -0.5 m and $+1.5$ m above MLLW. This zone overlaps the distribution of *L. hexactis*, though the two populations do not always peak at the same level. At most sites, large starfish were found lower on the shore than *O. borealis*, and the asteroids primarily occupied the larger crevices. Small starfish also occur in crevices, but live in relatively large numbers in holdfasts of *H. sessile* and various laminarians as well.

At Eagle Point, all individuals of both species were counted within 10 cm quadrats. There was a non-significant, though negative correlation between the occurrence of the two species. In general, no *L. hexactis* were found in quadrats containing high densities of *O. borealis*. The same held true for *H. sessile* holdfasts. At Pile Point, San Juan Island, two sites, one more exposed than the other, were examined in detail. At

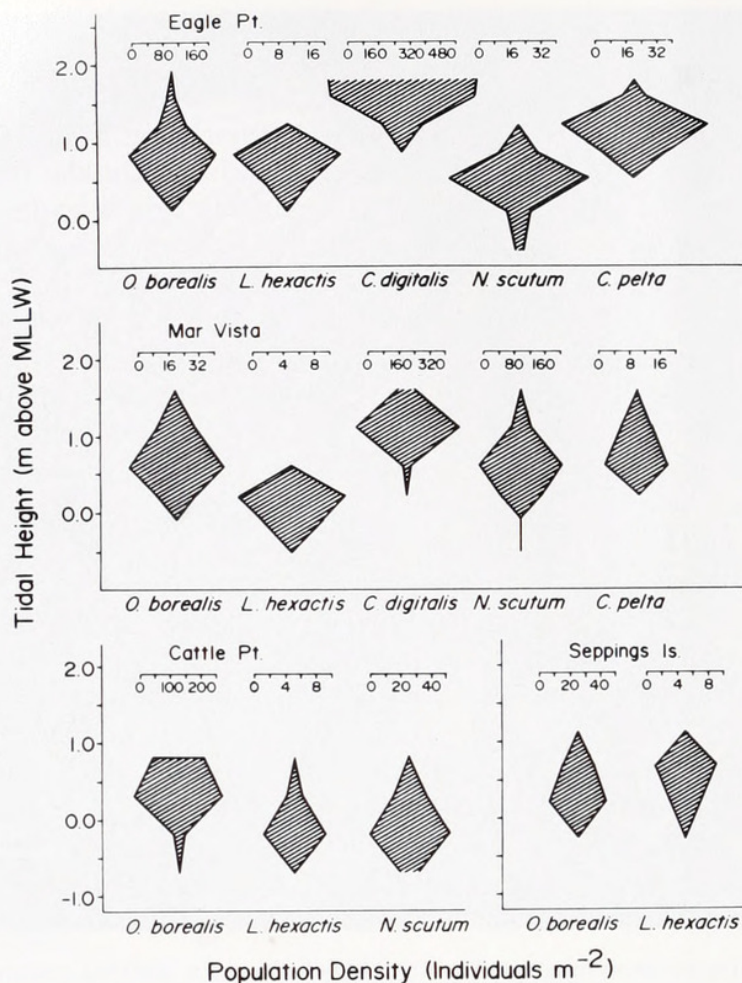


FIGURE 2. Vertical distributions of *Onchidella borealis*, *Leptasterias hexactis*, and associated limpets at four intertidal sites. Seppings Island is in Barkley Sound, British Columbia. All other sites are on the west side of San Juan Island, Washington state.

the more exposed site, only one *L. hexactis* was found, next to a holdfast. An average of 28.6 *O. borealis* (range: 13–64; $n = 8$) occurred in each holdfast. At the less exposed site, which was 200 m from the other site, higher densities of *L. hexactis* were found. *Leptasterias hexactis* in holdfasts were significantly smaller (mean = 12.9 mm; $n = 9$) than individuals occurring in cracks (mean = 44.3 mm; $n = 12$; $P < 0.001$, Mann-Whitney U-Statistic; Sokal and Rohlf, 1981). At the less exposed site, *O. borealis* were found primarily in shallow cracks above the level of the *L. hexactis*. Only one holdfast contained any *O. borealis*. The two species were never found within the same holdfast at either site.

Limpets, which occurred abundantly at all sites, showed a characteristic zonation pattern (Fig. 2). *Notoacmaea scutum* occupies virtually the identical zone as *O. borealis*. The lower limit of *Collisella pelta* is slightly higher than that of *O. borealis* and *N. scutum*, though the upper limit is at approximately the same level. *Collisella digitalis* overlaps the other species slightly, but peaks in its distribution much higher than *O. borealis*, *L. hexactis*, or any of the other limpets. These distributions suggest that all of the mollusc species except possibly *C. digitalis* should be available to *L. hexactis* as food.

Predatory invertebrates occurring in the same zones as *O. borealis* included asteroids, decapod crustaceans, fish, small polychaetes, nemerteans, and thaliid gastropods. Predation on *O. borealis* was never observed in the field.

TABLE I

Response of the polyclad flatworm Notoplana atomata to a dilute solution of repugnatorial gland secretion applied dorsally and ventrally

Substance applied	Surface	Response	No response
R. G. secretion	Dorsal	17	3
	Ventral	5	15
Seawater	Dorsal	0	20
	Ventral	0	20

A response consisted of "writhing" or active undulation of the margin. All of the two-way interactions are significantly different from random (Three-way log-likelihood [G] test: Sokal and Rohlf, 1981).

Encounters between Onchidella borealis and potential predators

Specimens of *Onchidella borealis* showed no response to *Notoplana atomata* and were never seen to fire their glands in response to the flatworm. Thick mucus removed from the ventral surface of the worms with a probe also did not elicit firing, though the snails curled their bodies in response to the mucus application. *Notoplana atomata* specimens demonstrated no apparent behavioral changes when encountering *O. borealis* in the laboratory ($n = 50$ trials with 5 individuals). Likewise, they seldom responded when placed in a small pool of seawater containing repugnatorial gland secretion (hereafter referred to as RGS). When RGS was applied dropwise to the dorsal surface, however, the worms undulated their margins rapidly (Table I). All of the two-way interactions in the contingency table were significant (Table I). Thus, RGS produces a different response than seawater, and worms respond differently to application of solution to the dorsal surface than to ventral application.

The hoplonemertean *Paranemertes peregrina*, which commonly occurs with *O. borealis* in Grappler Inlet, generally did not change course when encountering *O. borealis* in its path (4 course changes in 50 trials). The worms hesitated slightly when first encountering the snails, then resumed their course. The hesitation observed was not different from that seen when a worm encountered an inanimate object such as the blunt end of a pin. As *P. peregrina* dragged its body across the margin of *O. borealis*, the latter fired repugnatorial glands, but the secretions had no apparent effect on the speed or direction of locomotion of the worm. Worms were induced to respond (by changing their paths) by pipetting concentrated RGS directly on the head (27 course changes in 35 trials); seawater pipetted in an identical manner as a control had no effect (0 course changes in 35 trials). The interaction between the stimulus (RGS vs. seawater) and response (course change vs. no course change) was significant ($G = 66.986$, 2 d.f., $P < 0.001$).

Individuals of the gastropod *Searlesia dira* (4.56 ± 2.16 g wet wt.; variances reported here and subsequently are 1 Standard Deviation) altered their crawling paths in only 3 of 25 encounters with *O. borealis*. *Thais lamellosa* (13.82 ± 1.11 g wet wt.) changed its path in 4 of 25 staged encounters. More often, the shelled snails would crawl over *O. borealis*, or *O. borealis* would crawl up on the shell of the snail. Repugnatorial gland secretion applied to exposed regions of the head of the two gastropod species elicited retraction in 3 of 25 trials. Seawater elicited a similar retraction once in *S. dira*. The repugnatorial glands did not fire in most encounters between shelled gastropods and *O. borealis*.

The anomuran crab *Petrolisthes cinctipes* (range of wet weights: 0.72 g to 3.56 g) never consumed *O. borealis* in our experiments. Pooled results of the 5-hour experi-

TABLE II

Live and dead Onchidella borealis consumed, damaged, and not eaten by *Hemigrapsus nudus*

Prey condition (beginning)	Prey condition		
	Intact	Eaten	Damaged
Live	43	8	9
Dead	28	21	11

Data are pooled from 20 replicate pairs of dishes, each dish containing either three live or three dead *O. borealis* and one crab at the outset. The distribution of counts within the table differs significantly from random ($G = 9.44384$; $P < 0.01$).

ments with *Hemigrapsus nudus* (2.78 ± 1.00 g wet weight) are given in Table II. A few live *O. borealis* were eaten or damaged by the crabs, but significantly more dead ones were consumed. This suggests that although the defensive secretions of *O. borealis* are not completely effective against *H. nudus*, they probably reduce mortality. In many of the cases where animals were partly consumed (damaged), the foot and soft internal viscera were consumed and the mantle margin, where repugnatorial glands are located, was left intact.

The intertidal fishes used in laboratory trials, *Gobiesox meandricus* and *Apodichthys flavidus*, measured 7.3 ± 2.8 cm and 11.2 ± 3.6 cm long, respectively. In two identical runs with each species, each lasting five hours, and including five *Onchidella borealis*, none was eaten or mutilated.

The most dramatic responses to *O. borealis* were demonstrated by small asteroids. Total armspans of the individuals used are as follows: *Leptasterias hexactis*, 4.68 ± 0.54 cm; *Pisaster ochraceus*, 5.75 ± 1.77 cm; *Henricia leviuscula*, 9.85 ± 1.91 cm. Figure 3 shows a typical encounter sequence between *L. hexactis* and *O. borealis*. The glands of *O. borealis* almost always fired upon first contact with an asteroid tube foot. Often the margins of the mantle were flexed so that the gland openings were pointed upward toward the tube foot. Only the glands in the immediate vicinity of the tube foot fired. When the secretion touched the asteroid, the starfish began moving in another direction while simultaneously lifting the affected ray. Within the next few seconds, the ray was lifted to a vertical position, or sometimes flexed completely so that the aboral surface of the ray contacted the aboral surface of the disk. The responses of three asteroid species to live and dead *O. borealis* are given in Table III. In general, the starfish did not respond to dead snails and there were interspecific differences in the level of response to live snails (Table IV). *Henricia leviuscula* responded in the same manner as *L. hexactis* and *P. ochraceus* but less frequently and less dramatically. On one occasion, we exposed a small (20 cm diameter) subtidal asteroid, *Solaster stimpsoni*, to *O. borealis*. The starfish, which was at least two orders of magnitude larger than the snail, responded by curling its ray to the aboral side of the body. Repugnatorial gland secretion applied with a pipette to the ray of *L. hexactis* elicited the same response as a living *O. borealis*.

Experiments on the Leptasterias/Onchidella interaction

When *L. hexactis* were offered a choice of molluscan food items from the intertidal zone (*O. borealis*, *Collisella digitalis*, *Notoacmaea scutum*), they demonstrated a predictable hierarchy of preferences in both laboratory and field trials (Fig. 4). *Onchidella borealis* were never consumed. The most frequently consumed prey was the

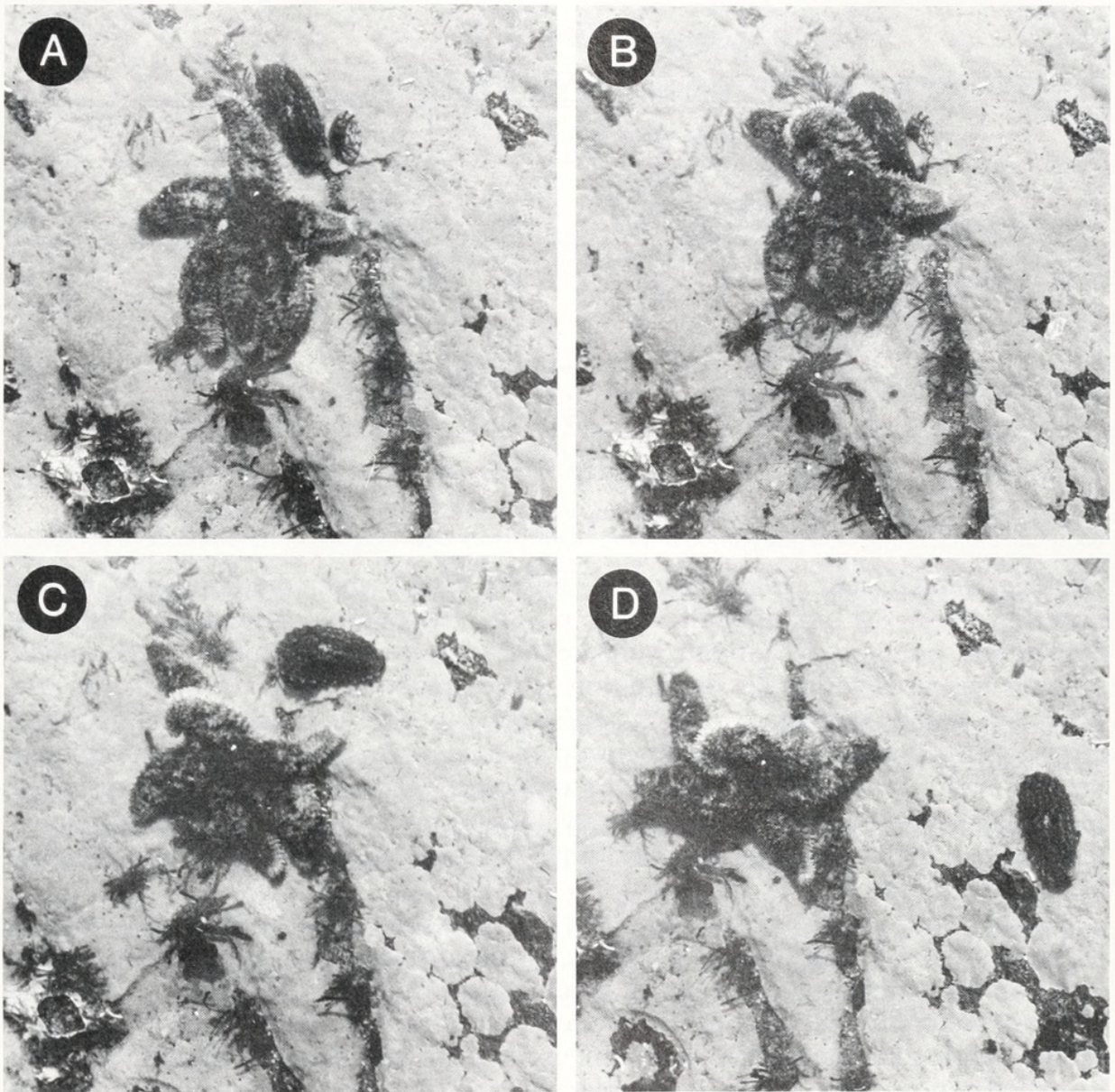


FIGURE 3. Staged encounter between *Onchidella borealis* and *Leptasterias hexactis* in a tidepool. A: Starfish touches *O. borealis* with tube feet; repugnatorial glands fire. B: Starfish curls arm aborally in response to secretions. C: *O. borealis* reverses direction of crawling while starfish remains stationary. D: *L. hexactis* continues to hold arm off substratum.

high intertidal limpet *C. digitalis*. *Notoacmaea scutum*, a limpet that occupies the same level of the intertidal zone as *L. hexactis* and *O. borealis*, was never consumed in laboratory experiments, but several individuals were taken during the neap tide period in the field experiments, possibly after the *C. digitalis* had all been consumed.

In the laboratory, there was a significant difference in the number of *L. hexactis* specimens remaining within holdfasts in the presence and absence of *O. borealis* (Fig. 5). Where *O. borealis* were present, the majority of starfish abandoned the holdfasts within the 2-h experimental period. Field experiments produced essentially the same result, except that the overall number of starfish remaining was lower than in the laboratory (Fig. 5).

DISCUSSION

Although interactions between molluscs and their potential predators have been studied extensively (for reviews see: Thompson, 1960; Edmunds, 1966; Todd, 1981;

TABLE III

Responses of three asteroid species to live and dead *Onchidella borealis*

Predator species	Condition of prey	Response				
		Aboral curl	Arm lift	Lateral movement	Combination	None
<i>Pisaster ochraceous</i>	live	1	26	15	5	3
	dead	0	0	2	0	48
<i>Leptasterias hexactis</i>	live	5	30	7	6	2
	dead	0	0	9	0	41
<i>Henricia leviuscula</i>	live	0	15	11	3	21
	dead	0	0	0	0	0

Responses are broken down into four categories. For the analysis in Table IV, all responses are pooled.

Faulkner and Ghiselin, 1983), these data are the first in which predator-prey interactions have been documented for a large number of potential predators of intertidal Onchidiids. In addition, our data indicate that the defensive secretion of *Onchidella borealis* has an effect on the distribution of the predatory seastar *Leptasterias hexactis*. The results indicate that *O. borealis* does not fire its repugnatorial glands in response to all potential predators, nor do all potential predators demonstrate flight behaviors in response to the glandular secretions of *O. borealis*. The most dramatic responses are found in intertidal asteroids that occupy the same approximate intertidal zone as *O. borealis* and consume small molluscs (primarily limpets) as a major portion of their diets.

Onchidella borealis did not fire their repugnatorial glands when encountering large polyclad turbellarians (*Notoplana atomata*) or when covered in flatworm mucus, even though the worms may be predators on *O. borealis* (E. P. M. Yau, pers. comm.). *Notoplana atomata* are sensitive to repugnatorial gland sections, but only on the dorsal side; the thick ventral mucus seems to effectively block the secretions in natural encounters. It may be significant that the only place in Barkley Sound where we have found *Notoplana atomata* abundant is in the same inlet and intertidal zone where the highest density of *O. borealis* is found. Additional work on the diet of the worm is needed.

The nemertean *Paranemertes peregrina* is sensitive to repugnatorial gland secretions only in the head region, even though the entire body of the worm stimulates firing of the repugnatorial glands. In the encounters we observed, the nemertean

TABLE IV

Log-likelihood analysis of the responses of three asteroid species to live and dead *Onchidella borealis*

Source of variation	d.f.	G	P
Species \times prey condition	4	24.656	0.05
Species \times response	4	41.717	0.01
Prey condition \times response	3	218.066	0.001
Species \times prey condition \times response	2	1.015	ns

Raw data (Table III) are pooled into two response categories (response, no response) for the analysis.

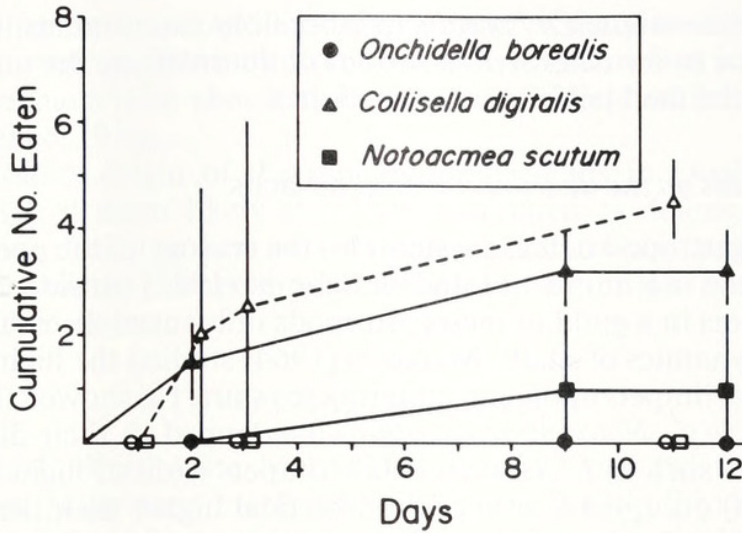


FIGURE 4. Cumulative number of *Onchidella borealis*, *Collisella digitalis*, and *Notoacmea scutum* consumed by *Leptasterias hexactis* in laboratory (solid lines and points) and field (broken lines and open points) experiments in which prey were replaced as eaten. Error bars are standard deviations. In lab trials ($n = 2$), each bowl contained 10 individuals of each potential prey species. Field cages ($n = 2$) each contained three individuals of each prey species.

never attacked *O. borealis* and seldom changed the direction of its movement in response to the snails. Predatory shelled snails, *Searlesia dira* and *Thais lamellosa*, showed no response to *Onchidella borealis*.

Onchidella borealis were apparently palatable to crabs (*Hemigrapsus nudus*); the crabs consumed dead snails readily in laboratory experiments. Live *O. borealis* were consumed less frequently, suggesting that the repugnatorial glands may reduce the predation pressure by crabs. However, our experiments with the crabs do not distinguish between the actual effects of the repugnatorial glands and other factors associated with live animals such as crawling behaviors, actively modified distributions,

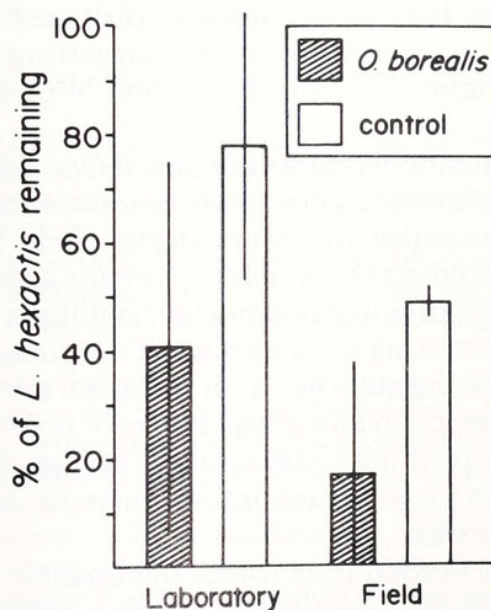


FIGURE 5. Percentage of *Leptasterias hexactis* remaining in holdfasts containing *Onchidella borealis* and no *O. borealis* in the laboratory and the field. Error bars are standard deviations.

etc. Fishes did not consume *O. borealis* in laboratory experiments, though it is not clear if this was due to the defensive secretions of the snails, to the unnatural laboratory setting, or to the food preferences of the fishes.

Effects of O. borealis on the distribution of L. hexactis

The effects of gastropod defense systems on the ecology of the potential prey species have been tested in a number of studies. Schmitt (1982) considered how different defense mechanisms in a guild of mesogastropods influenced distributional patterns and population dynamics of snails. Margolin (1964) studied the flight behaviors displayed by intertidal limpets upon encountering sea stars. He showed that species with effective defenses (e.g., *Notoacmaea scutum*) overlapped in their distribution with potential predators such as *L. hexactis*, while limpets without flight behaviors (e.g., *Collisella digitalis*) occupied a level of the intertidal higher than the predators. We found the same thing in this study. Like *N. scutum*, *O. borealis* are defended well against *L. hexactis* and overlap the predator in its distribution.

Rice (1985) has shown that a defensive mucus of the marine pulmonate *Trimusculus reticulatus* protects the snail from predation by the asteroid *Pisaster ochraceus*. However, Rice (1985) reports that, in the field, these two species commonly overlap in their distribution and can be found together in the same crevices. Conversely, our experiments suggest that although the distribution of *O. borealis* is not limited by predators, the small-scale distribution of the predatory asteroid *Leptasterias hexactis* may be influenced by high density populations of *O. borealis*. At some sites, the density of *L. hexactis* was highest just below the level of peak *O. borealis* density, but elsewhere, the two populations peaked at the same level (Eagle Pt.) or were juxtaposed (e.g., Seppings Island). Thus, the upper limit of *L. hexactis* appears not to be set by *O. borealis*. The definitive experiment would be to remove all *O. borealis* from a stretch of shoreline, then note any changes in the vertical distribution of *L. hexactis*.

Both *O. borealis* and small *L. hexactis* appear to use the holdfasts of *Hedophyllum sessile* as refuges. Onchidiids are readily knocked off the substratum by waves (Arey and Crozier, 1921) so the holdfasts probably serve as buffers from wave shock. Water motion is probably less critical for *L. hexactis*, as they cling securely to rocks and feed actively at high tide (Menge, 1972). Only small starfish are found within holdfasts of *H. sessile* and *Nereocystis luetkeana* specimens, suggesting that refuges from some unidentified source of mortality (perhaps desiccation or predators) are important to juvenile *L. hexactis*.

We have shown experimentally that specimens of *Onchidella borealis* have a negative effect on young individuals of *Leptasterias hexactis* within the holdfasts, probably because the latter are expelled by repugnatorial gland secretions. Although *L. hexactis* individuals leave holdfasts to which *O. borealis* have been added, it is likely that in the field, *L. hexactis* individuals never enter holdfasts occupied by *O. borealis* specimens. It would be interesting to determine if *O. borealis* returns to the same holdfast repeatedly, just as congeners home to the same crevice (McFarlane, 1980). If so, a given holdfast may be occupied exclusively by *O. borealis* for very long periods of time. Scarcity of unoccupied holdfasts in areas of high *O. borealis* density may increase mortality of *L. hexactis* juveniles or force them to occupy other refuges such as holdfasts lower in the intertidal.

Additional field work is needed to consider the possible effect of *O. borealis* on aspects of *L. hexactis* ecology. *Leptasterias hexactis* individuals use crevices for brooding their young (Chia, 1966; Menge, 1974) and as a refuge from competition with the larger forcipulate *Pisaster ochraceus* (Menge, 1974). Large numbers of *O.*

borealis occupying crevices could limit the amount of space available to *L. hexactis*, thus forcing the small starfish into more competitive encounters with *P. ochraceous*. Such encounters have been shown to decrease the individual fitness of *L. hexactis* (Menge and Menge, 1974).

The evolutionary origin of the repugnatorial glands in *Onchidella borealis* is unknown, though it seems likely that they originated as defensive structures. At present, they may function not only in defense, but as competitive "equalizers" allowing *O. borealis* to compete successfully for a limited microhabitat in the crowded intertidal zone.

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