CHEMICAL ATTRACTION OF NEWLY HATCHED OYSTER DRILLS

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ABSTRACT

Newly hatched oyster drills, *Urosalpinx cinerea* (Say), that had not eaten prey and had no prior experience in prey detection, were used to screen 25 potential attractants. Of these, odors of intact, living barnacles, *Semibalanus balanoides* and *Balanus eburneus* were most effective, optimally causing upstream migration in over 90% of the snails and retaining detectable activity after 200 fold dilution. The odor of a mixed bryozoan culture evoked a 70% and *Sabellaria vulgaris* a 30% response, whereas responses to *Crassostrea virginica*, oyster valves containing *Polydora websteri*, and *Trypetesa lampas* were low but still significant. Both rheotactic and chemotactic factors were involved in the upstream migration. Behavior reminiscent of trail search was observed in homogeneous dilute stimulus solutions. It is argued that the odor stimuli may be discrete molecules.

INTRODUCTION

The oyster drill *Urosalpinx cinerea* (Say), a predatory muricid gastropod, uses distance chemoreception (for reviews, see Carriker, 1955, 1957; Blake, 1962; Wood, 1968; Pratt, 1974; Ordzie and Garafalo, 1980) to locate a variety of shelled, sessile or virtually sessile prey (Carriker, 1955). Stimulated by an odor, the snail creeps upcurrent, locates the prey, grasps it with its foot, bores through the shell, and consumes the flesh (Carriker, 1955, 1969).

Indiscriminate consumption by *Urosalpinx cinerea* of commercially important species, its extreme hardiness, and *U. cinerea* densities from tens of hundreds per square meter (Carriker, 1955; Hancock, 1959; Wood, 1968) have resulted in numerous drill control attempts. For more than half a century control attempts have been marginally successful (Carriker, 1955). Chemical control by poisons has been unacceptable. There is a clear potential for chemical control based upon the mechanism of attraction to prey.

Results of several studies showed acute distance chemoreception of prey by *Urosalpinx cinerea* (Blake, 1962; Wood, 1968; Pratt, 1974; Ordzie and Garafalo, 1980). Blake (1960) demonstrated that stimulus potency is related to the metabolic activity of the prey. Wood (1968) and Pratt (1974) found that chemotactic responses are modified by diet, a phenomenon described as ingestive conditioning. Efficient testing of adult snails is impeded by their large size, slow speed, state of sexual receptivity and prior feeding experience.

Newly hatched drills have no prior predatory experience, show no cannibalism while in egg capsules, are sexually indifferent (an added bonus, see Wood, 1968) voracious miniature versions of the adult (Carriker, 1957), and should exhibit behaviors unmodified by experience (Carriker, 1957; Thorpe and Jones, 1937). They

Received 28 March 1981; accepted 25 March 1983.

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are excellent for low volume bioassays, being about 1 mm in shell height, and more active than adults (Carriker, 1957). Finally, newly hatched drills may be susceptable to biocontrol as they desiccate in a few hours (Carriker, 1957), and will starve to death in a few days at 23°C.

Egg capsules are deposited as long as adult snails remain active, and those deposited in late fall may over winter. One to fifteen newly hatched drills can be obtained from each egg capsule (Hancock, 1956). Thousands of capsules can be readily collected in the field by scraping them from firm substrates to which they are characteristically attached. Development of embryos in capsules can be either retarded by lowering, or accelerated by raising the temperature (Hancock, 1956). A laboratory hatchery of several tens of thousands of egg capsules occupying about two m³ of space can provide hundreds to thousands of fresh bioassay animals through most of the year.

This paper reports the results of a study designed to assess the potential for chemical control of depredation of the oyster *Crassostrea virginica* (Gmelin) by the oyster drill, *Urosalpinx cinerea*. Our objectives have been to develop a bioassay suitable for biochemical characterization of the molecules responsible for distance attraction of newly hatched snails and to determine potent sources of attractants.

MATERIALS AND METHODS

Egg capsule procurement and treatment

Urosalpinx cinerea egg capsules containing embryos at all stages of development were collected at the inner breakwater in Delaware Bay at weekly intervals between mid-June and October of 1980. Capsules were transported to the laboratory where they were cleaned of debris and stored in 28 g aliquots (~1000 capsules) at 18°C in 15 cm diameter finger bowls containing 200 to 400 ml of filtered (1 μ m) sea water. Rates of hatching and development were regulated by temperature (Hancock, 1956). At peak production there were approximately 30,000 egg capsules in the hatchery and 400 to 2,000 snails hatching daily. Newly hatched drills were stored, about 200 at a time, without food in 20 ml plastic cuvettes with plankton screening at both ends to allow exchange of water and metabolites. Cuvettes were stored in finger bowls of filtered sea water.

Stimulus preparation

Odor donor species were collected in local Delaware habitats, when possible, immediately prior to use. Animals not used immediately were stored for 1 to 2 days in the laboratory recirculating sea water system at 20 to 23°C.

Sea water (salinity 31 to 33‰) was trucked at biweekly or shorter intervals from the Indian River Inlet, Delaware, and stored in a 3000 liter holding tank separate from the main laboratory circulating sea water system at 21°C. At intervals, this sea water was pumped through a series of filters, the final one being a 1 μ m filter (Filterrite Corp., Timonium, MD). Filtered water was stored in 20 liter and 40 liter glass carboys until used.

Odors were prepared by placing a known wet weight of whole live organisms (1 to 800 g when possible $\simeq 200$ g whole wet weight) in a 4 liter aquarium, filling it with 1 μ m filtered sea water, and allowing it to stand at room temperature with aeration. Most odors were tested after standing for 2 to 4 h. Subsequently, the aquarium was refilled and the water tested again after standing for 18 to 24 h. In

the case of small biomasses (*e.g.*, the barnacle *Trypetesa lampas* and single prey individuals) volumes of sea water were reduced correspondingly.

Biomass of organisms used as stimulus sources varied widely. Serial dilutions of sea water from each potential source were tested to ensure a highly concentrated attractant was not overlooked. Relative strengths of active attractant preparations were determined on a gram live weight basis.

Test apparatus

The assay apparatus consisted of a solution reservoir connected to a flow regulator (Gilmont #2 flowmeter), a stop valve, an assay chamber, and a collection system fitted with a siphon relief. Components were connected by tygon tubing. Assay chambers were modified from a matched set of 2 ml borosilicate glass pipettes. Pipettes were chosen because the 0.1 ml divisions were 10 mm apart facilitating computation of distance traveled by snails, flow discharge, and current velocity. Tips of pipettes were removed at the 1.8 ml mark, mouthpieces were removed 2.5 cm above the 0 ml mark, and a right angle bend was added to the pipette so that the apex of the bend was at the 0.1 ml mark. All freshly formed edges were firepolished. The 1.8 ml end of each pipette was fitted into a tygon sleeve and could be readily rotated so that the bend in the pipette could be oriented with the open end of the pipette in any position between up and down. In the loading position the open end was up; in the running position the open end was down. During a run the downstream end could be connected to the collection system. The volume of the system, from the stimulus reservoir to the tip of the downstream end of the assay chamber, was 35 ml. In most experiments, four complete assemblies were used simultaneously.

Assay procedure

In the bioassays we used recently hatched Urosalpinx cinerea (collected from the capsules within three days) as test animals. All test animals were allowed to equilibrate to ambient temperatures (20-23°C) before an assay. Each test animal was used only once to eliminate any effects of prior exposure to the apparatus or to stimulus water. Preliminary tests were conducted at a variety of flow rates using the endogenous stimulus activity (no added stimulus) of freshly trucked sea water from Indian River Inlet. After several initial experiments with mixed prey stimulus, flow discharge was set to 7.5 ml/min, unless otherwise indicated. Each assay run was initiated by rotating the assay chamber into the load position, filling the chamber with test solution by opening the valve, closing the valve, and loading 10 to 40 test snails into the bore of a test chamber with a camel's hair paintbrush. Flow was restarted at Time 0. At this time the pipette was rotated to a position intermediate between run and load for 45 s. The 45 s period allowed each group of test animals to stabilize in the pipette. Snails landing on their foot attached immediately, and those landing on their shell generally attached within seconds (in agreement with Carriker, 1957). Any snail that crossed the 0.2 ml division of the pipette within 10 min after the start of flow was counted as a positive response. Those snails that attached but did not cross the 0.2 ml division were counted as not responding (Fig. 1). The distance chosen for a positive response effectively separated aroused and creeping snails from those that were just changing position. This distance was often traversed in less than 1 min by aroused snails. At least 35, and usually 50 or more



FIGURE 1. Pipette bioassays for chemotactic response of juvenile snails (1-2 mm shell height) to barnacle stimulus. Snails in top pipette migrate upcurrent in sea water bearing barnacle scent, while those in lower pipette remain stationary in a current of filtered, scent-free sea water. Load zone indicated by A and bracket. Positive response criterion 0.2 ml mark (B).

snails were tested in two or more replicate runs for all test solutions. The standard assay procedure was improved by reducing the background stimulus activity of filtered sea water by allowing it to stand several days. Response of snails to background cues was reduced four-fold from 20% to about 5% (G = 441.7 P < 0.005). This significant reduction in "noise" greatly improved the sensitivity of the assay.

Experiments and observations

Three series of experiments were performed. The first defined bioassay conditions. The effect of current velocities from zero to 360 cm/min was tested on the response of newly hatched snails to sea water with low endogenous attractant activity. Seven current velocities were examined with 100 snails each. The second series screened potential sources of attractant of Urosalpinx cinerea. It began with a mixed prey source and then tested individual species from that source. Finally other untested species were screened for attractant production. The mixed prey tests included: oysters (Crassostrea virginica), mussels (Mytilus edulis), barnacles (Balanus eburneus and Semibalanus balanoides), hydrozoans (Eudendrium sp.), polychaetes (Polydora websteri), and miscellaneous amphipods, isopods, and decapod crustaceans. In addition, during storage, sessile organisms had been in contact with the American eel, Anguilla rostrata, and the blue crab, Callinectes sapidus. Water from this mixed population was compared to a 1 µm filtered sea water control. Next, a series of filter feeding organisms were tested. Included were: hard clams (Mercenaria mercenaria); slipper limpets (Crepidula fornicata and C. plana); bay scallops (Argopecten irradians); small barnacles (Trypetesa lampas), which burrow into the columella of gastropod shells inhabited by hermit crabs; goose neck barnacles (Trilasmis inaequilaterale); and infaunal razor clams (Tagelus plebeius). After the series of tests with filter feeding organisms, additional organisms were screened that had not been tested and might release either attractants or molecules that could produce negative

CHEMICAL ATTRACTION OF OYSTER DRILLS

chemotaxis. Included were potential predators of oyster drills [lobsters (*Homarus americanus*); starfish (*Asterias forbesi*); and whelks (*Busycon carica*)], conspecifics, potential prey [periwinkles, (*Littorina saxatilis*)], tube worms (*Sabellaria vulgaris*), a mixture of encrusting bryozoans (*Membranipora tenuis* and *Schizoporella irror-ata*), and hermit crabs (*Pagurus pollicaris*). The third series used the most potent attractant and examined the effects of stimulus strength and flow on the creeping response of newly hatched snails.

Statistical analysis

Paired contingency comparisons were employed. Responding and nonresponding snails in an experimental group were compared to the same categories in a control group by the G statistic adjusted for unequal sample size and continuity (Sokal and Rohlf, 1969). Controls used to make comparisons were either the response to no added stimulus or to a 1:1000 dilution of a stimulus. The acceptance level chosen was P < 0.005. If G values with corresponding probabilities of 0.005 < P < 0.05 were obtained, experiments were repeated. By these criteria we theoretically made a type I error (*i.e.*, rejecting the hypothesis that frequency of response is independent of stimulus) in about 1 out of 100 tests.

RESULTS

To define the bioassay and to screen potential stimulus sources we performed 248 experiments testing 31,810 newly hatched *Urosalpinx cinerea*. These experiments were designed to investigate parameters a through g as follows:

a. Current velocity

Response of snails to flow increased dramatically from 3% with no-flow to about 20% with a current velocity of 30 cm/min (Fig. 2). There was a more gradual increase in percent response to current velocities from 30 cm/min to 190 cm/min. Maximal response of 33% for any of the current velocities tested was achieved at a velocity of 190 cm/min. The highest current velocity tested, 360 cm/min, resulted in a



FIGURE 2. Response of newly hatched snails to increasing current velocity with constant background stimulus activity. The assay interval was 10 min and the assay criterion for a positive response was extension of the tip of the siphonal canal beyond the 0.2 ml division of the assay chamber. Test animals that did not move this distance, but that attached were counted as non-responders. Bars represent 95% confidence limits for the samples.

decrease in the rheotactic response to 16%. These data established the flow rate of 10 ml/min to be used in studies of chemotactic response of snails to "mixed prey stimulus."

b. Mixed prey stimulus

The mixed prey stimulus was significantly (P < 0.005) active (Fig. 3) at three flow rates (100 cm/min, 86 cm/min, and 75 cm/min) and stimulated about 50% of the newly hatched snails to creep upcurrent.

c. Components of mixed prey stimulus

Experiments then assessed the contribution of each of the major species of mixed prey stimulus to the observed chemotactic response of the snails. The most potent stimulus came from barnacles. In addition to highly significant statistical results, the response of the snails to low dilutions of barnacle stimulus water was greater than 80%, and stimulus water could be diluted 200-fold or more (Fig. 4) and still retain significant (G test P < 0.005) activity. Both living *Crassostrea virginica* and empty valves of *C. virginica* containing *Polydora websteri* produced statistically significant stimulus activity. However, response of newly hatched snails never exceeded 21% (Fig. 3). Dilution of oyster stimulus water beyond 10-fold eliminated the response. Water from *P. websteri* in empty oyster valves lost significant activity at any dilution. Snails did not respond to the other 4 species tested.



FIGURE 3. Maximal percent response obtained to concentrations of every potential stimulus effluent tested. Responses were grouped into mixed prey, highly stimulatory, significantly stimulatory, non-stimulatory known prey, and nonstimulatory potential prey categories.



FIGURE 4. The response of newly hatched snails to a dilution series of *Balanus eburneus* stimulus water. Seven grams wet weight of barnacles (11 individuals) were placed in 850 ml of 1 μ m filtered sea water and allowed to incubate for two hours. Subsequently the activity response of recently hatched snails was tested over a range of concentrations of stimulus water diluted with 1 μ m filtered sea water. Full strength stimulus was considered as having a value of 1. Assay criterion was the same as that described in Figure 2. Flow discharges were 7.5 ml/min. Point represented by * was actually generated by assay of water with background stimulus activity.

d. Individual species stimulus: filter feeders

The first experiments on stimulus water of individual species suggested that not all potential prey of *Urosalpinx cinerea* release attractants that elicit responses from newly hatched snails. Accordingly, we next tested several additional filter feeding organisms. Only water from *Trypetesa lampas* was marginally active, eliciting a low (15%) but significant (P < 0.005) response from the drills (Fig. 3). Water from the six additional species did not stimulate the newly hatched predators to creep upcurrent.

e. Individual species stimulus experiments: other organisms

Of the 8 potential sources tested, only mixed bryozoans and tube worms produced attractants. Waters from mixed bryozoans stimulated up to a 70% response and were active when diluted tenfold. A stimulus associated with tube worms was active only when diluted 10-fold, and evoked a greater than 30% response. No obvious negative responses were made by snails to water from any of the potential predators and no other positive responses were observed.

In summary, screening experiments showed high percentage responses of newly hatched snails to chemoattractants released by intact living barnacles and bryozoans (Fig. 3). In addition, low potency chemoattractants were detected in water associated with tube worms, oysters, empty oyster valves infested with *Polydora websteri*, and

the barnacle *Trypetesa lampas*. Of the other 19 organisms tested, only the potpourri of mixed prey stimulus containing the "redolent bouquet" (Pratt, 1974) including stimuli from three species with known attractant-producing abilities was active.

f. Effect of flow

After determining that balanoid barnacles were a potent source of attractant, we tested flow discharge and stimulus concentrations. All rates of flow yielded comparable qualitative information about barnacle attractant concentration (Figure 5a). Although higher flows resulted in higher percent responses at high stimulus concentrations, statistical tests of results of all flows resulted in the same conclusions.

At the three highest flow rates, creep rate increased steadily with each increase in stimulus concentration. Creep rate for the lowest flow showed similar steady increases for intermediate stimulus concentrations with maximum at the 1:10 dilution. Creep rate decreased under conditions of low flow and highest stimulus concentration (Figure 5b). Although percent response did not increase at the lower stimulus concentrations, creep rates of those snails that responded were 25% to 78% higher for the three highest flow rates when rates at no added stimulus and the 1:1000 dilution of stimulus were compared. In general, there was high agreement between creep rate and log concentration for all flow rates.

g. Behavior of newly hatched snails

Newly hatched snails when exposed to homogeneous stimulus water raised the shell and waved the siphonal canal back and forth as described by Carriker (1957). In the presence of an active stimulus some individuals immediately raised their

Α



log Stimulus Concentration

FIGURE 5a. Effect of flow discharge on response of newly hatched snails to dilutions of same stimulus. *Balanus eburneus* stimulus was tested at dilutions and flow discharges shown and by standard assay criteria. Points represented by * were actually generated by assay of water with background stimulus activity.



FIGURE 5b. Response of newly hatched snails to various concentrations of *Balanus eburneus* stimulus at different flow discharges. Creep rate, the cm/active snail/min traveled by snails crossing the 0.2 ml division of assay chamber is plotted against log stimulus concentration with undiluted stimulus being taken as 1. * represents assay of water with background stimulus activity.

shells, waved them laterally, and began to creep rapidly, while others remained inactive for varying times and then crept upcurrent. In very dilute stimulus concentrations fewer snails became active, and those that were active did not creep as rapidly as snails exposed to higher concentrations. Exposed to a still weaker stimulus a few snails appeared to be inactive, but, after a 10 min interval, the apparently inactive snails had crept (often in groups but not following each other) up to 1 cm. Some snails crept continuously during the 10 min assay interval over a distance of 16 cm, while others moved for only a small percentage of the time. In the presence of low stimulus concentrations many snails moved upcurrent in a spiral path. In conditions of no stimulus a low percentage crept downstream. In high concentrations, stimulated snails generally crept straight upcurrent.

DISCUSSION

Central in the history of the laboratory study of distance attractants of *Urosalpinx* cinerea has been the choice between water with and without stimulus (Carriker, 1957; Blake, 1962; Wood, 1968; Pratt, 1974; and Ordzie and Garafalo, 1980). In our experiments, rather than requiring that test snails choose between two stimuli, they were scored as to whether or not they moved upcurrent in response to a single homogeneously mixed stimulus (Van Haaften and Verway, 1958; Phillips, 1975; and Lederhendler *et al.*, 1977). Advantages in asking this type of question include a) a homogeneous stimulus source as opposed to a source with unknown mixing characteristics; b) the repeated use of the same test solutions enabling modification and retesting of solutions (important in the isolation and characterization of the

active molecular components); and c) the opportunity to dilute solutions in a precisely defined manner. An anticipated disadvantage, a lack of specificity in the response, did not materialize. Savings in time and volume of stimulus waters when compared with previously published snail bioassay procedures are dramatic. The goal that the bioassay be useful for biochemical characterization of attractant molecules has been achieved.

The question of relative potency of stimuli can only be answered rigorously with purified compounds. However, a working understanding of the relative potencies of active waters is important in deciding which stimulus source to purify. We computed relative potencies of the four most potent stimuli, assuming that there is a linear relationship between stimulus strength and response. This is a conservative assumption as it minimizes differences in relative potencies. Computations show a four-fold difference between the relative potency of barnacle and bryozoan stimuli. Barnacle stimulus is over a hundred times more potent than that of tube worms and several thousand-fold more potent than that of oysters.

Odors from at least ten known prey of *Urosalpinx cinerea* and from many other organisms commonly associated with these snails were tested for chemoattractant activity with newly hatched *U. cinerea* (Fig. 3). Only water from bryozoans and *Balanus* spp. stimulated high percentages of snails to creep upcurrent. Curiously, though, adults of newly hatched snails readily consume all known prey species tested. Therefore, as hypothesized for drills by Pratt (1974) and reviewed for fish and crustaceans by Atema (1977, 1980), mechanisms in addition to distance chemoreception must be employed in the feeding response.

The snail predator-prey assemblage has been co-evolving for millions of years (Shrock and Twenhofel, 1953). We hypothesize that virtually every possible mechanism for chemolocation and for disrupting chemolocation has evolved. Testable mechanisms include: 1) chemical camouflaging as described by Fishlyn and Phillips (1980); 2) chemical diversion, *i.e.*, production of a molecule by one prey species, possibly oysters, that facilitates the predatory response to a second prey species, possibly barnacles (a monosodium glutamate effect) similar to that described by Rombauer and Becker (1973) and 3) chemical anosmia; *i.e.*, production of molecules by prey that render the predator unable to smell. It seems unlikely that the latter two mechanisms would evolve unless they were cost-effective (*i.e.*, by-products of other aspects of metabolism).

Our observation that newly hatched snails are attracted from a distance only to barnacles and bryozoans would appear to be in conflict with published work showing that adult *Urosalpinx cinerea* can locate *Argopecten irradians* from a distance (Ordzie and Garafalo, 1980) and some of our own work (Williams and Brown, unpub.) that demonstrates distance chemoattraction of adult *U. cinerea* to oysters. These apparent discrepancies can be readily explained by invoking the phenomenon of "ingestive conditioning" (Wood, 1968). That is, *U. cinerea* can be conditioned in certain circumstances to locate intact individuals of some species that it has previously consumed, given sufficient ingestive experience. This phenomenon is similar to that observed in feeding of tuna (Atema *et al.*, 1980) and lobsters (Derby and Atema, 1981), and in host location of pea crabs (Derby and Atema, 1980) and scale worms (Dimock and Davenport, 1971). Also, one might hypothesize that attractant preferences are manifested in a developmental sequence, similar to that demonstrated for water snakes, *Nerodia erythrogaster* (Mushinsky and Lotz, 1980).

Solutions presented to snails in the bioassay of this study were homogeneous and contained no concentration gradient. Therefore, the creeping response of snails was a product of the integration of stimulus molecule information with rheotactic information (Van Haaften and Verway, 1958; Phillips, 1975). Under ideal conditions creeping tended to be in a straight line. At other combinations of stimulus and flow, response of snails was not as high and their creeping behavior was also altered. At low stimulus concentrations, for example, responding snails often crept in spiral paths suggestive of a search behavior. A search mechanism would be beneficial to snails for location of potent stimulus trails. A second altered response was observed at high stimulus concentration and low flow. Responses in these conditions were lower than responses observed either at higher flow and the same stimulus concentration suggest that in calm water snails may use either secondary prey location mechanisms that are not dependent upon rheotactic information or that they may stop until a current or eddy provides additional rheotactic information about the location of the prey.

Newly hatched snails must travel a relatively long distance (generally several centimeters) from their capsules to their first prey. In addition to the obvious function of prey location, distance chemoreception hypothetically can serve secondary functions such as dispersal and predation avoidance. The newly hatched snail is probably the major dispersal stage of this species (Carriker, 1957). Furthermore, encapsulation of young stages should provide considerable selective pressure for mechanisms facilitating dispersal and minimizing predation. Other mechanisms functioning to maximize dispersal and minimize environmental hazards include positive thigmotaxis, negative geotropism at summer temperatures, positive phototropism to intermediate light levels, speed of movement, and the ability of young snails to raft on debris or on surface films with the aid of a proportionally large foot (Carriker, 1957). Given that the period associated with hatching is critical in the life history, it should be expected that every sense, including those involved in chemoreception, would evolve to direct newly hatched snails to a predator-free, desiccation resistant, well stocked habitat such as that inhabited by bryozoans and barnacles.

The specificity of response of newly hatched drills could be elicited at the molecular level by either a) a mixture of molecules, a chemical picture (Atema, 1977, 1980), or b) a small number (as few as one kind) of specific molecules, analogous to a word (Rittschof, 1980a, b) much like a hormone, relatively high in information content. Although both mechanisms are probably operative in different chemosensory systems and under different circumstances (and in fact may be logical extremes of the same mechanism), it is likely that the latter mechanism is operative here. Turbulence and mixing in the case of a single type of organism would simply dilute a chemical picture without altering its proportions. However, should more than one type of organism (each with its own molecular mixture of characteristic proportions) occur in an area, then turbulence and mixing would result in a mixture that did not resemble the proportions of any of the individuals. On the other hand, other than modification in background to signal ratio, specific chemical words would arrive at receptors as intact units even in turbulent and diverse environments. The latter requires that snails integrate complex flows with stimulus, which they do readily in flow systems resembling waterfalls and pools. Singular molecular forms carrying distinct messages occur universally in life systems as hormones. These are operative as attractants in slime molds (Bonner, 1959) and in distance chemoattraction of white blood cells (Schiffman et al., 1975; Showell et al., 1976) and in distance chemoattraction of hermit crabs to gastropod predation sites (Rittschof, 1980a, b).

ACKNOWLEDGMENTS

Thanks are extended to Langley Wood for providing the prototype bioassay and for incisive suggestions and stimulating discussions. We are grateful to Mr. Gregory

Gruber, Mr. Lyle Walsh, Mr. Jonathan Pennock and Ms. Josephine Rittschof for assistance in the investigation. We appreciate the loan of the lobsters collected in Delaware Bay by Mr. William Hall, the loan of the burrowing barnacles, *Trypetesa lampas*, also taken in the Delaware Bay by Mr. Todd Kamens, and to Mr. Michael Castagna for specimens of *Argopecten irradians* cultured in the Virginia Institute of Marine Science, Eastern Shore Laboratory, Wachapreague, Virginia. Finally, we would like to thank Dr. Julius Gordon, Mrs. Pamela Palinski, and Mrs. Julie Tigue for their particular contributions to this team effort.

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504

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Rittschof, Dan et al. 1983. "CHEMICAL ATTRACTION OF NEWLY HATCHED OYSTER DRILLS." *The Biological bulletin* 164, 493–505. <u>https://doi.org/10.2307/1541258</u>.

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