

Chemical Recognition of Prey by the Gastropod *Epitonium tinctum* (Carpenter, 1864)¹

BY

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(4 Text figures)

INTRODUCTION

CHEMORECEPTION is thought to be the most primitive and ubiquitous sense in marine invertebrates (WILSON, 1970). It is important in initiating and maintaining numerous interspecific and intraspecific relationships such as host-symbiont recognition, mating behavior and defensive interactions (DAVENPORT, 1966; McCAULEY, 1969; etc.). As early as 1918, scientists noticed that marine gastropods could locate food upcurrent at a distance, and fairly sophisticated experiments were conducted on chemoreception (COPELAND, 1918).

THORSON (1957) observed feeding in the ptenoglossan gastropod family Epitoniidae (Wentletraps). He called the Epitoniidae "temporary parasites," because between feedings they habitually left their host anemone and actively crawled or burrowed in nearby sand. Occasionally snails were found crawling far from the nearest anemone. The epitoniid *Opalia* feeds by everting its proboscis and inserting it into the soft base of *Anthopleura elegantissima* (Brandt, 1835), then sucking the body fluids. Although Thorson found *Epitonium tinctum* (Carpenter, 1864) around the base of *A. elegantissima*, he never observed feeding.

ROBERTSON (1961), after observing the feeding habits of several species of *Epitonium*, concluded that because some species can feed on at least two species of anemone, the snails may be non-specific and feed on any available anemone or other coelenterate. The wentletraps therefore cannot be considered parasitic but must be termed temporary ectoparasites. Further feeding observations on

one species suggested to Robertson that the genus *Epitonium* did not use chemosensory means to locate anemones: "*Epitonium rupicola* reacted to anemones only after being placed in contact with one, seemingly by chance. Thus, tactile stimuli appear to be the major means whereby anemones are located by this foraging wentletrap."

One might well ask why Robertson discarded the possibility of chemical recognition by *Epitonium* without testing it experimentally. Our preliminary observations demonstrated that when specimens of *E. tinctum* were held in still sea water at a distance of about 20 mm from *Anthopleura elegantissima*, snails reacted by extending their proboscises and performing searching movements. *Epitonium tinctum* was never observed extending the proboscis when held in still sea water without the anemone. Therefore, it seemed reasonable to assume that they might be receiving a chemical signal.

HOCHBERG (1971) observed *Epitonium tinctum* feeding daily during high tide periods on the tentacles of *Anthopleura elegantissima* (Figure 1). Initiation of the feeding process occurs by the rapid eversion of an acrembolic proboscis which rolls outward from the mouth, and contains the entire buccal mass. The wentletrap moves the extended proboscis through the water in a searching motion, until it comes in contact with an anemone tentacle. Initial proboscis contact with the tentacle consists of a series of touching and retracting responses by the snail that frequently produce no visible response from the anemone. The snail then either slips the tip of the proboscis over the anemone tentacle or slides the proboscis along the length of the tentacle until, presumably, a suitable location is found. Suddenly, the radula grips the tentacle. The anemone tissue is either cut or torn off by the radula, and upon retraction of the proboscis, in-

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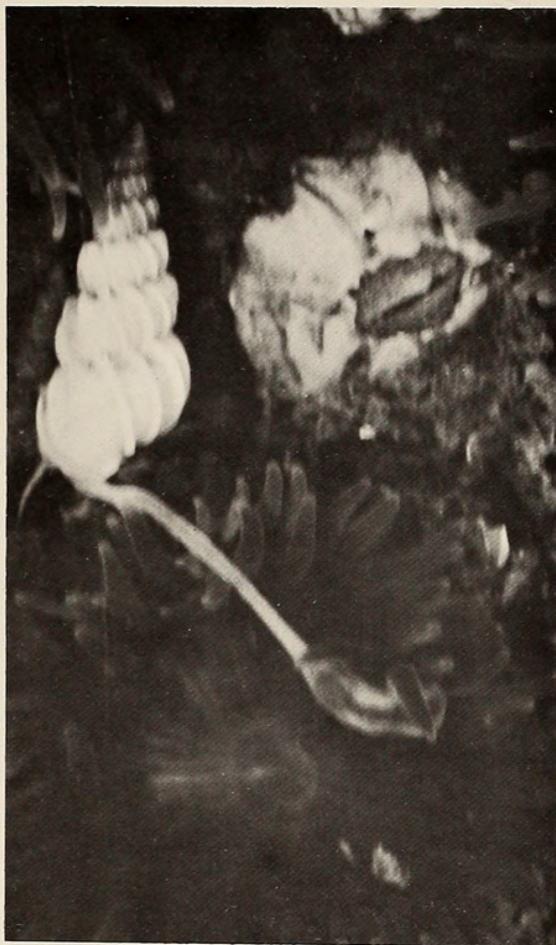


Figure 1

Epitonium tinctum
feeding on the tentacles of *Anthopleura elegantissima*

gested by the snail (HOCHBERG, *op. cit.*). *Anthopleura elegantissima* reacts with a localized tentacle retraction.

The following experiments were designed to determine if chemosensory recognition enables *Epitonium tinctum* to locate its prey, *Anthopleura elegantissima*. The specificity of any chemical attractant emitted from this anemone was tested against chemical emissions from both closely related and distantly related anthozoans to see if they also attract *E. tinctum*.

MATERIAL AND METHODS

Epitonium tinctum is commonly found in close association with sea anemones on rocks along the coast, from British Columbia, Canada, to the Gulf of California (STRONG, 1941). Snails used for the experiments were collected at low tides from the rocky intertidal area of Devereaux

Point, near Goleta, California. They were found either attached to the base of solitary or colonial *Anthopleura elegantissima* or burrowed in nearby sand. Animals were not fed for 24 hours prior to experimental trials because feeding behavior in the laboratory was seldom observed before this time. The snails were able to survive under laboratory conditions for about one week.

Colonies of *Anthopleura elegantissima* are found attached to rocks in wave-exposed areas. They occur chiefly in the mean lower intertidal region. Experimental animals were obtained from Goleta Point, Goleta, California. Individual anemones, attached to plastic containers floating in a large holding tank, and maintained on a diet of *Mytilus californianus* Conrad, 1837, remained healthy for months.

Anthopleura xanthogrammica (Brandt, 1835) is not found in the Santa Barbara intertidal zone. North of Point Conception it is commonly found in tide pools of the rocky intertidal area, where wave action brings an abundant supply of food. It occurs in open coast regions just below the mussel zone. Eight *A. xanthogrammica*, ranging in size from 5 to 12½ cm in diameter were collected at Hopkins Marine Station, Pacific Grove, California, and were shipped to the laboratory in thermos containers. They were maintained in the laboratory under the same conditions as *A. elegantissima* and remained healthy throughout the experimental period.

Tealia lofotensis (Danielssen, 1890) occurs in the Santa Barbara region in the subtidal area on the sides and undersurfaces of large rocks (HAND, 1955). Three small *T. lofotensis*, about 10 cm in diameter, were obtained from the subtidal zone off Goleta Point, Goleta, California. They survived well, attached to glass bowls and fed on a diet of *Mytilus californianus*.

Epiactis prolifera Verrill, 1896 has a wide range of habitat. It is found along the open coast, attached to rocks, seaweeds and eel grass. In the low intertidal region it is particularly common attached to the base of several species of brown algae (HAND, 1955). The *Epiactis* used for experimental purposes were collected in the intertidal region off Devereaux Point, near Goleta, California. A diet of *Mytilus californianus* sustained these animals in the laboratory for about 2 weeks.

The main habitat for *Metridium senile* (Linnaeus, 1767) in southern California is below the tide marks (HAND, 1955). Small *M. senile*, about 30 mm in diameter were brought to the laboratory attached to large *Mytilus californianus* from subtidal regions off Goleta Point. Both anemones and mussels were placed in a 4 l capacity bowl which received a constant supply of air and 20°C sea water. Anemones survived in the laboratory for about 2 weeks.

Corynactis californica Carlgren, 1936 mainly occurs in shallow sublittoral areas, attached to pier pilings or rocks. This colonial anemone species was brought into the laboratory from the pilings of the pier in Goleta State Park, Goleta, California, and placed in glass containers. The animals survived well throughout the experimental period.

Apparatus No. 1: Description and Application

An apparatus was designed and constructed to determine whether *Epitonium tinctum* would orient to various test anemones solely on the basis of chemical stimuli (Figure 2). Sea water from a common source was directed into 3 chambers. The 2 side chambers contained only sea water, while the center chamber housed the anemone to be tested. Effluent from each of the 3 chambers entered one of 3 arms of a plexiglass trough through a regulator valve. The valves could be adjusted to admit flow at an equal rate to each arm of the trough. The floor of the distal end of each arm was depressed 1½ mm to allow for the even flow of incoming water and to trap any particulate matter. Effluent from each arm then met in the stem of the apparatus forming 3 separate parallel streams, a sea water stream running along each side, and the "anemone labeled" stream in the center. Occasionally, fluorescein dye was added to check flow rates. In all controls and all experiments care was taken to scrub the apparatus before each trial to remove any snail secretions.

This apparatus was designed so that when an experimental snail was dropped into the central stream it would receive immediate directional stimulation from the labeled stream only. The function of the 2 unlabeled side streams was to render less likely thigmotactic response to walls, which frequently occurs in the conventional Y-tube apparatus. If the snail moved out of the central stream and into one of the other arms, or out the exit, one could assume they were repelled, or had received no stimulation from the central stream. Thus, a quick, simple, all-or-none response to the central stream stimulus could be tested for. The choices were scored (+) if the snail moved up the labeled stream, and (—) if it moved in any other direction.

One further advantage of this apparatus was that label reaching the experimental snail was less dilute than in a Y-tube apparatus (DAVENPORT, 1950). In a Y-tube, the experimental animal receives stimulation from 2 currents simultaneously, one containing label and the other containing sea water or effluent. Before these 2 currents reach the animal, which is placed some distance

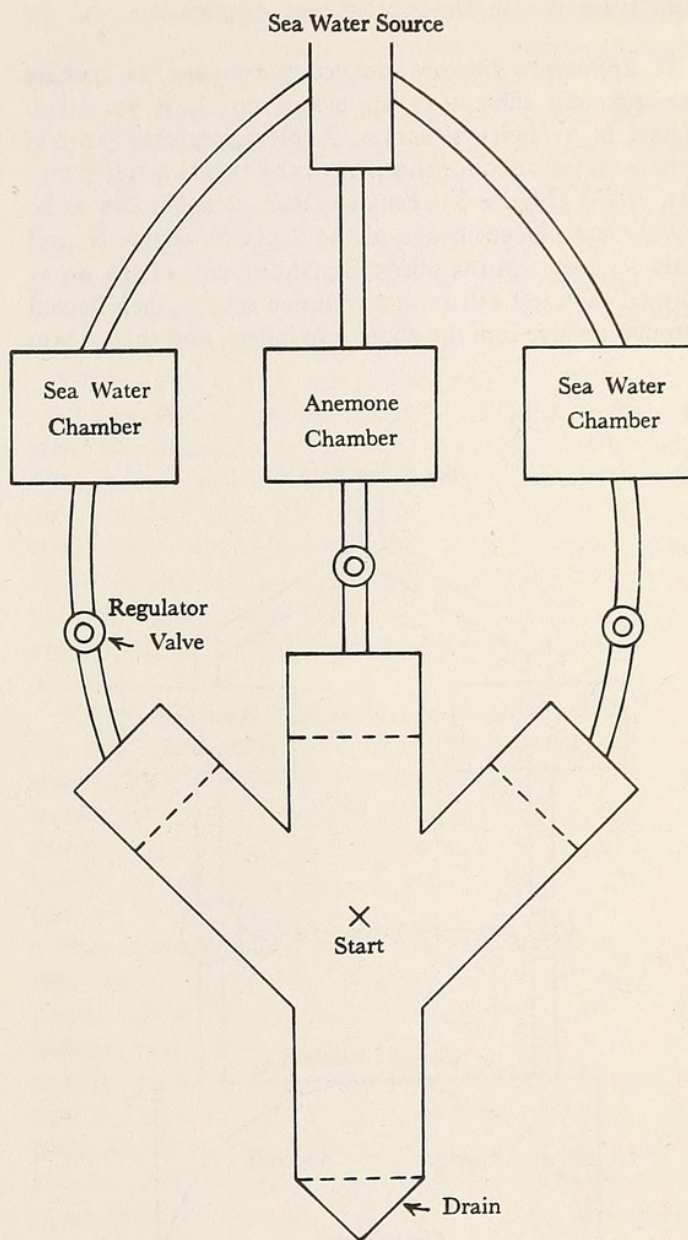


Figure 2
Apparatus No. 1

downstream, they undergo, as a result of turbulence, some mixing and hence dilution. In a single current system, such as apparatus no. 1, an experimental animal receives a maximum concentration of label and it is possible to test for a lower threshold of stimulation than in the Y-tube.

Apparatus No. 2: Description and Application

If *Epitonium tinctorum* showed a response to specific test-anemone effluent in apparatus no. 1, it was then placed in a choice situation. A plexiglass choice-arena apparatus was used for this part of the experiment (STEWART, 1970) (Figure 3). Equal masses of anemones to be tested were placed in one of the 2 plastic test cells, and plain sea water in the other. Equal amounts of sea water entered each test cell from a common source, then flowed through a valve into the choice chambers, and thence into

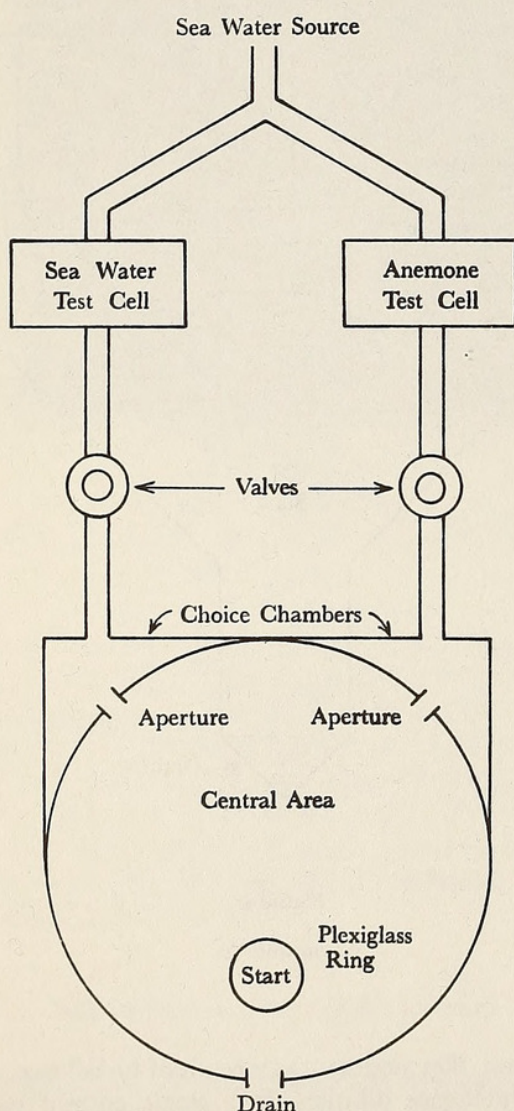


Figure 3
Apparatus No. 2

the 125mm diameter central area. The floor of each choice chamber was depressed 18mm below the level of the aperture into the central arena, in order to trap any solid matter as well as the experimental snails. The entire apparatus could be leveled before trials by means of 4 adjustable screws that formed the legs.

Flow rates were measured by the random addition of fluorescein dye and could be adjusted so that water from the 2 choice chambers would exactly bisect the central arena. An experiment was initiated by placing animals at the center of the arena in a plexiglass ring. The ring was removed at the beginning of each trial ("go"), and the snails were allowed to choose which stream they would follow and aperture they would enter. A (+) was scored if the snail entered the choice chamber with anemone effluent, and a (—) was scored if the sea water choice chamber was chosen. Introduction of anemone effluent to a particular test cell was randomized to control for possible differences in lighting, etc.

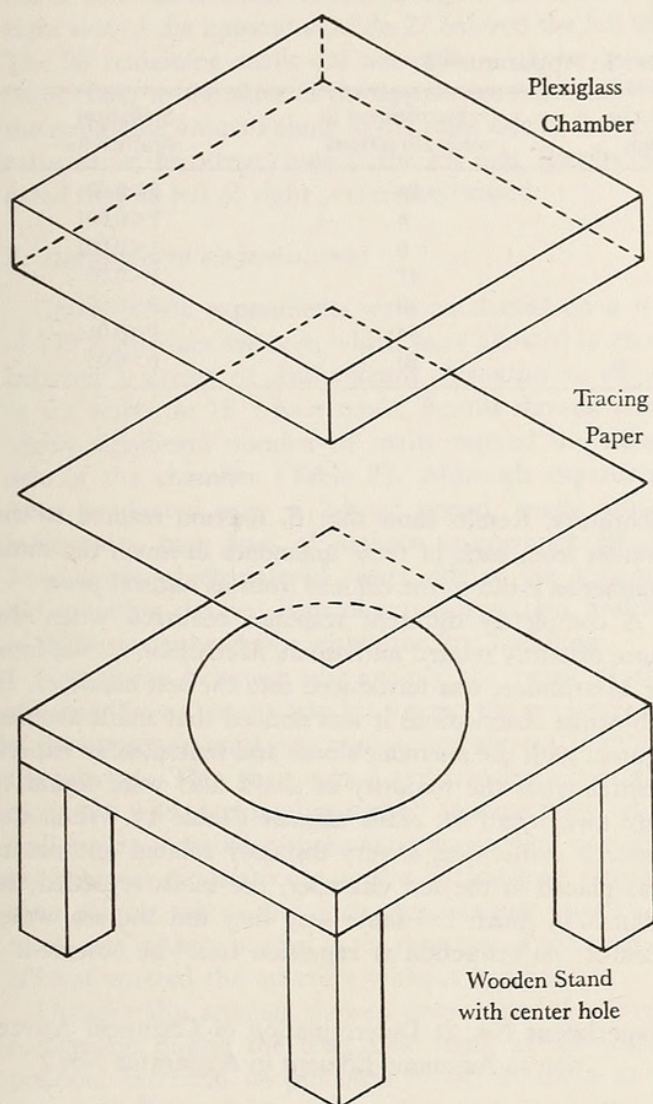
Apparatus No. 3: Description and Application

Orthokinetic and klinokinetic responses were tested for by comparing movements of individual snails in a uniform environment of anemone-effluent to manoeuvres in a sea water control. Anemone effluent was obtained by allowing approximately equal masses of test anemones to remain in stagnant 18°C sea water for 30 minutes. Snails, not fed for 24 hours, were placed at random in a 30cm by 40cm plexiglass chamber filled with either 1/ of "anemone effluent" or sea water (Figure 4). The

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Figure 4
Apparatus No. 3

transparent chamber was positioned over tracing paper on a wooden stand with a 22cm diameter circular hole in the center. The path of the individual snails was traced from below the stand and marked off in 1 minute intervals for periods of 5 to 10 minutes. Information obtained from the paths allowed the calculation of orthokinetic and klinokinetic responses.



RESULTS

Subjective Observations:

When placed at the base of large or small *Anthopleura elegantissima* in a bowl of still sea water, *Epitonium tinctum*, not fed for 24 hours, will extend their proboscises and begin searching until they come into contact with an anemone tentacle. Snails readily feed on tentacles by nipping off a piece of the side or sliding the proboscis over the tentacle tip and cutting off a portion of tissue about 2mm in length. The tissue, which can be seen through the semi-transparent proboscis, is then pulled into the body of the snail. Proboscis extension and feeding also occurred when a wentletrap was held in the water with

forceps at a distance of about 20mm from an anemone's tentacles. The anemone reacted by a localized retraction of several tentacles including the injured one.

Several *Epitonium tinctum* were placed near a specimen of *Anthopleura xanthogrammica*, which was turned on its side in order to bring the tentacles within reach of the snail. All snails were observed to approach the tentacles and crawl amongst them freely. After a few seconds of exploration some snails thrust out their proboscis and cut off a tentacle tip. The only reaction from the anemone was a retraction of the injured tentacle.

When a few snails were placed at the base of *Tealia lofotensis*, they showed no activity or interest in the anemone during the half hour observation period. One large *Epitonium tinctum* was then held with forceps about 20 mm from the anemone tentacles. Extension of the proboscis and striking the tentacle were observed. *Tealia lofotensis* reacted by vigorously contracting the injured tentacle. Other snails were placed near *Tealia* tentacles, and the typical feeding response was displayed a majority of times.

Epitonium tinctum readily fed on *Epiactis prolifera*. The process began with the usual proboscis extension and searching. After contact was made with the tentacles, the proboscis explored several of them extensively. Finally, a tentacle tip was enveloped and a portion, about 2mm in length, cut off. The anemone reacted with a violent contraction of all tentacles.

Several snails were held by forceps and lowered into a dish which contained *Metridium senile*. They were placed about 20mm from the tentacles, in the same fashion that other experiments were carried out. No searching movements were observed and *Epitonium tinctum* tentacles and proboscises seemed to avoid *M. senile* tentacles. Some of the wentletraps were then placed on mussels, near bases of the anemones. All snails turned away from the anemones. The movements of one animal were observed for about one half hour on the mussel, which was thickly populated with *M. senile*. At no time did the snail make contact with the anemones, instead, it avoided them by turning when it approached either base or tentacles. Later it was noticed that nematocysts from the base or tentacles of *M. senile* could kill *E. tinctum*, if snails were placed either on the anemone pedal disc or if they repeatedly came in contact with either the base or tentacles.

Ten *Epitonium tinctum* were then placed around the base of a *Corynactis californica* colony. No initial interest in the anemone was shown by the snails. Several snails approached the anemones and touched them without adverse effects. In these observations, and when held 20 mm away from the anemone tentacles with forceps, no feeding behavior was observed.

Table 1
Anemones versus Sea Water in Apparatus #1

Test Effluent	Animals tested (1 animal/trial)	(+) movement up center stream	(-) movement in other directions	Statistical significance
Sea Water (Control)	50	26	24	P>0.05
<i>Anthopleura elegantissima</i>	50	42	8	P<0.001
<i>Anthopleura xanthogrammica</i>	50	44	6	P<0.001
<i>Tealia lofotensis</i>	50	39	11	P<0.05
<i>Epiactis prolifera</i>	50	40	10	P<0.05
<i>Metridium senile</i>	50	6	44	P<0.01
<i>Corynactis californicus</i>	50	30	20	P>0.05

Experiment No. 1: Determination of Chemical Responsiveness to Anemone Effluent in Apparatus No. 1 (Table 1)

In a control situation, under overhead lights, with sea water flowing into all 3 arms, a degree of positive rheotaxis was exhibited. Out of 50 animals tested, 26 proceeded straight into the center stream. Of the 24 remaining snails, 9 entered the right arm, 7 entered the left arm and the other 8 turned toward the exit or failed to make a response.

Epitonium tinctorum was then exposed to a direct current of the effluent from its natural prey, *Anthopleura elegantissima*. Out of 50 snails tested, on a one animal per trial basis, 42 proceeded directly toward the anemone effluent, while 8 entered the sea water arms or went out the exit. *Epitonium* was then tested against *A. xanthogrammica*. Out of 50 trials, 42 snails proceeded directly to the effluent.

In the next group of trials, snails were exposed to the effluent from 2 anthozoans in the same family (Actiniidae) as *Anthopleura elegantissima*: *Tealia lofotensis* and *Epiactis prolifera*, which the snail readily ingested in the

laboratory. Results show that *E. tinctorum* reacted to the effluent from each of these anemones in much the same manner as it did to the effluent from its natural prey.

A completely different response occurred when the more distantly related anthozoan, *Metridium senile*, family Metridiidae, was introduced into the test chamber. In subjective observations it was noticed that snails avoided contact with the anemone's base and tentacles. In experimental trials the majority of snails also were found to turn away from *M. senile* effluent (Table 1). When *Corynactis californica*, a very distantly related anthozoan, was placed in the test chamber, the snails regarded the effluent in much the same way they did the sea water control: no attraction or repulsion could be observed.

Experiment No. 2: Determination of Chemical Attraction to Anemone Effluent in Apparatus No. 2

A. Controls:

Control trials initially were run with sea water on both sides of the apparatus to see if snails indicated a right or left preference. Out of 140 animals tested, in 10 2-hour

Table 2
Anemones versus Sea Water in Apparatus #2

Anemone	Trials	Total animals tested	Total responding to anemone effluent	Total responding to sea water	Non-runs	Statistical significance
<i>Anthopleura elegantissima</i>	19	159	78	6	75	P<0.001
<i>Anthopleura xanthogrammica</i>	12	100	54	2	44	P<0.001
<i>Tealia lofotensis</i>	14	170	28	26	116	P>0.05
<i>Epiactis prolifera</i>	12	144	28	18	98	P>0.05
<i>Metridium senile</i>	6	66	6	12	48	P>0.05

trials, conducted under overhead lights, 20 entered the right side of the apparatus while 22 entered the left side. The 98 remaining snails did not make a choice but instead clung to the sides of the apparatus. About 50% of the remaining animals clung to the right side of the apparatus while the others clung to the left side. Results indicated that no left or right preference existed.

B. *Anthopleura elegantissima*:

Choice arena experiments were conducted on a total of 159 *Epitonium tinctum*, which were allowed to choose between a stream of *Anthopleura elegantissima* effluent or sea water, in 19 2-hour trials. Results showed that a highly significant number of snails entered the effluent side of the chamber (Table 2). Although experiments were conducted over a 2-hour period, snails initially indicated a high level of activity to anemone effluent. Most snails which entered either side of the apparatus did so within the first hour of experimentation, and half of those made the choice within the first half hour.

Non-choice behavior was mainly the result of side-clinging. Several snails crawled toward the sea water side of the apparatus until they approached about 10 mm from the aperture. They then turned and crawled left or right along the wall, and finally stopped at some point on the wall for the remainder of the experiment. This side-clinging behavior did not occur on the *Anthopleura elegantissima* effluent side of the apparatus, because most of the snails that initially headed in the direction of the anemone effluent entered the aperture without hesitation.

Occasionally animals showed overt signs of chemical recognition during the tests. One snail, at the starting position, extended its proboscis in the direction of the anemone effluent. It then crawled about half the distance from the center to the anemone choice aperture and extended the proboscis again before entering.

C. *Anthopleura xanthogrammica*:

A series of experiments was conducted in which 100 *Epitonium* were allowed to choose between *Anthopleura*

xanthogrammica effluent and sea water in the choice area. Results again showed that a highly significant number of snails entered the effluent side of the chamber (Table 3). Snails showed a high degree of activity when initially exposed to effluent from this anemone, as was seen by the great number that moved from the starting position and entered the anemone effluent aperture within the first half hour of experimentation.

D. *Tealia lofotensis*:

Experiments were conducted on 170 *Epitonium* with *Tealia lofotensis* effluent in exactly the same manner. Statistically significant information could not be obtained confirming chemical detection of anemone effluent by the snails (Table 2). Wentletraps appeared to display a high degree of thigmotactic responses in the choice arena. Approximately 70% of all snails tested did not make a choice during the 2-hour trial period, due to side-clinging behavior. Even when animals were put into the start position after adhering to a side for about one hour, they tended to return to the same location where they had stopped before. Some snails were so sluggish that they did not even choose sides, but instead came to rest in the center of the arena. Since it was difficult to analyze all behavior in terms of (+) or (—), a record of the position of each non-choice snail, in terms of degrees away from each aperture, at the end of each trial was also kept (RESCH, 1972). No tendency for animals to congregate near the sea water or sea anemone aperture was demonstrated. Of the 30% of animals that did make a choice, many did so only after much hesitation. A record of the number of snails entering the anemone and sea water aperture per time interval indicated that most choices did not occur until the final hour of the 2-hour experimental period.

E. *Epiactis prolifera*:

In tests conducted on sea water versus effluent from *Epiactis prolifera*, the number of snails choosing *Epiactis* over sea water proved to be statistically insignificant

Table 3

Anthopleura elegantissima versus Anemones in Apparatus #2

Anemone	Trials	Total animals tested	Total responding to <i>Anthopleura elegantissima</i>	Total responding to other effluent	Non-runs	Statistical significance
<i>Anthopleura xanthogrammica</i>	4	50	12	15	23	P>0.05
<i>Tealia lofotensis</i>	8	84	32	3	49	P<0.05
<i>Epiactis prolifera</i>	8	84	43	9	34	P<0.05

(Table 2). Only 30% of the wentletraps tested actively made a choice during the experimental period, and the abundance of non-choice behavior again appeared to result from strong thigmotactic responses. Snails that actively made a choice did so more rapidly in *E. prolifera* effluent than in *Tealia lofotensis* effluent. A record of the number of choice responses per time interval showed that most choices were made by the wentletraps after only the first hour of the experimental period.

F. *Metridium senile*:

Unusual behavior was exhibited in the choice-arena experiments with *Metridium senile*. Out of a total of 65 animals tested, only 18 made a choice (Table 2). Most wentletraps turned 180° from the start position and moved toward the exit as soon as the center ring was removed at the beginning of each trial. Behavior that accounted for most of the non-choice was either migration of snails out the exit or side clinging on the sea water side of the apparatus. Very few snails clung to the anemone effluent side of the apparatus.

G. *Corynactis californica*:

Subjective observations showed that *Epitonium tinctorum* did not feed on or extend its proboscis toward the tentacles of *Corynactis californica*. Tests in apparatus no. 1 also indicated, statistically, that the snail did not behave differently in the presence of effluent from this anemone than it did in the sea water control. It was therefore assumed either that an attractant was not produced by *C. californica*, or if one was, its concentration was too low to effect a response. Since Apparatus no. 2 dilutes the anemone effluent more than Apparatus no. 1, no new information was likely to be gained by its use, so further experiments with *C. californica* were discontinued.

H. *Anthopleura elegantissima* versus other anemones:

In the next group of experiments, snails were tested in Apparatus no. 2 to see if they could distinguish between

effluent from their natural prey and effluent from the closely related *A. xanthogrammica*. Results showed that the snail could not distinguish between its natural prey and an anemone of the same genus (Table 3).

Experiments were also conducted in which *Epitonium* was given a choice between *Anthopleura elegantissima* and *Tealia lofotensis* effluents in the choice arena, and in subsequent tests, a choice between *A. elegantissima* and *Epiactis prolifera* effluents. In both cases the snails readily chose the effluent from their natural prey, *A. elegantissima*, over the other 2 anemones (Table 3). These results are supported by the previous experiments (anemones versus sea water - Table 2) in which snails exhibited a strong response to their natural prey, but no significant response to the 2 alternate anemones.

Experiment No. 3: Orthokinesis

Kinesis is a term used to describe a variation in locomotory activity which is dependent on the intensity of stimulation and not on the direction of stimulation (PATTEN, 1914). Orthokinesis is distinguished as a response in which the rate of forward movement depends on the intensity of stimulation (GUNN, KENNEDY & PIELOU, 1937). The objective of this facet of the study was to determine whether individual *Epitonium tinctorum* showed an orthokinetic response, in the form of an increase or decrease in velocity, in the presence of "anemone factor" as compared to sea water.

Experimental results showed that snails, in the presence of *Anthopleura elegantissima* effluent, increased their velocity significantly as compared to a sea water control. In 13 trials average distance traveled per minute in *A. elegantissima* effluent was 2.7 mm greater than in sea water (Table 4). Velocity also increased when snails were exposed to a uniform environment of *A. xanthogrammica* effluent, by an average of 2.58 mm per minute.

A decrease in distance traveled per unit time was noticed in *Tealia lofotensis* effluent as compared to sea water. Snail velocity decreased by 3.3 mm/min in the ane-

Table 4

Orthokinesis, Velocity in mm/min

Anemone Effluent	Trials	Average velocity in anemone effluent	Average velocity in sea water	Difference in velocity, effluent—sea water	Statistical significance
<i>Anthopleura elegantissima</i>	13	15.38	12.66	2.72	P<0.05
<i>Anthopleura xanthogrammica</i>	10	12.31	9.73	2.58	P<0.05
<i>Tealia lofotensis</i>	12	16.24	19.52	-3.28	P<0.05
<i>Tealia lofotensis</i> (repeat)	6	12.72	14.53	-1.81	P<0.05
<i>Epiactis prolifera</i>	10	13.93	14.25	-0.32	P>0.05
<i>Metridium senile</i>	8	19.96	17.66	2.30	P<0.05

mone effluent as compared to the sea water control. Experiments with *T. lofotensis* were conducted in July; the summer experiments were repeated in winter to determine if summer weather was somehow affecting snail responses. The results of the repeat experiments still indicated that snail velocity significantly decreased in the presence of *T. lofotensis* effluent.

Epiactis prolifera effluent introduced into the apparatus did not produce a statistically significant change in snail velocity. The effluent from *Metridium senile* produced an increase in the velocity of the snail. *Epitonium tinctum* increased its speed on the average of 2.3 mm/min in the presence of this anemone's effluent (Table 4).

Experiment No. 4: Klinokinesis

When some animals are placed in a nondirectional field of stimulation, a klinokinetic response is often exhibited. A klinokinetic response is defined by FRAENKEL & GUNN (1940) as one "in which the rate of random turning, or angular velocity, depends on the intensity of stimulation." There is no reason why such an animal should turn at a particular point, but the animal does turn and the direction of linear movement changes for no apparent reason. Animals may turn more frequently at high or low levels of stimulation, but the direction of turns is always random.

Klinokinetic responses for *Epitonium tinctum* were obtained by dividing the distance traveled per minute by the linear displacement per minute in anemone factor (SURTEES, 1964). The number obtained from this calculation was compared with the value obtained by dividing distance traveled per minute by linear displacement in sea water for the same animal. The calculated probability from experimental results, when *E. tinctum* was exposed to a uniform environment of stimulation from all anemones, was much greater than 10%, indicating that klinokinesis is not involved in the location of prey by *E. tinctum* (RESCH, 1972).

DISCUSSION

In the light of these experiments it can no longer be said that members of the genus *Epitonium* rely on purely tactile means to locate their prey. Choice-arena experiments indicate that *E. tinctum* can easily distinguish "prey factor" from plain sea water. In the presence of "prey factor" an increase in velocity indicates that an orthokinetic response is probably important in prey location. The fact that *E. tinctum* is not purely a tactile ani-

mal is of ecological significance. An orientation to and a physical activation by the effluent of *Anthopleura elegantissima* clearly allows this foraging species to locate its prey without difficulty.

Epitonium tinctum also will eat the tentacles of *Anthopleura xanthogrammica*, an anemone in the same genus as its natural prey. The snail also showed a strong positive response to the effluent from this anemone in the choice apparatus. Effluent from these two anemone species would appear to contain the same chemical agent, since *E. tinctum* could not distinguish between them under experimental conditions. Since the snail reacted exactly the same to *A. xanthogrammica* as to its natural prey in all experiments, and since *E. tinctum* may encounter *A. xanthogrammica* in some locations and prey on it naturally, it is not classified as an alternate prey in this study.

The wentletrap readily ingested tissues from 2 other members of the family Actiniidae, *Tealia lofotensis* and *Epiactis prolifera*, although geographical restrictions on these 2 species may make it less likely that the wentletrap would come in contact with them in nature. In Apparatus no. 1 the snail also oriented to effluent from these 2 anemones as long as it received immediate directional stimulation from them. Choice-arena attraction to these alternate prey was not demonstrated, however, so one could assume that even though a chemical attractant was emitted, its concentration was probably too weak to be detected. Distance traveled per minute by the snail in the presence of effluent from these 2 anemones decreased as compared to sea water, and at this time no suitable explanation can be given for this result.

Further experiments were conducted in which *Epitonium tinctum* chose between *Anthopleura elegantissima* and *Tealia lofotensis* effluent in the arena, and in subsequent tests snails chose between *A. elegantissima* and *Epiactis prolifera*. In both cases the snail readily chose the effluent from its natural prey over that from the other 2 anemone species. These results are supported by the previous anemone-versus-sea water experiments in the choice arena. These indicated that the snail was more strongly attracted to its natural prey than to sea water, while displaying a weaker response when choosing between the 2 alternate anemones and sea water. The obvious conclusion drawn from these results is that even though the snail could ingest anemone tissue from another genus, it showed a marked preference for its natural prey.

When tested against a more distantly related anthozoan, viz. *Metridium senile*, the snail avoided the base and tentacles and no feeding on this anemone took place. Further qualitative observations revealed that just touching the base of *M. senile* causes death to *Epitonium tinctum*. It is unknown whether just one touch or several are

required to cause death, and what is different about *M. senile* nematocysts or toxin that causes death to the wentletrap. *Anthopleura elegantissima*, *A. xanthogrammica*, *Tealia lofotensis* and *Epiactis prolifera* nematocysts are not only tolerated, but ingested without difficulty. Snails avoided the effluent of *M. senile* in both Apparatus no. 1 and no. 2.

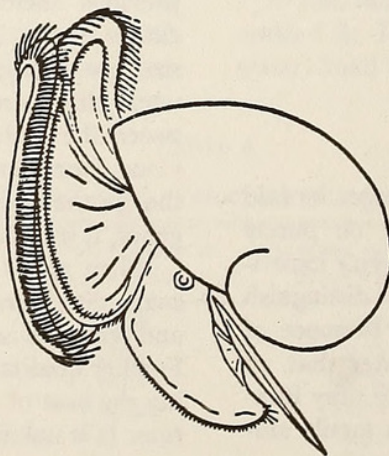
Corynactis californica (Order Corallimorpharia), a much more distantly related anthozoan, was also tested. *Epitonium* was neither attracted to this anemone nor repelled by it. Apparently it did not contain any of the attracting or repelling chemical substances in its secretions.

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Literature Cited

- COPELAND, MANTON
1918. The olfactory reactions and organs of the marine snails *Alectrion obsoleta* (Say) and *Busycon canaliculatum* (Linn.). Journ. Exp. Zool. 25: 177-227
- DAVENPORT, DEMOREST
1950. Studies in the physiology of commensalism. I. The polynoid genus *Arctonoe*. Biol. Bull. 98: 81-93
1966. The experimental analysis of behavior in symbioses. Sym-bioses 1: 381-429. Academ. Press Inc. New York
- FRAENKEL, GOTTFRIED S. & DONALD L. GUNN
1961. The orientation of animals: kineses, taxes, and compass reactions. Dover Publ. Inc., New York. x + 376 pp.
- GUNN, DONALD, JOHN KENNEDY & D. P. PIELOU
1937. Classification of taxes and kinesis. Nature 140: 1064
- HAND, CADET
1955. The sea anemones of central California. Part I. The corallimorpharian and athenarian anemones. Wasmann Journ. Biol. 12 (3): 345-375; text figs. 1-7 (7 January 1955)
1955. The sea anemones of central California. Part II. The endomyarian and mesomyarian anemones. Wasmann Journ. Biol. 13 (1): 37-99; text figs. 8-24 (3 October 1955)
1956. The sea anemones of central California. Part III. The acontarian sea anemones. Wasmann Journ. Biol. 13 (2): 189-251; text figs. 25-37 (14 February 1956)
- HOCHBERG, FRED G.
1970. Functional morphology and ultrastructure of the proboscis complex in *Epitonium tinctorum* (Gastropoda: Ptenoglossa). Abstr. & Proc. West. Soc. Malacol. 4th Ann. Meet. Asilomar, Calif.: 22-23
- MCCAULEY, JAMES E.
1969. Marine invertebrates, chemical signals, and marine products. Lloydia 32: 425-437
- PATTEN, B. M.
1914. A quantitative determination of the orienting reaction of the blowfly larva, *Calliphora erythrocephala*. Journ. Exp. Zool. 17: 213-280
- RESCH, CAREY
1972. Chemical recognition of prey in the gastropod *Epitonium tinctorum* (Carpenter). M. A. Thesis, Univ. Calif. Santa Barbara, 61 pp.
- ROBERTSON, ROBERT
1961. Wendletraps (Epitoniidae) feeding on sea anemones and corals. Proc. Malacol. Soc. London 35: 51-63
- STEWART, WILLIAM
1970. A study of the nature of the attractant emitted by the asteroid hosts of the commensal polychaete *Ophiodromus pugettensis*. Ph. D. Thesis, Univ. Calif. Santa Barbara: 86 pp.
- STRONG, ARCHIBALD MCCLURE
1941. Notes on *Epitonium (Nitidoscala) tinctorum* (Carpenter). The Nautilus 55 (2): 46-47
- SURTEES, G.
1964. Laboratory studies on dispersion behavior of adult beetles in grain. VIII. Spontaneous activity in three species and a new approach to analysis of kinesis mechanisms. Animal Behav. 12 (2-3): 374 to 377
- THORSON, GUNNAR
1957. Parasitism in the marine gastropod family Scalidae. Vidensk. Medd. Dansk Naturh. Foren. 119: 55-58
- WILSON, EDWARD O.
1970. Chemical communication within animal species. In: Chemical ecology, Ernest Sonderheimer & John B. Simone, eds. Acad. Press, London





Smith, C R. 1977. "CHEMICAL RECOGNITION OF PREY BY THE GASTROPOD EPITONIUM-TINCTUM." *The veliger* 19, 331–340.

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