ASPECTS OF THE BIOLOGY AND BEHAVIOR OF THE CHITON TONICELLA MARMOREA (FABRICIUS, 1780) (POLYPLACOPHORA, MOLLUSCA)

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ASPECTS OF THE BIOLOGY AND BEHAVIOR OF THE CHITON *TONICELLA MARMOREA* (FABRICIUS, 1780) (POLYPLACOPHORA, MOLLUSCA)

by

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ABSTRACT

The biology and behavior of the chiton, Tonicella marmorea (Fabricius) was studied, under both field and laboratory conditions. T. marmorea is nocturnal and found only sublittorally in Newfoundland waters. Studies showed that it moved as much as 200 centimetres in one feeding period and a mean distance of 35 to 40 centimetres each night. Daily observations of activity of a population, made during two experimental periods of approximately one month each, failed to demonstrate any seasonal pattern in the activity of the organism. No significant correlation was found between the duration of the dark photoperiod, or water temperature and actvity. Activity over a twenty-four hour period took place only during the dark hours. Individual specimens became active just before sunset and continued to move for 5 or 6 hours. Some specimens exhibited a second peak of activity, midway through the night, and a third, just before sunrise. Tonicella marmorea possesses the ability to "home" to a particular resting site, but was not observed to home regularly to the same site.

ACKNOWLEDGEMENTS

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INTRODUCTION

The present study stemmed from taxonomic studies of Polyplacophora (chitons) which the author conducted as a summer student at the Marine Sciences Research Laboratory, Memorial University of Newfoundland, at Logy Bay. Literature searches on three species of chitons native to Newfoundland waters, Tonicella marmorea (Fabricius, 1780), Tonicella rubra (Leloup) and Ischnochiton albus (Linnaeus), revealed little known of their biology. Originally the study was intended to encompass the autecology of these three species. However, it was concluded early in the program that this was unrealistic for a study period of only two years. As Tonicella marmorea was the largest and most common of the three, the focus of the study was changed to the biology and behavior of this chiton.

Although the literature contains many references to the biology of Polyplacophorans most of the studies were confined to specific aspects of their morphology and physiology and little information was available on the ecology or ethology of chitons. In 1919, Arey and Crozier conducted extensive investigations on the response of a littoral chiton, Chiton tuberculatus (Linnaeus), to stimuli of various types. This remains one of the most comprehensive works on the ethology of a Polyplacophoran to date. The contributions of Evans (1951), and Glynn (1970) were the only other major publications on chiton ecology, at the initiation of the present study. Langer (1972) studied the population structure of T. marmorea, T. rubra and I. albus at the same time as the present study was underway, and information from his study became available after field work for the present investigation had been completed.

Knowledge of the basic biology of Tonicella was limited to minor references in the literature. In order to better comprehend the behavior of the chiton, the author attempted throughout the study to gather as much baseline information on chiton biology as time permitted. Throughout the program, laboratory observations were verified, where possible, by investigations of an undisturbed field population of *T. marmorea*.

Evans (1951) found that responses to various environmental factors greatly affected the behavior and movement of *Lepidochitona cinereus* (Linnaeus) Similar experimentation to that designed by Evans was used in an attempt to evaluate the effect of individual environmental factors on the activity of *T. marmorea*.

With the exceptions of the works by Langer (1972) and Evans (1951), all previous studies on Polyplacophoran ethology were confined to littoral species. One of the observations common to these works was the ability of many chitons to "home" to particular sites on the substrate. As *Tonicella marmorea* is entirely sublittoral in Newfoundland waters, the question arose as to whether or not these chitons would "home", and, if so, what parameters affected their homing ability.

Studies to determine the daily activity periods of *T. marmorea* as well as the relationship between activity and various environmental parameters, were also conducted during the present program, since Glynn (1970), Lyman (1975) and Smith (1975) had found activity in several species of intertidal chitons to be related to both photoperiod and tidal height.

CHAPTER I

MATERIALS AND METHODS

Study Areas

Over a period of two years, from April 1972 to August 1974, specimens of Tonicella marmorea were collected from several areas in Newfoundland and one bay in Labrador (Figure 1). The main sampling areas in Newfoundland included Dyer's Gulch, Logy Bay; Tapper's Cove, Torbay, and Bread and Cheese Cove, Bay Bulls (Table 1). Most of the field observations quoted in the text were carried out in the vicinity of Dyer's Gulch, Logy Bay.

Dyer's Gulch is a short, narrow inlet of Logy Bay, north of the site of the Memorial University Marine Sciences Research Laboratory. A small fresh water stream enters the gulch at its south west extremity. The bottom type ranges from steep rock walls and rock outcrops at the head to boulders and pebbles at the mouth. Maximum water depth is 16 metres in the gulch and drops rapidly outside its mouth (Figure 2). The physical topography as well as the resident flora and fauna of the gulch were described extensively by Himmelman (1969) and Emerson (1974).

Sampling and underwater observations were carried out on the populations of T. marmorea present on the vertical rock walls located from points A to B, and C to D in Figure 2.

T. marmorea sampled from Labrador were collected during August 1972 in Saglek Bay, Labrador. This work was carried out while the author was Cruise Biologist aboard the C.S.S. Dawson of the Bedford Institute of

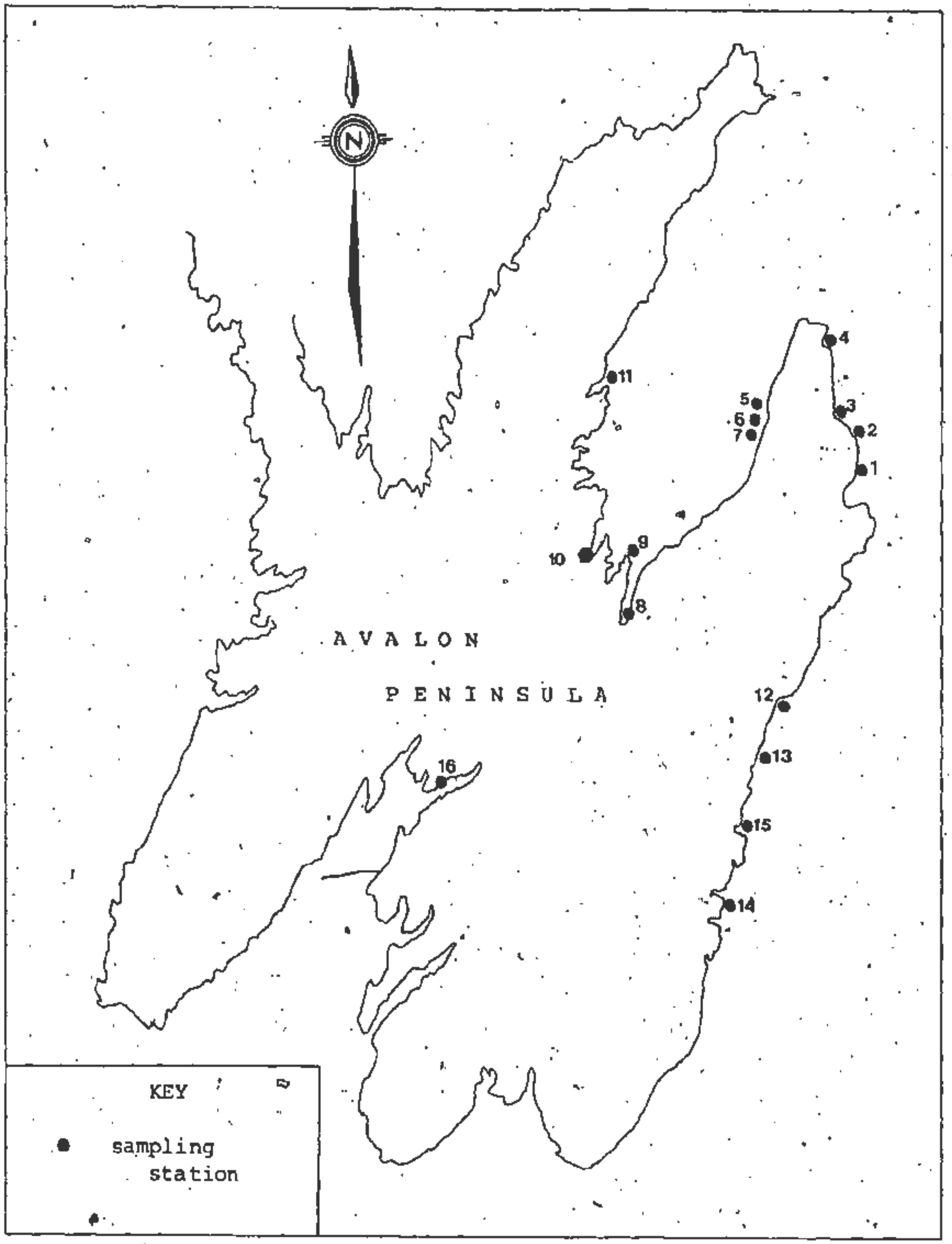

FIGURE 1: LOCATION OF AREAS ON THE AVALON PENINSULA, NEWFOUNDLAND, SAMPLED FOR TONICELLA MARMOREA.

TABLE 1: SAMPLING SITES IN NEWFOUNDLAND AND LABRADOR WITH RELATIVE ABUNDANCE OF TONICELLA MARMOREA AT EACH SITE

Location		Estimated Abundance of *Tonicella marmorea* per m.^{2}				
		0	5	5 - 10	10 - 15	15+
1)	Logy Bay					x
2)	Outer Cove	x				
3)	Torbay				x	
4)	Biscayan Cove				x	
5)	Portugal Cove				x	
6)	St. Phillip's		x			
7)	St. Thomas			x		
8)	Holyrood		x			
9)	Chapels Cove		x			
10)	Brigus		x			
11)	Carbonear Island		x			
12)	Bay Bulls					x
13)	Tors Cove			x		
14)	Fermeuse					x
15)	Cape Broyle		x			
16)	Salmonier			x*		
17)	Eastport, B.B.			x		
18)	Michael's Harbour, N.D.B.					x
19)	Saglek Bay, Lab.					x

* distribution restricted to the exterior surface of the valves of *Placopecten magellanicus* (Gmelin)

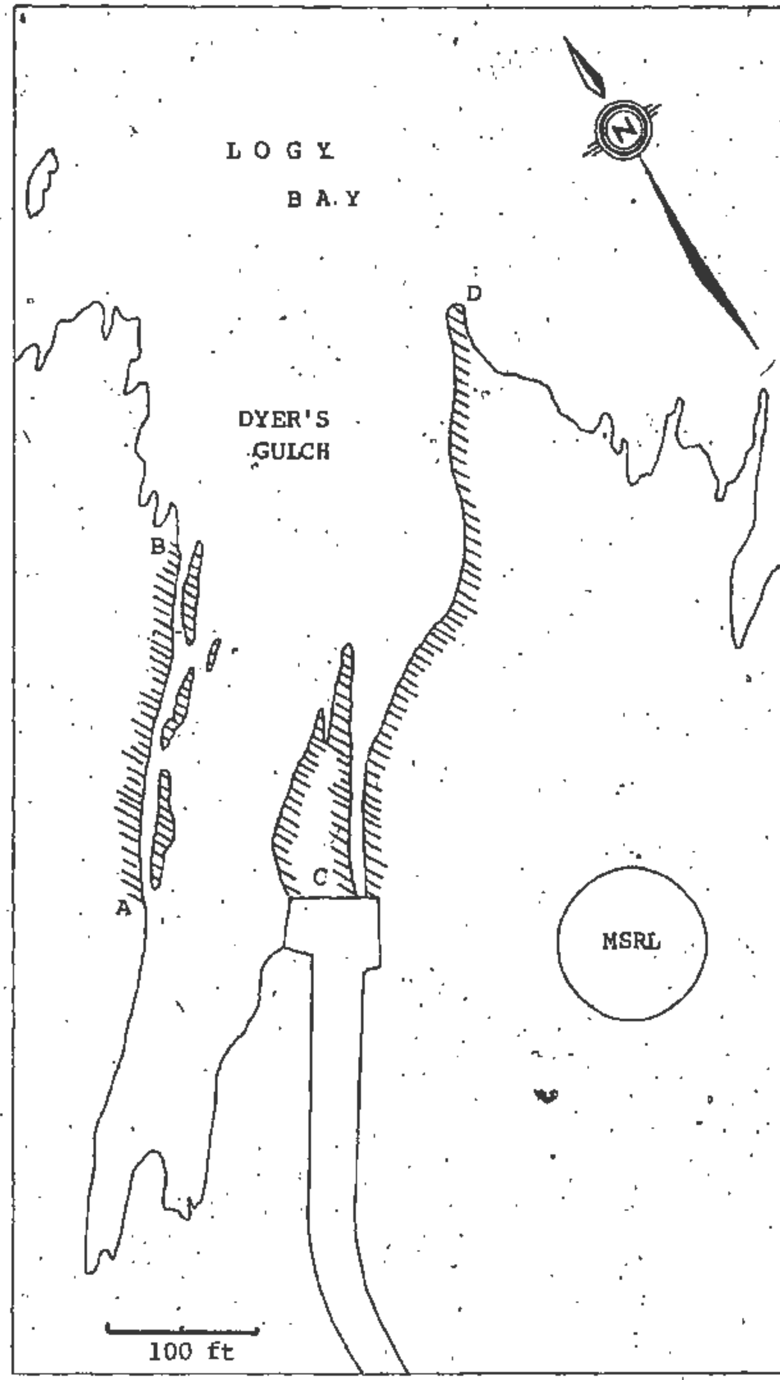

FIGURE 2: LOCATION OF STUDY AREAS (SHADED) IN DYER'S GULCH, LOGY BAY, NEWFOUNDLAND.

Oceanography, then on charter to the Faculty of Engineering and Applied Science, Memorial University of Newfoundland.

Collection and Holding of Specimens

All underwater observations and collections were made with the aid of SCUBA.

In order to obtain rough estimates of the population density of *T. marmorea* in the areas studied, several one metre square areas of bottom were selected at random and the number of specimens of *T. marmorea* recorded. The type of habitat and the position of specimens of *T. marmorea* were noted.

Large specimens of *T. marmorea* (more than 0.5 cm. long) were removed from the substrate by hand, or with a spatula. Because of the susceptibility of smaller specimens to injury during collection and handling, only large specimens were used during this study. Sizes therefore represent the mean maxima for each collecting site.

All specimens were transported to the laboratory in sea water immediately after collection. When possible, specimens transported long distances were refrigerated. *T. marmorea* was found to be hardy and survived periods of up to two days in unaerated sea water, which reached temperatures of up to 18° Celsius. At the laboratory specimens were placed immediately in holding tanks of circulating sea water.

Two basic types of holding and experimental tanks were used throughout the study. Initially the chitons were held in a fibre reinforced plastic tank. This tank was approximately 0.8 m. wide by 1.2 m. long, with a maximum water depth of about 10 cm.

The chitons were transferred to a second fibre reinforced plastic tank used mainly for experimental purposes. This tank was approximately 0.8 m.

by 4.9 m. with a maximum water depth of about 10 centimetres.

All tanks were continuously supplied with unfiltered sea water from Logy Bay. Temperatures in the tanks were usually 2-4 Celsius degrees above the ambient, subsurface temperature in the bay and therefore ranged from 0 to 12°C.

Unless otherwise noted, all holding and experimental tanks were supplied with a substrate consisting of rock particles 1 to 5 mm. in diameter, taken from Middle Cove. This particulate matter was rinsed and scattered over the tank bottom to a depth of 1 to 2 cm. Specimens of T. marmorea moving across the bottom of the tank displaced the particles, and left a clearly defined path.

Natural populations of algae, bryozoans and other microscopic marine organisms were allowed to develop on the sides and bottoms of the tanks and their contents, to provide food for specimens of T. marmorea.

All newly collected specimens were allowed a period of 24 to 48 hours from the time of capture, to acclimate to their surroundings. At the end of this period they were measured and tagged.

Measurement and Tagging

Each chiton was removed from the tank using a spatula and immediately transferred to a 5 x 8 cm. glass plate. The plate was immersed in a bowl of sea water placed in an ice bath. While on the glass plate, the length and width of each chiton was measured using vernier calipers.

Length was measured as the distance between the anterior and posterior margins of the girdle and width as the distance between the margins of the girdle at the fourth valve (Figure 3).

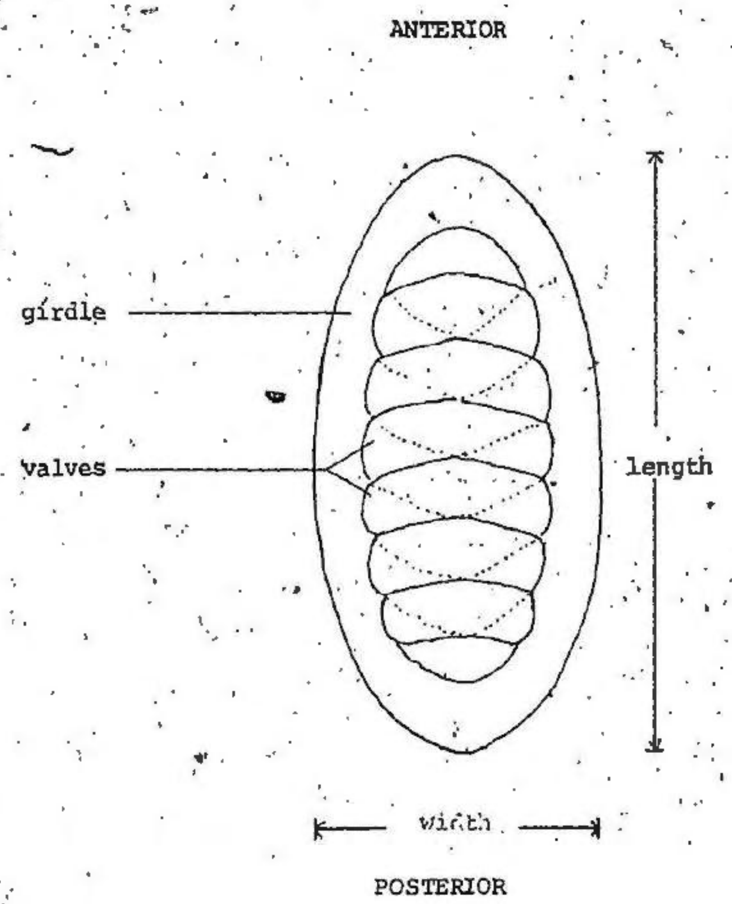

FIGURE 3: DORSAL VIEW OF TONICELLA MARMOREA SHOWING THE PARAMETERS OF LENGTH AND WIDTH.

Due to the nature of the experimental program a tagging method which would minimally interfere with the normal behavior of the animals was required. Several methods were tested including scratching the valves and removal of small portions of the girdle. Painting valves with nail lacquer or fast drying resins was also attempted.

None of these methods of tagging proved to be satisfactory. The clipped sections of the girdle were difficult to see when an animal was in a crevice, and grew back in 3 to 6 weeks. Scratches on the valves were quickly obscured by growths of bryozoans and algae. The various paints and resins used would not adhere to the damp, smooth exterior of the valves, and quickly flaked off. (As the photosensitive organs, or aesthetes, are located in small pits on the dorsal surface of the valves [Boyle,1972; Omelich,1967] excessive drying or blockage in this area was avoided.)

The most satisfactory method of tagging involved the attachment of small, plastic, handicraft beads to the girdle. These beads are approximately one mm. in diameter and are obtainable in a variety of colours from most handicraft stores. Only those beads with imbedded colour were satisfactory, as those which were painted lost their colour in water. The beads were attached singly, or in groups of two or three, to the right craniad portion of the girdle. The beads were threaded onto a needle using nylon suture thread. Before tagging the needle, thread and beads were rinsed in a solution of 70% ethyl alcohol to minimize infection. The needle was passed through the dorsal surface of the girdle at the base of the second valve, and emerged in the pallial groove. The thread was then looped around the girdle and secured to the beads with two half hitches

(Figure 4).

Weight was measured to the nearest tenth of a gram on an electronic balance. Before weighing, the chiton was removed from the water bath and blotted dry.

Measurement of length, width and weight were repeated every three months for each specimen of T. marmorea.

Meteorological information for the St. John's area was supplied by the Atmospheric Environment Service, Environment Canada; as recorded at the Torbay weather office.

At the laboratory, daily water temperatures in the tanks were recorded using a mercury bulb thermometer.

Predation

Information on predation was obtained from personal communication with other researchers working on predator species of Tonicella marmorea at Logy Bay, and from several experiments carried out at the laboratory.

Specimens of T. marmorea were placed in tanks containing cunners, Tautogolabrus adspersus (Walbaum), lobsters, Homarus americanus (Milne-Edwards), crabs, Cancer spp. and Hyas coarctatus (Leach), and sea-stars, Asterias vulgaris (Verrill). The "predator" species were not given any other food either during the experiment or for two days prior to the start of experimentation. The experiments varied from 24 hours to 72 hours in duration.

Feeding Behavior

Information on feeding behavior was obtained as a result of field

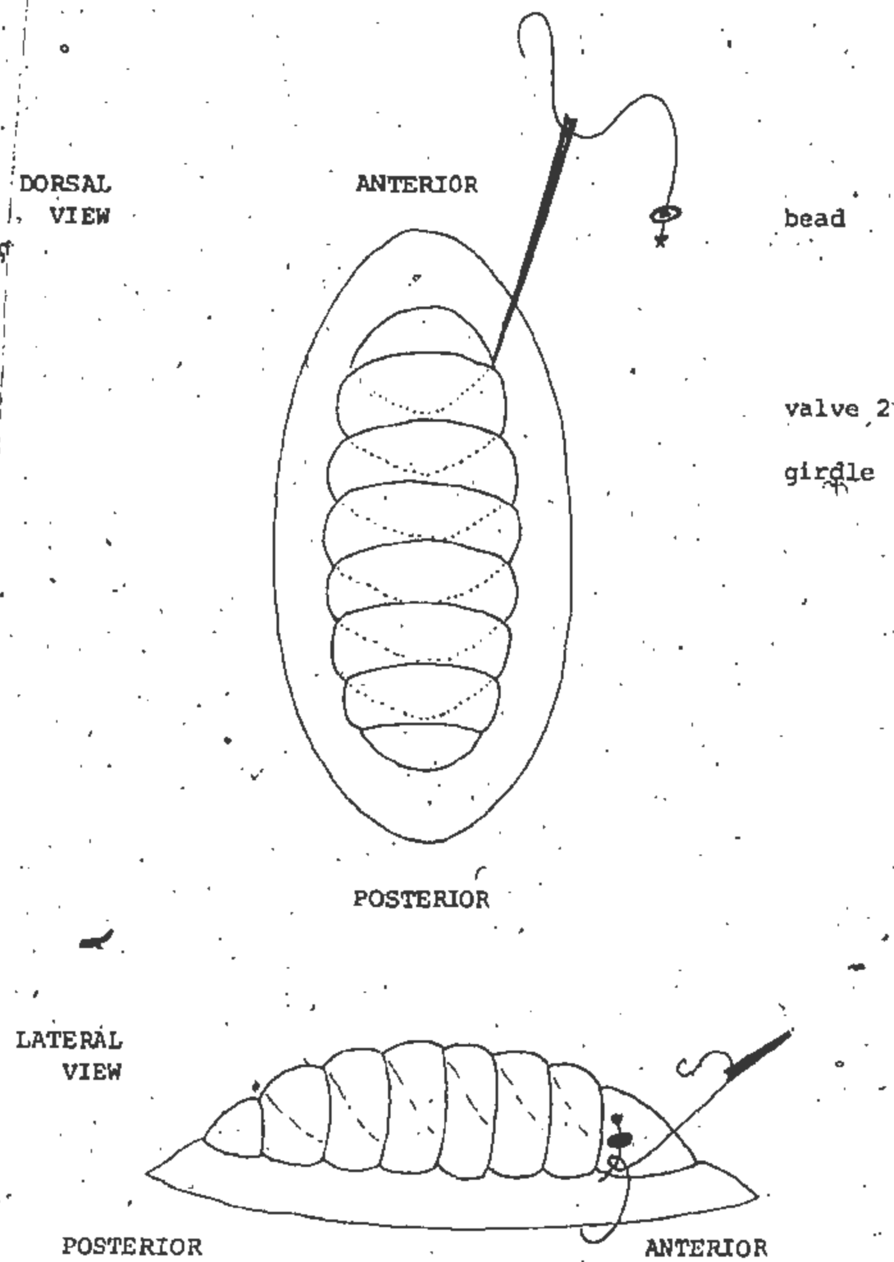

FIGURE 4: DORSAL AND LATERAL VIEWS OF TONICELLA MARMOREA SHOWING THE TAGGING METHOD.

observations and monitoring of laboratory populations kept in glass aquaria. In the field, animals were removed from the substrate and checked for radular activity. In the laboratory radular activity was observed through the glass walls of the aquaria and estimates made of the rate of radular movement and the periods of greatest feeding activity.

Reproduction and Development.

Spawning was observed in the laboratory only once during the study period. No observations were made of the spawning behavior of Tonicella marmorea in the field.

During the laboratory spawning incident ova and sperm were collected using pipettes. The gametes were placed in beakers of sea water in a holding tank. The water in the beakers was changed daily over the next twenty three day period. Microscopic examinations were made each day. On the tenth day after spawning small pieces of stone, mollusc shell and coralline algae were placed in the beakers to provide settling substrates for the larval chitons.

Photographs of the fertilized ova were taken using a Zeiss Photomicroscope with TRI-X, 400 ASA film.

Specimens of T. marmorea collected at Logy Bay at this time were killed and examined to determine the condition of the gonads.

Observations on the behavior of the larval T. marmorea were made throughout the twenty three day period of their development.

General observations of the behavior of adult specimens of T. marmorea were made in conjunction with other experimentation, both in the laboratory and in the field.

Response to Stimuli

A series of experiments was set up to test the response of *Tonicella marmorea* to stimuli such as touch, gravity and water currents. The experimental design was in part adapted from similar work by Arey and Crozier (1919) and Evans (1951).

(a) Thigmotaxis

The tactile response of various body surfaces on *T. marmorea* to touch by a blunt-pointed instrument was observed during a number of trials.

Furthur information on thigmotaxis was obtained through a series of experiments on dorsal contact. Four specimens of *T. marmorea* were placed in a glass aquarium which contained a raised sheet of glass, supported at the corners by small blocks of paraffin. The height of the sheet had been adjusted so that chitons travelling beneath the sheet would bring their dorsal surfaces into contact with it. Four additional specimens o *T. marmorea* were placed on the upper suface of the sheet.

(b) Geotaxis

On April 30, 1975 six specimens of *T. marmorea* were placed on a 1 x 1 m. sheet of rough fibreglass, which was then hung vertically in the water column of a 1.5 m. deep holding tank. The postion of the chitons on the sheet was checked at twelve hour intervals, for two days.

A second experiment using a 0.6 x 0.6 m. sheet of glass, was set up to test downward movement of chitons exposed to the air. Twenty specimens of *T. marmorea* were placed on the sheet (Figure5). The sheet was then placed in a vertical position, exposed to the air. Movement of the chitons

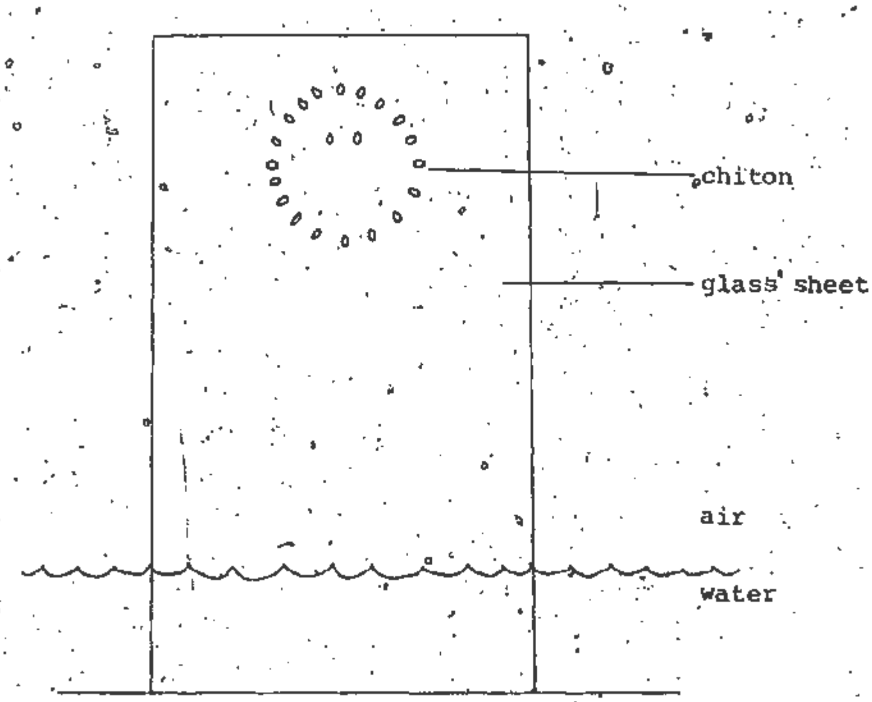

FIGURE 5. SCHEMATIC DRAWING OF THE GEOTAXIC TESTING APPARATUS USED TO DETERMINE THE RESPONSE OF TONICELLA MARMOREA TO GRAVITY, WHEN EXPOSED TO AIR.

was monitored for a period of 1.5 hours.

Another experiment of this type was run, using ten new specimens of T. marmorea. During this experiment a very light flow of directed on the animals to prevent dessication.

Each of these experiments was repeated once with new specimens of T. marmorea.

(c) Rheotaxis

The response of T. marmorea to turbulent water and currents was examined in a series of short experiments.

To assess the response to currents, ten specimens were placed randomly on a horizontal glass sheet 0.6 x 0.6 m. Ten other chitons were placed inside a 30 cm. piece of 7.6 cm. diameter poly-vinyl-chloride (PVC) tubing. Both groups of chitons were allowed to acclimate to their surroundings for one-half hour, after which time slow water currents were introduced across the surface of the glass plate, and through the PVC tubing. Observations on the response of specimens of T. marmorea to the water current were continued for one hour.

(d) Phototaxis and Response to Photoperiod

A number of experiments testing the response of T. marmorea to light were performed. All chitons tested were held in a 1 x 1 m. white plastic tank. The tank was supplied with sea water held at a depth of 12.7 cm. The tank was located in a portion of a wet bench directly in front of a large laboratory window. Artificial light was supplied by an adjustable electric lamp, model 12656, Lamp (Canada) Limited. The lamp was fitted with a 150 watt incandescent bulb. The light intensity on the dorsal surface of the valves of the chitons was approximately 1000 foot-candles.

Active specimens of T. marmorea were selected for this study. Only those chitons which moved at least 30 cm. per night were used. Chitons used ranged in length from 1.0 to 2.5 cm. All animals were allowed one-half hour to acclimatize to the tank before experiments were begun. At the end of this period the experimental regime was instituted. The experiment began when the first chiton moved.

Unless otherwise noted, all other lighting in the laboratory was off during this period, and the laboratory window was blocked by a sheet of black plastic.

As T. marmorea was observed both in the laboratory and the field to be active at night only, an experiment in which the normal light and dark cycles of the day were reversed was used to assess whether the nocturnal habit was triggered by light only, or if a circadian rhythym was also a factor. During this experiment ten chitons were placed in a controlled light chamber. Built of wood and impervious to light, the chamber consisted of a five-sided box which fitted over a 1.65 x 1 m. section of a wet bench. The top hinged lid contained three 100 watt incandescent lights, fixed at equal distances along the tank's length. A continuous supply of sea water kept the temperature constant. The lights were controlled by an automatic timer. During the first three days of the experiment the chamber had twelve hours of light followed by twelve hours of dark . On the fourth day the automatic timer was changed so that the next light period was twenty-four hours long and the artificial night fell during the normal daylight hours. The reversal of normal light and dark periods was continued for several days. During this period specimens of T. marmorea in the experimental chamber were monitored periodically to ascertain their activity patterns.

To further assess the most active period of the day for T. marmorea, 50 specimens were observed for a twenty-four hour period. Beginning at 1400 hours on April 9 and ending at 1400 hours the following day, the activity of the laboratory chitons was monitored every hour. The number of chitons moving and the distance moved each hour were recorded. During the night observations were made using short duration lighting with red light so as to disturb the animals as little as possible.

Movement

Attempts were made in the field to tag specimens of Tonicella marmorea underwater, or to replace tagged specimens to the areas from which they were originally sampled. Regular observations of the movements of these tagged animals was used to ascertain the role of "homing" in the behavior of the chiton.

An artificial habitat was created in the laboratory. It consisted of various types of rocks, shells and other possible resting sites placed in a 2.6 m. long section of a tank measuring 4.8 x 0.8 m. This section was gridded in 7.6 cm. squares. Approximately sixty tagged chitons were placed at various positions in the tank and allowed to acclimate to it for a period of seven days.

At the end of this period, the exact location of each chiton in the tank was noted on a scale drawing of the tank and observations were begun.

The chitons were allowed to move freely about the tank and were not disturbed in any way. At 1200 hours each day, the position of each chiton was recorded, and scale drawings made of the trails left in the sediment by the previous night's activity. The sketched trails were then measured and an estimate of total daily activity of each chiton obtained. Throughout the study, chitons often moved along the sides of the tank, or around the rock they rested on, leaving no observable trail. When this occurred, activity was estimated as the shortest distance between the two resting sites. If an animal returned to its original site, no activity was recorded for the period.

As this type of activity was limited to a small number of animals, it was not expected to greatly affect measurement of the total actvity of the population.

When changes in resting sites occurred, the straight line distance between the two sites was recorded, in order to establish whether or not T. marmorea possessed a home range.

Two studies of this type were carried out. The first ran from November 1 to December 7, 1973, a period of 37 days. The second was 29 days long, from March 14 to April 11, 1974. Daily water temperature was measured with a mercury bulb thermometer. Duration of the photoperiod, in hours per day, and radiation in Langleys per day, were obtained from the Atmospheric Environment Service, Environment Canada.

After the results had been tabulated, correlational co-efficients for activity per day versus water temperature, photoperiod, and radiation were computed using a Hewlett Packard Calculator-Computer, model 9810. The formulae used for the computations are given in Appendix I.

CHAPTER II: GENERAL BIOLOGY

RESULTS

Habitat Description

Tonicella marmorea, the mottled red chiton, is commonly found in the coastal waters of Newfoundland and Labrador at depths of 1 to 150 metres. (Abbott,1954). It is a small chiton, reaching approximately 3 cm. in length. Because of its distribution and outward appearance, it is often confused with Tonicella rubra the red northern chiton. T. rubra generally does not reach lengths of greater than 1.5 to 2.0 cm. and possesses minute, elongate scales which cover the girdle. The girdle of T. marmorea is naked.

The only other chiton common to these waters is Ischnochiton albus, the white northern chiton, which reaches lengths of 1 to 2 cm. Unlike T. rubra and T. marmorea, which are usually buff and red in colour, I. albus is always a pale cream to white. Throughout this study I. albus was sighted only twice; at Tapper's Cove, Torbay and at Portugal Cove, Conception Bay.

Because of their smaller size, I. albus and T. rubra tended to inhabit the smaller cracks and crevices of the hard substrate. T. marmorea, which is often more exposed, was the most commonly observed chiton.

T. marmorea can be found in abundance (>5 chitons per square metre) in most rocky, sublittoral zones of coastal Newfoundland. (Table 1). T. marmorea was never present in depths of less than 1 m. and usually was most abundant at 10 m. In areas of steep rock outcrop, T. marmorea was common in depths of 2 to 15 m., ranging to within 1 m. of the low water mark during the night and remaining during the day in depths greater than 2 m.

T. marmorea was never observed to move into the intertidal zone, throughout the period of this study. However, chitons taken from the field to the laboratory were often observed moving near the air-water interface. In this position the lateral edge of the girdle was exposed to the air. Occasionally a chiton was observed to crawl entirely out of the water. When this happened the chiton moved in a straight line distance of several centimetres away from the water's edge, eventually became immobile and sealed the girdle tightly to the tank wall. Even though the air/water interface was close at hand, these animals remained immobile and eventually died.

The distribution of T. marmorea did not appear to be affected by turbulence, except in such extreme areas as surf zones on a cobble beach. T. marmorea was not present in areas characterized by brackish water, heavy silting or sand. The major habitat requirement was a firm substrate such as rock outcrop or boulders. T. marmorea has been observed on stones or pebbles, less than 2 to 3 cm. in diameter.

T. marmorea is a nocturnal animal which begins to move in the hours just after sunset. During the night the larger chitons are readily observable on the upper surfaces of rocks or molluscan shells, and on exposed rock outcrops. They exhibit a definite photonegative response and, with the onset of dawn, move to shelter. Within two hours of sunrise, no chitons remain exposed.

The smaller chitons spend the daylight hours deep within crevices in the rock or encrusting coralline algae, or under stones. Even at night they are usually found within close proximity of their shelter, some never leave the crevice at all. The larger T. marmorea also seek shelter during the day under rocks and in crevices. However, these chitons may also been found beneath clumps of algae, or sponges or close to anemones, sea cucumbers, tunicates and other sessile marine organisms. As well, T. marmorea which live on boulders or rock outcrop imbedded in sand or silt often spend the daylight hours at the lowest edge of the substrate, partially buried in the sand or silt.

In most habitats frequented by T. marmorea during this program, coralline algae was found to be the dominant encrusting organism. Sponges, barnacles and bryozoans were present on the substrate, but were more limited in abundance and distribution than was the coralline algae. The daytime niches occupied by specimens of T. marmorea were often shared with organisms such as brittlestars, mussels, anemones, limpets and other chiton species.

Dyer's Gulch, Logy Bay is the location of one of the largest populations of T. marmorea studied during this program. It was assumed that this area would therefore possess many of the characteristics favourable to the survival of the chiton. The flora and fauna of Dyer's Gulch has been extensively described by Himmelman (1969) and Emerson (1974).

Colouration and Size

The mottled buff and red colouration of *Tonicella marmorea* made it difficult to distinguish from the background coraline algae and sponges. Variation in the patterns of mottling, as well as in the ratio of the buff to red colouration combined to produce colouration unique to each animal. Occasionally animals from a particular area appeared to be predominantly darker or lighter in hue than others. These differences were, however, of a very subtle nature, and not reliable as a method of discrimination between specimens sampled from different areas. No sexual dimorphism was evident in the external colouration of specimens of *T. marmorea* observed during this study period. Many of the chitons possessed bands of brilliant green in the dorsal surface of the girdle (Figure 6).

Also of note is an aquamarine colouration of *T. marmorea* found in Michael's Harbour, Notre Dame Bay (Figures 6 and 7). Five specimens with this peculiar colouration were collected and taken to the laboratory. Over the period of a year no changes were evident in the original colour and microscopic examinations were made to ensure that the colour was not a result of an encrusting algae or bryozoa. When preserved in 70% ethyl alcohol for 24 hours, the valves of these animals lost all colouration, unlike that of the other *T. marmorea* which retained, for the most part, their original colourations.

The mean maximum size range of each population of *T. marmorea* sampled is given in Table 2. Chitons sampled at Saglek Bay, Labrador, were significantly larger than chitons sampled from bays on the Newfoundland coast.

FIGURE 6: A NUMBER OF VARIATIONS IN THE COLOURATION OF SPECIMENS OF TONICELLA MARMOREA SAMPLED FROM SEVERAL LOCATIONS IN NEWFOUNDLAND.

FIGURE 7: COMPARISON OF THE UNUSUAL AQUAMARINE COLOURATION OF TONICELLA MARMOREA SAMPLED FROM MAICHAEL'S HARBOUR, N.D.B., AND THE 'NORMAL' COLOURATION OF TONICELLA MARMOREA SAMPLED FROM DYER'S GULCH, LOGY BAY.

(photographed against an atypical background)

TABLE 2: COMPARISON OF SAMPLE SIZE IN SPECIMENS OF <u>TONICELLA MARMOREA</u> SAMPLED FROM DIFFERENT AREAS OF NEWFOUNDLAND AND LABRADOR

Area	Mean Length (mm)	N	Mean Width (mm)	Mean Weight (gm)
Logy Bay	21.90	(39)	12.63	7.28
Notre Dame Bay	23.44	(10)	14.05	7.50
Fermeuse	19.00	(20)	11.35	5.34
Bay Bulls	21.09	(12)	12.07	6.53
Saglek Bay (Labrador)	38.62	(61)	19.44	37.09

Measurements of length, width and weight for individual animals, taken at three month intervals for one year did not demonstrate any trend in increase or decrease of size of T. marmorea. Variations in the size of these measurements were not large enough to be attributable to anything other than experimental error.

A number of chitons used in this study were kept in the laboratory for periods up to three years. Several of these animals died as a result of infections in the tagging area. Other causes of death included thermal stress resulting from accidental elevation of tank temperatures to 24°C, dessication and organ damage incurred during sampling. Data from animals which died during or shortly after experimentation was deleted.

Predation

During laboratory trials, T. marmorea was eaten by the seastar (Asterias vulgaris), crabs (Cancer spp.) and young lobsters (Homarus americanus). The chitons did not display any avoidance behaviour to any of these predators but responded to the initial touch of the seastar tube feet by clamping tightly to the substrate.

Asterias vulgaris when provided with other food such as capelin, Mallotus villotus (Miller) or mussels, Mytilus edulis Linnaeus did not eat Tonicella marmorea. The same was true for small crabs and lobsters.

Cunners (Tautogolabrus adspersus) did not eat specimens of T. marmorea exposed on the tank walls, but have been observed to actively prey on chitons in the field.[1] The cunner did not scrape chitons from the rock

[1] Personal communication with J.M. Green, 1973.

but bit completely through the protective valves and ate the soft visera.

Tonicella marmorea and Ischnochiton ruber are also preyed upon by the yellowtail flounder, Limanda ferruginea (Storer) and the winter flounder, Pseudopleuronectes americanus (Walbaum) (Barto-Wells, 1973).

Feeding Behavior

T. marmorea feedby rasping away encrusting flora and fauna from the substrate on which they moved. While feeding the animal moved in a straight line slowly over the substrate, holding the anterior margin of the girdle slightly above the substrate surface. The radula, which is long and equipped with large teeth, moved in and out at a rate of approximately 25 times per minute. Protrusion of the chemoreceptive subradular organs, as described by Fretter (1937), was not observed, but as food was abundant in the experimental tanks, their use may not have been required.

Laboratory observations of specimens of T. marmorea held in glass aquaria indicated that a close association between movement and feeding existed. Chitons which were stationary for periods of time exceeding two or three minutes did not exhibit any radular movement. Chitons which began moving over the glass walls of the aquaria were observed to initiate radular movement within seconds of the occurrence of the first pedal wave. In the field, animals distrubed during the dark hours while moving over the substrate had the radula extruded and in motion. Animals disturbed while at rest during the photoperiod did not exhibit radular activity. Similarly no radular activity was observed during the day in those animals clustered on glass walls of the aquaria. Chitons which were moving and feeding normally during the night hours would, if disturbed by artificial lights, either return rapidly to the home site or seek a new shelter. No feeding behaviour was observed during this movement.

The faeces of Tonicella marmorea were deposited as small cream coloured cylinders similar to those described by Arey and Crozier (1919) for Chiton tuberculatus. A 2.5 cm. long animal had a faecal pellet of 2 mm. in length and 0.5 mm. in thickness. They were emitted in mucoid chains of two or three which remained in the tanks for up to twenty four hours. No evidence of faecal masses were seen in the field. Detailed analysis of content was not carried out in this study, but preliminary examination indicated the presence of granular particles and fibrous tissues.

Defecation in T. marmorea occurred randomly throughout a 24 hour period, even while actively feeding at night.

Reproduction and Development

Spawning of Tonicella marmorea was observed only once during the study. On June 25, 1973, from approximately 1415 to 1630 hours, three females and three males spawned repeatedly in the holding tank at the laboratory.

All of the spawning chitons had moved to sunny, exposed positions on the upper surface of the rocks in the holding tank. The water temperature in the tank was 7°C. During spawning, the posterior edge of the mantle was lifted 2-3 millimetres (Figure 8). Sperm and ova were extruded from

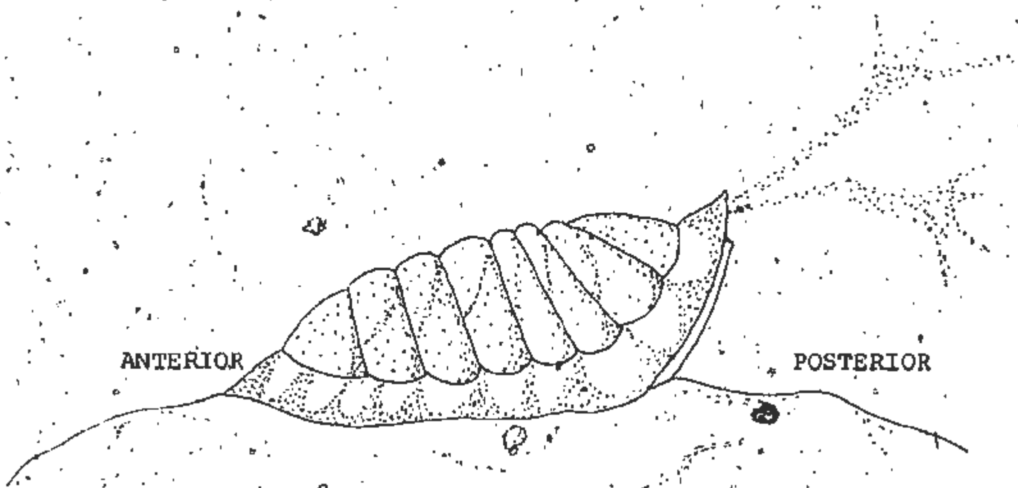

FIGURE 8: ILLUSTRATION OF A SPAWNING MALE SPECIMEN OF <u>TONICELLA MARMOREA</u>.

the region of the brachial chambers in two parallel streams. The sperm was milky-white in colour and quickly dispersed in the water. The bright red ova were emitted one or two at a time and were held together by a gelatinous material. During the period of observation the three females emitted 594 ova, of which 131 were collected (Table 3). Gastropods (Margarites spp) were observed actively eating the newly laid eggs.

Disturbance of the spawning behaviour occurred while the author was collecting sperm and ova with a pipette. The chitons so disturbed immediately ceased emission of gametes and lowered the girdle margin to the substrate. Spawning behaviour resumed within seconds of removal of the pipette.

The three females spawned continuously throughout the two and one half hour observation period, and stopped within five minutes of each other. Only one of the males was spawning initially. The others began about one hour after the initial observation. The tank contained more than thirty other mature chitons but no reaction was observed when sperm were released near each of them.

No other chitons spawned in the laboratory during the remainder of the study and no observations were made of chitons spawning in the field.

Three days after the laboratory spawning, specimens of T. marmorea from the laboratory and the field were examined and found to contain well developed ova & sperm. The gonadal tissue of the males is coloured milky-white while that of the females is bright red.

The ovum of T. marmorea is approximately 0.2 mm. in diameter (Table 4) and is enclosed in a hairy chorion (Figure 9). The ova and the newly fertilized zygotes were demersal. The chorion fibrils tended to

TABLE 3: SIZES OF SPAWNING TONICELLA MARMOREA, WITH NUMBERS OF OVA COLLECTED FROM EACH FEMALE, AFTER ONE HOUR OF SPAWNING.

Chiton	Length (cm)	Sex	Number of Ova
1	1.9	Female	93
2	2.0	Female	15
3	2.0	Female	23
4	2.4	Male	-
5	2.2	Male	-
6	2.2	Male	-

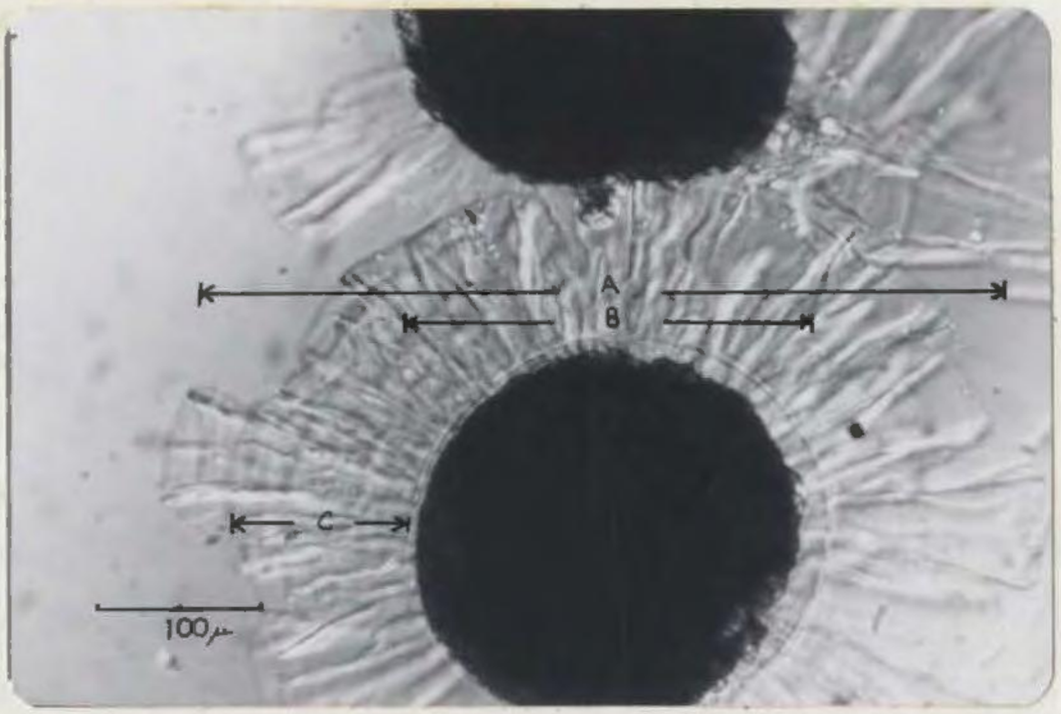

FIGURE 9: MICROPHOTOGRAPH OF TONICELLA MARMOREA OVUM/ZYGOTE, TAKEN FOUR HOURS AFTER SPAWNING.

A TOTAL DIAMETER OF OVUM/ZYGOTE
B DIAMETER OF THE CORE
C WIDTH OF THE CHORION FIBRILS

TABLE 4: SIZE (μ) OF THE OVUM/ZYGOTE OF TONICELLA MARMOREA FOUR HOURS AFTER SPAWNING. (REFER TO FIGURE 9 FOR EXPLANATION OF MEASUREMENTS).

Ovum/Zygote	(A) Total Diameter (μ)	(B) Core Diameter (μ)	(C) Width of Chorion (μ)
1	544.0	238.0	153.0
2	527.0	255.0	136.0
3	544.0	238.0	153.0
4	561.0	272.0	144.5
Mean	535.20	250.75	146.6

catch easily in any rough surface thus securing the ovum or zygote to the substrate.

Four days after spawning, on June 28, the first of the zygotes metamorphosed into trochophore larvae. Within twenty-four hours all viable zygotes had metamorphosed. The trochophore larvae were pale orange in colour and radially symmetrical (Figure 10C). Each possessed two flagellae at the anterior pole and were capable of swimming.

On July 10, twelve days after hatching, the larvae became flattened dorsoventrally. Two reddish cells such as those described for Lepidopleurus asellus (Spengler),(Christiansen, 1954) appeared on the ventral surface. Bands of clear cells appeared on the dorsal surface marking the beginning of the formation of shell plates (Figure 10D). These larvae were active and swam in a spiralling motion similar to that described for Lepidopleurus asellus (Christiansen, 1954)(Figure 11). At this stage the larvae appeared somewhat negatively phototropic and were found within 3-5 cm. of the substrate during the daylight hours. At night the larvae were most often near the surface of the water. At this time various types of substrate were placed in beakers.

On July 17, nineteen days after hatching, three larvae settled on a smooth pebble approximately 5 cm. in diameter. The newly settled chitons each possessed eight valves of a delicate pink colouration. They were approximately 1.0 mm. long and 0.5 mm. wide (Figure 10E). Within three days of settling all three chitons had become infested with a fungoid growth and died. No other settling occurred, although there were active larvae up to twenty five days after spawning.

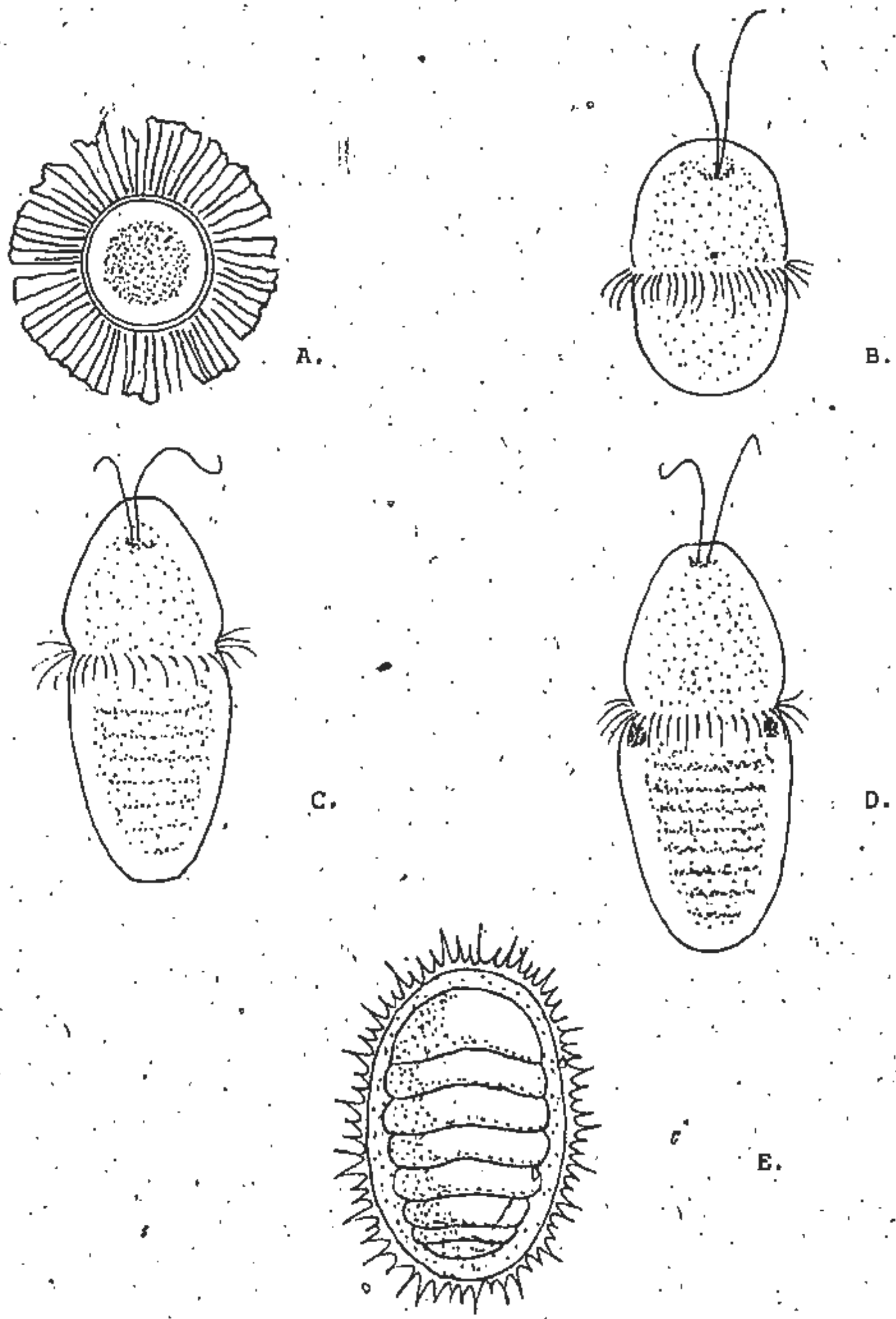

FIGURE 10: PHASES OF LARVAL DEVELOPMENT IN <u>TONICELLA MARMOREA</u> A. ZYGOTE B. TROCHOPHORE C. LARVA WITH VALVE DEVELOPMENT D. LARVA WITH OCELLS (EYESPOTS) E. SETTLED CHITON.

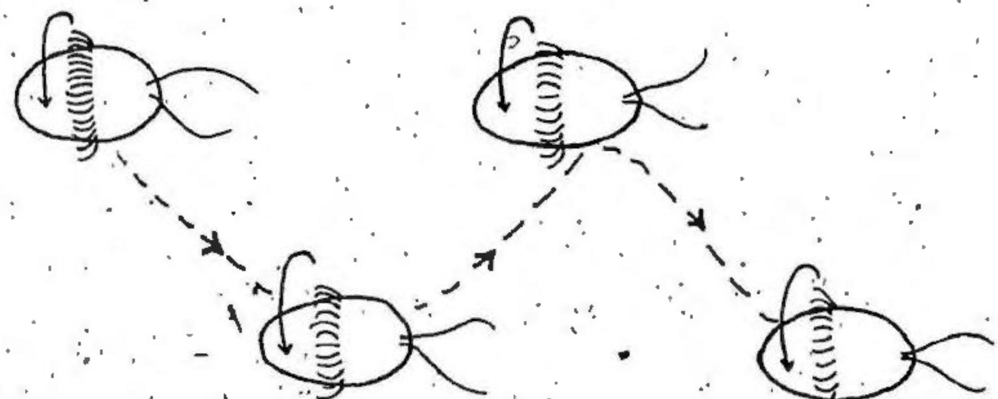

FIGURE 11: ILLUSTRATION OF THE SPIRAL SWIMMING MOTION OBSERVED IN THE TROCHOPHORE LARVAL STAGE OF TONICELLA MARMOREA (NOTE THE ROTATION OF THE LARVA AROUND ITS LONGITUDINAL AXIS)

General Observations on Behavior

Chitons cling to the substrate on which they live by means of suction created by the girdle and foot. When relaxed the girdle rests loosely on the substrate, with attachment due to the suction of the foot alone. When disturbed, however, the girdle is clamped hard to the substrate and the foot arched to provide greater suction. If the animal is removed from the substrate this clamping action continues and the animal rolls up in a manner not unlike that of the armadillo, with the anterior and posterior ends lying in close contact, often one above the other (Arey and Crozier, 1919). The author has observed instances when the curling action has been so severe that either the anterior or posterior portion of the viscera has been gouged by the opposite girdle and valves, resulting in death.

When in the curled position the chiton is involuntarily rolled over onto its side as a result of the curvature at its middorsal line. It is impossible for T. marmorea to right itself from this position, when on a flat, smooth substrate. The righting procedure involves straightening of the curl and extension of the girdle and foot towards the substrate. Unlike limpets (Gastropoda) chitons do not have the ability to extend the foot to the degree necessary to accomplish the righting manoeuvre on a flat surface. Observations made in the field of curled specimens of T. marmorea demonstrated that on an irregular surface, such as a pebble bottom, these chitons are able to extend the foot enough to obtain contact with some portion of the substrate and eventually right themselves.

Movement in chitons is the result of muscular waves which move anteroposteriorly along the foot (Parker, 1913; Crozier, 1919a; Hyman, 1967).

T. marmorea moves both forward and backward in this manner. Backward motion is accomplished by changing the direction of the pedal wave. *T. marmorea* was never observed to move backwards for distances greater than 2 cm. Sharp turns are effected by releasing the anterior and posterior portions of girdle and foot and pivoting the body mass on the attached, central portion of the foot. The chiton usually moves in a relatively straight line, as opposed to the zigzag fashion often characteristic of gastropods.

When *T. marmorea* was moving across a loosely packed substrate, such as gravel, the exterior margins of the girdle were lifted a fraction of a millimetre. When *T. marmorea* was moving across a solid substrate which had a light layer of sediment or gravel on it, the anterior portion of the girdle was kept close to the substrate surface and acted as a plow. This behavior ensured that small particles were moved out of the path of the chiton, and was possibly a protective mechanism to prevent fouling of the gills.

As was stated on page 21, *T. marmorea* is not normally found in sandy areas. The chiton will avoid moving on sand or mud, and has only been observed to do so when faced with a lack of food. However, specimens of *T. marmorea* were found on the valves of the deep sea scallop, *Placopecten magellanicus* (Gmelin) in Salmonier Arm, St. Mary's Bay. The bottom in this area was composed entirely of a fine, loosely-packed sand. No observations were made of *T. marmorea* moving over the sand, even though distances of up to 10 m. separated individual scallops.

Hyman (1967) stated that chitons avoid spiky rock surfaces, as well as mud and sand. Throughout the present study *Tonicella marmorea* was not observed to avoid sharp surfaces such as the edges of glass sheets and scallop shells. When attempting to move around such an edge the chiton was seen to approach it and release the anterior portion of the girdle and foot from the substrate. As the posterior portion continued to move forward, the anterior half " cast about " before bending forward until it touched the underside of the plate or shell. Once the anterior portion had attached, the posterior half was released and pulled around (Figure 12). This same behavior was observed when T. marmorea moved from the substrate onto a rock or shell, or vertical tank wall. The anterior portion was first released and reattached , then the posterior portion (Figure 13). T. marmorea was capable of these actions only because of its unique eight-plated shell and body musculature. This behavior also demonstrated the ability of the foot to localize suction , large enough to support the full body weight, in small areas of the foot surface.

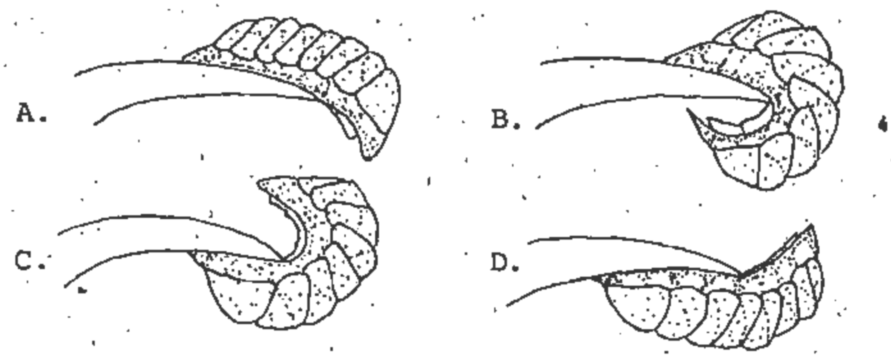

FIGURE 12: ILLUSTRATION OF A SPECIMEN OF <u>TONICELLA MARMOREA</u> MOVING AROUND A SHARP EDGE. A. RELEASING THE ANTERIOR PORTION OF THE FOOT AND GIRDLE. B. REATTACHING ON THE LOWER SURFACE. C. RELEASING THE POSTERIOR PORTION OF THE FOOT AND GIRDLE. D. REATTACHING.

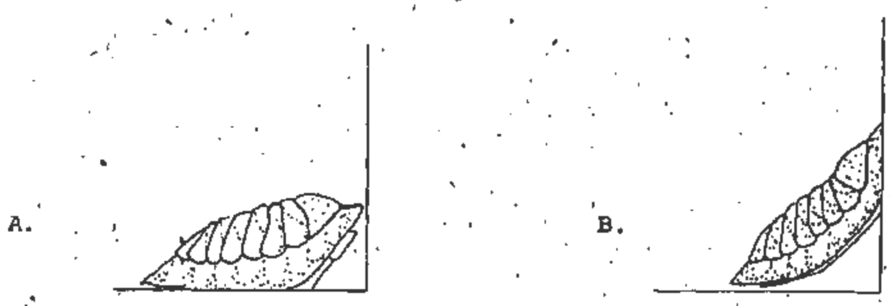

FIGURE 13: ILLUSTRATION OF A SPECIMEN OF <u>TONICELLA MARMOREA</u> MOVING FROM A HORIZONTAL TO A VERTICAL SURFACE. A. RELEASING ANTERIOR PORTION OF FOOT AND GIRDLE, ARCHING BODY. B. REATTACHMENT ON THE VERTICAL SURFACE, RELEASE OF THE POSTERIOR PORTION.

CHAPTER II: DISCUSSION

Although the members of the Polyplacophora bear perhaps the closest resemblence to the typified " ancestral mollusc " of any of the extant molluscan classes, the chitons are not primitive or simple molluscs. Through use of highly specialized morphological structures and complex behavioral mechanisms , the chitons of today are common throughout the world's oceans and have adapted to widely ranging environmental parameters. In comparison with many tropical, littoral species of the Polyplacophora, the biology and ecology of T. marmorea is not complex. The sublittoral niche it occupies does not experience such extremes as large daily temperature fluctuations and dessication, but the chiton has adapted in a number of ways so as to best survive in this area.

Langer (1972) found that the dominant species in a chiton population composed of T. marmorea, T. rubra and I. albus varied with increasing water depth. In his work in Eastport, Maine, Langer noted that T. rubra was the dominant species in the shallow sublittoral zone, and that the population size of this species decreased with increases in water depth. T. marmorea, however, was scarce in shallow water but increased in numbers with increasing depth. T. marmorea became the dominant species at the 7.5 metre station. The numbers of I. albus did not exceed the populations of either T. marmorea or T. rubra at any depth, but I. albus was most plentiful at a depth of 7.5 metres (Langer, 1975).

Although no detailed measurements of the distribution of these three species were made during this study, general observations on the distribution of T. marmorea and T. rubra would agree with the conclusions of Langer. I. albus, however, is not plentiful on the coast on Newfoundland.

Like many Polyplacophorans, T. marmorea possesses a mottled colouration which blends well with the coralline algae-covered rocks on which the chiton lives. The green banding present in the girdle of some of the specimens of T. marmorea sampled may be the result of algae growing on the girdle surface, as was observed for Chiton tuberculatus (Arey and Crozier, 1919).

Although measurements of length, width and weight were taken for laboratory specimens of T. marmorea, no reliable information on the rate of growth of this species was obtained. Variations in the size of individual chitons were of such small magnitude that experimental error probably accaounted for the entire fluctuation. Measurements of length and width are difficult to standardize in Polyplacophorans, as the animals possess great flexibility of body shape and size. Expansion and contraction of the spaces between the valves, and the girdle, as well as the ability to bend the body about the central axis, cause great variations in the size of the organism. There was a margin of error in the wet weight figures resulting from variations in the amount of water remaining after the animal had been blotted dry.

Growth rates for Polyplacophorans vary with the maximum attainable size of the animal. At Cape Cod, Massachusetts, Chaetopleura apiculata (Say), a subtidal species, reached its maximum size of 25 to 29 mm. in three years, was sexually mature in one year and probably lived to an age of four or five years (Grave, 1932). Glynn (1970) found that specimens of Acanthopleura granulata (Gmelin) grew at a mean rate of 3.8 mm. per month for the first year, and at a slightly slower rate thereafter. As the mean variation in lengths of the specimens of T. marmorea was only 1 or 2 mm. after a period of nine months, growth was assumed to have ceased in these animals.

Intertidal species of the Polyplacophora are preyed upon by fish, seastars, crustaceans, carnivorous molluscs, rodents and sea birds (Glynn, 1970; DeBevoise, 1975; Moore, 1975; Seiff, 1975). T. marmorea is protected from terrestrial predators by its sublittoral exhistance. Its colouration, nocturnal habits and inaccessibility by day may help to protect it from sublittoral predators. The abundance of this chiton in certain areas of coastal Newfoundland and Labrador indicated either its ability to avoid or escape predators or its undesirability as a major food source for many species. During laboratory trials, it appeared that T. marmorea had no sophisticated escape behavior. It also appeared that the chiton was a minor food source for most of its predators. Similar information on predation was obtained for subLittoral Tonicella lineata (Wood), a Pacific species very like Tonicella marmorea (Seiff, 1975).

The majority of chitons are herbivorous (Heath, [illegible]9; Arey and Crozier, 1919; Fretter, 1937; Glynn, 1970; Demopulos, 1975; Nishi, 1975; Ro[illegible] 1975; and Fulton, 1975). However, Barnawell (1959) reported carnivorous feeding in the Mopaliidae, where 15 to 60% of the gut contents of various species was composed of sponges, hydroids, polyzoans, annelids and small Mytilus. This phenomenon was attributed to the indiscriminate grazing action of the radula. Arey and Crozier (1919) reported that the radula of Chiton tuberculatus removed some of the rock surface, as well as the encrusting algae. Tonicella lineata feeds mainly on the corallinealgae in the Monteray Bay area of California (Demopulos, 1975). However, Langer[2] found no trace of $CaCO_3$ in the gut contents of more than two thousand specimens of Tonicella marmorea, and no evidence of feeding on coraline algae was observed during his study. Similarly no evidence of feeding on coraline algae was noted during the present study.

The nocturnal feeding habits of T. marmorea were not unusual for subtidal chitons. Demopulos (1975) found that feeding activity in the subtidal populations of T. lineata took place mainly during the dark hours. Similar behavior was also noted for Acanthopleura granulata and Chiton tuberculatus (Glynn, 1970). Glynn also noted that locomotory

[2] Personal communication with P. Langer, 1972

movements and feeding were closely related activities, and that chitons at rest do not feed.

Spawning behavior in T. marmorea was similar to that described in chiton species such as Chaetopleura apiculata (Grave, 1922); Lepidopleurus acetlus (Christiansen, 1954); Chiton marmoratus (Linnaeus) and Chiton squamosus (Linnaeus) (Metcalf, 1893); and Mopalia lignosa (Gould) (Watanabe and Cox, 1975). Unlike Mopalia lignosa, no movement of males or females of T. marmorea was observed during spawning.

Development of the trochophore larvae, and settling of the zygote of T. marmorea, did not differ significantly from development of other chitons (Grave, 1922; Christiansen, 1954; Watanabe and Cox, 1975), except with respect to the time intervals between the appearance of each developmental stage. This variation was difficult to standardize as the time required for development of the metamorphosed, settled chiton changed with the availability of preferred settling substrate. Watanabe and Cox (1975) found that metamorphosis in M. lignosa and M. muscosa was delayed or prevented by the lack of an appropriate settling substrate. Only two out of several hundred larvae underwent complete metamorphosis when glass was the only substrate available. Addition of Mytilus sp. shells to the tanks containing larvae of both species resulted in almost immediate metamorphosis. Similar responses were recorded for T. lineata (Barnes and Gonor, 1973). When presented with an assortment of settling substrate, metamorphosis of T. lineata occurred only on coraline algae. As only a small portion of the settling substrate offered to the larvae of T. marmorea during the present study was composed of coraline algae, the poor settlement and metamorphosis observed may have been the result of the absence of this, or other preferred substrate.

The information provided by this study on the biology of *Tonicella marmorea* is useful primarily as a source of baseline information. From this information more detailed work on specific aspects of the biology and habits of the organism can be performed, and possible explanations of the parameters affecting behavior and activity can be made.

CHAPTER III: BEHAVIOR AND MOVEMENT

RESULTS

Response to Stimuli

(a) Thigmotaxis

Tonicella marmorea responded immediately to tactile stimuli. The intensity of the response varied with the region of the body stimulated. The margins of the girdle reacted to touch by contracting medially a distance of several millimetres. Repeated stimulation usually resulted in the characteristic " clamping " action of the chiton. (The girdle is firmly attached to the substrate and the foot arched, providing a great deal of suction.) When in this position T. marmorea no longer responded to tactile stimuli and remained firmly fixed for periods varying from two to three minutes to three hours after the stimulus had been removed.

The dorsal and ventral surfaces of the girdle were not as sensitive as the margins, and responded with localized contractions to light touches of the probe. Stimulation of the anterior margin of the girdle caused the entire animal to react. The girdle section was rapidly withdrawn and the chiton backed away, turning so that the anterior end faced in a new direction. Moving chitons responded to tactile stimuli on the anterior girdle by immediate changes in direction, or " clamping ". No such response was exhibited when the posterior portion of the girdle was touched.

No response was exhibited when the dorsal surfaces of the valves were lightly touched with the probe. However, when the probe was allowed to remain in contact with the valves for several seconds, the animal clamped to the substrate. Spaces between the valves were sensitive , as was found by Arey and Crozier (1919) for Chiton tuberculatus. Tactile stimulation of this region resulted in a drawing together of the valves, to cover the stimulated area.

The central surfaces of the foot of T. marmorea was also very sensitive to touch. Animals lying on their dorsal surface, or moving so that a small portion of the foot was exposed responded to a quick jab by curling immediately.

T. marmorea did not show any tendency to aggregate beneath the glass plates. The four animals placed in the petri dishes tended to accumulate at the crevice formed where the sides met the bottom of the dish. No animals were found beneath the glass sheets. Of the four animals placed on the glass, three remained on the upper surface, one moved to the lower, released and lay on its back as there was not enough space to curl.

(b) Geotaxis

Of the six chitons placed on the submerged, vertical sheet of fibreglass, two did not move during the forty-eight hour period. The remaining four chitons moved randomly over the fibreglass during the dark hours and spent the daylight hours at various positions on the fibreglass sheet. No downward trend was observed in movements, and no preference was given to the lower edge of the sheet as a resting site.

The movement of T. marmorea on a vertical surface exposed to air were generally downward (Table 5, Figure 14). In two trials a total of 21 out of 36 chitons tested exhibited a downward orientation.

When the experiment was repeated using a light flow of water to prevent dessication, the results were very different (Table 5, Figure 15). For the most part the chitons, on contact with the water current, either clamped tightly to the glass or curled and dropped off. In all three trials only a little movement was detected and consisted mostly of slight shifts in position. A number of animals allowed portions of the girdle to release and set up small respiratory currents while the rest of the girdle remained firmly attached.

(c) Rheotaxis

As soon as the water current made contact with chitons on the glass sheet all of the animals clamped to the substrate. Within thirty seconds of the introduction of the water flow all ten chitons had released, curled and been moved into quiet water by the current. The same effect was observed with the chitons in the tubing. Repetition of the experiment with decreasing current strength served only to prolong the time before the

TABLE 5: GEOTAXIC RESPONSE OF TONICELLA MARMOREA WHEN EXPOSED TO AIR, WITH AND WITHOUT A DAMPENING WATER CURRENT.

	Number of Chitons	Orientation of Anterior Position of the Body				No Response	Curled
		Up	Down	Left	Right		
No water current	18	2	10	0	1	4	1
	18	3	11	1	0	3	0
Water current	11	1	0	3	0	4	3
	11	0	0	0	1	5	5
	11	0	1	1	0	5	4

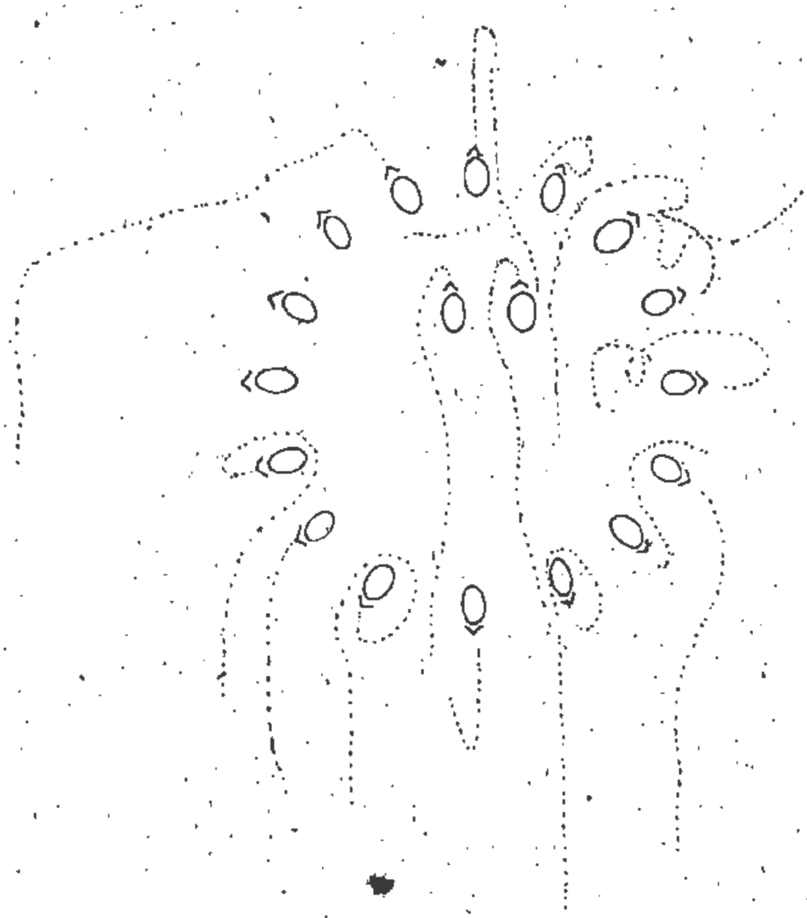

FIGURE 14: MOVEMENT OF 18 SPECIMENS OF <u>TONICELLA</u> <u>MARMOREA</u> AFTER ONE HOUR ON A VERTICAL GLASS SHEET, EXPOSED TO AIR AND WITHOUT A CONTINUOUS SUPPLY OF WATER.

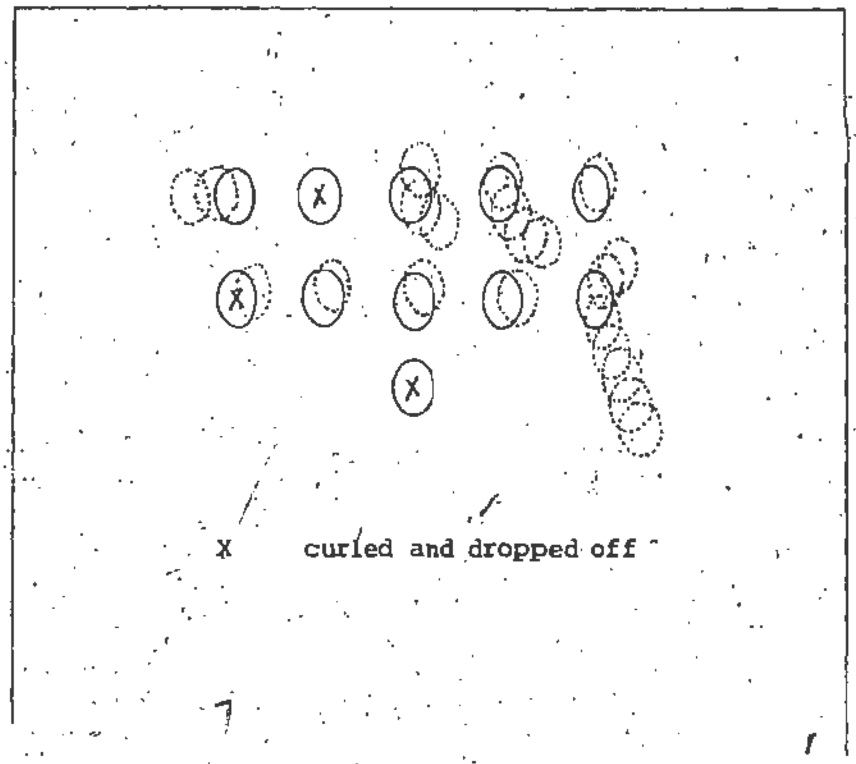

FIGURE 15: MOVEMENT OF 11 SPECIMENS OF <u>TONICELLA MARMOREA</u> AFTER ONE HOUR ON A VERTICAL GLASS SHEET, EXPOSED TO AIR BUT WITH A SLIGHT CURRENT OF WATER RUNNING OVER IT.

animals released and curled. Even with slight water flow, clamping was evident. None of the animals resettled until they were moved to quieter water.

(d) Phototaxis and Response to Photoperiod

Table 6 lists the responses of thirty-eight specimens of T. marmorea to a directional light source. Twenty-five of the thirty-eight test animals responded negatively to light. Of the remaining thirteen, five exhibited no response during the study period, seven moved to the left or right of the light source and one chiton moved toward the light.

Thirty of the thirty-eight chitons turned to move away from the light source. Of these, twenty-two turned to the right, whereas only eight turned to the left.

Chitons placed in the controlled light chamber immediately adjusted to the new light/dark cycle. No movement was observed during what would have been the normal dark cycle. Even though the cycles were interchanged a number of times, the chitons readily adapted to each new regime, moving only when the lights were off, no matter what the normal photoperiod was.

The results of the twenty-four hour activity study are given in Table 7, Figure 16. Movement was observed in twenty-eight of the fifty chitons studied. All activity took place between 1630 on April 9 and 0730 on April 10. The remaining 22 chitons were not observed to move during this period, remaining concealed beneath the small stones

TABLE 6: RESPONSE OF TONICELLA MARMOREA TO A DIRECTIONAL LIGHT SOURCE

Number of Chitons	Orientation of Anterior to Light				No Response
	Away from	Toward	Right	Left	
5	5				
4	3	1*			
3	3				
3	3				
3	2			1	
2	0		2		1
3	1			1	
3	2		1		
2	2				
8	3			1	4
2	1			1	
38	25	1	3	4	5

* chiton was covered in sand

TABLE 7: HOURLY ACTIVITY OF A POPULATION OF TONICELLA MARMOREA FROM 1630 HOURS, APRIL 9, TO 0930 HOURS, APRIL 10, 1974. (HELD UNDER NATURAL LIGHTING CONDITONS IN THE LABORATORY)

	ACTIVITY (cm.) PER HOUR PER CHITON																			
	1630 1730	1730 1830	1830 1930	1930 2030	2030 2130	2130 2230	2230 2330	2330 0030	0030 0130	0130 0230	0230 0330	0330 0430	0430 0530	0530 0630	0630 0730	0730 0830	Number Hours Active	Total Distance Travelled (cm)	Mean Distance Travelled (cm)	Standard Error
1	-	12	12	12	3	6	9	9	30	30	-	-	-	-	-	-	9	123.	13.67.	3.24
2	-	14	16	9	9	3	3	6	12	24	-	-	-	-	-	-	9	96	10.67	2.25
3	4	22	28	6	3	6	15	15	24	12	12	12	12	12	12	-	15	195	13.00	1.85
4	6	20	28	21	9	6	12	6	9	12	12	12	-	-	-	-	12	153	12.75	1.99
5	12	24	36	6	18	24	18	3	21	18	18	21	-	-	-	-	12	219	18.25	2.49
6	-	8	13	6	3	3	3	3	18	6	6	3	12	9	-	-	13	93	17.15	1.31
7	15	45	30	3	3	12	24	18	6	6	6	6	6	6	-	-	13	186	13.29	3.28
8	-	20	16	12	9	9	6	9	18	24	8	10	12	12	-	-	13	165	12.69	1.47
9	-	10	11	12	12	6	6	6	12	12	12	12	15	21	6	-	14	153	10.93	1.11
10	-	6	9	6	9	9	3	9	6	6	6	6	-	-	-	-	11	75	6.82	0.58
11	-	3	6	6	12	-	-	-	-	-	-	-	-	-	-	-	11	27	6.75	1.89
12	-	6	9	6	6	-	-	-	-	-	-	-	-	-	-	-	4	27	6.75	0.75
13	-	24	24	3	-	-	3	-	8	-	-	-	-	-	12	-	4	74	12.83	3.94
14	-	15	15	6	6	6	6	12	21	3	2	1	1	1	3	-	8	98	7.00	1.69
15	-	6	6	3	9	-	-	-	-	-	-	-	-	-	-	-	14	24	6.00	1.22
16	3	9	12	9	-	3	-	3	6	6	24	24	-	-	-	-	10	99	9.90	[illegible]
17	-	-	-	30	-	-	-	3	6	6	3	3	6	9	3	-	5	69	7.67	2.88
18	3	9	12	12	-	3	-	3	-	-	3	2	1	-	-	-	9	48	5.33	1.46
19	-	-	6	-	10	6	6	-	-	12	6	6	9	9	-	-	9	61	7.78	0.76
20	-	3	6	1	12	3	-	-	-	-	-	-	-	-	-	-	5	25	5.00	1.92
21	-	6	6	3	3	3	6	9	6	9	-	-	-	6	-	-	10	51	5.70	0.70
22	4	16	37	12	3	1	-	-	-	-	-	-	-	-	-	-	6	73	12.17	5.50
23	-	20	30	15	3	3	3	-	-	-	-	-	-	-	-	-	6	74	12.33	4.62
24	-	3	3	-	12	-	-	-	-	-	-	-	-	-	-	-	3	18	6.00	3.00
25	6	24	33	12	18	3	1	6	6	-	2	1	6	-	-	-	12	118	9.83	2.93
26	-	15	6	30	30	-	12	6	6	3	-	-	-	-	-	-	7	108	13.50	3.85
27	-	-	-	-	-	-	-	-	3	3	1	2	57	18	3	-	7	87	12.43	7.75
28	-	1		6	9	3	3	6	21	-	-	-	-	-	-	-	8	51	6.38	2.28
Total Activity per hour (cm)	53	341	412	247	211	118	139	132	239	192	121	121	137	103	39	0				
Mean Activity per hour (cm)	6.63	13.64	15.85	9.88	9.17	5.90	7.72	7.33	12.50	11.29	8.07	8.07	12.45	10.30	6.50	0				
Standard Error	1.58	1.97	2.16	1.51	1.34	1.13	1.46	1.01	1.82	1.98	1.68	1.84	4.66	18.5	1.80	0				
Number of Chitons Active	8	25	26	25	23	20	18	18	19	17	15	15	11	10	6	0				

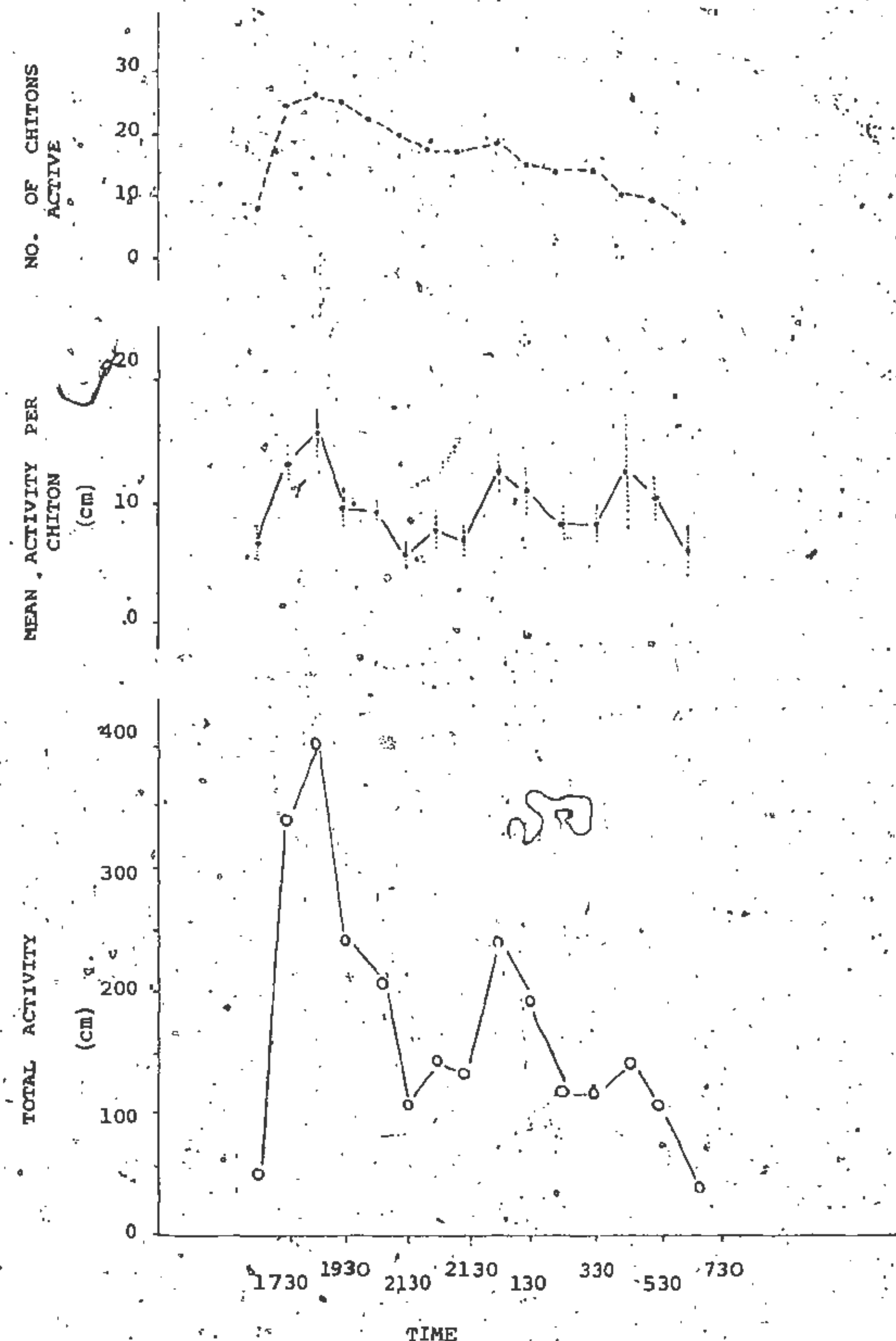

FIGURE 16: MEAN HOURLY ACTIVITY OF 28 SPECIMENS OF TONICELLA MARMOREA RECORDED DURING THE DARK HOURS OF A TWENTY-FOUR HOUR STUDY.

on the bottom of the experimental tank. Any activity which may have taken place while the chitons were so concealed was too small to have been significant in this study. Sunset on April 9 occurred at 1837, and sunrise on April 10 was at 0526.

T. marmorea was most active during the period just before and after sunset. Twenty-five of the twenty-eight active chitons were observed to commence movement at this time. The mean distance travelled per hour per active chiton during this period was 14.21 to 15.73 cm. For the remainder of the night the number of active chitons diminished. Those chitons which had not yet begun to move by 0130 remained inactive throughout the night. Also by 0130 many of the chitons which had been active earlier, had ceased movement.

A second activity peak, smaller than the first, was noted from 0030 to 0130 hours. Mean activity per chiton was 12.53 cm. Nineteen animals were active.

A third activity peak was noted to begin just before sunrise and lasted untill just after sunrise, 0430 to 0530. Mean activity per animal was 12.45 cm. Eleven animals were moving. From this time to 0830 hours, movement per animal, and total number of active animals, dropped rapidly. Activity from 0730 to 1430 hours was negligible.

Throughout the night few chitons moved at constant speeds. Most were observed to feed continuously for a few hours, then movement slowed before a second period of activity began. Not all chitons remained active during the entire night. The mean number of active hours per chiton was 9.0, even though the dark photoperiod was 11 hours. Mean total movement per chiton for this dark period was 92.50 cm. The total distance travelled per chiton ranged from 24 cm. to 219 cm.

Movement

The field studies on population movement were abandoned early in the program due to the failure to find a successful method of "in situ" tagging, or replacement of chitons in the field after tagging.

Laboratory studies on movement demonstrated that T. marmorea possessed the ability to return to a particular site or 'home'. The chiton accomplised this either by retracing its own trail, by following an old trail left by another chiton, or by taking an entirely new route. However, homing in specimens of T. marmorea studied during this program was not consistent. Changes in the resting site occurred frequently and at irregular intervals. Often a chiton would return to a resting site only once or twice, before moving to a new location. Instances of fifteen or twenty repeated homings to a single site were recorded during the program, but were rare. Great variation in the number of homings recorded existed between individual chitons, and no regular patterns of homing were established for each individual.

From March 14 to April 11, 1974, the movements of 44 chitons were monitored for 29 days, making a total of 1276 observations. During this period, 197 observations of homings (25% of observed movements) were made (Table 8). This figure represents individual instances when one chiton returned to a site for one day. Quite often the resting sites varied with each instance of homing.

Because of the irregularity of the homing response and the tendency to change resting sites, it was hypothesized that T. marmorea might be returning to a particular territory or home range. Of the 1276 observations made during this period, 454 chitons did not move. Of the

TABLE 8: FREQUENCY OF OCCURRENCE OF SPECIMENS OF *TONICELLA MARMOREA* AT VARYING DISTANCES FROM THE LAST OCCUPIED RESTING SITE. THE MOVEMENT OF 44 SPECIMENS OF *TONICELLA MARMOREA* WAS MONITORED FOR THE PERIOD MARCH 14 TO APRIL 11, 1974

		Distance (cm) from last resting site						
		0		1-10	11-20	21-30	31-40	41+
Number of Chitons Studied	Total Number of Observations	No Observed Movement	Observed Movement (Homing)					
44	1276	454	197	117	109	95	37	267

remainder, 314 (38.2%) were found within 10 cm. of the last resting site and 508 (61.8) were found at distances greater than 10 cm. As well, these distances applied only to the immediate last site. Specimens of T. marmorea were, after 10 days, often displaced as much as 100 cm. from the original resting site (Figure 17).

Chitons disturbed by lights while moving at night, often returned to the immediate last site. However, chitons displaced to a new area did not show any tendency to return to the capture site.

Great variation in the distance moved each night was observed between individual chitons, as well as between consecutive activity periods of the same chiton. Often animals which had been observed to move little and home regularly, for periods of up to two weeks, died shortly thereafter.

Throughout the study period T. marmorea demonstrated a definite tendency to remain in certain types of habitat (Table 9, Figure 18). These included the four corners of the tank, the crevices formed where the sides and bottom of the tank met, and the two areas composed mostly of 2 to 5 cm. diameter stones, coralline algae, rubble and mollusc shells. The least frequented sites were composed of artificial habitats such as glass flasks and jars, and pieces of PVC tubing. However, rocks which did not provide cracks and crevices into which the chitons could wedge, were also avoided. Sites composed of, or containing , live organisms such as anemones (Tealia spp.) and scallops (Placopecten magellanicus) were seldom used as resting sites.

T. marmorea was observed , both in the field and the laboratory, to occur in clusters or groups at resting sites. The composition of

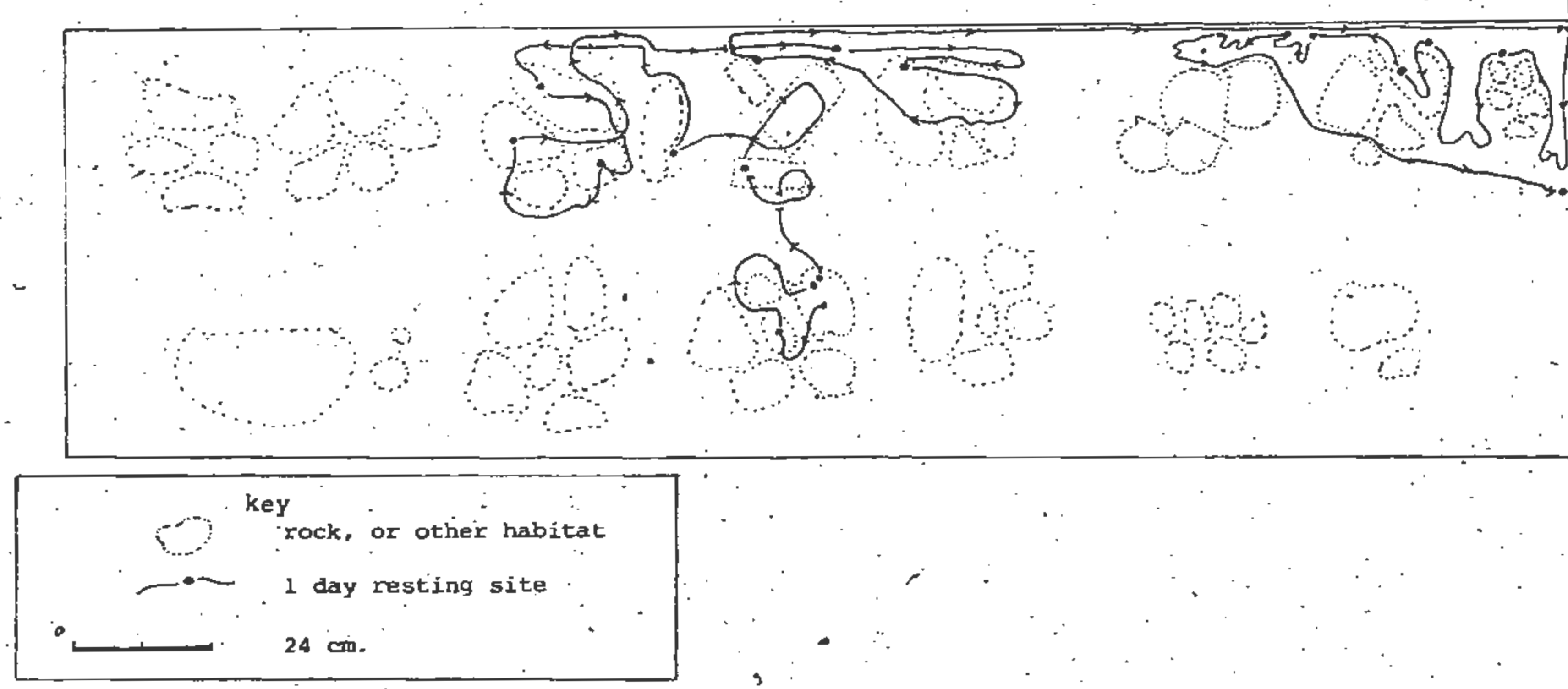

FIGURE 17: MOVEMENT OF A SPECIMEN OF <u>TONICELLA MARMOREA</u> OVER A 20 DAY PERIOD.

TABLE 9: FREQUENCY OF OCCURRENCE OF SPECIMENS OF TONICELLA MARMOREA ON VARIOUS TYPES OF HABITAT IN THE EXPERIMENTAL TANKS.

	Smooth Rock			Rough Rock		Artificial	Live	Scallop	Rubble****
	without crevices	with crevices	with coralline algae	without crevices	with crevices	Habitat*	Organisms**	Shells***	
Number of sites	11	11	2	17	2	3	3	3	2
Total occurrence	28	156	63	93	33	10	2	58	116
Mean per site	2.6	14.2	31.5	5.5	16.5	3.3	0.7	19.3	58.0

* glass sheets, PVC tubing
** P. magellanicus, Tealia spp.
*** P. magellanicus
**** small pebbles, coralline algae, and Mytilus edulis shells

10	198		3	8	1	2	5	9	4	1	4	3	4	4	2	5	1	1	4	2	6	9	2	3	3	4	6	10	6	3	1		5	98
9	4		3																															7
8																																		18
7	3	1					1					1										1												17
6													1				1								1	1			1			1		5
5	1																										1							2
4	7																											3						8
3	2																															1	2	7
2	4																															2		2
1	112	3	5	4	2	3	2	5	2	4	8	8	2	1	4		2	1	3	3	7	11	2	10	13	4	7	4	5	6	6	10	10	73
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34

24 cm.

FIGURE 18: SCHEMATIC DRAWING OF THE BOTTOM OF THE EXPERIMENTAL TANK SHOWING THE FREQUENCY OF OCCURRENCE OF EXPOSED SPECIMENS OF TONICELLA MARMOREA, PER GRID AREA.

the clusters observed in the laboratory changed as new recruits entered and others left. If the habitat consisted of a large rock with only one commonly frequented resting site, chitons new to the area were generally found at this site, whether or not other chitons were present. If the crevice was large and contained two or more chitons, the chitons would generally be clustered together at one end, rather than sparsely scattered over the crevice.

During the November-December study of long term activity of a laboratory population of T. marmorea, the mean distance travelled per chiton per night ranged from 10.3 cm. on December 3 to 71.7 cm. on November 17 (Table 10). The mean distance travelled per chiton per night for the study period was 37.6 cm.

In the March-April study activity ranged from a mean of 32.8 cm. on March 14 to 82.2 cm. on March 29 (Table 11). The mean distance travelled per chiton per night for the study period was 48.1 cm.

Considerable variation in the mean activity per night per chiton was evident in each study (Figure 19 and 20), as was the variation in movement each night in individual animals. No seasonal patterns of activity could be discerned either for mean activity per night per chiton, or for the activity of individual animals.

No significant correlation was found between mean activity per chiton per night and water temperature, photoperiod length, and daily radiation for the March - April study (Table 12). Similarly no significant correlation was found between mean activity per chiton per night and daily radiation for the November - December study. Significant correlations were found between the mean activity and the

TABLE 10: TOTAL DAILY ACTIVITY AND MEAN ACTIVITY PER CHITON PER DAY FOR A POPULATION OF TONICELLA MARMOREA FOR THE PERIOD NOVEMBER 1 TO DECEMBER 7, 1973.

Date		Total Activity (cm)	Number of Chitons	Mean Daily Activity per Chiton (cm)	Photo-Period (hrs)	Total Daily Radiation (Langleys)	Water Temperature °C
Nov.	1	3984	73	54.58	9.98	39	6.0
1973	2	2994	72	41.58		108	6.0
	3	2706	68	39.79	9.85	112	6.0
	4	2754	68	40.50		170	6.0
	5	2094	67	31.25	9.75	155	6.0
	6	2316	66	35.09		63	6.0
	7	3966	66	60.09	9.68	190	6.0
	8	3546	65	54.46		174	6.0
	9	3678	65	56.58	9.55	90	6.0
	10	1788	65	27.51		33	6.0
	11	2424	64	37.88	9.47	177	6.0
	12	2694	64	42.09		154	6.0
	13	2100	64	32.81	9.37	72	6.5
	14	3006	63	46.97		151	6.0
	15	4068	63	64.57	9.28	33	5.0
	16	2886	63	45.81		43	6.0
	17	4518	63	71.71	9.18	57	5.5
	18	3930	63	62.38		143	6.0
	19	2592	63	41.14	9.10	136	6.0
	20	1752	63	27.81		112	6.0
	21	2244	61	36.79	9.02	123	6.0
	22	2082	60	34.70		64	5.0
	23	2400	60	40.00	8.93	47	5.0
	24	2496	58	43.03		49	5.5
	25	2178	58	37.55	8.88	69	5.0
	26	1440	58	24.83		89	5.0
	27	1752	58	30.21	8.80	62	5.5
	28	2364	58	40.76		146	5.5
	29	1632	58	28.14	8.75	25	4.5
	30	1410	58	24.31		20	4.5
Dec.	1	1242	58	21.41	8.70	76	4.5
	2	744	58	12.83		52	4.5
	3	600	58	10.34	8.63	51	4.5
	4	1326	58	22.86		49	4.5
	5	1206	58	20.79	8.57	157	4.5
	6	1572	58	27.10		76	4.0
	7	1224	58	21.10	8.53	35	4.0
Total		87708.00	2301.00	1391.45	174.02	3402.00	201.00
Mean		2370.49	62.19	37.61	9.16	91.34	5.43
Standard Error		161.72	0.69	2.37	0.11	8.40	0.12
Number		37	37	37	19	37	37

TABLE 11: TOTAL DAILY ACTIVITY AND MEAN ACTIVITY PER CHITON PER DAY FOR A SAMPLE OF TONICELLA MARMOREA FOR THE PERIOD MARCH 14 TO APRIL 11, 1974

Date		Total Activity (cm)	Number of Chitons	Mean Daily Activity per Chiton (cm)	Photo-Period (hrs)	Total Daily Radiation (Langleys)	Water Temperature °C
March	14	1710	52	32.88	11.78	254	1.0
1974	15	1896	52	36.46		400	2.0
	16	2184	52	42.00	11.88	373	2.5
	17	2016	51	39.53			1.6
	18	2388	51	46.82	12.02	170	1.0
	19	1830	51	35.88		284	2.0
	20	2220	50	44.40	12.13	264	1.0
	21	3006	50	60.12		455	2.5
	22	3348	50	66.96	12.25	148	0.6
	23	2532	50	50.64		431	1.1
	24	2694	50	53.88	12.37	427	0.5
	25	2514	50	50.28		330	1.0
	26	3222	50	64.44	12.50	431	2.0
	27	3212	50	64.24		147	0.3
	28	2724	50	54.48	12.62	271	0.2
	29	4110	50	82.20		201	0.0
	30	2672	50	53.44	12.73	416	1.0
	31	2634	50	52.68		427	–
April	1	1638	50	32.76	12.83	321	2.0
	2	2674	50	49.56		–	0.5
	3	1956	53	36.91	12.95	196	1.5
	4	2448	53	46.19		306	1.2
	5	2220	53	41.89	13.07	99	0.2
	6	2274	53	42.91		216	0.0
	7	2220	53	41.89	13.18	335	0.2
	8	2754	53	51.96		486	1.0
	9	1824	53	34.42	13.30	561	1.0
	10	2346	53	44.26		112	1.0
	11	2196	53	41.23	13.42	312	0.5
Total		71266.00	1486.00	1395.31	189.03	8373.00	29.40
Mean		2457.44	51.20	48.11	12.60	310.11	1.05
Standard Error		101.89	0.25	2.14	0.14	23.67	0.14
Number		29	29	29	15	27	28

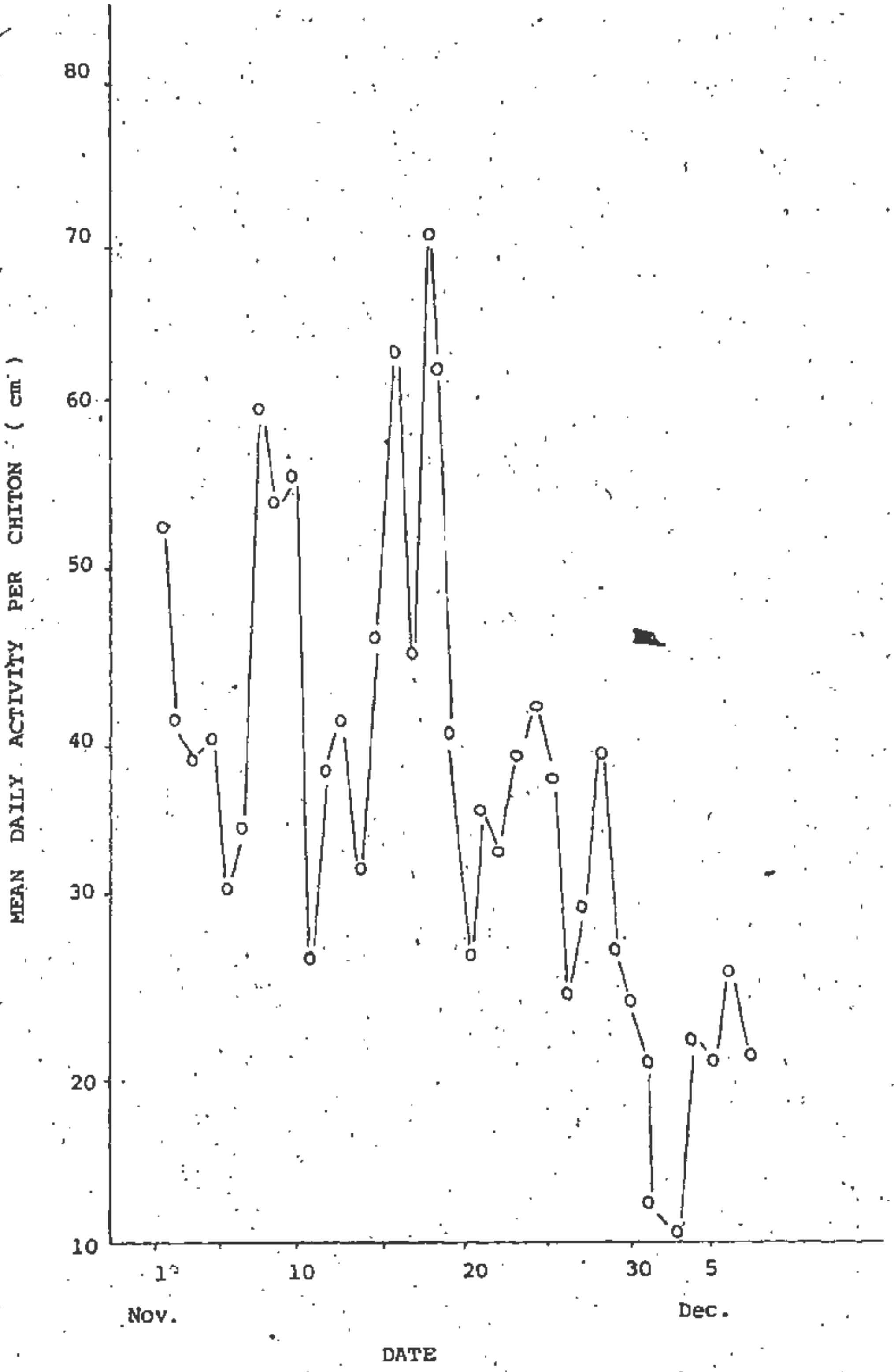

FIGURE 19: MEAN DAILY ACTIVITY FOR A LABORATORY POPULATION OF <u>TONICELLA MARMOREA</u> DURING THE PERIOD NOVEMBER 1 TO DECEMBER 7,1973.

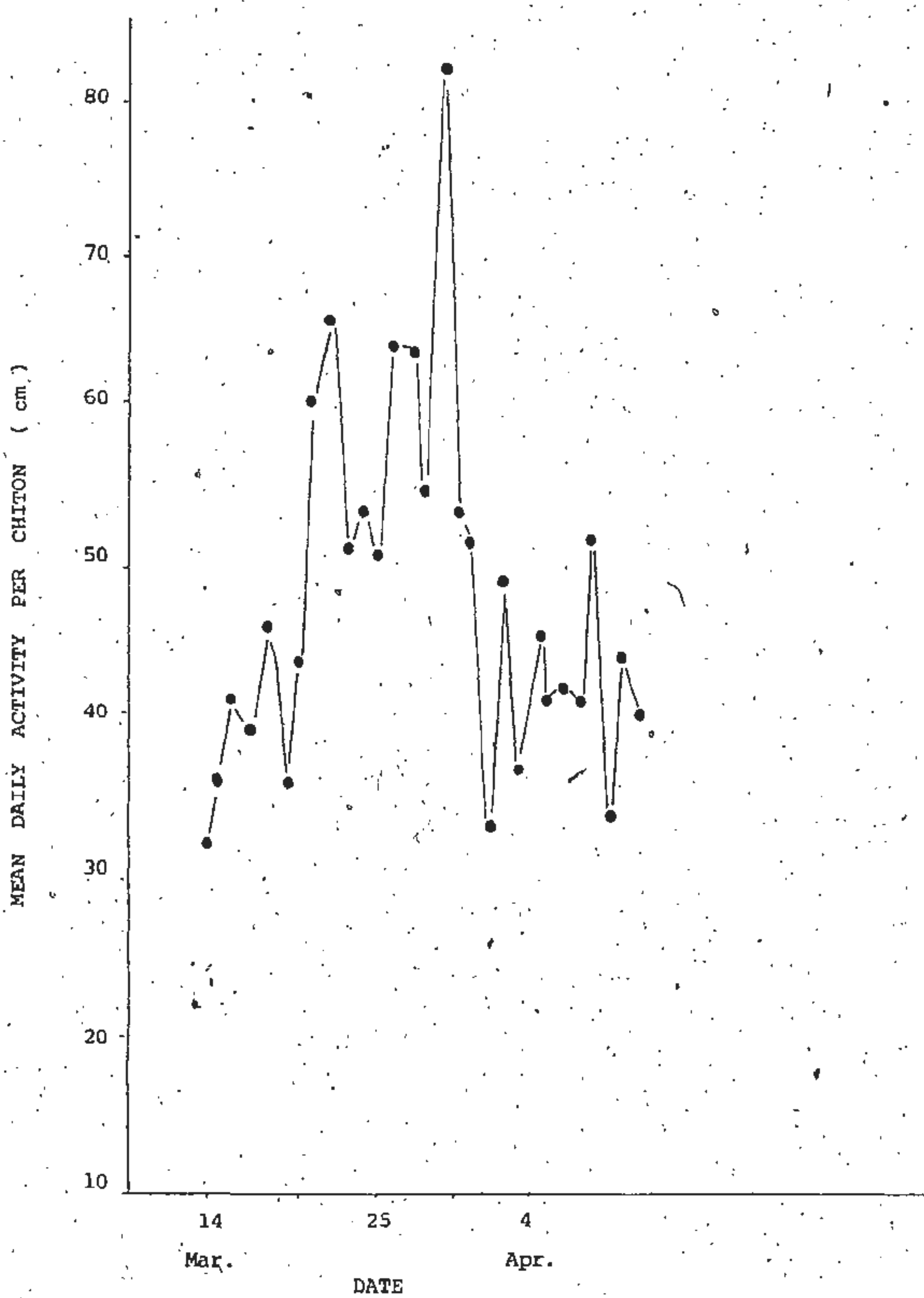

FIGURE 20: MEAN DAILY ACTIVITY OF A LABORATORY POPULATION OF TONICELLA MARMOREA DURING THE PERIOD MARCH 14 TO APRIL 11, 1974.

TABLE 12: COEFFICIENTS OF CORRELATIONS OF THE MEAN ACTIVITY PER SPECIMEN OF TONICELLA MARMOREA PER NIGHT AND SUCH FACTORS AS WATER TEMPERATURE, PHOTOPERIOD LENGTH, AND DAILY RADIATION, AS RECORDED FOR TWO ACTIVITY STUDY PERIODS, NOVEMBER-DECEMBER, 1973 AND MARCH-APRIL, 1974.

Mean Activity Per Chiton Per Night	Water Temperature (°C)	Light Photoperiod (hrs/day)	Daily Radiation (langleys)
NOVEMBER/DECEMBER			
Coef. of correlation	0.556	0.557	0.264
Degrees of freedom	35	35	35
t	2.73	2.74	1.51
$P_{.05}$	2.02	2.02	2.02
MARCH/APRIL			
Coef. of correlation	-0.00	-0.039	-0.079
Degrees of freedom	26	27	25
t	0.394	0.200	0.00
$P_{.05}$	2.06	2.04	2.06

water temperature and light photoperiod length for the November - December study (Table 12). This would imply that T. marmorea moves less as the dark hours of the night increase, and water temperature decreases. However, as no such correlation was found for the March - April study, and the mean movement was higher and the dark photoperiod shorter, the validity of this correlation is questionable.

CHAPTER III: DISCUSSION

The reactions of Tonicella marmorea to simple physical stimuli such as touch, gravity, turbulence and light were not unexpected from a chiton which is entirely subtidal in habitat in this area. Lepidochitona cinereus, the intertidal species tested by F.G.C. Evans (1951) for similar responses, demonstrated the effect interaction of responses to individual stimuli had on the overall behavior of the species. L. cinereus exhibited no response to dorsal stimuli, reacted negatively to light, and was capable of discerning both its direction and intensity, exhibited a positive geotaxic response when exposed to air, and none when submerged, and did not respond to gentle currents. The interaction of these responses resulted in the aggregation of the species beneath stones, when at low tide, and active feeding only when the variation in light intensities indicated that the tide had risen. This characteristic behavior has insured that L. cinereus is well adapted to meet the conditions of its intertidal existance.

When exposed to the same stimuli, T. marmorea reacted somewhat differently in some cases, and very similarly in others. Both species exhibited no response to dorsal contact stimuli. T. marmorea also had a definite negative response to light and could discern the direction of the source. When exposed to the air, T. marmorea exhibited a positive geotaxic response, but was much slower to react and move than was L. cinereus, the intertidal species. When submerged, no geotaxic response was evident. T. marmorea responded immediately to water currents, either by clamping tightly to the substrate, or curling and dropping off. In its subtidal habitat at Logy Bay, T. marmorea is not usually exposed to dessication. Turbulence does occur in areas in which the chitons are found, so that no advantage can be seen in the curling response to a current. The response to variations in light intensities enables T. marmorea to differentiate between light and dark photoperiods, and aids the chiton in finding resting sites which offer protection from the light cum predators.

The presence or absence of light was the main factor affecting daily activity in T. marmorea. During the twenty-four hour study, three main periods of activity were noted, one at dusk, one midway through the night and another at dawn. Glynn (1970) also noted that the nocturnal movements of specimens of C. tuberculatus were often separated into periods of high and low activity, and that the duration of movement varied with the individual.

Although no movement of T. marmorea was recorded for the daylight hours during this study, this may in part have been due to the lack of shaded areas in the experimental tanks. Chitons in the field were observed to move about when protected from the light ny overhanging rocks or seaweed. Movement in field populations was also noted during the daytime when there was heavy cloud cover or fog.

Homing has been recorded for a number of species of Polyplacophorans but all incidents of repeated homing have been confined to intertidal species (Crozier, 1921; Matthews, 1953; Thorne, 1967, 1968; Smith, 1975).

Returning to previous resting sites by specimens of T. marmorea, occurred frequently, but at irregular intervals. As well, there were few instances of sustained homing to a single site for periods greater than two or three days. For the most part, individuals of this species tended not to home to one particular site each night, but frequented a number of sites in a general area. Similar irregular patterns of homing have been observed for subtidal Tonicella lineata (Demopulos, 1975) and intertidal Cyanoplax hartwegii (Carpenter) (Lyman, 1975).

Homing in subtidal species of Polyplacophorans probably does not play an important role in the survival of the organism. Subtidal species are not exposed to such parameters as dessication, high daily fluctuation of temperature, or predation by terrestrial species. Consequently, the criteria which define a suitable resting site are few and the number of possible sites, many, lessening the need for a subtidal species to home. Intertidal chitons have many more criteria for selection of possible resting sites, and because of this the number of sites is low. Homing in an intertidal species often represents the development of a behavior necessary to the survival of the species.

The preferred resting sites of T. marmorea in the laboratory were not necessarily those which provided the greatest shelter from the light. Rather they offered either the combination of a vertical and a horizontal surface, or a crevice into which the animal could squeeze. Rough textured surfaces were preferred to smooth ones such as glass or plastic. Areas which contained sand or gravel as well as a crevice, so that the chiton could partially bury itself, were also preferred. A similar habitat preference was reported for Mopalia muscosa (Gould) (Smith, 1975).

Clustering of chitons at resting sites has not been described for other species. Smith (1975) reported that M. muscosa exhibited territoriality over its home range, and described encounters between resident chitons and intruders, which resulted in the departure of the intruder. No evidence of territoriality of any type was noted in the populations of T. marmorea studied. Often chitons at resting sites moved over other chitons or remained on top of others for the duration of the resting period.

During the long range activity studies conducted in November-December 1973 and March-April 1974, no seasonal pattern of activity was noted for the population of T. marmorea being observed. Although this may have been a reflection of the experimental method employed, it was concluded that the erratic movements of the population as a whole were probably the result of individual variations among chitons.

Individual variation of response was prevelant throughout the entire study and involved not only a difference in the reaction of individuals , but a difference in the reactions of a single individual to the same stimulus. Similar variation in the behavior and activity of chitons has been recorded for Cyanoplax hartwegii (Lyman, 1975) and Acanthopleura granulata (Glynn, 1970).

These variations in activity and behavior, coupled with the sensitivity of T. marmorea to even the slightest change in its environment, made the assessment of the 'normal' behavioral response of T. marmorea very difficult. In an attempt to reduce stress placed on organisms in the laboratory, all experiments were run using conditions as close to those of the natural environment as possible, without negating the original purpose of the study. However, recognition of the limitations of such a procedure, especially considering the sensitivity of the organism, has to be made before extrapolating the responses of a laboratory population of T. marmorea, to the responses one would expect from a natural population.

CHAPTER IV: SUMMARY

Tonicella marmorea has adapted well in both its biology and behavior to survival in its sublittoral niche. Its method of movement and the ability to contort the body shape made possible by the eight plates in the shell, enable it to utilize almost all areas of its habitat. T. marmorea possesses a pattern of colouration which blends well with the substrate on which it lives. This protective colouration coupled with the chiton's nocturnal behavior, subtidal habitat and relative inaccesibility to many species aid in protecting it from most predators. The chiton feeds on the numerous encrusting algaes which grow on the substrate. Reproduction is external and the pelagic larvae exhibit a preference for specific settling substrate.

T. marmorea exhibits no territoriality and shares its resting sites with members of the same or different species. The subtidal habitat, which offers few restrictions to movement, provides a large area for possible colonization by T. marmorea. As regular homing behavior in such a niche is not critical to the survival of the species, homing occurs irregularly, or not at all.

Activity of T. marmorea does correspond to a regular pattern based on the light/dark cycles of the day, but no seasonal patterns of activity were noted for the species, possibly due to the great variation in response between individual animals.

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APPENDIX I

STATISTICAL FORMULAE USED IN CALCULATIONS PERFORMED ON THE HEWLETT-PACKARD 9810 CALCULATOR/COMPUTER, (AS LISTED IN THE MODEL 9810A STAT PAC MANUAL).

MEAN $$\bar{x} = \frac{\sum_{i=1}^{k} f_i x_i}{\sum_{i=1}^{k} f_i}$$

STANDARD DEVIATION $$s_x = \sqrt{\frac{\sum_{i=1}^{k} f_i (x_i - \bar{x})}{\sum_{i=1}^{k} f_i - 1}}$$

STANDARD ERROR $$s_{\bar{x}} = \frac{s_x}{\sqrt{n}}$$

Number $$n = \sum_{i=1}^{k} f_i$$

COEFFICIENT OF CORRELATION $$r_{xy} = \frac{s_{xy}}{s_x s_y}$$

t $$t = r_{xy} \quad (n - 2) \; (1 - r_{xy})$$