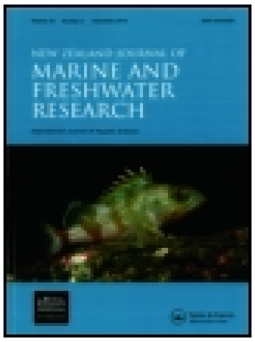

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ASPECTS OF THE ECOLOGY OF A LITTORAL CHITON, *SYPHAROCHITON PELLISERPENTIS* (MOLLUSCA: POLYPLACOPHORA)

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SUMMARY

On several Auckland shores, a littoral chiton, *Sypharochiton pelliserpentis* (Quoy and Gaimard, 1835), was widely distributed and common. At Castor Bay it was the commonest chiton, and its density equalled or exceeded that of the commonest limpet (*Cellana* spp.) over most of the inter-tidal range. Spot measurements of population density were made at other sites including exposed and sheltered shores. The smallest animals were restricted to the lower shore in pools or on areas of rock which were slow to drain. Exclusive of these small animals, the population structure was similar in pools and water-filled crevices situated either high or low on the shore. This was also true for populations of animals from drained surfaces, but, at both shore levels, the population structure in the two micro-habitats (pools and drained surfaces) was distinct.

Single measurements of salinity in the very small volumes of water in which chitons were living gave a range of 13.3–45.8‰. In laboratory experiments at normal temperatures this species could survive these fluctuations for the maximum time possible between tides. Desiccation experiments, in which weight loss was expressed as a percentage of total water content, showed weight loss to depend on size. No significant differences in weight loss were found between populations from the two shore levels and the two micro-habitats considered, though there were slight survival differences. Desiccation is probably an important factor influencing population structure, but loss of up to 75% of water content could be tolerated before 50% mortality occurred. Osmotic and desiccation stress evoked a characteristic behaviour pattern.

INTRODUCTION

The chiton fauna of New Zealand is extensive both in absolute numbers and in variety of species (Morton and Miller 1968). One species, *Sypharochiton pelliserpentis* (Quoy and Gaimard, 1835), is among the commonest and most widespread of shore molluscs (Knox 1953). It has a country-wide distribution (Suter 1913; Dell 1951; Powell 1961) and is common on most rocky shores (Iredale and Hull 1932). It lives at a wide range of shore levels and occurs mainly on rock surfaces rather than under stones. Several ecological papers include references to this species (Dellow 1950; Batham 1956, 1958, 1965).

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This paper presents qualitative and quantitative information on the abundance and distribution of *S. pelliserpentis* in relation to other chitons and some gastropods in selected localities. Measures of population density and population structure in different micro-habitats are included. Seasonal changes in population were not measured, quantitative studies being confined to April and May 1966 and 1967. Experiments were carried out on the adaptive responses of these animals to osmotic and desiccation stress, and how this may contribute to their ecological success is discussed.

Another species of *Sypharochiton, S. sinclairi* (Gray, 1843), was found by Johns (unpublished 1960) to be synonymous with *S. pelliserpentis.* Although Johns's thesis does not constitute a publication (Articles 8 and 9, International Code of Zoological Nomenclature 1961), his findings have been adopted here because the two species cannot be properly defined. He points out that the morphological characters on which *S. sinclairi* was based are very variable, and that it is unlikely to be reproductively isolated from *S. pelliserpentis.* Johns also concludes that the generic name *Sypharochiton* (Thiele, 1893) should be relegated to *Chiton* (Linnaeus, 1758). However, as the name *Sypharochiton* is in general use (Knox 1963; Batham 1965; Morton and Miller 1968) it is retained here. Names of all other molluscs are taken from Powell (1961) and other names are from Morton and Miller (1968). Details of ecological and experimental methods are placed at the beginning of the relevant section.

ECOLOGY

DISTRIBUTION IN SHELTERED CONDITIONS

Shore collections were made at Castor Bay, a moderately sheltered, gently sloping shore outside the Waitemata Harbour, for comparison with a series of collections at shores within the harbour, all of which are platforms of sandstone or mudstone of the Waitemata series. Many collections were made at Castor Bay, but at the harbour sites an approximate estimate of relative abundance was made, based on numbers collected in a standard collecting time (1 hour). As well as *Sypharochiton,* three important grazing gastropods were included: patellid limpets of the genus *Cellana* (*C. radians* and *C. ornata*), the turbinid *Lunella smaragda* (Gmelin, 1791), and the trochid *Melagraphia aethiops* (Gmelin, 1791). The results of this survey are summarised on a map of the region in Fig 1.

At Castor Bay, a wide range of chiton species is commonly found. Most of these live only under stones or in pools and crevices; however, *S. pelliserpentis* is also common on most open rock surfaces which are not heavily encrusted with algae. *Ancanthochiton zelandicus* may be found on open rock also, but fitting tightly into small crevices and depressions. At the level of low water spring tides, *Cryptoconchus porosus* (Burrow, 1815) and *Maorichiton* sp. sometimes occur on the upper surfaces of rocks as well. At the harbour entrance, a number of

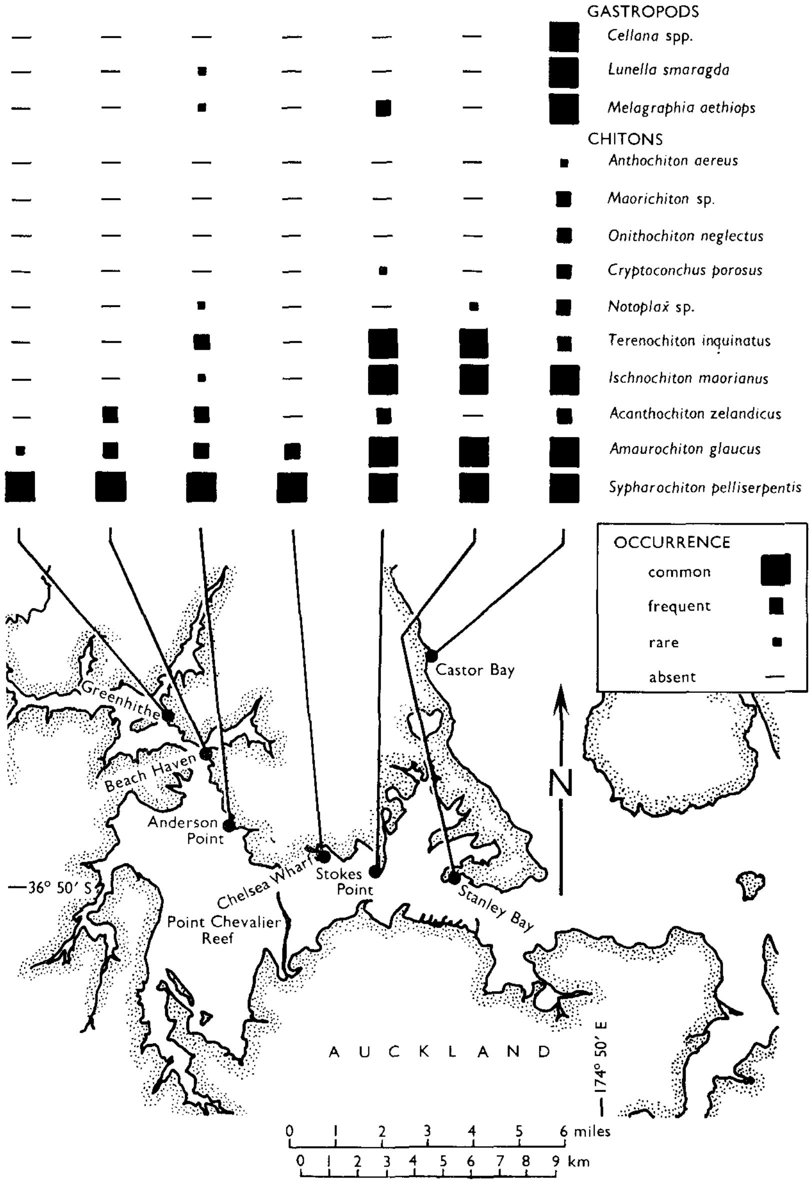

FIG. 1—Sketch map of Waitemata Harbour, Auckland, showing the relative abundance of chitons and certain gastropods at seven sites.

physical and faunal changes occur which become increasingly marked the further one progresses up the harbour. The most obvious of these, silting, reduces the available substrate by smothering the lower shore in a fine glutinous layer. Towards the head of the harbour, this mud layer becomes progressively thicker and higher on the shore. Movable rocks become encrusted with a complex fauna of sponges and tunicates on compacted oyster shells. Chitons rarely occur on such encrustations.

Sypharochiton pelliserpentis remained common at all sites within the harbour wherever a solid substrate was available, and very high densities were recorded. Although the upper harbour at Greenhithe is an area mostly of mud flats and mangroves, *Sypharochiton* is common there and apparently tolerates a high degree of silting (Fig. 2a). Of the other chitons present at Castor Bay, some are not found within the harbour, while others are progressively reduced in abundance (*see* Fig. 1). However, *Terenochiton inquinatus* (Reeve, 1847) reaches its maximum abundance within the harbour entrance on silted shores rich in organic debris.

At Westmere, a long basalt reef known as Point Chevalier Reef (Jillett 1968), Black Reef (Morton and Miller 1968) or Westmere Reef, extends ¾ mile into the harbour, almost at right angles to the shore. Its hard, pitted surface forms a substrate which contrasts with the soft, generally smooth mudstone nearby. The landward end is mud covered and colonised by mangroves, but off the northern end the bottom drops steeply to 20–23 m and there are fast tidal currents. By degree of silting, and floral and faunal changes, the reef may be divided into outer, central and inner regions, relative to the shore. The distribution of chiton species in these three regions is shown in Fig. 3.

The outer region is scoured by tidal currents and the rocks are relatively clean of surface silt. There is a good cover of brown algae here and *Cryptoconchus porosus* is conspicuous, being frequent on rock surfaces at the low water level of spring tides. *Ischnochiton maorianus* (Iredale, 1914) may be common and *Terenochiton inquinatus* frequent under movable rocks at the reef edge. The crest of the reef (accounting for most of the total reef width) is colonised by the rock oyster *Crassostrea glomerata* (Gould, 1850) and scattered barnacles. Here, the slightly sloping, drained surfaces support a large population of *Sypharochiton pelliserpentis* with frequent *Acanthochiton zelandicus* occurring in and between the edges of oyster shells, or tightly jammed into cracks in the basalt.

In the central region, the edges of the reef are still in water at extreme low water spring tides but the areas of movable rocks at low water are more restricted and muddier, and a complex fauna of sponges and tunicates encrusts large areas. Here, *Terenochiton inquinatus* is common but the other low-water chitons infrequent. The crest of the reef is dominated by barnacles with some *Crassostrea,* with *Sypharochiton pelliserpentis* and *Acanthochiton zelandicus* occurring as before. *Sypharochiton* also occurs frequently on the sides and lower surfaces of small rocks in pools on the reef surface.

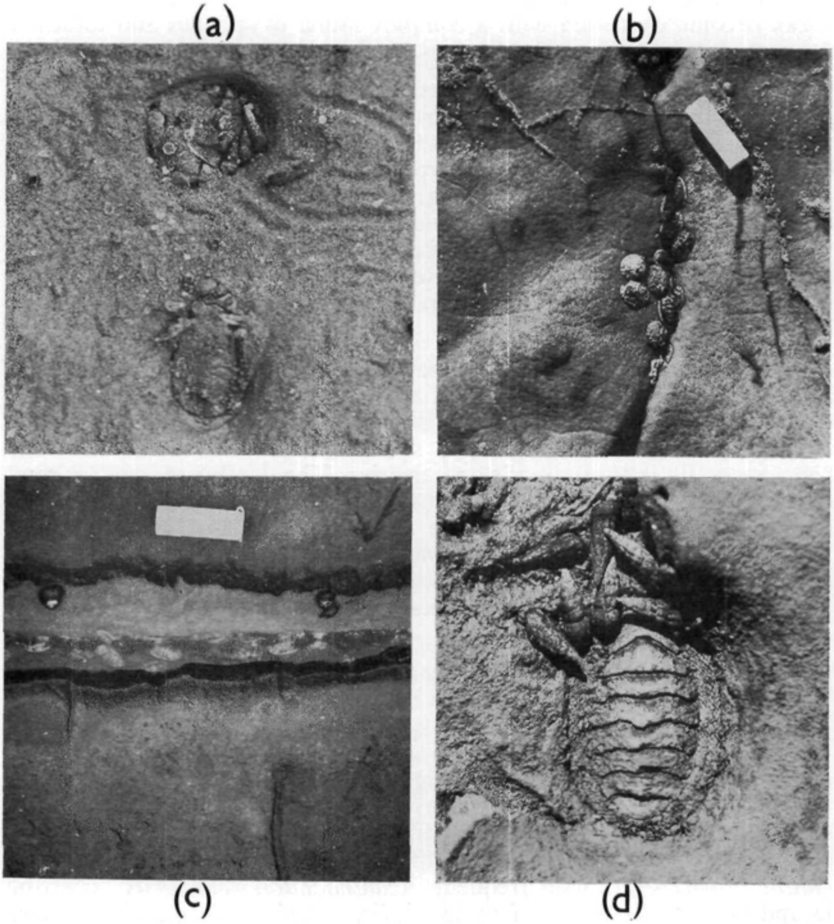

FIG. 2—*Sypharochiton pelliserpentis* (a)—two animals in "home" depressions, on heavily silted sandstone at Westmere; (b)—animals on a drained surface with limpets; (c)—animals in a water-filled crevice typical of this microhabitat; (d)—in a "home". (Specimen tube in (b) and (c) is 3 in. long.)

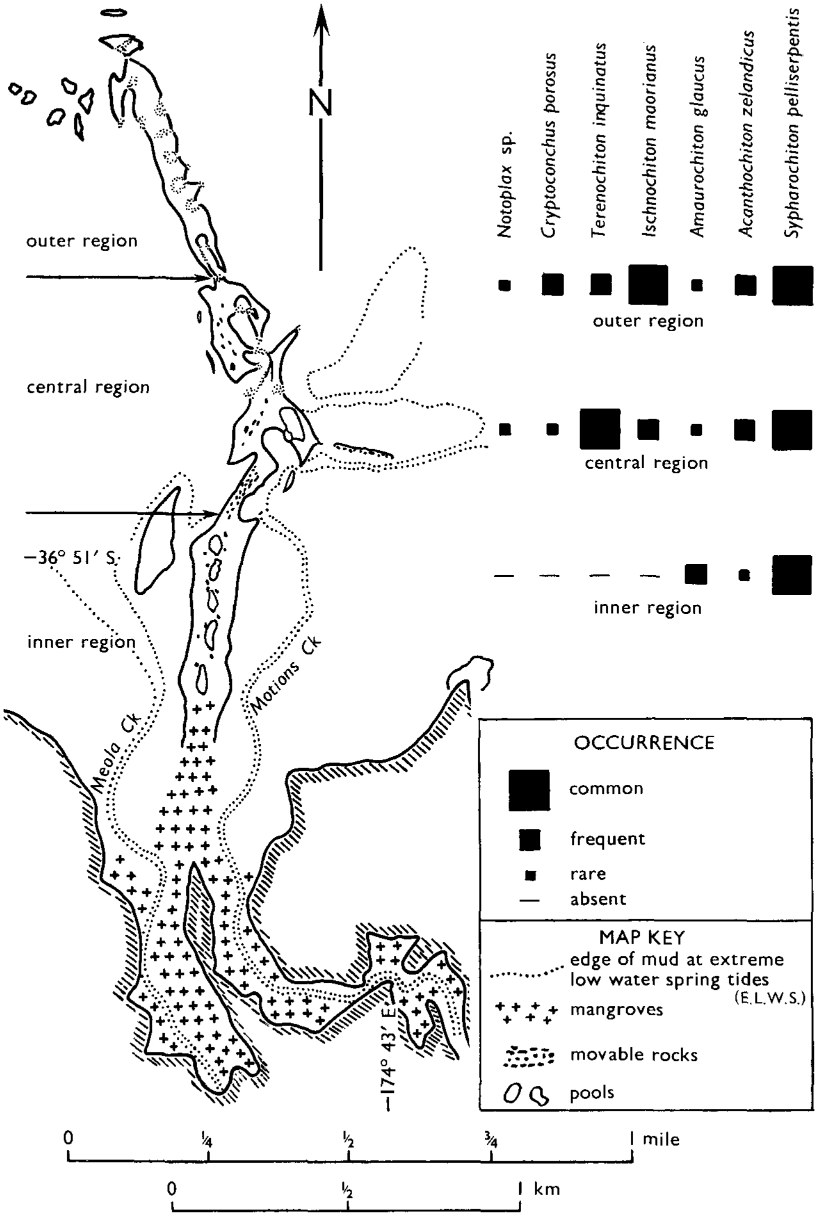

FIG. 3—Sketch map of Point Chevalier Reef, Waitemata Harbour, showing the relative abundance of chitons in three regions.

The inner region is drained completely at low water leaving a large expanse of fine mud on either side. Mud smothers the areas of loose rocks at the reef edges. The central crest of the reef is mostly bare of marine encrustation. Pools on the surface permit a stunted growth of some sponges and algae. The chitons of this region are *S. pelliserpentis* and *Acanthochiton zelandicus* on the reef surface and sometimes beneath stones. Of the other species, small numbers of *Amaurochiton glaucus* (Gray, 1828) are present beneath large stones embedded in mud at the reef edge.

POPULATION DENSITIES

Quantitative estimates of density were made by counting numbers of animals within a measured area. At Castor Bay the sample was taken from within a circle of radius 1 m (area 3.143 m^2), at other sites a square of side 1 m (area 1 m^2) or 0.5 m (area 0.25 m^2), but densities are expressed here as numbers per $metre^2$.

At Castor Bay, the sea has cut across dipping strata so that the shore platform is a succession of gullies and reefs, approximately parallel to each other and the shore line. The profile of a transect across this shore and the distribution of chitons along it is shown in Fig. 4. The surface of the outermost reef (a) is pitted and thickly encrusted with muddy *Corallina officinalis* and other small algae. At (b) the surface is similar. At (c) the boulders and movable rocks in the water-filled gully were sampled. The upper surfaces (under water) of these rocks were covered with *Corallina* and some of the fucoid *Hormosira banksii;* most of the chitons were on the lower surfaces. Site (d) was still covered by dense, muddy *Corallina* and no chitons were recorded. At (e) the *Corallina* cover was reduced and patchy but prevented the rock surface from draining completely, though at (f) the cover was less than 50% and most surfaces drained. At (g) macroscopic algae disappeared except in pools and barnacles formed a wide zone. At (h) the rock surface became rather pitted, trapping moisture in hollows, in which 81% of the sample occurred. At the last site, (i), most rock surfaces were drained and dried quickly as the tide receded, but 31% of the sample occurred in the moist depressions.

From the data on Fig. 4, *Sypharochiton pelliserpentis* is the commonest chiton; it reaches its maximum density at a higher shore level than the others but was absent from the water-filled gully (c). *Acanthochiton zelandicus* and *Maorichiton* sp. are common at low levels where there is continuous algal cover. *Notoplax violacea* (Quoy and Gaimard, 1835) and *Cryptoconchus porosus* were not recorded in the particular transect on which Fig. 4 is based, but they are included for completeness because they were usually found in small numbers at this locality.

The high density of *Sypharochiton* (50/m^2) shown in Fig. 4 is not unusual. Densities of 136/m^2 and 228/m^2 were recorded on pitted rock surfaces at Anderson Point, a site within the upper reaches of the harbour (*see* Fig. 1). However, on rock surfaces which are exposed to heavy surf, the density of *Sypharochiton* may be exceeded by that of

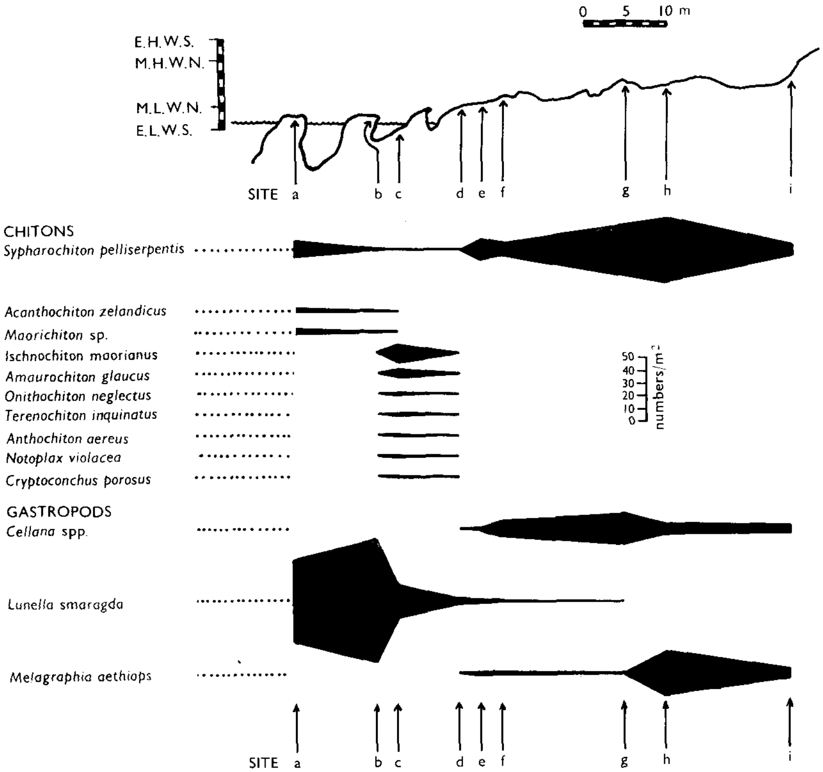

FIG. 4—Transect of the shore at Castor Bay showing sites sampled and the density of chitons and certain gastropods.

limpets. For example, at Piha (west coast of Auckland), the density of *Sypharochiton* was 20/m^2, while limpets of the genus *Cellana* reached 30/m^2 and *Notoacmaea* 18/m^2 in the same sample.

No attempt is made here to indicate average densities of *Sypharochiton pelliserpentis* on different shores. Fig. 4 shows just how much the density varies in relation to the physical and biological factors at any particular site. However, on most shores this species is widely distributed and has a high density relative to other animals.

POPULATION STRUCTURE

The size composition of the *Sypharochiton pelliserpentis* population sampled at Castor Bay was determined from collections of animals preserved in 70% ethanol. They were cleaned of encrusting organisms and surface-dried before weighing to the nearest 10 mg. They were then divided into size classes by weight at 1 g intervals, except that the animals below 0.1 g were separated from the rest of the under 1 g class (Fig. 5).

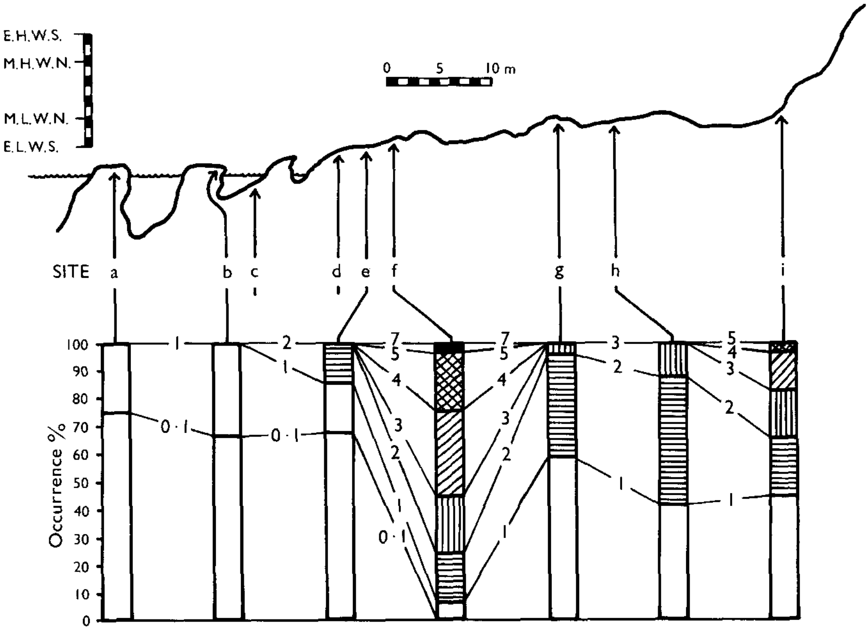

FIG. 5—Composition by weight of *Sypharochiton pelliserpentis* population at Castor Bay. The sizes and sites of the samples a–i are shown on Fig. 4. Numerals refer to the weight classes (g) into which samples were divided.

Animals of different sizes were not distributed equally; generally, animals of larger sizes occurred higher on the shore and smaller animals at lower levels. This pattern is modified by local factors, and larger animals occur where the rock surface is drained. "Drained" or "undrained" is a distinction between habitats which is relevant because of the varying amounts of possible exposure to desiccation of the animals therein. *S. pelliserpentis* is shown in drained and undrained micro-habitats in Fig. 2b and c. Intermediate habitats occur in small bodies of water which may dry up during the exposure period, and drained habitats also vary in the extent to which they retain moisture.

To compare directly the size of animals from these micro-habitats, an undrained crevice was selected high on the shore and another low down at the level of low water neap tides; every animal was collected along both crevices until samples of 50 were obtained. The drained surfaces adjacent to the crevices were then searched and every animal removed within a path about 1 m wide along the shore at the level of the crevice until 50 had been collected from each. The animals were treated and weighed as before, and the results shown in Fig. 6.

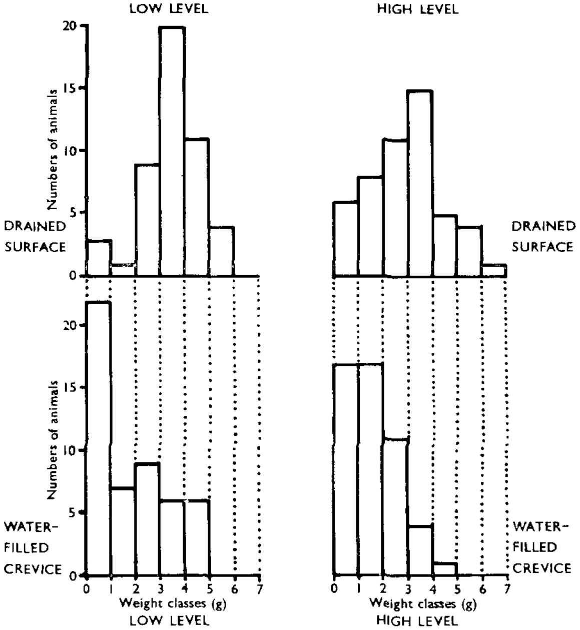

FIG. 6—Composition by weight of four samples of *Sypharochiton pelliserpentis* from different levels and micro-habitats at Castor Bay.

The two samples from each undrained crevice were essentially similar, but comparisons between the two types of micro-habitat showed marked differences in distribution of sizes within the population. The samples from the water-filled crevices included many small animals, but on the drained surfaces the 3–4 g size class was dominant. Thus the differences in size distribution within populations drawn from different micro-habitats may completely mask any relationship between size and level on the shore.

SALINITY FLUCTUATIONS

Sypharochiton pelliserpentis is a truly marine animal, neither extending into rivers nor normally living above high water neaps, except on exposed shores. Nevertheless, there may be rapid salinity fluctuations in two parts of its environment: within the harbour where the restricted water mass may be influenced by fresh water run-off, and in littoral pools and hollows on the shore by rainfall or evaporation.

Phillips and Grigg (1925, quoted by Hounsell 1935) and Hounsell (1935) recorded the maximum salinity range within the Waitemata harbour as 34.53–35.00‰; Powell's (1937) series of samples taken from the upper harbour towards the open sea showed a range of 29.63–35.00‰. Wallace and Newman's (1953) graphs of salinity fluctuations at several Auckland beaches during a tidal cycle showed ranges

TABLE 1—Extreme salinities measured in pools containing *Sypharochiton pelliserpentis* below high water level of neap tides, Castor Bay, Auckland, 1967–68. (Each depression of freezing point value (Δ) is the mean of three samples from the same pool, and each mean represents a different pool. The depression of freezing point value was converted to chlorinity using the tables of Barnes (1954) and to salinity from the Hydrographical Tables (Knudsen 1901).)

Weather conditions	Mean Δ (°C)	Chlorinity (‰)	Salinity (‰)
After heavy rain	1.46	15.0	27.0
	0.71	7.3	13.3
	0.96	9.9	17.9
	1.00	10.4	18.8
	0.72	7.5	13.6
After hot dry day	2.08	21.0	37.9
	2.53	25.4	45.8
	1.99	20.1	36.3
	1.72	17.5	31.6
	1.91	19.4	35.0
	2.43	24.4	44.0
	2.40	24.0	43.4
	2.21	22.2	40.1
	2.38	23.9	43.2
	2.48	24.8	44.8

of 32.57–35.19‰ (Mission Bay), 33.93–34.52‰ (Kohimaramara), 34.33–35.46‰ (St. Heliers) and 34.87–35.64‰ (Karaka). No data for seasonal salinity fluctuations in Waitemata Harbour are available, though Jillett (unpublished 1967) gave such data for two stations further out in Hauraki Gulf.

In pools more violent fluctuations can be expected. Lewis (1964) concluded that in general wide salinity fluctuations occur only in pools untouched by the tide for several days. In New Zealand, Ambler and Chapman (1950) reported fluctuations in salinity of 34.33–37.75‰ in a high-level pool of approximately 18.51 litres. However, in the small hollows and depressions in which many *Sypharochiton pelliserpentis* live, salinity fluctuations during a single low tide may be more extreme. Small bodies of water which were below the level of high water neap tides and in which chitons were living were sampled after heavy rain and at the end of a hot day.

The salinities were determined indirectly by the freezing-point depression of the samples (Boyle 1969). The results are summarised in Table 1; the total salinity range measured was 13.3–45.8‰. Although these were only spot determinations, they indicate the extent to which the micro-habitat is likely to differ from the general shore conditions for short periods. Johns (unpublished 1960) records that this species is not found where the salinity drops below 75% normal sea water (approximately 26‰) and Batham (1965) did not find *S. pelliserpentis* in salinities below 24‰.

OSMOTIC AND DESICCATION STRESS EXPERIMENTS

Animals removed to the laboratory for experiment were collected from Castor Bay and kept in perspex aquaria in clean sea water from the area of collection. The tanks were continuously aerated through porous stone diffusers, and perspex lids prevented significant evaporation. Animals clearly damaged by collection were rejected. After experimental exposure to osmotic or desiccation stress, animals were returned to fresh aerated sea-water for 24 hours. They were then removed and scored as alive, moribund or dead: 2, 1 or 0 respectively (Boyle 1969). Survival was calculated by expressing the score obtained as a percentage of the total score possible had all animals survived.

OSMOTIC STRESS

Recent work (Boyle 1969) has shown this species to be an osmoconformer. When exposed to fluctuations within the range 0–150% sea water, the internal osmotic concentration (measured by freezing-point depression of the pericardial fluid) adjusts to that of the medium. In 0% sea water, death occurs before equilibrium is reached. When exposed to reduced salinity, the animal clamps down on the substrate hard, thus reducing the rate at which equilibrium is attained.

Survival experiments were carried out on *S. pelliserpentis* in various concentrations of sea water. The salinity of the water from which the animals were collected and in which they were kept was determined either by inductive salinometer or by silver nitrate titration; the range was 34.2–35.7‰. Dilute media were prepared by adding "0% sea water" (2.5*M* $NaHCO_3$) to sea water from the same batch as that in which the animals were kept (Binyon 1961; Wells and Ledingham 1940; Pilgrim 1953). Concentrated media were prepared by evaporation (Gross 1954). Experimental media were kept at three controlled temperatures, 10°C ± 0.1°C, 20°C ± 0.5°C, and 30°C ± 0.1°C.

The results are summarised in Fig. 7, the data is for groups of 10 animals attached to glass plates at each temperature-salinity-time combination. At 10°C the aeration of some tanks may have been inadequate, and aeration was improved for later experiments. Significant mortality occurred at 10°C and 20°C only after 24 hours exposure to freshwater. At 30°C some mortality occurred after 10 hours in 50% sea water and nearly all were dead after 24 hours, in fresh water ("0% sea water") most animals were dead after only 6 hours exposure.

Skerman (1958) reports sea surface temperatures for Auckland harbour in which the lowest record is 8.7°C and the highest 24.4°C. No reports of frosts affecting the shore in Auckland could be found. With a mercury bulb thermometer (0.1°C divisions) and a battery-operated thermistor probe instrument the highest temperatures I recorded in small pools in which *S. pelliserpentis* was living were 30–32.5°C. The implications of this data and the previous spot measurements for salinity are that apparently *S. pelliserpentis* should survive any fluctuations in salinity to which it is exposed during a tidal cycle. Significant mortality would occur at >30°C with salinities of <50% sea water but this combination is unlikely to occur often.

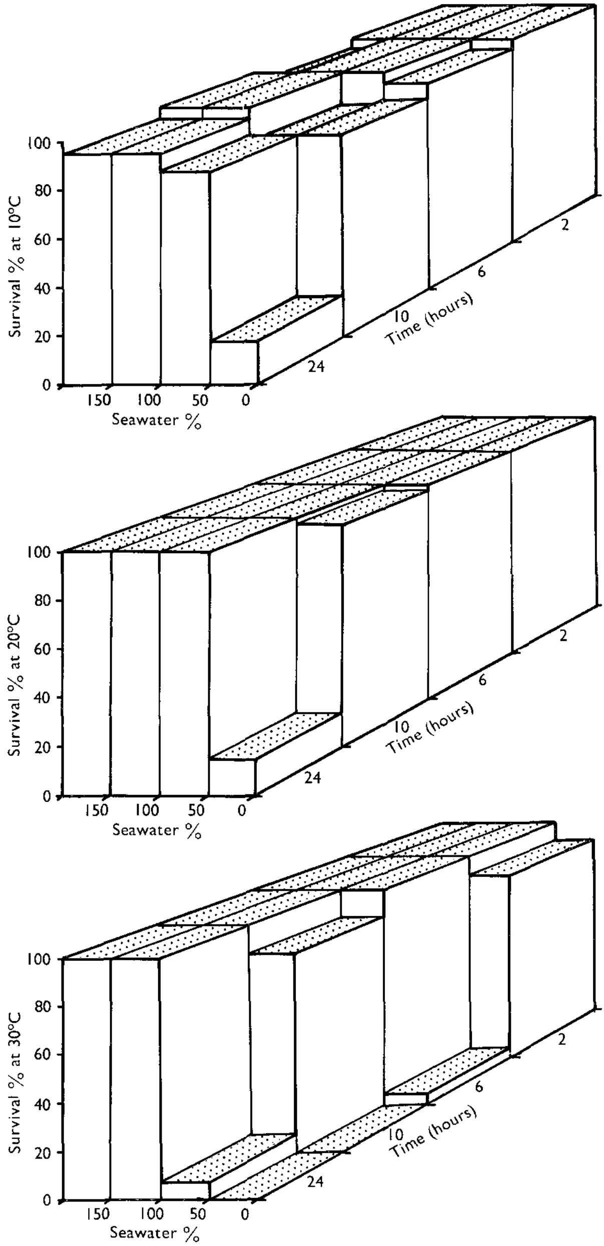

FIG. 7—Survival of *Sypharochiton pelliserpentis* from Castor Bay in various salinities at three temperatures (n = 10 at each temperature-salinity-time combination).

No correlation was established between the size of animal and its weight change or change in internal osmotic pressure, either before or after equilibrium had been reached. Although not tested directly, differential mortality between various sizes of animal is thus unlikely.

DESICCATION STRESS

Animals attached to weighed glass plates were removed from aquaria, lightly dried with a soft towel and weighed to the nearest 5 mg. They were then subjected to standard desiccating conditions in closed 10-l glass desiccators containing $\frac{1}{2}$ lb (226 g) of freshly dried self-indicating silica gel. Experiments were at room temperature (16–22°C). At defined intervals the plates were removed and weighed with the animals attached. Occasionally, an animal which had moved off the plate had to be replaced on it for weighing.

In closed desiccators, conditions are like those assumed by Ramsay (1935) for evaporation in still air. He points out that even if the partial pressure of water vapour at the surface of the drying agent is known, other factors such as the size and shape of the chamber, distance between the evaporating and drying surfaces, and the temperature and pressure of the system affect the rate of evaporation from the animals. Circulation of air within the chamber can considerably reduce these variables by bringing more of the air into contact with the desiccant and increasing the external diffusion gradient (Kensler 1967; Gibson 1970), though Bayne (1968) found this unnecessary. Because of the limitations of closed desiccators the relative humidity to which the animals were exposed cannot be estimated. However, in all experiments described here, when comparisons were to be made between two batches, the animals from each group were mixed in equal numbers and desiccated together. Approximately the same number of animals was used in each desiccator each time.

Water loss by individuals and groups of *Sypharochiton pelliserpentis* was measured as weight loss and expressed as a percentage of the water content. The water content of an animal was predicted from the regression equation:

$$\text{Water content} = 0.0468 + 0.3964 \,.\, \text{Wet weight (g)}$$

derived from a sample of 25 animals collected from Castor Bay which spanned the normal size range at that locality.

Animals from two levels (approximately low and high water level of neap tides) were collected from drained, gently sloping surfaces at Castor Bay. After 24 hours under standard desiccating conditions the weight loss of the two groups was measured and plotted against body weight using logarithmic co-ordinates (Fig. 8). The regression line for each set of data was fitted by the method of least squares for animals over 1 g. There was no significant difference (*t* test) between the two lines ($P = 0.5$). Desiccation was continued for 48 hours after which only three animals recovered, of which two were from the high-level group.

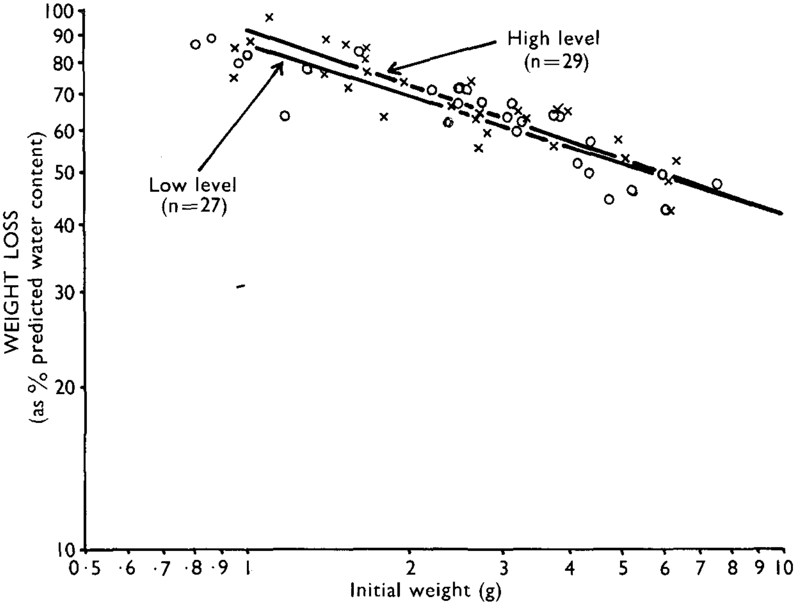

FIG. 8—Comparison of weight loss under standard desiccating conditions for 24 hours in two samples of *Sypharochiton pelliserpentis* collected from a high level (x) and a low level (o) at Castor Bay. Logarithmic co-ordinates. Regression lines, fitted by method of least squares, have the coefficients b = −0.35 (high level) and b = −0.31 (low level) for animals weighing >1g.

Animals from the drained and undrained micro-habitats at the high water level of neap tides at Castor Bay were compared by the same method. In each desiccator half of the animals were from the drained surface and half from the undrained. The pooled results for weight loss under standard desiccating conditions for 24 hours in two such experiments are shown in Fig. 9. There was no significant difference between the two regressions ($P = 0.1–0.05$). Except for one dead and another moribund from the water-filled crevice population, all animals recovered.

Many experiments were carried out using groups of 5 or 10 animals of approximately uniform size, weighed collectively on a glass plate. Weight of the animals and weight of water loss were expressed as mean values. Groups of animals weighed collectively from high and low levels gave some indication of survival differences after long periods of desiccation. For example a group of high-level animals from the shore at Westmere compared with a low-level group from Castor Bay (mean weights 4.92 g and 4.35 g respectively, $n = 10$ in both samples) lost 82.4% of their water content against 85% in the low-level sample; after 24 hours in recovery conditions none of the low-water group recovered but among the high-level group there were three moribund and one alive.

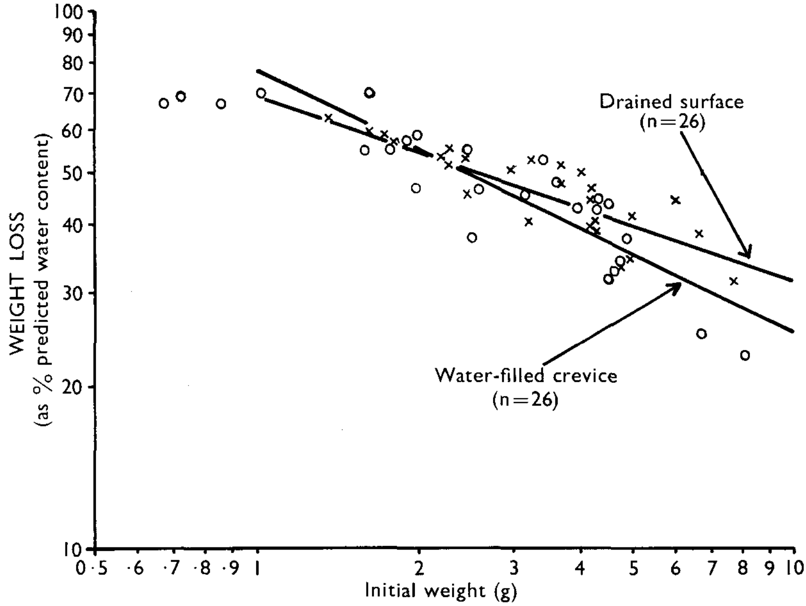

FIG. 9—Comparison of weight loss, under standard desiccating conditions for 24 hours, in two samples of *Sypharochiton pelliserpentis* from a drained surface (x) and a water-filled crevice (o) at approximately the high water level of neap tides at Castor Bay. Logarithmic co-ordinates. Regression lines fitted by method of least squares for animals over 1 g have the coefficients b = 0.35 (drained surface) and b = − 0.49 (water-filled crevice).

Animals desiccated with other chitons consistently lost less weight than individuals desiccated alone in the same nominal conditions. In each of two desiccators were placed five animals together on one weighed glass plate and another five on individual plates. The data from this experiment is shown in Fig. 10, where the two groups of 5 animals directly comparable with the 10 individuals are marked. All other data for groups of 5 or 10 *Sypharochiton pelliserpentis* desiccated collectively are included on the figure, to which regression lines were fitted for animals weighing over 1 g. Under the same conditions, individuals lose 10–20% more water than those of the same mean size desiccated collectively. After a total of 48 hours desiccation, only two of those weighed individually recovered; these were large animals of 4.3 g and 4.1 g which had lost 77.4% and 79.4% of their water content respectively. Animals in the group with the larger mean size (2.6 g) had lost on average only 59.8% of their water content and all of them recovered. Animals in the group of smaller mean size lost on average 78.5% water content and only 50% survived.

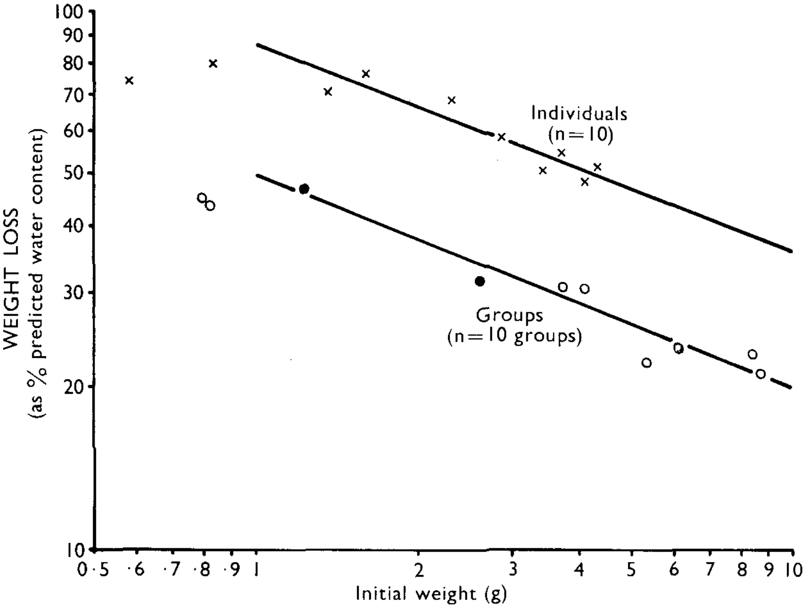

FIG. 10—Comparison of weight loss, under standard desiccating conditions for 24 hours, of 10 individual *Sypharochiton pelliserpentis* weighed separately (x), and 2 groups of 10 weighed collectively (●) from approximately the low water level of neap tides at Castor Bay; all other groups, 5 or 10 animals from Castor Bay or Westmere which were weighed collectively, are included as (o). Regression lines fitted by method of least squares for animals over 1 g have the coefficients b = − 0.38 (individuals) and b = − 0.39 (groups). Logarithmic co-ordinates.

The observed differences in weight loss of individuals and groups may be explained by their behaviour during desiccation. The behaviour patterns shows two phases:

(1) An initial, *active* or exploratory phase which may last 10 minutes to 1 hour. Animals desiccated collectively move rapidly to come into contact with one another, aggregate and cease moving. If the animals are desiccated individually this initial activity is prolonged; however, there seems to be no directional aspect, and movement is not continuous in one direction for long.

(2) A post-active phase, when the animals cease moving and clamp down tightly. The animal maintains a state of "tonic inactivity", in which crawling, respiratory movements and defaecation are inhibited but spawning apparently is not.

In control conditions—a desiccator containing cotton wool soaked in water maintaining 95–100% relative humidity—the chitons lost 2–8% of their water content in 24 hours (exceptionally and inexplicably one group lost 15%). None died during 48 hours in these conditions. The animals continued to move actively for long periods, and usually did not form defined aggregations.

The formation of aggregations in desiccating conditions considerably reduces the animals' collective surface area : volume ratio, and thus their rate of water loss. The absence in humid conditions of the clear behaviour patterns observed in drying conditions suggests that this behaviour is evoked by low humidity conditions and that, in the terminology of Fraenkel and Gunn (1961), it is a kinesis. In the field, *Sypharochiton pelliserpentis* usually do not aggregate on open rock, but typically congregate in areas of slightly higher humidity, crevices and hollows.

Observation of other littoral chitons in desiccators showed that both *Ischnochiton maorianus* and *Cryptoconchus porosus* are normally active and leave a mucus trail; movement often continues until adhesion is lost. *Guildingia obtecta* (Pilsbry 1893) (a littoral chiton from low on surf-exposed shores, Auckland west coast) shows little movement, but mucus and faeces are produced and the animal frequently becomes detached. *Amaurochiton glaucus* moves little; most animals clamp down but form no defined aggregations.

DISCUSSION

On the shores studied *Sypharochiton pelliserpentis* is a ubiquitous grazing mollusc. On fairly sheltered shores its numbers may exceed those of limpets, and in biomass this species sometimes outweighs all other grazing molluscs per unit area (W. J. Ballantine, pers. comm.). The population structure and responses to environmental stress provide clues to explaining this ecological success.

The experiments showed that *Sypharochiton pelliserpentis* is well adapted to both osmotic and drying stresses, which it resists by adopting patterns of behaviour tending to minimise the effects of the stress. Other types of behaviour in chitons, especially orientating behaviour to environmental stimuli and the way in which this may account for their position on the shore, have been described by Evans (1951) and Arey and Crozier (1919).

That tolerance of the effects of stress is well developed in *Sypharochiton* is illustrated by its ability to tolerate a mean loss of about 75% of the total body water before 50% mortality results. Tolerance of this nature can be regarded either as a specific physiological adaptation of tissues and metabolism, or attributable to the animal's simple organisation and lack of sensitivity to the stress, or partly to both.

The differences in population structure between water-filled crevices and adjacent drained surfaces at high and low levels probably stems from physical differences between the two micro-habitats, which differ widely in degree of exposure to desiccation. Experiments showed that mortality from desiccation is very much dependent on size, because the rate of dehydration of the animal is related to its surface area : volume ratio. On the shore, desiccation will selectively affect small animals less able to tolerate exposure to drying. Similarly, size could also affect the rate at which osmotic equilibrium is attained (though not the final equilibrium level), but this has not been detected (Boyle 1969); in small pools where the animals may be exposed to osmotic stress, the fluctuations of salinity did not appear to affect large and small animals differentially. However, apart from exposure to drying, there are many other differences in environmental factors between the micro-habitats which could relate to the observed difference in population structure.

Differential acclimation to water loss has not been shown in the *Sypharochiton* populations examined, though there are possibly slight survival differences; by comparison, in the limpet *Patella* low-level animals lose water faster than high-level animals of the same size (Davies 1969). As the animals grow they probably move from the water-filled crevice habitat to drained surfaces. Eventually, most adults permanently occupy elongate depressions or "homes" in the substrate (*see* Fig. 2d), to which they show "homing" behaviour (Johns unpublished 1960; Thorne 1968). Arey and Crozier (1919) report that in Bermuda the young animals of *Chiton tuberculatus* live under small flat stones on the upper shore. Larger animals live lower down under large boulders and on the walls of caves, while still larger animals "commonly occur freely exposed upon sunlit rocks, while those of maximal size (8 to 9 cm) are rarely found concealed in dark places".

Sypharochiton pelliserpentis can live for at least 24 hours in aerated sea water at 30°C. Temperatures of small chiton pools and of chitons on bare rock rarely reached a maximum of 32°C. Kenny (1958) working with the chiton *Clarvarizona hirtosa* showed the lethal temperature to be approximately 10°C above the highest recorded in the field, but Arey and Crozier (1919) for *Chiton tuberculatus* found environmental temperatures that were close to the lethal limit. In *Sypharochiton* temperature is probably of secondary importance in survival, but in combination with osmotic or desiccation stress high temperatures may cause increased mortality.

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