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Resource Partitioning in Seven Species of Sympatric Intertidal Chitons (Mollusca: Polyplacophora)

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ABSTRACT

RESOURCE PARTITIONING IN SEVEN SPECIES OF SYMPATRIC INTERTIDAL CHITONS (MOLLUSCA: POLYPLACOPHORA)

by

Richard D. Piercy

Space (intertidal height and location/exposure on the rock surface), and food (gut contents) were partitioned among 7 species of sympatric intertidal chitons: Mopaliidae - *Mopalia hindsii*, *M. ciliata*, *M. lignosa*, *M. muscosa*, and *Katharina tunicata*; and Ischnochitonidae - *Tonicella lineata* and *Cyanoplax dentiens*. Species distribution relative to intertidal height (-0.3m to +0.9m) showed significant differences. *M. hindsii*, *M. ciliata*, *M. lignosa*, and *T. lineata* preferred slopes or undersides of rocks while *M. muscosa*, *K. tunicata*, and *C. dentiens* occurred on the top horizontal surfaces or in more exposed habitats. Chitons differed significantly in their associations with *Lithothamnion*, macrophytic algae, *Ulva*, encrusting red algae (*Petrocelis* and *Hildenbrandia*), and invertebrates. Considerable overlap in food types occurred, however, significant differences in utilization of *Ulva* and diatoms and near significant differences in utilization of invertebrates, filamentous red algae, and *Lithothamnion* suggest food resource partitioning. Certain species appeared to "select" diatoms, *Ulva*, and invertebrates from eight food types available in the

microhabitat. Movement rates, activity, and behavior differed significantly in one tank experiment and may further ecologically separate the chiton species. However, field studies did not find significant differences among chiton species in distance moved, range of movement, and movement patterns.

LOMA LINDA UNIVERSITY

Graduate School

RESOURCE PARTITIONING IN SEVEN SPECIES OF SYMPATRIC INTERTIDAL CHITONS (MOLLUSCA: POLYPLACOPHORA)

by

Richard D. Piercy

A Thesis in Partial Fulfillment of the Requirements
for the Degree Master of Arts in Biology

December 1984

Each person whose signature appears below certifies that this thesis in his opinion is adequate, in scope and quality, as a thesis for the degree Master of Arts.

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LITERATURE REVIEW

The competitive exclusion principle states that if resources are limited and two species with similar requirements occur in the same area, one will outcompete and eliminate the other, i.e., no two species with identical requirements can occupy the same niche. A corollary of this principle is that if two or more sympatric species co-exist successfully, either: 1) resources are not limiting and competition is absent, or 2) competition has been reduced through means such as predation or resource partitioning.

Resource partitioning has been extensively examined as a possible mechanism that allows diverse assemblages of species with similar ecological requirements to exist. Hutchinson (1959) formulated the idea that species diversity and population size can at least partially be understood by examining the differential utilization of shared resources among sympatric species, i.e., resource partitioning. The extent to which any resource can be subdivided or partitioned partially determines the number of species utilizing that resource: the greater the partitioning, the greater the possible diversity. An understanding of resource partitioning may thus help us understand how taxonomic diversity is generated and maintained.

Marine intertidal communities contain groups of similar species occupying the same trophic level and similar niches in close proximity. As such they present excellent opportunities for studying resource partitioning. While much work on resource partitioning in marine invertebrates has been done, an understanding of the process, its extent, and overall significance in maintaining diversity is incomplete. A variety of studies dealing with a wide range of marine invertebrates point to the significance of resource partitioning in separating species along three main dimensions: space (habitat/microhabitat), food, and time (movement rates and activity patterns).

An extensive series of studies have been conducted on the gastropod genus _Conus_ by Kohn (1959, 1967, 1971), Kohn and Leviten (1976), Leviten (1978), and Leviten and Kohn (1980). Food types (prey species and prey size) as well as tolerance to physical stress (catastrophic rainstorms) may be responsible for separating species of _Conus_. Microhabitat and utilization of different time patterns for movement and feeding did not appear to segregate species.

Prey or food partitioning was again implicated as important in separating two intertidal predatory gastropods, _Thais lapillus_ (Linnaeus, 1758) and _Urosalpinx cinerea_ (Say, 1822) in a study by Jillson (1981). Competition for prey of a given size is reduced by preferential feeding on different prey species.

Bloom (1981) demonstrated the importance of habitat and food resource partitioning in ecologically separating six Pacific Northwest nudibranchs. The two guilds of species partition food resources along a gradient of sponge skeletal structure and partition space along a depth gradient.

Bloom proposed that a "watershed' effect based upon energy efficiency rather than competition has led to morphological and behavioral specializations among nudibranchs. Specialization occurred along a prey resource gradient to maximize net energy efficiency. Two different guilds of nudibranchs specialize on sponges at opposite ends of the gradient. As would be predicted from a watershed effect, intermediate forms would be less energy efficient and hence are absent. Differences in radular structure and in the digestive system permit increased efficiency in handling contrasting sponge tissue at opposite ends of the gradient.

Three species of turban snails (Tegula) partition space by having peak abundance at different depths (Riedman et al., 1980). A fourth species does not fall into this pattern. However, when found on kelp plants, these same four species show no difference in vertical distribution.

Before the term resource partitioning was defined, Test (1945) suggested the idea of resource partitioning in her work on several limpet species in the genus *Acmaea* (now classified into three genera: *Acmaea*, *Collisella*, and *Notoacmea*). Niche separation in these species is based on differences in substrate types, intertidal height, and food. Some species are eurytopic having broad niche dimensions such as *Collisella pelta* (Rathke, 1833), inhabiting a wide intertidal range and eating several types of foods. Others are stenotopic having much narrower niche dimensions, sometimes living only on a single type of algae on which they feed. *Notoacmea insessa* (Hinds, 1842), for example, lives almost exclusively on the kelp *Egregia menziesii* (Turner, 1808) on which it feeds.

Such ecological specialization might account for a large number of *Acmaea* species inhabiting the same intertidal zone. Test further maintained that eurytopic species may have given rise to stenotopic species through selection of individuals under different ecological conditions favoring variations in shell size, weight, sculpture, and aperture width. While helping to produce new species, these variations also defined new niches for those species.

Since Test's work, many studies have been conducted on or relating to resource partitioning in limpets. Haven (1971) found microhabitat to be important in separating *Collisella digitalis* (Rathke, 1833) and *C. scabra* (Gould, 1846). In zone 1 of the study site, *C. digitalis* was restricted to vertical or overhanging rocks whereas *C. scabra* preferred horizontal or gently sloping surfaces.

Data collected in Haven's (1971) study is in agreement with the work of Hewatt (1940) and Jessee (1968) in finding differences in behavior patterns between these same two species. *Collisella scabra* appears to be a homing species. The movement patterns of *C. digitalis* are less precise with respect to definite homing positions. In contrast to the strong homing tendencies of *C. scabra*, *C. digitalis* moves vertically in relation to seasons (Frank, 1965) and changing tides and surf (Miller, 1968). These behavioral differences are viewed as significant in producing niche separation between the two species.

Distance moved differs between these two species depending upon the angle of substrate (Collins, 1977). *Collisella scabra* moves less with increasing slope whereas *C. digitalis* moves more. These differences in movement may be related to distance traveled when foraging or to dessication tolerances. The two species both graze on microscopic films of algae and appear to compete for this resource (Haven, 1973).

Stress and dietary differences appear responsible for regulating distribution and abundance in three species of California abalones (Tutschulte, 1976). *Haliotis fulgens* Philippi, 1845 is more common in areas of high wave action than *H. corrugata* Gray, 1828 which is restricted to more sheltered sections in the subtidal region. Both of these species prefer drift algae as food whereas *H. sorenseni* Bartsch favors attached leaf kelps.

Although many species of chitons are common members of intertidal and shallow subtidal communities, few studies have dealt with resource partitioning in this group. Most ecological studies on chitons have examined distribution, movement patterns, and food preferences or some aspect related to these in a single species (Barnes, 1972; Caplan, 1970; Demopolus, 1975; Lyman, 1975; Mook, 1983; Nishi, 1975; Smith, 1975; and Westersund, 1975). A few investigations have examined two or more species usually in relation to a limited number of ecological parameters.

Barnawell (1954) arranged five species of the genus *Mopalia* in the following series from most to least tolerant of euryhaline conditions: *Mopalia hindsii* (Reeve, 1847), *M. muscosa* (Gould, 1846), *M. ciliata* (Sowerby, 1846), *M. hindsii var* Barnawell, 1954, to *M. lignosa* (Gould, 1846). *M. muscosa* was found to be the most abundant species in muddy habitats, indicating a tolerance to sedimentation as well as low salinities.

Differences in feeding habits also separate these same chiton species. A sequence from high to low percentage of animal versus plant material in gut contents follows a species pattern of: *Mopalia hindsii var*, *M. hindsii*, *M. ciliata*, *M. muscosa*, to *M. lignosa*.

Conner (1975) found differences in behavioral patterns and habitat in two common intertidal chitons, *Mopalia muscosa* and *Cyanoplax hartwegii* (Carpenter, 1855). *M. muscosa* is most abundant in unprotected areas, most active when submerged or awash, and exhibits territorial behavior. *Cyanoplax hartwegii* inhabits more protected areas, is most active when dry or awash, and is highly nomadic.

In a study by Fitzgerald (1975), neither *M. muscosa* nor *M. ciliata* exhibit "homing" (leaving and returning to the same spot during a single tidal cycle) although individuals move within a "home range" of about 1m. Young individuals of *M. muscosa* are negatively phototropic, moving away from a bright light. Older, larger chitons are photoneutral, being unaffected by the same light stimulus. Field observations showed young individuals are found beneath rocks during the day while larger chitons are found in more exposed habitats. The younger chitons move out from under the rocks at night. This behavior may separate age (size) classes of this species into different niches with greater possible utilization of the habitat.

Three species of subtidal chitons show a bathymetric distribution pattern (Langer, 1978). *Tonicella rubra* dominates in shallow water, *T. marmorea* (Fabricius, 1780) in deeper water. A third species, *Ischnochiton albus* (Linne', 1767) is particularly abundant at a depth of six meters. Separate feeding niches are delineated for the species by differences in proportions of three major prey items: diatoms, sponges, and protozoans.

Andrus and Legard (1975) characterize the microhabitat and vertical distribution of 12 species of chitons along the Monterey Peninsula of central California. Species show similarities and differences in chiton - algal/invertebrate associations, surf strength of habitat, vertical range, and substrate orientation and exposure.

Acanthopleura granulata Gmelin, 1791 and *Chiton tuberculatus* Linne', 1758 often coexist on wave-swept Caribbean shores composed of boulder-size rocks. The two species are spatially segregated, occupying different intertidal ranges with only occasional overlap (Glynn, 1970). Both species indiscriminately ingest numerous algae present within the feeding area. Diet does not appear to be significantly different although *C. tuberculatus* consumes a greater proportion of fleshy thalli of algae which are more common in its lower tidal habitat. Movement and feeding, equated in this study, differed between the species. *A. granulata* forages for 8 hours, *C. tuberculatus* for 6-7 hours.

Acanthopleura brevispinosa (Sowerby) and *A. gemmata* (Blainville) are two sympatric species of tropical chitons that demonstrate homing behavior. Chelazzi et al. (1983) have shown that different movement patterns in these species minimize zonal overlap during the night when they are most active, thus reducing interspecific competition for food. *A. gemmata* shows a stronger constancy in its homing along with a dominant downward component in movement. *A. brevispinosa* shifts its position more frequently. These differences in movement patterns may amplify the zonal separation between the species.

INTRODUCTION

The competitive exclusion principle states that no two species with identical requirements can occupy the same niche. A corollary of this principle is that if two or more species successfully coexist, then either: 1) resources are not limiting and hence competition does not exist, or 2) competition has been reduced through predation or resource partitioning.

Resource partitioning can be defined as the subdivision of an ecological parameter such as food or space into separate subsets each utilized by a different species. Since its initial proposal (Hutchinson, 1959), various studies have demonstrated the importance of resource partitioning in separating a variety of sympatric species.

Marine intertidal and subtidal communities contain groups of similar species occupying the same trophic level and having similar niches. As such, they present excellent opportunities for the study of resource partitioning. Food and space parameters as well as response to physical stress are commonly involved in niche partitioning in marine organisms.

As many as 10 to 15 different species of chitons occur in abundance in the intertidal and shallow subtidal zones in Puget Sound and Strait of Juan de Fuca in Washington, USA. Often many species coexist in the same locality. Their apparent similarity in food, behavior, and habitat warrants a closer examination of the individual niche each species occupies and presents a unique opportunity for studying resource partitioning in a group of sympatric species.

Most studies on niche dimensions in chitons have examined distribution, movement, and food preferences or some aspect related to these in a single species (Barnes, 1972; Caplan, 1970; Demopolus, 1975; Lyman, 1975; Mook, 1983; Nishi, 1975; Smith, 1975; and Westersund, 1975). A few have considered two or more species, usually in relation to a limited number of ecological parameters (Andrus and Legard, 1975; Barnawell, 1954; Chelazzi et al., 1983; Connor, 1975; Glynn, 1970; and Langer, 1978).

My study assumes that niche partitioning is the mechanism that allows diverse assemblages of sympatric chiton species to coexist. It attempts to discover to what extent two resources, space and food, are partitioned and whether or not movement, another niche dimension, contributes to niche separation. Seven species of chitons were studied. These included: *Mopalia hindsii* (Reeve, 1847), *Mopalia ciliata* (Sowerby, 1846), *Mopalia muscosa* (Gould, 1846), *Mopalia lignosa* (Gould, 1846) and *Katharina tunicata* (Wood, 1815) - Family Mopaliidae; and *Tonicella lineata* (Wood, 1815), and *Cyanoplax dentiens*

(Gould, 1846) - Family Ischnochitonidae. They were identified in Keys to the Marine Invertebrates of Puget Sound, the San Juan Archipelago, and Adjacent Regions (Kozloff, 1974).

MATERIALS AND METHODS

General

This study was conducted during the summer of 1983 at the Walla Walla College Marine Station near Anacortes, Washington, USA. The primary study site was on the south side of Deception Island near Deception Pass, located off Whidbey Island east of the Strait of Juan de Fuca. A large rock (approximately 8 x 4.5m) perpendicular to the shoreline and jutting out into the water was located where the 7 different chiton species were found. Limited data was gathered from a second study site near the state of Washington ferry dock at Anacortes. This was a less exposed habitat than at Deception Island. The substrate was primarily angular cobbles and pebbles with some sand and scattered boulders up to $2m^2$.

Transect lines, running parallel to the shoreline, were placed 0.5m apart across the rock surface at Deception Island. Numbered tags were fastened to these lines at 0.5m intervals providing a grid system which was used in sampling and determining individual chiton positions. Two sizes of quadrats were used in sampling: a 0.5 x 0.5m quadrat and a 0.0625 x 0.0625m quadrat. The smaller quadrat will be called the sampling quadrat and was a quarter section of the main, larger quadrat. Since the quadrat sampling technique proved unmanageable on the small boulders at the Anacortes ferry dock, each boulder was instead treated as a separate sampling unit.

Two methods were used in the marking of individual chitons both in the field and laboratory tanks. Generally, animals were tagged using a Dennison tagging gun with color coded plastic tags. Tags were inserted through the girdle and into the pallial groove. A different method was employed in the second tank experiment in which small strips of waterproof paper were letter coded and attached to one of the chiton plates with "super glue."

All specimens used in gut content analysis or laboratory tank experiments were collected at or near the study site at Deception Island.

<u>Space</u> - <u>Habitat/Microhabitat</u>

Extensive sampling of chiton species for microhabitat parameters including tidal height, slope of substrate, exposure, and % cover of algae and invertebrates was conducted to determine differences in microhabitat. Quadrats were placed consecutively along the transect lines. For each quadrat the percent cover of various algae and invertebrates was estimated. One of the four quarter sections (i.e., sampling quadrat) was randomly selected. All chitons in the sampling quadrat were identified and measured. Tidal height was determined for each sampling quadrat selected.

For each chiton within the sampling quadrat, the slope of substrate was measured using a Brunton compass. Microhabitat was further characterized for each chiton according to substrate type (rock, gravel/cobble, algae), degree of exposure (being in a pit, crack/crevice, groove, under algae, or fully exposed), position on rock (top, side, bottom), or the presence of large barnacles - primarily *Balanus cariosus* (Pallas, 1788). The algae within 10 cm of each chiton were also recorded.

Since the greatest diversity of chiton species occurred on the sloping sides of the rock, the total sloping perimeter of the rock was sampled. The top horizontal surface of the rock was less completely sampled with quadrats placed only between alternate transect lines.

At the Anacortes ferry dock two 50 m transect lines were laid down at the study site, one parallel to the shoreline, the other perpendicular. Fifteen random positions were chosen along each line. Boulders reaching to within 50 cm of the positions on the line were then sampled. The dimensions of each boulder were estimated and used in calculating species density.

Food

Gut contents were examined to determine food preferences of the six main chiton species. (*Mopalia lignosa* which was uncommon near the study rock was excluded). Animals were collected near the Deception

Island site during both low and high tides. SCUBA was used during high tides. After collection, animals were initially preserved in a 10% formalin solution, and later transferred to 70% alcohol. In those species in which material in the stomach and intestine was abundant, samples were removed and spread over 3 microscope slides. However, in Tonicella lineata and Cyanoplax dentiens, gut contents were often sufficient for only 1 or 2 slides. This was partly due to the small size of the animals.

A 1 x 1 cm ocular grid with 0.5mm square divisions was used to estimate the projected surface area of food items viewed. Each slide was scanned three times from left to right. Each time a possible food item was seen, an estimate of its projected surface area was obtained by comparing it to the number of squares it covered on the grid. This value was used to calculate the surface area occupied by a particular food item in the gut contents of each individual. From this area value the percent of that food in the diet was calculated for each individual and species.

Cell shape, size, and tissue structure were used in identifying various food items. Specific identification was not always possible. Most algal material could be identified to genus. Invertebrates were identified to a general taxonomic group such as amphipod, barnacle, hydroid, and polychaete.

Food categories, similar to Steneck and Watling (1982), were established based upon size, texture, and reliability of identification. The groups were: diatoms, filamentous red algae (e.g., *Polysiphonia*, *Pterosiphonia*, *Antithamnion*), *Ulva*, encrusting red algae (e.g., *Hildenbrandia*, *Petrocelis*), macrophytes (consisting of algae with several cell layers and forming large erect thalli usually branching or blade-like e.g., *Gigartina*, *Hedophyllum*, and *Fucus*), *Lithothamnion*, green filamentous algae (e.g., *Cladophora*), and invertebrates (barnacles, hydroids, bryozoa, polychaetes, nematods, bivalves, gastropods, and various larvae). Such "functional" groups appear to have ecological significance based upon toughness (including resistance to being scraped off a rock), size, and cellular structure which can be directly related to difficulty in grazing. These food groups, therefore, may be more important than particular algal or invertebrate species in comparing and analyzing chiton diets.

Movement

Movement differences among chiton species were analyzed and compared relative to rate, position, percent activity, range, and total distance in the field and in laboratory tanks. In the field study, positions of randomly chosen chitons were monitored relative to coordinates of the rock grid system 10 times over a 9 day period, followed by a hiatus of 10 days, and then 5 more times over a 10 day period (total time = 29 days). Observations at high tides were made using SCUBA. One night observation was made. Locations were plotted on a scale map of the rock grid system from which total distance moved, range of movement (maximum displacement between the two farthest points at which a chiton was observed) and vertical range (tidal height) were computed.

A concrete outdoor tank (dimensions = 2.5m x 1.2m x 1.2m) filled with running seawater was used for the laboratory study of chiton activity patterns, behavior, and movement rates. A grid system of 10cm x 10cm squares, drawn on the floor and sides, provided a means of plotting chiton positions. Each animal's location was recorded at two hour intervals. The tank was set up one week prior to the beginning of the experiment to allow a growth of diatoms as a food source. Water depth in the tank was maintained at 60 cm and controlled by a standpipe in the drain. The tank was drained and filled once each day corresponding to the times of the natural low tides. Water flow was automatically controlled with a Richdel solenoid operated water valve.

Two tank experiments were run, the first for 76 hours, the second for 32 hours. Distances moved were computed by plotting positions on a scale drawing of the tank. Mean rates were calculated for each species during a given time interval. Activity (percent of the total number of individuals per species that moved during a given time interval), level at which each animal was in relation to water depth (1 = within 10 cm of maximum water level, 2 = between maximum water level and tank floor, 3 = tank floor), and the number of surfaces occupied (1 = single surface, 2 = edge, 3 = corner) were also compared among species.

During the second tank experiment, small boulders containing a variety of algae and invertebrates were added to the bottom of the tank. In addition to the same four parameters in the first tank experiment, presence/absence on rocks and position on the rock (top, side, underneath, or below -- not attached) were added.

RESULTS

Table 1 summarizes the results obtained for all three aspects (space, food, and movement) of this study.

Space - Habitat/Microhabitat

Table 2 lists differences in species composition and density between the two study sites. In general, *Katharina tunicata* was much less dominant and *Mopalia* spp. more common at the ferry dock site than at the Deception Island site. Differences between sites in substrate, food availability, and wave energy may account for this.

Species distributions according to intertidal height are shown in Fig. 1. The tidal range of sampling was divided into three approximately equal intervals to test for any differences in distribution relative to high, to middle, and to low tidal regimes. For the Deception Island site, Chi square tests performed independently on each interval suggest significant ($p < 0.05$) species differences in relative abundance at the mid (-0.3 to +0.3) and at the high (+0.3 to +0.9) tidal range, but not at the low (-0.9 to -0.3) range.

Microhabitats relative to angle of substrate were also compared. Substrate angle was divided into 15 degree increments (from 0 to 90 degrees). The percent of each species occurring at each slope interval was computed. Differences in slope angle preference (one-way ANOVA, p <

0.05) existed among species at both sites.

At Deception Island, there were significant ($p < 0.05$) species differences in three of seven exposure categories (being under a rock or rock overhang, being on top of the rock, being among barnacles). No such differences were found at the ferry dock where most of the chitons were clustered under boulders.

Figure 2 shows the location of all chitons sampled at the Deception Island site. Note how Mopalia ciliata, M. hindsii, and Tonicella lineata primarily occupy the sloping sides of the rock, Cyanoplax dentiens the top, while Katharina tunicata ranges widely over both the sides and top. Only 50% of the top surface of the rock was sampled compared to the entire surface area of the sloping sides. (Therefore, density represented by the symbols in the two regions can not be directly compared).

A comparison of the chiton species with respect to relative percent cover of algae and invertebrates in the microhabitat is shown in Fig. 3. At Deception Island, species differed with respect to Ulva, to Lithothamnion, and to invertebrates ($p < 0.001$), and to encrusting red algae ($p < 0.05$). At the ferry dock site species differed with respect to invertebrates ($p < 0.01$), to Lithothamnion ($p < 0.05$), and to macrophytes ($p < 0.05$). Particularly note the high percent cover of Lithothamnion associated with Tonicella lineata at both sites.

Using only data for species common to both sites, a two-way ANOVA tested for species differences with respect to percent cover of algae and invertebrates among chiton species at both sites, between sites, and for a particular species between study sites (two-way interactions). There was a difference ($p < 0.05$) in cover of *Ulva*, diatoms, filamentous red algae, and filamentous green algae among chiton species over both sites. *Ulva* and invertebrates differed ($p < 0.01$) in cover between the two sites. *Ulva* was higher in the microhabitat of *M. muscosa* while invertebrates were higher in the microhabitat of *M. ciliata* at the ferry dock (ANOVA two-way interactions, $p < 0.05$).

FOOD

Chiton species differed (one-way ANOVA, $p < 0.05$) in the gut contents of *Ulva* and diatoms (Table 3), and possibly ($p < 0.10$) also of *Lithothamnion*, of filamentous red algae, and of invertebrates. Invertebrates (worms and amphipods) were frequently found associated with filamentous red algae in gut contents. Perhaps living among the filaments, they are ingested with the algae. Whole barnacles and barnacle plates were common in the gut contents of the *Mopalia* spp.

Similarities in gut contents appear between each of the following pairs of species (Table 3) based upon actual values of percent composition of diet and groupings made by the Duncan's Multiple Range Test which links species having values that are not significantly different: *Mopalia ciliata* and *M. hindsii*; *Katharina tunicata* and *M. muscosa*; *Cyanoplax dentiens* and *Tonicella lineata*. *M. hindsii* and *M. ciliata* are the most similar, with no clear distinction in any of the food categories, suggesting some other factor may separate them.

The ratio of percent contribution in gut contents to microhabitat percent cover may indicate the degree of selectivity in any of the eight food groups: the larger the value, the greater the selectivity (Fig. 4). In general, all species of chitons had a higher relative percent of diatoms in their diets than in their microhabitats. This is particularly noticeable for *Cyanoplax dentiens* and *Tonicella lineata*. Such an unusually high ratio may result from the ubiquitous presence of diatoms at the Deception Island site combined with ease of identification in gut contents and maximum preservation in the gut, or the high value may truly indicate real selectivity.

High gut content to microhabitat ratios of filamentous red algae in *Mopalia ciliata* and *M. hindsii* suggests that these two species select this item from the microhabitat. Similarly, *M. muscosa* appeared to select *Ulva*. Some food types (e.g., filamentous green algae) present in the gut contents but not seen in the microhabitat were probably overlooked in the field. Direct comparisons for the same individual as well as an increase in sample size are needed to confirm the evidence for selective feeding.

MOVEMENT

Field studies of distance moved and range revealed considerable variation among individuals of the same species, but species did not differ significantly (one-way ANOVA, $p > 0.05$). Movement patterns of representative chitons are plotted in Fig. 5. The concept of a home range rather than strict homing (returning to the same spot after one tidal cycle) best fits these patterns.

Table 4 presents data from the first movement experiment in the outdoor tank. The four species present differed with respect to three of four dependent variables: rates of movement, percent activity, and level of animal in tank (one-way ANOVA, $p < 0.05$). A distinct break separated the four species with respect to level (Duncan's Multiple Range Test). *Mopalia hindsii* and *Katharina tunicata* occupied higher levels in the tank than *M. muscosa* and *Tonicella lineata* which remained primarily on the tank floor.

Figure 6 (tank movement experiment 1) and Figure 7 (tank movement experiment 2) show movement and percent activity patterns for each species plotted in relation to the light/dark cycle, to tank and natural tidal cycle, and to time. Patterns among species appeared quite similar, predominantly showing one major peak per cycle. A few patterns suggested bimodal peaks.

For each animal in the experiment an analysis of variance (regression approach) was completed to obtain an estimate of the effects of time (each day divided into four six hour periods), light/dark, and tank tides (full, emptying, empty, and filling) on the four dependent variables (movement rates, percent activity, level of animal in the tank, and number of surfaces occupied). The species differed with respect to the effect of tank tides on each of the first three dependent variables. Katharina tunicata and Mopalia hindsii moved considerably more during tank high tides than M. muscosa and Tonicella lineata.

Light/dark also had an effect on movement rates ($p < 0.05$). Mopalia hindsii moved twice as far during the light as during the dark while the other three species showed little difference.

For those species and variables common to both tank experiments, relative values and positions based on the Duncan's Multiple Range test were fairly consistent with two exceptions. Mopalia muscosa had a higher movement rate in the first tank experiment than the second. Tonicella lineata had the highest level value in the second experiment compared to the lowest in the first. This can be explained by the fact that in the second experiment, individuals of T. lineata moved onto the rocks placed in the tank. In such cases their level was coded as a "2," increasing the species mean value. However, they never moved up along the sides of the tank to near the maximum water level. In the second tank experiment, there was no significant ($p > 0.05$) difference in any of the six dependent variables among the six chiton species (Table 5).

Tank tides and the light/dark cycle had significant effects (ANOVA regression approach, $p < 0.05$) on only one of six dependent variables, movement rates. *Katharina tunicata*, *Mopalia muscosa*, and *Tonicella lineata* moved considerably more than their mean values during tank filling. *M. ciliata* moved slightly more, and *M. lignosa* and *M. hindsii* moved less. During the remaining three tank tidal situations, no differences were found among the species. In contrast to the first tank experiment four species (*M. ciliata*, *K. tunicata*, *M. hindsii*, and *M. muscosa*) moved less during light than dark while the remaining two (*M. lignosa*, and *T. lineata*) moved more.

Differences in the results between the two movement experiments may be at least partially due to the fact that the animals were kept in small indoor tanks for several days before the start of the second experiment. During this time they did not experience consistent light/dark or tidal cycles, so that rhythms entrained by exogenous factors may have been altered. In contrast, during the first tank experiment the animals were placed into the outdoor tank and the experiment begun less than two hours after they were collected from the field.

Both tank experiments were done over relatively short time periods under artificial conditions with no real controls. Therefore, any conclusions based on results from these experiments can only tentatively be applied to the natural situation. The initial transfer from the field into the outdoor tank probably increased movement and activity. However, relative values and behavior do suggest species differences that warrant further investigation in both more controlled tank and field studies.

DISCUSSION

Differences in microhabitat parameters (i.e., tidal height, position and exposure on the rock surface, substrate slope, and chiton-algal/invertebrate associations) suggest the importance of space partitioning in separating chiton species. Owing to the somewhat limited area and tidal range sampled, the correlation of chiton species with intertidal height and depth may not have been shown adequately by this study. Langer (1978) has found a spatial separation of 3 species of chitons in relation to depth. Other studies by Andrus and Legard (1975) and Barnawell (1954) support indirectly the findings here that differences in exposure are important in spatially separating chiton species.

Andrus and Legard (1975) find Tonicella lineata to occur only in the presence of encrusting coralline algae. This same association appears in my study in which T. lineata had the highest percent cover of the encrusting calcareous alga Lithothamnion in its microhabitat, clearly separating it spatially from the other species.

Significant differences in gut contents and food group selection indicate resource partitioning of food groups. The high percent of Lithothamnion in the gut contents of T.

lineata agrees with similar findings of Demopulos (1975), Barnes (1972), and Barnes and Gonor (1973). The higher percent contribution of animal versus plant material in the gut contents of *Mopalia hindsii* and *M. ciliata* than in *M. muscosa* is in striking agreement with the observations of Barnawell (1954). This difference appears especially important in ecologically separating *M. ciliata* and *M. hindsii* from *M. muscosa*, which were quite similar in all other niche dimensions.

Radular structure (size and shape of teeth) and function as well as other digestive system modifications may account for differences in food preference. Barnawell (1954) found no correlation between the gut length and percent of animal versus plant material in diets of five species of *Mopalia*.

Movement may be related to foraging strategies and behavioral responses to changes in water level. Tank experiments revealed that *Katharina tunicata* frequently moved vertically following the water level while *Mopalia muscosa* remained on the tank floor. This may allow *K. tunicata* to move into areas where there are more high level macrophytes which it seems to prefer, and subsequently reduce competition between the two species. Since the tank experiments were uncontrolled and somewhat artificial, further field observations are needed. Similar behavioral differences help separate two sympatric Caribbean chitons

(Chelazzi et al., 1983) and two sympatric limpets (Collins, 1977).

Movement patterns in my field observations suggesting a home range have been found by other investigators (Lyman, 1975; Smith, 1975; and Fitzgerald, 1975) for the same chiton species examined here. Chelazzi et al. (1983) and Mook (1983), however, found evidence for strict homing to exact locations in Carribean chitons as a different movement pattern.

IMPLICATIONS

Partitioning of space (intertidal height and exposure) and food seem important in separating the chiton species. Whether this has resulted from competition or some other mechanism (e.g., predation, energy considerations) is not clear.

Space may be a limiting resource. Differences in utilization of that space suggest partitioning. There was indirect evidence for competition for space. *Katharina tunicata* was clearly the dominant species at the Deception Island study site, where the relative numbers of the other chiton species except for *Tonicella lineata* were much lower. This is especially true for *Mopalia muscosa*, which was the most similar to *K. tunicata* in its niche dimensions. At the ferry dock where the predominance of *K. tunicata* was much less, the relative numbers of *M. muscosa* and other Mopalia spp. were much greater.

Food did not appear to be a limiting resource in the microhabitats of the chiton species. Therefore, divergence in diet may not have resulted from competition.

Bloom (1981) has proposed an alternate explanation to competition as the impetus for resource partitioning in nudibranchs in what he refers to as a "watershed effect." In this model, niche is determined by optimization of energy efficiency in feeding. Two guilds of dorid nudibranchs specialize on sponges with different skeletal structures at opposite ends of a gradient in spicule development and concentration. He interprets this specialization and subsequent partitioning as a consequence of maximizing net energy efficiency rather than the result of direct competition. Differences in radular structure and in digestive modifications found in the two nudibranch guilds increase efficiency in processing sponge tissue at opposite ends of the gradient and appear to support this model. A lack of nudibranchs feeding on sponges in the middle of the gradient is further supportive evidence.

Such an explanation may partially apply to the diversity of diets in the chitons. Different food types such as those proposed by Steneck and Watling (1982), constitute a type of gradient based upon size, texture, and degree of difficulty in removal from the substrate. Barnawell's findings (1954) of a pattern of high to low percent of animal versus plant material in the diet of five species of the genus Mopalia, along with similar findings in my study, support the concept of a gradient of food groups with species feeding at different points along that gradient. In contrast to Bloom's (1981) model, however, chiton species feed along the entire length of the gradient, not just at opposite ends.

Hutchinson (1959) discusses as part of his answer to the question "Why are there so many kinds of animals?" two factors that seem related to the question of diversity in chitons: 1) the principle that communities like populations have ecological stability, and 2) the "mosaic nature" of the environment. Diverse communities of many different species are better able to persist than less diverse communities of fewer species for at least two reasons. A complex food web with many different links at the same level can better survive predation, stabilizing both the predator and prey populations. In addition, even though an invading species may reduce the niche and population size of an established species, it will lead to an increase in community stability by reducing possible fluctuations in population size of the original species. Thus, many species of similar chitons in contrast to a single or limited number of species may increase community stability and hence be important in indirectly influencing diversity.

Relatively small size of organisms coupled with diversified elements in the environment provide a wide range of conditions available. In chitons, which are mostly relatively small in size, a wide variety of microhabitats are available with differences in tidal exposure, light and temperature regimes, substrate, and micro-topography. Many types of algae and invertebrates are also accessible to the chiton radula as food. Such a large environmental mosaic makes a high degree of diversity possible.

Test (1945) suggests that eurytopic species with broad niche dimensions may have given rise to stenotopic species through selection of individuals under different ecological conditions favoring structural and physiological variations. She maintains that diversity in limpets (Acmaea) is a result of specialization, a narrowing of niche dimensions that eventually isolates groups which become different species. The mechanism for this process is not clear, however. How, for example, does reproductive isolation occur? Perhaps limpets that begin living in distinct microhabitats experience different environmental conditions (i.e., temperatures and exposure times) that may stimulate gamete production and trigger release at slightly different times, thus facilitating reproductive isolation.

If the ideas of Test are applied to taxonomic relationships in chitons, one or more eurytopic species should be present within a genus or family which have given rise to several stenotopic species. This framework may fit the genus *Mopalia*. When my data are combined with those of Barnawell (1954) and Andrus and Legard (1975), *Mopalia muscosa* appears eurytopic, with the remaining *Mopalia* species being somewhat more specialized either in microhabitat or food.

Competition may thus not be the sole driving force behind resource partitioning. Energy efficiency, community stability, the environmental mosaic, and relationships of eurytopic to stenotopic species may be equally linked to resource partitioning and chiton diversity.

TABLE 1

Summary of interpretation of important differences in the niches of the seven chiton species studied. Individual entries were chosen based both on the results of statistical tests comparing species differences and the author's own subjective interpretations.

	SPACE							FOOD		MOVEMENT						
	TIDAL HEIGHT		MICROHABITAT ORIENTATION[2]			ALGAL/INVERTEBRATE ASSOCIATIONS[2]		GUT CONTENTS[2]	FEEDING RATES (rasps/min)	FIELD	MOVEMENT RATES (cm/hr)	ACTIVITY	LEVEL	SURFACE	PRESENCE/ ABSENCE ON TANK ROCKS	POSITION ON ROCK
MOPALIIDAE																
Mopalia hindsii	narrow at MLLW	FD —	<45	FD —	overhang with barnacles	encrusting reds (soft)	FD —	filamentous reds,[1] invertebrates[1]	7	nomadic	9 (high tides-light)	0.55 (morning)	follows water level	2	present	side
Mopalia ciliata	broad	narrow at MLLW	<45	under	overhang with barnacles		invertebrates macrophytes	filamentous reds,[1] invertebrates[1]	7	nomadic	4	0.54	follows water level	2	present	side
Mopalia muscosa	narrow at MLLW	narrow at MLLW	0-90	sides[1]	top	encrusting reds (soft)	macrophytes	*Ulva*	7	home site	5	0.64	floor	2	present	side
Mopalia lignosa	—	narrow at MLLW	—	under	—		invertebrates		10	—	12	0.85	floor	2	present	under
Katharina tunicata	broad more +	narrow at MLLW	0-90	sides[1]	top with barnacles	*Ulva*, macrophytes[1]		macrophytes[ns]	8	nomadic	3 (high tides-pm)	0.45	follows water level	2	absent	side
ISCHNOCHITONIDAE																
Tonicella lineata	broad more -	narrow at MLLW	<45	under	overhang with barnacles	*Lithothamnion*	*Lithothamnion*	*Lithothamnion*	12	home site	2	0.39	floor	2	present	side
Cyanoplax dentiens	narrow only +	—	>45	—	top			Diatoms	—	—	—	—	—	—	—	—
STATISTICAL TEST	* (Chi square) high and mid regimes only	no test	* (ANOVA)	* (Chi square)	* (Chi square)	* (ANOVA)	* (ANOVA)	* (ANOVA)	ns (ANOVA)	ns (ANOVA)	* (ANOVA)	* (ANOVA)	* (ANOVA).	ns (ANOVA)	ns (ANOVA)	ns (ANOVA)

* indicates significant results for species differences ($p < 0.05$) in a statistical test

[1] indicates results for species differences with near significant values in a statistical test

[2] indicates columns whose entries are interpretations of species associations and preferences based on separate statistical tests performed on individual column categories

ns = species differences which were not statistically significant   MLLW = Mean low low water

TABLE 2

Comparison of species composition and density for the two study sites. The numbers in parentheses are the actual number of individuals counted. Owing to sampling of different size boulders, percent composition and density do not correspond directly with each other at the ferry dock.

	RELATIVE % COMPOSITION		AVERAGE DENSITY ($\#/m^2$)	
	Deception Island	Ferry Dock	Deception Island	Ferry Dock
Katharina tunicata	72 (163)	27 (13)	22	4
Tonicella lineata	17 (39)	10 (5)	6	3
Mopalia ciliata	5 (12)	20 (10)	2	2
Mopalia hindsii	2 (4)	—	1	—
Mopalia hindsii var	—	14 (7)	—	1
Mopalia muscosa	1 (3)	14 (7)	1	1
Mopalia lignosa	—	14 (7)	—	1
Cyanoplax dentiens	3 (5)	—	1	—

TABLE 3

Comparison of mean percent contribution of food categories in the gut contents of six chiton species. Sample size equals 8/species except 6 for *Cyanoplax dentiens*. Black lines represent the results of the Duncan's Multiple Range Test.

DIATOMS	M. ciliata	M. hindsii	M. muscosa K. tunicata	T. lineata	C. dentiens	
p = 0.04	44	48	49	62	94	
LITHOTHAMNION	C. dentiens	M. muscosa	K. tunicata	M. ciliata	M. hindsii	T. lineata
p = 0.08	0	1	3	6	7	16
SOFT ENCRUSTING REDS	M. muscosa C. dentiens	M. hindsii	M. ciliata	K. tunicata	T. lineata	
p = 0.5	0	1<	1	2	7	
FILAMENTOUS REDS	T. lineata C. dentiens	M. muscosa	K. tunicata	M. ciliata	M. hindsii	
p = 0.08	0	4	11	16	18	
FILAMENTOUS GREENS	M. hindsii	K. tunicata M. ciliata	M. muscosa	T. lineata	C. dentiens	
p = 0.2	1<	1	2	3	4	
ULVA	C. dentiens T. lineata	M. ciliata	M. hindsii	K. tunicata	M. muscosa	
p = 0.01	0	4	10	18	38	
MACROPHYTES	T. lineata	C. dentiens	M. muscosa	M. ciliata	M. hindsii	K. tunicata
p = 0.6	0	1	2	3	5	13
INVERTEBRATES	C. dentiens	K. tunicata	M. muscosa	T. lineata	M. hindsii	M. ciliata
p = 0.08	0	1	4	12	18	25

TABLE 4

Comparison of movement rates, percent activity, level, and surface among four chiton species during the first tank experiment. Values are species means. Sample size equals 10 for *Tonicella lineata* and *Katharina tunicata* and 9 for *Mopalia hindsii* and *M. muscosa*.

SQUARE ROOT OF DISTANCE MOVED/2 HOUR INTERVAL ($p < 0.05$)

T. lineata	*K. tunicata*	*M. muscosa*	*M. hindsii*
1.8	2.5	3.2	4.2
━━	━━		
	━━	━━	
			━━

ACTIVITY ($p < 0.001$)

0 = no individual moved/unit time, 1 = all moved/unit time

T. lineata	*K. tunicata*	*M. hindsii*	*M. muscosa*
.39	.45	.56	.64
━━	━━		
	━━	━━	
		━━	━━

LEVEL ($p < 0.05$)

1 = within 10 cm of maximum water level
2 = in between tank floor and maximum water level
3 = tank floor

M. hindsii *K. tunicata*	*M. muscosa*	*T. lineata*
1.9	2.7	2.8
━━		
	━━	━━

SURFACE ($p > 0.05$)

1 = floor or wall
2 = edge
3 = corner

T. lineata	*K. tunicata*	*M. hindsii* *M. muscosa*
1.6	1.7	1.8
━━	━━	━━

TABLE 5

Comparison of movement rates, percent activity, level, surface, presence/absence on rocks, and position on rocks for six chiton species during the second tank experiment. Values are species means. Sample size equals 5 for all species except 4 for *M. ciliata*.

SQUARE ROOT OF DISTANCE MOVED/2 HOUR INTERVAL ($p > 0.05$)

M. muscosa	*T. lineata*	*K. tunicata*	*M. hindsii*	*M. ciliata*	*M. lignosa*
2.0	2.1	2.2	2.4	3.4	4.4

ACTIVITY ($p > 0.05$)
0 = no individual moved/unit time
1 = all individuals moved/unit time

T. lineata	*M. ciliata*	*K. tunicata*	*M. hindsii*	*M. muscosa*	*M. lignosa*
0.44	0.51	0.53	0.54	0.56	0.77

LEVEL ($p > 0.05$)
1 = within 10 cm of maximum water level
2 = in between floor and maximum water level
3 = tank floor

T. lineata	*M. hindsii* *K. tunicata* *M. ciliata*	*M. muscosa*	*M. lignosa*
2.3	2.4	2.6	2.7

SURFACE ($p > 0.05$) 1 = floor or wall, 2 = edge, 3 = corner

M. lignosa	*M. muscosa*	*K. tunicata*	*M. hindsii*	*T. lineata*	*M. ciliata*
1.4	1.6	1.9	2.0	2.1	2.2

PRESENCE/ABSENCE ON ROCK ($p > 0.05$)
1 = on/touching rock
2 = not touching rock

M. ciliata	*M. hindsii* *T. lineata* *M. muscosa*	*M. ciliata*	*K. tunicata*
1.5	1.6	1.7	1.9

POSITION ON ROCK ($p > 0.05$)
1 = top, 2 = side, 3 = bottom and attached, 4 = bottom and not attached

K. tunicata	*M. hindsii*	*M. ciliata*	*M. muscosa*	*T. lineata*	*M. lignosa*
1.5	1.9	2.0	2.3	2.6	2.9

FIGURE 1: Percent of the total number of individuals for each species occurring at different tidal heights.

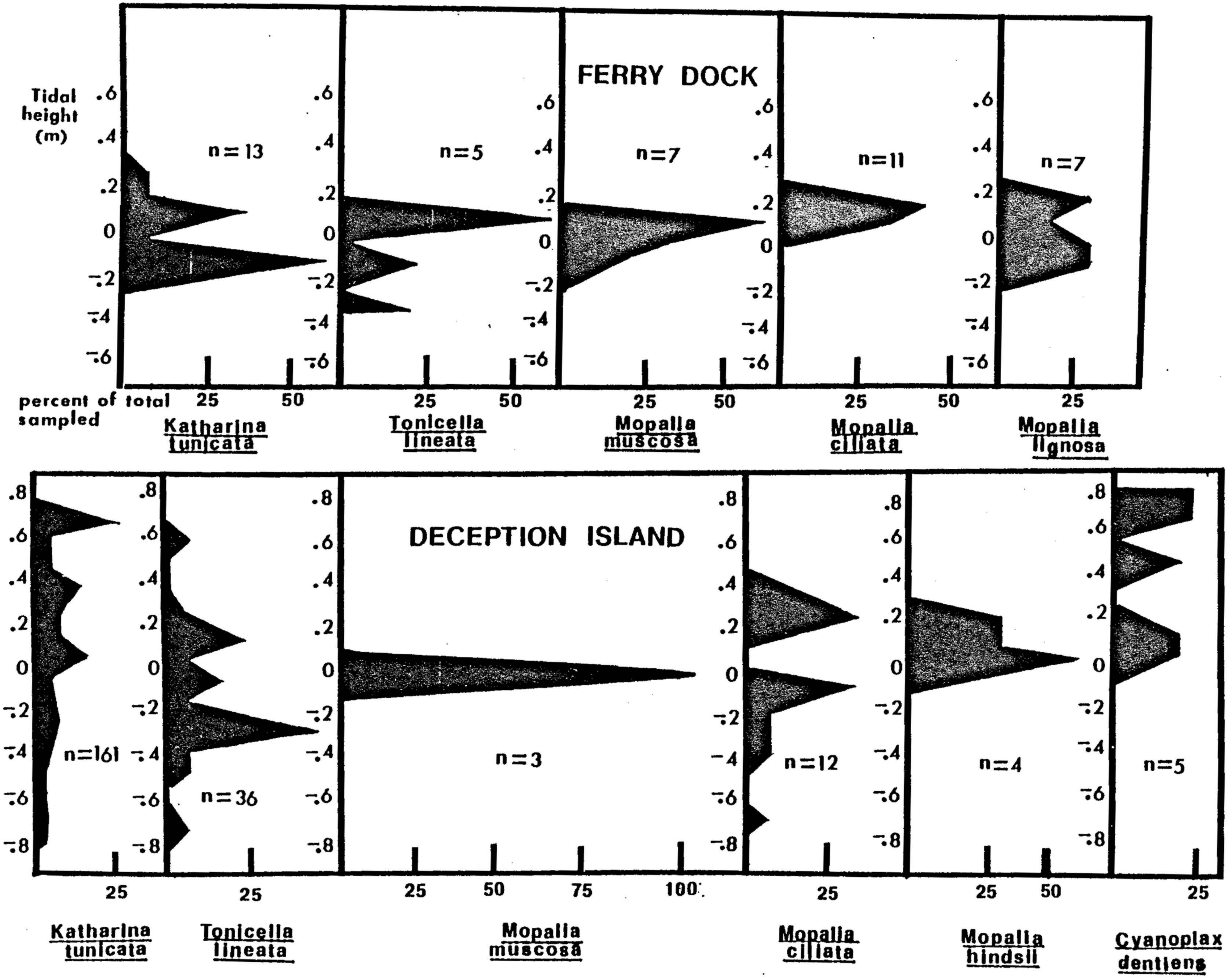

FERRY DOCK
Tidal height (m)
.6
.4
.2
0
-.2
-.4
-.6
percent of total sampled
25
50
n=13
Katharina tunicata
n=5
Tonicella lineata
n=7
Mopalia muscosa
n=11
Mopalia ciliata
n=7
Mopalia lignosa
DECEPTION ISLAND
.8
.6
.4
.2
0
-.2
-.4
-.6
-.8
25
50
75
100
n=161
Katharina tunicata
n=36
Tonicella lineata
n=3
Mopalia muscosa
n=12
Mopalia ciliata
n=4
Mopalia hindsii
n=5
Cyanoplax dentiens

FIGURE 2: Positions of all chitons sampled on the study rock at Deception Island. A contour line indicates points on the rock surface with the same tidal height.

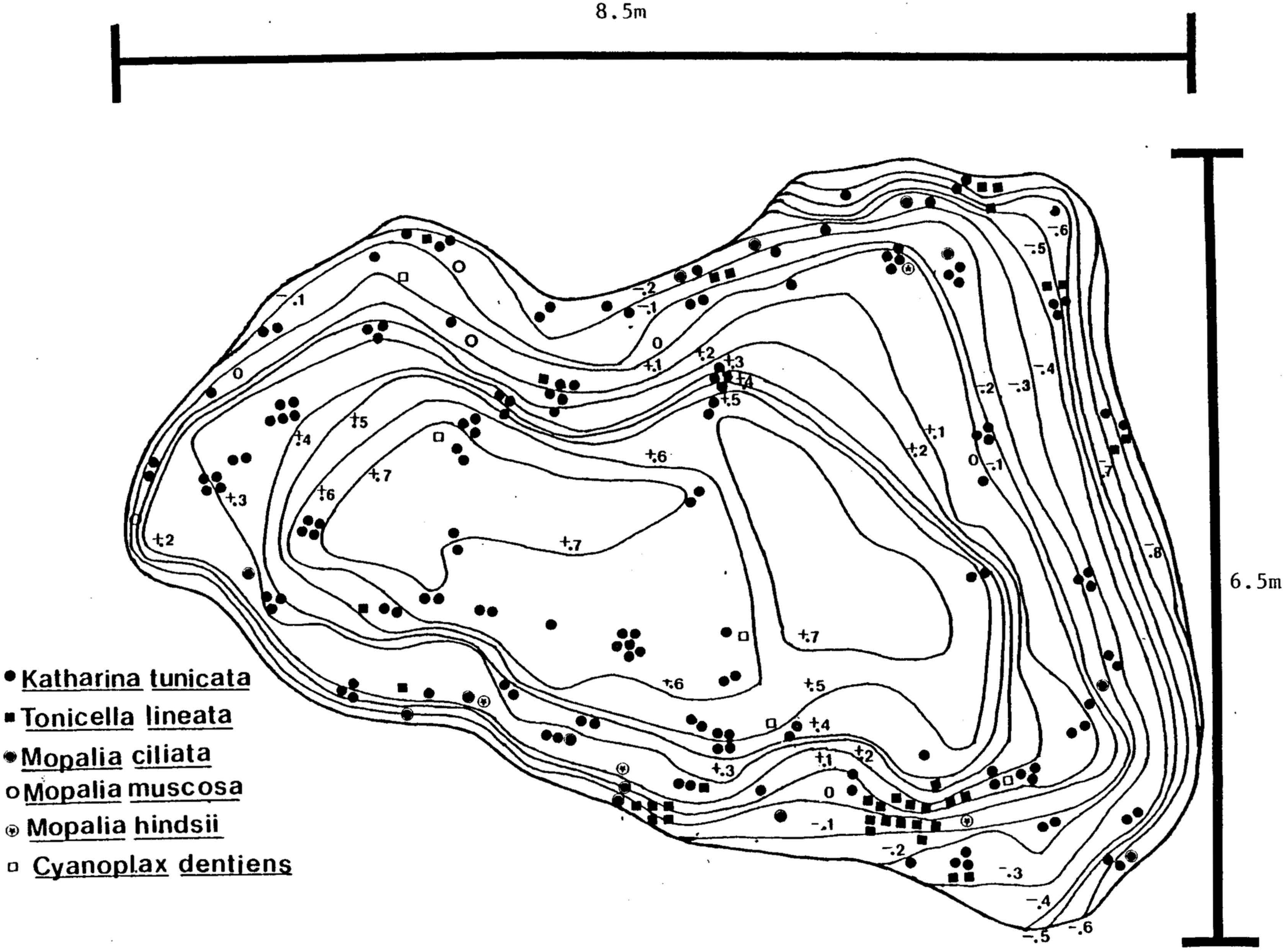

8.5m
6.5m
● Katharina tunicata
■ Tonicella lineata
◉ Mopalia ciliata
○ Mopalia muscosa
⊛ Mopalia hindsii
□ Cyanoplax dentiens
+.1
+.2
+.3
+.4
+.5
+.6
+.7
0
-.1
-.2
-.3
-.4
-.5
-.6
-.7
-.8

FIGURE 3: Comparison of the relative percent cover of seven algal categories and invertebrates in the microhabitat. Percent cover of a particular category for a chiton species was based only on those quadrats in which that species was present.

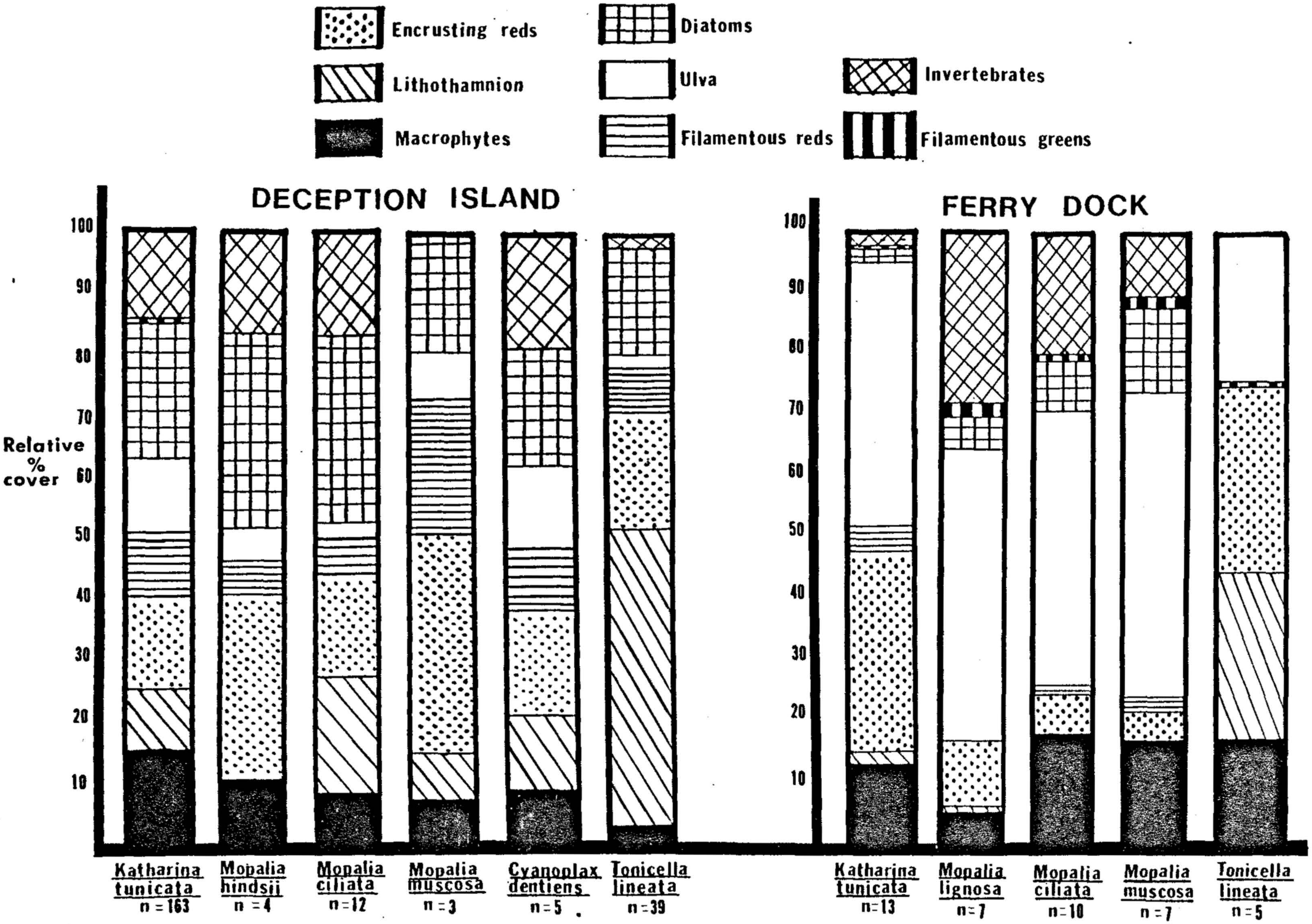
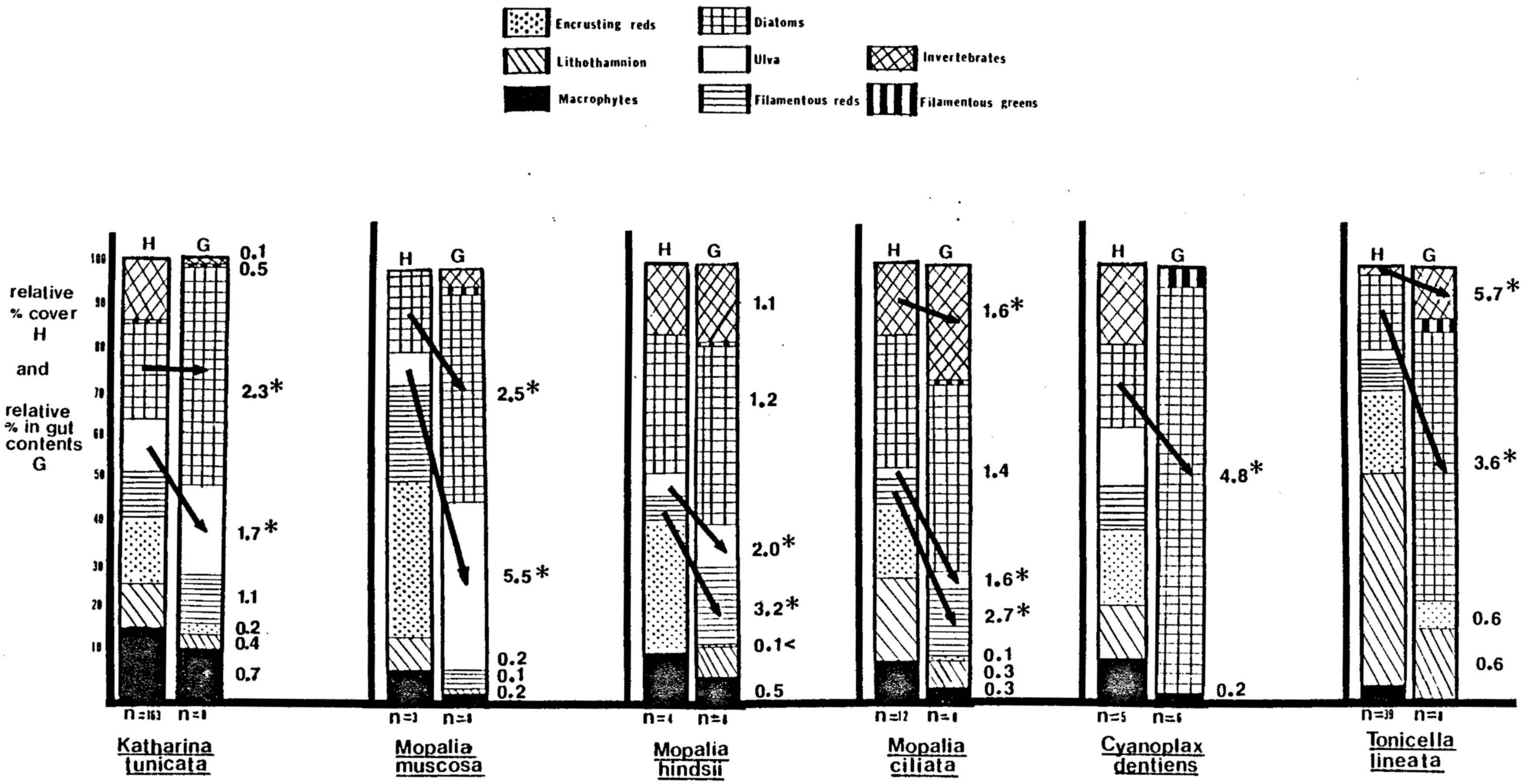

Encrusting reds
Lithothamnion
Macrophytes
Diatoms
Ulva
Filamentous reds
Invertebrates
Filamentous greens
DECEPTION ISLAND
FERRY DOCK
Relative % cover
100
90
80
70
60
50
40
30
20
10
Katharina tunicata n = 163
Mopalia hindsii n = 4
Mopalia ciliata n = 12
Mopalia muscosa n = 3
Cyanoplax dentiens n = 5
Tonicella lineata n = 39
Katharina tunicata n = 13
Mopalia lignosa n = 7
Mopalia ciliata n = 10
Mopalia muscosa n = 7
Tonicella lineata n = 5

FIGURE 4: Comparison of gut contents (G) with percent cover in the microhabitat (H) for the eight food groups and six chiton species studied on Deception Island. The value next to each bar section is the gut content to percent cover ratio for that item. Relatively large ratios (indicated with an asterisk) suggest "selectivity" in feeding.



Encrusting reds
Lithothamnion
Macrophytes
Diatoms
Ulva
Filamentous reds
Invertebrates
Filamentous greens
relative % cover H
and
relative % in gut contents G
100
90
80
70
60
50
40
30
20
10
H
G
0.1
0.5
2.3*
1.7*
1.1
0.2
0.4
0.7
n=163
n=1
Katharina tunicata
2.5*
5.5*
0.2
0.1
0.2
n=3
n=8
Mopalia muscosa
1.1
1.2
2.0*
3.2*
0.1<
0.5
n=4
n=8
Mopalia hindsii
1.6*
1.4
1.6*
2.7*
0.1
0.3
0.3
n=12
n=1
Mopalia ciliata
4.8*
0.2
n=5
n=6
Cyanoplax dentiens
5.7*
3.6*
0.6
0.6
n=39
n=1
Tonicella lineata

FIGURE 5: Plots of movement of selected individual chitons at the Deception Island study site. Each lettered symbol represents the position of a chiton on a particular date. If positions were different on two consecutive dates, points are connected with a black line indicating movement. If a lettered symbol is missing, the chiton could not be located on that date. Two identical views of the same rock are used to eliminate overlap of adjacent pathways.

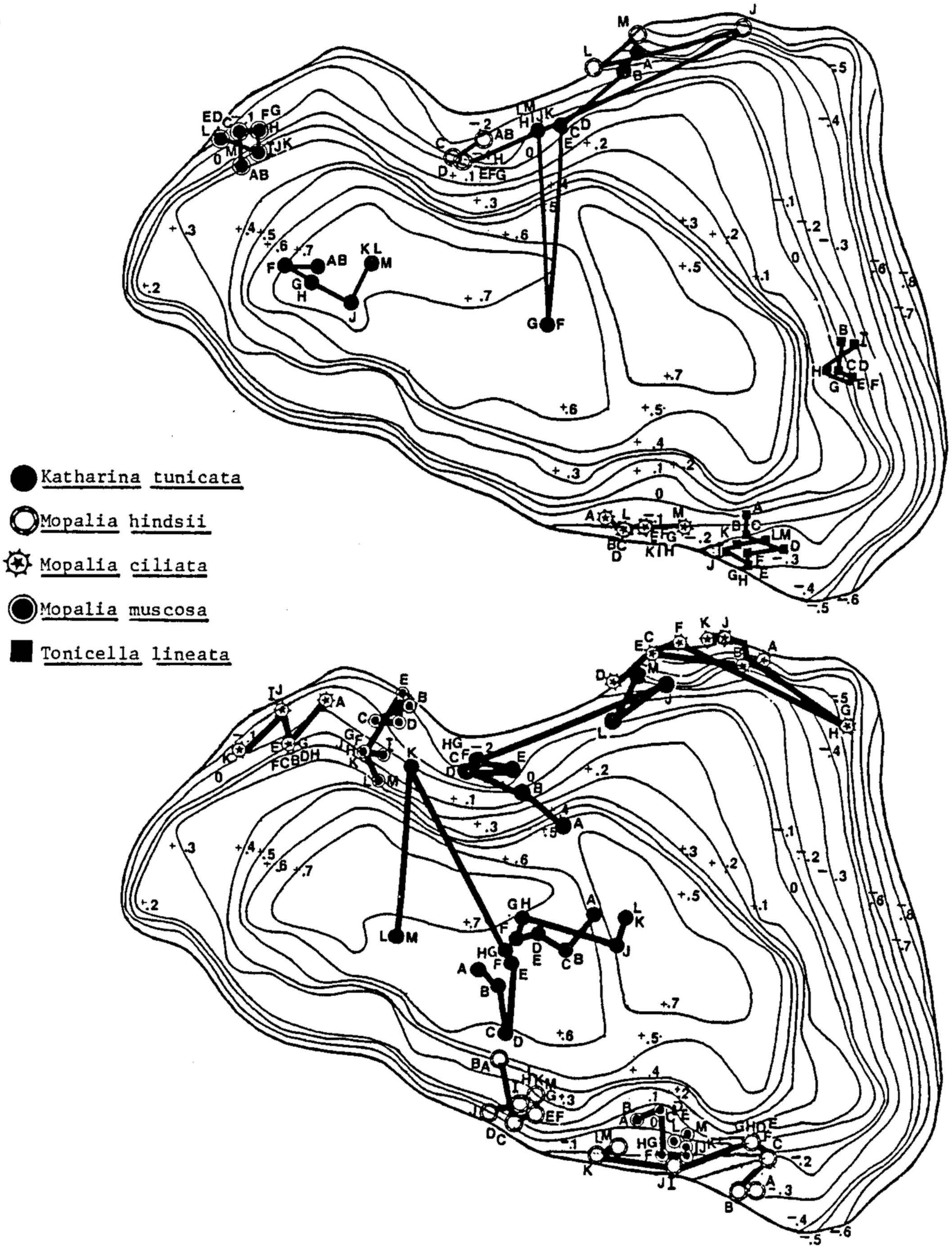

● Katharina tunicata
○ Mopalia hindsii
✪ Mopalia ciliata
◉ Mopalia muscosa
■ Tonicella lineata
+.7
+.6
+.5
+.4
+.3
+.2
+.1
0
-.1
-.2
-.3
-.4
-.5
-.6
-.7
-.8

FIGURE 6: Comparison of movement rates (mean distance moved/species/unit time) and activity (% of individuals moved/species/unit time) among four chiton species in an outdoor tank during a seventy-six hour period.

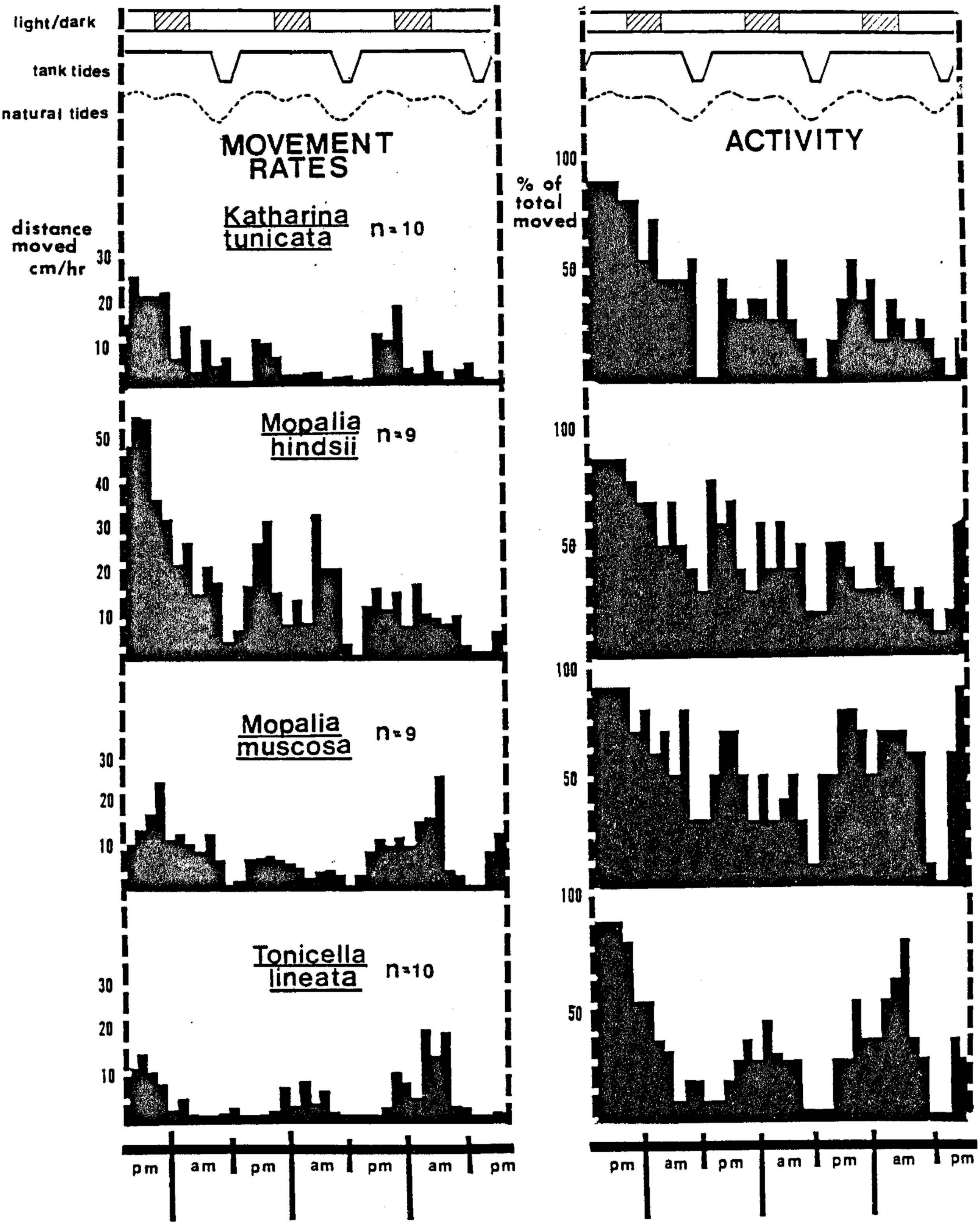

light/dark
tank tides
natural tides
MOVEMENT RATES
ACTIVITY
distance moved cm/hr
% of total moved
Katharina tunicata n=10
Mopalia hindsii n=9
Mopalia muscosa n=9
Tonicella lineata n=10
10
20
30
40
50
100
pm
am

FIGURE 7: Comparison of movement rates (mean distance moved/species/unit time) and activity (% of individuals moved/species/unit time) among six chiton species in an outdoor tank during a twenty-four hour period.

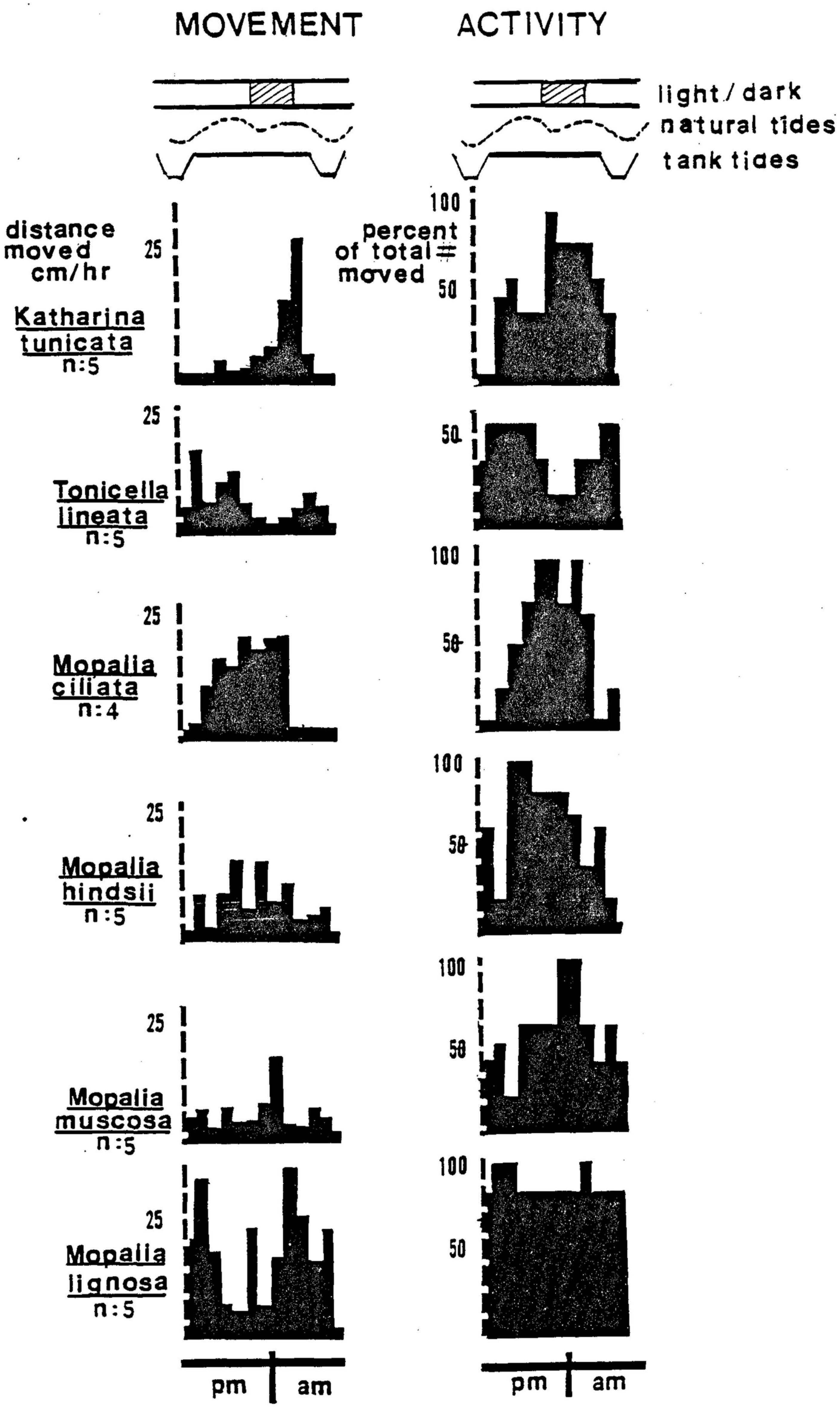

MOVEMENT
ACTIVITY
light / dark
natural tides
tank tides
distance moved cm/hr
25
percent of total # moved
100
50
Katharina tunicata
n:5
Tonicella lineata
n:5
Mopalia ciliata
n:4
Mopalia hindsii
n:5
Mopalia muscosa
n:5
Mopalia lignosa
n:5
pm
am

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TABLE 1

Exposure of chitons with respect to eight microhabitat parameters at the Deception Island site. Values are percent of the total number of individuals sampled/species.

microhabitat parameter species	under rock or overhang	groove	crevice, crack	under algae	pit	top of rock	side of rock	among barnacles
Katharina tunicata (n = 163)	1	39	2	10	0	17	81	70
Tonicella lineata (n = 39)	13	32	0	11	0	0	82	11
Mopalia ciliata (n = 12)	19	46	0	0	0	0	91	73
Mopalia hindsii (n = 4)	25	0	0	0	0	0	75	75
Mopalia muscosa (n = 3)	0	33	0	0	0	33	66	0
Cyanoplax dentiens (n = 5)	0	60	0	0	0	40	40	80

TABLE 2

Exposure of chitons with respect to eight microhabitat parameters at the Ferry dock site. Values are percent of the total number of individuals sampled/species.

microhabitat parameter species	under rock or overhang	groove	crevice, crack	under algae	pit	top of rock	side of rock	among barnacles
Katharina tunicata (n = 13)	51	0	0	0	0	0	75	0
Tonicella lineata (n = 5)	80	0	0	0	20	0	20	0
Mopalia ciliata (n = 10)	73	0	0	9	0	9	36	0
Mopalia muscosa (n = 7)	29	0	0	29	0	0	86	14
Mopalia lignosa (n = 7)	86	0	0	0	0	0	43	0

TABLE 3

Number of chitons and percent distribution (parenthesis) in relation to substrate slope for the Deception Island site.

slope angle	0-14	15-29	30-44	45-59	60-74	75-90
species						
Katharina tunicata (n = 163)	6 (4)	11 (7)	34 (21)	47 (29)	39 (24)	26 (16)
Mopalia muscosa (n = 3)	1 (33)	0 (0)	1 (33)	0 (0)	1 (33)	0 (0)
Mopalia ciliata (n = 12)	0 (0)	0 (0)	0 (0)	8 (67)	1 (8)	3 (25)
Mopalia hindsii (n = 4)	0 (0)	0 (0)	1 (25)	2 (50)	0 (0)	1 (25)
Tonicella lineata (n = 39)	0 (0)	0 (0)	4 (10)	12 (31)	13 (33)	10 (26)
Cyanoplax dentiens (n = 5)	1 (20)	2 (40)	1 (20)	0 (0)	0 (0)	1 (20)

TABLE 4

Number of chitons and percent distribution (parenthesis) in relation to substrate slope for the Ferry dock site.

slope angle	0-14	15-29	30-44	45-59	60-74	75-90
species						
Katharina tunicata (n = 13)	4 (31)	0 (0)	0 (0)	2 (15)	1 (7)	6 (46)
Mopalia muscosa (n = 7)	1 (14)	1 (14)	1 (14)	2 (29)	1 (14)	1 (14)
Mopalia lignosa (n = 7)	3 (43)	0 (0)	0 (0)	1 (14)	0 (0)	3 (43)
Mopalia ciliata (n = 10)	6 (60)	4 (40)	0 (0)	0 (0)	0 (0)	0 (0)
Mopalia hindsii var (n = 7)	2 (29)	0 (0)	0 (0)	4 (57)	1 (14)	0 (0)
Tonicella lineata (n = 5)	1 (20)	1 (20)	0 (0)	3 (60)	0 (0)	0 (0)

TABLE 5

Mean percent cover for seven algal categories and invertebrates in the microhabitat of chitons at the Deception Island site. Sample size equals the number of 0.5 x 0.5m quadrats in which a particular species was found.

species	Diatoms	*Ulva*	Fil. greens	Fil. reds	Encr. reds	*Lithothamnion*	Macrophytes	Invertebrates
Tonicella lineata (n = 16)	10	1	0	4	5	31	3	1
Mopalia muscosa (n = 3)	8	3	0	10	16	3	3	0
Mopalia hindsii (n = 4)	15	3	0	2	15	0	5	8
Mopalia ciliata (n = 10)	16	1	0	4	9	10	6	8
Katharina tunicata (n = 81)	12	5	1	5	8	6	9	7
Cyanoplax dentiens (n =5)	10	7	0	5	9	7	5	8
	$p>0.05$	$p>0.05$	* $p<0.01$	$p>0.05$	* $p<0.05$	* $p<0.01$	* $p<0.01$	$p>0.05$

p values are for one-way ANOVA tests run on each category

TABLE 6

Mean percent cover for seven algal categories and invertebrates in the microhabitat of chitons at the Ferry dock site. Sample size equals the number of 0.5 x 0.5m quadrats in which a particular species was found.

species	Diatoms	*Ulva*	Fil. greens	Fil. reds	Encr. reds	*Lithothamnion*	Macrophytes	Invertebrates
Tonicella lineata (n = 4)	0	9	1	0	11	10	6	0
Mopalia muscosa (n = 5)	7	29	1	1	3	0	10	6
Mopalia hindsii var (n = 6)	0	15	0	0	6	6	5	0
Mopalia ciliata (n = 10)	6	32	1	1	4	0	14	22
Mopalia lignosa (n =4)	4	28	1	0	6	1	3	15
Katharina tunicata (n = 10)	1	18	1	2	14	1	6	1
	* $p<0.05$	$p>0.05$	$p>0.05$	$p>0.05$	$p>0.05$	* $p<0.05$	* $p<0.01$	$p>0.05$

p values are for one-way ANOVA tests run on each category

TABLE 7

Feeding rates and duration of radular stroke for six chiton species. Mean values are given (± one standard deviation in parenthesis). Sample size equals the number of different individuals whose feeding rates were monitored using a contact microphone.

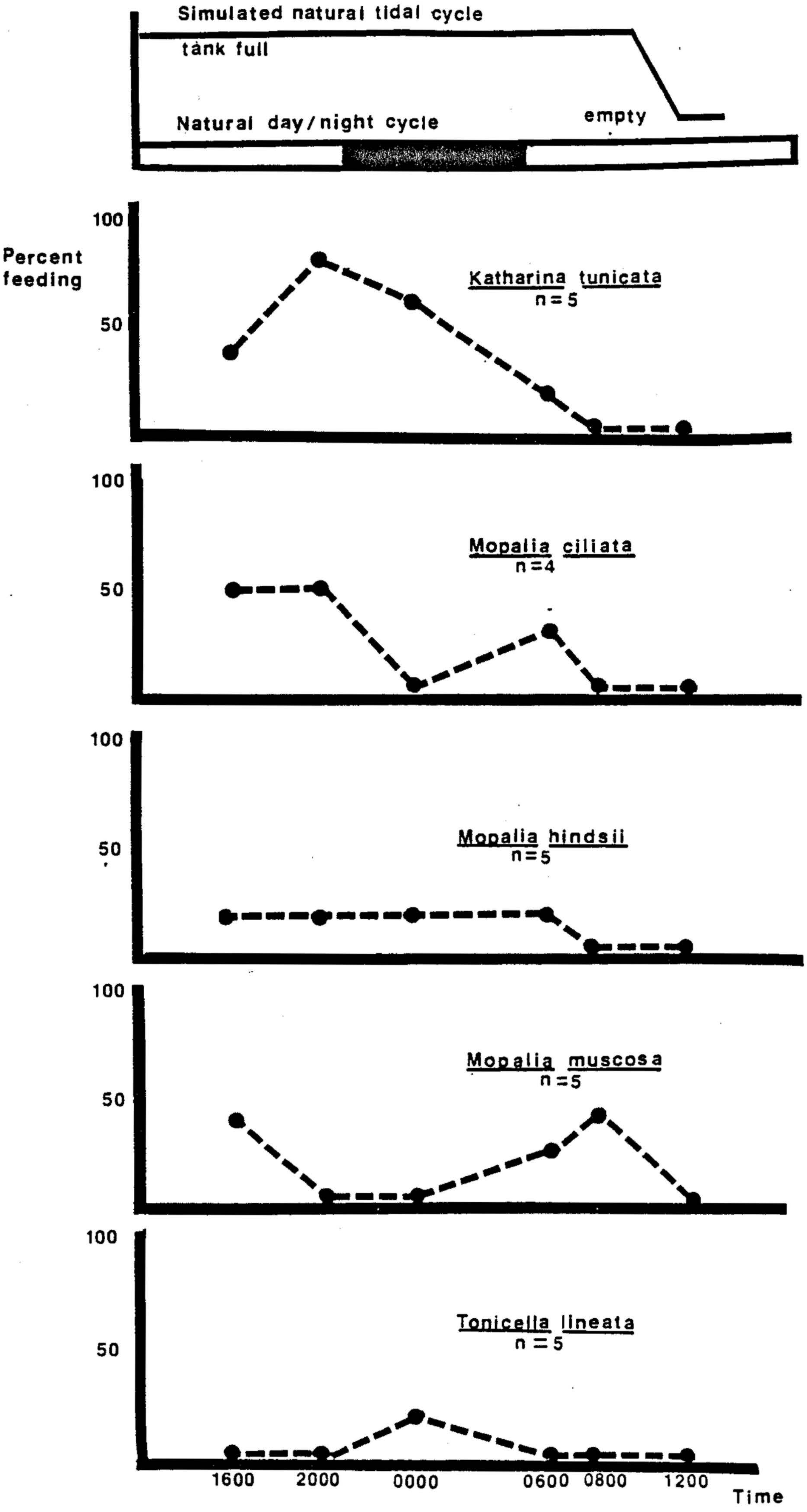
species	total # of observations	Feeding rate (rasps/min)	Duration of radular stroke (sec./rasp)
Katharina tunicata (n = 7)	11	8.3 (1.1)	2.1 (.2)
Mopalia hindsii (n = 4)	4	7.4 (2.0)	2.1 (.1)
Mopalia muscosa (n = 2)	5	7.4 (.7)	2.4 (.3)
Mopalia ciliata (n = 3)	4	7.6 (1.3)	2.2 (.3)
Mopalia lignosa (n = 2)	2	10.2 (1.7)	1.6 (.4)
Tonicella lineata (n = 1)	1	12.0	1.0 (.2)

TABLE 8

Movement of marked chitons at the Deception Island study site. Movement was tracked over an initial 9 day period and then extended through a 29 day period. Values given are means($\pm$ one standard deviation in parenthesis).

SPECIES	N	MEAN TOTAL DISTANCE MOVED OVER 9 DAYS (cm)	MEAN RANGE (cm)	MEAN VERTICAL RANGE (m)	N	MEAN TOTAL DISTANCE MOVED OVER 29 DAYS (cm)	MEAN RANGE (cm)	MEAN VERTICAL RANGE (m)
<u>Katharina tunicata</u>	10	188.7 (166.2)	104.6 (87.5)	.41 (.34)	9	343.5 (177.4)	170.1 (102.8)	.61 (.37)
<u>Mopalia ciliata</u>	5	203.4 (157.9)	99.8 (58.0)	.18 (.13)	2	294.5 (282.1)	161.0 (138.5)	.25 (.21)
<u>Mopalia muscosa</u>	6	136.7 (66.8)	73.2 (33.4)	.28 (.13)	3	177.0 (52.9)	64.7 (21.4)	.30 (.10)
<u>Mopalia hindsii</u>	4	114.8 (20.8)	63.0 (12.8)	.28 (.13)	3	363.3 (215.8)	191.3 (132.1)	.47 (.31)
<u>Tonicella lineata</u>	5	106.4 (27.0)	54.2 (21.7)	.22 (.04)	4	155.5 (64.1)	51.0 (10.6)	.28 (.10)

FIGURE 1: Percent feeding for chiton species held in an outdoor tank during the second tank experiment. Feeding sounds were monitored every four hours over one complete tidal cycle.


Simulated natural tidal cycle
tank full
empty
Natural day/night cycle
Percent feeding
100
50
Katharina tunicata
n=5
100
50
Mopalia ciliata
n=4
100
50
Mopalia hindsii
n=5
100
50
Mopalia muscosa
n=5
100
50
Tonicella lineata
n=5
1600
2000
0000
0600
0800
1200
Time