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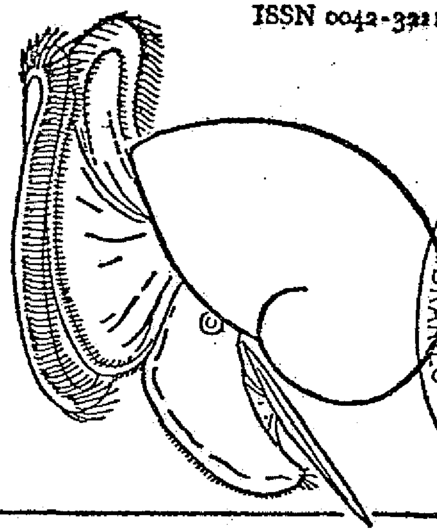

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Spatial Segregation of Four Species of Turban Snails

(Gastropoda : *Tegula*)

in Central California

BY

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(4 Text figures)

INTRODUCTION

FOUR SPECIES OF GRAZING TURBAN SNAILS of the genus *Tegula* are abundant in central California (ABBOTT & HADERLIE, 1980). Two of these species, *Tegula funebralis* (A. Adams, 1855) and *Tegula brunnea* (Philippi, 1848), are common in rocky intertidal communities; *T. funebralis* is abundant from mean lower low water (MLLW) to 1.5 m above MLLW, and *T. brunnea* is common below 0.5 m above MLLW. In addition, *Tegula pulligo* (Gmelin, 1791) and *Tegula montereyi* (Kiener, 1850) are common subtidally in kelp forests. LOWRY, MCELROY & PEARSE (1974) studied the distribution of the 3 subtidal species at one location within the middle of a kelp forest off Pacific Grove, California; the snails were associated with specific algae on the bottom as well as throughout the water column on fronds of giant kelp plants (*Macrocystis pyrifera*). In the present paper, we describe the horizontal and vertical distribution of all 4 species of *Tegula*, from the intertidal zone to the seaward edge of a kelp forest, at the same location as the LOWRY, MCELROY & PEARSE (1974) study. Distributions of the snails in early spring, when kelp biomass and canopy are minimal, are compared with their distributions in late summer, when kelp biomass and canopy development are maximal.

METHODS

Our study was conducted at Hopkins Marine Life Refuge in Monterey Bay off Pacific Grove, California. The habitat is very heterogeneous with a granite substrate interspersed with sand channels, pinnacles, cracks, and boulders. The substrate is covered with a lush understory of *Cystoseira osmundacea*, many species of red algae, and a dense algal-invertebrate turf of coralline algae, tunicates, bryozoans, solitary corals, sponges, vermetids, and many other encrusting organisms. The dominant, canopy-forming plant is the giant kelp *Macrocystis pyrifera*. A detailed description of the study area is provided in PEARSE & LOWRY (1974).

Sampling was done using SCUBA in March 1977 and again in August 1977 along a 300 m transect that extended from the intertidal zone seaward through the kelp forest to a depth of about 13 m (Figure 1). Nine stations were established along the transect at about 1.5 m increments of increasing depth beginning at the intertidal level

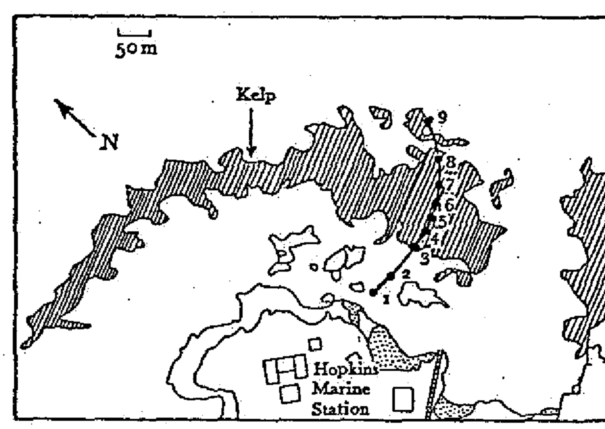

Figure 1

Hopkins Marine Life Refuge, Pacific Grove, California, showing the nine sampling stations transecting the intertidal zone, shallow subtidal zone and kelp forest (hatched). Drawn from an aerial photograph taken on June 14, 1978

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of 1.5 m above MLLW. Populations of *Tegula* spp. were sampled at each station in two ways, depending on whether they occurred on giant kelp plants or on the "bottom" which included algal-invertebrate turf and understory plants as well as rock and sand. At each station, approximately 200 individuals of *Tegula* spp. were collected from the bottom. Giant kelp plants were present only at stations 3 to 9; at these stations, snails were collected from the nearest giant kelp plant that extended up the water column to the surface. All snails were removed from the selected kelp plants in 1.5 m increments of increasing depth from the surface to the bottom; snails from each sample level were placed in a separate plastic bag. The snails were identified, counted and measured to the nearest mm in the laboratory.

The data were analyzed for relative frequency and size distribution of each species on the bottom and on kelp plants at each station. The relative frequencies of each species on kelp plants at each station also were calculated for each 1.5 m depth interval in the water column. Our sampling design did not provide estimates of the densities of each species along the transect because determining densities requires additional labor-intensive estimates of the number of snails per unit bottom area, per kelp frond and the density of kelp fronds at each station.

RESULTS

In March each of the 4 species of *Tegula* showed a distinct zone of abundance on the bottom from the intertidal zone to the seaward edge of the kelp forest (Figure 2). *Tegula funebralis* was restricted to the intertidal region from about 1.5 m above MLLW to 0.5 m below MLLW. *Tegula brunnea* occurred between 0.5 m to 7 m below MLLW. Near the shoreward edge of the kelp forest, at a depth of 3 m, nearly 90% of the turban snails on the bottom were comprised of *T. brunnea*. *Tegula montereyi* had a broad zone of distribution across the kelp forest, and except for a peak relative frequency of 50% at the 6 m depth, *T. montereyi* did not exhibit a clear dominance in relative frequency at any location. The relative abundance of *T. pulligo* on the bottom increased rapidly in the middle of the kelp forest at depths of 4 to 7 m. This species predominated in the seaward half of the kelp forest, with relative frequencies of 70% at a depth of 7 m to 100% at the 13 m depth.

The distribution of turban snails on giant kelp plants along the transect was similar to that of the snails on the bottom (Figure 2). *Tegula brunnea* was dominant on plants at the shoreward edge of the kelp forest. *T. pulligo* predominated on plants at the seaward portion, and *T. montereyi* occurred at low relative frequencies on plants throughout the middle of the kelp forest.

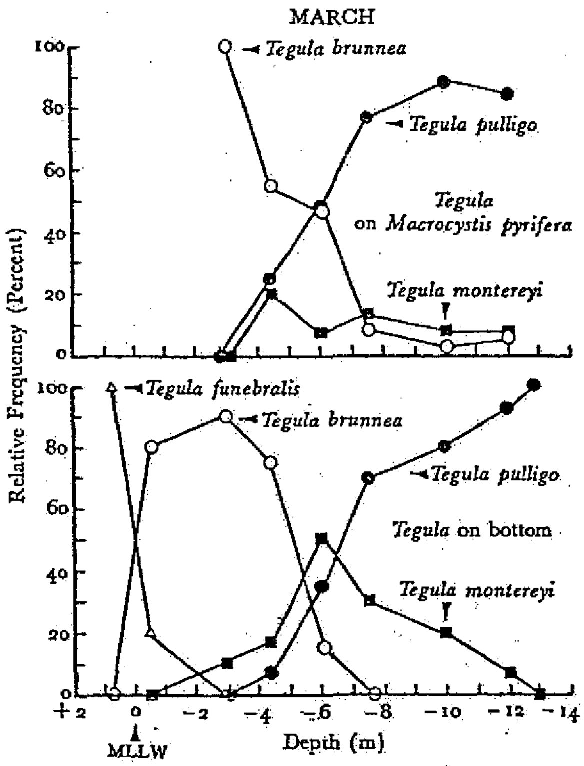

Figure 2

Distribution of four species of *Tegula* on the bottom and on giant kelp plants along the transect in March, 1977. The relative frequencies that each species comprised are plotted for each station. Snails on the bottom were sampled separately from snails on kelp plants. At each station, about 200 snails were collected from the bottom, and all snails were collected from single large kelp plants present at stations between depths from 3 to 12 m. Sample sizes for snails on kelp plants are shown in Figure 4

The pattern of zonation along the transect in August was remarkably similar to that in March for all 4 species, both on the bottom and on kelp plants (Figure 3). However, at 0.5 m depth *Tegula funebralis* occurred with higher relative frequency in August than in March and *T. brunnea* occurred at correspondingly lower frequency. *T. brunnea* was present at higher relative frequencies in August than in March at the 4 to 6 m depths, both on the bottom and on kelp plants. *Tegula montereyi* did not

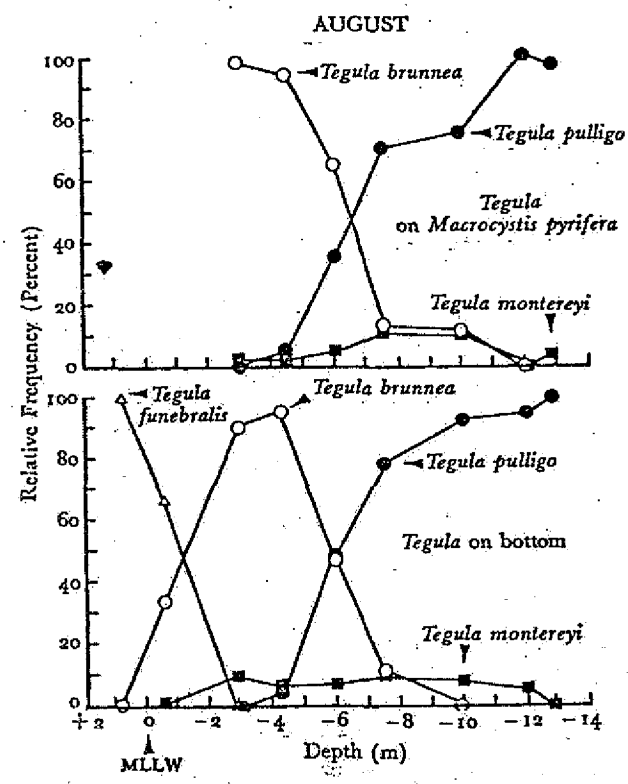

Figure 3

Distribution of four species of *Tegula* on the bottom and on giant kelp plants in August, 1977. Sampling procedures as explained in Figure 2

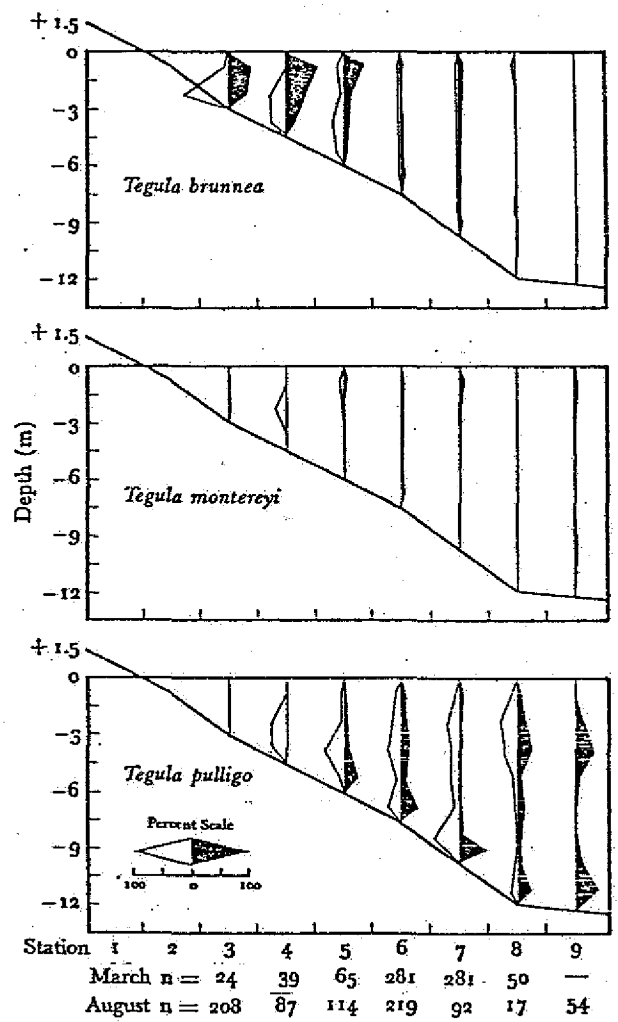

Figure 4

Vertical distributions of four species of *Tegula* on giant kelp plants at stations along the transect in March 1977 (open polygons) and August 1977 (solid polygons). The relative frequencies that each species comprised in the total number of snails collected from one large kelp plant at each station are shown for each 1.5 m interval of increasing depth from the surface to the bottom. Sample sizes for each sampling period and scale of relative frequency in percent are indicated

attain relative frequencies in the middle of the kelp forest as high in August as in March. The distribution and relative abundance of *Tegula pulligo* remained similar during both sampling periods.

The vertical distributions of turban snails on giant kelp plants did not show patterns of zonation that were as distinct as the horizontal distributions (Figure 4). *Tegula brunnea* in the shoreward part of the kelp forest showed a shift in relative abundance from the deeper portions of the plants in March up into the canopy in August. At the seaward stations, *T. brunnea* was generally evenly distributed throughout the water column at both sampling periods. *Tegula montereyi* occurred at about equal relative frequencies throughout the water column on kelp plants during both sampling periods. Similarly, *T. pulligo* was found at all depths on kelp plants with little apparent vertical zonation. However, in the middle of the kelp forest, there were proportionately fewer individuals of *T. pulligo* near the top of the plants in August than in March.

The size distribution of snails on the plants were similar to those found by Lowry, McElroy & Pearse (1974); individuals of *Tegula brunnea, T. montereyi* and *T. pul-*

ligo were smaller on the bottom, and in the lower portions of the kelp plants, than on the upper portion of the kelp plants.

DISCUSSION

Kelp forests are complex structural communities (PEARSE & GERARD, 1977) and closely related species often exhibit zonal patterns of distribution from the intertidal zone to increasing depths, *e.g.*, abalones (TUTSCHULTE, 1976); bryozoans (BERNSTEIN & JUNG, 1979); scorpaenid fish (HALLACHER, 1977; LARSON, 1980); and spider crabs (HINES, 1981). The 4 sympatric species of *Tegula* in the present study similarly exhibited a well-defined pattern of spatial segregation in the Hopkins Marine Life Refuge. *Tegula funebralis* occurred exclusively in the intertidal zone. *Tegula brunnea* was dominant from the low intertidal zone through the shoreward portion of the kelp forest, while *Tegula pulligo* dominated the seaward portion of the kelp forest. *Tegula montereyi* usually occurred at low relative frequencies throughout the kelp forest, with the highest relative abundance near the middle of the forest. This pattern of zonation was consistent both on the bottom and on the giant kelp plants, and it changed little seasonally.

The vertical distribution of the three species of *Tegula* on fronds of *Macrocystis pyrifera* showed no clear pattern of zonation in either March or August. However, in the shoreward portion of the kelp forest individuals of *T. brunnea* were more frequent and individuals of *T. pulligo* were less frequent in the kelp canopy in August than in March. LOWRY, MCELROY & PEARSE (1974) also found a vertical stratification with *T. brunnea* predominating in the canopy and *T. pulligo* predominating near the bottom. Their study was done near the center of the kelp forest (6-9 m depth) during August. Our more extensive sampling across the forest in March and August indicates that vertical stratification between these two species is very unstable.

Considering the marked seasonal changes in biomass and density of kelp plants in the Hopkins Marine Life Refuge (GERARD, 1976), the lack of substantial seasonal changes in the relative distribution of the different species of turban snails is surprising. Proliferation of kelp fronds in summer results in a tremendous increase in available substrate area at the sea surface, whereas winter storms greatly reduce the canopy cover. Moreover, winter storms probably knock many snails off the kelp fronds. The effect of the winter storm swells is most pronounced in shallower water, and may account for the seasonal shifts of *Tegula brunnea* on the plants of the shoreward portion of the forest.

The mechanisms maintaining the zonation pattern of the 4 species of *Tegula* in the Hopkins Marine Life Refuge are not apparent. The upper distributional limits of many intertidal species may be determined by physical factors or behaviors that avoid adverse physical factors (*e.g.*, WOLCOTT, 1973). In this respect, *Tegula funebralis* may be able to withstand temperature and desiccation stresses encountered in the intertidal area better than the other 3 species, thereby partially accounting for the near complete dominance of *T. funebralis* in the intertidal zone. However, such a physiological mechanism would not account for the observed lack of *T. funebralis* subtidally, or the zonation of the subtidal species.

Gradients of water turbulence and light could be important in determining the zonation patterns of the subtidal species. If, for example, individuals of *Tegula brunnea* were better able to maintain a grip on substrates in strong surge than those of *T. pulligo*, they might be expected to predominate in high-energy areas of the shallow subtidal zone and inner edge of the kelp forest. The zonation pattern of the snails also might be the result of pronounced dietary preferences for particular algal species limited to particular depths by specific light requirements. However, LOWRY, MCELROY & PEARSE (1974) found that all 3 subtidal species were widely distributed on different species of algae in the middle of the kelp forest, and all were found most frequently on giant kelp plants. Moreover, all 4 species have a high preference for *Macrocystis pyrifera* for food (unpublished observations; James M. Watanabe, pers. comm.). Considering the enormous abundance of giant kelp, both as attached plants and as pieces of plants on the forest floor (GERARD, 1976), competition among these snails for a limited food resource is unlikely, and differences in food preferences and availability probably cannot account for the subtidal zonation pattern. Furthermore, we have not observed any behavior in the field or laboratory that could be categorized as interference competition (*sensu* COLWELL & FUENTES, 1975) among any of these species.

Predation often limits the lower distribution of intertidal organisms, and in some areas predation by sea stars and whelks may determine the lower limit of *Tegula funebralis* (PAINE, 1969; B. MENGE, 1972; J. MENGE, 1974). Predation by rock crabs, *Cancer antennarius*, also could be important. These crabs cannot crack the shells of *Tegula brunnea* as easily as those of *T. funebralis* (ABBOTT & HADERLIE, 1980), and their presence in the low intertidal area might provide an explanation for the replacement of *T. funebralis* by *T. brunnea* in the shallow subtidal zone. However, individuals of *C. antennarius* are very scarce in the Hopkins Marine Life Refuge (Hines, in press), and the small number of crabs there is unlikely to have much impact on the large snail populations.

Sea stars are important predators in the subtidal kelp forest of the Hopkins Marine Life Refuge, and *Tegula* spp. are highly preferred prey of *Pisaster giganteus* in particular (Harrold, 1981). Watanabe (1980) found that high water movement and dense cover of red algae in the shallow subtidal area provided turban snails with some refuge from sea star predation. Snails within the kelp forest also may escape sea star predation by crawling up fronds of giant kelp plants (Harrold, 1981). However, sea otters, *Enhydra lutris*, in the Hopkins Marine Life Refuge eat large numbers of turban snails collected from the kelp fronds (Costa, 1978). The distributions and foraging patterns of all these different predators are not understood well enough to explain whether and how they might influence the distribution patterns of the subtidal species of *Tegula* in the Hopkins Marine Life Refuge.

Recruitment patterns may reflect and partly determine the distributions of the adult snails. Recruitment of *Tegula funebralis*, for example, is restricted to the intertidal zone (Paine, 1969). Moreover, Watanabe (pers. comm.) found distributional patterns of juvenile turban snails in the Hopkins Marine Life Refuge that were strikingly similar to those of the adults. Small juveniles (<5 mm diameter) of *T. brunnea* were most abundant on solid rock surfaces at depths less than 3 m, those of *T. pulligo* were mainly on shell fragments in the seaward portion of the kelp forest, and those of *T. montereyi*, were on shell fragments distributed throughout the forest. However, turban snails probably live at least for several years (Frank, 1975), and they are very mobile. More knowledge of the movements and life history of these snails clearly is needed before the mechanisms that maintain their distinct patterns of distribution will be revealed.

SUMMARY

1. Three species of turban snails display distinct patterns of zonation between the intertidal area and the seaward edge of the giant kelp forest in the Hopkins Marine Life Refuge, central California. *Tegula funebralis* is exclusively intertidal, *Tegula brunnea* is mainly shallow subtidal (0.5 to 7 m depth) in the shoreward portion of the kelp forest, and *Tegula pulligo* is mainly deeper (7 to 13 m depth) in the seaward portion of the kelp forest.
2. A fourth species, *Tegula montereyi*, occurs subtidally throughout the kelp forest, but does not dominate any particular zone.
3. The 3 subtidal species of *Tegula* are distributed snails in the Hopkins Marine Life Refuge were very throughout the water column on giant kelp plants, *Macrocystis pyrifera*, from the surface canopy to the bottom holdfasts, in the same pattern as their bottom distributions. *Tegula brunnea* is mainly on plants in the shoreward portion of the forest, *T. pulligo* is mainly on plants in the seaward portion of the forest, and *T. montereyi* is distributed more or less evenly on the plants. There is little distinct pattern of vertical distribution on the plants of any of the species of *Tegula*.
4. The patterns of distribution of the 4 species of turban similar in March and August, 1977, except that in August *Tegula brunnea* was most frequent in the canopy and *T. pulligo* was most frequent near the bottom of the plants.
5. Although recruitment patterns of juveniles reflect adult distributional patterns, the mechanisms maintaining these distributional patterns remain unclear. Tolerance to aerial exposure may permit *Tegula funebralis* to thrive in the intertidal zone, and lack of such tolerance may exclude the other species from this zone. Effective defense from predation and tolerance to high water turbulence may permit *T. brunnea* to dominate in the shallow subtidal, while *T. montereyi* and *T. pulligo* may escape predation in deeper waters by crawling up kelp fronds.

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