Reference: *Biol. Bull.*, 147: 386–396. (October, 1974)

THE DISTRIBUTION OF SIX SPECIES OF GASTROPOD MOLLUSCS IN A CALIFORNIA KELP FOREST

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Kelp forests are common features along temperate shores of much of the world. They are confined to shallow, rocky neritic zones where conditions of light, substrate and surge are suitable. Their productivity is very high, and much organic material flows through complex, but definable trophic structures (Miller, Mann and Scarratt, 1971; Mann, 1973). Spatial structures within these forests also are complex but definable, and many organisms occupy restricted habitats. Drach (1960) distinguished at least 8 types of rock habitats along the coast of Brittany, each with a discrete faunal assemblage. Within the kelp forests of California, vertical rock faces are commonly covered by sponges, anthozoans, byrozoans and ascidians, horizontal rock surfaces at similar depths are covered by algae and motile invertebrates such as decapods, gastropods and asteroids, while the undersides of loose rocks are the habitat for several species of brachyurans, amphineurans and ophiuroids (McLean, 1962, and personal observations). Within the range of the sea otter, rocky crevices are the main habitat of abalones and sea urchins (Lowry and Pearse, 1973).

Algae, in addition to rocks, provide habitats for many organisms. The holdfasts of *Macrocystis* spp. and *Nereocystis luetkeana* support an abundant and diverse fauna consisting primarily of polychaetes, decapods, amphipods, gastropods and ophiuroids (Andrews, 1925, 1945; Ghelardi, 1971). Andrews (1925) found that the stipes of *Nereocystis luetkeana* supported few animals while decapods, amphipods, isopods, gastropods and bryozoans were all abundant in the laminae. Wing and Clendenning (1971) found large numbers of micro-invertebrates associated with *Macrocystis* blades, especially blades that were encrusted with the bryozoan *Membranipora*. Clarke (1971) reported that the mysid *Acanthomysis sculpta* is found almost exclusively in *Macrocystis* canopies and within kelp forests this also appears to be the case for the shrimp *Hippolyte californiensis* (L. Lowry, unpublished data).

In the study reported here, we examined habitat specificity and differentiation among 6 species of closely related gastropods (family Trochidae) on 4 species of kelp forest algae. The snails were chosen because of their apparent ecological similarity (all predominantly subtidal browsing animals of similar sizes) and for ease of collection and identification. The algae were chosen because they provided the snails with a wide range of conditions. The giant kelp, *Macrocystis pyrifera*, is a perennial plant and the dominant alga in the kelp forest studied. Individual plants are anchored to the substrate by a large rhizomatous holdfast from which extend many fronds, each consisting of a central stipe bearing unilateral blades

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and pneumatocysts. The fronds extend through the entire water column and spread out on the surface to form a thick canopy. The brown alga, *Cystoseira osmundacea,* consists of small (less than 1 meter high), perennial vegetative portions from which massive reproductive fronds rise to the surface of the water from depths of 10 m or more. The reproductive fronds begin growing in mid-winter and break up and disappear by late summer. The vegetative portion of *C. osmundacea* is the main understory plant in our study area (density 1.6 individuals/m^2), while the reproductive portion adds seasonally to the canopy. The other two algae used in this study grow beneath the *C. osmundacea* vegetative fronds and are a major portion of the ground cover algae. These are the brown alga *Dictyoneuropsis reticulata* which has large blades (100×25 cm) that usually lie close to the bottom, and the red alga *Gigartina corymbifera* which is similar in growth form to *D. reticulata,* but with somewhat smaller blades (up to 50 cm long).

Methods and Materials

The study site was located off the northeast side of Point Cabrillo at Hopkins Marine Station, Pacific Grove, California. The area is described in more detail in Lowry and Pearse (1973). Collections were made by divers using scuba equipment during August, 1971, at five locations (depth 6–9 m) in the kelp forest. The plants were chosen arbitarily and all snails were removed from each plant chosen. Snails on *Gigartina* and *Dictyoneuropsis* were simply removed from the algae and put into plastic bottles. Snails from the vegetative and reproductive parts of *Cystoseira* were collected separately. For sampling *Macrocystis,* a line marked in meter intervals was used; snails from each one meter interval up to five meters from the bottom and those from above five meters (including the canopy) were kept separated. Using these procedures, a total of 85 *Macrocystis* fronds (from 6 separate plants), 60 *Cystoseira* plants, 315 *Dictyoneuropsis* blades and 440 *Gigartina* blades were sampled. The snails were then taken to the lab where they were identified, and the maximum basal diameter of each specimen measured to the nearest millimeter.

Results

Sizes and distributions of the species of snails

Calliostoma annulatum (Lightfoot, 1786). The least number of the 6 snail species collected was *C. annulatum.* They also had the smaller modal size (14 mm, see Fig. 1). Twenty-two of the 24 individuals collected were found on *Cystoseira,* 21 of these 22 were on the reproductive portions of the plants. Two individuals were found on *Macrocystis* and none on the ground cover algae (*Dictyoneuropsis* and *Gigartina*) (Table I).

Calliostoma canaliculatum (Lightfoot, 1786). This species was only slightly more common in our collections than *C. annulatum* and it had a very similar distribution. Five individuals were found on *Macrocystis,* but most (21 out of 27) were on the reproductive portions of *Cystoseira* and none were on the ground cover algae (Table I). The size-frequency distribution for this species (Fig. 1) shows

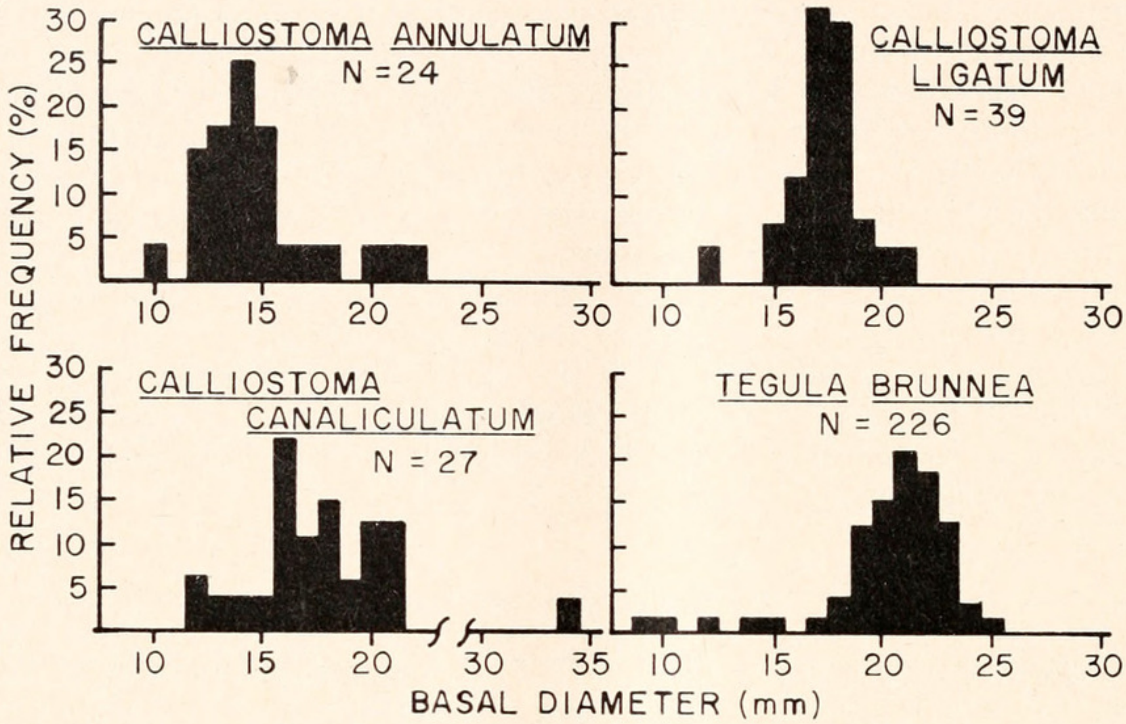

FIGURE 1. Size frequency distributions of the total collections of *Calliostoma* spp. and *Tegula brunnea*. The relative frequency is the per cent of the total collection for a given species that was in each 1 mm size class.

a single mode at 16 mm, and a predominance of large individuals (20–21 mm). The largest snail found (34 mm) belonged to this species.

Calliostoma ligatum (Gould, 1849). Twenty-nine out of 39 individuals of this species collected were found on *Cystoseira*, 13 of these were on the vegetative portions of the algae. Five individuals were found on *Macrocystis* and 5 on *Gigartina* (Table I). The size-frequency distribution (Fig. 1) shows a single mode at 17–18 mm.

Tegula brunnea (Philippi, 1848). One hundred eighty-seven out of 226 *T. brunnea* collected were from *Macrocystis*. Eleven were found on *Cystoseira*, 7 on the vegetative and 4 on the reproductive portions of the algae. Twenty-three specimens were found on *Dictyoneuropsis* and 5 were on *Gigartina* (Table I). The size frequency distribution (Fig. 1) shows a single mode at 21–22 mm.

TABLE I

Per cent of the total collection of each species of snail which was found on a given species of algae. N is the total number of individuals of each snail species collected.

Species	*Cystoseira* vegetative	*Cystoseira* reproductive	*Cystoseira* total	*Macrocystis*	*Dictyoneuropsis*	*Gigartina*	Total	N
C. annulatum	4	88	92	8	0	0	100	24
C. canaliculatum	4	77	81	19	0	0	100	27
C. ligatum	33	41	74	13	0	13	100	39
T. brunnea	3	2	5	83	10	2	100	226
T. montereyi	8	13	21	51	12	16	100	156
T. pulligo	12	19	31	39	21	9	100	404

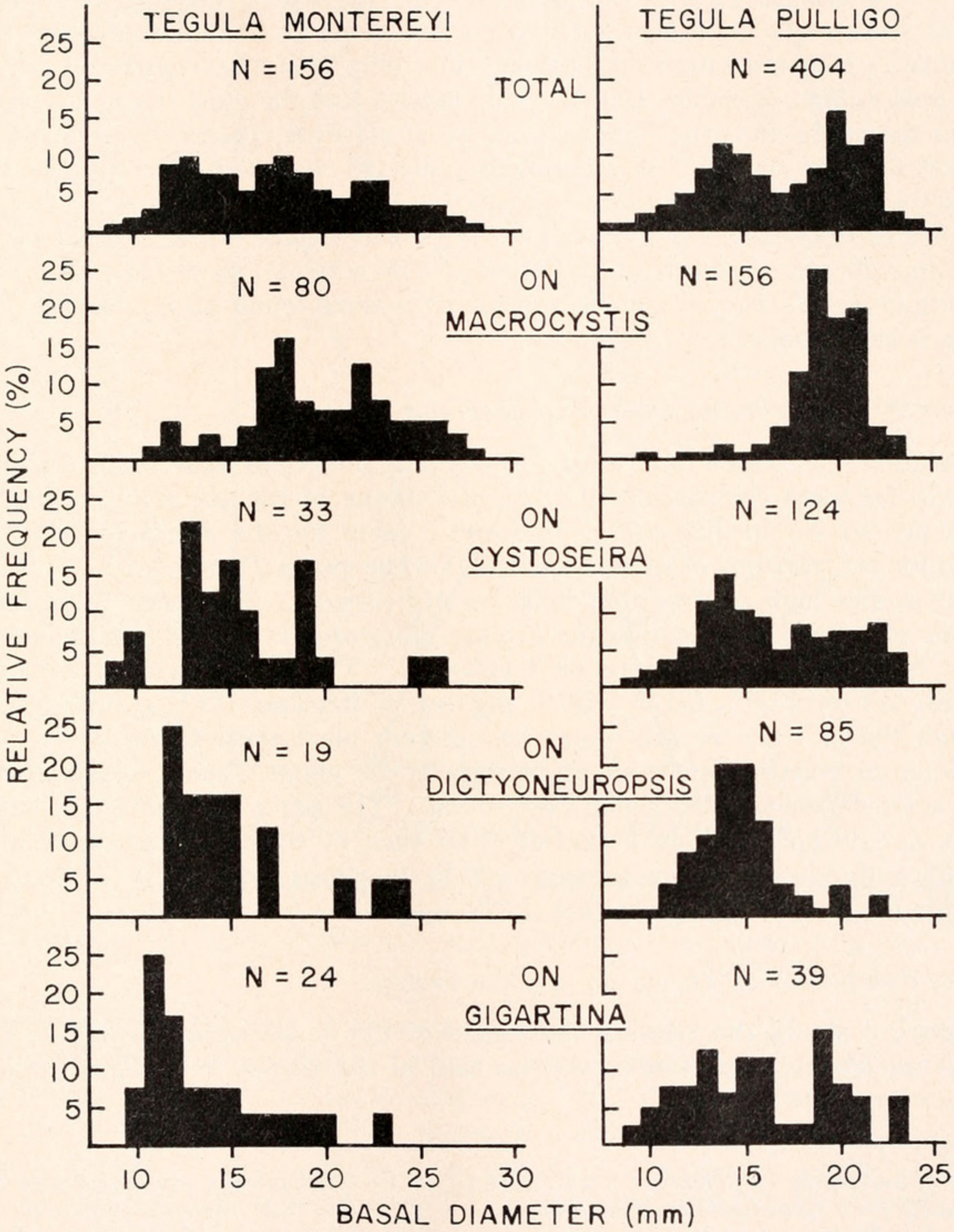

FIGURE 2. Size frequency distributions for the total collections and collections from each species of algae for *Tegula montereyi* and *T. pulligo*. The relative frequency is the per cent of the total collection or the collection from a given algal species that was in each 1 mm size class.

Tegula montereyi (Kiener, 1850). About half (80 out of 156) of the snails of this species collected were found on *Macrocystis*. Thirty-three were found on *Cystoseira*, a few more on the reproductive than on the vegetative portions of the plants. Nineteen were found on *Dictyoneuropsis* and 24 on *Gigartina* (Table I).

The size frequency distribution for the total collection of *T. montereyi* shows 3 modes, one at 13 mm, another at 18 mm and a third at 22–23 mm (Fig. 2). The modes at 18 and 22–23 mm are accounted for by a predominance of individuals of these size classes on *Macrocystis,* while the mode at 13 mm represents smaller individuals which were found mostly on *Cystoseira, Dictyoneuropsis* and *Gigartina.*

Tegula pulligo (Gmelin, 1791). This species was the most frequently collected snail in the study and was found regularly on all algal species investigated. One hundred fifty-six out of 404 individuals collected were on *Macrocystis,* 124 on *Cystoseira,* 85 on *Dictyoneuropsis* and 39 on *Gigartina* (Table I).

The size frequency distribution for the total collection shows 2 distinct modes at 14 and 20 mm, respectively (Fig. 2). As with *T. montereyi,* larger snails were found on *Macrocystis,* while smaller sizes were found on *Cystoseira, Dictyoneuropsis* and *Gigartina.*

Comparison of distributions among algal species

The figures in Table I were used to compute indices of association (Whittaker, 1952) to facilitate comparison of the distributions of the six snail species. The results are shown in Table II. The mean value for the similarity indices calculated for comparisons of species pairs within the genus *Tegula* is 68.3, due mostly to their similar high relative abundance on *Macrocystis.* The mean value for comparisons of species pairs within the genus *Calliostoma* is 66.6, due largely to their similar high relative abundance on *Cystoseira.* These mean values are not significantly different [t = 0.125 with 6 degrees of freedom (D.F.)] indicating that although the two genera are found on different algal species, the degree of distributional association found among species of the genus *Tegula* is similar to that found among species of the genus *Calliostoma.* The mean value for comparisons of species pairs which include a species from each of the 2 genera is 32.3. This is significantly lower than comparisons within the genus *Tegula* (t = 4.126, 6 D.F.) or within the genus *Calliostoma* (t = 3.504, 6 D.F.).

Vertical distribution of Tegula *spp. on* Macrocystis

Figure 3 shows the relative abundance of the 3 species of *Tegula* at various heights on *Macrocystis* plants. At the base of the plants, *T. pulligo* is the most

TABLE II

Indices of association (Whittaker, 1952) calculated from the distribution of snails shown in Table 1. The index for a species pair is calculated as $I_{A,B} = \sum_{i=1}^{5} \min(a,b)$ where a and b are the values given in Table 1 for species A and B in a given column and i represents the columns used. The vegetative and reproductive portions of Cystoseira *were considered separately; the values for total* Cystoseira *were not used in the calculations. The index has a maximum value of 100 (exactly equivalent distributions) and a minimum value of 0 (never found on the same species of algae).*

	C. annulatum	*C. canaliculatum*	*C. ligatum*	*T. brunnea*	*T. montereyi*
T. pulligo	31	42	53	56	81
T. montereyi	25	36	47	68	
T. brunnea	13	24	20		
C. ligatum	53	58			
C. canaliculatum	89				

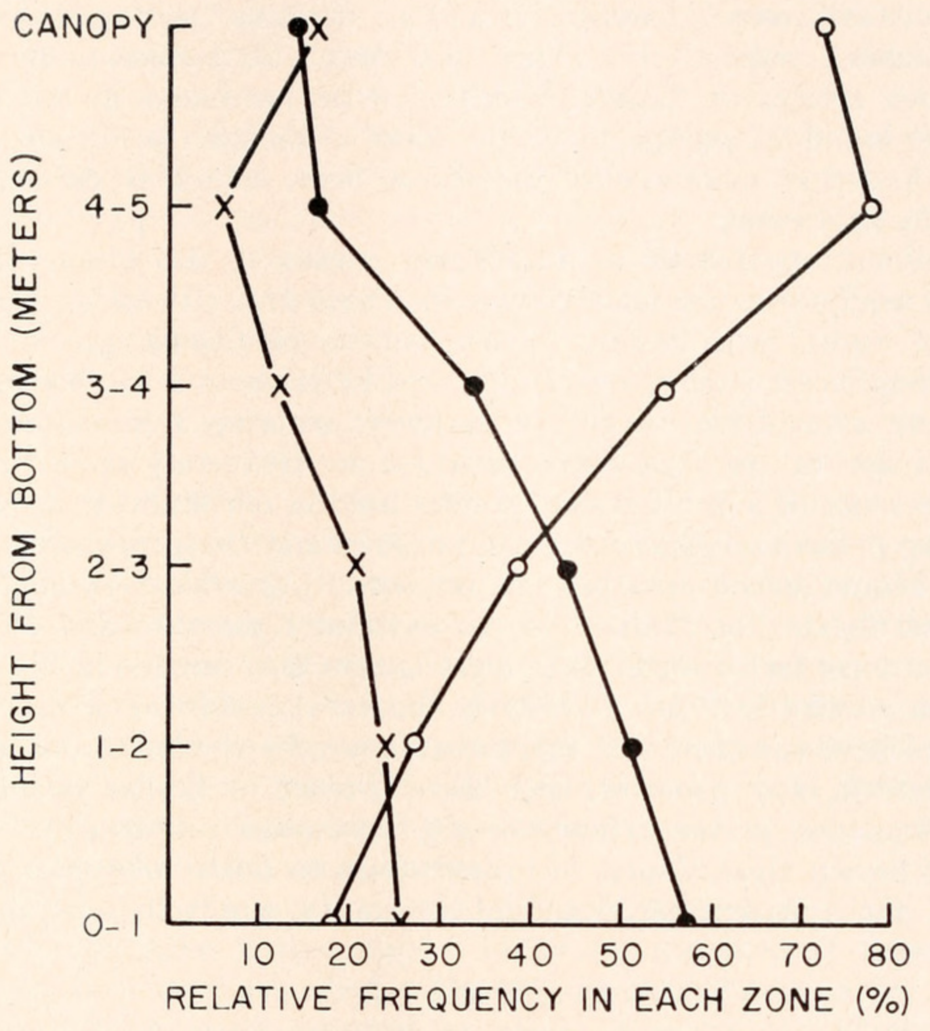

FIGURE 3. Vertical distribution of *Tegula* spp. on *Macrocystis*. The relative frequency is the per cent of the total collection of *Tegula* from a given zone which was made up by each individual species; open circle, *T. brunnea;* ×, *T. montereyi,* filled circle, *T. pulligo.*

common species (56%) and *T. brunnea* is the least common (18%). Moving up the plants, *T. brunnea* increases in relative abundance to become the most common species in the upper portions, comprising over 70% of the population in and just below the canopy. *Tegula pulligo* shows a corresponding decrease in relative abundance to become the least common species in the canopy (14%). *Tegula montereyi* shows little fluctuation in relative abundance, making up between 5 and 25 per cent of the population in all zones.

DISCUSSION

Habitat differentiation among the 6 species of trochid snails we studied has been noted briefly by earlier workers. *Calliostoma annulatum*, among the most beautiful of the West Coast snails, was reported by Keep (1887, page 80) to "crawl up the stems of the sea weed and rest near the surface of the water" during calm weather when specimens could be collected in quantities from boats. Smith and Gordon (1948) reported that all 6 species occur on kelp in the Monterey Bay region. In agreement with our observations, they found *Tegula brunnea* to be "near the surface" and *T. montereyi* and *C. ligatum* "farther down" and "well down the stalks," respectively. They also found *T. pulligo* to be scarcer than the other two species of *Tegula*, which is what we found in the kelp canopy; however, we found *T. pulligo* to be the most abundant trochid snail in the kelp forest and it occurs mainly near the forest floor, which is difficult to observe without scuba equipment.

Observations reported for four different studies in the Monterey Bay region using scuba equipment are summarized in Table III. There is little agreement among these studies with respect to distributions of *Tegula* spp. and *Calliostoma* spp. The kelp forest studied by Minter (1971) is about 2 km southeast of Point Cabrillo in an area of high exposure to surge, scouring and sedimentation. The substrate consists of low shale outcrops which are frequently sanded over. Minter noted the presence of 5 of the 6 snail species used in our study, and only mentioned them as being present on *Macrocystis*. *Cystoseira* and *Dictyoneuropsis* were present at the Del Monte Beach area but not common; *Gigartina* was not recorded. It would appear that either Minter did not examine *Cystoseira* and *Dictyoneuropsis* for snails, or some factor made these algal species less suitable in his study area.

The area studied by Faro (1970) is about 3 km northwest of Point Cabrillo and seems to have substrate and surge characteristics similar to our area. *Macrocystis, Cystoseria,* and *Gigartina* also were present in similar quantities. *Dictyoneuropisis* was not present; however *Dictyoneurum californicum* and *Costaria costata,* two brown algae similar in growth form to *Dictyoneuropsis,* were present. In spite of the apparent physical and vegetative similarities of the two areas,

TABLE III

Reported habitats of Tegula *spp. and* Calliostoma *spp. in Central California*

	McLean, 1962 Carmel Open Coast	Faro, 1970 Point Piños	Minter, 1971 Del Monte Beach	Lowry, McElroy and Pearse, this paper Point Cabrillo
Calliostoma annulatum	Juveniles common on rock walls, maximum development on *Macrocystis*	Common, found on bottom, but more often attached to large brown kelps	Scarce, on *Macrocystis*	Common on *Cystoseira*, especially reproductive fronds, few on *Macrocystis*
Calliostoma canaliculatum	Juveniles common on bottom rocks, maximum development on *Macrocystis*		Fairly common, on *Macrocystis*	Common on *Cystoseira*, especially reproductive fronds, few on *Macrocystis*
Calliostoma ligatum	Abundant on rock walls	Most common *Calliostoma*, distribution similar to *C. annulatum* but less common in turbulent areas	Failry common, on *Macrocystis*	Common on *Cystoseira* vegetative and reproductive fronds, few on *Macrocystis* and *Gigartina*
Tegula brunnea	Juveniles on rocks, adults on *Laminaria* and *Pterygophora*	Most common snail on bottom and holdfasts, seldom found on stipes or blades of kelp	Common on kelp fronds	Abundant on *Macrocystis*, especially in canopy, few on *Cystoseira*, *Gigartina*, and *Dictyoneuropsis*.
Tegula montereyi	Common on *Macrocystis*, *Laminaria* and *Pterygophora*	Common, found attached to kelps, most abundant on stipes and canopy of *Macrocystis*	Common on kelp fronds	Common on all species, larger on *Macrocystis*.
Tegula pulligo	Juveniles on rocks, adults on *Laminaria* and *Pterygophora*			Abundant on all species except *Gigartina*, larger on *Macrocystis*.

the reported distributions of snails are quite different, especially in the case of *T. brunnea* about which Faro (page 66) states that "unlike *Calliostoma* or *T. montereyi,* it was seldom found on the stipes or blades of kelp."

The area studied by McLean (1962) lies about 20 km south of Point Piños, and at the time studied, was a mixed *Macrocystis-Nerocystis* kelp forest. The area appears quite similar to Point Piños with the exception that the dominant canopy-forming alga was *Nereocystis luetkeana,* an anuual plant. The distributions reported by McLean agree somewhat with those given by Faro (1970) but little with the data from our study.

We found most of the individuals of all three species of *Calliostoma* on the reproductive fronds of *Cystoseira osmundacea.* These portions of the plants are seasonal and occur as part of the canopy from the late spring through the summer. In a study at Point Cabrillo carried out in the Fall of 1973, the reproductive fronds of *Cystoseira* were nearly absent, *Calliostoma annulatum* and *C. canaliculatum* were found almost exclusively in the upper portions of *Macrocystis,* while *C. ligatum* was found mostly on ground cover algae (especially *Gigartina*) and the rock bottom (University of California, Santa Cruz, unpublished reports for Neritic Ecology class, 1973). These seasonal differences, at least for *Cystoseira* and *Calliostoma,* may at least partly account for the differences seen among the different studies summarized in Table III. The differences may be further explained by differential responses of the snail populations to the physical, chemical and biological characteristics of the various areas.

The distribution of the snails on the different species of algae may reflect different food preferences of the snails. However, the food of these species of trochid snails has not been described. The species of *Calliostoma* we studied may feed more on sessile animals growing on plants, than on the plants themselves (James T. Carlton, personal communication), and their distributions therefore may be related to the distributions of the animal prey.

The three subtidal species of *Tegula* we studied probably are mainly herbivorous. *T. funebralis* in the adjacent intertidal is known to be mainly herbivorous, and it produces a wide array of enzymes to digest algal products (Galli and Giese, 1959). Moreover, all three species have been fed measurable amounts of algae, particularly *Macrocystis,* in the laboratory (University of California, Santa Cruz, unpublished reports of Neritic Ecology class, 1973). Many other kelp forest herbivores show definite food preferences for some species of algae, particularly for *Macrocystis* (Leighton, 1966). The tendency for the three species of *Tegula* we studied to be on *Macrocystis* suggests that this alga is also a preferred food item for these snails.

The results of between and within genus indices of association comparisons show that the three species of *Calliostoma* are very similarly distributed, being found almost exclusively on *Cystoseira.* The three species of *Tegula* were found primarily on *Macrocystis,* but some individuals were found on all species of algae investigated, and their indices of association are more widely distributed. Character displacement (Hutchinson, 1959) in terms of habitat selection therefore seems effective between the two genera, but less developed within each genus. Interspecific competition, if it exists, consequently might be expected to be most intensive between congeners. However, as indicated by Figure 3, species of the genus *Tegula* are differentiated in their vertical distribution on *Macrocystis* fronds. A similar means of differentiation may exist within the genus *Calliostoma* as *C. ligatum* was common on the vegetative (lower) portions of *Cystoseira* and was found on *Gigartina,* while *C. annulatum* and *C. canaliculatum* were found almost exclusively on the reproductive (upper) portions of *Cystoseira* and were never encountered on the ground cover algae (Table I). Further investigations are needed to elucidate the mechanisms allowing coexistence of these closely related gastropod species.

The bi- and trimodal size distributions of *Tegula pulligo* and *T. montereyi* (Fig. 2) suggest age classes in these snails. It is unlikely, however, that these are annual age classes and that the snails reach the size of 20 mm diameter in two to three years. Paine (1969) found that *Tegula funebralis* in the intertidal grows only about 1–4 mm per year, and 20 mm snails are about 15 years old. There seems little reason to believe that the subtidal species of *Tegula* grow at much higher rates. Rather, the bi- and trimodal size distributions we found probably reflect occasional years especially favored for recruitment, spaced several years apart. Such fluctuations in annual recruitment, with favorable years separated by several unfavorable years are known to occur in other marine animals (*e.g.,* asteroids, Loosanoff, 1964; and echinoids, Ebert, 1968).

McLean (1962) noted that juveniles of several species of snails were found mostly on bottom rocks. Bakus (1974), looking at snails in southern California kelp forests, noted that smaller individuals of *Norrisia norrisi* and *Tegula aureotincta* were located mainly on or in *Macrocystis* holdfasts or on the sea floor, while there were numerous larger individuals of both species on the stipes, pneumatocysts and blades of *Macrocystis.* Although rocks were not looked at in our study, the algae which lie close to the bottom had smaller individuals of *Tegula montereyi* and *T. pulligo* than did the larger, upright species of algae (Fig. 2).

North (1954) observed different size distributions in several populations of the intertidal gastropods *Littorina planaxis* and *L. scutulata.* He explained these size differences as being in part due to a greater ability of small snails to grip the rock substrate, resulting in a greater proportion of small individuals in areas exposed to heavy surge. Frank (1965) found that the intertidal limpet *Acmaea digitalis* shows a behavioral response to environmental conditions which involves an upward movement in the fall and winter followed by a lesser downward movement in the spring. This results in older, larger individuals being located higher in the intertidal. Paine (1969) found that larvae of the snail *Tegula funebralis* settle high in the intertidal, where its primary predator, the sea star *Pisaster ochraceus,* does not occur. When the snails are 5–6 years old, they migrate to a position lower in the intertidal where, as a consequence of the predatory activity of *Piaster* which reduces the density of *Tegula* populations, conditions are more suitable for growth and reproduction. More information is needed before it can be decided whether one of the above mechanisms, or another such as differential growth rates on different algal species or changes in habitat or food preference with age, is responsible for the size distributions observed in our study.

The question of how the distributions reported in this paper are established and maintained also remains. Bakus (1974) noted that a one-day period of heavy surge dislodged all *Norrisia norrisi* and *Tegula aureotincta* from the upper portions of *Macrocystis* plants. The same plants had "abundant" snails one month later.

In his area, Bakus considers the sheephead (*Pimelometopon pulchrum*) the principal predator on snails, particularly smaller individuals on or near the sea floor. Sheephead are not common in our study area; however, several species of predaceous asteroids (*Orthasterias koehleri, Pisaster brevispinus, P. giganteus,* and *Pycnopodia helianthoides*) are common (total density about 0.3 individuals/m^2). Feder (1963) has shown that escape responses to sea stars can influence the distribution of snails in the intertidal. It seems possible that adaptive responses to predators is at least one of the factors responsible for the snail size and species distributions we observed in the kelp forest at Point Cabrillo.

This work was conducted as part of a Stanford University summer course at the Hopkins Marine Station, Ecological Physiology (269H). The authors wish to thank the faculty and staff of Hopkins Marine Station for the use of facilities and equipment. We also thank Gerald J. Bakus, R. Andrew Cameron, James T. Carlton, William J. Kennedy, Mary W. Silver and Kathryn F. Truscott for invaluable comments and criticism of the manuscript. Final analysis and preparation of the manuscript was supported by NOAA Office of Sea Grant, Department of Commerce, under Grant No. USDC 04-3-158-22.

Summary

1. The summer distribution of 6 species of gastropod molluscs found in a kelp forest is analyzed. From 4 species of common macroalgae, 876 snails were collected.

2. *Tegula brunnea* was found primarily on *Macrocystis pyrifera*. *Tegula montereyi* and *T. pulligo* were fairly evenly distributed among the 4 algal species. *Calliostoma annulatum, C. canaliculatum,* and *C. ligatum* were all found primarily on the reproductive fronds of *Cystoseira osmundacea*. Indices of association are given which show that the mean distributional associations for pairs of species within the same genus are not significantly different for the 2 genera. When combinations involving members of the two different genera are compared to within genus combinations, the similarity was found to be significantly higher for the within genus combinations.

3. An analysis of populations of *Tegula* spp. on *Macrocystis* showed differences in species compositions at different heights on the plants. *Tegula pulligo* was relatively most common at the bottoms of the plants and least common in the canopy. *Tegula brunnea* showed the reverse trend.

4. A comparison of the size frequency distributions for *T. montereyi* and *T. pulligo* collected from the different species of algae showed that small individuals tend to be on the ground cover algae (*Gigartina corymbifera* and *Dictyoneuropsis reticulata*) and larger individuals on the large, upright *Macrocystis*.

5. Little agreement was found when comparing the distributions found in our study with those previously reported. This lack of agreement is probably due to differences among different areas as well as among different seasons.

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