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A comparative study of some population characteristics of Calyptraea fastigiata Gould, Crepidula lingulata Gould, and Crepidula nummaria Gould (Gastropoda, Prosobranchia)

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A COMPARATIVE STUDY OF SOME POPULATION CHARACTERISTICS OF CALYPTRAEA FASTIGIATA GOULD, CREPIDULA LINGULATA GOULD, AND CREPIDULA NUMMARIA GOULD (GASTROPODA, PROSOBRANCHIA)

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INTRODUCTION

Most marine gastropods of the family Calyptraeidae are protandrous filter feeders which group together by stacking. Being essentially sessile, movement is limited to the males moving about on the stack from one female to another. Several species of the group, however, do not display this stacking behavior; movement for them is probably much more extensive. Coe (1938b) reports that the males of *Crepidula lingulata* and *Crepidula nummaria*, two non-stacking species, associate with the females only during breeding periods, though they may be found in close proximity to them. The same holds true for the non-stacking European species, *Calyptraea chinensis* (Wilbur and Yonge, 1964). Nothing has been reported concerning the intraspecific behavior of the non-stacking American species, *Calyptraea fastigiata*. In fact, most of the information about the genus *Calyptraea* comes from work done on *C. chinensis* (Bacci, 1951; Pellegrini, 1949; Wyatt, 1957, 1960, 1961).

The major behavioral difference separating the two genera is the ability of *Crepidula* males, at least in the stacking forms, to be influenced by other members of the species, particularly females, into changing sex earlier or later than normal (Gould, 1919; Coe, 1938a, 1948). This is not the case for *C. chinensis* where all males of the same generation will transition at the same time regardless of association (Bacci, 1949, as reported by Hyman, 1967).

Most members of the family are found attached to hard surfaces such as rocks and shells (Coe, 1942a; Driscoll, 1967). Some inhabit the inside of gastropod shells, living in association with hermit crabs, while others are found attached to the outside of the shell (Coe, 1938a, 1942a; Moritz, 1938). As a family, they are found on rocky substrates and on hard surfaces which are raised off of soft bottoms (Fretter and Graham, 1962).

Competition for living space occurs between oysters and some members of the family. *Crepidula fornicata*, a stacking species introduced into England, forms masses inches deep over the bottom of oyster grounds; through the accumulation of faeces and pseudofaeces causes a deposition of mud that prevents oyster larvae from settling (Fretter and Graham, 1962).

Previous research has centered around the protandrous nature of the family. Very little work has been done on their general biology or autecology, especially in the non-stacking forms. It therefore seemed appropriate, in light of their possible economic importance, to make a comparative study of some of the population characteristics of several non-stacking members. Such items as habitat, vertical distribution, intraspecific association, size, reproductive behavior, and predator-prey relationships are considered.

For this purpose *Crepidula lingulata*, *Crepidula nummaria*, and *Calyptraea fastigiata* were chosen.

MATERIALS AND METHODS

Research was conducted between 1 March and 15 June 1974 at the University of Washington's Friday Harbor Marine Laboratories located on San Juan Island in the San Juan Archipelago, Washington. The primary study area was located just south of a cove known locally as Colin's Cove. Two other sampling areas located nearby were situated just north and south of the Cantilever Pier of the Friday Harbor Laboratories. A fourth sampling area, Smuggler's Cove, was located on the northwest side of San Juan Island (Figure 1). Three dredge hauls were made along the northeast side of the island between Friday Harbor Laboratories and Spieden Island. The first haul was east of Limestone Point at a depth of 50-65 fathoms on a shell fragment substrate over a mud bottom. The second dredge haul was between Speiden and Sentinel Islands at a depth of 21 fathoms on a solid bottom. The third haul, likewise on a solid bottom, was east of O'Neil Island at a depth of 25-30 fathoms.

The four sampling areas were typified by different substrates. The area south of Cantilever Pier was primarily a solid substrate with a gentle slope. A uniform substrate of small rocks (1-6 cm in diameter) lying upon silt characterized the site north of Cantilever Pier, whereas Smuggler's Cove was characterized by a steep incline with a substrate ranging from large rocks (diameter 12 cm and

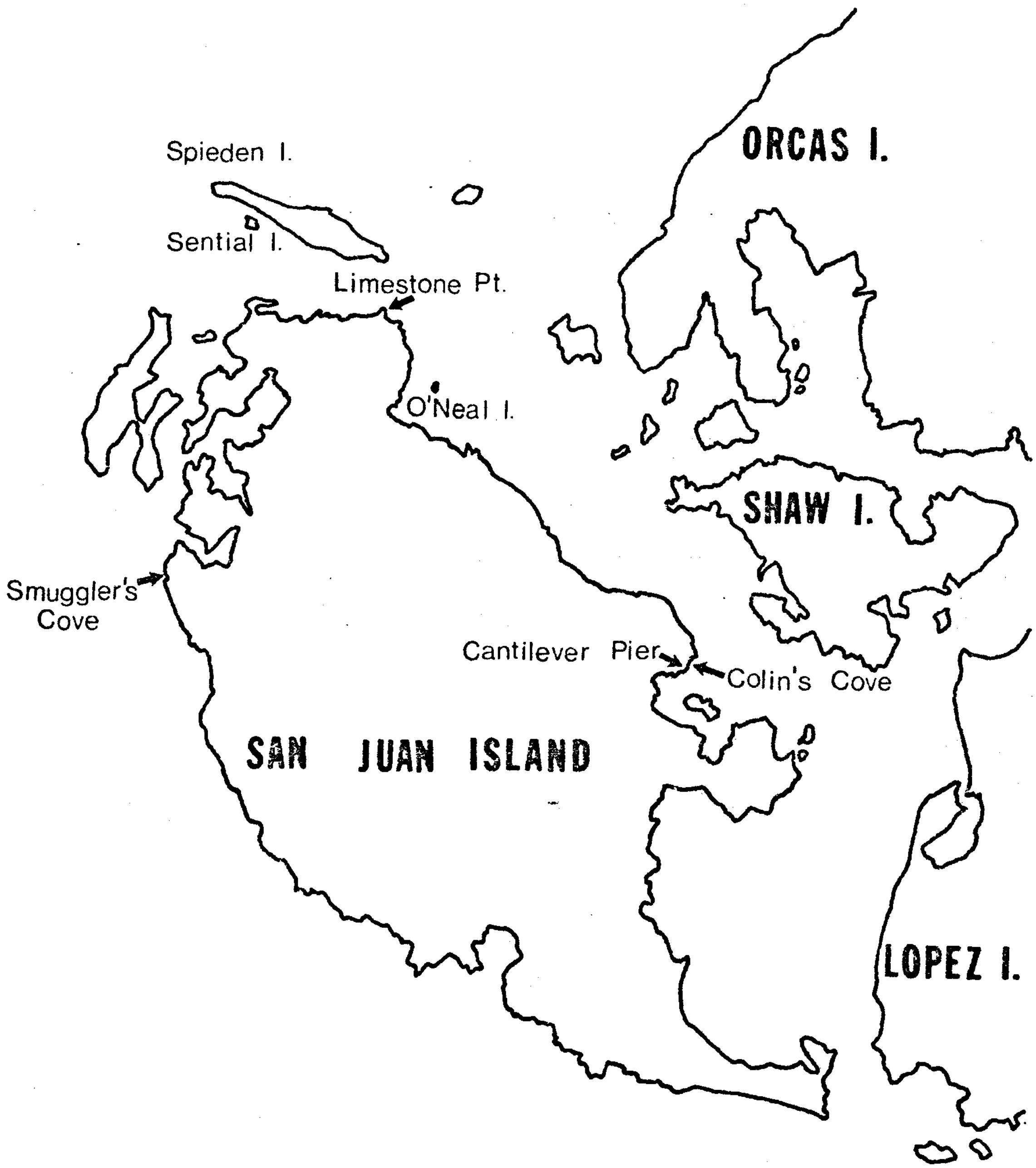


Figure 1

Study Areas on and in the Vicinity of San Juan Island over) to silt-free solid rock slopes and vertical cliffs. A substrate mixture was present in the Colin's Cove area. Solid rock was found at a depth ranging from 3-12 meters with a large loose rock area (both small and large rocks) at 9 meters. A small rock area lying upon solid rock was found at 12 meters, and this changed to a small rock area overlying silt which extended from 15-19 meters. At the 21-meter level the substrate had again become solid with overlying rocks. A vertical cliff was found at the 24-meter level. Small cliffs were found extending from 6-9 meters, 12-15 meters, and from 19-21 meters.

At each locality a sampling area 10 meters wide extending to a depth of 24 meters below MLLW was chosen. Only at North Cantilever did the width exceed 10 meters. This area was particularly chosen for its uniform substrate so that depth-related factors could be tested without regard to substrate. However, the area was frequently interspersed by solid slopes, making it necessary to exceed the 10-meter width. A transect line was placed at each locality, except North Cantilever, running from the surface to a depth of just over 24 meters. At each 3-meter vertical drop in depth a station was established for a total of eight stations. Correlation was made between these stations and the zero tide mark (MLLW). However, at North Cantilever only three stations were established. This was due to a lack of sampling time. These stations were chosen to represent a range of depths. Station #1 was at the 6-9 meter level, station #2 at the 15-18 meter level, and station #3 at the 24-27 meter level. For convenience these three stations were labeled 2, 5, and 8 respectively so that the station number would correspond to actual depth, as in other areas.

Samples were taken using a 1/4 m^2 quadrat divided into four 1/16 m^2 subareas. At Colin's Cove five 1/4 m^2 samples were taken at each station by randomly placing the quadrat five times. This resulted in 20 samples taken per station with a total of 160 samples for the entire area. Due to the lack of sampling time, all other areas were limited to one 1/4 m^2 quadrat sample per station. At South Cantilever this amounted to randomly placing the quadrat once and then collecting the four subareas. At Smuggler's Cove and North Cantilever the quadrat was randomly placed four times at each station and each time only one subarea, located in the lower left corner, was collected.

The location of each sample across the 10-meter width was randomly selected using a random numbers table. This was not done at North Cantilever. Here, because of the problem of ensuring a uniform substrate, the quadrat was blindly dropped, but only after the proper substrate was obtained. The actual day of collection was randomly selected for each 1/4 m^2 quadrat at Colin's Cove and South Cantilever and for each 1/16 m^2 subarea at Smuggler's Cove. This, however, was not done for the samples collected at North Cantilever. Randomization by day collected did not extend between areas. One area was started and finished before a new area was begun. South Cantilever was collected between 11-18 March; Colin's Cove between 12-30 March; Smuggler's Cove between 24-30 April; and North Cantilever between 10-23 May. It should be noted here that there was some overlap of days in the collection of South Cantilever and Colin's Cove. The number of samples taken was strictly based upon the available amount of time. The 160 samples at Colin's Cove placed the collected data for C. fastigiata and C. lingulata within ± 20 percent of the mean with 67 percent confidence. For C. nummaria, however, 265 samples were needed for the same confidence level. Both C. fastigiata at North Cantilever and C. lingulata at Smuggler's Cove fell within ± 20 percent of the mean at 67 percent confidence. All other collected data fell below this level of confidence.

The primary limitations imposed upon this sampling program was one of time. This resulted in the intense sampling of one area and the minor sampling of three others with the subsequent reduction in the level of confidence at the minor sampling areas. Further limitations were of a physical nature which would affect a SCUBA diver, such as currents, depth, and allowable bottom time.

HABITAT

The particular substrate upon which the organism was attached was noted during sampling. Such substrates as solid rock, vertical cliff, and loose rock were recorded. Loose rock was further classified according to size. This was determined by taking the longest measurement of the face upon which one or more of the animals were attached. This measurement was recorded once for each animal. Any one particular rock might have more than one face occupied and thereby provide more than one length. This method of determining preferred rock size was used over other methods, such as weight or total rock length, because of the false impressions these two might create. For example, a large rock might be buried, except for a small available surface area; or one might weigh more or less than another, due to difference in composition, and yet be the same size.

As already mentioned, the surface area length was recorded once for each animal present and not divided between them. This procedure might raise some questions, but since these organisms are filter feeders with the same opportunity for food and not grazers competing for feeding area, it is felt that the procedure was justified. Those individuals found on loose rock were further classified as to their general position on top of or under the rock. If the animals could be seen, regardless of actual position, they were considered to be on top; if they could not be seen, then, they were considered to be under.

Vertical distribution was established for each species at each sampling area. Means are reported in numbers per 1/16 m^2.

SIZE FREQUENCY

Lengths of all animals collected were taken by measuring the distance between the posterior and anterior edges of the shell. *Crepidula lingulata* and *C. nummaria* are reported to show deviations in form and size dependent upon the object to which they are attached (Coe, 1938b, 1942a). This could have an effect upon the measured length, but only one animal, a *C. lingulata*, was collected with any noticeable shell deformity. Two or three others, attached to oval rocks, had grown such that the anterior-posterior axis was slightly curved. Since the vast majority of animals displayed normal growth and were taken off substrates where growth was not hampered, it was felt that length measurements were adequate for size determinations.

SEX RATIOS

All individuals were placed into one of four sexual classes, being either neuters, males, transitionals, or females. Identification was determined visually by comparing the state of penis development (Figure 2). Those individuals with no external signs of a penis were labeled neuters; those with a penis were called males; those with a reduced stubby penis were considered transitionals; and those with only a rudiment were termed females. This classification was taken after Coe's (1938a) but modified so that all transitionals were lumped together.

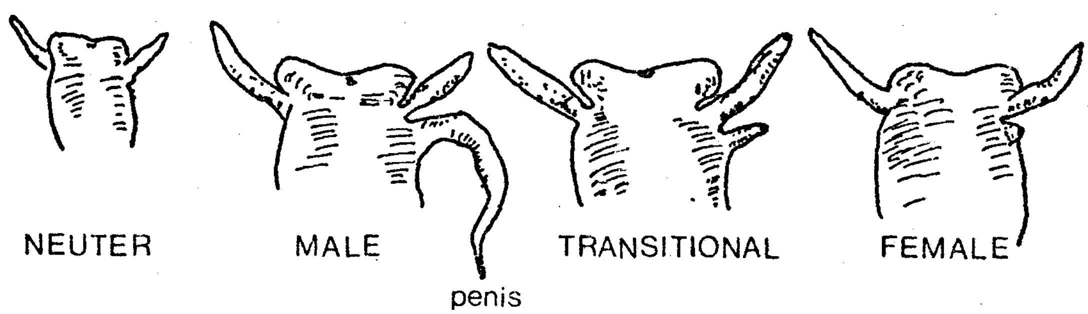


Figure 2

Anatomical Differences in Sexes

Neuter: No penis
Male: Penis present and well developed
Transitional: Reduced stubby penis
Female: Only a rudiment left

Very few neuters or transitional individuals of any species were found, so comparative tests between sexes were made using only males and females. Females of the species C. nummaria showed no rudiment that could be readily recognized and therefore could not be distinguished from neuters. Therefore, sex ratios and comparative tests involving sex ratios were not made for this species.

ASSOCIATIONS

Both intraspecific and interspecific associations were recorded. This included how many individuals of each species shared the same surface area along with the sex ratios of those sharing common surfaces. Percentages do not necessarily total 100 because one individual might well be in association with others of its own species and related species and therefore counted twice. The number of females with mounted males was noted as well as the number of females brooding egg capsules. Counts were made on the number of capsules per female and the number of eggs per capsule, plus measurements of capsule size.

PREDATOR-PREY RELATIONSHIPS

Predator-prey relationships were determined by both field and laboratory observations. In the field this consisted of turning sea stars to check prey selection. In the laboratory suspected predators were first starved and then placed with the potential prey. In order to observe the attack and any possible defense, the prey were first placed into round plexiglass containers. One side of the container was covered by plastic screen and the other was closed off by a rubber cork. This allowed enough water circulation to keep both predator and prey alive. The prey species were introduced to the containers 24 hours before a suspected predator in order to allow sufficient time for attachment. Any attack on a prey species could then be observed from any angle by simply rolling the plexiglass tube.

Predation pressure on those animals attached to the top of a rock versus those underneath and the pressure upon those on large rocks versus those on small rocks was checked. This was accomplished by setting up two areas within a sea-water table and covering the bottom with rocks in order to simulate the natural environment. In the first case 50 calyptraeids were added, 25 living on top and 25 living under rocks. Those under were placed in such a way that they were well off the substrate. Sea stars which had been starved were then introduced for one week. In the second case, calyptraeids occupying the smallest rocks were introduced with starved sea stars to determine if rock size offered protection from predation.

Radular action of the calyptraeids was observed by allowing them to attach to watch glasses and then observing them under a microscope while they were still submerged in a large bowl of water. By breaking a small hole in the shell on the left side, different materials could be introduced into the mantle cavity to see what action the animal might take against such foreign materials as tube feet, algae, and sand grains.

ANALYSIS

Comparative tests were run to determine the existing patterns for each species at each area where enough numbers were found to warrant it. Area patterns were then compared for differences. Differences between species were also determined statistically.

The various comparative tests used were t-tests and one-way analysis of variance for parametric data and 2xk contingency tables with chi-square or chi-square evaluations with expected numbers equal for non-parametric data. Linear regression analysis was run to determine correlation between depth versus size, rock size versus size, depth versus numbers per 1/16 m^2, and percent suitable substrate versus numbers per 1/16 m^2. All tests were run as two-tailed tests except those involving F-ratios and chi-squares. The probability level was always .05.

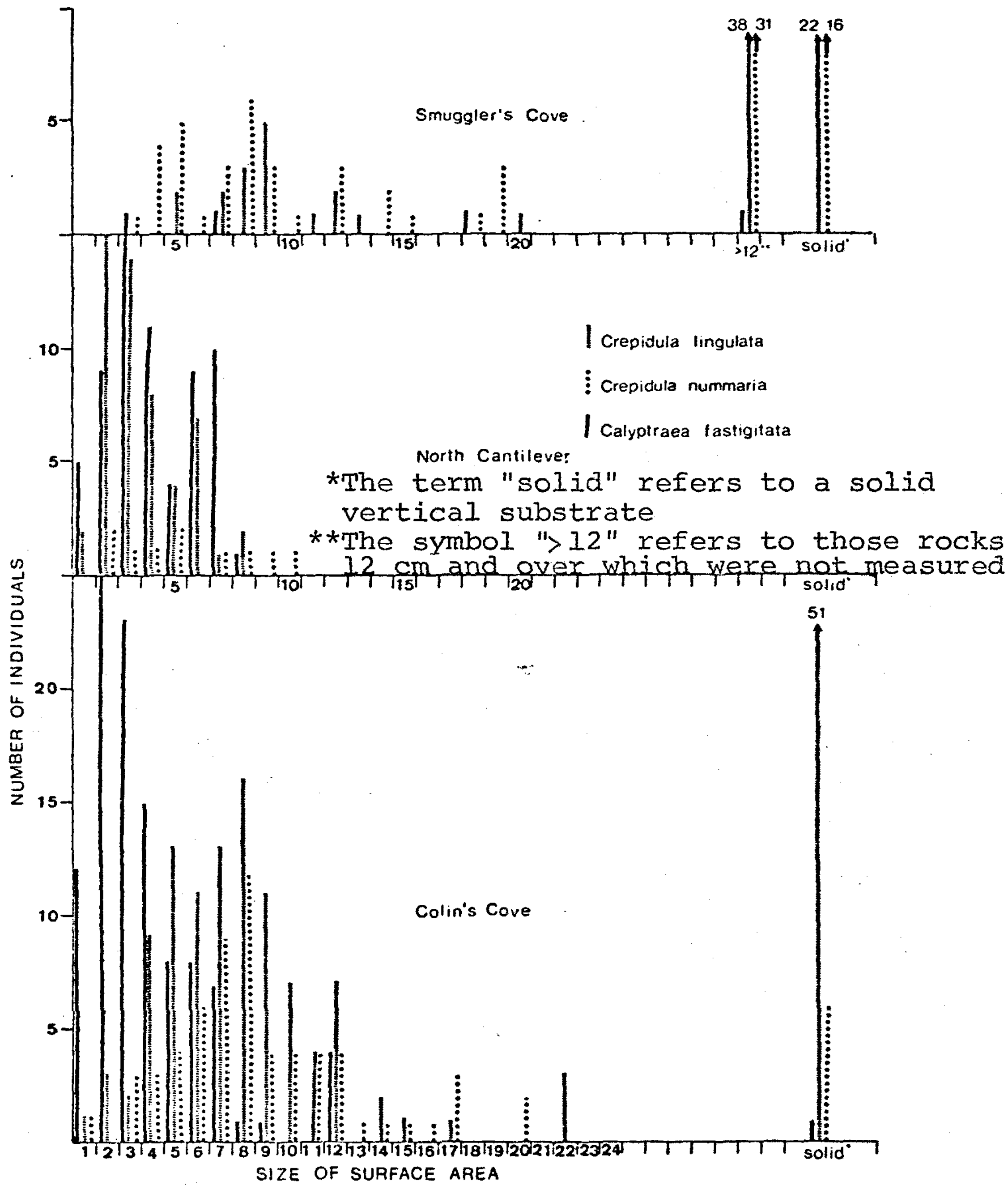
RESULTS

The following results are from a three and one-half month study and do not necessarily represent conditions throughout an annual cycle.

HABITAT

Of the numerous available habitats found on San Juan Island, the three species of calyptraeids under study were only found attached to hard surfaces. At Smuggler's Cove, both C. lingulata and C. nummaria were found on rough-walled vertical cliffs in equal numbers. This substrate provided 19-28 percent of the attachment sites for the two populations as opposed to 0 percent for C. fastigiata. However, the percentages dropped to almost zero for all three species when solid slopes were examined. A rocky substrate is the preferred habitat. Rock size was examined for each area and species resulting in the data shown in Figure 3. Some areas are excluded for certain species due to the lack of numbers collected. Range and mean rock size for each species and area are reported in Table 1. Calyptraea fastigiata prefers rocks measuring about 4.07 cm in length, whereas C. lingulata and C. nummaria prefer rocks measuring 7.44 cm and 9.32 cm respectively. Comparisons were made between rock sizes preferred by males and females for each species with

All sizes are in cm



*The term "solid" refers to a solid vertical substrate

**The symbol ">12" refers to those rocks 12 cm and over which were not measured

Figure 3

Size of Surface Area (Rock Size) Preferred for Each Locality

Table 1

Range and Mean Rock Size Preferred for Each Species[a]

Area	*C. fastigiata* Range	*C. fastigiata* Mean	*C. lingulata* Range	*C. lingulata* Mean	*C. nummaria* Range	*C. nummaria* Mean
Colin's Cove	1.0 to 12.0	3.77	1.0 to 22.0	7.90	1.0 to 20.0	8.53
North Canti-lever	1.0 to 12.0	4.28	1.0 to 8.0	3.60	2.0 to 10.0	5.5
Smuggler's Cove	ND[b]	ND	5.0 to 19.0	11.2	3.0 to 19.0	10.7
Dredge	1.0 to 8.0	3.93	ND	ND	ND	ND
Total Count	1.0 to 18.0	4.07	1.0 to 22.0	7.44	1.0 to 20.0	9.32

[a]Sizes listed in cm.

[b]ND = no data.

the result that there were no significant differences (see Table 11, Appendix) except for _C. fastigiata_ at Colin's Cove. The mean rock size for males there was 3.32 cm and for females 5.29 cm. The preferred rock size for _C. fastigiata_ was the same in all areas compared but such was not the case for _C. lingulata_ or _C. nummaria_ (Table 12, Appendix). If the three species are compared against each other, it is found that at Colin's Cove and at North Cantilever the three differ significantly in their preferences, but at Smuggler's Cove two of them, _C. lingulata_ and _C. nummaria_, do not differ (Table 13). When all areas are combined the result is an overall significant difference between the three species (Table 13 and Figure 4) with _C. fastigiata_ preferring the smallest rocks and _C. nummaria_ the largest.

Their position on the rock ranges from 69 percent found under the rocks for _C. fastigiata_ to 98.8 percent under for _C. nummaria_. _Crepidula lingulata_ was found under rocks about 85 percent of the time (Table 2). The difference in those found under rocks versus those on top was significant (Table 14, Appendix) as was the difference in those found on loose rock versus those on vertical cliffs (Table 15, Appendix).

Vertical distribution offers further evidence of substrate specificity. None of the three species show equal distribution with respect to depth except _C. fastigiata_ at North Cantilever (Tables 3 and 16). All other areas show

All sizes are in cm

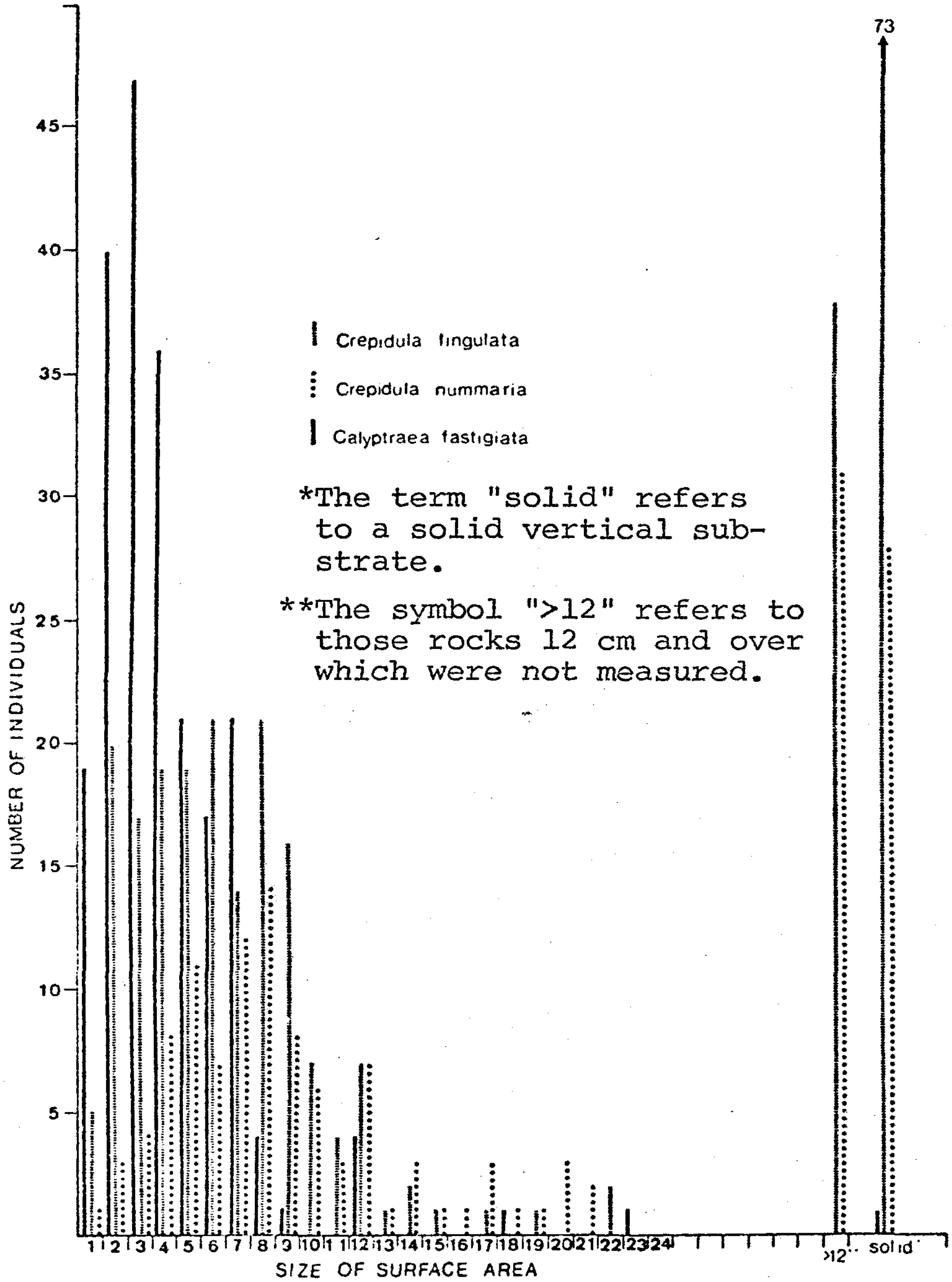


Figure 4

Size of Surface Area (Rock Size) Preferred with all Localities Combined

Table 2

Percentage of Those Species Found Underneath Rocks

Species	Colin's Cove	North Cantilever	Smuggler's Cove	Total Count
C. fastigiata	ND	69.41	ND	68.97
C. lingulata	ND	88.24	82.46	85.19
C. nummaria	ND	92.31	100.00	98.80

Table 3

Vertical Distribution (Numbers per 1/16 m^2)

Area	Depth	Description	*C. fastigiata*	*C. lingulata*	*C. nummaria*
Colin's Cove	1	100% solid slope	0.05	0.05	0.00
	2	99% solid slope, 1% loose rock	0.25	0.55	0.40
	3	50% cliff, 25% loose rock, 25% large rock	1.35	2.60	2.65
	4	50% solid slope, 50% loose rock	1.80	0.50	0.40
	5	1% solid slope, 99% loose rock	3.80	3.45	0.40
	6	1% solid slope, 99% loose rock	2.40	2.85	0.35
	7	75% solid slope, 15% cliff, 10% loose rock	0.45	3.10	0.50
	8	100% cliff	0.00	1.50	0.25
South Cantilever	1	100% large rocks	0.25	1.50	4.00
	2	100% solid slope	0.00	0.75	0.25
	3	100% solid slope	0.50	0.00	0.00
	4	100% solid slope	0.00	0.25	0.00
	5	100% solid slope	0.00	0.25	0.75
	6	100% solid slope	0.00	0.75	0.00
	7	100% solid slope	0.00	0.00	0.00
	8	100% solid slope	0.00	1.25	0.00
Smuggler's Cove	1	75% cliff, 25% large rocks	0.25	1.50	1.00
	2	25% solid slope, 75% cliff	0.00	0.75	3.25
	3	25% solid slope, 65% large rocks	0.00	2.50	5.25
	4	100% large rocks	0.00	5.50	6.50

Table 3 (Continued)

Area	Depth	Description	*C. fastigiata*	*C. lingulata*	*C. nummaria*
Smuggler's Cove	5	25% solid slope, 50% cliff, 25% large rocks	0.00	2.00	4.25
	6	50% solid slope, 25% cliff, 25% large rocks	0.25	3.75	0.25
	7	75% solid slope, 25% large rocks	0.00	2.25	0.00
	8	50% solid slope, 25% large rocks	0.25	1.50	1.00
North Canti-lever	2	100% loose rocks	6.75	2.50	2.25
	5	100% loose rocks	6.25	9.50	1.00
	8	100% loose rocks	8.50	3.00	0.00

density peaks at various depths corresponding to preferred substrate (Table 3 and Figure 5). Linear regression analysis was used to determine any correlation between density versus depth and density versus percent rocky substrate. Direct correlation was found for *C. fastigiata* at Colin's Cove with an r^2 value of .90 and for *C. lingulata* at Smuggler's Cove with an r^2 value of .56. No correlation was found for *C. lingulata* at Colin's Cove or for *C. nummaria* at either Colin's or Smuggler's Cove. Regression analysis on density versus depth revealed no correlation for any species at any location except for *C. lingulata* at Colin's Cove; however, the r^2 value was only .06.

Range of depth extended from 3 meters for all three species to 65 fathoms for *C. fastigiata* and *C. lingulata*. *Crepidula nummaria* extended to only 30 fathoms.

SIZE FREQUENCIES

Size averages are listed in Table 4 for all species and areas. Neuters and transitionals are listed for comparative purposes but are based on low numbers and in some cases on only one. Male size for *C. nummaria* at Smuggler's Cove is based on one individual and on three for the dredge samples. Sizes for neuters, transitionals, and females for *C. nummaria* are not listed due to problems already discussed.

Size differences were found between males and females for all species with males being significantly smaller than females (Table 19, Appendix, and Figures 6 and 7).

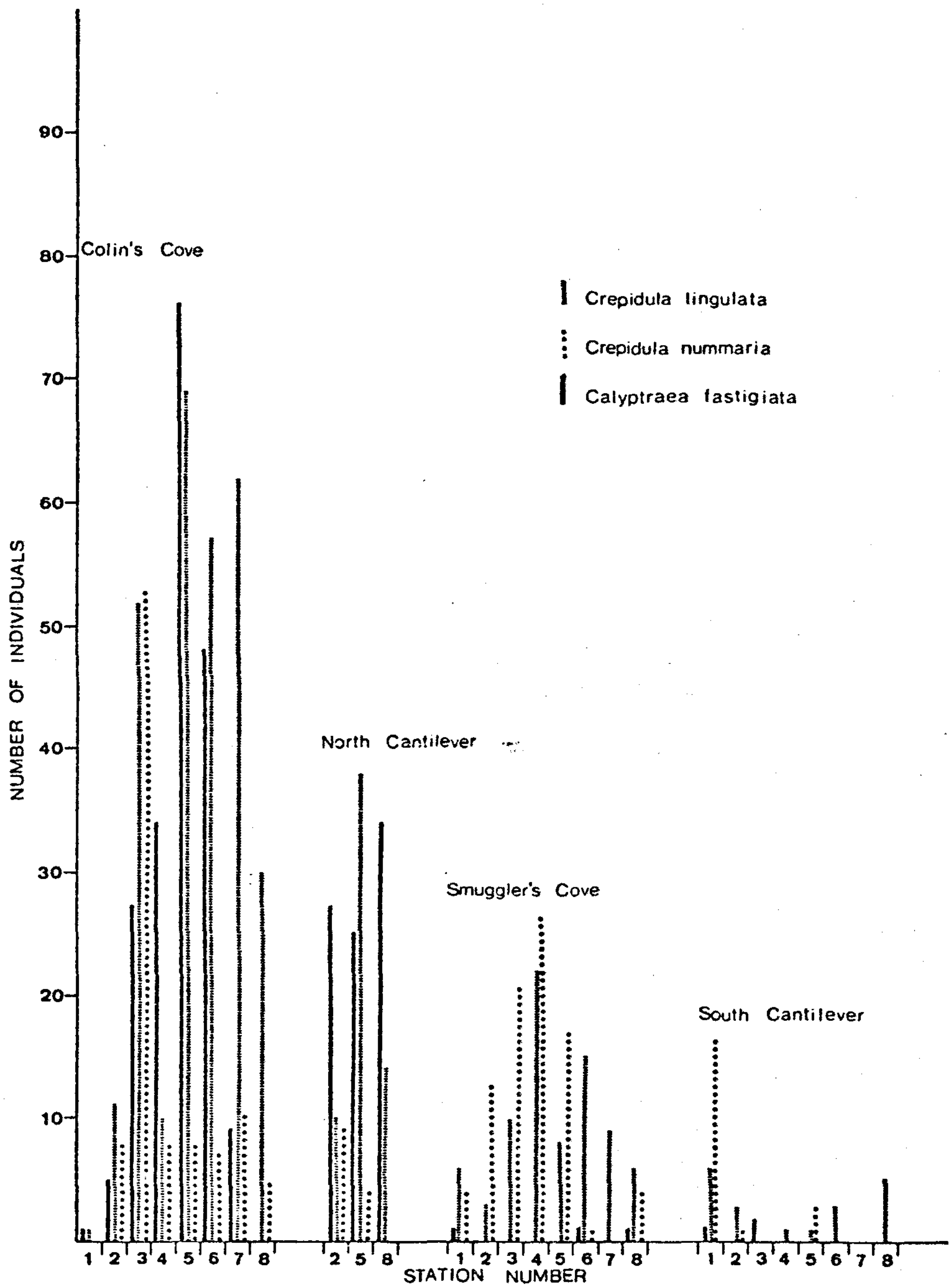


Figure 5

Vertical Distribution at Different Localities

Table 4

Mean Sizes[b] for Each Species at Different Localities

Area	Counts N[d]	M[d]	T[d]	F[d]	Total
C. fastigiata					
Colin's Cove	5.1	7.2	10.9	15.7	9.7
North Cantilever	ND[a]	6.8	10.6	14.7	9.9
Smuggler's Cove	ND	ND	ND	ND	ND
Dredge Samples	ND	9.0	10.7	15.1	12.3
Total Count[c]	5.1	5.7	10.8	15.3	9.1
C. lingulata					
Colin's Cove	3.0	6.9	8.4	13.2	11.3
North Cantilever	ND	6.6	8.5	14.3	10.7
Smuggler's Cove	ND	6.9	8.8	12.6	11.8
Dredge Samples	ND	ND	ND	ND	ND
Total Count[c]	5.7	6.9	9.4	13.7	11.6
C. nummaria					
Colin's Cove	ND	ND	ND	ND	13.7
North Cantilever	2.1	ND	ND	ND	13.0
Smuggler's Cove	ND	5.4	ND	ND	15.5
Dredge Samples	ND	ND	ND	ND	ND
Total Count[c]	2.1	5.4	ND	ND	

[a]ND = no data.

[b]All sizes are in mm.

[c]Sizes for total counts were figured from all localities and not just those listed here.

[d]N = neuters, M = males, T = transitionals, F = females, Total = total counts.

All sizes are in mm

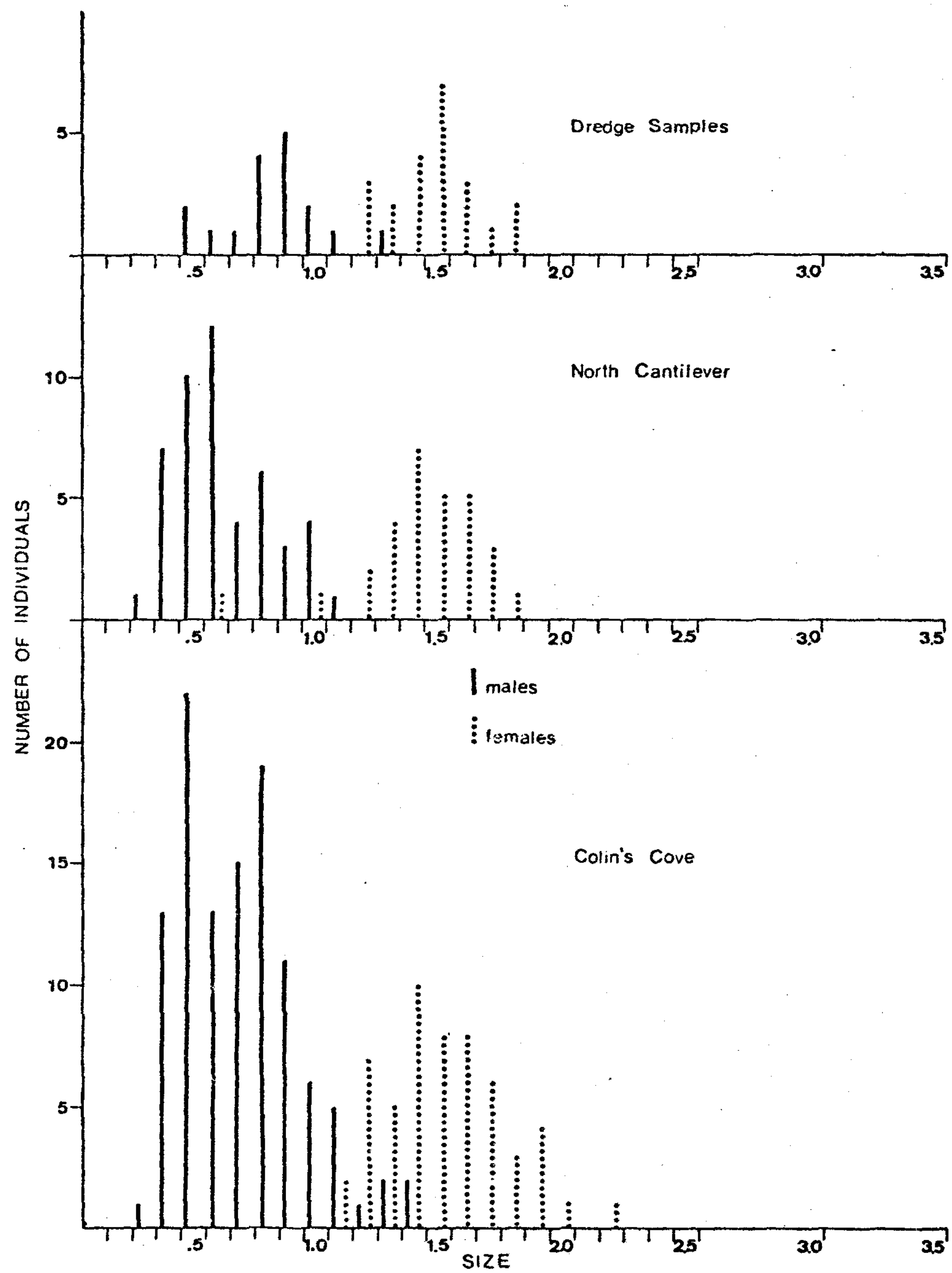


Figure 6

Size Frequency of C. *fastigiata* at Different Localities

All sizes are in mm

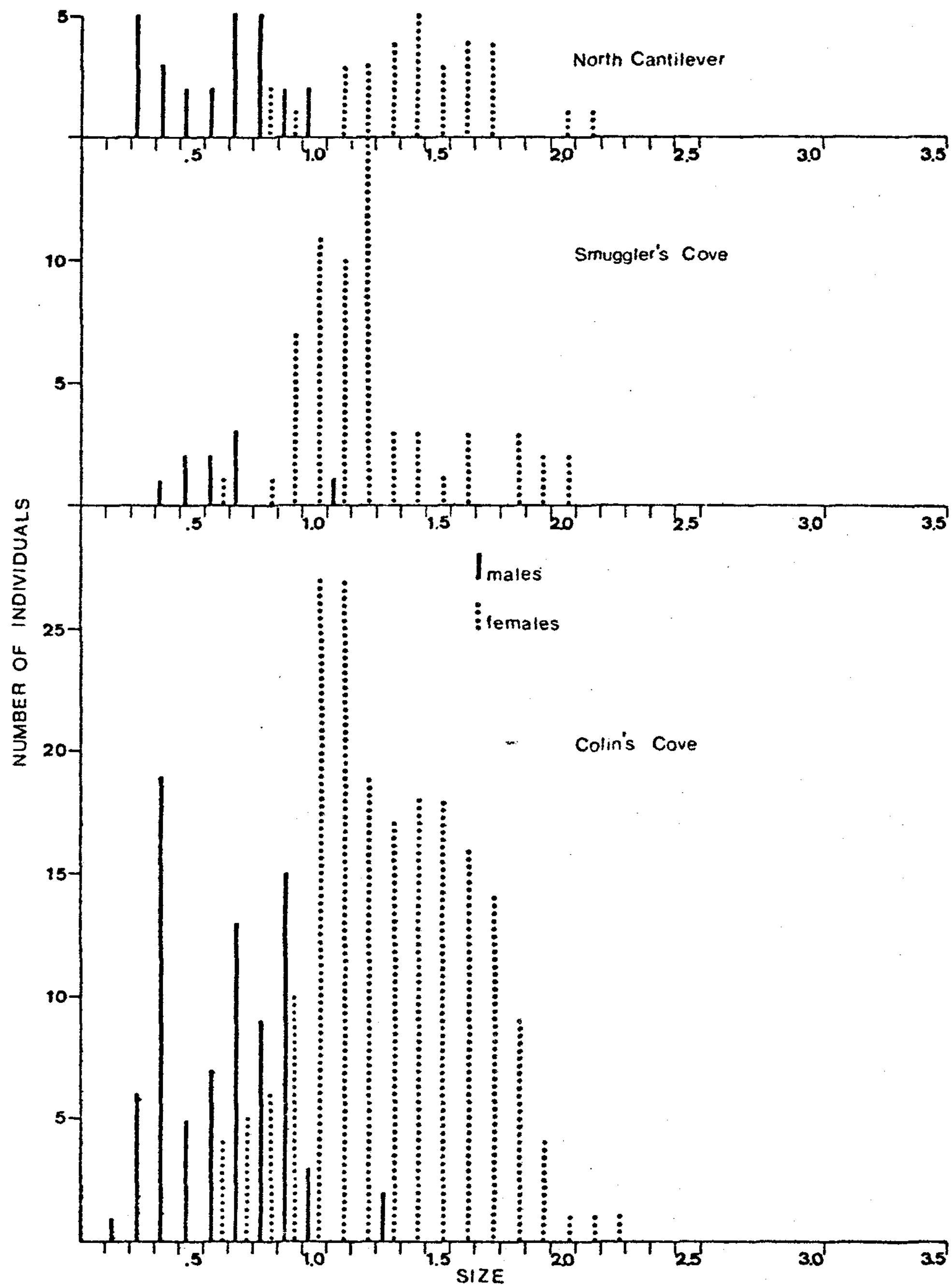


Figure 7

Size Frequency for C. lingulata at Different Localities

However, the average size for each sex was constant regardless of area (Table 20, Appendix). Size differences between species were negligible for both sexes except for C. fastigiata females at Colin's Cove, which were slightly larger (Table 21, Appendix).

Linear regression analysis was run against size versus depth and size versus rock size. The only correlation found between size versus depth was for C. fastigiata at Colin's Cove; however, the r^2 value was only .04. No correlation between size versus rock size occurred at Smuggler's Cove but correlation was shown for all three species at Colin's Cove. Crepidula lingulata was the only species to show correlation between size versus rock size at North Cantilever (Tables 22 and 23, Appendix). The r^2 values varied between .06 and .25 for those species showing significant regression between size versus rock size.

SEX RATIOS

Sex ratios are listed in Table 5 for each area and species except for C. nummaria as already explained. Neuters and transitionals are listed, though the numbers collected were small. However, only males and females were used for statistical comparisons, which were made by use of chi-squared evaluations (expected values equal) to show significant deviations from a 1:1 sex ratio.

Calyptraea fastigiata showed greater numbers of males at all areas except in the dredge samples, whereas

Table 5

Sex Ratios for Each Species at Different Localities[a]

Area	Neuters	Males	Transitions	Females
C. fastigiata				
Colin's Cove	1.98	64.85	5.94	27.23
North Cantilever	0.00	55.81	10.47	33.72
Smuggler's Cove	ND[b]	ND	ND	ND
Dredge	0.00	37.78	11.11	51.11
C. lingulata				
Colin's Cove	.69	27.34	2.77	69.20
North Cantilever	0.00	43.33	3.33	53.34
Smuggler's Cove	0.00	10.00	2.86	87.14
Dredge	9.09	18.18	0.00	72.73
C. Nummaria				
Colin's Cove	ND	ND	ND	ND
North Cantilever	ND	ND	ND	ND
Smuggler's Cove	ND	ND	ND	ND
Dredge	0.00	36.36	0.00	63.64

[a]Ratios are listed as percentages.

[b]ND = no data.

C. lingulata showed just the opposite (Table 5). The number of males and females differed significantly from each other for each species (Table 24, Appendix) and likewise differed significantly between each species (Table 25, Appendix). The sex ratio for *C. fastigiata* remained constant between Colin's Cove and North Cantilever, though it changed significantly for the dredge samples. *Crepidula lingulata* showed significant differences between all areas (Table 26, Appendix).

REPRODUCTIVE BIOLOGY

Table 6 gives the percentages of those females which were found to be brooding eggs at the time of collection.

Table 6

Percentages of Females with Eggs

Area	*C. fastigiata*	*C. lingulata*	*C. Nummaria*
Colin's Cove	18.18	4.5	9.09
North Cantilever	0.00	53.13	16.67
Smuggler's Cove	ND[a]	19.67	8.33
Dredge	0.00	ND	ND

[a]ND = no data.

This ratio, about 11 percent, remains fairly constant for *C. nummaria* at all areas collected but differs widely for the other two species. *Calyptraea fastigiata* drops from 18.18 percent at Colin's Cove to zero at North Cantilever whereas C. lingulata increases from 4.5 percent at Colin's Cove to 53.13 percent at North Cantilever. It should be noted that statistical comparisons were not made on these data and therefore the above differences and similarities might not be significant.

The mean number of capsules laid per female was 7.0 for C. fastigiata, 7.93 for C. nummaria, and 11.63 for C. nummaria. There were 8.41 eggs per capsule for C. fastigiata and 9.26 for C. nummaria. The number of eggs per capsule for C. lingulata was reported by Coe (1949) to be between 100 and 400 and this was confirmed. Dehnel (1955) reported that the number of egg capsules for C. nummaria varied from 4-12 and that each capsule varied in the number of eggs from 5-50.

The shape and structure of the capsules was described by Lebour (1937). In essence, for all three species, the capsules have the shape of a kernal of corn with the small end of each capsule lengthened into a thin strand which connects with other capsules at a common base attached to the substrate. Capsule sizes were not obtained for C. fastigiata, but for C. lingulata the length was 2.44 mm and the width 2.67 mm; for C. nummaria the length was 2.94 mm and the width 3.61 mm (Table 8).

Calyptraea fastigiata and C. nummaria brood their young to the crawling stage, whereas C. lingulata, as reported by Coe (1949), releases veligers into the plankton.

Table 7

Mean Number of Capsules per Female and Mean Number of Eggs per Capsule

Area	Capsules per Female			Eggs per Capsule		
	C. fastigiata	*C. lingulata*	*C. nummaria*	*C. fastigiata*	*C. lingulata*[b]	*C. nummaria*
Colin's Cove	7.0	9.0	7.78	8.41	100-400	10.33
North Cantilever	ND[a]	12.88	8.0	ND	100-400	8.63
Smuggler's Cove	ND	6.0	8.33	ND	100-400	6.68
Total Count	7.0	11.63	7.93	8.41	100-400	9.26

[a]ND = no data.

[b]Actual count not taken but confirmed to be within the range reported by Coe (1949).

Table 8

Mean Dimensions of Egg Capsules[a]

Species	Length	Width	Base Width
C. lingulata	2.44	2.67	.31
C. nummaria	2.94	3.61	.86

[a]Size listed in mm.

ASSOCIATIONS

Calyptraea fastigiata was found in association with itself and with other species fewer times than *C. lingulata* or *C. nummaria*. This level, about 13.5 percent, remained constant for all areas except North Cantilever where it jumped to 33.85 percent (Tables 9 and 27). *Crepidula lingulata* and *C. nummaria* varied between 31.03-50.00 percent in association each with itself, except at North Cantilever where *C. nummaria* dropped to 0 percent. This was due, no doubt, to the small numbers collected there. Sex ratios for those individuals found in intraspecific association did not vary significantly from a 1:1 ratio (Table 28, Appendix). Of the females collected, those found with mounted males in the mating position averaged between 2.5-10.91 percent.

PREDATOR-PREY RELATIONSHIPS

Natural predation on calyptraeids was only observed twice in the field but was induced on numerous occasions in the laboratory (Table 10). Of the various predators tested, *Lepasterias hexactis* and *Evasterias troschellii* proved to be the most voracious, often attacking and devouring one calyptraeid after another. Total length of attack from first contact to end of digestion lasted only 1-7 hours for *Lepasterias hexactis* and from 2-12 hours for *Evasterias troschellii*, depending upon the size of the prey,

Table 9

Percentages of Intraspecific and Interspecific Associations[a]

Area	Associations Intraspecific	Interspecific	Total
C. fastigiata			
Colin's Cove	13.46	8.65	20.19
North Canti-lever	33.85	9.23	38.46
Smuggler's Cove	ND[b]	ND	ND
Dredge	14.63	2.44	17.07
C. lingulata			
Colin's Cove	50.0	22.16	61.54
North Canti-lever	43.64	9.0	50.91
Smuggler's Cove	37.50	6.25	43.75
Dredge	ND	ND	ND
C. nummaria			
Colin's Cove	34.92	31.75	53.97
North Canti-lever	0.00	11.11	11.11
Smuggler's Cove	31.03	3.45	34.48
Dredge	ND	ND	ND

[a]Percentages do not total 100 percent since one individual could be experiencing both intraspecific and interspecific associations at the same time and would therefore be counted twice.

[b]ND = no data.

size of the sea star, and the degree of hunger. Although crabs were observed to crush the shell and feed on the calyptraeids in the laboratory, no evidence of this, such as crushed shells, was found in the field.

Table 10

List of Probable Invertebrate Predators

Predator	Observation[a] Laboratory	Field
Dermasterias imbricata	+	-
Evasterias troschellii	+	+
Lepasterias hexactis	+	-
Soloster stimpsoni	-	-
Ceratostoma foliata	-	-
Fusitriton orgegononsis	-	-
Ocenebra interfossa	-	-
Various crabs	+	-

[a]+ indicates confirmed observation; - indicates no observation.

The use of the radula to bite the tube feet of attacking sea stars was observed for all three species but to varying degrees of intensity. This action would cause an immediate release and withdrawal of a tube foot from under the shell. Each tube foot reacted independently and was removed only when it was bitten. This action delayed predation but in no case did it ever prevent predation.

The use of the radula for other than feeding purposes was further examined. Such objects as algae, tube feet, and sand grains were placed under the shell but with no more reaction than to be carried to the front of the shell either by ciliary currents or by being grabbed and held by the radula and then brought forward. From this point they were expelled from the shell by being pushed out by the head or again grabbed by the radula and carried to the shell's edge for elimination. *Calyptraea fastigiata* displayed a strange behavior of moving an inserted object forward by turning toward it and then placing the head beneath the mantle while leaving the left tentacle above and then moving forward to catch and move the inserted object. This was observed on several occasions as were both methods listed above. However, in no case was any real aggression shown as observed during a sea star attack. During sexing, it was often necessary to lift the head in order to observe the penis and this would almost always result in an aggressive attack on the metal probe. In another case, an *Ocenebra* moved immediately away after its foot, which had encroached slightly under the shell of *C. fastigiata*, was rasped by the radula.

DISCUSSION

A close examination of three species of Calyptraeidae, which inhabit the same general area, reveals a partitioning of the available substrate. Within each species no differences were found between male and female preferences except for *C. fastigiata* at Colin's Cove where females were found on significantly larger rocks than males. This difference might be due to individuals seeking larger rocks as they grow. Females of this species were not found predominantly on one rock size but distributed evenly on rocks measuring 1-5 cm. This might well indicate that younger, smaller females are inhabiting the smaller rocks and then moving to larger ones as they get older. However, it must be noted that no differences were found at North Cantilever or for the dredge samples. This might be explained by the fact that 78 percent of the dredged individuals were found on dead bivalve shells and that the substrate at North Cantilever was predominantly small rocks 1-2 cm in size. It is believed that at North Cantilever and for those dredged individuals that both males and females were forced onto substrates of the same size due to a lack of substrate diversity as found at Colin's Cove. The larger preferences of *C. lingulata* and *C. nummaria* provide no limitation problems for growth and therefore apply no pressure on a growing individual to move. Further evidence of this is offered in later discussion on the regression analysis of rock size versus individual size.

Calyptraea fastigiata did not differ in its preferred rock size from area to area but C. lingulata and C. nummaria did. Figure 4 shows C. fastigiata clustered on the low end of the scale and C. nummaria clustered significantly higher. However, C. lingulata does not show a definite cluster but rather maintains a constant level from the low end to the high end of the scale. This suggests that C. lingulata is an opportunist and can inhabit various rock sizes depending upon the nature of the substrate. Assuming this to be the case, then it would not be surprising to find a lack of correlation between areas for this species. However, correlation between areas would be expected for C. nummaria. Such is the case if those rocks from Smuggler's Cove measuring greater than 12 cm are eliminated from analysis. Smuggler's Cove had an almost uniform substrate of large rocks which resulted in the differences noted in the analysis. The fact that C. nummaria can and does occupy large rocks is itself significant. Coe (1938a, 1942a) and Dehnel (1955) found this species inhabiting the inside of empty gastropod shells. Only one such shell was collected during this study and it was from dredged samples. It is very possible that the habitat changes with depth. As would be expected, all three species differ significantly from each other in their substrate preference.

Analysis revealed that all three species were found on the undersides of rocks more frequently than on top, though to different degrees. Laboratory tests indicate that some degree of protection against predation is afforded those individuals on the undersides of rocks. It is assumed that rough-walled vertical cliffs likewise offer some selective advantage for *C. lingulata* and *C. nummaria* as a segment of their populations was found there. From personal observation, it is noted that sea stars were never found clinging to these cliffs, but were numerous in the loose rock areas and on solid rock slopes. Solid rock slopes produced the fewest numbers of individuals per square meter for any of the calyptraeids and therefore it must be assumed that it offers little protection against predation. This hypothesis is strengthened by the fact that solid sloped areas were interspersed among loose rock areas and therefore subject to the same physical conditions.

For all three species, vertical distribution can best be explained as being governed by availability of preferred substrate. Figure 5 shows density peaks which correspond to favorable substrate rather than depth or depth-related factors. Driscoll (1967) found that neither temperature nor depth were significant in controlling vertical distribution for *Crepidula plana*, *Crepidula fornicata*, or *Crepidula convexa*. Only at North Cantilever for *C. lingulata* does an unexplainable peak occur. Mean rock size for station 2 is 5.4 cm, but for stations 5 and 8 it is 3.2 cm, and yet station 5 has three times as many individuals. Regression analysis showed strong correlation between density and preferred substrate for C. fastigiata and C. lingulata at Colin's Cove and Smuggler's Cove respectively but not for other areas and not for C. nummaria. The lack of correlation for C. nummaria could be due to the small number of samples taken for this species. No correlation would be expected at North Cantilever since the substrate was 100 percent uniform. No explanation is given for the lack of correlation for C. lingulata at Colin's Cove. It should be noted, however, that if the analysis had been run as a one-tailed t-test than correlation would have been shown at an r^2 level of .41.

The degree of intraspecific and interspecific association, likewise, seems explainable in terms of preferred rock size. Mean rock size on which more than one individual is attached is always larger, though not necessarily significantly larger, than the mean rock size found for single individuals. Calyptraea fastigiata, which prefers smaller rocks, therefore shows fewer intraspecific and interspecific associations than C. lingulata or C. nummaria. This might be misleading, however. Numerous small rocks lying together present a greater surface area and more contact area than do large rocks. Calyptraea fastigiata would have little trouble crossing from one small rock to another but such would not be the case for C. lingulata and C. nummaria. Sex ratios for these intraspecific associations did not deviate from a 1:1 ratio even though when considering the entire population they did. Therefore these animals seem to be arranged in sexual groups. This appears to be in agreement with Coe's (1938b) finding for C. lingulata and C. nummaria. He also states that only temporary matings are the rule and to this end only about 8.5 percent of the females were found with mounted males.

Egg-laying data indicated that C. fastigiata was at the end of its breeding period in early March, whereas C. lingulata was just beginning. Crepidula nummaria maintained a constant egg-laying rate from March to middle June of about 11 percent. This low percentage over a 3½-month period might indicate, as Coe (1942a) states, that C. nummaria reproduces throughout the year.

Crepidula lingulata stands apart from C. fastigiata and C. nummaria in producing many more eggs per capsule, though the number of capsules per female are only slightly greater. It also differs by brooding its eggs only as far as the veliger stage (Coe, 1949) whereupon they are released into the plankton. These differences are indicative of an animal which experiences high wastage as opposed to C. fastigiata and C. nummaria which brood small numbers of eggs to the crawling stage and experience low wastage.

Decimation is overcome by the high productivity of the females within a population. It is therefore important to know sex ratios and how they might change throughout an annual cycle. During this study C. fastigiata maintained a large population of males in comparison to females, whereas C. lingulata did not. A large number of males would assure that all possible females were inseminated; and this would be important for an animal which produces few numbers of eggs per female. Superficially, it would seem that a large female population would be dependent upon the number of males and how many females they could inseminate in one season. However, Coe (1942b) found that in Crepidula onyx the sperm remained viable for more than a year and in sufficient quantity to fertilize 50,000 to 200,000 eggs. If this is the case with C. lingulata then mating may only have to occur every other year. This way a large population of females can be maintained for the production of great quantities of eggs. However, it must be emphasized that these species are protandrous and the sex ratios might not remain constant throughout the year. An annual study would have to be performed in order to draw absolute conclusions.

Females were found in all cases to exceed males in size. Sizes for C. lingulata and C. nummaria were reported by Coe (1936b, 1942a) and differ only slightly from those reported here (Table 4). These differences are probably not real but reflect only technique differences in sexing and measuring. Sizes have not been reported for C. fastigiata in the literature but for C. chinensis a shell length of 17 mm may be obtained (Fretter and Graham, 1962). Sizes appear to be constant regardless of area examined and do not differ between species for either males or females.

Differences were found (Tables 20 and 21, Appendix) but they seem to be isolated and not of general occurrence. The only correlation found between size and depth was for C. fastigiata at Colin's Cove with an r^2 value of .04. The value is so small that correlation is probably due to the high degrees of freedom which would detect very slight changes and not due to any real, or at least significant, correlation. However, correlation was shown between size of individual and size of rock at Colin's Cove. The r^2 value for C. lingulata was small (.06) and probably due to the large degrees of freedom. This is not surprising as C. lingulata prefers larger rocks and therefore, as already mentioned, would not experience the need to move as it grows but would remain on the rocks upon which it has settled. Crepidula nummaria had an r^2 value of .19 and C. fastigiata a value of .25. It is surprising that C. nummaria shows as high an r^2 value as it does since it should react the same as C. lingulata. However, no explanation is offered. The fact that C. fastigiata shows a value of .25 is not surprising as it probably moves to larger stones as it grows and therefore correlation should exist. The fact that it is only .25 reflects the mixed substrate of Colin's Cove. Here, small individuals can settle on a wide range of stones from small to large. Those on the smaller stones would move to larger rocks as they grow, but those on larger ones would have no need to move and hence the relatively small r^2 value. The correlation found at North Cantilever for

C. lingulata cannot be accounted for and with an r^2 of only .08 is probably not too important. The lack of correlation at Smuggler's Cove is due to the large rock substrate and hence the attachment of all sizes to large rocks with no need to move. The lack of correlation at North Cantilever for C. fastigiata and C. nummaria reflects the condition of the uniform substrate of small rocks.

No specific predators were found in the field but laboratory tests suggest that two sea stars are at least capable. Leptasterias hexactis and Evasterias troschellii fed heavily on calyptraeids in the laboratory. It must be remembered that these predators were starved and that only calyptraeids were offered. However, on two different occasions, Evasterias troschellii was observed in the field feeding on Crepidula. Feder (1959) and Mauzey (1968) reported occasional predation by Leptasterias hexactis, Orthasterias koeheri, and Pisaster ochraceus. Hancock (1955, 1958) reported heavy predation on C. fornicata by Asterias rubens and occasional predation by Crossaster papposus. He also reported that for Asterias rubens food preferences change with age. This suggests that all age classes of sea stars need to be checked for possible differences in preferred food. Other possible predators include Urosalpinx cinerea, Ocenebra sp. (Fretter and Graham, 1962), and Odostomia seminuda or other related species (Robertson, 1957).

Laboratory experiments indicate that those individuals attached to the undersides of rocks are afforded a high degree of protection from introduced predators. Attachment on small rocks, however, does not prevent predation. Fretter and Graham (1962) suggested that the mantle gland cells secrete upon stimulation a proteinaceous substance which, if not toxic, at least varies from repugnatorial to antiseptic. The use of the radula to bite and rasp seems to be more of a delaying action than an effective defense. In all cases the sea star eventually won. The degree to which the radula is used seems to be dependent upon the degree of irritation being received. A foreign object taken accidentally into the mantle cavity, if not handled by ciliary currents, would be leisurely removed with the help of the radula. However, a foreign object which causes a high degree of discomfort, such as a metal probe or the tube feet of an attacking sea star, would be ferociously attacked. Hancock (1958) reports that an exclusive diet of C. fornicata by Asterias rubens was not only inadequate for growth but that actual size reduction often resulted. This, then, might offer indirect protection.

CONCLUSIONS

The study of the field populations of three species of Calyptraeidae exhibiting the same anti-stacking behavior has revealed a basic resource partitioning.

All three prefer a loose rock substrate with negligible numbers found on solid substrate and with only 18-20 percent of C. lingulata and C. nummaria found on vertical cliffs and zero percent of C. fastigiata. The loose rock habitat is partitioned among the three with C. fastigiata occupying the smallest rocks (mean size 4.07 cm) and C. nummaria occupying the largest (mean size 9.32 cm). Crepidula lingulata seems to be an opportunist that can occupy the smallest to the largest but with a mean rock size preference of 7.44 cm. All three species prefer being underneath rocks but to varying degrees. Crepidula nummaria is found there almost exclusively whereas C. lingulata and C. fastigiata range from 67-88 percent respectively. Vertical distribution of all three species is based upon suitable substrate and not depth or depth-related factors. Numbers per square meter increase dramatically with suitable substrate.

The number of intraspecific and interspecific associations were greater for C. lingulata and C. nummaria due to their substrate preferences. Sex ratios for intraspecific associations did not deviate significantly from a 1:1 ratio.

This would indicate a grouping for sexual purposes since both populations did deviate from a 1:1 ratio when considered totally. All three species had about 8.5 percent of their females with mounted males.

Calyptraea fastigiata had high numbers of males as compared to females, whereas C. lingulata was just the opposite. High male counts would ensure that all females were inseminated, whereas a high female count would ensure maximum productivity. This conclusion, however, needs further substantiation from research on annual cycles. Egg laying and brooding behavior did support the hypothesis. Calyptraea fastigiata and C. nummaria laid few numbers of eggs per female and then proceeded to brood them to a young crawling stage. Crepidula lingulata, on the other hand, produced high numbers of eggs and then brooded them only until the veliger stage, at which time they were released into the plankton. Wastage would, therefore, be a problem for C. lingulata and maintenance of high productivity a necessity; whereas C. fastigiata and C. nummaria, with a low amount of larval wastage and low productivity, would need only to ensure total female insemination.

There were no significant size differences between the three species but within each species males were always significantly smaller than females. Size cannot be correlated with depth. However, correlation was found between individual size and rock size for C. fastigiata. This indicates that at least some of the population is moving from smaller rocks to larger ones as they grow. This is supported by the fact that _C. fastigiata_ was the only species to show a significant difference in the preferred rock size for males and females.

Well-established predators have not been found for any of the three calyptraeids. However, _Lepasterias hexactis_ and _Evasterias troschellii_ are at least capable of inflicting heavy losses with total length of attack lasting 1-12 hours. Individuals found under rocks are protected from predation by virtue of their position. The use of the radula to bite and rasp delays predation but does not halt it. The radula, besides being a feeding organ, is also used to remove irritants from under the shell.

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APPENDIX

Table 11

Analysis of Male-Female Differences in Preferred Substrate

Area	*C. fastigiata* df	*C. fastigiata* TS	*C. fastigiata* Reject Level	*C. fastigiata* Ho	*C. lingulata* df	*C. lingulata* TS	*C. lingulata* Reject Level	*C. lingulata* Ho
Colin's Cove	97	3.520	±1.988	Reject	101	1.458	±1.986	Accept
North Canti-lever	57	0.372	±2.003	Accept	-50	-1.621	±2.011	Accept
Smuggler's Cove	ND	ND	ND	ND	51	0.526	±2.009	Accept
Dredge	35	1.369	±2.032	Accept	ND	ND	ND	ND

Two-tailed t-test, α-level = .05.

ND = no data.

Table 12

Analysis of Substrate Difference Between Areas[a]

Species	df	F-ratio	Reject Level	Ho
C. fastigiata[b]	2;207	0.988	3.039	Accept
C. lingulata[c]	2;218	6.111	3.038	Reject
C. Nummaria[c]	2;134	8.862	3.063	Reject

[a]One-way analysis of variance, one-tailed test, α-level = .05.

[b]Areas compared are: Colin's Cove, North Cantilever, and the dredge.

[c]Areas compared are: Colin's Cove, North Cantilever, and Smuggler's Cove.

Table 13

Analysis of Substrate Difference Between Species[a]

Area	df	F-ratio	Reject Level	Ho
Colin's Cove[b]	2;268	55.51	3.033	Reject
North Canti-lever[b]	2;126	4.20	3.067	Reject
Smuggler's Cove[c]	1;117	1.32	3.924	Reject
Total[b]	2;563	98.93	3.00[d]	Reject

[a]One-way analysis of variance, one-tailed test, α-level = .05.

[b]Species compared are: *C. fastigiata, C. lingulata, C. nummaria.*

[c]Species compared are: *C. lingulata, C. nummaria.*

[d]Reject level listed is for infinity since interpolation was not possible with available tables.

Table 14

Analysis of Position Differences (on Top Versus Underneath)[a]

Species	North Cantilever df	North Cantilever χ^2	North Cantilever Reject Level	North Cantilever Ho	Smuggler's Cove df	Smuggler's Cove χ^2	Smuggler's Cove Reject Level	Smuggler's Cove Ho
C. fastigiata	1	12.812	3.8414	Reject	ND[b]	ND	ND	ND
C. lingulata	1	29.824	3.8414	Reject	1	15.056	3.8414	Reject
C. nummaria	1	9.308	3.8414	Reject	1	33.907	3.8414	Reject

[a] χ^2 evaluation: expected values equal, one-tailed test, α-level = .05.

[b] ND = no data.

Table 15

Substrate Comparison (Cliffs Versus Loose Rock)[a]

Species	df	χ^2	Reject Level	Ho
C. fastigiata	ND[b]	ND	ND	ND
C. lingulata	1	15.056	3.8414	Reject
C. nummaria	1	33.907	3.8414	Reject

[a]χ^2 evaluation, expected values equal, one-tailed test, α-level = .05.

[b]ND = no data.

Table 16

Analysis of Vertical Distributions[a]

Area	df	χ^2	Reject Level	Ho
C. fastigiata				
Colin's Cove	7	20.24	14.07	Reject
North Cantilever	2	1.56	5.99	Accept
Smuggler's Cove	ND[b]	ND	ND	ND
C. lingulata				
Colin's Cove	7	137.59	14.07	Reject
North Cantilever	2	24.40	5.99	Reject
Smuggler's Cove	7	25.81	14.07	Reject
C. nummaria				
Colin's Cove	7	157.57	14.07	Reject
North Cantilever	2	9.38	5.99	Reject
Smuggler's Cove	7	63.58	14.07	Reject

[a]χ^2 evaluation: expected values equal, one-tailed test, α-level = .05.

Table 17

Regression Analysis on Numbers per 1/16 m^2 Versus Percent Loose Rock[a]

Area	df	TS	Reject Level	r^2	Ho
C. fastigiata					
Colin's Cove	6	7.52	±2.447	0.90	Reject
Smuggler's Cove	ND[b]	ND	ND	ND	ND
C. lingulata					
Colin's Cove	6	2.02	±2.447	0.41	Accept
Smuggler's Cove	6	2.78	±2.447	0.56	Reject
C. nummaria					
Colin's Cove	6	0.923	±2.447	0.12	Accept
Smuggler's Cove	6	1.91	±2.447	0.38	Accept

[a]Linear regression analysis, two-tailed t-test, α-level = .05.

[b]ND = no data.

Table 18

Regression Analysis on Numbers per 1/16 m^2 Versus Depth[a]

Area	df	TS	Reject Level	r^2	Ho
C. fastigiata					
Colin's Cove	158	0.8427	±1.975	0.005	Accept
North Canti-lever	10	0.4974	±2.228	0.02	Accept
Smuggler's Cove	ND[b]	ND	ND	ND	ND
C. lingulata					
Colin's Cove	158	3.1671	±1.975	0.06	Reject
North Canti-lever	10	0.2808	±2.228	0.008	Accept
Smuggler's Cove	30	0.4058	±2.042	0.006	Accept
C. nummaria					
Colin's Cove	158	-0.7952	±1.975	0.004	Accept
North Canti-lever	10	-7.0209	±2.228	0.29	Accept
Smuggler's Cove	30	-1.2160	±2.040	0.05	Accept

[a]Linear regression analysis, two-tailed t-test, α-level = .05.

[b]ND = no data.

Table 19

Size Comparisons Between Males and Females

Area	*C. fastigiata* df	TS	Reject Level	Ho	*C. lingulata* df	TS	Reject Level	Ho
Colin's Cove	184	22.71	±1.973	Reject	277	15.85	±1.9865	Reject
North Canti-lever	75	15.33	±1.9925	Reject	55	10.58	±2.004	Reject
Smuggler's Cove	ND	ND	ND	ND	69	5.42	±1.9945	Reject
Dredge	37	10.12	±2.027	Reject	ND	ND	ND	ND

Two-tailed t-test, α-level = .05.

ND = no data.

Table 20

Size Comparisons Between Areas[a]

Species	df	F-ratio	Reject Level	Ho
Males				
C. fastigiata[b]	2,193	5.96	3.04	Reject
C. lingulata[c]	2,112	0.14	3.09	Accept
Females				
C. fastigiata[b]	2,103	1.61	3.09	Accept
C. lingulata[c]	2,289	2.98	3.03	Accept

[a]One-way analysis of variance, one-tailed test, α-level = .05.

[b]Areas compared are: Colin's Cove, North Cantilever, Dredge.

[c]Areas compared are: Colin's Cove, North Cantilever, Smuggler's Cove.

Table 21

Size Comparisons Between Species[a]

Area	df	TS	Reject Level	Ho
Males				
Colin's Cove[b]	209	0.08	±1.972	Accept
North Cantilever[c]	72	0.40	±1.993	Accept
Females				
Colin's Cove[b]	252	5.14	±1.969	Reject
North Cantilever[c]	58	0.98	±2.002	Accept

[a]Two-tailed t-test, -level = .05.

[b]Species compared are: C. fastigiata and C. lingulata.

[c]Species compared are: C. fastigiata and C. lingulata.

Table 22

Regression Analysis on Size Versus Depth[a]

Area	df	TS	Reject Level	r^2	Ho
C. fastigiata					
Colin's Cove	196	2.68	±1.973	0.04	Reject
North Canti-lever	84	-1.31	±1.989	0.02	Accept
Smuggler's Cove	ND[b]	ND	ND	ND	ND
C. lingulata					
Colin's Cove	285	-0.56	±1.468	0.001	Accept
North Canti-lever	57	-0.66	±2.0025	0.0007	Accept
Smuggler's Cove	71	1.00	±1.9935	0.001	Accept
C. nummaria					
Colin's Cove	97	1.81	±1.9845	0.03	Accept
North Canti-lever	11	-1.44	±2.201	0.16	Accept
Smuggler's Cove	83	1.60	±1.989	0.03	Accept

[a]Linear regression analysis, two-tailed t-test, α-level = .05.

[b]ND = no data.

Table 23

Regression Analysis of Size Versus Rock Size (Substrate Size)[a]

Area	df	TS	Reject Level	r^2	Ho
C. fastigiata					
Colin's Cove	100	5.77	±1.984	0.25	Reject
North Canti-lever	61	0.54	±1.9975	0.005	Accept
Smuggler's Cove	ND[b]	ND	ND	ND	ND
C. lingulata					
Colin's Cove	102	2.48	±1.984	0.06	Reject
North Canti-lever	52	2.09	±2.007	0.08	Reject
Smuggler's Cove	12	-0.08	±2.179	0.0005	Accept
C. nummaria					
Colin's Cove	61	3.79	±1.9995	0.19	Reject
North Canti-lever	8	.26	±2.306	0.01	Accept
Smuggler's Cove	26	1.77	±2.056	0.11	Accept

[a]Linear regression analysis, two-tailed t-test, α-level = .05.

[b]ND = no data.

Table 24

Analysis of Sex Ratios for Each Species[a]

Area	*C. fastigiata* df	*C. fastigiata* χ^2	*C. fastigiata* Reject Level	*C. fastigiata* Ho	*C. lingulata* df	*C. lingulata* χ^2	*C. lingulata* Reject Level	*C. lingulata* Ho
Colin's Cove	1	31.05	3.841	Reject	1	52.48	3.841	Reject
North Cantilever	1	4.69	3.841	Reject	1	0.62	3.841	Accept
Smuggler's Cove	ND[b]	ND	ND	ND	1	48.88	3.841	Reject
Dredge	1	0.90	3.841	Accept	ND	ND	ND	ND

[a]χ^2 evaluation, expected values equal, one-tailed test, $\alpha = .05$.

[b]ND = no data.

Table 25

Analysis of Sex Ratio Differences Between Species[a]

Area[b]	χ^2	TS	Reject Level	Ho
Colin's Cove	1	79.92	3.841	Reject
North Canti-lever	1	4.10	3.841	Accept

[a]2xK contingency table, χ^2 analysis, one-tailed test, α-level = .05.

[b]Species compared at both areas are: C. *fastigiata* and C. *lingulata*.

Table 26

Analysis of Sex Ratio Differences Between Areas[a]

Species	χ^2	TS	Reject Level	Ho
C. *fastigiata*[b]	2	11.49	3.841	Reject
C. *lingulata*[c]	2	18.85	3.841	Reject

[a]2xK contingency table, χ^2 analysis, one-tailed test, α-level = .05.

[b]Areas compared are: Colin's Cove, North Cantilever, Dredge.

[c]Areas compared are: Colin's Cove, North Cantilever, Smuggler's Cove.

Table 27

Analysis of Differences Between Areas for Intraspecific Associations[a]

Species	df	χ^2	Reject Level	Ho
C. fastigiata[b]	2	11.3	5.99	Reject
C. lingulata[c]	2	1.20	5.99	Accept
C. nummaria[c]	2	4.52	5.99	Accept

[a] 2xK contingency table, χ^2 analysis, one-tailed test, α-level = .05.

[b] Areas compared are: Colin's Cove, North Cantilever, Dredge.

[c] Areas compared are: Colin's Cove, North Cantilever, Smuggler's Cove.

Table 28

Analysis of Sex Ratios for Intraspecific Associations[a]

Area	*C. fastigiata*				*C. lingulata*			
	df	χ^2	Reject Level[b]	Ho	df	χ^2	Reject Level[b]	Ho
Colin's Cove	1	0.07	3.841	Accept	1	3.0	3.841	Accept
North Canti-lever	1	1.64	3.841	Accept	1	0.167	3.841	Accept
Smuggler's Cove	ND	ND	ND	ND	1	0.00	3.841	Accept
Dredge	1	0.00	3.841	Accept	ND	ND	ND	ND

[a] χ^2 evaluation, one-tailed test, α-level = .05.

[b] Reject level for the lower tail is 98069 x 10^{-9}.

A COMPARATIVE STUDY OF SOME POPULATION CHARACTERISTICS OF *CALYPTRAEA FASTIGIATA* GOULD, *CREPIDULA LINGULATA* GOULD, AND *CREPIDULA NUMMARIA* GOULD (GASTROPODA, PROSOBRANCHIA)

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M.S. Degree, April 1975

ABSTRACT

A comparative study of the field populations of *Crepidula lingulata, Crepidula nummaria,* and *Calyptraea fastigiata* indicated all three preferred a rocky substrate but favored different size rocks. Their positions on the rocks varied but the greatest numbers were found attached to the undersides. *Crepidula lingulata* and *C. nummaria* preferred larger rocks and were found in intraspecific associations more often than *C. fastigiata* which preferred smaller rocks. These associations occurred with a 1:1 sex ratio; however, the overall population did not. *Crepidula lingulata* had a high female count and *C. fastigiata* a high male count. Males, of all three species, were smaller in size than females.

Leptasterias hexactis and *Evasterias troschellii* were found to be possible predators. Protection was afforded those attached to the undersides of rocks. All three species used the radula to remove irritants from under the shell including the tube feet of attacking sea stars.

COMMITTEE APPROVAL:

VITA