

A COMPARISON OF GASTROPOD SPECIES DIVERSITY AND
TROPHIC STRUCTURE IN THE ROCKY INTERTIDAL ZONE
OF THE TEMPERATE AND TROPICAL WEST AMERICAS

by

ALAN CHARLES MILLER

A DISSERTATION

Presented to the Department of Biology
and the Graduate School of the University of Oregon
in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy

March 1974

APPROVED: Peter W. Frank
Peter W. Frank

VITA

NAME OF AUTHOR: Alan Charles Miller

PLACE OF BIRTH: Trona, California

DATE OF BIRTH: June 9, 1945

UNDERGRADUATE AND GRADUATE SCHOOLS ATTENDED:

Stanford University
University of Oregon

DEGREES AWARDED:

Bachelor of Arts, 1967, Stanford University
Master of Arts, 1968, University of Oregon

AREAS OF SPECIAL INTEREST:

Marine Ecology
Invertebrate Zoology
Community Trophic Structures

PROFESSIONAL EXPERIENCE:

Research Assistant, Department of Biology, University of Oregon,
1967-1968

Graduate Teaching Fellow, Department of Biology, University of
Oregon, 1968-1970, 1971-1973

AWARDS AND HONORS:

National Science Foundation Undergraduate Research Participation
Program, 1966

National Science Foundation Graduate Research Training Program,
Biology of Molluscs course, Hawaii, 1968

Organization for Tropical Studies Tropical Marine Biology course,
Jamaica and Panama, 1970

Atomic Energy Commission Grant for research at Eniwetok Atoll,
1970, 1971, 1973

Society of Sigma Xi Grants in Aid of Research, 1971

National Science Foundation Grant for Improving Doctoral
Dissertation Research in the Field Sciences, 1971-1972

PUBLICATIONS:

Miller, A. C., 1968. Orientation and movement of the limpet
Acmaea digitalis on vertical rock surfaces. Veliger 11
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feeding of Morula uva (Bolton) and Morula granulata (Duclos)
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(Abstract). In: Bakus, G.J. (editor), 1972. Marine studies
on the north coast of Jamaica. Atoll Research Bulletin 152:4-5

ACKNOWLEDGMENTS

The travel and equipment expenses were provided by the National Science Foundation Grant GA 29340, a Society of Sigma Xi Grants-in-Aid of Research award, the Department of Biology, University of Oregon, and the Alan and Susanne Miller Education Fund.

I thank my advisor Peter Frank for the time and assistance that he always willingly gave during my graduate years and in the preparation of this thesis. His optimism about life in general was inspirational. The thoughtfulness and hospitality provided by Marion and Peter Frank are also appreciated.

The time and advice provided by Robert Tate, Robert Terwilliger, Paul Rudy, Bayard McConnaughey, Local Board 145, Fred Bernstein, Tom Niesen, Snee Miller, and John Cubit helped in the completion of this study.

Special thanks are due to my wife Susanne who helped me during all stages of this study with advice and encouragement. She also served as a stabilizing force whenever my plans for adventures got unreasonable.

Thanks are also due to the ladrones for only taking our money and not our lives that night near Los Mochis, Mexico.

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INTRODUCTION

Many taxa of plants and animals tend to have an increasing number of species along a decreasing latitudinal gradient. This increased species diversity in the tropical regions compared to temperate areas has been reviewed by Fischer (1960) and has been discussed for mammals (Simpson, 1964; Fleming, 1973), plants and insects (Janzen, 1959, 1970), lizards (Pianka, 1967), birds (MacArthur, 1964; Recher, 1969), and gastropods (Therson, 1952; Kohn, 1971). Most of the authors before 1960 used compilations of zoogeographic lists to compare diversity and only in recent years have studies been done on similar, local habitats in the temperate and tropical zones.

Simpson (1964) says that the species diversity comparisons made by combining large geographic areas in the tropics or temperate zones are affected by two components: the number of habitats encompassed by the sample and the changes caused by ecological processes within habitats. For example, as Pianka (1966) indicates, Costa Rica has a whole range of habitats from low altitude tropical to middle altitude temperate to high altitude boreal. As one goes further north to higher latitudes, some of these habitats no longer exist so that the presence of more species in Costa Rica, as a geographic whole, is not surprising. The interesting question is that of what ecological processes allow more species to co-occur in tropical habitats than co-occur in similar habitats in the temperate zones.

The theories that have been suggested as possible explanations for the increased tropical diversity have been reviewed by Pianka (1966), using mostly zoological examples. Baker (1970) has commented on Pianka's review using botanical studies. Briefly, the theories are:

THE ECOLOGICAL AND EVOLUTIONARY TIME THEORY: The species diversity of a region is assumed to increase over time, and since the tropics have had more time to recover from major geological disturbances than have the temperate areas which have had recent glaciation, there should be more species in the tropics. Pianka (1966) cites evidence to cast doubt upon the plausibility of this theory, but Baker (1970) provides evidence from plants that suggests this theory may be important.

THE THEORY OF SPATIAL HETEROGENEITY: There might be a general increase in environmental complexity (i.e., more microhabitats) as one proceeds towards the tropics. The more heterogeneous a habitat is, the more diverse the flora and fauna should be since more different microhabitats exist to be exploited.

THE COMPETITION HYPOTHESIS: Natural selection in high latitudes is controlled mostly by the rigorous physical environment. In the tropics it is assumed that vagaries of the weather and other physical forces are not as severe and that the increased packing of species will be accommodated by biological interactions. The biological control of natural selection should produce smaller niche dimensions, such as more restricted food and microhabitat choices, thus allowing

more species to coexist.

THE CLIMATIC STABILITY THEORY: The regions with stable climates can allow the evolution of finer adaptations than those areas where the climate is more unpredictable because an organism must be more generalized to survive a wide range of variation. Finer adaptations can allow more species to divide up the resources differently. Also, a more stable climate could allow species to survive even if they were rare. If a unit of habitat can support the same number of individuals in the temperate and tropical regions, there could be more rare species in the tropical habitats.

THE PRODUCTIVITY HYPOTHESIS: The region with the greater productivity should have the higher species diversity. Pianka and Baker dwell at length on the evidence against this theory. Connell and Orias (1964) modify this theory by incorporating it into the climatic stability theory which makes it more plausible.

RATES OF SPECIATION VERSUS EXTINCTION THEORY: Baker (1970) argues that there are high rates of speciation and extinction under unstable conditions. In the tropics there are stable areas, like rain forests, near the unstable areas that can absorb some of the new species and prevent their rapid extinction; this increases the overall diversity.

THE PREDATION THEORY: Paine (1966a) proposes that there are more predators in the tropics which control the numbers of prey populations. This reduces the competition among the prey species. The reduced

competition among the prey for resources should allow additional species to exist at this trophic level which in turn may support different predator species. This contradicts the competition theory which says increased competition for resources rather than decreased competition increases diversity.

Some of the above theories overlap, and for any given situation the diversity observed may be a function of several of these concepts. Some recent studies have been directed to testing some of these theories.

There have been studies on several different taxa concerning the correlation of spatial heterogeneity with some measure of species diversity. Species diversity increases as the structural complexity of the habitat increases for birds (MacArthur, 1964; MacArthur, Recher, and Cody, 1966; Recher, 1969; Karr, 1971; Karr and Roth, 1971), for the gastropod genus Conus (Kohn, 1967), for some lizards (Pianka, 1967), for stream fish (Sheldon, 1968), and for some insects (Murdoch, Evans, and Peterson, 1972). In the bird studies foliage height categories were used to quantify the habitat structure for the communities. For the American lizards that Pianka (1967) studied, both vegetational vertical complexity and horizontal complexity (as measured by local distribution patterns of individuals of the plant species) correlated positively with lizard diversity. Kohn (1967, 1968) compared intertidal and subtidal substrates which differ in consistency and vertical complexity with the species diversity and density of individuals for one genus, Conus, of the coral reef

community in the tropics. Both the loose coral sand substrate and the flat limestone bench habitats have fewer Conus species than does the topographically complex subtidal coral reef habitat. However, the intertidal bench has a higher density of individuals. Kohn did not look at the gastropod community diversity as a whole; thus the relationship of the total diversity to these factors is unknown.

Some studies, however, suggest that structural diversity considered alone is not the best explanation for increased diversity. Pianka (1969) concludes that the total number of lizard species in Australian deserts is not explained by environmental structure alone, but also by climate and history. Fleming (1973) feels that the increase in diversity of forest bats in the tropics is qualitatively related not to vegetational structural heterogeneity, but appears to be due to utilization of new food resource bases such as fruit, nectar, blood, and animal matter. Temperate zone bats are primarily insect eaters. Orians (1969) concludes that although the birds he studied in tropical forests appeared to divide the habitat into finer vertical layers than similar temperate species, the presence of bird species which utilize different foods and foraging techniques than do birds in the temperate zone may be important too. The increase in tropical snake diversity is highly correlated with the increase in prey species (Arnold, 1972), and this is enough to explain most of the latitudinal variation. Arnold (1972) suggests that the number of prey species may be the most proximate variable influencing lizards in Pianka's studies rather than vegetational height or volume since

most lizards are carnivores.

Paine (1966a, 1971) and Porter (1972) working with marine systems where starfish are important predators and Harper (1969) in field situations with sheep as the dominant herbivora give evidence to support the theory that key predators can prevent resource monopolization (space in these studies) by a few species of prey so that more species can coexist in the system. If, in the absence of predators, these communities were allowed to reach higher successional stages, space could be monopolized by one or a few species (Auclair and Goff, 1971), but through the action of predators, the space monopolizing prey species populations are disrupted.

Paine (1966a, 1971) proposes that this control of community structure by predators may occur generally and says that the tendency for there to be more carnivorous species in the tropics would support this predation theory. The trend for increases in the relative number of carnivorous species along latitudinal diversity gradients exists in marine gastropods (Paine, 1966a; Keen, 1971), in zooplankton (Grice and Hart, 1962), and lizards (Pianka, 1967). However, if the number of potential prey species alone can cause an increase in predator species diversity as suggested by the studies of Arnold (1972) and Fleming (1973), then Paine's predation hypothesis might not be applicable to all taxa (Fleming, 1973). Also, as Moynihan (1971) has pointed out, on gross geographic terms, the relative number of species of eagles, hawks, and owls and terrestrial and fresh water Carnivora in the north temperate zone is either higher than or similar

to that of equivalent areas in the tropics. So the relative trend of greater numbers of carnivores in diverse tropical areas may not be true for all taxa.

Although there is greater marine gastropod species diversity in the tropical West Americas than in the temperate regions (Keen, 1971), both Paine (1966a) and Bakus (1967) report unexpectedly low gastropod diversity in some local intertidal areas which were examined qualitatively in Costa Rica.

The general purpose of this study was to examine quantitatively local rocky intertidal areas in Oregon, Mexico, and Costa Rica in order to compare the local species diversity and trophic structure of gastropod communities. The study is broken into sections seeking to provide answers to the following questions:

- A. How do exposed coast rocky intertidal areas in the temperate and tropical West Americas compare in relation to their gastropod and chiton community structure?
- B. Are there any physical factors that can be correlated with overall gastropod and chiton species diversity in temperate and tropical rocky intertidal areas?
- C. How is the increased species packing accomplished:
 1. Is there an increase in the "between habitat" component of diversity as predicted by MacArthur (1965), or are "within habitat" forces operating?
 2. Can the increase in diversity in the tropics be related to

the large increase in carnivorous gastropod species as suggested by Paine's hypothesis?

SITE DESCRIPTIONS AND METHODS

The localities of the transects are described in Table I, and Figures 1 and 2 are pictures of four transects comparing the general topography. Costa Rica was chosen as the tropical study area because the tidal ranges there are similar to those in Oregon (cf. U.S. Dept. of Commerce Tide Tables). The site in Mexico was picked to compare the tropical rocky intertidal communities in an area with a 1 m tidal range with the Costa Rican areas with a 3 m range. The Oregon transects were studied in the Spring and Summer of 1970, 1971, and 1972; the Costa Rican transects in January and February of 1972; and the Mexican transect in January, 1971.

Four of the six Oregon transects were made at Cape Arago State Park near Charleston, Oregon. Transects were done in North, Middle, and South Coves in order to sample areas with different wave exposures and topographies. The other two transects were made on the north-facing side of Cape Blanco which is approximately 15 miles north of Port Orford, Oregon.

The transect in Mexico is at Puerto Angelito, a small cove below the airfield at Puerto Escondido in the state of Oaxaca. Most of the rocky areas along this region of the Mexican coast consist of cliffs dropping into about 3 m of water so that it is difficult to find a rocky intertidal area with a horizontal component.

TABLE I. STUDY SITE DESCRIPTIONS

LOCALITY	LATITUDE	TIDAL RANGE	TRANSECT NAME (ABBREVIATION)	GENERAL DESCRIPTION	ROCK TYPE
Cape Arago, Oregon, U.S.A.	43.32°	2.1m	North Cove (NC)	cliff with high splash pool	sedimentary
			Middle Cove 1 (MC1)	ledge area with no loose boulders	" "
			Middle Cove 2 (MC2)	boulder field	" "
			South Cove (SC)	bedrock with outcrops and loose boulders	" "
Cape Blanco Oregon, U.S.A.	42.50°	2.2m	Cape Blanco 1 (CB1)	bedrock with outcrops and loose boulders	metamorphic
			Cape Blanco 2 (CB2)	bedrock with outcrops and loose boulders	" "
Puerto Escondido, Caxaca, Mexico	16.25°	0.8m	Puerto Escondido (PE)	ledge area with large tide pool and a few loose boulders	slightly metamorphic
Playa Hermosa, Guanacaste, Costa Rica	10.50°	2.7m	Playa Hermosa 1 (PH1)	bedrock with outcrops and loose boulders	basaltic
			Playa Hermosa 2 (PH2)	bedrock with outcrops and loose boulders	" "
			Playa Hermosa 3 (PH3)	bedrock with outcrops	" "

Sámara,
Guanacaste,
Costa Rica

9.87°

2.7m

Sámara 1 (S1)

flat bedrock, outcrops,
and loose boulders

slightly
metamorphic

Sámara 2 (S2)

flat bedrock, outcrops,
and much algal turf

" "

Sámara 3 (S3)

flat bedrock with
outcrops and tidepools

" "

Quépos,
Puntarenas,
Costa Rica

9.45°

2.5m

Quépos 1 (Q1)

large boulders

basaltic

Quépos 2 (Q2)

bedrock with outcrops
and loose boulders

" "

FIGURE 1. Photographs of the Oregon transects at
North Cove (left) and Middle Cove 1 (right).

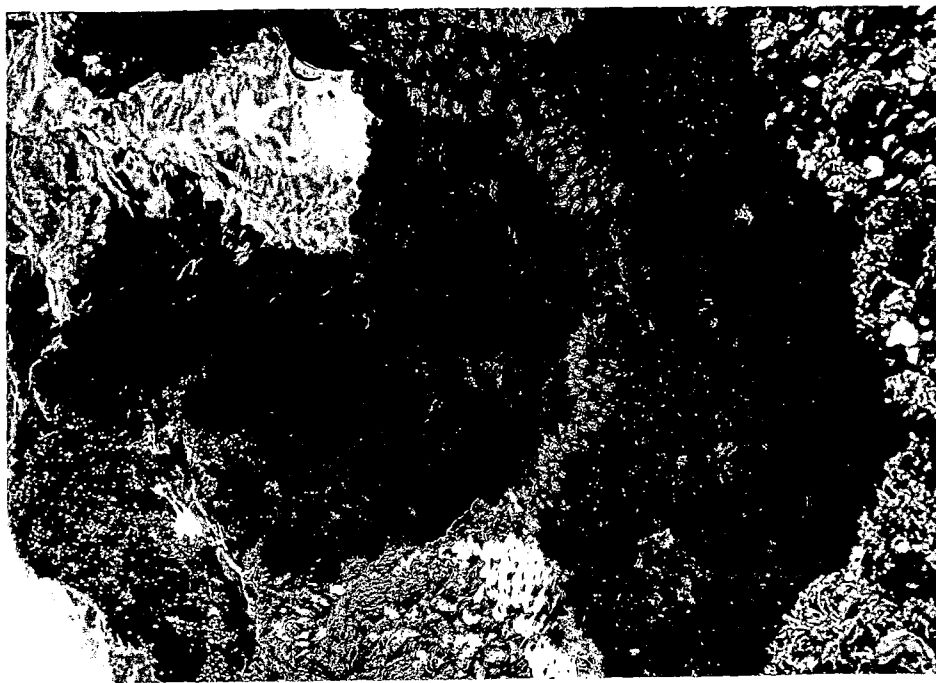
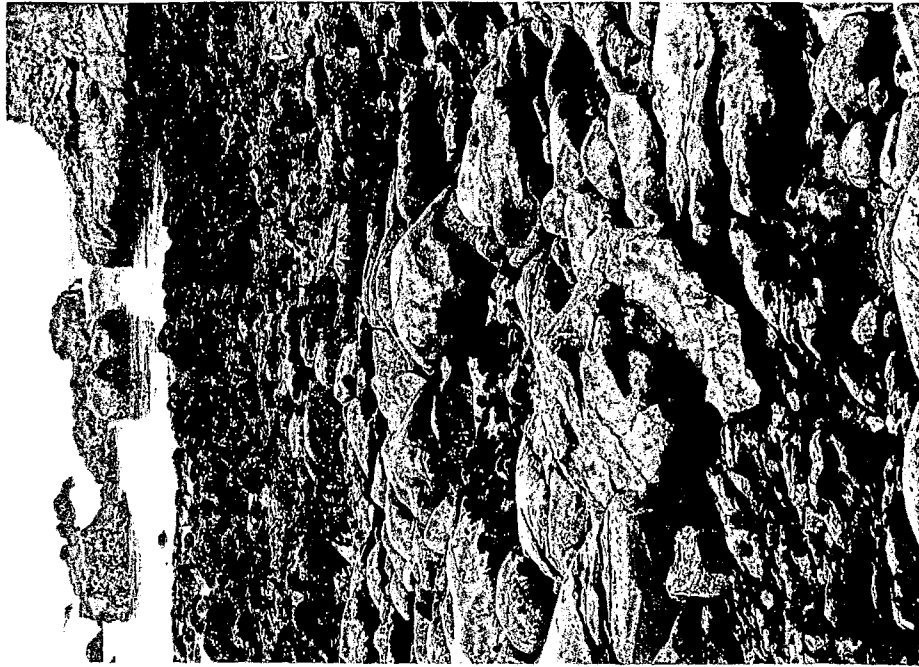
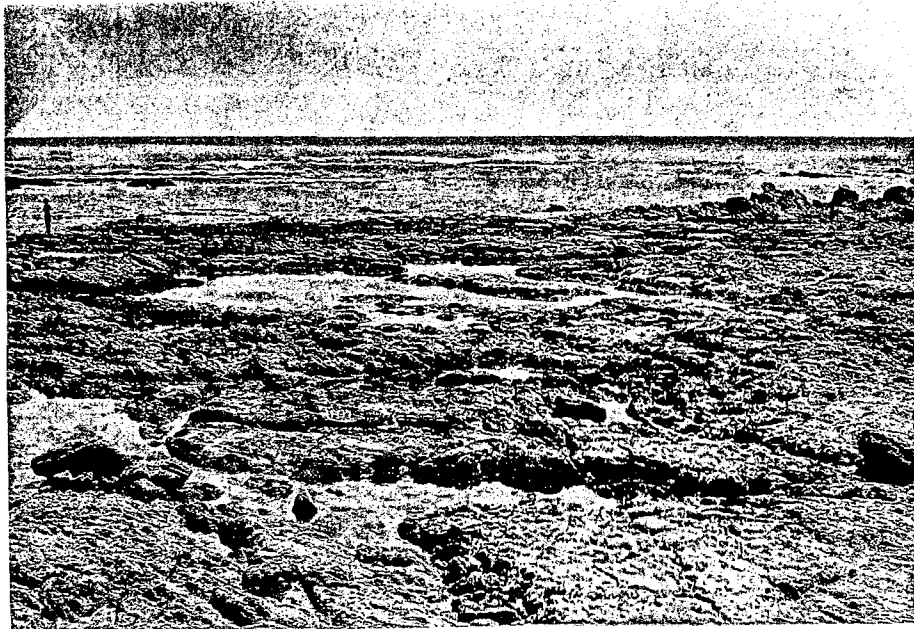
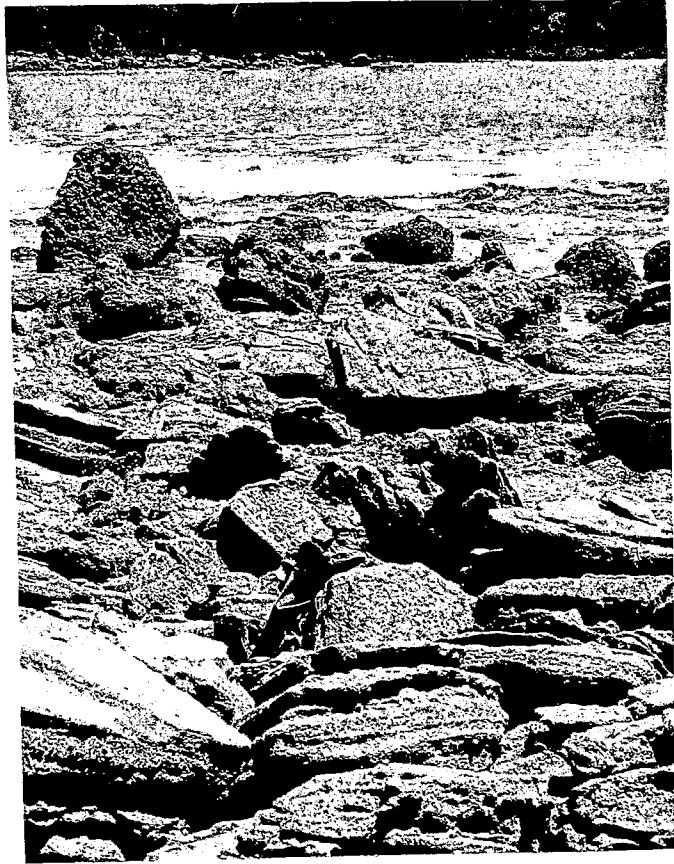


FIGURE 2. Photographs of the Costa Rican transects
at Quépos 2 (top) and Samara 2 (bottom).



At Playa Hermosa, a resort in a small bay about 7 miles north of El Coco (Playas del Coco), Guanacaste, Costa Rica, Hermosa 1 and Hermosa 2 transects were made on the southern side of the bay and Hermosa 3 on the more exposed northern side to sample differences in wave exposure. This area and Sámara are in the dry region of Costa Rica. The village of Sámara is 3 hours by automobile toward the coast from the town of Nicoya, Guanacaste, Costa Rica. An extensive intertidal flat is mostly protected by shallow rock reefs just offshore. The three transects here were picked in areas that differed in topography and in protection from waves by the reefs. The last two transects in Costa Rica were done at Playa Manuel Antonio, a small cove south of Quepos. Quepos 1 is on the southern side of the cove and Quepos 2 on the northern. This particular region is very wet with abundant terrestrial vegetation.

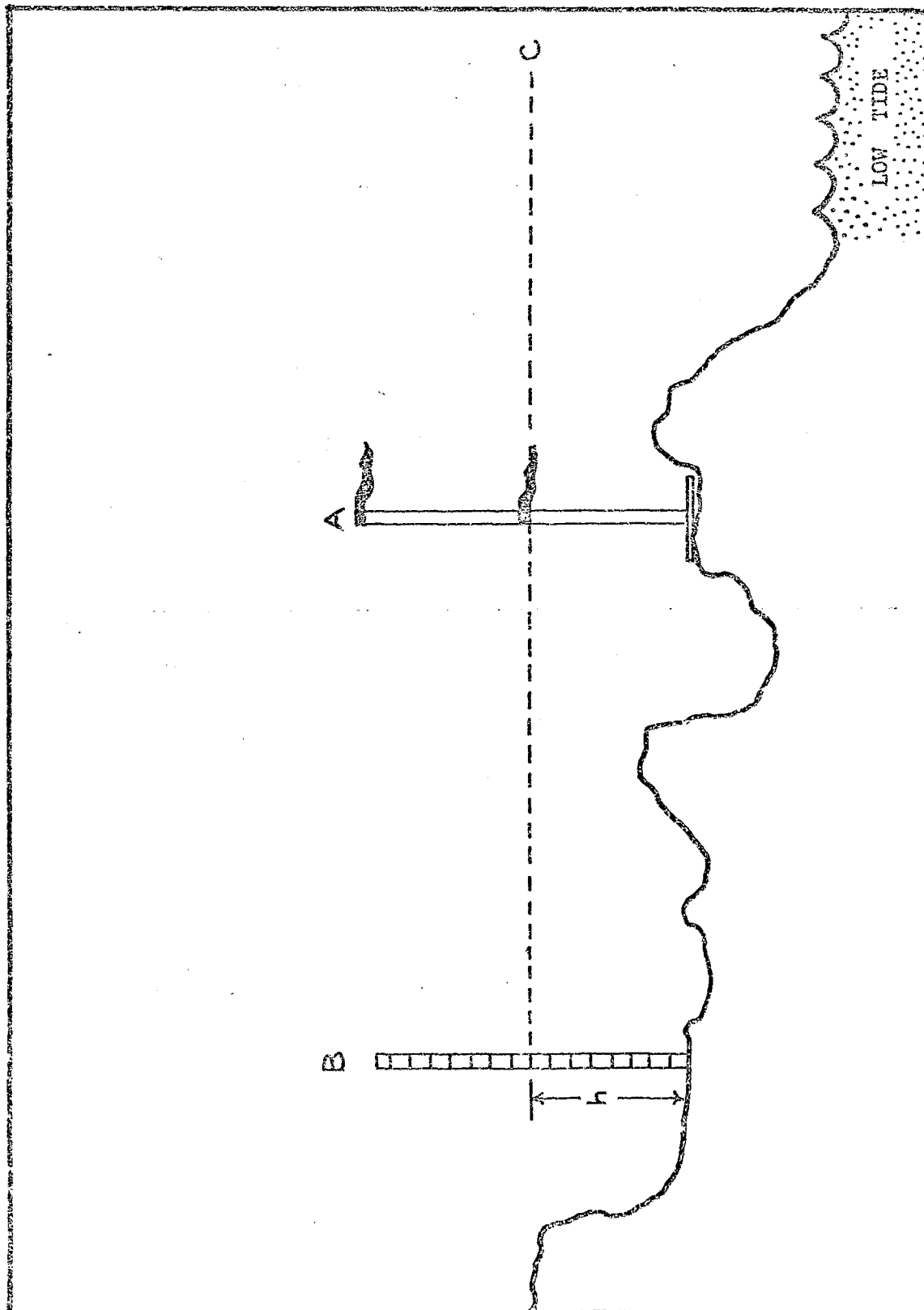
At each locality a general area was chosen that differed from the other transect areas in the immediate locality in terms of wave exposure and/or general topographic appearance. The base point for each transect was determined in the following fashion: a point was marked at the high tide drift line and the base point was placed a number of meters (between 0 and 50) chosen from a random numbers table from this point parallel to the high tide line. If the point picked sited a line perpendicular to the high tide line which crossed terrain impossible to sample (i.e., a big cliff), another random number was chosen. The transect was layed out by stretching taut a metric tape from the base point toward the water's edge at low tide.

The topography was quantified at 20 cm intervals within each meter sampled along the tape by using a surveying method to determine the height of the substratum in relation to a 0 m tide. The surveying method (Figure 3) consisted of a stationary (A) and a moving pole (B). The stationary pole was marked with one flag 1 m from the bottom of the pole and another flag 2 m from the bottom, while the moving pole was marked in 5 mm intervals from the bottom. Pole A was fixed in the lower intertidal and pole B was placed on the substratum next to the position on the tape at which a height reading was desired. Whatever point on pole B that visually lined up with one of the flags on pole A and the horizon (C) was the height reading (h) in cm for that position. When the tide had reached its lowest point for the day as determined from the U.S. Dept. of Commerce tide tables, the height of the base of the reference pole A above the water level was directly measured and the height readings were corrected accordingly.

The accuracy of the height of the low tide is limited by the atmospheric pressure, surf conditions, and the accuracy of the tide tables themselves. One major problem with comparing tidal heights between Costa Rica and Oregon is that 0 m tide is Mean Lower Low Water in Oregon, but it is based on Mean Low Water Spring Tides in Costa Rica. This means that the 0 m reference point in Costa Rica is actually lower than the same point in Oregon. Topographic profiles made for the transects using this method appear in Appendix 1.

Gastropods, chitons (hereafter lumped under the term gastropod), and asteroids were sampled by placing 1 m² quadrats across the transect

FIGURE 3. Diagram of the intertidal height survey method. See text for details.



line at arbitrarily set intervals according to the length of the transect and the time available to complete the work. For instance, South Cove was sampled for animals and height measurements every meter along the transect line while at Samera 3 the interval was every 5 m. Within each quadrat all starfish and snails, chitons, and nudibranchs were counted. Vermetids and octopuses, which occur in all the areas, were ignored. Due to difficulties in differentiating the numerous small Fossarius sp. from the similarly shaped and marked Littorina aspera in Costa Rica, these species were lumped. Similarly, Acmaea paradigitalis, which resembles A. digitalis in Oregon, were counted as A. digitalis in the Oregon transects. When Littorina spp. and Acmaea spp. occurred in high numbers, they were counted by randomly placing six 10 cm² quadrats within the 1 m² quadrat and the density per square meter was extrapolated from the average of these counts.

Although the positions of the species were also noted (under rocks, on top of rocks, etc.), it is important to remember that these positions were only for low tide periods; the positions at high tide for most tropical species are unknown to this author.

The prey of the carnivorous gastropods were determined from field observations and by collecting individuals in the field, isolating them in containers of sea water for up to 24 hrs, and then examining fecal pellets for prey hard parts with a microscope. Polychaetes, gastropods, chitons, most sipunculids, sponge, and barnacles and other crustaceans all have identifiable hard parts which are egested by the predator.

The volume of the gastropod and chiton species was estimated from shell measurements of representative individuals collected by the author (Appendices 4 and 5). This is a crude estimate of biomass and is only meant to provide a way of comparing relative, not average, sizes of the various species. I predict that if the actual biomass of each species were used, the trends would be similar to those found using the species volume estimates.

Species diversity was measured by simple species number, the Shannon-Wiener Information Statistic ($H' = -\sum_{i=1}^S p_i \log_e p_i$ where p_i is the proportion of the total of the i th category and S is the total number of categories (Pielou, 1966)), and H' VOLUME (using volume instead of individuals in the H' equation (Willim, 1968)). Because there is so much controversy regarding what statistic is a valid measure of species diversity and whether any of these statistics tell us anything biologically useful (Wager, 1972; Sanders, 1968; Huribert, 1971), I have chosen to refer primarily to the simple number of species when talking about species diversity in this paper. Another reason for using the number of species is that there are some rare species which are found regularly and which are important biologically to the community, but which are underemphasized using other diversity statistics (Pianka, 1966).

The index suggested by Whittaker (1960) to compare the similarity of groups of objects is used to compare the species makeup of pairs of transects. This index is defined as: $I = 1 - 0.5 \left(\sum_{i=1}^S a_i - b_i \right)$ where a_i is the proportion of species i of all species in transect A, b_i

the proportion in transect B, and s is the total number of species. The index has a value of 1.0 for complete similarity and 0.0 for complete dissimilarity.

The gastropod and chiton species identifications (Appendices 2 and 3) were made using McLean (1969), Keen and Doty (1942), and Rice (1971) for the Oregon species and Keen (1971) for the Costa Rican and Mexican species. Dr. James McLean at the Los Angeles County Museum also assisted me by identifying the turrids from Costa Rica and some of the uncommon Oregon species.

GASTROPOD COMMUNITY STRUCTURE COMPARISONS

The results of gastropod species diversity, abundance, and estimated volume appear in Table II and the herbivore-carnivore relationships for the different transects appear in Table III. Only the transects in Oregon and Costa Rica were compared statistically since the Puerto Escondido transect was sampled using 2 m^2 instead of 1 m^2 quadrats and the tidal range and the species pool are different from Costa Rica. The significantly lower similarity coefficients (Table IV) of the Mexico-Costa Rica comparisons compared to those occurring among Costa Rica-Costa Rica groupings ($t=3.088$, $P < .05$, 2 tail test) suggest that the species pools are somewhat different, probably because Costa Rica is several hundred miles south of Puerto Escondido, Mexico.

There is much variation in the total number of species, individuals, and densities of gastropods among the different transects in Oregon and Costa Rica; consequently, there is no significant difference between the temperate and tropical transects with respect to these three variables (Table II). Differences in species diversity as measured by H' are not significant either; however, the H' VOLUME measure is significantly higher in the Costa Rican transects. This is probably because the large carnivores occurring in small numbers now have a greater contribution to the diversity statistic than the numerous but smaller herbivore species. The reverse trend is true

TABLE II. COMPARISON OF SPECIES DIVERSITY, DENSITY, AND VOLUME OF GASTROPODS AND CHITONS IN EACH TRANSECT

	OREGON						COSTA RICA						MEXICO			
	NC	MC1	MC2	SC	CE1	CB2	PH1	PH2	PH3	S1	S2	S3	Q1	Q2	Oregon: Costa Rica Student's t	PE
Number of Species	13	18	28	36	19	22	27	28	15	33	34	29	38	26	1.471	42
Total Number of Individuals	486	1160	2400	9577	2711	1817	4780	708	1363	1125	711	1100	642	166	1.177	701
Number of m ² Quadrats	8	14	14	51	19	13	14	15	13	23	25	32	14	9		38
Gastropod Density per m ²	61	83	171	188	143	140	341	47	105	49	28	34	46	18	1.105	18
Estimated Total Volume per m ² (cc)	244	150	144	255	69	94	32	19	12	15	8	13	26	13	4.545**	24
H' ¹	1.28	1.52	1.26	1.55	1.04	1.63	1.23	2.25	0.83	1.71	2.12	1.84	2.49	2.41	2.121	2.66
H'VOLUME ¹	0.66	1.14	1.37	1.60	1.61	1.70	2.15	2.05	1.58	2.17	2.44	1.93	2.52	2.06	4.008**	1.28

*P < .05, 2 tail test

**P < .01, 2 tail test

¹ calculated using log_e

TABLE III. COMPARISON OF THE PROPORTION OF HERBIVOROUS AND CARNIVOROUS GASTROPODS AND CHITONS IN EACH TRANSECT

	OREGON						COSTA RICA						MEXICO			
	NC	MC1	MC2	SC	CB1	CB2	PH1	PH2	PH3	S1	S2	S3	Q1	Q2	Oregon: Costa Rica Student's t	PE
Number of Herbivorous Species	10	12	20	22	12	14	14	17	10	22	21	13	20	13	0.496	16
Herbivore Proportion of Total Individuals	.94	.97	.97	.94	.94	.95	.93	.63	.95	.85	.67	.46	.73	.72	3.995**	.68
Herbivore Proportion of Total Volume	.99	.98	.98	.96	.91	.92	.76	.69	.49	.61	.51	.28	.64	.52	8.188**	.73
Number of Carnivorous Species	3	6	8	14	7	8	13	11	5	11	13	16	18	13	2.406*	26
Carnivore Proportion of Total Individuals	.06	.03	.03	.06	.06	.05	.07	.37	.05	.15	.33	.54	.27	.28	3.992**	.32
Carnivore Proportion of Total Volume	.01	.02	.02	.04	.09	.08	.24	.31	.51	.39	.49	.72	.36	.48	8.188**	.27
Herbivore spp. to Carnivore spp. Ratio	3.3	2.0	2.5	1.6	1.7	1.8	1.1	1.5	2.0	2.0	1.6	0.8	1.1	1.0	2.460*	0.8

*P < .05; 2 tail test
**P < .01; 2 tail test

for the volume of gastropods and chitons per square meter: the temperate zone transects have higher values than those from Costa Rica in all cases. This may be due to the large sized herbivorous chitons and numerous, relatively large Tegula funebris found in the Oregon transects.

Although there appears to be no statistical difference between the average number of species found in the Oregon and Costa Rican transects, the species pool (total species) for Oregon (44) is much smaller than that of the Costa Rica samples (75). If the Mexico transect is included with Costa Rica, the joint species pool would increase to 96. Thus there is an increase in gastropod diversity with decreasing latitude when large geographic areas are considered.

The carnivorous species form 41%, 52%, and 51% among the Oregon, Costa Rican, and Mexico-Costa Rican species pools respectively. On the basis of the sampling, there is no difference in the number of herbivorous species between Oregon and Costa Rica, but there is a significant difference in the number of carnivorous gastropod species, with most of the Costa Rican transects having more carnivores than most of the Oregon ones (Table III). The results for the herbivore to carnivore ratios also indicate this trend. The herbivores make up a larger proportion of the number of individual gastropods and the volume in the temperate zone. The much larger contribution by the carnivores in Costa Rica to the volume of gastropods than to the number of individuals is due to the fact that many of the carnivorous species are larger than carnivores occurring in

Oregon (cf. Keen, 1971).

The presence of more rare species in the tropical transects is not firmly confirmed by these data. Most of the Costa Rican transects have a larger (although not significantly) percentage of species unique to that transect and significantly lower percentages of ubiquitous species (species occurring in all but one transect) than the Oregon transects (Table V).

If there are more rare species in Costa Rica, one would expect to find that when comparing two tropical transects the number of species not found in both would be higher than in a pair of Oregon transects. This was measured by computing coefficients of similarity (Whittaker, 1960) between all pairs of transects (Table IV). The Oregon transects have significantly higher similarities than the Costa Rican ones ($t=2.665$, $P < .05$, 2 tail test).

The case against more rare species occurring in the tropical transects is supported by Table VI and Figure 4. Karr and Roth (1971) defined a rare bird species as one whose individuals make up less than 2% of the community. Although this method is probably not useful for snail populations because some species are super-abundant, it was applied to my data to see what would happen (Table VI). There is no significant difference between Oregon and Costa Rica with regard to the percent of species comprising less than 2% of the total individuals in each transect ($t=0.120$, $P > .05$, 2 tail test) nor is there a difference in the percent of total individuals made up of "rare" species ($t=0.750$, $P > .05$, 2 tail test).

TABLE V. PROPORTION OF UNIQUE AND UBIQUITOUS (APPEARING IN ALL
TRANSECTS EXCEPT ONE) SPECIES IN EACH TRANSECT

Transect	Proportion of species unique to transect	Proportion of ubiquitous species
North Cove	.08	.69
Middle Cove 1	.06	.72
Middle Cove 2	.07	.50
South Cove	.19	.42
Cape Blanco 1	.05	.79
Cape Blanco 2	.04	.64
Playa Hermosa 1	.11	.30
Playa Hermosa 2	.11	.28
Playa Hermosa 3	.13	.47
Sámara 1	.13	.24
Sámara 2	.15	.21
Sámara 3	.10	.17
Quépos 1	.13	.21
Quépos 2	.08	.27
Oregon: Costa Rica Student's t	1.789	5.419*

*P < .01; 2 tail test

TABLE VI. THE RELATIVE RARENESS OF SPECIES IN OREGON AND COSTA RICAN TRANSECTS AS DEFINED BY KARR AND ROTH (1971)

TRANSECT	PROPORTION OF SPECIES WITH LESS THAN 2% OF THE TOTAL NUMBER OF INDIVIDUALS	PROPORTION OF THE TOTAL NUMBER OF INDIVIDUALS THAT ARE RARE SPECIES
NC	.54	.02
MC1	.67	.06
MC2	.86	.09
SC	.89	.14
CB1	.79	.08
CB2	.68	.06
PH1	.85	.05
PH2	.64	.09
PH3	.73	.02
S1	.79	.11
S2	.85	.18
S3	.79	.06
Q1	.71	.11
Q2	.65	.15

The regression lines for the number of species represented by one individual in a quadrat versus the total number of species in that quadrat (Oregon: $Y = 0.425X - 0.791$; Costa Rica: $Y = 0.430X - 0.245$) are not significantly different ($t=0.103$, 263 d.f., $P > .05$, 2 tail test). The results of this test also suggest that rare species occur with the same frequency in both cases.

The major problem with defining a rare species from the data is that the truly rare species may not have been sampled. Also, owing to such high numbers of some herbivorous snails like Littorina spp., it is very easy for most snails which occur in small numbers but which are frequently encountered to be less than 2% of the total individuals. The similarity of transects would also be expected to be lower in Costa Rica than in Oregon if the distributions of some species were patchy due to a specialization on some resource which is itself patchy.

Table VII shows that carnivores form the highest percentage of the unique species in both areas while herbivores are the most ubiquitous species. This may be in part due to the trophic pyramid effect, i.e., that there are relatively fewer individual carnivores compared to herbivores in a system because of energy losses from the herbivore through the carnivore trophic levels.

TABLE VII. THE RELATIVE CONTRIBUTION OF HERBIVOROUS AND CARNIVOROUS SPECIES TO THE NUMBER OF UNIQUE AND UBIQUITOUS SPECIES

	UNIQUE SPECIES		UBIQUITOUS SPECIES	
	OREGON	COSTA RICA	OREGON	COSTA RICA
PROPORTION OF HERBIVORES	.38	.37	.73	.88
PROPORTION OF CARNIVORES	.62	.63	.27	.12

SPECIES DIVERSITY AND PHYSICAL PARAMETER RELATIONSHIPS

Previous studies on birds and lizards suggest that for some communities certain physical parameters can be used to predict species diversity; therefore the relationship of species diversity to various physical parameters measured for the rocky intertidal transects was examined. The parameters used in this study are: wave exposure, the proportion of sample quadrats in the mid and low intertidal zone, the latitude of the transect, the proportion of sample quadrats containing the undersides of rocks as habitats, and two measures of topographic relief (Table VIII).

The degree of exposure of an intertidal area to wave shock is important in determining what kinds of organisms occur there (Lewis, 1964; Ricketts, Calvin, and Hedgpeth, 1968); therefore I made qualitative estimates of wave exposure for each transect. The resulting ranks (1 receives the lowest wave shock relative to the other transects; 5 the highest) appear in Table VIII. The surf was calm at all the Costa Rican sites during these studies so I had less of an idea of relative exposure there than at Oregon.

The less time an area is uncovered by the water, the less time it is exposed to the drying effects of the sun and air and the less chance there is of exposure to fresh water. For these reasons there should be more species in the mid and low intertidal zones which are uncovered less frequently than the high zone (Ricketts, Calvin, and

TABLE VIII. SUMMARY OF THE PHYSICAL PARAMETER MEASUREMENTS
FOR THE OREGON AND COSTA RICAN TRANSECTS

TRANSECTS	WAVE EXPOSURE	PROPORTION OF QUADRATS IN MID AND LOW ZONE	LATITUDE	PROPORTION OF QUADRATS WITH UNDERSIDES OF ROCKS	PROPORTION OF POSSIBLE CHANGES IN SLOPE DIRECTION	H' RELIEF
North Cove	5	.27	43.32 ^o	.00	.34	1.76
Middle Cove 1	4	.38	"	.14	.23	1.86
Middle Cove 2	2	.75	"	1.00	.55	1.95
South Cove	2	1.00	"	.53	.48	1.61
Cape Blanco 1	4	.70	42.50 ^o	.26	.29	1.76
Cape Blanco 2	4	.92	"	.54	.48	1.50
Playa Hermosa 1	3	.57	10.50 ^o	.50	.47	1.63
Playa Hermosa 2	3	.84	"	.40	.60	1.26
Playa Hermosa 3	4	.60	"	.08	.50	1.01
Sámara 1	1	.89	9.87 ^o	.35	.55	1.06
Sámara 2	2	.97	"	.60	.58	1.08
Sámara 3	1	1.00	"	.19	.63	0.60
Quépos 1	4	-	9.45 ^o	.79	.52	1.92
Quépos 2	4	.94	"	.67	.42	1.88

3

Hedgpeth, 1968). The more of the total area of a transect that is in these zones, the more species there could be because of the increased area for habitation receiving fewer physical stresses. Figures 4 and 5 show that there is a significant negative relationship ($P < .05$) between the number of gastropod species and intertidal height.

The separation height between high and mid intertidal for Oregon was taken as 174 cm based on C.M. Yonge's method of zonation (Ricketts, Calvin, and Hedgpeth, 1968) for California. Since the tropical intertidal areas are not as well studied and the tidal level reference point is different from that in Oregon, the upper height for the mid intertidal in Costa Rica was based on gastropod species assemblages.

The assemblage of gastropod species commonly occurring in the upper intertidal zone in Oregon was derived from Ricketts, Calvin, and Hedgpeth (1968). The species comprising the high intertidal assemblage are Littorina scutulata, Acmaea digitalis, A. pelta, and Thais emarginata. The Oregon snails living in the lower high and upper mid intertidal zones include: Acmaea scutum, Tegula funebris, and Thais lamellosa. The Costa Rican gastropod species that I feel correspond to the high intertidal Oregon species include: Littorina aspera, Nerita scabricosta, and Purpura patula; those in the high and upper mid intertidal would be Littorina modesta, Nerita funiculata, Planaxis spp., Tegula palliserpentis, and Acanthina brevidentata.

The high-mid intertidal junction point in Costa Rica was determined as the lowest height reading (120 cm) in the quadrats containing only those gastropod species corresponding to the high and

FIGURE 4. The relationship between height in the intertidal and species number for Oregon transects. The regression equation is: $Y = -20.10X + 241.40$.

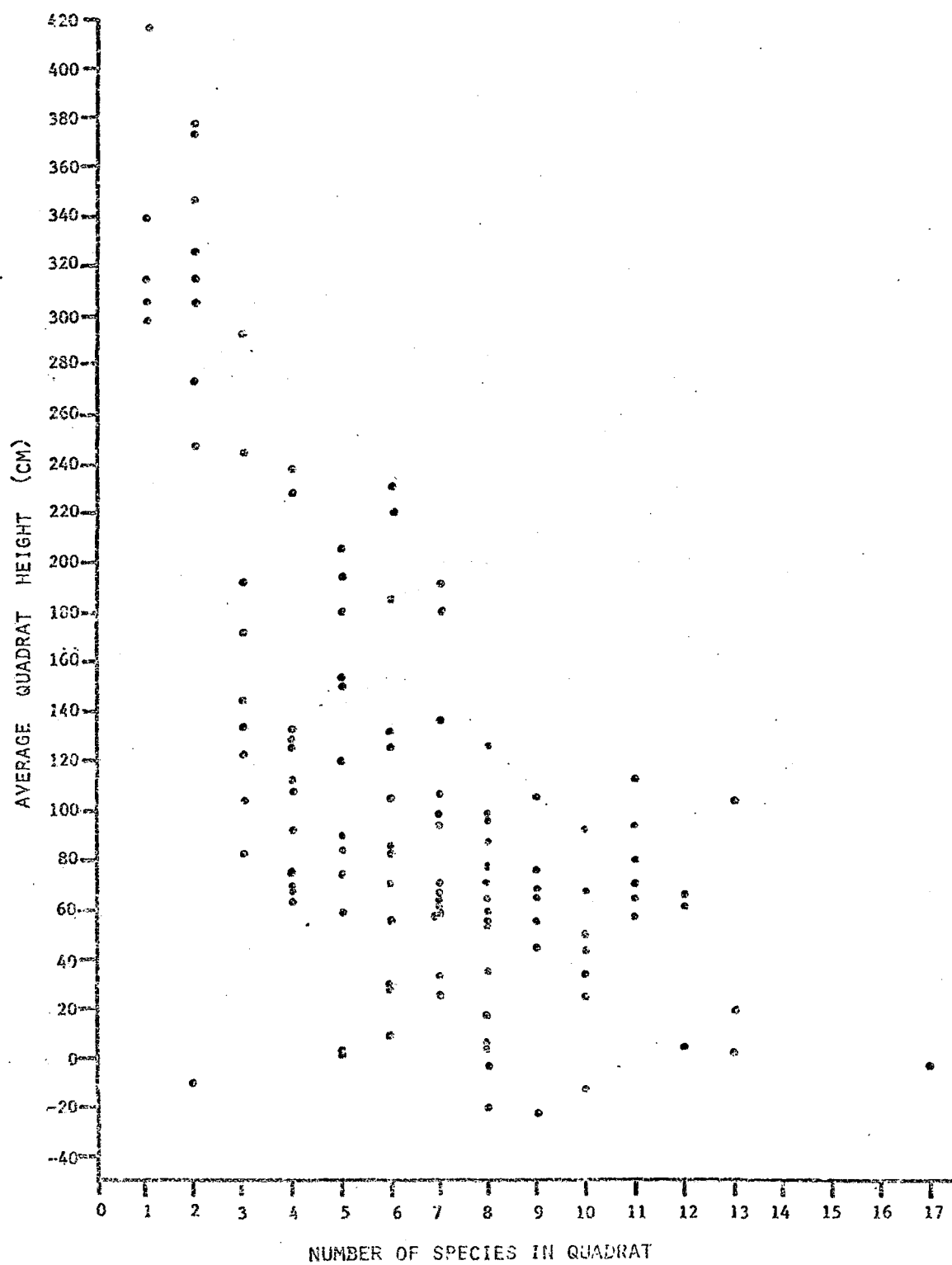
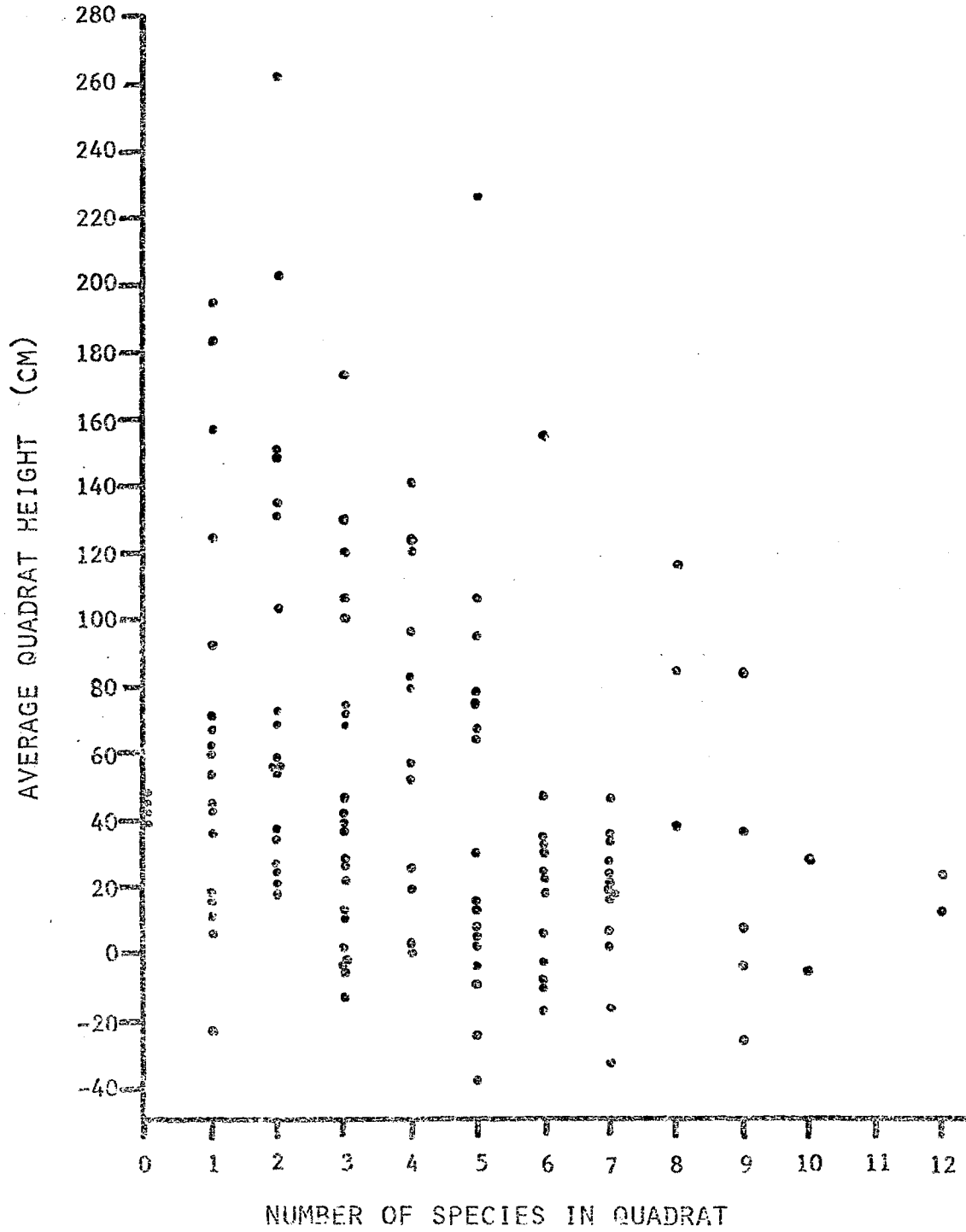


FIGURE 5. The relationship between height in the intertidal and species number for Costa Rican transects. The regression equation is: $Y = -6.10X + 76.90$.



upper mid intertidal species assemblage. Quépos 1 was not included in any calculations involving this parameter since most of the intertidal height measurements occurred on the tops of large boulders. This means that the average recorded heights of the individual quadrats are much higher than the actual intertidal height encompassed by each quadrat.

The number of individuals in quadrats from various heights in the intertidal zone are plotted in Figures 6 and 7. The quadrats with the higher number of individuals occur in the mid tide zone and the curve tapers off at both ends. The highest numbers of individuals per quadrat are due to the high numbers of Littorina spp. in the upper mid intertidal zone.

Latitude was included as a variable since it could include some parameters that are different in the tropics compared to the temperate zone, but which were not measured in this study. Factors like the amount of primary productivity, the year-round dependability of food availability, the length of the geologic time period without major physical catastrophes, and immigration rates could be larger or smaller in the tropics compared to the temperate zone; these could be encompassed by the latitude parameter.

Topographic features are important to intertidal organisms since exposure to wave shock and desiccation can be affected by the nature of the topographic relief such as crevices which provide shade, depressions for tide pools, and boulders to break the force of the waves. One might predict that an area with an extremely varied

FIGURE 6. The relationship between the number of individuals in a quadrat and the average height of the quadrat for the Oregon transects.

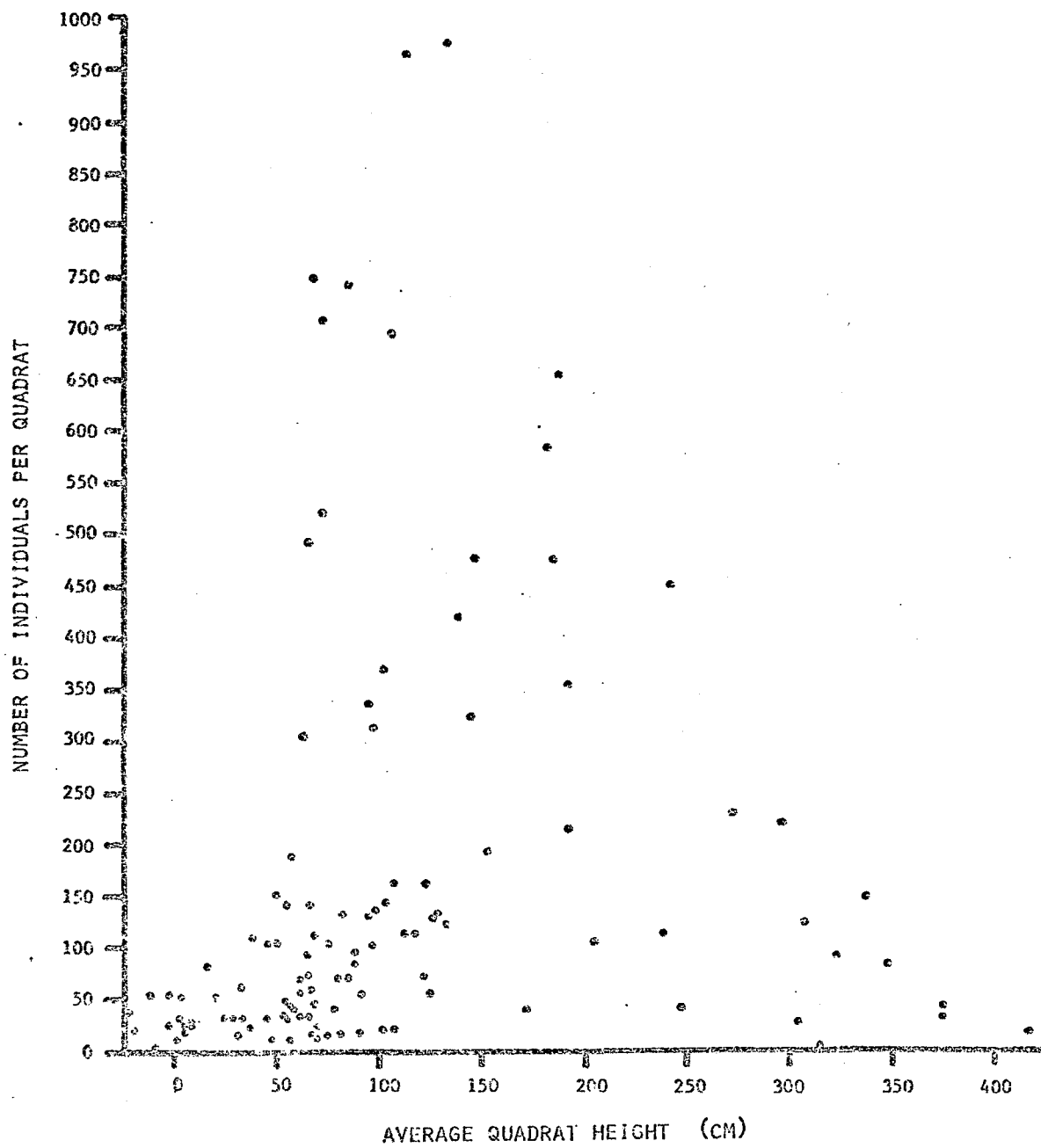
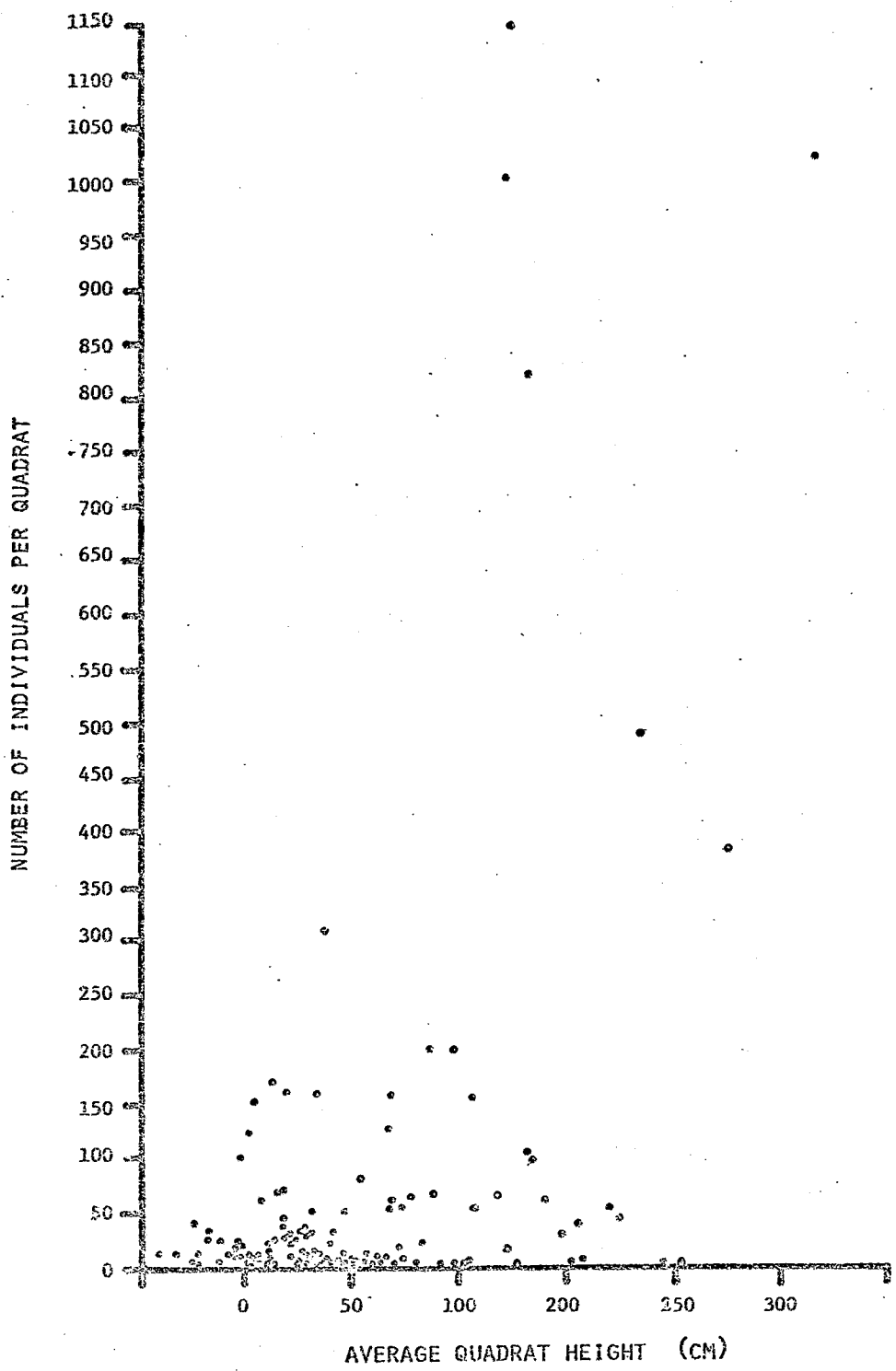


FIGURE 7. The relationship between the number of individuals in a quadrat and the average height of the quadrat for the Costa Rican transects excluding Quépos 1.



topography might support a larger species diversity than a flat area, other things being equal, since a greater variety of microhabitats would exist, each differing in the amount of exposure to waves and desiccation.

Three different measures of topographic complexity were determined for the transects: the availability of undersides of rocks, boulders, or ledges; the proportion of times the topographic relief reversed in slope direction; and the difference in heights between consecutive height readings along the transect lines.

The availability of undersides of rocks, boulders, or ledges increases the topographic complexity of an area and provides microhabitats that are more protected from desiccation and wave shock than areas with just bedrock. A significantly higher number of species, but not of individuals, are found in quadrats with this feature (Table IX) in both Oregon and Costa Rican transects. For this reason the proportion of sampled quadrats with these features available as a gastropod refuge was computed for each transect (Table VIII).

Topographic relief was quantified for each transect by using the intertidal height data taken at 20 cm intervals along the transect. These data were broken into two components: 1) the proportion of times that a change in direction of the slope of the transect line occurred between two consecutive data points and 2) the absolute difference between consecutive height readings.

TABLE IX. THE AVERAGE NUMBER OF SPECIES AND INDIVIDUALS FOUND IN QUADRATS WITH AND WITHOUT THE UNDERSIDES OF ROCKS AVAILABLE AS HABITATS FOR GASTROPODS. THE NUMBER OF QUADRATS IN EACH CATEGORY IS IN PARENTHESES.

AREA	AVERAGE NUMBER OF SPECIES IN QUADRATS WITH AVAILABLE UNDERSIDES OF ROCKS AND LEDGES		AVERAGE NUMBER OF SPECIES IN QUADRATS WITHOUT AVAILABLE UNDERSIDES OF ROCKS AND LEDGES		STUDENT'S t
OREGON	7.64	(55)	5.27	(63)	4.256*
COSTA RICA	5.73	(60)	3.26	(85)	5.750*

AREA	AVERAGE NUMBER OF INDIVIDUALS IN QUADRATS WITH AVAILABLE UNDERSIDES OF ROCKS AND LEDGES		AVERAGE NUMBER OF INDIVIDUALS IN QUADRATS WITHOUT AVAILABLE UNDERSIDES OF ROCKS AND LEDGES		STUDENT'S t
OREGON	167.10	(55)	139.90	(63)	0.713
COSTA RICA	42.90	(60)	94.4	(85)	1.892

*significant $P < .01$; 2 tail test

Component 1 provides an estimate of how often the topography changes since a flat or steadily sloping area would have a lower proportion of changes than found along a varied topography where the slope would change from positive to negative and vice-versa many times.

Component 2 was determined because knowing the proportion of times a change in slope occurs doesn't indicate the magnitude of the change. Categories were set up of 5 cm increments (0.0-4.9 cm, 5.0-9.9 cm, 10.0-14.9 cm, etc.) and H' (hereafter called H' RELIEF) was calculated for each transect with each 5 cm group as in i th class and the number of times that a difference of that magnitude occurred divided by the total number of height differences recorded as p_i . A flat topography would have a low H' RELIEF since most of the differences in height readings would be in the 0.0-4.9 cm category. The values of these two measures for each transect appear in Table VIII.

In order to assess which of these physical parameters might be more important in predicting diversity, a step-wise multiple regression was performed using the computer program BMD02R (Dixon, 1968). This program enters that independent variable (physical parameter) into the regression equation which makes the greatest reduction in the error sum of squares, has the highest partial correlation with the dependent variable (species diversity), and has the highest F value at each step (Dixon, 1968; Vuilleumier, 1970). It is probably unwise to make too much of the results of this

technique since the sample size is low and since wave exposure cannot be adequately quantified. Also note that Quépos 1 was not included owing to the previously mentioned problems of accurate intertidal height measurements for this transect.

Table X shows the results using the six physical parameters with the natural logarithm of the number of species in each transect. Natural log transformations were used in those cases where there was a higher r value than with untransformed data. This combination of physical factors explains 92.6% of the variation in the number of species found in the different transects. The three most important parameters (determined by significant F values) in order of importance are: wave exposure, the proportion of samples in the mid and low intertidal zones, and the H' measure of topographic relief. The number of species has a negative relationship with wave exposure and positive relationships with the two other significant parameters.

The same procedure was used to analyze the variation in H' and H' VOLUME using the physical parameters. The results for the multiple regression are presented in Tables XI and XII. The only significant physical parameter that might be useful in predicting species diversity as measured by H' is the proportion of a sample that is in the mid and low intertidal zones; this is a positive relationship.

The most important (significant) parameters in relation to the H' VOLUME statistic of diversity are the proportion of quadrats with the undersides of boulders or ledges available for utilization (positive relation), the latitude of the transect (negative relation),

TABLE X. RESULTS OF THE STEP-WISE MULTIPLE REGRESSION OF THE NATURAL LOG OF THE NUMBER OF GASTROPOD SPECIES ON THE PHYSICAL VARIABLES

INDEPENDENT PHYSICAL VARIABLE	CONTRIBUTION TO R ²	F VALUE	ORDER ENTERED INTO REGRESSION	SIGN OF THE REGRESSION EQUATION COEFFICIENT
WAVE EXPOSURE	0.6982	25.4507**	1	NEGATIVE
LOG _e PROPORTION OF QUADRATS IN MID AND LOW ZONES	0.1131	5.9984*	2	POSITIVE
LOG _e LATITUDE	0.0350	3.7536	4	NEGATIVE
LOG _e PROPORTION OF QUADRATS WITH UNDERSIDES OF ROCKS	0.0000	too low to be included	--	--
PROPORTION OF POSSIBLE CHANGES IN SLOPE DIRECTION	0.0006	0.0542	5	POSITIVE
H'RELIEF	0.0792	6.5116*	3	POSITIVE
TOTAL VARIATION EXPLAINED	92.6%			

REGRESSION EQUATION: \log_e number of species = 1.400 - 0.17(waves) + 0.470(\log_e mid-low) - 0.100(\log_e latitude) + 0.002(slope) + 0.386(H'RELIEF)

* significant P < .05 ** highly significant P < .01

TABLE XI. RESULTS OF THE STEP-WISE MULTIPLE REGRESSION OF THE NATURAL LOG OF THE H' MEASURES OF DIVERSITY ON THE PHYSICAL VARIABLES

INDEPENDENT PHYSICAL VARIABLE	CONTRIBUTION TO R ²	F VALUE	ORDER ENTERED INTO REGRESSION	SIGN OF THE REGRESSION EQUATION COEFFICIENT
LOG _e WAVE EXPOSURE	0.0486	0.7609	4	NEGATIVE
PROPORTION OF QUADRATS IN MID AND LOW ZONES	0.3210	5.1996*	1	POSITIVE
LOG _e LATITUDE	0.0377	0.5375	2	NEGATIVE
PROPORTION OF QUADRATS WITH UNDERSIDES OF ROCKS	0.0455	0.6849	5	NEGATIVE
PROPORTION OF POSSIBLE CHANGES IN SLOPE DIRECTION	0.0380	0.5337	6	POSITIVE
LOG _e H'RELIEF	0.0818	1.3155	3	POSITIVE
TOTAL VARIATION EXPLAINED	57.3%			

REGRESSION EQUATION: $\log_e H' = -0.560 - 0.240(\log_e \text{ waves}) + 0.014(\text{mid-low}) - 0.204(\log_e \text{ latitude}) - 0.009(\text{undersides}) + 0.021(\text{slope}) + 1.124(\log_e H' \text{ RELIEF})$

* significant P < .05 ** highly significant P < .01

TABLE XII. RESULTS OF THE STEP-WISE MULTIPLE REGRESSION OF THE NATURAL LOG OF THE H'VOLUME DIVERSITY MEASURES ON THE PHYSICAL VARIABLES

INDEPENDENT PHYSICAL VARIABLE	CONTRIBUTION TO R ²	F VALUE	ORDER ENTERED INTO REGRESSION	SIGN OF THE REGRESSION EQUATION COEFFICIENT
WAVE EXPOSURE	0.0000	too low to be included	-	-
LOG _e PROPORTION OF QUADRATS IN MID AND LOW ZONES	0.0366	4.4557*	3	POSITIVE
LATITUDE	0.2386	21.6158**	2	NEGATIVE
LOG _e PROPORTION OF QUADRATS WITH UNDERSIDES OF ROCKS	0.6510	20.5217**	1	POSITIVE
PROPORTION OF POSSIBLE CHANGES IN SLOPE DIRECTION	0.0026	0.2894	4	NEGATIVE
H'RELIEF	0.0010	0.0965	5	POSITIVE
TOTAL VARIATION EXPLAINED	93.0%			

REGRESSION EQUATION: $\log_e H'VOLUME = -0.765 - 0.000(\text{waves}) + 0.353(\log_e \text{mid-low}) - 0.010(\text{latitude}) + 0.055(\log_e \text{undersides}) - 0.003(\text{slope}) + 0.040(H'RELIEF)$

* significant $P < .05$ ** highly significant $P < .01$

and the proportion of quadrats in the mid and low intertidal (positive relation). These three parameters explain 92.6% of the variation in H'VOLUME while all six parameters together explain 93.0% (Table XII).

The high H'VOLUME values in Costa Rica (Table II) which result in the negative relationship of H'VOLUME species diversity with latitude are due to the fact that the low latitude Costa Rican transects have significantly higher species richness and evenness components of the H'VOLUME statistic than the Oregon transects (Table XIII). Because the volume of the individual species is more evenly distributed among all the species rather than a few species having all the volume, as in Oregon, the evenness components are higher which causes the H'VOLUME statistics to be larger. The reason for the different volumes of snails may have something to do with differences in productivity between Costa Rican and Oregon intertidal areas.

In the same manner the density per square meter and the volume per square meter of gastropods were entered as dependent variables on the physical factors (Tables XIV and XV). Density has no significant relation to any of the physical parameters. This may not be surprising since the density figures for any transect are largely dependent on whether Littorina spp. were encountered in the quadrats since they have densities so much higher than any other species (Appendices 2 and 3).

The volume per square meter (an estimate of biomass) is highly significantly related to the latitude of an area. This positive

TABLE XIII. COMPARISON OF THE SPECIES EVENNESS AND RICHNESS COMPONENTS OF H'VOLUME SPECIES DIVERSITY. EVENNESS IS $H'VOLUME/LOG_e S$ AND RICHNESS IS $(S-1)/LOG_e H$, WHERE S IS THE TOTAL NUMBER OF SPECIES AND N IS THE TOTAL VOLUME IN EACH TRANSECT.

TRANSECT	EVENNESS	RICHNESS
NC	0.053	0.259
MC1	0.396	2.221
MC2	0.410	3.548
SC	0.448	3.694
CB1	0.547	2.506
CB2	0.552	2.956
AVERAGE	0.401	2.531
PH1	0.653	4.257
PH2	0.615	4.787
PH3	0.582	2.771
S1	0.621	5.478
S2	0.692	6.188
S3	0.572	4.621
Q1	0.694	6.276
Q2	0.631	5.280
AVERAGE	0.632	4.957
STUDENT'S t	3.0289*	3.7349**

* significant $P < .05$; 2 tail test

** significant $P < .01$; 2 tail test

TABLE XIV. RESULTS OF THE STEP-WISE MULTIPLE REGRESSION OF THE NATURAL LOG OF THE DENSITY OF GASTROPODS ON THE PHYSICAL VARIABLES

INDEPENDENT PHYSICAL VARIABLE	CONTRIBUTION TO R ²	F VALUE	ORDER ENTERED INTO REGRESSION	SIGN OF THE REGRESSION EQUATION COEFFICIENT
LOG _e WAVE EXPOSURE	0.0000	too low to be included	-	-
PROPORTION OF QUADRATS IN MID AND LOW ZONES	0.0227	0.3164	2	NEGATIVE
LOG _e LATITUDE	0.2606	3.8771	1	POSITIVE
PROPORTION OF QUADRATS WITH UNDERSIDES OF ROCKS	0.0295	0.3767	4	POSITIVE
PROPORTION OF POSSIBLE CHANGES IN SLOPE DIRECTION	0.0599	0.8213	3	POSITIVE
H'RELIEF	0.0119	0.1359	5	NEGATIVE
TOTAL VARIATION EXPLAINED	38.0%			

REGRESSION EQUATION: $\log_e \text{ density} = 3.648 + 0.000(\log_e \text{ waves}) - 0.022(\text{mid-low})$
 $+ 0.672(\log_e \text{ latitude}) + 0.016(\text{undersides}) + 0.010(\text{slope})$
 $- 0.616(\text{H'RELIEF})$

* significant $P < .05$ ** highly significant $P < .01$

TABLE XV. RESULTS OF THE STEP-WISE MULTIPLE REGRESSION OF THE NATURAL LOG OF THE VOLUME OF GASTROPODS PER SQUARE METER ON THE PHYSICAL VARIABLES

INDEPENDENT PHYSICAL VARIABLE	CONTRIBUTION TO R ²	F VALUE	ORDER ENTERED INTO REGRESSION	SIGN OF THE REGRESSION EQUATION COEFFICIENT
LOG _e WAVE EXPOSURE	0.0171	1.8490	4	NEGATIVE
LOG _e PROPORTION OF QUADRATS IN MID AND LOW ZONES	0.0036	0.3219	6	NEGATIVE
LOG _e LATITUDE	0.8860	85.5179**	1	POSITIVE
LOG _e PROPORTION OF QUADRATS WITH UNDERSIDES OF ROCKS	0.0140	1.4005	2	NEGATIVE
LOG _e PROPORTION OF POSSIBLE CHANGES IN SLOPE DIRECTION	0.0027	0.2635	5	POSITIVE
H'RELIEF	0.0089	0.8835	3	POSITIVE
TOTAL VARIATION EXPLAINED	93.2%			

REGRESSION EQUATION: $\log_e \text{ volume} = -2.565 - 0.391(\log_e \text{ waves}) - 0.434(\log_e \text{ mid-low}) + 1.411(\log_e \text{ latitude}) - 0.391(\log_e \text{ undersides}) + 0.894(\log_e \text{ slope}) + 0.740(\text{H'RELIEF})$

* significant $P < .05$ ** highly significant $P < .01$

relationship is certainly a result of the large sized herbivores found in Oregon such as the chitons.

There is a danger in determining the relationships of these physical parameters individually with the diversity and volume measures since one physical variable may be influenced by another variable. Looking at one variable alone may show a relationship with diversity as determined by regression or correlation; however, when all the variables are compared to diversity in a multiple regression, the partial correlation of the one variable may change in sign and/or the significance of the relation. This happens with H'RELIEF. When correlated alone with the number of species, H'RELIEF has an $r = -0.120$, but in the stepwise regression the partial correlation is $+0.648$.

CARNIVOROUS GASTROPOD FOOD AND HABITAT PREFERENCES

Since the majority of the tropical transects do have more species than any of the Oregon transects except South Cove, the Costa Rican species pool is higher than Oregon's, and there is a significant increase in the number of carnivorous gastropod species in the tropical areas, the tropical communities must somehow accommodate snail species differently than temperate communities. In order to investigate this increased species packing, the divisions of the available food resources and intertidal habitats (as related to height above 0 m tide) were examined for carnivorous snails, which show the biggest increase in species diversity with decreasing latitude.

The prey preferences of the carnivorous gastropods found in Oregon and Costa Rican transects are presented in Table XVI and XVII. The range of prey items that can be eaten by a species and the number of feeding observations appear in Appendices 6 and 7. The preference for a particular prey was determined from individual feeding observations as follows: If 75% of the observations were in one prey category, the snail preferred this prey; if less than 75% of the observations were in one category, the two most common prey types consumed were considered as being preferred; if the two most common prey groups were involved in less than 70% of the feeding observations, the third highest preferred prey was included.

From the summary Table XVIII it can be seen that there are threefold increases in the number of gastropod species preferring polychaete and gastropod prey in Costa Rica compared to Oregon. Two food categories, sipunculid and fish, not utilized by the Oregon gastropods are exploited by tropical snails.

There is also a large increase in the number of snails preferring dead material in the tropics, due mainly to the numerous species of Columbellidae. Not enough work has been done to determine if all columbellids prefer dead material since it is difficult to know in most cases whether the prey an individual columbellid ate, or was found in the process of eating, was dead or injured to start with. It is certain that most of the columbellid species are attracted to dead and/or injured prey (Marcus and Marcus, 1962; Spight, pers. comm., Miller, pers. obs.). Members of the genus Columbella probably eat primarily plant material (Marcus and Marcus, 1962; pers. obs.).

All the carnivorous prosobranch gastropods that have been reported from the Oregon rocky intertidal zone (Keen and Doty, 1942) except Thais lima, Odostomia sp. (found outside the transect areas) and Vusitriton oregonensis (primarily subtidal but marginally intertidal) were found in the temperate transects. There are several species of nudibranchs which do occur intertidally that were not found in the transects. If these missing species were included in the summary food preference table, there would be an increase in the number of species in the coelenterate, tunicate, bryozoan, and sponge categories caused by the nudibranchs, and the parasitic and echinoderm

TABLE XVIII. SUMMARY OF THE PREY PREFERENCE CATEGORIES FOR THE CARNIVOROUS GASTROPOD AND CHITON SPECIES FOUND IN THE OREGON, COSTA RICAN AND MEXICAN TRANSECTS. * SPECIES EXIST BUT WERE NOT FOUND IN THE TRANSECTS: REFER TO THE TEXT FOR AN EXPLANATION.

AREA	SPONGE	COELENTERATES	SIPUNCULIDS	POLYCHAETES	LIVE, MOBILE CRUSTACEANS	BARNACLES	BIVALVES	GASTROPODS	BRYOZOANS	ECHINODERMS	TUNICATES	FISH	PARASITIC	DEAD ORGANISMS
OREGON	3	2	0	4	1	5	3	1	1	0*	1	0	2	3
COSTA RICA	1	1	2	13	0*	7	3	4	0	1	1	1	1	10
MEXICO	2	0*	1	8	0*	8	1	4	0	0*	2	1	1	4

categories would have one more species each due to Odostomia sp. and Fusitriton oregonensis (Eaton, 1971), respectively. I would predict that Thais lima feeds on barnacles and mussels.

All the categories of prey except those for fish and live, mobile crustaceans would show an increase in species numbers if intertidal gastropods not found in the Costa Rican and Mexican transects, but known to occur there, were included. For instance, the one species of Cymatium found in the Mexico transect also occurs in Costa Rica and eats gastropods; Purpura columellaris, feeding on barnacles and gastropods (Miller, pers. obs.), occurs in the high intertidal zone like P. patula but in different habitats; three different species of the vermivorous cones and turrids were encountered outside the transects; Vasum caestus, which eats polychaetes and sipunculids (Miller, pers. obs.), is essentially subtidal but can be found at extremely low tides, and more species of nudibranchs should occur intertidally (Keen, 1971) which should cause increases in the bryozoan, sponge, and coelenterate categories. The chiton Placiphorella blainvillii, which probably eats live, mobile crustaceans as does P. velata, in Oregon, was not found; but it does occur in Panama (Keen, 1971). The differences between temperate and tropical areas in the number of species in each feeding category would be more dramatic if all carnivorous species occurring in the Costa Rican rocky intertidal zone were included.

It should also be mentioned that two species of starfish, Pisaster ochraceus and Leptasterias hexactis, commonly occur in the temperate

zone transects (Appendix 2) and they feed on some of the same food categories as some of the gastropod species, as well as eating gastropods (Paine, 1969 ; Menge, 1972; Niesen, 1973). At Cape Arago State Park where this study was done, Niesen (1973) found that 83% of the 2,114 observations of Leptasterias hexactis feeding he made were on barnacles, 10% on gastropods, 4% on the polychaete Spirorbis sp., and 3% on bivalves and other prey. Niesen and I concur that L. hexactis less than 1 cm in diameter feed almost exclusively on Spirorbis sp.; both Amphissa columbiana and Ocenebra lurida also prey on this abundant serpulid. Pisaster ochraceus prefers mussels and barnacles but also eats gastropods (Feder, 1959; Paine, 1969) and thus overlaps with the diets of several gastropods. The Costa Rican intertidal areas examined in this study were devoid of starfish although a barnacle specialist, Heliaster sp., occurs in the high intertidal at Puerto Escondido, Mexico.

Another problem in defining food choices for gastropods occurs with species that appear to be indiscriminate grazers. Members of the herbivorous genus Calliostoma have been observed consuming hydroids at Friday Harbor, Washington (Spight, pers. comm.), and living coral (Miller, pers. obs. in Jamaica), but I feel that Calliostoma ligatum found in Oregon is basically an herbivore since its fecal pellets contain mostly plant material, and hydroids are not common enough to be a food source. On the other hand, the cowries (Cypraea) have been found to eat sponge and tunicates (Miller, pers. obs. in California,

Hawaii, and Costa Rica) and algae (Kay, 1960; Miller, pers. obs.). Cypraea cervinetta in Costa Rica is primarily a carnivore. I found some individuals on sponge and tunicates; fecal pellets from other individuals contained sponge spicules. Careful studies will have to be made on the feeding habits and digestive enzymes present to decide whether gastropods like Calliostoma spp. and Cypraea spp. and the polyplacophorans (chitons) are indiscriminate omnivores capable of digesting both plant and animal material or whether some species are strict carnivores and others herbivores.

Looking at the range of prey of the carnivorous species examined (Appendices 6 and 7), it is apparent that there is overlap among species. If food partitioning doesn't appear to be enough to separate the carnivorous species ecologically, perhaps habitat partitioning is. The intertidal height range of the populations of the carnivorous species is the one gross habitat dimension that I will consider, since it would not be accurate to describe microhabitat substratum preferences based only on the low tide observations that I made. This dimension was measured by averaging the six height readings for each quadrat in which the snail species were found and recording the average, two standard deviations above and below the average, and the range of heights in Figures 8, 9, and 10. For many snails only a few individuals were found, so it is hard to determine the true intertidal height range. Some species have the bulk of their populations in the subtidal zone so the few individuals of these species encountered probably represent the upper range of the

FIGURE 8. Intertidal height ranges for Oregon carnivorous gastropods and chitons. The rectangle encloses ± 2 s.d. from the mean. The dots represent the extremes of the range in the transects. The number of quadrats in which each species was found follows the species name. The number of individuals of each species found is in parentheses.

INTERTIDAL HEIGHT (cm)

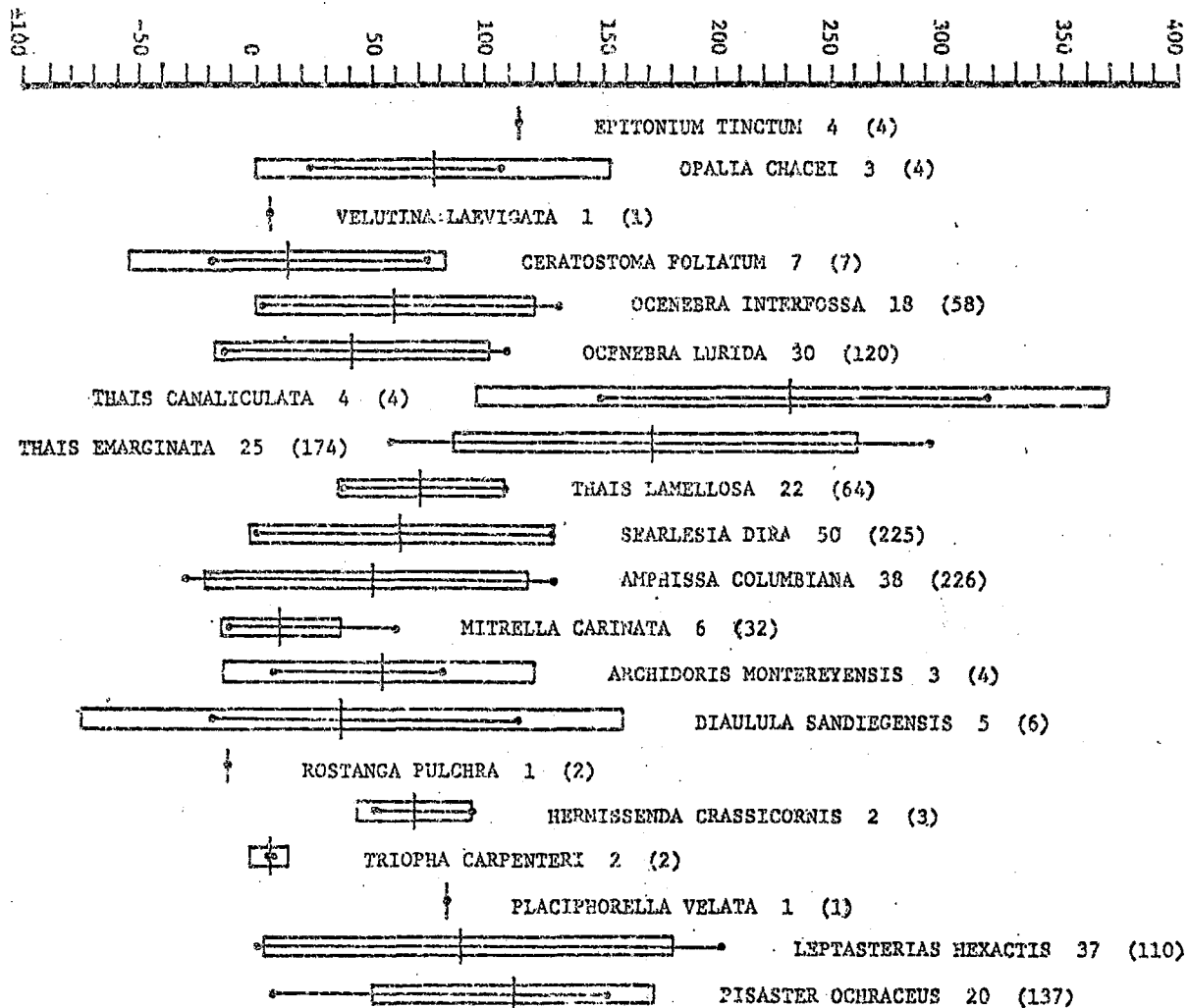


FIGURE 9. Intertidal height ranges for Costa Rican carnivorous gastropods excluding those found in Quepos I. The rectangle encloses ± 2 s.d. from the mean. The dots represent the extremes of the range in my transects. The number of quadrats in which each species was found follows the species name. The number of individuals of each species found is in parentheses.

INTERTIDAL HEIGHT (cm)

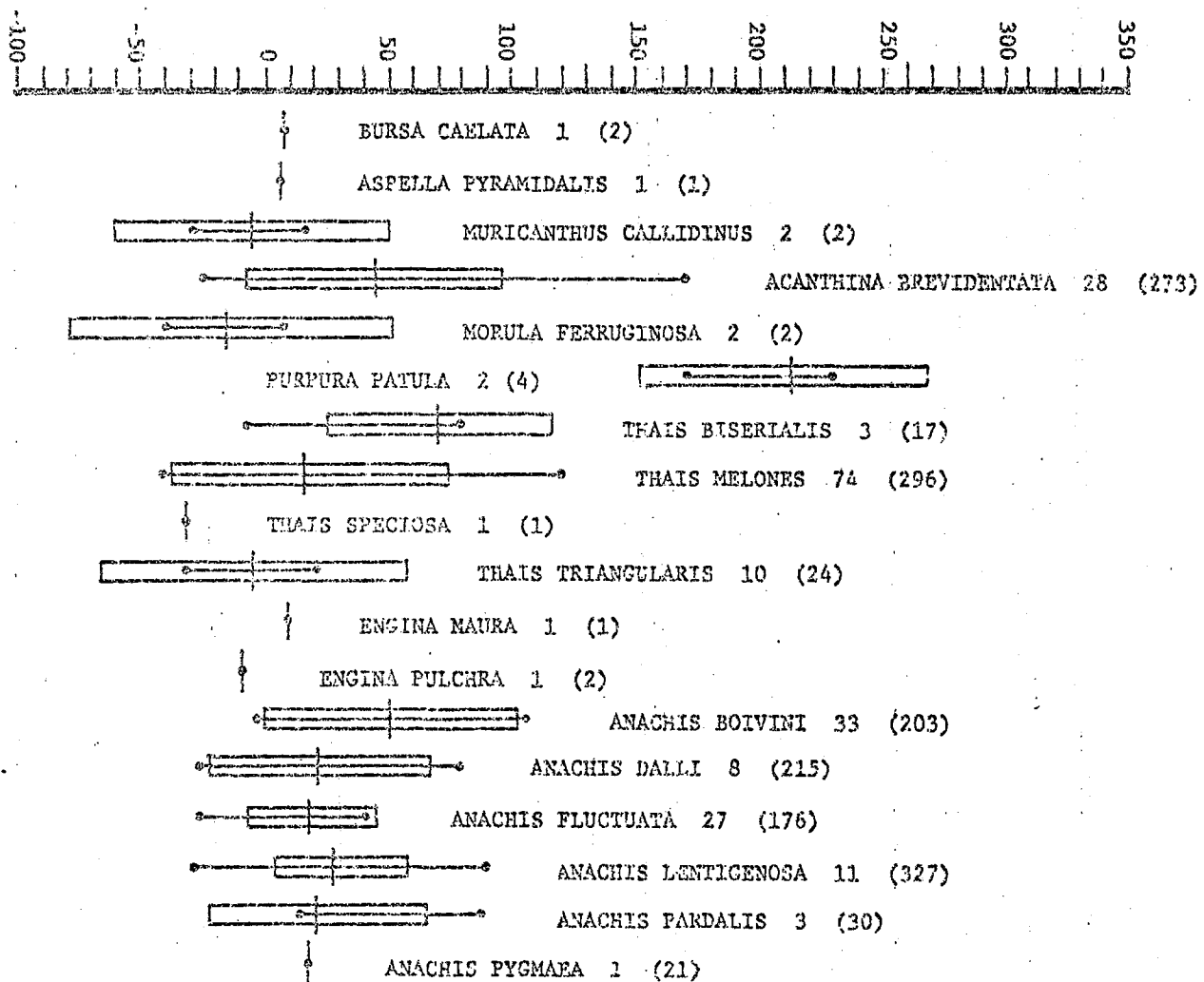
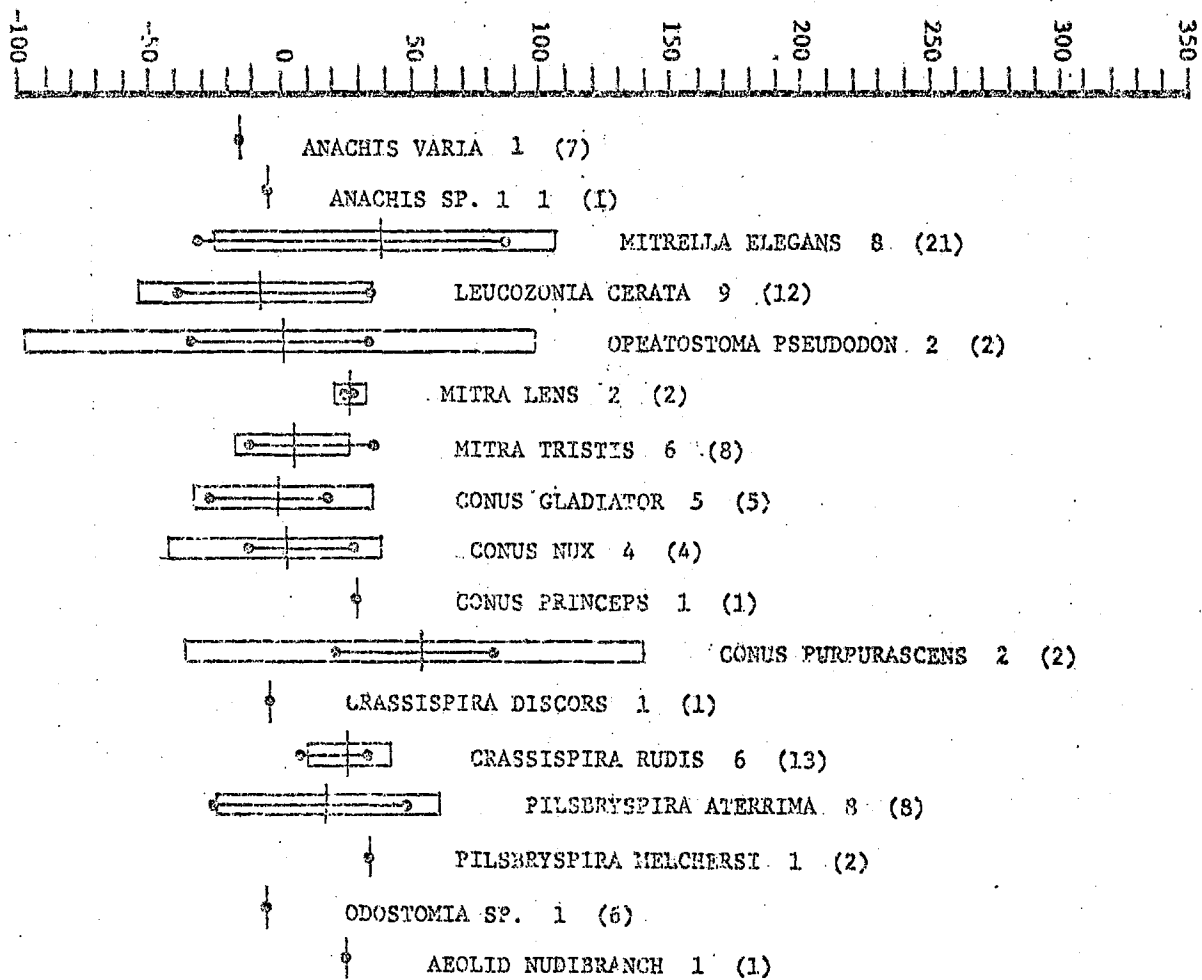


FIGURE 10. Intertidal height ranges for Costa Rican carnivorous gastropods excluding those found in Quépos I. The rectangle encloses ± 2 s.d. from the mean. The dots represent the extremes of the range in my transects. The number of quadrats in which each species was found follows the species name. The number of individuals of each species found is in parentheses.

INTERTIDAL HEIGHT (cm)



population or are refugee individuals. Some of the tropical species populations have patchy distributions so that, for this reason too, the intertidal height ranges recorded for species with only a few individuals are not to be considered complete ranges.

One major misrepresentation of intertidal range due to low numbers of observations is that for Thais canaliculata in Figure 9. This species is consistently found just below the bulk of the Thais emarginata populations where they occur together (Dayton, 1971; Miller, pers. obs.). The reason this did not show up in this figure is that one transect in which they were found (North Cove) has high wave exposure which raises the effective level of the sea (Lewis, 1964) and in this case creates a high tide pool where mussels, barnacles, and gastropods find a refuge.

Most of the species that do overlap to any extent in food preferences occupy different average intertidal heights. Tables XIX and XX show the results of t-tests used to compare the average intertidal heights of snail species populations whose food preferences are close and whose height distributions appear similar in Figures 9 and 10. The only two gastropod species in Oregon which might be competing for prey (if food were limiting population growth) and whose average intertidal heights coincide are Ocenebra lurida and Amphissa columbiana. However, A. columbiana consumes dead matter whereas O. lurida does not.

The starfish Pisaster and Leptasterias have significantly different average population heights in the intertidal (Table XVI).

TABLE XIX. COMPARISONS OF MEAN INTERTIDAL HEIGHTS FOR POPULATIONS OF SPECIES WITH SIMILAR FOOD RESOURCES. OREGON SPECIES.

PREY CATEGORY	SPECIES WITH PREY OVERLAP	INTERTIDAL HEIGHT COMPARISON t-VALUE
BARNACLES	THAIS EMARGINATA THAIS LAMELLOSA	18.150*
	OCENEBRA INTERFOSSA OCENEBRA LURIDA	3.596*
	OCENEBRA INTERFOSSA LEPTASTERIAS HEXACTIS	4.133*
	THAIS LAMELLOSA LEPTASTERIAS HEXACTIS	3.043*
	PISASTER OCHRACEUS LEPTASTERIAS HEXACTIS	4.550*
POLYCHAETES	AMPHISSA COLUMBIANA OCENEBRA LURIDA	1.621
	AMPHISSA COLUMBIANA MITRELLA CARINATA	6.850*
	LEPTASTERIAS HEXACTIS AMPHISSA COLUMBIANA	9.110*
DEAD MATTER	AMPHISSA COLUMBIANA SEARLESIA DIRA	4.700*
BIVALVES	THAIS LAMELLOSA CERATOSTOMA FOLIATUM	7.032*

*significant $P < .01$; 2 tail test

TABLE XX. COMPARISONS OF MEAN INTERTIDAL HEIGHTS FOR POPULATIONS OF SPECIES WITH SIMILAR FOOD RESOURCES. COSTA RICAN SPECIES.

PREY CATEGORY	SPECIES WITH PREY OVERLAP	INTERTIDAL HEIGHT COMPARISON t-VALUE
BARNACLES	ACANTHINA BREVIDENTATA THAIS BISERIALIS	3.784**
	ACANTHINA BREVIDENTATA THAIS TRIANGULARIS	8.992**
SIPUNCULIDS	MITRA LENS MITRA TRISTIS	1.440
GASTROPODS	THAIS BISERIALIS THAIS MELONES	7.779**
POLYCHAETES	CONUS NUX CONUS GLADIATOR	0.368
	CRASSISPIRA RUDIS PILSBRYSPIRA ATTERIMA	1.403
	PILSBRYSPIRA ATTERIMA CONUS GLADIATOR	1.475
DEAD MATTER	ANACHIS DALLI ANACHIS FLUCTUATA	2.598*
	ANACHIS BOIVINI ANACHIS DALLI	12.717**
	ANACHIS LENTIGINOSA ANACHIS DALLI	2.894*
	MITRELLA ELEGANS ANACHIS LENTIGINOSA	3.817**
	ANACHIS FLUCTUATA ANACHIS LENTIGINOSA ANACHIS DALLI ANACHIS BOIVINI	one factor analysis of variance; F=131.50 significant $P < .005$

* significant $P < .05$; 2 tail test

**significant $P < .01$; 2 tail test

Since both starfish species overlap to some extent in both food choice and intertidal range with several gastropod species and consume gastropods themselves (Feder, 1959; Paine, 1969; Menge, 1972; Niesen, 1973) they could exert considerable influence on gastropod population numbers. Paine (1969) suggests that although Pisaster ochraceus prefers mussels and barnacles, it can account for 16-31% of the mortality in Tegula funebris populations where the two species overlap. According to Menge (1972), Leptasterias hexactis in Puget Sound, Washington, can also significantly influence several gastropod populations such as Littorina spp. and Acmaea spp.

The division of resources by tropical carnivorous gastropods is more complicated with many more species appearing to share intertidal height ranges and/or prey preferences. This is especially true for the gastropods which prefer polychaetes such as the members of the genera Conus, Engina, and Leucozonia, and the five species of turrids. Kohn (1959, 1966, 1971) has shown that Conus spp. in most cases exploit different parts of the habitat and/or different species of polychaetes. It is expected that this occurs in the West American tropics too, but I do not have enough data to make similar statements. What the data that I do have from Mexico, Baja California, Jamaica, and Eniwetok Atoll suggest is that Engina and Leucozonia feed on sedentary polychaetes, the Conus spp. on errant polychaetes, and the turrids (which are very diverse in the tropical Americas) consume both sedentary and errant worms (Appendix 7).

The largest group of species encountered in the tropical transects is the columbellids (9 species). Except that most species are attracted to dead or injured animals, it is not known what any of these tropical species prefer to eat. The most common columbellid in the Oregon transects, Amphissa columbiana, has the most catholic of diets; along with the buccinid Searlesia dira (Lloyd, 1972; Miller, pers. obs.). Fecal pellet examinations made on various columbellid individuals in the tropical regions have revealed barnacle and other crustacean exoskeletons, polychaeta setae, and gastropod radulae, indicating that these species also feed on a number of prey categories. Not all columbellids are carnivorous, since members of the genus Columbella appear to feed on plant remains (Marcus and Marcus, 1962; Miller, pers. obs. from fecal pellet examinations). Cantharus spp. are also attracted to dead material and have a diverse diet according to fecal pellet remains. Some of the thaisids like Thais melones will eat carrion, but this is thought to be just opportunism, not an indication of preference in the sense defined.

The tropical gastropods that utilize barnacle and gastropod food resources appear to have more spatial separation than the other carnivores (Figure 10). Significance tests on the intertidal height averages were done for some pairs whose food resources overlapped (Table XX). Furpura columellaris shares the high intertidal habitat and food resources with P. patula but these species don't often occur in the same microhabitat. This suggests that some physical factor such as wave exposure may separate their distributions. Not enough

individuals of Mitra lens were found to determine if they ate different sipunculids than M. tristis. There also could be a partitioning of food on the basis of size in this case, since Mitra lens is twice as big as M. tristis. The partitioning of prey by size preference could be important for many snail species with some overlap in habitat and food choice. This type of partitioning is important in four species of Anolis lizards on the island of Bimini (Schoener, 1968).

The important aspect of how large the resource bases are with respect to the number of species eating that resource was not examined. It is entirely possible that food resources of the gastropods can overlap extensively if their populations are prevented from increasing by some other factor than competition for food and if the food resources are superabundant.

DISCUSSION

Local species diversity among gastropods and chitons, as measured by the number of species, is variable in the temperate and tropical areas studied. The tropical transects do not always have a higher species diversity nor is there a significant difference between the mean number of species found in Oregon and Costa Rican transects. A trend for increasing species diversity with decreasing latitude exists when large geographical areas are compared; the total number of different gastropod and chiton species in all Costa Rican transects (75) is much larger than that in all Oregon transects (44). The transect in southern Mexico has the largest number of species (52) of any, but its quadrat sizes were twice as large as in other transects.

When species diversity is examined using the diversity statistics which combine species number and abundance of individuals (H') or estimated relative biomass (H' VOLUME), more of a trend exists for individual Costa Rican transects to have a higher diversity than do individual Oregon transects (Table II). The average H' is not significantly higher for the Costa Rican transects, but the more biologically meaningful average H' VOLUME is. H' VOLUME is more meaningful than H' since it gives greater weight to the uncommon but large snails which occur more frequently in the tropics, such as the relatively big snail species Conus spp., Muricanthus spp., and Thais

melonae which are important predators in the community.

Of the physical parameters measured that might cause the variation in number of species found in the transects, wave exposure and the proportion of the transect in the mid and low intertidal zones were suggested as the most important variables by a stepwise multiple regression. A large portion (81%) of the variation in the number of species is explained by these two parameters (Table X). One measure of topographic relief (H'RELIEF) was the third most important significant parameter. However, its usefulness as a measure of topographic relief, like that of the change in slope direction measure, is in doubt.

It is hard to draw any conclusions concerning the influence of topographic relief on any of the dependent variables since the two measures are themselves negatively correlated ($r=-0.683$). For instance, compare the topographic profiles of Samara 3 with Middle Cove 2 (Appendix 1). Samara 3 is relatively flat (shown by a low H'RELIEF (Table VIII)), but it has a high "change in slope direction" value and a high species diversity. Middle Cove 2 has high values for both topographic measures and a similar diversity to Samara 3. Both transects differ in the other physical parameters (Table VIII), which may be more important in determining species diversity. For these reasons I do not consider that these two methods alone are entirely satisfactory for quantifying topographic relief; better methods are being investigated.

If the two pairs of transects from Oregon and Costa Rica that are most similar in the important physical parameters, as determined by the stepwise multiple regression, are compared (Table XXI), the numbers of species in the transects are very similar. The Whittaker similarity index comparing the number of measurements in the 5 cm height intervals computed for H'RELIEF are not particularly high, but the other differences between parameter values are small for the two transect pairs except, of course, the latitude.

If one is satisfied with defining species diversity as the simple number of species found, and if only samples of local intertidal areas are compared, theories of how and why there is more gastropod diversity in the tropics do not have to be invoked. Locally, the diversity isn't always greater in the tropics and physical factors similar in both the temperate and tropical rocky intertidal probably control the diversity.

Vertical spatial heterogeneity is probably not as important in determining diversity in this case as it is in other groups of animals like birds (MacArthur, 1964; MacArthur et al, 1966; Recher, 1969), lizards (Pianka, 1967), the gastropod genus Conus (Kohn, 1967), and fish (Sheldon, 1968). Fleming (1973), basing his conclusions on qualitative observations, thinks that the diversity of bats is also not primarily influenced by vertical spatial heterogeneity.

The H' measure of diversity is positively related to the proportion of the quadrats of a transect which occur in the mid and low intertidal zones; no other physical parameters show a significant

TABLE XXI. COMPARISON OF THE TEMPERATE AND TROPICAL
 TRANSECTS MOST SIMILAR IN THE IMPORTANT
 PHYSICAL PARAMETERS AS DETERMINED BY THE
 STEP-WISE MULTIPLE REGRESSION (**).

TRANSECT	NUMBER OF SPECIES	** WAVE EXPOSURE	** PROPORTION OF QUADRATS IN MID AND LOW INTERTIDAL	PROPORTION OF QUADRATS WITH THE UNDERSIDES OF ROCKS AVAILABLE	CHANGE IN SLOPE DIRECTION MEASURE	WHITTAKER OVERLAP VALUES OF THE RELIEF 5cm CATEGORIES
SOUTH COVE	36	2	1.00	.53	.48	
SÁMARA 2	34	2	.97	.60	.58	.80
CAPE BLANCO 2	22	4	.92	.54	.48	
QUÉPOS 2	26	4	.94	.67	.42	.73

relationship (Table XI). I am reluctant to make any conclusions about this relationship since the other diversity measures have significant relations with three variables, not just one. I also don't think H' is as meaningful a diversity statistic as is H' VOLUME. It is important to notice, however, that all three measures of diversity have significant positive relations with the proportion of mid and low intertidal quadrats in a given transect (Tables X, XI, and XII). This should not be unexpected since the more area in a sample containing microhabitats with reduced exposure to physiological stress, the more species one would expect to find there (Ricketts, Calvin, and Hedgpeth, 1968).

The difference in the number of species comprising the Oregon and Costa Rican species pools and the trend in the H' VOLUME values cannot be explained so easily. H' VOLUME has a significant positive relation to the proportion of quadrats having the undersides of rocks available as snail habitats and to the proportion of quadrats in the mid and low intertidal zones (Table XII). However, there are no significant differences among the Oregon and Costa Rican transects with respect to these two parameters and wave exposure (Table XXII), by which the diversity trends could be explained. The two measures of topographic relief are significantly different between the two areas; but since there are problems with these measures and they aren't significant contributors to the multiple regression of H' VOLUME on the physical parameters (Table XII), I don't feel that too much should be made of these differences. This leaves the

TABLE XXII: COMPARISON OF THE VALUES FOR THE PHYSICAL
PARAMETERS BETWEEN OREGON AND COSTA RICA

PHYSICAL PARAMETER	STUDENT'S t
WAVE EXPOSURE	1.1116
PROPORTION OF QUADRATS IN THE MID AND LOW INTERTIDAL	1.0101
PROPORTION OF QUADRATS WITH UNDERSIDES OF ROCKS AVAILABLE	0.1450
CHANGE IN SLOPE DIRECTION MEASURE OF TOPOGRAPHY	2.4162*
H'RELIEF	2.4590*

* significant $P < .05$; 12 d.f.; 2 tail test

latitudinal variable to explain the diversity differences.

The latitudinal parameter can include phenomena that are distinctly stronger in the tropics and weaker in the temperate zone, or vice versa. This would include things like a longer period of geologic history without major physical catastrophes in Costa Rica compared to Oregon, or the seasonality of the plant growing season. These kinds of differences are used as explanations in several of the theories on latitudinal gradients mentioned in the Introduction.

The increased number of species that causes the differences in species pools and in H'VOLUME diversity trends between Costa Rica and Oregon can come about by immigration and adaptive radiation. The increased diversity can be accommodated in the community by "within" and "between habitat" resource partitioning (MacArthur, 1965) resulting from the biological force of competition for limiting resources and/or the effects on population size due to predation (Paine, 1966a). Historical and present physical conditions in Costa Rica may be such that the rocky intertidal community has been structured through a combination of these biological processes in a manner different from that in Oregon.

Pianka (1966) and Baker (1970) both discuss reasons why there could be higher rates of evolution in the tropics, especially against the background of a "physically stable" geologic history, an almost constant, warm climate, and a more or less even availability of food on an annual basis.

The increase in the number of species in the species pool could have resulted, in part, by immigration. Immigration by gastropods with long-lived pelagic larvae could have occurred from the islands in the central Pacific via the North Equatorial Counter Current (Abbott, 1966) and also from the West Indian fauna when the land bridge between Central and South America was not fully formed. These possibilities for immigration could have added gastropod species which exploited food reserves like polychaetes and fish (Conus spp.) and sipunculids (Mitra spp.) to the fauna. Conus ebraeus, a widely dispersed Indo-Pacific species, is found in Costa Rica, as are Purpura pansa and Cypraea cervinetta which closely resemble West Indian species (Keen, 1971). The major trans-Pacific currents that move north from Asia toward the arctic and then down the North American coast to Oregon are cold currents. Larvae traveling in these currents must be physiologically able to withstand the low temperatures which would prevent migration of many gastropods.

The most obvious difference between the community structure in Oregon and Costa Rica is the significant increase in the contribution by carnivorous gastropods to the proportion of species, individuals, and volume of gastropods and chitons (Table III). The number of herbivorous gastropod and chiton species also increases in Costa Rica compared to Oregon, but not as much as carnivorous snail species do.

These tropical carnivorous snails are using food resources not eaten by Oregon snails (sipunculids and fish), and more species prey

on polychaetes and dead or injured prey. Since the rocky intertidal habitats in Oregon and Costa Rica are similar in that both contain sipunculids, small fish (2-5 cm long), polychaetes, and dead or injured organisms, this increase in carnivorous snail species which use more of the available food resources in the tropical rocky intertidal is probably an example of increased "within habitat" diversity (MacArthur, 1965).

That the higher tropical species diversity is attributable to an increase in the "within habitat" component of diversity due to different utilization of available food resources has been proposed for other animals also. In studies comparing terrestrial habitats in the temperate and tropical regions that appeared to be similar in vegetational structure, Karr (1971) and Orians (1969) agree that the major increase in tropical bird species seems to be due primarily to the increased exploitation of food resources which are more predictable in supply in the tropics; that is, an increase of the "within habitat" component of species diversity. Fleming (1973) thinks that the increase in mammal species in tropical habitats (forests) compared to similar temperate habitats is primarily due to the increase in bat species which is probably due, in turn, to the increased variety and year-round availability of certain kinds of food resources like fruit. McNab (1971) in his study on the trophic structure of bat communities also cites the increased diversity of food resources used by tropical bats as an important factor in the increase in bat diversity.

Further evidence that "within habitat" diversity forces are operating to increase gastropod diversity in the tropics can be found in protected sandy beach habitats. On a sandy beach inside Coos Bay, Oregon, there occur intertidally two species of Olivella which probably feed on detritus, and an uncommon predator, Polinices lewisii, which probably eats mostly bivalves but may take Olivella too. On a similar beach in Samara, Costa Rica, there occur Olivella columellaris (plankton feeder), Olivella morrisoni? (probably detritus eater), Agaronia propatula (preys on Olivella and bivalves), Natica chemnitzii (eats Olivella and maybe Agaronia and bivalves), and Natica grayi (eats Olivella and possibly bivalves). This increase in species diversity appears to be accommodated principally by an increase in the kind of food resources used (plankton and gastropods) compared to the temperate situations and by separation in space and time: the Olivella columellaris population follows the tide up and down the beach; Agaronia propatula resides in the mid and high tide zones; the Olivella morrisoni? is in the mid and low intertidal; Natica chemnitzii occurs in the mid tide zone; and N. grayi in the low intertidal zone.

Even though there is this increase in "within habitat" diversity in the tropics, local gastropod diversity is probably proximately controlled by local physical conditions like those mentioned. I may not have sampled in an area in Costa Rica where the physical conditions are such that the number of species present approaches the total species pool number. The Oregon transect with the highest percent of the species pool is South Cove with 82%; the highest percentage found

in Costa Rica is Quepos I with 51%. This also may be just due to problems with sampling in patchy habitats.

One of the problems with ascribing the diversity increases to an increase in "within habitat" diversity is that what I call a habitat (the rocky intertidal zone) is divisible into more than one microhabitat by the snails. Some of these microhabitats may be patchy in their distribution so that rocky intertidal areas, which I think are similar, may actually be different with respect to some microhabitat not easily discernible by me, but which determines whether a particular gastropod species is there or not. If this is the case, and it probably is for some snail species, there will also be a "between habitat" component of the total diversity which may be higher in the tropical areas thus favoring a higher species diversity (MacArthur, 1965).

The number of unique species in samples of similar, geographically close habitats can probably serve as an indicator of "between habitat" differences (Janzen and Schoener, 1968; Allan et al, 1973). Although the averages for the proportion of unique species in the Oregon and Costa Rican transects are not significantly different, the trend is for the Costa Rican transects to have a higher proportion of unique species (Table V). This trend and the fact that the similarity of species composition of geographically close transects tends to be lower in Costa Rica (Table IV) may indicate that there is greater "between habitat" diversity in Costa Rica.

These differences in unique species might be related to presence of more refugee species from mixed sand-mud-rock habitats in the area. Karr (1971), Orians (1969), Heyer and Berven (1973), and Patrick (1968) all stress that rare species could be refugees from surrounding areas and probably would not survive in the habitat under study. Certainly some of the rare snails in my Costa Rican transects (such as Opeato-
stoma pseudodon) are from the subtidal, but the total distribution is not known for most other species which are represented in the transects by only a few individuals.

In addition to refugee species or patchy microhabitats, the occurrence of unique species may be attributed to a sufficiently stable climate in Costa Rica that allows species with small numbers of individuals to survive (Baker, 1970). If this were the case, one would expect the increase between Oregon and Costa Rica in unique species to occur among both herbivore and carnivore species. The percentage of unique species which are herbivores and carnivores is similar for Oregon and Costa Rica; thus it appears that this may be occurring (Table VII). If the Costa Rican carnivore but not the herbivore proportion had increased, this might have been because the increase in species diversity is due mainly to secondary carnivores which are usually larger (in order to subdue prey) and rarer due to high energy requirements.

I think that the greater gastropod and chiton species diversity in Costa Rica can be primarily attributed to "within habitat" differences based mainly on the types of prey utilized. However,

there is probably also some increase due to the "between habitat" component of species diversity.

The increase in "within" and "between habitat" diversity in Costa Rica could have been influenced by competition, predation, and/or immigration. Without experimentation in the field, most of the evidence relating to the possibility of competition or predation as a structuring force in the community must be circumstantial or speculative.

I cannot supply any direct evidence supporting Paine's hypothesis that the large number of predatory gastropod species in Costa Rica should be reducing competition among the prey species for limiting resources and thus maintaining a high prey diversity which in turn can perhaps support more predators. Most of the increase in predator diversity is in species which eat fish, sipunculids, dead material, and polychaetes. With the exception of some families of polychaetes, these prey do not appear to be capable of monopolizing the space resource which Paine (1966a, 1971) feels is important in the rocky intertidal community.

If space in the intertidal could be limiting for some species (Paine, 1966a, 1971; Dayton, 1971), barnacles seem to be the only organism capable of monopolizing this resource in the absence of predation in Costa Rica. Mussels were not common in the areas studied and where they do occur they are usually about 1 cm in length. Algae do not appear to be a serious threat to space, since the standing crop is poor. Dawson (1962) describes the area around Quepos, Costa

Rica, as the most impoverished in the number of algal species that he has seen on the Pacific Coast. Six of the ten families of polychaetes that provide food resources for Costa Rican snails are tube builders which require space, but it would have to be demonstrated that some of these species could win in a competitive situation where space was limiting. In some places there are mats of Chaetopterus and sabellariid tubes (Puerto Escondido), so this might be a possibility. These mats of worm tubes are shelters for many different kinds of polychaetes, crustaceans, and small gastropods, so that the overall diversity is increased compared to a mass of barnacles.

In Costa Rica there are no large invertebrate carnivores like the starfish of the Oregon intertidal zone which consume large quantities of barnacles, bivalves, and gastropods (Paine, 1966a, 1971; Menge, 1972). The top invertebrate carnivores in my Costa Rican transects are four species of gastropods whose populations appear to occupy different habitats, probably based on intertidal height and wave exposure differences. As with the starfish in Oregon, these species do not rely only on gastropods for prey; they all eat barnacles also and probably could handle bivalves. Although these species do not have individuals the size of Pisaster, the population sizes can be substantial. Thus they could easily affect the abundance of other gastropods significantly.

I do not have data on prey abundance or species diversity so I cannot speculate as to whether the predators are a factor in permitting more prey species to coexist in Costa Rica, as Paine's

hypothesis predicts, nor whether the increase in gastropod carnivore diversity is correlated with an increase in prey diversity, as Arnold (1972) found for lizard species. The predation theory would predict the reverse. There is also a real possibility that the entire intertidal community is structured by intense fish predation (Bakus, 1969).

There is some evidence of a speculative nature that competition is a major structuring force in these rocky intertidal communities. When the intertidal height ranges (defined as the number of centimeters between two standard deviations above and two standard deviations below the average height of the quadrats in which a species was found) of the species appearing in five or more sample quadrats are compared in Oregon and Costa Rica, the ranges in Oregon are significantly wider ($t=2.460$; $d.f.=55$; $P<.05$; 2 tail test). This could support the idea that competition due to increased numbers of species in Costa Rica could lead to habitat contraction for some species while the food preferences for these species would remain similar (MacArthur and Pianka, 1966; MacArthur and Wilson, 1967).

This apparent reduction in habitat sizes for the Costa Rican gastropods may, however, be the result of an effective lowering of upper limits at which snails can survive in the tropical intertidal due to the higher heat stress. Notice in Figures 5 and 6 for the number of species in quadrats of certain average heights that the upper limit of the distribution of points in the Costa Rica graph meets the Y-axis at a much lower height than in that for Oregon.

In spite of the difference in how the zero tide base line is determined, I think the difference is real and probably due to desiccation factors. If there is a lowering of the effective intertidal height for physiological reasons, I would also expect the intertidal ranges of most species to shrink.

There has been some theoretical work on whether one should find generalist or specialist predators in a situation structured by competition (MacArthur and Pianka, 1966; MacArthur and Levins, 1964), but unfortunately I do not have enough data on most of the species consuming polychaetes or dead or injured prey in the tropics to comment too much on differences in prey specialists and generalists between the tropical and temperate zones. Many carnivorous species in both areas can handle at least two different types of prey (Appendices 6 and 7), so it should be possible to switch prey preferences if a type of prey becomes low in abundance or if local conditions preclude some prey species. This could stabilize the food web.

There is also the problem of how to define a specialist; is it a species which eats only one species of prey or is it one feeding on just one prey type which may include different genera and even families? For instance, there are several species eating polychaetes and there does appear to be a separation of these species on the basis of whether the polychaetes are tube-dwelling or benthic crawlers. It remains to be discovered whether those species that still feed on similar types of worms have spatial or temporal habitat separation

and eat similar species or if they actually specialize on different species.

The higher number of ubiquitous species in Oregon may mean that the Costa Rican gastropods have finer resource partitioning with patchy food and/or habitats. If competition has forced species to specialize on patchy resources, and if these resources are patchy enough so that my samples missed them in some transects or they weren't there at all, one would expect to find more unique species and fewer ubiquitous species in Costa Rica. On the other hand, a generalist would be better off in an environment where prey patches are small and dispersed (MacArthur and Pianka, 1966; Kohn, 1968), which is probably the case for some predators on polychaetes.

Still more speculatively, the fact that there is only one species of gastropod (Searlesia dira) in Oregon that does predictably attack live gastropods in parts of its range (Lloyd, 1972) may be due to competition from predation pressures by the starfish Leptasterias and Pisaster on gastropod populations. In the absence of starfish in Costa Rica, the species diversity of gastropod-eating snails has increased over evolutionary time. Of course, there may be physiological and other reasons why these differences occur.

The estimated volume of gastropods, which should approximate the trends that real biomass measurements would show, are very significantly positively related to the latitude (Table XII) and to no other physical parameter. As mentioned before, this is due to the presence in Oregon of large chitons, such as Cryptochiton.

stelleri and Katharina tunicata and the large populations of the relatively big herbivore Tegula funebris which can occur in numbers of over 100 per square meter. These particular herbivores are long lived and keep growing for many years. Tegula funebris lives to be over 30 years old (Frank, 1965) while the carnivorous Thais emarginata probably doesn't survive beyond 3-4 years (Miller, personal observation).

One might expect the tropical transects to have a lower estimated gastropod biomass if the sizes of the individual gastropods were comparatively small due to shorter longevity (high turnover) and if the populations were not superabundant; as Tegula funebris or Listorina spp. can be. Frank (1969) studied several species of tropical gastropods on Heron Island, Australia, and found that growth and, presumably, longevity of a number of these snails corresponds to his finding for temperate snails like Tegula funebris, Searlesia dira, and Diodora aspera. Thus it would seem that some tropical snails would be able to live as long and grow as large as temperate ones. This may be true for the large subtidal Strombus spp. in Costa Rica.

These volume differences between Costa Rica and Oregon molluscs also might be attributed to productivity differences, but there is no data on productivity for this area and one can't make predictions from the biomass of algae. Although Costa Rica has a more even growing season, there is a low standing crop of algae. This could be caused by the intense grazing by fish and invertebrates and the physiological

problems of heat stress in the intertidal. Oregon has the bulk of the algae produced in a spring bloom which lasts into the fall, but there is always an obvious standing crop of algae all year around.

The next steps in comparing community structure in the rocky intertidal areas in the temperate and tropical regions should be along the lines of designing exclosures to study the effect gastropods and fish are having on the invertebrate and algal populations, since the equivalent studies have been done in the temperate zone (Connell, 1961, 1970; Paine, 1966a, 1971; Dayton, 1972). The abundance and diversity of gastropod prey should also be measured to determine if there is a superabundance of food for the gastropods and if the gastropod diversity can be correlated with prey diversity (Arnold, 1972).

The community structure in the Costa Rican rocky intertidal zone is different from Oregon mainly due to the presence of so many carnivorous gastropods feeding on food types that exist in the temperate rocky intertidal but are not used by the predaceous gastropods present. The colder waters may indeed be hindering the radiation of carnivorous genera of gastropods prominent in the tropical trophic structure such as Conus, Cypraea, and Mitra. On the other hand, it may just be a matter of time, since the central California waters do have members of these genera subtidally; and the Columbellidae and Turridae occur in Oregon; but they have not radiated into many species, as they have in Costa Rica.

SUMMARY

Molluscs, along with some other groups, have an increasing number of species along a decreasing latitudinal gradient. There are several hypotheses regarding ecological processes that allow more species to co-occur in tropical habitats than in similar habitats in the temperate zone. This study examines how differences in physical variables and trophic structure affect local species diversity in similar rocky intertidal regions of the West Americas and relates these results to hypotheses put forth to explain diversity gradients.

Transects in rocky intertidal areas were done in Oregon, U.S.A., and Costa Rica, Central America, to compare gastropod and chiton species diversity and trophic relationships and food and habitat preferences of carnivorous gastropods. Several physical parameters of each transect were measured to determine if some relationship existed between them and species diversity. These parameters were: degree of wave exposure; proportion of quadrats in the transect in the mid and low intertidal zones; latitude; the proportion of quadrats which had the undersides of boulders or ledges available for habitation; and two measures of topographic relief.

The studies done at six sites in Oregon and eight sites in Costa Rica show that local gastropod and chiton species diversity is variable; the tropical sites do not always have a higher diversity. The species pool for the tropical transects (75) is greater than for

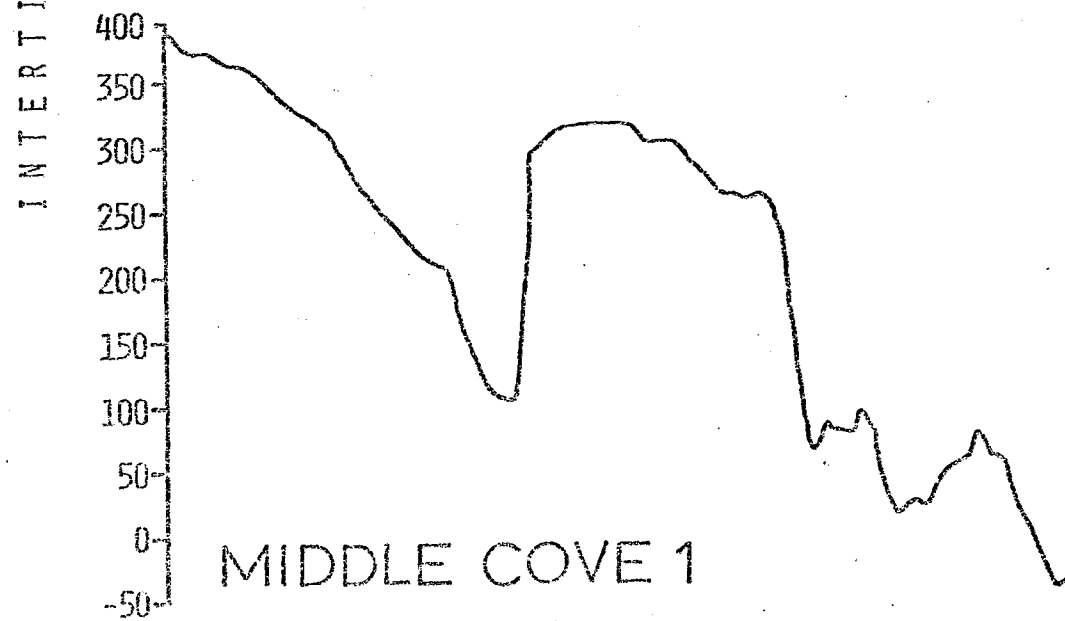
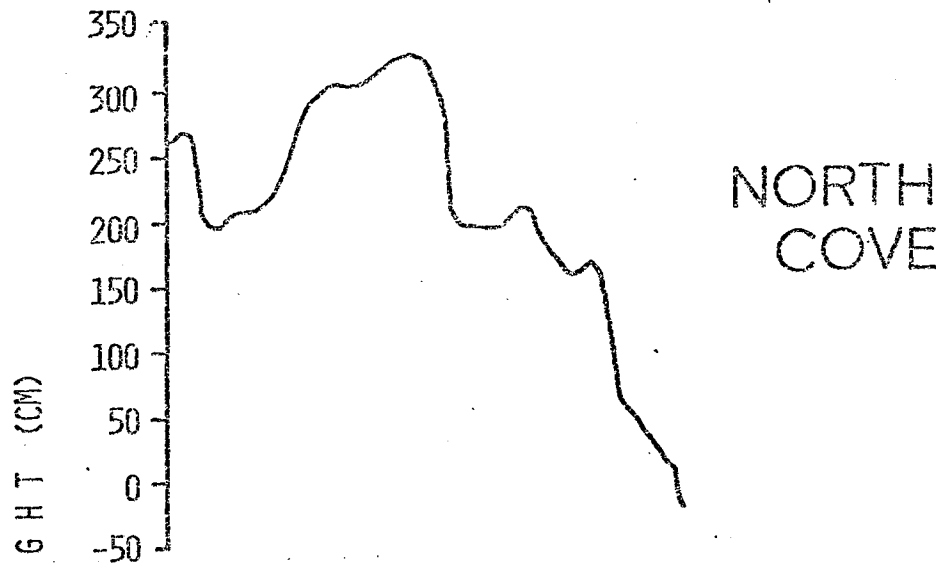
Oregon (44), so there is an increase in diversity in the tropics when larger geographic areas are considered. The tropical transects have a different trophic structure with many more carnivorous gastropod species than the Oregon transects. The density and estimated volume of snails per square meter is much higher in the temperate transects owing to the size and numbers of herbivorous individuals.

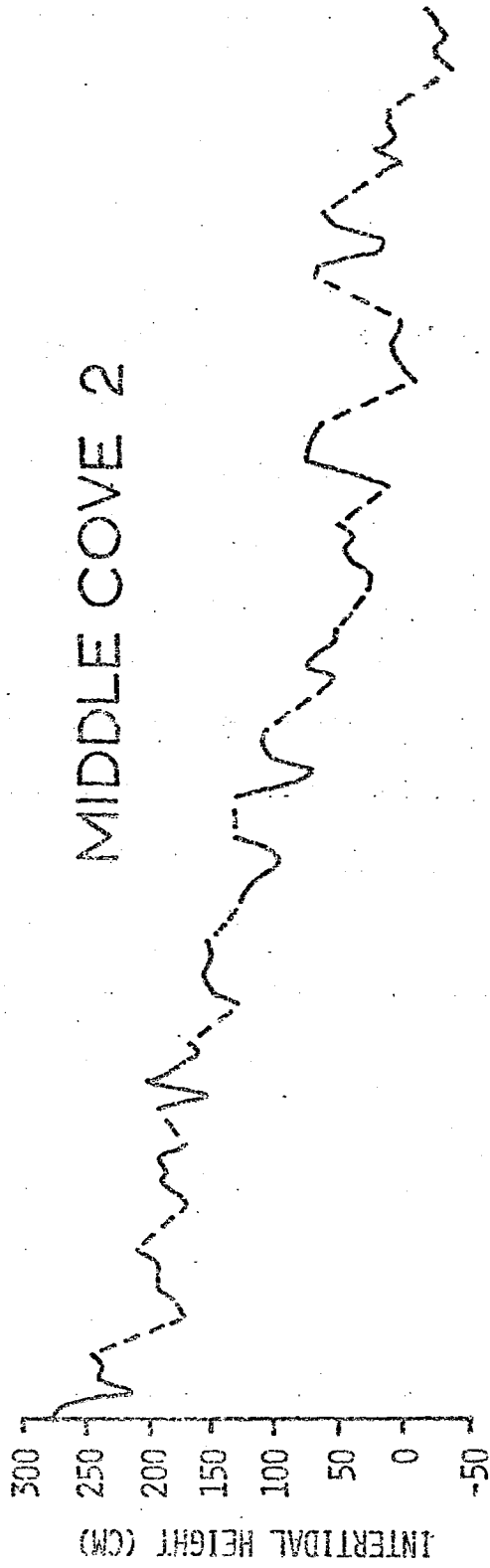
A stepwise multiple regression of the number of species on the physical parameters suggested that wave exposure is the most important variable influencing species diversity among the transects; the next two parameters in order of importance are the proportion of the transect that is in the high intertidal zone and the predictability of the topographic relief as measured.

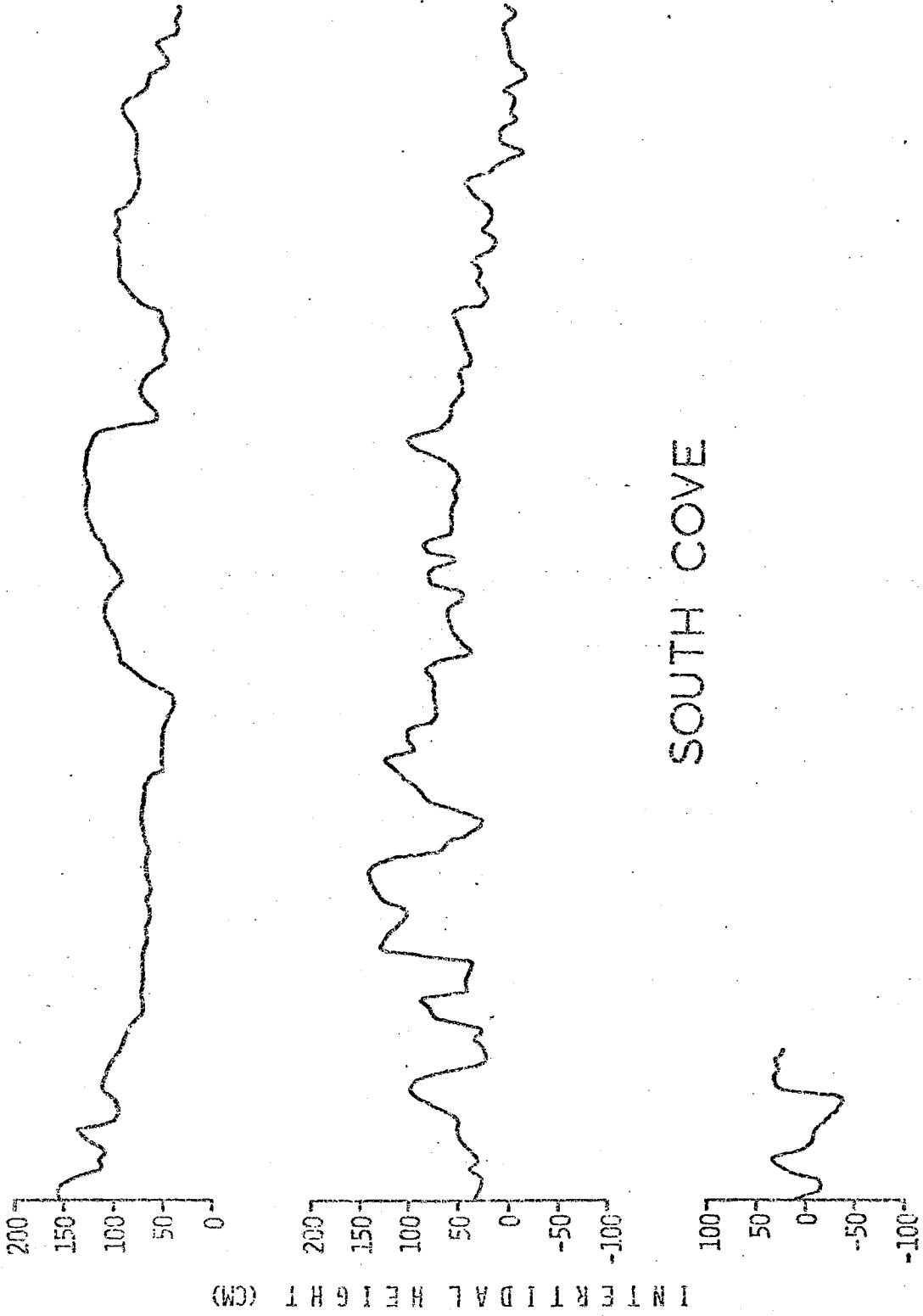
Most carnivorous gastropod species with overlapping intertidal height ranges use different food resources. The increase in carnivorous gastropod diversity in Costa Rica is mostly in species which utilize different food resources than do temperate zone snails, species that eat polychaete worms, and snails that prefer dead or injured organisms. Because of these feeding differences the tropical community trophic structure is much more complex than the temperate one.

APPENDIX 1

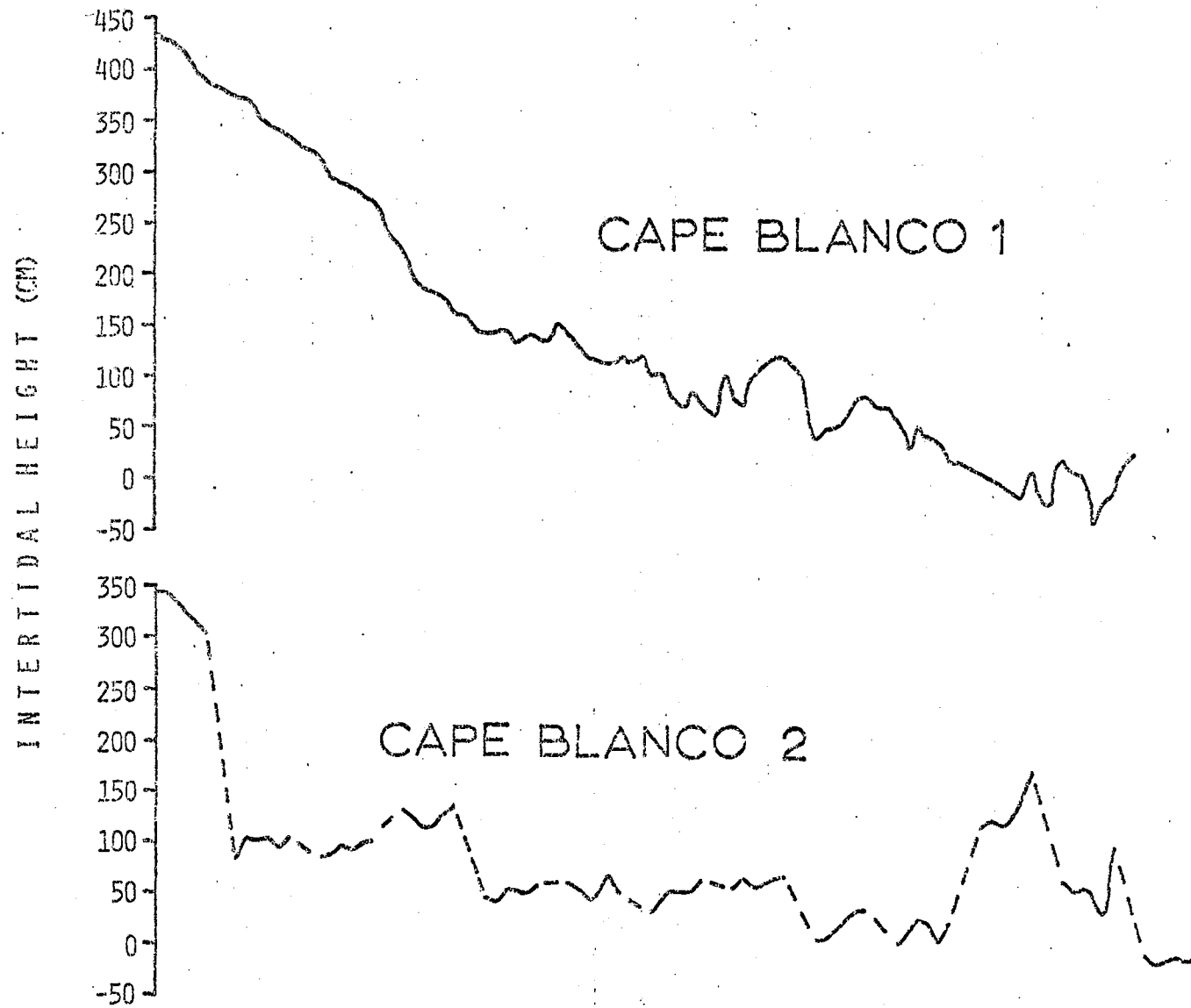
Topographic profiles of the transects in relation to the intertidal height. The profile line in transects not sampled every meter is broken. Note that the transect profiles for South Cove and Sámará 1, 2, and 3 are separated into sections.

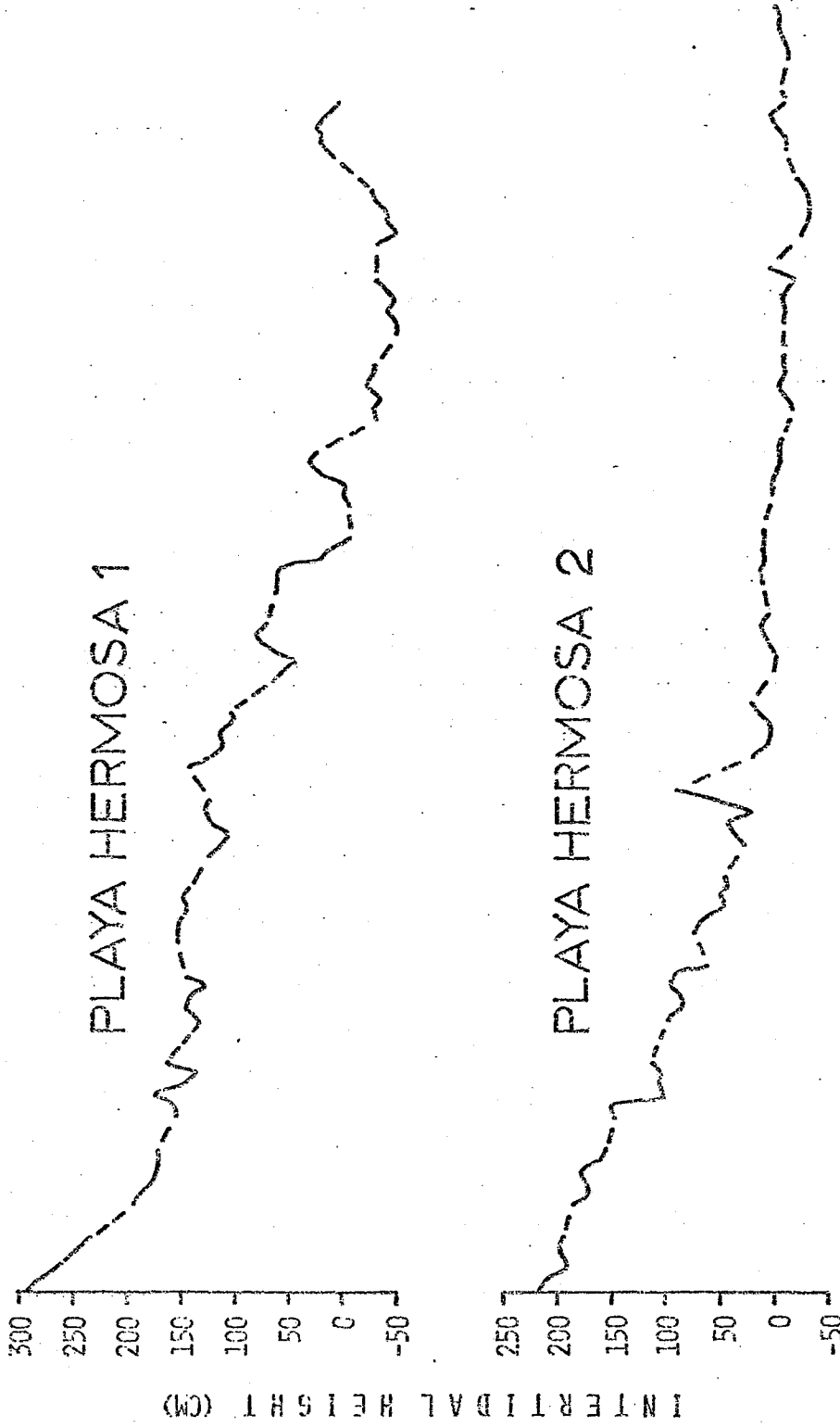


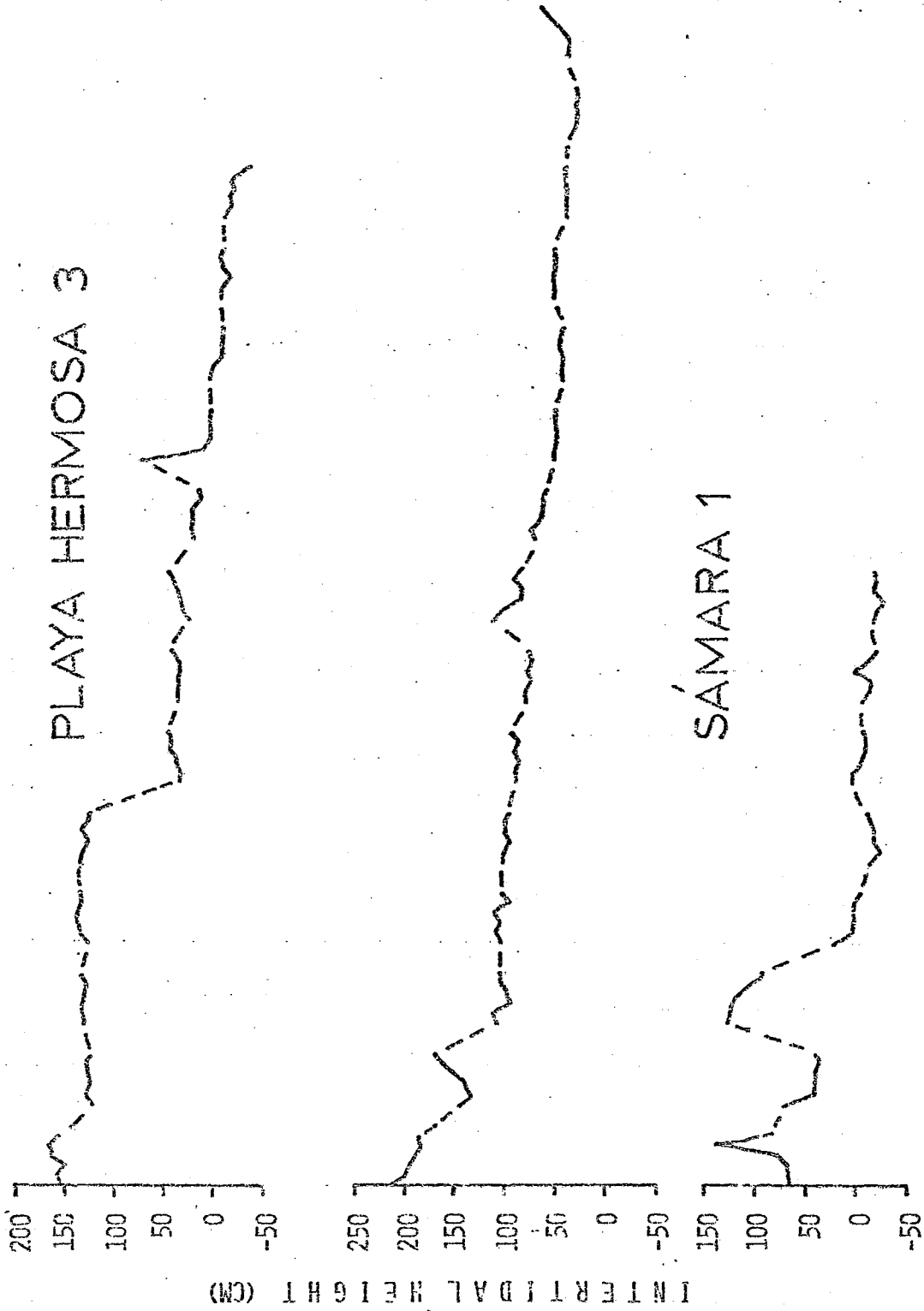


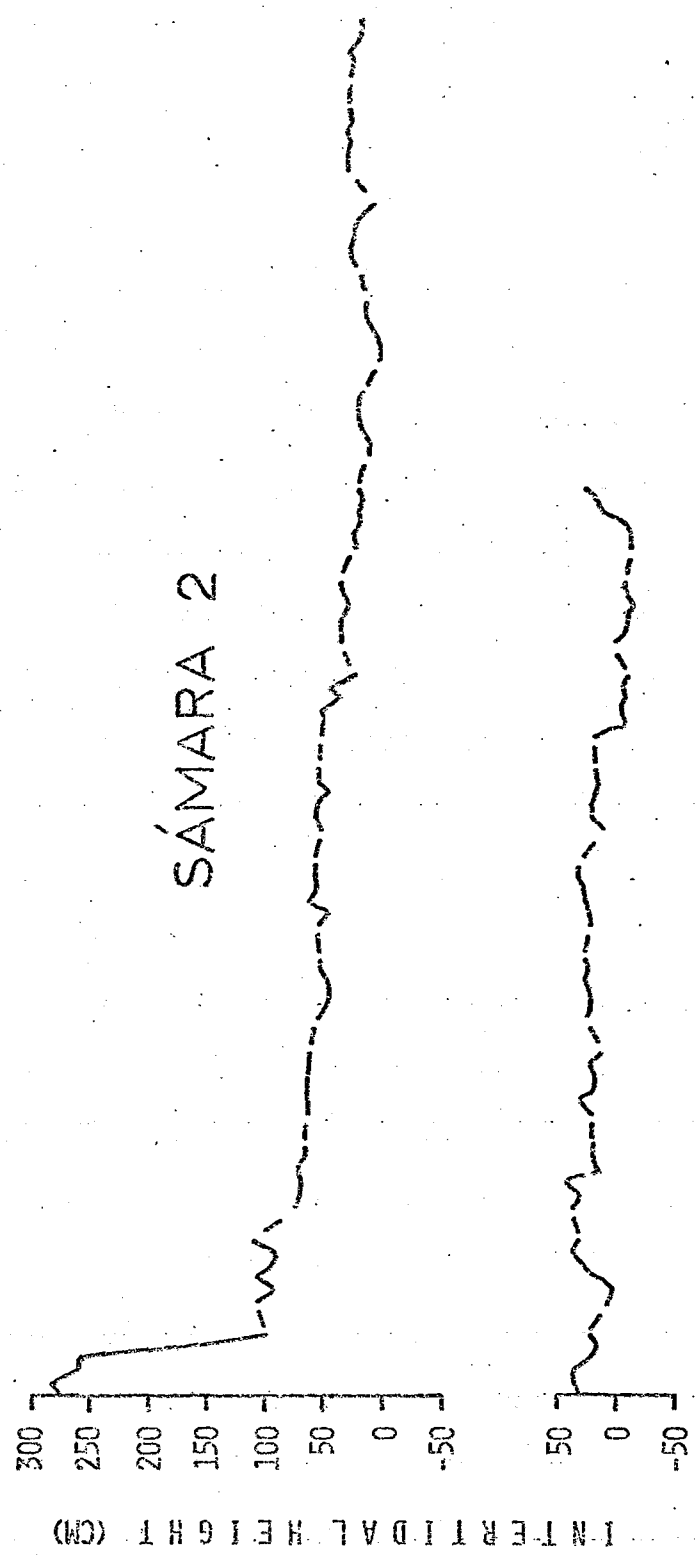


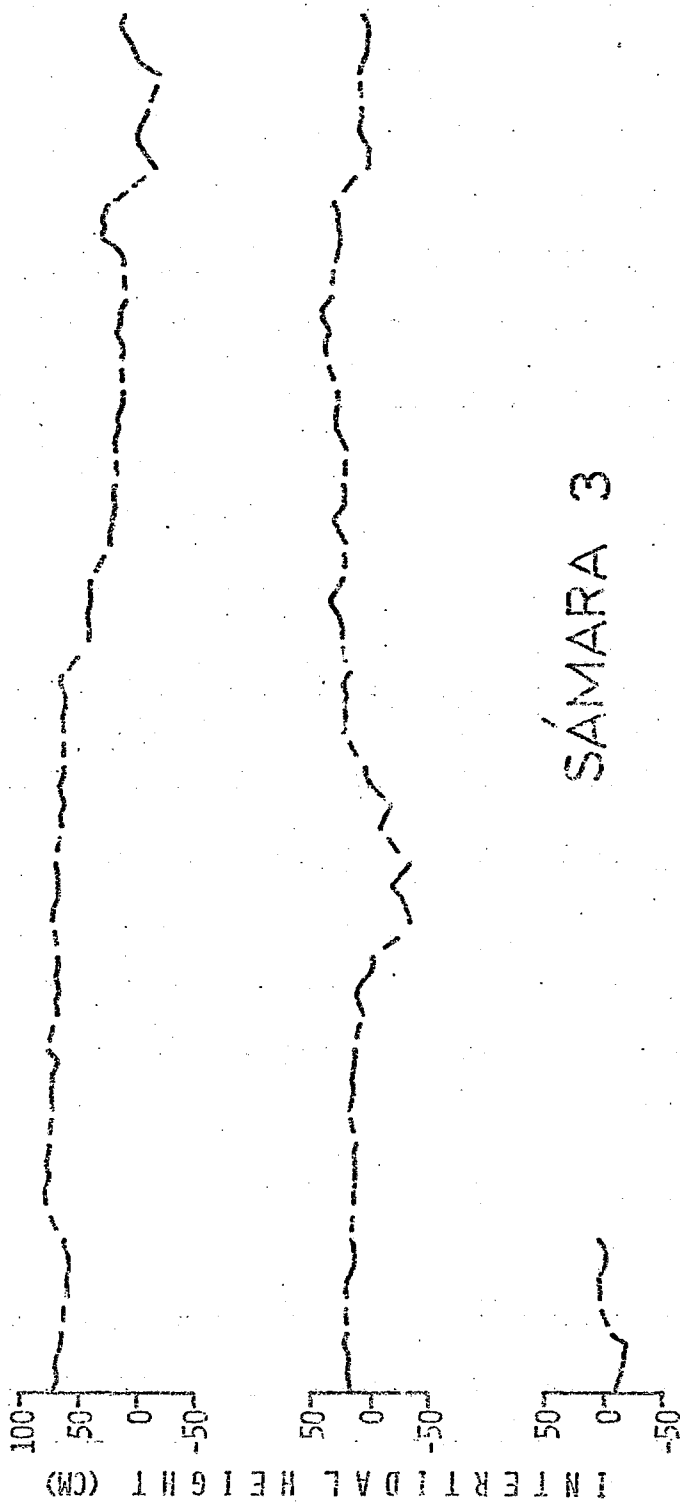
SOUTH COVE

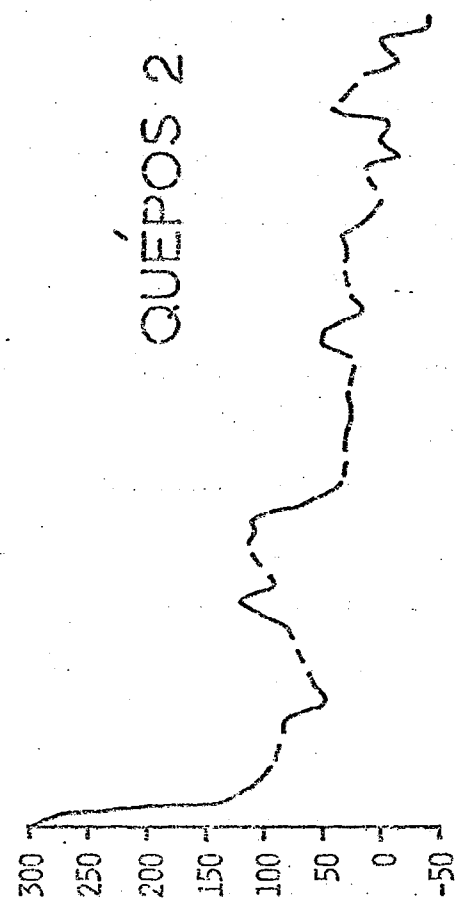
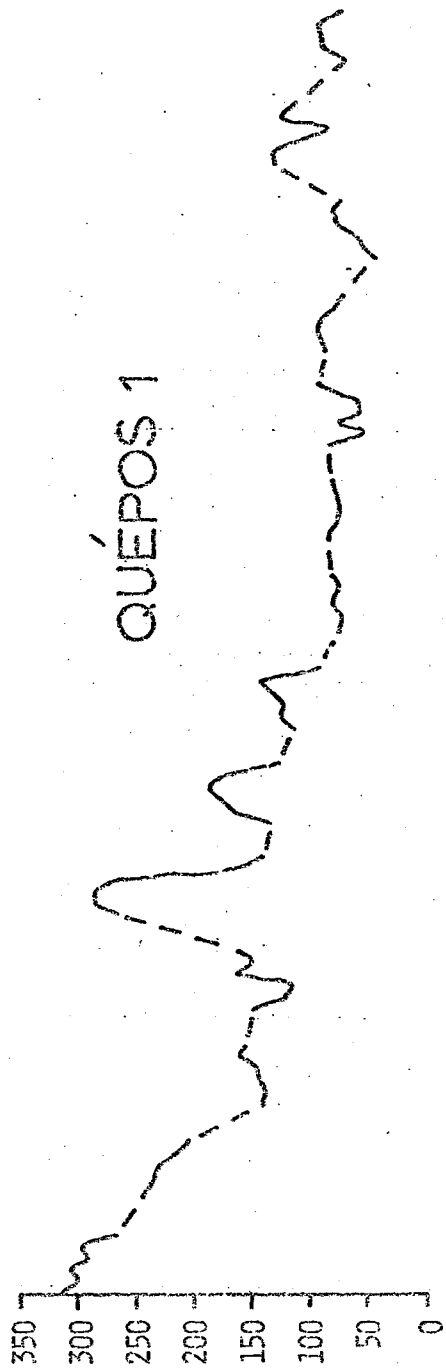












INTERTIDAL HEIGHT (CM)

APPENDIX 2. LIST OF SPECIES AND NUMBER OF INDIVIDUALS FOUND IN EACH

TRANSECT IN OREGON

Species	North Cove	Middle Cove 1	Middle Cove 2	South Cove	Cape Blanco 1	Cape Blanco 2
GASTROPODA: PROSOBRANCHIA						
<u>Diodora aspera</u> (Rathke, 1833)			3	5		
<u>Acmaea digitalis</u> Rathke, 1833	308	641	53	433	286	220
<u>Acmaea mitra</u> Rathke, 1833	1	8	15	9	1	3
<u>Acmaea pelta</u> Rathke, 1833	73	142	2	144	70	67
<u>Acmaea persona</u> Rathke, 1833			15			
<u>Acmaea scutum</u> Rathke, 1833		41	67	113	28	51
<u>Calliostoma ligatum</u> (Gould, 1846)		1	3	77	30	15
<u>Lirularia succincta</u> (Carpenter, 1846)			36	248	1	51
<u>Tegula funebris</u> (A. Adams, 1855)			530	2165		3
<u>Littorina scutulata</u> Gould, 1849		185	1532	5415	2050	928
<u>Lacuna carinata</u> Gould, 1848				75		350
<u>Pittina eschrichtii</u> (Middendorff, 1849)			13	110		1

	NC	MC1	MC2	SC	CB1	CB2
<u>Cerithiopsis columna</u> Carpenter, 1854	1		1	3		
<u>Cerithiopsis stejnegeri</u> Dall, 1884				10		
<u>Epitonium tinctum</u> (Carpenter, 1854)				1		
<u>Opalia chacei</u> Strong, 1937				4		
<u>Velutina laevigata</u> (Linnaeus, 1767)					1	
<u>Ceratostoma foliatum</u> (Gmelin, 1792)		1	1	5		
<u>Ocenebra interfossa</u> (Carpenter, 1864)		2	1	41	9	5
<u>Ocenebra lurida</u> (Middendorff, 1849)		5	18	76	17	4
<u>Thais canaliculata</u> (Duclos, 1832)	3				1	
<u>Thais emarginata</u> (Deshayes, 1839)	22	21	18	19	93	1
<u>Thais lamellosa</u> (Gmelin, 1791)			1	60		3
<u>Searlesia dira</u> (Reeve, 1846)			7	147	31	40
<u>Amphissa columbiana</u> Dall, 1916	2		31	147	19	28
<u>Mitrella carinata</u> (Hinds, 1844)			3	29		

	NC	MC1	MC2	SC	CB1	CB2
GASTROPODA: OPISTHOBRANCHIA						
<u>Archidoris montereyensis</u> (Cooper, 1862)		1		1		2
<u>Diaulula sandiegensis</u> (Cooper, 1862)				6		
<u>Rostanga pulchra</u> MacFarland, 1905				2		
<u>Hemissenda crassicornis</u> (Eschscholtz, 1831)						3
<u>Triopha carpenteri</u> (Stearns, 1873)				2		
GASTROPODA: PULMONATA						
<u>Oncidiella sp.</u>	23	55	2	61	34	
POLYPLACOPHORA						
<u>Cryptochiton stelleri</u> (Middendorff, 1846)				2		
<u>Cyanoplax dentiens</u> (Gould, 1846)		9	13	40	11	14
<u>Ischnochiton cooperi</u> (Carpenter in Pilsbry, 1892)			2	1		
<u>Katharina tunicata</u> (Wood, 1815)	20	18		4	9	8
<u>Mopalia cirrata</u> Berry, 1919			1			
<u>Mopalia hindsii</u> Reeve, 1847		3	1			
<u>Mopalia lignosa</u> Gould, 1846	2		11	14	2	5

	NC	MC1	MC2	SC	CBI	CB2
<u>Mopalia muscosa</u> Gould, 1846		2	2	16		
<u>Tonicella lineata</u> (Wood, 1815)	29	24	18	91	18	15
<u>Placiphorella velata</u> Carpenter in Dall, 1879		1				
chiton sp. 1	1			1		
chiton sp. 2	1					
ECHINODERMATA: ASTEROIDEA						
<u>Leptasterias hexactis</u> (Stimpson, 1862)	3	22	3	33	14	35
<u>Fisaster ochraceus</u> (Brandt, 1835)	3		1	4	76	53

APPENDIX 3. LIST OF SPECIES AND NUMBER OF INDIVIDUALS FOUND IN EACH TRANSECT IN MEXICO & COSTA RICA

Species ¹	Puerto Escondido	Playa Hermosa 1	Playa Hermosa 2	Playa Hermosa 3	Samara 1	Samara 2	Samara 3	Quepos 1	Quepos 2
GASTROPODA: PROSOBRANCHIA									
<u>Diodora inaequalis</u> (Sowerby, 1835)	1								
<u>Diodora pica</u> (Sowerby, 1835)					1				1
<u>Fissurella microtrema</u> Sowerby, 1835	6	1	1	1		1	2		
<u>Fissurella nigrocincta</u> Carpenter, 1856	1								
<u>Fissurella virescens</u> Sowerby, 1835		4	7		4	4	9	14	13
<u>Collisella atrata</u> (Carpenter, 1857)	211								
<u>Collisella discors</u> (Philippi, 1849)	37								
<u>Notoacmaea fascicularis</u> (Manke, 1851)		1			1	1		3	

	PE	PH1	PH2	PH3	S1	S2	S3	Q1	Q2
<u>Notoacmaea filosa</u> (Carpenter, 1865)					3				
<u>Scurria mesoleuca</u> (Menke, 1851)	1				1	4		3	
<u>Scurria stipulata</u> (Reeve, 1855)			2		4	2		3	1
<u>Tegula cooksoni</u> (E.A. Smith, 1877)					11	1	2	2	1
<u>Tegula globulus</u> (Carpenter, 1857)	38								
<u>Tegula peliiserpentis</u> (Wood, 1828)		7	5					25	1
<u>Arene sp.</u>								1	
<u>Turbo saxosus</u> Wood, 1828					5	5		1	
<u>Nerita funiculata</u> Menke, 1851		212	15	6	658	11	466	2	4
<u>Nerita scabricosta</u> Lamarck, 1822	57	71	39	3	12	3		18	6
<u>Littorina aspera</u> Philippi, 1846		1502	7	219	138	288		18	3
<u>Littorina modesta</u> Philippi, 1846	73	2601	8	1036	7	91		68	11

	PE	PH1	PH2	PH3	S1	S2	S3	Q1	Q2
<u>Rissoina effusa</u> Mörch, 1860			1						
<u>Turritella sp.</u>				1					
<u>Cerithium adustum</u> Kiener, 1841	1	1	1	2	4	11	1	1	
<u>Cerithium gemmatum</u> Hinds, 1844					40	1			
<u>Planaxis planicostatus</u> Sowerby, 1825		14	93		22			193	
<u>Hipponix panamensis</u> C.B. Adams, 1852		25	256	28	12			80	15
<u>Crucibulum sp.</u>	1								
<u>Erato sp.</u>	1								
<u>Cypraea arabicula</u> (Lamarck, 1811)	1								
<u>Cypraea cervinetta</u> Kiener, 1843								2	
<u>Cymatium lignarium</u> (Broderip, 1833)	1								

	PE	PH1	PH2	PH3	S1	S2	S3	Q1	Q1
<u>Bursa caelata</u> (Broderip, 1833)								1	2
<u>Aspella pyramidalis</u> (Broderip, 1833)									1
<u>Muricanthus callidinus</u> Berry, 1958		2							
<u>Muricanthus princeps</u> (Broderip, 1833)	3								
<u>Coralliophila costata</u> (Blainville, 1832)	1								
<u>Acanthina brevidentata</u> (Wood, 1828)	4	54	17		86		113	23	3
<u>Morula ferruginosa</u> (Reeve, 1846)	2	1						1	1
<u>Purpura columellaris</u> (Lamarck, 1822)	2								
<u>Purpura pansa</u> Gould, 1853	33					3			1
<u>Thais biserialis</u> (Blainville, 1832)			2	1			14		
<u>Thais melones</u> (Duclos, 1832)	13	22	39	46	31	34	100	41	25

	PE	PH1	PH2	PH3	S1	S2	S3	Q1	Q2
<u>Thais speciosa</u> (Valenciennes, 1832)	26	1							
<u>Thais triangularis</u> (Blainville, 1832)	46	3	4	15				7	2
<u>Cantharus gemmatus</u> (Reeve, 1846)	1								
<u>Cantharus sanguinolentus</u> (Duclos, 1833)	10							3	
<u>Engina maura</u> (Sowerby, 1832)									1
<u>Engina pulchra</u> (Reeve, 1846)					2				
<u>Engina tabogaensis</u> Bartsch, 1931	1							4	
<u>Anachis boivini</u> (Kiener, 1841)					27	42	136		
<u>Anachis dalli</u> Bartsch, 1931			43				172	3	
<u>Anachis fluctuata</u> (Sowerby, 1832)					8	124	44	4	
<u>Anachis lentigenosa</u> (Hinds, 1844)		236	89				1	71	1

	PE	PH1	PH2	PH3	S1	S2	S3	Q1	Q2
<u>Anachis pardalis</u> (Hinds, 1843)		1	29						
<u>Anachis pygmaea</u> (Sowerby, 1832)			21						
<u>Anachis varia</u> (Sowerby, 1832)					7				
<u>Anachis sp.</u>					1				
<u>Columbella fuscata</u> Sowerby, 1832	1								
<u>Columbella strombiformis</u> Lamarck, 1822	27					7			
<u>Columbella sp. 1</u>		1							
<u>Columbella sp. 2</u>			1						
<u>Mitrella elegans</u> (Dall, 1871)		1	12	1	1	6			
<u>Mitrella sp.</u>	20								
<u>Leucozonia cerata</u> (Wood, 1829)	10	4	2			1		3	5

	PE	PH1	PH2	PH3	S1	S2	S3	Q1	Q2
<u>Opeatostoma pseudodon</u> (Burrow, 1815)	1	1						1	1
<u>Mitra lens</u> Wood, 1828						1	1		
<u>Mitra tristis</u> Broderip, 1836	4	1			1	2	1	1	3
<u>Conus gladiator</u> Broderip, 1833	4	1	1			1	1	1	1
<u>Conus nux</u> Broderip, 1833	12				2		2		
<u>Conus princeps</u> Linnaeus, 1758							1		
<u>Conus purpurascens</u> Sowerby, 1833	1				1		1	2	
<u>Crassispira discors</u> (Sowerby, 1834)				1					
<u>Crassispira eurynome</u> Dall, 1919	1								
<u>Crassispira rudis</u> (Sowerby, 1834)						11	2		
<u>Pilsbryspira aterrima</u> (Sowerby, 1834)						5	3	1	

	PE	PH1	PH2	PH3	S1	S2	S3	Q1	Q2
<u>Pilsbryspira garciacubasi</u> Shasky, 1971	1								
<u>Pilsbryspira melchersi</u> (Menke, 1851)							2		
<u>Pilsbryspira</u> (undescribed)								2	
GASTROPODA: OPISTHOBRANCHIA									
<u>Odostomia</u> sp.						6			
<u>Bulla punctulata</u> A. Adams in Sowerby, 1850						4			
<u>Dolabrifera</u> sp.				2	4	9	4		
<u>Tridachiella diomedea</u> (Bergh, 1894)	5					13	8		
nudibranch sp.						1			
GASTROPODA: PULMONATA									
<u>Siphonaria gigas</u> Sowerby, 1825			1					21	
<u>Siphonaria palmata</u> Carpenter, 1857		9	1				1	2	53

	PE	PH1	PH2	PH3	S1	S2	S3	Q1	Q2
POLYPLACOPHORA									
<u>Acanthochitona rhodea</u> (Pilsbry, 1893)					2	6	2		1
<u>Acanthochitona</u> sp.	10								
<u>Callistochiton</u> sp.					1	1		1	
<u>Callistoplax ratusa</u> (Sowerby, 1832)	2								
<u>Chaetopleura</u> sp.					1		2		
<u>Chiton albolineatus</u> Broderip & Sowerby, 1829	14								
<u>Chiton articulatus</u> Sowerby, 1832	16								
<u>Chiton stokesii</u> Broderip, 1832		3	10	1	13		3	9	9
<u>Radsiella</u> sp. 1			1		14	10	4	1	
<u>Radsiella</u> sp. 2							2		
<u>Stenoplax limaciformis</u> (Sowerby, 1832)						1			

APPENDIX 4. ESTIMATED VOLUME IN CM³ OF INDIVIDUAL OREGON
GASTROPOD AND CHITON SPECIES USED IN CALCULATING
H¹ VOLUME FOR THE TRANSECTS.

SPECIES	VOLUME	SPECIES	VOLUME
GASTROPODA: FROSOBRANCHIA		<u>Thais canaliculata</u>	0.540
<u>Diodora aspera</u>	4.301	<u>Thais emarginata</u>	0.572
<u>Acmaea digitalis</u>	0.200	<u>Thais lamellosa</u>	3.159
<u>Acmaea mitra</u>	2.649	<u>Searlesia dira</u>	1.595
<u>Acmaea pelta</u>	2.362	<u>Amphissa columbiana</u>	0.286
<u>Acmaea persona</u>	2.264	<u>Mitrella carinata</u>	0.036
<u>Acmaea scutum</u>	1.242	GASTROPODA: OPISTHOBRANCHIA	
<u>Calliostoma ligatum</u>	1.344	<u>Archidoris montereyensis</u>	4.396
<u>Lirularia succincta</u>	0.026	<u>Diaulula sandiegensis</u>	4.251
<u>Tegula funebris</u>	2.547	<u>Rostanga pulchra</u>	0.056
<u>Littorina scutulata</u>	0.059	<u>Hemissenda crassicornis</u>	0.593
<u>Lacuna carinata</u>	0.009	<u>Triopha carpenteri</u>	0.884
<u>Bittium eschrichtii</u>	0.046	GASTROPODA: PULMONATA	
<u>Cerithiopsis columna</u>	0.014	<u>Oncidiella sp.</u>	0.032
<u>Cerithiopsis stejnegeri</u>	0.034	POLYPLACOPHORA	
<u>Epitonium tinctum</u>	0.151	<u>Cryptochiton stelleri</u>	2356.884
<u>Opalia chacei</u>	0.574	<u>Cyanooplax dentiens</u>	0.127
<u>Velutina laevigata</u>	0.066	<u>Ischnochiton cooperi</u>	0.127
<u>Coratostema foliatum</u>	4.955	<u>Katharina tunicata</u>	80.660
<u>Ocenebra interfossa</u>	0.269	<u>Mopalia cirrata</u>	0.961
<u>Ocenebra lurida</u>	0.319	<u>Mopalia hindsii</u>	23.399

<u>Mopalia lignosa</u>	20.488
<u>Mopalia muscosa</u>	19.386
<u>Tonicella lineata</u>	3.561
<u>Placiphorelia velata</u>	13.113
chiton sp. 1	0.113
chiton sp. 2	0.127

APPENDIX 5. ESTIMATED VOLUME IN CM³ OF INDIVIDUAL COSTA RICAN GASTROPOD AND CHITON SPECIES USED IN CALCULATING H' VOLUME FOR THE TRANSECTS.

SPECIES	VOLUME	SPECIES	VOLUME
GASTROPODA: PROSOBRANCHIA		<u>Rissoina effusa</u>	0.007
<u>Diodora inaequalis</u>	0.630	<u>Turritella</u> sp.	0.189
<u>Diodora pica</u>	0.022	<u>Cerithium adustum</u>	0.113
<u>Fissurella microtrema</u>	0.221	<u>Cerithium gemmatum</u>	0.042
<u>Fissurella nigrocincta</u>	1.450	<u>Planaxis planicostatus</u>	0.235
<u>Fissurella virescens</u>	1.016	<u>Hipponix panamensis</u>	0.336
<u>Collisella atrata</u>	1.597	<u>Craecibulum</u> sp.	1.065
<u>Collisella discors</u>	1.588	<u>Erato</u> sp.	0.059
<u>Notoacmaea fascicularis</u>	0.058	<u>Cypraea arabicula</u>	1.335
<u>Notoacmaea filosa</u>	0.154	<u>Cypraea cervinetta</u>	11.700
<u>Scurria mesoleuca</u>	0.269	<u>Cymatium lignarium</u>	0.425
<u>Scurria stipulata</u>	0.269	<u>Eursa caelata</u>	1.595
<u>Tegula cooksoni</u>	0.378	<u>Aspella pyramidalis</u>	0.019
<u>Tegula globulus</u>	0.236	<u>Muricanthus callidinus</u>	7.630
<u>Tegula pellisserpentis</u>	1.546	<u>Muricanthus princeps</u>	27.150
<u>Arene</u> sp.	0.007	<u>Coralliophila costata</u>	1.646
<u>Turbo saxosus</u>	1.701	<u>Acanthina brevidentata</u>	0.843
<u>Nerita funiculata</u>	0.151	<u>Morula ferruginosa</u>	0.667
<u>Nerita scabricosta</u>	0.798	<u>Purpura columellaris</u>	1.331
<u>Littorina aspera</u>	0.085	<u>Purpura pansa</u>	2.126
<u>Littorina modesta</u>	0.034	<u>Thais biserialis</u>	0.794

<u>Thais melones</u>	1.613	<u>Mitra tristis</u>	0.142
<u>Thais speciosa</u>	0.794	<u>Conus gladiator</u>	2.296
<u>Thais triangularis</u>	0.340	<u>Conus nux</u>	0.394
<u>Cantharus gemmatus</u>	1.418	<u>Conus princeps</u>	3.411
<u>Cantharus sanguinolentus</u>	0.832	<u>Conus purpurascens</u>	4.264
<u>Engina naura</u>	0.202	<u>Crassispira discors</u>	0.016
<u>Engina pulchra</u>	0.142	<u>Crassispira eurynome</u>	0.123
<u>Engina tabogaensis</u>	0.123	<u>Crassispira rudis</u>	0.132
<u>Anachis boivini</u>	0.132	<u>Pilsbryspira aterrima</u>	0.132
<u>Anachis dalli</u>	0.014	<u>Pilsbryspira garciacubasi</u>	0.085
<u>Anachis fluctuata</u>	0.232	<u>Pilsbryspira melchersi</u>	0.072
<u>Anachis lentigenosa</u>	0.014	<u>Pilsbryspira</u> (undescribed)	0.085
<u>Anachis pardalis</u>	0.016	GASTROPODA: OPISTHOBRANCHIA	
<u>Anachis pygmaea</u>	0.025	<u>Odestomia</u> sp.	0.004
<u>Anachis varia</u>	0.076	<u>Bulla punctulata</u>	0.396
<u>Anachis</u> sp.	0.072	<u>Dolabrifera</u> sp.	2.784
<u>Columbella fuscata</u>	0.756	<u>Tridachiella diomedea</u>	1.557
<u>Columbella strombiformis</u>	0.604	nudibranch sp.	0.268
<u>Columbella</u> sp. 1	0.104	GASTROPODA: PULMONATA	
<u>Columbella</u> sp. 2	0.059	<u>Siphonaria gigas</u>	2.599
<u>Mitrella elegans</u>	0.046	<u>Siphonaria palmata</u>	0.064
<u>Mitrella</u> sp.	0.005	POLYPLACOPHORA	
<u>Leucozonia cerata</u>	0.319	<u>Acanthochitona rhodea</u>	0.706
<u>Opeostoma pseudodon</u>	0.869	<u>Acanthochitona</u> sp.	0.961
<u>Mitra lens</u>	0.468	<u>Callistochiton</u> sp.	0.050

<u>Callistoplax retusa</u>	0.553
<u>Chaetopleura sp.</u>	0.254
<u>Chiton albolineatus</u>	2.539
<u>Chiton articulatus</u>	8.928
<u>Chiton stokesii</u>	3.416
<u>Radsiella sp. 1</u>	0.170
<u>Radsiella sp. 2</u>	0.170
<u>Stenoplax linaciformis</u>	0.981

APPENDIX 6. A LIST OF PREY OF CARNIVOROUS GASTROPODS AND CHITONS OF OREGON.
 *OBSERVATIONS WERE MADE ON A DIFFERENT SPECIES OF THE SAME GENUS.

<u>Predator</u>	<u>Prey</u>		<u>Number of Observations</u>	
	<u>Classification</u>	<u>Species</u>	<u>Present Study</u>	<u>Previous Studies</u>
PROSOBRANCHIA				
Epitoniidae				
<u>Epitonium tinctum</u>	Cnidaria Anthozoa	Sea anemones		*Robinson (1970)
<u>Opalia</u>	Cnidaria Anthozoa	<u>Anthopleura elegantissima</u>	4	
Velutinidae				
<u>Velutina laevigata</u>	Chordata Ascidiacea	tunicates		*Graham (1955)
	Cnidaria Hydrozoa	hydroids		*Graham (1955)
Muricidae				
<u>Ceratostoma foliata</u>	Mollusca Bivalvia	<u>Botula californiensis</u> <u>Saxicava</u> sp. <u>Zerfaea pilsbryi</u> <u>Protothaca staminea</u>	1 17 1 1	
<u>Ocenebra interfossa</u>	Arthropoda Cirripedia	barnacles	12	

<u>Ocenebra luxida</u>	Porifera	sponge	9	
	Annelida			
	Polychaeta			
	Sedentaria	<u>Spirorbis sp.</u>	13	
	Mollusca			
	Bivalvia	<u>Botula?</u>	1	
	Gastropoda	<u>Acmaea pelta</u>	3	
	Arthropoda			
	Cirripedia	barnacles	37	
Thalididae				
<u>Thais canaliculata</u>	Mollusca			
	Bivalvia	<u>Mytilus californianus</u>	26	Paris (1960)
	Arthropoda			
	Cirripedia	barnacles	7	Dayton (1971); Paris (1960)
<u>Thais emarginata</u>	Mollusca			
	Bivalvia	<u>Mytilus californianus</u>	14	
	Gastropoda	<u>Acmaea digitalis</u>	3	
		<u>Acmaea pelta</u>	1	
	Arthropoda			
	Cirripedia	Barnacles	78	Dayton (1971); Connell, (1970)
<u>Thais lamellosa</u>	Mollusca			
	Bivalvia	<u>Botula californiensis</u>	118	
		<u>Mytilus californianus</u>	3	
		<u>Pholadidea sp.</u>	1	
	Arthropoda			
	Cirripedia	barnacles	140	Dayton (1971); Connell, (1970)

Columbellidae			
<u>Amphissa columbiana</u>	Porifera	sponge	3
	Annelida		
	Polychaeta		
	Sedentaria	Cirratulidae	
		<u>Dodecaceria fistulicola?</u>	6
		unidentified	1
		Capitellidae	1
		Terebellidae	1
		Sabellariidae	
		<u>Sabellaria cementarium</u>	2
		Sabellidae	6
		Serpulidae	
		<u>Spirorbis</u> sp.	17
	Errantia	Nereidae	
		<u>Platynereis bicanaliculata</u>	10
		unidentified	1
	Mollusca		
	Gastropoda	<u>Acmaea pelta</u>	1
		<u>Littorina scutulata</u>	1
		unidentified	2
	Arthropoda	unidentified Crustacea	12
	Cirripedia	barnacles	10
	Carrion	dead fish	8
<u>Mitrella carinata</u>	Annelida		
	Polychaeta		
	Errantia	Nereidae	1
		unidentified	1
	Arthropoda	unidentified Crustacea	1

Succinidae					
<u>Searlesia dira</u>	Porifera	sponge	1		
	Annelida				
	Polychaeta				
	Sedentaria	Citratulidae			
		<u>Dodecacaria</u> sp.	3		
		Terebellidae			
		<u>Pista pacifica</u>	1		
		<u>Thelepus crispus</u>	1		
		unidentified spp.	2	2	Lloyd (1972)
		Sabellariidae			
		<u>Sabellaria cementarium</u>	1	3	Lloyd (1972)
		Sabellidae			
		<u>Pseudopotamilla ocellata</u>	2		
		unidentified spp.	5	1	Lloyd (1972)
		Serpulidae	3		
	Errantia	Nereidae			
		<u>Platynereis bicanaliculata</u>	2	13	Lloyd (1972)
		Ampharetidae			
		<u>Phyllocomus hiltoni</u>	1		
	Mollusca				
	Bivalvia	<u>Botula?</u>	1		
		various spp.		62	Lloyd (1972)
	Gastropoda	<u>Acmaea digitalis</u>	1	8	Lloyd (1972)
		<u>Acmaea pelta</u>	1	6	Lloyd (1972)
		<u>Acmaea scutum</u>	2	34	Lloyd (1972)
		<u>Tegula funebris</u>	7		
		<u>Littorina scutulata</u>		116	Lloyd (1972)
		<u>Thais lamellosa</u>		6	Lloyd (1972)
		Unidentified	2		
	Polyplacophora	<u>Katharina tunicata</u>		71	Lloyd (1972)
	Arthropoda	unidentified Crustacea	7		
	Cirripedia	barnacles	16	109	Lloyd (1972)
	Carrion	dead fish		16	Lloyd (1972)
		dead crabs		37	Lloyd (1972)

NUDIBRANCHIA

Dorididae

Archidoris

montereyensis

Porifera

unidentified sponge

6

Diaulula

sandiegensis

Porifera

Halichondria panicea

2

Cook (1961)

unidentified sponge

4

Rostanga pulchra

Porifera

Hymedesmia versicolor?

1

Ophiitaspongia pennata

Cook (1961)

Aeolididae

Hemissenda

crassicornis

Cnidaria

hydroids

Bertsch et al,
(1972)

Triopha carpenteri

Bryozoa

bryozoans

McBeth (1971)

POLYPLACOPHORA

Placiphorella velata

Arthropoda

live, mobile Crustacea

3

McLean (1962)

APPENDIX 7. A LIST OF PREY OF COSTA RICAN CARNIVOROUS GASTROPODS.

*OBSERVATIONS WERE MADE ON A DIFFERENT SPECIES OF THE SAME GENUS.

<u>Predator</u>	<u>Prey</u>		<u>Number of Observations</u>	
	<u>Classification</u>	<u>Species</u>	<u>Present Study</u>	<u>Previous Studies</u>
PROSOBRANCHIA				
Eratoidae				
<u>Erato</u> sp.	Cnidaria	Hexamerous corals		*Salvini-Plawen, (1972)
	Chordata	tunicates		*Graham (1955)
Cypraeidae				
<u>Cypraea arabacula</u>	Porifera	unidentified sponge	3	*Graham (1955)
<u>Cypraea cervinetta</u>	Porifera	unidentified sponge	5	
	Chordata	unidentified tunicate	1	Spight, unpubl. 1
Cymatiidae				
<u>Cymatium lignarium</u>	Mollusca			
	Gastropoda	probably eats other snails		*Miller, unpub. 2 *Houbrick & Frette (1969)
Bursidae				
<u>Bursa caelata</u>	Echinodermata			
	Echinoidea	probably eats sea urchins		*Miller, unpub. 3
Muricidae				
<u>Aspella pyramidalis</u>	Mollusca			
	Bivalvia	probably bivalves		*Spight, unpub.

<u>Muricanthus</u> <u>callidinus</u>	Mollusca Bivalvia	unidentified bivalves	9	
<u>Muricanthus princeps</u>	Mollusca Bivalvia	unidentified bivalves	8	Spight, unpub. ¹
Coralliophilidae <u>Coralliophila</u> <u>costata</u>	Cnidaria Zoanthidea	unidentified zoanthids	1	
Thaididae <u>Acanthina</u> <u>brevidentata</u>	Arthropoda Cirripedia	barnacles	32	80 Paine (1966b)
<u>Morula ferruginosa</u>	Arthropoda Cirripedia	barnacles	2	39 Paine (1966b)
<u>Purpura columellaris</u>	Mollusca Gastropoda	<u>Nerita funiculata</u> <u>Littorina aspera</u>	1 1	
	Arthropoda Cirripedia	barnacles	2	
<u>Purpura pansa</u>	Mollusca Gastropoda	<u>Littorina modesta</u> <u>Nerita funiculata</u> <u>Nerita scabricosta</u>	2 3 1	

<u>Thais biserialis</u>	Mollusca			
	Bivalvia	mussels & oysters	2	68 Paine (1966a); ¹ Spight, unpub.
	Gastropods	<u>Littorina aspera</u>	1	18 Paine (1966a,b)
	Arthropoda			unidentified snails
	Cirripedia	barnacles		11 Paine (1966a,b)
	Carrion			Paine, (1966 a)
<u>Thais melones</u>	Mollusca			
	Bivalvia	<u>Modiolus</u> sp.	3	
		unidentified oysters	5	Spight, unpub. ¹
	Gastropoda	<u>Fissurella microtrema</u>	1	
		<u>Fissurella virescens</u>	3	
		unidentified limpet	1	
		unidentified turbinid	1	
		<u>Nerita funiculata</u>	2	
		unidentified vermetids	5	
		<u>Cerithium adustum</u>	3	
		<u>Cerithium gemmatum</u>	3	
		unidentified thaisid	1	
		<u>Mitra lens</u>	1	
	Polyplacophora	<u>Acanthochitona</u> sp.	1	
		unidentified chiton	1	
	Arthropoda			
	Cirripedia	barnacles	1	Spight, unpub. ¹
Carrion	dead crab	1		
<u>Thais speciosa</u>	Mollusca			
	Bivalvia	unidentified bivalve	5	
	Gastropoda	unidentified limpet	2	
		unidentified vermetid	4	
		<u>Cerithium</u> sp.		Spight, unpub. ¹
		<u>Crucibulum</u> sp.	1	
		<u>Anachis</u> spp.	2	
	Polyplacophora	unidentified chiton	3	
Arthropoda				
Cirripedia	barnacle	16		

<u>Thais triangularis</u>	Arthropoda Cirripedia	barnacles	15	
Buccinidae				
<u>Cantharus gemmatus</u>	Arthropoda	unidentified Crustacea	2	
<u>Cantharus sanguinolentus</u>	Annelida			
	Polychaeta			
	Sedentaria	Sabellariidae		
		<u>Idanthyrus</u> sp.	1	*Miller, unpub. ⁴
	Errantia	Eunicidae		
		<u>Eunice sonora</u>	1	
	Mollusca			
	Polyplocophora	unidentified chiton	1	
	Arthropoda	unidentified Crustacea	2	
	Cirripedia	barnacles		*Miller, unpub. ⁴
<u>Engina maura</u>	Annelida			
	Polychaeta			
	Sedentaria	Chaetopteridae		
		<u>Mesochaetopterus minutus</u>	1	
<u>Engina tabogaensis</u>	Annelida			
	Polychaeta			
	Sedentaria	Cirratulidae		
		<u>Caulleriella</u> sp.	5	
		Spionidae		
		<u>Polydora</u> sp.	2	
Columbellidae				
<u>Anachis boivini</u>	Carriion	piece of meat	1	
<u>Anachis dalli</u>		attracted to freshly killed crab, limpet, and chiton		Spight, unpub. ¹

<u>Anachis fluctuata</u>	Annelida			
	Polychaeta			
	Sedentaria	Chaetopteridae	1	
	Errantia	Nereidae	1	
Fasciolaridae				
<u>Leucozonia cerata</u>	Annelida			
	Polychaeta			
	Sedentaria	Serpulidae		
		<u>Hydroides</u> sp.	6	
		<u>Pomatoceros</u> sp.	2	
		Sabellariidae		
		<u>Phragmatopoma lapidosa</u>	2	
		<u>Idanthyrus pennatus</u>	2	
		unidentified sp.	1	
		Spionidae		
		<u>Polydora</u> sp.	1	
	Mollusca			
	Gastropoda	unidentified vermetid	2	
	Arthropoda			
	Insecta	Lepidopteran wing scales (from detritus?)	1	
<u>Opeatostoma pseudodon</u>	Annelida			
	Polychaeta			
	Sedentaria	Spionidae		
		<u>Polydora</u> sp.	1	4 Paine (1966b)
	Arthropoda			
	Cirripedia	barnacles	17	
Mitridae				
<u>Mitra lens</u>	Sipunculida	unidentified sipunculid	2	
<u>Mitra tristis</u>	Sipunculida	<u>Phascolosoma</u> sp.	5	
		unidentified sipunculid	2	

Conidae					
<u>Conus gladiator</u>	Annelida				
	Polychaeta				
	Errantia	Amphinomidae			
		<u>Euprosina</u> sp.	1		
		Nereidae			
		<u>Pseudonereis</u> sp.	1		
		Eunicidae			
		<u>Nicidion cariboea</u>	2		
		<u>Eunice cariboea</u>	2		
		unidentified	2		
<u>Conus aux</u>	Annelida				
	Polychaeta				
	Errantia	Nereidae	1	Nybakken, pers.	
				comm.	
		Eunicidae	2	Nybakken, pers.	
				comm.	
<u>Conus princeps</u>	Annelida				
	Polychaeta				
	Errantia	Eunicidae		Nybakken, pers.	
				comm.	
		<u>Palola paloloides</u>	1		
		<u>Palola sicilienses</u>	1		
<u>Conus purpurascens</u>	Chordata				
	Vertebrata	live fish	2	Nybakken. (1967)	
Turridae					
<u>Crassispira rudis</u>	Annelida				
	Polychaeta				
	Sedentaria	Cirratulidae	1		
		Terebellidae			
	Errantia	Nereidae			
				*Miller, unpub. ⁵	
				13 *Miller, unpub. ⁶	

NUDIBRANCHIA

Aeolididae

unidentified sp. Cnidaria (probably) hydroids ?

- ¹Spight, T. M. Unpublished paper entitled: Organization of shallow water marine communities. I. Gastropods of a tropical rocky shore.
- ²Eniwetok Atoll; 4 Cymatium chlorostomum (Link) feeding on Morula granulata in mid intertidal zone.
- ³Eniwetok Atoll; Bursa bufonia (Gmelin) found eating urchins (3; also Kohn, pers. comm.), ophiuroid (2), and an amphinomid polychaete (1). No polychaete setae were ever found in the Costa Rican Bursa caelata fecal pellets.
- ⁴Baja California; Solenosteira macrospira Berry found eating barnacles (3) and sabellid polychaetes (3).
- ⁵Jamaica; Crassispira fuscescens (1).
- ⁶Baja California; Crassispira plato Pilsbry & Lowe found in mid tidal zone feeding on nereids (13).

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