COMPETITIVE INTERACTIONS AMONG THREE CRAB SPECIES IN THE INTERTIDAL ZONE

by

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This investigation describes and analyzes the competitive relationships between three brachyuran crab species which are often sympatric in the rocky intertidal areas of bays and estuaries along the Pacific coast of North America. First I describe the mechanism of competition between two congeneric shore crab species, Hemigrapsus nudus and H. oregonensis, in the middle and high intertidal zones at several locations in Coos Bay, Oregon. The evidence, from descriptive field sampling, small-scale habitat manipulations, and a species addition experiment indicates that the two species actively compete for refuge space along a gradient in rock sizes. Competition is mediated by size-related interference ability. In the near absence of one of the two, the resource utilization patterns exhibited by the species are virtually identical and biased toward progressively larger rocks. Larger rocks are thought to confer higher survivorship on resident individuals, owing to the inverse relationship between rock size and wave-induced disturbance rates. When the two species are sympatric, interspecific competition results in a distinct pattern of microspatial patchiness in which *H. nudus* dominates the largest rocks and most *H. oregonensis* are restricted to the locally abundant, but least stable smaller rocks. Competitive coexistence is facilitated by patchy physical disturbances and differences in the life history strategies employed by the two species: *H. oregonensis* rapidly achieves maturity and reproduces frequently while *H. nudus* individuals opt for enhanced growth rates, hence interference ability, by delaying maturity and reproducing less frequently. Competitive exclusion of *H. oregonensis* occurs only in habitats composed exclusively of large boulders or crevices, where disturbance rates are uniformly low and interference ability is at a premium.

The effects of a third competitor, *Cancer productus*, on the shore crabs in the lower intertidal zone are also considered. Methodology parallels that for the two species interaction. Analysis of the data, here only from a single site, indicates that the three species form a competitive hierarchy of *C. productus*, *H. nudus*, *H. oregonensis* in order from top to bottom. Both *Hemigrapsus* species are adversely affected by periodic invasions of *Cancer*. However, because *Cancer* also selectively occupies refuges

provided by large rocks, _H. nudus_ suffers disproportionately. As a result, periods of peak abundance of _Cancer_ and _H. nudus_ are mutually exclusive. Abundances of _Cancer_, the only osmoconformer of the three, are in turn negatively correlated with rates of freshwater input into the bay.

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TABLE OF CONTENTS

Chapter

I. THE ROLE OF SPATIAL HETEROGENEITY IN THE COMPETITIVE INTERACTION BETWEEN TWO CONGENERIC SHORE CRAB SPECIES.................. 1

Introduction 1
Animals and Their Treatment 4
Results...................................... 15
Discussion 70

II. COMPETITION FOR SPACE AMONG THREE CRABS IN THE ROCKY INTERTIDAL ZONE: THE EFFECTS OF CANCER PRODUCTUS ON COMPETITION BETWEEN TWO SHORE CRAB SPECIES............................ 78

Introduction................................. 78
Animals and their Treatment 81
Results...................................... 89
Discussion 114
General Discussion 122

APPENDIX 133

LITERATURE CITED 145

ILLUSTRATIONS

1. A Map of the Lower Coos Bay Region 9
2. Resource Utilization Curves for the Two Shore Crab Species in the Mid Zone at North Island as Determined by Stepwise Multiple Regression of Numbers of each Species as a Function of Rock Surface Area and its Square 17
3. Cumulative Percent of the Total Number of Individuals of Each Species in the Mid Zone at North Island as a Function of Rock Surface Area (100 cm^2 Classes) 19
4. Average densities of each <u>Hemigrapsus</u> species in the High and Mid Zones at North Island.......... 21
5. Resource Utilization Curves for Both Shore Crab Species in the High Zone at North Island... 22
6. Disturbance Rates of Rocks in 100 cm^2 Size Classes at North Island.............................. 25
7. Per Cent of the Total Rock Surface Area of Occupied Rocks Accounted for by Rocks <150 cm^2 as a Function of Total Shore Crab Density........... 27
8. Relationship Between the Size of Rock Occupied and the Size of Resident Individuals of Each Species at North Island 32
9. Mean Number of Individuals in 1-m^2 Quadrats in Which Rock Size Distributions were Experimentally Altered in the Mid Zone at North Island.... 37
10. Mean Number of Individuals in 1-m^2 Quadrats in Which Rock Size Distributions were Experimentally Altered in the High Zone at North Island.. 42
11. Average Density of <u>H. oregonensis</u> in the Mid Zone at South Island Plotted Against Time....... 48
12. Comparison of the Average Surface Area/m^2 of Rocks in 100 cm^2 Size Classes on North and South Island.................................... 51
13. Resource Utilization Curves for <u>H. oregonensis</u> in the Mid Zone at South Island.................. 52
14. Comparisons of the Mid Zone Resource Utilization Curves (Based on Biomass) for <u>H. oregonensis</u> at South Island and <u>H. nudus</u> at North Island.... 54
15. Resource Utilization Curves for Both Species in the Mid Zone at South Island Following the Addition of 5,500 <u>H. nudus</u> One Month Earlier.... 57
16. Resource Utilization Patterns, Shown as Mean Number ±1 S.E. in 100 cm^2 rock size classes, for <u>H. nudus</u> amd <u>H. oregonensis</u> in a cobble area at Fossil Point.......................... 60

. ILLUSTRATIONS (Cont.)

17. Size Frequency Distributions of the Shore Crab Species at Two Locations at Fossil Point.......... 62

18. Percentage of Adult Females of Both Species That Were Ovigerous at Each Field Survey......... 66

19. Percentage of the Total Number of Females in 5 mm Size Classes that Were Ovigerous at Any Time During the Study (January 1979-March 1980).. 68

20. Mean Monthly Discharge Rates from the Millicoma River Over the Course of the Study and Average Surface Salinity at North Island................ 85

21. Average Sizes of Individuals of Each Species Sampled at Various Times in the Permanent Quadrats at North Island......................... 90

22. Densities of the Three Crab Species in Permanent Quadrats in the Low Intertidal Zone at North Island 92

23. Relationship Between <u>Cancer productus</u> Density in Permanent Quadrats in the Low Zone and Rates of Discharge of the Millicoma River in 1978 and 1979.................................. 95

24. Size Distributions of Rocks in Permanent Quadrats in the Low Zone at North Island......... 98

25. Mean Biomass for the Three Crab Species in 200 cm^2 Rock Size Classes During Each Sample Period 103

26. Resource Utilization Curves for Each of the Three Crab Species.................................. 106

27. Relationship Between the Incidence of Rock Occupancy by <u>Cancer</u> and Rock Size, Shown at Months During Which <u>Cancer</u> Abundances Increased from Annual Minima to Annual Maxima During 1978 and 1979.................................. 108

28. Average Number of Each Species in Each of Two Types of 1 m^2 Quadrats in Which the Rock Size Distributions were Altered 112

29. Average Numbers of Each Crab Species in Each of Three Types of 1 m^2 Quadrats in Which Rock Size Distributions Were Altered 115

30. Summarizing Model of the Net Interactions Between the Species and the Effects of Physical Factors.. 116

31. Comparisons for All Three Crab Species of the Per Cent Increase in Size Which Results from a Single Molt, with Size Before Molting......... 144

TABLES

1. Size Frequency Distributions (%) of *H. oregonensis* and *H. nudus* Sampled Along the Permanent Transect in the Mid Zone at North Island............ 29
2. Size Frequency Distributions (%) of *H. oregonensis* and *H. nudus* Sampled Along the Permanent Transect in the High Zone at North Island....... 30
3. Results of *a posteriori* Simultaneous Test Procedure for Determining Differences Among the Estimated Regression Slopes of Size of Rock Occupied on Size of Resident Individuals........ 34
4. Size Frequency Distributions (%) of *H. oregonensis* and *H. nudus* censused in the Mid Zone Experimental Plots (Checkerboards) at North Island.. 40
5. Results of χ^2 Tests of Independence of the Size Distributions of Individuals Sampled Along the Permanent Transect and in the Mid Zone Experimental Plot at North Island 41
6. Results of χ^2 Tests of Independence of the Distributions of *H. nudus* among the Treatment Types in the Mid and High Zone Checkerboards.......... 44
7. Size Frequency Distributions (%) of *H. oregonensis* Sampled in the Mid Zone Along the Permanent Transect at South Island......................... 50
8. Results of Linear Regressions of Size of Rock Occupied and the Size of Resident *H. oregonensis* Individuals in the Mid Zone at South Island...... 55
9. Results of χ^2 Test of Independence Between the Size Distribution of Released and Recaptured *H. nudus* at South Island........................... 59
10. Parameters Used to Estimate Damp Weight from Carapace Width According to the Equation Weight (g) = b x Width (mm)÷...................... 88
11. Results of Stepwise Multiple Regressions of Biomass (g) for Each Species on Rock Surface (A, cm^2) and its Squared Term (A^2)............... 101
12. Results of Linear Regressions of Size of Rock Occupied on the Size of Resident *Cancer productus* Individuals in the Low Zone at North Island.. 109
13. Results of Experiment 3 on Predation by *Cancer* on the Shore Crabs.............................. 136
14. Results of Trials 4-6 on *Cancer* Predation.......... 138

TABLES (Cont.)

15. Numbers of Small (12-18 mm) *H. nudus* and *H. oregonensis* Killed over 7 Day Periods of Exposure to Large Individuals of either *Hemigrapsus* species 141

16. Survival of *H. nudus* and *H. oregonensis* of Various Sizes After 24-hr Exposure to Air at 16°C 143

CHAPTER I

THE ROLE OF SPATIAL HETEROGENEITY IN THE COMPETITIVE INTERACTION BETWEEN TWO CONGENERIC SHORE CRAB SPECIES

Introduction

The marine rocky intertidal zone has been an important source of information concerning the roles of species interactions in structuring biological communities. Connell (1961) demonstrated the importance of interspecific competition in determining the vertical distributions of barnacle species. Other studies have shown that predation (Dayton 1971, Paine 1966, Kitching and Ebling 1965, Menge 1976), by selective elimination of competitive dominants, may markedly influence community composition and species diversity.

Recent studies of intertidal ecology have tended to emphasize the effects of physical disturbance in structuring communities. Several authors (Dayton 1971, Levin and Paine 1974, Menge and Sutherland 1976, Connell 1978) have shown that random local disturbances may maintain species diversity by preventing regional monopolization of limiting resources by a few competitively dominant species. Selective stochastic disturbances appear to have similar, but more predictable results. In his study of an intertidal algal community, Sousa (1979) showed that disturbance (rock turnover) and its concomitant effects varied inversely over a gradient in rock sizes. Thus, although poor competitors may be outcompeted locally on large, stable rocks, these species persist in the community because of frequent disturbances among smaller, less stable rocks.

Perhaps the most fundamental generalization from these and other studies is that the extent to which any single factor, or combination of factors, determines community characterics is a function of the community under investigation (Osman 1977). However, almost without exception, the studies above have dealt exclusively with sessile and semisessile species which compete for space on rock surfaces. As there is a priori no compelling reason to believe that hypotheses generated from sessile communities should apply equally to other intertidal assemblages (Connell 1978), highly motile shore crab species (Hemigrapsus nudus and H. oregonensis) were chosen as the foci of the present study.

This report addresses aspects of the competitive interaction in the high and middle intertidal zones where the two species compete for refuge space under rocks. Like other highly motile competitors in the intertidal zone

(Vance 1972) and elsewhere (Grant 1972, Schoener 1974, Cody 1974), the spatial distributions of the two species at the regional level, or even within single isolated areas, suggest that evolved habitat or resource partitioning is the primary factor controlling species composition of this simple assemblage. However, I will argue, for this case at least, that any explanation which rests solely upon evolved partitioning is inadequate. In particular, I intend to show that when physical conditions are generally favorable for both species, the disturbance regime (defined by the rock size distribution and wave exposure) largely determines the species composition through its effect on the size structure of the crabs. Evidence for the proposed model comes from descriptive field sampling, small-scale habitat manipulations, and a species addition experiment. I will also address evidence concerning the reproductive strategies employed by the two species and their relationship to the competitive interaction. In general, the results show that when the two species are sympatric, *H. nudus* individuals dominate the most favorable portions of the contested resources (refuges provided by large, stable rocks), while interspecific competition forces most *H. oregonensis* individuals to occupy the least favorable portions of the available resources where mortality rates are relatively high. The evidence suggests that these patterns in resource utilization are brought about by differences between the species in size-related interference ability. The differences in interference ability are, in turn, related to the divergent life history strategies of the two species; H. nudus directs relatively more resources to growth and interference ability, while H. oregonensis opts for higher reproductive rates and greater colonizing ability. As a result, complete exclusion of H. oregonensis occurs only in habitats in which physical disturbance rates are uniformly low and interference ability is at a premium.

A third crab species, Cancer productus, was found to exert a major, albeit seasonal influence on the shore crabs in the low intertidal zone. For clarity, the effects of C. productus on the shore crab interaction are detailed elsewhere (Chapter II).

Animals and Their Treatment

Connell (1975) has reviewed the problems inherent in experimental manipulations of natural populations of highly motile species. In addition to the more obvious difficulties in performing treatments (species removals, etc.) more subtle but equally important problems arise in attempts to design adequate controls and in the interpretation of results, especially if aggressive encounters in part determine rates of movement of the species involved. These problems are to a large extent unavoidable and may be expected to become increasingly frustrating as the numbers of species and environmental complexity increase.

With these admonitions in mind and after initial failures to deduce potentially causal patterns in complex outer coast habitats, structurally and biologically simpler sites were sought and found among the rocky intertidal areas within Coos Bay, Oregon. In these habitats, the two *Hemigrapsus* species are more ideally suited to field studies: 1) they represent a dominant portion of the macrofauna, with densities commonly exceeding $100/m^2$; 2) individuals are easily sexed, measured, and identified even when they are small, and 3) as will be shown, they compete for space in discrete and quantifiable refuges (i.e., under rocks of known size and location).

The Species

Hemigrapsus nudus and *H. oregonensis* are the only eastern Pacific representatives of a brachyuran genus (Family Grapsidae) whose component species are distributed widely around the Pacific rim. Populations of the two species often occur sympatrically throughout their geographic ranges (Alaska to the Gulf of California, Rathbun 1917), although *H. nudus* is the more common on protected rocky outer coasts and *H. oregonensis* dominates on mud banks in the upper reaches of coastal estuaries (Ricketts et al. 1968, Hiatt 1948). Knudsen (1964) described the distributions of the two shore crabs in Puget Sound: rocky headlands are exclusively occupied by <u>H. nudus</u> while habitats composed of mud and gravel are occupied exclusively by <u>H. oregonensis</u>. Habitats in which the two species are sympatric are of an intermediate nature ("coarse to fine sand overlain with a fair supply of rocks and boulders"). Both species are omnivorous, may successfully inhabit all intertidal zones (Hiatt 1948, and personal observations), and are effective hyperosmotic regulators (Jones 1941). In addition, both species are aggressive yet gregarious, and when the opportunity is available, seek refuge from predators and exposure to physical factors, under rocks. Under these rocks, one often finds from one to many crabs (largely depending upon rock size) and these aggregations are often mixed species assemblages (Hiatt 1948, Todd and Dehnel 1960). It is important to note that <u>H. nudus</u> is typically the larger of the two species. It is rare, for example, to find <u>H. oregonensis</u> larger than 35 mm, although individual <u>H. nudus</u> may often exceed 50 mm in carapace width. Reproductive strategies will be discussed in a later section of the chapter (see Life Histories).

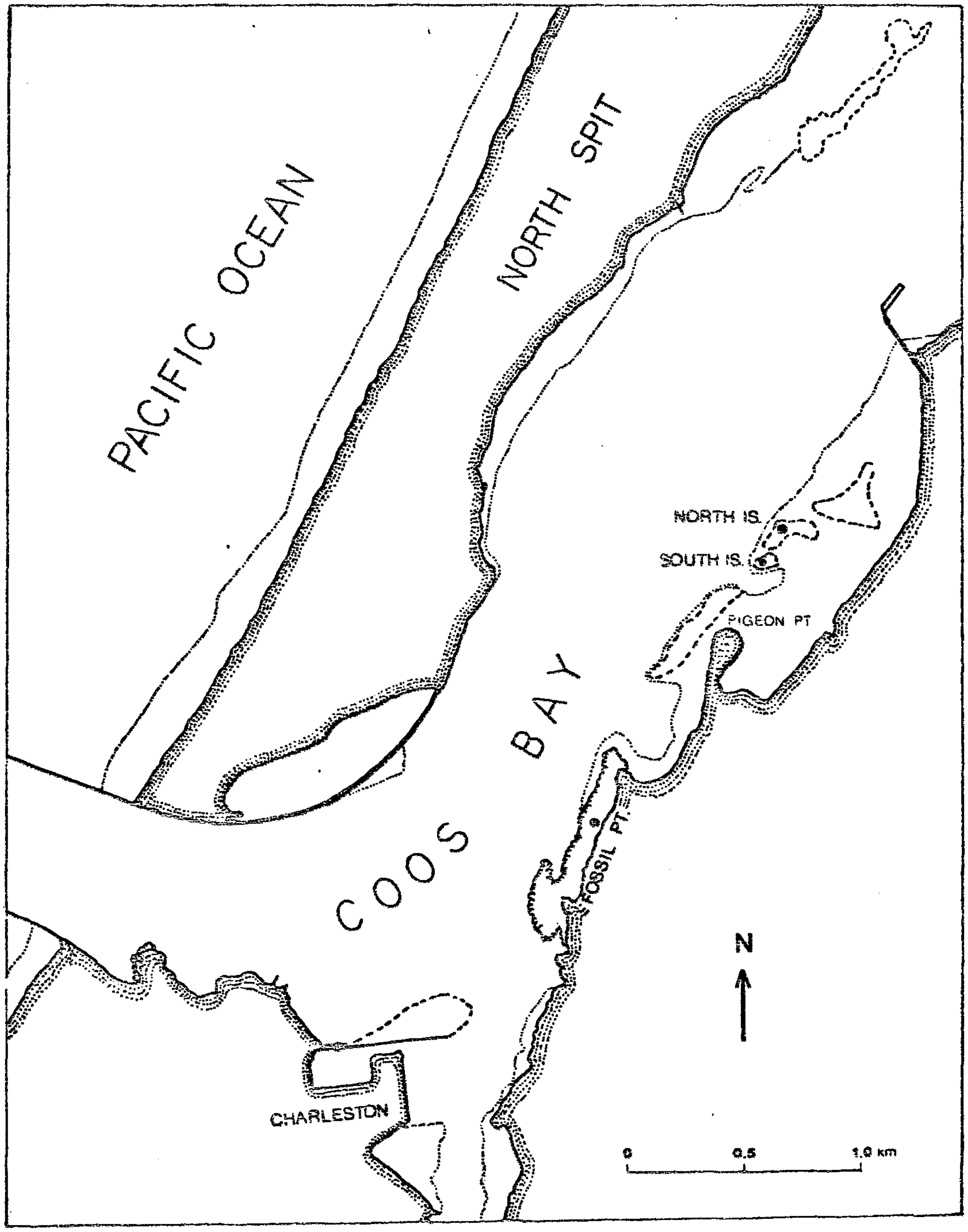
The Study Sites

All study sites are located in Coos Bay, Oregon (44°22'N, 124°18'W) on the central Oregon coast. In winter, the bay is characterized by strong southerly winds, frequent storms, low salinity (18 $^{o}/oo$ is the minimum recorded at a study site) and low surface water temperatures (8-10°C). Algal cover is generally sparse in all intertidal zones with *Ulva* and *Fucus* being the most common species. Summer conditions are generally milder and storms are markedly less frequent and severe. Algal blooms commonly occur in late spring and result in a dense canopy on rocks in the lower zones. *Ulva*, *Gigartina*, *Plocamium*, and *Odonthalia* are abundant. In the higher zones, however, algal cover is reduced, typically appearing as a short green turf composed primarily of *Ulva* and *Enteromorpha*. *Fucus* may become quite dense on isolated large rocks. Of the algal types, the shore crabs intensely graze only the more delicate greens and appear to be unable to utilize the tougher *Fucus*. With the onset of increased wave activity in the fall, algal cover quickly becomes reduced and returns to the characteristic winter conditions described above.

Unlike that of the algal community, faunal composition is not as distinctly seasonal. As mentioned above, shore crabs abound in numbers in all intertidal zones. In the low intertidal, barnacle (Balanus spp.) and mussel (Mytilus edulis) densities appear to be kept low by the predators Pisaster ochraceus and Thais lamellosa. Chitons (primarily Mopalia muscosa) and encrusting bryozoans are common on the undersides of large rocks. Higher in the intertidal, barnacles are common on rock surfaces while mussels appear to be restricted to the undersides of rocks. Littorina may recruit heavily but usually disappears after a short time. A large predaceous crab, Cancer productus, occurs in large numbers under rocks in the lower zone during periods of high salinity. The effect of these seasonal invasions on the shore crab populations is the subject of Chapter II.

The primary study site (Fig. 1) is an intertidal island (maximum elevation is 2.0 m above MLLW) covered by coarse sand and gravel overlain by cobble-sized rocks, most of which are a type of mudstone. Substrates in the lowest zone are somewhat finer, especially in winter when river discharge is high. A second study area is located adjacent to the south shore of the first and shares its general physical attributes, with one principal exception--it lacks a high intertidal zone (maximum elevation is 1.35 m above MLLW). Both sites, designated North and South Island, respectively, were created approximately 50 yrs

Fig. 1. A map of the lower Coos Bay region. Study sites are indicated with closed circles (●).


PACIFIC OCEAN
NORTH SPIT
NORTH IS.
SOUTH IS.
PIGEON PT
COOS BAY
FOSSIL PT.
N
CHARLESTON
0
0.5
1.0 km

ago by the deposition of dredging spoils. While both species are abundant on North Island, H. nudus is largely absent on South. Human disturbance on these islands is relatively unimportant owing to inaccessibility from the shore except at extreme low tides. Harbor seals (Phoca vitulina), however, haul out on the islands and render portions of the leeward sides unsuitable for the crabs.

Two other sites were less intensively studied. One of these, Fossil Point, is located on the eastern shore of the bay due east of the entrance. Being thus exposed, the area represents an intermediate between protected outer coast and typical estuarine rocky intertidal habitats with respect to wave action, salinity and species composition. Shore crabs are, for the most part, restricted to isolated patches of boulders and rubble which are interspersed among expanses of rocky reef in the mid zone. The second such area studied is on the leeward side of the breakwater at the Charleston small boat basin. At this site there are seldom, if ever, substantial waves and sediment loads in the water are often high. Cover for the shore crabs is provided by quarried igneous rocks which rest on fine muddy sediments. There is often a dense cover of Fucus and Balanus on the rock surfaces. Pachygrapsus crassipes, the lined shore crab, dominates crevices in the high zone and H. oregonensis is found in the mid and low zones.

H. nudus is virtually absent.

Sampling Procedures

In order to census the shore crab populations and to determine their resource utilization patterns, permanent transects were established normal to the shore at both North and South Island. Every 5 m along the transects, 1 m^2 quadrats were censused from the tops of the islands to approximately MLLW. Rocks within the quadrats were assigned to one of the following categories depending upon tidal height above MLLW: (a) low, 0-.75 m, (b) mid, .75-1.35 m, or (c) high, 1.35-2.0 m. At North Island there were 5 quadrats in the high and 7 in the mid zone. At South Island, which lacks a high intertidal zone, 5 quadrats were sampled in the mid zone. Data from the low intertidal zones are treated elsewhere (Chapter II). When crab densities were high, it was often necessary to limit the total area sampled, so that each survey could be completed within a tidal series.

For each rock larger than 150 cm^2, measurements included the maximum length of the rock and the width of the axis perpendicular to the first. Rock surface area was computed as the product of the two. Substrates under the rocks were categorized as muddy, muddy-sand, sandy, or sandy gravel. Each resident crab was classified by species, sex, and carapace width (to the nearest mm). Similar data were collected for smaller rocks only when the rock was occupied. Within each quadrat, the smallest rocks, those likely to harbor the fewest crabs, were checked and removed before any of the larger rocks were disturbed. This simple precaution effectively eliminated the possibility that individuals from denser aggregations might escape. Because of their relative scarcity, rocks larger than 600 cm^2 were occasionally sampled outside quadrats. Those chosen were the first encountered on either side of one of the quadrats. Transects were sampled quarterly beginning in January 1979 on North Island, and April 1979 on South Island. A total of 7,531 crabs under 1,347 rocks were sampled in this manner.

Estimation of Resource Utilization Functions

The crabs under study seek refuge beneath rocks which vary continuously over a gradient in size. Resource utilization is defined here as the mean number or biomass of individuals of each species as a function of rock surface area. If both species utilize refuge space beneath these rocks in a more or less random fashion, the probability of encountering an individual of either species per unit of rock surface area should depend only upon the total number or biomass of individuals ($\sum_{j=1}^{n} N_{ij}$) and the total refuge area ($\sum_{j=1}^{n} A_j$) sampled, but should be independent of the size of the rock sampled. Thus, the expected abundance of species i ($\hat{N}_{ij}$) under a rock of a given size (A_j) can be represented by the simple linear function

$$\hat{N}_{IJ} = a_i + \alpha_i A_j \tag{1}$$

where

$$\alpha_i = \sum_{j=1}^{n} N_{ij} / \sum_{j=1}^{n} A_j = \bar{N}_i / \bar{A},$$

and

$$a_i = \bar{N}_i - \alpha_i \bar{A} = 0 .$$

In essence, equation (1) states that under conditions of random utilization of refuge space, the density of individuals (N_{ij}/A_j) remains constant over the range of rock sizes. It is possible, however, for the observed resource utilization patterns to deviate significantly from the random pattern in a variety of ways, thereby indicating disproportionately high (or low) utilization of some portions of the resource axis. The density of individuals may, for example, increase ($\alpha_i > \bar{N}_i/\bar{A}$) or decrease ($\alpha_i < \bar{N}_i/\bar{A}$) asymptotically with increasing rock size. The former indicates "preference" for and the latter "avoidance" of large rocks. Alternatively, density as well as abundance may vary continuously with rock size, so that the relationship between abundance and rock size may be adequately described as a quadratic function,

$N_i = f(A^2)$. In general, any of the conditions above may be detected by solving the quadratic equation

$$\hat{N}_{ij} = b_i + \alpha_i A_j + \gamma_i A_j^2 \qquad (2)$$

where

$$b_i = \bar{N}_i - \alpha_i \bar{A} - \gamma_i \bar{A}^2$$

by stepwise multiple regression. Under conditions of random utilization, the variable A^2 should not explain a significant portion of the variance in N_{ij} (γ_i should equal 0), and as in equation (1), α_i should equal N_i/A and b_i (now equal to a_i) should equal 0. Any significant positive value for γ_i would indicate disproportionately high use (preference) for large rocks, as would any value for α_i greater than $\bar{N}_i/\bar{A}$ when $\gamma_i = 0$. Conversely, values of γ_i less than 0, or α_i less than $\bar{N}_i/\bar{A}$ when $\gamma_i = 0$ would indicate disproportionately low use of large rocks, etc. Interspecific differences may be determined by analysis of covariance (ANCOVA). Reasonable caution should be exercised in interpreting such results, however, since significant differences between the species' curves can be expected solely from differences in mean abundance.

Most analyses reported here were performed using numerical abundance rather than biomass as the dependent variable. The few instances in which the choice of variables leads to qualitatively different conclusions will be clearly indicated.

Of the problems inherent in this method, multicollinearity, the degree of correlation between A and A^2 is likely to be the most often encountered, especially when the range in rock sizes is small (e.g., see South Island under Results). Under such conditions, it is unlikely that both independent variables will successfully enter the regression equation regardless of the exact nature of the relationship. However, unless the curve of a species differs only slightly from that expected from random utilization, multicollinearity poses no serious limitations.

The methods used in small-scale habitat manipulations and a species addition experiment will be described in detail in the appropriate sections under Results.

Results

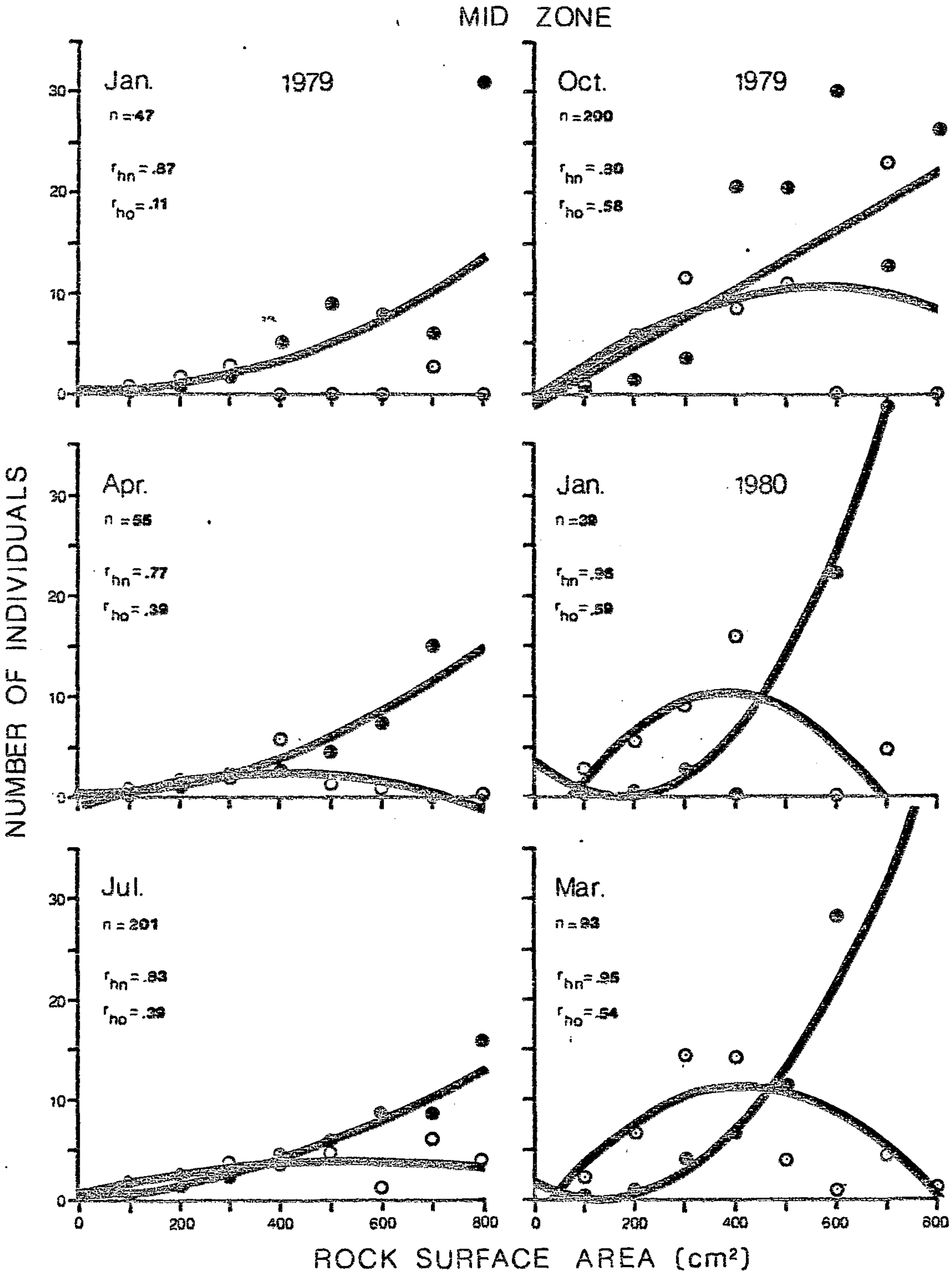
The major hypothesis developed here states that a distinct microspatial structure exists within the community as a direct result of interference competition and spatial heterogeneity in the physical environment. Furthermore, I will attempt to show that when conditions are otherwise favorable to both species, H. nudus enjoys a competitive advantage which is largely a function of the size structure of the crabs. Their size structure in turn is related to the rates of physical disturbance experienced by individuals throughout the habitat, and is consequently linked directly with the rock size distribution.

The results of the investigation are initially organized by study site. Those from North Island, where both species are abundant, are presented first and comprise the basis for the major hypotheses. The results from other study sites, South Island and Fossil Point in particular, are offered as suitable tests of the proposed competitive model. Finally, evidence concerning the timing and frequency of reproduction of the two competitors will be presented with the intent of eventually providing some insight into the underlying causes for the differences between the species in average competitive ability.

North Island

The results of stepwise regressions on the number of individuals per rock as a function of rock surface area for both species in the mid zone at North Island are shown in Figure 2, together with the means for 100 cm^2 rock size classes. Quite obviously, hypotheses predicting random utilization of rocks can be rejected. In general, _H. nudus_ densities increased significantly with rock surface area over the entire range of rock sizes in all months. In the single case (October 1979) in which _H. nudus_ numbers increased linearly with rock area, the regression

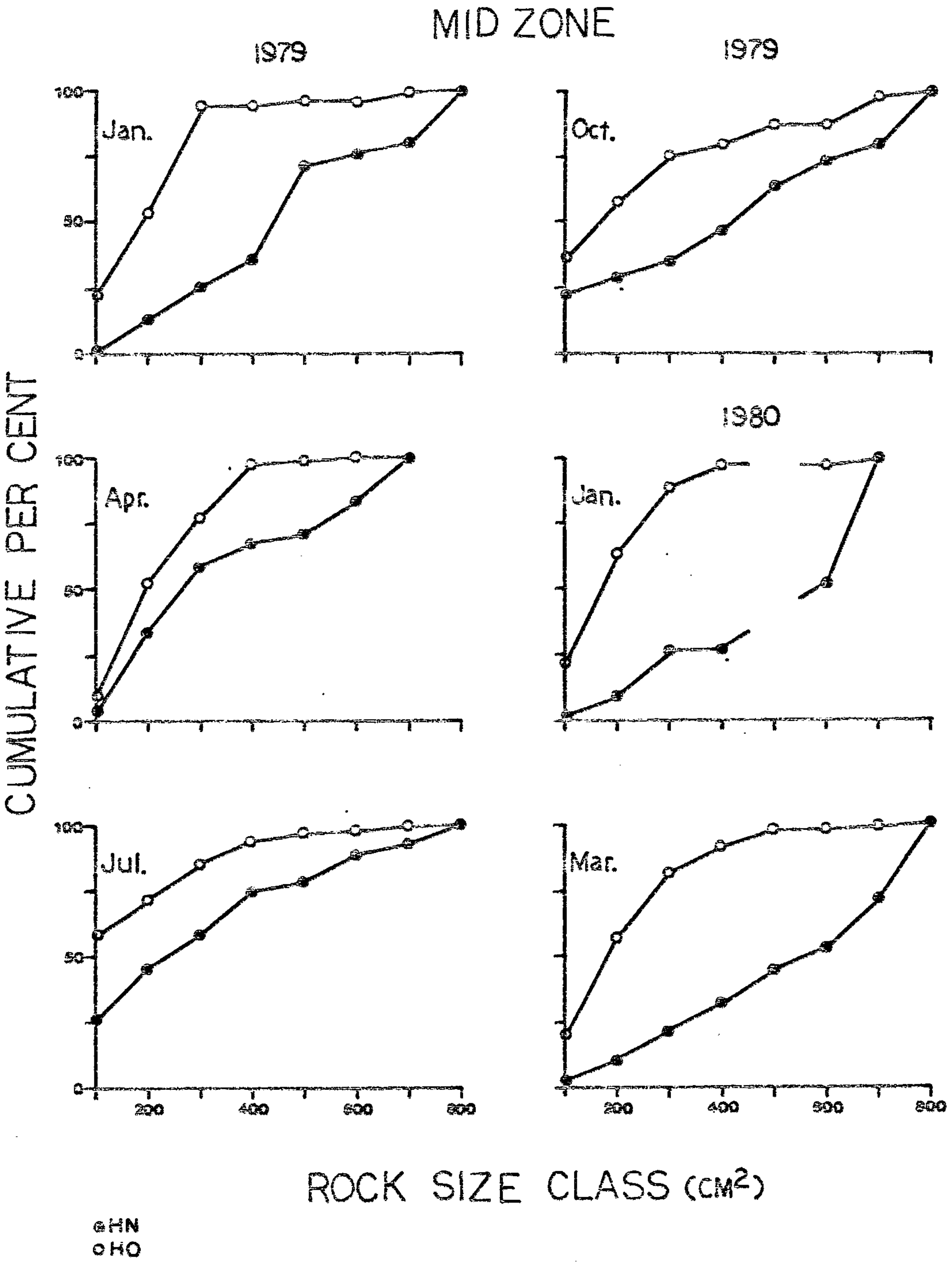
Fig. 2. Resource utilization curves for the two shore crab species in the mid zone at North Island as determined by stepwise multiple regression of numbers of each species as a function of rock surface area and its square (see text). All pairs of curves are significantly different ($P < .001$ in all cases, ANCOVA). Mean numbers of *H. nudus* (●) and H. oregonensis (o) in 100 cm^2 rock size classes are also shown.


MID ZONE
Jan.
1979
n = 47
r_{hn} = .87
r_{ho} = .11
Oct.
1979
n = 200
r_{hn} = .80
r_{ho} = .58
Apr.
n = 55
r_{hn} = .77
r_{ho} = .39
Jan.
1980
n = 39
r_{hn} = .96
r_{ho} = .59
Jul.
n = 201
r_{hn} = .83
r_{ho} = .39
Mar.
n = 93
r_{hn} = .95
r_{ho} = .54
NUMBER OF INDIVIDUALS
0
10
20
30
ROCK SURFACE AREA (cm²)
0
200
400
600
800

coefficient (0.028) differs significantly from the criterion for random utilization ($\overline{N}/\overline{A} = .019$, $t = 5.91$, $P < .001$). H. oregonensis densities, however, typically reached a maximum among intermediate-sized rocks and then declined with further increases in rock size. As is shown by the rock size class means, the decline was often sufficiently steep to result in a relatively poor fit to the quadratic model. Although the regressions for this species could in some cases be markedly improved by adding terms to the polynomial, the original intent in using the second order equation would be obscured. The apparent differences between the species were tested by comparing the pairs of regression equations by means of ANCOVA. In all months, the differences were highly significant ($P < .001$). Inclusion of the numerous unoccupied rocks smaller than 150 cm^2 in the analyses would merely depress both species curves near the origins without substantially altering the qualitative results.

A plot of the cumulative percent of each species' population with rock size (Fig. 3) shows that the bulk of the H. oregonensis population at any given time was found among the smallest rocks (<250 cm^2), while a similar fraction of the H. nudus population was accounted for only after much larger rocks were considered. When these results are viewed in conjunction with the rock size

Fig. 3. Cumulative percent of the total number of individuals of each species in the mid zone at North Island as a function of rock surface area (100 cm^2 classes).


MID ZONE
1979
1979
1980
Jan.
Oct.
Apr.
Jan.
Jul.
Mar.
CUMULATIVE PER CENT
100
50
0
200
400
600
800
ROCK SIZE CLASS (CM²)
● HN
○ HO

distribution, it is clear that most H. nudus individuals occupy a highly selective subset of the available rocks, while most H. oregonensis individuals are resident under locally abundant smaller rocks. Since the tide zone is otherwise physically homogeneous, rock size appears to be the sole environmental axis along which the species segregate. However, with increasing tidal height, H. nudus becomes increasingly abundant and H. oregonensis less so, so that in the highest zone at North Island H. nudus is always numerically dominant (Fig. 4). Except for the low numbers of H. oregonensis in the high zone, the species' resource utilization patterns (Fig. 5) are similar, at least qualitatively, to those already presented for the mid zone. In the high zone, however, H. nudus mean abundances, particularly among intermediate-sized rocks, appear to be slightly higher and are probably responsible for the more nearly linear form of the utilization patterns here. In two months (January and July 1979), the H. nudus patterns could not be distinguished from those that would have resulted from random utilization of space ($P > .20$) while analyses of the four remaining samples indicated disproportionately high use of large rocks ($P < .001$ in all cases). It is worth noting here that the interpretations of the former two analyses (January and July) are the only ones reported in the paper that are affected by the choice of dependent

Fig. 4. Average densities of each _Hemigrapsus_ species in the high and mid zones at North Island.

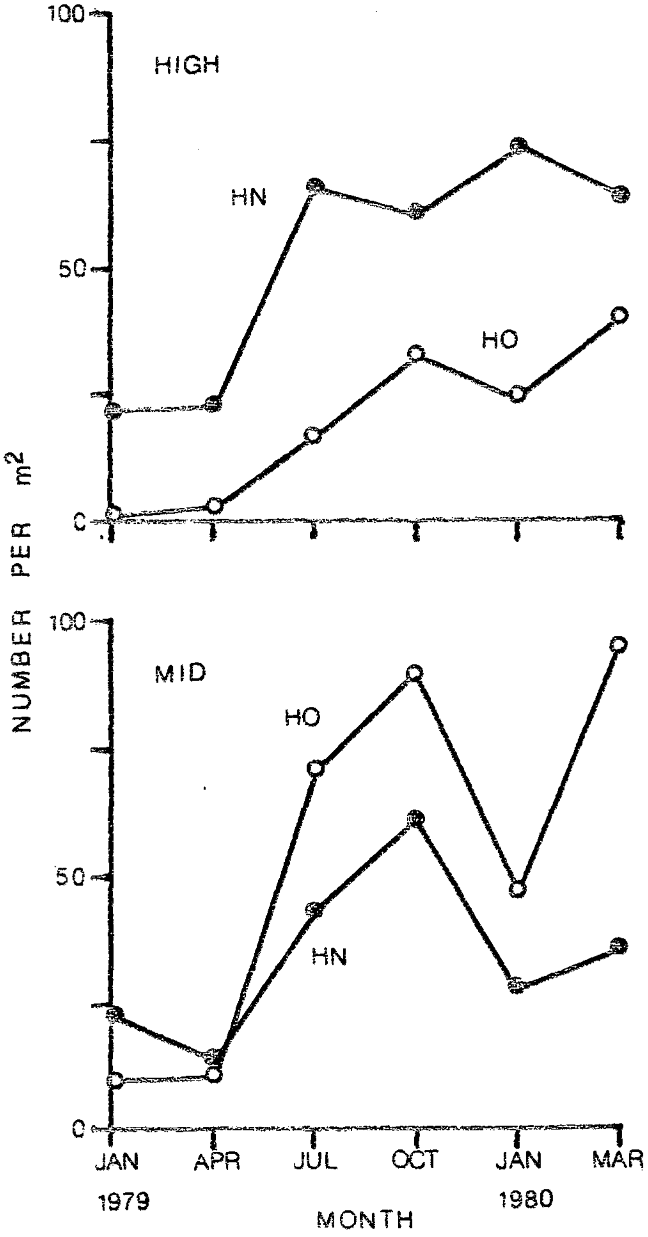
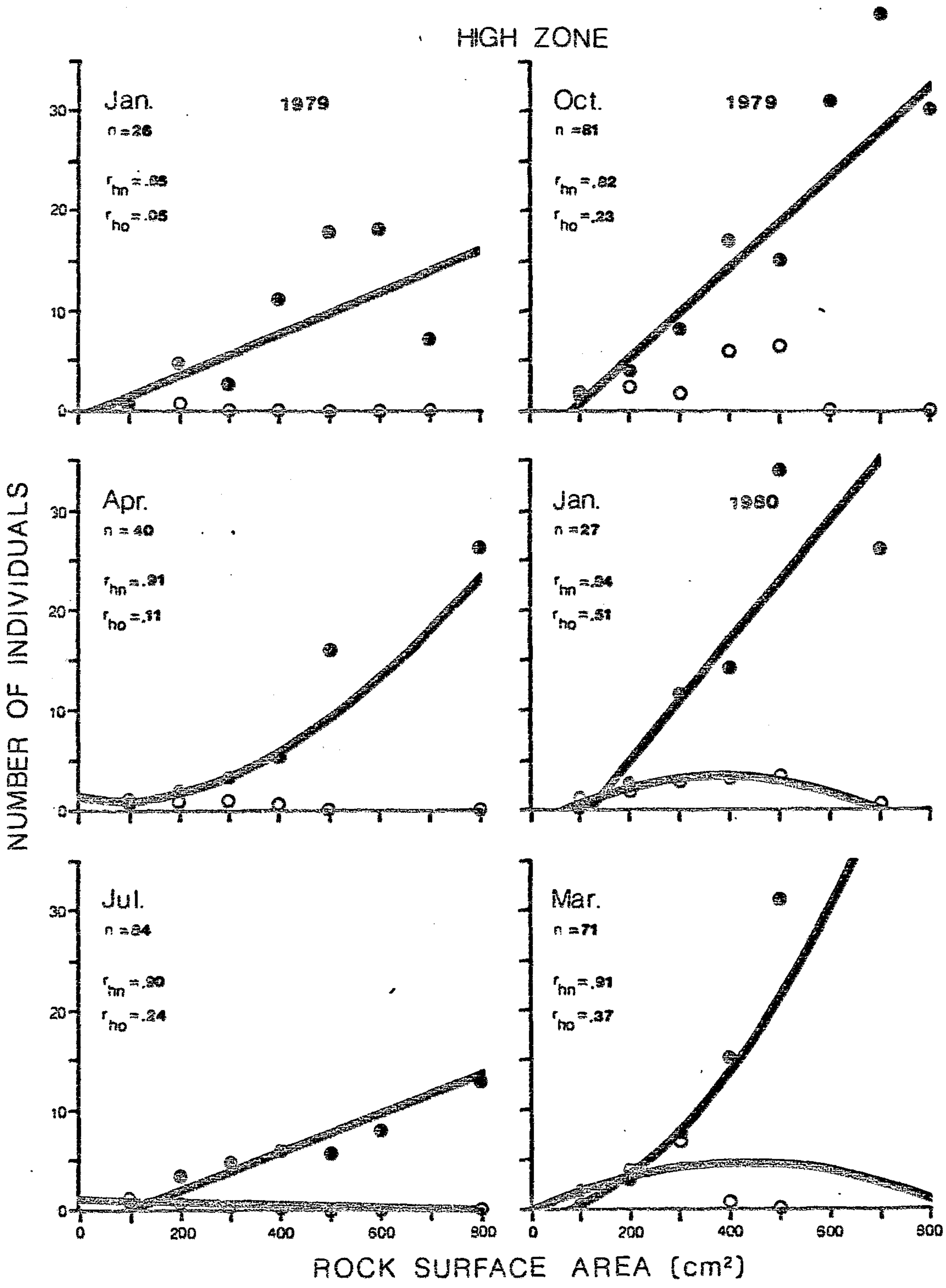

HIGH
HN
HO
MID
HO
HN
100
50
0
NUMBER PER m^2
JAN
APR
JUL
OCT
JAN
MAR
1979
1980
MONTH

Fig. 5. Resource utilization curves for both shore crab species in the high zone at North Island. Curves for *H. oregonensis* are not shown for those months in which the regressions were not significant. Mean numbers/rock in 100 cm^2 size classes are also shown for *H. nudus* (●) and *H. oregonensis* (o).


HIGH ZONE
Jan.
1979
n =26
r_{hn}=.85
r_{ho}=.05
Oct.
1979
n =81
r_{hn}=.82
r_{ho}=.23
Apr.
n = 40
r_{hn}=.91
r_{ho}=.11
Jan.
1980
n =27
r_{hn}=.94
r_{ho}=.51
Jul.
n =24
r_{hn}=.90
r_{ho}=.24
Mar.
n =71
r_{hn}=.91
r_{ho}=.37
NUMBER OF INDIVIDUALS
0
10
20
30
ROCK SURFACE AREA (cm²)
0
200
400
600
800

variables; had H. nudus biomass rather than numerical abundance been used, both analyses would indicate disproportionately high use of large rocks ($P < .001$).

Although the H. nudus resource utilization patterns in the high zone appear to be somewhat broader than in the mid zone, direct comparisons are seriously complicated by the fact that an unknown and potentially variable fraction of unoccupied rocks $<150\ \mathrm{cm}^2$ are not included in the data. At any given time, the fraction is undoubtedly greater in the high zone since H. oregonensis densities are generally quite low. In effect, to the extent that the high zone data are relatively more "preselected," the criteria for random utilization ($\overline{N}/\overline{A}$) are artificially increased and the results of comparisons less certain.

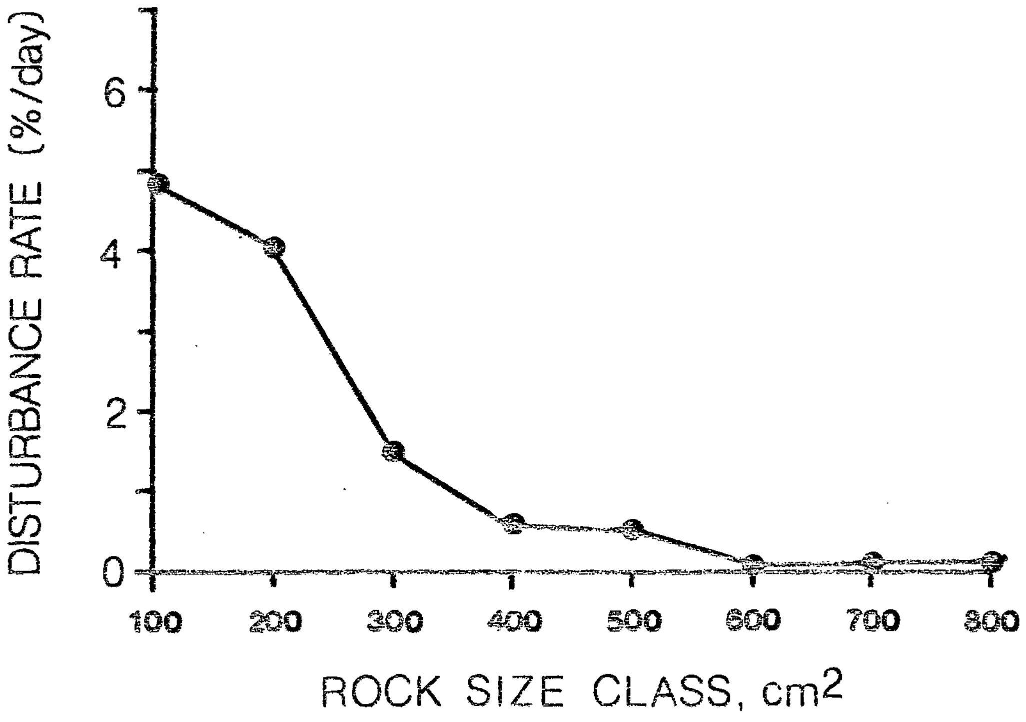
Refuge quality and acquisition

Rock cover is extremely important for both species. The results presented above strongly suggest that within a tidal zone, crabs do not perceive equal areas under different size rocks as being equal in "value." In addition, it was shown that there are marked differences between the species in the extent to which the rocks in any size class are utilized. In this section, a simple explanation for these patterns will be proposed.

The inverse relationship between the surface area and wave-induced disturbance rates of marked rocks at North Island (Fig. 6) is shown in data taken from two separate experiments in February and March 1980. A total of 135 rocks in known locations were marked and checked for movement at the end of 12 days. All rocks were between 0.3 and 0.5 m above MLLW. Seasonal differences in absolute rates of rock disturbance may be expected. During midsummer, for example, the bay is often quite calm and all rocks, except perhaps for the smallest, are probably equally stable. In contrast, during severe winter storms, substantial rock turnover may be expected in all but the largest rock size classes. Tidal height must also influence disturbance rates along the gradient in rock sizes. In general, rocks near MSL (mid zone) are subject to the greatest wave activity, since those higher up are less frequently submerged and those lower in the intertidal are protected by reason of increased depth. The relationship, more precisely a function of rock weight, has been discussed in detail in other recent papers (Osman 1977; Sousa 1979).

During periods of submergence, rocks serve as refuges from a host of marine predators (fish, Clemens and Wilby 1967; other crabs, Chapter II; diving birds, R. Lavelli, personal communication) and from damage and displacement to unfavorable areas as a result of wave activity. During low tides, rocks serve as buffers from

Fig. 6. Disturbance rates of rocks in 100 cm^2 size classes at North Island. Rates were computed as (no. disturbed/no. days elapsed). Based on data for a total of 135 marked rocks over two 12-day periods in February and March 1980, respectively.

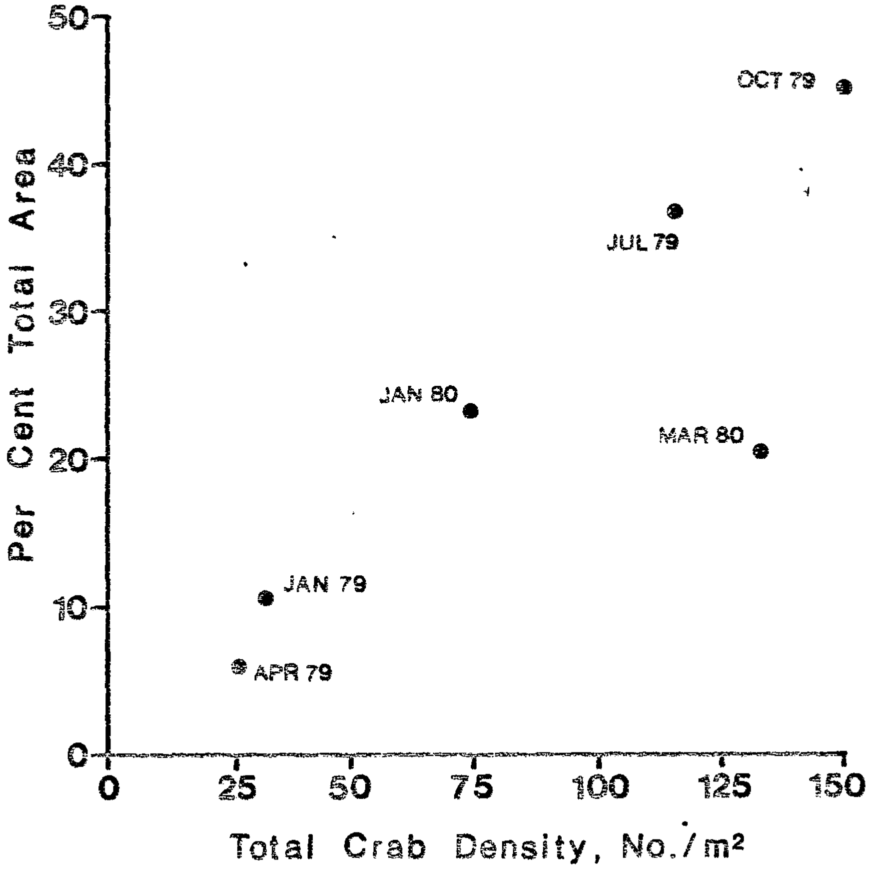

DISTURBANCE RATE (%/day)
6
4
2
0
100
200
300
400
500
600
700
800
ROCK SIZE CLASS, cm2

physical extremes (desiccation and varying temperatures) and provide protection from terrestrial predators such as gulls, crows, and (in other locations) raccoons (Ricketts et al. 1968). In nearly all instances, refuge quality can be expected to increase with rock size.

As stated previously, a large but unknown fraction of rocks in the smallest size class (<150 cm^2) were always unoccupied. Given the relatively high potential mobility of the animals and the low stability of these rocks, this is an unsurprising result. Occupancy rates in this size class should depend upon competitive pressures along the remainder of the resource axis. A comparison of the per cent of the total area of all occupied rocks that were <150 cm^2 with crab density (Fig. 7) strongly supports this hypothesis. The single deviant datum (March 1980) however, suggests that other factors, such as recent wave activity, are involved.

The simplest explanation for the seemingly different abilities of individuals of the two species to gain access under the larger, more stable rocks is that _H. nudus_ individuals are, on the average, larger and thus more aggressively competent than _H. oregonensis_ individuals. Reports in the literature on crab behavior (Hazlett 1970, Števčić 1971, Preston 1973, Evans et al 1976, Bovbjerg 1960, Warner 1970, Griffin 1968) repeatedly stress the

Fig. 7. Per cent of the total rock surface area of occupied rocks accounted for by rocks $<150\ cm^2$ as a function of total shore crab density. Data are from the mid zone at North Island.



Per Cent Total Area
0
10
20
30
40
50
Total Crab Density, No./m²
0
25
50
75
100
125
150
OCT 79
JUL 79
JAN 80
MAR 80
JAN 79
APR 79

correlation between individual size and intraspecific aggressive dominance. Although the evidence for interspecific aggression is less well developed (Preston 1973, Evans et al. 1976, Hiatt 1948), the results are similar.

It is apparent from the size distributions of the two species in the mid zone at North Island (Table 1) that the largest crabs are invariably *H. nudus* individuals, and that despite considerable overlap, the mean sizes of *H. nudus* are consistently greater (by 4-6 mm) than those for *H. oregonensis*. The distinctly bimodal *H. nudus* distributions, especially from January to July 1979, are probably due to the presence of individuals 2 or 3 years old. The unimodal *H. oregonensis* distributions are more likely those of an effectively annual species. Larger, presumably older individuals of both species may be found in a limited number of (other) habitats in the bay.

In the high intertidal, size distributions are usually similar to those in the mid zone but are biased toward smaller individuals (Table 2). Batie (1974) reported similar results for *H. oregonensis* in Yaquina Bay, Oregon. Field observations and data taken over a 2 year period in the low intertidal at North Island suggest that large *H. nudus* individuals preferentially occupy the lower reaches of the island while recruitment takes place primarily in the highest levels. Periodically, conditions

Table 1. Size frequency distributions (%) of *H. oregonensis* and *H. nudus* sampled along the permanent transect in the mid zone at North Island

Time	Species	Size Class (mm) ≤3	5	8	11	14	17	20	23	26	29	32	35	38+	n	Avg. size (mm)
(1979)																
Jan.	H.n.		3.2	9.7	4.5	5.8	9.1	14.3	27.3	14.3	6.5	2.6	1.9	0.6	154	20.4
	H.o.	5.7	5.7	7.1	14.3	27.1	21.4	7.1	10.0	1.4					70	14.0
Apr.	H.n.		7.1	15.2	8.1	8.1	10.1	11.1	16.2	10.1	10.1	4.0			99	18.1
	H.o.		2.5	6.2	19.8	39.5	17.3	9.9	3.7	1.2					81	14.4
Jul.	H.n.	0.5	2.3	14.7	28.1	13.8	7.4	4.1	3.2	13.8	5.1	4.6	0.9	1.4	217	16.7
	H.o.	2.0	11.2	27.7	33.1	19.3	4.2	1.7	0.8						357	10.3
Oct.	H.n.		8.7	25.2	35.0	14.0	7.3	4.8	2.0	2.0	0.6	0.6			357	14.8
	H.o.	0.7	3.2	31.8	41.5	15.4	5.2	1.7	0.2						402	10.8
(1980) Jan.	H.n.			14.9	28.4	39.2	10.8	2.7	1.4		1.4		1.4		74	13.4
	H.o.		11.6	49.7	24.9	9.9	3.9								181	9.4
Mar.	H.n.		0.3	16.2	28.2	22.8	15.0	5.4	4.5	3.6	2.4	0.9	0.6		333	14.4
	H.o.	9.7	9.1	42.4	27.1	8.7	2.5	0.4	0.2						528	8.7

Table 2. Size frequency distributions (%) of *H. oregonensis* and *H. nudus* sampled along the permanent transect in the high zone at North Island

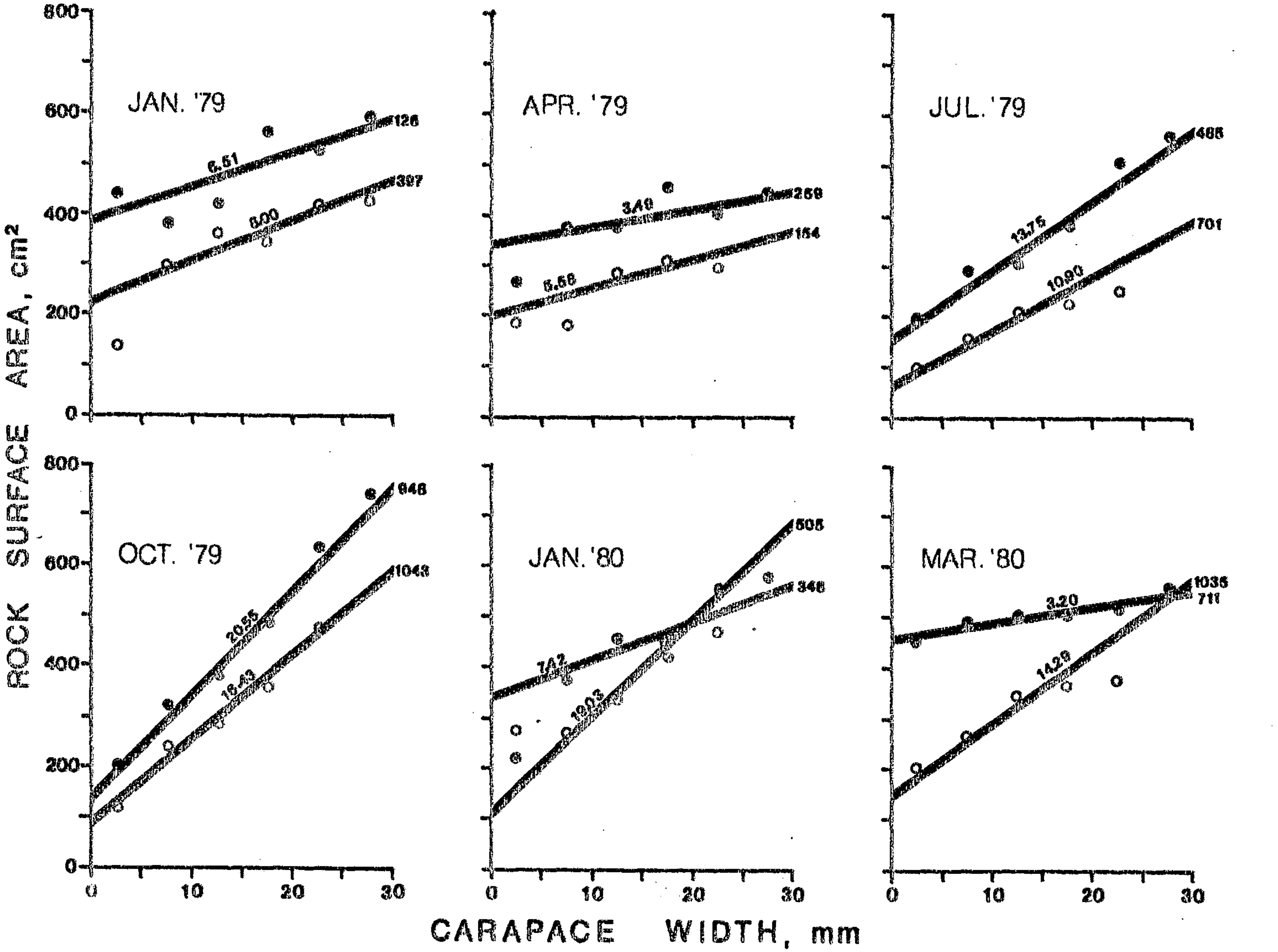
Time	Species	Size class (mm)													n	Avg. size (mm)
		≤3	5	8	11	14	17	20	23	26	29	32	35	38+		
(1979)																
Jan.	H.n.		27.7	44.6	6.3	3.6	4.5	2.7	5.4	0.9	4.5				112	10.0
	H.o.			40.0		40.0	20.0								5	13.2
Apr.	H.n.		6.1	13.9	13.9	13.0	9.6	6.1	7.8	17.4	8.7	2.6	0.9		115	17.6
	H.o.				17.6	29.4	11.8	23.5	17.6						17	17.1
Jul.	H.n.		1.5	11.6	19.1	25.6	6.5	1.0	4.5	14.1	9.0	2.5	2.0		199	16.2
	H.o.		18.2	30.3	30.3	12.1	3.0	6.1							33	10.1
Oct.	H.n.		0.2	11.7	29.1	32.3	14.9	5.0	2.7	2.0	1.2		0.5	0.2	402	12.9
	H.o.		5.4	35.1	39.3	13.1	4.8	1.8	0.6						168	10.4
(1980)																
Jan.	H.n.		2.3	34.7	28.9	17.9	9.8	2.3	2.3	0.6	0.6			0.6	173	11.4
	H.o.		10.2	53.1	30.6	4.1	2.0								33	9.0
Mar.	H.n.	0.8	2.3	24.8	27.5	23.3	14.0	3.5	2.3	0.4	0.8	0.4			258	12.5
	H.o.	16.7	11.7	47.5	18.5	4.9	0.6								162	7.7

become unfavorable for the large individuals in the low zone and many migrate upward. The marked change in the H. nudus size distributions between January and April 1979 is the result of one such migration. These relationships are described more fully elsewhere (Chapter II).

If individual size is the sole determinant of competitive ability, and survivorship is directly proportional to rock size, there should be positive correlations between the sizes of individuals and the sizes of the rocks that they occupy. Furthermore, there should be no differences between the species in this regard. Accordingly, linear regressions were performed on individual size with rock size for both species. Analysis of covariance was then used to test for significant differences between species. The results (Fig. 8) provide only partial support for the competitive mechanism. As predicted, larger crabs of both species occupy larger rocks than smaller conspecifics, but there are unexpected differences between the species. In two samples (January and March 1980), the H. oregonensis slopes are significantly higher than those for H. nudus ($P < .001$), and in all months the H. nudus intercepts are significantly greater ($P < .001$).

Over the range of overlap in sizes, H. nudus individuals occupy larger rocks than equal size H. oregonensis individuals. Several explanations which are not

Fig. 8. Relationship between the size of rock occupied and the size of resident individuals of each species at North Island. Mean sizes of occupied rocks in each 5 mm crab size class are also shown (*H. nudus* (●), *H. oregonensis* (o)). In all months, the intercepts for the two species differ significantly ($P < .001$ in all cases), and in January and March 1980, the slopes differ significantly ($P < .001$, ANCOVA). Sample sizes for each species are indicated at the right of each regression line. Estimated regression slopes are shown above the lines.


JAN. '79
6.51
126
6.00
397
APR. '79
3.49
259
6.56
154
JUL. '79
13.76
488
10.90
701
OCT. '79
20.56
948
16.43
1043
JAN. '80
7.42
605
19.03
346
MAR. '80
3.20
1036
711
14.29
0
200
400
600
800
0
10
20
30
ROCK SURFACE AREA, cm²
CARAPACE WIDTH, mm

necessarily mutually exclusive are possible. First, there may be intrinsic differences between the species in aggressive competence, "individual distance" requisites, or other behavioral factors. Second, it is possible that H. oregonensis fitness does not decline as rapidly with decreasing rock size as does H. nudus fitness. In consequence, selection for those traits that permit individuals to discriminate refuge quality would not be as intense. Finally, the results may reflect differences in the relative intensities of intra- and interspecific aggression. This effect could be expected to be most pronounced during the breeding season (as a reproductive isolating mechanism). Each of these alternatives will be discussed in later sections.

Aside from differences between the species, there are significant temporal differences within species. The differences between the regression coefficients were determined by an a posteriori simultaneous test procedure (Sokal and Rohlf 1969, p. 457). As can be seen from the results (Table 3), the slopes for H. nudus fall roughly into two groups, winter-spring and summer-fall. In general, there was a tendency for H. nudus of all sizes to be found under larger rocks in the winter and spring of both years. It may be significant that during the winter and spring of both years, H. nudus densities were relatively low, and

Table 3. Results of *a posteriori* Simultaneous Test Procedure for determining differences among the estimated regression slopes of size of rock occupied on size of resident individuals

A. Estimated regression coefficients for rock size on crab size

	Slope					
	a	b	c	d	e	f
Species	Jan9	Apr9	Jul9	Oct9	Jan0	Mar0
H. nudus	6.51	3.50	13.75	20.55	7.42	3.20
H. oregonensis	8.01	5.58	10.90	16.44	19.04	14.28

B. STP comparisons between regression coefficients

H. nudus $SS_{crit.05} = 696 \times 10^3$ *H. oregonensis* $SS_{crit.05} = 409 \times 10^3$

Species	Group	SS_{among} $(x10^3)$	Common Slope
H. nudus	All	6,572*	None
	a,b,c,e,f	2,081*	None
	a,b,d,e,f	6,197*	None
	a,b,e,f	252	5.21
	c,d	1,563*	None
H. oregonensis	All	684*	None
	a,c,d,e,f	457*	None
	b,c,d,e,f	568*	None
	c,d,e,f	316*	14.83
	a,b	299	6.81

∴ *H. nudus*: (Jan9,Apr9,Jan0,Mar0) ≠ Jul9 ≠ Oct9

H. oregonensis: (Jul9,Oct9,Jan0,Mar0) ≠ (Jan9,Apr9)

$*p < .05$

reproductive activity (measured as % mature females ovigerous, see Life Histories), and wave activity were high when compared to July and October 1979. Two clear groups emerged from the data for H. oregonensis; slopes for January and April 1979 were significantly lower than those for the remaining months of the study (July 1979 through March 1980). In this case, differences in density (relatively low in January and April 1979) provide the only readily apparent explanation for the differences between the slopes. Seasonality per se appears not to be a significant factor, either with respect to breeding activity or wave activity.

Experimental manipulation of rock size distributions

Due to the high correlation between rock size and species composition and the high variability in rock sizes both within and between transect quadrats, an attempt was made experimentally to alter species composition throughout 1 m^2 quadrats by manipulating the rock size distributions within these areas while maintaining a constant per cent cover. The following represent the ideal rock size distributions for the 4 treatments considered:

I. Eight 900 cm^2 rocks

II. Sixteen 450 cm^2 rocks

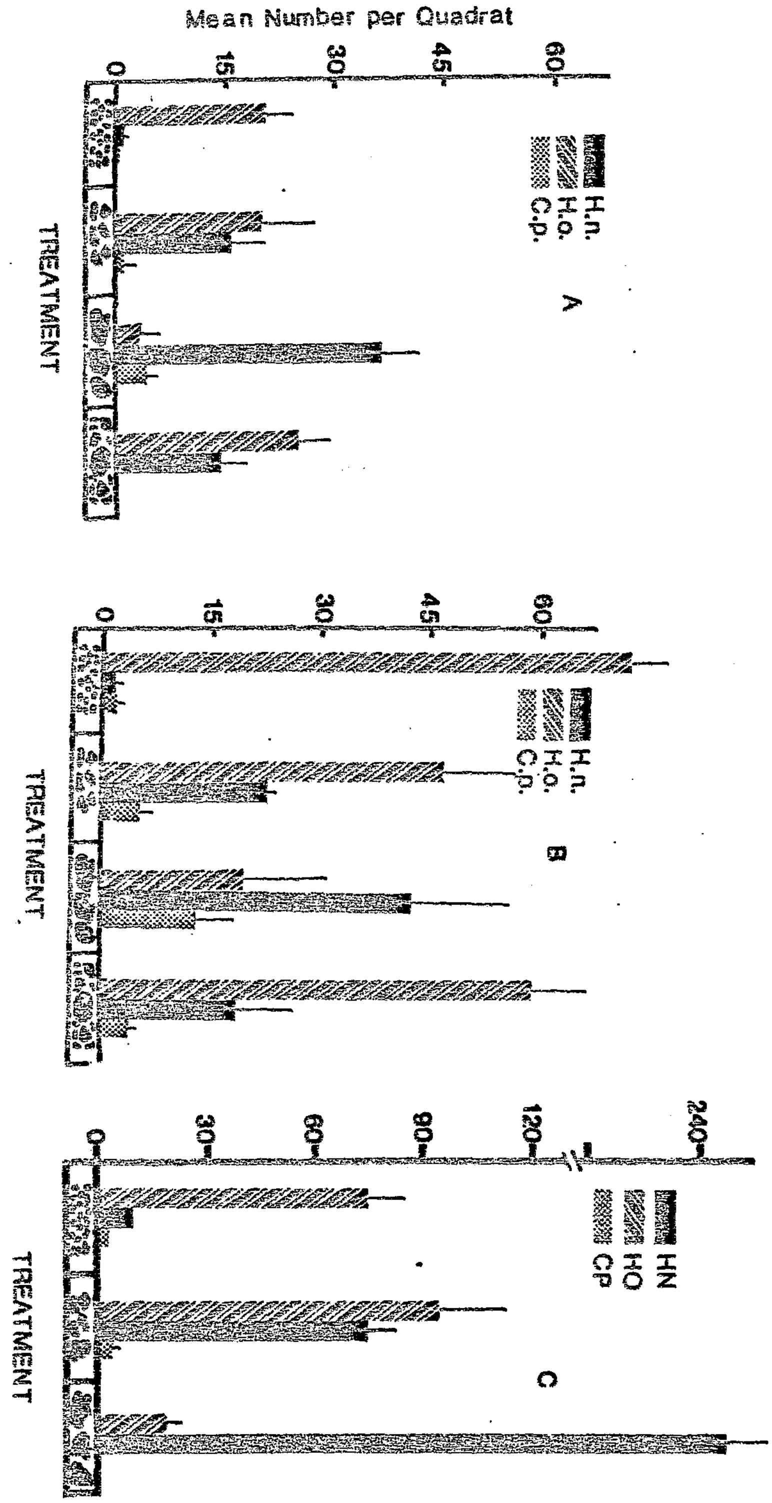
III. Forty-eight 150 cm^2 rocks

IV. Two or three 900 cm^2, five 450 cm^2, and sixteen 150 cm^2 rocks.

In practice, some allowance had to be made in order to maintain the same per cent cover in each cell when individual rock sizes varied from the ideal. Three replicate treatments were arranged in rows for a total of 12 cells per "checkerboard." Within rows, treatments were assigned randomly. Similar checkerboards were established in both the mid and high zones on North Island. In the mid zone, the experiments were censused in April, June, and September 1979. High zone experiments were censused in May, June, and September 1979. Treatment IV replicates (non-uniform distributions) were not sampled in either experiment during September, and the remaining data for September were derived from only two replicates of treatments I - III. Results of the mid intertidal experiments will be discussed first and will then be compared to the data obtained in the high intertidal.

The mean numbers of each species in the various treatments are depicted in Fig. 9. Data for the June census are complicated by the presence of considerable numbers of Cancer productus. Like H. nudus, individuals of this species exhibit a strong preference for large rocks. In addition, they are typically much larger than either shore crab species, and as such, they are effective competitors, particularly with H. nudus. For these reasons, a more detailed examination of the June results will be

Fig. 9. Mean number of individuals in 1-m^2 quadrats in which rock size distributions were experimentally altered (see text). Data are from the mid zone at North Island in a) April, b) June, and c) September 1979. Vertical bars represent ±1 S.E. Note that in (c) the scale for the vertical axis has been doubled.


Mean Number per Quadrat
0
15
30
45
60
H.n.
H.o.
C.p.
A
TREATMENT
0
15
30
45
60
H.n.
H.o.
C.p.
B
TREATMENT
0
30
60
90
120
240
HN
HO
CP
C
TREATMENT

deferred to a later section (Chapter II), and the following discussion will pertain primarily to the April and September experiments. These results show that the distributions of the species are similar to those predicted from analyses of single rocks sampled along the vertical transect. H. nudus individuals account for 92-93% of the total shore crabs in quadrats containing only large rocks and H. oregonensis individuals comprise 90-97% of the total in those containing only small rocks. Overlap between the species was, however, quite high in quadrats composed of intermediate-sized rocks (H. oregonensis = 56-57%) and in those treatments in which the rock size distribution was non-uniform. The increasing densities of potential colonists in the fall (Fig. 4) are reflected in the experiments as 1) an increase in the number of individuals/rock in all treatments, and 2) an increase in the frequency of occupied rocks in treatment III (.188 in April, .479 in September). All rocks in treatments I and II were occupied during both censuses.

These results are in keeping with those obtained along the vertical transect, and also show that nearly complete spatial separation of the species may be achieved by altering the rock size distribution. It should be noted, however, that the broader implications are limited by the fact that the treatment sets can only sample individuals from the established community in which they are embedded. One cannot, for instance, predict by extrapolation the relative abundances of the two species in another habitat composed solely of intermediate-sized rocks. It is, however, reasonable to ask whether the individuals so sampled are representative of those in the surrounding community. Accordingly, the overall structure of each species population as censused in the experimental plots (Table 4) was compared to the size structure as determined by random sampling along the vertical transect (Table 1). The results of χ^2 tests of independence (Table 5) show that in September there were more large individuals of both species than would be expected by chance ($P < .001$ for both); in April, the same was true only of H. nudus ($P < .001$). This nonrandom sampling undoubtedly can be attributed to the relatively high concentrations of large rocks within the plots when taken together with the positive linear relationship between crab size and the size of occupied rocks (Fig. 8). The extent to which this effect contributed to the general decline in large individuals sampled along the transect is unknown, but probably negligible.

Mean abundances for cells in the high intertidal plots (Fig. 10) reveal that H. oregonensis individuals were scarce in all three surveys, and that the numbers of

Table 4. Size frequency distributions (%) of <u>H. oregonensis</u> and <u>H. nudus</u> censused in the mid zone experimental plots (checkerboards) at North Island

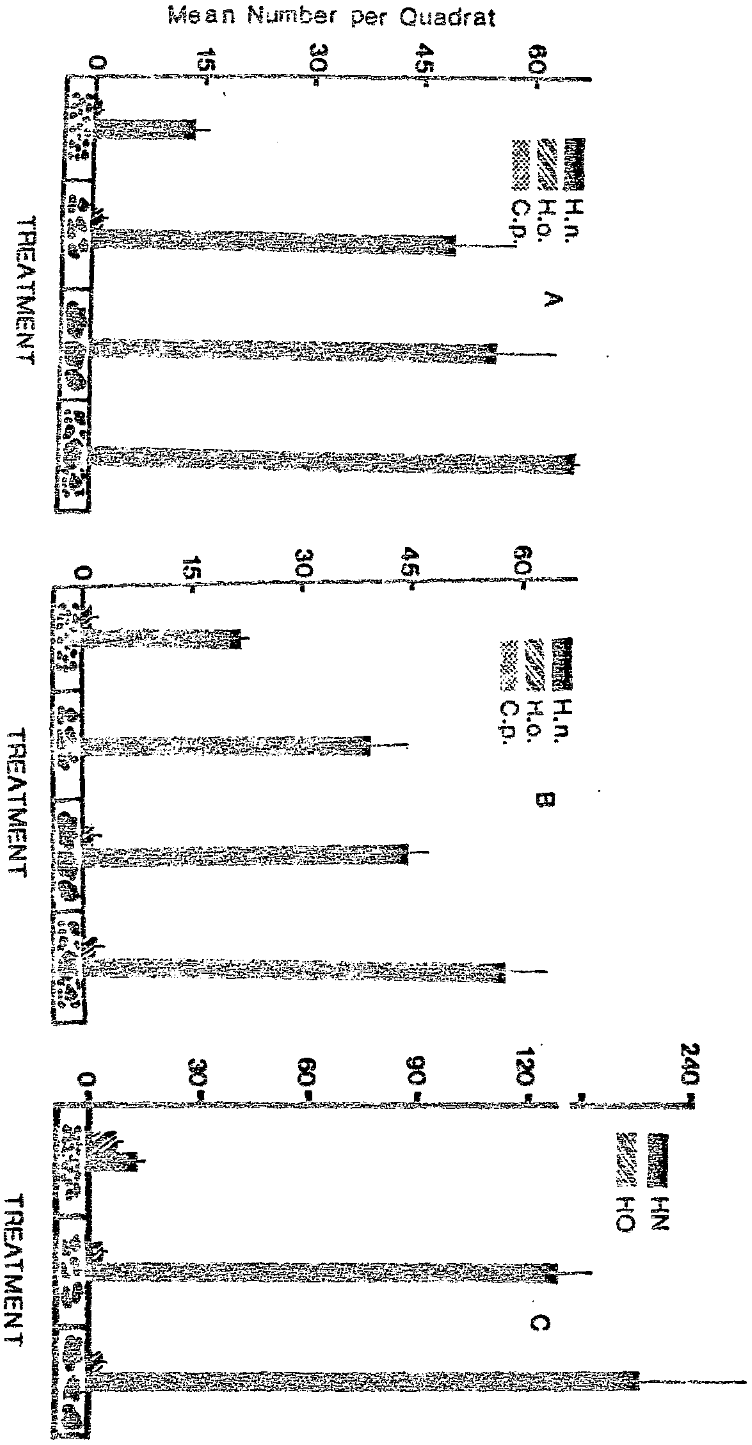
Date	Species	Size Class (mm)													n	Avg. Size (mm)
		≤3	5	8	11	14	17	20	23	26	29	32	35	38+		
Apr.	H.n.		3.0	1.0	1.0	0.5	2.0	5.0	30.2	30.7	20.3	4.5	1.5	0.5	202	24.7
	H.o.	1.5	6.8	2.4	14.1	32.5	26.2	8.7	6.3	1.5					206	14.7
June	H.n.	0.4	1.5	6.2	18.2	11.3	5.5	3.6	7.6	16.7	17.1	8.0	2.5	1.5	275	21.0
	H.o.	4.4	20.5	13.2	26.9	22.8	8.1	1.7	1.7	0.5	0.2				591	10.5
Sept.	H.n.				3.1	16.1	21.2	7.8	13.7	21.4	9.5	3.5	2.5	1.2	651	21.7
	H.o.		0.5	6.8	38.6	33.2	14.9	3.2	2.2	0.5					370	13.3

Table 5. Results of χ^2 Tests of Independence of the Size Distributions of Individuals Sampled Along the Permanent Transect and in the Mid Zone Experimental Plot at North Island

Size Class (mm)	April		June - July		Sept. - Oct.	
	H.n.	H.o.	H.n.	H.o.	H.n.	H.o.
≤ 3		(+) 1.18	(-) 0.03	(+) 3.80		(-) 2.76
5	(-) 2.59	(+) 1.95	(-) 0.48	(+)11.26		(-) 7.19
8	(-)23.59	(-) 2.34	(-) 8.93	(-)25.18	(-)56.53	(-)61.17
11	(-)10.05	(-) 1.19	(-) 5.30	(-) 2.88	(-)103.5	(-) 0.40
14	(-)12.79	(-) 0.82	(-) 0.64	(+) 1.28	(-)36.04	(+)25.53
17	(-) 3.10	(+) 1.95	(-) 0.71	(+) 5.15	(+) 6.39	(+)18.19
20	(-) 1.19	(-) 0.08	(+) 0.09	0.00	(+) 0.09	(+) 1.77
23	(+) 5.11	(+) 0.71	(+) 4.15	(+) 1.18	(+)17.40	(+) 6.05
26	(+)11.78	(+) 0.02	(+) 0.66	(+) 1.81	(+)59.85	(+) 2.09
29	(+) 4.08		(+)14.87	(+) 0.61	(+)19.27	
32	(+) 0.03		(+) 2.15		(+) 8.22	
35	(+) 1.47		(+) 1.75		(+) 4.65	
≥ 38	(+) 0.49		(+) .004		(+) 4.39	
ΣX^2	85.01	10.24	39.76	53.15	316.37	125.15
d.f.	11	8	12	9	10	9
P	<.001	>.20	<.001	<.001	<.001	<.001

Sign indicates more (+) or fewer (-) than expected in checkerboard size distribution.

Fig. 10. Mean number of individuals in 1-m^2 quadrats in which rock size distributions were experimentally altered (see text). Data are from the high zone at North Island in a) May, b) June, and c) September 1979. Vertical bars represent +1 S.E. Note that in (c) the scale for the vertical axis has been doubled.


Mean Number per Quadrat
0
15
30
45
60
H.n.
H.o.
C.p.
A
TREATMENT
0
15
30
45
60
H.n.
H.o.
C.p.
B
TREATMENT
0
30
60
90
120
240
HN
HO
C
TREATMENT

H. nudus individuals in treatments II and III (intermediate and small rocks) appear consistently greater than those in the same mid zone treatments. Surprisingly, the highest H. nudus densities occurred in treatment IV (nonuniform size distribution). It should be recalled that H. oregonensis clearly dominated those cells in the mid zone. H. nudus densities among the cells containing only large rocks were greater in the high zone in May but were not markedly different during June or September.

The simplest and most direct method of comparing the distributions of H. nudus individuals throughout the experimental cells is to compare the percentages of the species' total within each treatment type between zones. This approach also has the advantage of partially compensating for differences in crab densities between the zones. It is clear from the results of these comparisons (Table 6) that the proportions of the total H. nudus in each treatment type are not independent of tidal height ($P < .001$ in all months). In each instance, there were more H. nudus than expected among small and intermediate rock treatments in the high zone and fewer than expected in the large rock treatments. In May and June, there was also an unexpectedly large fraction among the quadrats in which the rock sizes were mixed. No data are available for these cells in the September census. As a corollary,

Table 6. Results of χ^2 tests of independence of the distributions of H. nudus among the treatment types in the mid and high zone checkerboards. Signs preceding the χ^2 values for each treatment indicate over- (+) or underrepresentation (-)

	Treatment									
	Small		Intermediate		Large		Mixed		Totals	
	χ^2	Exp.	χ^2	Exp.	χ^2	Exp.	χ^2	Exp.	χ^2	Exp.
April-May										
Mid	(-) 7.5	(11.2)	(-) 0.7	(53.0)	(+)16.6	(74.8)	(-)6.4	(63.1)	31.2	(202)
High	(+) 2.8	(29.8)	(+) 0.2	(142.0)	(-) 6.2	(200.2)	(+)2.4	(168.9)	11.6	(541)
	10.3	(41)	0.9	(195)	22.8	(275)	8.8	(232)	42.8***	(743)
June										
Mid	(-) 9.7	(25.8)	(-) 0.1	(65.8)	(+)10.9	(93.1)	(-)2.2	(90.2)	22.9	(275)
High	(+) 5.5	(45.2)	(+) 0.0	(115.2)	(-) 6.2	(162.9)	(+)1.3	(157.8)	13.1	(481)
	15.2	(71)	0.1	(181)	17.1	(256)	3.5	(248)	36.0***	(765)
Sept.										
Mid	(-) 0.4	(18.9)	(-)14.3	(199.4)	(+) 7.3	(432.8)			22.1	(651)
High	(+) 0.4	(22.1)	(+)12.2	(233.6)	(-) 6.2	(507.2)			18.8	(763)
	0.8	(41)	26.5	(433)	13.5	(940)			40.8***	(1414)

smaller rocks were more frequently occupied by *H. nudus* in the high than in the mid zone. In general, these results indicate that the *H. nudus* utilization pattern is somewhat broader in the high intertidal relative to the mid intertidal as was inferred from the transect data. There are, however, several factors aside from *H. oregonensis* density that vary with tidal height. Decreased wave intensity and decreased mean size of *H. nudus* in the high zone may have contributed to the differences. Decreased wave activity would have the effect of lessening the differences in refuge quality along the rock size axis.

To summarize the results obtained thus far:

1) The resource utilization patterns of the two species are markedly different, ostensibly as a result of competition for refuge space along the gradient in rock sizes. *H. nudus* was shown to prefer large rocks, while *H. oregonensis* individuals are apparently restricted to smaller rocks.

2) The quality of a rock as a refuge (as determined by wave-induced disturbance rates) is directly related to rock size.

3) The frequency of occupation of the smallest, least stable rocks is directly related to the total density of shore crabs.

4) Competitive ability, measured in terms of ability to gain access under preferred rocks, appears largely determined by individual size, and *H. nudus* individuals

are on the average larger than H. oregonensis individuals. There are, however, differences between the species that cannot be accounted for by size alone.

5) Nearly complete separation of the two species, over small areas at least, can be experimentally induced by manipulation of the rock size distribution.

6) Crab size structures, hence relative competitive abilities, are strongly affected by changes in the rock size distribution.

South Island

The evidence presented thus far for interspecific competition is based primarily on descriptive data. As such, it is inferential. In order concretely to demonstrate that the resource utilization patterns of H. oregonensis are the direct result of competition, it is necessary to show that those patterns are appropriately different when H. nudus is absent but conditions are otherwise the same. These conditions are very nearly met on South Island (Fig. 1) where H. nudus is comparatively scarce. Like North Island, South Island is composed of cobble-sized rocks overlying coarse sand and gravel. The two sites are separated by a narrow channel which has undergone substantial filling since the beginning of the study. The maximum elevation is 1.35 m above MLLW and the habitable mid intertidal is small (ca 230 m^2). In the low intertidal, rock cover is scant. The lack of a high zone is believed to be the most likely reason for the consistently low densities of H. nudus, since most recruitment for this species occurs there.

As on North Island, population density and resource utilization patterns were estimated by repeatedly sampling permanent quadrats along a transect normal to the shore. The quarterly surveys were begun in April 1979 and were continued until March 1980.

H. oregonensis densities on South Island (Fig. 11) were often twice those on North Island during the same months (Fig. 4). In March 1980 the difference was only about 50% (141 vs. $95/m^2$). However, the size distributions (Table 7) reveal that newly recruited individuals constituted a large fraction of the total. This was especially noticeable in winter when the majority of H. oregonensis >5 mm were killed, presumably by wave action, and the losses were replaced by heavy recruitment (Fig. 11). A similar phenomenon occurred on North Island, but recruitment was apparently insufficient to compensate for losses until the spring. The H. nudus individuals which were present on South Island seldom exceeded 15 mm and were usually found near the top of the island. Thus, although there was some interspecific competition, it was patchy

Figure 11. Average density of H. oregonensis in the mid zone at South Island plotted against time. Total density and the density of individuals ≥5 mm are shown.

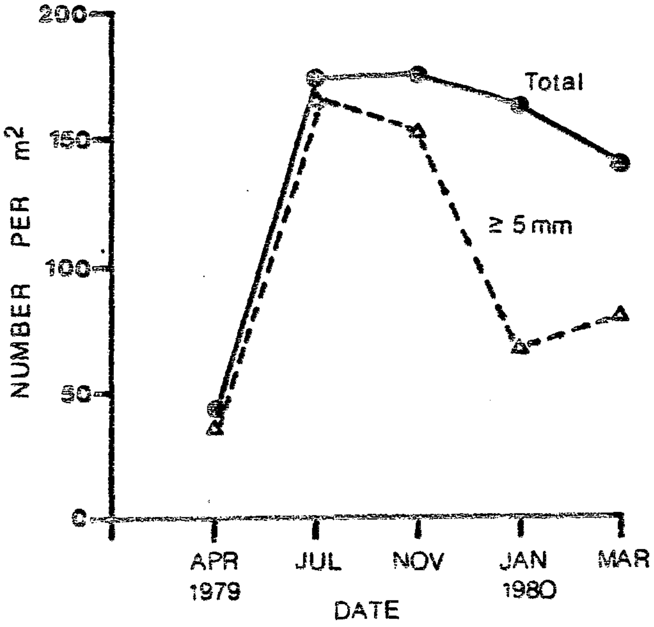

200
150
100
50
0
NUMBER PER m²
Total
≥ 5 mm
APR 1979
JUL
NOV
JAN 1980
MAR
DATE

Table 7. Size frequency distributions (%) of H. oregonensis sampled in the mid zone along the permanent transect at South Island

Time	Size Class (mm)									n	Avg. size (mm)
	≤3	5	8	11	14	17	20	23	26		
(1979)											
Apr.	4.9	33.3	16.9	17.1	16.5	5.9	3.1	2.0	0.4	508	9.5
Jul.	0.5	10.6	29.7	41.3	14.0	2.7	0.5	0.2	0.5	407	10.2
Nov.	10.4	26.5	31.9	18.6	7.7	3.2	1.4	0.5		442	8.2
(1980)											
Jan.	55.7	9.7	17.2	11.6	3.6	1.7	0.2	0.2		413	5.5
Mar.	33.5	19.4	22.0	17.5	5.0	1.4	0.9	0.2		635	6.6

and of comparatively low intensity. It is also worth noting that rocks >150 cm^2 constitute a markedly smaller portion of the available cover on South Island. The differences between the two sites are depicted in Fig. 12.

The mid zone resource utilization patterns for H. oregonensis on South Island (Fig. 13) are dramatically different from those obtained in North Island during the same months (Fig. 2). The most obvious distinction between the pairs of curves is that on South Island the mean number per rock continually increased over the range of rock sizes, while on North Island the means decreased after reaching maxima among intermediate-sized rocks. More importantly, using the same rationale described earlier, the density (number of individuals per cm^2 rock surface area) of H. oregonensis on South Island continually increased with rock size ($p < .001$ in all cases). It is tempting to compare these results (Fig. 13) with the resource utilization patterns for H. nudus at equivalent times and tidal heights on North Island (Fig. 2). It is clear from the figures that when given the opportunity, more (small) H. oregonensis can be physically accommodated within a given area than can (large) H. nudus. It is also clear that this does not imply that the former species exhibits a "greater preference" for large rocks. Some compensation for differences in the population size

Fig. 12. Comparison of the average surface area/m^2 of rocks in 100 cm^2 size classes on North and South Island. Data are pooled from all surveys.

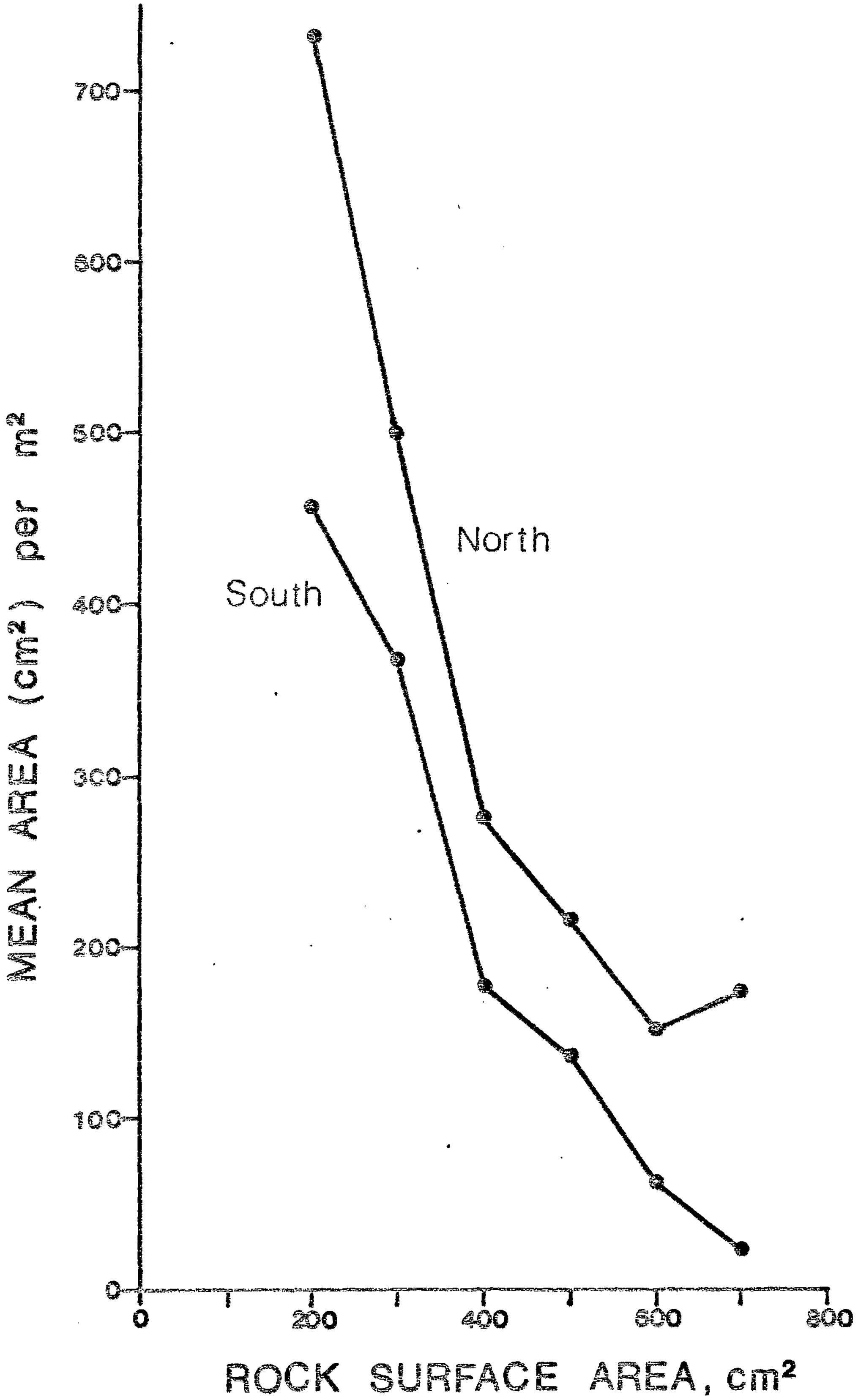
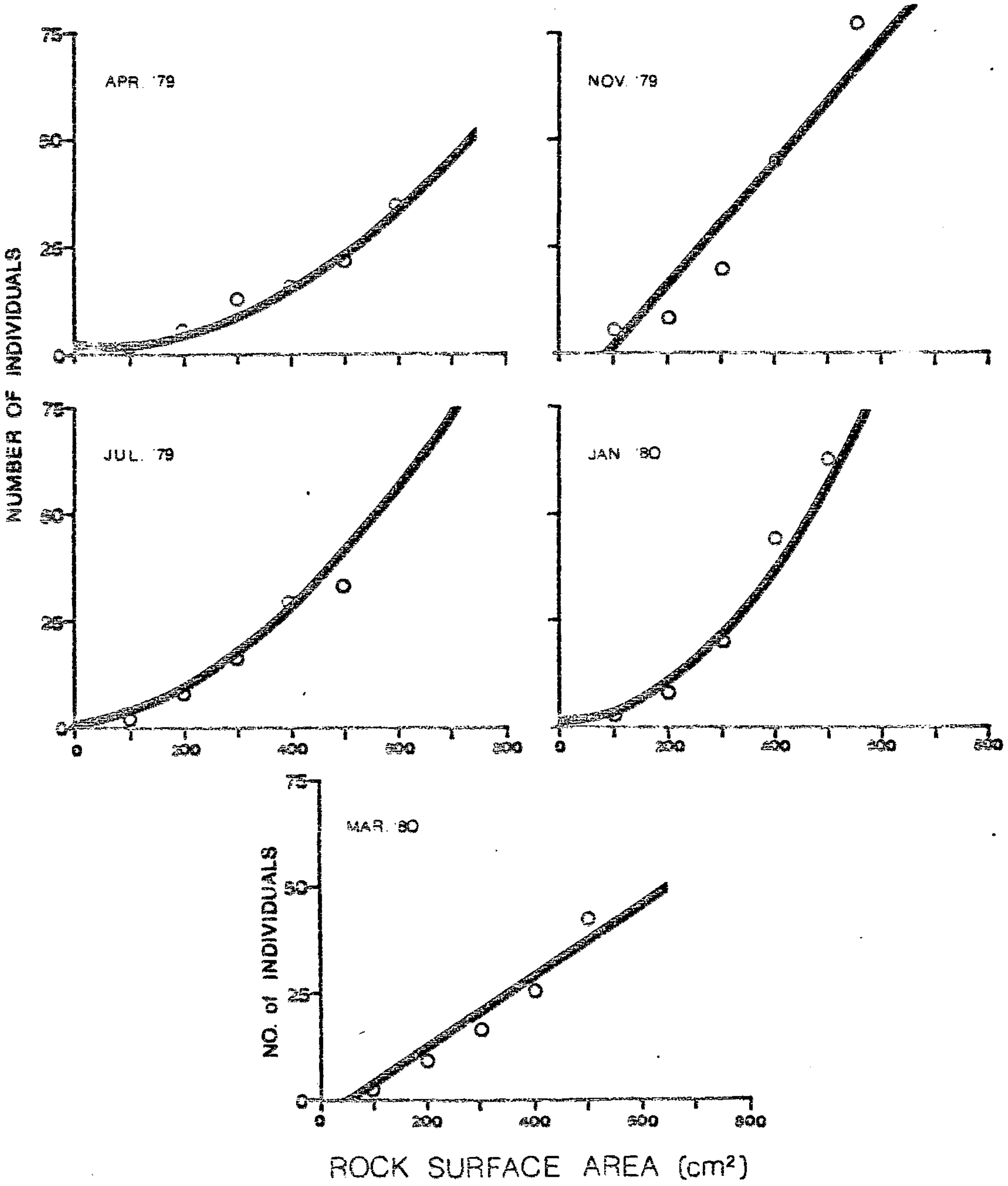

MEAN AREA (cm²) per m²
700
600
500
400
300
200
100
0
North
South
0
200
400
600
800
ROCK SURFACE AREA, cm²

Fig. 13. Resource utilization curves for *H. oregonensis* in the mid zone at South Island. Curves determined by stepwise multiple regression of number of individuals on rock surface area and its square. Mean numbers of individuals in 100 cm^2 rock size classes are also shown.


APR. '79
NOV. '79
JUL. '79
JAN. '80
MAR. '80
NUMBER OF INDIVIDUALS
NO. of INDIVIDUALS
0
25
50
75
0
200
400
600
800
ROCK SURFACE AREA (cm²)

structures can be made by substituting total biomass for numbers of individuals (Fig. 14). Of the five pairs of comparisons, the increases in total biomass were significantly greater for H. oregonensis on South Island in 2 months (July 1979, $P < .05$, and January 1980, $P < .01$), less in 2 months (April 1979, $P < .001$, and March 1980, $P < .001$), and in one pair (October-November 1979), the regressions were not significantly different ($P > .20$). However, for many of the same reasons cited earlier (differences in density and rock size distribution), it is difficult to ascribe precise meaning to the results.

From these results it is nonetheless reasonable to conclude that in the presence of considerable numbers of H. nudus (North Island), H. oregonensis individuals are competitively excluded from that portion of the limiting resource axis which they would preferentially exploit in the absence of such competition. Even so, highly significant positive correlations between the sizes of H. oregonensis individuals on South Island and the sizes of the rocks that they occupy (Table 8) suggest that size-related (intraspecific) interference continues to determine the probability that any given individual will gain access to the preferred refuge space.

A final test of the proposed competitive model was carried out between March and April 1980. Approximately

Fig. 14. Comparisons of the mid zone resource utilization curves (based on biomass) for *H. oregonensis* at South Island and *H. nudus* at North Island. Average biomasses in 100 cm^2 rock size classes are also shown.

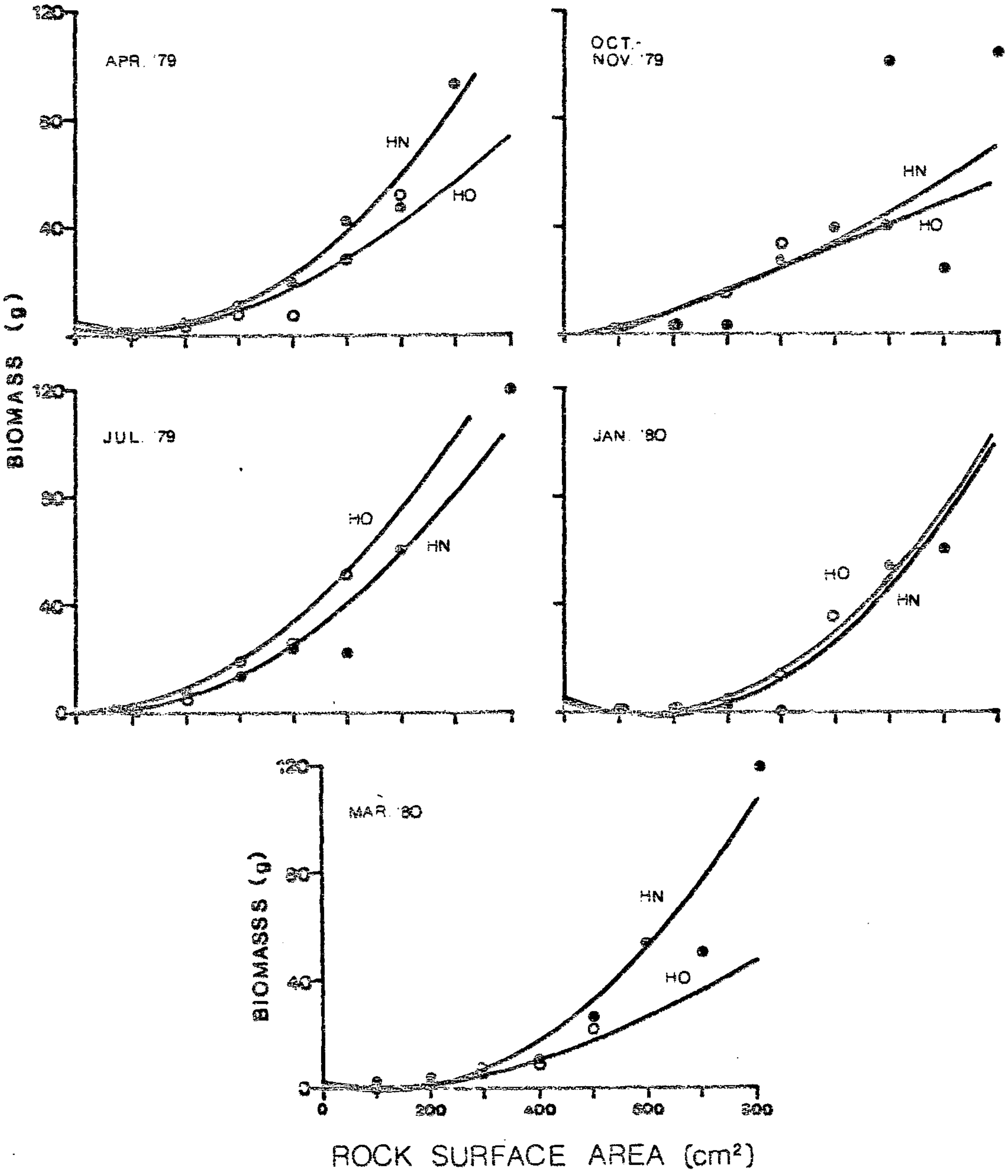
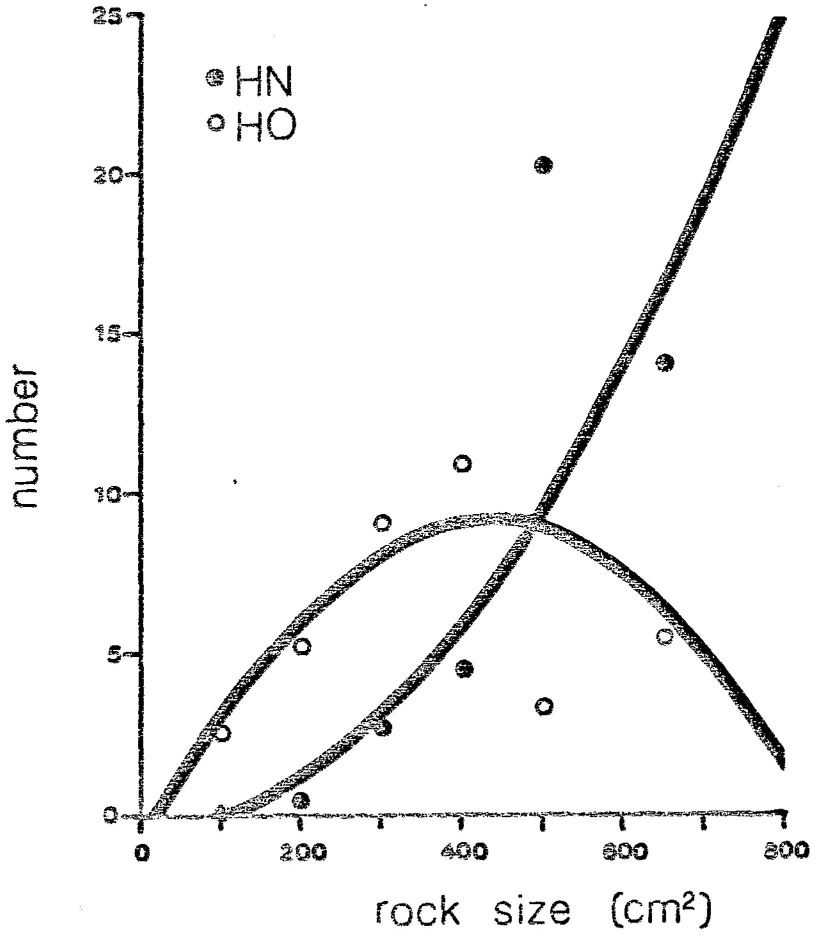

APR. '79
HN
HO
OCT.-
NOV. '79
HN
HO
JUL. '79
HO
HN
JAN. '80
HO
HN
MAR. '80
HN
HO
BIOMASS (g)
BIOMASSS (g)
0
40
80
120
0
200
400
600
800
ROCK SURFACE AREA (cm²)

Table 8. Results of linear regressions of size of rock occupied and the size of resident H. oregonensis individuals in the mid zone at South Island

Time	Slope	Intercept	d.f.	t	P
Apr. 79	11.22	252.5	506	5.9	<.001
Jul. 79	15.69	21.3	405	7.4	<.001
Nov. 79	4.79	374.8	440	2.1	<.05
Jan. 80	14.07	198.7	411	8.1	<.001
Mar. 80	14.17	232.8	633	8.7	<.001

5,500 H. nudus were collected from a nearby area (Pigeon Point) and released throughout the mid intertidal on South Island 4 days after the March 1980 transect survey. Since the low intertidal is, at best, a marginal habitat, the targeted area was small and relatively well defined. Assuming no mortality among those released, the addition was expected to result in an average H. nudus density of 25-30/m^2. The size structure of the released group was estimated from a semirandom sample of 413 individuals. After having been released, few individuals remained exposed when the area was covered by the tide 1-2 hours later. Four weeks later, the transect survey was repeated. In April, the H. oregonensis density had dropped to 55% of the previous month (79/m^2 vs 141/m^2) in the same quadrats. In addition, the H. oregonensis resource utilization pattern became deflected downward at the middle of the resource axis (Fig. 15, $P < .001$) as was characteristic of the North Island population, and was significantly different from the March pattern ($F = 39.15$, $P < .001$). The H. nudus resource utilization pattern (Fig. 15) shows that the density of individuals increased with increasing rock size and was significantly different from the H. oregonensis curve ($F = 12.41$, $P < .001$). The density of H. nudus individuals (16.6/m^2) was, however, markedly less than expected, and size classes >12 mm accounted for a

Fig. 15. Resource utilization curves for both species in the mid zone at South Island following the addition of 5,500 *H. nudus* one month earlier. Mean numbers of *H. nudus* in 100 cm^2 rock size classes are represented by closed circles, *H. oregonensis* by open circles.


● HN
○ HO
number
0
5
10
15
20
25
0
200
400
600
800
rock size (cm²)

disproportionately small fraction of the recaptures, even when the size distribution of the relatively small H. nudus resident on the island in March is taken into account (Table 9, $P < .01$). Of all the results from the experiment, this is the only one that was unexpected.

Fossil Point

As described earlier, shore crabs at Fossil Point are restricted to patches of rubble and boulders amid larger rocky reefs. A third grapsid, Pachygrapsus crassipes, is common here in rock crevices in the highest areas, and appears to be restricted to the zone just above that occupied by H. nudus.

In February 1980, a brief survey was conducted in two adjacent mid intertidal areas (ca 1.3 m above MMLW). One area is a small (20-25 m^2) patch of cobble-sized rocks overlying a sandy substrate. The second area, contiguous with the first, is a patch of boulders, some of which exceed 1 m in diameter. Substrates under the boulders range from solid rock to poorly drained sandy gravel.

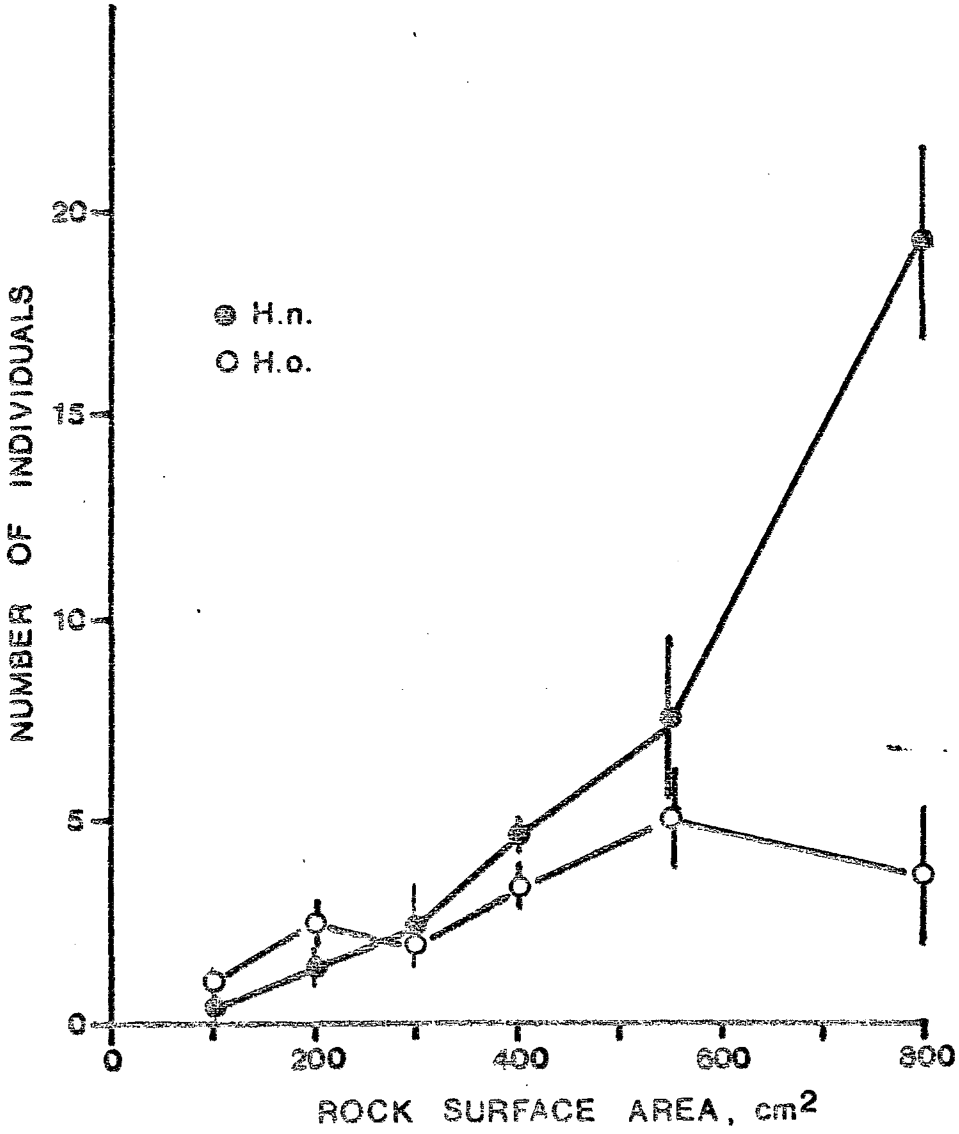
Within the first area, four randomly placed 1 m^2 quadrats were censused in the manner previously described for the major study areas. The resulting resource utilization patterns for the two Hemigrapsus (Fig. 16) are similar to those obtained at North Island during January (Fig. 2) and indicate that the area is, in general, favorable to both

Table 9. Results of χ^2 test of independence between the size distribution of released and recaptured H. nudus at South Island. Signs preceding χ^2 values indicate more (+) or fewer (-) than expected among recaptures

Size Class (mm)	Expected Frequency*	Number Expected	Number Observed	χ^2
≤8	.04	6.2	14	(+) 9.9
9-10	.13	21.4	32	(+) 5.3
11-12	.15	24.6	34	(+) 3.6
13-14	.21	34.9	28	(-) 1.4
15-16	.15	24.3	18	(-) 1.6
17-18	.14	23.7	20	(-) 0.6
19-20	.06	9.9	6	(-) 1.5
21-22	.05	7.7	6	(-) 0.4
23-24	.04	6.9	4	(-) 1.2
≥25	.03	5.4	3	(-) 1.0
Totals	1.00	165	165	26.5**

*Frequencies based on weighted distributions of resident and released H. nudus.

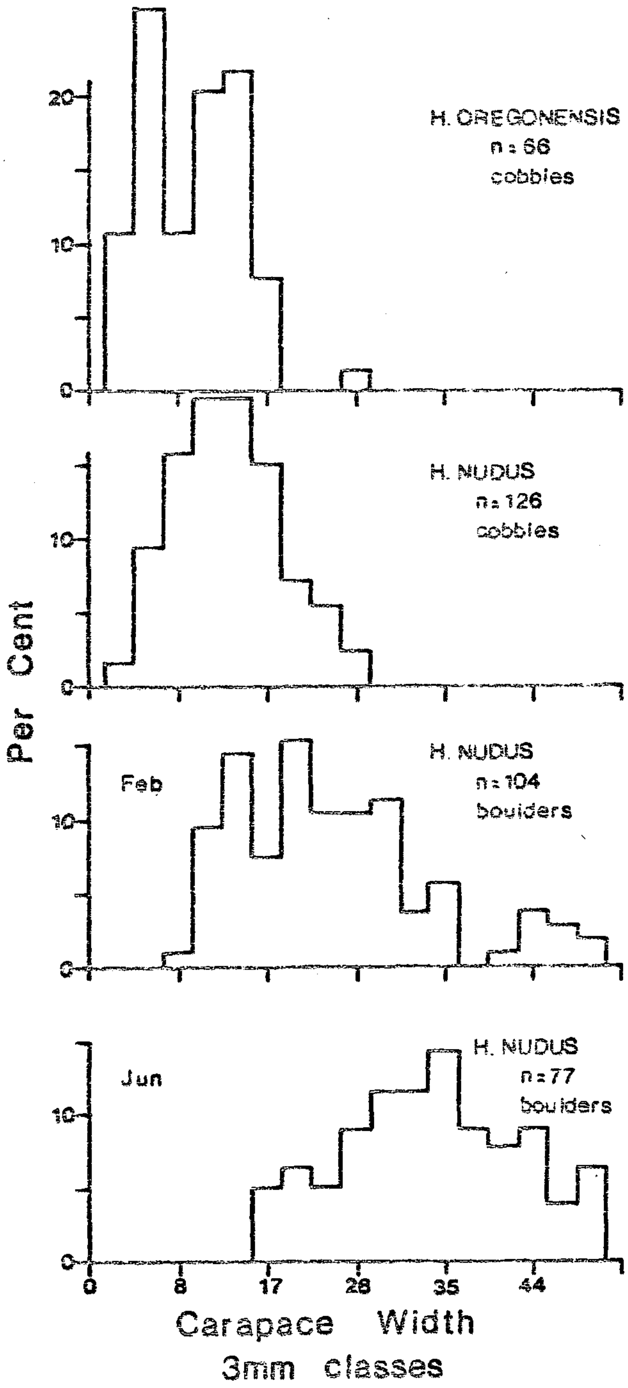
Fig. 16. Resource utilization patterns, shown as mean number ±1 S.E. in 100 cm^2 rock size classes, for H. nudus and H. oregonensis in a cobble area at Fossil Point.


NUMBER OF INDIVIDUALS
0
5
10
15
20
● H.n.
○ H.o.
0
200
400
600
800
ROCK SURFACE AREA, cm^2

species.

Sampling in the boulder field could not be done randomly since it proved impossible to turn over most of the rocks. Four relatively small boulders (mean surface area ca 2200 cm^2) were overturned and censused. In June 1980, 5 additional boulders (mean surface area ca 3800 cm^2) were censused in an area a few meters away. From the results of these brief surveys (Fig. 17), two conclusions can be drawn that are consistent with expectations of the model. First, while H. oregonensis is abundant at Fossil Point, it is completely absent in the boulder fields. In contrast to the cobble areas, H. nudus completely dominates the boulder fields. Secondly, the size structure of the H. nudus in the boulder fields is dramatically biased toward large individuals. To illustrate this last point, consider that 28 of 181 H. nudus individuals in the sample above were larger than 40 mm while only 21 of 6,876 H. nudus at North Island (from all sources) were in the same size category. Since it is unlikely that these boulders have been overturned in recent years, the area may be properly viewed as one in which competition has proceeded uninterrupted for some time.

Fig. 17. Size frequency distributions of the shore crab species at two locations at Fossil Point. Cobble area and the boulder field were sampled during February 1980. In both surveys, H. oregonensis was not found among the boulders.


H. OREGONENSIS
n = 66
cobbles
H. NUDUS
n = 126
cobbles
Feb
H. NUDUS
n = 104
boulders
Jun
H. NUDUS
n = 77
boulders
Per Cent
0
10
20
0
8
17
26
35
44
Carapace Width
3mm classes

Charleston Breakwater

To this point, the effects of different substrates on the two competitors have not been explicitly considered, since substrates at the study areas described above are relatively homogeneous (coarse sand and gravel). Substrate characteristics may, however, exert a powerful influence on the composition of the shore crab community. A brief description of the crabs present at the Charleston breakwater serves to illustrate this point, and in so doing, indicates the limits of the competitive model.

As a result of the lack of significant wave activity, substrates in the middle and lower zones on the inner (leeward) side of the breakwater are composed of very fine sand and mud. Rock surfaces are often covered with a thin layer of fine sediments, indicating high sediment loads in the water. On the outer (exposed) side, coarse sand predominates. Rocks on both sides are primarily quarried, igneous boulders, although smaller cobbles are present. Under the rocks on the inner side, _H. oregonensis_ is abundant and _H. nudus_ is virtually absent. The reverse is true on the outer surface of the breakwater. In general, _H. nudus_ is extremely rare in all rocky intertidal habitats in Coos Bay in which the substrates are predominantly muddy, regardless of the distribution of rock sizes (personal observation).

From these and similar observations (Olmsted and Baumberger 1923, Hiatt 1948, Dehnel 1960, Knudsen 1964, Low 1970) it appears reasonably certain that H. nudus is incapable of tolerating fine sediments. Hiatt (1948) noted that the tufts of setae covering the branchial incurrent openings is markedly reduced in H. nudus when compared to H. oregonensis. In consequence, H. nudus may literally suffocate under extremely turbid conditions. These observations also serve to illustrate that the pool of H. oregonensis recruits does not depend entirely upon reproductive output from those populations which co-occur with H. nudus. Instead, it is likely that populations in the numerous muddy areas in the estuary provide a large fraction of the available colonists.

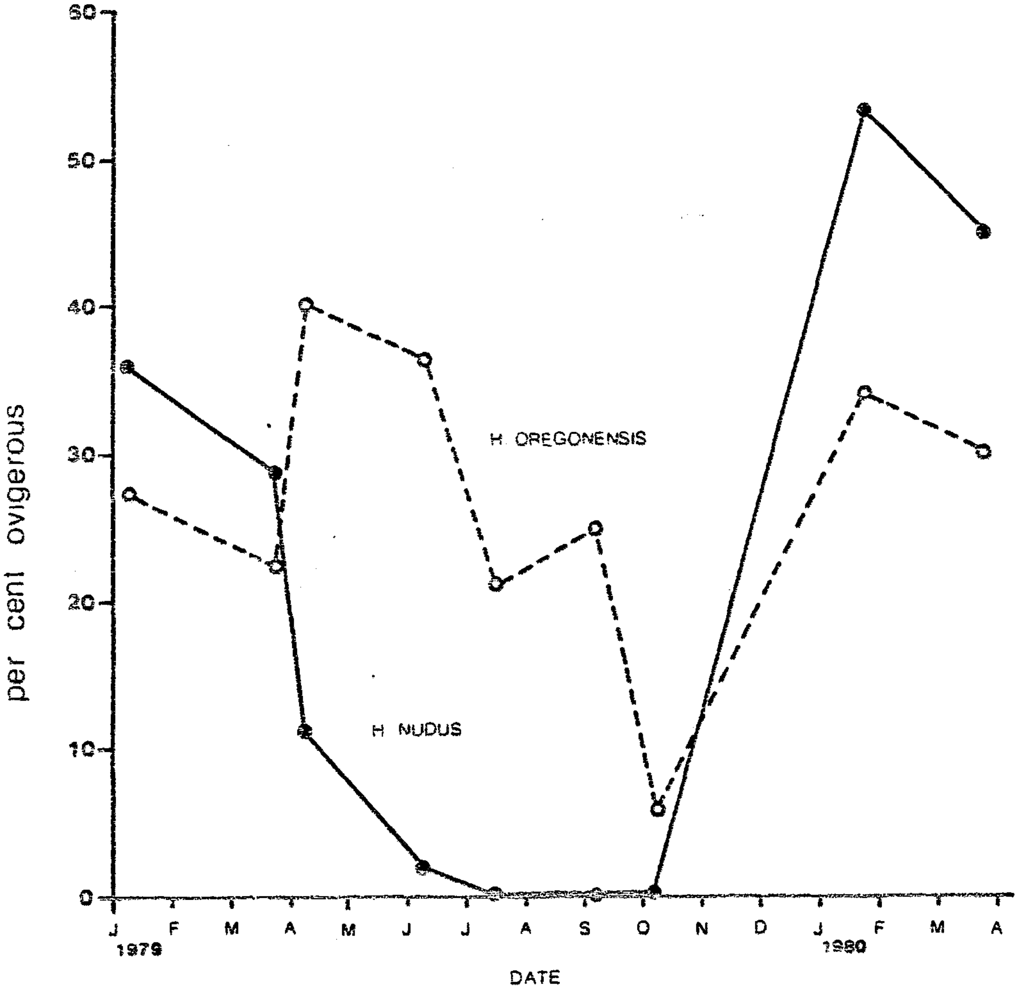
Life Histories

As in most crustaceans, female Hemigrapsus brood their eggs while the embryos develop into free-swimming planktonic larvae. Since the brood is carried externally, ovigerous females are readily detected during field surveys. Furthermore, since the brood period for individuals of both species is about 15 weeks (Knudsen 1964) it is unlikely that major reproductive events will be overlooked if the populations are sampled at quarterly intervals.

A plot of the percentage of mature ovigerous females (see below) at North Island during transect and checkerboard surveys shows that H. oregonensis has a markedly extended breeding season compared to H. nudus (Fig. 18). A large fraction of the mature females of both species were ovigerous during the winter months, but during summer, reproductive activity of H. nudus ceased while H. oregonensis females continued to reproduce. In his study of the reproductive patterns of crabs in Puget Sound, Knudsen (1964) concluded that this difference was due to the production of a second (summer) brood by H. oregonensis in contrast to the single (winter) brood produced by H. nudus. In both studies ovigerous H. oregonensis were found in all samples. The notion of a single winter brood in H. nudus is also consistent with the results of a study in Monterey Bay (Boolootian et al. 1959).

Aside from reproducing more frequently than H. nudus, H. oregonensis appear to begin reproduction at a smaller size. Estimates for the minimum size at maturity for H. oregonensis include 9 mm (Knudsen 1964), 8.6 mm (Willason 1980), and 6.5 mm (this study, average minimum was approximately 7.5 mm). The smallest ovigerous female H. nudus found by Boolootian et al. (1959) was 18mm, while Knudsen (1964) cites 11.9 mm as the minimum. In this study, I have found very few ovigerous H. nudus females <12 mm (minimum 11.7 mm) and an average minimum of about

Fig. 18. Percentage of adult females of both species that were ovigerous at each field survey. Data are taken from transect and checkerboard surveys at North Island.

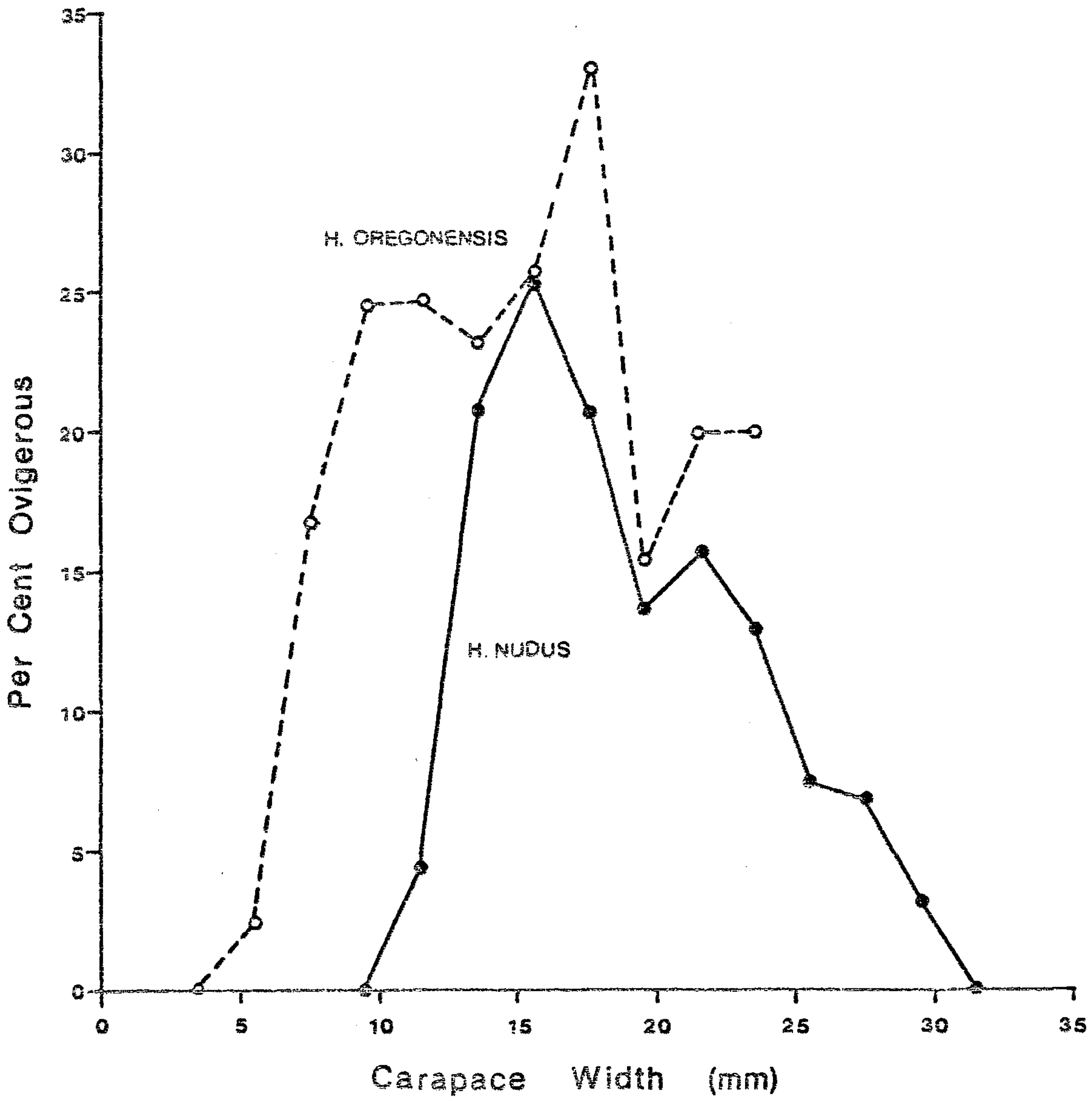

60
50
40
30
20
10
0
per cent ovigerous
H. OREGONENSIS
H. NUDUS
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
1979
1980
DATE

13.5 mm. In the graph above (Fig. 18), females larger than 7 mm and 13 mm were assumed to be mature for *H. oregonensis* and *H. nudus*, respectively.

A plot of the percentage of ovigerous females by size class is depicted in Fig. 19. The data shown were taken from North Island and are pooled without consideration of seasonal effects. In addition to showing the interspecific difference in size at first reproduction it is apparent from the graph that the fraction of berried females declines with size, particularly in *H. nudus*. Although not shown here, the *H. oregonensis* curve shows temporal variation wherein the winter peak is dominated by small females and the summer peak is dominated by larger females. This is consistent with the notion of a second brood, and pooling the data produces the plateau seen in Fig. 19. In contrast, the *H. nudus* curve does not vary appreciably in time. Although several explanations are possible, it would be premature to attach any special significance to this rather curious result since the data are from a single habitat and encompass only two annual breeding cycles. Observations of berried *H. nudus* females as large as 45mm at Fossil Point would, however, argue against explanations based on senescence.

Although the evidence is not direct, the results above suggest that molting frequency and hence annual

Fig. 19. Percentage of the total number of females in 5 mm size classes that were ovigerous at any time during the study (January 1979 - March 1980). Data are taken from transect and checkerboard surveys at North Island.


H. OREGONENSIS
H. NUDUS
Per Cent Ovigerous
Carapace Width (mm)
0
5
10
15
20
25
30
35

growth rates are lower for H. oregonensis. According to one study (Kuris 1971 cited in Kuris and Mager 1975) the growth increment resulting from a single molt (~15%), for H. oregonensis, is relatively independent of size so that the growth rate is primarily determined by molting frequency. Information gleaned from the literature (Kuris and Mager 1975, Olmstead and Baumberger 1923, C. Sidi unpublished data) and from my own limited field observations of recently molted crabs (see Appendix) suggests that the percentage increment resulting from a single molt is not substantially different between the species. There is to my knowledge no published information concerning the relative frequency of molting for the two species. However, it is reasonable to assume that the time (~3 mos) and energy invested in brooding and egg production may markedly decrease molting frequency. The second (summer) brood produced by H. oregonensis may be especially costly to annual growth since summer conditions (abundant food, warm temperatures, etc.) are probably ideally suited for growth.

Discussion

The results of this study demonstrate that the shore crabs *Hemigrapsus nudus* and *H. oregonensis* compete for refuge space along a gradient in rock size. Rock size and survivorship of resident crabs are thought to be closely linked inasmuch as rock size and wave-induced disturbance are inversely correlated. While both species prefer larger, more stable rocks in the absence of competition, interspecific competition results in a distinct pattern of microspatial patchiness in which *H. nudus* individuals dominate rocks in the largest size classes and *H. oregonensis* is restricted to smaller rocks. The smallest, least stable rocks are occupied in direct proportion to total shore crab density, an indicator of the competitive pressures along the remainder of the resource axis. At the level of the individual, competitive ability, measured in terms of ability to acquire preferred refuge space, is determined primarily by size. Positive correlations for both species between individual size and surface area of the rock occupied provide strong support for this assertion. Since *H. nudus* individuals are, on the average, larger than *H. oregonensis* individuals, the *H. nudus* population enjoys a competitive advantage.

Comparisons of the life history traits provide insights as to the underlying causes for the size-related competitive differences between the species. In particular, examination of the reproductive patterns revealed that H. oregonensis females become sexually mature at a smaller size and reproduce more frequently than H. nudus females. This strategy, which directs relatively more time and energy toward the production of potential colonists, must necessarily also result in the allocation of proportionately fewer resources to growth. Alternatively, by opting for delayed and infrequent reproduction, H. nudus individuals of the same age would gain an advantage in size and thus competitive ability and survivorship while paying for these in lowered fecundity. The rate at which fitness declines with increased frequency of disturbance is therefore probably greater for H. nudus since individual H. oregonensis are far more likely to produce successfully at least one clutch in the disturbance-free time interval. In a sense, H. oregonensis more effectively exploits environments in which average survivorship is low, while H. nudus sacrifices exploitation efficiency in favor of greater interference ability. When competition is interrupted by frequent but patchy physical disturbances, the species may thus be expected to co-occur in a spatial mosaic similar to that described above. However, if competition is allowed to proceed uninterrupted, interference ability becomes more important and a competitive equilibrium may be expected in which H. oregonensis is completely excluded.

Furthermore, since survivorship and rock stability are believed to be closely linked, crab size structure, and thus relative competitive ability, is determined to a large extent by the rock size distribution. Support for this notion comes from (1) the unexpectedly larger mean size of individuals of both species in the mid zone experimental plots at North Island when rock size distributions were deliberately altered, (2) the unexpectedly small fraction of large H. nudus among the South Island recaptures where large rocks are relatively uncommon, and (3) the dramatically higher mean and average maximum size of H. nudus among the boulders at Fossil Point. H. oregonensis is abundant in other habitats at Fossil Point, yet is conspicuously absent among the boulders. For these reasons, I believe that the boulder field and other similar habitats in the bay (e.g., the exposed side of the Charleston breakwater) represent mid-intertidal areas in which competitive equilibrium has been achieved, and that this equilibrium is attributable to the absence of physical disturbance and interference by other species. Under conditions in which substrates are silty or muddy the competitive model does not apply, since H. nudus is morphologically incapable of exploiting such habitats.

In contrast to the mid zone, the high intertidal at North Island is clearly dominated by H. nudus. Observations of sympatric populations of these crab species often yield similar findings (Hiatt 1948, Dehnel 1960, Knudsen 1964, Low 1970). Intertidal height is thus a second axis along which the species segregate. Differences in vertical distributions in other intertidal organisms are extremely well documented and are usually attributed to differential tolerance to exposure-related stress. Hiatt (1948) stated that H. oregonensis is less tolerant of exposure than H. nudus. I have also found that H. oregonensis is less tolerant to drying than H. nudus and that the young of both species are more susceptible than adults (see Appendix). Without refugia, few juveniles can survive longer than 12 hours (lab conditions) while many adults can survive for several additional hours. However, if provided with damp refuges, the young of either species can survive extremely long periods of exposure (>7 days) under field conditions in summer. Jones (1941) presented evidence that both species live well below their physiological limits to desiccation.

Comparisons of H. nudus distributions in the high zone with those in the mid zone showed that the resource utilization patterns in the high zone were significantly broader, with individuals tending to use intermediate-sized and small rocks more frequently and in greater numbers. Data from vertical transects and experimental plots are consistent in this regard. The high differs from the mid intertidal in several factors not all necessarily related to exposure: (a) *H. nudus* densities are greater, (b) *H. oregonensis* densities are lower, (c) wave action is less frequent, and (d) *H. nudus* individuals tend to be smaller. Since it is conceivable that any one of these factors alone could result in the patterns observed, it is impossible to determine which among them is most responsible. Likewise, it is not possible to distinguish between the effects of competition and increased exposure on the density of *H. oregonensis*. In light of the evidence above, it is not unreasonable to suppose that both interspecific competition and abiotic factors are involved, especially if it could be shown that crabs under small rocks (i.e., those available to *H. oregonensis* after competition) succumb more quickly to desiccation.

It was noted earlier that although there were significant positive correlations between the size of individual crabs and the size of the rocks that they occupy, the estimated intercepts for the H. *oregonensis* regressions were always significantly lower than for *H. nudus*.

The difference was most pronounced during winter. These findings indicate that the average rock size occupied by crabs of equal size depends upon the species. The reasons for this are not at present known, but several possibilities exist. For instance, to the extent that there are differences between the species in the rate at which fitness declines with decreasing rock size, selection pressures for behavioral traits (increased aggressive tendencies, etc.) that would permit individuals of a given size to acquire and maintain refuge space under larger rocks would be greater for H. nudus than for H. oregonensis. Put more simply, the motivation to compete for a quality refuge would be greater for the species with more to lose if it "settled" for a relatively poor one. Alternatively, H. oregonensis may have greater "individual distance" requisites (see Wilson 1975), thus causing individuals to avoid the more crowded larger rocks. Bovbjerg (1960) presented laboratory evidence which indicated that another grapsid, Pachygrapsus crassipes, is intolerant of close neighbors. Dispersal rates from an artificially crowded situation were high until the spacing of individuals reached an acceptable level. The extraordinary numbers of H. oregonensis under single rocks on South Island argue against this possibility. A third explanation is that the intensity of aggression may be greater between species than within species. In particular, it is likely that large H. nudus, which invariably occupy the largest rocks, are less aggressive toward conspecifics. Support for this hypothesis comes from laboratory experiments (Appendix) in which it was found that while large male H. nudus are voracious predators on small H. oregonensis, they engage in cannibalism far less frequently. If interspecific predation is considered as an extreme form of interference competition (von Ende 1979), these results are not in accordance with the widespread notion that interference competition should be directed primarily toward those individuals with whom niche overlap is highest (i.e., conspecifics), especially where kinship is not a complicating factor. Most of the evidence for the latter view comes from studies of interspecific territoriality in vertebrates (Low 1971, Orians and Willson 1964, Brown and Orians 1970, and see Lorenz 1964, Wilson 1975, Hazlett 1975, Darwin 1859).

Temporal differences in the relationship between crab size and rock size within the species may reflect differences in density (wherein small individuals tend to do more poorly with increased competitive pressures); or, for H. nudus in particular, seasonal differences in reproductive activity. Notably, smaller H. nudus tend to be found more often under larger rocks during the breeding season (winter-spring) than during the nonreproductive periods (summer-fall). It is therefore plausible that the winter assemblages are breeding aggregations, while the distribution of individuals in summer is determined strictly by size-related competitive ability. It may also be argued that in summer, small crabs have relatively less reason to compete for space under the largest rocks since wave action is less intense than in winter.

CHAPTER II

COMPETITION FOR SPACE AMONG THREE CRABS IN THE ROCKY INTERTIDAL ZONE: THE EFFECTS OF *CANCER PRODUCTUS* ON COMPETITION BETWEEN TWO SHORE CRAB SPECIES

Introduction

Interspecific competition is widely recognized as a major factor in determining the distributions of species in nature. Due to the potentially complex nature of such interactions, many empirical studies have been limited to describing contests between pairs of taxonomically and ecologically similar organisms. However, except under unique or rigorous physical conditions, pairs of competing species seldom interact in an ecological vacuum and interactions with other species in the community may unexpectedly alter the equilibrium densities of one or both competitors. Most notably, selective predation and herbivory have been show to stabilize competition between two or more prey species by disproportionately reducing the densities of competitive dominants (Paine 1966, Brooks and Dodson 1965, Sprules 1972, Menge 1976, among others).

It is also possible for the effects of interspecific competition to change unexpectedly in the presence of other competitors. MacArthur (1972) used the term "diffuse competition" to describe the combined effects of competition among several species. In laboratory studies of aquatic microcrustaceans, Neill (1974) showed that the interaction coefficients between pairs of competing species may depend upon the composition of the surrounding community. These higher order interactions are not readily incorporated into such theoretical constructs of community organization as the community matrix concepts and arguments concerning species packing. However, convincing evidence for higher order interactions among more than two competitors in nature is scarce (Wilbur 1972, Williams 1980). Davidson (1980) presented evidence for a desert ant community which suggested that the diffuse competition experienced by some species at equilibrium may actually decrease with greater species packing.

Among still other, primarily sessile assemblages, competition for space is mitigated by patchy physical disturbances which occur at a rate greater than the rate of return to competitive equilibrium (Connell 1978, Dayton 1971, Sousa 1979, Osman 1977). Despite apparently high niche overlap values, inferior competitors may persist indefinitely in such nonequilibrium assemblages as a result of their superior colonizing abilities and the continual provision of uncontested space.

Here, I will describe the interactions between three crab species which compete for refuge space under rocks in the marine intertidal zone. I have previously detailed the mechanism of competition between two of these species, *Hemigrapsus nudus* and *H. oregonensis*, in Coos Bay, Oregon (Chapter I). The study (reviewed below) emphasized the nonequilibrium nature of the competitive interaction in the middle and high intertidal zones where the two shore crabs are dominant members of the fauna, and influences by other species are minimal. The present study focuses attention on the low intertidal zone where a third competitor, *Cancer productus*, is seasonally abundant and exerts a powerful but unequal influence on each of the shore crab species. The results of field sampling conducted at regular intervals over a two year period, together with small-scale habitat manipulations support the contention that the relative abundances of *H. nudus* and *H. oregonensis* are determined primarily by seasonally variable competition with *Cancer productus* as well as by patchy physical disturbances.

The Animals and Their Treatment

The Species

Shore crabs

Hemigrapsus nudus and *H. oregonensis* are members of the brachyuran family Grapsidae. Both species occur abundantly in the rocky intertidal zones of bays and estuaries from Alaska to the Gulf of California (Rathbun 1918) where they are often sympatric. *H. oregonensis* may also inhabit burrows along the muddy banks of estuaries. *H. nudus* is intolerant of fine sediments but unlike its congener may be found abundantly under rocks along the protected outer coast. Both species are omnivorous and may be found in all intertidal zones. In addition, both species are effective osmoregulators in dilute seawater (Jones 1941, Dehnel and Carefoot 1965).

As mentioned above, I have previously examined the mechanism of competition between these species (Chapter I). The results of the study showed that these highly motile crabs aggressively compete for refuge space along a gradient in rock sizes. Since wave-induced disturbance rates were found to vary inversely with rock size, survivorship of resident crabs is believed to be closely correlated with the sizes of rocks they occupy. In the near absence of one of the two, the resource utilization patterns exhibited by the species are, within practical limits, identical and biased toward progressively larger rocks. However, when the two species are sympatric, interspecific competition results in a distinct pattern of microspatial patchiness in which H. nudus dominate the largest, most stable rocks and most H. oregonensis are restricted to the locally abundant, but least stable smaller rocks. Although evolved resource partitioning per se plays little role in the interaction, the life history strategies employed by the two species diverge markedly and tend to facilitate coexistence in spatially heterogeneous environments: H. oregonensis rapidly achieves maturity and reproduces frequently while H. nudus individuals opt for enhanced growth rates, hence greater interference ability, by delaying reproduction and reproducing less frequently. The relative advantage of either strategy, therefore, depends upon the rates of physical disturbance experienced by individuals throughout the habitat and is consequently linked directly to the rock size distribution. For example, when disturbance rates are uniformly low, as would be expected in habitats composed exclusively of large boulders or crevices, interference ability is at a premium and H. oregonensis may be excluded entirely. Conversely, when disturbance rates are uniformly high and no individual may survive long, interference ability loses importance and high reproductive rates are selectively and competitively advantageous.

Many habitats, such as the primary study site described below, lie somewhere between the two extremes: rock sizes are mixed and disturbances are frequent, but patchy in occurrence. Under these conditions, H. nudus may dominate the largest rock size classes but apparently lacks the colonizing ability necessary to offset the high mortality rates which individuals of either species may be expected to experience among the smaller rocks. These are exploited by H. oregonensis without significant interspecific interference.

Cancer productus

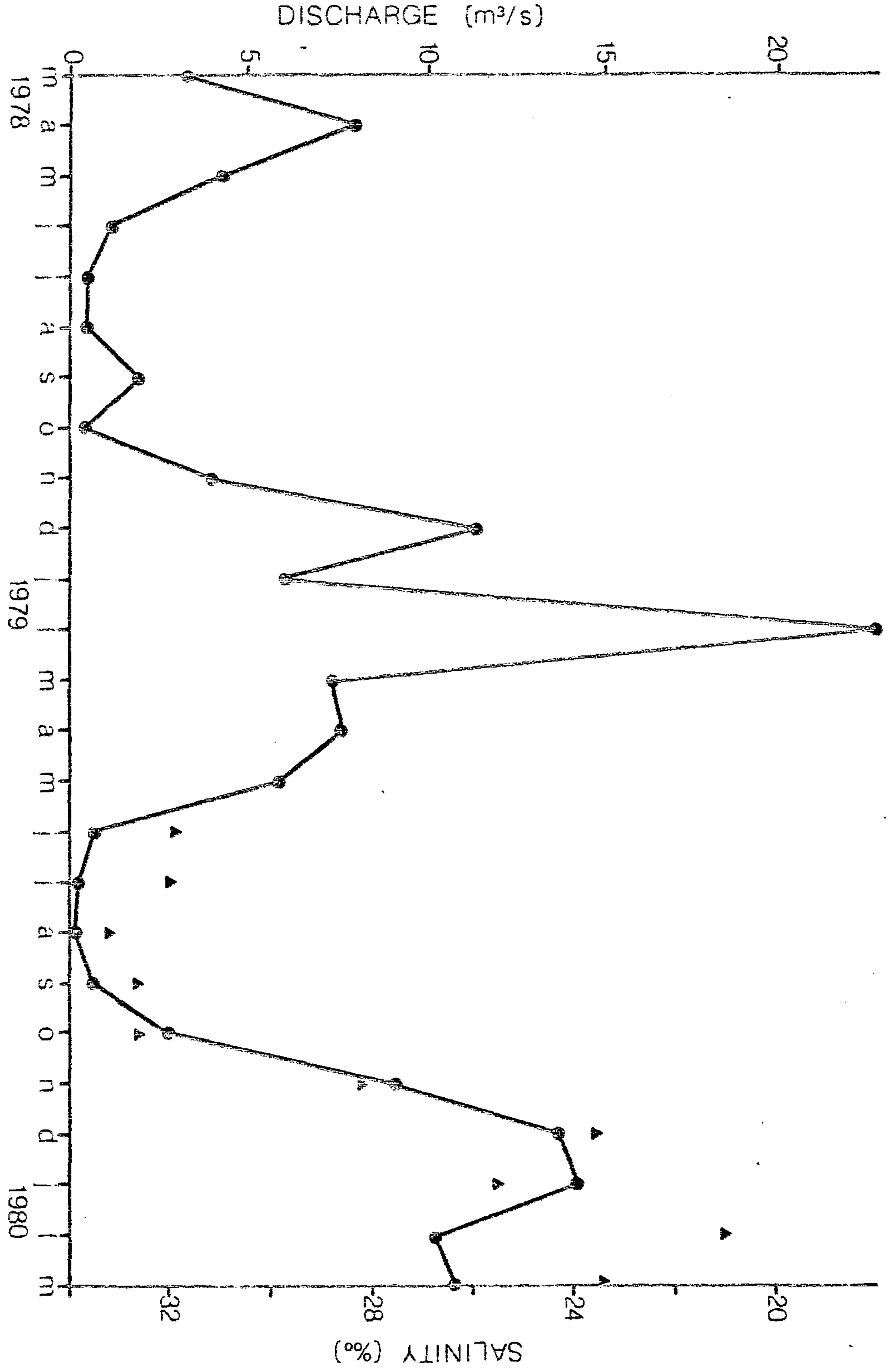
The intertidal distributions of the third crab species, C. productus, are seasonal and primarily restricted to the low zone. Unlike the Hemigrapsus species, C. productus is usually considered to be predaceous and subtidal in occurrence. In addition, C. productus individuals are relatively large (adults may reach 150-160 mm in carapace width while few shore crabs exceed 40 mm) and are apparently unable to regulate the concentration of body fluids in response to changes in ambient salinity (C. Holiday personal communication). It has been demonstrated or inferred that this species is an important predator on the intertidal whelk Thais (Bertness 1977, Connell 1978, Spight 1976) as well as on clams and oysters (Tegelberg and Simons 1978).

Captive individuals readily consume barnacles, limpets, and other crabs, including conspecifics.

The Study Site

The principal study site is an intertidal island in Coos Bay, (44°22'N, 124°18'W) on the central Oregon coast. The area, which I have designated as North Island, is located ca 3.7 km north and east of the bay entrance, and was created some 50 yr ago by the deposition of dredging spoils. The surface of the island is composed of cobble-sized rocks (25-1300 cm^2) which serve as refuges for the crabs. Substrates beneath the rocks are primarily sandy gravel, although finer sediments are common in winter. Wave action is sufficiently intense, especially during winter, to insure that most small and (many) intermediate-sized rocks are regularly overturned (Chapter I). Surface water salinity varies seasonally as a result of fluctuation in the discharge rates of the Coos and Millicoma rivers (Fig. 20). River flows are generally highest in late winter (February-March) and lowest in late summer (August-September); salinity patterns follow a reversed trend. A more complete description of the study area can be found elsewhere (Chapter I).

Fig. 20. Mean monthly discharge rates (●) from the Millicoma River over the course of the study (data from USGS) and average surface salinity (▲) at North Island. Salinity measurements were made at LLW.


DISCHARGE (m³/s)
0
5
10
15
20
SALINITY (‰)
32
28
24
20
m a m j j a s o n d
1978
j f m a m j j a s o n d
1979
j f m
1980

Sampling Procedures

In order to estimate the densities and resource utilization patterns of the crab populations, a permanent sampling grid was established in the low intertidal zone (ca 0.5 m above MLLW) at North Island. Within a designated 15x15 m area, three rows of eight 1 m^2 quadrats were established parallel to the shore. All quadrats were 1 m from those adjacent. Their corners were marked with metal pegs driven into the substrate. When censusing the grid, a wooden frame was placed over each quadrat and each rock was carefully removed and checked for the presence of individual crabs. Resident crabs, if any, were quickly placed in a container for sorting and measurement. For each occupied rock, measurements included the maximum length of the rock and the width of the axis perpendicular to the first. Rock surface area was defined as the product of the two. Each resident crab was classified by species, sex, and carapace width to the nearest mm. Small rocks (those likely to shelter the fewest crabs) were examined and removed before larger rocks were disturbed so as to minimize the chances of escape. The complete rock size distribution for each quadrat was determined only once (August 1978) from projected 35 mm transparencies of .25 m^2 sections. Measurements were calibrated using marked rocks and the wooden frame as references. The permanent grid was first surveyed in April 1978 and was surveyed a total of ten times in the first year. No data were collected during September or December 1978. Following the January 1979 census, experimental barriers were erected around 6 of the 8 columns of quadrats. Unfortunately, the barriers were remarkably ineffective. After several equally unsuccessful modifications, the experiment was discontinued and only 4-6 unaltered control quadrats were regularly sampled in the second year (April 1979 - March 1980).

Biomass estimates for individuals in the field were derived from log-log regressions of carapace width (to the nearest 0.1 mm) and damp weight (to the nearest 0.01 g) of animals collected from a single tidal height at the study site (Table 10). Animals missing appendages and those carrying eggs were not included in the samples intended for this use.

Other methods applying to a specific set of results will be described at the appropriate places under Results.

Table 10. Parameters used to estimate damp weight from carapace width according to the equation weight (g) = b x width (mm)^{a}

Species	Sex	b	a	n	r^2
H.n.	♂	4.653×10^{-4}	3.080	35	.97
	♀	6.318×10^{-4}	2.911	30	.96
H.o.	♂	3.853×10^{-4}	3.154	30	.94
	♀	4.955×10^{-4}	2.991	31	.96
C.p.	♂/♀	1.803×10^{-4}	2.947	30	.98

Results

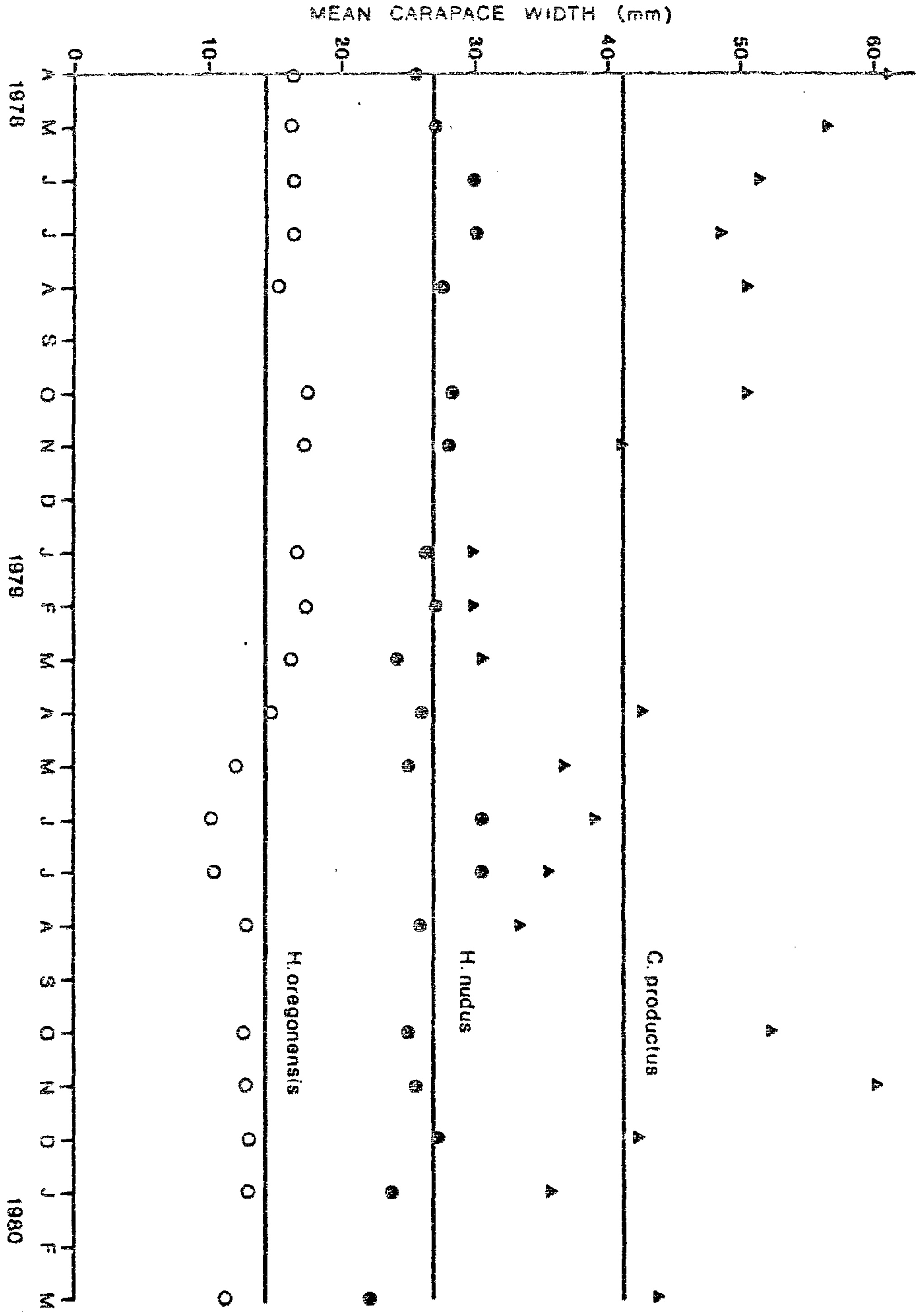
Field Sampling

Crab size structure

Both intra- and interspecific encounters between crabs are usually accompanied by some form of aggressive behavior, and the relative sizes of the contestants often provide a good index of competitive (aggressive) ability (see Chapter I for references). Although the point has not been rigorously tested, laboratory observations indicate that the three species considered here are not exceptional in this regard; larger individuals, regardless of species, are usually able to elicit retreat of smaller individuals. Commonly, but less often, when the size differences are great enough, the smaller of two contestants may be injured or killed and eaten. Individuals of all three species missing one or more appendages are commonly found in the field, despite considerable powers of regeneration.

The average size of individuals of each species over the course of the study (Fig. 21) suggests a distinct competitive hierarchy in which C. productus ($\bar{\bar{X}}$ = 41.5 mm) > H. nudus ($\bar{\bar{X}}$ = 27.0 mm) > H. oregonensis ($\bar{\bar{X}}$ = 14.2 mm). Among both C. productus and H. nudus at North Island, there is a marked tendency for small individuals to be found at higher tide levels. Since C. productus is primarily

Fig. 21. Average sizes of individuals of each species samples at various times in the permanent quadrats at North Island. Horizontal lines above the x-axis are drawn at the grand mean for each species.

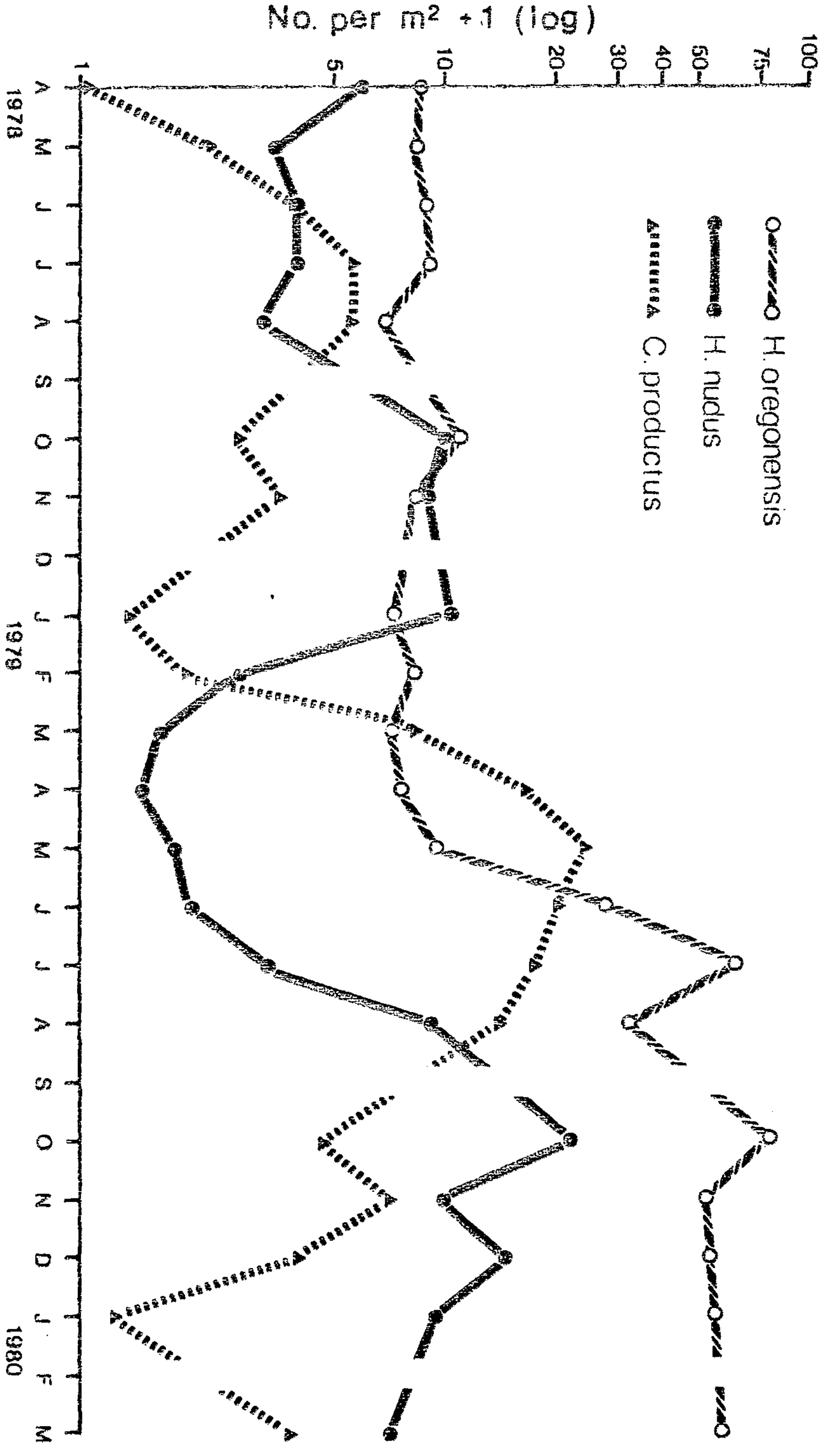

MEAN CARAPACE WIDTH (mm)
0
10
20
30
40
50
60
1978
A
M
J
J
A
S
O
N
D
1979
J
F
M
A
M
J
J
A
S
O
N
D
1980
J
F
M
H. oregonensis
H. nudus
C. productus

subtidal in occurrence, individuals in the low intertidal zone are typically among the smallest of the species. Selby (1981) reported few C. productus less than 90 mm in width in traps placed in the shallow subtidal zone at North Island, or among foraging individuals trapped in the intertidal zone at high tide. In contrast, H. nudus is strictly intertidal in distribution, and those individuals found in the low intertidal zone are among the largest of the species. In those months for which data are available, H. nudus in the low zone are 7-14 mm larger than population averages (see Chapter I for mid and high zone size distributions). These observations suggest that those individuals of both species which survive the physical rigors of higher tide levels eventually migrate to the more mesic portions of the vertical range of each. Batie (1975) reported similar evidence for H. oregonensis in Yaquina Bay, Oregon, although I have not been able to detect such a pattern for H. oregonensis at North Island.

Densities

From a plot of the densities of the three species over the course of the study (Fig. 22) it is clear that extreme variability in local abundance was common. All three species, for example, reached markedly higher densities in 1979 when compared to the previous year. In the

Fig. 22. Densities of the three crab species in permanent quadrats in the low intertidal zone at North Island.


No. per m² +1 (log)
100
75
50
40
30
20
10
5
1
H. oregonensis
H. nudus
C. productus
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
1978
1979
1980

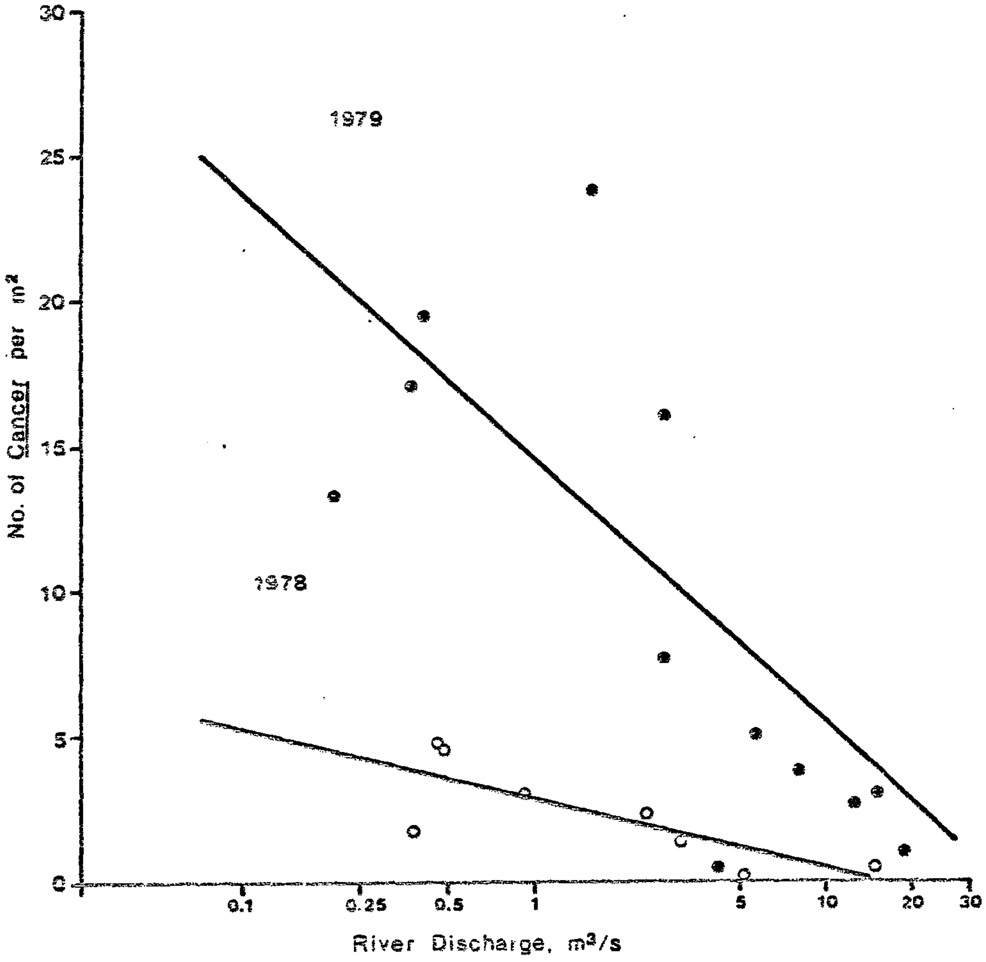
H. oregonensis population, densities consistently remained between 6-10/m^2 from April 1978 to May 1979 but increased rapidly to 62/m^2 by July 1979 and remained relatively high until the end of the study in March 1980 ($\bar{\bar{x}}$ = 51.6/m^2, S.D. = 16.2).

Aside from similar annual variability, the low intertidal densities of Cancer and H. nudus fell into distinct seasonal cycles. Minimum Cancer densities were recorded during the first month of the study (April 1978) and again during January 1979 and January 1980. Of the two periods of peak Cancer abundance, the first (July-August 1978) occurred somewhat later in the year than did the second (May-June 1979). Although the H. nudus population was also characterized by cyclic fluctuations in density, periods of H. nudus increase corresponded to periods of Cancer decrease, and vice versa. In general, these two species may be properly viewed as temporal replacements. The apparent absence of strictly seasonal changes in the H. oregonensis population provides a distinct contrast.

Seasonal distributions of Cancer productus, the only osmoconformer of the group, are most easily, but not completely accounted for by changes in local salinity (Selby 1981). As mentioned earlier, low winter and high summer salinities at the study site are largely determined by marked fluctuations in rainfall which affect the discharge rates of the Coos and Millicoma rivers (Fig. 20). Queen (1930) reported that incursions of C. productus to areas nearer the mouth of the Coos River are limited to late summer when river output is low. In contrast, C. productus is abundant throughout the year at Fossil Point, a site near the bay entrance where salinity variations are likely to be substantially lower (personal observation). In addition, large aggregations of adult kelp crabs, Pugettia producta, another osmoconformer (Gross 1957), regularly occur at Fossil Point in winter.

Although salinity at the study site was measured infrequently and only during the end of the study (June 1979-March 1980), mean daily discharge rates for the Millicoma River are available for the entire period (USGS, Water Resources Division). In order to assess the potential effects of recent freshwater dilution on C. productus abundances at North Island, regression analyses were performed on the species' average densities and average river discharge (m^3/s) during the week before each field survey. The results of the analyses (Fig. 23) tend to confirm the negative relationship between Cancer densities and river discharge rates during both 1978 ($P < .02$) and 1979 ($P < .01$). However, it is important to note that this explanation cannot adequately account for much of the variability in density during periods of low discharge (high salinity). In

Fig. 23. Relationship between *Cancer productus* density in permanent quadrats in the low zone and rates of discharge of the Millicoma River in 1978 and 1979. River discharge rates represent averages over 7 day periods preceding field surveys. Discharge rates from USGS.


30
25
20
15
10
5
0
1979
1978
No. of *Cancer* per m²
0.1
0.25
0.5
1
5
10
20
30
River Discharge, m³/s

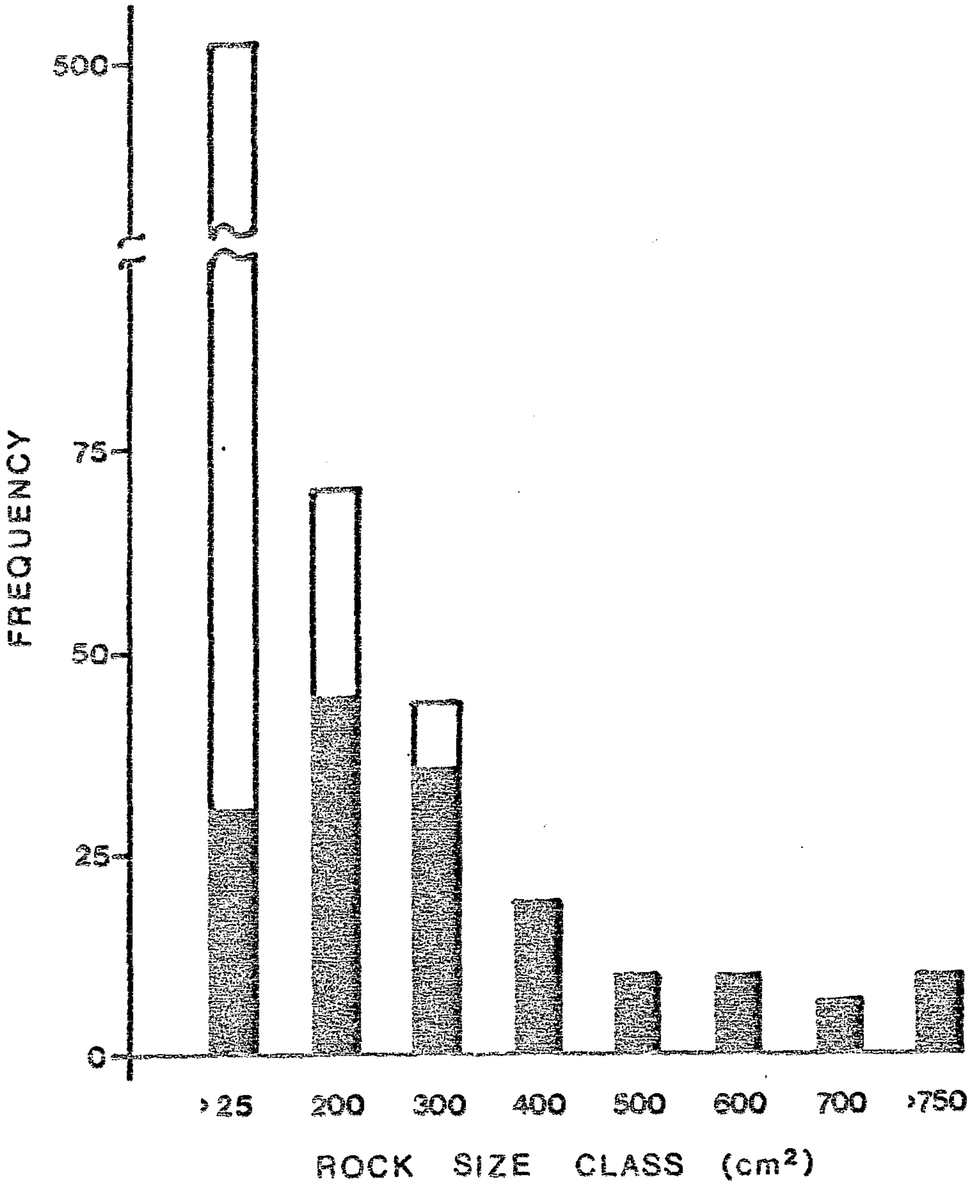
particular, during 1979 the observed densities in the spring (April-June) were substantially higher than predicted. The results of an exploratory study (Selby 1981) suggest that over short time intervals at least (12 hr), C. productus individuals are unaffected by salinities >19.5‰. Salinities near or below this limit were recorded at the study site only during midwinter.

When taken together, the results above clearly suggest that while C. productus may be physiologically incapable of permanently residing at North Island as a result of low winter salinities, fluctuations in the timing of peak abundances remain partially unexplained. In the next section, I will examine the limiting resource axis and describe the spatio-temporal distributions of the three species along that axis. From the results of these analyses, and a description of the size structure of the crabs (Fig. 21), I will argue that the contrasting patterns of abundance of the two shore crab species are due to unequal competition with C. productus.

Resource utilization patterns

Individuals of all three crab species seek refuge under rocks within the intertidal zone. I have shown earlier that refuge space is the primary limiting resource for which the two Hemigrapsus species compete and that the quality of refuge space is an increasing function of rock surface area (Chapter I). Wave-induced disturbance rates, for example, vary inversely with rock size (Chapter I, Sousa 1979, Osman 1977) and progressively larger rocks probably also provide increased protection from desiccation and temperature fluctuations during periods of exposure at low tide. From the size distribution of rocks in the permanent sampling grid at North Island (Fig. 24), it is apparent that the frequency of rocks in 100 cm^2 size classes decreases rapidly with increasing rock size so that the smallest rocks are locally abundant while the largest are relatively scarce. The photographs from which the distribution was calculated were taken during the August 1978 survey, and the portions of the available rocks in each size class that were actually occupied (by at least one crab) are also shown (Fig. 24). That only 7% of the rocks in the smallest class were occupied while all rocks >350 cm^2 were occupied attests to the high degree of selectivity employed by the crabs in seeking refuge space. In general, rocks in the smallest size class (<150 cm^2) in the mid zone at least are occupied in direct proportion to total crab density, an index of the competitive pressures along the remainder of the resource axis (Chapter I). The discussion below will be concerned only with the distributions of the three species among the rocks that were actually occupied

Fig. 24. Size distributions of rocks in permanent quadrats in the low zone at North Island. Closed bars represent the number of rocks occupied (by at least one crab) in each class in August 1978.


FREQUENCY
500
75
50
25
0
›25
200
300
400
500
600
700
›750
ROCK SIZE CLASS (cm²)

during each field survey.

Aside from the universal avoidance of small rocks indicated above, resource utilization patterns for each species within the set of occupied rocks can be ascertained by regression techniques described in Chapter I. The model employed is a quadratic equation in which a measure of the abundance of each species (number or biomass of individuals, N_i) is treated as the dependent variable and rock surface area (A) and its squared term (A^2) are independent variables. In the resulting equation

$$N_i = a_i + \alpha_i A + \gamma_i A^2$$

α_i and γ_i are the regression coefficients of rock surface area and its square, respectively. The term a_i is the estimated rock size at which the expected abundance of species i equals 0 (i.e., the intercept). If the species utilize rocks along the gradient in rock size in a more or less random fashion, each γ_i should equal 0 and each α_i should equal $\overline{N}_i/\overline{A}$. In essence, these conditions stipulate that the average abundance of each species per unit of rock surface area should be independent of rock size. Disproportionately high utilization of large rocks is indicated by values of $\gamma_i > 0$, or values of $\alpha_i > \overline{N}_i/\overline{A}$, whereas values of $\gamma_i < 0$ and those for $\alpha_i < \overline{N}_i/\overline{A}$ result from disproportionately low use of large rocks. Since the individuals of each species differ substantially in average size, and consequently in the amount of space each consumes under an occupied rock, biomass was considered in this case to be the more appropriate measure of species abundance. The use of numerical abundances would, however, not alter the conclusions but would result in a loss of clarity in interpretation.

The results of the stepwise multiple regressions (Table 11) described above, together with the average biomass/species in 200 cm^2 rock size classes (Fig. 25) provide important clues to the competitive relationships between the species. Before proceeding, it is useful to recall that both Hemigrapsus species, in isolation from each other, are preferentially distributed among large, stable rocks. When sympatric, however, only the competitive dominant, H. nudus, remains so (Chapter I). Although the resource utilization patterns of Cancer have not been documented in the complete absence of the shore crabs, the individuals of this species exhibited a significant preference for rocks in the largest size classes in 14 of the 20 monthly surveys. Four of the remaining six months (January, February, December 1979 and January 1980) correspond to months of minimum Cancer abundance and constitute a combined sample of only 45 individuals distributed among 320 rocks. In the two remaining months (June 1978 and August 1979), Cancer biomass increased linearly with rock size but

Table 11. Results of stepwise multiple regressions of biomass (g) for each species on rock surface area (A, cm^2) and its squared term (A^2). Data are from censuses of permanent quadrats in the low zone at North Island. Values for α and γ are regression coefficients for A and A^2, respectively. Rock size selectivity decisions were based on the sign of significant values for γ, or in their absence, on t-test comparisons of α with $\overline{N}_i/\overline{A}$ (see text).

Time	Species	Intercept	α ($x10^{-2}$)	γ ($x10^{-4}$)	n	r^2	Rock size selectivity[a]
Apr8	HO				147	.02ns	
	HN	-5.2	3.75***	1		.46	+ ***
	CP	-0.2		0.38***		.05	—
May8	HO				171	.01ns	
	HN	-3.5	2.98***	-1.96***		.18	-
	CP	4.6	-0.03***	0.74***		.44	+
Jun8	HO				210	.01ns	
	HN	-3.2	2.78***	-0.23*		.15	-
	CP	-2.7	3.64***			.16	R > .10
Jul8	HO				226	.01ns	
	HN	-0.7	1.76***			.12	R > .30
	CP	4.0		0.40***		.24	+
Aug8	HO				140	.00ns	
	HN	-1.0	1.43***			.14	R > .30
	CP	-6.8	6.54***			.38	+ **
Oct8	HO	0.8	2.41***	-0.28***	142	.08	-
	HN	1.4		0.72***		.38	+
	CP	-0.4		0.32***		.13	+
Nov8	HO	0.5	1.22**		183	.04	- ***
	HN	-1.2	2.57*	0.30***		.49	+
	CP	2.4		0.20***		.16	+
Jan9	HO	1.1	0.45*		93	.06	R > .10
	HN	2.1		0.74***		.63	+
	CP					.01ns	
Feb9	HO				143	.00ns	
	HN	-0.8	1.21***			.32	R > .10
	CP	-0.2	.30*				R > .20

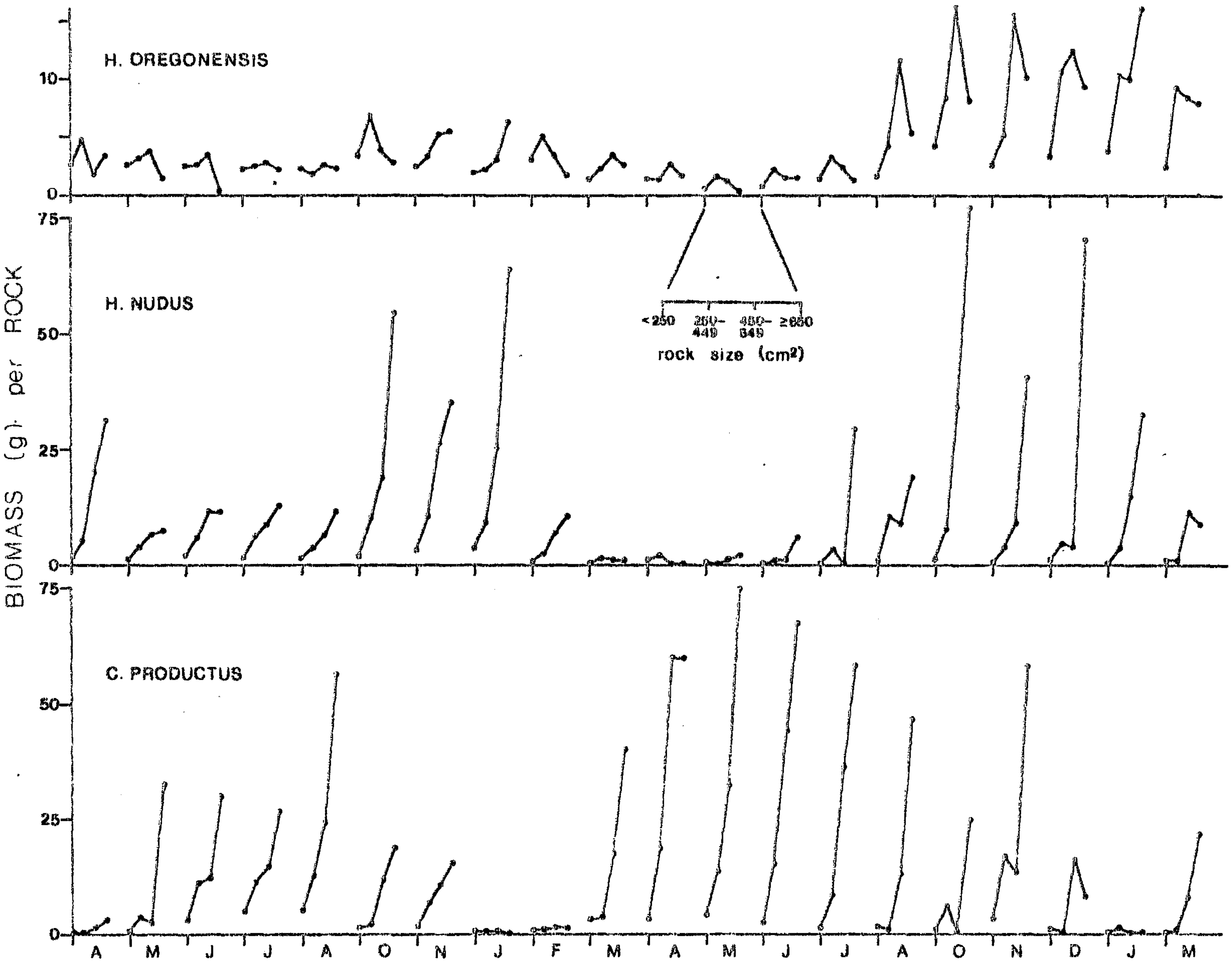
Table 11--Continued

Time	Species	Inter-cept	α ($\times 10^{-2}$)	γ ($\times 10^{-4}$)	n	r^2	Rock Size Selec-tivity[a]
Mar9	HO				173	.03ns	
	HN					.01ns	
	CP	6.8	-4.06***	1.00***		.57	+
Apr9	HO				35	.01ns	
	HN					.04ns	
	CP	-1.6		0.78***		.75	+
May9	HO				71	.03ns	
	HN	-0.2	0.24*			.08	R > .20
	CP	-8.7	9.38***			.49	+ *
Jun9	HO				114	.03ns	
	HN	-0.1		0.08***		.25	+
	CP	-4.9	8.12***			.55	+ **
Jul9	HO	0.9	0.70***	-0.05*	96	.12	-
	HN	1.9	-2.92***	0.63***		.82	+
	CP	-3.3	5.67***			.56	+ ***
Aug9	HO	0.1	2.06**	-0.15*	36	.27	-
	HN	-1.0	2.24***			.40	R > .20
	CP	-3.9	5.11***			.30	R > .10
Oct9	HO	1.2	2.84**	-0.18*	60	.18	-
	HN	-9.6	6.28***	0.41*		.85	+
	CP	-0.6		0.41***		.36	+
Nov9	HO	-1.2	3.35**	-0.20*	59	.26	-
	HN	-4.4	3.88***			.46	+ **
	CP	-5.7	7.75***			.36	+ *
Dec9	HO	-0.4	3.63***	-0.25**	46	.22	-
	HN	-19.3	9.10***			.51	+ **
	CP	-1.6	1.43*			.12	R > .20
Jan0	HO	2.4	1.83***		34	.35	R > .20
	HN	-7.0	4.10***			.46	+ **
	CP					.01ns	
Mar0	HO	-0.3	2.60***	-0.17***	40	.38	-
	HN	-6.0	4.46***	-0.30**		.26	-
	CP	-3.5	2.27***			.36	+ *

[a] (R)=random use, (+)=over- and (-)= underutilization of large rocks.

(*) $P < .05$ (**) $P < .01$ (***) $P < .001$

Fig. 25. Mean biomass for the three crab species in 200 cm^2 rock size classes during each sample period.


H. OREGONENSIS
H. NUDUS
C. PRODUCTUS
BIOMASS (g) per ROCK
0
10
0
25
50
75
0
25
50
75
<250
250-449
450-849
≥850
rock size (cm²)
A
M
J
J
A
O
N
J
F
M
A
M
J
J
A
O
N
D
J
M

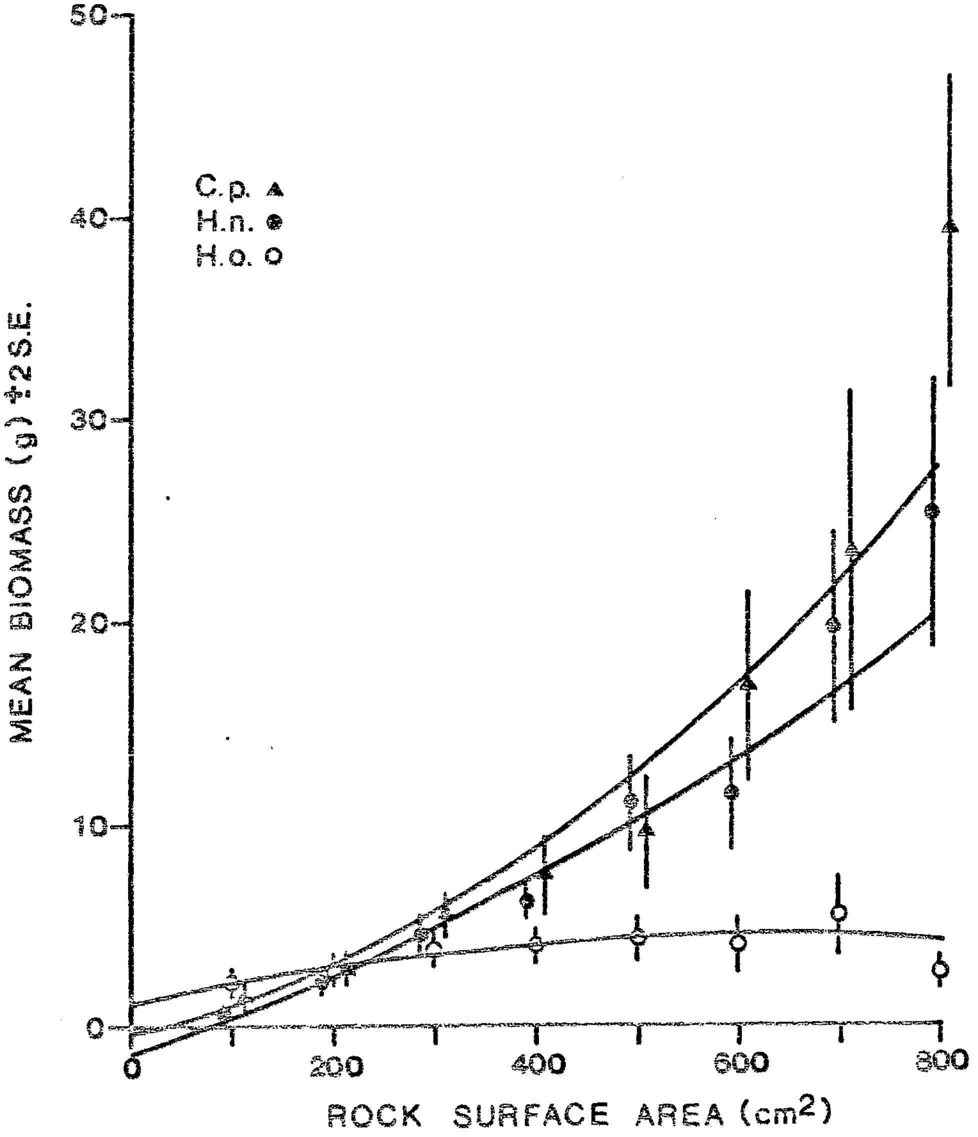
the increases were not significantly greater than the criterion values for random utilization ($\overline{N}_i/\overline{A}$).

Similarly, H. nudus individuals individuals exhibited a quantitative bias for larger rocks (10 of 20 months), but usually only during those months in which Cancer abundances were sufficiently low. Thus, during the peak of Cancer abundance in 1978 (May through August), H. nudus densities were reduced and the remaining individuals were distributed along the resource axis in a manner that could not be distinguished from random utilization (July and August) or so that large rocks were used less than expected by chance (May and June). During the second Cancer peak (March - August 1979), the results of the analyses for H. nudus are similar except that in June and July, individuals of this species exhibited a disproportionately high use of large rocks despite low overall densities.

In contrast to the other two species, H. oregonensis individuals never exhibited their intrinsic preferences for large rocks. In only 3 of the 20 surveys, H. oregonensis biomass increased linearly with rock surface area. In one such month (November 1978), the rate of increase was significantly lower than expected if the rocks along the gradient were used in a random manner ($P < .001$), while in January 1979 and 1980, the slopes were lower than, but not distinguishable from patterns of random utilization ($P > .05$).

It is possible to view these relationships in a somewhat simpler manner by treating the data from all monthly samples without considering temporal effects (Fig. 26). The average biomass for each species (±2 S.E.) in 100 cm^2 rock size classes is also shown. As is evident from an examination of the figure, the resource utilization patterns for Cancer and H. nudus are quite similar in that the biomass distributions of each are biased toward progressively larger rocks. In contrast, the rate of increase of H. oregonensis biomass declines with increasing rock size so that the average biomass/rock does not vary greatly between rock size classes. As a result of these patterns and the marked skewness in the overall size distribution of rocks (Fig. 24), the bulk (56.7%) of the total H. oregonensis biomass was distributed among the locally abundant and often unoccupied smaller rocks (<350 cm^2). These same rock size classes, however, accounted for far smaller fractions of the H. nudus and Cancer biomass totals (24.9% and 26.0%, respectively). Thus, Cancer and H. nudus use the same relatively scarce and universally preferred portions of the resource axis, but do so primarily at different times of the year. H. oregonensis, the smallest of the three competitors, achieves spatial, rather than temporal separation from the other species by using less intensely contested portions of the resource axis.

Fig. 26. Resource utilization curves for each of the three crab species. Based on data from permanent quadrats pooled without considering temporal effects. Regressions for all species are significant ($P < .001$). Mean biomass in 100 cm^2 rock size classes are also shown. Vertical lines represent ±2 S.E.


C.p. ▲
H.n. ●
H.o. ○
MEAN BIOMASS (g) ±2S.E.
0
10
20
30
40
50
0
200
400
600
800
ROCK SURFACE AREA (cm²)

Further evidence suggests that competition is not limited to contests between the different species. In _Cancer_, competition for refuge space between conspecifics is clearly indicated by the temporal patterns in the frequency with which individuals occupied rocks in the various size classes. Figure 27 shows these patterns over the months in both 1978 and 1979 in which _Cancer_ densities increased to annual maxima. More than half of the rocks >650 cm^2 were occupied by at least one _Cancer_ individual even at densities as low as $1.3/m^2$ (presumably at the expense of the _H. nudus_ population). Similar fractions of the rocks in the smaller size classes, however, became occupied only at substantially higher densities. In addition, of the _Cancer_ present during periods of peak abundance, there was often a significant tendency for the largest individuals to be distributed among the largest rocks and for smaller individuals to be found more often under progressively smaller rocks (Table 12). These results are clearly in accordance with the notion that individual size and aggressive ability are closely related. Similar relationships have been demonstrated for both shore crab species at higher tidal levels (Chapter I), but were found in very few instances in this study (not shown).

Fig. 27. Relationship between the incidence of rock occupancy (by *Cancer*) and rock size, shown at months during which *Cancer* abundances increased from annual minima to annual maxima during 1978 and 1979. Numbers below the lines indicate *Cancer* density (number/m^2) in the low intertidal zone.

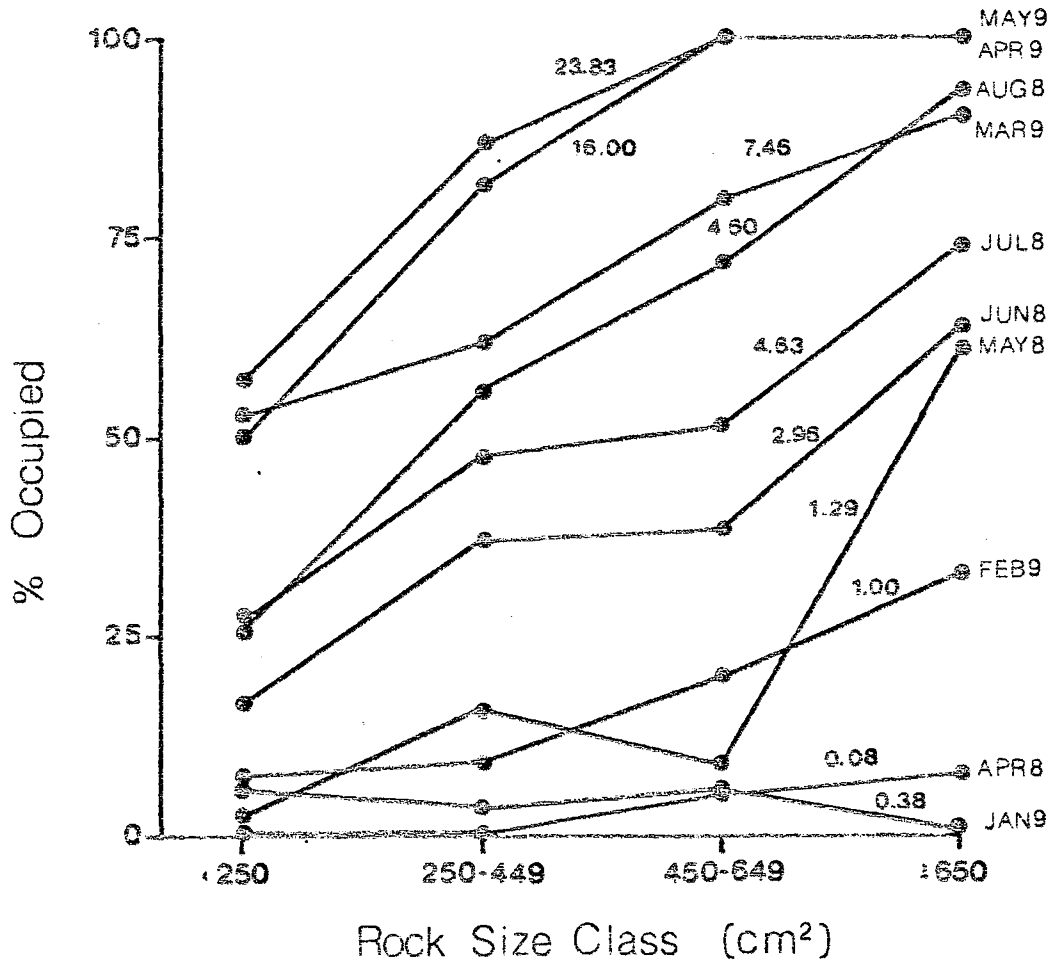

MAY9
APR 9
AUG 8
MAR9
JUL8
JUN8
MAY8
FEB9
APR8
JAN9
23.83
16.00
7.46
4.60
4.63
2.96
1.29
1.00
0.08
0.38
100
75
50
25
0
% Occupied
<250
250-449
450-649
≥650
Rock Size Class (cm²)

Table 12. Results of linear regressions of size of rock occupied on the size of resident *Cancer productus* individuals in the low zone at North Island

Date	Intercept	Slope	d.f.	t	P
(1978)					
Apr	N/A		(2)		
May	-441.6	18.97	29	4.73	<.001
Jun	269.7	3.28	69	1.40	ns
Jul	195.7	4.75	109	2.50	<.02
Aug	312.5	4.14	90	2.22	<.025
Oct	525.4	1.63	26	<1	ns
Nov	148.4	5.77	59	3.65	<.001
(1979)					
Jan	96.7	5.66	3	1.33	ns
Feb	408.4	3.19	22	<1	ns
Mar	364.6	3.63	177	2.58	<.01
Apr	325.9	6.93	94	3.38	<.001
May	402.5	5.84	141	3.10	<.01
Jun	379.0	4.98	114	3.46	<.001
Jul	248.8	5.80	66	2.09	<.05
Aug	581.7	3.60	51	1.14	ns
Oct	-111.7	12.93	16	2.00	<.05
Nov	119.7	7.71	22	1.07	ns
Dec	331.5	8.41	13	1.22	ns
(1980)					
Jan	N/A		(1)		
Mar	836.9	-1.03	9	<1	ns

Experimental Results

Within any given area in the mid intertidal zone at North Island, H. nudus and H. oregonensis were often more or less equally represented. However, nearly complete spatial separation of the two species could be induced within small areas by altering the rock size distribution (Chapter I). Similar experiments described below were carried out in the low intertidal zone.

Methods

The first of two designs used consisted of a 4x2 m rectangular area in which each of eight 1 m^2 quadrats were alternately covered with either small (<150 cm^2) or large (>500 cm^2) rocks resulting in 4 replicates of each of 2 treatments. One such plot was established in October 1978 adjacent to the permanent sampling grid (0.5 m above MLLW) and was censused 3 times at bimonthly intervals beginning in November 1978. In January 1979, a second low intertidal plot of the same design was placed ca 5 m from the first but at a slightly higher tidal level (0.75 m above MLLW), and was censused in March 1979. Each census merely entailed counting all individuals of each species in each quadrat.

The second experiment, a similar but slightly more elaborate version of the first, consisted of one replicate of each of 3 treatments randomly arranged within each of

3 rows for a total of nine 1 m^2 cells. The following represent the approximate rock size distributions in each of the three treatments considered:

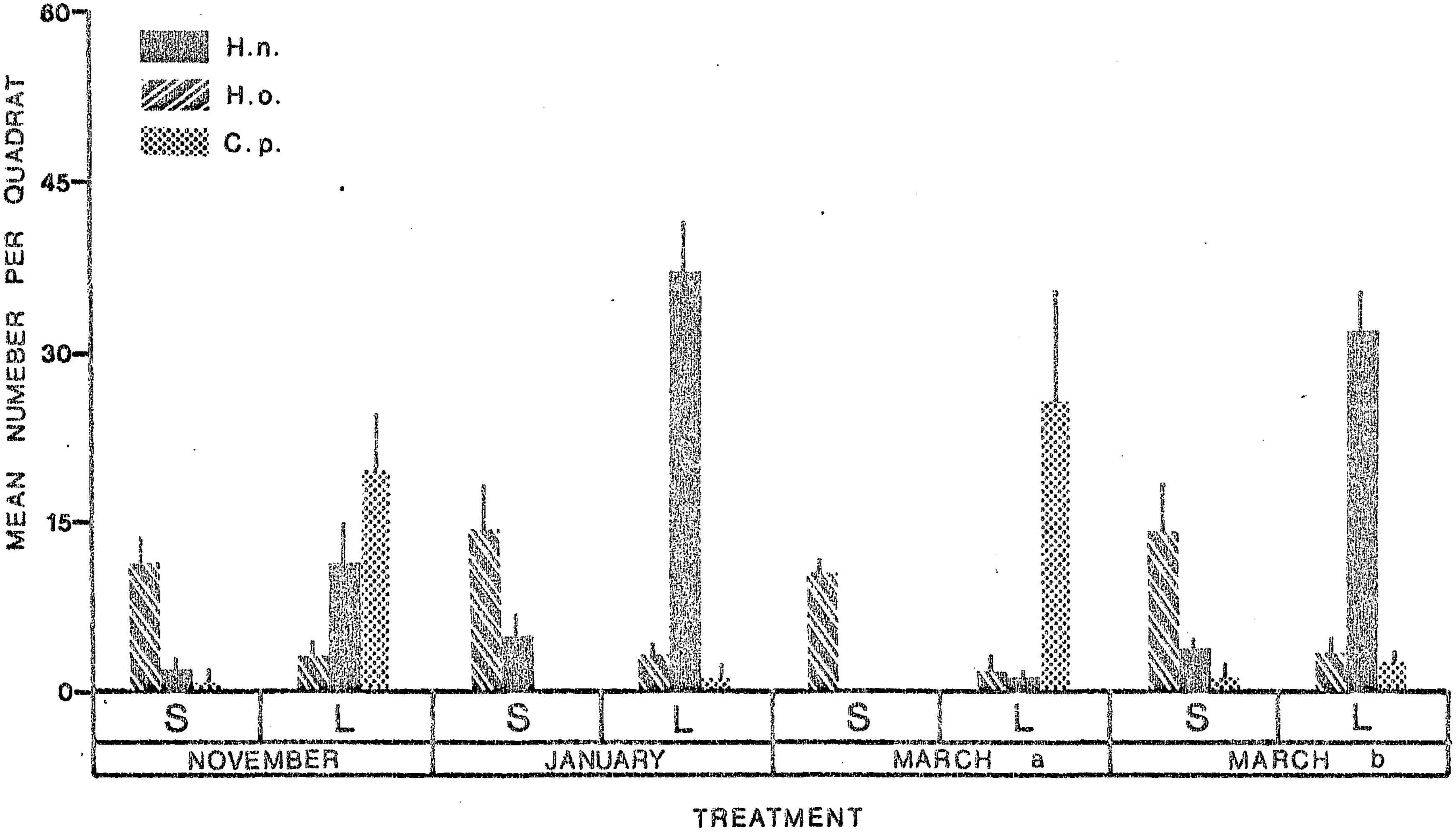
I. eight 900 cm^2 rocks
II. sixteen 450 cm^2 rocks
III. forty-eight 150 cm^2 rocks

The resulting "checkerboard" was established at 0.5 m above MLLW in April 1979 and was censused in May, June, September, and December 1979 as _Cancer_ abundances progressively declined from their peak. The census procedure was identical to that described earlier for the permanent grid. The results of this set of experiments are especially informative since the total amount of available refuge space did not vary appreciably between treatments and was known at all times. The average abundances of the species in each treatment consequently reflect a more direct and accurate assessment of resource utilization patterns than was obtainable with conventional sampling procedures.

Results

The results of the first experiments, shown as mean number/species in both treatment types (Fig. 28), deal only with the two extremes of the resource axis. At the November 1978 census, a time in which _Cancer_ densities were declining and _H. nudus_ densities were increasing,

Fig. 28. Average numbers of each species in each of two types of 1 m^2 quadrats in which the rock size distributions were altered (S = small rocks only, L = large rocks only). Vertical lines represent 1 S.E. Data from November 1978, January 1979, and March (a) 1979 were taken from a single experimental plot at ca 0.5 m above MLLW. Data for March (b) were taken from a second plot at ca 0.75 m above MLLW (see text).


60
45
30
15
0
MEAN NUMEBER PER QUADRAT
H.n.
H.o.
C.p.
S
L
S
L
S
L
S
L
NOVEMBER
JANUARY
MARCH a
MARCH b
TREATMENT

individuals of these two species were found in comparatively low numbers in quadrats containing only large rocks while both were scarce among small-rock quadrats. In January 1979, Cancer was nearly absent in the intertidal zone and H. nudus among the large rock treatments showed a 3-fold increase in density. By March, however, Cancer had reinvaded the intertidal zone and apparently displaced H. nudus among the larger rocks preferentially used by both species. Throughout the entire experiment, H. oregonensis maintained densities of 10.5-14.5/m^2 but only among those quadrats containing small, unstable rocks seldom used by either of the other two species.

On the same day in March when the lower plot was censused, Cancer remained scarce (1-2.5/m^2) only 5 m distant at the higher plot (Fig. 28), and H. nudus and H. oregonensis were distributed among the treatments as they had been in the lower plot during January. In effect, H. nudus appears to be "pushed" to progressively higher tidal levels as a result of intense competition with Cancer for preferred refuges. Owing to its usual marginal position along the resource axis, H. oregonensis does not appear to be similarly affected.

The results of the second set of experiments were gathered over a period of time in which Cancer densities declined from a peak in May to virtual absence in December

1979 (Fig. 29). Aside from the expected patterns of abundance for Cancer and H. nudus, the large numbers of H. oregonensis among the treatments containing large rocks are notable, especially in September ($54/m^2$) when the densities of both Cancer and H. nudus were low and in a state of transition. Although the numbers of H. oregonensis in these same quadrats were reduced by the H. nudus peak in December, the averages for this species remained relatively high ($31/m^2$).

Discussion

The intent of this report has been to demonstrate how the relative abundances of two closely related competitors, Hemigrapsus nudus and H. oregonensis, may be substantially altered by the presence of a third, more effective competitor. Contrary to expectations based solely upon the results of pairwise interactions, the low intertidal densities of the competitively dominant shore crab species, H. nudus, are clearly more adversely affected by competition with Cancer productus. A conceptual model showing the net effects of the three species on each other, as well as the effects of physical factors, is depicted in Fig. 30. Inferences concerning the role of sediments are drawn primarily from Chapter I (and see Hiatt 1948, Low 1971).

According to the model, individual competitive ability, the ability to acquire and maintain preferred refuge space, is based on aggressive competence, and is thus an increasing function of crab size. Significant positive correlations between the sizes of individuals and the sizes of

Fig. 29. Average numbers of each crab species in each of three types of 1 m^2 quadrats in which rock size distributions were altered. A = May 1979; B = June 1979; C = September 1979; D = December 1979. Vertical lines represent 1 S.E.

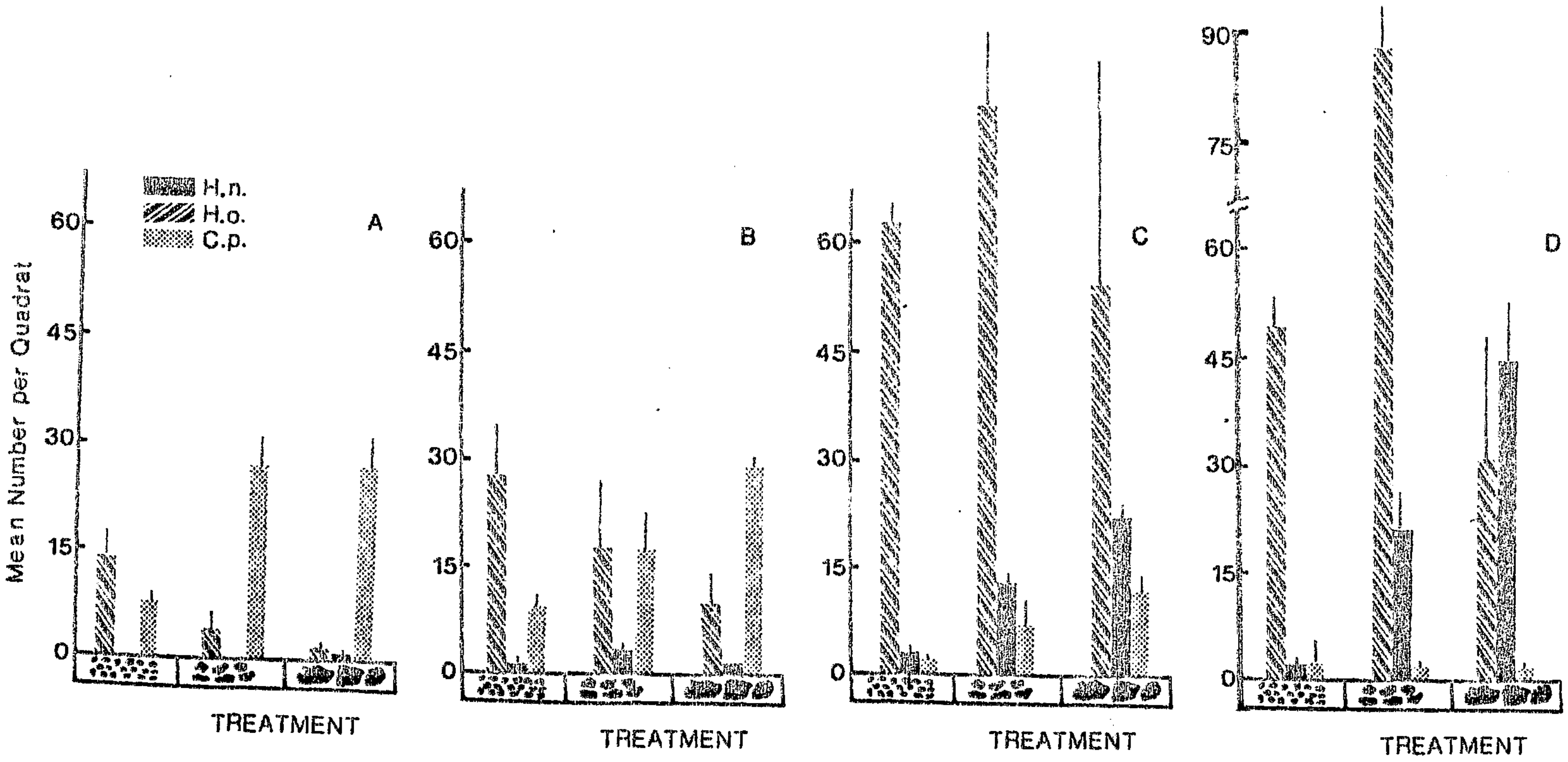
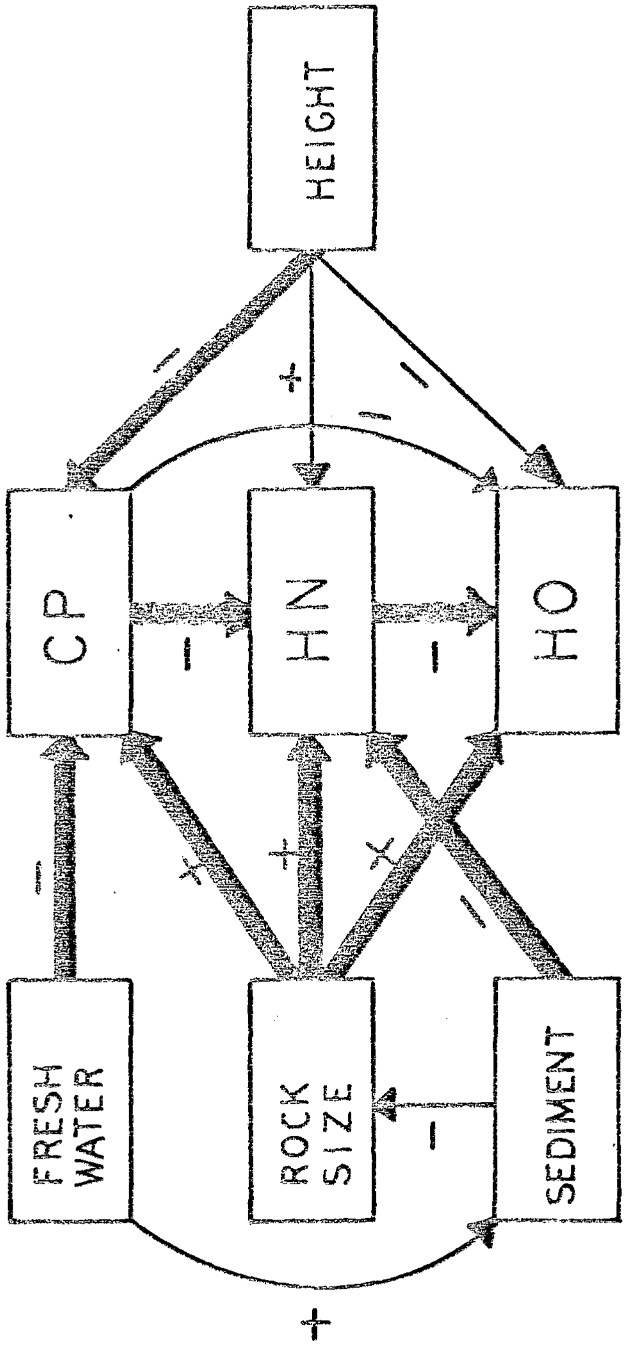

Mean Number per Quadrat
H.n.
H.o.
C.p.
A
B
C
D
0
15
30
45
60
75
90
TREATMENT
TREATMENT
TREATMENT
TREATMENT

Fig. 30. Summarizing model of the net interactions between the species and the effects of physical factors.


HEIGHT
CP
HN
HO
FRESH WATER
ROCK SIZE
SEDIMENT
−
+
−
−
−
−
−
+
+
+
−
−
+

the rocks that they occupy for both Hemigrapsus species (Chapter I) and Cancer (Table 3), are in accordance with this assertion. Under favorable conditions, then, the distributions of individuals of each species along the resource axis reflect the densities and sizes of conspecifics and those of the competitors' populations. Among the three species, there is a distinct rank-order in average size (Cancer > H. nudus > H. oregonensis), and thus also in average competitive ability. The competitive hierarchy is probably not strictly linear since some overlap in sizes is likely to exist in any given time period.

When Cancer is absent from the intertidal zone, or at very low densities, H. nudus dominates the largest rocks and H. oregonensis individuals are distributed as opportunity permits among smaller rocks. When physical disturbances and other biotic influences are minimal, competition between the shore crabs proceeds uninterrupted and H. oregonensis may be excluded entirely (Chapter I). The data presented in this chapter suggest that by periodically invading the low intertidal and, to a lesser extent, the mid zone, Cancer also interrupts this process of competitive displacement, but in a manner quite different from the effects of physical disturbances, which act principally on small, unstable rocks. Even at moderately low densities, such as at the onset of each cycle of invasion, Cancer individuals rapidly become distributed among most or all of the largest rocks, mainly at the expense of H. nudus. Occupation of smaller rocks by Cancer occurs only with subsequent increases in density and is much less extensive, even during months of peak abundance. Furthermore, the largest, most aggressively competent Cancer often tend to be resident under the largest rocks previously occupied by H. nudus, whereas progressively smaller Cancer individuals are more often found under rocks in the smaller size classes. In consequence, the contests between Cancer and each of the shore crab species are unequal in intensity. Many displaced H. nudus apparently retreat to higher tide levels where their appearance may be evidenced by a marked shift in population size structure (Chapter I).

According to this interpretation, then, periods of peak abundance of H. nudus and Cancer are mutually exclusive as a direct result of intense competition for limiting refuge space. Alternatively, it may be argued that the cyclic fluctuations in density are less directly related, or that the cycles are completely independent. In light of the evidence above, the original interpretation (competitive interference) seems to be the most reasonable explanation.

It is worth noting that the model does not imply that H. oregonensis, despite more constant densities, is unaffected by competition with Cancer. Indeed, it is rather certain that both Cancer and H. nudus have strong negative effects on H. oregonensis, although it may make little difference which of the two dominants is responsible at any given time for its distribution among the most marginal portions of the resource axis. If H. oregonensis directly benefits from the interaction between the two dominants, it does so only by taking advantage of larger rocks during those times in which Cancer and H. nudus densities are low and in a state of transition. The indirect benefits to H. oregonensis are essentially equivalent to the negative effects suffered by H. nudus (as a direct result of competition with Cancer). Potentially, these are: i) increased mortality during (or as a result of) displacement from the low zone, ii) loss of any benefits derived from inhabiting the most physically mesic portion of the species' vertical range, and iii) increased intraspecific competition among H. nudus in the high and mid zones.

In addition to being the only osmoconformer of the group, C. productus also appears to be the least adapted to withstand exposure in the intertidal zone. Captive Cancer, for example, are much more prone than either Hemigrapsus species to show obvious signs of stress when left unprotected for any length of time. Thus, although low salinities may account for the absence of Cancer in winter, the reasons for its presence in the intertidal zone during the remainder of the year are less clear. The simplest explanation rests upon the assumption that it wouldn't be there if it could do better elsewhere, and the observation that the Cancer found in the intertidal zone are small as compared to other conspecifics. Inasmuch as the intensity of predation by many strictly marine species (fish, diving birds, and other Cancer) increases with depth, it is likely that smaller individuals are temporarily ill-equipped for life in the subtidal region.

The subtidal adult Cancer represent a distinct subset of the species' population, both in distribution and perhaps in their effect on the shore crabs. During periods of submergence, large Cancer move into the intertidal zone to forage and have been observed in large numbers within the sampling grid (personal observation). The size distributions of individuals caught in baited traps set in the low intertidal zone at North Island (Selby 1981) are nearly completely nonoverlapping with the size distributions of Cancer resident in the zone at the same times (this study). While the model does not explicitly consider the effects of these large Cancer, they should not be entirely overlooked. Several investigators (Spight 1972 cited in Spight 1976, Connell 1970, Bertness 1977) have indicated that *C. productus* may be responsible for substantial mortality among intertidal *Thais* populations. Bertness (1977) found that up to 95% of the *T. lamellosa* and *T. emarginata* transplanted into an area of high *Cancer* density were killed by the crabs. Muntz et al. (1965) describe a similar role for *C. pagurus* in Lough Ine.

In the laboratory, *Cancer* readily consume shore crabs of either species, and exploratory studies have been carried out with the aim of determining if this activity might also affect the shore crab interaction (Appendix). The experiments were carried out in a plastic wading pool in which up to several equal-sized pieces of concrete block provided refuges for the shore crabs. Single large *Cancer* (>115 mm) were used in most experiments together with a variety of sizes and numbers of shore crabs. Under conditions in which refuge space was in short supply, predation was heaviest on those individuals unable to obtain refuge space (usually *H. oregonensis*). However, when refuge space was more amply provided (as is the case in the field) or when the predator had eliminated those prey who were without refuge space, predation fell most heavily on the largest shore crabs (usually large *H. nudus*). On many instances, we observed *Cancer* lifting the blocks, apparently attempting to dislodge the shore crabs underneath. Whether the observed size-selectivity is attributable to predator preference (i.e., actual preference or ease in handling) or to some behavioral characteristics of the prey is unknown. Small Cancer, such as those resident in the intertidal, do not choose the largest prey but instead appear to feed on any shore crabs below some maximum size.

There are several difficulties in extending these exploratory results to nature. The most serious and obvious is that the actual magnitude of Cancer predation on either shore crab species would be extremely difficult to quantify. Unlike the remains of snails, broken crab "shells" are quickly removed from the area by waves, or merely float away if decaying matter is left inside. Second, the experiments were performed in an unrealistic setting; the arena was easily searched and the refuges were all of the same size. In contrast, the natural setting is spatially complex, therefore presumably harder to search, and composed of refuges of all sizes, most of which are small (easily overturned) and occupied predominantly by H. oregonensis. Third, some mortality among small H. oregonensis occurred in the experiments even in the absence of Cancer. Subsequent laboratory observations have indicated that large H. nudus were probably responsible. In short, the answer to the question Who eats whom? is complex and not likely to be easily obtained in either the laboratory or the field.

General Discussion

The results of this and other studies have shown that age and size structure may markedly influence both the nature and outcome of interspecific competition. Among aggressive species (most notably arthropods and vertebrates), differences in size often determine interspecific dominance, and when size differences are great enough, interspecific predation (and cannibalism) commonly results and may accentuate competitive differences (von Ende 1979, Park et al. 1965, Wilbur 1972). However, even in cases where there is a marked difference between the species with respect to average maximum size, some portions of the "competitive dominant" species population are of necessity smaller and less aggressively competent that some members of the "competitive subordinate" population. So-called competitive reversals may thus be common between size classes of the two (or more) competitors' populations (unless smaller individuals are capable of exploiting some spatial or temporal refuge not accessible to larger individuals). Furthermore, as in the case of the shore crabs, when aspects of the physical environment (rock size distribution and wave action) set limits on the maximum size attainable by individuals of either species, it is clearly insufficient to treat the interaction as one between average individuals in a spatially homogeneous environment. However, even under relaxed assumptions, mathematical solutions to discrete-time models of such processes are not forthcoming. Serious complexities arise even in models of competition within single species age-structured populations. Roughgarden (1979, p. 345) stated that such models "rapidly lead into mathematical terra incognita."

Perhaps more importantly, traditional views of species interactions in both simple and more complex biological communities are generally based on the assumption that the component species' populations exist in equilibrium with their resources and have coevolved under saturated conditions (Pianka 1976). Among such coevolved assemblages, competitive interactions are believed to become progressively weaker (more efficient) as a result of selection for the avoidance of competition. This is usually achieved by specialization along one or more resource axes (niche diversification). Furthermore, it is held that such species coexist at equilibrium, in the absence of perturbations, by density-dependent regulation, and that in the event that the community is perturbed it will eventually return to the equilibrium state (Miller 1967, Pianka 1976).

Recent studies, however, suggest that disturbances may be a regular, rather than exceptional feature of some natural communities of sessile organisms (Dayton 1971, Levin and Paine 1974, Lieberman et al. 1979, among others). Still other investigators (Connell 1978, Sousa 1979, Osman 1977) offer convincing evidence that other sessile assemblages (tropical forests and coral reefs, intertidal algal communities, and subtidal epibenthic communities, respectively), seldom if ever exist at equilibrium and have probably evolved under nonequilibrium conditions. Nonequilibrium hypotheses which have been proposed by Connell (1978) and Sousa (1979) state that species interactions (usually competition) are intense, instead of being weak or finely tuned, and competitors coexist because of environmental disturbances, rather than despite them. Frequent, patchy disturbances continually provide uncontested space and interrupt the normal competitive processes which tend toward the elimination of inferior competitors. Since uncontested space is a predictable feature, inferior competitors may persist indefinitely in the system of patches by adaptations for colonizing ability and rapid achievement of maturity. In theory, niche overlap along the contested resource axis need not be less than unity.

In order to develop a cohesive general theory of community organization, it would be useful to know the extent to which these same processes are major factors in the evolution and organization of motile assemblages. Sousa (1979) predicted that closer examinations of motile organisms would reveal that many populations exist in a nonequilibrium state. The results presented here, if they have been interpreted correctly, suggest that several aspects of the shore crab interaction conform well to the expectations of the nonequilibrium hypotheses. It is worth noting that the life history traits of Hemigrapsus oregonensis, in particular, are not necessarily directly attributable to disturbance-related phenomena. It is equally likely that they arose in response to selection regimes in muddy areas where, for example, predation pressures (Willason 1980) may determine average survivorship and reinforce selection for early and frequent reproduction. Furthermore, selection for large size may be partially offset by the advantages of remaining inconspicuous. Despite this, it is clear that the concept of nonequilibrium assemblages is not limited to groupings of sessile species, and may eventually prove to be a powerful construct from which to view the dynamics of a variety of motile organisms. Logically, we may expect some differences between the two groups. I will point out only two of perhaps several which seem to be fundamental, if not obvious.

The first concerns the basic operational definitions. That is, how are we to distinguish between equilibrium and nonequilibrium communities? According to Sousa (1979), communities are in equilibrium when the relative and absolute abundances of species in a "local area" remain constant or exhibit long term stable oscillations. In nonequilibrium communities, by way of contrast, "the species composition in any area is usually changing and local populations often go extinct." The three-species assemblage in the low intertidal zone appears to conform reasonably well to the nonequilibrium criteria, as H. nudus is periodically replaced by Cancer productus during months of high salinity. At higher tidal levels, however, the interaction between the two Hemigrapsus species does not conform well to either definition. Indeed, in the absence of any knowledge concerning the actual mechanism of the interaction and the importance of patchy physical disturbances in determining species composition, the equilibrium definition might appear to be the more reasonable choice.

In this context, the important difference between motile and sessile assemblages is the manner in which biotic spatial heterogeneity is generated. According to the nonequilibrium view, biotic patchiness among sessile organisms is primarily due to local (e.g., rock level) variability in the length of time over which colonization and successional replacements (local extinctions) have proceeded. Local extinctions and continual changes in local species composition are thus not only characteristic but essential in explaining the coexistence of sessile competitors. Terms such as steady state and equilibrium, when they are appropriate at all, can have significance only in the absence of local disturbance or at the global level. Motile assemblages, such as the shore crabs, may also be characterized by continual change, but at a different level and with markedly different results. Local patches (rocks), for instance, cannot be viewed as competitively isolated components of the global (habitat wide or perhaps regional) system. Likewise, local assemblages of conspecific individuals cannot be treated as isolated populations subject to periodic extinctions by either local disturbances or local competition. Because disturbances are more or less predictably heterogeneous in space, some portions of the total available space are more intensely contested; because individuals are motile and differ in their abilities to acquire that space (based on individual age and species), the biotic structure is also spatially heterogeneous. Following a local disturbance, complete recolonization may occur in a matter of days. The new assemblage will presumably reflect the composition in the remainder of the habitat and will consist primarily of those individuals who are able to equal or better their current competitive and physical surroundings by occupying it. As a result, barring marked changes in the disturbance regime, the relative abundances of the two species in any rock size class are unlikely to change dramatically.

Continual changes in local species composition therefore need not be necessary or characteristic of systems in which motile competitors coexist in a nonequilibrium state. In order for such an assemblage to exist in a steady state which is statistically indistinguishable from the equilibrium conditions defined above, it would be minimally necessary to postulate constant, but still unequal recruitment. Admittedly, this is highly unlikely, especially since recruitment rates of many marine invertebrates are notoriously unpredictable and are often independent of the size of the local adult population (Thorson 1957, Coe 1956, 1957, Lough 1975). Chronically poor recruitment (not explicitly considered in any recent model) is thus also distinctly possible and could have profound consequences on the species composition of any community in which propagules are subject to independent sources of mortality.

The second way in which the model expectations for motile and sessile groups may diverge concerns the evolutionary tendencies toward specialization, or the lack thereof. In particular, it is probably significant that in all the empirical studies to date which tend to support the nonequilibrium view (Dayton 1971, Caman 1977, Sousa 1979, Lieberman et al. 1979, Connell 1978, and this study, among others), the contested resource has been space, and the competitors have been, in the main, generalists with respect to spatial utilization. Connell (1978) appears to suggest that in nonequilibrium communities, the relative lack of specialization which results in strong competitive interactions is fostered in part by the disturbance regime ("disruptions are so common that species assemblages seldom reach an ordered state") and partially by the general resource requirements of the species involved. Are intense competitive interactions merely characteristic of (some) nonequilibrium communities, or are they actually predicted by the model? If the latter view is correct, then diverse assemblages of specialist species would, by definition, conform more closely to equilibrium views of community organization and evolution.

Among motile species in general, food is probably more often cited as limiting. Even in those cases in which space is more often contested (e.g., rodents, Grant 1972), it is usually inextricably correlated with aspects of the predominant vegetation (grassland, shrubbery, woodland, etc.) which serve as sources of food and shelter. Since food items can vary in many respects (size, reproductive rate, defensive adaptations, time and season of availability, and nutritional value) there are abundant evolutionary opportunities for specialization, but only if the availabilities of these foods, or habitats, remain evolutionarily predictable (Oster and Heinrich 1976, Real 1980). The fact that many species have apparently specialized to become competitively superior at exploiting different food items, and that plants have evolved elaborate and specific defenses, makes it difficult to deny the validity of much of the traditional views (e.g., niche diversification). It is important to note, however, that predictable availability of sessile food items, for example, is not precluded by nonequilibrium hypotheses. Instead, the only unpredictable aspect of species composition in a nonequilibrium community may be the exact location within the larger system at which a species may be found at a given time. So long as the normal range of movements of a motile herbivore or pollinator is great enough to encompass a variety of patch types and the disturbance regime is such that a preferred food item always exists, specialization might still be advantageous. In the extreme form, it may be argued that by ensuring the regional persistence of many sessile species which might be otherwise competitively eliminated, local disturbances may promote "biological accommodation" at some trophic levels while tending to prevent it at others. It is therefore reasonable to question the usefulness of the "accommodated vs intense" dichotomy as being a generally applicable characteristic of interactions in either equilibrium or nonequilibrium assemblages. It is not satisfactory simply to assert that some trophic levels are in equilibrium while others are not, since the species composition and evolutionary tendencies of both may be subject to marked alteration depending upon the disturbance regime.

APPENDIX

This section contains the results of preliminary laboratory observations on i) predation on Hemigrapsus by Cancer productus; ii) interspecific predation and cannibalism among Hemigrapsus individuals, and iii) the tolerance of each shore crab species to desiccation. I conclude the section with a brief discussion of data concerning the growth increments which result from molting in all three species.

Predation by Cancer productus

Methods--The experimental results presented below were derived from observations of mortality among Hemigrapsus individuals exposed to predation by a single Cancer productus. The experiments were performed in the lab under constant temperatures (10 or 15°C) in a 1.8 m diameter plastic wading pool. Pieces of concrete block (ca 15x15 cm) provided refuge space for the shore crabs. Seawater, approximately 15 cm deep, was continuously filtered and changed when it was deemed necessary. Lighting was timed (12L:12D) although dim red light was frequently used to permit casual observation during the dark period. Individual shore crabs were marked with numbered plastic tags which were glued to their carapaces. Following a 5-day acclimation period in which the shore crabs were permitted to adjust to the surroundings, the Cancer was placed in the pool. On each day of the acclimation period and the predation period, mortality among the shore crabs was determined by visual inspection. During the first three experiments, the position of each individual was recorded, paying particular attention to those shore crabs not found under any of the refuges. Pertinent details of each experiment will be described below.

Results--In experiments 1 and 2, ten shore crabs of each of the two species (18-25mm) were placed in the pool together with 2 refuges. The size distributions of crabs of each species were approximately matched. Crabs that were killed were not replaced. During the acclimation period, 10-30% of the H. nudus and 70-90% of the H. oregonensis were apparently unable to acquire space under either of the blocks, indicating a rather severe shortage of refuge space. In both experiments, after the Cancer was introduced, mortality was highest among small individuals, and appeared to be initially higher among H. oregonensis in particular. The combined data for both experiments can be best summarized as follows: a) the per cent of the total observations made for each individual in which the crab was without shelter after the predator was added

(% time-out) was negatively correlated with survivorship ($r = -0.65$, $P < .001$, $n = 40$), and b) individual size and % time-out were also negatively correlated ($r = -0.44$, $P < .01$, $n = 40$). Thus, when refuge space is in short supply, small crabs are the least likely to obtain shelter and are also the most likely to be killed. Although comparisons between the species were not done, it was apparent that more _H. nudus_ (11) than _H. oregonensis_ (2) were always located under one of the refuges.

In order to reduce the severity of competition for refuge space, a total of 7 blocks were used in the third experiment. The number of shore crabs, however, was also increased (30 _H. nudus_ and 10 _H. oregonensis_). In addition, there was no effort to match the size distributions, so that the average sizes of _H. nudus_ and _H. oregonensis_ differed markedly (26.5 and 21.0 mm, respectively). Throughout the experiment, crabs that were killed were replaced with similar-sized conspecifics. During the acclimation period, a total of 14 small _H. oregonensis_ were killed (maximum size 19 mm). No mortalities were recorded during the acclimation period in the first two experiments. Table 13-A shows the size-ranks of those individuals that were killed following the introduction of the predator. In contrast to the results obtained from the first two experiments, predation was significantly

Table 13. Results of Experiment 3 on predation by Cancer on the shore crabs.

A. Size ranks of individuals killed on each day following the introduction of the predator (rank 1 = largest, rank 40 = smallest).

Day						
1	2	3	4	5	6	7
2½	4	13	3	11	1	1
12	5	16	4	18	5	
13	10	19	8			
16½	11	36				
18	14	38				
21½	25					

B. Results of χ^2 goodness-of-fit test on the distribution of mortalities among the shore crabs in each size-rank quartile

	Quartile			
	(Largest)			(Smallest)
	I	II	III	IV
Observed	10	12	2	2
Expected	6.5	6.5	6.5	6.5
χ^2	1.88	4.65	3.12	3.12
			χ^2 = 12.77**	

greater among large individuals (Table 13B). Of the 26 mortalities, 20 were among H. nudus and 6 were among H. oregonensis individuals (approximately in proportion to abundance). Only 20 of 256 recorded positions were for crabs unable to secure refuge space, indicating that competition for space was indeed reduced in comparison to the previous experiments. On many instances, we observed the Cancer successfully to dislodge shore crabs from their refuges by repeatedly lifting the blocks. Active pursuit always followed and was frequently successful.

In the last three experiments, 21 H. nudus and 7 H. oregonensis were placed in the pool together with 5 refuges. Individuals that were killed after the predator was introduced were not replaced, and no effort was made to record the positions of the crabs or to match the species' size distributions. In experiment 4, a large Cancer (125 mm) was used as the predator (as in experiments 1-3). In the last two trials, a small Cancer (75 mm) was employed. Since dead crabs were not replaced, the size-ranks of the individuals that died (Table 14) correspond to their rank on the day that the census was made. The results of the 4th trial (Table 14A) merely support the results of the third trial when refuge space is not seriously limiting, large individuals suffer higher-than-expected mortality, presumably as a result of active

Table 14. Results of trials 4-6 on *Cancer* predation

A. Trial 4. Size-ranks of individuals killed on each day following the introduction of a large *Cancer*.

		Day			
1	2	3	4	5	
1	1	3	none	4	χ^2 = 11.60**
2	2	18			
	14				
	16				

B. Trials 5 and 6. Size ranks of individuals killed on each day following the introduction of a small *Cancer*.

			Day			
	1	2	3	4	5	
Trial 5	none	24 25	12	16 17	none	χ^2 = 2.20 ns
Trial 6	none	13	none	13 22	13 14	χ^2 = 2.20 ns

χ^2 values based on goodness-of-fit of the distribution of mortalities among size-rank quartiles to a random pattern (25% in each quartile).

predation by large Cancer. Trials 5 and 6 (Table 14B), however, suggest that shore crabs beyond some size are relatively immune to predation by smaller Cancer, as might be expected. Some mortality occurred among small H. oregonensis during the acclimation period of each trial. These individuals were replaced before the Cancer was introduced.

Interspecific Predation and Cannibalism among Hemigrapsus

The experimental results presented here were obtained in an effort to clarify the reasons for mortality among small H. oregonensis during the acclimation periods of the preceding experiments when no Cancer were present. In each of the trials, 5 large H. nudus (>30 mm) or 5 large H. oregonensis (>25 mm) were placed in a 1.8 m diameter plastic pool together with 10 small crabs (12-18 mm) of both species or, alternatively, with 20 small individuals of only one of the species. Laboratory conditions (lighting, temperature, etc.) were identical with those described for the Cancer predation experiments, except that no refuges were provided. On each of 7 consecutive days, the crabs were censused; mortalities were noted and those that had been killed were replaced with similar-sized conspecifics. At the end of the week, the large crabs were removed, and on each of the following 5 days, censuses of the small crabs were repeated.

It is clear from the results (Table 15) that large crabs of both species commonly killed (and consumed) smaller individuals. Large H. nudus, however, preyed heavily on small H. oregonensis, but engaged in cannibalism far less frequently. In contrast, large H. oregonensis appeared not to be nearly so discriminating. Aside from raising an interesting question concerning the relative levels of intra- and interspecific aggression among competing species, these results strongly suggest that most of the deaths among small H. oregonensis in the acclimation periods of the experiments in the previous section can be justifiably attributed to H. nudus. It is equally likely that some mortality among these same individuals (following the introduction of Cancer) are also due to predation by H. nudus.

Desiccation Tolerance

In order to determine whether H. nudus and H. oregonensis differ in their ability to tolerate drying, I placed individuals of each species in open containers and noted mortalities at the end of 24 hours. All crabs had been immersed in seawater immediately before the start of each of 2 trials. No more than 3 individuals were placed in any single container so that the effects of

Table 15. Numbers of small (12-18 mm) *H. nudus* and *H. oregonensis* killed over 7 day periods of exposure to large individuals of either *Hemigrapsus* species. Mortality among small crabs in 5 day periods during which the large individuals were not present are also shown. Interspecific comparisons of mortality are from Wilcoxon two-sample tests.

	Trial							
	(1978)							
	1/09	1/21	2/02	2/10	2/18	3/19	4/01	
Large	5 HN	5 HO	5 HN	5 HN	5 HN	5 HN	5 HO	
Sm.HN	10	10	10	20	--	10	10	TREATMENT
Sm.HO	10	10	10	--	20	10	10	
Σ HN	7	3	0	0	--	2	5	NO. KILLED (Lg. crabs pres.)
Σ HO	18	4	9	--	19	9	5	
P	<.01	ns	<.025	<.001		<.05	ns	
Σ HN	0	0	0	N/A	--	0	0	NO. KILLED (Lg. crabs absent)
Σ HO	0	0	0	--	1	0	0	

aggregating were reduced (but not eliminated). The results (Table 16) show the number in each of 2 or 3 size classes that were alive at the start and at the end of the trial. In general, small individuals of either species survived poorly, and large *H. oregonensis* fared substantially worse than large *H. nudus*.

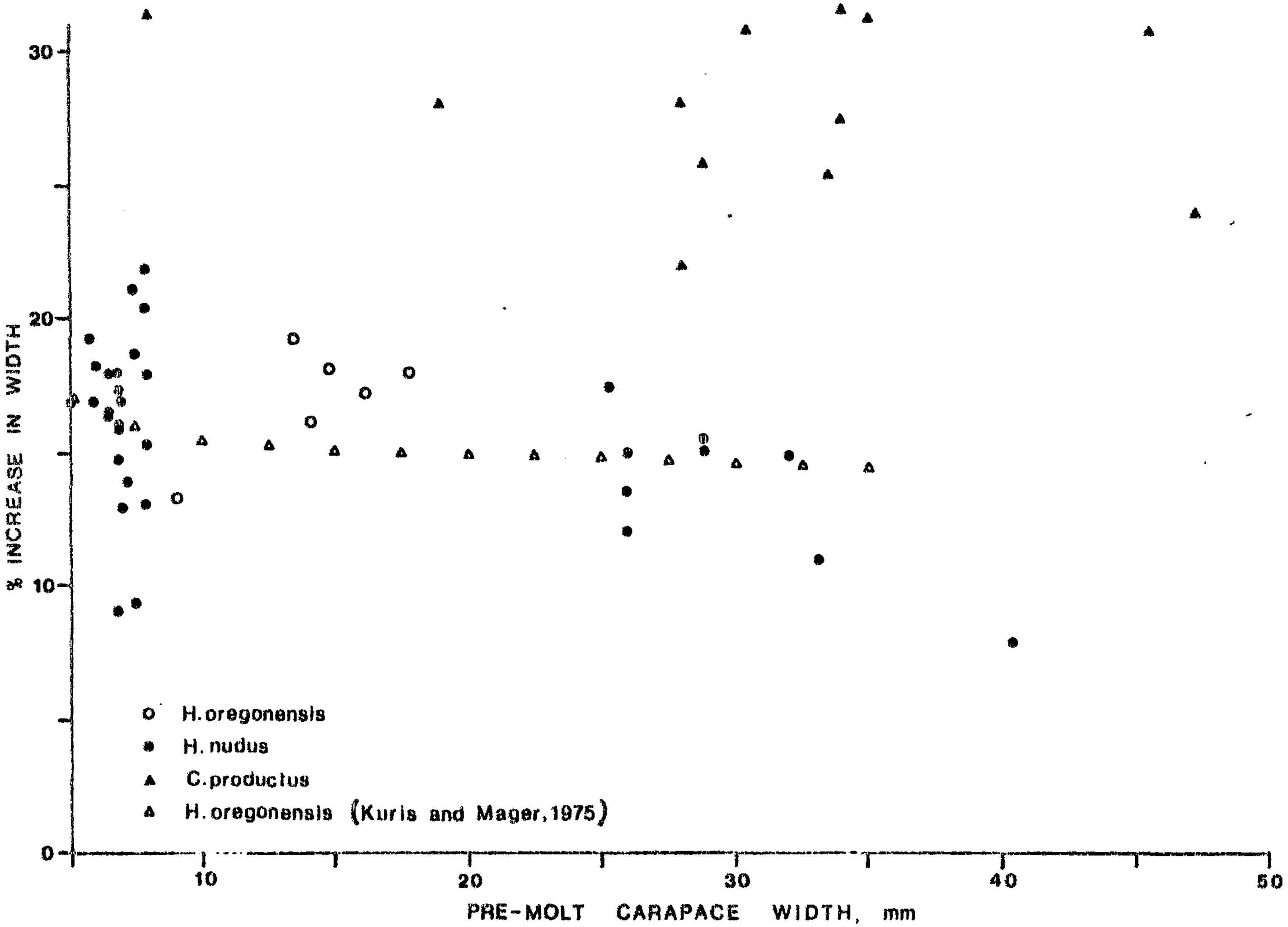
Increases in Size upon Molting

Over the course of the field and laboratory work involved in the project, I have had occasion to find recently molted crabs of all three species together with freshly cast-off exoskeletons. From such data and the results of others (Kuris and Mager 1975, C. Sidi, unpublished data), it is a simple matter to compute the percentage size increment at molting. The results (Fig. 31) indicate that there is no detectable difference between *Hemigrapsus nudus* and *H. oregonensis* in the percentage increase in size which results from a single molt. In consequence, any differences in the annual growth rates of the two species are probably attributable only to differences in the frequency with which molting occurs. In contrast, the percentage increase in size in *Cancer productus* is markedly higher than for either of the shore crab species.

Table 16. Survival of _H. nudus_ and _H. oregonensis_ of various sizes after 24-hr exposure to air at 16 C.

	Size Class		
	10-15 mm	20-25 mm	30 mm
H. oregonensis			
1.	10:2	10:5	
2.	10:2	10:6	
H. nudus			
1.	10:2	10:10	5:5
2.	10:1	10:10	5:5

(No. before:No. alive after)


30
20
10
0
% INCREASE IN WIDTH
10
20
30
40
50
PRE-MOLT CARAPACE WIDTH, mm
○ H. oregonensis
● H. nudus
▲ C. productus
△ H. oregonensis (Kuris and Mager, 1975)

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