

COEXISTENCE IN A KELP FOREST: SIZE, POPULATION DYNAMICS, AND RESOURCE PARTITIONING IN A GUILD OF SPIDER CRABS (BRACHYURA, MAJIDAE)¹

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Abstract. The population dynamics and resource partitioning of five species of spider crabs (*Loxorhynchus crispatus*, *Pugettia producta*, *Mimulus foliatus*, *Pugettia richii*, and *Scyra acutifrons*) were measured in a kelp forest on the central California coast. The distribution of the five species showed zones of peak abundances along a transect from the intertidal zone through the kelp forest to a deep reef. *P. richii* was the most abundant species with peak densities of 6 crabs/m² at the middle and inner edge of the kelp forest. *M. foliatus* was second most abundant with a peak of 3.5 crabs/m² at the middle and outer edge of the kelp forest. *S. acutifrons* had peak densities of about 3 crabs/m² at the outer edge of the kelp forest. *P. producta* had a peak of 2 crabs/m² in the intertidal zone. *L. crispatus* was present in low densities of about 0.5 crabs/m² from the middle of the kelp forest to the deep reef. The greatest combined density of spider crabs (11 crabs/m²) occurred at the middle of the kelp forest.

Densities of all five species in the main study area in the middle of the kelp forest showed a synchronous cycle with a maximum in late summer and fall and a decline in winter to a low in spring. The cycle appeared to be caused by a combination of density-independent mortality from winter swells and storm activity and by slower development and growth rates during the upwelling period of colder water temperatures. Brooding frequencies of all the species remained high year-round. Size-structures of the populations did not change during bimonthly sampling, indicating continuous recruitment. Size-frequency analysis of crab populations along the transect indicated that juveniles of *Pugettia producta* recruit into the intertidal and shallow *Phyllospadix* zones and migrate out into the kelp forest as they grow, but the other species did not have zones of recruitment separate from adult distribution. The diversity of predators which take spider crabs as a major portion of their diets indicated that the general level of predation pressure is high and may limit the overall population levels of the crabs. Predation by sea otters probably limits the density of *P. producta*, and the other four species are probably limited by fish predation. The crabs exhibit different color morphs, color change, and decorating behavior, which are adaptive for concealment from predators.

Size at maturity of the five species spanned an order of magnitude in carapace width from small *Scyra acutifrons* (1 cm) to large *Loxorhynchus crispatus* (10 cm). Mean body size of mature females and mean body size of the entire population of all pairs of species except *Mimulus foliatus*/*Pugettia richii* had ratios larger than Hutchinson's (1959) predicted value of 1.28. Body size may reflect limitations of the crabs' utilization of crevice refuges in the microhabitat.

Partitioning of the microhabitat resource was measured by substrate utilization. *Mimulus foliatus* had the largest microhabitat niche breadth and was found on most types of substrates, with an important refuge in kelp holdfasts. *Pugettia richii* was found primarily on the alga *Cystoseira osmundacea* and in coralline algal mats. *Scyra acutifrons* occurred in the interstices of algal/invertebrate turf, and *Loxorhynchus crispatus* was found on top of the turf. *Pugettia producta* occurred upon the kelp plants and had the narrowest microhabitat niche breadth.

Analysis of stomach contents showed partitioning of food resources. *Pugettia producta* was a strict specialist grazing on giant kelp, *Macrocystis pyrifera*. *Mimulus foliatus* and *Pugettia richii* also had narrow diets of mostly drift *M. pyrifera*. *Scyra acutifrons* had major food categories of detritus, sponge, and pieces of *M. pyrifera* trapped in the algal-invertebrate turf. *Loxorhynchus crispatus* was a dietary generalist foraging on a broad range of invertebrates and giant kelp.

Niche separation in the guild is multidimensional, and similar utilization of one resource is generally complemented by dissimilar utilization of another resource. Graphical analysis of niche separation for the three dimensions of microhabitat, food, and body size showed that *Pugettia producta* is an overall specialist and *Loxorhynchus crispatus* is a generalist. *Scyra acutifrons* also has a distinct niche within the algal invertebrate turf, but *Mimulus foliatus* and *Pugettia richii* exhibit extensive overlap in all of the parameters measured. However, the degree to which a species is a specialist vs. a generalist for a resource did not relate to the amount of niche overlap with the rest of the guild. Microhabitat resources appear to be the most important for niche separation and may also be explained as adaptations for minimizing predation.

Key words: *Brachyura*; crabs; diet; guild; kelp forest; *Loxorhynchus*; *Majidae*; microhabitat; *Mimulus*; niche breadth; niche overlap; population dynamics; *Pugettia*; resource partitioning; *Scyra*.

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INTRODUCTION

Analyses of resource partitioning have provided much of the evidence for competition as a mechanism which results in niche separation and coexistence of

ecologically similar species (see summaries by Schoener 1974, Diamond 1978). However, Wiens (1977) has questioned the existence of pervasive and continuous competition between species, because populations of potential competitors are seldom at equilibrium levels where resources become limiting. Some studies have emphasized the role of physical disturbance in regulating community structure by removing patches of long-lived dominant species (Connell and Slatyer 1977, Connell 1978). Others have contended that predation is the limiting factor which keeps population densities below levels required for competition (e.g., Paine 1966, 1969, Estes and Palmisano 1974, Menge and Sutherland 1976). Nevertheless, measurements of niche breadth and overlap continue to yield insights into patterns of community organization (e.g., Joern and Lawlor 1980, for grasshoppers), and the relationship of niche overlap and competition remains a subject of continued interest and debate (e.g., Hurlbert 1978, Abrams 1980).

Competition is extremely difficult to prove, both because it is advantageous for an organism to reduce or eliminate competition (Pianka 1976), and because most natural communities are so spatially and temporally variable that competition may be important only during limited episodes or "ecological crunches" (Wiens 1977). The most successful demonstrations of competition have been field systems in which a single resource was likely to be limiting and relatively easy to manipulate (e.g., Connell 1961, Dayton 1971, for competition for space in the intertidal zone; Vance 1972, for competition for shells by hermit crabs) and/or in which the behavioral attributes of interference competition provide ready identification of the mechanism of competition (e.g., Hallacher 1977, Larson 1980, for territoriality in fish, and many other cases of territorial defense). However, even if controlled experimental analysis of competition for a single resource is performed, or the competitive mechanism is identified, accurate measurements of competitive effects are difficult when several factors define the difference between two niches (Levins 1968) or when niche breadth is limited by diffuse competition from several competitors (Pianka 1974). Moreover, models of niche overlap and the interpretation of overlap values depend partly on whether those biological factors which are important in separating competing species are few and independent (May 1974), and many of the models are tautological (Peters 1976).

Difficulties in proving that competition is a mechanism of coexistence can be overwhelming in communities where analyses of resource utilization are most useful in determining patterns of community organization. These are the complex communities, which are often spatially and temporally variable, have many predators operating at several different trophic levels, have many potential competitors, and show multidimensional resource partitioning. Unequivocal proof of

competition is not necessarily the goal in these situations, because it would require that experimental manipulations be overly simplified in order to be technically feasible. The goals are first to determine the structure of guild organization at various trophic levels, and then to evaluate the adaptive significance of resource utilization and niche separation. Even for small, low trophic level species, which are most likely to be controlled by predation and/or disturbance (Menge and Sutherland 1976), measurement of resource partitioning provides an empirical key to understanding guild organization if analyzed in the context of the population dynamics and natural history of the component species.

This study analyzes the resource partitioning of five species of brachyuran crabs in the family Majidae (spider crabs), which coexist in the kelp forests off central California (Fig. 1). Kelp forests are highly productive and diverse ecosystems (North 1971), yet very little is known about the regulation of their community structure or about the basic biology and natural history of many of their principal component species. In central California, spider crabs are important trophic links in the food web of the system; they are common, small herbivores and omnivores which are preyed upon by octopuses, sea otters, and a wide variety of fishes. The five species of spider crabs are characterized by a similar morphology, a terminal molt at puberty when growth ceases, and marked sexual dimorphism (A. H. Hines, *personal observation*). However, the size of adults of different species spans an order of magnitude in carapace width from tiny *Scyra acutifrons* (1 cm) to large *Loxorhynchus crispatus* (10 cm) (Fig. 1). Almost nothing is known about their ecology. Boolootian et al. (1959) and Knudsen (1964) reported the reproductive cycles for *Pugettia producta* and *S. acutifrons*, and Wickstein (1977, 1978) described the diet and decorating behavior of *L. crispatus*. In the present study, I use comparisons of the population dynamics and observations of predation pressure on the crab populations to provide a context for analyzing the adaptive significance of patterns of resource partitioning of the five species. Several hypotheses about the causes of population cycles of the crabs are tested with measurements of reproductive activity, size-frequency analysis, and correlations with predation and weather patterns. Because the five species all have a similar body form but differ substantially in their size at sexual maturity, and because predictive correlations have been made about the overlap in sizes of similar coexisting species (Hutchinson 1959), crab size is combined with measurements of microhabitat and food niche breadth and overlap to analyze niche separation in the guild.

STUDY AREA AND SAMPLING METHODS

This study was conducted in the Hopkins Marine Life Refuge (HMLR) at Pacific Grove, California,

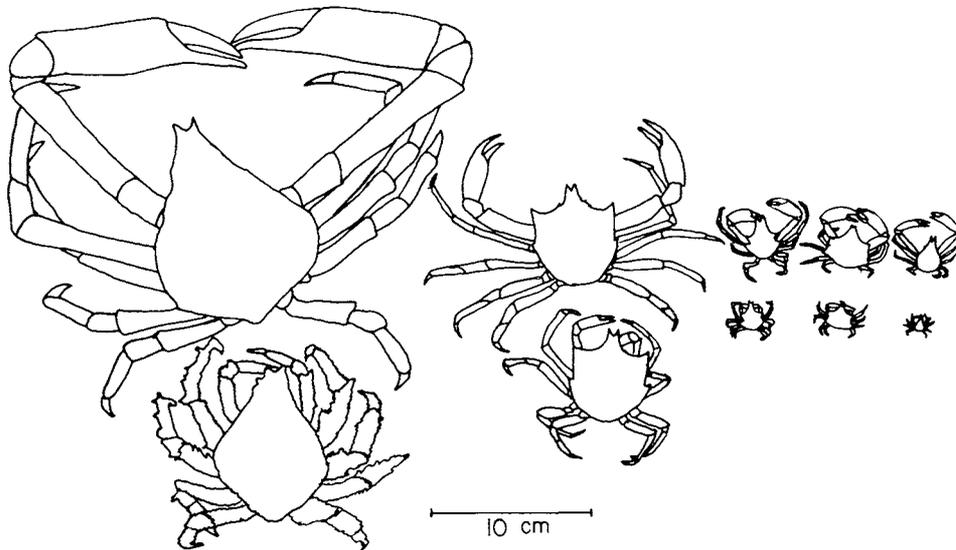


FIG. 1. Sexually mature males (top) and females (bottom) of five species of spider crabs. From left to right, they are *Loxorhynchus crispatus*, *Pugettia producta*, *Pugettia richii*, *Mimulus foliatus*, and *Scyra acutifrons*. Note the sexual dimorphism in size and chela allometry, as well as the differences in size at maturity among the species.

USA. Subtidally, HMLR is a rich giant kelp (*Macrocystis pyrifera*) forest. The habitat is very heterogeneous with a granodiorite substrate which is interspersed with sand channels, pinnacles, cracks, and boulders. The substrate is covered with a lush understory of *Cystoseira osmundacea*, many species of red algae and a dense algal-invertebrate turf of coralline algae, tunicates, byozoans, solitary corals, sponges, vermetids, and many other encrusting organisms. *Pugettia producta*, *Pugettia richii*, *Mimulus foliatus*, *Scyra acutifrons*, and *Loxorhynchus crispatus* are the most abundant brachyuran crabs in the HMLR kelp forest.

All sampling was done using scuba. The abundances and population structures of these crabs were surveyed during August 1978 with 10 quadrats placed randomly within each of six 500-m² stations along a transect running from the intertidal zone through the kelp forest to a deep reef in about 25 m of water outside the kelp forest (Fig. 2). The size of each of the quadrats was 1 m², except that *Pugettia producta* and *Loxorhynchus crispatus* were counted in 10-m² circular plots at stations 3–6. (See below for protocol for searching kelp fronds extending up to the canopy.) However, all of the detailed measurements of population dynamics and resource partitioning were done at a permanent 1600-m² study area in the middle of the kelp forest. At bimonthly intervals from January 1976 to August 1977, ten randomly placed 10-m² circular plots were sampled in the main permanent study area. For each plot sampled, all brachyuran crabs were identified and measured to the nearest millimetre across the carapace width, and mature females (as determined by abdominal allometry) were examined for

brooded eggs. Bimonthly determinations of brooding frequencies were supplemented by additional monthly samples of mature females. All crabs were examined in situ and replaced. The cryptic nature and small size of most of the crabs required picking carefully through the understory, turf, and substrate layers of the forest to find crabs. Although permanent plots are a better sampling design for measuring seasonal changes, random plots were used instead to minimize the effect of this sampling disturbance. In addition to the turf and understory layers of the kelp forest, complete fronds of *Macrocystis pyrifera* plants extending through the water column and forming the canopy layer were searched when their holdfasts occurred within a 10-m² plot. This ensured an appropriate protocol for censusing *P. producta* as well as the demersal species.

It is important to emphasize the painstaking care taken in sampling. Each 10-m² plot took an average of 40 min and as much as 90 min of bottom time to sample. Preliminary checks to determine the sampling error were run first by collecting all crabs from 10 plots and resampling for missed crabs. Although more crabs were overlooked in plots with higher crab densities and greater substrate complexity, only 1–7% of the crabs were missed per plot in the first samples. The size frequency distribution of the crabs found in the second collection did not differ significantly from that of the first collection (Kolmogorov-Smirnov test, $P > .05$). In a second check in October 1976, the densities of crabs in the standard census were compared with the number of crabs in independent, random 0.1-m² plots, which were sampled by chiseling off the algal-invertebrate turf and collecting it with an airlift suction device fitted with a 0.9-mm mesh bag. Mean

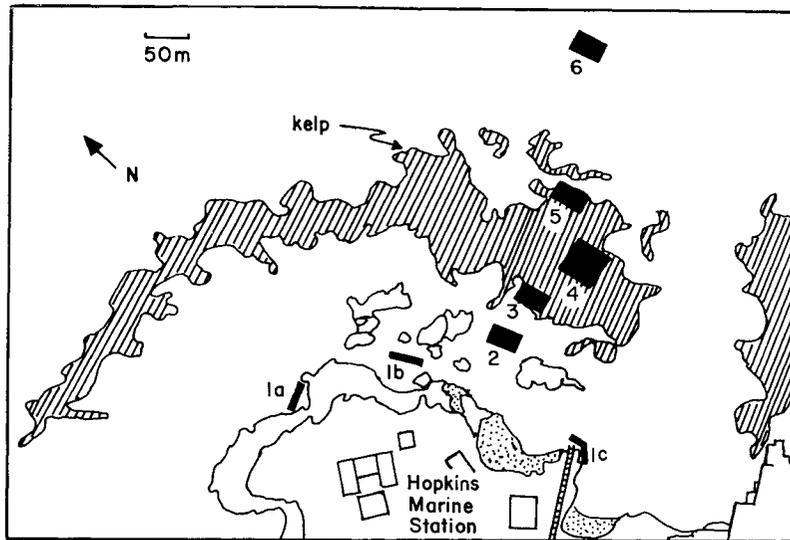


FIG. 2. Map of Hopkins Marine Life Refuge showing the locations of the six 500-m² stations along the transect at which crabs were sampled and the location of the main permanent 1600-m² study area in the center of the kelp forest. 1 = low intertidal station divided into three bands for a combined area equal to that of the other stations; 2 = *Phyllospadix* zone station; 3 = station at inner edge of kelp forest; 4 = main permanent station in middle of kelp forest; 5 = station at outer edge of kelp forest; 6 = deep reef station beyond kelp forest in 25 m of water.

densities of crabs in the two sampling methods were not significantly different (t tests, $P > .05$). However, mean densities of the airlift samples were about 100% larger than the standard census. This larger mean was entirely accounted for by small (<4 mm) crabs; densities of crabs >4 mm were nearly identical for the two sampling methods. Therefore, although crabs as small as 2–3 mm carapace width were often counted in the standard censuses, the number of crabs from the settlement stage (about 1–2 mm) to ≈4-mm size were not estimated accurately. Censuses of crabs >4 mm appear to be accurate.

The microhabitat utilization by the five species was measured in the study area during the October 1976 sampling period, when densities of crabs were high. All available substrate was categorized into 14 types, and the location of each crab in the 10 random 10-m² circular plots was recorded by substrate. The availability of each type of substrate was not measured, except that the average area covered by sand was estimated as 23% per plot.

Utilization of food resources by each species was measured by analysis of stomach contents of crabs collected from the main study area in August 1978. All crabs were collected from 26 randomly placed 1-m² quadrats and all *Loxorhynchus crispatus* and *Pugettia producta* were collected from surrounding 10-m² plots. The crabs were anesthetized with MgCl₂ within 1 h of collection and preserved in 10% Formalin/sea water. A subsample of each species of preserved crab was selected haphazardly, and their stomachs were removed and examined under a dissecting microscope. The diet composition of each species was calculated

from the following data. First, the fullness of each stomach was estimated as a percent of the total volume occupied by the contents. Second, the dissected contents of each stomach were identified to 21 fairly broad food categories, and the percentage by volume of each category was estimated. Because a full stomach provided more information about the diet of the crabs than an empty one, an average diet composition for each species was calculated using the fullness of the stomachs as a weighting factor as follows. The mean proportion of a food category in the diet is

$$p_i = \frac{\sum_{j=1}^n x_{ij}y_j}{\sum_{i=1}^{21} \sum_{j=1}^n x_{ij}y_j}$$

where x_{ij} is the proportion of the contents of the i th food category of the j th crab, and y_j is the fullness of the stomach of the j th crab.

Niche breadth and niche overlap for the microhabitat and food resources of the crabs were calculated using the simplest of the available indexes, as discussed in Colwell and Futuyma (1971). The niche breadth of the i th species was calculated as

$$B_i = 1 / \sum_j p_{ij}^2$$

where p_{ij} is the proportion of individuals of species i which is associated with resource state j . The proportional niche overlap between two species i and h was calculated as

$$C_{ih} = 1 - 1/2 \sum_j |p_{ij} - p_{hj}|$$

for the j resource states. The overall niche overlap of species i with the other four species was estimated by combining the frequencies of the other species associated with resource state j and recalculating the overlap as above.

Data for swell height were summarized from United States Weather Service records of marine surface observations made by ships in the region (Marsden Square 121). Water temperature data were summarized from daily surface measurements made by staff at Hopkins Marine Station.

RESULTS

Distribution

The distribution of the five species of spider crabs showed zones of peak abundances along the transect of six stations from the intertidal zone to the deep reef outside the kelp forest (Fig. 3). *Pugettia richii* was the most abundant species with peak densities of ≈ 6 crabs/m² at the middle and inner edge of the kelp forest and low densities at the other stations. *Mimulus foliatus* was the second most abundant with a peak of ≈ 3.5 crabs/m² at the middle and outer edge of the kelp forest, but it was not found in the intertidal zone or deep reef. *Scyra acutifrons* was the third most abundant species, and it peaked at ≈ 3 crabs/m² at the outer edge of the kelp forest and was moderately abundant at the middle of the kelp and deep reef stations. *Loxorhynchus crispatus* was present in low densities of ≈ 0.5 crab/m² from the middle of the kelp forest out to the deep reef. *Pugettia producta* (the kelp crab) was most abundant in the low intertidal zone with ≈ 2 crabs/m² found at about mean lower low water. About 1 kelp crab/m² was found in the *Phyllospadix* zone, and densities declined to only about 0.1 crab/m² in the kelp forest (including the canopy). This species was absent on the deep reef, where kelp does not occur. The greatest combined density of spider crabs (nearly 11 crabs/m²) occurred at the middle of the kelp forest, the location of the main permanent study area.

Population cycles

Densities of the spider crab populations in the permanent study area in the middle of the kelp forest showed a distinctly seasonal cycle for all five species (Fig. 4). Maximum densities of each species occurred in late summer and fall and declined rapidly in winter to low densities in spring. The relative species composition of the spider crabs remained quite constant throughout the cycle, and other species of brachyuran crabs (primarily *Cancer antennarius*, *Lophopanopeus bellus*, and *L. leucomanus*) remained at relatively low densities throughout the study period. A series of hypotheses about seasonal aspects of reproduction, recruitment, migration, predation, and, finally, physical factors, were examined to determine the cause of the population cycles.

Reproduction.—The first hypothesis was that sea-

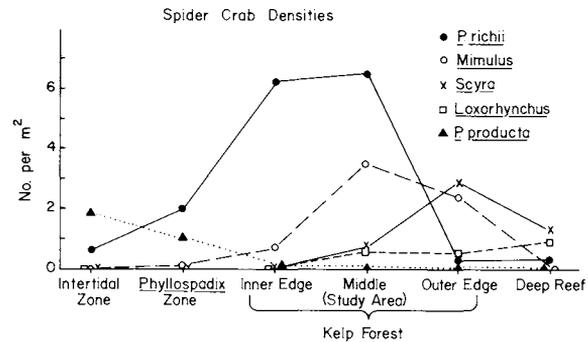


FIG. 3. Densities of spider crabs in August 1978 at six stations along the transect shown in Fig. 2.

sonal reproductive cycles were responsible for the population cycles. However, brooding activity of the crabs was high and relatively constant throughout the year, with $\approx 75\%$ of the mature females of a species brooding embryos at any time (Fig. 5). The one exception to this pattern was *Mimulus foliatus*, which had a period of lower incidence of brooding: $\approx 25\%$ of the mature females, in fall. Booloottian et al. (1959) and Knudsen (1964) report similar year-round brooding activity for *Pugettia producta* and *Scyra acutifrons*. For all five species, broods at all stages of development from freshly deposited to hatching were found at all times of year, and females of each species produce a succession of broods at 1–2 mo intervals with minimal delay between broods (A. H. Hines, *personal observation*). However, development rate of a brood to hatching for *P. producta* and larval development for other spider crabs is dependent on temperature (Goy et al. 1981, J. O'Brien, *personal communication*; A. H. Hines, *personal observation*). It is possible, therefore, that cold temperatures may result in a seasonal reduction in reproductive output by the crab populations (see Physical Factors below).

Recruitment and size-frequency analysis.—The second hypothesis was that the population cycle resulted from seasonal changes in recruitment rates, either as a result of, or independent from, reproductive output. However, analysis of the size structure of the populations did not show increases of small crabs which correlated with the cycles of population densities. Rather, the size-frequency distributions of the populations were fairly constant through time, with small and larger crabs present at all times of the year. The *Pugettia richii* population exemplifies this relative constancy of population structure (Fig. 6). Although the sample sizes of crabs measured at each sampling period reflected the cyclical changes in density, neither absolute nor relative size-frequency distributions showed any cyclical increases in small crabs. Plots of the cumulative size-frequency distributions of *Mimulus foliatus*, *Scyra acutifrons*, *Loxorhynchus crispatus*, as well as of *P. richii*, confirmed that the size frequencies of these crabs were not shifted to smaller

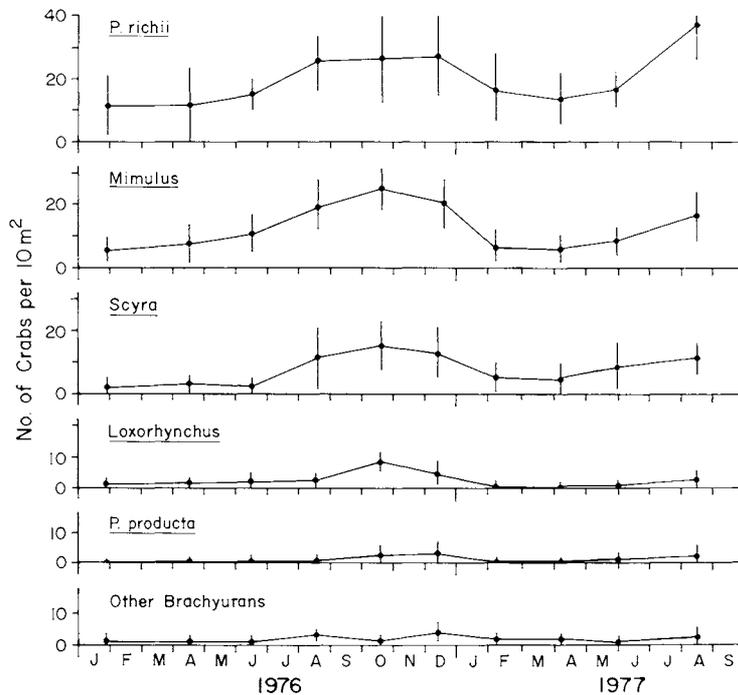


FIG. 4. Cycles of densities of spider crab populations at the main permanent study area in the middle of the kelp forest. Each point is the mean of 10 randomly placed 10-m² circular plots, and the 95% confidence intervals about the means are shown. Other brachyurans included *Cancer antennarius*, *Lophopanopeus bellus*, and *L. leucomanus*.

sizes during spring and early summer, nor were they shifted to larger sizes in fall, as might be expected from the density cycles (Fig. 7). Although the size frequencies of certain samples showed shifts in the expected direction, these shifts were not consistent between months of the same season or between years. For example, the cumulative frequency distribution of *S. acutifrons* was shifted to smaller sizes in June 1977, but it was not shifted in June 1976. The cumulative frequency distributions of *L. crispatus* appeared larger in February and April 1977, but the sizes of these samples ($N = 4$) were too small to be significant. The August 1976 sample of *L. crispatus* had one of the larger size-frequency distributions, but that in October 1976 had the smallest size structure. The bimonthly sample sizes of *Pugettia producta* were too small for size-frequency analysis, but small and large crabs of this species were found at all times of the year. Thus, although the population densities of these crabs went through seasonal fluctuations, the cycles apparently were not caused by seasonal changes in recruitment of small crabs.

Migration.—The third hypothesis examined was that seasonal migration into and/or out of the study area produced cycles in densities. This hypothesis had two components: (a) that migration followed recruitment into a "nursery ground," or (b) that migration occurred independently of recruitment. To determine

if the crabs had a nursery ground for recruitment, first the size-frequency distributions of the populations in the main study area were averaged over a 1-yr cycle (Fig. 8). The population structures of *Scyra acutifrons*, *Pugettia richii*, *Mimulus foliatus*, and *Loxorhynchus crispatus* in the main study area were similar in that these species all had many small crabs and fewer larger crabs. *Pugettia producta*, however, had a very different population structure of relatively many large and few small crabs. This indicated that although recruitment of small crabs into the study area in the middle of the kelp forest occurred for four of the species, small *P. producta* were not recruiting in this area. Analysis of the size structures of the populations of each species of spider crabs during August 1978 at each of the six stations along the transect from the intertidal zone to the deep reef showed that small *P. producta* were found in the *Phyllospadix* and the low intertidal zones, and progressively larger population structures were found toward the outer edge of the kelp forest (Fig. 9). The small kelp crabs in the intertidal and *Phyllospadix* zones were nearly always found in association with red algae, especially *Prionitis lanceolata*, and to a lesser degree, *Gelidium coulteri* and *Gastroclonium coulteri*. These crabs were a dark maroon color which matched the color of the red algae. *P. producta* in the kelp forest were nearly always associated with *Macrocystis pyrifera* plants, and

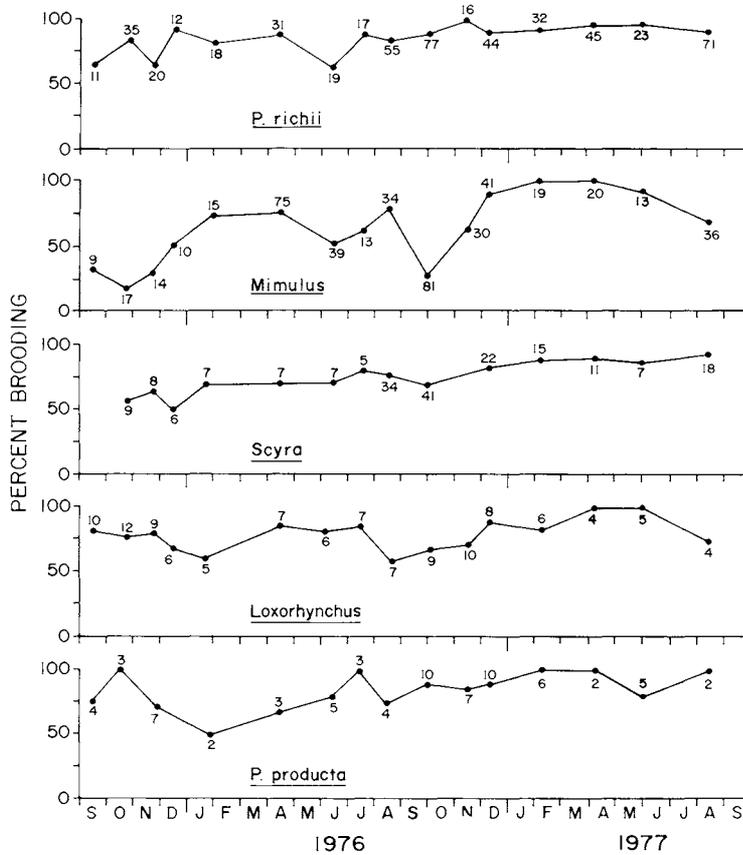


FIG. 5. Brooding frequencies of mature female spider crabs in the main study area. Numbers indicate the sample size of mature females of each species which were examined for the presence of brooded embryos.

most of these kelp crabs were a tan color that matched the brown algae. However, some of the smaller kelp crabs found at the inner edge and middle of the kelp were maroon, and these maroon crabs were found on *M. pyrifera*. *P. lanceolata* and other red algae within the kelp forest were searched carefully but did not have small kelp crabs associated with them. Therefore, most small *P. producta* apparently recruited onto red algae, especially *P. lanceolata*, in the intertidal and *Phyllospadix* zones and migrated out into the kelp forest as they grew, changing color from maroon to tan during the migration. Analyses of size-frequency distributions of the other four species of spider crabs indicated that they did not have this pattern of recruitment in one area and movement to another (Fig. 10). Both small and large crabs of the other four species were present together, except that only larger *P. richii* were found in the intertidal zone.

An hypothesis that seasonal migration independent of recruitment produced the population cycles was difficult to test, because most of the crabs were small (mean size was about 1 cm carapace width) and difficult to tag through the molt cycle. Moreover, it was not feasible in a complex subtidal habitat to search a

sufficiently large area to recapture crabs, because of the simple logistical problem of dilution. A few larger, terminal molt individuals of each species were tagged with a plastic band around the base of a walking leg or with plastic T-shaped fish tags inserted in the epimeral suture at the rear of the branchial chamber. Occasional resightings provided limited information about the potential ranges of movement of the crabs. Smaller crabs moved up to 10 m in 2 d, although most only moved 1-4 m. Large *Loxorhynchus crispatus* and *Pugettia producta* moved up to 40 m in a week, and one *L. crispatus* moved 200 m from its release site in 6 wk. Although these observations indicated that the crabs were capable of movement over considerable distances, most of the tagged crabs stayed in the general vicinity of their release point in the study area, and there was no net directional component to the movement. In fact, second and third sightings of some of the individuals, as well as short-term observations of the paths taken by wandering crabs, indicated that the crabs were milling around haphazardly. Extensive field observations at all times of year did not reveal any apparent seasonal migratory pattern for any of the species.

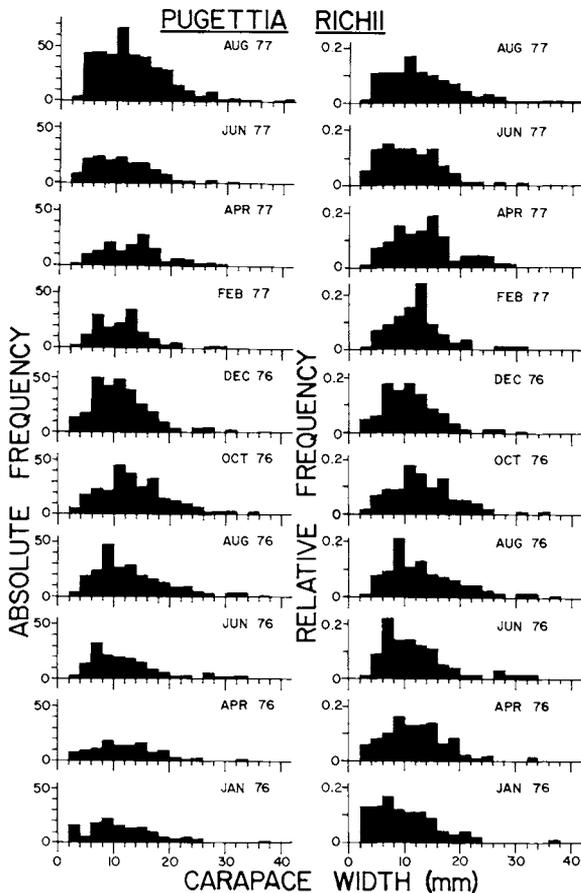


FIG. 6. Population structures of *Pugettia richii* in the main study area on each of the bimonthly sampling periods. Both absolute and relative frequency histograms are shown for each sampling period. Note that the absolute frequencies show the cyclical changes in numbers of crabs sampled, but there are no increases in relative abundance of small crabs.

Predation.—If predation rates fluctuated in a regular, seasonal way, they might have produced cycles of population density. There was an intense predation pressure on the spider crabs by a great variety of predators in the kelp forest. The magnitude of the predation pressure can be estimated from data on the densities, diets, and feeding rates of predators consuming spider crabs. For example, *Pugettia producta* made up $\approx 25\%$ of the prey items in the diet of sea otters (*Enhydra lutris*) which foraged daily at HMLR (Costa 1978, A. H. Hines, *personal observations*). In a study of the energetic requirements of sea otters and the energy value of their prey, Costa (1978) used this observation of the composition of the diet to estimate that a single sea otter in HMLR consumed about 48 *P. producta*/d to satisfy about 30% of its energy needs. An average of \approx one sea otter was present at HMLR on daily counts during the study period (A. H. Hines and J. S. Pearse, *personal observation*). The 1600-m² study area is about 3% of the total area of HMLR. If

it is assumed to have provided 3% (i.e., 1.4 crabs) of the 48 kelp crabs taken per day by an average otter, then over 500 kelp crabs were taken from the study area per year. At a mean density of 1 kelp crab/10 m² or 160 kelp crabs for the whole study area, this indicates over a three-fold turnover rate per year of the standing crop in the study area. Mature *P. producta* in the area were rarely found with fouling organisms growing on their carapace, nor were they found with calcified stumps of autotomized appendages, both of which are common for *P. producta* north of the range of sea otters. These observations indicated that the life span of *P. producta* after the terminal maturation molt was not very long at HMLR. This predation rate probably severely limited the densities of larger kelp crabs. Sea otters also foraged heavily on *Cancer* spp. and occasionally took large *Pugettia richii*, but they ignored the smaller crabs as a rule. Surprisingly, sea otters apparently rarely took large *Loxorhynchus crispatus*, which usually occurred exposed on the surface of rocks, and which do not appear to have any special escape or defense mechanisms from otters.

Many species of fish readily took small crabs of all five species, especially the bottom-dwelling species in the study area (Table 1). Average densities of these fish species were estimated from studies by Miller and Geibel (1973; Station A), Carr and Rhodes (1976), and personal data. Much of the information on diet of fish in kelp forests comes from studies in southern California (e.g., Quast 1968, Larson 1972, Love and Ebeling 1978), and Quast (1968) estimated that crabs were the second most important food category (behind gammarid amphipods) utilized by the total fish fauna in southern California kelp beds. Other studies in the region of the present study (e.g., Hallacher 1977; Roberts 1979) and numerous personal observations and samples of stomach contents confirm the importance of spider crabs in the diet of most of the fish species at the HMLR study site. *Mimulus foliatus*, *Loxorhynchus crispatus*, *Scyra acutifrons*, and *Pugettia richii* are major components in the diets of the demersal rockfish (family Scorpaenidae) *Sebastes chrysomelas*, *S. atrovirens*, and *S. caurinus*, as well as three species of small sculpins (family Cottidae) which were abundant on the bottom. For example, 15 *S. chrysomelas* collected from the area averaged 1.7 spider crabs per stomach. Sculpins frequently were observed feeding on crabs stirred up during bimonthly sampling. Larger bottom-dwelling predatory fish, including lingcod (*Ophiodon elongatus*), cabezon (*Scorpaenichthys marmoratus*), and kelp greenling (*Hexagrammos decagrammus*) also took large numbers of spider crabs up to 4–5 cm in carapace width. For example, kelp greenling caught in the area had as many as 11 *M. foliatus*, 5 *P. richii*, and 4 *S. acutifrons* per stomach, and cabezon had as many as 3 *L. crispatus*, 2 *M. foliatus*, 1 *P. richii*, and 1 *Pugettia producta* per stomach. The total number of fish feeding on spider crabs is estimated to

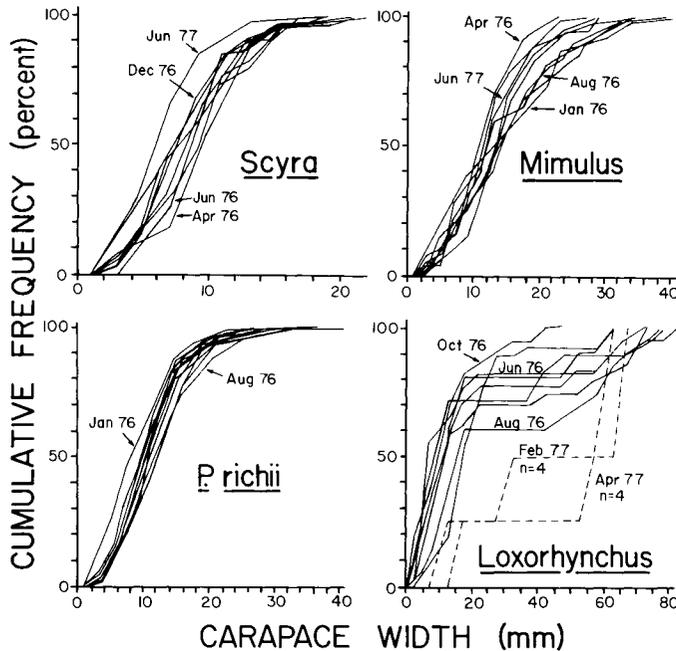


FIG. 7. Cumulative size-frequency distributions of *Pugettia richii*, *Mimulus foliatus*, *Scyra acutifrons*, and *Loxorhynchus crispatus* in the main study area for each of the bimonthly sampling periods. Cumulative frequency curves shifted to the left would indicate populations with smaller size structures; those shifted to the right would indicate larger size structures. The curves for February and April 1977 for *L. crispatus* had sample sizes of only four crabs. Sample sizes of *Pugettia producta* were too small for analysis.

average ≈ 2.2 fish/10 m² (Table 1). If an average fish were conservatively assumed to consume 1 crab/d, then at least 2 crabs/10 m² would be taken per day. At peak densities of ≈ 70 spider crabs/10 m² in late summer and fall, this rate of fish predation would result in a turnover of the spider crab population about once a month. Although preliminary results (A. H. Hines, *personal observation*) indicate that crab growth to the modal size of 1 cm takes 6–8 mo, indicating a somewhat slower turnover rate, it is clear that predation pressure from demersal fish had a major impact on spider crab populations.

In addition to sea otters and fishes, *Octopus* spp. were common in the kelp forest and are well known to feed extensively on crabs, but no octopus dens with piles of crab carapaces were found in the area. Also, the crabs themselves often eat other recently molted crabs in the laboratory, and crab parts were found in stomach contents of *Loxorhynchus crispatus* from the field (see Food Resource below).

All of these observations indicated great predation pressure on the spider crabs, particularly from predators using visual cues during foraging. Many aspects of the crabs' biology were clearly adaptive for minimizing the impact of these predators. All five of the species were extremely well camouflaged in their habitats as a result of their cryptic coloration and their ability to mimic the substrate by decorating their carapace with pieces of algae and invertebrates placed on

specially adapted hooked setae. *Pugettia producta* is capable of changing color between molts from maroon, which matches red algae, to tan, which matches kelp. *Pugettia richii* found on coralline algae were a pink color matching the substrate, while those on other substrates were a deep red or brownish red that blended well with foliaceous red algae or *Cystoseira osmundacea*. *P. richii* also frequently decorated its rostrum with pieces of algae, sponge, tunicates, and other material. *Mimulus foliatus* usually do not decorate, but it was found in a great variety of color morphs, ranging from the most common morph of reddish brown to all white to irregular patches of red and white. *Loxorhynchus crispatus* showed no color variation, but these crabs profusely decorated their carapaces with algae, bryozoans, sponge, hydroids, tunicates, and other materials. (See Wickstein 1978, for descriptions of decorations and behavior in *L. crispatus*.) In addition, small juvenile *L. crispatus* are covered with long, hairy setae that obliterated any profile resembling a crab and effectively made them appear like rocks covered with algae, bryozoans, or hydroids. Mature female *L. crispatus* are also quite pubescent, and mature males are thickly covered with short setae. Although individual *Scyra acutifrons* occasionally showed extensive decoration, most did not, and it had little color variation. Instead, most *S. acutifrons* resided within interstitial crevices which were inaccessible to most larger predators. All of the bottom-dwell-

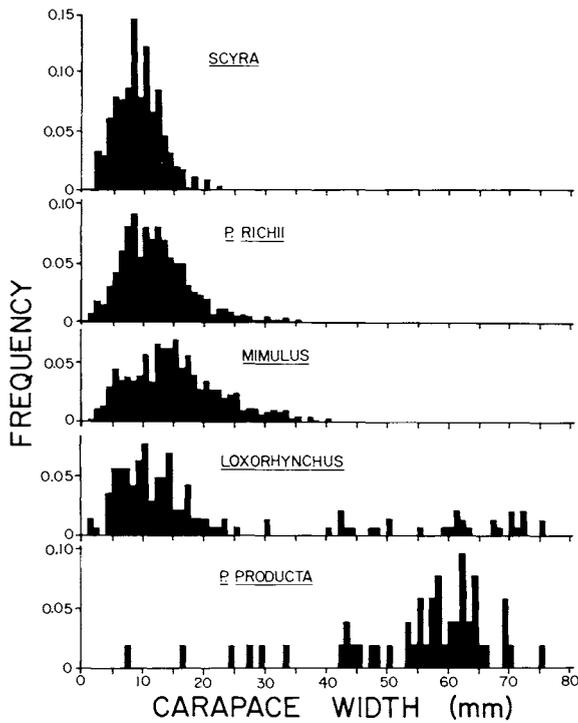


FIG. 8. Average size structures of populations of spider crabs at the main study area in the center of the kelp forest. Size-frequency histograms averaged for the six bimonthly sampling periods during 1976 are shown for each species. Note the paucity of small *Pugettia producta*.

ing species exploited cracks and crannies, were relatively slow moving, and all clung tenaciously to the substrate with sharp hooked dactils when disturbed. Only larger *P. producta* often moved rapidly

away when approached, and only this species pugnaciously and painfully pinched when handled.

Although predation was obviously an important source of mortality for these spider crabs, it was technically too difficult to manipulate experimentally total predation pressure on the populations. The crabs were mostly too small and motile to cage without seriously affecting water movement, light, and food availability. Similarly, the predators were too diverse and motile to cage all of them or to measure feeding rates without destructively sampling them (see Young et al. 1976 and Virnstein 1978 for discussions of the difficulty of manipulating predation pressure when a diverse array of a wide size range of predators is involved). Although there is strong enough circumstantial evidence that sea otter predation was probably limiting the population density of *Pugettia producta*, and fish predation was likely to have a major impact on the bottom-dwelling crabs, none of the important predators, including sea otters and most of the adult demersal fish, were markedly seasonal in their abundance. The total abundance of fishes in the study area was highest during summer, but this increase was primarily a result of midwater species (e.g., *Sebastes mystinus* and *Oxyjulus californica*), which have minimal impact on crabs (Miller and Geibel 1973, A. H. Hines, *personal observations*). Moreover, a cycle of increased number of predators in summer is contrary to increases in crab populations during the same period. However, some demersal species (e.g., *Ophidion elongatus*) were more active in the study area during winter, whereas juveniles of other species (e.g., *Sebastes* spp.) were abundant in summer (Miller and Geibel 1973). The net effect of seasonal reproductive cycles and migrations of fishes impacting crabs appears to be generally bal-

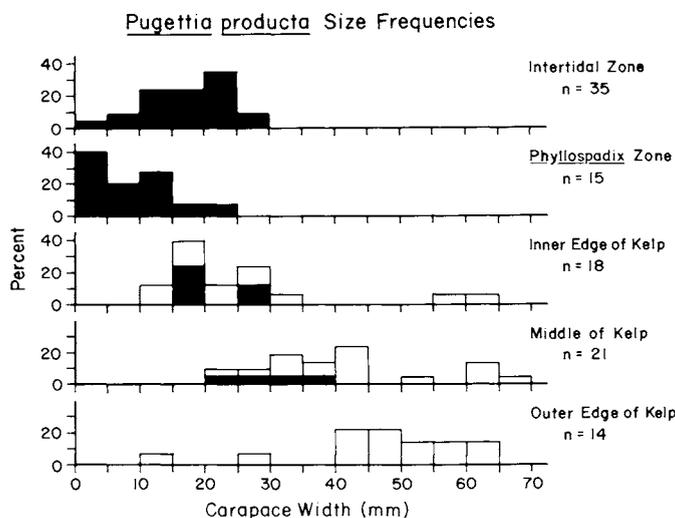


FIG. 9. Population structures of *Pugettia producta* at five stations from the low intertidal zone out through the kelp forest during August 1978. Small kelp crabs are apparently recruiting in the intertidal and *Phyllospadix* zones and migrating into the kelp forest. Solid bars on the histograms show the frequencies of maroon-colored crabs, which match red algal substrates, and open bars indicate frequencies of tan-colored crabs, which match kelp.

anced over the year, resulting in a high abundance of crab predators year-round. It is possible that some predators may switch their diets from crabs on a seasonal cycle (Love and Ebeling 1978, Roberts 1979). However, it is difficult to understand how total predation pressure from such a diverse array of predators could fluctuate in such a way as to produce a synchronized population cycle in all five of the species of crabs.

Physical factors.—With the apparent absence of any inherent cycle in brooding frequency, recruitment, migration, or predation pressure on the crabs, I propose that seasonal fluctuations in density-independent losses from winter wave activity and storms and/or changes in temperature-dependent rates of brood development and growth caused the synchronous cycles in the population densities of the crabs. Long-period winter swells from storms generated in the north Pacific appear to regulate the standing crop of *Macrocystis pyrifera* at HMLR (Gerard 1976, J. S. Pearse and A. H. Hines, *personal observation*). Not only is the standing crop of attached kelp regulated by winter swells, but the production and export of drift algae on the bottom is also a function of these swells (Gerard 1976), indicating that bottom communities are also strongly affected by the long-period swells. Most of the drift kelp moves out of the area along the bottom into deep offshore water during winter. The density cycle of spider crabs is negatively correlated with the cycles of monthly mean swell height, with one apparent exception in September 1976 (Fig. 11). However, unlike the winter season, increases in swell height during this month were caused by strong afternoon offshore winds, which produced only short-period swells that did not affect bottom communities at the depths of the study site. I suggest that long-period winter swells were a major cause of density-independent mortality which imposed a synchronous seasonal cycle on the crab populations by sweeping the crabs out of the system. My field observations during and immediately after storms indicate that in stormy winter weather the crabs do not seek shelter other than their normal affinity for refuges from predation.

Winter winds and storms also produce upwelling of cold water, and water temperature is closely correlated with the cycle of spider crab densities (Fig. 11). Because developmental rates of broods and larvae, and growth rates, are likely to be dependent on temperature (Goy et al. 1981, J. O'Brien, *personal communication*, A. H. Hines, *personal observation*), the productivity of the crab populations may be reduced during the colder period. The intense predation pressure would drive crab densities down when growth rates and productivity are reduced. Both density-independent losses from winter swells and/or reduction in temperature-dependent growth rates would affect all of the spider crabs in the same cyclical way, whereas biological factors are not likely to have caused the same cycle in all five species.

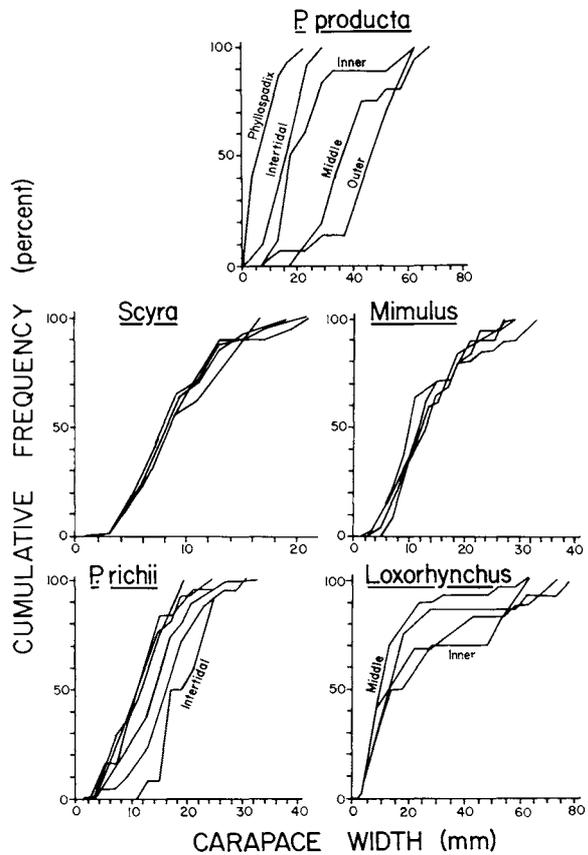


FIG. 10. Cumulative size-frequency distributions of populations of spider crabs at the six stations on the transect in Fig. 2 during August 1978. Cumulative frequency curves shifted to the left would indicate populations with smaller size structures; those shifted to the right would indicate larger size structures. Only *Pugettia producta* showed a pattern of different size structures in different zones.

Microhabitat resource partitioning

The microhabitat resource was clearly partitioned by the five species, although there was considerable overlap in the crabs' utilization of the substrates (Fig. 12, Table 2). *Pugettia richii* was found primarily on the bushy perennial portion of the brown understory alga, *Cystoseira osmundacea*, and in articulate coralline algae, *Bossiella* spp. and *Calliarthron* spp. *Mimulus foliatus* was found on many types of substrates, but it had an important refuge in holdfasts of giant kelp plants. *Scyra acutifrons* was found in the interstices of small cracks and invertebrate crusts formed by the vermetid *Petalocochus montereyensis* and under low red algae, especially *Rhodymenia* spp. Although *Loxorhynchus crispatus* appears to have had a large overlap in microhabitat utilization with *S. acutifrons*, this is in large part an artifact of the categorization of the substrates. *L. crispatus* was usually found upon the surface of the substrates, while *S. acutifrons* was nearly always found within the interstices. *Pugettia producta* was found almost exclusively upon the por-

TABLE 1. Densities of fish in Hopkins Marine Life Refuge kelp forest and occurrence of spider crabs in their diets.

	Density 10 m ² *	Diet				
		Frequency of crabs (%)	Reference			
Black and yellow rockfish (<i>Sebastes chrysomelas</i>)	0.073	30-80	Hallacher (1977); Larson (1972); Roberts (1970); <i>personal observations</i> †			
Kelp rockfish (<i>Sebastes atrovirens</i>)	0.277	3-30	Hallacher (1977); Larson (1972); Roberts (1979); <i>personal observations</i>			
Copper rockfish (<i>Sebastes caurinus</i>)	0.043	5-10	<i>Personal observations</i>			
Olive rockfish (<i>Sebastes serranoides</i>)	0.027	0-20	Hallacher (1977); Love and Ebeling (1978); Roberts (1979)			
Cabezon (<i>Scorpaenichthys marmoratus</i>)	0.026	70	O'Connell (1953); Quast (1968); <i>personal observations</i>			
Kelp greenling (<i>Hexagrammos decagrammos</i>)	0.120	30-80	<i>Personal observations</i>			
Painted greenling (<i>Oxylebius pictus</i>)	0.001	50-70	Quast (1968); <i>personal observations</i>			
Crevice kelpfish (<i>Gibbonsia montereyensis</i>)	0.043	5-20	Quast (1968); <i>personal observations</i>			
Sculpins (<i>Hemilepidotus hemilepidotus</i>) (<i>Clinocottus analis</i>) (Unidentified sp.)	1.031	10-50	<i>Personal observations</i>			
Rubberlip surfperch (<i>Rhacochilus toxotes</i>)				0.093	20-40	Quast (1968)
Black surfperch (<i>Embiotoca jacksoni</i>)				0.199	10	Quast (1968); <i>personal observations</i>
Kelp bass (<i>Paralabrax clathrus</i>)	0.289	5	Quast (1968); Love and Ebeling (1978)			
Total fish	2.222					

* From Miller and Geibel 1973; Carr and Rhodes 1976; *personal observations*.

† All personal observations are by A. H. Hines.

tions of giant kelp plants which extended through the water column to the surface. Qualitative observations on numerous night dives indicated that although *Cancer antennarius* was markedly nocturnal, none of the five species of spider crabs changed obviously in their level of activity or microhabitat selection. In summer, however, some adult *Pugettia richii* on *C. osmundacea* appear to move from the vegetative portion of the plant up onto the reproductive fronds in the evening hours (J. Aris, *personal communication*). None of the species of spider crabs showed any seasonal changes in activity (qualitative observations) or microhabitat (A. H. Hines, *personal observation*). Thus, *M. foliatus* had the largest microhabitat niche breadth and greatest overall microhabitat niche overlap, and *P. producta* had the narrowest microhabitat niche and lowest overall niche overlap within the guild (Table 2). As might be expected, pairwise niche overlap was greatest between the four bottom-dwelling species and smallest between these species and *P. producta*, which occurred upon the kelp plants. Again, the large pairwise niche overlap for *S. acutifrons* and *L. crispatus* is partially an artifact of not distinguishing crabs

occurring within the turf substrate (*S. acutifrons*) from those occurring on top of the turf substrate (*L. crispatus*).

Food resource partitioning

Analysis of the stomach contents of the crabs proved surprisingly easy if the crabs were preserved soon after collection, because the food items in the stomachs were in relatively large pieces which could be identified to broad categories, and because only the stomachs of *Scyra acutifrons* contained large amounts of detritus. The five species showed a spectrum of diets from *Pugettia producta*, which was a strict specialist on giant kelp (*Macrocystis pyrifera*), to *Loxorhynchus crispatus*, which was very much a generalist feeding on a great variety of items (Fig. 13; Table 3). *Mimulus foliatus* also showed a pronounced specialization on *M. pyrifera* (98.5% of its stomach contents). *M. pyrifera* comprised nearly 90% of the stomach contents of *Pugettia richii*, but several other food items were present in small quantities. In addition to large quantities of detritus, *Scyra acutifrons* had significant quantities of *M. pyrifera*, sand, and sponge

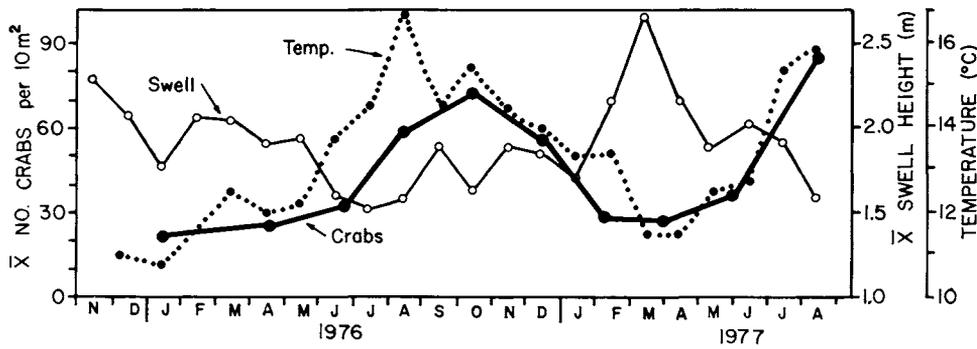


FIG. 11. Seasonal changes in monthly mean swell height (thin line), water temperature (dotted line), and total densities of spider crabs (thick line). Swell height data are from United States National Weather Service records of shipboard observations in the region (Marsden Square 121). Temperature data summarize surface measurements taken daily at Hopkins Marine Station. Crab densities sum the data for the five species in Fig. 4.

present in its stomach, as well as a few other items in minor quantities. The presence of significant quantities of *M. pyrifera*, sipunculids (*Phascolosoma agassizii*), sponge, sand, detritus, tube-dwelling and errant polychaetes, small *Cancer* and spider crabs, and an isopod species (*Idothea* sp.), as well as minor quantities of many other items in the stomachs of *L. crispatus* indicated that this species was a general omnivore. Wickstein (1977) reported a similarly diverse diet for *L. crispatus*. *P. producta* and *M. foliatus*, the species which specialized on *M. pyrifera*, had much fuller stomachs (averaging nearly 90% full) than the three species which had more diverse diets (averaging 46–65% full).

Although food availability was not assessed for the crabs, the microhabitat selection of each species and observations of their feeding behavior in the field and laboratory provided clues to their foraging patterns. *Pugettia producta* clearly grazed directly on the huge resource of attached *Macrocystis pyrifera* plants. *Mimulus foliatus* was probably eating the holdfasts and sporophylls of *M. pyrifera* plants, and it fed on drift *M. pyrifera* littering the bottom as well. *Pugettia richii* also fed on the abundant drift *M. pyrifera* on the bottom. *Scyra acutifrons* apparently fed heavily on the sand and detritus trapped in the interstices of the algae/invertebrate turf, and it also must have eaten small pieces of drift *M. pyrifera* which became trapped in interstices of the turf. *Loxorhynchus crispatus* was

often seen picking at the algae/invertebrate turf, removing sipunculids and other organisms from the interstices of vermetid (*Petalococonchus montereyensis*) mats. This crab appears to take opportunistically nearly anything it happens across, including drift *M. pyrifera* and dead and living invertebrates. *Cystoseira osmundacea* and many species of foliaceous and coralline red algae were available in abundance to the crabs, but none took these algae, except in trace quantities, even when starved in the laboratory. Thus *L. crispatus* had the broadest and *P. producta* the narrowest food niche breadth (Table 3). The greatest pairwise food niche overlap was between the three species which ate mostly *M. pyrifera*, but *S. acutifrons* and *L. crispatus* also had a large food niche overlap. *Pugettia richii* exhibited the greatest overall niche overlap within the guild, as a result of both feeding extensively on kelp and taking some invertebrates. *Scyra acutifrons* had the lowest overall niche overlap within the guild, due to its utilization of detritus, sponge, and a variety of invertebrates not taken by most of the species.

Body size

Hutchinson (1959) predicted that ecologically similar species should have a ratio of mean body size of at least 1.28, reflecting specialization for prey of different sizes. In similar contexts, several others (e.g., Ashmore 1968, Schoener 1969, 1970, Hespeneide

TABLE 2. Microhabitat niche breadth, pairwise niche overlap and overall niche overlap calculated from data for substrate utilization shown in Fig. 12.

	Niche breadth	Pairwise niche overlap				Overlap within guild
		<i>Pugettia producta</i>	<i>Loxorhynchus crispatus</i>	<i>Scyra acutifrons</i>	<i>Pugettia richii</i>	
<i>Mimulus foliatus</i>	4.62	.11	.40	.47	.43	.59
<i>Pugettia richii</i>	3.82	.13	.30	.31		.40
<i>Scyra acutifrons</i>	3.59	.05	.80			.43
<i>Loxorhynchus crispatus</i>	3.48	.05				.48
<i>Pugettia producta</i>	1.35					.13

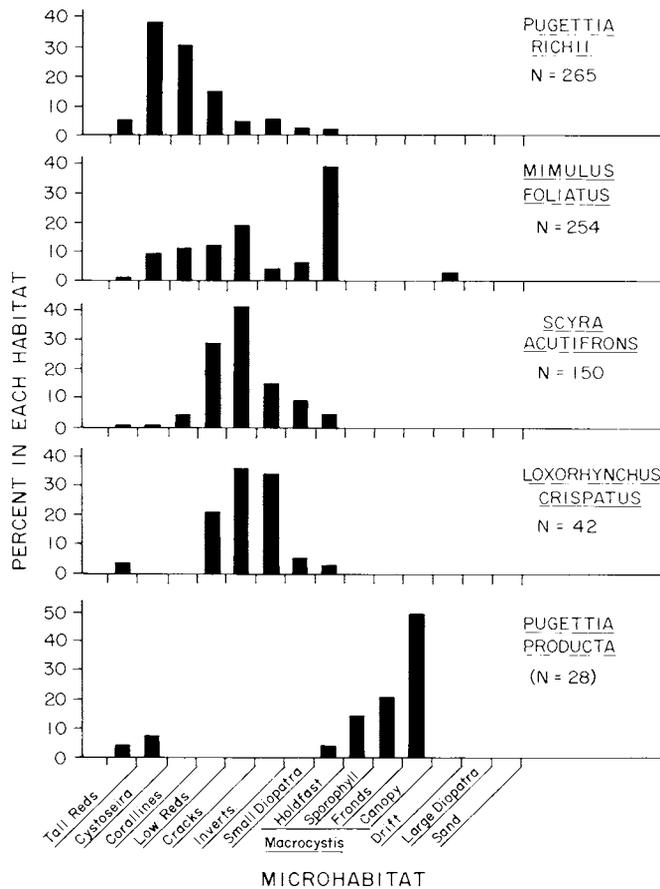


FIG. 12. Microhabitat partitioning by the five species of spider crabs in the main study area during October 1977. The frequency of occurrence of each species on 14 possible substrate types was recorded for all crabs in 10 randomly placed 10-m² circular plots. Additional random plots were sampled for *Pugettia producta* only, because of the low density of this species.

1973, Fraser 1976, Turner and Polis 1979) have analyzed body size as a reflection of the limits of resource utilization by similar species. Crabs in the family Majidae have a terminal molt at puberty (i.e., no molting and growth occurs after the molt at sexual maturation). They also show marked sexual dimorphism in size (males are larger) and chela allometry (males have larger chelae). For crabs in the present study, size at maturity may reflect differences in their abilities to

utilize crevices as refuges from predators, as well as reflecting utilization of the food resource.

Measurements of crabs during the bimonthly surveys showed that mature males and females of each species had a limited size range, and that the sizes at maturity of the five species spanned over an order of magnitude in carapace width from small *Scyra acutifrons* to large *Loxorhynchus crispatus* (Table 4). The ratio of mean size of mature females of *Mimulus fo-*

TABLE 3. Food niche breadth, pairwise niche overlap and overall niche overlap calculated from data on stomach contents shown in Fig. 13.

	Niche breadth	Pairwise niche overlap			Overlap within guild
		<i>Pugettia producta</i>	<i>Mimulus foliatus</i>	<i>Pugettia richii</i>	
<i>Loxorhynchus crispatus</i>	7.56	.19	.20	.19	.41
<i>Scyra acutifrons</i>	4.21	.26	.19	.21	.30
<i>Pugettia richii</i>	1.25	.89	.90		.63
<i>Mimulus foliatus</i>	1.03	.99			.57
<i>Pugettia producta</i>	1.00				.56

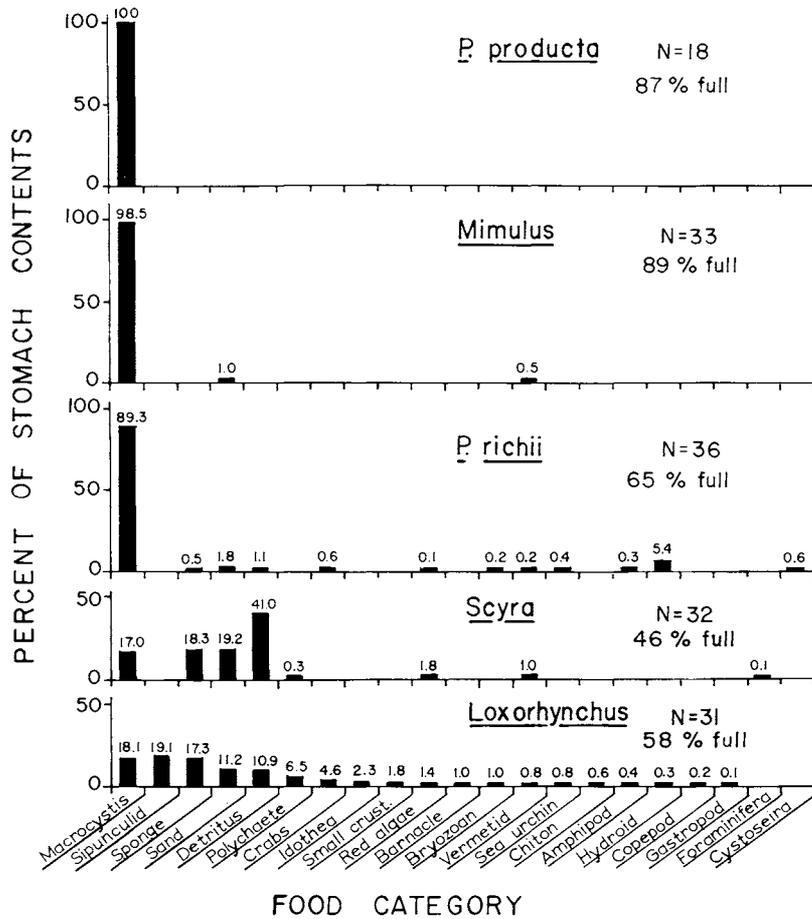


FIG. 13. Food resource partitioning by the five species of spider crabs in the main study area during August 1978. The numbers above each bar are the mean percentage of each of 21 food categories in the diets of each species, as calculated from analyses of stomach contents and adjusted by a weighting factor for the fullness of each crab stomach (see Methods). The sample size and mean fullness of stomachs of each species are indicated.

liatus and *Pugettia richii* was only 1.04 and that of *Pugettia producta* and *L. crispatus* was only 1.10, while all other pairs of species had ratios larger than Hutchinson's predicted value of 1.28. Note that in the main study area the modal sizes of the total populations of the four bottom species appeared to be similar, while that of *P. producta* was much larger (Fig. 8). However, ratios of mean size for the populations were greater than 1.28, except for the ratio of *P. richii* to *M. foliatus*. In both size at maturity and mean carapace width of the populations, *M. foliatus* and *P. richii* were nearly identical.

DISCUSSION

Under intense predation pressure, reduced development and growth rates during cold upwelling months appear to combine with winter storm mortality to produce the population cycles of all five species of spider crabs at HMLR. The crab populations are dynamic with high brooding frequencies and steady recruitment year-round, which cannot be responsible for

the cycles. Neither crab movement nor predation pressure on the populations appear to fluctuate in a regular, seasonal way. However, the array of predators in the kelp forest community which take spider crabs as a major portion of their diets indicates that the general level of predation pressure is very high. The circumstantial evidence indicates that predation from sea otters alone is sufficient to limit densities of *Pugettia producta*, and that the many species of demersal fish regulate densities of the other four bottom-dwelling species of crabs. Only *Loxorhynchus crispatus* attains a size large enough to preclude predation from most fish, and it is not often taken by sea otters. However, young *L. crispatus* are subject to the same fish predators as the smaller species. Therefore it is likely that predation limits the overall population levels of the crabs, while density-independent winter mortality and temperature-dependent production rates cause the synchronous population cycles within the limits set by predation.

Differences in microhabitat resource utilization

TABLE 4. Sizes of spider crabs at main study area. Measurements of carapace width in millimetres are indicated for mature males, mature females, and entire populations in six bimonthly samples in 1976. Hutchinson's ratios (1959) of larger to smaller species indicated a high degree of overlap when ratios were <1.28 .

	Size range carapace width (in mm)		Mature ♀♀		Population	
	mature ♂♂	mature ♀♀	Size ($\bar{x} \pm SD$)	Hutchinson's ratio	Size (\bar{x})	Hutchinson's ratio
<i>Scyra acutifrons</i>	13-24	6-15	9.4 \pm 2.2	1.6	8.7	1.40
<i>Pugettia richii</i>	18-42	9-33	15.4 \pm 3.7	1.04	12.2	1.21
<i>Mimulus foliatus</i>	16-40	7-33	16.0 \pm 4.3	3.7	14.8	1.49
<i>Pugettia producta</i>	52-72	52-72	59.7 \pm 4.4	1.1	51.8	2.35
<i>Loxorhynchus crispatus</i>	74-123	52-79	66.3 \pm 6.3		22.0	

combined with crypsis (i.e., color change, color variability, and decoration) impart different adaptive advantages for minimizing predation on each of the five species. *Scyra acutifrons*, *Mimulus foliatus*, and *Pugettia richii* each have important refuges in turf interstices, kelp holdfasts, and coralline mats, respectively. *Pugettia producta* occupies the kelp canopy, which provides an effective refuge from demersal fish preying on crabs. *P. producta* and *P. richii* can change color between molts to match their substrate more closely, whereas *M. foliatus* exhibits an array of color morphs, which are adaptive for its broad range of microhabitats and would provide a visual predator with an unpredictable search image. *Loxorhynchus crispatus* does not have a major spatial refuge, but it is the most cryptic of the species and relies heavily on setal and decorating camouflage for avoiding detection by predators. Thus, microhabitat selection in coordination with differences in camouflage allow the crabs to exploit different spatial refuges and strategies for concealment from predators.

The patterns of food utilization range from *Pugettia producta*, as a strict specialist on *Macrocystis pyrifera*, to *Loxorhynchus crispatus*, as a dietary generalist. *Loxorhynchus crispatus* is an omnivorous scavenger and predator which forages opportunistically over the algal-invertebrate turf. *Scyra acutifrons* exploits the rich resource of detritus trapped in the turf. It also feeds on sponge and small pieces of *M. pyrifera*, but it does not appear to prey on worms or small crustaceans, which are also abundant in the microhabitat. Although the *M. pyrifera* diets of *P. producta*, *Pugettia richii*, and *Mimulus foliatus* are narrow, the three species utilize a food item which is the most productive and abundant in the system, both in the form of attached plants for kelp crabs and drift kelp for the bottom species. These crabs appear to capture pieces of drift kelp with a waiting strategy similar to abalones and sea urchins at HMLR (Lowry and Pearse 1974). A waiting strategy minimizes movement and would thus also minimize detection by predators. It might at first appear unlikely that *M. pyrifera* in any form could be a limiting resource. Kelp biomass and production fluctuates seasonally in HMLR, but there

is always a large standing crop available for grazers (Gerard 1976). Drift kelp in HMLR accumulates in sand channels to a large peak standing crop during summer months of low water motion, but the rate of drift production is highest in winter months, when high swells and storm activity break up the kelp canopy and transport drift out of the forest into deeper waters (Gerard 1976). However, microhabitat distributions of *P. richii* and *M. foliatus* do not correspond with drift kelp (Fig. 12), so access to the bulk of the resource may be limited during summer when there is little movement of drift kelp for waiting crabs. Moreover, close association with drift kelp may be selected against because of the increased risk of being swept out of the system by swells. Because the diets of the four bottom-dwelling species do not correlate with their substrate distribution, utilization of food resources by these species can be considered largely independent of microhabitat, as assumed for the resource axes in a multidimensional niche analysis (May 1974). For *P. producta*, however, there is little else to eat except the *M. pyrifera* it occurs on, and utilization of the resource for food is clearly dependent on its utilization for substrate.

Differences in body size have been used as a partial measure of niche separation for guilds of gastropods (Kohn 1971), spiders (Waldorf 1976, Turner and Polis 1979), lizards (Schoener 1969, 1970), salamanders (Fraser 1976), birds (Ashmole 1968), and small mammals (Grant 1972). Size differences are usually interpreted as reflecting trophic separation, especially for predators which select prey on the basis of size. However, the differences in sizes of spider crabs in the present study probably do not relate to trophic differences, because there is no correlation between body size of a species and food niche breadth, and because none of the species appears to select food on the basis of size. The relationship of body size to a size parameter of microhabitat utilization has been studied for lizards and tree perches (Schoener 1970), snails and intertidal crevices (Emerson and Faller-Fritsch 1976), and hermit crabs and snail shells (Vance 1972). In this same vein, the ability of the spider crabs to utilize crevices as refuges from predators must be directly

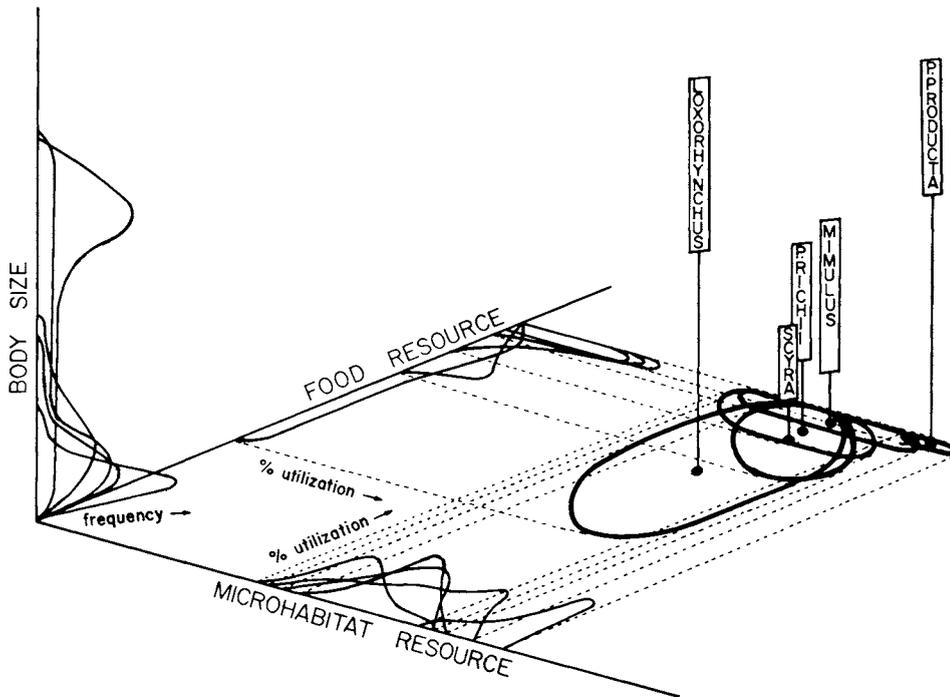


FIG. 14. A three-dimensional array illustrating niche separation of the five species of spider crabs. The two niche resource axes of microhabitat and food are combined with size-frequency distributions as a general measure of niche requirements. The size of the box containing the species names indicates the crab's size range at sexual maturity (carapace width in millimetres).

related to the size of the crabs. The three small bottom-dwelling species have different major microhabitat refuges, but *Loxorhynchus crispatus* and *Pugettia producta* do not. In addition to these major refuges, the crabs also utilize a great variety of depressions and crevices which are formed in all of the substrate surfaces, and which are difficult to quantify directly. Body size of the crabs may reflect the limits of utilization of this aspect of the microhabitat. Kohn and Nybakken (1975) used similar reasoning to relate body size of cone snails to the ability to utilize low-relief habitats lacking refuges from harsh physical conditions. Of the four bottom-dwelling species, only the *Mimulus foliatus*/*Pugettia richii* species pair show ratios of mean body size of the populations and mature females which are less than Hutchinson's (1959) predicted 1.28 value for coexistence. These two species are likely to use cracks of similar size, while other species are exploiting a different size range of crevices.

Resource partitioning by the spider crabs supports Schoener's (1974) generalization that niche separation is multidimensional, such that similar resource utilization between species for one niche dimension is complemented by dissimilarity along another dimension (Fig. 14). For example, *Pugettia producta* was very similar to *Mimulus foliatus* and *Pugettia richii* in food utilization, but it was quite distinct from the two

bottom-dwelling species in microhabitat breadth and body size. *Scyra acutifrons* and *Loxorhynchus crispatus* shared much of the same food resources and microhabitats, but they were the most disparate in size and sharply partitioned (within vs. on top of) the turf substrate. For the spider crabs, however, niche breadth for one resource does not necessarily correlate with niche breadth for another resource. For example, *Mimulus foliatus* had the greatest microhabitat niche breadth but a narrow diet, while *Pugettia producta* had the narrowest niche breadth for both resources. Moreover, the degree to which a species was a specialist vs. a generalist in utilization of a resource did not relate to the amount of niche overlap with the rest of the guild. *Mimulus foliatus* had the largest microhabitat niche breadth, and it had the greatest overall microhabitat niche overlap with the other species, but the highest overall food niche overlap occurred for *Pugettia richii*, a species with a rather specialized diet. Characterization of a species as a generalist or specialist requires a multidimensional description. Overall, *Loxorhynchus crispatus*, the largest species, clearly occupied the most generalized niche, and *Pugettia producta* had the most specialized niche.

Schoener (1974) also generalized that habitat dimensions are more important than food-related dimensions, which in turn are more important than temporal dimensions for niche separation. For the spider crabs

both habitat and food dimensions were important: microhabitat sharply separated *Pugettia producta* from the other crabs, and food separated *Scyra acutifrons* and *Loxorhynchus crispatus* from the species specializing on *Macrocystis pyrifera*. However, habitat probably is more important than the food dimension, given that much of the apparent overlap in microhabitat utilization between *S. acutifrons* and *L. crispatus* was an artifact produced by not scoring occurrence within a substrate differently from occurrence on top of the same substrate. Moreover, differences in size of the crabs probably reflected another aspect of microhabitat utilization, and the species were further segregated along habitat zones from the intertidal to the deep reef. Schoener (1974) suggests that habitat is less often the most important dimension for aquatic animals than it is for terrestrial animals. However, this definitely does not appear to be true for the few guilds of kelp forest animals which have been studied, most of which show patterns of major segregation by habitat, including bryozoans (Bernstein and Jung 1980), snails (Lowry et al. 1974), fish (Hallacher 1977, Larson 1977, 1980), and crabs in the present study. This discrepancy with Schoener's (1974) suggestion is at least in part due to his assumption of habitat homogeneity for benthic marine systems, whereas kelp forests are spatially complex. Abele (1974) surveyed a wide range of marine habitats and showed that the number of substrates is the most important factor in determining the number of species of decapod crustaceans present, and Jeffries (1966) demonstrated spatial and substrate partitioning in two species of *Cancer* crabs.

I did not attempt the difficult measurements of temporal changes in microhabitat utilization because my extensive field observations indicated that the temporal dimension is not important in niche separation of the spider crabs, either on a seasonal or a diurnal basis. This apparent similarity of temporal utilization of the environment is particularly curious considering the strongly seasonal nature of weather patterns impacting the crab populations and considering that the major species of fish preying on the crabs are active only during the day (Ebeling and Bray 1976). Why the crabs do not minimize the impact of these temporally predictable sources of mortality by, say, concentrating brooding activity in summer, or by concentrating foraging activity at night, remains an open question. Perhaps nocturnal predation by octopus balances selective pressures by daytime fish predation. Alternatively, food resources may be of such low quality, even though abundant as in the case of *Macrocystis pyrifera*, that the crabs must constantly search for and ingest food. If an individual's feeding efficiency is limiting, rather than actual resource depletion by competitors, there would be no selective pressure for temporal segregation.

Although many aspects of the patterns of resource

partitioning are understandable as adaptations for minimizing predation, the question remains whether competition is an important mechanism for maintaining the niche separation of the spider crabs. I have seen occasional intraspecific aggression between males, but I have never observed interference competition between any of the species. Crab densities may be below the carrying capacity of the environment much of the time as a result of predation and the population cycles, and carrying capacity itself may also fluctuate. May (1974) proposed that the maximum tolerable niche overlap between competing species should be relatively insensitive to environmental variability, but Wiens (1977) and others argued cogently that a fluctuating environment mitigates competition. Even though strategies of specialization vs. generalization do not necessarily reduce niche overlap for a resource, the overall niche specialization of *Pugettia producta* probably removes it from most potential competition. *Loxorhynchus crispatus* and *Scyra acutifrons* also appear to be sufficiently separate in multidimensional niche space that competition is unlikely. On the other hand, *Mimulus foliatus* and *Pugettia richii* exhibit extensive overlap in all of the niche parameters measured (Fig. 14), so exploitative competition is most likely between these two species. However, Colwell and Futuyma (1971), Dayton (1973), Connell (1975), Wiens (1977), and others have warned that neither high nor low niche overlap are accurate indicators of competition without experimental proof from controlled manipulations in the field. The problem remains that the effects of exploitative competition for, say, crevice refuges, are difficult to separate from effects of predation, and the complexities of resource utilization by the guild make it likely that any limitation of resources is multidimensional and highly unpredictable in space and time.

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