

Population effects of refuge dispersion for adult stone crabs (*Xanthidae*, *Menippe*)

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ABSTRACT: Refuge dispersion was manipulated for a hybrid stone crab population (*Menippe mercenaria* × *M. adina*) in the northeastern Gulf of Mexico. Den quality and quantity were controlled with prefabricated concrete modules (77 × 58 × 30 cm), each representing a resource (i.e. refuge) patch. Inter-patch distances differed among 3 treatments: a widely spaced, uniform patch pattern ('Wide'), an intermediate or mixed patch pattern ('Mixed'), and a closely spaced, uniform patch pattern ('Close'). Wide modules harbored significantly more crabs and larger crabs than did Mixed or Close modules. Sex ratios did not differ among treatments, but Wide modules harbored proportionately more mated pairs. Tagged crabs were not long-term residents of a single den, but crab resightings differed among treatments and were greater for females than males. We suggest that prey depletion on soft bottom is a function of refuge dispersion, and that the resulting resource mosaic determines local abundance of stone crabs, residency patterns by size and sex, and male mating success.

INTRODUCTION

For motile organisms, habitat is rarely homogeneous but rather a mosaic of resource patches in space and time, quality and abundance (Weins 1985). Such patchiness can create relative shortages of resources (Andrewartha & Browning 1961) and affect the spatio-temporal distribution and abundance of individuals within a population. Resource patchiness, for instance, is commonly considered an ecological determinant of breeding structure, or the mating system, within a population (e.g. Orians 1969, Emlen & Oring 1977). Correspondingly, patchiness of existing refuge or of habitat suitable for burrow construction affects mating prospects for several brachyuran crabs (Christy 1983, 1987, Wirtz & Diesel 1983, Abele et al. 1986, Diesel 1986a, Lindberg & Stanton 1989). Here we asked if population structure of stone crabs (genus *Menippe*) varies spatially with the dispersion of refuge patches.

For motile marine animals, conditions within habitat patches have been more readily manipulated than distances among habitat patches. Fricke (1980) altered coral patch size with consequent changes in the mating system of a damselfish, *Dascyllus marginatus*. Herr-

kind & Butler (1986) manipulated size, complexity, and prey content of natural and artificial algal patches to identify habitat preferences for settling spiny lobster postlarvae *Panulirus argus*. Similarly, habitat complexity and patch size have been tested for general population and community effects in reef-dwelling fishes (e.g. Molles 1978, Shulman 1984), and have been related to artificial reef function and design (Bohnsack 1989, Gorham & Alevizon 1989, Hixon & Beets 1989). Inter-patch distance has been manipulated mostly for fishes in the context of island biogeography theory and recruitment processes, specifically with respect to the proximity of patch reefs to large reef tracts or source pools (Molles 1978, Shulman 1985, Walsh 1985). Questions of relevant spatial scales have been raised for many studies of reef fish (see Ogden & Ebersole 1981, Sale et al. 1984).

Adult stone crabs, like other den-dwelling invertebrates such as *Homarus americanus* (Cobb 1971, Sheehy 1976, Ennis 1983, 1984a, b), *Panulirus argus* (Herrkind et al. 1975, Davis 1978), and *Octopus* spp. (Hartwick et al. 1984, Aronson 1986), are well suited for moderately large-scale field manipulations of resource patchiness because, in particular, their refuge can be identified, altered, or supplemented. South Florida stone crabs *Menippe mercenaria* occur subtidally where adults dwell in cavities of small rock outcrop-

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pings, excavate under hard substrata, or burrow into sand consolidated by seagrasses (Bert et al. 1978, pers. obs.). In mixed rock/seagrass habitats, Bert (1985) observed that males tended to occupy rock outcroppings while females occupied surrounding seagrass burrows. Northern Gulf of Mexico stone crabs *M. adina* (Williams & Felder 1986) burrow in intertidal oyster bars and subtidal consolidated mud (Powell & Gunter 1968, Perry et al. 1984, T. Bert pers. comm.).

A hybrid zone between these species extends in the northeastern Gulf of Mexico from about Apalachicola Bay to the Cedar Keys, Florida (Bert 1986, Williams & Felder 1986, Bert & Harrison 1988). At the northern end of this zone, Wilber (1989a) found partial habitat segregation, with *Menippe adina* and intermediate phenotypes predominating in intertidal oyster habitat, and equal proportions of phenotypes subtidally. We concentrate here on subtidal hard-bottom refuge at the southern end of the *Menippe* hybrid zone.

Given that stone crabs aggressively defend refuges (Sinclair 1977) where males sequester their mates (Savage 1971), and given that resource patchiness and defensibility are prime components of mating system models (e.g. Emlen & Oring 1977), one might expect refuge-defense polygyny (Christy 1987) to be manifested under favorable conditions of patch dispersion.

However, male stone crabs are more transient than females (Wilber 1989a) and engage in protracted mate guarding that is lengthened by the presence of competing males (Wilber 1989b). These factors suggest a female-centered, search-and-defend male mating strategy (Christy 1987, D. Wilber pers. comm.). With a pure refuge defense strategy, manipulations of refuge patch dispersion should yield clear differences in local population structure, i.e. predictable patterns of crab distribution, size and sex ratio. In contrast, a pure search-and-defend strategy should manifest no such treatment effects on these parameters. As a consequence of the coarse-scale sampling of treatment plots reported here, we suggest that stone crabs employ either a flexible search-and-defend or a patrol-and-defend (Christy 1987) mating strategy in which the male searching phase, and perhaps home ranging, is modified by the mosaic of refuge and food resources.

MATERIALS AND METHODS

Our study site was located in the northeastern Gulf of Mexico ca 16 km west of the University of Florida Marine Laboratory at Seahorse Key, Cedar Key, Florida (Fig. 1). Mean low water depth was 6.7 m and the

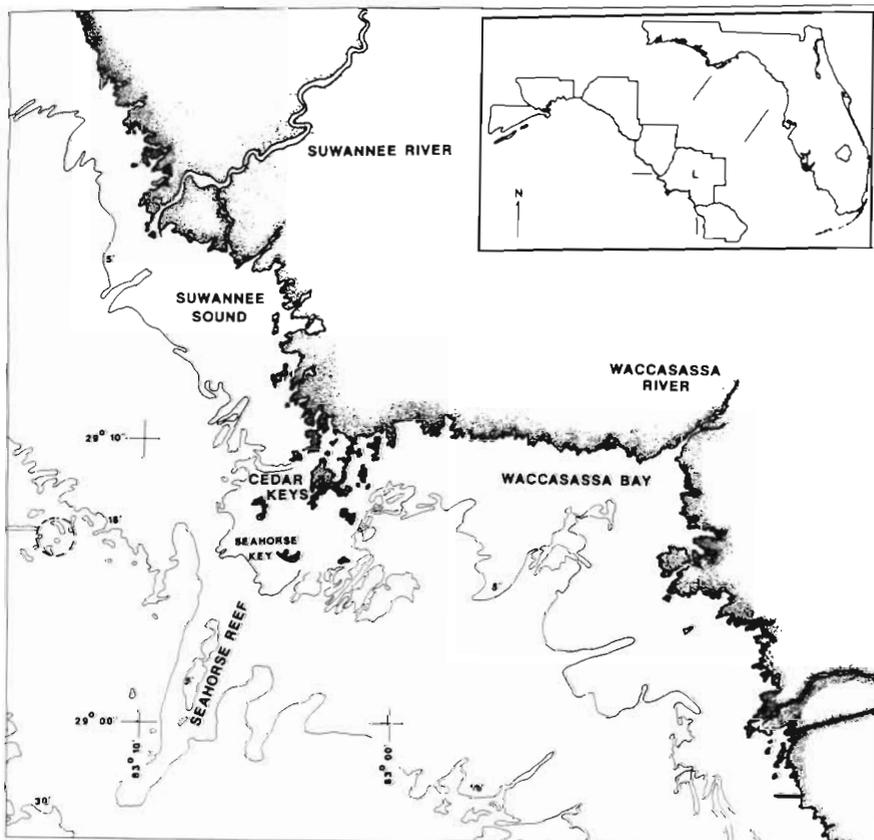


Fig. 1. Study site (dashed circle) west of the Cedar Keys, Levy County, Florida, USA. Insert shows position of Levy County (L) within approximate boundaries of the northeastern Gulf of Mexico *Menippe* hybrid zone

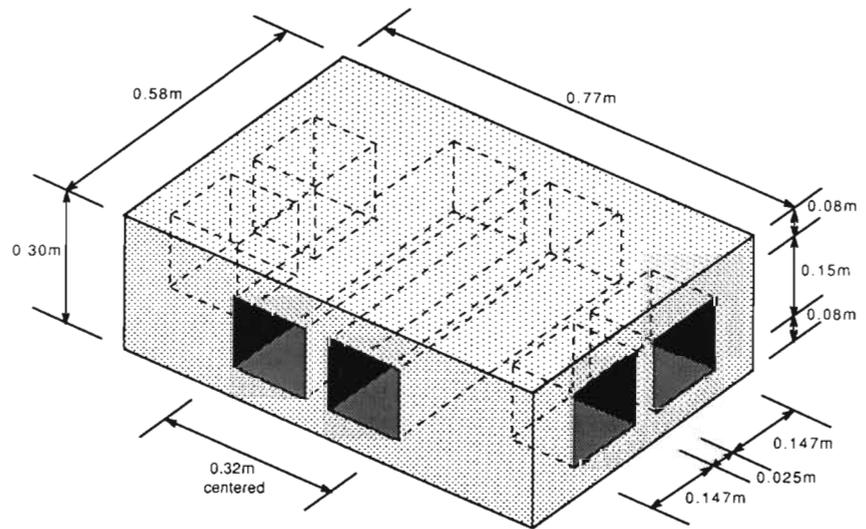


Fig. 2. Dimensions of stone crab modules used to control den quality while manipulating dispersion of den patches. Each end has 2 blind holes while holes in long sides are open-ended, for a total of 6 dens per module

bottom was sand/shell veneer overlying limestone bedrock.

Individual artificial reef modules simulated patches of aggregated, high-quality dens. Modules were fabricated from standard, 2-holed, concrete construction blocks ($20 \times 20 \times 40$ cm) embedded in reinforced concrete (Fig. 2). Each was calculated to weigh ca 77 kg in seawater and, by design, settled into the sand until den floors were even with the substratum. Earlier surveys of stone crabs in pre-existing artificial reefs showed that 50 of 63 total crabs occupied shallow dens excavated in sand under solid materials, while preliminary field tests indicated that stone crabs prefer horizontal cavities approximately level with the substratum as opposed to other configurations (Lindberg unpubl.). Extensive bottom surveys, within ca 12 km^2 surrounding the study site, revealed only sparse natural rock outcroppings smaller than one module, while throughout a broader area larger rock outcroppings rarely had more than one den per outcropping.

Treatment plots containing 36 modules each were interspersed within the 108 ha study site (Fig. 3). Modules were deposited by tug and barge in late August 1986, and were deployed by SCUBA divers using lift bags during the remaining summer, early fall, and subsequent summer. The manipulated independent variable was average inter-patch distance, resulting in 3 spatial patterns. A widely spaced, uniform patch pattern (hereafter 'Wide') had individual modules located in a grid at ca 60 m intervals. This distance corresponds to estimates of average net daily movements for free-ranging adult stone crabs (Bender 1971, Sullivan 1979). From laboratory studies Wilber & Herrnkind (1986) estimated the potential distance travelled daily by adult males to be greater than 200 m. At the other extreme, a closely spaced, uniform patch pattern ('Close') had all 36 modules/plot in a grid with

ca 2 m between module edges. As such, the distance around all modules in a Close plot approximated the distance between adjacent modules in a Wide plot. Plots of the intermediate or mixed patch pattern ('Mixed') contained 6 clusters of 6 modules each: Within a cluster, modules were ca 2 m apart, edge-to-edge; between clusters, the distance was at least 60 m, i.e. similar to the distance between Wide modules.

Modules were convenient sampling units per plot because occupancy was unambiguous, and the pre-

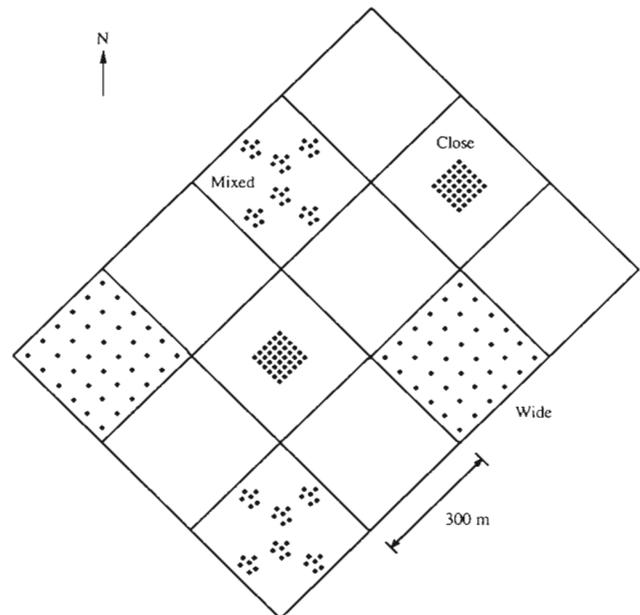


Fig. 3. Schematic for study site depicting interspersions of treatment plots and relative positions of 36 modules per plot. Each plot was 300×300 m, measured along nearly perpendicular LORAN C lines. Neither the modules nor the distances between them are drawn to scale

sence of one crab did not automatically preclude conspecifics from that or other modules.

Two non-destructive sampling strategies, exhaustive and subsampling, were employed during a period in the stone crab reproductive cycle when females molt and mate following their late summer release of larvae (Bert et al. 1986, Wilber 1989a). Exhaustive sampling was conducted during late August and early October, 1987 and 1988, and involved censusing all 36 modules on a plot in the shortest time possible ($\frac{1}{2}$ to 3 d plot⁻¹). Thus, only one plot per treatment could be censused within a week, but the same 3 plots were used for all exhaustive sampling periods. Subsampling was conducted during the weeks immediately following 1987 exhaustive sampling periods, and involved censusing 6 randomly selected modules per plot per week for all 6 treatment plots, i.e. $n = 12$ modules per treatment per week.

To census crabs in a module, paired SCUBA divers inspected each cavity visually or by touch. Stone crabs were pulled carefully from their dens by hand, and the following data were recorded: module identification, den identification, sex (if female, whether ovigerous or not), carapace width, right and left chela propodus lengths, side with crushing claw, and phenotypic characters scored according to Bert & Harrison (1988) for carapace color, claw color, carapace markings, claw markings, leg color, and leg banding. Measurements were taken to the nearest mm with plastic vernier calipers. A uniquely color-coded rubber band tag (Ennis 1984a) was then placed over the crusher claw merus, or cutter if crusher was missing, and the crab was returned to its original den. The 49 crabs on the Mixed plot during August 1987 exhaustive sampling were not tagged due to lack of time. If a crab found in a den had been previously tagged, it was disturbed only to the extent necessary to record its tag code and location. If a soft post-molt female was found, as much information as possible was gathered without handling her. Occasionally (<5% of observations), crabs seen under modules could not be extracted, but these were almost always from sub-adult size classes.

Statistical analyses were performed using PC-SAS Version 6 (SAS Institute Inc. 1985), except for hand-calculated G-tests. Parallel analyses were conducted for occupancy and crab size data collected during September and October subsampling periods. Occupancy data were square-root transformed to stabilize variance, and then tested by a split-plot design analysis of variance. Blocks were the southwestern and northeastern replicate plots while treatments were the sampling week and module spatial pattern (i.e. Wide, Mixed and Close). Sampling week was never significant ($p > 0.05$), nor was the block effect for September. For October, a significant block \times spatial pattern inter-

action required the final 1-way ANOVA with contrasts to be conducted by blocks. Crab size (mm carapace width) data collected during subsampling periods were also tested by a split-plot design analysis of variance; however, no transformations were necessary. Neither block nor sampling week effects were significant, so 1-way ANOVA's for spatial treatment effects are reported.

Occupancy data collected during August and October exhaustive sampling periods could not be transformed to satisfy parametric assumptions, so Kruskal-Wallis tests with chi-square approximations were conducted with Wilcoxon tests as follow-up. Crab sizes for each exhaustive sampling period were tested for treatment effects by 1-way ANOVA.

Sex ratios (f/m) could not be tested directly because one sex or the other was often absent from a module. Instead, the proportions of female crabs per occupied module (f/total on module) were tested for treatment effects.

RESULTS

Phenotypically, the stone crabs inhabiting experimental plots were predominantly intermediate and *Menippe mercenaria*-like hybrids (Fig. 4) and did not differ among treatments (ANOVA: $F = 0.24$, $df = 2$, $p = 0.79$). Twenty-eight mated pairs were observed, but only 32 mated individuals and 12 complete male-female pairs could be phenotypically scored because soft post-molt females, and sometimes their guarding males, could not be safely extracted from refuge. The 32 individuals proportionately represented the phenotype categories in Fig. 4 (Chi-square test: $\chi^2 = 9.18$, $df = 4$, $p > 0.05$). Too few complete pairs were

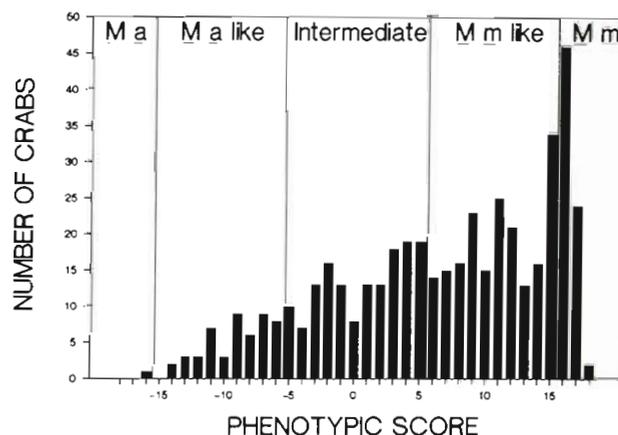


Fig. 4. *Menippe* spp. Frequency distribution of phenotypic indices (after Bert & Harrison 1988) obtained for all crabs sampled. *M a* and *M m* represent phenotypes of pure *M. adina* and *M. mercenaria*, respectively. Intermediate, *M a*-like and *M m*-like represent hybrid and backcrossed phenotypes

scored to test whether observed phenotype combinations differed from those expected by chance alone. However, the phenotype scores within male-female pairs ($n = 12$) were not correlated (Pearson's product moment: $r = 0.13$, $p = 0.68$).

The distribution of male-female pairs among treatment plots (Table 1) was proportional to the overall distribution of females ($G = 4.12$, $df = 2$, $p < 0.10$). However, significantly more pairs were found on Wide plots than would be expected from the overall distribution of males ($G = 6.34$, $df = 2$, $p < 0.05$).

Of the 511 crabs tagged and returned to their original dens during 1987 sampling periods, 75 (14.7%) were resighted at least once (Table 2). Of those, 15 (2.9%) were resighted twice, and 5 (1.0%) 3 times or more. Of the resighted crabs, 80% had changed modules but only 15% had changed plots. Females were resighted more often than males (goodness-of-fit G-test: $G = 6.08$, $df = 1$, $p < 0.025$). Dispersion of refuge patches affected the likelihood of resightings for both females ($G = 11.48$, $df = 2$, $p < 0.005$) and males ($G = 9.44$, $df = 2$, $p < 0.01$), with Close plots retaining more crabs than expected by chance and Wide plots retaining fewer. The average time at large between resightings was 19 d ($n = 101$ resightings, $SD = 25.11$ d). However, the average sampling interval for a given plot was 11.4 d ($SD = 6.01$), and only 6 of 36 modules per plot were censused during subsampling weeks. Eleven tags returned by commercial crabbers indicated net movements on the order of 10 to 12 km after up to 62 d at

large, but with no evident directional dispersal from the study site.

For all sampling periods, occupancy rates (crabs per module) were greatest on Wide plots, least on Close plots and intermediate on Mixed plots (Fig. 5, Table 3). In 1987, occupancy of the exhaustively sampled Wide plot was greater in August than in October (Kruskal-Wallis chi-square approximation: $\chi^2 = 9.40$, $df = 1$, $p = 0.002$), while neither Mixed nor Close plots differed over the same interval ($p > 0.25$). No crabs occupied plots during October 1988. Regression analysis of average occupancy rate versus subsampling week was not significant for Wide or Close plots ($p = 0.297$ and $p = 0.270$, respectively), but was significant for Mixed plots ($p = 0.01$, $Y = 0.15X + 0.88$) with r^2 only 0.069.

The differences in occupancy rates among treatments might be attributed more to females than to males (Fig. 6). In the 1987 exhaustive samples, male occupancy did not differ among plots while female occupancy differed greatly (Table 4). Both male and female occupancy differed significantly for the remaining sampling periods (Table 4), with a block effect in October 1987 subsampling data. Despite a seemingly greater effect on females than males, the proportion of crabs per occupied module that were female did not differ among treatments, except for the September 1987 subsampling period (Kruskal-Wallis test with chi-square approximation: $\chi^2 = 6.35$, $df = 2$, $p = 0.04$), when Wide = Mixed > Close (Wilcoxon tests, $p \leq 0.03$ for inequality).

Crab sizes were generally, but not always, greater from Wide and Mixed plots than from Close plots (Table 5, Fig. 7). Furthermore, the differences in mean crab size between Wide and Close plots, when significant differences existed, were apparently greater for males than for females (Fig. 7).

Table 1. *Menippe* hybrids. Distribution of mated pairs among treatments relative to the overall distributions of males and females

	Wide	Mixed	Close
No. of male-female pairs	19	6	3
Total no. of females	205	127	85
Total no. of males	115	62	69

Table 2. *Menippe* hybrids. Distribution of crab resightings by treatment and sex

	Wide	Mixed	Close	Total
Females				
No. tagged	181	72	60	313
No. resighted	22	13	21	56
on same plot	20	9	19	48
on same module	9	2	1	12
Males:				
No. tagged	107	41	50	198
No. resighted	5	3	11	19
on same plot	4	2	10	16
on same module	1	1	1	3

DISCUSSION

The dispersion of refuge patches affected local population structure of adult stone crabs, but the treatments also differed in crab densities or occupancy rates. The more widely spaced patches supported more crabs per unit reef. Four hypotheses potentially explain these differences: (1) a chance encounter hypothesis – rates of immigration into patches are lower for the more concentrated patches; (2) an agonistic hypothesis – rates of socially induced emigration from patches are inversely related to patch dispersion; (3) a predation hypothesis – rates of predator-induced emigration or mortality are inversely related to patch dispersion; and (4) a resource mosaic hypothesis – as refuge dispersion decreases, so too does access to prey on the soft bottom that surrounds such refuge. Shulman (1984) manipu-

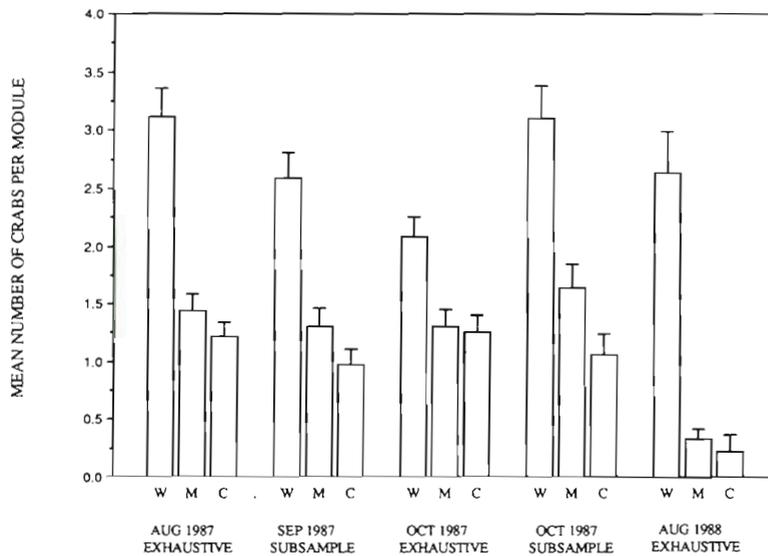


Fig. 5. *Menippe* hybrids. Average occupancy rates (\pm SE) of crabs on modules, by treatment for all sampling periods. Treatments are: Wide (W) = widely spaced, uniform patch pattern; Mixed (M) = intermediate or mixed patch pattern; Close (C) = closely spaced, uniform patch pattern. N = 36 for exhaustive sampling periods and 12 for subsampling periods

Table 3. *Menippe* hybrids. Effects of 3 refuge dispersion treatments on stone crab occupancy rates during exhaustive sampling and subsampling periods

Exhaustive sampling period	Kruskal-Wallis tests ^a		Wilcoxon pairwise comparisons ^b
	χ^2 (df = 2)	p	
Aug 1987	37.89	0.0001	Wide > Mixed = Close
Oct 1987	14.83	0.0006	Wide > Mixed = Close
Aug 1988	58.25	0.0001	Wide > Mixed = Close
One-way ANOVA's (df = 2) with contrasts following split-plot design			
Subsampling period	F	p	Contrasts ^c
Sep 1987	20.94	0.0001	Wide > Mixed = Close
Oct 1987			
SW block	41.39	0.0001	Wide = Mixed > Close
NE block	10.24	0.0002	Wide > Mixed > Close

^a SAS Kruskal-Wallis tests with chi-square approximations
^b p < 0.001 for all inequalities
^c p < 0.04 for all inequalities

lated refuge density and observed similar density patterns for juvenile reef fish, for which she posited hypotheses tantamount to (1) and (2). Although the 4 hypotheses are not mutually exclusive, our observed differences in stone crab population structure currently lead us to favor the resource mosaic hypothesis (4), in combination with mating strategies.

If one assumes that crabs immigrate into resource patches, like our study plots, by more or less straight-line ranging (e.g. *Panulirus argus*; Herrnkind et al. 1975), or even by random walks, then the probabilities of encountering modules would depend upon module dispersion. Chance alone should result in more crabs encountering Wide modules, because Wide modules occupy the greatest arc in the horizontal plane in which crabs move. If residency time after encounter with a

module is negligible, i.e. occupancy reflects only immigration, then differences in occupancy rates on the order we observed could be explained by the chance encounter hypothesis only with adequate migration rates through plots. At the other extreme, if residency time after encounter with a module is prolonged, then modules would become nearly saturated over time, and inherent differences in encounter rates would not be reflected in occupancy rates. Resighted crabs were generally found on their original plots, although most crabs in subsamples after exhaustive sampling were untagged, presumably new immigrants. The chance encounter hypothesis is impugned, although not totally eliminated, because this mechanism cannot also explain observed treatment effects on male and female crab sizes.

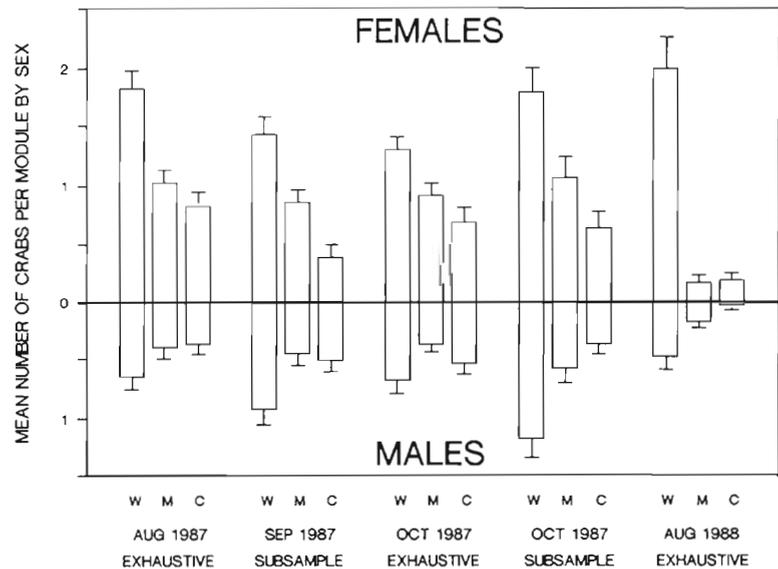


Fig. 6. *Menippe* hybrids. Average occupancy rates (\pm SE) of males and females on modules, by treatment for all sampling periods. (Abbreviations and sample sizes as in Fig. 5)

Short inter-patch distances in Mixed and Close plots, as compared to Wide plots, should result in greater encounter rates among crabs. Increased encounter rates under (2), the agonistic hypothesis, should increase the emigration of losers or subordinates (Lindberg & Frydenborg 1980). Asymmetries in size, sex and residency contribute to dominance in stone crabs; larger crabs, males, and residents have the advantage (Sinclair 1977). Conceivably, emigration yielding lower occupancy rates could occur in equilibrium with immigration, such that encounter rates in Mixed and Close treatments are maintained on a par with that of

Wide. If that were the case, however, we should observe large crabs and a reasonable number of males, i.e. more dominant individuals, remaining on these plots – which is the opposite of what we actually found.

By the same token, the more closely spaced patches could favor aggregation of predators and result in higher rates of induced crab emigration and mortality, i.e. the predation hypothesis (3). For this to underlie observed patterns of stone crab abundance and local population structure, large crabs would have to be most susceptible to predation or most inclined to emigrate, as large crabs of both sexes were under-represented in

Table 4. *Menippe* hybrids. Effects of 3 refuge dispersion treatments on male and female occupancy rates during exhaustive sampling and subsampling periods

Exhaustive sampling period	Sex (n)	Kruskal-Wallis tests ^a		Wilcoxon pairwise comparisons ^b
		χ^2 (df = 2)	p	
Aug 1987	M (50)	4.48	> 0.05	Wide > Mixed = Close
	F (133)	21.94	0.0001	
Oct 1987	M (56)	3.22	> 0.05	Wide > Mixed = Close
	F (105)	11.24	0.0036	
Aug 1988	M (24)	15.45	0.004	Wide > Mixed > Close
	F (86)	53.96	0.0001	
One-way ANOVA's (df = 2) with contrasts following split-plot design				
Subsampling period	Sex (n)	F	p	Contrasts ^b
Sep 1987	M (67)	3.57	0.03	Wide > Mixed = Close
	F (97)	20.6	0.0001	
Oct 1987 SW block	M (28)	17.98	0.0001	Wide = Mixed > Close
	F (37)	13.51	0.0001	
NE block	M (37)	9.40	0.0003	Mixed > Wide = Close
	F (72)	3.62	0.034	

^a Kruskal-Wallis tests with chi-square approximations

^b $p < 0.05$ for all inequalities

Table 5. *Menippe* hybrids. Effects of 3 refuge dispersion treatments on male and female sizes, i.e. carapace widths

	Sex (n)	One-way ANOVA		Scheffé's pairwise comparisons ^a
		F	p	
Exhaustive sampling period				
Aug 1987	M (50)	10.21	0.0002	Wide = Mixed ≥ Close Wide = Mixed > Close
	F (133)	6.43	0.002	
Oct 1987	M (56)	3.15	> 0.05	Wide = Mixed > Close
	F (105)	7.87	0.0007	
Aug 1988	M (24)	0.51	> 0.05	Wide > Mixed > Close
	F (85)	1.13	> 0.05	
Subsampling periods				
Sep 1987	M (67)	4.16	0.02	Follow-ups NS
	F (95)	0.46	> 0.05	
Oct 1987	M (64)	2.33	> 0.05	Wide > Mixed > Close
	F (106)	17.05	0.0001	

^a p < 0.05 for all inequalities

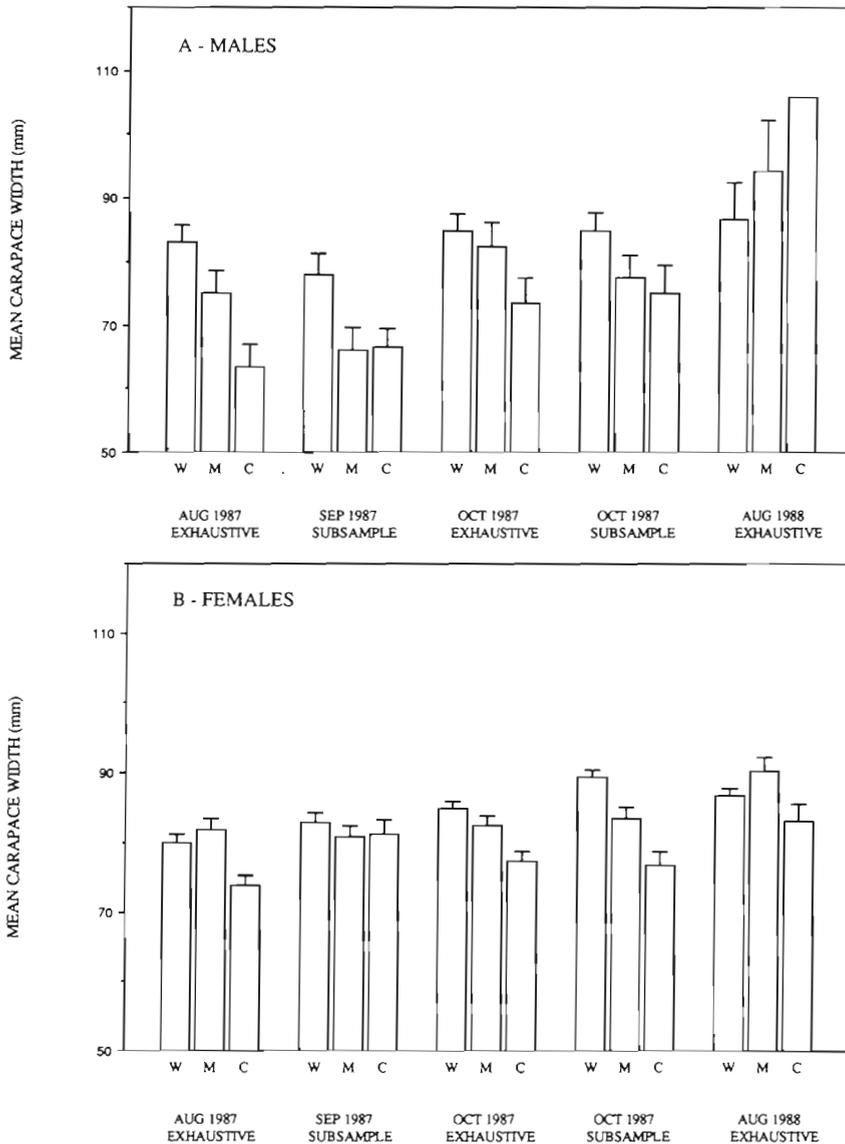


Fig. 7. *Menippe* hybrids. Average sizes (\pm SE) of (A) male and (B) female stone crabs from each treatment during all sampling periods. (Sample sizes listed in Table 5)

Close modules. Lindberg & Stanton (1989), however, found that the larger males of another xanthid expressed higher rates of refuge exchanges within groups than did smaller males and females, and furthermore, size did not matter in the rate of exchanges for females. If the same applies to stone crabs, then the predation hypothesis might explain the deficit of larger males on Close plots, but would not explain the deficit of larger females.

Moreover, the species which regularly occupy modules, and which might prey upon or induce emigration of stone crabs (including *Octopus vulgaris*), are the same among treatment plots, and their density patterns parallel those reported here for stone crabs (T. Frazer et al. unpubl.). The disappearance of stone crabs from all reef plots during the fall of 1988 might, in fact, be attributable to increased numbers of octopus throughout the study site (Lindberg et al. in press, T. Frazer et al. unpubl.).

Halos of relatively barren sand commonly surround reef structure as a consequence of consumers radiating out from their refuge to forage (Ogden et al. 1973, Davis et al. 1982); this mechanism is the basis for (4) the resource mosaic hypothesis. Stone crabs radiate from dens to prey upon bivalves, gastropods, echinoderms, and annelids (pers. obs.). One can easily envision concentric rings or 'isotrophs' of decreasing predation by crabs and increasing density of prey as a function of distance from dens. For an isolated single den occupied by a single crab, the gradient between isotrophs should be relatively steep compared to an aggregated patch of dens occupied by several crabs, like our Wide modules. However, as the inter-patch distance decreases, isotrophs from adjacent patches would overlap, further depressing prey numbers and necessitating greater foraging distances for stone crabs. Foraging movements directed away from depressed inter-patch areas might also be expected. Sampled prey densities do, in fact, increase with distance from our modules, and density gradients differ between Wide and Close modules (Frazer et al. unpubl.). In our current view, the mosaic of resources contributes to differing resource values of otherwise equivalent dens, and the dispersion of dens or den patches, in turn, helps structure the mosaic through actions of den occupants.

This resource mosaic, coupled with chance encounters and induced movements, should also yield a greater overall reproductive output by crabs occupying widely spaced reef modules. These modules harbored more and larger females than did other treatments, and larger females are more fecund (McRae 1950, Hines 1982). Stone crabs also exhibit size assortative mating with the males larger than their mates (Wilber 1989a), and larger males were found on Wide plots. As would be expected, the greater number of mated pairs from

the Wide treatment was proportional to the number of females but not to the number of males.

Consequently, our results suggest that resource dispersion also affects the expression of stone crab mating strategies and tactics (sensu Wootton 1984) which are not fully known. Large male stone crabs can obtain mates through take-overs and ensure their paternity through post-copulatory mate guarding (Wilber 1989b). Smaller males might also defer summer mating opportunities while molting to more competitive sizes in habitats less suited to reproduction (Wilber 1989a). An encounter rate competition strategy for males (sensu Christy 1987) is precluded by their protracted mate guarding (Savage 1971, Wilber 1989b). Likewise, purely resource centered, breeding site or refuge defense strategies (sensu Christy 1987; e.g. Christy 1983, Abele et al. 1986), which require defense of exclusive dens or territories, would not apply to stone crabs given joint occupancy of modules by more than one male and occasionally more than one pair, and low male den fidelity indicated by tag resightings (herein, and Wilber 1989a). Among the 4 remaining female-centered male strategies categorized by Christy (1987), neither the capture-and-defend nor the attract-and-defend strategies match Wilber's (1989b) description of pair formation observed in the laboratory. The questions, then, are whether male stone crabs engage in a pure search-and-defend or a patrol-and-defend strategy, and do females invoke male competition or choose among males?

When the mosaic of food and refuge is favorable, as it apparently was on Wide plots, we suggest that home ranging occurs for both sexes, with several dens occupied over time. Female den exchanges should be less frequent and home ranges smaller than those of males. Smaller, subordinate crabs, particularly males, should be induced to emigrate by repeated encounters with larger crabs. In this respect, stone crab strategies might include an element of resource-centered competition. Female stone crabs are not known to broadcast sexual receptivity as do portunid crabs, cited as examples of the search-and-defend strategy (Christy 1987). Nevertheless, if pair formation depends entirely on chance encounters among prospective mates, then one could consider the male strategy to be search-and-defend. On the other hand, if males recognize differences in female molt stages or impending receptivity within their home ranges, and direct their movements accordingly, then the patrol-and-defend strategy would apply (e.g. Diesel 1986a, b). In either case, the probability of mating encounters would be increased by greater crab densities and circumscribed movements induced by a combination of quality refuge patches and accessibility to prey.

A subsequent data set from these same plots (Frazer

et al. unpubl.) includes an example of the largest male on a Wide plot remaining there for at least 9 consecutive months, 10 resightings with females, and repeated occupancy of the same modules on opposite sides of the plot. The scenario above is credible, but will require intensive, fine resolution monitoring of movement and mating patterns, along with manipulations, to distinguish between a patrol-and-defend or search-and-defend strategy.

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