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Permeability of patch boundaries to benthic invertebrates: influences of boundary contrast, light level, and faunal density and mobility

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Abstract

This study empirically examines predictions concerning boundary permeability as a function of patch contrast (i.e., the magnitude of difference in measures across patch interfaces), light level, and faunal mobility and density, as well as relative rates of emigration and immigration. I assessed permeability using invertebrate transfer in a macroalgal-seagrass-sand landscape, with particular emphasis on the caridean shrimp *Thor floridanus*. Proportional emigration was estimated by staining algal fauna *in situ* using neutral red (a live immersion stain) and then later collecting all animals in the algal clumps and in the surrounding sand or seagrass. Permeability was in part a function of boundary contrast in this milieu; macroalgal patches were more of a closed system in sand than in seagrass. Contrary to predictions, proportional emigration across both the algal-seagrass and algal-sand boundaries was inversely related to faunal density. Another unexpected result was that the rate of change in emigration with increasing density was unaffected by differential contrast among habitat types. The observed enhanced permeability for more motile fauna was consistent with predictions. A related finding was that permeability was greater at night than during the day, probably as a function of increased nocturnal vagility of benthic fauna. Emigration was not in equilibrium with immigration at the temporal scale of this study (hours) for the majority of species tested. Emigration-immigration disequilibria should be most likely when the temporal scale is small, and in such cases caution should be exercised when extrapolating from one transfer parameter to the other.

Introduction

Most animals live within a mosaic of habitat patches, and the barrier posed by patch boundaries for mobile fauna is variable. Absolute boundaries barring all exchange probably do not exist (Wiens 1992). Literal islands, i.e., emergent land masses that are surrounded by water, lie towards the more isolated end of the insularity spectrum, at least for terrestrial organisms. Such isolates have "hard edges" (Stamps et al. 1987) or low "permeability" (Wiens et al. 1985). However, in other cases individuals of a given species may cross a boundary easily (a soft edge or highly permeable boundary). The level of relative patch isolation along this continuum is important, because individual space use is linked to population and metapopulation dynamics (Kareiva 1990, Wiens 1992, Wiens et al. 1993): random effects on recruitment, persistence, and mortality increase with increasing insularity (Sebens 1991). Further, Gilbert (1980), Stamps et al. (1987), and Burgess (1988) point out that predictions about animal movement derived from studies of systems with low permeability boundaries, for instance island biogeographic theory (MacArthur and Wilson 1967), may translate poorly into mosaics with high permeability boundaries. Several theoretical studies have developed predictions concerning boundary characteristics and associated emi-/immigration (Wiens et al. 1985, 1993, Stamps et al. 1987, Wiens 1992), and some recent reports have examined animal movement patterns in heterogeneous landscapes (e.g. Crist et al. 1992, Johnson et al. 1992, With 1994, Wiens et al. 1995, Crowe 1996). Tests of hypotheses about mosaic structure remain rare, however (Wiens 1995); the present study offers an empirical examination of predictions concerning boundary permeability as a function of contrast (*sensu* Kotliar and Wiens 1990, Hansen et al. 1992), light level, organism mobility and density, and emigration-immigration equilibria in a benthic marine mosaic.

Several authors (e.g. Bell and Hicks 1991, McNeill and Fairweather 1993, Robbins and Bell 1994, Irlandi et al. 1995) have called attention to the utility of seagrass systems for investigation of landscape processes. My work examines exchange of invertebrates (with emphasis on a dominant caridean shrimp, *Thor floridanus*) in a microlandscape consisting of discrete macroalgal clumps (*Laurencia* spp.) isolated in seagrass (*Thalassia testudinum*) and sand habitats. The macroalgae, seagrass, and sand components have high, intermediate, and low structural complexities (*sensu* McCoy and Bell 1991), respectively. The three substrata have the same rank order with regard to species richness and overall abundance of benthic fauna (Holmquist 1992); this rank order for fauna is consistent with findings from various sand-seagrass (e.g. Summerson and Peterson 1984, Wells et al. 1985) and seagrass-macroalgal (e.g. Lewis 1987, Holmquist in press) comparisons. Microlandscapes such as this system can serve as tractable testbeds for landscape hypotheses (Ims and Stenseth 1989, Turner 1989, Wiens et al. 1993).

Animals that move through a heterogeneous environment are likely to behave differently than those moving through homogeneous terrain (Foster and Gaines 1991); a corollary is that permeability of a patch boundary should be a function of the nature of the surrounding habitat (Janzen 1983, Kareiva 1983, Stamps et al. 1987). Boundary permeability may thus be a function of "contrast", i.e., the magnitude of difference in measures across patch interfaces (Kotliar and Wiens 1990, Hansen et al. 1992, Wiens et al. 1993). Macroalgae is more comparable to seagrass than sand in terms of complexity and potential refuge quality (e.g. Coen et al. 1981, Leber 1985) for small moving fauna. In addition to differences in complexity, the vertical dimension (Forman and Moore 1992) of the macroalgal-seagrass boundary is less than that of the macroalgal-sand boundary, because the macroalgae settle among the grassblades but rest

high above the surrounding habitat in sand. The macroalgal-seagrass boundary was of lower contrast than the macroalgal-sand boundary, and my first objective was a test of the hypothesis that permeability of the macroalgal boundaries would be higher in seagrass than sand.

Wiens et al. (1985) suggest that inter-patch transfer of animals should be density-dependent and more specifically that the rate of transfer should increase roughly exponentially with increasing density. They also suggest that the curve defining this increase in exchange as a function of density should have a greater slope for higher than for lower permeability boundaries. Testing these predictions was the second goal of the study.

Relatively sedentary organisms should be less likely to encounter boundaries than more motile fauna (Wiens et al. 1985, Wiens 1992). Further, more slowly-moving organisms may be more likely to perceive boundaries than are more vagile species (Kareiva 1982, Wiens et al. 1985, 1993, Wiens 1992, With 1994). The third aspect of this work was a comparison of inter-patch transfer for fauna known *a priori* to be relatively motile (caridean shrimp) versus more sedentary animals (molluscs and ophiuroids).

Invertebrates associated with benthic vegetation are generally more active at night (Brawley 1992), and the seagrass-algal fauna is no exception (e.g. Stoner 1980, Bauer 1985). Heck (1977) and Howard (1987), among others, have warned of the dangers of assuming that faunal assemblages of seagrass meadows documented during daylight are representative of the entire diel cycle. I hypothesized that boundary permeabilities should be higher in darkness than in daylight due to increased activity of most fauna at night, and a test of this hypothesis was my fourth objective.

Dempster et al. (1995a) note that the assumption of equivalent emigration and immigration may be flawed in many cases. Indeed, attempts to

determine reciprocal replacement of fauna based only on immigration data necessitates an assumption of equilibrium over a very short period of time, and conclusions concerning reciprocal interchange may not be warranted on a given temporal scale. The final goal of this work was a test of the null hypothesis of transfer equilibrium over a short time period.

Emigration can be used as a quantitative measure of permeability (Stamps et al. 1987), and the present paper examines emigration from algal clumps into the ambient seagrass or sand. My emigration estimates combine elements of both probability of boundary encounter and boundary crossing (Wiens 1992). These measures were generated by staining organisms *in situ* to provide a baseline against which cross-boundary transfer of animals could be judged (see Dempster et al. 1995b for a related approach using an insect system).

Methods

Study Area

Most field work was performed in a 250 square kilometer area (centered around 24° 53' N, 80° 50' W) of sand and seagrass habitats in southwestern Florida Bay, Florida, USA, near Long Key. The seagrass meadows are composed of *Thalassia testudinum* (turtle grass), *Halodule wrightii* (shoal grass), and *Syringodium filiforme* (manatee grass) but are dominated by the former species (area description in Holmquist et al. 1989a, b, Holmquist 1994, in press). Macroalgae occur year-round in both seagrass and sand habitats; *Laurencia poiteaui* is the most common species (mean size of clumps about 25 cm diameter). I also did field and lab tests of the faunal staining technique at the Florida State University Marine Laboratory (Florida panhandle, USA) and at the University of Puerto Rico's Isla Magueyes Laboratory (La Parguera, Puerto Rico, USA).

Field Work

I cast the core mensurative experiment as a 2 x 2 completely randomized factorial design (Factor 1= ambient habitat: sand or seagrass; Factor 2= light level: day or night). Thirty-two stations (sixteen in sand, sixteen in seagrass; one 25 cm-diameter clump of algae per station) were randomly chosen from the area described above, excluding shallow mudbanks, and apportioned among the four treatments. Each of the eight replicates consisted of one of each of the four treatments, and replicates were performed one month apart, i.e., the first in March, the next in April, etc. McClenaghan and Gaines (1976), Krebs (1992), and others argue that proportions, instead of numbers, of dispersers should be used as response variables when dispersal as a function of density is of interest and/or when the range of population densities is great. Both of these conditions obtained, and I estimated proportional emigration from macroalgae using a modification (Holmquist 1992, 1994) of an *in situ*, live-staining technique developed by Howard (1985, see also Edgar 1992). Howard's procedure involves the staining of a given area, sampling the area after a specified period of time, and determining the number of stained organisms (those that did not emigrate from the stained area) and unstained organisms (immigrants to the stained area). Because I wished to know the density of organisms originally present in the algal masses, I stained algal clumps and their associated fauna, but then later sampled the surrounding habitat as well as the algae. The latter method provides information on numbers of stained and unstained individuals both inside and outside of algal clumps (Fig. 1). Howard found substantial movement of crustaceans and molluscs within seagrass beds after 6 h, and I adopted this duration as my test period to allow comparison with Howard's homogenous system. Pilot sampling indicated that few

organisms emigrating from algal clumps moved out of a 1 m^2 area over a 6 h period, and abundances of stained animals found in the algal clumps together with stained animals collected in the surrounding square meter were similar to those in unmanipulated algal masses. Sampling the square meter of substrate surrounding an algal clump 6 h after staining should capture the majority of invertebrates emigrating from algal clumps. The proportion of original algal fauna emigrating during 6 h was thus estimated by:

$$\frac{\text{number of stained fauna in the ambient square meter}}{(\text{no. of stained fauna in ambient } m^2) + (\text{no. of stained fauna in algal clump}).}$$

Algal clumps were stained with neutral red as per the methods of Holmquist (1992, 1994). Clumps designated for "Day" samples were stained 10 h before sunset and the stations were sampled 3 h before sunset. "Night" algal clumps were stained 2 h before sunset and the clumps were sampled 5 h after sunset. Clumps were prevented from shifting position by a 2 mm diameter skewer pushed through the algae and into the substrate. After 6 h, I recovered the stained algal clumps by gently encircling the algae with a triangular dip net with 1 mm square mesh. Each clump and its associated fauna were placed in a 19 L bucket of seawater. I centered a 1 m^2 throw trap (droptrap; i.e., a box lacking lid or bottom that is cleared with a net), covered with 1 mm mesh, around the former position of the algal clump and used this apparatus to sample the ambient sand or seagrass. The throw trap and associated protocol is described in Holmquist (in press). The resulting "ambient" sample was placed in a second 19 L bucket of seawater. Both samples were immediately returned to the laboratory and sorted, because the stain is most visible in living organisms (Howard 1985). Fauna were sorted into four categories for each station:

"clump unstained", "clump stained", "ambient unstained", and "ambient stained" (Fig. 1). I identified specimens to species for most taxa at a later date.

Dempster et al. (1995b), in their study of insect movements, note the importance of careful consideration of potential problems stemming from marking fauna. Holmquist (1992) tested this neutral red technique on many invertebrate species with regard to 1) efficiency of field staining, 2) stain retention, 3) ability of the observer to discriminate stained versus unstained individuals, 4) differential mortality due to stain toxicity, and 5) incidental uptake of stain by unstained individuals from stained algae. Field staining was 94.8% (1.5 s.e.) efficient, and stain retention and correct discrimination in double-blind tests was 100% for 95% of the taxa; discrimination of stain status in crabs and penaeid and alpheid shrimps was difficult because of poor stain retention. I therefore did not score these taxa as either stained or unstained during the course of the study. Only one species (a hermit crab, also excluded from data) absorbed stain from stained algae, and there was no differential mortality due to stain contact.

There are several ways that staining could lead to overestimation of natural emigration from clumps. Disruption during the procedure could enhance emigration. Further, predation could increase due to increased visibility resulting from staining (unlikely because a dissecting microscope and considerable practice were necessary to reliably recognize staining in a number of species) or because of response of predators to my activity. I tested for such effects by comparing abundances of fauna in unstained clumps versus clumps which had been stained 6 h previously. These comparisons were made both during the day (n= 12 and 9 for unstained and stained clumps, respectively) and at night (n= 12 and 7 for unstained and stained clumps, respectively) because of the likelihood of any differential activity or predation

occurring as a function of light level. Algal clumps were collected, and associated fauna processed, as described above.

As noted above, pilot work indicated that few organisms emigrating from algal clumps moved out of the ambient square meter of substrate surrounding algal clumps. I further examined this possibility by sweeping the 8 square meters surrounding the throwtrap for each station used in the study with the bar seine and recording any stained fauna.

Analysis

I used an *F* test of the variance of the smallest sample versus the average variance of the other samples at the 0.25 level (Day and Quinn 1989) in conjunction with Cochran's test at the 0.05 level to test the null hypothesis of homogeneity of variance. Cochran's and *F* tests indicated moderate heteroscedasticity for the proportional emigration data, but angular (arcsine-square root) transformations resulted in homogeneous variance. Prior to transformation I substituted 0.5(1/n) and 1-(0.5(1/n)) where values were zero and one, respectively (Kirk 1982); n varied with species. Two-tailed paired *t* tests were used to compare emigration and immigration for "common" species (defined as having occurred in at least 10 algal clumps; these species represented > 91% of total individuals). I tested for differences in emigration as a function of substrate and light level via two-way ANOVAs for total individuals and the caridean shrimp *Thor floridanus* (this species accounted for about 70% of total individuals). Overall differences as a function of substrate and light level were tested by performing a sign test for emigration and immigration across all species found in at least 10 algal clumps. Analyses of both absolute and proportional emigration as a function of density were via linear regression using untransformed data.

Results

Although I had anticipated that abundances of fauna in unstained clumps might exceed abundances in stained clumps, number of fauna per algal clump did not differ in either day or night comparisons (P= 0.44 and P= 0.77, respectively; two-tailed, independent t tests on log-transformed data). Sampling outside of the square meter area yielded less than one stained organism/8 square meters. The occasional stained organisms collected were always caridean shrimp.

There was differential emigration of fauna from algae into the surrounding environment as a function of both substrate and light level. Emigration from algal clumps of both *Thor floridanus* and total individuals of all species combined was greater in seagrass than in sand (two-way ANOVAs: Substrate $F_{1,27}$= 20.965, P= 0.0001 and Substrate $F_{1,28}$= 16.252, P= 0.0004, respectively; Fig. 2). Emigration was also greater at night for *Thor* but not total individuals (two-way ANOVAs: Light $F_{1,27}$= 4.463, P= 0.0440 and Light $F_{1,28}$= 0.052, P= 0.8209, respectively; Fig. 2); Substrate x Light interactions were not significant. Most of the other species also demonstrated greatest exchange between algal patches and the surrounding habitat in seagrass and at night. Sign tests on all common species indicated that these trends were significant for both substrate (13 of 17 comparisons indicating greater exchange in seagrass; P= 0.039) and light level (14 of 18 comparisons showing greater exchange at night; P= 0.018).

The number of *Thor* emigrating from algal masses increased with density (Fig. 3), but proportion of *Thor* emigrating decreased with density (sand: P= 0.047; seagrass: P= 0.029, Fig. 4). Although the proportion of *Thor*

emigrating was higher in seagrass than in sand, the slopes for proportional emigration as a function of density were not different (P= 0.738; Fig. 4).

There was extensive exchange of fauna between algal masses and the ambient habitat over a 6 h period. About 20% of algal-associated organisms moved into the surrounding environment during this time (Fig. 5). Caridean shrimp were very active emigrants; 26% of the *Thor floridanus* population left the algal masses for the surrounding substrata. Fauna moving in from the surrounding substrate comprised 13% of the algal clump assemblage after 6 h (Fig. 5). The proportion of immigrants was particularly large for the shrimp *Periclimenes* (35%) and the gastropods *Cerithium* and *Nassarius* (about 20% each). Brittlestars demonstrated little movement in either direction. There was greater emigration of vagile fauna (caridean shrimp) versus more sedentary fauna (molluscs and brittlestars; one-tailed, independent t-test, P= 0.00020; Fig. 5), but there was no such difference for immigration (P= 0.16; Fig. 5).

Numbers of animals moving into clumps were not necessarily equivalent to those leaving clumps during a 6 h time period (Fig. 5). Means for the two movement parameters differed for six of nine species tested and for total individuals as well, and mean values for these two parameters differed by up to a factor of 20 for some species. Immigration exceeded emigration in some cases, but emigration was higher in other cases. This means-based evaluation is conservative; differences in movement into and out of individual algal clumps were much more extreme than these mean values.

Discussion

Howard (1985) voiced concern that altered activity levels of stained fauna or increased predation intensity on stained fauna were potential artifacts of the staining technique. My comparisons of epifaunal abundance in both

stained and unstained algal masses provided no evidence of such artifacts with this assemblage of fauna.

Boundary permeability was affected by contrast in the macroalgal-seagrass-sand milieu; macroalgal patches were more of a closed system in sand than in seagrass. Foster and Gaines (1991) note that there should be differences in behavior of animals moving through homogeneous versus heterogeneous terrain. The present investigation compares high and low contrast boundaries; Howard's (1985) study of movement of fauna in homogenous seagrass beds allows comparison with a "no contrast" edge or non-boundary. Howard found that about 46% and 15% of the caridean shrimp and gastropods, respectively, in a 0.56 m^2 area of seagrass was composed of individuals that immigrated into the area from surrounding seagrass over a 6 h period. I found 17% and 12%, respectively, of caridean shrimp and gastropod populations of algal clumps to be composed of individuals that moved into the clumps over a 6 h period. Caridean shrimp, therefore, demonstrate a decreasing progression of movement across these habitat configurations: homogenous seagrass> algal-seagrass boundary> algal-sand boundary. Gastropods showed a similar, albeit less pronounced, progression. Responses to boundaries can vary among organisms, even among different ontogenetic stages of the same species (Crowe 1996), and perceptions of study organisms and biologists are also often different (e.g. von Uexküll 1934, Turner 1989, Foster and Gaines 1991). Kolasa and Rollo (1991) distinguish between "measured heterogeneity" (a product of human perception) and "functional heterogeneity" (evidenced by study organism response). In this benthic mosaic, the two measures demonstrated some consistencies.

Wiens et al. (1985, see also Wiens et al. 1993) model rate of cross-boundary transfer as a roughly exponential function of density. If this

relationship held in the studied microlandscape, the proportional emigration data should demonstrate an increase with density and a positive slope. Alternatively, if rate of transfer were a direct linear function of density, the proportional data should have a slope of zero. However, the proportional data from both the algal-seagrass and algal-sand boundaries had significantly negative slopes when plotted against density. In addition, the Wiens et al. (1985) model predicts a greater slope for lower contrast boundaries than for higher contrast boundaries; the slopes for *Thor* in this benthic mosaic were not significantly different. In this microlandscape, the rate of change in emigration with increasing density was unaffected by differences in permeability.

Why was there a negative relationship between proportion of fauna emigrating and density? Other studies of emigration/dispersal (see Lidicker and Stenseth (1992) for a discussion of distinction and overlap) as a function of density have produced mixed results, some finding density-dependence (e.g. Service and Bell 1987, Herzig 1995) and others density-independence (e.g. Gaines and McClenaghan 1980, Holyoak and Lawler 1996). Krebs (1992) and Herzig (1995), among others, have suggested that there may be a threshold below which emigration is density independent but above which emigration is density dependent. The Wiens et al. (1985) model is not inconsistent with a density threshold for emigration expressed as proportion of the source population. At very low densities, i.e., on the near-horizontal portion of the Wiens et al. exponential curve, it seems that proportional emigration should initially decrease before ultimately increasing. Thus it may be that the densities in the algal clumps were below such a threshold. However, the densities encountered in this *in situ* study represent the range of densities (0-300 *Thor*/25 cm diameter clump) found in algal masses in this system (Holmquist 1992), although higher densities could occur under some set of optimal

conditions. It is also likely that many systems exhibit "density-vagueness" with regard to emigration, much as Strong (1986) has argued for population size, i.e., emigration may show a strong response to very low or high densities but be only vaguely related to density within a broad range of intermediate densities.

A variety of habitat and population characteristics influence patch choice (Rosenzweig 1991, Wiens et al. 1993) and may alter predicted effects of density on emigration. Animals are generally in a given patch for a reason, and there may be few emigrants from high quality patches, for instance, large patches (references in Ims 1995). Such differential patch quality could have led to the negative density dependence for proportional emigration in my study. However, algal patches were the same size and without apparent differences. Nonetheless, habitat heterogeneity at this scale is difficult for human observers to assess- a potential concern when using microlandscapes. The results from this benthic landscape could also have been influenced by the small scale of patchiness (Doak et al. 1992) and/or the small temporal scale of the individual replicate periods.

Permeability of the boundary between algae and the surrounding habitat, as measured by emigration, was greater for shrimp than for gastropods and ophiuroids. Howard (1985) found movement of crustaceans to generally exceed that of gastropods in homogeneous seagrass beds, and the differential boundary permeability conforms to predictions on the basis of vagility (Wiens et al. 1985, Wiens 1992). The higher permeability of the algal boundary for the more motile shrimp is probably a function of high boundary encounter rate rather than lack of ability to perceive boundaries, because some caridean shrimp have been shown to compete for occupancy of macroalgal clumps versus other habitats (Coen et al. 1981).

Boundary permeability was also a function of light level. Howard (1985) found gastropods in his seagrass system to be more active at night than during the day, but caridean shrimp were less active nocturnally than during daylight. In this study, both groups showed greater movement across the algal-ambient substrate interface at night. Enhanced nocturnal permeability was probably a result of generally greater, but non-directional, activity at night as a function of reduced risk of predation (Morgan 1990, Brawley 1992). It is also possible that the increased movement is in some cases directional, and that some of the larger and most active caridean shrimps emigrate from algal clumps shortly after dark to forage a short distance away in the surrounding habitat, as has been found in other marine systems in which complex and less-complex habitats are contiguous. As examples at larger spatial scales, both urchins (Ogden et al. 1973) and fishes (Robblee and Zieman 1984) harbor on corals during the day but forage in adjacent, less structurally-complex seagrass at night, and a variety of epibenthic predators shelter in seagrasses during the day but forage nocturnally on nearby unvegetated substrata (Summerson and Peterson 1984).

Emigration was not in equilibrium with immigration for the majority of species tested at the temporal scale of this study. Such disequilibria are probably the rule rather than the exception in real-world landscapes (Gustafson and Gardner 1996). The problems that asymmetrical transfer rates present for conclusions based on either emigration or immigration alone are a function of 1) the question asked, 2) the structure of the mosaic in question, and 3) the temporal scale. In the present study, net movements (see Wiens et al. 1985) into or out of the macroalgal clumps over a 6 h period were of interest. If the time frame was on the scale of weeks, it is likely that many more species would have demonstrated immigration-emigration equilibria. For instance, in this study, three times more *Thor* emigrated from algal clumps than were replaced

by immigration over 6 h; if this disparity continued for weeks, it is obvious that algal clumps would be rapidly defaunated. In some cases such differences will simply represent the variance in the system; in other cases such differences will be real and might, as an example, represent diel waves of emigration and immigration. As another example, Howard (1985) used immigration data alone to estimate general levels of movement in a seagrass bed. However, Howard's approach was sound because his goal was to estimate general levels of activity within a relatively homogenous habitat, i.e., there was no reason to expect net movement into, or out of, an arbitrarily-chosen 0.56 m^2 portion of seagrass meadow. Consideration of ecological equilibrium of any sort is scale-dependent (Wiens 1989), and emigration-immigration disequilibria are most likely to be a concern when the temporal scale is small and/or when boundary transfer is involved; in such situations, care should be taken when extrapolating from one transfer parameter to the other.

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Figure Legends

Fig. 1. Schematic showing central, initially-stained area (surrounding an algal clump) and outer "ambient" area (seagrass or sand). CS= "clump stained", i.e., organisms not leaving clump during 6 h; CU= "clump unstained", i.e., organisms moving into algal clump over 6 h; AS= "ambient stained", i.e., organisms moving out of algae into the surrounding square meter over 6 h; AU= "ambient unstained"; i.e., organisms in the square meter surrounding the algae after 6 h that were not in the algae during staining.

Fig. 2. Mean proportion of *Thor floridanus* (A) and total individuals (B) that moved from algal clumps to the ambient habitat over a 6 h period as a function of ambient habitat type and light level. Untransformed means and back-transformed 95% confidence intervals are provided. ANOVA results in text.

Fig. 3. Number of *Thor* emigrating from algae into sand (A) and seagrass (B) as a function of original density in algal clumps.

Fig. 4. Proportion of *Thor* emigrating from algae into sand (A) and seagrass (B) regressed on original density in algal clumps; 95% confidence intervals from linear regression.

Fig. 5. Mean proportion of individual taxa that moved from algal clumps into the ambient habitat over 6 h (emigration; ■) and mean proportion of individual taxa in algal clumps comprised of organisms which moved in from the ambient habitat over 6 h (immigration; □). Untransformed means and back-transformed 95% confidence intervals are provided. *P* values indicate results of

paired two-tailed *t* tests on angularly transformed data. Abbreviations indicate gastropods: (Mit) *Mitrella argus*, (Bul) *Bulla striata*, (Mod) *Modulus modulus*, (Cer) *Cerithium eburneum*, (Nas) *Nassarius* sp.; caridean shrimps: (Hip) *Hippolyte pleuracanthus*, (Tho) *Thor floridanus*, (Per) *Periclimenes americanus*; (Bri) brittlestars: dominated by *Ophiopsila riisei*, *Ophionereis squamulosa*, and *Ophionereis olivacea*; and (Tot) total individuals of all 78 taxa scored as stained or unstained in the study.

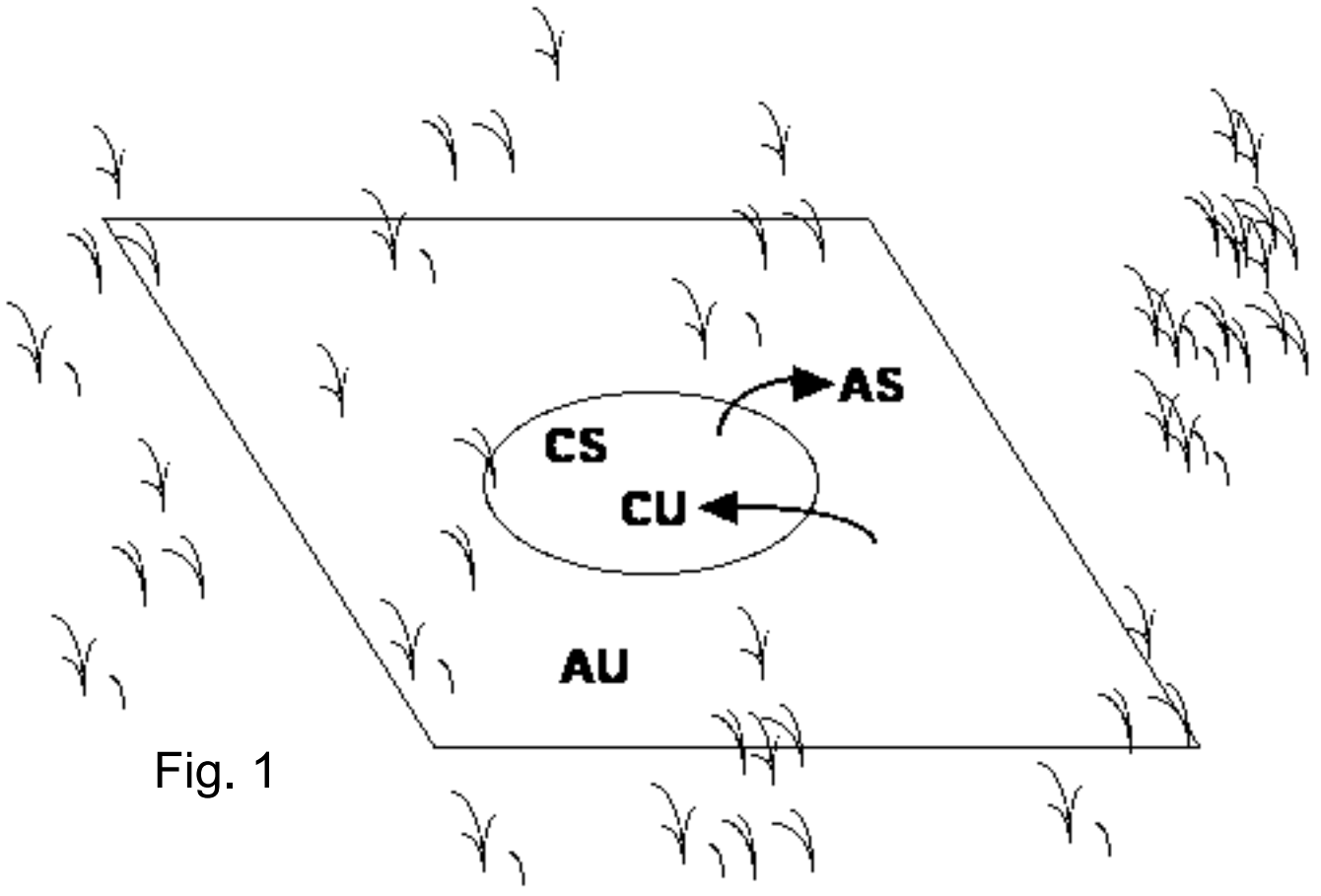


Fig. 1

$$\text{Clump emigrants} = \frac{AS}{AS+CS}$$

$$\text{Clump immigrants} = \frac{CU}{CU+CS}$$

$$\text{Ambient emigrants} = \frac{CU}{CU+AU}$$

$$\text{Ambient immigrants} = \frac{AS}{AS+AU}$$

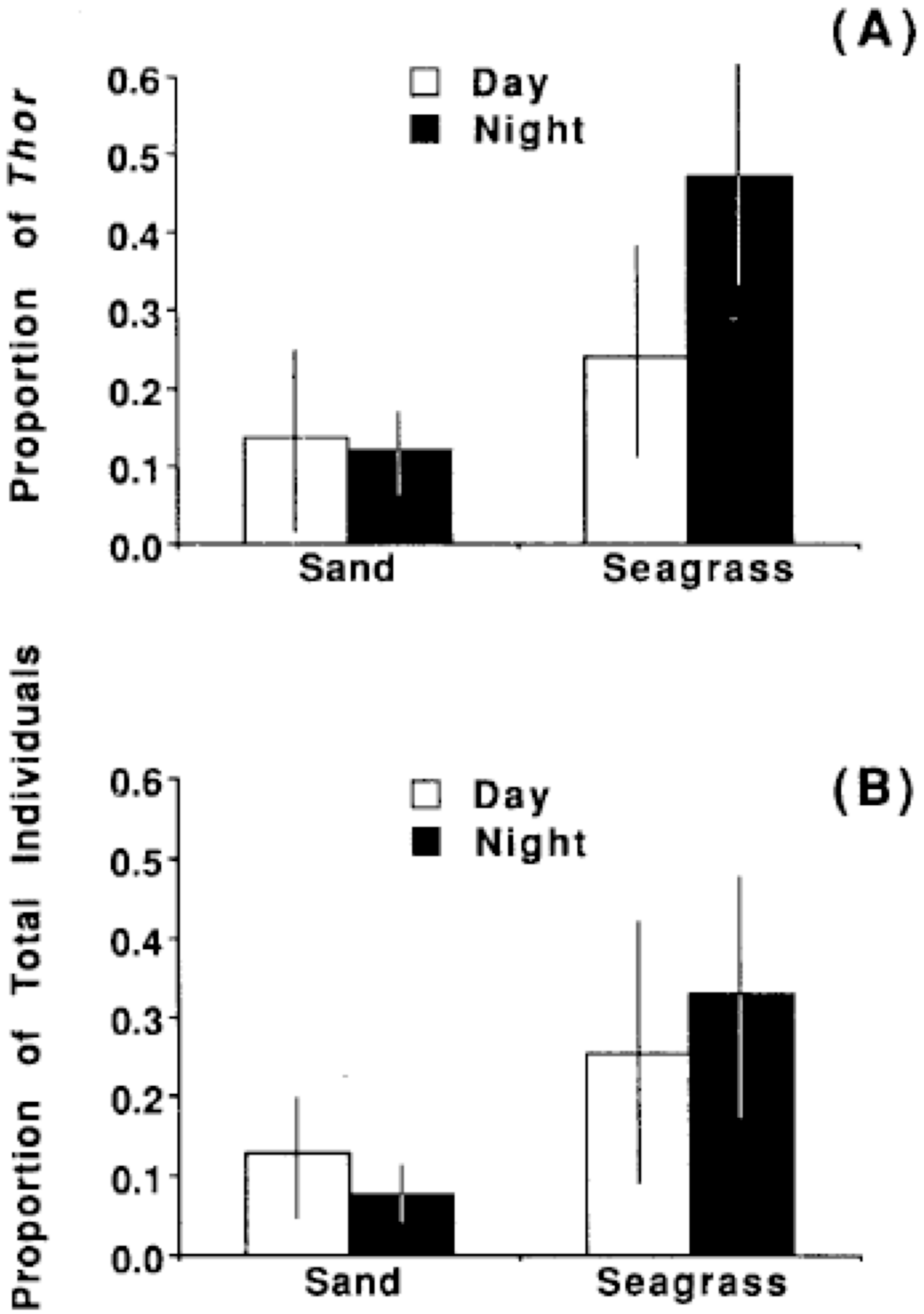
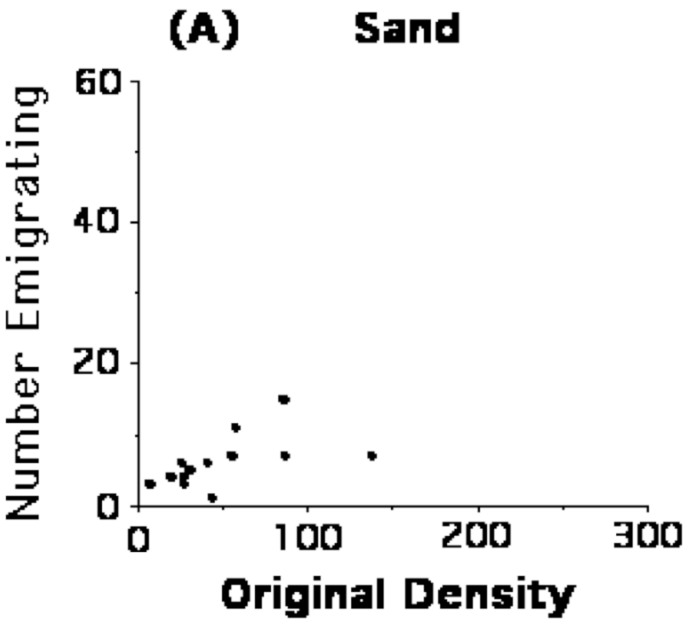

(A)
Proportion of *Thor*
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Day
Night
Sand
Seagrass
(B)
Proportion of Total Individuals
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Day
Night
Sand
Seagrass

Fig. 2


(A) Sand
Number Emigrating
60
40
20
0
0
100
200
300
Original Density

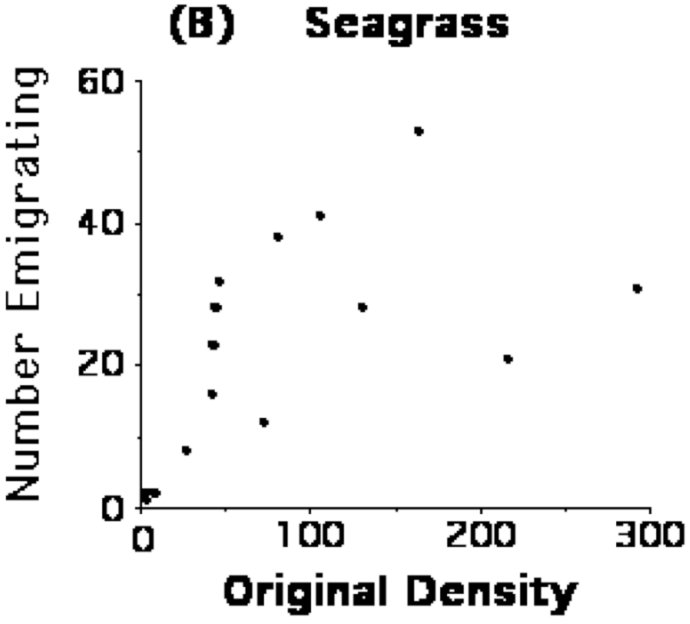
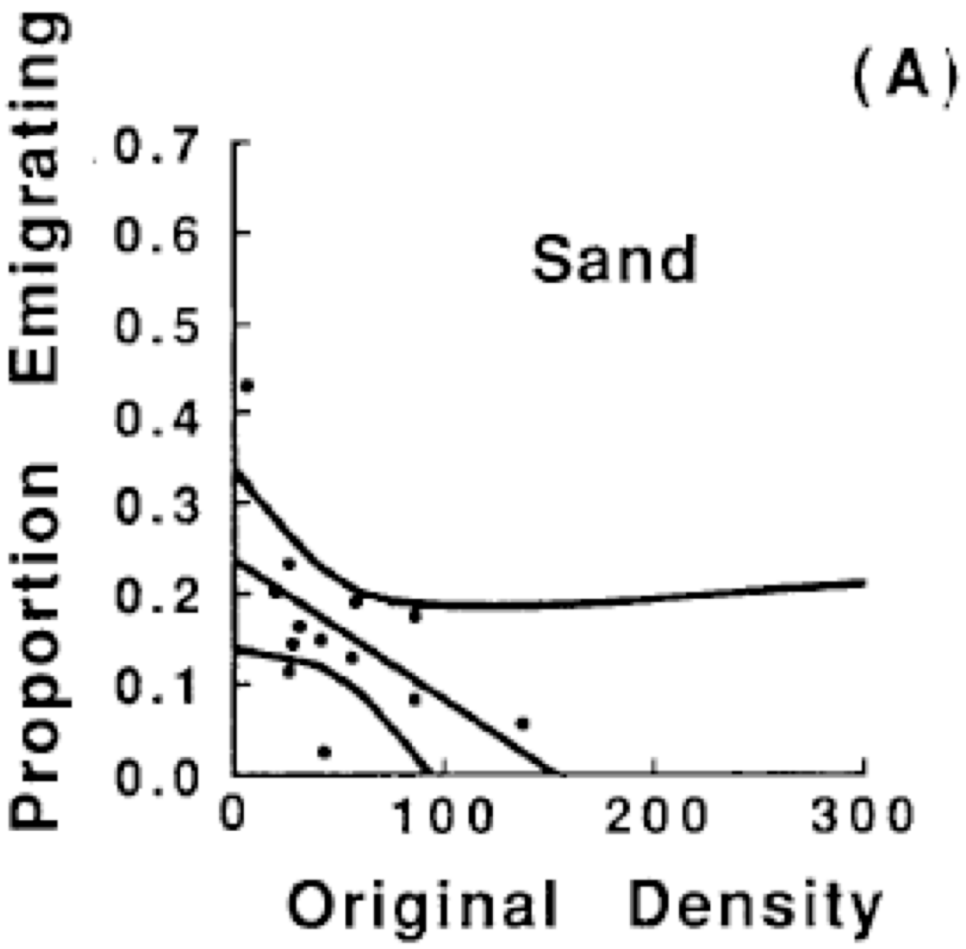

(B) Seagrass
Number Emigrating
60
40
20
0
0
100
200
300
Original Density

Fig. 3


(A)
Sand
Proportion Emigrating
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
0
100
200
300
Original Density

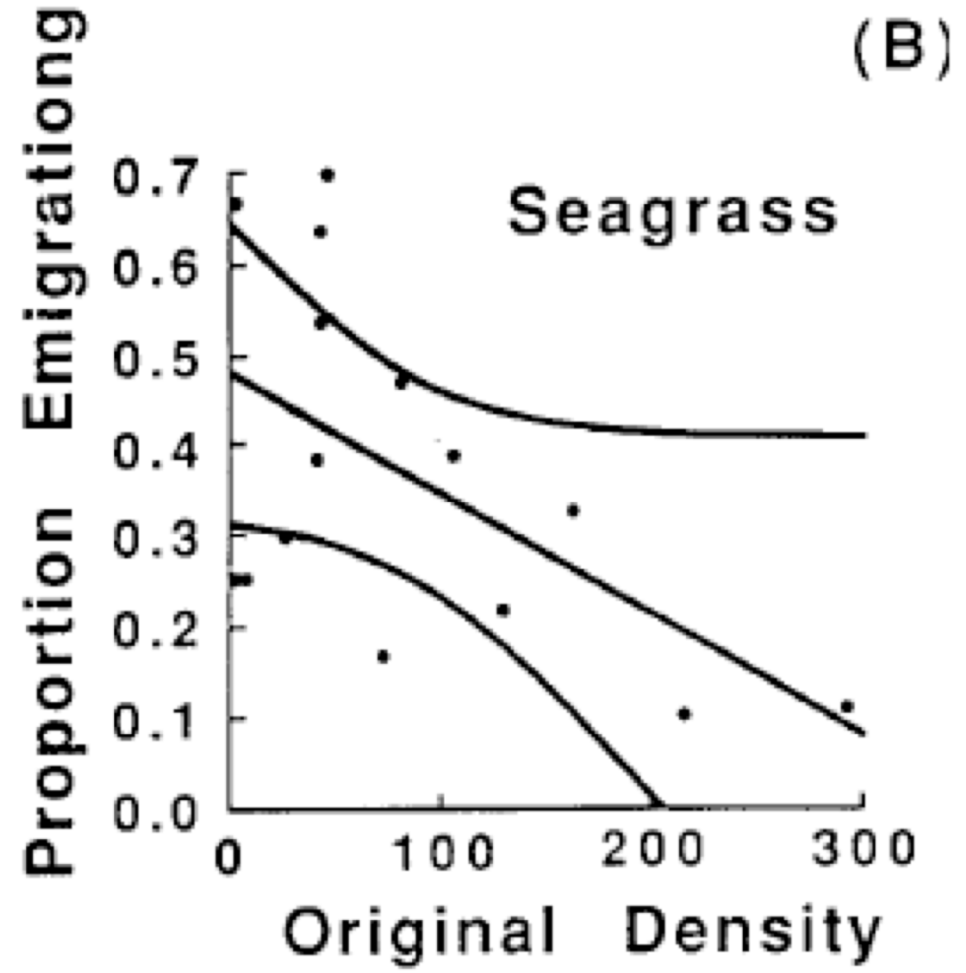

(B)
Seagrass
Proportion Emigrationg
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
0
100
200
300
Original Density

Fig. 4

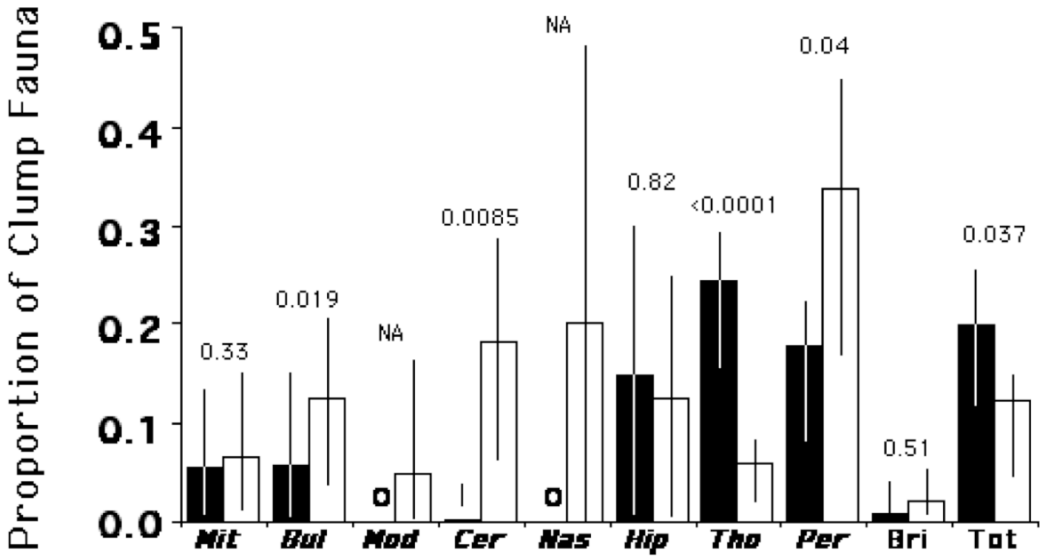

Proportion of Clump Fauna
0.5
0.4
0.3
0.2
0.1
0.0
0.33
0.019
NA
0.0085
NA
0.82
<0.0001
0.04
0.51
0.037
Mit
Bul
Mod
Cer
Nas
Hip
Tho
Per
Bri
Tot

Fig. 5