Oecologia (1993) 94:176–185

Oecologia

Habitat structure, conspecific presence and spatial variation in the recruitment of a temperate reef fish

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Received: 24 February 1992 / Accepted: 28 January 1993

Abstract. Pronounced spatial variation in recruitment occurs in many marine invertebrate and fish populations and is thought to be critical to the demography of these species. In this study I examined the importance of habitat structure and the presence of conspecific residents to spatial variation in larval settlement and recruitment in a temperate fish *Tautogolabrus adspersus*. I define settlement as the movement of individuals from the water column to the benthic habitat, while I refer to recruitment as numbers of individuals surviving some arbitrary period of time after settlement. Experiments in which standard habitats were stocked with conspecifics showed that resident conspecifics were not an important factor contributing to small-scale variability in recruitment. Further correlative analyses demonstrated that large-scale variation in recruitment could not be explained by variability in older age classes. By contrast, manipulations of macroalgal structure within a kelp bed demonstrated that recruitment was significantly higher in habitats with a dense understory of foliose and filamentous algae than in habitats with only crustose algae. Understory algae varied in their pattern of dispersion among sites, and the dispersion of fish matched that of the plants. In order to determine the effects of differences in patterns of algal dispersion on the demography of associated *T. adspersus* populations, I used experimental habitat units to manipulate patterns of dispersion. Settlement was significantly greater to randomly placed versus clumped habitats; however, no differences in recruitment between random and clumped habitats were detected. Because recruitment is a function of the numbers of settlers minus the subsequent loss of settlers, rates of mortality or migration must have been higher in the randomly placed habitats. These results are counter to the current paradigm for reef fishes which suggests that larval settlement is the crucial demographic process producing variability in population abundance. In this experiment patterns of settlement were modified by varying the patch structure of the habitat.

Key words: Recruitment – Settlement – Patch structure – Recruitment-limitation – Demography

Landscapes in both terrestrial and marine environments are composed of patches of habitat which vary in their physical and biogenic structure (e.g. Paine and Levin 1981; Addicott et al. 1987; Wiens 1989). Differential use of patches by individual organisms as well as the consequences of environmental heterogeneity on the structure of populations and communities have received increasing attention by both marine and terrestrial ecologists (Sale 1977, 1978; Sousa 1984; Fowler 1988; Wiens and Milne 1989; Møller 1991). Nonetheless, population models for reef fishes largely overlook how variability in the mosaic of patches forming the habitat may influence the dynamics of populations.

Reef fish generally have complex life cycles during which larvae and often eggs are pelagic and widely dispersed (Sale 1980). Following the pelagic phase, larvae or metamorphosed individuals settle (move from the water column to the benthic habitat). Thus, recruitment occurs by the addition of individuals to benthic populations through larval and post-larval settlement. In this context, I operationally define settlement as the permanent movement of individuals from the pelagic to benthic habitat and recruitment as the addition of individuals to the benthic population.

Recently, it has been argued that settlement of individuals from the water column to the adult habitat is the most important demographic process for both benthic and demersal marine populations (Underwood and Fairweather 1989; Doherty and Williams 1988). Consequently, emphasis has been placed on variability in the availability of pelagic propagules and subsequent variation in recruitment (e.g. Williams 1980; Grosberg 1982; Doherty 1983; Victor 1983; Gaines et al. 1985). In particular, the recruitment limitation model (Doherty 1981) asserts that sites are undersaturated with new settlers, and thus population density increases or decreases as settlement increases or decreases (Williams 1980; Doherty 1981, 1983; Victor 1983). Another incarnation of this model suggests that sizes of demersal populations are determined by the strength and variability of settlement and post-settlement processes (Forrester 1990). The distinction between these two, often confused, versions of recruitment limitation is critical (Forrester 1990). The former version predicts that abundances of cohorts

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Contribution number 278 from the Center for Marine Biology, University of New Hampshire

generated at settlement are not substantially modified by processes occurring after settlement. However, the latter interpretation proposes that the size of a demersal population may be affected by post-settlement processes, particularly if they are stronger or less variable than processes influencing settlement. (Forrester 1990).

Implicit in these models of recruitment limitation is that density-dependent interactions between demersal individuals and new settlers are of little importance. Resident conspecifics thus should not influence levels of recruitment. These models also make no allowance for the effects that variability in the structure of the habitat have on settlement. Therefore, the demography of local populations inhabiting areas which differ only in their patch structure (e.g. the sizes or dispersion of habitat patches) should not vary.

In this study I investigate the juvenile demography of a temperate reef fish, and ask if attributes of the habitat, including the presence of conspecifics can influence the relative contribution of pre- and post-settlement processes to variation in population abundance. Using both experimental and descriptive analyses, this study asks the following specific questions: 1) Are aggregations of recruits the result of attributes of the habitat? 2) Are settling post-larvae attracted to conspecifics? 3) Do differences in the dispersion of the habitat patches affect the relative importance of settlement and post-settlement loss to variation in recruitment?

Materials and methods

Study species

Cunner, *Tautogolabrus adspersus* (Pisces:Labridae), are common members of shallow subtidal communities in the Northwest Atlantic, occurring from intertidal zones (Whoriskey 1983) to depths greater than 90 m (Bigelow and Schroeder 1953). They occur in abundance from Conception Bay, Newfoundland, to New Jersey, and are occasionally found as far south as a Chesapeake Bay (Bigelow and Schroeder 1953).

Cunner spawn in early and mid summer (Dew 1976; Pottle and Green 1979). After a larval life averaging 18–21 days (Gleason and Reschiek 1990), fish settle to the demersal habitat. In the Gulf of Maine, cunner generally spawn in July and thus settlement of cunner occurs predictably in late summer, almost entirely in early August (Levin unpubl.). Young-of-the-year cunner appear to feed opportunistically on zooplankton and small benthic invertebrates (Chao 1972; Levin unpubl.). As juveniles, cunner are site-attached and do not stray far from cover, particularly that provided by macrophytes (Olla et al. 1975; Pottle and Green 1979; Levin 1991).

General methods

Field experiments and descriptive investigations were conducted during August and September of 1990 and 1991. Descriptive investigations were conducted at two spatial scales. For the purpose of this study, "small-scale" is defined as a scale of meters and "large-scale" refers to a scale of hundreds of meters. I refer to pigmented young-of-the-year fish as "recruits", 1+year old fish as "juveniles", and individuals > =2 years old as "adults".

Censuses of cunner were conducted at seven sites in the Gulf of Maine. These sites are numbered and described in table 1 and are representative of shallow subtidal habitats in the Gulf of Maine (Witman 1987; Chapman and Johnson 1990).

Quantifying patterns of recruitment

To determine large scale (among site) patterns of recruitment, densities of each age class were quantified by visually censusing randomly placed 15 × 1 m band transects in seven sites (Keast and Harker 1977; Lincoln-Smith 1988). Three to five minutes after the transect line was extended a diver carrying a 1 meter wide T-shaped bar to delineate the transect width swam over the line at a rate of eight to ten meters per minute and counted all fish (Sale et al. 1984). The three to five minute interval between extending and sampling the transect allowed fish to resume their normal behavior.

Additionally, the dispersion of fish within sites was examined. Two methods were used to assess patterns of dispersion in cunner recruits. Smaller scale patterns were determined at 5 sites by counting the number of recruits in randomly placed 0.25 m^2 quadrats. Larger scale patterns were also investigated at 4 sites by censusing numbers of recruits in randomly placed 15 × 1 m strip transects.

The standardized Morisita index of dispersion (I_p) was used to determine patterns of dispersion from both quadrat and transect data (Krebs 1989). This index ranges from -1.0 to $+1.0$, with 95% confidence limits at $+0.5$ and -0.5. I_p values>0 indicate aggregated patterns of dispersion, values<0 indicate a uniform pattern, and values$=0$ indicate a random pattern. Because this index is both independent of sample size and the density of the population, Myers (1978) argued that this index is one of the least biased measures of dispersion.

Dispersion of macrophytes was also quantified at two spatial scales. Percent covers of algae were enumerated by recording the type of algae under each of 45 points created by a grid of monofilament strung across randomly placed 0.25 m^2 quadrats. Dispersion of the coverage of upright (i.e. non-encrusting) macrophytes was determined using the standardized Morisita index of dispersion. Larger scale spatial patterns were also examined for the dominant macrophytes in the study sites. The T-square sampling procedure was used to assess the spatial pattern of these plants (Krebs 1989). This procedure compares the distance from a random point to the nearest plant with the distance from this plant to its nearest neighbor. The hypothesis of a random spatial pattern is tested using the Hines' test statistic for randomness (H_t). This sampling procedure samples a large area and is statistically robust (Krebs 1989).

Large-scale effects of conspecifics of recruitment

The effect of conspecifics on recruitment was assessed by examining the patterns of co-occurrence of recruits with juveniles (1+year) and with adults (>2+year) at all seven study sites. In August, recruits average 12 mm standard length (SL) (Levin, unpubl.), juveniles are greater than 51 mm SL (Bigelow and Schroeder 1953), and adults are at least 100 mm SL (Bigelow and Schroeder 1953). Because of the large size differences of these age classes, it was possible to unambiguously distinguish them while visually censusing transects.

A two factor analysis of covariance was used to simultaneously examine the effects of site, adult densities and juvenile densities on variation in recruitment (Winer et al. 1991). Prior to the analysis data were log transformed.

Small-scale effects of resident conspecific juveniles

Twelve standard habitat units (SHUs, after Sweatman 1985) were constructed and half of these were allocated equally between 2 sites. SHUs consisted of 2 cm diameter PVC pipe frames (1 m × 0.5 m)

Table 1. Location and description of sites used in this study

Site	Location	Description
1	Cape Neddick, ME 43°10′ N 70°36′35″ W	Rock ledge/urchin dominated area with sparse coverage of ephemeral and unpalatable algae
2	Nubble Island, ME 43°10′ N 70°36′30″ W	Rock ledge with high (>80%) cover of *Laminaria spp.* and a rich understory of red algae, mostly *Chondrus crispus*
3	Fort Point, NH 43°05′ N 70°44′ W	Sandy substratum with few large boulders surrounded by *Zostera marina* bed
4	Fort Foster, ME 43°04′ N 70°42′ W	Sandy/cobble substratum with *Zostera marina, Chondrus crispus* and scattered *Laminaria spp.*
5	Appledore Island, ME 42°59′ N 70°37′ W	Rock ledge with moderate cover (ca. 50%) of *Laminaria spp.* as well as a dense understory of *Codium fragile* and *Chondrus crispus*
6	Haley's Cove, NH 42°59′ N 70°36′30″ W	Rock ledge with dense cover of *Codium* and numerous filamentous species
7	Smuttynose Island, NH 42°59′ N 70°36′ W	Rock ledge/large boulders, dominated by urchins with very sparse cover of ephemeral algae

with five pieces of rope strung across each frame and 2 kelp fronds *(Lamanaria saccharina)* attached to each strand of rope. SHUs were fitted with PVC legs so they stood 0.5 m above the substratum to prevent burial in sandy areas. SHUs were isolated by at least 4 m from natural macrophytic structure and from each other.

All fish were removed from SHUs using the anaesthetic quinaldine at the start of the experiment. Six recruits were added to 3 SHUs at each site. This represented 1 standard deviation above the mean recruit density observed at site 1 in 1989. The remaining 3 SHUs at each site were left as controls. After adding recruits to SHUs, I observed that fish sought immediate shelter in the algae. The day following the addition of the recruits, I examined all SHUs. In all cases recruits had remained on the SHUs. The SHUs were censused for cunner recruitment three weeks (August 30, 1990) and five weeks (September 13, 1990) after the experiment was initiated. As cunner settle primarily during the month of August (Levin, unpubl.), the experiment was conducted during the entire settlement season for this species.

The hypothesis that recruitment to the SHUs did not vary between sites or experimental treatments was tested using a two-factor analysis of variance (ANOVA). Each sampling date was analyzed separately. A model I ANOVA was used in which both site and the addition of conspecific juveniles were considered fixed factors (Winer et al. 1991). Prior to analyses data were log transformed to meet the assumptions of parametric analyses (Winer et al. 1991).

Effects of macrophytes on recruitment

Previous descriptive work (Levin 1991) has shown that the presence or absence of cunner recruits could be predicted by the nature of the macroalgal assemblage at very small spatial scales. In particular, recruits were associated with fleshy upright algae rather than crustose species. An additional experiment was performed in August 1990 in order to determine if differences in the type of macroalgal cover could influence the density of recruits.

In this experiment, I manipulated the percent cover and type of macroalgae present within a kelp bed (site 2). In July 1990, immediately before cunner settlement had occurred, two circular plots 6 m in diameter with an area of 28.26 m^2 were created for each of three treatments. The first treatment consisted of removing all algae from the plot using putty knives and wire brushes. In the second treatment the kelp canopy was eliminated leaving only the filamentous and foliose understory. Because of the lack of canopy shade, this treatment became dominated by suntolerant filamentous and foliose species. In the final treatment, the control, macrophytes were not manipulated. One plot for each treatment was created in each of two areas. Within each area, plots were separated by at least 10 m, and the two areas were separated by 60 m. The surrounding habitat (kelp bed) was equivalent for all treatments.

At the end of the settlement season, four 0.25 m^2 quadrats were placed randomly within the central 12.56 m^2 of each of the 2 plots for each treatment. All recruits were visually censused within each quadrat. A one-way ANOVA with quadrats as replicates and areas as a blocking factor was used to test the null hypothesis that the density of recruits did not differ among treatments.

Consequences of small-scale patterns of dispersion

To determine the effects of habitat dispersion on the demography of juvenile cunner, an experiment was performed in which the spatial pattern of the macroalgal habitat was experimentally manipulated using SHUs. The SHUs used in this experiment were 0.5 m × 0.5 m with 0.5 cm^2 wire mesh across the top. Kelp was not attached, but filamentous algae was allowed to naturally colonize the SHUs. The experiment was performed adjacent to site 6 (Table 1) in Gosport Harbor at the Isles of Shoals, Maine. This site provided a protected and relatively level plain with sandy substrata at a depth of 4–10 m below mean low water. Forty eight contiguous plots (36 m^2) were established and 4 SHUs were positioned within the central 9 m^2 of each plot so that groups of SHUs were at least 6 m apart. Positioning of SHUs within active zones depended on treatment: 1) clumped – 4 SHUs were adjacent and touching to form a 1 m^2 square within the active zone; or 2) random – 4 SHUs were placed randomly within the active zone except that they were separated from each other by at least 1 m.

Each treatment was assigned randomly to half of the plots. The experiment was monitored on 11 of the 17 days of cunner settlement in 1991, and 2 days shortly after the settlement season. The number of translucent fish (settlers) and the number of pigmented young-of-the-year cunner (recruits) were recorded on each occasion. Settlers were assumed to remain translucent for no more than 24 h. Because of the close association of juvenile cunner with cover, the loss of fish between censuses was assumed to be due to mortality rather than demersal migration.

Prior to the analysis of settlement and recruitment, differences due to positioning of replicates within the study site were investigated. The study site was divided into 8 quadrants representing different compass directions. No differences in either settlement ($F = 0.798$ $p = 0.57$) or recruitment ($F = 1.54$ $p = 0.23$) were detected in different quadrants. Settlement was correlated with depth ($r = 0.731$, $p < 0.001$); however, the study site was divided into three depth ranges (4–6 m, 6–8 m, 8–10 m) and I ensured that equal numbers of replicates from each treatment were allocated to each depth zone.

Hypotheses about effects of experiment factors on demographic variables were tested using ANOVA. All analyses used a model where the experimental factor (clumped vs. randomly placed SHUs) was considered fixed and different sampling dates were considered random effects and a repeated measure (Winer et al. 1991). This model tested for differences in settlement or recruitment between experimental treatments over all dates sampled.

Results

Large-scale (among site) patterns of abundance

Recruitment varied significantly among sites (Fig. 1a, $F_{6,193} = 14.39$, $p < 0.001$). Sites 1, 2 and 3, averaged greater than 33 recruits per transect and received significantly higher recruitment than the other four sites (Tukey's HSD, $p < 0.05$). Additionally, sites 4, 5 and 7 averaged between 18 and 25 per transect and were statistically indistinguishable (Tukey's HSD $p > 0.05$); however, recruit densities at these sites were significantly greater than the density of recruits at site 6 (Tukey's HSD, $p < 0.05$).

Adult and juvenile densities also varied among sites (Figs. 1b and 1c; for adults, $F_{4,169} = 17.49$, $p < 0.001$; for juveniles $F_{4,162} = 8.145$, $p < 0.001$). Mean juvenile densities (3–4 fish per transect) were highest at sites 2 and 5 (Tukey's HSD $p < 0.05$). Mean juvenile densities between 0.5 and 2 fish per transect were observed at sites 1, 6, and 7, and these were significantly lower than the densities observed at sites 2 and 5 (Tukey's HSD $p < 0.05$). No juveniles were observed at sites 3 and 4. Sites 1 and 2 had the highest mean adult density with > 2 fish per transect (Tukey's HSD, $p < 0.001$). Sites 5, 6, and 7 had similar mean adult densities of < 1 fish per transect (Tukey's HSD $p > 0.3$). Adults were not observed at sites 3 and 4.

Small-scale (within site) patterns of abundance

At the small spatial scale examined (0.25 m^2), cunner recruits exhibited an aggregated pattern of dispersion in sites 1 ($I_p = 0.510$), 5 ($I_p = 0.512$) and 6 ($I_p = 0.541$); however in sites 2 ($I_p = 0.490$) and 7 ($I_p = 0.490$) fish were randomly dispersed. Recruits in sites which were separated by relatively small distances showed different dispersion patterns. Sites 1 and 2, for example were separated by ca. 100 m, yet fish at site 1 were aggregated and fish at site 2 were dispersed randomly. Cunner recruits were clumped at the larger spatial scale examined (15 m^2) at all 4 sites investigated (site 1 $I_p = 0.521$; site 2 $I_p = 0.532$; site 5 $I_p = 0.510$; site 6 $I_p = 0.516$).

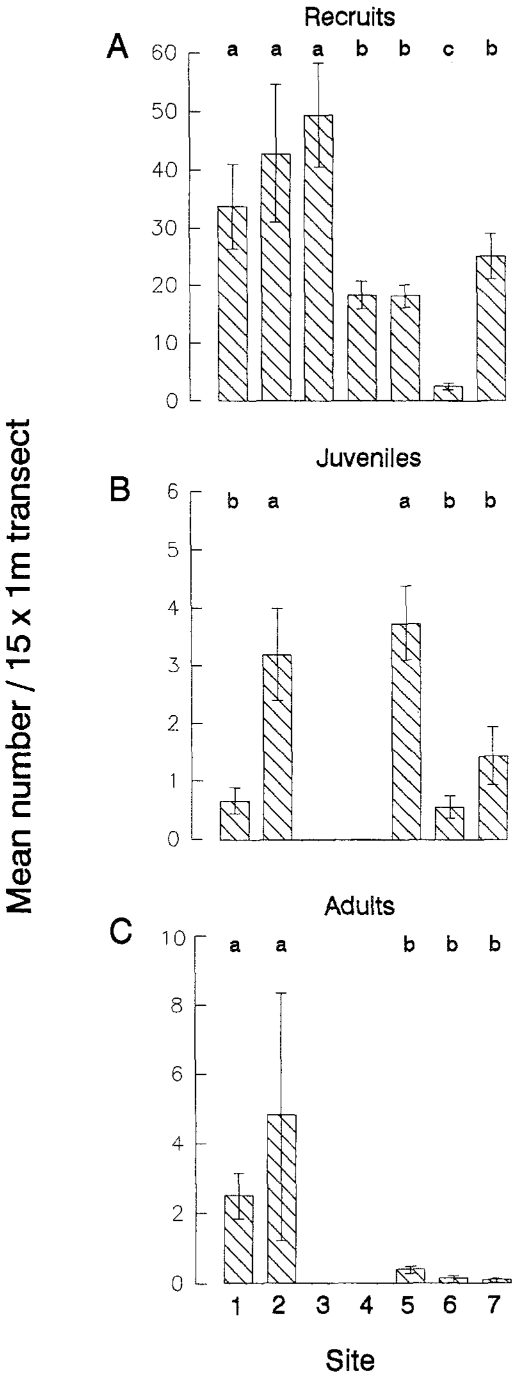

Fig. 1A–C. Mean density per 15 × 1 m strip transects of three age classes of *T. adspersus* at seven sites in the Gulf of Maine. Letters indicate sites which could not be distinguished statistically. Error bars represent ± 1 standard error

Large scale effects of conspecifics on variation in recruitment

Variability in recruitment was not consistently explained by variation in either juvenile or adult cunner abundance. A two factor analysis of covariance revealed that there were significant differences among sites in recruitment, but not a significant effect of juveniles or adults (Table 2).

Table 2. Two factor analysis of covariance testing the effects of site, juvenile density and adult density on recruit abundance. Sites 3 and 4 were omitted from the analysis because there was no variation in juvenile or adult density at these sites. Data were log (x + 1) transformed for the analysis

Source	SS	df	MS	F	*P*
Site (s)	67.376	4	16.844	11.982	<0.001
Adult (a)	0.232	1	0.232	0.165	0.69
Juvenile (j)	0.806	1	0.806	0.573	0.45
sxa	6.362	4	1.591	1.131	0.34
sxj	10.258	4	2.564	1.824	0.13
axj	0.014	1	0.014	0.01	0.92
sxaxj	6.817	4	17.04	1.212	0.31
Error	224.923	160	1.406		

Sites 3 and 4 were omitted from this analysis because no juveniles or adults were present at these sites. Despite the absence of older stage from these sites, there was still variability in recruitment comparable to other sites (Fig. 1).

There was also no relationship observed between numbers of recruits and the density of older stages among sites. Regression analyses of the mean density of recruits for each site versus the average density of both juveniles and adults were not significant ($P > > 0.05$).

Small-scale effects of resident conspecifics

Recruitment of cunner to SHUs did not vary significantly between sites on either date examined (Fig. 2). Additionally, no significant differences in recruitment were evident between those SHUs stocked with conspecifics and those left as controls (Fig. 2). On August 30, the mean number of recruits at on SHUs stocked with conspecifics was 39.5 (SE 3.96), versus 46.5 (SE 3.16) on SHUs which were not stocked.

There was a substantial decline in the number of recruits present on the SHUs after two weeks; however, the difference in recruitment between experimental treatments remained non-significant (Fig. 2). On September 13, SHUs stocked with conspecifics averaged of 16.83 (SE 2.65) recruits, and SHUs left as controls had a mean of 15.83 (SE 3.01) recruits.

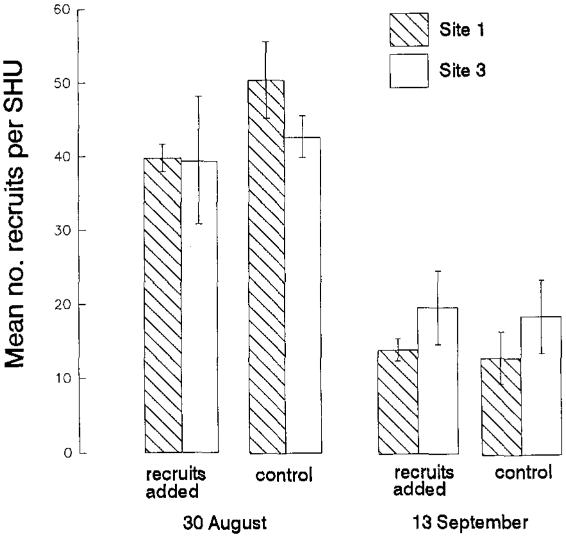

Fig. 2. Mean density of *T. adspersus* recruits at 2 sites on standard habitat units (SHUs) to which conspecifics were added or left as controls. Using a two way ANOVA, no difference was detected in recruit density either between treatments ($F = 1.56$, $P = 0.24$ for 30 August; $F = 0.116$, $P = 0.74$ for 13 September), or between sites ($F = 0.344$, $P = 0.57$ for 30 August; $F = 2.22$, $P = 0.17$ for 13 September). Error bars represent ± 1 standard error

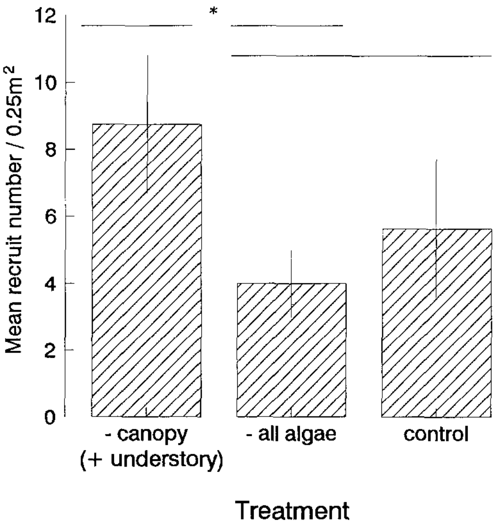

Fig. 3. Mean density of *T. adspersus* recruits in replicate experimental plots in which only the kelp canopy was removed, all fleshy algae were removed, and no algae were removed (control). Horizontal lines join bars which were not significantly different (Tukey's HSD $p > 0.05$). * indicates significance at $p < 0.05$. $N = 8$ quadrats for each treatment. Error bars represent ± 1 standard error

Effects of macrophytes on recruitment

The field manipulation of algal cover indicated that the presence of an understory without a kelp canopy increased recruitment of cunner (Fig. 3). While no difference in recruit density was detected between habitats without algae and those left as controls, there was significantly greater recruitment to habitats in which the canopy was removed than to those in which all algae were removed (Fig. 3, $F_{2,21} = 3.51$, $p = 0.048$) The density of recruits averaged 8.75 (SE 2.2) fish/0.25 m^2 in plots where only the canopy was removed, while in plots in which all algae were eliminated the mean was 4.00 (SE 1.3) recruits/0.25 m^2. Thus, the enhancement of the understory algal assemblage via canopy removal or the simply the absence of the kelp canopy resulted in a substantial increase in recruit density.

There was also a strong relationship between the dispersion of macroalgae and the dispersion of fish. At the smaller scale examined there was a high correlation (Spearman rank correlation coefficient = 0.895) between

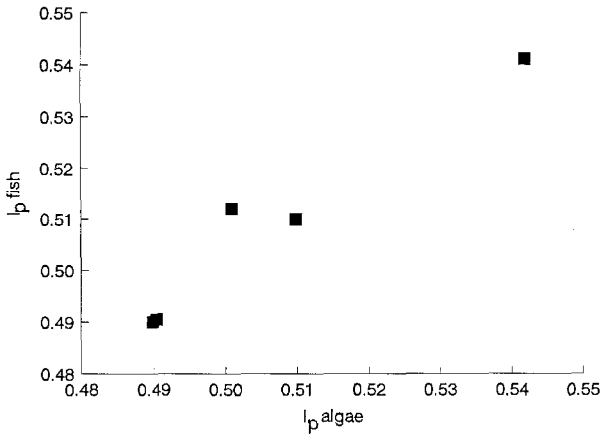

Fig. 4. The standardized Morisita's index of dispersion (I_p) for fish is plotted against the I_p for macroalgae for 5 sites. The spatial pattern for fish is highly correlated with that of the algae (Spearman rank correlation coefficient = 0.895)

Table 3. Repeated measures analysis of variance of settlement and recruitment on treatment (clumped vs. random) and sampling date

Source	SS	df	MS	F	*P*
A. Settlement					
Between subjects					
Treatment	23.24	1	23.24	10.53	0.006
Error	30.92	14	2.208		
Within subjects					
Date	55.06	10	5.506	0.84	<0.001
Date* Treatment	37.19	10	3.719	0.27	0.001
Error	159.23	140	1.14		
B. Recruitment					
Between subjects					
Treatment	6.88	1	6.88	0.77	0.40
Error	115.53	13	8.89		
Within subjects					
Date	17.18	11	1.56	2.50	0.007
Date* Treatment	2.63	11	0.24	0.38	0.96
Error	89.51	143	0.63		

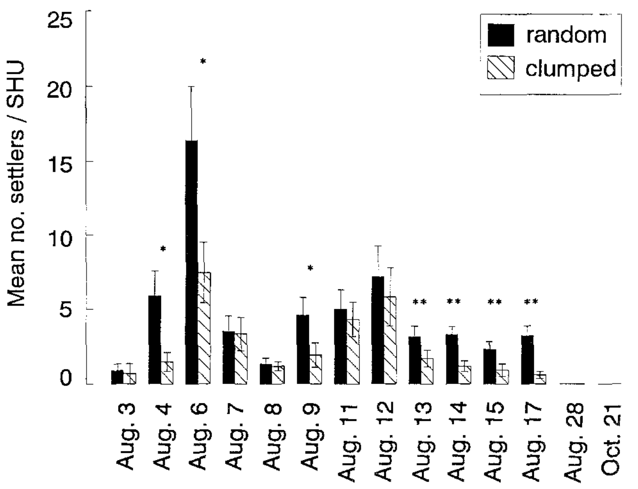

Fig. 5. Mean number of newly settled *T. adspersus* on randomly placed versus clumped sets of standard habitat units (SHUs) (area = 1 m^2). *, and ** indicate significance at $p < 0.05$ and $p < 0.01$ respectively by *t*-tests for each date. Results from repeated measures ANOVA determining significance over all dates are presented in Table 3a. Error bars represent ± 1 standard error

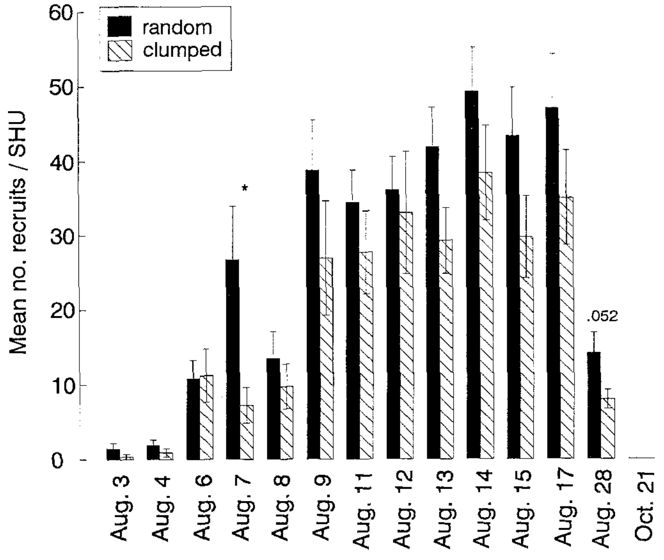

Fig. 6. Mean number of *T. adspersus* recruits on randomly placed versus clumped sets of standard habitat units (SHUs) (area = 1 m^2). *indicates significance at $p < 0.05$ by *t* test for each date. Results from repeated measures ANOVA determining significance over all dates are presented in Table 3b. Error bars represent ± 1 standard error

the standardized Morista's index for algae and for fish (Fig. 4). Because two different methods were used to assess algal and fish dispersion at the larger scale examined, I did not perform a correlation analysis; nonetheless, both algae and fish were clumped at this scale for each site investigated.

Consequences of small-scale patterns of dispersion

Both numbers of settlers and recruits on SHUs varied significantly during the sampling period (Table 3). These differences were due ostensibly to daily variability in the supply of pre-settlement fish and the subsequent accumulation of fish in the demersal habitat.

The relative importance of initial patterns of settlement and of mortality immediately after settlement varied between experimentally produced clumped and random habitats. Overall, there was significantly greater settlement to the random than the aggregated habitats (Fig. 5, Table 3). The total number of settlers observed averaged 54.75 (SE 5.96) on the random replicates versus 28.41 (SE 4.86) on the clumped SHUs. However, differences in the intensity of settlement between treatments varied with the sampling date (Table 3). As Fig. 5 illustrates there were some dates when settlement to the two treatments was similar, while on others settlement was higher to the random SHUs.

In contrast to patterns of settlement, no difference in the numbers of recruits over all dates was detected between random and aggregated habitats (Fig. 6, Table 3). Only on August 7, one day following the greatest pulse of settlement, was there a substantial difference in recruitment between the treatments. Although on 12 of 14 of the sampling dates the average number of recruits was higher on random SHUs than on clumped habitats, high variability within treatments resulted in a non-significant statistical result.

Recruitment is a function of the numbers of settlers minus the subsequent loss of settlers due to mortality and migration. Because I could not detect a difference in recruitment between the treatments, yet settlement was higher on random than clumped SHUs, mortality or migration of newly settled fish must have been greater on the randomly placed SHUs. Moreover, as censuses of the SHUs were performed frequently (often daily, Fig. 5 and 6) differential loss of newly settled fish must have occurred soon after settlement. Consequently, the difference between the clumped and random treatment which was set by settlement was subsequently reduced by differential mortality or migration.

Potential demersal predators occupying the SHUs were also enumerated. Sculpins *Myoxocephalus aeneus* were the only demersal predators observed and their densities did not vary between the treatments ($T = 0.84$, $p = 0.41$). The only other common animal inhabiting the SHUs was the crab *Cancer irroratus* and no difference in their densities was detected between the treatments ($T = 0.397$, $p = 0.70$).

Discussion

Spatial pattern of recruitment

Fish settling from the water column to the benthos require habitats in which they can obtain adequate food and cover so that they may mature and reproduce. By selectively settling in the presence of conspecifics these larvae would colonize sites where conspecifics have been successful in acquiring food and protection from predation. This appears to explain aggregated settlement in many sessile invertebrates and some reef fish (e.g. Highsmith 1982; Sweatman 1985). However, the clumped distribution of cunner recruits cannot be explained by this mechanism. In the present study, I did not detect higher recruitment on experimental habitats "seeded" with conspecifics, nor was any association of recruitment and conspecific density observed within or among sites.

These results corroborate the findings of several workers. Doherty (1983) performed experiments on the damselfish *Pomacentrus wardi*, in which the removal of resident conspecifics had no effect on levels of recruitment. Likewise, Jones (1984a) found that the removal of adult *Pseudolabrus celidotus* (Labridae) on temperate reefs had no effect on recruitment. By contrast, the presence of resident conspecifics enhanced recruitment of the damselfishes *Dascyllus aruanus* (Sweatman 1983, 1985; Forrester 1988), *Dascyllus retuculatus* (Sweatman 1985), *Dascyllus albisella* (Booth 1991), and *Chromis caerula* (Sweatman 1985) to experimental coral heads.

The experiments of Sweatman (1983, 1985) and Forrester (1988) were procedurally similar to mine; however, the results of this study differ in several respects from their findings. Densities of cunner recruits, corrected for differences in the sizes of the experimental habitats, were generally greater than Sweatman (1985) or Forrester (1988) observed for *D. aruanus* and *D. retuculatus*. Additionally, spatial variation in recruitment was much higher for *D. aruanus* (Forrester 1988) than for cunner. These differences may be the result of differences in the length and periodicity of the settlement season of the two species. All recruitment of cunner occurs within a one month period (Levin, unpubl.), whereas the recruitment season of *D. aruanus* is much longer (Sweatman 1985). As a result the outcome of an entire settlement season was observed in this study with only a relatively short time for high densities of fish to be lowered by mortality or emigration.

A strong relationship between the density of recruits and older stages could arise from a preference of settling fish for conspecifics, or could indicate that attributes of a habitat make it attractive to settling fish and provide resources necessary for survival to maturity. Species which use the same habitat throughout their life should show a positive relationship between the density of recruits and older stages as long as resources are not in short supply. Thus, for species such *Dascyllus aruanus*, in which recruits and adults occur in the same habitat, adults would be a reliable indicator of appropriate habitat. However, ontogenetic changes in resource requirements would make the presence of older conspecifics poor indicators of habitat quality for recruits. The absence of a relationship between recruits and older stages would thus be expected. For example, cunner recruits prefer macroalgal microhabitats, as is the case in many other fishes on temperate reefs (Wheeler 1980; Jones 1984a; Ebeling and Laur 1985; Carr 1989; DeMartini and Roberts 1990; Holbrook et al. 1990). However, as cunner grow, their dependence on macroalgal cover decreases and adults can often be seen in urchin dominated habitats where algal cover is sparse (Fig. 2, Pottle and Green 1979). Consequently, the presence of adult conspecifics would not be a reliable indicator of appropriate habitat for newly recruited cunner. Thus, unless older conspecifics, themselves, confer some fitness advantage, there is no expectation that cunner recruits, or recruits of other species with changing resource requirements, would be associated with older conspecifics.

It is more likely that settling larval cunner respond directly to attributes of the habitat than to the presence of conspecifics. Newly recruited cunner were found in higher densities in habitats in which the canopy was removed and only understory was present. This result agrees with previousl work which demonstrated an association of cunner results with microhabitats dominated by filamentous and foliose algae (Levin 1991). Additional laboratory experiments suggest this association is at least partially the result of active choice (Levin unpubl.). The role of differential mortality or migration among habitats was not investigated in this study and may also be important in determining patterns of recruitment. In addition, patterns of dispersion of recruits corresponded exactly to those exhibited by macrophytes in natural habitats or experimentally created habitats. Consequently, the dispersion of recruits at different spatial scales seems to be a response to patchiness of macrophytes.

Studies in other temperate systems have also noted that the dispersion of recruits appears to be influenced by habitat patchiness. On oyster reefs in Chesapeake Bay, Breitburg (1989, 1991) found that aggregation patterns of recently settled gobies *Gobiosoma bosci* were affected by topographic relief provided by rocks and the oyster reef. Jones (1984b), working on rocky reefs in New Zealand, found that 0+ year wrasses *Pseudolabrus celidotus* exhibited clumped patterns of dispersion, and suggested that the over-dispersion of these fish was, in part, a response to patchiness of appropriate habitat. Some plant species also show highly aggregated patterns of recruitment, and these also appear to the result of the dispersion of favorable microsites rather than effects of conspecifics (Fowler 1988). The present study, as well as those cited above, suggest that variation in spatial patterns of recruitment in many species may, in fact, be more predictable than current thinking would suggest.

Consequences of the spatial pattern of habitat on recruitment

In experimentally created habitats, settlement was higher to randomly placed than clumped habitats. However, no statistical differences in recruitment were detected between the two treatments. Consequently, initial patterns of settlement were modified by mortality or emigration to a greater extent in the random than in the clumped habitats.

The mechanisms producing these differences were not investigated; however, several non-mutually exclusive possibilities seem likely. First, although the actual areas of habitat were equal between the random and clumped treatments, if the attractiveness of the habitat extended some distance beyond their borders, than dispersed habitats would present a larger target to pelagic, pre-settlement fish. Therefore, a randomly moving pre-settlement fish would more likely encounter a random treatment than a clumped treatment, just as a propagule is more likely to colonize a larger than smaller island (MacArthur and Wilson 1967).

Second, while the densities of demersal predators did not vary between treatments, large schools of pelagic predators, particularly pollock *Pollachius virens*, were common. I frequently observed large schools of pollock feeding on cunner recruits living on SHUs and in natural habitats. As these predators moved through the experimental area, they too may come upon the randomly placed SHUs more frequently than the clumped ones. Larger aggregations of recruits may also suffer lower rates of predation due to the increased vigilance of the group or decreased foraging efficiency of the predator in large aggregations of fish (Hobson 1978). As a result, post-settlement mortality due to predation may have been greater on random than clumped SHUs.

Third, it is also conceivable that density dependent mortality due to competition or predation modified initial patterns of settlement. The best evidence for density dependence in reef fishes involves competition for food resources, which appears to affect growth rate more than mortality (Thresher 1983; Jones 1986, 1987; Forrester 1990); thus, it seems unlikely that competition was important to mortality occurring within the first 24 h after settlement. However, if predators respond to variability in the number of cunner recruits, density dependent mortality due to predation may be important (Gendron 1987).

Fish ecologists have investigated how the trade-offs between protection from predation and the quality of food govern patch selection (Mittelbach 1981; Werner et al. 1983; Schmitt and Holbrook 1985; Holbrook and Schmitt 1988). However, to my knowledge, the ways in which demographic processes vary with patch structure, particularly the dispersion of habitat types, had not been directly addressed for reef fish until this study. In terrestrial systems the spatial structure within habitats has been demonstrated to have significant impacts on demographic processes (Wiens 1976; Antonovis and Levin 1980; Addicott et al. 1987). Møller (1991), for example, found the patch structure of the habitat affected nest predation for several bird species. Variation in the spatial structure of the habitat can result in different degrees of aggregation in endophytophagus insects (Southwood and Kennedy 1983) and these differences may influence survival (Godfray 1986; Auerbach and Simberloff 1989; Faeth 1990), predation rates (Itamies and Ojanem 1977) or parasite load (Faeth 1990). Given the evidence gathered in other systems, it is not surprising that the dispersion of the habitat influenced the demography of juvenile cunner. However, counter to much current thinking, this result suggests that in order to understand the population dynamics of reef fishes, knowledge of what habitats settlers use and how subsequent losses vary with structural aspects of those habitats is critical.

Implications for models of recruitment-limitation

One generally accepted feature of reef fish populations is that they exhibit dramatic spatial and temporal fluctuations in recruitment (Doherty and Williams 1988). The significant spatial variation of recruitment in cunner certainly conforms with this belief. Nonetheless, the question relevant to the dynamics of populations is "does variability in recruitment exclusively determine abundance of demersal populations?" For this to be the case, settlement must be independent of the size of the resident population, and population size must be dependent on levels of settlement (Jones 1991).

No measurable effects of variability in the size of conspecific populations on recruitment were found in this study. This is consistent with the first requirement of recruitment-limitation. The second criterion of the model, however, is clearly not met. When the dispersion of patches was experimentally manipulated, variability in settlement between experimental treatments was not reflected as variation in the population of older fish (i.e. recruits). In this case density independent loss which was influenced by patch structure, or density dependent mortality or migration modified patterns of settlement differently in the two experimental habitats.

It is apparent that both rates of settlement and subsequent benthic mortality or migration may contribute to population fluctuations in demersal fishes (Warner and Hughes 1988). Recently several workers have called for a more pluralistic approach to the study of populations of reef fish (Warner and Hughes 1988; Jones 1987, 1990, 1991; Forrester 1990; Connell and Jones 1991; Sale 1991). The data presented here strongly support this argument. This study demonstrated that the relative importance of settlement and post-settlement mortality or emigration varies among experimental habitats of different structure, and it is evident that a singleprocess model cannot adequately explain the population dynamics of different reef fish species or of populations of single species in different habitats.

Acknowledgments. To P.F. Sale, T.P. Good, G.E. Forrester, L.G. Harris, A.C. Mathieson, R.R. Olson, R.R. Warner, and J.D. Witman, I offer gratitude for extensive comments on various aspects of this work. I thank P.F. Sale, M.A. Hixon, T.P. Good, R.R. Warner, and an anonymous reviewer for their comments on the manuscript. Thanks also to the staff of the Shoals Marine Lab, Capt. P. Pelletier and the crew of the R/V Jere Chase for providing logistical and moral support. Many thanks also to the divers who assisted me in the field, particularly J. Maret, L. Saabe, E. Wright, D. Lockett, B. McCarthy, and L. Neaveu. Most of all thanks to M.J. Levin. This work was supported by a development grant from New Hampshire/Maine Seagrant and NSF grant OCE-9102027 to P.F. Sale and P.S. Levin.

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