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Fine-scale temporal variation in recruitment of a temperate demersal fish: the importance of settlement versus post-settlement loss

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Abstract In order to understand variability in recruitment to populations of benthic and demersal marine species, it is critical to distinguish between the contributions due to variations in larval settlement versus those caused by post-settlement mortality. In this study, fine-scale (1–2 days) temporal changes in recruit abundance were followed through an entire settlement season in a temperate demersal fish in order to determine 1) how dynamic the process of recruitment is on a daily scale, 2) whether settlement and post-settlement mortality are influenced by habitat structure and conspecific density, and 3) how the relationship between settlement and recruitment changes over time. "Settlement" is considered to be the arrival of new individuals from the pelagic habitat, and "recruitment" is defined as the number of individuals surviving arbitrary periods of time after settlement. Replicate standardized habitat units were placed in 2 spatial configurations (clumped and randomly dispersed) and monitored visually for cunner (*Tautogolabrus adspersus*) settlement and recruitment every 1–2 days throughout the settlement season. The process of recruitment in *T. adspersus* was highly variable at a fine temporal scale. Changes in the numbers of recruits present on habitat units were due to both settlement of new individuals and mortality of animals previously recruited. The relative importance of these two processes appeared to change from day to day. The magnitude of the change in recruit number did not differ between the clumped and random habitats. However, post-settlement loss was significantly greater on randomly dispersed than clumped habitats. During several sampling dates, the extent of the change in recruit abundance was correlated with the density of resident conspecifics; however, on other dates no such relationship appeared to exist. Despite the presence of significant relationships between the change in recruit number and density, there was no evidence of either density-dependent mortality or settlement. Initially, there was a strong relationship between settlement and recruitment; however, this relationship weakened over time. Within 2 months after the cessation of settlement, post-settlement loss was greater than 99%, and no correlation remained between recruitment and the initial pattern of settlement. The results of this study demonstrate that the spatial arrangement of the habitat affects the rate and intensity of post-settlement loss. Counter to much current thinking, this study suggests that in order to understand the population ecology of reef fishes, knowledge of what habitats new recruits use and how mortality varies with structural aspects of the habitats is essential.

Key words Recruitment · Reef fish · Habitat structure Gulf of Maine · Temperate reef

Introduction

Habitats are frequently composed of mosaics of patches, some of which are used by a particular species while others are not (Addicott et al. 1987). Variation in the dispersion of preferred habitat patches within a habitat can have important consequences for the demography of many taxa. Theoretical studies have demonstrated the importance of the spatial arrangement of habitat patches for the persistence (Lomnicki 1978) as well as abundance (Taylor and Taylor 1977; Hanski 1985) of populations. Additionally, empirical investigations have shown that differences in the degree of spatial aggregation of individuals within a habitat can influence survivorship (Godfray 1986; Auerbach and Simberloff 1989; Faeth 1990), predation rates (Itamies and Ojanem 1977; Møller 1991) and parasite load (Faeth 1990). Fish

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ecologists have investigated how trade-offs between securing protection from predation and gaining high quality food govern patch selection (Mittelbach 1981; Werner et al. 1983; Schmitt and Holbrook 1985; Holbrook and Schmitt 1988). However, the ways in which demographic processes vary with the patch structure of a habitat, particularly the dispersion of preferred habitat types, has received surprisingly little attention for demersal or benthic marine fishes.

Pronounced differences in recruitment and subsequent local population abundance occur over a range of temporal and spatial scales in benthic invertebrates (Grosberg 1982; Caffey 1985; Olson 1985; Raimondi 1990), algae (Deyster and Dean 1986; Reed et al. 1988; Levin and Mathieson 1991) and demersal fishes (Williams and Sale 1981; Doherty 1983; Victor 1983; Jones 1984a; Sale et al. 1984; Carr 1991; Levin 1991). Predictive models for dynamics of populations of reef fish have recently emphasized the relative importance of larval supply, the settlement of larval and post-larval fish, and post-settlement growth and mortality (Jones 1991; Hixon and Beets 1993). As it has been difficult to measure settlement of fish in the field directly (but see Breitburg 1989, 1991; Levin 1993), most fish ecologists have measured recruitment. I define settlement as the time when an individual takes up permanent residence in the demersal habitat (Keough and Downes 1982), and recruitment as numbers of individuals surviving some arbitrary period of time after settlement (Connell 1985). Measured rates of recruitment equal the number of individuals that settle minus the fraction of fish that settle but die before being censused. The latter can be a significant fraction in some species, particularly if several days elapse between censuses of recruits (Doherty and Sale 1986; Sale and Ferrell 1988; Booth 1991).

How demersal fish populations are regulated has become an issue of vigorous debate. Historically, three hypotheses have been posed to explain variability in the distribution and abundance of fish. I present these hypotheses as alternatives; however, recent work has emphasized the need to adopt a more pluralist approach that does not view them as mutually exclusive (Doherty and Williams 1988; Warner and Hughes 1988; Doherty 1991; Hixon 1991; Jones 1991; Hixon and Beets 1993). One hypothesis, the "resource limitation hypothesis" asserts that the size of benthic populations is limited by the availability of resources. According to this model potential settlers are plentiful, and competition for resources (usually space or food) results in density-dependent rates of recruitment. The prediction from this model is that larval settlement and/or post-settlement survival is inversely related to the densities of conspecifics or ecologically similar individuals at the settlement site (Doherty 1983).

An alternative hypothesis, the "recruitment limitation" hypothesis, asserts that sites are undersaturated with new recruits and that sizes of populations are limited or determined by levels of recruitment (Doherty 1981, 1983; Victor 1983). This model predicts that settlement and post-settlement mortality are independent of the densities of conspecifics or potential competitors, and variation in settlement is expressed as variability in older age classes (Doherty 1983).

A third alternative, the "predation hypothesis" suggests that piscivores strongly influence the abundances of demersal fishes (Hixon 1991; Hixon and Beets 1993). This hypothesis asserts that predation pressure on individual fish is intense and abundances are kept low enough that resources, except those as refuges from predation, are seldom limiting. Thus variation in recruitment should result from variability in predation pressure.

Tests of these models for demersal fish populations have been conducted largely in coral reef habitats (e.g. Doherty 1983; Victor 1986; Jones 1987, 1990; Forrester 1990; Caley 1993; Hixon and Beets 1993). Recently, however, some workers have addressed the roles of settlement and post-settlement processes on temperate rocky reefs (Jones 1984a, b; Carr 1989, 1991; Connell and Jones 1991; Levin 1993). A major component of the structure of temperate reefs is macroalgal vegetation, and juvenile temperate reef fish are commonly associated with seaweeds (Wheeler 1980; Jones 1984a, b; Carr 1989, 1991; Holbrook et al. 1990; Levin 1991, 1993). The macroalgal structure of temperate reefs can vary considerably in space and time and is more ephemeral then the structure of tropical reefs (Dayton 1985; Chapman and Johnson 1990; Lambert et al. 1992).

The close association of juvenile fish with macrophytes may have a profound influence on the demography of fish populations. The dispersion of juvenile fish in habitats in which algae are clumped may also be aggregated (Jones 1984c, Levin 1993) thus influencing the small-scale density of fish and potentially affecting the processes that determine the size of local populations. In clumped habitats, locally high fish densities may result in resource shortages that might not occur in habitats that are randomly dispersed. If the ability of fish to find cover varies among habitats of different patch structure then the effects of predation may also vary among habitats. Thus, variability in the dispersion of seaweeds may affect the relative contributions of larval settlement and post-settlement mortality in determining local population size.

The purpose of this study was to test the predictions of population models for reef fishes using a temperate demersal fish in habitats of different patch structure. Changes in recruit abundance due to settlement, post-settlement loss or both were observed at a fine temporal scale (1–2 d) and the importance of habitat structure and resident fish densities to changes in the recruit population were examined. Specifically, I asked: 1) Are fine-scale temporal changes in recruit number influenced by the dispersion of habitat patches? 2) Are changes in recruit abundance affected by the density of resident conspecifics? 3) Is the relationship between settlement and recruitment sustained over time or affected by the dispersion of habitat patches?

Methods

Study species

Cunner *Tautogolabrus adspersus* Walbaum 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 Newfoundland, Canada to New Jersey, U.S.A. (Bigelow and Schroeder 1953). The larval life of cunner averages 18–21 days (Gleason and Reschiek 1990), and they settle to macroalgal habitats dominated by foliose and filamentous algae (Levin 1991, 1993). In the Gulf of Maine, cunner usually spawn in July and thus settlement occurs in late summer (Levin 1993b). In their first year, fish generally reach a length of 25–30 mm (Levin 1993b), and can eventually reach a maximum size of 300 mm (Bigelow and Schroeder 1953). As juveniles, cunner are site-attached and do not stray far from cover (Olla et el. 1975; Pottle and Green 1979; Levin 1991). Recent tagging experiments with newly settled fish have shown that cunner spend their first year within a few square meters (M. Tupper, Dalhousie University, unpublished data). Even as adults, home ranges of cunner are quite small ($< 3000\ m^2$) with most of their activity limited to core areas averaging $< 100\ m^2$. (Pottle and Green 1979; Bradbury 1993). Cunner overwinter in a torpid state within their home ranges (Green and Farwell 1971).

General methods

The study was conducted in April–October, 1991 in Gosport Harbor, Isles of Shoals, New Hampshire, USA (42°59′N 70°37′W). This site provided a protected, relatively level plain with sandy substrata at a depth of 4–9 m mean low water. In April an experiment commenced using standard habitat units (SHUs). SHUs were constructed from 0.5 cm wire mesh placed across a 0.5 m × 0.5 m frame fashioned from 1 cm diameter PVC pipe. Filamentous algae were allowed to colonize the mesh, and thus they provided a habitat similar to the one naturally used by young cunner. By July, 1991 algal coverage on all SHUs was approximately 100%, and levels of algal colonization to different SHUs appeared to be equal. To prevent burial by shifting sand, legs were attached to SHUs so they stood 0.5 m above the substratum. SHUs were placed in two spatial patterns: 1) clumped – 4 SHUs adjacent and touching to form a 1 m × 1 m square; and 2) random – 4 SHUs placed randomly except that they were separated from each other by no more than 1–2 m. Each set of 4 SHUs was separated from other sets and from natural habitat by at least 6 m. The physical differences between these habitats are summarized in Table 1. There were 12 replicates of each of the spatial patterns. As settlement and recruitment are negatively correlated with depth (Levin 1993), I ensured that equal numbers of replicates were allocated to each of 3 depth zones (4–6 m, 6–8 m, 8–10 m). Because juvenile cunner are extremely site-attached and SHUs were separated from each other and natural habitat, additions to the SHUs were expected to be the result of larval settlement rather than demersal migration.

SHUs were visually censused on 11 of the 17 days when cunner settlement was observed in 1991 (August 1–17) and on 2 more dates following the settlement season (August 28 and October 21). On August 26 Hurricane Bob passed approximately 4 miles from the study site. Thus, this sampling period included a potentially major disturbance. Visual censuses consisted of a diver counting all the fish while slowly circling the SHUs. Due to difficulties in locating all replicates, not all replicates were censused on the first 2 sampling periods. Since settling individuals are translucent and appear to assume full pigmentation 24 hours after settling, fish were scored as settlers only if they were translucent. My index of settlement underestimated settlement, but should have done so in a uniform fashion among replicates. Fish were recorded as recruits if they were fully pigmented. The entire surface of both clumped and random SHUs were easily observed by divers and the ability of divers to observe fish did not differ between treatments. Thus, it is unlikely that there was significant sampling bias between the two habitat types.

Data analysis

Changes in recruit abundance for each group of 4 SHUs were determined by subtracting the recruit number counted on one day from the recruit number counted on the next census (1 or 2 days later). The hypothesis that changes in recruit abundance were affected by the dispersion of habitat patches was tested using an analysis of variance in which the experimental factor (clumped vs. randomly placed SHUs) was considered a fixed factor and different sampling periods were considered a random factor and a repeated measure (Winer et al. 1991). Each group of 4 SHUs was considered a replicate. Because not all replicates on the first 2 sampling dates could be visited, Type III sums of squares were used to perform the ANOVA (Wilkinson 1990). Data were log transformed to meet the assumptions of analysis of variance. Probability plots and Bartlett's test indicated that data were approximately normally distributed and variances were homogeneous.

To determine if changes in recruit number were associated with the density of conspecifics on each set of 4 SHUs, regression analyses were performed in which the change in recruit number between two successive sampling periods was the response variable and the density estimated during the earlier period was the independent variable. In this analysis, the change in recruit number results from two different processes, settlement and post-settlement loss, that may act simultaneously and have opposite effects. The measured daily change is thus an index of the relative importance of settlement versus post-settlement loss during the sampling interval. This analysis is limited, however, since it masks the precise mechanisms producing the observed changes. Because changes in recruit density are influenced by both settlement and post-settlement loss, variation in the response variable is not constrained by the density of the resident population. For all regression analyses, residuals were examined to ensure they were approximately normally distributed, had a constant variance and were independent (Wilkinson 1990). Analysis of covariance was used to compare the slopes and intercepts of the regression lines for the clumped and random treatments.

Two null hypotheses were tested with the regression analyses. First, I tested the null hypothesis that the slope of the regression line did not differ from zero. A significant positive slope indicates that there was greater net growth in numbers of resident recruits on SHUs with higher resident densities. Similarly, a significant negative slope indicates that there was greater net loss of recruits on SHUs with higher densities.

A significant result from this analysis does not demonstrate density dependence, since greater post-settlement loss is expected on replicates with more fish. To test for density dependence, I further analyzed data for those sampling periods in which the slope of the line was significantly different from zero. My working hypothesis was that the slope of the regression line had a greater negative slope than the line expected from simply higher loss with higher densities. The expected line was generated from the data by determining the average proportional change in recruit number over the entire settlement season. The proportional change was determined by dividing the number of recruits present on a SHU at time $t+1$ by the number present at time t. Proportions for each SHU from all sampling dates during the settlement season were then averaged. This value was multiplied by a range of densities (0–100) and then plotted against that density to generate the expected line. A one-tailed t-test was then used to test the hypothesis that the observed regression line had a more negative slope than the expected line.

To investigate how these patterns of change might influence the recruit-settler relationship, I examined the relationship between the number of settlers I observed from August 1 through August 17 and the number of recruits on August 17, 28 and October 21. August 1 was the first date I observed a newly settled fish, and August 17 was 2 days after the last appearance of cunner pre-settlement fish in plankton tows conducted at the Isles of Shoals (Levin unpublished data). This approach is similar to the one used by Connell (1985) and Davis (1988). It suffers from the problem that the number of recruits is constrained by the number of settlers. Consequently, conventional significance tests of the correlation coefficient are not valid (McGuiness and Davis 1989). However, these data are presented to demonstrate a qualitative change in the recruit-settler relationship over time, and I do not attempt to draw statistical inferences from these data. Correlation coefficients are reported simply to illustrate changes in settler-recruit relationship over time.

I also examined the association between cumulative number of settlers I observed from August 1 through August 17 and the proportion of those settlers still present on the SHUs on August 17, 28 and October 21. The proportion of settlers present on the SHUs was determined by dividing the number of recruits by the cumulative number of settlers. Since fish were considered settlers only if they were still translucent when sighted, this is a conservative measure of settlement which underestimates settlement. Consequently, some proportions were greater than 1. The arcsine transformed data were analyzed using analysis of covariance to examine proportional loss with respect to initial density, date, and patch dispersion. An effect of initial density on the proportion of settlers remaining suggests mortality is density-dependent (McGuiness and Davis 1989).

Results

Fine-scale temporal patterns of change and the effect of habitat structure

Dramatic changes in recruit number were observed on a fine temporal scale; however, there were no consistent differences between clumped and random habitats in the change in recruit number (Fig. 1). There was frequently as much as a 10 fold difference in the mean change in recruit number among sampling periods. No pattern in the magnitude of change over the settlement season emerged. Large and small changes appeared interspersed with each other and occurred throughout the settlement season.

The sign of change (positive or negative) reveals whether larval settlement or post-settlement loss is of greater significance in producing the observed changes. A mean positive change indicates that gains from larval settlement were, on average, relatively greater than post-settlement losses. Likewise, a mean negative change suggests that post-settlement losses were larger than gains from settlement. Because cunner recruits are site-attached, and migration is rare (Tupper, unpublished data), loss of recruits is assumed to be due to mortality rather than migration. Figure 1 illustrates that the relative importance of settlement versus post-settlement mortality often varies on a daily basis. For example, during the August 6–7 sampling period larval settlement was of greater importance than post-settlement loss on the random treatment, while post-settlement loss was of more importance during the August 7–8 sampling period. The opposite was true for the clumped treatment. Here, post-settlement loss was more important than settlement during the August 6–7 period, while larval settlement dominated the August 7–8 sampling period.

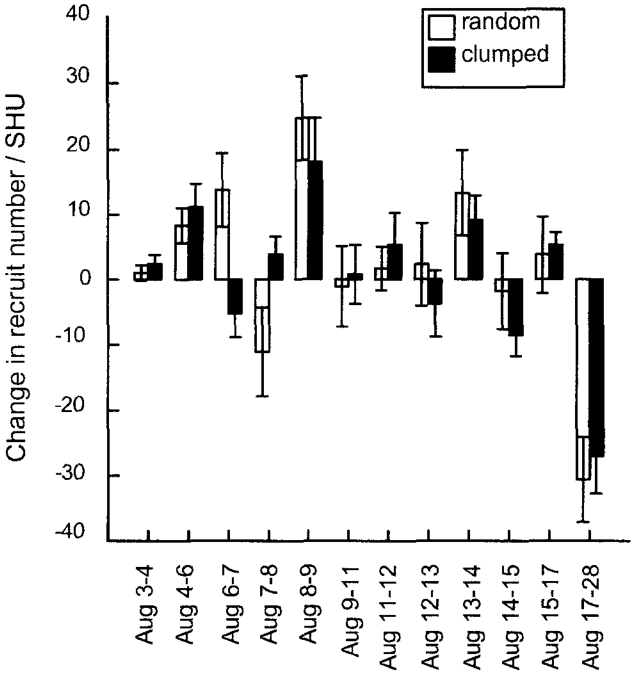

Fig. 1 The mean change between censuses in recruit number per set of 4 standard habitat units (SHUs) is plotted for each sampling period. A repeated measures ANOVA revealed that there were significant differences in the average change in recruit density among sampling dates ($F_{11,33} = 5.537$ $P < 0.001$); however, no difference was detected between clumped versus randomly placed SHUs ($F_{1,3} = 2.597$, $P = 0.20$). Error bars are ±1 SE

Table 1 A summary of differences between the clumped and randomly dispersed experimental habitats (SHUs) used in this study

	Treatment	
	Random	Clumped
Area of habitat	1 m^2	1 m^2
Bottom area covered by experimental replicates (including bare substratum between individual (0.25 m^2) habitat units)	ca. 4 m^2	1 m^2
Perimeter of habitat	8 m	4 m

The relationship between change in recruit abundance and initial density

Figure 2 summarizes the results of the 12 regression analyses examining the relationship between the change in initial density and recruit number for all 12 sampling periods. In no instance was the relationship influenced by the dispersion of the SHUs (ANCOVA, $p > > 0.05$). On 5 of the 12 sampling periods, there was a significant negative relationship between the change in initial density and recruit number (Fig. 2). In the other 7 sampling

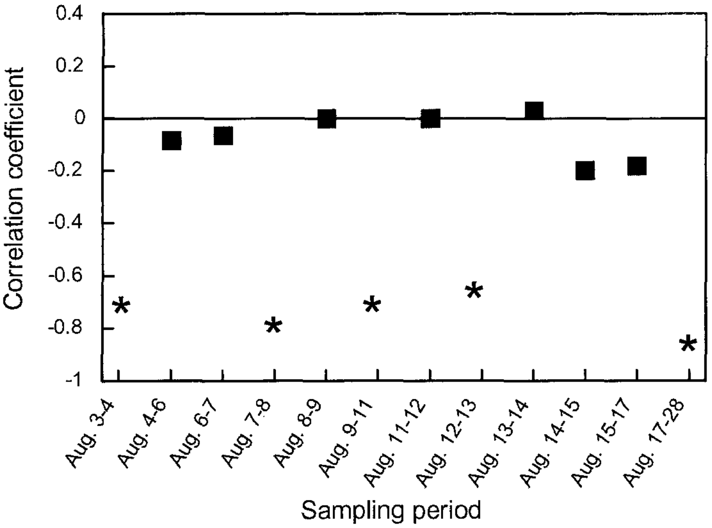

Fig. 2 The correlation coefficient between the change in recruit number per group of 4 SHUs and the initial density is plotted for each sampling period. Note that the last sampling period is 11 d while the other 11 sampling periods are 1–2 d. * indicates a significant relationship ($P < 0.05$) between the change in recruit number and initial density

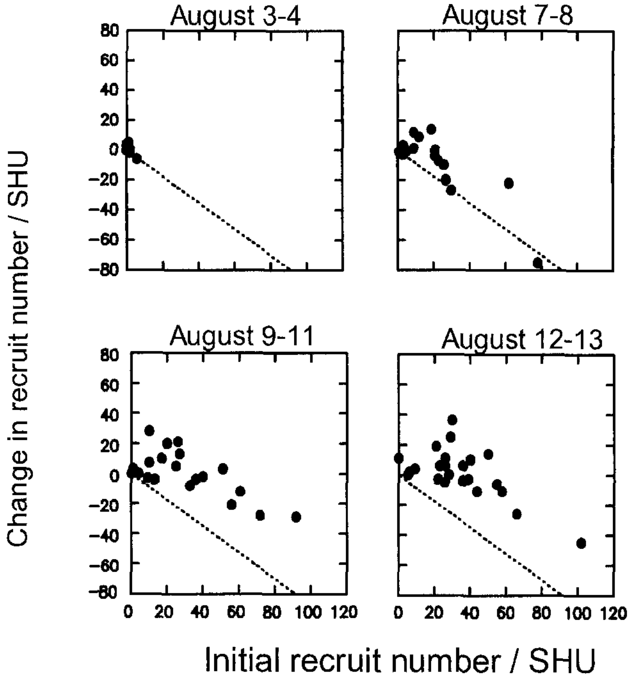

Fig. 3 For each sampling period during the 1991 settlement season (Aug. 1–17) in which the slope of the regression line was significantly different from zero (Fig. 2), the slope of the observed regression line is compared to the line expected if the change in recruit number is proportional to the density (slope = −0.872). For no sampling period tested was the observed slope significantly more negative than expected. (See text for details). The dashed line is the "expected" line

periods no relationship between change in initial density and recruit number could be detected (Fig. 2).

In order to determine if the significant relationships between changes in initial density and recruit number were the result of density-dependent processes, I tested the hypothesis that the slopes of the regression lines were more negative than would be expected simply if SHUs with greater densities of fish suffered higher losses. The August 17–28 sampling period was omitted from this analysis since this sampling period was longer than 1–2 day sampling interval used to derive the expected proportional change in recruit number. The mean proproportional change in recruit number. The mean proportional change in recruit number during the settlement season was 0.128. Thus, the line of the change in recruit number regressed against initial density is expected to have a slope of −0.872 (Fig. 3). The slopes of the observed regression lines were not significantly lower than the expected value for any sampling period (Fig. 3), and thus no evidence of density dependence was detected.

The recruit-settler relationship

There was a strong and positive relationship between cumulative settlement and recruitment on August 17 ($r = 0.75$, Fig. 4). One week following Hurricane Bob, the number of recruits was lower than on August 17, but a positive, albeit weaker, relationship between settlement and recruitment still existed ($r = 0.58$, Fig. 4). By October 21, a relationship between settlement and recruitment was no longer evident ($r = 0.004$) because few recruits remained on the SHUs (Fig. 4). In fact, by October 21 a total of 10 recruits of the 998 observed settlers remained. The loss of ca. 99% of the settlers was presumably due to mortality as a careful search of surrounding habitat also yielded very few recruits. This level of mortality was also observed in natural habitats and is typical for this species in the southern Gulf of Maine (Levin, unpublished data). Although settlement was greater to random than clumped SHUs (Fig. 4; see also Levin 1993), no difference in settler-recruit relationship between habitat treatments was apparent.

There was no relationship between the proportion of settlers that remained on August 17, August 28 and October 21 and the total numbers of settlers I observed throughout the settlement season (Fig. 5, Table 2). The proportion of fish that survived to the three sampling dates was similar on SHUs of varying densities. Consequently, at this temporal scale, there is no evidence of density dependence.

The dispersion of habitat patches did have an influence on the loss of settlers (Fig. 6, Table 2). A significantly higher proportion of fish was present on the clumped SHUs than on the randomly dispersed ones. This was particularly detectable on August 17 when the average proportion of fish present on the clumped treatment was ca. 40% greater than on the random treatment (Fig. 6). By October the average proportion of fish present was 14 times greater on the clumped treatment than on the random treatment. In fact, 8 of the 10 fish

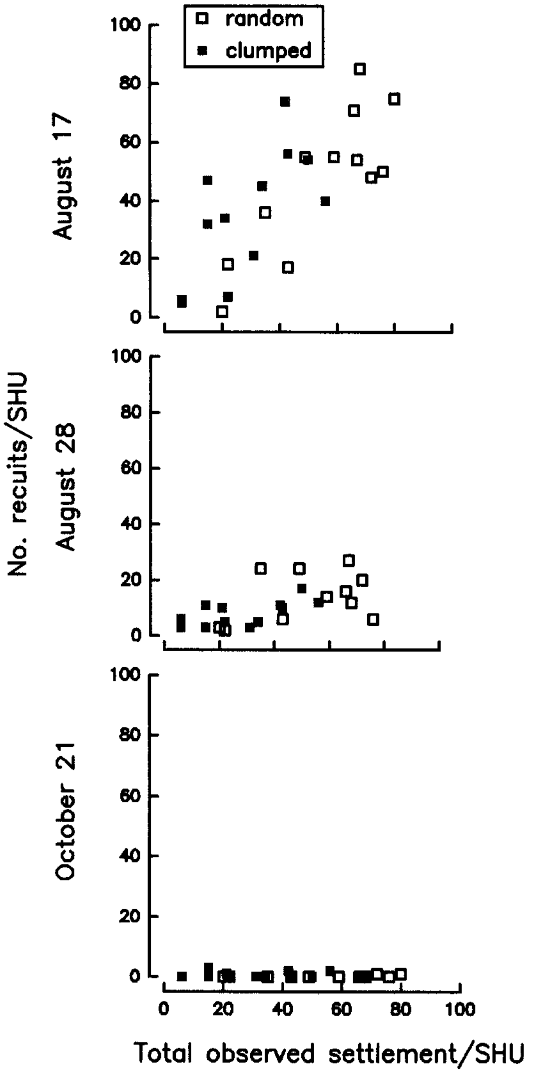

Fig. 4 Density of recruits on experimental habitats (SHUs) in random and clumped distributions for three sampling dates following the end of the settlement season vs. the total number of settlers observed during the settlement season. The correlation between the number of recruits and cumulative settlement weakens over time

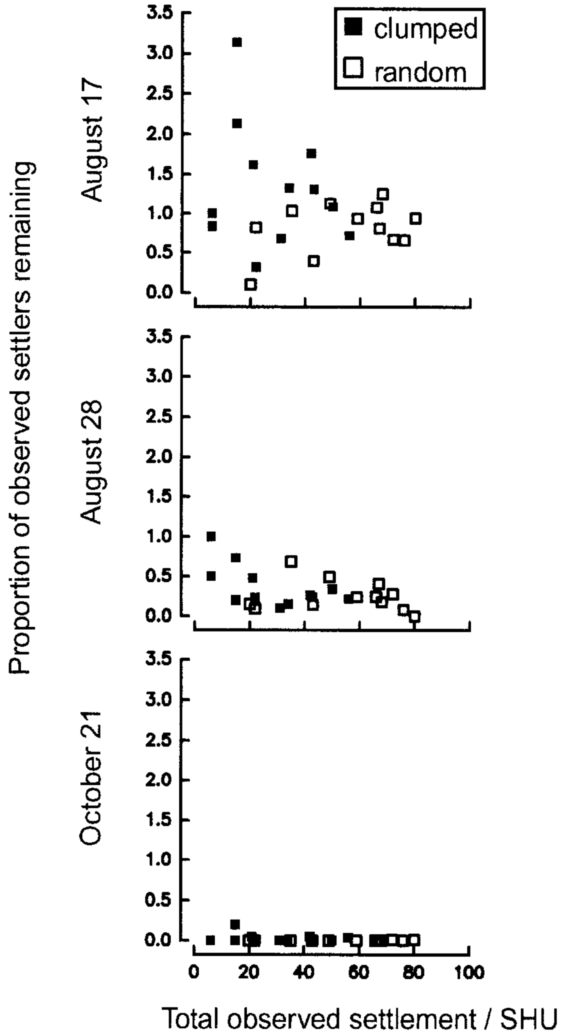

Fig. 5 The proportion of observed settlers remaining on each of 3 dates is plotted against the total observed settlement on each set of 4 SHUs. Proportions can be greater than 1 since a conservative measure of settlement was used (see methods). The relationship between the proportion of fish remaining and total settlement was not significant for any of the sampling periods ($R^2 = 0.04$, $P = 0.35$ on August 17; $R^2 = 0.15$, $P = 0.07$ on August 28; $R^2 = 0.02$, $P = 0.51$ on October 21)

that remained at the end of the experiment were on clumped SHUs.

Discussion

Settlement of post-larval *Tautogolabrus adspersus* occurs in a brief burst, which in 1991 lasted 17 days. During this time I observed 998 individuals settling to 24 m^2 of habitat (ca. 2.5 settlers $m^{-2}d^{-1}$). The process of recruitment in *T. adspersus* is very dynamic even at the fine temporal scale examined in this study. The magnitude of changes in recruit number, and the relative importance of settlement versus post-settlement loss both varied daily. Fine scale variability in changes in recruit numbers appeared to be density-independent and not influenced by the dispersion of the habitat. However, the proportion of settlers remaining at the end of the experiment was influenced by the dispersion of habitat patches. Post-settlement loss was greater in habitats composed of randomly dispersed patches versus aggregated patches. Post-settlement loss was high and variable, and the relationship between cumulative settlement and recruitment was present but weak. By the end of the experiment 99% of fish were gone. As a result, there was no realistic chance that spatial variation in settlement could be expressed as recruitment variation except as related to habitat patchiness.

It is unlikely that the apparent temporal decline in the strength of the correlation between recruitment and settlement was the result of migration from the experimental habitats. The habitats were isolated from each

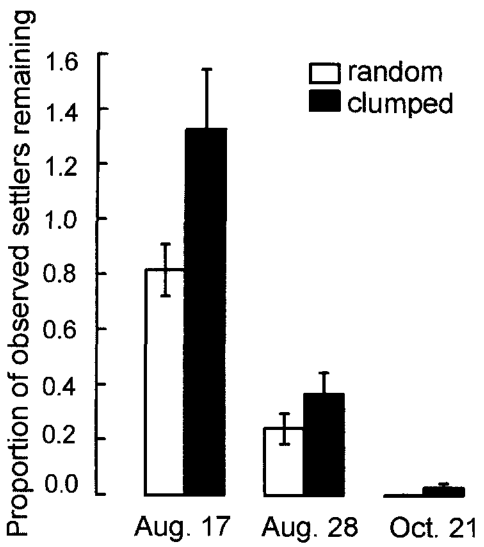

Fig. 6 The mean proportion of settlers remaining on random and clumped SHUs are shown for 3 dates. A significantly higher proportion of fish was lost from the random than the clumped SHUs. There was also a significant decline in the proportion of settlers remaining over time (Table 2). Error bars are ±1 SE

Table 2 Results of a two factor analysis of covariance used to determine if variation in the proportion on settlers remaining on experimental habitats changed with time, between experimental habitats of different patch structure (clumped vs. random), or was influenced by the number of settlers each replicate habitat received. Interaction terms that were not significant ($P > 0.1$) in the full model were removed from the model. Habitat refers to habitat dispersion treatment. *$P < 0.05$, ***$P < 0.001$

Source	SS	DF	MS	F
Habitat	0.096	1	0.096	4.945*
Date	2.027	2	1.013	51.925***
Settlement	0.022	1	0.022	1.141
Habitat X Settlement	0.055	1	0.055	2.818
Error	1.288	66	0.020	

other and from natural habitat by large distances, and these site-attached fish would have to cross large expanses of bare sand in the presence of large schools of mobile predators such as pollock *Pollachius virens*. Similar declines in abundances of *Tautogolabrus adspersus* recruits have been observed in the natural habitat surrounding the experiment as well as in sites throughout the southern Gulf of Maine for the last three years (Levin, unpublished data). For some species, however, emigration from settlement sites may be important to the demography of local populations (Sogard 1989).

The importance of the recruit-settler relationship for the interpretation of population and community studies

Since all fish populations experience some level of mortality, it is important to know the extent, timing and variability of mortality when inferences about settlement are to be drawn from infrequent recruitment surveys. If the dynamics of *Tautogolabrus adspersus* populations are typical, then studies that sample frequently may be able to draw inferences about settlement. On the other hand, for species, like *T. adspersus*, that suffer severe mortality in the first few weeks after settlement (Victor 1986; Shulman and Ogden 1987; Sale and Ferrell 1988; Hixon 1991), infrequent sampling to examine processes occurring at or around the time of settlement may result in erroneous conclusions (Booth 1991).

Models of community structure have been developed based on infrequent sampling. Sale and Douglas (1984), for example, proposed a model for the formation of assemblages of coral reef fishes on small patch reefs. From eight censuses conducted during a 33-month period they found that assemblages of fish on patch reefs possessed a structure which was temporally variable and largely independent of the reef structure. They suggested that vagaries in larval supply led to spatial and temporal variation in recruitment, and that assemblages on individual patch reefs were largely a product of this apparently stochastic variation. However, several of the common species found on the patch reefs that Sale and Douglas studied suffer high mortality as juveniles while others experience relatively low levels of mortality (Sale and Ferrell 1988). Consequently, the degree to which the patterns Sale and Douglas (1984) observed actually represented variable settlement may be species-specific. Thus, as Sale and Douglas (1984) noted, the composition of assemblages of fish is dependent on both settlement and subsequent loss, but the relative importance of these processes is likely to vary among species with different mortality schedules and cannot be determined from infrequent censuses.

A disintegration over time of the recruit-settler relationship can also influence the interpretation of population studies. Shulman and Ogden (1987) reported levels of mortality for Caribbean grunts similar to the level I observed for *Tautogolabrus adspersus*. Certainly, after only a short period of time, censuses of recruitment for these species have a great probability of yielding a distorted record of settlement. While extreme mortality may be unusual (cf Hixon 1991), precise data on settlement and subsequent rates of mortality are required to test models of population dynamics. Even moderate levels of mortality, particularly if it is variable, can weaken the recruit-settler relationship thus rendering any conclusions suspect (Warner and Hughes 1988; Jones 1991; Doherty 1991).

Implications for models of population dynamics

The principal prediction of the recruitment limitation model is that variation in settlement is expressed as variability in older age classes (Doherty 1983; Victor 1983; Doherty and Williams 1988). In order for densities of older fish to be controlled by levels of settlement, the size of the resident population must not affect rates of settlement and the size of the population must be dependent on levels of settlement (Jones 1991). Previous work (Levin 1993) has demonstrated that the presence of resident conspecifies does not influence levels of settlement in this species. However, because levels of mortality varied in habitats of different patch structure, spatial variation in settlement was not expressed as spatial variability in the abundance of older fish. The prediction of the recruitment limitation model is thus not supported for this species at the spatial and temporal scales examined in this study. Since the experiment was conducted for only one year, the significance of interannual variation of settlement on age structure is unknown. It remains possible that interannual differences in settlement would be reflected as variation in age class strength, and this would be consistent with the tenets of recruitment limitation.

The resource limitation model predicts that shortages of resources should result in density-dependent rates of recruitment. No evidence of density dependence was detected in this study. Moreover, the best evidence for density dependence in demersal fishes involves competition for food resources (Thresher 1983; Jones 1987; Forrester 1990). Competition for food appears to affect rates of growth and maturity more than survivorship (Peterson 1982; Jones 1987; Forrester 1990). Differential mortality, however, played an obvious and important role in determining the numbers of recruits at the end of the settlement season. Highly mobile predators, particularly pollock *Pollachius virens* were very common at the study site (pers. obs.), and I frequently observed schools of pollock foraging on cunner recruits on SHUs and in natural habitats. It is very likely that much of the post-settlement loss documented in this study was the result of predation. The loss of recruits was much greater on randomly dispersed than clumped SHUs. Despite higher levels of settlement in randomly dispersed habitats (Fig. 4; Levin 1993), at the end of the experiment 80% of the surviving recruits were on clumped habitats. The increased perimeter of randomly dispersed versus clumped patches may either increase the likelihood that mobile predators would detect a habitat patch or decrease the ability of recruits to hide from predators. In either case, predator pressure would be greater on randomly dispersed than clumped SHUs.

The results of this study support neither the recruitment nor resource limitation models, but provide circumstantial evidence for the predation hypothesis. The predation hypothesis predicts that abundances should be negatively related to the intensity of predation. As predation pressure was ostensibly related to the patch structure of the habitat, the results presented here are consistent with this hypothesis. Studies on coral reefs have demonstrated that the architecture of the habitat, particularly hole size and number, are important determinants of predation intensity (Shulman 1984, Hixon and Beets 1989, 1993). On temperate reefs increased biogenic structure is thought to reduce the impacts of predators (Holbrook and Schmitt 1988; Carr 1991). This study is the first to demonstrate the importance of the spatial arrangement of the habitat on the rate of post-settlement loss. It is important to note, however, that while predators, particularly pollock, were abundant and I observed pollock consuming large numbers of cunner recruits, there is no direct evidence that the mortality I observed was predominantly the result of predation.

At present, a cautious interpretation of these results is necessary. The study was only conducted at one site on artificial habitats, and detection of density dependence from a series of consecutive censuses is certainly more equivocal than experimental tests of density dependence. Recruitment (Levin 1993), macrophyte structure (Levin 1991, 1993), and predator abundance (pers. obs.) vary greatly among sites in the Gulf of Maine. Consequently, the relative effects of settlement and post-settlement loss on spatial and temporal variation in abundance may also vary. Nonetheless, this investigation adds to a growing number of studies that have established the necessity of considering post-settlement processes in models of demersal fish populations (Jones 1987, 1990; Shulman and Ogden 1987; Warner and Hughes 1988; Forrester 1990; Connell and Jones 1991; Caley 1993; Hixon and Beets 1993; Levin 1993).

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