

Small-scale recruitment variation in a temperate fish: the roles of macrophytes and food supply

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Synopsis

The availability of reef-related resources, particularly food and shelter can play a significant role in determining the distribution and abundance of reef fishes. Much of the structure on temperate reefs is provided by macroalgae, and variability in the density of temperate reef fishes at large spatial scales (100's of meters) can often be explained by variation in macroalgal cover or density. In this study I investigated the role of macrophytes and associated food resources on the recruitment of a temperate fish, *Tautoglabrus adspersus*, at a small spatial scale (0.25 m²). No relationship between the density of new recruits and the percent cover of kelp, foliose or filamentous algae was observed. Multiple regressions revealed that less than 8% of variability in recruitment could be explained by variability in macroalgal cover. However, recruits were found in higher abundance in patches containing many functional forms of seaweeds than in patches dominated by a single form. A wide variety of prey were available for use by cunner recruits; however, crustaceans and mussels were the only common components of their diet, and crustaceans were clearly the most preferred prey. The prey composition in patches where fish were present was compared to randomly selected patches. Significantly greater numbers of isopods, amphipods and newly settled mussels were present in patches where fish were present than in randomly selected patches. The data presented in this study contradict previous work that has shown algal structure to be important in determining patterns of abundance and food supply to be of little significance. A conceptual model is proposed suggesting that settling fish select habitats in a hierarchical manner largely based on their dispersal tendencies. Hierarchical selection of habitats results in different attributes of the habitat being selected during different life-history intervals.

Introduction

The demography of reef fishes in both tropical and temperate zones is affected by the interactive effects of patchiness in reef-related resources, particularly shelter from predators (Shulman 1984, Carr 1991a, Hixon & Beets 1993), and food (Schmit &

Holbrook 1985, Jones 1986, Forrester 1990). As juveniles, reef fishes generally have very small home ranges (Sale 1978), and some species suffer high early mortality (Shulman & Ogden 1987, Sale & Ferrell 1988, Levin 1994). The selection of appropriate habitat patches by juvenile fishes can thus have important consequences for the population dynam-

ics of these species. Since most reef fishes have pelagic larvae, colonization of patches usually occurs via the settlement of metamorphosed juveniles from the plankton to the demersal habitat. As a result, the covariance of larval settlement and reef-related resources is of great interest. In this paper settlement is operationally defined as the time when an individual takes up permanent residence in the demersal habitat (Keough & Downes 1982) and recruitment refers to the number of individuals surviving some arbitrary period of time after settlement (Connell 1985).

Variation in the abundance of fishes on temperate reefs, particularly at large spatial scales, can often be explained by variability in macroalgal structure (Jones 1988, Holbrook et al. 1990, Levin 1993a, Carr 1994). In addition, at small spatial scales the occurrence (presence/absence) of fish can be influenced by the presence of specific macroalgal habitats (Carr 1991b, Levin 1991). Algal habitats serve both as a source of food and as protection from predators (Ebeling & Laur 1985, Holbrook & Schmitt 1988). Macroalgal habitats vary extensively in space and time (Chapman & Johnson 1990, Lambert et al. 1992), thus offering associated fishes patches that differ in the quantity of food and/or quality of cover. In the few examples for temperate reefs examined thus far, effects of food resources on variability of recruitment seem slight (Jones 1984, Carr 1991a), but there appears to be a strong effect of algal habitat on the intensity of predation (Carr 1991a).

Although food supply has not yet been shown to influence recruitment variability, there are several reasons to suspect that it may, particularly at small spatial scales. Schmitt & Holbrook (1985) have shown that food richness rather than shelter potential is the major determinant of patch quality for juvenile black surfperch, *Embiotoca jacksoni*, in California. As a result, these fish choose algal patches based largely on food quality. Additionally, Jones (1986, 1987) and Forrester (1990) have shown that supplemental feeding of fish on coral reefs resulted in increased growth and/or earlier maturation rates.

While the data gathered to date suggest that large-scale variation in the abundance of recruits is affected by the density, cover, and/or height of sea-

weeds, a detailed study of how algal structure and associated food resources influence recruitment variation at small scales (meters) has not been conducted. In the present study I investigate patch use at a small spatial scale by a temperate demersal fish, *Tautoglabrus adspersus*, in the Gulf of Maine. Specifically, I ask: (1) What effect does small-scale variability in macroalgal cover have on variation in the abundance of newly recruited fish? (2) Do newly recruited fish have preferred prey? (3) Does the distribution of preferred prey influence spatial variation of recruitment?

Methods

Study species

Cunner, *Tautoglabrus adspersus*, are common members of rocky-reef communities in temperate waters of the western North Atlantic (Bigelow & Schroeder 1953). Cunner occur from intertidal zones (Whoriskey 1983) to depths greater than 90 m (Bigelow & Schroeder 1953), although newly recruited fish are most common in shallower depths (Levin 1993b). In the Gulf of Maine, the most intense period of cunner spawning occurs in July and early August (personal observation). Following a 18–21 day life as larvae (Gleason & Recksiek 1990), juvenile cunner settle to a wide range of habitats including both urchin-dominated areas and seaweed beds (Levin 1991). However, they are generally associated with macroalgal microhabitats (Levin 1991, 1993a). As juveniles, cunner have very small home ranges and do not stray far from algal cover (Olla et al. 1975, Pottle & Green 1979). Tagging studies have shown that cunner spend their first year within an area of a few square meters (M. Tupper unpublished data).

Adult cunner feed on a wide variety of motile and sessile invertebrates, particularly mussels, *Mytilus edulis* and *Modiolus modiolus*, urchins, *Strongylocentrotus droebachiensis*, and gastropods, *Lacuna vincta* and *Acmaea testudinalis* (Chao 1972, Green et al. 1984). During the spawning season, female and non-territorial males feed throughout daylight hours, while territorial males tend to feed more in

the morning (Green et al. 1984, 1985). Little published information exists on the diets of juvenile cunner. In 8 specimens (30–50 mm standard length) that Chao (1972) examined, micro-crustaceans (amphipods, isopods, copepods) dominated the diet. To my knowledge, no data exist concerning the diets of newly recruited cunner (10–12 mm standard length).

Macroalgae-recruitment relationships

The relationship between macroalgal cover and the density of newly settled recruits was investigated at two sites along the southern Maine coast near York, Maine (43° 10' N, 70° 36' W). In one site (site 1), filamentous, foliose and corticated macrophytes dominated the algal assemblage, while in the other site (site 2) the flora was dominated by kelps. Both sides were ca. 6.5 m in depth. Detailed descriptions of these sites are provided elsewhere (Levin 1991).

In order to estimate small-scale densities of cunner recruits, replicate 0.25 m² quadrats were placed randomly in each site (n = 81 in site 1; n = 79 in site 2). Randomization was accomplished using pairs of random numbers to indicate a compass direction and distance from a haphazard starting point. After counting all recruits, the percent cover of macroalgae in each quadrat was determined by recording the type of plant under each of 45 points created by a grid of monofilament line strung across the quadrat. Because previous work (Levin 1991, 1993a) has shown that erect, fleshy forms of algae are most attractive to settling fish, these were targeted in this study. Algae were grouped as kelps (*Lamanaria sacharina*, *L. digitata*, and *Agarum cribrosum*), foliose algae (*Ulva lactuca*) and branched algae (mostly *Ceramium* spp., *Polysiphonia* spp., *Desmarestia* spp., *Ahnfeltia plicata*). *Desmarestia* spp. can produce sulfuric acid (Thompson 1988), but were grouped with the other branched species because fish were often seen sheltering in *Desmarestia* and did not appear to respond differently to these species than to other branched species.

The null hypothesis that no relationship existed between algal cover and the density of recruits was examined using a multiple regression for each site.

Recruit density was the response variable in these analyses, and percent cover of kelps, branched and foliose algae were independent variables. Prior to the analyses, percent covers were arcsine transformed and recruit densities were log transformed (Zar 1984). Additionally, quadrats were grouped into 4 groups based on percent cover of seaweeds (0–25%, 26–50%, 51–75% and 76–100%). A likelihood ratio chi-square was used to test the hypothesis that the percentage of recruits in each of the 4 algal cover groupings was equal.

Fish diets and prey preference

To determine the types of prey cunner recruits consume, SCUBA divers collected 50 fish (< 15 mm SL) from Appledore Island, Maine (42° 59' N 70° 36' W) in the Isles of Shoals archipelago. This site is a granite ledge, ca. 6 m deep with a dense cover of the branched alga *Codium fragile*. Within 15 minutes of being captured, fish were placed in 10% buffered formalin. All collections were made in the morning hours when these fish were actively foraging. As cunner have no stomach and the intestine appears to act as a storage organ (Chao 1972), the entire alimentary tract of each fish was removed. Alimentary tracts were dissected and the contents examined under a dissecting scope. Prey were classified as specifically as possible; however, the poor condition of many species, particularly crustacea, made classification to even a suborder difficult. Consequently, when prey could not be identified to species, they were grouped to genus or family. The most common groupings were crustaceans (isopods, amphipods, copepods, etc.), worms (annelids and non-segmented), algal fragments, and ophiuroids.

Abundances of all potential prey available in the habitat had to be assessed in order to establish prey preference. To accomplish this, at Appledore Island, randomly selected 0.0625 m² quadrats (n = 17) were scraped clean with a putty knife and all the contents were collected using an airlift fitted with a 0.5 mm mesh collecting bag. This sampling procedure may have underestimated the densities of more mobile organisms, such as large amphipods

that could have swum away. The contents were frozen and later thawed in the laboratory where all animals and algae were separated. Algae were then damp-dried and weighed. All animals except mussels, amphipods, and isopods were then counted. As mussels, amphipods, and isopods were extremely abundant, densities of these taxa were estimated from random 1/16 sub-samples taken using a Folsom plankton splitter. Additionally, the total body length of common prey ($n > 500$ for each species) were measured using the Optimas image analysis system.

Two methods were used to measure prey preference. Manly's index α which is:

$$\alpha_i = r_i/n_i / (\sum r_j/n_j) \quad (\text{Krebs 1989}),$$

where r_i and r_j are the proportion of prey type i or j in the diet (i and $j = 1, 2, 3 \dots m$) and n_i and n_j are the proportion of prey types available in the environment. This index is a simple measure of preference derived from the probability that a predator will encounter a prey species and the probability of capture after encounter (Krebs 1989). The Manly's index indicates what the use of prey would be if all prey were equally available in the habitat.

As the assessment of preference is dependent upon the prey items the investigator chooses to include as 'available' in the habitat (Johnson 1980), I also measured prey preference using a rank preference index. Such indices produce a ranking of relative preference of prey items included in the analysis, and are thus not influenced by the exclusion of food items that are uncommon in the diet (Krebs 1989). Johnson's (1980) rank preference index is: $t_i = r_i - s_i$, where t_i is the rank difference, r_i is the rank of usage of resource types i ($i = 1, 2, 3 \dots m$) and s_i is the rank availability of resources that the investigator chooses to investigate.

Effects of prey distribution on recruitment

In order to test the hypothesis that small-scale spatial variation in recruitment is affected by the distribution of prey, I compared the densities and sizes of prey found in habitat patches with recruits versus

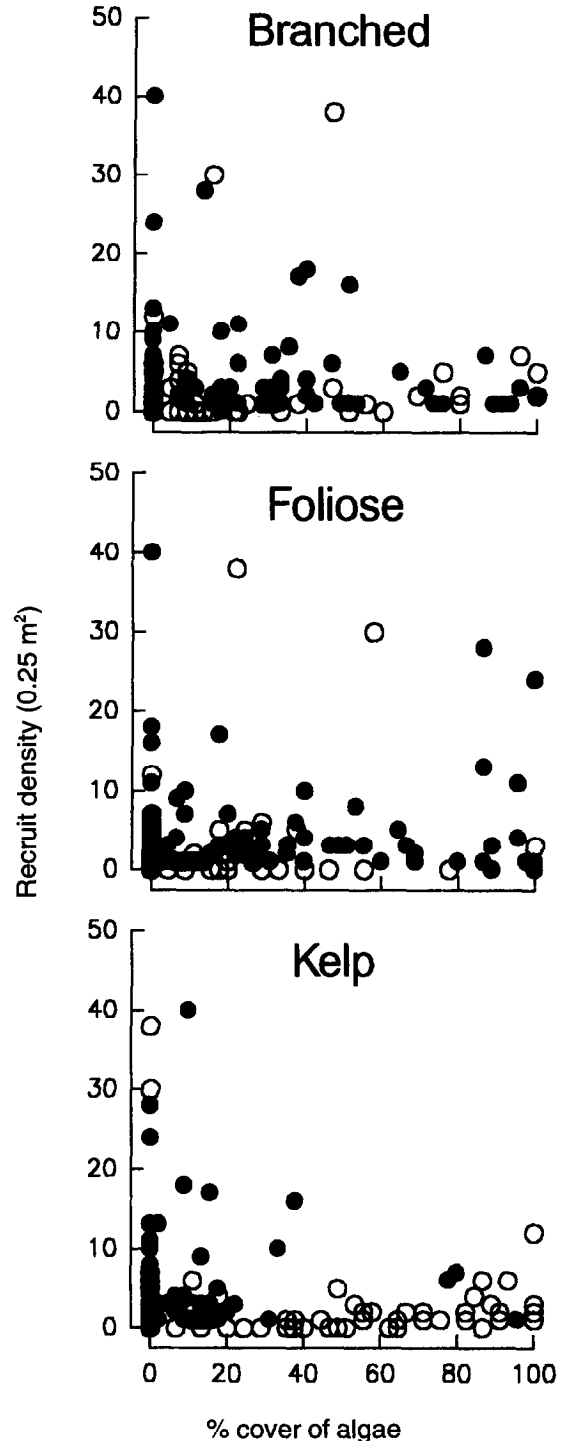


Fig. 1. The relationship between the density of newly recruited cunner with percent cover of kelp, foliose and branched algae are shown for two sites (site 1 – filled circles; site 2 – open circles). Variation in recruitment was not explained by variability in the algal assemblage.

those selected at random at Appledore Island. Quadrats (0.0625 m^2) were sampled with an airlift as described above. It is possible that the presence of fish altered the density or size distribution of the prey. However, since all quadrats were sampled in one day, these data should provide an accurate snap-shot of the association of cunner recruits with particular habitat patches at the time the samples were collected. T-tests on square root transformed data (Zar 1984) were used to test for differences in the average number of size of prey in patches with fish versus those sampled at random.

Results

Macroalgae-recruitment relationships

A total of 601 cunner recruits were censused in 160 quadrats. Mean density at site 1 was 3.25 fish m^{-2} while at site 2 recruit density averaged 1.0 fish m^{-2} . Among-quadrat variance was high with densities ranging from 0 to 160 fish m^{-2} . The mean total length of newly recruited fish at these sites was 12.1 mm (SE = 1.31, $n = 639$).

Macrophyte cover varied greatly between the two sites. In particular, average kelp coverage at site 2 was ca. 3 times greater than that at site 1 (Fig. 1). Among-quadrat variation in algal cover within sites was also high; the coefficient of variation for branched, foliose and kelp plants was greater than 100% at both sites. Nonetheless, no relationship between the density of newly recruited cunner and algal coverage was apparent. Multiple regressions with recruit density as the response variable and the cover of kelp, foliose and branched macrophytes as predictors explained less than 8% of the variance in recruit density and were not significant ($F_{3,81} = 2.349$, $p = 0.08$ for site 1, $F_{3,75} = 0.319$, $p = 0.81$ for site 2).

Further analysis revealed that the majority of recruits at both sites were in quadrats with < 25% branched algal, foliose algal or kelp cover (Fig. 2). In quadrats with < 25% branched algal cover, 67.9% of recruits were observed. Likewise, in quadrats with < 25% cover of foliose algae 62.9% of fish were observed, and 80% of recruits were found

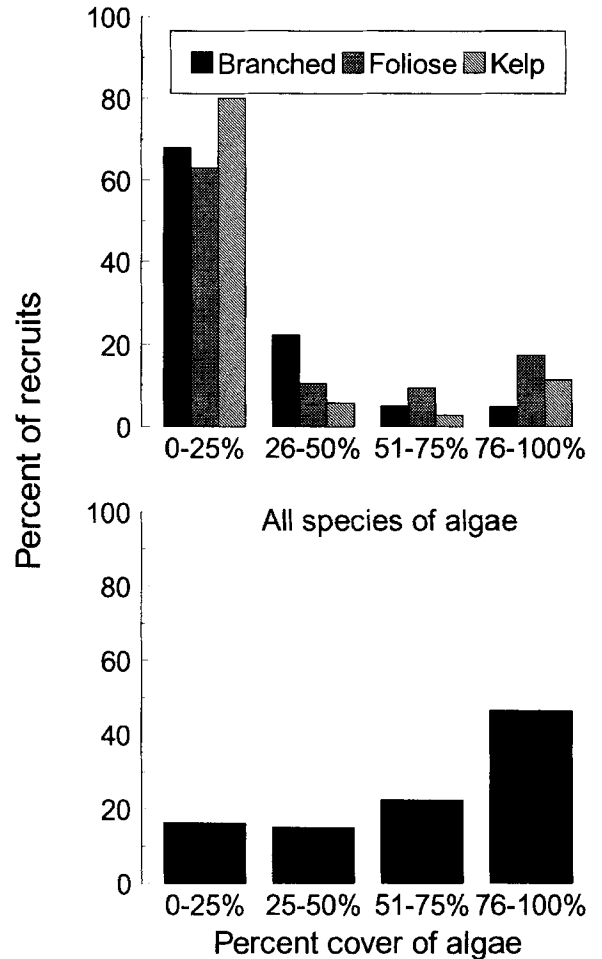


Fig. 2. The percent of recruits observed in quadrats grouped by percent cover of algae. When branched algae, foliose or kelp were examined alone, most fish were found in quadrats of low (< 25%) algal cover (Likelihood ratio chi square = 19.18, $p < 0.001$ for branched algae; Likelihood ratio chi square = 122.44, $p < 0.001$ for foliose algae; Likelihood ratio chi square = 80.77, $p < 0.001$ for kelp). When all algal forms are grouped, however, most fish were observed in quadrats with high algal cover (Likelihood ratio chi square = 61.95, $p < 0.001$).

where kelp cover was < 25%. However, when total algal cover is examined, most fish (68.9%) were found in quadrats with > 50% seaweed cover, and 46.6% percent of recruits were observed in quadrats with > 75% algal cover. These data indicate that when a single form of algae dominates a patch then recruit densities were low; however, when patches have high algal cover consisting of several forms then recruit densities were high.

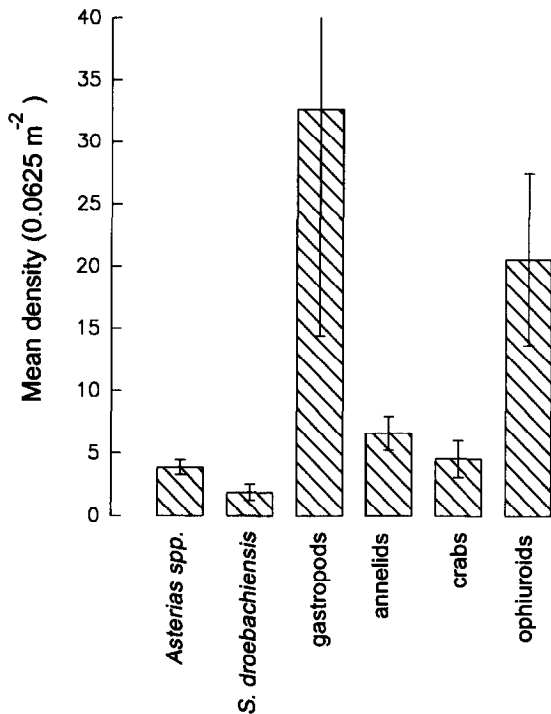


Fig. 3. The mean density (± 1 standard error) of potential prey for newly recruited cunner collected from Appledore Island. Samples were collected using an airlift fitted with a 0.5 mm mesh bag. Densities of amphipods, isopods and mussels were determined by sub-sampling and results are shown in Figures 4 and 5.

Fish diets and prey preference

At Appledore Island numerous species of benthic prey were abundant and available for use by newly recruited cunner (Fig. 3, 4). Newly settled mussels, *Mytilus edulis*, were common on filamentous and corticated macrophytes and were numerically dominant, with some estimates greater than 100 000 individuals 0.0625 m^{-2} (Fig. 4). Small crustaceans, particularly amphipods (both caprellids and gammarids) and isopods were also abundant.

Thirty-seven of the 50 fish examined from Appledore Island (74%) had ingested material in their alimentary tracts. Despite the variety of potential prey available in the environment, crustaceans and mussels were the only common taxa in the guts of cunner recruits. Crustaceans occurred in 70% of the alimentary tracts investigated, and mussels occurred in 34% of the fish. Algal fragments were found in 10% of the fish, and 4% of the fish contained other invertebrates particularly gastropods and worms.

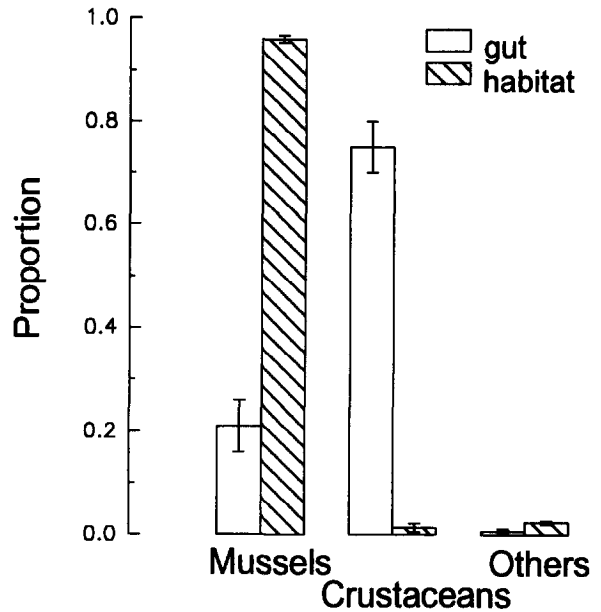


Fig. 4. The mean proportion (± 1 standard error) of mussels, crustaceans (amphipods, isopods) and other organisms found by random sampling of the environment and in the alimentary tracts of newly recruited cunner. Manly's α indicates that crustaceans were the preferred item for cunner recruits.

Three classes of prey items, crustaceans, mussels and algal fragments, were used to calculate Manly's index (α_i) values. Values above 0.33 indicate preference for a food type. Crustaceans were clearly a preferred food item ($\alpha_i = 0.96$) while mussels ($\alpha_i = 0.005$) and plants ($\alpha_i = 0.04$) were not selected as often. The same three prey groupings were used in the calculation of the rank preference index, and the results of this analysis corroborate the conclusions of Manly's index. Crustaceans were the most preferred prey while plants were the least preferred ($t_i = -0.8$ for crustaceans, 0.86 for mussels and 2.0 for macroalgae).

Effects of prey distribution on recruitment

I was unable to detect a difference in the quantity of algae between randomly selected patches and patches where fish were present ($T = 1.26$, $p = 0.22$). The average damp-dry mass of algae in randomly selected patches was 199.25 g (24.74 SE) while in patches with fish the mass was 270.27 g (42.80 SE). There were no obvious differences in species com-

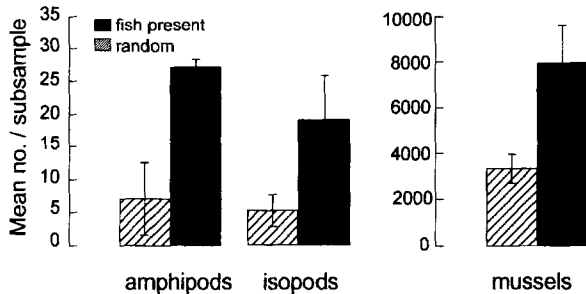


Fig. 5. The mean number (± 1 standard error) of amphipods, isopods and mussels in random 1/16 sub-samples of 0.0625 m^2 quadrats. For all species there were significantly more individuals found in quadrats with fish present versus those that were randomly sampled ($T = 4.66$, $p < 0.001$ for amphipods; $T = 3.38$, $p = 0.002$ for isopods; $T = 1.26$, $p = 0.015$ for mussels).

position of macroalgae in the patches, although this was not tested explicitly. All patches were dominated by *Codium fragile*.

Despite the similarity of algal habitat, there were substantial differences in the abundance of prey species in patches with fish and those selected at random (Fig. 5). There were ca. 4 times the number of isopods and amphipods, and more than twice the number of mussels in patches where fish were present than in randomly selected patches. This difference was evident even when the data were standardized by dividing animal densities by algal biomass. The standardized Morista's index of dispersion indicated that the prey were highly clumped in their distribution at the scale of 0.0625 m^2 ($I_p = 0.61$ for isopods, 0.51 for amphipods and 0.52 for mussels).

Additionally, the sizes of amphipods and isopods in random patches tended to be larger than in patches in which fish occurred. The mean total length of amphipods in patches with fish was 2.89 mm (0.04 SE), while in randomly selected patches amphipods averaged 3.80 mm (0.59 SE). Similarly, the length of isopods in patches with fish was 4.5 mm (0.05 SE), while in randomly selected patches they averaged 5.22 mm (0.15 SE). These differences were significant ($T = 8.48$, $p < 0.001$ for amphipods, $T = 1.799$, $p = 0.001$ for isopods). No difference in the average size of mussels between the two types of patches was apparent ($T = 1.799$, $p = 0.07$). Maximum shell length of mussels averaged 0.651 mm (0.03 SE) in patches with fish, and 0.606 mm (0.03 SE) in randomly sampled patches.

Discussion

Effects of macroalgae on recruitment

Macroalgae are often the major source of structure on temperate reefs. By providing juvenile fish with shelter from predation (Carr 1991a, Ebeling & Laur 1985) and foraging habitat (Schmitt & Holbrook 1985, 1990), macroalgae can play a critical role in the dynamics of populations of temperate fishes. Depending upon the species under investigation, the coverage of kelp canopy or understory algae has been shown to have a dramatic influence on recruitment variability (Carr 1989, 1991a, 1991b, 1994, Ebeling & Laur 1985, Holbrook et al. 1990, Jones 1984, 1988, Levin 1991, 1993b). However, the results from this study do not conform with this pattern. No relationship between the cover of erect macrophytes and densities of recruits was observed. Rather, in the present study, the species composition of algal patches and distribution of prey appear to be important factors determining the distribution of cunner recruits.

Differences in the spatial scale of interest may be the primary reason the results from this study do not coincide with the results of previous work (Wiens 1989, Levin 1992). I focused on very small-scale variability, while most other studies have examined patterns at much larger spatial scales. For example, several workers (Jones 1984, Holbrook et al. 1990, Carr 1989) have shown that a large amount of the variability in recruitment among sites can be explained by variation in algal cover or density. The same is true for cunner: in a study conducted in 1991 where sites were separated by 100's of meters, more than 70% of the among-site variation in mean levels of recruitment was explained by coverage of branched algae (Levin 1993b). The data presented here are not inconsistent with these findings; instead, they suggest what types of patches within algal beds fish are using.

Experimental studies manipulating algal structure have also generally been carried out at larger spatial scales than this study. For example, Jones (1984) manipulated algal cover in 300 m^2 plots and found much higher densities of juvenile fish in plots with high coverage. Similarly, Carr (1989) has ma-

nipulated algal cover in 150 m² and 8.55 m² plots and Levin (1993a) has manipulated algal cover in areas of 28.27 m². The results from these studies corroborate the results of Jones (1984). However, like the descriptive studies referred to above, they did not investigate how fish were distributed within algal patches. If prey were found in aggregations within these algal plots, then the results of this study predict that fish would be found in microhabitats rich in prey.

The distribution, but not abundance, of juvenile fishes has been shown to be influenced by attributes of the algal habitat at scales comparable to those of this study (Carr 1991b, Levin 1991). Levin (1991) investigated the determinants of small-scale variability in the abundance of juvenile cunner. He was able to predict the presence or absence of recruits by microhabitat characteristics; however, differences in density among patches were not related to microhabitat structure. Thus, for cunner and perhaps for other temperate fish, macroalgae appear to influence the distribution and abundance of juveniles at larger spatial scales, but at small scales differences in density can also be attributed to the variability in prey populations and species composition of algal patches.

Effects of food resources on recruitment variation

Previous work has suggested that food abundance does not explain differences in recruitment of larvae among habitats (Jones 1984, Shulman 1984, Carr 1991a). Additionally, Bray (1981) showed that young planktivorous reef fish, *Chromis punctipinnis*, would not leave shelter to forage on rich zooplankton patches although adults would. Thus, the distribution of these juvenile fish was also not affected by the distribution of prey. By contrast, within habitats, juvenile cunner appear to be associated with patches rich in prey. A causal relationship between prey abundance and recruitment of cunner cannot be established without experimental tests. Nonetheless, because the algal habitat was quite homogeneous at Appledore Island, it is unlikely that fish were responding directly to attributes of the algal habitat. The most parsimonious explana-

tion for these results is that juvenile cunner are responding to small-scale patchiness of their prey, particularly crustaceans.

Hierarchical habitat selection in heterogeneous environments

The ability of an animal to select a habitat depends upon the distance it disperses relative to the size of habitat patches (Morris 1992). Fish will only be able to discriminate among habitats if they encounter alternatives (Bell & Westoby 1986). As pre-settlement fish are advected across habitats, they have the opportunity to sample and ultimately select a habitat. Evidence that pre-settlement fish can prolong their pelagic lives (Victor 1986, Cowen 1991), presumably in the absence of appropriate conditions for settlement (Cowen 1991), supports the view that they are capable of distinguishing among habitats at relatively large spatial scales.

Juvenile reef fish do not disperse over large spatial scales (among habitats), and thus only have the opportunity to select among habitat attributes that are patchy at a smaller scale than their home range. The clumped distribution of prey at scales of 0.0625 m² and algae at scales of 0.25 m² (Levin 1993a) suggest that juvenile cunner would be exposed to patch boundaries and have the opportunity to make choices about what patches to use.

The cost and benefits of selection of habitats at various spatial scales should vary with the dispersal ability of an individual and thus during the ontogeny of fish. For a settling larva, the benefits of choosing an appropriate habitat type where it can survive, grow and reproduce are great; whereas, the costs of a continued search may not be too extreme for a pelagic pre-settlement fish (e.g. Cowen 1991). After settlement, the cost of a large-scale search for an optimal habitat is high because it forces the fish to leave shelter and travel through poor quality habitats. However, there is little cost to searching on a small-scale for the highest quality patch since fish would never stray too far from cover. The consequences of an incorrect choice at this scale are probably not as great as the selection of an inappropriate large-scale habitat. However, the benefits of such a

small-scale search are potentially great as the fish may be able to locate higher quality food patches or better shelter.

Given the potential differences in the costs and benefits of habitat selection at various spatial scales and during different ontogenetic stages, it is reasonable to hypothesize that fish recruiting to heterogeneous habitats select where to live in a hierarchical manner. Fish should first choose a habitat where there is a reasonable chance of survival. For many temperate reef fishes this is a macroalgal dominated habitat. Selection at this spatial scale would produce the among-site variation in recruitment observed by Jones (1984) and Holbrook et al. (1990). After settlement, fish should choose a patch within their home range that best meets their requirements for food and shelter. Thus, recruits should be located in specific algal patches (Carr 1991b, Levin 1991) that are rich in food resources.

This model of hierarchical habitat selection is similar to a model proposed by Bell & Westoby (1986, 1987) to explain the distribution of fish in seagrass beds. Their model suggests that just metamorphosed juveniles select the first seagrass bed they encounter, regardless of the physical complexity of the bed. After settlement fish select microhabitats within the seagrass bed that provide food and a high level of cover from predation. The prediction of this hypothesis is that abundances of fish are not correlated with attributes of the seagrass at large spatial scales. However, at small scales characteristics of the seagrass influence the distribution of fish. Both the hypothesis of Bell & Westoby and the hypothesis posed in this paper suggest that fish select habitats in a hierarchical manner. Nevertheless, because large-scale variation in recruitment of temperate reef fish is often related to variability in biogenic structure (Jones 1984, Holbrook et al. 1990, Levin 1993a), the model proposed by Bell & Westoby for seagrass fishes is not sufficient to explain large-scale patterns of distribution of fishes on temperate reefs.

The factors that produce variability in recruitment in demersal fishes are likely to vary with scale (Doherty & Williams 1988, Doherty 1991). The data presented here demonstrate that the well-established relationship between macroalgae and recruit-

ment of fishes on temperate reefs does not exist at small spatial scales for cunner. Rather, patchiness of food resources appears to be responsible for variability in recruit density at a scale of meters. This study underscores the importance of acknowledging that different mechanisms can produce variability in recruitment at different scales.

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