Responses of temperate reef fishes to alterations in algal structure and species composition

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ABSTRACT: Reef habitats in the South Atlantic Bight comprise only a small proportion of the available benthic habitat, but support enormous densities of fishes, invertebrates, and algae. Because these reefs are distant from shore and in deeper waters (usually >20 m), we know very little about the factors affecting the distribution of fishes or the structure of fish assemblages on these reefs. Our goal in this study was to determine how variance in macroalgal structure and species composition on reefs off the coast of North Carolina affects reef fishes. Manipulations of algal density and species composition in artificially created 1.5 m² plots indicated that: (1) patches with *Sargassum filipendula* had greater numbers and higher species richness of reef fishes than patches without algae; (2) fishes responded to variability in *Sargassum* density with high fish abundance in patches with higher algal density, but this response varied among fish species; (3) greater numbers of individuals and species of fish used *Sargassum* patches compared to patches of 2 other brown algae common in this region (*Zonaria* and *Dictyopteris*); (4) fish densities were higher in patches with taller algae and greater percent cover of algae. Many of the fishes using experimental patches were small, young-of-the-year individuals. Our results indicate that variability in the structure of seaweed beds on reefs in the South Atlantic Bight can influence the distribution and abundance of reef fishes. Although the algal beds in the South Atlantic Bight are more diminutive and less extensive than kelp beds of cold temperate waters, they may be a critical habitat for juvenile reef fishes in this region, and the algal species dominating the beds will have a large effect on their value as juvenile habitat.

KEY WORDS: Reef fish · Temperate reef · Habitat structure · Macroalgae · South Atlantic Bight · North Carolina · *Sargassum* · Recruitment

INTRODUCTION

Our current view of marine communities and populations emphasizes vagaries in the delivery of pelagic larvae to local populations and the extent to which adult populations reflect the supply of larvae (Gaines & Roughgarden 1985, Menge & Sutherland 1987, Doherty & Williams 1988, Underwood & Fairweather 1989). The recent focus by workers on larval supply and recruitment limitation has enhanced our understanding of marine populations; however, it is clear that post-settlement processes are also important in determining the sizes of populations (Forrester 1990, Jones 1991, Hixon & Beets 1993, Ólafsson et al. 1994).

Moreover, post-settlement processes may be influenced by attributes of the habitat. Hixon & Beets (1993), for example, demonstrated experimentally that hole size and number influenced the number of resident predators, and this set the upper limit of population size of newly recruited reef fishes in their experimental reefs in the Virgin Islands. Thus, a more pluralistic view of marine populations requires integrating the role of larval supply with the habitat requirements of older, demersal fish (Jones 1991).

Experimental studies of reef fish ecology have traditionally been conducted in coral reef habitats (Sale 1980, 1991). We therefore know much more about the ecology of tropical reef fishes and how they interact with their habitat than their temperate counterparts (Ebeling & Hixon 1991). Although temperate reefs themselves lack the tremendous topographic complexity of coral reefs, the extension of macroalgae above

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the reef provides structural complexity that may be uti-lized by fishes (Ebeling & Hixon 1991). Algal habitats and their associated invertebrates serve as a source of food (Coyer 1979, Holbrook & Schmitt 1988, Levin 1994a), and the structural complexity of these habitats provides a refuge from predation (Ebeling & Laur 1985, Carr 1991a, Anderson 1993). Recent work on temperate rocky reefs has indicated that macroalgae can influence initial patterns of recruitment (Jones 1984a, Carr 1989, 1991b, 1994a, Levin 1991, 1993) as well as patterns of adult abundance (Choat & Ayling 1987, Holbrook et al. 1990a, b, Anderson 1994, Carr 1994b). Thus, understanding how fishes respond to variability in seaweed beds may be critical to under-standing the dynamics of many populations of fishes on temperate reefs.

Most work on the fishes of temperate reefs has been conducted in kelp-dominated habitats in the Pacific (e.g. Hixon 1980, Larson 1980, Holbrook & Schmitt 1988, Jones 1988, Holbrook et al. 1990a, b, Anderson 1994, Carr 1994a) and in the Northwest Atlantic (Levin 1991, 1993, 1994b). Although kelps are absent from rocky outcroppings on the continental shelf of the South Atlantic Bight, USA, these reefs support exten-sive beds of smaller brown algae such as *Sargassum filipendula* (Fucales) and various genera of Dictyotales. These genera are the understory in some kelp-domi-nated locales (e.g. Carr 1989, Holbrook et al. 1990a, Schmitt & Holbrook 1990). Previous work on temperate reefs in other geographic regions suggests that sea-weed beds might be important habitats for fishes on reefs of the South Atlantic Bight; however, generaliz-ing from other geographic regions is problematic because of (1) the absence of kelps; (2) the dominance of algal species that occur only as understory species in other regions, but as canopy species in this region; and (3) the marked differences in the fish assemblages.

The goal of our study was to determine experimen-tally the effects of different algal habitats on the small-scale distribution of reef fishes in the South Atlantic Bight. Specifically we asked these questions: (1) Does the presence of algae influence the distribution of fishes? (2) Does variability in macroalgal density affect the density of fishes? (3) Does reef fish abundance and species richness vary among algal habitats composed of different species? (4) Is differential use of seaweed habitats by fishes the result of qualitative or quantita-tive differences among algal species?

METHODS

Study site and organisms. The continental shelf of the South Atlantic Bight is characterized by a complex sequence of rocky outcroppings with relief up to 10 m.

Although sand bottom covers most of the sea floor, about 15% of the shelf consists of exposed rocky out-croppings that support sponges, hydroids, corals and seaweed beds (Parker et al. 1983). On some reefs macroalgae form extensive beds along the top of the reef, while on other reefs algal coverage is sparse. Most of these reefs are distant from shore and in depths >20 m; consequently, virtually no experimental work has been conducted on the fishes of these reefs. Reefs in this region support a diverse assemblage of tropical and temperate fishes with greater than 114 species representing 43 families (Grimes et al. 1982, Sedberry & Van Dolah 1984). Tropical groups such as butterflyfishes, damselfishes and tropical labrids (e.g. slippery dicks *Halichoeres bivittatus*) are frequently found on the same reefs as other more temperate spe-cies such as black sea bass *Centropristis striata*.

Experiments were conducted at a 27 to 31 m deep reef located 43 km off the coast of Wilmington, North Carolina, USA (34° 10' 09" N, 77° 23' 12" W; Loran = 27186.0, 39157.2). The upper portion of the reef con-sists of flat hard substrate at a depth of 27 m. Near the reef edge, this substrate is generally free of sand and covered by a dense bed of brown algae dominated by *Sargassum filipendula*. Other brown algae including *Dictyopteris membranacea*, *Zonaria tournefortii*, *Dic-tyota* spp. and *Lobophora variegata* are also present and at times common, but less consistently abundant at this site than *Sargassum filipendula* (seaweeds will hereafter be referred to by their generic name). At other reefs in the region, *Zonaria*, *Lobophora*, *Dicty-opteris* or *Dictyota* can be the dominant seaweeds (Levin & Hay unpubl. data). At our study site, the algal bed extends from 3 to >30 m away from the reef edge depending on season and location along the reef. On one side of the reef edge, the reef drops rapidly to a sand plain at a depth of about 31 m. On its shallower side, the algal dominated portion of the reef merges into a sand-scoured flat that is very sparsely populated by corals, sponges and red and green algae. The rela-tive lack of benthic invertebrates and algae on this por-tion of the reef contrasts sharply with the biomass of algae that characterizes the reef at the same depth nearer to the reef edge.

Expt 1: Does the presence of algae influence the dis-tribution of fishes? To test the effect of macroalgae on the distribution of fishes, we performed an experiment in which we created 1.5 m^2 patches of algae on other-wise barren substratum adjacent to the reef. Algal patches were constructed by attaching natural densi-ties of *Sargassum* (21 plants m^{-2}, equivalent to 32 per patch) to four 1 m long ropes fastened with nylon tie wraps to two 1.5 m pieces of rebar (0.90 cm diameter metal rod) that were separated by 1 m and parallel to each other. We selected *Sargassum* because it was the

dominant large brown alga at our study site. For this experiment and all subsequent experiments, algae were collected from other parts of the reef and then attached *in situ* to rebar frames. Dry mass of *Sargassum* averaged ca 80 (SE = 5.2) g m^{-2}, while the dry mass of other common brown seaweeds such as *Dictyopteris* and *Zonaria* was much lower [dry mass of 26.3 (SE = 6.0) and 9 (SE = 3.3) g m^{-2}, respectively]. Two replicates of each treatment were arranged in blocks. Replicates within blocks were separated from each other by >2 m, and blocks were separated from each other by 7 to 8 m. The entire experimental array was positioned 15 m from the reef edge. On 25 May 1993, 8 *Sargassum* plots with 32 plants plot^{-1} and 8 control plots, consisting of only rope and rebar, were constructed. Fifteen days later we compared densities of fishes inhabiting *Sargassum* versus control plots.

Fishes were sampled by enveloping plots with an enclosure constructed of a square rebar frame (3 m^2) and plastic walls that were tied together at the top. The anesthetic quinaldine was injected under the plastic and all fishes were collected with dip nets and later identified and measured (standard length) in the lab. This method appeared to sample substrate-associated fishes adequately in that they generally retreated to the substratum when a diver approached. However, this method did not adequately assess densities of more mobile species such as grunts because they simply left the experimental patches as divers carrying the net enclosures approached. Paired *t*-tests were used to test for differences in the mean number of each fish species between treatments. Prior to analyses Bartlett's test was used to test for homogeneity of variances, and in all cases Bartlett's tests indicated that variances were not heterogeneous (p > 0.05). In addition, we used Fisher's exacts tests to examine differences in frequency of occurrence of fish between *Sargassum*-addition and control plots.

Expt 2: Does variability in macroalgal density affect the density of fishes? In this experiment we extended Expt 1 and examined whether fishes responded to variability in seaweed density. To do this we used an approach similar to that described for Expt 1. Replicate 1.5 m^2 plots were established on 8 July 1993 as described above. On the rebar-rope bases we attached either 4, 8, 16 or 32 *Sargassum* plants plot^{-1}. We employed a randomized blocked design such that all treatment levels were represented in each of 6 blocks.

Densities of fishes using algal patches were estimated 17 d later by visually censusing each replicate completely. Censuses followed procedures developed by Sale & Douglas (1981). A diver approached a patch and at a distance of 2 m slowly circled the patch while recording the number of active species hovering within 1 m of the patch. The diver then moved closer to

the patch and enumerated demersal species. Finally, the algae themselves were searched. Lengths of fishes were not explicitly examined; however, most fishes censused were either older juveniles (>50 mm TL, total length) or adults. Visibility at this site was good (>15 m), and fishes were easily observed and counted using this method. A blocked 1-way analysis of variance was used to test for differences in the mean number of fishes occupying patches of different densities. Bartlett's test for homogeneity of variances indicated that in all cases variances were homogeneous (p > 0.05). In addition, we examined differences in species richness among patches with different plant densities using 1-way ANOVA. While patches with greater density are expected to have higher species richness (Hurlburt 1971), we examined species richness without any correction for the density of fishes because we were interested in the number of species present on our algal patches regardless of density. Thus, our measure of species richness has a density bias but does suggest which patches have the greater potential for interspecific interactions.

Expt 3: Do algal species differ in their influence on local density and species richness of fishes? While *Sargassum* was the dominant canopy-forming alga at our study site, 2 other brown algae, *Dictyopteris* and *Zonaria*, were also common at this site, and dominate at some other reefs (Levin & Hay unpubl. data). Consequently, we asked if fish abundance and species richness varied among habitats composed of different algal species. On 21 July 1993, we created replicate 1.5 m^2 plots as before but with 16 plants each of either *Sargassum*, *Dictyopteris* or *Zonaria*. Nine *Sargassum* patches, 6 *Dictyopteris* patches and 6 *Zonaria* patches were assigned haphazardly to plots throughout the experimental array. These patches were constructed by removing algae used in Expt 2 from the plots and adding the appropriate algal species *in situ*. An unbalanced design was adopted for this experiment because limited bottom time prevented us from creating additional *Dictyopteris* or *Zonaria* plots. Patches were censused visually on 25 August 1993 using the methodology described above. Lengths of fishes were not explicitly examined; however, most fishes censused were either older juveniles (>50 mm TL) or adults. A 1-way ANOVA was used to test for differences in fish abundance and species richness among treatments.

Expt 4: Is differential use of seaweed habitats by fishes the result of qualitative or quantitative differences among algal species? The results of Expt 3 indicated that fish abundance was higher in *Sargassum* patches than in patches composed of *Dictyopteris* or *Zonaria*. Thus, we conducted an experiment to determine if the differential use of seaweed habitats is the result of some qualitative difference among the algae

(e.g. chemistry), or the result of quantitative differences, such as mean height or biomass, among our treatments. Replicate 1.5 m² plots (n = 7 for each treatment) were created on 26 August 1993 with the following 4 treatments: (1) 'tall': 16 unmanipulated *Sargassum* plants; (2) 'medium': 16 *Sargassum* plants from which an average of about 9 cm was removed from the bottom of each plant; (3) 'short': 16 *Sargassum* plants that were the same height as *Zonaria* plants (an average of about 26 cm was removed from the bottom of each *Sargassum* plant); (4) '*Zonaria*': 16 unmanipulated *Zonaria* plants. The height of each treatment was characterized by haphazardly selecting 3 plants in each plot and measuring them *in situ*. The percentage cover of algae of each treatment was also determined by centering a 1 m² quadrat with a grid of monofilament line forming 45 points over the plot and quantifying presence or absence of algae at each point. Fish densities were estimated visually on 7 September 1993 using the same methodology as Expts 2 and 3. Lengths of fishes were not explicitly examined; however, most fishes censused were either older juveniles (>50 mm TL) or adults. One-way ANOVA and post hoc Tukey's HSD tests were used to assess differences in fish abundances among the treatments. In all cases Bartlett's test indicated that variances were homogeneous.

We selected *Sargassum* and *Zonaria* for the above experiment because they co-occur at our site, are the dominant species in this region and have a similar relationship between weight and height (see 'Results'); consequently, when we shortened *Sargassum* plants we produced plants that were similar in both height and weight to *Zonaria*. Therefore, differences between *Sargassum* treatments and *Zonaria* would indicate that some qualitative differences between species result in differential habitat use by fishes. Differences among *Sargassum* treatments, but not between the short *Sargassum* and *Zonaria* treatment, would indicate that quantitative differences between these seaweeds result in different patterns of habitat use by fishes.

RESULTS

Expt 1: Does the presence of algae influence the distribution of fishes?

Reef fish abundance clearly increased in response to the addition of seaweeds to the sand-plain habitat (Table 1). Plots with 32 *Sargassum* plants attracted about 5 times as many total fishes as control plots made of only rope and rebar (*t*-test, p < 0.01). Every fish family was more abundant or more frequent on *Sargassum* plots than on control plots with these differences being significant for Blenniidae (primarily seaweed blennies *Parablennius marmorensus*) and Serranidae (primarily black sea bass *Centropristis striata*) (Table 1). Filefish (Balistids), blennies, and spottail pinfish (Sparidae) occurred only in plots with *Sargassum* (Table 1). The density of labridae (primarily slippery dicks *Halichoeres bivittatus*) doubled in response to *Sargassum* addition, but this increase was not statistically significant (Table 1).

From our experimental plots, we captured a total of 86 fishes representing 16 species. Species richness on algal patches averaged 4.0 (SE = 0.72) species plot⁻¹, and was significantly greater than the 1.4 (SE = 0.245) species plot⁻¹ captured on control plots (*t*-test, p = 0.006).

More than 60 % of the fishes collected in this experiment were less than 20 mm in total length, indicating that most of these fishes (other than blennies) were juveniles. The average total length of fish we collected was 42.8 mm (SE = 6.0).

Table 1. Mean (SE in parentheses) density of fishes, grouped by families, for 1.5 m² experimental plots that contained 32 *Sargassum* plants attached to a rope and rebar frame and plots with only rope and rebar (control). *t*-tests were used to detect differences between means. In addition, differences in frequency of occurrence were analyzed with Fisher's Exact Test. –: tests were not performed because means were 0 or frequencies were 100 %

Fish family	*Sargassum* addition plots	Control plots	*t*-test probability	Fisher's Exact Test probability
Balistid	1.3 (0.53)	0 (0)	–	0.075
Blenniid	2.3 (0.84)	0 (0)	–	0.005
Labrid	2.1 (0.69)	1.0 (0.63)	0.291	0.217
Serranid	2.4 (0.63)	0.6 (0.4)	0.036	0.035
Sparid	0.88 (0.40)	0 (0)	–	0.105
Other	0.63 (0.18)	0.4 (0.23)	0.471	–
Total	9.5 (2.1)	2.0 (0.32)	0.01	–

Expt 2: Does variability in macroalgal density affect the density of fishes?

When we manipulated *Sargassum* density (4, 8, 16, or 32 plants plot⁻¹) rather than just the presence or absence of plants, total fish density increased with increasing *Sargassum* density (Fig. 1); however, the relationship between fish density and plant density differed among species. Black seabass, for example, gradually increased in density as *Sargassum* density increased, but the fish were present in all treatments (Fig. 1). In contrast, spottail pinfish did not occur in the 4-plant treatment, occurred at very low densities

in the 8-plant treatment, but were abundant in both the 16-and 32-plant treatments (Fig 1). The response of slippery dicks differed from both of the previous species. Slippery dicks were rare in the 4-plant treatment but equally abundant in plots with 8, 16, or 32 plants plot^{-1}. This suggests that above some threshold density of *Sargassum*, increasing algal density did not affect the density of slippery dicks.
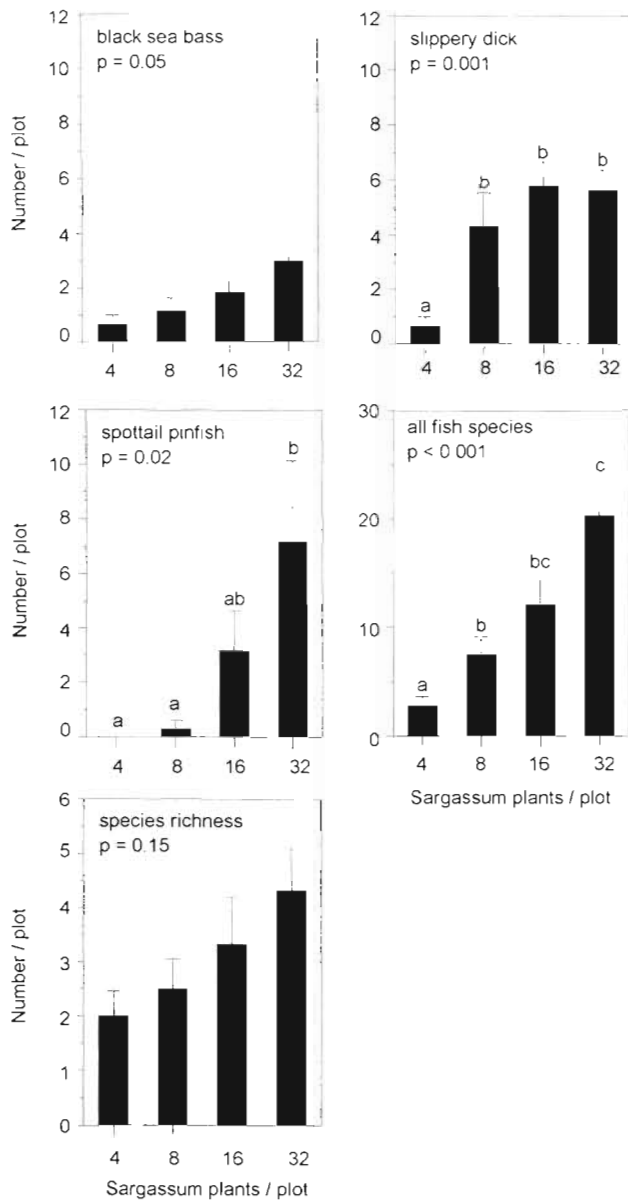
When we examined all species combined, there was a clear and significant effect of *Sargassum* density on fish abundance. Fish densities were more than 7 times greater on 32-plant plots than on 4-plant plots, and nearly 3 times as many fishes occurred on 32-plant plots as on 8-plant plots (Fig. 1). Fish species richness also appeared to increase with increasing *Sargassum* density, but this trend was not statistically significant (ANOVA, p = 0.15; Fig. 1).

Expt 3: Do algal species differ in their influence on local density and species richness of fishes?

When we held plant density constant at 16 plants plot^{-1}, but varied the species of brown seaweed used to create the seaweed patches, fishes strongly preferred plots composed of *Sargassum* to those composed of either *Dictyopteris* or *Zonaria* (Fig. 2). Total fish density on *Sargassum* plots was more than 8 times that
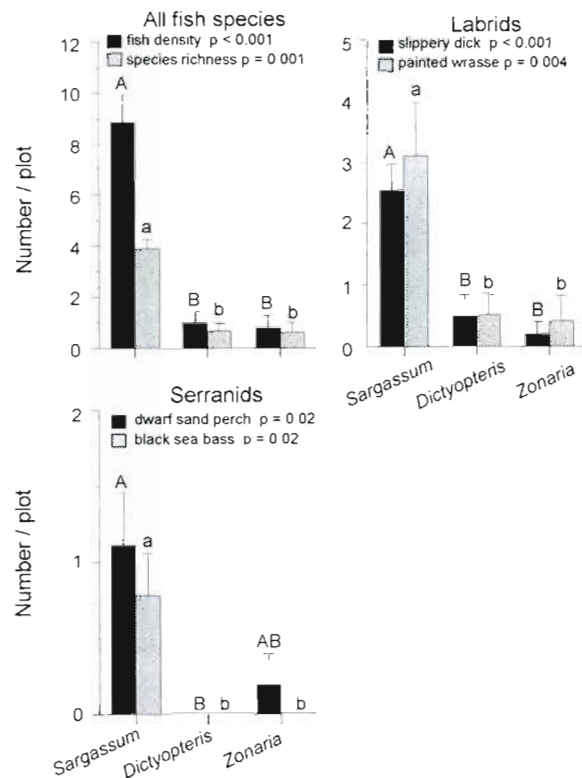

Fig. 1. Mean density of fish or fish species on experimental plots of varying *Sargassum* density (N = 6). p-values are from the overall ANOVA. Letters indicate means that were not significantly different in Tukey's HSD tests. No letters are present for black sea bass since differences could not be identified by Tukey's HSD tests. Error bars are 1 SE. Note that the y-axis scales differ among some graphs

Fig. 2. Mean density of fish or fish species on plots composed of 16 plants of either *Sargassum* (N = 9), *Dictyopteris* (N = 6), or *Zonaria* (N = 6). p-values are from the ANOVA. Letters indicate means that were not significantly different by Tukey's HSD test. Upper case letters refer to means designated by solid bars; lower case letters refer to means designated by hatched bars. Error bars are 1 SE. Note that y-axis scales differ among graphs
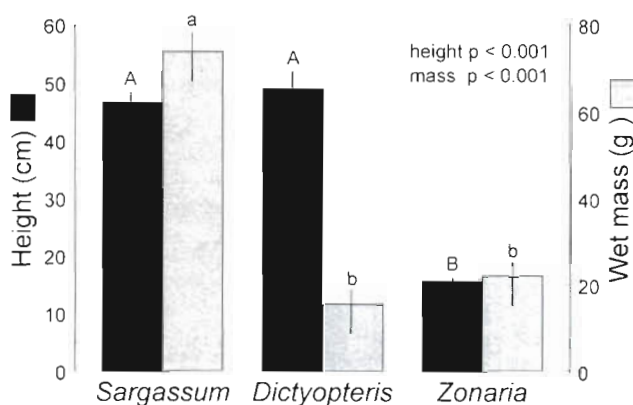
Fig. 3. Mean height and wet mass of individual *Sargassum*, *Dictyopteris*, or *Zonaria* plants. p-values are from ANOVA. Letters indicate means that were not significantly different by Tukey's HSD test. Upper case letters refer to means designated by black bars while lower case letters refer to means designated by hatched bars. Error bars are 1 SE

observed on either *Dictyopteris* or *Zonaria* plots (Fig 2; ANOVA, p < 0.001). Four fish species in 2 families comprised 96% of all the fishes we observed on these plots, and these 4 species showed patterns similar to those
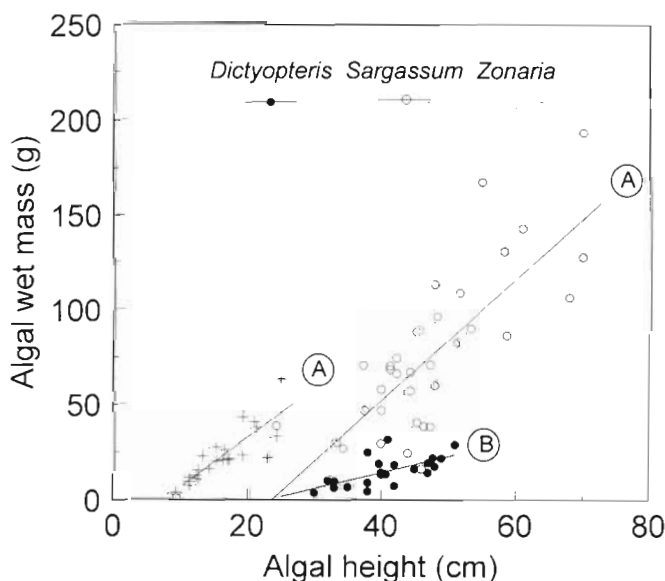

Fig. 4. Linear regression indicated that there was a significant relationship between wet mass and height for *Dictyopteris* ($r^2 = 0.42$, p < 0.001), *Sargassum* ($r^2 = 0.60$, p < 0.001), and *Zonaria* ($r^2 = 0.79$, p < 0.001). Analysis of covariance indicated that the slopes of the regression lines of mass versus height for *Sargassum* and for *Zonaria* do not differ from each other, but both are significantly greater than the slope for *Dictyopteris* ($F = 43.56$, p < 0.001). Letters indicate regression lines that were not significantly different from each other by Tukey's HSD tests

noted for total fish densities (Fig. 2). Slippery dicks and painted wrasses (Labridae) were both significantly more abundant in patches of *Sargassum* than in patches of *Dictyopteris* or *Zonaria*. Black seabass and dwarf sandperch (Serranidae) exhibited a similar pattern, with the exception that dwarf sand perch densities did not differ significantly between *Sargassum* and *Zonaria* plots (p = 0.09) even though densities in *Sargassum* were more than 5 times higher (Fig 2). Fish species richness was also much higher in *Sargassum* than in either of the other species' plots (Fig. 3; ANOVA, p < 0.001). The mean number of fish species per plot was 6 times higher in *Sargassum* patches than in either *Dictyopteris* or *Zonaria*.

Expt 4: Is differential use of seaweed habitats by fishes the result of qualitative or quantitative differences among algal species?

The species of brown algae we used in the above experiment differed from each other in secondary metabolite chemistry (Hay & Fenical 1988), the height and mass of algae represented by equal densities of plant, and probably numerous other attributes (Fig. 3). *Sargassum* and *Dictyopteris* plants averaged nearly 50 cm in height and were significantly taller than plants of *Zonaria* which averaged only 16 cm in height (Fig. 3). Additionally, the average *Sargassum* plant had a wet mass of 74 g and weighed significantly more than either *Zonaria* (22 g) or *Dictyopteris* (15 g) (Fig. 3). *Sargassum* and *Zonaria* plants also produce more biomass for a given height than *Dictyopteris* (Fig 4). The slopes of regression lines of weight versus height for *Sargassum* and for *Zonaria* did not differ from each other, but both were significantly greater than the slope for *Dictyopteris* (Fig. 4).

In this experiment, we constructed algal habitats made of equal densities of either short, medium, or tall *Sargassum*, or of unmanipulated *Zonaria*, which was similar to short *Sargassum* in height and the percentage cover it produces (Table 2). Additionally, because *Sargassum* and *Zonaria* have a similar height-weight relationship (Fig. 4), short *Sargassum* were similar in biomass to *Zonaria*. Fishes responded strongly to the taller *Sargassum* (Fig. 5). Total fish density in the tall *Sargassum* treatment was a significant 2 times greater than in the medium *Sargassum* treatment, and a significant 7 times greater than in the *Zonaria* or short *Sargassum* treatments (Fig. 5). This pattern was particularly evident in slippery dicks (a labrid), and in serranids (Fig. 5). Slippery dicks were absent from both the short *Sargassum* and *Zonaria* treatments and were 7 times more abundant on the tall than on the medium *Sargassum* plots (Fig 5). Similarly, when slip-

Table 2. Summary of the mean (SE in parentheses) algal height and algal cover resulting from plant height manipulations in Expt 4. ANOVA indicated significant differences among treatments in both height ($F = 33.66$; $p < 0.001$) and cover ($F = 17.07$; $p < 0.001$). Letters to the left of each mean in the table indicate means that were significantly different ($\alpha \leq 0.05$) in post hoc Tukey's HSD tests

Treatment	Height (cm) N = 18 plants	Percentage cover N = 7 plots
'Tall' *Sargassum*	A 43.22 (2.37)	A 46.43 (4.73)
'Medium' *Sargassum*	B 34.50 (3.63)	A 38.89 (6.31)
'Short' *Sargassum*	C 17.27 (0.83)	B 10.11 (1.79)
Zonaria	C 15.94 (1.08)	B 19.00 (1.24)

pery dicks were grouped with other labrids, abundances on tall *Sargassum* were significantly greater on tall versus medium *Sargassum* treatments, both of which had higher abundances than short *Sargassum* and *Zonaria* (Fig. 5). Serranids were also most abundant in tall *Sargassum* plots, less so in medium *Sargassum* plots, and occurred at low and similar abundance in both *Zonaria* and short *Sargassum* plots (Fig. 5). ANOVA indicated a significant difference in serranid densities among the treatments ($p = 0.048$), but differences could not be identified in subsequent multiple comparison tests (Tukey's HSD, $p > 0.05$ for all comparisons).

Because percentage cover of a patch was related to the mean height of plants in that patch ($r^2 = 0.21$, $p = 0.02$), height and percentage cover were partially confounded. In an attempt to distinguish between the effects of height and cover, we performed regression analyses using fish densities as the response variable and either percentage cover or the mean plant height in a patch as the independent variable. Both percentage cover and height explained a significant amount of variation in the total abundance of fishes (Fig. 6), with algal height appearing to explain more variance than percentage cover. Additionally, algal cover and height appeared to differentially affect the abundance of particular fish species. Dwarf sandperch densities were significantly affected by algal height ($r^2 = 0.31$, $p < 0.01$), but not cover ($r^2 = 0.05$, $p = 0.25$). Slippery dicks also responded more strongly to algal height ($r^2 = 0.61$, $p < 0.001$) than to algal cover ($r^2 = 0.31$, $p < 0.01$). In contrast to these patterns, young-of-the-year black sea bass (<50 mm TL) showed no response to variability in algal height ($r^2 = 0.04$, $p = 0.5$), but a weak, yet significant response to algal cover ($r^2 = 0.15$, $p < 0.05$).
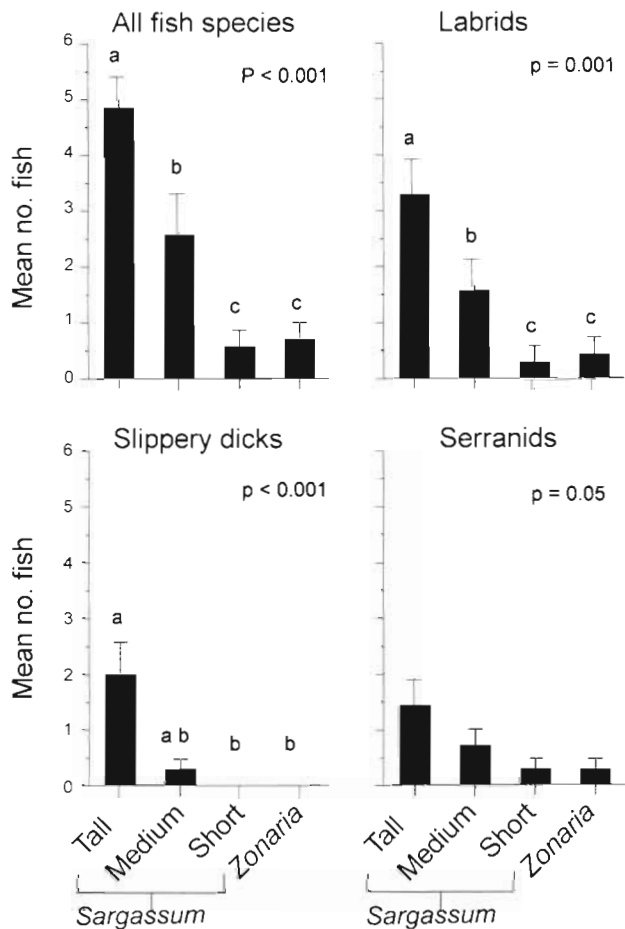

Fig. 5. Mean density of fish on experimental plots composed of 16 tall, medium, or short *Sargassum* plants, or on 16 *Zonaria* plants (N = 7; see Table 2 for details of experimental treatments). p-values are from the ANOVA. Letters indicate means that were not significantly different in Tukey's HSD tests. Error bars are 1 SE
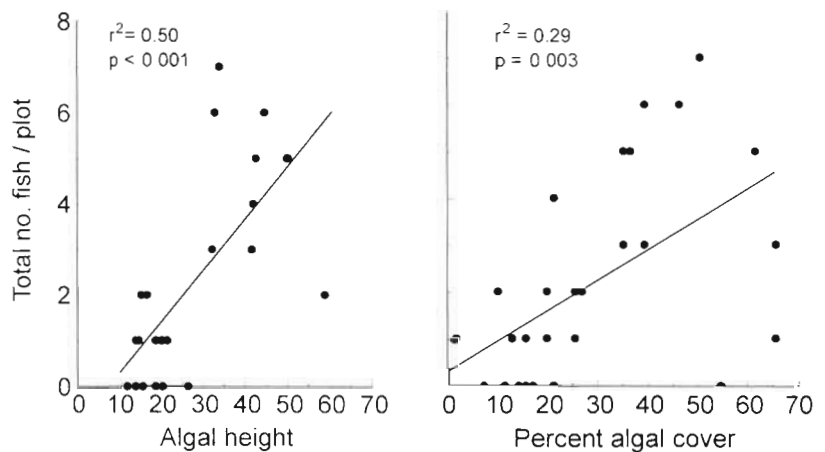

Fig. 6. Relationship between total density of fish (all species combined) and both algal height and percentage algal cover

DISCUSSION

Fishes, especially juveniles, in freshwater (Werner & Gilliam 1984), estuarine (Orth et al. 1984, Sogard 1989) and temperate marine (Holbrook et al. 1990a, b) habitats are frequently associated with submerged vegetation. Previous studies of how temperate reef fishes respond to macroalgae have focused on kelp-dominated communities of New Zealand, California, and New England, USA (Holbrook & Schmitt 1984, Jones 1984a, b, c, Ebeling & Laur 1985, Carr 1989, 1991b, 1994a, b, DeMartini & Roberts 1990, Holbrook et al. 1990a, b, Schmitt & Holbrook 1990, Levin 1991, 1993, 1994a, b, Anderson 1994). In these studies, kelp density and height are often important predictors of reef fish density and recruitment. This may occur, in part, because (1) large kelps such as *Macrocystis* extend continuously from the benthos to the water surface allowing the kelps to 'collect' recruits that might otherwise pass over the reef; or (2) this large vertical gradient provides the recruiting fish a spatial refuge from predators which tend to be more numerous near the benthos (Coyer 1979, Carr 1994b). As an example of the latter, recently settled kelp bass are most abundant in the upper portions of *Macrocystis* beds while their older, and cannibalistic, conspecifics are more abundant lower in the canopy (Carr 1994b). Presumably, as kelp bass increase in size, they become less susceptible to predation and migrate down the kelp canopy to the benthos and across the reef. Neither of the 2 processes described above is likely to occur on similar spatial scales in our study because the largest seaweeds in the South Atlantic Bight produce a canopy height of no more than about 0.5 m (Table 2). These seaweeds, therefore, extend through no more than 2% of the depth of the water column at our study site.

Although reefs in the South Atlantic Bight lack large kelps, presence and abundance of smaller seaweeds such as *Sargassum* still strongly influenced fish densities and species richness. Total fish density and species richness increased 5- and 3-fold, respectively, when *Sargassum* was added to an unstructured, sand-scoured portion of the reef. Because more than 60% of the fishes collected during this experiment were less than 20 mm long, we suspect that most were recent recruits (i.e. young-of-the-year). *Sargassum* abundance (rather than just presence or absence) also strongly affected fish densities and species richness. Fish densities increased 7-fold as *Sargassum* density was increased from 4 to 32 plants plot^{-1}.

Fish use of seaweed patches varied tremendously as a function of the algal species comprising the patch. When patches were constructed of equal densities of *Sargassum*, *Dictyopteris*, or *Zonaria*, total fish densities were 8 times higher on *Sargassum* plots than on plots of the other 2 seaweeds. Differences in fish density between *Sargassum* and *Zonaria* plots ultimately disappeared as we made *Sargassum* increasingly shorter by cutting it into smaller lengths. The finding that short *Sargassum* did not differ from *Zonaria* in height, percentage cover or use by fishes suggests that fishes used *Sargassum* plots more than plots composed of other algae because of the greater height, percentage cover or biomass provided by this species. The stronger association of fish densities with algal height as opposed to percentage cover suggests that some aspect of algal 3-dimensionality may be important in determining habitat quality for these fishes. This is also supported by the finding that tall *Sargassum* was more attractive to fishes than medium *Sargassum*, and these *Sargassum* treatments differed in height but not percentage cover.

Although many previous studies have documented strong correlations between kelp abundance and fish abundance, relatively few have assessed how different seaweed species or morphological types affect habitat utilization by fishes. On reefs in California, if the giant kelp *Macrocystis* is common, small turfs of algae and benthic animals dominate the understory, and foliose species such as *Sargassum*, *Dictyopteris*, and *Zonaria* are rare (Holbrook & Schmitt 1984, Carr 1989, Holbrook et al 1990a, b, Schmitt & Holbrook 1990). If *Macrocystis* is removed, smaller foliose species like *Sargassum*, *Dictyopteris*, *Zonaria*, and other foliose algae can become common (Carr 1989, Holbrook et al. 1990a, Schmitt & Holbrook 1990). Similarly, in New England, when laminarian kelp is removed, filamentous and foliose species dominate the algal assemblage (Levin 1993). Several studies have noted that small and large fishes respond differently when kelps are removed from these reefs. When Carr (1989) removed *Macrocystis* from transects within a *Macrocystis* bed, he found that use of areas without kelp declined for large fishes, but increased for smaller fishes that were attracted to the short understory algae, which included *Sargassum* and several Dictyotaceae (seaweeds that were common in our study) that increased in abundance following *Macrocystis* removal. In areas where reefs occur as either kelp beds or urchin barrens, small fishes that are dependent on the structure provided by seaweeds generally occur in kelp beds, while larger fishes that are independent of this structure often occur in high abundance over urchin barrens (Choat & Ayling 1987, Levin 1993). Thus, numerous studies from several geographic localities indicate that small, recently settled fishes depend heavily on algal-generated structure, but can become increasingly independent of such structure as they increase in size (Holbrook & Schmitt 1984, Jones 1984a, c, Ebeling & Laur 1985, Choat & Ayling 1987, Carr 1989, Holbrook et al. 1990, Levin 1993).

Some temperate reef fishes selectively settle in habitats with increased structural complexity (Jones 1984a, Levin 1993), while others settle randomly but experience high mortality in simple habitats and much lower mortality in more complex habitats (Connell & Jones 1991). These observations, as well as other investigations (Holbrook & Schmitt 1984, Jones 1984c, Ebeling & Laur 1985, Carr 1991a, Levin 1994b) suggest that predation may restrict new recruits and juvenile fishes to seaweed dominated areas of temperate reefs, where structural complexity is high. If successful recruitment and survival to early juvenile stages determines adult population size (e.g. Doherty & Fowler 1994), then variability in algal abundance could result in corresponding variability in fish populations (Anderson 1994, Carr 1994a).

Although there is a considerable literature on the potential importance of larval supply to the population dynamics of marine organisms (Underwood & Denley 1984, Doherty & Williams 1988, Roughgarden et al. 1988, Grosberg & Levitan 1992), recent work has shown or suggested that mortality of newly settled individuals, often as a result of predation, is critical in determining subsequent population size (Shulman & Ogden 1987, Hixon & Beets 1993, Levin 1994b). On temperate reefs, seaweeds can be critical components of habitat quality that determine survivorship of juvenile fishes. If these fishes become less dependent on seaweed-generated structure as they mature, then the regional abundance of seaweeds could ultimately affect adult populations that do not use seaweeds at all. As a possible example of this, at our study site, juvenile gag grouper and scamp grouper (<300 mm fork length) are found almost exclusively in the seaweed bed and begin using other, seaweed depauperate but structurally complex, portions of the reef only after they exceed the 300 mm size class (G. McFall & A. Hulbert, National Undersea Research Center, Wilmington, NC, unpubl. data).

If seaweeds are critical for juveniles but not adults, then the effects of periodic seaweed blooms could persist as strong year-classes of fishes long after the seaweeds are gone. In the South Atlantic Bight, about 85% of subtidal habitats are composed of sandy substrates that do not support seaweeds or reef fish. However, unusually large storms can remove the sand veneer from reefs and result in large increases in seaweed biomass (Renaud et al. unpubl.). These periodic expansions of algae could result in unusually high rates of fish recruitment. Moreover, for fishes, such as gag grouper, that settle in estuaries and migrate offshore after several months, the increased algal cover may increase available food and decrease mortality as they migrate >40 km to the reef habitat that they will occupy as adults. In other types of communities, asso-

ciations that protect juveniles during a critical early stage can create pulses of adults long after the protective symbiont is gone. In kelp beds, grazing on kelp sporelings by fishes is significantly reduced if the sporelings grow within patches of filamentous algae. If sporelings can survive this early stage, they rapidly achieve a size where fish grazing is no longer a threat (Harris et al. 1984). Similarly, spiny nurse plants in deserts prevent vertebrate grazers from killing young plants that later may persist in the presence of grazers even if the nurse plant dies (McAuliffe 1986).

From our experiments in North Carolina and from other work conducted in New England (Levin 1991, 1993, 1994b), New Zealand (Jones 1984a, b, 1988), and California (Ebeling & Laur 1985, Carr 1989, 1991a, b, 1994a, b, DeMartini & Roberts 1990, Holbrook et al. 1990a, b), it seems clear that seaweeds provide a critical habitat for settlement and early development of many temperate reef fishes. Despite the growing number of studies that document the importance of seaweeds to temperate reef fishes, there are few studies assessing what characteristics of seaweed beds are important to fishes. Understanding how various characteristics of algal beds influence settlement and subsequent retention of settlers on reefs would allow additional tools for the management of reef fisheries. For example, if a target fish population was limited by inadequate habitat for its early life stages, recruitment could be enhanced by (1) augmenting algal beds via the removal of urchins or the management of urchin outbreaks (Jones 1984a, Carpenter 1990); or (2) by the addition of sources of algal spores (Dayton 1973, Paine 1979).

In a recent review, Jones (1988) noted that characteristics of the habitat appeared to have a much greater effect on temperate reef fishes than the fishes have on the habitat. The recent emphasis on recruitment limitation and supply-side ecology in marine systems has produced a wealth of studies on physical and biological factors affecting larval supply. For temperate reef fishes, as well as many other organisms, we need to integrate these questions regarding larval delivery into a broader framework that includes an increased understanding of the habitat characteristics that cue larval settlement (e.g. Sweatman 1988) and significantly affect subsequent survivorship and growth.

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