

Habitat preference in newly settled coral trout (*Plectropomus leopardus*, Serranidae)

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Abstract. The densities of newly settled coral trout (*Plectropomus leopardus*, Pisces, Serranidae) were monitored in a variety of habitats on Green Reef in the Cairns section of the Great Barrier Reef to assess whether spatial patterns of recruitment are influenced by physical features of the substratum, and whether this species uses different habitats during its ontogeny. Surveys showed that small juveniles used sites that were significantly different from random and that these habitat associations changed as the fish grew larger. Specifically, coral trout recruited to level patches of rubble substrata $> 5 \text{ m}^2$ and subsequently shifted to high relief features. Densities of recruits were related to the amount of rubble substrata available.

Introduction

A significant component of the distribution and abundance of coral reef fishes can be explained by spatial heterogeneity within the environment (Smith and Tyler 1972; Luckhurst and Luckhurst 1978; Bell and Galzin 1984). In particular, newly settled reef fish often have restricted depth distributions and are associated with specific habitats (Ehrlich 1975; Sale 1980; Sale et al. 1980; Williams 1980; Doherty 1983; Eckert 1985). One explanation for these patterns is that larval fish possess precise habitat requirements at settlement and they actively select these sites (Sale et al. 1980).

Settlement sites selected by reef fish are known for only a few species (Leis 1991). Although numerous field studies have demonstrated apparent selection by juvenile damselfishes (Williams 1980; Sweatman 1988), and other reef-associated species (Sale et al. 1984; Eckert 1985), less is known about the habitat preferences of the juveniles of

large, carnivorous fish. In particular, little research has been devoted to the early life stages of serranids (Leis 1986; Richards 1990), primarily because they tend to be cryptic and rare; yet if serranids do select specific habitats at settlement, information about the characteristics of the preferred substratum could have important consequences for the management of this important commercial resource (Keener et al. 1988).

Coral trout, *Plectropomus leopardus*, are top carnivores and the most valuable food fish on the Great Barrier Reef (Williams and Russ 1994). With few exceptions, previous studies of this fish have concentrated on the adult phase and they have considered differences in density at whole-reef scales. Ayling et al. (1992) monitored the abundances of both juvenile and larger coral trout in front and back reef habitats on 26 reefs in the Cairns section of the Great Barrier Reef. They reported variation in the numbers of coral trout recruiting to each habitat, but attributed this to differential removal of predators due to fishing pressure. More recently, Doherty et al. (1994) used light traps to collect pre-settlement coral trout from sites in the same region, and reported spatial variation in catches, both between and within reefs.

These studies underscore the importance of selecting an appropriate sampling scale with which to measure patterns and processes (Ogden and Ebersole 1981). Measurement of patterns of habitat use for large, mobile fish such as coral trout may be complicated, not only because such fish are likely to relocate, but also because they may dramatically increase their range of movements during ontogeny (Davies 1995). Consequently, we might expect that habitat selection at settlement will be manifest over relatively small distances, reflecting both limited mobility and reduced sensory capabilities of these small fish. On the other hand, a sampling scale of kilometres may be necessary to detect changes in the fish-habitat associations of older juveniles. Therefore, several sampling scales may be needed to measure changes in habitat use during ontogeny.

The objectives of this study were three fold:

1. To characterise the specific sites occupied by newly settled coral trout

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2. To compare the habitat associations of newly-settled recruits with those of older fish, to establish whether ontogenetic shifts alter the distributions of growing coral trout
3. To determine appropriate sampling scales for measuring habitat associations of juvenile coral trout

Materials and methods

Study area

The study was conducted at Green Reef, in the central Great Barrier Reef Marine Park (Fig. 1), during September 1993–February 1994, and October 1994–February 1995. Four sites (S1–S4) were chosen around the periphery of the reef, at depths ranging between 8–15 m. Sites were selected in conjunction with another study (Doherty et al. 1994) which identified the presence of pre-settlement coral trout at these locations. S1 was designated the “primary area” and was used to make focused observations on newly settled fish. Within the primary area, a 50 × 50 m section was gridded and mapped in order to track the use of the environment by newly-settled coral trout.

Distribution and abundance among sites

Timed swims were used to assess the abundance of juveniles at each of the four sites. Each survey consisted of nine replicate 20 minute swims per site, covering a total area of approximately 1500 m². Replicates were separated by a short interval (3–5 minutes), during which divers were transported by boat to another haphazardly selected starting point. A zig-zag course was followed by divers, in order to include as many habitat types and depths as possible. One observer (PRL) methodically searched all habitats for the presence of juveniles. Standard lengths for all fish < 160 mm were estimated, and the associated habitats were recorded. The accuracy of size estimates was checked during a concurrent study, by capture and measurement of fish length. Two size classes were used in this study: 40–90 mm and 130–160 mm. Based on otolith studies, (Ferreira and Russ 1993) these size classes were considered to represent 0+ and 1+ fish (juveniles 90–130 mm were missing from the population during the sampling period). Sites were surveyed in December 1993 and 1994, and January 1994 and 1995.

Patterns of habitat use among sites

Point-intercept line transects were used to estimate percent habitat cover at each of the sites. Five replicate 50 m transects were placed haphazardly over the substratum, and 8 random points were selected along each transect. The substratum directly below each point was classified into one of four habitats: sand, rubble, live coral, and algae. The resulting 40 random points were used to determine the mean (\pm SE) cover for each of the categories.

Patterns of habitat use by 0+ fish within the primary site

In order to quantify habitat associations of newly settled fish and to determine their positions relative to prominent features in the environment, a 50 × 50 m section within the primary area was selected which contained relatively high numbers of recruits and offered a wide range of potential habitats. This section was subdivided into 10 × 10 m squares, and all features within each square (i.e. coral heads, rubble mounds, patches of macroalgae, etc.) were mapped with a resolution of approximately 50 cm. Habitat was quantified

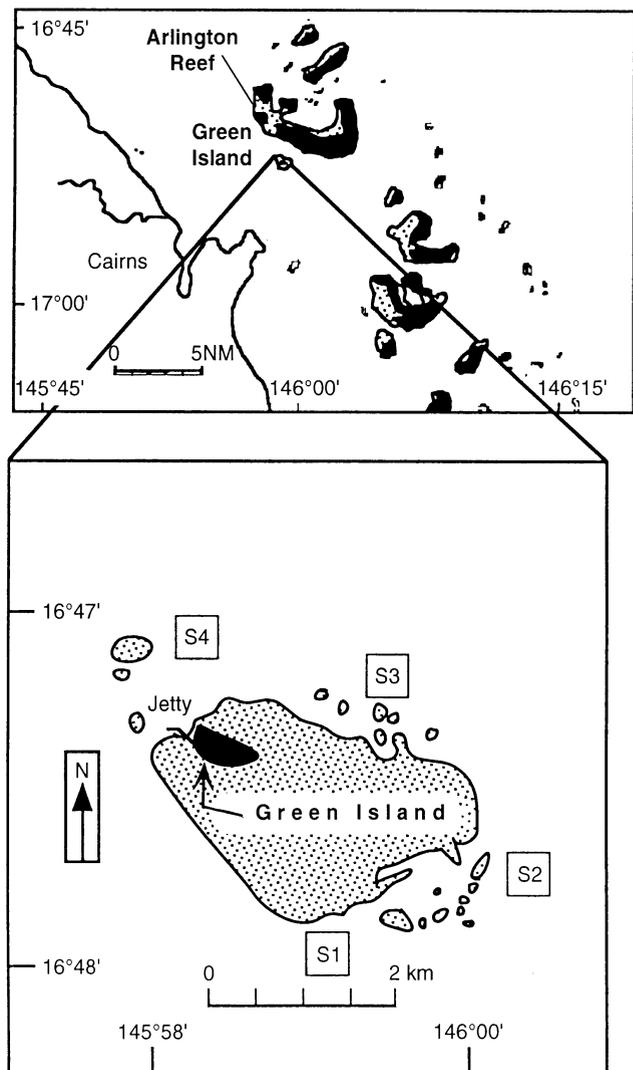


Fig. 1 Location of study sites at Green Reef. *Top*: position of Green Reef in the Cairns section of the GBR. *Bottom*: Green Reef, showing sites S1–S4 used in visual censuses. *Stippled area* reef platform

using six replicate point-intercept transects. The resulting 48 points were assigned to habitat categories as described already, with the exception that rubble habitats were subdivided into sand-rubble, rubble mounds, and dead coral, to allow for finer-scale partitioning of the environment (Table 1). Depth was 10–11 m.

The position of each juvenile was recorded during daily censusing of the grid between 8 December 1993 and 6 February 1994. Censuses required about 45 min to complete, and were conducted at different times of day to minimise effects of diurnal and tidal patterns. Juveniles undergo a pronounced shift in behaviour and diet at around 60 mm SL, when they become less cryptic and switch from crustacean prey to a mainly piscine diet (Light 1995). To determine whether these changes are accompanied by a corresponding habitat shift, newly settled fish were divided into two size classes: 40–60 mm (new recruits), and 61–99 mm (large recruits). Comparison of captured individuals with size estimates indicated that fish were correctly assigned to classes in > 95% of estimates.

In order to identify individuals, selected fish were marked and released. Fence nets were used to capture these juveniles ($n = 57$), and they were branded with individual marks using a 12 volt soldering tool. After branding and measurement, each fish was returned to the exact point of capture, usually within 10 min. Marks remained visible for two months, and observations of branded fish in

Table 1 Habitat types used in use/availability study, and descriptions

Habitat	Description
Sand/Rubble	Level expanses of sand bottom, covered with medium-grade rubble, (<10 cm along major axis)
Rubble mounds	Large (>10 m ²) piles of consolidated dead branching coral, often covered with macroalgae, rising to 5 m above bottom
Live coral	Hard and soft corals
Algae	benthic macroalgae, 5–15 cm in height
Sand	Uniform patches of sand containing little or no rubble
Dead coral	Rocks > 0.5 m

captivity and in the field indicated that fish were not adversely affected by the procedure. Daily positions of marked fish were recorded on an underwater map, and the most divergent observation points for each individual were connected to estimate home range. Subsequent plots of the area of these convex polygons and the number of resightings showed that home range was estimated reasonably with a minimum of twelve resightings. Consequently, the areas of fish with twelve or more resightings were used to indicate their positions relative to spatial reference points inside the grid.

The null hypothesis that juvenile coral trout use habitats in proportion to their availability was evaluated using two tests. First, resightings of all marked recruits were pooled and divided into the two size classes corresponding to new and large recruits. Frequency distributions of the number of fish seen on habitats were compared to habitat availability, using Chi-square tests. As a second test of habitat selection, the linear resource selection index, L , (Strauss 1979) was used to estimate habitat selection of individual fish:

$$L = r_i - p_i,$$

where r_i = relative utilisation of substratum i (i. e. number of associations of one individual with a habitat divided by the total number of resightings of that individual), and p_i = overall proportion availability of substratum i . Expected values of this index fall between ± 1 , with zero indicating random association and negative values indicating avoidance of the substratum. Selection indices were calculated for all fish resighted 12 or more times, and the means of new and large recruits were compared using Student's t-test. T-tests were also used to assess whether values were significantly different from zero for each habitat ($\alpha = 0.05$) (Morrissey and Gruber 1993).

Effect of sampling scale on measurement of habitat selection

To determine at what spatial scale settlement sites differed from randomly chosen sites, 33 recruits (mean SL 36.7 ± 1.2 mm, range 25–47 mm) were captured and measured during 1994–1995. For each fish, the surrounding habitat was quantified at three spatial scales using quadrats of nested size (1, 2, and 5 m squared), each divided into grids of 36 evenly spaced points. The surrounding habitat was classified under each point into one of 11 habitat categories, defined as: (1) rubble, (bits of dead coral <10 cm); (2) sand, (fine grained calcareous sediment); (3) algae, (e.g. *Halimeda*, *Sargassum*, *Caulerpa*); (4) rock, (dead coral >10 cm, firmly embedded in substratum); (5) live branching coral, (e.g. *Acropora*, *Pocillopora*); (6) live massive coral, (e.g. *Porites*, *Goniopora*); (7) live plate coral, (e.g. *Plerogyra*); (8) sponge; (9) soft coral; (10) consolidated rubble, (mounds of dead branching coral, rising 4–8 cm above the sea-bed); and (11) consolidated algae/rubble,

(similar to 10, but encrusted with turf and/or calcareous algae). To provide a valid comparison, null sites were selected using a compass and sets of two random numbers. The first random number in a set (integer between 1 and 8 inclusive) specified the compass quadrat (to the nearest 45°); the second (0–99 inclusive) determined the number of fin strokes to swim from the point of origin. Once the null position was determined, the surrounding habitat was quantified by the same procedures using the same three nested quadrats. The points underlying the quadrats were recorded as discussed.

Chi-square homogeneity tests on total counts for each of the 11 habitat groups were used to assess whether habitats selected at the three scales differed from each other. Principal components analysis (PCA) was used to reduce the data set to a smaller number of uncorrelated components, in order to identify trends in habitat use. Principal component axes (PCs) were characterised by their correlations with the original microhabitats: correlations were considered significant if they had an absolute magnitude greater than 0.5 (Paulissen 1988). Microhabitats selected by recruits were expressed as a subset of all microhabitats potentially available at each scale. Means and standard errors of eigenvalues along each PC axis were calculated, and significant differences between selected and random scores were identified at each of the three scales and for all scales combined, using Student's t-test ($\alpha = 0.05$) (Paulissen 1988).

Results

Distribution and abundance among sites

The pattern of distribution of recruits among sites at Green Island was relatively consistent between years (Fig. 2). S1 and S2 received the highest number of 0+ fish in both years sampled, but the overall magnitude was higher in the second year. When counts from both seasons were combined, 63 recruits were recorded from S1 and S2 compared to only three from the other two sites.

As with 0+ fish, one-year-old fish were slightly more abundant at S1 and S2. However, site by site comparison of the distributions of 0+ fish from the first season with distributions of 1+ fish from the second year, shows that despite a lack of recruits at S3 in 1993–1994, 1+ fish were present at this site during the following season, at densities equivalent to S1 and S2.

Analysis of variance of 0+ fish counts using years, months, and sites as fixed factors and number of fish seen per 20 min swim as the response variable, detected a significant interaction between year and site (Table 2). Multiple comparisons revealed higher abundances in 1994–1995, and for January censuses. Recruitment at S1 was significantly higher than at other sites (Tukey's test, $\alpha = 0.05$).

Counts of 1+ fish showed a similar rise in numbers during 1994–1995. A significant interaction was found between year and month (Table 3), indicating that the trend in the distribution pattern differed from that of 0+ fish. Multiple comparisons indicated a more even distribution of 1+ fish relative to recruits: there were no significant differences between abundances at S1, S2, and S3, and fish counts did not differ significantly between months.

Patterns of habitat use among sites

Analysis of transect data detected significant between-site differences in percent cover for rubble, sand, and algae,

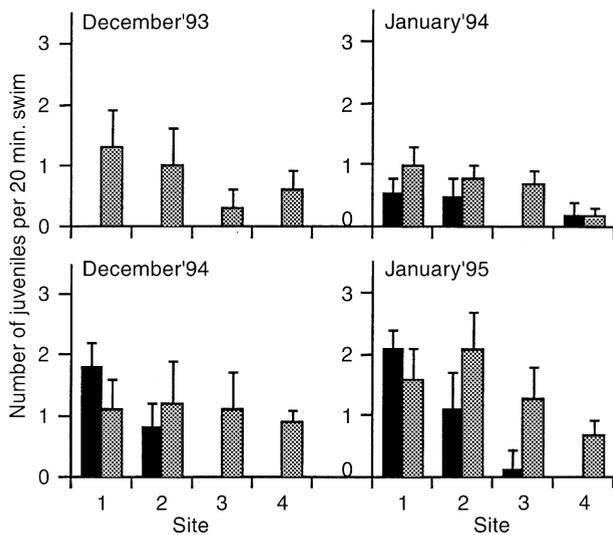


Fig. 2 Mean (\pm SE) number of juveniles seen per 20 min swim at sites around Green Reef ($n = 9$ swims per site). *Dark bars:* 0 + fish (recruits), *light bars:* 1 + fish

Table 2 A ANOVA of numbers of 0 + juveniles seen per 20 min swim during monthly timed swims at 4 sites around Green Reef. Assumptions of normality and homoscedasticity were met by the data (Cochran's test). **B** Tukey's test of number of juveniles seen per 20 min swim for the main effects of year, month, and site. Treatment levels not significantly different at the 0.05 level share an underline. Treatment levels are arranged in increasing order of juvenile abundance

A				
Source	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P</i>
Year	1	11.67	57.97	< 0.0001
Month	1	2.51	12.45	< 0.001
Site	3	9.56	47.48	< 0.0001
Year \times month	1	0.17	0.86	0.36
Year \times site	3	5.82	28.91	< 0.0001
Month \times site	3	0.40	1.97	0.12
Year \times month \times site	3	0.06	0.31	0.82
Residual	128	0.20		

B				
Main effect				
Year	<u>1993–1994</u>	<u>1994–1995</u>		
Month	<u>December</u>	<u>January</u>		
Site	<u>S4</u>	<u>S3</u>	<u>S2</u>	<u>S1</u>

and live coral (Table 4). S1 had the highest proportion of rubble substrata, while S4 had relatively high amounts of coral. S2 had the highest component of algae. Linear regression analysis of mean abundance of 0 + and 1 + fish with mean frequency of rubble cover at each site (Fig. 3) indicated a significant positive correlation for 0 + fish ($r^2 = 0.96$, $F = 47.3$, $P = 0.02$), but there was no significant correlation for 1 + fish ($r^2 = 0.46$, $F = 1.67$, $P = 0.33$).

Table 3 A ANOVA of numbers of 1 + juveniles seen per 20 min swim during monthly timed swims at 4 sites around Green Reef. Assumptions of normality and homoscedasticity were met by the data (Cochran's test). **B** Tukey's test of number of juveniles seen per 20 min swim for the main effects of year, month, and site. Treatment levels not significantly different at the 0.05 level share an underline. Treatment levels are arranged in increasing order of juvenile abundance.

A				
Source	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P</i>
Year	1	9.0	17.34	< 0.0001
Month	1	0.25	0.48	0.49
Site	3	3.72	7.17	< 0.0005
Year \times month	1	2.25	4.33	< 0.05
Year \times site	1	0.80	1.53	0.21
Month \times site	3	0.82	1.59	0.20
Year \times month \times site	3	2.0	1.8	0.20
Residual	128	0.52		

B				
Main effect				
Year	<u>1993–1994</u>	<u>1994–1995</u>		
Month	<u>December</u>	<u>January</u>		
Site	<u>S4</u>	<u>S3</u>	<u>S2</u>	<u>S1</u>

Table 4 A One way ANOVA of habitat cover at 4 sites around Green Reef, based on 40 random points per site. **B** Tukey's test of frequency of habitat at each site. Sites not significantly different at the 0.05 level share an underline. Sites are arranged in increasing order of frequency

A				
Source	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P</i>
Rubble	3	6.85	24.91	< 0.0001
Sand	3	16.07	21.42	< 0.0001
Algae	3	15.38	27.97	< 0.0001
Live coral	3	7.8	18.35	< 0.0001

B				
Habitat	<u>S3</u>	<u>S4</u>	<u>S2</u>	<u>S1</u>
Rubble	<u>S3</u>	<u>S4</u>	<u>S2</u>	<u>S1</u>
Sand	<u>S2</u>	<u>S1</u>	<u>S4</u>	<u>S3</u>
Algae	<u>S4</u>	<u>S3</u>	<u>S1</u>	<u>S2</u>
Live coral	<u>S2</u>	<u>S1</u>	<u>S3</u>	<u>S4</u>

Patterns of habitat use within a site

Fish-habitat associations were recorded for new recruits ($n = 169$), and large recruits ($n = 239$) seen during daily censuses of the 50×50 m grid. Number of resightings per fish ranged from 1 to 17. As analysing habitat associations from all resightings could bias results towards individuals resighted disproportionately more often, three observations were selected at random from the total observations of each juvenile, and were used to calculate use/availability indices. Frequency of sightings were inversely related to number of observations, thus the likelihood that random subsets represented the actual distributions of habitats remained consistent across observation numbers.

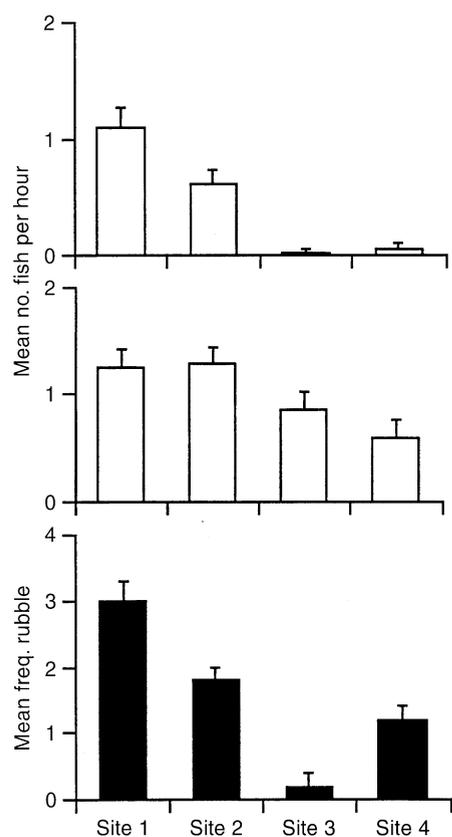


Fig. 3 Mean (\pm SE) number of juveniles seen during timed swims at 4 sites, and mean (\pm SE) frequency of rubble at each site. Counts of juveniles are pooled over two seasons ($n = 36$ swims per site). Frequency of rubble based on 40 random points (see text). *Top*: 0+ fish; *Middle*: 1+ fish; *Bottom*: frequency of rubble at each site

Comparison between numbers of juveniles seen on each habitat, with the availability of each habitat indicated a non-random assortment for both size classes. Habitats were used in proportions that varied significantly from their availability, in both new recruits ($X^2 = 92.1$, $df = 4$, $P < 0.0001$), and large recruits ($X^2 = 72.7$, $df = 4$, $p < 0.0001$). Sixty one percent of all sightings of new recruits were on the sand-rubble habitat, while this substratum took up only 24% of the total area (Fig. 4, Top). Large recruits were recorded most often on consolidated rubble mounds. Sightings on this habitat comprised 41% of all observations, while this substratum constituted only 21% of the total area (Fig. 5, Top).

Comparison of mean L values (preference/avoidance) for recruits seen twelve or more times also showed that new recruits (Fig. 4, Bottom) and large recruits (Fig. 5, Bottom) used habitats disproportionately to their availability within the grid. The greatest change in habitat use involved a transition from sand-rubble habitats to rubble mounds as fish increased in size. The use of sand-rubble was significantly different between the two size classes ($t = 5.2$, $P < 0.005$), as was the use of the rubble mound habitat ($t = -2.9$, $P < 0.05$). New recruits used the sand-rubble and live coral habitats in proportions which were significantly different from random ($t = 7.9$, $P < 0.001$; and $t = 5.6$, $P < 0.02$, respectively). Similarly large recruits used rubble mounds and live coral in proportions which

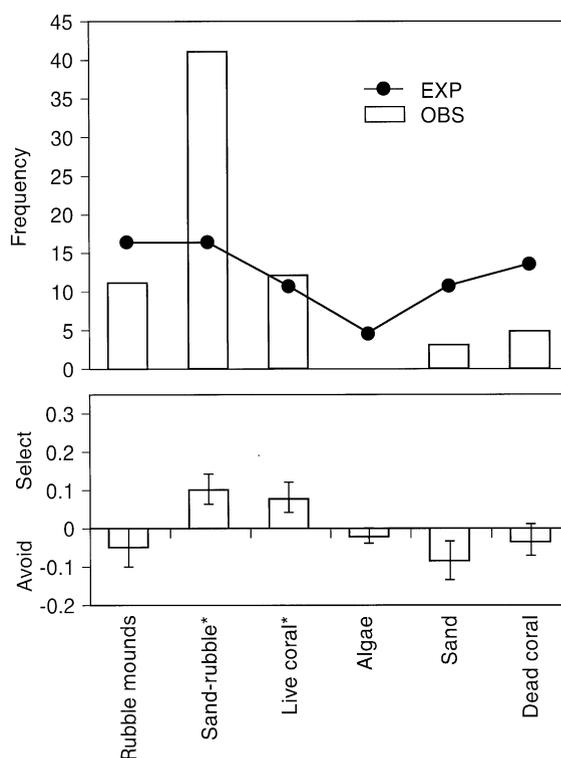


Fig. 4 *Top*: observed (*histogram*) and expected (*circles*) frequencies of observations of new recruits ($n = 72$) seen on habitats within 50×50 m mapped area. *Bottom*: mean (\pm SE) index of selectivity values for new recruits resighted 12 or more times ($n = 7$). *, significantly different from 0

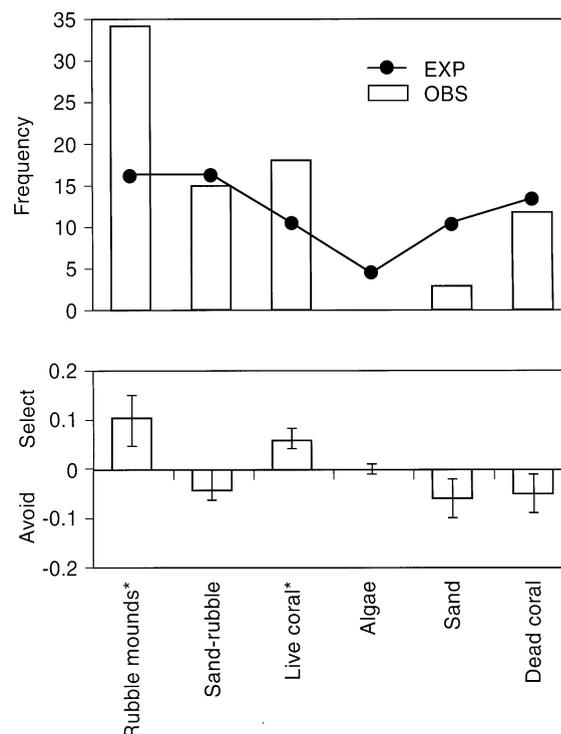


Fig. 5 *Top*: observed (*histogram*) and expected (*circles*) frequencies of observations of large recruits ($n = 85$) seen on habitats within 50×50 m mapped area. *Bottom*: mean (\pm SE) index of selectivity values for large recruits resighted 12 or more times ($n = 8$). *, significantly different from 0 (t -test, $P < 0.05$)

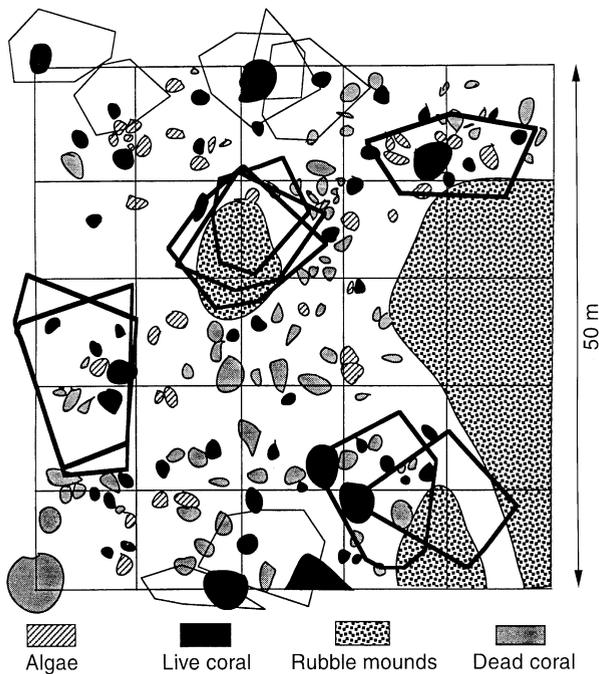


Fig. 6 Map of 50 × 50 m area used to monitor habitat associations of juveniles over time. *Polygons* represent the most divergent observation points for fish sighted 12 or more times ($n = 1.5$). *Light polygons* new recruits, *bold polygons*, large recruits

were statistically non-random ($t = 5.1$ $P < 0.002$; and $t = 5.60$, $P < 0.001$, respectively). Positions of large recruits were closely associated with high relief structures, and areas used by these fish tended to overlap (Fig. 6).

Effect of sampling scale on measurement of habitat selection

Mean frequencies of substrata cover for the 11 microhabitats were plotted for both selected sites and null sites

Table 5 Means (\pm SE) of PC scores for selected and random grids computed for the total data set and for each grid size. An asterisk denotes a significant difference between random and selected grids, using Student's t-test

		PC-1 Rubble (0.5)	PC-2 LM ^a (0.58)	PC-3 Sand (-0.54)
Correlation with PC				
Percent of variance		25.51	13.89	11.56
Scale	n ^b	Score (X \pm SE)	Score (X \pm SE)	Score (X \pm SE)
1 × 1	33	F ^c 1.1898 \pm 0.089	0.006 \pm 0.075	0.181 \pm 0.137
	33	R ^d -1.148 \pm 0.276***	0.129 \pm 0.303	-0.163 \pm 0.257
2 × 2	33	F 1.229 \pm 0.083	0.009 \pm 0.098	0.285 \pm 0.144
	33	R -1.066 \pm 0.278***	0.003 \pm 0.281	-0.081 \pm 0.234
5 × 5	33	F 1.174 \pm 0.085	0.148 \pm 0.100	0.253 \pm 0.118
	33	R -1.069 \pm 0.287***	0.541 \pm 0.283*	-0.136 \pm 0.179*
Total	99	F 1.197 \pm 0.049	-0.044 \pm 0.053	0.224 \pm 0.075
	99	R -1.095 \pm 0.160***	-0.133 \pm 0.179	-0.150 \pm 0.126**

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.0001$

^a Live massive coral

^b Number of grids

^c Fish-selected sites

^d Randomly selected sites

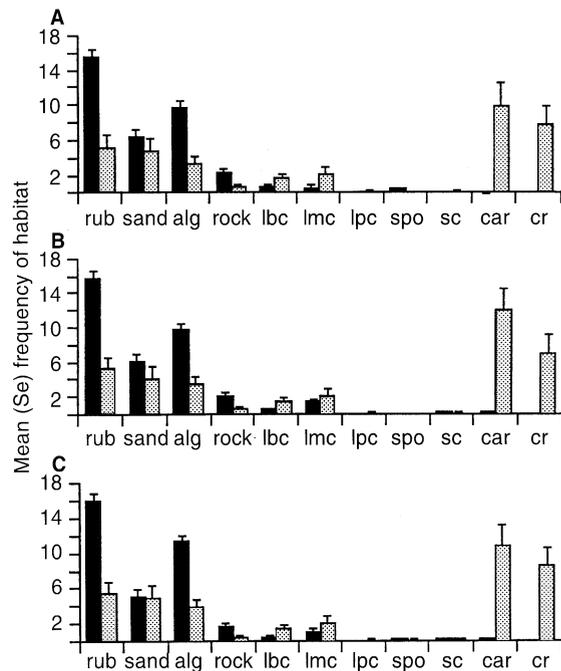


Fig. 7A–C. Mean (\pm SE) frequency of habitat types from nested grid study (see text). *Dark bars*, values for sites selected by recruits, *light bars*, random sites. Frequencies are based on 36 points within each grid. **A** 1 × 1 m grid; **B** 2 × 2 m grid; **C** 5 × 5 m grid. Habitat code: *rub*, rubble; *lbc*, live branching coral; *lmc*, live massive coral; *lpc*, live plate coral; *spo*, sponge; *sc*, soft coral; *car*, consolidated algae-rubble; *cr*, consolidated rubble

at the three scales (Fig. 7). There were significant differences between random and selected sites with regard to seven of the eleven microhabitats when data from all grids were pooled. Rubble, algae, and rock microhabitats were the most strongly selected categories as compared to null sites. Frequencies of live branched, live massive, consolidated rubble, and consolidated algal-rubble microhabitats were significantly higher in randomly chosen grids, indicating

that recruits tended to avoid these substrata. Chi-square contingency tests using the total frequency counts for each habitat group showed that the observed frequency distribution of the three grids differed significantly from each other: ($X^2 = 35.76$, $df = 14$, $P < 0.01$).

The first three components accounted for 51.0% of the variance in the raw data (Table 5). PC-1 was strongly positively correlated with rubble, algae, and rock substrata, and negatively correlated with rubble mounds and live branched coral. Thus PC-1 is interpreted as a relief gradient, with positive values denoting low relief features. PC-2 was strongly positively correlated with live massive, live

branched, and live plate coral, and hence describes a living/non-living gradient, with high values associated with live coral microhabitats, and low values representing rubble mounds and other primarily non-living substrata. The third PC was positively correlated with the sand microhabitat.

PC scores from all grids combined (total) showed significant differences between random and selected sites on PC-1 ($t = 13.5$, $P < 0.0001$) and PC-3 ($t = 2.4$, $P < 0.01$), but not on PC-2. When each grid size was analysed separately, selected and random sites differed at all three scales on PC-1. Only the 5×5 m grids showed significant

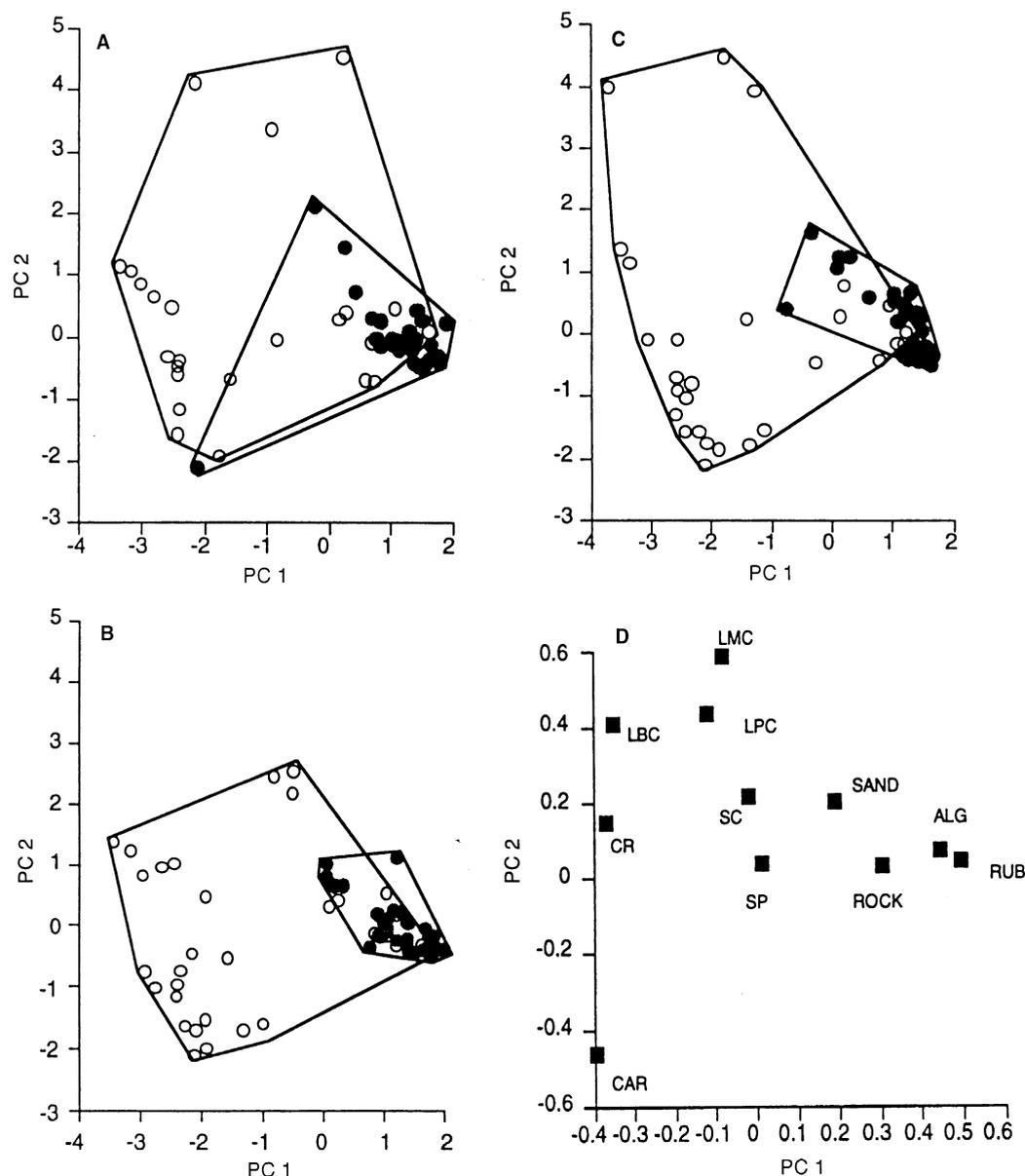


Fig. 8A–D. Eigenvalues of fish-selected sites ($n = 33$, filled symbols), versus randomly selected sites ($n = 33$, open symbols) at three spatial scales. The most divergent values for each group are connected to indicate habitat space relative to axes. **A** eigenvalues at 1×1 m scale; **B** eigenvalues at 2×2 m scale; **C** eigenvalues at 5×5 m scale; **D**

eigenvalues of habitats. All values plotted against PC 1 (25.5% of variance) and PC 2 (13.9% of variance). *LBC*, live branched coral; *LMC*, live massive coral; *LPC*, live plate coral; *SPO*, sponge; *SC*, soft coral; *CAR*, consolidated algae-rubble; *CR*, consolidated rubble

differences between random and selected sites on all three PC axes.

Plots of the eigenvalues for each grid size against the first two PCs indicated tight clustering of selected sites as opposed to random sites (Fig. 8A, B, C). Most recruits were strongly associated with low relief features which were intermediate on the living/non-living spectrum. Comparison of these plots with the biplot of habitats (Fig. 8D) shows that newly settled fish were primarily associated with rubble, algae, and rock habitats.

Discussion

Habitat associations of newly settled and growing juvenile coral trout are potentially important to the demography of adult populations. Recruits settled within patches of sand-rubble, and subsequently shifted to high relief features as they grew. Furthermore, their abundance at sites around Green Reef was correlated with the availability of the preferred habitat. On the other hand, distribution patterns for one year old fish were more dispersed at the whole reef scale, suggesting that older fish had moved from initial settlement sites.

The importance of selecting an appropriate sampling unit to measure fish-habitat associations was emphasised in a study by Roberts and Ormond (1987), in which pomacentrid abundances were strongly correlated with habitat at one scale, but not at another. Similarly, Ogden and Ebersole (1981), found that large artificial reefs were better indicators of change in community structure over time than small patch reefs. In the present study, the similar ability among all three grid sizes to discriminate between random and selected sites, (Fig. 8) indicated that the smallest grid size provided sufficient resolution to distinguish selected sites from random ones. Thus, coral trout probably respond to their environment at a scale of approximately 1 m² at the time of settlement, and a sampling unit of 1 × 1 m should provide the best compromise between precision and effort in future efforts to quantify settlement sites for this species.

Settlement sites were readily differentiated from randomly chosen sites, and had distinct microhabitat attributes as characterised by PCA. Most of the variation in the microhabitat data was described by a relief gradient (PC-1), and recruits were strongly associated with low relief features. These features, (rubble, algae, rocks) were ubiquitous within the settlement site, and appeared to facilitate predator avoidance by allowing recruits to search for prey while maintaining proximity to shelter.

The smallest recruits encountered in this study, (25 mm) had probably settled less than one week prior to capture. Mean size at settlement (as estimated from otolith analysis) was 17.9 (0.15) mm; growth rates were 1.05 (0.5) mm/day, and recruits were initially highly site-attached (Light 1995). Masuma et al. (1993), reported that coral trout reared during an aquaculture study were competent to settle at 20 mm SL. It is therefore likely that sites occupied by captured fish accurately represented microhabitats chosen at settlement.

Narrow microhabitat preferences at settlement have been documented for a number of reef species. Williams

(1980) found that two species of pomacentrids recruited to specific sections of patch reefs during three successive years. Sale et al. (1984) showed that sites occupied by eight species of newly settled reef fish could be discriminated from random sites in all but one case, although sites selected by individual species were not significantly different from each other. Ross and Moser (1995) presented evidence that pre-settlement gag, (*Mycteroperca microlepis*), an epinepheline serranid inhabiting coastal Atlantic waters, selectively recruited to sea-grass habitats. These habitats served as temporary "nurseries" from which they dispersed into surrounding habitats. Similarly, sites occupied by coral trout at settlement may represent centres of dispersal to other areas of the reef.

Compared to 0+ fish, the distribution pattern of 1+ fish at sites around Green Reef was more dispersed, suggesting that ontogenetic changes in movement may have altered spatial patterns established at settlement. Relatively high numbers of 1+ fish were recorded at S3 during 1994–1995, although none were seen there during 1993–1994. Furthermore, only one recruit was seen at this site during all surveys combined, suggesting that these older juveniles emigrated from nearby sites, probably S1 and S2. Behavioural observations of 0+ and 1+ fish indicate that older fish spend significantly more time moving, and less time under cover (Light 1995).

In addition to increased mobility, juveniles also shifted habitats early in life. At approximately 60 mm SL, initial preferences for sand-rubble changed to an association with high relief features. Similar shifts in habitat use by juvenile serranids have been reported in at least two other studies. Ross and Moser (1995) found that several months after settling on sea-grass beds, gag moved from these relatively low relief habitats into complex habitats such as jetties and pilings. In a study of another Atlantic epinephelid, juvenile (3–8 cm) Nassau groupers (*Epinephelus striatus*) were initially observed in close proximity to the sea bed, but moved into holes in the reef as they grew (Beets and Hixon 1994).

Distributions of newly settled coral trout were also correlated with the presence of rubble substrata at the whole reef scale. Green Reef is classified a fringing/planar reef (Black and Gay 1987), which is periodically disturbed by natural events including cyclones and *Acanthaster* outbreaks (Dight et al. 1990). S1 and S2 are located on the exposed southeast face, in a section of reef which has received the main impact of several cyclones in the past 30 years (George Craig personal communication). Habitat surveys around Green Reef recorded comparatively large amounts of rubble cover at these sites, which also received the highest recruitment during both seasons. The strong correspondence between recruit density and specific substrata suggests that distribution patterns may be the result of active selection of broad-scale regions of habitat.

A number of alternate explanations could also account for the uneven distribution of recruits around Green Reef. One suggestion is that recruits may be overlooked in certain habitats. This is unlikely, since sites recording the highest recruit numbers were also the most structurally complex and thus would presumably provide more hiding spaces than alternate sites.

Another possibility, differential delivery of larvae to sites, is suggested by hydrodynamic models predicting low residual displacement on the down stream side of reefs (Black 1993). Green Reef is influenced by the predominantly southward-flowing East Australian Current (Wolanski and Pickard 1985). Hence, if hydrodynamic trapping does occur behind reefs, the highest concentrations of pre settlement fish should be found at sites on the south edge of Green Reef. Indeed, the highest abundances of recruits were found at S1 and S2, both of which are located close to the south east corner of the reef. However, both light trap samples and visual censuses indicated that recruitment does occur at upstream sites, albeit at lower levels. Thus, models of distribution based solely on hydrographic features cannot account for the uneven distribution patterns seen among Green Reef sites.

The finding that recruits occupied specific microhabitats shortly after settlement suggests that larval coral trout were capable of identifying gross differences in habitat and reef morphology. Observations of such behaviour is available from both field (Sale et al. 1980; Eckert 1985) and laboratory studies (Marliave 1977). Spatial variability in coral trout recruitment at Green Reef may be due to broad-scale selection of regions within the reef, followed by differential movement and mortality at smaller scales. Despite large fluctuations in the magnitude of recruitment between years, the pattern of recruitment to sites was relatively constant, indicating that it may be a regular feature of the demography of coral trout on this reef. Further research will be necessary to establish the generality of this pattern on other reefs within the GBR.

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