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Effects of habitat on the recruitment variation of coral reef fishes.

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EFFECTS OF HABITAT ON THE RECRUITMENT VARIATION OF CORAL REEF FISHES

by
Paolo Usseglio

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ABSTRACT

Coral reef fish life cycles have two distinct phases that take place in different parts of their environment. Benthonic or pelagic eggs spawned by adults hatch into larvae that join the water column, after spending some variable time in it they settle back on to a reef. It is well documented that recruitment is highly variable across space and time. This variation can be a reflection of factor occurring during the pelagic larval phase, or during the settlement event. Prior to settlement the number of larvae settling to a given location could be a consequence of oceanographic features, as well as random events taking place during the pelagic larval phase which might affect the survival of larvae. Larvae then have been found to settle differentially to a preferred habitat. These associations have been studied at several spatial scales with contrasting results. In order to explore relationships between habitat and patterns of recruitment, we must first describe the habitat features found at a given location. Chapter two explored the effects that sampling intensity (i.e. number of sampling points or quadrats) and method (point-intercept vs. photo quadrats) have on the comprehensiveness and precision of percent cover estimates of substratum abundances. For both methods, comprehensiveness was least at the lowest level of sampling intensity, and rare substrata were not detected. Percent cover estimates obtained with either method were comparable in terms of precision. Inter-method comparison of sampling intensity revealed significant differences specific to particular substrata. The results obtained with the different sampling intensities employed in each method suggest that sampling at lower intensities is a viable option to increase levels of replication and/or savings in field time and costs, without compromising the precision or the comprehensiveness of the estimates obtained.

Chapter three assessed the degree to which habitat type can explain the spatial and temporal variation observed in the recruitment of 2 coral reef species. Even though, there was significant variation in substrate types throughout Mexico, Belize and Honduras, no clear spatial or temporal associations were detected between particular substrata and recruitment of either species. Our results suggest that large-scale variations in recruitment are affected by more than variation in substrate types and

therefore recruitment models focusing solely on substrata will fail to yield accurate information.

DEDICATION

To the awesome financial support
This university gives to grad students
Wink, wink, nudge, nudge

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ACKNOWLEDGMENTS

STATEMENT OF ORIGINALITY

"I certify that this thesis, and the research to which it refers, are the product of my own work, and that any ideas or quotations from the work of other people, published or otherwise, are fully acknowledged in accordance with the standard referencing practices of the discipline. I acknowledge the help and guidance of my supervisor Dr. Peter Sale, as well as Dr. Jake Kritzer, M.Sc. Paul Chittaro, Camilo Mora and Derek Hogan for critical review of early drafts of the chapters of this thesis"

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Chapter 1

General introduction

Introduction

Coral reef fish life cycles have two distinct phases that take place in different parts of their environment. First, adults spawn eggs (that may or may not be attached to the substratum) these eggs develop into larvae which enter the pelagic environment where they spend a variable amount of time ranging from weeks to months (Cowen 2002) before settling to a reef. This pelagic larval phase has been called a "black box" because it is very difficult to accurately assess the behavior and interactions of microscopic larvae immersed in trillions of liters of sea water. Following this pelagic phase larvae settle on to a reef to commence their juvenile life. Whether they settle to their reef of origin or to another reef is still a matter of much debate. It has been argued that populations of coral reef fish might be closed with self recruitment as the major contributor of larvae to the local population. On the other hand populations can be open because of the potential for long distance dispersal by larvae. Mora and Sale (2002) suggested that the answer might not lie at opposite ends of a continuum where populations are totally open or completely closed, but somewhere in the grey area where populations are both partially open and closed.

It is well documented that the recruitment of larvae that arrive to a given population is highly variable in both time and space, and at several spatial scales. Several mechanisms acting at different periods of the life cycle of coral reef fish have been proposed to explain this variation. The number of larvae settling to a given location could be a consequence of oceanographic features such as currents or eddies that can disperse or retain larvae from and to particular locations. Random events taking place during the pelagic larval phase might modify survival of larvae, and therefore affect the quantity of larvae competent to settle at a given location. Larvae have been found to settle differentially to a preferred habitat or to locations where conspecifics are abundant (Sweatman 1985), and this might account for spatial patterns in variation. Settlement does not assure survivorship, post-settlement events such as differential rates of mortality among sites, movement to preferred habitats, and competition with other fish may all influence the number of recruits observed at a given location.

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Studies have shown that larvae are behaviorally active during their late pelagic stage (Leis 1991). Larvae of some species exhibit strong swimming abilities (Stobutzki and Bellwood 1997). While the extent to which these behaviours are used in the natural environment is still a matter of debate, the possibility of larvae actively influencing their patterns of abundance and distribution is still possible.

Of the variation factors that may influence settlement and recruitment, habitat variation has been closely studied. Studies have suggested that recruitment patterns can be explained by habitat features (Sale 1979, Sweatman 1985, Carr 1991, McGehee 1995, Risk 1997, Holbrook et al. 2000, Levin et al. 1997, Tolimieri 1995, Tolimieri 1998a,b). The reef substratum can be viewed as a complex matrix in which fish can find shelter from predation and food. It is understandable then that different habitat types can provide different degrees of protection and food availability, which can be translated into higher abundances of recruits at "preferred" habitats.

In order to explore the relationships between habitat type and recruitment variation we must first describe the attributes that describe a habitat. A coral reef habitat is the assemblage of various substrata, therefore percent cover of each of the different substrata, both living and non, found in a particular area are often used as a proxy for habitat structure. Methods to quantify percent cover of habitat types can be divided into methods employing line transect and quadrat based approaches. Line transects can be sampled by recording substratum as segments along a line (Porter 1972),or by using a series of randomly or evenly distributed points along the centreline of the transect (Lucas 1977). Percent cover Quadrats can be used to quantify habitat composition by visually estimating the percent cover of each substratum within the quadrat (Goldberg 1973). Line transects can be sampled as a series of points along a line, therefore the number of points can be variable. There is a trade off between number of points and time spend in sampling a given transect. Researchers in coral reefs must often conduct studies in locations that are somewhat remote. It is at these locations that field time might be a limiting factor for our humble research allowances; therefore effective methods that yield accurate and homogeneous results are needed. Using fewer number of sampling points will lead to a decrease in field time per sampling unit, this in turn can

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allow us to increase our levels of replication. Chapter two explores the differences in the percent cover estimates obtained by using different numbers of sampling points by each line transects and quadrats analyzed by photography (photoquadrats henceforth). Complementary, chapter one also explores the way in which the two different approaches (line transects vs photoquadrats) describe the benthic community of a coral reef.

Describing the characteristics of the habitat is then the first step towards analyzing its effects on coral reef fish recruitment. These effects have been widely address in the literature for over 3 decades (Sale 1971, Sale *et al.* 1984, Jones 1988, Carr 1991, Booth 1992, Wellington 1992, Tolimieri 1995, Caselle and Warner 1996, Tolimieri 1998 a,b), and it is of general consensus that habitat features influence the abundance and distribution of coral reef fish. Recent evidence suggests that patterns of recruitment at small spatial scales (meters to hundreds of meters) can be a reflection of particular habitat attributes, however when these patterns are analyzed at larger spatial scales (several kilometers) the habitat-recruitment relationships tend to disappear (see but Tolimieri 1998b).

During 2002 our lab censused recruitment of fish at a number of sites across the Mesoamerican Barrier Reef System. Chapter three of this thesis explores the extent to which habitat can explain the variation in patterns of recruitment observed in these data. I selected two coral reef fish, *Thalassoma bifasciatum* and *Stegastes partitus* because they are numerically dominant in our database and because of their contrasting life histories. *T. bifasciatum* inhabits reef areas usually swimming freely over coral heads, inshore bays and sea grass beds. Feeds mainly on zooplankton and small benthic animals, but may also feed on ectoparasites of other fishes (Randall 1967). *S. partitus* is usually found in shallow coral reefs and isolated patch reefs in deeper water in close association with its substrate. It feeds primarily on algae but also on polychaetes, hydroids, copepods and ascidians (Cervigón 1993). As most pomacentrids this species is extremely territorial. This contrasting life histories will allow us to explore the relationships between habitat and recruitment in species with different habitat use.

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This study is also the first large scale effort to evaluate patterns of recruitment along the Mesoamerican Barrier Reef System (MBRS).

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Chapter 2

Effects of sampling intensity on estimates of percent cover obtained

with point-intercept and photo quadrat methods

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Introduction

The effects of habitat structure on reef fish communities have been widely addressed (Luckhurst and Luckhurst 1978, Bell and Galzin 1984, Jones 1988, Booth and Beretta 1994, Munday 2002). Several studies have suggested that species richness and biomass are related to attributes such as habitat richness (Ault and Johnson 1998), abundance of particular habitat types (Tolimieri 1998), and habitat complexity (Luckhurst and Luckhurst 1978, Jones and Syms 1998). In order to relate assemblages of fish or other mobile organisms to habitat characteristics, a reliable and effective quantitative method is needed to measure the contribution of the different substrata to the overall habitat structure.

Percent cover of each of the different substrata, both living and non-living, found in a particular area, is often used as a measure of habitat structure in coral reefs (Dodge *et al.* 1982; Lidell and Ohlhorst 1987; Chiapone *et al.* 2001). Percent cover data can be obtained by either recording substrata along a line transect or by deploying quadrats over an area. Determining percent cover on line transects can be done by one of two methods. Line intercept transects involve recording substrata as segments along a line (Porter 1972), whereas point-intercept transects involve recording substrata at a series of randomly or evenly distributed points along the centreline of the transect (Lucas 1977). Quadrats can be used to quantify habitat composition by visually estimating the percent cover of each substratum within the quadrat (Goldberg 1973). However, this visual estimation involves a high degree of subjectivity because the observer is constantly "guessing" the total coverage of a given substrata within the quadrat, instead of accurately estimating the area covered by it. Less subjective methods are to subdivide the quadrat into sub-quadrats, or impose a grid over the quadrat and record the substrata occurring under each intersection of the grid lines (Kinzie and Snider 1978).

Technological advances allow the use of still or video cameras to capture images of transects or quadrats, enabling storage of a permanent record of the area under study. Recording images also allows for more time for interpretation in the laboratory than is

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available in the field, and allows greater prospects for inter-observer comparisons. This can be particularly important when multiple observers will record data in different places as part of a large-scale, long-term monitoring program. Imaging software offers a precise and objective way to obtain percent cover estimates from such images. However, images with low graphical resolution might lead to misidentification errors during analysis. These methods are also more expensive and logistically complicated than methods that only require a slate, tape measure and pencil.

Marine ecologists and managers are often faced with the challenge of sampling a considerable amount of area in a short period of time, under tight budgets, or at depths that seriously constrain dive time. Under such conditions, field time can influence the level of replication. The number of replicates could be enhanced by using a faster method. For instance, photographing a quadrat in the field is faster than estimating percent cover *in situ*. However, additional time must be spent in the laboratory extracting data from the images. Another way of increasing the number of replicates would be to reduce the sampling intensity by recording substratum along each transect at larger intervals, therefore reducing the number of points, or by quantifying fewer quadrats.

Inter-method comparisons involve comparing the accuracy of each method when compared to the "real" percent cover of a given substrata. But because we cannot estimate this "real" value, accuracy of sampling cannot be determined by reference to known actual coverage. Nonetheless, one can measure the comprehensiveness, precision of estimates obtained, and time requirements for particular methods. Comprehensiveness is the extent to which all types of substrata are being successfully detected by each of the methods or sampling intensities employed. Precision refers to the degree of uncertainty in estimating the mean percent cover of a given substratum. Sampling time entails the amount of time involved in completing the collection and analysis of a single sampling unit (in the context of this study, a transect). This includes both field and laboratory time. In this study I assessed the effects that sampling intensity had on both the comprehensiveness and the precision of the percent cover

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estimates obtained when using point-intercept and photo quadrat methods on transects in reef habitat. Furthermore, I compared the estimates obtained by the two methods.

Methods

This study was conducted at Turneffe Atoll, Belize, Central America. Detailed descriptions of the atoll can be found in Garcia and Holtermann (1998). Thirteen 20 m long transects were haphazardly placed and sampled on coral reef habitat at the atoll at depths ranging between 5 and 15 m. Percent cover of the different substrata was estimated in each transect using both point-intercept and photo quadrat techniques. Substrata were grouped in categories following the CARICOMP protocol (CARICOMP 2001), in order to relate this study to a widely used monitoring program. From preliminary censuses of the study area, the maximum number of substrata observed was 15 (Table 1).

Point-intercept method: Substrata were recorded every 25 cm along the centreline of each transect. Then, four different levels of sampling intensity were simulated by selecting subsets of the data. Using every point along a transect gave the highest sampling intensity. By using only every second, third and fourth data point along each transect I produced two medium levels and one low level of sampling intensity. The number of sampling points per transect for each level of sampling intensity is provided in Table 2.

Photo quadrat method: A 50 x 50 cm quadrat was placed at every 1m mark along the transect and photographed with a Sea Life® reef master digital camera equipped with an external strobe. Images were captured with an optical resolution of 1280x960 dpi and image quality of 1.3 mega pixels. In the lab images were enhanced for colour saturation, contrast and brightness, and analysed following the planar point intercept grid method used by Kinzie and Snider (1978). Briefly, a grid with 36 intersections was projected on the computer screen over the quadrat, and the substratum underlying each of the intersections was then recorded. Different levels of sampling intensity were simulated by using every quadrat, every second, every third and every fifth. The

number of sampling points analyzed per transect by each sampling intensity is provided in Table 2.

Data analysis:

Within methods:

Comprehensiveness among sampling intensities within each method was graphically evaluated by comparing the presence/absence of the different substrata identified. If all substrata were successfully detected by all sampling intensities then they would be equal in terms of comprehensiveness. Failure of one of the sampling intensities to detect a given substratum would suggest differences in the degree to which all sampling intensities are successfully detecting all substrata. This assessment is testing the ability of the different sampling intensities to detect a given substratum but it is not giving us an estimate of how different they are. In order to test for significant differences in the estimates of percent cover for each substratum a one-way type I ANOVA was conducted, a MANOVA was not employed because this type of analysis would also test for differences in the percent cover among substrata, which for the purpose of this study is irrelevant. Percent cover estimates were arcsine square root transformed prior to analysis to achieve normality.

Different levels of sampling intensity might give similar results when only a small number of substratum categories are used. However, the addition of more substrata through finer taxonomic resolution might lead to greater differences among sampling intensities. Since point-intercept data were usually recorded to the species level, it was possible to investigate this possibility by using a suite of 42 substrata (Table 3). In instances when reliable species identification was not possible, the main substratum categories provided in Table 2 were used. This degree of taxonomic resolution was not possible for photographic data due to the limits of image quality when zooming to small areas, and so this finer scale analysis could only be done for the point intercept method. A one-way type I ANOVA was used to test for significant differences in the percent cover estimates obtained at each level of sampling intensity. A PCA analysis was used to graphically assess the ordination in space defined by habitat characteristics of all transects according to the sampling intensity employed to describe them. If the results obtained

Figure 3. Distribution of point-intercept transect data in a space defined by PCA Root I and II evaluating a suite of 42 different substrata. Individual transects are symbolized as shown in legend. H= sampling intensity every 25cm, 5=sampling intensity every 50cm, 7=sampling intensity every 75cm, L= sampling intensity every 100cm. b) Variable loadings of the PCA evaluating a suite of 42 substrata using the point-intercept method and different sampling intensities substrate codes as in table 3
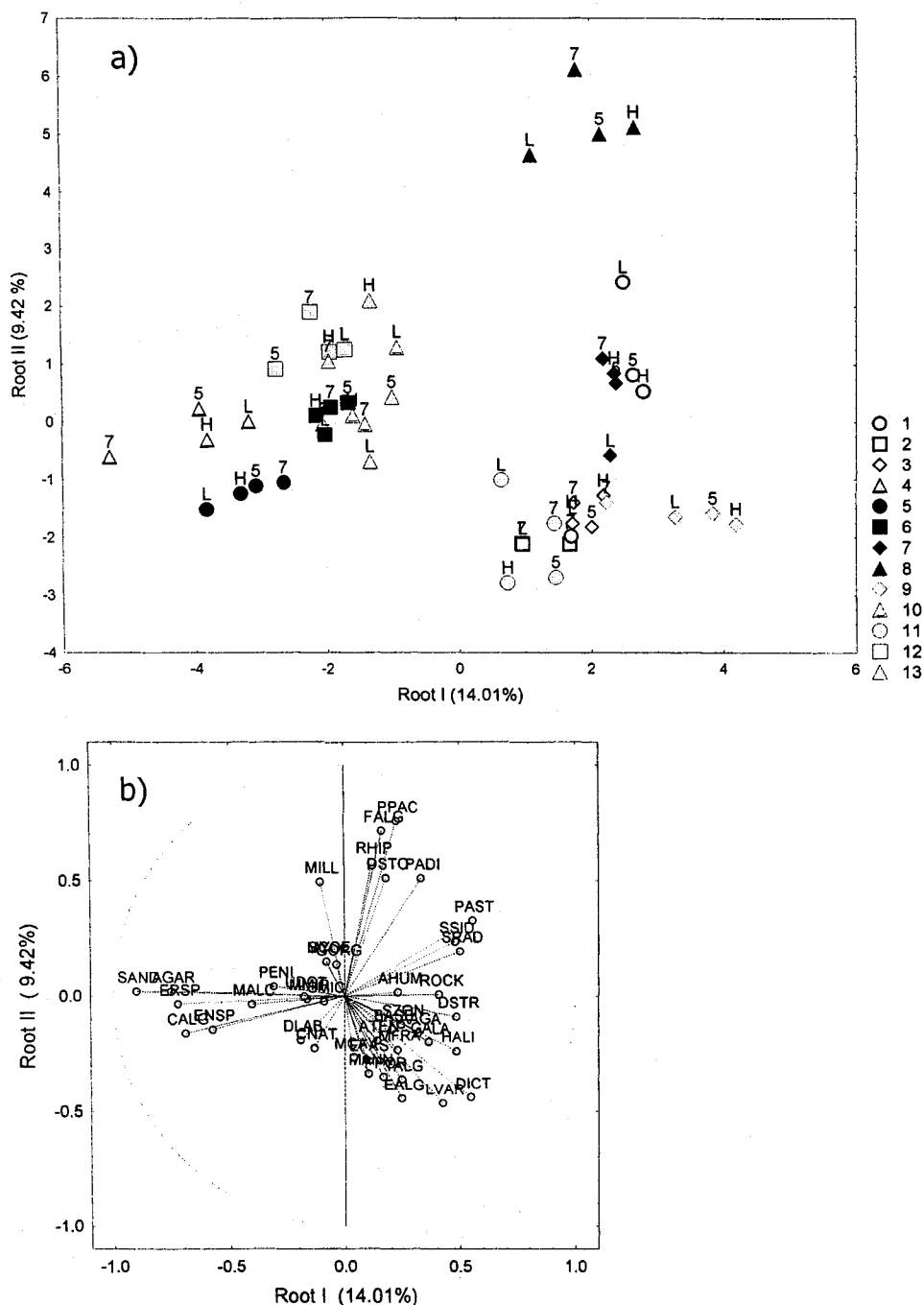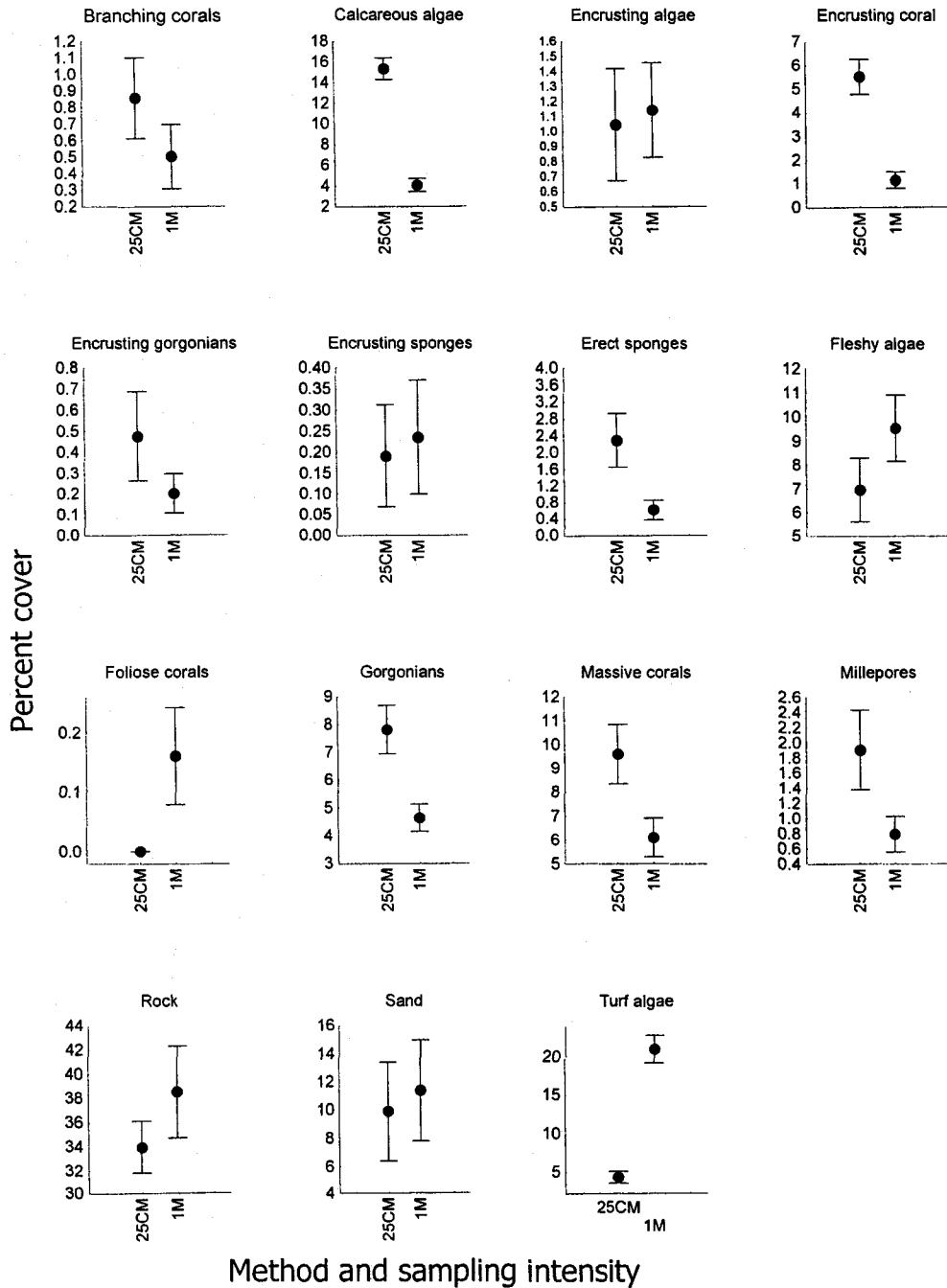
Figure 4. Percent cover estimates obtained with the highest sampling intensities of point intercept and photo quadrat methods. Error bars are standard errors.

Percent cover

Method and sampling intensity

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Chapter 3

Effects of habitat on the recruitment variation of coral reef fish across broad spatial scales

Introduction

Adult coral reef fish populations are shaped by processes acting at different stages of their life cycle. Prior to settlement, the quantity of larvae competent to settle to a given location can be influenced by physical patterns in currents, eddies and waves (Hauri *et al.* 1978, Williams *et al.* 1984, Cowen and Castro 1994, Hamner and Hauri 1977, Alldredge and Hamner 1980, Leis 1986, Lobel 1989, Shultz and Cowen 1994), and by random events happening during the pelagic larval phase. Larvae then can settle differentially to particular locations, which can be a reflection of factors such as conspecific abundance (Sweatman 1985, Levin 1994), and habitat type (Sale 1979, Sweatman 1985, Carr 1991, McGehee 1995, Risk 1997, Holbrook *et al.* 2000, Levin *et al.* 1997, Tolimieri 1995, Tolimieri 1998a,b). Post settlement events such as competition (Jones 1987, Forrester 1990), predation (Carr and Hixon 1995), and movement (Lewis 1997) can influence the abundance and distribution of new recruits on a given reef. Early views of adult coral reef populations produced models in which the importance of post-settlement processes was disputed. The lottery hypothesis (Sale 1977) and the recruitment limitation model (Victor 1983) did not consider post-settlement processes as important in organizing adult communities, whereas the competition model (Smith and Tyler 1972) and the predation disturbance model (Talbot *et al.* 1978) considered post-recruitment events important. Reef fish ecologist currently hold a view that considers both the events occurring before and after settlement as important shapers of adult coral reef fish communities.

Recruitment strength is an important factor in shaping reef fish populations. Recruitment is highly variable in both space and time (Williams and Sale 1981, Williams 1983, Sale *et al.* 1984, Doherty and Williams 1988, Caselle and Warner 1996, Tolimieri 1998b), but it might not be completely random. Spatial variation in recruitment can be attributed to one, or a combination, of factors that include: larval supply, habitat preferences at settlement, post-settlement movement to a preferred habitat, and differential mortality. Studies have shown that larvae may exhibit some form of active behaviour during their late pelagic stage (Leis 1991). Larvae of some species exhibit strong swimming abilities (Stobutzki and Bellwood 1997). The extent to which these

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behaviours are used in the natural environment is still a matter of debate, but larvae passively actively influence patterns of abundance and distribution. The abundance and distribution of new recruits in a reef may be influenced by the abundance of conspecifics (Sweatman 1985, Levin 1994), differential rates of survivorship after settlement (Wellington 1992), and habitat type (Sale 1979, Sweatman 1985, Carr 1991, McGehee 1995, Risk 1997, Holbrook *et al.* 2000, Levin *et al.* 1997, Tolimieri 1995, Tolimieri 1998a,b). The effects of habitat are especially important to understand in order to get an accurate idea of how anthropogenic changes in habitat might affect processes in coral reef fish.

Habitat preferences at settlement have been widely addressed in the literature (Sale 1971, Sale *et al.* 1984, Jones 1988, Carr 1991, Booth 1992, Wellington 1992, Tolimieri 1995). These preferences can affect recruitment rates in different ways according to the spatial scale over which they act. Tolimieri (1995) examined the effects of micro-habitat characteristics on small and large spatial scales in the recruitment variation in the three spot damselfish (*Stegastes planifrons*) in the U.S. Virgin Islands. He examined small scale microhabitat associations at a quadrat level in the island of St. Croix, and at larger scale across the islands of St. John, and Virgin Gorda, a scale that spanned over 150 km. The results from this study suggested that patterns of recruitment observed at small scales are influenced by microhabitat choice; however these effects did not scale up to explain the patterns of recruitment observed at larger scales (100's of km). Similarly Caselle and Warner (1996) working on St. Croix, found that certain features of habitat significantly predicted recruitment densities at a transect level. However, these features could not explain recruitment variation at a broader spatial scale (island wide pattern). Tolimieri (1998a) evaluated the small-scale effect of substrata on the recruitment of the stoplight parrotfish (*Sparisoma viride)* in Tague Bay St. Croix, U.S. Virgin Islands. His results showed that *S. viride* recruited in higher numbers to the coral *Porites porites* but there was no evidence of microhabitat choice at settlement, suggesting that differences in recruitment were the result of post-settlement processes. Finally using sites in St. croix, St. John, and Virgin Gorda, Tolimeri (1998b) approached the microhabitat-recruitment relationship of *Sparisoma viride* at three different spatial scales: small (meters), medium (100s of meters) and large (10s of kilometres). He found that

percent cover of *P. porites* was correlated with the abundance of recruits of *S. viride*, and that these effects did scale up to medium and large spatial scales. These results contrasted with his previous study, and suggest that processes that operate at small spatial scales can influence distribution and abundance patterns at larger scales for at least some species. However, young recruits of *S. viride* might be a more site-attached species that *T. bifasciatum*, which could explain the scaling up of the microhabitat effect across different spatial scales.

The previous results suggest that the relationship between habitat and recruitment variation is stronger at small spatial scales, and that it does not usually scale up to larger spatial scales (but see, Tolimieri 1998b). In these studies, temporal associations between habitat and recruitment variation were explored only at the scale of years by using the mean recruitment for that year. Since recruitment is highly variable during a given summer, the use of a mean value for a whole season might mask a pattern of higher and lower peaks and patterns of association with particular habitat features might be expected only at times of high recruitment.

The present study differs from its predecessors in two main aspects. This is the first study to evaluate patterns of recruitment of Caribbean species on a scale of hundreds of kilometres, although this has been done previously on the Great Barrier Reef. Because our data record recruitment of 2 focal species at both the new and full moon phases, treating each sampling period as an independent sample, we are able to explore temporal variation in the relationship between recruitment variation and microhabitat at large spatial scales. The main objectives of this study are: 1) to quantify the recruitment patterns of the labrid *Thalassoma bifasciatum* and the pomacentrid *Stegastes partitus*, 2) to investigate the extent to which habitat variation explains recruitment variation, and 3) to assess whether these relationships are constant through time and space.

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Methods

Study area

This study was conducted along the Mesoamerican Barrier Reef System (MBRS) from May to September 2002. The MBRS is the world's second largest barrier reef stretching almost 1000 km from the northern tip of Mexico's Yucatan Peninsula to the Bay Islands in Honduras. We sampled at four locations within the MBRS, Banco Chinchorro (BC), and Mahahual (MA), in Mexico, Turneffe Atoll (TA), in Belize, and Roatan Island (RI), in Honduras (Figure 1). Banco Chinchorro is located 30 km eastward from the Yucatan peninsula 100 km north from Turneffe Islands. It is roughly 47 km long, 18 km wide and extends over more than 700 km² (Jordan and Martin 1987). Turneffe atoll is located 51 km off the coast of Belize it has a maximum length of 48 km and a maximum width of 16 km. The Bay Islands of Honduras are located between 30 km and 50 km to the north of the Caribbean coast of Honduras. Roatan, the largest, is a long, narrow island orientated roughly east–west, with a maximum height above mean sea level of 233 m and an area of approximately 133 km².

At each of these locations, a series of sites was established. At BC six sites were established, one site near each of the northern and southernmost tip of the atoll, and two sites at each eastern and western sides of the atoll. MA consisted of three sites located at nearby reefs. TA had one site close to each of the northern and southernmost tips, three sites located along the eastern side and 2 sites located along the western side. At RI three northward oriented sites were established (Figure 1). Each site was divided into two positions according to depth (depth henceforth): shallow (3-5 m) and deep (10-14m). Each depth was a precisely defined GPS fix (Table 1) at which the boat was anchored when sampling. Sampling transects were then deployed within a roughly rectangular area centered on the anchoring position and extending approximately 120 m parallel to the reef face and 20 m perpendicular to it (Fig. 2)

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Study species

Spatial and temporal patterns of recruitment were estimated for two Caribbean coral reef fish species: the blue head wrasse, *Thalassoma bifasciatum*, and the bicolor damselfish, *Stegastes partitus*. The blue head wrasse is a small (12.5 cm total length) short lived (~3 years), sex-changing labrid that inhabits coral reefs and associated habitats, being most abundant near the top of reefs in shallow water (Claro 1994). This numerically abundant species can be seen spawning at midday throughout the year (Smith 1997), and has been extensively studied over the years. Young recruits settle to the reef after spending an average of 47.16 ± 0.36 (SE) days in the plankton at a standard length of roughly 1 cm (Caselle and Warner 1996). The bicolor damselfish is a small pomacentrid that attains a maximum standard length of 10 cm and settles at about 11 mm standard length (Sponaugle and Cowen 1996). It survives for up to 5 years (Caldow and Wellington 2003) feeding primarily on algae but also on polychaetes, hydroids, copepods and ascidians. As with most benthic feeding pomacentrids it is aggressively territorial but only around a small area (Lieske and Myers 1994)

Recruitment surveys

Visual surveys of *S. partitus* and *T. bifasciatum* were conducted concurrently at each location throughout the summer (May-August 2002). However, due to weather and other logistical constraints not all sites were visited over the entire summer. For instance, five census periods were conducted at Turneffe Atoll and Banco Chinchorro, and three at Mahahual and Roatan Island. Each census period included the monitoring of *S. partitus* and *T. bifasciatum* at each site, and was conducted within 7 days of a new or full moon.

At both positions two divers using fibreglass tape measures deployed a total of eight 30x1 m transects. Each transect was reeled out as the divers swam parallel to the reef and at a distance of 5-10 m from each other. Each diver estimated the width of the transect with a 1m wide t-bar that was marked at 50 cm, this mark was held over the centreline of the transect to ensure accuracy of width. The diver visually estimated

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standard lengths of new recruits and recorded all individual of either species with total length less than 2 cm within the 1m wide strip. We ensured the temporal independence in the data set by using published growth data and our own analysis using otoliths Using this criterion, we ensured that fish counted every two weeks were in fact new recruits and not 2-week-old-fish. To account for observer bias in the estimates of recruitment a series of calibrating and cross validating surveys were conducted at the beginning of the summer for all divers. Exercises included fish identification, and inter-observer comparisons of visual censuses.

Temporal and spatial variation in recruitment density, expressed as the mean number of individuals per transect, was explored using ANOVA. Each species was analyzed separately using a mixed model 4-way nested ANOVA, in which location, census period, site and position were independent factors with position nested within sites. Sites within locations were considered a random factor whereas all other factors were fixed. Because the number of levels for each factor varied among locations we calculated type II sums of squares to deal with the unbalanced nature of our sampling design (Langsrud 2002).

Habitat measurements

At each site, quantitative habitat assessments were obtained for six haphazardly arranged replicate 30 m long transects that were placed parallel to the reef crest at each depth. Any of 8 substratum categories were recorded on an underwater slate along each transect. Substrata were recorded every 25 cm using the point-intercept method (Porter 1972), yielding a total of 120 points per transect. Additionally, spatial complexity (rugosity henceforth) was estimated using a chain (Porter 1972). A 5m long brass chain (1.1 cm link size) was draped along the centreline of each transect starting at the 0 m, 10 m, and 20 m mark. Care was taken to ensure that the chain went under, over and around all fixed surfaces that were directly below the centreline of the transect. Rugosity was then calculated as the ratio of chain length over linear distance. A transect estimate was obtained by calculating the mean of the three sets of measurements performed.

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Habitat characteristics were quantified once during the summer at all study locations. To explore the patterns of variation in the percent cover estimates of each of the habitat characteristics across locations a mixed model three-way nested ANOVA was performed for each of the habitat characteristics quantified. Location, site and position were considered as three independent factors with position nested within site. Site was considered a random factor whereas location and position were fixed.

Habitat-recruitment relationships

Recruitment varies through time, however if fish have a strong association with particular habitat features these relationships should be constant through time. We conducted multiple regressions between the average number of recruits per transect at a given depth for each census period and the percent cover of all habitat categories recorded. Separate regressions were conducted for each census period. This analysis focuses on the temporal nature of the habitat-recruitment relationship; specifically we asked the question: is the relationship between recruitment and any given substrata consistent across all census periods? We used only TA data since it was the location for which we had the highest number of sites censused per census period relative to other locations.

We then examined the extent to which habitat features explain patterns of recruitment at large spatial scales (MBRS scale henceforth). For this we regressed the average number of recruits per transect at each site and depth across all census periods over the percent cover of all habitat categories recorded, we included all localities in this analysis. For these analyses recruitment data was log+1 transformed and percent cover of habitat categories was arcsine square root transformed.

Results

Temporal and spatial variation in recruitment

A total of 3211 and 2409 new recruits of *T. bifasciatum* and *S. partitus* respectively, were recorded during the sampling season over 1328 transects that covered an area of

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39840 m² over the Mesoamerican Barrier Reef System. The mean recruitment per transect for *S. partitus* and *T. bifasciatum* varied among locations peaking at RI with 4.5 ± 0.3 (SE)(n=128) and 6.3 ± 0.5 (SE)(n=128) respectively. Average number of recruits of *S. partitus* per transect in BC was 1.1 ± 0.1 (SE)(n=352), MA 2.3 ±- 0.2 (SE)(n=104), and TA 1.5 ± 0.1 (SE)(n=764). Mean number of recruits of *T. bifasciatum* per transect was similar across all remaining locations, BC 2.4 ± 0.2 (SE)(n=352), MA 1.8 ± 0.2 (SE)(n=104), and TA 1.7 ± 0.1 (SE)(n=764).

For recruitment of *S. partitus* ANOVA resulted in significant differences among census periods, locations, sites, and depths (Table 2). For most locations recruitment was higher in the shallow position than in the deep, however at TA there were no differences between depths (Figure 3a). RI had the highest number of recruits per position, being almost twice that observed at any other location (Figure 3a). There was considerable variation in recruitment among sites within each location (Figure 4 a, b), peaking at RI for the deep position and at TA for the shallow. There was no consistent pattern of recruitment at a given depth/site/location combination for a given census period (Figure 5). However, the highest number of fish per transect was consistently obtained at RI.

Recruitment patterns for *T. bifasciatum* were also variable between depths, among sites, locations and across census periods (Table 2). At each location and across all census periods the mean recruitment to the shallow depth was significantly higher than the recruitment received at the deep (Figure 3). There was an almost twofold difference in average recruitment between RI and all the other locations for either species at both depths (Figure 3). Within locations recruitment was variable among sites reaching a peak at RI, at both depths (Figure 4 b,c). Recruitment was variable across all census periods within each location. Peaks of recruitment at each location were reached around mid summer. For the deep strata, census periods two and three had the highest recruitment (Figure 6). In the shallow strata a similar pattern was observed with recruitment peaking at census periods two and three, with the exception of TA where census period 5 had the highest recruitment per transect (Figure 6). A consistent pattern of highest recruitment associated with a particular census period was not observed in any of the locations.

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Curiously RI had considerably higher recruitment rates than any of the other locations (Figure 3, 4, 5). Our sampling scheme ensured that teams of observers rotated consistently among locations. However, this was not the case for RI where all the sampling was done by a single observer. These patterns therefore, could have been the result of inter-observer differences. To explore this possibility, we performed inter-observer comparisons among observers in a set test of transects. These revealed no evidence of a given observer overestimating abundances of fish (Kritzer *et al.* in prep).

Recruitment variation did not correspond to lunar periodicity. The average recruitment across all locations for *S. partitus* was 1.9 ± 0.09 (SE) (n=680) fish per transect following the full moon and 1.6 ± 0.08 (SE) (n=668) fish per transect following the new moon. Similarly average recruitment for *T. bifasciatum* across all locations was 2.2 ± 0.12 (SE) (n=680) fish per transect following the full moon and 2.5 ± 0.13 (SE) (n=668) fish per transect following the new moon. T test resulted in no significant difference between the estimates obtained for either species at both the new or full moon phases ($p>0.05$).

Spatial variation in habitat

The percent cover of all habitat substrata measured across all study sites was highly variable. ANOVA resulted in significant differences among these habitat characteristics among locations, sites within locations and depths (Table 3).

Overall, these results support both temporal and spatial variation in the recruitment of *T. bifasciatum* and *S. partitus* and spatial variation in habitat features.

Relationship between habitat and recruitment

Temporal analysis

Multiple regression analysis resulted in no significant correlations between recruitment of *S. partitus* and any habitat feature at any given census period (Table 4). Conversely, recruitment of *T. bifasciatum* showed significant positive correlation in census period 2

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with rugosity and negative correlation with sponges. In census period 6 gorgonians were negatively correlated with abundance of this species (Table 5). Because the correlations were not consistent across all census periods these results suggest there is no constant temporal pattern of association between habitat features and the variation in the recruitment recorded for both species.

MBRS scale analysis

Habitat features accounted for 53% of the variation in recruitment of *T. bifasciatum*. Of all the habitat substrata measured only gorgonians were negatively correlated with abundance of this species (Table 6). For *S. partitus* habitat features explained 55% of the variation, there was a significant negative correlation between gorgonians and the recruitment of this species. Because RI exhibited higher levels of recruitment than any other location (Figure 3) we explored the extent to which this pattern was due to habitat differences between RI and all other localities. A PCA analysis was employed to assess which of the substrata quantified were driving differences among RI and other locations. The PCA resulted in two roots explaining 33.28% and 26.21% of the variation respectively. Graphical assessment showed that sites within RI were negatively correlated with principal component 2 and that they clustered away from other locations (Figure 7a). Visual interpretation of the variable loadings in the resulting ordination showed that principal component 2 was negatively correlated with algae and other substrata (Figure 7b). However, previous analysis resulted in no significant correlations between these substrata and the abundance of fish, which suggest that differences in the recruitment of either species across broader spatial scales cannot be explained by habitat variation alone.

Discussion

Spatial and temporal variation in recruitment

The results of this study indicate that recruitment patterns of *T. bifasciatum* and *S. partitus* are variable at both temporal and spatial scales. This in itself is not surprising

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since many authors have already found spatial and temporal patterns of recruitment variability in reef fishes (Williams and Sale 1981, Williams 1983, Sale *et al.* 1984, Doherty and Williams 1988, Caselle and Warner 1996, Tolimieri 1998a,b). Spatial patterns of recruitment for both species were highly variable across locations, peaking at RI where densities of *T. bifasciatum* were 3-4 times greater than at BC, MA and TA. For *S. partitus* density of recruits was almost twice that of other locations. This pattern however, could not be explained by variation in habitat across all study locations. Recruitment patterns for both species were also variable within each location. However, no discernible regional trend was detected. At a location level, the results for RI exhibited a gradient of decline in the abundance of both species from the west towards the centre of the island (Figure 4). A similar gradient was observed by Caselle and Warner (1996), they found that the abundance of recruits of *T. bifasciatum* followed a descending west-east gradient along the northern shore of the island, and a reverse pattern along the southern shore. They ruled out substrate differences as responsible for these patterns and proposed oceanographic processes that acted at spatial scales smaller than the island of St. Croix. However, in RI this trend could be the result of the small number of sites established, and because they do not span across the entire east-west northern shore of the island.

Choat *et al.* (1988) suggested that temporal patterns in recruitment could arise from stochastic oceanographic patterns that might affect larval delivery. The lack of correlation between particular habitat substratum and patterns of recruitment variation suggest that other processes are important shapers of these variations. Previous studies have linked lunar cycles to temporal patterns of recruitment (Robertson *et. al.* 1990, Doherty 1991). Our results however, did not find any consistent correlation between lunar phases and recruitment rates for any of the species under study. This, however, does not imply that lunar cycles are not responsible for recruitment variation to some degree. Our results only suggest that full and new phases of the moon are not driving big differences in recruitment, however we do not possess data to evaluate the effect of moon cycle during waxing and waning.

Deterministic processes such as habitat selection can result in variations in recruitment that will be fairly consistent over time, and if these processes are strong enough, this variation will also be consistent over larger spatial scales. It would be expected then that if some attributes of habitat were strongly correlated with recruitment rates, then sites in which this habitat attribute was more common would tend to have higher recruitment rates that sites with lower coverage of the habitat attribute. We explored this scenario by looking at associations between habitat attributes and patterns of recruitment.

Recruitment-habitat associations

Differential settlement could be the result of choice of habitat during settlement. In this case, at preferred habitats it would be expected to find higher abundances of individuals. Our results however, did not find correlations between any given habitat attribute and the recruitment patterns observed for either species that were consistent through time (Table 2a,b). At the MBRS scale we found a negative correlation between the percent cover of gorgonians and the recruitment of *S. partitus*. Across all locations sites that had higher percent coverage of gorgonians were high energy areas with low rugosity and composed of mostly flat pavement. *S. partitus* is often found around crevices and rubble that it uses for shelter, it is then comprehensible that places devoid of such features would exhibit lower number of recruits of this species. We do not possess data to assess if this pattern is due only to choice of habitat at settlement, or to post settlement events such as predation, competition or mortality, which differentially affect fish in different habitats.

Past studies have found evidence either in favour or against the effect that habitat variation has on recruitment variation. Topographic complexity (rugosity) has several times been identified as an important predictor of the diversity of reef fish assemblages (Talbot 1965, Risk 1972, Talbot and Goldman 1972, Luckhurst and Luckhurst 1978). Interestingly enough it was not important at the MBRS scale in our study, and it was only significant in one of the census periods for *T. bifasciatum* (Table 5). Caselle and Warner (1996) found that small-scale patterns of recruitment in St. Croix could be

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explained by habitat variation. In a series of papers (1995, 1998a) Tolimieri found strong relationships between recruitment of *Sparisoma viride* and *Stegastes planifrons* and particular species of coral in St. Croix, he concluded that habitat influences the distribution of organisms at small spatial scales (meters to 100's of meters); however these relationships are not maintained over larger scales (km to 10's of km)(see but, Tolimieri 1988b). Conversely, Sponaugle and Cowen (1996) found no relationship between recruitment of *S. partitus* and any of the habitat variables they measured. These different results can arise from differences at the spatial scales at which sampling was conducted. Both Caselle and Warner (1996), and Tolimieri (1995, 1998a,b) explored the habitat-recruitment relationship at a transect level, whereas in our study we explored site wide patterns. In accordance with their results, relationships found at small spatial scales are lost when the interactions are evaluated at larger spatial scales. Because we use the mean value of percent cover of a given substrate for each site, we lose the variation in the distribution of this attribute when we move from a transect to a broader spatial scale. It is also important to consider that habitat-recruitment variations might be species-specific. Whereas young recruits of *T. bifasciatum* can be observed among different substratum types, *S. viride* recruits tend to be more cryptic and in closest association with live corals whose structure ensures some degree of refuge (pers. Obs). Under this scenario Tolimieri's results can in fact be a reflection of differential intra-specific responses to preferred habitats that are strong enough to be detected even at larger spatial scales.

Based on previous studies we can safely conclude that although recruitment variation can be influenced by habitat at small spatial scales (meters), this by itself cannot explain large-scale patterns of recruitment. Our results agreed with a lack of temporal association between habitat features and recruitment patterns for either species. Our MBRS scale results suggest that even though recruitment of *S. partitus* is variable across census periods, the overall number of recruits is lower at locations where refuge is not generally available. Our efforts to explain recruitment variation have attempted to link recruitment variation to given habitat features. However, our findings suggest that an overall description of the habitat may be more effective to explain patterns of recruitment variation. Even though RI exhibited differences in the percent coverage of

specific substrata that were significant enough to cause it to cluster away from all other locations (Fig 7), these differences did not account for the greater number of recruits that were observed at this location. Because recruitment patterns are greatly variable they are likely to be caused by different factors that are acting before and after settlement, as has been suggested in the past. To better understand patterns of recruitment we will need to consider more factors such as oceanographic processes, patterns of larval availability, competition, and early post settlement mortality and movement.

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Tables

Table 1. GPS position of all sampling sites and depths established across the MBRS.

Location	Site	Depth	Latitude	Longitude
Banco Chinchorro	1	Deep	18°45.485	87°16.769
Banco Chinchorro	1	Shallow	18°45.136	87°17.349
Banco Chinchorro	2	Deep	18°39.454	87°13.692
Banco Chinchorro	2	Shallow	18°39.468	87°13.792
Banco Chinchorro	3	Deep	18°33.208	87°17.877
Banco Chinchorro	3	Shallow	18°33.228	87°17.944
Banco Chinchorro	4	Deep	18°23.721	87°24.156
Banco Chinchorro	4	Shallow	18°23.756	87°24.193
Banco Chinchorro	5	Deep	18°31.357	87°26.072
Banco Chinchorro	5	Shallow	18°31.390	87°26.133
Banco Chinchorro	6	Deep	18°39.080	87°24.295
Banco Chinchorro	6	Shallow	18°39.016	87°23.909
Mahahual	1	Deep	18°43.422	87°41.810
Mahahual	2	Deep	18°42.099	87°42.438
Mahahual	2	Shallow	18°42.110	87°42.477
Mahahual	3	Deep	18°38.618	87°43.135
Mahahual	3	Shallow	18°38.615	87°43.269
Turnefe atoll	1	Deep	17°35.295	87°44.631
Turnefe atoll	1	Shallow	17°35.290	87°44.715
Turnefe atoll	2	Deep	17°25.320	87°48.430
Turnefe atoll	2	Shallow	17°25.295	87°48.485
Turnefe atoll	3	Deep	17°19.076	87°47.549
Turnefe atoll	3	Shallow	17°19.087	87°47.594
Turnefe atoll	4	Deep	17°16.414	87°48.674
Turnefe atoll	4	Shallow	17°16.420	87°48.716
Turnefe atoll	5	Deep	17°10.390	87°53.246
Turnefe atoll	5	Shallow	17°10.442	87°53.293
Turnefe atoll	6	Deep	17°20.622	87°57.292
Turnefe atoll	6	Shallow	17°20.580	87°57.287
Turnefe atoll	7	Deep	17°26.212	87°54.805
Turnefe atoll	7	Shallow	17°26.206	87°54.725
Roatan island	1	Deep	16°22.730	86°28.810
Roatan island	1	Shallow	16°22.667	86°28.775
Roatan island	2	Deep	16°20.259	86°34.061
Roatan island	2	Shallow	16°20.235	86°34.028
Roatan island	3	Deep	16°16.204	86°36.159
Roatan island	3	Shallow	16°16.185	86°36.144

Table 2. Results of 4-way nested ANOVA of mean number of individuals of *S. partitus* and *T. bifasciatum* per transect recorded at all Locations. Significant p values are bold.

	Effect	DF	S. partitus			T. bifasciatum		
			MS	F	p	MS	F	p
Location	Fixed	3	5.728	7.258	**0.003**	5.826	8.837	**0.001**
site(location)	Random	15	1.099	15.581	**p<0.0001**	0.360	3.896	**0.001**
Census period	Fixed	6	0.050	0.705	0.646	1.005	10.873	**p<0.00**
Depth	Fixed	1	0.513	7.280	**0.007**	6.699	72.506	**p<0.00**
Error		1322	0.071			0.092		

Table 3. Results of the 3-way ANOVA of habitat categories among locations, among sites nested within locations and among depths. Significant p values are in bold.

	DF	Algae ms	Algae f	Algae p	Corals ms	Corals f	Corals p
Location	3	0.932	23.106	**p<0.001**	0.034	1.003	0.393
Site(Location)	12	0.125	3.098	**0.001**	0.472	13.886	**p<0.001**
Depth	1	0.004	0.095	0.758	1.158	34.083	**p<0.001**
Error	149	0.040			0.034		

	DF	Inert ms	Inert f	Inert p	Gorgonians ms	Gorgonians f	Gorgonians p
Location	3	3.038	109.128	**P<0.001**	0.127	11.750	**p<0.001**
Site(Location)	12	0.180	6.473	**P<0.001**	0.091	8.363	**p<0.001**
Depth	1	0.063	2.264	0.135	0.052	4.772	**0.030**
Error	149	0.028			0.011		

	DF	Other ms	Other f	Other p	Rugosity ms	Rugosity f	Rugosity p
Location	3	0.006	2.609	0.054	0.015	5.179	**0.002**
Site(Location)	12	0.012	5.160	**P<0.001**	0.050	17.453	**p<0.001**
Depth	1	0.020	8.629	**0.004**	0.038	12.966	**p<0.001**
Error	149	0.002			0.003		

	DF	Sponges ms	Sponges f	Sponges p
Location	3	0.114	18.247	**P<0.001**
Site(Location)	12	0.080	12.854	**p<0.001**
Depth	1	0.126	20.211	**p<0.001**
Error	149	0.006		

Table 4 Results from multiple correlations between mean number of recruits of *S. partitus* per transect across all sites and depths among all locations and percent cover of habitat categories (Significant p values are in bold).

	S. partitus Census period 1		*S. partitus* Census period 2		*S. partitus* Census period 3	
	Partial R^2	p	Partial R^2	P	Partial R^2	p
Algae	0.033	0.695	0.011	0.867	0.000	0.984
Corals	0.273	0.229	0.223	0.422	0.028	0.721
Gorgonians	0.224	0.283	0.208	0.440	0.135	0.418
Inert	0.000	0.973	0.003	0.931	0.094	0.503
Other	0.016	0.787	0.165	0.497	0.033	0.698
Rugosity	0.195	0.321	0.026	0.796	0.203	0.310
Sponges	0.119	0.448	0.092	0.619	0.497	0.077
	Multiple R^2	p	Multiple R^2	P	Multiple R^2	P
Whole model	0.343	0.884	0.460	0.877	0.764	0.187

	S. partitus Census period 4		*S. partitus* Census period 5		*S. partitus* Census period 6	
	Partial R^2	p	Partial R^2	P	Partial R^2	p
Algae	0.318	0.187	0.002	0.931	0.000	0.976
Corals	0.009	0.839	0.197	0.319	0.010	0.829
Gorgonians	0.000	0.976	0.255	0.248	0.017	0.782
Inert	0.343	0.167	0.018	0.773	0.010	0.828
Other	0.002	0.925	0.332	0.176	0.110	0.466
Rugosity	0.008	0.851	0.016	0.790	0.189	0.330
Sponges	0.121	0.445	0.060	0.595	0.180	0.342
	Multiple R^2	p	Multiple R^2	P	Multiple R^2	P
Whole model	0.674	0.344	0.666	0.360	0.648	0.395

	S. partitus Census period 7	
	Multiple R^2	p
Algae	0.009	0.841
Corals	0.021	0.756
Gorgonians	0.121	0.444
Inert	0.002	0.925
Other	0.017	0.779
Rugosity	0.071	0.564
Sponges	0.150	0.390
	Multiple R^2	p
Whole model	0.459	0.737

Table 5 Results from multiple correlations between mean number of recruits of *T. bifasciatum* per transect across all sites and depths among all locations and percent cover of habitat categories (Significant p values are in bold).

	T. bifasciatum Census period 1		*T. bifasciatum* Census period 2		*T. bifasciatum* Census period 3	
	Partial R^2	p	Partial R^2	P	Partial R^2	p
Algae	0.211	0.299	0.740	0.061	0.140	0.408
Corals	0.015	0.796	0.280	0.359	0.410	0.121
Gorgonians	0.003	0.913	0.401	0.251	0.114	0.458
Inert	0.171	0.356	0.669	0.091	0.045	0.647
Other	0.023	0.748	0.330	0.311	0.229	0.277
Rugosity	0.157	0.379	0.847	**0.027**	0.023	0.744
Sponges	0.419	0.116	0.950	**0.005**	0.320	0.186
	Multiple R^2	p	Multiple R^2	P	Multiple R^2	P
Whole model	0.640	0.410	0.969	**0.029**	0.495	0.678

	T. bifasciatum Census period 4		*T. bifasciatum* Census period 5		*T. bifasciatum* Census period 6	
	Partial R^2	p	Partial R^2	P	Partial R^2	p
Algae	0.273	0.229	0.014	0.803	0.355	0.158
Corals	0.002	0.919	0.000	0.980	0.000	0.998
Gorgonians	0.032	0.701	0.126	0.436	0.602	**0.040**
Inert	0.248	0.255	0.030	0.709	0.483	0.083
Other	0.043	0.655	0.127	0.432	0.239	0.265
Rugosity	0.071	0.564	0.000	0.989	0.144	0.400
Sponges	0.128	0.431	0.098	0.494	0.292	0.211
	Multiple R^2	p	Multiple R^2	P	Multiple R^2	P
Whole model	0.708	0.282	0.420	0.794	0.877	**0.046**

	T. bifasciatum Census period 7	
	Multiple R^2	p
Algae	0.267	0.235
Corals	0.122	0.443
Gorgonians	0.056	0.611
Inert	0.309	0.195
Other	0.010	0.831
Rugosity	0.017	0.778
Sponges	0.214	0.296
	Multiple R^2	p
Whole model	0.637	0.415

Table 6. MBRS scale results of multiple correlations between mean number of fish per transect per site per location per depth across all census periods and habitat features (significant p values are in bold).

	S. partitus		*T. bifasciatum*	
	Partial R^2	p	Partial R^2	p
Algae	0.046	0.351	0.007	0.718
Corals	0.054	0.313	0.019	0.550
Gorgonians	0.209	**0.037**	0.073	0.235
Inert	0.001	0.893	0.179	**0.056**
Other	0.046	0.351	0.004	0.797
Rugosity	0.128	0.111	0.001	0.914
Sponges	0.024	0.503	0.012	0.633
	Multiple R^2	p	Multiple R^2	p
Whole model	0.554	**0.016**	0.531	**0.024**

Figures

Figure 1 Study locations across the Mesoamerican Barrier Reef System. In clockwise order Banco Chinchorro (BC), Mahahual (MA), Turneffe Atoll (TA), and Roatan Island (RI). Numbers represent each sampling site.
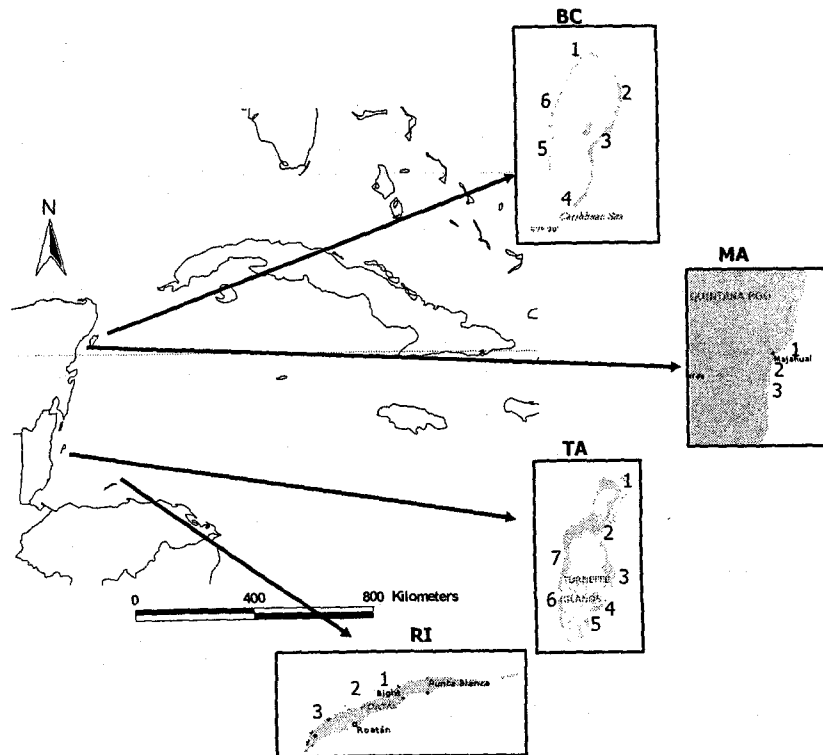
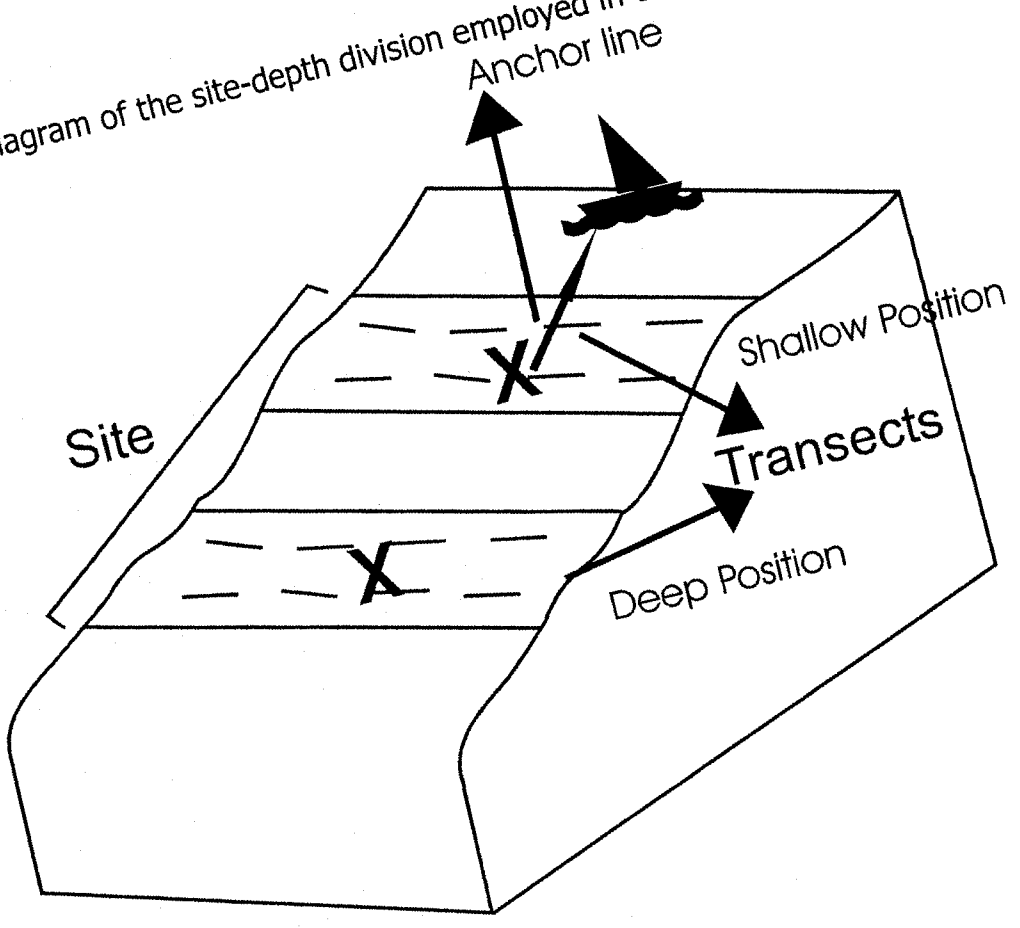**Figure 2** Diagram of the site-depth division employed in our sampling.

Anchor line

Site

Shallow Position

Transects

Deep Position

Figure 3 Mean recruitment of a) *T. bifasciatum* and b) *S. partitus* at each
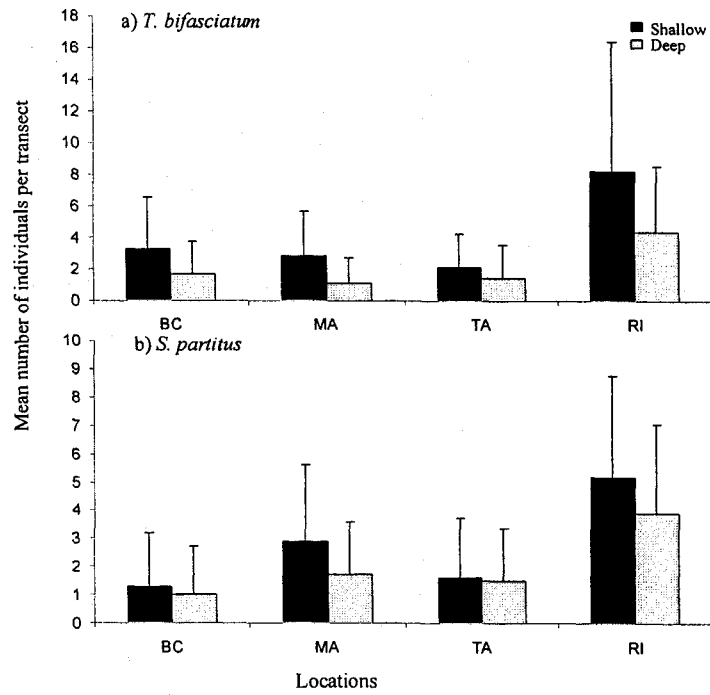location at two different depths across all census periods (Error bars are SD).

Figure 4 Variation in mean number of recruits of *S. partitus* (a-b) and *T. bifasciatum* (c-d) among sites within locations. Bars represent sites numbered as in Fig. 1. Error bars are SD of mean number.
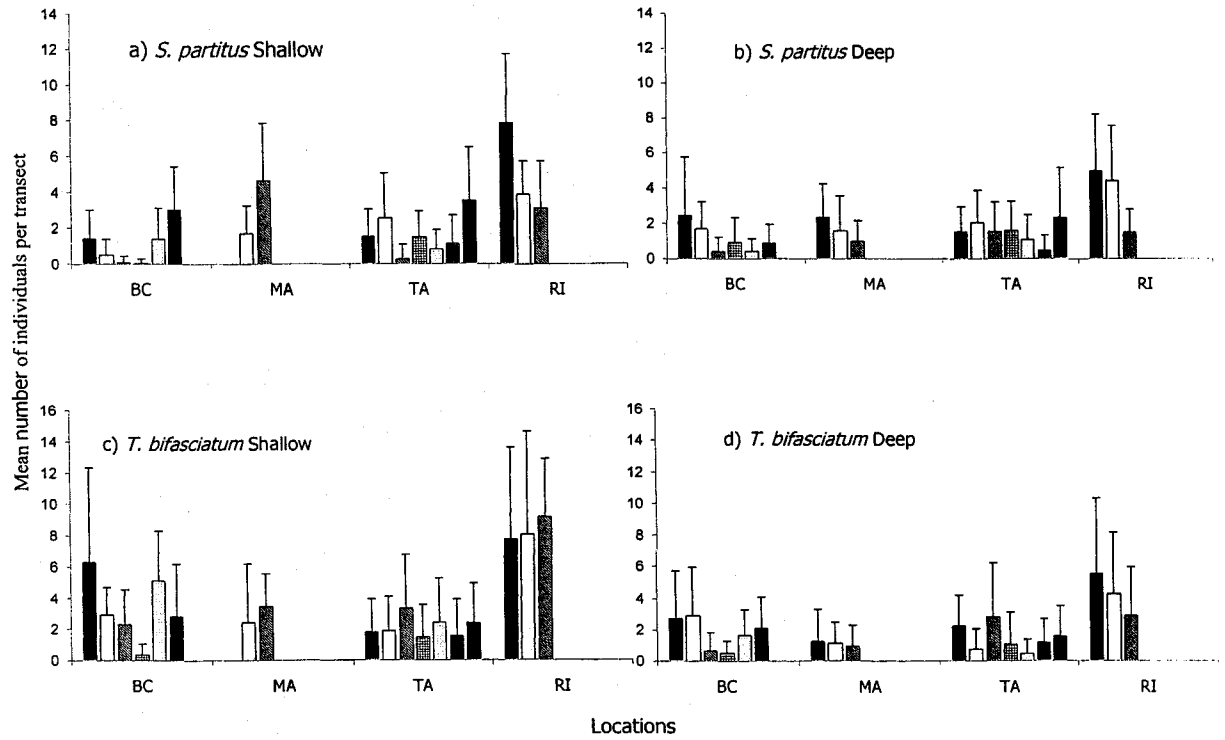
Figure 5. Variation in recruitment among census periods in 2002. Histogram shows the mean number of recruits per transect of *S. partitus* at each site for the 4 locations.(X denotes periods when sampling was not done, error bars are SD).
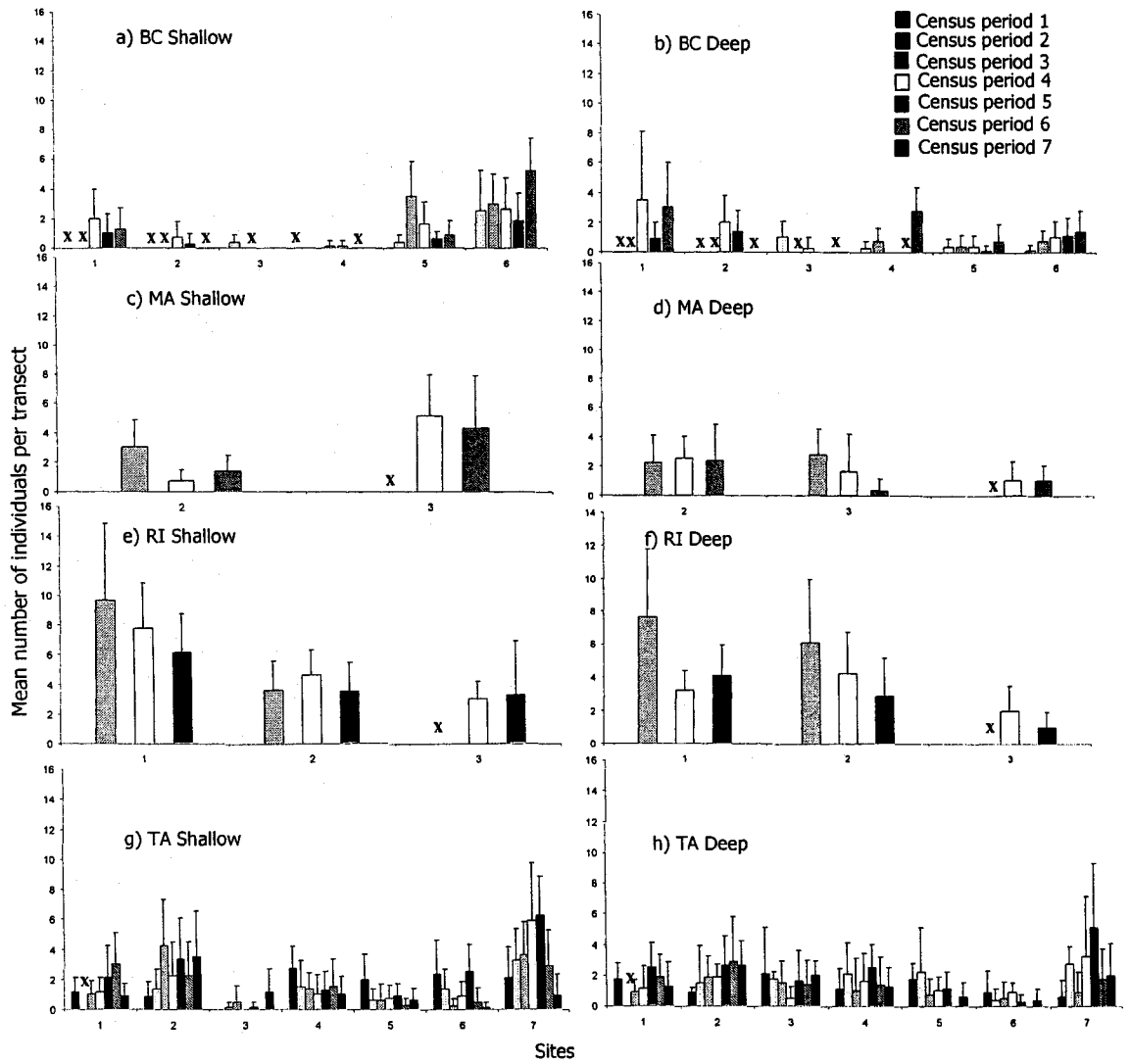
Figure 6. Variation in recruitment among census periods in 2002. Histogram shows the mean number of recruits per transect of *T. bifasciatum* at each site for the 4 locations.(X denotes periods when sampling was not done, error bars are SD).
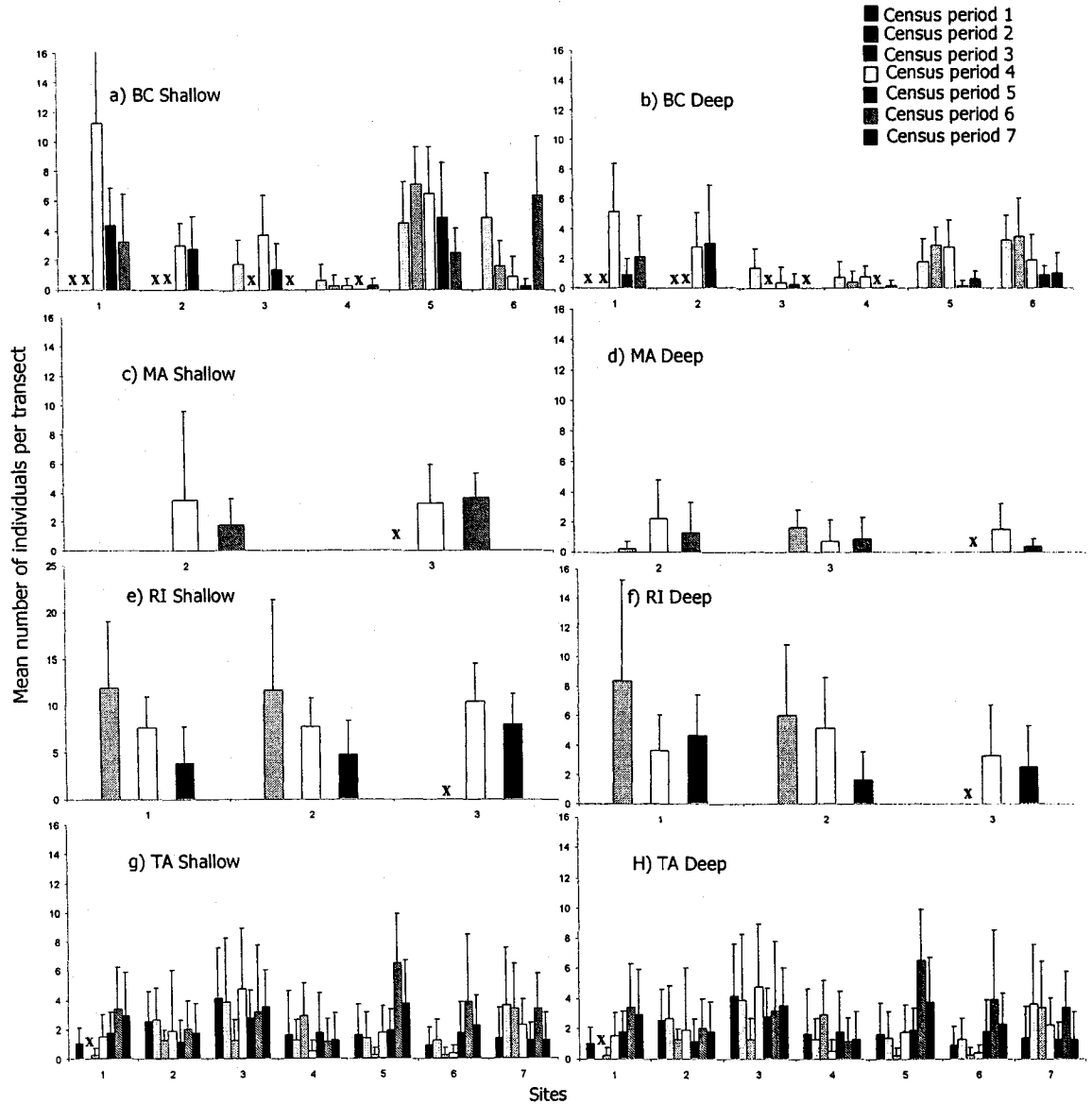

Legend:
- ■ Census period 1
- ■ Census period 2
- ■ Census period 3
- □ Census period 4
- ■ Census period 5
- ▓ Census period 6
- ■ Census period 7

a) BC Shallow
b) BC Deep
c) MA Shallow
d) MA Deep
e) RI Shallow
f) RI Deep
g) TA Shallow
H) TA Deep

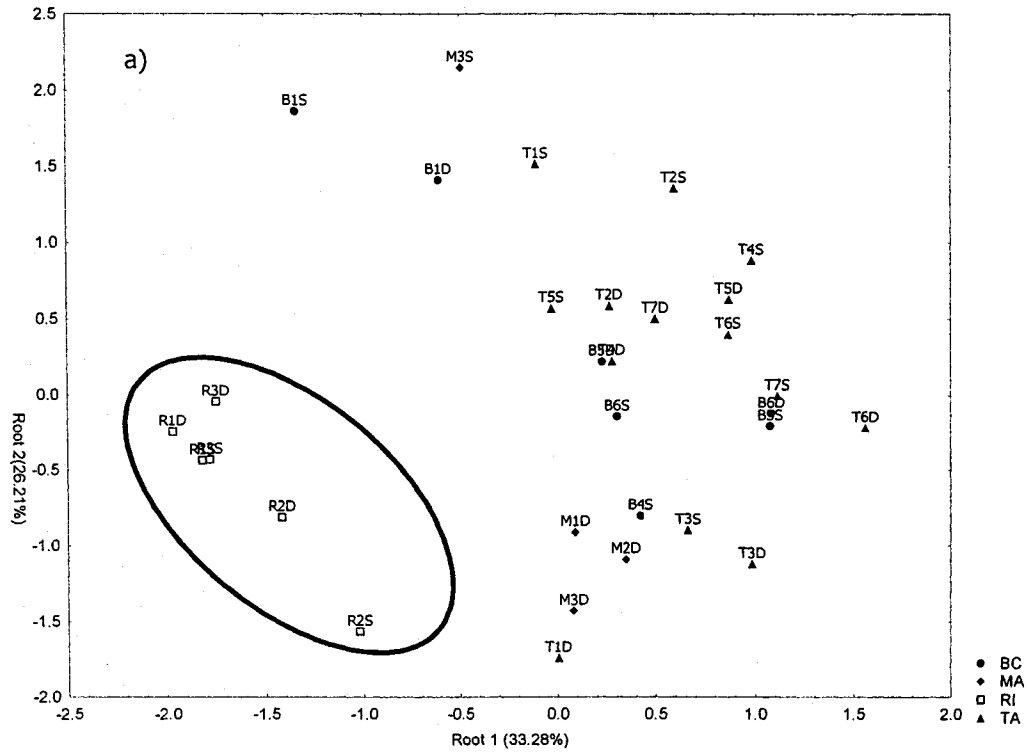Mean number of individuals per transect

Sites

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Figure 7 .a) PCA analysis of habitat features recorded at each depth across all locations. b) loadings of variables from the analysis used to interpret each root.

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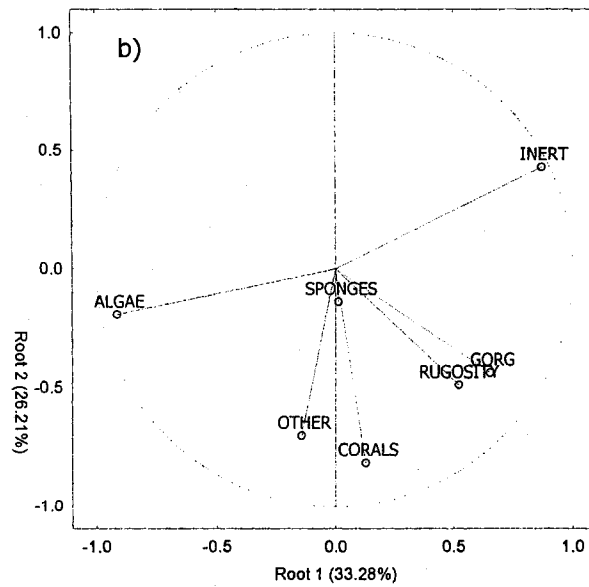
Chapter 4

General discussion and conclusions

General conclusions

The abundance and distribution of both adult and juvenile coral reef fishes has been explained to some extent by responses to spatial variation in habitat (Friedlander and Parish 1998, Carr 1991, Caselle and Warner 1996, Tolimieri 1998a,b). The study that spans the chapters of this thesis is aimed at elucidating the extent to which variations in habitat can explain the observed patterns of variation in recruitment of two species of coral reef fish in the western Caribbean. Given the great variation observed in the patterns of abundance and distribution of young recruits habitat alone seems unlikely to explain these variation on itself. We currently hold a view that patterns in abundance and distribution of coral reef fish are the result of multiple factors that act either at different times during the life cycle of the organism or in conjunction during a given part of the life cycle. These factors include several mechanisms that act at different periods of the life cycle of coral reef fishes. Among these are oceanographic features, random events taking place during the pelagic larval phase that might modify survival of larvae, differential settlement, and post-settlement events such as differential rates of mortality among sites, movement to preferred habitats, and competition with other fish. In al studies concerning reef fish the variation in recruitment has been found to be considerable in both space and time.

The estimation of percent cover of all the substrata found at a given location has often been used as a proxy for habitat structure. Traditionally percent cover has been assessed by recording substrata at points or segments along the centerline of a transect, or by estimating the percent cover of a given habitat feature encompassed by a quadrat, however there are several different methods in use for estimating percent cover in either case. Among these point intercept methods are generally acknowledged to be more precise. Chapter 2 was conceived as an experiment to evaluate the relative effectiveness of point intercept methods applied on line transects and in photoquadrats. Further, by varying the intensity of sampling (number of sampling points per line transect or quadrat) I was able to explore the precision (uncertainty among estimates) and the comprehensiveness (ability to detect all substrata) of the estimates obtained, as

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well as time employed per sampling unit. The relevance of this experiment lies in the fact that field research is usually conducted in remote locations where available field time becomes a limiting factor. Therefore the need for methods that will allow us to maximize the available time in terms of levels of replication and precision of our estimates when compared to other methods that might take longer time to perform.

The most important results in this study were that sampling a transect using a lower number of sampling points (20 vs 80 for point intercept, and 144 vs 720 for photoquadrats) did not affect the comprehensiveness or the precision of the estimates of percent cover obtained with either method. However, the lowest levels of sampling intensity employed with either method did not detect substrata with very low coverage, suggesting that while a lower number of sampling points will suffice to describe common substrata the rare ones might be missed. These results are highly relevant because they show that by recording substrata at lower sampling intensities we can significantly decrease the time spent per sampling unit (transect or quadrat), which can in turn be translated to an increase in our levels of replication.

Technological advantages allow us to record digital images that can be analyzed at a later date, and can be kept as a permanent record of the area under study. These methods involve more logistical support and require more equipment that is undoubtedly more expensive than a pencil, a slate and some underwater paper. I surveyed quadrats using an underwater digital camera, and then superimposed a grid on the quadrat image to carry out the point intercept sampling. When point intercept transects and quadrats were compared the results suggested that apart from some differences in percent cover that might have been attributable to observer bias, both methods described habitat features in a similar way. These results suggest that habitat characterization does not dramatically improve as a function of the technology employed to record it. In short, traditional pencil based methods yield information that is as comprehensive and precise as more sophisticated camera based approaches.

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Chapter three takes the ability to describe habitat and uses it to explore the relationship between habitat and patterns of recruitment for two species of coral reef fish. These relationships have been addressed in the literature on multiple occasions; however this is the first study in which data were collected on recruitment variation across broad spatial scales in the Caribbean. These relationships were explored at large spatial scale (MBRS system) and across several censusing periods for one atoll in the region.

Whether because of differential settlement to, or differential survival at preferred habitats, we might expect number of recruits to be higher here. Our results did not find any correlations that were consistent through time between habitat attributes and the recruitment patterns observed for either species. When patterns were analyzed at the MBRS scale we found a negative correlation between the percent cover of gorgonians and the recruitment of *S. partitus.* No correlations were found for *T. bifasciatum.*
Our data on fish and on habitat are all measured at the scale of a site –a region about 20x200 m in area within which replicate 30x1m long transects were deployed. Thus the lack of correlation between abundance of recruits and habitat does not refute earlier studies that have documented strong associations at smaller scales (e.g. Caselle and Warner 1996, Tolimieri 1995, 1998a, 1998b). Because recruitment patterns are greatly variable they are likely to be caused by different factors that are acting before and after settlement, as has been suggested in the past. Our data do suggest that association of fish and habitat are scale dependent, and that strong associations at small scales do not result in similar associations at larger scales of sites or regions. We are left with the fact that data on habitat variation among the sites does not account for the perceived spatial and temporal variations in recruitment of species. To better understand patterns of recruitment we will need to consider more factors such as oceanographic processes, patterns of larval availability, competition, and early post settlement mortality and movement.

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Vita auctoris

Paolo Usseglio was born in 1976 in San Andres Island, Republic of Colombia. He went to elementary and high school in the island but moved to the beautiful country of Costa Rica for his undergraduate education. He successfully graduated from the Universidad Nacional de Costa Rica in 2001 with a B. Sc, in Marine Biology. While at UNA Paolo swam for the university team winning several medals at the National University games of Costa Rica in 1998. He is currently working under the supervision of Dr. Peter Sale at the University of Windsor, he hopes to graduate in 2004 from his Masters program and move to a warm climate afterwards where he wishes to indulge in diving and water sports. However he expects to visit colder climates during the winter to enjoy snow based activities.

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