SPATIALLY AND TEMPORALLY PREDICTABLE FISH COMMUNITIES ON CORAL REEFS

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Abstract. Spatial and temporal variation in the distribution and abundance of site-attached fish species inhabiting small, isolated patches of coral reef has been attributed to variability in larval recruitment. However, the relative importance of settlement and postsettlement processes in determining the structure of fish communities in general, i.e., including non-site-attached species inhabiting large sections of contiguous reef, remains to be determined. Here, we examine the degree of spatial and temporal variation in community structure and population density of fish inhabiting sections of coral reef varying in size and connectivity.

To investigate spatial variability in fish community structure and population density, we surveyed 36 sites on contiguous reef and 39 patch-reef sites varying in size and isolation from neighboring patches. Ordination and regression analyses indicated that the structure of fish assemblages inhabiting contiguous reef varied predictably along habitat gradients. In contrast, intrinsic habitat characteristics, such as the shelter availability and the composition of the substratum, were apparently unrelated to the structure of fish assemblages on patch reefs. For sites on contiguous reef, multiple regression models explained a significant proportion of spatial variation in the population density of 10 site-attached and vagile species (including 90% of variation in the density of *Pomacentrus moluccensis,* a site-attached damselfish). For patch-reef sites, models of spatial variation in population density were significant for six species, five of which were not site attached. The overall pattern across most species was that patch-reef models were characterized by a reduced r^2 relative to corresponding models of contiguous-reef populations, but the reduction was substantially less for vagile species than for site-attached species.

Ordination analysis of temporal variability in community structure over two years suggested that none of the fish communities at the sites examined was in a consistent state of community succession. For most sites, community structure varied randomly over time, although at some sites, the structure of resident fish communities tended towards a stable position in multivariate community space. Across all sites, temporal change in community structure was significantly higher during periods of recruitment than at other times of the year, although there was little evidence to suggest that recruitment was the sole source of temporal variation. At most sites, the structure of fish assemblages fluctuated considerably during nonrecruitment periods. Patterns of temporal variation in the population density of four site-attached species indicated that population increases corresponding with pulses of recruitment were modified by postsettlement processes. For site-attached and moderately vagile species, overall temporal variability in assemblage structure increased significantly as sites became smaller and more isolated. Temporal variability in assemblages of highly vagile species was unrelated to survey area and connectivity.

Overall, the results of the analyses of spatial and temporal variability in fish community structure suggest that species' vagility and reef connectivity strongly influence the relative importance of recruitment and postrecruitment processes in determining local population density. Individuals of highly vagile species are able to move among isolated patches in response to habitat preferences or resource availability. Conversely, the continuous shelter provided by contiguous reef may allow sedentary species to migrate to more favorable areas. We suggest that for many fish species, including vagile species on patchy reef and site-attached species on contiguous reef, patterns in distribution and abundance established at recruitment are modified by postsettlement migration, which enhances the relationship between population density and habitat structure. Thus, while recruitment patterns may explain much of the spatial and temporal variation in populations of site-attached fish on small, isolated patch reefs, this result cannot necessarily be extrapolated to fish communities inhabiting large sections of contiguous reef.

Key words: community structure; contiguous reef; coral reef fish; habitat structure; ordination; patch reef; population density; recruitment; recruitment limitation; reef connectivity; regression; vagility.

INTRODUCTION

Early ecologists described coral reef fish communities as stable, equilibrial assemblages structured primarily by competitive interactions (Odum and Odum 1955, Hiatt and Strasburg 1960, Smith and Tyler 1972, 1973, Smith 1975, 1978). However, more recent studies have documented a high degree of spatial and temporal variation in the structure of coral reef fish assemblages (e.g., Sale and Dybdahl 1978, Williams 1980, Sale and Douglas 1984, Sale and Steel 1986, 1989, Sale et al. 1994). The apparent randomness in distribution and abundance of fish species has prompted the suggestion that coral reef fish communities are structured by stochastic processes, and in particular, by variation in recruitment (Sale and Dybdahl 1975, 1978, Talbot et al. 1978).

There has been much debate over the relative importance of recruitment and postrecruitment processes in structuring marine assemblages (see reviews by Underwood and Denley 1984, Lewin 1986, Roughgarden et al. 1986, Doherty and Williams 1988, Mapstone and Fowler 1988, Underwood and Fairweather 1989, Sale 1990, Doherty 1991, Fogarty et al. 1991, Jones 1991, Booth and Brosnan 1995). Recruitment of almost all coral reef fish species is by means of a pelagic larval stage, which lasts from weeks to months (Brothers et al. 1983, Thresher 1984). Oceanographic variability coupled with high mortality of pelagic larvae causes considerable spatial and temporal variation in larval recruitment at multiple scales (Eckert 1984, Sale et al. 1984b; Doherty 1987; reviewed by Richards and Lindeman 1987, Doherty and Williams 1988, Doherty 1991). However, it remains to be determined to what extent patterns established by stochastic recruitment are modified by postsettlement processes, such as competition for limiting resources (Smith and Tyler 1972, Thresher 1983a, Jones 1986, 1988, Forrester 1995, Robertson 1996), predation (Shulman et al. 1983, Shulman 1985, Hixon 1991, Hixon and Beets 1993, Carr and Hixon 1995), and migration (Robertson 1988a, b).

The recruitment limitation hypothesis is arguably the most widely accepted demographic model of coral reef fish populations. Its principal tenet is that populations are limited by an undersupply of larval recruits, i.e., there is insufficient recruitment to increase the population beyond the environmental "carrying capacity" at which density-dependent population regulation occurs (Williams 1980, Doherty 1981, 1983, Victor 1983, 1986). Thus, if recruitment patterns are not modified by postsettlement processes, the density of adult populations should reflect spatial and temporal variability in recruitment.

Recruitment of coral reef fishes has been studied using two main techniques. In the first, newly settled individuals are surveyed visually to determine distribution and abundance (e.g., Williams 1980, 1983, Victor 1986, Robertson 1988a, b, Robertson et al. 1993,

see also Williams et al. 1994), and in the second, otolith microstructure is examined to indicate the exact time of settlement (e.g., Victor 1982, 1983, 1986). In a recent study, Doherty and Fowler (1994a, b) used both techniques to estimate the extent to which temporal variability in recruitment explains spatial variation in the demography of two damselfish species at a number of sites on the southern Great Barrier Reef. They found that recruitment history explained almost entirely the spatial variation in the population age structure and abundance of both species. These results and those of a number of other studies (reviewed by Doherty and Williams 1988, Doherty 1991) have largely established the paradigm of recruitment limitation as the principal process driving the structure and dynamics of coral reef fish communities.

An important limitation of the majority of studies examining the ecology and dynamics of coral reef fish assemblages is that they have been conducted on patch reefs, i.e., outcrops of reef surrounded entirely by sand. In most studies, experimental patches have been small (area of patch reefs <30 m²; e.g., Sale and Dybdahl 1975, 1978, Williams 1980, Sale and Douglas 1984, Clarke 1988, Jones 1990), isolated (>8 m from neighboring patches; e.g., Williams 1980, Doherty 1983, Victor 1986, Clarke 1988, Jones 1990), and located in sheltered lagoons (e.g., Doherty 1983, Thresher 1983a, b, Sale and Douglas 1984, Clarke 1988, Doherty and Fowler 1994a,b). Furthermore, many researchers have focused exclusively on highly site-attached and/or territorial species (e.g., Williams 1980, Doherty 1981, Doherty 1983, Doherty and Fowler 1994a, b). Visual censusing is easier for species with small home ranges than for wide-ranging, highly vagile species, and small sedentary species are easy to capture and are ideal for experiments that involve manipulation of population density (e.g., Sweatman 1985, Jones 1987a, 1988, Forrester 1990). Similar advantages are gained by studying fish assemblages on small, isolated patch reefs (Sale 1984). These advantages underpin the paucity of studies examining populations of vagile species and fish assemblages on contiguous coral reef.

While there is good data on the population dynamics of site-attached species on isolated patch reefs, an understanding of the processes affecting patch-reef assemblages cannot necessarily be extrapolated to those inhabiting large, well-connected reef mosaics (Walsh 1985, Jones 1987b, 1988, Robertson 1988a, Sale 1991, Sale and Guy 1992, Sale et al. 1994). Here, we argue that assemblages of site-attached species inhabiting small, isolated patch reefs represent a special case with respect to the ecology and dynamics of coral reef fish communities. Moreover, we suggest that conclusions arising from the study of these systems do not necessarily apply to populations of vagile species or to fish assemblages inhabiting large sections of contiguous coral reef.

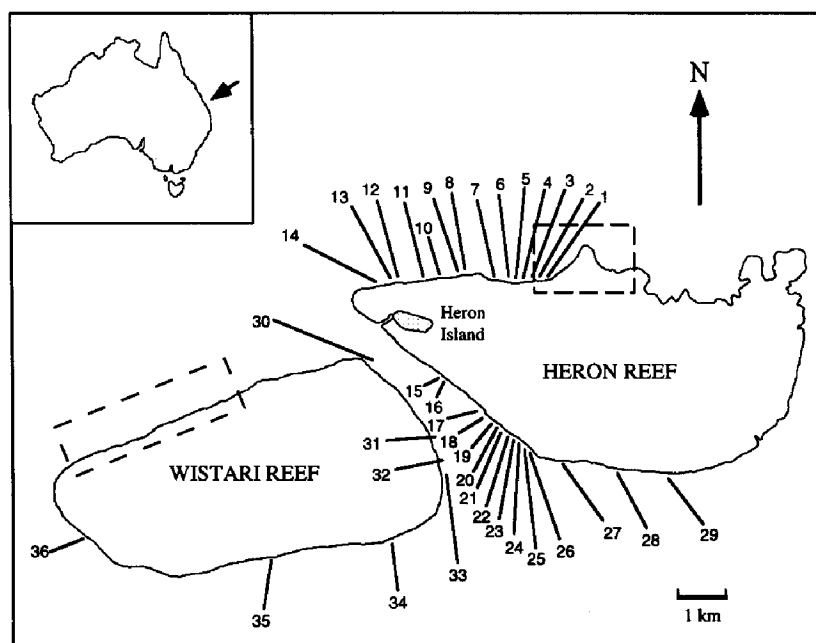The primary aim of our research was to quantify the

FIG. 1. Location of sites examined during the investigation of spatial variability in community structure. Locations of contiguous-reef sites are indicated by site numbers. Dashed squares indicate areas in which patch-reef sites were located.

degree of spatial and temporal variability in the structure of fish communities (species composition and relative abundances) and the density of fish populations on sections of contiguous reef and on patch reefs varying in size and isolation from neighboring patches. The study can be categorized conveniently into two parts (Study 1 and Study 2), namely examination of spatial and temporal variability in the distribution and abundance of coral reef fish species.

In Study 1, we investigated the degree to which spatial variation in fish community structure and population density is related to habitat characteristics (e.g., substratum characteristics, shelter availability). Specifically, we addressed the following questions: (1) How much spatial variation in fish community structure and population density is explained by variation in habitat structure alone? and (2) Does predictability in fish community structure and population density differ for fish species varying in vagility among sites on contiguous and patchy reef?

Previous studies of spatial variation in the structure of coral reef fish communities have been criticized for lacking a temporal component (Doherty 1983). Thus, to reduce ambiguity in our results, we conducted a concordant study assessing temporal variability in community structure and population density at sites varying in size and connectivity (Study 2). Over a 2-yr period, we repeatedly surveyed a range of sites from contiguous and patchy reef, with an aim to answering three main questions. (1) Is there any evidence that fish communities vary through time in a predictable direction (i.e., community succession) or fluctuate around a stable configuration? (2) Is the overall magnitude of temporal variability of a particular fish assemblage related to the size and connectivity of the survey patch and/or the vagility of the species comprising the assemblage? (3) Is there any evidence that recruitment

events are primarily responsible for temporal variation in fish community structure?

METHODS

Study sites

Research was conducted at adjacent Heron and Wistari reefs (23°21' S, 151°55' E) in the Capricorn Group, southern Great Barrier Reef. Both are platform reefs, consisting of a shallow lagoon surrounded by a continuous rim of coral comprising distinctive reef flat, crest, and slope habitats. All sampling was conducted on the outer reef slope, within a depth range of 4–15 m. On most sides of Heron and Wistari reefs, the reef slope consists of large tracts of contiguous coral reef. However, in a number of areas along the north side of both reefs, the slope is formed primarily by patch reefs that vary widely in size and in isolation from neighboring reef habitat.

Experimental design

In the examination of spatial variability in the structure of fish communities (Study 1), 36 sites on contiguous reef and 39 sites on patch reefs were surveyed once for fish community and habitat structure between October 1992 and October 1993. Locations of sites were varied as widely as practicable to minimize the possibility that local effects may mask general trends in community structure (Fig. 1). Patch-reef sites were chosen to vary along gradients of patch size and isolation from neighboring patches (connectivity).

As data on spatial variability were collected over a 1-yr period, it is possible that temporal variability in the structure of fish communities (e.g., seasonal effects) may have weakened overall relationships between community structure and habitat characteristics. Thus, analyses of spatial variation are likely to be conservative.

TABLE 1. Months during which surveys of temporal variation in fish community structure were conducted (Study 2).

Survey no.	Survey date
1	Feb 1993
2	Mar 1993
3	May 1993†
4a	Aug 1993
4b	Oct 1993‡
5	Nov 1993
6	Jan/Feb 1994
7	May 1994
8	Aug 1994
9	Nov/Dec 1994
10	Feb/Mar 1995

† First survey for three additional contiguous-reef sites (see *Methods: Experimental design*).

‡ First additional survey for seven additional patch-reef sites, no other sites surveyed (see *Methods: Experimental design*).

To investigate the degree of temporal variability in the structure of fish communities, a number of permanent sites were surveyed for fish community structure on multiple occasions over a 2-yr period (Study 2). In February 1993, three contiguous-reef sites and nine patch-reef sites were set up on the north side of Heron Reef. In May 1993, three more contiguous-reef sites were set up on the south side of Heron Reef, and in October 1993, seven more patch-reef sites were set up on the north side of Heron Reef. In general, surveys of fish community structure were conducted at ~3-mo intervals although additional surveys were conducted in the early stages of the study (Table 1).

Surveying of fish communities

At each contiguous-reef site, fish species abundance was recorded on a 10 × 10 m grid of 25 quadrats (each 4 m²) marked out by cords laid over the substratum. Each quadrat was surveyed for 2 min by a single diver on scuba (T. R. Ault throughout the study). All fish that were present or that entered the quadrat during the 2-min period were recorded, with the exception of small cryptic species (e.g., blennies and gobies), nocturnal species (e.g., cardinalfishes or soldierfishes), and semipelagic species not usually associated closely with the substratum (e.g., fusiliers and trevallies). Species that were usually present in large polarized schools (e.g., *Chromis atripectoralis, C. nitida, Cirrhilabrus punctatus*) were also excluded from statistical analyses.

During surveying of fish communities, the observer remained stationary or moved slowly, thereby reducing the likelihood of "herding" or frightening fish into or out of the grid. Although little diver-induced migration was observed, larger mobile species were recorded first as these were more likely to be disturbed than smaller site-attached species. Individuals that moved between quadrats during surveying were recorded once only.

The same method was used for sites located on patch reefs except that smaller grids of 4-m² quadrats were used as the area of each patch reef was <100 m². Unlike

the patch reefs commonly found in shallow lagoonal habitats, the patch reefs examined on the reef slopes of Heron and Wistari reefs were generally low in vertical relief relative to area and did not present a problem with the placement of quadrats.

Evaluation of surveying method

Surveying precision was evaluated by surveying a single site on contiguous reef (site 1; Fig. 1) three times in 3 h. Results were compared to surveys of all other contiguous-reef sites investigated in Study 1 (sites 2–36, Fig. 1) to determine if surveying precision was sufficient to resolve differences in community structure among sites. Similarity among surveys was estimated using the Bray-Curtis (BC) index of similarity on data that had been transformed to $\log(X + 1)$ (see Wolda 1981). Logarithmic transformation of the data ensured that BC scores were not dominated by abundant species. A cluster dendrogram summarizing similarity among sites was constructed using the unweighted pair-group method with arithmetic averaging (UPGMA).

Habitat measurements

At each site investigated during Study 1, several habitat parameters were measured, including water current velocity, mean depth, topographic complexity, substratum composition, and availability of shelter. Water current velocity was measured immediately after each survey by timing the movement of a neutrally buoyant object over a known distance at a height of 1 m above the substratum. Measurements were repeated three times and the results averaged. Mean depth was also measured immediately after each survey. As all sites were relatively homogeneous with respect to depth, an estimate of mean depth was obtained by averaging the depths of the shallowest and deepest part of each site. Topographic complexity (TC) was defined as $TC = (L_s - L_d)/L_d$ where L_d is the direct straight line length across the site, and L_s the "surface length" obtained by running a tape as closely as possible over the contours of the substratum (Risk 1972, Luckhurst and Luckhurst 1978, Sale and Douglas 1984). Parallel transects assessing topographic complexity were taken at 2-m intervals across each site and averaged. For each 4-m² quadrat, substratum composition was measured by a visual estimate of percentage cover of nine substratum types. Coral substrata included encrusting, digitate, branching, tabulate, massive, and soft corals. Noncoral substrata included dead coral rock (eroded dead coral, often covered with turf algae), rubble (fragments of coral rock <5 cm in diameter), and sand (sand and fragments <0.5 cm). Results for all quadrats were averaged to yield the mean substratum composition for each site. Shelter availability was measured by counting the number of holes that had a maximum depth equal to or greater than the minimum diameter of the hole entrance. Holes were placed in three size categories on the basis of minimum entrance diameter:
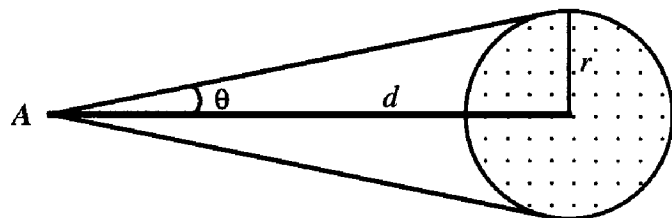
FIG. 2. The probability that an individual at A, which moves in a straight randomly chosen direction, will encounter a habitat patch of radius r is equal to θ/π (radians) or arctan $(r/d)/\pi$, where d is the distance from A to the center of the patch.

TABLE 2. List of species included in the analysis of spatial variation in community structure (Study 1), ranked in order of abundance.

Species	Family	Diel move-ment†
1) *Pomacentrus moluccensis*	Pomacentridae	SA
2) *Pomacentrus amboinensis*	Pomacentridae	SA
3) *Pomacentrus wardi*	Pomacentridae	SA
4) *Pomacentrus lepidogenys*	Pomacentridae	MV
5) *Chrysiptera rollandi*	Pomacentridae	SA
6) *Thallassoma lunare*	Labridae	HV
7) *Halichoeres melanurus*	Labridae	MV
8) *Amblyglyphidodon curacao*	Pomacentridae	MV
9) *Labrichthys unilineatus*	Labridae	MV
10) *Ctenochaetus binotatus*	Acanthuridae	HV
11) *Coris schroederi*	Labridae	MV
12) *Labroides dimidiatus*	Labridae	SA
13) *Labropsis australis*	Labridae	MV
14) *Scarus sordidus*	Scaridae	HV
15) *Stethojulis strigiventer*	Labridae	HV

† Diel movement: SA = site-atttached, MV = low–medium vagility, HV = high vagility.

small (3–10 cm), medium (10–20 cm), and large (>20 cm). Hole counts were converted to hole densities for analysis.

For each site examined during the study of temporal variation in community structure (Study 2), the composition of the substratum was estimated using the methods described. Surveys of substratum composition were made after the initial and final surveys.

Index of connectivity

Previous studies have suggested that for fish assemblages inhabiting patch reefs, the degree of isolation from neighboring patches can influence community structure (Molles 1978, Gladfelter et al. 1980, Walsh 1985). For all patch-reef sites investigated in this study, the degree of isolation of each site from neighboring patch reefs was estimated by an index of connectivity (C_i), which integrated the size and spatial arrangement of neighboring patches.

If an individual fish, at a distance d from a habitat patch of radius r (Fig. 2), moves in a straight, randomly chosen direction, the probability of the individual reaching the habitat patch is equal to θ/π or arctan$(r/d)/\pi$ (in radians). This value increases as the radius of the patch increases and the distance from the individual to the patch decreases. The probability measure can be likened to the "importance" of a neighboring patch of suitable habitat at distance d. Thus, the index of connectivity (C_i) is defined as the summed influence (probabilities) of surrounding habitat patches in all directions.

For patch-reef sites, connectivity (C) in one direction (compass bearing) was estimated in the following way. The presence or absence of suitable reef habitat (as opposed to bare sand or rubble providing little or no protection) was recorded at 1-m intervals over a 30 × 2 m belt transect radiating out from the patch, and C was calculated as:

$$C = \sum_{i=1}^{d} a_d(\arctan(r/d)/\pi)$$

where r is the radius of the patch and a_d is a binary parameter indicating the presence $(a_d = 1)$ or absence $(a_d = 0)$ of reef at a distance d along the transect. As most patch reefs sampled were approximately circular

or elliptical, r was estimated from patch area assuming each patch was a perfect circle. An average estimate of connectivity in all directions (C_t), was obtained by averaging C from eight belt transects radiating out from the site at 45° angles (N, NE, E, SE, S, SW, W, NW).

In calculating C_t, it is assumed that individuals move in a single constant direction and cannot sense or learn the location of suitable habitat patches. While these criteria are unlikely to be strictly met for many reef fish (see Bardach 1958, Reese 1989), C_t represents an estimate of connectivity that integrates the underlying biological assumptions with geographical data. Unlike other commonly used measurements (e.g., distance to nearest neighboring patch), C_t summarizes connectivity with a group of neighboring patches.

Analysis of spatial variability in fish community structure

To facilitate the identification of spatial patterns in fish community structure (Study 1), we limited the analysis to the 15 most common species (Table 2), with the exception of two species that were characterized by highly skewed distributions (*Pomacentrus australis, Assessor macneilli*). Data were transformed to improve normality, linearity, and homoscedasticity. Fish counts were converted to densities and transformed to log$(X + 1)$, percentage cover estimates were transformed to arcsin$\sqrt{X}$, and densities of small holes were transformed to log(X).

Bivariate scatterplots indicated that intercorrelations among most species were weak and nonlinear, and exploratory analyses using principal components analysis and canonical correlation analysis suggested that general linear techniques were unsuitable for describing interrelationships among species (indicated by inspection of principal component loadings and canonical variates). We used nonmetric multidimensional scaling

(MDS) to summarize similarities (Bray-Curtis) in fish community structure among sites on contiguous and patchy reef in two ordination dimensions (Kruskal 1964a, b, Faith et al. 1987, Minchin 1987, Clarke 1993). Final configurations were arranged so that the first dimension corresponded with the axis of maximal variation in MDS scores.

Although the analysis was limited to the 15 most common species, the area of some patch-reef sites was insufficient to support 15 species (due to the accumulation of species with increasing area). In the ordination of such sites, the absence of species due to small sample size would be treated as zero counts (densities). Thus, the position of small sites in ordination space may reflect sample size differences rather than true variation in fish community structure. To avoid this problem, we plotted the species/area curve for patch-reef sites and calculated, by interpolation from a fitted power curve, the sample area below which 15 species were unlikely to occur. Patch-reef sites with an area below the calculated threshold were excluded from the ordination analysis.

For both contiguous- and patch-reef sites, we used stepwise multiple regression (P to enter/remove = 0.15) to model the position of sites in MDS space using habitat variables as predictors. Separate regression models were constructed to predict scores (coordinates) along MDS dimension 1 and MDS dimension 2. To reduce the number of independent variables in the regression models, water current velocity and percentage cover of tabulate, boulder, and soft coral were excluded from analyses. Measurements of water velocity were negligible or slight at most sites (only 13 sites were characterized by a water current velocity in excess of 0.1 m/s), and tabulate, boulder, and soft corals were all minor components of the substrata of patch-reef and contiguous-reef sites. For the analysis of patch-reef data, survey area and C_t were included as independent variables.

Analysis of spatial variability in fish population density

To determine whether spatial variability in the population densities of the 15 common fish species was related to spatial variation in habitat structure, we used stepwise multiple regression to model the density of each species on contiguous- and patch-reef sites from habitat characteristics. For each species, two separate models were constructed, one to predict population density on contiguous-reef sites and one to predict population density on patch-reef sites. The independent variables in each model comprised the habitat variables used in the regression of MDS scores with the exception of survey area and C_t for patch-reef sites.

For models of patch-reef populations, it is possible that patch size (survey area) and connectivity (C_t) may account for some of the unexplained variability in population density (residual variability). Residual popu-

lation density may vary either predictably or unpredictably with patch size and/or connectivity. In the first case, residuals may become increasingly positive or negative as patches become larger and more connected. In the second case, overall variability in residual population density (residual magnitude, positive or negative) may be correlated with patch size and connectivity, indicating that the degree of unexplained variability in population density changes as patch reefs become larger and more connected. To test the effects of patch size and connectivity on models of fish population density based on patch-reef sites, we used multiple regression to predict residual population density with sign retained (untransformed) and residual population density transformed to absolute value, from survey area and C_t. The order of entry of independent variables into regression models of residuals was hierarchical with survey area entering first and C_t entering second. Thus, the effect of connectivity was evaluated after possible effects of sampling scale were accounted for. Significance of the variance explained by each variable as it entered the regression was evaluated by an F test (Sokal and Rohlf 1995).

Validation of multivariate analyses of spatial variability

In the multiple regression models of community structure and population density, the ratio of number of sites to number of independent variables was relatively low. Thus, it is possible that significant correlations between fish community structure and habitat structure may have arisen through random associations within the data. This potential problem is confounded by the use of stepwise regression, which tends to "overfit" a small data set and artificially elevate estimates of r^2 (Wilkonson 1979, Rencher and Pun 1980). It is recommended that stepwise regression solutions be validated by dividing the data set into two parts and performing identical analyses on each (Tabachnick and Fidell 1989). However, in Study 1, the number of sites examined from both contiguous and patchy reef was insufficient to allow division of either data set, so we evaluated the "robustness" of regression models through Monte Carlo testing of randomized data.

If differences in fish abundance among sites were due to spatial variation in some parameter other than the habitat characteristics measured (e.g., recruitment), there should be no significant difference between the total variance explained by models based on randomized data and models based on observed data. To test this null hypothesis, 50 randomized data sets were created. For contiguous- and patch-reef sites, the observed data set consisted of a matrix of dependent variables or Y matrix (density of each fish species) and a matrix of independent variables or X matrix (habitat measurements). Randomized data sets were created by "reshuffling" each column of the Y matrix in turn, such that observed abundances of each species were ran-

domly assigned to a new site. In this way, the correlation structure of the X variables was preserved and the effect of extreme Y values was maintained (Manly 1991). Thus, if models based on observed data were dominated by a small number of outlying data points, the models based on the randomized data would be influenced in the same manner.

Each randomized data set was analyzed using the same statistical techniques described above, i.e., analysis of variability in community structure by MDS and multiple regression, and analysis of variability in population density by multiple regression. As the number of analyses based on randomized data was relatively low (due to the time-consuming nature of the randomization procedure and subsequent analyses), we used the t distribution to test the null hypothesis. For each model, one-tailed t tests were conducted to determine whether r^2 from analysis of the observed data was significantly greater than r^2 values from analyses of randomized data sets (Sokal and Rohlf 1995: 227).

Analysis of temporal variability in fish community structure

For the investigation of temporal variation in the structure of fish communities (Study 2), the species pool was expanded to include most of the species surveyed, the exceptions being cryptic, nocturnal, pelagic and schooling species, and rare species, which were counted less than 15 times over the entire sampling period. For each site, similarity among repeat surveys was evaluated using the Bray-Curtis index on log-transformed data, and temporal variation in fish community structure was summarized by separate MDS ordinations in two dimensions. We examined each ordination diagram and tested for the nonrandom movement of each site through ordination space. The null hypothesis was that there was no directional bias to the movement of the site through community ordination space. Thus, if variability in community structure was random through time, progression of the site through ordination space should follow a random walk. For each site, we created 1000 randomized progressions, such that the position of the site moved with each repeat survey according to a random walk. Each random progression began at the same starting point in ordination space as the original solution and moved in a randomly chosen direction using the same magnitude of change for each transition as for the original MDS configuration. For each site, significance was evaluated by comparing the distance from the first survey to the final survey of the original ordination to the null distribution of distances from the 1000 randomized progressions (see Manly 1991, Potvin and Roff 1993).

At Heron and Wistari reefs, recruitment of most fish species is highly seasonal (November to February; reviewed by Doherty and Williams 1988, Doherty 1991). To test whether the structure of fish communities varied more during periods of peak recruitment than at other times of the year, we analyzed the similarity matrices (Bray-Curtis) underlying the MDS ordinations of each site. The magnitude of community change during recruitment and nonrecruitment periods was compared over 3-mo time intervals, i.e., recruitment periods (November–February) vs. nonrecruitment periods (February–May, May–August, August–November). For each site, we calculated the mean similarity of fish communities surveyed before and after each recruitment period (i.e., average Bray-Curtis similarity of surveys 5–6 and 9–10; see Table 1) and the mean similarity of fish communities surveyed before and after each 3-mo nonrecruitment period (i.e., average of surveys 1–3, 3–4a, 4a–5, 6–7, 7–8, 8–9; see Table 1). We were unable to test the mean similarity values directly because temporally autocorrelated measures of community similarity are not strictly independent (i.e., for a given input or loss of species, the degree of community change will depend on the composition of the community present initially). Instead, the difference between the mean similarities for recruitment and nonrecruitment periods was used as the test statistic. Data from sites were pooled into four habitat classes (contiguous-reef sites, large patch-reef sites >20 m², medium patch-reef sites 10–20 m², and small patch-reef sites >10 m²) and a one-way ANOVA was conducted to determine whether the difference in similarity varied among habitats. A paired t test was then conducted to determine whether the difference in mean similarity between recruitment and nonrecruitment periods differed significantly from zero (Sokal and Rohlf 1995: 356).

To examine overall temporal variation in the structure of fish communities in greater detail, we divided the species pool into three groups, based on a qualitative assessment of species' vagility (Table 3). For each site, we calculated a pairwise matrix of Bray-Curtis scores summarizing similarity among repeat surveys for each species group. We then used linear regression to model the mean pairwise similarity of repeat surveys conducted from November 1993 to March 1995 using C_t as the independent variable.

RESULTS

Evaluation of surveying method

Despite the overall high similarity in fish community structure among sites on contiguous reef (similarity of most sites >0.7), repeat surveys of site 1 were tightly clustered (Fig. 3). Thus, the surveying technique appears sufficiently robust to resolve consistent differences in community structure among sites harboring similar fish assemblages. A similar pilot study based on repeat surveys of a patch-reef site (31 m² in area, surveyed three times in 3 h) revealed very little variation among surveys. This result probably reflects reduced short-term variation in the structure of fish assemblages on patch reefs relative to contiguous reef

TABLE 3. Division of total species pool investigated during Study 2 (temporal variability) into three classes based on species' vagility.

Site-attached species	Low–medium vagility species	High vagility species
Pomacentrus moluccensis (P)	*Pomacentrus lepidogenys* (P)	*Thalassoma lunare* (L)
Pomacentrus amboinensis (P)	*Halichoeres melanurus* (L)	*Ctenochaetus binotatus* (A)
Chrysiptera rollandi (P)	*Amblyglyphidodon curacao* (P)	*Stethojulis strigiventer* (L)
Pomacentrus wardi (P)	*Labrichthys unilineatus* (L)	*Scarus sordidus* (S)
Labroides dimidiatus (L)	*Coris schroederi* (L)	*Anampses neoguinaicus* (L)
Dascyllus reticulatus (P)	*Labropsis australis* (L)	*Scarus niger* (S)
Assessor macneilli (Pl)	*Centropyge tibicen* (Po)	*Hemigymnus fasciatus* (L)
Pomacentrus australis (P)	*Cheilinus digrammus* (L)	*Hemigymnus melapterus* (L)
Pseudocheilinus hexataenia (L)	*Chaetodon aureofasciatus* (C)	*Gomphosus varius* (L)
Acanthochromis polyacanthus (P)	*Chaetodon rainfordi* (C)	*Thalassoma lutescens* (L)
Pseudochromis fuscus (Ps)	*Halichoeres margaritaceus* (L)	*Cantheschenia grandisquamis* (M)
Chrysiptera flavipinnis (P)	*Scolopsis bilineatus* (N)	*Sufflamen chrysopterus* (B)
Pomacentrus bankanensis (P)	*Cephalopholis boenak* (S)	*Scarus flavipectoralis* (S)
Plectroglyphidodon lacrymatus (P)	*Cheilinus chlorourus* (L)	*Anampses geographicus* (L)
Ogilbyina queenslandiae (Ps)	*Centropyge bispinosus* (Po)	*Choerodon fasciatus* (L)
Chrysiptera talboti (P)	*Pseudolabrus guentheri* (L)	*Chaetodontoplus meredithis* (Po)
Chaetodon trifascialis (C)	*Chaetodon trifasciatus* (C)	*Plectropomus leopardus* (S)
Amphiprion akindynos (P)	*Canthigaster valentini* (T)	*Diagramma pictum* (H)
Cypho purpurascens (Ps)	*Halichoeres prosopeion* (L)	*Siganus corrallinus* (Si)
Pseudochromis paranox (Ps)	*Centropyge bicolor* (Po)	*Synodus variegatus* (Sy)
Dascyllus trimaculatus (P)	*Chaetodon plebeius* (C)	*Siganus doliatus* (Si)
Dascyllus aruanus (P)	*Chaetodon kleinii* (C)	*Epibulus insidiator* (L)
	Chaetodon flavirostris (C)	*Lutjanus carponotatus* (Lu)
	Chelmon rostratus (C)	*Pomacanthus semicirculatus* (Po)
	Chaetodon melannotus (C)	*Zanclus cornutus* (Z)
	Pervagor aspricaudus (M)	*Parupeneus barberinoides* (Mu)
	Ostracion cubicus (O)	*Choerodon graphicus* (L)
	Bodianus axillaris (L)	*Cromileptes altivelis* (S)
	Neoglyphidodon melas (P)	*Zebrasoma scopas* (A)
	Paraluteres prionurus (M)	*Naso unicornis* (A)
	Oxymonacanthus longirostris (M)	*Choerodon schoenleinii* (L)
	Epinephelus merra (S)	*Siganus punctatus* (Si)
	Coris aurilineata (L)	
	Chaetodon baronessa (C)	
	Amblyglyphidodon leucogaster (P)	
	Coradion altivelis (C)	
	Epinephelus fasciatus (S)	
	Cephalopholis miniata (S)	
	Diploprion bifasciatum (S)	

Note: Species are listed in order of rank abundance. Family is indicated in parentheses. Family: P = Pomacentridae, L = Labridae, Pl = Plesiopidae, Ps = Pseudochromidae, C = Chaetodontidae, Po = Pomacanthidae, N = Nemipteridae, S = Serranidae, T = Tetraodontidae, M = Monacanthidae, O = Ostraciidae, A = Acanthuridae, B = Balistidae, H = Haemulidae, Si = Siganidae, Sy = Synodontidae, Lu = Lutjanidae, Z = Zanclidae, Mu = Mullidae.

due to decreased movement of fish into and out of the site.

Spatial variability in fish community structure

The 15 species retained for analysis belonged to four families and varied widely in vagility, ranging from site attached to highly vagile (Table 2). Our classification of species according to vagility was based on observations of rate and extent of movement of individual fish at the scale of surveying (10 × 10 m). For both habitats, the 15 species retained for analysis accounted for most of the fish community by number, representing 84 and 81% of all fish censused on contiguous- and patch-reef sites, respectively. For contiguous-reef sites, the two dimensional ordination solution from nonmetric multidimensional scaling (MDS) of the 15 most common species was very similar to the solution obtained from MDS analysis of the entire species pool. Similarly, MDS ordinations based on matrices of

Morista-Horn similarity produced comparable solutions to those based on Bray-Curtis similarity.

Interpolation from the species/area curve for patch-reef sites suggested that 15 species were unlikely to occur on patches with an area of <10 m^2 (Fig. 4). After exclusion of these sites, 24 patch-reef sites were retained for MDS analysis. The distributions of contiguous- and patch-reef sites along dimension 1 (x axis; Fig. 5) in ordination space were similar, but there was some separation along dimension 2 (y axis; Fig. 5).

Separate ordinations of contiguous- and patch-reef sites using MDS produced final configurations with stress values of 0.137 and 0.161. Stepwise regression models predicting MDS scores from habitat variables explained 82 and 76% of total variation in dimensions 1 and 2 for contiguous-reef sites (Table 4A), and 58% and 25% of total variation in dimensions 1 and 2 for patch-reef sites (Table 4B). For models based on contiguous-reef sites, r^2 values from the analysis of ob-
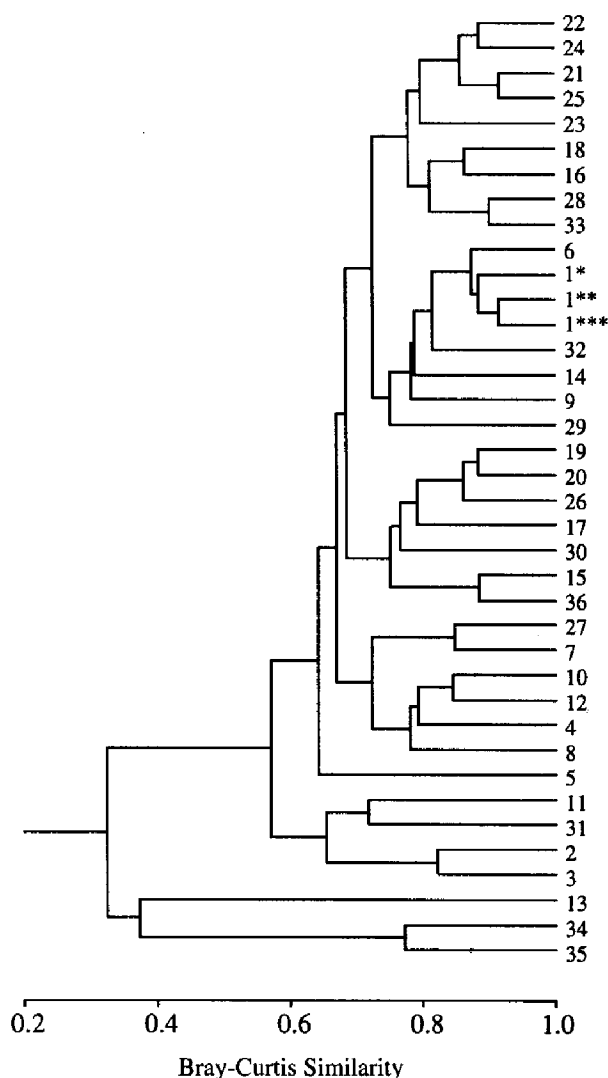
FIG. 3. Cluster dendrogram summarizing similarity among repeat surveys of site 1 (first, second, and third repeat surveys indicated by asterisks) and surveys of other sites examined on contiguous reef during Study 1.
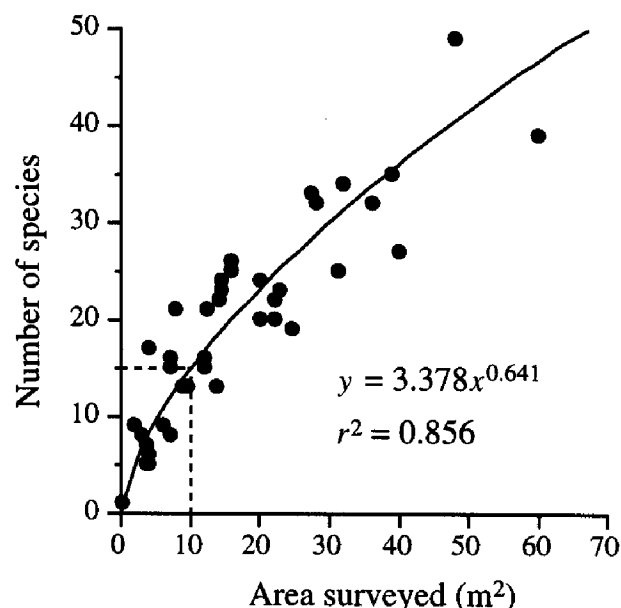

FIG. 4. Species/area curve for patch-reef sites examined in the investigation of spatial variability in community structure. Dashed lines indicate patch area below which 15 species are unlikely to occur.

$$y = 3.378x^{0.641}$$
$$r^2 = 0.856$$

served data were significantly higher than those obtained from analyses of randomized data (Table 5A), indicating that both models explained more variance than expected given the likelihood of chance associations within the data. For models based on patch-reef

sites, variation along MDS dimension 1 was significantly related to patch connectivity (Tables 4A, 5A). In contrast, the amount of variation along MDS dimension 2 explained by habitat characteristics (patch size) was not significantly higher than that expected by chance (Table 5B). This highlights the usefulness of the randomization procedure for statistical validation. For both models of patch-reef data (i.e., on MDS dimensions 1 and 2), the maximum r^2 obtained from analyses of randomized data exceeded 0.8.

Spatial variability in fish population density

Separate stepwise regression models predicting fish density from habitat characteristics at sites on contiguous reef varied widely in the proportion of variance explained, ranging from 0.1 for *Thalassoma lunare* to 0.9 for *Pomacentrus moluccensis* (Table 6A). *T* tests of observed and randomized analyses indicated that,

TABLE 4. R-squared, intercept, and regression coefficients for stepwise regression models of spatial variation in fish community structure. (A) models based on contiguous-reef sites, (B) models based on patch-reef sites.

MDS dimension	r^2	Intercept	Independent variable	Regression coefficient
A) Contiguous-reef sites ($n = 36$)				
MDS 1	0.816	−4.724	Small holes	1.348
			Digitate coral	3.778
			Branching coral	2.272
			Sand	1.535
			Topographic complexity	3.726
MDS 2	0.758	2.133	Sand	−2.766
			Rubble	−2.156
			Depth	−0.049
B) Patch-reef sites ($n = 24$)				
MDS 1	0.579	−1.35	C_t	0.656
MDS 2	0.247	0.565	Patch area	−0.023

Note: Dependent variable comprises scores (coordinates) from multidimensional scaling in two dimensions (MDS 1 and MDS 2). Variables are listed in order of stepwise inclusion into models.

TABLE 5. Comparison of r^2 for stepwise regression models of scores from multidimensional scaling in two dimensions (MDS 1 and MDS 2) based on observed data and randomized data. (A) models based on contiguous-reef sites, (B) models based on patch-reef sites.

MDS dimension	r^2 observed data	r^2 randomized data				t
		Max.	Min.	Mean	1 SE	
A) Contiguous-reef sites						
MDS 1	0.816	0.525	0	0.147	0.017	5.371†
MDS 2	0.758	0.492	0	0.137	0.016	5.611†
B) Patch-reef sites						
MDS 1	0.579	0.811	0	0.269	0.024	1.813*
MDS 2	0.247	0.814	0	0.313	0.033	−0.281

Note: $* P < 0.05$; $† P < 0.005$. For models of randomized data; max = maximum r^2, min = minimum r^2, SE = standard error of mean r^2. Significance was evaluated by one-tailed t test with 49 degrees of freedom.

for 10 species, models explained more significantly more variance that that expected from random associations within the data (Table 7A). These species included five damselfish (*P. moluccensis, P. wardi, P. amboinensis, Chrysiptera rollandi,* and *Amblyglyphidodon curacao*), three wrasses (*Halichoeres melanurus, Labrichthys unilineatus,* and *Coris schroederi*), one parrotfish (*Scarus sordidus*), and one surgeonfish (*Ctenochaetus binotatus*).

With the exception of *T. lunare,* all models of fish density on patch-reef sites explained less variation than corresponding models based on contiguous-reef sites (Table 6B). The reduction in r^2 was particularly noticeable for models of site-attached damselfish species, decreasing by 0.228 for *C. rollandi,* 0.233 for *A. curacao,* 0.372 for *P. moluccensis,* 0.419 for *P. wardi,* and 0.54 for *P. amboinensis.* In the models of these species on patch reefs, only that of *P. moluccensis* explained significantly more variance than analogous models of randomized data (Table 7B). For the more vagile spe-
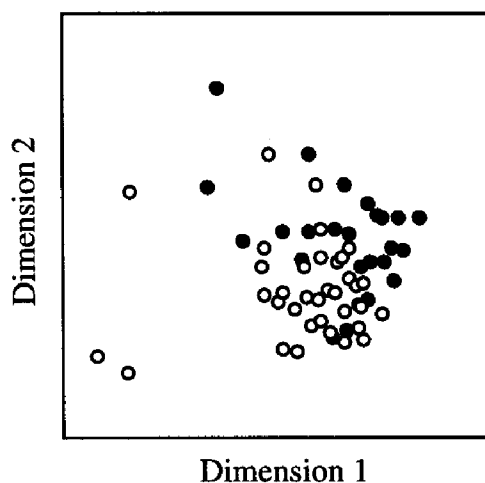

Dimension 1

FIG. 5. Multidimensional scaling of fish communities from contiguous (open circles) and patch-reef sites (closed circles) examined during analysis of spatial variability in community structure. Dimension 1 was aligned along the axis of maximal variation in MDS scores.

TABLE 6. Table of r^2 values, intercept, and regression coefficients for independent variables included in step-

Species	r^2	Intercept
A) Contiguous-reef sites		
P. moluccensis	0.90	0.06
P. amboinensis	0.70	−0.18
P. wardi	0.51	0.39
P. lepidogenys	0.37	−0.04
C. rollandi	0.54	−0.29
T. lunare	0.10	0.04
H. melanurus	0.52	0.05
A. curacao	0.56	0.00
L. unilineatus	0.66	0.00
C. binotatus	0.48	−0.09
C. schroederi	0.70	−0.04
L. dimidiatus	0.22	0.02
L. australis	0.28	−0.01
S. sordidus	0.57	0.07
S. strigiventer	0.26	0.05
B) Patch-reef sites		
P. moluccensis	0.53	0.14
P. amboinensis	0.16	−0.21
P. wardi	0.10	0.05
P. lepidogenys	0.21	−0.03
C. rollandi	0.31	−0.16
T. lunare	0.48	0.46
H. melanurus	0.43	−0.19
A. curacao	0.32	0.14
L. unilineatus	0.51	−0.10
C. binotatus	0.47	−0.02
C. schroederi	0.49	−0.16
L. dimidiatus	0.11	−0.02
L. australis	0.28	−0.01
S. sordidus	0.09	0.01
S. strigiventer	0.12	0.01

Note: Full names of fish species are given in Table 2.
† Independent variables: D = depth, TC = topographic complexity, EC = encrusting coral, DC = digitate coral, BC = branching coral, DCR = dead coral rock, R = rubble, S = sand, SH = small holes, MH = medium holes, LH = large holes.

cies, the reduction in r^2 from contiguous-reef models to patch-reef models was generally less, decreasing by 0.015 for *C. binotatus,* 0.092 for *H. melanurus,* 0.151 for *L. unilineatus,* 0.209 for *C. schroederi,* and 0.477 for *S. sordidus.* Furthermore, patterns of significance among models of vagile species on patch reefs were similar to those among models based on contiguous-reef populations, except that the model of *T. lunare* was significant for patch-reef sites while the model of *S. sordidus* was not (Table 7B).

It is unlikely that differences in the predictive ability of models based on contiguous- and patch-reef sites were due to major habitat differences among sites on contiguous and patchy reef. Two-tailed t tests of habitat characteristics indicated significant differences in only 4 of 11 habitat categories: proportion of branching coral, coral rubble, and dead coral and the density of medium holes (Table 8).

We tested the effects of patch size and connectivity on the six significant patch-reef models of population density using hierarchical multiple regression to predict

wise regression models of spatial variation in fish population density (dependent variable: individuals/m^2). (A) models of populations on contiguous-reefs sites, (B) models of populations on patch-reef sites.

Independent variables†										
D	TC	EC	DC	BC	DCR	R	S	SH	MH	LH
−0.02	···	···	1.01	0.34	−0.29	···	···	0.22	−0.01	−0.01
···	···	···	0.16	···	···	0.37	0.40	···	···	···
−0.01	···	···	···	−0.13	···	−0.21	−0.20	···	···	···
···	···	···	···	···	···	−0.26	−0.23	0.21	···	···
···	1.08	···	0.32	···	···	0.15	···	0.11	−0.02	···
···	···	···	···	···	···	···	···	···	0.01	···
−0.01	···	···	···	0.11	···	···	···	···	0.01	···
−0.01	···	0.13	···	0.19	···	···	···	···	···	···
···	···	0.07	···	0.11	···	···	−0.07	···	···	···
···	0.11	···	···	···	0.04	···	···	0.05	···	···
−0.01	···	···	···	0.06	0.05	0.11	···	···	···	···
···	···	···	···	···	···	···	−0.02	···	···	0.01
···	···	0.08	···	···	···	···	···	···	···	−0.01
−0.01	0.27	−0.09	···	···	···	···	−0.08	···	···	···
−0.01	···	···	0.12	···	···	···	···	···	<0.01	···
−0.06	···	···	0.80	···	···	···	0.27	0.40	···	···
···	···	···	···	···	···	···	···	0.34	···	−0.08
···	···	···	···	···	···	0.15	···	···	···	···
···	···	···	0.14	···	···	···	···	···	···	0.04
···	0.56	···	···	···	0.19	···	···	···	···	0.08
···	···	−0.24	···	···	···	−0.32	−0.29	···	···	···
0.01	···	−0.29	···	···	···	−0.16	···	0.36	···	···
−0.01	−0.23	···	···	···	···	0.12	···	···	···	···
···	···	···	0.07	0.10	−0.06	···	···	0.10	−0.01	···
−0.01	···	···	···	0.06	···	···	···	−0.13	−0.01	···
···	···	···	−0.14	···	···	···	0.19	0.18	···	−0.07
···	···	···	···	···	0.10	···	···	···	···	···
···	···	···	···	···	−0.06	···	···	0.04	···	0.01
···	···	···	···	···	···	0.05	···	···	···	···
···	···	···	···	···	···	0.06	···	···	···	···

residual scores from population density models from survey area and C_t (Table 9). For the model of *P. moluccensis*, both residuals with sign retained (RES) and residuals transformed to absolute value (RESABS) were correlated significantly with C_t. However, as semi-partial r^2 was larger for RES than for RESABS, the density of *P. moluccensis* appeared to vary predictably, rather than unpredictably, with patch connectivity, i.e., residuals from population models tended to increase with increasing connectivity, indicating that the density of *P. moluccensis* was higher on well- connected patch reefs than on isolated patch reefs (relative to other habitat elements). The only other significant effect was found for the model of *C. schroederi* in which the absolute values of residuals decreased as patch size increased. Thus, overall variability in the density of *C. schroederi* (as reflected by the magnitude of error in model predictions) decreased as patch area increased.

Temporal variability in fish community structure

From February 1993 to March 1995, a total of 6 contiguous-reef sites and 16 patch-reef sites were surveyed for temporal variation in the structure of resident fish assemblages. Sites were divided into four habitat classes: contiguous-reef sites, large patch-reef sites (>20 m^2), medium patch-reef sites (10–20 m^2), and

small patch-reef sites (<10 m^2) (Table 10). For most sites, there was little change in the composition of the substratum over the survey period (Table 11). Only the contiguous sites located on the south side of Heron Reef were characterized by a significant change in substratum composition, with an increase in the proportion of branching coral and decreases in the proportions of nonbranching coral and sand.

In general, the MDS ordinations of repeat surveys of each site were characterized by low levels of Kruskal stress (for all but four sites, stress was <0.1; Figs. 6–9). At all sites, the structure of resident fish assemblages did not vary in a constant direction and thus, did not appear to be in a predictable state of community succession. For most sites, movement of the site through ordination space did not differ significantly from a random walk, although the observed distance from the initial survey to the final survey fell consistently towards the lower end of the respective null distributions. For four sites, including the three contiguous-reef sites on the south side of Heron Reef, the distance from the initial survey to the final survey was significantly less than that expected on the basis of random variation (SC1, SC2, SC3, and SP4; Figs. 6D–F and 9D).

To test whether the degree of community change

TABLE 7. Comparison of r^2 for stepwise regression models of fish population density based on observed data and randomized data. (A) models based on contiguous-reefs sites, (B) models based on patch-reef sites.

Species	r^2, observed data	r^2, randomized data Max.	Min.	Mean	1 SE	t
A) Contiguous-reef models						
P. moluccensis	0.900	0.404	0	0.142	0.016	6.565**
P. amboinensis	0.697	0.410	0	0.179	0.018	4.081**
P. wardi	0.514	0.485	0	0.193	0.021	2.173*
P. lepidogenys	0.369	0.424	0	0.151	0.019	1.631
C. rollandi	0.542	0.446	0	0.132	0.016	3.614**
T. lunare	0.102	0.481	0	0.150	0.017	−0.395
H. melanurus	0.524	0.545	0	0.127	0.019	2.957**
A. curacao	0.556	0.445	0	0.177	0.017	3.187**
L. unilineatus	0.660	0.591	0	0.138	0.021	3.426**
C. binotatus	0.481	0.482	0	0.151	0.018	2.511**
C. schroederi	0.696	0.555	0	0.138	0.018	4.288**
L. dimidiatus	0.216	0.554	0	0.177	0.019	0.284
L. australis	0.280	0.491	0	0.154	0.018	0.968
S. sordidus	0.568	0.573	0	0.146	0.020	2.927**
S. strigiventer	0.258	0.611	0	0.136	0.019	0.879
B) Patch-reef models						
P. moluccensis	0.528	0.429	0	0.157	0.019	2.763**
P. amboinensis	0.157	0.679	0	0.172	0.020	−0.104
P. wardi	0.095	0.527	0	0.122	0.017	−0.229
P. lepidogenys	0.210	0.416	0	0.143	0.016	0.527
C. rollandi	0.314	0.790	0	0.168	0.024	0.863
T. lunare	0.476	0.417	0	0.136	0.016	2.967**
H. melanurus	0.432	0.509	0	0.140	0.017	2.451**
A. curacao	0.323	0.739	0	0.190	0.023	0.797
L. unilineatus	0.509	0.622	0	0.153	0.022	2.265*
C. binotatus	0.466	0.393	0	0.130	0.015	3.623**
C. schroederi	0.487	0.451	0	0.157	0.017	2.646**
L. dimidiatus	0.110	0.602	0	0.161	0.021	−0.332
S. sordidus	0.091	0.425	0	0.135	0.015	−0.414
S. strigiventer	0.122	0.495	0	0.148	0.018	−0.203

Note: For models of randomized data; max. = maximum r^2, min. = minimum r^2, SE = standard error of mean r^2. Significance was evaluated by one-tailed t tests with 49 degrees of freedom.
* $P < 0.05$; ** $P < 0.01$.

during periods of peak recruitment (dashed lines in left columns of Figs. 6–9) differed from that during other times of the year (solid lines in left columns of Figs. 6–9), the mean similarity of fish communities surveyed before and after each recruitment period (November– February) and the mean similarity of fish communities surveyed before and after each nonrecruitment period (February–May, May–August, August–November) were calculated for each site. A one-way ANOVA indicated that the difference between mean similarity val-

TABLE 8. Comparison of habitat characteristics of contiguous-reef and patch-reef sites investigated in the examination of spatial variability in fish community structure (Study 1).

Habitat variable	Mean ± SE from contiguous-reef sites ($n = 36$)	Mean ± SE from patch-reef sites ($n = 39$)	t
Depth (m)	9.38 ± 0.45	9.55 ± 0.24	−0.34
Topographic complexity	0.16 ± 0.01	0.18 ± 0.01	−0.10
Encrusting coral (%)†	16.26 ± 1.54	17.61 ± 2.30	0.24
Digitate coral (%)†	6.71 ± 0.84	6.84 ± 0.85	0.35
Branching coral (%)†	11.31 ± 1.81	5.0 ± 1.54	3.55*
Dead coral rock (%)†	29.0 ± 2.61	36.6 ± 2.34	−2.29*
Rubble (%)†	15.23 ± 1.20	5.73 ± 0.92	6.45*
Sand (%)†	10.3 ± 1.58	8.01 ± 1.54	1.58
Small holes (no./m²)‡	9.08 ± 0.68	10.51 ± 1.36	−0.40
Medium holes (no./m²)	1.14 ± 0.09	1.85 ± 0.30	−2.21*
Large holes (no./m²)	0.14 ± 0.02	0.18 ± 0.03	−1.21

Note: Results are from t tests with 73 degrees of freedom; SE = standard error, n = number of sites.
* $P < 0.05$.
† Transformed to $\arcsin(\sqrt{X})$ for analysis.
‡ Transformed to $\log(X)$ for analysis.

TABLE 9. Standardized regression coefficients and semipartial r^2 for patch area and connectivity (independent variables) upon entry into hierarchical regression models predicting the magnitude of residuals from population density models. Dependent variables: (A) residuals with sign retained, (B) residuals transformed to absolute value. Significance was evaluated by F tests.

Species	Patch area† Standardized coefficient	Patch area† Semi-partial r^2	Connectivity (C_i)‡ Standardized coefficient	Connectivity (C_i)‡ Semi-partial r^2
A) Residuals (sign retained)				
P. moluccensis	0.087	0.008	0.568	0.215**
T. lunare	−0.178	0.032	−0.084	0.017
H. melanurus	0.051	0.003	−0.079	0.004
L. unilineatus	0.309	0.095	0.001	<0.001
C. binotatus	0.020	<0.001	0.292	0.058
C. schroederi	−0.047	0.002	−0.303	0.062
B) Residuals (absolute value)				
P. moluccensis	0.060	0.004	−0.488	0.159*
T. lunare	−0.158	0.025	−0.262	0.046
H. melanurus	−0.112	0.012	−0.277	0.052
L. unilineatus	0.191	0.036	0.047	0.002
C. binotatus	0.092	0.008	−0.053	0.002
C. schroederi	−0.371	0.138*	−0.183	0.016

* $P < 0.05$; ** $P < 0.01$.
† df = 1, 37.
‡ df = 1, 36.

ues for recruitment and nonrecruitment periods did not vary significantly among habitats ($F = 2.598$, df = 3, 18, $P = 0.084$). As this variation was not significant, data were pooled over all habitats. A paired t test on the pooled data indicated that the similarity of fish surveys conducted before and after recruitment was significantly lower than the similarity of fish surveys conducted before and after nonrecruitment periods ($t = 6.084$, df = 21, $P < 0.001$), i.e., community change was higher during periods of peak recruitment. Nevertheless, the overall difference in similarity was low (mean and standard error 0.033 ± 0.006), and at most sites, there was considerable variation in community structure during nonrecruitment periods (indicated by relative lengths of solid and dashed lines in Figs. 6–9). Exceptions to this general pattern were the three contiguous-reef sites located on the south side of Heron Reef (sites SC1, SC2, and SC3; Figs. 6D–F). Here, the structure of resident fish communities was characterized by a marked shift following recruitment in 1994 (survey 6), but in subsequent surveys, community structure at all three sites had returned to a configuration similar to that prior to recruitment.

For medium- and high-vagility species, variation in the population density of individual species generally reflected the predominantly random patterns of overall community variation evident in most of the ordination analyses. However, some of the more common site-attached species displayed consistent patterns of temporal variation in population density, which were not evident from analyses of overall community similarity.

Across most contiguous-reef sites, the population density of the four most common species of site-attached damselfish, *Pomacentrus moluccensis*, *P. amboinensis*, *Chrysiptera rollandi*, and *P. wardi*, increased markedly following the 1994 peak recruitment period (Fig. 10). For some species (e.g., *C. rollandi* and *P. wardi*), there was also a smaller increase in population density at some sites following recruitment in 1995 (Fig. 10C, D). In all cases, the elevation of population density following recruitment in 1994 was temporary and the densities of all species had returned to near prerecruitment levels within 3 mo (Fig. 10).

Postrecruitment increases in the population size of the four common species of damselfish also occurred on many patch-reef sites. Following peak recruitment in 1994, there were often sharp increases in population densities, which declined over the subsequent 12 mo (Figs. 11–13). In general however, patterns of variation in the density of patch-reef populations were not as clear as those for contiguous-reef populations, particularly for small patch reefs (Fig. 13). The only exception was *P. moluccensis*. At nearly all sites where the mean density of *P. moluccensis* was higher than two individuals per square meter, populations demonstrated clear increases in population density during the peak recruitment period in 1994 with a subsequent rapid decline to prerecruitment levels (Figs. 11–13). For oth-

TABLE 10. Survey area and connectivity of sites surveyed for temporal variation in fish community structure (Study 2).

Site	Area surveyed (m²)	Connectivity (C_i)	Location	Date of first survey
A) Contiguous-reef sites				
NC1	100	9.4†	Northern reef slope	Feb 1993
NC2	100	9.4†	Northern reef slope	Feb 1993
NC3	100	9.4†	Northern reef slope	Feb 1993
SC1	100	9.4†	Southern reef slope	May 1993
SC2	100	9.4†	Southern reef slope	May 1993
SC3	100	9.4†	Southern reef slope	May 1993
B) Large patch-reef sites (>20 m²)				
LP1	28	2.56	Northern reef slope	Feb 1993
LP2	48	3.57	Northern reef slope	Feb 1993
LP3	32	2.98	Northern reef slope	Feb 1993
LP4	23	2.34	Northern reef slope	Oct 1993
LP5	28	3.28	Northern reef slope	Oct 1993
LP6	22	2.70	Northern reef slope	Oct 1993
C) Medium patch-reef sites (10–20 m²)				
MP1	20	2.35	Northern reef slope	Feb 1993
MP2	12	2.43	Northern reef slope	Feb 1993
MP3	16	2.46	Northern reef slope	Feb 1993
MP4	14	2.01	Northern reef slope	Oct 1993
MP5	15	2.78	Northern reef slope	Oct 1993
D) Small patch-reef sites (<10 m²)				
SP1	6	1.93	Northern reef slope	Feb 1993
SP2	4	0.91	Northern reef slope	Feb 1993
SP3	9	2.07	Northern reef slope	Feb 1993
SP4	7	0.72	Northern reef slope	Oct 1993
SP5	9	1.28	Northern reef slope	Oct 1993

† Maximum connectivity score for entirely connected reef in all directions (see *Methods: Index of connectivity*).

TABLE 11. Paired t tests of substratum characteristics from sites examined in the assessment of temporal variability in community structure (Study 2). Percentage cover of substratum types was measured after the initial and final surveys of fish communities.

Habitat category	Initial survey Mean	Initial survey 1 SE	Mean difference (final − initial)	df	t
A) Northern contiguous-reef sites					
Branching coral	7.25	3.60	1.60	2	3.78
Nonbranching coral	26.55	5.53	0.56	2	0.28
Dead coral rock	35.53	1.20	−0.76	2	−0.66
Rubble	19.87	3.25	−1.15	2	−0.61
Sand	10.80	4.80	−0.25	2	−1.29
B) Southern contiguous-reef sites					
Branching coral	13.19	2.27	6.84	2	21.38**
Nonbranching coral	42.80	8.07	4.83	2	5.82*
Dead coral rock	20.77	2.92	−2.01	2	−0.79
Rubble	17.28	5.05	−6.71	2	−2.49
Sand	5.96	1.85	−2.89	2	−6.55*
C) Patch-reef sites surveyed from Feb 1993 to Feb 1995					
Branching coral	5.17	2.34	−0.02	8	−0.08
Nonbranching coral	49.15	2.64	−3.66	8	−1.31
Dead coral rock	34.74	3.47	3.98	8	1.46
Rubble	4.94	1.96	1.32	8	1.55
Sand	6.00	1.68	−1.67	8	−1.71
D) Patch-reef sites surveyed from Oct 1993 to Feb 1995					
Branching coral	1.23	0.64	0.52	6	0.52
Nonbranching coral	42.20	6.02	4.01	6	1.58
Dead coral rock	40.21	6.44	−3.25	6	−1.04
Rubble	7.77	1.57	−0.73	6	−0.52
Sand	8.59	2.58	−0.56	6	−0.41

$* P < 0.05;$ $** P < 0.01.$

er species, the incidence of recruitment-correlated pulses in abundance and the rate of decline of population density following recruitment were lower on patch-reef sites than on contiguous-reef sites (Figs. 11–13).

At some patch-reef sites, the population densities of some species appeared to be in a state of decline during 1993 (Figs. 11–13). This may reflect the gradual attrition of individuals following the period of peak recruitment immediately prior to the commencement of the study. In general, this pattern was less obvious on contiguous-reef sites (with the possible exception of $P.$ amboinensis on NC2 and NC3; see Fig. 10B).

We investigated the relationship between the overall temporal variability in fish community structure, and patch area and connectivity using linear regression. However, as the correlation between patch area and connectivity was extremely high ($r = 0.989$; Table 10), we were restricted to using a single independent variable in the regression models. Connectivity (C_i) was used in preference to patch area as the formula for C_i incorporates patch area.

For assemblages of site-attached and moderately vagile species (Table 3), the mean pairwise similarity of repeat surveys conducted from November 1993 to March 1995 was positively and significantly related to patch connectivity (Tables 12 and 13). Thus, as the connectivity (and area) of habitat patches tended to increase, overall temporal variability in the structure of resident fish communities tended to decrease (Tables

12 and 13). In contrast, there was no relationship between mean similarity and connectivity for assemblages of highly vagile species (Tables 12 and 13).

DISCUSSION

Many studies emphasize the spatially and temporally stochastic nature of fish communities inhabiting coral reefs (Sale and Dybdahl 1975, 1978, Williams 1980, Sale and Douglas 1984, Sale and Steel 1986, 1989, Doherty and Williams 1988, Sale et al. 1994). Comparatively few suggest that community structure is predictable, and most that do have been conducted at large scales (10^3–10^5 m), unsuitable for detecting spatial and temporal variation at a local scale on individual reefs (e.g., Anderson et al. 1981, Roberts et al. 1992). In our study, we examined fish assemblages on Heron and Wistari reefs at a local scale (10^0–10^2 m), and were able to model successfully much of the spatial and temporal variability in community structure using habitat characteristics as predictors. This raises the important question of whether our results for Heron and Wistari reefs, which demonstrate that for many species (particularly site-attached species), fish assemblages are more predictable on contiguous reef than on small isolated patch-reefs, might apply more universally.

Despite equivalent sampling techniques to those used in our study, earlier researchers have generally been unsuccessful in predicting large proportions of variability in the distribution and abundance of com-
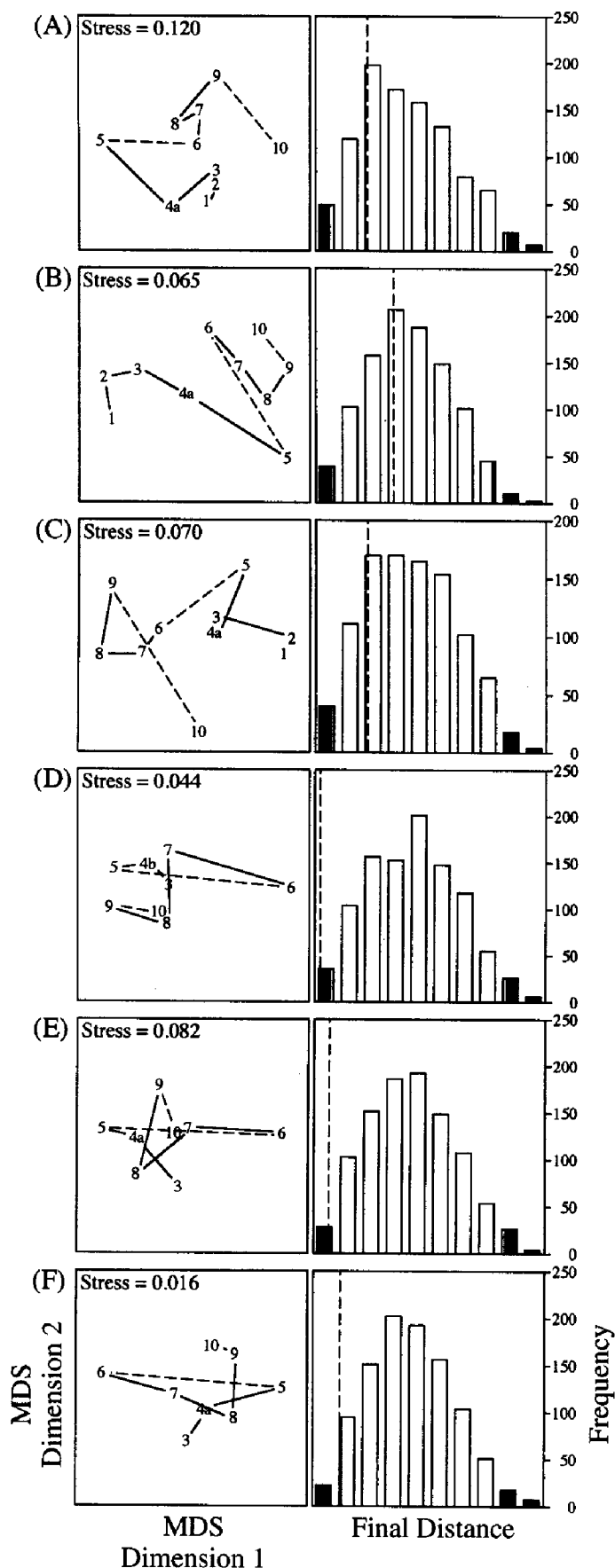
FIG. 6. Temporal variation in the structure of fish assemblages from contiguous-reef sites. Left-hand column: ordination by multidimensional scaling (numbers refer to sampling dates listed in Table 1; dashed lines indicate community change over peak recruitment periods between times 5–6 and 9–10). Right-hand column: difference in community structure as reflected by the observed distance from initial survey to final survey (dashed vertical line) compared to the null distribution of distances produced by 1000 random walks (see *Methods*). The test is significant if the observed distance falls within the shaded area indicating the significance region at α = 0.05. Sites are (A) NC1, (B) NC2, (C) NC3, (D) SC1, (E) SC2, and (F) SC3.

mon reef-fish species from habitat measurements (Thresher 1983b, Sale and Douglas 1984, Sale and Guy 1992). Much of this disparity in results may stem from differences in the experimental designs of our study and previous studies. First, we examined fish assemblages from both contiguous and patchy reef while many previous studies have been conducted entirely on small, isolated patch reefs (e.g., Sale and Dybdahl 1975, 1978, Sale and Douglas 1984, Clarke 1988). Second, our study was conducted entirely on the reef slope while most previous studies have been conducted in enclosed lagoons. Third, we examined fish species ranging widely in vagility whereas previous researchers have primarily examined site-attached or territorial species (Williams 1980, Doherty 1981, 1983, Doherty and Fowler 1994a, b).

Another important difference is that a number of workers have included schooling or cryptic species in their analyses while we did not (e.g., Talbot et al. 1978, Sale and Douglas 1984, Sale and Steel 1986, 1989, Sale et al. 1994). We excluded these species a priori from statistical analyses largely because they are difficult to survey accurately. In addition, patterns of movement and habitat utilization by schooling individuals are not independent; both are strongly influenced by the position of neighboring individuals (Partridge 1982). Large schools of fish are also less reliant on the reef substratum for protection from predators and territorial competitors than small groups of individuals (due to "safety in numbers," e.g., Pitcher 1973, Robertson et al. 1976), and seem to respond more readily to temporary environmental fluctuations, e.g., tidally induced currents carrying food particles (Hamner et al. 1988). Therefore, depending on schooling behavior, the inclusion of highly abundant schooling species in statistical analyses is unlikely to result in strong associations between fish abundance and the structure of the reef habitat. Moreover, the high abundance of schooling species may mask predictable patterns in the distribution and abundance of other nonschooling species.

In discussing our results, we highlight the differences between our study and those of previous workers, and suggest that the widely accepted notion that fish communities on coral reefs are stochastic in nature is largely the result of studies that have concentrated on the unique situation of site-attached species on small patch reefs.

Spatial variability in fish community and population structure

Our analysis of spatial variability using nonmetric multidimensional scaling and multiple regression sug-
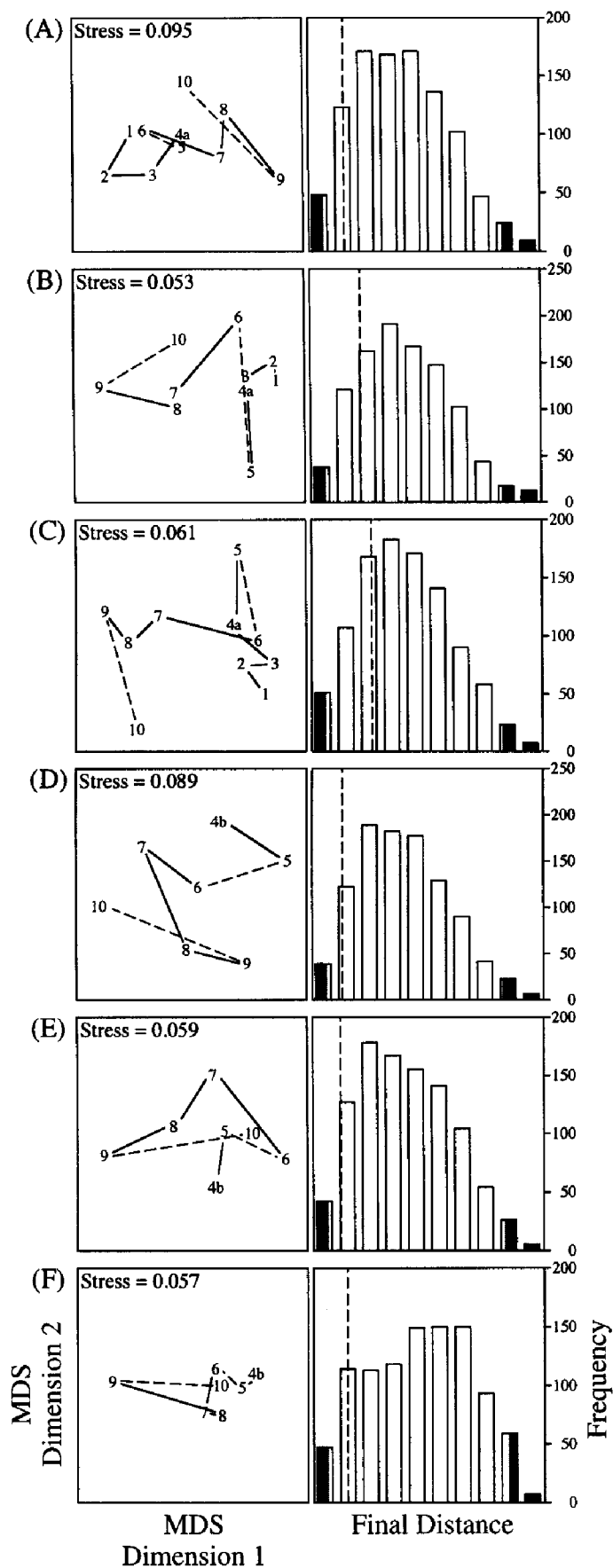
FIG. 7. Temporal variation in the structure of fish assemblages from large patch-reef sites. Left-hand column: ordination by multidimensional scaling (numbers refer to sampling dates listed in Table 1; dashed lines indicate community change over peak recruitment periods between times 5–6 and 9–10). Right-hand column: difference in community structure as reflected by the observed distance from initial survey to final survey (dashed vertical line) compared to the null distribution of distances produced by 1000 random walks (see

gests that on contiguous reef, the main axes of variation in the structure of fish communities are related to habitat composition. On contiguous reef, intrinsic habitat characteristics, such as substratum composition, depth, and topographic complexity, were strongly correlated with both MDS axes of community change (r^2 = 0.82 and 0.76). Thus, the organization of fish communities on contiguous reef appears nonrandom and varies predictably with habitat. In contrast, the main axes of community change on patchy coral reef were largely unrelated to intrinsic habitat properties. The only significant correlation was between community structure along the first ordination axis (MDS 1) and patch connectivity (r^2 0.58), suggesting that the structure of fish communities on isolated patches tends to differ from that on well-connected patches. Overall, the structure of resident fish assemblages on patch reefs was notably less predictable than those on contiguous reef.

Analysis of the distribution and abundance of individual species indicated that for many species, spatial variation in population density was related to spatial variation in habitat structure. While r^2 values varied widely among species and habitats (contiguous vs. patchy reef), some models were highly successful, e.g., r^2 of 0.9 for *Pomacentrus moluccensis* on contiguous reef. For models of population density based on contiguous-reef sites, statistical significance was unrelated to species' vagility. Models of 10 species (including four site-attached species, four species characterized by low-medium vagility, and two highly vagile species) explained significantly more variability than models based on randomized data. In contrast, of the six significant models of patch reef populations, five were based on species exhibiting medium or high vagility. Furthermore, while models of patch-reef populations were generally characterized by a reduction in r^2 relative to corresponding models of contiguous-reef populations, the reduction was substantially less for vagile species than for site-attached species. Clearly, vagility facilitates predictability in the spatial structure of fish populations in patch-reef habitats, and high reef connectivity enhances predictability in the spatial structure of populations of site-attached species.

Temporal variability in fish community structure

Ordination of temporal variability in fish community structure suggested that none of the fish assemblages on contiguous- or patch-reef sites was in a consistent state of community succession. For most sites, movement of the site through ordination space did not differ significantly from a random walk, suggesting that temporal change in community structure was unpredictable

←

Methods). The test is significant if the observed distance falls within the shaded area indicating the significance region at α = 0.05. Sites are (A) LP1, (B) LP2, (C) LP3, (D) LP4, (E) LP5, and (F) LP6.
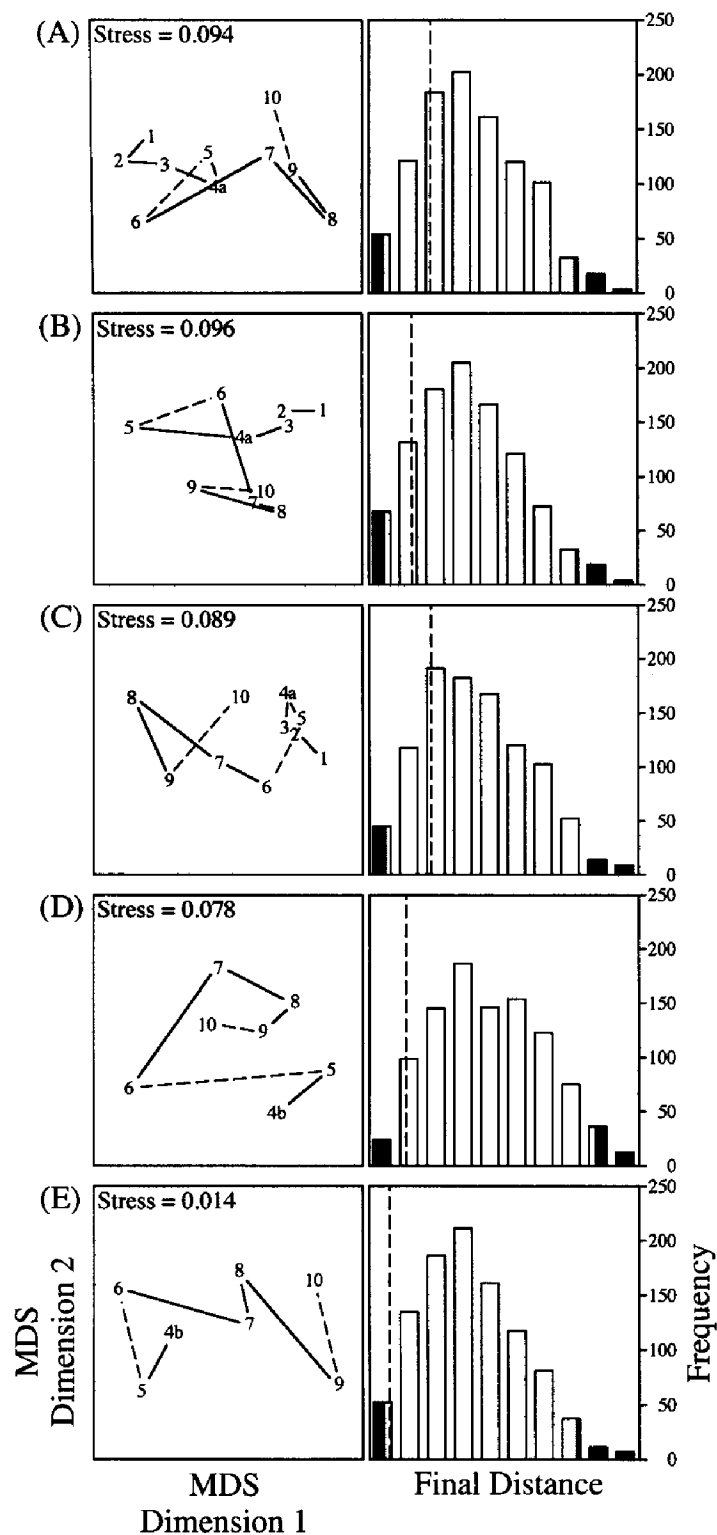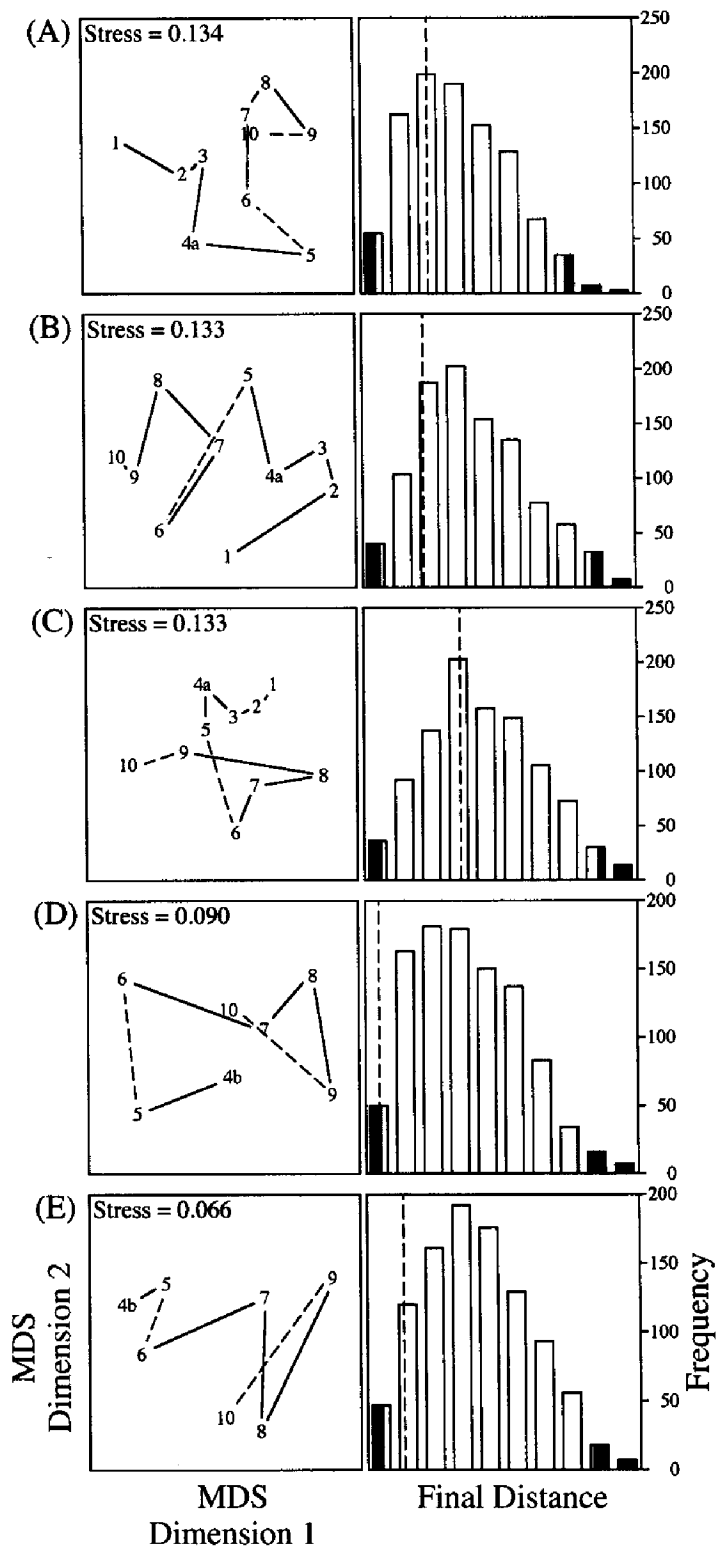
Fig. 8. Temporal variation in the structure of fish assemblages from medium patch-reef sites. Left-hand column: ordination by multidimensional scaling (numbers refer to sampling dates listed in Table 1; dashed lines indicate community change over peak recruitment periods between times 5–6 and 9–10). Right-hand column: difference in community structure as reflected by the observed distance from initial survey to final survey (dashed vertical line) compared to the null distribution of distances produced by 1000 random walks (see *Methods*). The test is significant if the observed distance falls within the shaded area indicating the significance region at α = 0.05. Sites are (A) MP1, (B) MP2, (C) MP3, (D) MP4, and (E) MP5.

Fig. 9. Temporal variation in the structure of fish assemblages from small patch-reef sites. Left-hand column: ordination by multidimensional scaling (numbers refer to sampling dates listed in Table 1; dashed lines indicate community change over peak recruitment periods between times 5–6 and 9–10). Right-hand column: difference in community structure as reflected by the observed distance from initial survey to final survey (dashed vertical line) compared to the null distribution of distances produced by 1000 random walks (see *Methods*). The test is significant if the observed distance falls within the shaded area indicating the significance region at α = 0.05. Sites are (A) SP1, (B) SP2, (C) SP3, (D) SP4, and (E) SP5.
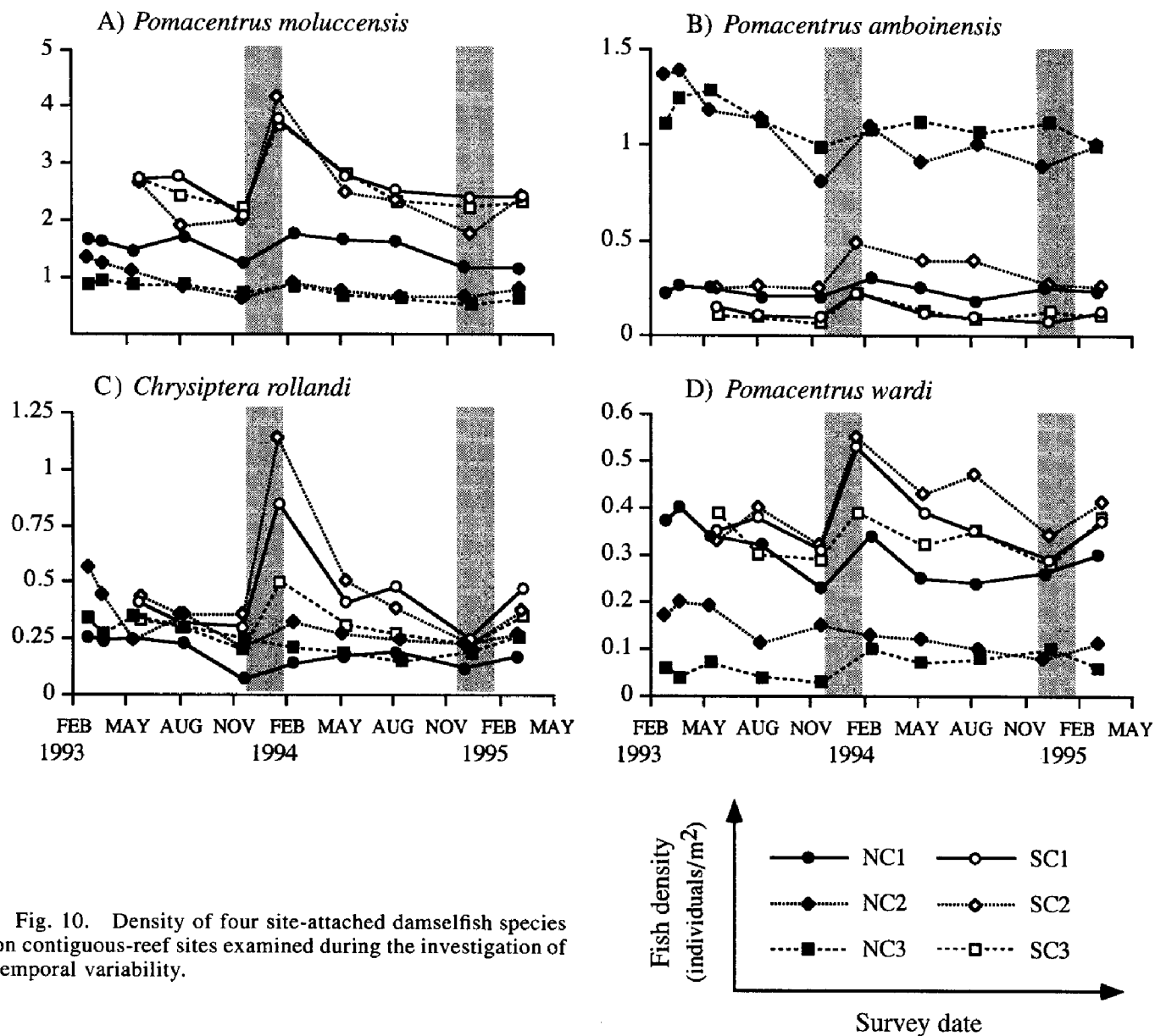
Fig. 10. Density of four site-attached damselfish species on contiguous-reef sites examined during the investigation of temporal variability.

in direction over the duration of the study. However, for four sites, the magnitude of temporal change in structure of resident fish communities was significantly less than expected on the basis of random fluctuation. For these sites, there appeared to be an "attractor" in community space, possibly reflecting a stable "equilibrium" state for the structure of resident fish communities. Three of these sites were located on the south side of Heron Reef, where the contiguous-reef slope is composed primarily of live coral (up to 90% cover) well protected from recent cyclones. Fish population density is also considerably higher on the south side of Heron Reef than on the north side. In this undisturbed habitat, the structure of resident fish communities displayed strong resilient stability (sensu Johnson and Mann 1988) following the effect of a strong recruitment pulse in early 1994. At all three sites, the marked shift in community structure coinciding with recruitment in 1994 was swiftly compensated for by an opposing shift evident in subsequent surveys.

Across all sites, temporal variation in the structure

of fish communities was significantly higher during periods of peak larval recruitment (November–February) than at other times of the year. However, the overall difference was small, and with the exception of the three contiguous-reef sites on the south side of Heron Reef, there was little evidence from the ordination analyses to suggest that recruitment was the sole process underlying temporal variation in fish community structure. At most sites, there was considerable variation in community structure during nonrecruitment periods.

Analysis of the mean similarity of repeat surveys among sites and species groups indicated that the degree of temporal variability in fish assemblage structure was related to species' vagility, patch size, and connectivity. Due to the high correlation between patch size and connectivity it was not possible to analyze separately the effects of each variable on community variation, so for the purposes of the discussion they can be considered in accordance. For site-attached and moderately vagile species, temporal variability in assemblage structure increased significantly
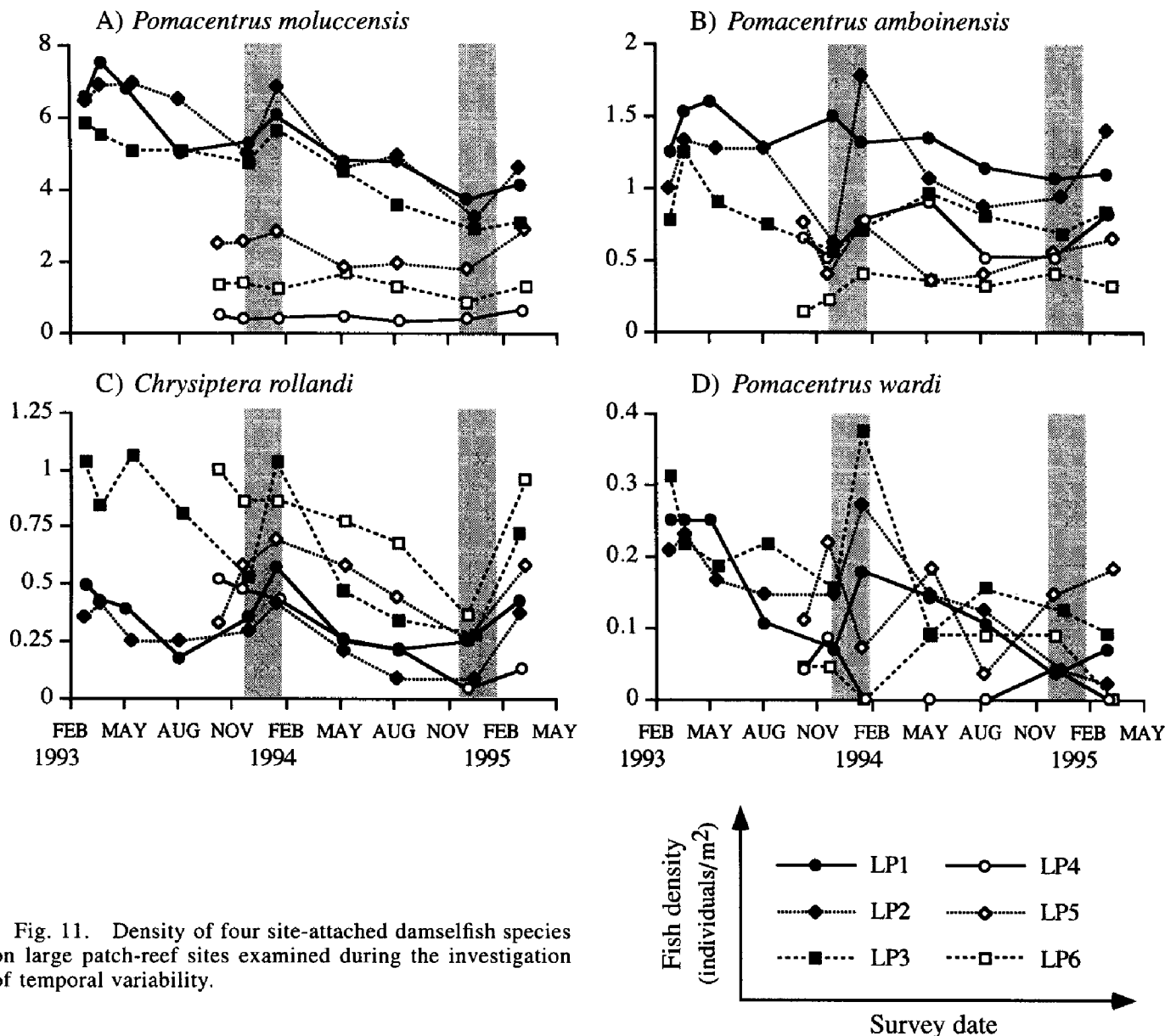
Fig. 11. Density of four site-attached damselfish species on large patch-reef sites examined during the investigation of temporal variability.

as sites became smaller and more isolated. In contrast, temporal variability in assemblages of highly vagile species was unrelated to patch size or connectivity. These results are consistent with the patterns revealed in the analysis of spatial variability. Overall, the analyses indicate that for site-attached species, spatial and temporal variability in community structure decreases significantly with increasing connectivity. However, as species' vagility increases, the relationship between variability in community structure and reef connectivity declines.

Importance of species' vagility and reef connectivity

The apparent importance of species' vagility suggests that migration is an important process affecting the structure of coral reef fish assemblages at local scales. This was also suggested by Robertson (1988a, b), who demonstrated that postsettlement migration of vagile surgeonfishes can dramatically alter the size and composition of fish populations inhabiting patch reefs (Robertson 1988a). Furthermore, he found that post-

settlement migration and mortality were more important than settlement events in determining population structure.

A possible consequence of high vagility is that individuals are better able to move among isolated patches in response to the availability of resources or to satisfy habitat preferences. Our results suggest that the relative importance of settlement and postsettlement processes in structuring fish assemblages may depend largely on the interaction between species' vagility and connectivity among sites. Where coral reef is fragmented into patches, resident fish assemblages assume a metapopulation structure and the degree to which patch reef populations are interconnected depends primarily on the vagility of the species and the proximity of neighboring patch reefs. In contrast, connectivity is maximized and postsettlement relocation is enhanced on contiguous reef since individuals do not have to traverse large stretches of open sand where shelter availability is low and the risk of predation is high (Sale and Guy 1992). Our data suggest that on contig-
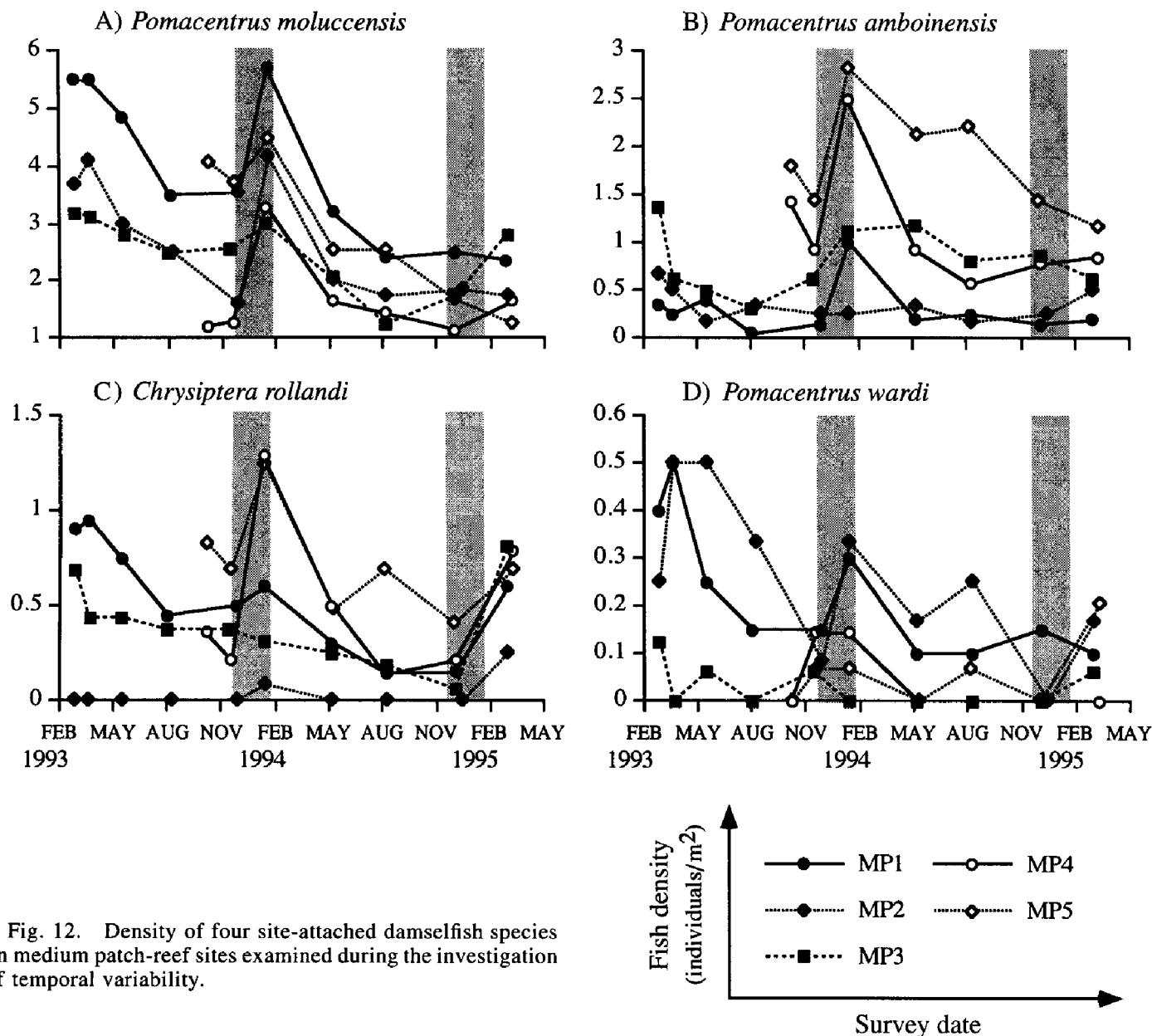
Fig. 12. Density of four site-attached damselfish species on medium patch-reef sites examined during the investigation of temporal variability.

uous reef, even relatively sedentary species are able to migrate to favorable areas with respect to habitat characteristics and/or population density, leading to a more predictable community structure. In contrast, on isolated patches, the density of site-attached species is largely unmodified by postsettlement migration, and distribution and abundance may be determined almost entirely by variability in recruitment (Doherty and Fowler 1994a, b). Thus, on patch reefs, community structure tends to fluctuate in both space and time according to variation in larval settlement.

*Role of recruitment in structuring coral-reef
fish communities*

In the analysis of temporal variability in fish community structure, community variation was significantly higher during periods of peak recruitment than during nonrecruitment periods. Nevertheless, the difference was small, and there was little indication that overall community change was driven solely by recruitment events. At the three contiguous-reef sites on

south Heron Reef (SC1, SC2, and SC3), a clear recruitment signal was evident in surveys conducted in February 1994, but subsequent surveys did not reveal a persistent shift in assemblage structure (Fig. 6D–F).

Similar patterns were apparent in the population densities of four common site-attached damselfish species (*Pomacentrus moluccensis, P. amboinensis, Chrysiptera rollandi, P. wardi*). Populations of all four species at many sites experienced peaks in abundance that coincided with periods of peak recruitment. These peaks were clearest for populations on contiguous-reef sites, but were also evident on several patch-reef sites. On contiguous-reef sites and those patch reefs where recruitment peaks were observed, the increases in population density in 1994 were temporary and the densities of all species returned to near prerecruitment levels within three months. Possible mechanisms for the postrecruitment declines in population density include mortality through competition or predation (density-dependent or density-independent), or migration to new areas following settlement.
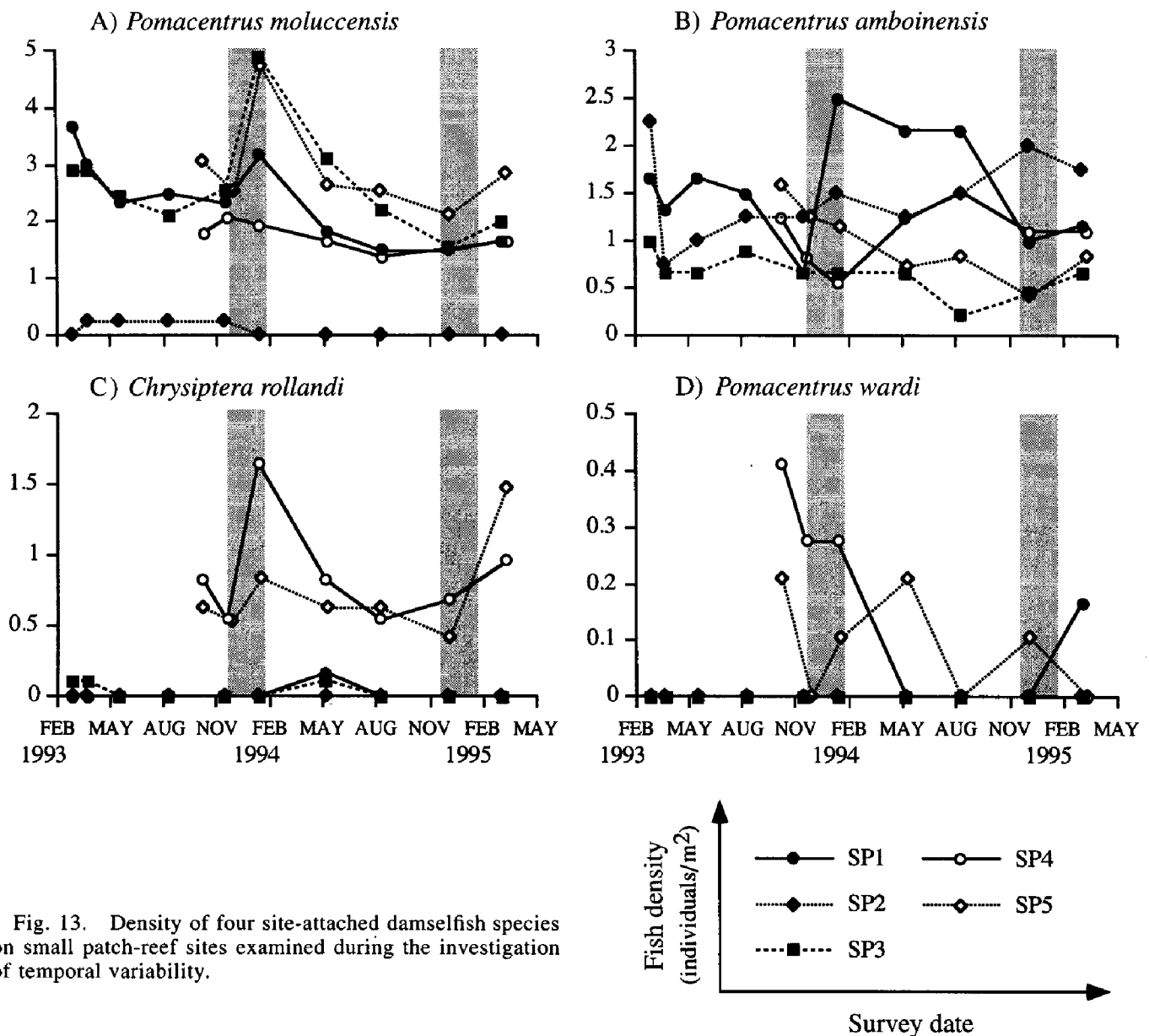
Fig. 13. Density of four site-attached damselfish species on small patch-reef sites examined during the investigation of temporal variability.

Recent manipulative studies suggest that both competition and predation may be important in modifying patterns of abundance established at recruitment. Predator removal experiments have indicated that the distribution and abundance of predators may have substantial effects on the density and size structure of local prey populations (Carr and Hixon 1995). Moreover, studies on Caribbean reefs have shown that density-dependent rates of survival and recruitment control population size in a species of goby (Forrester 1995), while interspecific competition among species of damselfish strongly influences patterns of habitat use and local abundance (Robertson 1996). Other studies have indicated that intraspecific competition may lead to density-dependent rates of growth (e.g., Doherty 1982, 1983, Jones 1987a, 1988, 1990, Forrester 1990).

We suggest that for many species, one of the first responses to pressure from competition (either from passive resource limitation or active resource exclusion) or predation may be migration to more favorable areas with a lower density of competitors or predators,

or a higher availability of resources (e.g., shelter). In freshwater fish, habitat use by prey species can be described by a "cost–benefit" analysis, which assesses the relative advantage of avoiding competition by utilizing more open habitats with higher food availability vs. the risk of increasing mortality by increasing exposure to predators (Werner et al. 1983, Power 1984). Similar mechanisms may affect habitat utilization by coral reef fish. For site-attached species on isolated patch reefs, the risk of migration over open sand may outweigh the potential benefits of a higher growth rate or enhanced survival in a more favorable habitat. In contrast, on contiguous reef, site-attached species may readily migrate to new areas with relatively low risk of predation.

For *P. moluccensis*, recruitment-correlated increases in population size and subsequent declines were evident at all sites on both contiguous and patch reefs with a background population density of >2 individuals/m². Similarly, in Study 1, we found *P. moluccensis* to be the only site-attached species for which the model of

TABLE 12. Summary of mean pairwise similarity (Bray-Curtis) for repeat fish surveys conducted at each site between November 1993 and February/March 1995.

Site	Mean and standard error of pairwise similarity		
	Site-attached	Medium vagility	High vagility
A) Contiguous-reef sites			
NC1	0.88 ± 0.01	0.78 ± 0.02	0.66 ± 0.02
NC2	0.89 ± 0.01	0.67 ± 0.02	0.70 ± 0.02
NC3	0.87 ± 0.01	0.63 ± 0.02	0.67 ± 0.02
SC1	0.87 ± 0.02	0.79 ± 0.01	0.64 ± 0.02
SC2	0.86 ± 0.02	0.70 ± 0.02	0.67 ± 0.02
SC3	0.87 ± 0.01	0.81 ± 0.01	0.68 ± 0.02
B) Large patch-reef sites (>20 m²)			
LP1	0.88 ± 0.01	0.67 ± 0.02	0.62 ± 0.02
LP2	0.84 ± 0.01	0.71 ± 0.01	0.69 ± 0.02
LP3	0.85 ± 0.01	0.64 ± 0.03	0.67 ± 0.02
LP4	0.75 ± 0.02	0.41 ± 0.03	0.64 ± 0.04
LP5	0.83 ± 0.01	0.45 ± 0.04	0.72 ± 0.02
LP6	0.81 ± 0.03	0.50 ± 0.03	0.68 ± 0.02
C) Medium patch-reef sites (10–20 m²)			
MP1	0.79 ± 0.02	0.50 ± 0.03	0.62 ± 0.02
MP2	0.76 ± 0.02	0.34 ± 0.05	0.62 ± 0.04
MP3	0.79 ± 0.01	0.46 ± 0.02	0.67 ± 0.02
MP4	0.76 ± 0.03	0.54 ± 0.03	0.59 ± 0.03
MP5	0.80 ± 0.02	0.56 ± 0.03	0.65 ± 0.02
D) Small patch-reef sites (<10 m²)			
SP1	0.82 ± 0.01	0.50 ± 0.04	0.67 ± 0.04
SP2	0.69 ± 0.03	0.15 ± 0.04	0.57 ± 0.04
SP3	0.81 ± 0.02	0.42 ± 0.04	0.49 ± 0.04
SP4	0.82 ± 0.02	0.44 ± 0.04	0.67 ± 0.04
SP5	0.81 ± 0.02	0.43 ± 0.04	0.69 ± 0.02

TABLE 13. Regression coefficients and r^2 for multiple regression models predicting mean pairwise similarity of repeat surveys (November 1993–February/March 1995) from site connectivity (C_i) (see Table 10).

Species group	Coefficient	r^2
Site-attached	0.011	0.510†
Medium vagility	0.038	0.587†
High vagility	0.005	0.114

† $P < 0.0001$.

in the population density of P. moluccensis on contiguous-reef and patch-reef sites respectively, with no information on previous recruitment levels.

There are a number of possible explanations for the apparent disparity between our results and those of Doherty and Fowler (1994a, b). First, it is possible that spatial variation in the intensity of recruitment and the density of adult populations among the lagoonal patch reefs examined by Doherty and Fowler (1994a, b) may have been similarly explained by variation in habitat structure, i.e., the patch reefs in lagoons characterized by high levels of recruitment and high adult population densities may have offered more favorable habitat to those in lagoons characterized by low recruitment and low adult numbers. Unfortunately, Doherty and Fowler (1994a, b) did not present comparative data on the structure of the patch-reef habitats in each of the lagoons examined.

Second, differences between the two studies may reflect differences in the spatial scale at which data were collected. Doherty and Fowler (1994a, b) investigated the relationship between recruitment and population density at the among-habitat scale (among lagoons) by averaging the results for replicate patch reefs within the lagoon of each reef. In contrast, we examined relationships between the distribution and abundance of fish species and habitat structure at the within-habitat scale (reef slope) by examining replicate sites individually. Thus, it is possible that relationships between habitat and fish community structure are only manifest at the within-reef scale while variation in recruitment among reefs sets background levels of population density. However, recruitment also varies considerably, both spatially and temporally, within reefs (see Doherty and Williams 1988), and despite the wide geographical separation of the sites examined in our study (across two coral reefs), we identified strong relationships between the densities of a number of fish species and habitat structure.

Finally, the apparent importance of recruitment and habitat structure in determining adult abundance may depend on the habitat zone in which the study was conducted. Our study was conducted entirely on the reef slope, which may receive higher levels of recruitment than the lagoonal patch reefs examined by Doherty and Fowler (1994a, b). In general, lagoonal systems are characterized by reduced water flow, and depending on the height and extent of the reef crest, some

spatial variation in population density on patch-reef sites was significant. P. moluccensis is the most abundant species of those we examined and recruits in high numbers to the reef slope. Thus, on isolated patch reefs on the reef front, postsettlement modification of population size in P. moluccensis may occur in the absence of migration because high densities of resident adult fish and high rates of recruitment may result in increased losses from competition and/or predation. Alternatively, individuals of P. moluccensis may migrate relatively large distances to neighboring patches because the detrimental effects of competition (due to high population densities) exceed the risk of exposure to predation. Preliminary evidence for early postsettlement migration by site-attached damselfish species has been collected by H. Sweatman for the Great Barrier Reef (H. Sweatman, personal communication).

Our results contrast with those of Doherty and Fowler (1994a, b), who found recruitment to limit the population densities of two site-attached damselfish (Pomacentrus moluccensis and P. wardi) on patch reefs within the lagoons of seven coral reefs, including Heron and Wistari reefs, on the southern Great Barrier Reef. They found that for P. moluccensis, mean levels of recruitment to each lagoon (averaged over 9 yr) explained 84% of variation in mean population density among lagoons. In contrast, at Heron and Wistari reefs, we were able to explain 90 and 53% of spatial variation

systems may be entirely isolated from oceanic currents at low tide (e.g., Heron Reef, Wistari Reef, and One Tree Reef on the Great Barrier Reef). This isolation may affect recruitment to lagoonal systems as the reef crest may act as a periodic barrier to larval movement (Sweatman 1985). In addition, the density of fish larvae in water entering lagoon systems over the reef crest and flat may decrease progressively as larvae encounter suitable substratum and begin to settle (Milicich and Doherty 1994). These factors may result in lower larval supply to lagoonal waters relative to the outer reef slope (Leis 1981). Fowler et al. (1992) found that for a species of butterflyfish at One Tree Reef, average recruitment over three years to a region of the leeward reef slope was higher than recruitment to various parts of the lagoon. Thus, much of the divergence between the results of our study and those of Doherty and Fowler (1994a) may stem from differences between a low-recruitment system (Doherty and Fowler 1994a) and a high-recruitment system (our study).

Alternative explanations for observed patterns

Overall, the results of our study suggest that for many fish species, there are significant relationships between population density and habitat structure, and the magnitude of these relationships is largely dependent on patterns of postsettlement migration. Nevertheless, there are several alternative perspectives on our results that must be addressed.

Studies of distribution and abundance have revealed that the recruits of many species of benthic coral reef fish display clear patterns of nonrandom habitat use (Sale et al. 1984a, Wellington 1992, Tolimieri 1995). It might be argued that the results of our investigation into spatial variability merely quantify these patterns. However, active habitat selection will not necessarily result in a linear relationship between fish abundance and resource availability. If local abundance is dependent entirely on recruitment to patches of suitable habitat, then the overall population density in a given area will be proportional to both habitat availability and larval supply. Thus, strong relationships between the distribution and abundance of fish species and habitat structure will only be evident if recruitment is uniform over the spatial scale at which these relationships are examined. In contrast, a number of studies have demonstrated variable recruitment over a range of spatial scales (10^1–10^5 m; Williams and Sale 1981, Doherty 1987, Fowler et al. 1992; reviewed by Doherty and Williams 1988).

Another possibility is that the structure of fish assemblages on contiguous reef is more predictable than that on patch reefs because recruitment itself is less spatially variable on large, connected areas of reef. Despite the numerous studies examining recruitment to patch reefs, very few have examined recruitment to contiguous reef. In addition, remarkably little is known about the processes through which pelagic larvae settle

and recruit to the demersal adult population (Sale 1990). A number of studies have demonstrated that some species are highly selective of microhabitat during settlement (Sale et al. 1984a, Shulman 1984, Tolimieri 1995). Booth (1992) suggests that visual cues may supplement chemical cues in facilitating habitat selection by settling larvae. If the magnitude of both visual and olfactory signals are related to the size and connectivity of habitat patches (e.g., large patches are more likely to be seen by drifting larvae), the intensity of recruitment may also vary with patch size and connectivity. This may explain why densities of *P. moluccensis* are significantly higher on well-connected patch reefs than isolated patch reefs.

It could also be argued that the decreased success of models based on patch-reef sites relative to models based on contiguous-reef sites was due to variation in sampling scale. Sale (1980) suggested that the deterministic view of coral reef fish communities emanating from large-scale studies (e.g., Gladfelter and Gladfelter 1978, Gladfelter et al. 1980, Anderson et al. 1981) may be a consequence of the central limit theorem, i.e., small-scale variability in spatial distribution and abundance may be smoothed out as spatial scale increases. However, if a reduction in sampling scale results in increased variation, we would expect the success of models predicting population density (as indicated by residual magnitude) to vary with patch size. With the exception of one species, *Coris schroederi*, the magnitude of error in models of fish density was unrelated to patch area.

Reduction in the scale of surveying may explain the significant negative relationship between temporal variability in the structure of assemblages of site-attached and medium-vagility species and patch area. For example, sampling at large spatial scales may be less precise than sampling at small spatial scales, leading to less evidence of temporal change. Nevertheless, an increase in the temporal variability of fish assemblages inhabiting small, isolated habitat patches relative to that of fish assemblages inhabiting large, well-connected habitat patches is also expected on the basis of metapopulation processes. Population fluctuation and local extinction as a result of stochastic demographic processes or catastrophic disturbances are more likely for small populations on small habitat patches than for large (MacArthur and Wilson 1967, Simberloff 1976, Harrison 1991). For these populations, persistence is highly dependent on interpatch migration to balance mortality (Harrison 1991). This may explain why an increase in reef connectivity significantly reduced temporal variability in assemblages of site-attached and moderately vagile species, and why temporal variability in assemblages of highly vagile species was unaffected by reef connectivity.

Conclusions

Our quantitative investigation of spatial and temporal variation in the distribution of coral reef fishes

sets the framework for appropriate questions to be addressed through manipulative experimentation. In the past, most manipulative experimentation on coral reef fishes has focused on identifying density-dependent or recruitment-dependent processes on isolated, lagoonal patch reefs. These experiments have generally ignored the effects of species' vagility, patch size, and connectivity. Therefore, we suggest that the appropriate question for the future is to compare the *relative* importance of recruitment and postrecruitment processes in structuring coral reef assemblages on patches of habitat varying in size, connectivity, and location (e.g., reef slope vs. lagoonal habitats). Manipulative experiments designed to identify intra- and interspecific interactions (such as those conducted by Sweatman 1983, 1985, Jones 1987a, b, 1988, 1990, Forrester 1995, Robertson 1996) must now be repeated on larger, well-connected habitat patches, which receive high rates of natural larval recruitment. These studies must now focus on migration as a potential structuring process rather than merely a confounding effect for the identification of other demographic processes.

The results of our study suggest that the importance of postrecruitment processes in modifying patterns of distribution and abundance established at recruitment increases as patch size and connectivity of the reef habitat increase. Most of the fish on coral reefs, commercial species in particular, inhabit large sections of contiguous reef, which comprise the majority of hard substratum on most reef systems. Despite this, most of the previous studies of coral reef fish community structure have focused on site-attached fish species inhabiting isolated patch reefs in coral reef lagoons. While it has been amply demonstrated that structure of fish assemblages on small, isolated patch reefs varies spatially and temporally with variation in recruitment (e.g., Doherty and Fowler 1994a, b), our work shows clearly that this result cannot necessarily be extrapolated to fish communities inhabiting large sections of contiguous reef.

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