Contribution to the Theme Section 'Seascape ecology'

Patterns of scale-dependency and the influence of map resolution on the seascape ecology of reef fish

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ABSTRACT: Detection and perception of ecological relationships between biota and their surrounding habitats is sensitive to analysis scale and resolution of habitat data. We measured strength of univariate linear correlations between reef fish and seascape variables at multiple spatial scales (25 to 800 m). Correlation strength was used to identify the scale that best associates fish to their surrounding habitat. To evaluate the influence of map resolution, seascape variables were calculated based on 4 separate benthic maps produced using 2 levels of spatial and thematic resolution, respectively. Individual seascape variables explained only 25% of the variability in fish distributions. Length of reef edge was correlated with more aspects of the fish assemblage than other features. Area of seagrass and bare sand correlated with distribution of many fish, not just obligate users. No fish variables correlated with habitat diversity. Individual fish species achieved a wider range of correlations than mobility guilds or the entire fish assemblage. Scales of peak correlation were the same for juveniles and adults in a majority of comparisons. Highly mobile species exhibited broader scales of peak correlation than either resident or moderately mobile fish. Use of different input maps changed perception of the strength and even the scale of peak correlations for many comparisons involving hard bottom edge length and area of sand, whereas results were consistent regardless of map type for comparisons involving area of seagrass and habitat diversity.

KEY WORDS: Landscape ecology · Scale · Coral reef · Home range · Habitat

INTRODUCTION

Recent studies have shown that the distribution and abundance of reef fish can be influenced by seascape factors such as the areas of adjacent seagrass, soft bottom, and hard bottom in the vicinity (Kendall et al. 2004a, Kendall 2005, Dorenbosch et al. 2006, Grober-Dunsmore et al. 2007, Pittman et al. 2007, Tuya et al. 2010). Many of these studies relied on particular benthic maps as a source of independent variables with which to establish relationships between fish and their surrounding habitat. Benthic maps are, however, abstract representations of actual seafloor features and have particular spatial and thematic characteristics that are profoundly affected by the processes and

source data used to produce them (Turner et al. 1989, Benson & MacKenzie 1995, Saura 2002, Andréfouët et al. 2003, Kendall & Miller 2008, Prada et al. 2008). Spatial characteristics include the number of patches, their size, shape, and edge length. Thematic characteristics include the number and types of categories used to describe seafloor features. For coral reef ecosystems, Andréfouët et al. (2003) found that map-based measurements of coral atolls differed by as much as 28% depending on the spatial resolution of satellite data. Kendall & Miller (2008) found that increasing thematic resolution greatly increased the number, diversity, and total edge length of map polygons, whereas changing the spatial resolution resulted in disproportionate changes in the area, perimeter, and other values

among feature types. Given the influence of spatial and thematic resolution on the quantification of seascapes, we hypothesized that map differences could influence the sensitivity of seascape ecological studies as well.

Map resolution may affect the detection and measurement of seascape influences on fish distribution in several ways. The amount of mapped habitat deemed essential to a particular species can be altered. Small or rare patches of habitat can be subsumed into larger features as map resolution is coarsened. Many species use edges or ecotones between habitat patches (Shulman 1985, Sweatman & Robertson 1994, Dorenbosch et al. 2005, Pittman et al. 2007, Valentine et al. 2007, Vanderklift et al. 2007), and such boundaries can be greatly simplified or even removed depending on map characteristics (Kendall & Miller 2008).

Seascape composition can affect fish ecology at several levels of biological organization. At the broadest level, species diversity, richness, and total abundance of fish have been partly explained by seascape variables (Kendall 2005, Grober-Dunsmore et al. 2007, Pittman et al. 2007). At lower levels of organization defined according to trophic roles or mobility and therefore with similar habitat or space requirements, fish guilds may have greater correlation with seascape elements when considered separately from the rest of the fish assemblage (Grober-Dunsmore et al. 2007). Individual species would be expected to have even higher correlation with seascape features without the added variability from multiple species of a guild that utilize slightly different niches or habitats. Highest fish–seascape correlations are expected for individual life stages of species considered separately. All such fish utilize the same discrete spatial scale and habitat types (Kendall et al. 2003, Grober-Dunsmore et al. 2007), and correlations would not be reduced by the added variability associated with the different scales of seascape utilization and habitat preferences among life stages.

The strength of fish–seascape correlations are likely scale-dependent and based on fish size, mobility, taxonomy, life stage, and habitat requirements (Kramer & Chapman 1999, Pittman et al. 2004, Kendall 2005, Grober-Dunsmore et al. 2007). Body size in some reef fish has been positively correlated to home range size (Kramer & Chapman 1999, Overholtzer & Motta 1999). Similarly, juveniles of a given species, by virtue of their relatively smaller size, are expected to interact with adjacent seascape features at shorter distances than adults (Kendall et al. 2003, Grober-Dunsmore et al. 2007). The abundance of those species that utilize a single rock, coral head, or burrow for most of their life history, termed resident species, would be expected to exhibit correlations only with habitat measures for their immediate vicinity. A good example are fish in

the genus *Stegastes*, which defend territories of 1 to 5 m^2 for food and breeding purposes (Itzkowitz 1977, Luckhurst & Luckhurst 1978). Those species that range more widely across larger or multiple habitat patches, termed mobile species, would not be expected to be correlated with just the habitats in the immediate vicinity of a focal patch and instead would have correlations with seascape features at distances of 10s to 100s of meters away. Examples include haemulids (Tulevech & Recksiek 1994, Burke 1995), acanthurids (Morgan & Kramer 2004), and scarids (Chapman & Kramer 2000, Mumby & Wabnitz 2002). Finally, those species that range widely across the seascape, termed transient species, would likely have correlations with seascape features at even greater distances. Such species include many fish in the families Carangidae and Lutjanidae (Chapman & Kramer 2000).

The scale of fish–seascape interactions can be identified by evaluating a local fish assemblage in relation to the surrounding mosaic of habitat patches (Irlandi & Crawford 1997, Pittman et al. 2004, Kendall 2005, Grober-Dunsmore et al. 2007, Vanderklift et al. 2007). The spatial extent of elements to include in such analysis is critical, and analyses should seek to systematically vary the spatial scale and distances over which fish and seascape associations are measured (Addicott et al. 1987, Wiens 1989, Riitters et al. 1997, Sale 1998, Kendall 2005). If the spatial extent used is too small, only weak fish–seascape correlations will be found, because seascape elements used by the taxa considered are not included in the analysis. Conversely, if the analysis is conducted at a spatial extent that is too broad, weak correlations will again be found, but this time because too many seascape elements not used by the taxa under consideration are being included. Correlations will be maximal at an intermediate extent that matches the scale of habitat use. Once quantified across a range of scales, correlation strength can be examined to find the scale that best correlates fish with their surrounding habitat. Use of this 'best' scale approach to empirically define the ecological scale has recently emerged in a handful of terrestrial (Pearson 1993, Karl et al. 2000, Ricketts et al. 2001, Steffan-Dewenter 2003, Holland et al. 2004, 2005) and marine studies (Kendall 2005, Grober-Dunsmore et al. 2007).

Both the scale and strength of fish–seascape correlations can be influenced by map resolution. If only the perception of correlation strength is altered, it is not a serious problem if the objective is merely to identify the scale of peak correlation. However, it is of concern if accurate measurement of correlation intensity is the goal. Of greater concern is when map type alters both correlation scale and magnitude, resulting in a complete misperception of a fish–seascape association.

The real seascape that fish inhabit and are influenced by is depicted in greatest detail by maps with very high spatial and thematic resolution. Thus, high-resolution maps are expected to yield the highest fish−seascape correlations when an association exists and also the lowest correlations when no association is present. Highly detailed maps are, however, costly and time-consuming to produce. Maps generalized into coarser thematic and spatial properties are cheaper and faster to produce, but these changes often have unknown consequences on the perception of fish−seascape correlations.

In the present study we investigated several interrelated aspects of ecological scale by simultaneously varying (1) the size of habitat measurements used as independent variables, (2) both the spatial and thematic resolution of map data, and (3) the life stage, mobility guild, and fish assembly groups used as dependent variables. Our complementary hypotheses (1 to 5, below) seek to disentangle the effects of these issues in detecting and accurately perceiving fish−seascape relationships:

(1) Reef fish are significantly correlated with seascape variables (area of sand or seagrass, length of hard bottom or reef edge, and habitat diversity).

(2) Correlation strength will vary with the spatial scale of the analysis.

(3) Thematic and spatial resolution of maps will affect correlation strength and scale. Highest resolution maps will yield the highest correlations.

(4) Range in correlation strength will be highest for individual life stages of species followed by guilds, and lowest for whole community metrics.

(5) Resident fish species will have highest correlation with seascape variables at shorter distances than mobile, followed by transient species, and juveniles of a given species will have highest correlation with seascape variables at shorter distances than adults.

MATERIALS AND METHODS

This study was based on the fish communities and seascape around Buck Island Reef National Monument (BIRNM), US Virgin Islands, which is comprised of seascape features typical of Caribbean coral reef ecosystems (Fig. 1). Dependent variables were based on fish surveys, and independent variables were based on 4 types of benthic maps.

Fish survey data. Underwater visual surveys were used to census fish on 588 sites on reefs and hard bottom within and around BIRNM between January 2002 and May 2006. Due to random placement, each site was surrounded by a unique combination of habitat elements. At each georeferenced site, a diver swam along a randomly selected compass heading for 15 min and recorded all fish within 5 cm size classes that were observed within a 25×4 m belt transect (100 m^2) to the lowest possible taxon.

A hierarchical approach was taken in selecting response variables to test hypotheses relating fish distribution at several organizational levels from whole community to particular life stages of individual species (Table 1, columns 1 & 2). Variables included total fish abundance and overall species richness; species richness and fish abundance within the mobility guilds of resident (R), mobile (M), and transient (T) (Grober-Dunsmore et al. 2007); and the abundance by life stage of 6 common reef fish species. The 6 species were chosen to include those with (1) representation from diverse family and trophic groups, (2) known life history and habitat preferences, and (3) relatively common occurrence in the study area across a range of seascape settings. Abundances of these species were also separated into juvenile and adult categories, respectively, for life stage-specific analysis.

Mapping and quantifying seascape structure. Four maps of the benthic habitat around BIRNM were produced using 2 levels of spatial and thematic resolution, respectively (Kendall & Miller 2008). Maps were created by visual interpretation of orthorectified aerial photographs (Kendall et al. 2001). A relatively large minimum mapping unit (MMU; size of the smallest feature to be mapped) of 4000 m^2 and a much smaller MMU of 100 m^2 were used. A hierarchical classification scheme was used to attribute maps at both spatial scales into 17 subcategories nested within 3 main categories in a scheme structurally similar to those used to produce reef ecosystem maps elsewhere (FMRI & NOAA 1998, Mumby & Harborne 1999, NOAA NCCOS 2004). Main categories were unconsolidated sediment, submerged vegetation, and hard bottom. Subcategories of unconsolidated sediment were sand and mud. Subcategories of submerged vegetation were seagrass and algae in varying degrees of patchiness. Subcategories of hard bottom were patch reefs, linear reefs, colonized pavement, bedrock, pavement with sand channels, spur and groove, and scattered coral/rock. Maps with 17 classes served as high thematic resolution maps. Subsequently, we dissolved the boundaries and aggregated the polygons of these high thematic resolution maps to the 3 thematic class level for use in the analyses as maps with low thematic resolution. This process resulted in 4 maps of BIRNM using the same approach but with different spatial and thematic characteristics (Fig. 2).

Four variables were selected to quantify seascape structure that were representative of broad classes of 'landscape pattern metrics' and suspected to play a role in reef fish community structure: (1) area of seagrass or
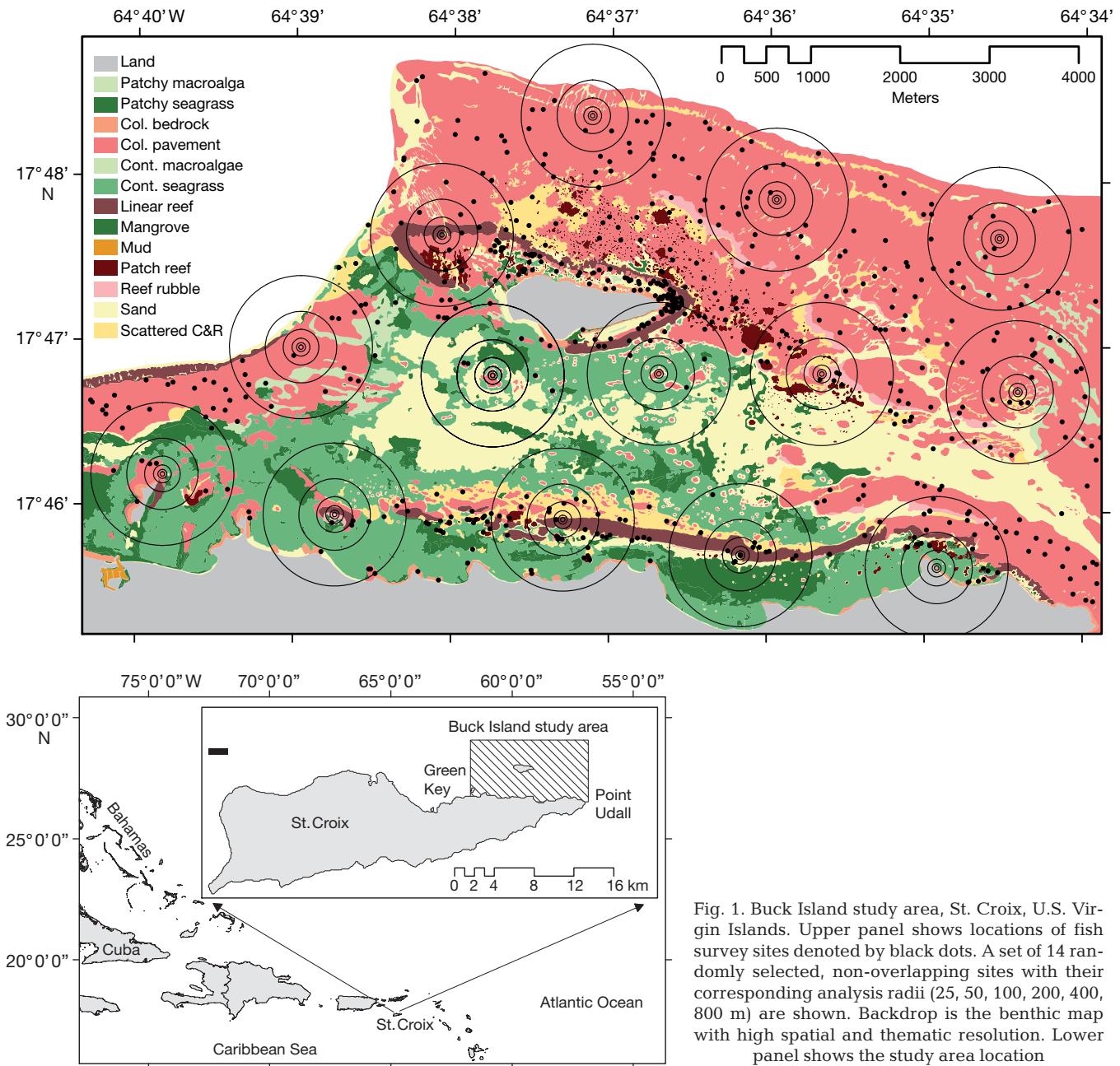
Fig. 1. Buck Island study area, St. Croix, U.S. Virgin Islands. Upper panel shows locations of fish survey sites denoted by black dots. A set of 14 randomly selected, non-overlapping sites with their corresponding analysis radii (25, 50, 100, 200, 400, 800 m) are shown. Backdrop is the benthic map with high spatial and thematic resolution. Lower panel shows the study area location

submerged aquatic vegetation (SAV), (2) length of hard bottom edge, (3) area of sand or unconsolidated sediment (map with high or low thematic resolution, respectively), and (4) habitat diversity (Shannon-Wiener Index). Area of seagrass around reefs is suspected to enhance abundance of lutjanids (snappers), haemulids (grunts), and other fish on reefs (Randall 1965, Ogden 1976, Kendall et al. 2003, Kendall 2005, Grober-Dunsmore et al. 2007). Reef edges have been implicated as a key ecotone shaping fish communities on reefs (Dorenbosch et al. 2005, Vanderklift et al. 2007), including piscivores (Shulman 1985, Sweatman & Robertson 1994, Valentine et al. 2007, Vanderklift et al. 2007), herbivores (Wernberg et al. 2006), and those species that use hard bottom as structural refuge but forage over soft bottom (Ogden 1976, Burke 1995). Sand and seagrass bottom provides settlement habitat for many reef fish species and may therefore eventually impact adult abundance on nearby reefs (Shulman & Ogden 1987, Shulman 1985, Parrish 1989). Diversity of habitat types may be positively correlated with the diversity of the fish community (Ward et al. 1999) and has been suggested as a surrogate for overall biodiversity in marine reserve selection (National Research Council 2001).

Table 1. Scale (m) of maximum fish–seascape correlation among all map types. SAV: submerged aquatic vegetation; (–) variable pairs with no correlations above |r| = 0.2 for any map type. Bottom rows summarize the changes in perception of fish–seascape correlation due to map type. [a] and [b] are defined in the bottom 2 rows and denote 2 types of altered perception. All 104 correlation plots are provided in the supplement at www.int-res.com/articles/suppl/m427p259_supp.pdf where numbers (Suppl. 1–Suppl. 4) and letters (Panels a–z) indicate seascape and fish variables, respectively (e.g. habitat diversity and fish abundance is Supplement 1, Panel a).

Fish variables	Habitat diversity Suppl 1	Seagrass/ SAV area Suppl 2	Sand/sedi- ment area Suppl 3	Hard bottom edge length Suppl 4	Panel
Whole community					
Fish abundance	–	–	–	–	a
Species richness	–	800[a]	800[bb]	800[ab]	b
Mobility guild					
Resident fish abundance	–	–	25[bb]	–	c
Resident species richness	–	800[a]	–	800	d
Mobile fish abundance	–	–	–	–	e
Mobile species richness	–	–	–	50[bbb]	f
Transient fish abundance	–	–	800[bb]	–	g
Transient species richness	–	–	800[bb]	–	h
Species (abundance)					
Acanthurus coeruleus					
Juvenile	–	–	–	800[aaa]	i
Adult	–	–	–	800[aab]	j
Total	–	–	–	800[aaa]	k
Cephalopholus fulvus					
Juvenile	–	800[a]	25[bb]	800[ab]	l
Adult	–	800	100[bb]	800[ab]	m
Total	–	800	25[bb]	800[ab]	n
Haemulon flavolineatum					
Juvenile	–	–	–	–	o
Adult	–	800	–	50[abb]	p
Total	–	800	–	50[abb]	q
Ocyurus chrysurus					
Juvenile	–	800[bbb]	–	–	r
Adult	–	–	–	–	s
Total	–	100[abb]	–	–	t
Sparisoma viride					
Juvenile	–	800[a]	–	800[aab]	u
Adult	–	400[a]	–	800[abb]	v
Total	–	–	–	800[aa]	w
Stegastes planifrons					
Juvenile	–	800[a]	–	800[ab]	x
Adult	–	800	–	800[a]	y
Total	–	800[a]	–	800[ab]	z
No. of comparisons with at least one map type with |r| > 0.2	0	14	7	17	
No. of times one of the other 3 map types had a peak |r| at the same scale but a significantly lower value. [a]each occurrence	na	8	0	22	
No. of times one of the other 3 map types had a peak |r| at a different scale. [b]each occurrence	na	5	14	17	

Multiscale analysis. The dominant scales at which components of the fish assemblage are correlated with their surrounding habitat mosaic were identified using a multi-scale approach. The seascape pattern metrics were calculated around each of the 588 fish survey sites within circular sample units for all 4 map types, respectively (Fig. 1). To determine which analysis scale 'best' related to a fish community variable, seascape metrics were calculated at a range of distances from very small, including only seascape elements directly at the fish census site, through broad scales that included the mosaic of habitat elements beyond the distance that fish were likely to be influenced. The smallest distance was 25 m to incorporate each 4 by 25 m fish survey. Habitat metrics were also calculated at increasing distances of 50, 100, 200, 400, and 800 m radii around each survey (Kendall 2005) (Fig. 1).

Univariate linear regression was used to determine the basic relationship between a given fish variable and the seascape variables at each analysis distance. The strength of the relationship as a function of spatial scale was evaluated using the Pearson correlation coefficient (r) that resulted from the regression. This was chosen over other regression-based statistics, such as R^2, to characterize relationships because it ranges from −1 to +1, and therefore both positive and negative relationships between variables can be perceived.

To maintain independence among samples, especially where larger analysis diameters (e.g. 800 m) would result in very similar seascape values around adjacent survey sites but maximize use of the data, a resampling approach was taken using the software Focus v2.1 (Holland et al. 2004). Based on distances between survey points, a non-overlapping subset of random survey sites was repeatedly drawn from the entire pool of 588 surveys (1 subset shown in Fig. 1). Preliminary analysis revealed that 1000 iterations of the resampling procedure and their corresponding correlation statistics produced a stable and unimodal set of r values with very low

Low spatial resolution (large MMU)								High spatial resolution (large MMU)
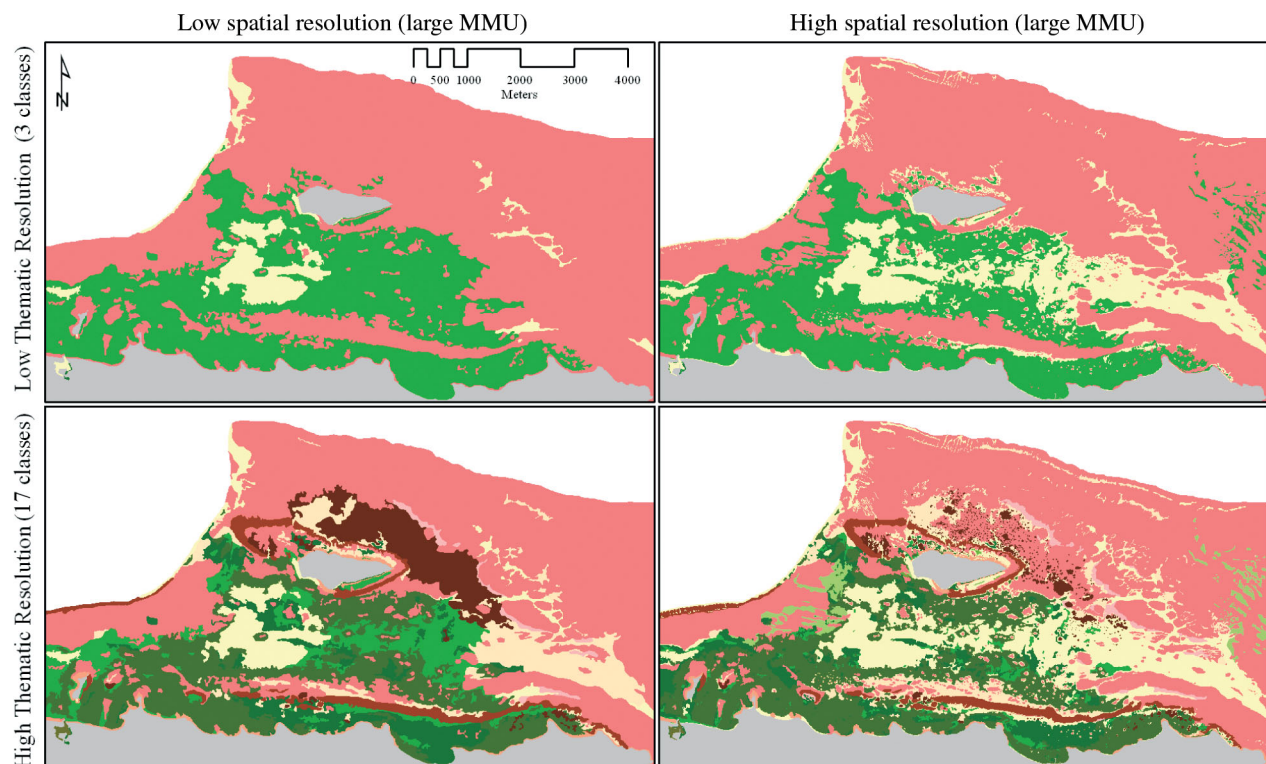

Fig. 2. Four map types of the study region. Counterclockwise from upper left is the map with low spatial and thematic resolution, low spatial but high thematic resolution, high spatial and thematic resolution, and high spatial but low thematic resolution. Grey denotes land. White denotes unmapped area beyond the shelf edge. Green tones denote seagrass/submerged aquatic vegetation categories. Tans denote sand/sediment categories. Reds denote coral reef/hard bottom categories. See Kendall & Miller (2008) for quantitative differences among maps

standard error for all variables and analysis scales. The sampling process was conducted at all 6 analysis scales for each combination of *x* and *y* variables, respectively. The mean and standard error of the correlation coefficients from each scale were plotted and the scale of greatest correlation (maximum |r|) was identified for each pair of fish and seascape variables. The resampling analysis was conducted for each of the 4 map types, and the results for each fish and seascape variable were plotted on the same chart to visualize the effect of map type on fish–seascape correlations.

Hypothesis testing. Four outcomes were possible for each fish–seascape combination in Table 1. The simplest case was when no correlation was found between a fish variable and seascape variable for any map type or analysis scale. Another possibility was that a significant correlation existed at one or more scales and all map types yielded similar results. It was also possible that one or more analysis scales yielded a significant correlation, but the results were different depending on the map type. In this case maximum |r| value among map types could occur at the same scale but achieve significantly different values, or maximum |r| values among map types could occur at entirely different scales. The results of each of the 104 fish and landscape

comparisons were tallied into one of these 4 categories using the rules defined in the hypotheses below.

Hypothesis 1. Reef fish are significantly correlated with seascape variables (area of sand or seagrass, length of hard bottom or reef edge, and habitat diversity): With Bonferroni correction for testing 6 scales at once, nearly all mean r values were significantly non-zero due to the very narrow standard error of the mean (SEM) values. Even r values between +0.1 and −0.1, which would account for <1% of the variability in the fish–seascape relationship, were statistically significant. To infer ecological relevance, a much higher and more conservative |r| of 0.2 was therefore selected as a cutoff for identifying more important ecological relationships and to reduce the probability of Type I errors.

Hypothesis 2. Correlation strength will vary with the spatial scale of the analysis: A simple ANOVA evaluated whether all 6 analysis scales yielded a maximum r value (|r| > 0.2) at the same scale for each fish–seascape variable pair and map type. Where a significant ANOVA was found, a Tukey's-type multiple means comparison determined which scales differed. A more conservative α = 0.001 was used to define significant differences due to the narrow SEM values that resulted from the resampling procedure.

Hypothesis 3. Thematic and spatial resolution of maps will affect correlation strength and scale. Highest resolution maps will yield the highest correlations: To evaluate the possibility that peak r values occurred at the same scale but had significantly different values among map types, the scale with the highest r value was identified and the mean r values among map types were tested for significant differences using a conservative Tukey's-type multiple means comparison procedure (α = 0.001). To evaluate the possibility that peak r values occurred at different scales for different map types, peaks in |r| values by map type were identified visually. The relative frequencies of these possible outcomes were tabulated for each seascape variable at the bottom of Table 1.

To determine if there was a map type that consistently had the highest or lowest |r| values for each of the 4 seascape variables, comparisons with significant results were evaluated further. When a |r| > 0.2 was present, maps yielding significantly higher or lower |r| than the rest were tallied for each seascape variable.

Hypothesis 4. Range in correlation strength will be highest for individual life stages of species followed by guilds and lowest for whole community metrics: Maximum |r| values for each of the 104 variable combinations were grouped and plotted by those that tested: (1) abundance of individual life stages (juvenile or adult) of particular species, (2) total abundance of particular species, (3) abundance or species richness of the mobility guilds, and (4) the whole assemblage variables of overall abundance or species richness. Plotted |r| values were separated by map type and coded by seascape variables. The range and distribution of extreme values was compared among levels of organization of the fish variables for each map type.

Hypothesis 5. Resident fish species will have highest correlation with seascape variables at finer scales than mobile, followed by transient species, and juveniles of a given species will have highest correlation with seascape variables at finer scales than adults: The scale of peak correlation between juveniles and a given landscape variable was identified for each map type and simply compared to the scale of peak correlation for adults. The distance of peak correlation of juveniles relative to adults was described as one of the following: juvenile < adult, adult < juvenile, or when the scale of peak correlation was the same for both of these life stages, juvenile = adult. The hypothesis that resident fish have higher correlations with seascape variables at finer scales than mobile, followed by transient fish, was evaluated in similar

fashion. Habitat diversity was not evaluated because r values were very low across all scales and no clear peaks in correlation were observed.

RESULTS

Hypothesis 1—Fish are correlated with seascape variables

Linear correlations between fish and individual seascape variables were low overall and explained a low percentage of the variability in fish distributions (see the supplement at www.int-res.com/articles/suppl/m427p259_supp.pdf). Of the 2496 mean r values calculated, only 220 (~11%) exceeded the selected significance level of |r| = 0.2. The strongest association was |r| = 0.5 between the abundance of *Cephalopholus fulvus*, a small grouper and the amount of hard bottom edge. Habitat diversity was not significantly correlated with any fish variable at any scale (Table 1) (e.g. Fig. 3).

Despite the lack of strong correlations between individual seascape variables and fish distributions, some relationships between fish and specific attributes of the seascape were found. Length of hard bottom edge was correlated with more of the fish variables (17) than any other seascape feature (Table 1). Species richness, resident species richness, mobile species richness, and abundance of all species except for *Ocyurus chrysurus* were related to length of hard bottom edge. Highest |r| values found with hard bottom edge length were for *Acanthurus coeruleus* adult and total abundance, *Cephalopholis fulvus* adult and total abundance (neg-
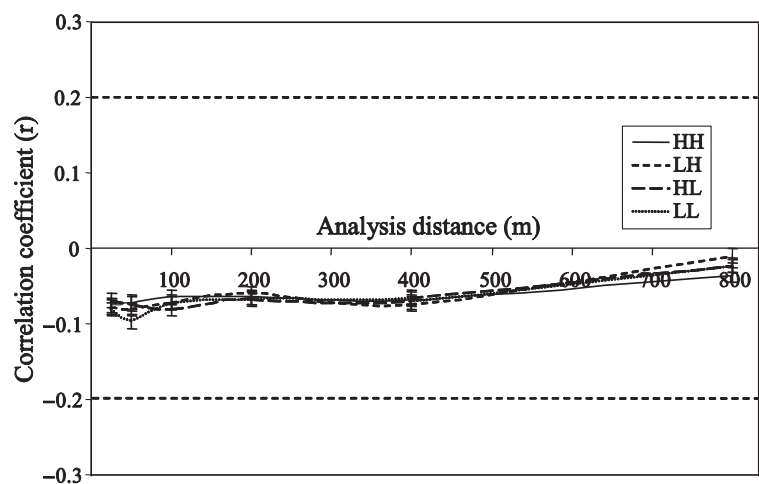

Fig. 3. Correlations of habitat diversity and fish species richness by analysis distance for all 4 map types. HH: map with high spatial and thematic resolution. LH: map with low spatial and high thematic resolution. HL: map with high spatial and low thematic resolution. LL: map type with low spatial and thematic resolution. Observations between the horizontal dashed lines (|r| < 0.2) denote non-significant results

ative correlations), and *Sparisoma viride* juvenile and total abundance. Area of seagrass/ SAV was correlated with total species richness, species richness of resident fish, and abundance of at least one life stage of all species considered except for *A. coeruleus* (Table 1). The highest |r| values found with seagrass/SAV were for *Stegastes planifrons* juvenile and total abundance, and *C. fulvus* juvenile, adult, and total abundance (negative correlations). Species richness and abundance of transients, abundance of residents, and overall species richness all had positive correlations with area of sand/sediment (Table 1).

Hypothesis 2 — Correlation strength varies with analysis radius

This hypothesis was accepted for all comparisons with significant r values, although the results differed by seascape variable (Table 1). Most peak correlations involving area of seagrass/SAV occurred at the broadest scale considered (800 m, e.g. Fig. 4). Transient richness and abundance had highest correlation at 800 m with sand/sediment area, whereas resident abundance had highest correlation at 25 m.

Patterns for correlations between individual species and seascape variables were less predictable (Table 1). The abundance of adult *Cephalopholis fulvus* had highest correlation with sand/sediment area at 100 m, whereas overall and juvenile abundance had highest correlation at 25 m. Most peak correlations with length of hard bottom edge occurred at the 800 m scale except for total and adult abundance of *Haemulon flavolineatum* and species richness of mobile species that occurred at 50 m. All peak |r| values showed positive relationships except for *C. fulvus*, which showed strong negative correlations.

Hypothesis 3 — Map resolution affects correlation strength and scale

Support for this hypothesis was equivocal among seascape variables, with spatial and thematic resolution influencing some results but not others. For fish–habitat diversity comparisons, all 4 map types yielded similar results, with |r| values rarely exceeding 0.1 across all scales (e.g. Fig. 3). For seagrass/SAV area, the scale of highest correlation was the same for all 4 map types in all but one of the 14 comparisons with significant results. In contrast, all sand/sediment area results were strongly influenced by map type. Maps of the same spatial resolution resulted in similar r values
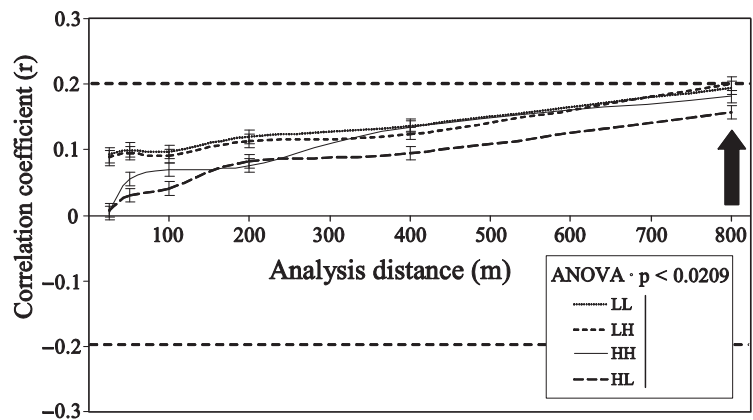

Fig. 4. Correlations of seagrass/submerged aquatic vegetation and *Haemulon flavolineatum* adult abundance by analysis distance for all 4 map types. Where a significant correlation was found (|r| > 0.2 as indicated by the horizontal dashed lines), the scale with the strongest relationship is noted with the black arrow. Vertical lines adjacent to the legend denote map types that have correlations that are not significantly different from each other at the scale with highest correlation. See Fig. 3 for abbreviations

at all spatial scales, whereas maps with differing spatial resolution resulted in very different values across scales (e.g. Fig. 5). More specifically, the abundance of adult *Cephalopholis fulvus* had highest correlation with sand/sediment area at 100 m, whereas overall and juvenile abundance had highest correlation at 25 m. These were perceived as positive relationships only when maps with low thematic resolution were used. For length of hard bottom edge, map type significantly influenced the results for all but one of the 17 comparisons with at least one |r| > 0.2. Only species richness of residents was consistently correlated with hard bottom edge by all 4 map types (Fig. 6). For the 16 other comparisons, use of different map types resulted in either significantly lower r at the same scale or even a peak in r at an entirely different scale.

Changes in perception of fish–seascape correlation due to map type are summarized at the bottom of Table 1 (i.e. either peak in correlation at different scale or peak at the same scale but different strength). Map type had no effect on correlations involving habitat diversity with no significant correlations observed with any map. When map type had an effect on the sand/sediment results, maximum |r| value occurred at completely different scales (14 occurrences) rather than simply peaking at the same scale but at a significantly lower value (0 occurrences). In contrast, seagrass/SAV and hard bottom edge relationships showed some of each type of difference. Overall, the 2 types of differences occurred with approximately equal frequency.

The number of times that each map type had the highest or lowest |r| value when a |r| > 0.2 was present is tallied in Table 2. Only hard bottom edge comparisons yielded a consistent pattern. Maps with high spa-
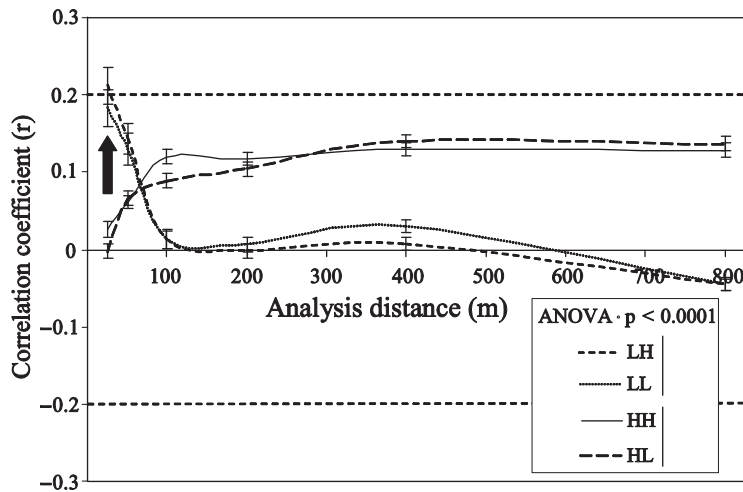
Fig. 5. Correlations of sand/sediment area and resident fish abundance by analysis distance for all four map types. See Figs. 3 & 4 for definitions and abbreviations
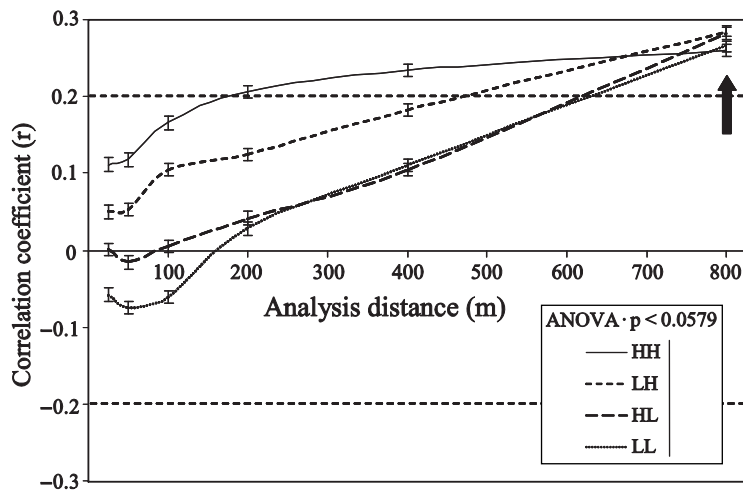

Fig. 6. Correlations of hard bottom edge and resident species richness by analysis distance. See Figs. 3 & 4 for definitions and abbreviations

tial and thematic resolution most often had |r| values significantly higher than other maps. Maps with low spatial and thematic resolution also had significantly lowest |r| values in the most comparisons. No single map type consistently differed from the others for the other 3 seascape variables.

Hypothesis 4 — Range in correlation strength varies by life stage, guild, and whole community variables

Maximum |r| values showed similar minima, maxima, and ranges among individual life stages of the 6 focal species and when all life stages were grouped together. Values for mobility guilds and whole fish community results were also similar to each other but

quite different from those based on individual species (Fig. 7). Findings were therefore grouped into these 2 broader categories, respectively. Of the 104 fish–seascape combinations tested, at least 11 of the highest maximum |r| values were for species-level analyses. This was true for all map types except for high spatial and low thematic resolution, which had only 4 of the highest values (Fig. 7d). Species-level analyses also had a higher range of values (~0.4), much higher than the range for guild or community comparisons (~0.2) (Fig. 7a–c). The exception was again for analyses based on maps with high spatial and low thematic resolution, which differed from this pattern in that the range of values was lower (~0.3) (Fig. 7d). Also of note, nearly all of the highest |r| values were for comparisons involving hard bottom edge length and seagrass/SAV, whereas nearly all of the lowest values were for correlations between habitat diversity and individual fish species.

Hypothesis 5 — Mobility guilds and life stage will affect distance of peak correlation

Overall, 38% (9 of 24) of the comparisons had maximum correlations at the same scale for resident, mobile, and transient species (Table 3). The next most common result (30%, 7 of 24 of the comparisons), occurred when transient species had a larger scale of correlation than either resident or mobile species (which had a common scale of peak correlation). The expected result of r value trends: resident < mobile < transient, occurred in only one of the 24 comparisons evaluated. Also of note, no fish–seascape correlations based on mobility yielded the same results for all 4 map types, and differences were unpredictable and inconsistent.

Overall, 56% (40 of the 72) of the comparisons evaluated had maximum correlation at the same scale for both adults and juveniles of a given species (Table 4). Juveniles had a finer scale of peak correlation in only 15% (11 of 72) of the comparisons, whereas adults had finer scales of peak correlation in 30% (21 of 72) of the comparisons. Of note, when a difference was found in comparisons involving seagrass/SAV, it was always that adults had a finer scale of peak correlation than juveniles. All 4 map types generally resulted in the same patterns. Exceptions to this were for *Ocyurus chrysurus* and *Cephalopholis fulvus*. For *O. chrysurus*, use of maps with high spatial resolution resulted in

Table 2. Tally of the number of times each map type had the highest or lowest |r| value when a significant result was present. SAV: submerged aquatic vegetation

Map resolution	Habitat diversity	Seagrass/ SAV	Sand/ sediment	Hard bottom edge length
Significantly highest |r| value				
High spatial high thematic	0	0	0	4
High spatial low thematic	0	0	0	0
Low spatial high thematic	0	0	0	1
Low spatial low thematic	0	1	0	0
Significantly lowest |r| value				
High spatial high thematic	0	0	0	0
High spatial low thematic	0	0	0	3
Low spatial high thematic	0	0	0	0
Low spatial low thematic	0	0	0	4

juveniles having finer scales of peak correlation than adults. When low spatial resolution was used, the inverse pattern was perceived. For *C. fulvus*, use of maps with high spatial resolution resulted in adults having finer scales of peak correlation than juveniles. When low spatial resolution was used, the inverse pattern was perceived. It should be noted that inference regarding scales of peak correlation by life stage are limited to only the 6 focal species tested, whereas results for mobility guilds a more broadly robust and are based on all species observed.
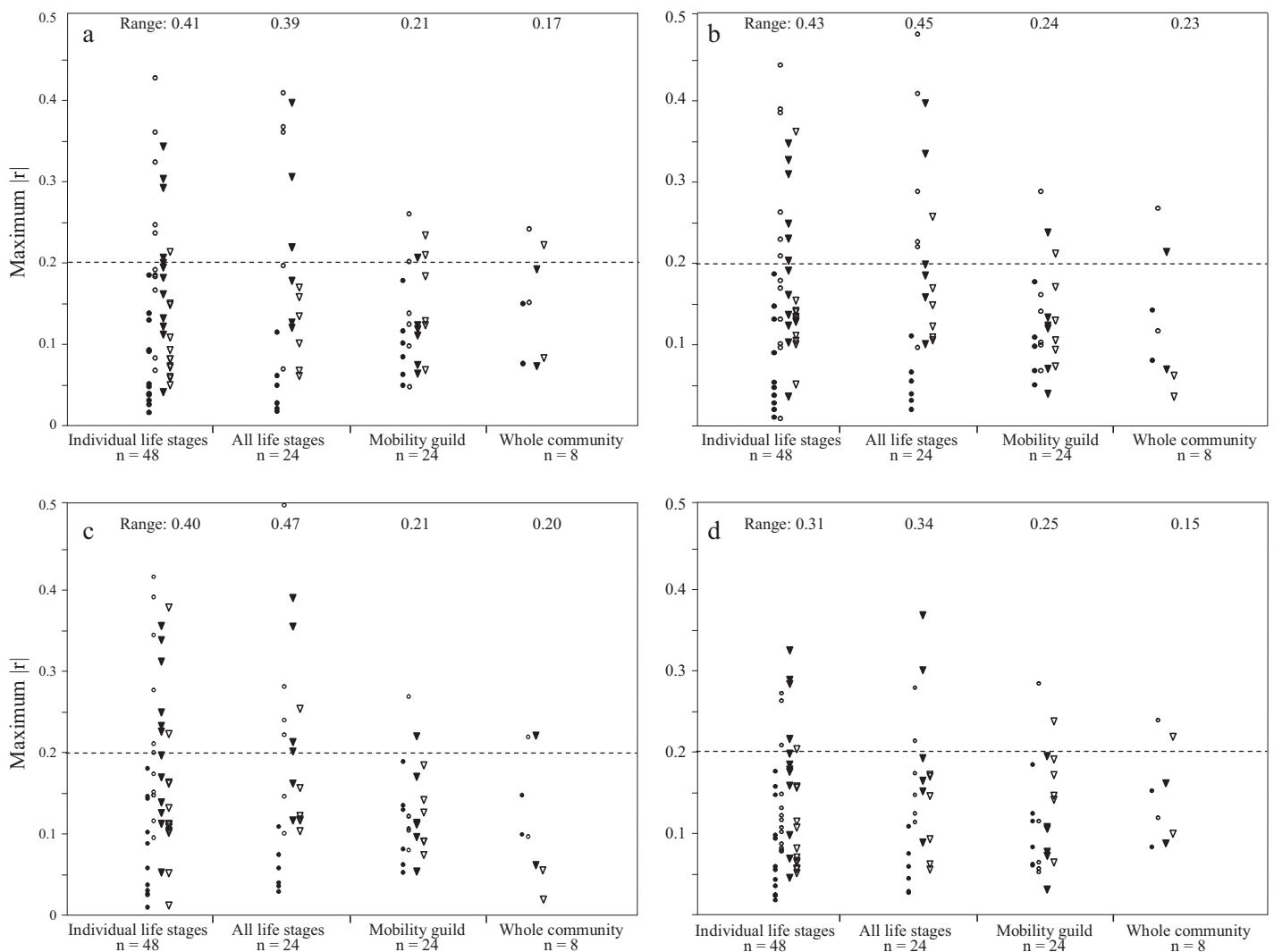

Fig. 7. Maximum |r| values for all 104 *x* and *y* variables investigated in the study using maps with (a) high spatial and thematic resolution, (b) low spatial and high thematic resolution, (c) low spatial and thematic resolution, and (d) high spatial and low thematic resolution. Results are grouped by level of organization of the fish variables. Symbols denote the landscape variables associated with each |r| value. •: habitat diversity; ○: hard bottom edge length; ▼: seagrass/SAV; ▽: sand/sediment

Table 3. Relative scale of maximum |r| values for resident (R), mobile (M), and transient (T) fish within the 4 map types. SAV: submerged aquatic vegetation

	High spatial high thematic	High spatial low thematic	Low spatial high thematic	Low spatial low thematic
Hard bottom edge length				
Fish abundance	R = M < T	M < R = T	R = M < T	R = M < T
Species richness	R = M = T	R = M = T	R = M < T	R = M = T
Seagrass/SAV				
Fish abundance	R = M = T	R = M < T	M < R < T	R < M < T
Species richness	R = M = T	R = M < T	R < M = T	R < M = T
Sand/sediment				
Fish abundance	R = M = T	T < R = M	R = M = T	R = M < T
Species richness	M < R = T	T < R = M	R = M = T	R = M = T

Table 4. Relative scale of maximum |r| values for juveniles (J) versus adults (A) of each of the 6 focal species within the 4 map types. SAV: submerged aquatic vegetation

	High spatial high thematic	High spatial low thematic	Low spatial high thematic	Low spatial low thematic
Hard bottom edge length				
Acanthurus coeruleus	J = A	J = A	J = A	A < J
Cephalopholis fulvus	J = A	J = A	J = A	J = A
Haemulon flavolineatum	J = A	J = A	J = A	J = A
Ocyurus chrysurus	J < A	J < A	A < J	A < J
Sparisoma viride	J = A	A < J	J = A	A < J
Stegastes planifrons	J < A	J = A	J = A	J = A
Seagrass/SAV				
A. coeruleus	A < J	A < J	A < J	A < J
C. fulvus	J = A	J = A	J = A	J = A
H. flavolineatum	J = A	J = A	J = A	J = A
O. chrysurus	A < J	A < J	A < J	A < J
S. viride	A < J	A < J	A < J	A < J
S. planifrons	J = A	J = A	J = A	J = A
Sand/sediment				
A. coeruleus	A < J	A < J	J = A	J = A
C. fulvus	A < J	A < J	J < A	J < A
H. flavolineatum	J = A	J = A	J < A	J < A
O. chrysurus	J = A	J = A	J = A	J = A
S. viride	J = A	J = A	J = A	J = A
S. planifrons	J < A	J < A	J < A	J < A

DISCUSSION

A central question asked in the present study is 'How much of the pattern in fish distribution can be explained using landscape variables?' The seascape pattern metrics selected for study were considered to be among those with the greatest explanatory power over fish distributions based on prior research. Results suggest, however, that each of the seascape variables studied here explain only a relatively small proportion (~25%) of the variability in the distribution of fish in coral reef systems.

Similar studies in a variety of systems have generally yielded a similar range of correlation values to those found here. Landscape variables explained 2 to 64% of the variability in bird and insect communities (Ricketts et al. 2001, Pearman 2002, Steffan-Dewenter 2003, Holland et al. 2004), and although less-studied, findings from multiscale studies of reef fish are similarly wide ranging, with 11 to 94% of the variability explained between seascape and fish variables (Kendall 2005, Grober-Dunsmore et al. 2007). Linear correlation between fish species richness on sand sites with area of nearby hard bottom reached maximum values of r = 0.33 in a separate study at BIRNM (Kendall 2005). Grober-Dunsmore et al. (2007) reported linear correlations between reef fish community variables and area of seagrass as high as 0.97 and were often in the range of ~0.5 to 0.6 around the nearby island of St. John, U.S. Virgin Islands. These differences in results for ecologically similar coral reef ecosystems from the same geographical area are likely the result of differences in sampling design between the 2 studies. Studies by Kendall (2005) and the results here were based on a large number of spatially random survey sites, whereas findings of Grober-Dunsmore et al. (2007) were based on a subset of selected coral reef sites chosen specifically to quantify the effects of variation in the amount of nearby seagrass cover and to minimize confounding variables such as differences in coral cover, rugosity, depth, and distance from shore. In contrast, our study provides a more comprehensive, ecosystem-wide measure of the strength of the relationships across the complete range of coral reefs in the study area.

What seascape variables had the highest or most correlations with the fish variables? Habitat diversity has been considered as a proxy for fish diversity in the selection of marine reserves (National Research Council 2001). Terrestrial studies have shown a relationship between habitat diversity and biotic diversity for a range of taxa (Kohn & Walsh 1994, Kerr & Packer 1997, Ricklefs & Lovette 1999, Fox & Fox 2000). However, our results suggest that habitat diversity is a very poor predictor of fish species richness or indeed any compo-

nent of the fish community considered. A possible explanation is that benthic maps of the type used here may not capture the aspects of habitat diversity to which fish respond. It is also possible that, although we evaluated a wide range of variables representing the fish assemblage, the species and assemblages considered may be habitat generalists or have considerable plasticity in suitable habitats (Ricklefs & Lovette 1999). Our results bolster growing evidence against using habitat diversity at the seascape scale, as depicted in benthic maps, as a proxy for predicting overall fish and biotic diversity (Donaldson 2002, Pittman et al. 2007, Grober-Dunsmore et al. 2008).

Area of seagrass/SAV was correlated with several of the fish community variables, including at least one life stage of most species tested. This confirms prior studies on species suspected of association with seagrass/SAV and further quantifies those relationships (Dorenbosch et al. 2005, 2006, Kendall 2005, Grober-Dunsmore et al. 2007, Valentine et al. 2007). Correlations were also found for species not previously thought to be related to area of seagrass (e.g. *Cephalopholis fulvus*, *Sparisoma viride*, and *Stegastes planifrons*). This demonstrates the importance of seagrass/SAV as an influence on fish distribution on reefs generally, not just those considered obligate users. It also indicates that a variety of direct and indirect mechanisms can operate that influence abundance of particular species or guilds. Sand/sediment area predicted several of the fish variables, although not as many as expected given this bottom type's role in settlement and foraging of many species.

Length of hard bottom edge was correlated with more of the fish variables than any other landscape feature. This underscores its role as an important habitat margin to a diversity of reef fish (Dorenbosch et al. 2005, 2006, Valentine et al. 2007). Edges between reef types and soft bottom often have high rugosity that offers structural refuge supporting a diversity of reef species (Pittman et al. 2007).

Correlations were found between diverse elements of the fish community and seascape features at a wide range of distances. Systematically changing the size of the analysis window and comparing fit among the models allowed the neighborhood that explains the highest amount of variability (highest |r|) in the fish data to be identified. The distance or neighborhood with the strongest correlation has been interpreted as the most ecologically influential or relevant scale for each combination of biotic and seascape variable (Holland et al. 2004, Kendall 2005). For many comparisons no significant relationships were found for any fish variables at any scale. In these instances, a number of factors may be responsible. Fish variables may be more closely related to a seascape variable not tested in this study, or the relationship may be non-linear and insensitive to

our linear-regression-based approach. It could also be that the seascape maps did not adequately capture the necessary detail of the seascape parameters that were tested. Fish may even be responding to seascape features beyond our maximum analysis distance.

Ecologically meaningful explanations are present for many of the observed patterns in neighborhood distance and associations with particular landscape variables. Species richness of fish was positively correlated with area of sand/sediment, area of seagrass/SAV, and length of hard bottom edge. Correlation with these variables increased with analysis distance such that maximum r values occurred at the 800 m scale, a broader scale of peak correlation than identified by prior research (400 m by Kendall 2005; 500 m by Grober-Dunsmore et al. 2007). It has long been thought that the area of surrounding seagrass increases the number of fish species on hard bottom sites by providing foraging areas for some species (Randall 1965, Ogden 1976, Nagelkerken et al. 2000), transfer of energy to reefs (Meyer et al. 1983, Meyer & Shultz 1985), nursery habitat (Dorenbosch et al. 2005, Adams et al. 2006, Dorenbosch et al. 2007, Verweij et al. 2008), and enhanced recruitment (Shulman & Ogden 1987, Cocheret de la Morinière et al. 2002). Similarly, area of surrounding sand bottom may result in enhanced recruitment to nearby hard bottom sites of the many species that initially settle in sand habitat to avoid reef and reef edge predators (Helfman et al. 1982, Shulman 1985, Shulman & Ogden 1987). Species richness may be enhanced by length of hard bottom edge through several mechanisms. Hard bottom edge must be transited for juvenile fish undergoing ontogenetic shifts following settlement in sand or seagrass (Shulman 1985, Shulman & Ogden 1987, Cocheret de la Morinière et al. 2002), it is a preferred hunting ground of some piscivores (Helfman et al. 1982, Quinn & Ogden 1984, Sweatman & Robertson 1994), and is the optimum location to seek structural refuge to minimize travel distance from reef to soft bottom for species that undergo such daily foraging migrations (Kendall et al. 2003, Tuya et al. 2010). Hard bottom edge represents a key ecotone habitat for many species (Wernberg et al. 2006, Valentine et al. 2007, Vanderklift et al. 2007), and also indicates the presence of bathymetric complexity between reef types or reef and soft bottom, which has been positively correlated with species richness of fish (Luckhurst & Luckhurst 1978, Gratwicke & Speight 2005a,b, Pittman et al. 2007).

Ecologically meaningful correlations were also found between individual species and seascape variables. Strong negative correlations were observed between *Cephalopholis fulvus* and length of hard bottom edge and area of seagrass/SAV. In both cases r values steadily decreased with analysis distance to a maxi-

mum at the 800 m scale. This species utilizes flat hard bottom often sparsely colonized by corals, sponges, and gorgonians (Pittman et al. 2008), a bottom type often described as pavement that typically covers broad areas (Kendall et al. 2004b). Hard bottom edges or a large area of seagrass nearby would mean that there is less of their preferred flat hard bottom habitat. Logical ecological correlations were also observed between seascape variables and *Haemulon flavolineatum* adult and overall abundance. This species feeds solitarily over seagrass and soft bottom at night but schools over reefs and hard bottom during the day (Randall 1965, Ogden 1976). Area of seagrass positively influenced abundance on reef sites by providing a large foraging area (Burke 1995, Nagelkerken et al. 2000, Kendall et al. 2003), especially at long analysis distances that may correspond to a broad foraging range. High correlation with hard bottom edge, especially at very short analysis distances, is logical, too, because optimality theory predicts that *H. flavolineatum* will utilize reef sites near reef edges (Kendall et al. 2003). Such proximity minimizes energy costs and daily travel time from resting sites on reefs to adjacent seagrass foraging areas. This relationship was apparent only when maps with high spatial and thematic resolution were used.

More difficult to explain were the strong correlations observed between other variables. For example, a positive correlation was observed between *Stegastes planifrons* and both area of seagrass/SAV and length of hard bottom edge. High correlations were measured at the 800 m analysis scale. This highly resident species settles directly onto reefs (Tolimieri 1995, Gutierrez 1998) and spends its benthic life associated with the same coral head or $<\sim 1$ m^2 territory (Luckhurst & Luckhurst 1978, Robertson et al. 1981). That either of these landscape variables or this analysis distance have a direct influence on fish abundance is doubtful. These seascape variables may instead be correlated with some other environmental factor, some indirect effect may be responsible, and we are reminded that correlation need not be obviously linked to causation.

In many comparisons, use of different input maps resulted in a changed perception of either the strength of peak correlation at a given scale, or the scale at which peak correlations occurred. The latter case represents a more serious problem in that both the spatial dimensions as well as the intensity of the relationship are perceived differently. Such events call for the most careful consideration of the consequences of relying on a particular map type. These 2 types of misperception occurred with different frequency depending on the seascape feature tested. Studies relying on the amount of hard bottom edge length and area of sand need to be cautiously interpreted due to the large number of cases where map type changed the perception of the

fish−seascape correlation. Spatial resolution of maps often completely changed the perceived relationships between fish and their area of surrounding sand/sediment. In all cases, use of high spatial resolution maps resulted in lower r values or even negative r values compared to low spatial resolution maps at the same analysis scale. Perception of correlation strength between fish and hard bottom edge also depended on the type of input maps used. While the general patterns of increasing correlation with scale were similar among all 4 map types, the values of the correlation were often significantly different. Maps of the study site exhibited a doubling of edge length for hard bottom features when high spatial resolution was used to create them (Kendall & Miller 2008). Many reef edges that fish interact with, such as small patch reefs in sand and sand channels in hard bottom, only appeared when high spatial resolution was used. In contrast, results were quite consistent for seagrass/SAV area regardless of map type. Continuous seagrass beds were characterized quite consistently at the 2 map scales used in the present study, but patchy beds showed large differences (Kendall & Miller 2008). For habitat diversity, all 4 map types performed similarly in that none had significant correlations with any fish variables.

Is there a particular map type that is best for seascape ecological studies of reef fish? Our results suggest that the answer depends on the seascape variables of interest. Maps with high spatial and thematic resolution had most of the significantly highest correlations for comparisons involving hard bottom edge, whereas maps with low spatial and thematic resolution were often lowest. This indicates that results of studies using hard bottom edge are likely inaccurate when using lower spatial or thematic resolution maps. In contrast, all 4 map types performed similarly for seagrass/SAV, indicating that even simple, inexpensive to produce maps do just as well as highly detailed, expensive, time-consuming maps in studies involving this variable. Also of relevance are the plots of maximum r values by level of organization of fish variables. All map types yielded a similar range of results except for maps with high spatial but low thematic resolution. This map type had lower sensitivity to detecting the highest and lowest peak correlations that were observed more consistently among the other map types. This indicates that mapping only a few bottom types with great spatial detail may be least effective in seascape ecological studies. Why such maps would perform more poorly than those with low thematic as well as low spatial resolution is unclear.

Maximum correlations between seascape variables and individual species achieved a wider range and more extreme values (highest and lowest) than comparisons involving either guilds or the entire fish

assemblage. Variables representing more than a single species had more moderate peak correlations. This is likely because the habitat preferences and scales of movement of the many species included in such variables get averaged together and limit extreme values. In contrast, individual species had both highest and lowest values since each species interacts with a more discrete set of habitats at similar scales. This pattern did not however, separate the results of individual life stages from all individuals of the focal species, as was expected, nor did it distinguish between mobility guilds and whole community metrics.

Scales of peak correlation were the same for juveniles and adults in over half of the comparisons. The expectation based on terrestrial literature (Holling 1992, Gehring & Swihart 2003, Holland et al. 2005), that juveniles would have a shorter distance of maximum correlation than adults, rarely occurred (but see Grober-Dunsmore et al. 2007). This suggests that seascape influences on the distribution of juvenile fish may operate at scales often as broad as those for their adult stages. Typical scales of seascape interaction for mobility guilds were somewhat more in line with expectations (Pearman 2002), in that transients had broader scales of peak correlation than either resident or mobile fish in a large number of comparisons. Still, however, scale of influence was the same for all 3 mobility guilds in many comparisons, again indicating that in many cases even resident fish are influenced by their surrounding seascape at distances as broad as those for transients. Despite peak correlation at similar scales, the mechanisms responsible are almost certainly indirect given present understanding of the very small home range of resident species and juveniles of the 6 focal species (Itzkowitz 1977, Luckhurst & Luckhurst 1978, Overholtzer & Motta 1999, Bell & Kramer 2000, Watson et al. 2002). Map type generally did not influence the results of peak scale for adult versus juvenile fish. In contrast, results of mobility guild analysis differed in unpredictable ways depending on map type, again indicating that caution be used when studying mobility guilds using a single map type.

Most prior seascape ecological studies base results on one type of map; whatever is available. Little consideration appears to have been given to the influence of map type on the conclusions reached. Terrestrial investigations have shown that the characteristics of input maps can influence results of landscape ecology studies (Stohlgren et al. 1997, Karl et al. 2000). Results here also suggest that use of a single map type in the marine environment can lead to an incomplete or even incorrect perception (i.e. undetected, weakly measured, inversely signed, thought to occur at the wrong scale) of habitat utilization and scale at which organisms interact with their seascape.

Based on the findings here, the following advice can be given to those interested in mapping coral reef ecosystems to study seascape ecology of reef fish, to model species distributions, or in making spatially explicit management decisions using benthic maps. Hard bottom should be mapped with high spatial resolution above all else since this most affects reef edge depictions. Time and money permitting, hard bottom should be mapped with high thematic resolution as well and separated into its various reef types. Many studies are presently concerned with hard bottom edge and proximity to hard bottom habitat (Sweatman & Robertson 1994, Dorenbosch et al. 2005, Wernberg et al. 2006, Valentine et al. 2007, Vanderklift et al. 2007, Tuya et al. 2010). Extrapolating their mostly *in situ* studies to seascape scales using benthic maps carries with it particular concerns. Sand should be mapped with high spatial resolution to pick up key features such as sand channels in hard bottom and halos separating hard bottom from seagrass (Kendall & Miller 2008). In contrast to these bottom types, seagrass mapped at coarse thematic and spatial resolution appear to effectively evaluate the seascape ecology of a variety of fish species and will result in similar values when more detailed maps are used. Given these findings, prior seagrass studies probably do not need to be concerned about their results changing if different map types were used (e.g. Pittman et al. 2004, Kendall 2005, Grober-Dunsmore et al. 2007). Results involving hard bottom or sand, however, could change measurably were different maps to be used as input. Habitat diversity, as measured by the type of benthic maps used here, is simply not representative of fish diversity or any other measure of the fish community at any scale and should not be considered as a surrogate or proxy variable for overall biodiversity. To keep these recommendations in perspective, however, seascape variables that were used here were for common bottom features. Habitat specialists that are obligate users of a particular reef type, for example, would need to be studied with a map of sufficient spatial and thematic complexity to capture such features.

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