ABSTRACT

DREW, CHRISTINA ASHTON. Spatial Ecology of Reef Fish in Backreef and Coral Reef Habitats. (Under the direction of David B. Eggleston.)

Understanding the spatial population dynamics of organisms is essential for effective ecological conservation and management. Landscape ecological theories consider the habitat composition and structure of landscapes at multiple spatial scales as drivers for population and community patterns. Yet, many of these theories have evolved through study of terrestrial systems, and a formal, predictive marine spatial ecology is needed to account for the unique characteristics of marine species and their environments. Marine systems present several conceptual challenges to established spatial ecological theories, because (1) pelagic larval dispersal strategies and life-histories incorporating ontogenetic habitat shifts make it difficult to identify population boundaries, (2) the decoupling of adult, larval, and juvenile populations means that a population's demographic rates are not associated with a single habitat patch, but rather a heterogeneous mosaic of habitats, and (3) hydrodynamic processes complicate predictions of landscape connectivity.

My research contributes to the development of marine spatial ecology by addressing the effects of local habitat patch characteristics, regional landscape structure, and hydrodynamics upon dispersal and recruitment of marine populations at multiple spatial scales. My focus was on the important shallow, coastal ecosystems that often serve as nursery habitat for many fish and crustacean species, and where habitat and hydrodynamics are likely to both play important roles in organism dispersal and survival. My research included three related studies: (1) a computer simulation model of passive and active dispersal strategies evaluated how organism dispersal behavior and landscape structure

interacted to influence dispersal and recruitment success; (2) a regression analyses tested the efficacy of both traditional (e.g. patch area, habitat diversity) and marine-specific (e.g. proximity to hydrodynamic corridors, habitat volume) landscape characteristics at multiple scales as predictors of juvenile fish population and community patterns at local scales (1 km) in Florida Keys mangroves; and (3) a retrospective analyses of island-wide, Caribbean habitat and fish population databases tested the degree to which adult reef fish population abundance and community structure correlate with nursery habitat variables.

I found that: (1) an organism's behavioral response to currents (whether to walk, swim, or drift) significantly influences organism recruitment success in heterogeneous landscapes and how organisms respond to landscape change; (2) the inclusion of marine-specific landscape characteristics (e.g. distance to nearest channel) greatly improves the predictive power of statistical models describing some fish population and community trends at local scales; and (3) the influence of nursery habitat on reef fish populations appears to be a localized effect that is minimized in regional, island-wide fish abundance datasets, such that regional-scale fish surveys likely highlight island-wide differences in reef structural complexity, rather than dependence on putative nursery habitats.

My research indicates that the spatial ecology of marine populations varies across spatial scales and among species. The behavioral strategies of dispersing individuals, as well as the patch- (100s meters) and landscape-scale (1 to 10s kilometers) characteristics of the habitat encountered by dispersing individuals, influence individuals' recruitment success and assemblage composition over larger scales. Even reef fish species in the same family or behavioral guild (e.g. feeding guild) have been observed to respond to distinct landscape and

patch scale habitat features. These observations support arguments in favor of multispecies, multi-scale, organism-based approaches for reef fish conservation and management, rather than simpler habitat patch based approaches. Contour maps of species probability functions, in particular, could make excellent use of multivariate regression models to map predicted species distribution to (1) aid in the identification of potential population density or diversity hot-spots for each species, (2) evaluate the relative benefits of alternative reserve designs to each species, and (3) identify gradients in habitat quality that would aid in the development of stratified sampling design.

SPATIAL ECOLOGY OF REEF FISH IN BACKREEF AND CORAL REEF HABITATS

by

CHRISTINA ASHTON DREW

A dissertation submitted to the Graduate Faculty of North Carolina State University in partial fulfillment of the requirements for the Degree of Doctor of Philosophy

MARINE, EARTH, AND ATMOSPHERIC SCIENCES

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This work is dedicated to Matthew, Matt, Mum, Dad, Rob,
and all my friends who keep me smiling.

Thanks.

BIOGRAPHY

Christina Ashton Drew was born 7 February 1973 in Augusta, Georgia, during a raging blizzard. Taking this unusual weather as a sign, Ashton's parents promptly moved to eastern Canada, and there she learned to enjoy all types of winter sports, as well as SCUBA diving in the icy waters of Halifax Harbour. Her parents also ensured that she developed a broad love of literature, travel, philosophy, and outdoor adventure. By the end of high-school, having successfully ruled out only music and astrophysics as future career choices, she decided it might be wise to pursue a very liberal-arts education. She chose Beloit College in Wisconsin, because it was the only school in North America to offer a minor in Museum Science. At Beloit, after experimenting with Modern Languages and Anthropology majors, and spending more semesters abroad than at Beloit, Ashton completed her Bachelor of Arts in Environmental Science in 1995. She immediately returned home to Nova Scotia, Canada, to complete a Master of Marine Management at Dalhousie University. Ashton then spent three years working as a wildlife and fisheries biologist and GIS technician for a consulting firm in British Columbia. Although it was wonderful to be paid to hike beautiful mountains, fish for salmon in remote streams, and cruise the inside passage, Ashton grew increasingly agitated as she could not pursue the many interesting research questions raised during the surveys conducted for clients. In 1998, Ashton moved to North Carolina to work for the Environmental Protection Agency while applying to graduate schools across the continent. Colleagues at the EPA introduced her to Dr. Dave Eggleston about the same time friends on her Ultimate Frisbee team introduced her to Matt Drew, and suddenly North Carolina seemed a great place to stay for a while. So, in 2000, she married Matt and started work on her

doctorate in Dave's lab at North Carolina State University. The following years had many ups and downs, but things picked up greatly when Matthew Gabrielle, a 9-year-old bundle of energy, came along in 2004 to join Matt in Ashton's cheering section. Now, with doctorate in hand, she hopes to find gainful employment somewhere nearer the ocean and much further north, so that she can teach her family to ski, play hockey, and perhaps SCUBA dive in some icy coastal waters.

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CHAPTER 1

Currents, landscape structure, and recruitment success along a

passive-active dispersal gradient

Drew, C.A. and D.B. Eggleston. In Press.

Landscape Ecology

ABSTRACT

There exists a gradient in dispersal behavior from passive to active, which reflects organisms' dependence upon currents versus self-propelled movement. We asked: Do currents modify organism-landscape interactions to influence recruitment success along this dispersal gradient? Using a spatially-explicit cellular model, we simulated the recruitment success of three generalized dispersal strategies (walkers, swimmers, and drifters) through hierarchically structured benthic landscapes. We evaluated the relative recruitment success (recruited population size, overall area occupied, time to recruit) of the three dispersal strategies in similar landscapes, as well as the consequences of varying the total proportion of habitat suitable for recruitment, and the scale and pattern of habitat patchiness on recruitment success. In the presence of currents, swimmers and drifters generally recruited over larger areas and in less time than walkers. Differences among the dispersal strategies' recruitment success were most pronounced when an intermediate number of good habitat cells (16 to 48 % of landscape) were broadly dispersed across the landscape. Although recruitment success always increased with increasing proportion of good habitat, drifters were more sensitive, and swimmers less sensitive, to these landscape changes than walkers. We also found that organisms dispersing within currents typically responded non-linearly (logarithmically or exponentially) to increasing proportion of total good habitat, whereas walkers more often responded linearly.

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INTRODUCTION

The absence of evidence defining connectivity between juvenile and adult habitats is a critical missing link in our understanding of marine population dynamics and our efforts to protect these populations (Beck et al. 2001; Gillanders et al. 2003). Hydrodynamic models of passive particles traveling in oceanic currents have provided insight into large-scale population processes and dispersal mechanisms linking adult and juvenile populations (Roberts 1997; Cowen et al. 2000; Gaines et al. 2003). Yet, juvenile mobile marine fauna spend an average of 13 months (range 8 days to 5 years) living and moving among nursery habitats in estuarine, coastal, or backreef environments prior to residing in adult habitat (Gillanders et al. 2003). Many of these species have complex life cycles that include one or more ontogenetic habitat shifts, during which they disperse over distances from a few meters to hundreds of kilometers (Beck et al. 2001; Gillanders et al. 2003), traverse complex habitats, and display strong species-specific habitat preferences (Eggleston 1995; Irlandi and Crawford 1997; Acosta 1999; Dahlgren and Eggleston 2000). The waters hosting these juveniles are characterized by complex, highly variable (both spatially and temporally) hydrodynamic patterns, where wind and tidal currents predominate. In addition, these juveniles are no longer pelagic larvae, but now actively interact with the benthos, seeking shelter and food resources as they move within complex habitat mosaics. High mortality in these environments could result in a decoupling of larval supply and adult abundances, such that high larval recruitment and high density of young juveniles would not serve as an indicator of future adult population density (Beck et al. 2001; Gillanders et al. 2003).

Species' interactions with currents may be described along a gradient from passively drifting (e.g. some insects, marine larvae, and seeds), to selectively using currents to orient or

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increase dispersal distance (e.g. some fish, marine mammals, and birds), to seemingly ignoring currents (e.g. some amphibians and small mammals). These different dispersal strategies correspond to differences in search area (size and shape) and directionality, and potentially impact the relative influence of landscape composition and configuration on recruitment success. For example, species utilizing currents for propulsion or orientation would be expected to display a more linear search pattern with directional flow and to spend more time dispersing above landscapes rather than through landscapes, relative to species that ignored currents. Species using currents for propulsion would move primarily downstream (e.g. Forward and Tankersley 2001; Gibson 2003; Thomas et al. 2003), while those using chemosensory cues within currents for orientation would likely move upstream (e.g. Schooley and Weins 2003). Despite the potential influence of currents on landscape scale organism dispersal, no study has comparatively evaluated how the potential differences in search area and directionality associated with currents may affect organism-landscape interactions along this passive-active dispersal gradient.

We developed a spatially explicit, cellular automata model to investigate how animal dispersal strategies interact with water currents and benthic landscape characteristics to influence the recruitment success of dispersing marine organisms at spatial scales of 1s to 100s km. The model was designed to simulate ontogenetic movement of juvenile species within nearshore, estuarine, or backreef habitats. Our model, however, could equally represent movement of some terrestrial organisms influenced by both aerodynamic currents and landscape composition and structure. We compared recruitment success of virtual dispersers as a function of three different dispersal strategies (walking, swimming, and drifting), and in response to the scale and pattern of habitat patchiness. The dispersal

strategy treatments differed in their movement ability (passive versus active horizontal dispersal), their response to currents (ignoring them versus utilizing them), and their potential search area (large versus small). The model was not intended to represent a specific species, but rather to explore the relative advantages of three dispersal strategies' unique dispersal "footprint" (e.g. search area size, shape, directionality) to recruitment success in diverse landscapes. We measured recruitment success in terms of population size (number of survivors), area (number of landscape cells occupied), and time (number of model iterations). We asked: 1) Do the unique characteristics of the three dispersal strategies result in significant differences in recruitment success within similar landscapes? 2) Does the recruitment success of the three strategies respond similarly to changing landscape characteristics? and 3) What is the relative influence of dispersal strategy and landscape characteristics upon recruitment success?

Many dispersal simulation models have investigated the interacting influences of organism behavior and landscape composition and structure on organism dispersal patterns, recruitment success, and subsequent population dynamics. Most of these studies of dispersal have focused on population dynamics (births, deaths, immigration, and emigration) within and between patches of suitable habitat within a matrix of unsuitable habitat (Fahrig and Merriam 1985; Fahrig 1988; Fahrig and Paloheimo 1988; With and Crist 1995; King and With 2002; Ovankainen et al. 2002; Krawchuk and Taylor 2003; Russell et al. 2003; Schooley and Weins 2003). Our dispersal simulation model differed from past models in several important ways: (1) we incorporated currents as an additional factor influencing organism dispersal, (2) our habitat classification system was unique by departing from traditional "good patch", "poor matrix" habitat designations, and (3) we did not model

reproduction due to our focus on recruitment success during ontogenetic habitat shifts rather

than metapopulation dynamics. These design differences, discussed in detail below,

represented what we perceived to be important distinctions between terrestrial and

concomitant marine environments and population dynamics.

METHODS

Modeling organism dispersal strategies

Separate models simulated three generalized dispersal strategies: (1) walking, (2) drifting,

and (3) swimming (Figure 1). Model organisms from all three strategies shared the same

perceptual range, habitat preference and mortality rates (Figure 1). The strategies differed in

their potential search area, ability to orient and move towards preferred habitat, and their

response to currents (Figure 2). Organisms' movement iterations were modeled in two stages

(active and resting) to simulate the selective tidal stream transport, or diel migration common

among marine organisms (review by Forward and Tankersley 2001). When actively

dispersing, organisms experienced the hydrodynamic currents as a uniform flow (constant

speed and direction) from left to right across all simulated landscapes. Resting organisms

sheltered in available benthic habitat and were not influenced by currents (see details below).

Walkers simulated organisms that move on or just above the seafloor, such as many

crustaceans, gastropods, and demersal fish (Figure 1a). Hydrodynamic currents did not

influence walkers' movement direction or range during active dispersal. Instead, the model

evaluated the neighboring eight landscape cells and assigned each a relative attraction value

based upon habitat quantity and the population density. Cells with abundant recruitment

habitat were more attractive to dispersing organisms than cells with sparse recruitment

habitat. Similarly, cells below carrying capacity were more attractive than cells at or above

carrying capacity. Individuals dispersed among the eight neighbor cells proportionate to the

neighboring cells' relative attraction value. Walkers could move one landscape cell per

iteration, in any direction.

The drifter model simulated the strategy of passive horizontal dispersal (Figure 1b).

This strategy is common to some species of crustaceans and bivalves, which rise up from the

seafloor to move with the currents and then recruit to the seafloor as they pass over suitable

substrates (Forward and Tankersley 2001; Gibson 2003). In the horizontal plane of the

model, drifters moved only in response to hydrodynamic currents and could not direct their

movement towards favorable habitat or away from crowded cells. They did, however,

exercise some control over their vertical movement by dropping into unoccupied habitat cells

that passed under their passive dispersal trajectory. Most drifters were transported up to two

cells in the direction of the current, while a small fraction were moved one cell to the right

(10%) or left (10%) of the current, simulating the effects of turbulent mixing.

Swimmers simulated the active dispersal of some fish and crustacean species (Figure

1c; Armsworth et al. 2001; Forward and Tankersley 2001; Gibson 2003). The combination

of neighboring habitat quantity, population density, and hydrodynamic currents determined a

swimmer's dispersal trajectory. Similar to walkers, swimmers' self-propelled movement was

limited to one cell in any direction. Swimmers could, however, utilize currents to extend

their search distance in the direction of a given currents' trajectory. The model allowed

swimmers to move one cell against the current in search of recruitment habitat, however, by

moving with the current, individual swimmers could move up to three cells.

Although our model simulated a linear flow regime, as a simplified representation of the selective tidal stream transport common among many dispersing marine organisms, our results, however, can be considered in light of other flow patterns. For example, if our three generalized dispersal strategies were simulated within a gyre current, we would predict that drifters would be retained, swimmers might gradually disperse beyond the gyre, while the current would not retain walkers, who move independent of current bias.

Modeling landscape patterns

All landscape cells contained some high quality recruitment habitat, but the relative abundance of high quality recruitment habitat, and therefore the carrying capacity, differed among cells. "Good" habitat cells held abundant recruitment habitat and could support a recruitment population of 100 individuals. "Poor" habitat cells contained sparse recruitment habitat and therefore had a carrying capacity of only ten individuals per cell. This quantitative, rather than qualitative definition of good versus poor habitat differs from most previous, terrestrially oriented, cellular models (e.g. Fahrig and Merriam 1985; With and Crist 1995), and is based on our observations of the ubiquitous distribution of recruitment habitat in both temperate and tropical coastal habitats at intermediate (1s to 100s km) spatial scales (Eggleston and Drew, unpublished data).

We assumed that all individuals could distinguish good and poor recruitment habitat, and that they would prefer the former. A penalty was applied to populations located within both good and poor habitat cells under conditions of overcrowding; all individuals in excess of the carrying capacity experienced a higher mortality rate (see mortality rates below).

We used a hierarchical clustering procedure called "Curdled" in the software program RULE (Gardner 1999) to generate 252 by 252 cell binary landscapes. We elected to use hierarchically structured landscapes because 1) they are considered more realistic representations of natural landscapes than randomly generated patterns (Lavorel et al. 1993), and 2) they allowed us to evaluate the relative importance of changing total proportion of good habitat versus the arrangement of habitat within the landscape.

In RULE, we specified three landscape generation levels (Figure 3). The coarsest level (Level 1) divided the whole landscape into forty-nine equal sections and specified that some cells within each section would be classed as good habitat. This ensured that patches of good habitat would be distributed across the entire landscape. Each Level 1 section was then subdivided further into thirty-six medium scale sections (Level 2). We varied the percentage of Level 2 sections that could contain good habitat from 20% to 80%, in increments of 20%. Finally, each Level 2 section that had been randomly selected to contain good habitat was subdivided into the thirty-six individual cells. At this finest scale, Level 3, we again varied the percentage of cells classified as good habitat from 20% to 80% in 20% increments.

The total proportion of good habitat (p_{tot}) was the product of the proportion of cells classified as good at Level 3 (p_{fine}) and Level 2 (p_{med}). Thus, we generated sixteen landscapes among which the total percentage of cells classified as good habitat varied from 4% to 64%. Early trials during the development of the simulation model assured us that the 252 by 252 cell matrix size was adequate to ensure that none of the dispersing individuals would encounter the landscape edges.

Modeling movement, mortality, and recruitment success

We incorporated active and resting dispersal phases into the models to simulate natural

dispersal patterns of many marine species, which commonly exhibit directed movement by

migrating in response to diurnal and tidal cycles (e.g. Forward & Tankersley 2001). Virtual

organisms dispersed only during the active phase and were forced to wait on the seafloor

during the resting phase, irrespective of behavioral strategy. As a consequence of this

movement pattern, walkers dispersed through the landscape cell-by-cell in a manner similar

to traditional, terrestrial cellular dispersal models, while swimmers and drifters experienced a

distinct interaction with the landscape. Poor habitat would not necessarily inhibit or redirect

the movement of swimmers and drifters, which move over rather than through the landscape

cells.

We applied mortality to populations within individual landscape cells at the transition

between the resting and active phases of dispersal. During this transition, the model

evaluated each landscape cell to locate individuals in excess of that cell's carrying capacity.

We assumed that these individuals would lack shelter from predators or sufficient food

resources, and would therefore experience a higher mortality rate per iteration ($37.88 * 10^{-4}$,

equivalent to an annual mortality rate of 0.75). The proportion of the population that had

safely recruited into the available recruitment habitat experienced a lower mortality rate of

$7.87 * 10^{-4}$ per iteration (equivalent to an annual mortality rate of 0.25). The natural

mortality rates of marine species are not well known and vary strongly depending upon the

species' growth rate and longevity (Froese and Pauly 2003). Our mortality rates

corresponded to those of a moderately long-lived fish species (Thompson and Munro 1977).

Following the mortality calculations, all surviving individuals in excess of a cell's carrying

capacity participated in the next active phase of dispersal by moving according to strategy-specific rules (Figure 1). Therefore, habitat quantity and species density together drove both immigration to and emigration from the individual landscape cells in our model. The model continued to iterate through resting and active phases until all surviving individuals successfully recruited into suitable habitat, herein referred to as "complete recruitment". We ran twenty repetitions for each dispersal strategy in each of the sixteen landscapes (20 repetitions x 3 dispersal strategies x 16 landscapes; total $N = 960$). Each dispersal and recruitment simulation commenced with a population of 30,000 individuals seeded to a central landscape cell, and continued until all surviving individuals successfully recruited. Only a single spatial location was seeded initially to eliminate potentially confounding effects of inter-population competition and overlap.

Three response variables measured recruitment success: (1) recruited population size, (2) area occupied, and (3) time to complete recruitment. We considered a dispersal strategy highly successful if it enabled a large proportion of dispersing individuals to quickly recruit over a broad extent. Increased survival would reflect a given dispersal strategy's ability to successfully locate high quality habitat while avoiding over-crowded situations. Recruitment over a broad extent would potentially enable the regional population to survive local perturbations, such as disease outbreak or habitat damage. Finally, rapid recruitment to habitats offering safe shelter from predators and high quality resources would allow individuals the best chance to survive and regain the energy expended during dispersal (McCormick 1998; Zollner and Lima 1999).

Data analyses

For models with large sample size and small variance, similar to our own, MANOVA procedures frequently reveal highly significant results for all main and interaction effects, even where observed differences in recruitment success responses are very small and the biological effects of the measured differences are likely trivial (Steidl and Thomas 2001). Therefore, we used the partial R^2 values calculated from a fully factorial MANOVA to estimate the relative influence of behavioral strategy, the proportion of good habitat at fine and medium spatial scales, and their interactions on recruitment success.

We contrasted recruitment success of the three behavioral strategies by fitting linear, logarithmic, and exponential models to the response slopes of recruitment success to increasing proportion of good habitat as an indicator of overall response strength. In this manner, we evaluated the shape of the response of dispersers to increasing the proportion of good habitat at fine scales (while holding the medium scale proportion constant), and medium scales (while holding the fine scale proportion constant), and for the overall total proportion of good habitat in the landscape. Akaike's Information Criterion (AIC) was then calculated to determine the relative fit of the three models (linear, logarithmic, exponential) to the data. AIC weights (Akaike 1973; Myung and Pitt 1997) provides an objective method of discerning which regression model explains more variability in the data while accounting for differences in sample size and the number of model parameters. We interpreted linear responses between recruitment success and landscape structure as indicative of consistent sensitivity to changing proportion of good habitat across all values of available good habitat, while non-linear responses indicated variable responses to incremental changes in the proportion of good habitat.

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We pooled the recruitment success data for organisms exposed to increasing proportion of good habitat at medium and fine scales because there was no difference at these scales. For example, the total proportion of good habitat in the landscape could be increased from p_{tot}=0.04 (p_{fine}=0.20 and p_{med}=0.20) to p_{tot}=0.12, either through the addition of good habitat cells at medium (p_{med} increased to p_{med}=0.60) or fine (p_{fine} increased to p_{fine}=0.60) spatial scales (Figure 3). Both scenarios resulted in similar recruitment success response curves; mean recruitment success did not vary significantly according to independent sample t-tests. This result of equal means was observed for all simulations with equal total proportion of good habitat but opposite landscape structure. Therefore, we pooled the data based on total proportion of good habitat for all further comparisons of the effects of the three dispersal strategies on recruitment success.

Simulations and model sensitivity analysis

In addition to the dispersal strategy and landscape treatment effects, our model contained two constant parameters that influenced the simulation outcomes: mortality rate and carrying capacity. Past research into the data requirements and sensitivity of spatially-explicit population models indicates that incorrect estimates of parameters such as dispersal mortality can result in significant prediction errors for dispersal success (Ruckelshaus et al. 1997). Therefore, a sensitivity analysis of the simulation results was conducted to understand how error in mortality rate and carrying capacity would affect the simulation outcome. This sensitivity analysis sequentially examined the influence of a 10% increase and 10% decrease in mortality rate and carrying capacity on recruitment success for each of the original forty-eight landscape-strategy combinations (Table 2).

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RESULTS

Relative recruitment success of the three dispersal strategies

When we measured recruitment success by the population size at complete recruitment (proportion of dispersing individuals that successfully recruit), the strategies that utilized currents (swimmers and drifters) were more successful than the walker strategy, which ignored currents (Figure 4a). Differences among the three strategies were generally greater for the area and time response variables, however, than for population size (Figure 4). Swimmers dispersed over a larger area and occupied more landscape cells than either drifters or walkers, which had much smaller potential search areas during each iteration of the model (Figure 4b). Swimmers also required the fewest model iterations to successfully locate and occupy recruitment habitat (Figure 4c). In comparison, walkers recruited somewhat slower than swimmers, but faster than drifters (Figure 4c). Thus, active dispersers recruited faster than passive dispersers, and organisms with a large potential search area recruited faster than those potentially searching a smaller area.

The rank order of the three dispersal strategies generally remained constant for a given response variable regardless of the proportion of good habitat in the landscape (Figure 4). As an exception, while drifters typically occupied more landscape cells than walkers, the opposite was true at the lowest ($P_{tot} = 0.04$) and the highest ($P_{tot} \geq 0.48$) modeled proportion of good habitat (Figure 4b).

The magnitude of the differences in recruitment success between dispersal strategies differed depending upon the proportion of good habitat and the response variable measured. Differences among the three dispersal strategies' mean recruited population size were greatest when the landscape presented an intermediate proportion of good habitat (Figure 4a:

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$0.16 < P_{tot} > 0.48$). Alternatively, for mean time to complete recruitment and mean area

occupied, differences among the dispersal strategies were most pronounced with a low

proportion of good habitat (Figures 4b and c: $P_{tot} < 0.40$). As the total proportion of good

habitat increased, the advantage of walker and drifter strategies relative to swimmers, as

measured in time and area occupied, diminished rapidly (Figures 4b and c).

Influence of increasing total proportion of good habitat

All three behavioral strategies benefited from increasing the proportion of good habitat;

however, the strength and shape of the recruitment response curves differed among strategies

and recruitment response variables (Figure 4). Overall, drifters were most sensitive (steepest

slope) to changes in the proportion of good habitat cover, particularly as the proportion of

good habitat increased from low ($P_{tot}= 0.02$) to moderate ($P_{tot} = 0.48$) levels, while swimmers

were least sensitive. Differences between the strategies were most pronounced for the

response variables time and area (Figure 4b and c).

All strategies' final recruited population size responded positively and exponentially

to increasing total proportion of good habitat (Figure 4a). This non-linear response was

slightly more pronounced for swimmers and drifters than for walkers, in that: (1) the

exponential models for swimmers' and drifters' population responses had higher adjusted R^2

values (adj. R^2 swimmer = 0.916, drifter = 0.945) than the walkers population response (adj.

R^2 walker = 0.884), and (2) AIC attributed no weight to the swimmer and drifter linear

models, while the walker response could have been described by the linear model (AICw

linear = 0.013). Thus, the ability to rise off the seafloor and disperse within currents

(swimmers and drifters) resulted in a strong exponential response, in contrast to walkers who

showed a more constant increase in final recruited population size over the same range of

landscape changes (Figure 4a). Currents and an organisms' ability to behaviorally respond to

currents did marginally affect landscape-organism interactions by increasing sensitivity to

habitat loss or gain when the total proportion of good habitat in the landscape was low, and

decreasing sensitivity when the total proportion of good habitat was high (Figure 4a).

Drifters showed a logarithmic increase of area occupied in response to increasing

good habitat, whereas walkers displayed a linear response to the same landscape change.

Swimmers displayed a general lack of response (all model adj. R^2 values < 0.047) due to very

high variability around the mean number of occupied cells, particularly at intermediate

proportions of good habitat (Figure 4b: $0.16 < P_{tot} < 0.48$). Although, swimmers and drifters

experienced similar recruitment success in terms of population size, swimmers settled over a

broader area because they more successfully encountered and settled within the cells hosting

sparse settlement habitat (e.g. the poor habitat cells). Drifters showed a logarithmic decrease

in mean time to complete recruitment in response to increasing the proportion of good

habitat. The responses of walkers (linear) and swimmers (exponential) were much less

pronounced (Figure 4c). Thus, recruitment time for organisms with small search area and the

inability to horizontally navigate towards good habitat appears more sensitive to landscape

changes than does the recruitment time for organisms with large search areas or directed

movement. For both the time and area response variables, a non-linear model best described

the responses of organisms utilizing currents (swimmers and drifters), while a linear model

best described the walker response (Figure 4b and c).

Relative influence of dispersal strategy and landscape structure on recruitment success

Although all interaction terms in the fully factorial MANOVA were significant, the partial R^2 values revealed that the main effects (behavioral strategy, proportion of good habitat at the coarse scale, and proportion of good habitat at the fine scale) explained most of the variability in recruitment success (Table 1). While landscape characteristics accounted for most of the variation in recruited population size (45% and 38% for coarse and fine scale, respectively), behavioral strategy explained most of the variation in area occupied by recruits (50%) and time to complete recruitment (54%).

Sensitivity Analysis

Our model was not overly sensitive to the constant values selected for mortality and carrying capacity (Table 2). In almost all cases, 10% changes in mortality or carrying capacity resulted in <10% change in all measures of recruitment success (Table 2). Changing the value of these constants also failed to affect the relative recruitment success of the three dispersal strategies in response to increasing total proportion of good habitat (Table 2).

DISCUSSION

The importance of currents and organism dispersal behavior in connecting distant habitat patches across broad spatial scales is well documented for a variety of terrestrial (e.g. Thomas et al. 2003; Nathan et al. 2005), aquatic (Nilsson et al. 2002; Elliott 2003), and marine (e.g. Wolanski et al. 1997; Botsford et al. 2001; Carr et al. 2003; Gaines et al. 2003) species. Likewise, regional habitat heterogeneity is recognized as essential to conserve species diversity (Tuomisto et al. 2003; Tews et al. 2004) and, particularly in marine

populations, to support some species' complex life-cycles that require multiple habitat types (Acosta 1999; Leslie et al. 2003). Yet, these three factors (currents, behavior, and habitat) are rarely explicitly considered together in the design of dispersal and recruitment studies, or in the evaluation of proposed habitat-based conservation strategies (but see: Schmitt and Holbrook 2002; Schooley and Weins 2003; Nathan et al. 2005). In this study we quantified the recruitment success of organisms simulating three generalized dispersal strategies within currents flowing across hierarchically structured landscapes that varied in the percentage of available recruitment habitat. We determined that (1) currents modify recruitment success of organisms dispersing through heterogeneous landscapes based on dispersing organisms' behavioral responses to those currents (whether to walk, swim, or drift).

Existing landscape ecology theory predicts decreased sensitivity to landscape structure as organism dispersal range increases, and as the total proportion of good habitat increases (Fahrig and Paloheimo 1988; King and With 2002). Thus, in comparing walkers (small search area, limited dispersal range) in this study, drifters (small area but longer range), and swimmers (larger area and longer range), it was not surprising that organism dispersal behavior in the presence of currents (whether to walk and ignore them, drift passively, or actively disperse within the currents) strongly influenced subsequent recruitment success during ontogenetic habitat shifts. It is important to consider the implications of these differences in the three strategies' recruitment success in the context of conservation and management planning, as well as experimental design and interpretation of recruitment studies.

Spatially explicit population models are often used to predict dispersal patterns among distant habitat patches for such diverse purposes as predicting the spread of invasive

species and diseases (With 2002), designing reserve networks that maximize propagule exchange to reduce extinction risk (Cabeza and Moilanen 2003), and postulating the effects of climate change on species distribution patterns (Iverson et al. 2004). Our results support a growing body of evidence demonstrating the importance of incorporating dispersal behavior into such spatially explicit population models (Lima and Zollner 1996; Russell et al. 2003). Models ignoring the role of currents and organisms' behavioral responses to currents would potentially underestimate the time passive drifters require to locate and occupy recruitment habitat, but overestimate the time required by active swimmers. Errors estimating time spent searching for suitable habitat could have significant effects on population models because several parameters, particularly those related to mortality (e.g. predation risk) and condition (e.g. energetic reserves), are often time dependent (Hiebeler 2004; Zollner and Lima 2005). Predictions of the number of successful recruits would also potentially be incorrect, as we found that organism-current interactions increased the number of individuals successfully recruiting to good habitat. Also, although walker-style models would also potentially provide an accurate prediction of the total area occupied by organisms that drifted, they would underestimate the area occupied by organisms that actively dispersed within currents, and thereby potentially underestimate the functional connectivity of the landscape for these species.

The potentially strong influence of dispersal behavior on recruitment success and the tendency of sparse habitat to accentuate the differences in recruitment success among the dispersal strategies point to several situations where knowledge of current-organism behavior could benefit conservation planning and monitoring. The high sensitivity of drifters and walkers to habitat loss relative to swimmers, as evidenced by their steep response to

increasing proportion of good habitat, suggests that species with these dispersal strategies would serve as the best focal or indicator species where habitat loss was a concern (Lambeck 1997). Likewise, conservationists considering alternative sites for protection may want to place a priority on the habitat essential to species that display walker or drifter behavior due to their sensitivity to habitat loss. Regarding the amount and configuration of habitat protected, several small protected areas would be expected to disproportionately benefit species dispersing actively within currents, as these species disperse and recruit over the largest area and therefore would be least susceptible to habitat fragmentation or localized perturbations. Although recruitment success always increased with increasing proportion of good habitat, the effect was not equal for all three dispersal strategies or among response variables. By actively moving within currents, swimmers potentially search a larger area, more rapidly than either drifters or walkers. As large search areas are known to decrease sensitivity to landscape changes by increasing the probability that the dispersing organism will encounter the desired habitat (Fahrig 1988), swimmers' relative insensitivity to varying the total proportion of good habitat was not surprising. It was surprising, however, that drifters were more sensitive to increasing proportion of good habitat than walkers. Both swimmers and drifters exhibited a more linear search pattern and could travel further into the landscape with each iteration relative to walkers. Increasing dispersal distance typically decreases sensitivity to landscape changes (Fahrig 1988), and linear and "nearly linear" search patterns, such as our drifter strategy, can be advantageous over strategies that follow a random-walk pattern (Zollner and Lima 1999). In our model, however, the ability to actively navigate towards good habitat ultimately had a greater influence on sensitivity to landscape change than did increasing dispersal distance. This sensitivity to landscape change likely

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reflected the passive nature of drifter dispersal; although drifters with their long, nearly linear search pattern more frequently encountered good habitat patches, they could not disperse laterally to fully occupy these patches.

The potential for currents to increase the linear distance an organism travels became important, however, when we considered the shape of the recruitment success response curve as we increased the proportion of good habitat. The longer search distances of drifters and swimmers corresponded to non-linear responses for the area occupied by recruits and final population size. For these non-linear responses, increasing the proportion of good habitat from low to intermediate levels was more beneficial than increasing the proportion of good habitat from intermediate to high levels. In contrast, the recruitment success of walkers, which could actively control their horizontal movement but could not utilize currents to extend their search area, increased linearly with increasing proportion of good habitat. Therefore, for walkers, any gain or loss of good habitat had a corresponding effect upon recruitment success.

All dispersal studies, whether terrestrial or marine, face a common challenge: while behavioral decisions are often made in response to fine spatial resolution of environmental cues (e.g. habitat quality or the presence of conspecifics), the cumulative response of these decisions are generally observed at the population and community levels over broad spatial scales. In terrestrial dispersal simulation studies, the challenge of representing fine scale spatial habitat heterogeneity in large scale models has led to the predominance of patch-corridor-matrix model design, where (1) populations reside and reproduce within patches and emigrate to new patches via corridor or matrix habitat, and (2) each landscape cell is considered either suitable or unsuitable for dispersal or reproduction. This patch-corridor-

matrix approach has been found effective to predict dispersal pathways and population dynamics for many species, including invertebrates (e.g. Johnson et al. 1992; Firle et al. 1998; Jonsen et al. 2001; Goodwin and Fahrig 2002), vertebrates (e.g. Fahrig and Merriam 1985; Zollner and Lima 1997), and even seeds (e.g. Tewksbury et al. 2002). Alternatively, models of marine organism dispersal typically emphasize hydrodynamic currents rather than complex benthic habitat mosaics. Although our landscapes did contain hierarchically structured habitat patches, our classification of landscape cells departed from the traditional patch-corridor-matrix model by assuming that all landscape cells within dispersal range would contain at least some habitat suitable for settlement. This classification undoubtedly contributed to the absence of an effect of landscape structure on recruitment success (e.g. increasing the proportion of good habitat at fine scales or at medium scales had the same effect). However, dispersal by currents is thought to reduce marine organisms' response to landscape patchiness by enhancing movement over inhospitable habitat (Darcy and Eggleston 2005), increasing the grain at which dispersing organisms respond to habitat heterogeneity (Kotliar and Wiens 1990), and thus potentially reducing the relevance of traditional patch-corridor-matrix representations of benthic landscape structures to dispersal studies in marine systems.

Our results have important implications for spatial scaling in ecological experiments. Identifying the appropriate spatial scales for population modeling and empirical ecological studies remains a significant challenge. Allometric scaling studies conducted on terrestrial species to relate species size to such factors as home range or mean and maximum dispersal distance (Sutherland et al. 2000), have not typically accounted for the effects of currents. Our model highlights how organism-current interactions could influence these and other

scaling relationships of importance in landscape ecology. Currents potentially alter

allometric relationships such that smaller, less mobile species would be able to travel further

than expected based solely on their size or average movement speeds. Kinlan and Gaines

(2003) noted that dispersal by sedentary marine species (whose larvae swim or drift in ocean

currents) was typically one to two orders of magnitude greater than estimated maximum

dispersal distances of terrestrial plants. A review by Carr et al. (2003) similarly concluded

that dispersal distances are much greater in marine systems. The failure of allometric

measures to account for currents may help explain why marine experiments modeled after

successful terrestrial landscape projects, using similarly spatial scales and similarly species,

can fail to measure significant landscape effects on dispersal (Darcy and Eggleston 2005).

In general, our study supports major conclusions from predominately terrestrially

oriented simulation literature: both organism behavior and landscapes influence dispersal

patterns, and should be considered in conservation management or experimental design,

particularly when either behavior (e.g. limited range, limited orientation ability) or landscape

structure (e.g. limited suitable habitat or the presence of dispersal barriers) limit dispersing

individuals' access to suitable habitat patches. However, our research highlights the need to

jointly consider the influence of currents, dispersal behavior, and landscape structure on

dispersing organisms' recruitment success wherever currents potentially play an important

role in shaping dispersal pathways and subsequent population and community dynamics.

The unique dispersal footprints associated with different behavioral dispersal strategies in

this study differed in the magnitude and shape of their response to landscape changes. The

nature of these differences in recruitment success could not have been predicted by

individual search area or distance alone, but rather by the combined effects of currents on organism search area, distance traveled, and directionality of dispersal.

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Table 1. Sum of squares and partial R^2 values from a fully factorial MANOVA testing the main and interaction effects of dispersal strategy, proportion of good habitat at the coarse spatial scale, and proportion of good habitat at the fine spatial scale on recruitment success. R^2 values are shown for all main effects. None of the interaction effects exceeded $R^2 = 0.05$.

Source	DF	Sum of Squares	Partial R^2
RECRUITED POPULATION SIZE			
Strategy	2	16192	0.0508
Coarse	3	144393	0.4526
Fine	3	123025	0.3856
AREA OCCUPIED BY SUCCESSFUL RECRUITS			
Strategy	2	3347073	0.4995
Coarse	3	788411	0.1177
Fine	3	689005	0.1028
TIME TO COMPLETE RECRUITMENT			
Strategy	2	113611	0.5370
Coarse	3	35460	0.1676
Fine	3	31919	0.1509

Table 2. Summary of sensitivity analyses of a ± 10% change in mortality and carrying capacity on mean recruitment success of organisms displaying three different dispersal strategies: (1) walk, (2) drift, and (3) swim. Both annual mortality rate (AMR) and the equivalent daily mortality rate (DMR) are presented. Sensitivity analyses of recruitment success to mortality and habitat carrying capacity were evaluated against the original model for each dispersal strategy using the following response variables: (1) mean recruited population size (Pop), (2) mean area occupied by recruits (Area), and (3) time to complete recruitment (Time). The effects of changing mortality and carrying capacity were minor and did not affect the rank order of recruitment success or the strength and shape of the recruitment success response curve with increasing proportion of good habitat in the landscape.

| | Percent Change in Constant | Settled Individuals' Mortality AMR (DMR) | Dispersing Individuals' Mortality AMR (DMR) | Carrying Capacity of Poor Habitat # Individuals | Carrying Capacity of Good Habitat # Individuals | Percent Change in Response Variable Mean | | | | | | | | |
| | | | | | | Walk | | | Drift | | | Swim | | |
						Pop	Area	Time	Pop	Area	Time	Pop	Area	Time
Original Model	N/A	0.25 (0.000787)	0.75 (0.003788)	10	100	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Mortality Rate Sensitivity	+10 %	0.275 (0.000880)	0.825 (0.004761)	10	100	-3.2	-0.1	-5.0	-9.1	-8.0	-10.0	-2.4	1.4	-7.7
	-10 %	0.225 (0.000698)	0.675 (0.003072)	10	100	0.9	-0.5	2.1	2.9	3.2	3.5	0.7	-0.4	2.3
Carrying Capacity Sensitivity	+10 %	0.25 (0.000787)	0.75 (0.003788)	11	110	6.8	4.4	-2.7	6.4	-0.3	-5.2	8.9	5.7	-3.7
	-10 %	0.25 (0.000787)	0.75 (0.003788)	9	90	-7.4	-4.9	3.2	-7.7	2.2	5.9	-9.4	-6.4	4.1

FIGURE LEGENDS

Figure 1. Three movement behaviors: A) Walking, where an individual may move in any direction based upon habitat preference; B) Drifting, where an individual cannot move against or perpendicular to the current; and C) Swimming, where an individual can move in any direction, however, the current significantly biases potential movement. The dark arrow on the right indicates direction of current flow. The white diamonds represent individual organisms, with the potential movement trajectories identified by the fine arrows. The gray areas indicate the potential search area of the individuals. Notice that the area, shape and perimeter of the search areas vary between movement strategies. The daily mortality rates correspond to annual mortality rates of 0.25 when recruited to good habitat, and 0.75 while dispersing in search of good habitat. Simulated currents flowed from left to right across all landscapes.

Figure 2. Conceptual design of model illustrating how movement strategy characteristics (search area size, ability to orient and move towards preferred habitat, and whether the strategy uses currents) are shared by two strategies but differ for the third strategy. This design allowed us to distinguish which of the three characteristics were driving observed differences among strategies. If the model outcome appeared as shown in A, the shared characteristics of the two strategies with high recruitment success is their ability to utilize currents (swimmers and drifters), while the strategy with lower recruitment success (walkers) does not utilize currents. In B, the characteristic that distinguishes organisms with high recruitment success from those with lower recruitment success is their respective search areas (large for swimmers, but small for walkers and drifters).

Figure 3. Schematic of three of the 16 hierarchically structured cellular landscapes used to manipulate the scale and pattern of habitat patchiness. The dark cells represent areas with abundant settlement habitat and, therefore, high carrying capacity (referred to as "good" habitat in the text). The white cells indicate areas that offer sparse settlement habitat and limited carrying capacity within the cell's area (referred to as "poor" habitat in the text). Comparison of the images A and B illustrates how adding good habitat at the fine scale generated small, tightly clumped patches of good habitat separated from one another by expanses of poor habitat. Alternatively, as shown by comparing images A and C, adding good habitat at the medium scale generated a dispersed pattern with fewer dense patches of good habitat, but also fewer open expanses of poor habitat than observed when habitat was added at fine scales.

Figure 4. Effects of dispersal strategy (walk, drift, swim) and total proportion of good habitat in the landscape on recruitment success as measured by (A) mean recruited population size (represented as the proportion of dispersers that successfully recruit), (B) mean area occupied by successful recruits, and (C) mean time to complete recruitment. Each series of symbols represents the nine distinct P_{tot} values obtained from the sixteen model landscapes. Individual symbols represent the mean of twenty ($P_{tot} = 0.04, 0.36, 0.64$), forty ($P_{tot} = 0.08, 0.12, 0.24, 0.32, 0.48$), or sixty ($P_{tot} = 0.16$) model repetitions. Error bars show one standard deviation above and below the mean. The model type, adjusted R^2 values, P-values, and AIC weights are shown in the table to the right of each figure. For each dispersal strategy, the models are listed from best to worst fit based on their AIC weights. The best fitting models are illustrated on the figures.

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Common Characteristics:

Perceptual range:
- 8 neighboring landscape cells

Habitat preferences:
- Prefer sites with abundant shelter to sites with sparse shelter
- Prefer sites below carrying capacity to sites at or above carrying capacity

Daily mortality rate:
- $7.87 * 10^{-4}$ when recruited
- $37.88 * 10^{-4}$ while dispersing

A) WALK   B) DRIFT   C) SWIM

Strategy-Specific Characteristics:

	A) WALK	B) DRIFT	C) SWIM
Self-propelled mobility:	Yes, 1 cell	No	Yes, 1 cell
Current influences movement:	No	Yes	Yes
Moves above or through benthos:	Through	Above	Above
Controls movement direction:	Yes	No	Yes
Potential search area per time step:	8 cells	8 cells	16 cells

Figure 1. Summary of the characteristics of three generalized dispersal strategies: walkers, drifters, and swimmers.

Figure 2. Conceptual design of model.

Increase proportion of good habitat at fine scale

Increase proportion of good habitat at medium scale

A
P_{tot} = 0.04
P_{med} = 0.2
P_{fine} = 0.2

B
P_{tot} = 0.12
P_{med} = 0.2
P_{fine} = 0.6

C
P_{tot} = 0.12
P_{med} = 0.6
P_{fine} = 0.2

Poor habitat   Good habitat

Direction of flow across all landscapes
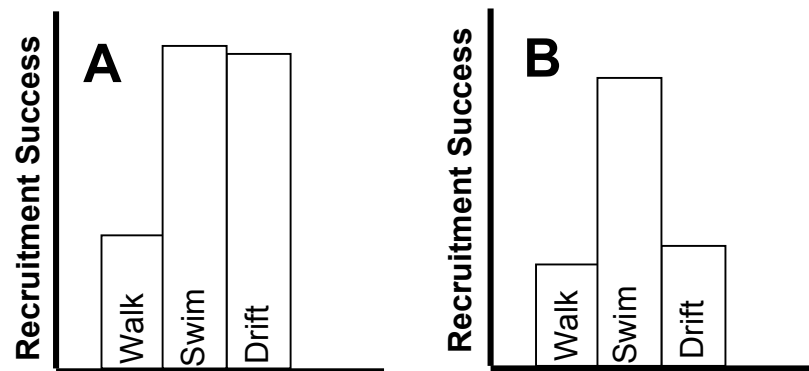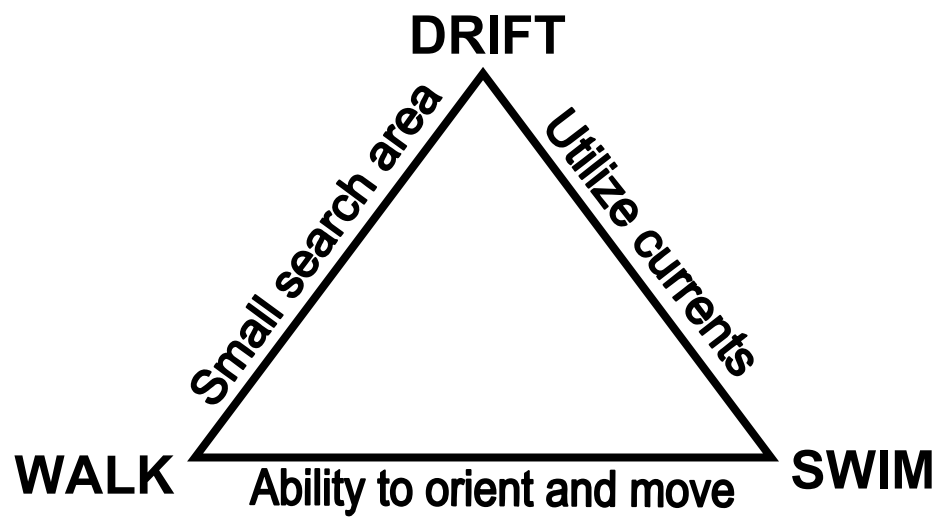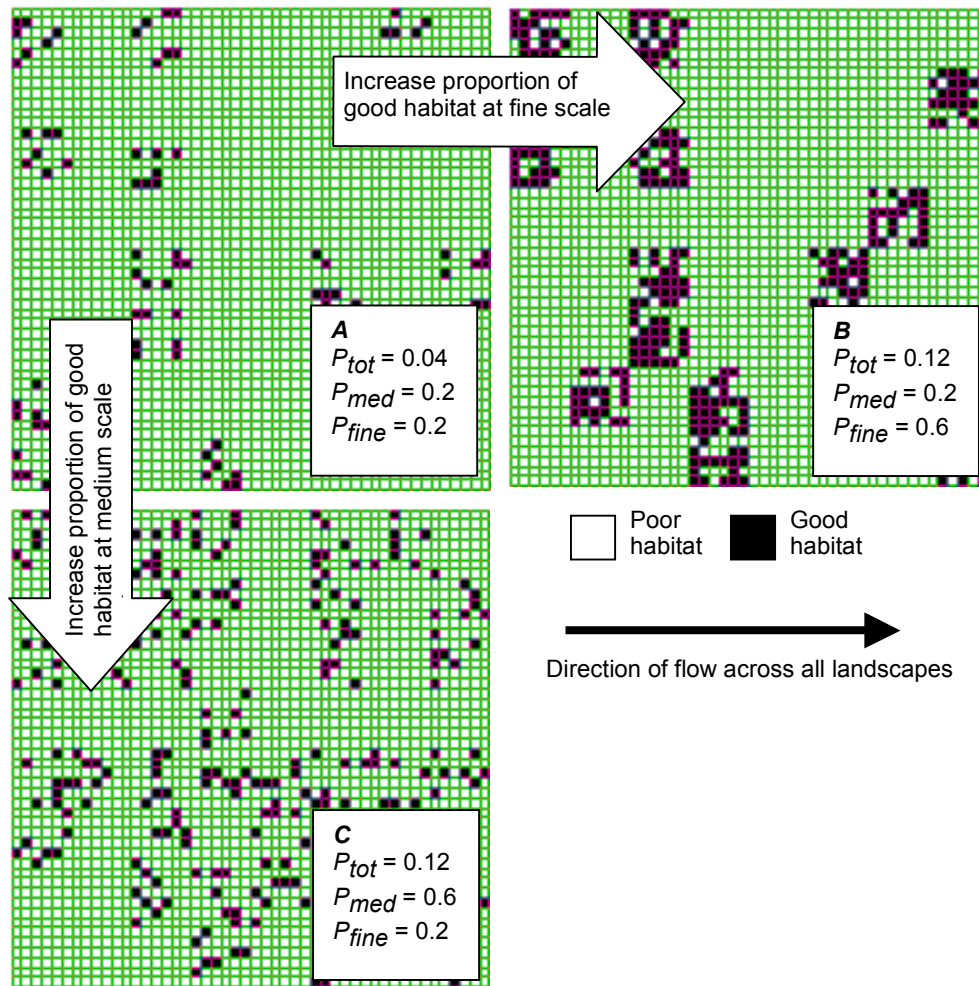
Figure 3. Hierarchically structured landscapes.
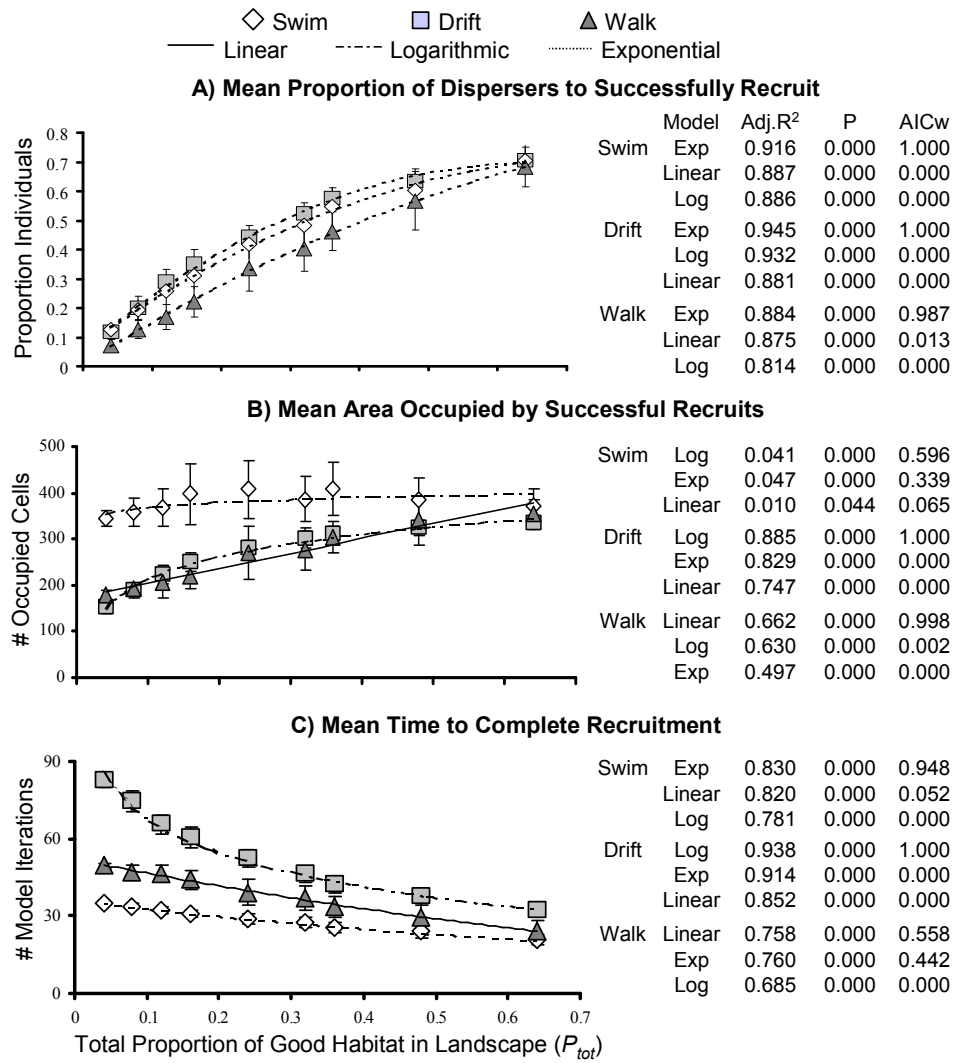
Figure 4. Recruitment success of three dispersal strategies fit to linear, logarithmic, and exponential models.

CHAPTER 2

Local juvenile fish densities in Florida Keys mangroves correlate with

regional landscape characteristics.

Drew, C.A. and D.B. Eggleston. In Review.

Marine Ecology Progress Series

ABSTRACT

Although nursery habitat patches of similar type (e.g. mangroves) are often lumped together for research and conservation purposes, juvenile fish density and diversity can vary greatly among patches of the same habitat type. Such variability in abundance could arise from variability in larval supply or from differences in habitat characteristics that influence juvenile habitat selection, recruitment success, and survivorship. We used backwards elimination, multiple regression models to test relationships between juvenile fish density and diversity, and patch- (100's m) and landscape-scale (1 km) habitat characteristics in mangrove prop root habitats of the Great White Heron National Wildlife Refuge in the lower Florida Keys, USA. Our results demonstrated that: (1) variability in juvenile fish density in mangrove backreef habitats correlates strongly with landscape-scale habitat characteristics; (2) each species' density correlates to a unique combination of patch or landscape characteristics; and (3) juvenile fish diversity is not strongly correlated to either patch- or landscape-scale habitat characteristics. Based on individual species' strong correlation with the landscape data (benthic, terrestrial, and bathymetric habitat characteristics), considering a site's landscape context could greatly aid in (1) selecting fish species and sites for experiments to test nursery habitat hypotheses, and (2) implementing conservation strategies based upon habitat surrogates or quotas (e.g. protect 20% of mangrove habitat to conserve fish species associated with mangroves as juveniles). We also support the use of habitat contour mapping and individual-based modeling as alternative tools to prioritize backreef nursery habitat sites for conservation, because these methods can account for the unique responses of individual species to habitat variability at multiple spatial scales.

INTRODUCTION

Understanding organisms' perceptions of and responses to landscape heterogeneity and connectivity is essential for effective ecological conservation and management (Doak and Mills 1994; Poiani et al. 2000; Collinge 2001). The need for such understanding is particularly urgent in marine environments given present initiatives to identify and conserve nearshore estuarine and marine ecosystems that serve as nursery habitats for many marine fish and invertebrate species (Beck et al. 2001). Significant effort has been applied towards clarifying the functional definition of nursery habitat and developing hypothesis-driven criteria for delineating these sites (Beck et al. 2001). Empirical studies have shifted focus from simply demonstrating the presence of juveniles within nursery habitats, to investigating the relative value of different nursery habitats (Dahlgren and Eggleston 2001) and studying linkages between nursery and adult populations (Gillanders et al. 2003) by correlating the presence of juvenile habitat to the abundance and distribution of adult populations (Nagelkerken et al. 2002; Halpern 2004). These papers demonstrate that (1) juvenile fish growth and survival do differ among backreef habitats, and (2) adult fish density sometimes correlates positively with the neighboring presence (versus absence) of nursery habitat. These studies do not, however, demonstrate how landscape-scale habitat composition, configuration, and connectivity affects organism distribution and abundance patterns.

Relatively little is known about how marine species perceive or respond to variation in habitat characteristics at the landscape scale (Beck et al. 2001). Published research does, however, suggest important differences between terrestrial and marine spatial ecology. While terrestrial species-area relationships predict greater species diversity in larger patches, several marine studies have found longer patch perimeters may attract more immigrants,

support higher survival rates, and have greater species diversity than large patches (Eggleston et al. 1998; Eggleston et al. 1999; Hovel and Lipcius 2002). Species-area curves also appear steeper for marine species than for their terrestrial counterparts (Chittaro 2002). When Halpern (2004) investigated the relationship between adult coral reef fish densities, the size of mangrove nursery habitat, and proximity of mangrove patches, he found no significant relationships between adult densities and these patch characteristics, suggesting that patch area and patch isolation by distance play less important roles in marine systems than in terrestrial systems. Halpern (2004), however, did observe a highly significant log-linear relationship between adult reef fish density and island-wide mangrove area for one unfished species (*Gerres cinereus*). This landscape-scale correlation agrees with the results obtained by Mumby et al (2004) and Nagelkerken (2002), supporting the argument that correlations between adult fish population density and nursery habitat area are scale-dependent. In contrast, a study of island biogeographic theory applied to the benthic macrofauna of Danish estuaries concluded that habitat area did not influence species richness, but that habitat isolation (measured as the restriction of water flow between estuarine and oceanic waters, rather than physical distance) did significantly influence community structure (Josefson and Hansen 2004).

We examined the relationships between juvenile fish population density and diversity, and mangrove habitat characteristics in the Florida Keys, USA. Mangrove prop roots are important nursery habitat for many tropical reef fish species (Nagelkerken et al. 2000b; Cocheret de la Morinière et al. 2002; Nagelkerken et al. 2002; Eggleston et al. 2004b; Halpern 2004; Mumby et al. 2004). Eggleston et al. (2004a) described fish population density, diversity, and habitat features at 31 mangrove sites in the Great White Heron

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National Wildlife Refuge, Florida Keys, USA. Their data reveal significant variation in fish species diversity, overall fish population density, and population density of individual fish species among the mangrove stations (Eggleston et al. 2004a). They did not, however, find a relationship between total fish population density or diversity and local habitat features (water depth, distance visible into mangrove prop roots, and canopy height).

In this study, we extend the data analysis by Eggleston et al. (2004a) by focusing on juvenile fish species living within and along-side the mangrove prop roots. Our approach is novel in that, rather than simply focus on the ecology of the life-stage found in mangrove habitat and the characteristics of the immediate mangrove microhabitats, we incorporated independent variables that (1) reflected the highly mobile and complex life-history of each individual species, and (2) considered both the patch- (100s square meters) and landscape-scale (including bathymetric, benthic, and terrestrial landscape features within 1 km radius from each survey site) characteristics of mangroves. For example, we hypothesized that the relative quality of two mangrove sites might not simply reflect microhabitat or patch characteristics (e.g. water depth), but also regional landscape conditions such as proximity to oceanic larval sources for pelagic-spawned species, or proportional cover of seagrass in neighboring waters for species that depended on this resource in earlier or later life-stages. We asked: (1) Can patch and landscape characteristics serve as useful indicators of juvenile fish population and community structure? and (2) Does the inclusion of marine-specific, landscape-scale metrics, such as distance from oceanic larval pools or distance from hydrodynamic channels, increase statistical models' ability to describe population and community variability?

METHODS

Study Site

The refuge is part of a network of protected areas designed to conserve the ecological and economic resources of the Florida Keys ecosystem. The refuge, located on the north (Gulf of Mexico) side of the lower Florida Keys, extends west of Marathon Key from the middle of Seven Mile Bridge to the eastern end of Key West (Figure 1), and was established in 1938 to protect migratory birds such as herons and egrets from commercial exploitation. Neither commercial nor recreational fishing is restricted within the park, except within certain vessel exclusion zones near important colonial nesting sites (e.g. frigate birds, *Fregata* sp.). Most of the refuge area (~784 km^2, 99%) is designated as intra- or subtidal wilderness marine habitat, including mangroves, seagrass beds, hardbottom, macroalgal beds, sand flats, and coral reefs. The hydrography of the area is influenced both by the Gulf of Mexico and the Florida Current, and species composition in the area likely reflects recruitment from both water masses (Eggleston et al. 2004c).

Fish and Fish Habitat Surveys

In July-August 2002 and August 2003, Eggleston et al. (2004a) performed the first systematic survey of fish and fish habitat across a mosaic of five habitat types within the refuge. These surveys documented fish density, diversity, and size structure, as well as habitat characteristics, at 31 randomly selected mangrove island sites. The survey methods had been developed and tested in similar habitat elsewhere in the Florida Keys (Eggleston and Dahlgren 2001; Eggleston et al. 2004b). Each island was surveyed once, as near as possible to a daytime high tide, because (1) most fish species only shelter within the prop

roots during the day (Rooker and Dennis 1991), and (2) mangrove habitats do not experience significant nocturnal-diurnal changes in species composition (Rooker and Dennis 1991). At each island, two to four snorkelers performed 10-minute visual surveys of fish populations within and alongside the mangrove prop roots. Snorkelers recorded individual fish by species and length to nearest centimeter (except counts of fish at a given size within large schools of baitfish were estimated by hundreds or thousands). Each snorkeler also measured their survey distance and estimated the water depth, distance visible into prop roots (effective survey width), and canopy height within their section. GPS coordinates were obtained as close to the mangrove fringe as possible, central to the total length of mangrove coastline surveyed by all snorkelers. Snorkeler's fish counts were standardized by area searched (fish per 100 m^2), and then both fish and habitat observations were averaged across all snorkelers at a given site. Of the 31 mangrove sites surveyed by Eggleston et al. (2004a), 22 were defined as spatially independent at the 1 km regional-scale used in our landscape analyses (sites separated by greater than 1 km). These sites, spread across the refuge, were the sample units of our study (Figure 1), rather than individual islands (entire islands were rarely surveyed) or individual snorkelers' surveys (a form of pseudo-replication).

Juvenile fish density and diversity were extracted from the data collected by Eggleston et al. (2004a). Juvenile fish were identified based on maximum length data (cm total length, TL) presented in the Life History Data Tool in FishBase (Froese and Pauly 2000). All fish less than one third of the maximum length were classified as juveniles; this method is reliable for several Caribbean mangrove and seagrass fish species (Nagelkerken and van der Velde 2002; Nagelkerken and van der Velde 2004). Of the greater than 280,000 fish representing 45 species in 25 families observed in the refuge mangroves, just over

200,000 fish of 37 species in 20 families were identified as juveniles. Most of these juvenile fish (97.2%) were from the families Atherinidae, Clupeidea, and Engraulidae (hereafter referred to as the ACE complex), which swam in large schools along the mangrove fringe of some islands. The next most abundant species, *Lutjanus griseus*, accounted for 2% of total juvenile fish sightings, or 64.7% of non-ACE complex juvenile fish sightings. Other species accounting for greater than 1% of the non-ACE juvenile species sightings were: *Eucinostomus melanopterus* (14.1%), *Archosargus rhomboidalis* (3.1%), *Anisotremus virginicus* (2.7%), *Gerres cinereus* (2.6%), *Ablennes hians* (2.4%), *Sphyraena barracuda* (2.3%), and *Lutjanus apodus* (1.6%). Many juvenile species were present at only one mangrove site, and only ten species or families were present at ten or more of the 22 sites included in this study. Our species density analyses included only these ten species and families (Table 1), but the diversity analyses included all species. At each site, we calculated the juvenile fish density (total and for individual species) and species diversity. Species diversity was measured as Shannon's evenness index (Washington 1984) and species density (Gotelli and Colwell 2001). Species density was represented both as the observed mean total species density for each site, and rarefied to a common density of individuals to match the lowest observed density among mangrove sites (150 individuals per 100m^2) (Sanders 1968; Gotelli and Colwell 2001).

The field data from the refuge fish and fish habitat surveys (Eggleston et al. 2004a) reported the following patch characteristics for each mangrove site: mean water depth at the mangrove margin, mean depth visible into prop roots, and mean mangrove canopy height (Table 2). All three variables were included in our study.

Landscape Characteristics

We tested the relationships between juvenile fish density and diversity, and characteristics of three landscapes: benthic, bathymetric, and terrestrial. The Florida Keys Benthic Habitats atlas (Florida Marine Research Institute 1998) provided digital, shallow-water (< 2 m) benthic cover data. These data supported the identification and mapping of six benthic habitat types: continuous seagrass, patchy seagrass, patch reef, platform margin reef, hardbottom, and barren. Specific descriptions of each habitat type may be found in this benthic atlas' metadata files (Florida Marine Research Institute 1998). Areas deeper than 2 m were labeled as ocean. This digital atlas also provided bathymetric data, which facilitated the identification of major channels and the 10 m isobaths surrounding the refuge. The Florida Vegetation and Land Cover atlas (Florida Fish and Wildlife Conservation Commission 2004) provided digital data characterizing 17 natural (e.g. forested) and semi-natural (e.g. golf course) terrestrial land cover types, 4 land cover types indicative of human disturbance, and 1 water class. We extracted the data for mangrove swamp, scrub mangrove, salt marsh, tidal flat, high impact urban, and low impact urban classes, and then combined all other vegetation and land cover classes into the single category: other non-tidal land. Specific descriptions of terrestrial habitat types may be found in this land cover atlas' metadata files (Florida Fish and Wildlife Conservation Commission 2004).

Once all landscape data were assembled into ArcView 3.2a GIS, circular buffers measuring 1 km in radius were generated around each mangrove survey site's central coordinates (Figure 1). We used the PatchGrid Fragstats software extension of ArcView to calculate landscape metrics such as the total number of habitat types, the total number of patches, overall mean patch size, and habitat patch diversity and evenness for the region

surrounding each site (Table 2). When measuring the proportional cover of a given benthic

habitat type, for example seagrass, we calculated both (1) the proportion of the entire 1 km

radius buffer area designated as seagrass, and (2) the proportion of the buffer region's

benthic habitat area (excluding the terrestrial area) within the buffer designated as seagrass.

The same two measures were calculated for proportional cover of terrestrial habitat types.

We also measured the linear distance from the mangrove station to both the Gulf of Mexico

and Atlantic Ocean 10 m isobaths, as well as to the nearest major channel (Table 2).

Statistical Analyses

We initially intended to employ clustering and nonmetric multidimensional scaling

ordination techniques to search for correlations between mangrove sites' (1) fish community

structure, and (2) the independent patch- and landscape-scale habitat variables. The data,

however, did not support such an approach. Community ordination techniques illustrate and

describe community structure according to correlation and covariation among the species,

and therefore require that some species be positively or negatively correlated (McCune and

Grace 2002). None of the juvenile fish species at the 31 mangrove sites exhibited significant

correlation at the Bonferroni-corrected, experiment wide probability level of 0.05 (Table 3).

Analysis of species co-occurrence patterns (Gotelli 2000) confirmed the results of the

Pearson correlation analyses. The juvenile fish community C-score indicated that there was

only slightly less co-occurrence than expected by chance (marginally significant at

$p(obs \geq exp) = 0.039$), and there were no species that never occurred together (checkerboard

analysis was non-significant). These results suggest that juvenile fish species observed at the

31 mangrove sites are distributed independent of one another. We therefore chose to proceed

with a series of linear regression models to test juvenile species-habitat correlations independently for each species.

We employed a series of backwards elimination, multiple regression models (removal of independent variables at probability F = 0.10) to measure correlations between fish density and diversity, and mangrove habitat characteristics. To meet assumptions of normality and homogeneity of variances associated with multiple regression models, it was necessary to transform the data and remove outliers. The juvenile fish density data were log transformed, due to the high variation (several orders of magnitude) in species density among mangrove sites. The independent patch and landscape variables were square root, log, or arcsine transformed depending upon the shape of the raw data's distribution (Legendre and Legendre 1998). Following transformation, data points greater than two standard deviations from the mean for average Euclidean distance (univariate mean for the dependent variable and multivariate mean for the independent variables) were labeled as outliers and excluded from the analyses (McCune and Grace 2002).

Each regression model included multiple patch- or landscape-scale independent variables and one dependent variable (first with individual fish species' density, then with total juvenile fish density and diversity indices). Given our low sample size (sample size from 9 to 22), we were cautious not to overfit the models by including too many independent variables in the model (Legendre and Legendre 1998). The patch-scale model was always initiated with three independent variables: water depth, mangrove canopy height, and distance visible into prop roots. The number of independent variables entered in the landscape-scale model varied from five to seven depending upon (1) knowledge of the species life history (e.g. distance from the Atlantic Ocean was included for species believed

to spawn in the Atlantic, but not necessarily for species believed to spawn locally or in the Gulf of Mexico), and (2) species habitat requirements (e.g. proportional cover of seagrass within 1 km was included for species known to inhabit or feed within seagrass during at least one life stage, such as *Archosargus rhomboidalis*). These data were gathered through searches of the peer-reviewed literature, personal communications, and unpublished field observations. In some cases, two or more independent variables deemed important were highly correlated, such that inclusion of both variables would cause problems associated with high multicollinearity. In these cases, the landscape model was run repeatedly, once with each of the correlated variables included, and we reported the reduced model that explained the greater percentage of the overall variability according to the adjusted R^2 values.

RESULTS

Juvenile fish density and diversity are weakly related to mangrove patch characteristics. The mangrove patch-scale characteristics, water depth and distance visible into prop roots, explained some variation in juvenile fish population density among mangrove sites (Table 4). Based on removal of independent variables when probability of F=0.10, the backwards elimination, multiple linear regression models found solutions for five of the ten juvenile fish species present at a minimum of ten survey sites. Water depth was the only variable included in these reduced models, with the exception of the model for *L. griseus*, which included both water depth and the distance visible into prop roots. Juvenile Clupeidae, Gerreidae, *L. griseus,* and *S. barracuda* were found at shallower sites, while juvenile *A. virginicus* was positively associated with depth. *L. griseus* juvenile densities were highest at mangrove sites that had shallow, narrow prop root margins (short distance visible into prop roots). Based

upon the adjusted R^2 values, patch characteristics, when significant, accounted for between 16.0% (*S. barracuda*) and 46.2% (Gerreidae) of the variability in juvenile fish density. There was a weak positive relationship between juvenile fish Shannon Evenness Index and the canopy height of mangrove sites in the refuge (Table 4, adjusted $R^2 = 0.129$).

In some cases, juvenile fish density is strongly related to landscape characteristics. Landscape models described more of the variability in juvenile fish density among mangrove sites than patch models for seven of the ten species groups (Table 4: Atherinidae, Clupeidae, Engraulidae, *L. apodus*, *L. griseus*, *A. rhomboidalis*, and *S. barracuda*). Based on adjusted R^2 values, landscape models explained 15.6% (*L. apodus*) to 90.8% (Atherinidae) of the observed variability in juvenile fish density among sites where species were present. The reduced multiple regression model solutions were unique for each species. For example, Atherinid juvenile density was highest along the margins of islands with high perimeter/area ratios, distant from the Atlantic Ocean 10 m isobath, and surrounded by low diversity benthic habitat (likely barren habitat, since there was no univariate relationship between juvenile Atherinid density and either seagrass or hardbottom cover). Juvenile Clupeids were found in highest density in areas where several islands were clustered together distant from major channels. Juvenile Engraulid density showed a positive relationship with the distance to the Gulf of Mexico 10 m isobath, while juvenile *L. griseus* occurred in higher densities with increasing distance from the Gulf of Mexico and at islands with large perimeter area ratios, relatively distant from major channels.   Juvenile *L. apodus* density was positively associated with benthic habitat diversity. *A. rhomboidalis* juvenile density, however, was negatively associated with benthic habitat diversity as these fish were more common at sites with extensive, continuous seagrass beds surrounding clustered mangrove islands. Finally, *S.*

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barracuda juveniles occurred in higher densities at more isolated islands, nearer the Atlantic Ocean 10 m isobath.

Juvenile fish diversity is weakly related to landscape characteristics. There was no statistical relationship between juvenile fish species Shannon Evenness Index and mangrove landscape characteristics (Table 4). Juvenile species density, however, was positively related to island perimeter-area ratio and the proportion of seagrass habitat covering the surrounding seafloor (Table 4). The reduced model including these two independent variables accounted for 43.2% of the variability in juvenile species density among mangrove sites, based on the adjusted R^2 values. The relationship between rarefied species density (species density per 150 individuals sampled) and mangrove landscape characteristics was much weaker than that observed for the total observed species density. Rarefied species density was also positively related to the proportion of seagrass habitat in the 1 km buffer area, but this model only accounted for 14.9% of the variability in species density.

DISCUSSION

Mangrove islands, often assumed to be important nursery habitat for many juvenile tropical fish species of both commercial and ecological importance (but see: Sheridan and Hays 2003; Chittaro et al. 2005), display high variability in juvenile fish density and diversity. In the refuge, we found that regression models that incorporated landscape-scale habitat characteristics often explained more of the variability in observed juvenile fish abundance than those that incorporated patch-scale habitat characteristics. Patterns of juvenile fish diversity were only weakly related to patch- and landscape-scale habitat characteristics. These results have important implications for (1) the design and interpretation of experiments

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that address the role of mangroves as nursery habitat and (2) the development of habitat-based fisheries management and conservation efforts.

. The presence of high, species-specific patterns of variability in fish density among mangrove sites in the refuge, suggests that the value of mangrove islands as nursery habitat for any given species covers a continuous range from poor to excellent quality at multiple spatial scales. Yet, the spatial scale of marine ecological experimental design is commonly constrained by practical considerations, and, particularly in field experiments, by our human sensory perspective. Research of organism-habitat associations is often scaled down to consider species microhabitat utilization (1-10's meters), as these characteristics frequently drive individual mortality risk (Eggleston 1995; Dahlgren and Eggleston 2001; Laegdsgaard and Johnson 2001; Ellis and Bell 2004; Darcy and Eggleston 2005). For example, most studies investigating juvenile fish habitat selection and mortality in mangrove habitat have focused on microhabitat features such as water depth (Laegdsgaard and Johnson 2001; Ellis and Bell 2004), light availability (Ellis and Bell 2004), prop root density or complexity (Laegdsgaard and Johnson 2001), and prop root fouling (Laegdsgaard and Johnson 2001). While these habitat features have been shown to influence microhabitat usage by juvenile fish during daily foraging and resting behaviors, it has been unknown whether the importance of these features could be scaled up to explain or predict patterns of variability in fish population density among mangrove islands.

When we considered some typical microhabitat characteristics at the slightly larger patch-scale (100's m), water depth did describe a significant portion of variability in the density of some juvenile fish species, with higher juvenile densities generally associated with shallower sites. However, most species' juvenile fish density also exhibited strong

correlation with landscape-scale habitat characteristics. Past research investigating the

nursery role of mangrove habitat at large spatial scales has commonly compared population

density or abundance data within binary or categorical units, such as presence versus absence

of mangrove habitat (Nagelkerken et al. 2002; Dorenbosch et al. 2004), or mangrove versus

seagrass or reef habitat (Chittaro et al. 2005). For organisms that disperse broadly and

experience one or more ontogenetic habitat shifts, however, landscape-scale habitat

characteristics, such as the relative abundance and connectivity of different habitat types at

scales larger than the organisms' daily movement patterns, may influence local population

density and diversity as strongly as local habitat conditions (Rose 2000). If landscape

context is important, than binary presence/absence style treatment of nursery habitat would

represent too coarse a scale to evaluate the role of mangroves as nursery habitat because it

would introduce high variability around the population response means by potentially

grouping mangroves that do play a nursery role with those that do not. For example,

although numerical data are not published, such high variability is observed in Chittaro et

al.'s (2005) figures for several mangrove sites (and other habitat types). Experimental

evaluation of mangrove's role as nursery habitat must take into account individual species

ecology and not group all mangrove habitat together as a single class, because (1) there is

high variability in juvenile density among mangrove habitats, (2) the pattern of high and low

juvenile density sites is unique for each species, (3) these population patterns do reflect

landscape scale habitat features, and (4) the relationships between juvenile fish density and

landscape-scale habitat features are often significant only as multivariate responses. The

grouping of all mangrove habitat into a single class, particularly in cases where only a small

proportion of the mangroves may actually serve as high quality nursery habitat, could mask

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any significant nursery effect. In terrestrial studies, species-habitat relationships are recognized to be complex, multivariate and multi-scale. Further study of marine nursery habitats should be conducted in conjunction with research into the landscape-scale ecological responses of juvenile fish.

The same observations described above (e.g. highly variable fish density and diversity, with each species' variability reflecting a unique suite of patch- and landscape-scale habitat characteristics) have implications for marine conservation and management. Research focused on developing conservation strategies often treat all habitat of a given type as similar and are developed to protect a fixed proportion of different habitat types. For example, Leslie et al. (2003) recommended a "simulating annealing approach" to marine reserve network design based upon their analyses of the Florida Keys using the same benthic habitat data and the same spatial scale (1 km) that we employed in this study. Their approach builds reserve networks by selecting individual habitat patches until a predefined percentage of each habitat type is included, while minimizing reserve area and perimeter to facilitate community acceptance and logistic oversight of the reserve (Leslie et al. 2003). While treating all mangroves as equal may not be a problem if the majority of mangroves are targeted for conservation, if only a small percentage of the mangrove habitat is to be protected (Leslie et al. 2003 consider 10-30% habitat protection), alternative research designs, all protecting the same amount of mangrove habitat, could have very different conservation benefits for different species.

A common conservation practice is to regionally protect a diverse range of habitat types (e.g. seagrass, mangroves, patch reefs over 10s to 100s kilometers) as a means to protect regional species diversity. Our measure of benthic habitat diversity quantified the

landscape-scale benthic habitat diversity (within 1km buffer) associated with individual mangrove sites, and allowed us to test whether habitat diversity, important at regional scales, was also an important factor influencing local species diversity. We did not find any association between landscape-scale (1 km) benthic habitat diversity surrounding a mangrove site (benthic Shannon diversity index) and juvenile fish diversity within mangrove habitats of the refuge. Furthermore, where landscape-scale benthic habitat diversity did appear as a significant independent variable in a species density model, local juvenile fish diversity was negatively associated with habitat diversity (Atherinidae and *A. rhomboidalis*).

Although our research did not identify a single or small suite of habitat characteristics that might serve as an indicator or surrogate for aiding in reserve site selection for all species, our research does support the conclusion that mapped landscape characteristics can provide useful insight into individual juvenile fish species distribution and abundance patterns. Also, the inclusion of simple metrics that accounted for unique features of marine organisms' life history (e.g. distance to Gulf of Mexico for species believed to spawn in Gulf waters, or distance from channels as potential dispersal corridors) was important for several species. That such mapped habitat data and simple life-history knowledge could be used to construct regression models explaining a large proportion of variability in juvenile fish population density is promising, in that the technology for mapping benthic, terrestrial, and hydrographic landscape features are increasingly accessible and affordable. Several recent publications have suggested alternate approaches to species conservation and management that could effectively utilize these data in multispecies, multiscale, organism-based approaches (rather than simpler habitat patch based approaches) that seem advisable given our results. For example, Rose (2000) argues for the importance and feasibility of uncovering

sources of variability in marine populations, and he describes several successful examples of integrating individual based models, life history theory, and multidisciplinary studies into conservation planning. Fischer et al. (2004) describe contour mapping (visually similar to topographic maps) as a means to intuitively represent habitat quality at multiple, continuous scales. Contour maps could make excellent use of multivariate regression models to map predicted species distribution to (1) aid in the identification of potential population density or diversity hot-spots for each species based on multivariate criteria, (2) evaluate the relative benefits of alternative reserve designs to each species, and (3) identify gradients in habitat quality that would aid in the development of stratified sampling design.

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Table 1. Summary of juvenile fish density and diversity data.   Juvenile fish density values
are presented for species or families present at 10 or more of 22 spatially independent
mangrove sites (sites separated by at least 1 km). Each species at each site was represented
by one value: the mean density of juvenile fish per one hundred square meters based on fish
counts by multiple divers simultaneously deployed for 10 minutes at each site. Species in
some families were grouped due to the difficulty of distinguishing juveniles of these species.
Juvenile fish diversity values reflect all observed species, rare and common, and again
represent the mean from multiple surveys at each site. We report the average (AVE),
standard deviation (SD), minimum (MIN), and maximum (MAX) mean fish density and
diversity. Note that mean fish density varies one or more orders of magnitude for all species
and the standard deviations around the mean density are very high.

Juvenile Fish Density		N	AVE	SD	MIN	MAX
Atherinidae	Silversides	15	21.6	36.7	1.15	143
Ablennes hians	Flat needlefish	10	0.131	0.145	0.010	0.467
Anisotremus virginicus	Porkfish	10	0.059	0.029	0.013	0.100
Archosargus rhomboidalis	Seabream	11	0.129	0.139	0.017	0.500
Clupeidae	Herrings, menhaden	13	8.56	21.7	0.080	79.4
Engraulidae	Anchovies	15	41.6	59.5	0.533	183
Gerreidae	Mojarras	20	0.436	0.516	0.014	1.59
Lutjanus apodus	Schoolmaster	14	0.055	0.104	0.007	0.411
Lutjanus griseus	Gray snapper	22	0.880	1.023	0.065	4.21
Sphyraena barracuda	Great barracuda	21	0.033	0.034	0.008	0.163
Total fish density (excluding ACE species)		22	124.8	106.1	18.8	434.9
Juvenile Fish Diversity						
Shannon Evenness Index		22	0.336	0.141	0.132	0.599
Total species density		22	8.27	2.16	5.00	13.00
Rarefied species density		22	4.93	1.72	2.04	7.82

Table 2. Summary of the habitat data from 22 spatially independent mangrove sites (sites separated by at least 1 km; N = 22) within the refuge. Patch data were quantified during field surveys (Eggleston et al 2004a), and benthic, terrestrial, and bathymetric landscape data were taken from digital maps (see text for details).

Mangrove Patches	Average	Standard deviation	Minimum	Maximum
Mean water depth (m)	1.5	0.9	0.5	3.8
Mean canopy height (m)	5.4	1.4	3.8	8.9
Mean distance visible into prop roots (m)	2.9	1.3	0.8	6.6
Benthic Landscapes				
Total seagrass area (m^2)	2.21×10^6	6.96×10^5	6.49×10^5	3.11×10^6
Continuous seagrass area (m^2)	1.49×10^6	8.98×10^5	1.26×10^5	2.77×10^6
Hardbottom area (m^2)	6.29×10^5	7.52×10^5	0.00	2.41×10^6
Bare area (m^2)	2.80×10^4	9.32×10^4	0.00	3.80×10^5
Shannon Diversity Index	0.88	0.25	0.42	1.26
Terrestrial Landscapes				
Island perimeter/area ratio	0.042	0.046	0.004	0.184
Swamp mangrove area (m^2)	2.20×10^5	2.72×10^5	2.83×10^3	9.93×10^5
Marsh area (m^2)	4.07×10^3	1.63×10^5	0.00	7.70×10^4
Number of mangrove patches	0.82	3.42	0.00	16.00
Bathymetric Landscapes				
Distance to nearest major channel (m)	1973	1499	100	5200
Distance to Gulf of Mexico (m)	14673	6798	8200	34800
Distance to Atlantic Ocean (m)	21877	3941	12400	28000

Table 3. Pearson correlations of log transformed mean juvenile fish density at all mangrove sites (N=31). Four significant correlations (two-tailed) are highlighted in bold, however, none of these four relationships are significant after Bonferroni-correction of the probability level to account for multiple simultaneous tests (Bonferroni corrected probability level = $0.05/45 = 0.001$).

		Atherinidae	Clupeidae	Engraulidae	Ablennes hians	Gerreidae	Lutjanus griseus	Sphyraena barracuda	Anisotremus virginicus	Lutjanus apodus
Clupeidae	Pearson	0.019								
	P	0.920								
Engraulidae	Pearson	**-0.377**	-0.273							
	P	**0.037**	0.137							
Ablennes hians	Pearson	0.042	0.098	0.045						
	P	0.823	0.600	0.811						
Gerreidae	Pearson	**-0.402**	-0.057	0.304	0.168					
	P	**0.025**	0.762	0.097	0.368					
Lutjanus griseus	Pearson	-0.089	-0.003	-0.252	-0.096	-0.097				
	P	0.635	0.986	0.172	0.606	0.604				
Sphyraena barracuda	Pearson	0.018	0.002	0.082	0.277	0.286	0.306			
	P	0.922	0.991	0.662	0.131	0.119	0.095			
Anisotremus virginicus	Pearson	0.165	-0.083	-0.089	0.129	**-0.408**	0.093	-0.144		
	P	0.375	0.658	0.635	0.488	**0.023**	0.617	0.440		
Lutjanus apodus	Pearson	-0.162	-0.063	0.306	0.225	0.293	-0.048	0.306	0.176	
	P	0.384	0.737	0.094	0.223	0.110	0.797	0.094	0.342	
Archosargus rhomboidalis	Pearson	0.155	**0.365**	-0.319	-0.019	0.140	0.028	0.180	-0.233	-0.351
	P	0.404	**0.043**	0.080	0.921	0.453	0.883	0.333	0.208	0.053

Table 4. Results of multiple regression analyses to test the relationship between juvenile fish density and diversity, and mangrove site and landscape characteristics in refuge. Site independent variables included in the reduced regression models included: water depth, and distance visible into prop roots (distance visible). Landscape independent variables included in the reduced regression models included: proportion of benthic habitat within 1 km radius covered with continuous seagrass beds (continuous seagrass), proportion of benthic habitat within 1 km radius covered with either patchy and continuous seagrass beds (total seagrass), benthic habitat Shannon diversity within 1km radius (benthic sdi), mangrove island perimeter-area ratio (island p/a), number of mangrove swamp patches within a 1 km radius (swamp number), proportion of terrestrial habitat within 1 km radius covered with mangrove forest (mangrove area), distance to the Atlantic 10 m isobath (atlantic), distance to the Gulf of Mexico 10 m isobath (gulf), distance to the nearest major channel (channel). See text for the criteria used to identify the most parsimonious regression model. Significance of regression beta coefficients noted with asterix (*** < 0.001; ** <0.01, * <0.1).

Table 4 (continued)

Dependent Variable	Site Model	N	Adj. R^2	Landscape Model	N	Adj. R^2
Juvenile Fish Density						
Atherinidae (Silversides)	no solution	15	n/a	atlantic = -0.713*** island p/a = 0.382** benthic sdi = -0.476***	13	0.908
Ablennes hians (Needlefish)	no solution	10	n/a	no solution	10	n/a
Anisotremus virginicus (Porkfish)	water depth = 0.647*	10	0.347	no solution	10	n/a
Archosargus rhomboidalis (Seabream)	no solution	11	n/a	continuous seagrass = 0.545* swamp number = 0.625* benthic sdi = -0.643*	11	0.706
Clupeidae (Herring, Menhaden)	water depth = -0.685*	9	0.394	swamp number = 0.439* channel = -0.931**	9	0.784
Engraulidae (Anchovies)	no solution	15	n/a	gulf = 0.487*	15	0.178
Gerreidae (Mojarra)	water depth = -0.700**	20	0.462	swamp number = -0.561** channel = -0.323*	20	0.401
Lutjanus apodus (Schoolmaster)	no solution	14	n/a	benthic sdi = 0.470*	14	0.156
Lutjanus griseus (Gray snapper)	water depth = -0.550* distance visible = -0.479*	20	0.228	gulf = -0.220* island p/a = 0.769*** channel = -0.330	20	0.638
Sphyraena barracuda (Great barracuda)	water depth = -0.457*	18	0.160	atlantic = 0.377* swamp number = -0.835***	16	0.752
All juveniles except ACE species	water depth = -0.643** distance visible = -0.455*	21	0.302	Mangrove area = -0.740***	19	0.528
Juvenile Fish Diversity						
Shannon Evenness Index	canopy height = -0.413*	22	0.129	no solution	22	n/a
Total Species Density	no solution	22	n/a	island p/a = 0.517** total seagrass = 0.444*	20	0.432
Rarefied Species Density	no solution	22	n/a	total seagrass = 0.435*	22	n/a

FIGURE LEGENDS

Figure 1. Map of Great White Heron National Wildlife Refuge study area in Florida Keys,

USA, showing mangrove survey sites as light blue dots. Examples of the diverse terrestrial

(A) and benthic (B) habitats within 1 km radius buffers are shown for four stations.
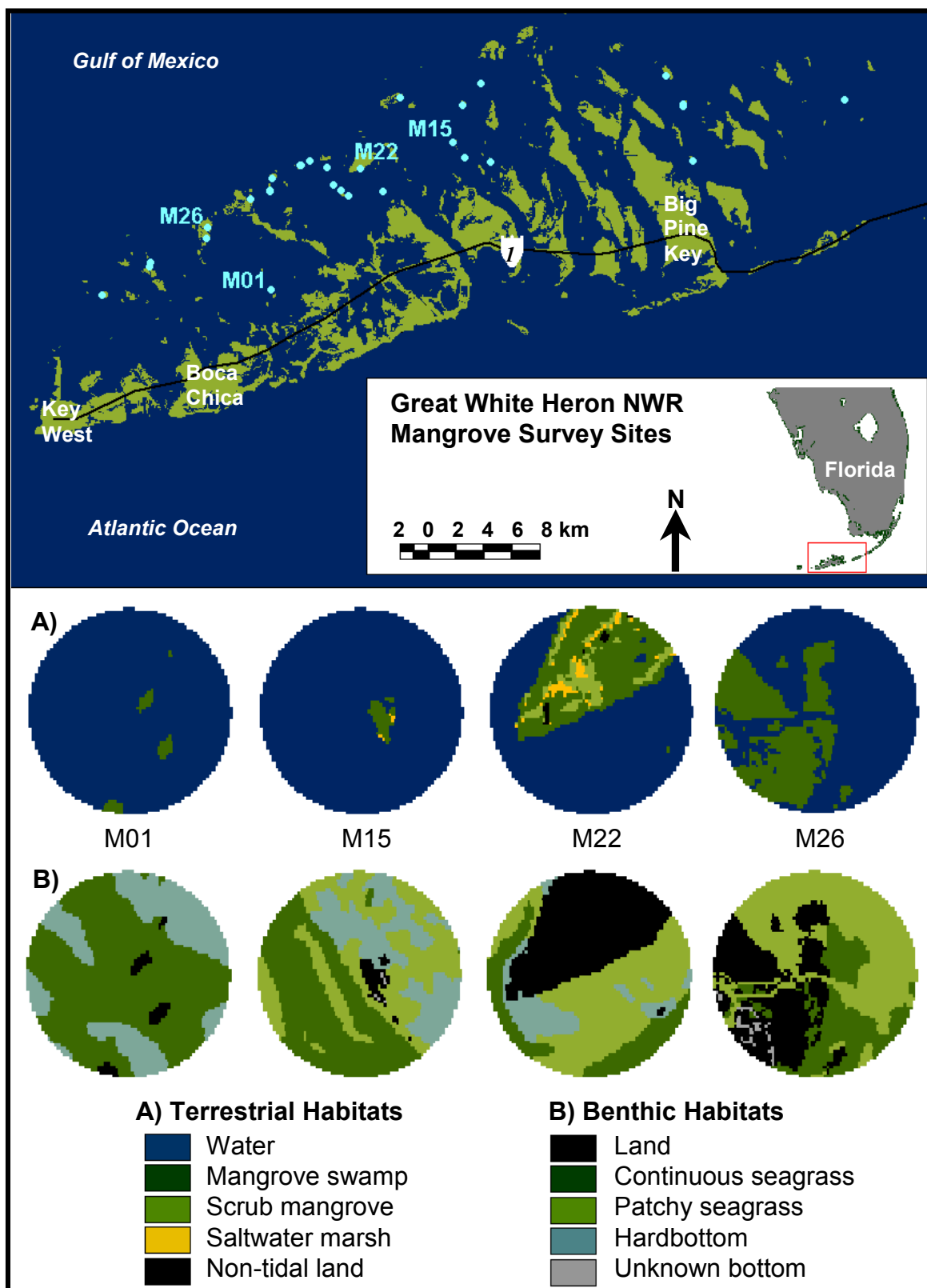
Figure 1. Map of study area and four example study site landscapes.

CHAPTER 3

Effects of backreef nursery habitat on Caribbean reef fish

at island-wide scales

ABSTRACT

In surveys of Caribbean reef fish communities, high local densities of reef fish species on coral reefs often correlates positively with proximity to mangroves and seagrass habitats. We investigated whether this local reef fish, nursery-habitat association applied at larger spatial scales by testing whether island-wide patterns of reef fish abundance similarly correlate with island-wide abundance of mangrove and seagrass habitats. We targeted 33 common reef fish species: 17 species with nursery-associated juvenile stages and 16 species with reef-associated juvenile stages. Island-wide reef fish abundance scores were calculated from the Reef Environmental Education Foundation (REEF) roving diver transect survey database. Island-wide habitat data were gathered through literature review and online databases. We used a combination of clustering and non-metric, multidimensional scaling ordination to examine the relationship between island-wide reef fish assemblage structure and gradients in nursery habitat characteristics. A series of simple and partial Mantel tests partitioned the variation in species abundance among four components: species with nursery-associated juveniles, species with reef-associated juveniles, habitat characteristics, and geographic space. We found no relationship between the island-wide abundance scores of species with nursery-associated juveniles and island-wide nursery habitat abundance. We did, however, observe strong correlations (1) between islands' community structure based on abundance scores of species with reef-associated juveniles and islands' mangrove habitat variables, and (2) between islands' community structure based on abundance scores of species with reef- and nursery-associated juveniles. These results could be suggestive of strong indirect rather than direct effects of nursery habitat on reef fish species with nursery-associated juvenile stages. More likely, however, the tendency for nursery habitats to locally (1-10 km scales)

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enhance reef fish populations and alter species composition is masked at larger spatial scales (100-1000 km) by the combined effect of (1) differences in reef structural complexity among islands, (2) recreational diver bias towards structurally complex, "healthy" reefs, and (3) uneven sampling of reefs near and far from backreef nursery habitats. We suggest that the influence of nursery habitat on nursery-associated fish abundance scores is a localized effect that is minimized in regional, island-wide fish abundance datasets. Instead, regional-scale fish surveys may highlight island-wide differences in reef structural complexity.

INTRODUCTION

Backreef habitats, such as seagrass meadows and coastal mangrove forests, provide services essential to the effective conservation and management of tropical reef fish (Beck et al. 2001; Gillanders et al. 2003; Mumby et al. 2004). Seagrass and mangrove habitats are known to (1) trap sediments and pollutants that might otherwise damage delicate corals (e.g. Kitheka 1997; Duke et al. 2005), (2) export nutrients and particulate organic matter potentially promoting the growth of corals and other sessile reef organisms (e.g. Dittmar and Lara 2001), and (3) shelter high densities of many juvenile reef fish species (Nagelkerken et al. 2000a; 2000b; 2002; Nagelkerken and van der Velde 2002; Dorenbosch et al. 2004; Eggleston et al. 2004b; Mumby et al. 2004; Chittaro et al. 2005). Backreef habitats have received the most attention for their role as potential nursery habitats that can enhance reef fish density and diversity.

Mangrove and seagrass habitat area are the most common measures of nursery habitat availability in studies exploring the influence of backreef nursery habitats on Caribbean reef fish communities (Halpern 2004 and references therein). Research on mangrove and

seagrass as nursery habitat, however, has led to mixed conclusions regarding the influence of these habitats on adult reef fish populations. Simple measures of habitat area typically used in these studies might not provide the best indicator of nursery habitat availability and influence on reef fish assemblages, and could account for some of the conflicting results from studies conducted in different regions of the Caribbean. In particular, several factors related to the spatial configuration of nursery habitat could influence reef fish assemblages in backreef and reef habitats, as well as reef fish movement between these habitats. For example, factors potentially confounding studies of nursery habitat influence on reef fish assemblages include: (1) varying quality of nursery habitat with regards to mangrove or seagrass species diversity, hydrology, exposure to wave action, disturbance, and other microhabitat features (Eggleston 1995, Laegdsgaard and Johnson 2001; Halpern 2004; Chittaro et al. 2005), (2) isolation versus connectivity of nursery and reef habitat (Gillanders et al. 2003; Dorenbosch et al. 2004; Halpern 2004; Mumby et al. 2004), (3) the proportion of coastal habitat defined as nursery versus non-nursery habitat type, (4) clumped versus dispersed distribution of mangroves along coastlines, and (5) recruitment limitation to juvenile habitat due to relative scarcity of adult habitat, and vice versa (Halpern 2004).

Connectivity and microhabitat features are known to mediate the impact of nursery habitat on neighboring reef fish populations. The proportion of coast as nursery habitat, the distribution of nursery habitat patches, and the relative abundance of nursery versus adult habitat, however, are not addressed in the literature. A large, island-wide perspective on the role of nursery habitat would consider not only the locally targeted nursery and reef habitat patches, but also the spatial configuration of these patches within the broader, landscape context. Surveys of juvenile fish in mangrove habitats have demonstrated that some fish

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species do respond strongly to large-scale (1-10s km) landscape features (Drew and Eggleston in review). For example, multiple regression models incorporating landscape-scale variables such as distance to major channels, the number of distinct mangrove patches, and regional benthic habitat diversity, determined that between 15.6% and 90.8% of the variability in juvenile fish density among mangrove sites in the lower Florida Keys for several species was driven by these landscape-scale metrics (Drew and Eggleston in review).

In this study, we measured the degree to which reef fish community structure correlated with mangrove and seagrass area at 26 Caribbean islands, but we also examined four additional landscape-scale characteristics of nursery habitat quantity that may influence nursery habitat and reef fish connectivity, which have not been previously addressed: (1) the areas of specific types of mangrove habitat (estuarine, lagoon, or coastal fringe), (2) mangrove area per kilometer of coastline, (3) number of mangrove patches, and (4) mangrove area per square kilometer of reef habitat. In particular, we asked the following questions: (1) How is reef fish abundance related to the abundance and type of nursery habitat? (2) After accounting for geographic gradients, is there a relationship between reef fish abundance and nursery habitat? and (3) Do patterns of abundance differ between reef fish with nursery-habitat and reef-habitat associated juvenile stages?

METHODS

Nursery Habitat Data

Our study focused on individual islands distributed across the Caribbean region. We searched the peer-reviewed and gray literature, as well as online databases, for island-wide estimates of the following: coastline length, mangrove area, reef area, and seagrass area. We sought

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these data to quantify the amount of nursery habitat per kilometer of coastline, the amount of

nursery habitat per reef area, and the number of distinct nursery habitat patches. Study sites

were selected based on the availability of regional mangrove, reef, and seagrass data (Table

1). Although many countries and agencies have sponsored detailed habitat studies that

include local measures of coastal benthic resources at individual sites, there are few

published estimates of mangrove, reef, and seagrass area at national or island-wide levels.

Habitat data (mangrove, reef, and seagrass data) were gathered from regional reports issued

by multinational governmental and non-governmental organizations, including the World

Conservation Monitoring Center's World Atlas of Coral Reefs (Spalding et al. 2001) and

World Mangrove Atlas, (Spalding et al. 1997), an FAO forestry report (Wilkie and Fortuna

2003), the Seas at the Millennium series (Sheppard 2000), and a UNECSO-published review

of regional mangrove cover (Bacon 1993). These publications summarized results from

extensive searches of primary literature, government documents, and personal

communications. Several of the more recent publications heavily cited the older review by

Bacon (1993). Coastline lengths (Table 1) were calculated from 1:250,000 scale digital maps

(The Nature Conservancy 2006). The latitude and longitude (decimal degrees) of each

islands' landmass center defined its geographic location.

The use of data from diverse sources, particularly gray-literature and secondary

sources, required careful attention to data quality, particularly the comparability of measures

collected by different agencies, in different years, using different methods. For example,

measures of coast length are sensitive to spatial data resolution, and measures of seagrass or

reef extent are sensitive to both the maximum water depth of the survey and the habitat

classification system employed. Measures of mangrove habitat are also sensitive to the

classification system used. Many reports either group all mangroves together (e.g. lumping interior salt pond and coastal mangrove habitats), or group all wetland vegetation types together (e.g. marsh, salt ponds, mangrove), and only one review reported detailed mangrove cover data by mangrove type (Bacon 1993). We minimized such variability in our data by: (1) using only documents that clearly identified their methods and data sources, (2) using only sources published in peer-reviewed journals or official reports, (3) drawing only upon one source for each environmental parameter, and (4) researching regional rates of habitat loss or gain to identify any sites experiencing rapid habitat change where data across parameters from different years would be less compatible.

Reef Fish Data

Since 1994, the Reef Environmental Education Foundation's (REEF) Fish Survey Project has been collecting fish data from volunteer divers across the Caribbean, and maintaining these data in a publicly-accessible, online database (http://www.reef.org/). REEF volunteers use a Roving Diver Technique, which involves swimming freely throughout a dive site and recording every observed fish species that can be positively identified (Schmitt and Sullivan 1996). Divers report species observed, the relative abundance of each species, and dive bottom time. From these data, REEF calculates a weighted density average and sightings frequency for each species (REEF 2005). The weighted density average indicates the log-scale abundance category in which a given species was most often sited, and ranges from 1 (single fish) to 4 (over 100 fish). Sightings frequency is a measure of the percentage of surveys in which a species was observed. For comparison among sites, REEF recommends multiplying the weighted density average by the sightings frequency to obtain a species

abundance score that accounts for sites with zero sightings of a given species. Although gathered by volunteers, the data are of high quality and useful for research purposes (Schmitt and Sullivan 1996; Pattengill-Semmens and Semmens 1998; Semmens et al. 2004). In addition, we included only data from Expert surveys (data from individuals who have conducted at least 35 surveys and have obtained a score of at least 90% on an advanced fish identification quiz (REEF 2005), to further minimize errors associated with fish misidentification or miscounting.

Our study focused on 33 fish species commonly associated with reef habitat as adults (Table 2). Several of these species have significant economic value to commercial fisheries (e.g. *Haemulon flavolineatus, H. sciurus, Lutjanus apodus, L. mahogoni, Scarus iseri, and Sparisoma aurofrenatum*), and all species could be considered of value to the marine tourism industry and maintenance of biodiversity.

Previous work by Nagelkerken et al. (2000a) identified 17 of these species as having nursery-associated juvenile stages, while the juveniles of the remaining 16 species were more commonly associated with reef habitat (Table 2). Although these designations were assigned based on field studies in Curaçao, all species are common throughout the region and similar juvenile fish habitat associations have been observed in the Florida Keys (Eggleston et al. 2004a; Eggleston et al. 2004b), St. Croix (Adams and Ebersole 2002), Belize (Mumby et al. 2004), and a regional study comprising data from sites in Belize, Mexico, and the Bahamas (Chittaro et al. 2005). At least one species, *Scarus guacamaia*, has been noted to have a functional dependency on mangrove nursery habitat, such that local extinction followed after the removal of mangroves (Mumby et al. 2004). There are a few notable examples of documented juvenile fish habitat associations contrary to those observed by Nagelkerken et

al. (2000a). For example: (1) juvenile *Scarus iseri, Haemulon flavolineatum, H. plumeri, Chaetodon capistratus*, and *Sparisoma chrysoptera*, which were more common in reef and rubble habitat in St. Croix (Adams and Ebersole 2002), than in seagrass and macroalgal nursery habitats (mangroves were not surveyed), and (2) *Sparisoma aurofrenatum* juveniles had higher proportional abundance in nursery than reef habitat in data gathered from Bahamas, Mexico, and Belize (Chittaro et al. 2005). Such differences in species habitat associations among sites suggest either some geographic variability or flexibility in species habitat requirements (Halpern 2004), or local variability in the quality of reef and backreef nursery habitat at the study locations (Chittaro et al. 2005).

The REEF online database was queried between 20 December 2005 and 20 January 2006, and we downloaded fish sightings frequency and average weighted density data for all 33 species in each of the 26 study regions (Table 2).

Statistical Analyses

Our overall hypothesis was that reef fish community structure, as represented by an assemblage of 33 common species, would vary along gradients in backreef nursery habitat abundance. In particular, we predicted that the abundance scores of reef fish species with nursery-associated juvenile stages would be higher in regions where nursery habitat was abundant than where nursery habitat was scarce. We also predicted that the abundance scores of reef fish species with reef-associated juvenile stages would be lower (if recruitment of fish species from nurseries displaces reef species) or similar (if nursery and reef species coexist without displacement) in regions where nursery habitat was abundant than where nursery habitat was scarce. Although our analysis refers exclusively to reef fish surveyed in

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reef habitat, we will refer to the reef fish species with nursery-associated juvenile stages and those with reef-associated juvenile stages simply as "nursery-associated fish" and "reef-associated fish", respectively. The term "reef fish" will be used to refer to both of these groups inclusively.

The nature of our data, which focused on common reef fish species and uncommon measures of habitat characteristics, presented a unique challenge in terms of statistical analysis. The criteria of our reef fish and habitat search led us to identify 26 potential island study sites (Table 1), which were broadly distributed across the region. Most reef fish species were observed at most sites. Not all habitat data were available for each site; yet, statistical techniques comparing community and habitat data commonly require that both datasets contain the same number of sample sites. Therefore, we defined five separate datasets to address our overall hypotheses: (1) All Mangroves, (2) Coastal Mangroves, (3) All Reefs, (4) Mangrove Reefs, and (5) All Seagrass. Each dataset included all reef fish species, but differed in the number of study sites, depending upon which aspect of nursery habitat was under investigation (Table 1). All Mangroves = total mangrove area (including interior and coastal mangrove forests together), coastline length, and the ratio of total mangrove area to island area at 26 islands. Coastal Mangroves = estuarine mangrove area, fringe mangrove area, the number of coastal mangrove patches (includes estuarine, fringe, and lagoon patches), and the ratio of coastal mangrove area to coastline length at 19 sites. All Reefs = total reef area and the ratio of reef area to coastline length at 10 sites. Mangrove Reefs = total reef area, the ratio of total coastal mangroves to coastline length, and the ratio of total coastal mangroves to reef area at 7 sites. All Seagrass = total seagrass area and the ratio of seagrass area to coastline length at 8 sites. The distinction between total mangrove

area versus coastal mangrove area was necessary because a comparison of the total mangrove area against more detailed estimates of three coastal mangrove habitat types (coastal fringe, estuarine, and lagoon mangroves) revealed that total mangrove area could grossly overestimate the mangrove area accessible to marine fish (Table 1). All nursery habitat data were monotonically transformed as necessary to reduce the influence of extreme outliers, and these transformations generally had the effect of normalizing the data (as indicated by skew, kurtosis, and a Kolmogorov-Smirnov test).

Given the wide range in sample sizes (N ranges 7 to 26), not all datasets could be evaluated with the same statistical procedures. Table 3 provides a summary of our hierarchical approach for statistically analyzing the relationships between backreef nursery habitats and Caribbean reef fish at island-wide scales. In particular, this table summarizes which tests employed each of the five nursery habitat datasets and which analyses considered reef fish abundance patterns at the assemblage versus the species level. Our hierarchical approach to statistically testing our hypotheses involved three steps. First, we examined relationships between reef fish abundance and the quantitative characteristics of coastal mangrove habitat using a combination of clustering and non-metric, multidimensional scaling ordination techniques (Table 3, Step 1) (McCune and Grace 2002; Urban et al. 2002). Second, we used a series of simple and partial Mantel tests (Table 3, Step 2) to partition the variance in reef fish populations due to space from that due to the coastal mangrove's habitat characteristics (Legendre and Troussellier 1988). These tests focused on the All Mangroves and Coastal Mangroves datasets. All Mangroves, with N=26, offered the best representation of the study sites in species space for clustering and ordination. The Coastal Mangroves dataset, however, offered the best compromise between sample size (N=19, large enough to

effectively run the Monte Carlo tests) and ecological relevance (best capturing differences in nursery habitat abundance among islands). Third, we examined correlations (accounting for latitude and longitude) between reef fish abundance scores and nursery habitat data (using all nursery habitat datasets) to identify which reef fish species most strongly correlated with one another and with the nursery habitat characteristics (Table 3, Step 3).

Clustering and Non-metric Multidimensional Scaling Ordination

To begin, the 26 All Mangrove study sites were grouped based on Bray-Curtis dissimilarity in species abundance scores using the flexible beta (β = -0.25) linkage method (PC Ord v 4.25; McCune and Mefford 1999). Due to our focus on common species, the transformations commonly applied to equally weight the contribution of common and rare species were not necessary; species data (1) exhibited only moderate variability across study sites (coefficient of variation (CV) of species totals = 66.70%), and (2) were not heavily skewed (average skew = 0.407). The resulting dendrogram, which describes the dissimilarity between sites based on species composition, was scaled according to Wishart's objective function (Wishart 1969), and measures the information lost as sites are clustered together, and converted to percent information remaining (McCune and Grace 2002). The dendrogram was pruned to define groups at the 50% information remaining level.

Next, we performed a non-metric multidimensional scaling ordination, based on the same Bray-Curtis dissimilarity matrix as was used for the clustering procedure, to more closely examine the relationships among study site clusters. This ordination is a non-parametric approach that is not only independent of assumptions of equal sample size or homogeneity of variance, but also is less sensitive to outliers, sample clumping, and uneven

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spacing of samples along ordination axes relative to other ordination techniques (McCune and Grace 2002). Data characteristics that can cause problems during the ordination and the associated Monte Carlo tests, such as extreme outliers, the presence of a single super-abundant species, or very many zeros, were not present in our data.

Study site clusters were plotted in the reduced ordination space following varimax rotation to aid interpretability (McCune and Grace 2002). Kendall's Tau quantified correlations between reef fish species ordination scores and (1) the abundance scores of individual reef fish species, (2) the Coastal Mangrove habitat variables, and (3) geographic location as latitude and longitude. By plotting these correlations in ordination space as joint plots, we could: (1) identify reef fish species strongly contributing to regional similarity among sites (e.g. within clusters), (2) determine whether gradients in nursery-associated and reef-associated fish correlated with distinct axes or clusters, (3) evaluate whether clusters aligned along gradients in the quantity of coastal mangrove, and (4) evaluate whether clusters aligned along latitudinal or longitudinal gradients. This entire procedure, clustering and ordination, was repeated for the Coastal Mangrove dataset (Table 3).

Variance Partitioning and Path Analysis with Mantel Tests

Two common concerns when studying relationships between community structure and environmental conditions across large spatial scales are the possibility of strong latitudinal gradients, or spatial autocorrelation, among study sites (Legendre and Troussellier 1988; Borcard et al. 1992; Urban et al. 2002). Therefore, we examined the simple and partial Mantel correlations between reef fish species compositional dissimilarity, nursery habitat dissimilarity, and geographic distance (Urban et al. 2002). Mantel tests provided a simple

means of measuring the correlation between two dissimilarity or distance matrices of two variables, while controlling for the shared influence of a third variable. In addition, the pattern of significant and non-significant simple and partial correlations, combined with the relative strength of the significant correlations, supports the development of causal models to guide future hypothesis development (Legendre and Troussellier 1988; Legendre 1993). We evaluated a series of possible causal models by comparing the predictions indicated by alternative model pathways against the results of our simple and partial Mantel tests. The configuration of the model (and thus the number of different models evaluated) was restricted such that: (1) site geographic position could not be a dependent variable, and (2) differences in mangrove habitat characteristics among sites could be dependent on geographic distance, but not on dissimilarity in reef- or nursery-associated species assemblages.

We focused on the Coastal Mangrove dataset (N=19), because, of the five datasets examined, this one provided the greatest detail regarding mangrove habitat characteristics, while also maintaining an adequate sample size for these analyses. Three Bray-Curtis dissimilarity matrices defined distances between sites, as defined by: (1) differences in the abundance scores of reef-associated species (RFISH), (2) differences in the abundance scores of nursery-associated species (NFISH), and (3) differences in coastal mangrove habitat characteristics (MANG). A Euclidian distance matrix calculated from islands' geographic coordinates represented the spatial distance between island sites (SPACE). The first set of simple Mantel tests evaluated the simple correlation between each possible pair of distance matrices. We then computed the partial Mantel correlations by (1) creating new matrices containing the residuals of linear regressions between each possible pair of distance and

dissimilarity matrices, and (2) performing Mantel tests on the resulting residual matrices.

For example, a partial Mantel test on the residuals of the regressions of NFISH on SPACE

and MANG on SPACE, allowed us to measure the correlation between the distances in

NFISH and MANG while controlling for any shared effect of SPACE. This analysis, with

four simple and twelve partial Mantel tests, also enabled us to evaluate the correlation

between the dissimilarities in reef- and nursery-associated fish assemblages, first directly,

and then accounting for any shared influence of space and mangrove nursery habitat. All

partial Mantel tests were performed with PC Ord software using unstandardized residuals

from linear regressions in SPSS statistical software. Monte Carlo randomization (5000 runs

per test) provided the probability of committing a Type 1 error associated with each Mantel

test. All probability values were Bonferroni-corrected to account for simultaneous testing.

Kendall's Tau Correlation Tests

Mantel tests measure the correlation between distance matrices, not the original data, and

therefore cannot indicate the sign of correlative relationships. To measure the direction and

magnitude of correlations between the abundance scores of nursery-associated fish, reef-

associated fish, and nursery habitat we exported the original fish and habitat data to SPSS.

We included the habitat variables from the Coastal Mangrove, All Reefs, Mangrove Reefs,

and All Seagrass datasets (estuarine mangrove area, lagoon mangrove area, fringe mangrove

area, number of coastal mangrove patches, coastal mangrove area per kilometer coastline,

coastal mangrove area per square kilometer reef, reef area, and seagrass area). We (1)

normalized the fish species data by square-root transformations, (2) applied log

transformations where necessary to normalize the habitat data, (3) obtained the

unstandardized residuals from multivariate linear regression of fish abundance, and then

habitat variables, on latitude and longitude to remove the influence of geographic space, and

(4) measured the correlations between these residuals with a Kendall's Tau non-parametric

test statistic. The Bonferroni correction was considered too conservative for such a large

number of simultaneous tests (reef-associated with nursery associated fish = 272 correlations;

reef-associated fish with nursery habitat = 128 correlations; and nursery-associated fish with

nursery habitat = 136 correlations), so we used Holm's procedure (Box 1.3: Legendre and

Legendre 1998) to calculate adjusted probability values for each correlation and control for

inflated Type 1 errors.

RESULTS

Island reef fish assemblages differ along strong geographic gradients and weaker

habitat gradients

The cluster dendrogram and the ordination joint plot illustrated dissimilarities in the

abundance scores of 33 reef fish species between the 26 All Mangrove island study sites.

The cluster analysis indicated the study sites grouped into six clusters with approximately

50% information remaining (Figure 1). The compositions of the six clusters illustrate a

strong geographic component to the reef fish assemblages; island-scale reef fish assemblages

are generally clustered according to their location within the Caribbean region (Figure 2).

Only four islands did not cluster by geography: (1) Mustique, geographically located in the

Windward Islands but clustered with the southwestern islands of the Netherlands Antilles, (2)

St. Martin/St. Maarten, geographically located in the Leeward Islands, but clustered with the

Windward Islands, and (3) Cluster C, which included Tobago and St. Thomas from opposite ends of the Lesser Antilles (Figure 2).

For the ordination, the greatest reduction in stress was achieved with two axes (Figure 3: final stress = 12.66, final instability over 20 iterations = 0.0008). The six clusters occupied distinct portions of the ordination space, with the exception of Cluster C, which overlapped with Cluster A such that Tobago's position in species space more closely approximated its position in geographic space than suggested by the dendrogram. Although the clusters generally did not overlap, neither did islands within clusters appear tightly grouped. Such equal spacing among sites within and between groups is often indicative of a continuous, rather than discontinuous, relationship of species with underlying habitat gradients.

The joint plot (Figure 3) illustrates the magnitude and direction of relationships of the variables with the ordination scores. The vertical axis defines a gradient in abundance scores of nursery- and reef-associated fish species. Moderate to high abundance scores for four species with nursery-associated juveniles are strongly associated (Kendall's Tau > 0.500) with Clusters B and E: *Haemulon sciurus*, *Lutjanus apodus*, *Ocyurus chrysurus*, and *Sphyraena barracuda*. Moderate to high abundance for *Chromis multimineata*, *Myripristis jacobus*, and *Haemulon chrysargyreum*, three reef fish species with reef-associated juvenile stages distinguish Clusters A and D. Clusters A and E are widely separated along the horizontal axis, which is associated with a gradient in the abundance scores of *Haemulon flavolineatum* (nursery-associated) and *Stegastes dorsopunicans* (reef-associated). None of the All Mangroves habitat variables strongly correlated with either axis (Kendall's Tau > 0.500). At lower Tau cut-offs (Kendall's Tau = 0.200 to 0.300), however, correlation vectors

for all habitat variables aligned along the vertical axis, pointing in the same direction as the nursery fish species. Latitude and longitude were both strongly correlated with the vertical axis, and oriented in the same direction as correlation vectors of the nursery-associated fish species.

Cluster analysis and ordination of the abundance scores for reef fish in the Coastal Mangrove dataset (N=19; figures not shown) revealed similar patterns, with respect to the alignment of geographic, nursery-associated, and reef-associated fish along the same axis, as described for All Mangroves (Figures 1, 2, and 3). The only exception was that, with fewer sites, the Coastal Mangrove dendrogram defined fewer distinct clusters than the All Mangrove analysis: three Coastal Mangrove clusters were distinguished with approximately 35% information remaining and 6.10% chaining. The ordination joint plot illustrated that the two major groups could be defined geographically as occupying the northwest versus southeast perimeter of the Caribbean Basin, with the dividing line running through the Virgin Islands. A smaller, third group of sites was not as spatially cohesive (Tobago grouped with St. Croix and St. Thomas).

Reef-associated fish more strongly correlate with mangrove habitat gradients than do nursery-associated fish

The simple Mantel tests (Table 4) identified a very strong association between RFISH and NFISH (simple Mantel r: 0.908 (p<0.001)). Unexpectedly, there were no significant correlations between NFISH and either MANG or SPACE. In contrast, there was a significant simple correlation between RFISH and MANG (simple Mantel r: 0.132 (p<0.001). RFISH was also correlated with SPACE (simple Mantel r: 0.158 (p<0.001). The

partial Mantel tests (Table 4) indicated that even accounting for SPACE or RFISH, NFISH was not significantly correlated with MANG. Systematic comparison of our Mantel results against the predictions indicated by different possible causal models (not shown) led to the final diagram shown in Figure 4. This was the only model to both (1) meet the restrictions set out in the methods (e.g. SPACE and MANG could not be dependent on RFISH or NFISH) and (2) have all predictions met by the computed Mantel results. This model indicates that dissimilarity among the nursery-associated fish assemblages does not reflect distance in geographic space, nor dissimilarity in nursery habitat characteristics among the 19 Caribbean islands. Rather, dissimilarity among the nursery-associated fish assemblages correlates with dissimilarity among the reef-associated fish assemblages.

Few correlations between fish species and nursery habitat variables, but many between reef- and nursery-associated fish species

The results of Kendall's Tau non-parametric correlation tests (Appendix) complemented the Mantel results. There was very little support for a relationship between island-scale backreef habitat characteristics and backreef nursery-associated fish. For example, only four percent (6 of 136) of the correlations indicated statistically significant relationships (Holm's adjusted probability ≤ 0.050) between the abundance scores of nursery-associated fish and nursery habitat characteristics. Three of these significant relationships were positive: the abundance scores of (1) *Haemulon plumerii* (Tau = 0.430) and (2) *Lutjanus analis* (Tau = 0.627) with fringe mangrove area, and the abundance scores of (3) *Ocyrurus chrysurus* (Tau = 0.571) with seagrass area. The three negative correlations were: the abundance scores of (1) *Chaetodon capistratus* (Tau = -0.471) and (2) *Scarus iseri* (Tau = -0.452) with estuarine

mangrove area, and the abundance scores of (3) *Acanthurus chirurgus* (Tau = -0.584) with reef area.

Six percent (8 of 127) of the simultaneous tests of reef-associated fish and nursery habitat were significant. Six of these tests described significant negative correlations: *Stegastes dorsopunicans* with (1) estuarine mangrove area (Tau = -0.398), (2) seagrass area (Tau = -0.539), and (3) area coastal mangroves per square kilometer of reef (Tau = -0.720), and (4) *Halichoeres bivittatus* (Tau = -0.491), (5) *Stegastes planifrons* (Tau = -0.400) with fringe mangrove habitat, and (6) *Halichoeres radiatus* (Tau = -0.720) with area coastal mangroves per square kilometer of reef. The two significant positive correlations were between *Sparisoma aurofrenatum* and (1) fringe mangrove area (Tau = 0.415) and (2) area coastal mangroves per kilometer of coastline (Tau = 0.500).

A much larger percentage (24 percent; 64 of 272 correlation tests) of the reef- with nursery-associated fish correlated with one another than with the island-wide nursery habitat variables. Positive correlations between reef- and nursery-associated species were three times more common than negative correlations. Seventy-seven percent (49 of 64 significant correlations) of the correlations documented significant positive species associations. Twenty-three (15 of 64) of the significant correlation tests measured negative correlations between the abundance scores of reef- and nursery-associated species. *Chromis multimineata*, in particular, was negatively associated with several nursery-associated fish (6 species). Note that, in all cases, these correlations are measured at the island-wide scale and may not indicate local positive or negative patterns in co-occurrence.

DISCUSSION

While the nearby (within 10 km) presence of nursery habitat has a strong positive influence on Caribbean reef fish density and diversity (Cocheret de la Morinière et al. 2002; Nagelkerken et al. 2002; Dorenbosch et al. 2004; Eggleston et al. 2004b), the influence of nursery habitat at larger, regional scales (100s to 1000s kilometers) appears to be insignificant relative to other environmental variables. In general, we did not observe a positive association between the abundance scores of nursery-associated reef fish and the quantity of mangrove nursery habitat available at island-wide scales. The absence of an island-wide correlation between nursery-associated fish and mangrove nursery habitat quantity was consistent through the ordination and Mantel tests. Even after accounting for spatial gradients in the data, the correlation between nursery-associated fish and mangrove nursery habitat dissimilarity matrices was small (Table 4) and non-significant after Bonferroni-correction of the probability level.

Most research investigating the role of mangroves as nursery habitat for reef fish has focused on either microhabitat (Laegdsgaard and Johnson 2001) or local-scale population and community patterns (Cocheret de la Morinière et al. 2002; Nagelkerken et al. 2002; Dorenbosch et al. 2004; Eggleston et al. 2004b). Even where studies have been conducted to compare island-wide patterns of reef fish and nursery habitat associations (Nagelkerken et al. 2002), the reefs surveyed have been in close proximity to the nursery habitat (e.g. located near the mouth of shallow embayments encompassing the nursery habitat) at the islands where nursery habitat was present. These studies identify the influence of nursery habitat on reef fish populations as primarily a localized effect enhancing the density of nursery-associated fish species. For example, in Curaçao, although some nursery-associated fish do

appear on reefs distant (>10 km) from nursery habitats, the density of nursery-associated

species is consistently higher on reefs proximate (<1 km) to bays with nursery habitat

(Dorenbosch et al. 2004). Based on these results, and the results of other studies of

Caribbean nursery-associated fish population trends, we had predicted that the REEF roving

diver surveys would document higher abundance scores for nursery-associated species at

islands with higher abundances of nursery habitat (Table 5, #1); this was not the case.

We did observe significant differences between islands' reef fish communities. We

suggest that these differences reflect island-wide differences in the quality of coral reef

habitats (Table 5, #2), and that this regional factor outweighs the influence of island-wide

differences in nursery habitat quantity on reef fish community structure. Healthy coral reefs

are typically characterized by high structural complexity, and reef structure is known to

mediate fish behavioral interactions and distribution patterns (Hixon and Menge 1991;

Eggleston et al. 1997; Almany 2004b; Almany 2004a; Semmens et al. 2005). Species

richness and fish abundance increase with increasing rugosity, variety of growth forms,

percentage hard substrate, and variety of refuge hole sizes (Gratwicke and Speight 2005).

This positive correlation between reef fish abundance and reef structural complexity has been

observed for both nursery- and reef-associated fish species (Almany 2004b; Gratwicke and

Speight 2005). In this study, Bonaire, an island noted for the high quality and diversity of its

reef habitat, but possessing relatively little nursery habitat, had the highest abundance scores

for both nursery-associated and reef-associated species on the coral reefs of all island study

sites. Unfortunately, coral reefs are declining globally, with an estimated 80% decline in

hard coral cover in the Caribbean over the past three decades (Gardner et al. 2003), due to

coral disease, hurricane damage, and algal-phase shifts. These declines, however, have not

been equal in all regions and the structural status of coral reefs is, therefore, highly variable across the Caribbean Basin.

Given that recreational (e.g. tourist) divers collect the majority of the REEF fish data, we suspect that, at any given island, REEF survey sites (1) are preferentially located on the most structurally complex available reefs with the highest local fish densities and diversities, and (2) likely do not equally sample reefs near and far from backreef nursery areas. If this is true, then locally enhanced adult densities of nursery-associated fish species (Table 5, #1) could easily be missed due to (1) the absence of survey data from reefs near nursery habitat, or (2) averaging the results from many sites far from and relatively few sites near nursery habitats. Under the same set of assumptions (i.e., diver bias towards structurally complex reefs, and regional variability in reef structural complexity), any difference between islands' reef structural complexity (Table 5, #2) and fish response to that structural complexity, would be identified by the REEF data. In addition, REEF survey methods and differences in island-wide reef structural complexity would explain (1) the failure to observe a significant association between nursery-associated fish abundance and island-wide quantity of nursery habitat, and (2) the predominant pattern of positive correlation between individual nursery- and reef-associated fish species abundance scores observed in this study.

The mean island-wide abundance score of all nursery-associated reef fish species was always lower than the mean island-wide abundance score of all reef-associated species. Yet, REEF divers regularly encountered nursery-associated fish at all islands, even those islands with little or no mangrove nursery habitat. If the presence of nursery-habitat benefits primarily local reef fish populations (Dorenbosch et al. 2004), then the presence of nursery-associated fish, regardless of the quantity of nearby mangrove nursery habitat, suggests

either: (1) nursery-associated fish are facultative and enjoy much greater flexibility to use alternative habitats during juvenile stages than is typically assumed (Sheridan and Hays 2003; Dorenbosch et al. 2004), or (2) alternative habitats (e.g. those not typically categorized as significant nursery habitat) have much higher export of nursery-associated species than previously assumed based on studies of juvenile density.

Our results suggest a hierarchical framework for addressing regional reef conservation goals. For example, although the positive effect of mangrove nursery habitat on reef fish species does not appear to scale-up from local to regional, island-wide spatial scales, this result does not contradict the many studies identifying mangroves as important nursery habitats at smaller, local spatial scales. Mangroves and other backreef nursery habitats do positively influence reef fish populations and their protection is essential to manage and conserve healthy reef fish communities (see citations in Table 5, #1). We suggest that at the coarsest level, considering islands across the Caribbean, sites should first be prioritized for conservation of nursery-associated reef fish species based on structural complexity and diversity of local reef systems. Next, at a given island, reef sites might be prioritized based on nursery habitat availability (e.g. Beck et al. 2001) and landscape context (e.g. distance from channels and larval sources, benthic habitat diversity near the nursery habitat) of available mangrove habitats (Drew and Eggleston in review). Finally, finer scale patch and microhabitat characteristics, such as prop root complexity and water depth in mangrove habitats (e.g. Laegdsgaard and Johnson 2001; Verweij et al. 2006), would be examined to identify sites most likely to promote high growth and survival of nursery species.

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Table 1. Data for nine island-wide habitat variables at 26 study sites distributed across the Caribbean region. These habitat variables are: coastline length (Coast), log-transformed total mangrove area (Mang), estuarine mangrove area (Est), lagoon mangrove area (Lag), coastal fringe mangrove area (Fri), number of coastal mangrove patches (includes estuarine, lagoon, and fringe mangrove patches (Num), seagrass area (Seag), and reef area (Reef). The total number of REEF expert roving diver surveys reporting fish data for each site is also provided (Surv). Data sources are indicated by superscripts next to the column headers, and these letters correspond to the following sources: (a) World Mangrove Atlas, (b) The Nature Conservancy, (c) Bacon 1993 report, (d) Seas at the Millennium, and (e) REEF (see text for web-addresses). The cluster labels refer to the results of the cluster dendrogram in Figure 1. The four-letter site abbreviation codes are used in all figures. Dataset refers to the five subsets of the habitat data used in our analyses: (1) All Mangroves, (2) Coastal Mangroves, (3) All Reefs, (4) Mangrove Reefs, and (5) All Seagrass (see text for details).

Table 1 (continued)

Study Site	Dataset	Coast[b] (km)	Mang[a,c] (km^2)	Est[c] (km^2)	Lag[c] (km^2)	Fri[c] (km^2)	Num[c]	Seag[d] (km^2)	Reef[a,d] (km^2)	Surv[e] (#)
Cluster A										
Aruba (ARUB)	1, 3, 4	105	2.92	na	na	na	na	35.2	9.9	49
Bonaire (BONA)	1, 3, 4	120	0.79	na	na	na	na	104	43.72	4714
Curaçao (CURA)	1, 3, 4	169	0.55	na	na	na	na	4.94	45.6	1011
Mustique (MUST)	1, 2	18	0.12	0.000	0.000	0.000	1	na	na	25
Cluster B										
St. Eustatius (EUST)	1, 4, 5	21	0	na	na	na	na	82	1.80	33
St. John (JOHN)	1	71	0.26	na	na	na	na	na	na	179
Tortola (TORT)	1, 2	78	1.39	0.000	0.000	0.908	17	na	na	502
Virgin Gorda (VIRG)	1, 2	50	0.09	0.000	0.000	0.086	4	na	na	79
St. Kitts (KITT)	1	83	0.70	na	na	na	na	na	na	60
Cluster C										
St. Thomas (THOM)	1, 2	78	3.54	0.000	0.000	3.450	1	na	na	550
Tobago (TOBA)	1, 2, 3	160	2.00	1.000	0.000	1.000	11	0.64	na	171
Cluster D										
Barbados (BARB)	1, 2, 4, 5	96	0.16	0.080	0.000	0.010	9	na	90	134
Dominica (DOMI)	1, 2, 4, 5	150	0.10	0.040	0.000	0.000	4	na	70	160
St. Vincent (VINC)	1, 2	92	0.03	0.014	0.000	0.011	4	na	na	421
Grenada GREN)	1, 2, 4, 5	246	1.49	0.030	0.000	0.610	10	na	160	111
St. Lucia (LUCI)	1, 2, 4, 5	164	1.58	0.723	0.000	0.493	17	na	90	20
St. Martin (MART)	1, 3, 4, 5	77	0	na	na	na	na	27.99	6.92	37
Cluster E										
Saba (SABA)	1, 4, 5	15	0	na	na	na	na	na	0.14	90
St. Croix (CROI)	1, 2, 3	104	6.48	1.000	0.000	0.100	2	na	na	313
Cluster F										
Cayman Brac (BRAC)	1, 2	42	0.36	0.000	0.000	0.246	2	na	na	55
Grand Cayman (GCAY)	1, 2, 3	133	71.00	0.000	0.000	49.29	3	25	na	402
Little Cayman (LCAY)	1, 2	37	10.40	0.000	0.000	1.030	1	na	na	658
Grand Turk (TURK)	1, 2	24	3.58	0.000	1.980	0.000	2	na	na	166
Salt Cay (SALT)	1, 2, 3	16	2.01	0.000	0.200	0.000	1	56	na	28
New Providence (NEWP)	1	96	37.26	na	na	na	na	na	na	86
West Caicos (WCAI)	1, 2	27	5.65	0.000	0.000	0.010	1	na	na	93

Table 2. Mean sighting frequency (SF%), mean average weighted density (D), and mean relative abundance scores (RA) of 33 common reef fish species from the 26 All Mangrove study sites, with standard deviations (sd). Sighting frequency and density data were downloaded from the online REEF database between 20 December 2005 and 20 January 2006. Relative fish abundance was calculated for each site as RA = SF% * D. Nursery- and reef-associated juvenile designations are from Nagelkerken et al. 2002.

Table 2 (continued)

Fish Species	Common Name	Code	D (sd)	SF% (sd)	RA (sd)
Reef Fish with Nursery-associated Juvenile Stages ("nursery-associated fish" in text)					
Acanthurus chirurgus	Doctorfish	acchi	2.0 (0.3)	0.46 (0.22)	0.95 (0.58)
Chaetadon capistratus	Foureye butterflyfish	chcap	2.1 (0.2)	0.84 (0.15)	1.82 (0.44)
Gerres cinereus	Yellowfin mojarra	gecin	1.5 (0.7)	0.13 (0.17)	0.26 (0.35)
Haemulon flavolineatum	French grunt	hafla	2.4 (0.2)	0.87 (0.10)	2.12 (0.40)
Haemulon parrai	Sailors choice	hapar	1.6 (0.7)	0.11 (0.11)	0.23 (0.25)
Haemulon plumierii	White grunt	haplu	1.7 (0.3)	0.32 (0.29)	0.59 (0.56)
Haemulon sciurus	Bluestriped grunt	hasci	1.9 (0.3)	0.50 (0.31)	0.98 (0.65)
Lutjanus analis	Mutton snapper	luana	1.3 (0.6)	0.14 (0.16)	0.20 (0.23)
Lutjanus apodus	Schoolmaster	luapo	2.1 (0.3)	0.60 (0.30)	1.30 (0.73)
Lutjanus griseus	Gray snapper	lugri	1.9 (0.7)	0.15 (0.14)	0.33 (0.35)
Lutjanus mahogoni	Mahogany snapper	lumah	2.2 (0.2)	0.66 (0.17)	1.49 (0.44)
Ocyurus chrysurus	Yellowtail snapper	occhr	2.4 (0.4)	0.75 (0.21)	1.83 (0.67)
Scarus coeruleus	Blue parrotfish	sccoe	1.0 (1.1)	0.03 (0.05)	0.04 (0.08)
Scarus guacamaia	Rainbow parrotfish	scgua	1.0 (0.8)	0.03 (0.05)	0.05 (0.07)
Scarus iseri	Striped parrotfish	scise	2.5 (0.3)	0.72 (0.21)	1.86 (0.62)
Sparisoma chrysopterum	Redtail parrotfish	spchr	1.7 (0.3)	0.32 (0.19)	0.57 (0.37)
Sphyraena barracuda	Great barracuda	spbar	1.4 (0.2)	0.35 (0.19)	0.50 (0.30)
Reef Fish with Reef-associated Juvenile Stages ("reef-associated fish" in text)					
Acanthurus bahianus	Ocean surgeonfish	acbah	2.7 (0.3)	0.91 (0.07)	2.43 (0.40)
Acanthurus coeruleus	Blue tang	accoe	2.6 (0.3)	0.94 (0.07)	2.48 (0.39)
Canthigaster rostrata	Sharpnose puffer	caros	2.1 (0.2)	0.86 (0.10)	1.80 (0.33)
Chromis multimineata	Brown chromis	chmul	3.4 (0.5)	0.89 (0.12)	3.04 (0.72)
Haemulon chrysargyreum	Smallmouth grunt	hachr	2.5 (0.7)	0.43 (0.34)	1.14 (0.98)
Halichoeres bivittatus	Slippery dick	habiv	2.5 (0.3)	0.49 (0.20)	1.25 (0.64)
Halichoeres maculipinna	Clown wrasse	hamac	2.2 (0.4)	0.55 (0.23)	1.26 (0.63)
Halichoeres radiatus	Puddingwife	harad	1.7 (0.3)	0.48 (0.21)	0.84 (0.46)
Mulloidichthys martinicus	Yellow goatfish	mumar	2.7 (0.2)	0.85 (0.10)	2.28 (0.42)
Myripristis jacobus	Blackbar soldierfish	myjac	2.5 (0.5)	0.74 (0.23)	1.97 (0.88)
Sparisoma aurofrenatum	Redband parrotfish	spaur	2.7 (0.2)	0.93 (0.05)	2.50 (0.27)
Sparisoma viride	Stoplight parrotfish	spvir	2.6 (0.2)	0.91 (0.06)	2.35 (0.35)
Stegastes dorsopunicans	Dusky damselfish	stdor	2.1 (0.3)	0.31 (0.16)	0.66 (0.42)
Stegastes planifrons	Threespot damselfish	stpla	2.4 (0.4)	0.66 (0.18)	1.63 (0.67)
Stegastes partitus	Bicolor damselfish	stpar	3.4 (0.4)	0.93 (0.05)	3.15 (0.44)
Thalassoma bifasciatum	Bluehead	thbif	3.4 (0.2)	0.96 (0.03)	3.26 (0.25)

Table 3. Summary of hierarchical approach for statistically analyzing the relationships

between backreef nursery habitats and Caribbean reef fish at island-wide scales.

Table 3 (continued)

Purpose: (1) quantify and describe community-level dissimilarity in reef fish assemblages among island study sites, and (2) describe community structure in relation to islands' nursery habitat variables and geographic position.

Analysis	Ordination Variables	Independent Variables	N
1	• All 33 reef fish species abundance scores (dissimilarity matrix)	• All Mangroves • Space (latitude and longitude)	26
2	• All 33 reef fish species abundance scores (dissimilarity matrix)	• Coastal Mangroves • Space (latitude and longitude)	19

Major Results: (1) All Mangroves habitat variables do not correlate with ordination axes, (2) Coastal Mangrove habitat variables do correlate with ordination axes, but this relationship is much weaker than the correlation of axes with latitude and longitude, and (3) individual nursery- and reef-associated species' abundance correlation vectors align along the same axis as habitat and space vectors.

Step 2: SIMPLE AND PARTIAL MANTEL TESTS

Purpose: (1) quantify and isolate the relationships of reef-associated and nursery-associated fish assemblages with geographic distance from their relationship with differences in nursery habitat, (2) quantify and isolate the relationship between dissimilarity in reef-associated and nursery-associated fish assemblages, and (3) develop a hypothetical causal model to summarize relationships among distance and dissimilarity matrices.

Analysis	Correlation Variables	N
3	• Reef-associated fish species abundance scores (dissimilarity matrix) • Nursery-associated fish species abundance scores (dissimilarity matrix) • Coastal Mangroves (Euclidian distance matrix) • Space (Euclidian distance matrix)	19

Major Results: (1) Assemblage dissimilarities of reef-associated and nursery-associated species are strongly correlated, (2) distance in space and nursery habitat characteristics more strongly correlate with reef- than with nursery-associated species

Step 3: KENDALL'S TAU CORRELATION TESTS

Purpose: (1) identify how many and which individual reef fish species positively and negatively correlate with nursery habitat variables, and (2) identify how many and which individual nursery-associated fish species positively and negatively correlate with reef-associated fish species.

Analysis	Dependent Variables	Independent Variables	N
4	• 17 nursery-associated fish species' abundance scores (individual species)	• Coastal Mangroves • All Reefs • Mangrove Reefs • Seagrass	varied
5	• 16 reef-associated fish species' abundance scores (individual species)	• Coastal Mangroves • All Reefs • Mangrove Reefs • Seagrass	varied
6	• 17 nursery-associated fish species' abundance scores (individual species)	• 16 reef-associated fish species' abundance scores (individual species)	26

Major Results: (1) few reef- or nursery-associated species abundance scores correlate with habitat variables, (2) few reef- and nursery-associated species abundance scores negatively correlate, and (3) many reef- and nursery-associated species abundance scores positively correlate

Table 4. Results of simple and partial Mantel tests for the Euclidian distance matrix of island latitude and longitude (SPACE) and three Bray-Curtis dissimilarity matrices calculated from (1) the abundance scores of reef fish with reef-associated juvenile stages (RFISH), (2) the abundance scores of reef fish with nursery-associated juvenile stages (NFISH), and (3) the multivariate measures of coastal mangrove habitat (MANG). Simple Mantel statistics and associated probabilities appear above the diagonal. Partial Mantel statistics are shown below the diagonal. Dot notation indicates the variable controlled for in each partial test. Probability levels were Bonferroni-corrected to hold the overall significance level for each set of simultaneous tests at the 0.05 level (0.05/6 = 0.0083 for six simple tests; 0.05/12 = 0.0042 for twelve partial tests). Significant correlations are indicated with bold font.

Nursery and Reef Juvenile Fish with Coastal Mangroves (N=19)			
	NFISH	**RFISH**	**MANG**	**SPACE**
NFISH	-	**0.904** (0.0002)	0.108 (0.0168)	0.109 (0.0102)
RFISH	• SPACE **0.389** (0.0002) • MANG **0.394** (0.0002)	-	**0.132** (0.0002)	**0.158** (0.0002)
MANG	• SPACE 0.289 (0.0056) • RFISH 0.132 (0.0862)	• SPACE **0.441** (0.0002) • NFISH **0.354** (0.0002)	-	0.223 (0.0586)
SPACE	• MANG **0.273** (0.0018) • RFISH 0.053 (0.1860)	• MANG **0.554** (0.0002) • NFISH **0.492** (0.0002)	• RFISH -0.126 (0.1224) • NFISH 0.065 (0.1060)	-

Table 5. Summary of local and regional factors that potentially influence island-wide relative abundance of Caribbean reef fish. We failed to reject our original hypotheses, which were based upon research suggesting a positive correlation nursery-associated fish abundance scores and nursery habitat presence and distance from reefs. We suggest that the influence of nursery habitat on nursery-associated fish abundance scores is a localized effect that is minimized in regional, island-wide fish abundance datasets. Instead, regional-scale fish surveys may highlight island-wide differences in reef structural complexity.

Local and regional factors		Predicted influence on nursery-associated fish	Predicted influence on reef-associated fish	References
1. Nursery habitat presence and distance from reef	Present and Near	+	ns	(Nagelkerken et al. 2000b; Laegdsgaard and Johnson 2001; Cocheret de la Morinière et al. 2002; Nagelkerken et al. 2002; Nagelkerken and van der Velde 2002; Gillanders et al. 2003; Dahlgren and Marr 2004; Dorenbosch et al. 2004; Mumby et al. 2004; Chittaro et al. 2005)
	Absent or Far	-	ns	
2. Reef structural complexity	High	+	+	(Sale and Douglas 1984; Hixon and Menge 1991; Holbrook et al. 2002; Almany 2004b; Almany 2004a; Gratwicke and Speight 2005; Semmens et al. 2005)
	Low	-	-	

FIGURE LEGENDS

Figure 1. Cluster dendrogram of Bray-Curtis dissimilarity in the abundance scores of 33 reef fish species across 26 island study sites. Linkage was performed by the flexible beta method (β = -0.25), resulting in 4.87% chaining. Dendrogram was scaled according to Wishart's Objective Function, converted to percent information remaining. Six clusters are present with 50% information remaining.

Figure 2. Map of 26 island study sites (black) illustrating that our study sites (1) cover the entire Caribbean region, and (2) display a geographic gradient in cluster membership. Island four-letter name codes are defined in Table 1. The letter following each island's name code identifies its cluster membership, as defined by the dendrogram in Figure 1.

Figure 3. Non-metric multidimensional scaling ordination joint plot, with varimax rotation, of study sites (islands) in species space based on Bray-Curtis dissimilarity in the abundance scores of 33 reef fish species. Study site symbols refer to the six clusters defined by the dendrogram in Figure 1. Vectors indicate the direction and strength of Kendall's Tau correlations (cut-off Tau > 0.500). The settings for the ordination in PC Ord were as follows: randomized starting configurations, 500 runs with real data, up to 500 iterations, 500 iterations to evaluate stability, step down in dimensionality from 6 axes, and stability criterion equal to 0.00001.

Figure 4. Hypothetical causal model as supported by the results of simple and partial Mantel tests. The relationships predicted by this particular arrangement of variables in the model are listed, along with correlation r-statistics calculated by Mantel tests. The r-statistics are presented for all significant correlations while non-significant correlations are indicated with "ns" (based on Bonferroni corrected probability levels). An example interpretation of this figure would be that reef-associated fish abundance patterns respond to geographic gradients and differences in nursery-habitat variables, while nursery-associated fish abundance patterns reflect the differences in reef-associated fish abundance patterns rather than differences in geographic or nursery-habitat characteristics. See Table 3 for all t-statistics and associated p-values.
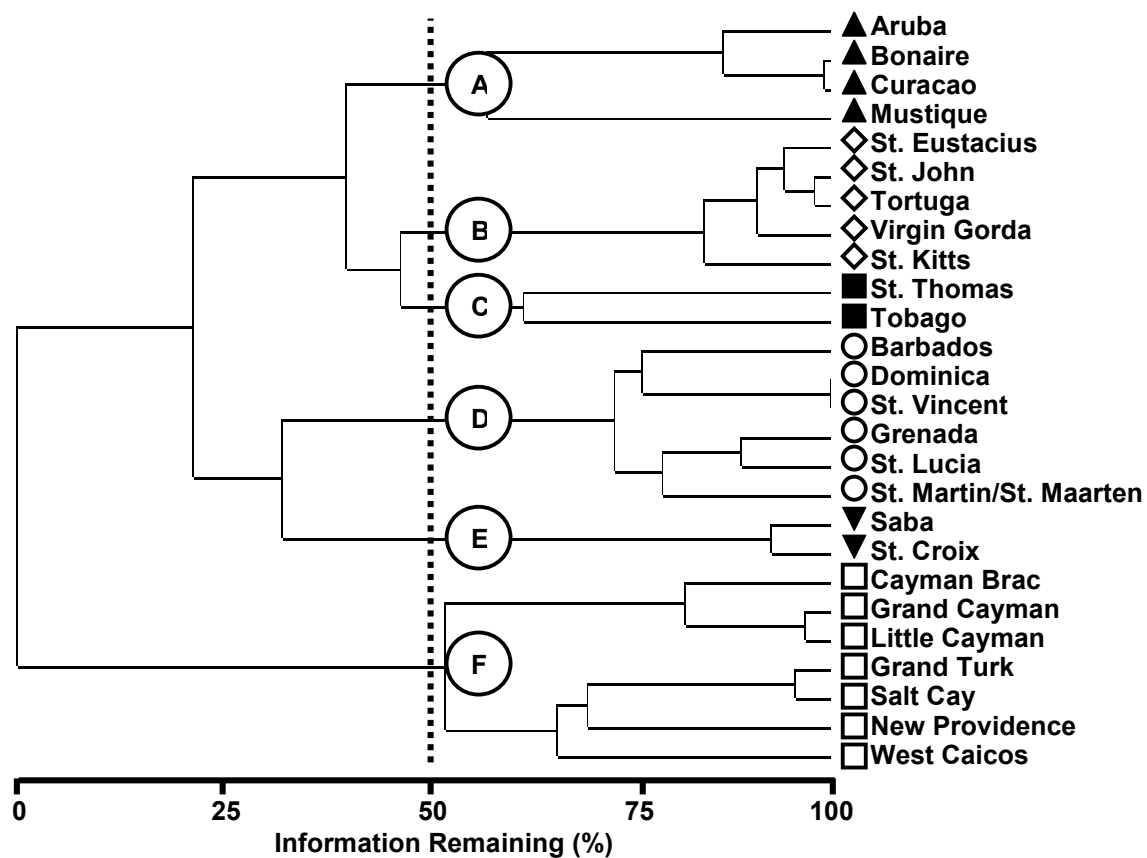
Figure 1. Dendrogram of 26 Caribbean islands based on dissimilarity of reef fish species assemblages
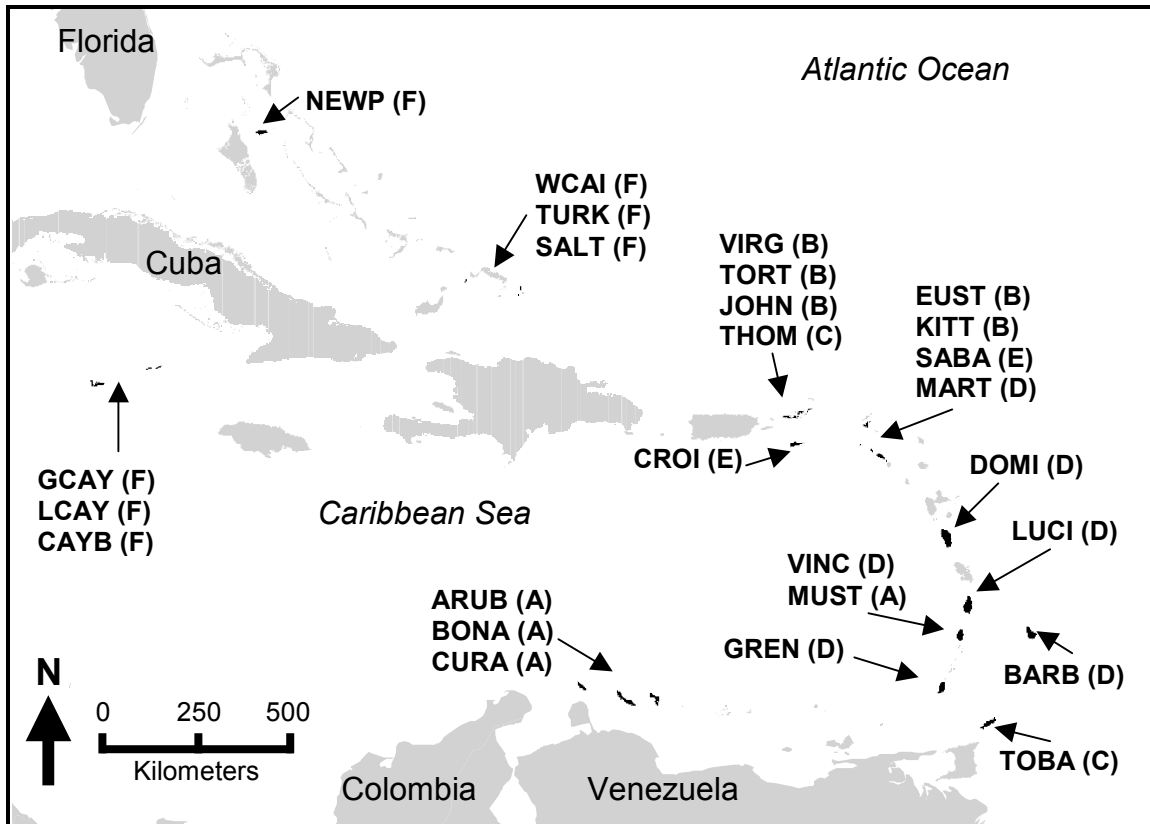
Figure 2. Map of 26 island study sites showing cluster membership
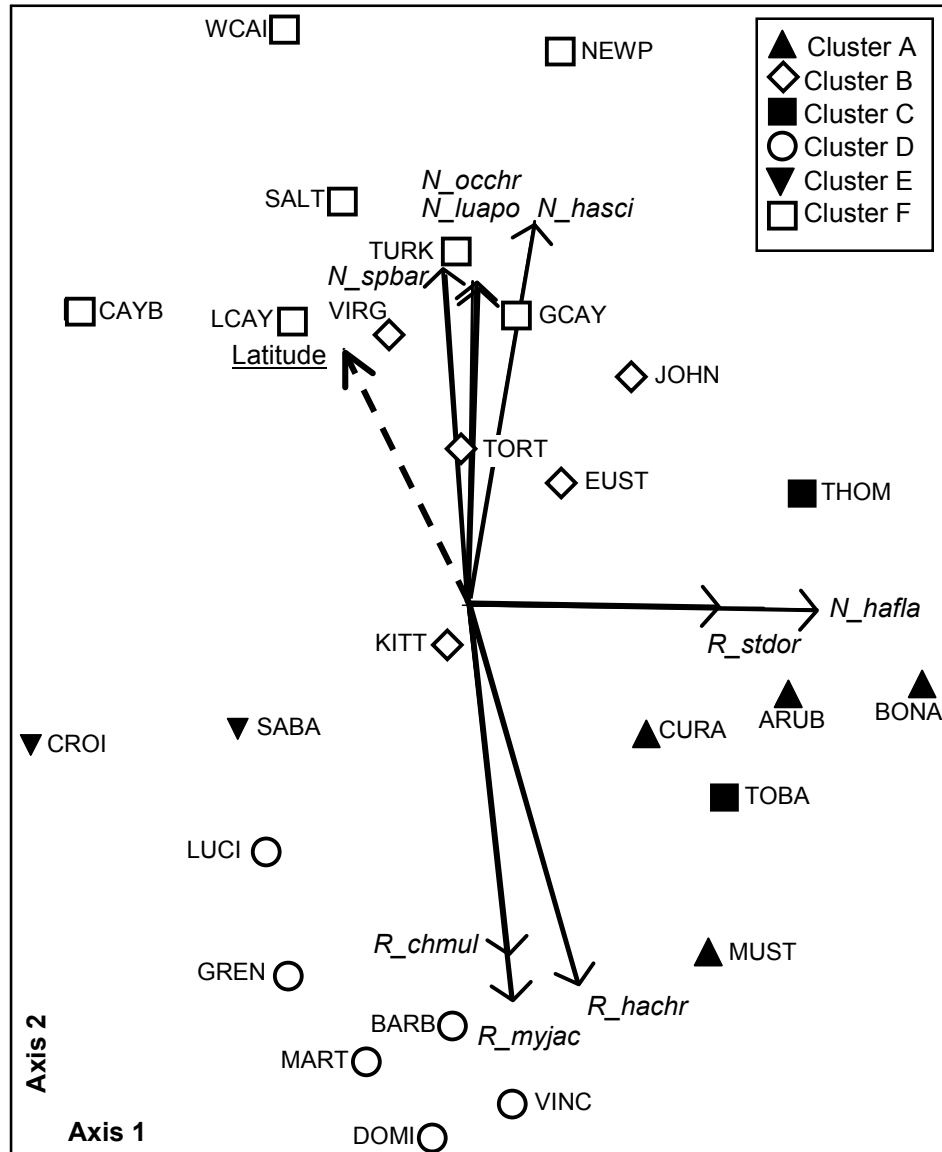
Figure 3. Non-metric multidimensional scaling ordination joint plot of islands in species space
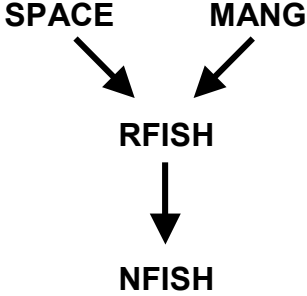
Hypothetical Causal Model	Model Predictions	Computed Results
SPACE **MANG**	RFISH • NFISH ≠ 0	0.904
	SPACE • RFISH ≠ 0	0.158
	MANG • RFISH ≠ 0	0.132
RFISH	SPACE • MANG = 0	ns
	(SPACE • RFISH) • MANG ≥ SPACE • RFISH	0.554 > 0.158
	(MANG • RFISH) • SPACE ≥ MANG • RFISH	0.441 > 0.132
	(MANG • NFISH) • RFISH ≥ MANG • NFISH	ns = ns
	(SPACE • NFISH) • RFISH ≥ SPACE • NFISH	ns = ns
NFISH	(MANG • NFISH) • SPACE ≥ MANG •NFISH	0.289 > ns
	(SPACE • NFISH) • MANG ≥ SPACE • NFISH	0.237 > ns

Figure 4. Hypothetical causal model as supported by results of simple and

partial Mantel tests

APPENDIX

Community analyses based on distance (dissimilarity) matrices can indicate the presence of

correlative relationships, but not the sign of the correlations. Therefore, we measured

Kendall's Tau correlations between each dependent and independent variable to provide an

indication of whether (1) relationships between variables were positive or negative, (2) the

similarity between communities reflects correlated distribution patterns of few or many

species, and (3) correlations between fish species and nursery habitat, or among fish species.

We performed this analysis in SPSS, a software program that can account for missing data by

using pair-wise deletions (see variable N values in tables below). There were 17 nursery-

associated reef fish species, 16 reef-associated reef fish species, and eight nursery habitat

variables. We performed three sets of correlation tests: (1) reef fish species with nursery-

associated juvenile stages and nursery habitat variables ($k = 136$ simultaneous tests), (2)

sixteen reef fish species with reef-associated juvenile stages and nursery habitat variables ($k

= 128$), and (3) reef fish species with nursery-associated juvenile stages and reef fish species

with reef-associated juvenile stages ($k = 272$).

Holm's method (Holm 1979; Legendre and Legendre 1998) adjusts p-values to

account for increased probability of Type 1 error due to multiple, simultaneous tests. This

test is a sequentially rejective multiple test procedure, where we (1) ranked p-values from

least to greatest, (2) adjusted the p-values according to the equation $p_i' = (k - i + 1)p_i$, (3)

examined the rank order of the adjusted p-values to replace smaller with the larger of two p-

values wherever the rank order has been reversed (such that both p-values took the value of

the larger p-value), and (4) compared the adjusted p_i' to the unadjusted α significance level

and made the statistical decision (Legendre and Legendre 1998). This adjustment method is

recommended (Legendre and Legendre 1998) due to its simplicity and much greater power than the Bonferroni-correction (α/k), particularly for very large sets of multiple tests.

LITERATURE CITED

Holm, S. 1979. A simple sequentially rejective multiple test procedure. Scandinavian Journal of Statistics 6:65-70.

Legendre, P., and L. Legendre. 1998. Numerical Ecology, 2nd English edition. Elsevier, New York.

Table 1. Kendall's Tau correlations between nursery-associated fish abundance scores and nursery habitat characteristics. Significant correlations (based on Holm's corrected probability) are highlighted in gray.

Nursery- associated Reef Fish Species		Log Estuarine Coastal Mangrove Area	Log Lagoon Coastal Mangrove Area	Log Fringe Coastal Mangrove Area	Log Number of Coastal Mangrove Patches	Log Coastal Mangrove Area per km Coastline	Log Seagrass Area	Log Reef Area	Log Coastal Mangrove per Reef Area
Acanthurus chirugus	Kendall's Tau	-0.235	-0.169	0.113	-0.275	-0.015	0.143	-0.584	-0.309
	Sig. (2-tailed)	0.227	0.414	0.533	0.141	0.934	0.621	0.020	0.347
	N	17	17	17	17	17	8	10	7
Chaetodon capistratus	Kendall's Tau	-0.452	0.231	0.113	-0.197	0.235	0.357	-0.270	-0.309
	Sig. (2-tailed)	0.020	0.265	0.533	0.293	0.187	0.216	0.281	0.347
	N	17	17	17	17	17	8	10	7
Gerres cinereus	Kendall's Tau	-0.380	0.293	0.083	-0.024	0.324	0.214	-0.045	0.000
	Sig. (2-tailed)	0.051	0.158	0.648	0.900	0.070	0.458	0.857	1.000
	N	17	17	17	17	17	8	10	7
Haemulon flavolineatum	Kendall's Tau	-0.380	0.169	0.038	-0.008	0.132	0.143	0.000	0.000
	Sig. (2-tailed)	0.051	0.414	0.835	0.966	0.458	0.621	1.000	1.000
	N	17	17	17	17	17	8	10	7
Haemulon parrai	Kendall's Tau	-0.054	0.262	0.023	-0.181	0.265	0.214	0.000	0.309
	Sig. (2-tailed)	0.780	0.206	0.901	0.333	0.138	0.458	1.000	0.347
	N	17	17	17	17	17	8	10	7
Haemulon plumerii	Kendall's Tau	-0.163	-0.323	0.430	0.102	0.132	-0.214	0.180	0.514
	Sig. (2-tailed)	0.403	0.119	0.018	0.584	0.458	0.458	0.472	0.117
	N	17	17	17	17	17	8	10	7
Haemulon sciurus	Kendall's Tau	-0.325	0.262	0.143	-0.149	0.309	0.071	-0.090	0.103
	Sig. (2-tailed)	0.094	0.206	0.430	0.424	0.084	0.805	0.719	0.754
	N	17	17	17	17	17	8	10	7
Lutjanus Analis	Kendall's Tau	-0.072	-0.385	0.627	0.275	0.191	0.000	0.449	0.309
	Sig. (2-tailed)	0.710	0.063	0.001	0.141	0.284	1.000	0.072	0.347
	N	17	17	17	17	17	8	10	7

Table 1 (continued)

Nursery- associated Reef Fish Species		Log Estuarine Coastal Mangrove Area	Log Lagoon Coastal Mangrove Area	Log Fringe Coastal Mangrove Area	Log Number of Coastal Mangrove Patches	Log Coastal Mangrove Area per km Coastline	Log Seagrass Area	Log Reef Area	Log Coastal Mangrove per Reef Area
Lutjanus apodus	Kendall's Tau	-0.108	0.262	0.098	0.055	0.294	0.000	-0.225	-0.206
	Sig. (2-tailed)	0.577	0.206	0.589	0.768	0.099	1.000	0.369	0.530
	N	17	17	17	17	17	8	10	7
Lujanus griseus	Kendall's Tau	-0.217	0.231	0.038	-0.149	0.250	0.429	-0.135	-0.206
	Sig. (2-tailed)	0.265	0.265	0.835	0.424	0.161	0.138	0.590	0.530
	N	17	17	17	17	17	8	10	7
Lutjanus mahogoni	Kendall's Tau	-0.054	0.200	-0.264	-0.212	-0.132	0.000	0.090	-0.206
	Sig. (2-tailed)	0.780	0.334	0.146	0.256	0.458	1.000	0.719	0.530
	N	17	17	17	17	17	8	10	7
Ocyurus chrysurus	Kendall's Tau	-0.217	-0.077	0.174	-0.008	0.088	0.571	-0.180	0.000
	Sig. (2-tailed)	0.265	0.710	0.339	0.966	0.621	0.048	0.472	1.000
	N	17	17	17	17	17	8	10	7
Scarus coeruleus	Kendall's Tau	-0.181	0.323	-0.174	-0.102	0.162	0.071	0.090	0.103
	Sig. (2-tailed)	0.353	0.119	0.339	0.584	0.365	0.805	0.719	0.754
	N	17	17	17	17	17	8	10	7
Scarus guacamaia	Kendall's Tau	0.018	0.077	0.008	0.244	0.191	0.000	-0.405	-0.514
	Sig. (2-tailed)	0.926	0.710	0.967	0.192	0.284	1.000	0.106	0.117
	N	17	17	17	17	17	8	10	7
Scarus iseri	Kendall's Tau	-0.452	0.385	-0.053	-0.212	0.221	0.357	-0.315	-0.103
	Sig. (2-tailed)	0.020	0.063	0.771	0.256	0.217	0.216	0.209	0.754
	N	17	17	17	17	17	8	10	7
Sphyraena barracuda	Kendall's Tau	0.036	0.046	0.249	-0.039	0.250	-0.071	0.225	0.411
	Sig. (2-tailed)	0.853	0.824	0.170	0.833	0.161	0.805	0.369	0.210
	N	17	17	17	17	17	8	10	7
Sparisoma chrysopterum	Kendall's Tau	-0.090	-0.015	0.128	0.181	0.191	-0.500	-0.090	-0.514
	Sig. (2-tailed)	0.642	0.941	0.480	0.333	0.284	0.083	0.719	0.117
	N	17	17	17	17	17	8	10	7

Table 2. Kendall's Tau correlations between reef-associated fish abundance scores and nursery habitat characteristics. Significant correlations (based on Holm's corrected probability) are highlighted in gray.

Reef-associated Reef Fish Species		Log Estuarine Coastal Mangrove Area	Log Lagoon Coastal Mangrove Area	Log Fringe Coastal Mangrove Area	Log Number of Coastal Mangrove Patches	Log Coastal Mangrove Area per km Coastline	Log Seagrass Area	Log Reef Area	Log Coastal Mangrove per Reef Area
Acanthurus bahianus	Kendall's Tau	-0.054	-0.169	0.189	-0.118	0.132	0.429	-0.315	-0.206
	Sig. (2-tailed)	0.780	0.414	0.299	0.528	0.458	0.138	0.209	0.530
	N	17	17	17	17	17	8	10	7
Acanthurus coeruleus	Kendall's Tau	0.018	-0.046	0.113	-0.071	0.206	0.214	-0.225	-0.103
	Sig. (2-tailed)	0.926	0.824	0.533	0.705	0.249	0.458	0.369	0.754
	N	17	17	17	17	17	8	10	7
Canthigaster rotratum	Kendall's Tau	0.072	0.231	0.008	0.322	0.162	-0.071	0.045	0.000
	Sig. (2-tailed)	0.710	0.265	0.967	0.084	0.365	0.805	0.857	1.000
	N	17	17	17	17	17	8	10	7
Chromis multimineata	Kendall's Tau	0.145	-0.262	0.068	-0.134	-0.015	0.143	-0.045	-0.309
	Sig. (2-tailed)	0.457	0.206	0.709	0.474	0.934	0.621	0.857	0.347
	N	17	17	17	17	17	8	10	7
Halichoeres bivittatus	Kendall's Tau	-0.289	0.385	-0.491	-0.212	-0.118	0.214	-0.180	-0.206
	Sig. (2-tailed)	0.137	0.063	0.007	0.256	0.510	0.458	0.472	0.530
	N	17	17	17	17	17	8	10	7
Haemulon chrysargyreum	Kendall's Tau	0.127	0.077	-0.159	-0.008	-0.074	0.071	-0.360	-0.617
	Sig. (2-tailed)	0.515	0.710	0.383	0.966	0.680	0.805	0.151	0.060
	N	17	17	17	17	17	8	10	7
Halichoeres maculipinna	Kendall's Tau	0.018	-0.385	0.249	-0.134	-0.029	-0.214	-0.270	-0.411
	Sig. (2-tailed)	0.926	0.063	0.170	0.474	0.869	0.458	0.281	0.210
	N	17	17	17	17	17	8	10	7
Halichoeres Radiatus	Kendall's Tau	-0.325	0.231	-0.143	-0.197	0.000	0.071	-0.360	-0.720
	Sig. (2-tailed)	0.094	0.265	0.430	0.293	1.000	0.805	0.151	0.028
	N	17	17	17	17	17	8	10	7

Table 2 (continued)

Reef-associated Reef Fish Species		Log Estuarine Coastal Mangrove Area	Log Lagoon Coastal Mangrove Area	Log Fringe Coastal Mangrove Area	Log Number of Coastal Mangrove Patches	Log Coastal Mangrove Area per km Coastline	Log Seagrass Area	Log Reef Area	Log Coastal Mangrove per Reef Area
Mulloidicthys martinicus	Kendall's Tau	-0.181	0.015	-0.008	-0.212	0.000	0.214	-0.180	-0.206
	Sig. (2-tailed)	0.353	0.941	0.967	0.256	1.000	0.458	0.472	0.530
	N	17	17	17	17	17	8	10	7
Myripristis jacobus	Kendall's Tau	0.289	-0.046	0.128	0.149	0.147	-0.214	-0.180	-0.206
	Sig. (2-tailed)	0.137	0.824	0.480	0.424	0.410	0.458	0.472	0.530
	N	17	17	17	17	17	8	10	7
Sparisoma aurofrenatum	Kendall's Tau	-0.054	0.108	0.415	0.181	0.500	-0.143	-0.225	-0.103
	Sig. (2-tailed)	0.780	0.603	0.022	0.333	0.005	0.621	0.369	0.754
	N	17	17	17	17	17	8	10	7
Stegastes viride	Kendall's Tau	-0.289	0.231	0.128	0.024	0.294	0.286	-0.449	-0.309
	Sig. (2-tailed)	0.137	0.265	0.480	0.900	0.099	0.322	0.072	0.347
	N	17	17	17	17	17	8	10	7
Stegastes dorsopunicans	Kendall's Tau	-0.398	0.231	-0.294	-0.322	-0.118	0.357	-0.539	-0.720
	Sig. (2-tailed)	0.041	0.265	0.105	0.084	0.510	0.216	0.031	0.028
	N	17	17	17	17	17	8	10	7
Stegastes partitus	Kendall's Tau	0.217	-0.262	0.264	0.102	0.162	-0.357	-0.180	-0.411
	Sig. (2-tailed)	0.265	0.206	0.146	0.584	0.365	0.216	0.472	0.210
	N	17	17	17	17	17	8	10	7
Stegastes planifrons	Kendall's Tau	-0.217	0.385	-0.400	-0.055	-0.118	0.429	-0.360	-0.309
	Sig. (2-tailed)	0.265	0.063	0.028	0.768	0.510	0.138	0.151	0.347
	N	17	17	17	17	17	8	10	7
Thallisoma bifasciatum	Kendall's Tau	0.018	0.293	-0.159	-0.149	0.206	-0.071	-0.225	-0.411
	Sig. (2-tailed)	0.926	0.158	0.383	0.424	0.249	0.805	0.369	0.210
	N	17	17	17	17	17	8	10	7

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Table 3. Kendall's Tau correlations between nursery-associated and reef-associated fish abundance scores. Significant correlations (based on Holm's corrected probability) are highlighted in gray.

Table 3 (continued)

Reef-associated Reef Fish	Nursery-associated Reef Fish	Acanthurus chirurgus	Chaetodon capistratus	Gerres cinereus	Haemulon flavolineatum	Haemulon parrai	Haemulon plumerii	Haemulon sciurus	Lutjanus analis	Lutjanus apodus	Lutjanus griseus	Lutjanus mahogoni	Ocyurus chrysurus	Scarus coeruleus	Scarus guacamaia	Scarus iseri	Sphyraena barracuda	Sparisoma chrysopterum
Acanthurus bahianus	Kendall's Tau	0.009	0.280	0.243	0.200	0.003	0.095	0.046	0.015	-0.003	0.212	0.040	0.231	-0.046	-0.046	0.151	0.003	-0.280
	Sig. (2-tailed)	0.947	0.045	0.082	0.152	0.982	0.494	0.741	0.912	0.982	0.128	0.774	0.098	0.741	0.741	0.280	0.982	0.045
	N	26	26	26	26	26	26	26	26	26	26	26	26	26	26	26	26	26
Acanthurus coeruleus	Kendall's Tau	0.298	0.126	0.249	0.194	0.354	0.102	0.335	0.034	0.397	0.452	-0.163	0.138	-0.040	0.243	0.058	0.206	0.268
	Sig. (2-tailed)	0.033	0.366	0.074	0.165	0.011	0.467	0.016	0.808	0.004	0.001	0.243	0.321	0.774	0.082	0.675	0.140	0.055
	N	26	26	26	26	26	26	26	26	26	26	26	26	26	26	26	26	26
Canthigaster rotratum	Kendall's Tau	-0.169	-0.132	0.126	0.034	-0.028	-0.071	-0.022	0.034	-0.071	-0.286	0.292	-0.206	-0.052	0.120	-0.015	-0.212	0.157
	Sig. (2-tailed)	0.225	0.343	0.366	0.808	0.843	0.612	0.877	0.808	0.612	0.040	0.036	0.140	0.708	0.390	0.912	0.128	0.261
	N	26	26	26	26	26	26	26	26	26	26	26	26	26	26	26	26	26
Chromis multimineata	Kendall's Tau	-0.249	-0.274	-0.102	-0.182	-0.182	-0.298	-0.471	-0.169	-0.446	-0.231	0.348	-0.323	-0.243	-0.194	-0.108	-0.329	-0.231
	Sig. (2-tailed)	0.074	0.050	0.467	0.193	0.193	0.033	0.001	0.225	0.001	0.098	0.013	0.021	0.082	0.165	0.440	0.018	0.098
	N	26	26	26	26	26	26	26	26	26	26	26	26	26	26	26	26	26
Halichoeres bivittatus	Kendall's Tau	0.298	0.163	0.372	0.317	0.145	0.114	0.286	0.009	0.212	0.280	-0.040	0.175	0.292	0.317	0.231	-0.003	0.280
	Sig. (2-tailed)	0.033	0.243	0.008	0.023	0.300	0.415	0.040	0.947	0.128	0.045	0.774	0.209	0.036	0.023	0.098	0.982	0.045
	N	26	26	26	26	26	26	26	26	26	26	26	26	26	26	26	26	26
Haemulon chrysargyreum	Kendall's Tau	-0.077	0.218	0.071	0.015	-0.218	-0.348	-0.077	-0.243	0.009	-0.034	0.335	-0.089	-0.071	0.114	0.052	-0.243	-0.095
	Sig. (2-tailed)	0.582	0.118	0.612	0.912	0.118	0.013	0.582	0.082	0.947	0.808	0.016	0.523	0.612	0.415	0.708	0.082	0.494
	N	26	26	26	26	26	26	26	26	26	26	26	26	26	26	26	26	26
Halichoeres maculipinna	Kendall's Tau	0.286	0.003	0.163	0.083	-0.065	0.114	0.065	0.058	0.015	-0.040	0.145	-0.058	-0.262	0.108	-0.015	-0.077	0.145
	Sig. (2-tailed)	0.040	0.982	0.243	0.552	0.643	0.415	0.643	0.675	0.912	0.774	0.300	0.675	0.061	0.440	0.912	0.582	0.300
	N	26	26	26	26	26	26	26	26	26	26	26	26	26	26	26	26	26

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Table 3 (continued)

Reef-associated Reef Fish	Nursery-associated Reef Fish	Acanthurus chirurgus	Chaetodon capistratus	Gerres cinereus	Haemulon flavolineatum	Haemulon parrai	Haemulon plumerii	Haemulon sciurus	Lutjanus analis	Lutjanus apodus	Lutjanus griseus	Lutjanus mahogoni	Ocyurus chrysurus	Scarus coeruleus	Scarus guacamaia	Scarus iseri	Sphyraena barracuda	Sparisoma chrysopterum
Halichoeres radiatus	Kendall's Tau	0.397	0.249	0.335	0.280	0.108	0.065	0.348	-0.003	0.409	0.268	0.022	0.114	0.046	0.342	0.046	0.095	0.231
	Sig. (2-tailed)	0.004	0.074	0.016	0.045	0.440	0.643	0.013	0.982	0.003	0.055	0.877	0.415	0.741	0.014	0.741	0.494	0.098
	N	26	26	26	26	26	26	26	26	26	26	26	26	26	26	26	26	26
Mulloidicthys martinicus	Kendall's Tau	-0.009	0.237	0.225	0.206	-0.040	-0.071	0.114	-0.015	0.065	0.292	0.206	0.298	0.132	0.182	0.108	0.169	-0.003
	Sig. (2-tailed)	0.947	0.090	0.108	0.140	0.774	0.612	0.415	0.912	0.643	0.036	0.140	0.033	0.343	0.193	0.440	0.225	0.982
	N	26	26	26	26	26	26	26	26	26	26	26	26	26	26	26	26	26
Myripristis jacobus	Kendall's Tau	-0.311	-0.040	0.034	-0.071	-0.194	-0.274	-0.274	-0.182	-0.126	-0.046	0.335	-0.126	0.052	-0.034	-0.120	-0.071	-0.132
	Sig. (2-tailed)	0.026	0.774	0.808	0.612	0.165	0.050	0.050	0.193	0.366	0.741	0.016	0.366	0.708	0.808	0.390	0.612	0.343
	N	26	26	26	26	26	26	26	26	26	26	26	26	26	26	26	26	26
Sparisoma aurofrenatum	Kendall's Tau	0.040	0.212	0.286	0.280	0.071	0.237	0.286	0.231	0.138	0.108	-0.052	0.200	0.095	0.194	0.354	0.108	0.058
	Sig. (2-tailed)	0.774	0.128	0.040	0.045	0.612	0.090	0.040	0.098	0.321	0.440	0.708	0.152	0.494	0.165	0.011	0.440	0.675
	N	26	26	26	26	26	26	26	26	26	26	26	26	26	26	26	26	26
Stegastes viride	Kendall's Tau	0.175	0.434	0.495	0.415	0.206	0.163	0.397	0.009	0.335	0.342	-0.114	0.323	0.169	0.231	0.551	0.108	0.009
	Sig. (2-tailed)	0.209	0.002	0.000	0.003	0.140	0.243	0.004	0.947	0.016	0.014	0.415	0.021	0.225	0.098	0.000	0.440	0.947
	N	26	26	26	26	26	26	26	26	26	26	26	26	26	26	26	26	26
Stegastes dorsopunicans	Kendall's Tau	0.385	0.335	0.262	0.342	-0.077	0.077	0.237	-0.065	0.163	0.206	0.046	0.237	0.218	0.378	0.194	-0.003	0.095
	Sig. (2-tailed)	0.006	0.016	0.061	0.014	0.582	0.582	0.090	0.643	0.243	0.140	0.741	0.090	0.118	0.007	0.165	0.982	0.494
	N	26	26	26	26	26	26	26	26	26	26	26	26	26	26	26	26	26
Stegastes partitus	Kendall's Tau	-0.077	-0.138	0.034	-0.009	-0.292	-0.065	-0.163	0.003	-0.138	-0.169	0.311	-0.274	-0.108	0.151	-0.169	-0.206	0.126
	Sig. (2-tailed)	0.582	0.321	0.808	0.947	0.036	0.643	0.243	0.982	0.321	0.225	0.026	0.050	0.440	0.280	0.225	0.140	0.366
	N	26	26	26	26	26	26	26	26	26	26	26	26	26	26	26	26	26
Stegastes planifrons	Kendall's Tau	-0.151	0.182	0.403	0.298	-0.071	-0.188	-0.003	-0.243	-0.040	0.052	0.138	0.095	0.323	0.249	0.434	-0.280	-0.022
	Sig. (2-tailed)	0.280	0.193	0.004	0.033	0.612	0.179	0.982	0.082	0.774	0.708	0.321	0.494	0.021	0.074	0.002	0.045	0.877
	N	26	26	26	26	26	26	26	26	26	26	26	26	26	26	26	26	26
Thallisoma bifasciatum	Kendall's Tau	0.114	0.138	0.249	0.169	-0.102	-0.132	0.188	-0.151	0.114	0.058	0.169	-0.009	0.083	0.305	0.169	-0.003	0.169
	Sig. (2-tailed)	0.415	0.321	0.074	0.225	0.467	0.343	0.179	0.280	0.415	0.675	0.225	0.947	0.552	0.029	0.225	0.982	0.225
	N	26	26	26	26	26	26	26	26	26	26	26	26	26	26	26	26	26