

## Interpreting space use and behavior of blue tang, *Acanthurus coeruleus*, in the context of habitat, density, and intra-specific interactions

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### Synopsis

We hypothesized that blue tang, *Acanthurus coeruleus*, territories on sites with low biogenic structure would be larger than territories on sites with relatively high biogenic structure due to differences in the amount and distribution of resources. We tested this hypothesis by tracking blue tang over uncolonized pavement and reef crest, two habitat types at opposite ends of the habitat structure spectrum. We recorded density, feeding rates and aggression events in order to evaluate our findings in the context of a territory model and the ideal free distribution model. Territories of *A. coeruleus* averaged nearly four times larger on pavement sites than on reef crest sites. Conversely, densities of *A. coeruleus* were significantly lower on pavement sites. While there was no significant difference in the average rates of movement between habitats, average turning angles were significantly higher on reef crest. There were no significant differences in feeding rates between habitats, suggesting that higher territory sizes and lower densities may allow fish on uncolonized pavement to match resource acquisition of fish on reef crest. The insignificant difference of aggression encounters between habitats suggests that movement and density differences among habitats are not solely legacies of differential settlement.

### Introduction

Habitat structure and quality in the marine environment are in a state of flux globally (Watling & Norse 1998). Nowhere are these changes more obvious than in coral reef systems, where alarming reports of reef destruction and degradation from anthropogenic and natural disturbances are common (Ginsburg 1994, GCRMN 2002). In Caribbean reefs, the cumulative effects of disease, bleaching, and anthropogenic disturbance have

significantly reduced coral cover, resulting in decreased biogenic structure (GCRMN 2002, Gardner et al. 2003). In addition to these impacts, increases in atmospheric carbon dioxide will likely decrease coral calcification rates, resulting in weaker skeletons, reduced extension rates, and increased susceptibility to erosion (Kleypas et al. 1999, Kleypas et al. 2001). Changes in habitat structure are known to affect the movement of organisms in other systems (e.g., spotted owls in patchy forests) (Lande 1988). Thus effective long-

term conservation of coral reef fishes requires an understanding of how existing habitat influences behavior, how habitats are distributed, and how impending habitat changes will likely alter behavior in the future.

For most reef fishes, the amount and distribution of resources is a function of local benthic habitat (Williams 1991). Degraded reefs lose biogenic structure (Szmant 1991, Aronson et al. 1994, Edmunds 2002), which generally reduces the availability of food, shelter, and settlement areas for reef fish (Kohn 1968, Kaufmann 1983). We expected that differences in resource availability resulting from decreased habitat complexity would yield corresponding differences in fish movement among habitats. Since habitat complexity varies enormously across a reef complex and among reef sites, we simplified the evaluation of habitat by considering two habitat types that best represent the morphological 'end-points' of degradation on Caribbean reefs: uncolonized pavement sites, and reef crest sites. Specifically, we hypothesized that reef fish territories on sites with little or no biogenic structure (uncolonized pavement) would be larger than territories on sites with relatively high biogenic structure (reef crest) due to assumed differences in the amount and distribution of resources. To test this hypothesis we surveyed the movements of *Acanthurus coeruleus* (Pisces: Acanthuridae – blue tang) over the two different habitat types. To evaluate possible drivers of movement differences between habitats, we collected information on abundance, feeding rates, and aggressive interactions.

### Methods

In July, 2000, we tracked a total of 57 fish (between 14–25 cm fork length) over two uncolonized pavement sites and two reef crest sites on Andros Island, Bahamas, using facilities at the Forfar Field Station. We distributed our data collection effort evenly over the two habitat types.

Uncolonized pavement was characterized by flat, low relief, solid carbonate rock, often covered by a thin sand veneer, with sparse coverage of macroalgae, hard coral, gorgonians, and other sessile invertebrates that did not obscure the underlying carbonate rock (Mumby & Harborne

1999)<sup>1</sup>. Reef crest was characterized by the nearly emergent segment of a reef lying between the back reef and fore reef zones (Mumby & Harborne 1999)<sup>1</sup>. Reef crest habitat had high rugosity (from live and dead *Acropora palmata*), relatively high live coral cover, and included some spur-and-groove formation on the forereef side of the crest. *A. coeruleus* were easily located on both habitat types. On four occasions we 'tracked' a stationary object so that we could evaluate measurement error in the tracking technique. At each survey site, we conducted eight transects using the Atlantic and Gulf Rapid Reef Assessment protocol to record density of fishes<sup>2</sup>. During an AGRRA belt transect, a surveyor traversed a 2 m wide by 30 m long area over a period of 6–8 min by paying out a 30 m tape reel. Surveyors used a 1 m t-bar to help visualize a 2 m<sup>3</sup> survey area while traversing the transect. During the transect surveyors recorded all *A. coeruleus* entering the survey area.

### Study organism

*Acanthurus coeruleus* is a common, widely distributed obligate reef resident on Caribbean reefs<sup>3</sup>. It is a predominant member of the large mobile herbivore trophic guild, and likely plays an important role in reef communities (Ogden & Lobel 1978, Hay 1984, Lawson et al. 1999). *A. coeruleus* is a typically solitary forager, although adults will occasionally join large schools to forage on algae in well defended territories of damselfishes (Foster 1985). In previous studies of habitat use by *A. coeruleus*, fish were in the highest abundances on the reef crest and inner fore reef, although individuals were present in all zones from

<sup>1</sup> Kendall, M.S., C.R. Kruer, K.R. Buja, J.D. Christensen, M. Finkbeiner and M.E. Monaco 2002. Methods used to Map the Benthic Habitats of Puerto Rico and the U.S. Virgin Islands. NOAA Biogeography Program, website: <http://biogeonos.noaa.gov/projects/mapping/caribbean/startup.htm>

<sup>2</sup> AGRRA. 2003. Atlantic and Gulf Rapid Reef Assessment, RSMAS University of Miami. website: <http://www.coral.noaa.gov/agra/>

<sup>3</sup> REEF. 2004. Reef Environmental Education Foundation. World Wide Web electronic database, website: <http://www.reef.org>

the back reef to the outer fore reef (Lewis & Wainwright 1985, Lawson et al. 1999).

While *A. coeruleus* is not typically the target of commercial or sport fisheries, it is important to subsistence fishers (Munro 1974, Robertson 1988, Garrison et al. 1998). In places where subsistence fishing pressure is particularly intense, the density of Acanthurids can be highly depressed; the dramatic loss of coral cover in Jamaica following the 1983 mass mortality of *Diadema antillarum* was attributed to the compounding effect of intensive fishing on herbivorous fishes in the region (Liddell & Ohlhorst 1986), allowing algae to outcompete corals (Hughes 1994).

#### *Tracking technique*

We quantified *A. coeruleus* movement by geo-referencing the path of a fish during a 20 min period. We used Garmin GPS units connected to data loggers (Palm Pilot m100) to record the location of a focal fish at 1–3 second intervals (depending on the rate at which GPS units were able to update position fixes) while tracking the fish on snorkel or SCUBA. Since Selective Availability was turned off in the Spring of 2000, the absolute accuracy of non-differential GPS units has increased to within 5 meters 95% of the time, while precision over a short time period is substantially greater<sup>4</sup>. Use of GPS units out over open water where interference and factors such as multipath are negligible further improves both the accuracy and consistency of position estimates.

To conduct a survey, a surveyor located a focal fish, and then followed the fish for 20 min while keeping a float with a GPS datalogger directly above the fish. The first 5 min of each 20-min survey period were intended to acclimate the fish to the presence of the surveyor, and were not used in the data analysis. In water shallower than 3 m, the surveyor lagged behind the fish to minimize the surveyor influence on fish behavior (Reese 1978). During the latter 15 min of the survey period, the surveyor recorded both the number of con-specific aggressive encounters and the number of grazing

bites taken. We classified aggressive encounters as responses of a focal fish to another (such as lateral displays, bites, or chases) that resulted in terminations of previous behavioral activities, excluding courtship and spawning (van Rooij et al. 1996b, Mumby & Wabnitz 2002). We recorded bites by counting the number of times the focal fish contacted the substrate with its mouth. Fish would often take several bites from the same location in rapid succession; in these instances we counted each bite independently. During the survey, the observer noted unique characteristics of the focal fish so as to avoid re-tracking the same individual in subsequent surveys. On consecutive days, observers tracked fish from different areas within each site to minimize the possibility of re-tracking.

#### *Data analysis*

We imported fish paths into ArcView 3.2 and analyzed them using the Animal Movement Analysis extension (Hooge & Eichenlaub 1997) to determine minimum convex polygon (MCP) territory size, average turning radius (0–180°), and average movement rate ( $\text{m s}^{-1}$ ) for each fish. We excluded two fish that were tracked over uncolonized pavement from the study because they swam in a relatively straight line throughout the tracking period, and were thus assumed to be non-territorial ‘wanderers’. Wandering is a specific social mode of *A. coeruleus* described by Morgan & Kramer (2004) in which non-territorial individuals swim relatively rapidly and high over the substrate. Wanderers are assumed to be in search of foraging sites, new territories, or cleaning stations. We imported all data into SAS software for analysis (SAS Institute Inc. 2003). For the sake of consistency and ease of comparison, we completed all analyses using the SAS procedure PROC NLMIXED. PROC NLMIXED is a flexible procedure that allows for multiple levels, random and fixed effects, and a variety of response distributions. To test for significant differences in the number of aggression events and the densities of *A. coeruleus* between habitat types we fitted a generalized mixed model with a Poisson response. We used a Poisson response because both the density and aggression data are the result of counts and have a pronounced right skewed distribution. Habitat type was modeled as a

<sup>4</sup> NGS. 2000. National Geodetic Survey, National Ocean Service, National Oceanic and Atmospheric Administration, Department of Commerce. National Geodetic Survey Website: <http://www.ngs.noaa.gov/>

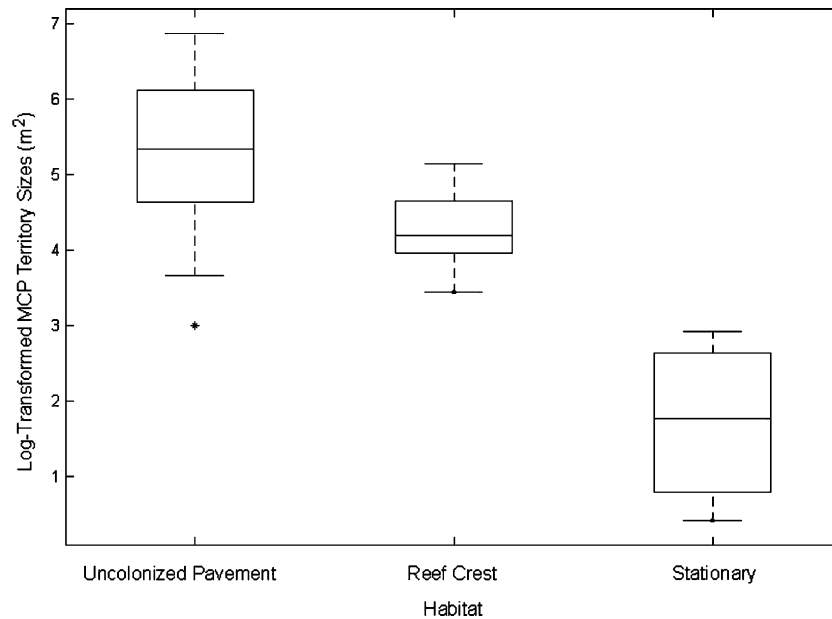


Figure 1. Box plot of the log-transformed MCP territory sizes of *A. coeruleus* in different habitat types, and the log-transformed MCP areas calculated from surveys of stationary objects. The upper and lower ends of the boxes represent the 75th and 25th percentiles, and the whiskers depict the extent of the data. The centerline represents the median. Outliers are identified by an '\*'. Note that the mean territory sizes presented in the results section are for untransformed data and thus do not directly correspond to the box centers.

fixed-effect predictor, and sites were modeled as random-effect predictors nested within habitat. To account for likely differences in bite counts, territory sizes, turning radii, and movement rates between habitats we fit the same model effects as above, but assumed a normally distributed response. We log-transformed the MCP territory sizes in order to meet the assumption of normality.

## Results

We tracked 30 *A. coeruleus* on reef crest sites and 27 on pavement sites over a period of 4 days.

There were significant differences in the size of *A. coeruleus* territories between habitats (Figure 1); territories from both habitat types differed significantly from the average MCP territories calculated from the stationary object surveys ( $\bar{X} = 8.49 \text{ m}^2$ ,  $SE = 3.91$ ; Table 1). Territories on uncolonized pavement sites ( $\bar{X} = 292.43 \text{ m}^2$ ,  $SE = 48.35$ ) averaged nearly 4 times the size of territories on reef crest sites ( $\bar{X} = 76.59 \text{ m}^2$ ;  $SE = 6.27$ ). The density of *A. coeruleus* on the reef crest ( $\bar{X} = 0.10 \text{ m}^2^{-1}$ ,  $SE = 0.02$ ) was over 4 times higher than the density of *A. coeruleus* on uncolonized pavement ( $\bar{X} = 0.02 \text{ m}^2^{-1}$ ,  $SE = 0.01$ ;  $T_3 = 6.23$ ,  $p = 0.008$ ). All *A. coeruleus* MCP

Table 1. Differences in the least squared mean values of log transformed MCP territory sizes calculated from tracks of fish on reef crest (RC), uncolonized pavement (UP), and the tracks of a stationary object (ST). Each row gives the  $p$ -value for pair-wise comparisons of RC, UP, and ST. Note that there are only two degrees of freedom in analyses comparing stationary object surveys since all stationary data are from one site; the model thus accounts for random effects of 3 sites as compared to 4 for comparisons of territory sizes between the two different habitat types.

Habitat	Habitat	Standard error	DF	$t$ value	$p >  t $
RC	ST	0.419	2	5.98	0.03
RC	UP	0.21	3	-3.57	0.04
ST	UP	0.422	2	-8.43	0.01

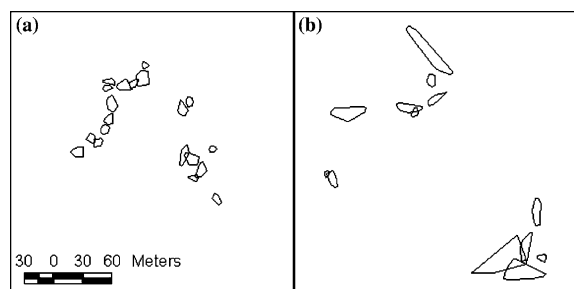


Figure 2. Maps depict MCP territories for tracked fish on one of the reef crest survey sites (a) and one of the uncolonized survey sites (b). Each polygon represents the MCP of an individual fish. The appearance of territory 'clusters' within sites results from survey effort on different days. Daily survey areas were offset in order to avoid unintentionally re-tracking individuals.

territories from one reef crest site and one uncolonized pavement site are shown in figure 2 for illustrative purposes.

While there were significant differences in the average turning radius of fish between reef crest ( $\bar{X} = 105.30^\circ$ ,  $SE = 2.50$ ) vs. uncolonized pavement sites ( $\bar{X} = 72.97^\circ$ ,  $SE = 3.28$ ;  $T_3 = 7.26$ ,  $p = 0.02$ ), movement rates between reef crest ( $\bar{X} = 0.194 \text{ m s}^{-1}$ ,  $SE = 0.008$ ) and uncolonized pavement ( $\bar{X} = 0.226 \text{ m s}^{-1}$ ,  $SE = 0.012$ ) were not significantly different ( $T_3 = 0.77$ ,  $p = 0.50$ ; Figure 3). Aggression rates ( $\bar{X} = 0.064$  aggressions  $\text{min}^{-1}$ ,  $SE = 0.018$ ) and feeding rates

( $\bar{X} = 17.39$  bites  $\text{min}^{-1}$ ,  $SE = 0.85$ ) on the reef crest were not significantly different from aggression rates ( $\bar{X} = 0.08$  aggressions  $\text{min}^{-1}$ ,  $SE = 0.015$ ;  $T_3 = 0.88$ ,  $p = 0.44$ ) and feeding rates ( $\bar{X} = 12.51$  bites  $\text{min}^{-1}$ ,  $SE = 1.1$ ;  $T_3 = 0.69$ ,  $p = 0.54$ ) on uncolonized pavement. Note that for all results the degrees of freedom for the t-statistic are the number of survey sites minus one.

## Discussion

Differences in the manner in which fishes use space on a reef influence the effectiveness of a diversity of management endeavors, including reserve design and density assessments (Kramer & Chapman 1999). Quantitative characterizations of habitat-mediated reef fish movements are clearly important tools for resource managers tasked with conserving fisheries in the face of increasing anthropogenic impacts. However, such characterizations must be interpreted in the context of spatial-ecological theory in order to gain insight into the mechanisms driving differences in behavior and abundance.

The lower abundances and larger territories of *A. coeruleus* on uncolonized pavement vs. reef crest can be explained by differences in habitat complexity and the amount of available resources between the two habitat types. Because uncolon-

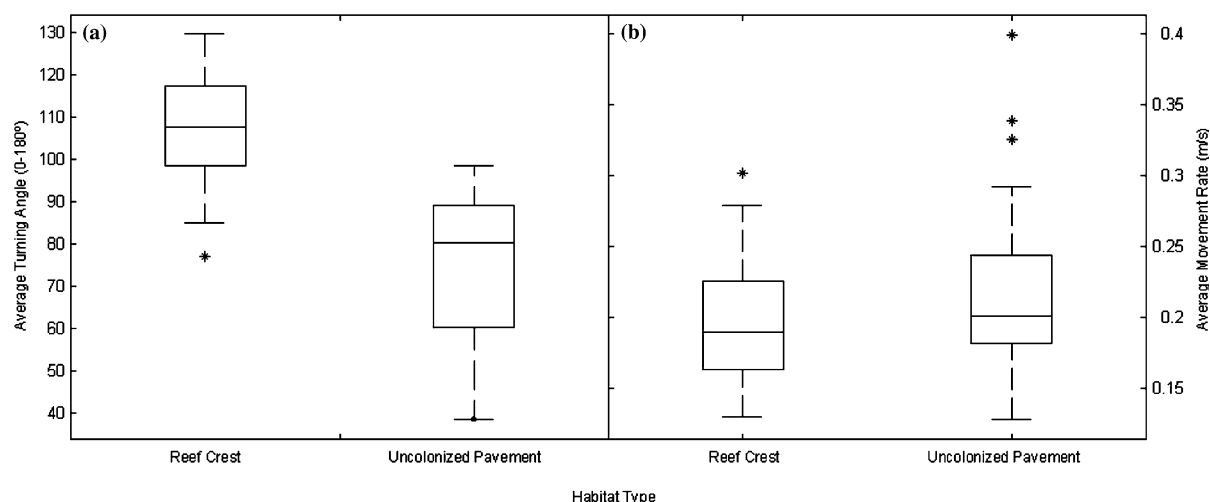


Figure 3. Box plots of the average absolute value of turning angles (a) and the average rate of movement (b) of *A. coeruleus* in different habitat types. The upper and lower ends of the boxes represent the 75th and 25th percentiles, and the whiskers depict the extent of the data. The centerline represents the median. Outliers are identified by an '\*'.

ized pavement is less rugose and has less substrate suitable for algal growth than reef crest, uncolonized pavement is less complex and less productive (Bruggemann et al. 1994, Russ 2003). Increasing habitat complexity results in decreasing interference competition (Uttley 1980, Crowley et al. 1987, Anholt 1990), which in turn may allow a higher number of individuals to occupy a patch (Jensen 1987). Thus, differences in competitive interactions mediated by habitat complexity may contribute to the differences in the average territory size and density of *A. coeruleus* between habitat types. Fretwell & Lucas (1970) and Fretwell (1972) proposed the ideal free distribution (IFD) model to explain the distribution of individuals across habitats with different resource levels. In the IFD model, animals distribute themselves such that all individuals are able to acquire the same amount of resources; if resources differ between habitat patches, then the density of individuals will differ correspondingly. Several studies of Caribbean reef fish have documented changes in the density of large mobile herbivores in response to altered resource levels in a manner consistent with the predictions of the IFD model (McClanahan et al. 2000, Williams et al. 2001, McClanahan et al. 2002). Our results are also consistent with the predictions of the IFD in that there were fewer individuals in less productive habitat. Furthermore, the larger territory sizes of fish on uncolonized pavement suggest that larger areas are needed to procure similar resources in less productive areas.

Observed differences in territory size between the two habitats may be due to differences in the density of *A. coeruleus*, rather than to differences in habitat quality as we have postulated (Gust 2002, Mumby & Wabnitz 2002). Levin et al. (2000) found that the distribution of *Stegastes planifrons* (three-spot damselfish) did not conform to the IFD model, and postulated that the virtual absence of post-settlement relocations resulted in local densities that reflected recruitment success rather than resource availability. Hixon's (1980) model for optimal territory size in an energy maximizing animal predicts that, all else being equal, increases in competitor density will result in smaller territories, decreased time spent feeding, and increased time spent defending territories. While we documented significant differences in

territory size between habitats, there were no significant differences in the aggression encounters or the amount of time spent feeding. In other words, despite markedly different densities of fish, aggression and rates of resource usage were similar between the two habitats, contrary to the predictions of a territory model under the assumption of equal habitat quality across patches. Thus, it is reasonable to assume that the differences in territory size are due at least in part to differences in habitat complexity and productivity.

The similar rates of movement between habitats may have resulted from the optimization of net energy gain, or may be a direct consequence of the behaviors of *A. coeruleus* under the constraint of their morphology. Energy maximizing animals should only alter rates of movement when doing so leads to a net energy gain. Increases in the rate of movement within a territory while holding time investment in food acquisition and defense constant will yield a decrease in the daily net energy gain for a territorial animal (Korsmeyer et al. 2002). The similar rates of movement in the two habitat types fit with our expectations of *A. coeruleus* as energy maximizing territorial animals, given that the time budgets of the fish within the two habitats were similar. However, movement rates may not be 'chosen' based on optimizing net energy gain, but rather mandated to a certain extent by the morphology of the species. Drucker & Lauder (2000) hypothesized that stability and maneuverability were functions of the force exerted by a swimming fish, and subsequently noted a morphologically mediated tradeoff between movement rate and maneuverability. In the case of *A. coeruleus*, rates of movement may thus be set by the maneuverability requirements of foraging and territory defense rather than by optimizing net energy gains. Future efforts to track *A. coeruleus* across a broad array of habitat characteristics will likely yield the information necessary to evaluate relative support for these two different hypotheses.

Traditional visual methods for collecting data on movement in reef fish involve a snorkeler or SCUBA diver recording the location of a fish as it travels across a grid placed on a reef prior to tracking (Samoilys 1997, Jones 2002), or by periodically flagging its location and subsequently measuring distances between marks (Shapiro 1987,

van Rooij et al. 1996a, Overholtzer & Motta 1999, Bell & Kramer 2000). The GPS based survey method employed in this study represents an improvement over previously published visual methods because it does not require site preparation prior to data collection, and it provides nearly continuous position data useful for deriving rates and turning radii. Based on the stationary object tracking, position error of up to 3 m can be expected using the technique. As such, previously described visual survey methods such as the flagging technique would likely yield more accurate data on territory sizes for fishes that are highly site-philopatric such as damselfish or perhaps even juvenile *A. coeruleus*. Future studies employing the GPS based survey method should collect stationary object surveys as we have done to demonstrate that the data have sufficient precision to characterize territories (i.e., MCPs from stationary object surveys are significantly smaller than the MCPs of fish territories). In our experience, *A. coeruleus* did not noticeably alter their behavior in response to the presence of a snorkeler following the 5-min acclimation period. It is possible, however, that the behaviors of fish were imperceptibly altered. Despite the extensive use of visual observations in reef fish behavioral investigations, to our knowledge no study has attempted to identify and characterize behavioral bias associated with the presence of a diver. Combining a high resolution acoustic tagging method such as Radio Acoustic Positioning and Telemetry (RAPT) with intermittent visual observations would likely uncover such behavioral biases if they exist (O'Dor et al. 2001, Parsons et al. 2003).

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