Habitat association, disturbance dynamics, and the role of spatial scale in structuring coral reef fish assemblages

Thesis submitted by

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in March 1998

for the degree of Doctor of Philosophy

in the Department of Marine Biology

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18 Oct 1998

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Abstract

Understanding how patterns and processes at one scale are related to those at other scales is of central importance in developing ecological theory. However, in order for scaling rules to be useful to empirical ecologists, they must have a rational, measurable, and critically examinable basis. In this study I consider the role spatial scale plays in structuring coral reef fish assemblages and how habitat structure may mediate scaling rules for the assemblage.

The relationship between a population's mean and variance provide a measure of whether that population is indeed scale dependent. I counted fish and measured habitat variables in 701 transects, allocated across 12 habitat zones. Slopes of the power plots for most species lay between 1 and 2 which indicated that the variance, as a proportion of the mean, of small samples was lower than in large samples and hence scale-dependent. 28% of the variation of the data set was explained by habitat variables which indicated that a large percentage of the scale dependence could be modelled by habitat variables alone.

Peaks of variability associated with changes in scale are indicators of the scales at which organisms are spatially structured. It has been hypothesised that coincident variance peaks are indicators of common scales of organisation and thus should also correspond to the scale of maximal correlation. I tested this idea by quantifying fish-habitat associations at different scales on contiguous coral reefs. I mapped fish and habitat to a 3x3m resolution in 24 30x30m grids and then progressively aggregated adjacent squares and recalculated the correlation between fish and benthic cover, physical reef structure, and locality over 9 spatial scales ranging from 9-225m^2. Both fish and habitat variables were patchy at the smallest scale, yet maximal correlation occurred at larger scales (>54m^2). A complex suite of responses were found among fish taxa, with some species associated simply with benthic cover and locality, while others were associated with complex interactions between different types of habitat measures. The scale of maximal correlation was not indicative of the scale at which fishes responded to their environment. Maximal correlation was found when the likelihood of the occurrence of a particular fish species and the likelihood of the occurrence of

preferred habitat type were symmetrised. In other words, the scale of measurable fish-habitat association was a measurement of the optimal scale at which predictability of fish given habitat type, and predictability of habitat type given fish were maximised.

Studies carried out on small patch reefs have provided the basic information from which much ecological theory of coral reef fishes has been derived. However no published studies have attempted to document what scaling effects exist in coral reef systems, and whether we can extrapolate or interpolate between studies carried out on different scales. I mapped randomly selected patch reefs, ranging in size from $0.26m^2$ to $63.5m^2$, and censused the resident fish fauna. I then partitioned variation amongst reef area, reef shape and patchiness, and benthic cover. Species responded in a variety of ways to reef parameters. Some species were strongly area-dependent, others were well predicted by reef shape and patchiness, and a considerable number of species were well predicted by the benthic cover of the reef. Further groups of species were associated with combinations of these factors. In order to measure the effect of scaling up or down, I divided the data set into small, medium, and large reefs, recalculated regression equations and measured the predictive ability of each equation. Surprisingly equations derived from the smaller reefs were better predictors of larger reefs than vice versa. As a consequence, the lessons drawn from experiments carried out on small reefs can, in the light of prior information, be cautiously, and with strong caveats, applied to large reefs. Central to these scaling rules is the incorporation of habitat as an explanatory variable.

To establish the bounds within which habitat may influence fish assemblage structure, I carried out two experiments. First, I experimentally reduced coral cover in 10x10m quadrats on contiguous reef from 55% to 47%, 43%, and 34% and monitored the assemblage over two years. Contrary to what might be expected from many correlative studies, all fish species considered were resistant, at this scale and level, to habitat disturbance. However, a large portion of variation in the fish assemblage was explainable by spatial and temporal variables. It is hypothesised that spatial-temporal structure at the landscape level may moderate local disturbance to habitat structure on contiguous reef.

The second disturbance experiment was carried out on small patch reefs. To re-evaluate the current models of reef fish assemblage organisation, I implemented a factorial combination of direct (by fish removal) and indirect disturbance (by habitat alteration) and monitored the experiment over two years. Habitat disturbance generated strong, predictable changes in the fish assemblage which explained almost half the variation in the data set. In contrast, direct disturbance generated a lesser and shorter-term effect. The results from this experiment supported a model of reef fish assemblages as deterministic (within broad bounds), yet weakly interacting systems, the determinism of which was mediated by habitat.

This study supports the initial premise that scaling rules for coral reef fish assemblages are mediated by habitat. As a consequence, habitat structure must be included into a general theory of coral reef fish ecology. An important precursor to the successful incorporation will be the parameterisation of the spatio-temporal dynamics of habitat structure, and the scales and forms of responses to habitat disturbance that fishes can be expected to make. Scale, far from being a black-box within which incongruous results are filed, can exert rational, mechanistic effects which can be incorporated both into the theoretical and empirical development of coral reef fish ecology.

Acknowledgements

I would like to thank my supervisor, Dr Geoff Jones, for granting me free rein to pursue the lines of inquiry that took my fancy, and furthermore picking up the tab courtesy of his Australian Research Council grant. I thank Geoff also for his many conversations, ideas, and criticisms that have served to focus my research over the years. The Australian Museum's Lizard Island Research Station provided the logistical support without which I could not have spent the many diving hours required to address the questions that I found interesting. Many thanks to the directors, Anne Hoggett and Lyle Vail, and support staff, Lance and Marianne. I thank also the numerous and varied diving assistants who bore with me, wondering how it was possible to look at the same piece of rock for 30 minutes and still retain enough enthusiasm to relish the thought of looking at another rock for a further half hour *ad infinitum*. Extra special thanks to Tara Anderson for her patch-reef map drawing and image analysis skills; her copious proof reading; graphical and word processing expertise; long discussions about what's wrong with science (we *can't* be wrong, can we?); her tireless perfectionism during the latter stages of this thesis - long after I ceased to care what it looked like; and her perennial love and support.

STATEMENT ON SOURCES
DECLARATION

I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institute of tertiary education. Information derived from the published or unpublished work of others has been acknowledged in the text and a list of references is given.

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