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Journal of Experimental Marine Biology and Ecology 324 (2005) 157–169

Journal of EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY

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Spatial patterns of Yucatan reef fish communities: Testing models using a multi-scale survey design

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Received 31 October 2003; received in revised form 17 January 2005; accepted 7 April 2005

Abstract

Using a hierarchical multi-scale survey design, we examined the spatial patterns of reef fish communities and tested ecological models concerning the relative importance of reef geomorphology and anthropogenic pressure possibly driving community structure. Canonical redundancy analysis was used as a form of multivariate analysis of variance (MANOVA) to asses differences in reef fish community composition at two spatial scales: broad (10^5 m) and intermediate (10^4 m). Surveys were conducted on the east coast of the Yucatan Peninsula (Mexican Caribbean fringing reef), including regions and reefs which differed in geomophologic structure and human use. Seven hundred and fourteen line transects were distributed among 13 reef localities belonging to different regions established a priori. Transects covered four types of reef habitat: lagoon, front, slope, and terrace. Tests of significance were based on permutation procedures. Significant differences among regions were found for the lagoon, slope, and terrace fish communities, consistent with the geomorphologic model, but it is only in the reef lagoon that they were consistent with the anthropogenic model, which may indicate an effect of coastal human activities. Significant differences among reefs within regions were observed, which could be associated with local environmental gradients. Canonical nested MANOVA was an appropriate method for testing ecological hypotheses about the functioning of complex biological systems. The use of a surveying strategy that explicitly incorporated the spatial structure represents an important contribution of this paper to coral reef fish ecology.

Keywords: Anthropogenic disturbance; Canonical analysis; Nested survey design; Reef-fish community; Reef geomorphology; Spatial analysis; Yucatan Peninsula

1. Introduction

Awareness of the importance of the spatial structure of complex ecosystems like coral reefs, and the

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doi:10.1016/j.jembe.2005.04.011

communities which inhabit them, is growing. Ecologist know that the spatial organization of the elements of an ecosystem is important for functioning (Legendre, 1993), although it is rarely integrated in the survey methodology and analysis of the results. This is an important reason why many ecological surveys across space do not lead to clear conclusions. Fortunately, the state of knowledge, research procedures, statistical methods, and technology now make it possible to understand spatially-structured data.

1.1. Theoretical framework

According to hierarchy theory, complex stable systems are often hierarchical (Allen and Starr, 1982). Physical forces acting at broad spatial scale can generate identifiable structures at finer scales. Taking this theory into account, we can picture the reef environment as being structured by broad-scale physical mechanisms, like geomorphology or current dynamics, generating broad and relatively homogeneous zones; inside these, finer-scale biotic processes dominate in spatially structuring the environment (Legendre, 1993). Understanding how information is transferred across scales is a fundamental problem in ecology (Levin, 1992). The patterns and processes we discover will depend strictly on the extent at which we examine the system (Sale, 1998).

Some studies have analysed spatial variation of reef fish community structure over broad extents or across a variety of extents (Fowler et al., 1992; Adjeroud et al., 1998; Eagle et al., 2001; Gust et al., 2001; Bellwood et al., 2002). Many others have analysed particular processes of reef fishes on small areas like coral heads and patch reefs (e.g. Clarke, 1988; Doherty and Fowler, 1994; Sale et al., 1994). According to Ault and Johnson (1998), assemblages of species inhabiting small, isolated patch reefs represent a special case in the general ecology and spatial dynamics of reef fishes.

Spatial patterns may results from deterministic processes, or from processes inherent to the community causing spatial autocorrelation, or both (Legendre et al., 2002). Field observations often present a combination of spatial dependence on environmental factors, which provides for the broad-scale spatial structures, and spatial autocorrelation, which produce the finer-scale structures. Although different ecological processes are capable of generating similar patterns, the quantification of spatial patterns may provide clues as to the identity of these processes (Borcard and Legendre, 1994; Leihold and Gurevitch, 2002).

Testing ecological hypotheses on reef fish communities has been an objective of scientists for many years: “Scientifically, the understanding of the relationships of reef fishes to each other and to their environment has grown by leaps, and the reef fish system promises to become a standard system for testing ideas in ecology” (Ehrlich, 1975 in Sale, 1991). Different theories and models have been proposed to explain ecological structures of reef fish communities, primarily focused on processes such as recruitment (Doherty, 1991) and predation (Hixon, 1991), and the effect of habitat structure (Jones and Syms, 1998; Syms and Jones, 2000). Scientists now generally agree that many different factors and processes are important in governing reef fish communities (Waltho and Kolasa, 1996; Caley et al., 1996). Some of these factors are more important in the early life stages of fishes (from larval to pre-settlement) and are often operating at broad scale; others are acting during subsequent life stages (from settlement to adult) and are operating at smaller scale (Casselle and Warner, 1996; Doherty, 2002; Lecchini and Galzin, 2003).

Several natural factors, geomophologic, historical, ecological, and biological have been hypothesized to explain the spatial variation in reef fish community structure (Harmelin-Vivien, 1989). Alternatively, positive anthropogenic effects, like human interventions to protect coral reef fauna by the creation of marine reserves, or negative, through habitat disturbance by activities like fishing and tourism, have been suggested as causes of spatial variation on fish species assemblages (Russ, 2002). Human activities could have a direct effect on fish species by removal of individuals, or indirect effects resulting from damage to the coral reef habitat (Russ, 1991). New ideas have led ecologists to pay attention to spatial scaling; one of them is the role of disturbances as modifiers of community patterns and dynamics (Schneider, 1994).

1.2. Explanatory models

At the onset of this study, two complementary explanatory models were considered to describe the distribution patterns found in the species composition