From Habitat Mapping to Ecological Function: Incorporating Habitat into Coral Reef Fisheries Management

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ABSTRACT

Ecosystem-based fisheries requires management to consider habitat functions, but how this can be accomplished is often not clear. While habitats represent species and life-stage distributions, more important is how knowledge of habitat abundance, distribution and spatial arrangement can be used to identify spatially explicit, key ecological functions necessary for sustaining fisheries production. Multivariate numerical models are tools for identifying potential production centers, but ecological function can only be incorporated if input data are appropriately designed and scaled, and outputs are appropriately evaluated. We address key functions related to connectivity (ecological flows) using a two-part approach. First, habitats are subdivided to reflect differences in represented fauna, but with particular emphasis on differential habitat use across both species and ontogenetic stages within species, thus ensuring that the habitats needed to support all ontogenetic stages will be represented. Resulting habitats should be in near proximity to enhance the probability of connectivity at the local scale. Second, the known limits of connectivity are defined in terms of distance or locations. These limits are then used to assess the suitability of results. For Puerto Rico, habitats were divided into 22 subcategories [reef/colonized hard bottom (8), uncolonized hard bottom (4), unconsolidated substrate (2), seagrass (3), mangroves (3)], with subcategories relating benthic and/or fish community structure to habitat type, geomorphology and cross-shelf position. For example, mangroves were subdivided into lagoonal, shoreline edges and mangrove keys to account for both community differences and nursery functions. Larval connectivity was 40 km; ontogenetic connectivity requires full cross-shelf representation.

KEY WORDS: Ecosystem-based management, Puerto Rico, coral reef ecosystems, Marxan, MPAs

De la Cartografía de Hábitats a la Función Ecológica: Incorporando el Hábitat en el Manejo de las Pesquerias de Arrecifes de Coral

El manejo de las pesquerías basada en los ecosistemas requiere que se considere las funciones del hábitat, pero en la manera en cómo esto se puede lograr a menudo no es clara. Si bien los hábitats representan las especies y su distribución durante el ciclo de vida, más importante es cómo el conocimiento de la abundancia del hábitat, su distribución y arreglo espacial se puede utilizar para identificar funciones claves ecológicas, en un manera espacialmente explícita, necesarias para el sustento de la producción pesquera. Para este estudios proponemos la integración de modelos numéricos multivariados como herramientas útiles para identificar centros potenciales de producción, pero la función ecológica sólo se puede incorporar si la escala de los datos de entrada está debidamente diseñada, y los resultados se evalúen adecuadamente. Hemos logrado relacionar las funciones claves del hábitat con la conectividad (caudales ecológicos), utilizando dos enfoques. En primer lugar, los hábitats se subdividen para reflejar las diferencias en la fauna representada, pero con especial énfasis en los distintos usos del hábitat entre las especies y a través del estado ontogenético de las especies, garantizando así la representación de los hábitats necesarios para apoyar todas las etapas ontogenéticas. Los hábitats resultantes deben estar muy cerca de aumentar la probabilidad de conectividad a una escala local. En segundo lugar, los límites conocidos de la conectividad se definen en términos de distancia o lugares. Estos límites se utilizan para evaluar la sustentabilidad de los resultados. Para Puerto Rico, los hábitats se dividieron en 22 subcategorías [arrecife / fondo duro colonizados (8), sin colonizar fondo duro (4), el sustrato no consolidadas (2), algas marinas (3), los manglares (3)], con subcategorías relacionando el béntico y / o las estructuras de comunidades de peces a el tipo de hábitat, la geomorfología y la posición a través de la plataforma. Por ejemplo, los manglares se subdividieron en lagunas costeras (manglar de franja) y cayos, esto para tener en cuenta las diferencias tanto en la comunidades y las funciones del hábitat como guardería. Para este estudio se define la conectividad larval a 40 km; lo necesario para que la conectividad ontogenética esté representada a través de toda la plataforma.

PALABRAS CLAVE: Manejo de ecosistemas, Puerto Rico, los ecosistemas de arrecifes de coral, Marxan, áreas marinas protegidas.

De la Cartographie d'habitats á La Fonction Ècologique: En Incorporant l'Habitat dans le Maniement des Pêcheries de Récifs de Corail

MOTS CLÉS: Maniement des pêcherries, Puerto Rico, function ècologique, MPAs

INTRODUCTION

The maintenance of ecosystem resilience will become an increasingly important goal within the framework of ecosystem-based fisheries management. Ecosystem-based management must focus on the health and productive capacity of the system, and the identification and protection of key habitats will be critical for protecting ecosystem integrity and function. The importance of maintaining resilience is evident, considering that ecosystem models, and even single-species stock assessment models, are limited in defining the productive capacity of the system and the potential impacts of exploitation, especially in data poor scenarios. While previous studies (e.g., Cerveny 2006, Cerveny et al. 2011) have shown that some habitats are particularly important over a range of species, these are embedded within an overall seascape where separation of habitats for most management purposes would be extremely difficult. Additionally, habitat use is not constant for many species undergoing ontogenetic migration, so management must consider the complete suite of habitats required across the community of exploited species. Thus, the more practical alternative to foster ecosystem resilience is to target protection for selected areas that are critical to the productive capacity of the system over large scales. The rationale for maintaining ecosystem resilience is to maintain ecological function. The question then becomes one of design: What are the guidelines to be used in selecting such priority areas that will help maintain ecological function (i.e., self maintenance) across a range of spatial scales? What emerges is to develop a network of targeted areas, where ecological linkages are conserved within and between these areas. It is convenient, then, to consider linkages at these two scales; ecologically this can be done by dividing them into one dealing with ecological exchange among habitats within a local area (habitat connectivity), and another dealing with long-distance dispersal between areas (larval connectivity).

How do we incorporate these principles using available information without having to conduct new and exhaustive site-specific surveys of species distributions along with detailed movement/dispersal studies? The key is to use habitats as proxies for distributions and arrangement of habitats to facilitate connectivity. Habitats have been used as a proxy for mapping the distribution of marine communities (Airamé et al. 2003, Leslie et al. 2003, Sala et al. 2002). Habitat information can be readily obtained from a variety of sources such as aerial photography (NOAA/NOS/Biogeography Team 2002), satellite (Mumby and Harborne 1999) and sonar (Prada 2002) imagery, bathymetry or even knowledge of basic geomorphology (Ballantine 1997a,b). More difficult is to preserve ecological function using these habitat proxies. Roberts et al. (2003) presented general considerations for using habitat distributions to preserve ecological function, and several studies have attempted to apply these to some degree (Airamé et al. 2003, Leslie et al. 2003, Sala et al. 2002).

In practice the identification of key areas for conservation concern is complex due to the high number of ecological factors involved, the incomplete nature of most data sets, and potential for conflicting goals. Site selection, thus, involves a multivariable system were each element can be differently considered according to the local characteristics and/or needs. Numerical models can be used as a tool to realize such evaluations in an objective manner based on predetermined assumptions and goals. However, to incorporate ecological flows into the identification of key habitat areas, model implementation requires that the available data (e.g., habitat distributions, bathymetry, etc.) and scale of analysis are structured so that the relevant ecology of the system is accounted for.

Our objective is to show how existing data for a tropical coral-reef ecosystem (Puerto Rico) can be structured to incorporate marine communities and ecological function. Specifically, we concentrate on the goal of maintaining representation and connectivity, realizing that these are intertwined in terms of the ecological functions associated with maintaining species viability and community composition. The functions considered here are the provision of food, shelter and a source of recruits. In general, habitat is used as a surrogate for species distributions. However, given that ecological functions occur at different scales for different organisms, our premise is that at small scales these functions are subsumed within the definition of habitat, *i.e.*, the place that is natural for the life and growth of an organism. At larger scales, however, one must account for the flow of organisms and materials across the seascape that would support those species dependent on movement across habitats (e.g., ontogenetic migrations, feeding migrations), with connectivity being aided by proximity. Our approach, then, will be to divide the seascape into a series of habitats that not only refine representation, but also whose proximity in space will, as a function of model optimization, foster connectivity at larger spatial scales and hence ecological function.

Our analysis consists of the following steps:

i) Review of the knowledge base of habitats relative to the issues of representation and connectivity to identify what features, and at what scales, should be targeted for inclusion;
ii) Arrange habitat data to reflect targets identified in Step 1;
iii) Develop criteria for assessing success. Throughout this process, emphasis is given to data derived from fishes.

METHODS

Guidelines for Using Habitat as a Proxy for Species Distribution: The Role of Structure and Location

Reef invertebrate (Kendall et al. 2001, McGehee 1994, 1997, Prada et al. 2008) and fish (Luckhurst and Luckhurst 1978, Prada 2002) community composition depends on the type of habitat structure. One of the most important structural factors is relief or rugosity (Foley 2003, Friedlander and Parrish 1998, McCormick 1994, Roberts and Ormond 1987, Syms and Jones 2000). The interesting question, then, is how finely habitat structure needs to be partitioned to reflect significant differences in associated community structure. For example, off La Parguera, Puerto Rico, Prada et al. (2008) identified 21 different types of benthic habitat based on structural features as determined using side-scan sonar, each with a quantitatively different benthic community composition, while for all of Puerto Rico Kendall et al. (2003) distinguished 24 different habitats based on aerial photography. Given that real differences in community composition were observed at these levels of habitat differentiation, a first rule would be to let the number of primary habitat classes be determined by the quality of available habitat data.

Changes in community structure arise not only from significant differences in habitat structure but also from landscape effects. Thus, habitats such as reef, mangroves and seagrass should be further subdivided according to their location within the larger habitat mosaic. Important landscape factors include depth, position with respect to fore or back reefs (Kimmel 1985), nearshore/offshore position (Friedlander et al. 2003), patch size (Acosta and Robertson 2002, Ault and Johnson 1998, Prada 2004), and salinity where applicable (Austin 1971). For example, location of structure impacts community composition through differential settlement (*e.g.*, inshore nursery areas and subsequent ontogenetic migration (Appeldoorn et al. 2003, Lindeman 1997, Nagelkerken and van der Velde 2003) or through the availability of surrounding feeding habitat (Appeldoorn et al. 2003, Kendall et al. 2003, Pitman et al. 2007). That differences in community composition arises due to connectivity processes (water flow, species movements) means that partitioning habitats is not independent from the issue of habitat connectivity.

Habitat Connectivity and Ecological Function

While seagrass beds support a myriad of fish and invertebrates, forming unique communities (*e.g.*, Bouchon-Navaro et al. 2004, Christensen et al. 2003, Friedlander et al. 2003), they also form important linkages to other marine communities through two mechanisms:

i) Export of organic matter, either dissolved (Ziegler and Benner 1999a,b) or particulate (detritus), and
ii) The movement of fishes and invertebrates. The latter occurs either through their role as nursery areas and subsequent ontogenetic migration (Appeldoorn et al. 1997, Cocheret et al. 2002, Murphy 2001, Nagelkerken et al. 2002, Nagelkerken and van der Velde. 2003, Stoner 2003) or through daily cross-habitat feeding migrations (Dennis 1992, Hobsen 1973, Ogden and Zieman 1977, Meyer et al. 1983, Rooker and Dennis 1991) of reef and mangrove associated species.

Mangroves, because of their effect on water flow, water quality and shading, create a unique marine habitat. Mangrove prop roots provide vertical relief for shelter and structure for the attachment of sessile organisms such as sponges, mollusks and algae (Burkholder and Almodovar 1974, Rodriguez and Stoner 1990). As with seagrass beds, mangroves form important linkages to other communities. Detrital nutrient input into coastal waters, which support the coastal fauna (Boto and Bunt 1981, Bunt et al. 1982, Odum and Heald 1972), with the extent of export being a function of the nature of the sediment, fauna present, the degree of ebb and flow tidal fluctuations, and the volume of water flow (Camacho and Bagarinao 1987, Montague et al. 1987).

The functional relationship between mangrove and fish fauna is complex. A variety of fishes use mangrove areas for feeding (Austin and Austin 1971). Few feed directly on mangroves or mangrove litter, but rather feed on crustaceans associated with the litter (*e.g.*, crabs, ostracods, harpactacoids) or other mangrove associated fishes. Many other fishes, while using mangroves as nursery areas (see below), do not rely on mangrove production for nutrition (Cocheret et al. 2003). Proximity to non-mangrove areas, such as coral reefs may influence fish species composition in the mangrove (Parrish 1987).

Mangroves prop roots serve as important nursery areas for coral reef fishes (Cocheret et al. 2004). Such nursery areas are only found in clear, reasonably high salinity waters (Nagelkerken et al. 2002), and are located only in the narrow band bordering the mangrove water interface. Thus, these are limited to the outer margin of coastal mangroves and the mangrove keys found on emergent reefs. Typical species utilizing mangroves as nursery areas include the grunts, snappers, surgeonfishes and parrotfishes (Appeldoorn et al. 2003, Cocheret et al. 2002, Murphy 2001, Nagelkerken et al. 2002, Nagelkerken and van der Velde 2003). For most species, mangrove nurseries appear to be opportunistic, but the number of individuals, especially of subsequent adults, can be greatly reduced when suitable mangrove nurseries are absent or at some distance (Appeldoorn et al. 2003, Mumbry et al. 2004, Nagelkerken et al. 2002).

Enclosed mangrove lagoons support communities distinct from those associated with coral reefs, and in particular they can serve as important nursery areas. In Puerto Rico, Austin (1971) divided lagoons nursery communities into two types based on salinity. Lagoons with salinity < 20 ‰) are characterized by the sleepers (Eleotridae), soles *(Achirus* sp.), swordfin snook (*Centropomus ensiferus*), mosquito fish (*Gambusia* sp.), and in some areas by introduced talapia. Those with salinity > 38 ‰ are characterized by snook (*C. undecimalis*), mullet (*Mugil curema*), most mojarras (Gerreidae), and the needlefish (*Strongylura* sp.).

Scale of Habitat Connectivity

Marine reserves must preserve connectivity among habitats if ecosystem function is to be maintained, and that connectivity results from two processes: the movement of water (*e.g.,* dissolved organic matter) and the movement of individual organisms among habitats. For purposes of marine reserve design, the movements of fishes are used to assess the latter, due both to data limitations with respect to other taxa and the fact that fishes constitute the taxon most directly impacted by harvesting.

In reef ecosystems, there are significant differences in the distances that some species will move out from settlement/nursery areas (Aguilar-Perera 2004, Appeldoorn et al. 2003), but there does not seem to be any inherent limitation on this capability within a species given similar arrangements of required habitat (Appeldoorn et al. 1997, 2003). Since many species migrate ontogenetically across the full width of a shelf, this aspect should be incorporated into any local area targeted for conservation.

There do appear to be limitations on the degree of lateral (alongshore) movement, and these may reflect a number of processes. In the U.S. Virgin Islands, Beets and Muhlstein (unpublished) found reefs adjacent to seagrass beds to have different assemblages compared to those not close to seagrass beds. This may reflect both settlement/ontogenetic movement processes as well and feeding migration processes of older juveniles and adults (*e.g*., Kendall et al. 2003). Similar results were observed in Providencia (Appeldoorn *et al*. 2003, Friedlander *et al*. 2003) comparing patch reefs near and far from nearshore recruitment areas/habitats. There, limitations both on ontogenetic processes and feeding migrations were evidenced. Feeding migrations were generally limited to a few hundred meters. Detailed movement studies using acoustic telemetry (Beets et al. 2003, Holland et al. 1993, 1996, Tulevech and Recksiek1994, Zeller 1997) show ordinary daily movements of typical species to be fairly limited in spatial dimension (100s meters), with movements of several kilometers representing maximum excursions.

Scale of Larval Connectivity

The goal of maintaining larval connectivity is to ensure the maintenance of populations within protected areas (and by corollary those populations in between). Larval exchange must be significantly greater than that necessary to just maintain gene flow. Several lines of argument suggest the extent of such flow is limited to the order of 40 km. Empirical observations of fish larval distributions (Ojeda Serrano 2002, Pagan 2002, Ramírez-Mella and García-Sais 2003, Rojas 2002; Rojas-Ortega and García Sais 2002) and current flows (Appeldoorn et al. 1994, 2000; Ojeda-Serrano 2002) show limited movement of nearshore larvae into offshore environments. High resolution models (Pagan 2002) incorporating shelf topography tend to show low levels of both advection and dispersal, with distances of 40 km over a typical one-month larval duration. Models of actual flow at the time of larval sampling (Ojeda Serrano 2002) show strong congruence between the abundance and size of larvae and current speeds and direction. These models further suggest that alongshore movement dominates. This is additionally supported by studies showing the Mona Passage to act as a biogeographic boundary for some shallow-water taxa (Baums et al. 2005, Taylor and Hellberg 2003) and studies of larval distributions and current flows (Ojeda Serrano 2002, Rojas 2002, Rojas-Ortega and García Sais 2002) suggest little exchange between Puerto Rico and Mona Island, representing a minimum distance of 40 km. In the only study within this part of the Caribbean were self recruitment was actually measured, Swearer et al. (1999), found self recruitment in St. Croix to occur on a spatial scale of about 40 km, but this was for a species whose minimal larval life is significantly longer than the average for many species.

Mapping Habitats

The available data for Puerto Rico consists of habitat and species distributions. Benthic habitat distributions were taken primarily from NOAA/NOS/Biogeography Team (2002), based on subcategories of reef and colonized hard bottom (8), uncolonized hard bottom (4), unconsolidated substrate (2), seagrass (3), macroalgae (3), mangroves. Habitat areas are resolved to a minimum mapping unit of one acre (~ 4000 m^2) but cover only about 38% of the shelf area. Habitats are also classified as occurring in one of seven geomorphic zones ranging from the shoreline to the shelf edge. Additional habitat data were taken from environmental sensitivity maps (NOAA 2001), particularly with respect to coastlines (*e.g.*, rocky, sand beach) and wetland distributions.

Coral reef habitats were divided on the basis of both type of reef and geomorphic zone. Combinations of location and reef type chosen were designed primarily to reflect expected differences in community structure. Unfortunately, the inshore – offshore classification as used in the NOS Benthic Habitat Map does not generally provide the cross-shelf subdivision needed to address the scales of ontogenetic migration and differential species utilization. This is because almost all reef areas are categorized as being in the bankshelf stratum, regardless of the width of the shelf. Types of reefs were lumped into the following three groups based on size and relief:

i) Colonized pavement (with and without sand channels) and Colonized bedrock. These represent flat or low relief areas of variable size and colonization, typically by gorgonians and sponges, with few hard corals.

ii) Linear reef, Spur-and-groove and Large patch reef. There represent large reef structures providing high vertical relief and a continuous expanse of habitat. Some of these are emergent, and they typically represent fore reef or shelf-edge zones.
iii) Small patch reefs and Scattered coral.

These represent small patches of reef, often offering 1-3 m of vertical relief, that occur within an extensive matrix of sand or sand-algal plain. The zone classification was based largely on depth and location relative to emergence, and hence water flow. The five resulting classes were as follows:

i) Lagoon, Reef crest and Shoreline intertidal. This grouping represents mostly shallow habitats, often utilized as nursery areas, and are associated with emergent reefs or backreef waters.
ii) Backreef. This zone is also associated with emergent reefs; it is deeper but more sheltered area relative to the first.
iii) Bankshelf. This is by far the most extensive zone, covering most of the shelf, and is not associated with emergent reefs. Depths typically range from 7 to 20 m (the latter representing the limits of habitat recognition from aerial photographs).
iv) Bankshelf escarpment, and
v) Forereef. These two zones represent forereef environments differing in their locations. The latter is associated with emergent reefs, while the former is associated with shelfedge reefs.

The NOS Benthic Habitat Map separates seagrasses according to percentage cover, but these were pooled in our analysis. However, sea grass beds were divided into three categories based on zone (position along the shelf) as follows:

i) Backreef and reef crest zones were pooled. These represent emergent reef associated areas that often serve specific settlement/nursery functions. These areas are typically of medium density and have a clean, coralline sand base.
ii) Lagoon and shoreline intertidal zones were pooled. These consist of shallow, nearshore seagrass, often very dense, with a silty bottom.
iii) Deep sea grass beds within the bankshelf and forereef zones were combined.

Based on the available data, three sets of mangrove data were developed. Two attempted to isolate that aspect of mangrove habitats that serve as nursery areas for fishes. The first of these was the line representing the mangrove-water interface and was derived from data obtained from the Environmental Sensitivity Index Atlas for Puerto Rico (NOAA 2001). The second included just the mangroves associated with offshore keys or similar structures, with these obtained from the NOS Habitat Map. The third data set constituted the coastal (i.e., without the keys) marine mangroves. This data set was area-based and represents mangroves that potentially contribute to the marine system through the export of nutrients/biomass, as well as serving as a surrogate for mangrove associated species, which range from nesting birds to prop root invertebrate communities. Breakdown of habitat types based on community structure and function are represented in Table 1.

Criteria for Assessing Model Performance

There is no direct way to quantify ecological function to assess the suitability of model results. However, qualitative assessments can be made using ecological criteria (Table 1) derived from the rationale for habitat classification developed here (which is based on functional arguments) and spatial scales needed to maintain larval and habitat connectivity (Table 2). For these criteria, model results can be compared to these criteria, and if the criteria are not met, model parameters (e.g., clustering, stratification into subareas) would need to be changed and the model run again.

DISCUSSION

The purposes of this study were:

i) To establish an ecological basis for habitat classification of tropical marine systems for use in numerical optimization models such that these models would incorporate ecological function in ensuing results,
ii) To establish specific ecological criteria, especially with respect to connectivity, for assessing model performance, and
iii) To implement this approach by structuring available data for Puerto Rico. Further investigation into implementing this approach is given in Pagan et al. (2011).

While no data set can represent the full range of ecological complexity and no model can capture the full range of ecological function, attention to what is known of both ecological complexity and function and how available data can reflect these should lead to more accurate and robust results upon which to base management actions. And, while it is difficult to assess fully the future impact of potential large scale management actions, comparing results against established ecological criteria should significantly improve decision making over results based on biodiversity targets alone.

Given sufficient data coverage of the insular platform, implementation of modeling using Marxan or similar programs should identify what amounts to areas of high diversity and productivity. In a context where most habitats can be considered essential for at least some species, these areas constitute a higher order of essential fish habitat (Cerveny et al. 2011). More importantly, such areas would be considered critical hubs in the series of overlapping networks (habitat connectivity, larval connectivity, food webs). Network theory and practical examples from elsewhere (Buldyrev et al. 2010) illustrate that failure of critical hubs in interconnected networks can lead to a cascading collapse of system function. Thus, conservation of these hubs should be a management priority and a keystone of maintaining system resilience.

Table 1. Breakdown of habitat types to maximize ecological function from available data for Puerto Rico, based on community structure and function.

Habitat	Description/Function
Reef	
Type:	
Colonized pavement (with/without sand channels) and Colonized Bedrock	Flat/low relief. Gorgonians, sponges, few corals
Linear Reef, Spur and Groove, Large Patch Reef	Large structures, high relief; include forereef, with some emergent
Small patch reefs and scattered coral	Small patches of reef, 1-3 m of relief within matrix of sand/algal plain
Location:	
Forereef	Windward margin of emergent reefs
Lagoon, Reef Crest, Shoreline intertidal	Shallow, associated with emergent reefs; settlement and nursery area
Back Reef	Associated with emergent reefs, deeper and more sheltered
Bankshelf	Outer shelf, 7-20 m deep; not associated with emergent reefs
Bankshelf Escarpment	Deep forereef at shelf edge
Seagrass (*Location*)	
Backreef and Reef Crest	Associated with emergent reefs; medium seagrass density; clean coarse sand; settlement and nursery area
Lagoon and Shoreline Intertidal	Shallow, dense seagrass; silty bottom and shelter areas
Deep Seagrass	Feeding ground
Mangroves (*Location*)	
Shoreline Edges	Coastal nursery habitat for reef fish
Mangrove Keys	Coral cay nursery habitat for reef fish
Coastal Mangroves	Habitat for proproot/lagoon fishes/nesting birds, etc.; export nutrients/ biomass

Table 2. Criteria for assessing if area selections retain ecological function.

Criterion	Metric
Maximum spacing among reserves	40 km
Habitats included within area	All
Habitat dispersal within area	Coastline to Shelfedge
Habitat separation	10^2 – 10^3 m

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