A Spatial Framework for Assessing Cross-Shelf Habitat Use Among Newly Settled Grunts and Snappers

KENYON C. LINDEMAN, GUILLERMO A. DIAZ,
JOSEPH E. SERAFY and JERALD S. AULT
Division of Marine Biology and Fisheries
RSMAS/University of Miami
4600 Rickenbacker Causeway
Miami, FL 33149 USA

ABSTRACT

The differential use of nursery habitats by grunts and snappers (Haemulidae and Lutjanidae) across a complex coastal seascape was examined using a cross-shelf habitat (CSH) framework. The framework explicitly defined structural bottom types, cross-shelf physical strata, and associated spatial features on scales ranging from 0.01 m^2 to 1x10^3 km^2. These habitat attributes were combined using matrices which integrated an axis representing structural bottom types with an axis representing physiographic cross-shelf strata. The framework identified 10 cross-shelf strata, most encompassing over 15 natural bottom types for the shelf area of Biscayne Bay, Florida. The resulting matrices contained 169 cells which represent potential cross-shelf habitats. The hypothesis that utilization of cross-shelf habitats by grunts and snappers was uniform was not supported by 30 years of prior literature or museum materials, and new field surveys of the Biscayne Bay area. In terms of bottom types, newly settled stages of *Lutjanus griseus* and *Anisotremus surinamensis* (< 20 mm SL) were not recorded from hard structures and seagrasses, respectively. Distributions of newly settled *Lutjanus synagris* were broader; they occurred in both grassbeds and on hard structures. Structurally-identical habitats were often used differently based on their cross-shelf positioning. Habitat utilization patterns ranged from opportunistic to highly specialized. For example, *L. synagris* was estimated to use approximately 64 cross-shelf habitats for settlement, while *A. surinamensis* used 10. Opportunistic use of structural habitats at settlement characterized seven of 21 grunt and snapper species. The CSH framework facilitated nursery area identification on several spatial scales and may provide a template for identifying habitats essential for fish production.

KEY WORDS: Habitat use, Haemulidae, Lutjanidae

INTRODUCTION

Tropical coastal areas often support high diversities of habitats and fishes under considerable anthropogenic pressures. Modification of differing habitats may produce population-scale effects on valuable fishery species (Peters and Cross, 1992; Butler *et al.*, 1995). Therefore, comparative information on habitat

use among key species can aid the management of both coastal habitats and fisheries. In the United States, U.S. Virgin Islands, and Puerto Rico, the need for explicit habitat assessment tools has increased with the mandate to characterize essential fish habitat and habitat areas of particular concern in fishery management plans (NOAA, 1996).

The concept of habitat is one of the most unstandardized in marine ecology. In part, this is due to the multiple variables influencing the spatial distributions of organisms in dynamic aquatic systems (Downing, 1991). Habitat characterization necessarily involves observer-introduced simplifications of many abiotic and biotic variables. Many approaches have focused on one of two basic categories: a) water column characteristics (e.g., Coutant, 1985; Bulger *et al.*, 1993); or b) structural bottom-types (e.g., Luckhurst and Luckhurst, 1978; Bell *et al.*, 1987; Jones, 1988).

Diverse approaches for characterizing habitats exist. Many coastal permitting agencies with direct responsibilities for habitat management have used the classification of Cowardin *et al.* (1979). This system consists of five primary components from palustrine to marine, with successive sublevels based on hydrology and generic structural types. The overall framework of the Sly and Busch (1994) lake classification is similar and Dethier's (1992) marine classification is also based on small refinements to the Cowardin *et al.* (1979) system. Many of these systems are employed as one-dimensional lists of mixed structural and physiographic attributes over an undefined range of spatial scales. To compare habitat use or estimate habitat values, many agencies have also used habitat suitability indices. These estimate optimum habitat conditions from the literature on a given species and compare these with conditions in a given area (Terrell, 1984). Nelson (1987) suggested that many species are typically insensitive to the small changes in chemical and physical variables used in habitat suitability indices and that they are best suited for species with low mobility and specific habitat requirements.

Assessing species distributions across an entire shelf, and on the finer scale of structural bottom types, is limited by the absence of spatial frameworks which incorporate both water quality and structural attributes within a cross-shelf continuum. For example, tools are needed which compare fish use of red mangrove prop-root habitats or grass beds among the differing salinity and turbidity regimes of mainland areas versus those of emergent islands across the shelf. Such a framework should explicitly characterize several spatial scales across heterogeneous seascapes and, importantly, be usable by non-scientists administratively charged with coastal construction permitting decisions in areas with varying levels of baseline data. It should also be adaptable to differing geographic regions and employ a cross-shelf structure to aid visualization of ontogenetic migrations.

386

We developed a spatial framework for assessing habitat use in the Biscayne Bay shelf area of southeast Florida following the above goals. The specific objectives in developing this cross-shelf habitat (CSH) framework were to: a) define spatial scales for structural bottom-types and their physiographic backdrops (cross-shelf strata); b) integrate these features using a matrix that combines a structural axis and a physiographic axis in a geographically logical manner; and c) apply a CSH framework to estimate distributional patterns of fishes among the primary habitats of a heterogeneous coastal seascape.

The CSH framework was used to identify distributional patterns of early stages of grunts and snappers (Haemulidae and Lutjanidae), abundant fish families with over 20 species in southeast Florida. First, the range of structural bottom types and cross-shelf physical strata available to demersal fishes of the Biscayne Bay shelf area was characterized using CSH matrices based on existing databases. Second, the cross-shelf distributional boundaries of newly settled stages of three species of grunts and snappers were identified over several spatial scales. Third, we identified several structural and physiographic patterns common to the settlement habitats of 21 grunt and snapper species of the Biscayne Bay shelf area.

METHODS
Habitats and Cross-shelf Strata
A framework containing five spatial scales was developed (Table 1). Two of these scales were emphasized: structural habitats and cross-shelf strata. Habitats were defined as structural bottom-types on spatial scales of 0.1-1 m^2 that provide shelter or trophic resources (Table 2). Twenty-one natural habitat types were identified and assigned mnemonic acronyms (Table 2). These structural bottom types were based on: 1) field observations in Florida, the Bahamas, and seven Antillean islands from Cuba to Barbados; and 2) reviews of existing aquatic habitat classifications (e.g., Cowardin *et al.*, 1979; Terrell, 1984; Dethier, 1992; Bulger *et al.*, 1993; Sly and Busch, 1994).

Ten cross-shelf strata, with spatial scales ranging from 1 - 1,000 km^2 (Table 1), were postulated to extend from inshore mainland areas to the outer shelf edge of the Biscayne Bay area. These strata were based on: a) bathymetry; and b) cross-shelf positioning relative to emergent sediment- and reef-derived structures (Key Biscayne through Elliot Key; following Hoffmeister, 1974). Five of these strata were within Biscayne Bay and are shown in Figure 1 with their acronyms. Five others extended from oceanic channels of the Bay to the outer shelf edge. From inshore to offshore, these were: channel axis (CA, 0- 2 m); windward inshore (WI, 0 - 2 m); windward subtidal (WS, 2 - 10 m); midshelf (MS, 10 - 20 m); and outer shelf (OS, >20 m). The ten cross-shelf strata are proxies for gradients of other physical variables (e.g., salinity, turbidity, wind exposure) that

can distribute in semi-continuous bands across the shelf. Since fish usage of similar structural habitats may vary along physically different sections of shelves, cross-shelf strata can represent environmental gradients following Keddy (1991), who suggested that such gradients are useful but often overlooked research tools.

Cross-Shelf Habitat Matrices

By superimposing structural habitats (Table 2) on the vertical axis and cross-shelf strata (Figure 1) on the horizontal axis, a cross-shelf habitat (CSH) matrix of primary habitat combinations of the Biscayne Bay seascape was produced (Figure 2). Intersections of individual habitat types and cross-shelf strata formed cells within the matrix termed cross-shelf habitats. For example, one cross-shelf habitat is *Syringodium* grass within a mainland subtidal cross-shelf stratum (Figure 2). A second cross-shelf habitat is *Syringodium* grass within a leeward subtidal stratum. Several combinations of spatial scales can be examined depending on the organisms, life stages, and processes of interest. The distributional patterns of a species within a CSH matrix were termed habitat mosaics. These represented combinations of cross-shelf habitats on scales of 1 - 1,000 m^2 (Table 1).

Data Sources

Habitats — To estimate relative abundances of submerged habitats within Biscayne Bay, GIS-compatible information was obtained from a detailed map of bottom communities based on aerial surveys and underwater observations (DERM, 1983). Habitat distributions and areas were extracted for the north-central through southern portions of the bay from the Rickenbacker Causeway on the north end, to the southern boundary of Biscayne National Park (near Long Arsenicker Key). References to the Bay therefore refer to this large central and southern portion (Figure 1) and not the northernmost section above the Rickenbacker Causeway.

Depth contours for cross-shelf strata within Biscayne Bay were based on the area between three pairs of isobaths: a) 0 - 1 m (inshore); b) 1 - 2 m (subtidal); and c) > 2 m (basin axis) (Figure 1). Contours were created using Arc-Info from bathymetric data from the National Ocean Service and Biscayne National Park. The contours created from the original data did not exactly follow the original depth profiles of the complex system of banks in the west-central bay known as the Safety Valve (between Key Biscayne and Ragged Key). To create usable GIS polygons, the depth contours of this area had to be simplified by treating all bottom types as if in the 0 - 1 m depth range.

Table 1. Spatial scales characterized by a cross-shelf habitat (CSH) framework. Measured heterogeneity: observer-introduced standards and measures. Functional heterogeneity: organismal attributes that may operate at observer-introduced scales (following Kolasa and Rollo, 1991)

	Measured Heterogeneity			Functional Heterogeneity	
Scale	Descriptor	CSH Example		Biotic Scale	Biotic Process
0.0-0.1 m^2	Microhabitat	Peripheral prop root - sediment interface		Individual	Growth, Predation, Feeding
0.1-1 m^2	Habitat	*Rhizophora* mangrove (MR) Table 2		Individual, Population	Growth, Predation, Feeding, Recruitment
1-1,000 m^2	Habitat Mosaic	Black margate nursery areas (Figure 6)		Individual, Population, Multi-species assemblages	Growth, Predation, Feeding, Recruitment
1-10^3 km^2	Cross-shelf strata	Mainland Subtidal (Figure 1)		Population, Multi-species assemblages	Predation, Feeding, Recruitment
>10^3 km^2	Ecosystem	South Florida		Multi-species assemblages	Local Extinction, Speciation?

389

Table 2. Natural strutural habitats (0.1 - 1m²) of southeast Florida which can be utilized by coastal fishes and invertebrates. SAV: submerged aquatic vegetation.

Habitat Category	Acronym	Natural Habitat type	Number of Microhabitats[1]
Coastal trees	MR	Mangrove - Red (*Rhizophora mangle*)	5
	ET	Erided Trees (*Avicennia, Casuarina,* others)	3
Grasses and	GT	Grass - *Thalassia* type: tall, wide blades	5
Algae (SAV)	GS	Grass - *Siringodium* type: tall, thin blades	5
	GH	Grass - *Halodule* type: short, thin blades	4
	GM	Grass - Mixed, two or more grass spp.	5
	GA	Grass - Algae, grass and macroalgae spp.	5
	AA	Algae - Attached (*Halimeda, Caulerpa*)	3
	DM	Detached Macrophyte piles, (e.g. wrack)	3
	DD	Detached Drift macrophytes (e.g. *Sargassum*)	3
Sediments	SF	Sediments - Fine (e.g. mud)	3
(Barebottom)	SC	Sediments - Course (e.g., sand)	3

Table 2 (continued).

Habitat Category	Acronym	Natural Habitat type	Number of Microhabitats[1]
Hardbottom	EH	Exposed Hardbottom	3
and	ML	Mixed - Low density invertebrates ($<2/m^2$)	4
Invertbrates	CL	Corals - Low relief growth forms; domal	4
	IP	Invertebrate - *Phragmatopoma* worm reefs	3
	IM	Invertebrate - Miscellaneous (e.g., *Diadema*)	3
	IS	Invertebrate - Sponges	3
	CG	Corals - Gorgonians	3
	MH	Mixed - High density invertebrates ($>3/m^2$)	5
	CH	Corals - High relief growth forms; branching	5

1 - Microhabitats summarized in Lindeman (1977), Table 2.14)
2 - Includes gorgonians, sponges, corals, and associated invertebrate taxa.

MI = Mainland Inshore (0-1m)

MS = Mainland Subtidal (1-2 m)

BA = Basin Axis (>2 m)

LS = Leeward Subtidal (1-2 m)

LI = Leeward Inshore (0-1 m)

Key
Biscayne

25°30' N

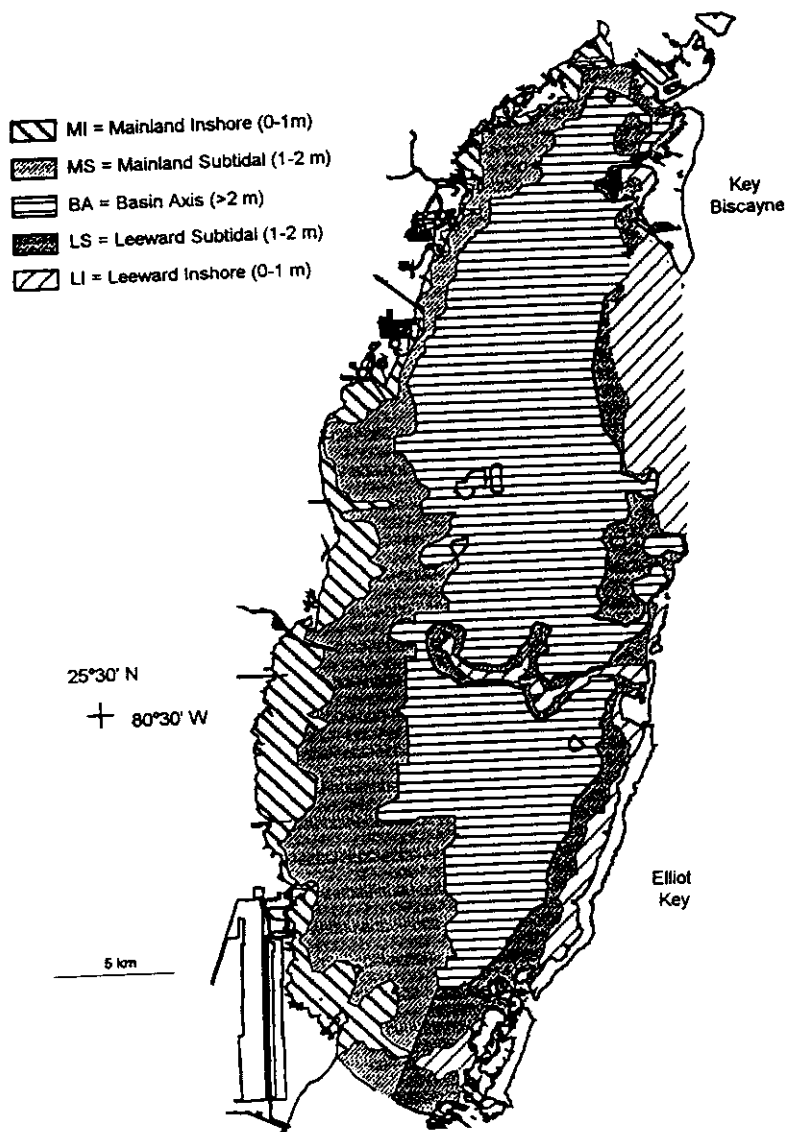+ 80°30' W

Elliot
Key

5 km

Figure 1. Five cross-shelf physical strata of central and southern Biscayn Bay, Florida USA. Characteristics of these strata and those outside of the bay are summarized in the text.

CROSS-SHELF STRATA SPATIAL SCALE (1-10³ KM²)

			Estuarine				Barrier Island				Reef		
Habitats:													
Category	Type	MI	MS	BA	LS	LI	CA	WI	WS	MS	OS
Trees	MR			■			■		■	■	■
H	ET			■			■				
A	GT										■
B	GS										■
I Grasses	GH									■	■
T &	GM									■	■
A Algae	GA										■
T	AA										
	DM										■
S	DD										■
C Sediments	SF										
A	SC										
L	EH	■									
E	ML	■				■					
	CL	■				■					
.1- Hard-	IP	■	■	■	■	■			■	■	■
1 bottom/	IM										
M² Inverts.	IS						■				
	CG	■			■		■				
	MH	■									
	CH	■	■	■	■	■	■	■			

Figure 2. CSH matrix integrating natural structural habitats and cross-shelf strata of the Biscayne Bay shelf area, Florida USA. Spatial scales ranging from 1 to 10⁶ m² are represented (Table 1). Habitat and cross-shelf strata acronyms are from Table 2, Figure 1 and text. Habitats abstent from specific cross-shelf stata are shaded.

Fish Distributions — Haemulids (grunts) and lutjanids (snappers) were emphasized as they are abundant, economically valuable, and well-documented in the Biscayne Bay literature and museum collections. Twenty-one species were examined in total, three using detailed CSH matrices: black margate (*Anisotremus surinamensis*), gray snapper (*Lutjanus griseus*), and lane snapper (*L. synagris*). Within these species, the distributions of two early demersal life stages were examined: a) newly settled (~6.5 - 20 mm in grunts, 10 - 25 mm in snappers); and b) early juveniles (~20-50 mm in grunts, ~25 - 70 mm in snappers) following Lindeman (1986; 1997). Since spatial distribution patterns of these early stages have not been documented for most grunts and snappers, the primary objective was to characterize the distribution of these stages among structural bottom types and physical strata using CSH matrices. The null hypothesis predicted that distributions of species at both the cross-shelf and structural habitat scales would be uniform. The black margate was used as the initial example of CSH matrix construction due to a specialized and easily represented pattern of cross-shelf habitat use.

Three primary data sources were used to estimate distributional boundaries and patterns of habitat use among early demersal grunts and snappers. First, the information on fishes of natural habitats of the Biscayne Bay shelf area was consulted. This included the following: Roessler (1965), Voss *et al.* (1969), Low (1973), de Sylva (1976), Berkeley and Campos (1984), Campos (1985), Bohnsack et al. (1992), Serafy *et al.* (1997), Lindeman (unpubl. data), and Ault et al. (unpubl. data). Several studies had useful information on early stages of grunts and snappers; the natural cross-shelf habitats surveyed in these studies are summarized in Figure 3. Second, examinations of specimens and museum logs from over fifty collections from the Biscayne Bay area in the former University of Miami fish museum (now deposited at the Florida Museum of Natural History) were made. Third, some cross-shelf habitats for which no information was available were surveyed visually. These included over 10 natural and artificial structural-types (e.g., mangrove prop roots, rip-rap boulders) within several cross-shelf strata (e.g., leeward subtidal, windward inshore). To document occurrences and identifications, collections of newly settled stages were made using handnets paired with handheld fine-mesh screens, seines, or wheel-mounted pushnets. Voucher specimens of newly settled stages of grunts and snappers from previously uncollected habitats were deposited in the Florida Museum of Natural History, Univ. of Florida (UF) and the United States National Museum, Smithsonian Institution.

By definition, nursery areas can include immature stages that are much older than the early demersal stages emphasized in the present study. In the CSH matrices, primary *nursery areas* were cross-shelf habitats where newly settled individuals were commonly recorded by one or more of the above information

sources. Early juveniles may have been commonly recorded, or absent, from these areas. Secondary nursery areas were cross-shelf habitats where early juveniles were commonly recorded, but newly settled stages were infrequent or absent. In addition to broad nursery areas, two subcategories based on the occurrence of only newly settled stages were identified. Primary *settlement areas* were cross-shelf habitats where newly settled stages were documented from multiple studies or in high abundances from one study. Secondary settlement areas were cross-shelf habitats where one or two sources have documented newly settled stages in moderate or low abundances.

In cross-shelf habitats for which information was available (Figure 3), the use of zeros as distributional estimates in CSH matrices was based on the complete absence of a species despite multiple sampling efforts over various temporal scales. This was reinforced when congeners of the same sizes were routinely recorded. However, survey information was not available for various cross-shelf habitats, particularly those offshore (Figure 3). Distributional estimates for such cross-shelf habitats were therefore based on the extrapolation of species occurrence patterns from similar structures and cross-shelf strata, and the absence of any contradictory evidence. For example, detailed fish surveys of natural deep-reef habitats off Biscayne Bay were limited or unavailable. However, no early stages of black margate have been recorded from: 1) any museum collections from Florida Keys deep reefs, 2) informal observations by knowledgeable researchers in the area, and 3) the literature on such habitats for the entire range of the black margate. Therefore, distributional patterns for cross-shelf habitats not indicated in Figure 3 were inferred from available evidence. Using exclusions to define outer distributional boundaries (in this case, zeros in CSH matrices) is testable and can be useful for identifying pattern in complex systems (see Platt, 1964).

RESULTS

Biscayne Bay Habitat Characterization

Twenty-one structural habitats and 10 cross-shelf strata were identified within a cross-shelf habitat matrix for the Biscayne Bay shelf area (Figure 2). The 210 cells within this matrix exceeded the number of actual cross-shelf habitats available to early demersal stages of fishes, as many structural habitats do not occur within certain cross-shelf strata (e.g., mangrove habitats do not occur within basin axis, midshelf, and other physiographic strata). Forty-one of such cells were identified (shaded cells in Figure 2). Therefore, a total of 169 natural cross-shelf habitats were estimated to be available to early stages of fishes (unshaded cells in Figure 2). In addition, 58 artificial cross-shelf habitats can also be identified in the Biscayne Bay shelf area (Lindeman, 1997).
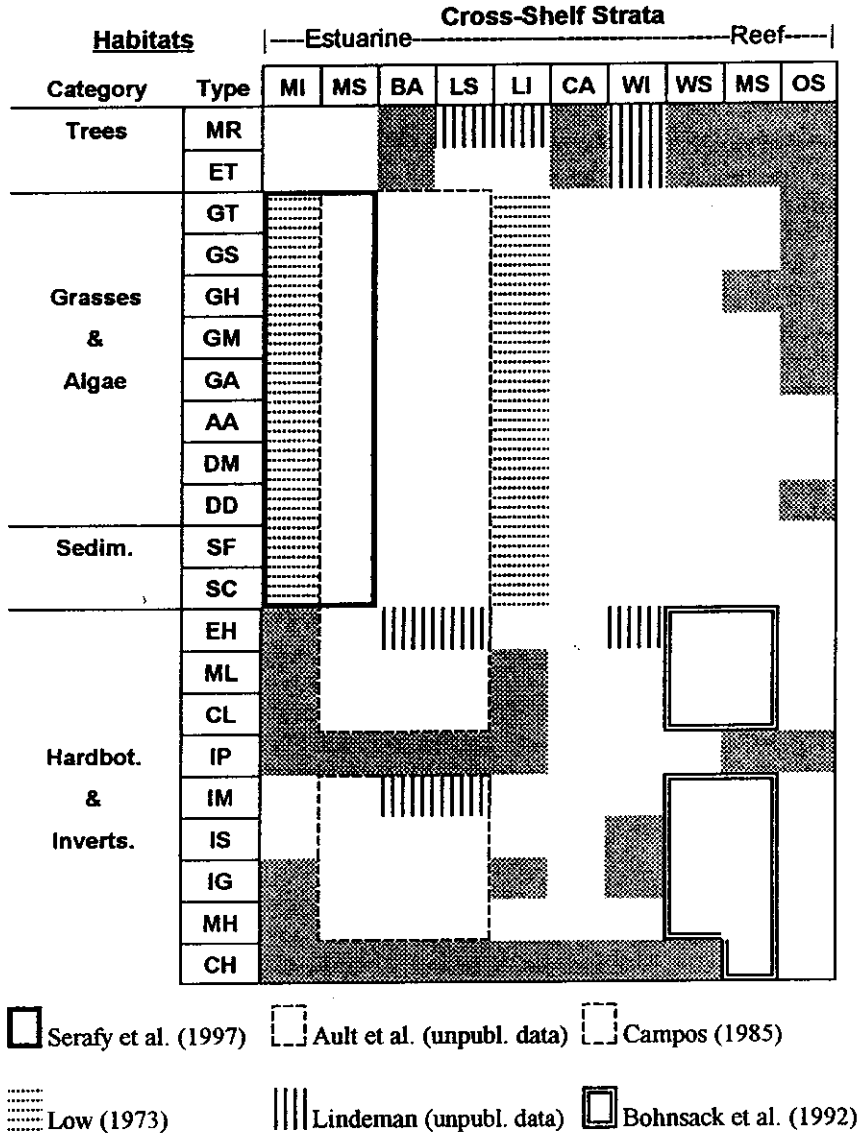
Figure 3. Habitat-specific sampling efforts in prior studies of Biscayne Bay shelf area fishes. Not comprehensive; surveys consulted in present work emphasized.

The high dimensionality of the cross-shelf habitat matrix exceeded the habitat-specific information in the available GIS files for Biscayne Bay (based on DERM, 1983). Due to this and potential temporal shifts in habitat distributions since map construction, all structural habitats were collated into three basic categories to estimate areal coverages in the Bay. The submerged aquatic vegetation (SAV) category included all habitats that could be defined as grasses and algae (Table 2). The barebottom category included all habitats dominated by unconsolidated sediments, whether fine or coarse. The hardbottom category contained consolidated bedrock habitats and associated invertebrate fauna (Table 2). Relative areas of other habitat types in the CSH matrix (e.g., mangroves) could not be compared as adequate GIS data were unavailable.

At the cross-shelf scale, the CSH matrix for Biscayne Bay identified five physiographic strata. By combining the three clustered habitat categories with the five cross-shelf strata, a 15-cell CSH framework was obtained for which areal GIS data from the Bay were available (Figure 4). In terms of structural habitat quantity, SAV was most widely distributed, covering approximately 79% (404 km^2) of the Bay. The most abundant cross-shelf habitat combination in the Bay was SAV within the basin axis stratum. SAV coverage was three times greater within the mainland subtidal cross-shelf stratum than leeward subtidal stratum. Hardbottom area was greatest within the mainland subtidal stratum in the southern Bay. Large areas of sedimentary habitat in the northern bay contain low-relief mixtures of shell hash and mud, reflecting prior dredge excavations for land fill. Open sedimentary area was greatest within the basin axis (Figure 4).

Cross-shelf Habitats and Settlement

Distributional information was combined using CSH matrices to: a) estimate the outer spatial boundaries of settlement across the shelf; and b) identify key settlement habitats among representative species of grunts and snappers. Although important, temporal variations were not detailed. The present estimates of distributions at settlement are for August. This is a period of substantial settlement for many grunt and snapper species based on known patterns of reproduction (García-Cagide *et al.*, 1994) and settlement (McFarland *et al.*, 1985; Halvorsen, 1994; Lindeman and Snyder, in press; Lindeman *et al.*, MS; Maddox, pers. comm.) in the northern Caribbean. The majority of information on fish use of natural structural habitats in the study area was from within Biscayne Bay, not the euhaline shelf area outside of the Bay (Figure 3).

Black Margate — Based on existing literature, museum holdings, and current field studies in the Biscayne Bay shelf area, rank abundances for newly settled and early juvenile stages within each cross-shelf habitat were estimated (Figure 5). The zeros across the matrix reflect a complete absence of any records of early stages of black margate from these cross-shelf habitats. Early demersal stages of

black margate were only recorded from three cross-shelf strata, all associated with shallow areas of windward barrier islands and channels (Figure 5). Newly settled stages occurred outside or within channels, but rarely on leeward sides. Although less information is available, no records of newly settled stages exist from areas deeper than ten m. Structural habitat use was also highly restricted. There is no evidence that any life stages utilize habitats comprised exclusively of seagrass at any depth.

Potential primary and secondary settlement sites were identified in Figure 6 by eliminating habitats of uncommon occurrence. A total of eight cross-shelf habitats within 0 - 10 m depths and consisting of invertebrates and hardbottom, were identified as primary or secondary settlement sites. Substantial vertical relief was a feature of all of these habitats. Black margate early stages were relatively cryptic, positioning under overhangs and within crevices.

Gray Snapper and Lane Snapper — In the literature on Biscayne Bay area fishes and in the University of Miami museum collections now catalogued at UF, gray snapper occurred commonly in grassbeds. However, there was an absence of surveys and collections from other habitats (Figure 3). In visual observations and collections in the present study, newly settled stages (< 2.5 cm) were present in grassbeds, but consistently absent from mangrove and hardbottom habitats. Juvenile stages were more widely distributed, particularly on the habitat scale, associating with a variety of hard structures, as well as SAV (Figure 7). Newly settled stages of gray snapper were rarely recorded from cross-shelf strata outside inlets, despite their abundance within cross-shelf strata in or west of channels. A total of 62 cross-shelf habitats were estimated to serve as primary or secondary nursery sites for newly settled and early juvenile stages of gray snapper (Figure 7). For newly settled stages, almost all nursery areas were associated with differing combinations of seagrasses leeward of barrier islands. Early juveniles were frequently associated with a broad variety of structural habitats, including grassbeds, mangrove prop and drop roots, and hardbottom areas (Figure 7).

Although abundances were rarely high, early demersal stages of lane snapper have been recorded from almost every structural habitat type of the Biscayne Bay area (Figure 8). This includes mangrove trees, grasses and algae, and hardbottom/invertebrate structure. As in gray snapper, differential habitat use occurred between life stages. This was most apparent in red mangrove prop-root canopies that were utilized primarily by early juveniles (Figure 8). Newly settled stages have been rarely observed or collected in these habitats. Sixty-six cross-shelf habitats with nursery value were estimated after eliminating uncommonly used cross-shelf habitats (Figure 8). Early stages occurred among all cross-shelf strata from the mainland shoreline of Biscayne Bay to depths of at least ten m offshore. However, collections and observations suggested that early

juvenile stages utilized leeward and windward barrier island inshore strata more commonly than strata further inshore.
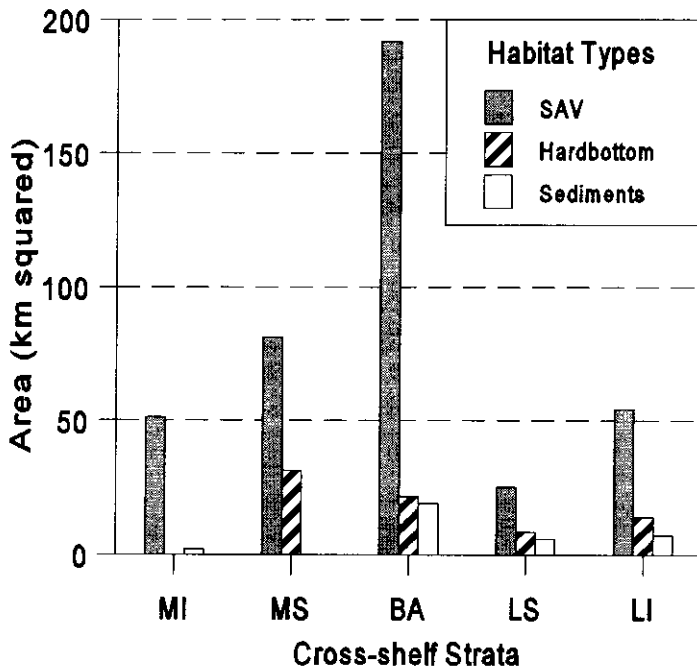

Figure 4. Spatial coverage of three clustered habitat types in Biscayne Bay, Florida USA. Stratified according to five cross-shelf strata (Figure 1). MI: Mainland Inshore (0 - 1 m): BA: Basin Axis (> 2m); LS: Leeward Subtidal (1 - 2 m); LI: Leeward Inshore (0 - 1 m); SAV; Submerged Aquatic Vegetation.

HABITAT USE PATTERNS   Species: Black margate, *A. surinamensis*
Season: Summer   Life Stages: NS:EJ

Habitats Category	Type	MI	MS	BA	LS	LI	CA	WI	WS	MS	OS
Trees	MR	0 0	0 0	▨	0 0	0 0	▨	0 0	▨	▨	▨
	ET	0 0	0 0	▨	0 0	0 0	▨	0 0	▨	▨	▨
Grasses & Algae	GT	0 0	0 0	0 0	0 0	0 0	0 0	0 0	0 0	0 0	▨
	GS	0 0	0 0	0 0	0 0	0 0	0 0	0 0	0 0	0 0	▨
	GH	0 0	0 0	0 0	0 0	0 0	0 0	0 0	0 0	▨	▨
	GM	0 0	0 0	0 0	0 0	0 0	0 0	0 0	0 0	0 0	▨
	GA	0 0	0 0	0 0	0 0	0 0	0 0	0 0	0 0	0 0	▨
	AA	0 0	0 0	0 0	0 0	0 0	0 0	0 0	0 0	0 0	0 0
	DM	0 0	0 0	0 0	0 0	0 0	0 0	0 0	0 0	0 0	0 0
	DD	0 0	0 0	0 0	0 0	0 0	0 0	0 0	0 0	0 0	▨
Sedim.	SF	0 0	0 0	0 0	0 0	0 0	0 0	0 0	0 0	0 0	0 0
	SC	0 0	0 0	0 0	0 0	0 0	0 0	0 0	0 0	0 0	0 0
Hardbot. & Inverts.	EH	▨	0 0	0 0	0 0	0 0	1 1	2 2	2 2	1 1	0 0
	ML	▨	0 0	0 0	0 0	▨	1 1	1 2	1 2	0 1	0 0
	CL	▨	0 0	0 0	0 0	▨	1 1	1 2	1 2	0 1	0 0
	IP	▨	▨	▨	▨	1 1	2 2	2 2	▨	▨	▨
	IM	0 0	0 0	0 0	0 0	0 0	0 0	0 0	0 0	0 0	0 0
	IS	0 0	0 0	0 0	0 0	0 0	0 0	▨	0 0	0 0	0 0
	IG	▨	0 0	0 0	0 0	▨	0 0	▨	0 0	0 0	0 0
	MH	▨	0 0	0 0	0 0	0 0	1 1	1 1	1 1	0 1	0 0
	CH	▨	▨	▨	▨	▨	▨	▨	▨	1 1	0 0

(Cross-Shelf Strata)

Figure 5. Estimated habitat use patterns of newly settled (NS - left value) and early juvenile (EJ - right value) stages of black margate of the Biscayne Bay area. Habitat and cross-shelf strata acronyms in Table 2 and text. Each rank approximates an order of magnitude: 0 - absent or rare; 1 - uncommon; 2 - occasional; 3 - abundant (modified from Starck, 1968). Shaded cells: habitats absent from specific cross-shelf stata.

HABITAT USE PATTERNS   **Species:** Black margate, *A. surinamensis*
Season: Summer   **Life Stages:** Newly settled : Early juvenile

<u>Habitats</u>   Cross-Shelf Strata

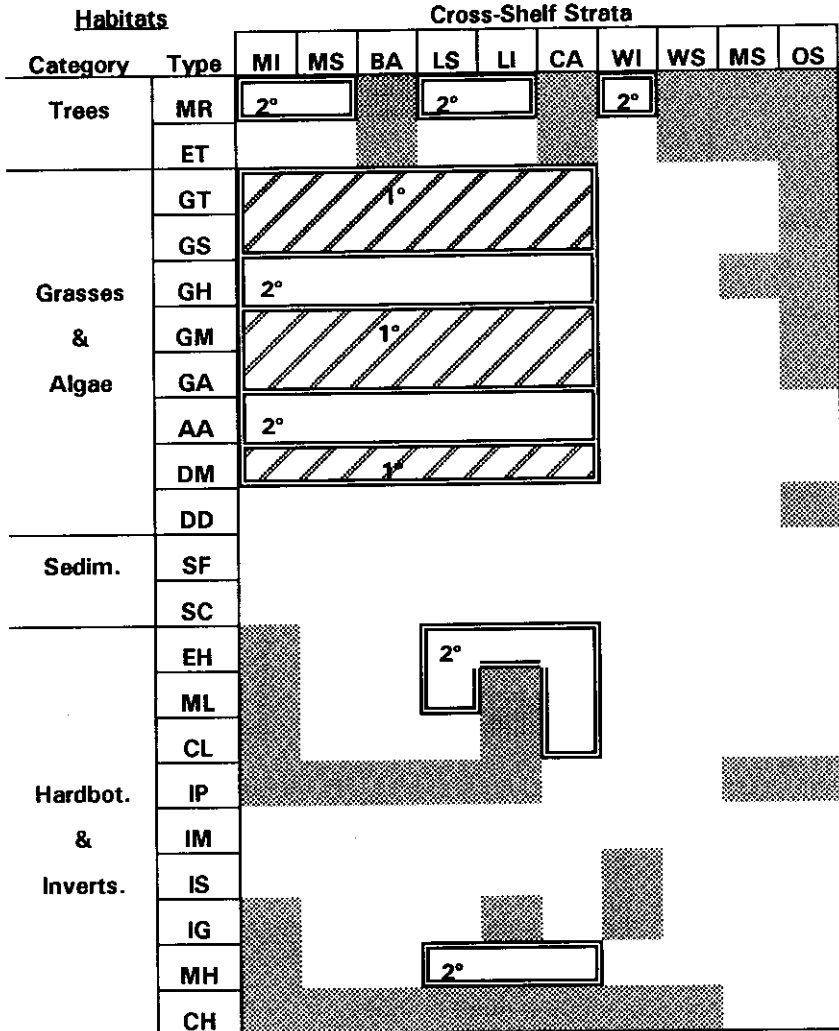| Category	Type	MI	MS	BA	LS	LI	CA	WI	WS	MS	OS
Trees	MR										
	ET										
Grasses	GT										
	GS										
	GH										
&	GM										
Algae	GA										
	AA										
	DM										
	DD										
Sedim.	SF										
	SC										
	EH						1°				
	ML						2°				
	CL										
Hardbot.	IP										
&	IM										
Inverts.	IS										
	IG										
	MH										
	CH										
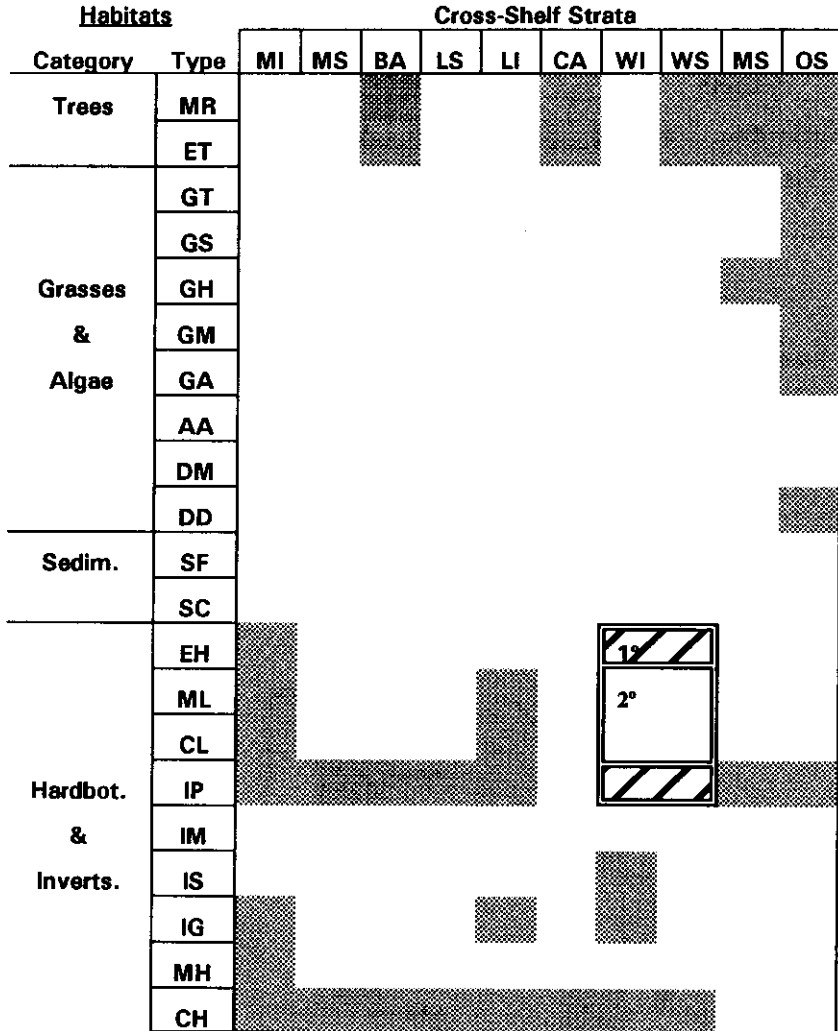
Figure 6. Estimated primary nursery areas (1°, with diagonal fill) and secondary nursery areas (2°) for *Anisotremus surinamensis*, Biscayne Bay shelf area. Distribution and rank abundance estimates of newly settled and early juvenile stages given in Figure 5.

NURSERY SITES   **Species:** Gray Snapper, *Lutjanus griseus*
Season: Summer   **Life Stages:** Newly settled : Early juvenile

Habitats		Cross-Shelf Strata									
Category	Type	MI	MS	BA	LS	LI	CA	WI	WS	MS	OS
Trees	MR	2°			2°			2°			
	ET										
Grasses & Algae	GT				1°						
	GS										
	GH	2°									
	GM			1°							
	GA										
	AA	2°									
	DM			1°							
	DD										
Sedim.	SF										
	SC										
Hardbot. & Inverts.	EH				2°						
	ML										
	CL										
	IP										
	IM										
	IS										
	IG										
	MH				2°						
	CH										

Figure 7. Estimated primary nursery areas (1°, with diagonal fil) and secondary nursery areas (2°) for *Lutjanus griseus*, Biscayne Bay shelf area.

NURSERY SITES   **Species:** Lane Snapper, *Lutjanus synagris*
Season: Summer   **Life Stages:** Newly settled : Early juvenile
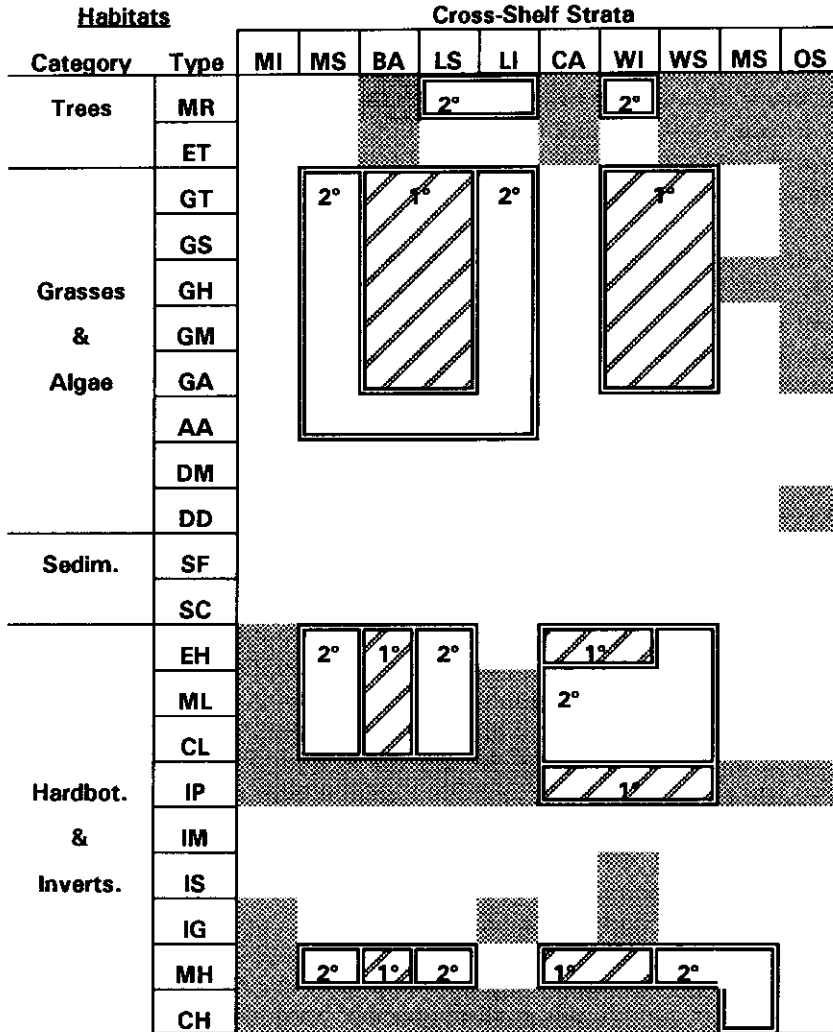
Figure 8. Estimated primary nursery areas (1°, with diagonal fill) and secondary nursery areas (2°) for *Lutjanus synagris*, Biscayne Bay shelf area.

Estimated primary and secondary settlement areas of gray and lane snapper differed within Biscayne Bay (Figure 9). Limited GIS data on specific habitat types within the broad SAV, sedimentary, and hardbottom categories (summarized in the Biscayne Bay Habitat Characterization section) resulted in plots which represent fish distributions at only these broad habitat categories among the five cross-shelf strata within the Bay (Figure 1). However, the fundamental patterns within the detailed CSH matrices were still present. Settlement areas of gray snapper were concentrated in inshore grassbeds and did not include hardbottom (the blank area in the gray snapper plot in Figure 9). In contrast, newly settled lane snapper occurred over a wider range of structural habitats, including hardbottom.

Spatial Comparisons of Settlement Among Grunt and Snapper Species —
Cross-shelf habitat use was also characterized for newly settled stages of 18 other grunt and snapper species of the Biscayne Bay area using prior studies, museum materials, and surveys in the present study. Coarse attributes of distributional patterns were estimated at both the structural habitat and cross-shelf scales (Figure 10). This format summarized existing information on the occurrence of newly settled stages among vegetated habitats only, hardbottom habitats only, or both structural types (vertical axis). On the cross-shelf scale (horizontal axis), five patterns were identified ranging from settlement only at shallow areas inside the Bay, to settlement only in outer shelf areas. The distributional patterns summarized here may change with additional information on settlement in haemulids and lutjanids.

At settlement, four snapper species showed specialized distributions at both the structural habitat (grassbed) and inshore cross-shelf scales (top left in Figure 10). Two grunt and one snapper species showed specialized distributions within both the structural habitat (hard structure) and offshore cross-shelf scales (bottom right in Figure 10). Four grunts and one snapper were estimated to settle primarily on hard structures in shallow areas outside of barrier islands. The bluestriped grunt (*Haemulon sciurus*) was specialized in terms of cross-shelf distribution, but not structural habitat use (Figure 10). The porkfish (*Anisotremus virginicus*) was specialized for habitats (hard structures) but not for cross-shelf strata. Only one species, the tomtate (*H. aurolineatum*), was clearly opportunistic at both habitat and cross-shelf strata scales (Figure 10). However, the three grunts and three snappers within the "shallow - inside and outside barrier island" and "seagrass and hard structure" categories can also be considered opportunistic in their use of structural habitats. Of the 21 species considered (12 grunts and 9 snappers), 14 appeared to show a high degree of specialization in the use of structural habitats or cross-shelf strata at settlement (eight grunt and

six snapper species). Seven species were considered opportunistic (four grunt and three snapper species).

▨ Primary settlement areas   ▱ Secondary settlement areas

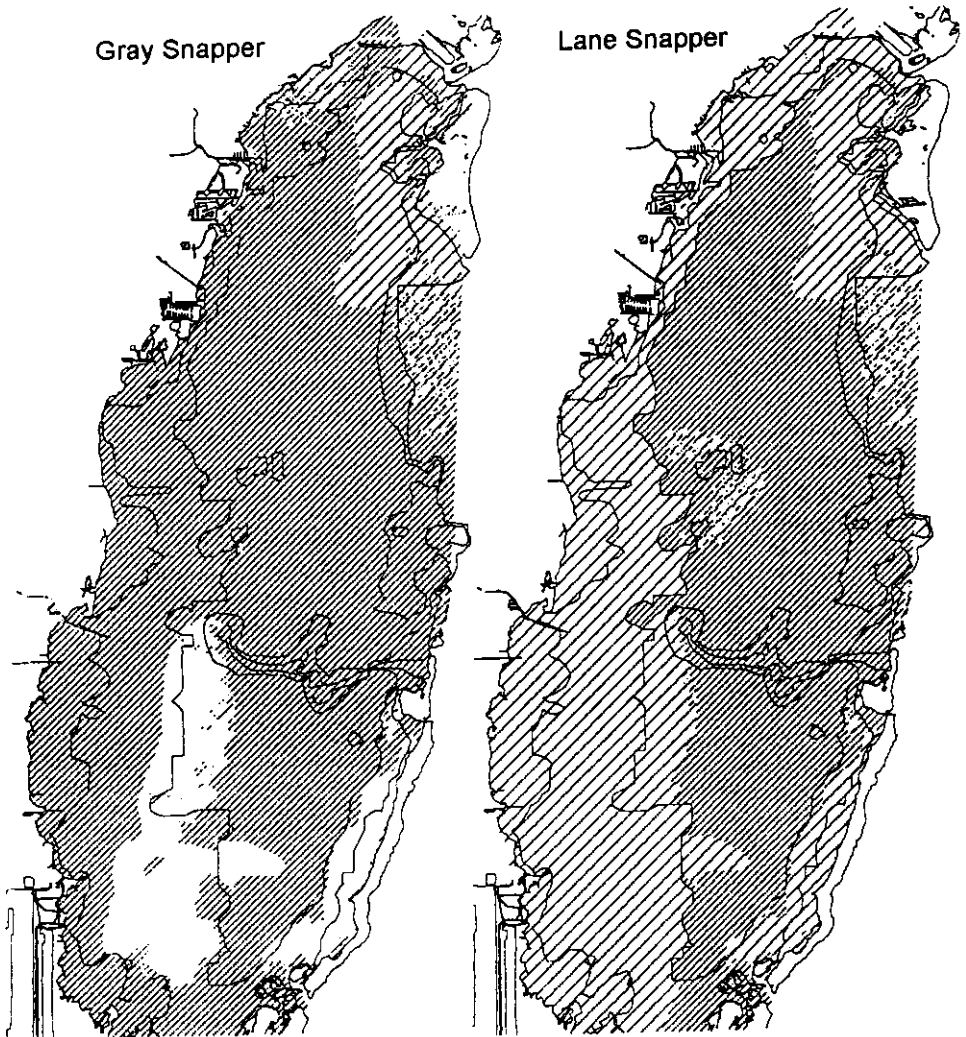Gray Snapper   Lane Snapper

Figure 9. Preliminary estimates of gray and lane snapper (*Lutjanus griseus* and *L. synagris*) settlement areas in central and southern Biscayne Bay, Florida USA. One and two meter isobaths shown.

Habitat Categories	Cross-shelf Positioning				
	Shallow (<10 m)				
	Inside Barrier Island	Inside & Outside Barrier Island	Outside Barrier Island	Shallow & Deep	Deep (>10 m)
Seagrass	Mutton Snapper Gray Snapper Dog Snapper Cubera Snapper				
Seagrass & Hard Structure	Bluestriped Grunt	Lane Snapper Yellowtail Schoolmaster Sailors Choice White Grunt French Grunt		Tomtate	
Hard Structure			Black Margate Smallmouth Grunt Caesar Grunt Spanish Grunt Mahogony Snapper	Porkfish	Striped Grunt Cottonwick Blackfin Snapper

Figure 10. Structural habitats and cross-shelf areas occupied by newly-settled stages of haemulids (< 2 cm SL) and lutjanids (< 2.5 cm) of the Biscayne Bay shelf area.

DISCUSSION
Cross-shelf Habitat Use in Snappers and Grunts

Early demersal habitat use in the three species assessed with CSH matrices showed several clear patterns. These patterns are summarized here and compared with information on these species from other studies in southeast Florida. In all species, distributions of early demersal stages at both cross-shelf and structural habitat scales were not uniform. Both newly settled and early juvenile stages of black margate associated exclusively with hard structure within shallow cross-shelf strata. In contrast, newly settled gray snapper used grassbeds almost exclusively and were rarely recorded from hardbottom. Early juvenile gray snapper were more opportunistic than newly settled stages, using grassbed, mangrove, and hardbottom habitats. Available evidence suggests that lane snapper is highly opportunistic during both early demersal stages. Lane snapper showed broader distributional patterns at both the habitat and cross-shelf strata spatial scales (Figure 8). For example, newly settled lane snapper occurred on hardbottom as well as grassbed habitats (Figure 9).

Few other studies have documented early habitat use in the black margate. At nearshore hardbottom habitats approximately 150 km north of Biscayne Bay, this species ranked fifth in abundance of 86 total taxa censused (Lindeman and Snyder, in press). The majority of these individuals were newly settled or early juvenile life stages. This pattern was similar to that of the hardbottom habitats and windward inshore/windward subtidal strata of the CSH matrix for the Biscayne Bay area. Black margate have never been recorded from pure stands of seagrass.

Starck (1970) summarized information available through the 1960s for gray snapper in the Florida Keys and concluded that settlement stages and early juveniles primarily used grassbeds before migrating to hard structure in deeper waters. In the Florida Bay area, early juveniles have been examined indirectly or directly in various studies, including Odum and Heald (1972), Thayer _et al._ (1987), Sogard _et al._ (1987), Hettler (1989), Rutherford _et al._ (1989), and Chester and Thayer (1990). These studies found gray snapper to be the most abundant lutjanid in the northern and eastern areas of this complex estuary. In grassbeds of the Indian River Lagoon, gray snapper was the most frequently occurring and second most abundant snapper collected (Gilmore, 1988). All early life stages of gray snapper were uncommon at nearshore hardbottom habitats outside of barrier islands of the southern Indian River Lagoon (Lindeman and Snyder, in press). None of these studies contradict any components of the CSH matrix patterns constructed for gray snapper in Biscayne Bay: a) newly settled stages used grassbeds inside the Bay, not hardbottom or mangrove structures, and b) early juveniles were more opportunistic, using grassbeds, hardbottom and mangrove structures in and out of the Bay.

Despite their usage of many structural habitats in inshore areas, information on early stages of lane snapper from southeast Florida was sparse. In the Florida Keys, Starck (1970) reported that juveniles were common in grassbeds. Juveniles of lane snappers were the most abundant snappers collected in grass habitats of western Florida Bay (J. Colvocoresses, pers. com). In the grassbeds of the Indian River Lagoon, lane snapper were the most abundant and second most frequently collected snapper species (Gilmore, 1988). Lane snapper, primarily present as newly settled stages, were the most abundant snapper on nearshore hardbottom reefs off the southern Indian River Lagoon (Lindeman and Snyder, in press). These studies do not contradict the CSH matrix patterns for lane snapper in Biscayne Bay: a) newly settled stages used both grassbeds and hardbottom inside and outside the Bay; and b) early juveniles used grassbeds, hardbottom and mangrove structures in and out of the Bay. The absence of newly settled life stages of gray and lane snapper from mangrove habitats may result from concentrated predation pressure by seasonally-resident juvenile stages.

Cross-shelf Habitat Frameworks

Research Applications — A CSH framework for the Biscayne Bay area fostered the logical organization of a complex shelf system into multiple habitat components on both structural and physiographic scales despite incomplete distributional data on both habitats and fishes (almost universal constraints). When integrated with a GIS system, the framework was spatially explicit and quantified relative habitat areas. Due to their architecture, CSH matrices can also aid the design of stratified random sampling surveys (Ault *et al.*, MS). When applied to several life stages, the matrices can identify patterns of inshore colonization and successive offshore movements. Habitat sampling by fishes during the early stages of ontogenetic habitat shifts (Helfman *et al.*, 1982) may involve shifts in cross-shelf positioning. Such fine-scale movements may also be assessed using CSH frameworks, if adequate temporal data is available. Differences in the pre-settlement biology of late-stage larvae underlie many differences in post-settlement spatial patterns. CSH approaches may aid examination of the cross-shelf immigration of early-settling species, such as grunts, which may not undergo discrete, "drop and stay" settlement events (Lindeman *et al.*, MS).

Distributional information from the matrices was easily comparable with a variety of other studies. This suggests potential value in applying CSH matrices to other regions for comprehensive inter-regional comparisons of habitat use across continental and insular shelves. The structural habitats composing the rows of CSH matrices (Table 2, Figure 2) can represent the majority of coastal habitat types in the central western Atlantic. Therefore, customizing only the cross-shelf strata axis for the region under study creates

cross-shelf habitat matrices that are standardizeable among regions. This may permit the characterization of habitat use among different regions, while maintaining standard spatial scales. Application of this attribute in the examination of selected biogeographic hypotheses of Caribbean fish distributions may also be feasible (Lindeman, 1997).

Habitat and Fisheries Management Applications — Agencies evaluating coastal construction permits under federal, state, and local administrative rules need habitat frameworks which explicitly characterize multiple spatial scales and are usable by non-scientists. For many coastal fishes, it has long been known that juvenile stages occur in shallower water than adults (Starck, 1970; Odum and Heald, 1972; Nakamura *et al.*, 1980; Nelson *et al.*, 1991). However, there has been a chronic need for detailed habitat-specific information across the shelf. This is now amplified by new agency guidelines for evaluating essential fish habitat impacts during permit reviews (NOAA, 1996). Very few front-line permitting agencies have good habitat or fish distribution data on a site-specific basis, or GIS technology. CSH matrices can permit logical, comparative assessments of life stage specific distributions over several spatial scales (e.g., structural habitat and physical strata) in data-poor environments.

The geographic and biotic complexity organized by cross-shelf habitat matrices may aid the ranking of critical areas for settlement and growth of early stages. The primary and secondary nursery areas identified within Figures 7 and 8 for gray and lane snapper may reflect multiple levels of essential fish habitat in habitat plans used by fishery management councils. For example, primary settlement areas could warrant designation as habitat areas of particular concern, and secondary settlement areas as essential fish habitat. Management tools such as marine reserves also require precise identification of the spatial linkages between habitat use and fishery production (Plan Development Team, 1990). CSH matrices may aid the design of reserves by identifying key habitats which link ontogenetic habitat shifts between settlement and spawning areas.

Superimposing distributional mosaics of multiple life stages upon CSH matrices has parallels in landscape ecology (sensu Hanski and Simberloff, 1996). Since many fish populations possess an ontogenetic structure with differing levels of interconnectivity, principles of metapopulation biology on an intrapopulation scale may also be applicable to cross-shelf frameworks. For example, the graphic fusion of metapopulation biology and landscape ecology represented in Wiens (1996, Figure 3) could reflect a plot of an "ontogenetic metapopulation" upon a cross-shelf seascape within a larger population. Grunts, snappers, and other wide ranging species with semi-open populations (after Caley *et al.*, 1996) may be appropriate test cases to apply metapopulation biology and landscape ecology within a fishery management context.

Limitations — The CSH framework has limitations, many of which can be resolved by greater data availability. Some geomorphological configurations are too complex to be simplified into a series of semi-continuous cross-shelf strata. For example, Florida Bay on the southern boundary of peninsular Florida contains over 230 low relief islands (Enos, 1989), hundreds of channels, and over a dozen sizable basins. Important features such as channels can be represented in some areas such as Biscayne Bay. However, in other instances, channels and mainland canals do not easily position within CSH matrices. In these cases, such features may be treated as modifiers using refined versions of approaches discussed in Cowardin *et al.* (1979).

The diversity of cross-shelf habitat types identified by a CSH framework precludes any one standard sampling gear, making inter-habitat comparisons problematic. Limited data for many cells can also impede the full application of the framework (i.e., the theory may be "ahead" of the available data). However, it is better to have a thorough spatial framework with an incomplete database than no comprehensive framework and the same incomplete database. If a study is totally focused within one habitat and is not intended to be comparative, a CSH framework may be of little use.

Boundaries among microhabitats, habitats, and cross-shelf strata (Table 1) are rarely explicit in the field. The transition areas of differing ecotones may have important characteristics of their own. However, ecotonal characteristics cannot be comparatively analyzed unless their component habitats are first characterized. The complex attributes of ecotones are partially addressed by use of habitat mosaics. However, additional work is needed to account for transitional ecotones. Microhabitat-scale stratifications (0.01 - 0.1 m^2) are also possible (Lindeman, 1997, Table 2.14) and may aid the examination of fine-scale habitat selection.

Accurately characterizing relative habitat use can be confounded by temporal variations in species occurrences. Spatial distribution estimates in the present study were for late summer, a period of high abundance of newly settled stages for most grunt and snapper species. The coarse nature of this temporal scale was a function of the study objectives (primarily involving distributional boundaries) and the available data, not the actual CSH framework. Multiple time-scales and temporal data can be incorporated within individual or multiple CSH matrices according to study objectives and data availability. On diel scales, the cross-shelf habitat mosaics used by many haemulids and lutjanids contract and expand with light and dark periods. Cyclical temporal shifts will not confound CSH approaches and stratification of day/night differences in cross-shelf habitat use is primarily limited by data availability.

Opportunities for Synthesis — Approaches to the organization of complex spatial systems to represent the distributions of dynamic organisms are unavoidably diverse. At the level of the population and above, the concept of "habitat" underlies almost all efforts to describe pattern or infer causality. Therefore, no evaluation of existing approaches can be fully comprehensive and no approach ideal. However, many new tools for habitat assessment are becoming available due to data-processing advances and new biological information. For example, with advances in GIS technology and population modeling theory, various assessment issues can be addressed in spatially-explicit manners by habitat suitability modeling and habitat affinity indices (Christenson *et al.*, 1997; Monaco *et al.*, 1998). In addition, bioenergetic models using growth potential as a proxy for habitat use are now available to predict the production rates of differing habitats (Ault *et al.*, in press).

Several attributes of CSH matrices (e.g., assessment of structural habitats among geographically standardized cross-shelf strata; management utility in data-poor environments) appear to have value in describing and analyzing the ontogeny of habitat use in coastal fishes. Perspectives on habitat use which involve the entire shelf are becoming more frequent (Winemiller and Leslie, 1992; Dennis, 1992; Newman and Williams, 1996; Appeldoorn *et al.*, 1997). Particularly useful approaches will result from the merging of the new generation of population modeling tools with new empirical data on ontogenetic variations in the use of cross-shelf habitats.

ACKNOWLEDGEMENTS

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