COASTAL HABITAT CONNECTIVITY OF REEF FISHES FROM SOUTHWESTERN PUERTO RICO

By

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ABSTRACT

In the western Atlantic, despite increasing concerns about designing and implementing an integrated approach in coastal conservation and management, the ecological relationships (i.e., habitat connectivity) for reef fishes between mangroves, seagrass and shallow-water coral reefs have received relatively little attention. Whereas the fish community of southwestern Puerto Rico, off La Parguera, has been extensively studied, little information is available analyzing the relative importance of these coastal shallow-water habitats in terms of nursery value and ontogenetic habitat shifts. Based on underwater visual censuses, the present study determined the pattern and extent of habitat use in post-settlement fishes and how these processes may change during ontogeny, leading to a quantification of habitat connectivity. The study was divided in three components: (1) presenting a baseline characterization of the fish community structure along an inshore-offshore, cross-shelf gradient from Montalva Bay to Turrumote, (2) evaluating the nursery value of these habitats, and (3) providing evidence for ontogenetic migrations and habitat shifts. There were significant differences in community structure and spatial distribution of fishes among these habitats, revealing an unequal spatial pattern. Among the dominant groups were Haemulidae, Pomacentridae, Scaridae, Labridae, Lutjanidae, and Acanthuridae. The nursery value of a given habitat was species specific, and not only mangroves or seagrass but a combination of habitats exhibited high densities of juveniles; however, Romero Key was more important and may function as a transition point from bay habitats to coral reef habitats further away. Most strata along this gradient showed a high proportional abundance of juveniles of selected species;

however, there was a preponderance of high densities of juveniles in shallow-water strata (0-3 m depth), whereas the adults were found in deeper strata (3-10 m). Results were consistent with ontogenetic migrations for many of the fish species studied, displaying species specific migratory routes from mangroves and seagrass to deep reefs, and from shallow to deeper reefs. This lead to the idea that certain “corridors” may exist along the inshore-offshore habitat gradient. The findings highlight the relevance of including the habitat connectivity in coastal shallow-water areas for the conservation and management strategies for the marine ecosystem.

RESUMEN

En el Atlántico oeste, a pesar de la creciente preocupación sobre el diseño e implementación de una visión integral para el manejo y conservación costera, las relaciones ecológicas (i.e., conectividad de hábitat) de peces arrecifales entre mangles, pastos y arrecifes coralinos de aguas someras, han recibido poca atención. Si bien la comunidad íctica del suroeste de Puerto Rico, frente a La Parguera, ha sido estudiada substancialmente, poca información está disponible para analizar la importancia relativa de estos hábitats costeros de aguas someras en términos del valor como vivero y los cambios ontongenéticos del hábitat. Utilizando censos visuales submarinos, el presente estudio determinó el patrón y extensión de uso de hábitat en peces post-asentados y cómo estos procesos cambian durante la ontogenia, permitiéndo la cuantificación de conectividad de hábitat. El estudio se dividió en tres componentes: (1) caracterización básica de la estructura comunitaria del ensamble de peces a lo largo de un gradiente cercano y distante a la costa a través de la plataforma desde Bahía Montalva hasta Turrumote, (2) evaluación del valor de vivero para estos hábitats, y (3) proveer evidencia de migraciones ontogenéticas y cambios de hábitat. Hubo diferencias significativas en la estructura comunitaria y distribución espacial de peces entre estos hábitats, revelando un patrón espacial no uniforme. Entre los grupos dominantes figuraron Haemulidae, Pomacentridae, Scaridae, Labridae, Lutjanidae, and Acanthuridae. El valor de vivero fue específico para cada especie, dado que no solamente un hábitat sino la combinación de hábitats exhibió densidades altas de juveniles; sin embargo, cayo Romero fue más importante, y quizá funcione como sitio de transición en hábitats de bahía hacia hábitats

coralinos distantes. La gran mayoría de los estratos a lo largo del gradiente mostró una abundancia proporcionalmente alta de juveniles de las especies seleccionadas; no obstante, hubo preponderancia de densidades altas de juveniles en aguas someras (0-3 m profundidad), mientras que los adultos se encontraron en estratos profundos (3-10 m). Los resultados fueron consistentes con migraciones ontogenéticas para muchas de las especies estudiadas que exhibieron rutas migratorias específicas desde mangles y pastos hacia arrecifes profundos y de arrecifes someros hacia profundos. Esto generó la idea de la existencia de “corredores” entre los hábitats cercanos y distantes a la costa. Los hallazgos destacan la relevancia de incluir la conectividad del hábitat en áreas costeras someras para estrategias de conservación y manejo del ecosistema marino.

DEDICATION

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CHAPTER 1: GENERAL INTRODUCTION AND OUTLINE OF DISSERTATION

In the western Central Atlantic, shallow-water environments (e.g., mangroves, seagrass, and coral reefs) are under continuous stress due to coastal development (e.g., dredging, building), pollution, and overfishing (Jackson et al. 2001; Hughes et al. 2003; Bellwood et al. 2004). Fishing, as the most widespread and ancient exploitative activity, exerts direct and indirect impacts on coastal ecosystems, greatly modifying the population structure and habitat of associated marine organisms (Russ 1991; Jennings and Kaiser 1998). Historically, overfishing has produced severe declines in fish populations world-wide (Jackson et al. 2001) and many heavily exploited stocks have collapsed despite regulation using traditional fishery management approaches (Botsford et al. 1997; Hilborn et al. 2003). In the Caribbean, artisanal fishing has been able to produce differences in fish assemblages and benthic habitats (Hawkins and Roberts 2004).

Despite increasing concerns about designing and implementing an integrated approach in coastal conservation and management, the ecological relationships (i.e., habitat connectivity) between mangroves, seagrass and coral reefs have received relatively little attention (Beck et al. 2001; Gillanders et al. 2003). While these coastal habitats are ecologically connected to each other (Beck et al. 2001), the quantification of relationships and importance of adjacent habitats for coral reef associated fish species has been elucidated only recently (Nagelkerken et al. 2000; Adams and Ebersole 2002; Cocheret de la Morinière et al. 2002; Dorenbosch et al. 2004; Mumby et al. 2004;

Chittaro et al. in press). Fundamental ecological research on the habitat connectivity is urgently needed for the development of sound coastal conservation and management.

At least two major categories of connectivity are commonly recognized due to the typical life history (i.e., two-phase life cycle) of the vast majority of reef associated fishes and invertebrates: (1) pre-settlement connectivity and (2) post-settlement connectivity. The former involves a combination of larval behavior (i.e., chemical detecting, swimming speed and performance, etc.) and oceanographic conditions (i.e., current patterns, eddies, waves), leading to either inshore retention or offshore advection of larvae in given geographical areas (Roberts 1997; Cowen et al. 2000; Sponaugle et al. 2002; Mora and Sale 2002). Post-settlement connectivity involves biological and physiological changes in juveniles that settle in areas (i.e., nursery) different to those of adults, and progressively migrate (i.e., post-settlement life cycle migration) from settlement areas using intermediate habitats as they grow (i.e., ontogenetic changes) until reaching deeper, adult habitats (Appeldoorn et al. 1997; Lindeman et al. 2000; Nagelkerken et al. 2000; Dahlgren and Eggleston 2000; Cocheret de la Morinière et al. 2002). In addition, this connectivity also involves other kinds of migrations, such as those related with feeding (Ogden and Zieman 1977) and spawning (Zeller 1998).

A given marine habitat is considered a nursery if juveniles occur at higher densities, have lower rates of predation or higher rates of growth compared to other habitats, and also if the habitat contribution, in terms of juveniles per unit area to the production of adults, is greater than that from other habitats harboring also juveniles (Beck et al. 2001). In the western Atlantic, mangrove and seagrass beds in estuarine and

non-estuarine bays function as nurseries for several marine organisms (e.g., crustaceans, mollusks, and fishes) (Parrish 1989; Roberts 1996; Beck et al. 2001). However, in the Indo-Pacific such a function is partial for some regions (Blaber 1980; Laegdsgaard and Johnson 1995), while for others it is not important (Quinn and Kojis 1985); this has produced contradictory results (Thollot 1992).

Mangroves, seagrass beds, and shallow coral reefs are important habitats functioning as nursery grounds for several reef associated fishes (Thayer et al. 1987; Baelde 1990; Ley et al. 1999; Nagelkerken et al. 2000). Among the most important reasons why juveniles of several fish species use mangroves and seagrass beds as nurseries include, (1) shelter from predators (Parrish, 1989) due to habitat structural complexity, (2) high abundance of food (Odum and Heald 1972; Ogden and Zieman 1977; Laegdsgaard and Johnson 2001), and (3) planktonic larvae reception due to extensive habitat coverage (Parrish 1989).

The life history of reef fishes is characterized by two-phase cycle, exhibiting a planktonic larval stage and a benthic stage (i.e., juvenile and adults) (Sale 1980; Leis 1991). However, many fish species settle on habitats completely different than that of adults (Shulman and Ogden 1987; Eggleston 1995), providing relatively different environmental and habitat conditions to juveniles; thus, it may be considered as another stage in the life cycle. Thus, such fish species have a life history comprised by a three-phase cycle: larvae (planktonic), juvenile (benthic), and adult (benthic). Juveniles of these fishes are commonly found in high densities in non-reef habitats (e.g., mangroves, seagrass, algal clumps, reef lagoons, bays), whereas adults are almost exclusively found

on the coral reef itself (Parrish 1989; Nagelkerken et al. 2000; Adams and Ebersole 2002, Cocheret de la Moriniere et al. 2002). In addition, these fish species showing juveniles utilizing off-reef habitats (i.e., mangroves and seagrass) as nursery areas, display ontogenetic habitat shifts or post-settlement life cycle migrations (PLCMs, Cocheret de la Morinière et al. 2002) in which they progressively migrate to coral reefs as adults (Parrish 1989; Jones 1991; Eggleston 1995; Dahlgren and Eggleston 2000). Such habitat shifts are commonly inferred through the size or age structure of populations in different habitats over time (Jones 1991). Furthermore, juveniles are able to select particular habitat conditions based on the "minimize μ/g hypothesis" which establishes that juveniles maximize growth rate and minimize risk of predation (Werner and Gilliam 1984).

Despite that mangroves and seagrass beds harbour high densities of juvenile commercially important fishes, it is not known to what extent the nursery production contributes to the fishery yields in coral reefs (Roberts 1996; Beck et al. 2001; Gillanders et al. 2003). In the western Atlantic, many studies on fish communities from estuaries have focused on mainland coasts (Thayer et al. 1987; Ley et al. 1999), while relatively little attention has been paid to island locations (Baelde 1990; Rooker and Dennis 1991; Nagelkerken et al. 2000; Nagelkerken et al. 2002) containing non-estuarine bays and lagoons in Caribbean islands (Nagelkerken and van der Velde 2002). Few studies have attempted to study fishes from mangroves, seagrasses and shallow reefs simultaneously (Nagelkerken et al. 2000; Murphy 2001; Cocheret de la Morinière et al. 2002), and some

studies used more than one methodology to compare these habitats (Thayer et al. 1987; Acosta 1997).

The habitat connectivity has been recently a matter of concern for designing and implementing no-take marine reserves (NTMRs), as an attempt to set up ecologically meaning conservation and management regulations in the western Atlantic (Appeldoorn et al. 2003; Friedlander et al. 2003; Sale and Ludsin 2003; Mumby et al. 2004). An increasing interest on marine protected areas (MPAs), and specifically no-take marine reserves (NTMRs) as management tools, has been adopted for compensating the stock collapses (Roberts and Polunin 1991; Roberts et al. 2003; Lubchenco et al. 2003). While the idea of using NTMRs is not new (Guénette et al. 1998), it is relatively recent that their use has not only been scientifically supported (Roberts et al. 2001; Gell and Roberts 2003), but also socially adopted (Ballantine 1995). The main goal of NTMRs is to put aside one specific portion of the marine ecosystem from exploitation, including not only the marine organisms but also associated habitats (Lubchenco et al. 2003). In terms of biology and conservation, NTMRs can only be effective if the different life stages of the species under exploitation are fully protected either within one, large area or within a series of smaller areas representing connected habitats through the movement of fishes. Two of the most basic tenets of NTMR design are that all habitats have to be represented and the reserve network be self-sustained (Ballantine 1995). Therefore, optimal design of NTMRs must include habitats essential for fishes to complete their life stages (i.e., from larval settlement to adulthood). In order to link habitat types with fish communities it is necessary to identify habitat requirements for fish species according to life stage (e.g.,

juveniles and adults), their dispersal range and pathways, and the availability and distribution of essential (i.e., nursery, spawning) habitats (e.g., mangroves, seagrass, and shallow-water coral reefs) within the areas to be protected (Lindeman et al. 2000).

Although the fish community of southwestern Puerto Rico has been extensively studied (Austin 1971; Austin and Austin 1971; Kimmel 1985; Rooker and Dennis 1991; Dennis 1992; McGehee 1994; Acosta 1997; Appeldoorn et al. 1997; Murphy 2001; Foley 2003; Christensen et al. 2003), little information is available analyzing the relative importance of mangroves, seagrass beds, and shallow-water coral reefs in terms of the nursery value and ontogenetic habitat shifts.

The present study aims to determine the pattern and the extent of habitat use in post-settlement reef fishes, and how these change during ontogeny, leading to a quantification of habitat connectivity. This study, planned within the context of NTMR design, focuses on the continuum of mangroves-seagrass-coral reefs to (1) offer a baseline characterization of the community structure (e.g., diversity, distribution, abundance) of the fish assemblage along an inshore-offshore, cross-shelf gradient from a bay (i.e., Montalva) to a proposed NTMR (i.e., Turrumote); (2) elucidate the nursery value of mangroves, seagrass and coral reefs for a group of selected fish species, and (3) offer evidence of ontogenetic migrations (or PCLMs) and habitat shifts. Emphasis is on the juveniles and adults of commercially (e.g., Lutjanids, Haemulids) and ecologically (e.g., Acanthurids, Scarids) important species. The study specifically addresses these goals within the context of the proposed NTMR at Turrumote Key, off La Parguera, Puerto Rico, and adjacent areas, e.g., Corral Key and Montalvo Bay, which are also

found within an existing MPA, the La Parguera Natural Reserve. The objectives of the present study are the following:

1.-To determine which fish species of commercial and ecological importance, are found in the mangrove-seagrass-coral reef continuum and how they are distributed in terms of habitat type and depth in the study area (Turrumote, Corral and Montalva Bay).

2.-To investigate if the combination of habitat and depth (i.e., strata) along the cross-shelf inshore-offshore gradient differs in terms of proportional abundance of juveniles and density of juveniles of commercially and ecologically important fishes.

3.-To examine if there is any connectivity among strata and biotope (i.e., mangroves, seagrass, shallow coral reefs) based on ontogenetic habitat shifts.

Chapter 2 is a baseline characterization of the ichthyofauna associated with the inshore-offshore, cross-shelf gradient from a bay to corral reefs, and outlines the spatial distribution and community structure (e.g., diversity, density) of commercially (e.g., Haemulids, Lutjanids) and ecologically (e.g., Acanthurids, Scarids) important fishes, identifying which species are associated to which habitat and the degree of utilization patterns.

Chapter 3 investigates variations in the proportional abundance of juveniles and juvenile densities of reef-associated fish species in mangrove and seagrass as nurseries, and how that use differs from the use of shallow-water coral reefs, as an attempt to test the null hypothesis (H_o) that there are no differences in juvenile fish densities among mangroves and seagrass of a non-estuarine bay and shallow-water coral reefs of lagoon areas.

Chapter 4 examines whether reef-associated fishes show ontogenetic habitat shifts within a section of La Parguera shelf, specifically along the seaward gradient Montalva Bay-Corral Key-Turrumote Key by comparing site-specific size-frequency distributions to infer fish habitat transitions and potential distance of movement using cluster analyses.

Chapter 5 provides a general discussion of those three chapters, and additionally elucidates the relative importance and nursery value of mangroves, seagrass in relation to the post-settlement life cycle migrations or ontogenetic migrations of fishes in the Caribbean and the usefulness of a better comprehension of ecological interrelationships in these habitats for the implementation of marine reserves.

CHAPTER 2: SPATIAL DISTRIBUTION OF MARINE FISHES ALONG A CROSS-SHELF GRADIENT CONTAINING A CONTINUUM OF MANGROVE-SEAGRASS-CORAL REEFS IN SOUTHWESTERN PUERTO RICO

INTRODUCTION

Tropical marine ecosystems in coastal areas experience multiple underlying processes in structure and composition at different spatial and temporal scales (McCoy and Heck 1976; Birkeland 1997; Hubbard 1997). Shallow coastal areas containing mangroves, seagrass and coral reefs are among the most diverse and productive in the world (Beck et al. 2001; Valiela et al. 2001; Gillanders et al. 2003). Fish assemblages associated with these areas vary greatly at several spatial scales (Nagelkerken et al. 2000; Christensen et al. 2003).

The spatial habitat characteristics of shallow coastal areas represent a mosaic of substrates potentially offering many benefits to fishes according to species, life history traits, and life stage (Sale 1991; Jones and McCormick 2002). Patterns of reef fish distribution in mangroves, seagrass beds and shallow-water coral reefs may result either from behavioral responses to preferred habitats in terms of resource availability (e.g., space, shelter, food; Jones 1991) and reproduction (Robertson 1991) or ecological interactions, such as differential survival among different habitats through predation and competition (Hixon 1991; Roberts 1996).

While many studies on the fish communities of mangroves, seagrass, and coral reefs are available for the western Atlantic (Thayer et al. 1987; Baelde 1990; Sedberry and Carter 1993; Ley et al. 1999), the vast majority are concentrated on continental coasts

and examine the fish community of either one or two biotopes (e.g., mangrove, seagrass) at a time using different methodologies (e.g., fish collection and underwater visual censuses [UVC]). Relatively few studies from Caribbean islands (e.g., Curaçao and Bonaire) have attempted to explicitly delineate the fish community from the mangrove-seagrass beds-coral reefs along a continuum (Nagelkerken et al. 2000; Cocheret de la Morinière et al. 2002).

Whereas the fish community of southwestern Puerto Rico has been extensively studied (Austin 1971; Austin and Austin 1971; Kimmel 1985; Rooker and Dennis 1991; Dennis 1992; McGehee 1994; Acosta 1997; Appeldoorn et al. 1997; Murphy 2001; Christensen et al. 2003; Foley 2003), the spatial distribution of marine fishes along a cross-shelf, inshore-offshore gradient, including the mangrove-seagrass bed-coral reef continuum, and the processes that underlie these, have not been fully elucidated. One factor contributing to this has been the bias resulting when multiple survey methods are used. A major effort was devoted by Kimmel (1985), who developed a novel methodology of underwater visual census for characterizing various fish assemblages off La Parguera, and identified at least 3 groups of fishes: (1) associated with most coral reefs, (2) associated with few coral reefs, (3) associated with non-reef biotopes (e.g., inshore, lagoon, seagrass, mangroves).

The present study in southwestern Puerto Rico compares the spatial distribution and community structure (e.g., density, species richness, diversity) of fish species commonly associated with coral reefs, but along a inshore-offshore gradient having a component containing a mangrove-seagrass-coral reef continuum (i.e., Montalva Bay-Romero) and another component with absence of mangroves but having mostly coral

reefs (i.e., Corral-Turrumote). I tested the null hypothesis that no difference in the community structure and spatial distribution of fishes among these components occurred.

MATERIALS AND METHODS

Study site

The study was conducted at the eastern part of La Parguera, southwestern shelf of Puerto Rico from January 2003 to May 2004. This shelf has a complex physiography, including submerged and emergent reefs (Morelock et al. 1977) and a variety of biotopes (e.g., mangroves, seagrass beds, algal plains, sandy-mud lagoons, and patch reefs) (Kimmel 1985). Selected locations of study, along an inshore-offshore gradient and including the mangrove-seagrass-coral reef continuum, were Montalva Bay, Romero Key, Corral Key, and Turrumote (Fig. 1). Reasons for selection of such locations were based on the presence of a proposed marine reserve offshore (i.e., Turrumote) and the proximity of this reserve to bay (i.e., Montalva) and shallow-water coral reefs. Montalva Bay (17° 57’ 55” N; 66° 59’34” W) is a non-estuarine, coastal system (3.7 km^2) fringed by mangroves (*Rhizophora mangle* predominantly) and shallow water areas (i.e., sand, mud), covered with seagrass beds (*Thallassia testudinum* predominantly). Romero Key (17° 56’ 52” N; 66° 59’48” W), located 2.3 km from shore and at the entrance of Montalva bay, is an emergent reef (0.7 km^2) with relatively small mangrove areas (i.e., prop-root areas not sufficient to be surveyed in this study) and shallow reef and seagrass bed areas (*Thallassia testudinum*, predominantly). Corral Key (17° 56’ 43” N;67° 00’34” W), located 2.9 km from shore and off Montalva Bay, is also an emergent reef (1.5 km^2) with shallow coral reefs and seagrass beds (*Thallassia testudinum*, predominantly) and

little mangrove areas (i.e., prop-root areas not in water as to be surveyed). At the end of the inshore-offshore gradient lies Turrumote (17° 56' 12" N; 67° 01'09" W), in which there is a proposed marine reserve (7.6 km^2). This little emergent Key (0.1 km^2) is located at mid distance between the coastline and the insular shelf edge (4.6 km) and its reef system is composed of emergent coral reefs and several submerged reefs with an extensive hard ground, low relief platform. It has no mangrove areas, a very small patch of seagrass (16 m^2), and mostly shallow and deeper coral reefs; in addition, it has profuse soft-coral (e.g., gorgonians) areas.

Study design

A stratified sampling procedure was applied to investigate the variability of fish densities along the mangrove-seagrass-coral reef continuum following an inshore-offshore gradient. Based on the presence (or absence) and the proximity of mangrove habitats in relation to the location of the proposed marine reserve in Turrumote Key, at least two segments along the gradient were arbitrarily recognized to determine differences or similarities in their corresponding fish community assemblages: Montalva-Romero and Corral-Turrumote. At each location, 2 to 4 major strata were selected according biotope (e.g., mangrove, seagrass, coral reef), depth (e.g., shallow: 0-3 m, deep: 3-10 m) and wave exposure (e.g., fore reef, back reef). At each stratum, 3 sites were randomly selected and located at the eastern, middle and western parts of each stratum to cover a greater extent. At each site, 10 transects (i.e. 100 m^2) were sampled, totaling for 1 000 m^2 per site or 3 000 m^2 per stratum (see Table 1).

Fish censuses

The community structure of non-cryptic, diurnally active reef fishes in the mangrove-seagrass-coral reef continuum was surveyed using an adaptation of the underwater visual census (UVC) based on belt-transects (Brock 1954). This is a non-destructive technique for estimating reef fish populations that enables the researcher to select specific species, requires only one worker, and is relatively rapid and inexpensive (Fowler 1987; Bellwood and Alcala 1988). Potential disadvantages of the UVC include variations in duration and swimming speed (Kimmel 1985; Lincoln Smith 1988), fish length estimation, species identification, and fish behavior (Brock 1982), and transect width (Cheal and Thompson 1997). Despite these potential disadvantages, the UVC allows for the rapid estimates of relative abundance, biomass, and length frequency distributions of reef fishes. For this reason, UVC is the most practical and extensively technique used to study a wide range of demersal species taken by shallow-water fisheries on coral reefs (Nagelkerken et al. 2000; Appeldoorn et al. 2003).

For the present study, the selected transect dimension was 25 m length by 2 m from each side of the transect line (25 x 4 m). Such a dimension was chosen for 3 reasons: (1) it immediately rendered an area of 100 m^2 per replicate (i.e., transect), (2) comparisons with previous works could be made, and (3) it was amenable for use at the three biotopes selected (i.e., mangroves, seagrass, and coral reefs). Duration of transect survey (i.e., fish count) was standardized to less than 20 min per transect, and the censuses were conducted at least 15 min after laying down the transect line on the bottom to allow normal fish community behavior to resume after setting the line on the bottom. SCUBA was used in deeper locations (> 5 m), while snorkeling was used during shallow

surveys (< 5 m), mainly in the mangrove prop-roots and seagrass beds. Transect surveys were conducted diurnally from 8:00 to 12:00 hrs. Transect width in the mangrove prop-roots was adapted as much as possible to the selected transect dimension, but in some instances was less than 2 m to each side of transect line. Fishes included were only those entering the transect area. Individuals of all recognizable, non cryptic (with some exceptions, Grammatidae, Holocentridae), and diurnally active species were recorded. Species of *Eucinostomus* (Gerreidae) were not easily to identify, thus they were pooled as *Eucinostomus* spp. Similarly, some juveniles of Haemulidae that were not properly identified to species were pooled as *Haemulon* spp. Nomenclature for species followed that of Eschmeyer (1998). For schooling fishes (e.g., *Haemulon flavolineatum*, *Acanthurus coeruleus*, *Lutjanus apodus*) forming groups of more than 50 individuals, previous essays were performed to calibrate estimation of number of individuals by using counting techniques for shorebirds (Haig 2004).

Statistical analysis

Fish species density, relative abundance, and diversity were estimated per stratum (e.g., Mangrove Inside, Shallow Back Reef-Romero) and biotope (e.g., mangrove, seagrass). Species diversity was calculated from the Shannon-Weaver Diversity index (Ludwig and Reynolds 1988), $H' = \Sigma P_i \ln P_i$, where P_i is the proportion of the total number of individuals occurring in species i, while evenness (J') was calculated accordingly, $J' = H' / \ln S$, where S is the total number of species (Pielou 1977). Fish densities were calculated as the total number of individuals per species divided by the total area surveyed per stratum (i.e., 3 000 m^2) and expressed per 100 m^2, while relative

species abundances (%) were calculated as the proportion of all individuals for each species divided by the total individuals per stratum. Normality was determined using Kolmogorov-Smirnov 1-sample test after square root data transformation (Sokal and Rohlf 1995). To compare fish densities, abundance, and species richness among strata and biotope, a one-way ANOVA was used, while a Tukey-Kramer HSD (Honestly Significant Difference) test was used for multiple comparisons ($\alpha = 0.05$).

Cluster analysis, performed after square root transformation using the Multivariate Statistical Package (MVSP ©), was used to compare mean fish densities for each stratum along the inshore-offshore, cross-shelf gradient. The nearest neighborhood method was used in combination with the Bray-Curtis coefficient. A Detrended Correspondence Analysis (DCA) was done on square root transformed mean fish densities using the MVSP program to study the spatial distribution of fish and associations among strata along such a gradient.

RESULTS

A total of 52 138 fishes were recorded, along an inshore-offshore, cross-shelf, gradient (i.e., along the 16 selected strata), representing 102 species and 2 groups (*Eucinostomus* spp. and juvenile *Haemulon* spp.) belonging to 32 families (Table 2, 3). At the Montalva-Romero segment, 25 736 individuals (94 species, 2 groups, 29 families) were identified, while at the Corral-Turrumote segment, 26 402 individuals (93 species, 2 groups, 28 families) were found.

One-way ANOVA revealed significant differences in mean fish density among strata along the inshore-offshore, cross-shelf gradient ($F_{15, 464} = 36.04$, $p < 0.0005$; Fig. 2,

Table 6). Mean densities at SFR and DFR Romero were significantly higher (Tukey-Kramer HSD) compared to the rest of strata along the gradient. Mean densities of mangroves and seagrass strata at Montalva Bay were comparable to those at SBR and DFR Turrumote, but lower to those of Romero; the lowest densities were found in mangroves and seagrass of Montalva Bay and seagrass of Romero and Corral.

At least 17 fish species in 7 families were among the most common in terms of relative abundance, representing 76 % of the total individuals along the inshore-offshore gradient (Table 4). At least 15 species represented 71% of the total abundance at Montalva-Romero and the 75% at Corral-Turrumote (Table 5). Numerically dominant families along the inshore-offshore gradient included Haemulidae, Pomacentridae, Scaridae, Labridae, Lutjanidae, and Acanthuridae (Figure 3a, b). The fish assemblage at Montalva-Romero was dominated ($N/100m^2$) by Haemulidae (11.8), Scaridae (8.2), Pomacentridae (8.8), Acanthuridae (3.7), and Lutjanidae (3.4) (Table 2; Fig. 3a). Dominant species ($N/100m^2$) were *H. flavolineatum* (4.8), *Sc. taeniopterus* (2.7), *H. plumieri* (2.24), *S. dorsopunicans* (2.11), and *H. sciurus* (2.08) (Figure 4a). Haemulidae dominated not only in the mangroves but also in the seagrass beds, either inside or outside Montalva Bay. Lutjanidae dominated mostly the mangroves, with *Lutjanus apodus* (inside: mean ± SE = 0.24 ± 0.8; outside: 0.59 ± 3.1) as main species, and Scaridae in the seagrass beds with *Sc. taeniopterus* as main species (inside: 0.23 ± 3.6; outside: 0.65 ± 5.5).

In Romero Key, the seagrass was dominated by Haemulidae and Scaridae, with *H. flavolineatum* (mean ± SE = 0.33 ± 2.1) and *S. atomarium* (Scaridae, 0.32 ± 0.9) as the main species (Table 2; Fig. 4a). In shallow coral reefs (0-3 m deep), the back reef (SBR)

was dominated by Haemulidae and Pomacentridae, with *H. flavolineatum* (1.2 ± 22.9) and *S. dorsopunicans* (0.46 ± 1.2) as main species, while the fore reef (SFR) was dominated by Pomacentridae, Scaridae, and Labridae, with *T. bifasciatum* (0.67 ± 1.5), *S. dorsopunicans*, (0.60 ± 1.2), and *S. viridae* (0.54 ± 1.4), as main species. The deep fore reef (DFR, 3-10 m) was dominated by Haemulidae and Pomacentridae, with *H. chrysargyreum* (Haemulidae, mean ± SE = 0.74 ± 14.8), *T. bifasciatum* (0.52 ± 1.0), *A. saxatilis* (0.46 ± 1.6), and *S. dorsopunicans* (0.44 ± 0.7), as main species (Table 2; Fig. 4a).

Pomacentridae, Scaridae, and Labridae dominated at the Corral-Turrumote component (Table 3, Fig. 3b), with *T. bifasciatum* (3.28), *S. dorsopunicans* (2.98), and *H. bivittatus* (2.60) as dominant species (Fig. 4b). In Corral Key, *H. plumieri* (mean ± SE 0.49 ± 1.6) was dominat at the seagrass beds, while in the SBR and SFR strata *H. flavolineatum* (0.94 ± 11.8) and *T. bifasciatum* (0.48 ± 0.9) were dominant, respectively. Lastly, in DFR, *G. loreto* (0.41 ± 2.0) was dominant. In Turrumote Key, the DBR was dominated by *H. bivittatus* (0.53 ± 1.5), the SBR and SFR were dominated by *H. bivittatus* (0.39 ± 0.9) and *S. dorsopunicans* (0.49 ± 1.5), respectively, while the DFR was dominated by *S. dorsopunicans* (0.31 ± 0.8) (Table 3; Fig. 3b, 4b).

Mean diversity and mean species richness at Montalva-Romero and Corral-Turrumote components were significantly different among strata (diversity: $F_{15, 32}$= 13.96, $p < 0.0005$; species richness: $F_{15, 32} = 13.76$, $P < 0.0005$; Table 6). At Montalva-Romero, mean diversity was significantly higher at coral reefs relative to that of mangroves and seagrass beds, but it was not significantly different among these latter biotopes, while species richness in mangroves was higher than that of seagrass beds, but

lower than that of coral reefs. At Corral-Turrumote, diversity was significantly higher at coral reefs relative to that of seagrass beds, while at coral reefs it was significantly different among strata ($F_{6, 14} = 7.61$, $p < 0.001$); diversity in deep reefs was significantly higher relative to that of shallow coral reefs. Species richness of seagrass was substantially lower relative to that of coral reefs, but species richness was not significant different among coral reef strata. By comparing all the strata along the gradient from Montalva Bay to Turrumote, the species richness values in mangroves of Montalva were not significantly different to those from shallow, back and fore reefs of Turrumote, and shallow and deep fore reefs of Corral (Table 6).

Cluster analyses on mean fish densities of the more abundant species along the inshore-offshore, cross-shelf gradient, revealed a consistent spatial distribution according to biotope by separating the ichthyofauna associated with mangroves, seagrass and that of shallow (back and fore) reefs, and deep fore reefs (Fig. 6). Two major clusters could be distinguished, which corresponded to (1) mangroves and seagrass, and (2) shallow and deep coral reefs: within the former, mangroves were separate from seagrass; within the reef strata, the pattern was more complex, with clustering representing an interaction among sites, depths, and reef position. For example, shallow back reefs of Romero and Corral clustered together but were distinct from that of Turrumote. All shallow fore reef sites occurred together. The deep back reef of Turrumote was similar to that of deep fore reefs of the remaining locations, but separated from its own deep fore reef.

Detrended correspondence analysis (DCA) applied to the more abundant fish species showed a spatial pattern in density distribution (Fig. 7). Three major groupings were distinguished, which corresponded to mangroves and seagrass, shallow and deep

reefs at Romero, and shallow and deep reefs of Corral and Turrumote. In the mangroves, *Sphyraena barracuda*, *Lutjanus griseus*, *Archosargus rhomboidalis,* and *Diodon holocanthus* reached highest densities. The more dense species, such as *Haemulon flavolineatum, H. sciurus* and *Lutjanus apodus* formed the second grouping occurring at the middle of the Montalva-Romero gradient, with highest densities in mangroves and coral reefs. At the southern end of the Montalva Bay-Turrumote gradient, typical coral reef fishes, such as *Halichoeres bivittatus, Stegastes dorsopunicans, S. leucostictus,* and *Halichoeres radiatus,* reached their highest density.

Some species were restricted either to mangroves and seagrass or any stratum in coral reefs (i.e., shallow back reef, shallow fore reef and deep fore reef), while others were widespread along the gradient. In terms of relative abundance per stratum, there were some species that dominated over others. At least 9 species were restricted to coral reefs: *Chromis cyanea, Chromis multilineata, Gramma loreto, Halichoeres maculipinna, Microsphatodon chrysurus, Sparisoma aurofrenatum, Stegastes partitus, Acanthurus coeruleus* and *Thalassoma bifasciatum*. Others were restricted either to mangroves or seagrasses: *Archosargus rhomboidalis, Diodon holocanthus, Eucinostomus* spp., *Ocyurus chrysurus, Haemulon chrysargyreum, H. plumieri, H. sciurus, Sphyraena barracuda* and *Sparisoma atomarium*. At least 11 fish species of 8 families were relatively widespread along the gradient: Acanthuridae (*Acanthurus bahianus, A.chirurgus*), Haemulidae (*Haemulon flavolineatum*, Lutjanidae (*Lutjanus apodus*), Pomacentridae (*Stegastes dorsoponicans, S. leucostictus*), Scaridae (*Scarus taeniopterus, Sparisoma viridae*), Chaetodontidae (*Chaetodon capistratus*), Gerreidae (*Gerres cinereus*), and Labridae (*Halichoeres bivittatus*). However, of these 11 species, there were some species more

prominent than others in terms of relative abundance. At Montalva-Romero, *H. flavolineatum* was widespread along the strata from mangroves to SBR, but relatively absent from deeper reefs (Table 7a, b), while at Corral and Turrumote it was dominant at SBR only. *Haemulon plumieri* was dominant at seagrass, exhibiting relatively low abundance at SBR and almost absent from deeper reefs. *L. apodus* was dominant at mangroves only, and *S. dorsopunicans* was dominant at shallow and deeper reefs.

DISCUSSION

Of the approximately 693 fish taxa documented for the Puerto Rican plateau (Dennis 2000), the inshore-offshore shelf gradient in the present study from southwestern Puerto Rico represented only 16% of this total number of species (i.e., 102). Kimmel (1985), using a novel UVC methodology, found 250 species but over a greater area of coverage, and including cryptic fish species (e.g., gobiids, bleniids). Another study, also covering a greater extent and using a combination of gillnets and UVCs, recorded 86 and 56 species, respectively (Acosta 1997). A more recent study (Christensen et al. 2003) using only UVC, on the shelf off La Parguera, documented 123 species; however, they also included many cryptic species.

In the present study, the inshore-offshore shelf gradient containing a mangrove-seagrass-coral reef continuum, revealed an unequal spatial pattern in the distribution of fish communities. There were significant differences in community structure and spatial distribution of fishes among mangroves, seagrass beds, and coral reefs. Furthermore, the fish community structure at Montalva-Romero was relatively different in terms of species composition and density to that of Corral-Turrumote. The fish communitiy inside the

Montalva Bay, i.e., mangroves and seagrass, was typical of that found in other inshore areas of the western Atlantic (e.g., Curaçao, Bonaire, Nagelkerken et al. 2000; Belize, Sedberry and Carter, 1993; and Florida, Thayer et al. 1987; Ley et al. 1999), and was characterized by Haemulidae, Lutjanidae and Sphyraenidae. On the other hand, in Corral-Turrumote, which is relatively distant (~ 2 km from the shoreline inside Montalva Bay) and characterized by emergent reefs with negligible (i.e. Corral) to complete absence (i.e. Turrumote) of mangrove prop-root areas, the fish community was comprised by typical fish species of families more commonly associated with coral reefs, such as Pomacentridae, Labridae, Scaridae and Acanthuridae

Kimmel (1985) found 3 species-groups of fishes according to their habitat associations and occupying characteristic biotopes along the La Parguera shelf; however, the ichthyofauna can be divided into reef and non-reef assemblages. Whereas spatial overlap persists for many species, less intra- than inter-biotope variability exists for respective fish distributions. Kimmel (1985) found that non-reef biotopes (i.e., mangroves and seagrass) presented characteristic species due to the attributes provided by these biotopes; however, these biotopes often contained species more representative of coral reefs, since the latter biotopes may exhibit a nursery function for coral reef fishes.

Based on the species groups that Kimmel (1985) elucidated for the fish assemblages off La Parguera, the more abundant species found in this study for the Montalva Bay-Romero segment (e.g., *H. flavolineatum*, *S. taeniopterus*, *H. plumieri*, *H. sciurus*), belong to the Kimmel's category of ubiquitous or associated with most coral reefs, with one exception (i.e., *S. dorsopunicans*) allocated in the category of associated with few coral reefs. In the segment Corral-Turrumote, most species (e.g., *T. bifasciatum*,

H. flavolineatum, *Sc. taeniopterus*) fell into the first category with two exceptions (i.e., *S. dorsopunicans*, *H. bivittatus*) allocated in the next category. In the case of the next Kimmel's category (i.e., non-reef biotopes), at least 5 species (e.g., *L. griseus*, *S. testudineus*, *A. rhomboidalis*, *G. cinereus*, *H. parrai*) and the *Eucinostomus* species complex, were found mainly at mangroves and seagrass of Montalva Bay.

At Montalva-Romero, the fish community of SFR-Romero showed the highest density relative to the other strata and locations, followed by DFR-Romero, while at Corral-Turrumote, the fish community of SFR-Corral exhibited the highest density compared with the remaining strata, followed by DBR-Turrumote. In terms of species richness, SFR-Romero showed higher values relative to the remaining strata in the Montalva-Romero component, while DFR-Corral exhibited higher values compared to other strata in the Corral-Turrumote component. As expected, the mean fish density, mean species richness, and diversity along the cross-shelf gradient was higher at coral reef stratum relative to mangroves and seagrass strata. However, the total species richness in mangroves was as high as that of SFR-Corral, and SBR and SFR of Turrumote. The total density of these latter strata was twice as high as that of mangrove stratum. Plausible reasons explaining highest fish densities in coral reefs compared to mangroves and seagrass are that coral reefs offer greater structural complexity and availability of shelter (Roberts and Ormond 1987; Friedlander and Parrish 1998). Likewise, among the possible reasons for comparable species richness between mangroves and shallow (back and fore) reefs is the structural complexity of the mangrove prop-roots. Cocheret de la Morinière et al. (2004), working in Curaçao, argued that the attractiveness of mangrove vegetation for

some reef associated fish species may be influenced by the structural complexity of the habitat along with the availability of shade.

Some fish species were more widespread than others, which may be explained by life stage (i.e., juvenile or adult) and associated preferences for certain habitats in relation to shelter, food availability, and reproduction. Most species of Haemulidae and Lutjanidae were widespread regardless of habitat type along the cross-shelf, inshore-offshore gradient, while most species of Acanthuridae, Scaridae, Pomacentridae, and Labridae were commonly associated to shallow (back and fore) and deep reefs. In terms of habitat use along the cross-shelf gradient, *H. flavolineatum* was the most widely distributed fish species, being found in most of the strata in high relative abundances.

Other species showed restrictions for certain strata or biotopes, either exclusively at coral reefs or mangroves and seagrass, or a combination. Among Pomacentridae and Labridae, *Stegastes dorsopunicans* and *S. leucostictus*, and *Halichoeres bivittaus* were found in mangroves and seagrass, but in relatively low abundance compared with that of coral reefs.

Among commercially important fish species, notable was the almost complete absence of serranids. *Cephalopholis cruentata* and *Epinephelus guttatus* were the only commercially important serranids found in this study, with the former being in low abundance preferentially at deep coral reefs of Corral; but at least three individuals recorded from mangrove, whereas the latter accounting just for two individuals offshore (i.e., Turrumote). Among Lutjanidae, *Ocyurus chrysurus* is considered the most commercially important snapper (i.e., landed weight) in Puerto Rico (Matos–Caraballo 2002); however, it represented only 20% of all lutjanids recorded. *Lutjanus apodus* (53%)

was the most abundant lutjanid, but its commercial value is not as high as that of *O. chrysurus*. Probable reasons for absence of some serranids and the relatively low abundance of some snappers may be related to their preferences for outer regions of the shelf, avoidance behavior, and overfishing.

In general, this study of the cross-shelf, inshore-offshore gradient, in southwestern Puerto Rico showed that the patterns of habitat use by the fish community are species specific and related to habitat type (i.e., mangrove, seagrass, reef), with habitat use or location being limited for some species and wider for others. Another important aspect revealed in this study is the versatility of working at the species level, rather than family level only (e.g., Christensen et al. 2003), for better elucidation of the differential habitat use for fish species within the same family. In locations west of my study area(e.g., Collado, Pelotas), Murphy (2001) found that fish communities along the continuum of mangrove-seagrass-shallow were not uniformly structured, but instead varied species composition and life stages according to features of the physical environment. Such variations were evident between small-scale structural attributes of the substratum (i.e., habitat types) and on a large scale between shelf locations that vary in depth, exposure to currents, and distance from shore (i.e., geomorphic zones). Similar results in relation with associations of fish communities with variable shelf locations and exposure to currents were revealed by Foley (2003). Christensen et al. (2003), working at larger dimensional scales in southwestern Puerto Rico, found distinct patterns of habitat use across the seascape, indicating that habitat type was more important than cross-shelf location for determining spatial patterns in fishes at the family and generic levels. However, patterns within and among species may be more complex.

The patterns of fish community structure along the mangrove-seagrass-coral reef continuum and adjacent areas (i.e., Corral-Turrumote) examined in this study did not consider species life stages (i.e., juvenile, adults) and associated interactions during processes such as post-settlement, migration, and differential mortality. High densities observed in Romero may reflect the presences of both, juveniles and adults; obviously, because of cumulative mortality, it is expected to be more juveniles than adults. There is the possibility that Romero is located in a transition point in terms of fish densities in between Montalva Bay and Turrumote (including Corral) since the latter location exhibited the highest density at the shallow fore reef (SFR). Determination of habitat use patterns according to life stages along a cross-shelf, inshore-offshore gradient is needed to understand the relative value of habitats in terms of nursery areas or the possibility of ontogenetic shifts in habitat requirements by looking at changes in fish size structure. It would then be possible to infer degrees of habitat connectivity by species migrating among habitats during post-settlement ontogeny (Lindeman et al. 2000; Nagelkerken et al. 2000; Appeldoorn et al. 2003). Knowing the nursery value of various habitats and ontogenetic migration routes (Appeldoorn et al. 1997; Lindeman et al. 2000; Cocheret de la Morinère et al. 2002) would facilitate conservation and management actions, such as designing no-take marine reserves (NTMRs) and improving the proposed NTMR protected areas in adjacent areas to the Turrumote Key.

Conclusions

1) There were significant differences in community structure and spatial distribution of fishes among mangroves, seagrass beds, and coral reefs. The fish community structure at Montalva-Romero was relatively different in terms of species composition and density to that of Corral-Turrumote. At the former, the more abundant fish families were Haemulidae, Lutjanidae, and Sphyraenidae, while at the latter were Pomacentridae, Labridae, Scaridae, and Acanthuridae

2) Fish mean densities at mangroves and seagrass strata of Montalva Bay were comparable to those at SBR and DFR Turrumote, but lower than those of Romero; while the lowest density was found in mangroves and seagrass of Montalva Bay and seagrass of Romero and Corral.

3) Most species of Haemulidae and Lutjanidae were widespread, regardless of habitat type along the cross-shelf, inshore-offshore gradient. Most species of Acanthuridae, Scaridae, Pomacentridae, and Labridae were commonly associated to shallow (back and fore) and deep reefs.

4) Notable among commercially important fish species was the almost complete absence of serranids and low abundance of some lutjanids (e.g, *Ocyurus chrysurus*).

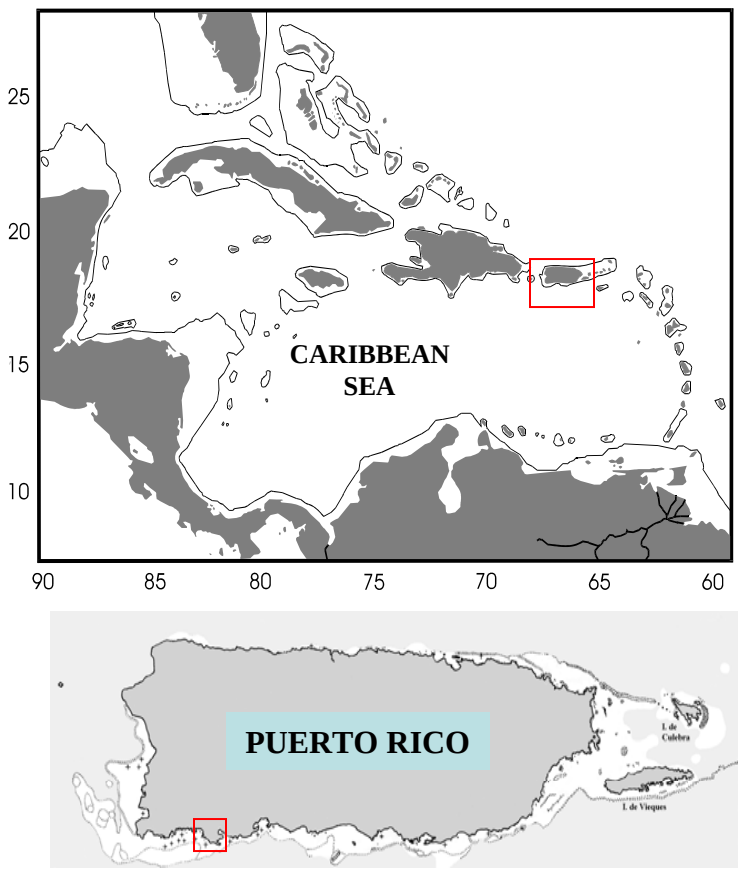
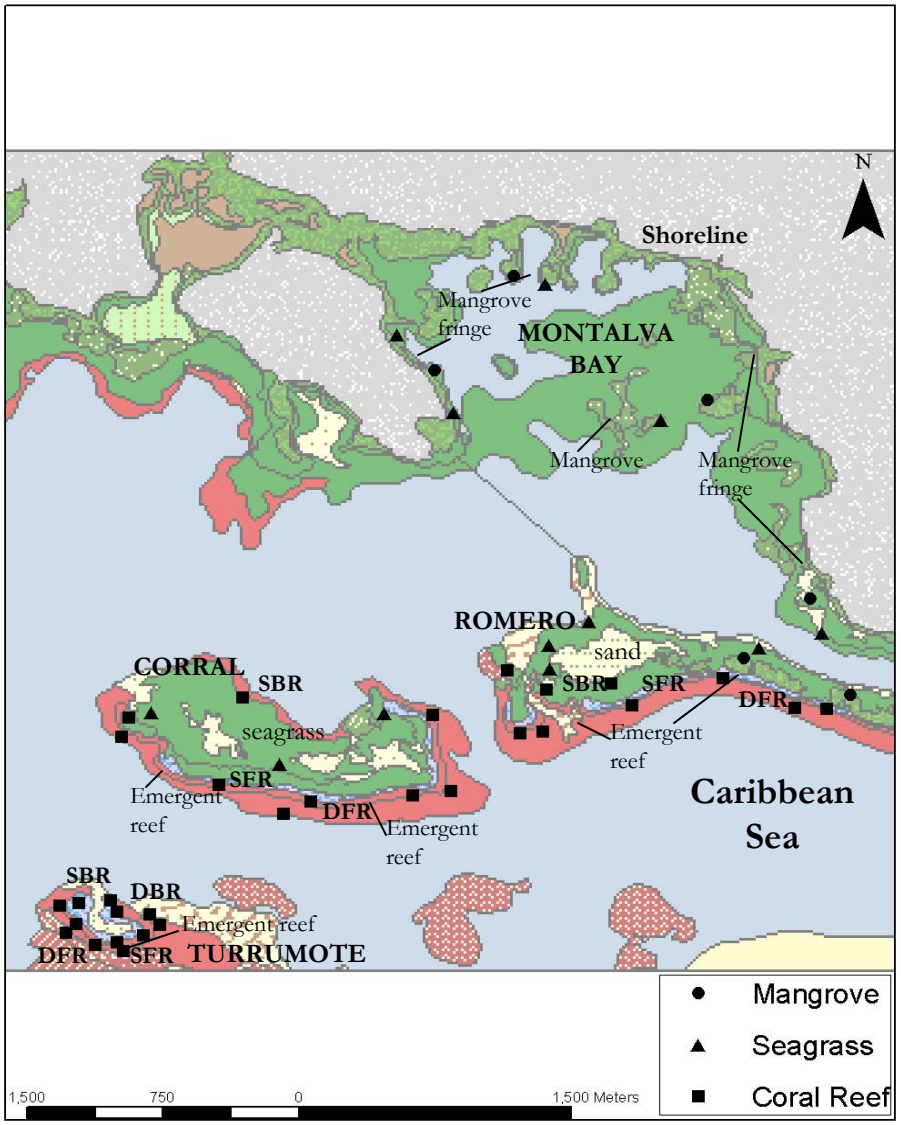


Fig. 1. Map of Puerto Rico showing study area and locations with sites in the various strata (i.e., SBR, DFR) and biotopes (i.e., mangroves, seagrass, coral reefs). SBR: shallow back reef, SFR: shallow fore reef, DFR: deep fore reef, DBR: deep back reef.



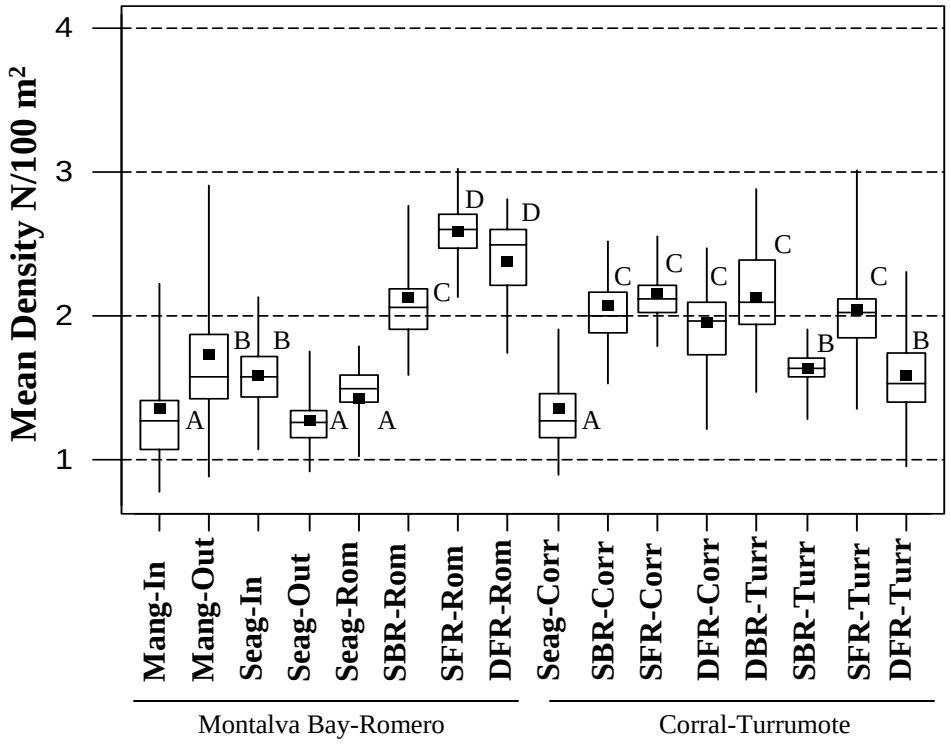


Fig. 2. Mean density of fish per stratum along the Inshore-Offshore, cross-shelf gradient from Montalva Bay to Turrumote, southwestern Puerto Rico. Groups with the same letter are not significantly different from one another as determined from the Tukey-Kramer HSD test. Little black squares denote mean values, boxes are 95% confidence limits, and lines within boxes are medians. Data were square root transformed for analysis.

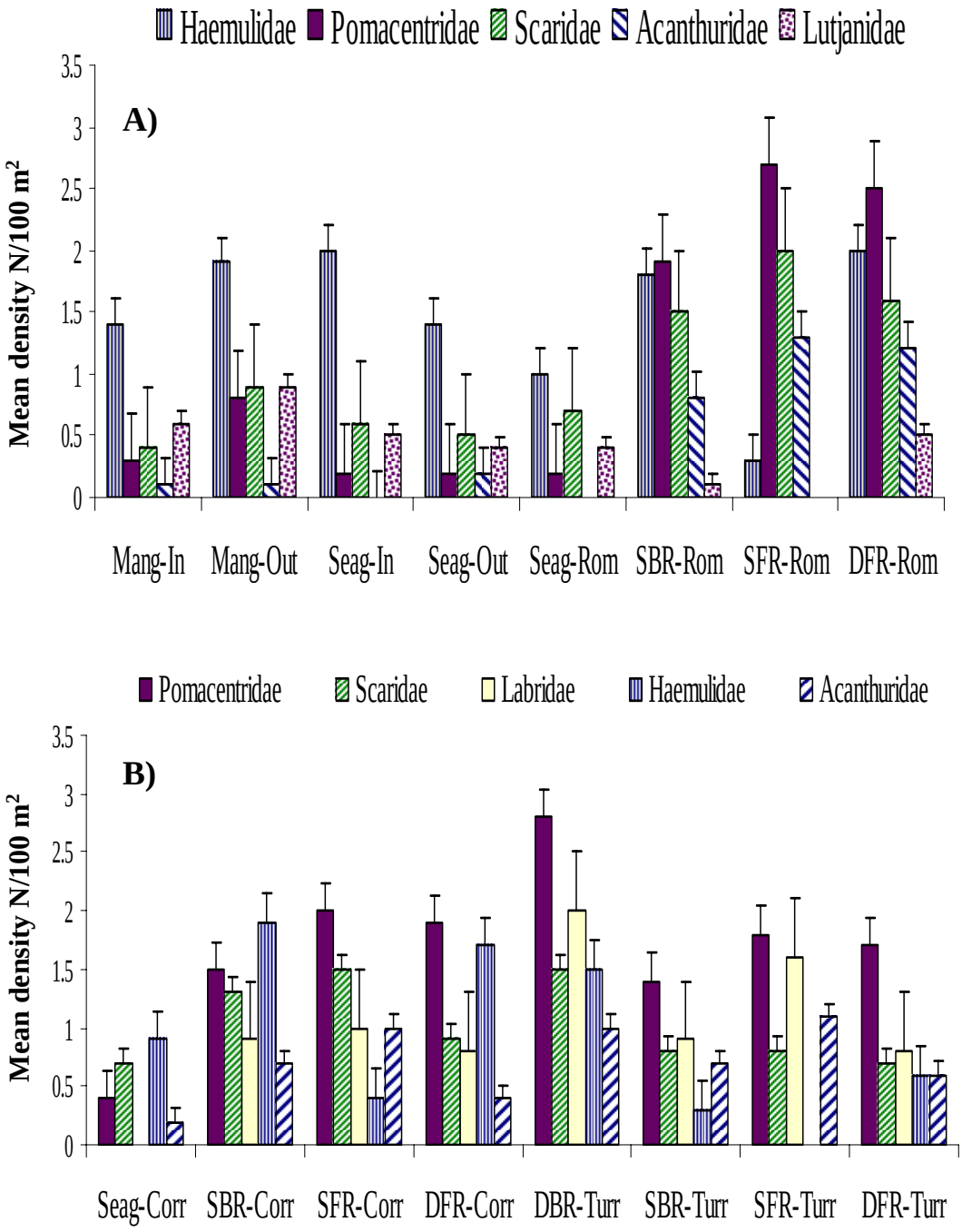


Fig. 3. Mean densities of more abundant fish families per stratum at A) Montalva Bay-Romero and B) Corral-Turrumote along the inshore-offshore, cross-shelf gradient.

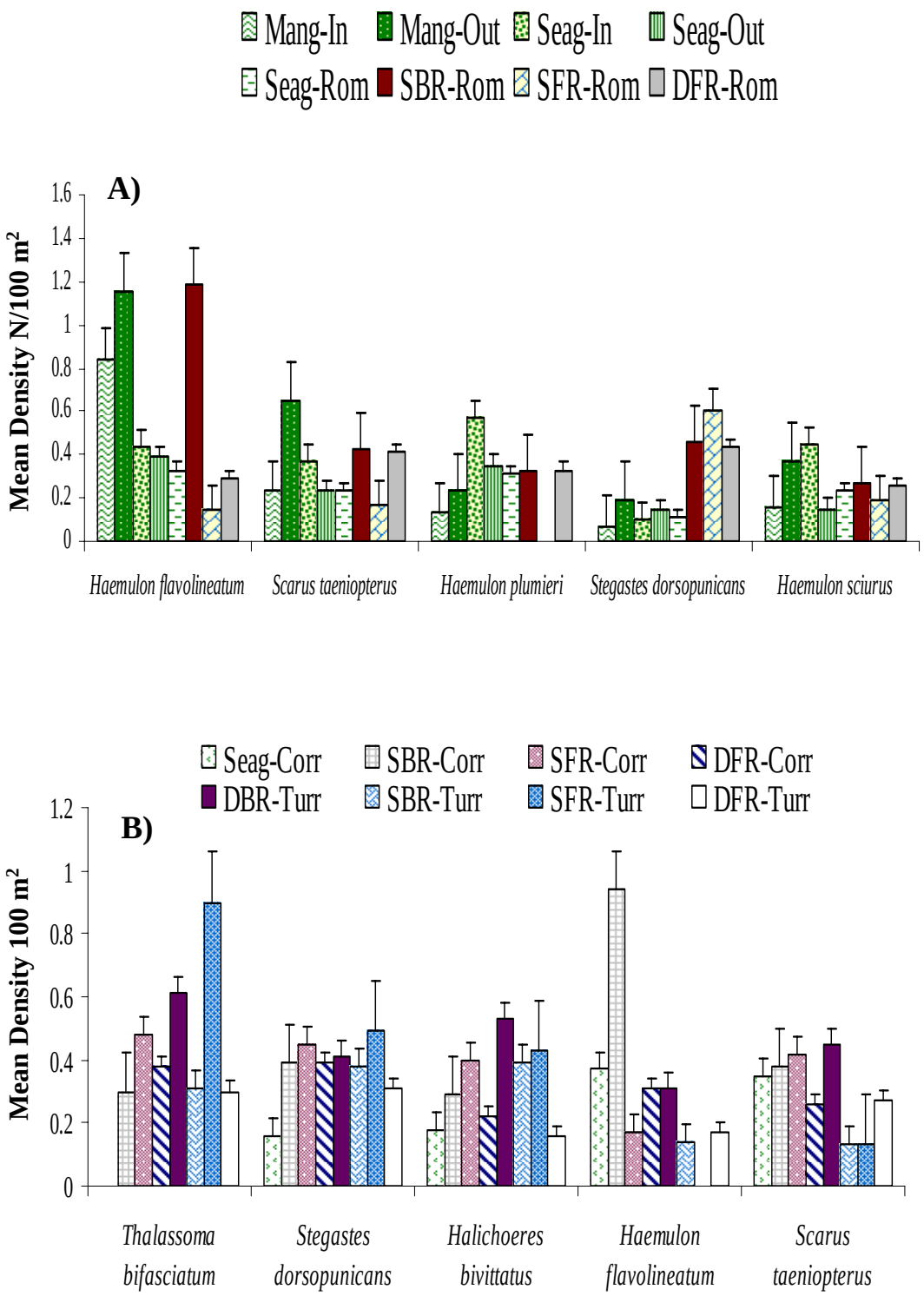


Fig. 4. Mean density of more abundant fish species per stratum at A) Montalva Bay-Romero and B) Corral-Turrumote along the inshore-offshore, cross-shelf gradient in southwestern Puerto Rico.

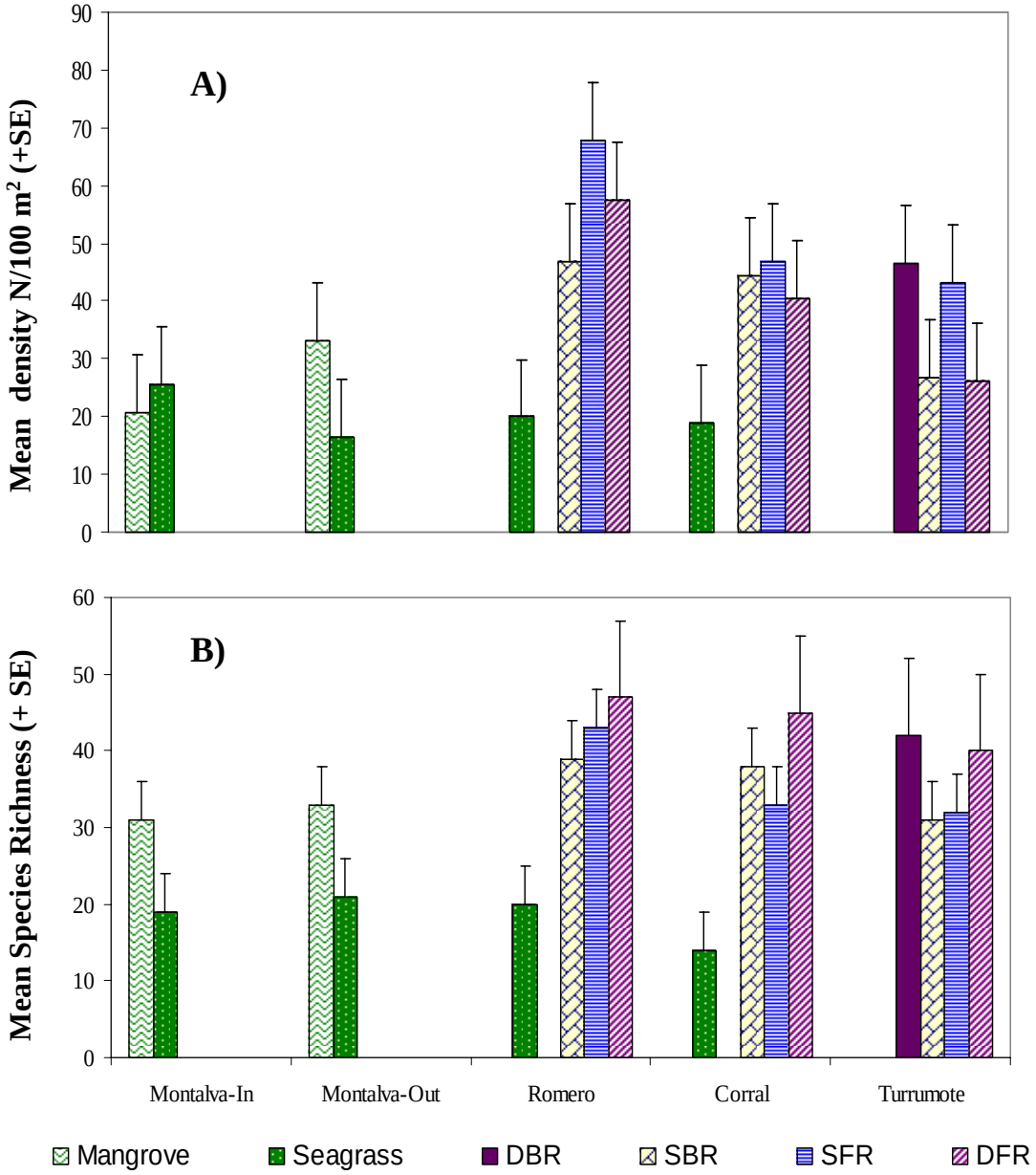


Fig. 5. A) Mean fish density and B) species richness (Nspp/100 m^2) according to location and stratum along the inshore-offshore gradient.

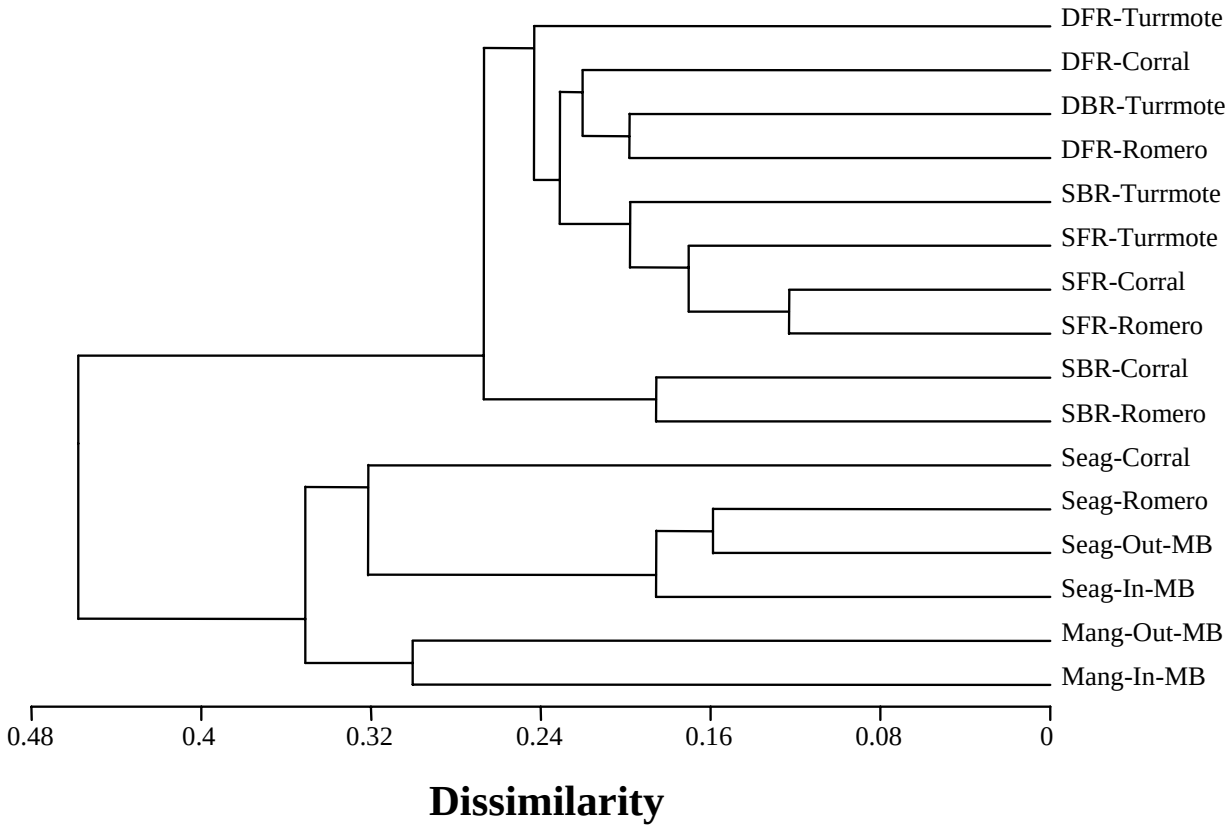


Fig. 6. Hierarchical dendrogram of cluster analysis of mean fish species densities (100 m^2) per stratum along the inshore-offshore gradient (i.e,, Montalva Bay-Turrumote) in southwestern Puerto Rico. MB: Montalva Bay, Mang: mangroves, Seag: seagrass, SBR: shallow back reef, SFR: shallow fore reef, DFR: deep fore reef, DBR: deep fore reef.

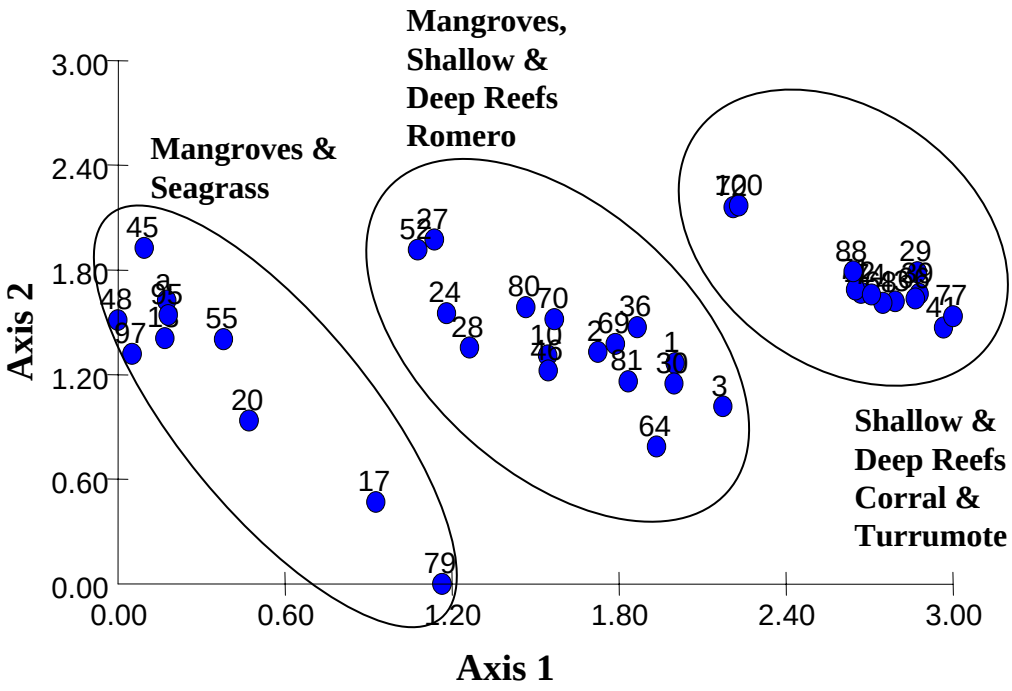


Fig. 7. Detrended correspondence analysis of square root transformed fish mean densities (N/100 m^2) of more abundant species per stratum along the inshore-offshore, cross-shelf gradient. Number codes refer to species in Tables 2 and 3, respectively.

Table 1. Sampling intensity, stratum, depth, and transect area surveyed along the inshore-offshore gradient in southwestern Puerto Rico. Every site represents 1 000 m^2 (i.e., a site is 10 transects of 100 m^2 each). In Montalva Bay, the 12 sites for mangroves and seagrass were split into 2 strata (Mang-In, Seag-In) inside the bay and 2 strata (Mang-Out and Seag-Out) outside the bay, with 3 sites per strata.

Location	**No. of Sites**	**Mangrove**	**Seagrass**	**Shallow Back Reef (SBR) 0-3 m**	**Deep Back Reef (DBR) 3-10 m**	**Shallow Fore Reef (SFR) 0-3 m**	**Deep Fore Reef (DFR) 3-10 m**
Montalva	12	6	6	-	-	-	-
Romero	12	-	3	3	-	3	3
Corral	12	-	3	3	-	3	3
Turrumote	12	-	-	3	3	3	3
Transect area (m^2)	48 000	6 000	12 000	9 000	3 000	9 000	9 000

Table 2. Mean fish density (N/m^2 ± SE) in 8 strata at the Montalva-Romero segment of the cross-shelf gradient in southwestern Puerto Rico, along a inshore-offshore gradient. SBR = shallow back reef, SFR = shallow fore reef, DFR = deep fore reef, DBR deep back reef. Depth: shallow is 0-3 m depth and deep is 3-10 m. Every stratum corresponds to 3 sites of 1 000 m^2 each (10 replicates of 100 m^2) of surveyed area 0 = species absent; + = species present in low numbers to calculate mean density (few individuals only in 1 stratum). Strata definitions in text. Numbers in bold are summed densities for all species belonging to a single family per stratum. Nomenclature follows Eschmeyer (1998).

Location	MONTALVA BAY					ROMERO		
Sites	3	3	3	3	3	3	3	3
Family/Species/Strata	Mang In	Mang Out	Sg In	Sg Out	Seagrass	SBR	SFR	DFR
Acanthuridae	**0.1**	**0.1**	**0.0**	**0.2**	**0.0**	**0.8**	**1.3**	**1.2**
1. *Acanthurus bahianus*, ocean surgeon	0	+	0	0.08 ± 0.3	+	0.25 ± 0.7	0.32 ± 0.6	0.35 ± 1.0
2. *Acanthurus chirurgus*, doctorfish	0.10 ± 0.7	0.07 ± 0.3	0.16 ± 0.6	0.14 ± 0.5	0.11 ± 0.3	0.29 ± 1.0	0.38 ± 1.1	0.37 ± 1.1
3. *Acanthurus coeruleus*, blue tang	0.04 ± 0.2	0.06 ± 0.8	0	+	0	0.22 ± 0.5	0.61 ± 1.7	0.44 ± 1.0
Aulostomidae								
4. *Aulostomus maculatus*, trumpetfish	0	0	0	0	0	+	+	0
Balistidae								
5. *Balistes vetula*, queen trigger fish	0	0	0	0	0	0	+	0
6. *Melichthys niger, black durgon*	0	0	0	0	0	0	+	0
Bothidae								
7. *Bothus lunatus*, peacock flounder	0	+	0	0	0	0	0	0
Carangidae								
8. *Caranx latus*, horse-eye jack	+	+	+	0	0	0	0	0
9. *Caranx crysos*, blue runner	0	0	0	0	0	0	0	+
Chaetodontidae	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.2**	**0.3**	**0.3**
10. *Chaetodon capistratus*, foureye butterflyfish	0.11 ± 0.5	0.08 ± 0.3	0.16 ± 0.4	0.09 ± 0.3	0.08 ± 0.2	0.18 ± 0.8	0.16 ± 0.3	0.20 ± 0.6
11. *Chaetodon ocellatus*, spotfin butterflyfish	0	0	0	0	0	0	0	+
12. *Chaetodon striatus*, banded butterflyfish	0	+	0	0	+	0.05 ± 0.3	0.11 ± 0.3	0.10 ± 0.7
Diodontidae								
13. *Diodon holacanthus*, balloonfish	0.14 ± 1.0	0.08 ± 0.3	0.06 ± 0.3	0.04 ± 0.2	0.09 ± 0.3	0.05 ± 0.3	0	0
14. *Diodon hystrix*, porcupinefish	0	+	0	0	0	0	+	0
Ephippidae								
15. *Chaetodipterus faber*, atlantic spadefish	0	0	0	0	0	0	0	0
Fistularidae								
16. *Fistularia tabacaria*, bluespotted cornetfish	0	0	0	+	0	0	0	0
Gerreidae	**0.2**	**0.2**	**0.0**	**0.6**	**0.0**	**0.5**	**0.0**	**0.0**
17. *Gerres cinereus*, yellowfin mojarra	0.06 ± 0.3	0.06 ± 0.3	0	0.14 ± 1.6	0	0.08 ± 0.4	0.14 ± 0.6	0.20 ± 0.7
a. *Eucinostomus* spp., mojarra	0.11 ± 0.4	0.17 ± 1.5	0.38 ± 1.7	0.45 ± 3.9	0.40 ± 2.0	0.38 ± 1.2	0	0
Grammatidae								
18. *Gramma loreto*, fairy basslet	0	0	0	0	0	0	0	0.40 ± 0.9
Haemulidae	**1.4**	**1.9**	**2**	**1.4**	**1.0**	**1.8**	**0.3**	**2.0**
19. *Anisotremus surinamensis*, black margate	0	0	0	0	0	0	+	0
20. *Anisotremus virginicus*, porkfish	0.07± 0.3	0.11 ± 0.6	0.08 ± 0.7	+	0	0	+	0.13 ± 0.4
21. *Haemulon aurolineatum*, tomtate	0	+	+	0.47 ± 7.6	0.18 ± 0.7	+	0	0
22. *Haemulon carbonarium*, caesar grunt	0	0	0	0	0	0	+	+
23. *Haemulon chrysargyreum*, smallmouth grunt	0	0	0	0	0	0	+	0.74 ± 14.8
24. *Haemulon flavolineatum*, french grunt	0.84 ± 10.1	1.15 ± 10.3	0.44 ± 2.1	0.39 ± 1.9	0.33 ± 2.1	1.19 ± 22.9	0.15 ± 0.5	0.29 ± 1.1
25. *Haemulon macrostomum*, spanish grunt	0	0	0	0	0	0	0	0
26. *Haemulon parrai*, sailors choice	0.04 ± 0.3	0.08 ± 0.3	0	0	0	0	+	0.23 ± 0.6
27. *Haemulon plumieri*, white grunt	0.13 ± 2.3	0.23 ± 1.6	0.57 ± 2.1	0.35 ± 1.4	0.31 ± 1.1	0.32 ± 2.0	+	0.33 ± 0.7
28. *Haemulon sciurus*, bluestriped grunt	0.16 ± 1.3	0.37 ± 2.5	0.45 ± 1.5	0.15 ± 0.7	0.23 ± 1.0	0.27 ± 1.6	0.19 ± 0.9	0.26 ± 1.0
b. *Haemulon* spp., grunts	0.23 ± 2.1	+	0	0	0	0	0	0
Holocentridae	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.1**	**0.3**
29. *Holocentrus adscensionis*, squirrelfish	0	+	0	0	0	+	0.07 ± 0.2	+
30. *Holocentrus rufus*, longspine squirrelfish	+	0.12 ± 0.7	0	+	0	0.08 ± 0.7	0.08 ± 0.3	0.09 ± 0.2
31. *Myripristis jacobus*, blackbar soldierfish	0	0	0	0	0	+	+	0.18 ± 1.1
32. *Sargocentron vexillarius*, dusky squirrelfish	0	+	0	+	0	+	+	0
Kyphosidae								
33. *Kyphosus sectatrix*, bermuda sea chub	+	0	0	0	0	0	+	0
Labridae	**0.0**	**0.2**	**0.0**	**0.0**	**0.1**	**1**	**1.6**	**1.4**
34. *Bodianus rufus*, spanish hogfish	0	0	0	0	0	0	0.07 ± 0.3	0.07 ± 0.4
35. *Clepticus parrai*, creole wrasse	0	0	0	0	0	0	0	0
36. *Halichoeres bivittatus*, slippery dick	+	0.09 ± 0.5	0.14 ± 0.3	0.09 ± 0.2	0.11 ± 0.4	0.35 ± 0.8	0.43 ± 0.8	0.37 ± 1.0
37. *Halichoeres cyanocephalus*, yellowcheek wrasse	0	0	0	0	0	0	0	0

Table 2. Cont..

38. *Halichoeres garnoti*, yellowhead wrasse	0	0.07 ± 0.6	0	0	0	+	0	0.20 ± 1.2
39. *Halichoeres maculipinna*, clown wrasse	0	0	0	0	0	0.15 ± 0.8	0.24 ± 0.6	0.18 ± 0.6
40. *Halichoeres poeyi*, blaekear wrasse	0	0	0	0	0.07 ± 0.3	0	+	0
41. *Halichoeres radiatus*, puddingwife	0	0	0	0	0	0.07 ± 0.6	0.18 ± 0.4	0.12 ± 0.4
42. *Lachnolaimus maximus*, hogfish	0	0	+	0	+	0.10 ± 0.3	0	0
43. *Thalassoma bifasciatum*, bluehead wrasse	+	+	0	0	0	0.37 ± 0.6	0.67 ± 1.5	0.52 ± 1.0
44. *Xyrichtys splendens*, green razorfish	0	0	0	0	0	0	0	0
Lutjanidae	**0.6**	**0.9**	**0.5**	**0.4**	**0.4**	**0.1**	**0.0**	**0.5**
45. *Lutjanus analis*, mutton snapper	0	0	0.08 ± 0.7	0.11 ± 0.4	0.11 ± 0.2	0.10 ± 0.4	+	0
46. *Lutjanus apodus*, schoolmaster	0.24 ± 0.8	0.59 ± 3.1	0.16 ± 0.4	0.09 ± 0.3	0.11 ± 0.3	0.13 ± 0.4	0.23 ± 0.9	0.23 ± 0.7
47. *Lutjanus cyanopterus*, cuber snapper	+	+	0	0	0	0	0	0
48. *Lutjanus griseus*, gray snapper	0.19 ± 1.7	0.16 ± 1.4	0.17 ± 0.7	0.09 ± 0.5	0.08 ± 0.6	+	0	+
49. *Lutjanus jocu*, dog snapper	0.14 ± 1.2	0	0	0	0	+	0	0
50. *Lutjanus mahogoni*, mahogany snapper	+	0.13 ± 1.0	0	0	0	0	+	0.17 ± 1.3
51. *Lutjanus synagris*, lane snapper	+	+	0	0	0	0	0	0
52. *Ocyurus chrysurus*, yellowtail snapper	0.05 ± 0.3	0.07 ± 0.4	0.14 ± 0.5	0.09 ± 0.3	0.09 ± 0.5	0.09 ± 0.5	0	0.15 ± 0.7
Mugilidae								
53. Mugil cephalus	0	+	0	0	0	0	0	0
Mullidae	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.3**	**0.0**	**0.3**
54. *Mulloidichtys martinicus*, yellow goatfish	0	+	0	+	+	0.11 ± 1.5	0.12 ± 0.5	0.11 ± 0.3
55. *Pseudupeneus maculatus*, spotted goatfish	0.04 ± 0.3	+	0.11 ± 0.5	0.06 ± 0.3	0.10 ± 0.3	0.17 ± 1.2	0	0.15 ± 0.5
Muraenidae								
56. *Gymnothorax funebris*, green moray	0	+	+	+	0	0	+	0
57. *Gymnothorax moringa*, spotted moray	0	+	0	0	0	0	+	0
Ophichthidae								
58. *Myrichthys breviceps*, sharptail eel	0	0	0	0	0	0	0	0
Pempheridae								
59. *Pemperis shomburgki*, glassy sweeper	0	0	0	0	0	0	0	0
Pomacanthidae								
60. *Pomacanthus arcuatus*, grey angelfish	0.05 ± 0.7	0	0	0	0	0	+	0.06 ± 0.5
61. *Pomacanthus paru*, french angelfish	+	+	0	0	0	0	+	+
62. *Holacanthus ciliaris*, queen angelfish	0	+	0	0	0	0	+	0
63. *Holacanthus tricolor*, rock beauty	0	0	0	0	0	0	0	0
Pomacentridae	**0.3**	**0.8**	**0.2**	**0.2**	**0.2**	**1.9**	**2.7**	**2.5**
64. *Abudefduf saxatilis*, sergeant major	0.06 ± 0.3	0.10 ± 0.6	0	0	0	0.27 ± 0.9	0.61 ± 1.7	0.46 ± 1.6
65. *Abudefduf taurus*, night sergeant	0	0	0	0	0	0	+	0
66. *Chromis multilineata*, brown chromis	0	0	0	0	0	+	0.38 ± 1.1	0.44 ± 1.9
67. *Chromis cyanea*, blue chromis	0	0	0	0	0	0	0	+
68. *Microsphatodon chrysrurus*, yellowtail damselfish	0	0	0	0	0	0.25 ± 0.7	0.54 ± 1.1	0.32 ± 0.9
69. *Stegastes dorsopunicans*, dusky damselfish	0.07 ± 0.4	0.19 ± 1.2	0.10 ± 0.8	0.14 ± 1.3	0.11 ± 0.5	0.46 ± 1.2	0.60 ± 1.2	0.44 ± 0.7
70. *Stegastes leucostictus*, beaugregory	0.06 ± 0.3	0.15 ± 0.8	0.09 ± 0.3	0.12 ± 0.3	0.12 ± 0.4	0.28 ± 0.9	0.23 ± 0.8	0.23 ± 0.7
71. *Stegastes partitus*, bicolor damselfish	0	+	0	0	+	0.35 ± 0.9	0.34 ± 1.5	0.34 ± 1.0
72. *Stegastes planifrons*, threespot damselfish	0.13 ± 2.0	+	0	0	0	0.28 ± 0.6	0	0.28 ± 0.8
73. *Stegastes variabilis*, cocoa damselfish	0	0.33 ± 2.8	0	0	0	0	0	0
Scaridae	**0.4**	**0.9**	**0.6**	**0.5**	**0.7**	**1.5**	**2.0**	**1.6**
74. *Scarus aurofrenatum*, redband parrotfish	+	+	0	0	0	0.26 ± 0.8	0.35 ± 0.7	0.29 ± 0.8
75. *Scarus taeniopterus*, princess parrotfish	0.23 ± 3.6	0.65 ± 5.5	0.37 ± 1.5	0.23 ± 1.1	0.23 ± 0.5	0.42 ± 1.2	0.17 ± 1.6	0.41 ± 1.9
76. *Scarus vetula*, queen parrotfish	0	0	0	0	0	0	0.32 ± 0.8	0.23 ± 1.1
77. *Sparisoma atomarium*, greenblotch parrotfish	0	0	0.19 ± 0.4	0.21 ± 0.7	0.32 ± 0.9	0	0	0
78. *Scarus chrysopterum*, redfin parrotfish	0	0	0	0	0	0.20 ± 0.9	0.14 ± 0.3	+
79. *Sparisoma radians*, bucktooth parrotfish	+	0.09 ± 0.9	0	0	0	0	0	0
80. *Sparisoma rubripinne*, redfin parrotfish	0.05 ± 0.4	0.06 ± 0.3	0	0	0	0.17 ± 1.3	0.46 ± 1.1	0.16 ± 0.6
81. *Sparisoma viride*, stoplight parrotfish	0.07 ± 0.4	0.13 ± 0.9	+	0.09 ± 0.5	0.15 ± 1.7	0.42 ± 1.2	0.54 ± 1.4	0.48 ± 1.3
Scorpaenidae								
82. *Scorpaena plumieri*, spotted scorpionfish	+	0	0	0	0	0	0	0
Sciaenidae								
83. *Odontoscion dentex*, reef croacker	0	0	0.22 ± 0.6	0	0	0	0	0
Serranidae						**0.2**	**0.1**	**0.1**
84. *Cephalopholis cruentata*, graysby	0	0	0	0	0	0	0.04 ± 0.2	0.04 ± 0.2
85. *Epinephelus guttatus*, redhind	0	0	0	0	0	0	0	0
86. *Epinephelus adscensionis*, rock hind	0	0	0	0	0	0	0	0
87. *Hypoplectrus aberrans*, yellowbelly hamlet	0	0	0	0	0	+	0	0
88. *Hypoplectrus chlorurus*, yellowfin hamlet	+	+	0	0	0	0.07 ± 0.4	0.04 ± 0.2	0.06± 0.2
89. *Hypoplectrus indigo*, indigo hamlet	0	0	0	0	0	0.05 ± 0.4	+	+
90. *Hypoplectrus nigricans*, black hamlet	0	0	0	0	0	+	0.04 ± 0.2	0
91 *Hypoplectrus puella*, barred hamlet	+	0	0	0.07 ± 0.7	+	0.04 ± 0.3	+	+

Table 2. Cont..

92. *Hypoplectrus unicolor*, butter hamlet	+	0	0	0	+	+	+	0.04 ± 0.3
93. *Rypticus saponaceus*, greater soapfish	0	0	0	0	0	0	0	+
94. *Serranus tigrinus*, harlequin bass	0	0	0	0	0	0	0	0
Sparidae								
95. *Archosargus rhomboidalis*, sea bream	0.06 ± 0.3	0.11 ± 0.9	0.20 ± 0.4	0.08 ± 0.9	0.09 ± 0.4	0.13 ± 0.5	+	0
96. *Calamus pennatula*, pluma	0	0	0	0	0	+	+	0
Sphyraenidae								
97. *Sphyraena barracuda*, great barracuda	0.15 ± 0.5	0.13 ± 0.3	0.05 ± 0.2	+	0.06 ± 0.3	+	0	0
Syngnathidae								
98. *Hippocampus reidi*, longsnout seahorse	+	0	0	0	0	0	0	0
Synodontidae								
99. *Synodus intermedius*, lizard fish	0	0	+	+	0	+	+	+
Tetraodontidae								0
100. *Canthigaster rostrata*, sharpnose puffer	+	0.07 ± 0.4	0	0	0	0.17 ± 1.2	0	0.11 ± 1.3
101. *Sphoeroides testudineus*, checkered puffer	0.05 ± 0.3	0.08± 0.4	+	+	0	0	0	0
102. *Sphoeroides spengleri*, bandtail puffer	0	0	0	+	+	0	0	+

Table 3. Mean fish density (N/m^2 ± SE) in 8 strata at the Corral-Turrumote segment of the cross-shelf gradient in southwestern Puerto Rico SBR = shallow back reef, SFR = shallow fore reef, DFR = deep fore reef, DBR deep back reef. Depth: shallow is 0-3 m depth and deep is 3-10 m. Every stratum corresponds to 3 sites of 1 000 m^2 each (10 replicates of 100 m^2) of surveyed area. 0 = species absent; + = species present in low numbers (i.e., few individuals only in 1 stratum). Strata definition in text. Numbers in bold are summed densities for all species belonging to a single family per stratum. Nomenclature follows Eschmeyer (1998).

Location	CORRAL				TURRUMOTE			
Sites	3	3	3	3	3	3	3	3
Family/Species/Strata	Seagrass	SBR	SFR	DFR	DBR	SBR	SFR	DFR
Acanthuridae	**0.2**	**0.7**	**1.0**	**0.4**	**1.0**	**0.7**	**1.1**	**0.6**
1. *Acanthurus bahianus*, ocean surgeon	0.14 ± 0.5	0.16 ± 0.4	0.31 ± 0.8	0.17 ± 0.5		0.21 ± 0.7	0.23 ± 0.7	0.16 ± 0.5
2. *Acanthurus chirurgus*, doctorfish	0.08 ± 0.6	0.29 ± 0.9	0.37 ± 1.8	0	0.35 ± 1.3	0.24 ± 0.9	0.43 ± 0.4	0.18 ± 0.5
3. *Acanthurus coeruleus*, blue tang	0	0.27 ± 0.9	0.43 ± 1.1	0.25 ± 0.8	0.38 ± 1.3	0.27 ± 0.8	0.45 ± 1.1	0.24 ± 1.2
Aulostomidae								
4. *Aulostomus maculatus*, trumpetfish	0	0	+	0.04 ± 0.2	+	+	+	+
Balistidae								
5. *Balistes vetula*, queen trigger fish	0	0	0	0	0	0	0	0
6. *Melichthys niger, black durgon*	0	0	0	0	0	0	0	0
Bothidae								
7. *Bothus lunatus*, peacock flounder	0	0	0	0	0	0	0	0
Carangidae								
8. Caranx latus, horse-eye jack	0	+	0	0	0	0	0	0
9. *Caranx crysos*, blue runner	0	0	+	0	0	0	+	0
Chaetodontidae	**0.0**	**0.3**	**0.3**	**0.2**	**0.2**	**0.2**	**0.0**	**0.2**
10. *Chaetodon capistratus*, foureye butteflyfish	+	0.30 ± 1.0	0.18 ± 0.3	0.17 ± 0.5	0.17 ± 0.4	0.10 ± 0.3	0.08 ± 0.3	0.12 ± 0.4
11. *Chaetodon ocellatus,* spotfin butterflyfish	0	0	+	0	0	0	0	0
12. *Chaetodon striatus,* banded butterflyfish	0	0.04 ± 0.2	0.12 ± 0.6	0.05 ± 0.3	0.08 ± 0.2	0.06 ± 0.2	+	+
Diodontidae								
13. *Diodon holacanthus*, balloonfish	+	+	0	0	0	0	0	0
14. *Diodon hystrix*, porcupinefish	0	+	+	0	+	+	+	+
Ephippidae								
15. *Chaetodipterus faber*, atlantic spadefish	0	0	0	0	0	0	0	0
Fistularidae								
16. *Fistularia tabacaria*, bluespotted cornetfish	+	0	0	0	0	0	0	0
Gerreidae	**0.0**	**0.0**						
17. *Gerres cinereus*, yellowfin mojarra	0	0.07 ± 0.6	0.13 ± 0.9	0	0.15 ± 1.4	+	0	0
a. *Eucinostomus* spp., mojarra	0.49 ± 6.7	0	0	0	0	0	0	0
Grammatidae								
18. *Gramma loreto*, fairy basslet	0	0	0	0.41 ± 2.0	0.42 ± 1.4	0	0	0.30 ± 0.8
Haemulidae	**0.9**	**1.9**	**0.4**	**1.7**	**1.5**	**0.3**	**0.0**	**0.6**
19. *Anisotremus surinamensis,* black margate	0	+	0	+		0	0	0
20. *Anisotremus virginicus*, porkfish	0	0	0	+	0.12 ± 0.8	0	0	+
21. *Haemulon aurolineatum*, tomtate	0	0	0	0.19 ± 0.5	0.22 ± 1.1	0	0	+
22. *Haemulon carbonarium*, caesar grunt	0	0	+	0.19 ± 1.7	0	0	0	0
23. *Haemulon chrysargyreum*, smallmouth grunt	0	0	0.11 ± 0.2	0.19 ± 1.8	0	0	0	0.16 ± 0.9
24. *Haemulon flavolineatum*, french grunt	0.37 ± 1.5	0.94 ± 11.8	0.17 ± 0.8	0.31 ± 2.2	0.31 ± 1.0	0.14 ± 1.8	+	0.17 ± 1.5
25. *Haemulon macrostomum*, spanish grunt	0	0	0	+	0	0	0	0
26. *Haemulon parrai*, sailors choice	0	+	+	0.24 ± 1.0	0.29 ± 1.2	0	0	0
27. *Haemulon plumieri*, white grunt	0.49 ± 1.6	0.85 ± 5.3	0	0.37 ± 3.3	0.30 ± 1.4	0.14 ± 0.5	0	0.17 ± 0.9
28. *Haemulon sciurus*, bluestriped grunt	+	0.16 ± 1.2	0.10 ± 0.4	0.23 ± 0.9	0.25 ± 1.1	+	0.11 ± 0.6	0.09 ± 0.6
b. *Haemulon* spp. grunts	0	0	0	+	0	0	0	0
Holocentridae	**0.0**	**0.2**	**0.0**	**0.2**	**0.3**	**0.0**	**0.3**	**0.0**
29. *Holocentrus adscencionis*, squirrelfish	0	+	0.06 ± 0.3	0.05 ± 0.2	0.14 ± 1.9		0.07 ± 0.3	0.07 ± 0.4
30. *Holocentrus rufus*, longspine squirrelfish	+	0.15 ± 1.0	0	0.06 ± 0.4	0.11 ± 0.7	0.06 ± 0.2	0.08 ± 0.3	0.08 ± 0.4
31. *Myripristis jacobus*, blackbar soldierfish	0	0.09 ± 0.5	0	0.05 ± 0.3	0	0	0	0
32. *Sargocentron vexillarius*, dusky squirrelfish	+	0	+	0	0	+	0.15 ± 0.7	0
Kyphosidae								
33. *Kyphosus sectatrix*, bermuda sea chub	0	0	0	+	0	0	+	0
Labridae	**0.0**	**0.9**	**1.0**	**0.8**	**2.0**	**0.9**	**1.6**	**0.8**
34. *Bodianus rufus*, spanish hogfish	0	0	+	+	0.10 ± 0.7	+	+	+
35. *Clepticus parrai*, creole wrasse	0	0	0	0	0	0	0	0.24 ± 1.8
36. *Halichoeres bivittatus*, slippery dick	0.18 ± 0.5	0.29 ± 0.6	0.40 ± 0.9	0.22 ± 1.1	0.53 ± 1.5	0.39 ± 0.9	0.43 ± 0.9	0.16 ± 1.5
37. *Halichoeres cyanocephalus*, yellowcheek wrasse	0	0	0	0	0	+	0	+
38. *Halichoeres garnoti*, yellowhead wrasse	0	0	+	0.11 ± 0.3	0.16 ± 0.8	0	0	0.12 ± 0.6
39. *Halichoeres maculipinna*, clown wrasse	0	0.12 ± 0.6	0.16 ± 0.4	0.10 ± 1.2	0.43 ± 1.3	0.11 ± 0.3	0.18 ± 0.6	+

Table 3. Cont..

40. *Halichoeres poeyi*, blackear wrasse	+	0.08 ± 0.3	+	0	0	0	0	0
41. *Halichoeres radiatus*, puddingwife	0	0.07 ± 0.3	0.10 ± 0.3	+	0.10 ± 1.2	0.11 ± 0.4	0.08 ± 0.2	0
42. *Lachnolaimus maximus*, hogfish	0	0	0	+	0.04 ± 0.2	0	0	+
43. *Thalassoma bifasciatum*, bluehead wrasse	0	0.30 ± 0.8	0.48 ± 0.9	0.38 ± 1.0	0.61 ± 1.4	0.31 ± 0.7	0.90 ± 7.0	0.30 ± 1.3
44. *Xyrichtys splendens*, green razorfish	0	0	0	0	0	+	0	0
Lutjanidae	**0.0**	**0.0**	**0.0**	**0.3**	**0.4**	**0.0**	**0.0**	**0.0**
45. *Lutjanus analis*, mutton snapper	+	0	0	+	0	0	0	**0**
46. *Lutjanus apodus*, schoolmaster	0	0.23 ± 1.4	0.13 ± 0.2	0.18 ± 0.6	0.21 ± 0.8	0.13 ± 0.8	0.29 ± 6.2	0.19 ± 2.0
47. *Lutjanus cyanopterus*, cuber snapper	0	0	0	+	0	0	0	0
48. *Lutjanus griseus*, gray snapper	0	0	0	0	0	+	0	+
49. *Lutjanus jocu*, dog snapper	0	0	0	+	0	+	+	0
50. *Lutjanus mahogoni*, mahogany snapper	0	+	0	+	0	0	0	+
51. *Lutjanus synagris*, lane snapper	0	0	0	0	0	0	0	0
52. *Ocyurus chrysurus*, yellowtail snapper	0.07 ± 0.3	+	0	0.08 ± 0.6	0.23 ± 0.8	0	+	0.07 ± 0.4
Mugilidae								
53. Mugil cephalus, striped mullet	0	0	0	0	0	0	0	0
Mullidae								
54. *Mulloidichtys martinicus*, yellow goatfish	0	+	+	+	0.09 ± 0.7	0.13 ± 0.3	+	0.12 ± 0.7
55. *Pseudupeneus maculatus*, spotted goatfish	+	+	+	+	+	+	+	0
Muraenidae								
56. *Gymnothorax funebris*, green moray	0	0	0	0	0	0	0	0
57. *Gymnothorax moringa*, spotted moray	0	+	0	+	0	0	+	+
Ophichthidae								
58. *Myrichthys breviceps*, sharptail eel	+	0	0	+	0	0	0	0
Pempheridae								
59. *Pemperis shomburgki*, glassy sweeper	0	0	0	+	0	0	0	0
Pomacanthidae								
60. *Pomacanthus arcuatus*, grey angelfish	0	0	+	+	0.06 ± 0.2	0	+	+
61. *Pomacanthus paru*, french angelfish	0	+	0	+	0	0	+	0
62. *Holacanthus ciliaris*, queen angelfish	0	+	0	0	0	0	0	0
63. *Holacanthus tricolor*, rock beauty	0	0	0	0	0	0	0	+
Pomacentridae	**0.4**	**1.5**	**2.0**	**1.9**	**2.8**	**1.4**	**1.8**	**1.7**
64. *Abudefduf saxatilis*, sergeant major	0	0.23 ± 1.4	0.38 ± 1.2	0.19 ± 0.4	0	0.18 ± 0.7	0.18 ± 1.5	0.13 ± 1.5
65. *Abudefduf taurus*, night sergeant	0	0	0	0	0	0	0	0
66. *Chromis multilineata*, brown chromis	0	+	0.40 ± 3.4	0.29 ± 1.3	0.52 ± 1.7	0.26 ± 1.5	0.38 ± 2.0	0.28 ± 1.7
67. *Chromis cyanea*, blue chromis	0	0	0	+	0.52 ± 3.2	+	0	0.26 ± 1.2
68. *Microsphatodon chrysrurus*, yellowtail damselfish	0	0.24 ± 1.1	0.38 ± 0.8	0.23 ± 0.9	0.31 ± 2.9	0.23 ± 0.6	0.38 ± 0.9	0.16 ± 0.7
69. *Stegastes dorsopunicans*, dusky damselfish	0.16 ± 1.0	0.39 ± 1.0	0.45 ± 0.5	0.39 ± 1.2	0.41 ± 0.9	0.38 ± 0.8	0.49 ± 1.5	0.31 ± 0.8
70. *Stegastes leucostictus*, beaugregory	0.25 ± 0.5	0.19 ± 0.6	0.23 ± 0.9	0.23 ± 0.5	0.31 ± 0.6	0.15 ± 0.3	0.14 ± 1.0	0.14 ± 0.4
71. *Stegastes partitus*, bicolor damselfish	0	0.23 ± 0.8	0.23 ± 1.1	0.26 ± 0.5	0.33 ± 1.1	0.20 ± 0.7	0.22 ± 1.1	0.24 ± 0.8
72. *Stegastes planifrons*, threespot damselfish	0	0.25 ± 1.1	0	0.31 ± 1.5	0.38 ± 1.3	0	0	0.17 ± 0.5
73. *Stegastes variabilis*, cocoa damselfish	0	0	0	0	0	0	0	0
Scaridae	**0.7**	**1.3**	**1.5**	**0.9**	**1.5**	**0.8**	**0.8**	**0.7**
74. *Scarus aurofrenatum*, redband parrotfish	0	0.19 ± 0.6	0.36 ± 0.8	0.21 ± 0.5	0.36 ± 1.0	0.20 ± 0.5	0.20 ± 0.6	0.18 ± 0.5
75. *Sparisoma taeniopterus*, princess parrotfish	0.35 ± 1.8	0.38 ± 2.3	0.42 ± 0.9	0.26 ± 0.9	0.45 ± 1.0	0.13 ± 0.4	0.13 ± 0.4	0.27 ± 2.3
76. *Scarus vetula*, queen parrotfish	0	0	0	0	0	0	0	0
77. *Sparisoma atomarium*, greenblotch parrotfish	0.35 ± 0.9	0.19 ± 0.9	0	0	0	0	0	0
78. *Scarus chrysopterum*, redfin parrotfish	0	0.15 ± 0.6	0.25 ± 0.7	0	0.33 ± 2.8	0.12 ± 0.3	0.18 ± 0.7	0
79. *Sparisoma radians*, bucktooth parrotfish	0	+	0	0	0	0	0	0
80. *Sparisoma rubripinne*, redfin parrotfish	0	0	0.14 ± 0.6	0	0	0.13 ± 0.3	0.07 ± 0.7	0
81. *Sparisoma viride*, stoplight parrotfish	+	0.40 ± 1.0	0.35 ± 1.0	0.38 ± 3.3	0.37 ± 1.2	0.24 ± 0.6	0.25 ± 0.5	0.26 ± 0.7
Scorpaenidae								
82. *Scorpaena plumieri*, spotted scorpionfish	0	0	0	0	0	0	0	+
Sciaenidae								
83. *Odontoscion dentex*, reef croacker	0	+	0	+	0	0	0	0
Serranidae	**0.0**	**0.1**	**0.0**	**0.0**	**0.3**	**0.0**	**0.0**	**0.3**
84. *Cephalopholis cruentata*, graysby	0	+	+	+	0.06 ± 0.3	+	+	0.04 ± 0.1
85. *Epinephelus guttatus*, redhind	0	0	0	+	0	+	0	0
86. *Epinephelus adscensionis*, rock hind	0	0	0	0	0	0	0	+
87. *Hypoplectrus aberrans*, yellowbelly hamlet	0	+	0	0	+	+	0	+
88. *Hypoplectrus chlorurus*, yellowfin hamlet	0	0.05 ± 0.2	0.05 ± 0.2	0.05 ± 0.2	0.08 ± 0.3	+	0.04 ± 0.2	0.05 ± 0.2
89. *Hypoplectrus indigo*, indigo hamlet	0	0.05 ± 0.2	0	0	0	+	0	+
90. *Hypoplectrus nigricans*, black hamlet	0	+	+	0	0	0	+	+
91 *Hypoplectrus puella*, barred hamlet	0	0.05 ± 0.2	0	+	0.04 ± 0.2	0		0.04 ± 0.2
92. *Hypoplectrus unicolor*, butter hamlet	0	+	+	+	+	+	+	0.05 ± 0.2
93. *Rypticus saponaceus*, greater soapfish	0	0	0	0	0	0	0	0
94. *Serranus tigrinus*, harlequin bass	0	0	0	0	0.12 ± 1.5	0	0	0.09 ± 0.2

Table 3. Cont..

Sparidae								
95. *Archosargus rhomboidalis*, sea bream	0	0.06 ± 0.5	+	0	0	0	0	0
96. *Calamus pennatula*, pluma	0	0	0	0		0	+	0
Sphyraenidae								
97. *Sphyraena barracuda*, great barracuda	+	+	0	0	+	0	0	+
Syngnathidae								
98. *Hippocampus reidi*, longsnout seahorse	0	0	0	0	0	0	0	0
Synodontidae								
99. *Synodus intermedius*, lizard fish	0	+	0	0	+	0.04 ± 0.3	+	+
Tetraodontidae								
100. *Canthigaster rostrata*, sharpnose puffer	0	0.08 ± 0.5	0	0.09 ± 0.7	0.19 ± 0.8	0	0	0.15 ± 0.5
101. *Sphoeroides testudineus*, checkered puffer	0	0	0	0	0	0	0	0
102. *Sphoeroides spengleri*, bandtail puffer	+	+	0	0	0	0	0	+

Table 4. Total abundance, density (N/100 m^2), and relative abundance (%) for the 17 more abundant species in the inshore-offshore gradient shelf in southwestern Puerto Rico. Rel. Abund: relative abundance.

Species	Family	Total Abundance	Density	Rel. Abund.
Haemulon flavolineatum	Haemulidae	4 150	8.65	8.0
Stegastes dorsopunicans	Pomacentridae	3 723	7.76	7.1
Thallasoma bifasciatum	Labridae	2 962	6.17	5.7
Sparisoma viride	Scaridae	2 955	6.16	5.7
Scarus taeniopterus	Scaridae	2 888	6.02	5.5
Acanthurus coeruleus	Acanthuridae	2 816	5.87	5.4
Halichoeres bivittatus	Labridae	2 812	5.86	5.4
Haemulon plumieri	Haemulidae	2 612	5.44	5.0
Acanthurus chirurgus	Acanthuridae	2 300	4.79	4.4
Microsphatodon chrysurus	Pomacentridae	1 971	4.11	3.8
Sparisoma aurofrenatum	Scaridae	1 915	3.99	3.7
Stegastes leucostictus	Pomacentridae	1 553	3.24	3.0
Lutjanus apodus	Lutjanidae	1 483	3.09	2.8
Chaetodon capistratus	Chaetodontidae	1 472	3.07	2.8
Acanthurus bahianus	Acanthuridae	1 391	2.90	2.7
Stegastes partitus	Pomacentridae	1 329	2.77	2.5
Haemulon sciurus	Haemulidae	1 302	2.71	2.5

Table 5. Total abundance, density (N/100 m^2), and relative abundance of the 15 more abundant fish species (in 7 families) at the Montalva-Romero and Corral-Turrumote segments along the inshore-offshore, cross-shelf gradient in southwestern Puerto Rico. Rel Abund: relative abundance.

Montalva Bay-Romero				
Species	**Family**	**Total abundance**	**Density**	**Rel. Abund**
Haemulon flavolineatum	Haemulidae	3 053	12.72	11.86
Scarus taeniopterus	Scaridae	1 556	6.48	6.05
Stegastes dorsopunicans	Pomacentridae	1 497	6.24	5.82
Haemulon plumieri	Haemulidae	1 459	6.08	5.67
Sparisoma viride	Scaridae	1 262	5.26	4.90
Lutjanus apodus	Lutjanidae	1 137	4.74	4.42
Thalassoma bifasciatum	Labridae	1 112	4.63	4.32
Halichoeres bivittatus	Labridae	1 078	4.49	4.19
Haemulon sciurus	Haemulidae	1 072	4.47	4.17
Acanthurus coeruleus	Acanthuridae	1 064	4.43	4.13
Acanthurus chirurgus	Acanthuridae	966	4.03	3.75
Microsphatdon chrysurus	Pomacentridae	821	3.42	3.19
Stegastes leucostictus	Pomacentridae	713	2.97	2.77
Abudefduf saxatilis	Pomacentridae	701	2.92	2.72
Chaetodon capistratus	Chaetodontidae	677	2.82	2.63
Corral-Turrumote				
Species	**Family**	**Total abundance**	**Density**	**Rel. Abund**
Stegastes dorsopunicans	Pomacentridae	2 226	9.28	8.43
Thalassoma bifasciatum	Labridae	1 850	7.71	7.01
Acanthurus coeruleus	Acanthuridae	1 752	7.30	6.64
Halichoeres bivittatus	Labridae	1 734	7.23	6.57
Sparisoma viridae	Scaridae	1 693	7.05	6.41
Acanthurus chirurgus	Acanthuridae	1 334	5.56	5.05
Scarus taeniopterus	Scaridae	1 332	5.55	5.05
Sparisoma aurofrenatum	Scaridae	1 252	5.22	4.74
Haemulon plumieri	Haemulidae	1 153	4.80	4.37
Microsphatodon chrysurus	Pomacentridae	1 150	4.79	4.36
Haemulon flavolineatum	Haemulidae	1 097	4.57	4.15
Acanthurus bahianus	Acanthuridae	895	3.73	3.39
Stegastes leucostictus	Pomacentridae	840	3.50	3.18
Stegastes partitus	Pomacentridae	808	3.37	3.06
Chaetodon capistratus	Chaetodontidae	795	3.31	3.01

Table 6. Average species richness (S), Shannon diversity (H'), Evenness (J'), total species, and total density per stratum (N/100 m^2). Strata with the same letters are not significantly different from one another ($\alpha = 0.05$) according to Tukey-Kramer HSD test.

Location	S	H'	J	Total Species	Total Density
Montalva					
Mang-In	31a	2.45a	0.72	43	57.7
Mang-Out	33a	2.43a	0.69	52	96.5
Seag-In	19b	2.31a	0.78	27	71.2
Seag-Out	21b	2.41a	0.79	33	45.6
Romero					
Seag	20b	2.40a	0.80	29	48.4
SBR	39c	2.97b	0.81	52	139.6
SFR	43c	2.99b	0.79	60	203.7
DFR	47c	3.36d	0.87	51	172.3
Corral					
Seag	14d	1.93c	0.72	23	53.2
SBR	38c	2.77b	0.76	56	133.1
SFR	33a	2.87b	0.82	45	140.6
DFR	45e	3.15d	0.83	64	111.6
Turrumote					
DBR	42e	3.26d	0.87	49	139.6
SBR	31a	2.80b	0.81	44	80.6
SFR	32a	2.72b	0.78	45	129.2
DFR	40e	3.14d	0.85	58	78.8

Eucionostomus spp. (N = 720) and *Haemulon* spp. (N = 372) were not included.

Table 7a. Relative abundance (%) of main species per stratum at Montalva Bay-Romero.

	Montalva Bay				**Romero**			
	MangIn	MangOut	SgIn	SgOut	Seag	SBR	SFR	DFR
Haemulon flavolineatum	33.6	27.4	14.3	23.2	17.0	14.4	*	*
Lutjanus apodus	12.3	18.2	*	*	*	*	*	3.5
Sparisoma atomarium	*	*	*	10.0	18.3	*	*	*
Thalassoma bifasciatum	*	*	*	*	*	5.5	9.2	6.1
Stegastes dorsopunicans	*	*	*	*	*	9.8	8.9	7.7
Haemulon plumieri	*	*	23.8	22.5	17.6	*	*	*
Acanthurus coeruleus	*	*	*	*	*	*	9.0	6.8
Sparisoma viride	*	*	*	*	*	8.2	8.0	7.0
Scarus taeniopterus	*	9.4	11.8	*	*	6.0	6.4	*
Halichoeres bivittatus	*	*	*	*	*	7.6	*	4.7
Sphyraena barracuda	7.6	*	*	*	*	*	6.3	*
Haemulon sciurus	*	10.4	15.8	*	*	*	*	*
Microsphatodon chrysurus	*	*	*	*	*	*	8.0	4.4
Acanthurus chirurgus	*	*	*	*	*	*	*	5.0
Total	**53.4**	**65.5**	**65.7**	**55.6**	**52.9**	**51.5**	**55.7**	**45.2**

* = not computed. See text for strata code definitions.

Table 7b. Relative abundance (%) of main species per stratum at Corral-Turrumote.

	Corral				**Turrumote**			
	Seag	SBR	SFR	DFR	DBR	SBR	SFR	DFR
Haemulon flavolineatum	13.4	12.7	*	*	*	*	*	*
Lutjanus apodus	*	*	*	*	*	*	*	*
Sparisoma atomarium	19.0	*	*	*	*	*	*	*
Thalassoma bifasciatum	*	*	*	5.7	6.1	9.6	15.3	4.2
Stegastes dorsopunicans	*	6.2	9.0	9.0	7.6	13.6	10.5	8.5
Haemulon plumieri	26.8	9.5	*	3.7	4.0	*	*	*
Acanthurus coeruleus	*	*	9.2	5.6	4.9	8.6	10.8	4.5
Sparisoma viride	*	9.1	*	9.4	5.0	*	*	7.3
Scarus taeniopterus	*	*	9.1	3.8	8.0	*	*	*
Halichoeres bivittatus	*	6.2	8.5	*	4.6	14.5	9.7	*
Sphyraena barracuda	*	*	*	*	*	*	*	*
Haemulon sciurus	*	*	*	*	*	*	*	*
Microsphatodon chrysurus	*	*	7.5	*	*	*	7.6	*
Acanthurus chirurgus	*	6.4	6.4	4.3	*	6.3	*	*
Total	**59.1**	**50.1**	**49.6**	**37.2**	**40.2**	**52.7**	**54.1**	**24.6**

* = not computed. See text for strata code definitions.

CHAPTER 3: VARIATIONS IN JUVENILE FISH DENSITY AMONG MANGROVES, SEAGRASS, AND SHALLOW-WATER CORAL REEFS IN SOUTHWESTERN PUERTO RICO

INTRODUCTION

In the western Atlantic, shallow-water habitats in coastal zones have vast areas of mangroves and seagrass important for adult and juvenile stages of many marine organisms (Parrish 1989; Roberts 1996; Beck et al. 2001). Larvae of some reef-associated fish species apparently do not settle on the coral reef itself, but rather in alternative off-reef habitats, such as mangroves and seagrass beds. These shallow-water habitats are known to be nursery areas because of the large numbers of juveniles observed compared to other areas (Parrish 1989).

Mangroves and seagrass beds function as nurseries for juveniles of marine organisms (e.g., crustaceans, molluscs, and fishes) having a two-phase life cycle (Roberts 1996; Beck et al. 2001). However, in the Indo-Pacific the nursery function of these habitats is elusive (Blaber 1980; Laegsgaard and Johnson 1995; Quinn and Kojis 1985). A given habitat is considered “nursery” if juveniles occur at higher densities, have lower rates of predation or higher rates of growth compared to other habitats, and also if the habitat contribution, in terms of juveniles per unit area to the production of adults, is greater than that from other habitats harbouring also juveniles (Beck et al. 2001).

Most reef fishes have a life history including a two-phase cycle, where the larvae are planktonic and the juveniles and adults are benthic (Sale 1980; Sweatman 1985; Leis 1991). However, many fish larvae settle on habitats completely different than that of adults (Shulman and Ogden 1987; Eggleston 1995), which adds another stage (i.e.,

benthic juvenile) differing in environmental and habitat conditions. Thus, many reef fishes have a life history comprised by a three-phase cycle: larvae (planktonic), juvenile (benthic), and adult (benthic). Juveniles of reef fishes are commonly found in high densities in non-reef habitats (e.g., mangroves, seagrass, algal plains, lagoons), while adults are found almost exclusively in the coral reef itself (Parrish 1989; Roberts 1996; Nagelkerken et al. 2000; Adams and Ebersole 2002; Cocheret de la Moriniere et al. 2002).

Among the most important reasons why juveniles of several reef-associated fish species use mangroves and seagrass beds as nurseries habitats include (1) shelter from predators due to habitat structural complexity (Parrish 1989), (2) high abundance of food (Odum and Heald 1972; Ogden and Zieman 1977; Laegdsgaard and Johnson 2001), and (3) planktonic larvae reception due to extensive habitat coverage (Parrish 1989). However, it is possible that juveniles could select particular habitat conditions based on the "minimize μ/g hypothesis", which establishes that fish juveniles maximize growth rate and minimize risk of predation (Werner and Gilliam 1984). According to Beck et al. (2001), nursery habitats, compared to other habitats, support greater contributions to adult recruitment from any combination of the following factors: density, growth, survival of juveniles, and movement to adult habitats.

Despite that mangroves and seagrass beds harbour high densities of juveniles of commercially important fishes, it is not yet known to what extent the nursery production contributes to the fishery yields in coral reefs (Roberts 1996). In the western Atlantic, many studies on fish communities from estuaries have focused on mainland coasts (Thayer et al. 1987; Yanez-Arancibia 1988; Ley et al. 1999), while relatively little

attention has been paid to island locations (Baelde 1990; Rooker and Dennis 1991; Nagelkerken et al. 2000; Nagelkerken et al. 2002) with non-estuarine bays and lagoons in Caribbean islands (Nagelkerken and van der Velde 2002).

Some recent studies have investigated the fish communities from mangroves, seagrasses and shallow coral reefs simultaneously (Nagelkerken et al. 2000; Murphy 2001), while others have used more than one methodology to compare these habitats (Thayer et al. 1987; Acosta 1997). In Curaçao, Nagelkerken et al. (2000) recognized at least 17 reef fish species for which juveniles were highly abundant in bays. They grouped those fishes as “nursery species”, i.e., those species whose juveniles use bay habitats as a nursery but when adults occur in the coral reef. This suggests that these nursery species depend on the presence of seagrass beds and mangroves as a nursery habitat. At the same location, Cocheret de la Morinière et al. (2002) inferred Post-Settlement Life Cycle Migration patterns of juveniles from mangroves and seagrasses into the shallow-water coral reefs for nine of those species. Nagelkerken et al. (2002) determined that densities of several fish species on coral reefs in some Caribbean islands are a function of the presence of nearby mangroves and seagrass beds. In addition, Adams and Ebersole (2002) found in St. Croix, Virgin Islands, that lagoonal patch-reef areas of bank-barrier reefs are preferred nursery habitats for many reef fishes.

Although the fish community of southwestern Puerto Rico has been extensively studied (Austin 1971; Austin and Austin 1971; Kimmel 1985; Rooker and Dennis 1991; Dennis 1992; McGehee 1994; Acosta 1997; Appeldoorn et al. 1997; Murphy 2001; Christensen et al. 2003), little information is available analyzing the relative importance of mangroves, seagrass beds, and shallow-water coral reefs as nursery areas.

In the present study on the La Parguera shelf, southwestern Puerto Rico, I investigated the extent to which 20 selected, reef-associated fish species use the mangrove and seagrass as nurseries and how that use differs from the use of shallow-water coral reefs. The null hypothesis (i.e., H_o) is that there are no differences in fish juvenile densities between mangroves, seagrass beds and shallow-water coral reefs of lagoon areas.

MATERIALS AND METHODS

Study site

The study was conducted at the eastern part of La Parguera, on the southwestern shelf of Puerto Rico from January 2003 to May 2004. This shelf has a complex physiography, including submerged and emergent reefs (Morelock et al. 1977), and a variety of biotopes (e.g., mangroves, seagrass beds, algal plains, sandy-mud lagoons, and patch reefs) (Kimmel 1985). Selected locations of study along the mangrove-seagrass-coral reef continuum and within an inshore-offshore gradient, included: Montalva Bay, Romero Key, Corral Key, and Turrumote (Fig. 1). Reasons for selection of such locations were based on the presence of a proposed marine reserve offshore (i.e., Turrumote) and the proximity of this reserve to a bay (i.e., Montalva) and shallow-water coral reefs. Montalva Bay (17° 57’ 55” N; 66° 59’34” W) is a non-estuarine, coastal system (3.7 km^2) fringed by mangroves (*Rhizophora mangle* predominantly) and shallow water areas (i.e., sand, mud), covered with seagrass beds (*Thallassia testudinum* predominantly). Romero Key (17° 56’ 52” N; 66° 59’48” W), located 2.3 km from shore and at the entrance of Montalva bay, is an emergent reef (0.7 km^2) with relatively small mangrove

areas (i.e., prop-root areas not sufficient to be surveyed in this study) and shallow reef and seagrass bed areas (*Thallassia testudinum*, predominantly). Corral Key (17° 56' 43" N; 67° 00'34" W), located 2.9 km from shore and off Montalva Bay, is also an emergent reef (1.5 km^2) with shallow coral reefs and seagrass beds (*Thallassia testudinum*, predominantly) and little mangrove areas (i.e., prop-root areas not in water as to be surveyed). At the end of the inshore-offshore gradient lays Turrumote (17° 56' 12" N; 67° 01'09" W), in which there is a proposed marine reserve (7.6 km^2). This little emergent Key (0.1 km^2) is located at mid distance between the coastline and the insular shelf edge (4.6 km) and its reef system is comprised by emergent coral reefs and several submerged reefs with an extensive hard ground, low relief platform. It has no mangrove areas, a very small patch of seagrass (16 m^2), and mostly shallow and deeper coral reefs; in addition, it has profuse soft-coral (e.g., gorgonians) areas.

Study design

A stratified sampling procedure was applied to investigate the variability of fish densities along the mangrove-seagrass-coral reef continuum following an inshore-offshore gradient. At each location, 2 to 4 major strata were selected according to biotope (e.g., mangrove, seagrass, coral reef), depth (e.g., shallow: 0-3 m, deep: 3-10 m) and wave exposure (e.g., fore reef, back reef). At each stratum, 3 sites were randomly selected, but located as possible, at the eastern, middle and western parts of each stratum in order to cover a greater extent. At each site, 10 transects (i.e. 100 m^2) were sampled, totaling for 1 000 m^2 per site or 3 000 m^2 per stratum (Table 1). For Montalva Bay, the strata selection was based on biotope (i.e., mangrove and seagrass) and distance from

shore (i.e., inside the bay or outside the bay), resulting in 2 strata for mangroves (i.e., Mang-In and Mang-Out) and 2 for seagrass beds (i.e., Seag-In and Seag-Out). For Romero Key, selection was based on biotope (i.e, seagrass and coral reef), wave exposure (i.e., back reef, fore reef) and depth (i.e., 0-3 m and 3-10 m), resulting in 1 strata for seagrass beds (i.e., Seag-Rom), 2 strata for shallow coral reefs (i.e., shallow back reef and shallow fore reef, SBR and SFR) and 1 strata for deep coral reefs (i.e., deep fore reef, DFR). For Corral Key (i.e., Seag-Corr, SBR, SFR, and DFR), selection was similar to Romero Key. In the case of Turrumote, the same criteria applied; however, since the seagrass bed area is negligible, the resulting strata were 2 for shallow reefs (i.e., shallow back reef and shallow fore reef, SBR and SFR) and 2 for deep reefs (i.e. deep back reef and deep fore reef, DBR and DFR).

Fish censuses

Of the 103 fish species recorded in the various strata along the inshore-offshore gradient (see Chapter 2), 20 species were selected in this study based on (1) high relative abundance (see Chapter 2) compared to other species along the inshore-offshore gradient, (2) commercial (fisheries, aquarium trade; e.g., Haemulidae, Lutjanidae) and ecological importance (coral feeders, herbivores; e.g., Acanthuridae, Scaridae), and (3) documented evidence of at least 13 of them as nursery species (Nagelkerken et al. 2000; Cocheret de la Morinière et al. 2002). The term “nursery species” refers to those fish species of which the juveniles use a given biotope (e.g., bay, mangrove, seagrass) as a nursery where their density is higher compared to other biotopes (Cocheret de la Morinière et al. 2002), while “reef species” refers to those species of which all life stages are commonly found on the

coral reef (Nagelkerken et al. 2000). The selected species consisted of 4 grunts (Haemulidae): *Haemulon flavolineatum*, *H. plumieri*, *H. sciurus*, *H. parrai*; 3 surgeon fishes (Acanthuridae): *Acanthurus bahianus*, *A. chirurgus*, *A. coeruleus*; 5 parrotfishes (Scaridae): *Sparisoma aurofrenatum*, *S. chrysopterum*, *S. rubripinne*, *S. viride*, and *Scarus taeniopterus*; 4 snappers (Lutjanidae): *Lutjanus apodus*, *Ocyurus chrysurus*, *L. griseus*, *L. mahogoni*; 1 butterflyfish (Chaetodontidae): *Chaetodon capistratus*; 1 barracuda (Sphyraenidae): *Sphyraena barracuda*; 1 mojarra (Gerreidae): *Gerres cinereus*, and 1 damselfish (Pomacentridae): *Abudefduf saxatilis*. Recognition of juveniles of the selected fish species recorded in this study was based on documented maturation sizes available in literature (Nagelkerken 2000; García-Cagide et al. 2001) and Fishbase (at www.fishbase.org; Froese and Pauly 1993).

The selected fish species were studied using an adaptation of the underwater visual census based (UVC) on belt-transects (Brock 1954). This is a non-destructive technique for estimating reef fish populations that enables one to select specific species, requires only one worker, and is relatively rapid and inexpensive (Fowler 1987). Potential disadvantages of the UVC relate to variations in swimming speed (Lincoln Smith 1988), transect width (Cheal and Thompson 1997), fish length estimation (Bellwood and Alcala 1988), species identification (Brock 1982), and replicate number (Samoilys and Carlos 2000). Despite these potential disadvantages, the UVC allows rapid estimates of relative abundance, biomass, and length frequency distributions of reef fishes. For this reason, the UVC is the most practical and extensively used technique to study a wide range of demersal species taken by shallow-water fisheries on coral reefs (Nagelkerken et al. 2000; Christensen et al. 2003; Appeldoorn et al. 2003).

For every individual of the selected species observed within belt-transects, the body length in centimeters of forked length (FL) was recorded. Each transect was 25 m by 2 m each side of the line transect (25 x 4 m). Such a dimension was chosen for three reasons: (1) it immediately renders an area of 100 m^2 per replicate (i.e., transect), (2) comparisons with previous works can be made, and (3) it is amenable for use at the three biotopes selected (i.e., mangroves, seagrass, and coral reefs). For reducing potential bias and improve accuracy of fish length estimation, wooden fish models of several lengths (5-40 cm) tied to the reef bottom (Rooker and Recksiek 1992) were used as calibration objects before starting the study. Furthermore, transect duration (i.e., fish count) was standardized to less than 20 min per transect, and censuses were conducted at least 15 min after laying down the transect line on the bottom to allow fish normal behavior to resume after setting the line on the bottom. SCUBA was used in deeper locations (> 5 m), while snorkeling was used during shallow surveys (< 5 m), mainly in the mangrove prop-roots and seagrass beds. Transect width in the mangrove prop-roots was adapted as much as possible to the selected transect dimension, but in some instances was less than 2 m to each side of the transect line. For schooling fishes (e.g., *Haemulon flavolineatum*, *Acanthurus coeruleus*, *Lutjanus apodus*) forming groups of more than 50 individuals, previous essays were performed to calibrate number estimation by using counting techniques for shorebirds (Haig 2004).

Statistical analysis

In order to test the null hypothesis of no difference among habitats in terms of probable nursery potential, the proportional abundances of juveniles of the 20 selected

species were calculated and compared using a one-way ANOVA among (1) strata and biotope and (2) species among strata and biotope along the gradient using the multiple comparison Tukey HSD test ($\alpha = 0.05$) (Sokal and Rohlf 1995). Homogeneity of variances was tested with a Bartlett's test, and normality was tested using the Kolmogorov-Smirnov 1-sample test after square root data transformation. Strata or biotopes having more juveniles relative to adults will exhibit higher juvenile proportions compared to a strata or biotope having more adults or relatively few juveniles (Chittaro et al. in press).

RESULTS

A total of 28 758 individuals of the 20 selected fish species (in 7 families) were recorded among mangroves, seagrass beds, and coral reefs (Table 2). Juveniles accounted for 80% of this total, showing a proportion greater than 60% per stratum; some strata (e.g., seagrass) reached a proportion of 100% (Fig. 2; Table 3). By pooling species per stratum (or biotope) and analyzing the juvenile proportional abundance per shelf gradient component, there was a significant difference between inshore and offshore ($F_{12, 191} = 4.41$, $p < 0.0005$; Fig. 3). The proportional abundance of juveniles was higher at mangroves, seagrass beds, and shallow reefs of Montalva Bay and Romero compared to shallow and deep coral reefs of Corral and Turrumote. There was a significantly higher proportional abundance of juveniles in shallow back reef (i.e, SBR) of Romero and mangroves and seagrass of Montalva Bay relative to shallow and deep fore reefs (i.e., SFR and DFR) of Romero ($F_{4, 76} = 7.64$, $p < 0.0005$; Table 3). However, at Corral and Turrumote, there was no significant difference ($p > 0.05$) in juvenile proportional abundance among strata, with the exception of seagrass stratum in Corral that had a

100%, but the remaining strata exhibited more than 50% in proportional abundance of juveniles.

In terms of mean juvenile density (N/100 m^2) per stratum and biotope for selected species, there were significant differences among strata ($F_{15, 437} = 13.15$, $p < 0.0005$; Fig. 4) and biotope ($F_{4, 423} = 14.42$, $p < 0.0005$; Fig. 5). Fish densities at SBRs, SFRs, and DFRs of Romero and Corral, and mangroves-out and seagrass-in of Montalva Bay were significantly higher than those of the remaining strata. The lowest density was found in DFR of Turrumote. However, analyzing the juvenile densities per biotope, the SFRs and SBRs from all locations showed higher juveniles densities compared with mangroves, seagrass beds, and DFRs, while mangroves had higher juvenile densities compared with seagrass beds and DFRs (Fig. 6, 7).

Of the 20 selected fish species, *H. flavolineatum* (14.4%) had the greatest relative abundance (including juveniles and adults), followed by *S. viride* (10.2%), *Scarus taeniopterus* (10%), *A. coeruleus* (9.7%), and *H. plumieri* (9%; Table 2). Since the proportional abundance of juveniles per species was greater than 70% in the majority of strata, with the exception of *H. parrai* (18%), *L. mahogoni* (30%), *A. bahianus* (46%), *A. coeruleus* (57%), and *C. capistratus* (27%; Fig. 2), the mean juvenile density per stratum was compared to determine variations among strata rather than comparing the proportional abundance of juveniles for each species per stratum along the inshore-offshore gradient.

The juvenile mean density of *H. flavolineatum* was significantly higher (biotope: $F_{4, 225} = 7.83$, $p < 0.0005$) at mangroves, seagrass and SBRs relative to SFRs and DFRs (Fig. 6, 7), while at the level of individual stratum was significantly higher (strata $F_{10, 219}$

= 3.26, $p < 0.001$) at mangroves, seagrass beds of Montalva bay and SBR of Romero, compared to SBRs and DFRs of Corral and Turrumote, respectively (Fig. 8-11). Mangroves were the most important biotope in terms of juvenile fish density (Table 4). However, juvenile mean densities of *H. plumieri* (strata: $F_{7, 156} = 9.32$, $p< 0.0005$) and *H. sciurus* (strata: $F_{5, 107} = 11.43$, $p < 0.0005$; biotope: $F_{4, 108} = 11.80$, $p< 0.0005$) were significantly higher at seagrass relative to mangroves and coral reefs. Seagrass and mangroves were the most important biotope (and strata) for *H. plumieri* and *H. sciurus*, respectively (Table 4).

The juvenile mean density of *Lutjanus apodus* was significantly higher at mangroves relative to seagrass and coral reefs (biotope: $F_{3, 133} = 6.17$, $p <0.001$; Fig. 6, 7). Density at mangrove-out in Montalva bay was significantly higher than that at the remaining strata ($F_{6, 130} = 6.79$, $p < 0.0005$; Fig. 8-11). Mangroves were the most important biotope (Table 4). However, the juvenile mean density of *Ocyurus chrysurus* was significantly higher in seagrass and DBR of Turrumote relative to mangroves and the other coral reef strata (strata: $F_{5, 76} = 8.25$, $p < 0.0005$; biotope: $F_{3, 78} = 11.32$, $P < 0.0005$; Fig. 6, 7; Table 4). *L. griseus* was found almost exclusively in mangroves and seagrass, but its density was very low and not significantly different (Table 4).

The juvenile mean density of *Acanthurus chirurgus* was significantly higher at all SBRs relative to SFRs and DFRs (biotope: $F_{5, 281} = 31.48$, $p < 0.0005$; Fig. 6, 7), being significantly higher at the SFRs and DFRs of Romero and Corral relative to mangroves and seagrass, and coral reefs of Turrumote ($F_{15, 271} = 12.76$, $p < 0.0005$; Fig. 8-11; Table 4). *A. coeruleus* showed higher densities at all SFRs relative to SBRs and DFRs ($F_{3, 237} = 11.82$, $p < 0.0005$; Fig. 6, 7), while exhibited higher densities at the SFR of Turrumote

relative to the other coral reefs of Corral and Romero ($F_{9, 231} = 5.24$, $p < 0.0005$; Fig. 8-11; Table 4). *A. coeruleus* was almost absent from mangroves and seagrass, similarly to *A bahianus*; however, this latter species showed no significant differences in mean density among strata and biotopes.

The juvenile mean density of *Sparisoma aurofrenatum* was significantly higher at all SFRs relative to the remaining biotope ($F_{2, 233} = 12.96$, $p < 0.0005$; Fig. 6, 7), showing significantly higher density at SBR and SFR from Romero and DBR of Turrumote relative to the other reef strata of Corral and Turrumote (strata $F_{9, 227} = 12.37$, $p < 0.0005$; Fig. 8-11; Table 4), but being completely absent from mangroves and seagrass. Densities of *Scarus taeniopterus* were not significantly different at the level of biotopes, but were higher at SBR, SFR and DFR of Romero relative to the other strata (strata $F_{14, 259} = 6.36$, $p < 0.0005$; Fig. 8-11; Table 4). *Sparisoma viride* showed significantly higher densities at SBRs (biotope: $F_{3, 246} = 2.60$, $p < 0.053$; Fig. 6, 7; Table 4) compared to the other coral reefs, but absent from mangroves and seagrass, and exhibited significantly higher densities at all strata of Romero and SBR of Corral relative to the other coral reefs (strata: $F_{9, 240} = 9.02$, $p < 0.0005$; Fig. 8-11; Table 4). Juvenile mean density of *S. chrysopterum* was significantly higher at all SFRs relative to SBRs (biotope: $F_{1, 81} = 18.34$, $p < 0.0005$), and significantly higher at the SBR of Romero relative to the other strata (strata: $F_{5, 77} = 10.45$, $p < 0.0005$; Table 4); however, it was absent from mangroves and seagrass (Fig. 6-11).

The mean juvenile density of *Chaetodon capistratus* showed a significantly higher density at SBRs relative to seagrass, mangroves, and DFRs (biotope: $F_{3, 103} = 15.23$, $p < 0.0005$), being significantly higher at the SBR Corral and seagrass of

Montalva bay relative to the remaining strata, including mangroves and other seagrass strata (strata: $F_{7, 99} = 8.40$, $p < 0.0005$; Table 4). *Abudefduf saxatilis* showed higher densities at SFRs and DFRs relative to SBRs and mangroves (biotope: $F_{3, 127} = 31.47$, $p < 0.0005$; Table 4), while it was significantly higher at SFR and DFR of Romero and SFR of Corral relative to the remaining strata (strata: $F_{9, 121} = 27.03$, $p < 0.0005$); it was absent from seagrass (Fig 6-11).

Sphyraena barracuda and *Lutjanus griseus* exhibited a restricted distribution to mangroves and seagrass only, but their juvenile mean densities were not significant different either among strata or biotope. The remaining fish species, *L. mahogoni, Gerres cinereus*, *Haemulon parrai*, and *Sparisoma rubripinne* were not statistically compared because of their low density per stratum.

DISCUSSION

The majority of strata, and consequently biotopes, along the inshore-offshore gradient in southwestern Puerto Rico showed a higher proportional abundance of juveniles (80%). However, there were differences in juvenile fish densities among mangroves, seagrass beds and shallow-water coral reefs. In the section Montalva Bay-Romero, there was a greater density of juveniles compared with Corral-Turrumote, which may be explained by the presence of more heterogeneous habitats (e.g., mangroves, seagrass, and shallow coral reefs). At the segment Montalva Bay-Romero, the stratum SFR of Romero had the highest density of juveniles and the lowest was in seagrass Romero, while at the Corral-Turrumote segment, the SBR of Corral showed the highest density and DFR of Turrumote accounted for the lowest density. In terms of biotopes, the

seagrass showed a higher density of juveniles compared to that of mangroves. The highest juvenile density along the 2 segments (i.e., Montalva Bay, Romero, Corral, Turrumote) was at Romero (e.g., SFR and DFR). At the level of biotope (i.e., mangrove, seagrass, SBRs, SFRs, DFRs), the highest juvenile density was found at SFRs from all locations. The preponderance of Romero as showing the highest density of juveniles of the selected species is relevant, which could be due to the closeness to the mangrove fringe and seagrass areas in Montalva Bay compared to the other locations. There is the possibility that Romero may be a transition point, as reflected from the high fish densities, for these species in their plausible displacement in between Montalva Bay and adjacent off-shore areas (e.g. Corral and Turrumote).

Preferences for strata or biotope for the selected 20 species were species-specific. Among Haemulidae, while *Haemulon flavolineatum* was widespread along the inshore-offshore gradient, its density was higher at Montalva Bay-Romero, mainly at mangroves, seagrass and SBRs. In constrast, *H. plumieri* and *H sciurus* showed a more restricted distribution, with juveniles more dense at seagrass. *H. parrai* presented a low density of juveniles, exhibiting a higher proportion of adults mainly at deeper reefs. Among Lutjanidae, while juveniles of *Lutjanus apodus* were found not only in mangroves but also in coral reefs, they exhibited a preference for mangroves in terms of higher density. In contrast, juveniles of *Ocyurus chrysurus* showed preferences for seagrass and deeper reefs in Turrumote compared with mangroves and more inshore coral reefs, and *L. griseus* showed restricted preference for mangroves only. *L. mahogoni* was more commonly found offshore, but in very low juvenile densities. Among the Acanthuridae, juveniles of *Acanthurus chirurgus* were widespread along the inshore-offshore gradient,

but densities were high at shallow coral reefs compared with mangroves and seagrass, while *A. coeruleus* juveniles were absent from these latter biotopes and highly dense at shallow coral reefs. *A. bahianus* juveniles did not show any preference for strata, but it was relatively absent from mangroves and seagrass implying that prefers coral reefs. In Curaçao, *L. apodus* and *H. sciurus* presented strong preference for mangroves over seagrass, *L. griseus* was also strongly associated with mangroves, and *A. bahianus* was not present in mangroves, while *H. flavolineatum* and *Ocyurus chrysurus* used both habitats (Cocheret de la Morinière et al. 2002); however, these two latter preferred seagrass as nursery areas (Nagelkerken et al. 2000).

Among the Scaridae, juveniles of *Scarus taeniopterus* were widespread along the inshore-offshore gradient, but they exhibited higher densities at shallow and deep fore reefs compared with other biotopes. None of the juveniles of the remaining selected species of Scaridae were found either at mangroves or seagrass, but showed high preferences for either shallow or deep coral reefs. In constrast, *S. viride* used seagrass as nursery areas in Curaçao (Nagelkerken et al. 2000). While juveniles of *Chaetodon capistratus* and *Abudefduf saxatilis* showed preferences for either shallow back or fore reefs, compared with mangroves and seagrass, juveniles of *Sphyraena barracuda* showed preferences for mangroves at inshore and *Gerres cinereus* for shallow and deep coral reefs offshore. However, *Ch. capistratus* showed preferences for mangroves as most important nursery biotope in Curaçao (Nagelkerken et al. 2000).

The importance of mangroves and seagrass as nursery habitats has been documented for many regions in the western Atlantic (Parrish 1989; Sedberry and Carter 1993; Nagelkerken et al. 2000; Cocheret de la Morinière et al. 2002). As shallow-water

habitats, mangroves and seagrass often have greater abundance of juvenile fishes compared to coral reefs. The former are considered as nursery areas because of the presence of higher densities of juveniles compared to the latter (Parrish 1989; Adams and Ebersole 2002; Dorenbosch et al. 2004). Higher densities of juveniles in mangroves and seagrass have been attributed tofood availability (Ogden and Ziemann 1977), structural complexity (Parrish 1989; Cocheret de la Morinière et al. 2004), shade (Cocheret de la Morinière et al. 2004), reduced predation (Robertson and Blaber 1992), and planktonic larvae reception due to habitat extensive coverage (Parrish 1989).

Nagelkerken et al. (2000) and Cocheret de la Morinière et al. (2002) working in Bonaire and Curaçao used terms such as “nursery species”, “bay species” and “reef species” for categorizing fishes that show differential use of habitat according to life stage. It is important to mention that this categorization is relative to the conditions of study area. All fish species under consideration are reef associated species as adults, but some are “off-reef” species as juveniles. Such a distinction was used here in this study of Puerto Rico for comparative reasons and to discern preferences of some reef fishes as juveniles for habitats other than coral reefs (e.g., mangroves, seagrass). Therefore, of the 20 fish species selected in southwestern Puerto Rico, at least 13 are the same “nursery species” of Nagelkerken et al. (2000), whereas 7 are “reef species”. In Curaçao, Nagelkerken et al. (2000) found that seagrass was the most important nursery for *H.flavolineatum, H. sciurus, O. chrysurus, A. chirurgus,* and *S. viridae*; mangroves for *L. apodus, L. griseus, S. barracuda,* and *C. capistratus*; and shallow-water coral reefs for *H. chrysargyreum, L. mahogoni, A. bahianus,* and *A saxatilis*. However, in southwestern Puerto Rico, while relatively abundant on mangroves and seagrass, *H. flavolineatum,*

Lutjanus apodus, *O. chrysurus*, *H. sciurus*, and *Haemulon plumieri* showed greater preference for shallow coral reefs as nursery areas. Similar departures were found by Nagelkerken et al. (2001) where *H. flavolineatum*, *C. capistratus*, *G. cinereus*, and *L. mahogoni* were not strictly dependant on mangroves and seagrass as nurseries, but used alternative nursery areas, such as shallow coral reefs.

In southwestern Puerto Rico, even more dramatic was the high proportional abundance of juveniles in the vast majority of strata regardless of biotope along the inshore-offshore gradient. The remaining nursery species (e.g., *A. bahianus*, *S. chrysopterum*, *L. mahogoni*, *Gerres cinereus*, *H. parrai*, *Chaetodon capistratus*), with the exception of *Sphyraena barracuda* and *L. griseus* that were restricted to mangroves, did not present consistent preferences for mangroves and seagrass, but for either shallow or deep coral reefs as nursery areas.

In Curaçao, Nagelkerken et al. (2002) found on islands lacking mangroves a complete absence or low densities of 11 of the 17 fish nursery species previously identified (Nagelkerken et al. 2000), implying a very important nursery function of mangroves and suggesting that the densities of some fish species on coral reefs are a function of the presence of nearby bays containing mangroves and seagrass beds as nurseries. In Florida, Lindeman et al. (2000) elucidated the facultative and obligate association (i.e., dependence) for 26 fish species for estuarine bays and lagoons, from which at least 2 species of Lutjanidae (i.e., *L. griseus*, *L. cyanocephalus*) showed estuarine dependency, whereas the remaining species, including 7 of the nursery species (*L. apodus*, *L mahogani*, *O. chrysurus*, *H. flavolineatum*, *H. plumieri*, *H. sciurus*, *H. parra*) used bay and lagoon habitats opportunistically. In the Colombian Caribbean,

Appeldoorn et al. (2003) revealed the relative importance of nearshore habitats containing seagrass and mangroves as nursery areas compared to offshore habitats. Halpern (2004) determined that the relative importance of mangroves as a limiting resource for *L. apodus* and *G. cinereus* was more evident on island-size wide scale. In contrast, Chittaro et al. (in press) approaching the relative importance of mangroves, seagrass, and coral reefs as nursery areas and using estimates of fish density, assemblage composition and relative rates of predation across three locations in the Caribbean (i.e., Bahamas, Belize and Mexico) found that not all mangroves and seagrass offer nursery function and such a function may be limited to a few species. Dorenbosch et al. (2004) found that some fish species use the shallow coral reefs as alternative nursery and did not depend strictly on the presence of bays with seagrass beds and mangroves as nurseries.

In this study from southwestern Puerto Rico, density was the attribute used for determining the relative importance of biotopes and strata as potential nurseries. The study showed that the importance of mangroves and seagrass in terms of harboring high densities of juveniles of the selected 20 species was relative and species-specific, since in the majority of cases shallow coral reefs (i.e., shallow back and fore reefs, 0-3 m depth) were even more important than mangroves and seagrass. In adjacent areas in Puerto Rico, Dennis (1992) found that whereas fish juvenile density in mangroves was greater than that of seagrass, the greater abundance of seagrass and coral reefs convey these latter habitats greater importance as settling areas. Likewise, in Curaçao, Nagelkerken and van der Velde (2002) found that mangroves had similar juvenile densities to those from shallow coral reefs. In addition, Chittaro et al. (in press) when examining juvenile and adult densities in mangroves, seagrass, and coral reef habitats at sites in several

Caribbean locations found that juvenile densities were not always greater in mangroves and seagrass and were rarely significantly greater. In contrast, Mumby et al. (2004) showed that mangroves are indeed important, serving as intermediate nursery habitat that may increase the survivorship of juvenile fishes (e.g., *Scarus guacamaia*), strongly influencing the community structure of fishes in adjacent coral reefs of the Caribbean.

The term "nursery area" as surrogate of mangroves or seagrass should be used with discretion, since these biotopes also harbor an adult community. Chittaro et al. (in press) argued that based on density, assemblage composition and relative rates of predation, not all mangrove and seagrass beds appear to offer nursery function. Furthermore, the nursery function of some mangrove areas in northeastern Florida Bay may not be viable due to drastic environmental fluctuations (Ley et al. 1999). However, other areas represent important nurseries for lutjanids (e.g., *L. griseus*) and sciaenids (e.g., *Cynoscion nebulosus*) (Rutherford et al. 1989). The nursery value of mangroves and seagrass in the Indo-Pacific is dubious, since many studies have presented contradictory results (Thollot 1992), and in the particular case of mangroves from Kenya (Indian Ocean), juvenile fishes did not show evidences of using mangroves as shelter (Huxham et al. 2004). Consequently, generalizations about the nursery role of mangroves and seagrass in the Caribbean should be avoided. Chittaro et al. (in press) highlighted the need to avoid generalizations about mangroves and seagrass having nursery related functions if estimates of density are the only method to confirm nursery potential. Therefore, in order to determine if a given habitat is a nursery, many approaches have to be examined simultaneously, such as: density, survival, growth, and displacement among habitats (Beck et al. 2001).

Mark-recapture studies of juveniles in nursery areas could determine the size, distance, and location at which the juveniles or early adults re-locate. Such a study to determine the patterns of displacement of tagged grunts (*H. flavolineatum*) at selected locations off La Parguera shelf is currently ongoing (Bouwmeester 2004). Another approach to determine the nursery value involves measuring the macronutrient and trace-element ratios in fish otoliths as a unique tracer of the temporary residence in nursery habitats (Gillanders 2002). Comparison of genetic structure of fishes from many locations is another approach to elucidate the origin of juveniles (Palumbi 2003). In Curaçao, comparisons of dietary changes between juveniles and adults of at least 9 nursery fish species (Cocheret de la Mornière et al. 2003) using stomach contents and stable isotopes showed that the juveniles and adults of these reef fish species are separated ecologically and spatially for a considerable period of time.

It was evident that, for the species studied in this work, either one or a combination of biotopes is crucial as nursery areas based on habitat preferences. Several studies have shown that many fish species undergo post-settlement life cycle migrations (Cocheret de la Morinière et al. 2002) or also known as cross-shelf ontogenetic migrations (Appeldoorn et al. 1997; Lindeman et al. 2000; Nagelkerken et al. 2000; Dahlgren and Eggleston 2000). The extent that this occurs in southwestern Puerto Rico, and the impact this post-settlement process may have on understanding the complexities of habitat use and potential for stage-specific nursery functions has not been fully investigated. Only for *H. plumieri*, have ontogenetic migrations been previously documented in the region (Appeldoorn et al. 1997).

Recently, there is a trend to modify traditional fisheries management by incorporating an ecosystem-based approach for a sustainable use of the marine environment (Garcia et al. 2003; Browman et al. 2004), along with the use of no-take marine reserves (NTMRs). Ideally, this means that the conservation and management strategies for the marine ecosystem must be oriented not only to a local scale but that they must also incorporate the habitat relevance into a larger regional scale (e.g., large marine ecosystems, Sherman and Duda 1999; biogeochemical provinces, Longhurst 1998). Any conservation or management action taken to protect the fish assemblages through the use of NTMRs, must include not only certain coral reef areas but also their associated inshore habitats, such as mangroves and seagrass. Incorporating the vast mosaic of structural habitat heterogeneity along a habitat continuum is a plausible and strongly recommended alternative for providing an inter-linkage approach for the protection of reef fishes based on life history characteristics and habitat association. If more fish species experience ontogenetic migrations along the inshore-offshore gradient of southwestern Puerto Rico; then, it would be of primal importance to include the whole mosaic of habitats along the continuum of mangroves-seagrass-coral reefs from Montalva Bay to the proposed NTMRs in Turrumote Key, including Romero and Corral keys, as a composite NTMRs for protecting not only essential adult and nursery ground but also the “corridors” of potential post-settlement fish connectivity.

Conclusions

1) The majority of strata along the inshore-offshore shelf gradient showed a high proportional abundance of juveniles (80%).

2) Preferences for strata or biotope for the selected 20 species were species specific.

3) The present study from southwestern Puerto Rico showed that not only mangroves and seagrass are important in terms of harboring high densities of juveniles of the selected 20 species, but also shallow coral reefs (i.e., shallow fore reef). Juvenile proportions (but not necessarily densities) were greater inshore.

4) Mangroves were important for *L. apodus*, *L. griseus*, and *S. barracuda*. Mangroves and SBR were important for *H. flavolineatum*. Mangroves and seagrass were important for *H. sciurus* and *G. cinereus*. Seagrass were important for *O. chrysurus* and *H. plumieri*. SBR and SFR were important for *A. bahianus, A. coeruleus, A. chirurgus, S. viride, S. chrysopterum, S. aurofrenatum, Ch. capistratus, L. mahogoni, A. saxatilis, Scarus taeniopterus, Sparisoma rubripinne,* and *H. parrai*.

5) For the majority of fish species, the juveniles were found in shallow-water strata, while the adults were found in deeper-water strata. However, for some species (e.g., L. *griseus, L. apodus, S. chrysopterum*) adults co-occurred with the juveniles in the same strata.

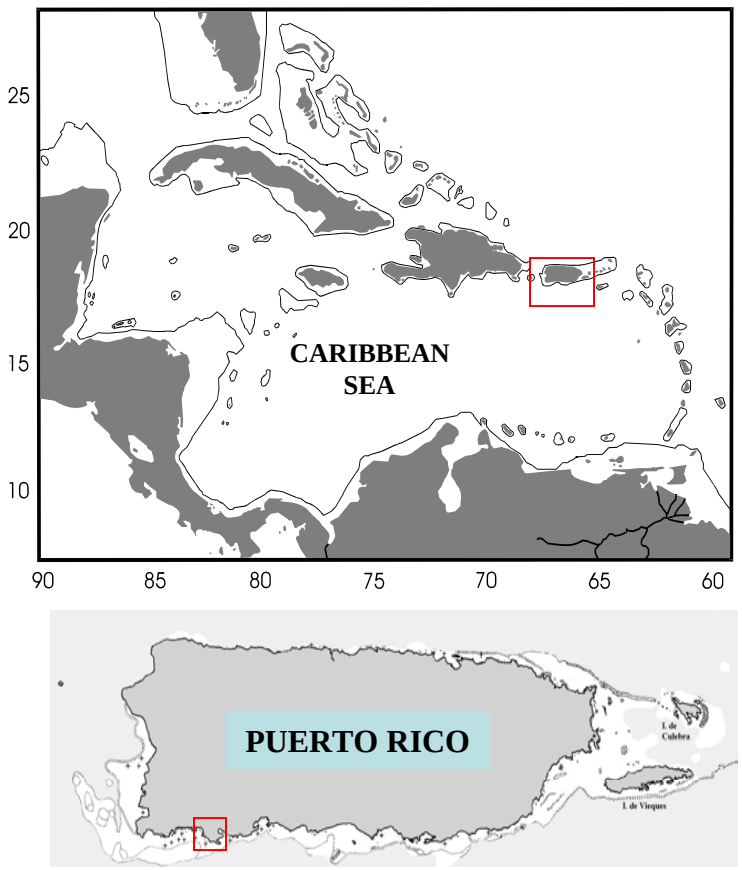
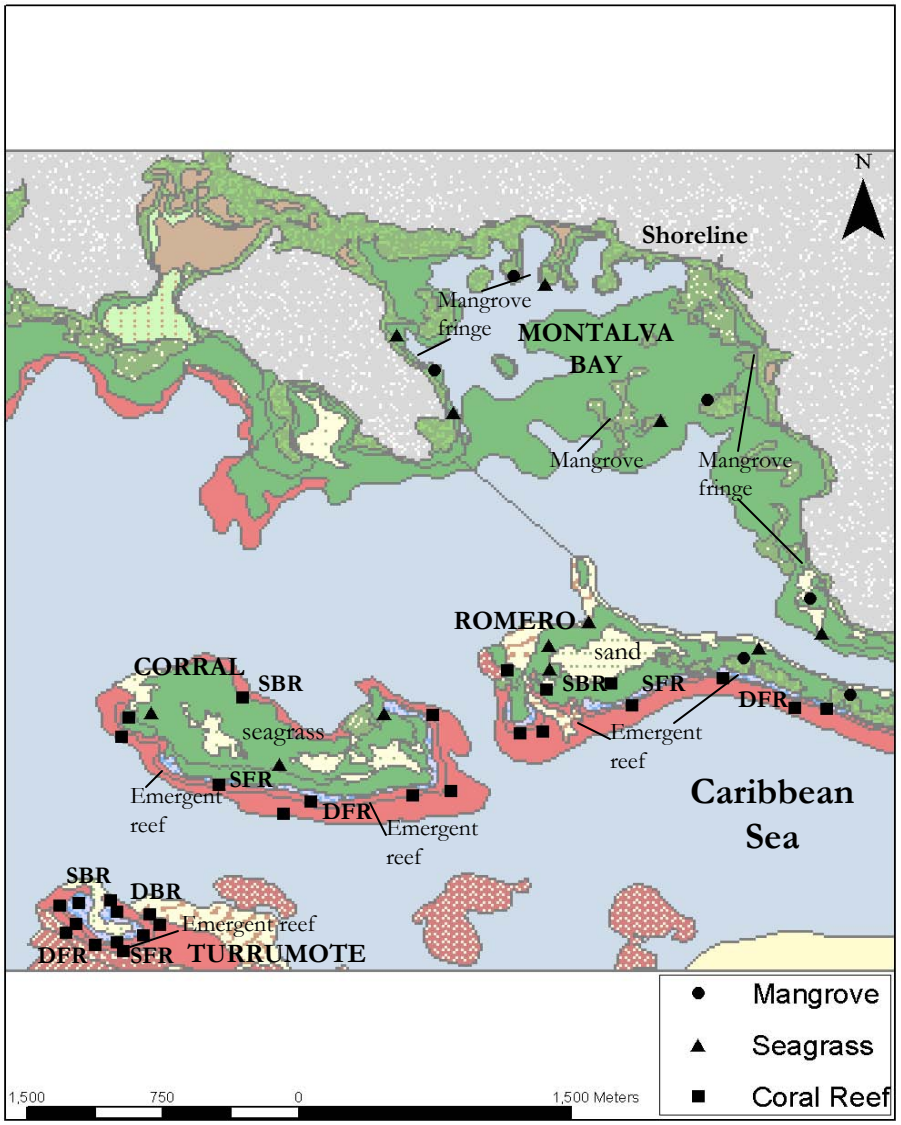


Fig. 1. Map of Puerto Rico showing study area and locations with sites in the various strata (i.e., SBR, DFR) and biotopes (i.e., mangroves, seagrass, coral reefs). SBR: shallow back reef, SFR: shallow fore reef, DFR: deep fore reef, DBR: deep back reef.



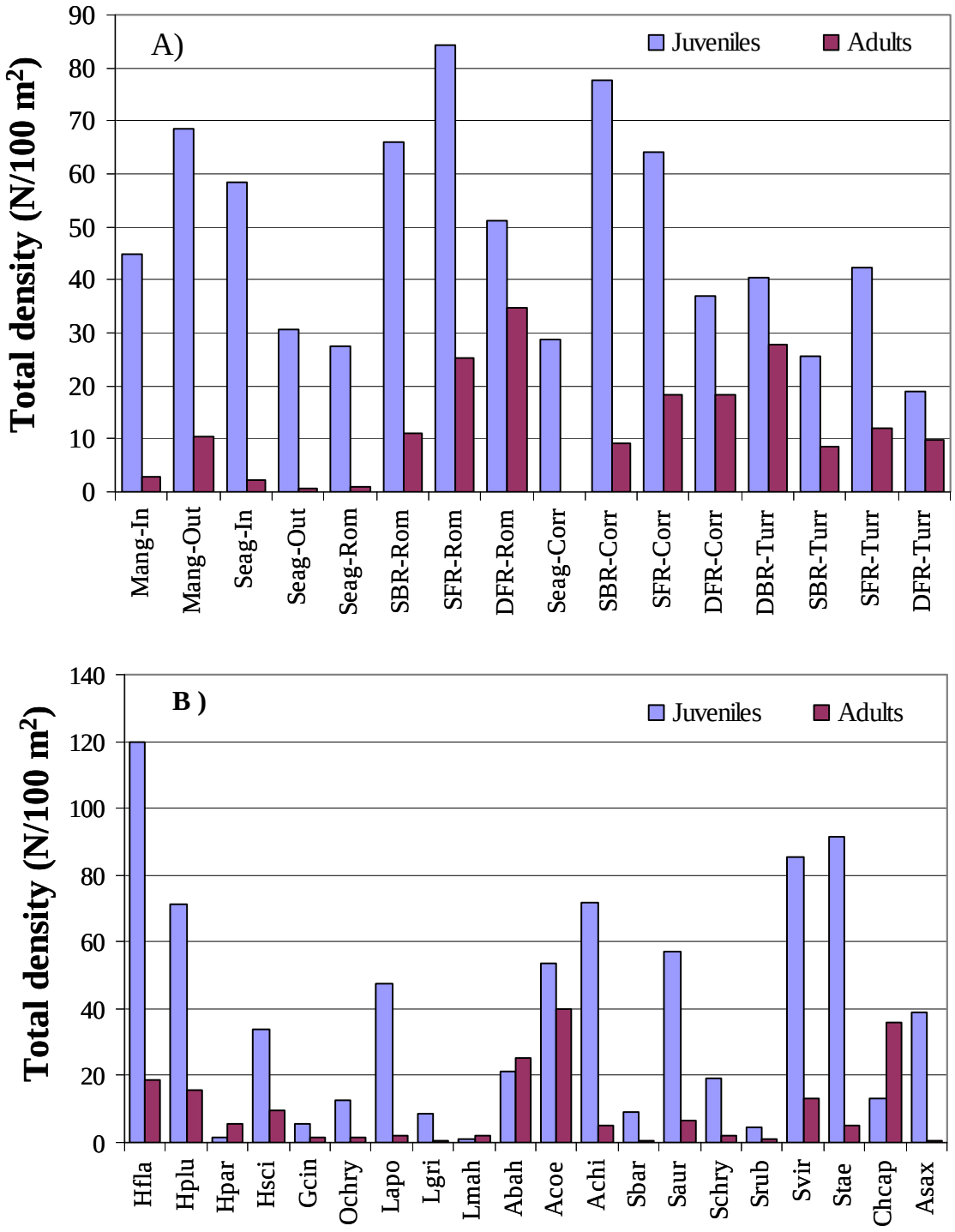


Fig. 2. Total density (N/100 m^2) of juveniles and adults per stratum A) along the inshore-offshore gradient, and B) for juveniles and adults of the 20 selected species. N = number of individuals. See Table 2 for species codes.

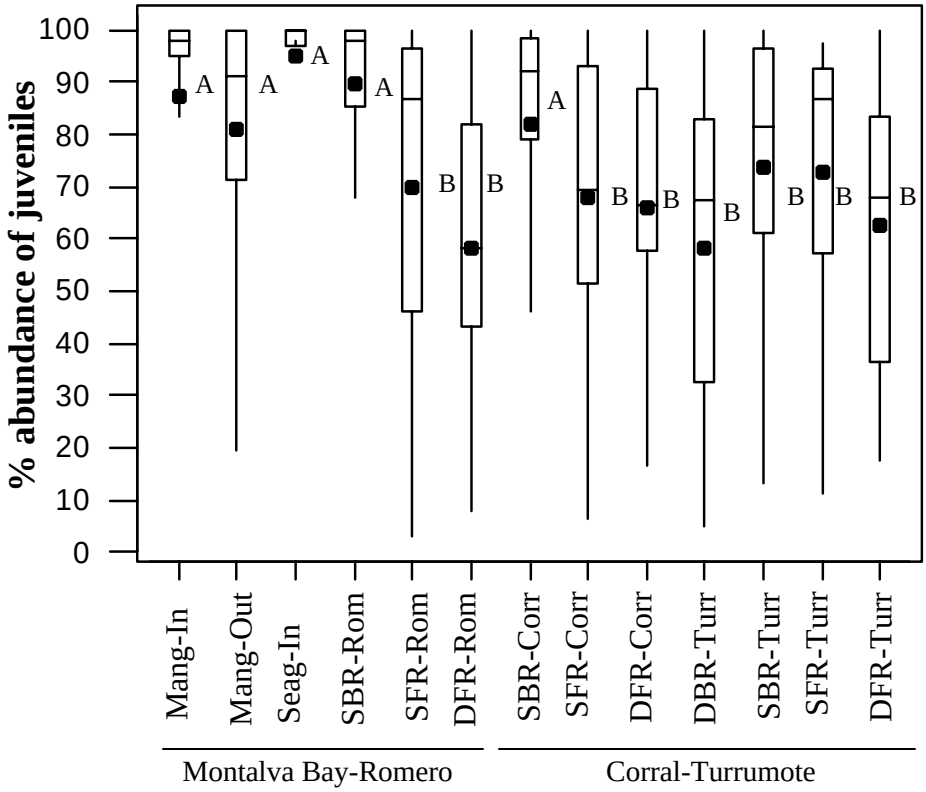


Fig. 3. Percent abundance of juveniles among strata along the inshore-offshore gradient. Groups with the same letter are not significantly different from each other as determined by Tukey-Kramer HSD test (α =0.05). Data were arcsine transformed for analysis; however, proportionality is shown in the graph. Data from SeagOut, Seag-Rom, and Seag-Corr were not included because they were 100% in proportional abundance of juveniles. SBR: shallow coral reef, SFR: shallow fore reef, DFR: deep fore reef, DBR: deep back reef. Whiskers (i.e., vertical lines: upper and lower limits; Box: 95% C.I., black square: mean; lines in boxes: medians. See text for meaning of strata labeling.

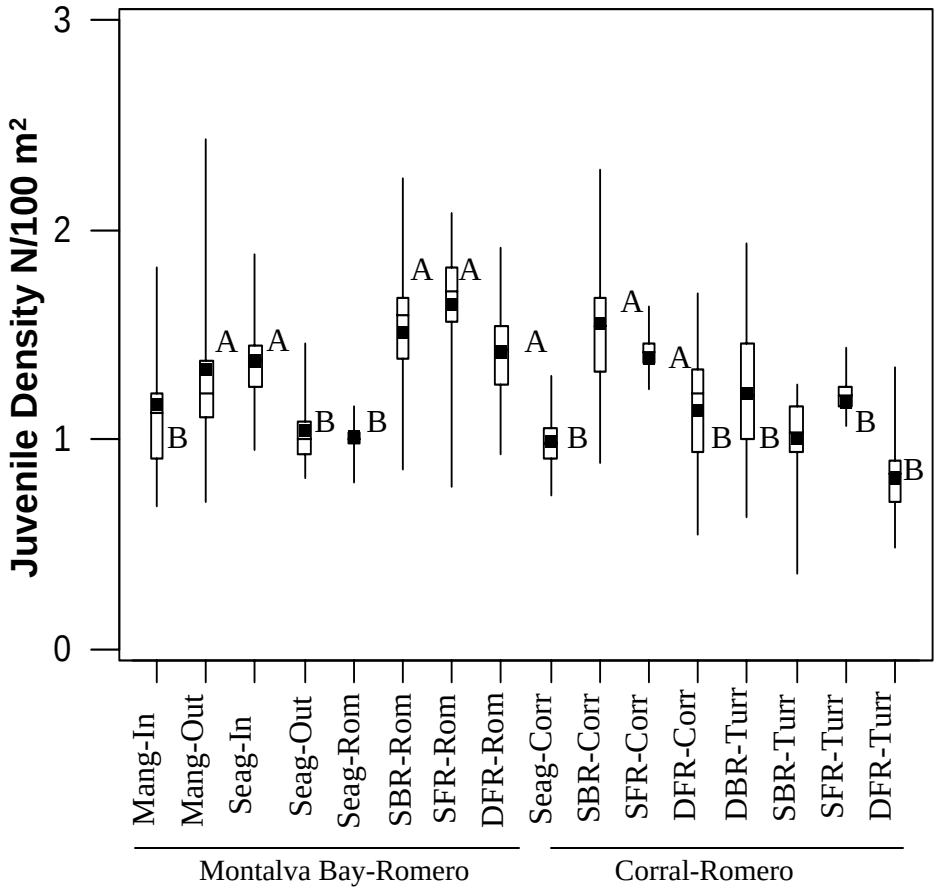


Fig. 4. Mean density of juveniles per stratum along the inshore-offshore gradient. Groups with the same letter are not significantly different from each other as determined by the Tukey-Kramer HSD test ($\alpha = 0.05$). Data were square root transformed for analysis. Whiskers (i.e., vertical lines: upper and lower limits; Box: 95% C.I., black square: mean; lines in boxes: medians. See text for meaning of strata labeling.

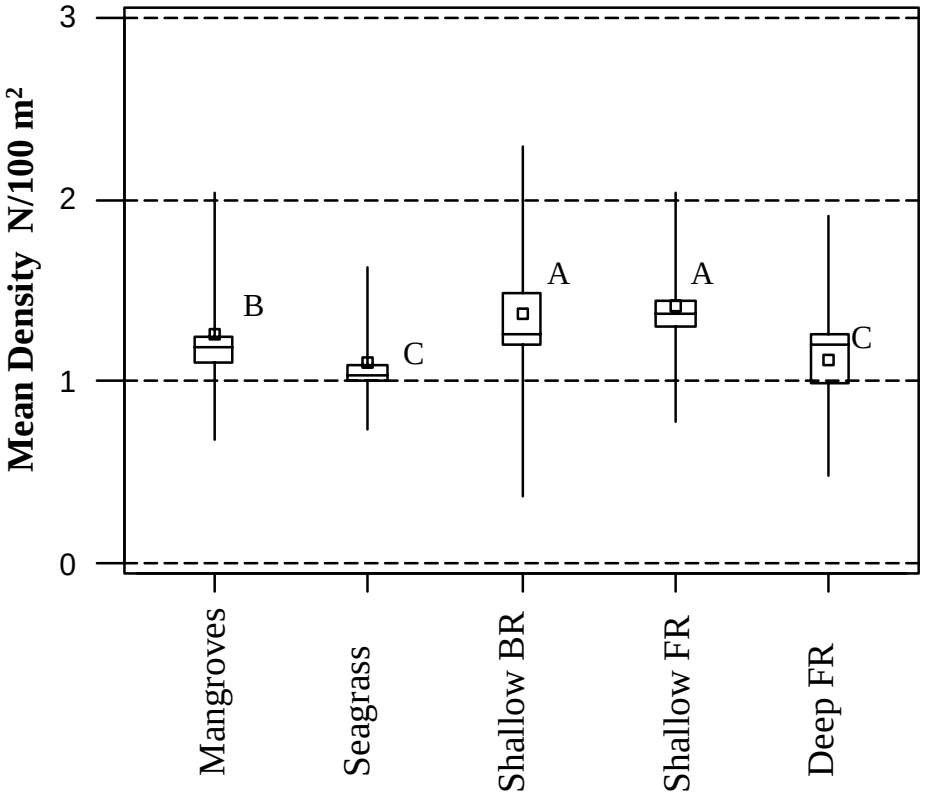


Fig. 5. Mean density of juveniles per biotope along the inshore-offshore gradient. Groups with the same letter are not significantly different from each other as determined by the Tukey-Kramer HSD test ($\alpha = 0.05$). Data were square root transformed for analysis. Boxes represent 95% confidence limits, small squares inside the boxes are means, and the whiskers are upper and lower limits. Lines inside are medians. BR: back reef, FR: fore reef.

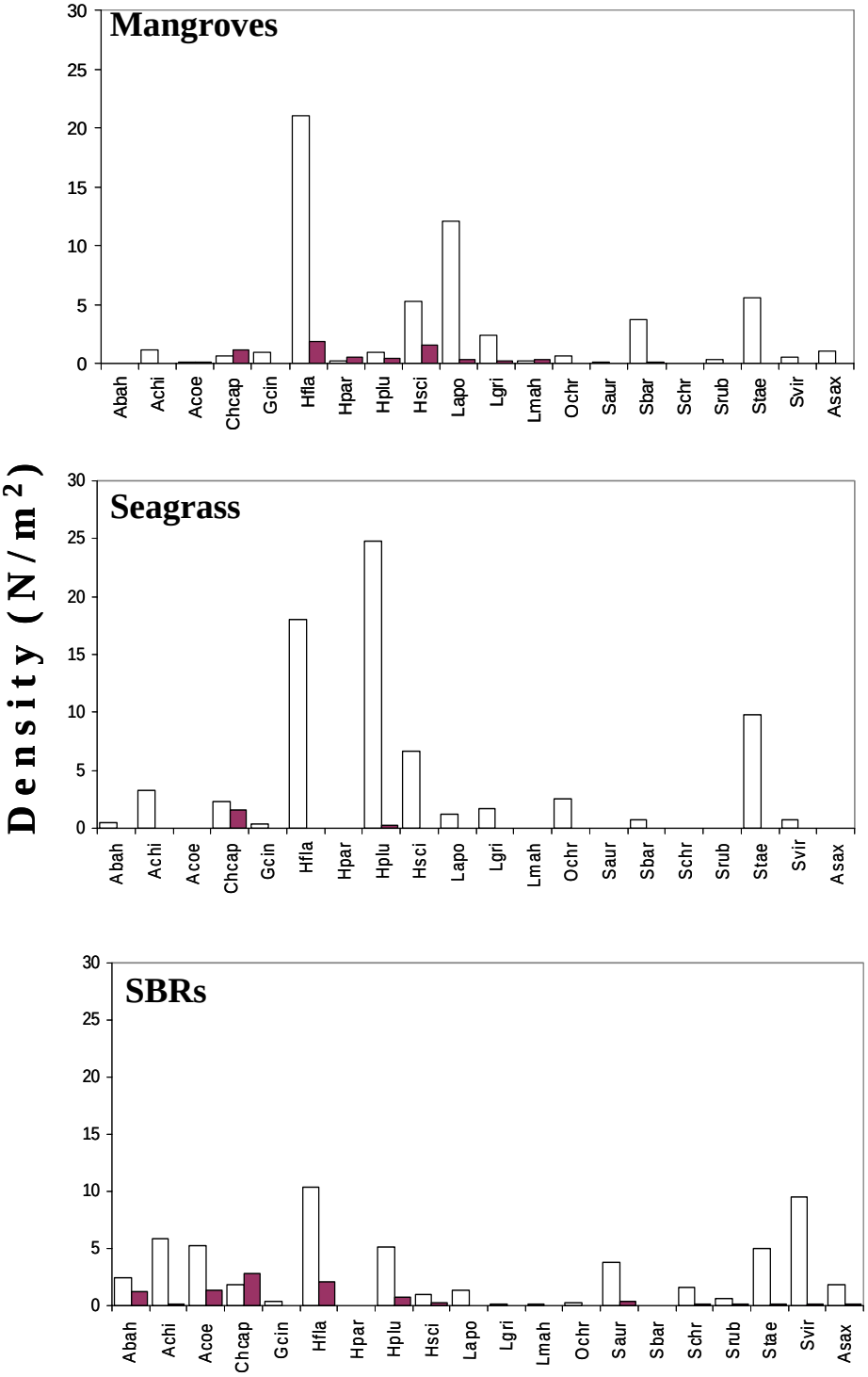


Fig. 6. Total density per 100 m^2 of juveniles and adults according to species and strata per biotope. X-axis refers to species, while Y-axis refers to density. SBRs: shallow back reefs. Open bars: Juveniles, Dark bars: Adults. See Table 2 for species codes.

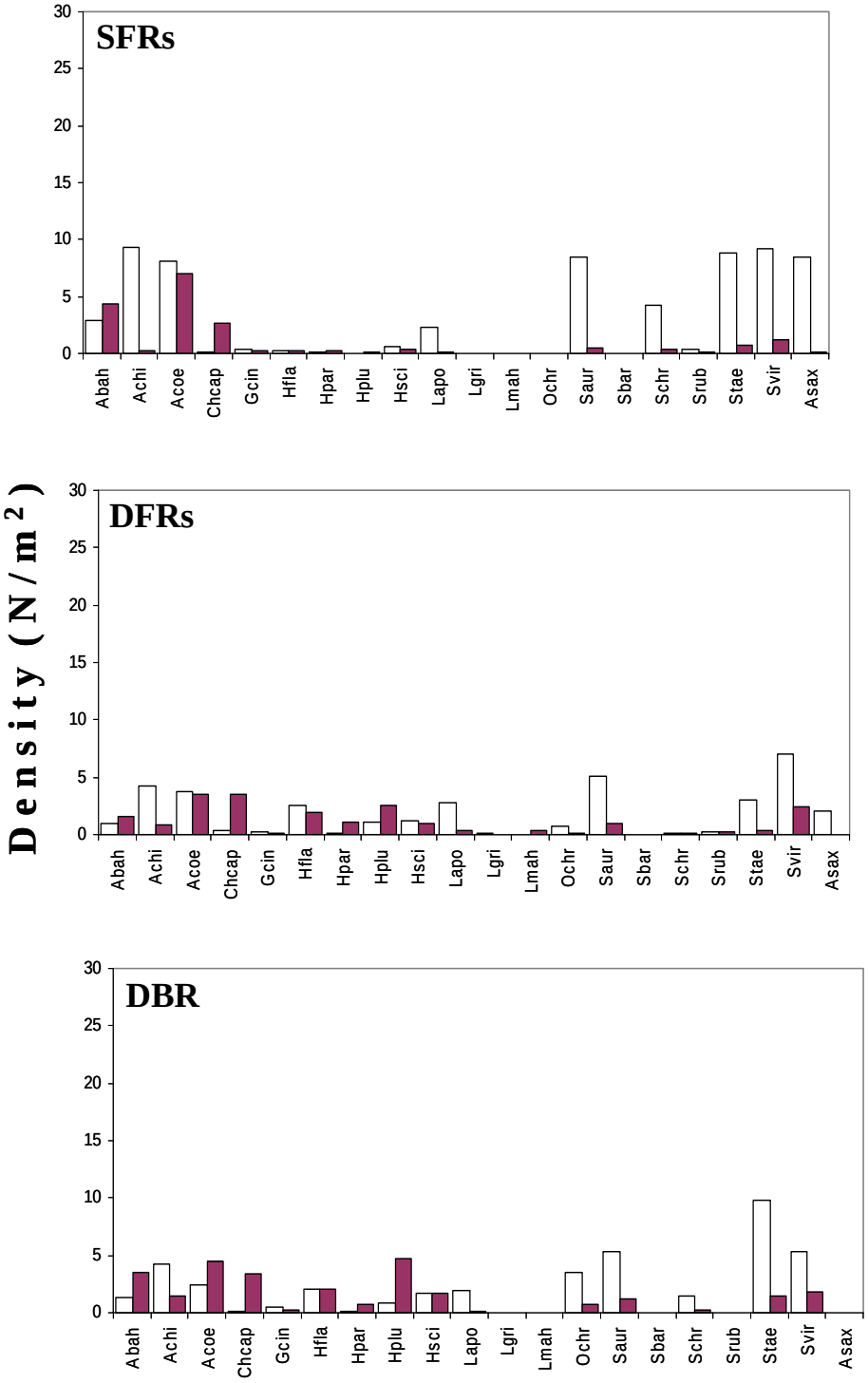


Fig. 7. Total density per 100 m^2 of juveniles and adults according to species and strata per biotope. X-axis refers to species, while Y-axis refers to density. SFRs: shallow fore reefs, DFRs: deep fore reefs, and DBR: deep back reef. Open bars: Juveniles, Dark bars: adults. See Table 2 for species codes.

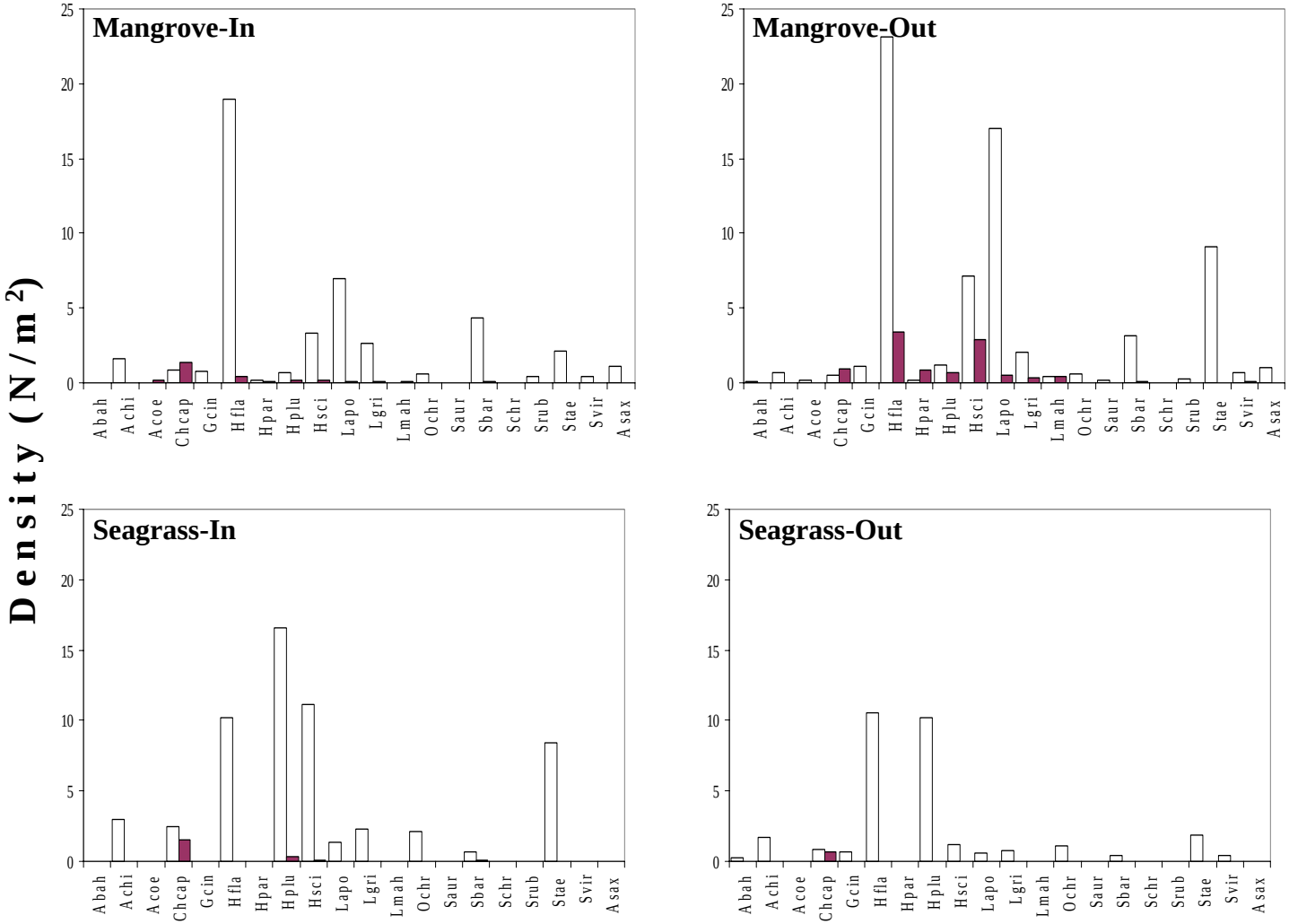


Fig. 8. Total density (N/100 m^2) of juveniles and adults per stratum and species for Montalva Bay. X-axis refers to species, while Y-axis refers to density. Open bars: Juveniles, Dark bars: Adults. See Table 2 for species codes.

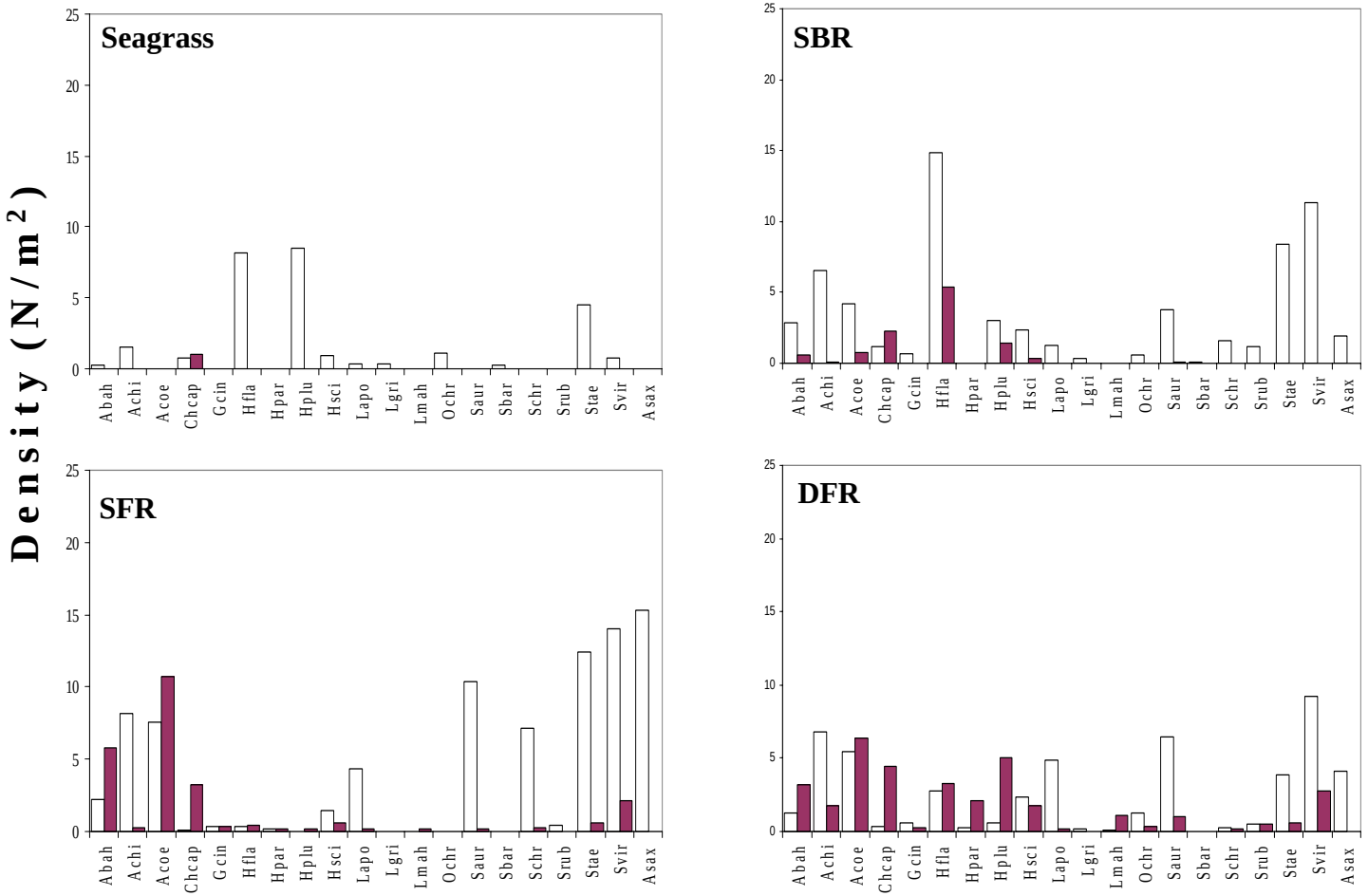


Fig. 9. Total density (N/100 m^2) of juveniles and adults per stratum and species for Romero key. X-axis refers to species, while Y-axis refers to density. Open bars: Juveniles, Dar bars: Adults. SBR: shallow back reef, SFR: shallow fore reef, DFR: deep fore reef. See Table 2 for species codes.

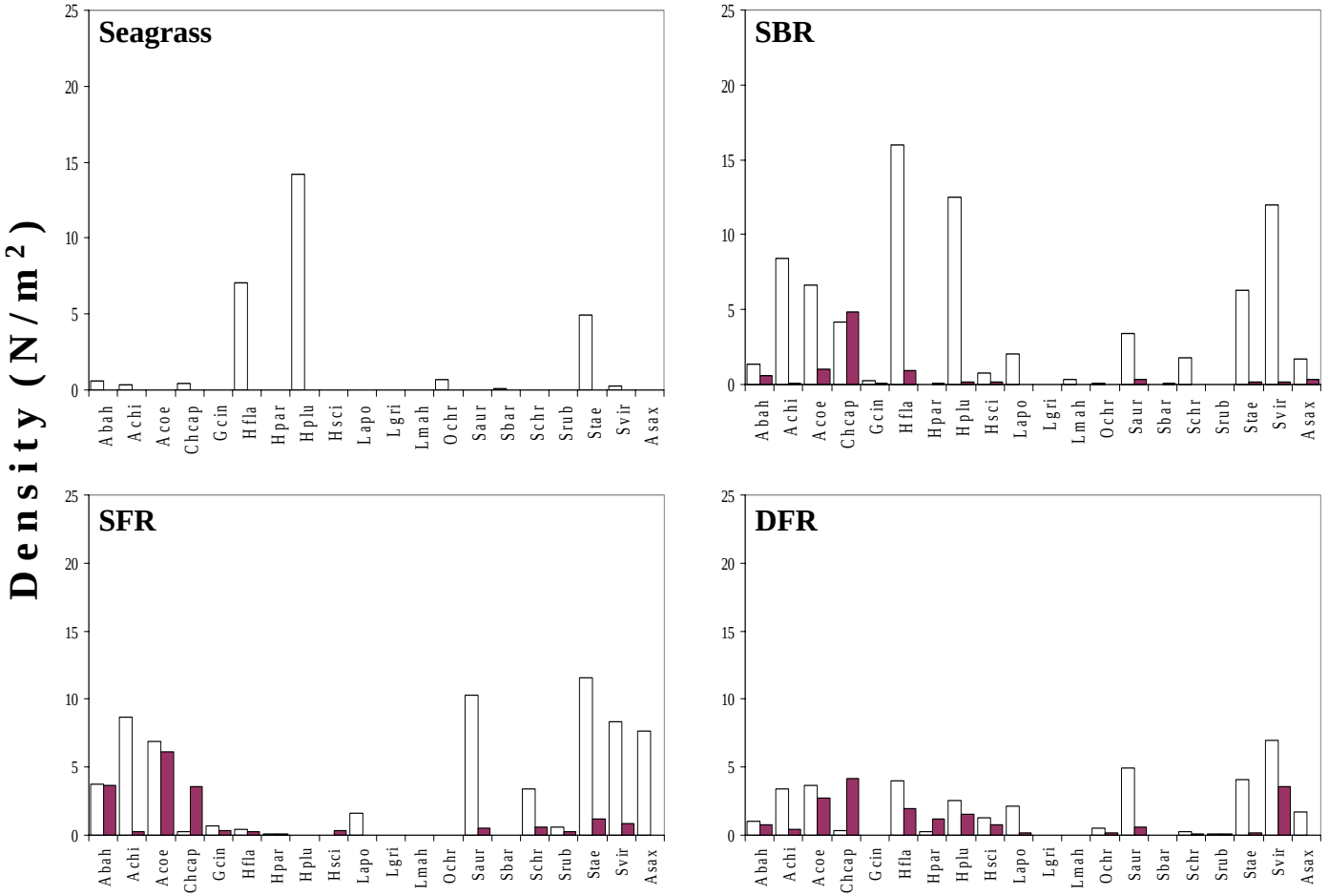


Fig. 10. Total density (N/100 m^2) of juveniles and adults per stratum and species for Corral key. X-axis refers to species, while Y-axis refers to density. Open bars: Juveniles, Dark bars: Adults. SBR: shallow back reef, SFR: shallow fore reef, DFR: deep fore reef. See Table 2 for species codes.

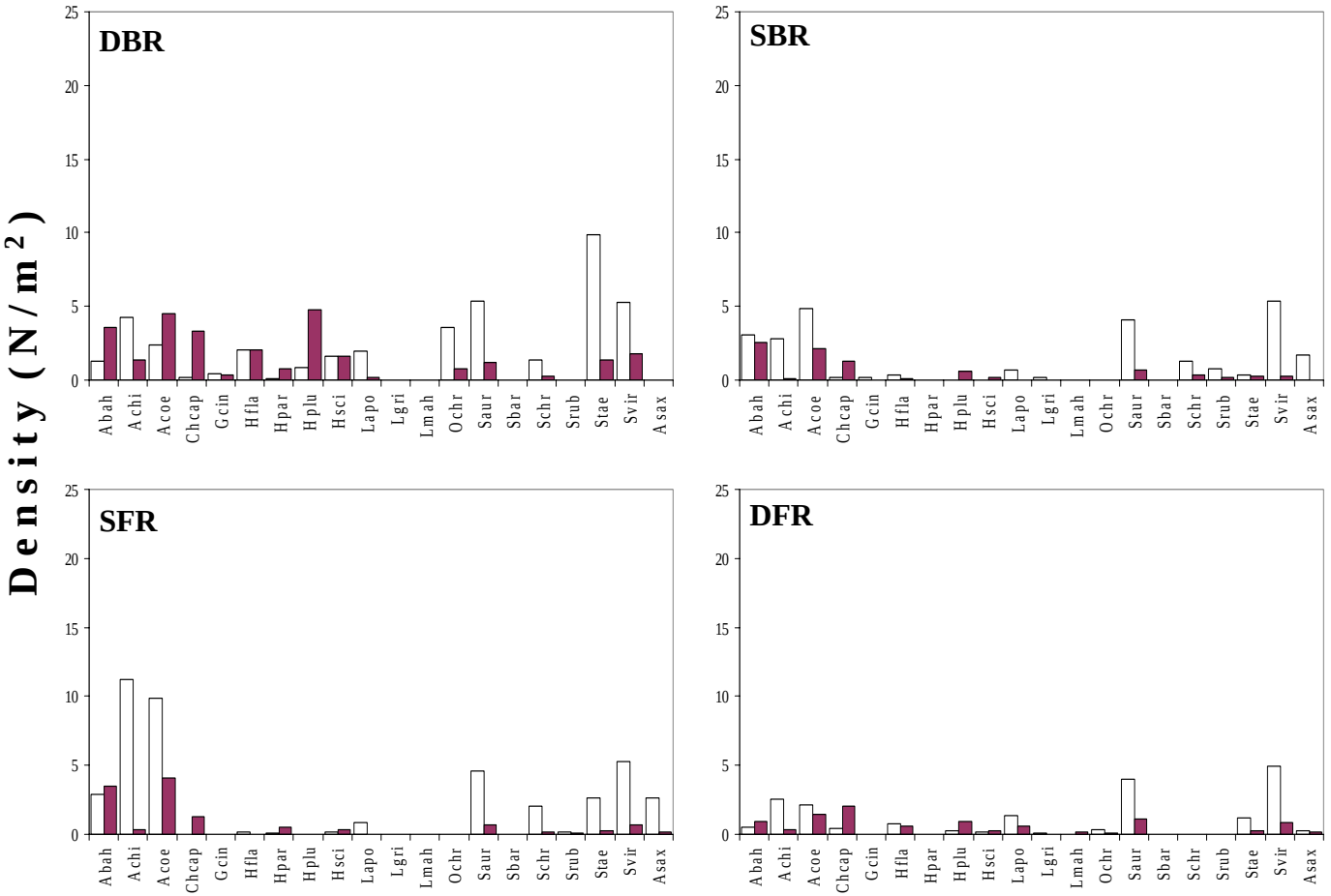


Fig. 11. Total density (N/100 m^2) of juveniles and adults per stratum and species for Turrumote key. X-axis refers to species, while Y-axis refers to density. Open bars: Juveniles, Dark bars: Adults. DBR: deep back reef, SBR: shallow back reef, SFR: shallow fore reef, DFR: deep fore reef. See Table 2 for species codes.

Table 1. Sampling intensity, stratum, depth, and transect area surveyed along the inshore-offshore gradient in southwestern Puerto Rico. Every site represents 1 000 m^2 (i.e., a site is 10 transects of 100 m^2 each). In Montalva Bay, the 12 sites for mangroves and seagrass were split into 2 strata (Mang-In, Seag-In) inside the bay and 2 strata (Mang-Out and Seag-Out) outside the bay, with 3 sites per strata.

Location	**No. of Sites**	**Mangrove**	**Seagrass**	**Shallow Back Reef (SBR) 0-3 m**	**Deep Back Reef (DBR) 3-10 m**	**Shallow Fore Reef (SFR) 0-3 m**	**Deep Fore Reef (DFR) 3-10 m**
Montalva	12	6	6	-	-	-	-
Romero	12	-	3	3	-	3	3
Corral	12	-	3	3	-	3	3
Turrumote	12	-	-	3	3	3	3
Transect area (m^2)	48 000	6 000	12 000	9 000	3 000	9 000	9 000

Table 2. Maturation sizes, percent of juveniles, total density, and relative species abundance (%) of the 20 selected fish species. Maturation data taken from Nagelkerken et al. (2000), García-Cagide et al. (2001), and Fishbase (www.fishbase.org, Froese and Pauly 1993). According to Nagelkerken et al. (2000) N: nursery species, R: reef species (see text for definition).

Species	**Codes**	**Group**	**Maturation size (cm, FL)**	**% Juveniles**	**Density (100 m^2)**	**%**
Haemulon flavolineatum	Hfla	N	10	86	138.4	14.4
H. plumieri	Hplu	N	10	82	87.1	9.1
H. parrai	Hpar	N	10	18	7.1	0.7
H. sciurus	Hsci	N	15	78	43.4	4.5
Gerres cinereus	Gcin	N	15	80	7.1	0.7
Ocyurus chrysurus	Ochr	N	15	91	14.0	1.5
Lutjanus apodus	Lapo	N	20	96	49.4	5.2
L. griseus	Lgri	N	15	95	9.2	1.0
L. mahogoni	Lmah	N	10	30	2.8	0.3
Acanthurus bahianus	Abah	R	10	46	46.4	4.8
A. coeruleus	Acoe	R	10	57	93.9	9.8
A. chirurgus	Achi	N	15	94	76.7	8.0
Sphyraena barracuda	Sbar	N	40	96	9.3	1.0
Sparisoma aurofrenatum	Saur	R	15	90	63.8	6.7
S. chrysopterum	Schry	N	15	91	21.1	2.2
S. rubripinne	Srub	R	15	79	5.5	0.6
S. viride	Svir	R	15	87	98.5	10.3
Scarus taeniopterus	Stae	R	15	95	96.3	10.0
Chaetodon capistratus	Chcap	N	5	27	49.0	5.1
Abudefduf saxatilis	Asax	R	10	98	39.8	4.1
Total				**80**	**59.9**	

Table 3. Total density, percent of juveniles, species richness (S), and relative fish abundance (%) for the 16 strata along the inshore-offshore gradient.

Strata	Density ($100\ m^2$)	Percent of Juveniles	S	%
Montalva Mang-In	47.6	94	17	4.97
Montalva Mang-Out	78.9	87	19	8.23
Montalva Seag-In	60.4	97	11	6.30
Montalva Seag-Out	31.4	98	15	3.28
Seag-Romero	28.5	96	13	2.97
SBR-Romero	77.2	86	19	8.05
SFR-Romero	109.5	77	15	11.43
DFR-Romero	86.1	60	19	8.98
Seag-Corral	28.7	100	10	2.99
SBR-Corral	86.9	89	18	9.06
SFR-Corral	82.3	78	15	8.59
DFR-Corral	55.4	67	16	5.78
DBR-Turrumote	68.4	59	16	7.13
SBR-Turrmote	34.4	75	16	3.59
SFR-Turrmote	54.5	78	13	5.68
DFR-Turrmote	28.5	66	14	2.98
Total	**59.9**	**80**	**20**	

Mang: Mangrove, Seag: Seagrass, SBR: Shallow back reef, SFR: Shallow fore reef, DFR: Deep fore reef.

Table 4. Strata containing highest densities of juveniles and adults of fish species along the inshore-offshore gradient in southwestern Puerto Rico. Gray areas refer to most important strata (relative abundance > 20 % of either juveniles or adults among strata). + = important strata (relative abundance 10-20%). MB: Montalva Bay; SBR: shallow back reef; SFR: shallow fore reef; DFR: deep fore reef; DBR: deep back reef; FL: forked length.

Species	Maturation size (cm, FL)	Mangrove-In-MB	Mangrove-Out-MB	Seagrass-In-MB	Seagrass-Out-MB	Seagrass-Romero	SBR-Romero	SFR-Romero	DFR-Romero	Seagrass-Corral	SBR-Corral	SFR-Corral	DFR-Corral	DBR-Turrumote	SBR-Turrumote	SFR-Turrumote	DFR-Turrumote
Haemulon flavolineatum	10																
Juvenile		+	+				+				+						
Adult			+			+		+				+	+				
Haemulon plumieri	10																
Juvenile				+	+					+	+						
Adult								+				+	+				
Haemulon parrai	10																
Juvenile		+	+					+	+				+				
Adult		+					+				+	+					
Haemulon sciurus	15																
Juvenile		+	+	+													
Adult		+					+					+					
Gerres cinereus	15																
Juvenile		+	+	+		+		+				+					
Adult							+	+				+	+				
Ocyurus chrysurus	15																
Juvenile				+					+					+			
Adult								+					+				
Lutjanus apodus	20																
Juvenile		+	+						+								
Adult		+													+		
Lutjanus griseus	15																
Juvenile		+	+	+													
Adult			+														
Lutjanus mahogoni	10																
Juvenile			+														
Adult			+					+									
Acanthurus bahianus	10																
Juvenile							+	+				+			+	+	
Adult								+	+			+		+		+	
Acanthurus coeruleus	10																
Juvenile								+	+	+	+	+				+	
Adult								+	+			+		+		+	
Acanthurus chirurgus	15																
Juvenile								+			+	+				+	
Adult							+						+				
Sphyraena barracuda	40																
Juvenile		+	+														
Adult			+														

Table 4, cont.

Species	Maturation size (cm, FL)	Mangrove-In-MB	Mangrove-Out-MB	Seagrass-In-MB	Seagrass-Out-MB	Seagrass-Romero	SBR-Romero	SFR-Romero	DFR-Romero	Seagrass-Corral	SBR-Corral	SFR-Corral	DFR-Corral	DBR-Turrumote	SBR-Turrumote	SFR-Turrumote	DFR-Turrumote
Sparisoma aurofrenatum	15																
Juvenile								+	+			+					
Adult									+					+	+	+	+
Sparisoma chrysopterum	15																
Juvenile								+				+				+	
Adult								+				+			+	+	+
Sparisoma rubripinne	15																
Juvenile							+		+			+			+		
Adult									+			+					
Sparisoma viride	15																
Juvenile							+	+	+		+	+					
Adult								+	+				+	+			
Scarus taeniopterus	15																
Juvenile			+					+				+		+			
Adult								+	+			+		+			
Chaetodon capistratus	5																
Juvenile				+							+						
Adult								+			+	+	+				
Abudefduf saxatilis	10																
Juvenile								+	+			+					
Adult											+						

CHAPTER 4: ONTOGENETIC HABITAT SHIFTS IN FISHES ASSOCIATED TO CORAL REEFS FROM SOUTHWESTERN PUERTO RICO

INTRODUCTION

In the Caribbean, mangroves and seagrass beds represent important nursery habitats for many reef fish species (Parrish 1989; Roberts 1996; Nagelkerken et al. 2000; Adams and Ebersole 2002). The nursery function of such habitats is related to the availability of food, shelter, and reduced predation for high densities of juveniles (Parrish 1989; Beck et al. 2001; Laegdsgaard and Johnson 2001). However, in the Pacific, the nursery value of mangroves and seagrass is elusive (Thollot 1992).

During post-settlement many fish species using either mangroves or seagrass as nurseries, perform progressive ontogenetic migrations or post-settlement life cycle migrations (PLCMs, Cocheret de la Morinière et al. 2002), from such nursery shallow-water habitats (e.g., mangroves and seagrass) to adult deeper habitats (e.g, coral reefs) to complete their life cycle (Parrish 1989; Eggleston 1995; Dahlgren and Eggleston 2000; Appeldoorn et al. 1997; Lindeman et al. 2000). These ontogenetic habitat shifts are commonly inferred through the size or age structure of populations in different habitats over time (Jones 1991). As the fish grows, it takes a combination of behavioral decisions related with foraging demands, predator avoidance or reproduction (Lima and Dill 1990; Utne et al. 1993) that are reflected in their patterns of spatial distribution (Williams 1991). Such decisions vary due to changes in morphology and increases in body size during ontogeny, and consequently ecological needs for appropriate habitat change accordingly (Ludwig and Rowe 1990). Net results of habitat selection and utilization are thought to arise from trade-offs between maximizing growth rate (*g*) and minimizing

predation risk (μ), which has been suggested as the minimize μ/*g* hypothesis (Werner and Gilliam 1984).

Studies on the ecology of early juvenile fishes have focused on damselfishes (Pomacentridae) and labrids (Labridae) which settle directly onto coral reefs (Doherty 1991). However, recent studies of medium and top level predators of commercial importance, such as grunts (Haemulidae), groupers (Serranidae), snappers (Lutjanidae) from Caribbean islands (Appeldoorn et al. 1997; Lindeman et al. 2000; Nagelkerken et al. 2000; Dahlgren and Eggleston 2000; Nagelkerken and van der Velde 2002; Christensen et al. 2003; Appeldoorn et al. 2003), have illustrated the importance that off-reef habitats have in relation to ontogenetic migrations.

While the reef fishes of Puerto Rico have been extensively studied (Austin 1971; Austin and Austin 1971; Kimmel 1985; Rooker and Dennis 1991; McGehee 1994; Acosta 1997; Murphy 2001; Christensen et al. 2003; Foley 2003), little information is available on the extent of connectivity in terms of ontogenetic shifts (Appeldoorn et al. 1997) along the mangrove-seagrass-coral reef continuum. A previous study (Chapter 3) has elucidated that there are differences in the distribution of juveniles and adults in southwestern Puerto Rico, but studies analyzing habitat use across fish size ranges to indicate processes of species-habitat interactions and connectivity are lacking.

To investigate whether 20 selected fish species, along an inshore-offshore, cross-shelf gradient in southwestern Puerto Rico, showed evidences of conducting ontogenetic habitat shifts, I compared site-specific size-frequency distributions to infer such post-settlement life cycle migrations (PLCMs) involving habitat transitions along a inshore-offshore gradient from a bay to coral reefs. In this study, I investigated the spatial

patterns of habitat use of fish species along the inshore-offshore gradient using multivariate analysis (i.e., cluster) based on size-frequency distributions and relative density per size class to elucidate ontogenetic cross-shelf migrations and the degree of habitat connectivity between mangrove, seagrass, and shallow-water coral reefs from bay habitats to coral reefs.

MATERIALS AND METHODS

Study site

The study was conducted at the eastern part of La Parguera, southwestern shelf of Puerto Rico from January 2003 to May 2004. This shelf has complex physiography, including submerged and emergent reefs (Morelock et al. 1977) and a variety of biotopes (e.g., mangroves, seagrass beds, algal plains, sandy-mud lagoons, and patch reefs) (Kimmel 1985). Selected locations of study, along an inshore-offshore gradient and including the mangrove-seagrass-coral reef continuum, were Montalva Bay, Romero Key, Corral Key, and Turrumote (Fig. 1). Reasons for selection of such locations were based on the presence of a proposed marine reserve offshore (i.e., Turrumote) and the proximity of this reserve to bay (i.e., Montalva) and shallow-water coral reefs. Montalva Bay (17° 57’ 55N; 66° 59’34W) is a non-estuarine, coastal system (3.7 km^2) fringed by mangroves (*Rhizophora mangle* predominantly) and shallow water areas (i.e., sand, mud), covered with seagrass beds (*Thallassia testudinum* predominantly). Romero Key (17° 56’ 52” N; 66° 59’48” W), located 2.3 km from shore and at the entrance of Montalva bay, is an emergent reef (0.7 km^2) with relatively small mangrove areas (i.e., prop-root areas not sufficient to be surveyed in this study) and shallow reef and seagrass

bed areas (*Thallassia testudinum*, predominantly). Corral Key (17° 56' 43" N; 67° 00'34" W), located 2.9 km from shore and off Montalva Bay, is also an emergent reef (1.5 km^2) with shallow coral reefs and seagrass beds (*Thallassia testudinum*, predominantly) and little mangrove areas (i.e., prop-root areas not sufficient in water to be surveyed). At the end of the inshore-offshore gradient lays Turrumote (17° 56' 12" N; 67° 01'09" W), in which there is a proposed marine reserve (7.6 km^2). This little emergent key (0.1 km^2) is located at mid distance between the coastline and the insular shelf edge (4.6 km) and its reef system is comprised by emergent coral reefs and several submerged reefs with an extensive hard ground, low relief platform. It has no mangrove areas, a very small patch of seagrass (16 m^2), and mostly shallow and deeper coral reefs; in addition, it has profuse soft-coral (e.g., gorgonians) areas.

Study design

A stratified sampling procedure was applied to investigate the variability of fish densities along the mangrove-seagrass-coral reef continuum following an inshore-offshore gradient. At each location, 2 to 4 major strata were selected according biotope (e.g., mangrove, seagrass, coral reef), depth (e.g., shallow: 0-3 m, deep: 3-10 m) and wave exposure (e.g., fore reef, back reef). At each stratum 3 sites were randomly selected, but located as possible, at the eastern, middle and western parts of each stratum in order to cover a greater extent. At each site, 10 transects (i.e. 100 m^2) were sampled, totaling for 1 000 m^2 per site or 3 000 m^2 per stratum (Table 1). For Montalva Bay, the strata selection was based on biotope (i.e., mangrove and seagrass) and distance from shore (i.e., inside the bay or outside the bay), resulting in 2 strata for mangroves (i.e.,

Mang-In and Mang-Out) and 2 for seagrass beds (i.e., Seag-In and Seag-Out). For Romero Key, selection was based on biotope (i.e, seagrass and coral reef), wave exposure (i.e., back reef, fore reef) and depth (i.e., 0-3 m and 3-10 m), resulting in 1 strata for seagrass beds (i.e., Seag-Rom), 2 strata for shallow coral reefs (i.e., shallow back reef and shallow fore reef, SBR and SFR) and 1 strata for deep coral reefs (i.e., deep fore reef, DFR). For Corral Key (i.e., Seag-Corr, SBR, SFR, and DFR), selection was similar to Romero Key. In the case of Turrumote, the same criteria applied; however, since the seagrass bed area is negligible, the resulting strata were 2 for shallow reefs (i.e., shallow back reef and shallow fore reef, SBR and SFR) and 2 for deep reefs (i.e. deep back reef and deep fore reef, DBR and DFR).

Fish censuses

Of the 103 fish species recorded in the various strata along the inshore-offshore gradient (see Chapter 2), 20 species were selected in this study based on (1) high relative abundance (see Chapter 2) compared to other species along the inshore-offshore gradient, (2) commercial (e.g., fisheries, aquarium industry, Haemulidae, Lutjanidae) and ecological importance (e.g., herbivores, Acanthuridae, Scaridae), (3) documented evidence for 13 of them as nursery species (Nagelkerken et al. 2000; Chapter 3), and (4) documented evidence for many on performing ontogenetic migrations (Nagelkerken et al. 2000; Nagelkerken and van der Velde 2003; Cocheret de la Morinière et al. 2002; Appeldoorn et al. 2003; Christensen et al. 2003). The selected species consisted of 4 grunts (Haemulidae): *Haemulon flavolineatum*, *H. plumieri*, *H. sciurus*, *H. parrai*; 3 surgeon fishes (Acanthuridae): *Acanthurus bahianus*, *A. chirurgus*, *A. coeruleus*; 5

parrotfishes (Scaridae): *Sparisoma aurofrenatum, S. chrysopterum, S. rubripinne, S. viride*, and *Scarus taeniopterus*; 4 snappers (Lutjanidae): *Lutjanus apodus*, *Ocyurus chryrsurus, L. griseus*, *L. mahogoni*; 1 butterflyfish (Chaetodontidae): *Chaetodon capistratus*; 1 barracuda (Sphyraenidae): *Sphyraena barracuda*; 1 mojarra (Gerreidae): *Gerres cinereus*, and 1 damselfish (Pomacentridae): *Abudefduf saxatilis*. Recognition of juveniles of the selected fish species recorded in this study was based on documented maturation sizes available in literature (Nagelkerken 2000; García-Cagide et al. 2001) and Fishbase (at www.fishbase.org; Froese and Pauly 1993).

The selected fish species were studied using an adaptation of the underwater visual census (UVC) based on belt-transects (Brock 1954). This is a non-destructive technique for estimating reef fish populations enabling the researcher to select specific species, requiring only one worker, and is relatively rapid and inexpensive (Fowler 1987). Potential disadvantages of the UVC relate to variations in swimming speed (Lincoln Smith 1988), transect width (Cheal and Thompson 1997), fish length estimation (Bellwood and Alcala 1988), species identification (Brock 1982), and replicate number (Samoilys and Carlos 2000). Despite these potential disadvantages, the UVC allows rapid estimates of relative abundance, biomass, and length frequency distributions of reef fishes. For this reason, the UVC is the most practical and extensively used technique to study a wide range of demersal species taken by shallow-water fisheries on coral reefs (Nagelkerken et al. 2000; Christensen et al. 2003; Appeldoorn et al. 2003).

For every individual of the selected species observed within the belt-transects, body length in centimeters of forked length (FL), grouped in size classes of 5 cm, was recorded. Each transect was 25 m by 2 m each side of the line transect (25 x 4 m). Such a

dimension was chosen for three reasons: (1) it immediately renders an area of 100 m^2 per replicate (i.e., transect), (2) comparisons with previous works can be made, and (3) it is amenable for use at the three biotopes selected (i.e., mangroves, seagrass, and coral reefs). For reducing potential bias and improve accuracy of fish length estimation, wooden fish models of several lengths (5-40 cm) tied to the reef bottom (Rooker and Recksiek 1992) were used as calibration objects before starting the study. Furthermore, transect duration (i.e., fish count) was standardized to less than 20 min per transect, and the censuses were conducted at least 15 min after laying down the transect line on the bottom to allow fish normal behavior to resume after setting the line on the bottom. SCUBA was used in deeper locations (> 5 m), while snorkeling was used during shallow surveys (< 5 m), mainly in the mangrove prop-roots and seagrass beds. Transect width in the mangrove prop-roots was adapted as much as possible to the selected transect dimension, in some instances it was less than 2 m at each side of the transect line. For schooling fishes (e.g., *Haemulon flavolineatum*, *Acanthurus coeruleus*, *Lutjanus apodus*) forming groups of more than 50 individuals, previous essays were performed to calibrate number estimation by using counting techniques for shorebirds (Haig 2004).

Statistical analysis

For each of the 20 selected fish species, evidence of ontogenetic migration/habitat shifts was taken as changes in the length composition of the samples obtained across the inshore-offshore, of shelf gradient. To compare the community structure of the fish species between the different strata along the inshore-offshore gradient, a cluster analysis was used. Densities per species and size classes for each stratum were transformed to

percentages of total composition of a given species and were square root transformed for cluster analyses using the program Multivariate Statistical Package 3.1. The average-linkage method (with weighted pair group average) was used in combination with the Bray-Curtis coefficient.

RESULTS

A total of 28 758 individuals of the 20 selected fish species in 7 families were recorded among mangroves, seagrass beds and coral reefs, along an inshore-offshore gradient (i.e., Montalva Bay to Turrumote). Cluster analysis of Haemulidae exhibited a spatial separation in stratum (or biotope) use among the size classes and species (Fig. 2). Juveniles were found in mangroves, seagrass, and SBRs, while adults were mainly found at SFRs and DFRs. Given the entire species size range (i.e., including juveniles and adults), *Haemulon flavolineatum* dominated in terms of density over its related species in mangroves, SBR Romero and SBR and SFR Corral, while *H. plumieri* dominated in seagrass and *H. sciurus* in SFRs of Romero and Turrumote (Fig. 3). At Montalva Bay-Romero, juveniles of *Haemulon flavolineatum* (0-10 cm) and *H. sciurus* (0-15 cm) were mainly found in mangroves and seagrass of Montalva bay and seagrass of Romero, respectively; while at Corral-Turrumote, *H. flavolineatum* occurred at SBR Corral and *H. sciurus* occurred at DBR Turrumote (Fig. 4, 5). Adults of *H. flavolineatum* (> 10 cm) were more common at SBR and DFR of Romero (with the former stratum as the most important in terms of density), while adults were common at DFR Corral. Adults of *H. sciurus* (> 15 cm) co-occurred with juveniles at mangroves of Montalva Bay, while at Turrumote they were common at DFR. Many small adults of *H. flavolineatum* (10-15

cm) used the SBR of Romero as an intermediate stratum in their ontogenetic shift from mangroves and seagrass beds of Montalva bay to the deeper coral reefs off Romero (Fig. 4), while many adults of *H. sciurus* (15-20 cm) used the mangroves as intermediate stratum for reaching deeper coral reefs of Romero. Juveniles of *H. plumieri* (0-10 cm) were mostly found at seagrass of Montalva Bay and Romero and seagrass of Corral, while the adults were more common at SBR and SFR of Romero and DBR and SBR of Turrumote. DFR Romero and DFR Corral were important for juveniles of *H. parrai* (0-10 cm), while the adults (> 10 cm) mostly occurred at SFR Romero and DBR Turrumote (Fig. 5).

Cluster analysis of Lutjanidae, also showed a spatial separation in stratum use among the size classes and species (Fig. 6). While juveniles of some species were mainly found in seagrass and mangroves (e.g., *Lutjanus apodus*), juveniles of others were mainly found in SBRs or SFRs (e.g., *Ocyurus chrysurus*) (Fig. 7, 8). *Lutjanus apodus* dominated in terms of density over its related species in mangroves and SBRs, SFRs and DFRs (Fig. 3). Juveniles of *L. apodus* (0-20 cm) were mainly found in mangroves of Montalva Bay and SBR Corral. Juveniles of *Ocyurus chrysurus* (0-15 cm) were mainly found at seagrass of Montalva; however, juveniles and adults (>15 cm) co-occurred at DFR Romero and DBR Turrumote. Juveniles (0-10 cm) and adults (>10 cm) of *L. griseus* were found mostly at mangroves and seagrass of Montalva and Romero, with the mangrove-in stratum as important for adults, but as the most important nursery habitat for juveniles. Juveniles (0-10 cm) and adults (>10 cm) of *L. mahogoni* were common at mangroves, but DFR Romero was the most important stratum for adults.

Cluster analysis of Scaridae revealed a spatial separation in habitat use among the size classes and species (Fig. 9). Out of the 5 species, only 2 (i.e., *Sparisoma viride* and *Scarus taeniopterus*) as juveniles were mainly found in mangroves and seagrass, while the other species shown preferences as juveniles for SBRs and SFRs strata (Fig. 10, 11). *Scarus taeniopterus* dominated in terms of density over its congeners in most of the inshore-offshore gradient strata, while *Sparisoma viride* dominated mainly in shallow and deep coral reefs (Fig. 12). Juveniles of *Sparisoma rubripinne* (5-15 cm) and *Scarus chrysopterum* (0-15 cm) were mainly found at SBR Romero and SBR Corral for the former and SBR Turrumote for the latter. Juveniles of *S. taeniopterus* also were found in SFR Romero and SFR Corral, and DBR Turrumote. Adults of *S. rubripinne* were mostly found in DFR Romero and SFR Corral, while adults of *S. taeniopterus* were found at SFR and DFR Romero and SFR Corral and DBR Turrumote, being these latter the most important strata in terms of density for adults. Juveniles of *Sparisoma aurofrenatum* (0-15 cm) and *S. viride* (0-15 cm) were mainly found at SBR, SFR and DFR Romero at inshore, and SBR and SFR Corral at offshore. The most important nursery stratum for *S. aurofrenatum* was SFR Romero, whereas juveniles of *S. viride* did not show a marked preference. Adults of *S. aurofrentaum* were mainly found at SFR Romero and SFR Corral, and most of the strata in Turrumote, while adults of *S. viride* were mainly found at SFR and DFR Romero and DFR Corral and DBR Turrumote. DFR Corral was the most important habitat for adults of *S. viride*. Juveniles of *S. chrysopterum* were mainly found at SFR Romero and SFR Corral, but the former was the most important nursery stratum. Adults of *S. chrysopterum* were also found at SFR Romero and SFR Corral

where this latter was the most important stratum in terms of density; adults also occurred at most of the strata of Turrumote.

Cluster analysis of Acanthuridae revealed a spatial separation in habitat use among the size classes and species (Fig. 13). *Acanthurus chirurgus* dominated in terms of density over its congeners in most of the strata along the inshore-offshore gradient, followed by *A. coeruleus* mainly in the coral reefs (Fig. 12). Juveniles of *Acanthurus chirurgus* were found in most of the strata, including mangroves and seagrass, but they were mainly found at SBR and SFR of Romero and Corral, respectively; adults shown similar distribution, but SFR Romero was the most important stratum. Juveniles of *A. coeruleus* had similar distribution to that of *A. chirurgus*, but the former was not found in mangroves; adults also shown preferences for the SFR of Romero. Juveniles of *A. bahianus* were mainly found at SBR and SFR of Romero, SFR of Corral, and SFR and DFR of Turrumote, while adults shown a similar distribution to that of *A. coerulues* (Fig. 14, 15).

Juveniles of *Gerres cinereus* (0-15 cm) and *Sphyraena barracuda* (0-40 cm) were mainly found at mangroves and seagrass of Montalva Bay (Fig. 16). In the latter, juveniles were mostly found in mangroves. Adults were found at the SFR Romero, DFR Corral and DBR Turrumote in the case of *G. cinereus*, and in seagrass mainly in the case of *S. barracuda*, with some individuals of the latter at deeper coral reefs. Juveniles of *Abudefduf saxatilis* (0-10 cm) were commonly found at SFR and DFR Corral; these strata being the most important as a nursery. Adults were mainly found at SBR Corral (Fig. 16, Table 2). Juveniles of *Chaetodon capitstratus* (0-5 cm) were mainly found at seagrass of

Montalva Bay and SBR Corral, and adults (>5 cm) were commonly found at SFR Corral (Fig. 17, Table 2).

Considering the 20 species with no distinction of life stage (i.e., juveniles or adults), a cluster analysis revealed that among Haemulidae only *H. flavolineatum* and *H. plumieri* occurred in a single cluster, consequently showing similarity in strata use (i.e., mainly seagrass and mangroves, Fig. 18). Among the other taxa, none occurred in similar clusters within families, but appeared in separated clusters, which means different strata use along the inshore-offshore gradient.

DISCUSSION

One of the major trends elucidated in this study stems on the wide variety of responses the fish species exhibited within families along the inshore-offshore gradient, which reflects a differential habitat use according to life stage. The species-specific examinations of spatial variations in length-frequency distributions sustain the idea that many fish species conduct migratory displacements from nursery areas to adult grounds. Of the 20 species selected in this study, at least 17 showed clear evidences of a progressive difference in habitat use, with preferences for certain strata or biotope according to species, size class, and consequently maturation stage (i.e., juvenile or adult). Juveniles were mainly observed in shallow-water strata (i.e., mangroves, seagrass, SBR, SFR), while size (i.e., adults) were mainly found in deeper strata (i.e., DFR, DBR).

Nagelkerken et al. (2000) and Cocheret de la Morinière et al. (2002) working in Curaçao used terms such as “nursery species”, “bay species” and “reef species” for categorizing fishes that show differential use of habitat according to life stage. However,

it is important to note that this categorization is relative to the conditions of their study area. All fish species under consideration are reef associated species as adults, but some are “off-reef” species as juveniles. Nevertheless, the terminology from Curaçao studies is also used here for comparative reasons and to discern preferences of some reef fishes as juveniles for habitats other than coral reefs (e.g., mangroves, seagrass). Therefore, of the 20 selected species, 13 species are considered nursery species, while 7 are reef species. The nursery species showed an ontogenetic migration from mangroves and seagrass into coral reefs, while the reef species exhibited a migration from shallow-water coral reefs (i.e., SBRs) to deeper reefs.

Among the 13 “nursery species”, with the exception of *C. capistratus*, all showed evidence of a given migration among habitats. Many showed an apparent migration from mangroves to coral reefs using seagrass as intermediary site. However, *L. griseus* exhibited a displacement from seagrass to mangrove habitats. Among the 7 “reef species”, *Acanthurus coeruleus*, *A. bahianus*, *S. aurofrenatum*, *S. rubripinne,* and *S. viride* showed preferences for shallow-water coral reefs (i.e., SBRs) as nurseries, and progressively moved toward deeper reefs. However, for acanthurids, few juveniles of *A. bahianus* were also found in mangroves. Lastly, *A. saxatilis* used shallow coral reefs as nurseries, but its ontogenetic migration was not so evident since juveniles co-occurred with adults in the same strata.

Inferences of fish ontogenetic migrations were not only from mangroves to coral reefs, using seagrass as intermediate habitat, but also from shallow-water coral reefs (i.e., back and fore reefs, 0-3 m depth) to deeper reefs (3-10 m depth). However, at Corral and Turrumote, with few to no mangrove prop-roots migration was from seagrass to deeper

reefs, in the case of Corral, and from SBR to either DFR or DBR in Turrumote. In terms of absolute densities of the 20 selected species, it was possible to infer for many species an ontogenetic migration directed from mangroves (M) to coral reefs (CR), using the seagrass (S) as intermediate habitat. However, other species (*H. plumieri, S. taeniopterus, and O. chrysurus*) showed an apparent directionality from S to CR, while still others (*A. bahianus, A. coeruleus, S. chrysopterum*) showed directionality from SBRs to DFRs.

In Curaçao, 16 of the 20 selected species from southwestern Puerto Rico showed a clear difference in habitat utilization between small (juvenile) and large (adult) fishes, which indicated an ontogenetic migration across the reef shelf from shallow-water nursery areas to deeper-water habitats (Nagelkerken et al. 2000; Cocheret de la Morinière et al. 2002). Nagelkerken and van der Velde (2003) distinguished three cross-shelf ontogenetic patterns in habitat use in Curaçao and Bonaire: (1) for nursery species, migration was inferred to occur from bay habitats to coral reefs, and (2) for reef species, migration occurred from shallow coral reefs to deeper coral reefs, and (3) for both species, migration occurred from channel reef to bay and then outer reefs. In southwestern Puerto Rico, in nearby locations to the study area, Christensen et al. (2003) found that many species of Haemulidae, Lutjanidae and Scaridae, showed ontogenetic shifts in habitat preferences, migrating from mangroves and seagrass to deeper reefs. In Florida, Lindeman et al. (2000) distinguished at least 50 species of several families showing a degree of ontogenetic cross-shelf migration; many of them included species of Haemulidae, Lutjanidae, Serranidae, and Sparidae.

As Appeldoorn et al. (1997) hypothesized, at least three scenarios on cross-shelf ontogenetic migrations for fishes are viable: (1) where suitable adult habitat exists across

a shelf, displacement distances vary greatly, (2) where a gap exists between the distribution of juvenile and adult habitats, the variation in migration is less with fish moving less distances, and (3) where the shelf is narrow, fish movements tend to be short because habitats are close regardless the distribution. In southwestern Puerto Rico, while the shelf is wide (thus, the distance from mangroves to the shelf edge is large), the present study only included the extent from inshore to mid-shelf (i.e., Montalva bay to Turrumote). Therefore, juvenile habitat was relatively close to adult habitat, which was reflected in the relatively high proportional abundance of juveniles in the majority of strata surveyed high (see Chapter 3). Thus, in many instances juveniles and adults co-occurred in the same habitat type. Consequently, along the inshore-offshore segment surveyed in the present study (at least 4 500 m from shoreline to Turrumote), the distance traveled by juveniles during their potential ontogenetic migrations from "off-reef" habitats (i.e., mangroves and seagrass) to reach deeper adult habitats may be relatively short.

For some fish species, the ontogenetic migrations may be partial, which is reflected in the apparent variability the same species exhibit among different geographic regions. Conceivable reasons why ontogenetic migrations may vary among regions may be explained by the geographic characteristics of the shelf, the closeness of available coral reef habitats, and the scale dimension of mangroves and seagrass with respect to that of coral reefs; all of these in conjunction with season. For instance, in the Biscayne Bay, on Florida's southeastern coast, ontogenetic migrations have been evident for *L. apodus* and *S. barracuda*, but not for *L. griseus*, *H. parrai*, and *H. sciurus* (Serafy et al. 2003). Plausible reasons for these latter species not exhibiting clear evidences of

ontogenetic migrations in Biscayne Bay, which is reflected their reduced density in the coral reef, may be related to (1) fishing pressure on reefs, (2) expandability of habitat use in mangroves, and (3) sex-specific habitat preferences (Serafy et al. 2003).

In this study, the relative importance of mangroves, seagrass, and coral reefs as interconnected "corridors" for the selected fish species conducting ontogenetic migrations was elucidated. The results were based on indirect evidence of ontogenetic migrations based on size-frequency distribution changes in relative density of size classes along the inshore-offshore, cross-shelf gradient. Nonetheless, a recommended approach to further substantiate direct evidence would be through tagging fish juveniles. A mark-recapture study over a vast size range of individuals of ontogenetic migratory species (e.g., *H. flavolineatum*, *L. apodus*) in nursery areas would determine the distance and location to where they re-locate, either still as juveniles or as early adults, confirming the preponderance of ontogenetic migrations. A study to determine the patterns of displacement of tagged grunts (*H. flavolineatum*) in several locations off La Parguera shelf is currently ongoing, and includes locations within the present study area. Another approach to validate ontogenetic migrations would involve measuring macronutrient and trace element ratios on fish otoliths, providing a unique trace of the temporary residence of given life stages of fish species in nursery habitats (Gillanders 2002). Comparisons of diet of nursery species have proven an effective approach to gain insights into the ontogenetic migrations of fish species. Although other factors may theoretically initiate or promote the migration patterns, the ontogenetic dietary changes may reflect the nursery-to-coral reef migrations (Cocheret de la Morinière et al. 2003).

Marine protected areas (MPAs), and in special no-take marine reserves (NTMRs), are important tools for conservation and management (Lubchenco et al. 2003; Roberts et al. 2003). The main goal of NTMRs is to put aside one specific portion of the marine ecosystem from exploitation, protecting both the organism and the habitat (Lubchenco et al. 2003). Shallow-water habitats (e.g., mangroves, seagrass, and shallow-water coral reefs) have proven importance for many marine species as nursery or adult areas (Nagelkerken et al. 2000; Beck et al. 2001). Documenting the relative importance of these habitats as nurseries and allocating other essential habitats (i.e., nursery, spawning, and growth) is crucial for the design of NTMRs (Nagelkerken and van der Velde 2003; Appeldoorn et al. 2003; Friedlander et al. 2003). To link habitat types with fish communities, it is necessary to identify habitat requirements for fish species according to life stage (e.g., juveniles and adults), their dispersal range and pathways, and the availability and distribution of essential habitats within the areas to be protected (Lindeman et al. 2000). In the MPA off La Parguera, Turrumote Key has been proposed as a NTMR; however, Turrumote does not include inshore, off-reef habitats such as those of Corral, Romero, and Montalva Bay. The implications of post-settlement habitat connectivity for the selected fish species along this inshore-offshore gradient are of concern in terms of conservation and management strategies. In this study, the mosaic of habitats along the continuum, from bay habitats (i.e., Montalva Bay) to shallow-water habitats of Turrumote Key showed species-specific patterns of relative importance in terms of juvenile and adult densities. In management, excluding any essential habitat type from protection along this continuum may promote a gap in local connectivity between

reef, and either feeding or nursery habitats, fostering a “bottleneck” at which fish population maintenance might be affected.

An ecosystem-based approach, in conjunction with NTMRs, is a novel scientific strategy that is altering traditional fishery management by incorporating an ecological meaning to management under the premise that the value to humanity of the whole ecosystem is much greater that the sum of its parts (Browman et al. 2004). By ecosystem-based approach, the emphasis is given to protecting the habitat within a larger regional context (i.e., large marine ecosystems, Sherman and Duda 1999; biogeochemical provinces, Longhurst 1998) rather than a local strategy. However, since still novel, there are differences in opinion on how to scale the approach, either from top-down or bottom-up. On this respect, an emerging integration of social and socio-economic components onto ecology would be decisive to better define the process of the new fishery management. Nonetheless, under the ecological perspective, there is an increasing need to determine the characteristics of the habitat in conjunction with the ecology that many fishery-targeted species (e.g., Lutjanidae, Haemulidae, Serranidae) exhibit, such as knowing the characteristics of larval and post-settlement connectivity and the influence that habitat quality has on basic biological processes (e.g., reproduction, spawning aggregations, growth, feeding) (e.g., Lindeman et al. 2000; Appeldoorn et al. 2003; Mumby et al. 2004).

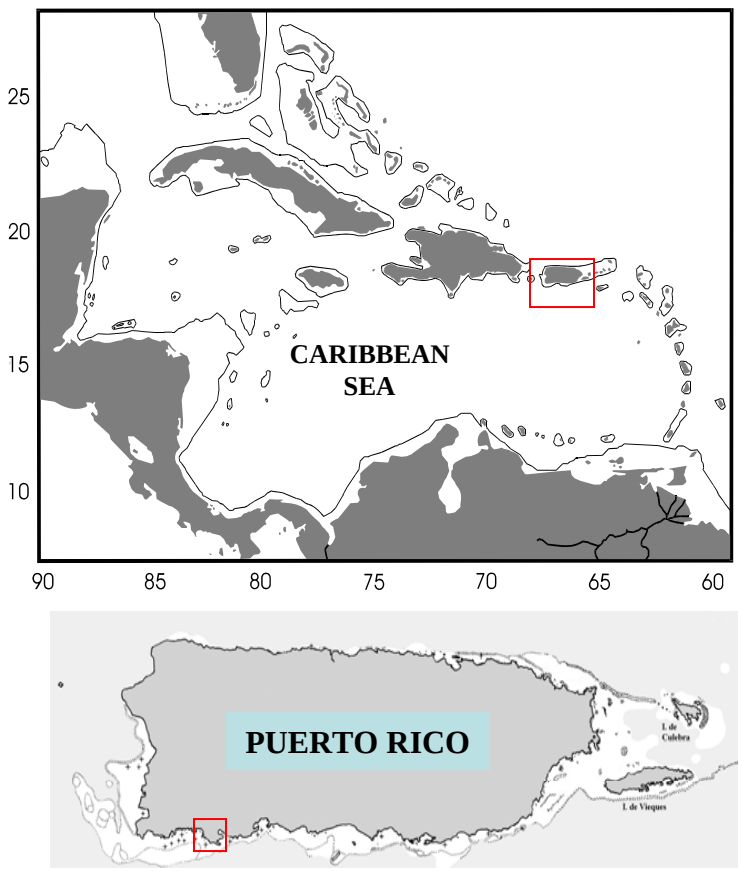
Conclusions

1) Of the 20 species selected in this study, at least 17 showed clear evidences of a progressive difference in habitat use, with preferences for certain strata or biotope which implies ontogenetic migrations or PLCMs. Among the 13 “nursery species”, at least 12 showed evidence of migration among habitats.

2) Apparent directionality of migration was from mangroves, seagrass and shallow back reefs to deeper reefs in Montalva Bay-Romero, while in Corral-Turrumote such an apparent directionality was from seagrass and shallow back reefs to deeper reefs.

3) The inshore-offshore segment surveyed represented a dimension distance of approximately 4,500 m from shoreline to Turrumote (but approximately of 2,000 m from shoreline to deeper reefs of Romero). Consequently, the potential distance traveled by juveniles during their potential ontogenetic migrations from nursery areas to reach deeper adult habitats may be relatively short.

4) One of the major trends elucidated in this study stems was the wide variety of responses the fish species exhibited within families along the inshore-offshore gradient reflected in differential habitat use according to life stage.



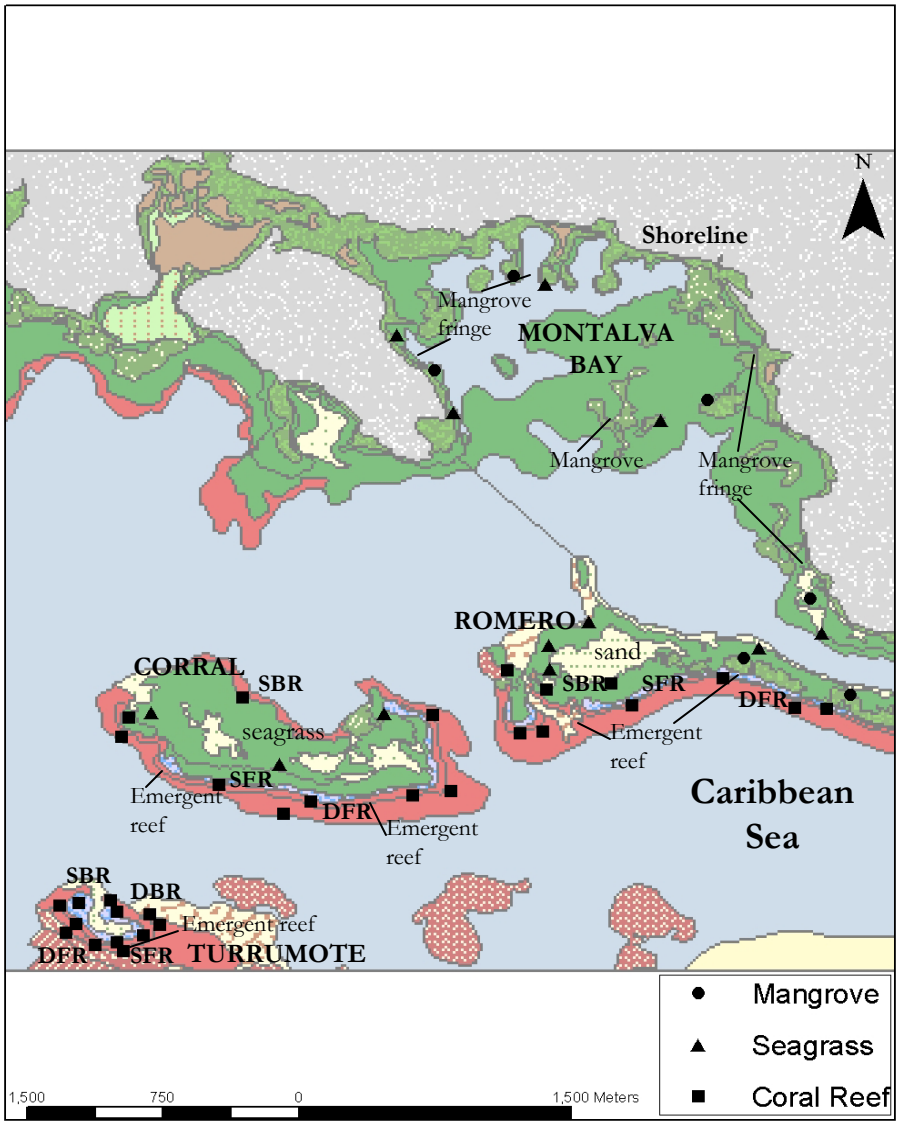


Fig. 1. Map of Puerto Rico showing study area and locations with sites in the various strata (i.e., SBR, DFR) and biotopes (i.e., mangroves, seagrass, coral reefs). SBR: shallow back reef, SFR: shallow fore reef, DFR: deep fore reef, DBR: deep back reef.

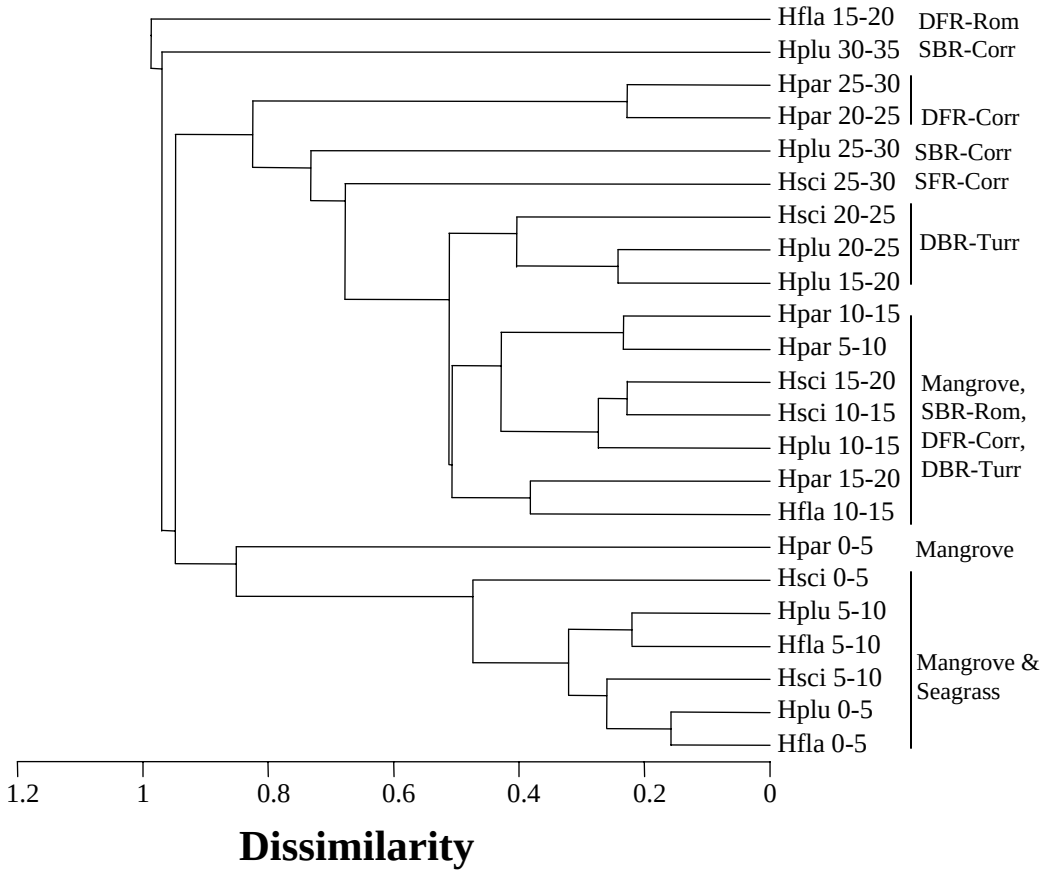


Fig. 2. Cluster analysis of size classes of Haemulidae per stratum along the inshore-offshore gradient (i.e., Montalva Bay-Turrumote). Numbers indicate size classes in forked length (cm). Hfla: *Haemulon flavolineatum*, Hsci: *H. sciurus*, Hplu: *H. plumieri*, Hpar: *H. parrai*. See text for code strata definitions

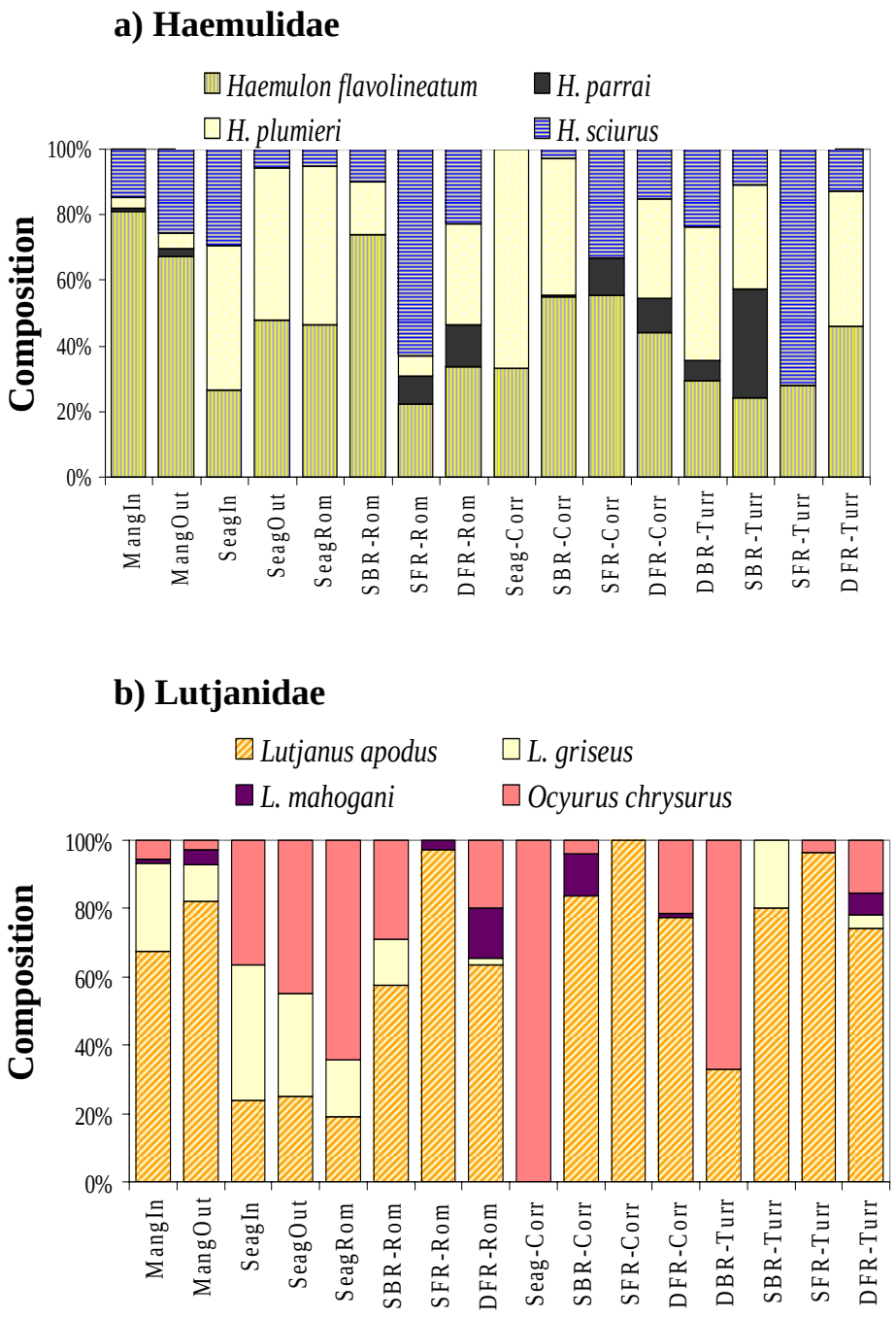


Fig. 3. Percentage composition of total density of related species of a) Haemulidae and b) Lutjanidae for each stratum along the inshore-offshore gradient.

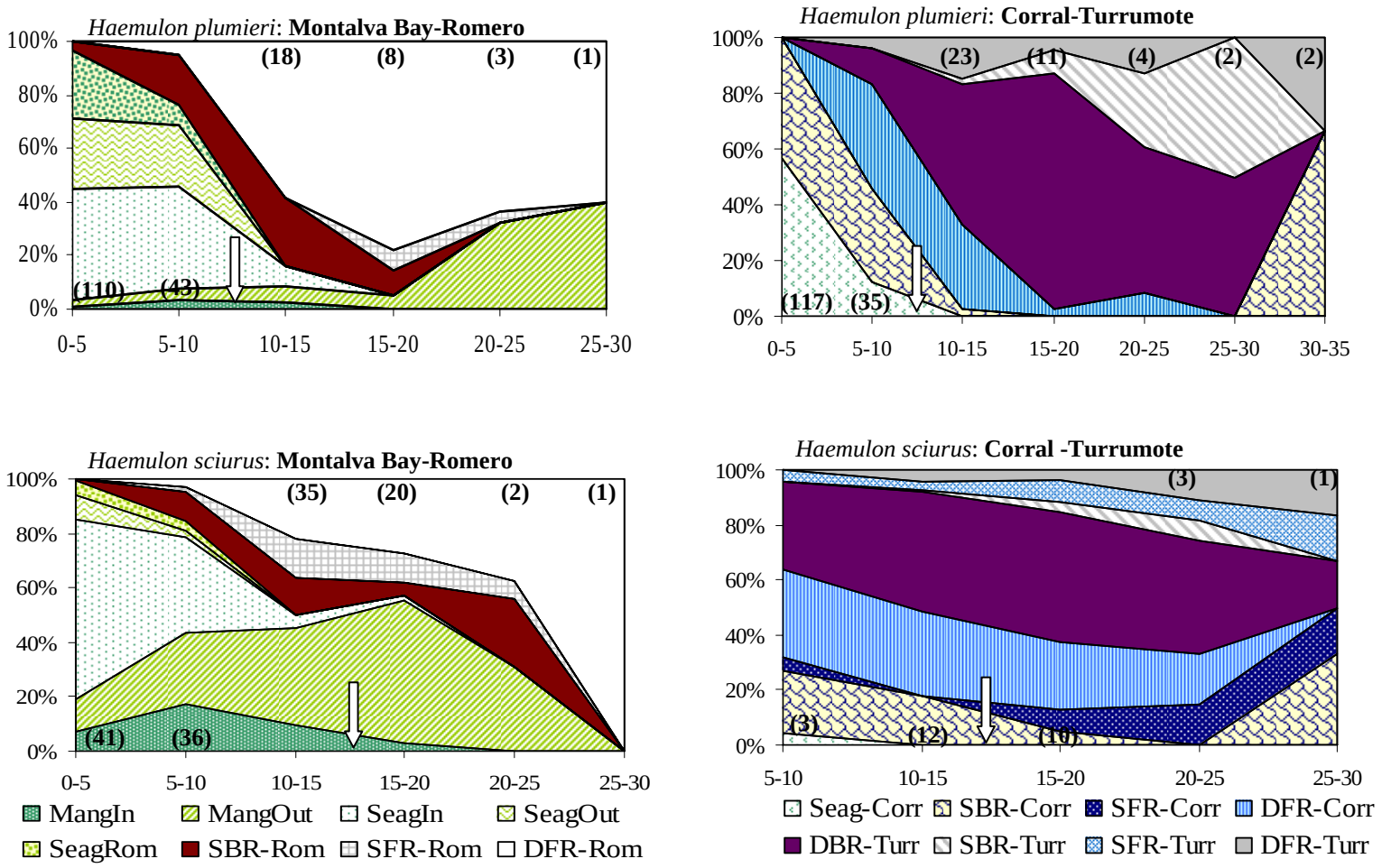


Fig. 4. Size-frequency diagrams of species of Haemulidae at the strata along the inshore-offshore gradient. X-axis refers to size classes in centimeters of forked length, while Y-axis refers to relative density. The arrows indicate approximate size of sexual maturation (see Table 2). See text for code strata definitions. Values in parenthesis are average number of individuals per size class per strata.

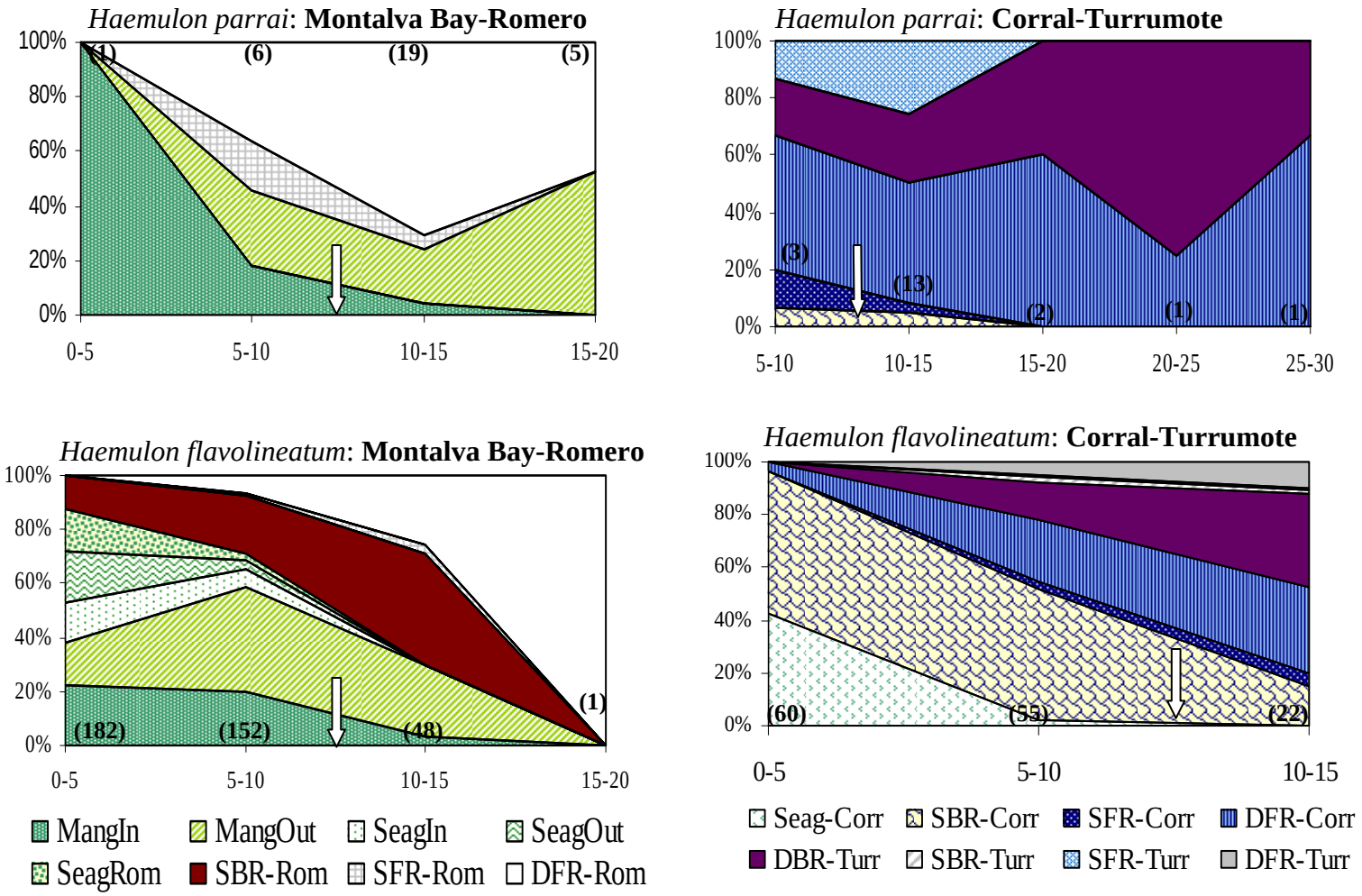


Fig. 5. Size-frequency diagrams for species of Haemulidae in the strata along the inshore-offshore gradient. X-axis refers to size classes in centimeters of forked length, while Y-axis refers to relative density. The arrows indicate approximate size at sexual maturation (see Table 2). See text for code strata definitions. Values in parenthesis are average number of individuals per size class per strata.

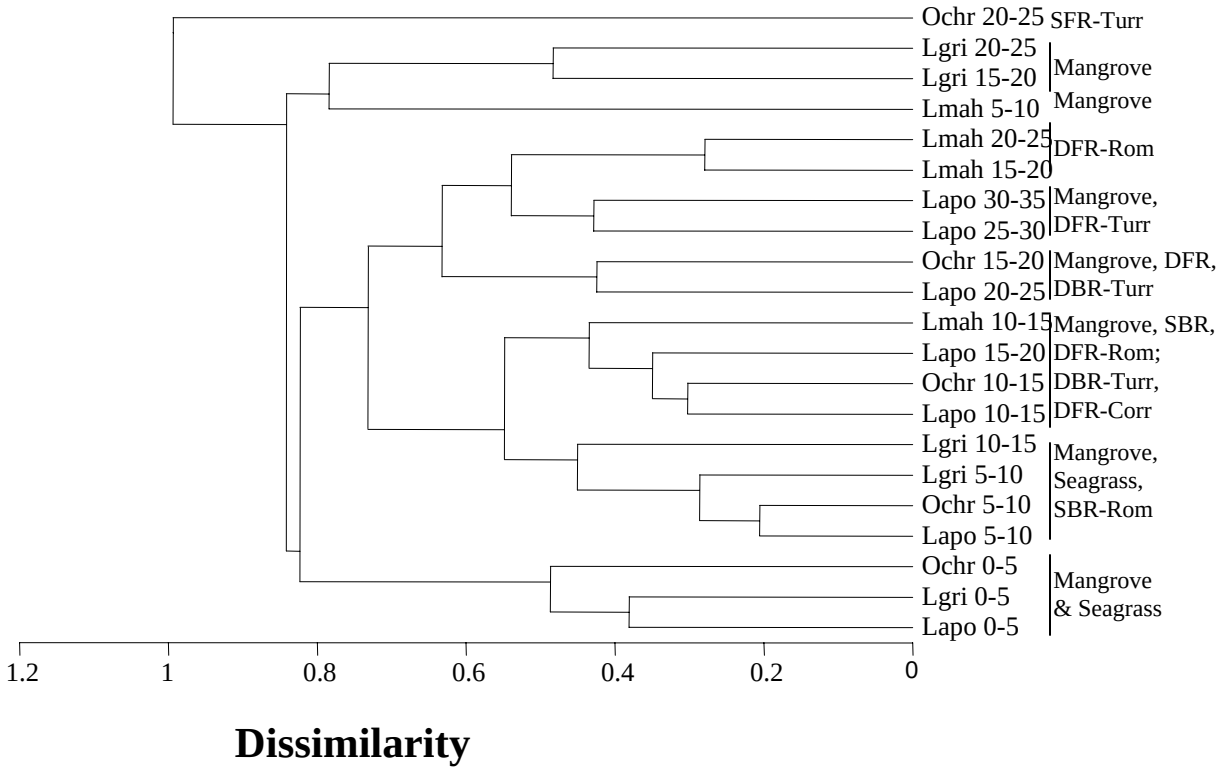


Fig. 6. Cluster analysis of size classes of Lutjanidae per stratum along the inshore-offshore gradient (i.e., Montalva Bay-Turrumote). Numbers indicate size classes in forked length (cm). Lapo: *Lutjanus apodus*, Lmah: *L. mahogoni*, Lgri: *L.griseus*, Ochr: *Ocyurus chrysurus*. See text for code strata definitions.

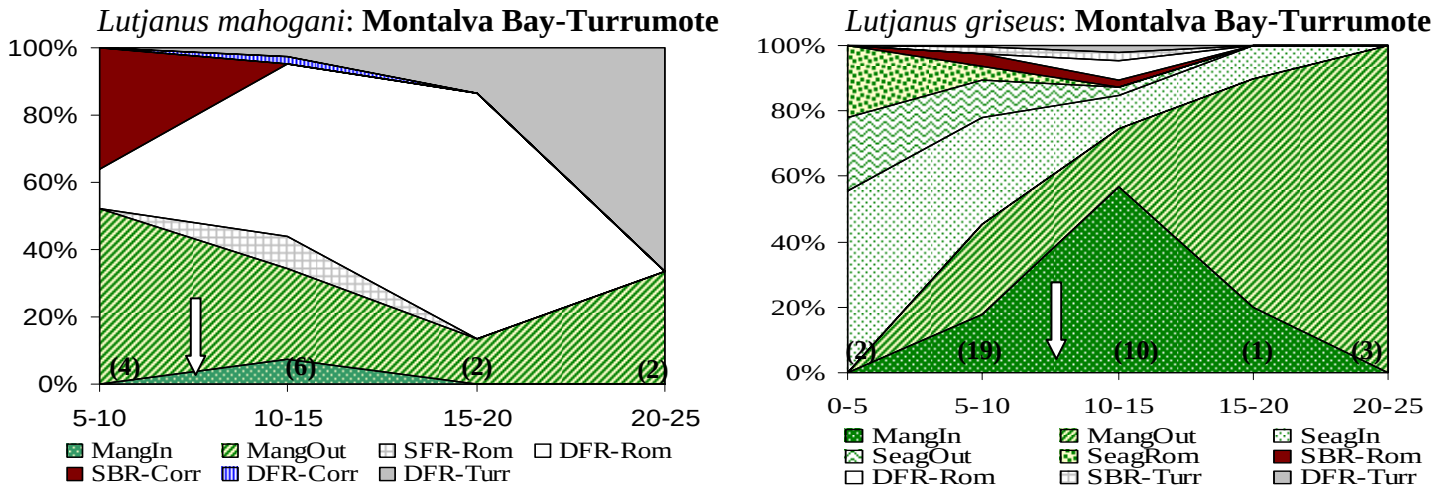


Fig. 7. Size-frequency diagrams for species of Lutjanidae in the strata along the inshore-offshore gradient. X-axis refers to size classes in centimeters of forked length, while Y-axis refers to relative density. The arrows indicate approximate size of sexual maturation (see Table 2). See text for code strata definitions. Values in parentheses are average number of individuals per size class per strata.

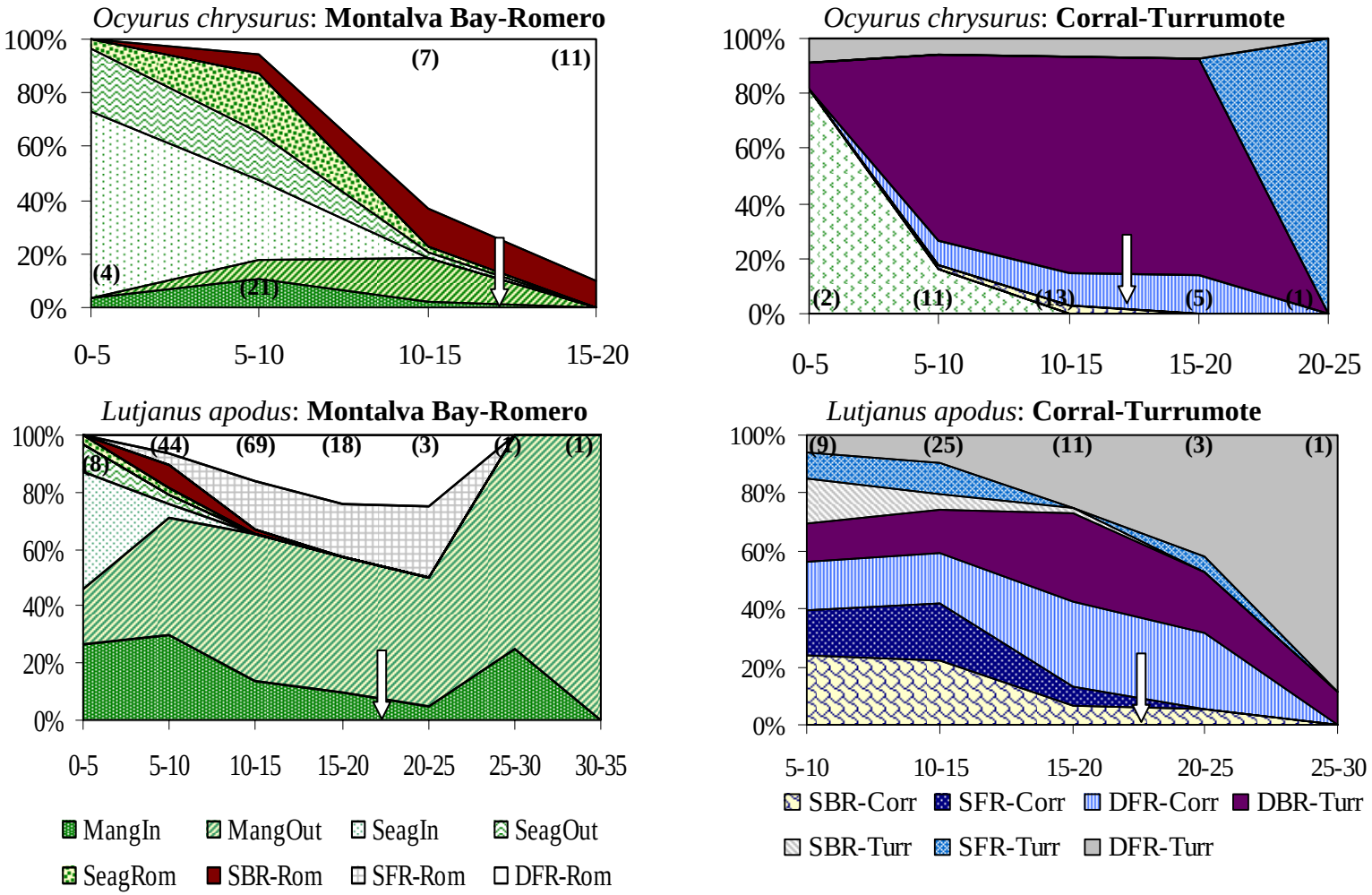


Fig. 8. Size-frequency diagrams for species of Lutjanidae in the strata along the inshore-offshore gradient. X-axis refers to size Classes in centimeters of forked length, while Y-axis refers to relative density. The arrows indicate approximate size of sexual maturation (see Table 2). See text for code strata definitions. Values in parentheses are average number of individuals per size class per strata.

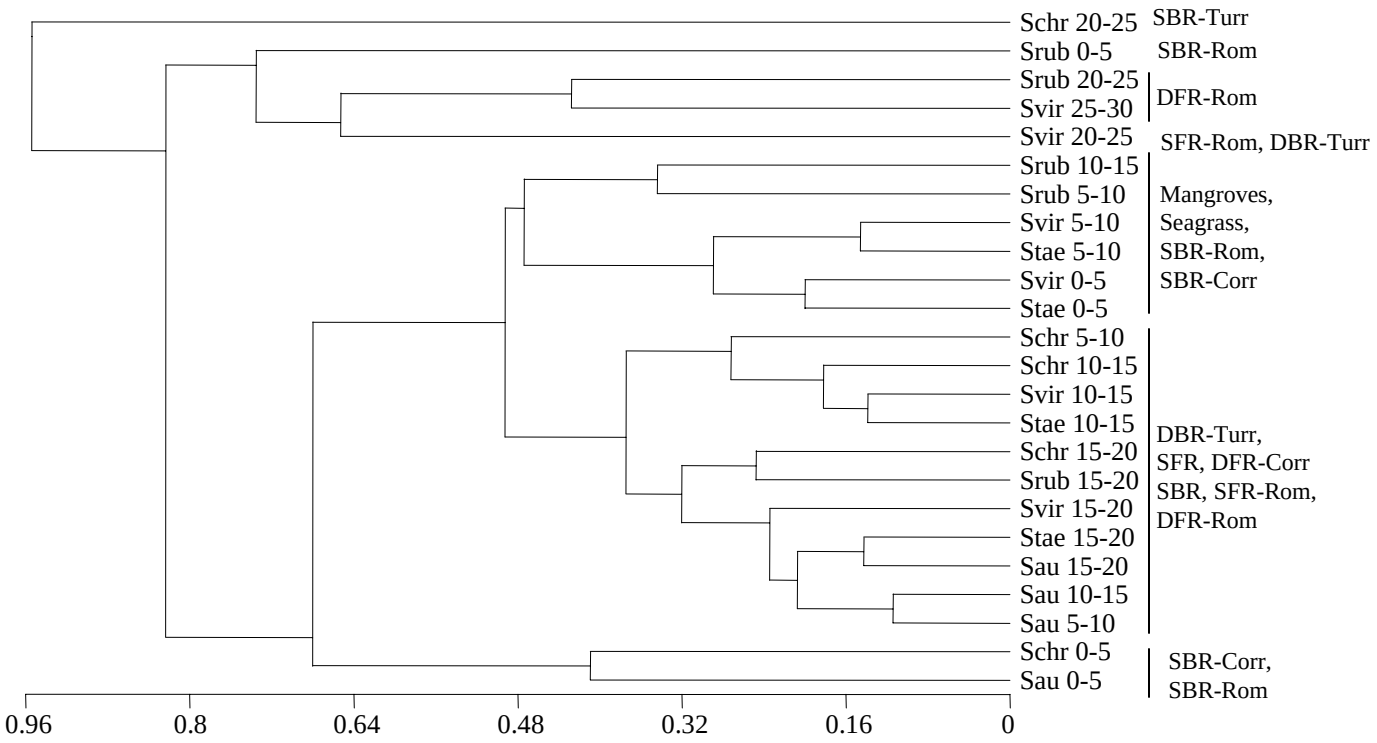


Fig. 9. Cluster analysis of size classes of Scaridae per stratum along the inshore-offshore gradient (i.e., Montalva Bay-Turrumote). Numbers indicate size classes in forked length (cm). Saur: *Sparisoma aurofrenatum*, Schr: *S. chrysopterum*, Srub: *S. rubripinne*, Svir: *S. viride*, Stae: *Scarus taeniopterus*. See in text code strata definitions.

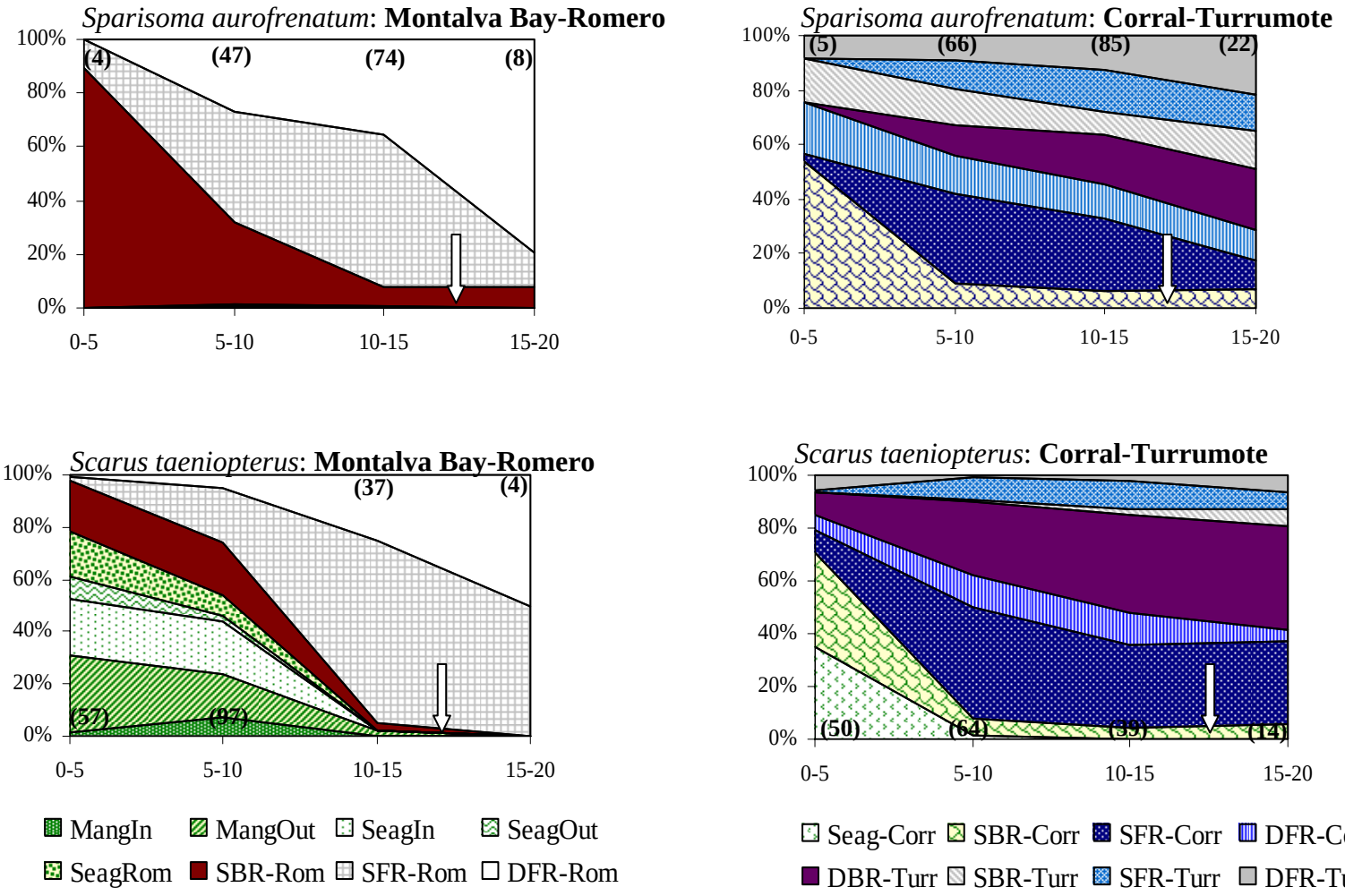


Fig. 10. Size-frequency diagrams of species of Scaridae at the strata along the inshore-offshore gradient. X-axis refers to size classes in centimeters of forked length, while Y-axis refers to relative density. The arrows indicate approximate size of sexual maturation (see Table 2). See text for code strata definitions. Values in parentheses are average number of individuals per size class per strata.

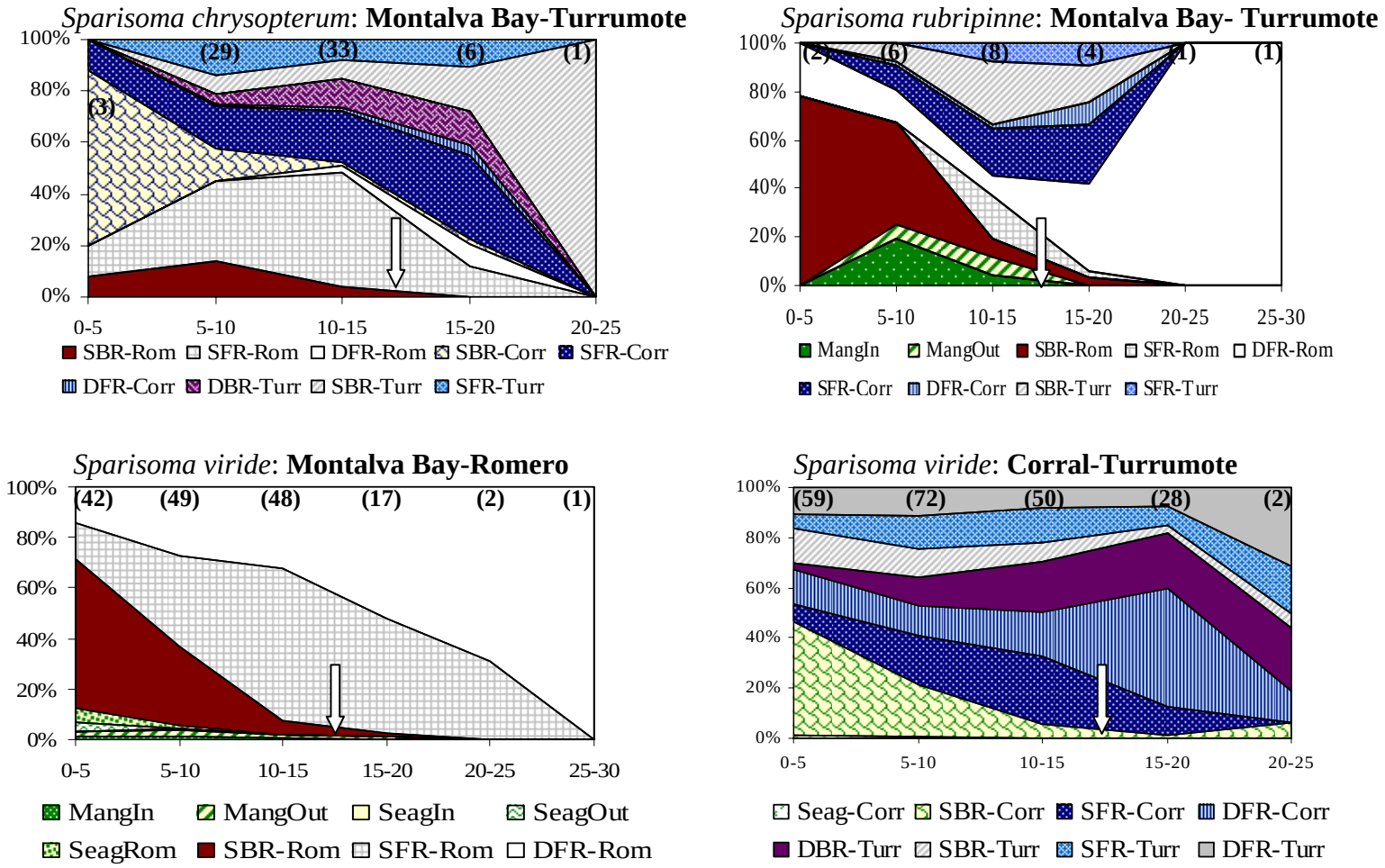


Fig. 11. Size-frequency diagrams of species of Scaridae at the strata along the inshore-offshore gradient. X-axis refers to size classes in centimeters of forked length, while Y-axis refers to relative density. The arrows indicate approximate size of sexual maturation (see Table 2). See text for code strata definitions. Values in parentheses are average number of individuals per size class per strata.

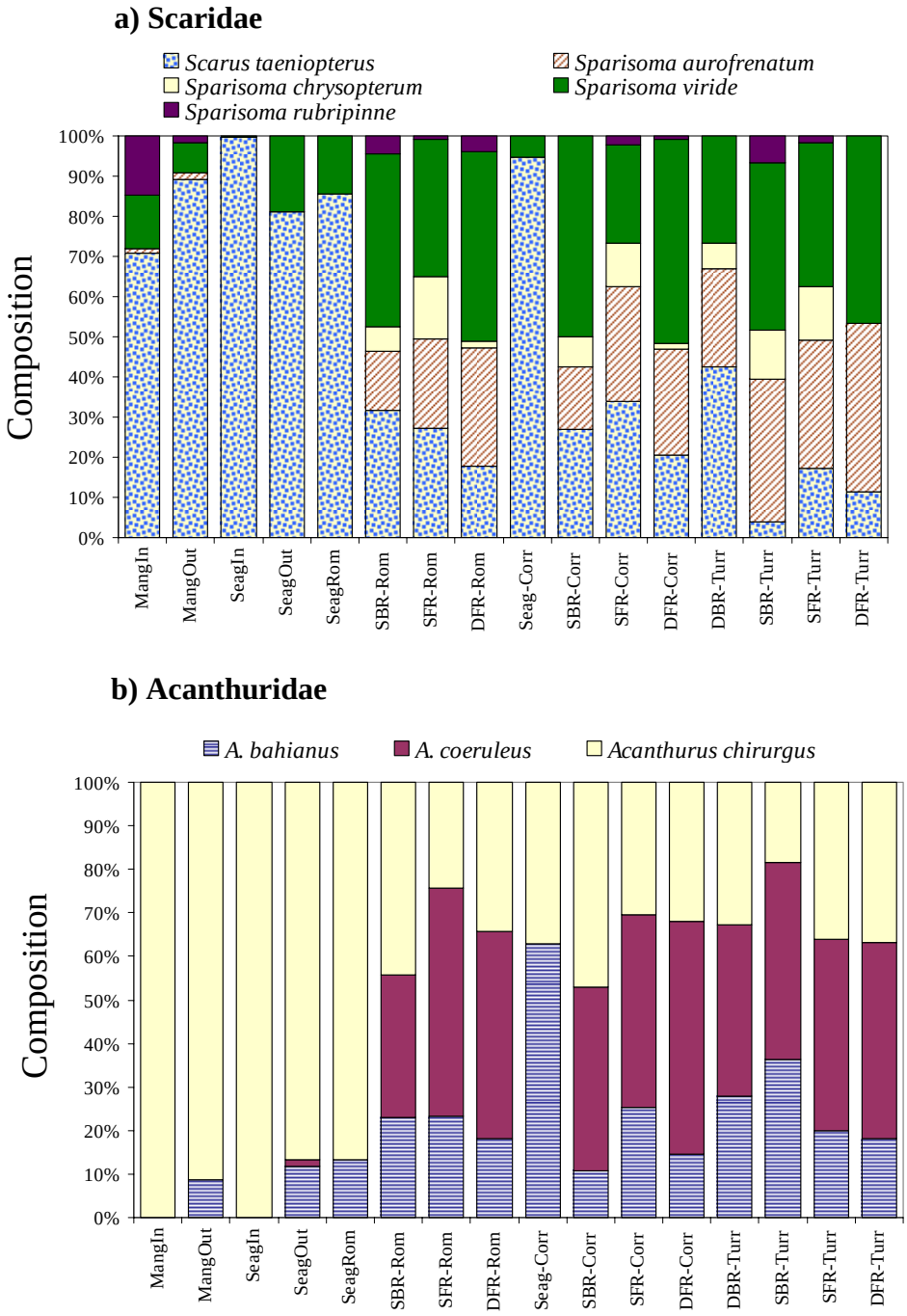


Fig. 12. Percentage composition of total density of related species of a) Scaridae and b) Acanthuridae for each stratum along the inshore-offshore gradient.

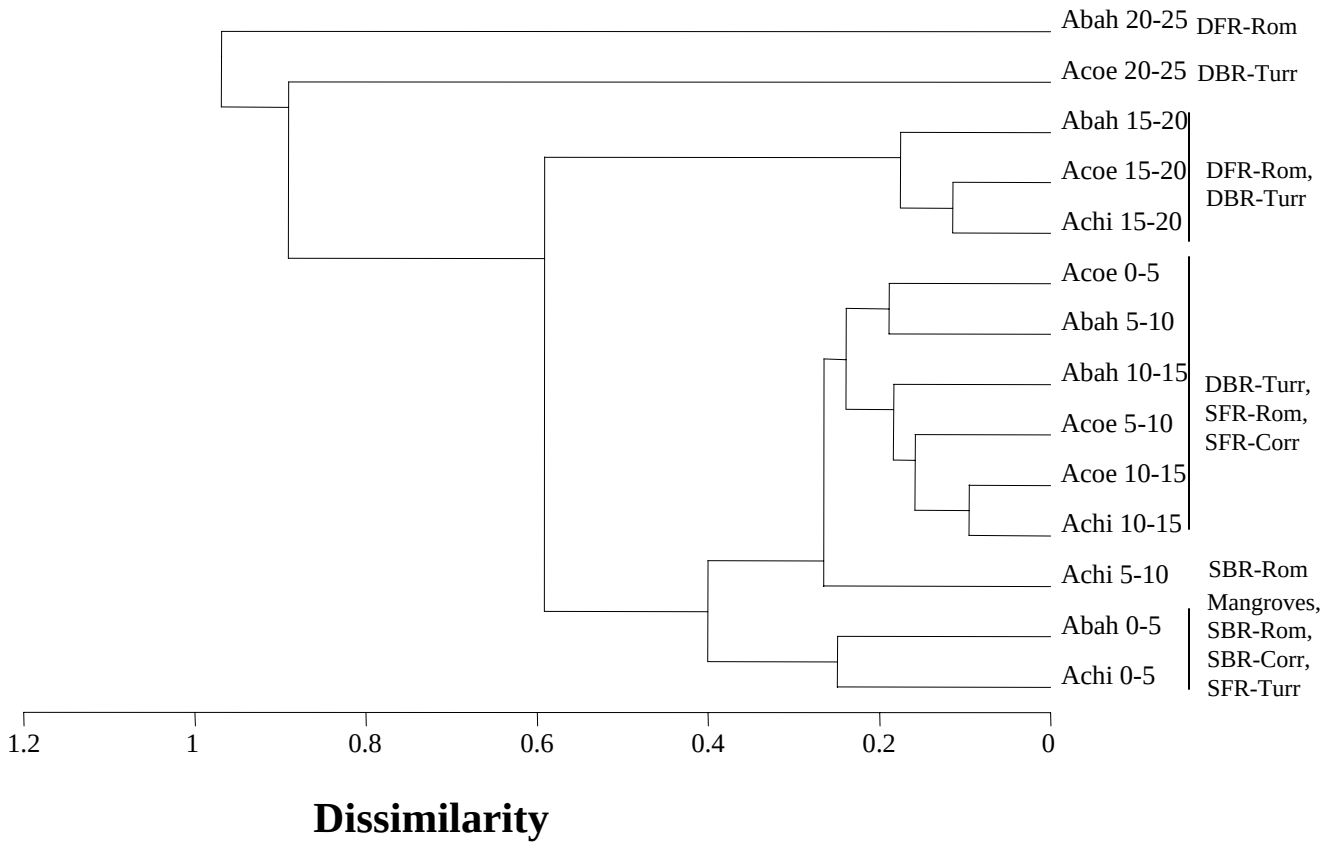


Fig. 13. Cluster analysis of size classes of Acanthuridae per stratum along the inshore-offshore gradient (i.e., Montalva bay-Turrumote). Numbers indicate size classes in forked length (cm). Abah: *A. bahianus*, Acoe: *A. coeruleus*, Achi: *A. chirurgus*. See text for code strata definitions.

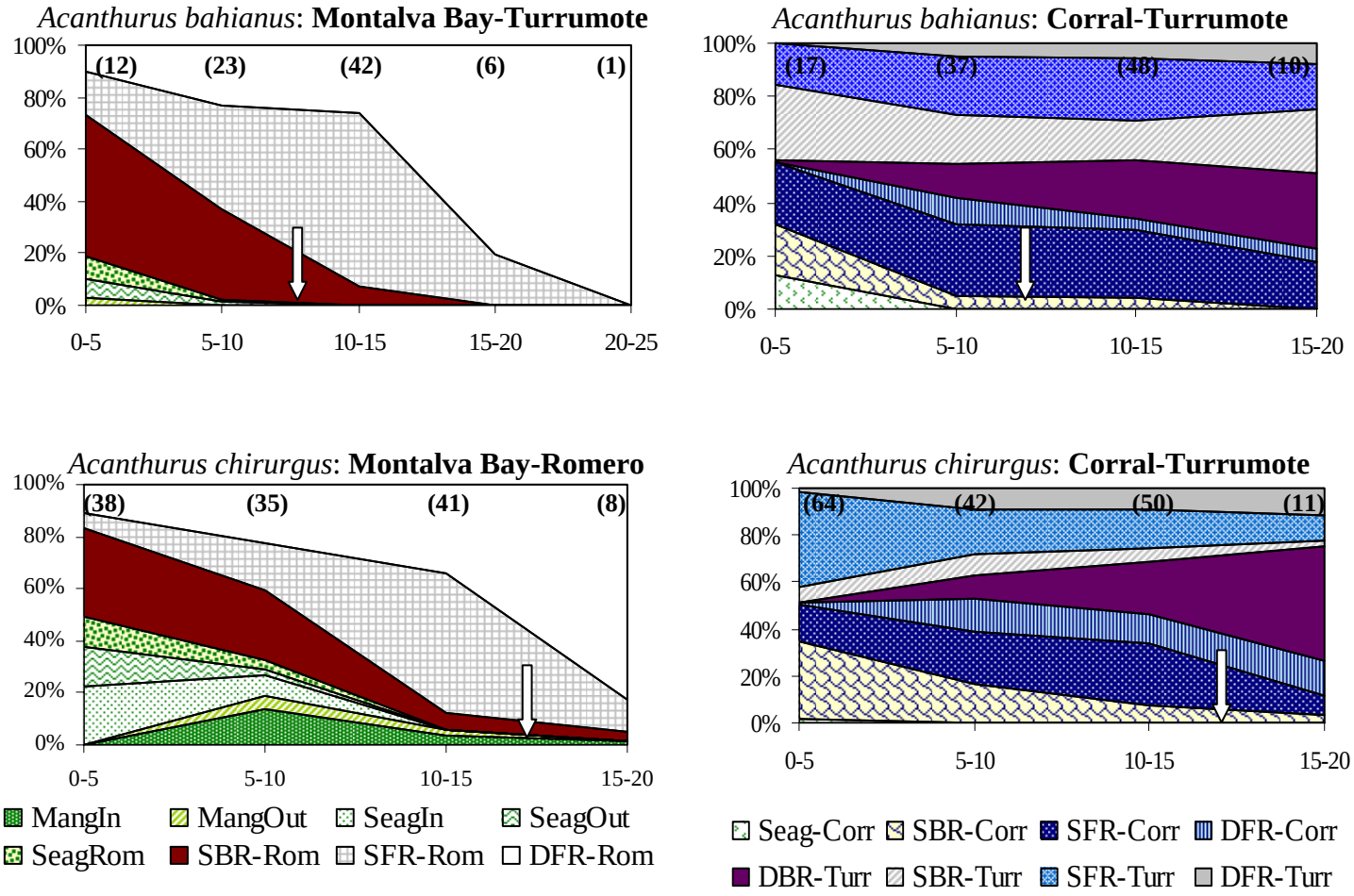


Fig. 14. Size-frequency diagrams for species of Acanthuridae in the strata along the inshore-offshore gradient. X-axis refers to size classes in centimeters of forked length, while Y-axis refers to relative density. The arrows indicate approximate size at sexual maturation (see Table 2). See text for code strata definitions. Values in parentheses are average number of individuals per size class per strata.

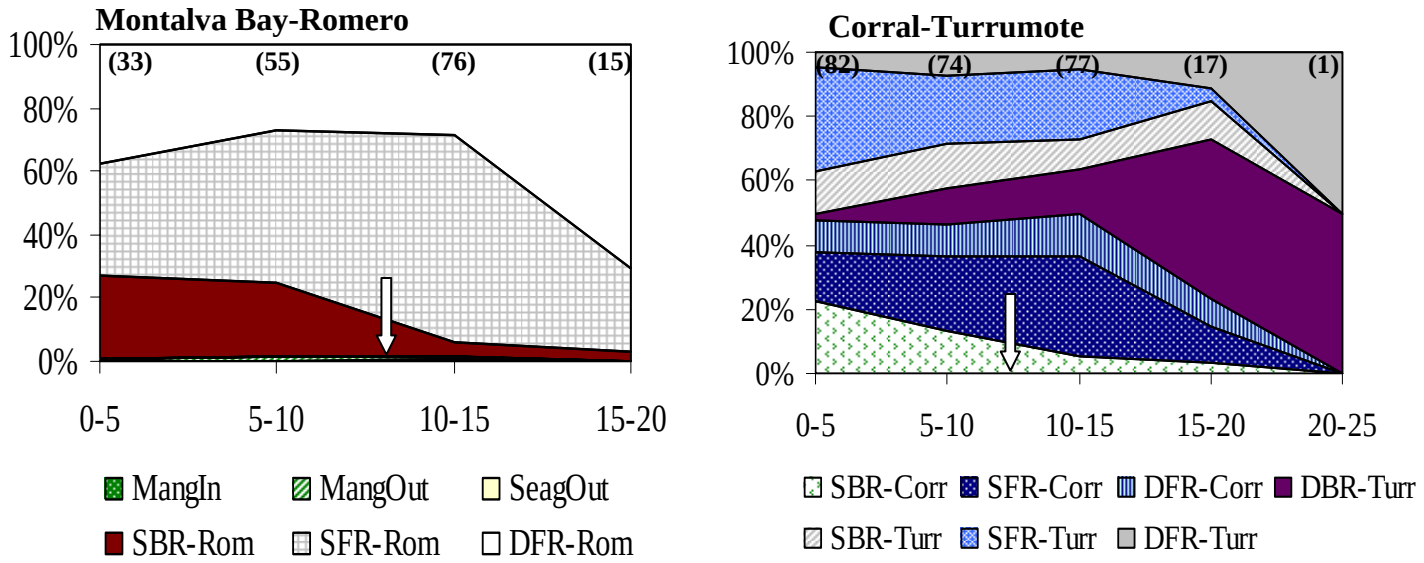


Fig. 15. Size-frequency diagrams for *Acanthurus coeruleus* in the strata along the inshore-offshore gradient. X-axis refers to size classes in centimeters of forked length, while Y-axis refers to relative density. The arrows indicate approximate size at sexual maturation (see Table 2). See text for code strata definitions. Values in parentheses are average number of individuals per size class per strata.

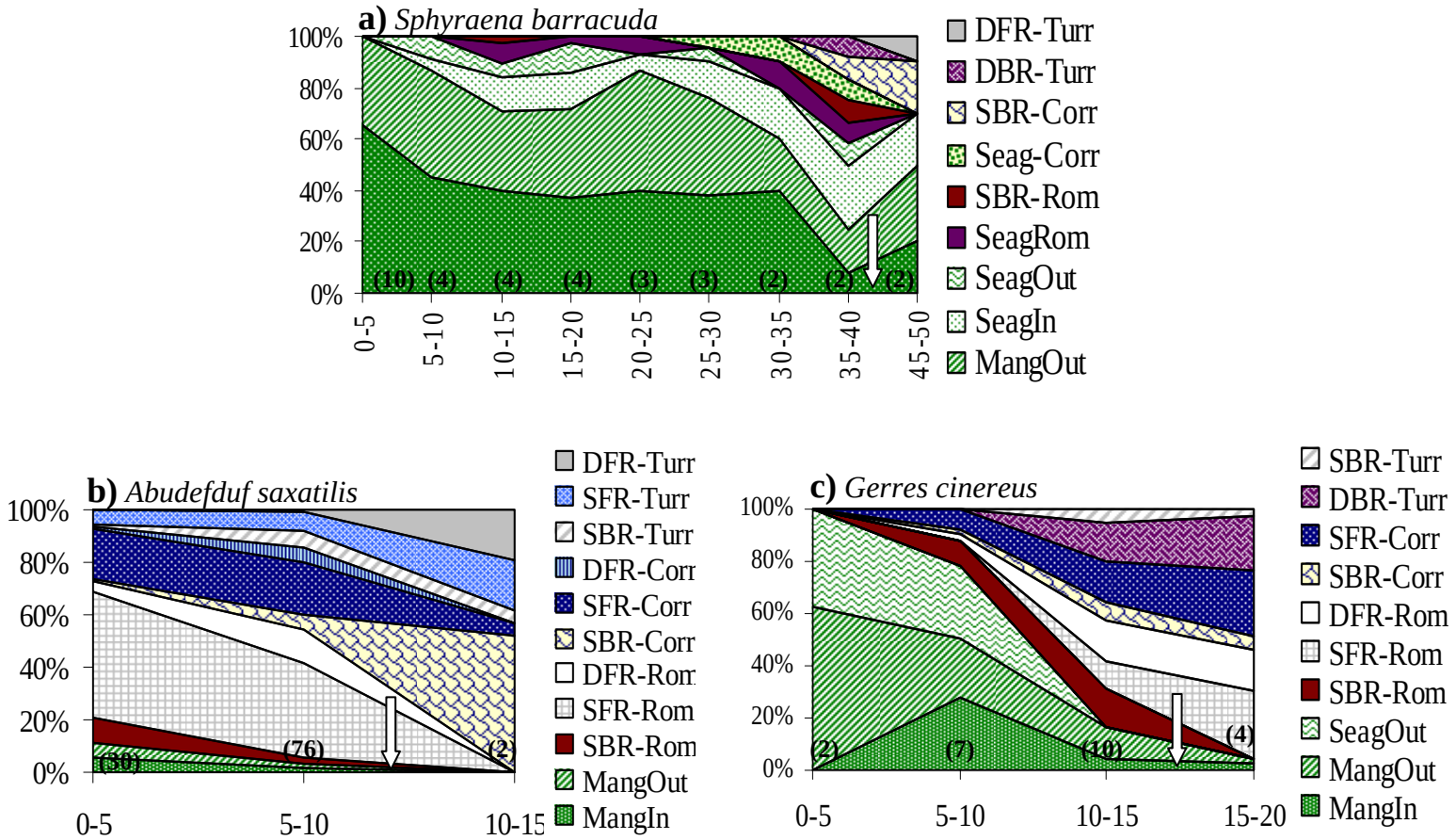


Fig. 16. Size-frequency diagrams of species of Sphyraenidae a), Pomacentridae b), and Gerreidae c), at strata along the inshore-offshore gradient (Montalva Bay-Turrumote). X-axis refers to size classes in centimeters of forked length, while Y-axis refers to relative density. The arrows indicate approximate size of sexual maturation (see Table 2). See text for code strata definitions. Values in parentheses are average number of individuals per size class per strata.

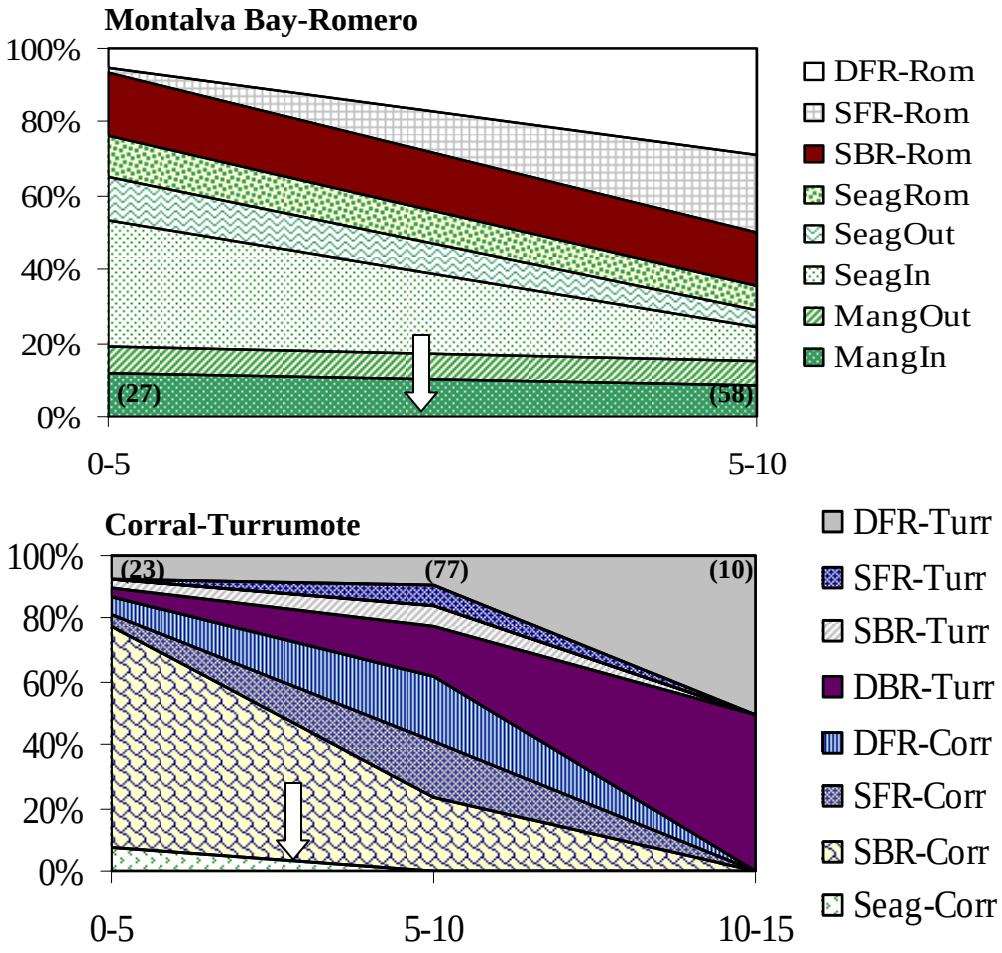


Fig. 17. Size-frequency diagrams of species of *Chaetodon capistratus* along the strata of the inshore-offshore, cross-shelf gradient. X-axis refers to size classes in centimeters of forked length, while Y-axis refers to relative density. The arrows indicate approximate size at sexual maturation (see Table 2). See text for code strata definitions**.** Values in parentheses are average number of individuals per size class per strata.

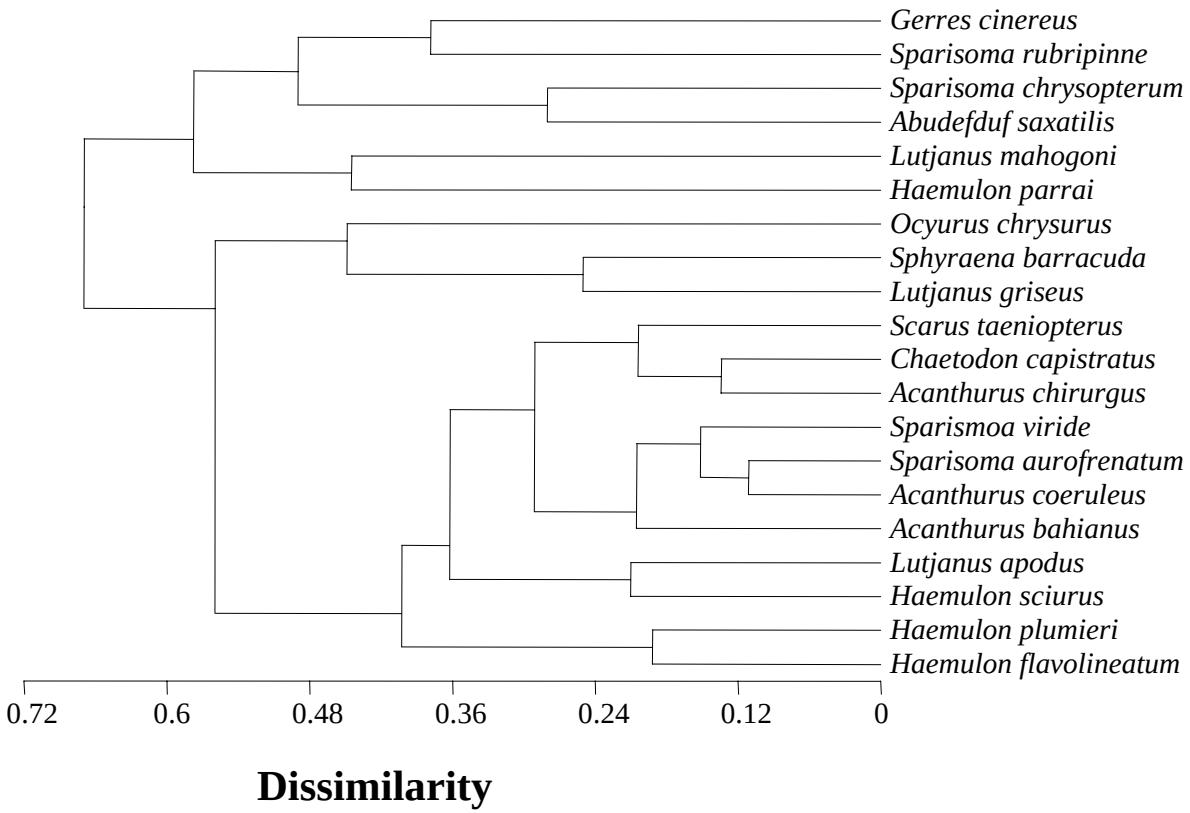


Fig. 18. Cluster analysis of the 20 selected fish species on the relative abundance of all size classes per stratum along the inshore-offshore gradient (i.e., Montalva Bay-Turrumote).

Table 1. Sampling intensity, stratum, depth, and transect area surveyed along the inshore-offshore gradient in southwestern Puerto Rico. Every site represents 1 000 m^2 (i.e., a site is 10 transects of 100 m^2 each). In Montalva Bay, the 12 sites for mangroves and seagrass were split into 2 strata (Mang-In, Seag-In) inside the bay and 2 strata (Mang-Out and Seag-Out) outside the bay, with 3 sites per strata.

Location	**No. of Sites**	**Mangrove**	**Seagrass**	**Shallow Back Reef (SBR) 0-3 m**	**Deep Back Reef (DBR) 3-10 m**	**Shallow Fore Reef (SFR) 0-3 m**	**Deep Fore Reef (DFR) 3-10 m**
Montalva	12	6	6	-	-	-	-
Romero	12	-	3	3	-	3	3
Corral	12	-	3	3	-	3	3
Turrumote	12	-	-	3	3	3	3
Transect area (m^2)	48 000	6 000	12 000	9 000	3 000	9 000	9 000

Table 2. Maturation sizes, percent of juveniles, total density, and relative species abundance (%) of the 20 selected fish species. Maturation data taken from Nagelkerken et al. (2000), García-Cagide et al. (2001), and Fishbase (www.fishbase.org, Froese and Pauly 1993). According to Nagelkerken et al. (2000) N: nursery species, R: Reef species (see text for definition).

Species	**Maturation size (cm, FL)**	**Species group**	**Density (100 m^2)**	**%**
Haemulon flavolineatum	10	N	138.4	14.4
H. plumieri	10	N	87.1	9.1
H. parrai	10	N	7.1	0.7
H. sciurus	15	N	43.4	4.5
Gerres cinereus	15	N	7.1	0.7
Ocyurus chrysurus	15	N	14.0	1.5
Lutjanus apodus	20	N	49.4	5.2
L. griseus	15	N	9.2	1.0
L. mahogoni	10	N	2.8	0.3
Acanthurus bahianus	10	R	46.4	4.8
A. coeruleus	10	R	93.9	9.8
A. chirurgus	15	N	76.7	8.0
Sphyraena barracuda	40	N	9.3	1.0
Sparisoma aurofrenatum	15	R	63.8	6.7
S. chrysopterum	15	N	21.1	2.2
S. rubripinne	15	R	5.5	0.6
S. viride	15	R	98.5	10.3
Scarus taeniopterus	15	R	96.3	10.0
Chaetodon capistratus	5	N	49.0	5.1
Abudefduf saxatilis	10	R	39.8	4.1
Total			**59.9**	

CHAPTER 5: GENERAL DISCUSSION

Connectivity has recently become a matter of concern for designing and implementing no-take marine reserves (NTMRs) in many places in the western Atlantic (Appeldoorn et al. 2003; Friedlander et al. 2003; Sale and Ludsin 2003; Mumby et al. 2004). At least two major categories of connectivity are commonly recognized due to the typical life history of the vast majority of reef associated fishes and invertebrates: pre-settlement or larval connectivity and post-settlement or juvenile/adult connectivity. The former is related to a combination of larval behavior (e.g., chemical detecting, swimming speed and performance, etc.) and oceanographic conditions (e.g., current patterns, eddies, waves), leading to either inshore retention or offshore advection of larvae in given geographical areas (Roberts 1997; Cowen et al., 2000; Sponaugle et al. 2002; Mora and Sale 2002). Connectivity concerns at least three major processes: (1) life cycle migration, the post-settlement life cycle migrations (PLCM, Cocheret de la Morinière et al. 2002), also known as cross-shelf ontogenetic migrations (Lindeman et al. 2000) or simply ontogenetic migrations (Appeldoorn et al. 1997; Nagelkerken et al. 2000), (2) feeding migrations (Beets et al. 2003), and (3) spawning migrations (Claro and Lindeman 2003).

The PLCMs or ontogenetic migrations are related to biological and physiological changes in juveniles that settle in areas (i.e., nursery) different from those of adults, and progressively migrate as they grow from those areas using intermediate habitats until reaching deeper, adult habitats. Contributing factors to such migrations are (1) growth (Shulman 1985), (2) predator avoidance (Werner and Gilliam 1984), (3) swimming improvement (Hyndes et al. 1997), (4) gonad development (Helfman et al. 1982), and (5)

changes in feeding strategy (i.e., from zoobenthivory to piscivory; Muñoz and Ojeda 1998).

The functionality of mangroves and seagrasses as nurseries in the western Atlantic for many fishes is commonly accepted (Parrish 1989; Beck et al. 2001; Mumby et al. 2004); but generalizations must be avoided, since not all mangroves and seagrass appear to offer nursery function (Chittaro et al. in press). In contrast, the nursery function of these habitats appears not to be generally accepted for the Indo-Pacific due to contradictory results (Thollot 1992; Huxham et al. 2004). In the western Atlantic, until recently, few studies were available on the relative importance of mangroves and seagrass as nurseries for fishes (Austin 1971; Ogden and Zieman 1977; Rooker and Dennis 1991), but quantitative studies using size-frequency data to study fish preferences for nursery habitats have been increasing (Nagelkerken et al. 2000; Cocheret de la Morinière 2002; Appeldoorn et al. 2003; Dorenbosch et al. 2004). Several hypotheses have been established about the ecological benefits of seagrass and mangroves as nursery habitats for fishes from the western Atlantic: food availability (Ogden and Zieman 1977; Laegsdgaard and Johnson 2001), shelter (Parrish 1989), shade (Cocheret de la Morinière et al. 2004), high turbidity, low predation (Blaber 1997), and low abundance of piscivorous (Parrish 1989). However, these hypotheses are not mutually exclusive; a species may favor a given habitat (i.e., mangroves, seagrass, and shallow-water coral reefs) due to a combination of preferences.

The present dissertation in southwestern Puerto Rico aimed to first elucidate the reef-associated fish assemblage in an inshore-offshore, cross-shelf, gradient from Montalva Bay to Turrumote containing a mangrove-seagrass-coral reef continuum and a

proposed marine reserve without mangroves and seagrass habitats (i.e., Turrumote). Then, the relative importance of mangroves, seagrass, and coral reefs as nursery habitats for at least 20 selected fish species was determined, and their post-settlement connectivity was inferred through elucidating the ontogenetic cross-shelf migrations or PLCMs among such shallow-water habitats.

The baseline study (Chapter 2) showed differences among shallow-water habitats (e.g., mangroves, seagrass, and coral reefs) in the fish community structure. The fish assemblage, composed by 102 species in the inshore-offshore, cross-shelf gradient from Montalva Bay to Turrumote, showed species specific preferences for mangroves, seagrass, and shallow and deep coral reefs. The fish assemblage along the Montalva Bay-Romero segment was characterized by species typical from inshore bays, while that of Corral-Turrumote segment exhibited typical reef-associated fish species. At the former, the fish families most represented were Haemulidae, Lutjanidae, and Sphyraenidae, typical of inshore, bay habitats, while at the latter were Pomacentridae, Labridae, Scaridae, and Acanthuridae. Most species of Haemulidae and Lutjanidae were widespread, regardless habitat type along the cross-shelf, inshore-offshore gradient. Most species of Acanthuridae, Scaridae, Pomacentridae, and Labridae were commonly associated with shallow (e.g., back and fore) and deep reefs. Notable among commercially important fish species was the almost complete absence of serranids and low abundance of some lutjanids (e.g, *Ocyurus chrysurus*).

The fish community structure along the mangrove-seagrass-coral reef continuum was not uniform. Differences in the community structure of the fish assemblage along the continuum may be related to habitat heterogeneity in terms of availability of shelter and

food and ongoing fish migrations (e.g., feeding, spawning, ontogenetic). Certain species (e.g., *L. griseus, S. barracuda*) exhibited marked preferences for mangroves compared with other habitats, while others (e.g., *H. flavolineatum*) were widespread along the continuum but showing life stage preferences (i.e., juveniles) for certain strata (e.g., mangroves and shallow back reefs).

The relative importance of mangroves, seagrass, and coral reefs in terms of nursery function in southwestern Puerto Rico for the selected 20 fish species (Chapter 3) proved to be slightly different from that exhibited by the same species in other areas of the Caribbean (i.e., Bonaire, Belize, Curaçao; Nagelkerken et al. 2000; Cocheret de la Morinière et al. 2002). The vast majority of strata along the inshore-offshore shelf gradient showed a proportionally high abundance of juveniles, and preferences by fishes for a given stratum (or biotope) were species specific. Therefore, the importance of mangroves and seagrass as nurseries in terms of harboring high densities of juveniles was species-dependent, since for certain species the shallow coral reefs (i.e., shallow back and fore reef) exhibited higher densities. In species-specific cases, mangroves were important for *L. apodus*, *L. griseus*, and *S. barracuda*, whereas a combination of mangroves and shallow back reef were important for *H. flavolineatum*. Mangroves and seagrass were important for *H. sciurus* and *G. cinereus*, whereas seagrass were important for *O. chrysurus* and *H. plumieri*. Lastly, shallow back reefs and shallow fore reefs were important for *A. bahianus, A. coeruleus, A. chirurgus, S. viride, S. chrysopterum, S. aurofrenatum, C. capistratus, L. mahogoni, A. saxatilis, Scarus taeniopterus, Sparisoma rubripinne*, and *H. parrai*. For the majority of fish species, the juveniles were found in shallow-water strata, while the adults were found in deeper-water strata. However, for

some species (e.g., L. *griseus, L. apodus, S. chrysopterum*) adults co-occurred with the juveniles in the same strata.

Inferences about the PLCMs or ontogenetic migrations for the selected fish species along the inshore-offshore, cross-shelf gradient in southwestern Puerto Rico were elucidated by quantification and analysis of size-frequency distributions (Chapter 4). Of the 20 selected species, at least 17 showed clear evidences of a progressive difference in habitat use, with preferences for certain strata or biotope, implying ontogenetic migrations or PLCMs. However, among the 13 "nursery species", at least 12 showed evidences of migration among habitats; among the other 2, one showed low abundances and habitat restriction (i.e., mangroves), while the other one showed similar preferences for many strata as nurseries. Among the 7 "reef species", at least 6 showed the migration; the other remaining showed similar preferences for many strata (i.e., mainly coral reefs). An apparent directionality of migration occurred from mangroves, seagrass and shallow back reefs to deeper reefs in Montalva Bay-Romero, while in Corral-Turrumote such an apparent directionality was from seagrass and shallow back reefs to deeper reefs.

In this study, the relative fish nursery value of the mangrove-seagrass-coral reef continuum (Chapter 3) and the evidence of PLCMs or ontogenetic migrations (Chapter 4) were deductively elucidated using underwater visual censuses (UVCs) based on relative fish densities. However, direct evidence of nursery functionality of given habitats and their relative contribution of juveniles to adjacent areas and distance traveled may be substantiated by complementing UVCs with mark-recapture techniques, otolith microchemistry (Gillanders 2002), genetic structure comparisons (Palumbi 2003), and comparisons of dietary changes (Cocheret de la Morinière et al. 2003), not only for a

given geographic area but also for a combination of several areas under different hydrodynamic and geomorphological regimes.

From a geographical perspective, in the western Atlantic not all mangroves and seagrass are similar in terms of providing nursery function (Chittaro et al. in press), but mangroves may substantially contribute for the replenishment of certain fish species (e.g. *Scarus guacamaia*, Mumby et al. 2004). The mangrove and seagrass habitats harbor their own invertebrate and vertebrate community (Valiela et al. 2001) and also have other intrinsic values, such as supporting fisheries, and controlling sediment movement, wave action, and coastal erosion (Alongi 2002). Consequently, instead of providing a complete relevance to given habitats separately (e.g., mangroves, seagrass or shallow-water coral reefs) as nurseries, it would be more important to view the mosaic of habitats as a continuum and integral component of the post-settlement connectivity of marine organisms. The whole continuum may offer a combined function as a species-specific nursery and adult grounds rather just than visualizing an allocated value.

Sound conservation and management strategies in coastal zones should be based on integral approaches to protect marine habitats using NTMRs taking into consideration the ecological relationships (i.e., connectivity) between habitats not only locally (i.e., nation-wide), but more importantly into a larger regional scale (i.e., large marine ecosystems, e.g., Sherman and Duda 1999; biogeochemical provinces, e.g., Lunghurst 1998). In fact, the value that an interlinked mosaic of habitats may offer in terms of providing essential attributes (e.g., shelter, food, spawning grounds and nursery areas) for many species would be even more important than protecting the species individually. The use of NTMRs (Lubchenco et al. 2003; Roberts et al. 2003) incorporating a range of

habitats (Lindeman et al. 2000), following an ecosystem-based approach (Browman et al. 2004) is a promising conservation and management alternative, recently being scientifically endorsed, to provide an ecological-based management approach for wisely use and protect the coastal resources. However, a crucial component of an ecosystem-based management, NTMRs, and MPAs would be the linking process between the resource (e.g., fish), fishermen, and government regulators (Browman et al. 2004; Hilborn et al. 2004); in other words, considering humans in the ecosystem management would provide incentives to ameliorate the historic cascade effects of fishing on the marine ecosystem (e.g., Jackson et al. 2001).

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