

**Distribution patterns of reef fishes in southwest Puerto Rico, relative to structural habitat, cross-shelf location, and ontogenetic stage**

By

Kassandra Cervený

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Approved by:

\_\_\_\_\_  
Conrad Recksiek, Ph.D.  
Member, Graduate Committee

\_\_\_\_\_  
Date

\_\_\_\_\_  
Paul Yoshioka, Ph.D.  
Member, Graduate Committee

\_\_\_\_\_  
Date

\_\_\_\_\_  
Richard S. Appeldoorn, Ph.D.  
Chair, Graduate Committee

\_\_\_\_\_  
Date

\_\_\_\_\_  
Edgardo Ojeda, Ph.D.  
Representative of Graduate Studies

\_\_\_\_\_  
Date

\_\_\_\_\_  
Nilda E. Aponte, Ph.D.  
Departmental Director, Marine Science

\_\_\_\_\_  
Date

## ABSTRACT

This work applies a Cross-Shelf Habitat (CSH) framework to delineate habitat usage patterns for twenty-eight species from five families of common reef fishes (Acanthuridae, Serranidae, Haemulidae, Lutjanidae, Scaridae) in the southwest of Puerto Rico. This framework incorporates both habitat types and geomorphic zone of the insular shelf to create a matrix of individually unique cross-shelf habitats. Habitat maps of 24x4 meter strip transects and counts of 21,877 fishes (using visual census) on mapped habitats provided the data applied to the CSH framework. Patterns emerge in habitat usage. The *Inner Shelf – windward intermediate* geomorphic zone is of importance for all lifestages of sampled species, while for non-adult life stages *Low Relief Dead Coral* is the most important habitat type overall. These usage patterns can aid in the conservation efforts in marine and fishery science by delineating not only habitat of importance but also the location of that habitat on the shelf.

## RESUMEN

Este trabajo utiliza la distribución de habitáculos a través de la plataforma ‘CSH’ (por sus siglas en inglés) como el marco de trabajo para delinear los patrones de uso de éstos, por veintiocho especies comunes de peces arrecifales pertenecientes a cinco familias (Acanthuridae, Serranidae, Haemulidae, Lutjanidae y Scaridae). Este marco incorpora a ambos, los tipos de hábitat y las zonas geomórficas de la plataforma insular, para generar numerosos otros habitáculos individuales únicos a través de la plataforma. Para proporcionar los datos al marco de “CSH” se levantaron mapas de habitáculos por medio de transectos lineales en forma de franjas de 24 por 4 metros y se contó por medio de censos visuales un total de 21,877 peces, en los mismos hábitat descritos. Los patrones emergen según su uso; Al interior de la Plataforma – la zona geomórfica intermedia de barlovento resulta importante para todos los estadios de vida de las especies estudiadas, así como es importante para los estadios de vida “no adultos”, el hábitat de coral muerto de bajo relieve. El conocimiento de los patrones de uso puede contribuir a los esfuerzos de conservación de las ciencias marinas y pesqueras no solamente delineando los hábitat de importancia, sino también por la ubicación de ese hábitat en la plataforma.

Singularly dedicated to David Spencer.

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# INTRODUCTION

Many fishes utilize a variety of habitats ontogenetically as they develop through various life stages, e.g., newly settled, early and late juveniles, sub-adults, adults (Appeldoorn et al., 1997; Lindeman, 1997). Warner and Gilliam (1984) hypothesized that preferred fish habitat is selected by balancing the need for refuge while maximizing growth. While some Caribbean studies document fish habitat use over life cycles, there is a lack of characterization of differential habitat use during ontogenetic migrations in terms of the cross shelf continuum. Appeldoorn et al. (2003) showed a progressive increase in fish length for snappers and grunts as distance increases away from presumed near-shore settlement sites. In Curaçao, Cocheret de la Morinière et al. (2002, and 2003a, b) showed ontogenetic migrations, also known as *Post-settlement Life Cycle Migrations*, from mangrove and seagrass habitats (nursery habitats) to offshore reef habitats. Nagelkerken et al. (2000, 2001) supported the nursery value of mangroves, seagrass and shallow-water coral reefs for fishes, with fish using nearshore seagrass and mangrove habitats in juvenile stages before moving offshore to reef habitats as adults. In Biscayne Bay, Lindeman (1998) thoroughly defined habitat use across the shelf for snappers and grunts at differing times in their life cycle, but his study was limited not only by the number of species investigated but also by the simplicity of the locale itself. In Puerto Rico, Appeldoorn et al. (1996) and Hill et al. (2003) found that differences in size and frequency distributions of fish populations were consistent through time and across habitats within the coral reef system of La Parguera. Hill et al. (2003) further suggested that establishing habitat maps and species densities within habitats

allowed for more fine scale analysis of habitat-species relationships and further extrapolation to total population sizes.

One critical factor limiting the understanding of species distributions and displacements across shelf habitats has been the lack of a spatial framework that considers structural attributes along a shelf continuum (Lindeman et al., 1998). Ideally, such a framework should address three points. First, quantitative work needs to evaluate the preferences of reef fishes for using mangrove, seagrass and reef across the full range of environmental conditions available, from the coastline to offshore areas (Lindeman, 1998); thus it must represent the full range of habitat alternatives. Second, the framework must be adaptable to the quality and scale of the available habitat information. The approach normally taken is a hierarchical classification scheme, where sub-habitat classifications (e.g., dense seagrass, sparse seagrass) can be pooled, when necessary into a coarser habitat category e.g., seagrass, or submerged aquatic vegetation (SAV). Such hierarchical classification schemes are to some degree dependent upon the technology used for discriminating habitat, with examples being those of habitats resolved from diver based assessments (Lindeman et al., 1998), satellite based imagery (Mumby and Harborne, 1999), aerial photographs (Kendall et al., 2001; NOAA/NOS/Biogeography Team, 2002), and sidescan sonar (Prada, 2002). Third, the evaluation of preferential habitat use must also address variations in habitat quality due to changes in geomorphology, particularly in a cross-shelf context. This allows for quantification of situations where more than one location of the habitat exists (e.g., mangrove habitats that occur along the shore and also in association with offshore emergent reefs). Lindeman et al. (1998) developed a Cross-Shelf Habitat

(CSH) framework that accounts for such differences. The framework is in the form of a matrix with structural habitats listed on the side (in a hierarchical fashion) and cross-shelf geomorphic zones presented in a linear order across the top. Thus, Lindeman's framework allows for characterization to occur at several spatial scales across heterogeneous marine habitats by incorporating habitats in singularity, as well as the cross shelf strata on which they were found, essentially creating a new "cross shelf habitat" moniker for that particular habitat.

Lindeman et al. (1998) first implemented the CSH framework with diver-observed data (e.g., transect data, point counts) in mind. This had two advantages: (1) data were collected at the small scales ( $\sim 1 \text{ m}^2$ ) at which most fish interact with their environment, and (2) data collection was not dependent on the existence of any detailed habitat map. Hill et al. (2003) considered CSH-based mapping to provide a more "robust" sampling of habitat features and their linkages to fish distributions because the mapping method considered all species encountered, thus allowing for a more in-depth sample for fisheries management purposes, while at the same time its flexibility allows detailed sampling to occur without prior habitat map information. This latter point is critical because detailed habitat maps are not available for most reef systems, regardless of management need.

Currently the study of ontogenetic habitat use across the cross-shelf continuum has only been used for limited species over a simple marine environment (Biscayne Bay has only a single barrier reef, and the Curaçao-based studies examined a simple bay and channel system). The simplicity of a marine system may limit the extrapolation of results to more complex systems. Murphy (2001) used the CSH framework to establish habitat use patterns

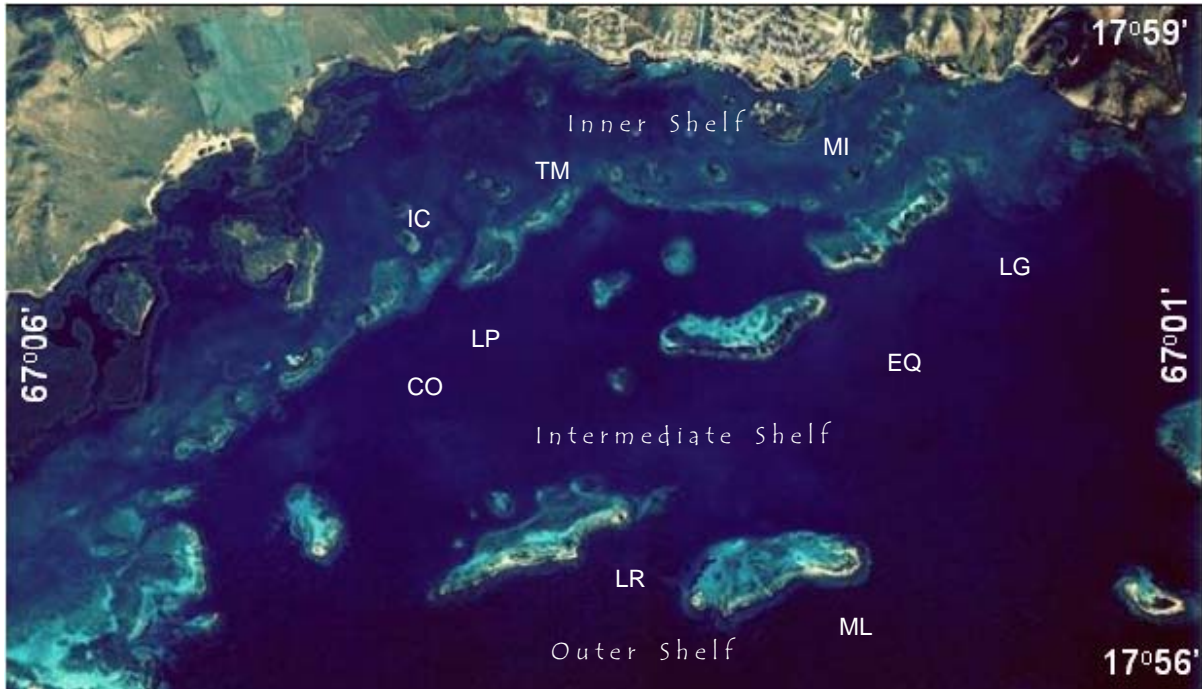
of a limited group of reef fishes in the more complex habitat of La Parguera, PR. However, he concentrated only on the mangrove and seagrass habitats, thereby limiting the understanding of habitat use across the shelf. Christiansen et al. (2003) also attempted to link fish distributions to habitat and cross-shelf position in the La Parguera area, but they primarily restricted their study to the analysis of family distributions. This limited the interpretation of fish habitat use and cross-shelf position as one species could dominate the family in simple terms of numbers, skewing the resulting distribution data (e.g., French grunts, *Haemulon flavolineatum*, in Haemulidae). While these studies have demonstrated the validity and practicality of the CSH approach, limitations of environment (simple systems), habitats investigated (only mangroves and seagrasses), and pooled species distributions (families not species) have impeded the full application of the CSH framework and a complete understanding of habitat use within coral reef ecosystems. Investigating the ontogenetic variations in habitat use across many fish species within a complex ecosystem will eventually allow for a greater understanding of how fish perceive and utilize their environment, enhance our understanding of habitat linkages, and identify critical habitat from a multi-species perspective. A necessary first step is to determine species-specific patterns of habitat use through ontogeny.

The primary objective of this study was to utilize a previously conceived cross-shelf habitat framework for La Parguera, Puerto Rico (Appendix A.1, see Recksiek et al. 2001) to assess the spatial distribution patterns of five Caribbean reef fishes (e.g., Acanthuridae, Haemulidae, Lutjanidae, Serranidae, Scaridae) and how these vary over ontogeny within a complex habitat assemblage.

The species selected for evaluation were chosen based on their economic and ecological importance. In addition to species-specific distribution patterns, information for all species was combined to see if certain cells (cross-shelf habitats) had greater importance for the protection of habitat and biodiversity. The protection of these cross-shelf habitats will be essential for the conservation of the highest biodiversity of these groups.

## Methods

The southwest coast of Puerto Rico, within the La Parguera shelf (17°58.3' N, 67°02.8' W), constitutes the area of study. Although the climate consists of both wet and dry seasons through the summer and winter months, respectively, the area is characterized by low rainfall. Trade winds prevail from the east and southeast throughout the year. The shelf edge is approximately 12 km from shore, and there are a series of three emergent reef lines (Figure 1) between it and the shoreline that act as breakwaters. The nearshore environment of La Parguera is composed of *Thalassia testudinum* beds and mangrove coastline dominated by *Rhizophora mangle*. The three reef lines stratify the insular shelf into inner, middle, and outer shelf reef sites, and define the cross-shelf classification (Recksiek et al., 2001; Appeldoorn et al., 2001, Kimmel, 1985).



**Figure 1. Inshore area of La Parguera, Puerto Rico, showing the three shelf regions and the location of major emergent reefs. Inner emergent reefs: CO = Collado, LG = La Gata, LP = Las Pelotas. Intermediate emergent reef: EQ = Enrique. Outer emergent reefs: ML = Media Luna, LR = Laurel. Other sites: IC = Isla Cueva, MI = Magueyes Island field station, , TM = Tres Marias.**

This study sampled sites across this local seascape (Figure 2). The six inner shelf sites, *Collado*, *Isla Cueva*, *Tres Marias*, *El Palo*, *La Gata* and *Las Pelotas* are approximately 1.5 km from shore, while the middle shelf site, *Enrique* is 2 km from shore. *Enrique* is a large spanning reef, taking up the majority of this zone, and for this reason, there is no comparable replicate site for this middle shelf reef zone. *Laurel*, *Margarita* and *Media Luna*, the outer emergent reefs, lay approximately 3.5 km from shore.



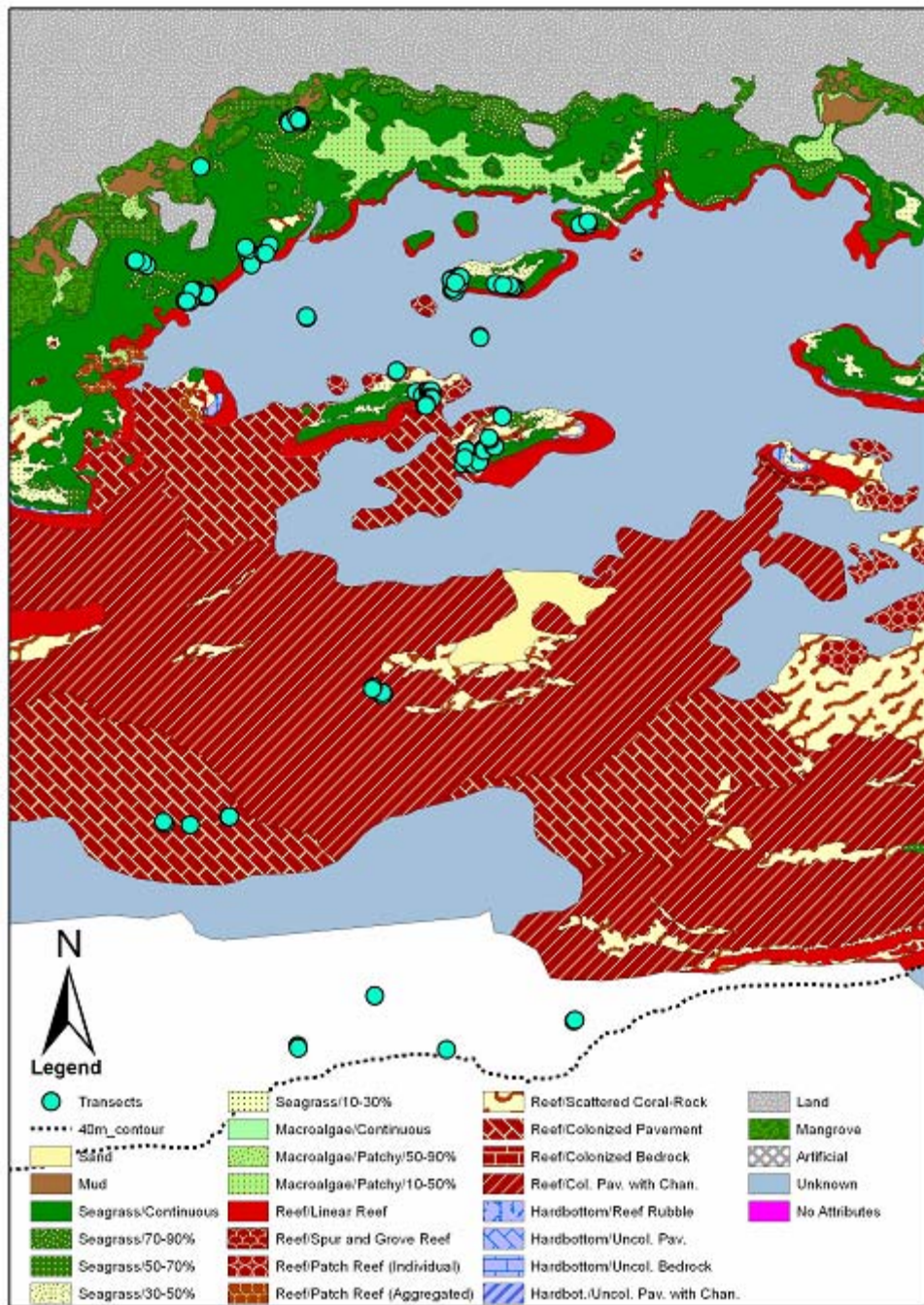


Figure 2. Transect sites surveyed in La Parguera, Puerto Rico, 1996-2000, superimposed on a benthic habitat map (NOAA/NOS/Biogeography Team, 2002). The edge of the insular shelf is approximated by the 40-m depth contour.

In this study *habitat type* is based on benthic substratum on small spatial scales (1 m<sup>2</sup>) according to its structure. In contrast, *geomorphic zones* are based on the cross-shelf geomorphology (depth, distance from shore, current/wave exposure, wind exposure, etc.) at large scales. The combination of the two define *cross-shelf habitat*. The axes of habitat type and geomorphic zone form a framework of spatially arranged cells, with each unique cell signifying an individual cross-shelf habitat. Thus, a habitat can occur multiple times over the cross shelf continuum, but each CSH framework cell represents a unique combination of habitat type and location across the shelf. By estimating the abundance of each species (or life stage: early juvenile, juvenile, adult) for each cell, the framework reveals preferential habitat use. This effectively produces a “map” of the marine environment for each species, allowing for the identification of key cells within it. By treating abundance data by life stage, the CSH framework highlights usage patterns over ontogeny. These patterns can then be compared across families for key habitat usage. When compared across all species, the key cells (cross-shelf habitats) for conservation efforts can be easily chosen, as the usage patterns can be clearly seen.

The insular shelf of La Parguera, Puerto Rico has been characterized (Appeldoorn et al., 2001 and Recksiek et al., 2001) utilizing the cross-shelf habitat framework as derived from its original application in Biscayne Bay, Florida (Lindeman, 1998.) Thirty-six geomorphic zones were identified using bathymetry and cross-shelf positioning relative to emergent mangrove islands and reefs (Lindeman et al., 1998.) Twenty structural habitat types were also determined (Lindeman et al., 1998.) Of the possible 720 cross-shelf habitats

(36 geomorphic zones x 20 structural habitat types), 521 were judged by Appeldoorn et al. (2001) to occur in the La Parguera area (Appendix A.2).

A modified framework to characterize the habitat and geomorphology of the La Parugera shelf was used in this study (Appendix A.3). The deep shelf edge geomorphic zones were not sampled due to the depth limits on SCUBA diving. Instead, an additional zone, “Near Shelf Edge,” was added to the Cross-Shelf Habitat Framework in an attempt to record changes in species distributions expected at the edge of the insular shelf. Emphasis in this study was given to the patterns around emergent reefs, and the reef top geomorphic zone, which applies to non-emergent reefs, was not sampled. Because there was only one intermediate reef, it was not sampled to the same degree as the inner and outer reefs and sampling was oriented toward a separate study on seagrass and mangrove habitats (Murphy, 2001). In addition, it was difficult to adequately delineate in the field the central channel axis zone on the single intermediate reef. For these, just the leeward and windward zones were used. Furthermore, the “Invertebrate-Sponge” habitat was redefined. As originally conceived, sponge bottom habitat was defined as one dominated by large barrel sponges, a habitat thought not to occur in La Parguera. However, broad areas of encrusting sponge were discovered, and the “invertebrate-sponge” label was used to classify this habitat type.

All surveys followed Recksiek et al. (2001) and Murphy (2001). Underwater visual census was utilized to characterize habitat type and fish distribution along random transects (each 4x24m). Two advantages of this census method are linkages between habitat and fish distribution and estimation of fish size (i.e., length.). Snorkel and SCUBA techniques were used for these habitat and fish surveys.

First, broad sites (~25 sites) (Figure 2) were chosen according to the cross shelf strata developed for the La Parguera area. To ensure the inclusion of a variety of microhabitats, the site was pre-surveyed to identify broad patches of “uniform” habitat; transects were then randomly placed within these areas. Each transect was surveyed three times. The first survey generated the habitat map; the second and third surveys (on a different day) were used to record mobile and sedentary fish species, respectively. Habitat type along each transect was surveyed using a 1m<sup>2</sup> quadrat by the surveying diver. Sixteen habitat types were included in this study. (Table 1) Positions of individual fish or schools were recorded on the transect habitat map. For schools, the numbers of fish (for each species) were estimated, along with the minimum and maximum length. All size data were reported in total length (Murphy, 2001). All fieldwork was completed from 1996 to 2000 (Murphy, 2001 and Foley, 2004). Species surveyed covered 54 species in 13 families for a total of 31,354 individuals. This paper studies 28 species in five families. (Table 2)

**Table 1. Habitat definitions used during the diver-based habitat surveys of La Parguera, Puerto Rico, 1996-2000. Habitats were mapped at a scale of 1 m<sup>2</sup>.**

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**Coral High Relief (CH):** Greater than 50% live coral, which is a branching coral species, and therefore a complex structure, that provides refuge between branches. E.g., *Acropora cervicornis*, *Porites porites*, *Millepora* sp.

**Coral Low Relief (CL):** Greater than 50% live coral. These are live corals that aren't elevated off the bottom, nor are branching species. These are then smooth, flattened or rounded corals that don't have a complex structure to them, therefore they don't offer hiding places or refuges within the coral structure itself. E.g., *Montastrea* sp.

**Dead High Relief (DH):** Greater than 50% dead coral that is structurally intact. The colony has died but its original structure persists. E.g. Dead *Acropora cervicornis* or *Porites porites* skeletons that still offer hiding spaces.

**Dead Low Relief (DL):** This is mostly hard bottom with little or no relief off the bottom and therefore no protective hiding areas to larger fish. Importantly though, this is still the original framework of the coral structure.

**Mixed Low Relief (ML):** Here is an indiscernible mix of habitat categories, where no one type can be determined as the dominant cover. Structure is still simple and low relief, therefore not offering suitable hiding space.

**Mixed High Relief (MH):** Here is an indiscernible mix of habitat categories, where no one type can be determined as the dominant cover. Structure is complex and high relief, therefore offering suitable hiding space.

**Grass with small invertebrates (GI):** Greater than 50% seagrass occupied by "small" sized invertebrates such as a *Favia fragum* coral, a little patch of *Acropora cervicornis*, small sponges, small patches of zooanthids. Unfortunately, this idea of small is a bit ambiguous here and does depend a bit more in what the individual observer considers "small".

**Grass with large invertebrates (GL):** Greater than 50% seagrass with "large" sized invertebrates such a large patches of *Acropora cervicornis*, large patches of zooanthids mixed in with the seagrass, and some mounding corals found alone among a bed of seagrass.

**Grass *Thalassia* (GT):** Greater than 50% *Thalassia testudinum* seagrass species that does not include any other major structural invertebrates within a meter square quadrat.

**Grass and Algae (GA):** Greater than 50% coverage of any seagrass species mixed with attached or detached algal clumps (E.g., *Dictyota* sp., *Ulva lactuca*).

**Algae (AA):** Greater than 50% coverage of algae within a meter square quadrat and is therefore dominated by algae cover of any kind, including: detached, attached, mat or turf for examples.

**Rubble (RB):** Greater than 50% coverage in a meter square quadrat of broken coral pieces or fragments. Coral material is no longer living and is no longer in the original structure. This habitat is unique from dead coral in that the fragments have potential to move with current and wave regime.

**Coral/Gorgonian (CG):** Greater than 50% in a meter square quadrat of gorgonians species. These are often attached to some hard structure, often live coral and therefore, the habitat classification system includes corals in the category name. Gorgonians may provide hiding space for larger individuals. But is considered a low relief habitat since the refuge space is not as desirable as high relief coral.

**Sand coarse (SC):** Greater than 50% coarse sand composition. Coarse sand is more commonly observed at shallow depths.

**Sand fine (SF):** Greater than 50% fine sand composition. Fine sand is more commonly observed at depths of at least 50 ft.

**Invertebrate sponge (IS):** A category used to define large barrel sponges that can be used as hiding spaces by small fishes. Was also used to classify large encrusting colonies of *Cliona* sp. that are often found encrusting on dead coral or rubble pieces.

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**Table 2. Species List with lifestage sizes (and relevant source), number of individuals and number of encounters for the La Parguera, Puerto Rico study**

SCIENTIFIC NAME	COMMON NAME	# of Individuals	# of Encounters	Early			Size Class Citation
				Juvenile (cm)	Juvenile (cm)	Adult (cm)	
<i>Acanthurus bahianus</i>	Ocean Surgeonfish	697	389	1-7	8-14	15+	Munro 1983, Ross, 1982
<i>Acanthurus chirurgus</i>	Doctorfish	877	314	1-7	8-14	15+	Munro 1983, Ross, 1982
<i>Acanthurus coeruleus</i>	Blue Tang	621	437	1-6	7-13	14+	Munro, 1983
<i>Epinephelus adscensionis</i>	Rock Hind	4	4	1-7	8-15	16+	Garcia-Cagide, 2001
<i>Cephalopholis cruentata</i>	Grasby	11	11	1-7	7-13	14+	Fishbase, 2005
<i>Cephalopholis fulva</i>	Coney	19	19	1-8	8-16	16+	Munro, 1983
<i>Epinephelus guttatus</i>	Red Hind	9	9	1-12	13-24	25+	Munro, 1983
<i>Haemulon carbonarium</i>	Ceasar Grunt	52	26	1-7	8-21	22+	Munro, 1983
<i>Haemulon chrysargyreum</i>	Smallmouth Grunt	85	29	1-7	8-17	18+	Munro, 1983
<i>Haemulon flavolineatum</i>	French Grunt	7023	471	1-7	8-14	15+	Munro, 1983
<i>Haemulon macrostomum</i>	Spanish Grunt	7	7	1-7	8-28	29+	Munro, 1983
<i>Haemulon parra</i>	Sailors Choice	24	24	1-7	8-16	17+	Lindeman, 1998
<i>Haemulon plumieri</i>	White Grunt	1100	199	1-7	8-15	16+	Munro, 1983
<i>Haemulon sciurus</i>	Bluestriped Grunt	347	114	1-7	8-17	18+	Munro, 1983
<i>Haemulon striatum</i>	Striped Grunt	75	75	1-7	8-16	17+	Lindeman, 1998
<i>Lutjanus analis</i>	Mutton Snapper	2	2	1-10	11-27	28+	Munro, 1983
<i>Lutjanus apodus</i>	Schoolmaster	329	209	1-11	12-26	27+	Munro, 1983
<i>Lutjanus griseus</i>	Gray Snapper	23	15	1-10	11-24	25+	Starck, 1971
<i>Lutjanus synagris</i>	Lane Snapper	60	34	1-9	10-19	19+	Munro, 1983
<i>Sparisoma aurofrenatum</i>	Redband Parrotfish	555	408	1-7	8-14	15+	Munro, 1983
<i>Sparisoma chrysopterygum</i>	Redtail Parrotfish	577	353	1-8	9-16	17+	Ross, 1982
<i>Sparisoma iseri</i>	Striped Parrotfish	7087	828	1-7	8-15	16+	Fishbase, 2005
<i>Sparisoma radians</i>	Bucktook Parrotfish	840	840	1-2	3-5	6+	Humann, 1994
<i>Sparisoma rubripinne</i>	Yellowtail Parrotfish	205	156	1-8	9-16	17+	Ross, 1982
<i>Sparisoma taeniopterygum</i>	Princess Parrotfish	403	136	1-8	9-16	17+	Fishbase, 2005
<i>Sparisoma viride</i>	Stoplight Parrotfish	785	580	1-8	9-16	17+	Munro, 1983, Ross, 1983
<i>Scarus guacamaia</i>	Rainbow Parrotfish	40	40	1-8	9-16	17+	Ross, 1982
<i>Scarus vetula</i>	Queen Parrotfish	20	18	1-8	9-16	17+	Ross, 1982

Data were managed using *Microsoft Excel* (2002) and *Access* (2002) including statistical manipulation and CSH framework generation. *ArcView* (version 3.1) and *GeoMedia (InnerGraph)* were used to digitize the transect habitat maps to obtain habitat areas. The habitat areas of each transect allowed for the calculation of habitat-specific density for each fish species.

The data collected on minimum/maximum length and numbers of individuals per school were used to generate habitat-specific length/frequency distributions. Within-school length distributions were assumed to be uniform between the minimum and maximum lengths recorded. Density-based length frequencies within each habitat type were then combined from different transects within the same geomorphic zone. The Central Limit

Theorem was invoked to assume this process led to Gaussian distributions. As densities cannot simply be added, the weighted averages were used for combination purposes. This method takes into account the area of the habitat that an individual was encountered over. This procedure gives greater weight to fish encountered over a small area of a specific habitat in a larger available matrix of habitats, in effect recognizing that this habitat may be of particular importance. Thus, the importance of that small habitat area is not lost in the combination of densities for the resulting CSH frameworks.

The result of this process was the density, by size class, of fish within each combination of habitat type and geomorphic zone, i.e., cross-shelf habitat. The length-frequency distributions were used to calculate density by life stage within each cross-shelf habitat. Three stages were considered: early juveniles, juveniles and adults. To determine adult size ranges, size at first maturity was used (if available) or size and pigmentation patterns as reported in the literature (Starck, 1970; Ross, 1982; Munro, 1983; Humann, 1994; Lindeman, 1998; Fishbase, 2005). Size and pigmentation patterns were also used in differentiating juvenile and early juvenile length ranges (Lindeman, 1997). If juvenile and early juvenile information were unavailable, the range between zero and the adult stage was divided by half with the lower being designated as early juvenile and the higher as juvenile (Murphy, 2001). The size ranges of life stages are presented in Table 2.

To depict habitat use for each species by life stage, density data were grouped into quartiles. For each species' life stage, all occurrences were listed in increasing order of density. After this ranking was established, it was split into quartiles. If fewer than four occurrences were observed, each occurrence was assigned to a quartile starting at the lowest

one. The quartile group of each cell in the CSH framework was then coded (by shading), which gives a graphical view of the cross-shelf habitats used and their relative importance.

## Results

Twenty-five sites (Figure 2) were sampled along the cross-shelf gradient, with data collected for 185 transects. The areas of cross-shelf habitats sampled in this study ranged from 0.07 m<sup>2</sup> to 96 m<sup>2</sup>. Approximately 21,900 fish were sampled through the 5 families (28 species.) More than half (64%) of the total fish abundance were made up of two species (32% each Striped Parrotfish and French Grunt). Eighty-eight percent of the total fish abundance was found in two families (Scaridae and Haemulidae). Densities within the cross-shelf habitats ranged from 0.0012 fish/m<sup>2</sup> (Blue Tang) in low relief, dead coral dominated habitats in the Inner Shelf – Windward Intermediate geomorphic zone to 12 fish/m<sup>2</sup> ( French Grunt) in high relief, dead coral dominated habitat in the Inner Shelf – Leeward Shallow geomorphic zone.

This study encountered three cross-shelf habitats that were not initially expected (Appendix A.3). These additional occurrences are in the outer shelf area, with two instances in bare rubble, and one in coral with high relief habitat areas.

### **Acanthurids**

Across three acanthurid species (*Acanthurus bahianus*, *A. chirurgus*, and *A. coeruleus*) 2,200 individuals were observed.



### *Acanthurus bahianus*

Surgeonfishes showed a distinct ontogenetic shift in cross-shelf habitat use. Early juveniles were found in a mix of habitats (Appendix B.1.a). Seagrass areas in protected shallow inner shelf habitats supported high densities. These included the leeward side and leeward channel axis of the inner emergent reef line, as well as adjacent to inshore mangrove keys. The only other area with seagrass occurred on windward intermediate zone of the inner emergent reef line, and this too supported high densities of early juveniles. This zone also had high densities in areas of mixed low-density corals, while moderate densities were also found in protected areas of low relief dead corals. A second area supporting high densities of early juveniles occurred along the leeward and channel axis zones of the outer emergent reef. Here the primary habitat types were low relief areas of live or dead corals or gorgonians. Additionally, early juveniles were found in lower abundance in a variety of cross shelf-habitats, thus showing some flexibility in habitat use. However, no early juveniles were found associated with the broad shelf areas, regardless of cross-shelf position; distributions were always associated with emergent keys or reefs.

The distribution of large juveniles (Appendix B.1.b) shows a shift in cross-shelf habitat use relative to early juveniles. Reduced densities are found on inner shelf sites, with no occurrences associated with keys inshore of the inner reef line. Seagrass and low relief dead coral habitat-types still dominated on the inner shelf. Whereas some early juveniles were found along seagrass habitats on the middle reef line, larger juveniles were more abundant here but were limited to hard bottom habitats of rubble and gorgonians. Highest densities of large juveniles were found associated with the outer emergent reef and outer

shelf habitats, predominately on a mix of consolidated substrata, including both low and high relief areas. Moderate densities were found on the broad outer shelf and at near shelf-edge locations.

Adult distribution patterns (Appendix B.1.c) continued the above shift in habitat use. Only low densities were found over the inner shelf, and none within seagrass habitats there. Adults were largely restricted to the outer shelf, with a clear shift evident into deep areas (windward deep, shelf outer, near shelf-edge, as well as leeward deep). In these areas, a mixture of low relief habitats dominated. High densities of adults were also found along the forward margins of the channel axis in areas of mixed corals.

In summary, early juveniles of the ocean surgeonfish occur largely in shallow areas, with inshore seagrass habitats being important. However, patterns of habitat use in show a general shift during ontogeny toward the outer shelf, toward progressively deeper habitats, and toward the exclusive use of consolidated substrata.

### *Acanthurus chirurgus*

Doctorfish did not show as clear an offshore movement as surgeon fish, but instead had a consistent high-density presence in the inner shelf, windward intermediate zone across most habitat types (Appendix B.2.a.) The early juvenile distribution was similar to the ocean surgeonfish.

Larger juvenile distribution patterns show a shift from vegetation dominated habitats to coral dominated ones (Appendix B.2.b) with the exception of the continued use of the Inner Shelf- Windward Intermediate zone. The lowest densities were found in non-coral covered habitats (vegetation and sediment.) The highest densities were found in the coral

dominated outer shelf sites (channel axis and leeward) and in that inner shelf site. Although found in the vegetated habitats in the inner shelf, the majority of the larger juveniles were more densely populating the coral habitats.

The adult distributions of doctorfish (Appendix B.2.c) continued to illustrate the shift from vegetation to coral cover. Except for the Inner Shelf – Windward Intermediate zone, no adult occurrences were in vegetation. The highest densities were found in gorgonian dominated as well as mixed high relief coral and low coral relief areas. Additional to the clear habitat shift, a cross shelf trend appears with high densities being found in the windward margin of the channel axis areas of the outer shelf.

The highest densities of doctorfish occur in vegetated habitats (seagrasses and algae) with the leeward margins being of importance. Habitat usage patterns clearly shift during ontogeny from this habitat to a coral dominated one as well as out from the inner shelf towards the shelf edge. In addition to this, the Inner Shelf – windward intermediate geomorphic zone played an important role through all lifestages of this species.

### *Acanthurus coeruleus*

The distribution patterns of blue tangs shared the distinct ontogenetic shift in cross-shelf habitat usage with the ocean surgeonfish. (Appendix B.3.a-c) The early juvenile distribution was also very similar to that of the ocean surgeonfish. Seagrass habitats within the protected inner shelf were of importance to the early juveniles, as were the coral dominated areas of the inner and outer shelf. (Appendix B.3.a) The only windward seagrass zone supporting this lifestage occurred within the inner reef line. The Inner Shelf –

windward intermediate zone was of clear importance to this lifestage - supporting high densities.

The larger juvenile lifestage distribution exhibits a changing trend in cross-shelf habitat use relative to the early juveniles. (Appendix B.3.b) A reduction in the densities of occurrences in vegetated habitats as well as within the inner shelf supports this ontogenetic shift. The larger juveniles were most densely associated with the outer shelf zones directly adjacent to the channel axis and windward of it in coral dominated habitats. In fact, the distribution of this lifestage was almost exclusively restricted to non-vegetated habitats. Dead coral habitats dominated the inner shelf in this lifestage similar to the early juvenile stage. High densities of this lifestage occurred in the outer shelf in the channel axis zones and the immediately adjacent ones. Leeward zones in the outer shelf were also supportive of high densities of this life stage.

Adult distribution patterns (Appendix B.3.c) maintained the trend noted above in habitat use. Only limited occurrences of adults were found in the inner shelf and none within vegetated habitats. Those inner shelf occurrences were found within the windward intermediate zone that has been shown to be of unique importance. This life stage was mainly restricted to the outer shelf with a mixture of habitat use within.

Blue tang early juveniles were found to have a wide habitat use, with vegetated areas being of importance. There is, however, a trend seen shifting the habitat use from vegetation to coral dominated areas as well as from the inner shelf to increasingly deeper areas.

## Serranidae

Four species, 43 individuals, were observed in this study: *Epinephelus adscensionis*, *Cephalopholis fulva*, *Cephalopholis cruentata*, and *Epinephelus guttatus*. Most encounters and highest densities occurred in the outer shelf area with no great trend in ontogenetic shifts seen.

### *Epinephelus adscensionis*

Rock hind encounters were limited in this study. Only the juvenile lifestage was encountered and that was limited to the deeper zones of the outer shelf (Appendix B.4.a).

### *Cephalopholis fulva*

The juvenile lifestage of the coney was also limited, but occurred exclusively in the deeper reaches of the outer shelf (Appendix B.5.a). The highest density for this lifestage was in rubble habitat and secondarily in low relief areas of mixed corals. The adult coney distribution was also restricted to the deeper zones of the outershelf, concentrated in gorgonian and low relief coral habitats (Appendix B.5.b). Coneys showed a shift from rubble as juveniles to habitats without rubble as adults.

### *Cephalopholis cruentata*

As with the three other members of this family, graysby juvenile encounters were observed in the outer shelf in the deeper zone (Appendix B.6.a). As adults, graysbys split encounters between the outer shelf and inner shelf, but both mainly within windward geomorphic zones (Appendix B.6.b). The Inner Shelf – windward intermediate geomorphic zone surfaces again as crucial habitat supporting high densities of graysbys.

### *Epinephelus guttatus*

The distribution pattern of the red hind shows a distinct preference for windward habitats (Appendix B.7.a-c). The early juvenile lifestage of this specie was restricted to the

outer shelf windward zone, both in deep (shelf outer) and shallower zones (windward shallow) (Appendix B.7.a).

The juvenile lifestage shows a more indiscriminate use of the shelf, with the highest densities focused in windward zones of the outer shelf in deeper water (Appendix B.7.b). A secondary grouping of red hind densities were within the intermediate shelf and inner shelf, windward of the channel. The primary habitats supporting high densities of red hind in all three shelf zones were low relief coral. Mixed corals of low relief and bare rubble were two secondary habitats found of importance in both the intermediate and outer shelf.

The adult distributions were again limited to deeper zones of the outer shelf (Appendix B.7.b). These densities were found concentrated in coral dominated habitats (mixed corals of low relief and gorgonians.)

The distribution patterns of red hinds demonstrate the importance of the windward geomorphic zones as well as low relief and low relief coral dominated habitats.

## **Haemulidae**

Eight species, 8,713 individuals, of Haemulidae were observed in this study: *H. carbonarium*, *H. chrysargyreum*, *H. flavolineatum*, *H. macrostomum*, *H. parra*, *H. plumieri*, *H. sciurus*, and *H. striatum*. All but *H. sciurus* and *H. striatum* showed an ontogenetic movement from the inner shelf areas toward outer shelf areas; while this trend was distinct in some species, in others it was overlain on to a broad patterns of habitat use distributed across the shelf. *H. sciurus* showed movement from submerged aquatic vegetation habitat types across to coral dominated habitats with age. The adult encounters of the Haemulidae family show a shelf-ward trend.

### *Haemulon carbonarium*

The distribution pattern of Caesar grunts showed a clear ontogenetic shift across the shelf (Appendix B.8.a-c). Early juveniles exclusively were found in the inner shelf and in shallow waters (>2m) (Appendix B.8.a). The distribution pattern of the larger juveniles shows the shift in cross-shelf habitat usage (Appendix B.8.b). Habitat usage begins to move across the shelf towards the shelf edge as well as into continuously deeper waters. The windward reach of these geomorphic zones showed to be an important component of this shift (windward shallow, windward intermediate, channel windward.) Coral habitats dominate this specie's usage patterns; however, there is an instance of moderate density found in seagrass habitat. The highest densities are supported in the intermediate shelf in the geomorphic zone immediately adjacent to the channel axis. Secondary high densities were found in the leeward deep zone of the outer shelf. Moderate densities were found in coral dominated habitats (dead coral, both low and high relief and high relief living coral) of the windward side of the inner shelf.

The entirety of the adult distribution of this grunt was restricted to the outer shelf (Appendix B.8.c). The highest densities of this lifestage were concentrated in the leeward shallow zone with consolidated substrata.

To summarize, Caesar grunts are found as early juveniles in shallow waters of the inner shore then progressively move into deeper waters as well as toward the shelf edge with size.

### *Haemulon chrysargyreum*

The distribution pattern of smallmouth grunts shows the importance of windward geomorphic zones for this particular species (Appendix B.9.a, b). The juvenile stage has the

highest densities located shallow to intermediate depth (0-8m) on the windward side of the channel both in the inner and outer shelf (Appendix B.9.a). Moderate densities were also found in the channel axis of both of these areas. All of these encounters were in coral dominated habitats. The highest densities used dead coral with low relief while moderate and low densities were found in areas of high relief both among living and dead coral. Two geomorphic zones were of distinct importance for this species: Inner Shelf – windward intermediate and Outer Shelf – channel windward.

The adult distribution trends tightened up into those two geomorphic zones (Appendix B.9.b). It is interesting to note that the highest density for this lifestage was not found in coral dominated habitat, but in algae. The moderate densities were found back in the coral habitats. The high relief coral habitats were of strict importance in the Outer Shelf – channel windward zone. The lowest densities of the adult lifestage were found in the inner shelf among dead coral habitats.

Smallmouth grunts occur mainly in windward reaches of coral dominated habitats as juveniles and within two very specific geomorphic zones (Inner Shelf – windward intermediate and Outer Shelf – channel windward) as adults.

### *Haemulon flavolineatum*

French grunt distribution patterns show a shift in cross-shelf habitat usage with increasing size. Early juveniles were found to have an indiscriminate habitat use (Appendix B.10.a). Seagrasses in protected shallow inner shelf habitats supported high densities. These included the leeward side and leeward channel axis of the inner, intermediate and outer emergent reef line, as well as adjacent to the inshore mangrove keys and channel leeward



areas. Moderate to high densities were also found in protected areas of dead coral (both high and low relief) and living coral of high relief.

Another area supporting high densities of early juveniles occurred along the leeward channel axis zone of the intermediate shelf. In this zone, the bare rubble and low relief living coral were of importance. Additional to these, high densities of this lifestage could be found on the channel axis and leeward (including deep leeward areas) of the outmost emergent reef. Again coral of low relief were important habitat; as was bare rubble, mixed corals of high relief and living coral with high relief. No early juvenile occurred windward outside of the protected inshore reef break.

Larger juvenile French grunts show the beginning of a shift in habitat use relative to the first stage (Appendix B.10.b). Reduced densities were found in the innermost shelf sites. Vegetation and dead coral dominate the habit usage of the inner shelf. Higher abundances are beginning to be seen away from vegetated areas and more in hard bottom habitats, such as corals and gorgonians in both the inner and intermediate shelf. High densities begin to be seen windward of the channel axis in this lifestage. Three geomorphic zones are illuminated in importance to this lifestage: Inner Shelf – windward intermediate and Intermediate Shelf – channel leeward and channel windward.

Moderate densities are found along the leeward and windward side of the channel axis of the outer emergent reef. The deep leeward side of this same reef is also of moderate importance. Occurrences also creep toward the shelf edge with low densities in the outer shelf's windward intermediate, shelf outer and near shelf edge zones.

The distribution of adults continued the shift in habitat use (Appendix B.10.c). The highest densities were found in the outer shelf, while the inner shelf had lower densities of occurrences and have almost completely abandoned the vegetated habitats. The majority of the fish occurrences also were at the channel axis or windward, leaving most of the protected leeward inner shelf barren of this species. No adult French grunts were found in the intermediate shelf. The highest densities of the adults occurred in the leeward side of the outermost emergent reef with moderate to high densities in the channel axis and windward of it.

In summation, the French grunt had an indiscriminate use of habitat in the early juvenile stage, with high use of vegetated habitats and preference for protected geomorphic zones. As fish grew, they moved out of the protected shelf into deeper waters as well as into hardbottom substrate.

#### *Haemulon macrostomum*

There were limited occurrences in the early juvenile lifestage of the Spanish grunt. The occurrences were in the inner shelf in dead coral dominated areas of low relief on the windward side (Appendix B.11.a). Spanish grunts showed similar patterns of juvenile use as their early juvenile habitat usage (Appendix B.11.b). The coral dominated habitats of the windward margin of the inner most emergent reef hosted the larger juvenile Spanish grunts.

#### *Haemulon parra*

Only the two juvenile stages of sailor's choice were observed in the surveys. The one occurrence of early juveniles were found in the leeward mangrove habitat of the inner reef line (Appendix B.12.a), which also harbored some larger juveniles (Appendix B.12.b), but

they were also found on the windward side of the inner reef at shallow and intermediate depths over dead coral.

*Haemulon plumieri*

White grunt distribution patterns showed a shift in cross-shelf habitat usage. Early juveniles re found in an array of habitats, but mainly in the protected leeward side of the emergent reef (or channel axis and leeward) (Appendix B.13.a). No windward zones were preferred habitat for white grunts at this lifestage. High densities were found in the protected leeward waters of the outer shelf. Moderate densities were found in the inside inner shelf reef both in mangrove and seagrass habitats as well as in dead coral (high and low relief) and living coral (high relief.) Low densities were found in seagrass dominated leeward areas within the protection of the intermediate reef break and moderate to high densities within the leeward reach of the outer shelf.

The larger juvenile distribution of the white grunt showed the initial stages of the ontogenetic shift in habitat use (Appendix B.13.b). Moderate densities of this lifestage began to be seen in windward areas as well as higher densities in coral dominated habitats. The highest densities of this lifestage were encountered in the high relief corals (both in the inner shelf and outer shelf.) The leeward deep geomorphic zone of the outer shelf harbored high densities of this lifestage. There was reduced usage of the protected inner shelf vegetated areas.

Adult density distributions are mostly concentrated in coral dominated windward zones. Only two occurrences of vegetation-dominated habitats are seen of importance to this life stage, an emergent reef mangrove area and a windward seagrass area. Mixed coral (high

and low densities) had high densities of fish preference and usage both in the inner shelf and outer, and gorgonians in the windward side of the inner shelf. High relief coral provided a medium density use for the white grunt in both channel and windward zones of the inner and outer shelf.

In summary, white grunts moved out from protected areas on the shelf towards the shelf edge with increasing size. Like French grunts, white grunt adults show more of a trend toward the shelf, rather than a strict occurrence in that geomorphic zone. This increasing size also showed a shift in habitat preference from vegetation to an almost exclusive use of coral dominated substrates.

### *Haemulon sciurus*

Bluestriped grunt patterns of distribution showed a shift in usage trends with ontogenetic growth. All occurrences of early juveniles were encountered on the leeward side of the emergent reef in both the inner and intermediate shelf (Appendix B.14.a.). Highest densities of this lifestage were found in mangrove habitats and in habitats dominated by grass and algae.

The larger juveniles moved out of the protected geomorphic zones and vegetated habitats and into windward areas and coral dominated habitats as they began their ontogenetic shift (B.14.b). High densities were encountered in the channel and windward of it in the inner shelf in high relief coral, high relief mixed corals, and gorgonian habitats. Dead corals of low relief supported low densities of this fish within the inner shelf. On the intermediate shelf, high densities were still limited to mangrove areas. A single high density usage in the outer shelf was also on the windward side of the channel in low relief coral.

The adult distribution of bluestriped grunts was generally restricted to windward areas in consolidated substrate (Appendix B.14.c). Low densities of this lifestage were encountered in the inner shelf zone (both windward and leeward of the emergent reef and channel.) The other exception to the windward statement is the Intermediate Shelf – channel leeward seagrass cross-shelf habitat that had a high density use by this fish. High densities clustered in the Inner Shelf – windward intermediate geomorphic zone; the highest being in high relief mixed corals and high relief dead corals. High relief corals as habitat, whether dead or alive, were consistently used by this lifestage as preferred habitat.

To summarize, bluestriped grunts had a specific use of vegetated, protected cross-shelf habitat use as early juveniles before shifting to less protected and deeper waters characterized by consolidated substrata.

### *Haemulon striatum*

The distribution pattern of striped grunts implies a movement with increasing size across the shelf and into deeper waters. The early juvenile encounters were minimal, only on the leeward side of the channel in the intermediate shelf in habitats of high relief: one in a seagrass area and the other in high relief living coral (Appendix B.15.a). The highest densities of the larger juveniles are found in the exact same location as the early juveniles, but moderate and low densities are found in the outer shelf in protected leeward areas as well as in areas windward of the channel (Appendix B.15.b). The outer shelf encounters both occurred in areas of low relief dead coral.

The adult distribution of the striped grunts occurred exclusively in the leeward margin of the outer emergent reef in areas of low relief dead coral (Appendix B.15.c). In summary,

striped grunts are seen leaving the protected intermediate leeward areas as early juveniles for more wind driven and deeper waters of the outer shelf as larger juvenile and adults.

## **Lutjanidae**

Four species, 414 individuals were sampled in this project – *L. analis*, *L. apodus*, *L. griseus*, and *L. synagris*. *L. apodus* showed strong movement across the shelf with increasing size.

### *Lutjanus analis*

With only early juvenile and juvenile encounters, mutton snapper distribution pattern shifts are hard to imply from the data of this study. The distribution of the early juveniles shows a preference for protected and vegetated habitats. All densities occurred leeward of the emergent reef and mostly within the inner shelf (one instance in the outer shelf) (Appendix B.16.a). The larger juveniles were observed in similar cross-shelf habitats (Appendix B.16.b). To summarize, mutton snapper juveniles of all sizes prefer vegetated habitats in the protected areas shoreward of the emergent reef on the shelf.

### *Lutjanus apodus*

Schoolmaster distribution patterns show a distinct shift in cross-shelf habitat usage with ontogeny. Early juveniles were mainly in vegetated protected areas (Appendix B.17.a). Protected seagrass and mangrove habitats leeward of the emergent reef of both the inner and intermediate shelf were preferred habitat for the highest densities of early juvenile schoolmasters. High relief live coral in the shallow lee side of the inner emergent reef also supported high densities of this lifestage. Unconsolidated habitat (coarse sediment) in the shallow lee of the intermediate shelf also supported moderate densities. This habitat was often adjacent to the afore mentioned mangrove and live coral areas.

With increasing size, the juveniles moved from the protection of vegetated and leeward sites to more coral dominated habitats and out onto the shelf (Appendix B.17.b). The highest densities of the juvenile lifestage were found clustered in the outer shelf channel axis and windward in a variety of coral type habitats (dead, living and mixed, high and low relief, and strictly gorgonians.) High densities also occurred in the leeward of the emergent reef in the outer shelf in similar coral habitats. Moderate densities within the inner shelf were mainly grouped into dead coral (high and low relief) bare rubble, and live coral (within the windward intermediate geomorphic zone.) Low densities of this lifestage were in similar vegetation habitats relative to their early juvenile distribution.

The adult lifestage moved exclusively to the outer shelf (Appendix B.17.c). The highest densities of adults were in mixed low densities and gorgonian habitats in the shallow leeward zone, while the lowest were in low relief coral areas dominated by dead corals in the intermediate depths of the windward exposure. In summary, schoolmaster snappers moved from an early juvenile preference of protected vegetated habitats into more coral dominated exposed areas with increasing size.

### *Lutjanus griseus*

The distribution patterns of the gray snapper imply a shifting trend in cross-shelf habitat usage. There is a clear early juvenile preference for vegetated habitats on the protected lee side of the inner emergent reef (Appendix B.18.a). The highest density of this lifestage was, however, encountered in high relief coral dominated habitat of that zone. With increasing size, juveniles expand out toward the intermediate shelf. Highest densities were found in the same cross shelf habitats as early juveniles, but use of intermediate mangrove

habitats replaces that of inner mangroves. Some juveniles were also found on less protected zones in the inner shelf dominated by low relief dead corals.

In summary, gray snappers show a preference for protection and vegetation as an early juvenile, but tend to move out from those areas with increasing size. The Inner Shelf – leeward shallow zone with high relief coral was vital for both lifestages of this fish.

### *Lutjanus synagris*

Lane snapper distribution patterns showed a mix of cross-shelf habitat use through all lifestages. Vegetated habitats in the protected leeward side of emergent reefs (inner and intermediate shelf) are clearly preferred habitats for the early juvenile lifestage (Appendix B.19.a). The highest density for this lifestage occurred in the channel axis of the inner shelf in low relief coral, while moderate densities occurred in the windward reaches of the inner shelf in low relief dead corals and in unconsolidated substrate of the intermediate shelf.

The larger juveniles are seen to move out from the protection of the inner shelf and are found in high densities in the channel axis (low relief coral, high relief dead coral) and windward of the channel (algae dominated habitat and seagrass) (Appendix B.19.b). Moderate densities are found in similar habitats relative to the early juvenile stage in protected mangrove and seagrass habitats. Moderate densities are also found in the outer shelf in coral dominated habitats (low relief dead coral and high relief living coral) in intermediate and deeper waters.

The adult distribution was exclusively in the outer shelf intermediate depth, windward of the channel (Appendix B.19.c). This single habitat used was in unconsolidated sediment (coarse). In summation, lane snappers show a preference for protected vegetated habitats in



the early juvenile stage before shifting to less protected, deeper and more coral dominated habitats.

## **Scaridae**

Nine species, consisting of 10,512 individuals, were analyzed in this study - *Sparisoma aurofrenatum*, *S. chrysopterum*, *S. iseri*, *S. radians*, *S. rubripinne*, *S. taeniopterus*, *S. viride*, *Scarus guacamai* and *Scarus vetula*. Generally, a variety of habitats across the shelf are utilized throughout ontogeny in these species, yet within this pattern there is a differential shift in relative abundance from the inner to the outer shelf. There is no clear trend in these encountered species for a shelf-ward shift with increasing age, nor is there a clear trend of movement from submerged aquatic vegetation dominated habitats to coral dominated habitats. The Inner Shelf-windward intermediate zone is important to four of the nine species (redband parrotfish, redband parrotfish, striped parrotfish, and rainbow parrotfish.) The remaining species show an indiscriminate shelf use across their life history.

### *Sparisoma aurofrenatum*

The distribution pattern of redband parrotfish shows an indiscriminate habitat usage across all lifestages with a slight shift toward the shelf edge with increasing size. Geomorphic zones appear to be of higher importance for early juveniles in comparison to specific habitats (Appendix B.20.a). The Inner Shelf – windward intermediate through a variety of habitats support high densities, as does Intermediate Shelf – channel leeward and Outer Shelf – channel windward., windward shallow, intermediate and deep. High densities were also found in the channel axis of the inner shelf.

Larger juveniles were found in similar geomorphic zones relative as early juveniles (Appendix B.20 b). The highest density groupings occurred windward of the channel on the

outer emergent reef in coral dominated habitats (and two algae habitats in those same geomorphic zones.) The windward extent of the inner emergent reef supported another grouping of high densities, as did the leeward and windward margins of the channel axis of the immediate emergent reef. Low densities of redband parrotfish were found in vegetated habitats associated with the channel axis and protected inshore areas of the inner shelf.

The distribution of adults is similar in composition to the previous lifestages in that certain geomorphic zones seem to be critical (Appendix B.20.c). Inner Shelf – windward intermediate, and Outer Shelf – channel axis, channel windward, windward shallow intermediate and deep, and leeward deep were all zones supporting high densities of adult redband parrotfish. Outer Shelf – shelf outer and Intermediate Shelf – channel leeward and windward all supported lower densities and less diverse preferred habitat. The adult shift to the outer shelf can be seen in the decline in relative densities in the inner and intermediate shelf geomorphic zones and the abandonment of habitats inshore of the intermediate windward zone of the inner emergent reef. There is also a relative decline in the use of vegetated habitats

In summary, geomorphic zones seemed to be of stricter importance to this species rather than cross-shelf habitats. Grass habitats with large invertebrates were found to be of importance for two of the three lifestages. Coarse unconsolidated sediment habitats were also preferred habitats across the lifestages and shelf location.

### *Sparisoma chrysopterum*

Similar to the redband parrotfish, redband parrotfish seem to have a stronger affiliation to geomorphic zone rather than ontogenetic shift through the cross-shelf habitats. Early

juveniles showed preference for vegetated habitats across all three shelf breaks. The strength of that preference declines with distance from shore, with only minor use of seagrass habitats on the outer shelf (Appendix B.21.a). Protected zones inshore of the first emergent reef break supported high densities of this lifestage in the vegetated habitats, while moderate densities were found in sediment and dead coral dominated habitats. Seagrass and mangrove habitats in protected intermediate shelf areas were moderately important. High densities of this lifestage were also found in coral and algae dominated Outer Shelf – channel axis and windward zones.

Larger juveniles showed a slight shift in habitat usage (B.21.b). The high densities of this lifestage are found moving out from protected inshore areas to windward inner shelf zones as well as reducing preferred habitat in vegetated areas for those with consolidated substrate. The Inner Shelf – windward intermediate geomorphic zone still supports high densities through this lifestage. High relief coral and mixed coral habitats in the outer shelf also continues to support high densities. Bare rubble as well as low relief coral (dead and living) continues to be preferred habitat with an increase in rubble usage.

As adults, redbtail parrotfish show strong affiliations to the Inner Shelf – windward intermediate geomorphic zone (Appendix B.21.c), with highest densities in coral habitats. Unconsolidated sediment and seagrass habitats also supported moderate densities. Moderate to high densities were also supported in the coral dominated habitats of the Outer Shelf – leeward shallow and channel windward zones.

In summary, redbtail parrotfish show great affinity for geomorphic zones in terms of preference rather than habitat. The Inner Shelf – windward intermediate stands alone as the

highest importance for this species. Inner Shelf – leeward shallow, Outer Shelf – channel axis and channel windward were also of importance to this species. Cross-shelf habitat usage did show a shift in distribution trends out of protected inshore areas for less protected and less vegetated habitat types with increasing fish size.

### *Sparisoma iseri*

Striped parrotfish showed a clear shift in cross-shelf habitat preference. Early juveniles were found in a wide variety of cross-shelf habitats (Appendix B.22.a). Vegetated habitats in protected areas leeward of the inner emergent reef line supported high densities, as did those in the channel axis and those on the inner forereef at intermediate depths. The coral dominated habitats of the inner shelf in the channel axis zones and the shallow and intermediate windward zones hosted high densities of early juveniles, as did dead coral habitats leeward of the inner emergent reef. Leeward of the intermediate emergent reef this species also had moderate density in seagrass habitats.

A second area supporting high densities of early juveniles occurred along the channel axis and adjacent zones of the outer emergent reef. Dead coral habitat across the outer shelf geomorphic zones also supported high densities of this lifestage. Unconsolidated coarse sediment was also a preferred habitat type for this fish, as every density possible was found in this habitat across all three shelf breaks. Additionally, early juveniles of lower abundance were found in a variety of cross-shelf habitats indicating flexibility in habitat use at this stage.

Larger juveniles showed a reduction in mix of cross-shelf habitat preference (Appendix B.22.b). High densities were still found in protected seagrass and mangrove habitats of the protected inner emergent reef as well seagrass in the channel axis. The Inner

Shelf – windward intermediate geomorphic zone supported a moderate density through vegetated and coral dominated habitats. Seagrass habitats associated with emergent reefs in the intermediate shelf also hosted moderate densities of this lifestage, as did the channel windward zone of the intermediate shelf. High densities were located in unconsolidated coarse sediment and dead, high relief coral windward of the outer emergent reef. Dead coral (both high and low relief) was preferred habitat type for this lifestage.

Adult striped parrotfish completely abandoned the inner shelf and most of the intermediate shelf (Appendix B.22.c). All high densities occur in coral rich habitats windward of the channel axis in the outermost emergent reef. Most were associated with the emergent reef line, but rubble areas on the broad plain of the outer shelf (shelf outer) also supported high densities.

In summary, early juvenile striped parrotfish have a wide flexibility in habitat usage that narrows with increasing fish size. Fish generally move out of the vegetated habitats and into unprotected waters, primarily along the outer shelf as adults.

#### *Scarus guacamaia*

Only a limited number of rainbow parrotfish were observed in this study. All were located in the coral dominated habitats (low relief and dead coral high relief) of the Inner Shelf – windward intermediate geomorphic zone (Appendix B.23.a).

#### *Sparisoma radians*

Bucktooth parrotfish were generally restricted to a few specific geomorphic zones and cross-shelf habitats across the three lifestages. Early juveniles had high densities in seagrass habitats leeward of the outer emergent reef (Appendix B.24.a). High highest density

was also encountered in the channel axis of the inner emergent reef in low relief dead coral habitat.

Larger juveniles occupied the same cross-shelf habitats as early juveniles, but additionally there was a strong movement into seagrass habitats further inshore (Appendix B.24.b). Highest densities were found in the channel axis of the inner emergent reefs. The shallow leeward zones of both the inner and intermediate shelf hosted moderate densities. Seagrass habitats within the protection of the inner emergent reef had low densities of usage.

Adults continued using primarily vegetated habitats, but those associated with the outer emergent reef were restricted to the shallow leeward margin. However, additional new areas of coral habitat were used by adults in low relief live and dead corals of the inner channel axis, and in moderate density along the outer channel axis in low relief dead coral.

In summary, this fish has an opposite trend with increasing size, showing movement from offshore to inshore.

### *Sparisoma rubripinne*

The distribution patterns of yellowtail parrotfish show a slight trend of cross-shelf habitat usage change with ontogeny. The early juvenile high densities cluster in protected seagrass and mangrove habitats behind the inner emergent reef (Appendix B.25.a).

Additionally, lower densities were found in some coral dominated habitats leeward of the channel axis of the inner and outer emergent reefs. Only along the inner reef line were early juveniles found in windward areas, with high densities observed in shallow areas of high relief coral.

Larger juveniles showed a shift from protected inshore habitats out across the shelf as well as into more coral dominated habitats (Appendix B.25.b). Densities of this lifestage mirrored those of early juveniles with respect to protected inshore vegetated and dead coral habitats. Inshore, use of windward habitats shifted from shallow to intermediated depths, while individuals were now found associated with the intermediate emergent reef, primarily along the leeward channel axis. Moderate to high densities were also found scattered throughout the outer shelf. Distribution was extended further offshore, with high densities found in the deep windward margin of the outer emergent reef (dead mixed low relief corals) and in sand areas of the broad outer plain (shelf outer).

Adults showed an almost complete evacuation from the vegetated habitats (the only sea grass still used was at intermediate depths of the inner fore reef) to those of consolidated substrate (Appendix B.25.c). High densities were found in the windward intermediate zone of the inner reef line and again in the deep windward margin of the outer emergent reef.

In summation, yellowtail parrotfish show an ontogenetic shift in cross-shelf habitat usage. Moving out of protected geomorphic zones and vegetated habitats, the yellowtail parrotfish shifted to more coral dominated habitats out across the shelf.

### *Sparisoma taeniopterus*

The distribution pattern of the princess parrotfish shows a trend of cross-shelf habitat shift. Early juveniles had highest densities in coral-dominated habitats, with scattered densities across the seagrass habitats of leeward reaches of all shelf breaks (Appendix B.26.a). Highest densities were found in the leeward margins of the intermediate reef channel axis and the windward channel axis of the outer reef. The three outermost

geomorphic zones supported early juveniles in bare rubble areas and in dead and mixed low relief coral habitats.

Larger juveniles were distributed across the outer shelf coral habitats and along the Intermediate windward channel, having abandoned the inner shelf and most seagrass habitat (Appendix B.26.b). Within the outer shelf, the distribution was shifted to the deeper geographic zones most offshore (shelf outer, near shelf edge). Two incidences of sediment habitats also occurred in the windward outer shelf. The shallow and deep leeward zones of the outer reef supported moderate densities of juveniles.

Adult princess parrotfish distributions were generally similar to that of large juveniles, but were more restricted in the habitats in which they were observed (Appendix B.26c). In the intermediate windward channel, high densities were only observed in low relief dead coral habitat, and no observations were found in unconsolidated substrate. Moderate densities were still found on the outer shelf leeward of the emergent reef (low relief dead coral and high relief living coral) as well as on the outer plain and near shelf edge zones (low relief dead and mixed coral habitats).

In summary, princess parrotfish show a shift in cross-shelf habitat preference with ontogeny, moving from a variety of habitats including vegetated ones and zones, including protected inner shelf ones to coral dominated windward sides of reef and out into the outer shelf.

### *Scarus vetula*

The distribution patterns for the queen parrotfish were limited in this study to the early juvenile and juvenile lifestages. The early juvenile habitat preference was for low relief



coral dominated windward intermediate habitats of both the inner and outer shelf (Appendix B.27.a). The larger juveniles retained a preference for low relief coral habitats but showed a shift in preference to the windward shallow zone of both shelf areas (Appendix B.27.b).

In summation, there is a trend implied that with increasing size, *S. vetula* moves into shallower waters.

### *Sparisoma viride*

Stoplight parrotfish showed a slight migration during ontogeny within a pattern of broad habitat use. The early juvenile lifestage showed high density habitat usage in the coral dominated habitats of the inner shelf (Appendix B.28.a). Channel axis zones and the shallow and intermediate windward zones supported high densities, with low to moderate densities also occurring in seagrass habitats. Additionally, mangrove and seagrass habitats in the protected waters shoreward of the inner emergent reef hosted low to moderate densities of this lifestage.

Generally, larger juveniles had similar geomorphic zone use relative to the early juveniles (Appendix B.28.b). Overall, the use of seagrass habitats was greatly reduced except for areas associated with the intermediate windward zone of the inner reef. On the outer shelf, a similar pattern was observed for juveniles as for early juveniles, but a wider variety of coral habitats were used and higher densities were supported.

By the adult stage, while still occupying a variety of cross-shelf habitats, stoplight parrotfish had reduced their high-preference areas (Appendix B.28.c). On the inner shelf the high relief and seagrass-invertebrate habitats of the intermediate windward zone were key. In the intermediate shelf the areas of high density occurred on low relief habitats of the

windward channel margin. Across the outer shelf, stoplight parrotfish were found in both high and low relief habitats, but highest densities were found on the shallow leeward and windward margins of the emergent reef

In summary, stoplight parrotfish have many geomorphic zones that are of high importance in terms of preferred habitats (Inner Shelf – windward intermediate, Intermediate Shelf – Channel windward, Outer Shelf- channel axis, channel leeward and windward), and they use a mix of coral and vegetated habitats. There is also a shift seen in cross shelf habitat usage with increasing size, in that stoplight parrotfish move out of vegetated habitats into consolidated coral substrate as well as offshore.

## **Habitat Distribution Patterns**

### *Vegetation*

The highest percentages of observed density quartiles occur in inner shelf area decreasing to the outer shelf. The majority of the habitats responsible for any outer shelf occurrences are the Algae-Attached and Grass-Algae habitat types. The observed quartile densities were comprised of early juvenile (52%,) juveniles (36%,) and adults (12%).

### *Sediments*

Fifty-two percent of all observed quartile densities in the sediment category occurred in the outer shelf, and 77% of those observed sediment quartiles occurred in the early juvenile (41%) and juvenile (37%) lifestages.

### *Hardbottom and Invertebrates*

Seventy-three percent of all observed quartile densities occurred in the early juvenile (41%) and juvenile (32%) lifestages, and 60% of the observed quartile densities occurred in the outer shelf, with 29% in the inner shelf and 10% in the intermediate shelf.

## **Life Stage Distribution Patterns**

### *Early Juveniles (nursery habitats)*

Fifty-two percent of observed quartile densities in the vegetated habitats were for early juveniles, while 88% were for early juveniles and juveniles combined (Table 3). Fifty-seven percent of those observed quartile densities for early juveniles and juveniles in the vegetated habitats occur in the inner shelf geomorphic zone, 20% in the intermediate shelf and 10% in the outer shelf. Across all habitat types, 45% of all observed quartile densities occurred in the inner shelf, 16% in the intermediate shelf, and 39% in the outer shelf.

### *Juveniles*

Thirty-six percent of the observed quartile densities within the vegetated habitat grouping were of juveniles, while 41% of the observed quartile densities in the hardbottom and invertebrate habitat group were of this lifestage. In the geomorphic zones, juveniles were prominent both in the inner (37%) and outer (46%) shelf.

### *Adults*

Adults showed similar percentages of quartile densities in the sediment (23%) and hardbottom/invertebrate (26%) habitats, while the vegetated habitats had low observed quartile densities 12%. In terms of geomorphic zones, the adults showed highest observed quartile densities in the outer shelf (60%) followed by the inner shelf (33%) and intermediate shelf (7%).

**Table 3. Percentages of observations per shelf location per lifestage per habitat in La Parguera, Puerto Rico. Column percentages for habitats sum to 100. The last column (% per Lifestage) is the sum across rows.**

Lifestage and Shelf Location	% in Vegetation	% in Sediments	% in Hardbottom/ Invertebrates	% in All Habitats	% per Lifestage
<b>Early Juvenile Inner</b>	33.9	9.6	10.6	16.9	44.8
Early Juvenile Intermediate	11.1	13.3	3.5	6.1	16.1
Early Juvenile Outer	7.1	13.3	18.1	14.8	39.1
<b>Juvenile Inner</b>	23.8	7.2	11.3	14.5	36.5
Juvenile Intermediate	8.7	10.8	5.7	6.8	17.1
Juvenile Outer	3.3	22.9	24.3	18.4	46.3
<b>Adult Inner</b>	8.7	4.8	6.9	7.3	32.6
Adult Intermediate	1.4	2.4	1.6	1.6	7.0
Adult Outer	2.1	15.7	18.0	13.5	60.5

## Key Cross-Shelf Habitats

Key cross-shelf habitats within the framework were identified within each species (Appendix C) and then grouped here by family. Key cross-shelf habitat was identified according to occurrence within each species lifestage framework.

### *Acanthuridae*

The distribution patterns of key cross-shelf habitats of the Acanthuridae family generally reflect the patterns of the individual members. Early juveniles had fifteen primary key habitats, grouped mostly in shallow inshore areas of vegetation and dead coral, and low relief coral areas of the shallow outer shelf (Appendix C.1.a). Key cross-shelf habitats of larger juveniles are reduced in the inner and intermediate shelf, with a notable grouping of secondary key habitats in high relief areas of intermediated depth on the inner shelf fore reef (Appendix C.1.b). Most key habitats were clustered in coral habitats along the channel and windward zones of the outer emergent reef. There were five primary key cross shelf habitats, three of which occur in rubble areas of the channel margin. Windward exposed shallow and

intermediate low relief dead coral and gorgonians also are primary key cross-shelf habitats. Offshore of the outer emergent reef the only key habitat (secondary) for juveniles was exposed algae on the outer plain.

The adult distribution of key cross-shelf habitats show that the windward intermediate zone of the inner emergent reef continues to be key for this family with two primary key cross-shelf habitats (low relief dead coral and gorgonians) and three secondary (seagrass, sand, and high relief dead coral) (Appendix C.1.c). On the outer shelf, rubble habitat of the leeward channel continued to be of primary importance, while a scattering of secondary key habitats occur in low and high relief areas extending from the channel axis out to the near shelf edge.

### *Serranidae*

There were no shared key cross-shelf habitats for the early juvenile groupers. No primary key cross-shelf habitats were found in the larger juveniles (Appendix C.2.a), but four areas of secondary importance occurred in low relief coral/rubble and gorgonian areas of the outer plain and near shelf edge. The outer plain continued to be of importance for adults (Appendix C.2.b), with a primary key cross-shelf habitat in deepwater gorgonian areas, and a secondary key habitats in low relief mixed corals.

### *Haemulidae*

The grunt family key cross-shelf habitats reflected the ontogenetic shifts across the shelf seen for individual species. Early juveniles had a single secondary key cross-shelf habitat in the shallow lee of the first emergent reef in low relief coral (Appendix C.3.a). Primary key cross-shelf habitat for juveniles (Appendix C.3.b) was in the intermediate

windward zone of the inner reef (low relief dead coral) as was a secondary key cross-shelf habitat in high relief dead coral. Other secondary key cross-shelf habitats were grouped in high relief coral areas in the inner channel axis and windward of it. Mangroves in shallow lee margins of the inner and intermediate emergent reefs were secondary key cross-shelf habitats. Low relief coral windward of the outer channel also was a secondary key cross-shelf habitat.

Adult grunts have no shared primary key cross-shelf habitats (Appendix C.3.c). Secondary key cross-shelf habitats are found in the omni-important intermediate windward zone of the inner reef (high relief dead coral and high relief mixed corals), as well as in the outer channel axis (high relief corals) and the outer plain (low relief mixed corals).

### *Lutjanidae*

The early juvenile snappers have no shared primary key cross-shelf habitats, but eight secondary ones (Appendix C.4.a). Mostly grouped inshore of the first emergent reef, the key cross shelf habitats were largely in seagrass and mangrove areas with one instance in high relief coral. Two secondary key cross-shelf habitats were found beyond this reef break, on in low relief coral of the Inner Shelf – windward intermediate zone and one in the seagrass areas of the protected shallow waters of the intermediate shelf.

The distribution of larger juveniles reflects species movements out of vegetated and inshore areas (Appendix C.4.b). The Inner Shelf – windward intermediate zone again hosts secondary key cross-shelf habitats (dead coral) as does the shallower windward waters in algal dominated habitats. The mangrove habitats of shallow leeward waters inshore of the

emergent reef break in both the inner and intermediate shelf also have secondary key cell occurrences.

No primary or secondary key habitats were identified for adult snappers.

### *Scaridae*

Only a single primary key cross-shelf habitat occurs for early juvenile scarids, in grass-algal areas of the shallow leeward waters of the outer shelf reef (Appendix C.5.a). Secondary key cross-shelf habitats are found grouped in the Inner Shelf – windward intermediate zone (seagrass, dead corals, and gorgonians), Intermediate Shelf – channel leeward zone (seagrass, low relief mixed coral, and high relief coral), and along the emergent reef in the channel leeward (rubble and low relief dead coral), channel windward (dead coral, high relief mixed coral, and low relief coral), and windward shallow (low relief dead coral) zones. The protected water inshore of the inner emergent reef has two secondary key cross-shelf habitats (seagrass and low relief dead coral).

There were no primary key cross-shelf habitats for larger juveniles (appendix C.5.b). The Inner Shelf- windward intermediate zone continues to play an important role in both seagrass habitats as well as dead coral dominated ones. Two other seagrass key cross-shelf habitats occur in the Inner Shelf – leeward shallow and Intermediate Shelf – channel leeward zones. The remaining key areas occur windward of the channel axis in low relief coral habitats of the intermediate (rubble and low relief coral) and outer reefs, representing an offshore movement from the leeward channel areas used by early juveniles. Similarly, key juvenile habitats extended out onto to outer plain.

Adults continued this movement of key habits into deeper and less protected waters (Appendix C.5.c). The Inner Shelf – windward intermediate zone continues to be of importance in high relief mixed and dead corals. Scattered secondary key habitats occurred on the outer shelf from the channel axis to the outer plain in low relief and gorgonian areas.

## Discussion

Recent works investigating variable habitat usages of reef fishes (e.g., Lindeman 1997, Lindeman et al. 1998, Nagelkerken et al. 2000, 2004, Cocheret de la Morinière et al. 2002) were based on environments and reefscapes of a lower complexity than the study area in La Parguera, Puerto Rico. As a consequence, those studies were unable to delineate habitat usage and its change during ontogeny in more complex environments involving multiple reef lines and variable depths across the shelf. The present study across a complex shelf has elucidated variable habitat utilization patterns as they change across geomorphic zones and through ontogeny, but the application of the cross-shelf habitat framework also allows broader scale patterns to be easily constructed and interpreted.

As in this study, Murphy (2001) found life stages were differentially distributed throughout available habitats, with juveniles grouping in vegetated habitats. Murphy, however, stated that the juveniles of certain reef fishes (French grunt, doctorfish, ocean surgeon, stoplight parrotfish, redbtail and yellowtail parrotfishes) occurred in all habitats, but that adults occurred exclusively in coral areas. In contrast, this study showed every one of the stated species had some occurrence outside of coral reef dominated habitats in the adult



lifestage. French grunts and doctorfish were two of the six specifically named species by Murphy (2001) shown in this study to have high densities in vegetated areas as adults. Rooker and Dennis (1991) stated that offshore mangrove habitats act as staging points for intermediately sized French grunts during their ontogenetic shift from nursery habitats to adult habitats in coral reefs. This was supported in the present study, as moderate densities of juveniles were found there, but adults did not use this cross-shelf habitat. However, still higher juvenile densities were found in other coral and vegetated habitats in the inner and intermediate shelves.

Christiansen et al. (2003) found lutjanid adults largely inhabited bank-shelf reef zones (outer shelf reef zones) and early juveniles inhabited the inner lagoon vegetated areas, and these patterns were corroborated in the present study. Additionally, they found adult haemulids characteristically inhabited the outer lagoon area and shelf zone, while early juveniles and juveniles were closely associated with the inner lagoon, inner and outer lagoon mangroves, and inner and outer lagoon submerged vegetation areas. Kendall et al. (2003) found similar results for French grunts in St. Croix. While the present study supports the observations for French grunts, the family-wide analysis for haemulids showed vegetative habitats not to be key nursery areas. Only a few, but abundant species (e.g., French, bluestriped grunts) utilize these habitats. The unweighted pooling of individual grunts across species used by Christiansen et al. (2003) allowed these few species to dominate the observed trends. For parrotfishes, as in the present study, Christiansen et al. (2003) found that striped parrotfish and princess parrotfish exhibited ontogenetic shifts in habitat preference, with bucktooth parrotfish predominantly within vegetated habitats throughout all

stages, a pattern opposite of the rest of the scarids, which are generally found on reef structure.

Studies in Curaçao, with its compressed and simpler marine system, showed similar habitat use patterns. Ocean surgeonfish, doctorfish, French grunts, Bluestriped grunts, schoolmaster snappers, gray snappers, striped parrotfish, and princess parrotfish all showed an increase in size from the vegetated habitats to the coral dominated habitats (Cocheret de la Morinière et al., 2002). Nevertheless, some interesting differences occurred. In Curaçao, ocean surgeonfish only settled at the mouth of the bay before migrating to reef habitat, and therefore never occupied mangrove and seagrass habitats further inshore, while in La Parguera inshore mangroves and seagrass habitats supported moderate to high densities of early juveniles. Gray snappers were found primarily in mangroves, and to a lesser degree seagrass beds in Curaçao (Cocheret de la Morinière et al., 2002; Nagelkerken et al., 2000), but while seagrass and mangroves were utilized in La Parguera the highest densities were found in inshore areas of high relief corals. Juvenile schoolmaster snappers and bluestriped grunts used mangroves and seagrass areas almost exclusively in Curaçao (Cocheret de la Morinière et al., 2002; Nagelkerken et al., 2000), but in La Parguera, these species had a more diverse distribution, which included coral reef areas as preferred habitat. Striped parrotfish and French grunts in Curaçao tended to settle initially in seagrass and mangrove areas at the mouth of the bay before moving into these same habitats further inshore (Cocheret de la Morinière et al., 2002). Early juvenile French grunts in La Parguera were found in a variety of shallow habitats across the shelf. Routinely, newly settled fish are associated with structure, e.g., sea urchin spines (Lindeman 1985) or small coral colonies in

seagrass (Hill 2001), but generally are not found along the inner most mangroves and seagrass areas. In the present study, the early juveniles observed in these latter habitats were at the larger size range of this lifestage and may have moved into these locations from settlement sites associated with the protected habitats of the inner reef line. In contrast to the French grunt, observations of striped parrotfish in Curaçao seem to be fundamentally different from those in the present study. Early juveniles were found at a wide variety of depths, habitats, and cross-shelf zones, including widespread use of all coral habitats associated with the outer emergent reef down to the deeper margins of the fore reef.

Lindeman (1997) and Lindeman et al. (1998) in Biscayne Bay presented cross-shelf habitat distributions for newly settled and early juveniles of two snappers and one grunt analyzed in the present study, and these can be used to more directly compare species behavior in systems of different complexity. For gray snapper, the two studies showed similar results, with seagrass and high relief coral habitats being most important and mangroves also being important in La Parguera. In Biscayne Bay, these habitats were located inside the one reef line, while in La Parguera all occurrences were inside the inner most emergent reef line. Interestingly, between the two studies there is an almost exact reversal of cross-shelf habitats considered of primary and secondary importance. For lane snappers, key habitats in Biscayne Bay were mangrove, seagrass and corals located on both shallow leeward and windward sides of the barrier reef, and the inner basin in Biscayne Bay was also considered an important zone. In La Parguera, the same habitats were important, but no early juveniles were observed in the inner basin (shelf inner), nor on the fore reef. All occurrences were inside the inner most emergent reef line. Striped grunts showed a very

restricted distribution in Biscayne Bay, being found in only in coral habitat and only on the outer shelf. There were few observations of early juvenile striped grunts in La Parguera, but the primary habitat was also coral, and this occurred on the leeward channel of the intermediate reef line. In the same zone, some were also observed in seagrass with invertebrate habitat.

Appeldoorn et al. (2003) studied differential habitat use at several temporal scales in grunts and snappers at Providencia (San Andres Archipelago, Colombia), including ontogenetic migrations in both windward and leeward directions across the platform. There is general agreement between this and the present study concerning general patterns of movement and habitat use. For example, grunts showed a wide distribution, with French grunts having the broadest, most opportunistic spread, but with juveniles still favoring nearshore sites. Juveniles of bluestriped grunts were more restricted and had highest preference for nearshore nursery areas, particularly mangroves. Gray snappers showed only little dispersal away from vegetated habitat. Interestingly, of those species that did disperse in Providencia, they generally dispersed to deeper zones to the lee side of the island, especially the bluestriped grunt and schoolmaster snapper. While both species showed strong inshore-offshore ontogenetic shifts from protected vegetated areas to coral habitats on the outer shelf, the geomorphology of La Parguera precludes such a migration in a leeward direction.

System complexity plays a role in the comparison of other studies to this one. Simple systems can be viewed as natural models, which reduce natural variations relative to some process or pattern of interest, such as ontogenetic habitat shifts. Simple systems may not,

however, give a full range of behavior (e.g. habitat plasticity) or full insight on how to convert findings to management practices in other (possibly more complex) systems. Aguilar Perera (2005) used methods similar to those used in Curaçao (Cocheret de la Morinière et al., 2002; Nagelkerken et al., 2000) to study size-specific distributions of fishes in La Parguera to the east of the present study along a cross-shelf gradient extending out to the outer most emergent reef. Patterns observed differed from those in Curaçao due to the greater geomorphic complexity at La Parguera, and generally agreed closely with the results of the present study. Both Aguilar's and the present study indicate these species show variable degrees of flexibility in patterns of habitat use, suggesting that actual patterns observed at any specific location may be due to local patterns in habitat availability. Lindeman (1979), Nagelkerken et al. (2001) also demonstrated flexibility in habitat use in some species, most epitomized by the French grunt. Additionally, other studies have shown habitat use to be dependent not only on the relative amount of available habitat, but on the general proximity of shelter to feeding areas (Appeldoorn et al., 2003; Kendall et al., 2003; Nagelkerken and van der Velde, 2004).

Overall, the patterns observed across all species identify inshore mangrove and seagrass areas as important areas for early juveniles. This functional nursery for fishes inhabiting coral reefs as adults is well documented from studies in Panama (Weinstein and Heck, 1979), Belize (Sedberry and Carter, 1993), Curacao (Nagelkerken et al., 2000), Bonaire (Nagelkerken et al., 2000), and Puerto Rico (Appeldoorn et al. 1997, Hill 2001; Murphy, 2001; Aguilar Perera, 2004; Foley et al., 2004, in press). These habitats are within close proximity to coral reefs and are non-estuarine. Shallow, well vegetated habitats

provide refugia for smaller fishes that can then shift to a more open habitat type like coral dominated areas as they gain a larger size. However, the present study also identified the role of coral habitats as nursery areas for some species, and this seems to be underappreciated in the literature.

This work was done on a small scale – smaller than management can operate. Therefore, protection on the level of individual cross-shelf habitats (cells within the framework) is operationally impossible, but protection at some larger scale would effectively protect multiple cross-shelf habitats. This work was also done on a single species scale, which is not conducive to integrated coastal and fisheries management. By managing at a larger scale and taking a more holistic view of fish groups, management can be a more science grounded ecosystem based management endeavor.

Essential Fish Habitat (EFH) was defined in the 1996 (Amended) Magnuson-Stevens Fishery Conservation and Management Act as “those waters and substrate necessary to fish for spawning, breeding, feeding, or growth to maturity” (16 U.S.C. 1802 (10)). This definition views EFH within the context of single species management, which becomes impractical in a multispecies or ecosystem-based approach when the summed EFH’s of all species would identify practically all areas of the seascape. As such, there would be no basis for prioritizing areas for conservation or management.

An advantage of using the cross-shelf habitat framework is that it easily lends itself to combining results from individual species into a multispecies context. By viewing EFH on a larger scale and finding common key cross-shelf habitats among species, efforts for conservation can target groups of species, lifestages, families, etc. Two combined

frameworks are developed here. One framework targets areas of priority use, by life stage, based on addition across species as the simplest first approach to the problem. To construct this framework, each cross-shelf habitat was scored according to the highest quartile density observed in any species (Appendix D.1-3). Thus, for example, a cell given highest priority had at least one species for which that cross-shelf habitat showed the highest density quartile. This framework illustrates essential fish habitats based on importance to any species. Although the range of cross-shelf habitats is broad (the sum of all species), those cells of highest priority are more restricted. In addition, Appendix D.1 clearly shows the role of coral habitats as nursery areas for coral reef fishes, and that these are located in the windward areas of in inner emergent reef and across the reef structure on the intermediate and outer reefs.

As important as knowledge of the areas of habitat use, knowledge of those areas not key is equally illuminating. This is revealed by identifying all cross-shelf habitats that were not essential fish habitat to any species at any life stage, i.e., the blank cells of Appendix E. The result allows for an initial survey of habitats nominated for conservation to be more narrowly targeted to habitats actually utilized by reef fishes.

In the second approach, a framework was constructed on the basis of the frequency of importance a particular cross-shelf habitat had across all species. This approach removes the disproportional effect that abundant and ubiquitous species give to the first approach (Appendix D). For this framework, cross-key shelf habitats were sorted into three groups of primary, secondary and tertiary importance. Primary key cross-shelf habitats are defined as those cells including 90% or more of the sampled species. Secondary key cross-shelf

habitats were defined as occurring in 50%-90% of the sampled species, and tertiary as 25-50%. This was done by life stage for all species (Appendices F).

Early juveniles across all species sampled shared many key cross-shelf habitats. Two of these were of secondary importance (50-90% of all species samples occurred in the cell), while 34 were of tertiary (25-50%) importance (Appendix F.1). The interesting aspects of this analysis are the groupings. Vegetated areas of the inner shelf shoreward of the channel axis constitute about a third of the sites, with mangrove and *Thalassia* areas being particularly important. Low relief dead coral areas on the inner shelf were also important. Another cluster can be seen in the Outer Shelf, in coral dominated areas associated with the emergent reef.

Key cross-shelf habitats in the juvenile stage (Appendix F.2) are more scattered than those for early juveniles. Leeward shallow mangrove and *Thalassia* habitats (both Inner and Intermediate Shelf) remain important, as does use of dead coral habitats on the inner and outer shelf, but now more toward the windward of the emergent reef lines. The only key area identified on the outer plain was the mixed coral low relief habitat.

Three secondary and nine tertiary key habitats were identified for adults (Appendix F.3). By this stage most fish have moved out of the vegetated areas and into the coral dominated habitats of the inner and outer shelves. The Inner Shelf – windward intermediate zone is particularly important. Dead low relief coral associated with the outer emergent reef was also important, and importance of the mixed coral low relief habitat of the outer plain increased.



Certain limitations restricted this work; most specifically, for reasons of logistics and costs, all zones across the shelf were not sampled, and unequal effort was applied across the three shelf sections. Short term sampling cannot capture the entirety of the variability of the system and the species; however, the results can offer a view into the cross-shelf habitat usage of species and lifestages (e.g., Williams, 1986, Fowler, 1990, Green, 1996). Also, as fishing pressure in La Parguera is quite high, the results of this study may be somewhat different than those from within an unexploited area. No-take marine reserves in this area could to provide control areas for future scientific study.

Marine conservation efforts can more successfully achieve their objectives both in protection and enhancement when properly informed of the critical habitat for their target species. This study brings into sharp relief the importance of the Inner Shelf – windward intermediate zone for all lifestages of reef fishes, and the clustering of younger lifestages in both vegetation dominated areas and shallow low, dead coral dominated areas. Marine and fisheries management efforts can now use this work to target conservation efforts on a lifestage, family or species level.

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# Appendices

**Appendix A - Cross-shelf habitat framework integrating structural habitat types and geomorphic zones of La Parguera, Puerto Rico shelf area, as presented in Appeldoorn et al. (2001).**



## Appendix A.1

Cross-shelf habitat framework integrating structural habitat types and geomorphic zones of La Parguera, Puerto Rico shelf area, as presented in Appeldoorn et al. The cross-shelf habitat matrix is composed of 720 cells, of which 521 occur in La Parguera.

		Geomorphic Zones (Cross-shelf Strata)																																					
		Inner Shelf										Intermediate Shelf										Outer shelf																	
Depth Range (m)		0-2 Mainland Inshore	0-2 Leeward Inshore	0-2 Windward Inshore	2-20 Shelf Inner	0-2 Leeward Shallow	0-2 Reef Top	0-2 Channel/Leeward	>2 Channel Axis	0-2 Channel Windward	0-1 Windward Shallow	1-8 Windward Intermediate	8-17 Windward Deep	>14 Shelf Middle	3-20 Leeward Deep	0-3 Leeward Shallow	5-3 Reef Top	5-3 Channel/Leeward	0-3 Channel Axis	5-3 Channel Windward	5-3 Windward Shallow	3-10 Windward Intermediate	10-18 Windward Deep	3-20 Leeward Deep	0-3 Leeward Shallow	5-5 Reef Top	0-3 Channel/Leeward	>3 Channel Axis	0-5 Channel Windward	0-5 Windward Shallow	5-10 Windward Intermediate	10-18 Windward Deep	18-33 Shelf Outer	16-34 Near Shelf Edge	14-25 Bank Top	16-23 Bank Windward	>18 Bank Deep		
Habitat Types																																							
Mangrove-Red																																							
Grass-Thalassia																																							
Grass-Syringodium																																							
Grass-Mixed																																							
Grass-Algae																																							
Grass w/Small Invertebrate																																							
Grass w/Large Invertebrate																																							
Algae-Attached																																							
Detached Macrophyte																																							
Sediment-Fine																																							
Sediment-Coarse																																							
Rubble-Bare																																							
Mixed-Low relief																																							
Dead coral-Low relief																																							
Coral-Low relief																																							
Invertebrate-Sponge																																							
Coral-Gorgonium																																							
Mixed-High relief																																							
Dead coral-High relief																																							
Coral-High relief																																							

## Appendix A.2

Cross-shelf habitat framework integrating structural habitat types and geomorphic zones of La Parguera, Puerto Rico shelf area, as presented in Appeldoorn et al. The cross-shelf habitat matrix is composed of 720 cells, of which 521 occur in La Parguera.

		Geomorphic Zones (Cross-shelf Strata)																																					
		Inner Shelf										Intermediate Shelf										Outer shelf																	
Depth Range (m)		0-2 Mainland Inshore	0-2 Leeward Inshore	0-2 Windward Inshore	2-20 Shelf Inner	0-2 Leeward Shallow	0-2 Reef Top	0-2 Channel/Leeward	>2 Channel Axis	0-2 Channel Windward	0-1 Windward Shallow	1-8 Windward Intermediate	8-17 Windward Deep	>14 Shelf Middle	3-20 Leeward Deep	0-3 Leeward Shallow	5-3 Reef Top	5-3 Channel/Leeward	0-3 Channel Axis	5-3 Channel Windward	5-3 Windward Shallow	3-10 Windward Intermediate	10-18 Windward Deep	3-20 Leeward Deep	0-3 Leeward Shallow	5-5 Reef Top	0-3 Channel/Leeward	>3 Channel Axis	0-5 Channel Windward	0-5 Windward Shallow	5-10 Windward Intermediate	10-18 Windward Deep	18-33 Shelf Outer	16-34 Near Shelf Edge	14-25 Bank Top	16-23 Bank Windward	>18 Bank Deep		
Habitat Types																																							
Mangrove-Red																																							
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Rubble-Bare																																							
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Dead coral-Low relief																																							
Coral-Low relief																																							
Invertebrate-Sponge																																							
Coral-Gorgonium																																							
Mixed-High relief																																							
Dead coral-High relief																																							
Coral-High relief																																							

### Appendix A.3

Cross-shelf habitat framework integrating structural habitat types and geomorphic zones of La Parguera, Puerto Rico shelf area, as presented in Appeldoorn et al. (2001). The cross-shelf habitat matrix is composed of 660 cells, of which 529 occur in La Parguera.

		Geomorphic Zones (Cross-shelf Strata)																																			
		Inner Shelf										Intermediate Shelf										Outer Shelf															
		Leeward Inshore	Windward Inshore	Shelf Inner	Leeward Shallow	Reef Top	Channel Leeward	Channel Axis	Channel Windward	Windward Shallow	Windward Intermediate	Windward Deep	Shelf Middle	Leeward Deep	Leeward Shallow	Reef Top	Channel Leeward	Channel Axis	Channel Windward	Windward Shallow	Windward Intermediate	Windward Deep	Leeward Deep	Leeward Shallow	Reef Top	Channel Leeward	Channel Axis	Channel Windward	Windward Shallow	Windward Intermediate	Windward Deep						
Depth Range (m)		0-2	0-2	2-20	0-2	0-2	0-2	>2	0-2	0-1	1-8	8-17	>14	3-20	0-3	.5-3	.5-3	0-3	.5-3	.5-3	3-10	10-18	3-20	0-3	.5-5	0-3	>3	0-5	0-5	5-10	10-18	18-33	16-34				
<b>Habitat Types</b>																																					
Mangrove-Red																																					
Grass-Thalassia																																					
Grass-Syringodium																																					
Grass-Mixed																																					
Grass-Algae																																					
Grass w/small Invertebrate																																					
Grass w/Large Invertebrate																																					
Algae-Attached																																					
Detached Macrophyte																																					
Sediment-Fine																																					
Sediment-Coarse																																					
Rubble-Bare																																					
Mixed-Low relief																																					
Dead coral-Low relief																																					
Coral-Low relief																																					
Invertebrate-Sponge																																					
Coral-Gorgonium																																					
Mixed-High relief																																					
Dead coral-High relief																																					
Coral-High relief																																					

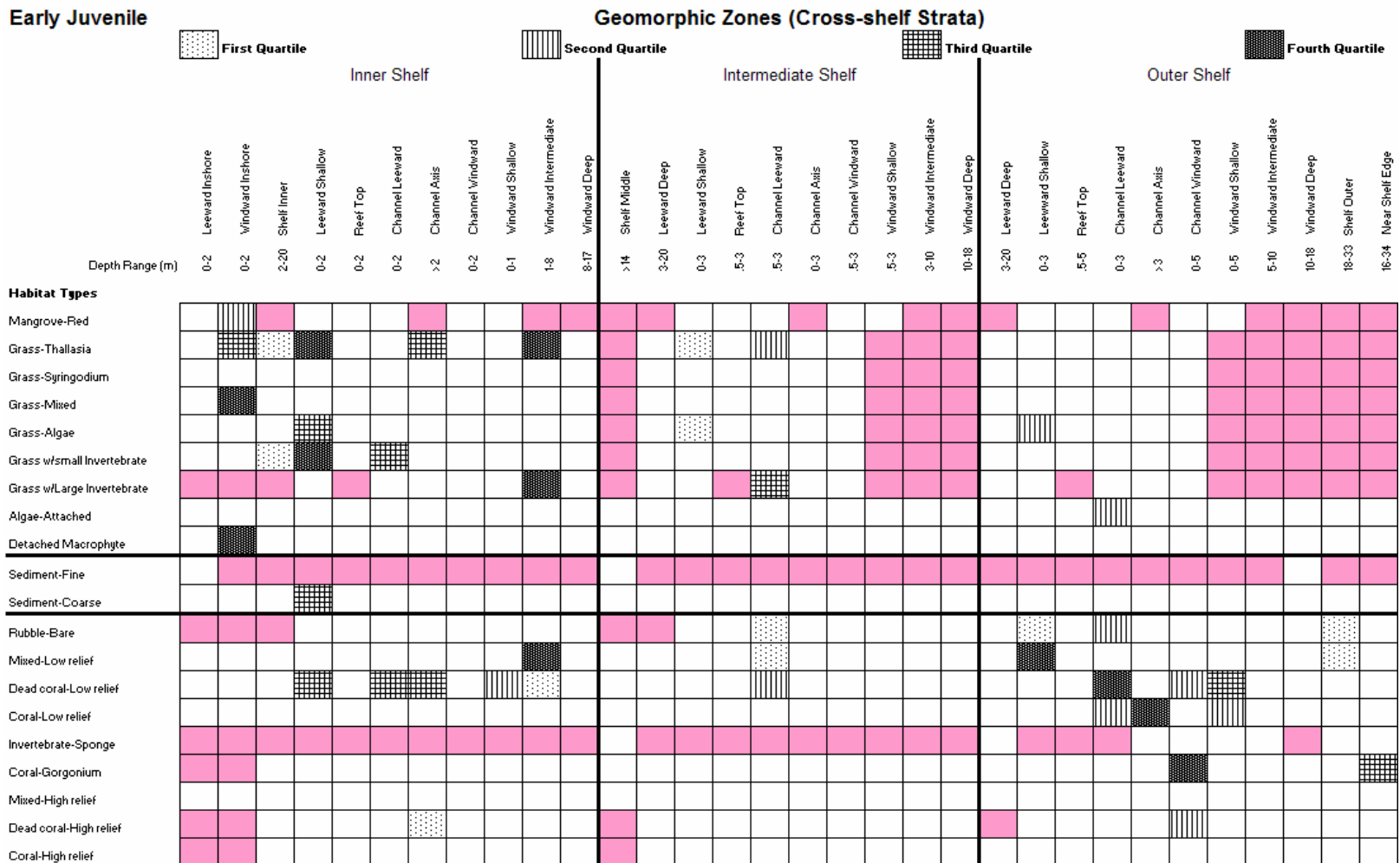
**Appendix B - Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.**

**Appendix B.1.a**

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

***Acanthurus bahianus***

**Early Juvenile**

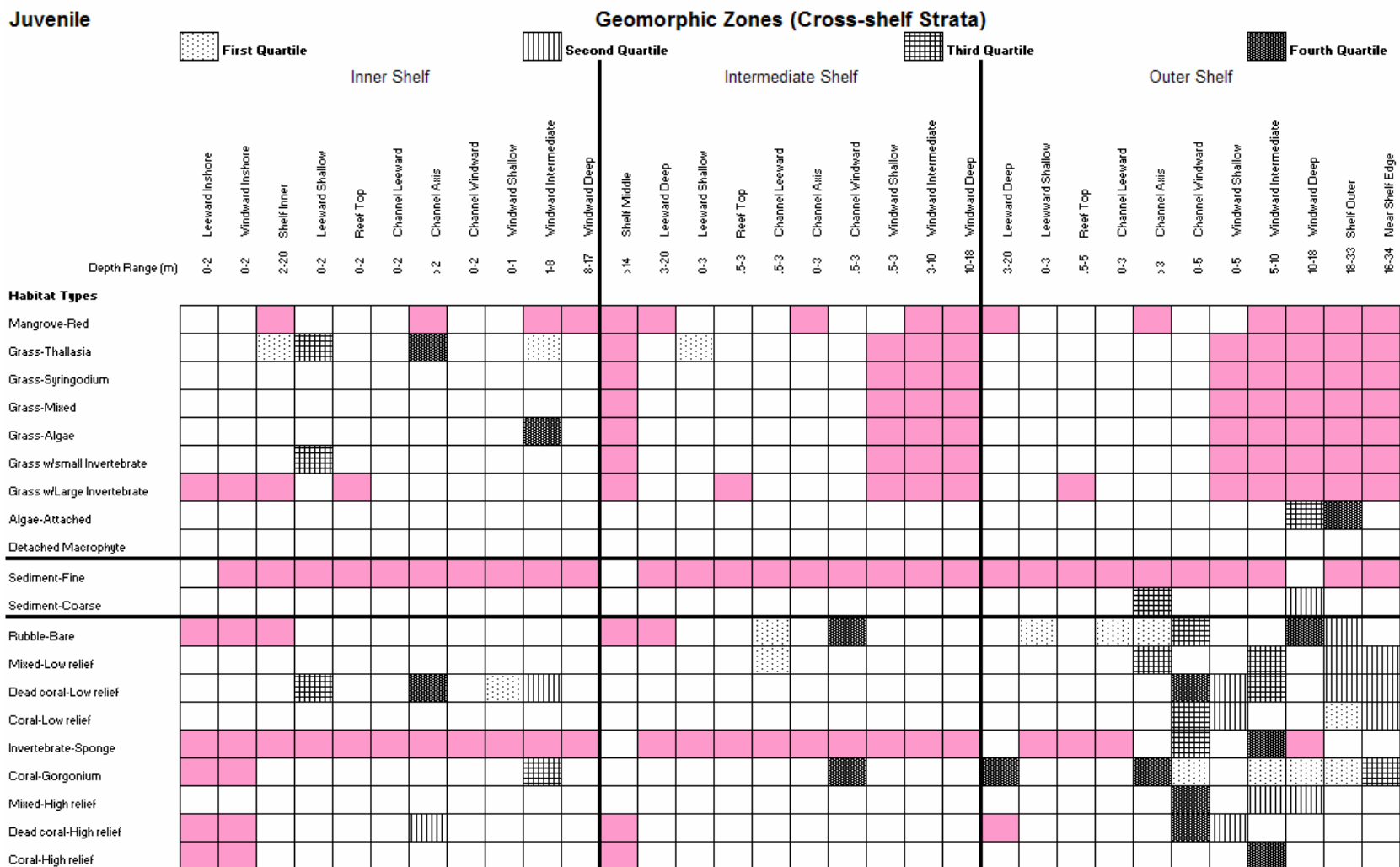


**Appendix B.1.b**

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

***Acanthurus bahianus***

**Juvenile**

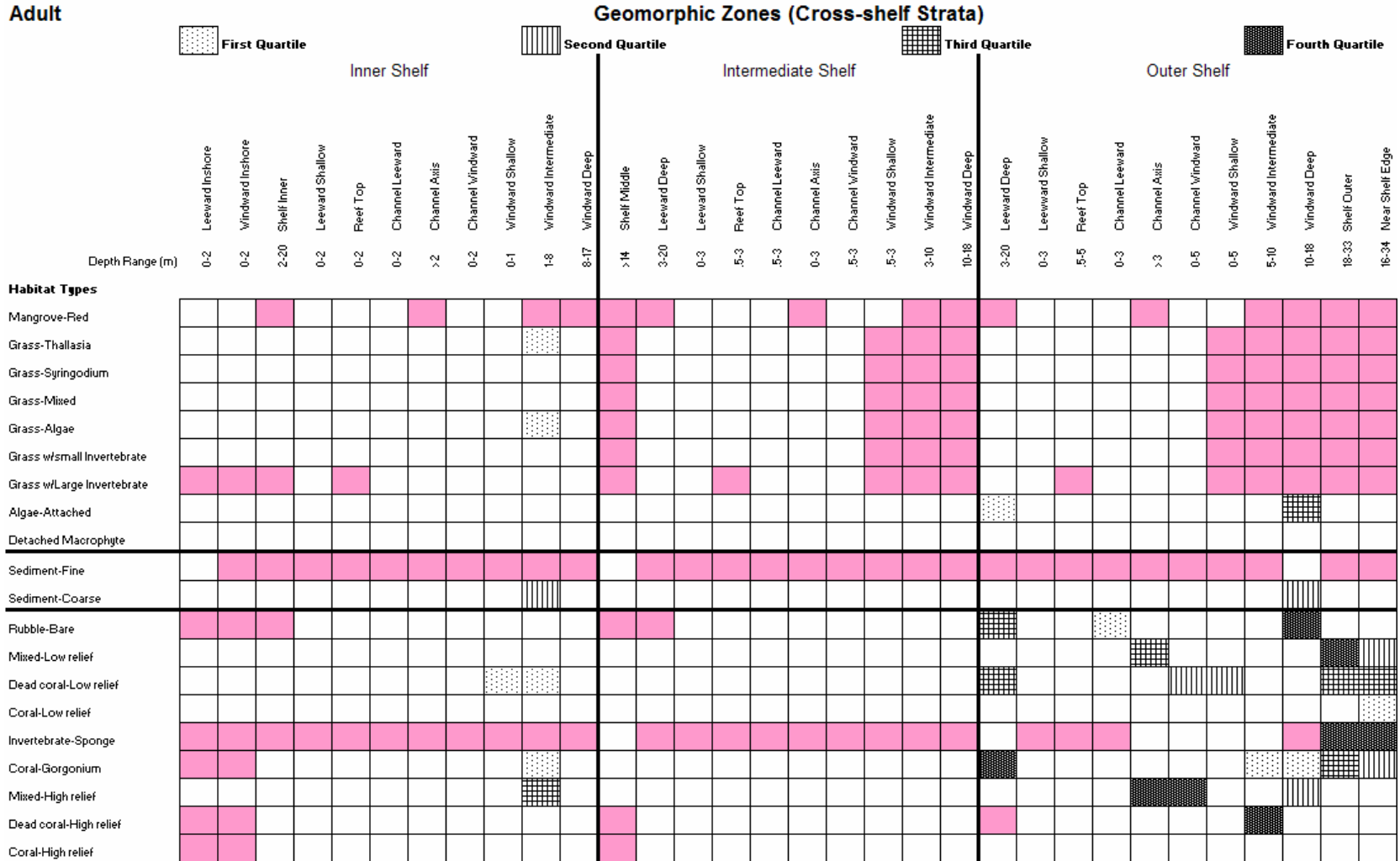


### Appendix B.1.c

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

#### *Acanthurus bahianus*

Adult

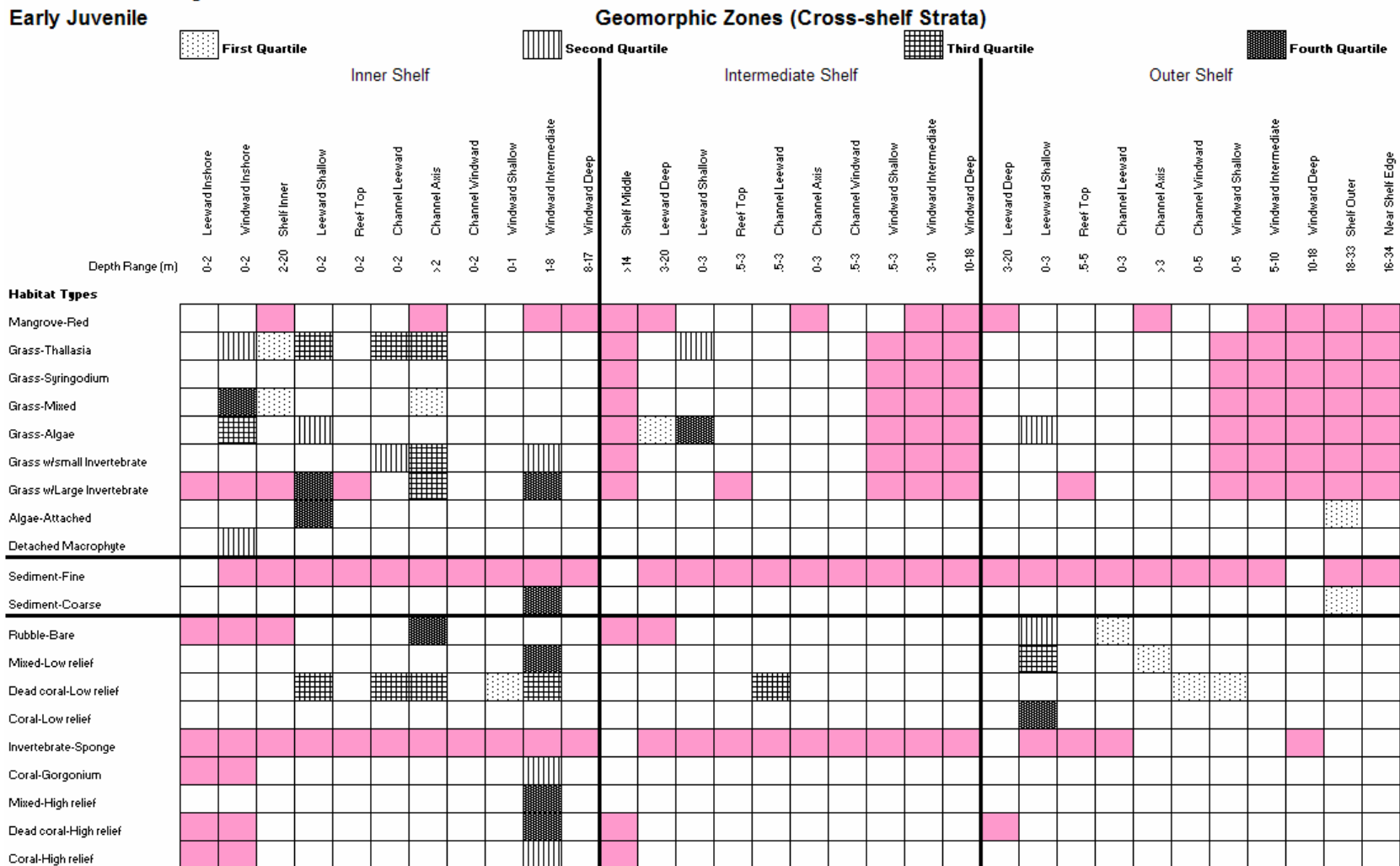


**Appendix B.2.a**

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

***Acanthurus chirurgus***

**Early Juvenile**



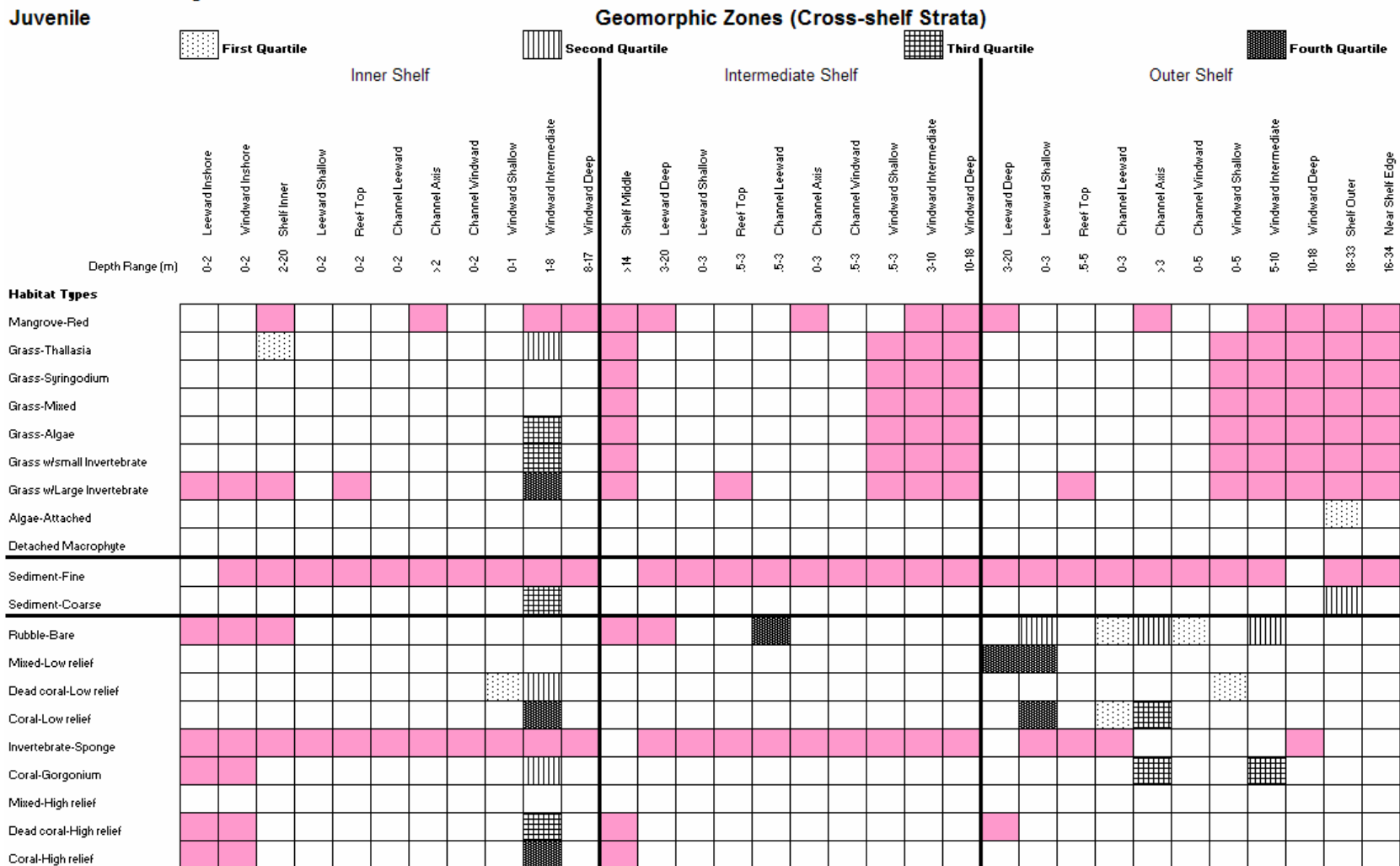


### Appendix B.2.b

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

#### *Acanthurus chirurgus*

#### Juvenile

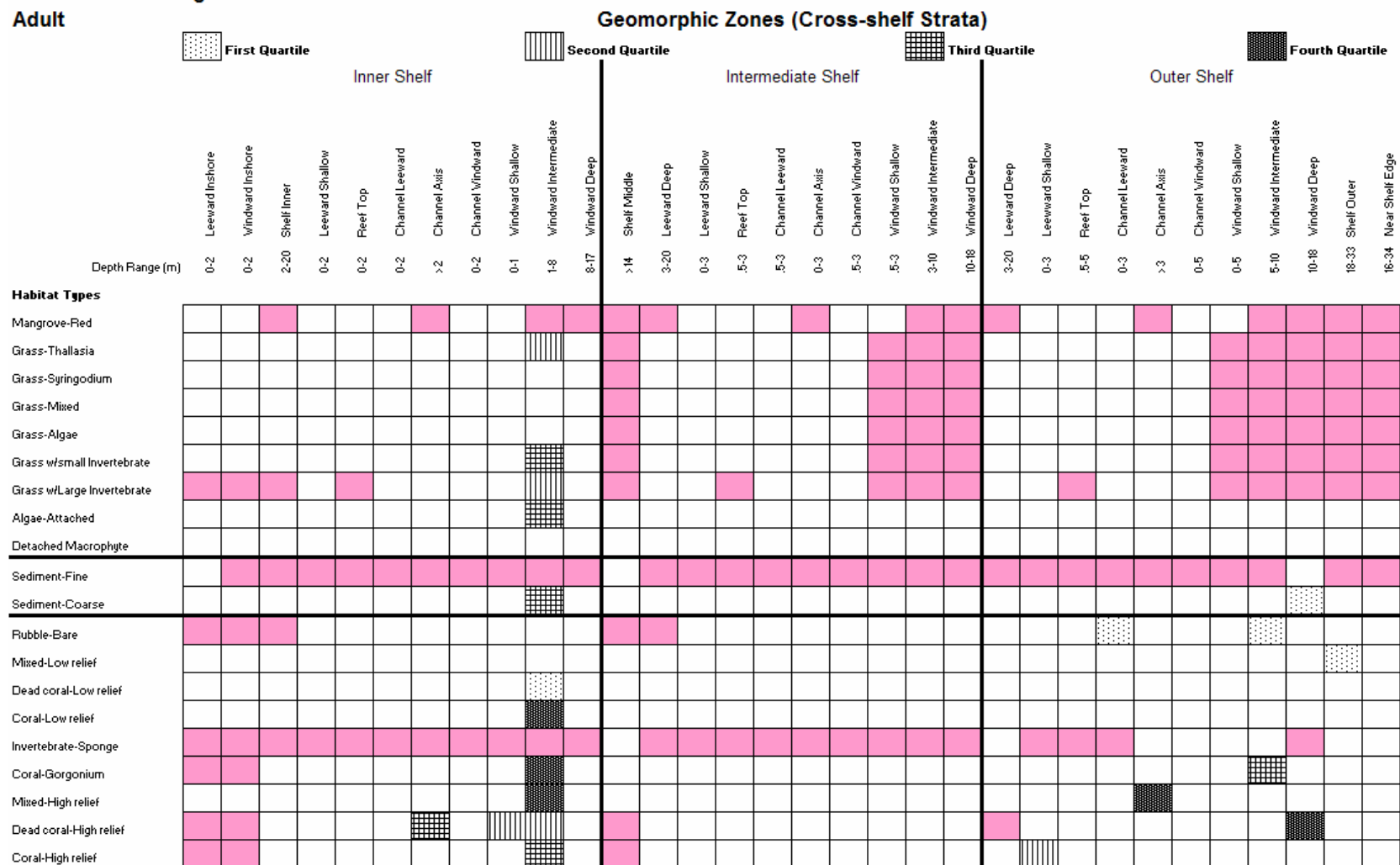


### Appendix B.2.c

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

### *Acanthurus chirurgus*

#### Adult

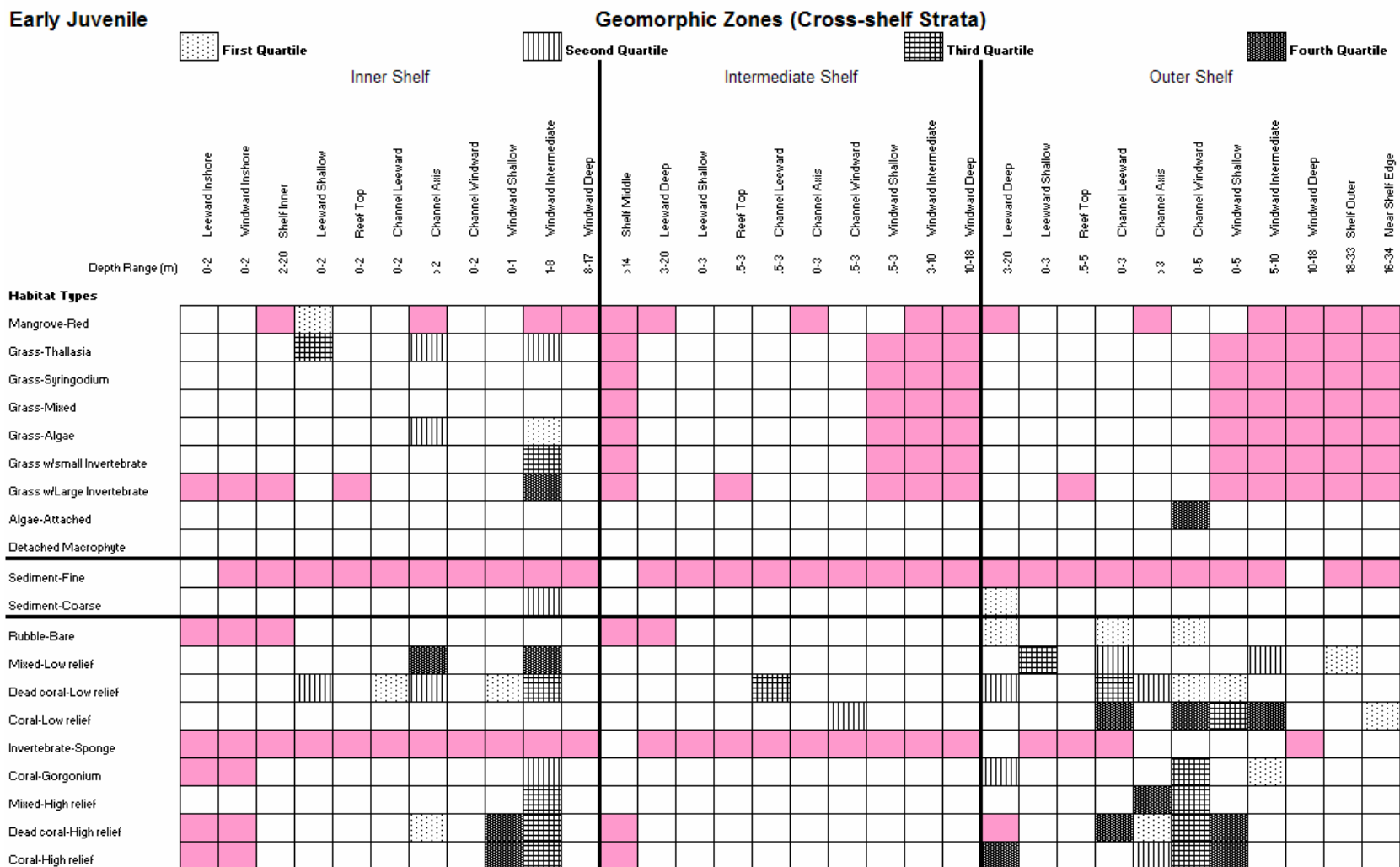


### Appendix B.3.a

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

#### *Acanthurus coeruleus*

#### Early Juvenile

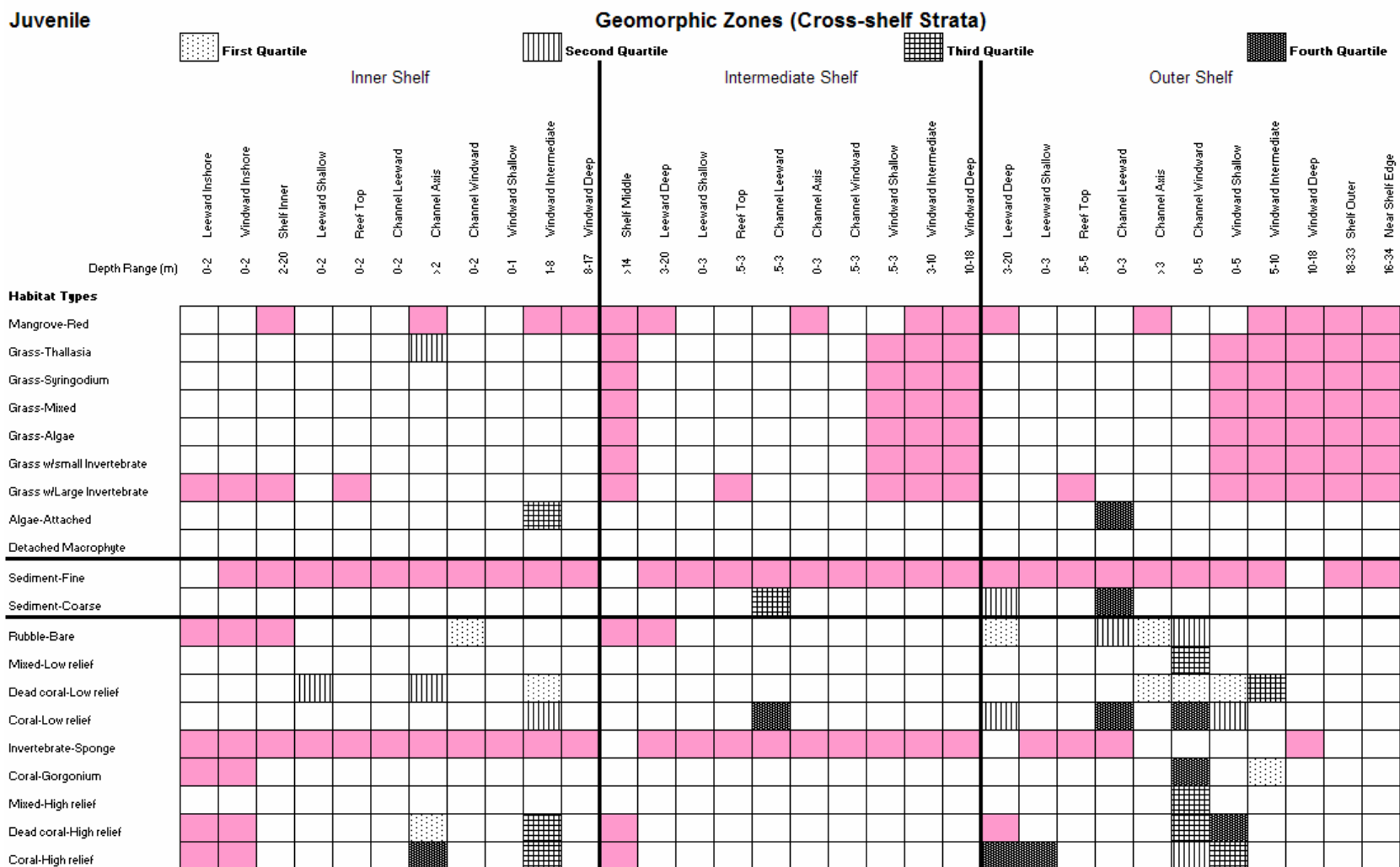


### Appendix B.3.b

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

#### *Acanthurus coeruleus*

#### Juvenile

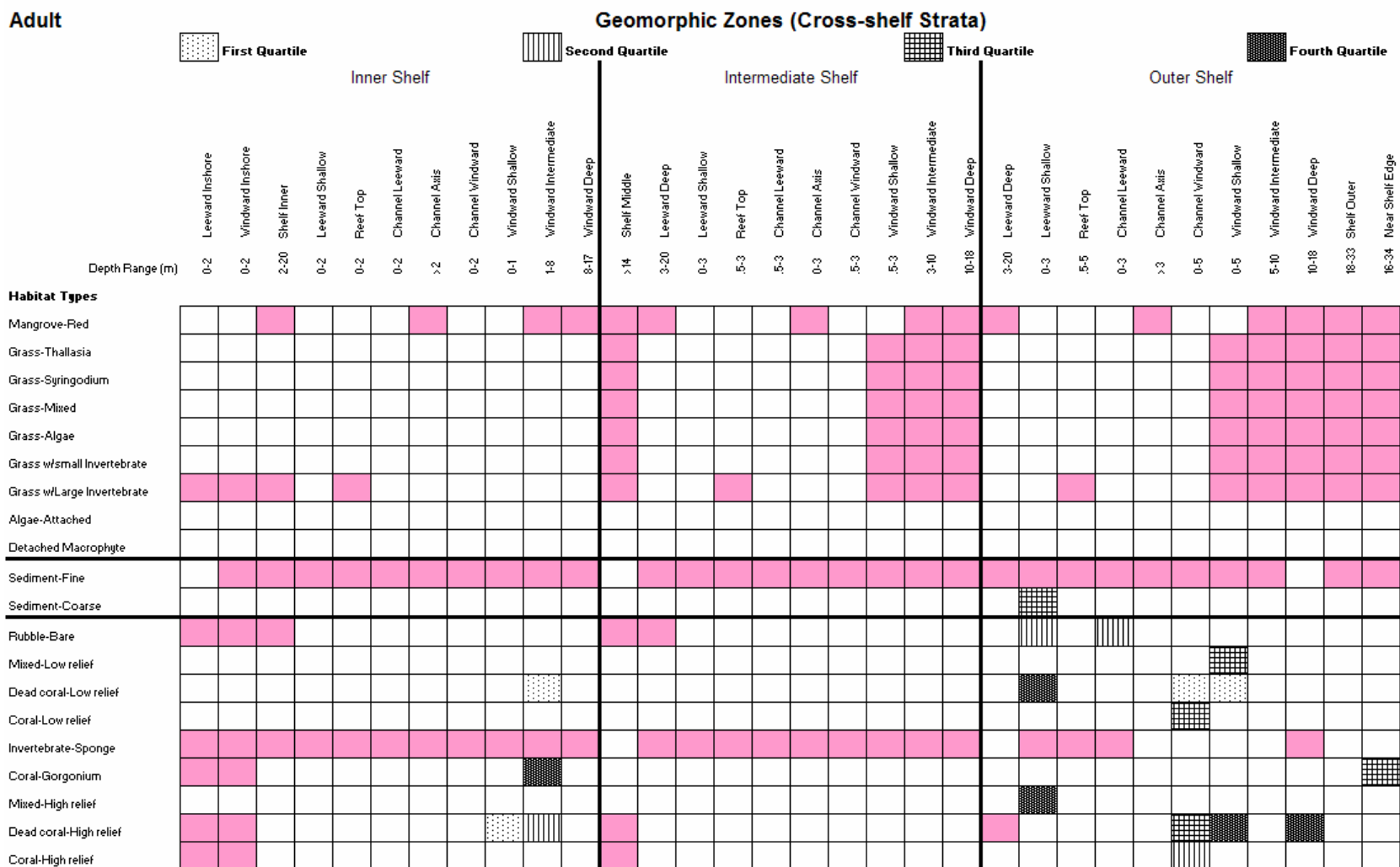


### Appendix B.3.c

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

#### *Acanthurus coeruleus*

Adult

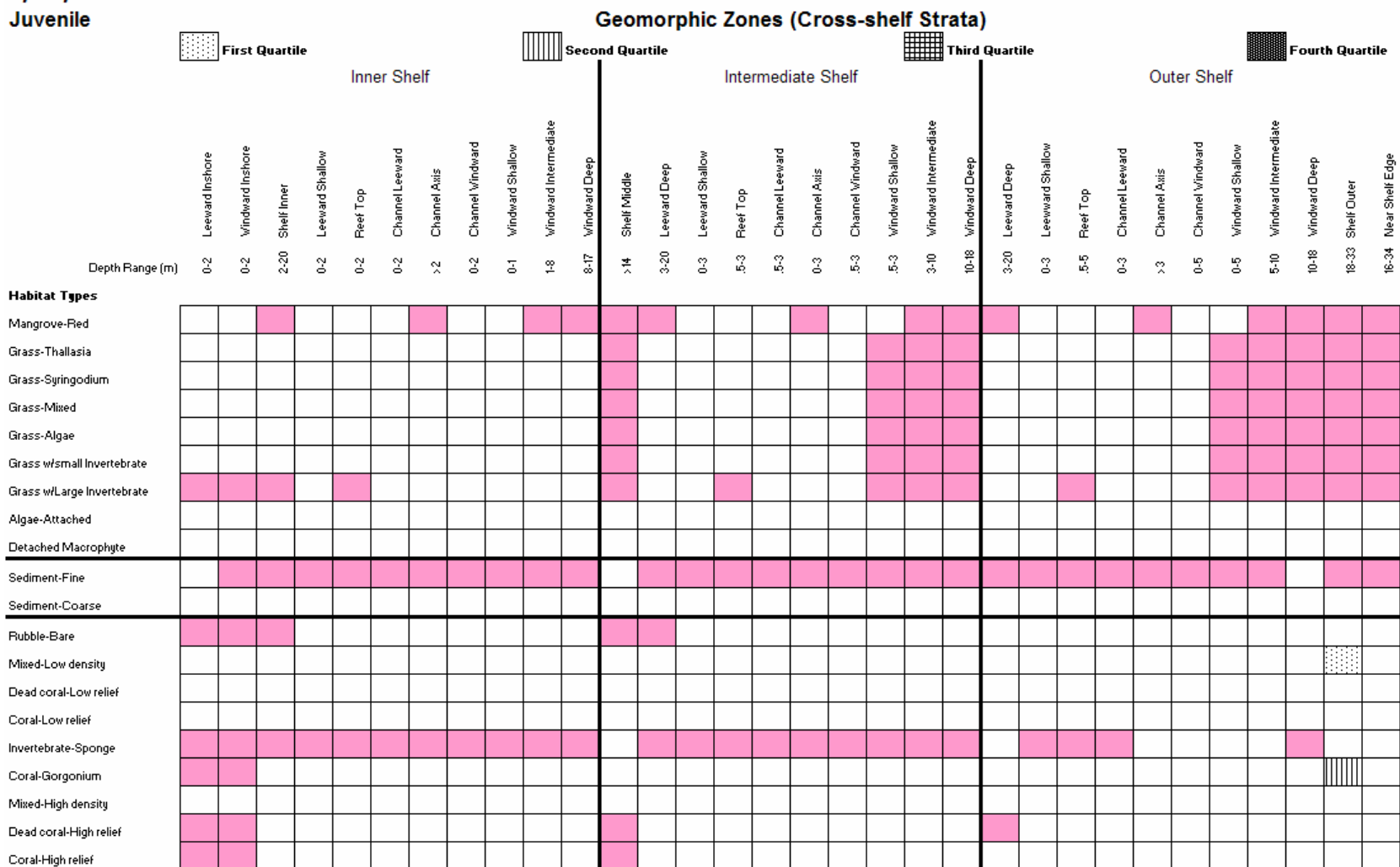


### Appendix B.4.a

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

#### *Epinephelus adscensionis*

#### Juvenile

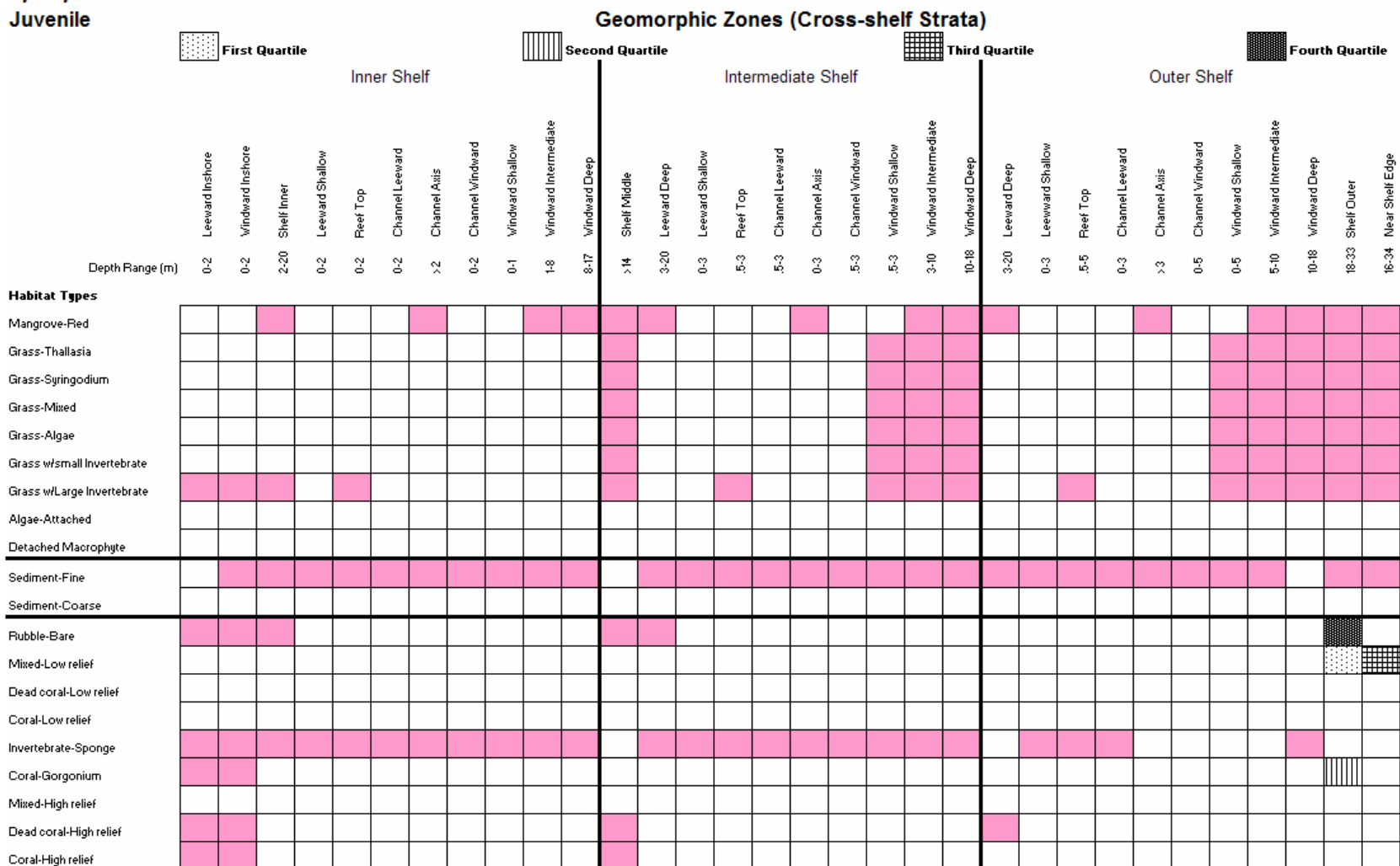


### Appendix B.5.a

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

#### *Epinephelus fulvus*

#### Juvenile

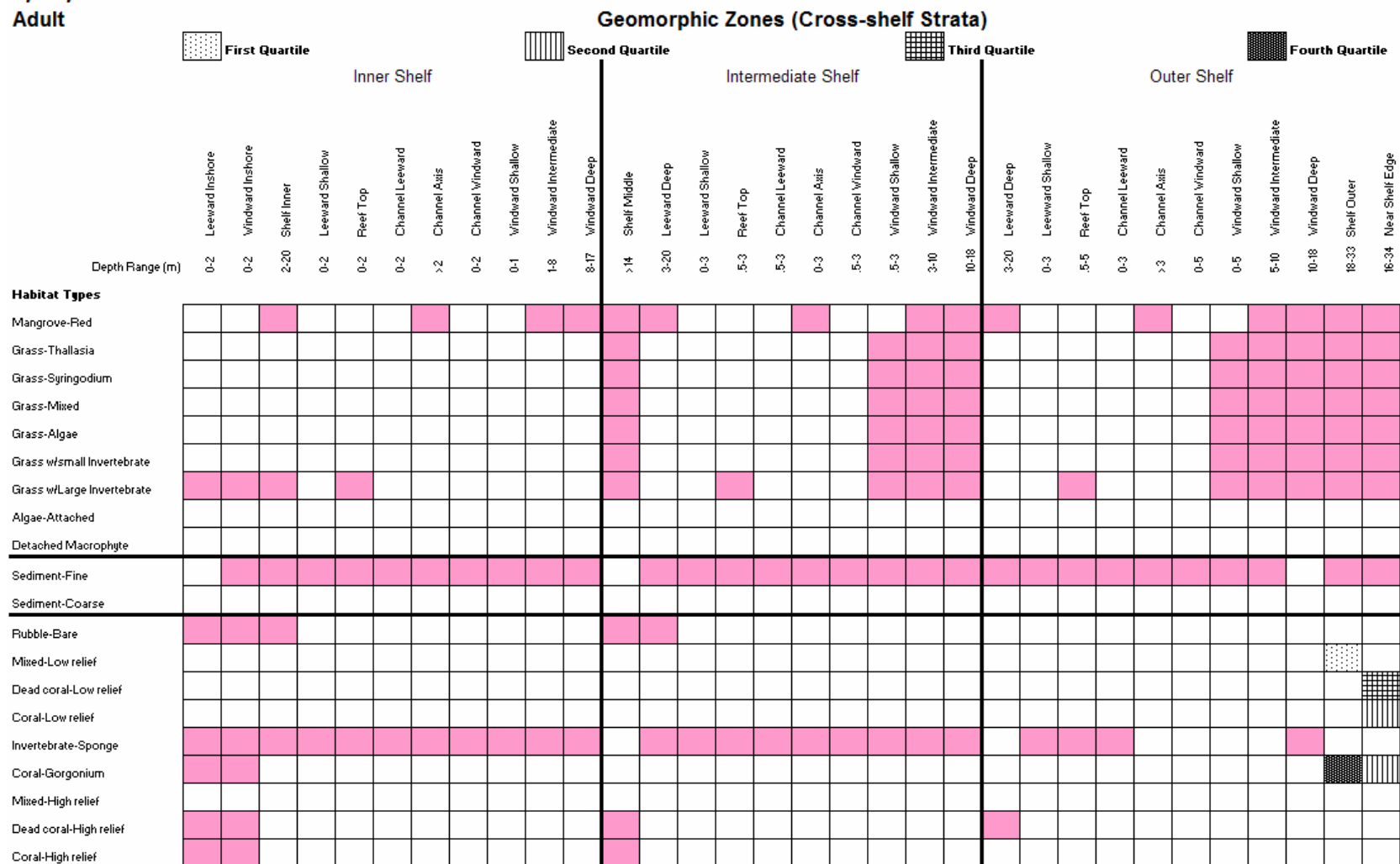


### Appendix B.5.b

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

#### *Epinephelus fulvus*

#### Adult



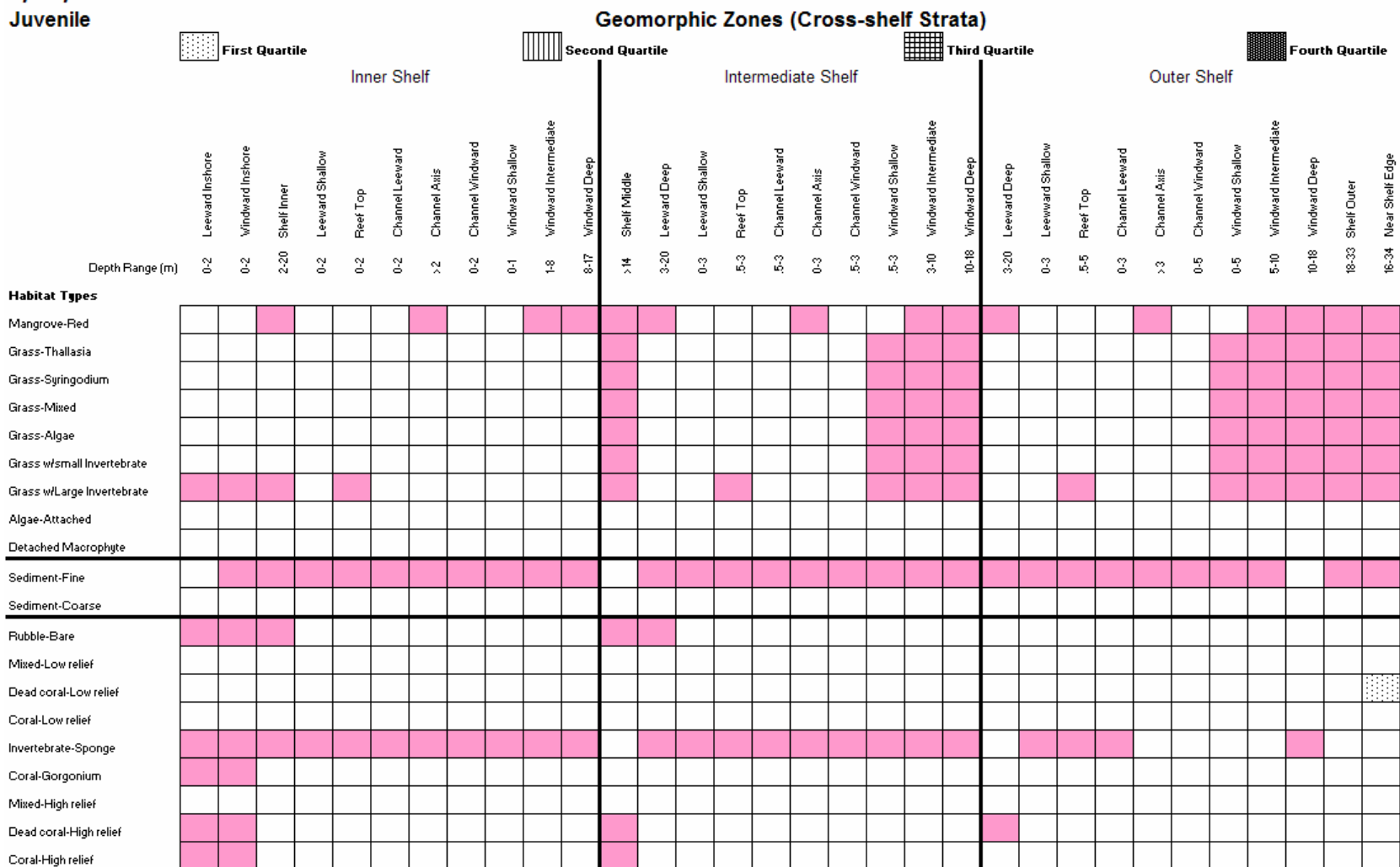


### Appendix B.6.a

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

### *Epinephelus cruentatus*

### Juvenile

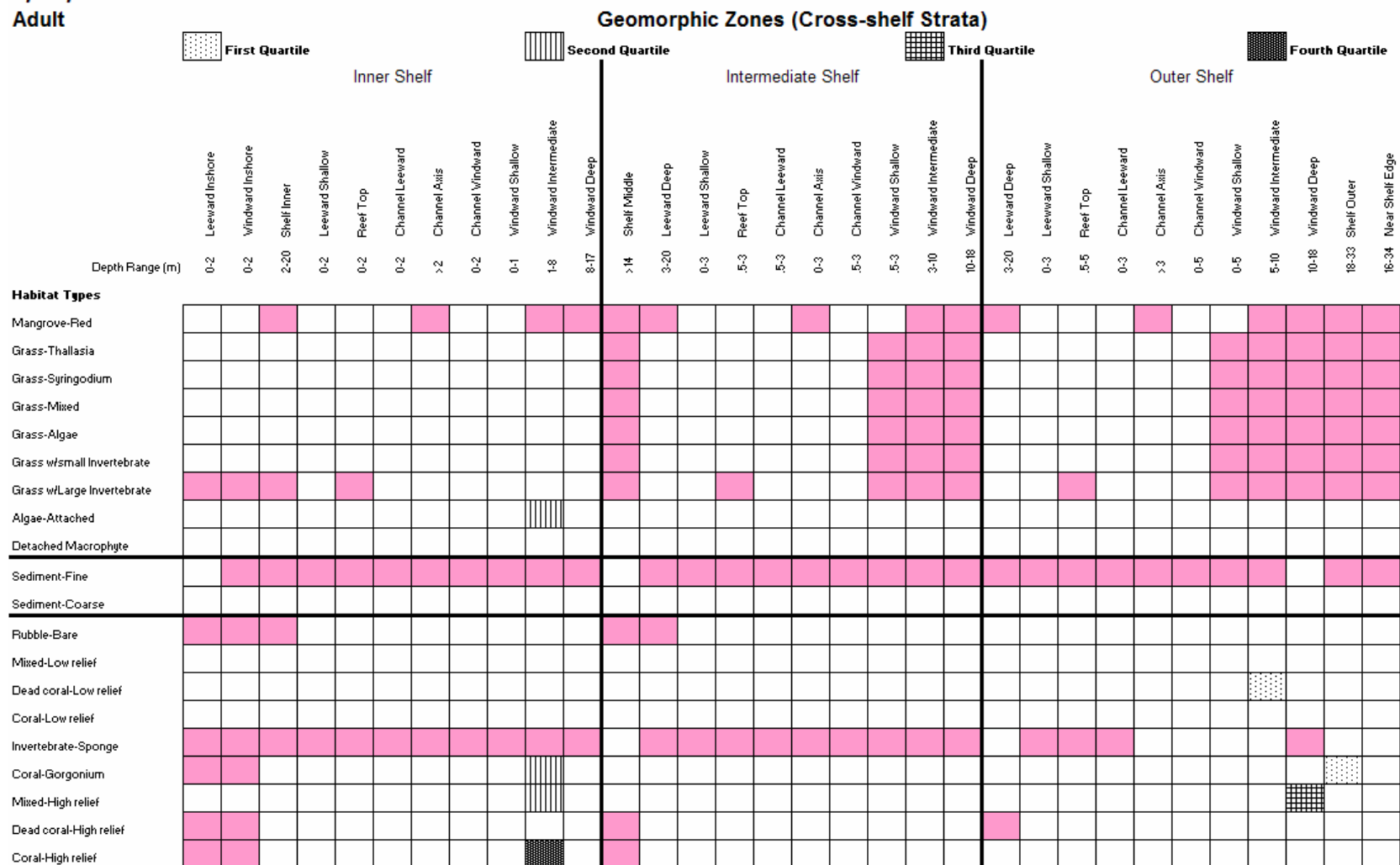


### Appendix B.6.b

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

### *Epinephelus cruentatus*

### Adult

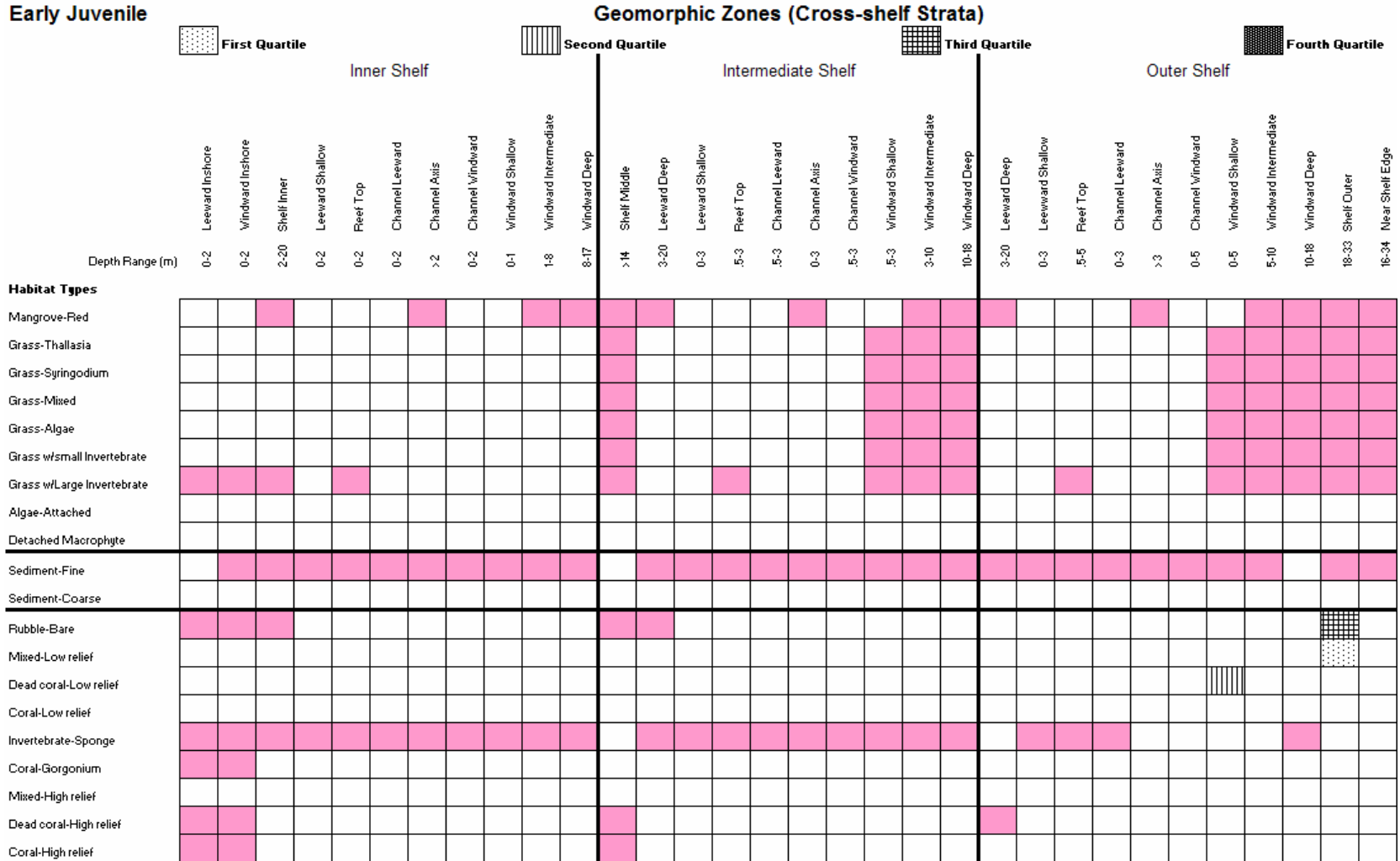


**Appendix B.7.a**

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

***Epinephelus guttatus***

**Early Juvenile**

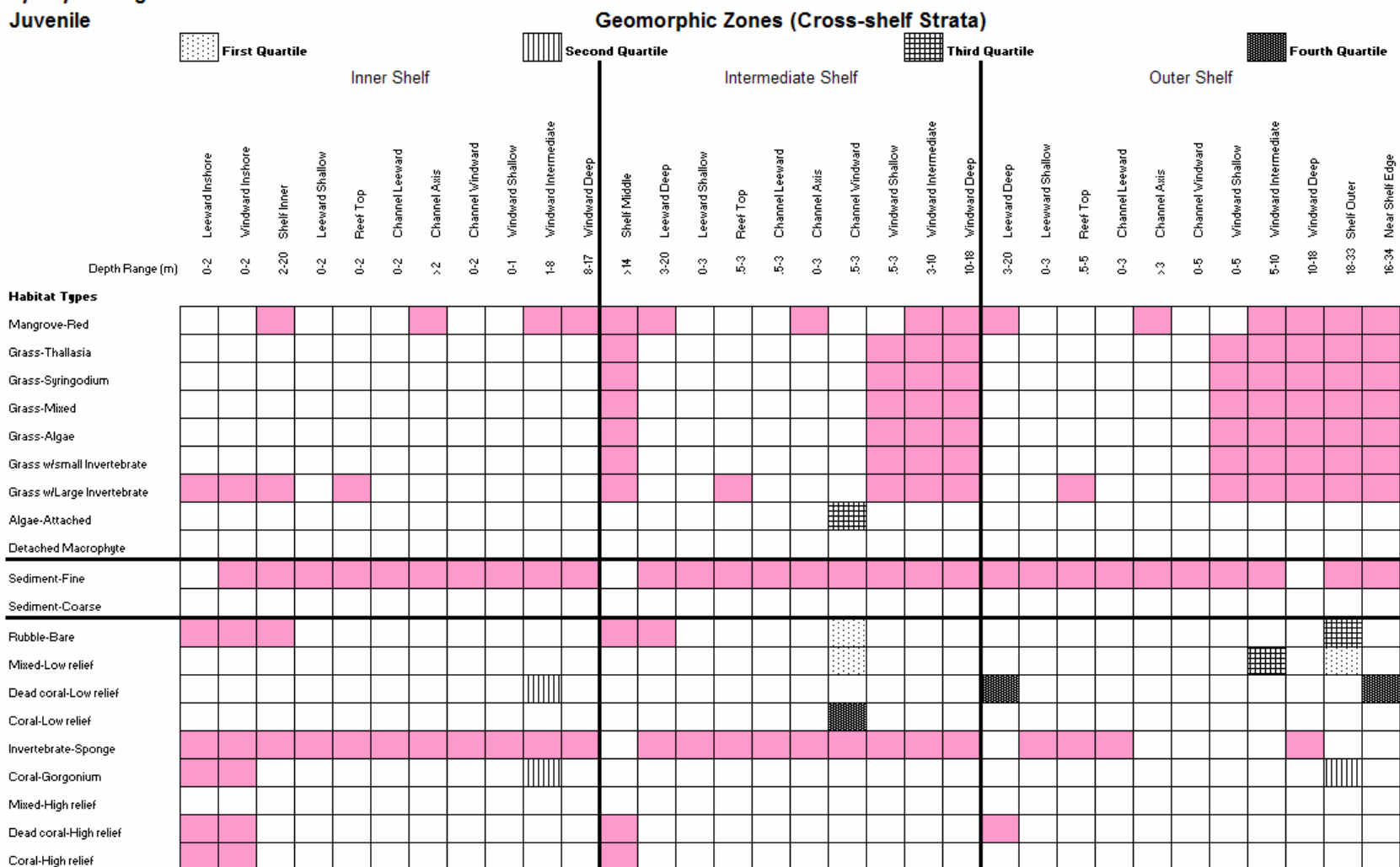


### Appendix B.7.b

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

#### *Epinephelus guttatus*

#### Juvenile

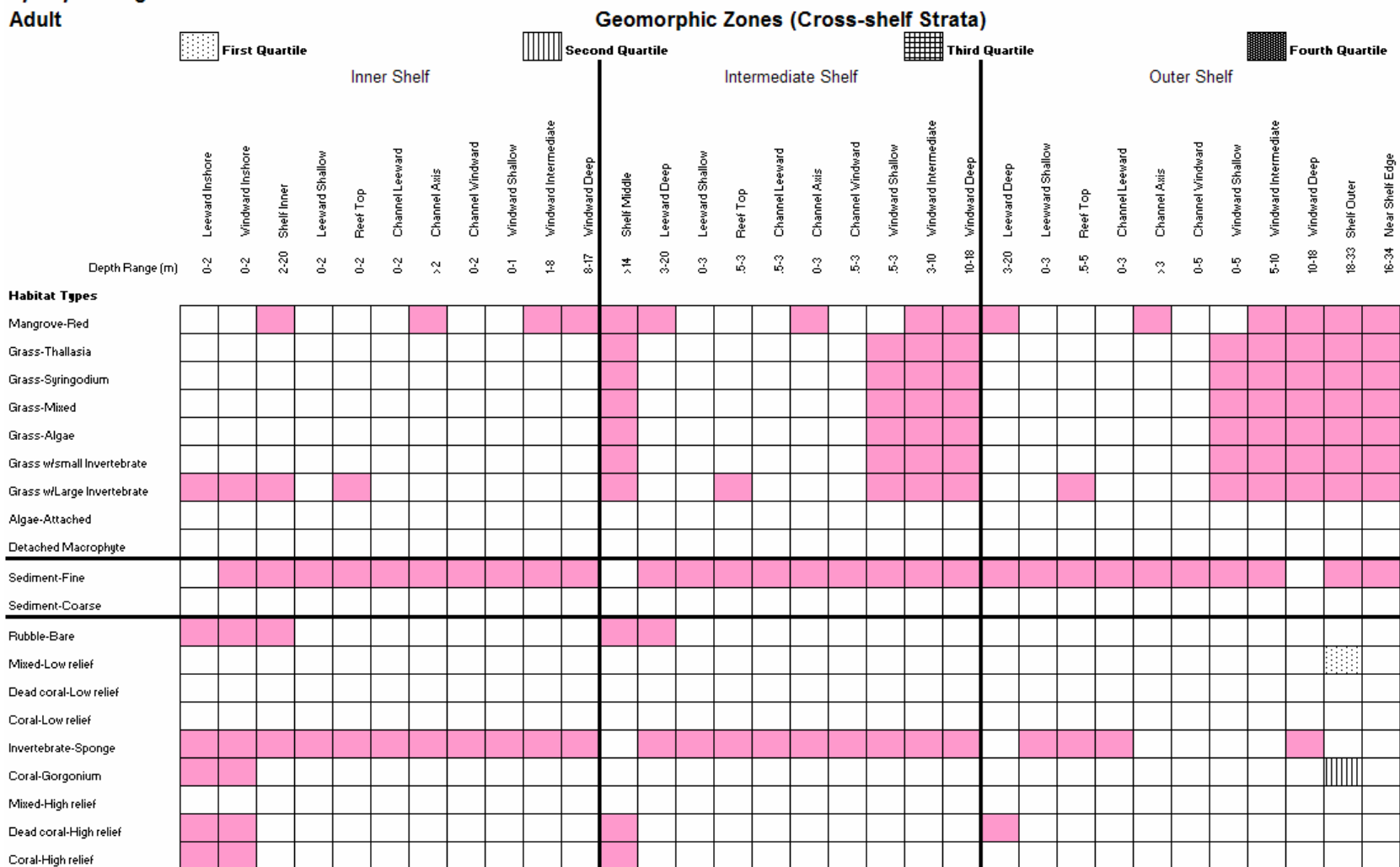


### Appendix B.7.c

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

#### *Epinephelus guttatus*

#### Adult

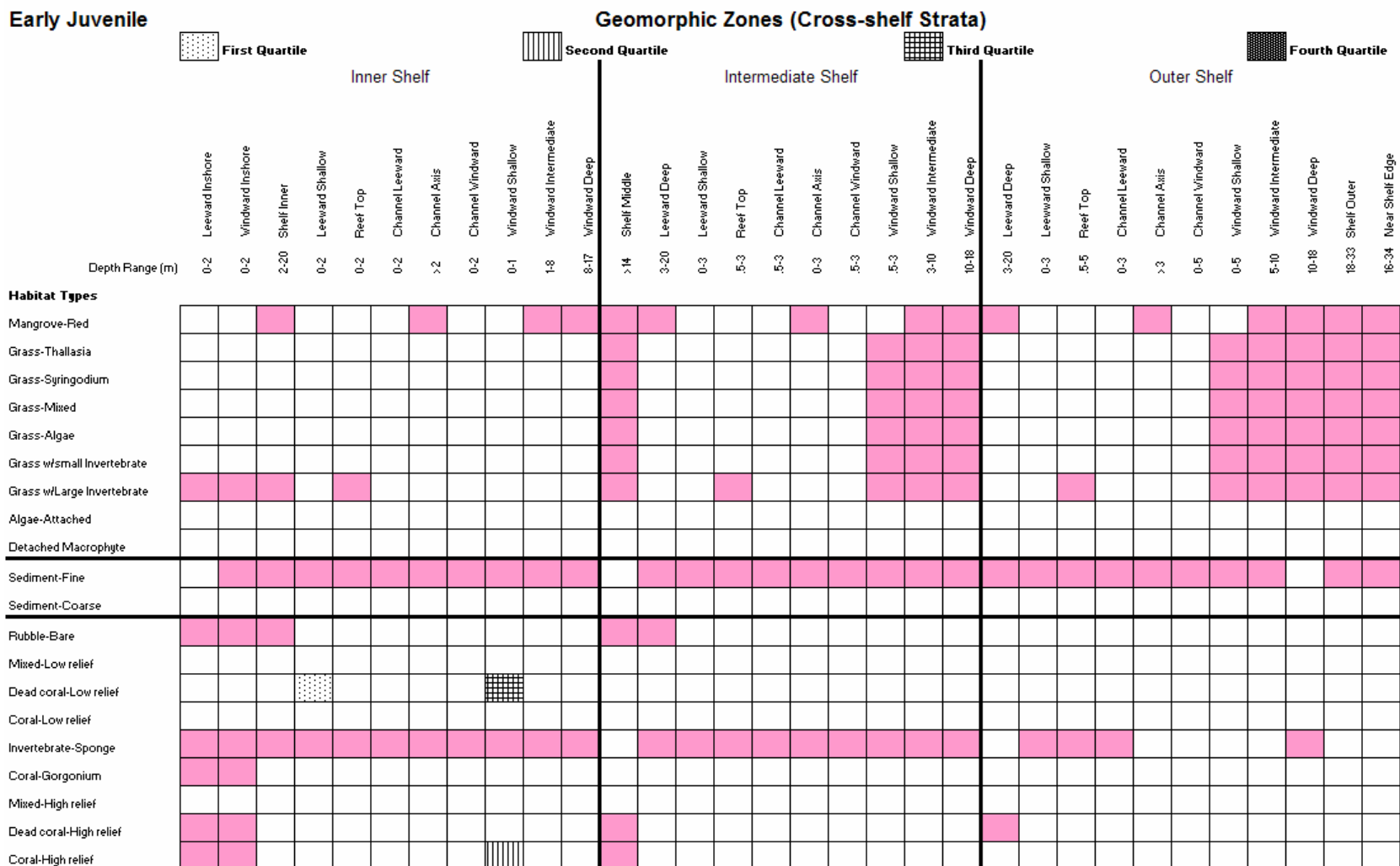


### Appendix B.8.a

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

#### *Haemulon carbonarium*

#### Early Juvenile

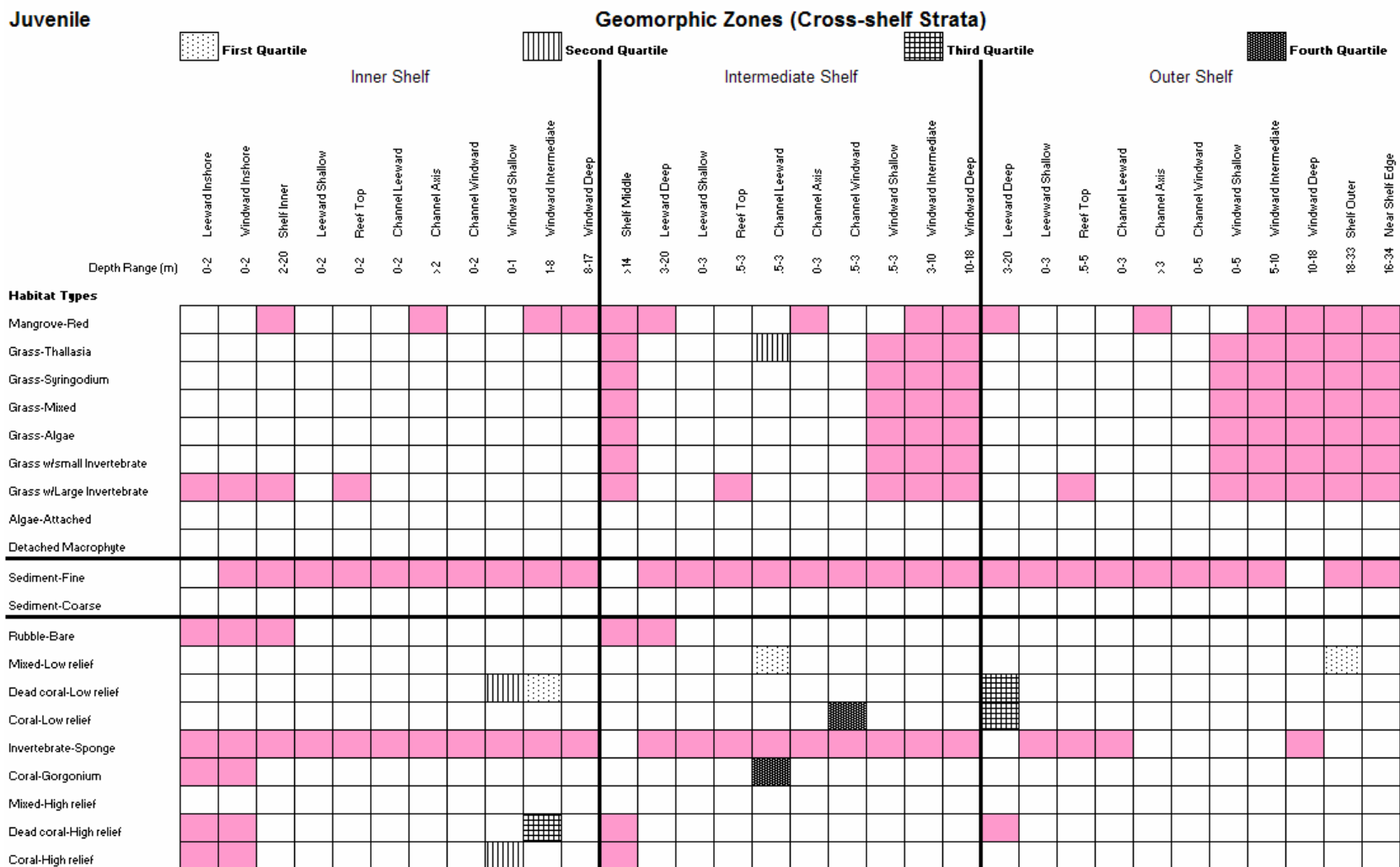


### Appendix B.8.b

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

#### *Haemulon carbonarium*

#### Juvenile

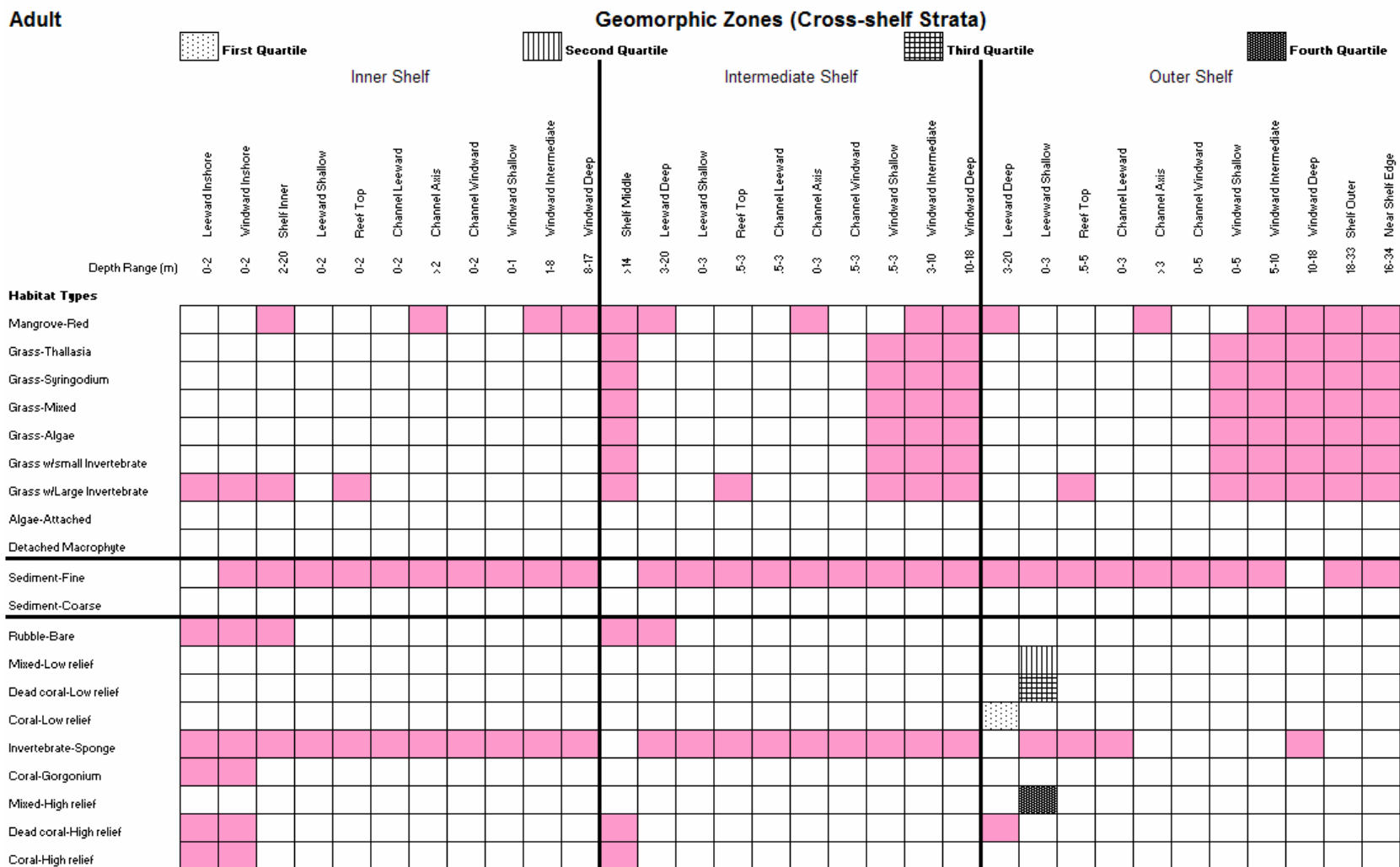


### Appendix B.8.c

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

#### *Haemulon carbonarium*

#### Adult



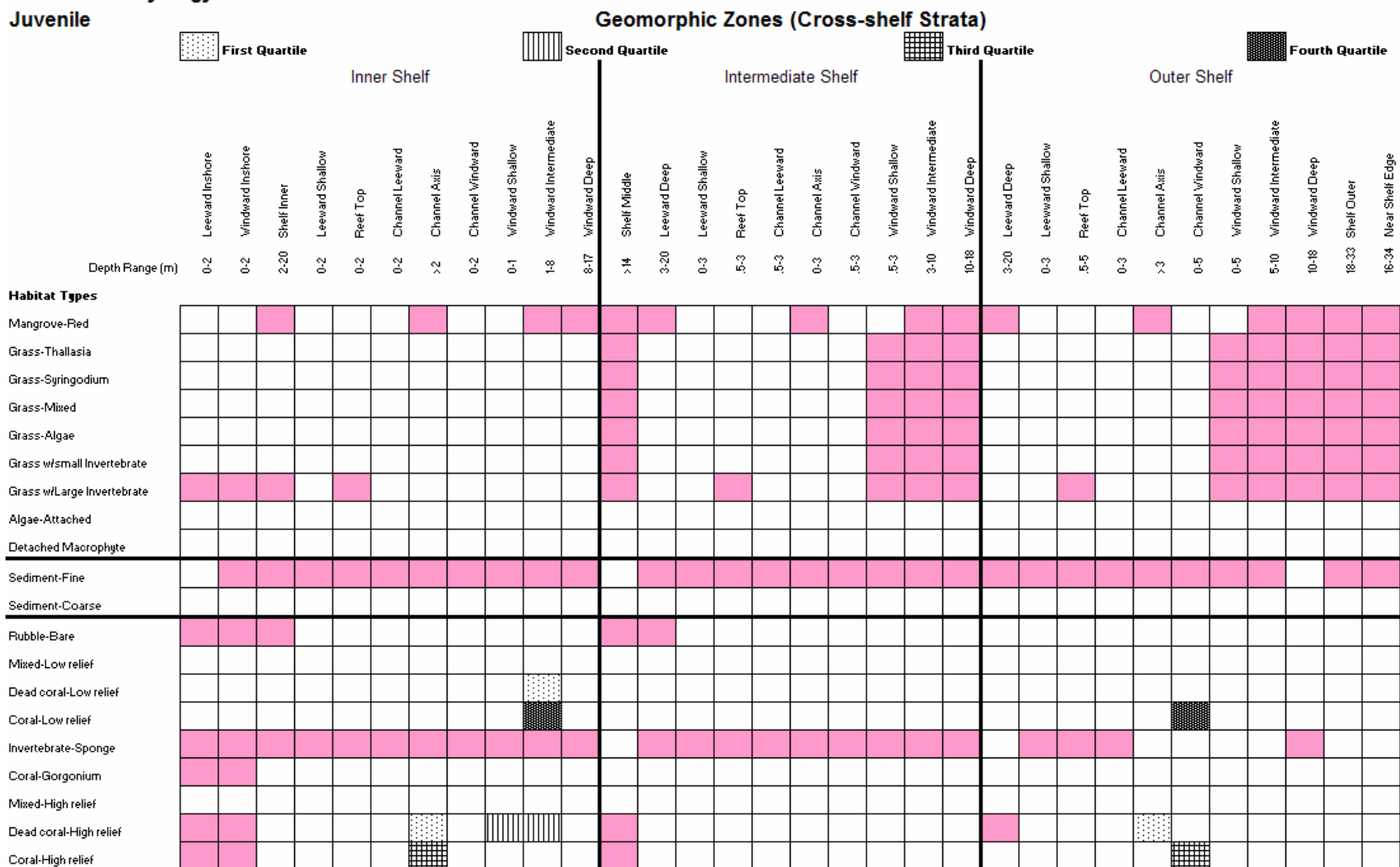


### Appendix B.9.a

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

### *Haemulon chrysargyreum*

### Juvenile

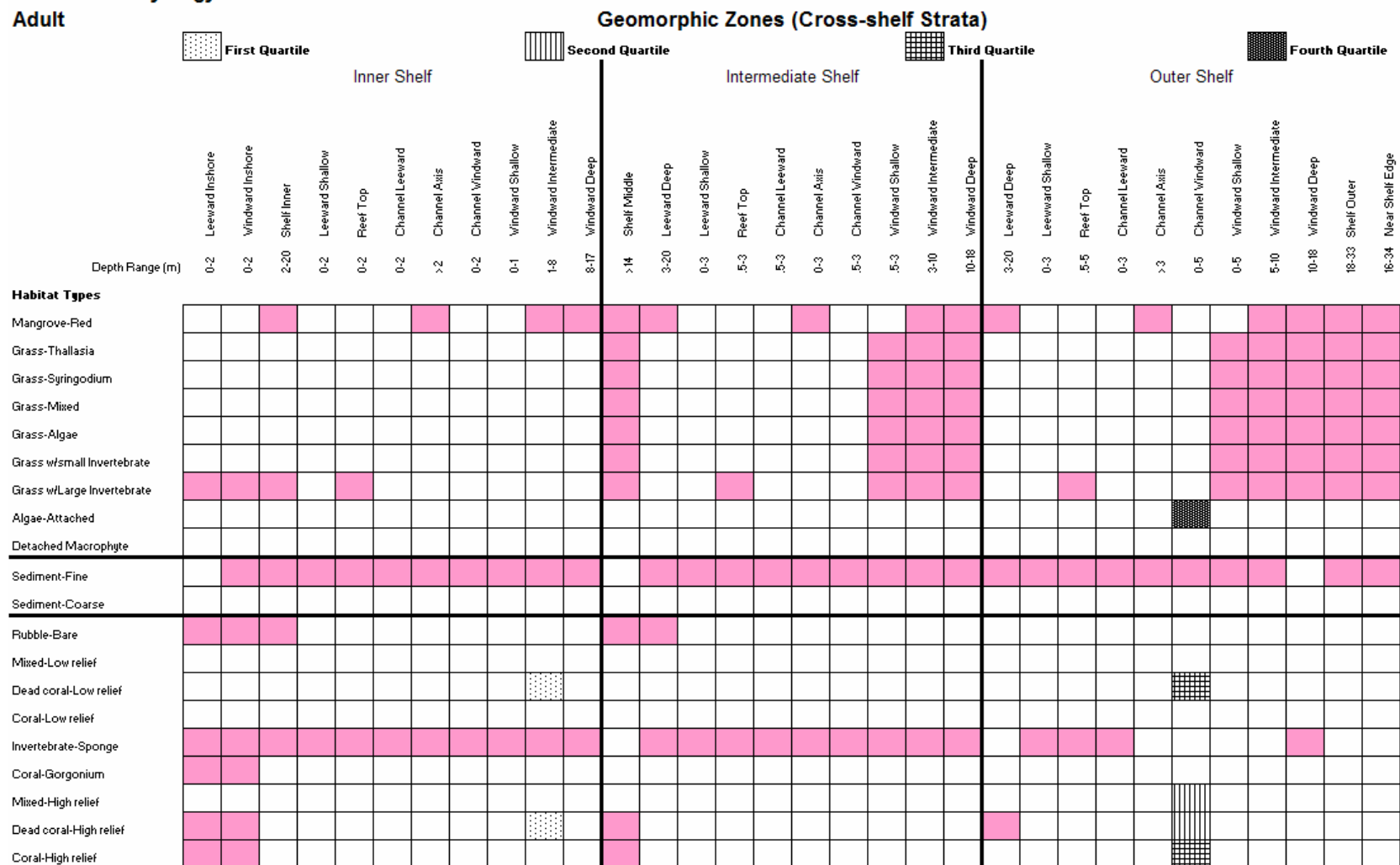


### Appendix B.9.b

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

#### *Haemulon chrysargyreum*

Adult

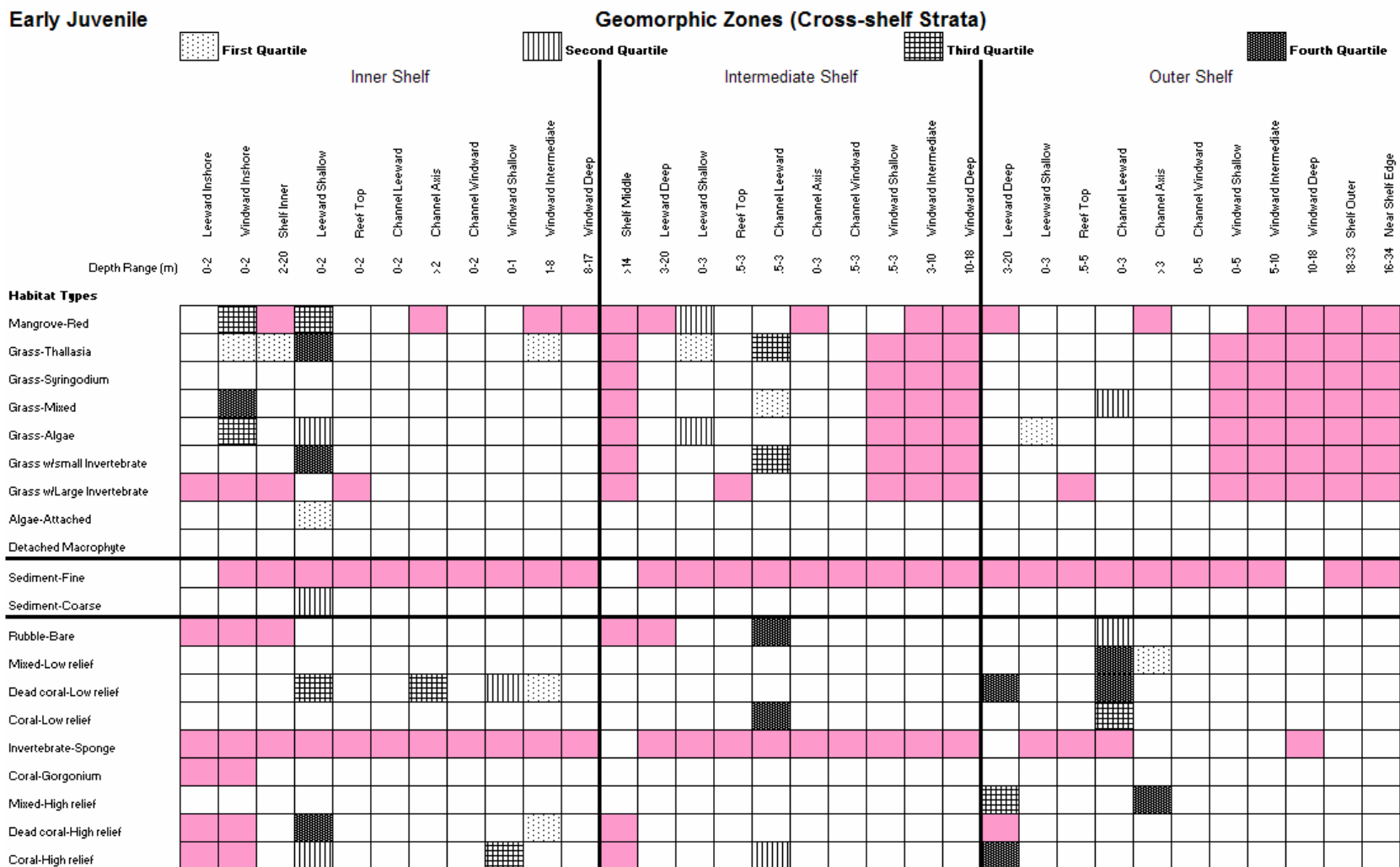


**Appendix B.10.a**

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

***Haemulon flavolineatum***

**Early Juvenile**

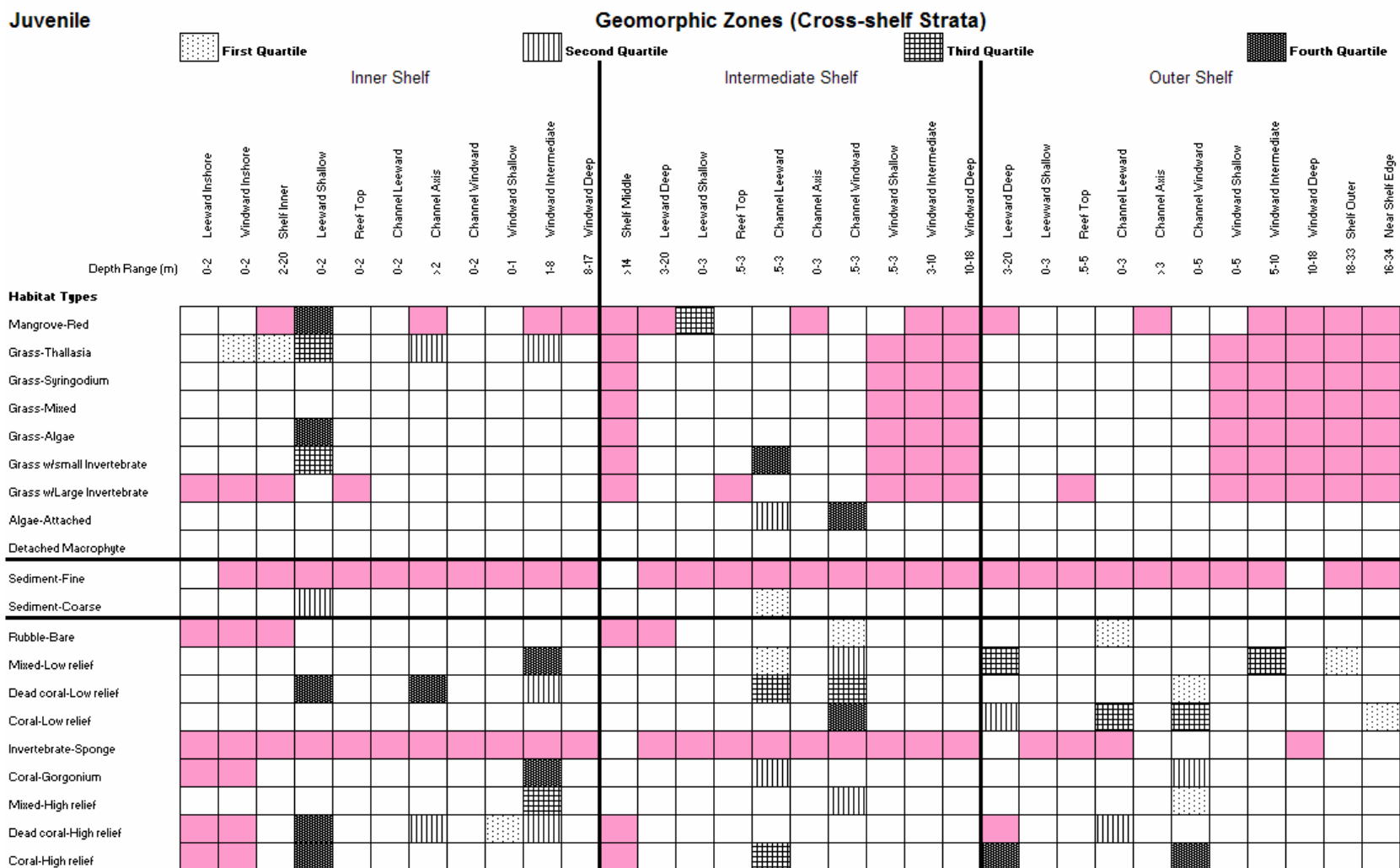


### Appendix B.10.b

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

#### *Haemulon flavolineatum*

#### Juvenile

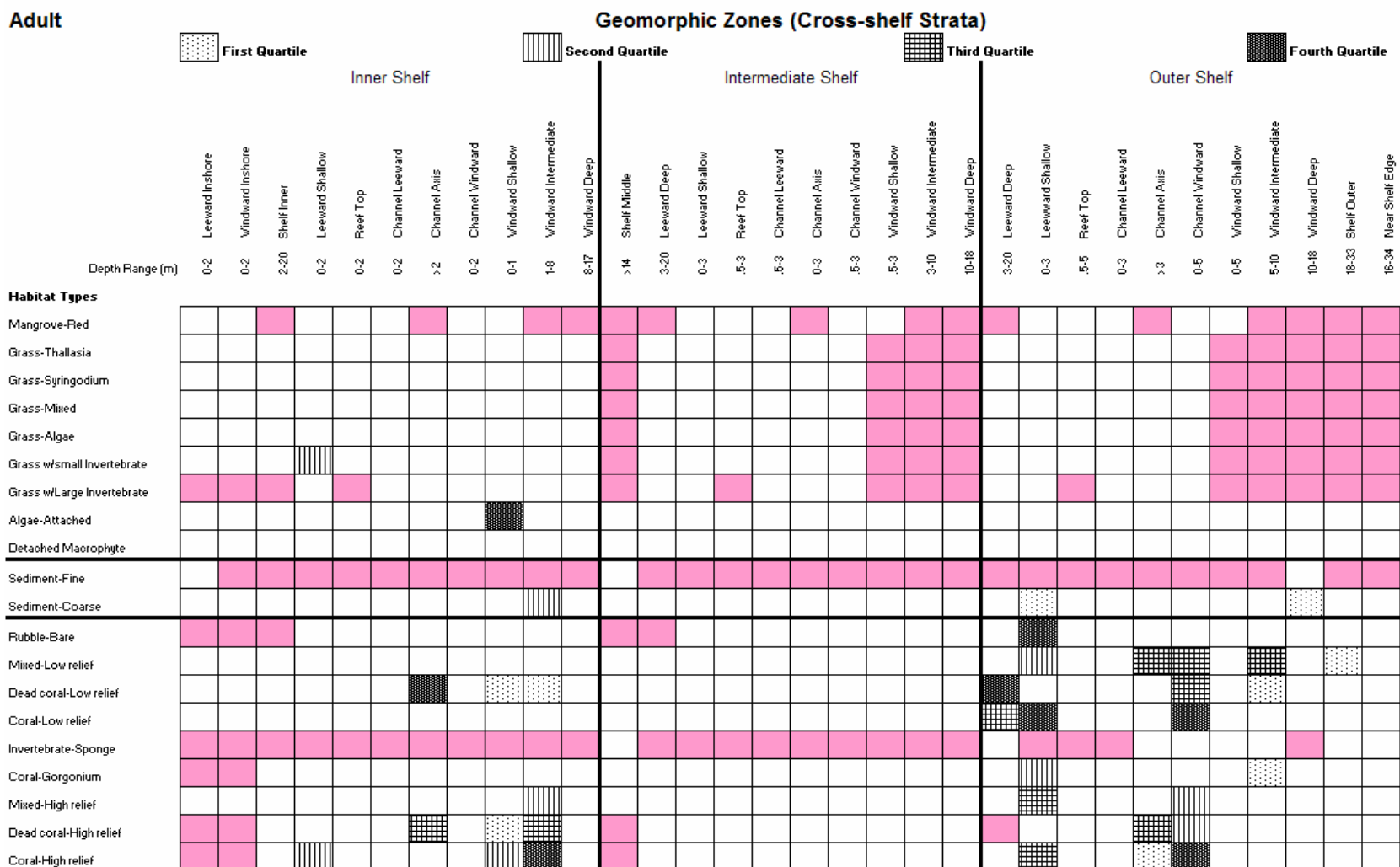


### Appendix B.10.c

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

#### *Haemulon flavolineatum*

#### Adult

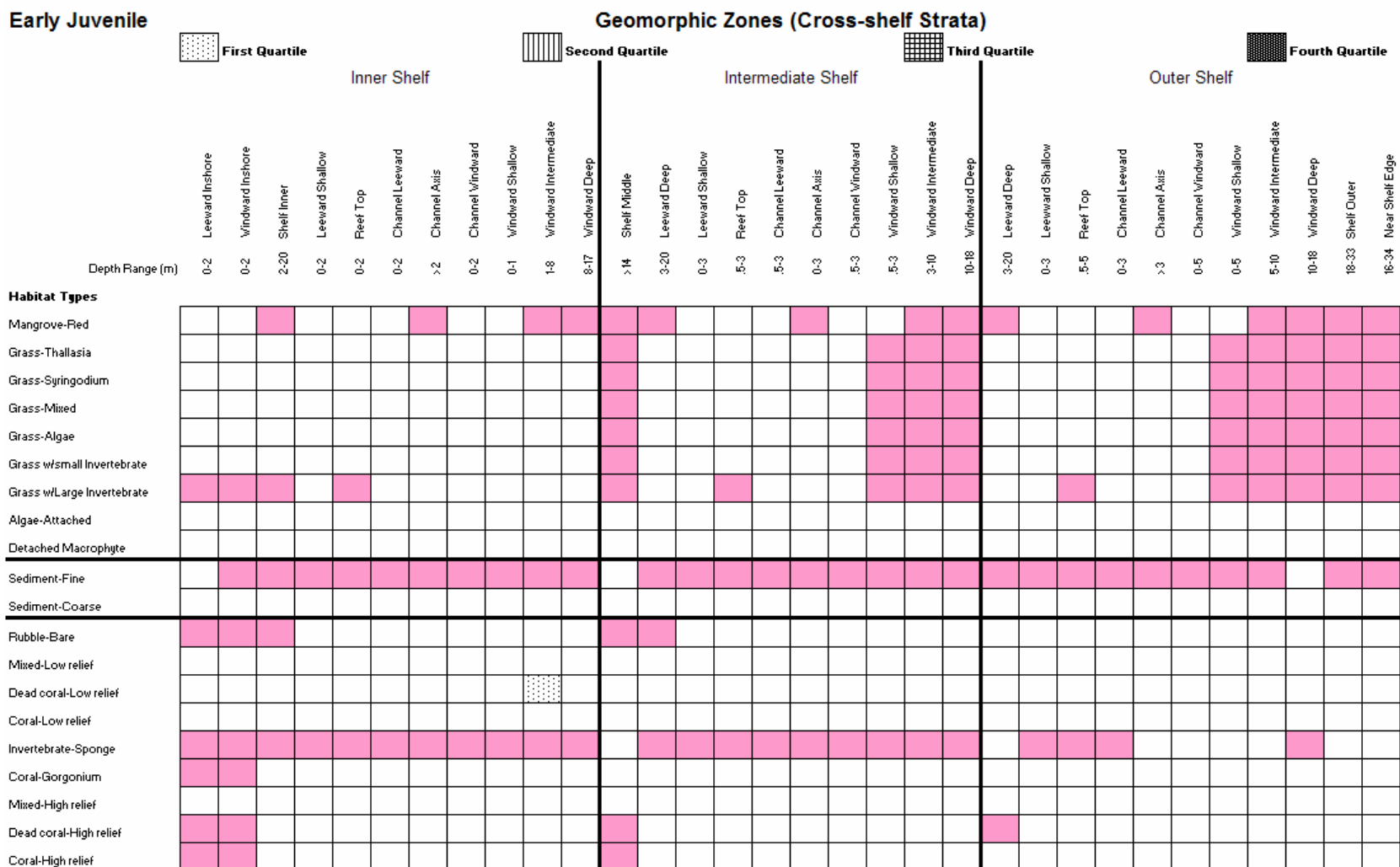


### Appendix B.11.a

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

#### *Haemulon macrostomum*

#### Early Juvenile

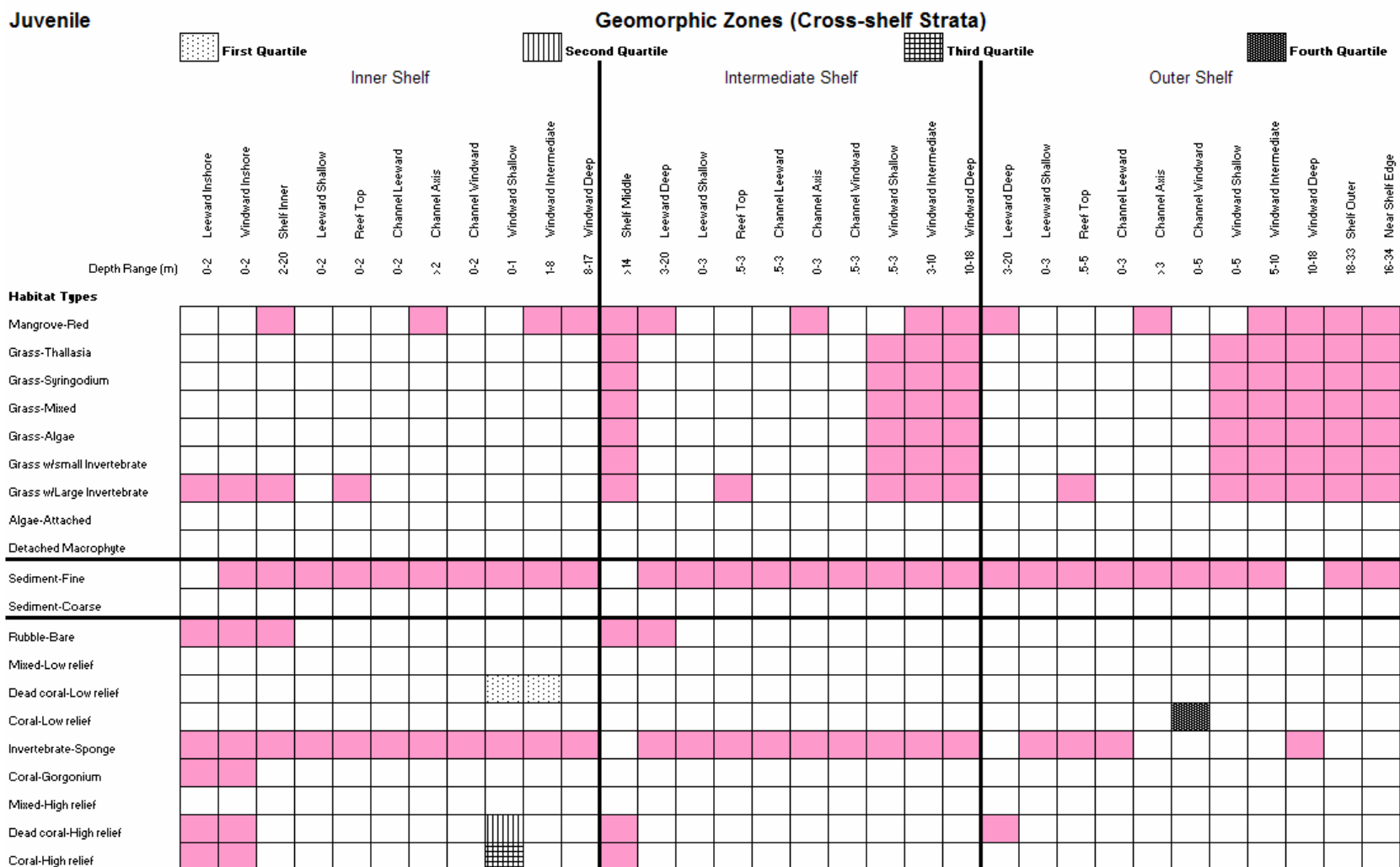


### Appendix B.11.b

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

#### *Haemulon macrostomum*

#### Juvenile

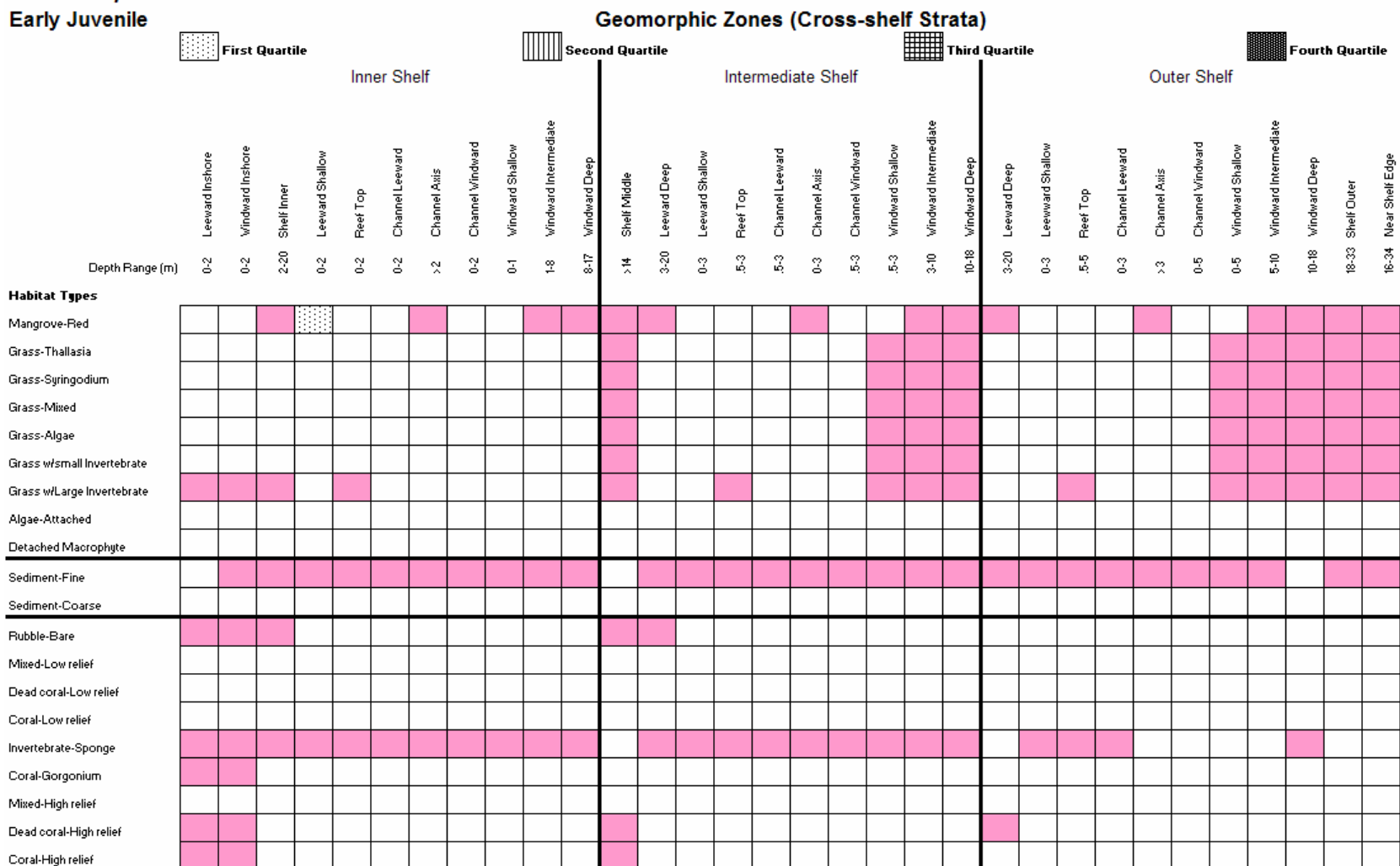


### Appendix B.12.a

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

#### *Haemulon parra*

#### Early Juvenile



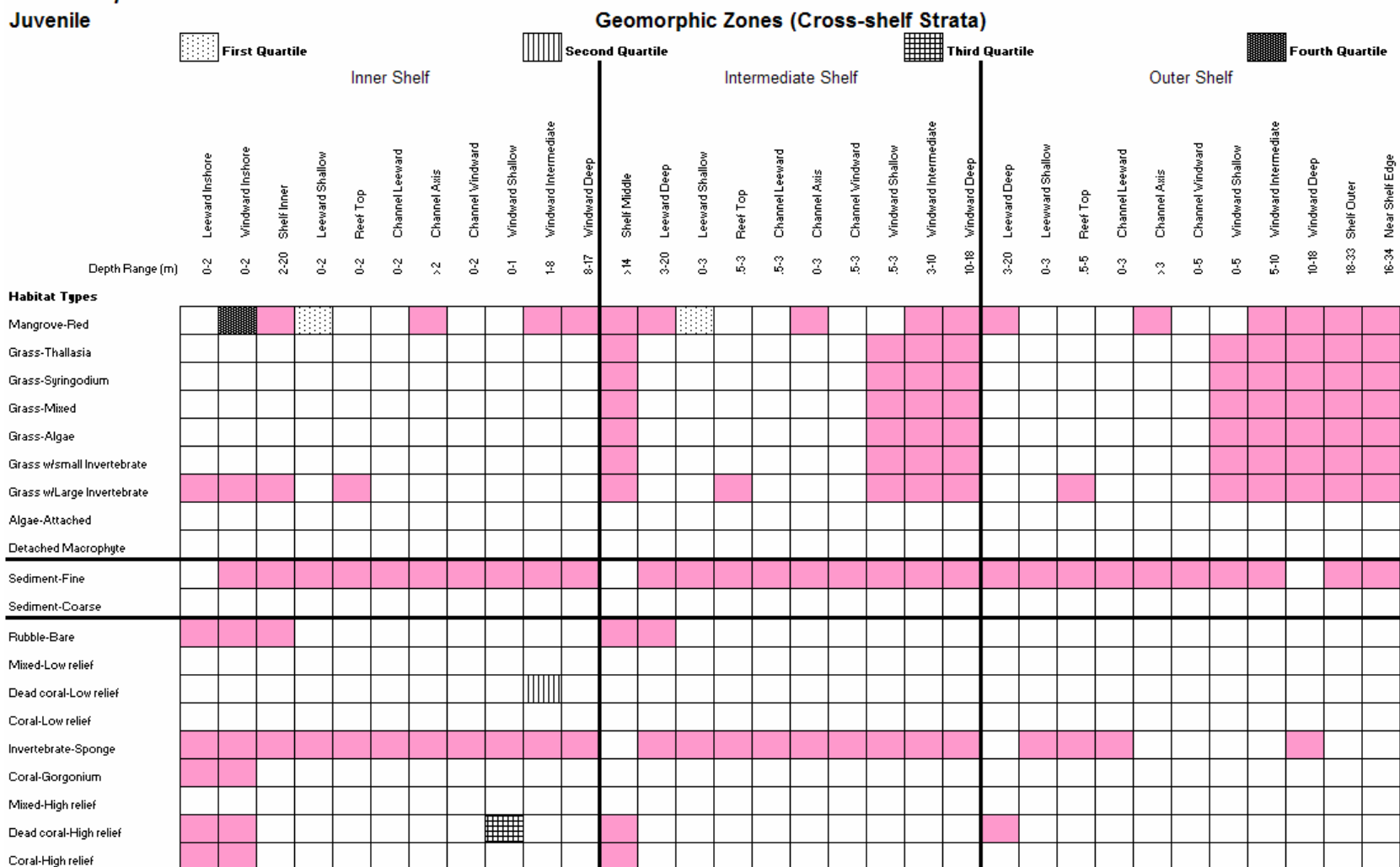


### Appendix B.12.b

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

#### *Haemulon parra*

#### Juvenile

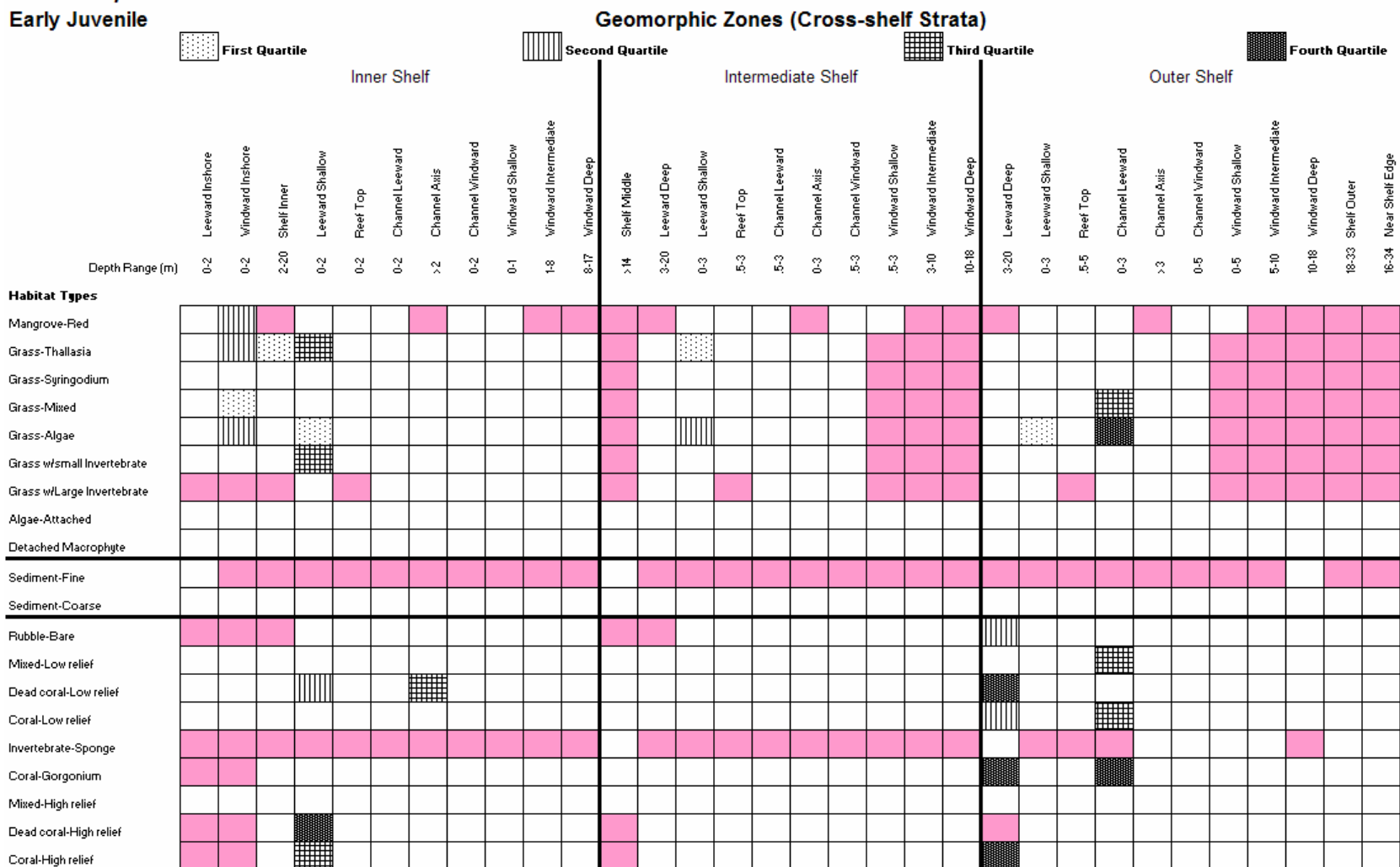


### Appendix B.13.a

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

#### *Haemulon plumieri*

#### Early Juvenile

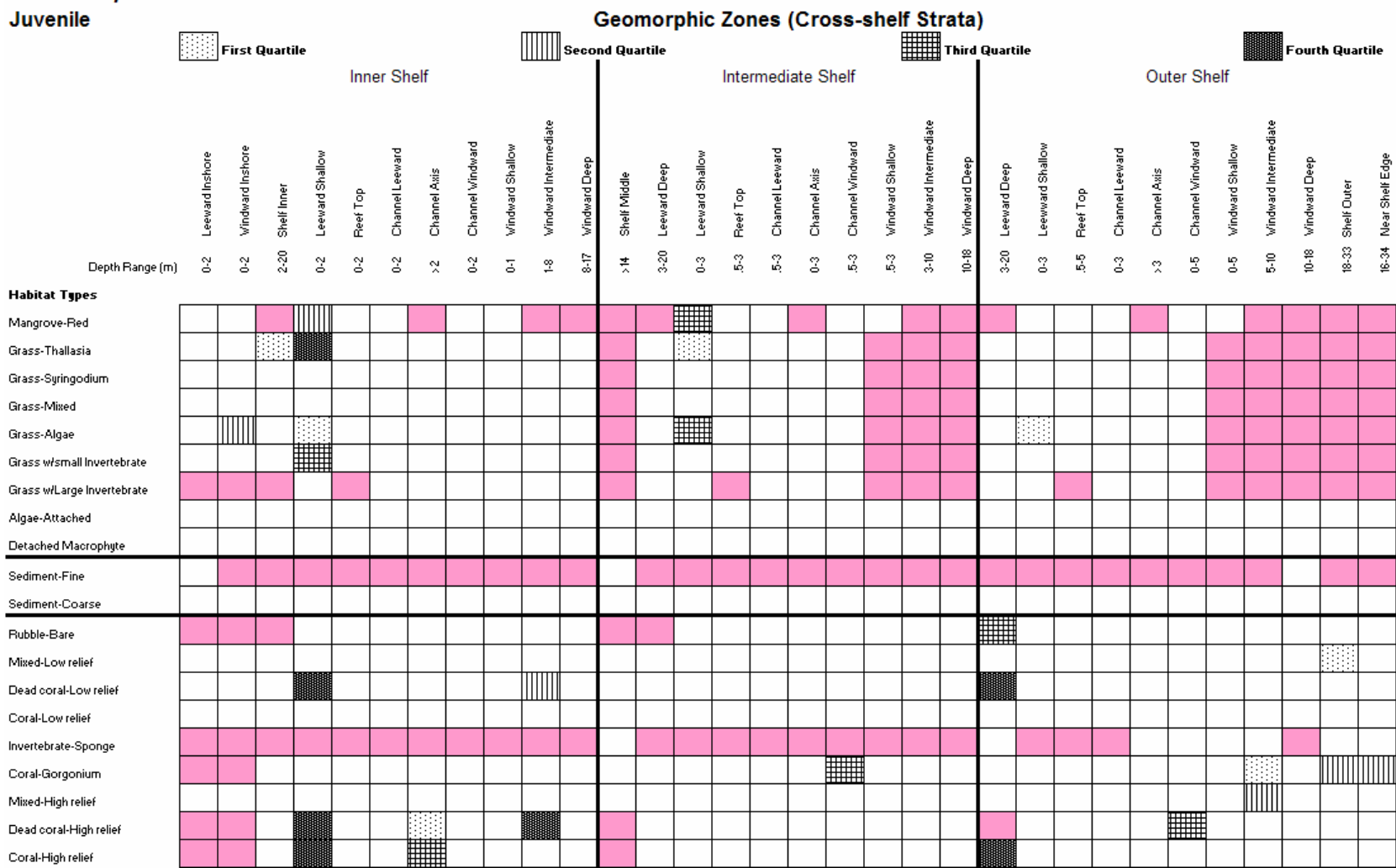


**Appendix B.13.b**

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

***Haemulon plumieri***

**Juvenile**

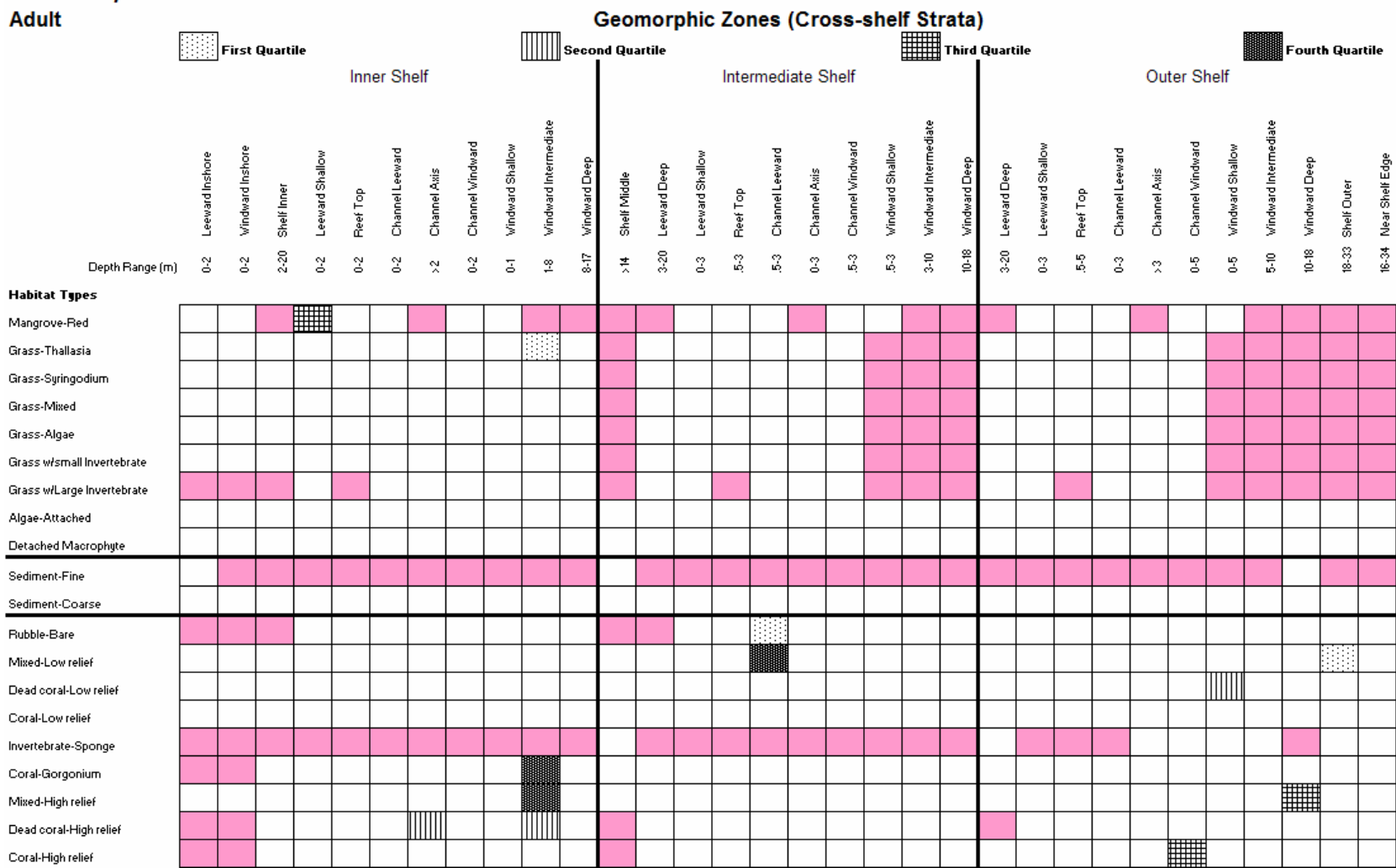


**Appendix B.13.c**

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

***Haemulon plumieri***

**Adult**

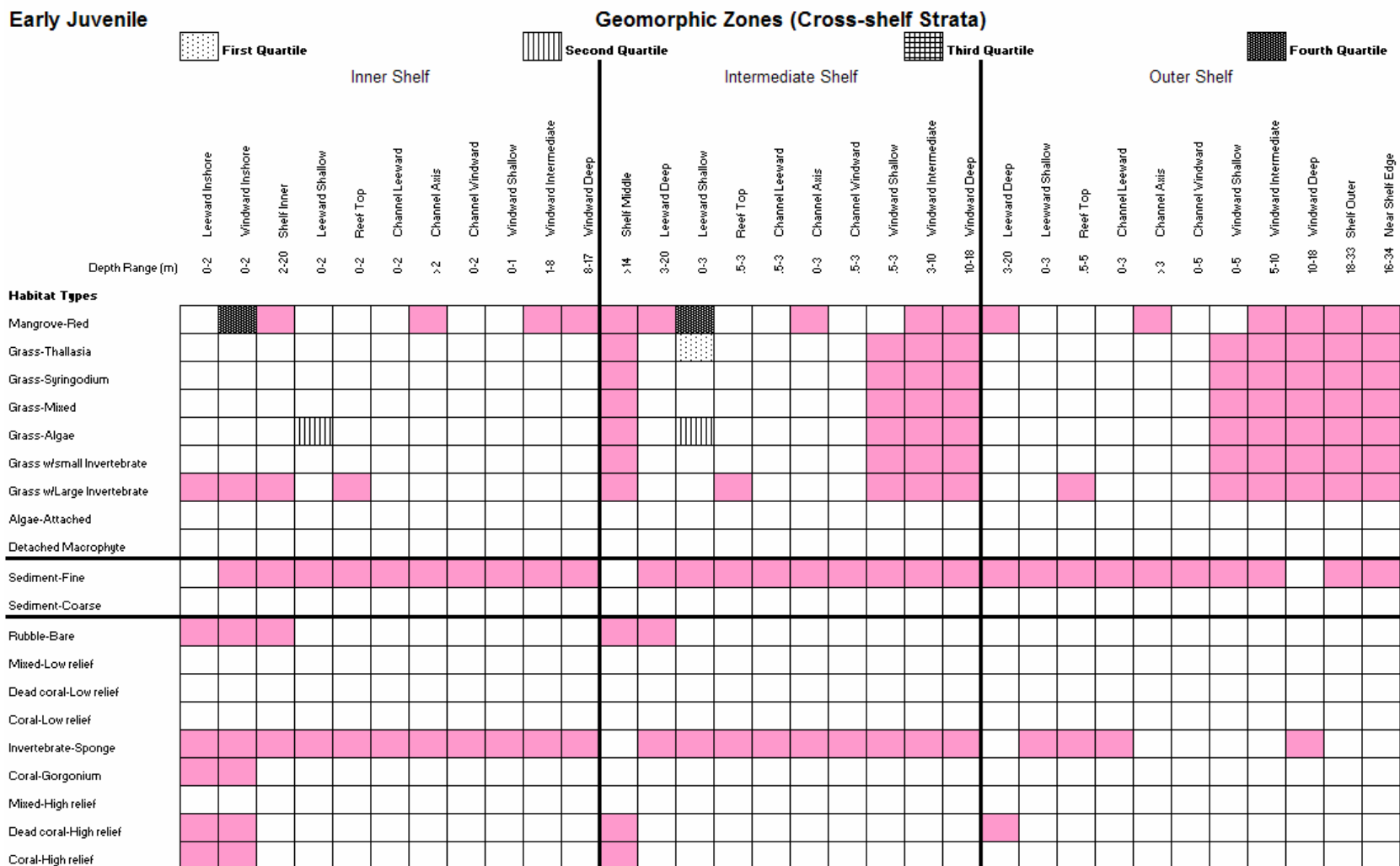


### Appendix B.14.a

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

#### *Haemulon sciurus*

#### Early Juvenile

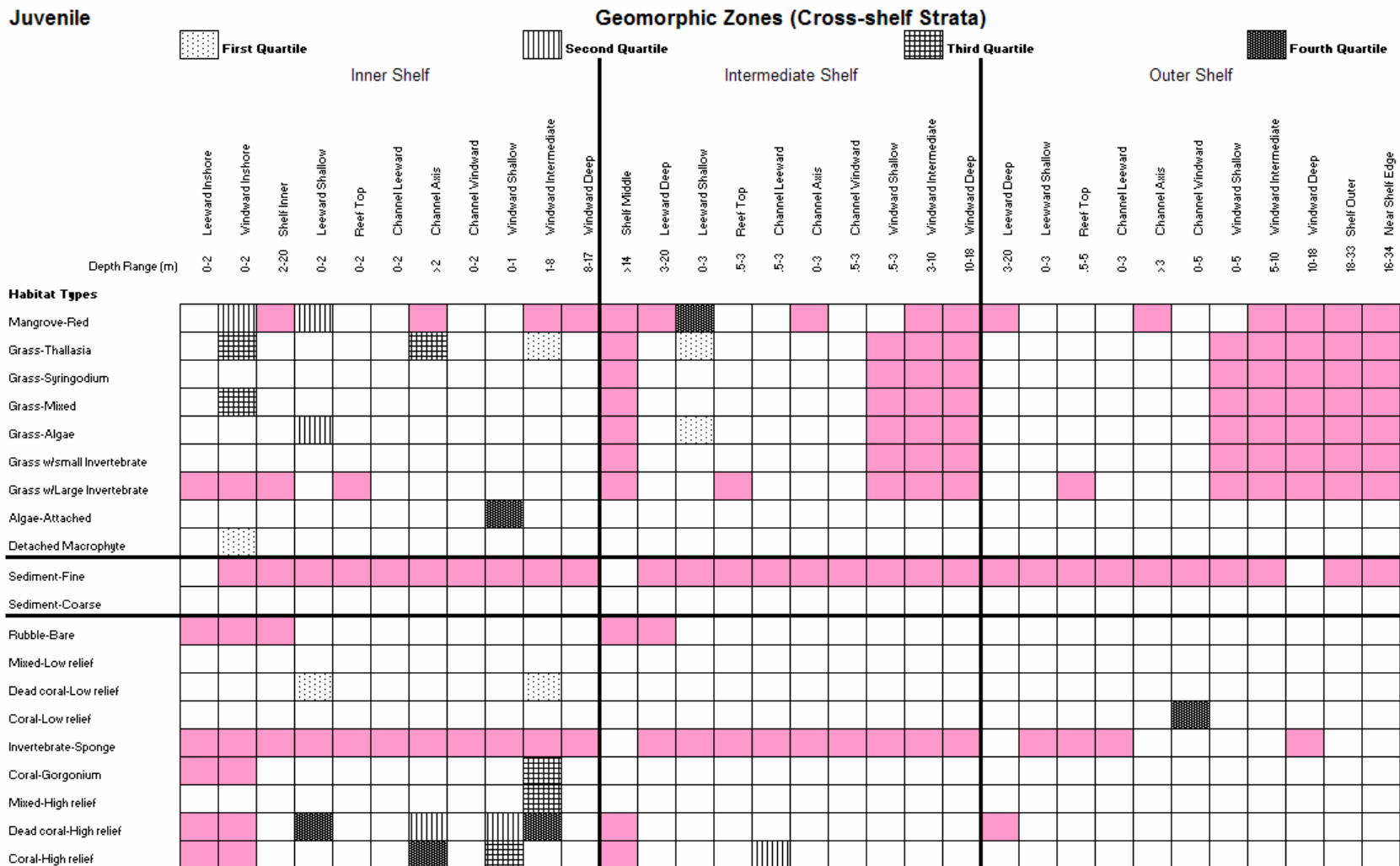


**Appendix B.14.b**

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

***Haemulon sciurus***

**Juvenile**

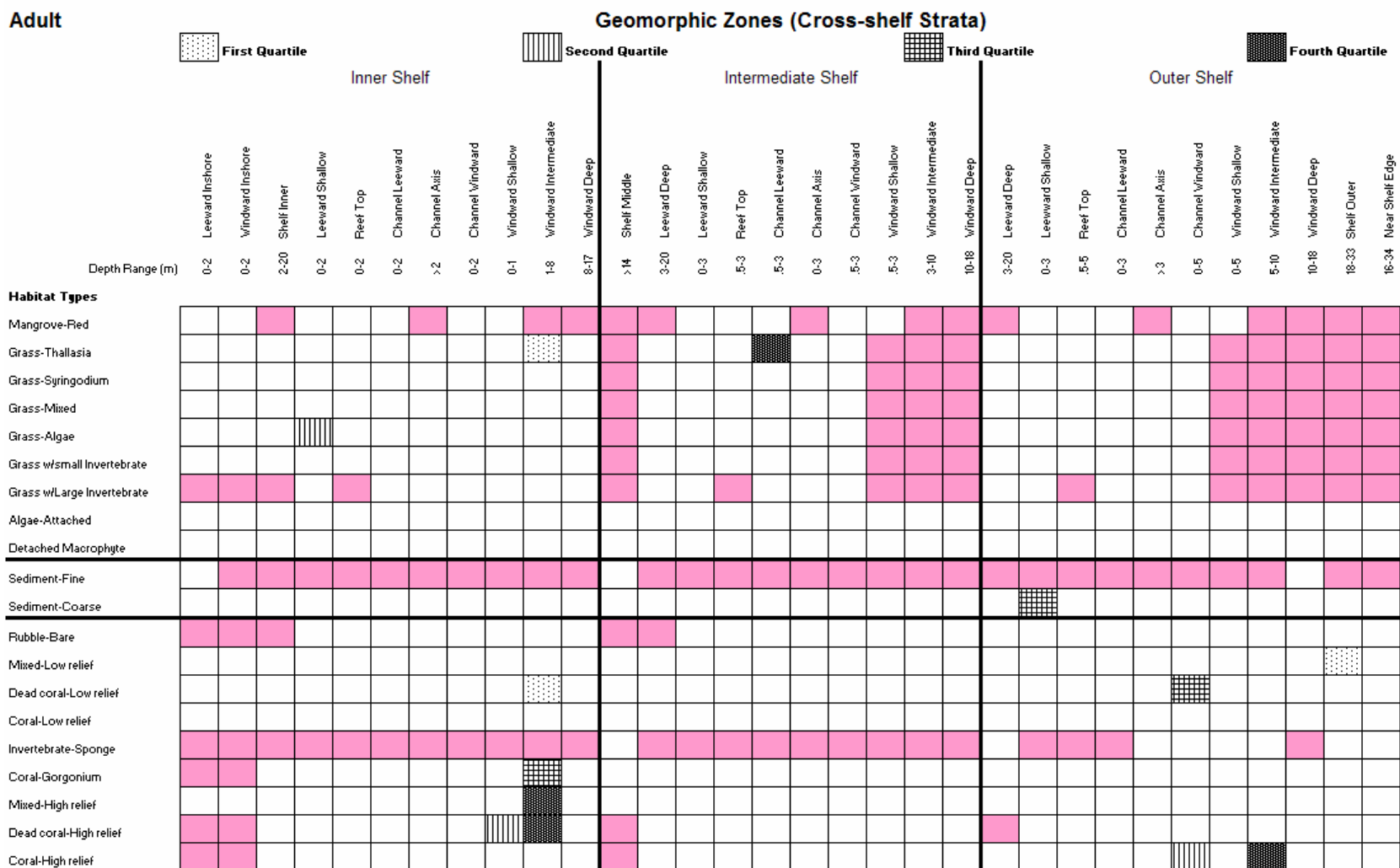


### Appendix B.14.c

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

#### *Haemulon sciurus*

#### Adult

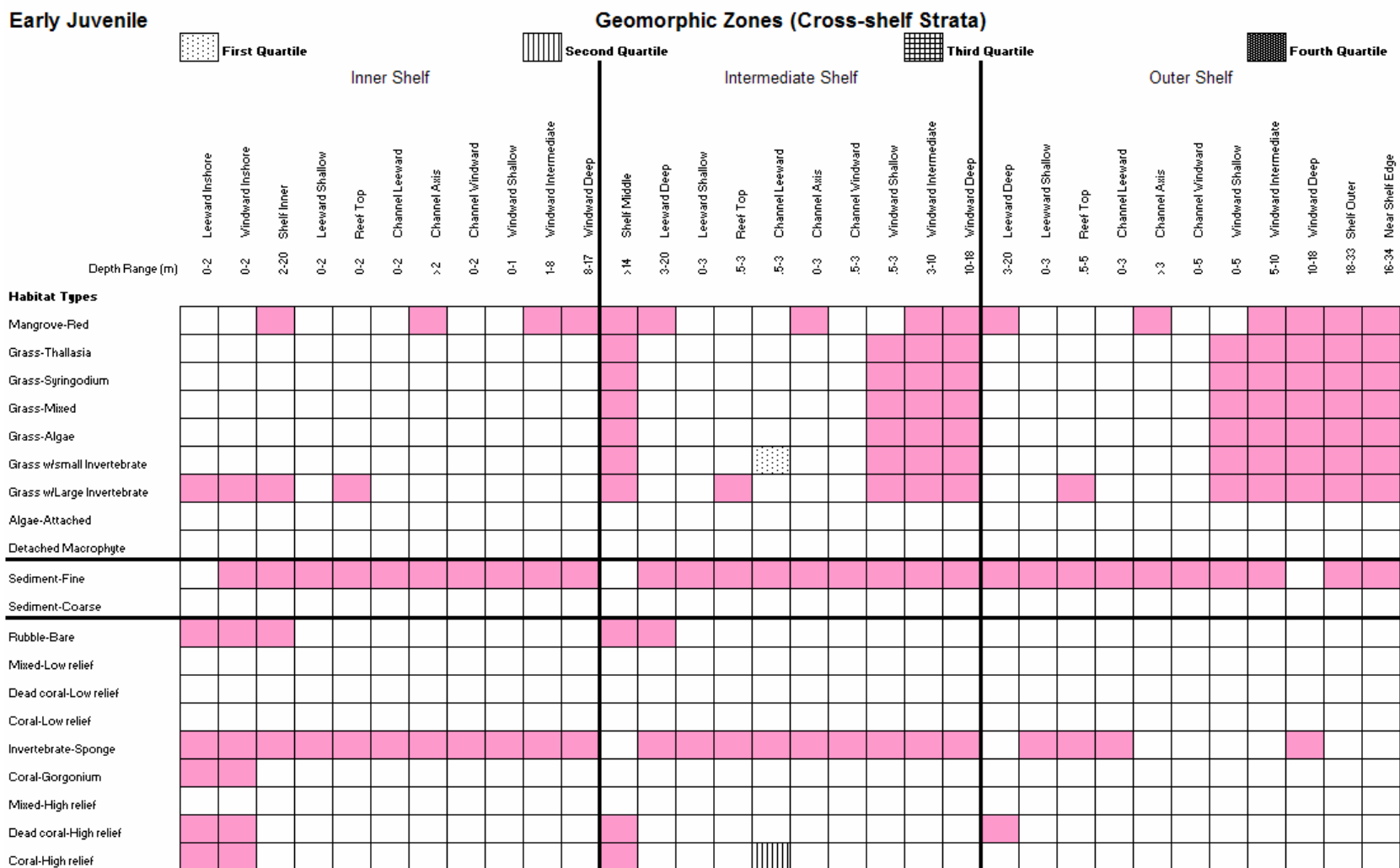


### Appendix B.15.a

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

#### *Haemulon striatum*

#### Early Juvenile



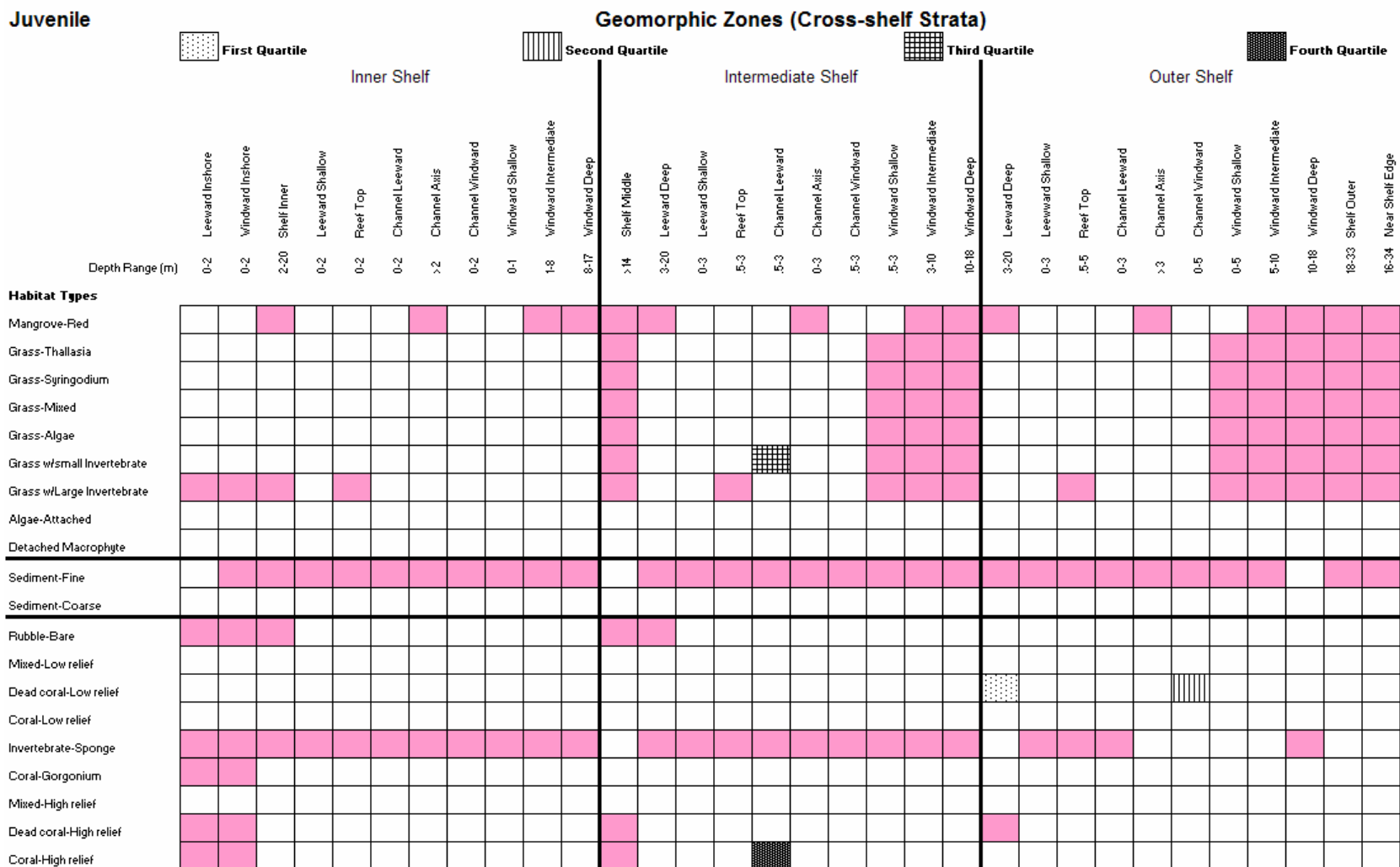


**Appendix B.15.b**

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

***Haemulon striatum***

**Juvenile**

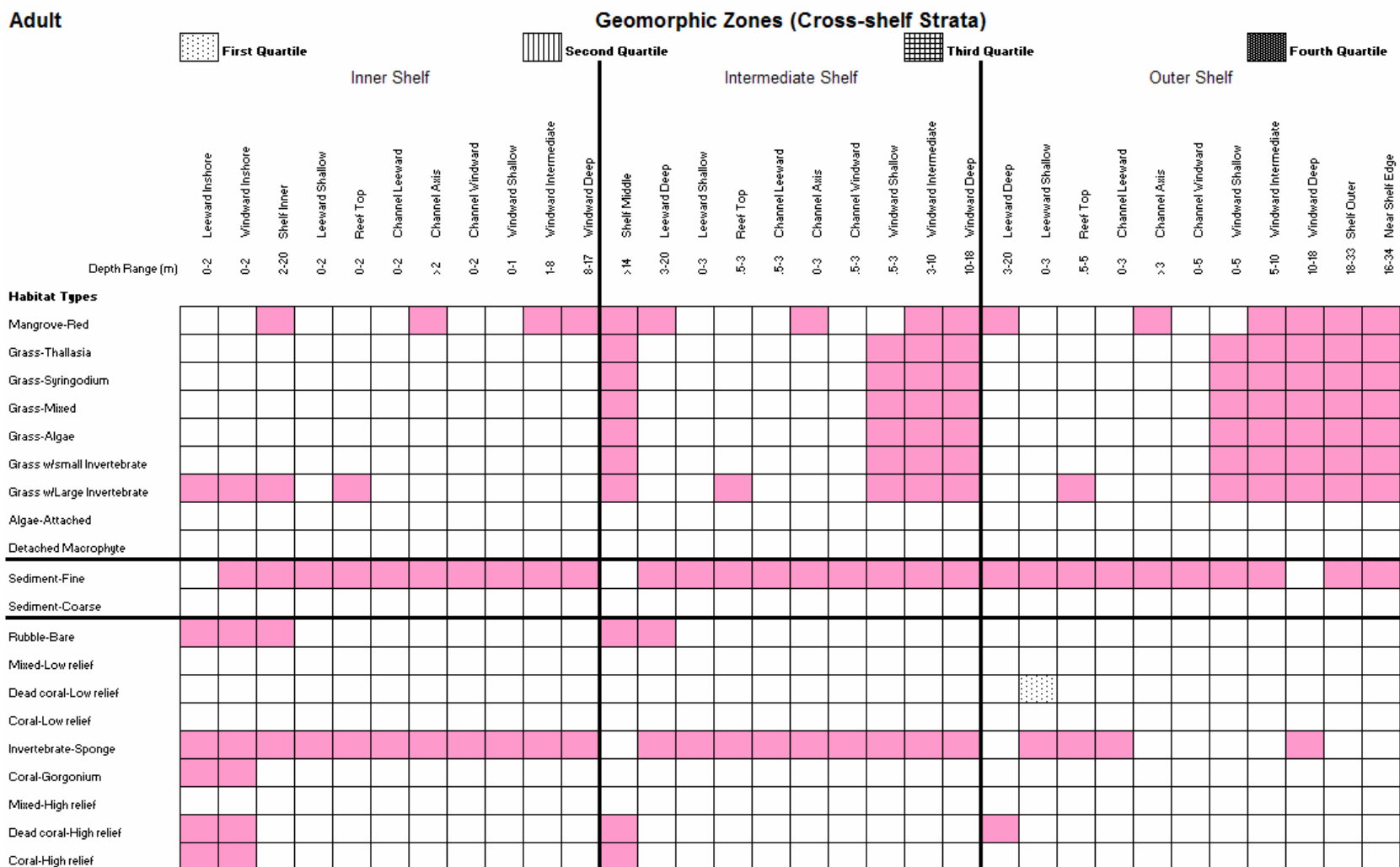


**Appendix B.15.c**

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

***Haemulon striatum***

**Adult**

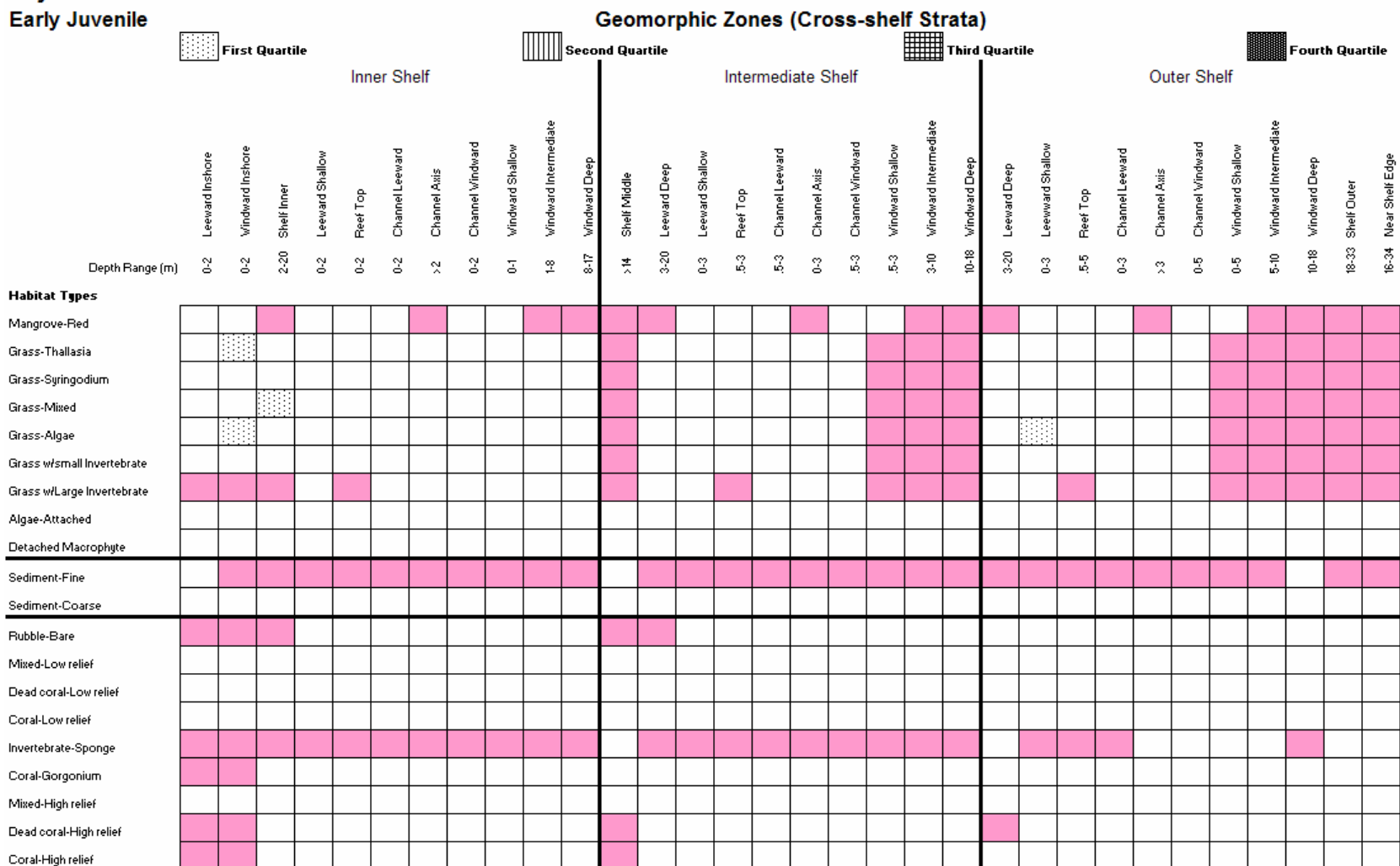


**Appendix B.16.a**

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

***Lutjanus analis***

**Early Juvenile**

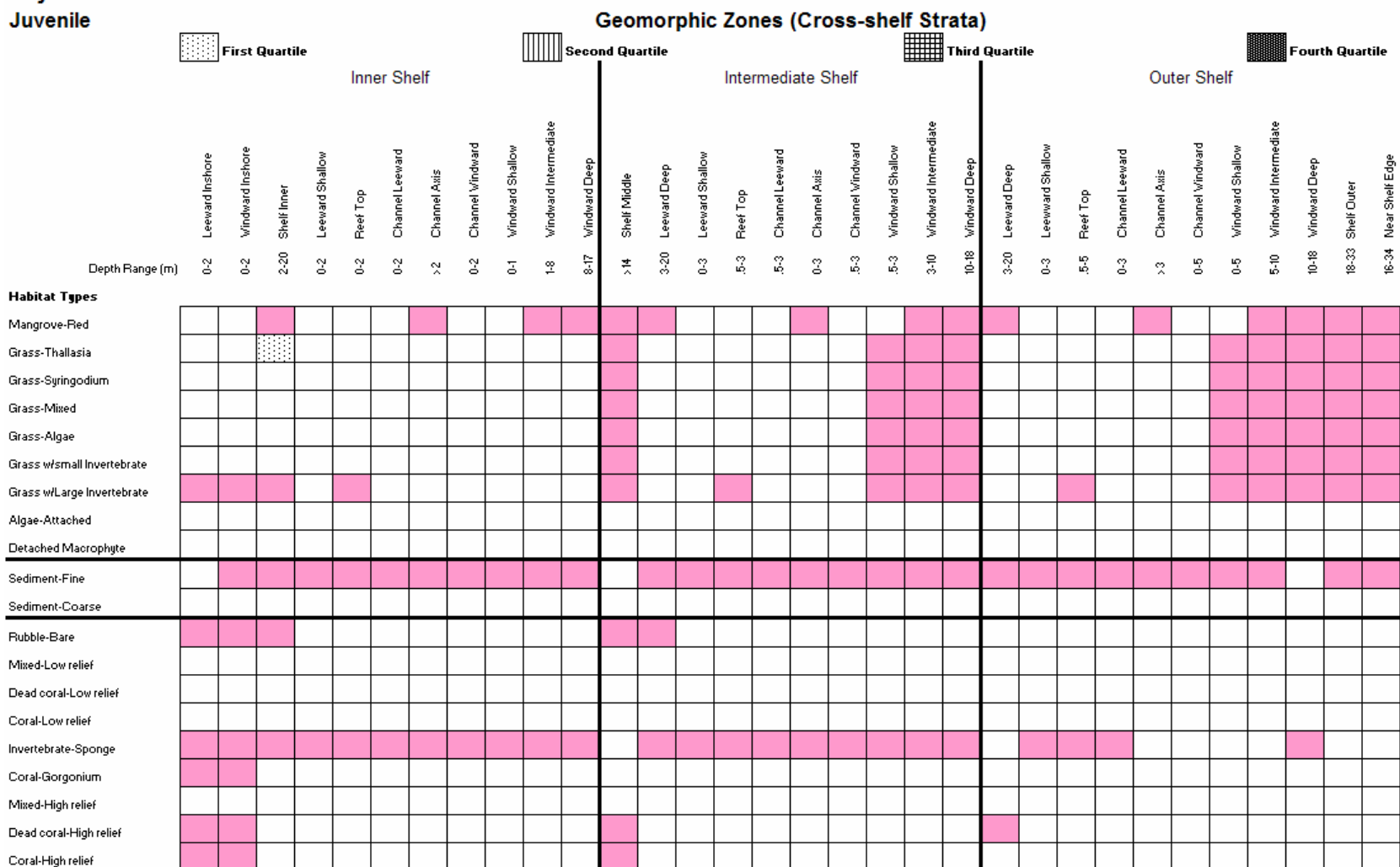


**Appendix B.16.b**

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

***Lutjanus analis***

**Juvenile**

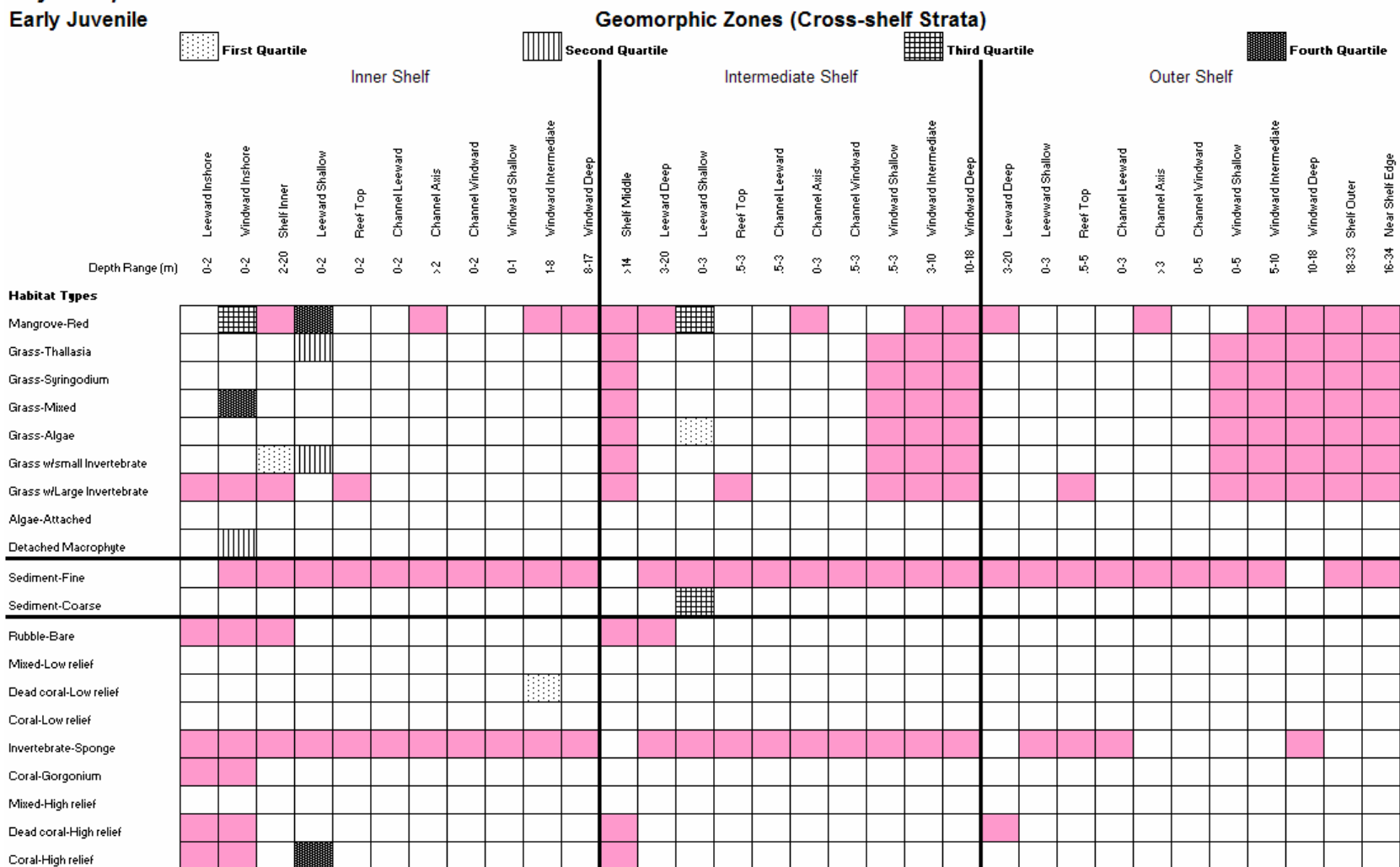


**Appendix B.17.a**

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

***Lutjanus apodus***

**Early Juvenile**

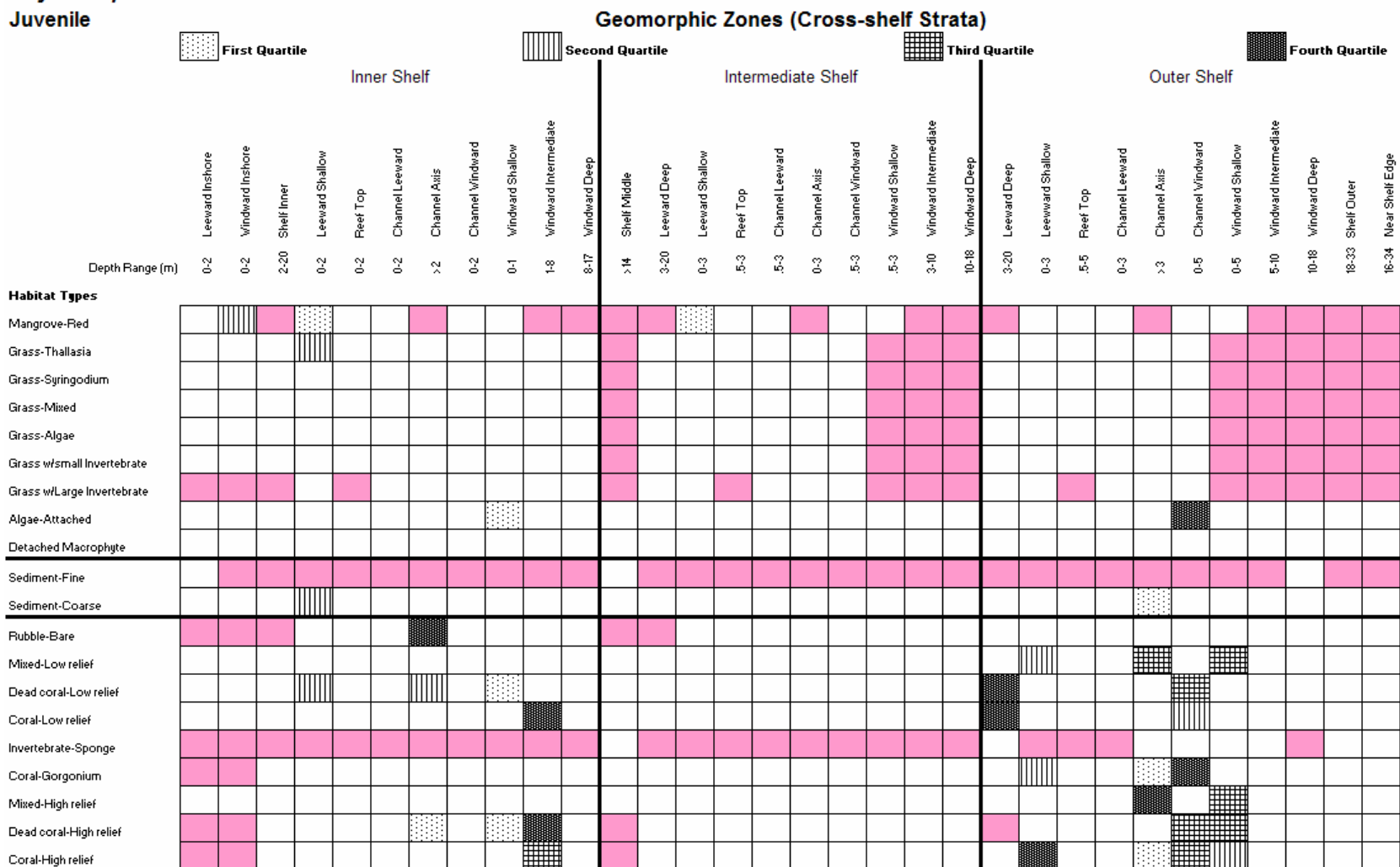


### Appendix B.17.b

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

#### *Lutjanus apodus*

#### Juvenile

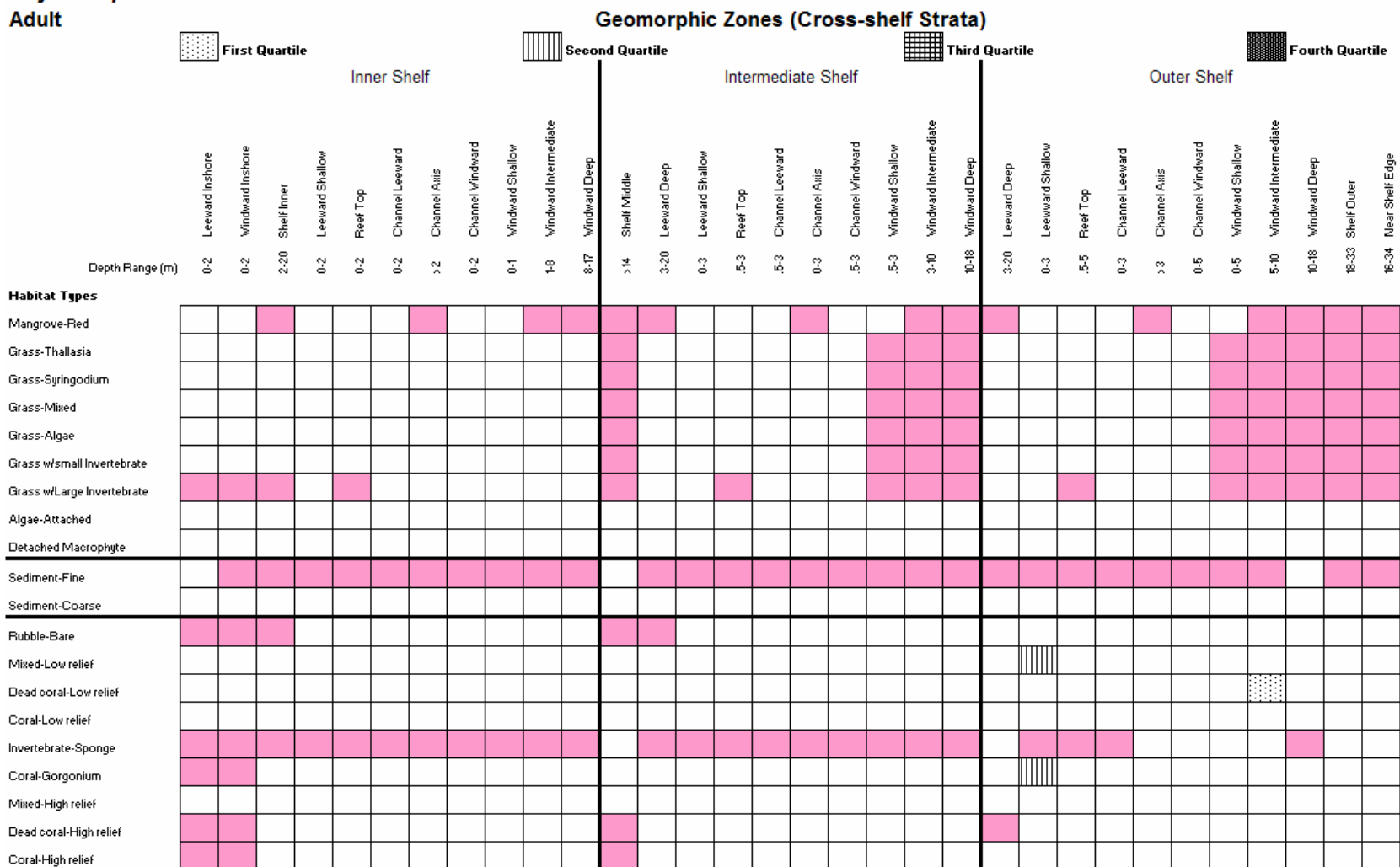


**Appendix B.17.c**

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

***Lutjanus apodus***

**Adult**

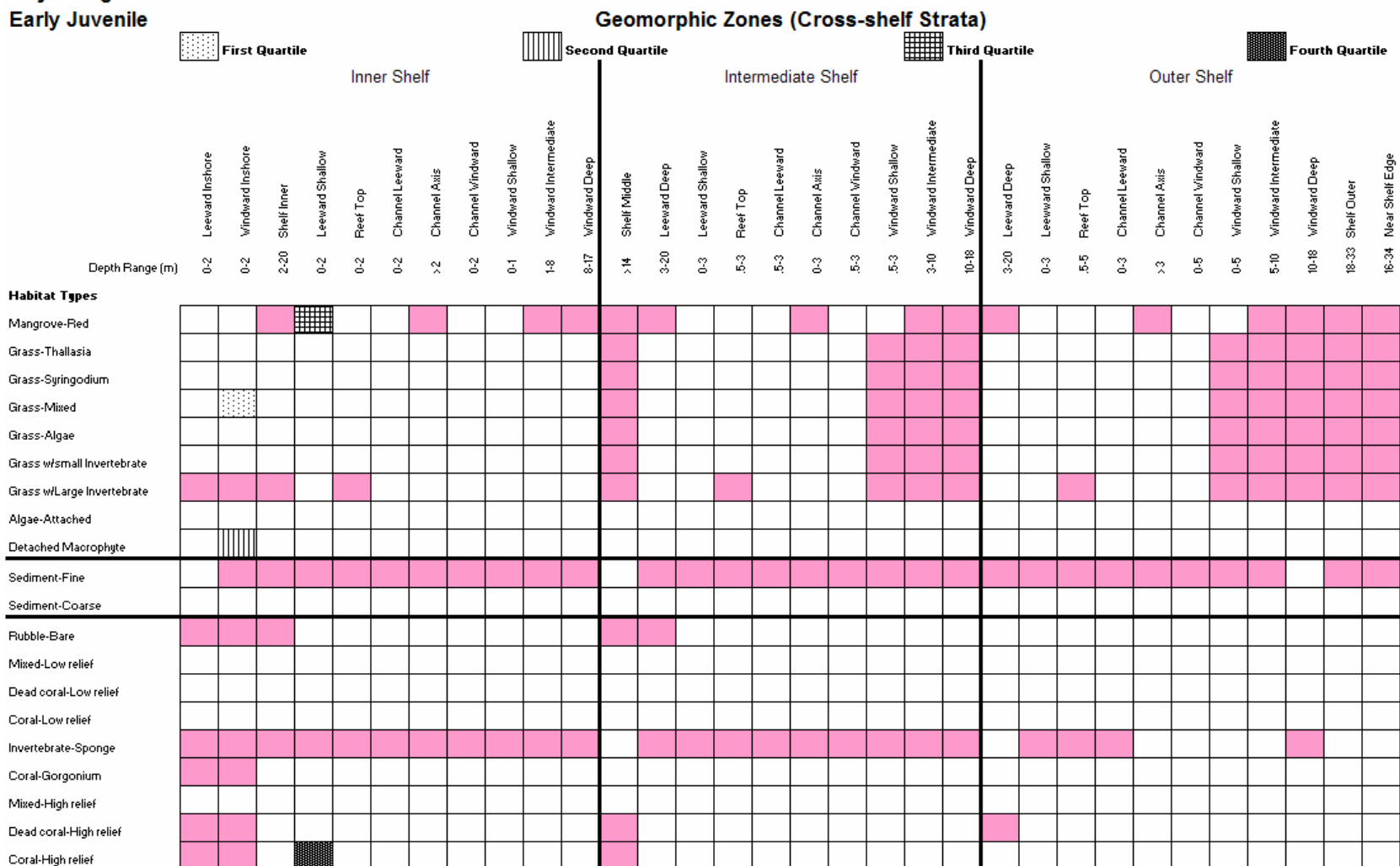


### Appendix B.18.a

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

#### *Lutjanus griseus*

#### Early Juvenile



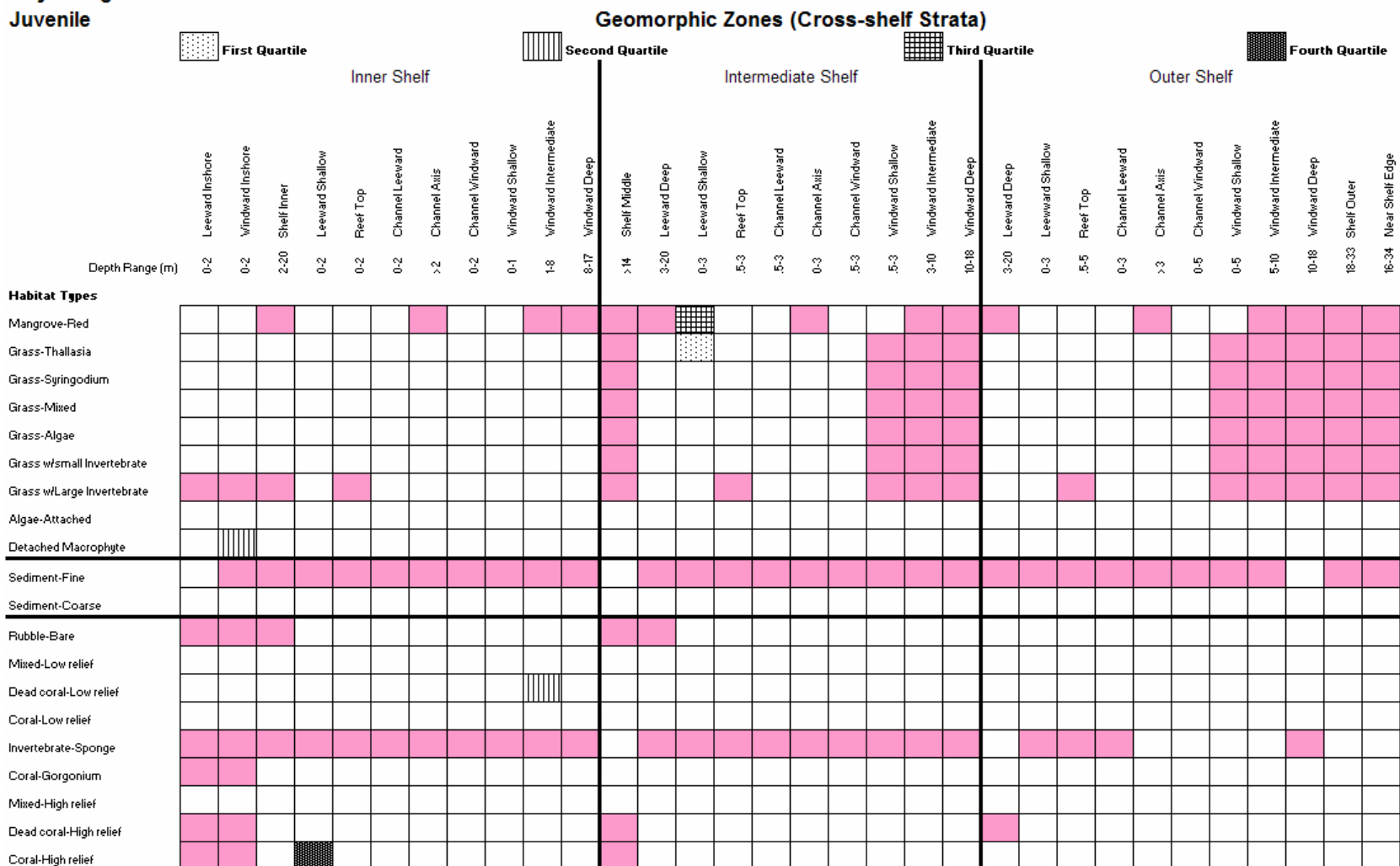


### Appendix B.18.b

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

#### *Lutjanus griseus*

#### Juvenile

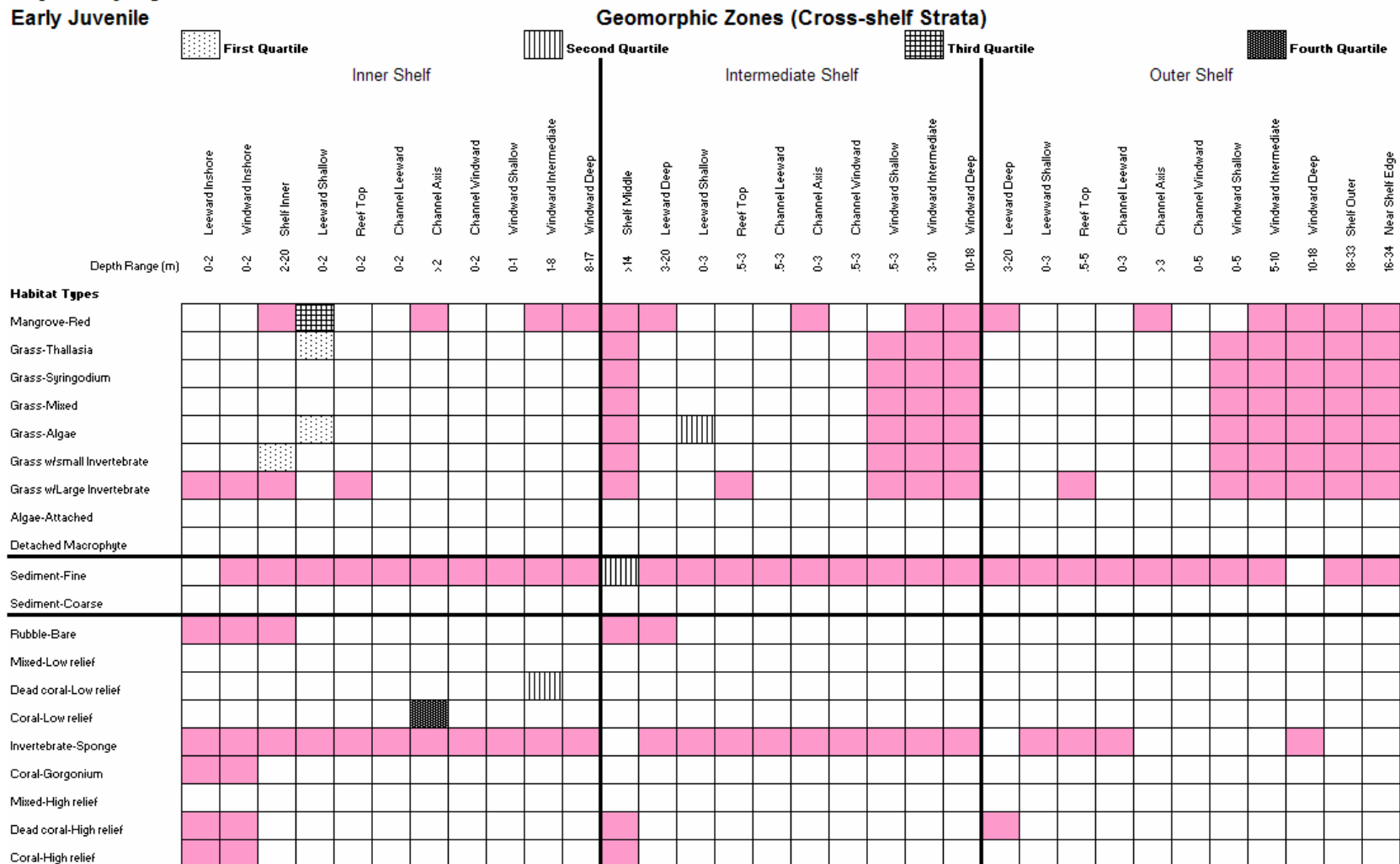


**Appendix B.19.a**

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

***Lutjanus synagris***

**Early Juvenile**

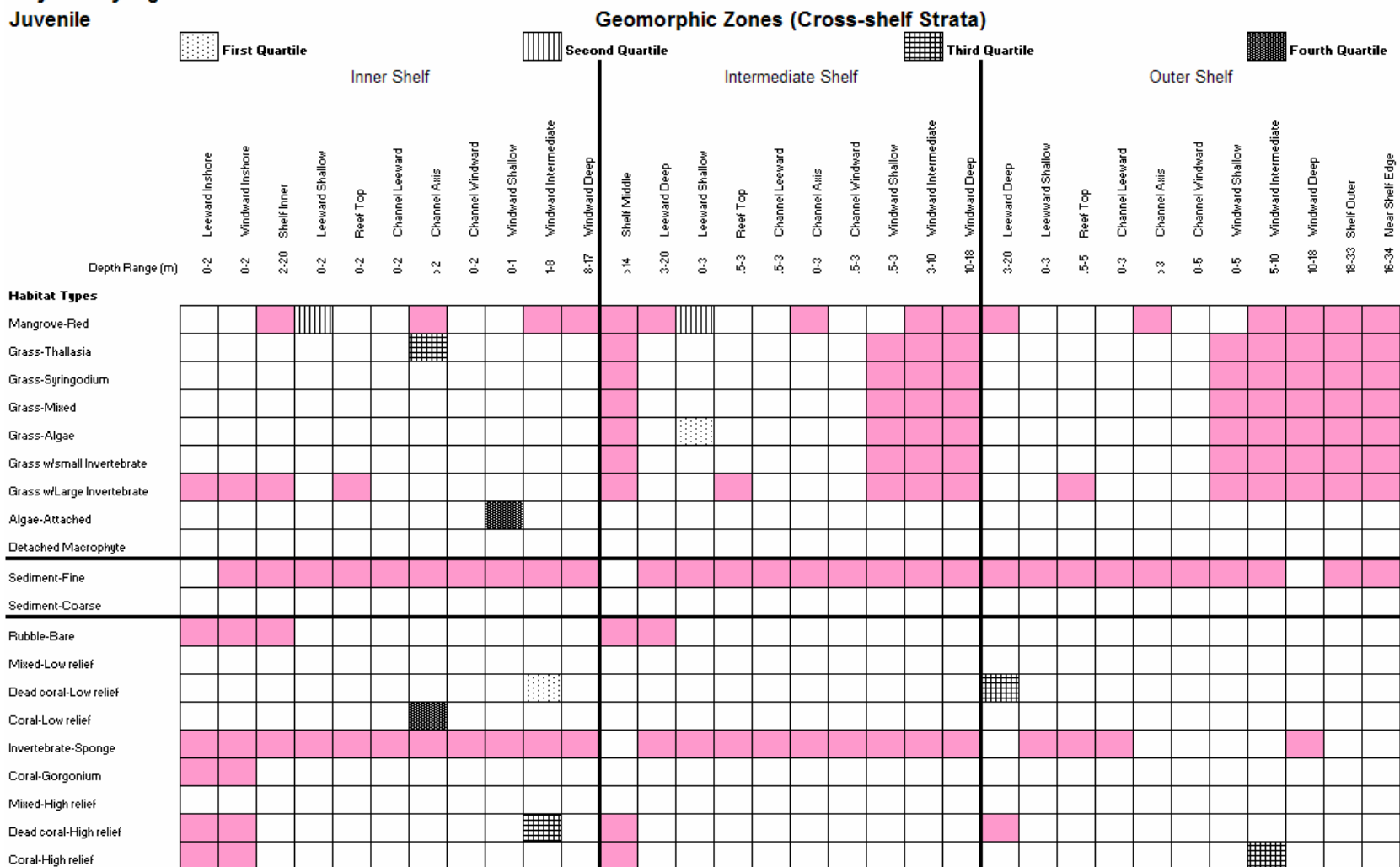


### Appendix B.19.b

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

#### *Lutjanus synagris*

#### Juvenile

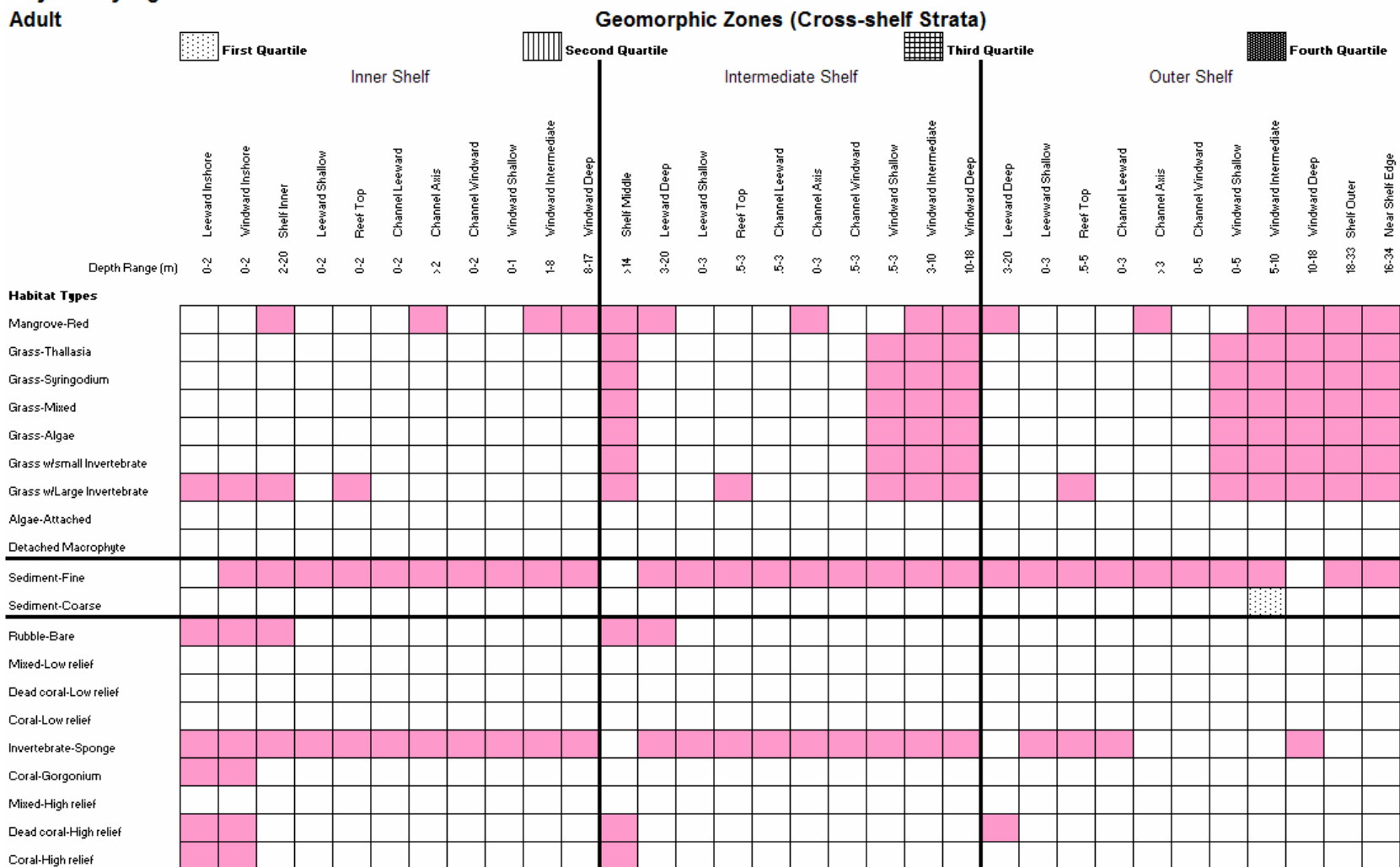


**Appendix B.19.c**

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

***Lutjanus synagris***

**Adult**

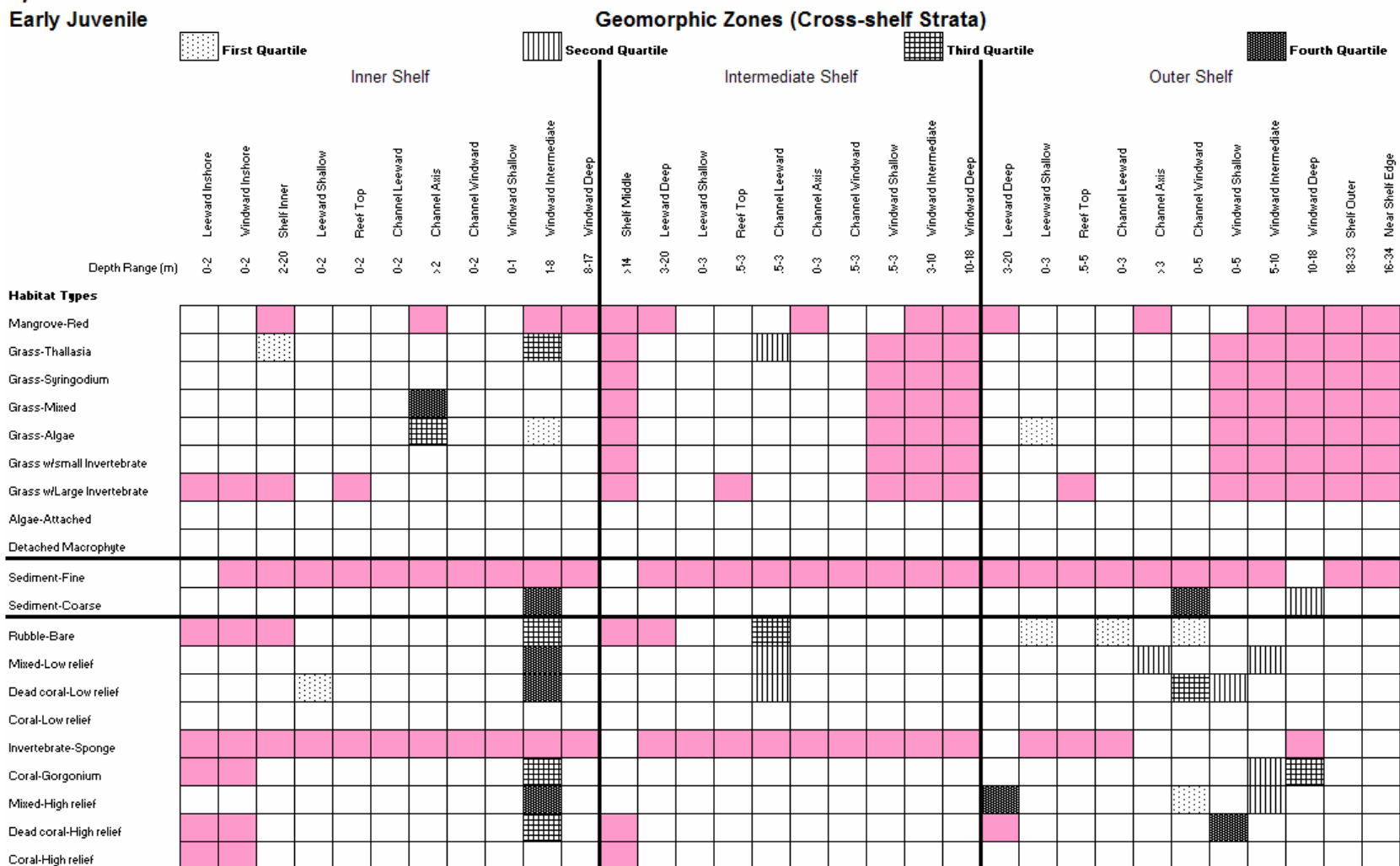


### Appendix B.20.a

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

#### *Sparisoma aurofrenatum*

#### Early Juvenile

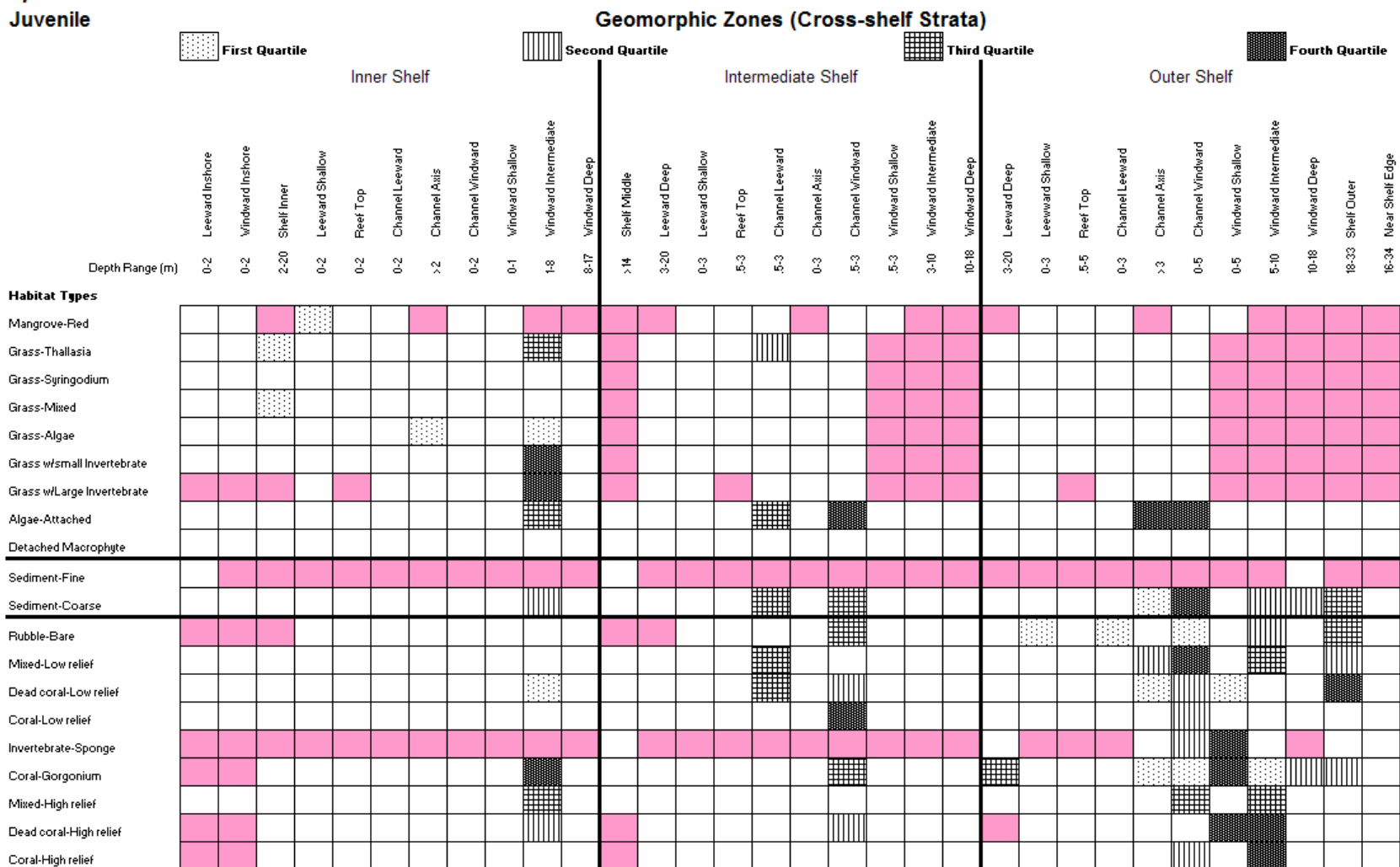


**Appendix B.20.b**

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

***Sparisoma aurofrenatum***

**Juvenile**

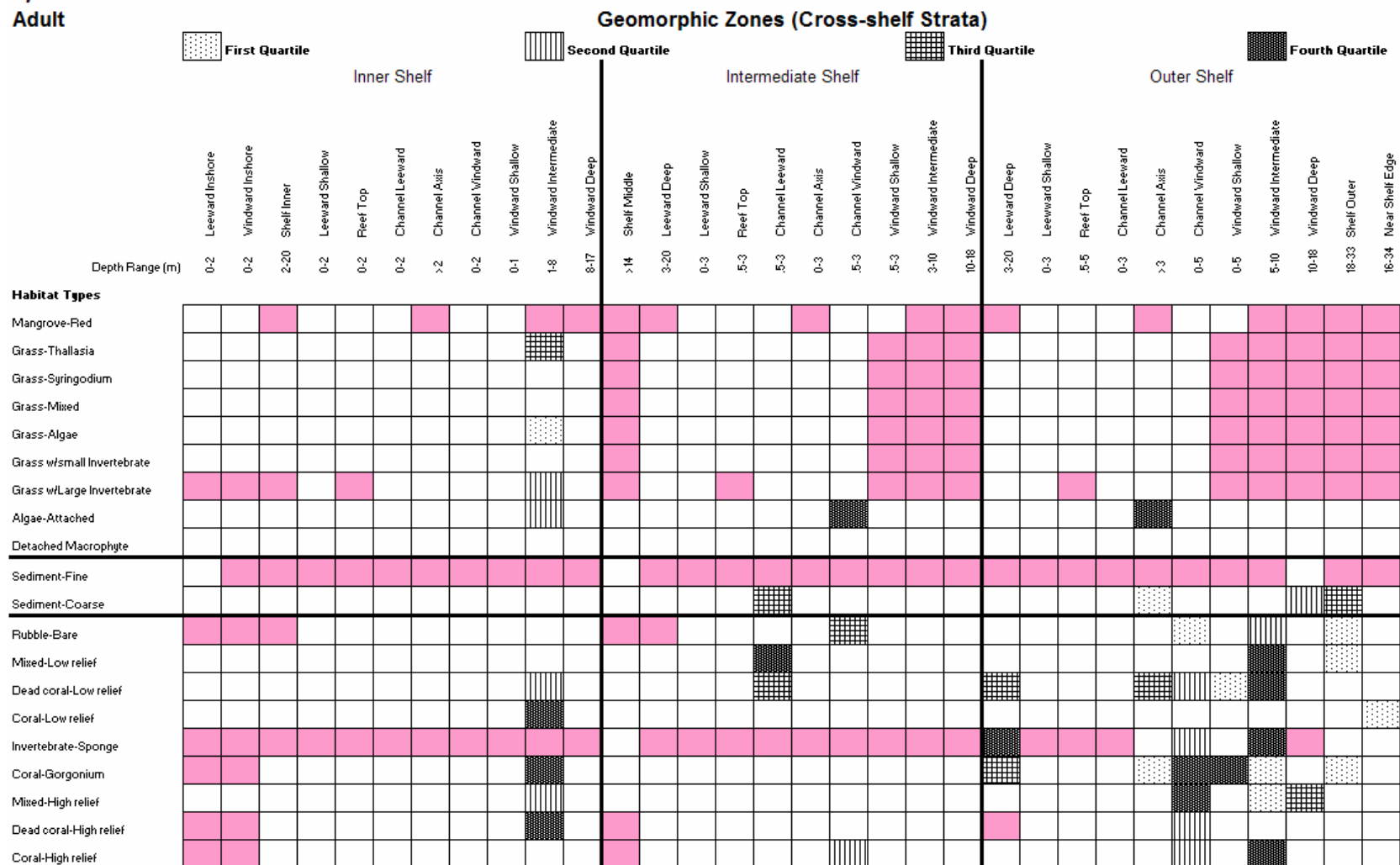


### Appendix B.20.c

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

### *Sparisoma aurofrenatum*

Adult

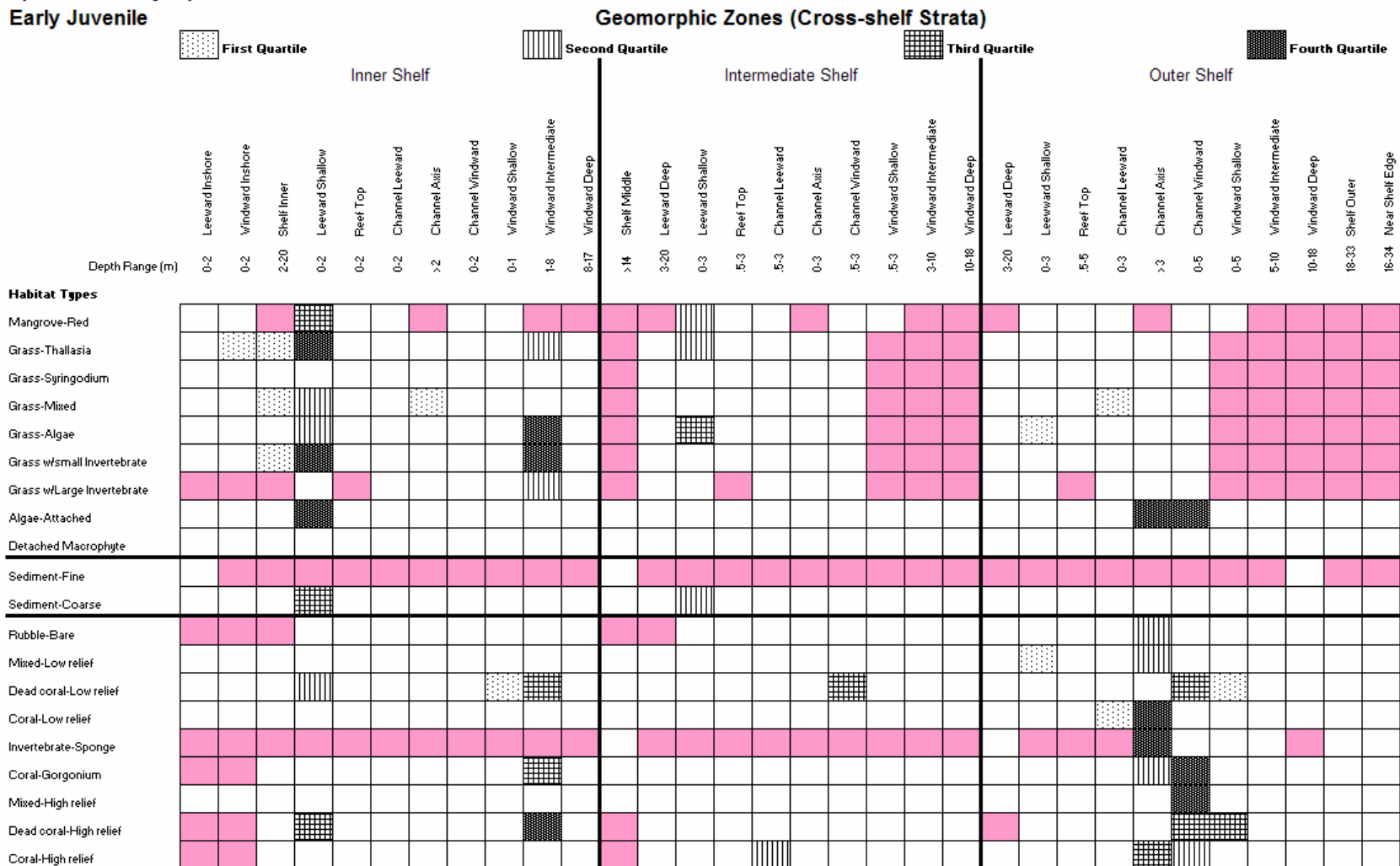


**Appendix B.21.a**

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

***Sparisoma chrysopterum***

**Early Juvenile**



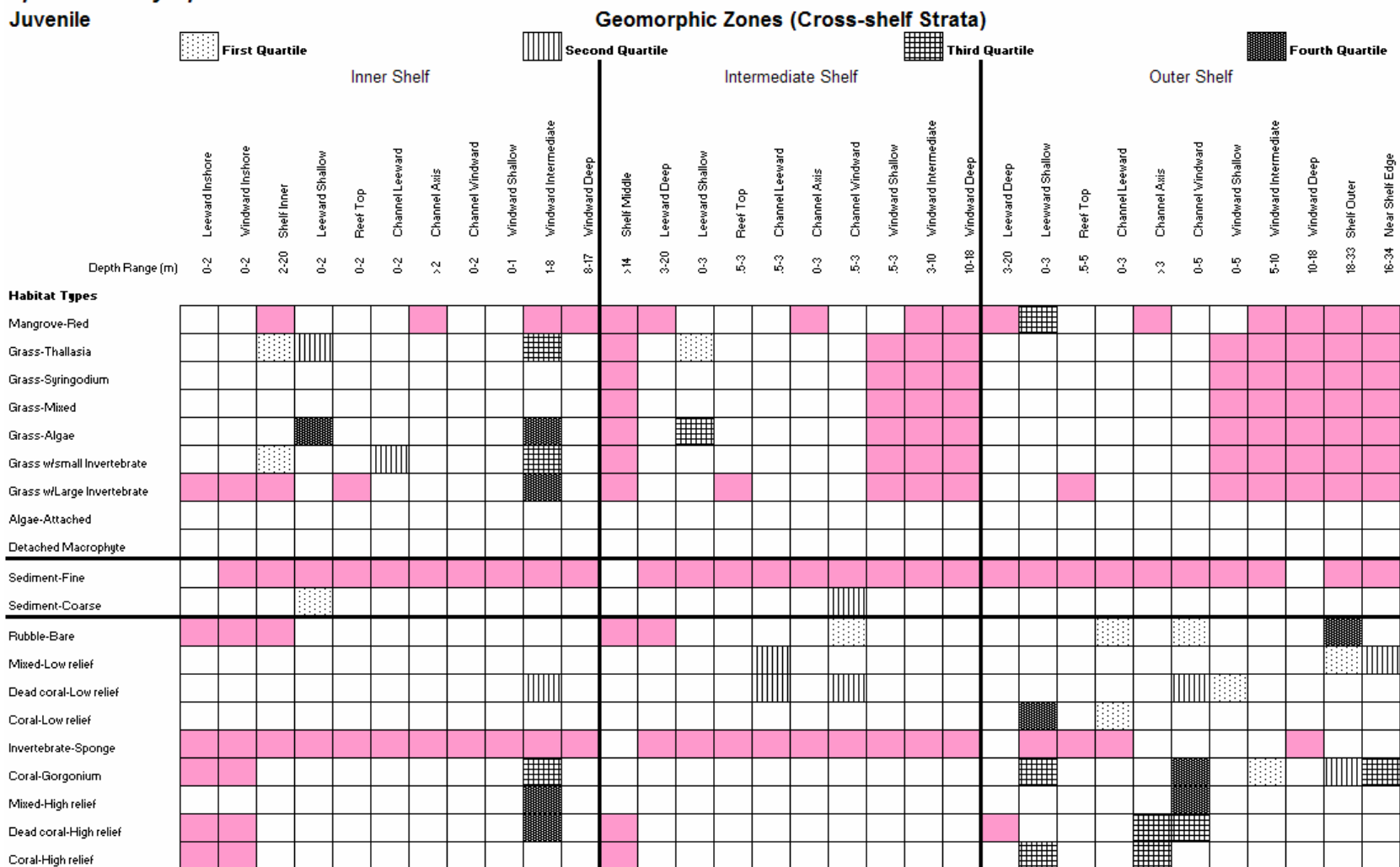


**Appendix B.21.b**

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

***Sparisoma chrysopterus***

**Juvenile**

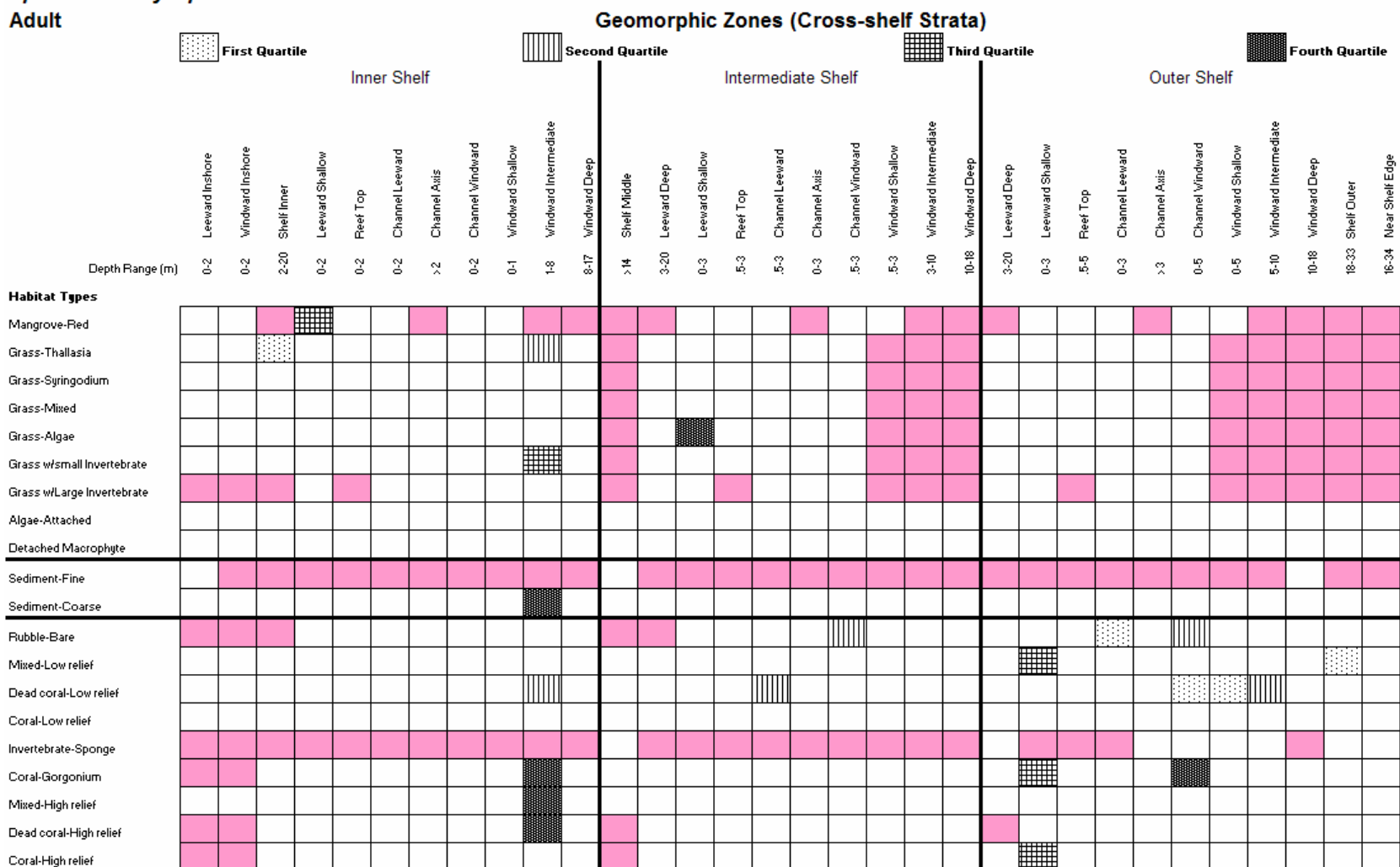


### Appendix B.21.c

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

### *Sparisoma chrysopterum*

Adult

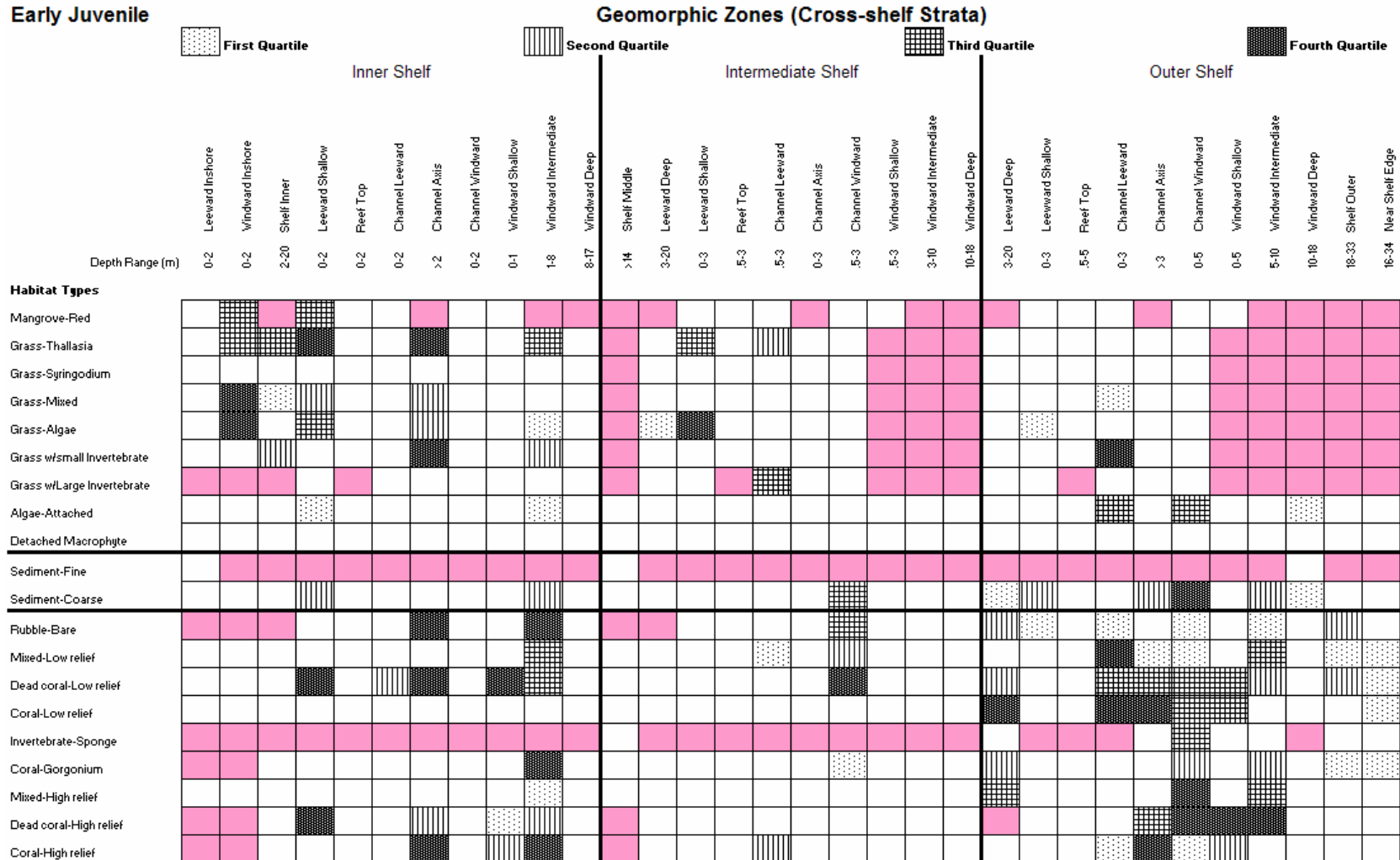


### Appendix B.22.a

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

#### *Sparisoma iseri*

#### Early Juvenile

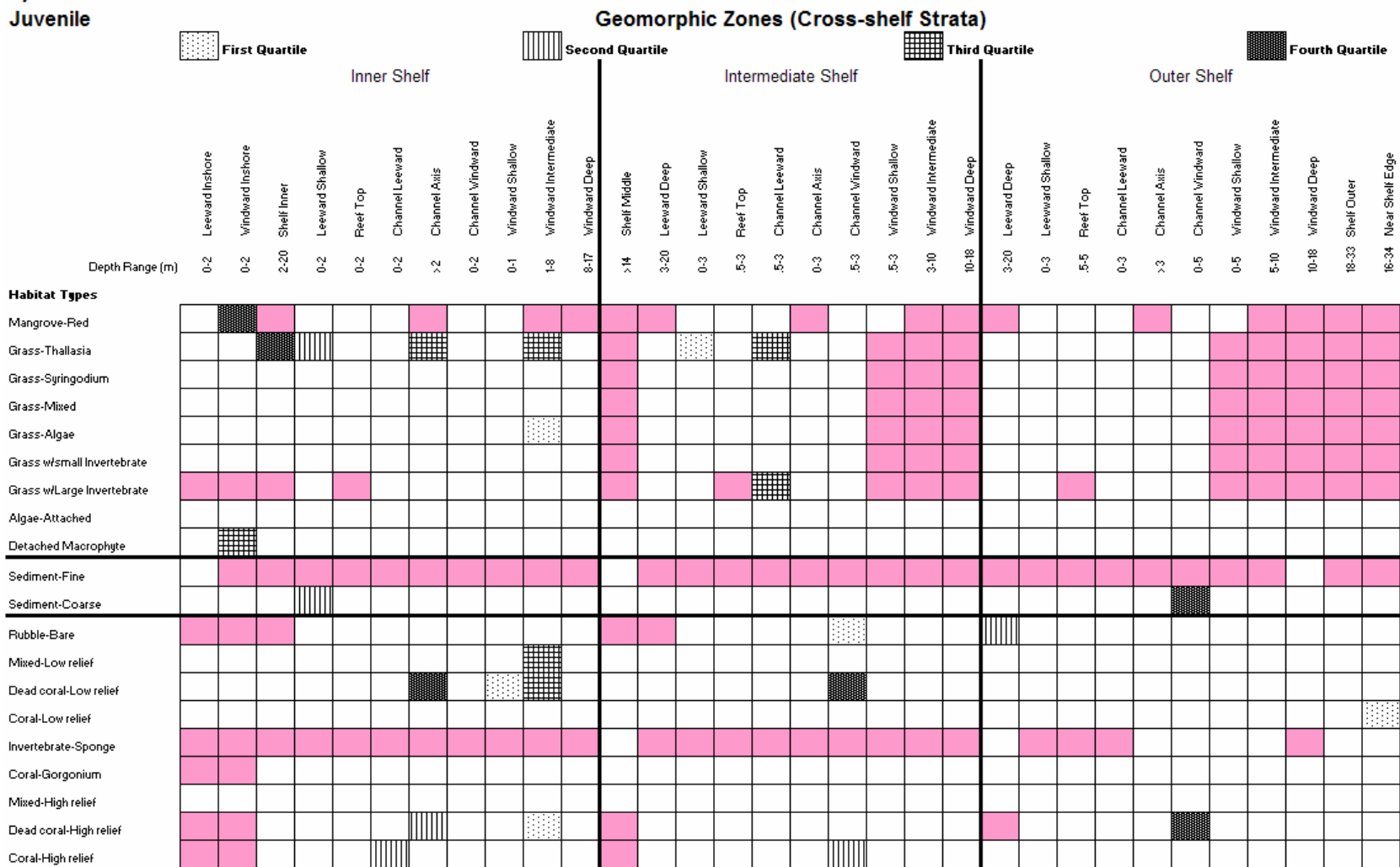


**Appendix B.22.b**

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

***Sparisoma iseri***

**Juvenile**

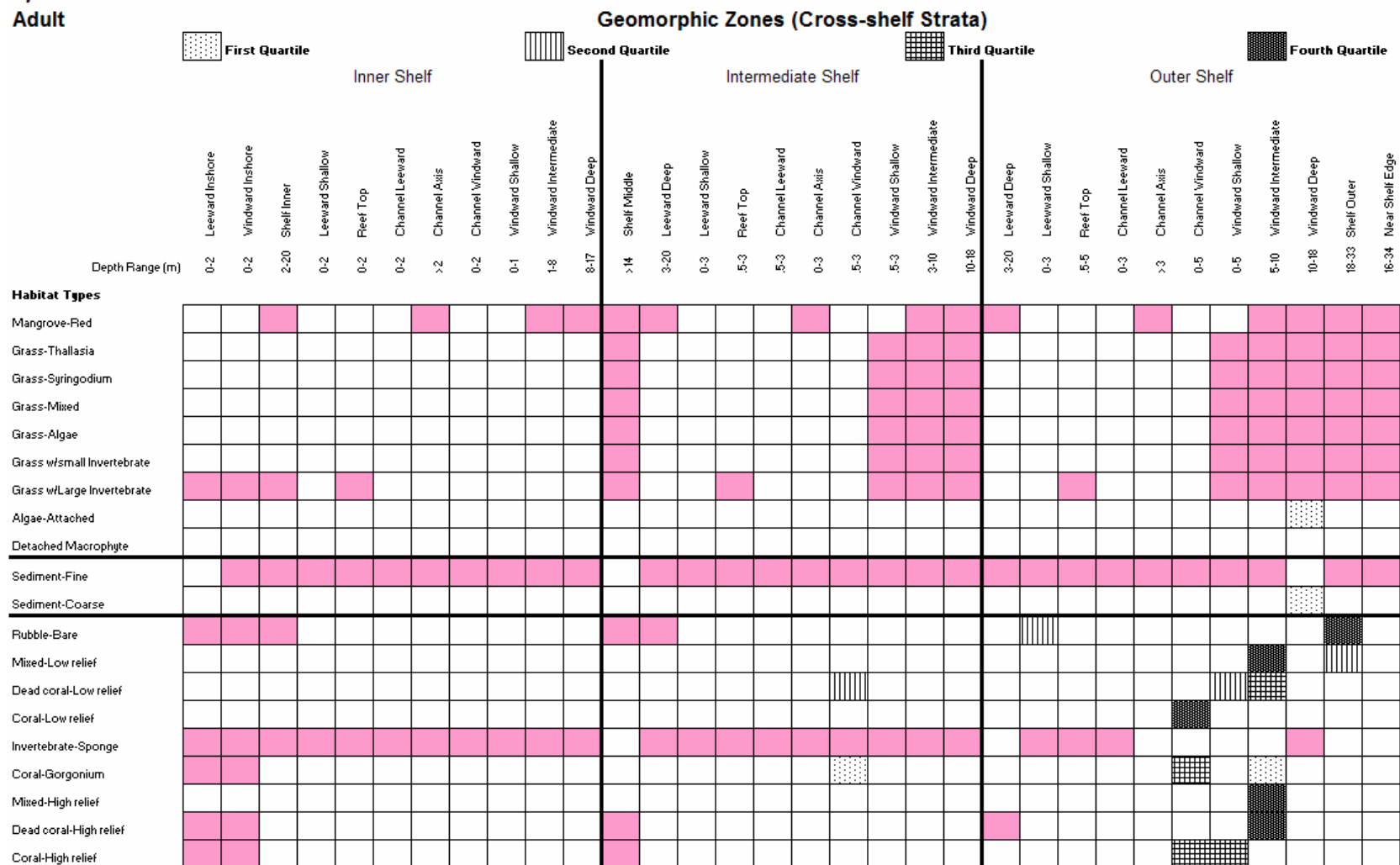


### Appendix B.22.c

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

#### *Sparisoma iseri*

#### Adult

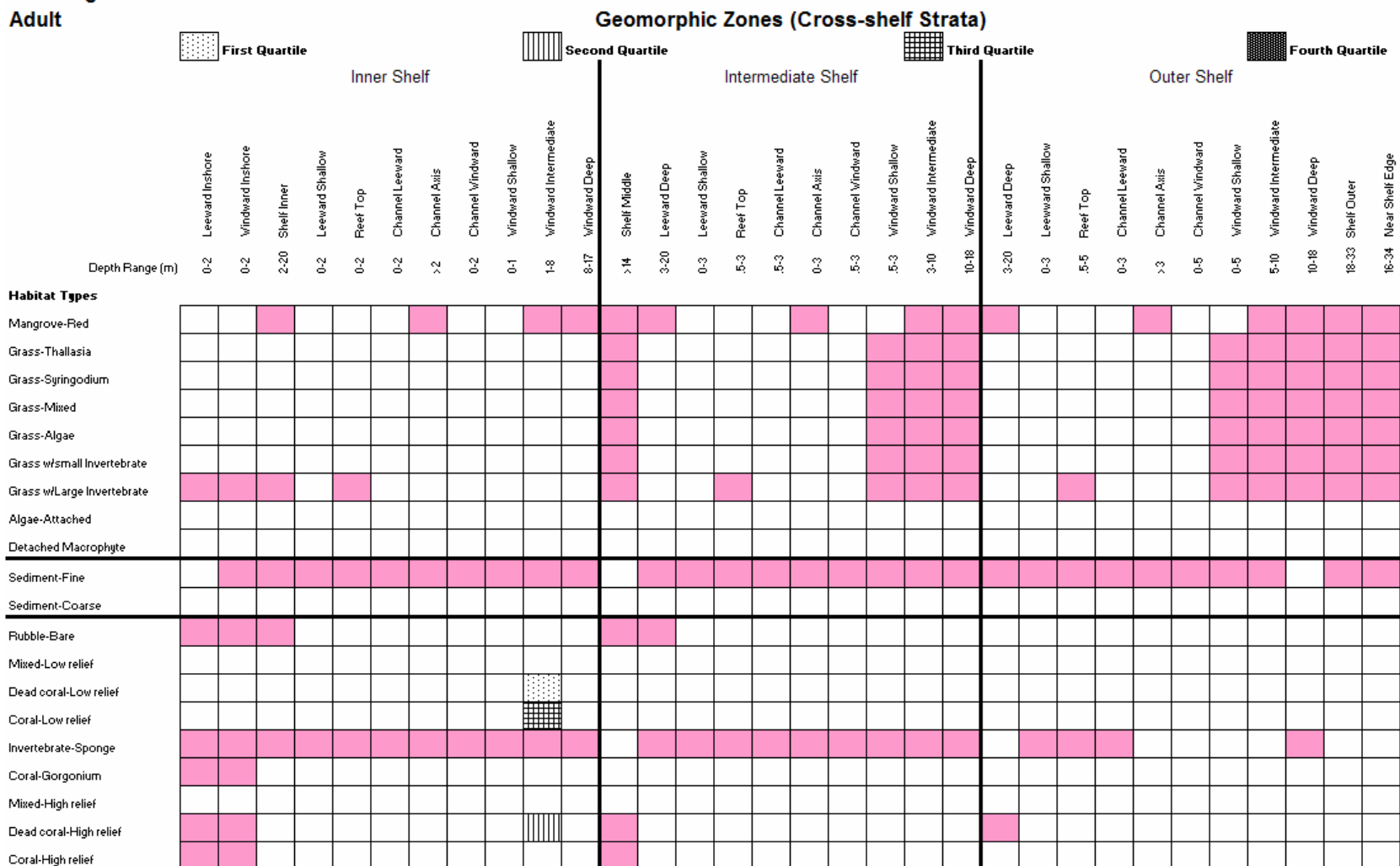


### Appendix B.23.a

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

#### *Scarus guacamaia*

#### Adult

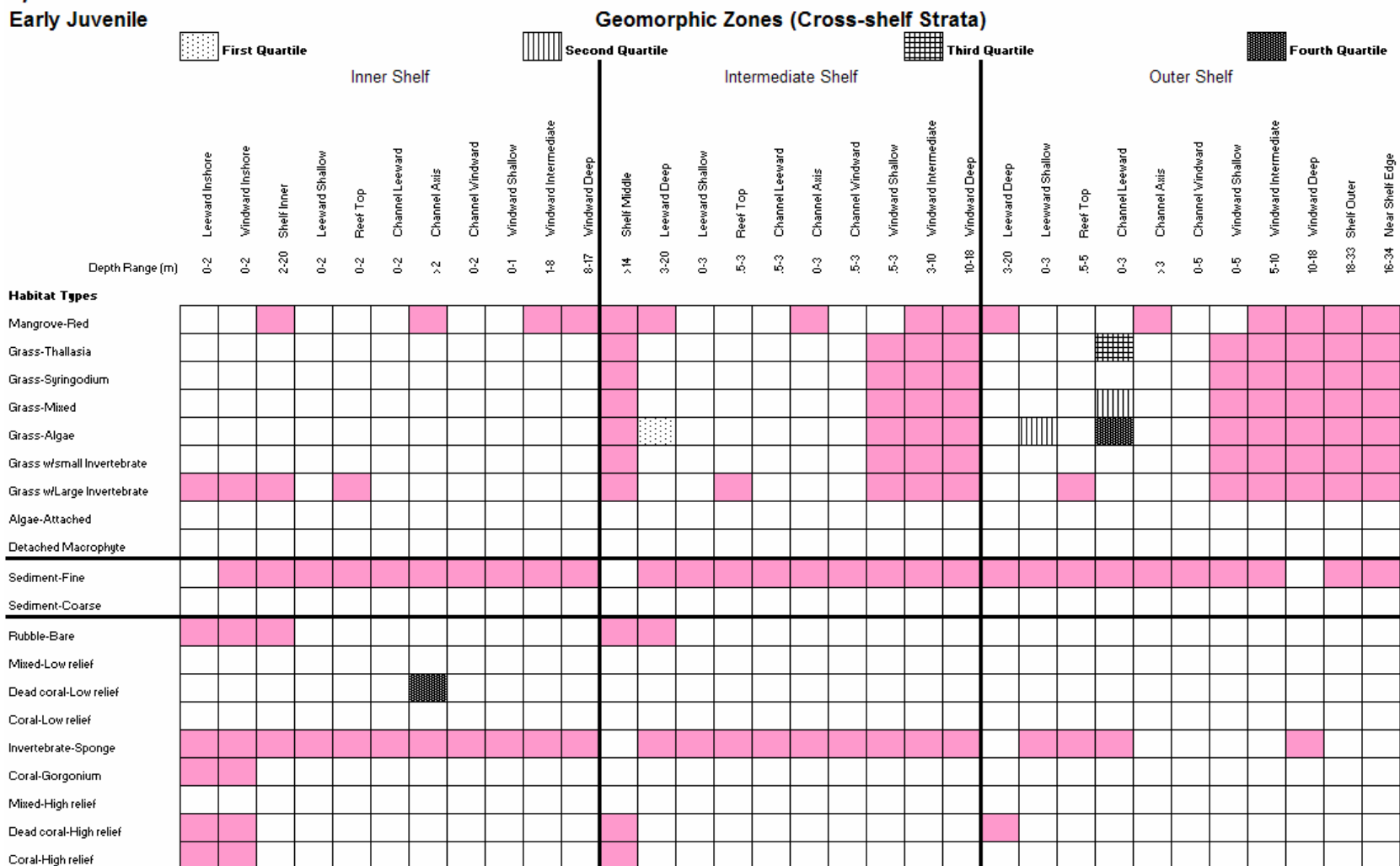


### Appendix B.24.a

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

#### *Sparisoma radians*

#### Early Juvenile

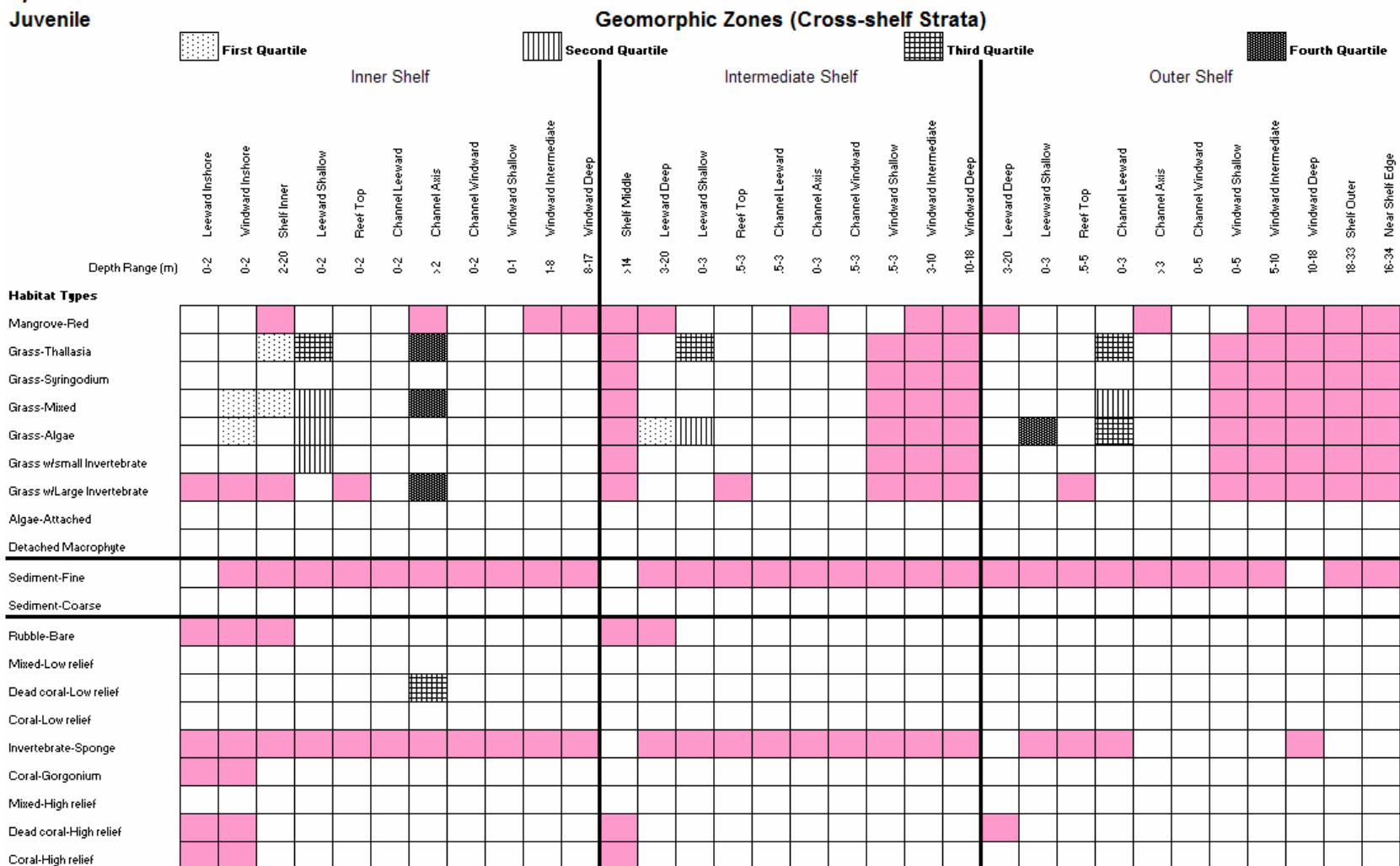


### Appendix B.24.b

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

#### *Sparisoma radians*

#### Juvenile



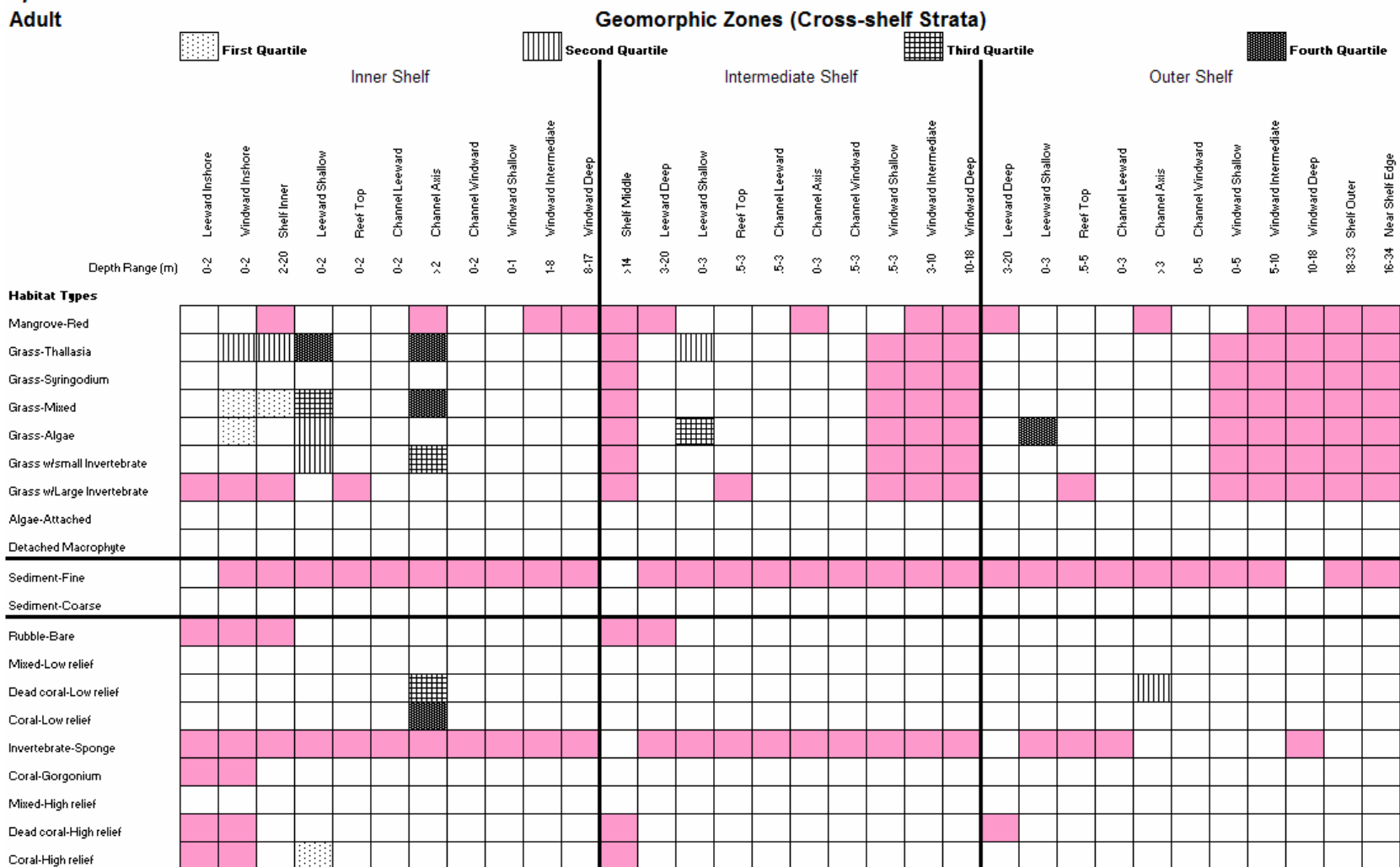


**Appendix B.24.c**

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

***Sparisoma radians***

**Adult**

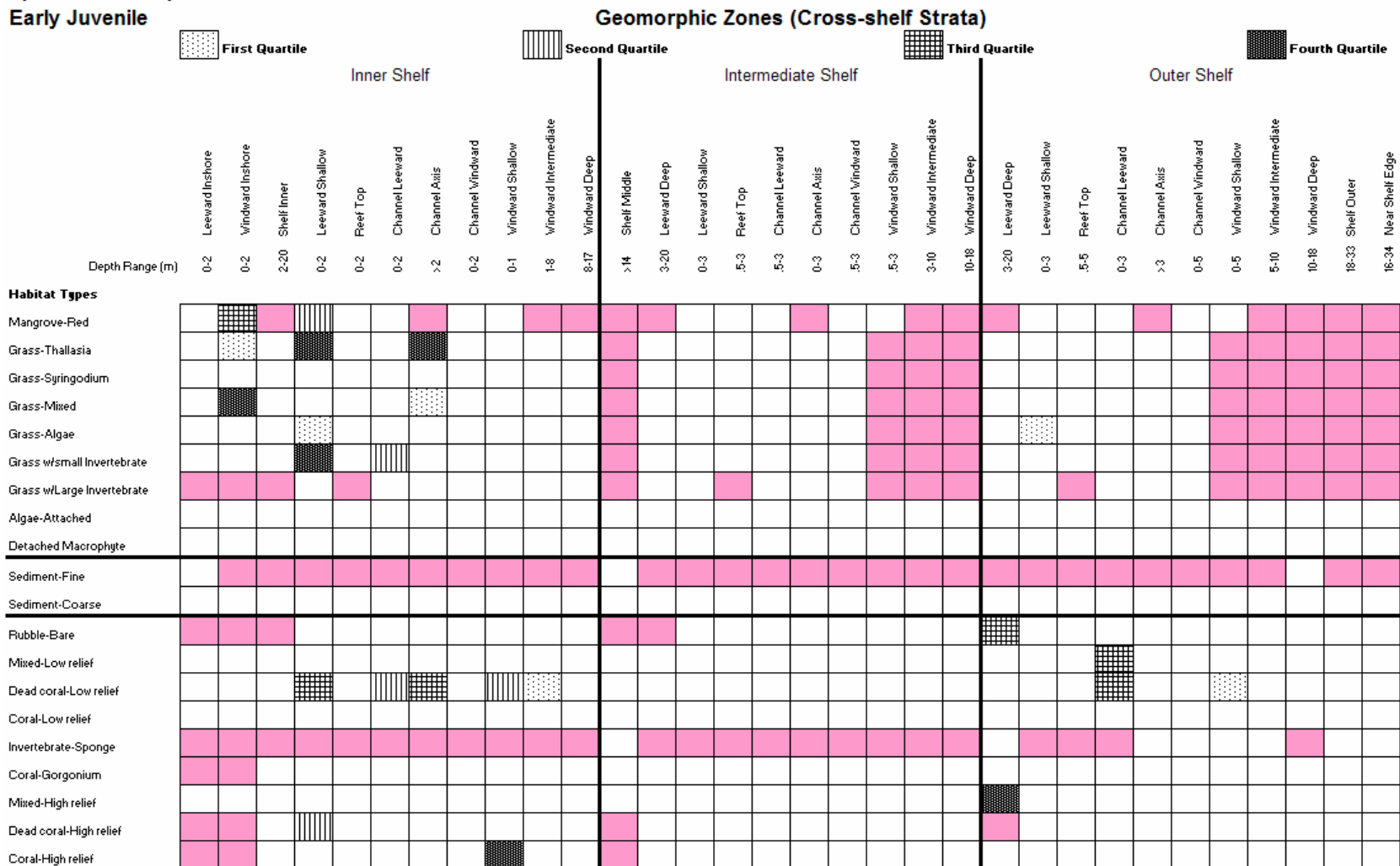


**Appendix B.25.a**

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

***Sparisoma rubripinne***

**Early Juvenile**

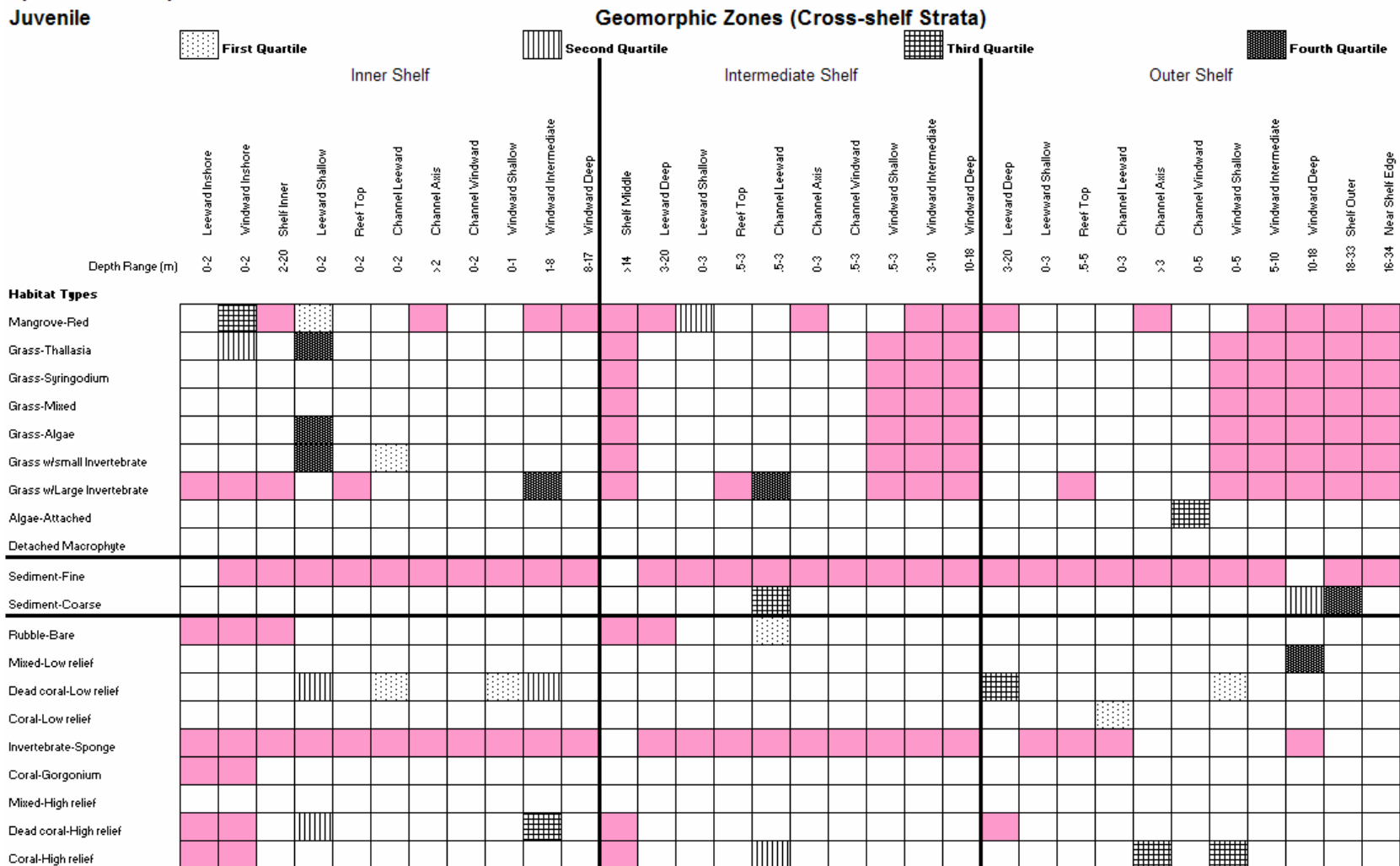


**Appendix B.25.b**

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

***Sparisoma rubripinne***

**Juvenile**

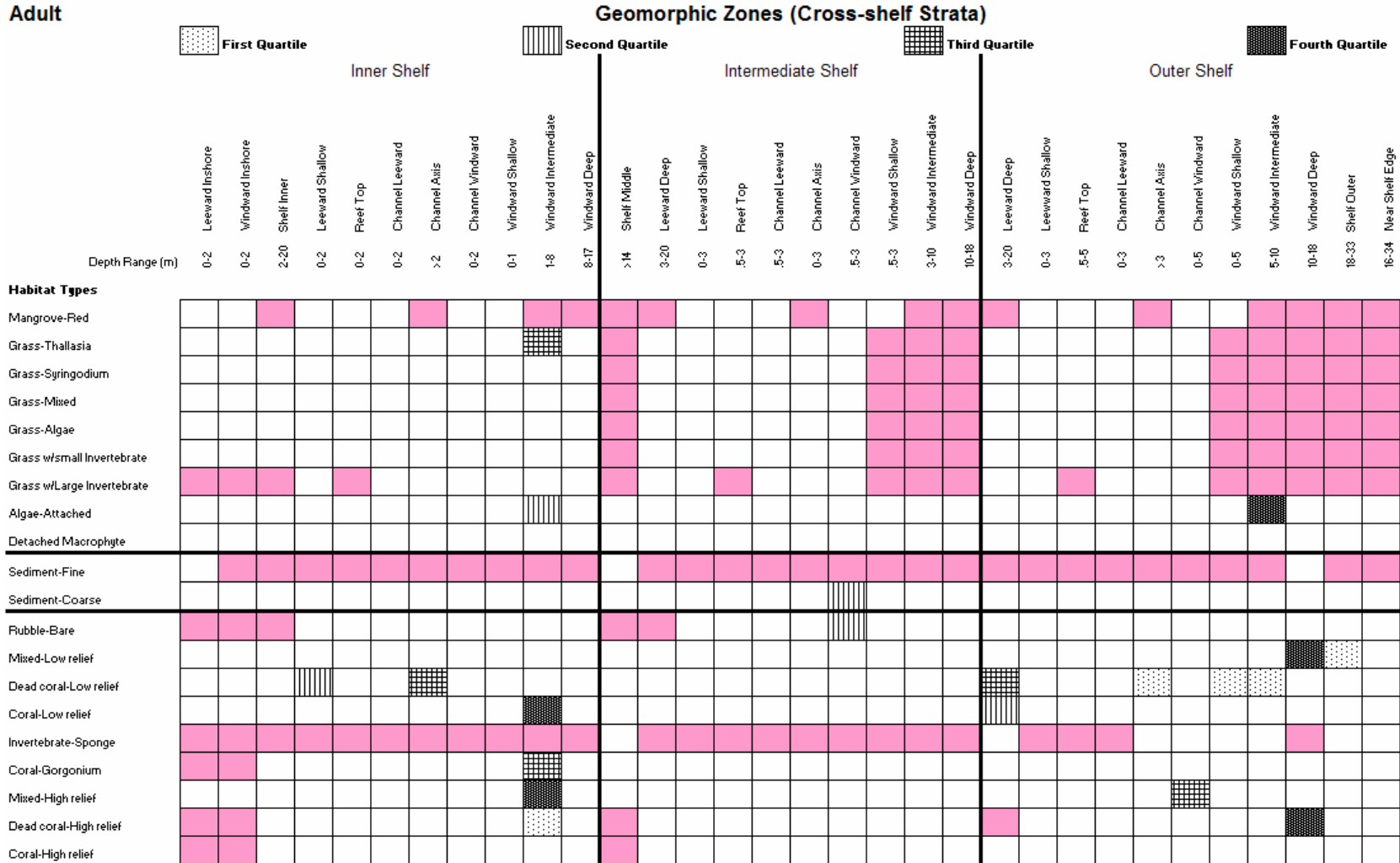


**Appendix B.25.c**

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

***Sparisoma rubripinne***

**Adult**

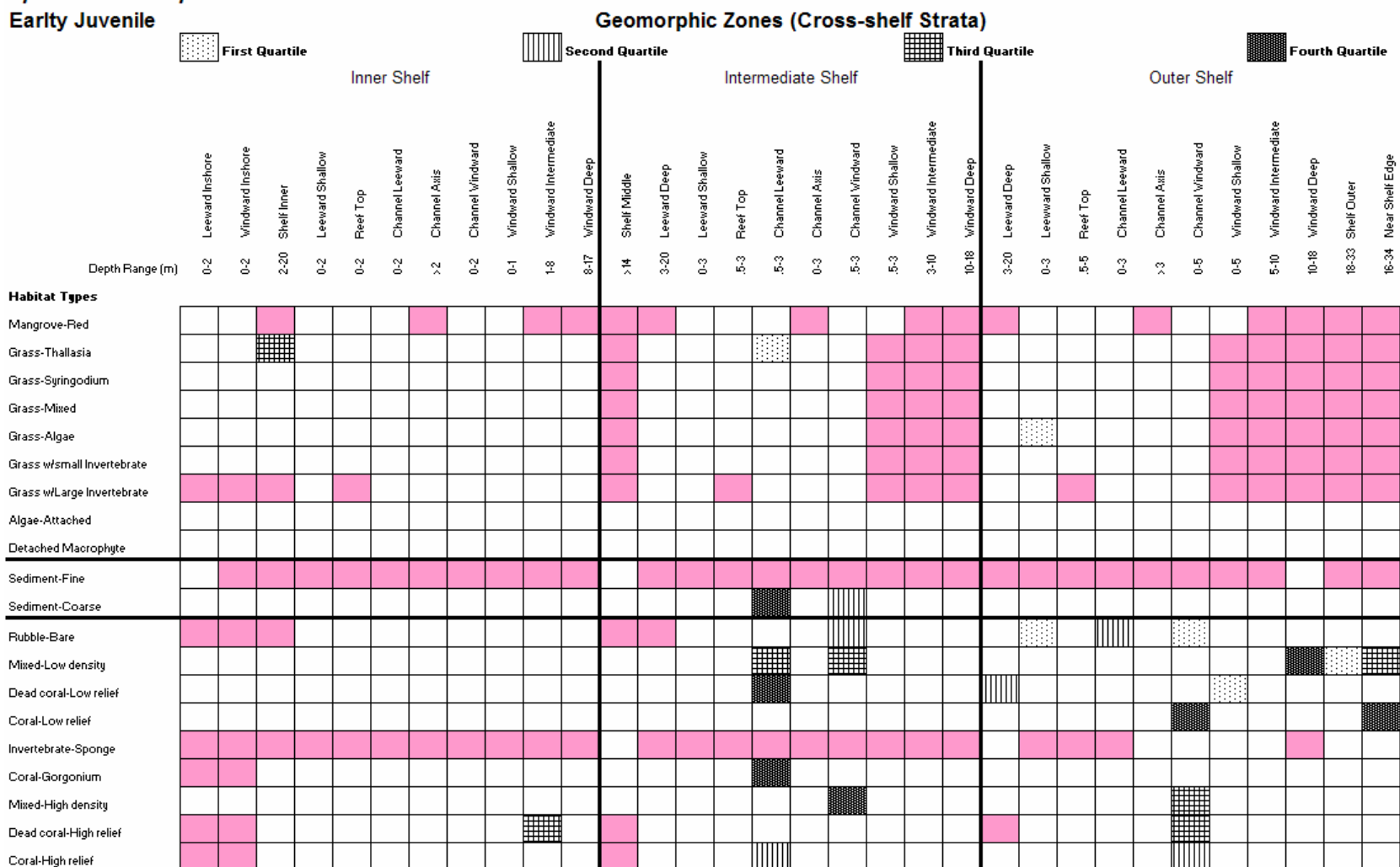


### Appendix B.26.a

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

#### *Sparisoma taeniopterus*

#### Early Juvenile

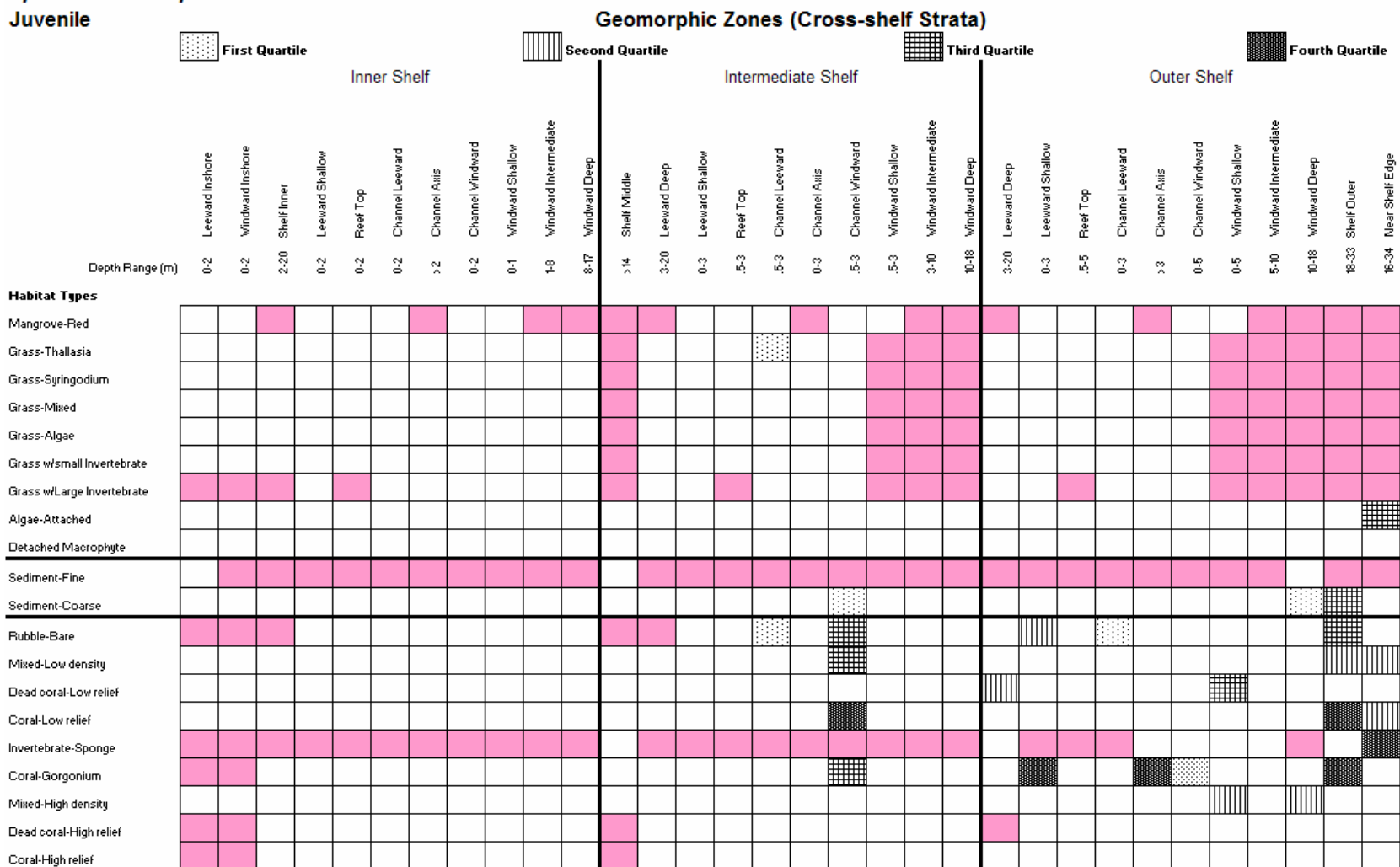


**Appendix B.26.b**

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

***Sparisoma taeniopterus***

**Juvenile**

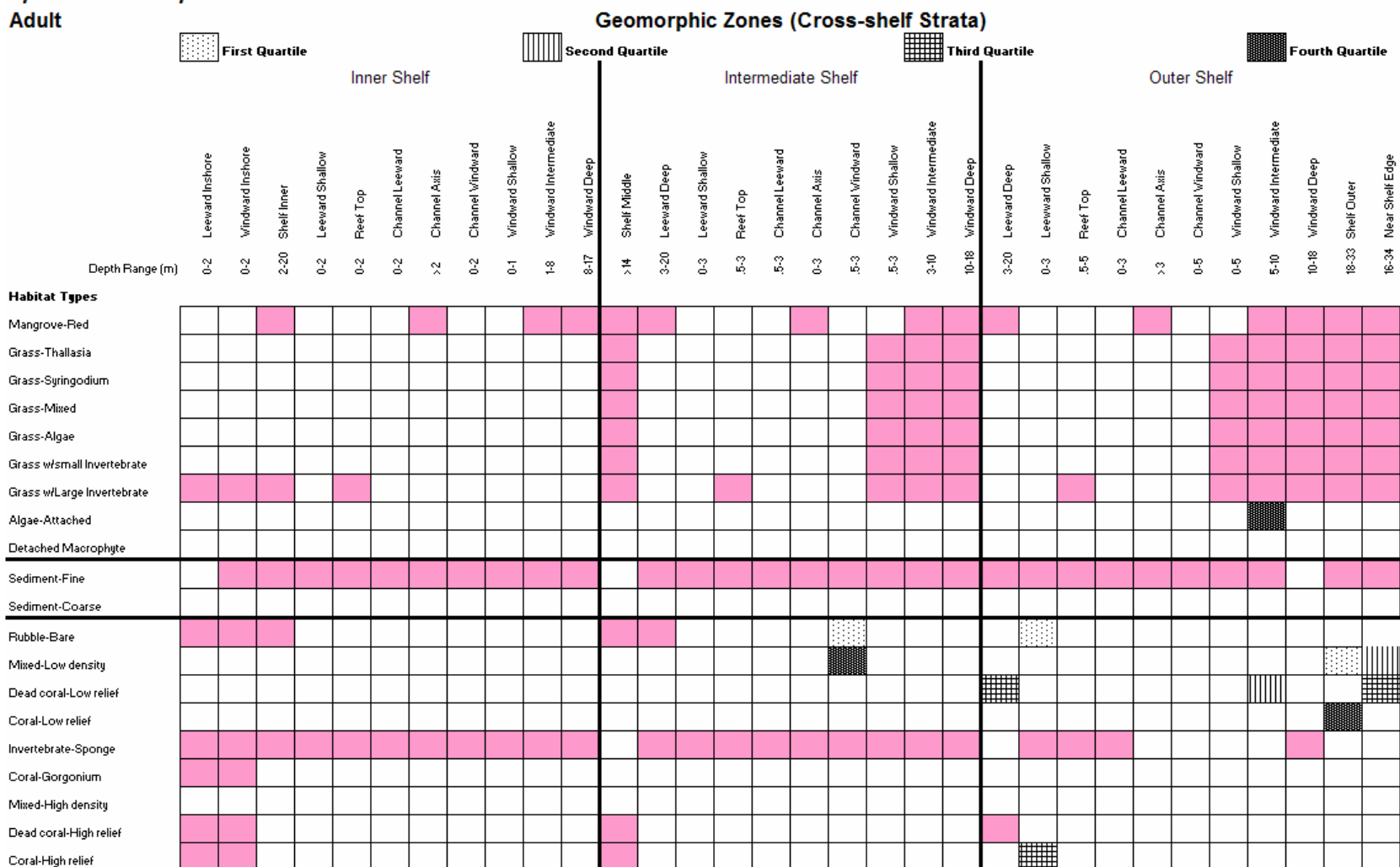


**Appendix B.26.c**

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

***Sparisoma taeniopterus***

**Adult**

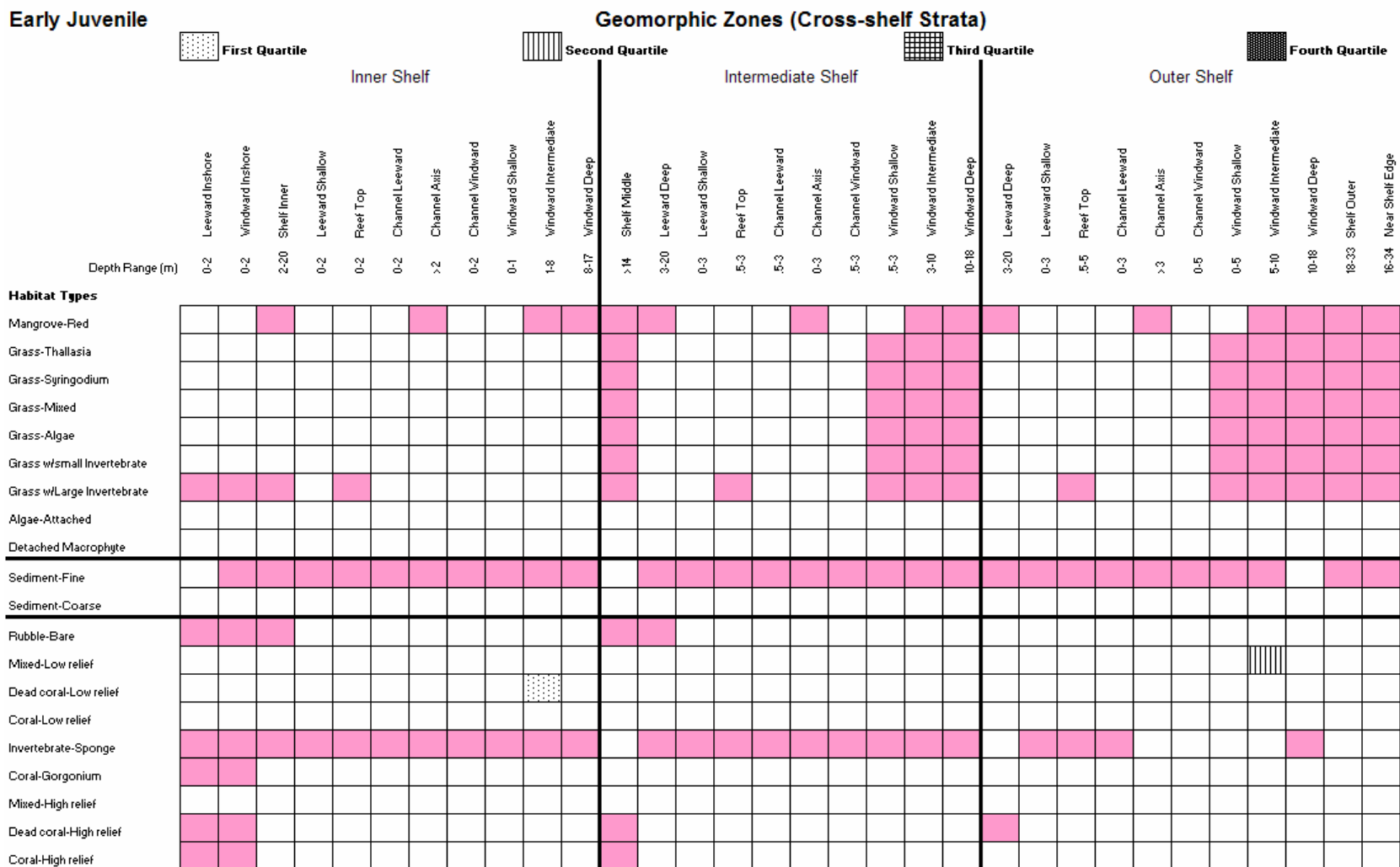


**Appendix B.27.a**

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

***Scarus vetula***

**Early Juvenile**



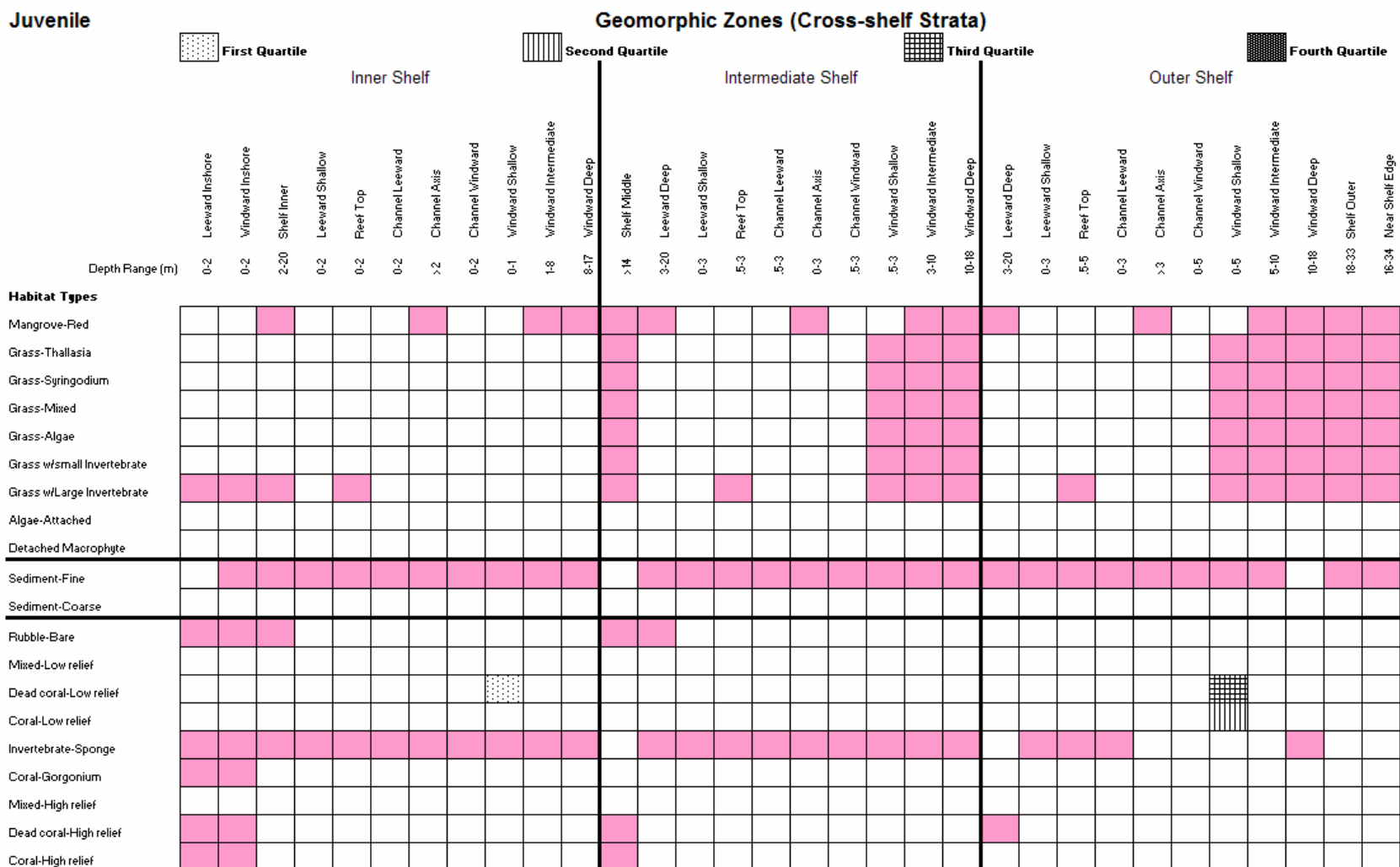


**Appendix B.27.b**

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

***Scarus vetula***

**Juvenile**

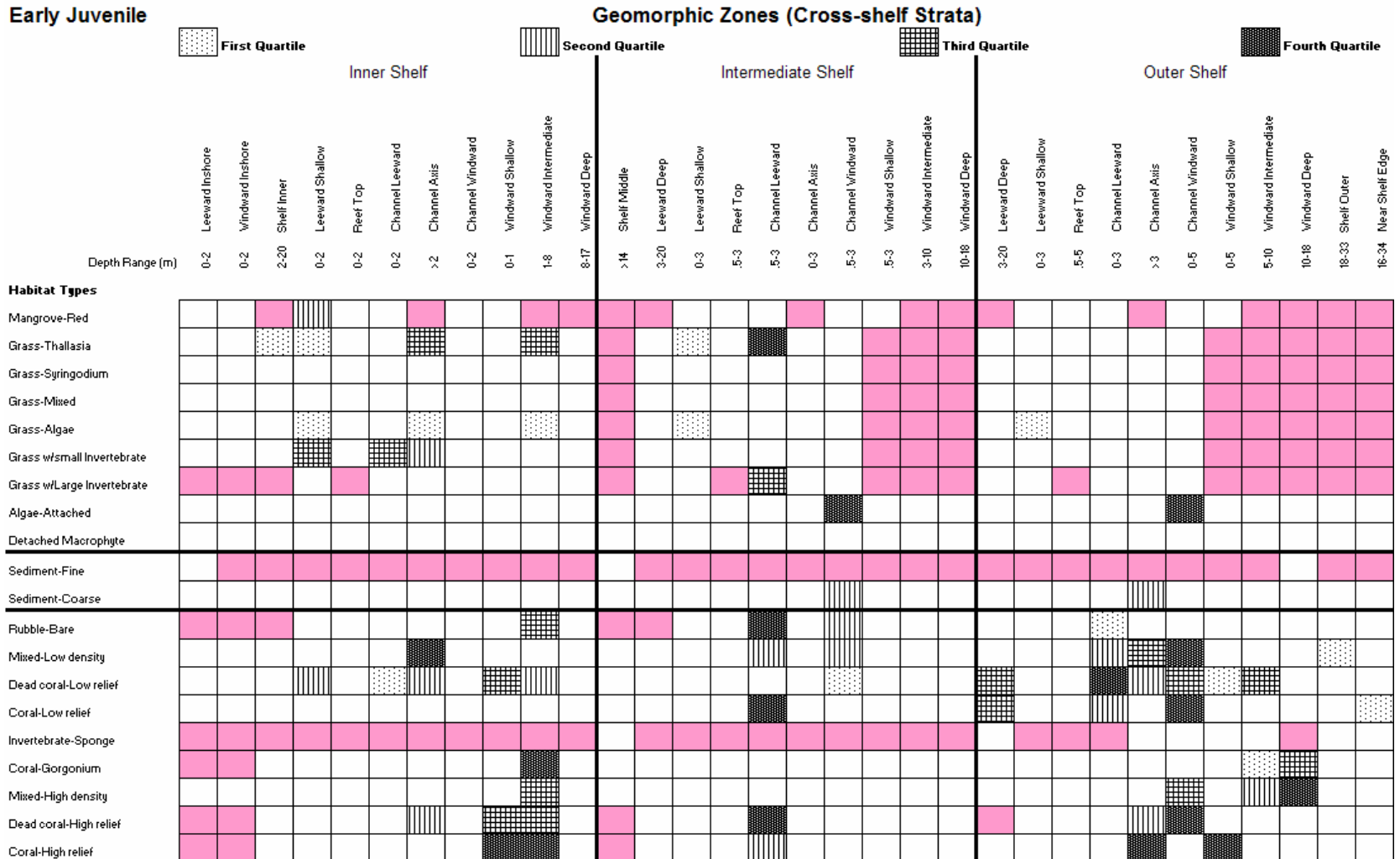


# Appendix B.28.a

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

## *Sparisoma viride*

### Early Juvenile

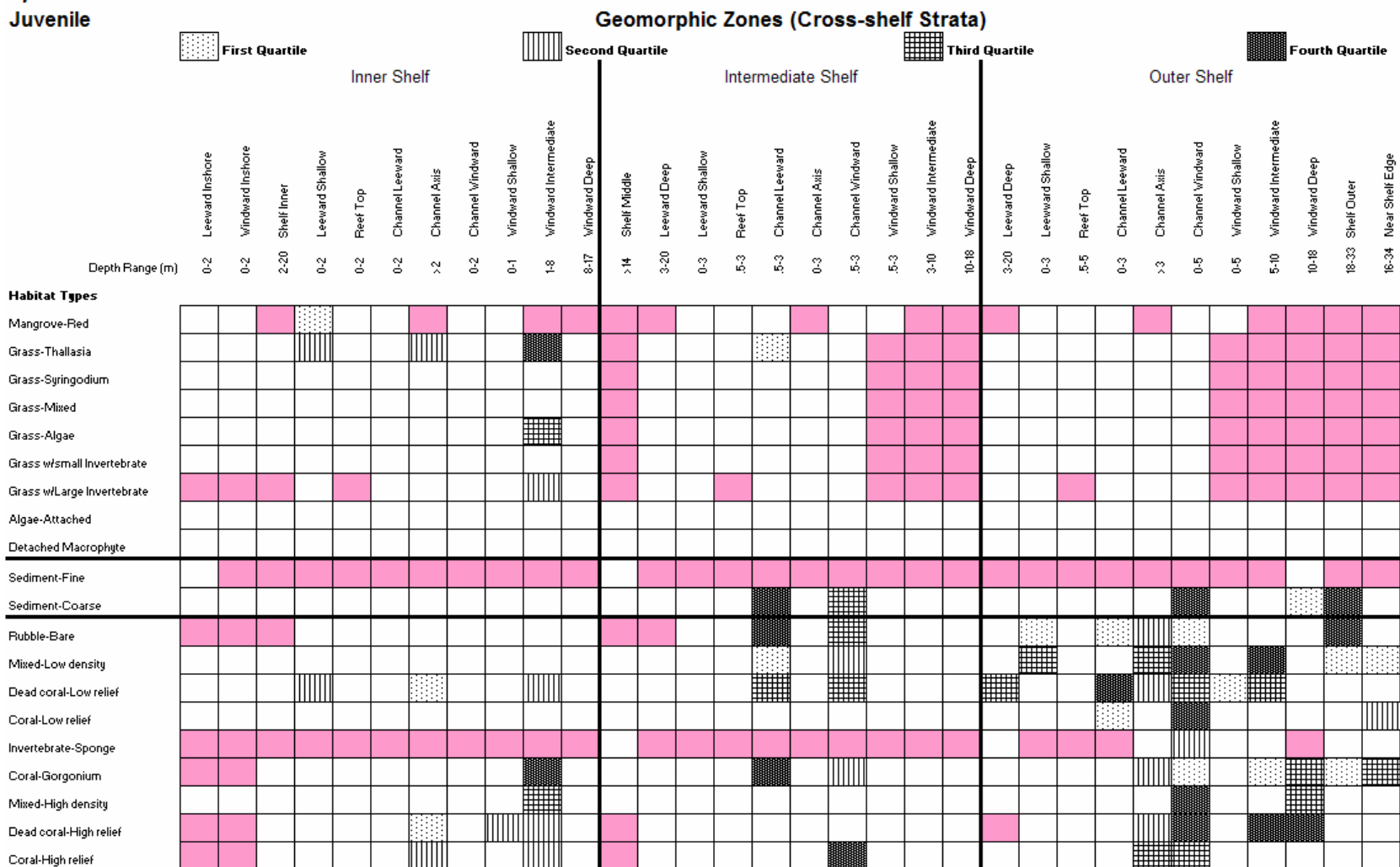


**Appendix B.28.b**

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

***Sparisoma viride***

**Juvenile**

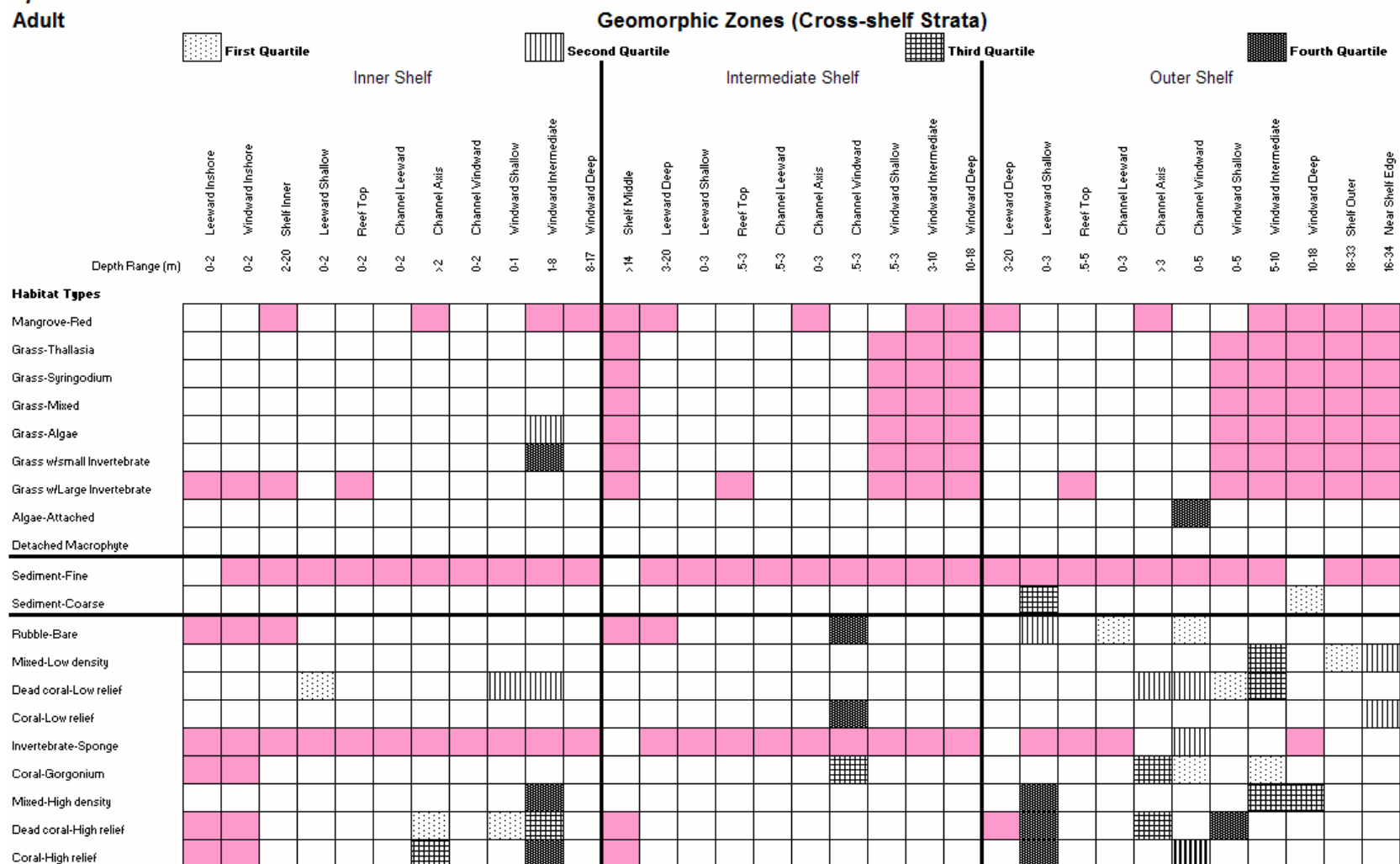


**Appendix B.28.c**

Relative fish density, by quartiles for each cross-shelf habitat of La Parguera, Puerto Rico sampled in this study.

***Sparisoma viride***

**Adult**



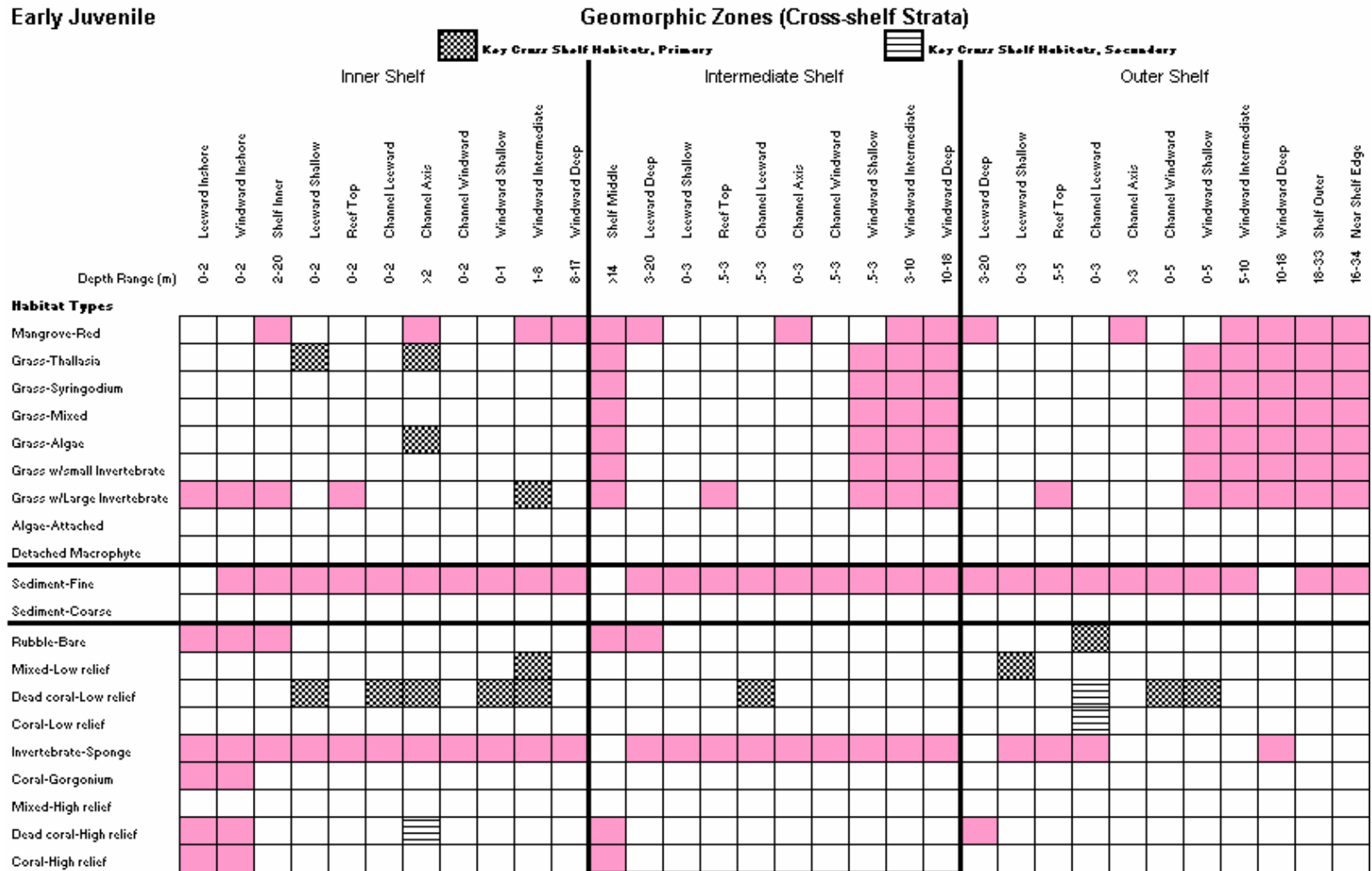
**Appendix C - For each family pooled, relative fish density, by quartiles, for each cross-shelf habitat of La Parguera, Puerto Rico samples in this study.**

### Appendix C.1.a

For each family pooled, relative fish density, by quartiles, for each cross-shelf habitat of La Parguera, Puerto Rico samples in this study.

#### *Acanthuridae*

#### Early Juvenile

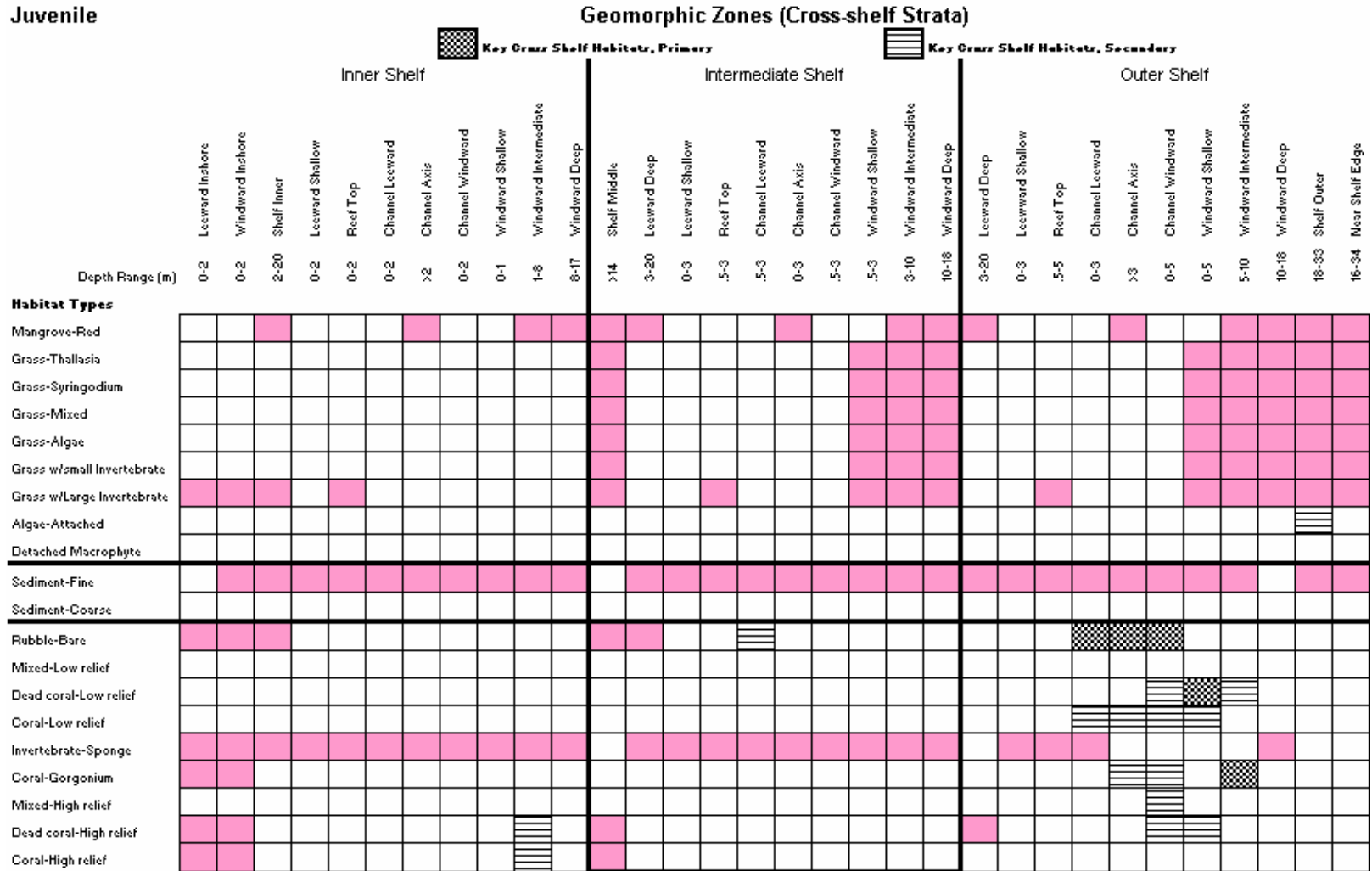


**Appendix C.1.b**

For each family pooled, relative fish density, by quartiles, for each cross-shelf habitat of La Parguera, Puerto Rico samples in this study.

**Acanthuridae**

**Juvenile**

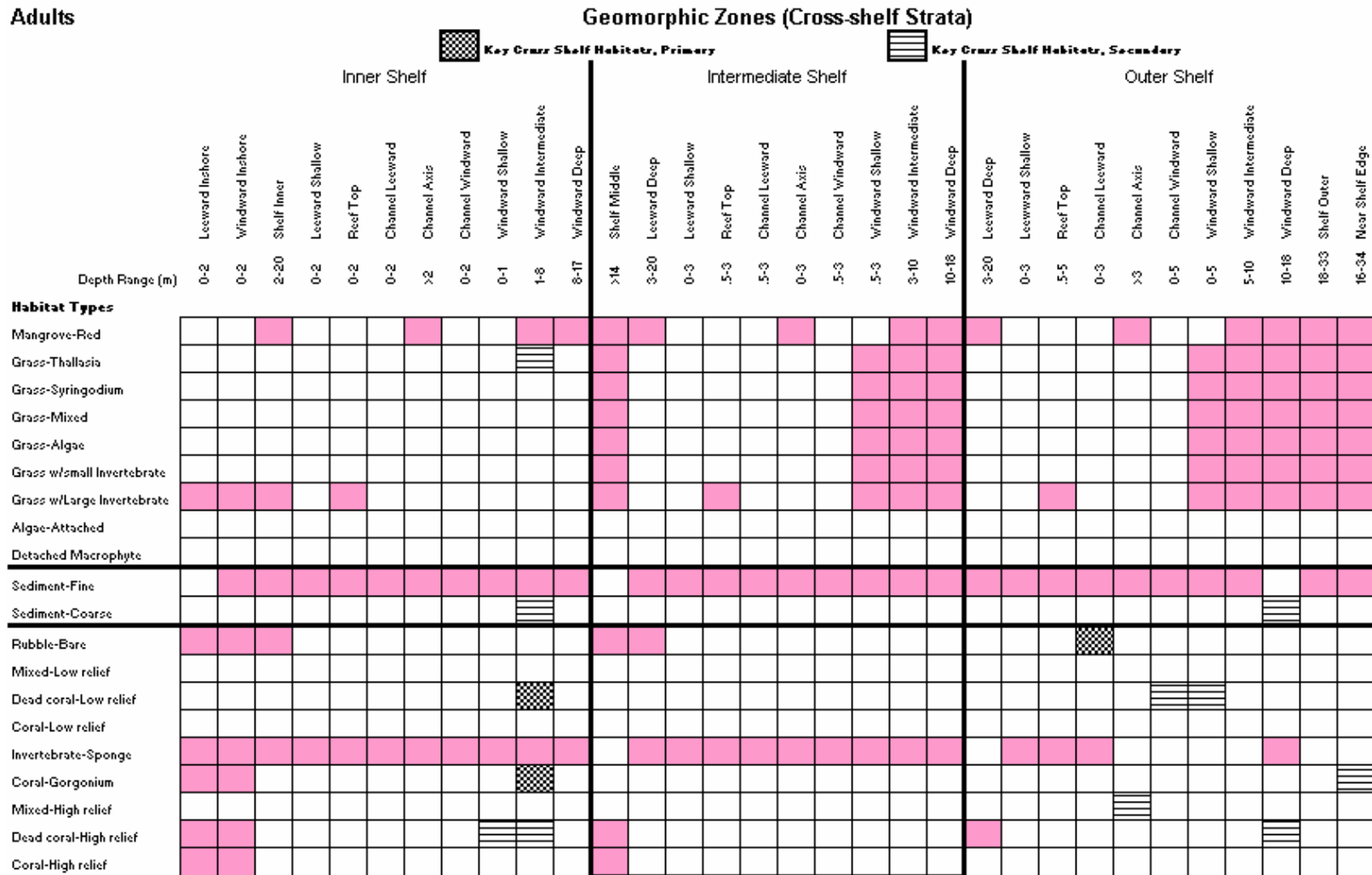


**Appendix C.1.c**

For each family pooled, relative fish density, by quartiles, for each cross-shelf habitat of La Parguera, Puerto Rico samples in this study.

**Acanthuridae**

**Adults**



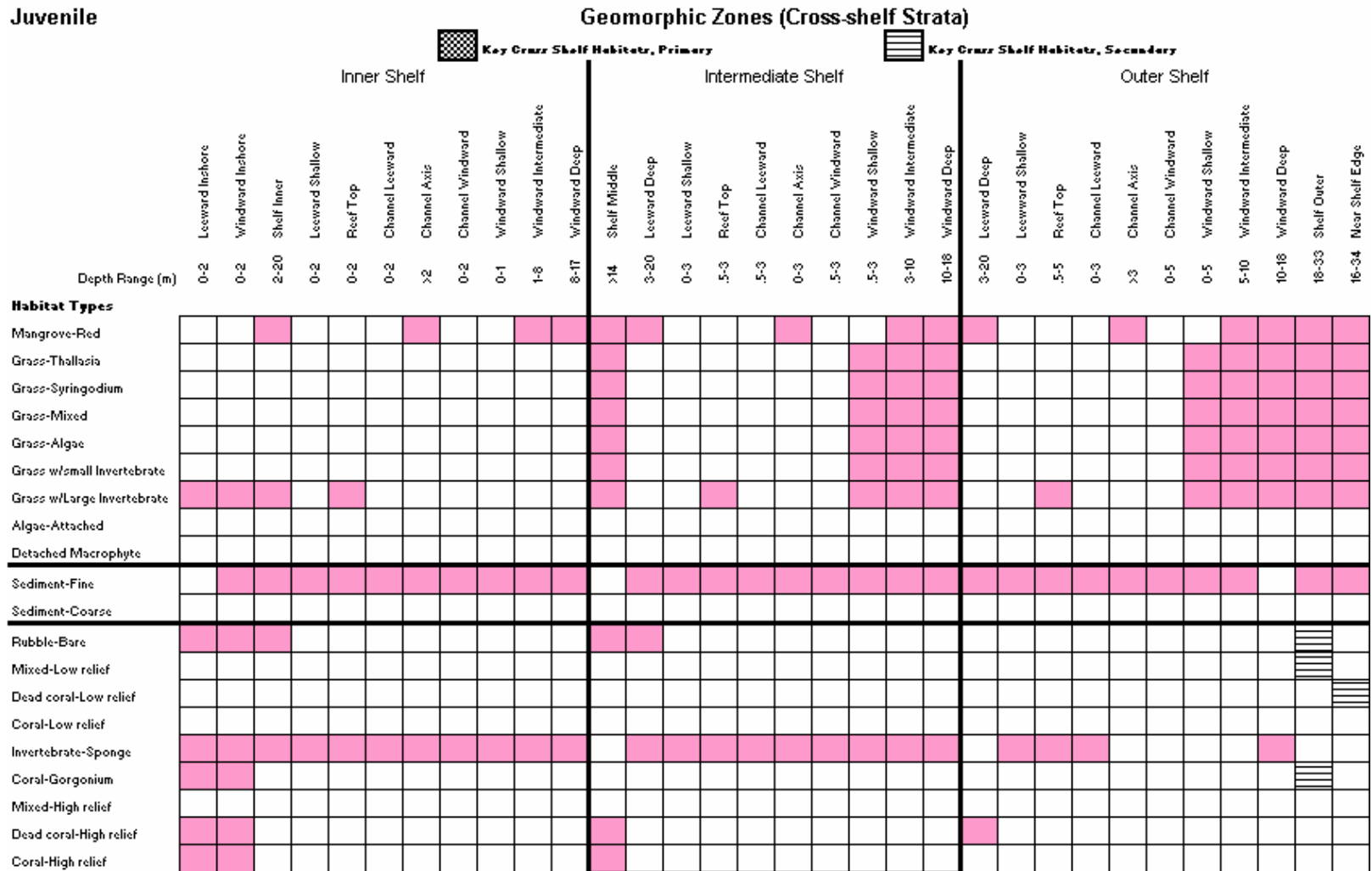


**Appendix C.2.a**

For each family pooled, relative fish density, by quartiles, for each cross-shelf habitat of La Parguera, Puerto Rico samples in this study.

**Serranidae**

**Juvenile**

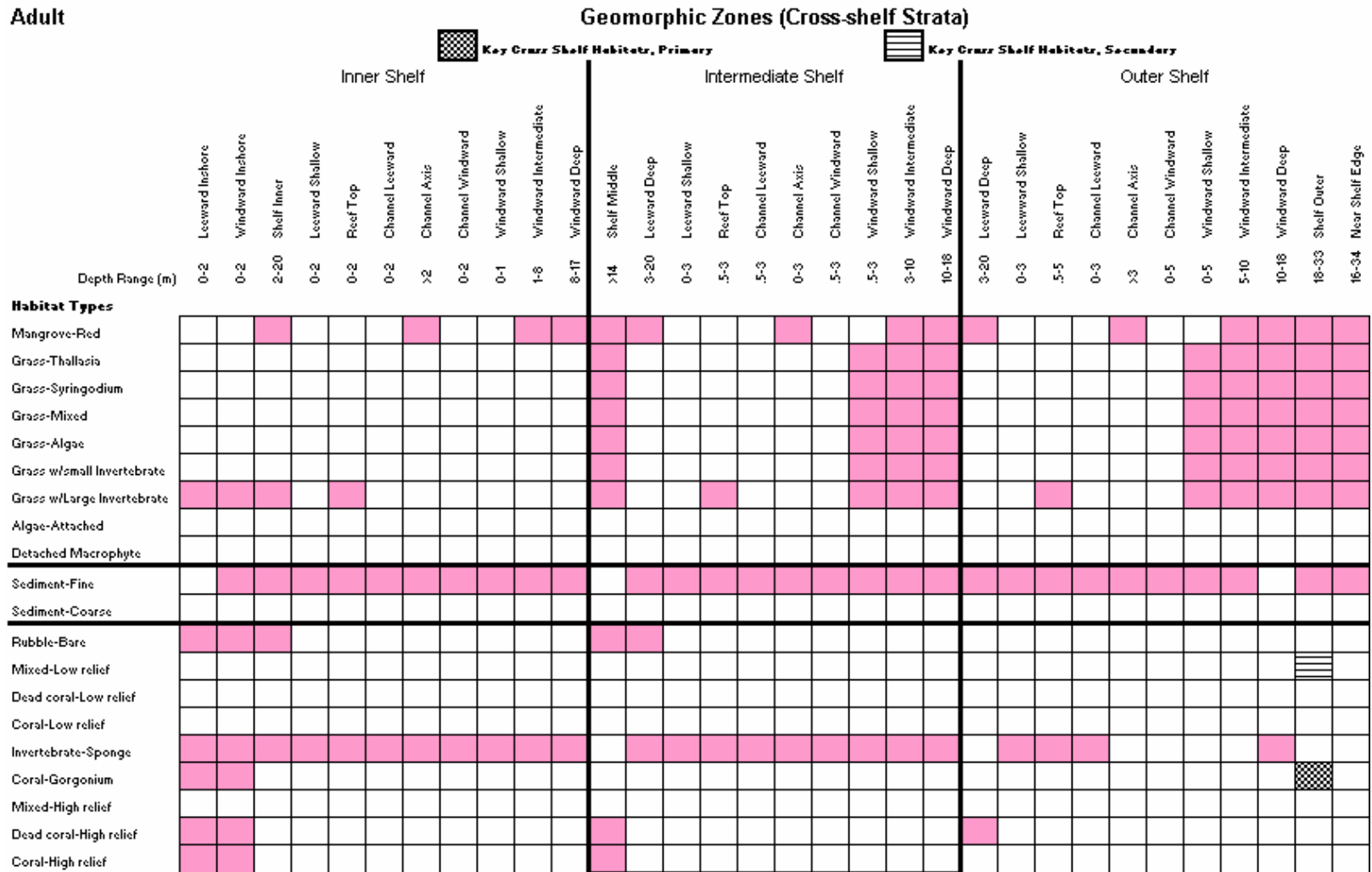


**Appendix C.2.b**

For each family pooled, relative fish density, by quartiles, for each cross-shelf habitat of La Parguera, Puerto Rico samples in this study.

**Serranidae**

**Adult**



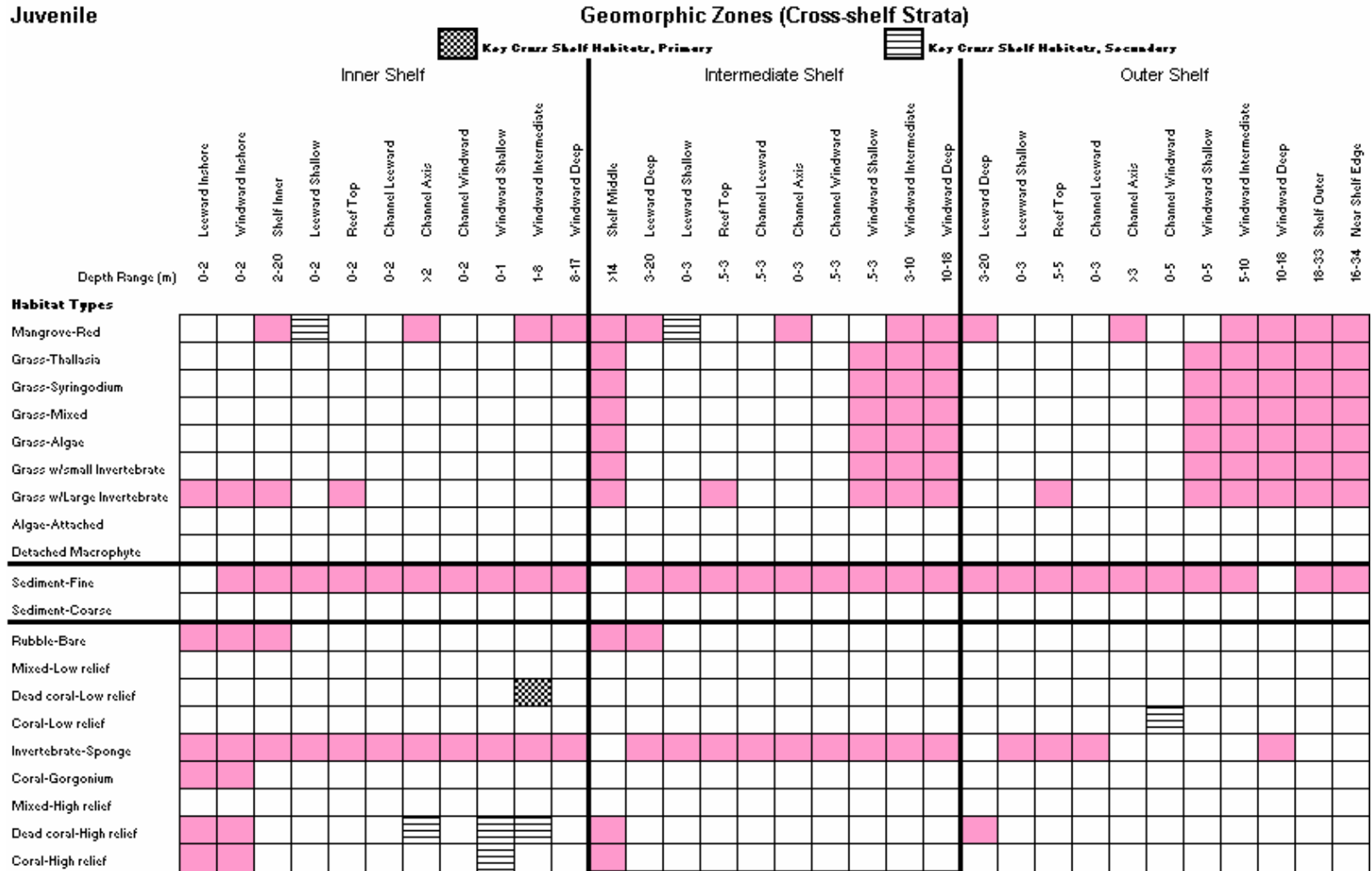


### Appendix C.3.b

For each family pooled, relative fish density, by quartiles, for each cross-shelf habitat of La Parguera, Puerto Rico samples in this study.

#### *Haemulidae*

#### Juvenile

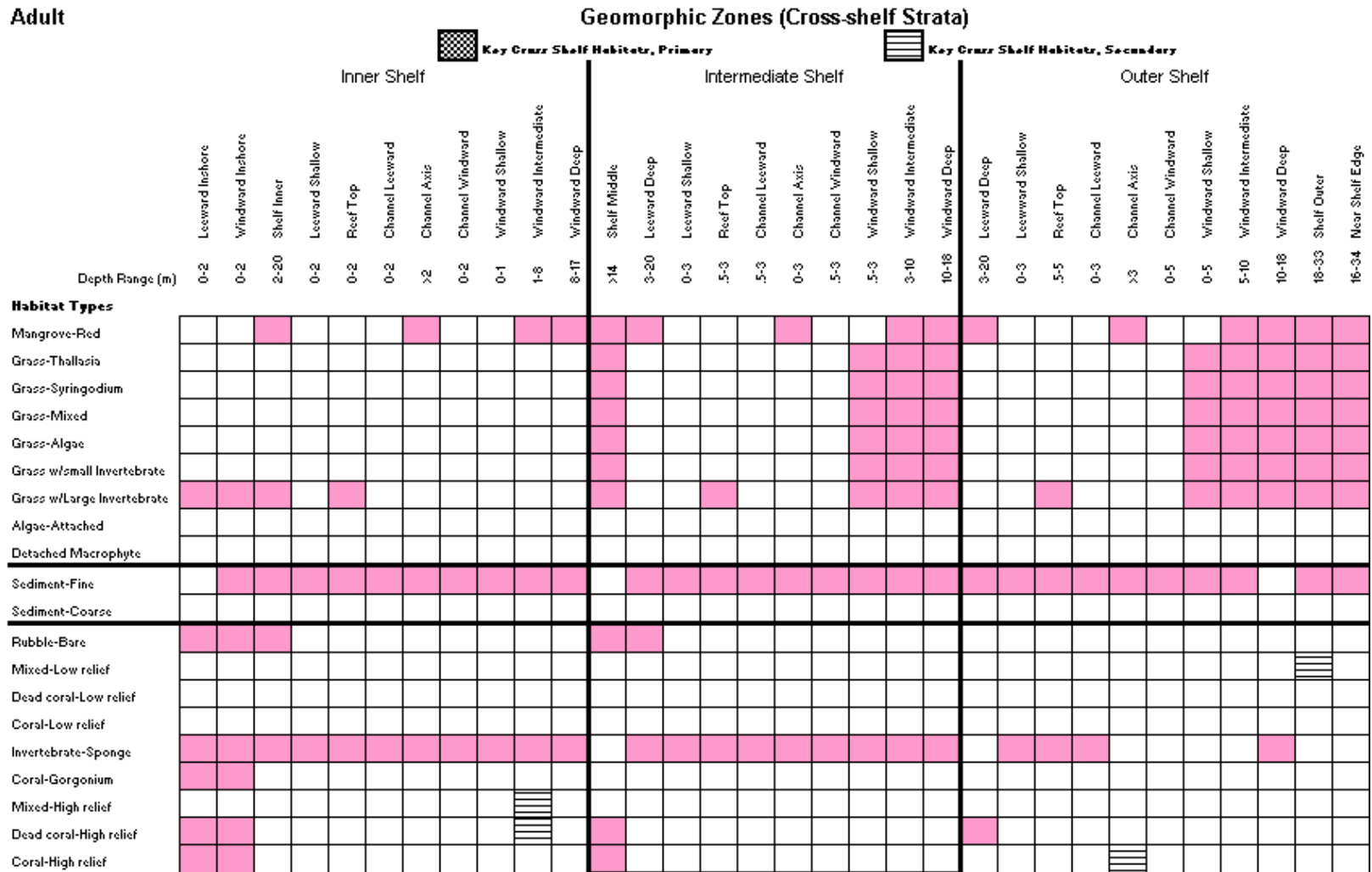


**Appendix C.3.c**

For each family pooled, relative fish density, by quartiles, for each cross-shelf habitat of La Parguera, Puerto Rico samples in this study.

**Haemulidae**

**Adult**

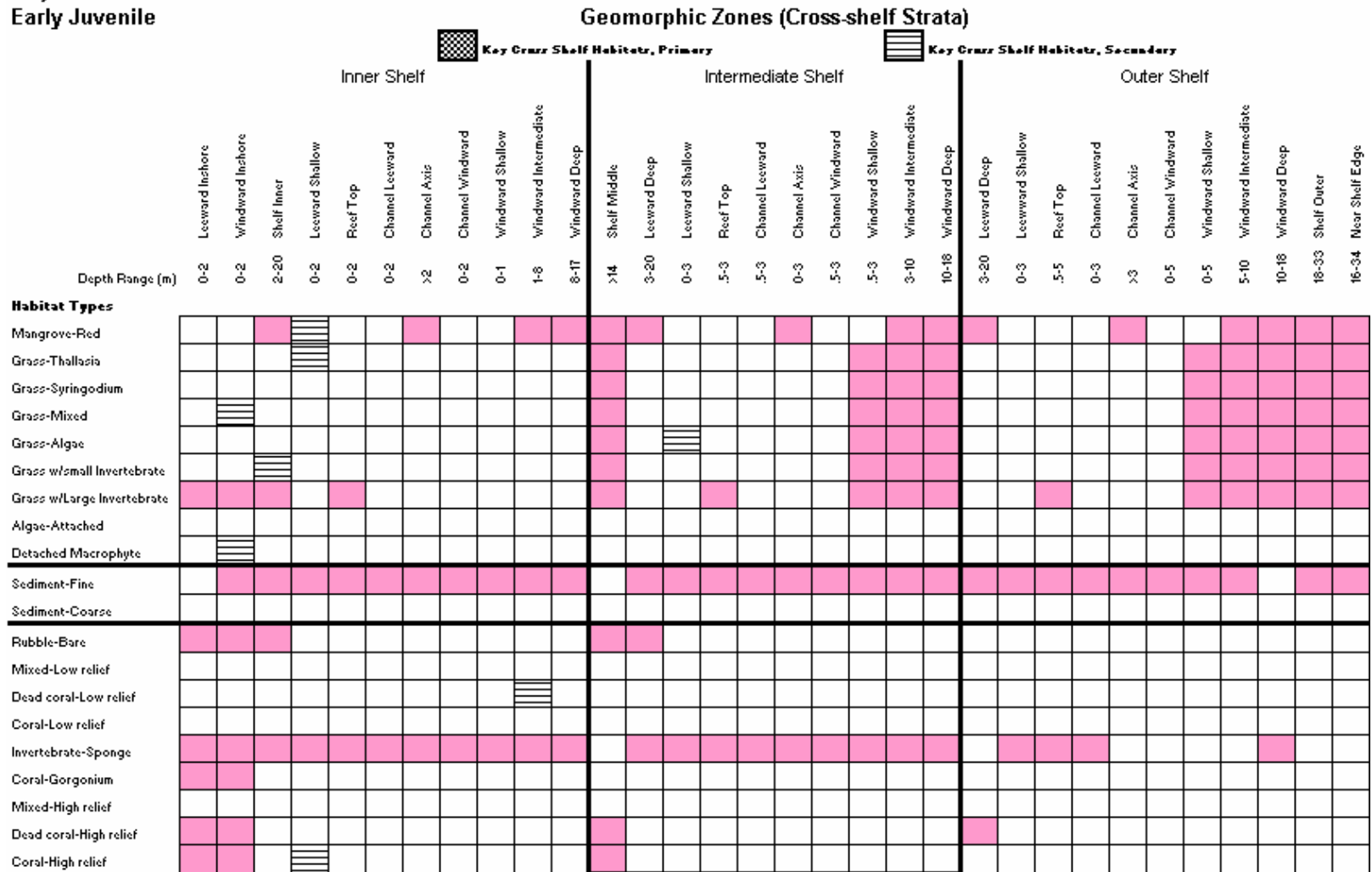


### Appendix C.4.a

For each family pooled, relative fish density, by quartiles, for each cross-shelf habitat of La Parguera, Puerto Rico samples in this study.

#### *Lutjanidae*

#### Early Juvenile

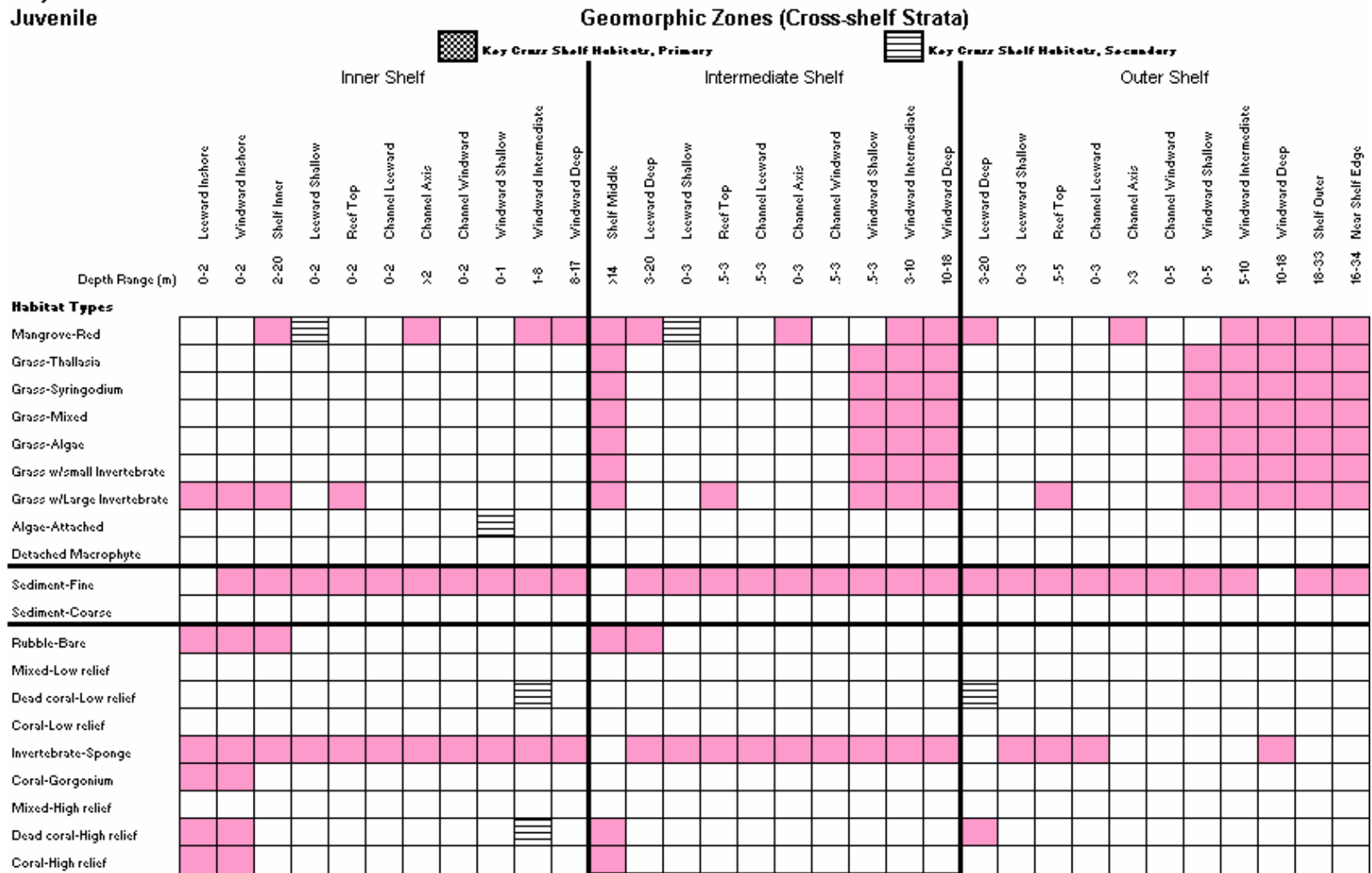


### Appendix C.4.b

For each family pooled, relative fish density, by quartiles, for each cross-shelf habitat of La Parguera, Puerto Rico samples in this study.

#### *Lutjanidae*

#### Juvenile

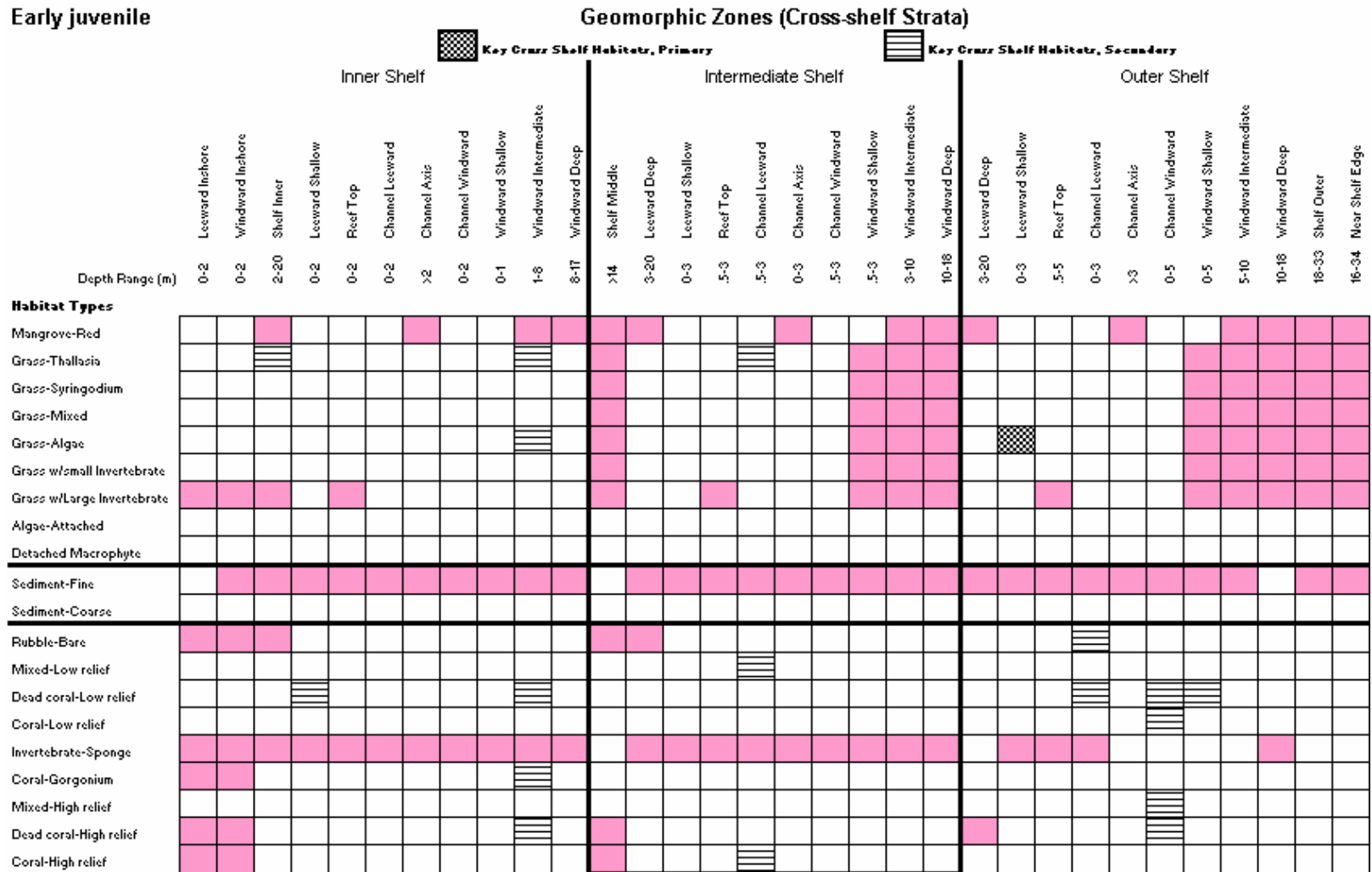


**Appendix C.5.a**

For each family pooled, relative fish density, by quartiles, for each cross-shelf habitat of La Parguera, Puerto Rico samples in this study.

**Scaridae**

**Early juvenile**





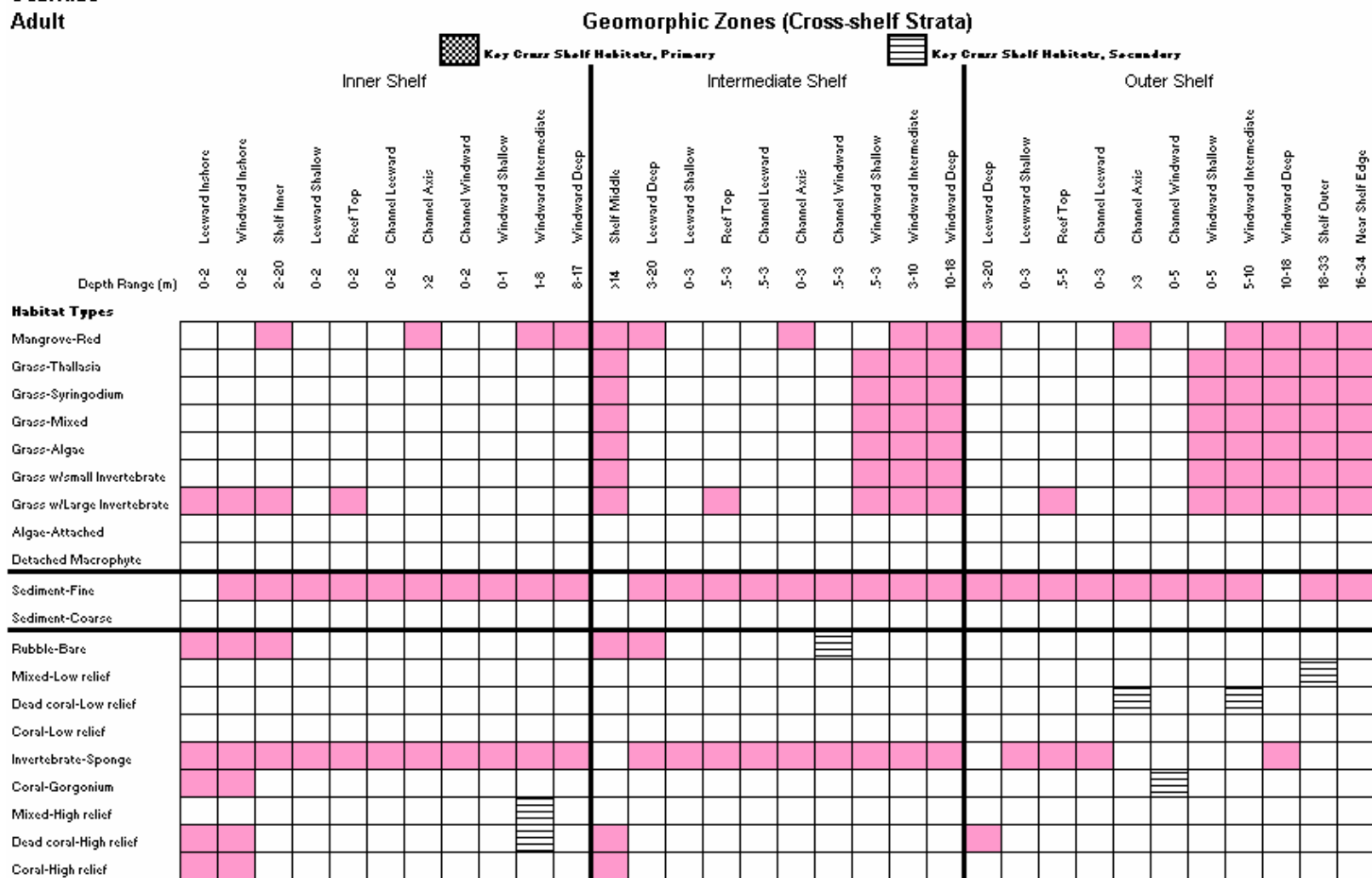


### Appendix C.5.c

For each family pooled, relative fish density, by quartiles, for each cross-shelf habitat of La Parguera, Puerto Rico samples in this study.

#### *Scaridae*

#### Adult

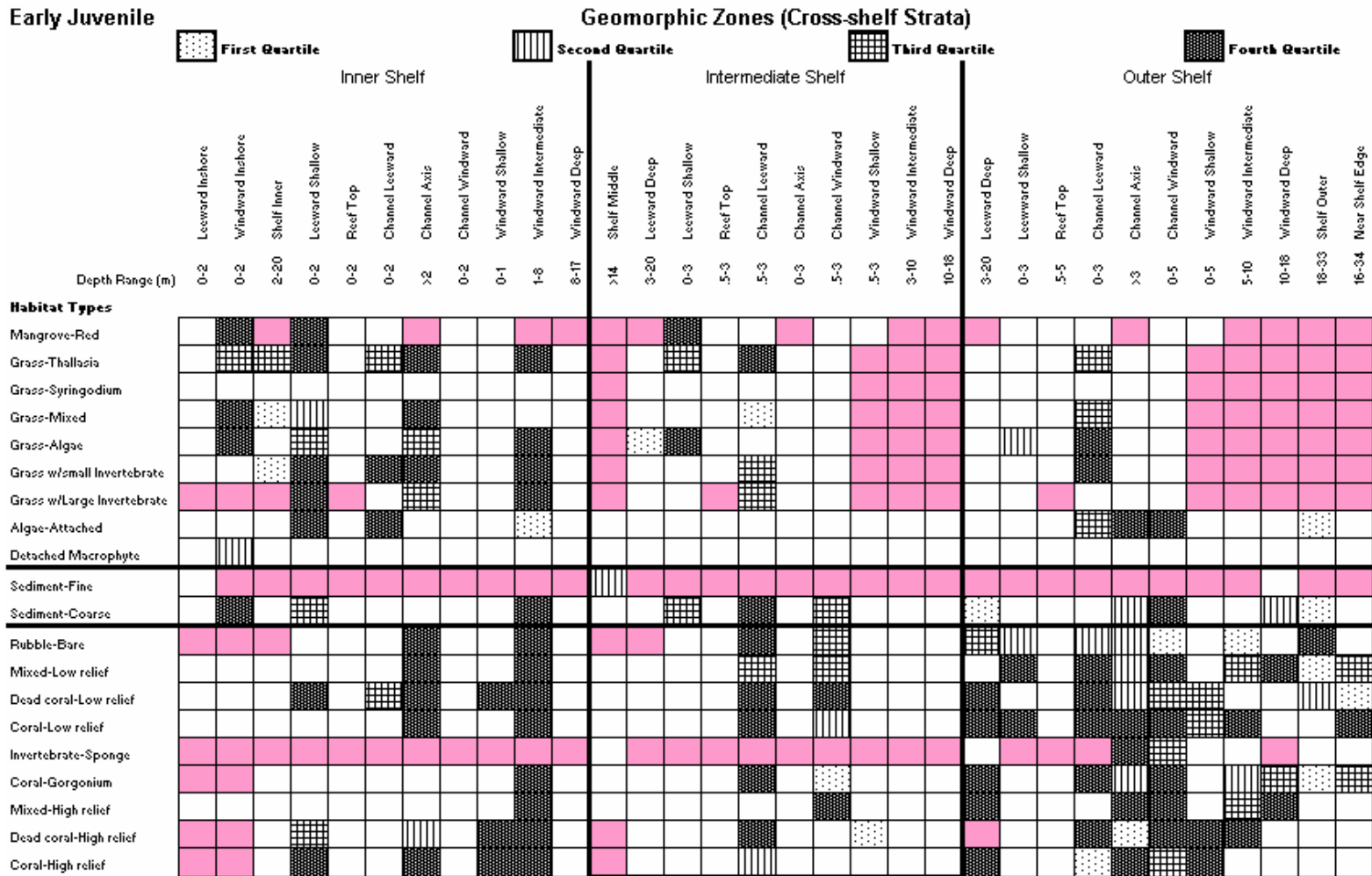


**Appendix D - Maximum relative fish density, by quartiles, for each cross-shelf habitat of La Parguera, Puerto Rico observed across all species (see text for details).**

### Appendix D.1

Maximum relative fish density, by quartiles, for each cross-shelf habitat of La Parguera, Puerto Rico observed across all species (see text for details).

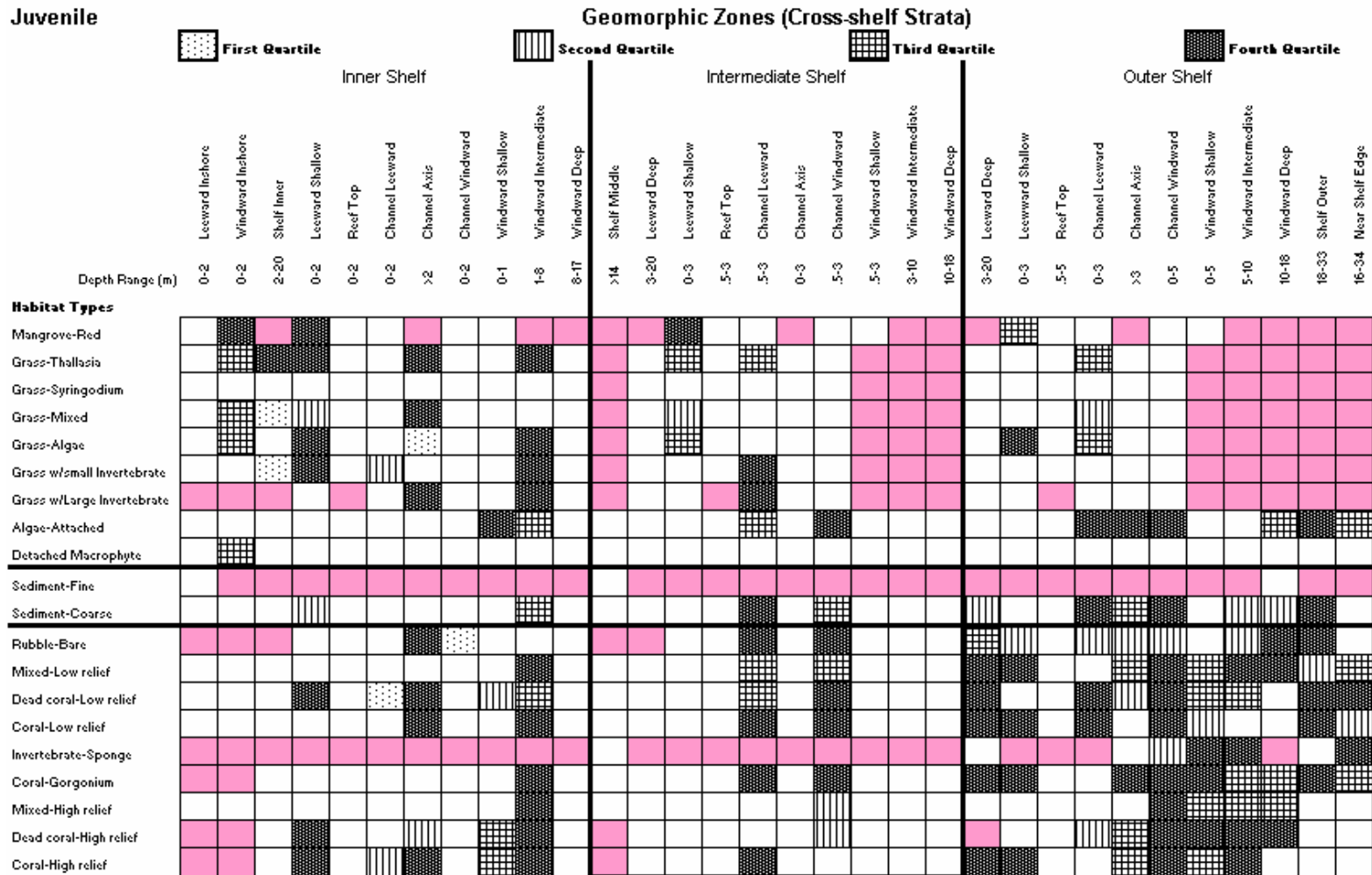
#### Early Juvenile



### Appendix D.2

Maximum relative fish density, by quartiles, for each cross-shelf habitat of La Parguera, Puerto Rico observed across all species (see text for details).

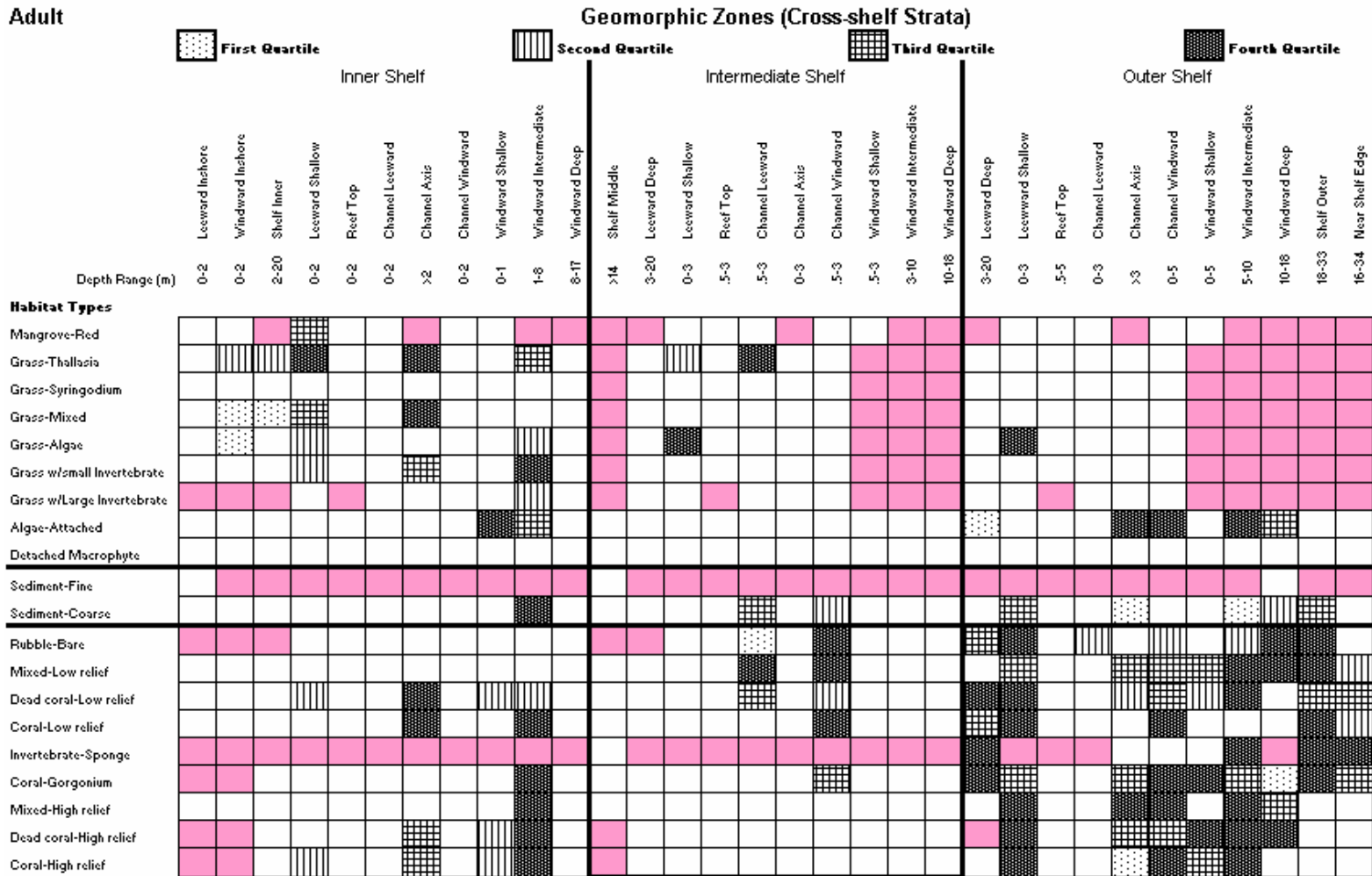
#### Juvenile



### Appendix D.3

Maximum relative fish density, by quartiles, for each cross-shelf habitat of La Parguera, Puerto Rico observed across all species (see text for details).

#### Adult



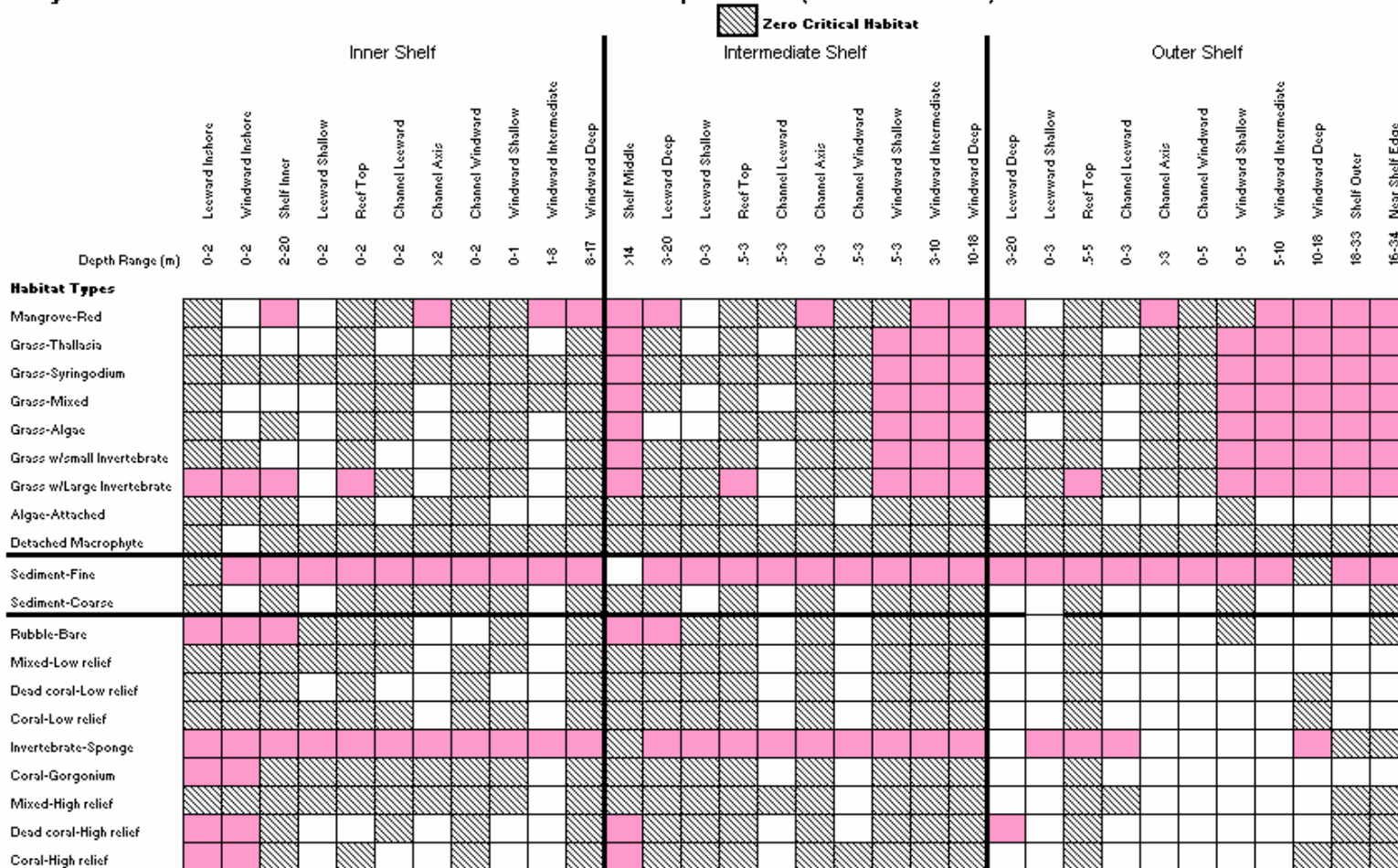
**Appendix E - Cross-shelf habitat framework integrating structural habitat types and geomorphic zones of La Parguera, Puerto Rico shelf area. Shaded cells do not occur locally, cross-hatched cells had zero encounters in all species in all lifestages of this study.**

## Appendix E

Cross-shelf habitat framework integrating structural habitat types and geomorphic zones of La Parguera, Puerto Rico shelf area. Shaded cells do not occur locally, cross-hatched cells had zero encounters in all species in all lifestages of this study.

### Early Juvenile

### Geomorphic Zones (Cross-shelf Strata)



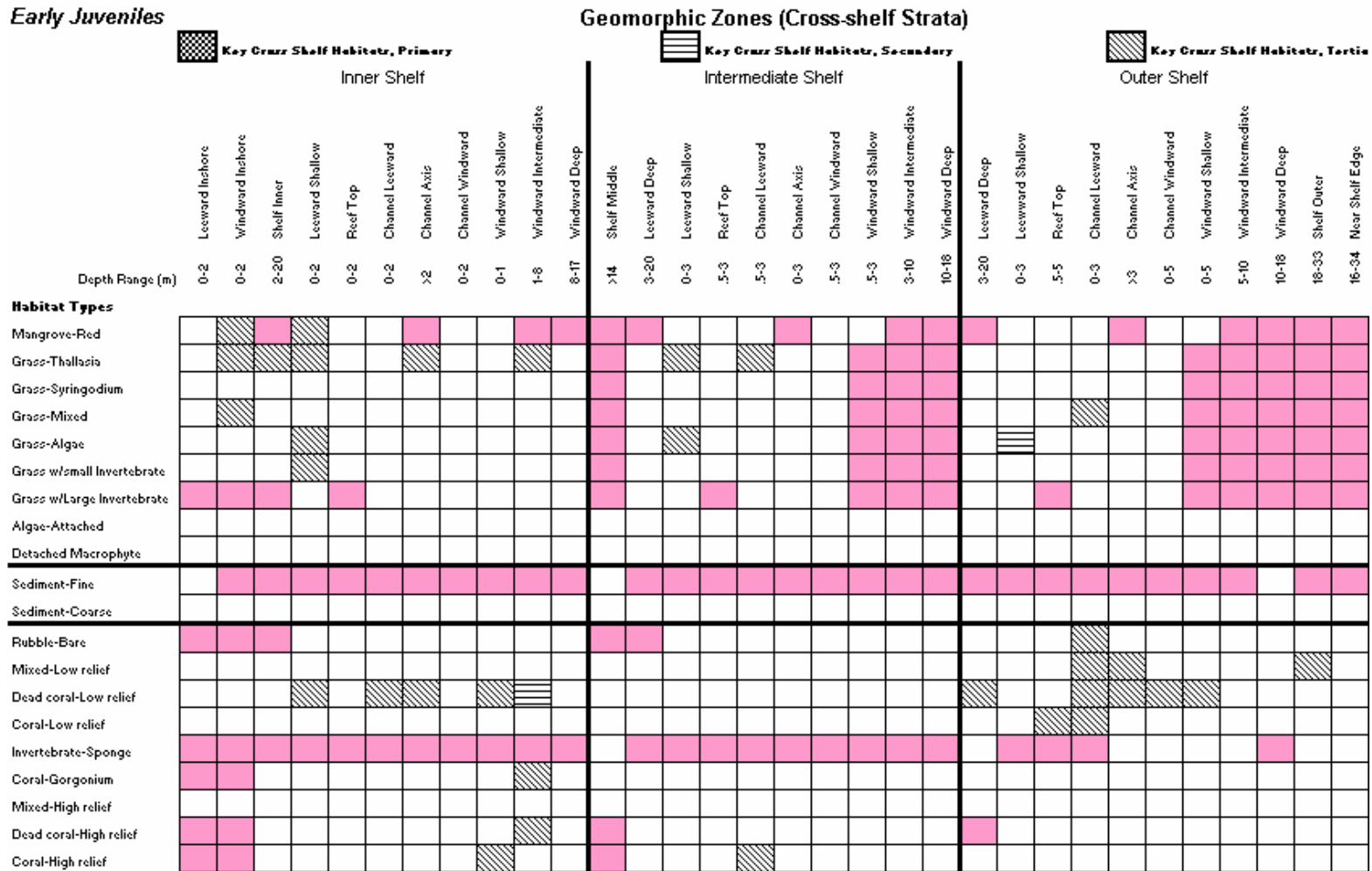


**Appendix F - Relative key cross-shelf habitats of La Parguera, Puerto Rico determined by frequency of occurrence across all fish species (see text for details).**

# Appendix F.1

Relative key cross-shelf habitats of La Parguera, Puerto Rico determined by frequency of occurrence across all fish species (see text for details).

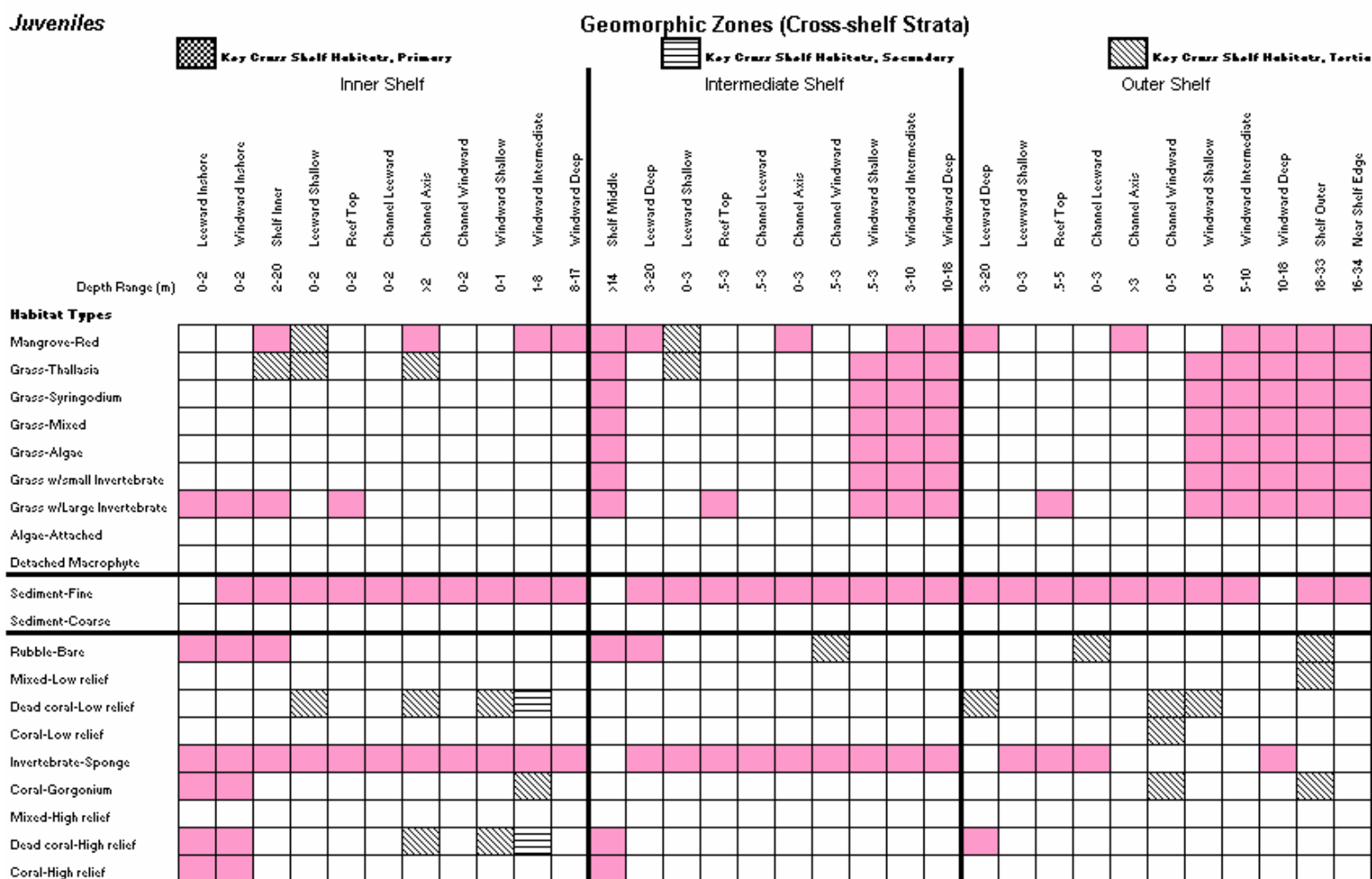
## Early Juveniles



## Appendix F.2

Relative key cross-shelf habitats of La Parguera, Puerto Rico determined by frequency of occurrence across all fish species (see text for details).

### Juveniles



### Appendix F.3

Relative key cross-shelf habitats of La Parguera, Puerto Rico determined by frequency of occurrence across all fish species (see text for details).

#### Adults

