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FISH DENSITY, DIVERSITY, AND SIZE-STRUCTURE WITHIN MULTIPLE BACK REEF HABITATS OF KEY WEST NATIONAL WILDLIFE REFUGE

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ABSTRACT

Tropical and subtropical back reef habitats such as seagrass meadows, mangrove prop-roots, and channels bisecting mangrove islands presumably serve as important nursery areas for numerous fishes. This study provides an initial step towards identification of the nursery role of specific habitats within multiple back reef habitats by quantifying fish density, diversity, and size-structure, and was part of a larger study that used aerial photographs, ground-truthing, and GIS software to map putative nursery habitats in the Key West National Wildlife Refuge (KWNWR). Visual surveys assessed fish density, diversity, and size-structure in the Lakes and Marquesas regions of the KWNWR over a 3-mo period and across the marine habitats of concern (seagrass, channels, mangroves, hardbottoms, patch reefs, offshore reefs). A combination of band transects and 10-min surveys provided a more complete overall species assessment than either method in isolation. Mangrove prop-root habitats contained the highest relative mean density and diversity of fish, with abundant forage fish such as silverside minnows (Atherinidae) and herrings (Clupeidae), as well as a high number of piscivores such as gray snapper *Lutjanus griseus* (Linnaeus, 1758) and barracuda *Sphyraena barracuda* (Walbaum in Artedi, 1792). Channel habitats contained the greatest diversity of microhabitats, and contained a relatively high diversity of fish compared to seagrass. Channel habitats typically harbored juvenile snappers (Lutjanidae), grunts (Haemulidae), and forage fish (Atherinidae). Qualitatively, we observed greater numbers of relatively large gamefish, as well as rare and threatened species in channel and mangrove habitats than any other habitat. Conversely, seagrass contained higher fish densities than channels. Increases in the size-frequency of certain species, such as *S. barracuda*, *Pomacanthus arcuatus* (Linnaeus, 1758), and *Gerres cinereus* (Walbaum in Artedi, 1792), from back-reef habitats such as seagrass and mangroves, to channels and eventually patch and offshore reefs were suggestive of ontogenetic patterns of habitat use. In contrast, the smallest stages of *L. griseus* were found exclusively in seagrass, but remaining size classes, including adults, were found at all of the habitats surveyed. In contrast, the smallest size classes of *Halichoeres bivitattus* (Bloch, 1791), *Lutjanis synagris* (Linnaeus, 1758) and *Haemulon sciurus* (Shaw, 1803) were found in nearly all of the habitats examined. We found no relationship between fish density and diversity, or seagrass shoot density and blade height. Inclusion of seagrass, mangrove, and channel habitats in future studies of reef fish growth, survival, and emigration should produce a more complete picture of their nursery role in tropical back reef environments.

This publication is part in a series of papers resulting from a scientific workshop held at the Caribbean Marine Research Center (December 2001) to evaluate the importance of back reef systems for supporting biodiversity and productivity of marine ecosystems. Tropical and subtropical back reef habitats such as seagrass meadows and mangrove prop-roots presumably serve as important nursery areas for numerous reef fishes (Weinstein and Heck, 1979; Stoner, 1983; Sogard et al., 1987; Morton, 1990; Eggleston, 1995; Ley et al., 1999; Nagelkerken et al., 2000; Dahlgren and Eggleston, 2001, Laegdsgaard and Johnson, 2001). These habitats are thought to intercept large numbers of larvae and provide abundant food resources and protection from predators (Parrish, 1989; Dahl-

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gren and Eggleston 2000; Laegsgaard and Johnson, 2001). Fish eventually migrate from these nursery habitats to nearshore patch reefs and offshore reefs as they mature. The term "back reef nursery" implies that juvenile fish density and ecological processes such as growth, survivorship, and emigration success should be enhanced compared to adjoining juvenile habitat types (Beck et al., 2001). A habitat is a nursery if its contribution per unit area to the production of individuals that recruit to adult populations is greater, on average, than production from other habitats in which juveniles occur (Beck et al., 2001). The ecological processes operating in nursery habitats, as compared with other habitats, must support greater contributions to adult recruitment from any combination of four factors: (1) density, (2) growth, (3) survival of juveniles, and (4) movement to adult habitats (Beck et al., 2001). There are very few data that compare animal density and ecological processes across multiple, structurally complex habitats that characterize tropical and subtropical back reef environments (Nagelkerken et al., 2000; Beck et al., 2001). This study provides an initial step towards identification of the nursery role (sensu Beck et al., 2001) of specific habitats within multiple back reef habitats by quantifying fish density, diversity and size-structure, and was part of a larger study that mapped putative nursery habitats in the KWNWR and quantified distribution and abundance of Caribbean spiny lobster in these habitats (Eggleston and Dahlgren, 2001).

The Florida Keys marine ecosystem in the U.S. supports important commercial and recreational fisheries for both fish and invertebrates [e.g., snapper, Lutjanidae; grouper, Serranidae; Caribbean spiny lobster, *Panulirus argus* (Latreille, 1804); stone crab, *Menippe mercenaria* (Say, 1818)], as well as a marine-based tourism industry. Despite the ecological and economic significance of the Florida Keys coral reef ecosystem, it is faced with a growing number of threats including water quality degradation (Lapoint and Clark, 1992), habitat loss (Robblee et al., 1991; Durako, 1994; Herrnkind et al., 1997), and overfishing (e.g., Ault et al., 1998). These multiple insults have led to the Florida Keys coral reef ecosystem being classified as an "ecosystem-at-risk" (NMFS, 1996). To conserve this threatened ecosystem, a network of protected areas is being established to safeguard its living resources.

The first protected area in the Florida Keys was the Key West National Wildlife Refuge (KWNWR), established in 1908. Marine habitats within the KWNWR include mangroves, seagrass meadows, hardbottom, macroalgal beds, sand flats, and coral reefs. Both recreational and commercial fishing are allowed within a majority of the KWNWR. Although most of the refuge consists of shallow bank and seagrass habitats interspersed with mangrove islands, it also contains numerous patch reefs within Hawk Channel to the south and north towards the Gulf of Mexico. Within the KWNWR are two smaller areas referred to as the "Lakes" and "Marquesas" (122 km^2; Fig. 1). These smaller areas contain a complex mosaic of habitat types including seagrass, channels, macroalgal meadows, hardbottoms, mangroves, and patch reefs. In this study, we 1) mapped the distribution and aerial cover of habitats for reef fish in the "Lakes" and "Marquesas," 2) quantified fish density, diversity, and size-structure across the mosaic of five habitats described above, as an initial step towards identification of the nursery role (sensu Beck et al., 2001) of these habitats, and 3) quantified the relationship between fish abundance and specific habitat features.

Methods and Materials

Habitat Mapping and Sampling Sites

The KWNWR is a rectangular-shaped (82° 10′ W × 24° 40′ N, 81° 49′ W × 24° 27′ N) area measuring 766.9 km^2. Initial site and habitat reconnaissance was conducted during July, 1999 by ground-truthing aerial photographs (1:48,000; obtained from the National Ocean Service, NOAA) of the Lakes (24° 35′ N, 82° 55′ W) and Marquesas (24° 36′ N, 82° 8′ W) regions with a small (7 m) boat, and by snorkeling and SCUBA diving. We identified six habitats within which to quantify the density, diversity, and size-structure of fish: 1) submerged mangrove (*Rhizophora mangle* L.) prop-roots; 2) channels bisecting mangrove islands or seagrass shoals; 3) subtidal seagrass beds; 4) inshore hardbottoms; 5) inshore patch reefs; and 6) offshore reefs (Fig. 1). We digitized the aerial photographs and estimated areal cover of seagrass beds (both subtidal and intertidal) and channels, as well as the perimeter of mangroves, using GIS ArcView software. We were unable to delineate hardbottom and reef habitats because these substrates were not clearly visible.

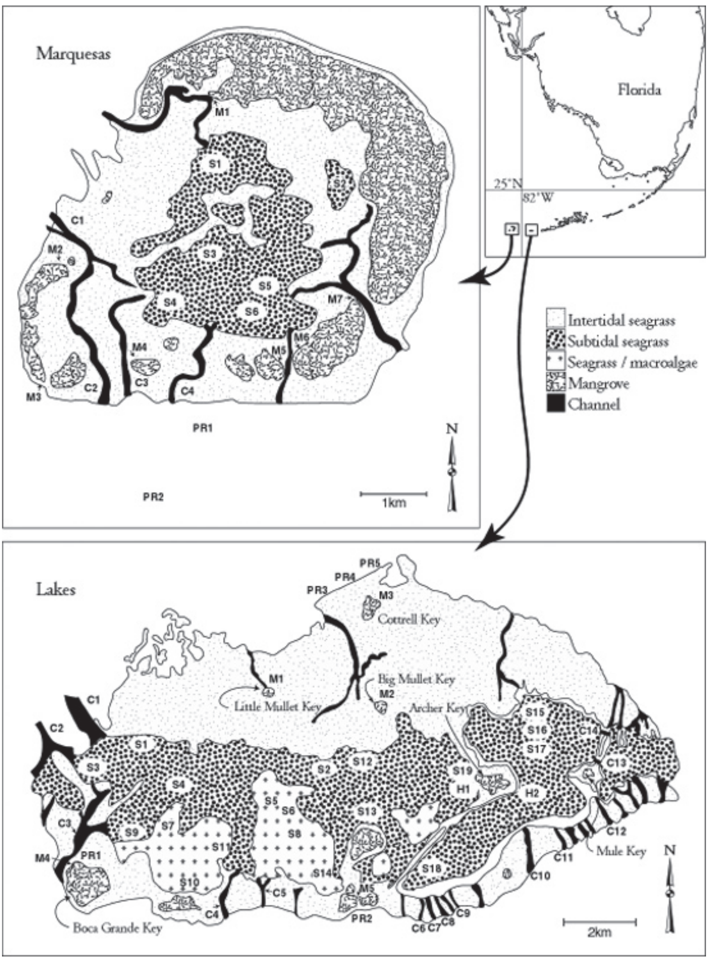

Figure 1. Schematic of habitat types and locations of sampling stations within the Lakes and Marquesas regions within the Key West National Wildlife Refuge (KWNWR), Florida. Habitat maps were generated with ground-truthed, geo-referenced, and digitized aerial photographs (1:48,000 scale obtained from the National Ocean Services, NOAA). C = channel habitats, S = seagrass habitats, M = mangrove habitats, H = hardbottom habitats, and PR = patch reefs. Alphanumerics (e.g., M1, S1, etc.) are sample sites. See text for details regarding the sampling approach.

Fish Density and Microhabitat Features

We used visual survey techniques to rapidly assess the distribution and abundance of reef fishes in the Lakes and Marquesas regions over a 3-mo period and across the marine habitats of concern (seagrass, channels, mangroves, hardbottoms, patch reefs, offshore reefs). All surveys were conducted during the day when water visibility exceeded 10 m, and during a 7-d window bracketing the new moon each month so as not to confound fish counts with possible variation in abundance due to diel and lunar variation in migration behavior (Helfman et al., 1982; Rooker and Dennis, 1991; Kasai et al., 2000 and references therein).

We used a stratified random survey procedure for fishes in subtidal seagrass beds (Fig. 1), and randomly chose channels, mangroves, hardbottoms, patch reefs, and offshore reefs to survey fish. The areal cover of seagrass and channels was ~3–6 times greater in the Lakes than in the Marquesas (see below), thus our sample size for seagrass and channels was ~4 times higher in the Lakes than in the Marquesas. Fish counts were conducted with two general approaches, each using SCUBA divers: 1) visual band transects, which provided density estimates, and 2) 10-min surveys with visual estimates of area searched, which provided an additional, although cruder, measure of density. During September 2002, we assessed the accuracy of our visual estimates of distance traveled during 10-min swims in seagrass and mangroves that were located in the nearby Great White Heron National Wildlife Refuge.

Habitat-Specific Surveys

Seagrass.—To sample fishes in seagrass, a grid system containing cells measuring ~200 × 200 m was superimposed over a navigational chart of each region. We then randomly chose 19 cells and six cells at the Lakes and Marquesas, respectively, and used SCUBA divers to quantify fish density, diversity and size-frequency, as well as habitat characteristics, in each cell. If a randomly chosen cell corresponded to an intertidal seagrass bed, we randomly chose another cell until a subtidal seagrass site was selected. Two parallel band transect lines (60 × 2 m) were then placed as close as possible to the center latitude and longitude coordinates for each grid cell using a GPS. The transects were located parallel to each other ~100 m apart, and were identified with floats at the ends. Divers initiated their surveys ~20 min after the transect lines were deployed, and began at the downstream edge of each cell such that divers began their survey by swimming against the current. All counts within a single band were made by two divers; the first diver would count fishes and the second diver quantified habitat characteristics (see below). Fish total length (TL) was estimated to the nearest 1 cm by comparing a fish to a ruler attached perpendicular to the far end of a 70 cm rod held out from a diver (Eggleston, 1995; Eggleston et al., 1997). This device helped avoid underwater magnification problems in estimating fish sizes. Divers counting fishes slowly swam along each transect and used a 2-m long PVC-pipe to delineate the 2-m band width. Although estimates of fish size were made at the resolution of 1 cm, fish sizes were compared among habitats by categorizing size distributions into 5-cm size classes. The 2-m PVC-pipe was also slowly pushed through seagrass or macroalgae to "herd" small, cryptic fishes for periodic enumeration. The response variable produced from the band transects was the density (no. 120 m^{-2}) of fishes.

There is often a positive relationship between macrophyte structural complexity (e.g., seagrass shoot density and biomass) and fish density in macroalgal and seagrass systems (Carr, 1994; Eggleston, 1995; Levin and Hay, 1996). Thus, we measured seagrass habitat characteristics (mean shoot density and blade height) adjacent to each band transect within a grid cell (N = 2 $cell^{-1}$). Seagrass shoot density was quantified by blindly tossing a 0.07 m^2 quadrat near the starting point of each band transect. Individual seagrass shoots and mean blade height (mean of 10 haphazardly chosen shoots measured with a ruler) within a quadrat were counted by SCUBA divers. After seagrass characteristics were measured within a quadrat, percent cover of six benthic habitat categories (each covering > 1% of the total area) were estimated along each 2 × 60 m band to the nearest 5%: (1) seagrass (*Thalassia testudinum* Banks & Soland. ex Koenig, *Syringodium filiforme* Kuetz., *Halodule* sp.); (2) *Laurencia* sp. (including *Laurencia*-covered coral clumps); (3) other macroalgae (including *Penicillus* sp., *Udotea* sp., and *Halimeda* sp.); (4) relatively large sponges [primarily *Speciospongia vesparia* (Lamarck, 1814)]; (5) coral (predominantly *Porites porites* (Pallas, 1766) including both live and dead coral rubble); and (6) sand (usually sand or a thin sand veneer over rock). To increase the accuracy of estimates, habitat data were recorded every 20 m and then combined for each band. In our previous studies using these techniques (Eggleston, 1995; Dahlgren and Eggleston, 2001), two divers independently estimated percent cover along a given transect, which never varied much between divers (< 10% in all cases; Dahlgren and Eggleston, 2001). Therefore, we used one diver per transect to quantify habitat characteristics in this study. Diver estimates, however, were averaged across transects to reduce individual diver bias.

After a band transect was completed, divers continued to swim up-current in a straight line, and initiated a timed (10 min) visual survey for fishes. The timed transect started ~10 m from the end of the band transect to reduce the chance of counting the same fishes. At the end of the 10-min survey the diver surfaced, visually estimated the distance back to the band transect float, and subtracted 10 m to estimate the total distance traveled. The distance traveled averaged 120 m. During September 2002, we used a differential GPS (accurate within 3 m) on a research boat to assess the accuracy of diver estimates of distance traveled. We compared diver estimates of distance traveled with the known distance from latitude/longitude points taken at the start and end of the 10-min swim. Although divers tended to over-estimate the distance traveled (mean = + 4.5 m, SE = 4.9 m, N = 12), there was no significant difference between diver estimates of distance traveled and distances measured with the differential GPS (paired t-test, $t = 0.90$, $P = 0.39$). Thus, diver estimates of distance traveled in seagrass were relatively accurate. The width of the 10-min transect was determined by water visibility, which averaged 10 m. Thus, the 10-min survey in seagrass covered an estimated average area of 1200 m^2. Although this method of estimating distance traveled was somewhat crude, it provided an estimate of fish densities and variance that could be used to 1) estimate required sample sizes for future studies, 2) make relative comparisons of density across structurally complex habitat types, and 3) qualitatively compare fish density between band transect and timed swim survey methods. The mean values between the two surveys within a seagrass cell (i.e., two band transects and two, 10-min swims) served as a single replicate (N = 19 and six at the Lakes and Marquesas, respectively).

Channel Habitats.—Channel habitats measuring 2–4 m deep that bisect mangrove islands and intertidal seagrass (Fig. 1) probably serve as important conduits for ontogenetic migrations of some species from nursery habitats within the Lakes and Marquesas to offshore reefs. In total, 14 and four channels were randomly chosen from available channels at the Lakes and Marquesas, respectively (Fig. 1). Two separate band transects and two separate 10-min surveys were conducted within each channel as described above for seagrass. We quantified fishes and habitat characteristics as described above for seagrass habitats, with the additional quantification of sponge habitat characteristics. The mean values for fish density and habitat characteristics between the two surveys (two bands or two, 10-min surveys) within a channel served as a single replicate (N = 14 and four at the Lakes and Marquesas, respectively). The average estimated area searched during 10-min surveys in channel habitats was 1000 m^2.

Large sponges were a relatively common feature of channel bottoms probably due to high tidal current speeds (1–1.5 m s^{-1}), which scoured the bottom providing a hard substrate for sponge attachment, and delivered a high concentration of suspended food for these suspension-feeders. The total number of sponges and sponge volume per transect (120 m^2) was estimated by divers. We estimated sponge volume by measuring the radius (r) and height (cm) of each sponge with a ruler, and then treating each sponge as a cylinder and multiplying height by πr^2.

Hardbottom Habitats.—Within seagrass beds in the Lakes region, we observed hardbottom areas that were devoid of seagrass but contained solution holes, sponges, and coral rubble, and were typically 1–4 ha in area. These hardbottom areas were absent for the most part in the Marquesas, and relatively uncommon in the Lakes (H1 and H2 located east and west of "Archer Key"; Fig. 1). Hardbottom habitats provided some of the only crevices available for crevice-dwelling fishes (e.g., Serranidae) within large seagrass beds, and so were included in our Lakes surveys during September (N = 2 hardbottom sites). Fishes and habitat features were quantified using both band transect and timed survey methods, as described above for seagrass habitats. The average estimated area searched during 10-min surveys in hardbottom areas was 400 m^2.

Mangroves.—Snorkelers conducted 10-min surveys for fishes in mangrove prop-root habitats. Snorkel was used instead of SCUBA to avoid becoming entangled on the prop-root canopy while searching the shallow interstices of the prop-root canopy. Each mangrove survey was conducted by 2–4 snorkelers surveying non-overlapping areas, with the mean values between divers used in statistical analyses (N = 5 and seven in the Lakes and Marquesas, respectively). We estimated the area covered during a 10-min search by recording the distance that we could reliably count fish within the prop-root canopy (~2–4 m), and by placing floats at the beginning and end of a survey. After a particular survey was completed, we visually estimated the linear distance surveyed between the floats marking the beginning and end of a transect, and accounted for indentations along the mangrove fringe, which would add distance to the distance traveled. During September 2002, we used a tape measure to assess the accuracy of diver estimates of distance traveled. We compared diver estimates of distance traveled with the known distance from laying out a tape measure along the mangrove fringe that was surveyed. In this case, divers tended to underestimate the distance traveled (mean = –1.75 m, SE = 2.35 m, N = 20); however, there was no significant difference between diver estimates of distance traveled and distances measured with the underwater tape measure (paired t-test, t = -0.75, P = 0.47). Thus, diver estimates of distance traveled along the mangrove fringe were relatively accurate. Our estimates of linear distance traveled during a 10-min search ranged from 10–80 m, and averaged 38 m. The average estimated area covered during 10-min surveys in mangrove prop-root habitats was 152 m^2. Although we randomly chose seven out of all available mangrove habitats to sample at the Marquesas, we were restricted to five mangrove areas in the Lakes (Fig. 1) because all of the other mangrove areas were inaccessible by boat due to extremely shallow water.

Nearshore Patch and Offshore Reefs.—We counted reef fishes at all patch reef sites that we could locate near the Lakes (N = 5) and Marquesas (N = 2; Fig. 1) with the 10-min survey method. Patch reefs consisted primarily of clusters of patch coral heads surrounded by seagrass south of the Marquesas, and a series of ledges, hardbottoms, and patch heads north of Cottrell Key in the Lakes (Fig. 1). We also used this survey method to quantify the abundance of fishes at the following randomly chosen offshore reefs within the KWNWR: “Sand Key,” “Western Dry Rocks,” “Coalbin Rocks,” and the eastern portion of “Cosgrove Shoals.” These offshore reefs are not shown on Figure 1, but were located 12–15 km south of the Lakes and Marquesas along the southern boundary of the KWNWR. Fish counts and sizes were estimated as described above for seagrass habitats, but with four divers. The divers surveyed areas that were 90º in the opposite direction of each other. We used the mean counts from a total of four divers per reef in statistical analyses. The areas searched per diver during 10-min surveys of *patch reefs* ranged from 300–700 m^2 and averaged 600 m^2. The areas searched per diver during 10-min surveys of *offshore reefs* ranged from 1000–1700 m^2, and averaged 1500 m^2. In summary, the band-transect and 10-min survey methods were used in seagrass, channel, and hardbottom habitats, whereas only the 10-min survey method was used in mangrove prop-roots, patch reefs, and offshore reefs.

Statistical Analyses

We examined the effects of region (Lakes vs Marquesas) on the mean density of reef fishes in seagrass, mangrove, channel, and patch reef habitats with separate t-tests. We used separate t-tests, rather than an ANOVA approach that would include habitat type as a factor, because we did not know how the accuracy of our visual survey techniques compared across habitat types, and because of widely different search areas across habitat types (e.g., 152 m^2 for mangroves and 1200 m^2 for seagrass). For example, animal diversity often increases with area searched (Rosenzweig, 1995). The response variables from the band transect and timed surveys were the mean densities of: 1) fishes (including atherinids, which dominated the counts in many surveys); 2) fishes without atherinids; 3) fish families; and 4) fish species. The data were log of (x + 1) transformed when necessary to meet the assumptions of normality (tested with a Kolmogorov-Smirnov test) and homogeneity of variances (tested with Levene’s test). We calculated the mean density of fishes in hardbottom and offshore reef habitats, but did not statistically contrast these data across regions (Lakes vs Marquesas) because hardbottoms were only sampled in the Lakes, and offshore reefs were located well outside of the Lakes and Marquesas.

A forward, stepwise multiple regression model was used to examine the relationship between habitat characteristics and reef fish density measured during band transects in seagrass and channel habitats. Separate models were used for seagrass and channels. For seagrass, the regression model included as independent variables: 1) seagrass shoot density, 2) mean seagrass blade height, and 3) the percent cover of *Thalassia*, *Syringodium*, *Halodule*, *Laurencia*, other macroalgae, sponges, coral, and sand. For channel habitats, the independent variables were similar to those of seagrass, with the addition of 1) sponge density and 2) mean sponge volume. Alpha to enter and remove factors from the model was 0.10.

Results

Habitat Areal Cover and Microhabitat Characteristics

The most visible components of the landscape in aerial photographs of the Lakes and Marquesas were mangrove-fringed islands, dense seagrass beds, shallow intertidal seagrass, and channels (Fig. 1). Intertidal seagrass was the most extensive habitat in terms of areal cover at both regions (Table 1), with an area of 58.27 km^2 and 14.52 km^2 at the Lakes and Marquesas, respectively. The second most extensive habitat was subtidal seagrass beds (Table 1). The areal cover of subtidal seagrass beds was ~6 times greater at the Lakes (37.89 km^2) than at the Marquesas (5.7 km^2). Diver surveys covered an estimated total subtidal seagrass area of ~0.05 km^2 and ~0.02 km^2 at the Lakes and Marquesas, respectively (Table 1). The areal cover of channels was ~3 times greater at the Lakes (5.6 km^2) than at the Marquesas (1.65 km^2). We surveyed ~0.007% and 0.006% of channel habitats at the Lakes and Marquesas, respectively (Table 1). The perimeter of mangrove fringe surrounding small islands (keys) within the KWNWR was slightly higher in the Marquesas (33.22 km) than in the Lakes (20.55 km).

Within subtidal seagrass beds, seagrass percent cover (primarily *Thalassia*) was always extremely high at the Marquesas, ranging from 94–100% (Appendix 1). We did not observe any appreciable areas that contained a mixture of seagrass and macroalgal beds at the Marquesas, whereas we sometimes observed a mosaic of both dense and moderate density seagrass interspersed with macroalgal meadows at the Lakes. Seagrass percent cover in transects at the Lakes ranged from a low of 5–14% in areas that contained a mixture of seagrass and macroalgal beds (e.g., stations S6, S14, Appendix 1), to a high of 100% (Appendix 1). The primary species of seagrass counted in quadrats at the Lakes and Marquesas was *T. testudinum* (Appendix 1), although we observed expansive beds of *Syringodium filiforme* and *Halodule* sp. at both the Lakes and Marquesas, particularly in channel habitats at the Marquesas. Although mean seagrass shoot count and blade height was higher in the Marquesas than the Lakes (Table 2), the mean values did not vary significantly by region (t-test; $P > 0.05$). Mean water depths in subtidal seagrass meadows were ~1.5 m in both the Lakes and Marquesas.

In general, channel habitats contained more diverse microhabitats than seagrass beds, with macroalgal clumps (*Laurencia* sp. + "other macroalgae") providing the greatest percent cover (mean = 27%), followed by sand (mean = 25%) and seagrass (mean = 24%) (Appendix 2). Sponges were absent in one of four channels in the Marquesas and two of 14 channels in the Lakes (Appendix 2). The mean density and volume of sponges in

Table 1. Estimates of areal cover of fish habitat in the Lakes and Marquesas regions of the KWNWR estimated from ground-truthed, geo-referenced, and digitized aerial photographs using ArcView software. Also provided are estimates of percent areal cover by a particular habitat within a region, and estimates of areal cover of visual surveys (band transects vs 10-min surveys) by divers. Estimates of areal cover for band transects was based on the number of seagrass or channel stations sampled in a region × 2 replicate transects/location (e.g., S1, C1, etc.) × 120 m^2. Estimates of areal cover for 10-min diver surveys were based on the number of seagrass or channel stations sampled in a region × 2 replicate transects/location × 1200 m^2. See text for details concerning areal cover of diver surveys. N/A = habitat not available to sample. BT = band transects and 10-min = 10-min surveys.

	Areal cover in km^2 and (% cover) within a region	
Habitat	Lakes	Marquesas
Subtidal seagrass	37.89 (34%)	5.70 (26%)
Intertidal seagrass	58.27 (52%)	14.52 (66%)
Seagrass/macroalgal beds	10.81 (10%)	N/A
Channels	5.60 (4%)	1.65 (8%)
	Perimeter (km)	
Mangroves	20.55	33.22
	Area surveyed (km^2)	
Subtidal seagrass* (BT)	0.0046	0.0014
Subtidal seagrass* (10-min)	0.0456	0.0144
Subtidal seagrass* (total)	0.0502	0.0158
Channels (BT)		0.0010
Channel (10-min)		0.0096
Channels (total)		0.0106

* Includes seagrass/macroalgal beds for the Lakes region

channel habitats did not differ between the Lakes and Marquesas (Table 3; t-test, $P > 0.05$).

Fish Density, Diversity, and Size-Structure.

We conducted a total of 248 diver surveys (124 band transects and 124 timed surveys combined) during a 21 d period in August–October, 1999 in the KWNWR, and recorded density, diversity, and size-structure of 114 species of fish representing 42 families (Appendix 3). We also observed commercially important stone crabs, queen conch (*Strombus gigas* Linnaeus, 1758) and Caribbean spiny lobster, as well as mating pairs of horseshoe crabs [*Limulus polyphemus* (Linnaeus, 1758)] within the KWNWR, but did not record their numbers or estimate size-frequencies. We also observed juvenile goliath grouper [*Epinephelus itajara* (Lichtenstein, 1822), ~30 cm TL] and Nassau grouper [*Epinephelus striatus* (Bloch, 1792); ~20 cm TL] residing in mangrove and crevice habitats outside of our surveys. Nassau and goliath grouper are federally protected species in the U.S.

Comparisons of Band Transect vs 10-min Surveys.—Similarity in the number of fish families, genera, and species between band transects and 10-min surveys was ~0.50 (Table 4). Divers swimming band transects often observed small, cryptic species such as newly settled *L. griseus*, *L. synagris*, and *G. cinereus* that were missed during 10-min swims, whereas divers conducting 10-min swims observed more large, transient fish species. Higher numbers of fish families, genera, and species were observed during 10-min surveys than in band transects (Table 4). There were 57 unique species observed in 10-min surveys, and eight unique species observed in band transects. Examples of

Table 2. Mean, range, standard deviation, and sample size for shoot count and blade height in subtidal seagrass beds in the Lakes and Marquesas regions of the KWNWR.

	Lakes	
	Shoot count (no. 0.07 m^{-2})	Blade height (cm)
Mean	26.23	29.74
Range	12.00–43.00	15.50–47.35
Standard deviation	10.7	9.52
n	18	18
	Marquesas	
Mean	31.3	36.50
Range	16.50–43.00	27.30–45.10
Standard deviation	11.4	6.29
n	6	6

unique species observed during 10-min surveys included: yellow jack *Caranx bartholomaei* Cuvier in Cuvier and Valenciennes, 1833, tarpon *Megalops atlanticus* Valenciennes in Cuvier and Valenciennes, 1847, red drum *Scianops ocellatus* (Linnaeus, 1766), and lemon shark *Negaprion brevirostris* (Poey, 1868). Examples of unique species observed during band transects included: foureye butterflyfish *Chaetodon capistratus* Linnaeus, 1758, Hamlets *Hypoplectrus* sp., and Gobies *Ioglossus* sp. Thus, the band transect and 10-min survey methods appear to be complementary in terms of characterizing fish diversity in backreef habitats.

Habitat-Specific Rank Order of Fish Abundance

Seagrass Habitats.—The fish fauna inhabiting seagrass beds often consisted of patchily distributed and tightly packed schools of silversides and herrings (Atherinidae and Clupeidae, respectively), which were typically located near the surface of the water column. Schools of demersal snapper (family Lutjanidae, primarily gray snapper, *Lutjanus griseus*), mojarras (family Gerreidae, *Gerres* spp.), sea bream (family Sparidae, *Archosargus rhomboidalis* (Linnaeus, 1758)), and juvenile grunts (family Haemulidae, primarily *Haemulon sciurus* and *H. plumieri*) were observed amongst the seagrass blades and bottom. We sometimes observed tarpon (*M. atlanticus*) and bonnethead sharks *Sphyrna tiburo* (Linnaeus, 1758) outside our band transects or after the 10-min surveys were complete. The most numerically abundant fish family inhabiting seagrass during band

Table 3. Mean, range, standard deviation and sample size for sponge count and sponge volume in channel habitats in the Lakes and Marquesas regions of the KWNWR.

	Lakes	
	Sponge count (no. 120 m^{-2})	Sponge volume (cm^3)
Mean	22.27	15,679.2
Range	0.00–99.00	105.20–46352.70
Standard deviation	35.2	17,679
n	14	7
	Marquesas	
Mean	23.50	16,283.90
Range	0.00–33.50	717.10–33283.00
Standard deviation	17.20	16,283.10
n	3	3

Table 4. Total number of fish families, genera, species, and unique species observed during band transects and 10-min surveys at the Lakes and Marquesas regions of the KWNMR during July–October, 1999. The Jaccard Index indicates the similarity of fish species, where 1 equals complete similarity.

	Band transects	10-min surveys	Jaccard index
No. of families	4	48	0.577
No. of genera	42	66	0.514
No. of species	73	122	0.500
No. of unique species	8	57	N/A

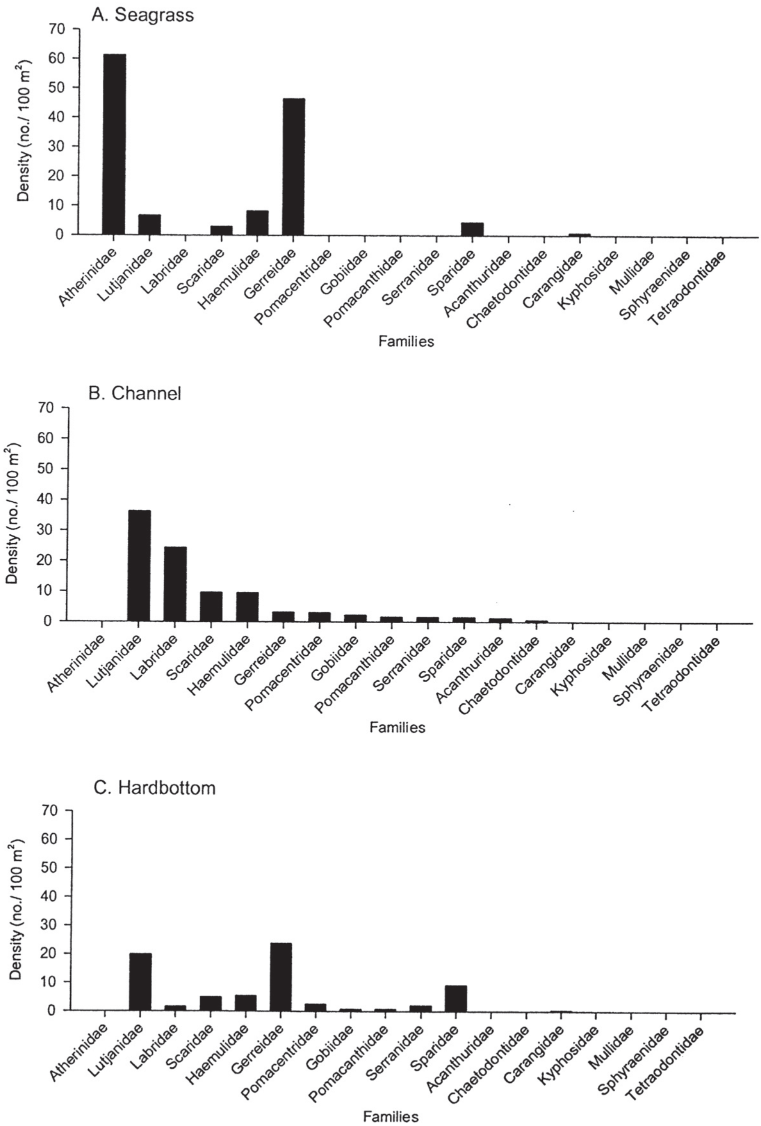

Figure 2. Rank order of abundance of fish from band transects in (A) seagrass, (B) channel, and (C) hardbottom habitats pooled across the Lakes and Marquesas regions of the KWNWR.

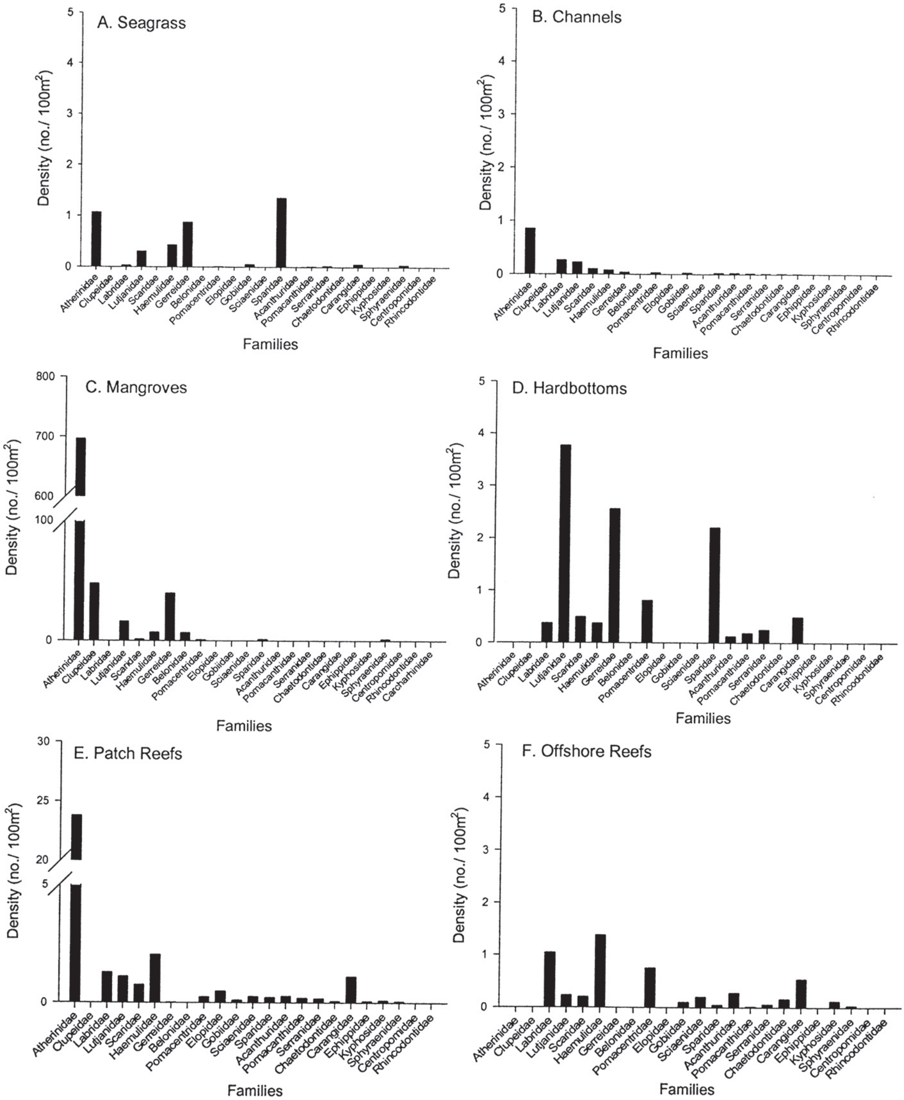

Figure 3. Rank order of abundance of fishes from 10-min surveys in (A) seagrass; (B) channel; (C) mangrove; (D) hardbottom; (E) patch reef; and (F) offshore reef habitats pooled across the Lakes and Marquesas regions of the KWNWR. Note different y-axis values for (C) and (E).

transects was Atherinidae, followed by Gerreidae, Haemulidae, and Lutjanidae (Fig. 2A). Conversely, the family Sparidae (primarily *Archosargus rhomboidalis*) had the highest density in seagrass using 10-min surveys, followed by Atherinidae, Gerreidae, Haemulidae, and Lutjanidae (Fig. 3A). Estimates of fish density from band transects were generally higher than 10-min surveys (Figs. 2A,3A).

Channel Habitats.—The most striking feature of fish assemblages inhabiting channel habitats during band transects was the relatively high number of fish species and families compared to seagrass (Figs. 4C,D). Upon entering the water at channels and before we began our transect surveys, we often saw sharks (primarily nurse sharks, *Ginglymo-*

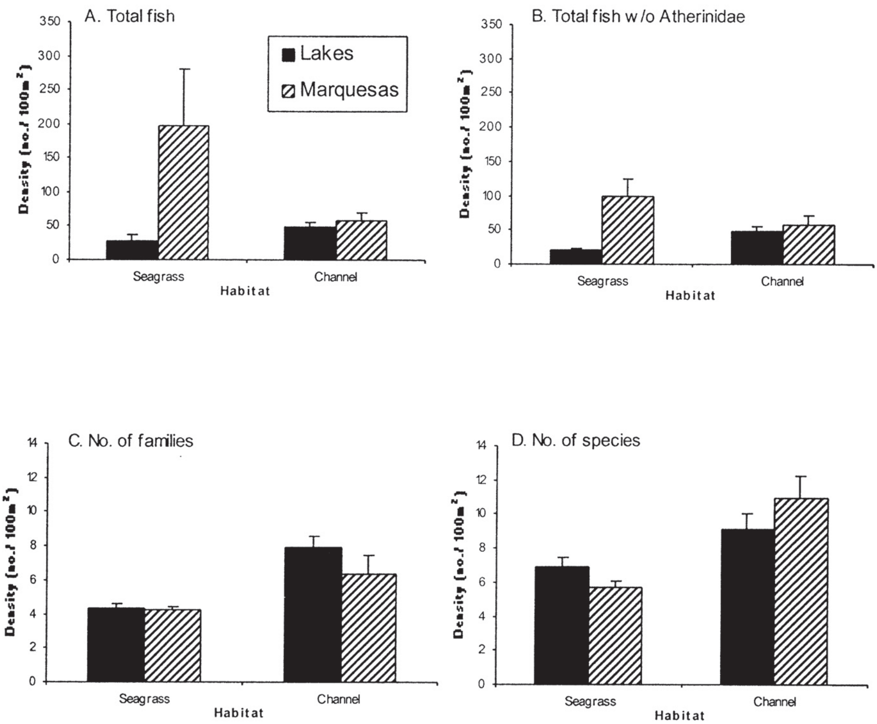

Figure 4. The effects of region (Lakes vs Marquesas) and habitat (seagrass, channels) on the mean (+ 1 SE) (A) density of fish; (B) fish without atherinids; (C) number of fish families; and (D) number of fish species measured with band transects. See text for details of statistical analyses.

stoma cirratum (Bonnaterre, 1788), lemon sharks, *Negaprion brevirostris*, and bonnethead sharks, *Sphyrna tiburo*), turtles [primarily loggerhead, *Caretta caretta* (Linnaeus, 1758) and green turtles, *Chelonia mydas* (Linnaeus, 1758)], and tarpon (*M. atlanticus*). These species typically swam out of the survey area by the time we initiated our 10-min surveys. The family Lutjanidae (snappers) had the highest density in channel habitats in band transects, followed by Labridae (wrasses), Haemulidae (grunts), and Scaridae (parrotfishes) (Fig. 2B). The most common species of lutjanid was *L. griseus*, followed by *Lutjanis synagris*. During the 10-min surveys within channel habitats, the family with the highest density was Atherinidae, followed by Labridae (*Halichoeres bivittatas*), Lutjanidae, and Scaridae (Fig. 3B). The top five families present in channel habitats were similar when the band transect and 10-min survey rank order of abundance indices were compared (Figs. 2B,3B). The exception was schooling atherinids, which were not commonly observed during band transects when divers were searching methodically for more cryptic species.

Hardbottom Habitats.—Within seagrass beds near "Archer Key" in the Lakes, there were several low relief hardbottom areas that were devoid of seagrass but contained solution holes, small sponges and patch corals (Fig. 1). These hardbottom areas represented some of the only crevice-type structure available within relatively large, monotypic stands of seagrass. The fish family with the highest density in hardbottom habitats was Gerriedae, followed by Lutjanidae, Sparidae, Haemulidae, and Scaridae (Fig. 2C).

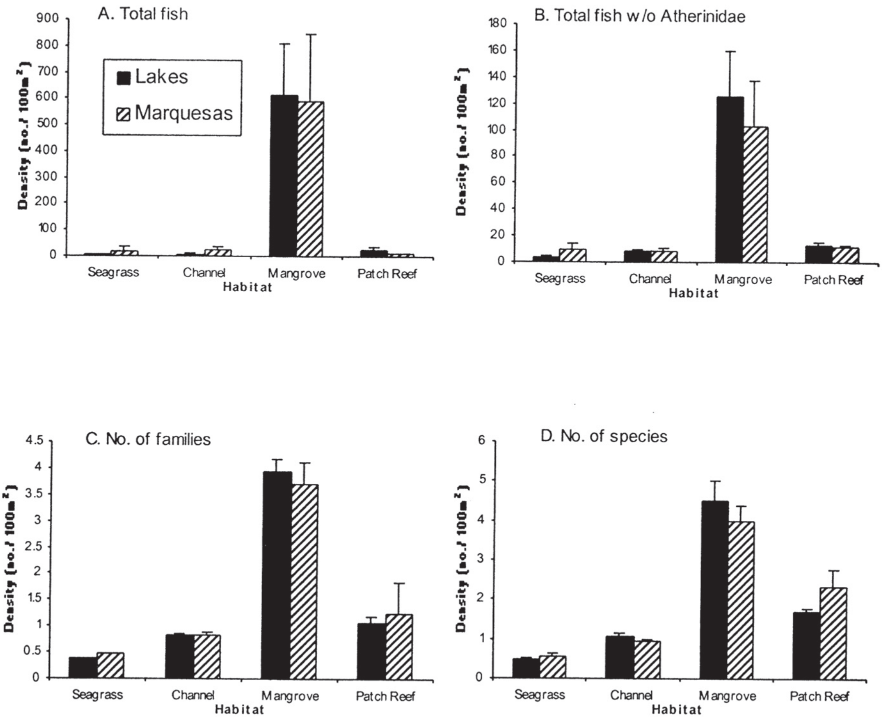

Figure 5. The effects of region (Lakes vs Marquesas) and habitat (seagrass, channels, mangrove, patch reefs) on the mean (+ 1 SE) (A) density of fishes; (B) fishes without atherinids; (C) number of fish families; and (D) number of fish species measured in 10-min surveys. The numbers above each histogram in (A) denote the number of sampling sites. See text for details of statistical analyses.

During the 10-min surveys, Lutjanidae had the highest density, followed by Gerreidae, Sparidae, and Pomacentridae (Fig. 3D). Lutjanidae was the top family in both band transect and 10-min surveys in hardbottoms; however, estimated densities were 5-times higher in band transects than 10-min surveys (Figs. 2C,3D).

Mangrove Habitats.—The most striking feature of fish assemblages inhabiting mangrove prop-root habitats was the extremely high density and diversity of fish (Fig. 5), and the clear domination by the family Atherinidae (silverside minnows; Fig. 3C), which often hovered along the mangrove fringe in tightly packed schools containing 1000s of individuals. The family Atherinidae had the highest density of any fish family across all habitats surveyed. The second most abundant fish family in mangroves was the Clupeidae (herrings; Fig. 3C), which also formed pelagic schools along the mangrove fringe, followed by the families Gerreidae, Lutjanidae (primarily *L. griseus*), and Haemulidae (primarily *Haemulon aurolineatum* Cuvier, 1830 and *H. sciurus*), which swam in schools among the mangrove prop-roots. Several relatively large (> 40 cm TL) gamefish species were observed residing within the mangrove prop-root canopy including tarpon *M. atlanticus*, snook *Centropomus undecimalis* (Bloch, 1792), and red drum *Sciaenops ocellatus*. We also observed Cubera snapper *Lutjanus cyanopterus* (Cuvier in Cuvier and Valenciennes, 1828). Although not included in our 10-min surveys, we also observed the following species in mangrove habitats: lemon shark *N. brevirostris*, silver porgy *Diplodus argenteus* (Valenciennes, 1830) and the mangrove terrapin *Malaclemys terrapin rhizophorarum* (Fowler, 1906).

Patch Reefs.—Patch reef habitats had the second highest densities of fish after mangrove habitats, and were dominated by Atherinidae (skewed by three patch reefs), followed by Haemulidae (primarily *Haemulon plumieri* (Lacépede, 1801) and *H. sciurus*), Labridae (primarily *H. bivittatas*), Lutjanidae (primarily *L. griseus* and *L. apodus*), and Carangidae [primarily *Caranx ruber* (Bloch, 1793), *Caranx latus* Agassiz in Spix and Agassiz, 1831, *Caranx crysos* (Mitchill, 1815)] (Fig. 3E).

Offshore Reefs.—The most abundant fish families residing in offshore reefs were Haemulidae (primarily *Haemulon flavolineatum* (Desmarest, 1823) and *Haemulon plumieri*), followed by Labridae (primarily *H. bivittatus* and *Halichoeres garnoti*), Pomacentridae (primarily *Chromis multilineata* (Guichenot, 1853) and *Abudefduf saxatilis* (Linnaeus, 1758)), Carangidae (primarily *Caranx ruber, Caranx latus, Caranx crysas*), and Acanthuridae [primarily *Holocentrus marianus* Cuvier in Cuvier and Valenciennes, 1829 and *Holocentrus adscensionis* (Osbeck, 1765)] (Fig. 3F).

Effects of Region and Habitat Type on Fish Density

Band Transects.—In seagrass, there were significantly higher numbers of fish at the Marquesas than at the Lakes, regardless of whether or not atherinids were included (Fig. 4A,B; t-test, $P < 0.04$). Conversely, in channels, there was no significant difference in total numbers of fishes between the Lakes and Marquesas (Fig. 4A,B; t-test; $P > 0.14$). There was also no difference in the number of fish species and families between the Lakes and Marquesas, irrespective of habitat type (Fig. 4C,D; t-test; $P > 0.26$). Qualitatively, there was a trend towards higher diversity (fish species and families) in channels than seagrass, despite relatively higher total numbers of fishes in seagrass (Fig. 4A,B). Higher diversity of fishes in channels may have been due to the relatively high diversity of microhabitats in channels (e.g., sponges, macroalgae, seagrass, corals; Appendix 2).

10-Min Surveys.—There were significantly higher total numbers of fishes observed at the Marquesas than the Lakes, which was similar to the pattern observed during band transects (Fig. 5A,B; t-test; all $P < 0.04$). There was no significant difference in the total numbers (with and without Atherinids) and diversity (species and families) of fishes between the Lakes and Marquesas in mangrove and patch reef habitats, and no difference in fish diversity between the Lakes and Marquesas in seagrass (Fig. 5, t-test; all $P > 0.18$). Qualitatively, the mean density and diversity of fishes was 3–5 times higher in mangroves than seagrass, channel, or patch reef habitats (Fig. 5). This pattern of highest fish abundance and diversity in mangroves was consistent across both regions (Fig. 5).

Relationship Between Fish Density and Microhabitat Features

Although there was a positive trend between the density of lutjanids and seagrass shoot density, there was no significant relationship between fish density and any of the microhabitat features measured (multiple regression, all $P > 0.09$). The lack of a relationship between fish abundance and habitat characteristics (e.g., seagrass shoot density, blade height, % macroalgal cover) may have been due to the relatively low number of samples taken to characterize seagrass (i.e., one 0.07 m^2 quadrat per transect line), or the generally high amount of habitat available. For example, seagrass shoot density in the Marquesas was very high, and percent cover averaged 95%. In the Lakes in areas where seagrass percent cover was somewhat lower, these areas contained a mixture of alterna-

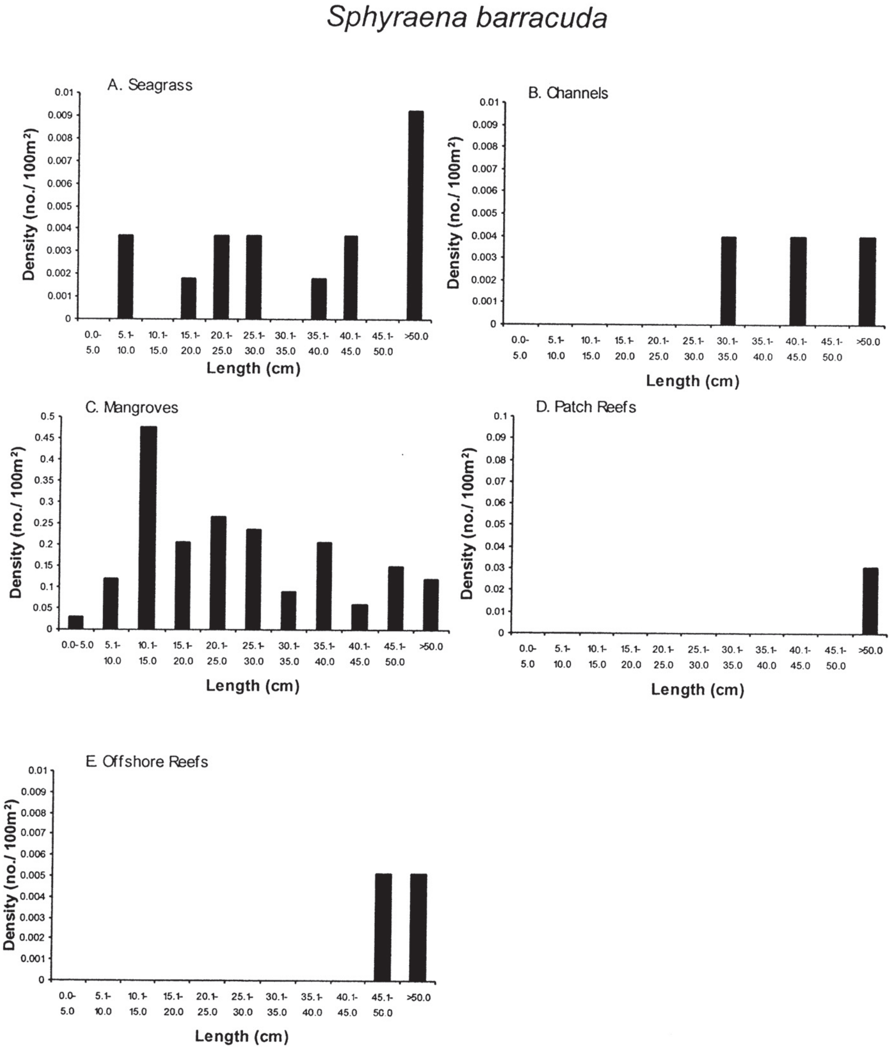

Figure 6. The size frequency distribution of *Sphyraena barracuda* (barracuda) observed during 10-min surveys in (A) seagrass; (B) channels; (C) mangroves; (D) patch reefs; and (E) offshore reefs for the Lakes and Marquesas regions pooled. Note different y-axis values in (C).

tive microhabitats such as coral rubble and clumps of macroalgae (primarily *Laurencia* spp.).

Ontogenetic Habitat Shifts

We examined body size-specific habitat use in several species as a possible indicator of ontogenetic habitat shifts. One of the clearest examples of size-specific habitat use was barracuda *Sphyraena barracuda* (Walbaum, 1792). The size-frequency of *S. barracuda* shifted from a mixture of size classes in seagrass and mangroves, to only the largest stages in channels, patch reefs, and offshore reefs (Fig. 6). Gray angelfish *Pomacanthus arcuatus* (Linnaeus, 1758) also demonstrated size-specific habitat use, with the smallest sizes in seagrass, hardbottom and channel habitats, and largest sizes in offshore

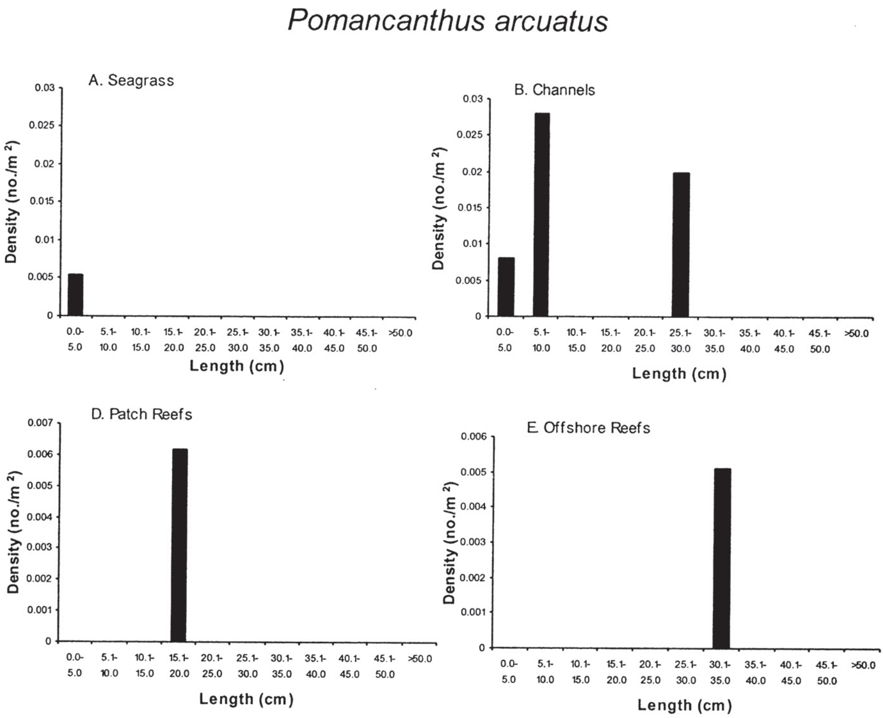

Figure 7. The size frequency distribution of *Pomacanthus arcuatus* (gray angelfish) observed during 10-min surveys in (A) seagrass; (B) channels; (C) patch reefs; and (D) offshore reefs for the Lakes and Marquesas regions pooled. Note lower density on y-axes of (C) and (D).

reefs (Fig. 7). Similarly, the smallest *Gerres cinereus* (Walbaum, 1792) (yellowfin mojarra) were found in seagrass, channels and mangrove habitats, and only the largest size class occurred on patch reefs (Fig. 8). Although the smallest size classes of *L. griseus* (gray snapper) occurred in seagrass, the largest size classes were observed in all habitats (Fig. 9). Certain fish species appeared to use both back-reef and offshore reef habitats as early juvenile habitat; these species included *Lutjanus synagris* (lane snapper; Fig. 10), *H. bivitatttus* (slippery dick; Fig. 11), and *H. sciurus* (bluestripped grunt; Fig. 12).

Discussion

In this study we provide an initial assessment of the nursery role (based solely on daytime fish densities) of multiple, structurally complex tropical backreef habitats for fish, with comparisons of fish species composition and size-structure to reefs located offshore. The combination of band transects and 10-min surveys provided a more complete overall species assessment than either method in isolation. Based on visual surveys, mangrove habitats in the KWNWR contained the highest relative mean density and diversity of fishes, with abundant forage fish such as silverside minnows (Atherinidae) and herrings (Clupeidae), as well as a high number of piscivores such as *L. griseus* (gray snapper) and *S. barracuda* (barracuda). Thus, based solely on the density criterion for identifying nursery habitats (Beck et al., 2001), mangroves appear to be the most important backreef nursery habitat in the KWNWR. An important caveat to this conclusion,

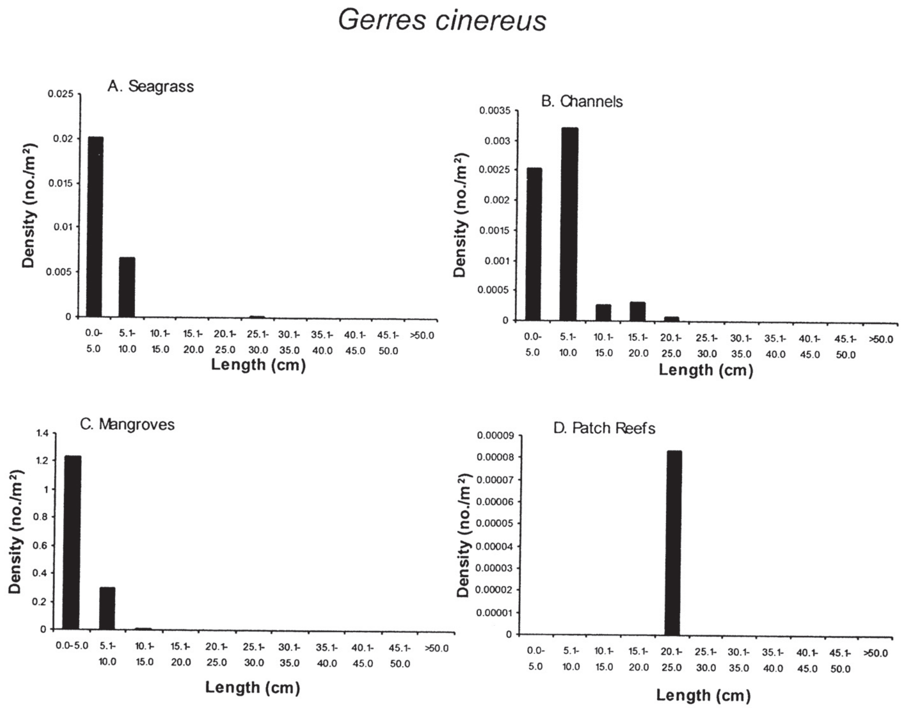

Figure 8. The size frequency distribution of *Gerres cinereus* (yellowfin mojarra) observed during 10-min surveys in (A) seagrass; (B) channels; (C) mangroves; and (D) patch reefs for the Lakes and Marquesas regions pooled. Note different y-axis values.

however, is the nocturnal use of nearby seagrass meadows by mangrove fishes (pers. obs.). Mangrove prop-roots provide small juvenile fish with an architecturally complex substrate that provides maximum food availability and minimizes the risk of predation (Laegdsgaard and Johnson, 2001). Mangrove fishes probably also rely on food in adjacent seagrass meadows during nighttime foraging, such that the nursery role of mangroves is invariably linked to nearby seagrass habitat. Channel habitats contained the greatest diversity of microhabitats, and contained a relatively high diversity of fish compared to seagrass. Channel habitats typically harbored juvenile snappers (Lutjanidae), grunts (Haemulidae), and forage fish (Atherinidae). Qualitatively, we observed greater numbers of relatively large gamefish, as well as rare and threatened species in channel and mangrove habitats than any other habitat. Conversely, seagrass contained higher fish densities than channels. Increases in the size-frequency of certain species, such as *S. barracuda*, *P. arcuatus*, and *G. cinereus*, from backreef habitats such as seagrass and mangroves, to channels and eventually patch and offshore reefs were suggestive of ontogenetic patterns of habitat use. In contrast, the smallest stages of *L. griseus* were found exclusively in seagrass, but remaining size classes, including adults, were found at all of the habitats surveyed. In contrast, the smallest size classes of *H. bivitattus*, *L. synagris*, and *H. sciurus* were found in nearly all of the habitats examined.

Potential Sampling Biases.—We used visual survey techniques to rapidly assess fish distribution and abundance patterns in the Lakes and Marquesas regions over a 3-mo period and across a broad range of marine habitats (seagrass, channels, mangroves,

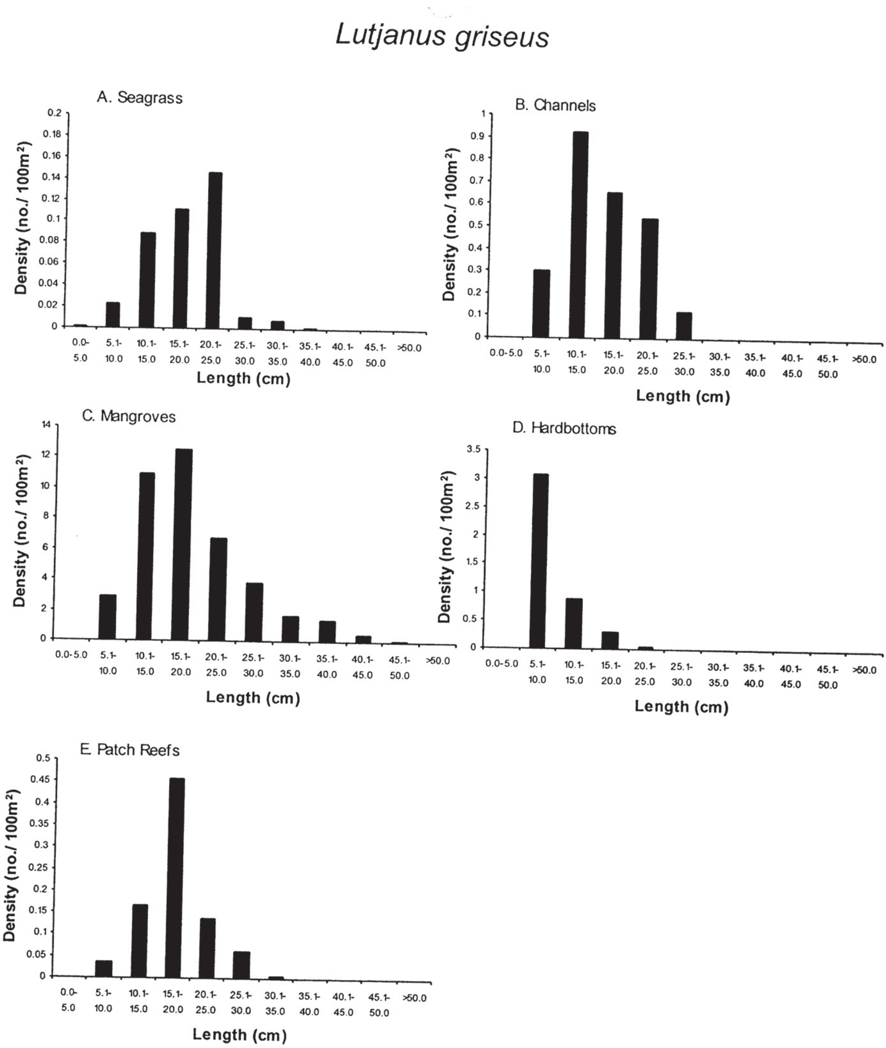

Figure 9. The size frequency distribution of *Lutjanus griseus* (gray snapper) observed during 10-min surveys in (A) seagrass; (B) channels; (C) mangroves; (D) hardbottoms; and (E) patch reefs for the Lakes and Marquesas regions pooled. Note different y-axis values.

hardbottoms, patch reefs, offshore reefs). We recognize that some of the differences observed between fish abundance and diversity and the six habitats surveyed may be due to differences in the efficiency of our visual survey methods across habitats, as well as area searched. Poor water visibility and the cryptic nature of certain fish species in complex benthic habitats can reduce the accuracy and precision of visual survey techniques. For example, very small stages (0–5 cm TL) of serranids and sparids were absent from our 10 min surveys, but present in our band transects, in which divers spent more time slowly searching through seagrass and crevice habitats than in 10-min surveys. Moreover, some fish fled divers before they could be identified or their size estimated. We tried to reduce habitat- and observer-specific biases in our visual survey techniques through the use of 1) divers with experience in identifying coral reef fishes; 2) replicate surveys within a given sampling cell or site; 3) slow and methodical searches in complex benthic habitats;

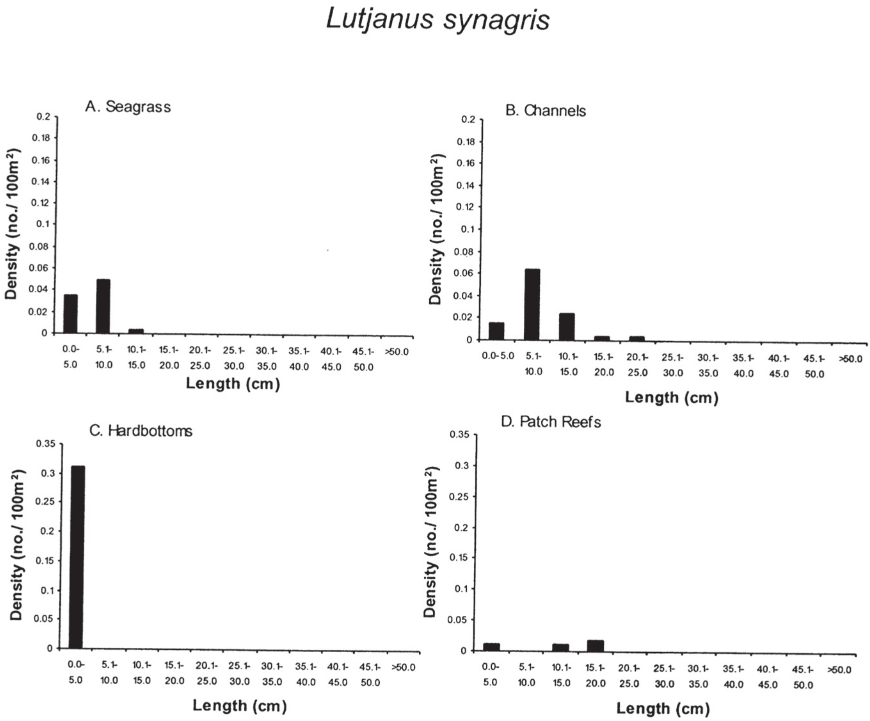

Figure 10. The size frequency distribution of *Lutjanus synagris* (lane snapper) observed during 10-min surveys in (A) seagrass; (B) channels; (C) hardbottoms; and (D) patch reefs for the Lakes and Marquesas regions pooled. Note different y-axis values.

4) a complementary combination of band transect and timed surveys in many habitat types; 5) waiting for fish that initially fled an area to return; and 6) conducting visual surveys when water visibility was high (> 10 m). This use of a complementary combination of band transect and timed surveys likely increased the accuracy with which we assessed both cryptic species, such as recently settled lutjanids and gerreids, as well as more transient species such as large snappers, jacks, and barracuda. For example, the density of relatively small *G. cinereus* was up to 50 times greater in band transects than 10-min surveys, which was likely due to divers using the 2-m PVC-pipe that delineated the 2-m band width to methodically "herd" small fish from within the interstices of the seagrass canopy. Conversely, transient *S. barracuda* were rarely observed during band transects in seagrass, but were commonly observed during 10-min surveys. In a related study, Schmitt et al. (2002) employed a combination of roving diver surveys and band transects to assess coral reef fish assemblages off southeastern Hispanola. Roving diver surveys involved a diver swimming around a reef site for ~45–60 min, recording all fish species observed (Schmitt et al., 2002). Although roving diver surveys did not provide estimates of fish density, they did provide a rapid assessment of fish species presence and absence, and when combined with transect surveys, provided a more complete assessment of fish assemblages than either survey technique alone (Schmitt et al., 2002).

Accurate measures of fish density for our 10-min surveys depended on accurate estimates of distance surveyed. We assessed the accuracy of our visual estimates of distance traveled in seagrass and mangrove habitats, and although we slightly overestimated and

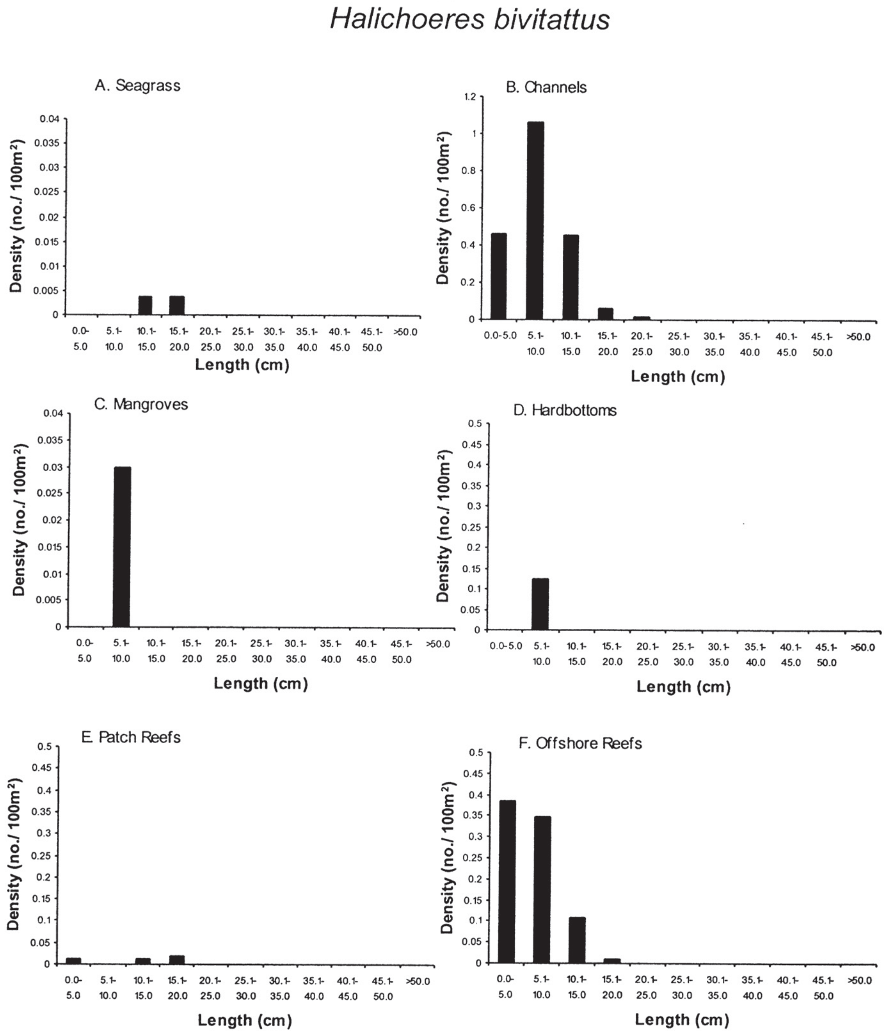

Figure 11. The size frequency distribution of *Halichoeres bivitattus* (slippery dick wrasse) observed during 10-minute surveys in (A) seagrass; (B) channels; (C) mangroves; (D) hardbottoms; (E) patch reefs; and (F) offshore reefs for the Lakes and Marquesas regions pooled. Note different y-axis values.

underestimated distance traveled in seagrass and mangroves, respectively, our estimates of distance traveled did not differ significantly from the actual distances measured using a differential GPS system on a boat (seagrass) or a tape measure (mangroves). Thus, our visual estimates of distance traveled during 10-min surveys were relatively accurate. The efficiency of our visual survey methods was likely similar to or higher than trawling in seagrass (e.g., 16–69% efficient; Kjelson and Colby, 1977), or block-net and rotenone sampling methods in mangroves (~75%; Thayer et al., 1987), but may have been lower than the use of drop-nets in seagrass (Nagelkerken et al., 2000).

There are fundamental sources of bias when comparing animal diversity across different habitat types when search area is different, or different areas are searched within a given habitat. We tried to reduce bias associated species/area relationships (Rosenzweig,

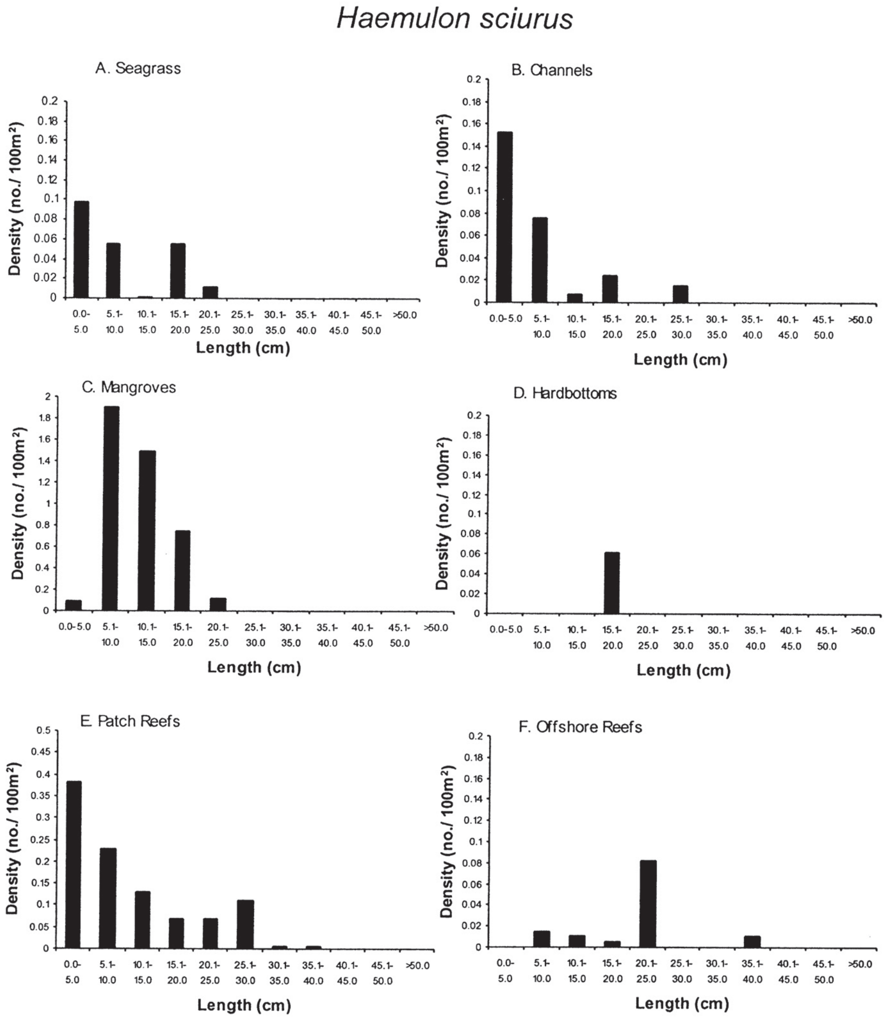

Figure 12. The size frequency distribution of *Haemulon sciurus* (bluestripped grunt) observed during 10-min surveys in (A) seagrass; (B) channels; (C) mangroves; (D) hardbottoms; (E) patch reefs; and (F) offshore reefs for the Lakes and Marquesas regions pooled. Note different y-axis values.

1995) by not making statistical comparisons of fish diversity across habitat types, and by standardizing area searched for a given habitat type according to its relative availability when making comparisons between regions. For example, we surveyed ~3 times more channels in the Lakes than the Marquesas because there was ~3 times greater areal cover of channels in the Lakes than the Marquesas. Qualitatively, it does not appear that area searched was a critical determinant of fish diversity in this study given that the habitat with one of the lowest areas searched, mangroves, had much higher diversity than habitats with much greater areas searched (e.g., seagrass and channels).

Habitat Characteristics.—The Lakes and Marquesas regions within the KWNWR contain a relatively large and diverse mosaic of habitats for fishes (this study) and Caribbean spiny lobster (Eggleston and Dahlgren, 2001). The use of aerial photographs was critical in (1) designing our field surveys that targeted the most conspicuous habitat types in the KWNWR, (2) efficiently navigating this shallow region, and (3) determining samples sizes within a given habitat and region based on the areal cover of the habitat. The major limitation to relying on the aerial photographs was the inability to see patch reefs and hardbottom habitats. We overcame this limitation by hiring local guides at the initiation of the study. These local guides were especially helpful in terms of identifying hardbottom "lobster holes" not indicated on navigational charts.

We found significantly higher fish densities at the Marquesas than the Lakes regions. The reason for the higher fish densities in the Marqueasas than the Lakes is unclear, but may have been due to a combination of factors including, but not limited to: (1) higher seagrass density at the Marquasas (31.3 shoots 0.07 m^{-2}) than the Lakes (22 shoots 0.07 m^{-2}) (although the trend was not significant and there was 81% greater seagrass areal cover at the Lakes), (2) 40% more mangrove perimeter at the Marquesas than the Lakes, and (3) relatively close proximity of the Lakes to Key West, which may have resulted in poorer water quality and greater fishing pressure than in the Marquesas.

We did not observe any obvious areas of seagrass or sponge die-off, as indicated by denuded mud patches, as has been seen in nearby Florida Bay (Robblee et al., 1991; Durako, 1994; Butler et al., 1995; Herrnkind et al., 1997). Seagrass percent cover was high (75–100%) in areas outside of macroalgal beds, with relatively high average shoot densities (467–500 shoots m^{-2}) and blade heights (30–37 cm), compared to similar measurements in Florida Bay (Durako, 1994), Mexico (Gallegos et al., 1993), and the Bahamas (Eggleston, 1995).

Density and Diversity of Fish in Back-Reef Habitats.—The density of fish in seagrass was similar to that in mangroves when atherinids were removed; however, the diversity of fish in mangrove fringe and channel habitats was greater than in adjacent seagrass meadows. Overall, the fish species present in the Lakes and Marquesas appeared somewhat transitional between the more subtropical estuarine environment of Florida Bay basins, and the tropical oceanic environment of the Bahamas and Caribbean. For example, in seagrass, we tended to find greater numbers of reef fish species (e.g., haemulids and lutjanids) than did Sogard et al. (1987) in Florida Bay, whereas they found greater abundances of more estuarine fish from the families Cyprinodontidae (killifishes) and Batrachoididae (toadfishes). Similarly, Thayer et al. (1989) working in seagrass, found greater numbers of more estuarine fish such as Cyprinodontidae, Batrachoididae, as well as spotted seatrout *Cynoscion nebulosus* (Cuvier in Cuvier and Valenciennes, 1830) and pinfish *Lagodon rhomboids* (Linnaeus, 1766), and fewer species of reef fish than our study. The fish assemblages observed by Ley et al. (1999) working along an estuarine salinity gradient in Florida Bay mangrove prop-roots were dominated by the families Engraulidae and Atherinidae, which was similar to this study; however, they found higher numbers of more estuarine fishes such as Poeciliidae (mosquitofish) and Cyprinodontidae than we did. Conversely, we identified greater numbers of more estuarine species in mangrove habitats than did Rooker and Dennis (1991), who worked in mangroves in Puerto Rico that were in close proximity to coral reefs.

Our visual estimates of fish density (converted to fish ha^{-1} for comparative purposes) in seagrass in the Lakes and Marquesas using band transects ranged from a low of $\sim 3 \times 10^3$ fish ha^{-1} in the Lakes to a high of $\sim 2.5 \times 10^4$ fish ha^{-1} in the Marquesas. Our fish density estimates are within the range of those reported from other tropical and subtropical seagrass systems. For example, using otter trawls in Florida Bay seagrass beds and channels, Thayer and Chester (1989) reported an average density of 2×10^3 fish ha^{-1}. Using throw-traps in Florida Bay, Sogard et al. (1987) observed highest mean densities of 11

× 10^4 fish ha^{-1} in seagrass bank habitats in Florida Bay. Adams (1976) used throw traps in eelgrass (*Zostera marina* L.) beds in North Carolina and found an average density of 1.8 × 10^4 fish ha^{-1}, and Weinstein and Brooks (1983) found densities <10^3 fish ha^{-1} in Chesapeake Bay seagrass beds using an otter trawl.

Ontogenetic Habitat Shifts.—Ontogenetic habitat shifts from back-reef to offshore reefs were observed for some species. One of the clearest examples of an ontogenetic habitat shift was *S. barracuda*, in which the smallest size class was found exclusively in mangroves, and the largest size class in all habitats. A similar ontogenetic habitat shift was reported for *S. barracuda* in Bonaire, Netherlands Antilles (Nagelkerken et al., 2000). Other species that showed relatively strong evidence for ontogenetic habitat shifts, particularly from seagrass and channels to reefs, included *G. cinereus* and *P. arcuatus*. Conversely, the smallest size class of *L. griseus* occurred exclusively in seagrass, with adult stages occupying all habitats. A similar pattern was observed for *L. griseus* in Bonaire (Nagelkerken et al., 2000).

The fish families and species (Appendix 1) identified during patch reef and offshore reef surveys in this study were similar to those reported from elsewhere in the Florida Keys (Bohnsack and Bannerot, 1986; Ault et al., 1998) and Dry Tortugas (Rydene and Kimmel, 1995). For example, Bohnsack and Bannerot (1986) reported a total of 117 species of fish observed in 160 visual surveys from the forereef at Looe Key, Florida. Their species assemblages were dominated by haemulids, labrids, pomacentrids, and acanthurids (Bohnsack and Bannerot, 1986). The jacks (Carangidae) comprised ~10% of the reef fish in this study, but less than 5% off of Looe Key (Bohnsack and Bannerot 1986). Although bluehead wrasse *Thalassoma bifasciatum* (Bloch, 1791) was the predominant labrid at Looe Key (Bohnsack and Bannerot, 1986), the slippery dick (*H. bivittatus*) was the most common labrid in this study.

In conclusion, mangroves (based on 10-min surveys) and seagrass (based on band transects) appear to be key nursery habitats for fishes, particularly given that seagrass consistently harbored the smallest size classes of many species, and mangroves contained the highest density and diversity of fishes. Although channels containing large sponges represented only 0.06% of the total area of the Lakes and Marquesas, they contained the highest diversity of microhabitats, and a relatively high diversity and density of fishes. Moreover, we qualitatively observed more sharks, gamefish (e.g., tarpon), and turtles in channels than any other habitat. Channels also provide a likely corridor for fishes migrating from back reef habitats such as seagrass and mangroves to patch reef and offshore reefs (Parrish, 1989). Thus, inclusion of seagrass, mangrove, and channel habitats in future studies of reef fish growth, survival, and emigration should produce a more complete picture of their nursery role (sensu Beck et al., 2001) in tropical back reef environments.

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Appendix 1. Habitat characteristics from seagrass habitats within the Lakes region of the KWNWR. Shoot counts and blade heights are 0.07 m^{-2}. Percent cover is 120 m^{-2}. Counts represent the average of two band transects within a sampling station (grid cell). N/A indicates that measurements were not taken.

				% Cover										
Region	Station	Shoot Ct	Blade Ht	*Thalassia*	*Syringodium*	*Halodule*	Station	Shoot Ct	Blade Ht	*Laurencia*	Other Macroalgae	Sponge	Coral rubble	Sand
Lakes	S1	31.0	25.8	99.3	0.0	0.0	S1	31.0	25.8	0.7	0.0	0.0	0.0	0.0
	S2	41.5	42.4	99.7	0.0	0.0	S2	41.5	42.4	0.0	0.3	0.0	0.0	0.0
	S3	22.0	31.4	54.0	0.0	0.0	S3	22.0	31.4	0.0	25.0	0.0	0.0	21.0
	S4	43.0	47.7	99.5	0.5	0.0	S4	43.0	47.7	0.0	0.0	0.0	0.0	0.0
	S5	18.0	27.0	17.5	0.0	0.0	S5	18.0	27.0	17.5	20.5	3.7	0.0	40.8
	S6	N/A	N/A	14.2	0.0	0.0	S6	N/A	N/A	26.7	7.4	0.0	0.0	51.7
	S7	37.0	31.7	68.3	0.0	0.0	S7	37.0	31.7	2.5	22.5	0.0	0.0	6.7
	S8	12.0	23.6	75.8	0.0	8.3	S8	12.0	23.6	13.0	2.9	0.0	0.0	0.0
	S9	43.0	36.1	85.8	0.0	0.0	S9	43.0	36.1	0.0	10.7	0.0	0.0	3.5
	S10	20.5	18.1	21.7	0.0	0.0	S10	20.5	18.1	6.7	29.1	3.3	2.5	36.7
	S11	21.0	19.3	15.0	0.0	0.0	S11	21.0	19.3	22.5	40.0	5.0	2.5	15.0
	S12	21.0	39.6	100.0	0.0	0.0	S12	21.0	39.6	0.0	0.0	0.0	0.0	0.0
	S13	12.5	16.9	75.0	0.0	0.0	S13	12.5	16.9	0.0	11.7	0.0	0.0	13.3
	S14	N/A	N/A	5.0	0.0	0.0	S14	N/A	N/A	5.0	40.0	0.0	0.0	50.0
	S15	36.5	41.5	99.2	0.0	0.0	S15	36.5	41.5	1.0	0.2	0.0	0.0	0.0
	S16	19.0	15.5	50.0	0.0	0.0	S16	19.0	15.5	0.0	15.1	1.7	0.0	33.2
	S17	27.5	26.9	97.0	0.0	0.0	S17	27.5	26.9	0.0	0.5	0.0	0.0	2.5
	S18	15.5	25.4	99.2	0.0	0.0	S18	15.5	25.4	0.0	0.3	0.0	0.0	0.5
	S19	18.5	29.5	93.8	0.0	0.0	S19	18.5	29.5	0.0	6.2	0.0	0.0	0.0
Marquesas	S1	40.5	27.3	99.0	0.0	0.0	S1	40.5	27.3	0.0	0.2	0.0	0.0	0.8
	S2	40.5	45.1	96.2	0.0	0.0	S2	40.5	45.1	0.0	0.0	0.0	0.0	3.8
	S3	43.0	38.5	94.0	0.0	0.0	S3	43.0	38.5	1.0	4.8	0.0	0.0	0.2
	S4	24.0	33.2	94.7	0.0	0.0	S4	24.0	33.2	0.0	3.3	0.0	0.0	2.0
	S5	16.5	34.4	95.5	0.0	0.0	S5	16.5	34.4	0.0	0.0	0.0	0.0	4.5
	S6	23.0	40.8	100.0	0.0	0.0	S6	23.0	40.8	0.0	0.0	0.0	0.0	0.0

Appendix 2. Habitat characteristics (120 m^{-2}) from channel habitats within the Lakes region of the KWNWR. Counts represent the average of two band transects within a sampling station. N/A indicates that measurements were not taken.

Region	Station	Sponge count	% Cover												
			Sponge volume	*Thalassia*	*Syringodium*	*Halodule*	*Laurencia*	Station	Sponge count	Sponge volume	Other Macroalgae	Sponge	Coral rubble	Sand
Lakes	C1	3.0	N/A	20.8	39.2	0.0	0.0	C1	3.0	N/A	19.2	0.0	0.0	20.8
	C2	4.5	3,308.4	0.0	0.0	0.0	1.8	C2	4.5	3,308.4	64.0	0.0	7.5	26.7
	C3	3.5	N/A	5.0	0.0	0.0	0.0	C3	3.5	N/A	75.0	0.0	0.0	20.0
	C4	N/A	N/A	0.0	0.0	0.0	37.5	C4	N/A	N/A	50.0	0.0	12.5	0.0
	C5	25.5	3,348.9	15.0	0.0	0.0	14.2	C5	25.5	3,348.9	18.5	0.5	21.0	30.8
	C6	N/A	N/A	3.3	0.0	0.0	43.8	C6	N/A	N/A	51.9	0.0	0.0	1.0
	C7	29.0	10,474.5	21.7	0.0	0.0	18.2	C7	29.0	10,474.5	28.4	0.0	0.0	31.7
	C8	0.0	N/A	44.2	10.0	1.7	0.0	C8	0.0	N/A	23.3	0.0	0.0	20.8
	C9	N/A	N/A	66.7	0.0	0.0	0.0	C9	N/A	N/A	3.3	0.0	0.0	30.0
	C10	0.5	N/A	61.7	0.8	0.0	0.0	C10	0.5	N/A	7.5	0.0	0.0	30.0
	C11	2.5	105.2	26.3	0.0	2.5	6.3	C11	2.5	105.2	13.6	0.0	0.0	51.3
	C12	2.5	24,875.2	15.0	0.0	0.0	29.2	C12	2.5	24,875.2	15.0	0.0	0.0	40.8
	C13	83.0	46,352.7	8.3	0.0	0.0	38.9	C13	83.0	46,352.7	14.8	24.4	0.0	13.6
	C14	99.0	32,803.1	3.3	0.0	0.0	0.0	C14	99.0	32,803.1	56.7	18.3	0.0	21.7
Marquesas	C1	33.0	717.1	5.8	16.7	70.5	0.0	C1	33.0	717.1	2.3	0.0	0.0	4.7
	C2	33.5	33,283.0	15.0	40.0	20.8	12.2	C2	33.5	33,283.0	2.7	0.8	0.0	8.5
	C3	8.0	17,144.1	13.3	26.7	0.0	0.0	C3	8.0	17,144.1	45.0	5.0	0.0	10.0
	C4	0.0	0.0	16.7	46.6	0.0	0.0	C4	0.0	0.0	0.0	0.0	0.0	36.7

Appendix 3. List of fish families and species observed during band transects and timed surveys at the Lakes and Marquesas regions of the KWNMR during July–October, 1999. Habitat codes are: C (channels), H (hardbottoms), M (mangroves), PR (patch reefs), R (offshore reefs) and S (seagrass).

Family	Species	Habitats of occurrence
Acanthuridae	*Acanthurus bahianus*	C, PR, R
	Acanthurus chirurgus	C, H, PR, R
	Acanthurus coeruleus	C, PR, R
	Acanthurus sp.	
Atherinidae	sp.	M, S
Balisitidae	*Balistes capriscus*	C
	Monacanthus tuckeri	R, S
Batrachoididae	*Opsanus* sp.	C
Belonidae	sp.	M, S
Blennidae	sp.	C, PR, R
Carangidae	*Caranx bartholomaei*	H, S
	Caranx crysos	M, PR, R
	Caranx latus	PR
	Caranx ruber	C, H, PR, R, S
	Caranx sp.	PR
Carcharhinidae	*Negaprion brevirostris*	C
Centropomidae	*Centropomus undecimalis*	M
Chaetodontidae	*Chaetodon capistratus*	C, PR, R, S
	Chaetodon ocellatus	C, PR, R
	Chaetodon striatus	C, PR, R
Clinidae	*Malococtenus* sp.	C, R
Clupeidae	sp.	M, PR, S
Cyprinidae	sp.	M, S
Dasyatidae	*Dasyatis americana*	C, PR
Echeneidae	*Ecenies* sp.	R
Elopidae	*Megalops atlanticus*	M, PR, C
Ephippidae	*Chaetodipterus faber*	PR
Exocoetidae	*Hemirhamphus brasiliensis*	S
Fundulidae	*Fundulus* sp.	H, S
Gerreidae	*Eucinostomus melanopterus*	S
	sp.	S
Gobiidae	*Coryphopterus glaucofraenum*	C, H, PR, S
	Gobiosoma oceanops	PR, R
	Ioglossus sp.	C, S
Haemulidae	*Anisostremus virginicus*	C, H, M, PR, R, S
	Haemulon aurolineatum	C, M, PR, R, S
	Haemulon flavolineatum	C, H, M, PR, R, S
	Haemulon macrostomum	M, PR, S
	Haemulon parra	C, H, M, PR, R
	Haemulon plumieri	C, H, M, PR, R, S
	Haemulon sciurus	C, H, M, PR, R, S
	Haemulon sp.	C, M, PR, S

Appendix 3. Continued.

Family	Species	Habitats of occurrence
Holocentridae	*Holocentrus adscensionis*	R
	Holocentrus marianus	R
Kyphosidae	*Kyphosis sectatrix*	C, M, PR, R
Labridae	*Bodianus rufus*	R
	Halichoeres bivittatus	C, H, M, PR, R, S
	Halichoeres garnoti	R
	Halichoeres maculipinna	R
	Halichoeres poeyi	R
	Halichoeres radiatus	C, PR, R
	Lachnolaimus maximus	C, H, PR, R, S
	Thalassoma bifasciatum	C, R
Lutjanidae	*Lutjanus griseus*	C, H, M, PR, S
	Lutjanus analis	C, H, M, PR, S
	Lutjanus apodus	C, H, M, PR, R, S
	Lutjanus cyanopterus	M
	Lutjanus jocu	M
	Lutjanus mahogoni	R
	Lutjanus synagris	C, H, PR, S
	Ocyurus chrysurus	C, PR, R, S
Mullidae	*Mulliodichthys martinicus*	R
	Opisthognathus aurifrons	R
Ostraciidae	*Lactophrys quadricornis*	PR
Pomacantidae	*Holacanthus bermudensis*	C, PR
	Holacanthus ciliaris	C, PR, S
	Pomacanthus arcuatus	C, PR, R, S
	Pomacanthus paru	C, H, PR, S
	Pomacantus sp.	C
Pomacentridae	*Abudefduf saxatilis*	C, H, M, PR, R
	Chromis cyanea	R
	Chromis multilineata	R
	Microspathadon chrysurus	PR, R
	Stegastes fuscus	C, H, PR, R
	Stegastes leucostictus	C
	Stegastes partitus	C, H PR, R, S
	Steagastes planifrons	R
	Stegastes sp.	PR, R
	Stegastes variabilis	C, PR, R
Rhincodontidae	*Ginglymostoma cirratum*	C
Scaridae	*Scarus* sp.	C, R, S
	Scarus coeruleus	H, R
	Scarus croicensis	C, PR, R, S
	Scarus guacamaia	C, M, PR
	Scarus taeniopterus	C, H, PR, R, S
	Scarus vetula	M, R
	Sparisoma aurofrenatum	C, H, PR, R, S
	Sparisoma chrysopterum	C, H, M, PR, R, S
	Sparisoma radians	C, H, PR, S
	Sparisoma rubripinne	C, M, PR, R
	Sparisoma viride	C, H, M, PR, R, S

Appendix 3. Continued.

Family	Species	Habitats of occurrence
Sciaenidae	*Equetus acuminatus*	C, PR, S
	Equetus umbrosus	PR, R
	Odontoscion dentex	PR, R
	Sciaenops ocellatus	M
Serranidae	*Diplectrum formosum*	C, H, S
	Epinephelus adscenionis	PR
	Epinephelus cruentatus	PR
	Epinephelus itajara	M
	Epinephelus morio	C, PR
	Epinephelus striatus	C, H
	Hypoplectrus puella	C, PR
	Hypoplectrus sp.	C, PR, R, S
Serranidae	*Mycteroperca bonaci*	C, M, PR, R
	Mycteroperca phenax	PR
	Rypticus maculatus	C, M, PR, R
	Serranus tabacarius	R
	Serranus tigrinus	R
Sparidae	*Archosargus probatocephalus*	PR
	Archosargus rhomboidales	C, H, M, PR, S
	Calamus bajonado	C, PR, R
	Calamus penna	H
	Lagodon rhomboidales	C, M , S
Sphyraenidae	*Sphyraena barracuda*	R
Syngnathidae	*sea horse* sp.	S
Synodontidae	*Synodus* sp.	S
Tetraodontidae	*Canthigaster rostrata*	R
	Diodon hystrix	PR
	Sphoeroides spengleri	C
	Sphoeroides testudinus	C
Urolophidae	*Urolophus jamaicensis*	C, PR, R, S