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Biodiversity and Ecosystem Function of Shallow Bank Systems within Florida Keys National Marine Sanctuary (FKNMS)

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Cover

Cover photo by John Burke shows the diverse fish and benthic flora and fauna of a channel bottom within the Moser Channel Bank System during a flooding tide.

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Abstract

Bank systems, clusters of shallow banks and associated channels located in the shallow waters between Florida Bay and the Florida Keys, are distinctive benthic features of Florida Keys National Marine Sanctuary (FKNMS). The banks are aggregations of *Porites* coral rubble and *Halimeda* sand covered with a veneer of seagrass, macroalgae and a wide diversity of invertebrate taxa. Bank systems provide a mosaic of essential fish habitat, such as juvenile nurseries and foraging and sheltering grounds for adults, including high densities of economically important reef fishes. Surveys of three bank systems (Moser Channel, Bamboo, and Channel Key Banks) showed that their associated fish assemblages consistently resembled assemblages of coral reefs and had higher diversity and biomass than the assemblages of surrounding basins. As in most reef fish assemblages, a high proportion of the biomass of the bank system community consisted of "homing" species that shelter in channels during the day and forage nocturnally in surrounding habitats. The species composition and the high density and diversity of the fish assemblage indicate bank systems provide a key structural component supporting the biodiversity and productivity of the FKNMS. Given their integral role in the ecology of the FKNMS and the vulnerability of bank systems to environmental and anthropogenic stressors, we recommend they receive additional protection through inclusion in a management zone better suited to protect the structure and function of these critical habitats.

Key Words

Florida Keys National Marine Sanctuary, Reef fish, Macroalgae, Seagrass, Benthic Habitat, Channels, Banks, Biodiversity, Conservation, Marine Zone

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INTRODUCTION

Background

The Florida Keys lie in a transition zone between the warm temperate southeastern Gulf of Mexico (GOM) and the more tropical oligotrophic environment of the Florida Straits. This transition occurs where the West Florida Shelf (WFS) gradually shoals from its deeper regions to seagrass meadows, hard bottom features, tidal flats and mangrove habitats along the northern fringe of emergent islands in the Florida Keys (FMRI 2000).

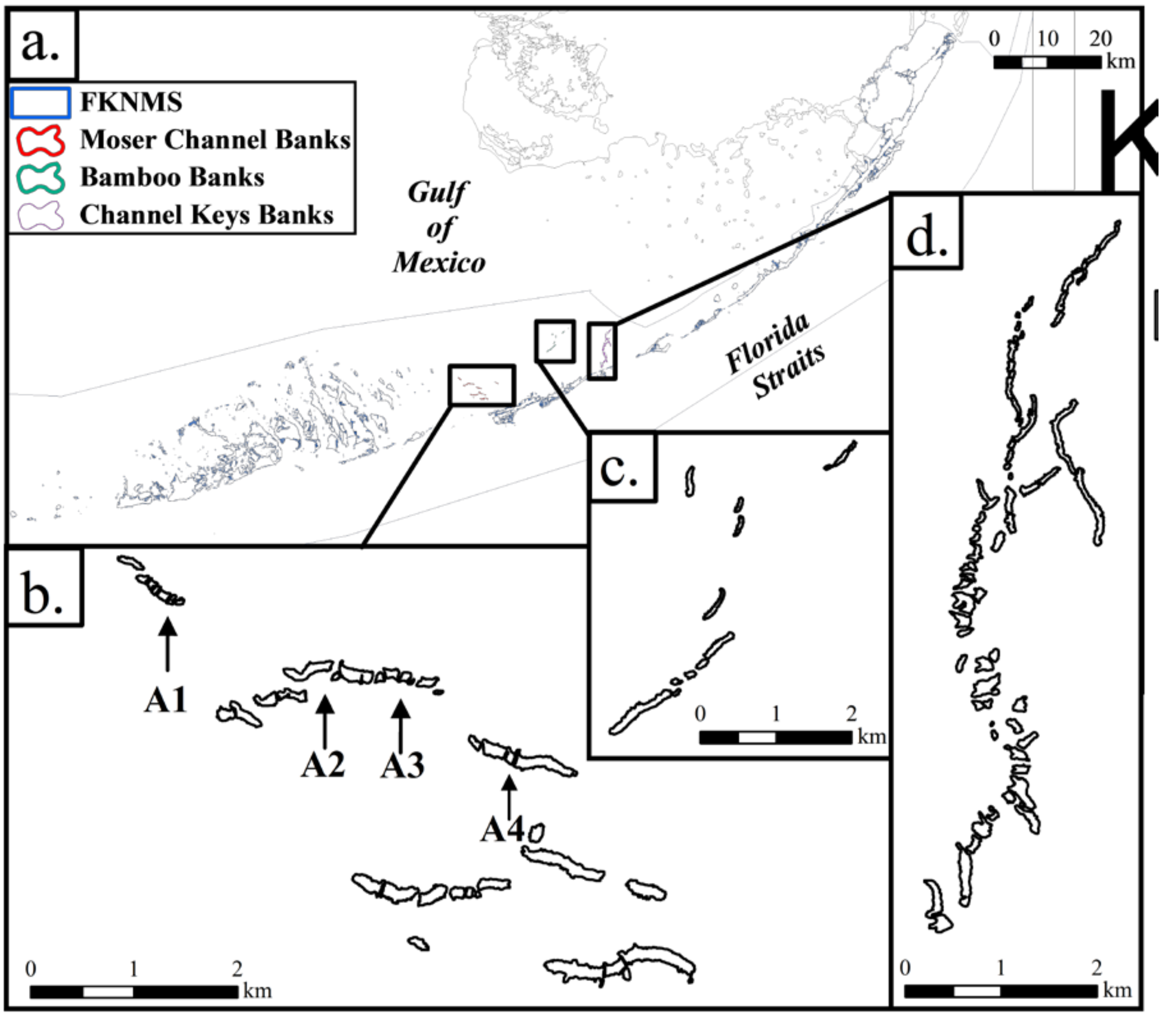

Figure 1. Study area: a) Location of bank systems sampled within FKNMS between 2002 and 2006, b) Moser Channel Banks System (MCBS) containing focal sampling locations A1, A2, A3 and A4, c) Bamboo Banks System (BBS), d) Channel Keys Banks System (CKBS).

South of the Keys, the rapidly flowing warm oligotrophic waters of the Florida Straits and the widespread distribution of exposed bedrock favors the development of reef building coral communities (Schomer and Drew 1982). North of the Keys the development of coral reefs is limited by the cooler and more variable temperatures, a less oligotrophic water column, and the widespread prevalence of unconsolidated biogenic sediments. Reef building communities of the shallow shelf north of the Keys generally occur as dispersed colonies of gorgonians, several species of hard corals and sponges (Phillips et al. 1990). Such reef building communities are typically found on hard substrates with minimal relief (<3 m) and are widely dispersed among the seagrass meadows and macroalgal beds which are the dominant components of benthic habitat in shallow waters on the WFS (Iverson and Bittaker 1986, Zieman and Zieman 1989, FMRI 1998, FMRI 2000, Peterson and Fourqurean 2001, Fonseca et al. 2008). The Middle Keys region (between Lower Matecumbe and Little Duck Keys) is of particular importance to this transition due to strong hydrodynamic exchange between the GOM and the Florida Straits that occurs there (Smith and Lee 2003). The east-west oriented Middle Keys are bisected by several large passes (e.g. Moser Channel, Grassy Key Pass, Channel 5) through which, in addition to strong tidal exchange, there is a net transport of Gulf of Mexico waters to Hawk Channel and the Florida Straits (Smith 1994).

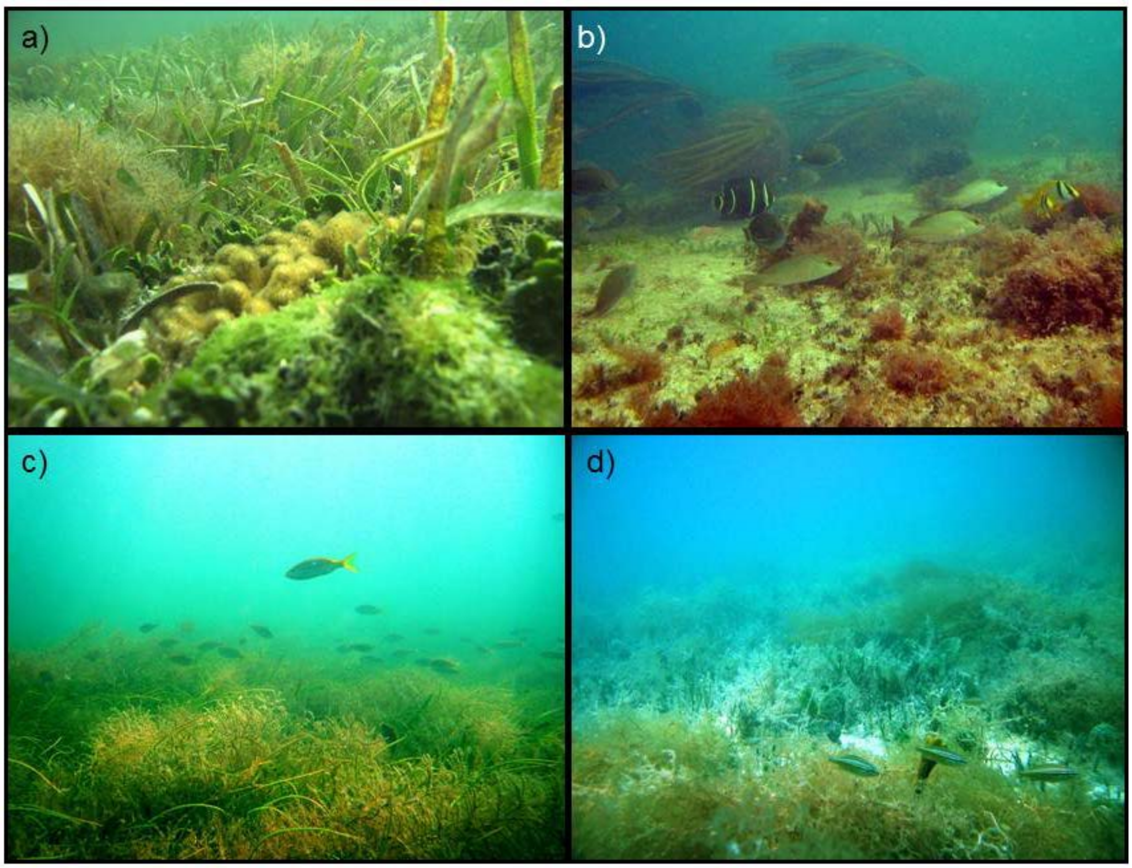

Figure 2. Photographs of a) bank top, b) channel, c) bank margin, d) and basin habitats associated with Moser Channel Banks System illustrating the sampling strata defined for the ecological investigation of bank systems

A distinctive feature of the Gulf side of some Middle Key tidal passes are bank systems (Figure 1) consisting of complex networks of banks, channels and their interface with the surrounding basin. These banks are stable features of the landscape as they accumulate calcareous materials at a pace sufficient to keep up with rising sea level (Neumann and Macintyre 1985). The banks associated with Long Key Pass have been described geologically as Holocene reef mounds whose formation was initiated approximately 2000 ybp (McNeill 1988). Typically banks rise approximately 2 to 5 meters above the surrounding bottom with sloping sides covered by dense sessile floral and faunal communities. Despite the strong tidal currents associated with banks, this biotic blanket stabilizes its foundation of large volume of *Porites* spp. coral rubble, fragments of molluscs, *Halimeda* sands and lime mud. With the exception of slack tide, flow over the banks and through the channels between adjacent banks is continuous and results in the development of distinct substrates as well as differences between the floral and faunal characteristics of the bank tops, their slopes, associated channels and the surrounding basins (Figure 2). McNeill (1988) recognized the existence of three ecological zones on an individual bank controlled primarily by tidal circulation and periodic exposure. The tops and sloping sides of the banks are stabilized by communities of tropical seagrasses, calcareous and fleshy macroalgae, sponges, and other invertebrate taxa (Figure 2a). In the channels, currents erode sediments exposing the bedrock and providing substrate for sessile invertebrates and macroalgae (Figure 2b). On their margins, banks provide shelter from the tidal currents allowing accumulation of sediment and development of dense mixed meadows of seagrasses and macroalgae (Figure 2c). Thus a bank system provides a structured mosaic of habitats whose ecological role may be analogous to that of a coral reef, to the extent that, like coral reefs they provide focal points of biodiversity and biological activity.

Conservation issue

Bank systems represent conspicuous features within Florida Keys National Marine Sanctuary (FKNMS) and although largely unstudied may play an important ecological role. FKNMS, established by Congress in 1990 in response to the deterioration of the marine ecosystem in South Florida, now encompasses 9,933 km^2 of marine habitat including virtually the entire Florida Reef Tract, all of the mangrove islands of the Keys, and a large portion of the region's seagrass meadows (Florida Keys National Marine Sanctuary Comprehensive Science Plan 2002, Fourqurean et al. 2001). While the sanctuary provides protection for all habitats within its boundaries, zoning within the sanctuary assists in the protection of the biological diversity of the marine environment in the Keys. Of the six zone types currently utilized, three (Sanctuary Preservation Areas, Ecological Reserves, and Special Use Areas) are fully protected no-take areas where all consumptive activities are prohibited (ONMS 2011). Sanctuary Preservation Areas and Ecological Reserves are primarily associated with the coral reef tract and thus, limited geographically to the ocean side of the Keys. There are also four National Wildlife Refuges within the boundaries of the sanctuary, which are administered by the U.S. Department of Interior's Fish and Wildlife Service. These regulated areas primarily focus on the preservation of specific terrestrial or avian species (e.g. key deer, great white heron) rather than the protection of marine habitats that are integral to the function of South Florida's subtidal ecosystem. The National Wildlife Refuges do manage some marine areas. There are 20 wildlife management areas (WMAs) in Great White Heron and Key West National Wildlife Refuges and these are co-managed with the Sanctuary. While they were established to protect the great white heron/other birds, they also protect sea turtle nesting areas on small mangrove island beaches and protect seagrass by establishing no motor zones where needed.

FKNMS's focus on the protection of coral reef resources has its roots in the early conservation movement within the keys. A meeting of scientists and conservationists at the Everglades National Park in 1957 to discuss the demise of the coral reef resources of South Florida led to the 1960 creation of John Pennekamp Coral Reef State Park, the world's first underwater park (Office of National Marine Sanctuaries. 2011). Subsequent designation of highly protected areas within the Keys and including the 2001 establishment of the Tortugas Ecological Reserve have focused primarily on the bank barrier reef system.

While coral reefs have historically received the strongest protection, the inclusion within the FKNMS of the extensive shallow waters on the bay side of the Keys implicitly recognized the importance of other habitats to the health of the ecosystem. These shallow marine habitats are structured primarily by fast growing vegetation (seagrass, macroalgae and mangrove) (Schomer and Drew 1982, Fourqurean et al. 2001) and are expected to be more resilient to disturbance than habitats structured by the slower growing hard corals. Bank systems may represent an exception to this generality as much of their structure is made up of *Porites* rubble that may have taken hundreds to thousands of years to accumulate (McNeill 1988). Recent studies suggest that bank systems are particularly vulnerable to motor vessel injuries which compromise the bio-physical integrity of bank systems (Sargent et al. 1995, Kenworthy et al. 2002, Whitfield et al. 2002, Kirsch et al. 2005, SFNRC 2008, Uhrin et al. 2011). As a consequence of the proximity to tidal passes and the Atlantic Intracoastal Waterway, some bank systems experience a large volume of recreational and commercial vessel traffic. Vessel groundings and propeller scaring are common both on banks that do not have proximal aids to navigation as well as those that do (Figure 3). Recent estimates suggest that the shallow seagrass banks in FKNMS experience between 250 and 500 vessel groundings per year, which are particularly severe when they occur in a bank system that is subjected to high currents (Sargent et al. 1995, Kenworthy et al. 2002, Kirsch et al. 2005, Uhrin et al. 2011). Groundings immediately destroy a portion of the protective veneer of plants and sessile invertebrates on the bank tops and margins of the release channels. Where natural recovery is impeded, erosion from strong currents and severe storms further destabilizes and enlarges the injuries and threatens to fragment the banks (Whitfield et al. 2002, Uhrin et al. 2011).

The impact of changing water quality is also a concern for bank system due to instability of water quality in "upstream" areas. The impact of deterioration of water quality upstream from the sanctuary was clearly demonstrated in the late-1980's to mid-1990's when an extensive area of south Florida waters experienced impaired water quality associated with the algal blooms originating in the vicinity of Florida Bay (Durako et al. 2002). The cascade of ecological effects included seagrass and sponge die offs which reduced fish and shellfish habitat in the surrounding areas, including the newly established FKNMS. Changes in water management practices, critical to the health of the South Florida system (Hunt and Nuttle 2007, Comprehensive Everglades Restoration Plan Report to Congress 2010) will mean increased flow of freshwater and nutrients from the Everglades into Florida Bay and will certainly affect systems "downstream", including the bank systems of FKNMS. Further monitoring of the structure and function of bank systems and other South Florida habitats likely to be impacted by water management changes would be prudent. Because the long-term mean volume transport from the western margin of Florida Bay and the southeastern Gulf of Mexico is southeastward over the bank systems and through the main tidal passes out to the reef tract (Lee and Smith 2002), bank systems may have an important biophysical role in filtering sediments and nutrients, buffering the coral reefs south of the Keys from the full impact of shelf and bay waters .

Figure 3. Aerial photograph showing an attempt to extricate a large vessel from a grounding site on a bank top within the Moser Channel Banks System. This particular bank has been severely damaged by multiple vessel groundings.

Objectives

Recognizing the widespread distribution and potential threats to bank systems of the middle Florida Keys, we conducted a series of surveys to investigate their ecological role in FKNMS. Benthic habitat, macroalgal and fish communities were surveyed to allow comparison between banks systems and their surrounding habitat. Detailed analysis is focused on fishes due to their ecological and economic importance in the region. Fishes, with their high motility and complex life histories, are important contributors to the linkages between benthic habitats (e.g. Burke et al. 2009). Fishes are also a major contributor to the economics of the Keys, supporting tourism and important commercial and recreational fisheries. Specifically, we designed and implemented surveys to address the following questions:

1) Do bank systems focus biological activity and biodiversity?
2) What ecological services are bank systems likely to provide?

To answer these questions we:

1) Investigated seasonal, annual and spatial variability of bank system resources,
2) Compared resources of three bank systems,
3) Compared the resources of bank systems to those of the surrounding habitat, and.
4) Monitored behavior of bank system fishes.

Results of these surveys are relevant to questions regarding the functional importance of bank systems in the ecology of the South Florida's coral reef ecosystem.

MATERIALS AND METHODS

Study Area

Three bank systems located north of the middle Florida Keys were surveyed (Figure 1). Each bank system consisted of a cluster of associated banks, the channels between the individual banks and the interface or bank margin between these system elements and the relatively flat surrounding bottom which we subsequently refer to as basin habitat (Figure 4a, b). The most intensively studied bank system contained 42 banks which collectively we refer to as the Moser Channel Banks System (MCBS), due to its location north of the large tidal pass known as Moser Channel (Figure 1b). The long axis of individual banks and the orientation of closely associated banks within MCBS was generally east-west. To the northeast of MCBS is a relatively smaller aggregation of nine banks named Bamboo Banks which, with their associated channels and interface with the surrounding basin, we refer to as the Bamboo Bank System (BBS). The collective orientation of the nine banks within the BBS is generally NE-SW (Figure 1c). Unlike MCBS, BBS is not in close proximity to a particular tidal pass and consequently is subject to lower tidal currents. East of the BBS is the Channel Key Bank System (CKBS) which bridges the extensive basin between the middle Keys and Florida Bay and experiences strong flow associated with the tidal pass between Long Key and Conch Key. CKBS consists of a chain of approximately 70 closely associated banks originating at Channel Key slightly north of the tidal pass at Long Key and extending NNE to the extensive flats of Arsenic Bank at the western margin of Florida Bay (Figure1d).

Sampling strata

The study area was stratified relative to habitat types to allow estimation of natural resources and their distribution relative to bank systems and their surrounding habitat. To define strata geographically the perimeters of each bank system, of the individual channels and associated banks were delineated using aerial photography and a geographic information system (GIS). We defined four sampling strata, representing morphologically defined habitats of the study area's benthic landscape (Figure 4a). Bank tops were the shallow area that crowned the sloping sides of banks. Channels were the laterally constrained passes between adjacent banks. The bank margin was the perimeter of an aggregation of banks where their sloping sides graded to the flat surrounding habitat. The basin was the area of uniform depth surrounding a bank system and was further stratified relative to distance from the margin of the bank system (Figure 4b). Depending on the objective to be addressed, fixed or randomly selected stations within the four strata were sampled during annual surveys, 2002 through 2006 (Table 1).

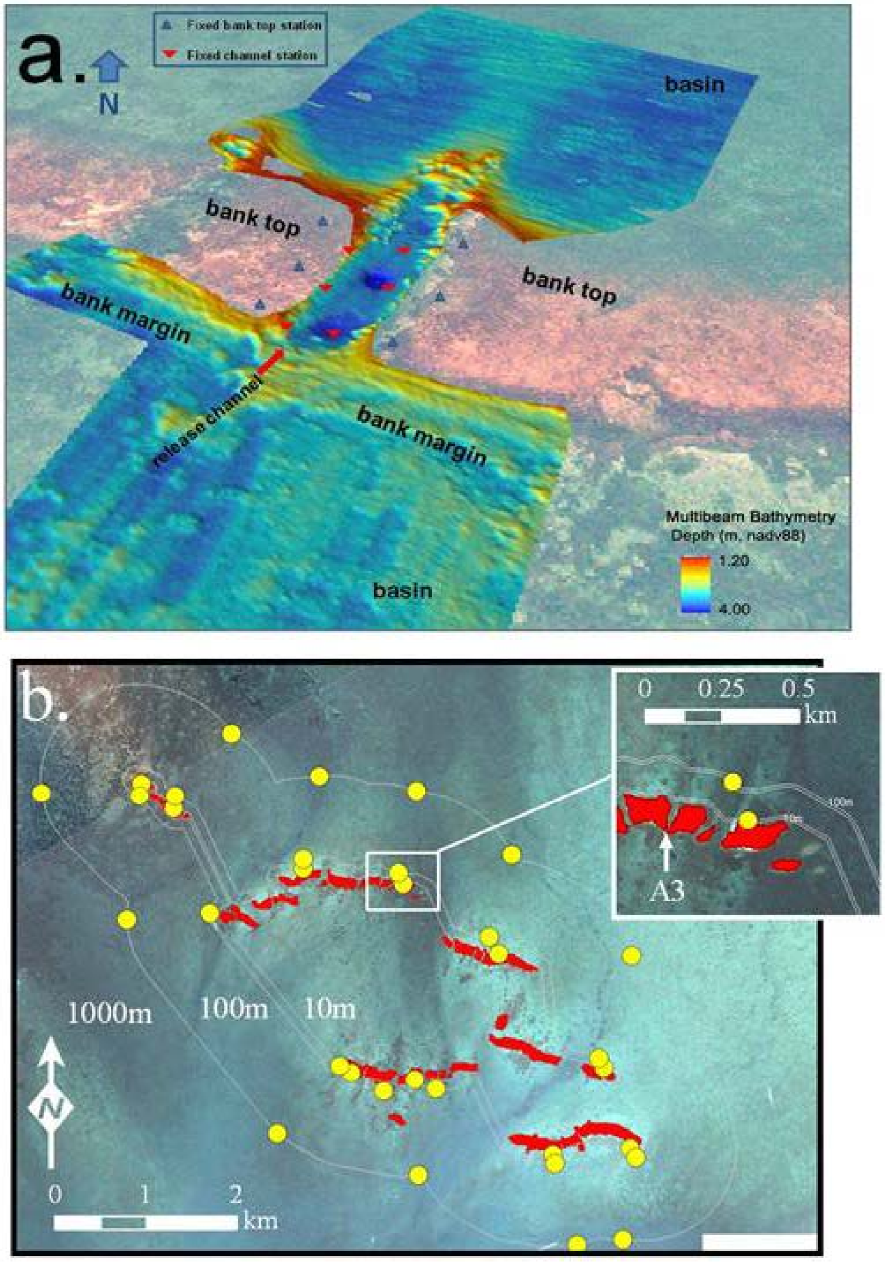

Figure 4. a) Detail of the features of a focal area A2 within the Moser Channel Banks System showing sampling strata (channel bank top, bank margin and basin) and the locations of fixed channel and bank top stations within the focal area. b) Aerial photograph of the Moser Channel Banks System and 10, 100, and 1000 meter perimeters and the randomly selected sampling sites (yellow dots) surveyed in 2006. Inset shows detail around focal area A3 and location of a 10 and 100 meter stations.

Table 1. Summary of surveys conducted between 2002 and 2006 within and around three bank systems; Moser Channel Banks System (MCBS), Bamboo Banks System (BBS), Channel Key Banks System (CKBS). Survey were distinguished by their target; fish (F) habitat (H) and macroalgae (M), the sampling strata in which the surveys were conducted and in the case of MCBS whether the stations were located in selected focal areas, repeatedly sampled over time or randomly selected.

		2002		2003		2004		2005		2006	
Banks System	Sampling strata	F	H	F	H	F	H	F	H	F	M
MCBS Focal Area and Basin Transect Stations	Channel	36	-	36	-	24	24	24	-	24	24
	Bank top	36	-	36	-	24	24	24	-	24	24
	Bank Margin	-	-	-	-	-	-	24	-	-	-
	Basin	-	-	-	-	6	-	48	12	-	-
MCBS Stratified Random and Basin Transect Stations	Channel	-	-	-	-	14	-	-	-	-	-
	Bank top	-	-	-	-	14	-	-	-	-	-
	Basin	-	-	-	-	6	-	-	-	44	18
BBS Stratified Random and Basin Transect Stations	Channel	-	-	-	-	6	-	6	6	6	24
	Bank top	-	-	-	-	6	-	6	6	6	24
	Basin	-	-	-	-	6	-	6	12	16	9
CKBS Stratified Random and Basin Transect Stations	Channel	-	-	-	-	40	-	30	15	30	30
	Bank top	-	-	-	-	40	-	30	15	30	30
	Basin	-	-	-	-	6	-	6	-	36	9

Fish Surveys

Surveys of the fish communities were conducted by scuba divers at stations within the four sampling strata. Fish survey provided an estimate of fish (and lobster) abundance, diversity and biomass using a modified stationary point count based on an established procedure (Bohnsack and Bannerot 1986). Once settled on the bottom at the geographically fixed station, a scuba diver counted all fishes present or that entered a cylindrical space with an estimated diameter of six meters for a period of five minutes. When a school of fishes entered the cylinder it was assumed that all fish present in the school entered. All fishes observed were identified to the lowest taxonomic category possible based on visual identification criteria (Humann and Deloach 2002). Total lengths of all fish counted were estimated to length intervals (<5 cm, 5-10 cm, 10-15 cm, 15-20 cm, 20-25 cm, 25-30 cm, 30-35 cm). Sizes of fish greater than 35 cm were estimated to the nearest decimeter.

Most surveys within MCBS were conducted at fixed stations with repeated measurements providing estimates of seasonal and inter-annual variability of the fish community. Sampling of fixed stations within MCBS was conducted in every year of this study (2002 – 2006). Fixed stations were located within focal areas, each of which consisted of two adjacent banks and the channel that divided them. Focal areas were selected to represent the range of physical variability found in MCBS. For example, the focal area identified as A1 had gently sloping banks, the channel was relatively wide and the bottom was covered with unconsolidated sediments and dense seagrass. In contrast, the banks at focal area A4 had steeper sides and its channel was relatively narrow with a floor consisting primarily of exposed portions of the underlying limestone bedrock covered in places by coarse sand, invertebrates and macroalgae. To account for spatial variability within each focal area, six fixed sites were sampled within an area's channel and three fixed sites on each of the channel's two defining banks (Figure 4a). To provide a warm/cold seasonal comparison of fish communities, fixed stations within channel and bank top strata of six focal areas were surveyed in the summer of 2002 and in February 2003. To provide an estimate of inter-annual variability of the fish community, fixed stations of four of the six focal areas sampled in 2002 and 2003 (focal areas A1, A2, A3 and A4, Figure 1) were resampled each June from 2004-2006.

To determine the distribution of fishes relative to MCBS and surrounding habitat the abundance of fishes at fixed stations within MCBS's four focal areas were compared to abundance at the margin of MCBS and in the surrounding basin. The fish community of the basin surrounding MCBS was investigated along eight transects that originated at either end of the focal area channels (A1, A2, A3, A4). These transects were sampled at 0.1, 0.2, and 1 km distances from the margin of the MCBS. The fish community at the bank system margin was sampled at the foot of the bank slope on both sides of the channels of focal areas A2 and A4.

To test for evidence of a common pattern of fish distribution relative to bank systems, randomly selected stations and stations at set distances along transects were surveyed. Randomly selected channel and bank top stations in MCBS, BBS and CKBS were surveyed in 2004. Each system's channels and their adjacent bank pairs were sequentially numbered and sample locations were selected at random. Individual sampling sites within a channel and on the adjacent banks were set on either side of the deepest portion of the channel. The distribution of fishes within the basins surrounding the three bank systems was investigated at set distances along transects aligned at a right angle to the bank system margin. Sampling effort varied between years due to variation in the time available for sampling basin transects. Distances of sampling locations from the banks system was varied by year in an effort to better resolve the distribution of basin fishes relative to bank system margins. In 2004, two transects originating at the margins of each of the three bank systems were sampled at distances of 50 m, 500 m and 1,500 m. In 2005, in addition to previously described sampling of MCBS basin, BBS and CKBS basins were each sampled along two transects at 100 m, 200 m and 1000 m distances from their margins. In 2006 basin stations at distances of 10 m, 100 m, and 1000 m from the margins of the three bank systems were sampled. In order to randomly select these basin stations, polygons that defined the three respective distances from a bank system were designated (Figure 4b) and sites were located on a radius that originated at a randomly selected point along the ten meter perimeter using Hawth's Tools in ArcGIS.

Crepuscular Behavior

Crepuscular behavior of fishes was investigated on a single date in 2006 within one of MCBS's channels. Two stationary dive teams were located approximately 10 m up and down current from an area of the channel which held schools of both gray snapper (*Lutjanus griseus*) and white grunts (*Haemulon plumieri*) which were expected to exhibit crepuscular migrations. The divers performed species counts and activity observations every five minutes for a period of an hour starting approximately 30 minutes before sunset.

Benthic Habitat

SCUBA divers quantified benthic habitats of fish survey stations by visually estimating the coverage of flora and fauna in four 0.25 m^2 quadrats. Abundance of seagrass species, macroalgae, exposed abiotic substrate (hard-bottom, sand), sponges, octocorals, and corals were assessed using a modified Braun-Blanquet scale (Braun-Blanquet 1972, Kenworthy et al. 1993, Fourqurean et al. 2001). Macroalgae were further categorized as either upright calcareous, upright fleshy or turf (Atlantic and Gulf Rapid Reef Assessment 2006). Finally, octocorals and corals within each quadrat were counted. Observations of cover at each site sampled were categorized as: 0 = species or taxa absent from a quadrat, 0.1 = species or taxa represented by a solitary individual, 0.5 = species or taxa represented by a few individuals, 1 = species or taxa represented by many individuals (<5% cover), 2 = species or taxa represented by many individuals (5% - 25% cover), 3 = species or taxa represented by many individuals (25% - 50% cover), 4 = species or taxa represented by many individuals (50% - 75% cover), and 5 = species or taxa represented by many individuals (75% - 100% cover). Because habitat surveys were more time consuming than fish surveys, monitoring station within MCBS could only be visited once during the study and only a subset of the randomly selected stations could be sampled to provide inference relative to habitat variation among sampling strata, the three bank systems and their basins. We assumed that a single survey of the fixed stations within MCBS provided a reasonable estimate of its habitat over the entire survey period. Repeated visits conducted by fish survey teams during their annual surveys in MCBS indicated that this assumption was reasonable. Habitat surveys were initiated in 2004 when all stations within the four focal areas within MCBS were sampled, allowing a comparison between and among the bank tops and channels. Habitat surveys of subsets of the randomly selected stations in BBS and CKBS and basin habitat surveys in MCBS and BBS were conducted in 2005 (Table 1).

Macroalgal Survey

Surveys to compare the macroalgal assemblages of channels, bank tops, and basins were conducted in June, 2006. Four channels and their adjacent bank tops in the MCBS, three in BBS and five in CKBS were sampled using a design analogous to that used for fishes and benthic cover. At each site, divers collected all macroalgae contained within six 100 cm^2 quadrats within the channel. The same procedure was followed for the adjacent bank habitats so that six bank top collections of macroalgae were also made per site. Basins of the three bank systems were sampled along transects at three pre-determined distances (10 m, 100 m, and 1000 m) from the closest bank. Two transects (six sites) were surveyed around MCBS and only one (three sites) around both BBS and CKBS because of time constraints. Three replicate quadrat samples were collected at each site. Algal samples were stored on ice during transport from the field to the lab where they were identified to species of the lowest taxa possible. To determine dry weights of macroalgal genera, samples were rinsed thoroughly with fresh water, separated to genus, and dried to a constant weight at 100°C. Dried algae samples were then ashed for four hours at 480-500°C. Ash-free dry mass (AFDW, as mg/100cm^2) was obtained by subtracting the mass of the ash from the dry weight.

Data Analysis

Benthic habitat Braun-Blanquet cover data was converted to percent cover using the mid-point of each categorical range following Lepš and Hadincova (1992). For each cover category, density (D) was calculated as:

$$D_i = \frac{\sum_{j=1}^{n} Sij}{n}$$

Where D_i = density of species/taxa *i*,
j = site number from 1to *n*, the total number of sites sampled, and
S*ij* = the Braun-Blanquet score for species/taxa *i* in site *j*.

Macro algal ash-free dry weights (AFDW, as mg/100 cm^2) were log transformed to normalize distributions and homogenize variance and analyzed with a general linear model (Proc GLM, SAS) for the contribution of three sampling strata (bank top, channel, basin), the three bank systems and the interaction of strata and bank system.

For each fish species observed, mean number, mean total length and mean biomass were calculated to provide spatial, temporal, and overall estimates of species abundance, length, and biomass for each of the sampling strata. We assumed that our efficiency at counting and estimating the lengths of fishes was equal between sampling locations. Species specific biomass estimates for each sample were calculated from estimated lengths and length-weight regression coefficients for each species obtained from Fish Base (Froese and Pauly 2006). A fish's length was assumed to equal the midpoint of the length interval within which it was counted and mean lengths for species or groups were calculated for each survey. As an indicator of how common a species was in surveys, percentage sighting frequencies (%SF) were calculated as percentage of all counts within which a species was observed. To provide an indicator of the trophic structure of bank systems, all fish species observed were classified into one of six general feeding guilds; piscivore, benthic carnivore, invertivore, planktivore, omnivore and herbivore based on the trophic description provided by Fish Base (Froese and Pauly 2006). Feeding guild biomass estimates were calculated by summing the biomass of all species within each of the guilds. As an indicator of the diversity of fishes among sampling strata, the Shannon index was calculated based on counts of all fishes that were identified to the species level.

Annual variability of the fish community among the four focal areas within MCBS was analyzed using repeated measures analysis of variance. For fish count, diversity, and biomass data, repeated measurements from fixed stations nested within areas (A1, A2, A3, A4) were examined for the contribution of area, year and the interaction of year and area with a mixed model (Proc MIXED, SAS). The model specified a spatial distance correlation structure for the repeated measurements that accounts for the different time intervals between sampling periods. Fish abundance and biomass estimates were transformed [log10 (estimate + 1)] to normalize distributions and homogenize variances.

To investigate the distribution of fishes relative to the MCBS, fish abundance from surveys of the four sampling strata (bank top, channel, bank margin and basin) from two (A2, A4) focal areas within MCBS was analyzed. Fish counts for stations from the four strata nested within the two areas (A2, A4) were analyzed with a nonparametric generalized linear model specifying a negative binomial distribution (Proc GENMOD, SAS). This allowed an analysis of untransformed fish counts for the contribution of strata, area and their interaction to fish abundance.

To compare fish communities among the three bank systems and their common habitats, random survey data from 2004 was analyzed to investigate variability in fish population metrics among sampling strata nested within bank system. Fish abundance (counts) for stations randomly selected from strata (bank top, channel, basin) of the three bank systems (MCBS, BBS, CKBS) were analyzed with the previously described nonparametric generalized linear model (Proc GENMOD, SAS) for the contribution of strata, system and their interaction. The comparable data for diversity and biomass were transformed (log10 (estimate + 1)) to normalize distributions and homogenize variance and analyzed with a general linear model (Proc GLM, SAS).

To compare variation in basin fish abundance and diversity relative to distance from the three bank systems, survey data from randomly selected stations sampled in 2006 was analyzed. Models were designed to provide inference relative to the contribution of distance (10, 100, 1000m) nested within basin (MCBS, BBS, CKBS basin) and the interaction of distance and basin. As in previous analyses, a generalized linear model (Proc GENMOD, SAS) was used to analyze count data and a general linear model (Proc GLM, SAS) was used to analyze diversity estimates.

RESULTS

Benthic Habitats

Benthic communities appear more variable within channels than on banks tops based on percent cover estimates of MCBS's four focal areas. Seagrasses consistently dominated the benthic community of bank tops (Figure 5a). Macroalgae was also important biological cover (Figure 5a) with 36 species identified in MCBS bank top samples (Appendix 1). Macroalgae dominated benthic coverage in three of four focal area channels (Figure 5b). Habitat within these three channels can be described as "hard bottom" scoured by tidal currents that prevented the accumulation of sediment, leaving the underlying limestone either exposed or covered by a thin veneer of coarse sand. The lack of a stable layer of unconsolidated substrate in channels at focal areas A2, A3 and A4 limits growth of seagrasses, favoring macroalgae and turf algae capable of attaching to hard substrate. In contrast to these hard bottom channels, the channel in A1 had more and thicker unconsolidated sediment and was therefore covered with seagrass. Sessile invertebrates, though accounting for a small percentage of the benthic cover, were common on both bank tops and in channels. On bank tops, the coral *Portites divaricata* and various sponges and bryozoans as epiphytes on seagrass were common (Figure 2a) while in channels, loggerhead sponges and large octocorals were relatively common (Figure 2b).

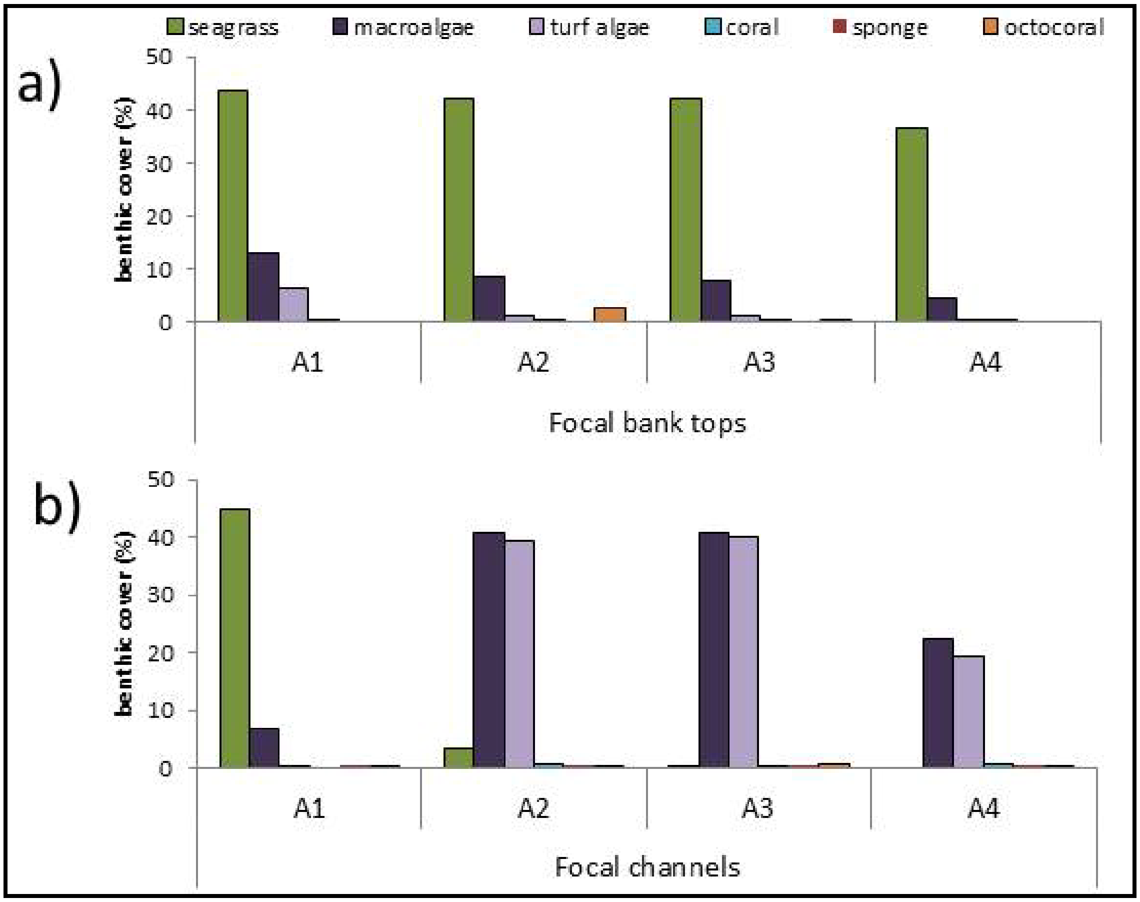

Figure 5. Percent cover estimates derived from Braun-Blanquet scores for sessile benthic floral and faunal categories within a) channels b) bank tops of four focal areas (A1, A2, A3, A4) within the Moser Channel Banks System.

Benthic habitats of the three bank systems were similar in many respects; however, differences were apparent in channel habitats and the macroalgal community of BBS relative to MCBS and CKBS. Comparison of benthic cover showed that bank top habitats of all three bank systems consisted of dense mixed beds of seagrass, macro- and turf algae (Figure 5, 6a). *Thalassia testudinum* was the most abundant seagrass followed by *Syringodium filiforme* on all bank tops. *Halodule wrightii* was a minor component of the seagrass community at BBS and CKBS, but it was not detected in the MCBS system. In contrast to bank tops, the channel habitats differed between systems. Mixed vegetation beds dominated by seagrass were observed in BBS while macroalgae dominated coverage in CKBS channels, with seagrass representing less than 5% of coverage (Figure 6b). This difference in channel habitat appears to reflect the variation observed among the focal area channels of MCBS. BBS channel habitats resembled the soft bottom channel at focal area A1 while CKBS channel habitats were similar to the hard bottom channels A2, A3 and A4 which were more typical of the MCBS system (Figure 5b). Likely related in part to this difference in channel habitats among systems, the macroalgal community of BBS had lower species richness and lower dry weight than MCBS or CKBS (Appendix 1, Figure 7 a, b). Analysis of macroalgal dry weights samples relative to system, strata and their interaction indicated that only system was a significant factor ($p<0.05$). Macroalgal dry weights of Bamboo Banks System strata averaged 0.6 kg m^{-2} approximately, half the average dry weights of both Moser Channel and Channel Key Banks. Examination of mean ash free dry weights (AFDW) for eight common species shows that *Halimeda*, the most important genera in terms of weight, contributed far less in Bamboo Banks strata than in Moser Channel and Channel Key Bank Systems (Figure 7).

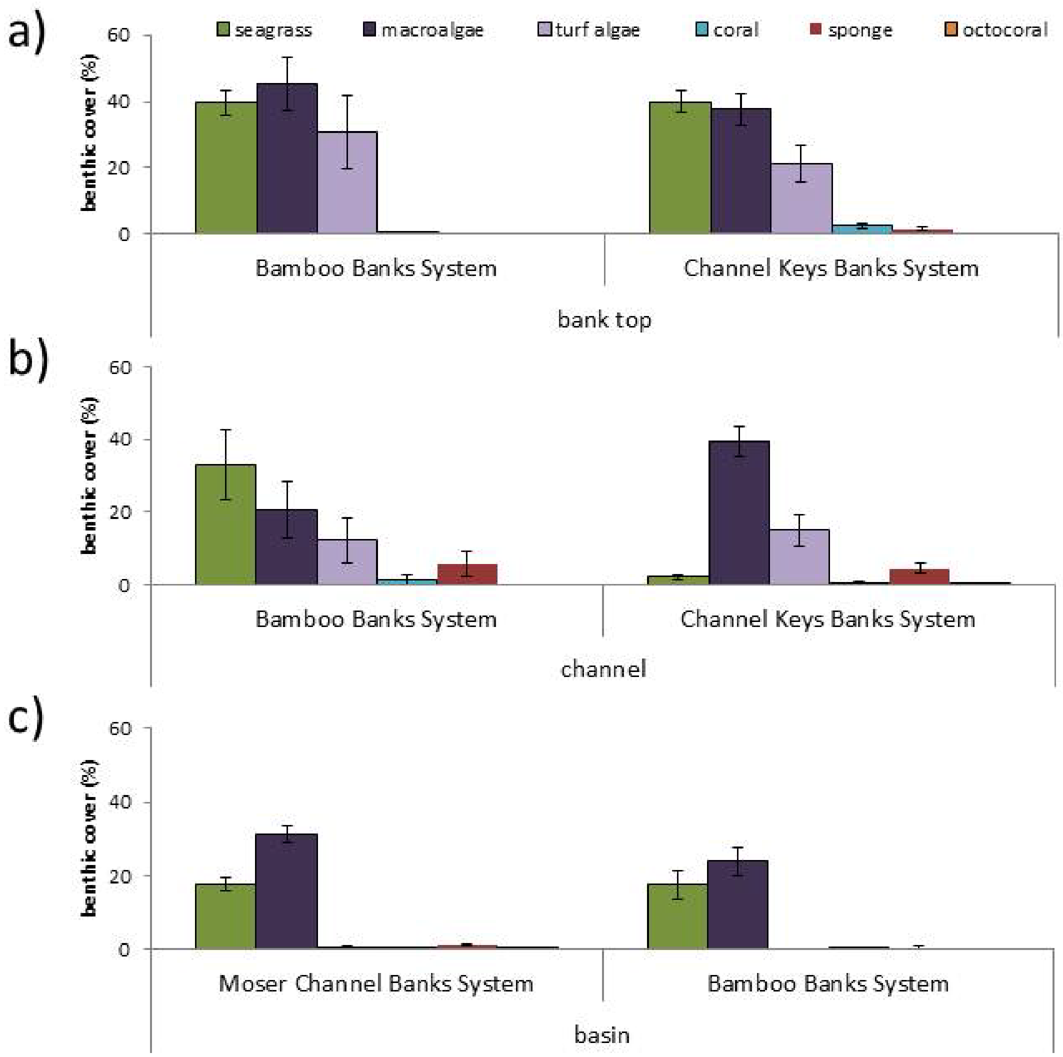

Figure 6. Comparison of percent cover (mean ± std err) of benthic floral and faunal categories for a) banktops, b) channels of Bamboo and Channel Key bank systems, and c) the basins surrounding Moser Channel and Bamboo Banks systems. Percent cover estimates were derived from the mid-points of Braun-Blanquet scores.

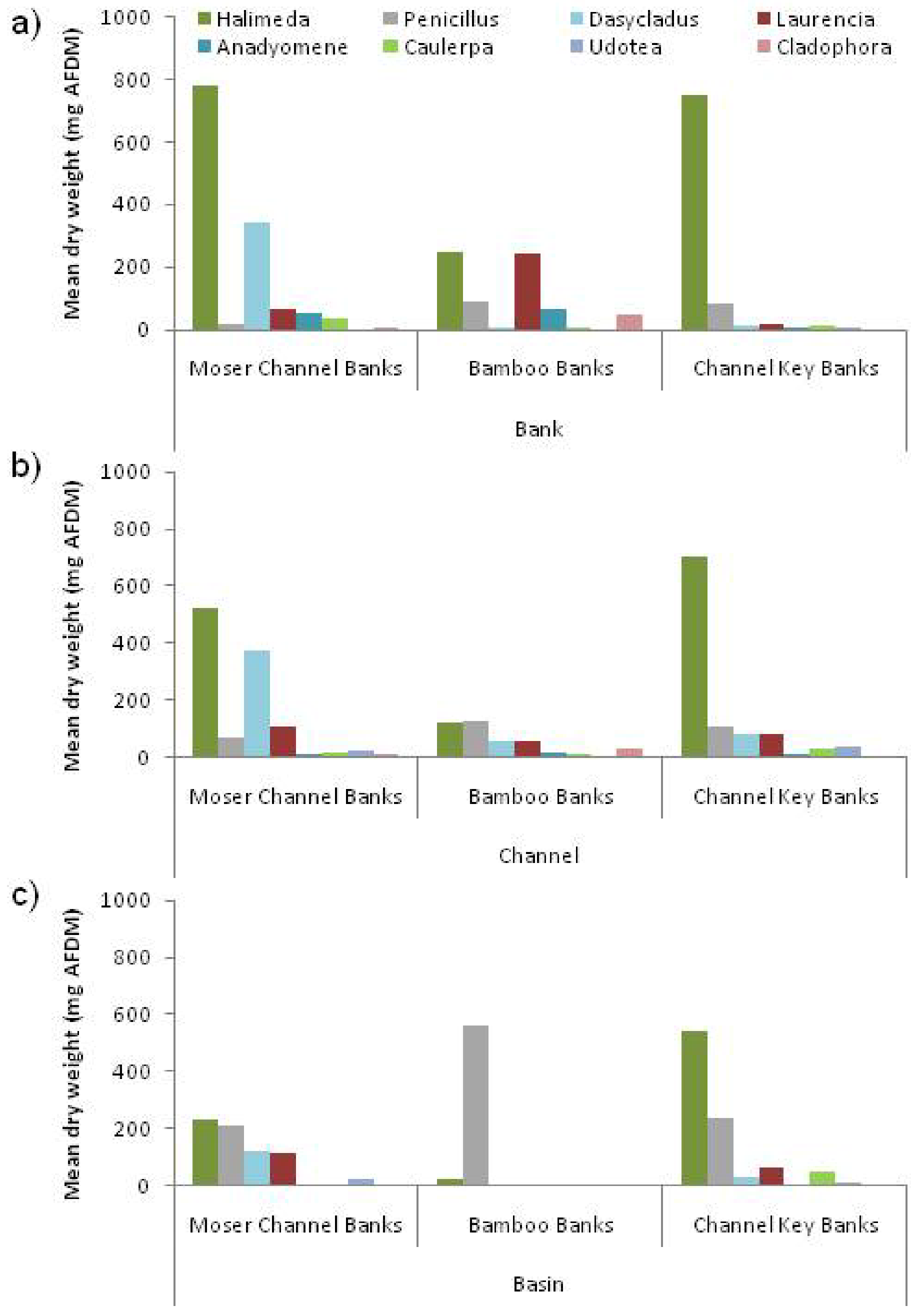

Figure 7. Mean dry weights ash free dry weight (AFDW) (mg) of common macroalgae genera from a) bank top, b) channel and c) basin sampling strata of three banks systems. Genera were limited to those with an overall mean AFDW/100 cm2 > 10mg and to those that occurred in at least four of the nine possible system/strata levels. Genera are ordered by their overall mean AFDW.

Bank system habitats appeared more diverse than the basin habitat that surrounded them, based on both benthic coverage data and macroalgae species richness (Figure 6). Basins surrounding MCBS and BBS were similarly dominated by mixed beds of seagrass and macroalgae (CKBS's basin was not sampled due to time constraints). Macroalgae coverage was on average higher than seagrass; however, seagrasses dominated by *T. testudinum* exceeded 10% in both basins. Turf algae had very low coverage values in basins (Figure 6c), but generally exceeded 10% on bank tops and in channels of BBS and CKBS where sponges were also an important component of the benthos (Figure 6b). A similar dichotomy was evident in the macroalgal surveys which showed higher species richness in the bank system than in the surrounding basins. A total of 69 species were identified among bank top, channel, and basin strata (Appendix 1). Bank top and channel strata of all three bank systems had substantially higher numbers of macroalgal species than in their respective basins.

Fish Community

MCBS Fish Community

Surveys from MCBS showed that this bank system sheltered a fish community of high diversity, abundance and biomass compared with the surrounding basin. Point count surveys within and around MCBS identified 73 species among 30 families representing over 13,000 individuals and six feeding guilds (Appendix 2). Mean counts showed the most abundant fishes were reef associated species belonging to the snapper, grunt and parrotfish families. Invertivores represented the most important feeding guild in terms of species richness (21 species) followed by omnivores (16), herbivores (15), benthic carnivores (14), piscivores (7) and planktivores (4). Six species had overall mean counts >1 for bank system associated strata including; two benthic carnivores (gray snapper, *Lutjanus griseus*; yellowtail snapper, *Ocyurus chrysurus*), two invertivores (white grunt, *Haemulon plumeri;* bluestriped grunt, *Haemulon sciurus*) and two herbivores (striped parrotfish, *Scarus iserti*; redband parrotfish, *Sparisoma aurofrenatum*). These fishes were also the most abundant species encountered in the basin surrounding MCBS, though in lower abundance (Appendix 2).

Seasonal, Annual and Spatial Variation of Fishes in MCBS Focal Areas

The fish communities of MCBS channels and banktops changed dramatically between June 2002 and February 2003, indicating seasonal variation in fish utilization of these habitats (Figure 8). In June 2002, the fish community was more diverse, abundant and evenly distributed among stations (41 species or species groups; 38±7 individuals sample^{-1}, n=72) than in the following February (20 species or species groups, 27±16 individuals sample^{-1}, n=72). In June, benthic carnivores, invertivores and herbivores dominated counts in both channel and bank tops, whereas, planktivores dominated the counts in both strata during February (Figure 8a). The high variability of counts during winter was due to the patchy occurrence of schooling planktivores including anchovies (*Anchoa sp.*) and ballyhoo (*Hemiramphus sp.*) which were the majority of fish encountered. Total biomass was an order of magnitude higher in June (6.1 ± 2.0 kg sample^{-1}) than in February (0.53 ±0.37 kg sample^{-1}) (Figure 8b).

Annual sampling of fixed stations within MCBS's focal areas showed fish communities exhibited significant annual and spatial variation. Though analysis of repeated June surveys (2002, 2004, 2005, 2006) of bank top and channels indicated that year was generally the most important source of variation for fishes, focal area was also a

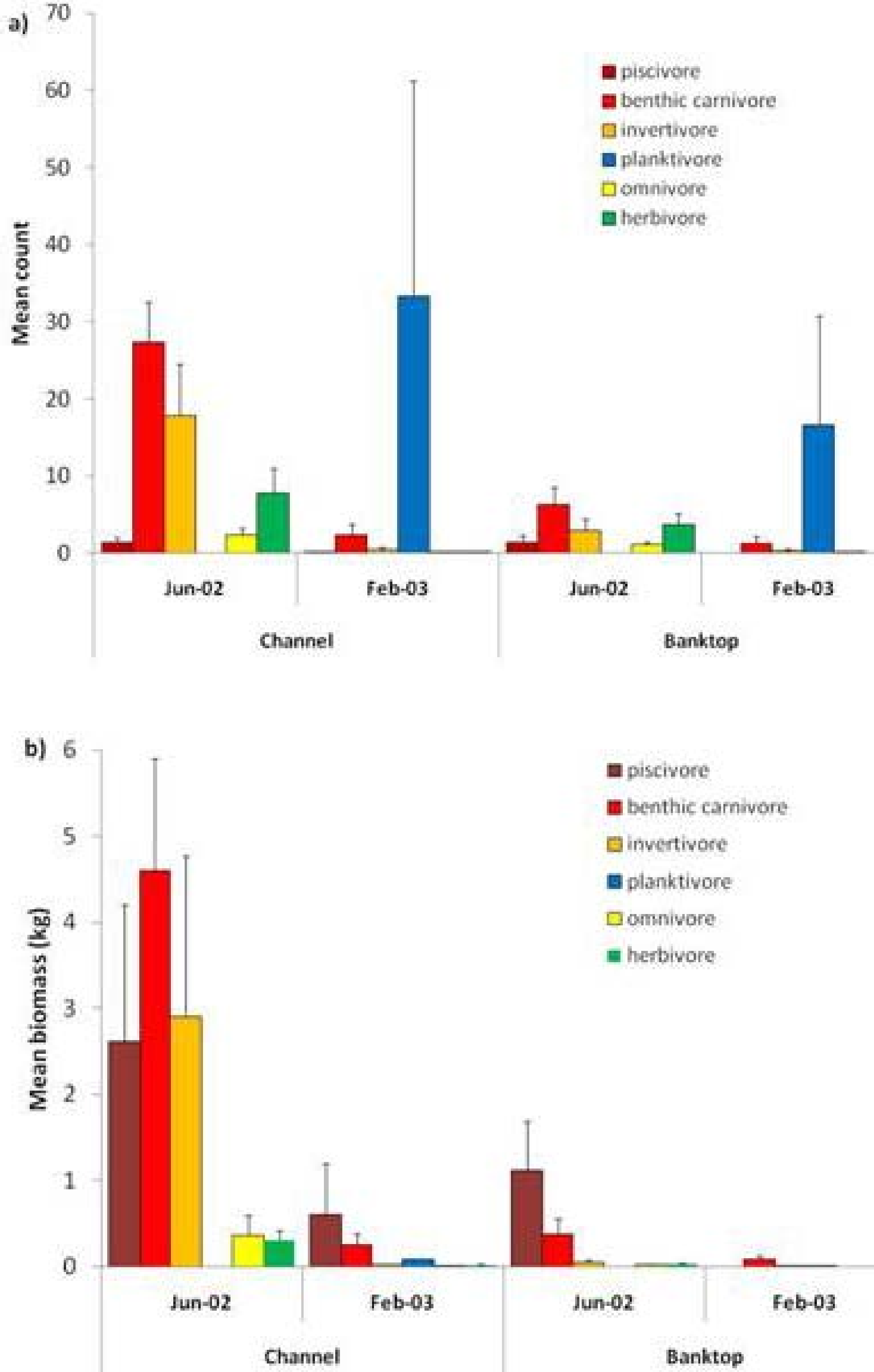

Figure 8. Seasonal comparison of June 2002 with February 2003 fish communities of the Moser Channel Banks System, partitioned among feeding guilds for a) abundance (mean count ± std err) and b) biomass (kg ± std err) in channel and bank top strata.

highly significant factor for fish abundance and diversity on bank tops (Table 2a) and biomass and diversity in channels (Table 2b). Contrasts indicated that fish diversity of both bank top and channel habitat of focal area A1 was significantly higher than most other focal areas (Table 2a, b; Figure 9). A1 also appeared to have higher fish abundance on bank tops and lower biomass in channels and higher diversity than other focal areas (Figure 9a-c). The comparatively low fish biomass of A1's channel, and the high fish diversity of both its channel and bank tops suggest that the fish community or habitat utilization of this

Table 2. Summaries of a mixed model repeated measures analyses of the dependence of a) bank top and b) channel fish community metrics on Moser Channel Banks System focal area (A1, A2, A3 and A4), year of sampling (2002, 2004, 2005, 2006) and the year*area interaction. Variation in fish abundance (Log_{10} (total fish count+1)), b) biomass (Log_{10} (fish biomass+1)) and c) diversity (Shannon index) were analyzed separately for bank top and channel strata. Twenty four fixed sites were surveyed on both bank tops and channels in each of the four years the survey was conducted. Contrasts to distinguish differences (p<0.05) among areas are provided where a significant difference was detected among areas and a significant interaction between area and year was not.

	Dependent variable	Sources of Variation	DF	F value	Pr>F
a)	Bank top fish count	Area	3	6.10	0.002
		Year	3	12.3	<0.0001
		Year*area	9	3.99	0.0004
	Bank top fish biomass	Area	3	2.63	0.07
		Year	3	7.24	0.0003
		Year*area	9	1.72	0.10
	Bank top fish diversity	Area	3	*9.47*	0.0008
		Year	3	*8.75*	<0.0001
		Year*area	9	*1.62*	0.14
	Contrasts among focal areas bank top fish diversity	A1 vs A2	1	*21.26*	0.0012
		A1 vs A3	1	*8.80*	0.013
		A1 vs A4	1	*27.51*	0.0008
b)	Channel fish count	Area	3	0.42	0.76
		Year	3	11.3	<0.0001
		Year*area	9	4.02	0.0004
	Channel fish biomass	Area	3	5.66	0.003
		Year	3	5.45	0.002
		Year*area	9	2.69	0.01
	Channel fish diversity	Area	3	*5.62*	0.007
		Year	3	*3.21*	0.03
		Year*area	9	*1.63*	0.14
	Contrasts among focal areas channel fish diversity	A1 vs A2	1	*2.47*	0.14
		A1 vs A3	1	*8.32*	0.01
		A1 vs A4	1	*15.2*	0.002

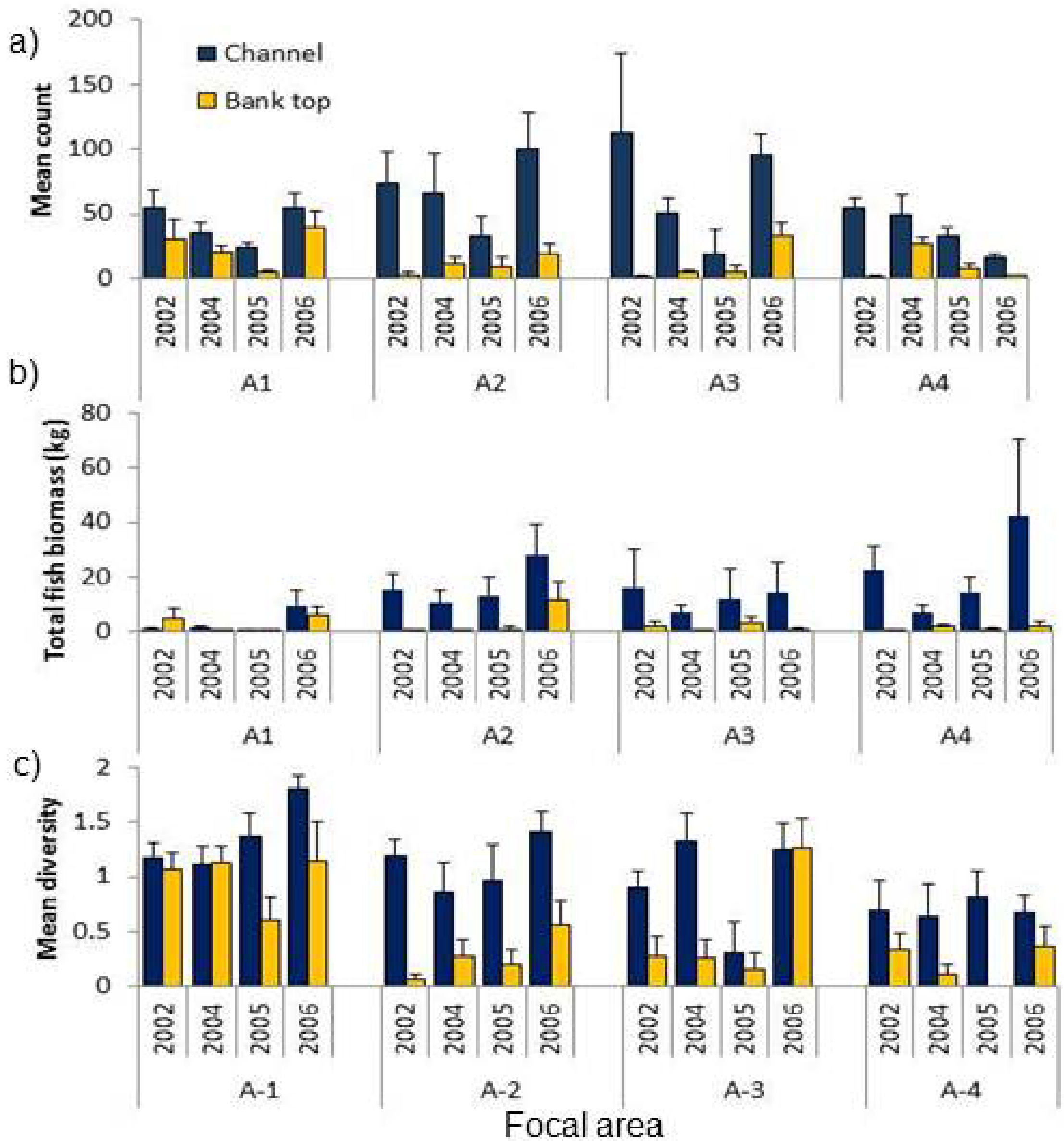

Figure 9. **Fish a) abundance (mean count ± std err) b) biomass and c) diversity in channel and bank top strata of four focal areas (A1, A2, A3, A4) within the Moser Channel Banks System during June of 2002, 2004, 2005 and 2006.**

area differs fundamentally from the other three areas. Although the same fish families dominated the communities of the four areas, the relative importance of snappers tended to be lower in A1's channel and bank tops than in other areas (Figure 10). Examination of the abundance and size of the two principal bank system snappers among the four channels showed that distribution of both species varied relative to focal area. Gray snapper density was low in A1, but consistently high in the other three channels. In contrast, yellowtail snapper density was consistently higher though there size was lower in A1 than in the other focal channels (Figure 11).

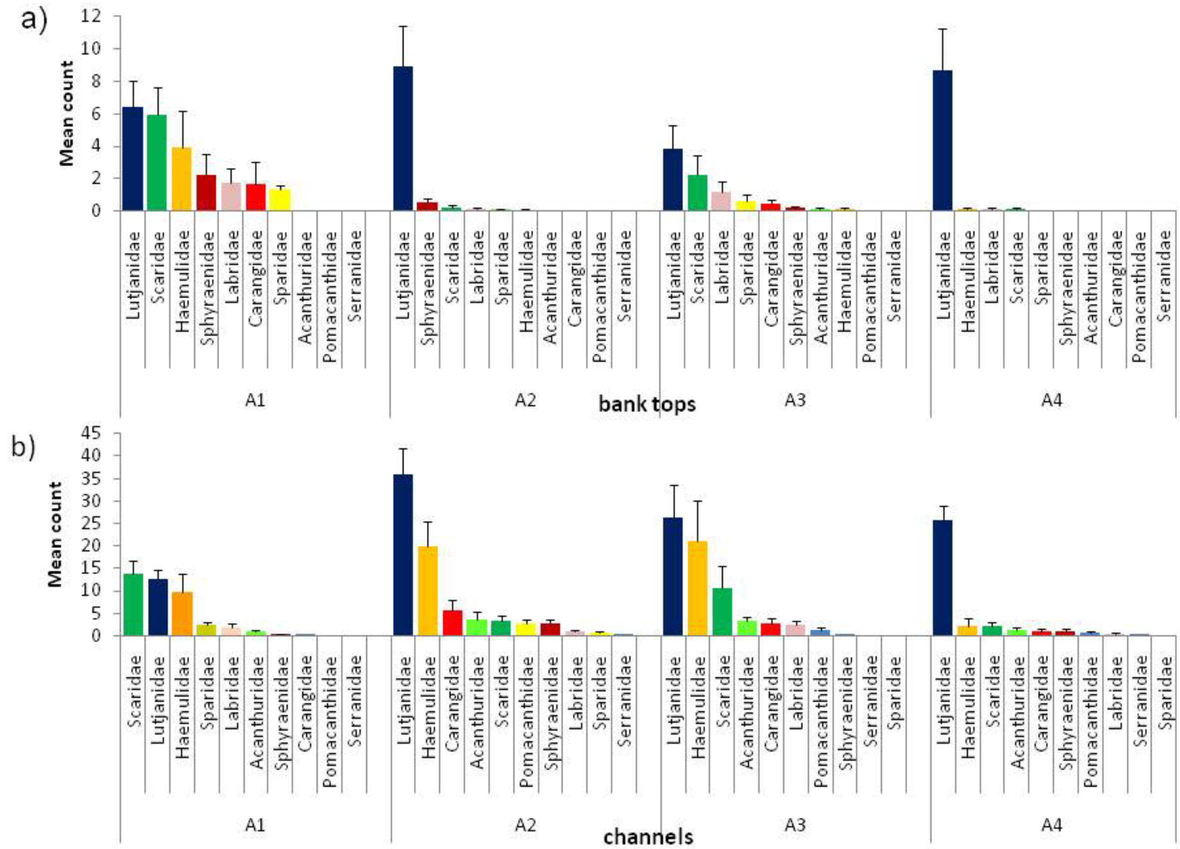

Figure 10. Comparison of the abundance of common fish families (mean count ± std err) associated with a) bank tops and b) channels of Moser Channel Banks System during June surveys.

Examination of mean lengths for numerically abundant families in the focal channel confirmed that the average size of fishes in A1 were uniformly smaller than in other areas (Figure 12). Generally mean lengths corresponded to those of juveniles in A1 and adults in A2, A3 and A4. This dichotomy in terms of life history stage indicated the channel at A1 was utilized as a nursery rather than adult habitat, likely due to differences in benthic cover among the focal channels (Figure 5b)**.**

Despite considerable variation in fishes between years and among the focal areas of MCBS, sampling strata common to all of the focal areas could be distinguished from one another based on their fish communities. Abundance, biomass and diversity of fishes were generally higher in channels than on bank tops (Figure 9a-c). To compare the fish abundance of bank tops, channels to the margin of MCBS and the surrounding basin, we analyzed a balanced data set from two of MCBS focal areas surveyed in 2005. Analysis of fish counts at basin stations located at increasing distance (100, 200, 1000 m) from the channel mouths at focal areas A2 and A4 indicated that abundance did not differ significantly relative to distance from the bank system (SAS, Proc Genmod, p>0.05). After pooling the basin samples by focal area, an analysis relative to area, strata (habitat) and their interaction indicated habitat was the only significant factor affecting fish abundance (Table 3). Examination of mean abundances showed the two areas shared a similar pattern relative to habitat; fish abundance at the bank system margin was similar to that of channels and significantly higher than that of bank tops or basins (Figure 13).

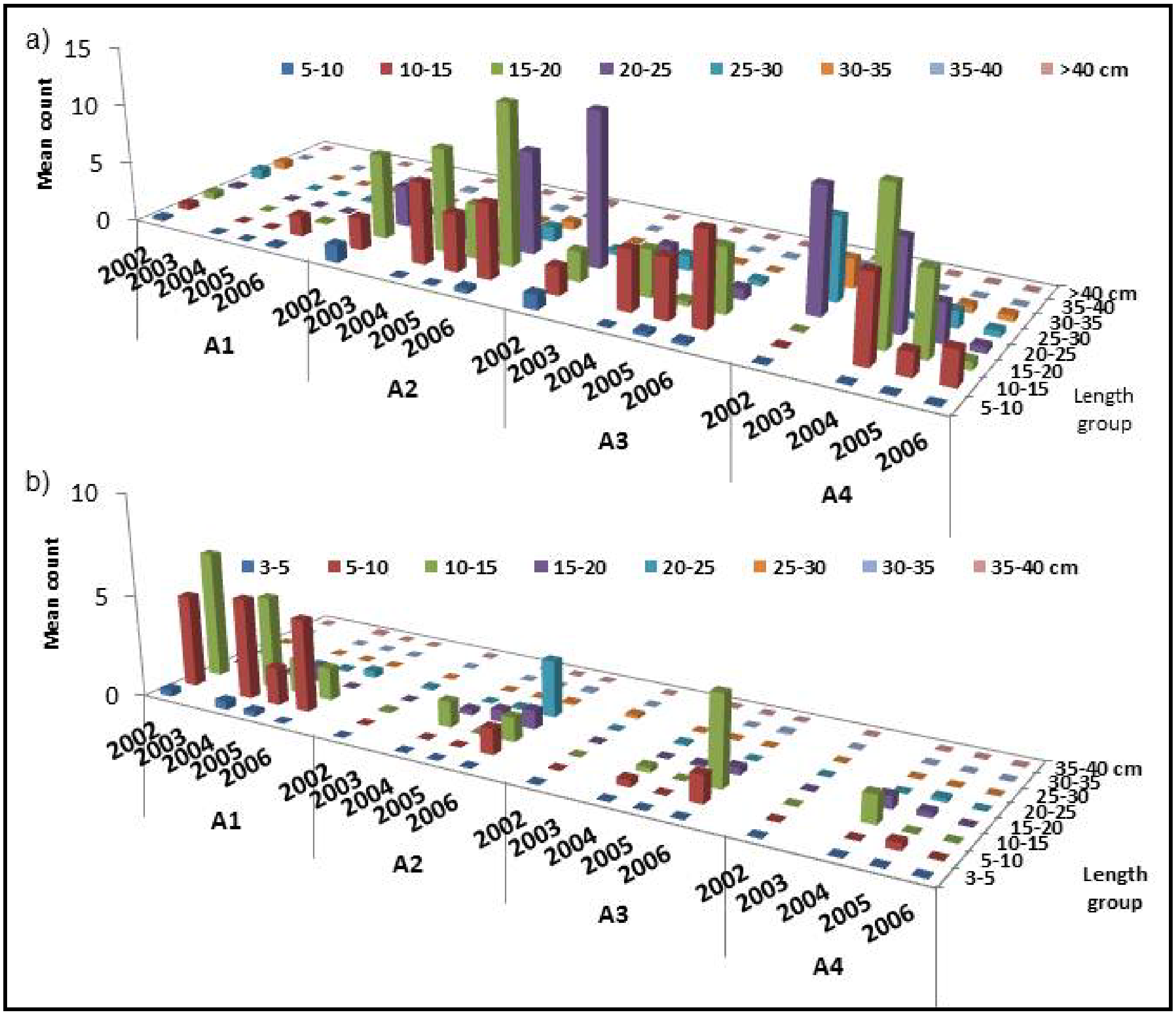

Figure 11. Abundance and size distribution of (a) gray and (b) yellowtail snapper in the four focal areas within the Moser Channel Banks System. Different color bars indicate different length groups.

Table 3. Summary likelihood ratio statistics from a generalized linear model analyses of fish abundance (total count) relative to focal area (A2 and A4) within Moser Channel Banks System, strata (channel, bank top, bank margin and basin) and the interaction of area and strata. Contrasts to distinguish differences among strata are provided.

Dependent variable	Sources of variation	DF	ChiSq	Pr>ChiSq
Total fish count	Area	1	0.87	0.35
	Strata	3	26.75	<0.0001
	Area*Strata	3	0.15	0.99
Contrasts	Basin vs Channel	1	23.7	<0.0001
	Basin vs Bank margin	1	19.2	<0.0001
	Basin vs Bank top	1	7.8	0.005

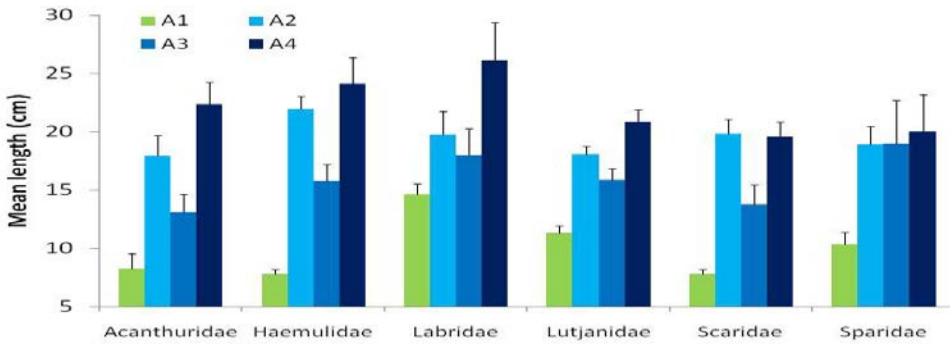

Figure 12. Fish lengths (mean cm ± std err) for numerically dominate reef fish families for focal areas (A1, A2, A3, A4) within the Moser Channel Banks System.

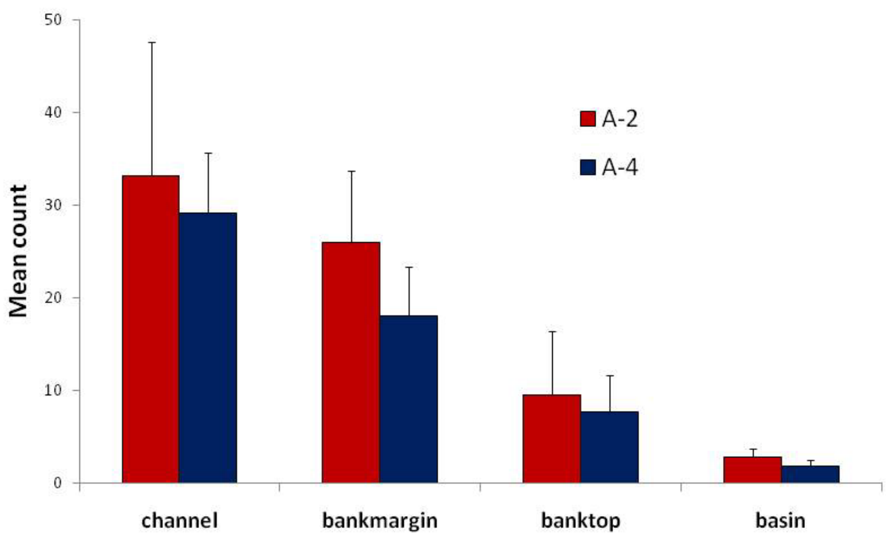

Figure 13. Total fish abundance (mean count ± std err) in the four sampling strata associated with two focal areas (A2, A4) from 2005 surveys within the Moser Channel Bank System.

To determine how the sizes of fishes varied relative to sampling strata, mean lengths of six species with highest %SF was calculated based on the entire data set. Generally, the greatest mean length for all species was observed in the channels though both the gray snapper and bucktooth parrotfish, *Sparisoma radians* exhibited little variation in mean length among strata (Figure 14). Greatest variation in size among strata was evident for the two grunt species and the doctorfish, *Acanthurus chirurgus*. For these species, the disparity in size between fish observed in the channel and other strata suggest there is habitat segregation among life history stages, with adults occurring primarily in the channels and juveniles in other strata. Mean lengths suggest that the white grunt utilizes bank tops during the early juvenile phase and bank margins as advanced juveniles and channels as adults.

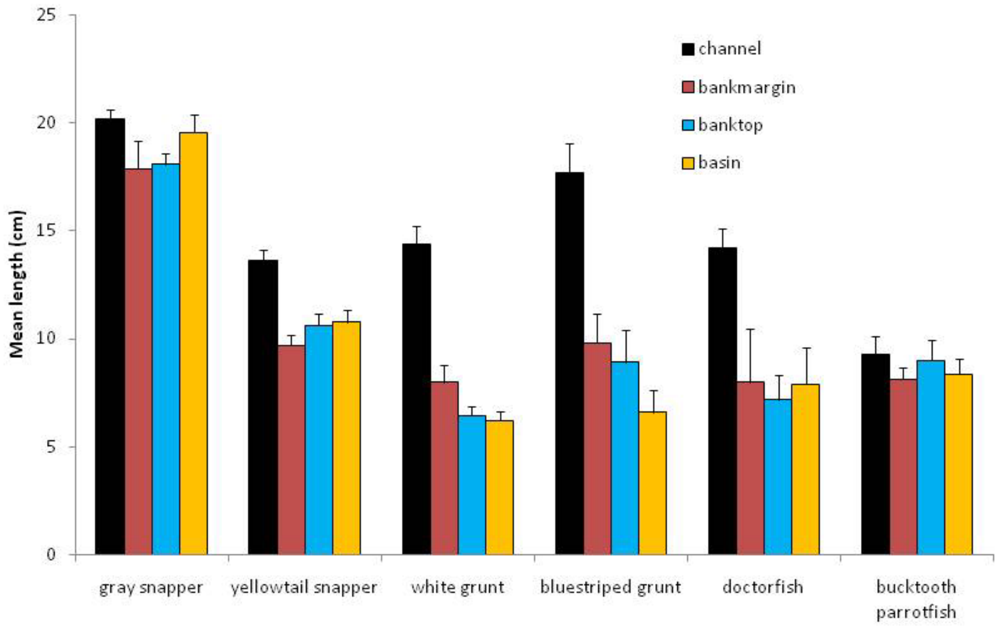

Figure 14. Mean lengths (± std err) of six abundant species of fishes relative to strata sampled within and around Moser Channel Bank System (MCBS).

Crepuscular Behavior of MCBS Fishes

Crepuscular observations within a channel during and following sunset revealed marked behavioral, density and species composition changes during this period. Observers recorded declines in fish density at both the up and down stream observation locations as the light level declined (Figure 15a, b). Prior to sunset redband parrotfish, doctorfish and white grunts were the dominant species present at the upstream observation site (Figure 15a). At the upstream location redband parrotfish departed abruptly prior to 2000 hr followed by doctorfish whose disappearance from the site was more gradual. White grunt density increased during the second observation period before declining. Behavioral changes were evident among the white grunts during the observation period. At the onset of observations white grunts maintained a loose aggregation of resting fish. During the second observation as density increased, larger white grunts exhibited feeding behavior and chased smaller white grunts whose activity also increased. As activity increased density declined and disappearance of grunts from the site occurred just prior to predicted twilight. At the downstream site the doctorfish was the most abundant species. Doctorfish numbers declined over the observation period and the species disappeared prior to the onset of twilight (Figure 15b). White grunts were not observed at the downstream site during the observation period though they had been observed there earlier in the day. Grey snapper, which like white grunts are known to exhibit nocturnal feeding migrations, were present and disappeared from counts between sunset and twighlight. Just prior to twighlight four spiny lobsters, (*Panulirus argus*) in a closely spaced line moved down- current through the observation site. Just after twighlight a stone crab was observed emerging from its lair and a black grouper appeared in the observation area.

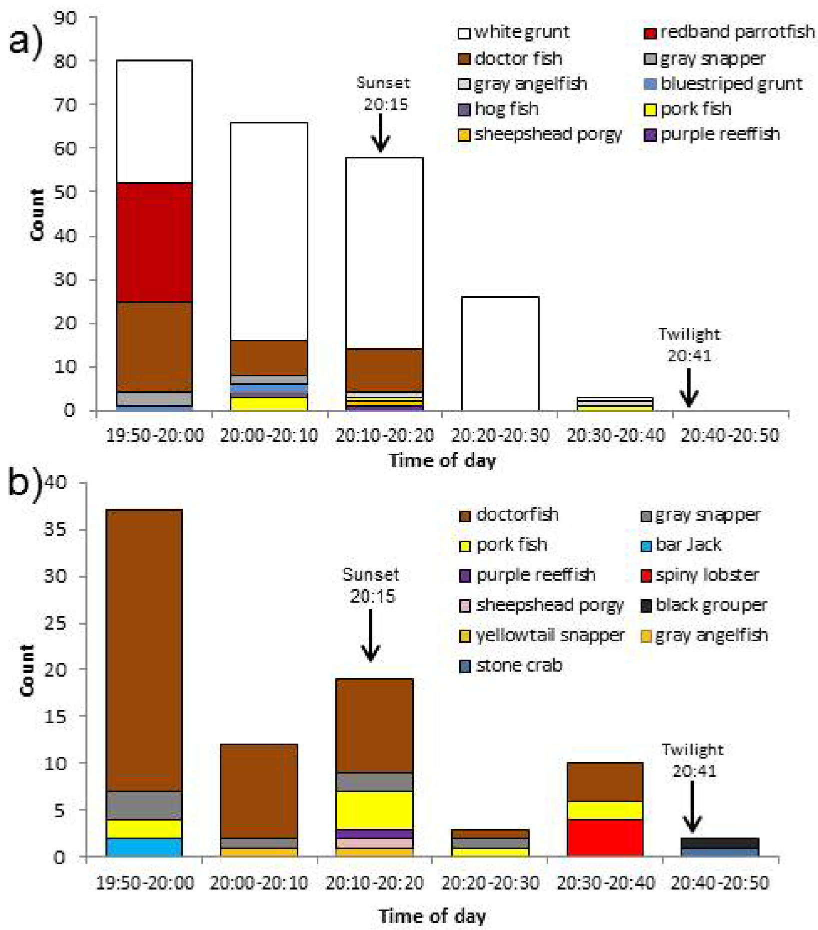

Figure 15. Abundance of fishes a) up-current and b) down-current of a day time habitat of fishes in the Moser Channel Banks System during the crepuscular period. Point counts at ten minute intervals were conducted to determine the change of abundance and species composition of fishes.

Variation in Fish Communities among Bank Systems

Fish communities of all three bank systems were dominated by many of the same reef associated species. The 15 species with highest percent sighting frequencies (%SF) for the three bank systems include members of 11 fish and a single crustacean family (Figure 16). Five parrotfish species, three snappers, three grunts, two wrasses, two angelfishes, two sparids, a single Scianid (highhat), a gerrid (flagfin moharra), a serranid (sand perch), greater barracuda, doctorfish, and the spiny lobster were among the top 15 species in terms of %SF in at least one of the systems. Seven species all associated with reef habitats of the region were common to the lists of the three banks systems: yellowtail and gray snappers, white and bluestriped grunts, doctorfish, bucktooth parrotfish and gray angelfish, *Pomacanthus arcuatus*.

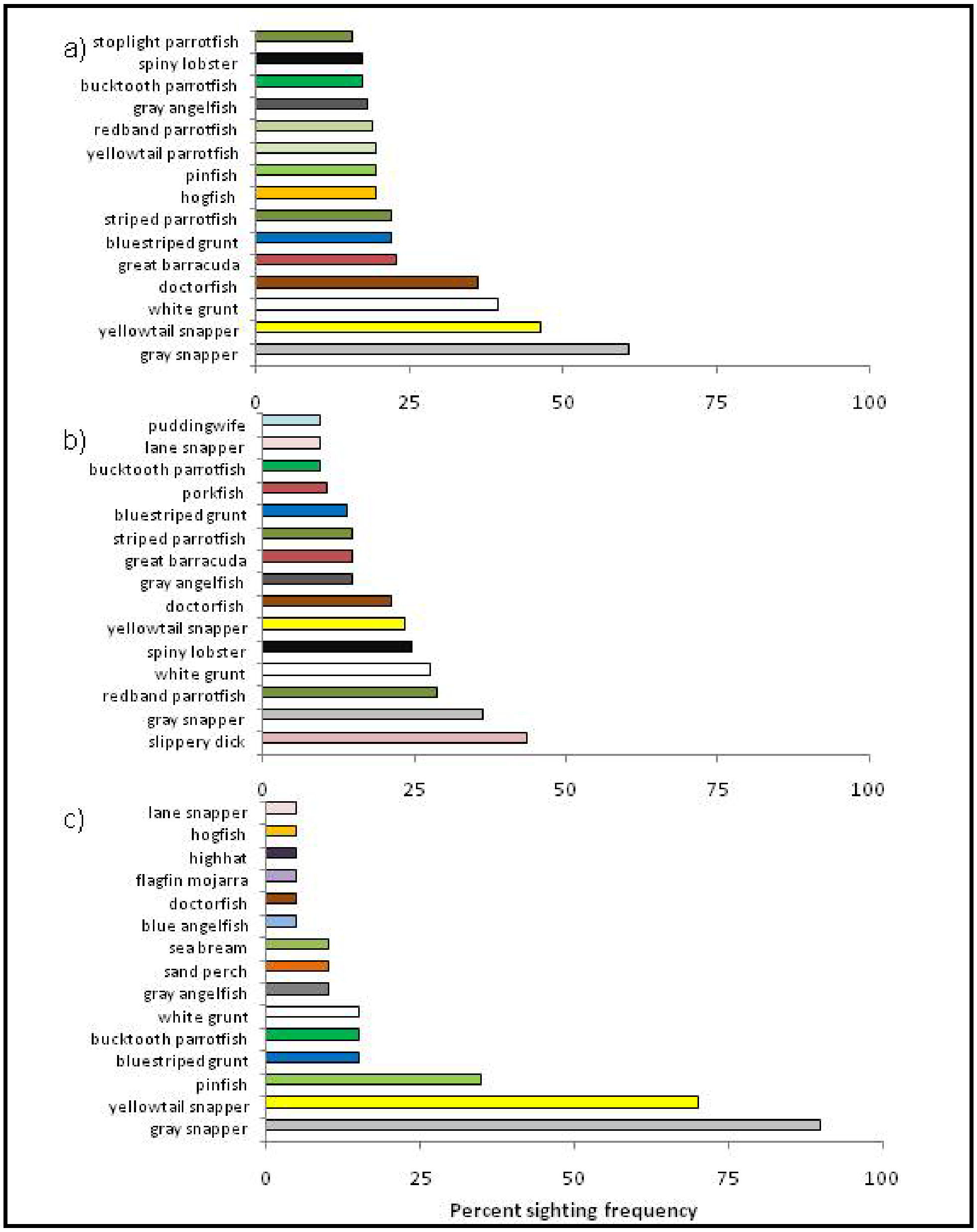

Figure 16. Species with highest percent sighting frequency within channels of a) Moser Channel Banks System, b) Channel Key Banks System, and c) Bamboo Banks System.

The fish communities of the different bank system exhibited similar patterns relative to sampling strata. Analysis of data from randomly selected stations surveyed in 2004 showed that fish abundance, biomass, and diversity varied significantly between strata, but not between bank systems or relative to the interaction of strata and system (Table 4). The common pattern of channels having greater fish biomass and diversity than bank tops or basins is illustrated by their feeding guild biomass estimates (Figure 17). These estimates also show that the pattern of greater biomass and diversity in channels was considerably stronger within MCBS and CKBS than in BBS where the mean biomass was relatively low in the channels.

Table 4. Summaries of analyses of the dependence of a) total fish counts, b) total fish biomass and c) fish community diversity on bank system (Moser Channel Banks System, Bamboo Banks System, Channel Key Banks System), strata (channel, bank top, basin) and their interaction.

	Dependent variable	Source of variation	DF	Chi-square	Pr>ChiSq
a)	Fish abundance	System	2	2.13	0.35
	Total fish count	Strata	2	3.99	0.04
		System*Strata	4	2.20	0.33
				F	Pr>F
b)	Fish biomass	System	2	0.48	0.62
	Log_{10}(biomass+1)	Strata	2	4.11	0.04
		System*Strata	4	0.15	0.86
c)	Fish diversity	System	2	1.14	0.33
	Shannon Index	Strata	2	10.70	0.002
		System*Strata	4	2.20	0.12

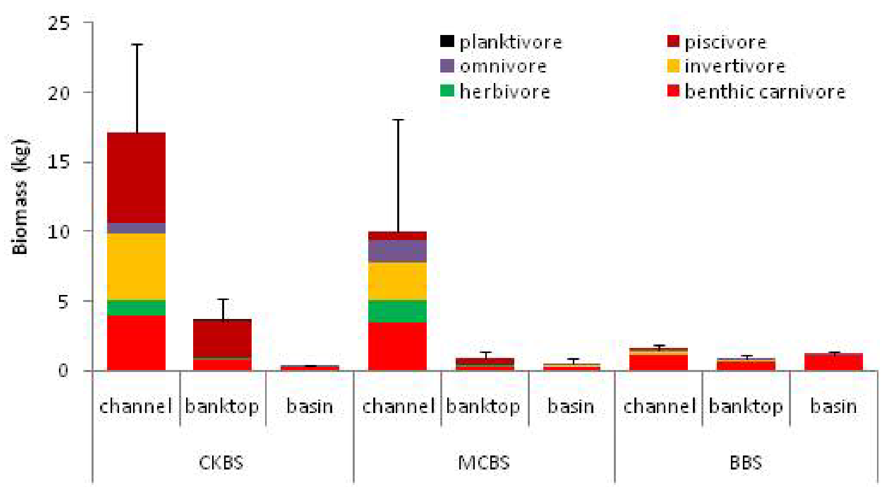

Figure 17. Mean biomass (kg ± std err) of fishes partitioned among feeding guilds for channel , bank top and basin strata of Channel Key Banks System (CKBS), Moser Channel Banks System (MCBS) and Bamboo Banks System (BBS) estimated from randomly selected locations within and around each system.

Differences in fish abundance and diversity were evident among the banks system basins; however, a common pattern of distribution consisting of elevated fish abundance close to the bank system margin was common to all three systems (Figure 18). Fish abundance was significantly higher around MCBS than CKBS and the difference in abundance between BBS and CKBS basins approached significance (Table 5a; Figure 18a). Fish diversity of both MCBS and BBS basins was significantly higher than CKBS's basin (Table 5b; Figure 18b).

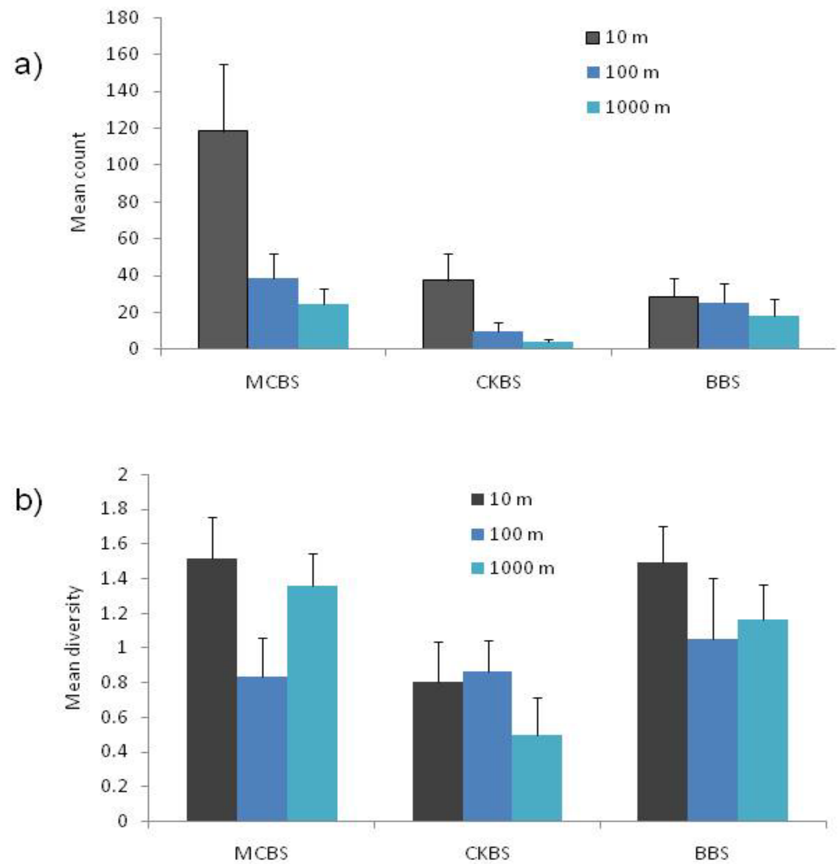

Figure 18. (a) Number of fish (mean + std err) from surveys conducted in basins surrounding each of three bank systems sampled at distance of 10m, 100m, and 1000m from those systems. (b) Diversity (mean Shannon index +/- std err) of these basin fish communities sampled at distance of 10m, 100m, and 1000m from bank systems. MCBS, Moser Channel Bank System; CKBS, Channel Key Bank System; BBS, Bamboo Bank System.

Examination of the fish community relative to distance from the bank system margins revealed that proximity to banks was positively associated with fish abundance but not diversity. Fish abundance was significantly higher at 10 m than at other distances (100 and 1000 m) sampled (Table 5a). In contrast, fish diversity did not differ significantly relative to distance from banks (Table 5b, Figure 18b).

Table 5. Summaries of a) generalized linear model analysis of total fish counts and b) general linear model analysis of variance, of fish diversity (Shannon Index) among basins (Moser Channel Banks Basin (MCBB), Bamboo Banks Basin (BBB), Channel Key Banks Basin (CKBB)) and distance (10m, 100m, 1000m) out into the basin from a bank system. Contrasts among basins and distances (p<0.05) are provided.

a)	Dependent variable	Sources of variation	DF	Chi-square	Pr>ChiSq
	Total fish count	Basin	2	18.42	0.0001
		Distance	2	13.55	0.0011
		Basin*Distance	4	3.06	0.54
		Contrasts among Basins			
		BBB vs MCBB	1	2.04	0.15
		MCBB vs CKBB	1	18.29	<0.0001
		BBB vs CKBB	1	2. 53	0.06
		Contrasts among Distances			
		10 m vs 100 m	1	9.13	0.0025
		100 m vs 1000 m	1	2. 53	0.11
b)	Dependent variable	Sources of variation	DF	F	Pr>F
	Diversity	Basin	2	5.15	0.009
		Distance	2	1.92	0.16
		Basin*Distance	4	1.31	0.28
		Contrasts among Basins			
		BBB vs MCBB	1	0.0	0.99
		MCBB vs CKBB	1	9.07	0.004
		BBB vs CKBB	1	5.05	0.03

DISCUSSION

Benthic Habitat

The high diversity and biomass of bank system sessile communities relative to their surrounding basins enhances the complexity of these seascape features. Plants dominated all habitats surveyed in terms of benthic cover; however, the two basins surveyed revealed a simple pattern compared to the bank top and channel strata of bank systems. Seagrass and macroalgae coverage values were generally higher and turf algae was a frequent component of bank top and channel habitat communities, but not basin habitats. The more topographically (and presumably environmentally) complex bank systems supported on average more than twice as many macroalgal species as the nearby basins variation (Appendix 1). This is analogous to the relationship observed in terrestrial environments where topographic variation is positively correlated with species richness of plants (Benayas and Scheiner 2002, Grace et al. 2011).

The diversity and biomass of sessile animals can be expected to be similarly enhanced by the more complex bank systems. The presence of abundant hard substrates and strong tidal currents in channels provide an ideal environment for attachment and growth of sessile invertebrate filter feeders. Recent studies of deep sea and mesophotic corals implicated factors such as high topography, currents (Baco-Taylor et al. 2006), rugosity and availability of limestone (Bridge et al. 2011) as the most significant abiotic factors explaining distribution of benthic macro-fauna. Similarly, habitats of high topographic variability have been correlated with high biomass and diversity of sponges (Ruetzler et al. 2000). Biomass of certain motile invertebrates was also apparently elevated within bank systems. For example, spiny lobsters were abundant in hard bottom channel where crevasses in the limestone floor and large sponges provided refuges (Figure 19) but were rarely observed during basin surveys.

Figure 19. Lobster, *Panulirus argus* shelters in channel habitat; a) loggerhead sponge, b) limestone bedrock crevasse.

Fish Community

Comparison of Banks System and Coral Reef Fish Communities

Bank systems north of the middle Keys may play an ecological role similar to that played by coral reefs in the coastal ocean to the south in the Florida Straits. During warm months, bank systems have an abundant and diverse fish community dominated by reef fish species whose biomass (within channels) is similar to that found on Caribbean coral reefs (Bauer and Kendall 2010). Of the 11 families represented by frequently sighted species in the bank systems, Sale (1991) lists nine as important on coral reefs. Four of these families are considered among the families to be most characteristic of the coral reef community (Sale 1991): the parrotfishes (represented by five frequently sighted species), wrasses (three species), angelfishes (two species) and surgeonfish (one species). The high biomass of reef fish within banks systems may be due in part to the high topographic variability of bank systems. High relief (Parrish and Boland 2004) and the height of habitat architecture (Gratwicke and Speight 2005) have been recognized as important predictors of reef fish biomass. Thus, these bank systems appear to fill many roles commonly associated with coral reefs.

Though bank system fish communities were dominated by reef associated species, differences in seasonal utilization appear to distinguish bank systems and coral reefs. Unlike Florida's coral reefs which appear to support a relatively stable community year round (Smith 1976), observations made in MCBS during February of 2003 indicate that reef fishes utilize this habitat seasonally. Bank system fishes likely exhibit a seasonal migration through the several passes in the keys to the deeper reefs of the Florida Straits as water temperature declines during the winter. A return migration or colonization probably occurs in the spring. Assuming most reef fishes leave bank systems during cold months, our observations suggested that some adult fishes and schools of fish exhibited homing behavior to specific locations within bank systems. Examples of observations that suggested the occurrence of homing by individuals and groups were sightings of a pair of exceptionally large pork fish, *Anisotremus virginicus*, associated with a coral head within MCBS's A2 channel in successive June sampling periods, observation of a goliath grouper, *Epinephelus itajara*, approximately 2 m in length that occupied the same CKBS channel in three consecutive years, and the observation of a school of adult lookdowns, *Selene vomer*, and an associated school of spade fish, *Chaetodipterus faber*, in the same location of the same CKBS channel in each of the three summers this site was sampled (Figure 20).

Variation in the seasonal suitability of bank system environment for reef fishes as well as differences in habitat may limit the diversity of bank system fish community and influence the distribution of biomass among feeding guilds relative to the community that utilizes nearby oceanic coral reefs. Diversity index values of MCBS's fish community were approximately half that of the reef fish communities studied recently in the US Caribbean (Bauer and Kendall 2010) or the coral reefs associated with the Tortugas Banks (Burke unpublished data) . This lower diversity appeared primarily due to the absence or rarity of fishes whose specialized feeding mechanisms allow the coexistence of large numbers of closely related and morphologically similar species on coral reefs (Hobson 1974). The limited coverage provided by the coral community in bank system likely explains the limited numbers of coral feeding fishes and pomacentrid species which use branching corals for protection (Oehman and Rajasuriya 1998) .

Figure 20. Schools of lookdowns, *Selene vomer,* and spade fish, *Chaetodipterus faber,* were observed in a single channel in Channel Key Bank System but were present there during three successive June sample periods.

Many such reef fish species spend virtually their entire life history associated with reefs (Sale 1991) which serve as settlement and nursery sites for early stages of development and foraging and resting grounds for adults. For these sedentary reef species, bank systems may not represent suitable habitats as their utilization could require significant post settlement movement to avoid cold temperatures during winter.   Also noticeably rare or absent from our bank system surveys were specialized reef fish planktivores such as members of the genus *Chromis* and the bluehead wrasse, *Thalassoma bifasciatum*. Factors such as the shallow water depth, high average current velocity and lack of preferred prey may limit utilization of bank systems by this feeding guild. A similar difference in the importance of planktivores has been reported among coral reefs differing in landscape characteristics. In a comparison of reef communities of the central Pacific and Virgin Islands Gladfelter et al. (1980) concluded that the major trophic difference between the two communities could be attributed to environmental differences between the reefs; the oceanic influence in the Pacific favored planktivores while the grass beds and its invertebrate community surrounding the Virgin Island reef favored benthic carnivores. Bank systems of FKNMS also appear to provide favorable habitat for benthic carnivores, however; the bank system's benthic carnivores appear less diverse than those associated with coral reefs. Rare or missing from the banks systems were small diurnally active benthic carnivores, such as seabasses of the genus *Serranus* and *Hypoplectrus* (hamlets), many of the wrasses of the genus *Halichoeres and* cleaner species such as the neon goby, *Gobiosoms oceanops*, and wrasse of the genus *Bodianus*. In contrast to these specialists, the benthic carnivores common in bank systems were generalists including snappers (Lutjanidae), grunts (Haemulidae), jacks (Carangidae) and porgys (Sparidae) (Appendix 2) characterized by a large mouth suitable for seizing exposed prey that lack heavy armor or noxious components as defense against predators (Hobson 1974). Unlike the more specialized coral reef benthic carnivores which feed on the reef during daylight hours, generalized carnivores feed primarily during the night or during crepuscular periods and generally exhibit feeding migrations away from resting grounds.

Ecological Significance of Banks Systems for Fishes

The seasonal utilization of bank systems by both adult and juvenile fishes normally associated with coral reefs of the region suggests that utilization of bank systems provides substantial benefits. Utilization of bank systems may be analogous to the seasonal utilization of temperate and sub-tropical estuaries which are presumed to enhance growth and survival of coastal fishes (Warlen and Burke 1990) by providing critical habitat, abundant food resources and facilitation of the transitions between life history stages. The consistently high diversity and biomass of the fishes within bank systems and the enhanced abundance of juvenile fishes observed in the immediate vicinity of these systems relative to the surrounding basins suggests that these seascape features concentrates fish. Elevated above a comparatively homogeneous basin landscape, the structurally complex features of bank systems provide microhabitats of harder bottom structures embedded within a largely vegetated and relatively homogeneous landscape dominated by seagrasses and macroalgae. The resulting diversity of biophysical environments provides a wide range of substrates for sessile plants and invertebrates, and functional habitat for epibenthic fauna and fishes. The geographic location of the bank systems places them directly in the regular tidal exchange and the net transport of water between the more temperate Gulf of Mexico and the oligotrophic Atlantic. Such locations position bank systems to intercept larval transport as well as migrating juveniles and adults of a wide diversity of fishes moving between these larger ocean and bay features. Because of their strategic location and the integrated nature of their structural components, bank systems can play an important role in the life histories of fishes and allow efficient transitions as their feeding and sheltering requirements change with growth. Observed differences in the size and abundance of fishes within and around bank systems are likely driven by a variety of abiotic and biotic factors whose relative importance varies ontogenetically (Craig and Crowder 2000). The gradation in size of species such as white and bluestriped grunt among adjacent bank system habitats suggest these species minimize ontogenetic movements and accompanying risk within bank systems. The presence of schools of juvenile yellowtail snapper, doctor fish, redband and striped parrotfish, bar jacks (*Carax ruber*), barracuda and intraspecific schools of grunts associated with bank tops and bank slopes suggest that these shallow, densely vegetated environments represent preferred nursery habitats. Banks systems represent emergent landscape features likely to facilitate school formation, a critical step in the survival strategy of many species (Neill and Cullen 1974).

Though our study was not designed to distinguish the relative importance of bank systems attractive to fishes, our description of the community's variation relative to the physical structure and associated benthic cover does provided a basis for considering what aspects of bank systems are attractive to the fish community. The physical variation provided by bank systems relative to surrounding basins is likely a causal factor in the observed concentration of fishes.

Channels also served as nurseries, apparently dependent on the type of benthic cover. Fish communities of hard bottom and seagrass dominated channels in MCBS differed in size distribution, as well as the relative abundance and ranking of common reef fish families. Juvenile yellowtail snapper appeared to be attracted to a seagrass dominated environment while the gray snapper, represented by advanced juvenile and adults, appeared to avoid it. Numbers of jacks and barracuda were lower in the seagrass dominated channel (A1) compared to the more typical hard bottom channels (A2, A3, A4). Our observations showed that the strong tidal currents within channels and over bank tops tended to flatten the grass bed canopy into a physically dense and visually opaque feature, ideal for the concealment and sheltering of small fishes and invertebrates. Such seagrass features can be expected to enhance survival and growth by shielding early juveniles from both the powerful currents and foraging piscivores while they feed on epiphytic and benthic invertebrates and passing plankton (Figure 21).

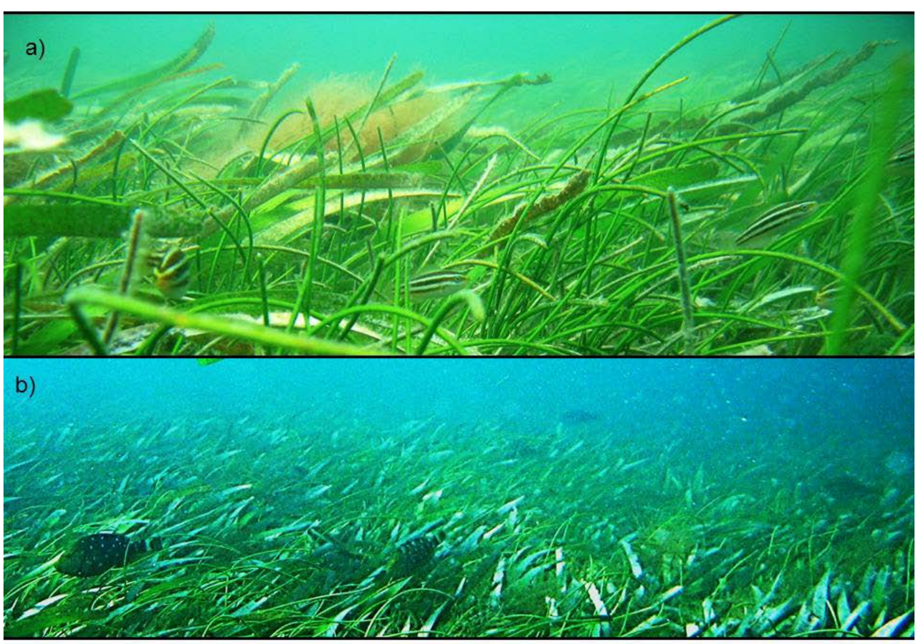

Figure 21. Juvenile reef fish in bank system seagrass beds; a) striped parrotfish and grunts in the canopy on a bank top, and b) stoplight parrotfish in a seagrass dominated channel.

Bank systems appear to offer a transitional habitat between Florida Bay and the ocean by providing feeding and resting grounds for a range of adult and maturing coral reef fishes. For the most abundant bank system species, the gray snapper, the lack of early juveniles and consistently high concentrations of maturing juveniles and recently matured adults suggests that the bank systems represent important secondary nursery grounds that act as stepping stones between the seagrass bed and mangrove habitats of juveniles (Lara et al. 2008) in Florida Bay and coastal ocean reefs that represent adult habitat.

Bank systems provide sheltering and feeding grounds for both nocturnally and diurnally active adult fishes. The presence and behavior of schools of generalized carnivores such as grunts and snappers within bank systems indicates these habitats provide daytime resting grounds allowing for the exploitation of surrounding basins at night. Such species are known to rest on reefs (Ogden and Erlich 1977, McFarland et al. 1979) and among the prop roots of mangroves (Rooker and Dennis 1991, Burke et al. 2009) during the day. During the crepuscular period they migrate to surrounding soft-bottom habitats to feed and home to their resting ground the next morning (Quinn and Ogden 1984). The behavior exhibited by white grunt within MCBS during the crepuscular period matches the behavior of grunts migrating from reefs to surrounding feeding grounds (Ogden and Erlich 1977, McFarland et al. 1979). The disappearance of grunts (Figure 22) and snappers from bank system channels as night fell strongly suggests that they migrate to the surrounding basins for nocturnal feeding. The high abundance and biomass of these nocturnal predators within bank systems suggest they exert significant predation pressure on prey communities of surrounding basins. In contrast to these nocturnal predators, the

Figure 22. White grunt school resting in a Channel Key Banks System hard-bottom channel.

relatively abundant day time feeding piscivores associated with bank systems such as barracuda (*Sphyraena barracuda)*, yellow jacks (*Caranx bartholomaei*), blue runners (*Caranx crysos*) and cero mackerel (*Scomberomorus regalis*) are probably attracted to these systems due to the high abundance of potential prey that shelter there. Large herbivores and invertivores also appear to be attracted to bank systems and the frequent observation of sea turtles, nurse sharks(*Ginglymostoma cirratum*), large spotted eagle rays (*Aetobatus narinari*) and southern stingrays (*Dasyatis americana*) suggests that these species forage and rest in the bank systems.

The importance of individual bank systems to the fish community can be expected to differ due to variation in system size, benthic cover and location within the broader landscape. The interaction of geography and system topography is likely of great importance. For example CKBS provides a series of shallow stepping stones between Florida Bay and adjacent oceanic systems. Such a corridor of favorable habitat may be of particular importance as a migration pathway between Florida Bay, the west Florida Shelf and the Florida Straits for estuarine-dependent marine species of the region. The relatively low biomass within BBS compared to MCBS and CKBS was likely related to system size and differences in benthic cover; however, geographic location and related differences in currents and potentially resulting differences in colonization rates of fishes may also be important. MCBS and CKBS are more closely associated with major passes and thus more accessible to the deep waters of the Florida Straits and the reef tract than BBS. Proximity to passes affects the energy regime as it influences both tidal flow and the net transport of water from the Gulf to Hawk's Channel and the Florida Straits (Smith 1994). BBS is likely to experience relatively weaker tidal currents and consequently greater deposition and retention of sediments. The abundance of seagrass and scarcity of exposed limestone in channels of BBS may reduce their attractiveness for larger fishes that were associated with attached invertebrates (sponges, gorgonians and hard corals) and the complex limestone floors and strong currents characteristic of many channels in MCBS and CKBS. Clearly the linkages among these bank systems and the more charismatic and visible keys habitats (corals and mangroves) needs to be established given the potentially critical role they may play as intermediate habitats and as a reservoir or buffer for fishes utilizing and moving between systems.

Threats to Bank Systems

The structural and biological integrity of banks systems can be severely compromised by boat groundings and is susceptible to negative impacts due to fishing and human activities that affect water quality. Damage to bank systems due to grounding and prop scars related to fishery and recreational boating activities are an ongoing problem in the FKNMS (Sargent et al. 1995, Kirsch et al. 2005, Uhrin et al. 2011). Aerial imagery and damage assessments bear witness to the frequency of injuries due to boat bank encounters (e.g., Figure 4). Vessel groundings destabilize banks by damaging their protective veneer of plants and animals and making them vulnerable to erosion by tidal currents (Whitfield et al. 2002). As their physical structure erodes so too must their ecological role.

While fishing boats likely damage banks physically our surveys did not suggest that fish communities of banks systems were subject to over-fishing. Monitoring of fixed stations within the MCBS over a period of four years showed that fish community metrics lacked a trend consistent with adverse human pressure such as over-fishing. Numbers, and to a lesser extent, biomass of bank system fishes declined during most of the study period (2002-2005), a pattern that might be consistent with fishing pressure; however, this apparent trend disappeared at most locations in 2006. Annual biomass estimates for feeding guilds lack evidence of a decline in biomass of groups targeted by fishermen (benthic carnivores and piscivores) relative to non-target groups (herbivores, omnivores, planktivores and invertivores), a trend expected in a heavily exploited reef community (Russ and Alcala 1989). Despite their sheltered location and proximity to populated areas, we observed relatively few fishermen in bank systems during our June surveys. Given the considerable biomass of commercially important species observed in channels this was surprising and may reflect a mismatch in the size distribution of target species associated with bank systems and current preferences of fishermen. Length frequency distribution of gray and yellowtail snapper within bank systems, the two most important commercial species by weight in regional landings (D. Glockner, NMFS SEFSC, Miami, personnel communication), show that the majority of individuals were smaller than the size currently targeted by fishermen. Yellowtail snapper ranged from early juveniles to adults; however, the majority was juveniles 5-15 cm in length. Adult yellowtail, though relatively rare, were observed to exceed 30 cm in length. The majority of grey snapper were 10-25 cm in length and adults exceeding 40 cm were rarely reported. Despite the lack of fishing pressure, we did encounter a variety of objects (lengths of PVC pipe, a cement mixer) that we presumed were dumped in channels to serve as lobster casitas. While conducting similar work during August coinciding with the spiny lobster recreational season, we were forced to abandon survey efforts due to the number of vessels navigating the area. Thus, problems related to fishing likely vary temporally and could increase due to changes in factors such as climate, human demographics, and the economy.

A threat to the fish community of bank systems may emerge in the form of the invasive lionfish. Diet of the lionfish show that it impacts primarily small fishes (Morris and Akins, 2009), and banks might represent a rich feeding ground for this species. On the other hand, lionfish may have difficulty adapting to the strong currents and seagrass dominated habitats which appear to challenge piscivores with strong swimming abilities, such as the jacks and barracuda. Periodic inspection of these habitats for presence of lionfish is recommended.

Based on their strategic location between large marine systems, their historical persistence and their impact on the distribution and abundance of fishes, the ecological role played by bank systems within the south Florida coral reef ecosystem is likely to be important. Damage to the structural integrity of bank systems caused by boats groundings might be halted and degradation of their ecological functions reversed by management actions. For example the incidence of damage to coral reefs by ship grounding dropped precipitously (Florida Keys National Marine Sanctuary Revised Management Plan. 2007) following the “Area To Be Avoided” designation in 1990 and the protection of selected FKNMS coral reefs with Sanctuary Preservation Area (SPA) status,. While damages to bank systems are caused primarily by pleasure craft rather than the cargo ships that impacted coral reefs, identifying bank systems as areas of special concern on charts and restricting the activities permitted within them should provide some protection. SPAs currently do not exist north of the middle Keys, but this zone type could potentially protect the bank systems from further degradation by improving marking and forbidding extraction of resources. Designation of bank systems as wildlife management areas with closed zones and restrictions on access by motorized vessels should also be effective in reducing damage. While designation of bank systems within special management zones should reduce the fragmentation of these systems due to boat grounding, it would not protect them from deterioration of water quality. Water management plans in the region should consider potential downstream effects of water management practices and water quality monitoring should be conducted to allow documentation of impacts to the ecological status of bank systems.

Summary

1) Bank systems of FKNMS provide ecological services that in many respects are analogous to those provided by coral reefs.

2) Topographic complexity, varying substrates and diverse benthic flora and sessile fauna within bank systems provides a mosaic of habitats that concentrate fishes relative to the surrounding basin environments.

3) Bank systems shelter a high diversity and biomass of fishes, providing nursery grounds for juvenile reef fish as well as resting and foraging grounds for adults.

4) Generalized nocturnal carnivores utilize bank systems as they would a coral reef, as daytime resting grounds. Their feeding migrations can be expected to impact communities of the topographically simpler habitats adjacent to bank systems.

5) Proximity of bank systems to tidal passes between the Gulf and Atlantic appears to affect habitat quality and their utilization by fishes. Systems located near tidal passes are likely to provide stepping stones for estuarine dependent marine species transiting to the coral reefs of the coastal ocean.

5) Vessel groundings, pose an immediate threat to the physical integrity of bank systems and the ecological services these seascape features provide.

Appendix

Appendix 1. **Total number of macroalgal species observed, mean species richness and percent sighting frequency for bank top (BT), channel (C) and basin (B) strata within and across three bank systems of FKNMS.**

	Moser Channel Banks System			Bamboo Banks System			Channel Key Banks System			Bank system strata			
	BT	C	B	BT	C	B	BT	C	B	BT	C	B	
	Number of species observed												Total
	36	39	24	33	29	8	27	48	16	52	58	30	69
	Mean species richness												Mean
	21	21	9	19	12	3	13	24	10	17	19	8	15
Species	Percent sighting frequency												Mean
Laurencia intricata	100	100	67	60	80	33	75	100	100	77	92	75	79
Halimeda incrassata	75	100	33	100	80	100	100	50	67	92	77	67	78
Penicillus capitatus	75	75	0	100	80	100	50	100	50	77	85	50	70
Penicillus dumetosus	75	75	33	80	100	0	50	75	83	69	85	50	64
Halimeda opuntia	50	50	0	80	100	33	100	100	50	77	85	33	63
Rhipocephalus phoenix	50	75	0	20	100	100	100	100	17	54	92	33	62
Halimeda monile	25	50	0	40	100	100	75	50	67	46	69	58	56
Halimeda tuna	100	25	0	100	100	0	100	75	0	100	69	0	56
Dasycladus vermicularis	75	50	0	40	60	0	100	75	17	69	62	8	46
Hypnea spinella	50	25	0	60	80	0	100	75	0	69	62	0	43
Wrightiella tumanowiczii	75	50	33	0	20	33	25	75	50	31	46	42	40
Dictyosphaeria cavernosa	100	0	0	80	60	0	100	0	17	92	23	8	40
Batophora oerstedii	75	25	0	60	100	33	0	25	33	46	54	25	39
Udotea looensis	50	25	33	20	60	100	0	25	33	23	38	50	39
Anadyomene stellata	100	25	0	0	60	0	100	50	0	62	46	0	37
Udotea flabellum	0	50	33	40	60	67	25	50	0	23	54	25	36
Amphiroa fragilissima	75	25	0	40	40	0	75	50	0	62	38	0	34
Champia parvula	50	0	0	20	60	33	50	75	0	38	46	8	32
Acetabularia crenulata	0	50	67	0	40	0	50	25	50	15	38	42	31
Laurencia poitei	50	25	0	0	20	33	50	75	0	31	38	8	28
Dictyota cervicornis	0	25	0	40	40	0	50	75	17	31	46	8	27
Caulerpa racemosa	0	0	0	20	80	0	50	75	17	23	54	8	27
Caulerpa prolifera	25	0	0	60	0	33	75	25	17	54	8	17	26
Gracilariopsis lemaneiformes	0	25	0	40	60	100	0	0	0	15	31	25	25
Halimeda discoidea	100	0	0	0	20	0	50	50	0	46	23	0	24
Avrainvillea fulva	0	0	0	0	20	0	100	75	17	31	31	8	24
Gelidiella acerosa	75	25	0	0	80	0	0	25	0	23	46	0	23
Laurencia papillosa	50	25	0	40	60	0	0	0	0	31	31	0	19
Dictyota menstrualis	0	0	0	60	20	0	0	50	33	23	23	17	18
Caulerpa sertularoides	25	0	0	0	80	0	25	25	0	15	38	0	17
Cladophora sp.	75	25	0	0	0	0	50	0	0	38	8	0	17
Caulerpa paspaloides	50	0	0	0	20	33	25	0	17	23	8	17	16
Halymenia floresia	25	25	0	0	60	0	0	0	17	8	31	8	14
Neomeris annulata	0	0	0	20	20	0	50	25	0	23	15	0	13
Udotea luna	0	0	0	20	20	0	0	50	17	8	23	8	12
Valonia macrophysa	50	0	0	20	0	0	25	0	0	31	0	0	11
Chaetomorpha gracilis	0	0	0	0	0	0	50	25	17	15	8	8	10
Gracilaria tikvahie	0	0	0	0	40	0	0	50	0	0	31	0	10
Chondria leptacremen	0	0	0	0	20	67	0	0	0	0	8	17	10
Dictyota sp.	0	0	0	0	0	0	25	50	0	8	15	0	8
Udotea sp	0	0	0	0	0	0	25	50	0	8	15	0	8
Anadyomene saldenhae	0	25	0	20	20	0	0	0	0	8	15	0	7
Caulerpa mexicana	0	0	0	0	40	0	0	25	0	0	23	0	7
Ceramium sp.	0	0	0	0	40	0	0	25	0	0	23	0	7
Dasya baillouviana	0	25	0	0	40	0	0	0	0	0	23	0	7
Digenea simplex	0	0	0	0	60	0	0	0	0	0	23	0	7
Penicillus pyriformis	25	0	33	0	0	0	0	0	0	8	0	8	6

Bryopsis hypnoides	50	0	0	0	0	0	0	0	0	15	0	0	6
Caulerpa cupressoides	25	25	0	0	0	0	0	0	0	8	8	0	6
Cladophora albida	0	0	0	0	0	0	25	25	0	8	8	0	6
Dictyota pulchella	0	0	0	0	0	0	50	0	0	15	0	0	6
Jania sp	50	0	0	0	0	0	0	0	0	15	0	0	6
Polysiphonia spp.	0	25	0	0	0	0	0	25	0	0	15	0	6
Dictyota mertensii	25	0	0	0	20	0	0	0	0	8	8	0	5
Gracilaria damaecornis	0	25	0	0	20	0	0	0	0	0	15	0	5
Acanthophora spicifera	0	0	0	0	40	0	0	0	0	0	15	0	4
Dasya ocellata	0	0	0	0	40	0	0	0	0	0	15	0	4
Halimeda lacrimosa	0	0	0	20	20	0	0	0	0	8	8	0	4
Halimeda simulans	0	0	0	0	0	0	0	0	33	0	0	17	4
Udotea ocidentalis	0	0	0	0	0	0	0	0	33	0	0	17	4
Agardhiella subulata	0	0	0	0	0	0	25	0	0	8	0	0	3
Caulerpa ashmeadii	0	0	0	0	0	0	0	25	0	0	8	0	3
Ceramium cruciatum	0	0	0	0	0	0	0	25	0	0	8	0	3
Gelidiopsis intricata	25	0	0	0	0	0	0	0	0	8	0	0	3
Herposiphonia tenella	0	0	0	0	0	0	25	0	0	8	0	0	3
Lomentaria baileyana	0	0	0	0	0	0	25	0	0	8	0	0	3
Gracilaria blodgettii	0	0	0	0	20	0	0	0	0	0	8	0	2
Gracilaria bursa-pastoris	0	0	0	0	20	0	0	0	0	0	8	0	2
Spyridia filamentosa	0	0	0	0	20	0	0	0	0	0	8	0	2

Appendix 2. **Families and common names of fish and lobster species observed within the Moser Channel Bank System and the surrounding basin during surveys conducted from 2002-2006. Fishes were assigned to one of six feeding guilds: P, piscivore; BC, benthic carnivore; I, invertivore; PL, planktivore; O, omnivore; H, herbivore. Overall mean counts and lengths and their standard errors for each species are provided for four sampling strata; channel (N=162), bank top (N=162), bank margin (N=46) and the basin (N=104) surrounding Moser Channel Banks System. Families which were only observed during the February 2003 survey are identified with an *. Surveys of bank margin and basin strata were all conducted during the month of June.**

			Channel				Bank top				Bank margin				Basin			
Family	Common name	Trophic group	Mean count	stderr	Mean length	stderr	Mean count	stderr	Mean length	stderr	Mean count	stderr	Mean length	stderr	Mean count	stderr	Mean length	stderr
Lutjanidae	gray snapper	BC	13.62	1.77	18.66	0.53	3.23	0.63	17.29	0.78	2.93	0.90	17.93	1.44	1.19	0.30	19.61	1.05
	yellowtail snapper	BC	3.45	0.61	12.93	0.65	2.43	0.58	10.39	0.57	5.59	1.46	9.73	0.52	1.44	0.32	10.23	0.59
	lane snapper	BC	0.14	0.04	9.14	0.85	0.01	0.01	7.50		1.17	0.20	9.32	0.58	0.25	0.07	9.58	0.94
	schoolmaster	BC	0.01	0.01	7.50		0.01	0.01	12.50		0.07	0.07	12.50		0.06	0.04	17.50	2.50
Haemulidae	white grunt	I	4.94	1.48	14.13	1.13	0.43	0.11	8.68	1.05	6.33	2.10	9.59	0.94	2.63	0.54	6.75	0.48
	bluestriped grunt	I	3.09	0.94	16.80	1.54	0.50	0.33	8.60	1.05	1.76	0.76	11.22	1.37	0.30	0.13	8.03	1.34
	porkfish	I	0.46	0.13	15.59	2.07	0.01	0.01	5.75	1.75	0.02	0.02	7.50		0.01	0.01	7.50	
	tomtate	I	0.32	0.18	8.33	1.06	0.00	-			0.85	0.49	9.85	2.55	0.36	0.25	3.50	0.50
	sailors choice	I	0.06	0.03	17.35	2.70	0.04	0.03	3.79	0.69	0.09	0.05	3.00	0.50	0.01	0.01	2.50	
	french grunt	I	0.00	-			0.00	-			0.24	0.16	7.50	0.00	0.02	0.02	7.50	
Scaridae	striped parrotfish	H	2.72	0.77	6.10	0.30	1.00	0.32	6.09	0.39	2.54	0.91	6.94	0.72	0.55	0.25	5.84	0.63
	redband parrotfish	H	1.23	0.41	12.28	0.94	0.49	0.21	11.25	0.67	2.93	0.84	10.78	0.61	0.67	0.18	10.46	1.12
	bucktooth parrotfish	H	0.56	0.14	7.70	1.02	0.40	0.11	7.33	0.55	0.52	0.18	9.64	0.83	0.22	0.07	9.75	0.79
	yellowtail parrotfish	H	0.50	0.12	18.07	1.46	0.02	0.01	9.17	1.67	0.09	0.06	7.50	0.00	0.05	0.03	12.50	0.00
	rainbow parrotfish	H	0.26	0.12	25.15	1.99	0.02	0.02	25.00		0.00	-			0.00	-		
	stoplight parrotfish	H	0.23	0.06	9.63	1.00	0.14	0.05	7.20	0.30	0.59	0.22	8.87	1.14	0.08	0.04	7.25	1.23
	blue parrotfish	H	0.08	0.04	19.21	3.94	0.00	-			0.07	0.05	5.75	1.75	0.00	-		
	redtail parrotfish	H	0.06	0.04	17.50	0.00	0.00	-			0.00	-			0.00	-		
	princess parrotfish	H	0.04	0.03	10.63	6.88	0.00	-			0.00	-			0.00	-		
	midnight parrotfish	H	0.01	0.01	17.50		0.00	-			0.00	-			0.00	-		
Carangidae	yellow jack	P	0.76	0.25	46.95	6.96	0.03	0.03	55.00		0.00	-			0.12	0.12	45.00	
	bar jack	BC	0.33	0.22	24.50	5.15	0.48	0.27	10.36	1.49	2.17	2.17	7.50		0.59	0.48	8.08	1.18
	blue runner	BC	0.23	0.14	36.43	1.71	0.00	-			0.00	-			0.00	-		
	lookdown	BC	0.26	0.25	47.50	28.83	0.00	-			1.09	1.09	7.50		0.00	-		
Sparidae	pinfish	O	0.44	0.11	10.66	1.38	0.35	0.08	9.96	0.76	1.61	0.53	9.22	0.86	1.08	0.38	8.43	0.50
	Sheepshead porgy	I	0.35	0.07	17.59	1.24	0.18	0.04	12.98	1.57	0.59	0.13	9.04	0.90	0.09	0.03	14.33	2.55
	sea bream	O	0.14	0.05	18.17	2.08	0.14	0.05	12.01	1.86	0.20	0.10	17.50	2.24	0.06	0.03	15.50	2.55
Labridae	slippery dick	I	0.63	0.21	14.88	1.42	0.38	0.15	11.12	1.17	1.52	0.64	11.28	0.98	0.34	0.14	11.69	1.49
	hogfish	I	0.25	0.06	22.99	1.48	0.02	0.01	8.75	3.15	0.22	0.09	10.25	2.40	0.07	0.03	16.27	4.14
	puddingwife	I	0.02	0.01	16.25	4.27	0.01	0.01	4.00	0.00	0.04	0.03	7.50	0.00	0.00	-		
	rosy razorfish	I	0.01	0.01	17.50		0.00	-			0.02	0.02	7.50		0.00	-		
	yellowhead wrasse	I	0.02	0.02	12.50	2.89	0.00	-			0.00	-			0.00	-		
	bluehead wrasse	PL	0.00	-			0.09	0.07	9.17	1.67	0.00	-			0.00	-		
Acanthuridae	doctorfish	H	1.51	0.34	15.04	1.05	0.04	0.02	5.40	0.86	0.17	0.13	8.00	2.47	0.17	0.08	7.91	1.66
	ocean surgeonfish	H	0.02	0.02	17.50		0.00	-			0.00	-			0.00	-		
	blue tang	H	0.01	0.01	4.00		0.00	-			0.00	-			0.00	-		
Sphyraenidae	great barracuda	P	0.67	0.19	66.67	9.22	0.55	0.21	53.43	6.85	0.37	0.28	125.2	9.37	0.05	0.02	112.5	23.8
Pomacanthidae	gray angelfish	O	0.60	0.17	21.42	1.61	0.00	-			0.02	0.02	7.50		0.05	0.05	20.50	
	blue angelfish	O	0.05	0.03	18.44	1.39	0.00	-			0.00	-			0.01	0.01	7.50	
	french angelfish	O	0.01	0.01	7.50		0.00	-			0.00	-			0.00	-		

Family	Common name	Trophic group	Channel Mean count	Channel stderr	Channel Mean length	Channel stderr	Bank top Mean count	Bank top stderr	Bank top Mean length	Bank top stderr	Bank margin Mean count	Bank margin stderr	Bank margin Mean length	Bank margin stderr	Basin Mean count	Basin stderr	Basin Mean length	Basin stderr
Pomacanthidae	queen angelfish	O	0.10	0.04	16.58	1.59	0.00	-			0.00	-			0.00	-		
	rock beauty	O	0.00	-			0.00	-			0.37	0.37	8.09		0.00	-		
Palinuridae	spiny lobster	O	0.77	0.20	32.94	2.12	0.03	0.02	30.83	4.41	0.07	0.05	4.50	3.00	0.01	0.01	1.50	
Gerreidae	yellowfin mojarra	I	0.03	0.02	27.50	5.00	0.02	0.01	24.17	1.67	0.11	0.07	14.17	4.41	0.00	-		
	flagfin mojarra	I	0.01	0.01	7.50		0.32	0.31	10.83	6.01	0.50	0.44	6.83	2.83	0.20	0.19	4.88	0.88
Serranidae	sand perch	BC	0.06	0.03	13.97	2.77	0.00	-			0.52	0.14	8.50	0.67	0.33	0.08	10.02	1.31
	red grouper	BC	0.02	0.01	27.50	7.64	0.00	-			0.02	0.02	22.50		0.01	0.01	32.50	
	barred hamlet	BC	0.01	0.01	7.50		0.00	-			0.00	-			0.00	-		
	gag grouper	P	0.01	0.01	30.00	2.50	0.00	-			0.00	-			0.00	-		
	black grouper	P	0.01	0.01	27.50		0.00	-			0.04	0.04	12.50		0.00	-		
Sciaenidae	highhat	I	0.21	0.08	5.03	0.46	0.03	0.02	2.88	0.38	0.00	-			0.01	0.01	1.50	
	jackknife fish	I	0.01	0.01	7.50		0.00	-			0.00	-			0.00	-		
	cubbyu	I	0.01	0.01	4.00		0.00	-			0.00	-			0.02	0.02	4.00	
Holocentridae	squirrelfish	I	0.07	0.05	15.67	0.17	0.00	-			0.00	-			0.00	-		
Pomacentridae	dusky damselfish	O	0.01	0.01	4.00	0.00	0.00	-			0.00	-			0.00	-		
	beaugregory	O	0.01	0.01	7.50		0.00	-			0.00	-			0.00	-		
	cocoa damselfish	H	0.01	0.01	4.00		0.00	-			0.00	-			0.00	-		
	sergeant major	O	0.00	-			0.04	0.03	6.45	1.05	0.00	-			0.00	-		
Kyphosidae	chub	H	0.06	0.04	24.17	1.67	0.00	-			0.00	-			0.00	-		
Chaetodontidae	spotfin butterflyfish	O	0.02	0.01	7.50	0.00	0.00	-			0.00	-			0.00	-		
	banded butterflyfish	I	0.01	0.01	7.50		0.00	-			0.00	-			0.00	-		
	foureye butterflyfish	I	0.01	0.01	4.00		0.00	-			0.00	-			0.00	-		
	reef butterflyfish	O	0.01	0.01	12.50		0.00	-			0.00	-			0.00	-		
Gobiidae	bridled goby	O	0.01	0.01	4.00		0.00	-			0.00	-			0.00	-		
	neon goby	O	0.01	0.01	7.50		0.00	-			0.00	-			0.00	-		
Tetraodontidae	bandtail puffer	I	0.01	0.01	7.50		0.01	0.01	12.5		0.02	0.02	7.50		0.02	0.01	5.75	1.75
	sharpnose puffer	O	0.00	-			0.01	0.01	7.5		0.00	-			0.00	-		
Scombridae	cero mackerel	P	0.01	0.01	75.00		0.00	-			0.00	-			0.00	-		
Carcharhinidae	bull shark	P	0.00	-			0.01	0.01	195.0		0.00	-			0.00	-		
Rhincodontidae	nurse shark	I	0.00	-			0.00	-			0.02	0.02	135.0		0.00	-		
Urolophidae	yellow stingray	I	0.01	0.01	37.50		0.00	-			0.02	0.02	32.50		0.00	-		
Myliobatidae	spotted eagle ray	I	0.01	0.01	37.50		0.00	-			0.00	-			0.00	-		
Balistidae	fringed filefish	I	0.00	-			0.00	-			0.00	-			0.01	0.01	4.00	
Mullidae	spotted goatfish	I	0.01	0.01	4.00		0.00	-			0.00	-			0.01	0.01	7.50	
Ostraciidae	scrawled cowfish	I	0.01	0.01	7.50		0.00	-			0.02	0.02	12.50		0.00	-		
Diodontidae	striped burrfish	I	0.00	-			0.00	-			0.00	-			0.02	0.01	17.50	5.00
Exocoetidae*	ballyhoo	PL	0.62	0.62	17.50		0.00	-			0.00	-			0.00	-		
Atherinidae*	silversides	PL	0.62	0.62	1.50		0.00	-			0.00	-			0.00	-		

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