Assessment of Spatial Management Practices for Enhancing Fish Populations in Bermuda

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Non-Technical Summary

The future of coral reef ecosystems is threatened by a broad range of anthropogenic disturbances. Tightly interdependent coral and fish communities face degradation from excessive rates of overfishing, sedimentation, eutrophication, coral disease and global warming. With the rapid degeneration of coral reef communities in the Caribbean over the past three decades, Bermuda may soon be a regional bastion of relatively unaffected ecosystem function. Past fisheries and habitat management has played an essential role in maintaining the integrity of local reefs, and may have afforded Bermuda's reefs greater resiliency against imminent threats, such as global warming. However, adaptive conservation measures will be required to optimize the recovery of fish communities from historical overexploitation and to safeguard ecosystems in the face of continuing anthropogenic impacts.

The aims of this study were twofold. First, we sought to evaluate the effectiveness of current Marine Protected Areas (MPA's hereafter) in promoting the abundance and biomass of fishes. Second, we examined how fish populations are distributed across Bermuda's reef platform, in order to identify regions and habitats of high biodiversity or significance to harvestable and ecologically-important species.

Findings of the first study component – assessing the performance of current MPA's – revealed few differences in fish abundance or community structure between protected and unprotected areas. While these results conformed to those of one previous study, our study found that more data is required to confirm that MPA's are not enhancing fish populations within the reserves. With confidence, this study can assert that large benefits are not afforded to current MPA's by protected status. But we must also stress that less obvious effects cannot be ruled out without substantially more data. Furthermore, it is unclear whether any lack of enhancement would be related to (i) insufficient sampling to detect trends in fish abundance, (ii) subtle responses of fish communities to protection,

(iii) uniformly light fishing pressure inside and outside MPA's, or (iv) logistical difficulties of effectively enforcing these reserves. Nonetheless, it is apparent that some modifications to the current MPA system, such as larger reserve sizes, might better address the biology and ecology of key species. Such modifications might facilitate the recovery of Bermuda's fish populations from the lingering effects of historic overexploitation.

Through extensive surveying of fish communities across the reef platform, the second part of this study documented a large degree of variation in community structure over relatively small distances. In broad terms, fish community structure differed most between lagoon reef habitats and offshore rim/fore reefs. However, within these reef zones, there were also differences in productivity and ecology over even smaller spatial scales. In this context, this study identified three main areas and habitats of key importance to fish communities across the reef platform. The first of these areas were small sub-habitats of rim reefs adjacent to tidal passes which appeared to host large numbers of species as well as significant populations of herbivorous and carnivorous fish alike. A second key area notable for species richness and abundances of commercial species was a region roughly corresponding to the North Shore Coral Reef Preserve. Some of the importance of this area was also attributable to the inclusion of a third significant type of habitat, nearshore reefs. The particular significance of this habitat is seen in the fact that the majority of fish species studied – including several important commercial species - heavily used inshore fringing and patch reefs as juvenile habitat. It seemed likely that this habitat supplemented the nursery functions of seagrass beds and mangrove roots and probably also seeded offshore populations.

Virtually none of the ecologically-significant habitats are currently protected through MPA delineations. Thus, the overall implication of our findings is that any future modifications to local MPA coverage would better conserve ecosystem integrity – and thus safeguard resources and ecological function - if they accounted for and represented these ecological "hotspots".

Acknowledgements

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Chapter 1

Assessing the Effectiveness of Current Marine Protected Areas (MPA's) at Enhancing Bermuda Fish Populations

Introduction

Bermuda supports the most northerly coral reef system in the world, with the large majority of the species being derived from tropical Atlantic reefs. The extension of subtropical systems to Bermuda's high latitude can be attributed to the transport of warm waters by the Gulf Stream. Although Bermuda lies to the east of this flow, vortices bring water of subtropical origin to the islands. These eddies are infrequent, but are believed to provide larval transport of warm-water species to the islands (Hateley, 1994; Glasspool, 1994). While Bermuda provides a high latitude outpost for Caribbean species, it supports a much reduced species assemblage with only about one third of the shallow-water coral species recorded from Jamaica (Thomas and Logan, 1992) and a similarly under-represented icthyofauna (Smith-Vaniz *et al*., 1999).

Bermuda is very well studied with over 4,500 documents chronicling the island's natural history since man's arrival in 1609. Accounts of the earliest explorers describe islands uninhabited by humans but rich in fish, birds and sea turtles. Such primal abundance existed that the founder of the Bermuda colony, Admiral Sir George Somers, reportedly caught so many fish in half an hour that they sufficed the whole company for one day (Smith-Vaniz *et al.*, 1999). However, it was not long after colonization that concern was expressed over the impact of the unregulated harvest of marine life. In 1627 the first restrictions regarding the harvesting of fish were implemented in response to concern that the practice of processing pilchards and fry to make oil was causing a "scarcity of bait for necessary fishing" (Smith-Vaniz *et al.*, 1999). Numerous fisheries laws, including spatial closures, size restrictions and species protections, were enacted over the ensuing centuries in order to regulate harvestable marine resources.

Fast forwarding to the mid-20th Century, the Bermuda Government received an optimistic report on the potential of local fish resources (Bardach, 1958a), resulting in the active promotion of the commercial fishery. This coincided with a rapidly expanding resident and tourist population that placed a high demand on fish. Incentives were offered to encourage investment in more sophisticated gear. Fish pots were soon widely used and fishing pressure increased greatly through the use of more and larger traps. Unfortunately, exploratory reports proved overly optimistic, projecting an annual catch far greater than that which was ever realized. Yet with the substantial investment in the industry, fishers were obliged to maintain levels of exploitation to pay off their debts, leading to an unsustainable harvest.

Commencing as early as 1963, spatial restrictions on fish pot use began. But it was not until 1972 that the more comprehensive Fisheries Act was passed. The Act created a broad legislative framework for coordinated fisheries management which included provisions for establishing seasonally protected areas and/or species. However, despite the seasonal closure of two known grouper spawning sites around the island, by the early 1980's it was apparent that the groupers could not support the sustained heavy fishing pressure. Landings of most of these species plummeted; large serranids became rare.

Previously shunned herbivorous species became the mainstay of the fishery, with groupers becoming the bycatch (Butler *et al.*, 1993). There was strong anecdotal evidence that grazers such as scarids (now legally protected), were also substantively reduced in number through pot fishing. A series of increasingly restrictive management tactics were enacted in an unsuccessful attempt to revive grouper stocks: *Mycteroperca venenosa, M. microlepis, M. tigris, Epinephelus striatus, E. morio* and *Alphestes afer* are now considered to have been effectively extirpated in Bermuda.

Concurrent with the 1990 closure of the fish pot fishery - and in recognition of Bermuda's increasing marine tourist market - local dive operators requested that a series of 9 permanent moorings installed at popular dive sites be incorporated as protected areas under the 1972 Fisheries Act. Such protection meant that all fishing activities were prohibited at these sites within a radius of between 300 and 1000 metres. The intention was to reduce user conflicts by separating SCUBA divers and fishermen, as well as to minimize anchor damage from dive boats – but not explicitly to enhance fish populations. One further permanent mooring was added to a shipwreck site in 1996, followed by a further 19 permanent dive site moorings in 2000 at the most frequently visited dive sites (Fig. 1). These small, disconnected sites constitute the only designated permanent Marine Protected Areas (MPA's hereafter). Furthermore, there is some skepticism within the community that these sites serve as a magnet to the dive community and therefore concentrate higher levels of destructive recreational activity at them. It is very important to note that these MPA sites were not created with the goal of enhancing fish populations within their area, but rather to prevent fishers from interacting with divers.

Regardless, fish populations in Bermuda's MPA's may be structured by both historic patterns of overexploitation and current impacts of human recreation. Moreover, the size and configuration of these reserves undoubtedly also influence their effectiveness at conserving and restoring ecosystem integrity. Little data exists for assessing whether MPA's have benefited fish populations concurrent with their intended function of protecting the aesthetics of popular dive sites. However, considerable evidence from other countries suggests that spatial protection of key habitat from fishing can indeed enhance fish populations and restore historic ecosystem function to degraded areas.

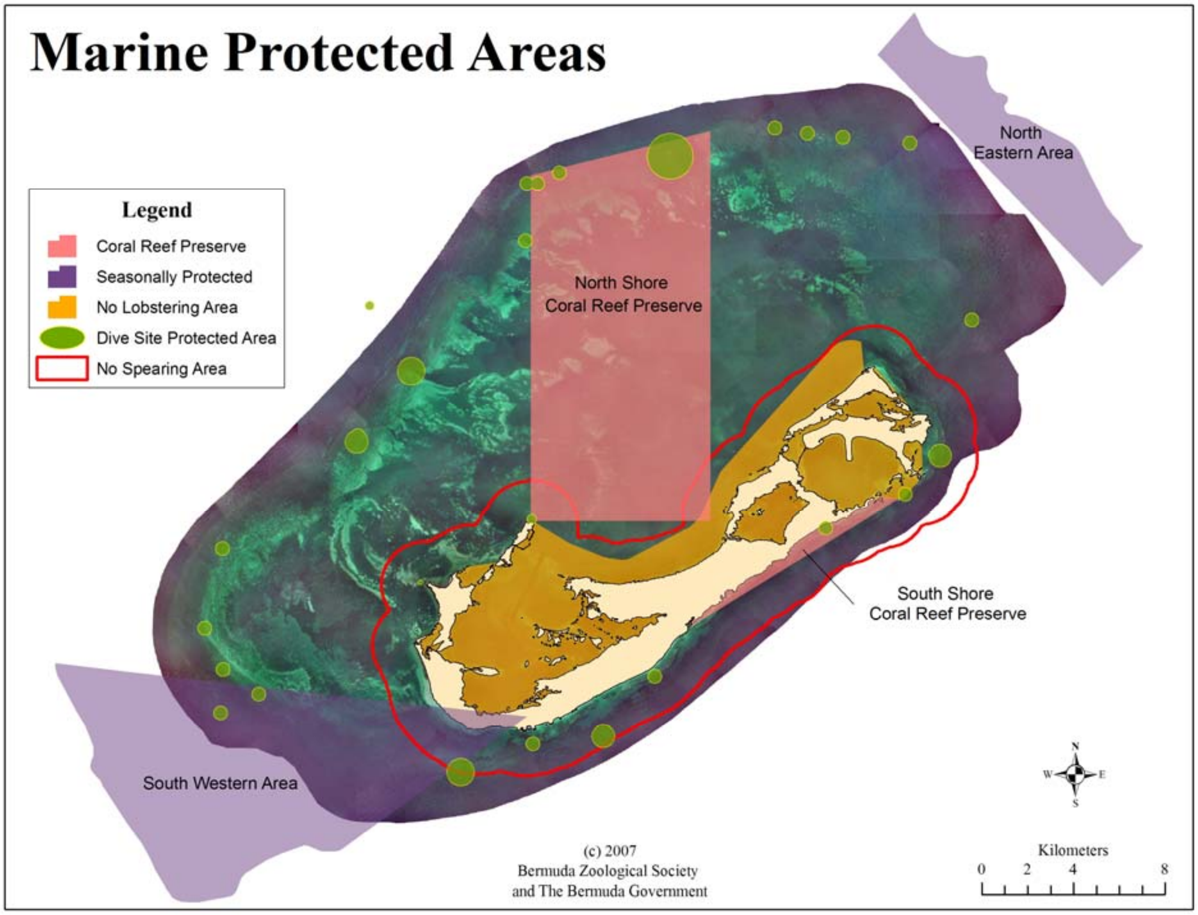

Fig. 1. Map designating current protected areas in on the Bermuda platform. Coral Reef Preserves (in pink) afford the least protection, with fishing permitted, yet prohibition of harvesting benthos. Seasonally Protected Areas (in orange) prohibit fishing between May 1st and August 31st to protect spawning serranids. Finally, fully protected MPA's (in green) offer mooring buoys to minimize anchor damage and prohibit any harvest.

Effective MPA's may initiate the enhancement in abundance and size of exploited, high trophic level predators (*e.g.* Mumby *et al.,* 2007b; Ojeda-Martinez *et al.*, 2007; Unsworth *et al.*, 2007; Watson *et al.*, 2007). Furthermore, these effects are not necessarily confined to target species. MPA's can initiate recovery of diverse components of fish assemblages by addressing the interactions among multiple species (Botsford *et al.*, 2003; Baskett *et al.,* 2007). Accordingly, the abundances of non-target species may be significantly affected by permanent spatial closures. Examples of this are the top-down control of lower-trophic species by increased predator abundance (Micheli and Halpern*.,* 2005; Mumby *et al.*, 2006) and the unexpected enhancement of other non-commercial species through complex, non-linear mechanism (Watson *et al.,* 2007). Other indirect ecosystem benefits of successful spatial protection may also include prevention of biodiversity loss from anthropogenic disturbance (Pitcher, 2001; Micheli *et al.,* 2004), resiliency to increasing incidences of coral bleaching and diseases (Hughes *et al.,* 2003), and enhanced fisheries production and community recovery outside reserve boundaries (Guidetti, 2007).

From 2001 to 2003, the Marine Environment Programme (MEP, unpublished technical report) surveyed fish populations at several Bermuda MPA's and control sites,and concluded no demonstrable protection effect was afforded by current reserves. This remains the only study to examine in detail the structure of fish populations in protected areas. This present report thus aims to add current and supplemental data to these findings by assessing the effectiveness of fish populations inside and outside four MPA's using different surveying protocols (AGGRA, supplemented by REEF roving diver). More importantly, however, this analysis is a component of a larger initiative (Bermuda Reef Ecosystem Assessment and Monitoring - BREAM) for mapping local ecosystems.

In this chapter, we address whether MPA's are functioning to maximum effect and if any modifications are necessary to improve their performance. In turn, results provide context for Chapter 2, where spatial patterns in fish populations across the reef platform are used to delineate areas of ecological importance for the consideration of future spatial protection.

Methods

AGRRA surveys

The Atlantic and Gulf Rapid Reef Assessment (AGRRA) Version 4.0 fish protocol was adopted as the standard methodology for fish census studies (www.agrra.org). The AGRRA fish protocol, designed to provide a "snapshot" characterization of functionally important fish indicators is widely accepted throughout the Western Atlantic, so our adoption of this protocol allows for regional comparisons to be made. Surveys were conducted at four MPA's (North Rock, Eastern Blue Cut, Snakepit and Southwest Breaker) and six control sites (Conch Rock, Creole Canyon, Angelfish Pass, Mini-Snakepit, Snapper Rocks, and Diadema Plateau). Fish were enumerated by two SCUBA divers, conducting a total of ten 30 x 2 meter belt transects per site. Transects were laid haphazardly and away from other divers to minimize any bias related to diver-activity. When surveying, divers swam slowly in a randomly determined direction while an attached spool of transect line unraveled to signal completion of the transect. Surveyors received prior training using a T-bar to more accurately gauge fish size as well as model cut-out fish suspended in the water of varying sizes and body shapes for practice. Each survey transect took typically 6-8 minutes. Any fish encountered within a lane bounded one meter on either side of the transect and upwards to the surface was counted and assigned to one of six visually-estimated total length categories (<5cm, 10-20cm, 20-30cm, 30-40cm, and >40cm). The smallest size category captured juvenile fish and constituted a modification of AGRRA 4.0 protocol. One other minor modification was the inclusion of *Cephalopholis fulva* and *Cephalopholis cruentata* (formerly *Epinephelus fulvus* and *E. cruentatus*, respectively) as locally important serranids.

REEF roving diver fish surveys

To ensure coverage of less abundant fish species and those not included in AGRRA protocol, a roving diver fish census was performed for each site using the Reef Environmental Education Foundation (REEF) protocol (Schmitt *et al.*, 1998). This protocol involved a prolonged period of swimming observation (at least 30 minutes) where all fish species seen were recorded. Species were categorized by abundance and recorded as "Single" (1 fish), "Few" (2-10 fish), "Many" (11-100 fish) or "Abundant"

(>100 fish; REEF, 2007). This particular method takes account of more cryptic species likely to be overlooked in the belt transects and is therefore a more valuable measure of species richness.

Statistical analysis:

Fish densities were calculated for fish species and functional guilds (see Appendices 1-2 for groupings), standardized to $100m^2$. From these densities, biomasses were calculated by using species-specific power functions of the form $W = aL^b$ to convert lengths, derived from visually-estimated categories, into weights ($g/100m^2$; Marks and Klomp, 2003). As length categories comprised intervals and not exact measurements, lower and upper limit biomasses were estimated based on the lower and upper length limit of each size category. REEF abundance scores were the product of REEF density scores of species across sites and their sighting frequency across sites. Density scores were calculated by the following equation:

$$D = \frac{[(nS \times 1) + (nF \times 2) + (nM \times 3) + (nA \times 4)]}{nS + nF + nM + nA}$$

where nS is the total number of sites for which the “Single” category was recorded for a species, nF for the “Few” category, nM for “Many” and nA for the “Abundant” category. Sighting frequency was the percentage of all sites at which a species was sighted.

Univariate statistical analyses were performed on data using JMP 6 to compare mean densities, biomasses and abundances of fish in MPA’s with those of control sites. Data not normally distributed were transformed by either square-root, fourth-root, logarithmic (base 10) or Box-Cox transformations. If data still did not conform to a normal distribution, analyses were still conducted but earmarked for cautious interpretation.

Multivariate ordinations of AGRRA density (limited to AGRRA species) and REEF abundance data were performed using PRIMER 6 software. AGRRA density data was first square-root transformed to down-weight abundant species. REEF abundance data was analyzed untransformed as the abundance categories (*e.g.* “few”: 2-10 fish) conformed to a quasi-logarithmic scale. Bray-Curtis similarity matrices were calculated for both REEF and AGRRA data prior to cluster analysis which used the complete linkage method. Clusters were then plotted on an MDS ordination at levels of similarity that revealed the most information about relationships among sites. SIMPROF routines on cluster analysis (9999 permutations) tested for the significance of internal structure in dendograms and thus which clusters had statistical evidence supporting their divergence.

ANOSIM routines (9999 permutations) were performed on square-root transformed AGRRA and untransformed REEF data, to test for differences among the *a priori* groupings of reef treatment; MPA or control. In case of significant ANOSIM differences, One-way SIMPER routines (9999 permutations) were employed to establish which species contributed most to dissimilarities among significantly different reef zone species assemblages.

User group surveys

Survey questionnaires were sent to all dive operators in Bermuda to assess the effectiveness of MPA's as tools for management of user groups and sensitive habitat (raw data not included in this report). Questions addressed the following themes: (i) MPA usage patterns by dive operators, (ii) the degree to which MPA's alleviate user conflict, (iii) the perceived extent of protection conferred by MPA status, and (iv) the sufficiency of current MPA coverage.

Results

Relative contributions of functional guilds at MPA's and control sites

A total of 46 species from the AGRRA protocol species list (AGRRA, 2005) were recorded from 60 AGRRA transects across ten MPA and control sites. These ten sites corresponded to both control sites for Snakepit and Eastern Blue Cut MPA's, while North Rock and Southwest Breaker MPA's each had only one control site surveyed (Conch Rock and Diadema Plateau, respectively).

Overall, the similarities in functional guild contributions to total species richness, abundance, density, and biomass between MPA's and control sites suggested highly similar functional structures between protected and unprotected reefs. REEF roving diver survey data, which was not limited to indicator species, recorded 122 species recorded across the platform - 73 of which were found in MPA's and 75 at control sites. Proportions of functional guilds in relation to total species richness were remarkably uniform in pooled MPA and pooled control site groupings (Fig. 2). The only notable difference was a higher proportion of piscivores at control sites, which equated to four additional species than observed at MPA's. Herbivores, while not the most speciose guild, were the numerically dominant group in both MPA's and controls (Fig. 3-4). Even though striking similarities in functional guild contributions occurred between pooled MPA's and pooled control sites, REEF abundance data suggested that herbivores might be marginally more dominant in MPA's (Fig. 3). This trend appeared to be borne out by density data for AGRRA species, which suggested slightly higher contributions of select herbivores to total fish density in MPA's than control sites (Fig. 4). In terms of biomass, AGRRA herbivores were again the overwhelmingly dominant functional guild and contributed equally to total biomass in both MPA's and control sites (Fig. 4).

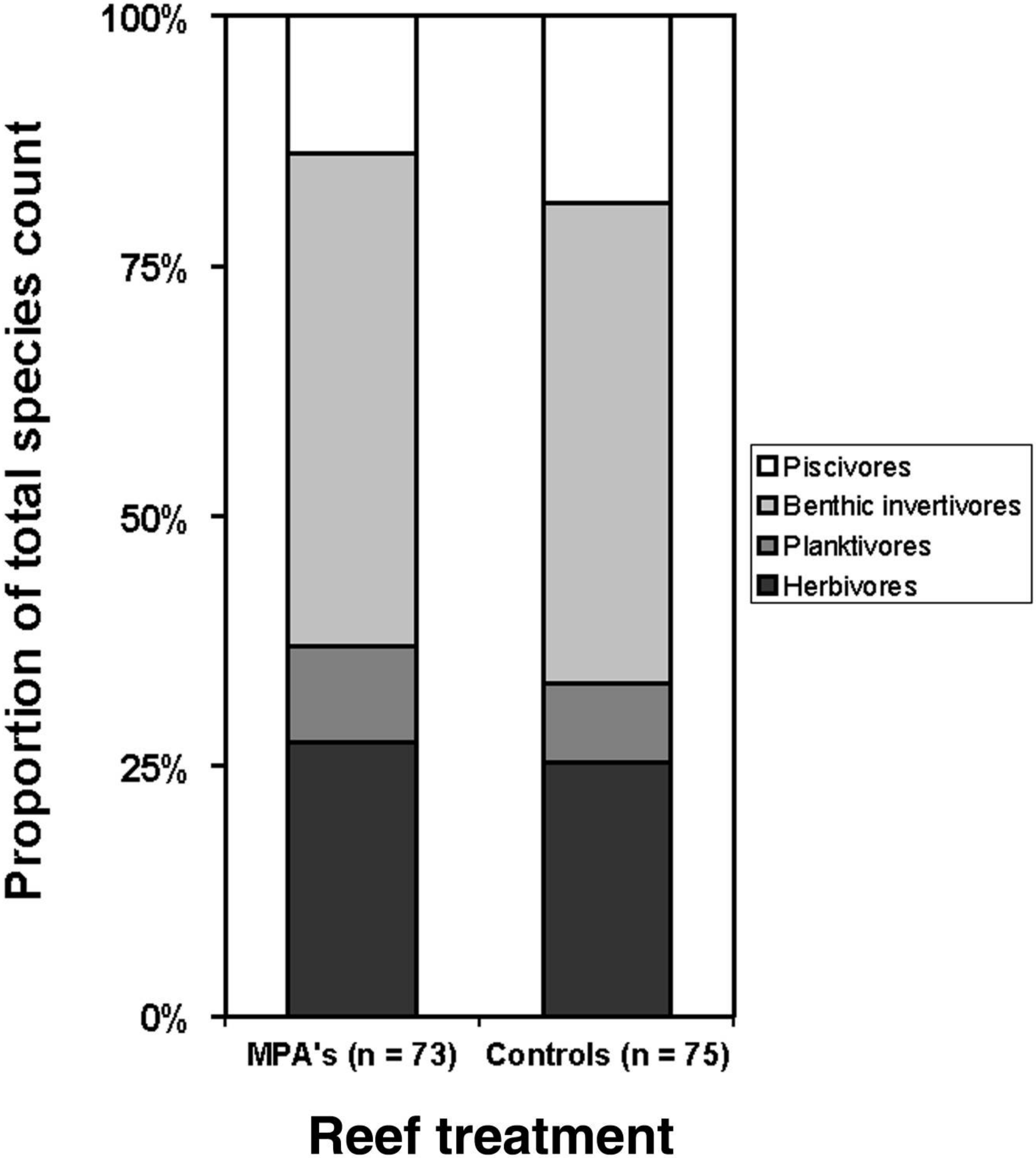

Fig. 2. Contribution (%) to total species richness of four functional guilds for pooled MPA sites and pooled control sites. Data derived from REEF roving diver surveys. n is total species richness.

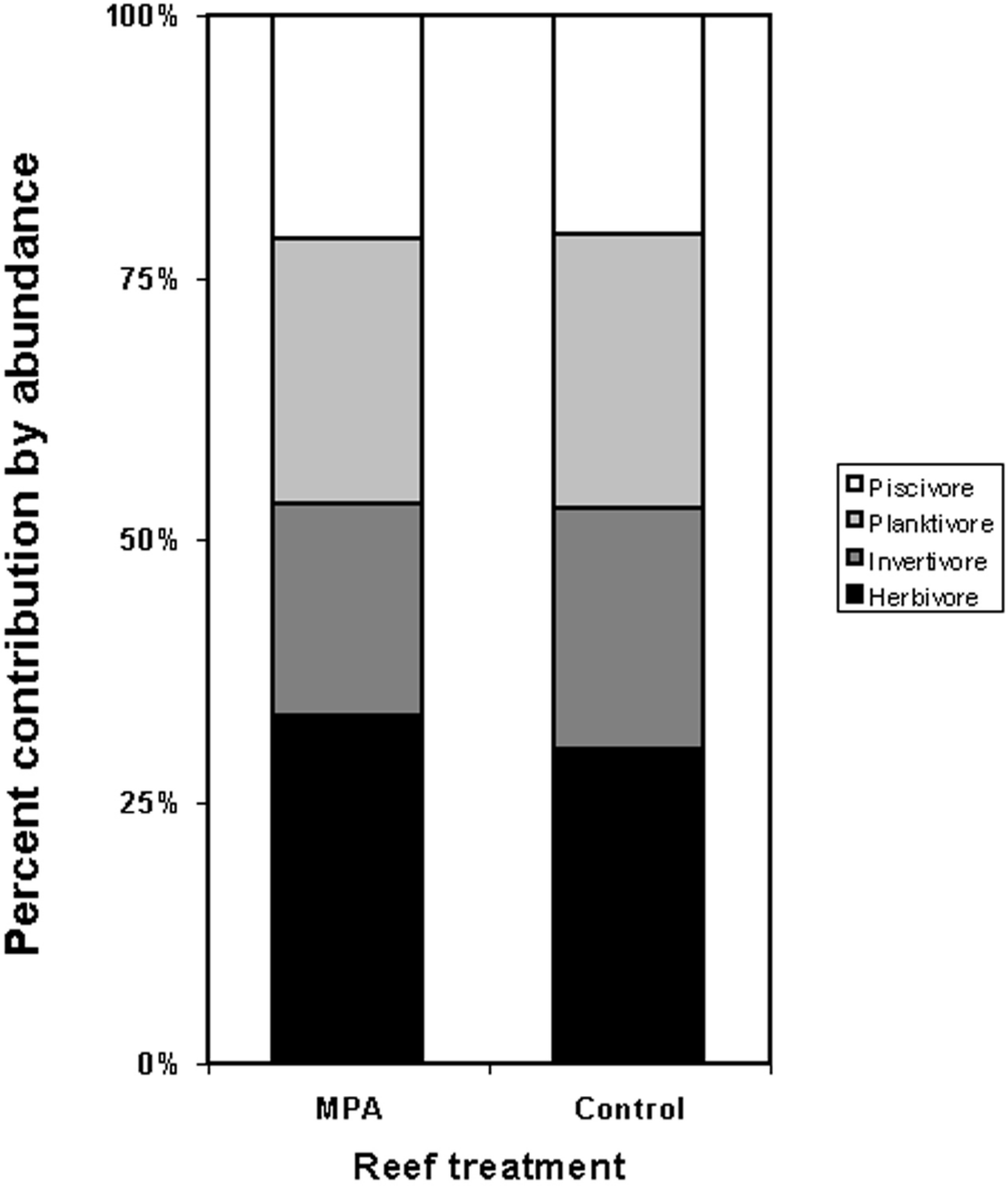

Fig. 3. Contribution (%) to total REEF abundance of four functional guilds for pooled MPA sites and pooled control sites. Data derived from REEF roving diver surveys.

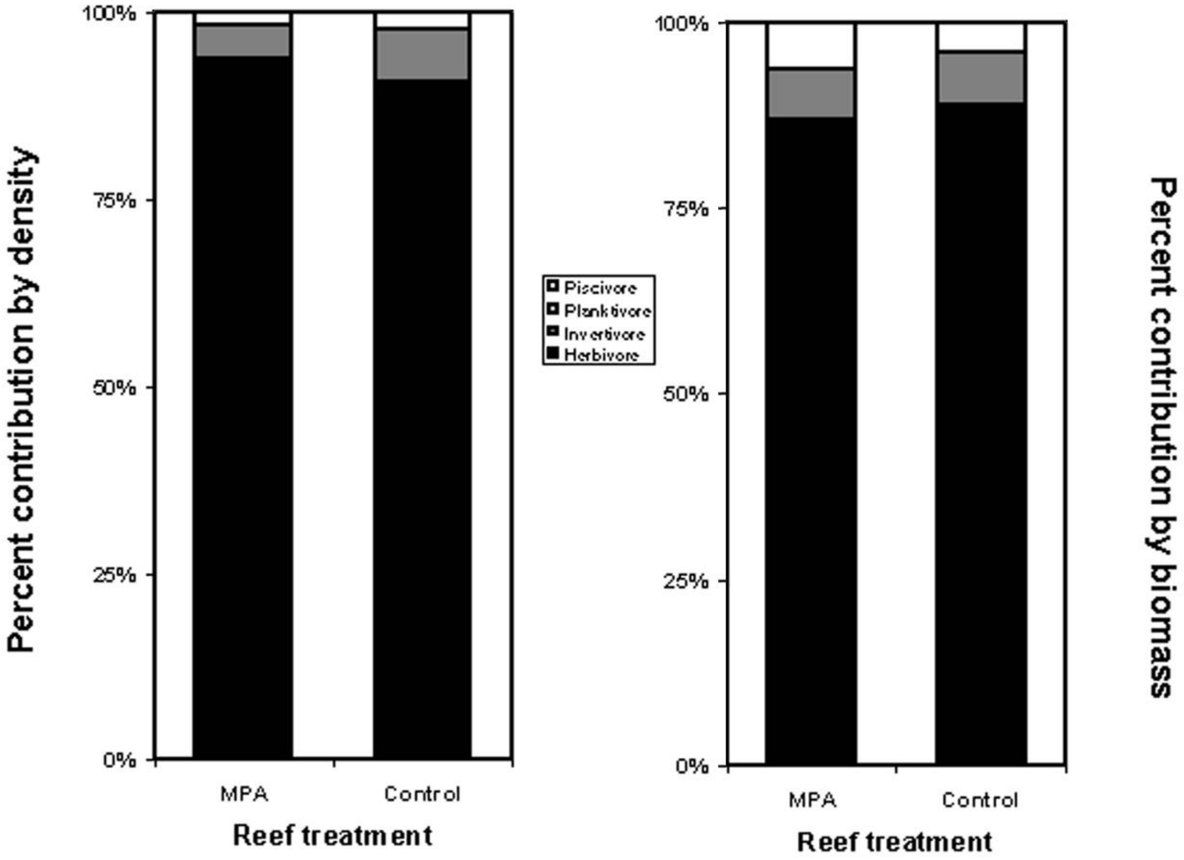

Fig. 4. Contribution (%) to total AGRRA density (left) and biomass (right) of four functional guilds for pooled MPA sites and pooled control sites. Data derived from AGRRA fish surveys.

Density, biomass and abundance at MPA's and control sites

Pooled densities of functional guilds

Absolute densities and biomasses of functional guilds (and species of commercial or recreational importanct) also showed a high degree of similarity among at pooled MPA's and pooled control sites (Fig. 5-6). For instance, mean densities of commercial species were uniformly low, averaging 1.17 ± 0.25 fish / 100 m^2 at MPA's and 1.00 ± 0.15 fish / $100m^2$ at control sites. Piscivores occurred at similarly low densities at MPA's and control sites (1.17 ± 0.25 and 0.97 ± 0.15 fish / $100m^2$, respectively). Invertivores were found at slightly higher densities, and shared similar means in MPA and control sites

(2.92 ± 0.47 and 3.03 ± 0.40, respectively). As suggested by relative densities, herbivores occupied by far the dominant functional role in both protected and unprotected areas. Additionally, only in herbivores did the means differ to any great extent (63.54 ± 11.55 and 39.69 ± 3.68 fish / 100m^2 for MPA's and control sites, respectively). Density data for pooled sites consistently failed to conform to a normal distribution for parametric tests, even after several transformations (Appendix 3). However, as t-tests are more robust to assumptions of normal distribution than to those of equal variances, tests were conducted but with the intention for conservative interpretation of results. In any event, no significant differences were found between pooled MPA's and pooled control sites for any functional guild (Appendix 3).

For all functional guilds, the mean biomasses in MPA's were statistically indistinguishable from the control grouping. Upper estimates of piscivore and commercial species biomass were higher at MPA's than at control sites, but were also characterized by high variance around the means. Herbivores contributed greatly (up to 9427 g / 100 m^2) to the biomass of reef fish in both MPA's and control sites. Contrary to results based on fish density, mean herbivore biomass (lower estimate) was greater in the control grouping (3162.68 ± 406.28 grams / m^2) than the MPA grouping (2744.58 ± 313.29 grams / 100m^2). This difference of means, however, was also non-significant.

While pooling sites and consolidating species data into functional groups allowed for increased power to detect statistical differences, it was still low on average (0.33 ± 0.14). Thus, even though means were often highly similar, some of the above non-significant findings may result from insufficient resolution rather than non-significance in entire populations.

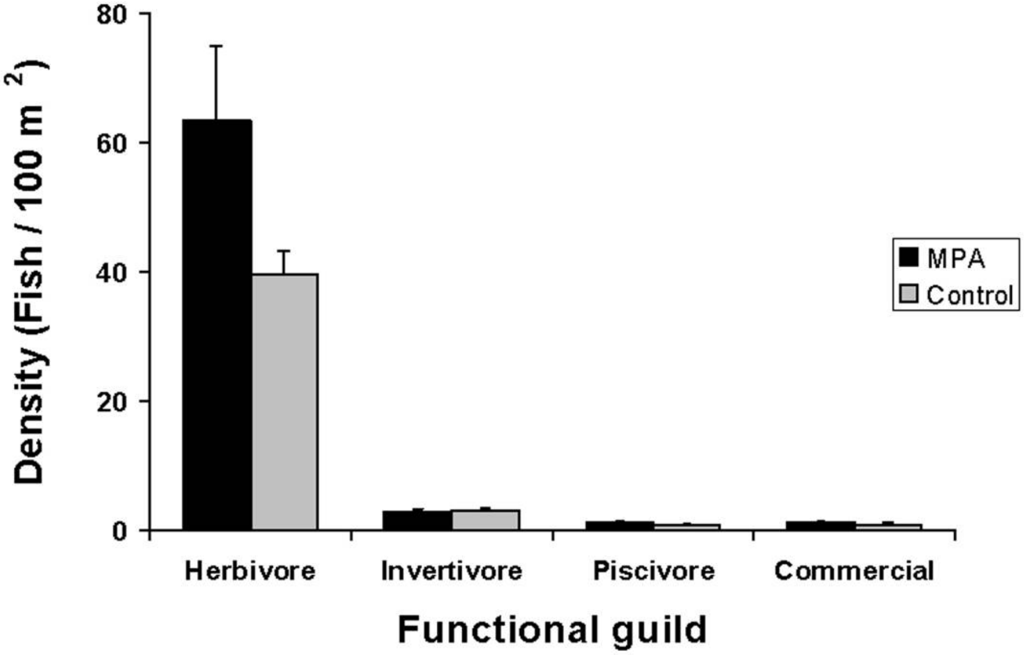

Fig. 5. Mean density of AGRRA fish species (fish / 100m^2) for pooled MPA sites and pooled control sites, categorized by functional guild and commercial species. Data are means ± standard error.

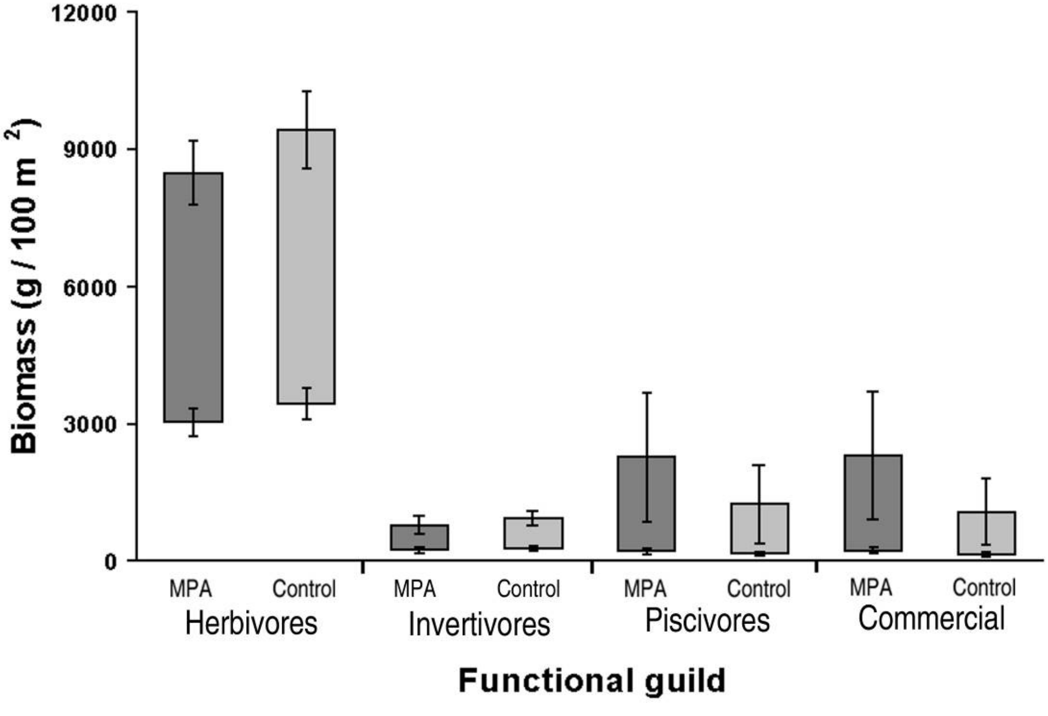

Fig. 6. Mean biomass of AGRRA fish species (g / 100m^2) for pooled MPA sites and pooled control sites, categorized by functional guild and commercial species. Biomass reported includes lower and upper possible limits, calculated from minimum and maximum lengths in AGRRA protocol size categories. Data are means ± standard error.

Pooled densities of key species

A comparison of the densities of key scarids in pooled MPA's with those at pooled control sites found no statistically significant differences among them. All common scarids were found in far higher densities than the most common piscivores. These scarid densities also showed no clear differences between MPA's and controls. Mean density was almost identical between the MPA and control site groupings for most common scarid species (Fig. 7), with two exceptions. *Sparisoma viride* densities in MPA's (4.48 ± 0.50 fish / 100m^2) exceeded controls (3.56 ± 0.38 fish / 100m^2), though, again, the difference was not significant. *Scarus taeniopterus*, by far the most abundant scarid, mirrored the general trend of the herbivore guild and exhibited a greater MPA mean density (42.42 ± 11.20 fish / 100m^2) than the control means (18.83 ± 3.76 fish / 100m^2). However, many of the *S. taeniopterus* individuals in the MPA grouping were counted at just two sites, and the resulting large variance around the mean and low power (Appendix 3) precluded detecting any statistical differences.

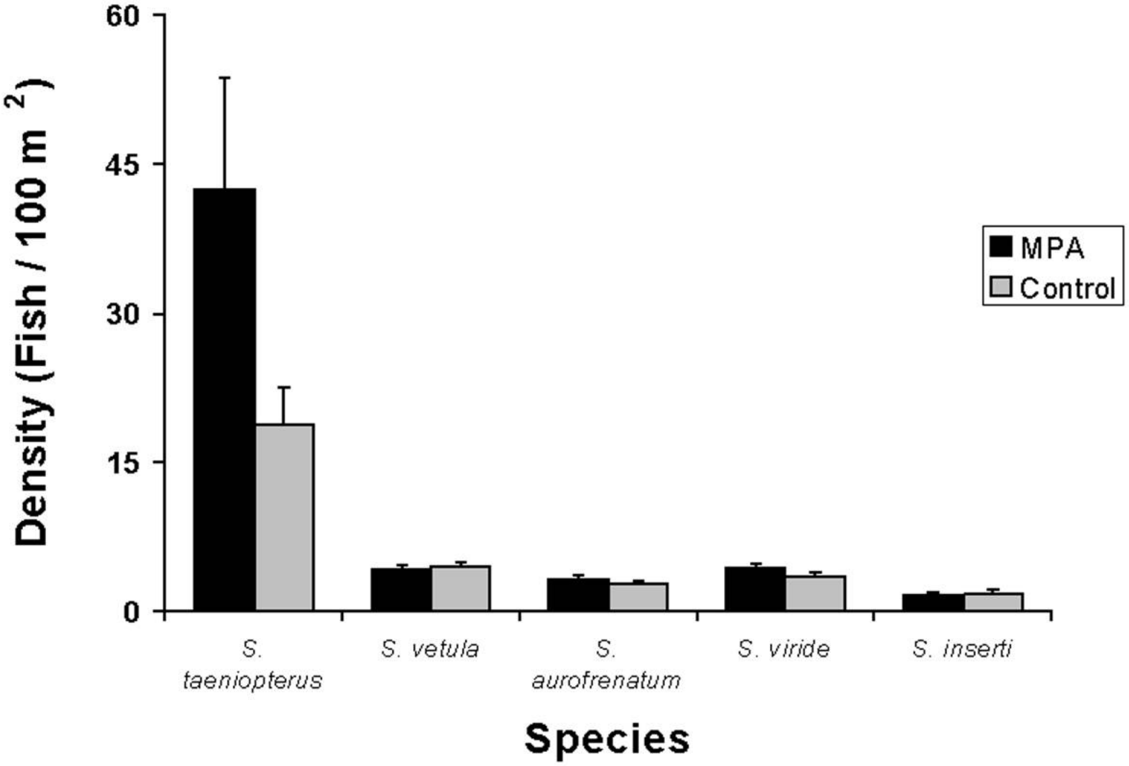

Fig. 7. Mean densities of some key AGRRA herbivorous species (fish / 100m^2) for pooled MPA sites and pooled control sites. Data are means ± standard error.

Among piscivores and commercial species, *Cephalopholis fulva* exhibited the greatest mean density (0.67 ± 0.17 and 0.69 ± 0.15 fish / 100m^2 in MPA's and controls, respectively; Fig. 8). The largest piscivore, *Mycteroperca bonaci*, was found only at low densities (0.04 ± 0.04 and 0.03 ± 0.03 fish / 100m^2). Another serranid, *Epinephelus guttattus*, found at only slightly higher densities than *M. bonaci* (0.11 ± 0.05 fish / 100m^2) at the control sites, was absent in MPA's. The snappers, *Lutjanus griseus* and *Ocyurus chrysurus*, presented differences between MPA and control site means that were substantial for the latter (0.17 ± 0.12 and 0.03 ± 0.03 fish / 100m^2, respectively). The large variance around the means, however, meant that these differences were not statistically significant. *Carangoides ruber* similarly exhibited higher mean densities in MPA's without statistical significance.

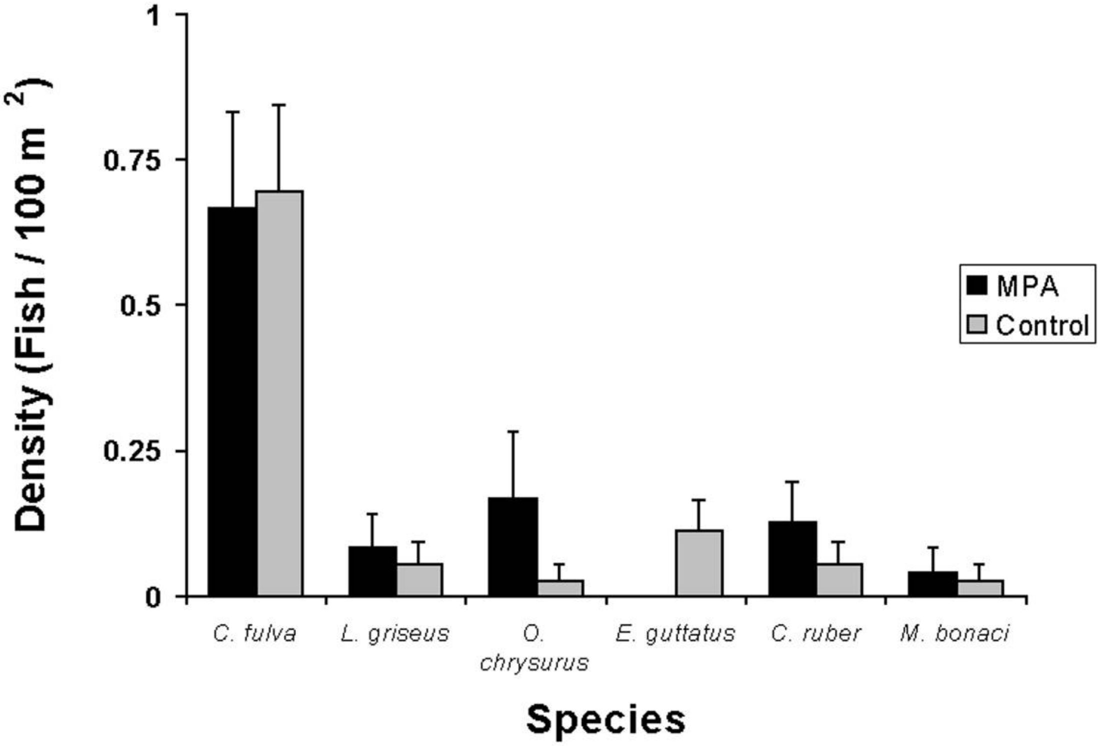

Fig. 8. Mean densities of some key AGRRA piscivorous species (fish / 100m^2) for pooled MPA and pooled control sites. Data are means ± standard error.

Other abundant herbivores of the rim reef, the acanthurids, displayed a pattern of lower densities in MPA's than control sites (Fig. 9). Mean densities of A*canthurus coeruleus* and *Acanthurus bahianus* were similar, and both species occurred in MPA's at comparable densities to control sites. Only moderate variance occurred around mean densities for both of these species, and made it likely that non-significant t-test results (Appendix 3) truly reflected the null hypothesis of no difference in fish density among MPA's and control sites. *Acanthurus chirurgus* occurred in the lowest densities of the acanthurids (0.21 ± 0.14 and 0.19 ± 0.08 fish / 100m^2 for MPA's and controls, respectively) and also showed no significant differences between MPA's and control means.

Three pomacentrids occurred in moderate densities at both the MPA's and control sites (Fig. 10). While *Stegastes leucostictus, Stegastes variablis* and *Stegastes planifrons* are not counted in AGRRA protocol, they are graphed here individually (but not included in

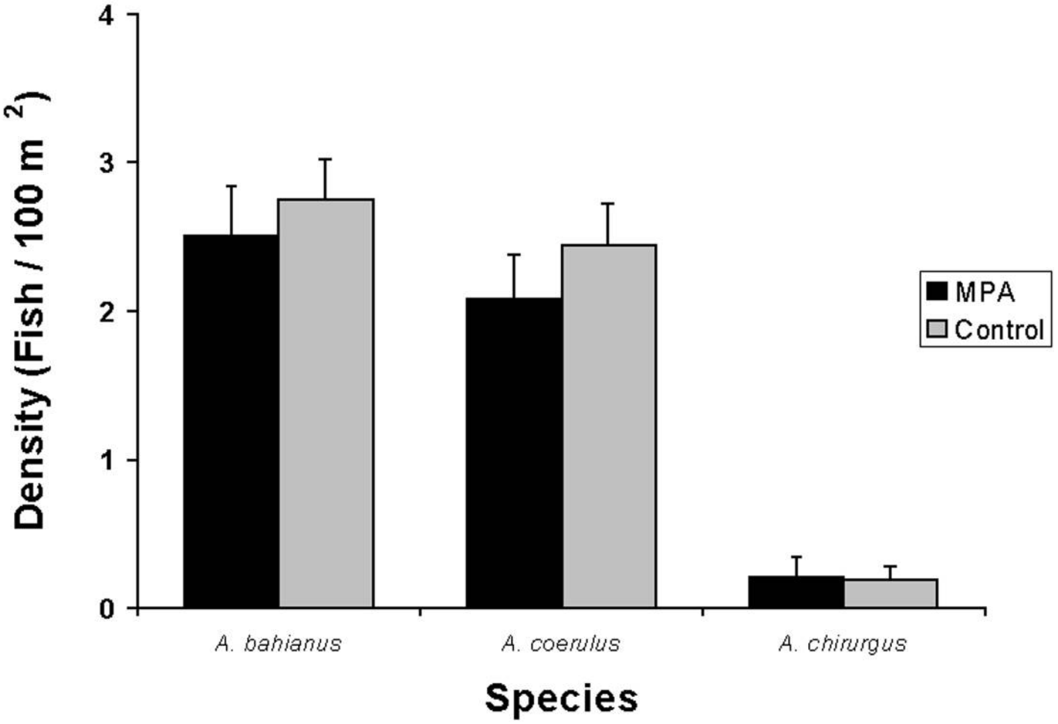

Fig. 9. Mean densities of some key AGRRA acanthurid species (fish / 100m^2) for pooled MPA sites and pooled control sites. Data are means ± standard error.

functional guild or multivariate groupings) for their significance to coral reef ecology. Furthermore, *S. leucostictus* and *S. variablis* densities are combined here due to the difficulties in distinguishing some of their color phases in the field.

Microspathodon chrysurus was the dominant pomacentrid on both MPA reefs (2.50 ± 0.36 fish / 100m^2) and control reefs (1.94 ± 0.27 fish / 100m^2 ; Fig. 10). Mean densities of *S. planifrons* were also higher in MPA's (1.08 ± 0.25 fish / 100m^2) than in control sites (0.75 ± 0.29 fish / 100m^2). *S. leucostictus/variablis* densities were the lowest of the pomacentrids, while the control mean density (0.92 ± 0.19 fish / 100m^2) was identical to the MPA mean (0.92 ± 0.24 fish / 100m^2). However, none of these differences among means were significant.

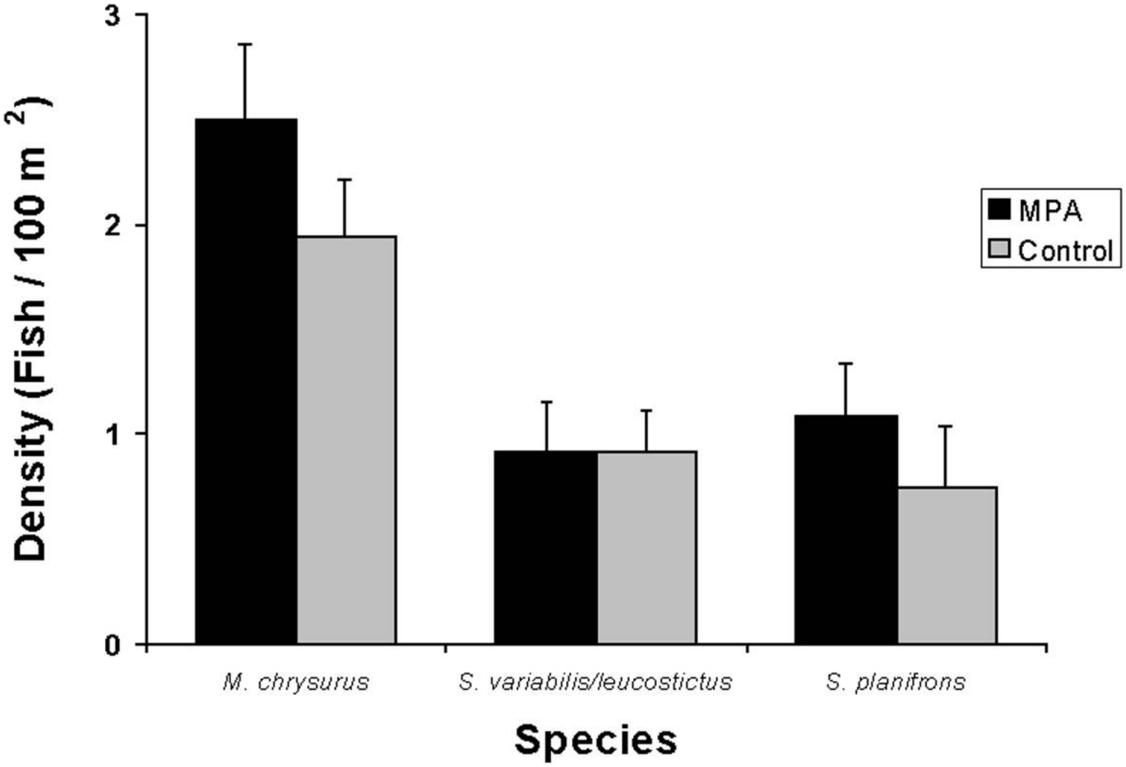

Fig. 10. Mean densities of some key pomacentrid species (fish / 100m^2) for pooled MPA sites and pooled control sites. *S. variabilis* and *S. leucostictus* pooled due to difficulties differentiating in field. Data are means ± standard error.

Of key invertivores, *Chaetodon capistratus* occurred in the highest densities (Fig. 11). Moderate densities of this species were found at both MPA's (1.67 ± 0.34 fish / 100m^2) and control sites (1.92 ± 0.35 fish / 100m^2). *Haemulon flavolineatum* also occurred in relatively high densities. Mean density of this species in MPA's was higher (0.54 ± 0.16 fish / 100m^2) than that of control sites (0.33 ± 0.10 fish / 100m^2), and though variance was relatively small, the difference was marginally non-significant. Another haemulid, *Haemulon sciurus*, was found at low but equivalent densities in MPA's (0.08 ± 0.06 fish / 100m^2) and control sites (0.08 ± 0.05 fish / 100m^2) despite its commercial importance. Finally, densities of *Bodianus rufus* peaked in MPA's (0.21 ± 0.11 fish / 100m^2), but were only marginally lower – and did not differ significantly – from control site densities (0.31 ± 0.09 fish / 100m^2). Similar to functional groupings, comparisons between pooled MPA's and pooled control sites for individual species were characterized by low statistical power (0.16 ± 0.03).

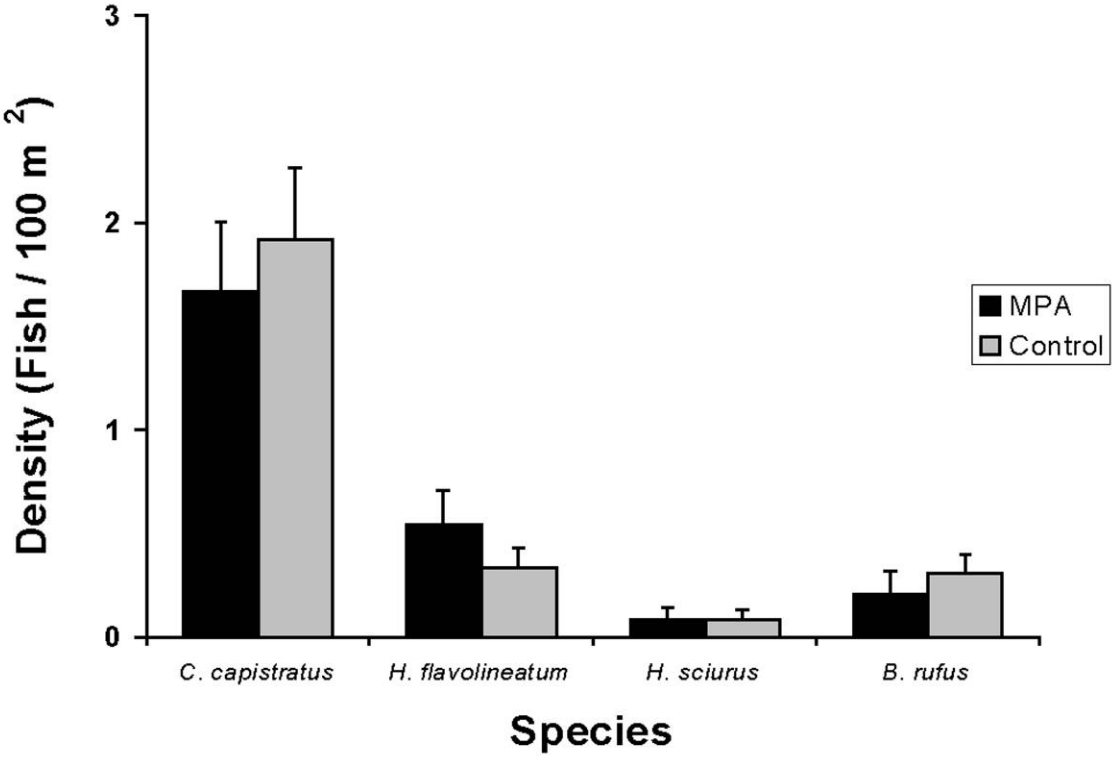

Fig. 11. Mean densities of some key AGRRA invertivorous species (fish / 100m^2) for pooled MPA sites and pooled control sites. Data are means ± standard error.

Pooled abundance of key families

Like with AGRRA data, REEF roving diver data revealed high abundances of acanthurids, scarids and pomacentrids in both MPA's and control sites (Fig. 12). Unlike that data, however, REEF data also indicated high abundance of labrids across sites, reflecting the inclusion of several common species (*e.g. Thalassoma bifasciatum*) in this protocol. Despite all lutjanids and most common serranids being included in AGRRA protocol, REEF data appeared to yield relatively higher abundances for these families than suggested by AGRRA data. Indeed, lutjanids shared comparable REEF abundance scores with chaetodontids. In constrast, scarids appeared to be a less dominant family than implied by AGRRA data.

Mean abundance of families in MPA's exceeded those at control sites for five of the seven most abundant families. Though most means were similar and no differences were significant, three families showed sizeable differences between MPA and control means. Higher pomacentrids means in MPA's were attributable mainly to higher abundances of *Stegastes partitus, Stegastes planifrons* and *Stegastes leucostictus*. Greater mean abundance of serranids in MPA's were attributable not to higher abundances in commercially-important species, but instead to *Paranthias furcifer* and *Rypticus saponaceus*. Higher lutjanid abundance in MPA's, however, was a result of the greater abundance of one commercially-important snapper, *Lutjanus griseus*.

Density of functional guilds and species at local scales

Comparing densities of functional guilds and species at single MPA's and an associated control site revealed some localized differences that were obscured when MPA's or control sites were pooled. However, by and large, no statistical differences were detected among sites (Appendix 3).

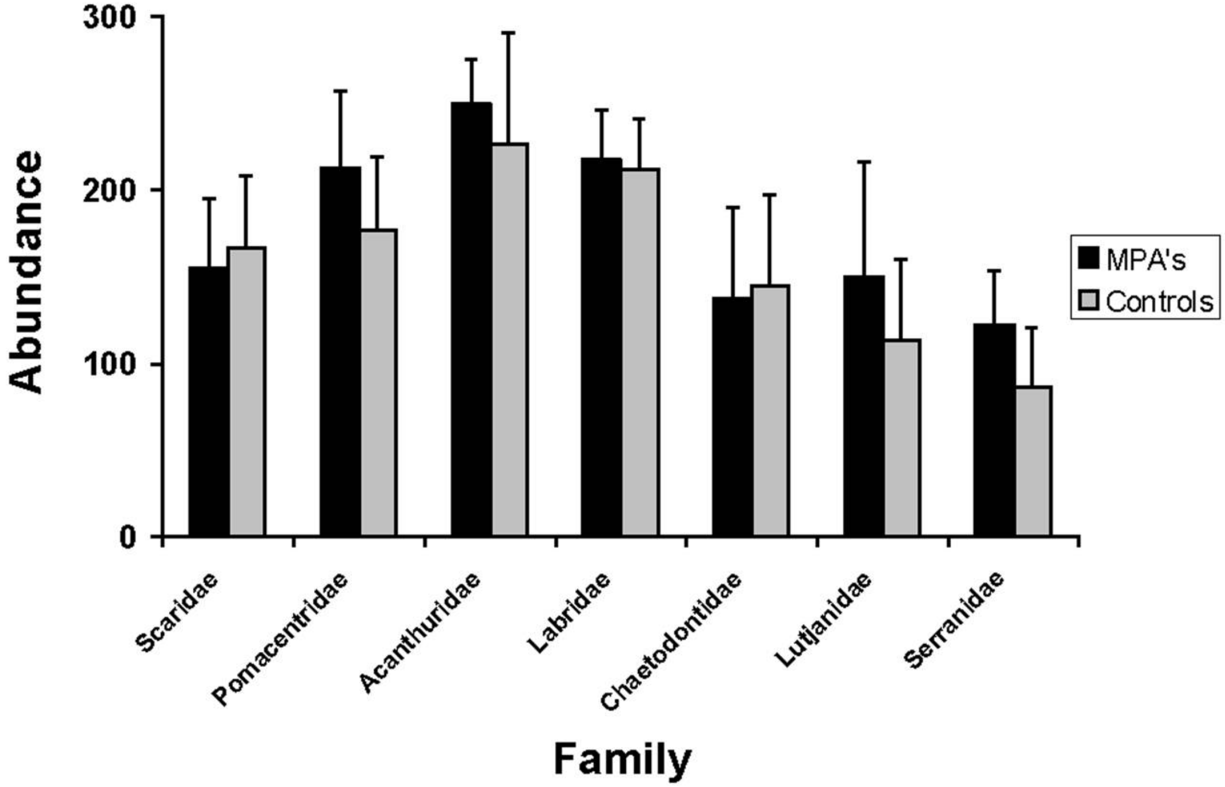

Fig. 12. Mean abundance of the most common families for pooled MPA sites and pooled control sites, based on REEF roving diver data. Data are means ± standard error.

The densities of functional guilds displayed considerable variation among sites. For example, mean herbivore density spanned a five-fold range between Southwest Breaker and North Rock MPA's (Fig. 13). The low power of statistical tests (0.12 ± 0.02) made it difficult to ascertain any consistent differences between MPA and control functional guild densities (Appendix 3). Nonetheless, mean values were not consistently higher or lower in MPA's than controls and likely indicates considerable variation from region to region rather than consistent trends among single MPA's and their associated control sites.

Despite low mean power (0.19 ± 0.02), some statistical differences were detected in single species densities between MPA's and their control sites. These differences were predominantly in herbivorous species that were consistently encountered during surveys. For instance, *Sparisoma viride* occurred in significantly higher densities at North Rock MPA than at the control site (t = -2.153, p = 0.045; Fig. 15). Similarly, *Sparisoma aurofrenatum* densities peaked in Eastern Blue Cut MPA over the control site (t = -2.212, p = 0.040; Fig. 15). The pomacentrid, *Stegastes variabilis / leucostictus*, was also found in significantly higher densities in Eastern Blue Cut MPA than in the control site (t = -2.794, p = 0.0167; Fig. 16). Finally, significant differences were found for *Scarus inserti* (t = 2.642, p = 0.026; Fig. 15), but in this case, density was highest at the control site. However, data for *Scarus inserti* and *Stegastes variabilis / leucostictus* were not normally distributed and results must therefore be interpreted cautiously for these two species.

No invertivores, piscivores or commercial species were found to differ in density between MPA's and their control sites. These species were typical found at low densities and their absence from many transects may have sufficiently increased variance and decreased power to obscure and real differences. However, it may be concluded that any large differences in densities between sites would have been detected despite the low power of tests with these species (Appendix 3).

Size frequency distributions at MPA's and control sites

Size frequency distribution of functional guilds

Insufficient numbers of fish were surveyed to create size frequency distributions for all AGRRA species. For this reason, distributions were generated by pooling MPA sites and control sites. Similar to density data, size frequency distributions by functional group revealed few consistent differences in cohort structure between MPA's and control sites. Distributions of herbivores, however, revealed one interesting difference between protected and unprotected areas (Fig. 17a). Specifically, the proportions of total herbivore counts were higher in control sites than MPA's for all size categories except for 0 – 5 cm. This length category contributed 25% more to the total herbivore count at MPA's than controls, though these juveniles appeared to dominate herbivore populations at both.

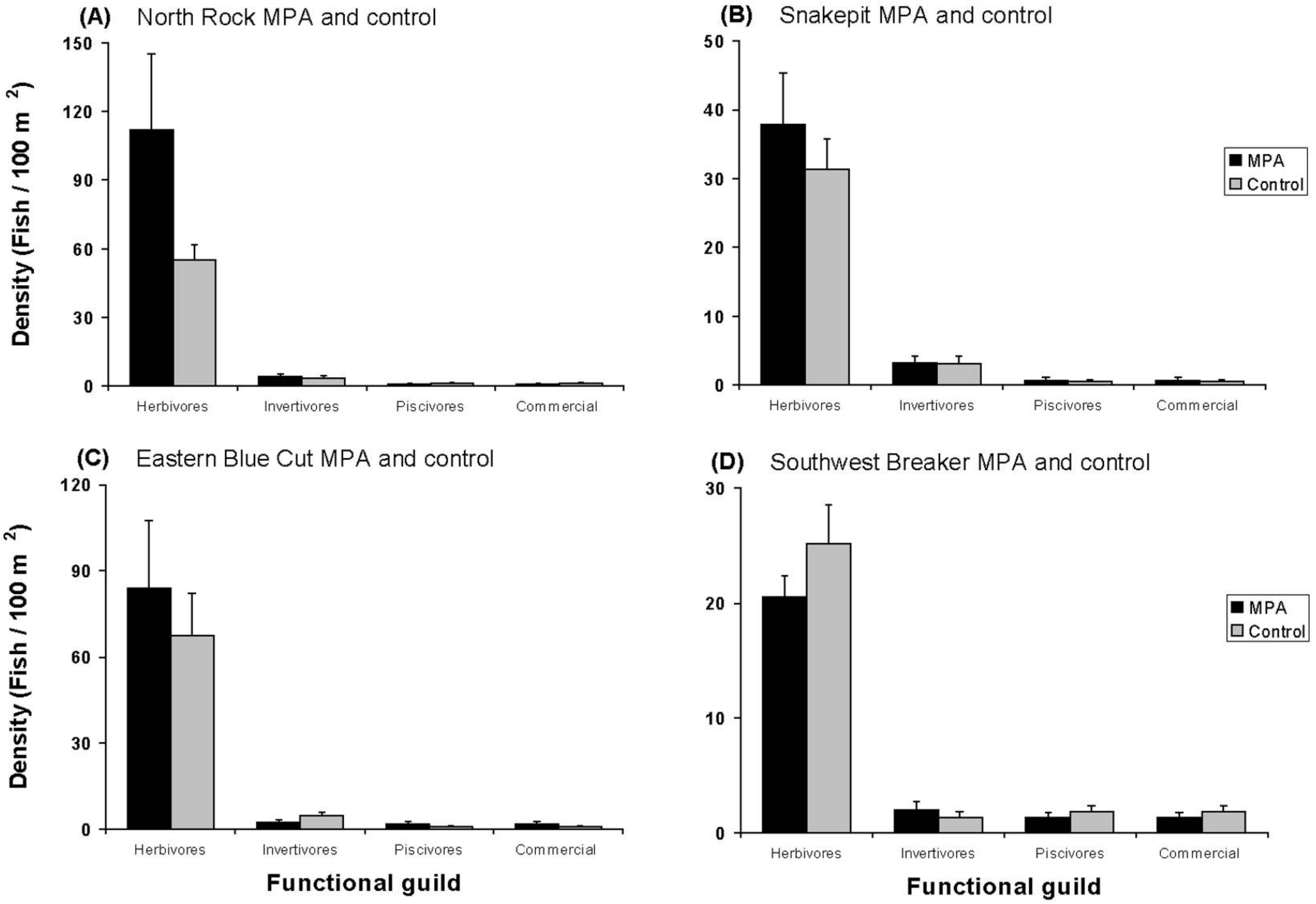

Fig. 13. Comparison of mean densities of functional guilds at **(a)** North Rock MPA, **(b)** Snakepit MPA, **(c)** Eastern Blue Cut MPA, and **(d)** Southwest Breaker MPA with one associated control site each. Data are means ± standard error.

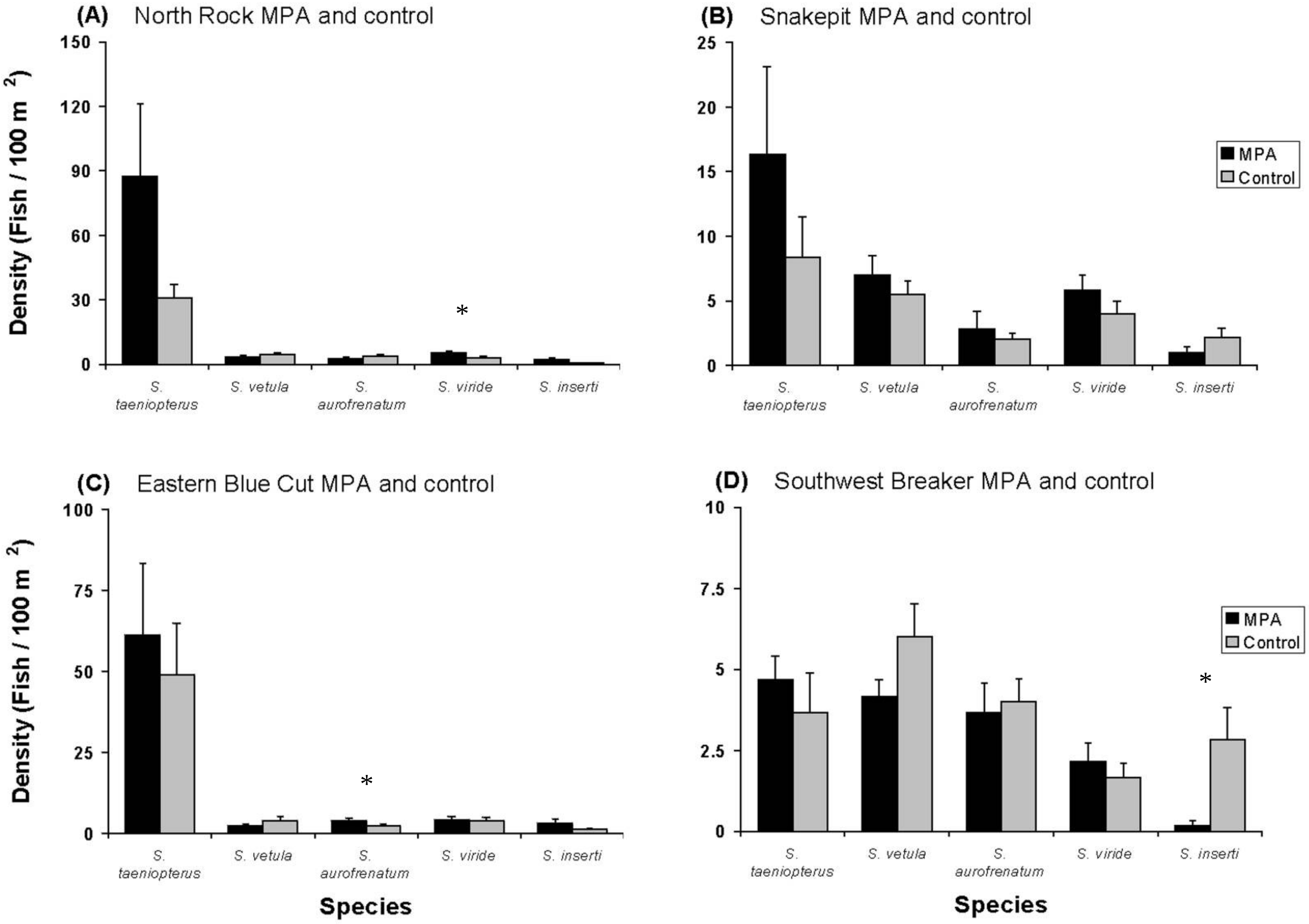

Fig. 14. Comparison of mean densities of the five most abundant scarids at **(a)** North Rock MPA, **(b)** Snakepit MPA, **(c)** Eastern Blue Cut MPA, and **(d)** Southwest Breaker MPA with one associated control site each. Data are means ± standard error. * denotes significantly different pair.

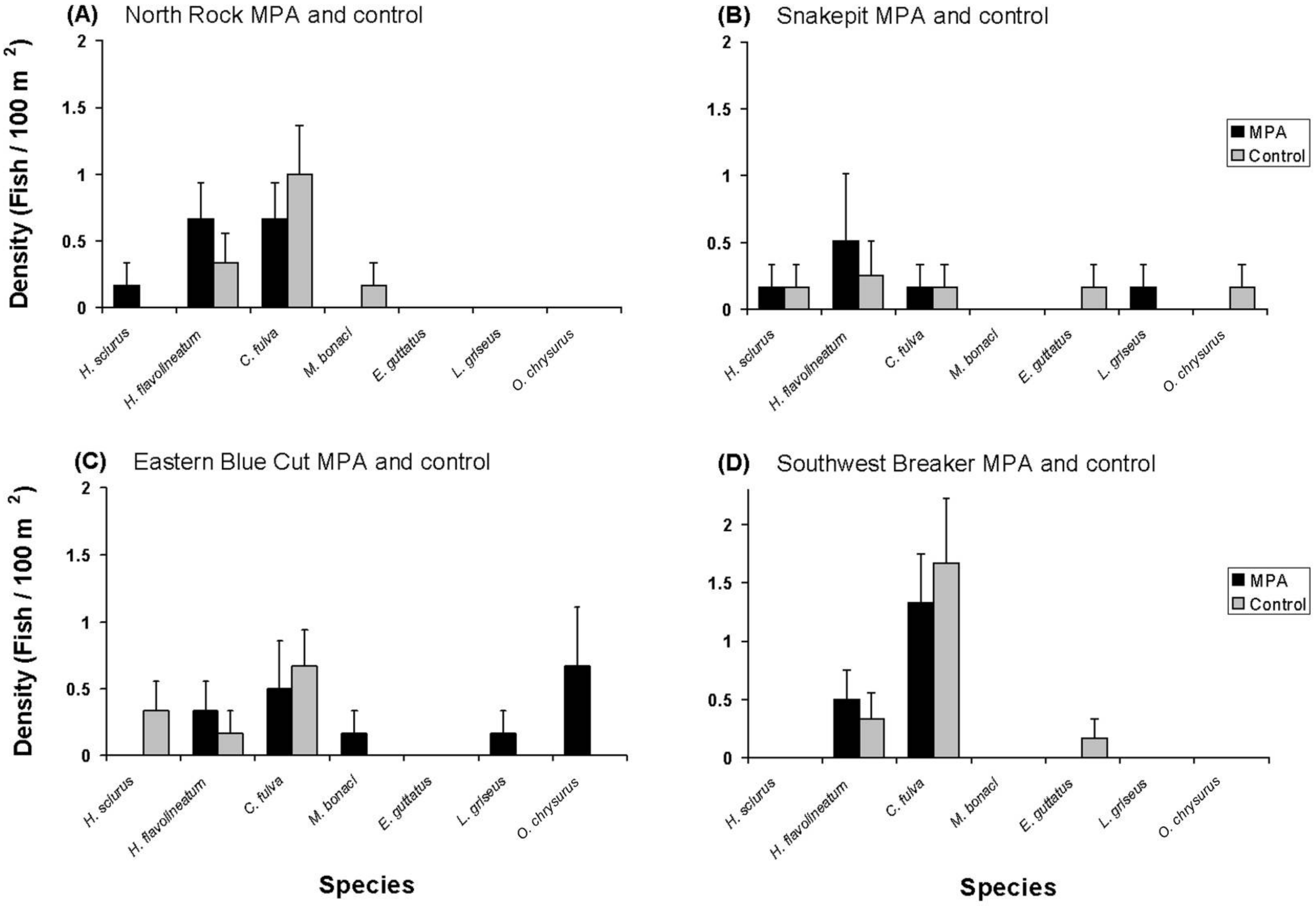

Fig. 15. Comparison of mean densities of seven key carnivorous species at **(a)** North Rock MPA, **(b)** Snakepit MPA, **(c)** Eastern Blue Cut MPA, and **(d)** Southwest Breaker MPA with one associated control site each. Data are means ± standard error.

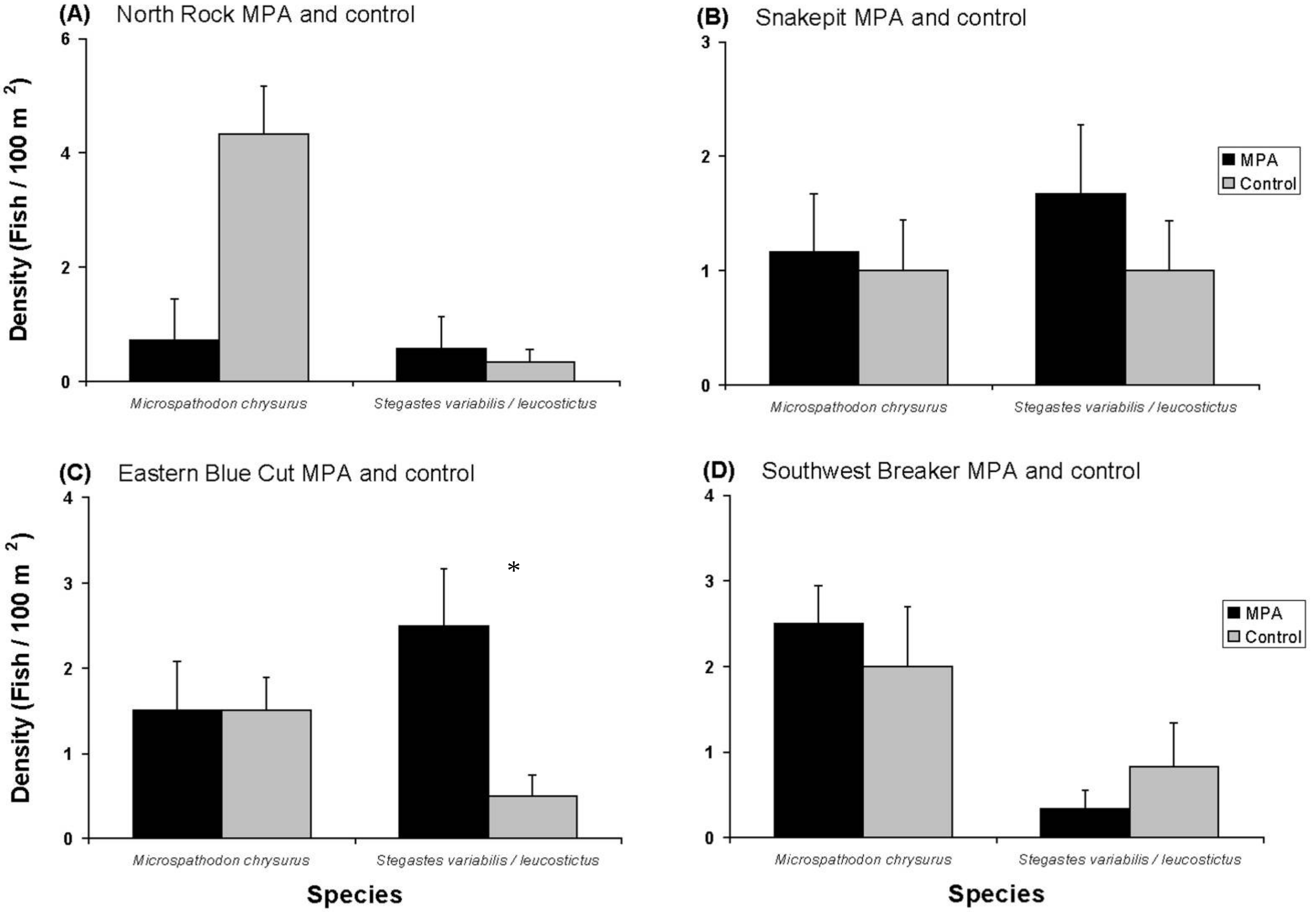

Fig. 16. Comparison of mean densities of key pomacentrids at **(a)** North Rock MPA, **(b)** Snakepit MPA, **(c)** Eastern Blue Cut MPA, and **(d)** Southwest Breaker MPA with one associated control site each. *S. variabilis* and *S. leucostictus* pooled due to difficulties differentiating in field. Data are means ± standard error. * denotes significantly different pair.

Invertivores exhibited similar size frequencies at MPA's and control sites (Fig. 17b). The only notable differences occurred in the two size classes under 10 cm. Control sites alone recorded invertivores in the 0 – 5 cm category, while 6 – 10 cm fish occurred at almost twice the proportion in MPA's than control sites.

Size frequency distributions of piscivores and commercial species were virtually identical, probably reflecting the importance of piscivores in fisheries (Fig. 17c-d). Distributions for both groups were skewed towards larger sizes. Only MPA's recorded fish in the 6 – 10 and 31 – 40 cm size ranges, though the overall contribution of these categories was minor. MPA sites tended to have a higher proportion of fish greater than forty cm in length than control sites. Due to the low abundance of piscivores in general, however, the higher contribution of 40+ cm fish in MPA's is attributable to the observation of just one additional fish than in control sites.

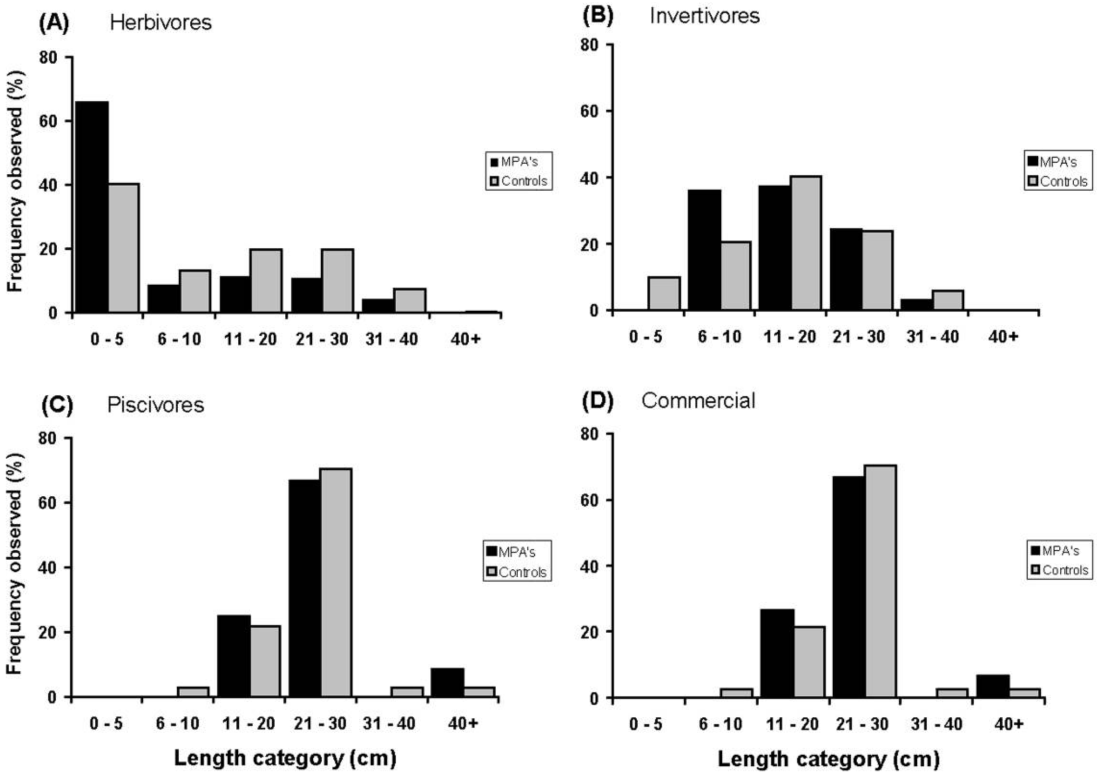

Fig. 17. Size frequency distribution of AGRRA species functional groups at MPA's and control sites. Functional groups represent (A) herbivores (n = 1547, 1419), (B) invertivores (n = 70, 122), (C) piscivores (n = 24, 37), and (D) commercial species (n = 30, 37).

Size frequency distributions of key species

As size frequency distributions require sufficient numbers of fish to capture population-wide trends, distributions of key species at MPA's and control sites were primarily confined to abundant herbivores and invertivores. The piscivore, *Cephalopholis fulva*, however, was found in sufficient numbers to demonstrate highly comparable size distributions at both MPA's and controls (Fig. 18).

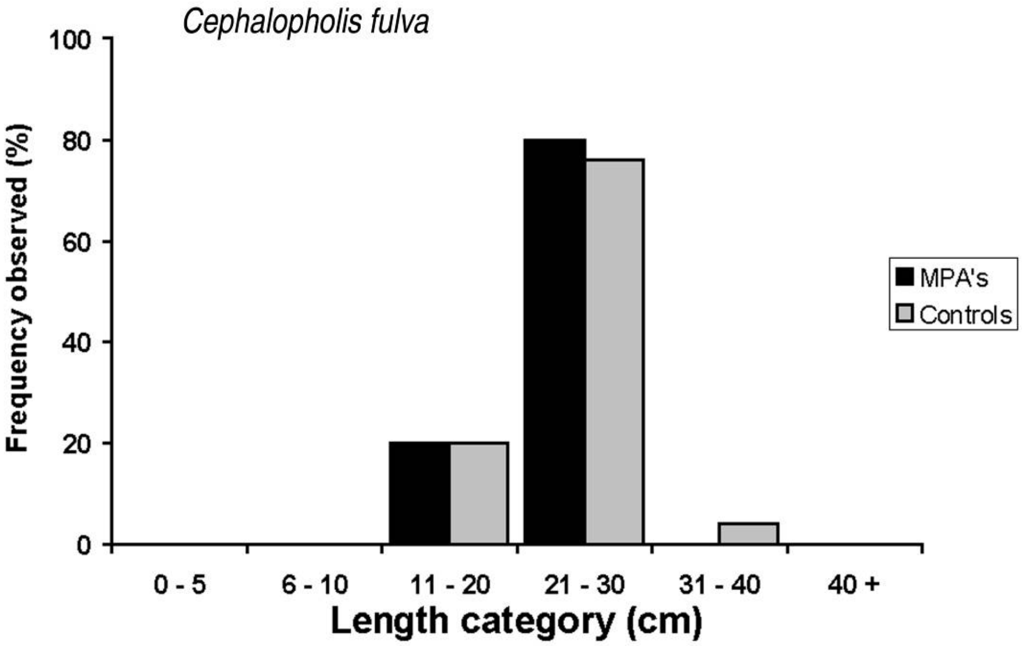

Fig. 18. Size frequency distribution of the commercially important serranid, *Cephalopholis fulva*, at MPA's and control sites MPA: n = 15. Control: n = 25.

Scarids size distributions also differed little between MPA and control sites. Distributions of *Sparisoma viride*, for example, were almost identical (Fig. 19). *Scarus vetula* exhibited a uniform distribution in intermediate size classes, and only in the 6 – 10 cm category did the MPA frequency differ somewhat from the control frequency (Fig. 20). Populations of *Scarus taenopterus* were characterized by high proportions of juveniles in the 0 – 5 cm range (Fig. 21). Proportions of this size class in MPA's exceeded those in control sites, while the reverse was true of control proportions for all other size classes. The same pattern was evident in *Sparisoma aurofrenatum*, with juveniles relatively more abundant in MPA's and with marginally higher proportions of the remaining size classes at control sites (Fig. 22).

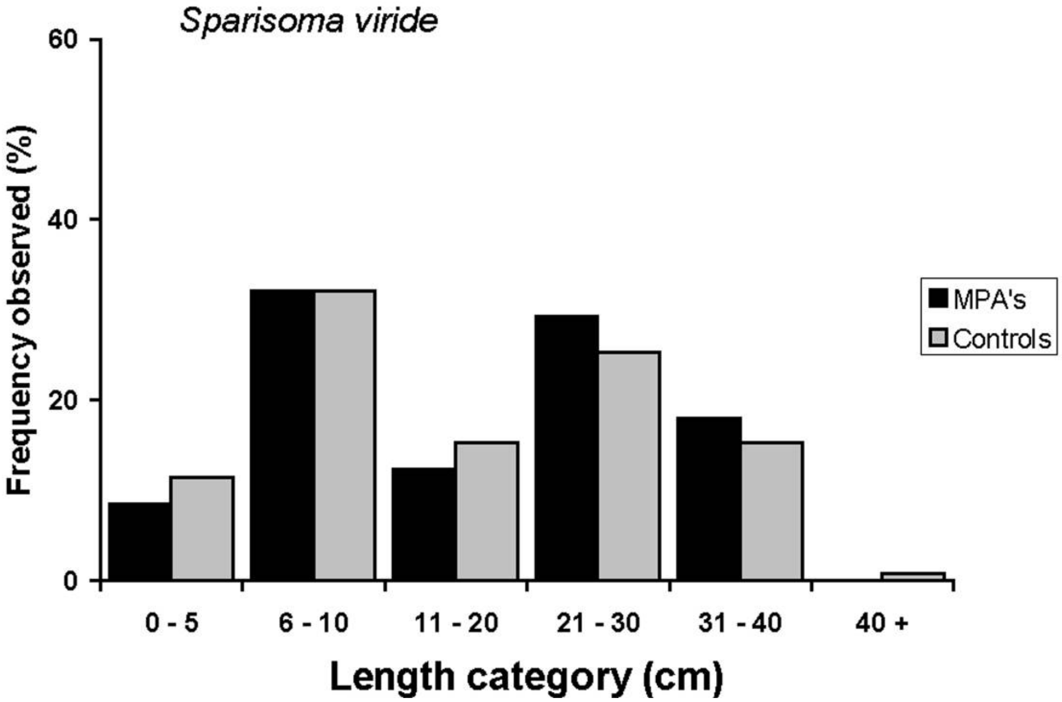

Fig. 19. Size frequency distribution of the scarid, *Sparisoma viride*, at MPA's and control sites MPA: n = 106. Control: n = 131.

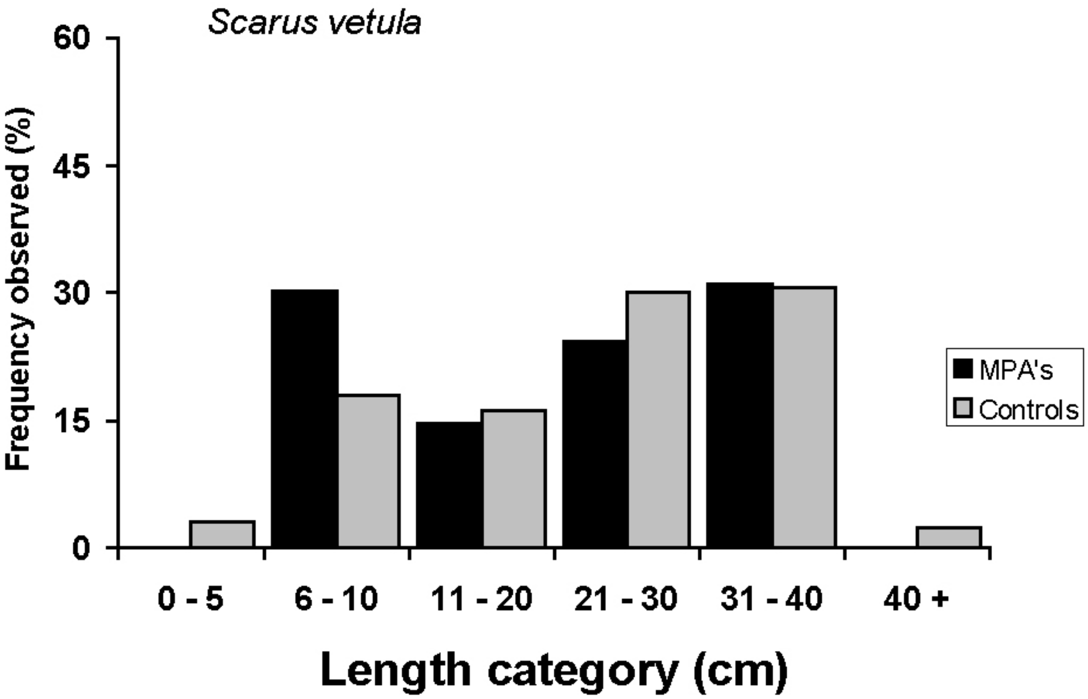

Fig. 20. Size frequency distribution of the scarid, *Scarus vetula*, at MPA's and control sites MPA: n = 103. Control: n = 167.

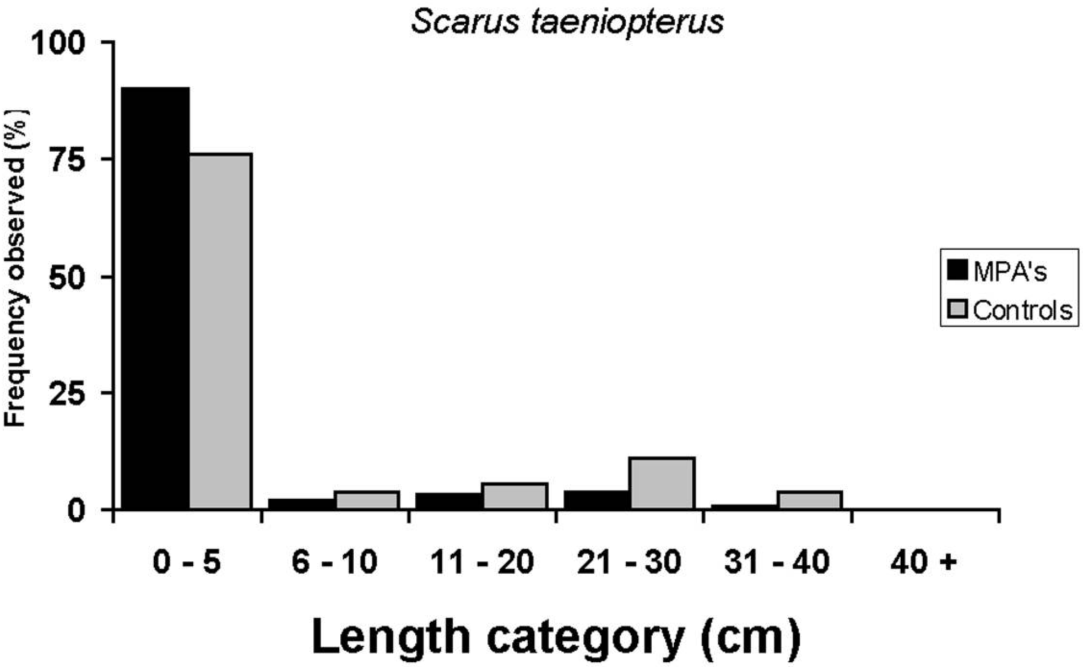

Fig. 21. Size frequency distribution of the most abundant scarid, *Scarus taeniopterus*, at MPA's and control sites MPA: n = 1075. Control: n = 678.

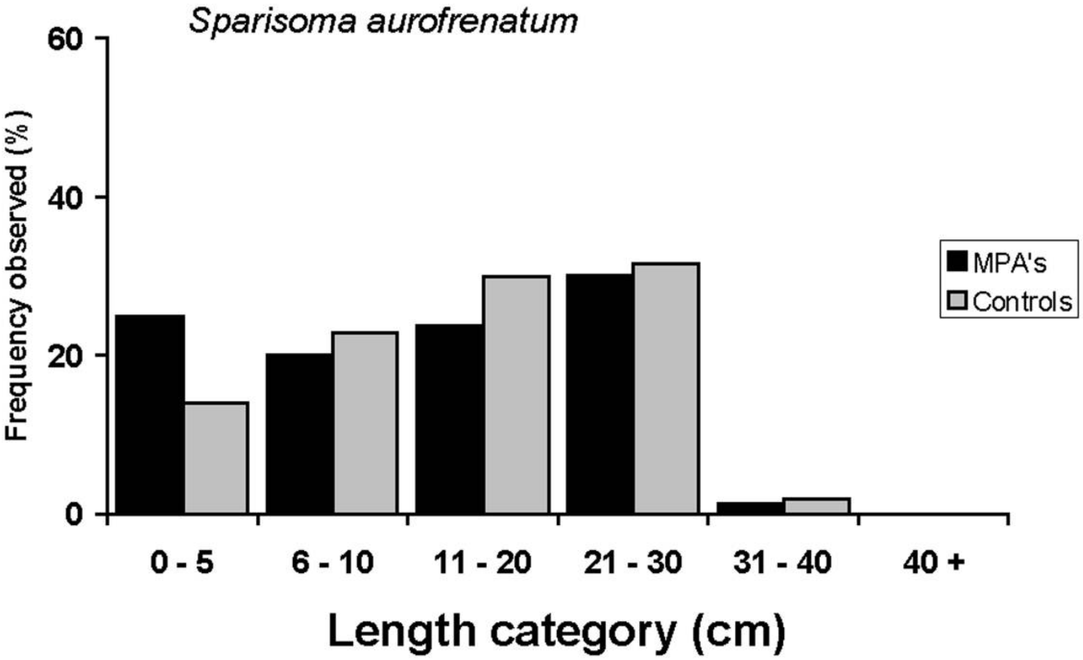

Fig. 22. Size frequency distribution of the scarid, *Sparisoma aurofrenatum*, at MPA's and control sites MPA: n = 80. Control: n = 114.

Size distributions of the key herbivore, *Acanthurus bahianus*, were highly similar, with only a slightly higher contribution from the 6 – 10 cm category at control sites (Fig. 23). The pomacentrid, *Stegastes leucostictus/variablis*, also exhibited similar distributions inside and outside the protected areas (Fig. 24). Distributions of another pomacentrid, *Microspathodon chrysurus*, in contrast, differed markedly in proportions of 0 – 5 and 6 – 10 cm fish between MPA's and control sites. Fish in the smallest size class were relatively more abundant at MPA's, while 6 -10 cm fish were relatively more abundant at control sites (Fig. 25). Fish in the 6 – 10 cm range also had higher proportions at control sites for the invertivore, *Chaetodon capistratus* (Fig. 26). This species was absent as juveniles in MPA's.

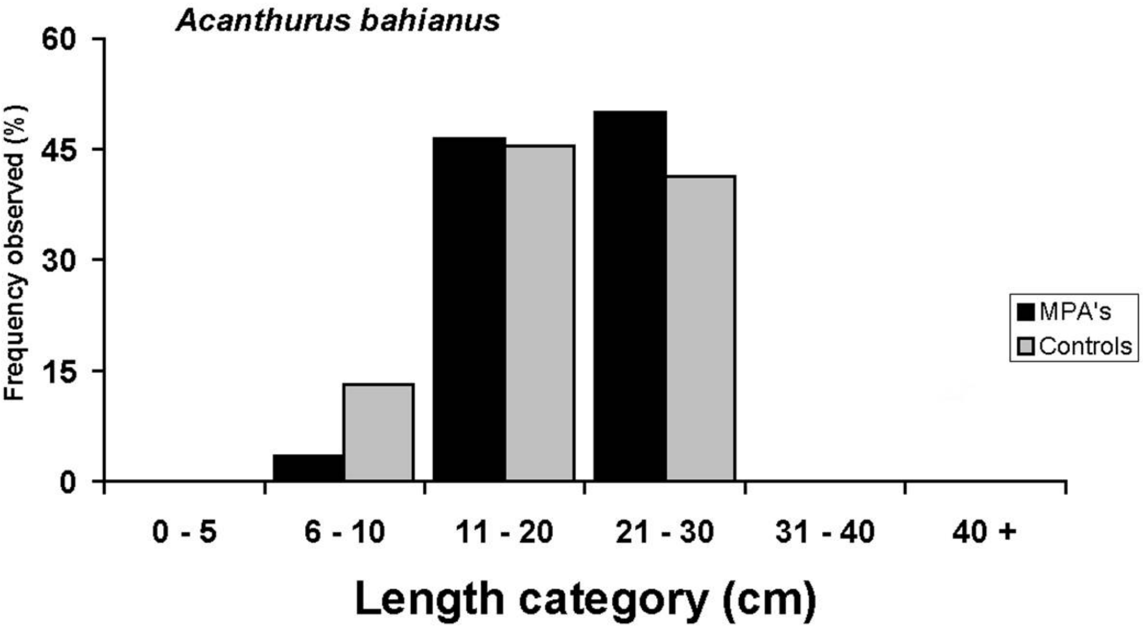

Fig. 23. Size frequency distribution of the abundant acanthurid, *Acanthurus bahianus*, at MPA's and control sites MPA: n = 58. Control: n = 99.

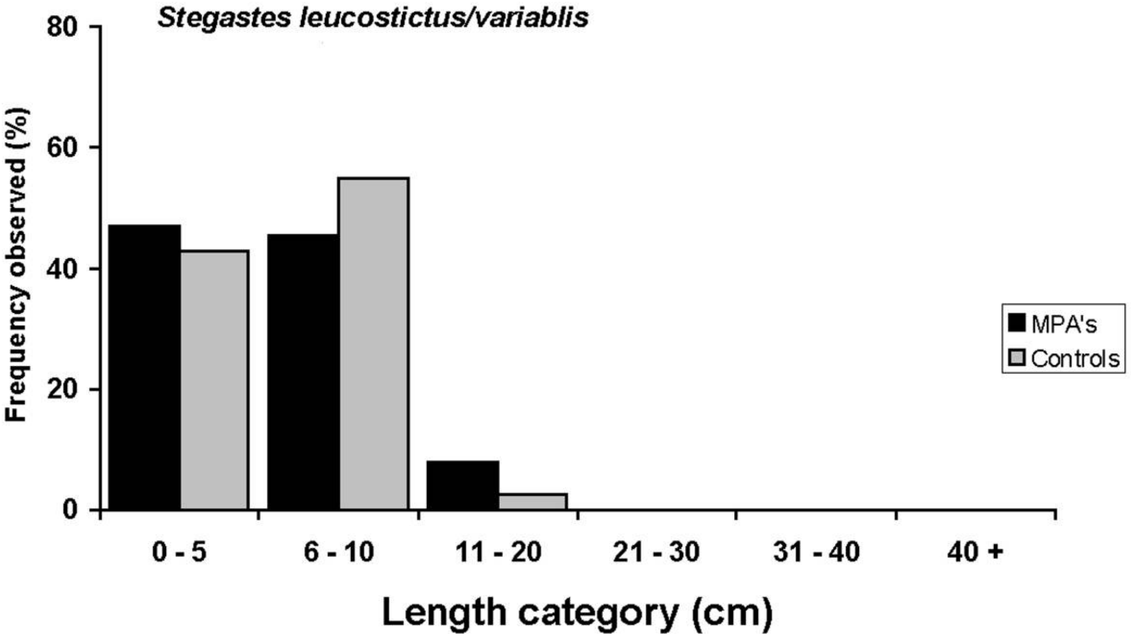

Fig. 24. Size frequency distribution of the abundant pomacentrids, *Stegastes leucostictus* and *S. variablis*, at MPA's and control sites. Both species were combined due to difficulties distinguishing the species with certain colour phases MPA: n = 64. Control: n = 42.

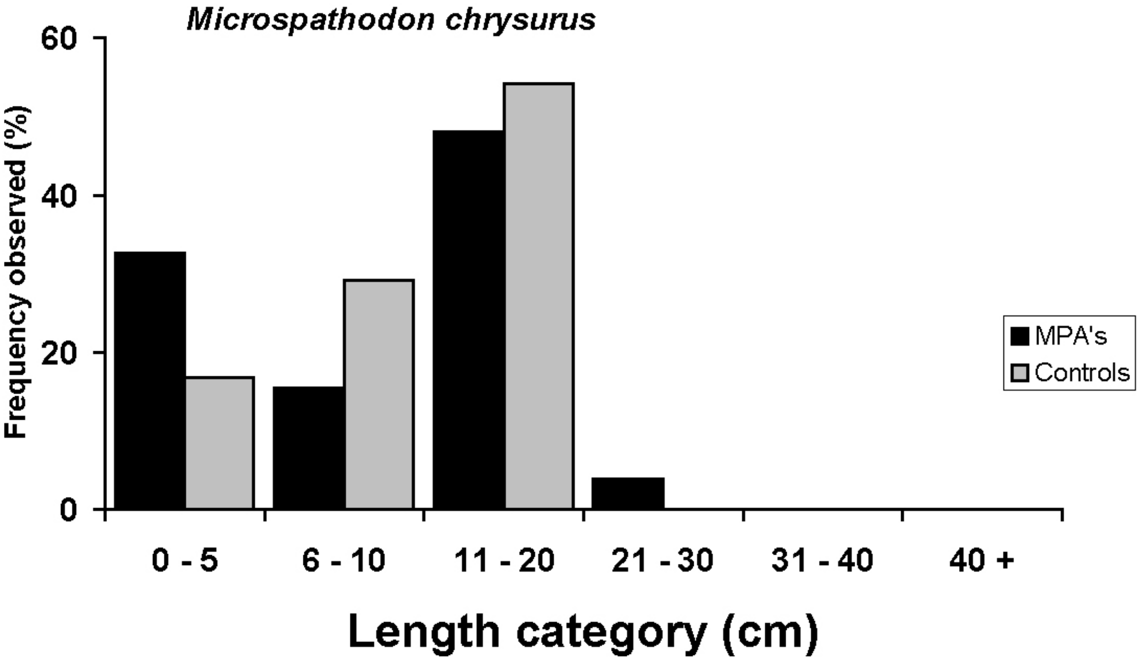

Fig. 25. Size frequency distribution of the abundant pomacentrid, *Microspathodon chrysurus*, at MPA's and control sites. MPA: n = 52. Control: n = 72.

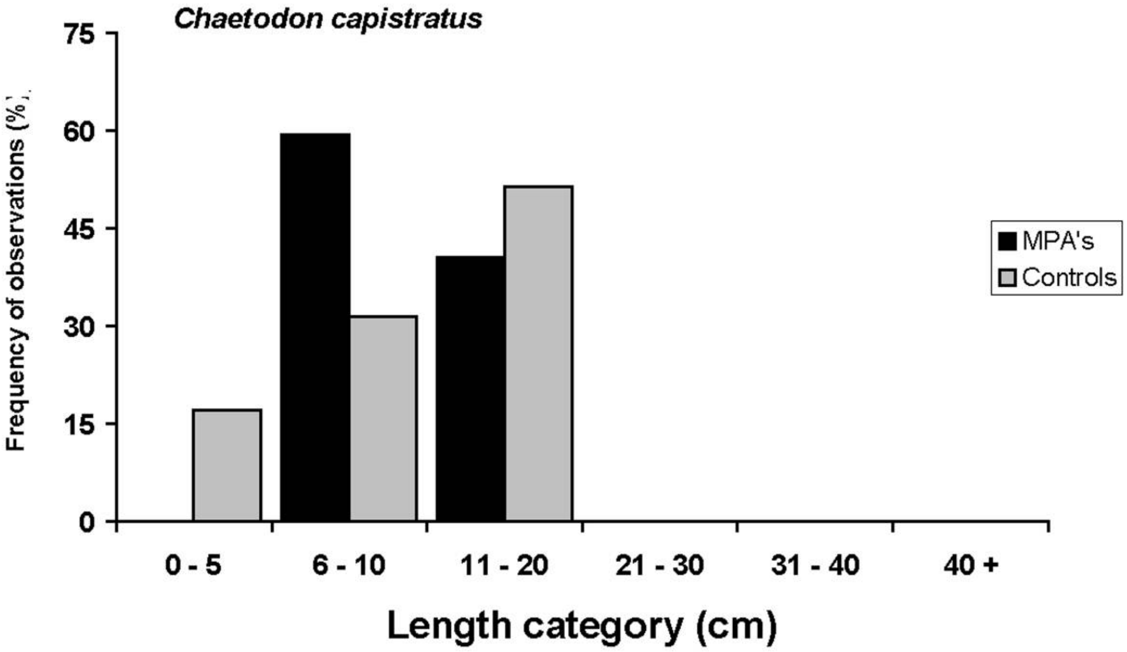

Fig. 26. Size frequency distribution of the abundant chaetodontid, *Chaetodon capistratus*, at MPA's and control sites. MPA: n = 37. Control: n = 70.

Differences in composition of MPA and control assemblages

AGGRA species assemblages in MPA's and control sites

ANOSIM routines of multivariate density data comparing MPA and control groupings of sites revealed no statistical differences in assemblage structures (R = 0.147, p = 0.190). Furthermore, visual examination ordination of the square root-transformed data revealed no consistent clustering of MPA or control sites (Fig. 27). Two clusters were apparent at 70% similarity, but each isolated three control sites intermingled with MPA sites. MPA's ordinated with large distances between sites, with one MPA (3065 - Snakepit) failing to cluster with any other sites. The widespread ordination pattern suggested even less consistency in protected site assemblages than those of control sites. SIMPROF routines supported the lack of consistent differences among sites of any type by finding no evidence for the significance of any of the clusters.

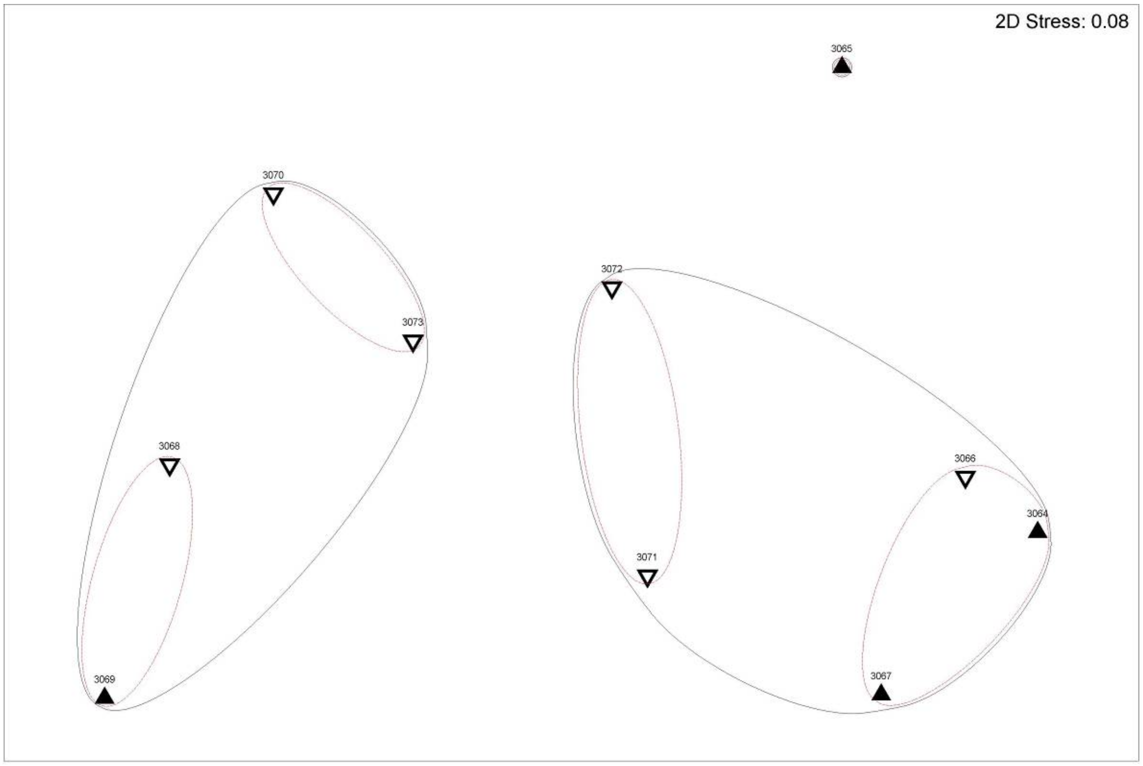

Fig. 27. MDS ordination of square-root transformed density data for all AGRRA species at MPA and control sites, overlaid with clusters of 70% similarity (black contours) and 75% similarity (red contours). ▲ = MPA, ▽ = control site.

REEF species assemblages in MPA and control sites

Similar to multivariate AGRRA data, ANOSIM routines of untransformed REEF data suggested no statistical differences between the structure of MPA and control fish assemblages (R = 0.15, p = 0.183). Subsequent ordination of REEF data showed no distinct clustering of MPA and control site assemblages (Fig. 28). MPA's were again widely dispersed among control sites with only one control site cluster above 80% similarity. SIMPROF routines again found no statistical evidence to support the existence of these site clusters. The result, again, implies no consistent differences in species composition and abundance among MPA's, control sites or any combinations of these sites.

Fig. 28. MDS ordination of untransformed REEF roving diver survey data for all species at MPA and control sites, overlaid with clusters of 65% similarity (black contours) and 80% similarity (red contours). ▲ = MPA, ▽ = control site.

Discussion

This study employed metrics from two surveying protocols, AGRRA and REEF roving diver, to test for differences in fish density, biomass, abundance and assemblage composition between MPA's and corresponding control sites. The two protocols, one limited to only key species, captured different aspects of fish assemblages in MPA's and control sites. REEF data (encompassing all species), for example, provided comparative species richness data and better indications of actual ecosystem function than AGRRA protocol. On the other hand, AGRRA data offered size class information and more precise estimates of fish density and biomass, albeit for fewer species. Despite some significant differences, the results suggested little variation in (i) assemblage structure, (ii) key species abundance or biomass, and (iii) size frequency distributions between protected and unprotected reefs protected and unprotected reefs. While statistical power was generally low for detecting differences among MPA's and control sites, the findings rule out the existence of large variations among protected and unprotected assemblages. This study thus lends support to the idea that current spatial protection on rim reefs in Bermuda has not resulted in large-scale alteration or enhancement of fish populations. Such a result is not surprising considering that parrotfish are protected across the region, and most other herbivorous, planktivorous and invertivorous fish are not harvested locally. Only piscivorous fish such as groupers and snappers are likely to benefit from the protection provided by the permanently buoyed MPA sites. In this case the small size of the MPA sites may be preventing a significant MPA effect from being found in these fished species, or perhaps management is not working effectively. This may be the case since there are reports of fishers targeting MPA sites after 5 pm, at night or during stormy weather, when fisheries wardens are not actively patrolling.

Functional organization of MPA's and control sites

In terms of species richness, fish density and biomass, the general functional organization of both MPA and control reefs was highly comparable. Indeed, no significant differences existed between reef types for any functional guild when sites of similar protection treatment were pooled or when single MPA's were compared with their corresponding control site. In all cases, herbivory dominated the functional organization of the assemblage. Scarid densities contributed most to this predominance, paralleling their dominant grazing position in the Caribbean subsequent to the decline of the sea urchin, *Diadema antillarum* (Mumby *et al.*, 2006). The lower mean herbivore density observed at pooled control sites, while not significantly different from that of MPA's, countered expectations. Significant differences between single MPA's and their control sites for individual herbivore species similarly countered expectations and suggested that higher statistical power may have allowed detection of differences in herbivore guild densities.

Herbivore abundance is most often expected to decrease as a trophic response to increasing predator densities in protected habitats (Micheli and Halpern 2005; Mumby *et al.*, 2006; Sonnenholzner *et al.*, 2007). However, Mumby *et al.* (2006, 2007b) noted increases in scarid densities in a Bahamian MPA similar to the higher means noted here. Two mechanisms were suggested for these increases. First, spatial protection released scarids from targeted harvest, as occurs across the Bahamas, and spurred their recovery (Mumby *et al.,* 2006). This mechanism is unlikely in Bermuda as all scarids have been protected from harvest since 1989. Any local protection effects would thus be indirect food web responses. Mumby *et al.* (2007a) proposed that high abundances of large-bodied scarids in MPA's might counter any top-down control of increased predator abundance. This could indeed be the case in Bermuda, where large scarids are abundant. On the other hand, the large range of herbivore densities and variability among MPA-control pairs suggests spatial heterogeneity of abundance among all sites rather than consistent differences among MPA's and control sites.

Even though mean densities of herbivores at pooled MPA sites were suggestive of enhancement over control densities, biomasses indicated the opposite trend. Here, the higher biomass estimates at control sites implied a higher proportion of small herbivores at MPA's. It must be noted that variance - likely related to high herbivore densities at some sites (*e.g.* North Rock MPA) - was too substantial to detect any statistical differences. However, higher proportions of the juveniles of some abundant herbivore species may support differences in biomass between MPA's and control sites. Specifically, the higher proportions of juvenile *Scarus vetula, Scarus taeniopterus*¸

Sparisoma aurofrenatum, and *Microspathodon chrysurus* found in MPA's could explain the lower biomass of sites characterized by high herbivore densities. Interestingly, as only large-bodied scarids would escape predation by any enhanced piscivore populations in MPA's (Mumby *et al.*, 2006), we would have expected juveniles of such species to be less common than in unprotected areas. Again, though, without better resolution of differences in abundance or size frequency distributions, protected areas cannot be conclusively demonstrated to offer refuge to large numbers of juvenile or adult herbivores.

The similar mean densities and biomasses of invertivores, piscivores and commercially / recreationally important species in MPA's and control sites suggested that these functional groups were also little-influenced by protected status. This is perhaps surprising given that piscivorous and commercial species often exhibit the most dramatic responses to spatial protection (Ojeda-Martinez *et al.*, 2007; Unsworth *et al.*, 2007; Watson *et al.*, 2007). The apparent low abundance of carnivores thus contrasts with findings that describe broad enhancement of these functional guilds in protected areas, but agrees with a previous, local MPA assessment (MEP, unpublished technical report). Even though statistical power was low, not finding differences in piscivore or commercial species densities between MPA's and control sites might be considered support for similar previous findings (MEP, unpublished technical report). This prior assessment attributed the low abundance of piscivores inside and outside MPA's to the residual effects of historical overexploitation of these commercially-important species.

On the whole, the resemblance of functional organization between pooled MPA's and pooled control suggests that protected areas in Bermuda do not appear to have initiated the broad enhancement of higher trophic levels (*i.e.* piscivores), as reported elsewhere (Guidetti and Sala, 2007; Unsworth *et al.*, 2007). Furthermore, densities of herbivores varied greatly among regions, suggesting that natural spatial variation in this functional guild might have been greater than the resolution of trends between protected and unprotected reefs. However, the lack of broad enhancement of high trophic levels at the relatively coarse level of functional guilds is perhaps not surprising for three reasons.

First, the piscivore and commercial species densities reported here are generally lower than those reported in the balance of the Caribbean (Kramer, 2003). The high variance incurred by sampling at such low densities may thus obscure true differences among means. Second, where life history traits differ among species sharing a functional guild, increases in one species may be cancelled out by neutral or negative responses to protection in other species. Third, localized ecosystem and assemblage responses to protection may mask more obvious indications of enhancement in MPA's. Therefore, failure to detect increased abundance of any functional guild does not necessarily imply that no species effects are conferred by protected status. Rather, assessment of key species may be better suited to revealing trends obscured at the level of functional guilds.

Key species in MPA's and control sites

In addition to the functional organization of MPA's and control sites being highly similar, densities and size distributions of key species generally agreed between protected and unprotected habitats. However, some differences were apparent. Comparisons on the local scale between an MPA and its control site suggested that some scarids displayed spatial idiosyncrasies in abundance. For example, the significant differences in MPA and control abundance for *Sparisoma aurofrenatum, Sparisoma viride* and *Scarus inserti* in only one of four MPA-control pairings indicate spatial variability in species abundances among sites. However, whether or not this is a protection effect is unclear. The higher mean densities of *Sparisoma viride* in all MPA's than control sites (significant in the North Rock pairing) is suggestive of consistent enhancement of this species on protected reef, yet not statistically robust across all pairings.

A similarly suggestive pattern of consistent population enhancement in MPA's existed for *Scarus taeniopterus.* This herbivore exhibited higher mean densities in all MPA's than control sites, but none of these pairings were statistically significant. As with the herbivore guild in general, this pattern runs contrary to expectation. We predicted that enhanced predator populations resulting from a release in fishing pressure would result in lower abundances of prey items such as *S. viride* and *S. taeniopterus*. While Mumby *et al.* (2007b) noted an absence of top-down control of large-bodied scarids in MPA's, the high proportions of juvenile *S. taeniopterus* at some Bermuda MPA's make the local absence of top-down control unlikely. But, on the other hand, the apparently comparable densities of piscivores in MPA's and control sites at least suggests that predators are not sufficiently more numerous in MPA's to exert far greater top-down control of herbivore populations. Thus, while a mechanism for enhanced scarid populations in MPA's in not clear, it is perhaps a useful reminder that responses to protection may be non-linear. Watson *et al.* (2007), for example, reported increased abundance of several species not targeted by fisheries concurrent with target species. While such enhancements depend on a species' position in the ecosystem, they often result from complex interactions that make their prediction or interpretation difficult.

It is unclear whether region-specific differences in the relationship between MPA and control abundances of scarids result from (i) failure to detect actual responses to protection at some sites, (ii) varied responses to protection in different MPA-control pairings, or (iii) responses to varied local conditions other than degree of protection. While it is possible that the low power of univariate statistics resulted in failure to detect differences between sites, a similar previous study with more replication than this study did not report any major differences either (MEP, unpublished technical report). Furthermore, the inconsistent direction (*i.e.* higher or lower in MPA's than controls) of non-significant differences in means of *Sparisoma aurofrenatum* and *Scarus inserti* again hint that if protection responses do exist, they must be locally varied (*e.g.* Guidetti and Sala, 2007).

Even though densities of *S. taeniopterus* could be uniformly higher in MPA's, local variation appears to occur in juvenile dispersal also. For instance, the high variance around pooled data for this species reflected the occurrence of large numbers of juveniles at only two MPA's (North Rock and Eastern Blue Cut). Furthermore, high variance in comparing single MPA's to control sites resulted from the patchy distribution of these fish within sites. Such spatial variation in juvenile *S. taeniopterus* – or adult *S. aurofrenatum* and *S. inserti* – densities might arise from small-scale differences in habitat distribution, hydrology or food web structure. Whether and just how many of these factors are influenced by habitat protection, however, is beyond the resolution of this study. It is thus unclear as to whether differences in scarid abundances in MPA's and controls represent true protection effects or responses to minor variations in environmental and community conditions across space.

Differences in the abundances of some pomacentrids between MPA's and control sites were also suggested by both REEF and AGRRA data. Pooled site means were highest for *Microspathodon chrysurus* and *Stegastes planifrons* in MPA's, but did not differ significantly. In contrast, while pooled site means were equivalent for *Stegastes variabilis / leucostictus*, densities of this species were significantly higher in Eastern Blue Cut MPA than the control site. As with other species, though, this pattern did not hold true for the means of other MPA-control pairings. This might again be attributable to regional differences, lack of statistical resolution or, perhaps, an artifact of combining the two pomacentrid species for ease of census.

Higher densities of pomacentrids in even just one MPA were unexpected for two reasons. First, as with scarids, we may expect the top-down limitation of small herbivores – and not their increase - from any increase in predator populations due to habitat protection (Ojeda-Martinez *et al.*, 2007). Second, the association of high abundances of some "algal-farming" pomacentrids with coral loss and reef degradation (Jones *et al.,* 2006) makes the occurrence of such abundance in protected habitat potentially paradoxical. The greater proportion of juvenile *M. chrysurus* in MPA's than control sites, hinted that it was higher recruitment in protected areas that drove increased - but not significantly different - mean density. While degraded habitat may favour the settlement of some pomacentrid species (Feary *et al.*, 2007), there is also some precedent for protected areas, which can conserve spatial heterogeneity, in providing better growth conditions for some species (Retzel *et al.,* 2007). However, the widespread abundance of herbivores in Bermuda to facilitate coral recruitment (Mumby *et al.,* 2007a-b) and the lack of physically destructive fishing or boating practices (*e.g.* dynamite), makes it most unlikely that protected reefs offer any more structural heterogeneity than unprotected ones.

Uncertainties in the ecology and ecosystem effects of Bermuda's pomacentrids also make it difficult to attribute increased abundance of pomacentrids in MPA's to any habitat degradation. Furthermore, contradictory indications of abundance in MPA's and controls confound interpretation. For instance, while the coinciding higher REEF abundance pomacentrids in protected areas may appear to support the trends suggested by densities of *M. chrysurus* and *S. planifrons* and *Stegastes variabilis / leucostictus*, a closer assessment reveals that the higher pomacentrid REEF abundance in MPA's is attributable not only to *S. planifrons* or *M. chrysurus*, but to different species *Stegastes partitus*. Acknowledging the mismatch of species responsible for higher MPA means between the REEF and AGRRA data, as well as the high variance around MPA and control means, we might regard higher pomacentrid abundance in MPA's as either too ambiguous to draw conclusions or spurious.

The observed correlation between chaetodontid density and spatial complexity has lead to their suggested use as indicators of reef health (Brokovich and Baranes, 2005). The slightly higher mean density of *Chaetodon capistratus* in control sites would thus appear unusual, except that high variance again makes this relationship very uncertain. At best we may conclude that they are abundant and important fish in both protected and unprotected habitats. Results from coral assessments of the study sites further indicate high variability in coral community composition among all sites rather than relating to level of habitat protection (Murdoch *et al.,* 2007), making consistent differences in chaetodontid densities in MPA's and control sites unlikely anyway. This lack of consistent trend probably also relates to the low incidence in Bermuda of fishing or boating practices destructive to physical habitat. Densities and size frequencies of chaetodontid species, as in almost all other key species, thus reveal no tangible distinction between protected and unprotected coral reefs.

Very weak evidence existed to suggest any higher abundances of piscivore or commercial species in MPA's. Mean densities of *Ocyurus chrysurus* and *Carangoides ruber*, for example, were higher in MPA's than controls sites, but the high mobility of these species - coupled with high variance around means - suggests that this is not the influence of site protection. Rather, any suggested differences in means might just be an artifact of sampling species with low site fidelity using a “snapshot” approach. The densities and size frequency distributions of other key commercial species, such as *Cephalopholis fulva*, *Haemulon sciurus* and *Mycteroperca bonaci*, possibly reinforced the absence of a protection effect on either fish numbers or population size structure in MPA’s, though sample sizes were clearly an issue. However, such a finding would concur with the study by the Marine Environment Programme (unpublished technical report) which also described the uniform distribution of piscivores and commercial species across MPA boundaries.

The insubstantial evidence for increased abundance of target species in MPA’s contrasted with other studies outside Bermuda. Increases in serranid densities and size, for example, were characteristic of a large Bahamian no-take zone. Unsworth *et al.* (2007) similarly documented a 30% increase in serranid density in just five years at an Indonesian coral reef MPA of comparable size to those studied here. Despite the likelihood that these increases occurred in the context of heavier fisheries exploitation outside the protected area than seen in Bermuda, the lack of any positive trend in density or biomass at MPA’s for these species is surprising. It must be acknowledged, however, that AGRRA surveys produced few observations of these relatively rare piscivores and commercial species that likely affected density estimates. Consequently, even AGRRA data from the most common serranid (*Cephalopholis fulva*) would have insufficient statistical power to detect the same 30% increase in density detected by Unsworth *et al.* (2007).

REEF roving diver surveys appeared to better capture the abundances of rarer commercial species than AGRRA surveys. Variances around means were still quite high, but this protocol provided estimates of rarer piscivores that were relatively higher than those produced by AGRRA. In the case of REEF data for serranids, the responsibility of *Paranthias furcifer* and *Rypticus saponaceus* densities for the higher MPA mean suggest that prohibition of fishing is not directly responsible for that greater mean, as neither species has great commercial significance. The higher mean abundance value of lutjanids in MPA’s, in contrast, was attributed to *Lutjanus griseus*, a valuable commercial species. The same weak pattern in AGRRA could liberally be interpreted as suggesting a protective role of MPA's for this species. *Lutjanus griseus* indeed shares several characteristics of a species that respond to habitat protection, such as the ability to pair-spawn rather than aggregating to reproduce (pers. obs.), a relatively high fecundity, and significant commercial value. However, despite these promising characteristics and some indications of increased *Lutjanus griseus* abundance in MPA's from both data sets, such a trend is also quantitatively unsubstantiated - again due to the considerable uncertainty surrounding means.

The lack of resolution in metrics of both AGRRA density and REEF abundance of rarer species appears to be related to the relatively low abundances of piscivores and commercial species in Bermuda. Lutjanid and serranid densities presented here, for example, generally undercut by 50% AGRRA densities reported for seven regions spanning from the Bahamas to Brazil (Kramer, 2003). The low numbers and patchy distribution of predators on Bermuda's reefs thus appear to demand higher levels of replication to assess trends in abundance to an adequate degree. The considerable variance around mean densities of even some common herbivores, however, may also reflect the use of a protocol like AGRRA, developed for use on continuous swathes of reef, not the patchy, morphologically-heterogeneous reefs of Bermuda.

MPA and control assemblages

At the broader level of species assemblages, equally-paltry evidence existed for differences in ecosystem structure or function between MPA's and control sites. While increased species diversity has been described for MPA's (Micheli and Halpern, 2005; Tittensor *et al.,* 2007), species richness at Bermuda MPA's and control sites matched almost exactly. Similarly, the proportions of total species comprising functional groups at protected and unprotected sites were highly comparable. This finding contrasts with observations that functional groups, such as piscivores, exhibited greater integrity and redundancy (in terms of species) in protected areas (Micheli and Halpern, 2005).

The lack of multivariate evidence for separate and distinct MPA and control assemblages in ordinations of both species density and abundance data, further suggests the absence of large-scale changes to ecosystem composition or function by habitat protection. If protection were a defining factor, we would perhaps expect MPA's to ordinate distinctly from control sites based on the direct enhancement of targeted commercial species as well as indirect effects on some non-target species (Ojeda-Martinez *et al.*, 2007; Watson *et al.*, 2007). Of course, if sampling was indeed insufficient as suggested by univariate power analysis, site means used for multivariate analyses may be similarly unrepresentative of actual species abundances. Nonetheless, the lack of any significant clustering whatsoever at least suggests that no consistent large-scale differences exist between MPA's and control sites. Ordination of sites based on abundances of multiple species thus probably reflects either "noise" related to uncertainty around means or the influence of other environmental factors on assemblages. It must be conceded, however, that MPA sites do disperse more widely in ordinations, perhaps reflecting a greater heterogeneity in species composition and/or abundance than in control sites. This difference in dispersion could be interpreted as locally-varied assemblage responses to protection resulting from differences in local ecosystem organization (Guidetti and Sala, 2007), but the limited ordinated-distances of MPA's from their associated control sites within the same region weakens this possibility. Indeed, it is also possible that the dissimilarity of MPA assemblages reflects not responses to protection, but the historic selection of diverse and complex sites for MPA creation.

Assessment of MPA effectiveness

In evaluating the effectiveness of existing MPA's as safeguards of ecosystem integrity, species diversity and populations of key fish species, we wish to answer several questions:

- Is data quality sufficient to infer the degree of conservation offered by MPA's?
- Do trends indicate conservation of ecological integrity?
- What factors account for the performance of MPA's?
- What modifications to current design might enhance the functioning of MPA's?

Data quality

The selection of sites in this study granted a representative view of Bermuda's MPA's and a valuable opportunity for comparison to previous studies. For instance, the fairly widespread distribution of MPA's across the reef platform allowed the capture of regional differences in reef ecosystems. Furthermore, the study sites chosen were all reefs whereas the majority of MPA's in Bermuda encompass shipwrecks which might confound comparisons via different rates of community recovery from grounding damage. Finally, site selection enhanced the quality of data by mirroring the sites selected by a prior study (MEP, unpublished technical report) at three of four MPA's, thus providing greater context for the interpretation of results.

The use of two surveying protocols offered complementary approaches that provided the means for quantitative estimates of density and biomass for some key species as well as additional data on the entire range of Bermuda reef species. While these protocols were a powerful combination for co-indicating trends, neither by itself provided fine resolution of differences between MPA's and control sites. Accordingly, the uniformly low power of AGRRA density metrics, even when sites and species of functional guilds were pooled, potentially compromised comparisons between protected and unprotected sites. Unfortunately, this effect was most pronounced for patchily distributed piscivores and commercial species, which are most likely to respond to protective measures. The implication of this poor resolution of trends is that, on Bermuda reefs, replicates within sites must be greatly increased to approach density estimates with appropriately lower variance. Analogous to the necessity for high sampling intensity in space, Gerber *et al.* (2007) found that several years of data were required for sufficient precision to make informed judgements about effectiveness of habitat protection. With this in mind, future comprehensive assessments of the effectiveness of Bermuda's MPA's would need to be on a far larger scale than this component study.

Despite the poor resolution of trends, data quality was sufficient to detect some differences in fish densities between MPA's and control sites. The possibility exists that further significant differences were obscured by high variances and low statistical power as some patterns in mean densities were suggestive of consistent differences but not statistically substantiated. Moreover, interpretation of the causes of differences in fish density were complicated if differences were detected among one pair of MPA and control sites, but missed in others. However, in the absence of statistical evidence, it is equally possible that differences between MPA and control densities truly did not exist for most species. Indeed, the resemblance of functional organization and assemblage structures in protected and unprotected areas offered some evidence that reef protection did not significantly alter fish populations. Furthermore, the prior study of these MPA's suggests this to be the case (MEP, unpublished technical report). We may thus draw certain limited conclusions from the data. Acknowledging inadequate replication, the many consistent similarities in community structure between protected and unprotected reefs allow us to conclude that we have detected differences where they are moderately large. This study of MPA effectiveness thus provides an assessment of any sizeable changes in community structure across sites, but not weak signals of protection effects.

Effectiveness of current spatial protection

Whether MPA's have succeeded in conserving the ecological integrity of Bermuda's reef fish assemblages largely depends upon the reasons why protected areas and non-protected areas appear to resemble each other. User group surveys, for example, report little evidence of degradation of physical habitat yet do see signs of illegal fishing in Bermuda's MPA's. No estimates exist for the magnitude of poaching, so it is unclear whether protected areas resemble unprotected ones because they are inadequately protected, because the entire rim-reef enjoys little fishing pressure, or because more subtle trends in abundances were not detected. For instance, Samoilys *et al.* (2007), found strict enforcement of no-take zones to most affect the success of local fish assemblage recovery. Bermuda's historic fishing pressure is implicated as at least one major factor in the limited response to protecting habitat by the contrast between the documented past abundance of serranids and lutjanids (Bardach and Menzel, 1956; Lavett-Smith, 1958) and the low densities described here and elsewhere (Smith *et al.*, 2002; MEP, unpublished technical report). The Marine Environment Programme (unpublished technical report) also attributed the low abundances of commercial species in MPA's to slow recovery of all populations from the over-exploitation of fish traps until 1990.

If historic fishing pressure has indeed precluded effective MPA functioning, the lack of an increase in exploited species commensurate with habitat protection may reflect the life history traits (*e.g.* fecundity, larval dispersion distances) and relative scarcity of those overexploited species. Of the large serranids, for example, only *Mycteroperca bonaci* has recovered to moderate populations, while others (*e.g. Epinephelus striatus)* still occur very rarely. Equal abundances of these commercial fish, species that should respond most to fishing prohibition, inside and outside MPA's would thus reflect populations of recovering species with insufficient fecundity, numbers or spatial protection to respond rapidly to protective measures. In such a scenario, MPA's would be judged to have preserved the ecological integrity of a recovering fish assemblage, but because of limitations set by life history traits of species not enhanced it. Before this position is adopted, however, better resolution of abundances trends as well as rates of illegal fishing in MPA's should be estimated to distinguish widespread trends in recovering fish populations from local cases of poor MPA enforcement.

The few cases of differences in densities between MPA's and control sites were not easily attributable to effects of habitat protection, which further obscures the role of MPA's in conserving ecological integrity. For example, differences in the abundances of some scarid species at MPA's and controls in some pairings but not others raised the question of whether natural variance among reefs or regions was greater than differences caused by habitat protection. Similarly, if species components of fish communities responded differently to protection in different regions, greater ambiguity would be assigned to assessing the effectiveness of habitat protection. Trends such as the abundance of adult *Sparisoma viride* and juvenile *Scarus taeniopterus* in MPA's provide tantalizing evidence for successful enhancement in MPA's of herbivores essential to coral reef health (Mumby *et al.,* 2007a). In the end, however, too many questions about response mechanisms are raised to offer conclusive proof of effective MPA functioning. Along the lines of prior assessments (MEP, unpublished technical report), we might –

with appropriate caveats regarding low statistical power - view this assessment as providing no further evidence for effective enhancement of fish populations by MPA's.

Bermuda's MPA's were not originally conceived to preserve representative habitats or fish populations on the reef platform, but rather aimed to prevent anchor damage to popular dive sites. For this reason, regardless of current MPA functioning, modifications to the current system based on the distributions of key species, functional groups and assemblages might better conserve ecosystem integrity. For instance, it seems unlikely that herbivores, protected under current law, would benefit directly from further spatial protection, though indirect trophic effects from greater ecosystem protection might occur. In contrast, as most commercial species occur at low densities and appear not to have benefited greatly from habitat protection, moulding MPA sizes and configurations to life and distributional characteristics of these species may hold promise for their future enhancement. For example, species with disparate juvenile and adult habitat (*i.e.* most commercial species – see Chapter 2), higher mobility (*e.g.* carangids and some lutjanids) or long-distance larval dispersal (*e.g.* serranids) might benefit from larger reserves or networks of protected key habitats (Botsford *et al.*, 2003). The identification of population sources and sinks and nursery habitats would be essential in this endeavour and would further inform configuration of protected areas (see Chapter 2).

This study has tentatively demonstrated a similarity in fish assemblages inside and outside protected areas. Whether this similarity reflects current levels of MPA enforcement or the interaction of MPA configurations and ecological characteristics of Bermuda's fish assemblages cannot be addressed by this study. While much greater levels of sampling are essential to achieving confirmation of these indications, results suggest that large enhancements of fish populations are not initiated by current spatial management practices. Accordingly, in Chapter 2, we examine the spatial characteristics of fish assemblages across the platform to explore the possible modification and enhancement of Bermuda's MPA programme.

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Chapter 2

Evaluating Current Management Practices for Spatial Protection of Bermuda Fish Populations: Identifying Under-Represented and Critical Habitats

Introduction

Response of fish populations to over-exploitation and recent protection

The closure of the fish pot trap fishery in 1990 was another step forward in Bermuda's rich history of progressive marine resource management. Although the ban on this gear type came only after considerable declines in populations of reef fish (Butler *et al.,* 1993), its implementation appears to have halted further losses (Hodgson, 2000). In addition, several other forward-looking measures of ecosystem management have accompanied the fish pot ban. For example, the current no-take status of all scarids is a rare example among western Atlantic countries of protecting herbivores in coral reef communities (Aronson and Precht, 2006). Indeed, the prohibition on harvesting these key species may have spared these key herbivores from overexploitation and prevented the phase shifts towards the macroalgal dominance observed on many Caribbean reefs in the last few decades (Mumby *et al.,* 2006).

Subsequent to the fish pot ban, the protected status of most large serranids (*Epinephelus striatus, E. morio, Alphestes afer, Mycteroperca venenosa, M. microlepis,* and *M. tigris*) was spurred by the virtual removal of these apex predators from Bermuda's reefs and further demonstrates Bermuda's steps towards comprehensive ecosystem management. The additional seasonal-closure of two serranid spawning grounds (principally *Epinephelus guttatus*) has probably also prevented the demise of populations of the remaining viable species. Combining these restrictions on fish harvest with the protected status of all corals since 1978 and two sizeable coral reserves, the legislative regime controlling Bermuda's reef system now resembles that of a marine park; the principle exception being the acceptance of fishing by hook and line for more common species. However, despite these progressive measures, fish assemblages still bear the signs of historical overexploitation and only gradual recovery (MEP, unpublished technical manuscript).

Immediately following the closure of the trap fishery, the Division of Fisheries instituted a visual census programme to monitor the recovery of coral reef fish populations with monthly surveys at four sites outside the rim reef. Our understanding of temporal trends in fish abundance and community structure of recovering assemblages are thus limited to only certain habitat types and based only on few sites. Nonetheless, the data collected were suitable for analysis of some trends in the fish selected taxa. For example, the abundance of the five parrotfish species being monitored has increased by a factor of 2 to 3 over the baselines established in the first year of the study (Hodgson, 2000). However, this same study found that *Cephalopholis fulva*, the only commonly recorded grouper species, had not exhibited any significant change in abundance since the fish trap closure.

The likely recovery of some scarids but sustained low abundance of serranids suggests that while fish assemblages are in a state of recovery, some species still lag behind. Whether shifts from historic community composition to that of today can be reversed remains to be seen.

Coral reef communities respond to disturbance in complex, non-linear ways such that the loss of certain key fish species or functional guilds (herbivores, piscivores, planktivores, invertivores) can have indirect effects not only on the whole fish community, but can also affect the entire ecosystem. For example, while heavy fishing pressure in Bermuda obviously reduced abundances of many species directly, a few non-target species appear to have increased in number. Notable amongst these were *Balistes capriscus,* and *Kyphosus sectatrix* (Ward, pers. comm.), whose populations may have been enhanced by reduced competition, reduced predation, or other complex food web shifts. However, other indirect effect of selective overexploitation may be more insidious. In particular, reductions of certain herbivores on reefs around the globe have been reported to negatively impact coral and enhance algal cover (Munro and Williams, 1985; Roberts, 1995). Similarly, predators are thought to exert considerable influence on sustaining the integrity of all levels of reef ecosystems (*e.g.* Mumby *et al.,* 2006). Meanwhile, the reverse relationship – the strong coupling of fish assemblage health of that to benthic integrity – may readily be seen by the catastrophic alterations of fish assemblages during intense coral bleaching events (Graham *et al.,* 2007). Recovery and maintenance of productive and resilient coral reef ecosystems thus relies on effectively preserving not only components of fish and benthic communities but the full complement of trophic and ecological interactions among the species comprising this interrelated ecosystem. Protective measures must therefore target those areas and habitats with the greatest ecological value to key species and ecosystem function alike.

Towards ecosystem conservation and enhancement through spatial protection

Marine Protected Areas (MPA’s hereafter), when tailored to the needs of local fish assemblages, can initiate recovery and complement traditional fisheries management by addressing multiple and interacting species through spatial protection (Botsford *et al.*, 2003; Baskett *et al.,* 2007). In effect, the prohibition of fishing and other damaging activities, such as anchoring, conserves ecosystem integrity by safeguarding all ecological components evident at the scale of the reserve. Specific indirect benefits of such spatial management may also include prevention of biodiversity loss from anthropogenic disturbance (Micheli *et al.,* 2004), resilience to increasing incidences of coral bleaching and diseases (Hughes *et al.,* 2003), and enhanced fisheries production outside reserve boundaries (Guidetti, 2007). In contrast, arrays of single-species fisheries regulations may not preserve the diversity of functional and ecological relationships comprising an ecosystem (Pitcher, 2001).

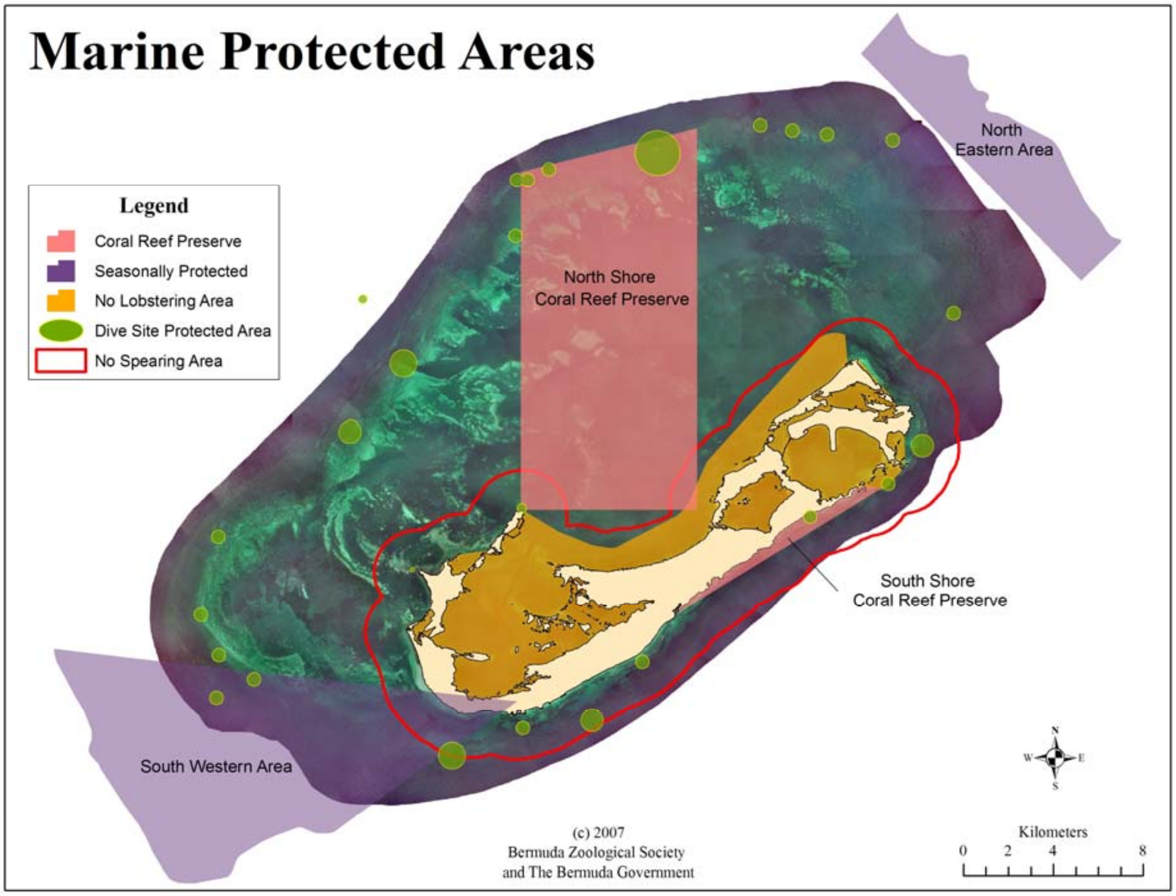

Fig. 1. Map designating current protected areas in on the Bermuda platform. Coral Reef Preserves (in pink) afford the least protection, with fishing permitted, yet prohibition of harvesting benthos. Seasonally Protected Areas (in purple) prohibit fishing between May 1st and August 31st to protect spawning serranids. Finally, fully protected MPA's (in green) offer mooring buoys to minimize anchor damage and prohibit any harvest.

Currently, Bermuda hosts 31 small no-take MPA's, two seasonal no-take zones, spearfishing and lobstering exlusion zones, and two coral reef preserves where fishing is permitted but all benthos are protected (Fig. 1). Though numerous, these reserves only permanently protect ~ 2% of Bermuda's coral reef ecosystem. As the newly enacted Protected Species Act 2003 mandates the development of recovery plans for critical habitats that support threatened species, conservation of intact ecosystems through MPA's may prove highly relevant in the near future. Investigations for modifying Bermuda's MPA system are especially relevant for two additional reasons. First, current MPA's were not originally intended as fish refuges and thus may not reflect optimal design. Second, some evidence suggests that these MPA's may not be facilitating the recovery of ichthyofauna inside or outside reserves (Chapter 1; MEP, unpublished technical manuscript).

Despite considerable study of Bermuda's reef platform, knowledge of the spatial distributions of key species and fish assemblages requisite for informed MPA development do not exist. To date, Bermuda reef community research has focussed on small-scale patterns observed on a few individual reefs. Similarly, established fish census programs have concentrated on a few selected reef sites, and provide only limited data on critical nursery habitats and other ecologically significant areas. Indeed, the paucity of data for many taxa and regions precludes any assessment of broad trends in species composition and abundance across the reef platform. Only Ward (1999) has paid explicit attention to the spatial distributions of adult fish - in a study of Bermuda's seagrass beds - where he noted significant variation with location and season in assemblage composition. High variability has been demonstrated in hierarchical analyses of coral assemblages from other jurisdictions, such as the Florida Reef Tract (Murdoch and Aronson, 1999), which suggests that the current Bermuda reef community data is insufficient for extrapolation to the entire 750 km^2 platform. Greater resolution of small-scale variations in fish species and assemblages is thus essential to the continued management of coral reef ecosystems and harvestable resources.

This study seeks to address the gaps in spatial understanding and protection of Bermuda's coral reef ecosystem by (i) expanding the range of observations to include fringing, patch, rim and fore reef environments, (ii) dramatically increasing the number of sites sampled and, therefore, the resolution of spatial trends in fish populations and (iii) providing information for more comprehensive management and implementation of MPA's based on spatial distribution patterns of key species and species assemblages. Particular attention is paid to identifying habitats that foster high biodiversity, critical life history stages of threatened species, important ecological services and harvestable resources.

Methods

AGRRA surveys

The Atlantic and Gulf Rapid Reef Assessment (AGRRA) Version 4.0 fish protocol was adopted as the standard methodology for fish census studies (www.agrra.org). The AGRRA fish protocol, designed to provide a "snapshot" characterization of functionally important fish indicators is widely accepted throughout the Western Atlantic, so our adoption of this protocol allows for regional comparisons to be made. Surveys were conducted at four MPA's, six control sites and 94 synoptic sites across the reef platform. Fish were enumerated by two SCUBA divers, conducting a total of ten 30 x 2 meter belt transects per site. Transects were laid haphazardly and away from other divers to minimize any bias related to diver-activity. When surveying, divers swam slowly in one direction while an attached spool of transect line unraveled to signal completion of the transect. Surveyors received prior training using a T-bar to more accurately gauge fish size as well as model cut-out fish suspended in the water of varying sizes and body shapes for practice transects. Each transect survey took typically 6-8 minutes. Any fish encountered within a lane bounded one meter on either side of the transect and upwards to the surface was counted and assigned to one of six visually-estimated total length categories (<5cm, 10-20cm, 20-30cm, 30-40cm, and >40cm). The smallest size category captures juvenile fish and constitutes a modification of AGRRA 4.0 protocol. One other minor modification is the inclusion of *Cephalopholis fulva* and *Cephalopholis cruentata* (formerly named *Epinephelus fulvus* and *E. cruentatus*, respectively) as locally important serranids.

Fish densities were calculated for fish species and functional guilds (see Appendix 1 for groupings), standardized to $100m^2$. From these densities, biomasses were calculated by using species-specific power functions of the form $W = aL^b$ to convert lengths, derived from visually-estimated categories, into weights ($g/100m^2$; Marks and Klomp, 2003). As length categories comprised intervals and not exact measurements, lower and upper limit biomasses were estimated based on the lower and upper length limit of each size category.

REEF roving diver fish surveys

To ensure coverage of less abundant fish species and those not included in AGRRA protocol, a roving diver fish census was performed for each site using the Reef Environmental Education Foundation (REEF) protocol (Schmitt *et al*., 1998). This protocol involved a prolonged period of swimming observation (at least 30 minutes) where all fish species seen were recorded. Species were then categorized by abundance and recorded as “Single” (1 fish), “Few” (2-10 fish), “Many” (11-100 fish) or “Abundant” (>100 fish; REEF, 2007). REEF abundance scores were the product of REEF density scores of species across sites and their sighting frequency across sites. Density scores were calculated by the following equation:

$$D = \frac{[(nS \times 1) + (nF \times 2) + (nM \times 3) + (nA \times 4)]}{nS + nF + nM + nA}$$

where nS is the total number of sites for which the “Single” category was recorded for a species, nF for the “Few” category, nM for “Many” and nA for the “Abundant” category. Sighting frequency was the percentage of all sites at which a species was sighted. This particular method takes account of more cryptic species likely to be overlooked in the belt transects and is therefore a more valuable measure of species richness. REEF species groupings for functional guilds are listed in Appendix 2.

Statistical analysis:

Multivariate ordinations of AGRRA density (limited to AGRRA species) and REEF abundance data were performed using PRIMER 6 software. AGRRA density data was first square-root transformed to down-weight abundant species. REEF abundance data was analyzed untransformed as the abundance categories (*e.g.* "few": 2-10 fish) conformed to a quasi-logarithmic scale. Bray-Curtis similarity matrices were calculated for both REEF and AGRRA data prior to cluster analysis which used the complete linkage method. Clusters were then plotted on an MDS ordination at levels of similarity that revealed the most information about relationships among sites. SIMPROF routines on cluster analysis (9999 permutations) tested for the significance of internal structure in dendograms and thus which clusters had statistical evidence supporting their divergence.

ANOSIM routines were performed on square-root transformed AGRRA and untransformed REEF data, to test for differences among the *a priori* groupings of reef zone; fringing, patch, rim and fore reef. Subsequent One-way SIMPER routines were employed to establish which species contributed most to dissimilarities among significantly different reef zone species assemblages. Contributions were reported for only the ten and fifteen most influential species for AGRRA and REEF data, respectively.

Geospatial mapping:

Spatial distributions of densities of important AGRRA species were mapped using ArcMap 9.2. Prior to mapping, data were sorted into juvenile and adult categories based on species-specific lengths at ontogeny.

Results

Spatial variation in species richness

Of 122 species recorded from 100 sites across the Bermuda platform, a maximum of 103 were observed on patch reefs (Fig. 2). Rim reefs, as a whole, harboured a similar number of species to patch reefs. Substantially fewer species (~80) were found to inhabit fringing and fore reefs. However, as these reef zones were also the least sampled, this result may very well reflect insufficient sampling. Examining species richness at individual sites across the platform suggested that a string of rim reefs to the north, mostly concentrated in the North Shore Coral Reef Preserve, held the greatest numbers of species (Fig. 3). Many of these sites of high richness also corresponded to no-take MPA's (Snakepit, Eastern Blue Cut, and Southwest Breaker) or their associated control sites. Some patch reefs in the north, central lagoon exhibited comparable species richness to the MPA's and their controls, but these were interspersed with sites of lower richness.

Functional guilds were represented in relatively constant proportions of total species richness among fringing, patch, rim and fore reefs (Fig. 2). The relative composition of each reef zone corresponded closely to the overall composition across the platform, suggesting a somewhat constant scaling of species contribution to functional guilds across habitats. The most obvious differences occurred on fringing reefs, which had a higher proportion of herbivore species and a lower proportion of planktivores than other reef zones. Fore reef also revealed a lower proportion of piscivores. Within all reef zones, benthic invertivores were the most speciose guild, followed closely by herbivores. Redundancy was low for piscivores and least for planktivores.

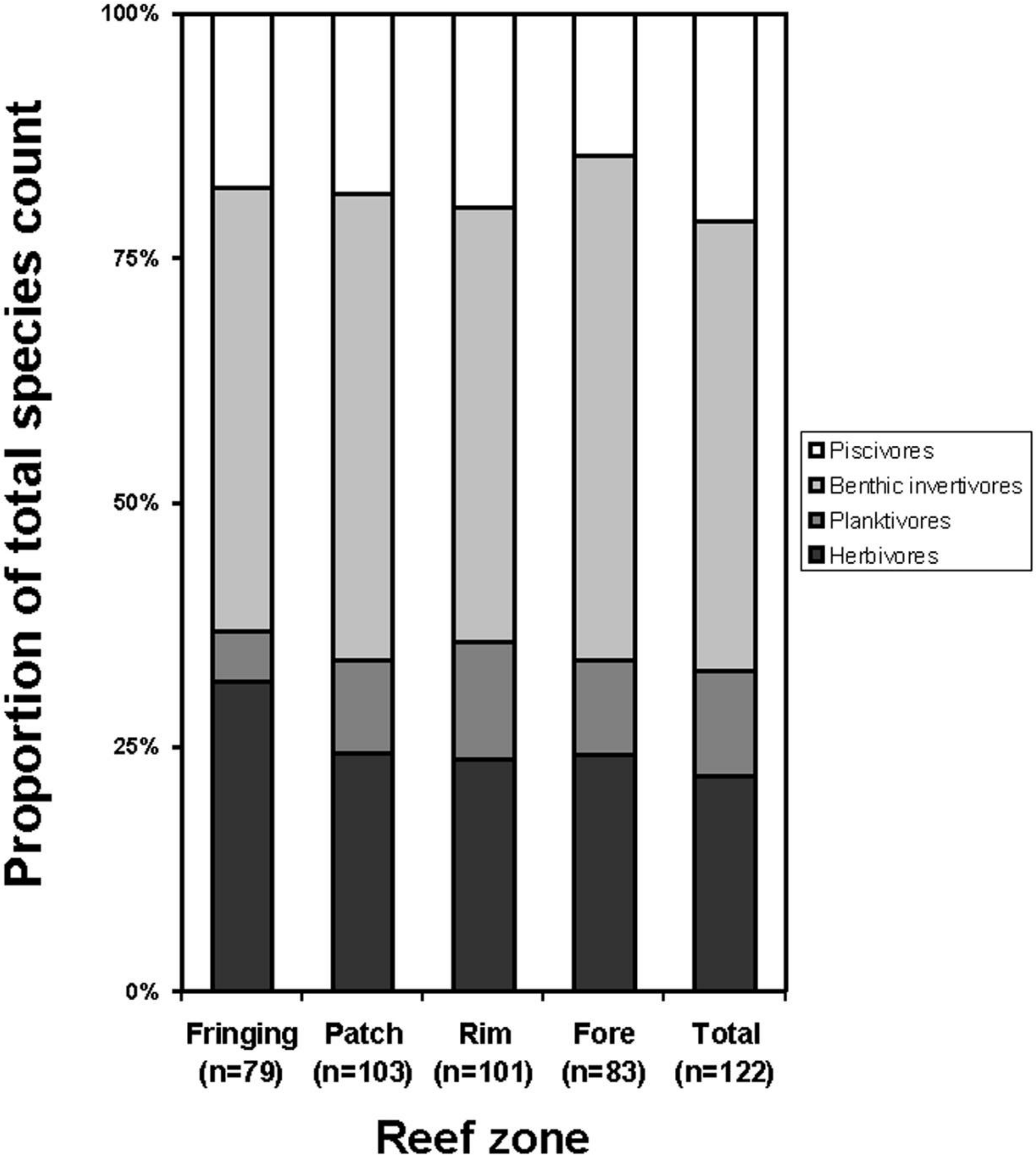

Fig. 2. Proportion of total species richness comprised by functional guilds (herbivores, benthic invertivores, planktivores and piscivores) at different reef zones and overall on the Bermuda reef platform. n denotes number of species observed.

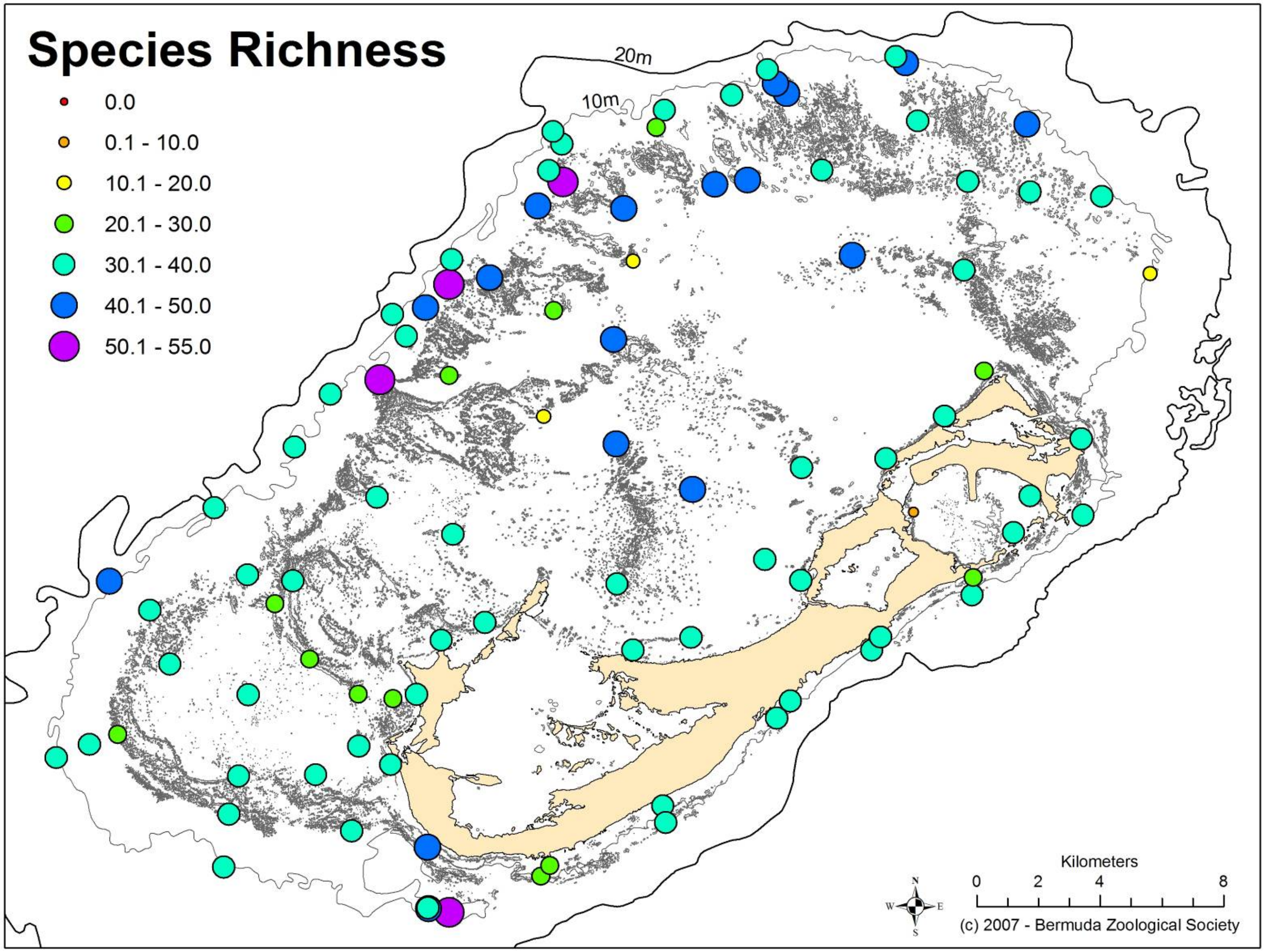

Fig. 3. Fish species richness derived from REEF roving diver surveys at 100 sites across the Bermuda reef platform.

Variation in community structure of reef zone assemblages

AGRRA data

Fish density and biomass estimates, derived from AGRRA surveys, suggested that considerable variation existed in the functional organization of the four reef zones. In particular, densities hinted that herbivores were relatively more numerically dominant on rim and fore reefs than fringing or patch reefs (Fig. 4). In constrast, planktivores were the dominant functional guild of inshore waters. Relative contributions of functional guilds to total biomass for the four reef zones indicated that herbivores on fringing and patch reefs contributed relatively more to total community composition by mass than was suggested by densities. Thus, these inshore reef zones might be characterized by low numbers of larger herbivores than rim and fore reef.

Absolute biomasses of herbivores in different reef zones suggested a similar pattern to the relative contributions of herbivores to assemblages at different reef zones (Fig. 5). However, absolute densities of herbivores indicated that actual numbers of herbivores were actually fairly comparable among reef zones. Invertivores were still most dominant in terms of number and biomass on fringing and patch reefs (Fig. 6). Piscivores occurred at remarkably similar densities in all reef zones (Fig. 7). Like invertivores, densities of commercial species also appeared to peak on fringing reef, though biomasses were fairly comparable among all reef zones (Fig. 8).

Although broad differences in functional organization were apparent among generalized reef zones, geospatial maps of relative functional guild contributions at each site indicated variation in community composition at more localized scales (Fig. 9). For example, while planktivores were of general significance to both fringing and patch reef communities, they had particularly high absolute densities and relative importance at sites in the central, north lagoon. Herbivores showed a similar tendency of dominance along the northern rim of the reef platform. In contrast, invertivores and piscivores showed only weak indications of such regional dominance.

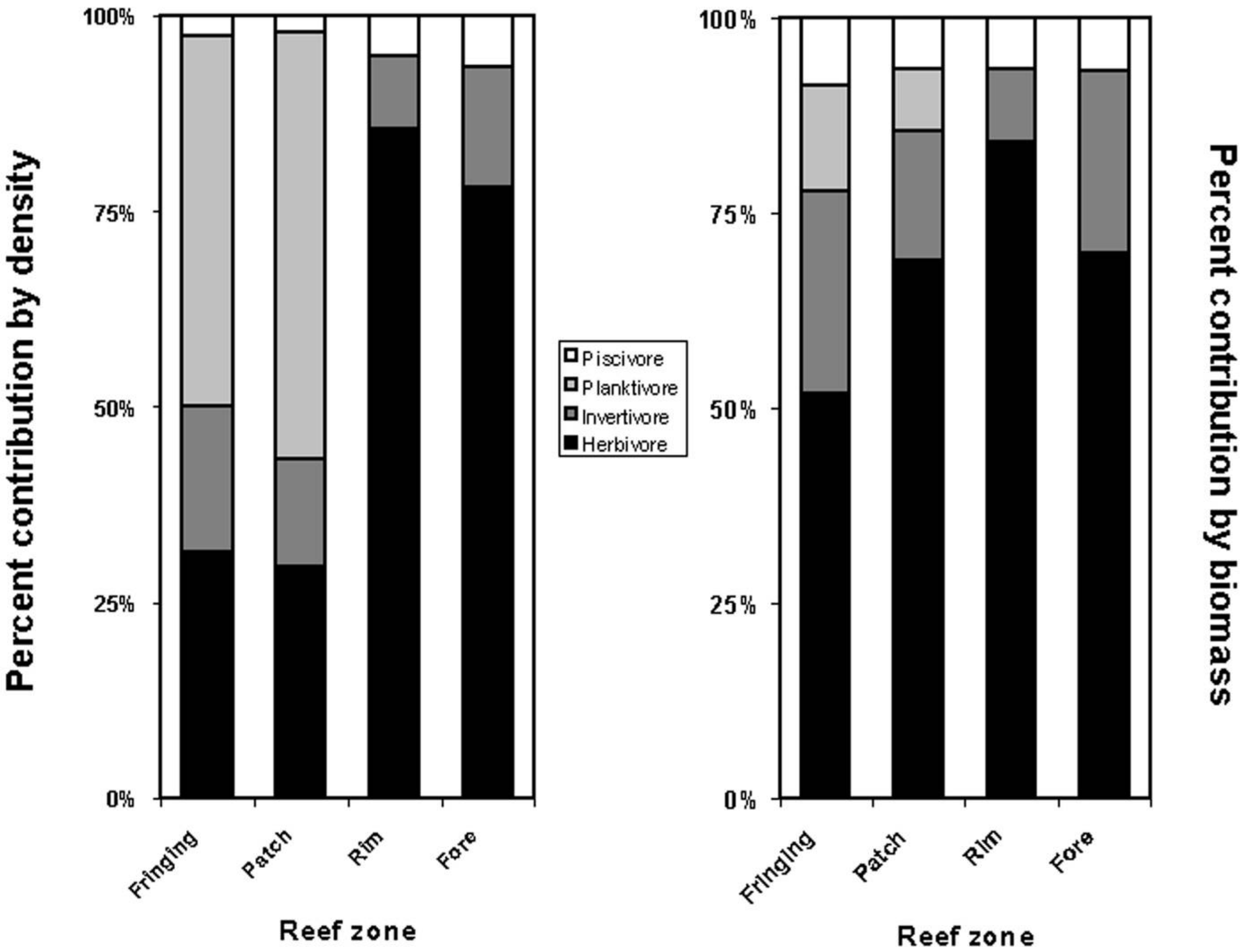

Fig. 4. Proportion of total density (at left) and total biomass (at right) comprised by functional guilds (herbivores, benthic invertivores, planktivores and piscivores) at different reef zones on the Bermuda reef platform. Data derived from AGRRA surveys at 104 sites.

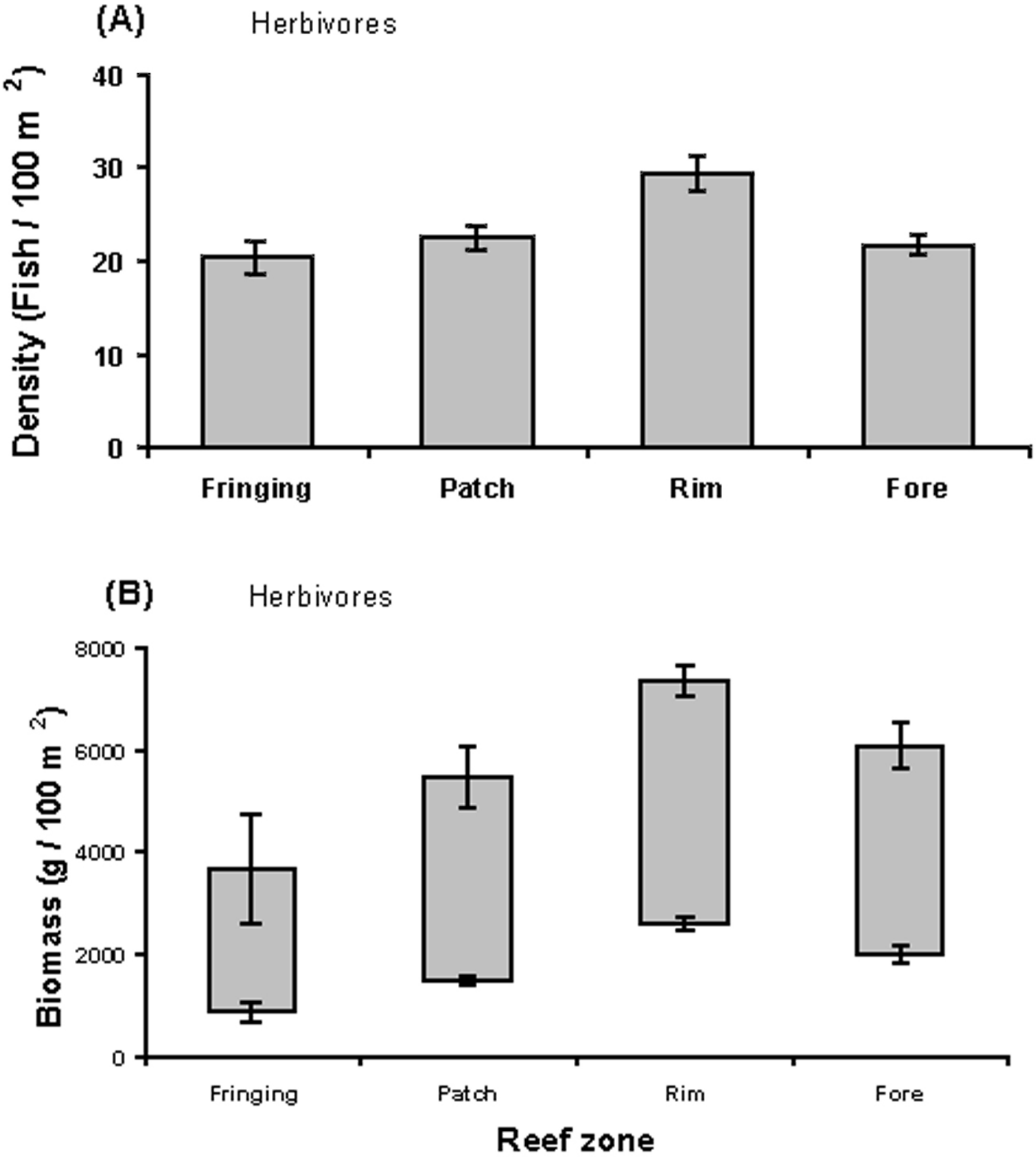

Fig. 5. Mean **(a)** density and **(b)** biomass of herbivores at fringing, patch, rim and fore reefs, derived from AGRRA survey data at 104 sites. Biomass reported includes lower and upper possible limits, calculated from minimum and maximum lengths in AGRRA protocol size categories. Data are means ± standard error.

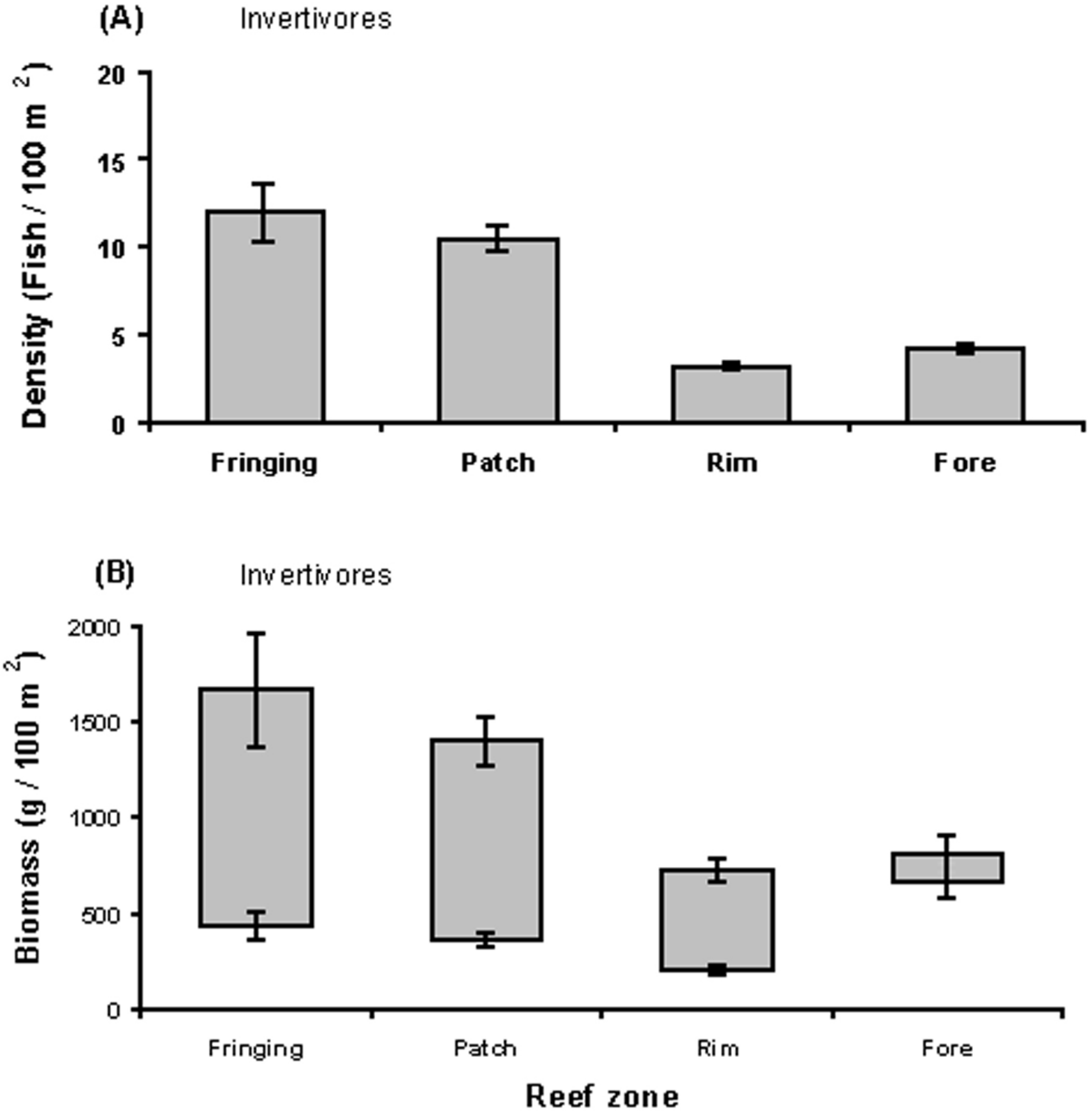

Fig. 6. Mean **(a)** density and **(b)** biomass of invertivores at fringing, patch, rim and fore reefs, derived from AGRRA survey data at 104 sites. Biomass reported includes lower and upper possible limits, calculated from minimum and maximum lengths in AGRRA protocol size categories. Data are means ± standard error.

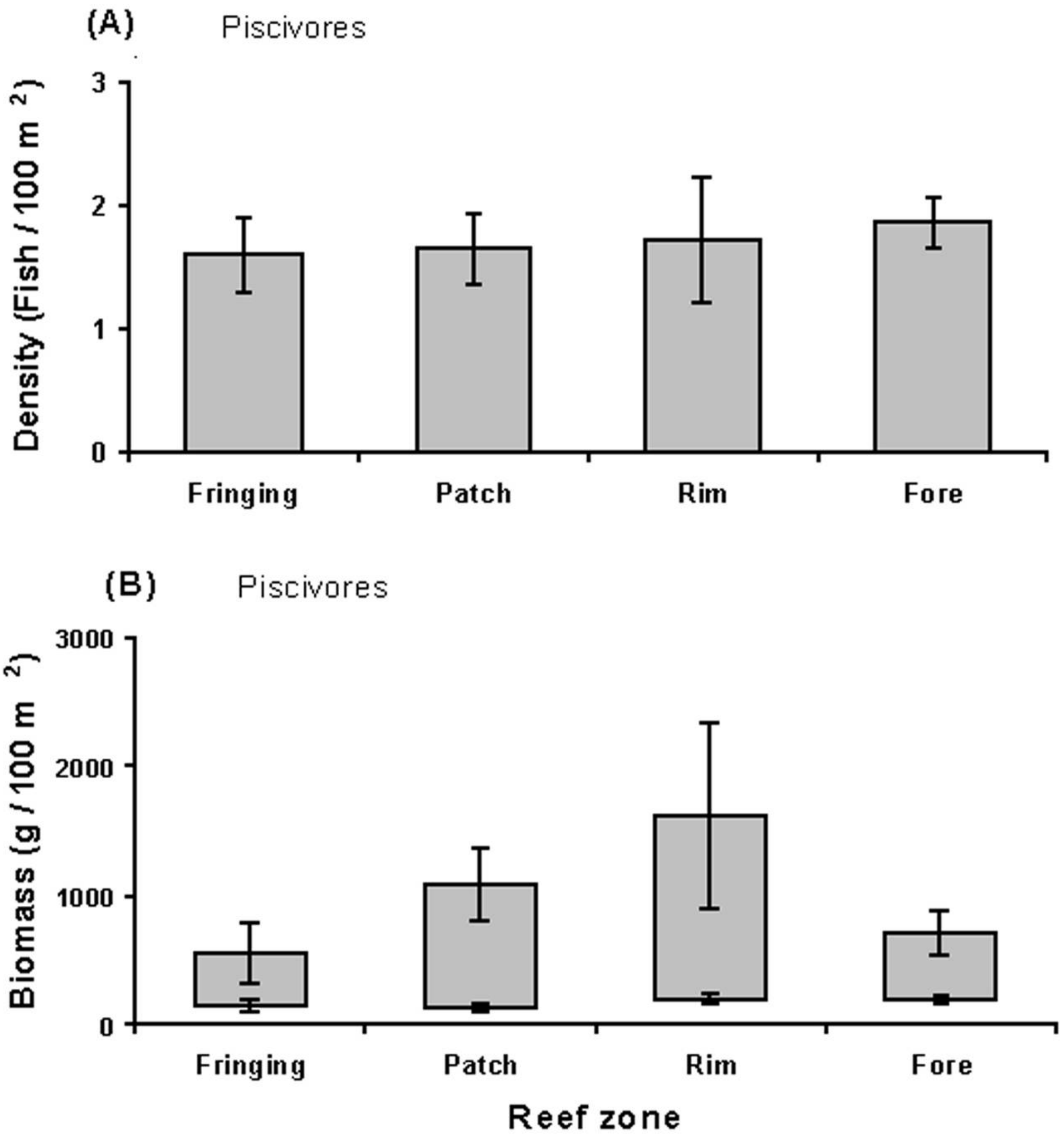

Fig. 7. Mean **(a)** density and **(b)** biomass of piscivores at fringing, patch, rim and fore reefs, derived from AGRRA survey data at 104 sites. Biomass reported includes lower and upper possible limits, calculated from minimum and maximum lengths in AGRRA protocol size categories. Data are means ± standard error.

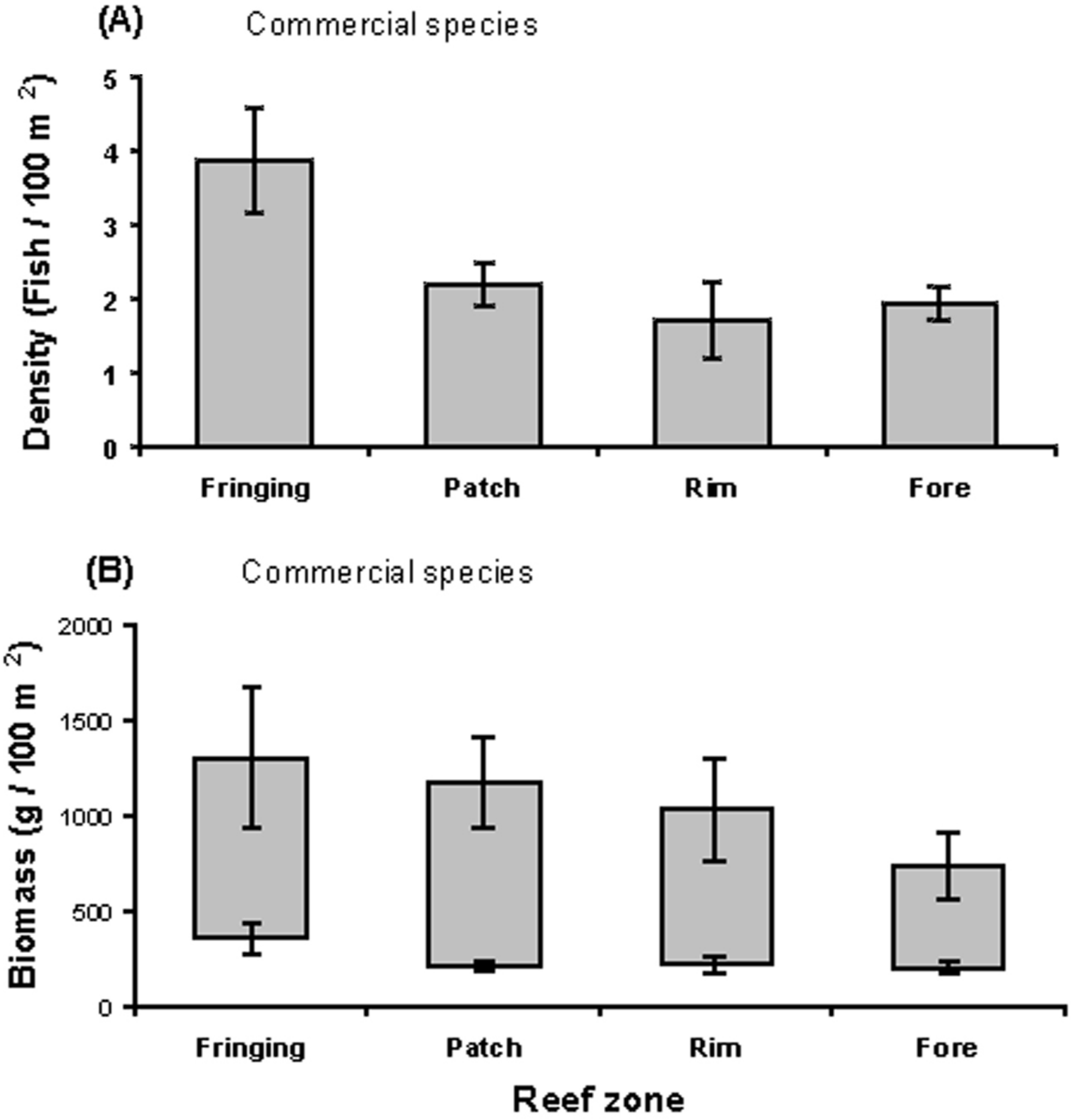

Fig. 8. Mean **(a)** density and **(b)** biomass of commercial species at fringing, patch, rim and fore reefs, derived from AGRRA survey data at 104 sites. Biomass reported includes lower and upper possible limits, calculated from minimum and maximum lengths in AGRRA protocol size categories. Data are means ± standard error.

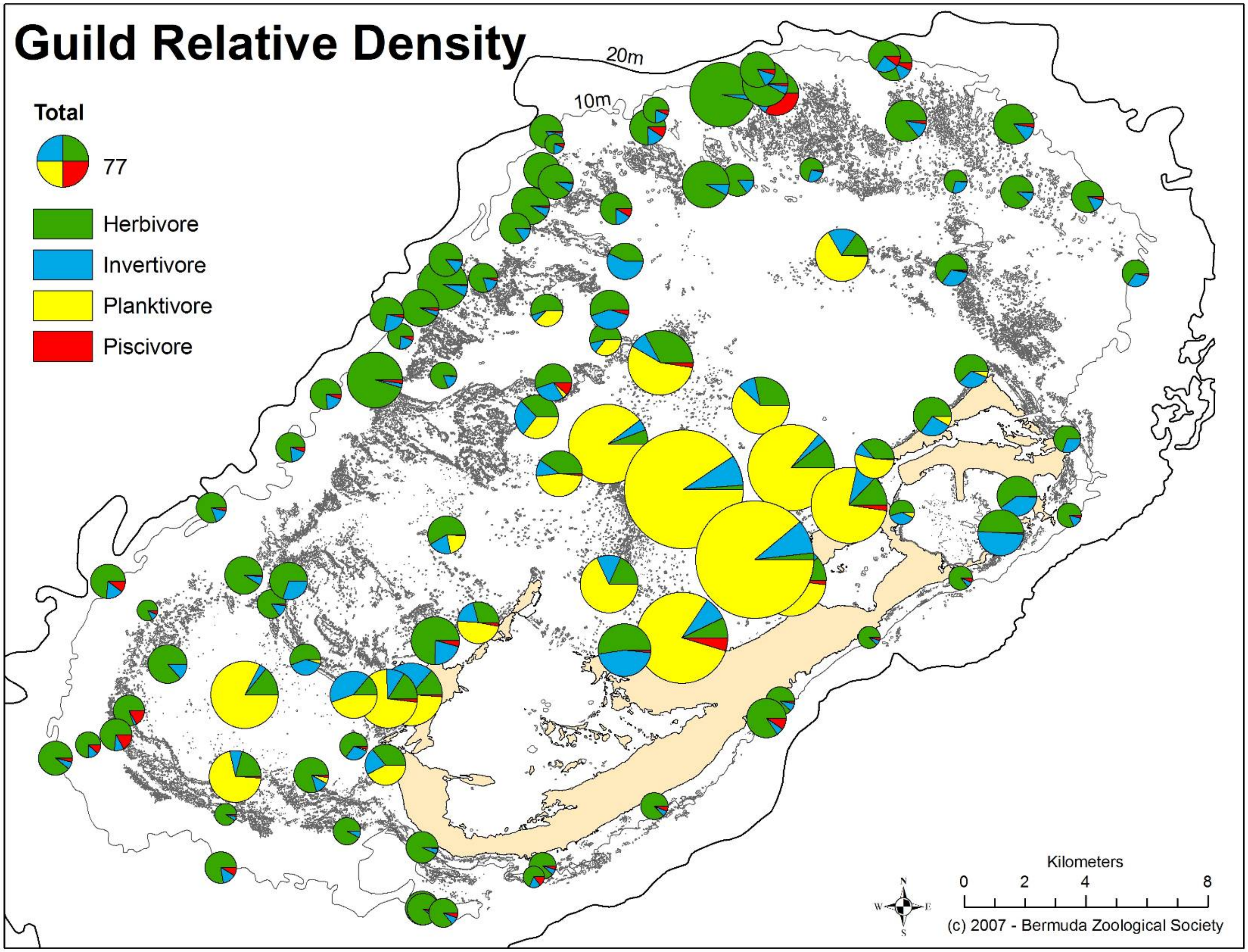

Fig. 9. Relative density, derived from AGRRA surveys, of functional guilds at sites across the Bermuda platform.

Spatial distributions of functional guilds across the reef platform were a response to combinations of three generalized distributions in species that comprised guilds. Specifically, species were generally distributed with either (i) peak density on fringing and patch reefs *i.e.* lagoonal (Fig. 10), (ii) uniform density among all reef zones *i.e.* lagoonal and offshore (Fig. 11) or (iii) peak density on rim and fore reefs *i.e.* offshore (Fig.12). Table 1 lists species commonly recorded on AGRRA surveys and their approximate distributions across the reef platform.

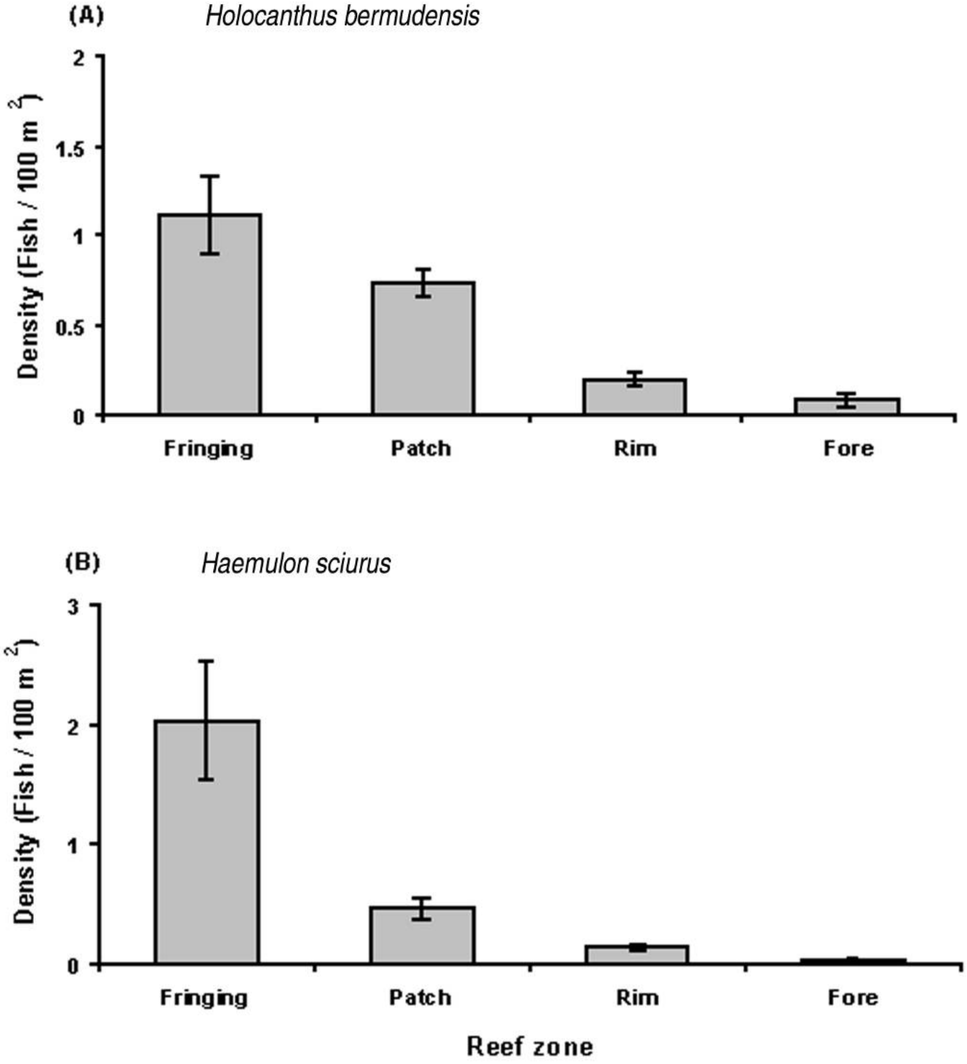

Fig. 10. Densities of **(a)** *Holocanthus bermudensis* and **(b)** *Haemulon sciurus*, derived from AGRRA surveys, as examples of species with peak density on lagoonal reefs.

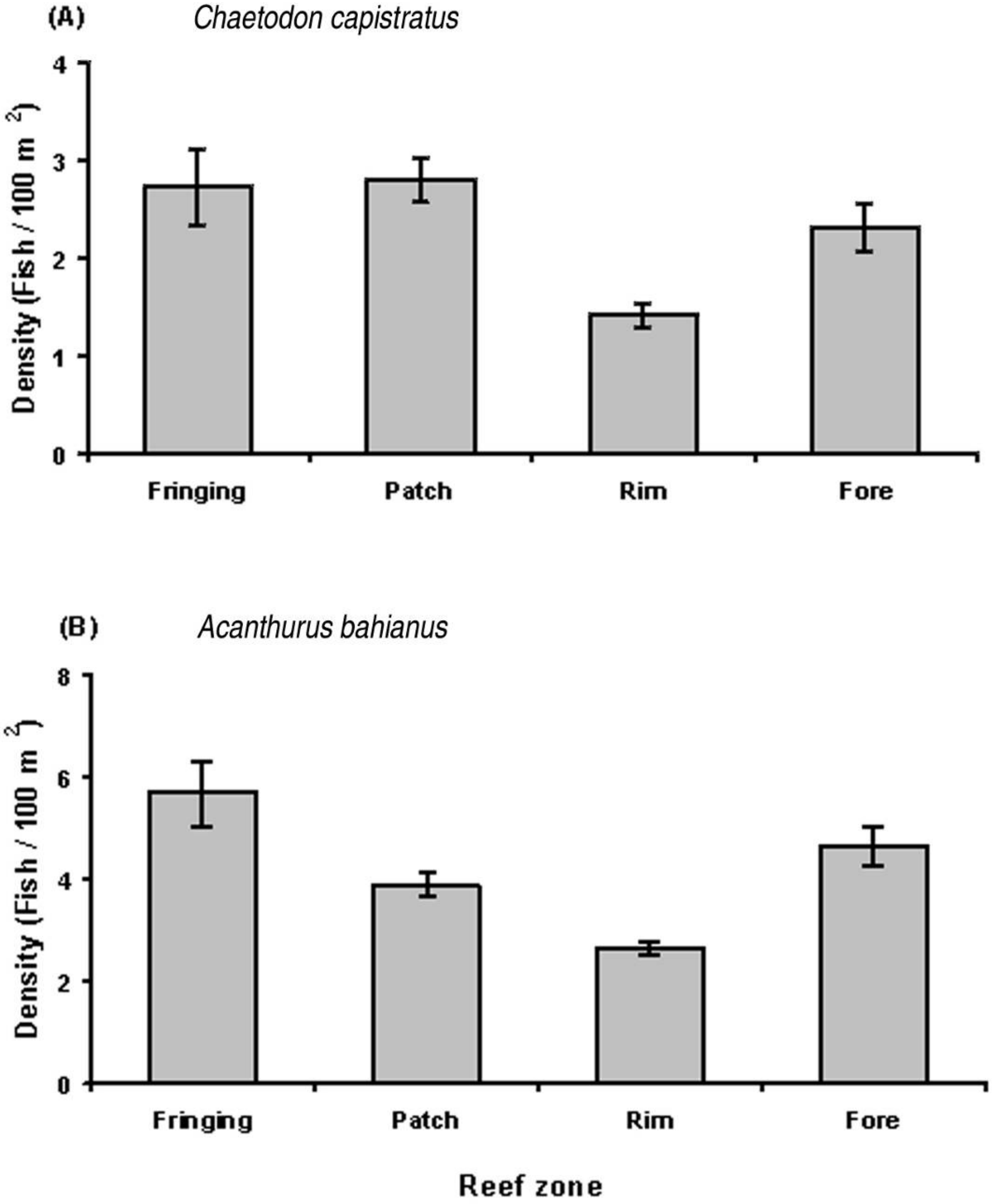

Fig. 11. Densities of **(a)** *Chaetodon capistratus* and **(b)** *Acanthurus bahianus*, derived from AGRRA surveys, as examples of species with relatively uniform densities on both lagoonal and offshore reefs.

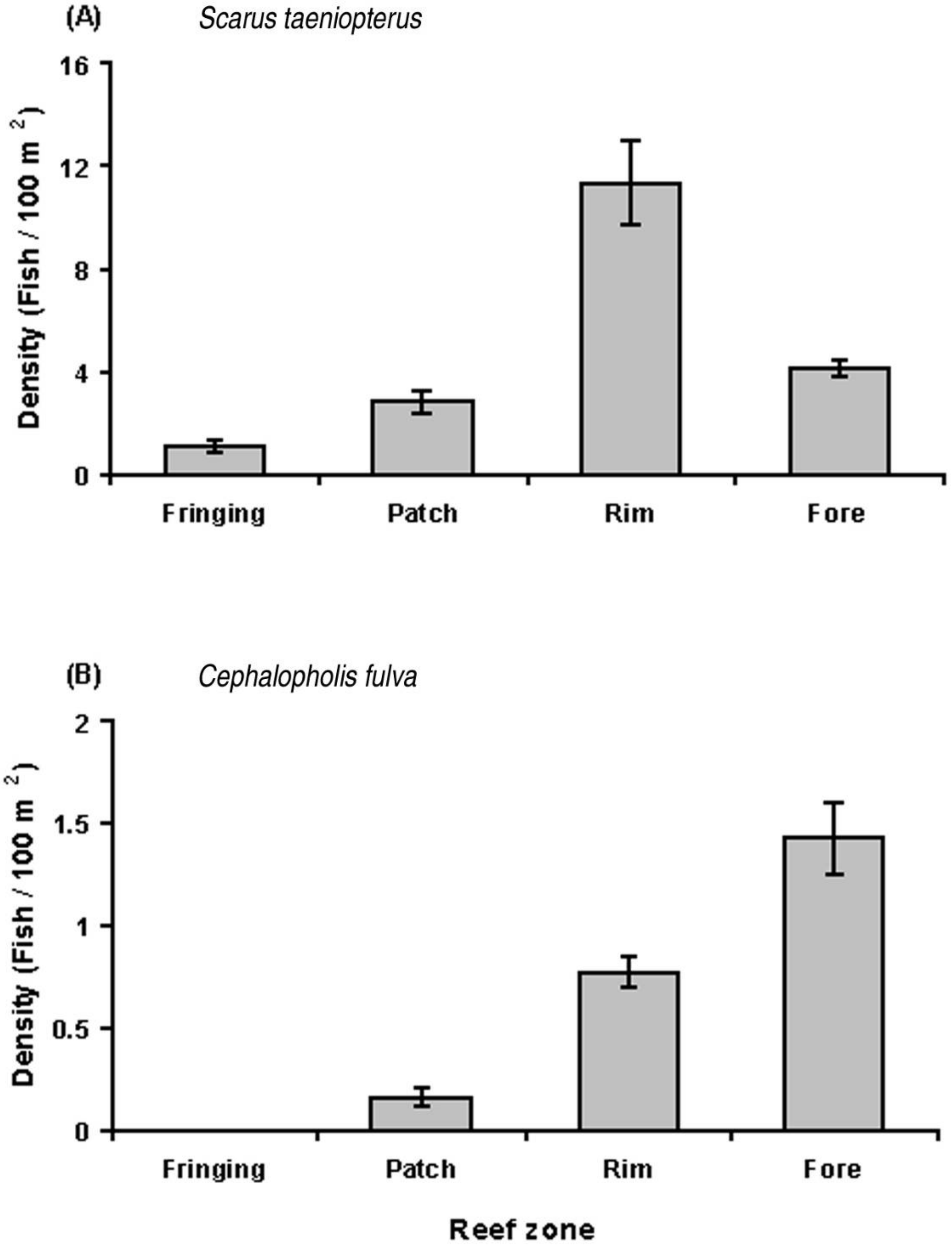

Fig. 12. Densities of **(a)** *Scarus taeniopterus* and **(b)** *Cephalopholis fulva*, derived from AGRRA surveys, as examples of species with peak density on offshore reefs.

Table 1. Generalized Distributions of Key Species, Based on AGRRA Densities Across the Bermuda Platform.

Lagoonal	**Offshore**	**Lagoonal and Offshore**
Scarus guacamaia *Scarus inserti* *Acanthurus chirurgus* *Stegastes variabilis/leucostictus* *Chaetodon ocellatus* *Holocanthus bermudensis* *Haemulon sciurus* *Haemulon flavolineatum* *Haemulon aurolineatum* *Lachnolaimus maximus* *Lutjanus synagris* *Lutjanus griseus* *Ocyurus chrysurus*	*Sparisoma aurofrenatum* *Scarus taeniopterus* *Scarus vetula* *Acanthurus coerulus* *Microspathodon chrysurus* *Cephalopholis fulva*	*Sparisoma viride* *Sparisoma chrysopterum* *Acanthurus bahianus* *Chaetodon capistratus* *Epinephelus guttatus*

Multivariate ANOSIM procedures tested whether the varied spatial distributions of individual species resulted in significant differences in assemblage structure among the four reef zones. Results reinforced the trend suggested by univariate plots; that these differences occurred most consistently between the lagoonal reef types (fringing, patch) and the offshore reef types (rim, fore). Only fringing-patch and rim-fore reef pairings did not exhibit highly significant differences (Table 2). These differences indicated considerable assemblage heterogeneity between all habitats that were not adjacent, with the single exception of adjacent patch and rim reef zones which differed significantly. The marginally non-significant rim-fore reef pairing indicates that some variation, though not statistically resolved, may exist across the border of those adjacent habitats also.

Table 2. Results of ANOSIM Comparing AGRRA Species Densities Among Reef Zones on the Bermuda Reef Platform.

Reef zone comparison	**R-statistic**	**p-value**
Overall	0.350	**0.0001**
Fringing - patch	0.051	0.228
Fringing - rim	0.783	**0.0001**
Fringing - fore	0.815	**0.0001**
Patch - rim	0.434	**0.0001**
Patch - fore	0.320	**0.0001**
Rim - fore	0.111	0.052

One-way SIMPER routines, which identified the greatest sources of variation among fish assemblages, also suggested that functional organization varied across reef zones concurrent with differences in assemblage composition (Tables 3-6). *Haemulon aurolineatum* proved to contribute most to the dissimilarity between significantly different reef zones. The ratio of dissimilarity to standard deviation was high when fringing reef assemblages were compared to rim and fore reef assemblages, but less so when those offshore assemblages were compared to that of patch reefs. The lower ratio, and thus higher standard deviation, when patch reefs were compared result from the more patchy distribution of *H. aurolineatum* on those reefs compared to on fringing reefs (Fig. 38). *H. aurolinateum* thus accounted for much of the assemblage differences between inshore and offshore reefs, but had less discriminatory power on patch reefs owing to the absence of this species on patch reefs far from shore. The simultaneous ecological influence of this species may clearly be seen its sole responsibility for the inshore dominance of the planktivore guild. Again, this dominance was particularly evident at sites to the west end of the island and in the central north lagoon (Figs. 9, 38).

Scarus taeniopterus and *S. inserti* also consistently contributed to differences in assemblages along a gradient from inshore to offshore (Tables 3-6). *S. taeniopterus* was most characteristic of rim and fore reefs, while the opposite trend was true of *S. inserti*, which peaked in abundance on lagoonal reefs. The acathurids, *Acanthurus bahianus* and *A. chirurgus*, were additional, important herbivores that peaked in abundance on fringing and patch reefs. Other significant herbivores, such as *Scarus vetula, Acanthurus coerulus, Sparisoma viride,* and *Microspathodon chrysurus,* appeared to be most characteristic of rim and fore reef, where they greatly influenced the structure of assemblages there. The net effect of the finer distributions of these species was the apparent repositories of the herbivore functional guild on rim and fore reef to the north of the lagoon (Fig. 9).

Table 3. Results of One-way SIMPER Analysis Comparing the Contribution of the Ten Most Influential Species to the Dissimilarity of Fringing and Rim Reef Assemblages. AGRRA densities are square root transformed. Average dissimilarity over 9999 permutations between assemblages was 54.47%.

Species	**Rim density**	**Fringing density**	**Dissimilarity / St. Dev.**	**% Contribution**
Haemulon aurolineatum	0.40	4.14	1.14	16.63
Scarus taeniopterus	2.61	0.94	1.03	7.89
Scarus inserti	1.02	2.31	1.07	6.71
Acanthurus coerulus	1.37	0.31	1.76	4.90
Haemulon flavolineatum	0.80	1.92	1.16	4.86
Acanthurus bahianus	1.46	2.27	1.36	4.65
Scarus vetula	1.96	0.94	1.85	4.53
Microspathodon chrysurus	1.11	0.17	2.05	4.12
Haemulon sciurus	0.23	1.14	1.32	3.92
Sparisoma viride	1.69	0.85	1.61	3.73

Table 4. Results of One-way SIMPER Analysis Comparing the Contribution of the Ten Most Influential Species to the Dissimilarity of Fringing and Fore Reef Assemblages. AGRRA densities are square root transformed. Average dissimilarity over 9999 permutations between assemblages was 52.62%.

Species	**Fringing density**	**Fore density**	**Dissimilarity / St. Dev.**	**% Contribution**
Haemulon aurolineatum	4.14	0	1.14	16.86
Scarus inserti	2.31	0.94	1.12	7.13
Cephalopholis fulva	0	1.16	2.68	5.35
Haemulon flavolineatum	1.92	0.72	1.22	5.31
Scarus taeniopterus	0.94	2.01	1.86	4.99
Acanthurus coerulus	0.31	1.33	1.43	4.95
Haemulon sciurus	1.14	0.06	1.47	4.68
Acanthurus chirurgus	1.16	0.33	1.45	4.14
Acanthurus bahianus	2.27	2.02	1.17	3.74
Microspathodon chrysurus	0.17	0.86	1.62	3.30

Table 5. Results of One-way SIMPER Analysis Comparing the Contribution of the Ten Most Influential Species to the Dissimilarity of Patch and Rim Reef Assemblages. AGRRA densities are square root transformed. Average dissimilarity over 9999 permutations between assemblages was 49.02%.

Species	Patch density	Rim density	Dissimilarity / St. Dev.	% Contribution
Haemulon aurolineatus	3.83	0.40	0.87	17.18
Scarus taeniopterus	1.43	2.61	1.02	8.17
Scarus inserti	2.51	1.02	1.26	8.15
Haemulon flavolineatus	2.16	0.80	1.26	6.72
Microspathodon chrysurus	0.28	1.11	1.86	4.43
Acanthurus coerulus	0.65	1.37	1.56	4.00
Scarus vetula	1.30	1.96	1.57	3.85
Chaetodon capistratus	1.55	1.05	1.00	3.74
Acanthurus chirurgus	0.84	0.65	1.06	3.61
Cephalopholis fulva	0.09	0.78	1.70	3.54

Table 6. Results of One-way SIMPER Analysis Comparing the Contribution of the Ten Most Influential Species to the Dissimilarity of Patch and Fore Reef Assemblages. AGRRA densities are square root transformed. Average dissimilarity over 9999 permuations between assemblages was 47.64%.

Species	Patch density	Fore density	Dissimilarity / St. Dev.	% Contribution
Haemulon aurolineatum	3.83	0	0.85	17.16
Scarus inserti	2.51	0.94	1.33	8.61
Haemulon flavolineatum	2.16	0.72	1.34	7.29
Cephalopholis fulva	0.09	1.16	2.32	5.47
Scarus taeniopterus	1.43	2.01	1.39	4.41
Acanthurus coerulus	0.65	1.33	1.24	4.11
Microspathodon chrysurus	0.28	0.86	1.61	3.70
Chaetodon capistratus	1.55	1.30	1.09	3.61
Acanthurus chirurgus	0.84	0.33	0.95	3.61
Sparisoma aurofrenatum	1.03	1.56	1.51	3.23

Carnivores were seldom captured by AGRRA surveys and their virtual absence from the list of influential species to assemblage structure reflects their low densities. However, the piscivore, *Cephalopholis fulva*, partially drove differences between inshore and offshore assemblages. Its absence on fringing and patch reefs, except for a few occurences just inside the rim, made its presence on rim and fore reefs a distinguishing feature between those two broad assemblages (Fig. 42). Moreover, the peak in piscivory found on rim and fore reefs (Fig. 9, 7b) likely derives from the presence of this species. In contrast, the strong inshore association of the invertivore, *Haemulon sciurus,* makes the presence of these species a key difference from inshore to offshore reef habitats. Additionally, the presence of this species may account for a generally higher relative abundance of invertivores inshore suggested by AGRRA data (Fig. 9). *H. sciurus*, a commercial species, also appears to have a particular preference for fringing reefs in any sheltered, lagoonal areas (Fig. 36).

ANOSIM, SIMPER and geospatial maps of AGRRA data suggest that differences between inshore and offshore fish assemblages hinge on habitat preferences of some abundant and representative species of functional groups. The absence of most carnivores from the list of influential species implies that minor transformation of AGRRA data may be insufficient to illustrate the role of these species in differentiating assemblages. REEF data has the benefit of conforming to a quasi-logarithmic scale which may serve to highlight the roles of rarer species in distinguishing assemblages, as well as including abundant species that were not included in AGRRA protocol.

REEF data

Estimates of the relative abundance of functional guilds at difference reef zones, derived from REEF survey data, contrasted with indications from AGRRA data (Fig. 13). REEF abundance scores showed that herbivores were still the most numerically dominant guild on all reef types, but were represented in more comparable proportions in them. Furthermore, with the inclusion of all observed species, the relative abundances of other functional guilds were greater. These results thus indicate a greater similarity of functional composition among reef zones as well as a greater balance of contributions by guilds than suggested by AGRRA data.

Despite differences in functional composition estimates, ANOSIM comparisons of fish assemblage composition at different reef zones, derived from REEF fish abundance data, almost exactly replicated reef zone differences calculated from AGRRA data (Table 7). Again, all reef zones differed significantly from others except fringing-patch and rim-fore reef pairings. Assemblages again appear not to differ across boundaries of adjacent habitat except for between patch and rim reefs.

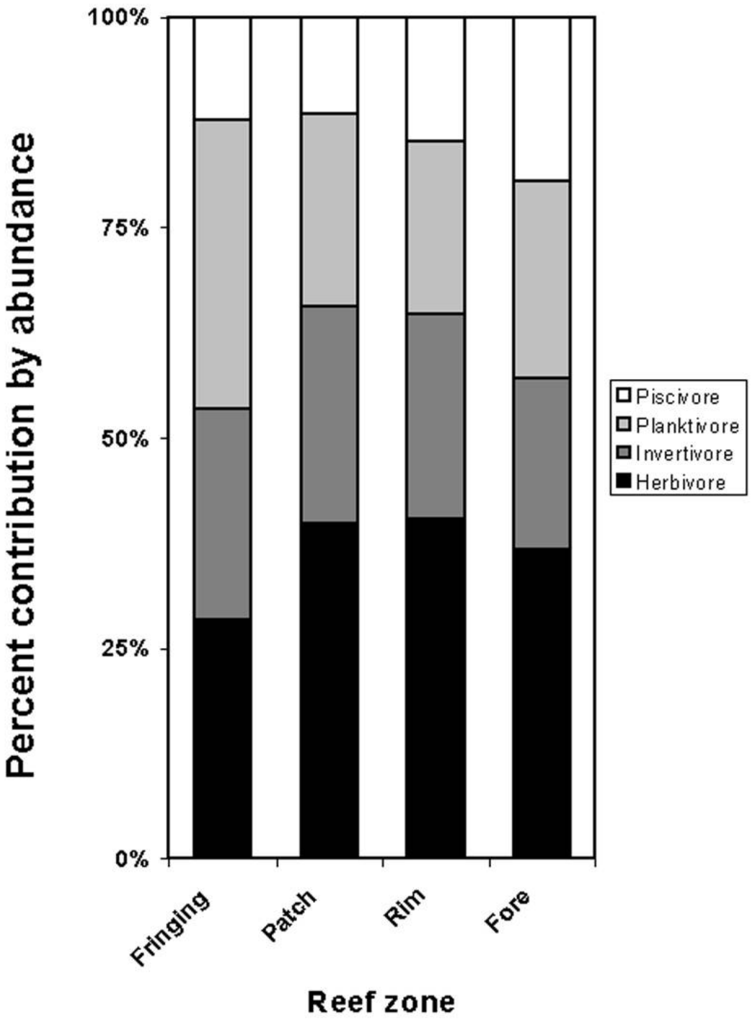

Fig. 13. Proportion of total abundance comprised by functional guilds (herbivores, benthic invertivores, planktivores and piscivores) at different reef zones on the Bermuda reef platform. Data derived from REEF roving diver surveys at 100 sites.

Table 7. Results of ANOSIM Comparing Species Densities from REEF Roving Diver Surveys Among Reef Zones on the Bermuda Reef Platform.

Reef zone comparison	**R-statistic**	**p-value**
Overall	0.396	**0.0001**
Fringing - patch	0.072	0.237
Fringing - rim	0.728	**0.0001**
Fringing - fore	0.811	**0.0001**
Patch - rim	0.427	**0.0001**
Patch - fore	0.490	**0.0001**
Rim - fore	0.197	0.200

Unlike with *Haemulon aurolineatum* in AGRRA data (Tables 3-6), no single species contributed disproportionately to the dissimilarity between assemblages. Instead, many species contributed more uniformly to the variation (Tables 8-11), probably reflecting the inclusion of many more species with REEF protocol. *H. aurolineatum* abundance still played a role in distinguishing inshore from offshore habitat, but was joined in that capacity by another abundant planktivore, *Thalassoma bifasciatum*. In contrast to *H. aurolineatum,* this labrid characterized rim and fore reefs rather than inshore reefs. The offshore presence of this species thus appears most responsible for the similar proportions of planktivory in the inner lagoon and on the rim suggested by REEF abundances (Fig. 13).

Abundances of invertivores derived from REEF data, which included many more species than AGRRA data, implied that the inshore dominance of invertivory was, in fact, an artifact of the limited number of species surveyed (Tables 8-11). In particular, while *Halichoeres bivittatus* abundance helped differentiate fringing reef assemblages from those further offshore, the offshore influence of non-AGGRA *Halichoeres garnoti,* and *Bodianus rufus* appeared to balance out the offshore dearth of invertivory suggested by AGRRA. Other inshore pomacentrids also appeared to contribute considerably to differences among assemblages. Specifically, high lagoonal abundances of *Stegastes planifrons* and *Stegastes leucostictus* were consistent features of assemblages on those reefs. Moreover, it is primarily the abundances of these species that account for the slightly higher proportions of invertivory on several inshore reefs off the west end of Bermuda (Fig. 9).

Similar to AGRRA data, SIMPER analysis of REEF abundances indicated the importance of herbivorous species in distinguished rim and fore reefs from fringing and patch reefs (Tables 7-10). The most abundant herbivores (*e.g. Microspathodon chrysurus, Scarus taeniopterus*, *Sparisoma aurofrenatum, Stegastes variabilis*) were again the most influential. Also concurring with AGRRA trends, rim sites at the northern, northwest and northeast boundaries of the North Shore Coral Reef Preserve appeared to be important to this functional guild (Figs. 9,1).

Greater relative abundances of piscivores in REEF data indicate that these surveys better captured the occurrence of carnivores on Bermuda's reefs than AGRRA surveys (Tables 8-11). Accordingly, the common serranid, *Cephalopholis fulva*, played a more obvious role in differentiating lagoonal assemblages from offshore groupings than with AGRRA data. The preference of offshore habitat by this species (Fig. 42) accounts almost exclusively for the relatively high abundances of the piscivore guild on rim and fore reef. The offshore northern and northwest regions were particularly important in this capacity (Fig. 9). In contrast to offshore reefs, the moderate abundance of piscivores on inshore reefs likely reflects the occurence of *Lutjanus griseus* and *Ocyurus chrysurus* (Figs. 45 - 46). While *Cephalopholis fulva* presence and absence exerted moderated influence on assemblage structure, the negligible influence of other piscivores in differentiating assemblages across reef zones parallels their low abundances on all reefs.

Table 8. Results of One-way SIMPER Analysis Comparing the Contribution of the Fifteen Most Influential Species to the Dissimilarity of Fringing and Rim Reef Assemblages. REEF abundances are untransformed. Average dissimilarity over 9999 permutations between assemblages was 53.78%.

Species	**Fringing abundance**	**Rim abundance**	**Dissimilarity / St. Dev.**	**% Contribution**
Halichoeres garnoti	0.22	2.68	2.45	2.98
Haemulon aurolineatum	2.44	0.12	1.68	2.83
Thalassoma bifasciatum	1.33	3.44	1.34	2.82
Microspathodon chrysurus	0.11	2.35	2.1	2.72
Cephalopholis fulva	0.11	2.29	2.26	2.62
Halichoeres maculipinna	0.22	2	1.72	2.26
Scarus taeniopterus	1.11	2.56	1.28	2.16
Halichoeres bivittatus	3	1.35	1.28	2.08
Coryphopterus - personatus/hyalinus	2.33	2.35	1.1	2.07
Stegastes planifrons	2.11	1.15	1.22	2.01
Stegastes leucostictus	1.89	1	1.27	1.99
Stegastes variabilis	1.78	1.24	1.25	1.97
Halichoeres radiatus	1.11	2.53	1.29	1.94
Sparisoma aurofrenatum	1.33	2.32	1.2	1.92
Bodianus rufus	0.67	1.91	1.63	1.89

Table 9. Results of One-way SIMPER Analysis Comparing the Contribution of the Fifteen Most Influential Species to the Dissimilarity of Fringing and Fore Reef Assemblages. REEF abundances are untransformed. Average dissimilarity over 9999 permutations between assemblages was 58.04%.

Species	**Fore abundance**	**Fringing abundance**	**Dissimilarity / St. Dev.**	**% Contribution**
Halichoeres bivittatus	0	3	5.04	3.52
Cephalopholis fulva	2.88	0.11	3.73	3.3
Halichoeres garnoti	2.59	0.22	2	2.83
Haemulon aurolineatum	0	2.44	1.72	2.8
Thalassoma bifasciatum	3.53	1.33	1.42	2.73
Microspathodon chrysurus	2.29	0.11	2.11	2.57
Scarus taeniopterus	3	1.11	1.29	2.38
Stegastes planifrons	0.41	2.11	1.39	2.33
Sparisoma aurofrenatum	2.82	1.33	1.19	2.17
Coryphopterus - personatus/hyalinus	1.06	2.33	1.3	2.16
Haemulon sciurus	0.41	2.11	1.65	2.09
Halichoeres maculipinna	1.88	0.22	1.57	2.08
Acanthurus chirurgus	0.82	2.33	1.51	2.07
Stegastes leucostictus	0.29	1.89	1.25	2.06
Canthigaster rostrata	1.88	0.22	1.58	2.04

Table 10. Results of One-way SIMPER Analysis Comparing the Contribution of the Fifteen Most Influential Species to the Dissimilarity of Patch and Rim Reef Assemblages. REEF abundances are untransformed. Average dissimilarity over 9999 permutations between assemblages was 49.24%.

Species	**Patch abundance**	**Rim abundance**	**Dissimilarity / St. Dev.**	**% Contribution**
Haemulon aurolineatum	2.48	0.12	1.46	3.11
Microspathodon chrysurus	0.4	2.35	1.81	2.64
Thalassoma bifasciatum	1.83	3.44	1.18	2.48
Cephalopholis fulva	0.48	2.29	1.76	2.42
Stegastes planifrons	2.63	1.15	1.41	2.4
Halichoeres garnoti	1.03	2.68	1.45	2.31
Kyphosus sectatrix	0.93	2.26	1.34	2.27
Halichoeres maculipinna	0.58	2	1.57	2.17
Stegastes variabilis	2.2	1.24	1.34	2.17
Coryphopterus - personatus/hyalinus	2.75	2.35	1.09	2.15
Stegastes leucostictus	2.1	1	1.31	2.1
Bodianus rufus	0.6	1.91	1.55	1.94
Halichoeres radiatus	1.28	2.53	1.23	1.93
Coryphopterus glaucofraenum	1.33	1.5	1.17	1.91
Halichoeres bivittatus	2.2	1.35	1.2	1.9

Table 11. Results of One-way SIMPER Analysis Comparing the Contribution of the Fifteen Most Influential Species to the Dissimilarity of Patch and Fore Reef Assemblages. AGRRA REEF abundances are untransformed. Average dissimilarity over 9999 permutations between assemblages was 52.49%.

Species	**Fore abundance**	**Patch abundance**	**Dissimilarity / St. Dev.**	**% Contribution**
Haemulon aurolineatum	0	2.48	1.49	3.12
Cephalopholis fulva	2.88	0.48	2.47	3.1
Stegastes planifrons	0.41	2.63	1.83	2.91
Halichoeres bivittatus	0	2.2	1.92	2.75
Coryphopterus - personatus/hyalinus	1.06	2.75	1.48	2.6
Microspathodon chrysurus	2.29	0.4	1.81	2.52
Thalassoma bifasciatum	3.53	1.83	1.22	2.4
Stegastes leucostictus	0.29	2.1	1.49	2.37
Kyphosus sectatrix	2.41	0.93	1.37	2.36
Halichoeres garnoti	2.59	1.03	1.44	2.35
Stegastes variabilis	1.41	2.2	1.37	2.08
Halichoeres maculipinna	1.88	0.58	1.48	2.06
Sparisoma aurofrenatum	2.82	1.53	1.18	2.05
Acanthurus chirurgus	0.82	1.7	1.23	1.93
Scarus inserti	1.59	2.8	1.17	1.9

Small-scale variation in fish assemblage composition

AGGRA data

Cluster analysis of density data for AGRRA species revealed the existence of several distinct fish assemblages across the reef platform at spatial scales smaller than those delineated by reef zones. SIMPROF routines confirmed a statistically sound internal structure to the relationships supporting the existence of these assemblages (Fig. 14). However, evidence for distinct clusters only extended to a resemblance of ~50%. Thus, only relatively coarse resolution and differentiation of assemblages was possible.

An ordination of the square-root transformed densities of AGRRA species reinforced the distinction between inshore and offshore fish assemblages suggested by ANOSIM, as well as more subtle delineations of inshore assemblages (Fig. 15). The first of three clusters represents an offshore fish assemblage, with 98.4% of sites (n = 64) in this cluster falling into the categories of fore, rim or patch reefs immediately inside the rim. The only exception to this pattern (site 2039) was a fringing reef to the southwest that lies fairly close to the reef edge.

The two other broad clusters describe inshore fish assemblages (Fig. 15). The cluster in the center of the ordination appears to primarily reflect fish communities inshore at the eastern and western extremes of the island. 76.5% of sites (n = 17) in this cluster correspond to this habitat east or west of the central, north lagoon. The remaining sites (n = 4) lie within a small area south of Snakepit MPA in the north lagoon.

The final cluster seems to primarily describe an assemblage of the central, north lagoon. 65.4% of sites (n = 26) in this cluster fall into this area. Of the sites which do not (n = 9), most of these (n = 6) lie in one small area off the west end of the island. This area is characterized by high densities of haemulids, chaetodontids and inshore scarids (Figs. 22-24, 36-38).

While the three clusters seen at 30% similarity correspond well to inshore, offshore and lagoonal zonation on the reef platform, the statistically-robust clusters seen at ~50% similarity in the SIMPROF test fail to conform to obvious patterns in habitat distributions (Fig. 15). This lack of meaningful clustering at higher levels of similarity may reflect the incomplete species register comprising AGRRA protocol. The absence of some abundant species (*e.g. Thalassoma bifasciatum*) and many rare species in the protocol may thus obscure some true differences among assemblages. REEF data, which accounts for all species observed, may thus provide better resolution of fine distinctions among small scale assemblages.

REEF data

SIMPROF routines indicated the significance of relationships between clusters, based on REEF abundance data, to a higher level of resemblance (~60%) than was possible with AGRRA data (Fig. 18). As in AGRRA ordinations and suggested by ANOSIM, untransformed REEF data grouped into two dominant clusters; one representing a fish assemblage of the fore and rim reefs (plus some patch reefs adjacent to the rim) and another reflecting an inshore assemblage common to fringing and almost all patch reefs (Fig. 19). Greater levels of resemblance, however, also revealed the existence of assemblages at finer spatial scales.

Inshore cluster: At greater levels of resemblance, sub-clusters within the inshore cluster revealed more specific types of fish assemblages. At 40% similarity, for example, two west-end sites paralleled the AGRRA cluster off the west end and appeared to reflect an assemblage of reefs adjacent to inshore seagrass beds. These sites were characterized by high abundances of haemulids (*H. sciurus, H. flavolineatum,* and *H. aurolineatum*; Figs. 36-38), the absence of several of the most widespread scarids (Figs. 21, 22, 26), and numbers of *Scarus guacamaia* (Fig. 20) and *Sparisoma radians* (data not included).

Other sub-clusters represented similarly fine distinctions, such as one describing an assemblage of the southern lagoon in the lower North Shore Coral Reef Preserve. These sites are typified by high abundances of *Haemulon aurolineatum* and *H. flavolineatum* (Figs. 37-38). Central lagoon sites formed exclusive clusters probably based on abundances of some species not so common elsewhere. Some ecologically and commercially important examples include *Mycteroperca bonaci* (Fig. 40), *Lachnolaimus maximus* (Fig. 39), *Holocanthus bermudensis* (Fig. 35), *Chaetodon* spp. (Figs. 33-34) *Acanthurus chirurgus* (Fig. 27), *Lutjanus griseus* (Fig. 45), *Ocyurus chrysurus* (Fig. 46) and *Lutjanus synagris* (Fig. 44). One further trend that may set these southern lagoon sites apart from others is the virtual absence of several key herbivores (*Acanthurus bahianus* [Fig. 28]*, Sparisoma viride* [Fig. 21] *, S. chrysopterum* [Fig. 22]*, S. aurofrenatum* [Fig. 23] and *Scarus inserti* [Fig. 24]) from the reefs in the southern region of the North Shore Coral Reef Preserve.

One other such sub-cluster appeared to capture fish community composition on very isolated patch reefs, where *Haemulon sciurus* was present in relatively larger numbers than other offshore patch reefs. Otherwise, no other differences in community composition were readily discernable, raising the possibility of subtle differences in presence and abundance only apparent across the entire assemblage.

By and large, other high resolution sub-clusters included various combinations of inshore east and west end sites, or combinations of west and central lagoon sites. These patterns suggest, first of all, commonalities in community structure between reefs at the east and west ends of the island. However, no single species appears primarily responsible for this clustering. In contrast, commonalities between west end and north, central lagoon sites are unambiguous. For example, in common with central lagoon sites, west end reefs share high AGRRA densities of *Haemulon aurolinatum* (Fig. 38)*, Lutjanus griseus* (Fig. 45) and *Ocyurus chrysurus* (Fig. 46).

Offshore cluster: The other dominant cluster, comprised of sites near the edge of the reef platform, also indicated meaningful assemblages at finer levels of site-association. One cluster was dominated by the four MPA and four control sites (surveyed for a related assessment of MPA benthic protection). While the trend is not apparent from AGRRA data (Fig.16), all of these sites harbour higher REEF abundances of all functional groups than average rim reefs and appear to represent rim reefs adjacent to tidal passes (Fig. 17).

Overall, outer reef sites to the northeast of the island tended to share clusters with those from the southwest, indicating common community structures between those two regions. The low densities of *Scarus taeniopterus* (Fig. 25)*, Sparisoma viride* (Fig. 21) and *Sparisoma chrysopterum* (Fig. 22) characteristic of both sections of the outer reef may be the main sources of resemblance for these sites. These regions might thus represent assemblages depauperate in herbivores relative to the adjacent northern outer reef, where most herbivores were particularly abundant (Figs. 5, 9). The few sites surveyed on south shore tended to associate with the northeast region suggesting that they may exhibit assemblage characteristics common to both regions. Again, though, this may be attributable to the relative scarcity of *Scarus taeniopterus* on south shore and the northeast region.

A third, smaller cluster existed also and included fringing, patch and a single fore reef site. In terms of assemblage species composition and abundance, the fore reef site appeared to bear little resemblance to the remaining sites in the cluster. The resemblance of these remaining sites, however, was likely greatly influenced by the low species richness and dominance of pomacentrids there (Figs. 3, 31). The smaller cluster evident at the 60% similarity level may, therefore, reflect a degraded subset of inshore reefs, overrun by damselfish. This cluster appears to be distinguishable from another sub-cluster of the inshore grouping by the low abundance of labrids at these sites.

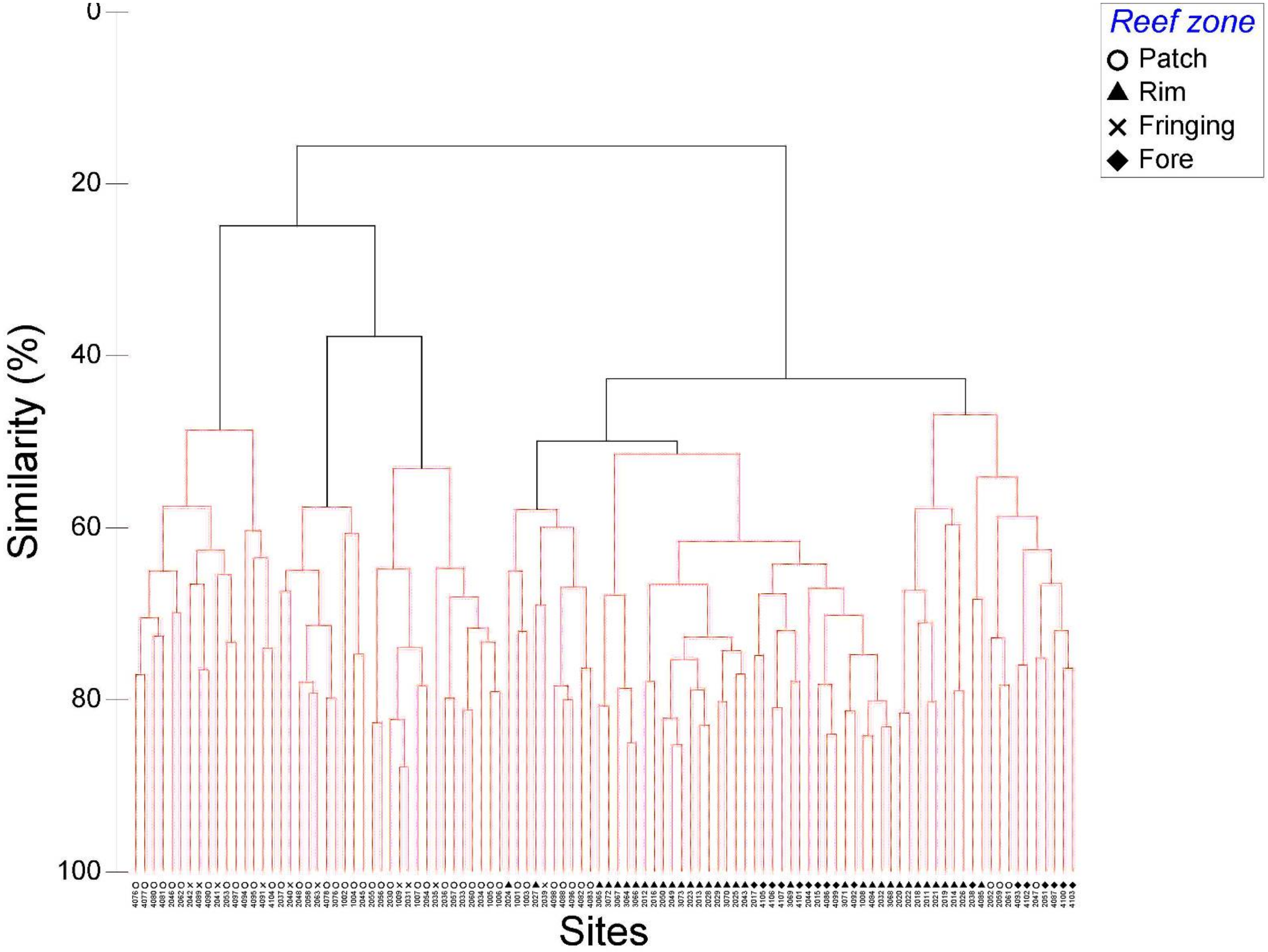

Fig. 14. Cluster analysis of square root transformed AGGRA density data for 104 sites across the Bermuda platform and subjected to SIMPROF testing for significance of relationships among clusters. Black lines denote clusters with sufficient evidence (95%), based on permutations, of significant internal structure.

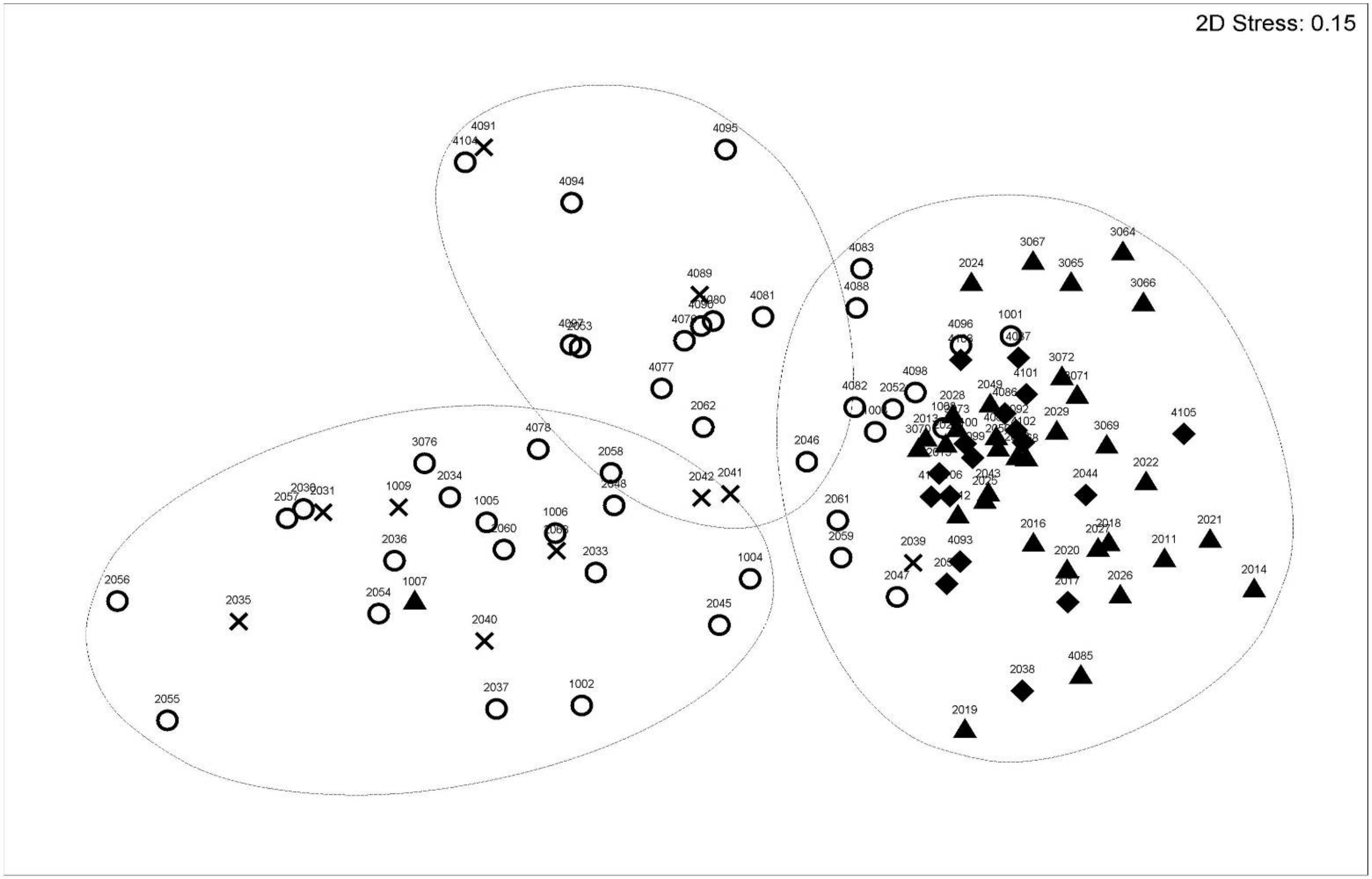

Fig. 15. MDS ordination of square-root transformed AGRRA species density data for 104 sites across the Bermuda platform, overlaid with clusters of 30% similarity. ✕ = fringing, ○ = patch, ▲ = rim, ◆ = fore. 2D stress value displayed in upper right of plot.

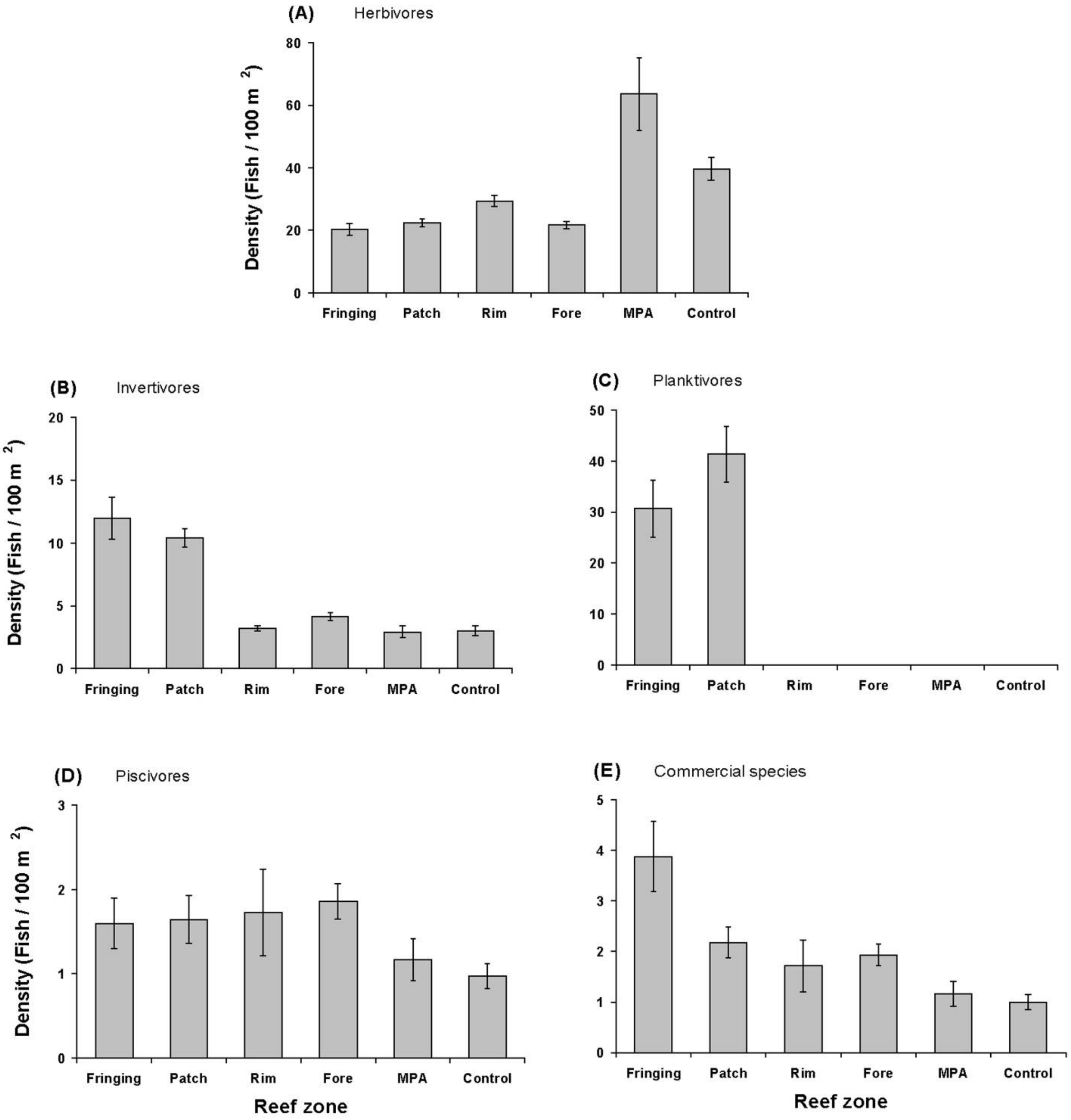

Fig. 16. Mean density of functional guilds across different reef zones, MPA's and MPA control sites on the Bermuda platform, derived from AGRRA survey data: **(a)** herbivores, **(b)** invertivores, **(c)** plantivores, **(d)** piscivores, and **(d)** commercial species. Data are means ± standard error

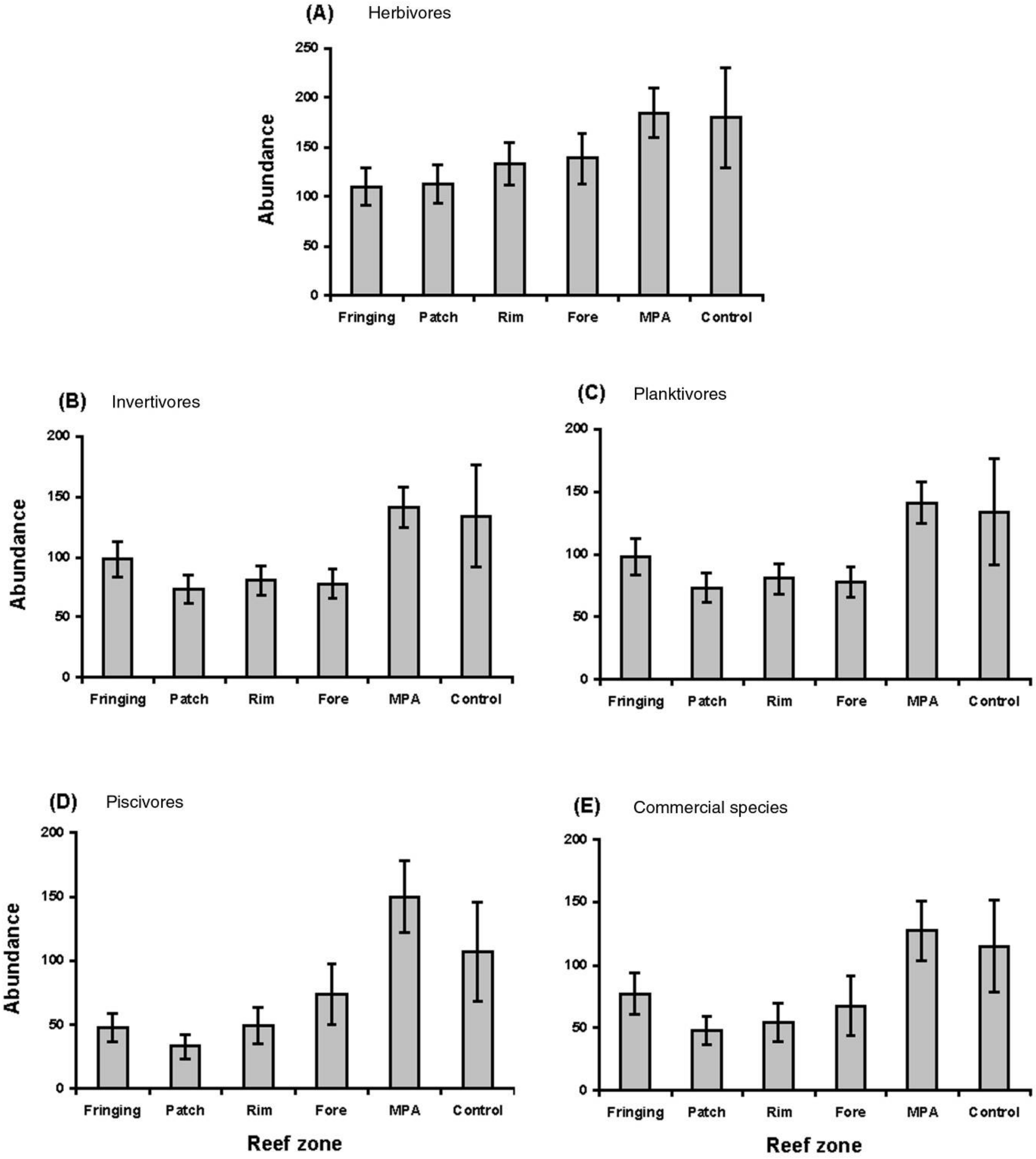

Fig. 17. Mean abundance score of functional groups across different reef zones, MPA's and MPA control sites on the Bermuda platform, derived from REEF roving diver survey data: **(a)** herbivores, **(b)** invertivores, **(c)** plantivores, **(d)** piscivores, and **(d)** commercial species. Data are means ± standard error.

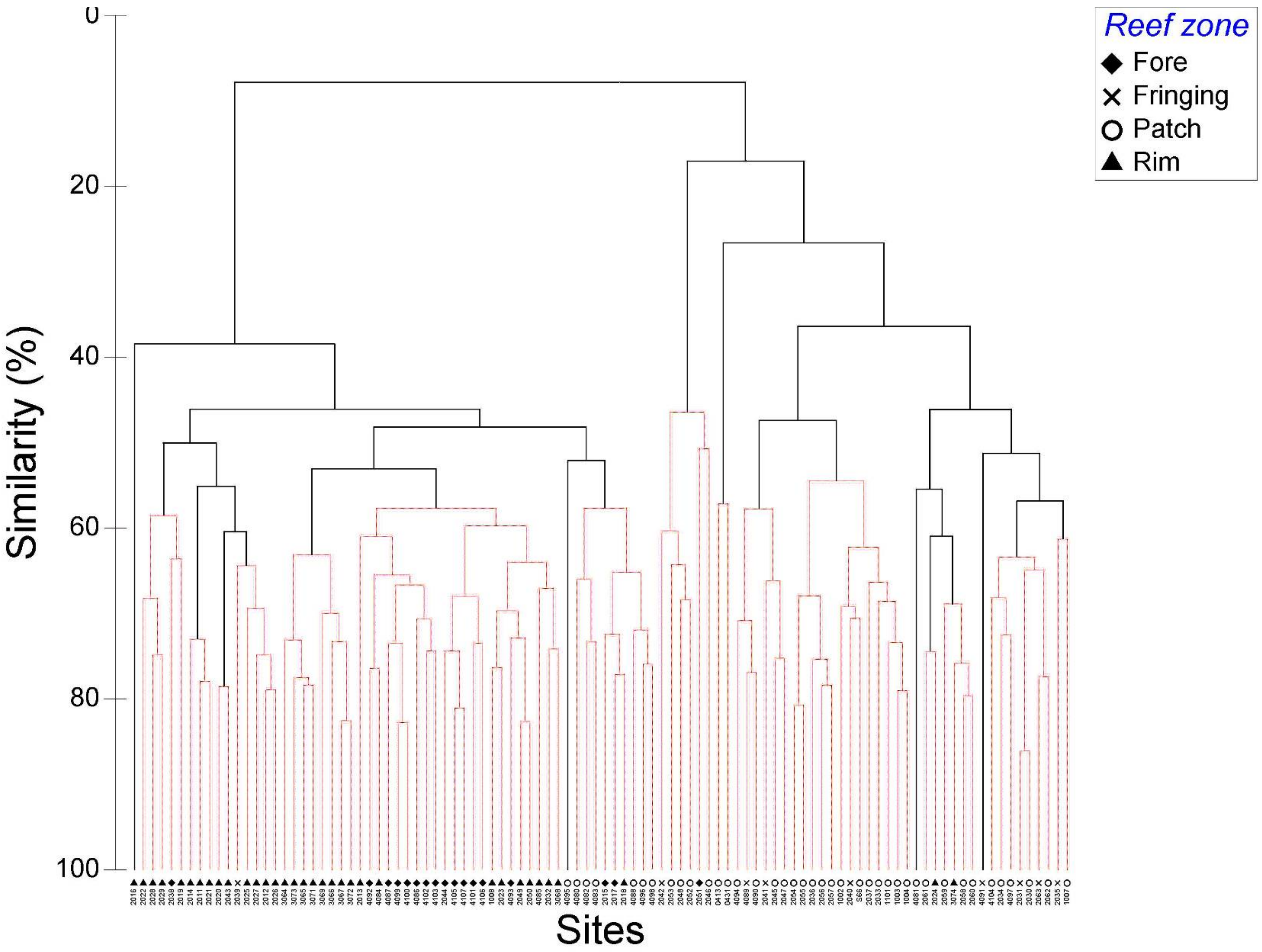

Fig. 18. Cluster analysis of untransformed REEF abundance data for 100 sites across the Bermuda platform and subjected to SIMPROF testing for significance of relationships among clusters. Black lines denote clusters with sufficient evidence (95%), based on permutations, of significant internal structure.

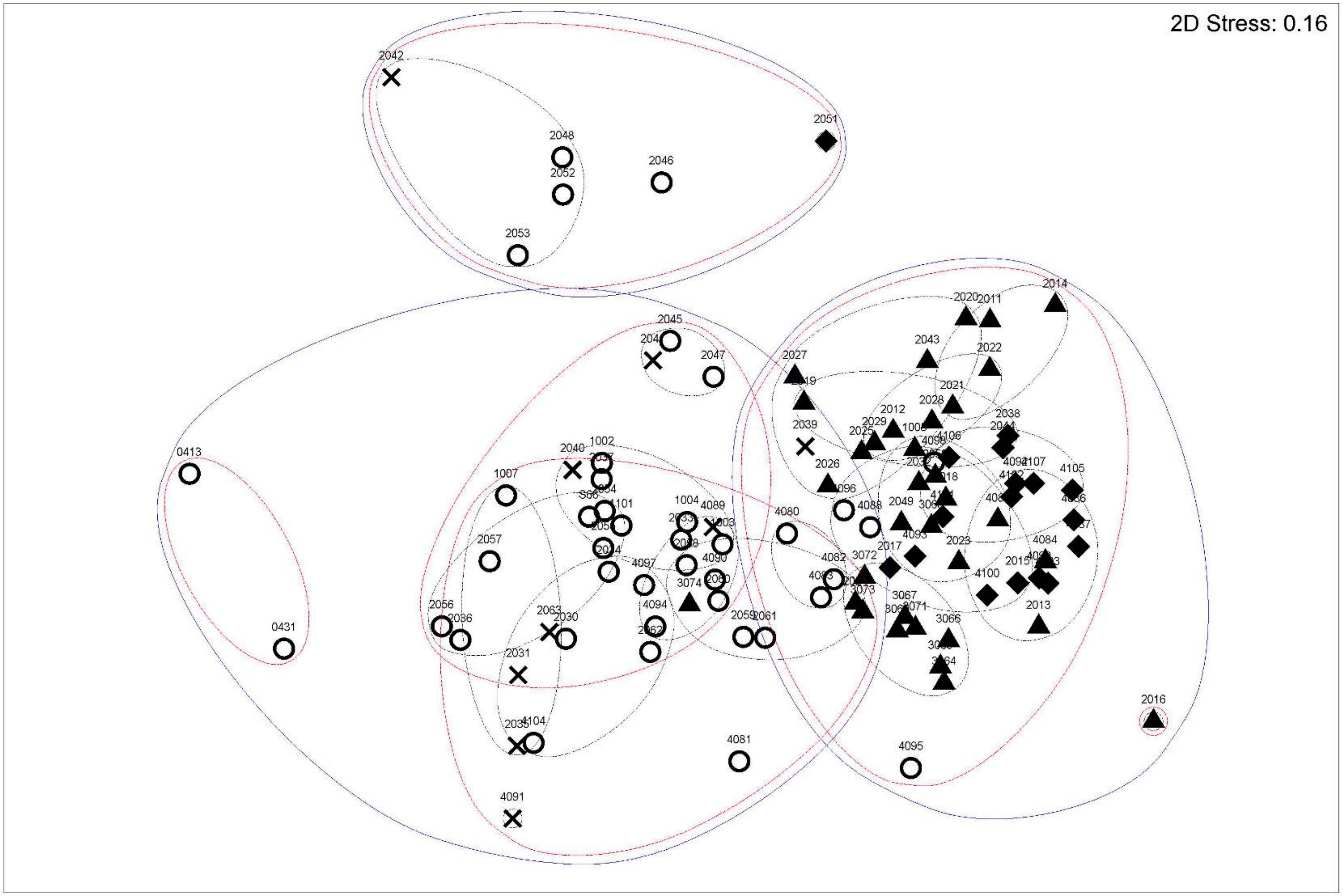

Fig. 19. MDS ordination of untransformed REEF abundance data for 100 sites across the Bermuda platform, overlaid with clusters of 20% similarity (blue contours), 40% similarity (red contours) and 60% similarity (black contours). ✕ = fringing, ○ = patch, ▲ = rim, ◆ = fore. 2D stress value displayed in upper right of plot.

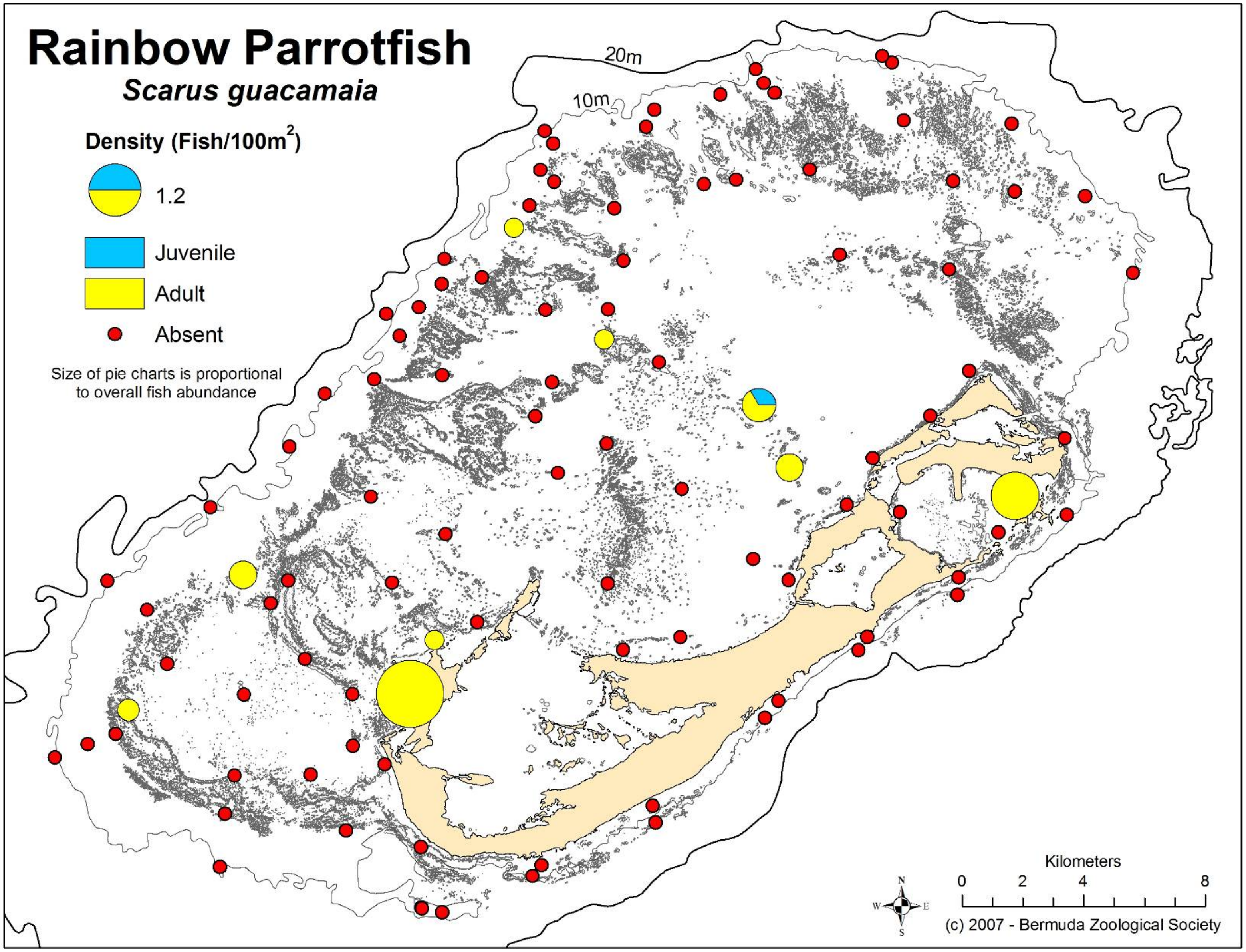

Fig. 20. Geospatial map illustrating juvenile and adult densities, derived from AGGRA surveys, of *Scarus guacamaia.*

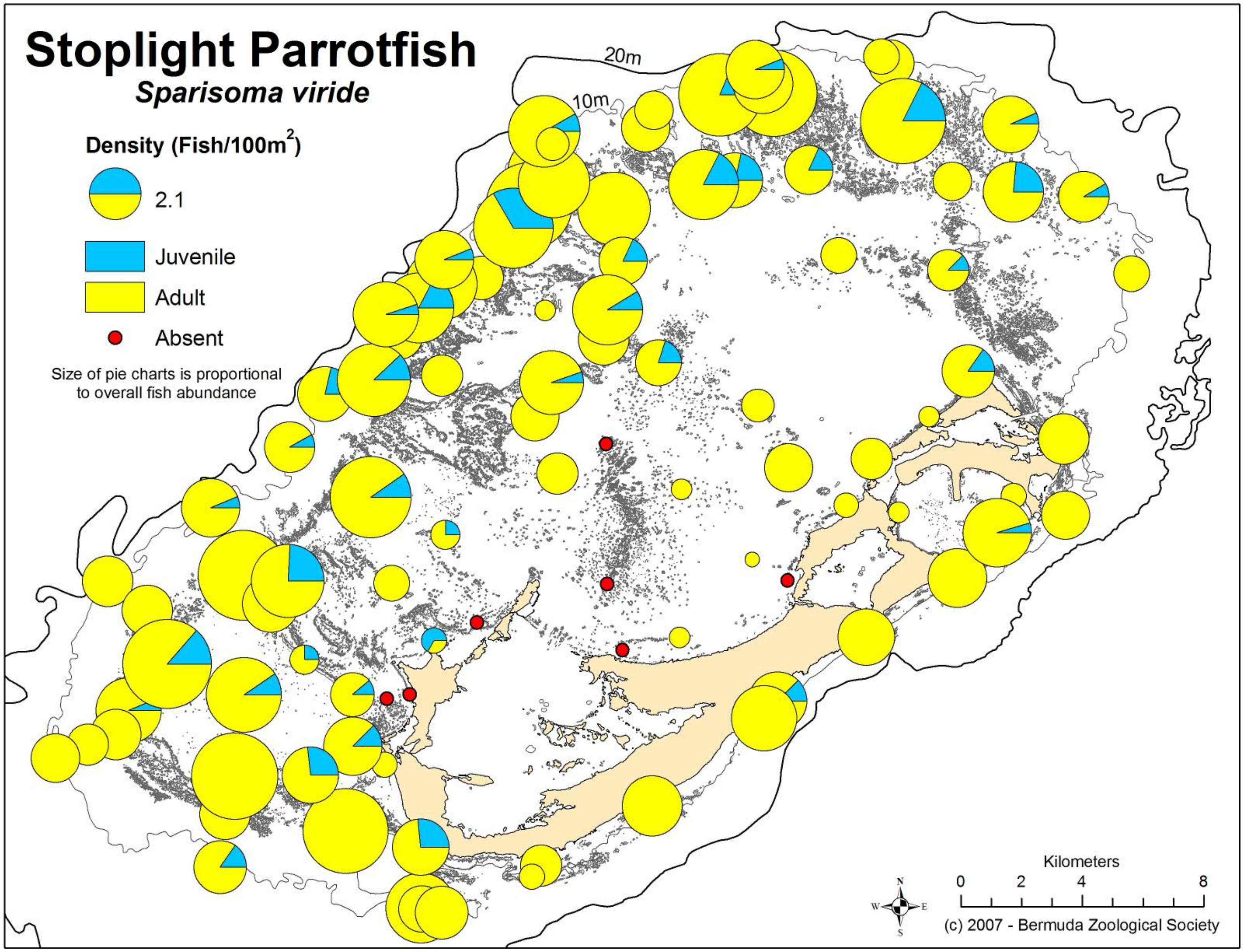

Fig. 21. Geospatial map illustrating juvenile and adult densities, derived from AGGRA surveys, of *Sparisoma viride.*

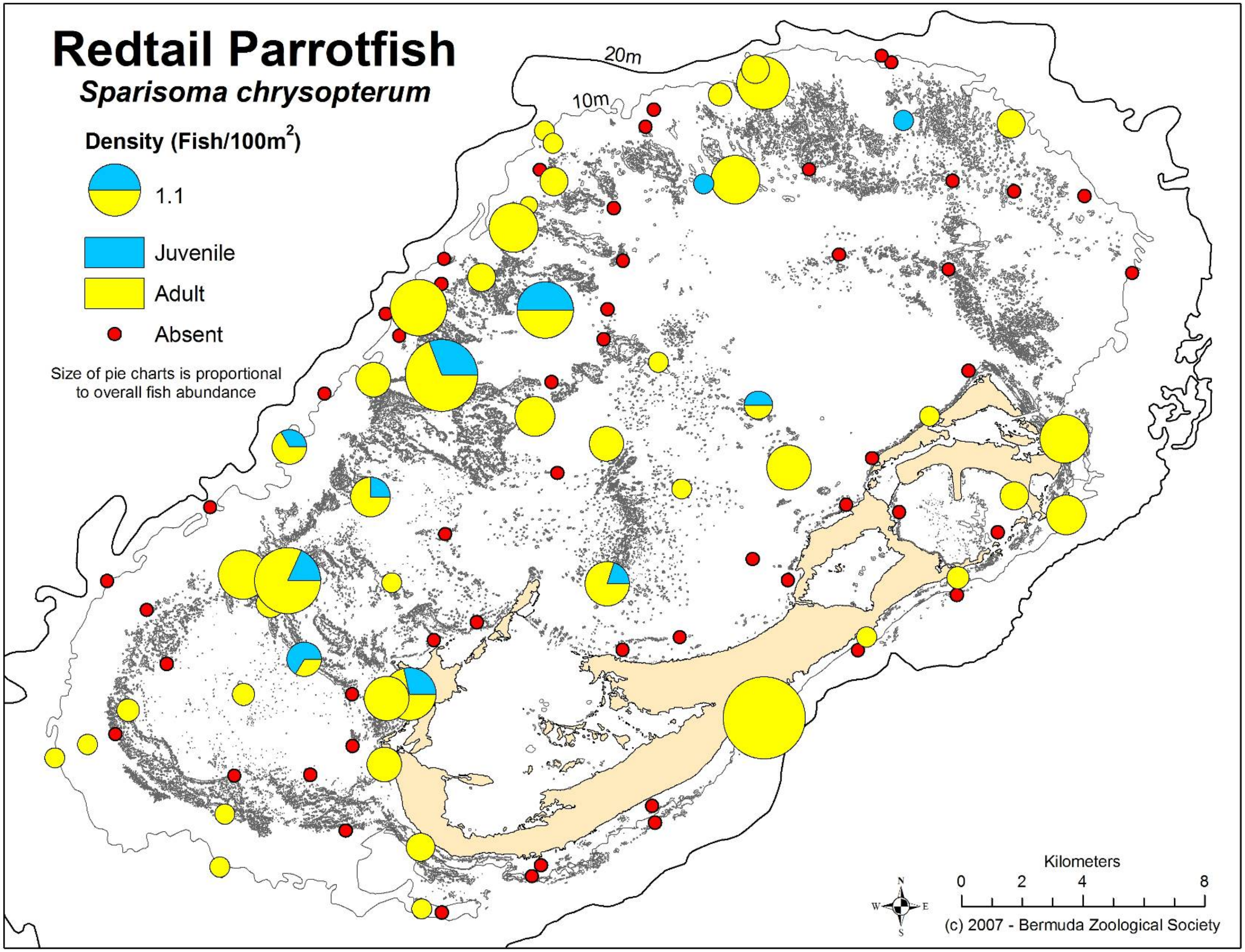

Fig. 22. Geospatial map illustrating juvenile and adult densities, derived from AGGRA surveys, of *Sparisoma chrysopterum.*

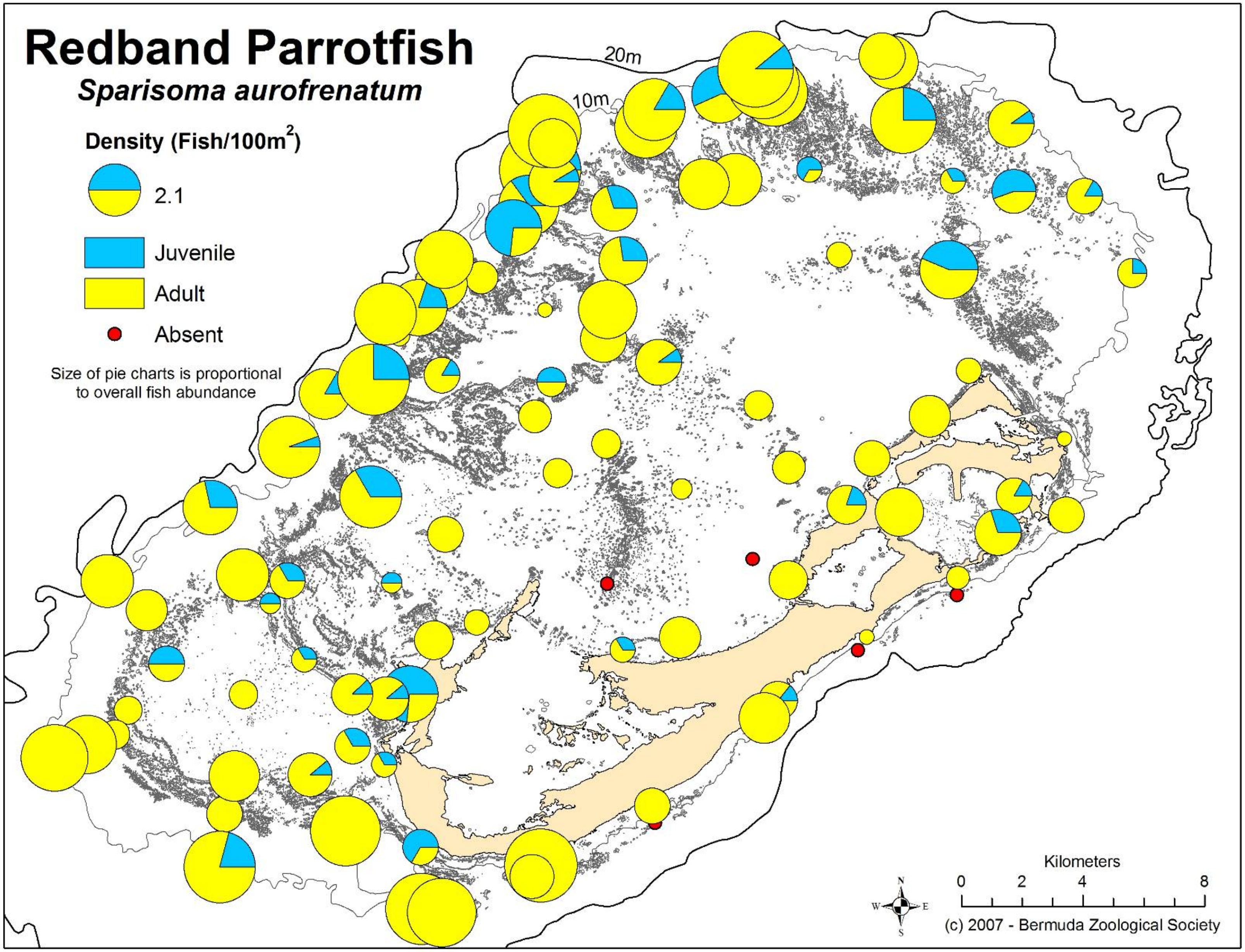

Fig. 23. Geospatial map illustrating juvenile and adult densities, derived from AGGRA surveys, of *Sparisoma aurofrenatum.*

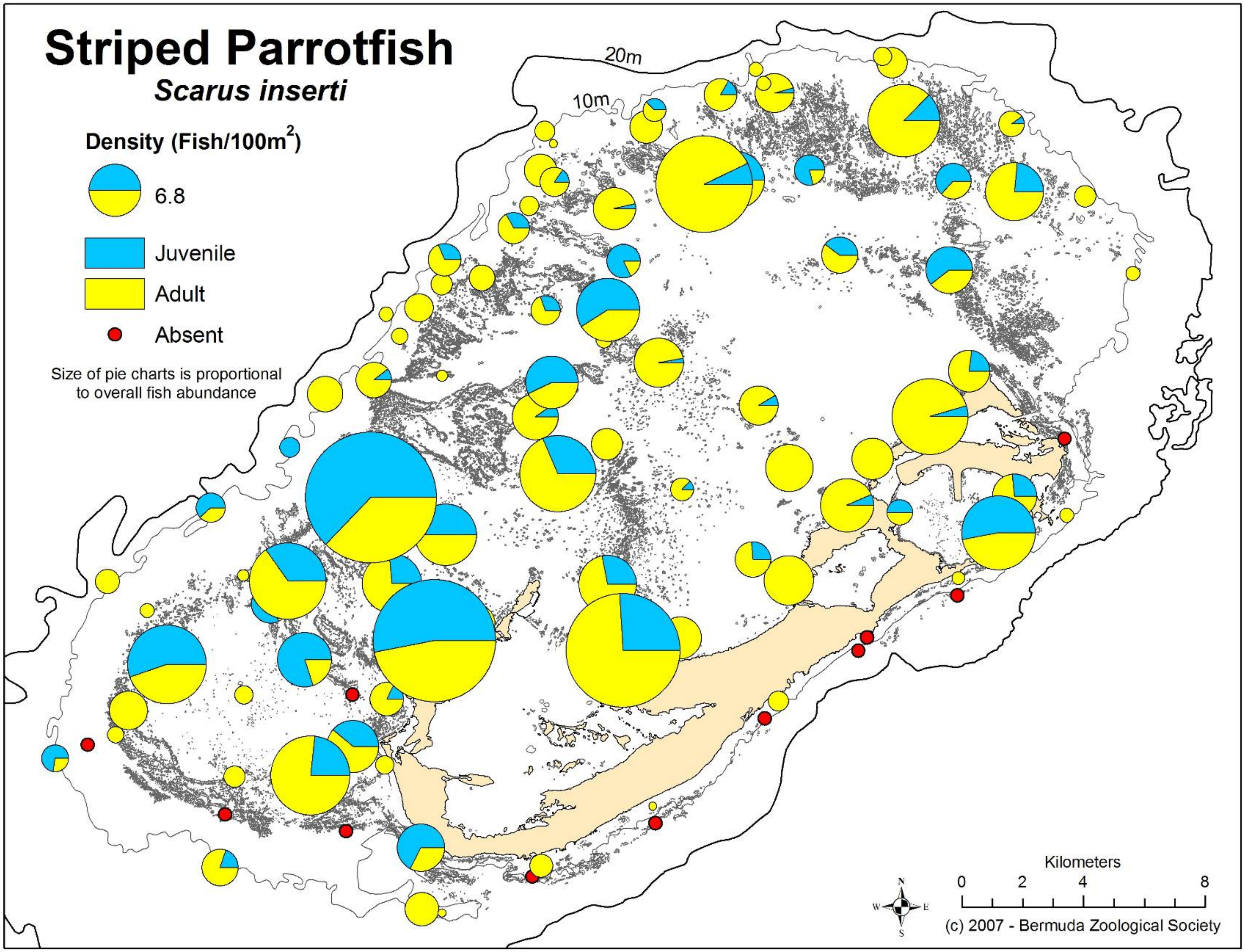

Fig. 24. Geospatial map illustrating juvenile and adult densities, derived from AGGRA surveys, of *Scarus inserti.*

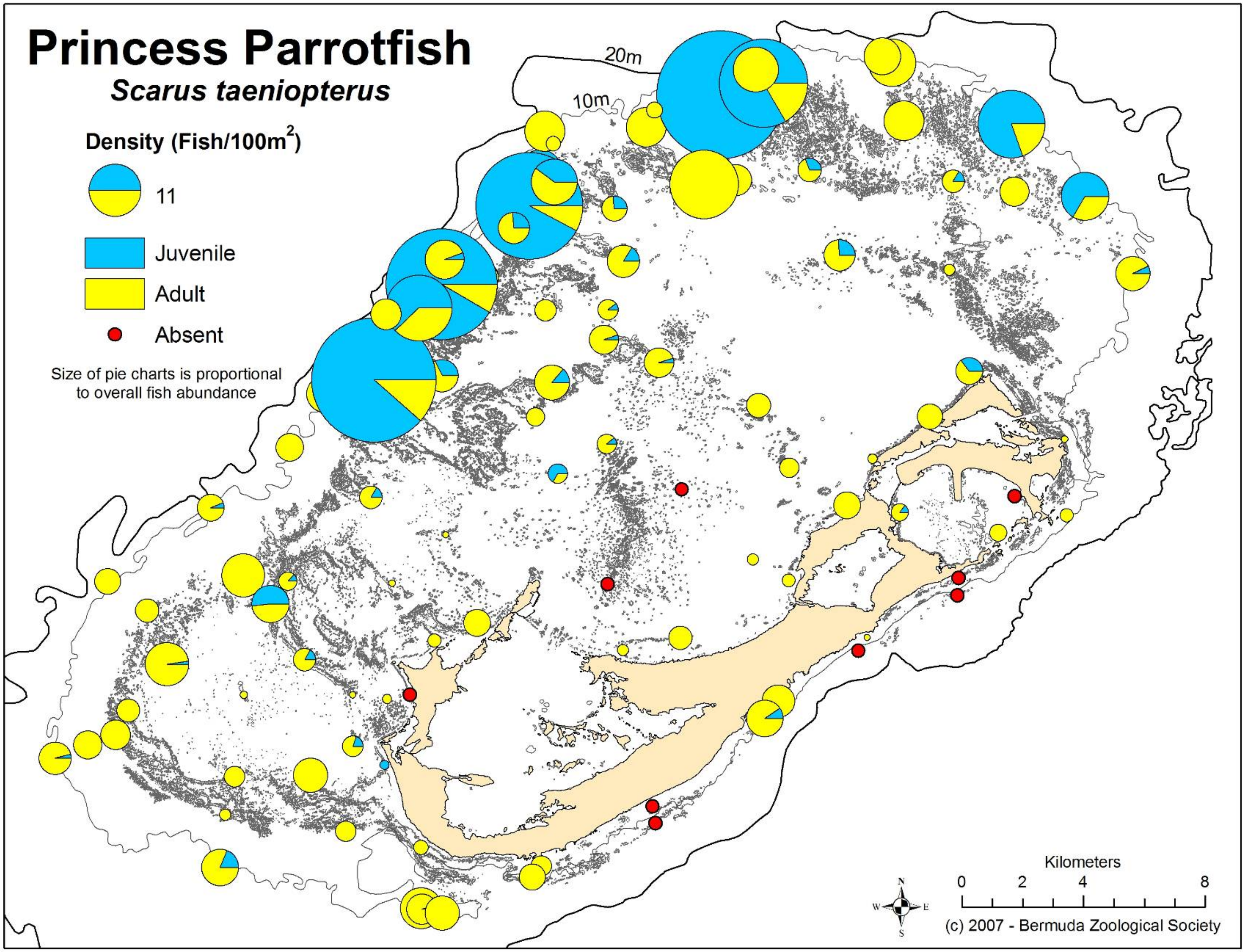

Fig. 25. Geospatial map illustrating juvenile and adult densities, derived from AGGRA surveys, of *Scarus taeniopterus.*

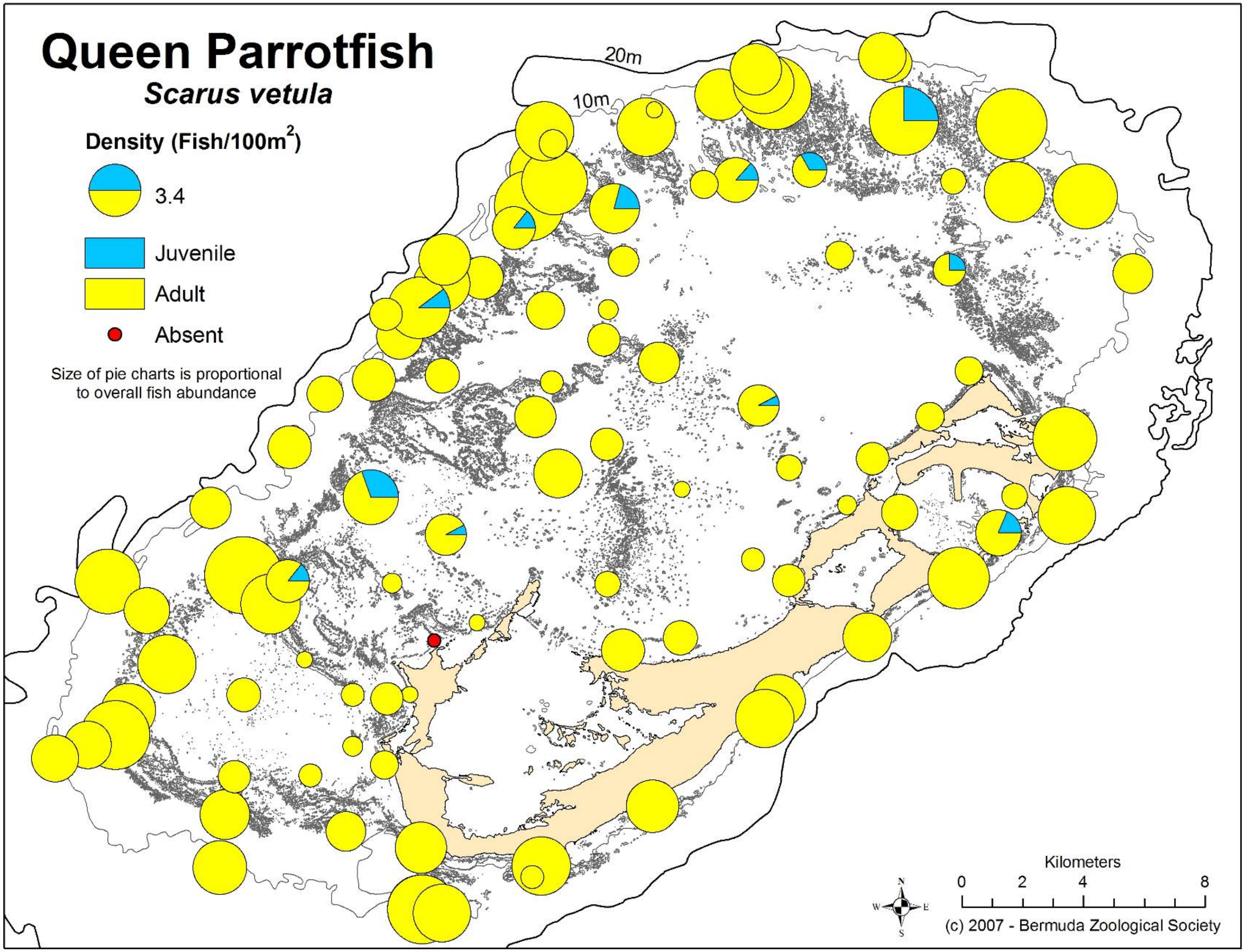

Fig. 26. Geospatial map illustrating juvenile and adult densities, derived from AGGRA surveys, of *Scarus vetula.*

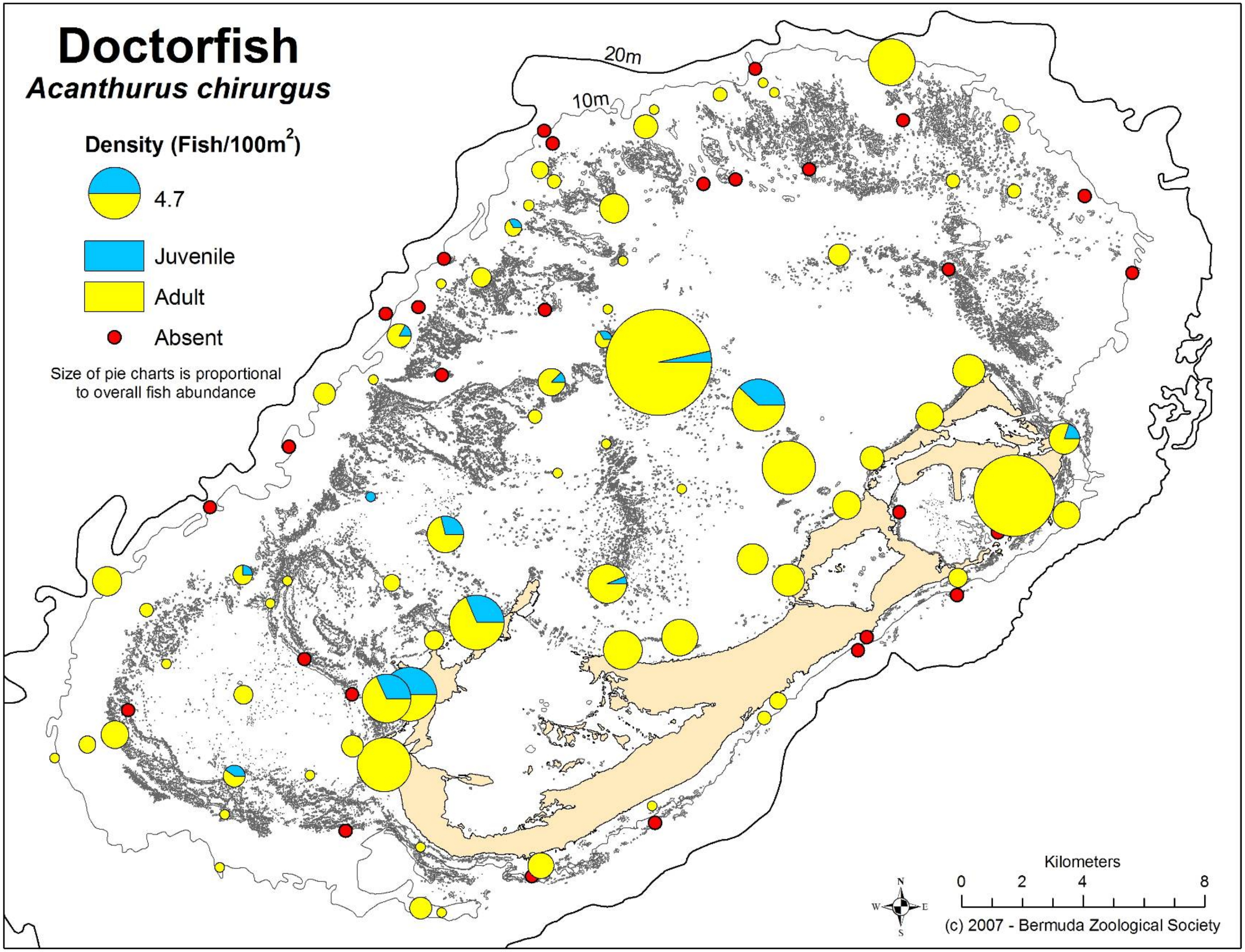

Fig. 27. Geospatial map illustrating juvenile and adult densities, derived from AGGRA surveys, of *Acanthurus chirurgus.*

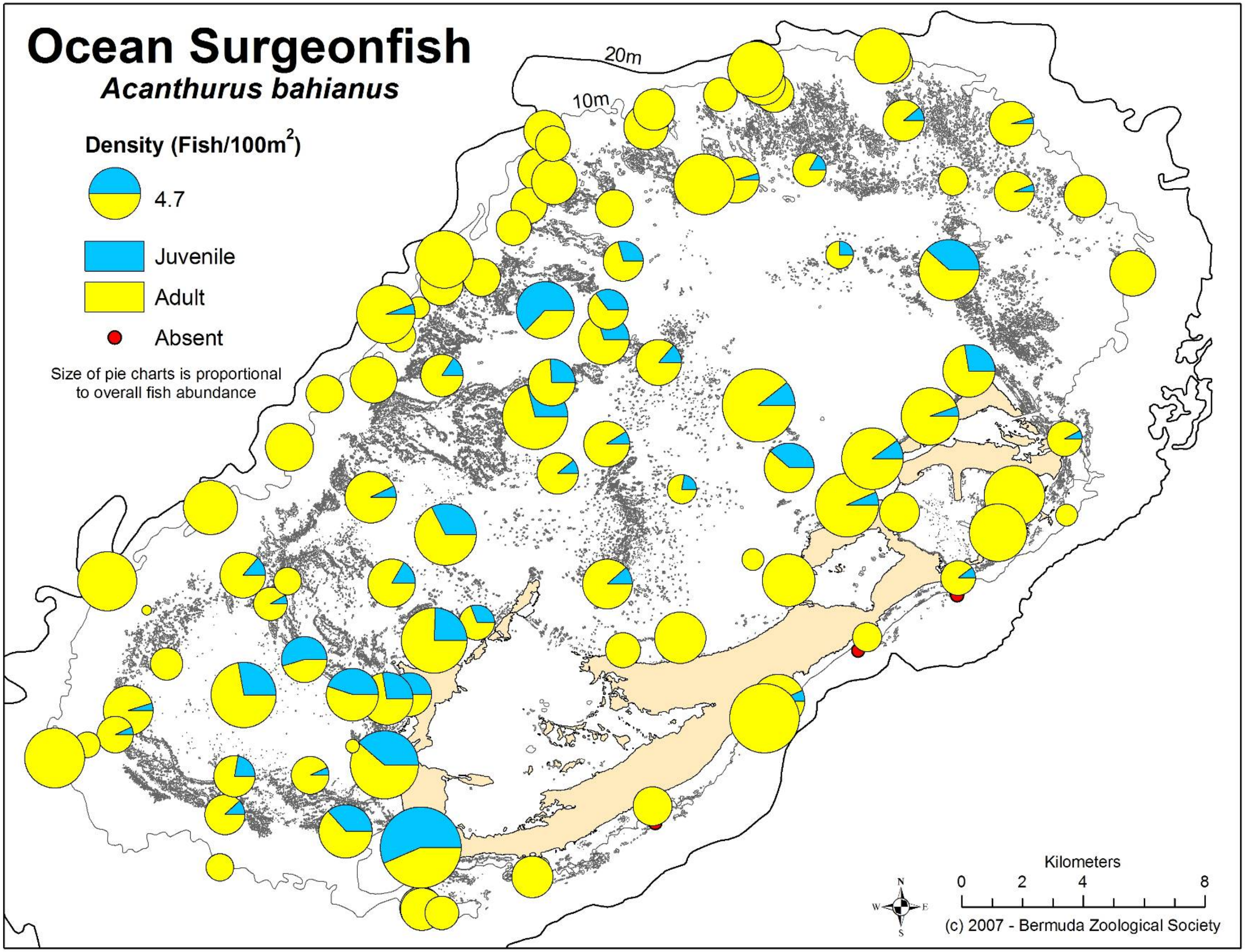

Fig. 28. Geospatial map illustrating juvenile and adult densities, derived from AGGRA surveys, of *Acanthurus bahianus.*

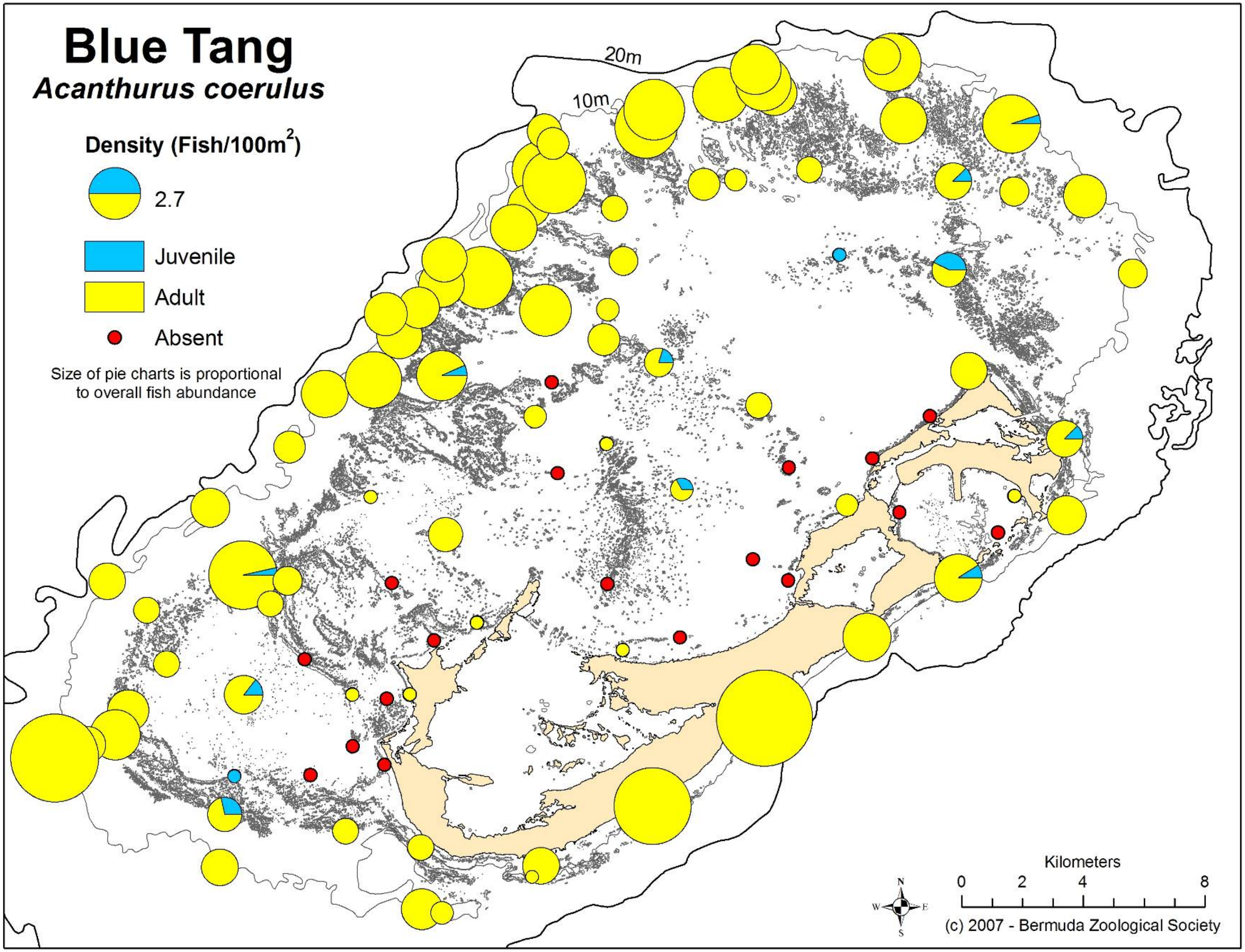

Fig. 29. Geospatial map illustrating juvenile and adult densities, derived from AGGRA surveys, of *Acanthurus coerulus.*

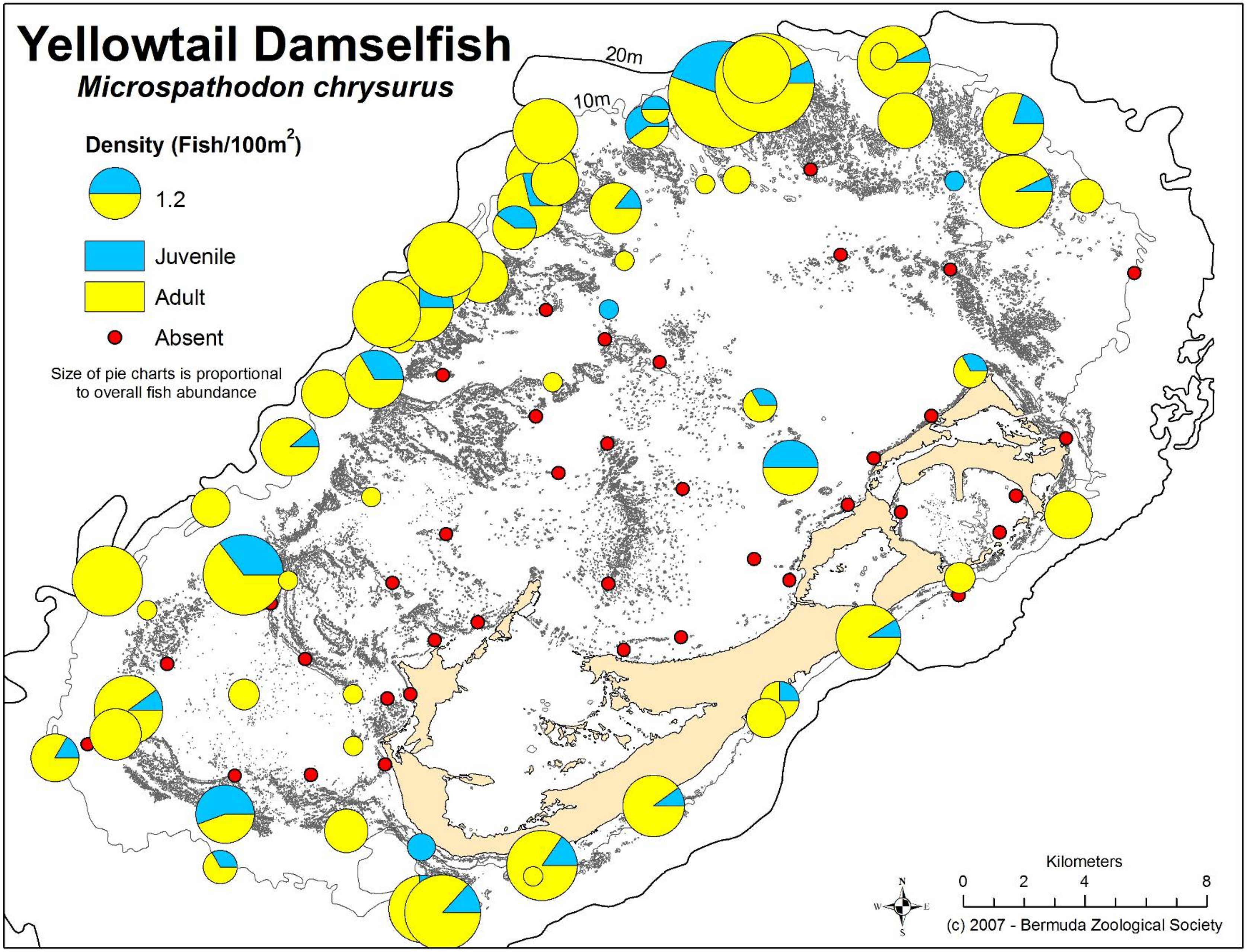

Fig. 30. Geospatial map illustrating juvenile and adult densities, derived from AGGRA surveys, of *Microspathodon chrysurus.*

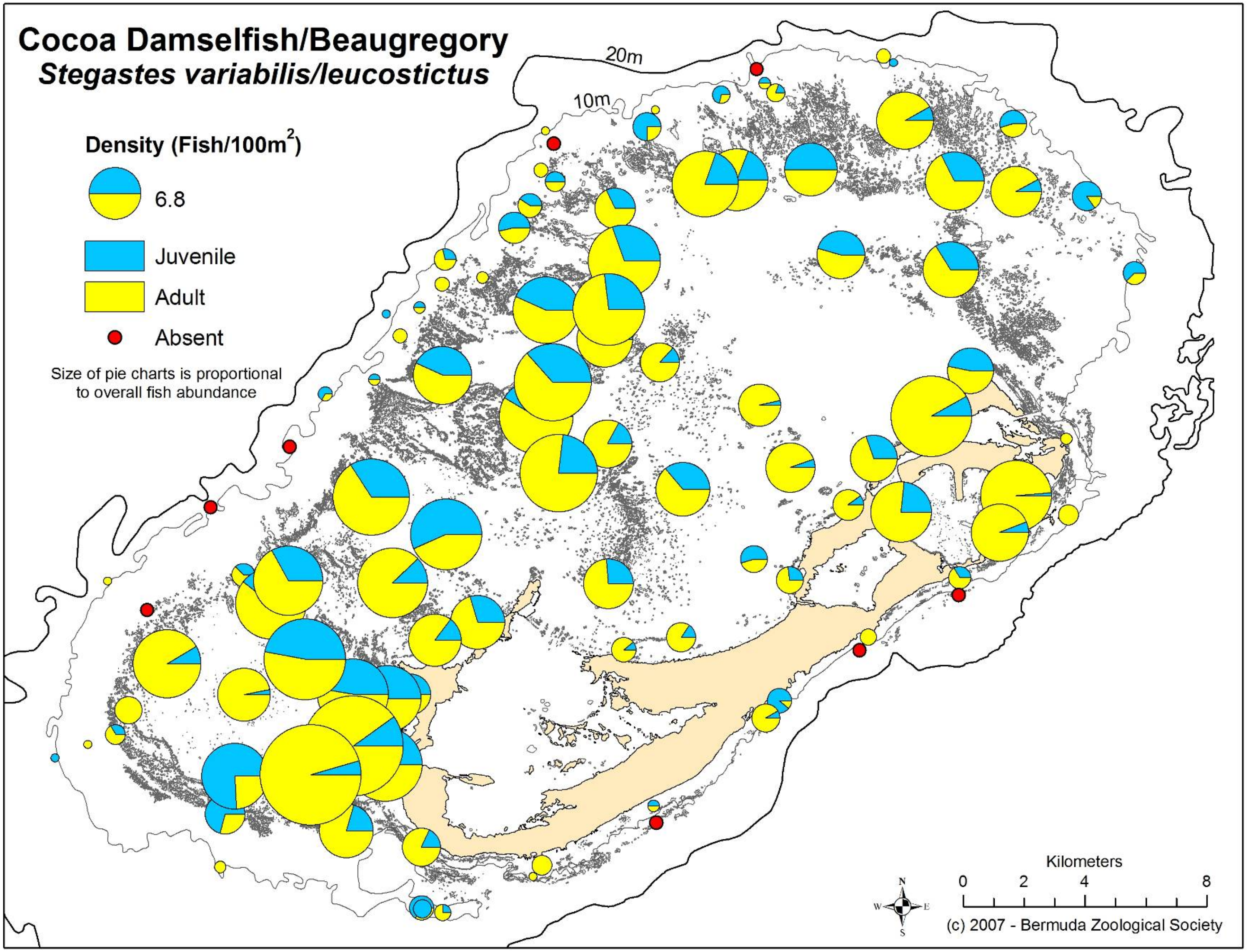

Fig. 31. Geospatial map illustrating juvenile and adult densities, derived from AGGRA surveys, of *Stegastes variabilis / leucostictus.*

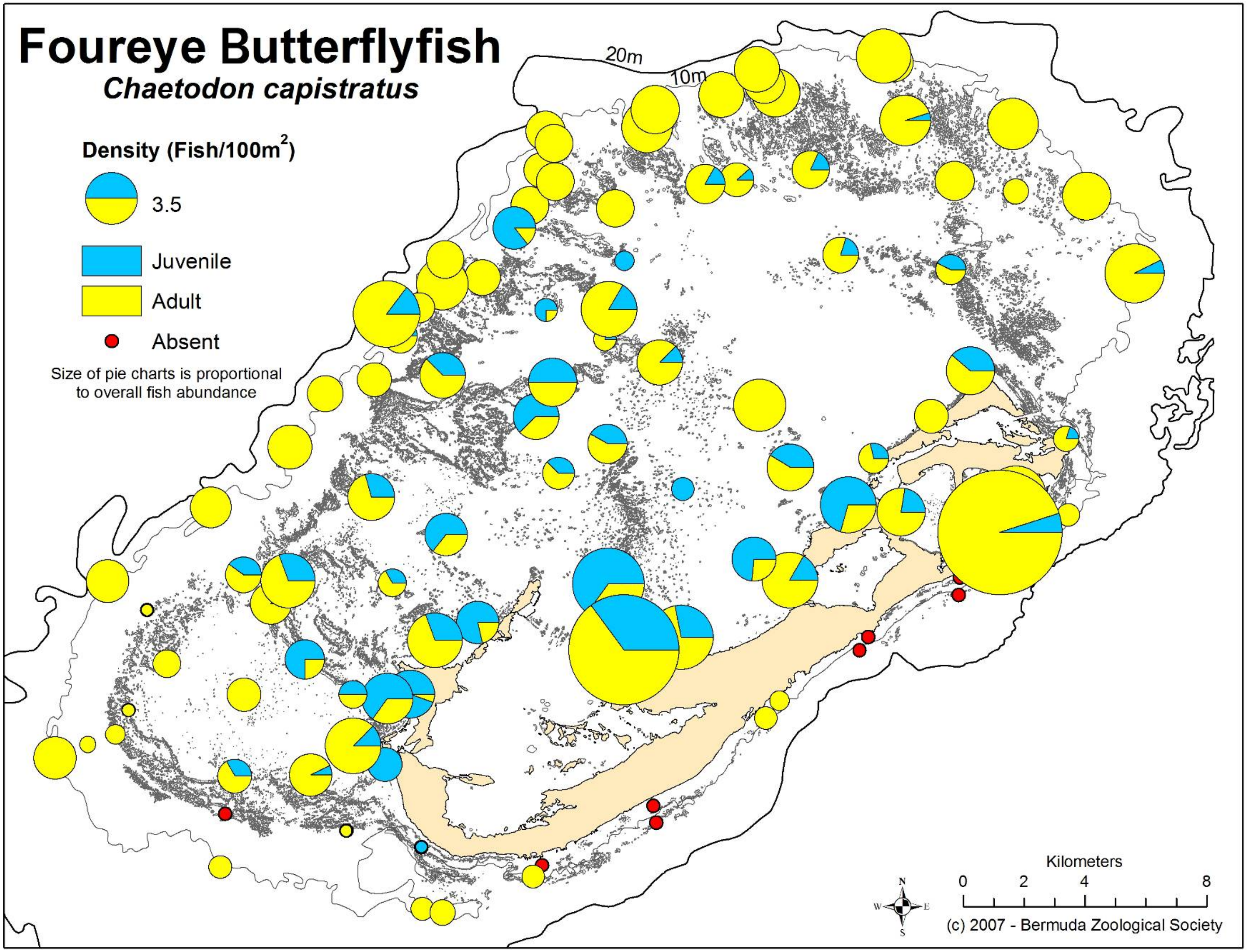

Fig. 32. Geospatial map illustrating juvenile and adult densities, derived from AGGRA surveys, of *Chaetodon capistratus.*

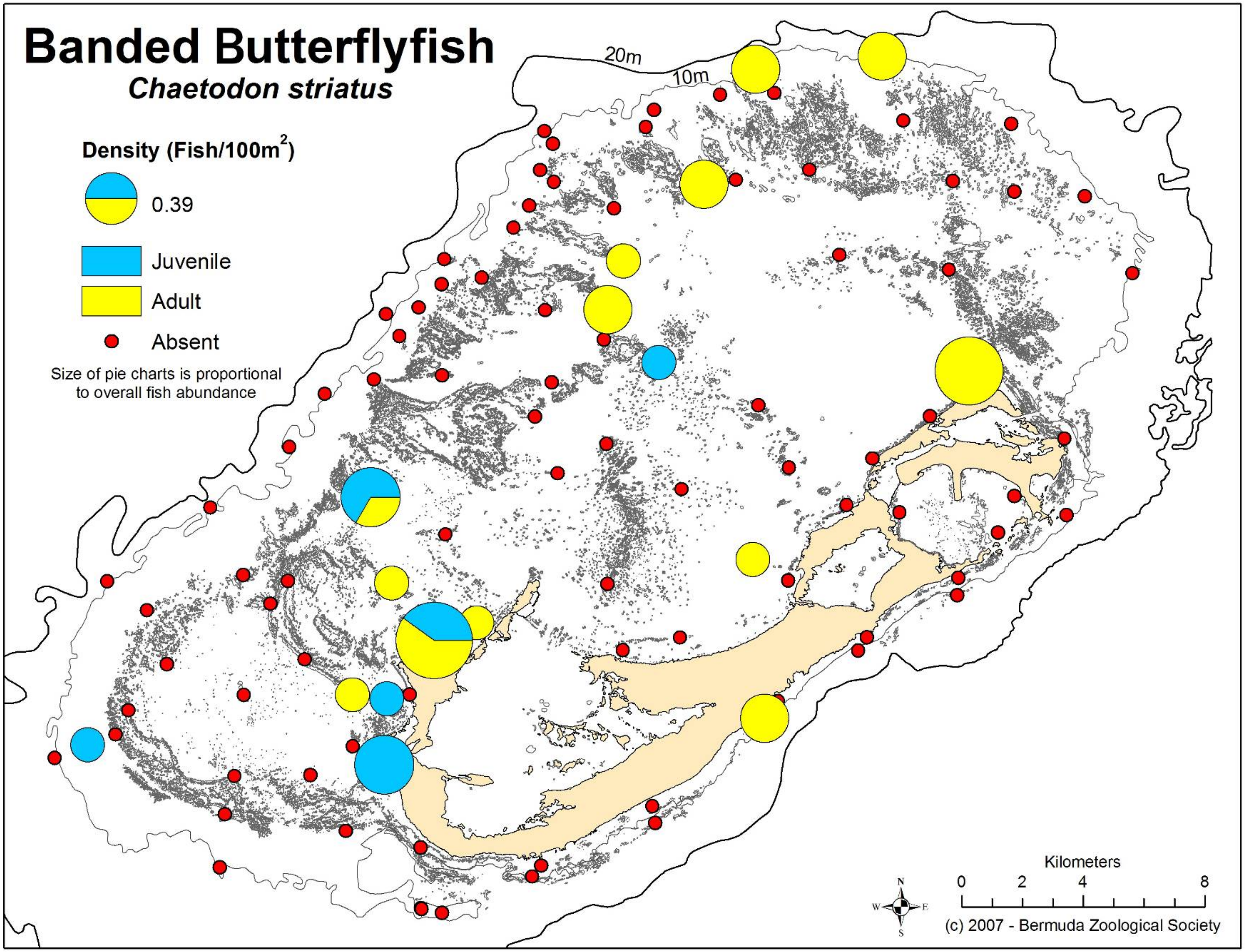

Fig. 33. Geospatial map illustrating juvenile and adult densities, derived from AGGRA surveys, of *Chaetodon striatus.*

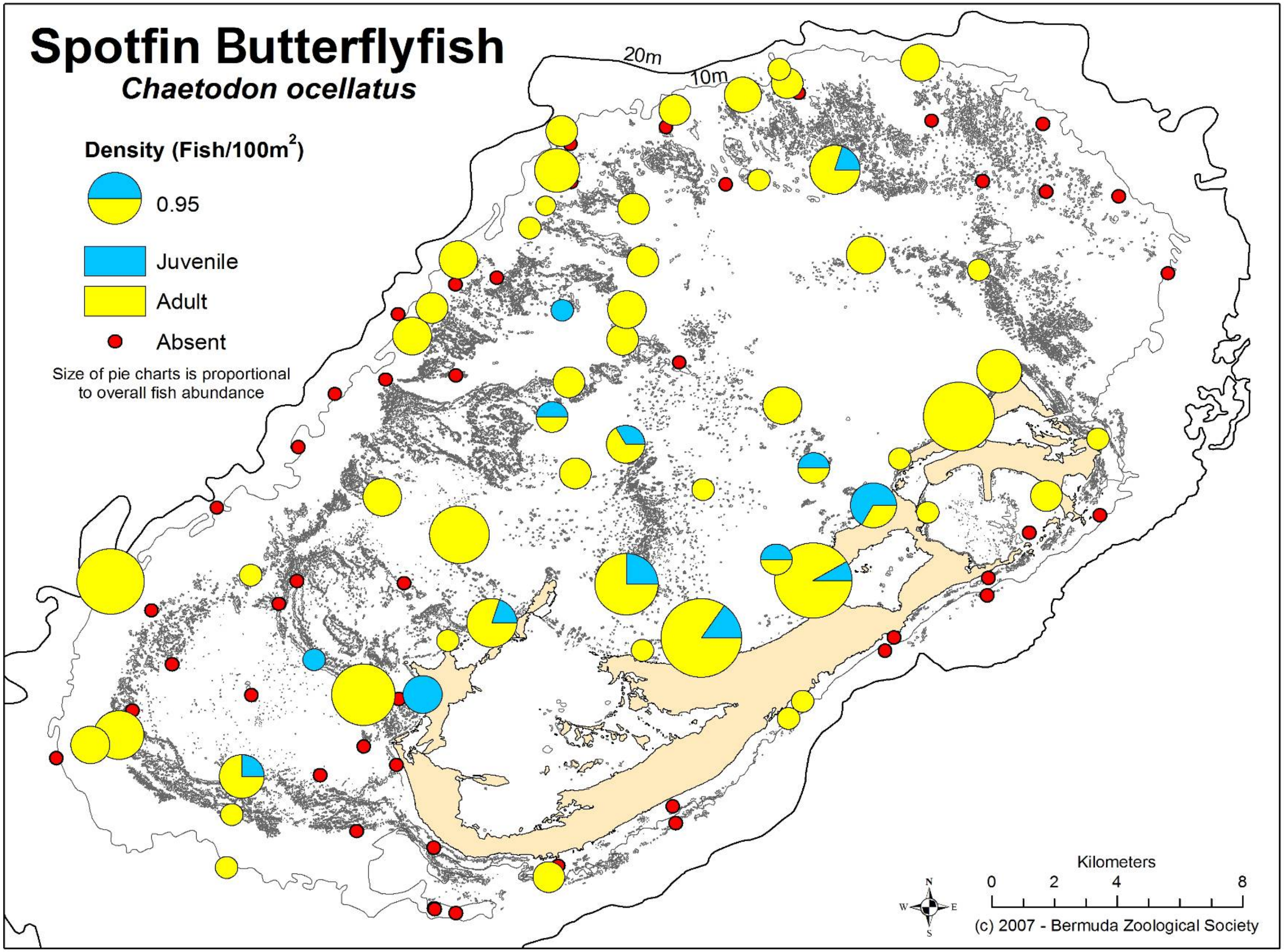

Fig. 34. Geospatial map illustrating juvenile and adult densities, derived from AGGRA surveys, of *Chaetodon ocellatus.*

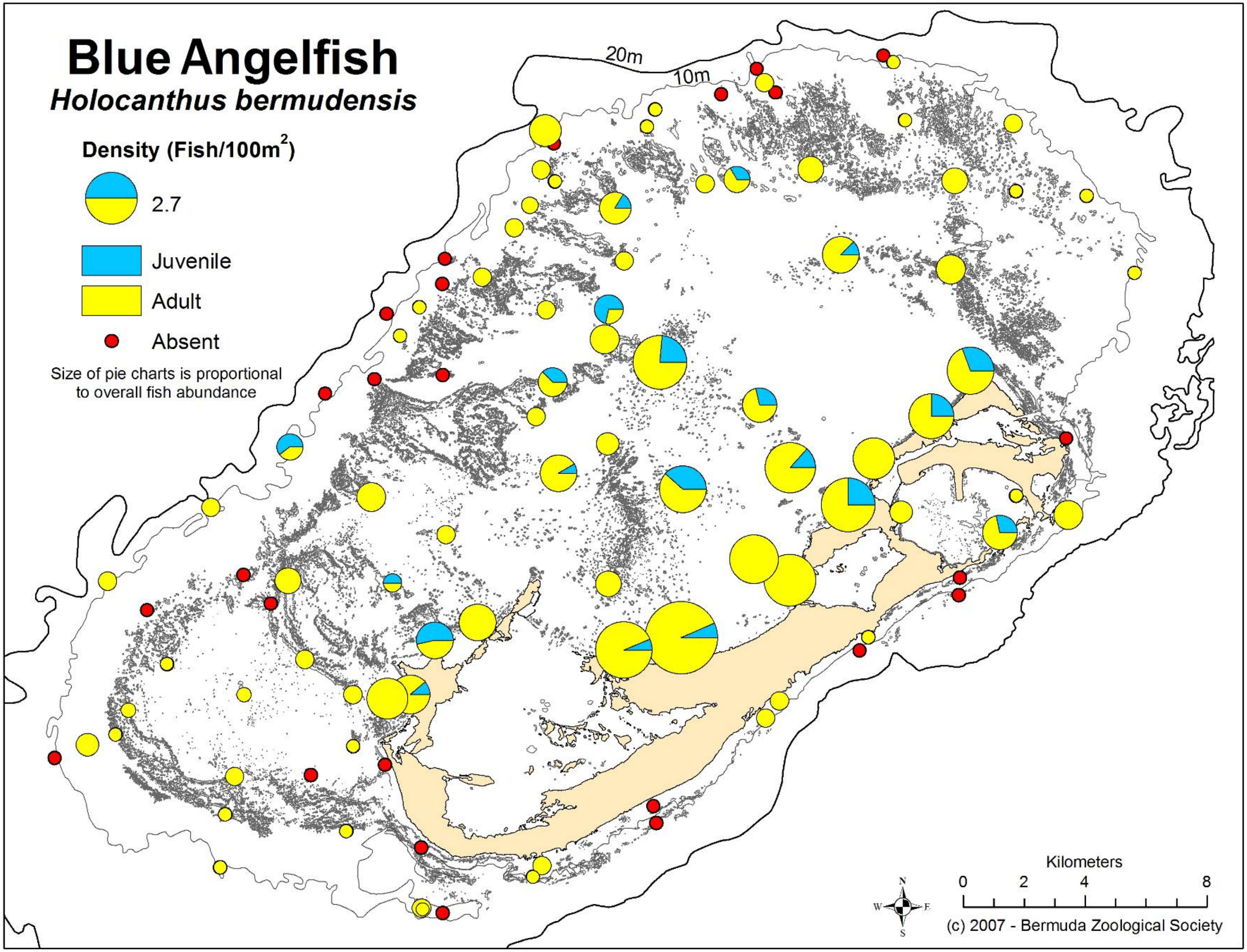

Fig. 35. Geospatial map illustrating juvenile and adult densities, derived from AGGRA surveys, of *Holocanthus bermudensis.*

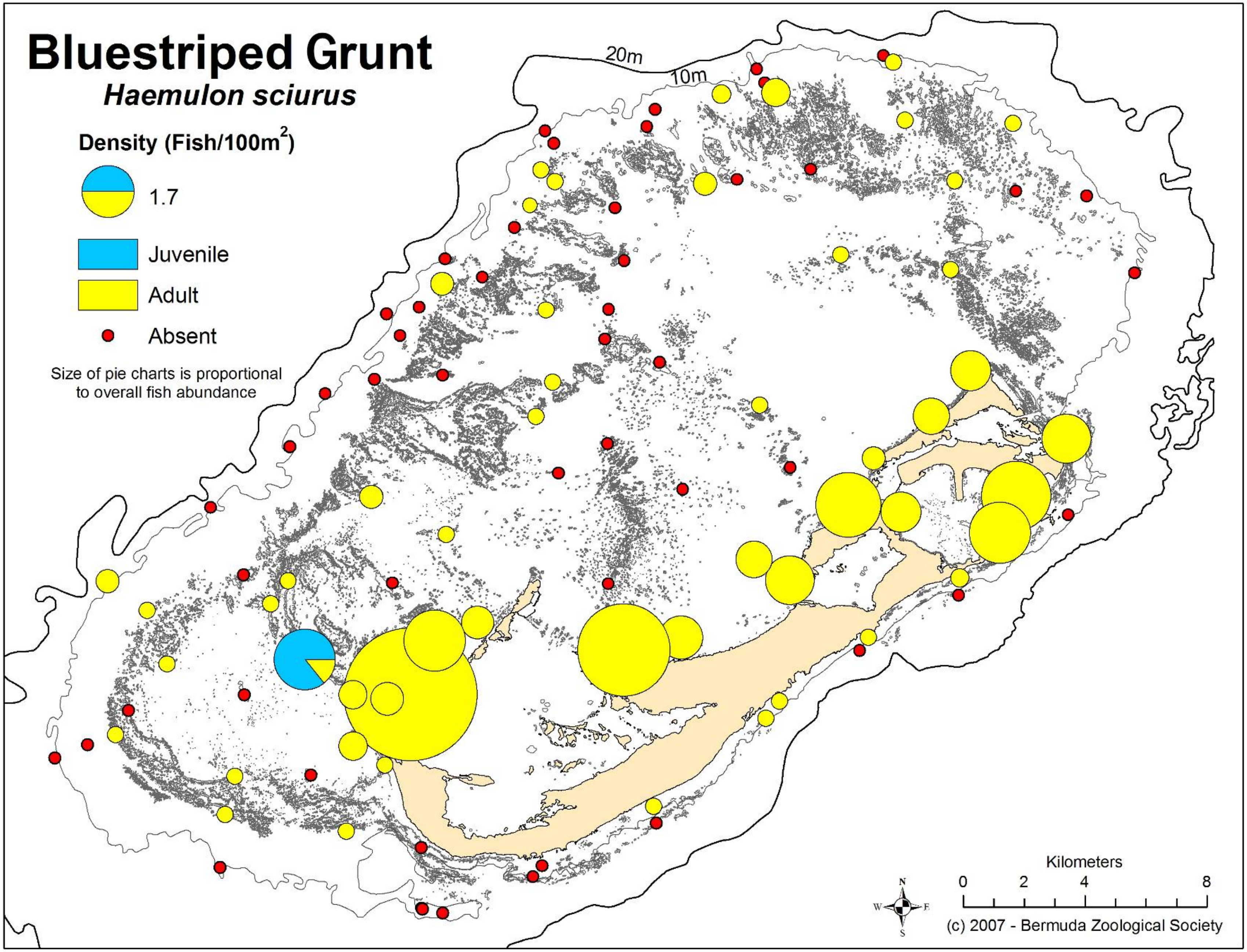

Fig. 36. Geospatial map illustrating juvenile and adult densities, derived from AGGRA surveys, of *Haemulon sciurus.*

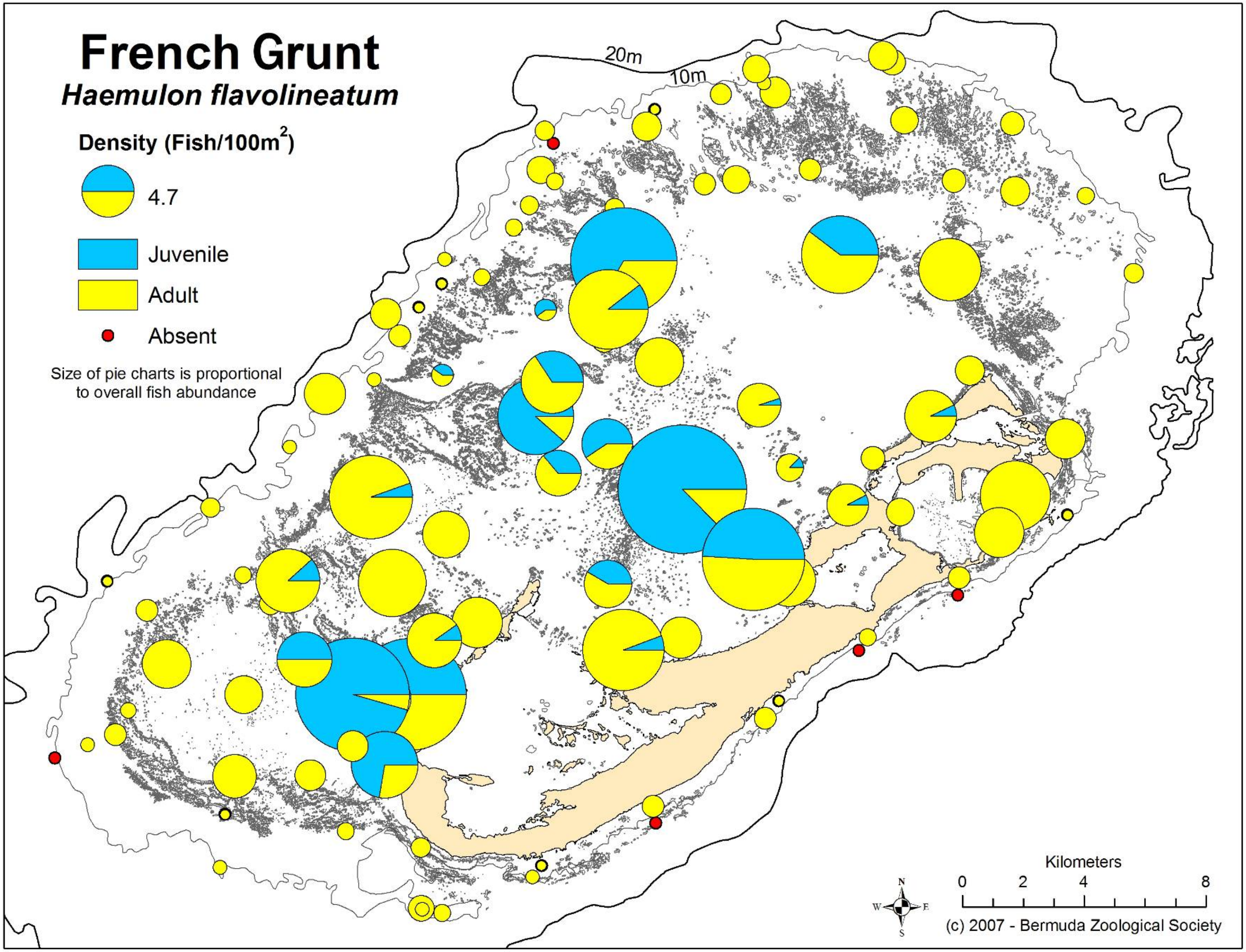

Fig. 37. Geospatial map illustrating juvenile and adult densities, derived from AGGRA surveys, of *Haemulon flavolineatum.*

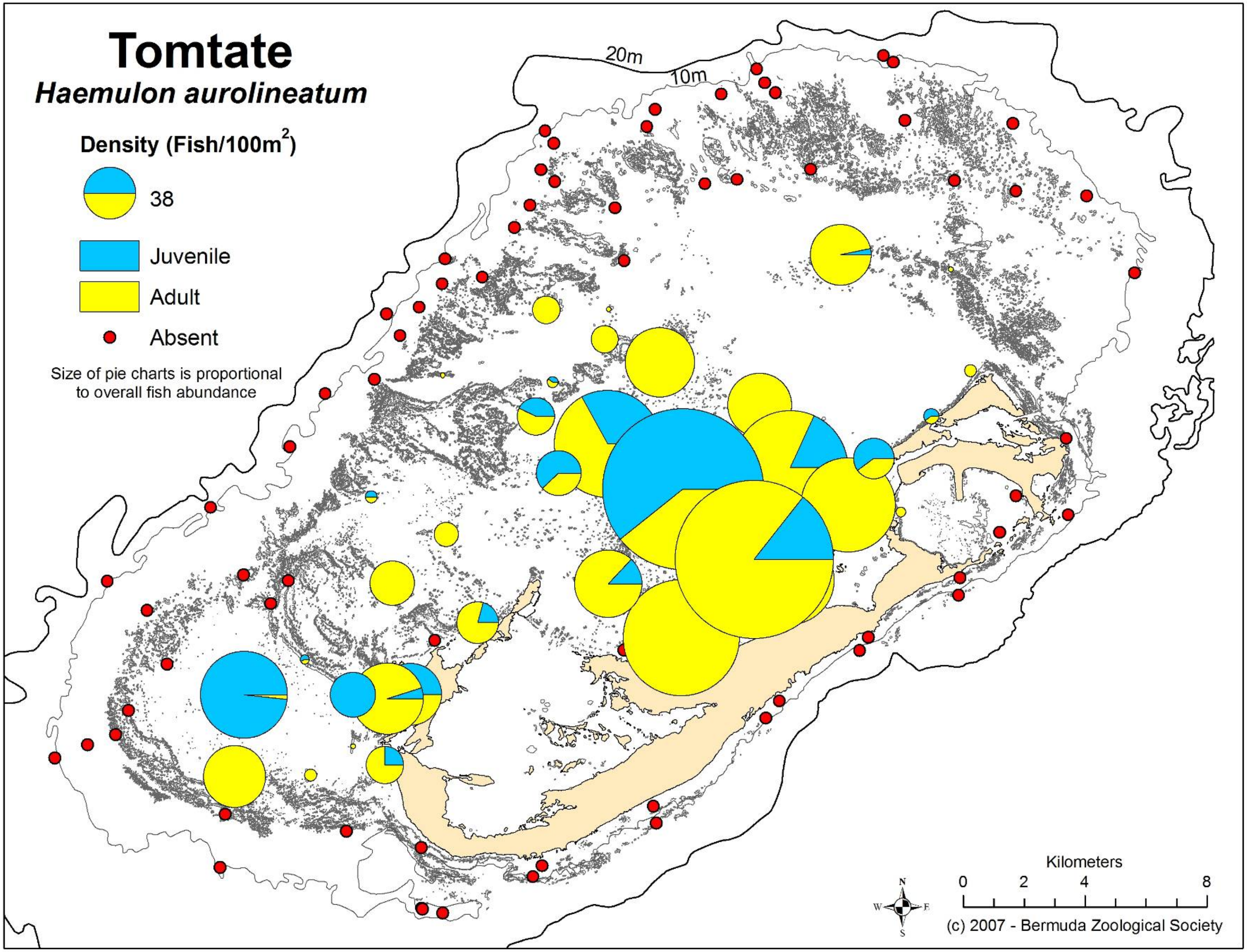

Fig. 38. Geospatial map illustrating juvenile and adult densities, derived from AGGRA surveys, of *Haemulon aurolineatum.*

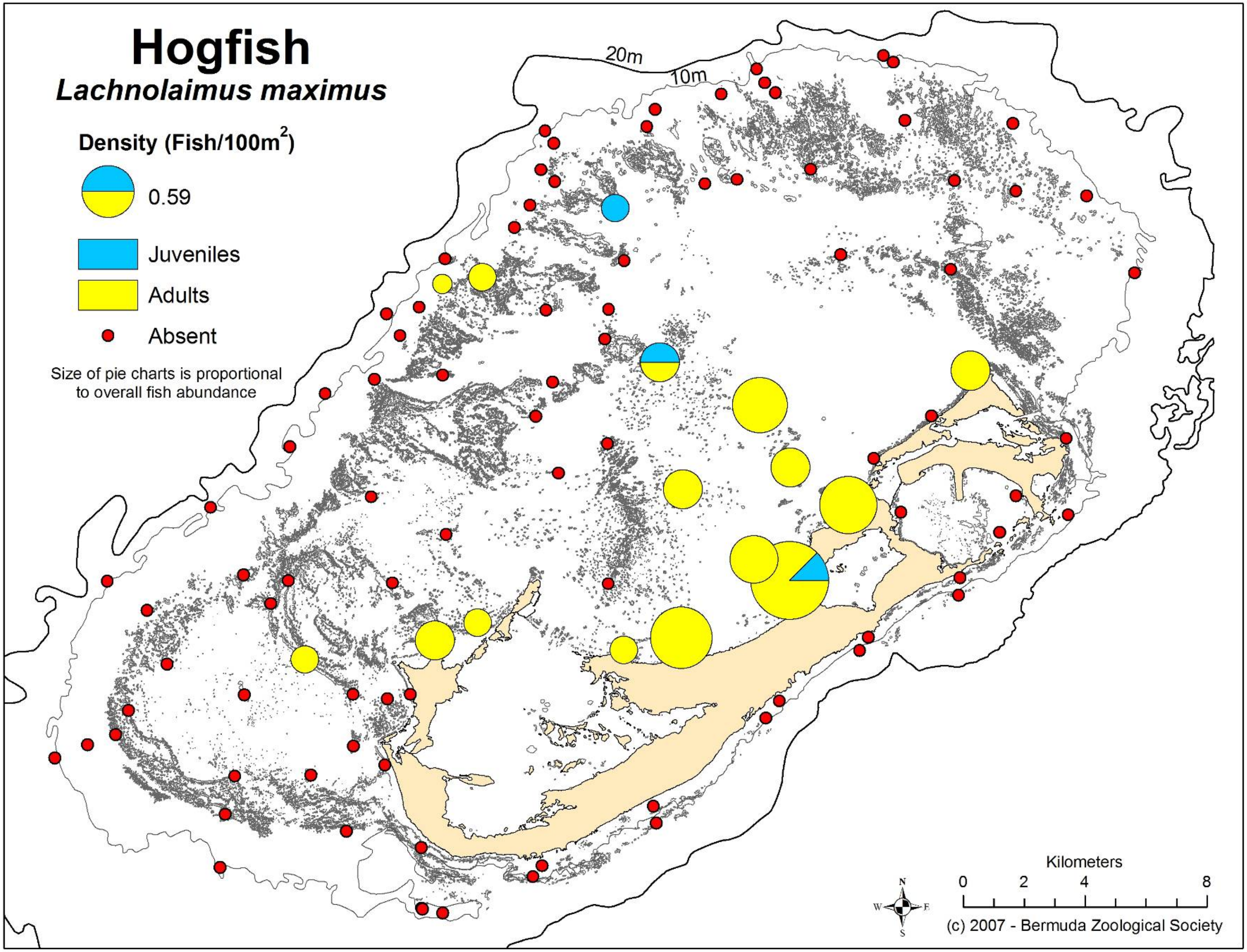

Fig. 39. Geospatial map illustrating juvenile and adult densities, derived from AGGRA surveys, of *Lachnolaimus maximus.*

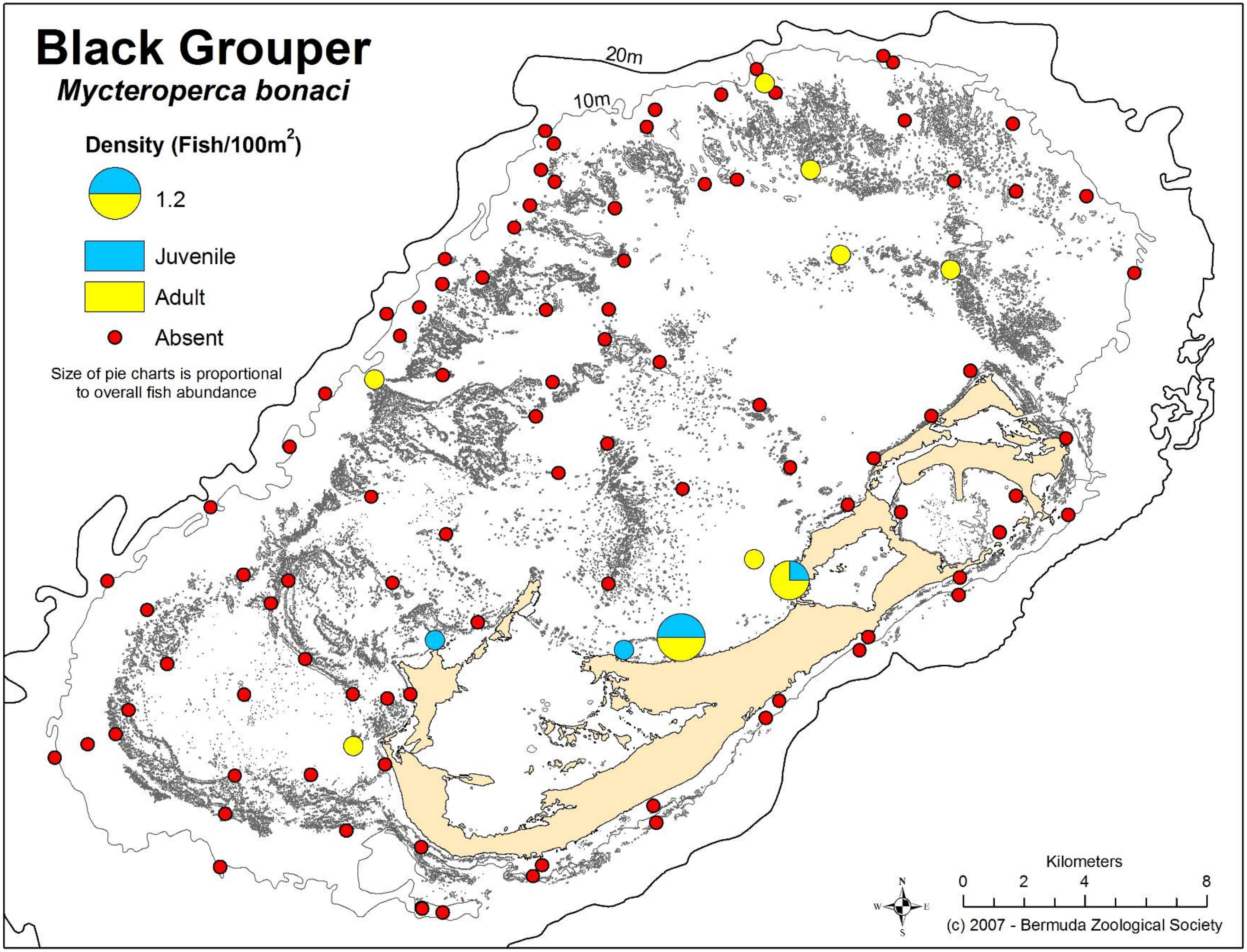

Fig. 40. Geospatial map illustrating juvenile and adult densities, derived from AGGRA surveys, of *Mycteroperca bonaci.*

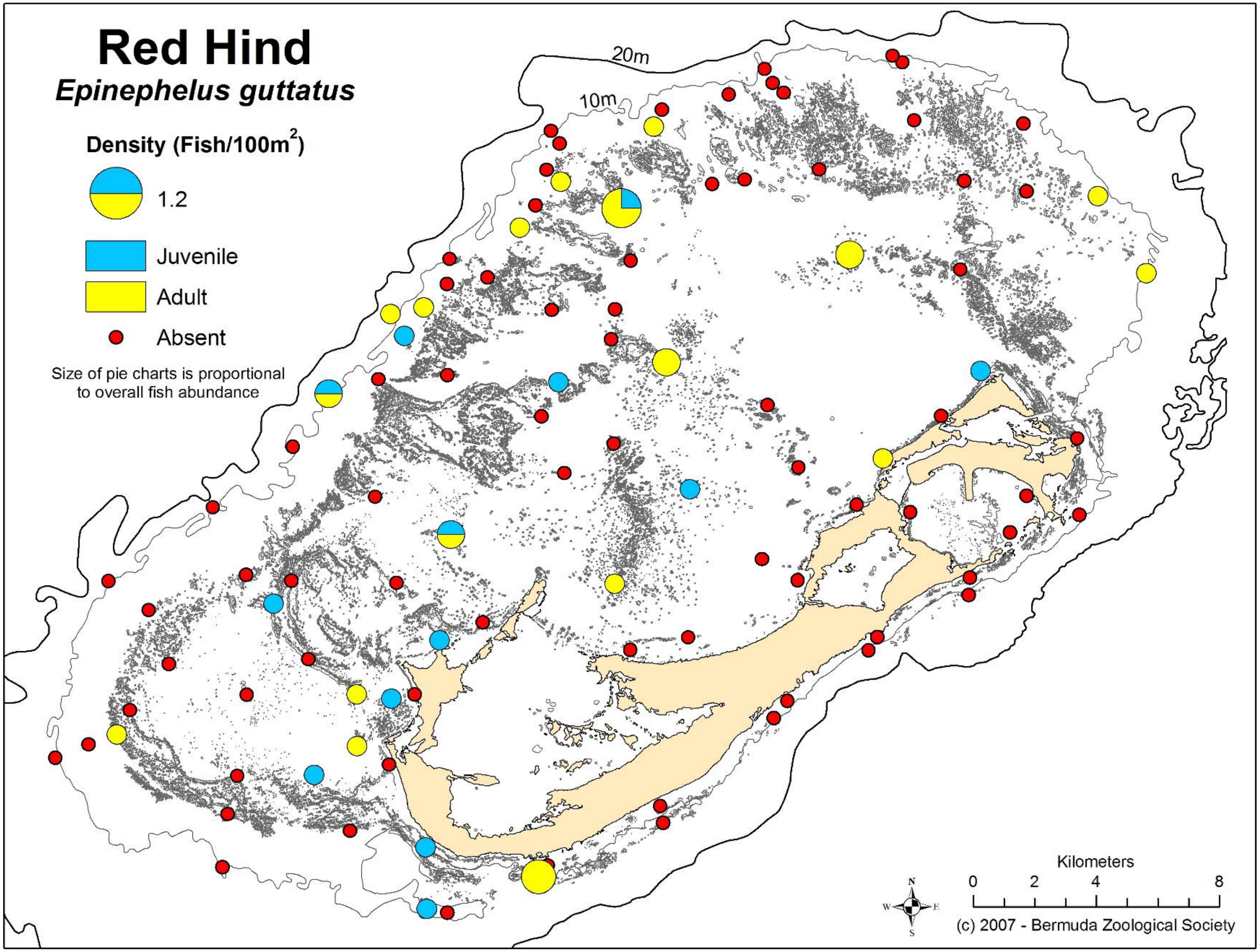

Fig. 41. Geospatial map illustrating juvenile and adult densities, derived from AGGRA surveys, of *Epinephelus guttatus.*

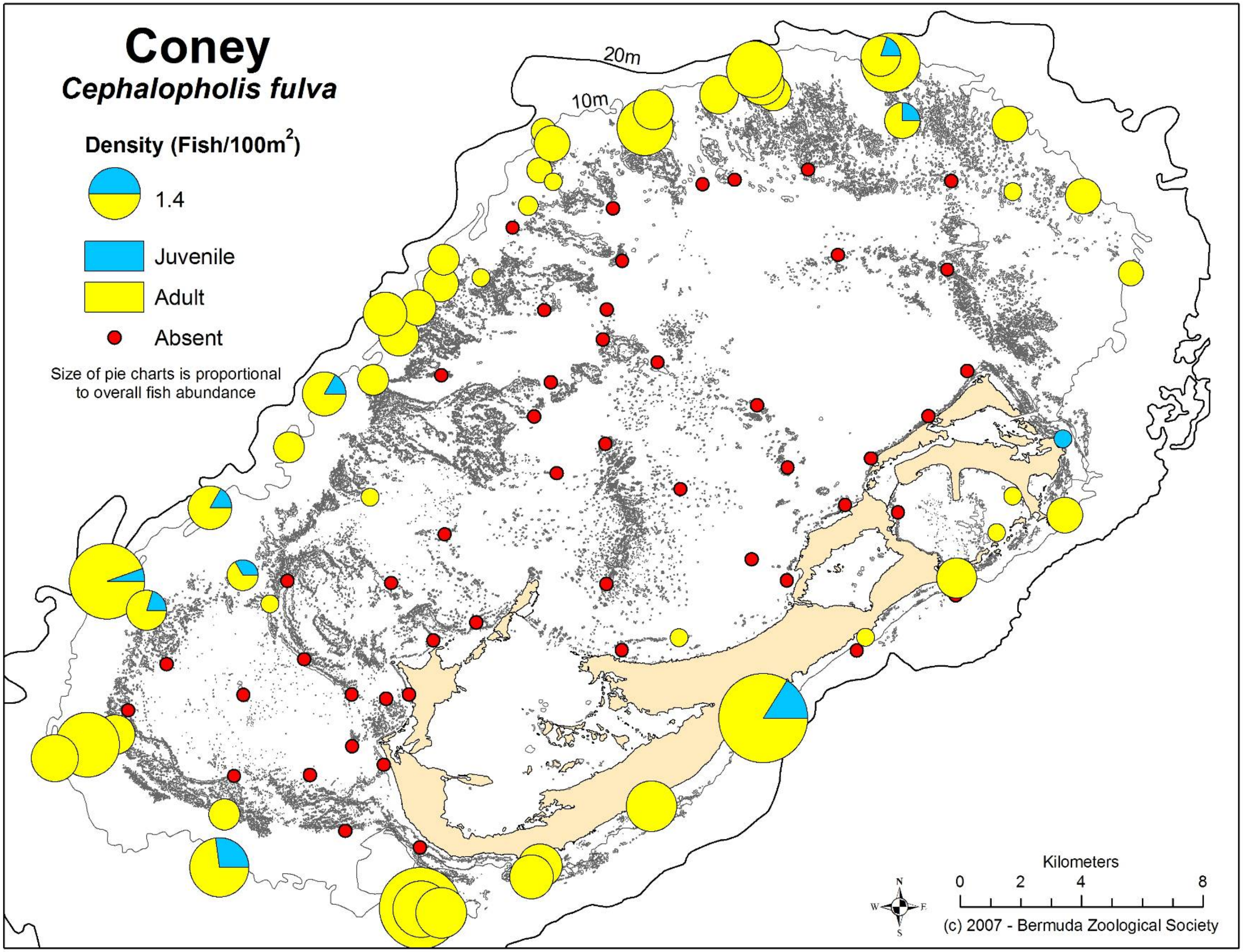

Fig. 42. Geospatial map illustrating juvenile and adult densities, derived from AGGRA surveys, of *Cephalopholis fulva.*

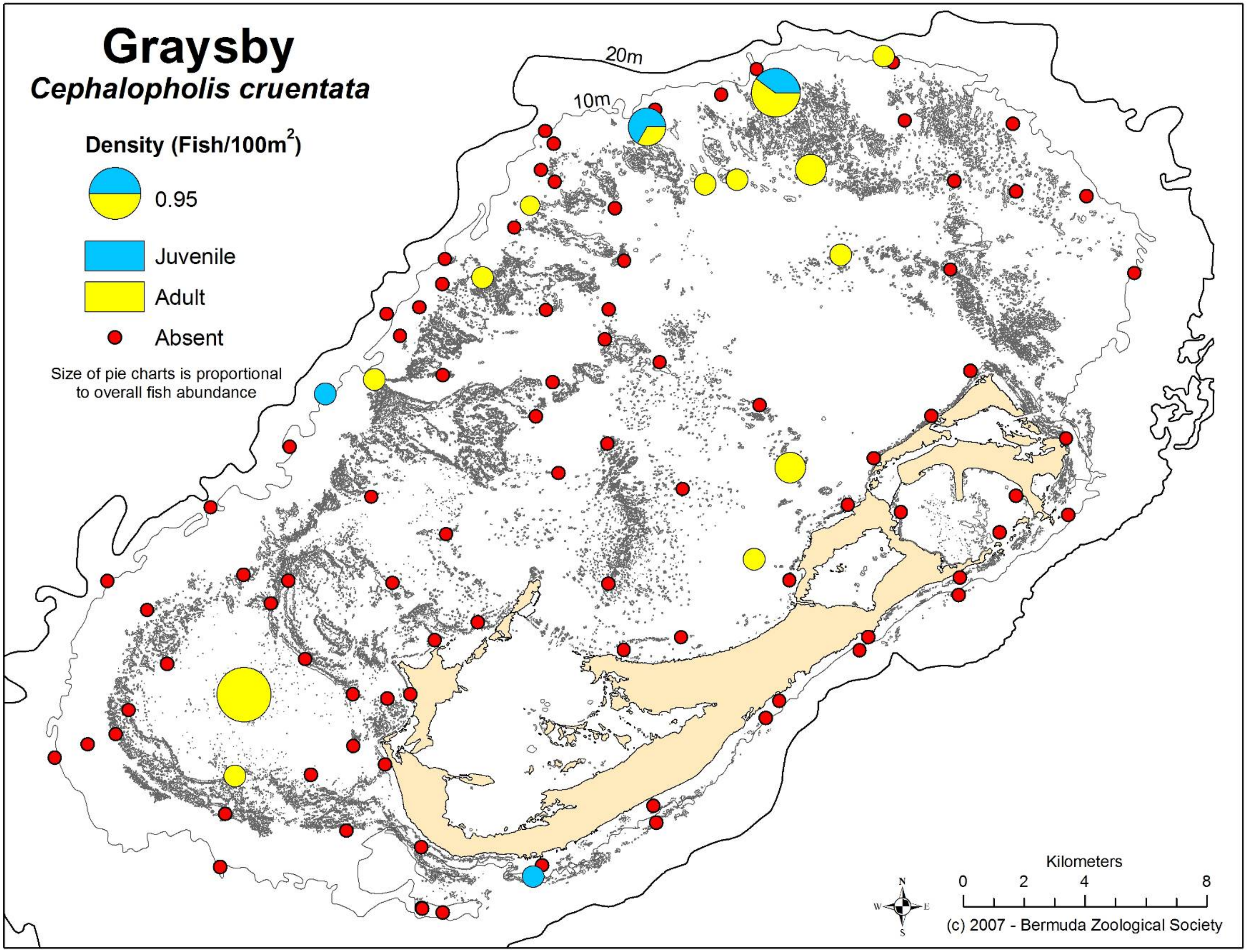

Fig. 43. Geospatial map illustrating juvenile and adult densities, derived from AGGRA surveys, of *Cephalopholis cruentata.*

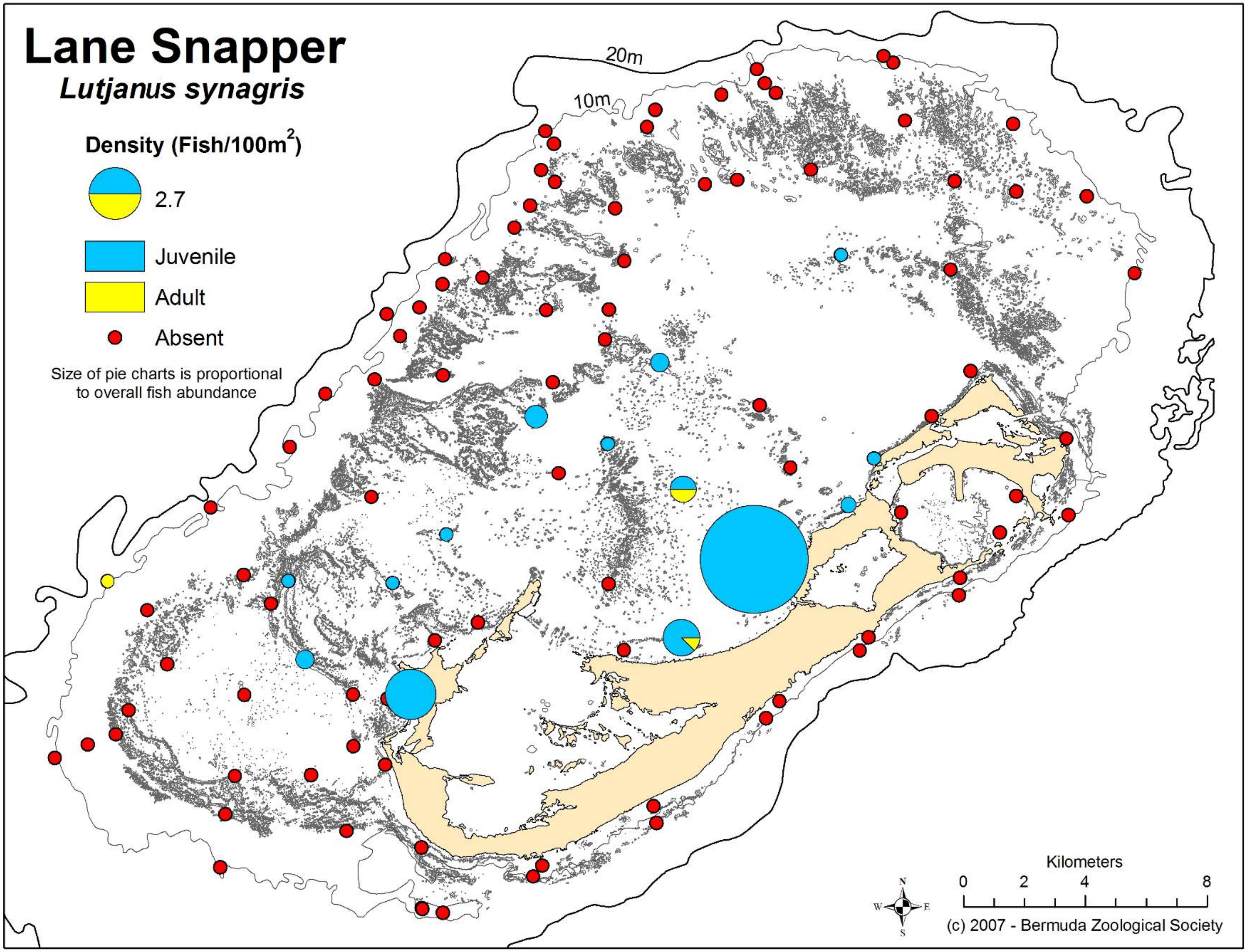

Fig. 44. Geospatial map illustrating juvenile and adult densities, derived from AGGRA surveys, of *Lutjanus synagris*.

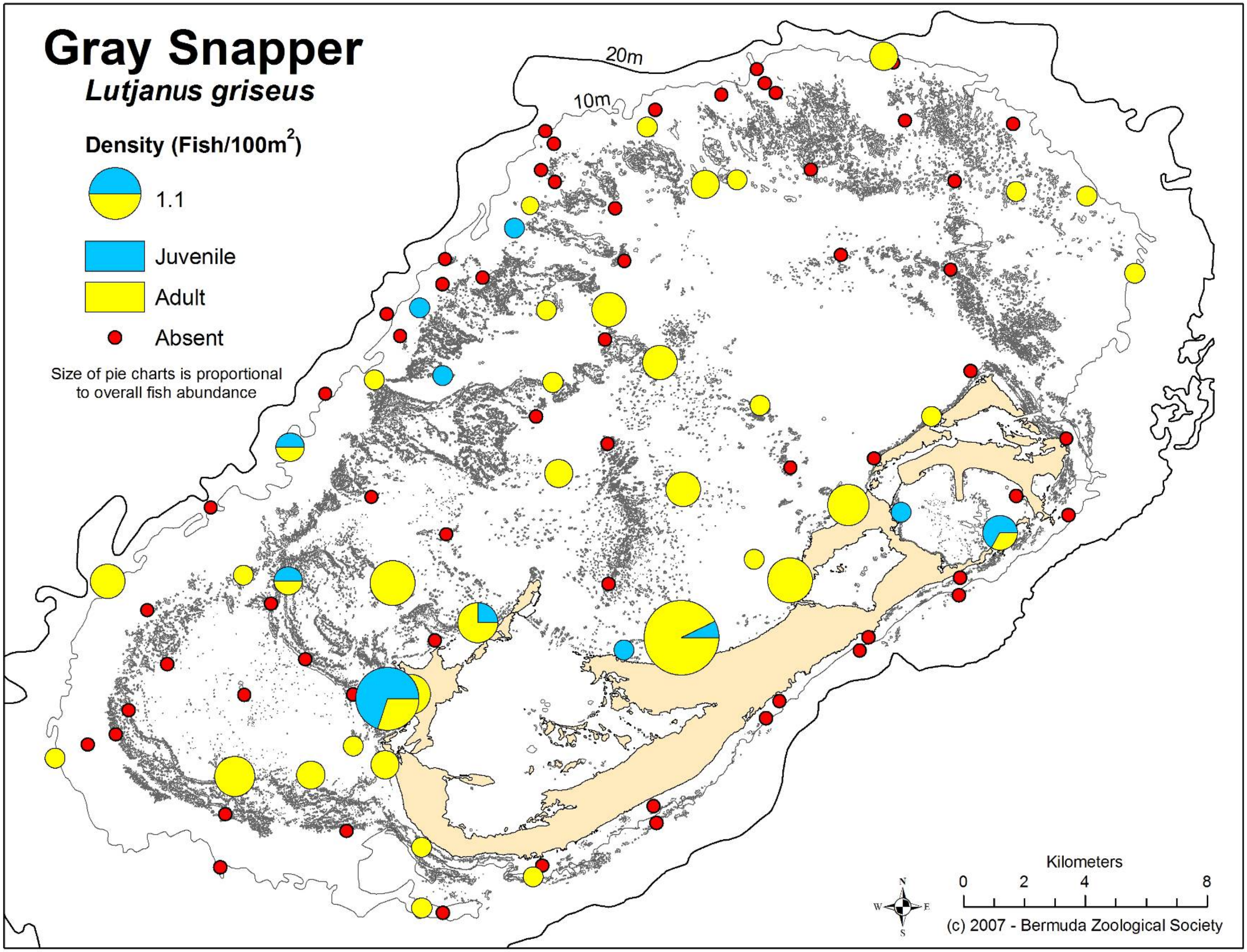

Fig. 45. Geospatial map illustrating juvenile and adult densities, derived from AGGRA surveys, of *Lutjanus griseus.*

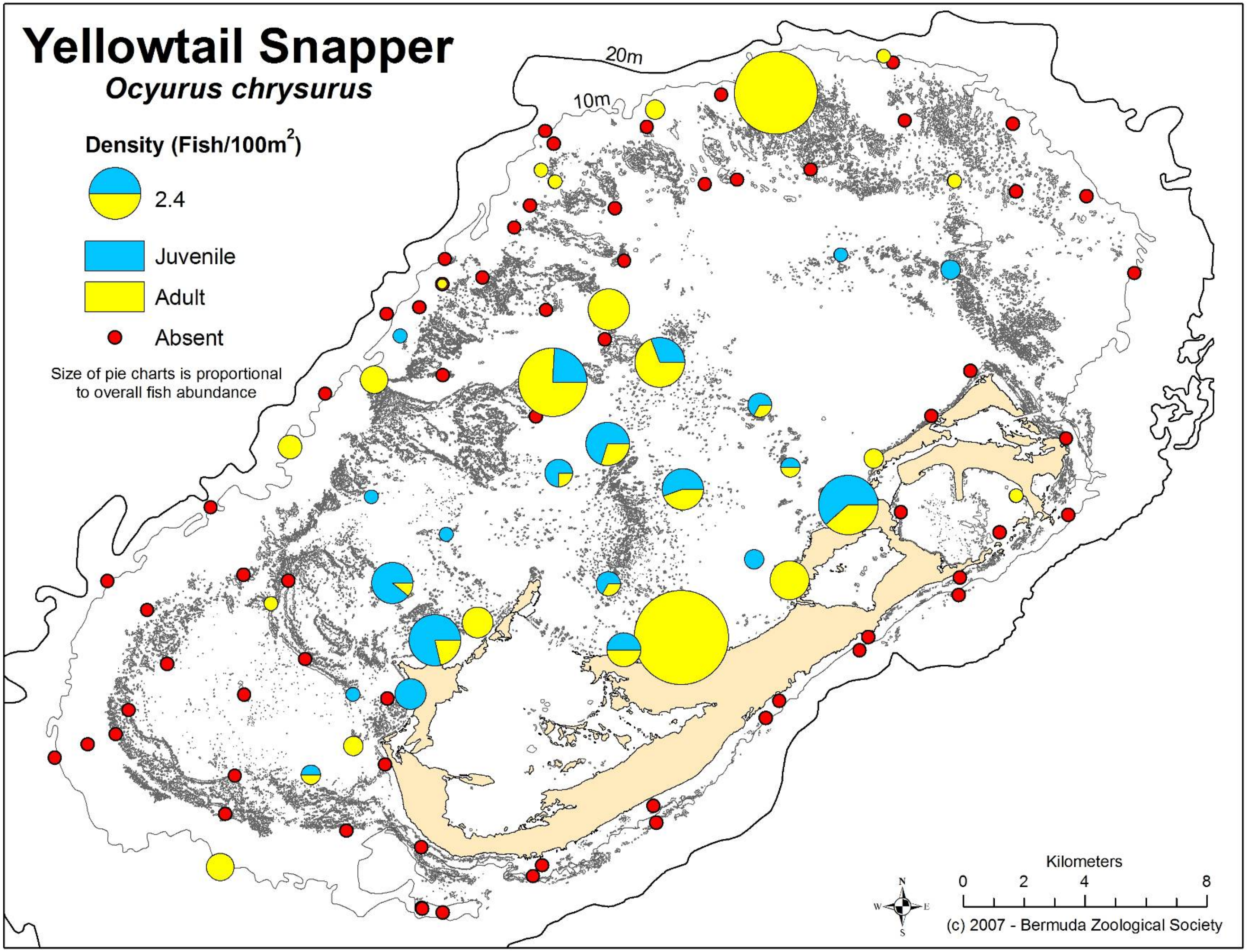

Fig. 46. Geospatial map illustrating juvenile and adult densities, derived from AGGRA surveys, of *Ocyurus chrysurus.*

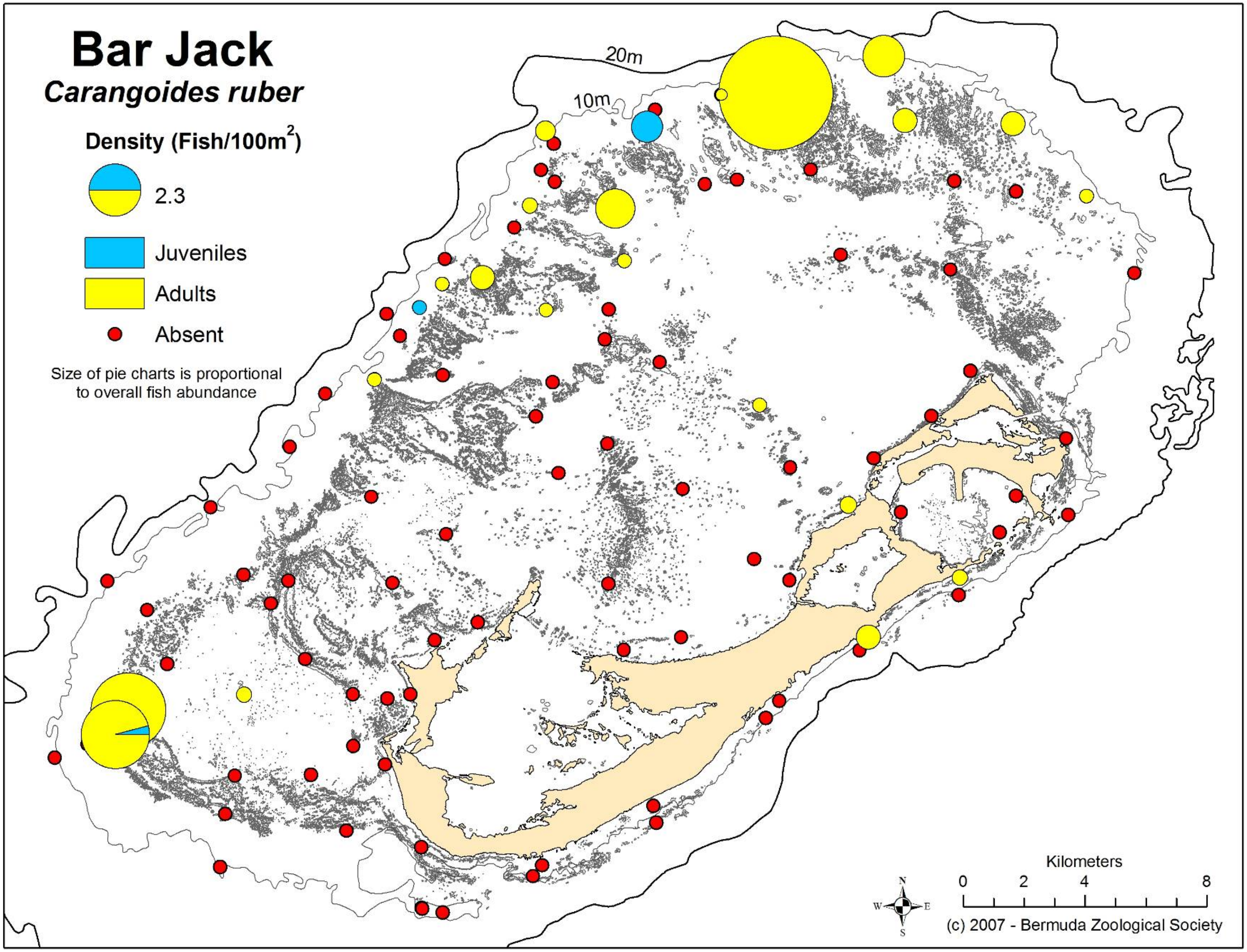

Fig. 47. Geospatial map illustrating juvenile and adult densities, derived from AGGRA surveys, of *Carangoides ruber.*

Juvenile habitat use by key species

Geospatial maps provided valuable data for key species that occupy different habitats at various life history stages, especially those using juvenile habitat. In general, inshore habitat appeared significant for juveniles of many species. For instance, of the species for which AGRRA density data was sufficient to infer habitat preference for both juveniles and adult (n = 24), fully 58% of species heavily used lagoonal patch or fringing reef as juveniles (Table 12). This trend is further reinforced by the scarcity of juveniles of any species on the exposed south shore reefs (Figs. 20-47). Only 17% of species exclusively used rim and fore reefs as juvenile habitat. Geospatial mapping of juvenile and adult densities further illustrated the significance of inshore habitat to those species characteristic the lagoon as well as those whose adult abundance peaks on offshore reefs (*e.g. Acanthurus bahianus* [Fig. 28]).

Table 12. Habitat Important to Juveniles of Key Species, Based on Geospatial Maps of AGRRA Densities Across the Bermuda Platform.

Lagoonal	**Offshore**	**Lagoonal and Offshore**
Scarus inserti	*Scarus taeniopterus*	*Sparisoma aurofrenatum*
Sparisoma chrysopterum	*Scarus vetula*	*Sparisoma viride*
Scarus coerulus	*Cephalopholis fulva*	*Acanthurus coerulus*
Acanthurus bahianus	*Cephalopholis cruentata*	*Holocanthus bermudensis*
Acanthurus chirurgus		*Stegastes variabilis/leucostictus*
Chaetodon capistratus		*Epinephelus guttatus*
Chaetodon ocellatus		
Chaetodon striatus		
Haemulon flavolineatum		
Haemulon aurolineatum		
Mycteroperca bonaci		
Lutjanus griseus		
Lutjanus synagris		
Ocyurus chrysurus		

Of the AGRRA species that used inshore juvenile habitat, about half appeared to recruit uniformly across the platform. Other species, however, exhibited finer distributions of juvenile distribution within inshore habitats. For example, *Haemulon aurolineatum* (Fig. 38), *H. flavolineatum* (Fig. 37), *Lutjanus griseus* (Fig. 45) and *Ocyurus chrysurus* (Fig. 46) all appeared to peak in large numbers on fringing and patch reefs both in the central, north lagoon and at the west end of the island. However, the ubiquitous herbivore species that were conspicuously rare on these reefs as adults (*Acanthurus chirurgus* [Fig. 27], *Sparisoma viride* [Fig. 21], *S. aurofrenatum* [Fig. 23], *S. chrysopterum* [Fig. 22], and *Scarus inserti* [Fig. 24]) were similarly scarce as juveniles. Rather, their juveniles were otherwise widespread or concentrated off the west end of Bermuda (*e.g. Acanthurus chirurgus* and *Scarus inserti*).

Other key species displayed similarly idiosyncratic spatial distributions of juveniles. Young *Epinephelus guttatus* (Fig. 41) were most often seen to the west and southwest of the island, proximate to their protected spawning grounds. Juveniles of another important commercial species, *Haemulon sciurus* (Fig. 36), were only observed at a single western site. The commercial lutjanid, *Lutjanus synagris* (Fig. 44), was also found on shallow reefs in this area, but was more often found on reefs in the central lagoon adjacent to adult deep lagoon habitat. In this way, the species was comparable to *Holocanthus bermudensis* (Fig. 35), which was also distributed as juveniles along the margins of the central lagoon. The commercial serranid, *Cephalopholis fulva* (Fig. 42), displayed the highest proportion of juveniles in the regions of highest overall density, offshore in the northwest and southwest. Three important herbivores also appear to have restricted areas of juvenile habitat. Distributions of *Scarus vetula* (Fig. 26) and *S. taeniopterus* (Fig. 25) juveniles reveal a distinct preference for outer patch reefs rim reefs north of the central lagoon. *S. taeniopterus* juveniles, in particular, were abundant at several MPA and control sites. The distribution of *Acanthurus bahianus* (Fig. 28) juveniles also favoured a relatively small region, inshore reefs off the west end of the island.

Discussion

This study used metrics from two different survey protocols (REEF roving diver and AGRRA) to examine spatial patterns in fish abundance and assemblage composition over relatively small spatial scales on the Bermuda reef platform. Unsurprisingly, correspondence between the two protocols was not exact. For example, AGRRA surveys appeared to overestimate the relative contribution by density and biomass of invertivores and planktivores on inshore reefs because important species of those functional guilds on offshore reefs were not included in the protocol. Most widespread piscivores were included in AGRRA protocol, yet still the broader areas covered by REEF roving diver surveys better captured the relative abundances of these rarer species. In addition, REEF data allowed a complete species register for estimates of species richness. However, for common species, the rigorous counting method in AGRRA protocol probably resulted in abundance estimates that were closer to actual means than estimates derived from the broad intervals represented by the four abundance categories in REEF protocol.

Despite differences in emphasis and resolution between REEF and AGRRA protocol, most trends were mutually indicated by both data sets. Moreover, the approaches were often complimentary. For instance, the full compliment of REEF species provided for a more ecologically-relevant basis for detecting multivariate patterns in assemblage distributions than when using AGRRA data. In turn, the higher resolution of abundance trends for select species offered by AGGRA data in geospatial maps enhanced the interpretation of those multivariate differences among fish assemblages. Findings from both data sets indicate a large degree of variation in fish assemblage composition over relatively small spatial scales across the Bermuda reef platform. The causes of such variation are typically complex and interrelated, and may include local differences in productivity, hydrology, structural heterogeneity, community organization, larval dispersion rates or fishing pressure. An analysis of factors influencing the spatial partitioning of Bermudian fish assemblages, however, is outside the scope of this study. Instead, the differences apparent among reef morphologies and regions of the reef platform have suggested some biotopes or geographical regions whose importance to key species or ecosystem function warrant conservation. Specifically, these findings have highlighted the following:

i) the need for the effective functioning and coverage of MPA's
ii) the under-representation of certain reef types as key habitats for fish
iii) the existence of geographically distinct sub-habitats within reef types that host unique assemblages of fish
iv) the rationale for more informed and coordinated management of protected areas

The need for better coverage and functioning of MPA's in Bermuda

Current MPA coverage represents less than two percent of Bermuda's reef platform, while large no-take reserves designed to conserve ecosystems and sustain fisheries ideally comprise at least 30% of marine areas (Pitcher, 2001). This disparity, coupled with the widespread low abundances of high trophic fish (including MPA's; see Chapter 1), suggests that habitat protection in Bermuda is not working to maximum effect. The moderate densities of herbivores and low densities of piscivores and commercial species across the Bermuda platform compared to a range of Caribbean islands (Kramer, 2003; Newman *et al.*, 2006) suggest reef fish populations are, indeed, either in recovery or at a carrying capacity. The virtual extirpation of several large serranids and the subsequent dominance of small serranids (*e.g. Cephalopholis fulva)* also indicate major shifts in competition of predation dynamics (Chiappone *et al.*, 2000) on Bermuda's reefs. The historic abundance of serranids and lutjanids prior to the widespread use of fish traps illustrates the formerly high carrying-potential of the island's reefs. Bermuda's fish populations are thus presumed to be in recovery under protective measures (see Hodgson, 2000) but potentially limited by a combination of factors: altered ecosystem organization, life history traits of key species, selection by low-to-moderate fishing pressure across the platform, and any degradation of key habitats. Consequently, whether or not current MPA's positively affect fish populations, modified no-take zones that account for distributions and life history patterns of target species may be more successful than current ones. In contrast to the original delineation of MPA's, which aimed to prevent anchor damage at popular dive sites, an ecosystem approach based on spatial data could accommodate the protective needs of those most sensitive species while conserving the ecosystem integrity of areas of general ecological importance.

Significant habitats under-represented by current MPA coverage

This study found that current MPA's, concentrated on the rim, covered only a small proportion of the varied habitats and ecologically-important areas of the reef platform. The most fundamental differences between the amply covered rim reef habitat and other reef types were apparent in functional modes of the species dominating those habitats. Interestingly, the proportions of species comprising functional groups were fairly constant between fringing, patch, rim and fore reef habitats. The fewer sites at the fringing and fore reef likely under-sampled the species present in these habitats. On the other hand, the striking resemblance in proportions with their neighbouring patch and fore reef habitats perhaps suggest that these basic proportions would not vary much with more sampling. While the causes of functional group uniformity across reef types are unclear, it is apparent that functional redundancy, in terms of species, was highest in herbivores and invertivores and lowest in piscivores and planktivores. This trend in functional redundancy suggests a degree of resiliency to herbivory and invertivory on all reef types (Micheli and Halpern, 2005), yet piscivorous and planktivorous functions that would be more impacted by species loss from habitat degradation or exploitation. From historical records (Smith-Vaniz *et al.*, 1999), planktivores appear to have never been a speciose guild in Bermuda and may be naturally limited in species richness by dispersal or other environmental factors such as food limitation within the relatively oligotrophic waters of Bermuda. In contrast, the virtual removal of several functional piscivores by overfishing (*i.e. Epinephelus striatus*, *E. morio*, *Mycteroperca tigris*, *M. interstitialis*, *M. venenosa*, *M. microlepis*, *Alphestes afer*) has greatly reduced the functional redundancy and resiliency of this guild. Instead of enhancing functional resiliency, the gradually increasing populations of *M. bonaci* may be pre-empting the recovery of other large serranids. From a purely functional perspective, this implies the importance of preventing the loss of historically-overexploited, high-trophic species on all reef types for the maintenance of resilient predatory functions on coral reefs.

Fundamental differences between reef types were evidenced by variation among assemblages and the functional differences among the predominant species. For example, differences in the relative and absolute densities and biomasses of functional guilds among reef zones suggest that these areas may host communities of contrasting structure and function. Furthermore, regions within reef zones appear to host similar variation. For instance, the preference of rim and fore reef by many scarid species (*e.g. Scarus vetula, Sparisoma aurofrenatum, Scarus taeniopterus*) and the degree to which herbivorous species structured offshore assemblages implies ecological significance of this habitat to this functional group. Indeed, the high densities of *Scarus taeniopterus* at northern rim sites suggests the localized importance, and perhaps nursery function, of rim reefs. Their preference of rim reef habitat may reflect higher algal growth on the low coral cover substrate of the rim. The moderate densities of other scarids (*e.g. Scarus inserti*) and acanthurids on fringing and patch reefs illustrate the importance of these habitats to herbivores and the ubiquitous and adaptable nature of this functional group.

The apparent dominance of invertivores in fringing and patch reef fish assemblages, indicated by both univariate and multivariate comparisons of AGRRA data, may reflect a distinct community dynamic existing on inshore reefs that does not exist offshore. Invertivory as a characteristic of inshore assemblages is paralleled by REEF data, despite the inclusion of several additional offshore labrid species under this protocol. The predominance of invertivores on inshore reefs is mostly driven by the abundance of *Haemulon aurolineatum*. However, larger invertivores also appear to prefer this lagoonal habitat. For example, strong associations with fringing reefs exist for the commercial species, *Haemulon sciurus*, as well an inshore preference by *Lachnolaimus maximus* . The almost exclusive use of lagoonal reefs (and intervening sedimentary habitats) by the vital commercial invertivore, *Lutjanus synagris*, further emphasizes the importance of inshore reefs to commercial interests as well as an entire guild of Bermuda’s ichthyofauna. Moreover, the anecdotal preference of patch reefs by spearfishers (MEP, unpublished technical report) highlights the risks of not protecting areas of this habitat.

Piscivores, like herbivores, generally peaked in abundance on rim and fore reefs. Perhaps unsurprisingly, this pattern parallels the distribution of the most abundant piscivore, *Cephalopholis fulva*. While key habitat for this species, offshore reefs may not be essential habitat for the entire functional group, but only the currently dominant one. For example, the commercial lutjanids, *Lutjanus griseus* and *Ocyurus chrysurus*, were found in the greatest densities not on offshore reefs, but on fringing and patch reefs – a trend reinforced by prior studies (Luckhurst and Ward, 1992; Nagelkerken, pers. comm.). While higher estimates of serranids from REEF surveys suggested that AGRRA may have inadequately captured abundances, greater inshore density appeared to be true for the large, commercial serranid, *Mycteroperca bonaci.* Inshore reefs, on the whole, thus may have a greater ecological value for piscivores and commercial species as a whole.

Perhaps the most compelling indication of the ecological value of inshore reefs is the apparent nursery function they serve for many species. That the vast majority of the 25 species (for which size data was sufficient) associated with inshore reefs as juveniles indicates a significant ecological service provided by this habitat across taxa. Similar results were also reported by Huijbers *et al.* (in press). The differential use of habitat during various stages in a species' life history implies the necessity to protect each associated habitat to safeguard the entire life cycle of target species. Such protection would also conserve valuable ecological functions. For example, juvenile *Acanthurus bahianus* closely associate with inshore reefs (also documented by Robertson *et al.,* 2005) along with other juvenile herbivores (this study and Nagelkerken, pers. comm.), but their large adult populations across the reef platform ensure grazing in all reef zones. Similarly, *Chaetodon capistratus* juveniles were found almost exclusively in the lagoon. Adult chaetodontids inshore and offshore form a close association with coral reefs and their dietary selectivity implies ecological value in structuring coral assemblages (Berumen *et al.,* 2005). Spatially explicit protection across a variety of habitats may not be essential for all species, as some species (*e.g. Epinephelus guttatus* and *Sparisoma viride*) seem to share uniform size-distributions across all reef types. However, the uneven spatial distributions in the majority of species demand consideration in the creation of effective MPA's.

The considerable differences in habitat use by key species and functional groups alike suggest greatly different community structure and function, presumably adapted to local patterns in resource availability, hydrology and community interactions. The partitioning of communities along rough lines of reef morphology also implies the need for protection of representative biotopes that conserve both ecosystem integrity and the populations of key species. In particular, rim and fore reefs appear to be significant habitat for herbivores. The high species richness of many reefs along the northern rim suggests that this habitat is also important for maintaining assemblage biodiversity. The concentration of sites with high species richness along the rim perhaps reflects steep gradients of environmental conditions and sub-habitats in the transition from lagoon to fore reef biotopes. Although 31 MPA's (totaling ~ 14 km^2) currently protect such rim habitat, at least two sites of highest species richness (50 – 55 species) occur outside reserves. Other rim reefs high in species richness similarly lie in under-protected sub-habitats of this reef.

The great ecological significance of fringing and patch reefs as juvenile habitat for species from all functional guilds, as well as many commercial species, indicate these reef zones as significant and under-represented habitats. Similar to rim reefs, some patch reefs in the central, north lagoon harbour high species richness. The patchy distributions of these species rich reefs within the North Shore Coral Reef Preserve suggest considerable environmental heterogeneity over small spatial scales within the lagoon. In turn, this scattered distribution also points to the difficulty of preserving these "hotspots" of species diversity without large reserves. However, the importance of inshore reefs as critical habitat for both juveniles and adults of a large proportion of Bermuda's reef species demonstrates the need for protecting entire assemblages where they are most rich.

A rough framework for conserving inshore reefs already exists in Bermuda's system of MPA's. Two seasonally-protected areas exist, one to the island's northeast and one to the southwest, whose placement protects from harvest the offshore spawning aggregations of *Epinephelus guttatus.* The southwestern no-take zone also includes a significant proportion of fringing, patch and rim reef in addition to fore reef, and thus acts as a seasonally-active reserve for these biotopes. With the exception of two small protected areas (H.M.S. Vixen and Commissioner's Point), the southwestern protected area is the only no-take zone that covers any inshore reef habitat. While the occurrence of more juvenile *Epinephelus guttatus* off the west end and southwest of the island may reflect some "spill-over" recruitment from protected spawning aggregations, there is evidence that rotating closures may not be effective for protecting permanently-resident assemblages unless closure is continuous for many years (Williams *et al.*, 2006). Furthermore, establishing a permanent reserve here may encompass some low-qaulity habitat and overlook areas of greater ecological value elsewhere on the reef platform.

The highest densities of *Stegastes variablis* or *S. leucostictus* occurred inshore in the southwest region. Such large populations of these species, which can lead to excessive mortality of corals, may indicate degradation of those reefs already. Thus, while current seasonal reserves play a significant role in conserving remaining serranid stocks, permanent reserves designed to conserves entire communities would be better placed in areas of more uniformly high habitat quality. Data from this study point to the existence of reef areas and sub-units of habitat within reef zones that host higher species richness, higher abundances of key species and important ecological functions. For reasons of higher productivity or unusual community attributes, these sub-habitats may indeed prove to be better options for spatial protection.

Small-scale assemblages within reef zones

Ordination of both multivariate AGRRA and REEF data at coarse levels of resemblance revealed distinctions between inshore and offshore fish assemblages. The occurrence of multiple inshore assemblages in both data sets might be thought to reflect greater variation in environmental conditions within the lagoon. We would expect this greater diversity of fish assemblages within the lagoon as a result of the patchy distribution of reefs within the lagoon (Belmaker *et al.*, 2005; Nunez-Lara *et al.*, 2005) as well as the existence of adjacent back-reef habitats such as seagrass and algal beds (Grober-Dunsmore *et al.,* 2007). It seems, however, that comparable diversities of smaller-scale assemblages exist both within the lagoon and on the offshore reefs as seen by the similar number of sub-clusters in each environment. Small-scale environmental heterogeneity thus appears to influence assemblage structure on the continuous swathes of rim and fore reef as well as within the obviously varied lagoonal habitats. The existence of distinct assemblages in adjacent rim and patch reef habitat further suggests a role of this morphological feature in diversifying environmental conditions along the transition from lagoonal to offshore waters.

The most striking example of fish assemblages associating with offshore reef sub-habitats was the tight clustering of all but one of the MPA's and control sites. The clustering of these sites corresponds well to the similarity in fish abundances at MPA's and control sites, yet does not explain why these sites cluster distinctly from other rim reefs. The higher abundances of fish at these sites in all functional groups, though, indicate them as being highly productive. The studied MPA's, originally chosen for their value as dive sites, appear to have captured a sub-habitat of rim reefs with high fish abundance – a situation distinct from average rim reef conditions. This sub-habitat also appears to promote high species richness. Control sites have never had any spatial protection, but were chosen to be comparable in all other aspects to MPA's. The common feature tying these sites together is likely the presence of adjacent tidal passes. AGRRA densities at these sites do not indicate higher abundances of all functional guilds at these sites, perhaps reflecting the limited number of species included in this protocol. Nonetheless, the data do suggest that this sub-habitat might enhance herbivore populations. In fact, high AGRRA densities of juvenile *Scarus taeniopterus* and *S. vetula* raise the possibility of this sub-habitat's use as a nursery. The concentration of tidal passes along the northern rim an associated profusion of *Scarus taeniopterus, Sparisoma viride* and *S. chrysopterum* may also account for the clustering of northeast and southwest sites which have far smaller populations of these species. REEF data shows that all functional groups are more abundant on rim reefs adjacent to tidal passes. Higher mean densities of commercial species at these sites than at other rim sites further attest the productivity of this sub-habitat. While seven or eight MPA's afford protection to this sub-habitat, approximately thirty additional tidal passes, mostly in the northwest quadrant of the reef platform, lack any protective measures. Considering the apparent significance of this sub-habitat across taxa, current MPA coverage of these features may be insufficient.

Small, highly-isolated patch reef sites in the lagoon also ordinated together and appear to harbour fish assemblages distinct from other inshore reefs. The abundance of resident *Heamulon sciurus* has previously been found to be characteristic of these reefs (Bardach and Menzel, 1956; Bardach, 1959) and was confirmed here. These fish apparently account for, in part, the higher proportion of carnivores on these isolated reefs reported by Bardach (1959). The dramatic decline of *Epinephelus striatus, E. guttatus* and *Mycteroperca* spp. on these reefs since Bardach's surveys, however, seems to have reduced carnivore abundance and shifted carnivore dominance towards *Lutjanus griseus, Cephalopholis fulva* and *Haemulon sciurus*. Additional importance of this sub-habitat is suggested by the fact that juveniles of the rare serranid, *Myteroperca intersitialis,* were only sighted on isolated patch reefs. It is perhaps occasional use of patch reefs by rare species such as this that result in the high species richness of some patch reefs. Due to insufficient replicates of this highly-isolated patch reefs, it is unclear whether species richness is lower in this sub-habitat than on other patch reefs as would be predicted from higher predation rates observed in isolated habitats (Almany *et al.*, 2007). While the isolation of these reefs by deep (~ 15m) sand flats would be thought to reduce migration and encourage even more disparate assemblages among patches (Nunez-Lara *et al.*, 2005), the assemblage composition remains quite stable among isolated reefs. *Lutjanis synagris* is known to form spawning aggregations in summer over intervening sand areas, such as Murray's Anchorage (Bardach and Mowbray, 1955) in summer, but the mobile nature of these schools makes their targeted spatial protection problematic. Isolated patch reefs and their surrounding deep sand flats appear to form a consistent and important sub-habitat for many carnivores and fall within the species-rich patch reef ecosystem. However, no MPA's currently include this sub-habitat.

Ordinations of both AGRRA and REEF data indicated that neighbouring habitats may exert a structuring effect on inshore reef fish assemblages. The clustering of some reefs adjoining seagrass beds provides a good example. These reefs were typified by large numbers of haemulids, which commonly use seagrass meadows as juvenile habitat (Nagelkerken *et al.,* 2000; Smith *et al.*, 2002; Verweij and Nagelkerken, 2007). Also observed were numbers of the inshore parrotfish, *Scarus guacamaia,* and a seagrass specialist, *Sparisoma radians.* This finding supports the observation that both species richness and composition of fish assemblages are greatly influenced by spatial context and the proximity of other habitats (Smith *et al.,* 1998; Grober-Dunsmore *et al.*, 2007). It has been suggested that, with mangroves and seagrass habitats being relatively rare habitats in Bermuda, patch reefs fulfill a role as nursery habitat for many species (Huijbers *et al.,* in press). However, the directed recruitment of *Lutjanus griseus* and *Haemulon sciurus* (Huijbers *et al.,* in press) and the existence of distinct assemblages on neighbouring reefs still support the local, albeit relatively lesser, significance of these uncommon back-reef habitats. Thus, with a view to conserving whole-ecosystem processes, the connectivity of reefs to seagrass habitats cannot be ignored. This may be especially relevant for the rare serranids, *Epinephelus morio*, *Mycteroperca microlepis* and *Alphestes afer* which were formerly common throughout the reefs (Lavett-Smith, 1958; Andersen, 1987) but typically inhabit seagrass beds and adjacent patch reefs for at least one life stage (Lavett-Smith, 1958; MEP, unpublished technical report; pers. obs.).

Other back-reef habitats may exhibit significant connectivity with reefs and merit attention when implementing MPA’s. Mangroves, for example, provide nursery habitat for several reef species (Nagelkerken *et al.*, 2000) including important herbivores, *Lutjanus griseus* (Faunce and Serafy, 2007) as well as other commercial species, and a now rare predator, *Lutjanis apodus* (Mowbray, 1965; Verweij *et al.,* 2007; pers. obs.). It has been suggested elsewhere that *Scarus guacamaia*, the largest herbivore in the western Atlantic, may indeed be completely dependent as juveniles on mangrove habitat. On the other hand, Bermuda populations of this fish may use patch reefs to the same effect, as do many other species more closely associated with mangroves in the Caribbean (Huijbers *et al.,* in press). Other inshore habitats, such as algal beds, play a less known role than mangroves in structuring fish assemblages. It is possible, though, that lagoonal assemblages like the one bordering the south ship channel may reflect the influence of this habitat (*e.g.* Garrison *et al.,* 2004). Because adjacent habitats appear to exert such influence on assemblages, protecting them and enhancing their recovery may require some estimates of connectivity to adjacent habitats and their inclusion in MPA’s.

In contrast to other assemblages reflecting productive habitats, one ordination cluster identified sites characterized by low coral cover, low overall fish abundance, low species richness and high proportions of pomacentrids. These sites were concentrated inshore and mostly at the west end of Bermuda, though two sites were widespread. This wide distribution suggested that different mechanisms might be responsible for the local degradation of coral reef habitat and structuring of the fish assemblage. The low coral cover at Walsingham, for example, may reflect coral loss and community shifts from the historic dredging of Castle Harbour (Flood *et al.*, 2005) and provide amenable habitat for pomacentrids (Feary *et al.*, 2007) and other members of this degraded reef assemblage. In contrast, the extremely shallow depths of west end sites may serve to exclude predators and provide a refuge for populations of pomacentrids whose algal-gardening reduces coral cover (Jones *et al.*, 2006).

Another pattern in clusters from REEF ordinations suggested two similar assemblages existing close to shore at the two extremes of the island. Interestingly, this pattern corresponds closely to the axis of tidal drainage across the platform. While no single species appeared to conform to the distribution of the assemblage, the moderate-to-low species richness in both areas may be common structure shared by both communities. Given the position of both areas at the extremes of an axis of tidal flow, it is thus possible that these relatively species-poor assemblages owe their similarity to the influence of hydrology on habitat or larval dispersal. As with degraded reefs associated with pomacentrids, the existence of clusters reflecting assemblages of low abundance and species richness offers two benefits. First, it provides insight into mechanisms resulting in the local loss of species abundance and richness while, at the same time, reminds us of the close interaction between benthic community structure and fish assemblage composition. Second, it reveals areas of inconsequential ecological value that may be omitted when considering which areas most warrant protection.

In some cases during this study, it was not be possible to link environmental conditions to assemblage structure. This difficulty no doubt arises from the confluence of many interacting physical and ecological gradients to create local conditions. In these complex situations we may thus only identify areas that support these varied assemblages and assess their importance. Ordinations provided distributions for many assemblages, but some relationships recurred enough to infer ecological significance and suggest strong environmental gradients at work. For instance, a recurring focus of inshore clusters was the central, north lagoon. Surrounded by deep (~15m) sand and mud bottoms, these large patches of reefs apparently support a distinct assemblage that may shares similarities with the west end assemblage. Additional importance of this habitat may be the use of reefs bordering deep lagoon by juvenile *Lutjanus synagris* and *Holocanthus bermudensis.*

The most distinctive confluence of fish distributions in the north lagoon occurred in an area approximately represented by the North Shore Coral Reef Preserve. Here, an overwhelming abundance of juvenile and adult *Haemulon aurolineatum* and *H. flavolineatum* may bolster numbers of the piscivores, *Lutjanus griseus, Ocyrurus chrysurus* and *Mycteroperca bonaci.* Furthermore, high abundances of *Holocanthus bermudensis*, *Lachnolaimus maximus, Chaetodon capistratus, Chaetodon striatus* and *Acanthurus chirurgus* make this area important to the ecology of all functional groups in the north lagoon. While AGRRA and REEF data did not agree on whether herbivore abundance is lower on these reefs than other inshore areas, the relatively low densities of both juvenile and adult *Acanthurus bahianus, Sparisoma viride , S. chrysopterum, S. aurofrenatum,* and *Scarus inserti* suggest at least a divergent community composition. Species richness data also identify this area as one of the only repositories of biodiversity in the lagoon. While mechanisms behind these patterns are unclear, identifying this area and others like it provides invaluable data towards informed management of marine resources.

Similarities between the assemblage of the central, north lagoon and ones inshore off the island’s west end suggest this assemblage to also be ecologically significant. The relationship between the assemblages appeared to hinge primarily on the shared abundance of the haemulid so characteristic of inshore habitats, *Haemulon aurolinateum.* High abundances of *Lutjanus griseus* and *Ocyurus chrysurus* also connected these assemblages across space and reinforced the importance of these areas to commercial fisheries. The west end assemblage also seems to play an important role as a juvenile area for the abundance herbivore, *Acanthurus bahianus.* The occurrence of juvenile *Haemulon sciurus* only at one west end site may indicate this area as a nursery for this species. However, while *H. sciurus* does spawn in aggregations and could recruit in small areas, the importance of mangroves for juveniles of this species (Mumby *et al.,* 2004) may mean that their actual nursey habitat was not surveyed by this study. But regardless of these west end community attributes, the greater densities of most species (except some widespread herbivores) and higher species richness in the central lagoon assemblage suggest that this area represents greater ecological value for conserving whole ecosystem attributes.

At higher levels of resemblance, offshore clusters in ordinations did not follow exactly the same patterns of ecological significance as inshore ones. Specifically, instead of an emphasis on the central lagoon and the east and west ends of the island, offshore reefs showed consistent similarities between the northeast and southwest regions. One common factor of the northeast and southwest assemblages was the low abundances of *Scarus taeniopterus, Sparisoma viride* and *S. chrysopterum*. These assemblages thus share similar community composition, but one possibly based on the virtual absence of some species. Thus, by default, the species-rich and productive northern and northwest offshore regions likely represent better choices for additional protection than the northeast or southwest offshore region.

The northeast region also appeared to cluster often with the south shore. The association of these regions suggests that these assemblages may be considered ecologically similar for purposes of MPA creation. However, the lower abundances of all fish in the northeast region indicate this area to be a generally poor choice for habitat protection. The associated south shore community appears to have similarly low abundances and species richness. In addition, the absence of juveniles of most species suggests that populations are generally not self-seeding and may depend on subsidy of post-recruits. The absence of lagoonal habitat for juvenile recruitment on the exposed and narrow shelf of south shore may be responsible for this. Thus, spatial protection on this coast would thus not encompass many discrete and viable populations of key species.

This study has not explicitly measured the stability of fish assemblages over time. As the overwhelming majority of sites were sampled in the summer season, confidence in site comparisons is high. What is unaccounted for, however, is whether species composition and abundance changes seasonally or inter-annually. However, the consistent agreement in species abundance and composition at site in the same reef zone sampled over three years suggests a broad temporal stability in assemblages. Seasonal movements of some fish species undoubtedly occur. *Lutjanus griseus*, for example, leaves fringing reefs for the winter (pers. obs.). Large scarids also abandon shallow reefs when water temperatures fall (Bardach, 1958b). However, since most species remain on even shallow reefs during the winter and migrating species presumably return to the most productive habitats, informed selection of MPA's should ensure protection of healthy habitat and of fish during at least the summer period of highest fishing pressure.

Rationale for informed modifications to current MPA coverage

The severe depletion of target species by historical fishing practices and resulting species shifts towards non-target species (Link, 2007) saw a steep decline in herbivores and carnivores alike and brought several serranids to commercial extinction (Smith-Vaniz *et al.*, 1999). The subsequent no-take status of scarids appears to have lead to their recovery (Hodgson, 2000). Moreover, as herbivorous may counter impaired coral recruitment from macroalgal overgrowth, the continued protection of scarids and all their reef habitats may, in turn, afford reefs greater potential for recovery in the face of increasing global coral mortality from pathogens and bleaching (Aronson and Precht, 2006). Six of the most impacted serranid species also enjoy year-round protection from harvest. In contrast to scarids, though, these serranids have remained at extremely low densities. As no more protection from direct exploitation may be afforded these rare species, it is hoped that conservation of intact ecosystems may spur their recovery. The goal of restoring the abundance of several large serranids, however, may be complicated by trophic shifts that have occurred in response to the historic overexploitation of target species. For example, a comparison between rim reef densities of herbivores between this study and that of Bardach (1959) reveals an approximately doubled abundance of acanthurids today and along with an elevenfold increase in scarid abundance. While different surveying methods introduce some uncertainty to these figures, the magnitudes of differences suggest that herbivore populations, at least on rim reefs, have likely been enhanced during the last fifty years. The contemporaneous high abundance of carnivores further suggests the historic top-down control of herbivores through predation of juveniles and illustrates the significant shifts in species composition and functional group dominance that have shaped today's assemblages in ways that may or may not be reversible.

Despite the challenge of reversing some ecosystem shifts (Pinnegar *et al.,* 2000; Pitcher, 2001), there is mounting evidence that the maintenance of ecosystems free of the selective forces of fishing and other human activities, such as boat anchoring, may reverse to a fair degree the species and regime shifts initiated by overexploitation of fish populations (Pitcher *et al.,* 2000; Tittensor *et al.*, 2007; Watson *et al.*, 2007). This reversal can result from surprisingly minor and unpredictable alterations in the non-linear organization of communities. An interesting example of this phenomenon was the simple occurrence of a rare batfish on Australian coral reefs that enabled the reversal of a regime shift towards macroalgal overgrowth (Bellwood *et al.*, 2007). The documented recovery of rare and overexploited carnivores as well as whole community structure (Micheli *et al.*, 2004; Mumby *et al.,* 2006; Watson *et al.*, 2007), further suggests that conservation of ecological integrity through protecting key connected habitats might foster conditions necessary for the recovery these formerly common species (Micheli *et al.,* 2004). Failing this, restocking of formerly common species has been proposed as a supplement to habitat protection (Pitcher, 2001). Though perhaps equally important as recovering rare species, effective protection of ecosystem integrity will likely enhance other currently exploited species, non-target species and habitats that increasingly face stressors of fishing, boat anchoring, sedimentation, nutrient loading and marine and terrestrial development.

Priority areas for conservation are those that are under-represented by the current MPA system and those areas that exhibit unusual importance to key species, functional groups or fish assemblages. The importance of areas to fish populations were thus assessed with reference to (i) patterns of community organization across reef zones, (ii) distributions and habitat requirements of key species, (iii) the influence of connected habitat on assemblage composition and (iv) the existence of sub-habitats with extraordinary ecological value.

Perhaps the most pressing need for protection exists within the lagoon of the Bermuda reef platform. The importance of these reef zones to higher trophic fish (Bardach and Menzel, 1956; Bardach 1959) - as well as the extensive use by juveniles of many key species - suggest that these areas are vital to the broader ecosystem and viability of offshore assemblages too. The patchy distribution of piscivores and commercial species, however, suggest the need for informed and spatially-targeted protection as well as large reserves to encompass these populations. In addition, the influence of adjacent habitats, such as seagrass, on assemblage composition and the significance of them to certain commercial species suggest that MPA's within the lagoon would achieve maximum effect by including a mosaic of related habitats. An ideal configuration of such a seascape preserve would thus include significant areas of bare sand, seagrass and algal beds, mangroves and fringing and patch reefs. The southwestern region might suit these requirements and be more palatable to Bermuda's public as the area already encompasses a seasonally-protected area. An inshore MPA in that region would omit few distinct assemblages. However, the possible degradation of these reefs already, coupled with the only moderate numbers of commercial species there, might reduce the worth of conserving that region. The north lagoonal assemblage from the southern ship channel up to at least the rim roughly conforms to the North Shore Coral Reef Preserve and appears to be more ecologically distinctive than the southwest region. This exceptional area would harbour (i) species-rich patch reefs significant to juveniles and adults of many commercial and non-commercial species, (ii) distinct isolated patch reef communities, and (iii) an inshore reef-sand-seagrass complex important to juvenile lutjanids (*Lutjanus* *griseus* and *Ocyurus chrysurus*) and serranids (*e.g. Epinephelus morio, Mycteroperca bonaci*).

Current numbers of MPA's on the rim reef are reassuring. However, two shortcomings may be addressed in the future. First, the high productivity rim reefs adjacent to tidal passes are protected by 6-7 MPA's, but increased coverage of these sub-habitats would benefit conservation efforts by preserving fish populations where they are naturally highest. New offshore MPA's should first be established surrounding the tidal pass sub-habitat. Again, an extension north of the North Shore Coral Reef Preserve would capture several examples of this sub-habitat. Alternatively, the northwest region appears to harbour a significant concentration of this habitat as well as impressive populations of most fish species.

The second shortcoming of current MPA's on the rim reef is their uniformly small size. For instance, while *Epinephelus guttatus* may exercise considerable site fidelity (Bardach, 1958b), small MPA's provide less protection for adults migrating towards spawning aggregations and represent smaller "targets" for settlement of widely dispersed larvae (Roberts, 1997; Botsford *et al.,* 2001; Botsford *et al.*, 2003). The typically greater larval dispersion for higher trophic levels (Kinlan and Gaines, 2003) reinforces the need for sufficiently large MPA's to contain viable populations of piscivorous and commercial species. Moreover, the likely low rates of larval subsidy to Bermuda from down-current Caribbean islands (Glasspool, 1994) highlights the importance of protected habitats that preserve large, self-seeding stocks. Indeed, Newman *et al.* (2006) noted that Caribbean reef fish assemblages approaching a recovered state only occurred in large (~100 km^2), old reserves. In Bermuda, the consolidation of several smaller MPA's may be considered towards enhancing reserve size. Such a large-sized MPA would be consistent with the aim of an ecosystem reserve by protecting fish populations at most scales of dispersion and movement present in the assemblage (Botsford *et al.*, 2003; Kinlan and Gaines, 2003; Baskett *et al.*, 2007).

Though this study generated little data on fore reef populations, the observed greater REEF abundance of piscivorous and commercial species plus the historical occurrence of larger serranids in this reef zone (Bardach and Menzel, 1956), suggest offshore reef reserves might benefit from the inclusion of this habitat. Pitt (2003) proposed incorporating serranid spawning locations on fore reefs into permanent MPA's or creating corridors to protect fish while undergoing spawning migrations.

This chapter has presented spatial patterns of ecological importance to fish assemblages across the Bermuda reef platform towards their incorporation into modifications to the current MPA system. The identification of regions, habitats and sub-habitats that lack appropriate protection of fish assemblages has suggested some requirements for the effective protection of ecosystems supporting Bermuda's fish populations. An ideal reserve would capture the functional organization, biodiversity, juvenile habitat and productivity of each reef zone in the areas which are most ecologically significant, while maintaining sufficient reserve size and connectivity between habitats. Spatial, logistical and political challenges make realization of this difficult. However, the region roughly delineated by the North Shore Coral Reef Preserve appears optimum for safeguarding representative and significant fish assemblages. Due to the close connectivity of reef fish assemblages with benthic community structure (*e.g.* Graham *et al,* 2007; Wilson *et al.,* 2007), as well as the intrinsic value of those communities, future modifications of current MPA coverage may aim to also optimize benthic protection. After all, only a synthesis of spatial trends for both benthic and demersal communities can hope to protect the areas of greatest overall ecological significance to Bermuda's coral reef ecosystem. Reserves of sufficient size and enforcement would fulfill the function not only of safeguarding ecosystem integrity and associated services but also providing an insurance policy against future chance events or mismanagement (Pitcher, 2001). Indeed, sustained recovery of fish populations and their viability into the future likely depends on the coordinated establishment of a new generation of MPA's informed by a spatial understanding of key ecological resources.

References

Almany G.R., Peacock L.F., Syms C., McCormick M.I., Jones G.P. 2007. Predators target rare prey in coral reef assemblages. *Oecologia*. 152(4): 751-761.

Andersen R. 1987. Bermudian handline fishing in the sailing sloop era: a fisherman's account. In: *The Fishing Culture of the World.* Ed. Gunda, B. p 777- 801.

Aronson R.B., Precht W.F. 2006. Conservation, precaution and Caribbean reefs. *Coral Reefs.* 25: 441-450.

Bardach J.E. 1958a. *Bermuda Fisheries Research Program – Final Report.* Bermuda Trade Board. Hamilton, Bermuda. 59 pp.

Bardach J.E. 1958b. On the movements of certain Bermuda reef fishes. *Ecology.* 39(1): 139-146

Bardach J.E. 1959. The summer standing crop of fish on a shallow Bermuda reef. *Limnology and Oceanography.* 4: 77-85.

Bardach J.E., Menzel D.W. 1956. Field and laboratory observations on the growth of some Bermudae reef fishes. In: *Proceedings of the Gulf and Caribbean Fisheries Institute: 9th Annual Session.* p 106-112.

Bardach J.E., Mowbray L.S. 1955. Bermuda Fisheries Research Program Progress Report #2. 96 pp.

Baskett M.C., Micheli F., Levin S.A. 2007. Designing marine reserves for interacting species: Insights from theory. *Biological Conservation.* 137(2): 163-179.

Bellwood D.R., Hughes T.P., Hoey A.S. 2007. Sleeping functional group drives coral reef recovery. *Current Biology.* 16: 2434-2439.

Belmaker J., Shashar N., Ziu Y. 2005. Effects of small-scale isolation and predation on fish diversity on experimental reefs. *Marine Ecology Progress Series.* 289: 273-283.

Beruman M.L., Pratchett M.S., McCormick M.I. 2005. Within-reef differences in diet and body condition of coral-feeding butterflyfishes (Chaetodontidae). *Marine Ecology Progress Series.* 287: 217-227.

Botsford L.W., Hastings A., Gaines S.P. 2001. Dependence of sustainability on the configuration of marine reserves and larval dispersal distance. *Ecology Letters*. 4(2): 144-150.

Botsford L.W., Micheli F., Hastings A. 2003. Principles for the design of marine reserves. *Ecological Applications.* 13: 525-531.

Brokovich E., Baranes A. 2005. Community structure and ecology of butterflyfishes (Chaetodontidae) in the Gulf of Aqaba (northern Red Sea). *Aquatic Conservation:Marine and Freshwater Ecosystems*. 15: S45-S58.

Butler J.N., Burnett-Herkes J., Barnes J.A., Ward J. 1993. The Bermuda fisheries: a tragedy of the commons averted? *Environment.* 35(1): 6-33.

Chiappone M., Sluka R., Sealey K.S. 2000. Groupers (Pisces: Serranidae) in fished and protected areas of the Florida Keys, Bahamas and northern Caribbean. *Marine Ecology Progress Series*. 198: 261-272.

Faunce C.H., Serafy J.E. 2007. Nearshore habitat use by gray snapper (*Lutjanus griseus*) and bluestriped grunt (*Haemulon sciurus*): environmental gradients and ontogenetic shifts. *Bulletin of Marine Science.* 80(3): 473-495.

Feary D.A., Almany G.R., McCormick M.I., Jones G.P. 2007. Habitat choice, recruitment and the response of coral reef fishes to coral degradation. *Oecologia*. 153: 727-737.

FishBase. 2007. World Wide Web. Visited: 10/2007. http://www.fishbase.org.

Flood V.S., Pitt J.M., Smith S.R. 2005. Historical and ecological analysis of coral communities in Castle Harbour (Bermuda) after more than a century of environmental perturbation. *Marine Pollution Bulletin.* 51: 545-557.

Garrison V.H., Rogers C.S., Beets J., Friedlander A.M. 2004. The habitats exploited and the species trapped in a Caribbean island trap fishery. *Environmental Biology of Fishes.* 71(3): 247-260.

Gerber L.R., Wielgus J., Sala E. 2007. A decision framework for the adaptive management of an exploited species with implications for marine reserves. *Conservation Biology.* 21(6): 1594-1602.

Glasspool A.F. 1994. *Larval distribution, population structure and gene flow in Bermuda's reef fish.* PhD Thesis. University College of North Wales. Gwynedd, UK. 186 pp.

Graham N.A.J., Wilson S.K., Jennings S., Poulinin N.V.C., Robinson J., Bijoux J.P., Dow T.M. 2007. Lag effects in the impacts of mass bleaching on coral reef fish, fisheries and ecosystems. *Conservation Biology.* 21(5): 1291-1300.

Grober-Dunsmore R., Frazer T.K., Lindberg W.J., Beets J. 2007. Reef fish and habitat relationships in a Caribbean seascape: the importance of reef context. *Coral Reefs.* 26(1): 201-216.

Guidetti P. 2007. Potential of marine reserves to cause community-wide changes beyond their boundaries. *Conservation Biology.* 21(2): 540-545.

Guidetti P., Sala E. 2007. Community-wide effects of marine reserves in the Mediterranean Sea. *Marine Ecology Progress Series*. 335: 43-56.

Hately J.G. 1994. Stock discrimination and stock enhancement in western Atlantic groupers. ODA Project Interim Report 7.

Hodgson A.D. 2000. *Marine Resources and the Fishing Industry in Bermuda: A Discussion Paper.* Ministry of the Environment Technical Report. 495 pp.

Hughes T.P., Barid A.H., Bellwood D.R., Card M., Connolly S.R., Folke C., Grosberg R., Guldberg O., Jackson J.B.C., Kleypas J., Lough J.M., Marshall P., Nyström M., Palumbi S.R., Pandolfi J.M., Rosen B., Roughgarden J. 2003. Climate change, human impacts and the resilience of coral reefs. *Science*. 301: 929 – 933.

Huijbers C.M., Grol M.G.G., Nagelkerken I. In press. Shallow patch reefs as alternative recruitment habitats for some mangrove/seagrass associated species in Bermuda. *Revista de Biología Tropical.*

Jones G.P., Santana L., McCook L.J., McCormick M.I. 2006. Resource use and impact of three herbivorous damselfish on coral reef communities. *Marine Ecology Progress Series.* 328: 215-224.

Kinlan B., Gaines S. 2003. Propagule dispersal in marine and terrestrial environments: A community perspective. *Ecology.* 84(8): 2007-2020.

Kramer P.A. 2003. Synthesis of coral reef health indicators for the western Atlantic: results of the AGRRA program (1997-2000). p. 1-57. In: Status of Coral Reefs in the Western Atlantic: Results of Initial Surveys, Atlantic and Gulf Rapid Reef Assessment (AGRRA) Program. 630 pp.

Lavett-Smith C. 1958. *The Groupers of Bermuda*. Reprinted from *Final Report – Bermuda Fisheries Research Program*. Bermuda Trade Development Board. Hamilton, Bermuda. 18 pp.

Link J.S. 2007. Underappreciated species in ecology: "ugly fish" in the northwest Atlantic Ocean. *Ecological Applications.* 17(7): 2037-2060.

Luckhurst B.E., Ward J.A. 1992. *Analysis of Trends in Bermuda's Fishery Statistical Database from 1975-1990 with Reference to Fishery Management Measures Implemented During this Period.* Division of Fisheries Report. 19 pp.

MEP (Marine Environment Programme). Unpublished technical report. *Assessment of Reef Fish Populations in Bermuda's Marine Protected Areas.* Bermuda Institutes of Ocean Science. 92 pp.

Marks K.W., Klomp K.D. 2003. Appendix two: Fish biomass conversion equations. In: *Status of Coral Reefs in the Western Atlantic: Results of Initial Surveys, Atlantic and Gulf Rapid Reef Assessment (AGRRA) Program.* Ed. Lang J.C. National Museum of Natural History. Washington D.C. 630 pp.

Micheli F., Halpern B.S. 2005. Low functional redundancy in coastal marine assemblages. *Ecology Letters.* 8(4): 391-400.

Micheli F., Halpern B.S., Botsford L.W., Warner R.R. 2004. Trajectories and correlates of community change in no-take marine reserves. *Ecological Applications.* 14(6): 1709-1723.

Mowbray L.S. 1965. *A Guide to the Reef, Shore and Game Fish of Bermuda*. 64 pp.

Mumby P.J., Edwards A.J., Arias-González J.E., Lindeman K.C., Blackwell P.G., Gall A., Garczynska M.I., Harborne A.R., Pescod C.L., Renken H., Wabnitz C.C., Llewellyn G. 2004. Mangroves enhance the biomass of coral reef fish communities in the Caribbean. *Nature.* 427: 533-536.

Mumby P.J., Dahlgren C.P., Harborne A.R., Kappel C.V., Micheli F., Brumbaugh D.R., Holmes K.E., Mendes J.M., Broad K., Sanchirico J.N., Buch K., Box S. Stoffle R.W., Gill A.B. 2006. Fishing, trophic cascades, and the process of grazing on coral reefs. *Science*. 311: 98-101.

Mumby P.J., Hastings A., Edwards H.J. 2007a. Thresholds and the resilience of Caribbean coral reefs. *Nature.* 450: 98-101.

Mumby P.J., Harbarre A.R., Williams J., Kappel C.V., Brumbaugh D.R., Micheli F., Holmes K.E., Dahlgren C.P., Paris C.B., Blackwell P.G. 2007b. Trophic cascade facilitates coral recruitment in a marine reserve. *Proceedings of the National Academy of Science.* 104(20): 8362-8367.

Munro J.L., Williams D.M. 1985. Assessment and management of coral reef fisheries: biological, environmental and socioeconomic aspects. *Proceedings of the Fifth International Coral Reef Congregation.* 4: 545-581.

Murdoch T.J., Aronson R. B. 1999. Scale dependent spatial variability of coral assemblages along the Florida Reef Tract. *Coral Reefs.* 18(4): 341-351.

Nagelkerken I.A. Personal communication. 2007. Radboud University Nijmegen, The Netherlands.

Nagelkerken I., Dorenbosch M., Verberk W.C.E.P., Cocheret de la Marinière E., Vander Velde G. 2000. Importance of shallow water biotopes of a Caribbean bay for juvenile coral reef fishes: patterns in biotope association, community structure and spatial distribution. *Marine Ecology Progress Series.* 202: 175-192.

Newman M.J.H., Paredes G.A., Sala E., Jackson J.B.C. 2006. Structure of Caribbean coral reef communities across a large gradient of fish biomass. *Ecology Letters*. 9: 1216-1227.

Nunez-Lara E., Anas-Gonzalez J.E., Legendre P. 2005. Spatial patterns of Yucatan reef fish communities: testing models using a multi-scale survey design. *Journal of Experimental Marine Biology and Ecology.* 324(2): 157-169.

Ojeda-Martinez C., Bayle-Sempere J.T., Sanchez-Jerez P., Forcada A., Valle C. 2007. Detecting conservation benefits in spatially protected fish populations with meta-analysis of long-term monitoring data. *Marine Biology*. 151(3): 1153-1161.

Pinnegar J.K., Poulinin N.V.C., Francour P., Badalmenti F., Chemello R., Harmelin Vivien M-L., Hereu B., Milazzo M., Zabala M., D'Anna G., Pipitore C. 2000. Trophic cascades in benthic marine ecosystems: Lessons for fisheries and protected areas management. *Environmental Conservation.* 27(2): 179-200.

Pitcher T.J. 2001. Fisheries managed to rebuild ecosystems? Reconstructing the past to salvage the future. *Ecological Applications.* 11(2): 601-617.

Pitcher T.J., Watson R., Haggan N., Guenette S., Kennish R., Sumaila U.R., Cook D.,Wilson K., Leung A. 2000. Marine reserves and the restoration of fisheries and marine ecosystems in the South China Sea. *Bulletin of Marine Science.* 66(3): 543-566.

Retzel A., Hansen A.D., Gronkjaer P. 2007. Otolith growth of Springer's demoiselle, *Chrysiptera springeri* (Pomacentridae, Allen and Lubbock), on a protected and non-protected coral reef. *Journal of Applied Ichthyology.* 23(5): 568-572.

REEF, 2007. Reef Environmental Eduation Foundation. World Wide Web Publication. http://www.reef.org. Visited 10/2007.

Roberts C.M. 1995. Effects of fishing on the ecosystem structure of coral reefs. *Conservation Biology.* 9(5): 988-995.

Roberts C.M. 1997. Connectivity and management of Caribbean coral reefs. *Science.* 278: 1454-1457.

Robertson D.R., Ackerman J.L., Choat J.H., Posada J.M., Pitt J. 2005. Ocean surgeonfish, *Acanthurus bahianus*. I. The geography of demography. *Marine Ecology Progress Series.* 295: 229-244.

Samoilys M.A., Martin-Smith K.M., Giles B.G., Cabrera B., Anticamara J.A., Brunio E.O., Vincent A.C.J. 2007. Effectiveness of five small Philippines' coral reef reserves for fish population depends on site-specific factors, particularly enforcement history. *Biological Conservation.* 136(4): 584-601.

Schmitt E.F., Wells Feeley D., Sullivan-Sealey K.M. 1998. *Surveying Coral Reef Fishes: A Manual for Data Collection, Processing and Interpretation of Fish Survey Information for the Tropical Northwest Atlantic.* Media Enterprise. Nassau, Bahamas. 84 pp.

Smith S.R., Pitt J.M., Webster G. 2002. *Benthic Monitoring Report – Summary Report*. Bermuda Biological Station for Research Report.

Smith S.R., Hellin D.C., McKenna S.A. (Environment Bermuda). 1998. *Marine Environmental Impact Studies on the Thermal Effluent Released from the Tynes Bay Incinerator and Ash Waste Disposal in Castle Harbour.* Bermuda Biological Station for Research Special Publication 35. 205 pp.

Smith-Vaniz W.F., Collette B.B., Luckhurst B.E. 1999. *Fishes of Bermuda: History, Zoogeography, Annotated Checklist and Identification Keys*. American Society of Ichthyologists and Herpetologists Special Publication 4. 424 pp.

Sonnenholzner J.I., Ladah L.B., Lafferty K.D. 2007. Cascading effects of fishing on Galapagos rocky reef communities. *Marine Ecology Progress Series*. 343: 77-85.

Thomas M.L., Logan A. 1992. *A Guide to the Ecology of Shoreline and Shallow-water Marine Communities of Bermuda.* Bermuda Biological Station for Research Special Publication 30. 346 pp.

Tittensor D.P., Micheli F., Nystrom M., Worm B. 2007. Human impacts on the species-area relationship reef fish assemblages. *Ecology Letters.* 10(9): 760-772.

Unsworth R.K., Powell A., Hukom F., Smith D.J. 2007. The ecology of Indo-Pacific grouper (Serranidae) species and the effects of a small scale no take area on grouper assemblage, abundance and size frequency distribution. *Marine Biology.* 152(2): 243-254.

Verweij M.C., Nagelkerken I. 2007. Short and long-term movement and site fidelity of juvenile Haemulidae in backreef habitats of a Caribbean embayment. *Hydrobiologia*. 592(1): 257-270.

Verweij M.C., Nagelkerken I., Hol K.E.M., van den Beld A.H.J.B., van der Velde G. 2007. Space use of *Lutjanus apodus* including movement between a putative nursery and a coral reef. *Bulletin of Marine Science.* 81(1): 127-138.

Ward J.A.D. Personal communication. 2007. Bermuda Department of Conservation Services.

Ward J.A.D. 1999. Bermuda's coastal seagrass beds as habitats for fish. MSc thesis. University of Glasgow. 96 pp.

Watson D.L., Harvey E.S., Kendrick G.A., Nardi K., Anderson M.J. 2007. Protection from fishing alters the species composition of fish assemblages in a temperate-tropical transition zone. *Marine Biology.* 152: 1197-1206.

Williams I.D., Walsh W.J., Miyasaka A., Friedlander A.M. 2006. Effects of rotational closures on coral reef fishes in Waikiki-Diamond Head Fishery Management Area, Oahu, Hawaii. *Marine Ecology Progress Series.* 310: 139-149.

Wilson S.K., Graham N.A., Pratchett M.S., Jones G.P., Poulunin N.V.C. 2006. Multiple disturbances and the global degradation of coral reefs: are reef fishes at risk or resilient? *Global Change Biology*. 12: 2220-2234.

Appendix 1. AGRRA species comprising functional guilds

Functional guild*	**Common name**	**Species**
Herbivores	Blue tang	*Acanthurus coerulus*
	Doctorfish	*Acanthurus chirurgus*
	Ocean surgeonfish	*Acanthurus bahianus*
	Blue parrotfish	*Scarus coerulus*
	Greenblotch parrotfish	*Sparisoma atomarium*
	Midnight parrotfish	*Scarus coelestinus*
	Princess parrotfish	*Scarus taeniopterus*
	Queen parrotfish	*Scarus vetula*
	Rainbow parrotfish	*Scarus guacamaia*
	Redband parrotfish	*Sparisoma aurofrenatum*
	Redtail parrotfish	*Sparisoma chrysopterum*
	Stoplight parrotfish	*Sparisoma viride*
	Striped parrotfish	*Scarus inserti*
	Yellowtail (redfin) parrotfish	*Sparisoma rubripinne*
	Yellowtail damselfish	*Microspathodon chrysurus*
	Black durgon	*Melichthys niger*
	Cocoa damselfish / beaugregory†	*Stegastes variabilis/leucosticus*†
Invertivores	Bluestriped grunt	*Haemulon sciurus*
	Caesar grunt	*Haemulon carbonarium*
	French grunt	*Haemulon flavolineatum*
	Lane snapper	*Lutjanus synagris*
	Gray triggerfish	*Balistes capriscus*
	Orangespotted filefish	*Cantherhines pullus*
	Slender filefish	*Monacanthus tuckeri*
	Whitespotted filefish	*Cantherhines macrocerus*
	Banded butterflyfish	*Chaetodon striatus*
	Foureye butterflyfish	*Chaetodon capistratus*
	Longsnout butterflyfish	*Chaetodon aculeatus*
	Reef butterflyfish	*Chaetodon sedentarius*
	Spotfin butterflyfish	*Chaetodon ocellatus*
	Hogfish	*Lachnolaimus maximus*
	Spanish hogfish	*Bodianus rufus*
	Blue angelfish	*Holocanthus bermudensis*
	French angelfish	*Pomacanthus paru*
	Queen angelfish	*Holocanthus ciliaris*
	Townsend angelfish	*Holocanthus bermudensis*
Planktivores	Tomtate	*Haemulon aurolineatum*
Piscivores	Black grouper	*Mycteroperca bonaci*
	Red hind	*Epinephelus guttatus*
	Gray snapper	*Lutjanus griseus*

Piscivores (continued)	Yellowtail snapper	*Ocyurus chrysurus*
	Bar jack	*Carangoides ruber*
	Great barracuda	*Sphyraena barracuda*
	Coney	*Cephalopholis fulva*
	Graysby	*Cephalopholis cruentata*
	Rock hind	*Epinephelus adscenionis*
Commercial species	Bar jack	*Carangoides ruber*
	Bluestriped grunt	*Haemulon sciurus*
	Black grouper	*Mycteroperca bonaci*
	Coney	*Cephalopholis fulva*
	Graysby	*Cephalopholis cruentata*
	Red hind	*Epinephelus guttatus*
	Rock hind	*Epinephelus adscenionis*
	Gray snapper	*Lutjanus griseus*
	Lane snapper	*Lutjanus synagris*
	Yellowtail snapper	*Ocyurus chrysurus*
	Gray triggerfish	*Balistes capriscus*
	Hogfish	*Lachnolaimus maximus*

* Species were categorized by functional group based on their predominant component of their diet, as reported on FishBase (www.fishbase.org).

[†] Inclusion of *Stegastes variabilis/leucostictus* is a modification of AGRRA 4.0 protocol.

Appendix 2. Functional guild groupings for species seen on REEF surveys.

Functional guild*	**Common name**	**Species**
Herbivores	Blue tang	*Acanthurus coerulus*
	Doctorfish	*Acanthurus chirurgus*
	Ocean surgeonfish	*Acanthurus bahianus*
	Blue parrotfish	*Scarus coerulus*
	Greenblotch parrotfish	*Sparisoma atomarium*
	Midnight parrotfish	*Scarus coelestinus*
	Princess parrotfish	*Scarus taeniopterus*
	Queen parrotfish	*Scarus vetula*
	Rainbow parrotfish	*Scarus guacamaia*
	Redband parrotfish	*Sparisoma aurofrenatum*
	Redtail parrotfish	*Sparisoma chrysopterum*
	Stoplight parrotfish	*Sparisoma viride*
	Striped parrotfish	*Scarus inserti*
	Yellowtail (redfin) parrotfish	*Sparisoma rubripinne*
	Yellowtail damselfish	*Microspathodon chrysurus*
	Black durgon	*Melichthys niger*
	Seaweed blenny	*Parablennius marmoreus*
	Pearl blenny	*Entomacrodus nigricans*
	Barred blenny	*Labrisomus nuchipinnis*
	Bridled goby	*Coryphopterus glaucofraenum*
	Tiger goby	*Gobiosoma macrodon*
	Goldspot goby	*Gnatholepis thompsoni*
	Masked/glass goby	*Coryphopterus personatus/hyalinus*
	Bermuda chub	*Kyphosus sectatrix*
	Bicolor damselfish	*Stegastes partitus*
	Cocoa damselfish	*Stegastes variabilis*
Invertivores	Bluestriped grunt	*Haemulon sciurus*
	Caesar grunt	*Haemulon carbonarium*
	French grunt	*Haemulon flavolineatum*
	Cottonwick	*Haemulon melanurum*
	White margate	*Haemulon album*
	Pigfish	*Orthopristis chrysoptera*
	Lane snapper	*Lutjanus synagris*
	Ocean triggerfish	*Canthidermis sufflamen*
	Gray triggerfish	*Balistes capriscus*
	Orangespotted filefish	*Cantherhines pullus*
	Slender filefish	*Monacanthus tuckeri*
	Fringed filefish	*Monacanthus ciliatus*
	Scrawled filefish	*Aleuterus scriptus*

Invertivores (cont.)	Whitespotted filefish	*Cantherhines macrocerus*
	Banded butterflyfish	*Chaetodon striatus*
	Foureye butterflyfish	*Chaetodon capistratus*
	Longsnout butterflyfish	*Chaetodon aculeatus*
	Reef butterflyfish	*Chaetodon sedentarius*
	Spotfin butterflyfish	*Chaetodon ocellatus*
	Hogfish	*Lachnolaimus maximus*
	Spanish hogfish	*Bodianus rufus*
	Blue angelfish	*Holocanthus bermudensis*
	French angelfish	*Pomacanthus paru*
	Queen angelfish	*Holocanthus ciliaris*
	Townsend angelfish	*Holocanthus bermudensis*
	Flamefish	*Apogon maculates*
	Redspotted hawkfish	*Amblycirrhitus pinos*
	Hairy blenny	*Labrisomus nuchipinnis*
	Mottled mojarra	*Eucinostomus lefroyi*
	Orangespotted goby	*Nes longus*
	Dusky squirrelfish	*Sargocentron vexillarium*
	Longspine squirrelfish	*Holocentrus rufus*
	Clown wrasse	*Halichoeres maculipinna*
	Puddingwife	*Halichoeres radiatus*
	Slippery dick	*Halichoeres bivittatus*
	Yellowhead wrasse	*Halichoeres garnoti*
	Sand tilefish	*Malacanthus plumieri*
	Spotted goatfish	*Pseudopeneus maculates*
	Yellow goatfish	*Mulloidichthys martinicus*
	Honeycomb cowfish	*Acanthostracion polygonia*
	Scrawled cowfish	*Acanthostracion quadricornis*
	Smooth trunkfish	*Lactophrys triqueter*
	Rock beauty	*Holocanthus tricolor*
	Beaugregory	*Stegastes leucostictus*
	Sergeant major	*Abudefduf saxatilis*
	Threespot damselfish	*Stegastes planifrons*
	Glasseye	*Heteropriacanthus cruentatus*
	Greater soapfish	*Rypticus saponaceus*
	Barred hamlet	*Hypoplectrus puella*
	Jolthead porgy	*Calamus bajonado*
	Saucereye porgy	*Calamus calamus*
	Pinfish	*Lagodon rhomboids*
	Bermuda bream	*Diplodus bermudensis*
	Bandtail puffer	*Sphoeroides spengleri*
	Balloonfish	*Diodon holocanthus*
	Porcupinefish	*Diodon hystrix*
	Sharpnose puffer	*Canthigaster rostrata*
Planktivores	Brown garden eel	*Heteroconger longissimus*

Plankivores (cont.)	Bermuda halfbeak	*Hemiramphus bermudensis*
	Tomtate	*Haemulon aurolineatum*
	Bluehead wrasse	*Thalassoma bifasciatum*
	Green razorfish	*Xyrichtys splendens*
	Rosy razorfish	*Xyrichtys martinicensis*
	Creole wrasse	*Clepticus parrae*
	Glassy sweeper	*Pempheris schomburgki*
	Blue chromis	*Chromis cyanea*
	Creole fish	*Paranthias furcifer*
	Silversides	Atherinidae, Clupeidae etc.
Piscivores	Black grouper	*Mycteroperca bonaci*
	Red hind	*Epinephelus guttatus*
	Gray snapper	*Lutjanus griseus*
	Yellowtail snapper	*Ocyurus chrysurus*
	Bar jack	*Carangoides ruber*
	Great barracuda	*Sphyraena barracuda*
	Coney	*Cephalopholis fulva*
	Graysby	*Cephalopholis cruentata*
	Rock hind	*Epinephelus adscenionis*
	Trumpetfish	*Aulostomus maculates*
	Eyed flounder	*Bothus ocellatus*
	Peacock flounder	*Bothus lunatus*
	Almaco jack	*Seriola rivoliana*
	Blue runner	*Carangoides chrysos*
	Sharksucker	*Echeneis naucrates*
	Goldentail moray	*Gymnothorax miliaris*
	Spotted moray	*Gymnothorax moringa*
	Red lionfish	*Pterois volitans*
	Nassau grouper	*Epinephelus striatus*
	Peppermint basslet	*Liopropoma rubre*
	Yellowmouth grouper	*Mycteroperca interstitialis*
	Snowy grouper	*Epinephelus niveatus*
	Southern sennet	*Sphyraena picudilla*
	Sand diver	*Synodis intermedius*
	Bluestriped lizardfish	*Synodus saurus*
	Round scad	*Decapterus punctatus*
	Makerel scad	*Decapterus mararellus*
Commercial species	Bar jack	*Carangoides ruber*
	Bluestriped grunt	*Haemulon sciurus*
	Black grouper	*Mycteroperca bonaci*
	Coney	*Cephalopholis fulva*
	Graysby	*Cephalopholis cruentata*
	Red hind	*Epinephelus guttatus*
	Rock hind	*Epinephelus adscenionis*
	Gray snapper	*Lutjanus griseus*

Commercial species (continued)	Lane snapper	*Lutjanus synagris*
	Yellowtail snapper	*Ocyurus chrysurus*
	Gray triggerfish	*Balistes capriscus*
	Hogfish	*Lachnolaimus maximus*
	Creole fish	*Paranthias furcifer*
	Mackerel scad	*Decapterus mararellus*
	Blue runner	*Carangoides chrysos*
	Almaco jack	*Seriola rivoliana*
	Saucereye porgy	*Calamus calamus*
	Jolthead porgy	*Calamus bajonado*

* Species were categorized by functional group based on their predominant component of their diet, as reported on FishBase (www.fishbase.org).

Appendix 3. Results of t-tests comparing densities of fish at MPA's and control sites.

Comparisons correspond to Figs. 5-16 (Chapter 1) and include pooled MPA sites and pooled control sites, as well as comparisons between individual MPA's and control sites. Significant p-values presented in bold type.

Site grouping	**Species**	**Normal?**	**Equal variances?**	**Power**	**t-statistic**	**dF**	**p**
Pooled	Herbivores	No	No	0.6188	1.97	98	0.055
	Invertivores	No	Yes	0.5360	0.178	98	0.859
	Piscivores	No	Yes	0.1088	-0.713	98	0.478
	Commercial	No	Yes	0.0930	-0.612	98	0.542
	Scarus taeniopterus	No	No	0.6272	-1.996	47.9	0.052
	Scarus vetula	No	Yes	0.0805	0.517	98	0.606
	Sparisoma aurofrenatum	No	Yes	0.1312	-0.835	98	0.406
	Sparisoma viride	No	Yes	0.2588	-1.324	98	0.189
	Scarus inserti	No	Yes	0.0757	0.475	98	0.636
	Cephalopholis fulva	No	Yes	0.0517	0.122	98	0.904
	Lutjanus griseus	No	Yes	0.0694	-0.413	98	0.681
	Ocyurus chrysurus	No	No	0.2767	-1.161	43.5	0.252
	Epinephelus guttatus	No	No	0.3811	1.673	98	0.098
	Carangoides ruber	No	Yes	0.1516	-0.931	98	0.354
	Mycteroperca bonaci	No	Yes	0.0594	-0.289	98	0.773
	Acanthurus bahianus	No	Yes	0.0875	0.572	98	0.569
	Acanthurus coerulus	No	Yes	0.1380	0.868	98	0.387
	Acanthurus chirurgus	No	Yes	0.0510	-0.094	98	0.925
	Microspathodon chrysurus	No	Yes	0.2391	-1.261	98	0.210
	Stegastes variabilis/ leucostictus	No	Yes	0.0500	0.000	98	1.000
	Stegastes partitus	No	Yes	0.1271	-0.814	98	0.418

Site grouping	**Species**	**Normal?**	**Equal variances?**	**Power**	**t-statistic**	**dF**	**p**
	Chaetodon capistratus	No	Yes	0.0777	0.493	98	0.623
	Haemulon flavolineatum	No	No	0.2153	-1.107	65.5	0.272
	Haemulon sciurus	No	Yes	0.0500	0.000	98	1.000
	Bodianus rufus	No	Yes	0.1032	0.679	98	0.499
North Rock	Herbivores	Yes (Log_{10})	No	0.1259	-0.844	18	0.410
	Invertivores	Yes	Yes	0.0836	-0.426	17.5	0.675
	Piscivores	No	Yes	0.0941	0.647	18	0.529
	Commercial	No	Yes	0.0941	0.637	18	0.529
Snakepit	Herbivores	Yes (Log_{10})	Yes	0.0518	-0.132	18	0.897
	Invertivores	Yes (Sqrt)	Yes	0.0531	-0.173	18	0.865
	Piscivores	No	Yes	0.0644	-0.372	18	0.714
	Commercial	No	Yes	0.0644	-0.372	18	0.714
Eastern Blue Cut	Herbivores	Yes (Log_{10})	Yes	0.0500	0.013	18	0.990
	Invertivores	Yes	Yes	0.3242	1.587	18	0.130
	Piscivores	No	Yes	0.2316	-1.292	18	0.213
	Commercial	No	Yes	0.2316	-1.292	18	0.213
Southwest Breaker	Herbivores	No	Yes	0.2065	1.201	18	0.245
	Invertivores	No	Yes	0.1060	-0.728	18	0.476
	Piscivores	No	Yes	0.1091	0.747	18	0.465
	Commercial	No	Yes	0.1091	0.747	18	0.465
North Rock	*Scarus taeniopterus*	Yes (Sqrt)	No	0.1171	-0.795	11.0	0.444
	Scarus vetula	Yes	Yes	0.2620	1.395	18	0.180
	Sparisoma aurofrenatum	Yes	Yes	0.2679	1.414	18	0.174
	Sparisoma viride	Yes	Yes	0.5308	-2.153	18	**0.045**
	Scarus inserti	No	Yes	0.3647	-1.704	18	0.106
Snakepit	*Scarus taeniopterus*	Yes (Sqrt)	Yes	0.1214	-0.820	18	0.423
	Scarus vetula	Yes	Yes	0.1248	-0.838	18	0.413
	Sparisoma aurofrenatum	No	No	0.2341	-0.594	11.4	0.564
	Sparisoma viride	Yes	Yes	0.2077	-1.206	18	0.244

Site grouping	**Species**	**Normal?**	**Equal variances?**	**Power**	**t-statistic**	**dF**	**p**
	Scarus inserti	No	Yes	0.2635	1.400	18	0.179
Eastern Blue Cut	*Scarus taeniopterus*	Yes (Log_{10})	Yes	0.0645	0.373	18	0.713
	Scarus vetula	No	Yes	0.2106	1.217	18	0.239
	Sparisoma aurofrenatum	Yes (Sqrt)	Yes	0.5529	-2.212	18	**0.040**
	Sparisoma viride	Yes	Yes	0.0513	-0.114	18	0.910
	Scarus inserti	No	Yes	0.1266	-0.848	18	0.408
Southwest Breaker	*Scarus taeniopterus*	No	Yes	0.1025	-0.705	18	0.490
	Scarus vetula	Yes	Yes	0.3261	1.593	18	0.129
	Sparisoma aurofrenatum	Yes	Yes	0.0585	0.286	18	0.778
	Sparisoma viride	No	Yes	0.1022	-0.709	18	0.487
	Scarus inserti	No	Yes	0.7052	2.642	9.5	**0.026**
North Rock	*Haemulon sciurus*	No	No	0.1575	-1.000	18	0.331
	Haemulon flavolineatum	No	Yes	0.1464	-0.949	18	0.355
	Cephalopholis fulva	No	Yes	0.1060	0.728	18	0.476
	Mycteroperca bonaci	No	Yes	0.1575	-1.000	18	0.331
	Epinephelus guttutus	-	-	-	-	-	-
	Lutjanus griseus	-	-	-	-	-	-
	Ocyurus chrysurus	-	-	-	-	-	-
Snakepit	*Haemulon sciurus*	No	Yes	0.0500	0.000	18	1.000
	Haemulon flavolineatum	No	Yes	0.0589	-0.293	18	0.773
	Cephalopholis fulva	No	Yes	0.0500	0.000	18	1.000
	Mycteroperca bonaci	-	-	-	-	-	-
	Epinephelus guttutus	No	Yes	0.1575	1.000	18	0.331
	Lutjanus griseus	No	Yes	0.1575	-1.000	18	0.331

Site grouping	**Species**	**Normal?**	**Equal variances?**	**Power**	**t-statistic**	**dF**	**p**
	Ocyurus chrysurus	No	Yes	0.1575	1.000	18	0.331
Eastern Blue Cut	*Haemulon sciurus*	No	No	0.2951	1.500	9	0.168
	Haemulon flavolineatum	No	Yes	0.0878	-0.600	18	0.556
	Cephalopholis fulva	No	Yes	0.0644	0.372	18	0.714
	Mycteroperca bonaci	No	Yes	0.1575	-1.000	18	0.331
	Epinephelus guttutus	-	-	-	-	-	-
	Lutjanus griseus	No	Yes	0.1575	-1.000	18	0.331
	Ocyurus chrysurus	No	No	0.2951	-1.500	9	0.168
Southwest Breaker	*Haemulon sciurus*	-	-	-	-	-	-
	Haemulon flavolineatum	No	Yes	0.0754	-0.493	18	0.628
	Cephalopholis fulva	No	Yes	0.0741	0.480	18	0.637
	Mycteroperca bonaci	-	-	-	-	-	-
	Epinephelus guttutus	No	Yes	0.1575	1.000	18	0.331
	Lutjanus griseus	-	-	-	-	-	-
	Ocyurus chrysurus	-	-	-	-	-	-
North Rock	*Stegastes variabilis / leucostictus*	No	No	0.1796	-1.095	11.7	0.295
	Microspathodon chrysurus	Yes	Yes	0.0715	-0.454	18	0.655
Snakepit	*Stegastes variabilis / leucostictus*	No	Yes	0.1716	-0.885	18	0.388
	Microspathodon chrysurus	No	Yes	0.0564	-0.249	18	0.806
Eastern Blue Cut	*Stegastes variabilis / leucostictus*	No	No	0.7526	-2.794	11.5	**0.017**

Site grouping	**Species**	**Normal?**	**Equal variances?**	**Power**	**t-statistic**	**dF**	**p**
	Microspathodon chrysurus	No	Yes	0.0500	0.000	18	1.000
Southwest Breaker	*Stegastes variabilis / leucostictus*	No	Yes	0.1357	0.896	18	0.382
	Microspathodon chrysurus	No	Yes	0.0885	-0.605	18	0.554