Spatial patterns and habitat associations of targeted reef fish in and around a marine protected area in St. Croix, U.S. Virgin Islands

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Abstract

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As marine protected areas (MPAs) become an increasingly popular method to address global declines of coral reef ecosystems, understanding how to gauge no-take reserve effectiveness through both simple metrics and spatially quantitative methods is imperative for robust design and management. In order to be an effective fisheries management tool, it must be shown that MPAs do not simply displace fishing effort, but can actually increase the biomass or density of fish in adjacent fisheries. Net export of adult fish to surrounding waters, termed the spillover effect, is one way MPAs may function to replenish fish stocks. The ability to detect the spillover effect using simple metrics of abundance and biomass for five highly targeted species was tested for an MPA in the US Virgin Islands. Moreover, it is equally important for managers to understand linkages between reef fish biomass patterns and associated habitat at multiple scales. Habitat characteristics that influence distribution patterns of targeted reef fish can be explored through spatial statistics and spatial multivariate models. In this study, the specific aim was to further evaluate seascape and local site habitat metrics to find how spatial scales of habitat composition and configuration can be used together cohesively to understand reef fish distribution patterns. In addition, global and local spatial regression models were compared to determine if there is non-stationarity of ecological processes across management zones. Results of this study reinforce the complexities of fish-habitat interactions, which make detection of spillover difficult using simple metrics. However, using a combination of both multi-scale spatial habitat metrics and local regression methods can aid in MPA management and design.

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Introduction

Coral Reef Systems in Decline

Coral reef communities have experienced severe declines due to overfishing, pollution, disease and global change (Bellwood et al. 2003). In the Caribbean, coral cover has declined on average from 50% to 10% over the last three decades. The region-wide decline of two primary reef building species, *Acropora palmata* and *Acropora cervicornis*, have resulted in a loss of reef complexity and habitat for reef fish and macroinvertebrates (Gardner et al. 2003; Bellwood et al. 2003). The resilience of reefs, or their ability to recover from both natural and human impacts, has been compromised by accelerating global change, and has resulted in rapid phase shifts from coral-dominated to macroalgae- dominated systems (Bellwood et al. 2003). In the U.S. Virgin Islands specifically, live coral cover has declined, algal cover has increased, seagrass densities have declined, and the abundance of large reef fish has sharply decreased (Rogers & Beets 2001; Fabricius et al. 2005).

Unsustainable fishing practices have stressed fish stocks for decades and since the 1980s fish catches have declined and stocks have collapsed (Pauly et al. 2002; Jackson et al. 2001). Although reef fish fisheries account for only 2 to 5% of global fisheries extraction, they provide a disproportionately large amount of protein to tropical and underdeveloped regions with growing populations (Pauly et al. 2002). Reef fish landings are generally believed to be under-reported and many have posited that reef fish fisheries may be inherently unsustainable (Newton et al. 2007; Pauly et al. 2002). Caribbean reef assemblages may be particularly vulnerable to overfishing because there is less redundancy in functional groups as compared to assemblages in the Pacific (Bellwood et al. 2003). The U.S. Virgin Islands is no exception; reef fisheries in the USVI have been rated as “overexploited” and there is evidence that changes to reef fish assemblages began over 30 years ago, even before widespread habitat degradation began to change the character of coral reefs (Rogers & Beets 2001; Newton et al. 2007). Commercial fishing is a vital part of the local economy on St. Croix, and is of cultural and social importance. Traps, handlines and seines are the primary form of extraction and over 180 species of reef fish are targeted (Rogers & Beets 2001).

While reef fish populations have been under stress from over-harvesting for decades with relatively well-known effects, the results of coral declines and habitat degradation on reef fish communities are not as well studied. However, recent declines in Caribbean reef fish density include lower-trophic level species and have not been confined to heavily targeted species. This provides evidence that habitat degradation has begun to affect reef fish communities (Paddock et al. 2009). Over 75% of Caribbean coral reef species have declined in abundance, with species most directly dependent on coral health showing the greatest declines. This is consistent with the finding that reductions in live coral cover and over-all reef destruction affects reef fish abundances and diversity (Jones et al. 2004). Local habitat degradation caused by land-based pollution and sedimentation is now likely to be compounded by the effects of global change and ocean acidification, further threatening coral reef communities and their associated fish assemblages (Hoegh-Gulberg et al. 2007).

Role of MPAs in Coral Reef Management

Marine protected areas (MPAs) are increasingly being used as a tool for marine conservation and to enhance the resilience of marine ecosystems. MPAs have been shown to increase live coral cover and fish biomass inside their boundaries (Evans 2004). However, the use of no-take zones as a method to manage fisheries is still contentious (Russ et al. 2003). In order to be an effective fisheries management tool, it must be shown that MPAs do not simply displace fishing effort, but can actually increase the biomass or density of fish in adjacent fisheries. One way that MPAs could achieve this is through the spillover effect, which is a net export of adults across no-take boundaries. This emigration of individuals across a reserve boundary has been shown to create a decreasing gradient of biomass, abundance or density with increasing distance from the boundary (Russ et al. 2003; Kramer and Chapman 1999; Forcada et al. 2009). Evidence of the spillover effect has been found in both tropical and temperate systems (Abesamis et al. 2005; Forcada et al. 2009).

The magnitude of spillover and the distance over which it is effective is dependent on many factors. Targeted (fished) species are more likely to show the spillover effect than unfished species. Abesamis et al. (2006) found that the gradient of abundance across boundaries for targeted fish species in a no-take area in the Philippines could not be explained by habitat effects alone, while the distribution of non-targeted species was more likely to be dictated by habitat quality. They also found that in the absence of fishing pressure outside the boundaries, the spillover effect was less apparent. Higher mobility species with larger home ranges may display greater magnitudes of spillover that extend greater distances outside the boundary (Abesamis et al. 2006). The size and age of a reserve is expected to influence the magnitude and detectable range of the spillover effect, however, because most studies have focused on long-established, small MPAs, empirical evidence to test this hypothesis has not yet been collected (Halpern et al. 2010).

Habitat structure, in terms of both complexity and connectivity, can also influence the amount of spillover. Marine environments are extremely patchy, which can act as a barrier for reef fish movement. Cross-boundary heterogeneity could therefore be hypothesized to negatively affect spillover (Forcada et al. 2008). In three Mediterranean reserves, Forcada et al. (2009) found that while there was significant export of adults of targeted fish species across boundaries in continuous sea grass beds, boundary areas interspersed with sandy patches were not conducive to movement (or emigration).

In addition to factors that can cause differences of magnitude and extent of spillover, there are confounding factors that can make spillover difficult to detect. Habitat effects can either falsely enhance or mask the spillover effect. Many no-take areas are created in areas of existing high habitat quality. Such is the case with Buck Island Reef National Monument, which was created to protect “one of the finest marine gardens in the Caribbean Sea” (U.S. President Proclamation 1984). If MPAs encompass the best habitat in a particular area, then enhanced fish biomass inside and surrounding the MPA could be attributable to good habitat quality as opposed to protection. For example, Claudet et al. (2010) found that habitat characteristics and quality were more important determinant of species composition and abundance than the status of protection. Therefore, if gradients consistent with the spillover effect are observed, they must be shown to result from protection and not habitat features. Alternately, habitat quality could be uniform across the MPA boundary or even greater outside the boundary, which could counterbalance and therefore mask any effect of spillover if it were occurring. Therefore it is important to consider habitat quality when evaluating MPA effectiveness and fisheries spillover (Garicia-Charton et al. 2004; Forcada et al. 2008). A study of Buck Island Reef National Monument and Virgin Islands National Park, two MPAs located in the U.S. Virgin Islands, found no significant increases in abundance or size of fishes inside the protected areas compared with outside the MPA boundary (Rogers & Beets 2001).

As with all spatially explicit ecological questions, issues of scale and design of monitoring programs can affect the research outcomes. While the exact distance over which spillover occurs differs between studies, most agree that it is very localized. In a review of empirical evidence of spillover, Halpern et al. (2010) estimated that on average, the spillover effect was measurable up to a distance of 800 m from reserve boundaries. Harmelin-Vivien et al. (2008) observed the spillover effect in 6 Mediterranean reserves, concluding that the benefits to fishers extended on the order of hundreds of meters from the boundary. However, even this small increase of biomass or abundance outside the reserve was often enough to compensate fishers for lost fishing grounds, and indeed led to increasing catches (Halpern et al. 2010). Home ranges of many highly mobile fish exceed “sampling units common in MPA assessments,” complicating the study design and detection of spillover (Claudet 2010).

Habitat Associations

Just as habitat quality can affect the magnitude and detectability of spillover, environmental and habitat characteristics have been shown to strongly influence spatial distribution patterns of reef fish. Both protection status and habitat associations must therefore be examined to understand the distribution of reef fish. While studies have historically focused on habitat features of the local sample location (e.g., depth, structural complexity and percent coral cover), there has been increasing emphasis on patch and landscape habitat variables that focus on sample location context in a larger habitat mosaic. Reef fish distribution is therefore not simply dependent on site characteristics in isolation, but also the characteristics of the surrounding environment (Pittman et al. 2004).

Structural complexity of benthic habitats has been shown to be one of the most important determinants of reef fish biomass and species richness. Structural complexity offers refuge from predators and forage habitat (Alvrez-Filip 2009; Gratwicke & Speight 2005; Friedlander & Parrish 1998). Reef height has been found to be less important than the rugosity and number of small holes in the substratum (Gratwicke & Speight 2005). Biomass and species diversity can also differ by depth. For example, Friedlander et al. (2003) observed higher biomass of reef fish at shallower sites, but higher diversity at deeper sites in a study of Hawaiian coral reefs. Higher coral cover has been found to correspond with higher reef fish biomass and small changes in cover can have a large effect on abundance and species richness (Bell & Galzin 1984). Growth rates of reef fishes can also be affected by percent coral cover, with damselfish growth rates significantly higher where coral cover is higher (Feary et al. 2009). Coral cover is important to consider in addition to reef complexity because structure persists after the death of coral tissue. Although rugosity and coral cover are related, because they are not direct functions of one another, both must been considered in monitoring schemes (Alvarez-Filip 2011).

Habitat context, defined as "the spatial pattern of surrounding habitat patches," has been found to affect reef fish assemblages in the Caribbean. The spatial characteristics of habitat structure can be describe by pattern metrics which are informative of individual patches of similar habitat (i.e. patch size, patch area, patch perimeter) or metrics which illustrate the complex pattern of a mosaic of those patches across the whole landscape (i.e. landscape diversity, number of patches, average patch size). These metrics may also be derived for any give subset of a landscape such as the region within a set radius of a site (Grober-Dunsmore 2008, Pittman et al. 2003). Grober-Dunsmore et al. (2008) found in the U.S. Virgin Islands that the perimeter-to-area ratio of patches and the number of patches were the best indicators of fish abundance. Despite this finding, the authors went on to concluded that overall the landscape metrics performed poorly as indicators of fish abundance and concluded that at the scale of several patch reefs, fish assemblage structure was not well predicted by landscape metrics of habitat diversity. They also concluded that different reef species may respond to metrics differently, making analysis of the entire reef assemblage difficult. While patch composition was strongly related to fish parameters, reef configuration and reef size were not (Grober-Dunsmore 2008; Pittman et al. 2004). Several studies have shown that the amount of seagrass nearby is one of the most important seascape habitat characteristic affecting both reef fish abundance and diversity (Grober-Dunsmore et al 2007; Pittman et al. 2007; Kendall et al.2003).

One of the larger implications of many of these patch and landscape metrics is that they correspond to the degree of habitat connectivity, which affects how reef fish move through their environment. Habitat connectivity appears to play a large role in reef fish movements and therefore distribution. Chapman and Kramer (2000) found reef fish in Jamaica to high site fidelity, despite occasional movements up to 500m. They also found that areas of sand and rubble measuring more than 20m between reef acts as a natural barrier that can prevent fish movement.

Spatial Pattern Analysis

The concept of landscape ecology has been applied to terrestrial ecosystems for decades, but its application to marine environments is just now beginning to become more pervasive (Pittman et al. 2011). The emerging field of seascape ecology seeks to link ecological process with spatial and temporal patch patterns over multiple scales (Bostrom et al. 2011). In a special theme section on seascape ecology, Pittman et al. (2011) suggest that the most pressing challenge and objective in seascape ecology “is to determine the mechanisms by which spatial patterns influence key ecological process.” Because the use of landscape metrics in marine and coral reef environments is relatively new, the strength of relationships between different terrestrially-derived metrics and reef fish characteristics is still being tested. Of particular interest in marine spatial ecology is determining ecological thresholds for patch and landscape metrics (Bostrom et al. 2011). In addition to patch and landscape metrics, a variety of spatial statistics can help reveal quantitative relationships between reef fish distribution and habitat that may lead to the ability to link pattern to ecological process. Spatial regression techniques, both global and local, are a further application of spatial statistics that show graphically the relationship between multiple variables and fish distribution patterns.

Global spatial statistics require that processes that control spatial distribution and pattern of the location and attributes of data be uniform across the study area. The consequence of this assumption is that a model of the process would exhibit spatial stationary in the mean and variance of the random function. The output of a global statistic is a single value or function for the entire extent of the study area; for example, the mean or standard deviation. Ordinary least squares (OLS) is one such global statistical model that assumes processes are stationary or homogeneous (Fortin & Dale 2005). OLS also assumes that the “observations used for fitting models are independent,” or not autocorrelated (Zhang 2004). Zhang identifies three types of dependence in forest ecology that violate this assumption: nested autocorrelation, temporal autocorrelation and spatial effects which include spatial autocorrelation and non-stationarity. These violations of independence also apply to marine data. Ecological data most often follows Tobler’s law, “Everything is related to everything, but near things are more related than distant things” (Tobler 1970). Autocorrelation of error or residuals can result in measures of model fit to be misleading in their spatial representation of pattern. To address non-stationarity or heterogeneity of ecological data, a local statistic can be used. A geographically weighted regression is an example of a local statistic that addresses the variation of the strength relationships and processes across space (Fotheringham et al. 2002).

A geographically weighted regression (GWR) is a local spatial statistic that evaluates the relationships among spatial variables such that the nearer observations exert greater influence over the expected model estimate. The resulting estimates can be mapped in order to examine local variation in the model. This analysis can be especially informative to fisheries managers because it can indicate how processes that shape fish distribution fluctuate across MPA boundaries and management zones. However, GWR has been applied sparingly to fisheries data, and has not yet been used to help describe tropical reef fish distribution. Windle et al. (2009) used a GWR to evaluate spatial distribution of cod in the Northwest Atlantic and found that a local statistic outperformed global techniques. Moreover, marine data tend to be highly patchy and fisheries data in particular is often zero-inflated and interspersed with extremely high fish observations (Pennington 1996). Marine environmental gradients tend to be stark and the resultant data are difficult to normalize and describe using parametric techniques (Windle et al. 2009). A geographically weighted regression could be a way to address these confounding characteristics of fisheries and marine ecosystem data.

Site Description

Buck Island Reef National Monument (BUIS) was created in 1961 under the Antiquities Act and is managed by the National Park Service. The monument included the 17- acre Buck Island and 704 acres of the surrounding waters for the purpose of "protecting Buck Island sand its adjoining shoals, rocks, and undersea coral reef formations" and to preserve "one of the finest marine gardens in the Caribbean Sea"(U.S. President Proclamation 1984). The original management plan included a zone on the western end of the island that allowed for limited resources extraction, while the zone on the eastern portion of the Monument restricted all forms of harvest (Figure 1). In 2001, under the U.S Coral Reef Initiative, the boundaries of the monument were expanded to encompass additional marine habitat bringing the total area of the monument to 19, 015 acres. The boundary of the expanded Monument were primarily determined by political methods, rather than following biological rational. All fishing, both recreational and commercial, is now banned within the marine protected area and rangers enforce this closure.

The St. Croix East End Marine Park (STXEEMP) was created by the local U.S. Virgin Islands government in 2003, and is the first territorial marine park in the U.S. Virgin Islands. STXEEMP encompasses the eastern end of the island and extends from the high tide mark to three miles off shore. It is nestled against Buck Island Reef National Monument. There is a diversity of ecosystems within the park including coral reefs, seagrass beds, mangroves forests, salt ponds, colonized pavement and sandy beach (TNC 2002). The primary management goal of the park is the "sustainable use of natural ecosystems" and to meet this goal, four management zones or use areas (no take, recreation, turtle wildlife, and open) were established within the park (DPNR 2005). The no-take zones are located in nearshore environments and are designed to protect reef, seagrass, and mangrove communities. Fishing and harvesting are prohibited within the no-take zones. Turtle wildlife areas are located adjacent to nesting beaches and in those area, net fishing, jet skiing and any other activity that might disturb nesting turtles are prohibited. Recreation areas are designed for swimming, snorkeling, and diving, and activities that would inhibit recreation are not allowed. The majority of the park is comprised of open areas in which fishing, harvesting and all recreational activities are allowed (TNC 2002). Although the park was created in 2003, funding for buoys to demarcate the different zones was not secured until 2011. In fall 2011, marker buoys were installed; however, there has been no enforcement of no-take and turtle wildlife areas to date. Because of this delay in the implementation of signage and enforcement, the area encompassed by the park expansion has not yet realized the benefits of protection.

Research Goals

I used data from fish observations and benthic monitoring over a 10 year period to determine whether spatial pattern could be detected within each of five highly-targeted reef fish species, and if so, to determine whether the patterns are consistent with those proposed for other coral reef systems. I explored the utility of the data for evaluating the spatial effectiveness of current management options through comparison of univariate versus multivariate methods, local versus global spatial statistics, and landscape- to local-scale metrics.

Research Questions

Q1. Is the spillover effect detectable in and around Buck Island Reef National Monument?

  Q1.1. Is the spillover effect detectable using simple metrics of abundance and biomass versus distance?

  Q1.2. Can weighted standard deviational ellipses help indicate magnitude and direction of spillover?

  Q1.3. Do significant hotspots or outliers of abundance fall inside the park boundaries?

Q2. How can model performance be improved given the data?

  Q2.1. Is model performance improved by use of a multivariate spatial model that considers habitat associations in addition to protection status?

  Q2.2. Does a combination of local, patch and landscape metrics improve model performance?

Q2.3. Does a local statistic (GWR) measurably improve spatial distribution model performance over a global statistic (OLS)?

I use the results of these analyses to consider whether and how spatial analytical approaches can contribute to management of reef fish in and around Buck Island Reef National Monument.

Methods

Study Site

St. Croix is located in the Eastern Caribbean, west of Puerto Rico, and is the largest and southern-most of the U.S. Virgin Islands. It is separated from St. Thomas and St. John by the Puerto Rican trench and is thus ecologically semi-isolated. The study area is located on the north side of the east end of St. Croix and includes Buck Island Reef National Monument and the St. Croix East End Marine Park (Figure 1).

Buck Island is formed from Cretaceous volcaniclastic rocks that were deposited by turbidity flows of volcanic fragments. Reefs began to form around Buck Island in the Pleistocene, about 125,000 years ago. Today, a linear reef with a high reef crest forms a protective barrier around the east, north-east and south-east of Buck Island. Inside the main reef complex is a shallow lagoon, ranging from 120 m to 240 m wide, that is primarily comprised of sand, carbonate pavement and scattered patch reef. On the north side of the island outside the reef crest are abrupt, intermittent patch reefs called “haystacks” composed of *Acropora palmata* fragments that were cemented together starting around 1000 years ago. (Hubbard 1991). The south forereef is covered with *Acropora palmata* and newly recruited *Diploria* spp. Buck Island Reef National Monument protects linear, patch and spur and groove reef, colonized and uncolonized pavement and seagrass beds, as shown in the area habitat map (Figure 1).

Data Collection

All analysis is based on data collected by NOAA’s National Centers for Coastal Ocean Science through the Caribbean Coral Reef Ecosystem Monitoring Program. Starting in 2001, NOAA’s Biogeography Branch began sampling in and around Buck Island Reef National Monument with the goal “To spatially characterize and monitor the distribution, abundance, and size of both reef fishes and macro-invertebrates” and relate them to the benthic habitat (NOAA 2008). A random stratified sampling scheme was created based on the 2001 NOAA Biogeography Program nearshore benthic habitat maps and NOS bathymetry models. Refer to Figure 1 for the study area and all locations sampled between 2001 and 2010. At each survey location, two divers use a belt transect to characterize fish and benthic habitat.

To quantify fish abundance, the first diver began the observational survey by slowly rolling out a tape measure at a pre-selected random compass bearing. The dimensions of the transect were 25m long and 4m wide (2 meters on each side of the tape). A standard sampling period of 15 minutes per transect was used. The surveyor recorded fish to the species level and the fork length of each fish was categorized into 5cm increment bins, while those larger than 35cm were measure to the nearest centimeter. After finishing the fish survey, the diver used 2 randomly selected positions along the tape measure to lay a chain in order to collect rugosity measurements.

As the fish observer slowly rolled out the tape measure, the second diver laid a 1m x 1m quadrat at randomly selected distances every 5 meters along the 25m long tape. First the depth at each quadrat position was recorded. Next, the abiotic and biotic footprint within each quadrat was observed. The abiotic footprint was equal to 100 percent and included substrate beneath any living organisms. Percent cover of living organisms, including algae, seagrass, live corals, sponges, and gorgonians, was recorded and when added to bare substrate, equaled 100 percent. At the quadrat level, canopy height and biota abundances were recorded. At the transect level, abundance of queen conch, lobster and long-spined urchin, as well as absence or presence of coral reef structures within 3 meters of the transect were recorded.. A more detailed survey methodology can be found at: http://ccma.nos.noaa.gov/ecosystems/coralreef/reef_fish/protocols.aspx

The number of locations sampled per year ranged between 150 and 250. In most years, locations were sampled in the fall between August and November and then the winter or spring, between January and April. In two years, 2008 and 2010, locations were sampled only in the fall. Refer to Table 1 for a break-down of survey locations by year, season and protection status. In early years (2001 and 2002), the study area was much narrower and focused in and around the old park boundary. In 2003, the study area was expanded to the full extent of the study of area shown in Figure 1.

Data Analysis

I chose to analyze spillover and spatial patterns of five commercially fished species based on catch data, conservation need, and frequency of occurrence in the ecological surveys. For example, while mutton snapper (*Lutjanus analis*) is highly targeted and also has high conservation value, the frequency occurrence is low, making spatial analysis difficult. This study therefore focuses on two small grouper, coney (*Cephalopholis fulva*) and red hind (*Epinephelus guttatus*), yellowtail snapper (*Ocyurus chrysurus*), redband parrotfish (*Sparisoma aurofrenatum*) and queen triggerfish (*Balistes vetula*).

Grouper and snapper are among the most valuable commercially fished species on St. Croix, however they are particularly susceptible to overfishing because of their late reproductive maturity, long life history, complex age-structure and their tendency to form spawning aggregations. These spawning aggregations can include hundreds to thousands of fish and are disproportionately targeted by fishermen due to their spatial and temporal predictability. Grouper are protogynous hermaphrodites, meaning that they begin their life cycle as females and become males later in life. Males are thus typically much larger than females and selective fishing of large males can alter the community structure of the fish populations (Nemeth 2005). Under intense commercial fishing pressure in the U.S. Virgin Islands, the Nassau grouper fishery collapsed in the 1970s and was replaced by a fishery for smaller grouper species, such as red hind, coney and grasby. By the next decade, these species were also in severe decline (Karras & Agar 2009). In addition to grouper and snapper, parrotfish are also highly targeted on St. Croix. While traps have historically been the dominant gear type used on St. Croix, the use of gill and trammel nets and associated catch has increased and now exceeds annual trap catches. Parrotfish are the primary targets and comprise 56% of the annual gill and trammel net catch. As parrotfish populations have begun to decline due to fishing, damselfish, which feed on live corallites, have increased in abundance (Toller & Tobias 2005).

Queen triggerfish is primarily trap-caught and in the U.S. Virgin Islands, consisted of 10-15% of the total fisheries catch (Manooch & Drennon 1987).

Spillover

I used the original boundary established for Buck Island Reef National Monument (BUIS) instead of the current (expanded) park boundary that was established in 2001 (Figure 1). A previous study at BUIS examined spatial patterns of reef fish in and around the current boundary. They found higher biomass of some targeted species, including parrotfish and coney, on hardbottom habitat inside the park. However, biomass and density of predator groups, such as snapper, were higher outside the park (Pittman 2008). There is anecdotal evidence that the original BUIS boundary is more accepted by stakeholders and therefore there may be less affected by poaching. To examine changes in abundance and size over the study period, I plotted abundance, biomass, and biomass size class versus distance from the BUIS boundary. For biomass and abundance, I combined observations across all years in a single plot, and then made a plot for each year from 2004 to 2010. I made a single plot of biomass size classes from 2004-2010. I excluded from analysis all sample locations in which observations for a given species were zero. Since spatial statistics are designed to evaluate the association of observations as a function of the distance and direction apart of those observations, only the occurrence of species and their location in space was used. As a measure of distance from the original BUIS boundary, I used the shortest distance from each survey location to the boundary, determined using the Near tool in AcrGIS 10.0. In this analysis, the original BUIS boundary itself was set at zero. Survey locations inside the BUIS boundary were assigned a negative value that became increasingly negative with distance from the boundary, and those outside were assigned a positive value. A decline in abundance and biomass with increasing distance outside reserve boundary is consistent with the spillover effect.

Spatial Pattern Analysis

To further examine spatial patterns of reef fish abundance, I plotted a standard deviational ellipse for fish biomass and Local Morans I of fish abundance for each of the five species examined. To examine magnitude and direction of reef fish distribution outside the original BUIS boundary, unweighted and weighted standard deviational ellipses were compared for each species. Local Morans I was used to measure non-stationarity to reveal hotspots, and to identify outliers that vary from the global statistic (Anselin 1995).

The mean center is a simple measure of the geographic center of the reef fish biomass data that is calculated by plotting the average x value versus the average y value. Changes in the mean center over time or in weighted versus unweighted data help show corresponding changes in spatial distribution. Similarly, standard deviational ellipses (SDE) can be used to elucidate changes in average spatial distribution with the added elements of direction, magnitude and concentration or dispersion (Yuill 1971). The mean center and standard deviational ellipse of reef fish biomass were calculated for each of the five targeted species using the Spatial Statistics Toolbox in ArcGIS 10.0. First, the mean center and the SDE were calculated for all sample locations outside the original BUIS boundary as a baseline of overall sample location distribution. Then, each species was analyzed separately using only non-zero values and observations at samples locations outside the original BUIS boundary. The x and y axes of the SDE were set at one standard deviation from the mean center. The unweighted mean center and SDE were compared to the mean center and SDE of the weighted data. The weight assigned to each observation is an attribute value related to the intensity of observation. The weight value simulates the number of observations at each location equal to the weight value, and therefore influences the pattern in the spatial distribution.

Maps displaying each species' weighted and unweighted mean center and SDE were created, along with accompanying tables that give quantitative characteristics of the mean center and SDE that help describe mean distribution, orientation, magnitude and concentration or dispersion (Yuill 1971). Rotation is degree of the major axis, measured clockwise from north (0 degrees). The ratio is the proportion of the data that falls within the ellipse, while the concentration is the percent that falls within the ellipse. The eccentricity is a measure of flatness or elongation of the ellipse and is calculated using the following equation (Yuill 1971):

Eccentricity = length of focus/length of major axis

Local Morans I, a local statistic, returns a value for each observation instead of one average value for the entire study area. Generally, Local Morans I provides a measure of autocorrelation and similarity between observations as a function of distance. It can be used to map hotspots and coldspots and spatial outliers (Anselin 1995). In order to examine statistically significant clustering across the study area, an interpolated surface of abundance using the Inverse Weighted Distance (IDW) technique was first performed. The IDW tool in ArcGIS 10.0 was used. Cell size and power were left blank, search radius was variable, and the processing extent was set to the study area. The raster output was then converted back to a simplified polygon and used as the input for the Local Morans I. The conceptualization of spatial relationships was set to inverse distance. The results were mapped.

Multivariate Models

To explore the relationship between reef fish biomass and habitat associations and protection status, spatial multivariate regression models were constructed for each of the five targeted species. Landscape and local habitat characteristics were compared and the most significant variables were included in the models. Non-stationarity of the data was examined by comparing the global spatial statistic to a local spatial statistic using the same optimal model inputs.

Input variables were selected based on previous findings reported in the literature. To test the importance of landscape and local metrics, variables at both spatial levels were selected. At the local level, depth, rugosity, and hard coral cover were used as model inputs. At the landscape level, distance from the original BUIS boundary (with distances inside assigned a negative value and those outside a positive value), as well as proportion of sand, macroalgae, uncolonized pavement, seagrass, and hard coral cover within a 250 meter radius of each locations. Lastly, the distance of the sample location from the center of a nearest linear or patch reef was calculated.

The proportion of coral reef habitat in a 250 m radius buffer around each location was determined by using the Intersect polygons with Raster tool provided by the Geospatial modeling Environment toolbox (http://www.spatialecology.com/gme). The NOAA fine scale Buck Island habitat map created in 1999 was first converted to a 5 km raster layer, using the "ID" field as the value captured in the raster. The GME tool was run using the 250m buffered points and the habitat raster. Results were appended to the table associated with the 250m buffer layer. The column outputs were in numeric categories "HABV1"- "HABV35". Using field calculator, these categories were combined into 5 fields: coral reef, mangrove, macroalgae, seagrass, uncolonized hardbottom and sand. The percent composition of each class was again determined using field calculator.

To calculate the distance of each sample location from the center of the nearest linear or patch reef, the sample locations were overlaid on the NOAA fine scale habitat map. Using the Feature to Point tool in Data Management, a new shapefile containing the centroids of all the polygons was created. Next, linear and patch reef locations were selected and the select set was exported into a new shapefile. Then the Near tool was used to find the distance between each sample location and the nearest center of a patch of linear reef.

The most significant and non-collineated variables that optimize model performance were selected using a number of metrics in JMP and ArcGIS 10.0. First, because the data were not normally distributed, a square root transformation was used. Next, in JMP 9.0, I used the multivariate scatterplot matrix and Pearson correlation coefficient matrix to examine the relationship between variables and find significant variables. Variables with a Pearson correlation coefficient of at least an absolute value of .3 were used as the independent variables in a standard least squares model fit. Significant variables with low t-probabilities were selected and the variance inflation factor (VIF) for each variable was examined to find multicollinearity among the variables, with large VIFs indicating collinearity. When two or more variables had high VIFs, different combinations of the variables were tried. In these cases, the most significant variable with the lowest t-probability was used. Once the significant variables with low VIFs were identified, they were entered into an ordinary least squares (OLS) model in ArcGIS 10.0.

OLS makes several assumptions that must be recognized. OLS assumes that 1) the process under study is stationary; 2) there is no multicolinearity among the explanatory variables; 3) the residuals are not autocorrelated; and 4) that the relationship between the variables is linear (ArcGIS help menu). The Akaike Information Criterion (AIC) is a measure of model performance. The lower the AIC, the better the model fit (Fotheringham et al. 2002). A difference of 3 AIC units is generally considered the minimum amount that indicates better model performance (Fotheringham et al. 2002). The R-squared value is also a measure of model performance, with the best R-squared being 1.0. An R-squared value of 1.0 indicates that the model explains 100 % of the variation in the spatial distribution of the response variable.

After the OLS models were run, the non-stationarity of the strength of relationships between each coefficient and the dependent variable was assessed using a geographically weighted regression (GWR). The same optimum variables used in the OLS were used in the GWR. An adaptive bandwidth that uses larger spatial kernels when data are scarce and smaller when data are more abundant was applied (Fotheringham et al. 2002). This adaptive kernel technique could be especially useful for species such as queen triggerfish and red hind, which have lower smaller abundances and biomass. The intent is to compare both the AIC and adjusted R-squared of the OLS and GWR to determine whether the use of a local statistic over a global statistic improves model performance. The OLS and GWR R-squared also can be compared to the linear, univariate model used to examine spillover and determine whether the multivariate model is a better fit.

The residuals of each OLS and geographically weighted regression model were mapped to display possible clustering or autocorrelation. The coefficients of each explanatory variable of the GWR were mapped as a raster surface that shows the strength of the relationship between the given variable and fish biomass. The potential use of GWR t-values to "delineate distinct zones of species" and show environment interaction relationships has been noted by others (Windle 2009). An objective of this study was to test whether this approach can be used to discern how these relationships change across protection status, which in turn could help inform management.

Results

Spillover

The data do not offer compelling evidence for the spillover effect at Buck Island Reef National Monument. None of the five species investigated exhibited a significant negative gradient in abundance, biomass, or size class biomass with distance away from the reserve, nor does the spillover effect become detectable with increasing age of the expanded no-take reserve between 2004 and 2010 (Figures 2-16). The majority of plots show increasing abundance and biomass with increasing distance from the original BUIS boundary.

Because spillover was not detected using simple metrics, the standard deviational ellipses of biomass cannot be used to determine magnitude and direction of spillover. Orientation and shape of SDE are most affected by the shape of the study area, which can be clearly seen in Figures 17-21 (Yuill, 1971). While the SDE cannot be used in this case to further analyze spillover, the weighted SDEs do indicate the spread and patterns of biomass. For example, the SDE for queen triggerfish is elongated with a high eccentricity, which indicates that biomass is probably heavily biased towards a few areas (Figure 18). Alternately, the weighted SDE of red hind is almost identical to the SDE of the study area and the concentration is relatively low. This is probably the case because areas of high biomass are well dispersed throughout the study area (Figure 19).

The IDW interpolated surfaces show that areas of high fish abundance varied between species, (Figure 22). The results of the IDW and weighted SDEs are in good agreement with respect to fish abundance. Areas of high abundance of coney are located along the northern portion of the study area. Queen triggerfish are concentrated in the northeast corner of the study area, while yellowtail snapper occur in high abundance in the south and west, with a noticeable lack in the northeast corner. Areas of high abundance of red hind and redband parrotfish are relatively evenly distributed across the study area.

The results of the local Morans I analysis show that many of the areas of high abundance in the IDW were not statistically significant hotspots or outliers (Figure 23). Abundance of coney has only a small number of high-high clusters along the northern boundary of the study area. The modeled distribution of queen triggerfish suggests hotspots in the northeast corner of the study area, however low number of these observations throughout the study area influences this result. Although red hind showed areas of high abundance in the IDW interpolated surface, most were not statistically significant hotspots, except those in the southwest portion of the study area. There were only a few hotspots of yellowtail snapper abundance along the north shore of St. Croix and the southwestern corner of the study area. The hotspots or outliers that do exist for each species are found both inside and outside the original BUIS boundary.

Improved Model Performance

Spatial multivariate models that included habitat associations in addition to protection status improved model performance. Significant independent variables differed between species and included a mix of local and landscape metrics. However, rugosity and depth were significant for all species and distance to the center of the nearest linear or patch reef was significant for all species except red hind. Table 2 shows significant variables for each of the five species and table 3 shows model performance. Model performance was moderate for both coney and redband parrotfish, and was less good for queen triggerfish, red hind, and yellowtail (Table 3). Coney and redband parrotfish are most abundant and have the highest overall biomass, suggesting that in this analysis, more data improves model performance, although the results for queen triggerfish are not consistent with this observation.

Significant variables were selected to minimize the VIF, so the final models did not display any problems in multicolleniarity. However, there were some issues with the models that could contribute to their poor performance. The Jarque-Bera statistics was significant for all species, indicating that residuals could be autocorrelated. A global Morans I did reveal that the residuals are autocorrelated at the .95 confidence level. Figure 24 displays maps of the distribution of OLS residuals. This could be a result of model misspecification, such as missing an explanatory variable or non-linear relationship between the variables (ArcGIS Help Menu). A scatterplot matrix of each independent variable versus species biomass showed non-linear relationships between most of the variables, and even with a square-root transformation, fish biomass was not normally distributed. It is difficult to identify the exact cause of the Jareque-Bera statistic’s significance. Neither the maps of OLS residuals, nor the local Morans I maps immediately revealed patterns that could lead to the discovery of other relevant explanatory variables. In such a complex system with biological, chemical, physical and geological controls, it is difficult to incorporate all explanatory variables accurately in a simple multivariate model.

The associations between the independent variable and fish biomass, given by the coefficients, did not always follow what would be expected from the literature, and differed significantly by species. For example, the biomass of coney displayed a strong positive association with the proportion of uncolonized pavement within 250m, red hind showed a moderate positive association with proportion of macroalgae within 250m, and redband parrotfish and yellowtail snapper displayed a weak negative association to distance to the center of the nearest patch or linear reef (Figure 24). The associations with landscape variables appeared to be less predictable than local variables. For example, all species showed a moderate to strong association with rugosity, which has been demonstrated over and over again in the literature. Coral cover had only a weak positive association with coney and redband parrotfish, which suggests that rugosity is more important than live coral cover in determining fish distribution.

The Koenker statistic was significant for all species except yellowtail snapper, which could indicate non-stationarity or local variation (ArcGIS Help Menu). This problem might be solved by using a local statistic, such as GWR, that allows for variation in relationships across the study area.

Using a geographically weighted regression for multivariate analysis of targeted reef fish distribution increased model performance for all species. Both the adjusted R-squared and the AIC reflected better model fit for the local spatial regression (Table 3). AIC scores were minimized by a margin of 170 to 30, indicating that GWR outperformed OLS by a significant amount.

The local regression model of coney biomass showed the greatest improvement in model performance, so coefficient raster surfaces were created to examine non-stationarity of associations across the study area (Figure 25). Proportion of uncolonized pavement, proportion of coral reef and rugosity had strong to moderate positive associations with coney biomass. The strength of the relationship between each variable and biomass differed significantly across the study area, with proportion of uncolonized pavement ranging from 4.7 to 21.5. Several of the variables have stronger associations with reef fish biomass distribution within the BUIS boundary. Distance to nearest linear or patch reef and proportion of coral reef have the strongest association to biomass within the BUIS boundaries.

Discussion

I was able to detect no evidence of spillover from BUIS using simple metrics of abundance, biomass and size classes. This result was consistent across all five species investigated. There are several reasons why the spillover effect may not be detectable. First, habitat quality could be limiting the rate of fish production inside BUIS, with the consequence that spillover is too low to detect. Buck Island is surrounded by a shallow water lagoon with low structural complexity, with lower fish biomass than that of surrounding areas. Consequently, habitat attributes could cause low biomass within the reserve. Forcada et al. (2008, 2009) were able to discern the difference between the influences of habitat versus the effect of protection using advanced statistical techniques that differ from the spatial analytical tools I applied.

The sampling design used to obtain the data may not be optimal for this type of spatial analysis. Because I used pre-existing data, I was not able to adjust my sampling design for the specific intent of detecting gradients in biomass. Although the existing data have the advantage of temporal and spatial richness, it is possible that a different sampling scheme could have had a greater power to detect differences. For example, in addition to SCUBA visual surveys, Abesamis et al. (2005) used hook and line sampling outside the reserve to further estimate increased catch and biomass.

Garcia-Charton et al. (2004) argue that it is important to consider both abundance and biomass when examining short ecological gradients because where fish sizes differ, abundance and biomass can reveal different spatial patterns. Alternately, in one of the first studies to identify the spillover effect, Rakitin and Kramer (1996) used both abundance and catch data and found the largest detectable distance of spillover outside the reserve because they were able to use abundance estimates obtained from both observation and extraction (Halpern et al. 2010). Because fishing pressure outside reserve boundaries is a key component in creating a spillover gradient, it is important to estimate fishing pressure in waters outside the reserve. This study could be substantially improved by inclusion of data to indicate fishing for targeted species around the park.

In addition, I examined spillover at only one scale: the full extent of the study area. However, most studies have found that the spillover effect is detectable only at a few hundred meters from the reserve boundary (Harmelin-Vivien et al., 2008). Using such a large study area with a large expanse outside the reserve boundary, up to 5000m, could conceal more localized spillover.

Alternatively, it is possible that the spillover effect negligible or absent. Habitat and environmental characteristics are important in the determination of reef fish distribution. It is possible that these environmental and habitat characteristics are more important than protection status in this area. This, especially in combination with varying amounts of fishing pressure along the boundaries, could contribute to the lack of a spillover effect.

Standard deviational ellipses are a simple tool that can be used to measure direction and magnitude of distribution. Export of reef fish outside protected areas is probably not directionally uniform and SDEs could be used to find areas of high spillover. SDEs could prove particularly useful in examining reef fish biomass spillover outside of MPAs. SDEs would be most useful when abundance or biomass inside a protected area is higher than outside, and when there is a decreasing gradient of abundance or biomass outside the boundary. A more symmetrical study area could be more sensitive to changes in direction and magnitude of spillover.

Although I did not detect a spillover effect at Buck Island Reef National Monument, in comparing the SDE with the hotspot analysis, one can see how shifts in the location, orientation and eccentricity between the unweighted and weighted biomass ellipses reflect the location of hotspots and could be used to track spillover. The high eccentricity and shift of the ellipse to the northeast of the queen parrotfish SDE corresponds to the concentration of hotspots. The same result is visible when comparing stoplight parrotfish SDE and the location of hotspots; the SDE is shifted to the haystack area north of Buck Islands where the majority of hotspots are located.

The local Morans I analysis helps to clarify why weighted and unweighted ellipses are similar; either areas of high biomass are well distributed, are near the center of the SDE, or have no large peaks with consistent biomass over the study area. Redband parrotfish and red hind offer two examples of this. Redband parrotfish biomass is well distributed over the study area, while red hind is well distributed with few peaks.

The hotspots or outliers, however, differed substantially between species, suggesting that each species is utilizing the habitat differently and environmental interactions that help determine spatial distribution are different for each. The hotspots or outliers do not appear to be influenced by protection status. No one area demonstrated a concentration of hotspots common to all species. A few areas of high complexity did show hotspots common to a few of the species. The linear reef along the coast of St. Croix, the haystacks north of Buck Island and far southwestern corner of the study area are hotspots for at least a few species.

The observation that fish species do not congregate uniformly across areas of high rugosity suggests that there exists further habitat specialization between species. Explanatory variables other than rugosity can help determine distribution and these explanatory variables are likely to differ for each species, even within the same family.

The multivariate regression models performed better than the simple univariate regression models. Inclusion of both local and landscape metrics resulted in the best fit model for each species. Model performance for both OLS and GWR varied depending on species. Model fit was best for coney and redband parrotfish and was poorest for yellowtail snapper. It is possible that, among species with poor model fit, an explantory variable was missing. Alternately, it is possible that some reef fish are not the habitat specialists that they are believed to be with the result that it could be very difficult to model their distribution. The most significant explanatory variable for some species deviated from the expected based on what is known of reef fish behavior and habitat preferences. For example, the moderate positive association between red hind biomass and proportion of macroalgae was not expected. It is possible that proportion of macroalgae is related to some other environmental characteristic that is driving the positive association. Overall, with a sampling scheme that shows a snapshot in time of ecological processes that determine reef fish distributin, it is unlikely that a simple multivariate model will be able to perfectly describe a complex system. It is unlikely that any variable will have equal influence over fish distribution patterns over all time.

While distance from the original BUIS boundary was significant for some species, it had a weak positive association, suggesting that biomass actually increased sightly with increasing distance from the boundary. Again, the multivariate models show that habitat charactersitics may have a greater influence over distribution than protections status. It is important to consider that the current boundaries of BUIS were in large part determined by political and logistical means, rather than a cohesive ecological unit that is connected to the STXEEMP.

The improvement of the local GWR over the global OLS regression models shows that local statistics at varying strengths of relationships between variables should be considered in reef fish management. In this study, proportion of coral reef and distance to nearest patch or linear reef have the strongest association to biomass within or near the boundary of the BUIS. This once again highlights the importance of considering habitat associations and quality in reef fisheries management.

Conclusion

Although simple metrics of abundance, biomass and size classes of biomass did not reveal a detectable spillover effect outside the BUIS original boundary, the results of this study reenforced the importance of habitat associations in the pattern of reef fish distribution throughout the study area. Rugosity and proportion of coral reef within 250m were significant variables for five and four species respectively. So while I did not find evidence of the spillover effect, protection of coral reef habitat that provides structurally complex habtat for reef fish is vital to the persistence of reef fish assemblages. Mutiple scales of analysis at local, patch and landscape levels must be performed to understand reef fish distribution and how protection status and habitat associations affect patterns of fish abundance. Local spatial regression methods such as GWR enhance model performance by accounting for the non-stationarity of processes that determine reef fish distribution patterns and could be useful in MPA management. Overall, this study points to the importance of spatial methods in examining MPA effectiveness and in managing our marine resources.

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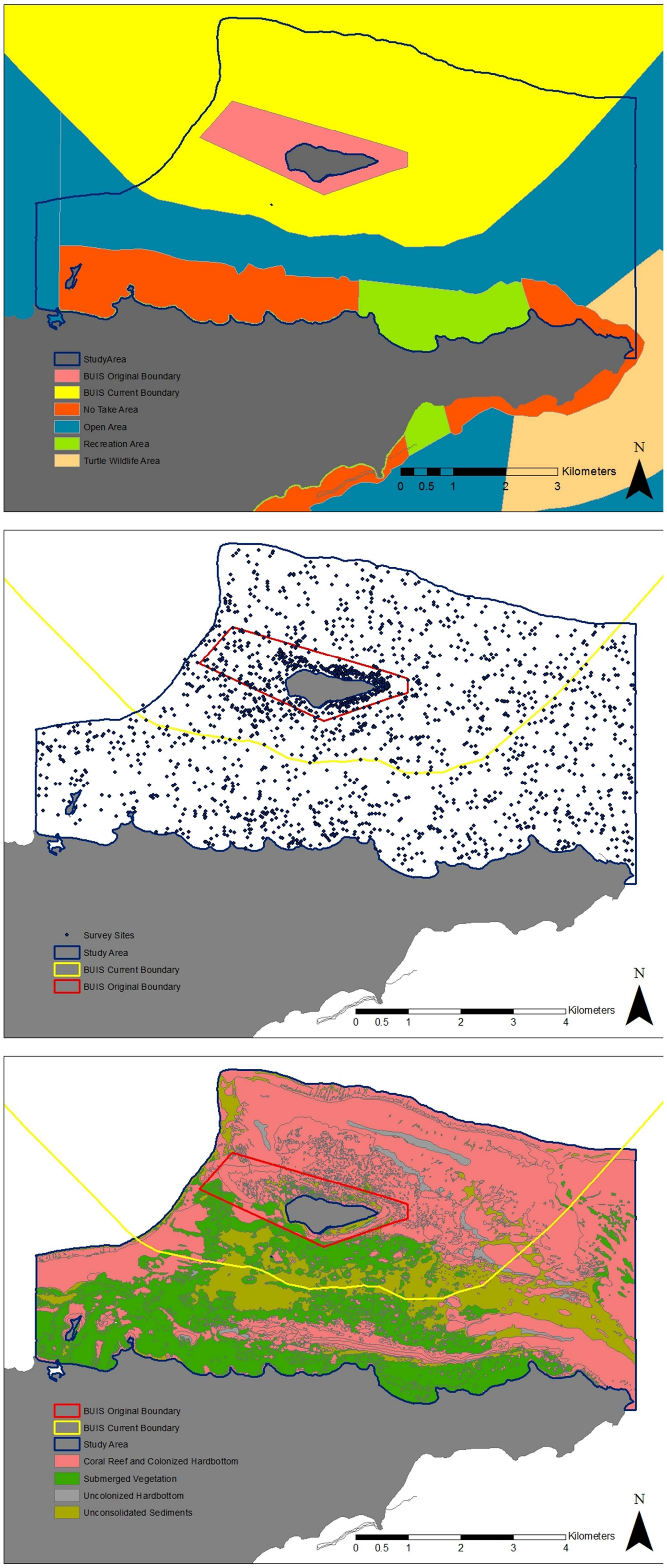


Figure 1. Maps of study site management zones, sample location and benthic habitat.

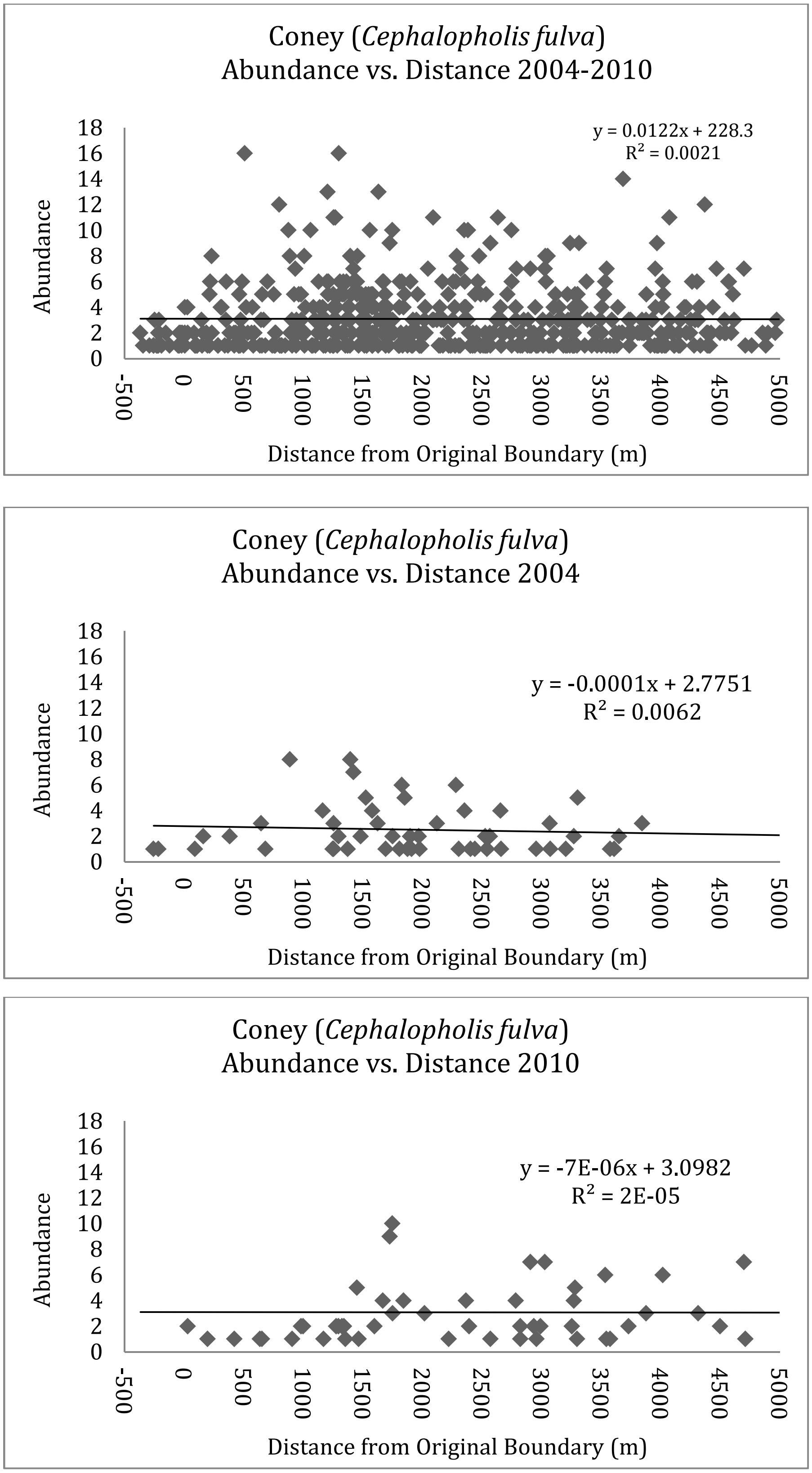
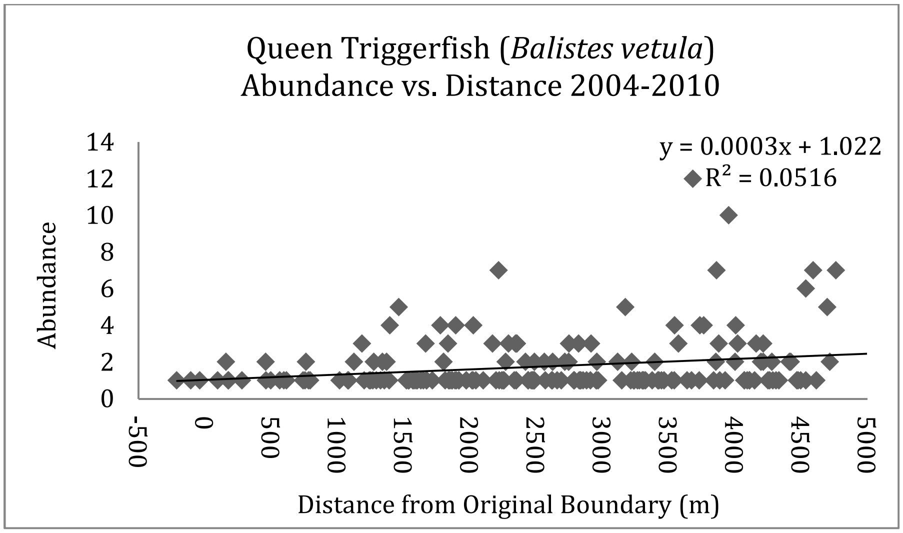
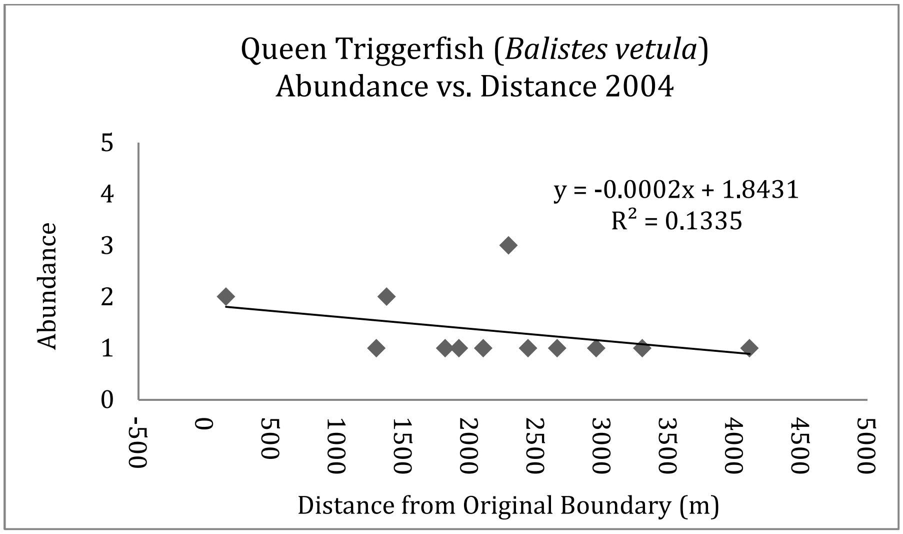


Figure 2. Abundance of coney with distance from the original BUIS boundary.





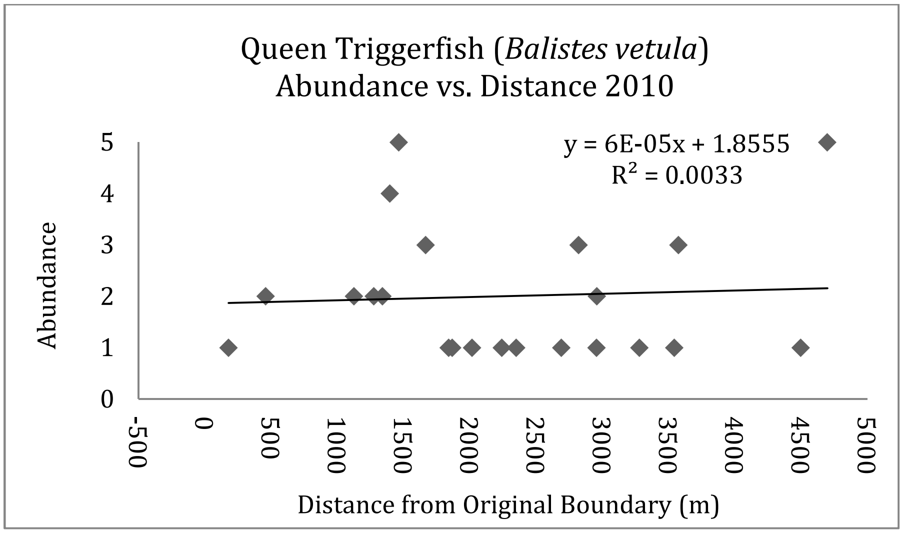


Figure 3. Abundance of queen triggerfish with distance to the original BUIS boundary

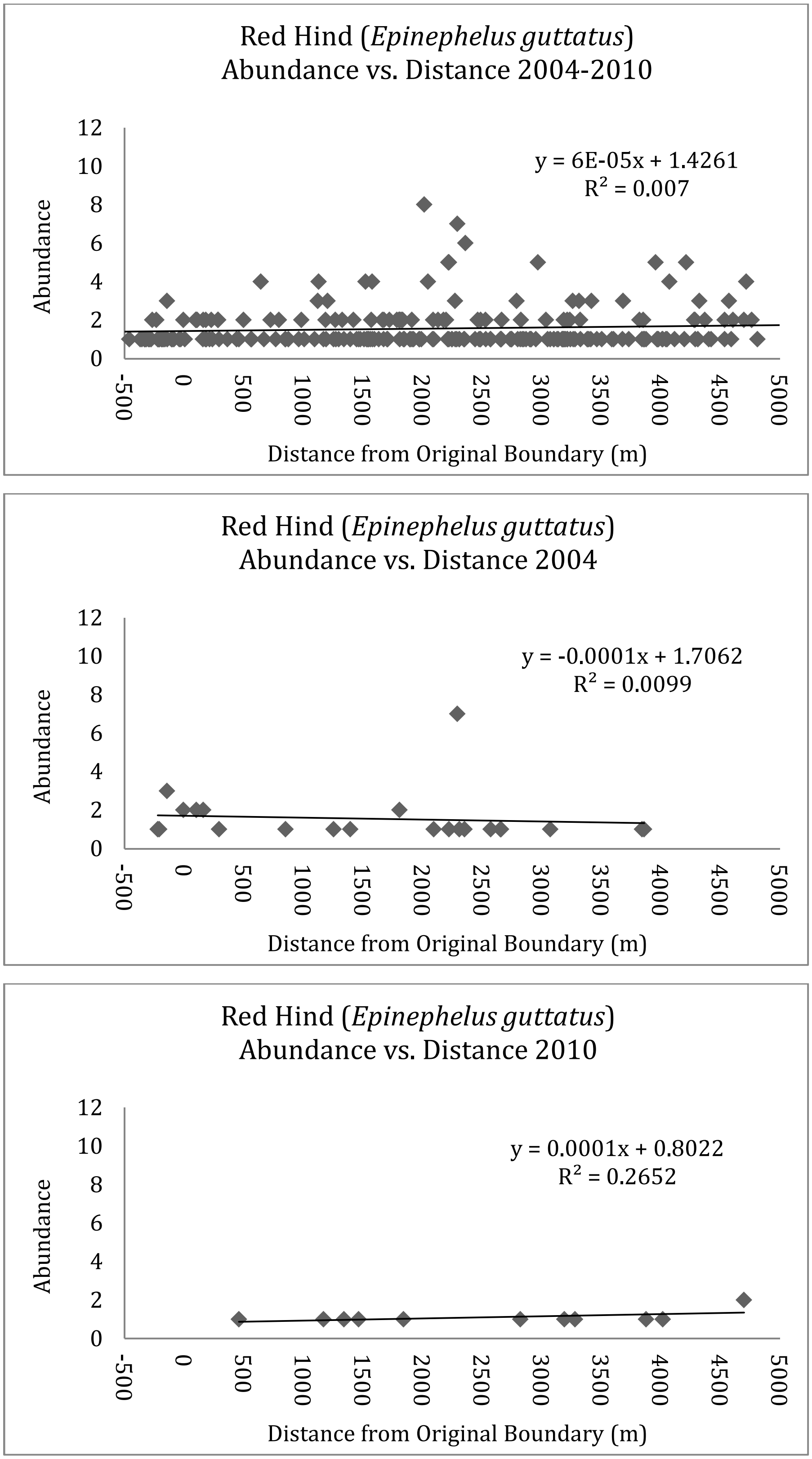


Figure 4. Abundance of red hind with distance to the original BUIS boundary.

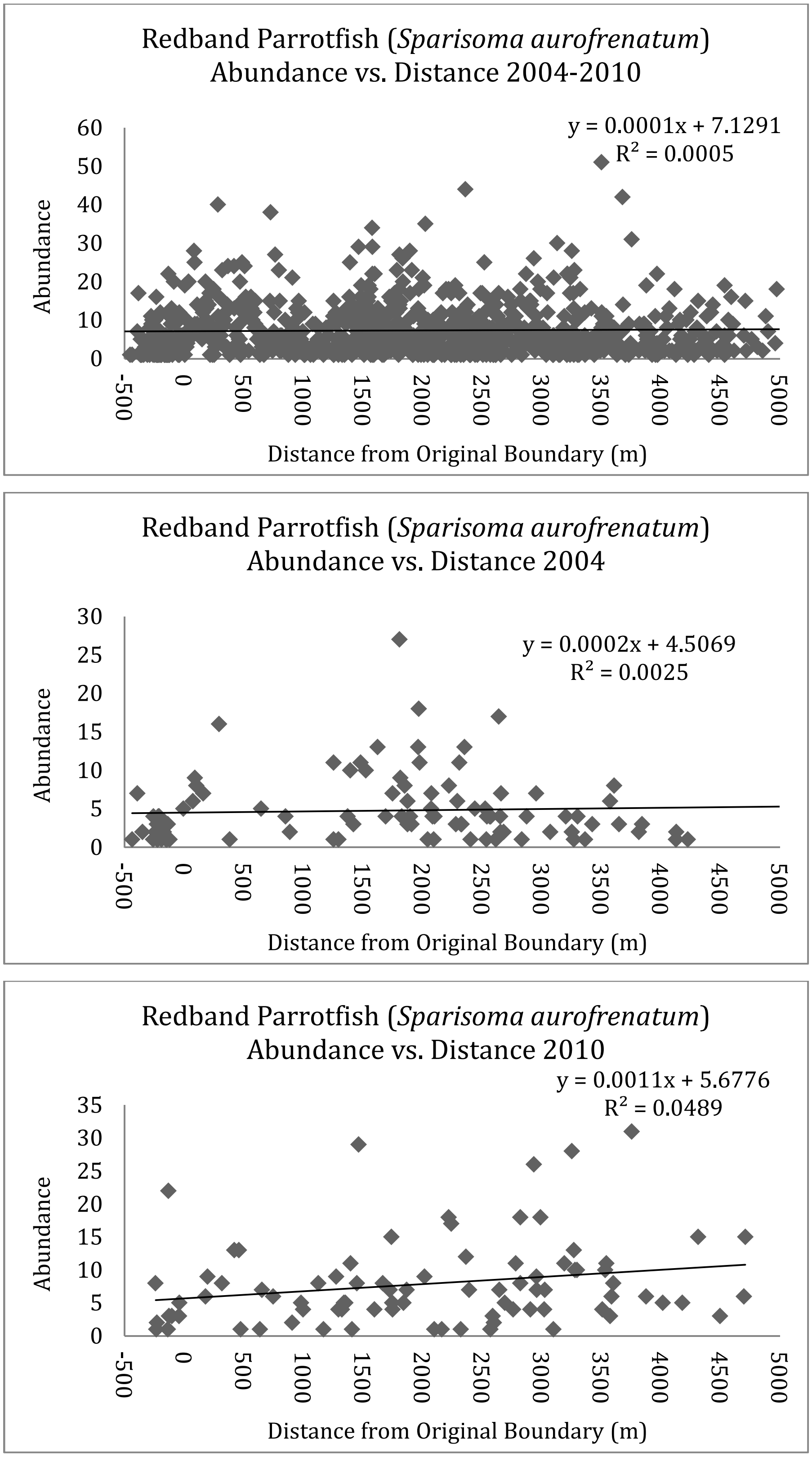
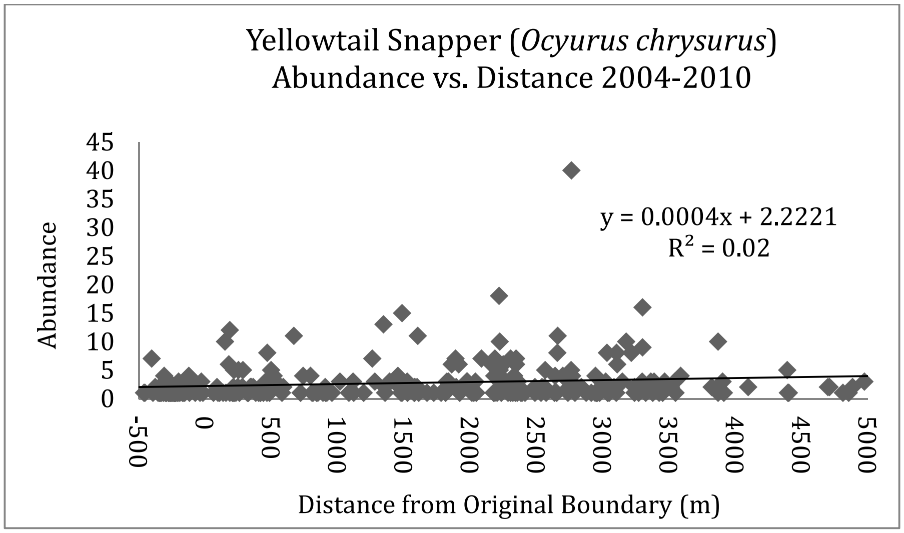
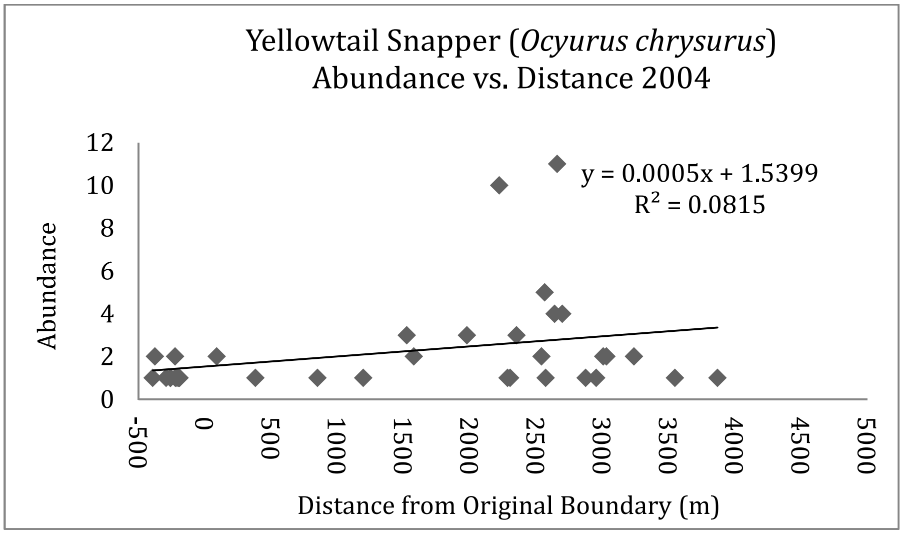


Figure 5. Abundance of redband parrotfish with distance to the original BUIS boundary.





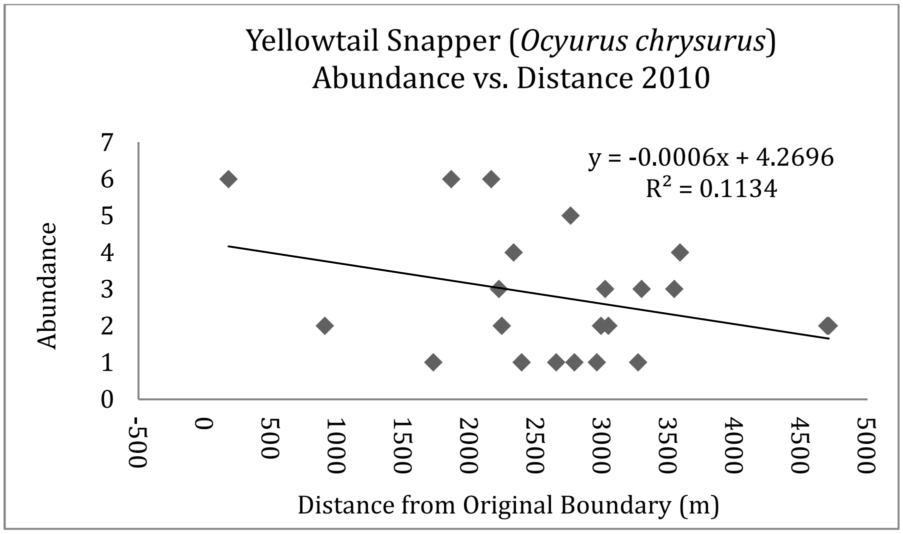


Figure 6. Abundance of yellowtail snapper with distance from the original BUIS boundary.

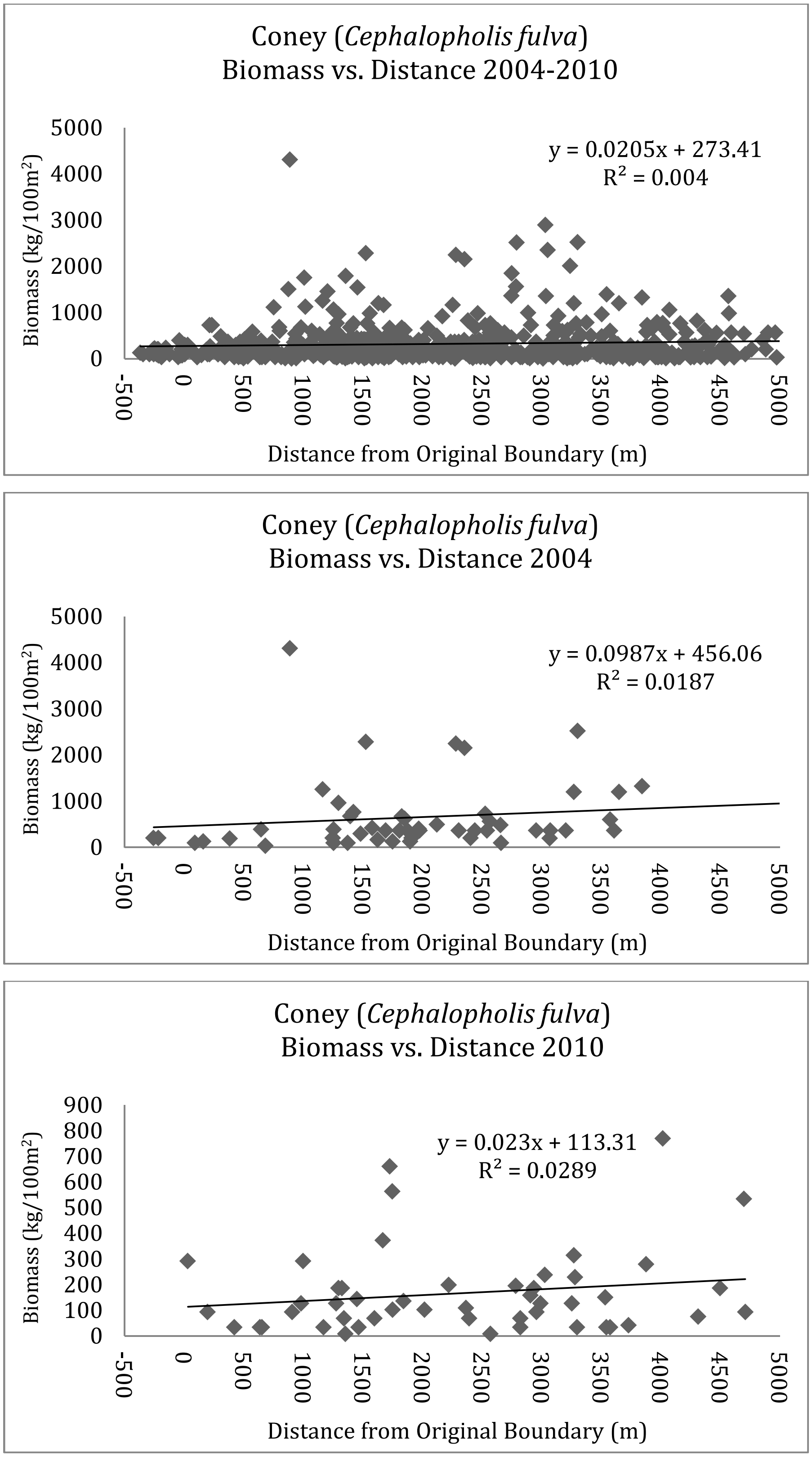
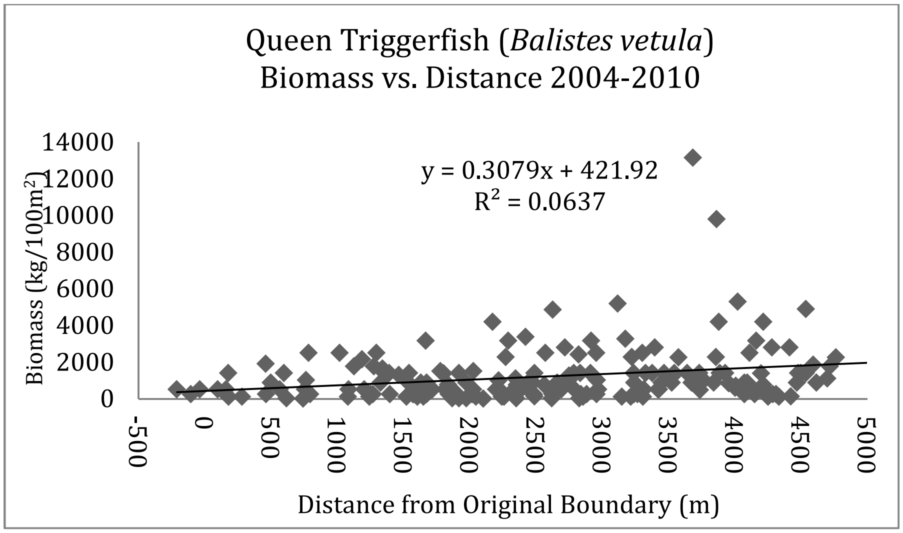
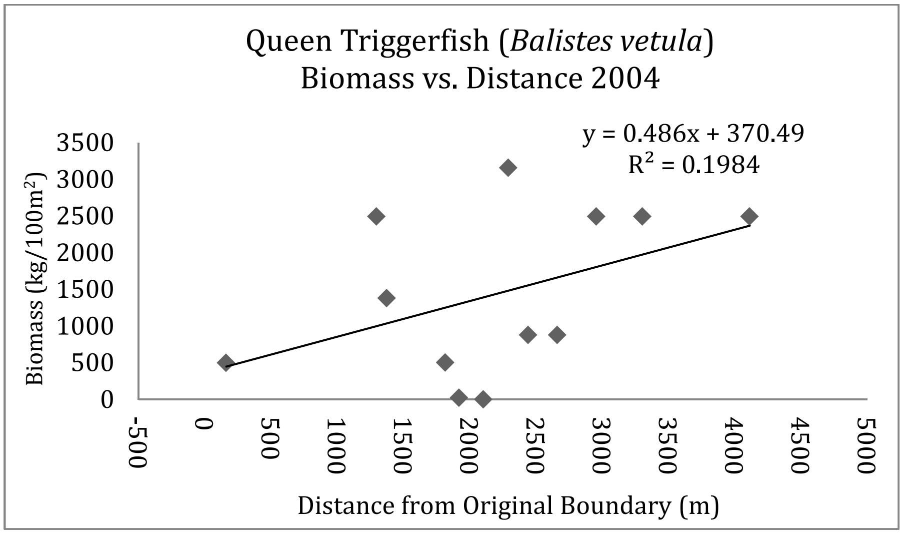


Figure 7. Biomass of coney with distance to the original BUIS boundary.





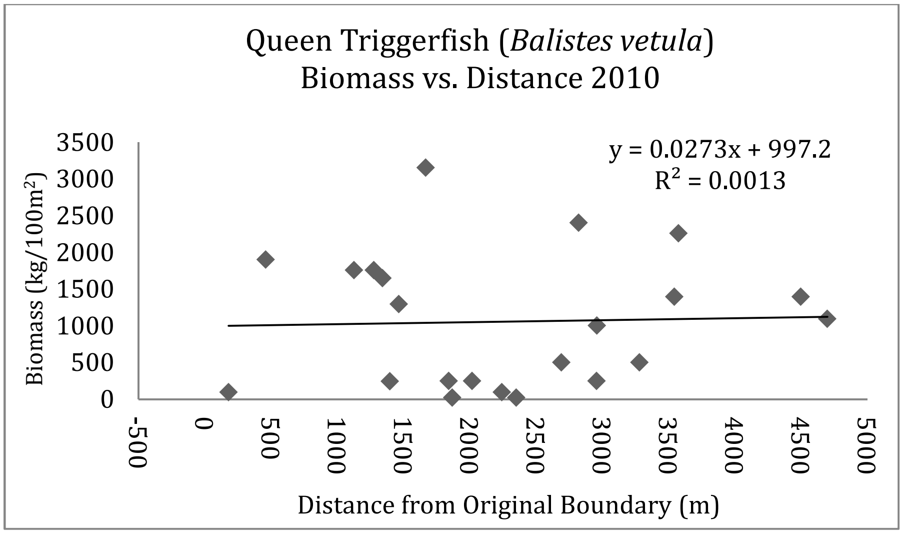
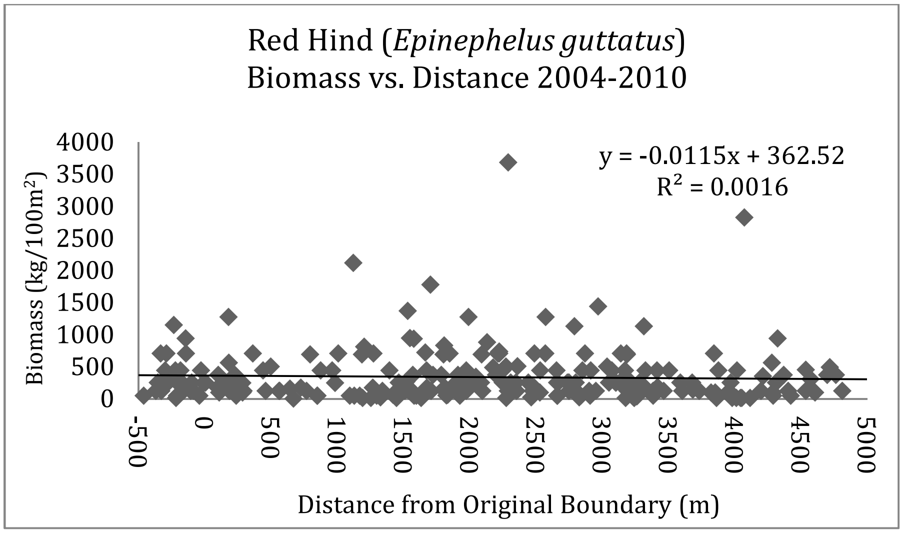
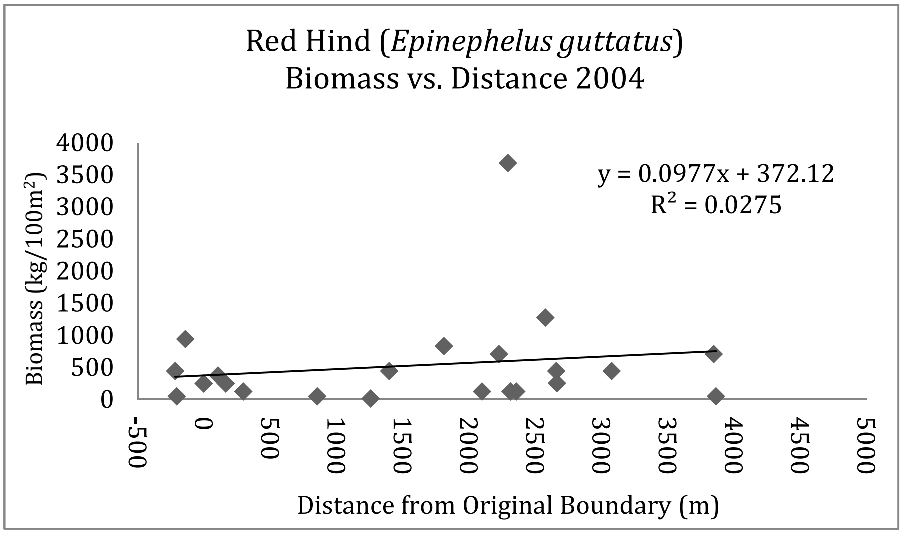


Figure 8. Biomass of queen triggerfish with distance to the original BUIS boundary.





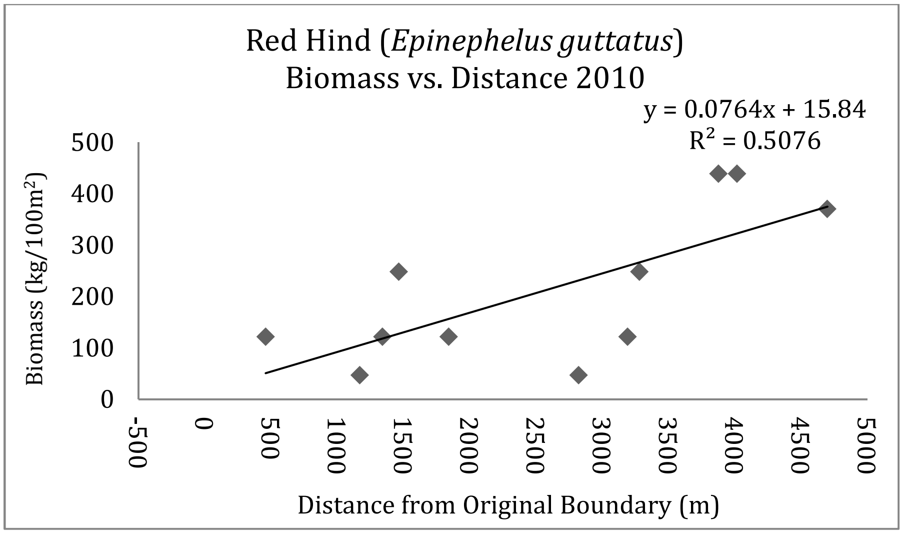
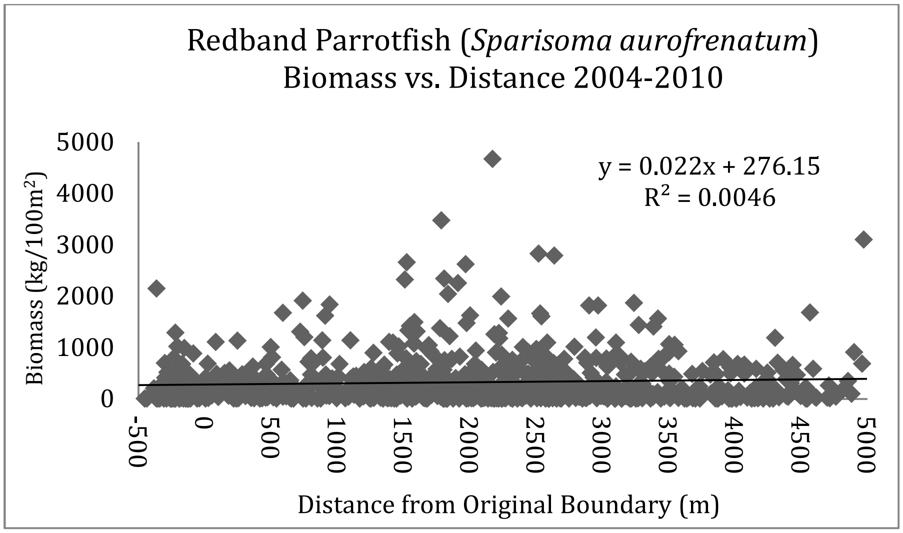
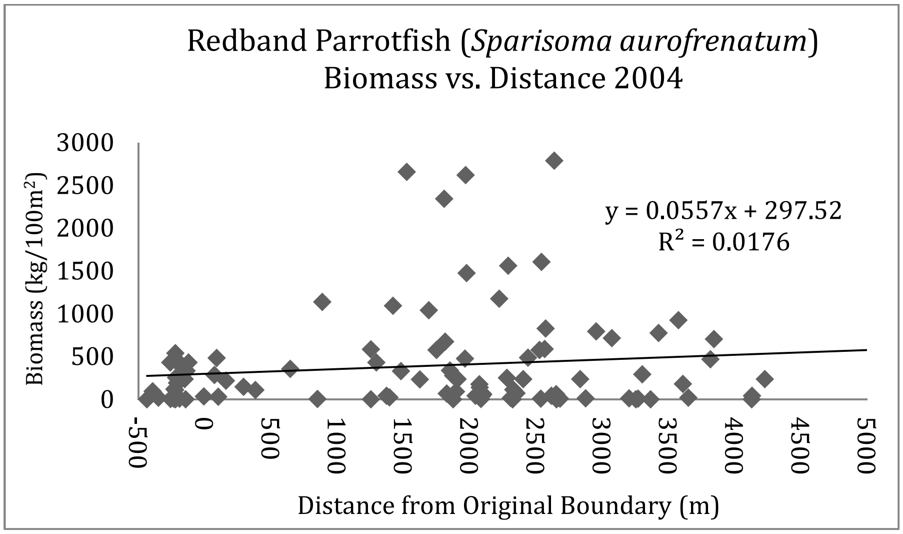


Figure 9. Biomass of red hind with distance from the original BUIS boundary.





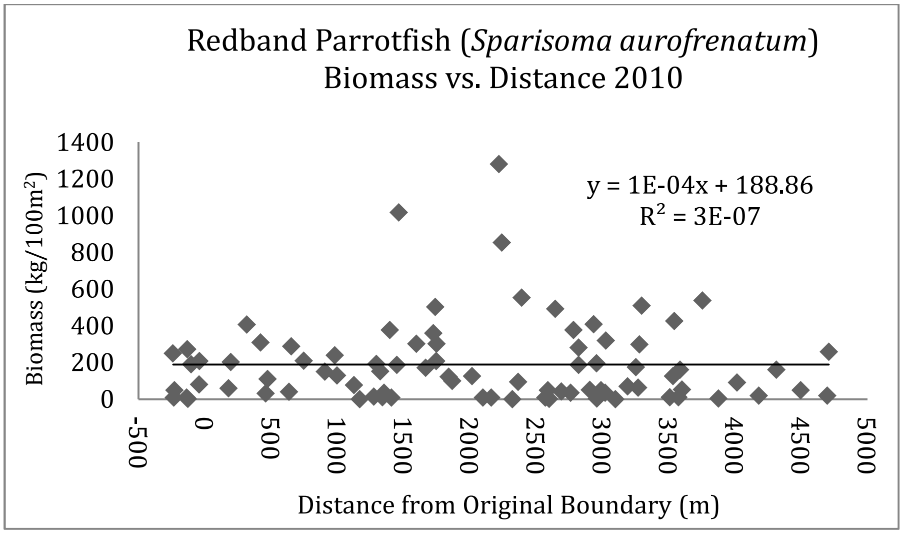
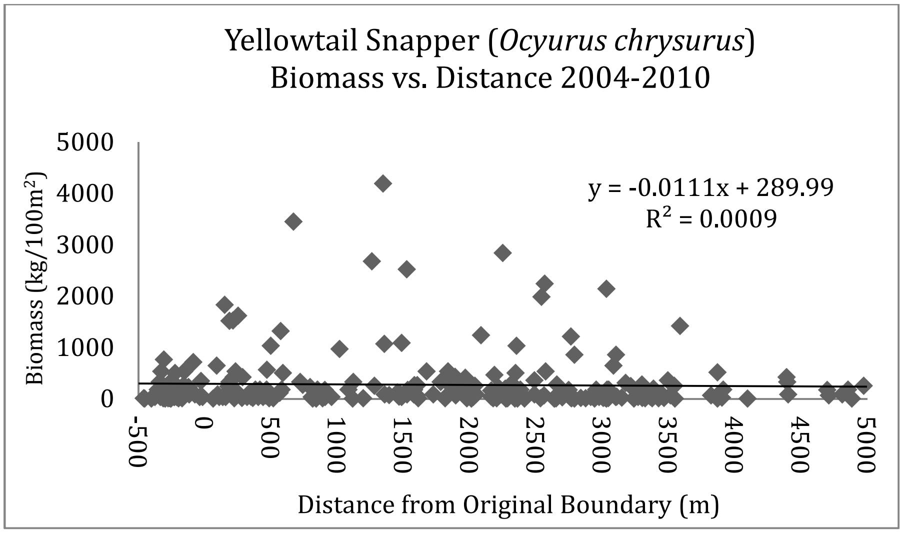
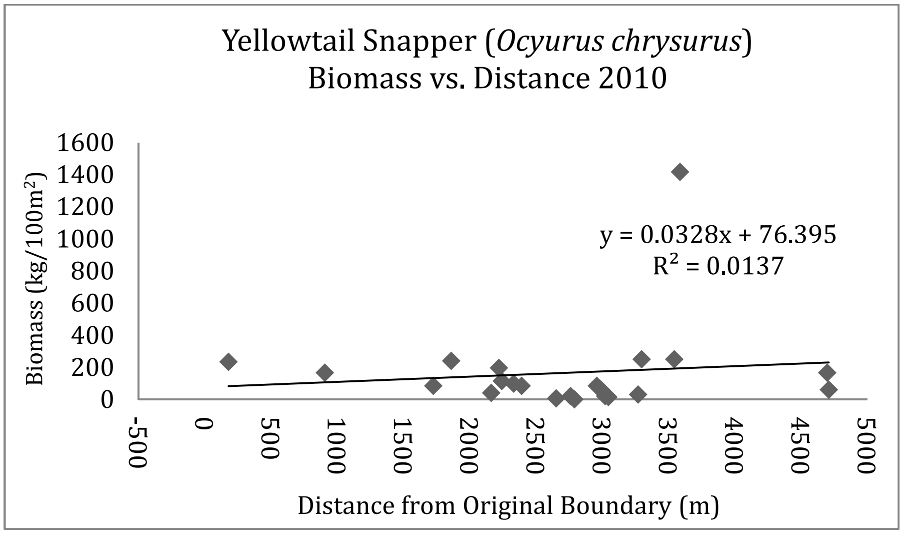


Figure 10. Biomass of redband parrotfish with distance to the original BUIS boundary.





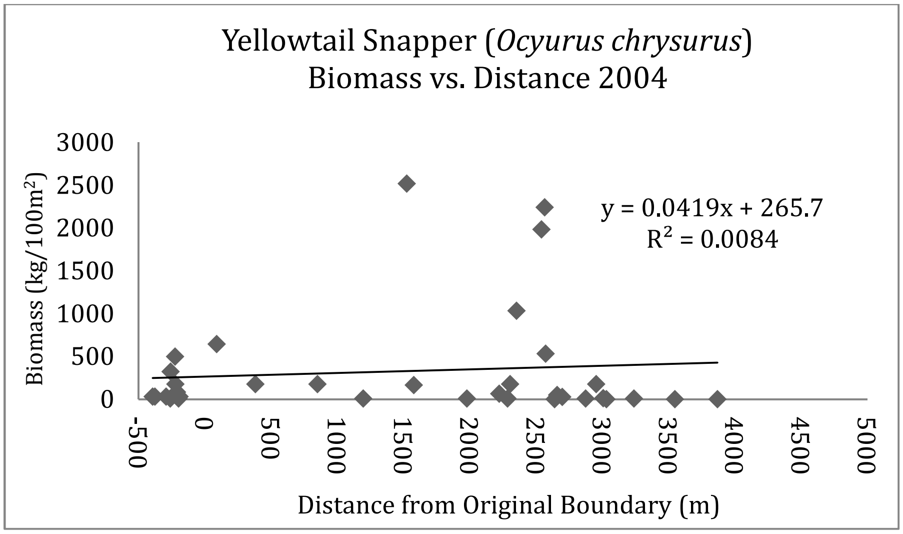
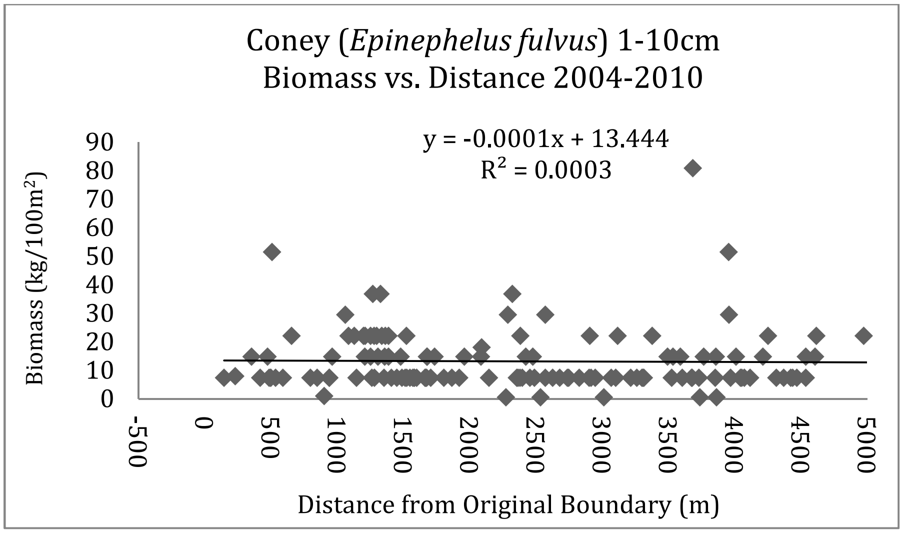
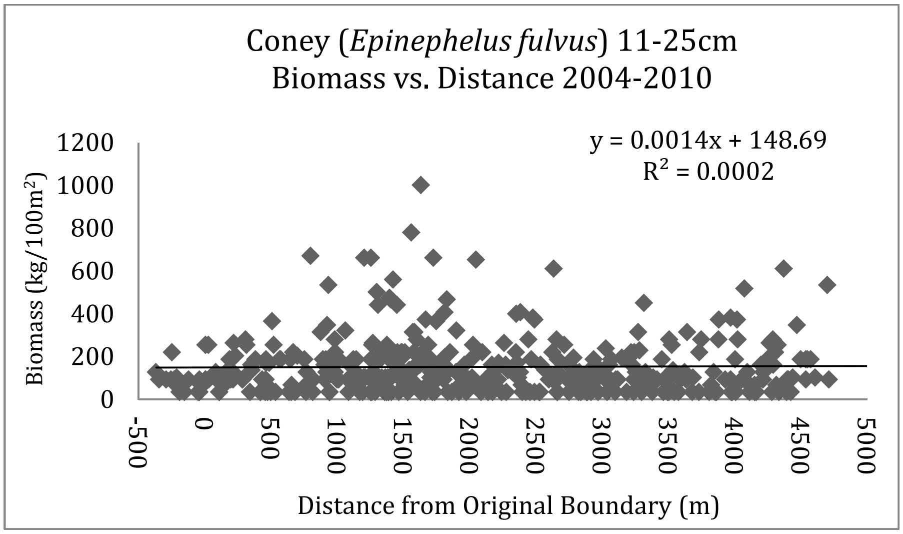


Figure 11. Biomass of yellowtail snapper with distance to the original BUIS boundary.





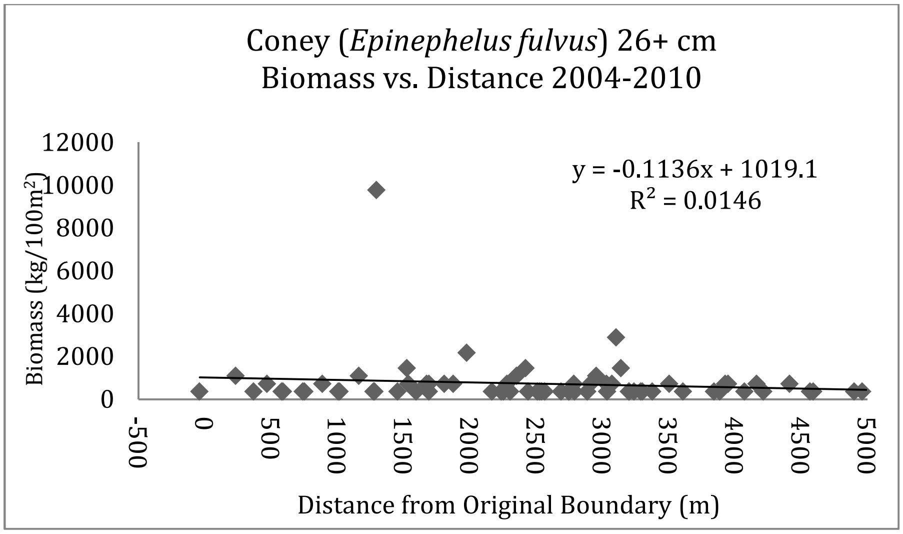
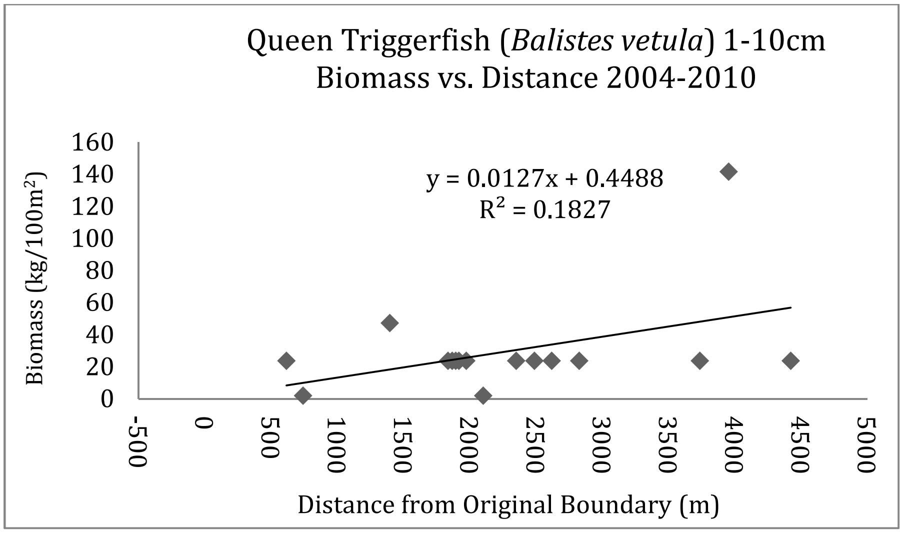
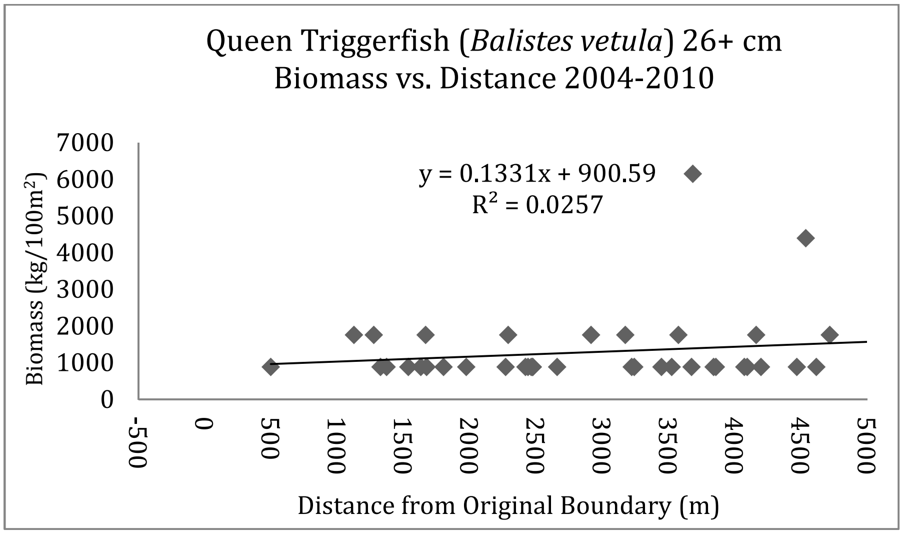


Figure 12. Biomass of coney by size class with distance from the original BUIS boundary.





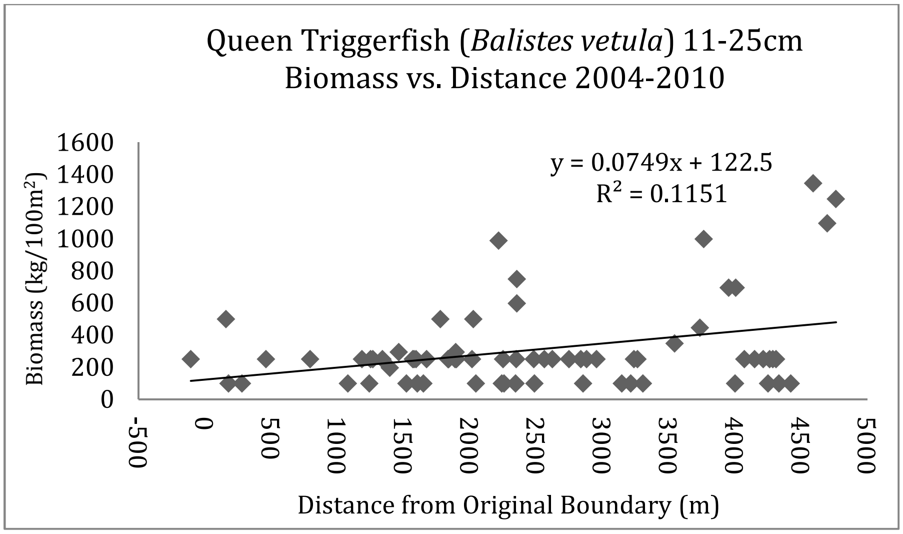


Figure 13. Biomass of queen triggerfish by size class with distance from the original BUIS boundary.

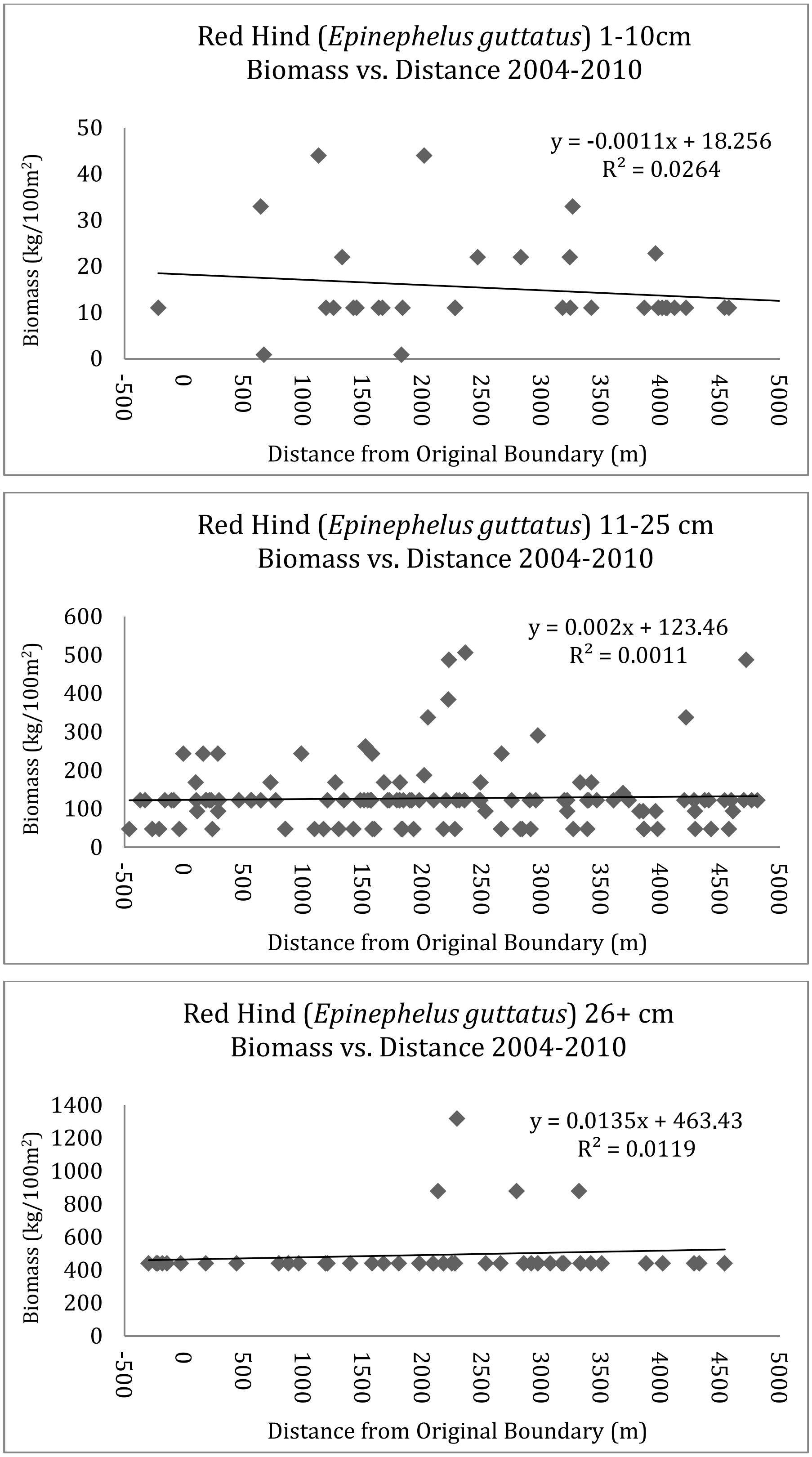
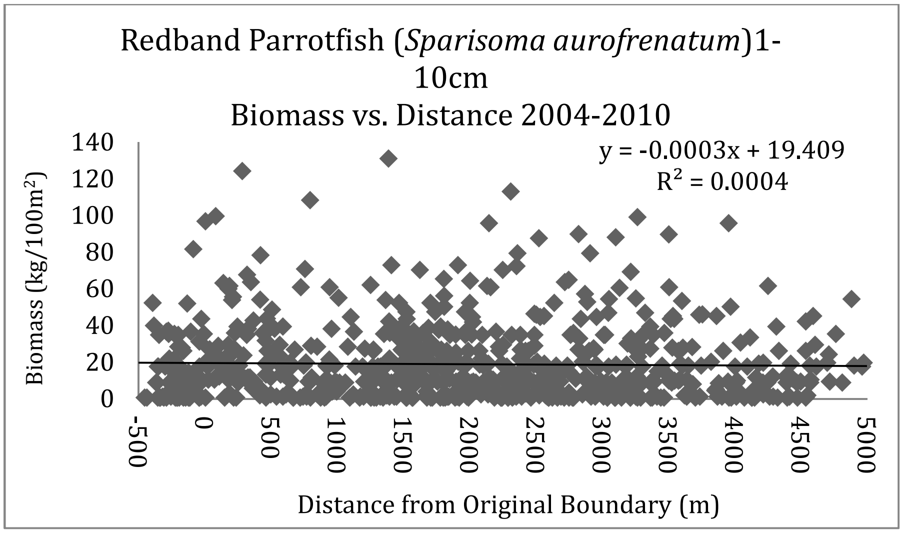
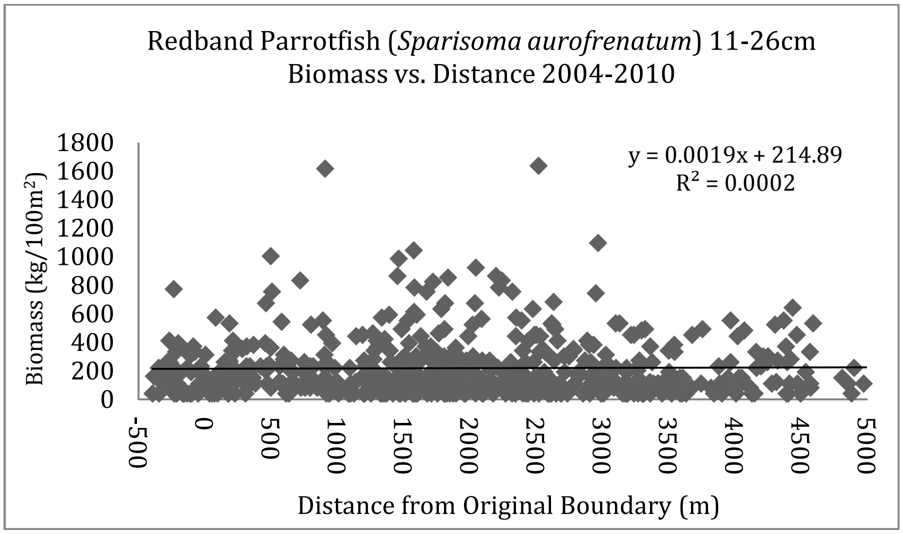


Figure 14. Biomass of red hind by size class with distance from the original BUIS boundary.





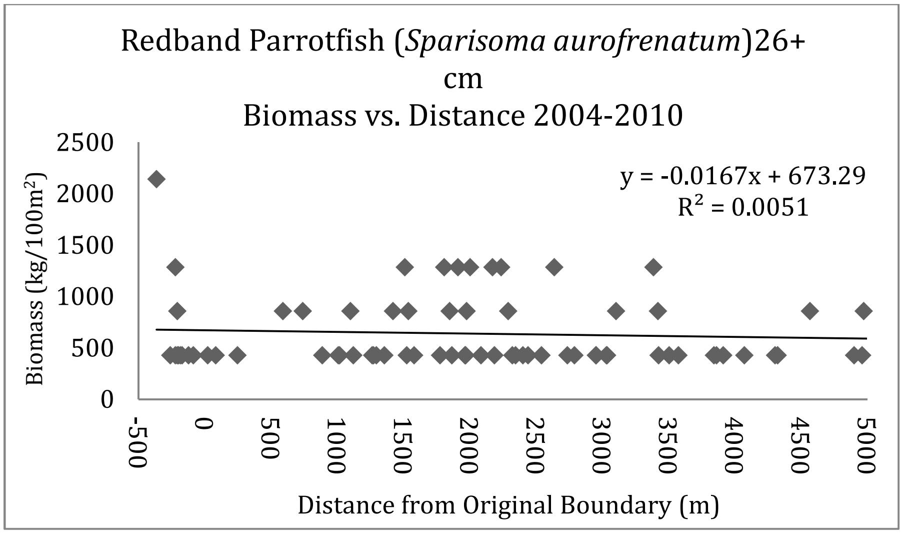


Figure 15. Biomass of redband parrotfish by size class with distance from the original BUIS boundary.

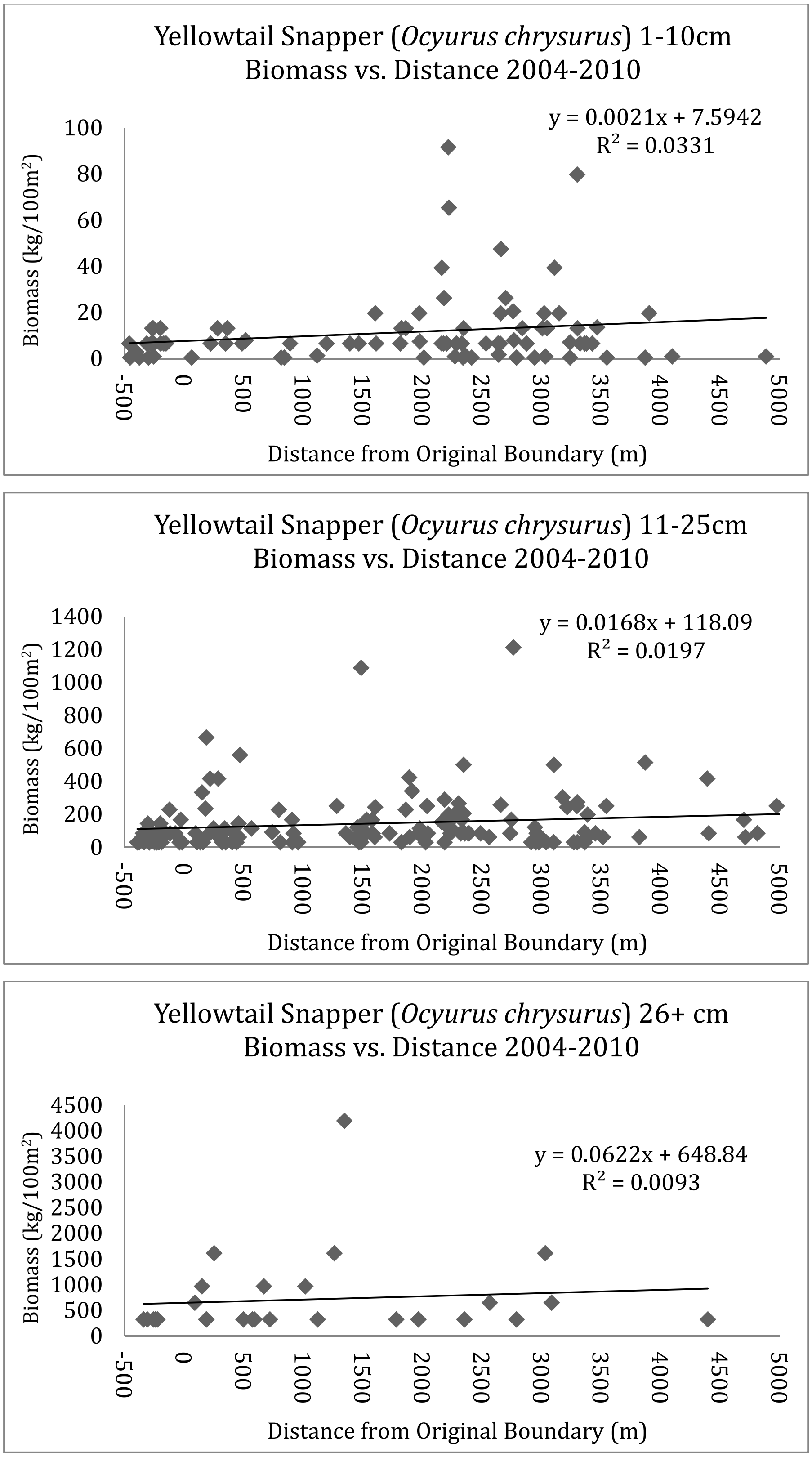
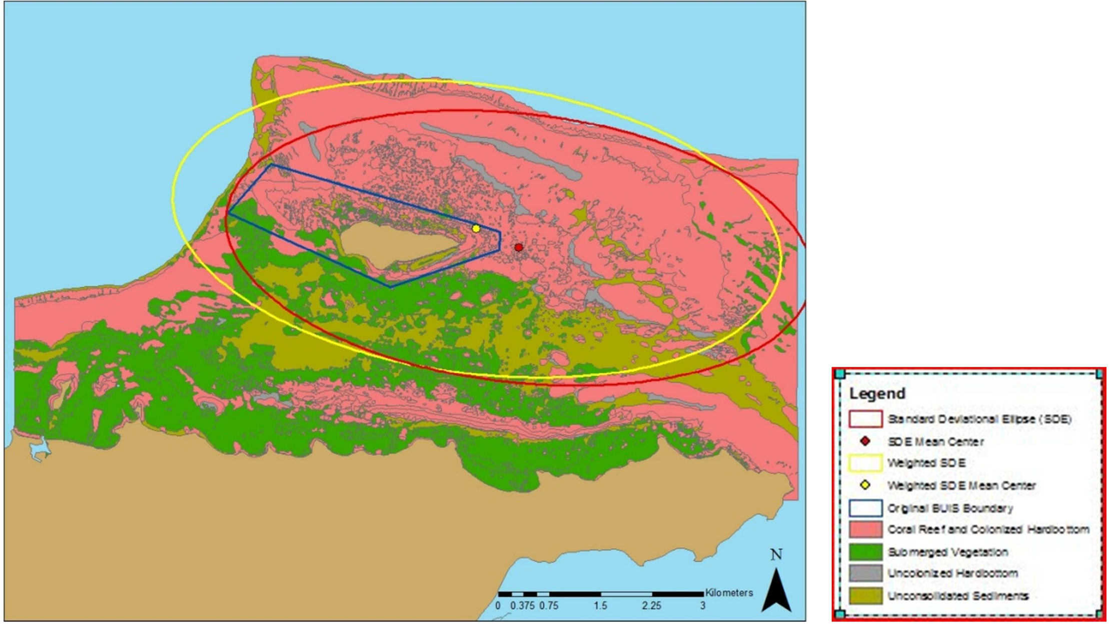
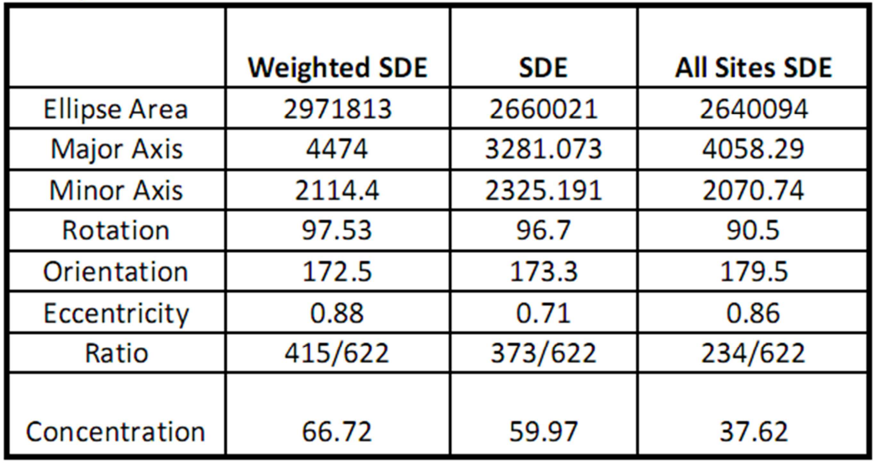


Figure 16. Biomass of yellowtail snapper by size class with distance from the original BUIS boundary.

Coney Weighted vs Unweighted SDE

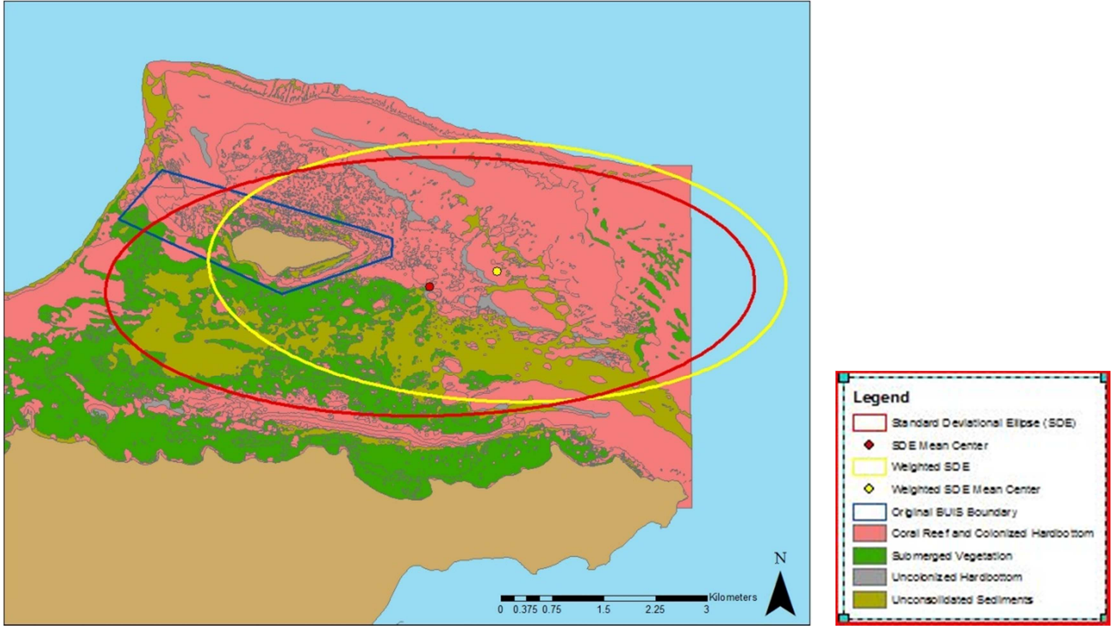


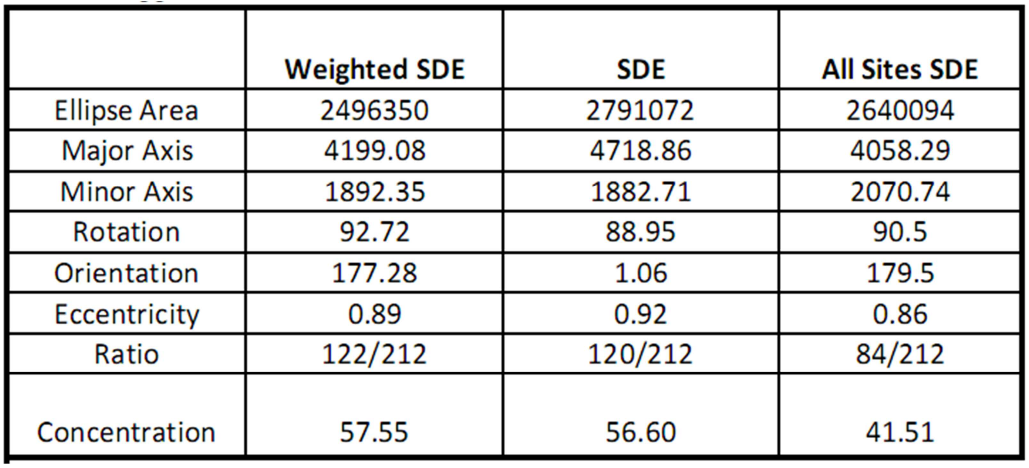


	Weighted SDE	SDE	All Sites SDE
Ellipse Area	2971813	2660021	2640094
Major Axis	4474	3281.073	4058.29
Minor Axis	2114.4	2325.191	2070.74
Rotation	97.53	96.7	90.5
Orientation	172.5	173.3	179.5
Eccentricity	0.88	0.71	0.86
Ratio	415/622	373/622	234/622
Concentration	66.72	59.97	37.62

Figure 17. Standard deviational ellipse of coney.

Queen Triggerfish Weighted vs Unweighted SDE

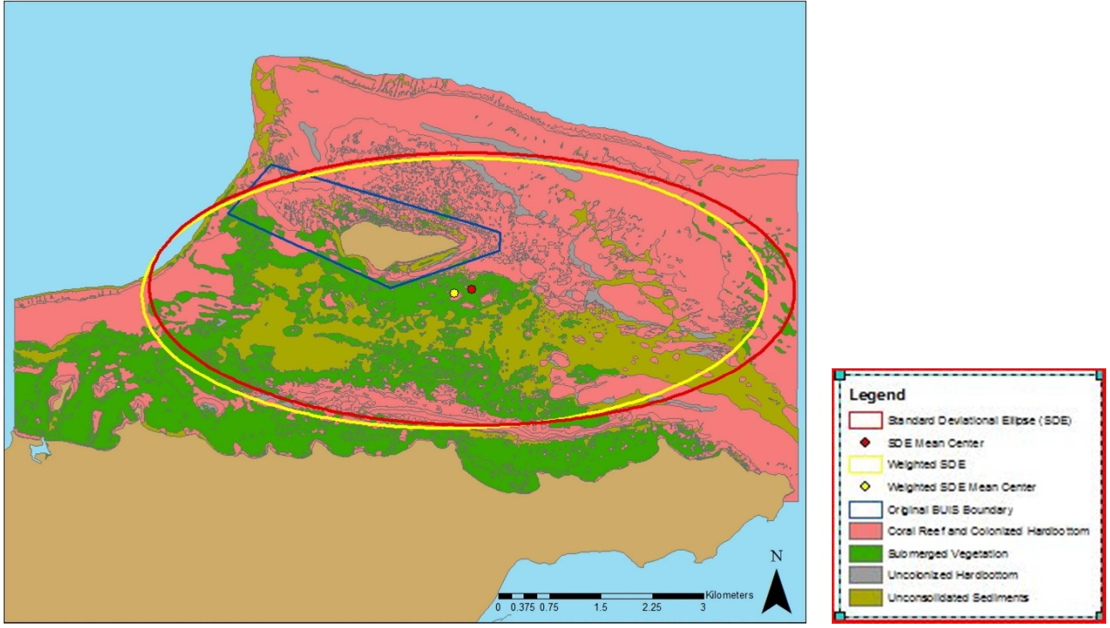


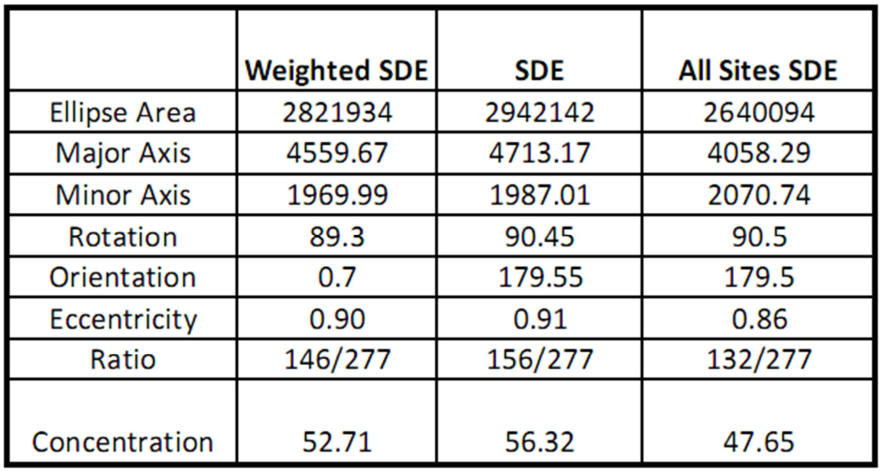


	Weighted SDE	SDE	All Sites SDE
Ellipse Area	2496350	2791072	2640094
Major Axis	4199.08	4718.86	4058.29
Minor Axis	1892.35	1882.71	2070.74
Rotation	92.72	88.95	90.5
Orientation	177.28	1.06	179.5
Eccentricity	0.89	0.92	0.86
Ratio	122/212	120/212	84/212
Concentration	57.55	56.60	41.51

Figure 18. Standard deviational ellipse of queen triggerfish.

Red Hind Weighted vs Unweighted SDE

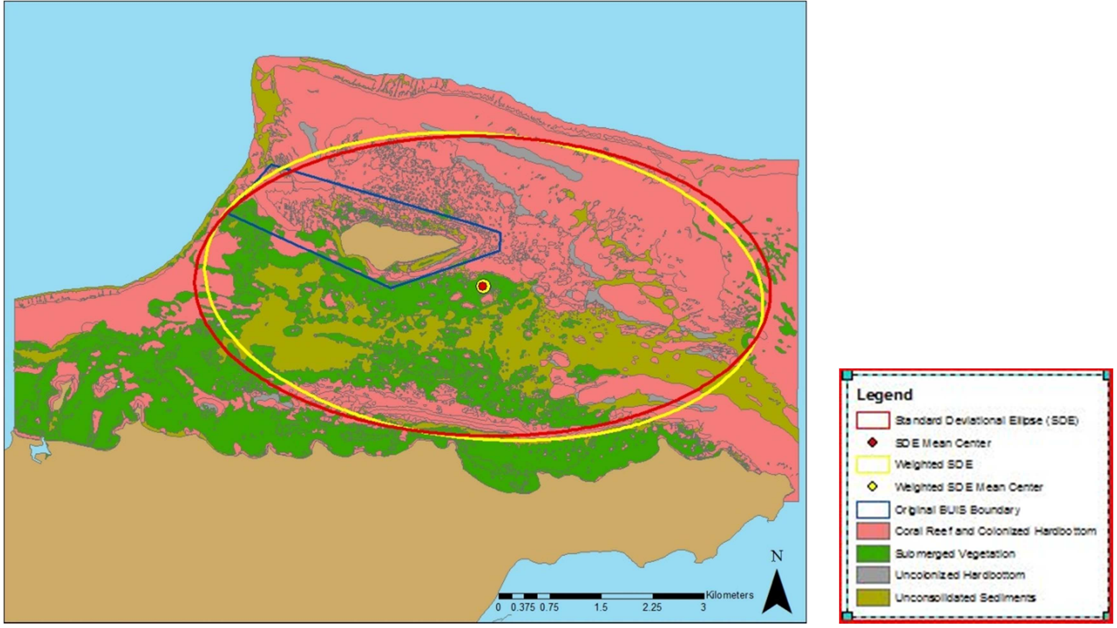


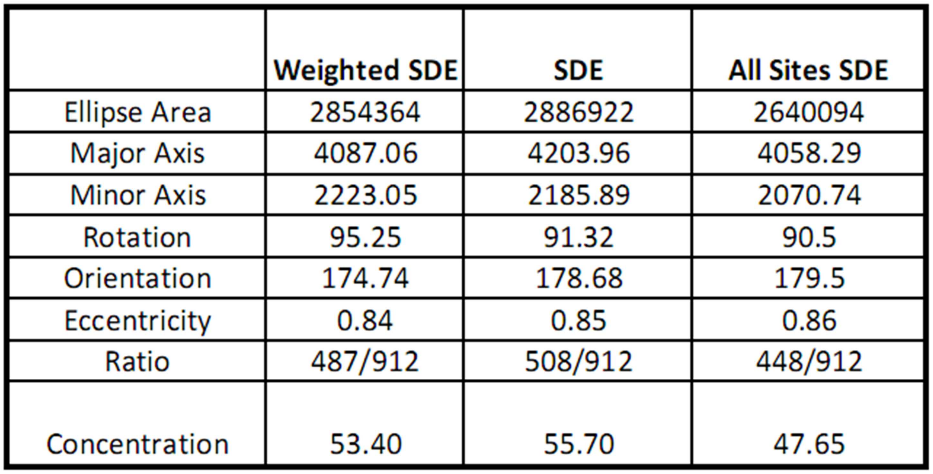


	Weighted SDE	SDE	All Sites SDE
Ellipse Area	2821934	2942142	2640094
Major Axis	4559.67	4713.17	4058.29
Minor Axis	1969.99	1987.01	2070.74
Rotation	89.3	90.45	90.5
Orientation	0.7	179.55	179.5
Eccentricity	0.90	0.91	0.86
Ratio	146/277	156/277	132/277
Concentration	52.71	56.32	47.65

Figure 19. Standard deviational ellipse of red hind.

Redband Parrotfish Weighted vs Unweighted SDE

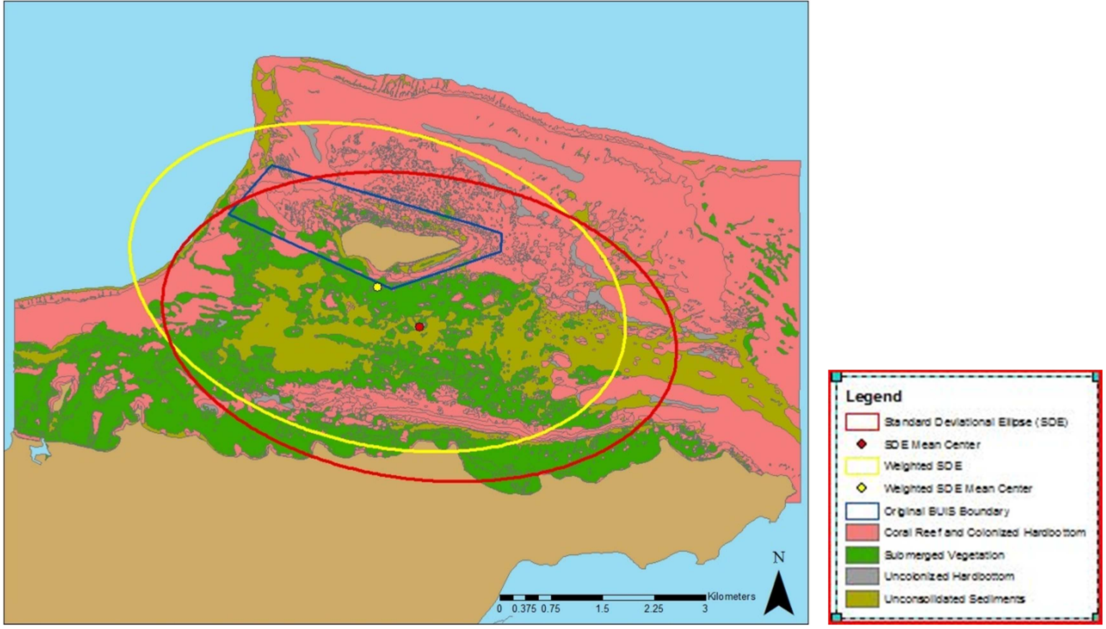


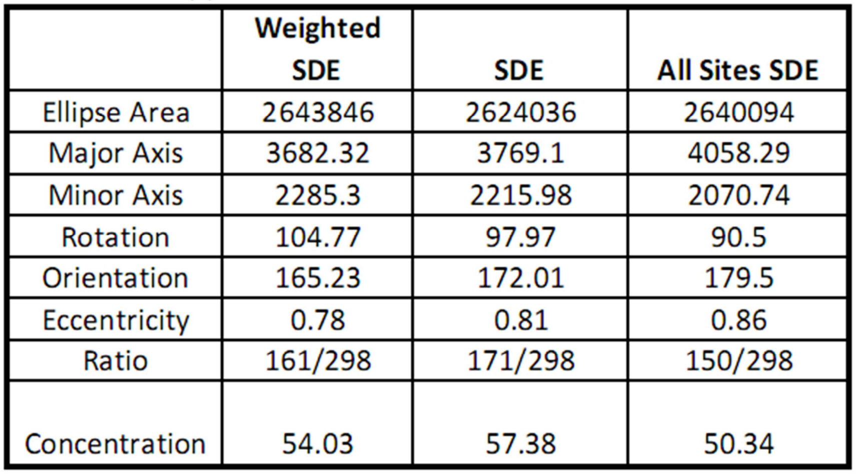


	Weighted SDE	SDE	All Sites SDE
Ellipse Area	2854364	2886922	2640094
Major Axis	4087.06	4203.96	4058.29
Minor Axis	2223.05	2185.89	2070.74
Rotation	95.25	91.32	90.5
Orientation	174.74	178.68	179.5
Eccentricity	0.84	0.85	0.86
Ratio	487/912	508/912	448/912
Concentration	53.40	55.70	47.65

Figure 20. Standard deviational ellipse of redband parrotfish.

Yellowtail Snapper Weighted vs Unweighted SDE





	Weighted SDE	SDE	All Sites SDE
Ellipse Area	2643846	2624036	2640094
Major Axis	3682.32	3769.1	4058.29
Minor Axis	2285.3	2215.98	2070.74
Rotation	104.77	97.97	90.5
Orientation	165.23	172.01	179.5
Eccentricity	0.78	0.81	0.86
Ratio	161/298	171/298	150/298
Concentration	54.03	57.38	50.34

Figure 21. Standard deviational ellipse of yellowtail snapper.

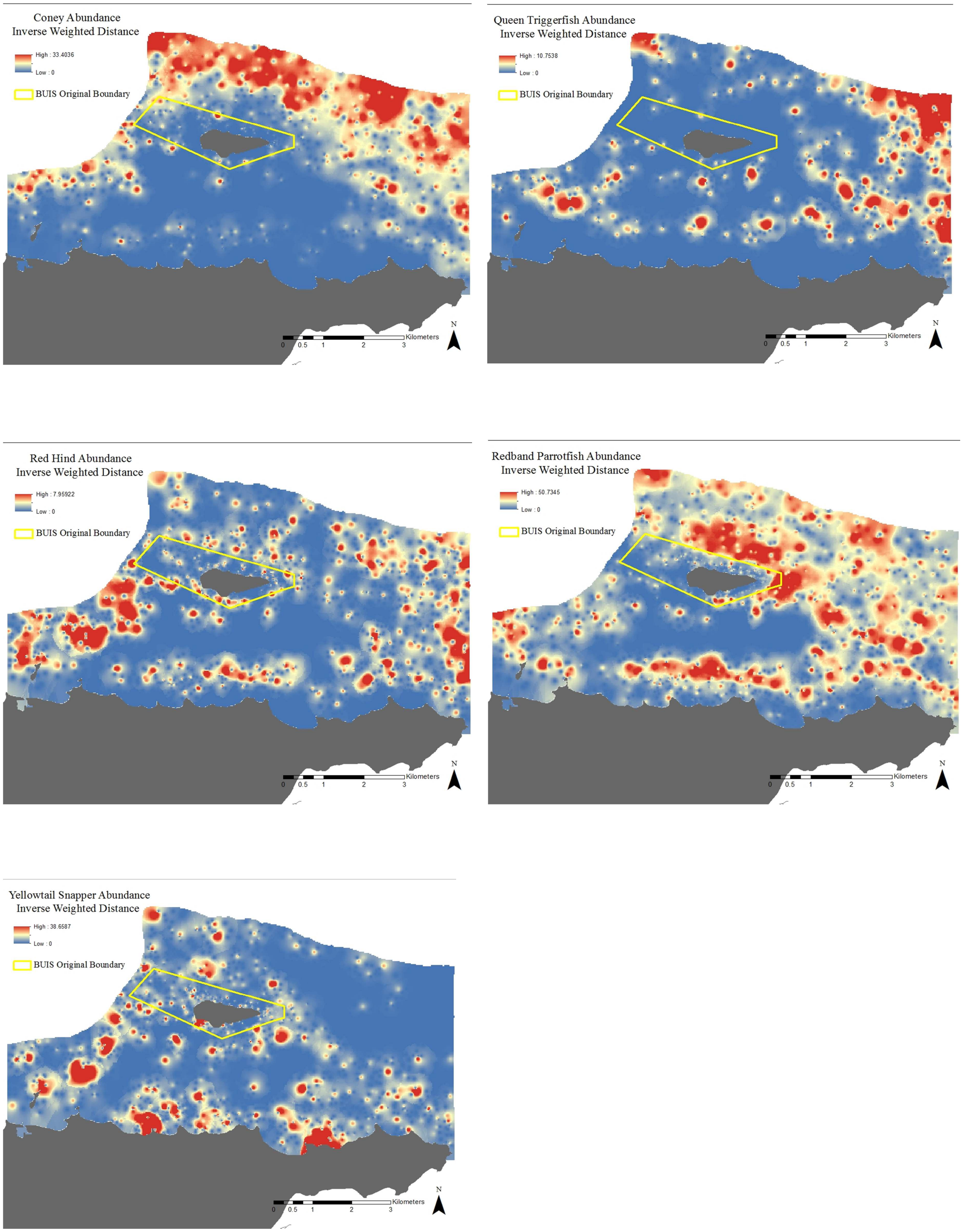


Figure 22. Inverse weighted distance interpolated surfaces of abundance.

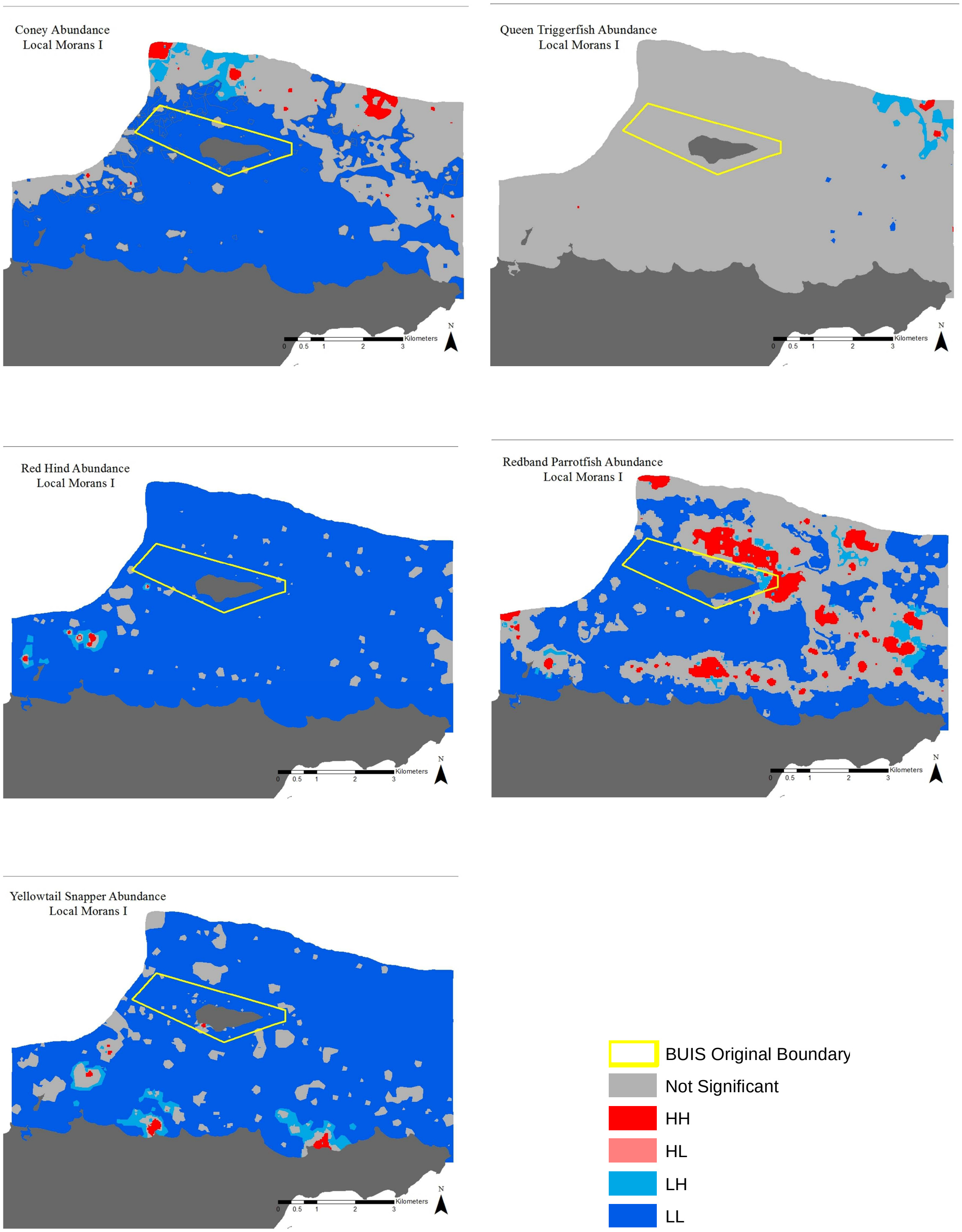


Figure 23. Local Morans I analysis of abundance.

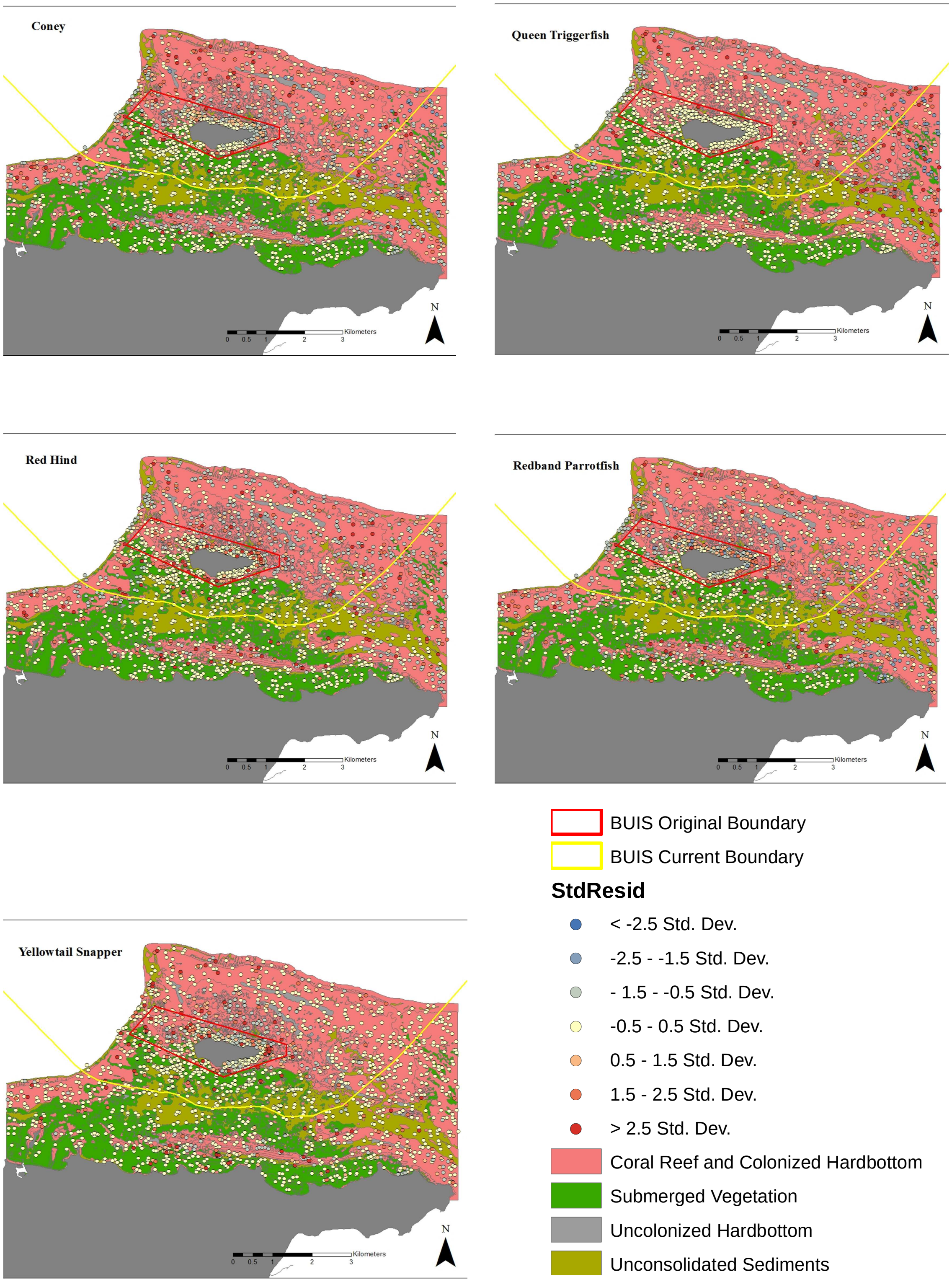


Figure 24. Residuals of the OLS analysis.

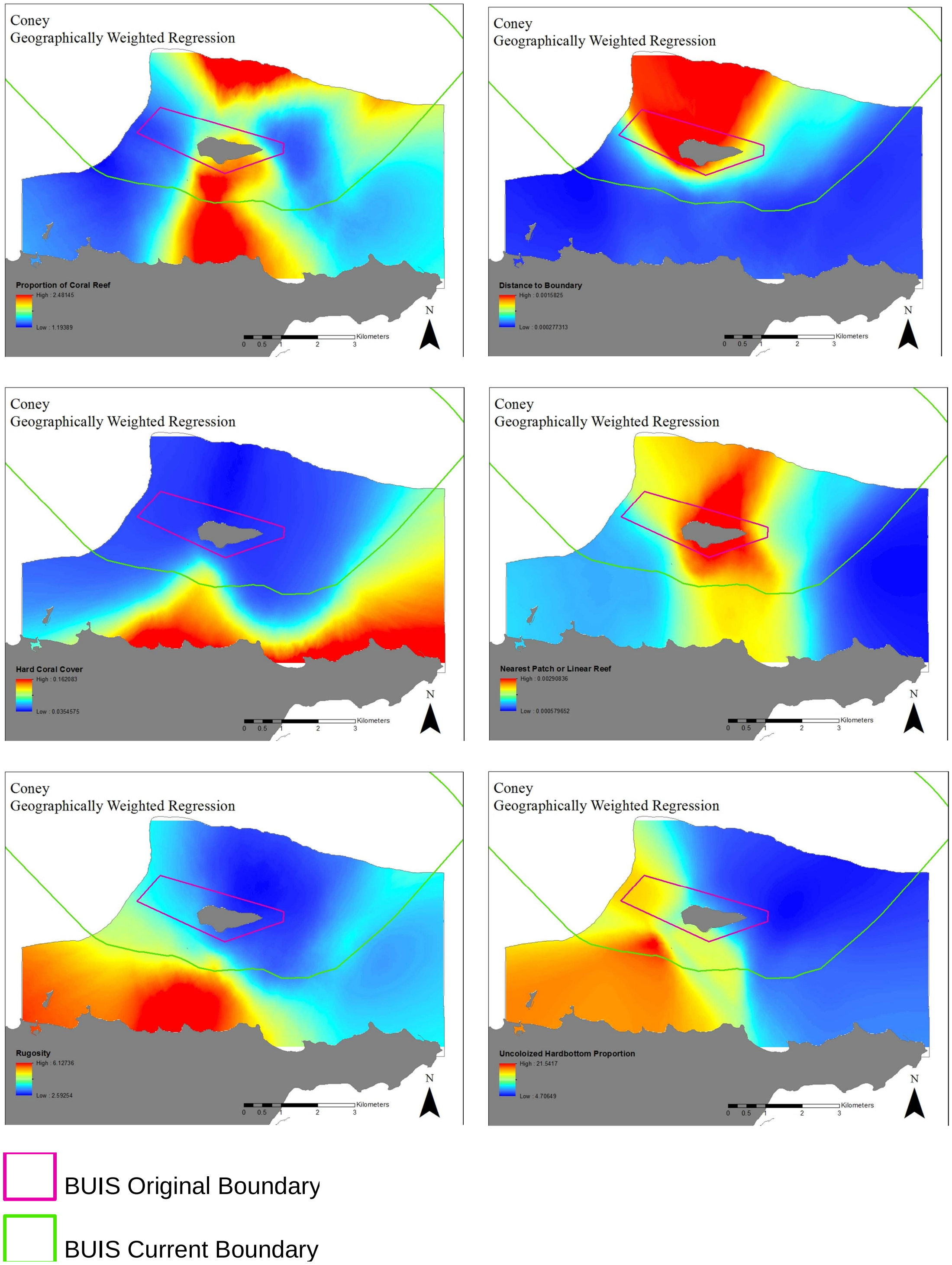


Figure 25. Geographically weighted regression coefficient surfaces for coney.

Table 1. Distribution of sample locations inside and outside the original BUIS boundary.

		All	**Fall**	**Spring**
2001	Total	186	70	116
	Inside	105		
	Outside	81		
2002	Total	152	70	82
	Inside	68		
	Outside	84		
2003	Total	246	129	117
	Inside	72		
	Outside	174		
2004	Total	194	130	64
	Inside	44		
	Outside	150		
2005	Total	247	121	126
	Inside	33		
	Outside	214		
2006	Total	244	124	120
	Inside	31		
	Outside	213		
2007	Total	122	122	—
	Inside	19		
	Outside	103		
2008	Total	242	120	122
	Inside	33		
	Outside	209		
2009	Total	222	122	100
	Inside	27		
	Outside	195		
2010	Total	122	122	—
	Inside	14		
	Outside	108		
All Years	Total	1977	1130	847
	Inside	446		
	Outside	1531		

Table 2. Results from the OLS regression model. Shows explanatory variable coefficients.

	Local Variables		
	Rugosity	Hard Coral Cover	Max Depth
Coney	4.5389	0.0750	0.0261
Queen Triggerfish	5.7419		0.0695
Red Hind	4.1925		0.0385
Redband Parrotfish	25.6972	0.0789	0.0789
Yellowtail Snapper	5.3421		0.0211
All	*		*

	Landscape Variables						
	Nearest Patch or Linear Reef	Distance to Boundary	Coral Reef Proportion	Seagrass Proportion	Macroalgae Proportion	Uncolonized Pavement Proportion	Sand Proportion
Coney	0.0038	0.0005	10.0063			25.5747	
Queen Triggerfish	0.0048	0.0007	2.9753				
Red Hind			2.4886		8.9558		
Redband Parrotfish	-0.0019	0.0010	8.6770				
Yellowtail Snapper	-0.0013					-11.8617	
All	*					*	

Table 3. Multivariate regression model fit. Compares the results of the OLS and GWR.

	OLS					GWR	
	R-squared	AIC	Koenker Statistic	Jarque-Bera Statistic	Auto-correlated	R-squared	AIC
Coney	0.2804	14033.52	*	*	Yes	0.3467	13859.7
Queen Triggerfish	0.1631	14895.04	*	*	Yes	0.1966	14836.1
Red Hind	0.0405	13424.15	*	*	Yes	0.0721	13380.3
Redband Parrotfish	0.2841	14402.6	*	*	Yes	0.3262	14306.4
Yellowtail Snapper	0.0191	13340.48		*	Yes	0.0507	13309.8
All	—	—	—	—	—	—	—