Assessment of Benthic Fauna Communities on Florida Keys' Shallow Banks as an Indicator of Prey Availability for Bonefish (*Albula vulpes*)

[photo courtesy of Mac Stone]

Final Project Report to the Bonefish and Tarpon Trust

May 2013

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EXECUTIVE SUMMARY

The decline of bonefish (*Albula vulpes*) throughout the Florida Keys, particularly in Florida Bay which historically was an epicenter of the Florida bonefishery, is a tremendous concern due to their status as an indicator species and the importance of the fishery for the Keys' economy. This study utilized a bottom-up trophic approach, examining the bonefish prey base as a possible cause of the population decline. Specifically, the goals of this 1-year study were to compare patterns of bonefish abundance using available data, and to examine spatial (regional) and temporal (decadal) variation in benthic fauna communities of the Florida Keys to determine the extent that prey abundance may influence bonefish abundance and distribution.

Trends in bonefish abundance were assessed using a 19-question questionnaire that targeted known, experienced Florida Bay fishers (conducted independent of this study, 2010-2012). Prey sampling was conducted three times in 2012 (March, July and October) at five study sites: Cross Bank, Buchanan Bank and 9-Mile Bank in the Upper Keys, Sands Cut in Biscayne Bay, and Sawyer Keys in the Lower Keys. Benthic and canopy-dwelling fish and invertebrates were collected using 1-m^2 throw traps, modeling sampling design and protocols after those of Powell et al. (1987) who described fish and decapod communities in Florida Bay in the 1980s (repeated by Matheson et al. (1999) in the 1990s). Seagrass beds at each site were characterized using 15.3-cm diameter cores and estimates of cover during each sampling event. Comparisons were made of seagrass characteristics and community structure, abundance and biomass of fish and invertebrates among sites, and with collections made in the 1980s and 1990s at Cross and Buchanan.

Key Findings:

- The Lower Keys had the least reported overall decline in bonefish and the highest abundance of bonefish prey and other invertebrates, while the Upper Keys/Florida Bay had the greatest reported overall decline in bonefish and a lower abundance of bonefish prey and other invertebrates.
- Cross Bank and 9-Mile Bank had tremendous intra-annual (seasonal) variation in benthic prey community structure and low prey abundance compared to all other sites. The prey community (structure and standing stock) at Buchanan Bank was more similar to that of Biscayne Bay than to the other Upper Keys sites.
- No discernible relationship was observed between seagrass abundance and benthic prey abundance, as Sawyer (Lower Keys) had the least seagrass and the highest prey abundance, while Cross Bank had the most seagrass and the lowest prey abundance.
- While our data indicate lower bonefish prey abundance at two of the three Upper Keys/Florida Bay sites, relative to other regions, decadal comparisons do not suggest benthic prey abundance at these sites decreased to a great extent (if at all) over the last three decades. These findings suggest it is unlikely that prey limitation is the primary cause of the recent decline in the Florida Bay bonefish population. We suggest other factors that may also be contributing to the bonefish decline in Florida Bay.

CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Coastal and estuarine ecosystems are currently declining on a global scale. While these systems are dynamic by nature, their transformation has dramatically accelerated worldwide over the past two centuries. Second only to exploitation as a cause of this ecosystem change, habitat destruction is responsible for nearly half of the depletions and extinctions of coastal species worldwide (Lotze et al. 2006). In the past 60 years, we have seen a marked increase in nitrogen and phosphorus loads, primary productivity, eutrophic plankton, oxygen depletion and losses of epiphytic diatom communities associated with seagrasses (Cloern 2001, Jackson et al. 2001), leading to a substantial decline in nursery habitat for estuarine and nearshore species. The consequent collapse of pelagic and inshore food webs and decline in fisheries is most pronounced in the Northern Hemisphere (Pauly et al. 1998). While the last 50-100 years have seen a slowdown in the decline of large vertebrates in coastal ecosystems, trends in the deterioration of populations of smaller consumers and water quality continue (Lotze et al. 2006).

Human alteration of the flow of surface water throughout the Greater Everglades into Florida Bay has been well described. Documented deleterious effects of reduced freshwater flow into Florida Bay include mass mortality of seagrasses, mangrove dieback, reduced recruitment of pink shrimp, snook and redfish, marked changes in the abundance of small prey fish, lowered reproductive success of osprey, roseate spoonbills and other species of wading birds, and shifts in the distribution of manatees and crocodiles (McIvor et al. 1994, Lorenz 1999, 2013, Lorenz et al. 2002, 2009). Given the physical changes that have occurred (and continue) in Florida Bay, negative impacts on the ecological services provided by seagrasses and other critical habitats continue to be fully realized and documented.

Bonefish (*Albula vulpes*) are a critical component of the Florida Keys' ecological, recreational, and economic identities. Founded in Florida Bay, the sport of shallow-water sight fishing began drawing worldwide attention to our region after World War II as leisure fishing became a popular pastime. Since that time, the mystique of bonefishing continues to draw locals and tourists alike to the flats of the Keys. Annual censuses (2003-2010) estimate a mean population of 316,805 bonefish in the Florida Keys (201 bonefish/mi^2) (University of Miami 2010). As bonefishing is a pillar of the Keys recreational fishing industry (Florida Fish & Wildlife Conservation Commission), each bonefish represented in the census represents approximately $3,500/year ($75,000 over its lifetime) to the Florida economy, making the fishery one of the most valuable in the world.

In the Keys, bonefish are considered an ecological indicator species due to their high mobility and benthic-based diet (Larkin et al. 2010, Larkin 2011). Once centered in the Upper Keys, this region's bonefish fishery has deteriorated since the 1970s, with a more dramatic decline in the past five years (P. Frezza, unpublished personal interviews). Bonefish currently are comparatively scarce on banks that they historically utilized heavily. Importantly, while the Upper Keys bonefish population has greatly diminished, populations in the Lower Keys and Biscayne Bay appear to have remained more stable. While the exact nature of the decline is unknown, it is suggested that changes in the flats community, particularly the benthic prey-base, is a likely cause.

The marked decline seen in recent years in the Upper Keys bonefish population emphasizes the timely need to address potential threats to the Keys' bonefish fishery. Furthermore, these changes are certainly indicative of the ecological health of this region and may serve as a forewarning of future impacts to other recreational or commercial fisheries. This study examines one potential driver of change in the Upper Keys' bonefish population with the goal of identifying what changes in ecosystem management can be made to benefit our bonefish fishery.

With no evidence of disease or increased predation affecting Keys' bonefish populations, we employ a bottom-up trophic approach to provide insight into ecosystem function. The benthic, primarily crustacean diet of bonefish (Crabtree et al. 1998) may be especially sensitive to environmental change (e.g., habitat loss, changes in salinity, declines in water quality) in this ecosystem, as these taxa tend to be less mobile than larger and free-swimming species. Support for this approach includes previous studies documenting declines in Chesapeake Bay blue crab populations in response to reduced water quality and loss/fragmentation of seagrass habitat (Mizerek et al. 2011), reduced recruitment of Florida Bay juvenile pink shrimp in response to environmental changes (Browder et al. 1999, Ehrhardt and Legault 1999), and observed diet shifts in Charlotte Harbor snook in response to alterations of freshwater flow into estuarine creeks (Adams et al. 2009).

Successful estuary and coastal zone restoration relies on both historical reference points and current assessments of the degree and drivers of degradation in an ecosystem context (Pikitch et al. 2004, Balmford et al. 2005). The objective of this study is to provide scientifically-based factual information on the state of bonefish habitat in the Upper Keys compared to historical conditions and conditions of bonefish habitats in nearby marine environments.

The specific goals of this study were to:

(1) Examine spatial variation in benthic fauna communities of the Florida Keys (the Upper Keys, Biscayne Bay, and the Lower Keys) to determine the extent that prey availability may influence the abundance and distribution of bonefish.

(2) Describe temporal changes in benthic prey communities in the Upper Keys concurrent with the decline in the bonefish fishery.

(3) Compare patterns of bonefish abundance (historic and present) using available data (including interviews with local/experienced fishers').

(4) Develop a hypothesis as to how variation in benthic fauna communities, seagrass beds, and physicochemical factors have contributed to observed changes in bonefish habitat use in the Florida Keys.

BACKGROUND

Bonefish in Florida Bay

Anecdotal reports from long-time fishers of Florida Bay suggest a dramatic reduction in bonefish abundance in recent years. In the absence of a reliable long-term dataset, experienced fishers may be a critical source of information on historical changes in this fishery. Independent of this study, between 2010 and 2012 surveys of known, long-time fishers with exceptional knowledge of Florida Bay bonefish were collected (all data reported here: P. Frezza, unpublished data). These data will be submitted for peer review publication in Summer 2013. The goal of this survey was to characterize and quantify trends and establish a historical baseline of the bonefish population of Florida Bay through information gained from long-time guides and anglers of the region. A deliberately non-random sampling design was chosen to target interviewees in an attempt to survey all or most fishers with the greatest experience and reputation within the fishery. The survey consisted of a hardcopy questionnaire that included several questions used to assess the respondent's background and experience, and 19 short-answer, multiple-choice, or closed ended/fixed-response questions about their perception of the Florida Bay bonefish population. All interviewees were initially contacted by phone or in person to request their participation in the survey to maximize return rate (return rate=97%). Here, we report data collected to date (N=64) for questions relevant to this study. Respondents were encouraged to use log books or records when available. Notably, unless otherwise noted, all survey questions were specific to Florida Bay, not the Lower Keys, Biscayne Bay, or the oceanside of the Upper Keys.

Survey Findings

Experience of respondents ranged from 12 to 64 years, with an average of 35.7 (±1.5) years bonefishing in Florida Bay. The effective period of record was 1948-present. Seventy-three percent of respondents had ≥30 years' experience, while 13% had ≥50 years' experience. Eighty-four percent of respondents work or have worked professionally as guides in Florida Bay, with an average of 26.5(±1.7) years of professional guiding. Of the 92% of respondents who were still bonefishing in Florida Bay, 73% were working guides.

All but one of the 64 respondents reported they believe the bonefish population in Florida Bay has declined over the course of their career. Most respondents (88%) reported that they feel there are currently "many fewer" bonefish compared to when they first started bonefishing, while others reported "fewer" (11%) or "no change" (1%). No respondents reported a perceived increase. When respondents started bonefishing in the Bay, 95% defined the fishing as "excellent" or "very good", while currently (or when they stopped bonefishing), 84% define the fishing as "poor" or "terrible." Almost half (48%) of respondents described this bonefish decline as "steady." This was the most common description of the trend of the decline with anglers of all experience levels except anglers with ≤20 years' experience, who pointed to "certain/specific years" or "a single episode/event" (Fig. 1).

Respondents were asked to estimate their perceived decline in bonefish abundance since they started fishing (multiple-choice categories used 10% increments: 10%, 20%, etc.). The mean perceived decline was 78(±2)%, with no correlation between perceived decline and angler experience (Pearson's r(62)=0.02). When asked to identify the 5-year period when they detected the largest decline in the number of bonefish in Florida Bay, 87% of anglers responded that some part of that period fell between 2005 and the present. In terms of bonefish catch, a strong negative correlation between the reported maximum bonefish caught/day and the year they were caught was reported (Pearson's r(61)=-0.43, P<0.01; Fig. 2). The average maximum bonefish caught/day was 26(±5) in the 1970s, 18(±2) in the 1980s, 17(±2) in the 1990s, and 12(±1) in the 2000s.

When asked about the average change in the size of bonefish in Florida Bay over the course of their career, 17% of respondents said bonefish are "bigger" or "much bigger," 30% said there is no change in size, and 53% said bonefish are "smaller" or "much smaller." Ninety-one percent of respondents indicated the percentage of days/year that they spent targeting bonefish in Florida Bay decreased, with 77% of them citing "lack of fish" as the primary reason. Seventy percent of guides say a declining bonefish population has had a negative economic effect on their guiding business.

Discussion

In the absence of a meaningful or reliable long-term dataset (e.g., catch or abundance data), local fishers' knowledge may be the best or only source of information to document historical changes in local marine fish species abundance (Pitcher and Pauly 1998, Johannes et al. 2000). In recent decades, the field of fisheries science and management has increasingly relied upon informal data to document the historical status of and highlight 'shifting baseline' issues with marine species (Neis et al. 1999, Sadovy and Cheung 2003). By only using standard forms of data collection or datasets, we felt we would not adequately document shifts in local bonefish abundance.

We are aware of three appropriate quantitative bonefish abundance data sets specific to the upper Keys region: (1) bi-annual visual Keys bonefish surveys, (2) Everglades National Park guides' trip reports, and (3) bonefish tournaments of Islamorada, Florida. All three data sources were considered for their usefulness in assessing bonefish population trends. The limitations with each of these datasets (described below) led us to choose a questionnaire-based survey method to describe patterns of bonefish abundance, both historic and present. It is our belief that this offered the most valid representation of the trends in the Florida Bay bonefish population.

(1) The visual bonefish surveys (Ault et al. 2008a) are an excellent source of information for monitoring trends in bonefish abundance throughout the Keys, but the relatively short period of record (2003-present) currently prohibit any interpretation of long-term trends.

(2) Everglades National Park guides' trip reports provide a 36-year record of 'catch' statistics. During this time, the logbooks used in these surveys have gone through a number of design changes which confound data analyses. Non-

compliance with logs was an issue until the reporting became mandatory for guides in 2007. In 1990, a ‘species preferred’ line was added to the survey which provides an opportunity for guides to indicate the species they are targeting. This could allow for insight into relative fish abundance of sport fishes in the future.

(3) Islamorada bonefish tournament data provide a 44-year record with information on number of bonefish caught, dates of each tournament, hours of fishing, number of participants, and gear used. These data were analyzed and reported by Larkin (2011). Unfortunately, no information are retained on *where* bonefish are caught, prohibiting examination of regional variation. Currently there is no limit to the distance that anglers can travel to target bonefish during these tournaments. Personal communication with tournament anglers (P. Frezza) indicates that currently, many anglers are travelling great distances (>40 miles) to preferred locations. Further, there is no way to account for or correct for advancements in technology and increased skill level of anglers which almost certainly affect catch rates.

Finally, while datasets 2 and 3 quantify catch rates, we do not feel that ‘classic’ catch statistics gained through tournament records or creel surveys are a good indicator for representing bonefish abundance or trends in the Florida Keys. Because bonefish are a species that are extraordinarily difficult to catch and are thought to be highly-adaptive to increased fishing pressure, classic catch statistics may be misleading. Furthermore, it is believed that a diminishing bonefish population, difficulty of finding, hooking and landing remaining fish and the competitive nature of tournaments have been the driver for sophisticated advancements in fishing technology that have made it possible to continue to sustain catches. In the last decade alone, tremendous advancements have been made in shallow water fishing gear including continued improvement in designs of: hooks, lines, leaders, fly material, rods, boats and sunglasses. These points, along with a noted increase in angler and guide skill level, lend credence to the notion that the shallow water fishery ‘catch’ may remain unchanged or even increase over extended periods of time with a concurrent decline in fish abundance. This is a phenomena that was recently chronicled with tarpon by a highly-decorated tournament angler (Mill 2013).

Through personal communication with experienced anglers and guides, it was found that in recent years upper Keys anglers were commonly travelling away from what was once the epicenter of the bonefish fishery (Islamorada) to destinations in the Biscayne Bay region or the lower Keys to target bonefish. We feel this reduced effort in the Upper Keys is another indication of a diminishing population of bonefish in the Upper Keys region. Due to this apparent regional change, the question of perceived change in bonefish abundance in other regions of the Keys was also explored during our survey. When asked to rate the change in bonefish abundance over the course of their angling careers in four regions outside of Florida Bay, 96% of respondents indicated bonefish abundance had “decreased” or “decreased greatly” on the oceanside of the Upper Keys, 81% indicated bonefish abundance had “decreased” or “decreased greatly” in Biscayne Bay, 72% indicated bonefish abundance had “decreased” or “decreased greatly” in the Middle Keys, and 40% indicated bonefish abundance had "decreased" or "decreased greatly" in the Lower Keys (Fig. 3). Interestingly, 40% of respondents indicated bonefish abundance had "increased" or "increased greatly" in the Lower Keys (20% indicated no change). It is noteworthy that a number of anglers targeting bonefish in the Key West and Marquesas region reported the greatest %increase in fish abundance.

Conclusions

Responses from this survey indicated fishers believe the population of bonefish utilizing Florida Bay is 22% of what it was in the early 1950s, when the first fishers surveyed came into the fishery. Our failure to find a relationship between angler experience and their perceived decline in bonefish abundance reinforced our belief that the greatest decrease in bonefish abundance occurred in relatively recent years. Respondents reported a gradual decline in bonefish beginning in the mid-1960s (accelerating in the late-1970s), with several periods of notably rapid decline. Two of the largest periods of bonefish decline indicated by fishers corresponded with the timing of the two major algal bloom events that occurred in Florida Bay over the past 50 years: the early-1990s and 2007-08. However, the single greatest year of decline that was reported, 2010, corresponded to a severe, extended period of cold temperatures that resulted in remarkable mortality of vertebrate life throughout the southern Everglades and Florida Bay (Hallac et al. 2010). It should be emphasized, however, that significant decline in bonefish abundance was occurring prior to the cold event of 2010.

Bonefish prey communities

Examination of food webs is a logical first step in understanding species decline. While the relative importance of top-down (predator-controlled) versus bottom-up (resource-controlled) food-web regulation is a classic debate in trophic ecology (e.g., Hairston et al. 1960, Hunter and Price 1992, Power 1992, Abrams 1993, Polis et al. 1996), Florida Bay's recent history of changes in nutrient status, algal growth, and resulting changes in seagrass communities (Fourqurean and Robblee 1999, Fourqurean et al. 2002, Richardson and Zimba 2002, Boyer et al. 2009, Glibert et al. 2009) suggests examination of bottom-up impacts of bonefish prey on the bonefish population is highly appropriate. Furthermore, Lorenz (2013) reviewed the population declines of numerous vertebrate species in Florida Bay and found that most studies implicate reduced prey resources as the most likely reason for these declines. Finally, suggested links between shifts in bonefish growth rate and their diet (Larkin 2011) further justify a focus on assessing the status of prey populations and the need to better understand trophic linkages.

Bonefish diet

In addition to anecdotal observations of seasoned bonefishers, our current understanding of bonefish diet comes from stomach content analyses of captured individuals. Stomachs of bonefish collected in Puerto Rico (Warmke and Erdman 1963) and the Bahamas (Colton and Alevizon 1983) were dominated by mollusks (56% by volume and 39% by dry weight, respectively), while crustaceans (particularly swimming crabs (Portunidae) and mud crabs (Xanthidae)) were also very important. In the Florida Keys (primarily Marathon to Key West), Bruger (1974) found bonefish stomachs were dominated by crustaceans, particularly penaeid shrimp (pink, white and brown; Penaeidae), snapping shrimp (Alpheidae), swimming crabs and mud crabs. Notably, gulf toadfish were absent from bonefish stomachs in this study.

Crabtree et al. (1998) examined stomach contents of 385 bonefish captured in the Florida Keys (oceanside), Florida Bay and Biscayne Bay and compared these data with invertebrate and fish prey availability to infer selectivity. Overall, stomachs were dominated by five taxonomic groups (% by weight): mud crabs (29.9%), gulf toadfish (17.2%), swimming crabs (10.9%), snapping shrimp (9.2%), and penaeid shrimp (7.7%). While stomach contents of Florida Bay bonefish differed somewhat from that of oceanside Keys' bonefish, the same prey taxa dominated in both areas. Prey selectivity was inferred through comparisons with aquatic fauna data from 1-m^2 throw trap collections on the oceanside (Middle Keys to Elliot Key) and data from those made by Matheson et al (1999) in Florida Bay (Buchanan Bank). On the oceanside, bonefish fed selectively on snapping shrimp, mud crabs, northern pink shrimp (*Farfantepenaeus druorarum*) and gulf toadfish, selecting against small, abundant species of grass (Palaemonidae) and cleaner (Hippolytidae) shrimp. In Florida Bay, bonefish fed selectively on mud crabs, snapping shrimp, gulf toadfish, northern pink shrimp, and blue crabs (*Callinectes* spp.) and selected against small, abundant species of grass and cleaner shrimp, in addition to abundant code gobies (*Gobiosoma robustum*). Seasonal shifts in stomach contents were seen, but were subtle, with the same taxonomic groups dominating year round.

Variation in bonefish prey with size has been reported in several studies. In the Bahamas, bonefish >416 mm fork length (FL) consumed more mud crabs, spider crabs (Majidae), snapping shrimp and prey fish than smaller bonefish (Colton and Alevizon 1983), with prey fish mainly found in bonefish >575 mm FL. They also reported that small bonefish consumed more blue crabs than large bonefish. In the Keys, bonefish >439 mm FL consumed more decapods and prey fish than smaller bonefish, but no blue crabs were found in the stomachs of bonefish <440 mm FL, although they were consumed in large numbers by larger bonefish (Crabtree et al. 1998). While all previous studies described here focused on relatively large bonefish captured using hook-and-line, a study in the Florida Keys used beach seines to collect 407 young-of-the-year (YOY) bonefish (Snodgrass 2008). They found the most important prey items for YOY were polychaetes, amphipods, copepods, shrimp, and other decapods. They also found that with increased YOY size, there was a decrease in the importance of amphipods and an increase in the importance of crabs as prey items.

Previous assessments of prey species on Florida Bay mud banks

In the mid-1980s, an extensive study was conducted in an effort to describe the ecology of shallow water bank habitats of Florida Bay. Specifically, Powell et al. (1987) examined how physical parameters (e.g., wind velocity and direction, water turbulence, variation in water level) shaped the distribution and abundance of resident species. Six sites were established, four in northern Florida Bay (Oyster, Dump, Eagle and Coon Keys), and two in southern Florida Bay (Cross and Buchanan Banks), and demersal and pelagic fauna communities were quantified using 1-m^2 throw traps and gill nets, respectively. Demersal fauna sampling was repeated by Matheson et al. (1999) to detect and describe any variation due to the recent seagrass die-off, phytoplankton blooms and other ecosystem changes that had occurred in the late 1980s and early 1990s. In both studies, sampling efforts spanned the three hydrologic seasons of Florida Bay: dry season (Feb-March 1984, Jan 1985, Mar 1994), early-wet season (May 1984, May-Jun 1985, June 1995, May 1996) and late-wet season (Sep 1984, Sep 1985, Sep 1994, Sep 1995). Relevant to the study reported here, we focus only on observations from each study at Cross and Buchanan banks, as these are historic bonefish forage grounds.

Powell et al. (1987) found that of all study sites, the seagrass bed at Buchanan was richest, with the highest seagrass density and standing crop. Seagrass at Cross was similar to Buchanan (both were relatively lush turtle grass-dominated meadows), but was more sparse. Because fauna abundance was usually highest on the leeward side of the bank (with no difference in community structure), a single leeward transect/site was used in sampling repeated by Matheson et al. and in our reported study. While the fauna of Florida Bay are primarily temperate in nature (Tabb et al. 1962, Holmquist et al. 1989), Buchanan had several common 'tropical' species due to water exchange with the Atlantic (tropical species were more rare at Cross). In addition to the intra-annual seasonality observed in both fish and decapods, Powell et al. reported significant, and often marked, inter-annual variation in fish and decapod abundance. For example, the abundance of 5 of 10 fish species increased 100% between the first and second years of the study; the abundance of all grass shrimp species also increased during this time. On a smaller temporal scale, densities of fish and decapods captured in throw traps showed little to no response to tidal fluctuations.

Decadal comparisons made by Matheson et al. (1999) indicated an overall decrease in seagrass canopy-dwelling fauna and an increase in benthic fauna from the mid-1980s to the mid-1990s. While seagrass beds at Cross and Buchanan were relatively lush, they noted a significant decrease in standing crop, attributed to a decrease in canopy height, as no change in shoot density was observed. Few inter-decadal differences were seen in the fauna community at Buchanan, although they did note an increase in canopy crustaceans, zostera shrimp, and gulf toadfish. The abundance of fauna at Cross generally decreased from the mid-1980s to the mid-1990s. Significant decadal changes were observed in canopy crustaceans (50% decrease), benthic crustaceans (50% decrease), canopy-resident fish (70% decrease), and two species of benthic fish: code goby (25% decrease) and gulf toadfish (125% increase).

These previous studies provide a valuable opportunity to examine changes in fauna (bonefish prey) communities in Florida Bay from the mid-1980s to present, a period of notable bonefish decline in this region.

METHODS

Study Design

Five study sites were selected based on Principal Investigators' (PIs) local knowledge of bonefish populations and communication with sport fishermen and guides (Fig. 4; Table 1). Sites in the Upper Keys represent locations that historically supported excellent bonefish fisheries, but have recently experienced marked population declines, while sites in Biscayne Bay and the Lower Keys represent locations that currently support bonefish fisheries.

Buchanan Bank (Fig. 5): The Buchanan Bank site experienced nearly-full Atlantic tidal influence, but was located 5 mi from the nearest ocean exchange (Channel 2 Bridge). The tide was slightly attenuated, experiencing an average annual tidal range of approximately 1.75 ft.

Cross Bank (Fig. 6): While the Cross Bank site was also under Atlantic tidal influence, the site location was situated approximately 4 mi from both Snake Creek and Tavernier Creek, which were the nearest passes to the ocean. These creeks have far less transport capacity than the passes situated near the Buchanan Bank site, therefore tide was attenuated even more so than at Buchanan. Average annual tidal range at the Cross Bank site was approximately 1 ft.

9-Mile Bank (Fig. 7): The 9-Mile Bank site was under Gulf of Mexico semi-diurnal tidal influence, with greater amplitude than the neighboring Atlantic. Average annual tidal range at was 2.75 ft.

Sands Cut (Fig. 8): The Sands Cut site was located just inside the pass separating Sands Key and Elliott Key and received nearly-full Atlantic Ocean semi-diurnal tide, with an average annual tidal range of approximately 2 ft.

Sawyer Keys (Fig. 9): Like the 9-Mile Bank site, the Sawyer Key site was under Gulf of Mexico semi-diurnal tidal influence. Average annual tidal range was 3 ft.

Three sampling events were conducted in 2012, corresponding to the three ecologically distinct seasons of Florida Bay (described by Powell et al. 1987): (1) the middle of the dry season (March 2-20), (2) the first half of the wet season (July 3-13), (3) the second half of the wet season (October 1-5).

Field Sampling

Construction of sampling devices (1-m^2 throw trap, corer) and sampling protocols followed those described by Powell et al. (1987) and Matheson (1999). At each site, a 70-m transect was established parallel to the bank on its leeward side. Transect location was selected such that water depth was ≈50 cm deeper than the top of the bank upon arrival (early morning). Physical data (water temperature (^{o}C), salinity (psu), specific conductance (mS/cm), and dissolved oxygen (mg/L and %saturation)) were measured at the top and bottom of the water column at the beginning and end of the sampling day using a Hydrolab® Quanta Water Quality Monitoring System. Six 1-m^2 throw-trap samples were collected along the transect (approximately every 10 m), with successive trap locations shifted (perpendicular to the bank) with tidal fluctuations to maintain a consistent trap depth. Care was also taken to avoid selecting trap locations not representative of the site due to propeller scars or other physical disturbances.

Each throw-trap was cleared with a 3-mm mesh seine until three successive passes yielded no organisms other than gastropods or mud crabs (minimum of 10 passes). Sea cucumbers were enumerated and measured (total length) but not retained. Seagrass litter and drift algae collected in each trap were retained and returned to the lab. Water depth, seagrass species present, %seagrass cover and %macroalgae cover were recorded for each trap. Two 15.3-cm diameter cores were also taken at the outside edges of each trap to quantify seagrass beds. All samples were frozen for preservation prior to laboratory analyses.

Laboratory Processing

Core samples were processed by identifying seagrass species and recording blades/shoot for each shoot. Length (cm) and width (mm) were recorded for each blade of five randomly selected shoots. All blades were scraped to remove epiphytes, rinsed in 10% HCl, dried at 40°C for 48 h, and weighed. Metrics used for data analysis included *shoot density* (no. shoots/m^2) for each species, *canopy height* (maximum blade length; mm), *leaf area* (average blade area (length x width) x total number of blades; cm^2/m^2), and *standing stock* (dry weight; g/m^2).

Seagrass litter from each trap was sorted from drift and/or calcareous algae. Litter was squeezed dry, air-dried for 30 minutes and weighed (g/m^2). Drift and calcareous algae were also air-dried (as above) and weighed.

Fauna samples were fixed in 10% formaldehyde and preserved in 70% EtOH. Specimens were identified to lowest feasible taxonomic level (e.g., species for most fishes, family for most crustaceans) and enumerated. Length (standard length (SL) for fishes, carapace length (CL) for shrimp, carapace width (CW) for crabs; mm) and wet mass (g) were recorded for most specimens, although total mass by size class was recorded for some large samples. Shells were removed from bivalves prior to weighing, but were included in weights of gastropods and hermit crabs to avoid destruction of specimens.

Data Analyses

Analyses of data collected in this study focused on variation among study sites, and conclusions took into account regional differences among sites (Florida Bay vs. Biscayne Bay vs. Lower Keys). All abundance and biomass data were ln(y+1)-transformed and %cover data were arcsine(√y)-transformed prior to analyses to fulfill assumptions of normality. Inter-site variation in seagrass shoot density (no./m^2), canopy height (mm), leaf area (cm^2/m^2), seagrass biomass (g dry weight/m^2), seagrass litter (g wet weight/m^2), drift and calcareous algae (g wet weight/m^2), and %cover of seagrass and algae was analyzed using 1-way analysis of variance (ANOVA). A combination of multivariate and univariate techniques was used to examine variation in aquatic fauna communities. Community analyses focused on abundance (no./m^2) of common taxa (incidence ≥10%). Spatial variation in fish and invertebrate community structure was described using 1-way ANOSIM based on a standardized Bray-Curtis dissimilarity matrix (Clarke 1993, Clarke and Warwick 1994). Similarity percentage breakdown (SIMPER) was used to describe observed community variation, and non-metric multidimensional scaling (nMDS) was used to help visualize patterns. Univariate analyses (ANOVA) focused on fauna abundance and biomass (g wet weight/m^2). All results reported from ANOVA are based on type-III sums-of-squares (Shaw and Mitchell-Olds 1993).

RESULTS

Inter-Site Variation

Physical

Water depth within throw traps ranged from 32 to 115 cm ($\overline{X}$=52.6±1.3 cm). Due to known temporal variation, small sample sizes prohibited quantitative comparison of physical data, but several trends were apparent. Water temperature was similar among sites, and was lower in the dry season than the early- or late-wet seasons (Fig. 10). Salinity and specific conductance were notably lower at Cross than other sites, and sites generally experienced a decrease in these variables from the dry season to the late-wet season (Fig. 11).

Vegetation

Turtle grass (*Thalassia testudinum*) was the most abundant vegetation encountered at all sites. In core samples, 99.5% of seagrass shoots were turtle grass, while 0.3% were manatee grass (*Syringodium filiforme*) and 0.2% were shoal grass (*Halodule wrightii*). Replicate seagrass cores from one sampling location (Sawyer, throw 5, early-wet season) were removed from the data set as outliers prior to analyses, as they contained no seagrass. Total shoot density varied among study sites ($F_{4,10}$=89.19, P<0.001, R^2=0.973) with shoot density at Cross 1.8X higher than 9-Mile and Buchanan (which were similar), 2.5X higher than Sands, and 5.6X higher than Sawyer (Fig 12a). Canopy height did not vary among sites ($\overline{X}$=207 mm; $F_{4,10}$=2.413, P=0.118, R^2=0.491). Leaf area varied among study sites, with lower leaf area at Sawyer than most sites (Fig 12b).

Seagrass standing stock was generally higher at 9-Mile and Cross (which were similar) than the other sites ($F_{4,10}$=10.161, P=0.002, R^2=0.803), although there was overlap in some pairwise comparisons (Fig. 12c). Calcareous algae standing stock was higher at Sands, Sawyer and Buchanan (which were similar) than at 9-Mile and Cross (which were similar) ($F_{4,10}$=22.915, P<0.001, R^2=0.902; Fig 12d).

In throw traps, %cover of algae was 3.6X higher at 9-Mile and Sawyer (which were similar) than other sites (which were similar) ($F_{4,10}$=12.0, P=0.001, R^2=0.828; Fig. 13). Total percent cover and %cover of seagrass also varied among sites (total %cover: $F_{4,10}$=7.97, P=0.004, R^2=0.761; seagrass %cover: $F_{4,10}$=17.56, P<0.001, R^2=0.875), lower at Buchanan and Sawyer than other sites (Fig. 13). Biomass of seagrass litter was 3.9X greater at 9-Mile, Cross and Sands (which were similar) than at Buchanan and Sawyer (which were similar) ($F_{4,10}$=18.462, P<0.001, R^2=0.881; Fig 14). Biomass of algae (calcareous and drift) was generally highest at 9-Mile and Sawyer and lowest at Sands, although there was considerable overlap in pairwise comparisons ($F_{4,10}$=8.338, P=0.003, R^2=0.769; Fig. 14).

Fauna

We collected a total of 9,779 invertebrates from 41 taxa (including gastropods, bivalves, cephalopods, annelids, xiphosurans, crustaceans and echinoderms; Table 2). Community analyses focused on decapods, as they were the most abundant invertebrate taxa and are those with the greatest importance to bonefish. Decapod community structure varied significantly among sampling sites (Global R=0.760, P=0.001). Intra-site variation was less than inter-site variation at each site (Fig. 15), with the exception of Cross which exhibited a great deal of variation between sampling events. Decapod communities at Sands, Sawyer and Buchanan were more similar to each other than to the other two sites. SIMPER analysis revealed decapod communities at each site were characterized as follows, with prominent taxa listed in order of decreasing %similarity:

> <u>Sands</u>: snapping shrimp (Alpheidae), mud crabs (Xanthidae), spider crabs (Majidae), cleaner shrimp (Hippolytidae) (cumulative similarity=83.56%)
>
> <u>Sawyer & Buchanan</u>: mud crabs, snapping shrimp, cleaner shrimp, grass shrimp (Palaemonidae) (cumulative similarities=75.40% and 77.63%, respectively)
>
> <u>Cross</u>: cleaner shrimp, snapping shrimp, mud crabs (cumulative similarity=74.37%)
>
> <u>9-Mile</u>: cleaner shrimp, mud crabs, grass shrimp (cumulative similarity=80.71%)

Univariate analyses of invertebrates focused on the abundance and biomass of common taxa (incidence≥10%; Table 2). Significant inter-site variation was observed in 10 of 15 common taxa (Table 3). Cross had a higher abundance of snails than Sands and Sawyer, and higher bivalve abundance than Sawyer (Fig. 16a,b). Echinoderms were more abundant at Buchanan than 9-Mile and Sands (Fig. 16c). Sawyer had the highest abundances of snapping shrimp, grass shrimp, spider crabs and mud crabs, while lowest abundances of invertebrate taxa were most often seen at 9-Mile and Cross (Fig 17). Buchanan frequently had higher abundances of invertebrate taxa than 9-Mile and Cross, with abundances often similar to those seen at Sands and/or Sawyer. Total invertebrate abundance was higher at Sawyer than most other sites (Fig. 18). Similar patterns were seen in analyses of biomass.

We collected a total of 1,131 fish from 35 taxa (Table 4). Fish community structure varied significantly among sampling sites (Global R=0.810, P=0.001), and intra-site variation was less than inter-site variation at each site (Fig. 19). The fish community at Sands was most different from other sites and exhibited the most variation among sampling events. SIMPER analysis revealed fish communities at each site were characterized as follows, with prominent taxa listed in order of decreasing %similarity:

Sands: gulf toadfish (*Opsanus beta*) (cumulative similarity=83.58%)

9-Mile: rainwater killifish (*Lucania parva*), Gulf toadfish (cumulative similarity=77.47%)

Cross: gulf toadfish, fringed pipefish (*Anarchopterus criniger*), rainwater killifish, code goby (*Gobiosoma robustum*) (cumulative similarity=79.30%)

Buchanan: gulf toadfish, code goby, sea robin (Triglidae), banded blenny (*Paraclinus fasciatus*) (cumulative similarity=85.15%)

Sawyer: code goby, gulf toadfish, banded blenny, dwarf seahorse (*Hippocampus zosterae*) (cumulative similarity=81.50%)

Univariate analyses of fish data focused on the abundance and biomass of common taxa (incidence≥10%; Table 4). Significant inter-site variation was observed in 5 of 11 common taxa, with most variation attributed to local abundance of a taxon at a site. Compared to other sites, fringed pipefish were most abundant at Cross, rainwater killifish were most abundant at 9-Mile, sea robins were most abundant at Buchanan, and dwarf seahorse were most abundant at Cross and Sawyer (which were similar) (all 'significant' pairs, Tukey's pairwise P≤0.05) (Table 5, Fig. 20). Code goby were less abundant at Sands than Sawyer and 9-Mile, which were similar. Similar patterns were seen in analyses of biomass.

We also focused specifically on taxa identified as known bonefish prey items in Florida Bay (Crabtree et al. 1998): mud crabs, snapping shrimp, gulf toadfish, pink shrimp (*Farfantepennaeus duorarum*) and blue crabs (*Callinectes*). While crustaceans were generally identified to family-level in this study, previous studies in this region of Florida Bay (Matheson et al. 1999) suggest most penaeid shrimp (Penaeidae) are pink shrimp and most swimming crabs (Portunidae) are blue crabs, which supported the use of these higher taxonomic levels for this analysis. The total abundance of bonefish prey varied significantly among study sites ($F_{4,10}$=80.38, P<0.001, R^2=0.970), with abundance at Sawyer greater than that of Buchanan and Sands (which were similar) which were greater than the abundance at 9-Mile and Cross (which were similar) (Tukey's pairwise P<0.05; Fig 21). Total biomass of bonefish prey showed a similar trend among sites, but variation was not statistically significant ($F_{4,10}$=2.35, P=0.125, R^2=0.484).

Decadal Comparisons

Decadal comparisons were made for Buchanan and Cross Banks by graphing (mean±SE) and visually comparing data. While we were able to obtain raw physical, vegetation, and fauna abundance data from the 1990s effort, quantitative analyses were not possible without access to the original 1980s data set (means reported here are those reported by Powell et al. (1987)). Expressions of differences or similarities among decades are qualitative only, and are based upon overlap between means or mean±SE.

Physical

Average water temperature showed no decadal variation at Buchanan, but water temperature at Cross appeared to be lowest in the 1980s and highest in 2012 (Fig. 22a). The total range of this variation, however, was less than the daily fluctuation range (2.3°C-5.8°C) reported by Powell et al. (1987). Average salinity showed no decadal variation at Buchanan, but at Cross, salinity appeared lower in 2012 compared to the earlier studies, which were similar (Fig. 22b).

Vegetation

Comparisons of seagrass data from this study with those collected in 1980s and 1990s is challenging due to the unavailability of raw data from the 1980s study and the nature of data reported in grey and peer-reviewed literature. Conclusions from visual comparisons of reported means (described above) often do not follow those from non-parametric statistics computed and reported by Matheson et al. (1999). For this reason, here we discuss visual comparisons of our data with those of the 1990s (for which we have raw data) and the conclusions of the non-parametric comparisons of 1980s and 1990s data. At Buchanan, most seagrass metrics appeared similar among decades (Fig. 23). Standing crop, however, decreased from the 1980s to 1990s (apparently driven by decreased canopy height), while 1990s and 2012 standing crops were similar. At Cross, standing crop also decreased from the 1980s to 1990s, but was higher in the present study than in the 1990s; the difference/similarity between 1980s and present standing stock are unclear. While shoot density and leaf area did not vary between the 1980s and 1990s, they appeared to increase from the 1990s to present. Canopy height at Cross appeared higher in 2012 than in previous decades (Fig. 23).

Fauna

Total abundance of crustaceans appeared lower at both Buchanan and Cross, than in previous decades (Fig. 24). This trend could not be attributed to any taxonomic group, however, as 1980s samples had a particularly high abundance of cleaner shrimp, 1990s samples had a particularly high abundance of hermit crabs, mantis shrimp (Buchanan only) and pink shrimp, and 2012 samples had a particularly high abundance of snapping shrimp and mud crabs (at Buchanan only)(Fig. 25). No apparent decadal difference was observed in benthic, canopy-resident, canopy-transient or pelagic fish (Fig. 26).

DISCUSSION

Water conditions and habitat structure

Water temperature, salinity and conductivity varied seasonally as would be expected in this subtropical ecosystem. Detailed temperature and salinity profiles were not recorded in this study, and our small sample size (N=3 sampling events) allowed only a coarse evaluation of trends in water conditions. Water temperature tracked seasonal air temperature patterns (highest in summer months, lowest in winter months) and salinity and conductivity (inversely) tracked seasonal rainfall patterns (highest in dry season, lowest in late wet season). Compared to other sites, Cross had lower salinity and conductivity, and the smallest range of seasonal temperature variation. This is likely due to its relative proximity to freshwater inputs from the Everglades and distance from Atlantic inflows, compared to other sites (Nuttle et al. 2000).

Seagrass communities at our study sites were dominated by turtle grass, as described in previous studies (e.g., Zieman et al. 1989). Generally, habitat structure for bonefish prey was similar at two of our three Upper Keys sites (9-Mile and Cross), while Buchanan (Upper Keys) was more similar to our Biscayne Bay and Lower Keys sites. Habitat structure at each site can be summarized as follows:

- Cross and 9-Mile (Upper Keys) had high seagrass shoot density (highest at Cross), leaf area, standing stock, %cover, and litter biomass, and low calcareous algae standing stock. Biomass of drift algae was higher at 9-Mile than Cross.
- Buchanan (Upper Keys) had seagrass shoot density similar to that of 9-Mile (relatively high), but seagrass standing stock, %cover, and litter biomass were among the lowest of all sites. Standing stock of calcareous algae was higher at Buchanan than the other Upper Keys sites, but similar to sites in the Lower Keys and Biscayne Bay.
- Sands (Biscayne Bay) had relatively low seagrass shoot density, leaf area, standing stock, and %cover, but had higher seagrass litter biomass and less drift algae biomass (lowest of all sites) than would be expected from seagrass core analyses.
- Sawyer (Lower Keys) had the lowest seagrass shoot density, leaf area, and seagrass litter biomass of all sites. Seagrass %cover and standing stock were also lower than most sites. All algae metrics (%cover, standing stock of calcareous and biomass of drift) were higher at Sawyer than at most other sites.

Between the 1960s and 1970s, Florida Bay's heterogeneous seagrass meadows, comprised of a mosaic of turtle grass and shoal grass monocultures, shifted to a more homogeneous system dominated by turtle grass; this shift was concurrent with a notable decline in game fish, a correlation many guides believed was causal (Tilmant 1989). At both Buchanan and Cross, seagrass standing stock declined from the 1980s to 1990s, reflecting the large-scale seagrass die-off that occurred in Florida Bay (Durako 1994). At Buchanan, contemporary standing stock estimates are similar to those of the 1990s (remaining lower), while standing stock has increased at Cross. Unfortunately, the nature of our analyses did not allow us to assess whether the current standing stock at Cross is lower than, or has returned to or exceeded that of the

1980s. Traditionally, higher seagrass standing stock is associated with higher infauna abundance (Stoner 1980, Orth et al. 1984, Hemminga and Duarte 2000), although the potential importance of some degree of habitat heterogeneity cannot be overlooked (Bologna and Heck 2002).

Spatial and temporal trends in bonefish prey

We observed inter-site variation in the structure of both fish and invertebrate communities. The fish community was largely dominated by gulf toadfish, as observed in previous studies. Fish community structure at our Biscayne Bay site was the most different from other sites and displayed slightly more seasonal variation than other sites. While the driver of this variation is unclear, it may be notable that the record of several tropical taxa (e.g., parrotfish, damselfish) were unique to this site and may be an indication of greatest proximity to and/or exchange with hard bottom and patch reef habitats of the Atlantic (Robblee and Zieman 1984). Overall, the invertebrate community was dominated by decapod crustaceans, particularly snapping shrimp, mud crabs, spider crabs, cleaner shrimp and grass shrimp. It is notable that while this study (unlike Powell et al. (1987) and Matheson et al. (1999)) included all invertebrates in collections, only a few non-decapods were common and little consistent inter-site variation was observed in any of these taxa. The effectiveness of the 1-m^2 throw trap in collecting these other taxa is unknown. Invertebrate communities were similar at Buchanan (Upper Keys), Lower Keys, and Biscayne Bay sites, and showed minimal season variation compared to communities at the other two Upper Keys sites which were very different (from each other and from other sites) and varied widely among sampling events.

Patterns of fauna abundance among study sites follow (generally inversely) those seen in the seagrass community, with Buchanan (Upper Keys) more similar to our Biscayne Bay and Lower Keys sites than to the other Upper Keys sites. Our Lower Keys site had the highest abundance of most species of shrimp and crabs. Buchanan (Upper Keys) generally had a higher abundance of fauna than the other Upper Keys sites, usually equivalent to those in Biscayne Bay and/or the Lower Keys. While we did detect statistically significant variations, we saw no interpretable patterns in the abundance of fish among study sites or regions suggesting that dynamics of fish communities may be more complex than we were able to detect through this sampling design.

Comparison of the three regions sampled in this study suggests the most bonefish prey in the Lower Keys, and the least bonefish prey in the Upper Keys (specifically, 9-Mile and Cross Banks), with Biscayne Bay and Buchanan (Upper Keys) falling in-between. This closely follows the pattern of perceived changes in bonefish abundance reported by experienced fishers, who indicated the Lower Keys bonefishery as most stable and the Florida Bay bonefishery as having seen the greatest decline, with Biscayne Bay falling in-between. Counterintuitive from a habitat-availability perspective, patterns of seagrass abundance were inverse those of prey abundance, with seagrass meadows most dense in the Upper Keys and least dense in the Lower Keys, and indicating bonefish abundance is not positively correlated with seagrass coverage. Regardless of prey abundance, however, it is important to acknowledge the feeding style of bonefish, and their reduced feeding ability in a dense seagrass environment (P. Frezza, personal observation). Together, these findings can be combined to produce a logical conceptual framework: *In the Lower Keys, sparse seagrass beds supporting a high abundance of bonefish prey are able to support a stable bonefishery, while in the Upper Keys/Florida Bay, dense seagrass beds with a lower abundance of bonefish prey support a collapsing bonefishery*. This conceptual framework alone, however, fails to support the decadal trends we observed in the Upper Keys.

From the 1980s to 1990s, decreases were reported in the abundance of nearly all fauna (Matheson et al. 1999). Between the 1990s and the present, we observed a decrease in crustaceans at both sites (Buchanan and Cross), but an increase in our 'bonefish prey' metric at Buchanan (abundance of 'bonefish prey' at Cross was similar to 1990s). No change from the 1990s was seen in fish abundance. The dramatic decline of the Upper Keys/Florida Bay bonefishery since the 1990s in the absence of a dramatic decline in bonefish prey at our study sites during this time period suggests our conceptual framework is overly simplified and incomplete. In fact, the Florida Bay conceptual ecological model (Rudnick et al. 2005) proposes bonefish prey (benthic grazers, pink shrimp, fish community) can be influenced by a host of stressors, including an altered salinity regime, nitrogen and phosphorus inputs, pesticides and mercury, and fishing pressure. While a decrease in prey may likely have been part of the cause of the decline seen since the 1980s (and perhaps even earlier), prey abundance alone does not appear to explain the dramatic decline in Florida Bay bonefish that has occurred in recent years (since 2006). The high intra-annual variability observed in prey communities (particularly invertebrates) at Cross and 9-Mile, however, is of particular concern. This variability may be a sign of a more complex food web and/or one with a high degree of temporal variability (Menge and Sutherland 1976). This high variability also suggests the small sample size (one study year) may be inadequate for characterizing or comparing the fauna community structure and standing stock.

Food web considerations

The nature of the potentially-complex trophic interactions in this ecosystem, and the uncertainty that remains about bonefish predator-prey relationships should not be overlooked. While predation is classically considered the dominant organizing interaction in trophically-complex communities (Menge and Sutherland 1976), trophic dynamics of this Florida Bay food web are not well described. In this study, we observed notable seasonal shifts in the community structure of bonefish prey communities at two of three Upper Keys sites. While we were unable to make inter-decadal comparisons of seasonal changes in the prey community (and are thus, unable to determine if this seasonal variation occurred when the bonefish population was more stable), seasonal variation in prey communities at our other sites (sites with more stable bonefish populations) were relatively minimal. It is unclear how these dramatic seasonal shifts in the prey community affect bonefish, or if an adequate prey-base remains year round at these sites. Furthermore, it is unclear whether this variation is an indication of the relative stability of this food web (Pimm 1984), or its susceptibility to other ecological perturbations (discussed below).

Food web theory predicts a decline in the Florida Bay bonefish population (in absence of other ecosystem changes) would result in a trophic cascade that would resonate into lower trophic levels (Heithaus et al. 2008). The release of bonefish prey from predation pressure would visibly increase prey abundance, unless either (1) the abundance of another predator increased to compensate for the lost predator (keeping prey populations stable), or (2) prey abundance also decreased due to another environmental variable. In Florida Bay, we failed to see a release of bonefish prey from predation pressure following the recent bonefish decline (on the contrary, we observed an overall decrease in abundance of crustaceans). Anecdotally, there is no indication that the abundance of an equivalent predator increased following the bonefish decline (questionnaire respondents volunteered that the abundance of other predators like sting rays, nurse sharks, bonnethead sharks and cowfish also declined during this time). This suggests a decrease in both predator and prey populations in Florida Bay, with the magnitude of the prey decline likely masked or dampened by the simultaneous predator decline, the cause of which is unknown. While a decline in bonefish prey does not appear to be the only factor leading to bonefish decline, data collected in this study emphasize the need to better understand these trophic interactions and their implications for the Florida Bay bonefishery. Furthermore, regardless of other environmental stressors affecting bonefish directly, it is unclear whether the current prey population in Florida Bay is sufficient to support a healthy bonefish population.

Limitations of this study

While the study reported here allowed us to assess spatial and temporal trends in bonefish prey abundance, concurrent with declines in the Florida Bay bonefishery, we acknowledge several apparent limitations of the study design, data analysis, and our ability to fully address all questions outlined in our study goals.

Study design

As with many studies where time/effort is weighed against project cost, the greatest limitation of this study is that of replication (spatial and temporal). While describing prey populations outside the Upper Keys where bonefish are more abundant provided an excellent context for interpreting the ability of Upper Keys' fauna to support a healthier bonefish population, additional study sites in Biscayne Bay and the Lower Keys would have bolstered our confidence in inferring regional variation from site differences. More importantly, however, the narrow temporal scope of this study (1 year) provided significant limitation. We observed tremendous variation in invertebrate community structure at two of three Upper Keys sites between sampling events. An additional year (or two) of sampling would help us better understand the nature of these community changes, and would likely strengthen comparisons among sites by reducing variation. Powell et al. (1987) noted dramatic variation (two-fold increase) in fauna abundance between consecutive study years. This magnitude of inter-annual variation could cause us to misinterpret (if the direction of variation is not consistent) or underestimate (if the magnitude of variation is not consistent) spatial trends. Juxtaposing our average fauna abundance from 1-year with the 3-year data sets of Powell et al. and Matheson et al. (1999) can cause similar misinterpretations.

Bonefish diet

Inherent bias in the nature of gut content analyses certainly limits (the magnitude of which is unknown) our ability to infer predator-prey dynamics from variation in fauna communities. All fish gut content analyses offer a 'snapshot in time' of fish diet, but the composition of a gut at one point in time is affected by many unquantifiable factors unrelated to the actual composition of the diet (Baker et al. 2013). In all previous studies of adult bonefish summarized in the beginning of this report, individuals were captured using hook-and-line, presumably during daylight hours, thereby limiting the temporal scope of our 'snapshots.' The rate of digestion of organisms is usually unknown (Hyslop 1980), which can potentially overestimate the presence of slow-digesting taxa while underestimating the presence of fast-digesting taxa. In this study, the importance of soft-bodied prey, such as worms and mollusks, are likely underestimated. While the effective biomass of worms and mollusks (shells excluded), was relatively small in this study, highly abundant small fish (esp. killifish, gobies) may be difficult to differentiate in gut content analyses and do represent significant fauna biomass. The importance of these small fishes due to their abundance (as a source of predator attraction and cumulative energetic gain), may well be underestimated. Additionally, due to limitations in the sampling scope and scale of the study conducted by Crabtree et al. (1999), seasonal and habitat-related variability (e.g., bottom type, water depth) in bonefish diet is unknown. Despite (and acknowledging) these biases, gut content analysis likely remains the most efficient, and cost-effective method for describing bonefish diet. Care must be taken, however, to consider these limitations when using gut contents to infer prey availability. In this study, we presented analyses of both 'prey taxa' and other abundant taxa (including taxa not documented as important bonefish prey), and both should be considered. Stable isotope analysis (particularly, $\delta^{13}C$ and $\delta^{34}S$) would likely be an effective tool to strengthen our understanding of trophic pathways in this system (Fry et al. 1999, Chasar and Chanton 2005).

Data analyses

In addition to the study design limitations described previously, our decadal comparisons were largely limited by our inability to obtain raw data files from earlier studies. We were not able to obtain any raw data from the 1980s effort. Data presented here are from (geometric) means reported in the project final report (Powell et al. 1987). Comparison of these means with the same data reported by Matheson et al. (1999), who reported seagrass parameters and fauna taxonomic groupings as box-and-whisker plots, raised question about the nature of the 1980s data (suggesting high variability). Obtaining these raw data would allow us to use parametric statistics to quantitatively detect and describe decadal variation in both fauna communities and seagrass parameters.

Abundance data were obtained from the 1990s effort, but no fauna biomass data were available from either the 1980s or 1990s studies. Analysis of biomass data will help to better elucidate patterns in prey abundance. For example, while cleaner shrimp (Hippolytidae) were often the most abundant taxon at a study site in a given sampling event, their biomass relative to larger species is relatively insignificant (e.g., a single pink shrimp). Additionally, with seagrass beds serving as nursery grounds for many species, a variety of size classes (with small size classes often in great abundance) can be found; the collective biomass of these different size classes can be significant. We continue to work with earlier PIs to acquire all of these data.

Other factors potentially contributing to the bonefish decline

Although this study does not rule out a change in food resources as the underlying problem, it is unlikely that it is the only factor contributing to the bonefish decline. Numerous studies have demonstrated that physical stress caused by the exhaustive exercise of ’playing' a fish while angling can result in sub-lethal metabolic and osmotic disruption in the fish (e.g., Mazeaud et al. 1977) that are typically more exaggerated than in higher vertebrates (Wells et al. 1986, Wood 1991, Kieffer 2000). This weakened and compromised state could open the individual up to predation or diseases. Repeated capture of the same fish could result in cumulative impacts that lead to mortality (Muoneke and Childress 1994) which could be compounded by any large mortality that may have occurred during the 2010 low temperature event (i.e., fewer fish under consistent fishing pressure). This point emphasizes the argument that under a diminished population, any mortality to bonefish as a result of a catch and release fishery becomes more problematic. Furthermore, repeated disturbance from increased boating activity on the flats and in adjacent basins and channels in Florida Bay could exacerbate this problem or be a source of dispersal or decline unto itself. An aerial survey of boater use in the marine waters of Everglades National Park (Ault et al. 2008b) indicated that boater use had increased 2.5 times between the 1970s and 2007.

There are myriad possible disturbance factors associated with water quality and contaminants. Unmonitored toxins in both the sediment and water column could be altering health, behavior and reproduction in bonefish and/or their prey base. For example, endocrine disruptors may be affecting the reproductive activity in any part of this food web including the bonefish themselves. Pesticides, including chemicals used for mosquito control, could likewise be having the same effect. Biocides, such as endosulfans, have been found in Florida Bay with likely origins in the south Dade County agricultural areas where they were widely used. Runoff from these agricultural lands into Florida Bay via the Everglades has been well established. Atmospheric deposition of contaminates such as methyl mercury could also cause these types of problems. Bioamplification, the process by where toxins are more highly concentrated the higher in food chain an organism is can exacerbate the effect of contaminants. The sheer diversity of possibilities with contaminants makes this line of investigation daunting but bioassays of bonefish tissue for many of the common or most likely culprits may be instructive.

Factors associated with greenhouse gases may also be problematic for bonefish. Ocean acidification could potentially be having a profound effect on the bonefish invertebrate prey base. Increasing variability in temperatures could also be a factor, as colder continental air masses push through the Keys, stimulating mortality events. These temperatures may be ameliorated by high tidal exchange in Biscayne Bay and the Lower Keys, but may be lethal in the relatively low tidal exchange, expansive shallow-water Florida Bay region. Other populations of bonefish in the Bahamas, Caribbean and Central America would not be as severely affected by these cold fronts.

Florida Bay differs from other regions of the Keys and many other regions of the Caribbean where bonefish are present in that historically the area functioned as an estuary. Drainage of the Everglades, alterations to hydrology, and continued stresses on water resources have shifted the ecosystem to where it has become a saline lagoon, experiencing periods of extended hypersalinity. Altered salinity and hydrologic parameters within Florida Bay have been documented to have measurable negative impacts on vertebrate fauna and their habitats (Lorenz 2013). It is possible that bonefish have fallen into the ecological cascade that has resulted from diversion of fresh water which increased hydrologic stresses on primary then secondary producers, culminating in population declines at the top of the food web.

Prior to the commercial fishing ban in Florida Bay in 1985, many thousands of bonefish were killed as bycatch. Although ranked as the least likely cause of the recent declines in bonefish by the angler survey (out of a choice of seven possibilities), the implications of this period of high mortality on future generations of this long-lived species cannot be entirely discounted.

Next Steps

Based on the findings from this study, we suggest a number of options to facilitate the primary objective of BTT's *Florida Keys Initiative*: determining potential causes for declines in bonefish population and enacting measures to correct problems and restore the population.

First, we recommend expanding the temporal scope of this prey-based study in order to increase replication and to match the temporal scale of previous studies (Powell et al. in the 1980s and Matheson et al. in the 1990s). This increased sample size would help us to better understand the high inter-annual variability in prey communities we observed in 2012. Furthermore, increasing the spatial scale of this study through replication at additional sites in Biscayne Bay and the Lower Keys would strengthen our confidence in inferring regional variation in prey abundance from observed inter-site variation.

In addition to biological analyses, chemical analyses of the Florida Keys' shallow seagrass beds could provide further insight into the cause of the recent declines in the population of bonefish in the Upper Keys. Synthetic chemicals found in the environment are often resistant to environmental degradation, and thus, persist in the environment for long periods of time. Chemicals of concern include pesticides, PCBs, dioxins, petroleum hydrocarbons, and polycyclic aromatic hydrocarbons (PAHs), among others. Many of these chemicals have been classified as endocrine disruptors, whereas others are likely to reduce reproductive success of affected organisms. Chemical analysis of sediment and seagrass samples from areas experiencing declines in bonefish populations for the presence of synthetic chemicals could be compared to control sites in which bonefish populations have remained more stable over the past decades.

Qualitative, as well as quantitative, data on the presence of persistent, synthetic chemicals could be obtained via extractions of these chemicals from sediment and seagrass samples followed by analysis using high performance liquid chromatography mass spectrometry (HPLC/MS).

The benefit of marine protected areas for bonefish within the Florida Keys region should be addressed in great detail. This can be accomplished through engagement in habitat protection initiatives through management options within Everglades National Park and the Florida Keys National Marine Sanctuary. Disturbance from boats and other water activities within shallow-water habitat should also be examined with regards to providing safe habitat for bonefish within the Keys. Zoning changes, such as non-combustion or pole/troll areas, offer management options to ensure bonefish safety and should be considered paramount when judging such areas against arguments for boating access.

We encourage the continued engagement on the management of bonefish through state fisheries regulations. Special interest given to bonefish in recent years by fisheries managers, both within the State and National Park Service, has lead toward progress on conservation efforts of bonefish through legislation. However, we feel advocating for state regulations that would prohibit removal of bonefish from the water during catch and release fishing should be promoted. Such a rule would ensure the best possible management practice for bonefish while still allowing for a fishery. Bonefish appear to have declined and are continuing to decline to levels at which extreme management options such as this should be considered to ensure their survival.

Finally we suggest support of Everglades Restoration initiatives, such as further bridging of the Tamiami Trail and completion of the second phase of the C-111 Project, at the Federal and State level which will lead toward increased freshwater flows and more estuarine conditions in Florida Bay.

ACKNOWLEDGEMENTS

We are grateful to the following guides and anglers who offered their knowledge and assistance with selecting sampling sites in Florida Bay, Biscayne Bay and the Lower Keys: Bob Branham, Charlie Causey, Brian Esposito, John Kipp, Mark Krowka, Diego Rouylle, Rick Ruoff, and Dexter Simmons. Equipment preparation/maintenance and field assistance was provided by April Geisler, Mike Kline, Mac Stone, Adam Chasey and Allie Curtze. We thank Ed Matheson for providing us with data from the 1990s Florida Bay fauna study and Bill Loftus for assistance with fish identification.

This research was funded by the Bonefish Tarpon Trust (BTT) as part of the BTT Keys Initiative. We thank the members of and contributors to BTT for their support (financial, political, and otherwise) of ecological research aimed at preserving the Florida Keys bonefish population and the ecosystem they depend on.

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Table 1. Sampling dates and coordinates of the start and end of each study transect corresponding to each sampling event.

			Transect Start		Transect End	
Site	Season	Date	LAT (N)	LON (W)	LAT (N)	LON (W)
9-Mile	Dry	3/20/12	24°56’04.20”	80°51’01.30”	24°56’03.70”	80°50’59.10”
	Early-wet	7/3/12	24°56’04.26”	80°51’01.25”	24°56’03.41”	80°50’58.62”
	Late-wet	10/1/12	24°56’03.50”	80°51’01.10”	24°56’03.89”	80°50’58.58”
Buchanan	Dry	3/6/12	24°55’06.40”	80°45’17.30”	24°55’05.50”	80°45’14.70”
	Early-wet	7/13/12	24°55’06.49”	80°45’17.16”	24°55’05.75”	80°45’14.96”
	Late-wet	10/3/12	24°55’06.32”	80°45’17.67”	24°55’05.87”	80°45’14.87”
Cross	Dry	3/2/12	25°00’26.86”	80°34’47.85”	25°00’26.30”	80°34’44.90”
	Early-wet	7/11/12	25°00’26.85”	80°34’47.64”	25°00’26.13”	80°34’45.01”
	Late-wet	10/2/12	25°00’26.67”	80°34’47.57”	25°00’25.92”	80°34’44.83”
Sands	Dry	3/9/12	25°29’25.00”	80°11’01.90”	25°29’26.70”	80°10’59.20”
	Early-wet	7/10/12	25°29’23.53”	80°11’01.59”	25°29’24.46”	80°10’59.05”
	Late-wet	10/4/12	25°29’22.65”	80°11’00.96”	25°29’24.93”	80°10’59.19”
Sawyer	Dry	3/12/12	24°44’41.30”	81°34’0510”	24°44’39.00”	81°34’04.60”
	Early-wet	7/6/12	24°44’41.37”	81°34’05.07”	24°44’38.90”	81°34’04.76”
	Late-wet	10/5/12	24°44’41.27”	81°34’05.27”	24°44’38.77”	81°34’04.85”

Table 2. Incidence (%I), relative abundance (%RA) and total abundance (N) of all invertebrate taxa collected in this study.

		%I	%RA	N
Mollusca				
Gastropoda	gastropod (unidentified)	43.3	0.9	85
Astraea phoebia	long-spined star shell	3.3	<0.1	3
Bulla striata umbilicata	common Atlantic bubble	1.1	<0.1	2
Cerithium atratum	dark cerith	1.1	<0.1	1
Cerithium leburneum	ivory cerith	4.4	<0.1	4
Cerithium spp.	cerith spp.	1.1	<0.1	1
Columbella rusticoides	rusty dove shell	2.2	<0.1	3
Diodora spp.	keyhole limpet	2.2	<0.1	2
Fasciolaria spp.	tulip shell	5.6	0.1	6
Jaspidella jaspidea	jasper dwarf olive	3.3	<0.1	3
Lima pellucid	Antillean file shell	2.2	<0.1	2
Lithopoma tectum americanum	American star shell	6.7	0.1	6
Natica spp.	moonsnail	1.1	<0.1	1
Prunum apicinum	common Atlantic marginella	43.3	0.8	77
Turbo castanea	chestnut turban	30	1.8	176
Bivalvia	bivalve (unidentified)	36.7	0.6	56
Arcopsis adamsi	Adams' miniature ark	1.1	<0.1	1
Argopecten gibbus	calico scallop	6.7	0.1	12
Argopecten irradians	bay scallop	2.2	<0.1	3
Carditamera floridana	broad-rimmed cardita	20	0.5	50
Chione cancellata	cross-barred venus	35.6	1.1	109
Pteria colymbus	Atlantic wing oyster	7.8	0.1	8
Tellina iris	iris tellin	1.1	<0.1	1
Tellina lineate	rose petal tellin	1.1	<0.1	1
Tellina similis	candy stick tellin	7.8	0.1	8
Cephalopoda				
Octopoda	octopus (unidentified)	1.1	<0.1	1
Annelida	worm (unidentified)	77.8	6.1	594
Arthropoda				
Xiphosura				
Limulus polyphemus	Atlantic horseshoe crab	1.1	<0.1	2

		%I	%RA	N
Crustacea	crustacean (unidentified)	17.8	0.2	20
Stomatopoda	mantis shrimp	13.3	0.2	15
Amphipoda	amphipod	26.7	0.7	69
Isopoda	isopod	50	1.5	149
Alpheidae	snapping shrimp	86.7	17.7	1733
Hippolytidae	hippolytid shrimp	91.1	23.0	2247
Palaemonidae	palaemonid shrimp	75.6	7.4	723
Penaeidae	penaeid shrimp	45.6	0.9	90
	shrimp (unidentified)	67.8	2.1	209
Paguroidea	hermit crab	63.3	2.4	238
Majidae	spider crab	64.4	6.2	603
Xanthidae	mud crab	96.7	19.2	1882
Portunidae	swimming crab	20	0.2	24
	crab (unidentified)	1.1	<0.1	2
Panulirus argus	Caribbean lobster	5.6	0.1	5
Echinodermata				
Asteroidea	sea star	32.2	0.5	46
Ophiuroidea	brittlestar	68.9	3.7	357
Holothuroidea	sea cucumber	64.4	1.5	149
TOTAL INVERTEBRATES				9,779

Table 3. ANOVA of the abundance and biomass of common invertebrate taxa among study sites in 2012 (Buchanan, Cross, 9-Mile, Sands, Sawyer).

		Abundance			Biomass		
Common name	Taxon name	$F_{4,10}$	P	R^2	$F_{4,10}$	P	R^2
Snails	Gastropoda	**6.14**	**0.009**	**0.711**	**4.41**	**0.026**	**0.638**
Bivalves	Bivalvia	**4.96**	**0.018**	**0.665**	**7.12**	**0.006**	**0.740**
Worms	Annelida	0.89	0.503	0.263	0.45	0.774	0.151
Echinoderms	Echinodermata	**6.34**	**0.008**	**0.717**	2.40	0.119	0.490
Mantis shrimp	Stomatopoda	2.69	0.093	0.518	**4.44**	**0.026**	**0.640**
Amphipods	Amphipoda	**3.61**	***0.046**	**0.590**	1.26	0.350	0.334
Isopods	Isopoda	0.94	0.479	0.273	1.47	0.282	0.370
Snapping shrimp	Alpheidae	**147.48**	**<0.001**	**0.983**	**42.48**	**<0.001**	**0.944**
Cleaner shrimp	Hippolytidae	**5.45**	**0.014**	**0.686**	**4.48**	**0.025**	**0.642**
Grass shrimp	Palaemonidae	**41.56**	**<0.001**	**0.943**	**72.21**	**<0.001**	**0.967**
Penaeid shrimp	Penaeidae	1.97	0.176	0.440	0.93	0.487	0.270
Hermit crabs	Paguridae	**16.69**	**<0.001**	**0.870**	**10.85**	**0.001**	**0.813**
Spider crabs	Majidae	**30.66**	**<0.001**	**0.925**	**38.77**	**<0.001**	**0.939**
Mud crabs	Xanthidae	**87.41**	**<0.001**	**0.972**	**9.56**	**0.002**	**0.793**
Swimming crabs	Portunidae	2.86	0.081	0.534	3.30	0.057	0.569
Total Crustaceans		**8.33**	**0.003**	**0.769**	**40.10**	**<0.001**	**0.941**
Total Invertebrates		**9.56**	**0.002**	**0.793**	**20.10**	**<0.001**	**0.889**

* model is significant ($P \leq 0.05$) but pairwise comparisons (Tukey) reveal no significant relationships.

Table 4. Incidence (%I), relative abundance (%RA) and total abundance (N) of all fishes collected in this study.

Species		%I	%RA	N
Abudefduf saxatilis	sergeant major	1.1	0.1	1
Anarchopterus criniger	fringed pipefish	26.7	5.2	59
Atherinomorus stipes	hardhead silverside	2.2	2.7	30
Blenniidae	blenny (unidentified)	2.2	0.2	2
Chasmodes saburrae	Florida blenny	2.2	0.3	3
Cosmocampus albirostris	whitenose pipefish	3.3	0.3	3
Cosmocampus elucens	shortfin pipefish	7.8	0.6	7
Ctenogobius stigmaturus	spottail goby	4.4	0.8	9
Cyprinodon variegatus	sheepshead minnow	1.1	0.1	1
Diodon holocanthus	porcupine puffer	1.1	0.1	1
Eucinostomus spp.	Mojarra	11.1	1.1	12
Floridichthys carpio	goldspotted killifish	5.6	0.8	9
Gobiosoma bosc	naked goby	1.1	0.1	1
Gobiosoma ginsburgi	seaboard goby	1.1	0.1	1
Gobiosoma robustum	code goby	65.6	15.4	174
Haemulidae	grunt (unidentified)	13.3	1.3	15
Hippocampus zosterae	dwarf seahorse	18.9	2.2	25
Lagodon rhomboides	Pinfish	15.6	1.7	19
Lucania parva	rainwater killifish	37.8	24.5	277
Lutjanus griseus	gray snapper	2.2	0.2	2
Lutjanus synagris	lane snapper	1.1	0.1	1
Micrognathus spp.	pipefish (unidentified)	22.2	4.8	54
Microgobius gulosus	clown goby	1.1	0.1	1
Myrophis punctatus	speckled worm eel	4.4	0.4	4
Ogilbia cayorum	Key brotula	5.6	0.9	10
Opsanus beta	gulf toadfish	86.7	25.5	288
Paraclinus fasciatus	banded blenny	35.6	5.2	59
Paraclinus marmoratus	marbled blenny	7.8	0.7	8
Scaridae	parrotfish (unidentified)	3.3	0.3	3
Stephanolepis spp.	Filefish	4.4	0.4	4
Syngnathus floridae	dusky pipefish	2.2	0.4	4
Syngnathus louisianae	chain pipefish	1.1	0.1	1
Syngnathus scovelli	gulf pipefish	1.1	0.1	1
Syngnathus spp.	pipefish (unidentified)	3.3	0.4	5
Triglidae	sea robin	13.3	2.1	24
	fish (unidentified)	13.3	1.1	13
TOTAL FISH				1,131

Table 5. ANOVA of the abundance and biomass of common fishes among study sites in 2012 (Buchanan, Cross, 9-Mile, Sands, Sawyer).

		Abundance			Biomass		
Common name	Taxon name	$F_{4,10}$	P	R^2	$F_{4,10}$	P	R^2
Banded blenny	*Paraclinus fasciatus*	**3.79**	***0.040**	**0.603**	**4.12**	**0.032**	**0.622**
Code goby	*Gobiosoma robustum*	**4.67**	**0.022**	**0.651**	**3.92**	**0.036**	**0.611**
Dwarf seahorse	*Hippocampus zosterae*	**7.14**	**0.006**	**0.741**	**6.71**	**0.007**	**0.729**
Fringed pipefish	*Anarchopterus criniger*	**4.79**	**0.020**	**0.657**	**4.10**	**0.032**	**0.621**
Grunts	*Haemulon* spp.	0.71	0.604	0.221	0.79	0.559	0.240
Gulf toadfish	*Opsanus beta*	1.63	0.242	0.394	2.01	0.169	0.445
Mojarra	*Eucinostomus* spp.	0.91	0.495	0.267	1.04	0.434	0.294
Pinfish	*Lagodon rhomboids*	1.57	0.255	0.386	0.48	0.751	0.161
Pipefish	*Micrognathus* spp.	1.30	0.334	0.342	1.33	0.324	0.347
Rainwater killifish	*Lucania parva*	**23.89**	**<0.001**	**0.905**	**8.13**	**0.003**	**0.765**
Searobin	Triglidae	**43.67**	**<0.001**	**0.946**	**9.19**	**0.002**	**0.786**
Total Fish		3.07	0.069	0.551	1.25	0.353	0.332

* model is significant ($P \leq 0.05$) but pairwise comparisons (Tukey) reveal no significant relationships

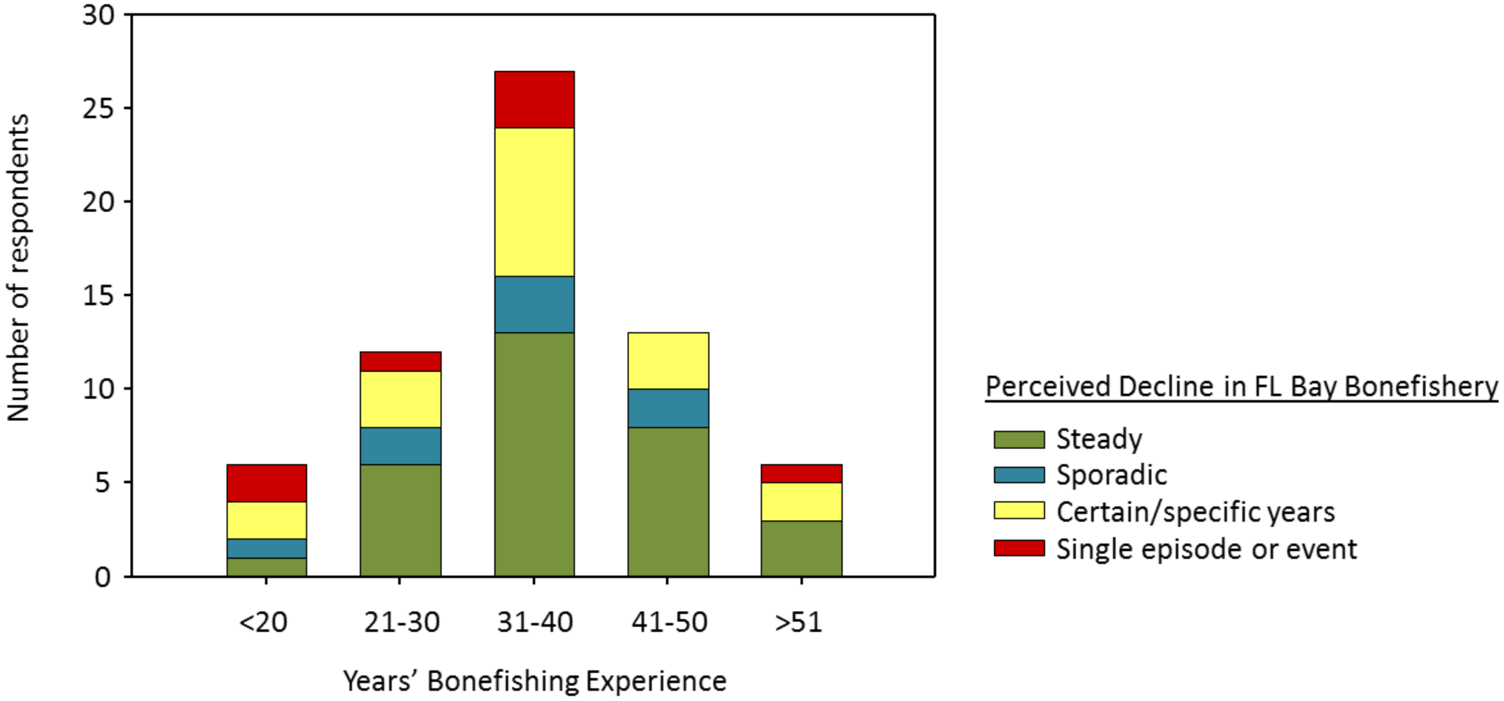

Fig. 1. Perceived characterization of the decline in the Florida Bay bonefishery as reported by respondents with varying degrees of bonefishing experience.

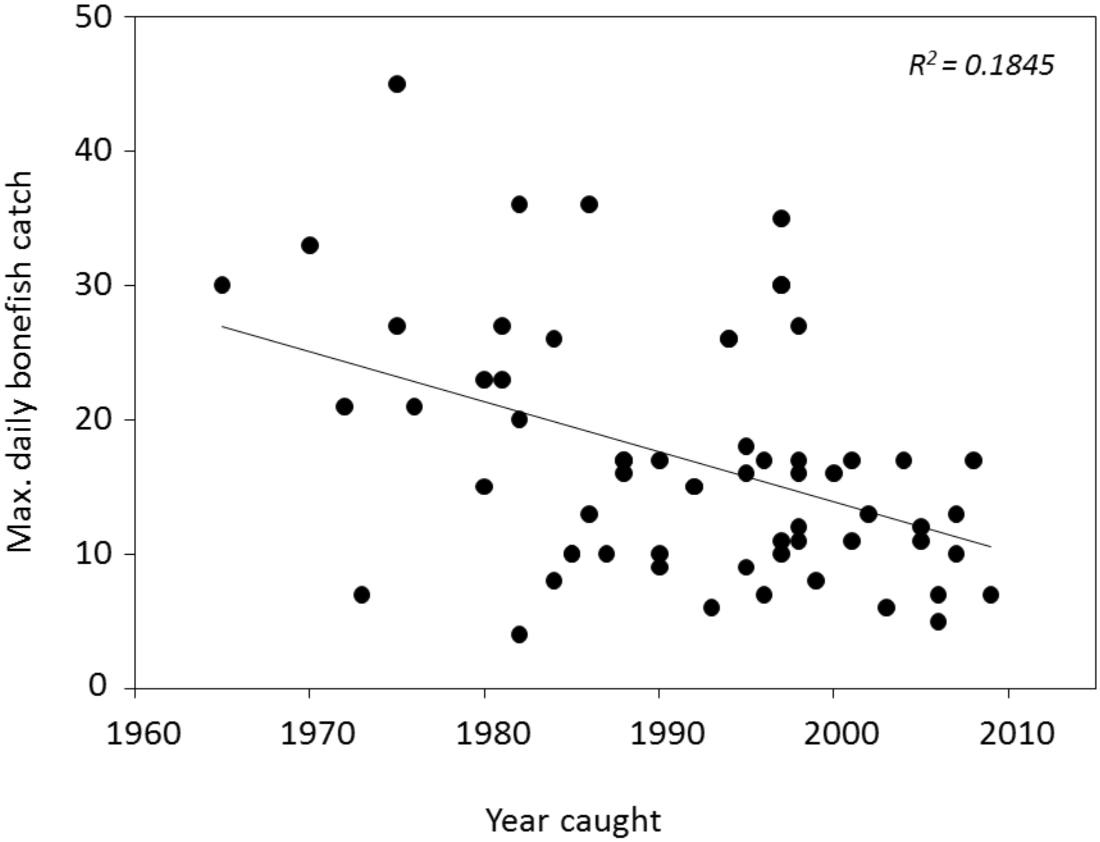

Fig. 2. Correlation between career-to-date maximum daily bonefish catch and the year caught, as reported by questionnaire respondents.

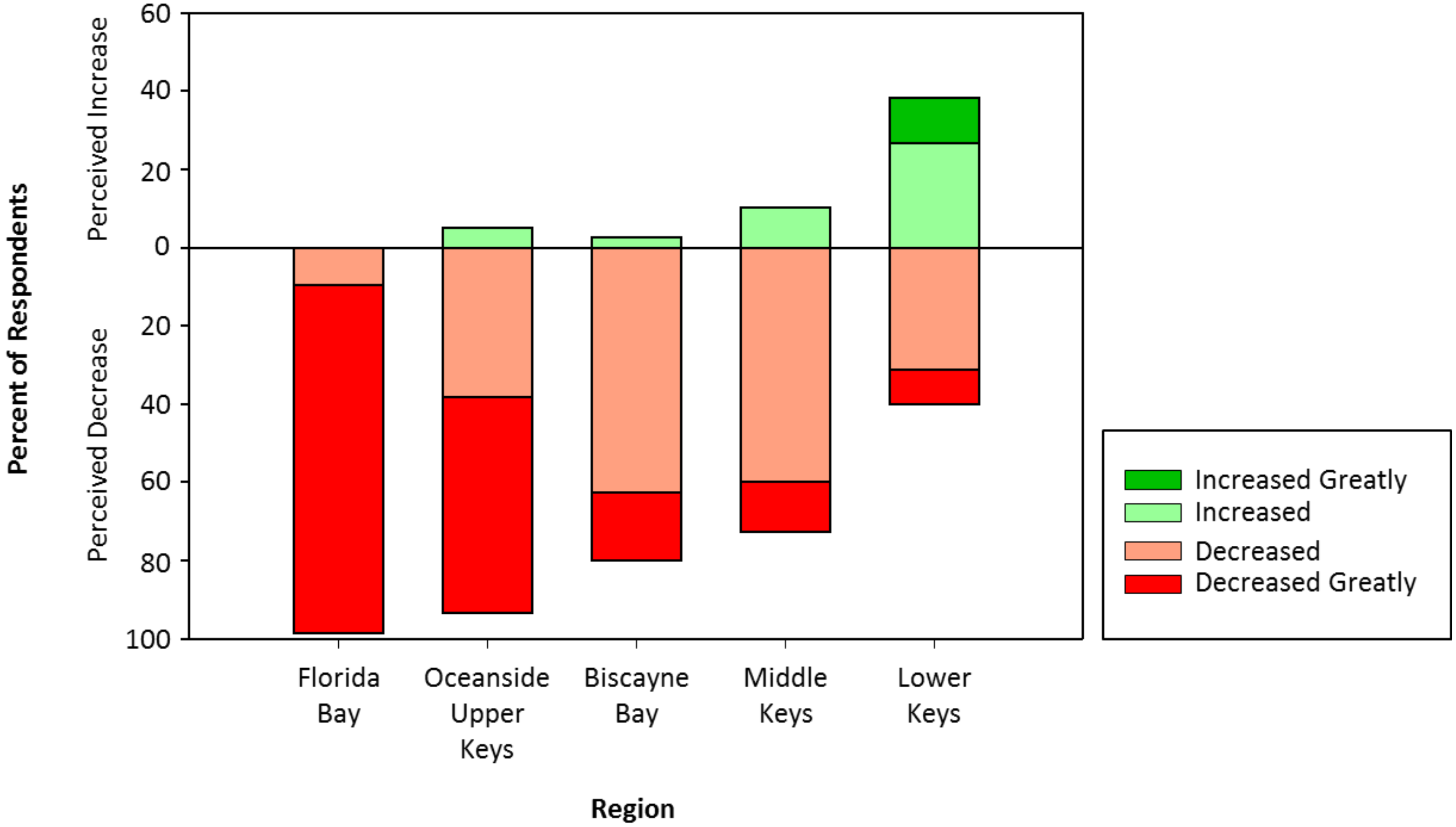

Fig. 3. Percent of questionnaire respondents reporting a perceived increase or decrease in bonefish in five South Florida regions.

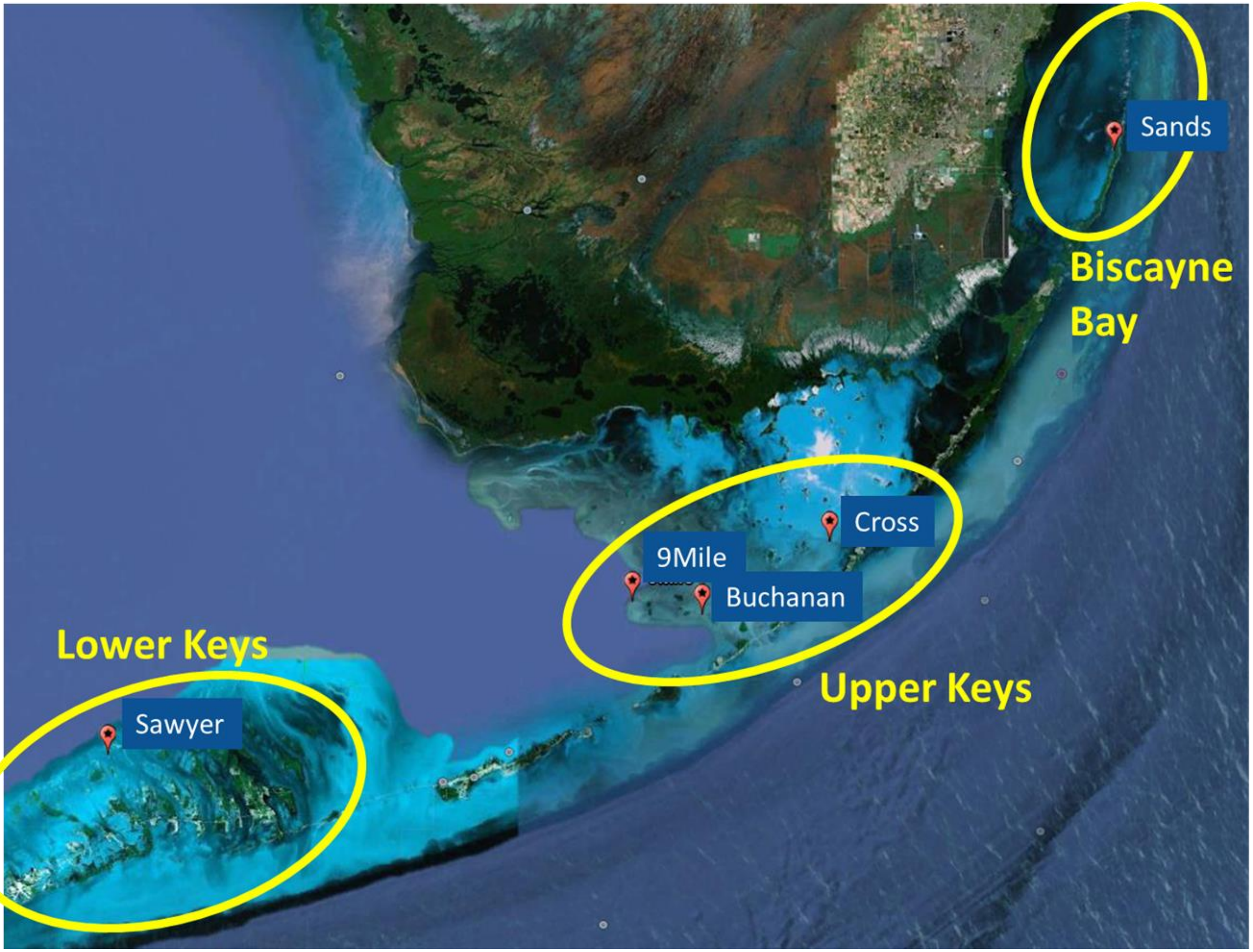

Fig. 4. Location of the five study sites in the Lower Keys, Upper Keys and Biscayne Bay. Buchanan and Cross were also sites of fish and decapod studies in the 1980s and 1990s.

Fig. 5. Location of the study site at Buchanan Bank. Red line represents the sampling transect orientation and location in July 2012.

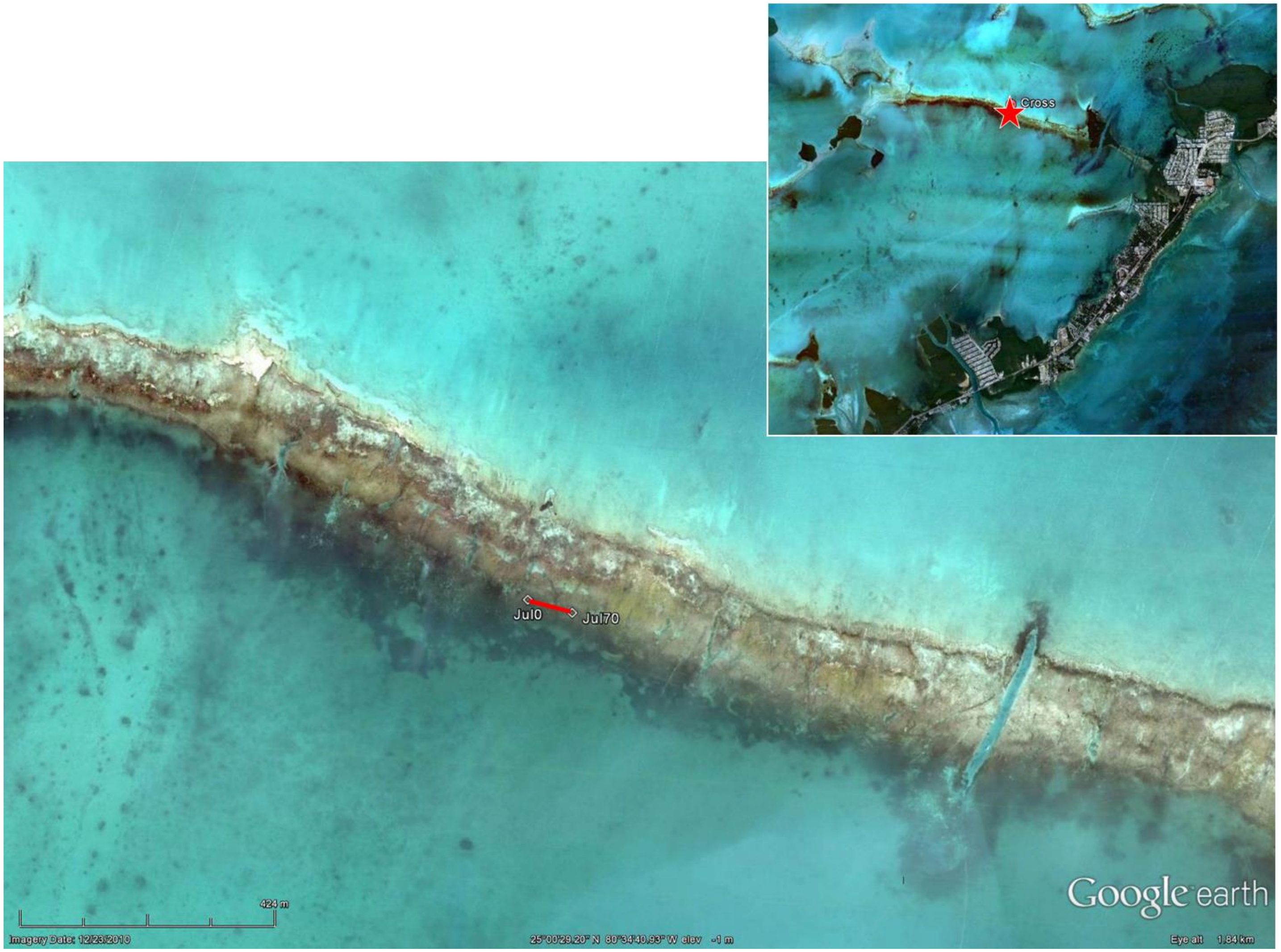

Fig. 6. Location of the study site at Cross Bank. Red line represents the sampling transect orientation and location in July, 2012.

Fig. 7. Location of the study site at 9-Mile Bank. Red line represents the sampling transect orientation and location in July, 2012.

Fig. 8. Location of the study site at Sands Cut. Red line represents the sampling transect orientation and location in July, 2012.

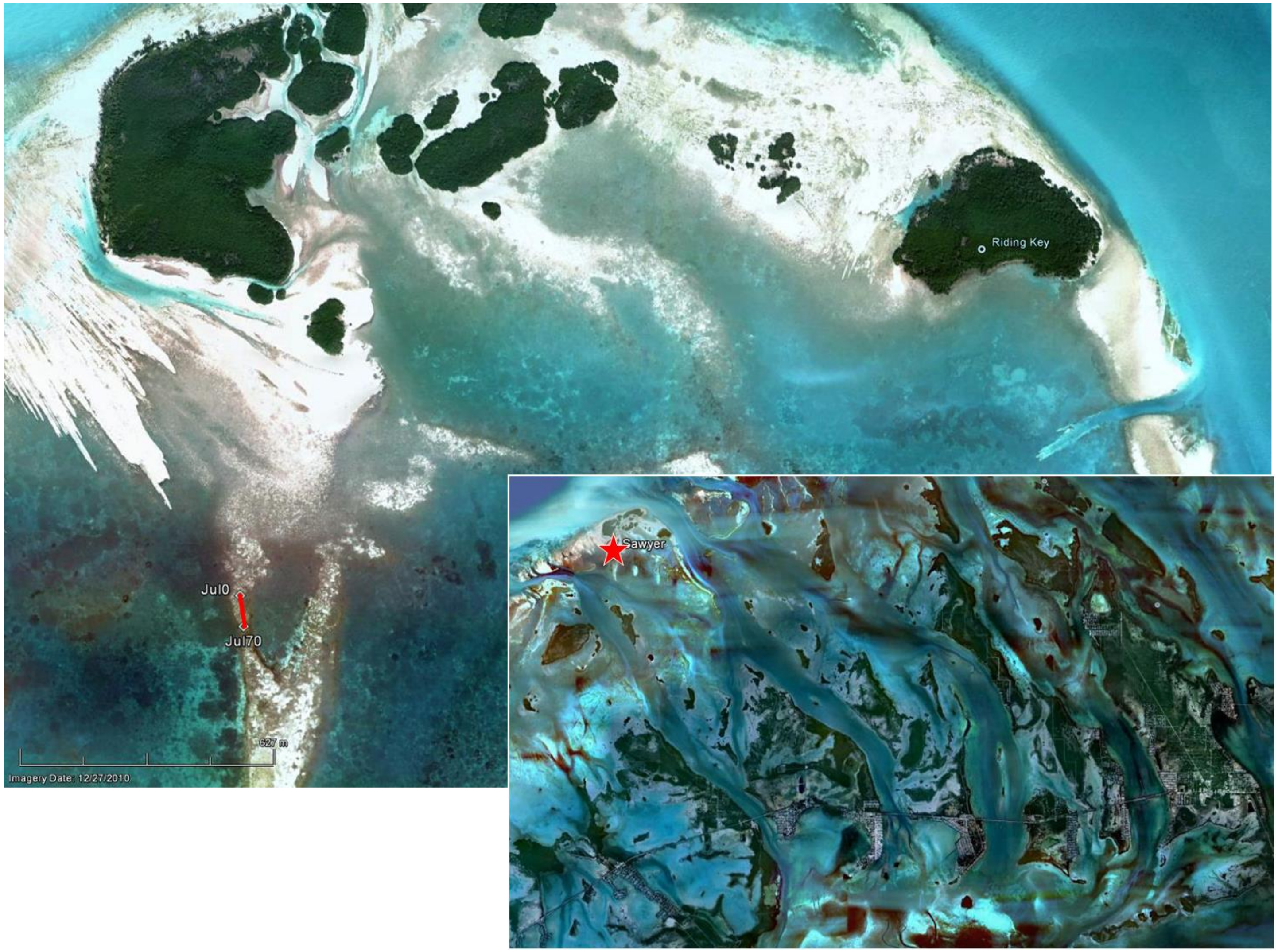

Fig. 9. Location of the study site near the Sawyer Keys. Red line represents the sampling transect orientation and location in July, 2012.

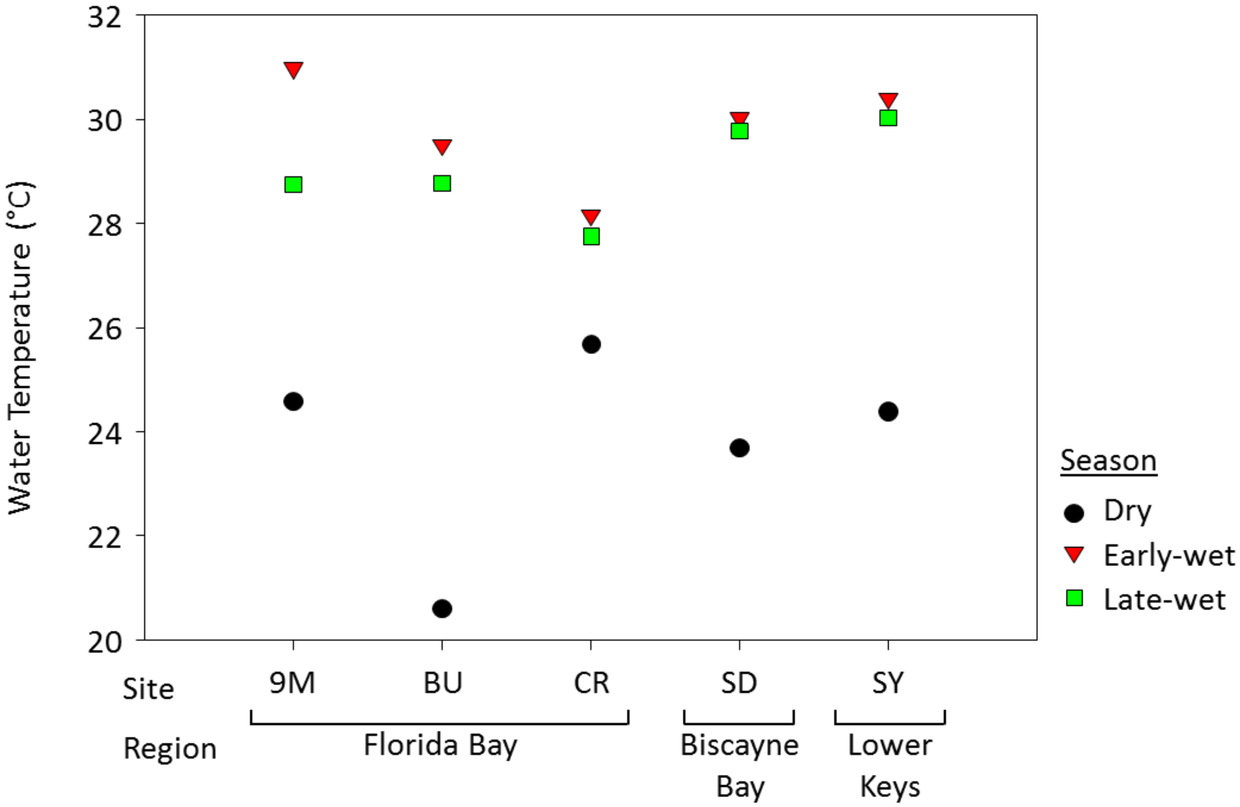

Fig. 10. Water temperature (°C) recorded at each site (9M=9-Mile, BU=Buchanan, CR=Cross, SD=Sands, SY=Sawyer) during each sampling event in this study.

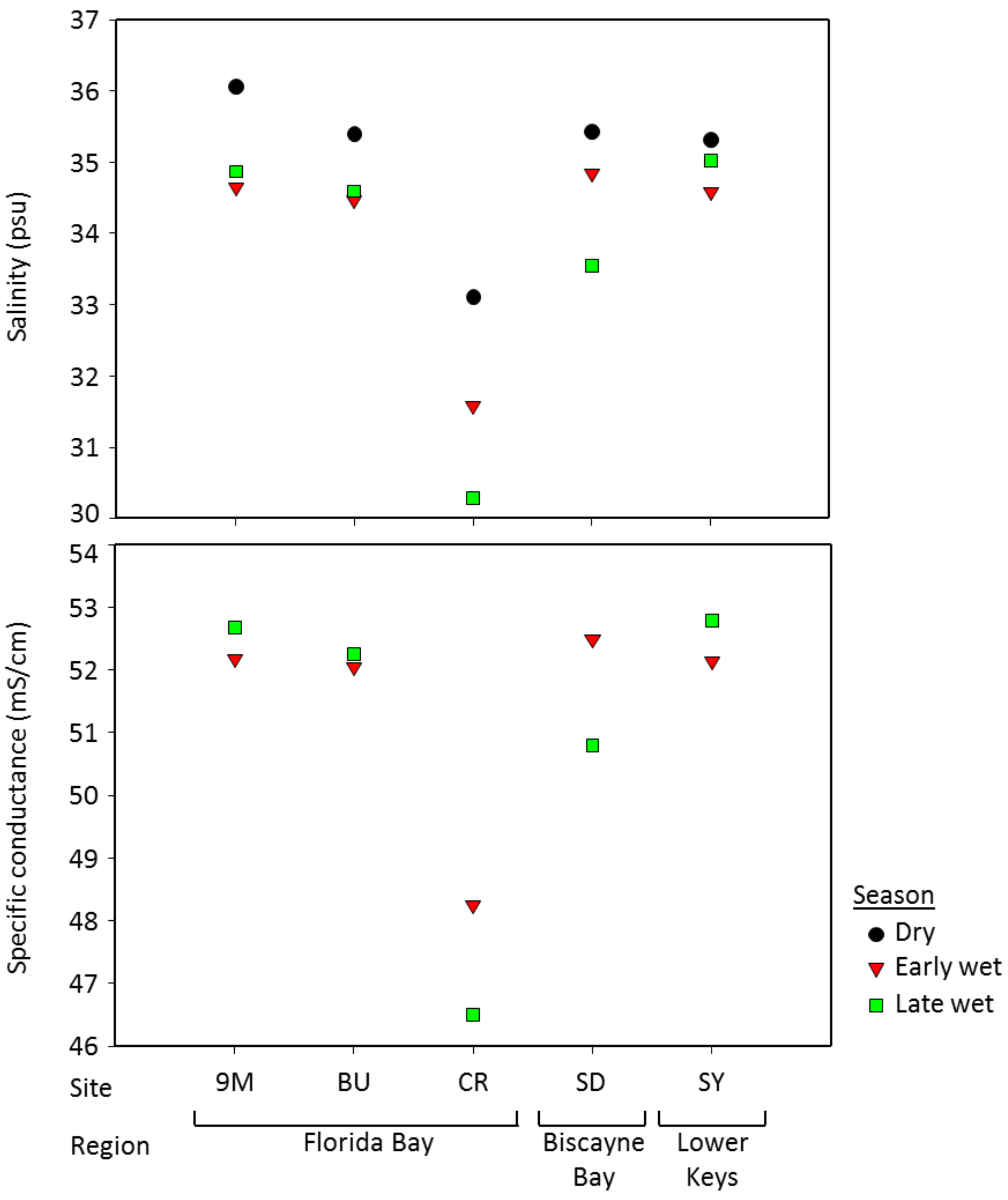

Fig. 11. Salinity (psu) and specific conductance (mS/cm) recorded at each site (9M=9-Mile, BU=Buchanan, CR=Cross, SD=Sands, SY=Sawyer) during each sampling event in this study. Specific conductance was not recorded in the dry season.

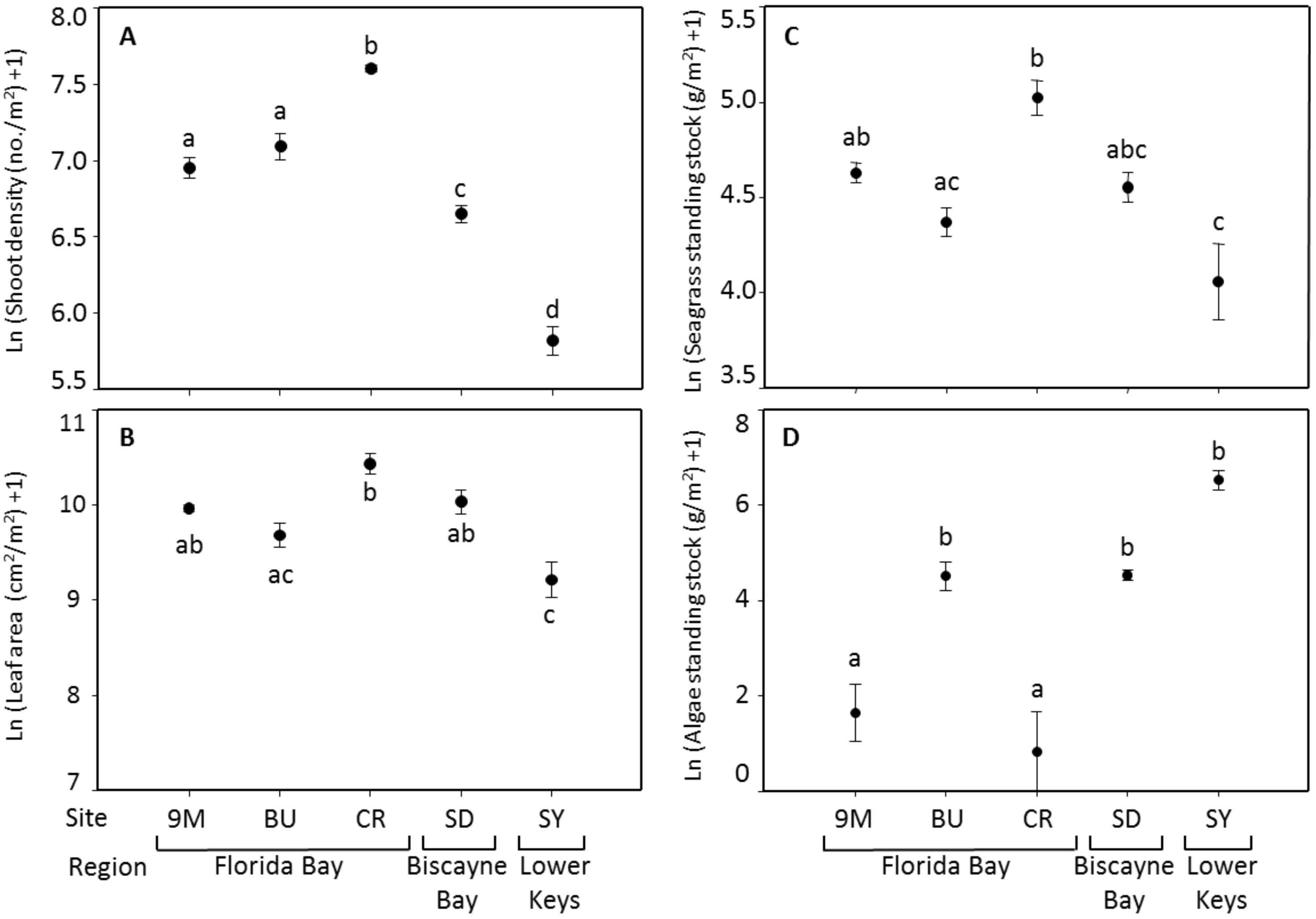

Fig. 12. Average of seagrass metrics from cores collected at each site (9M=9-Mile, BU=Buchanan, CR=Cross, SD=Sands, SY=Sawyer) in this study: A) shoot density (no./m^2), B) leaf area (cm^2/m^2), C) seagrass standing stock (g dry mass/m^2), D) calcareous algae standing stock (g dry mass/m^2). Error bars represent ±1 SE.

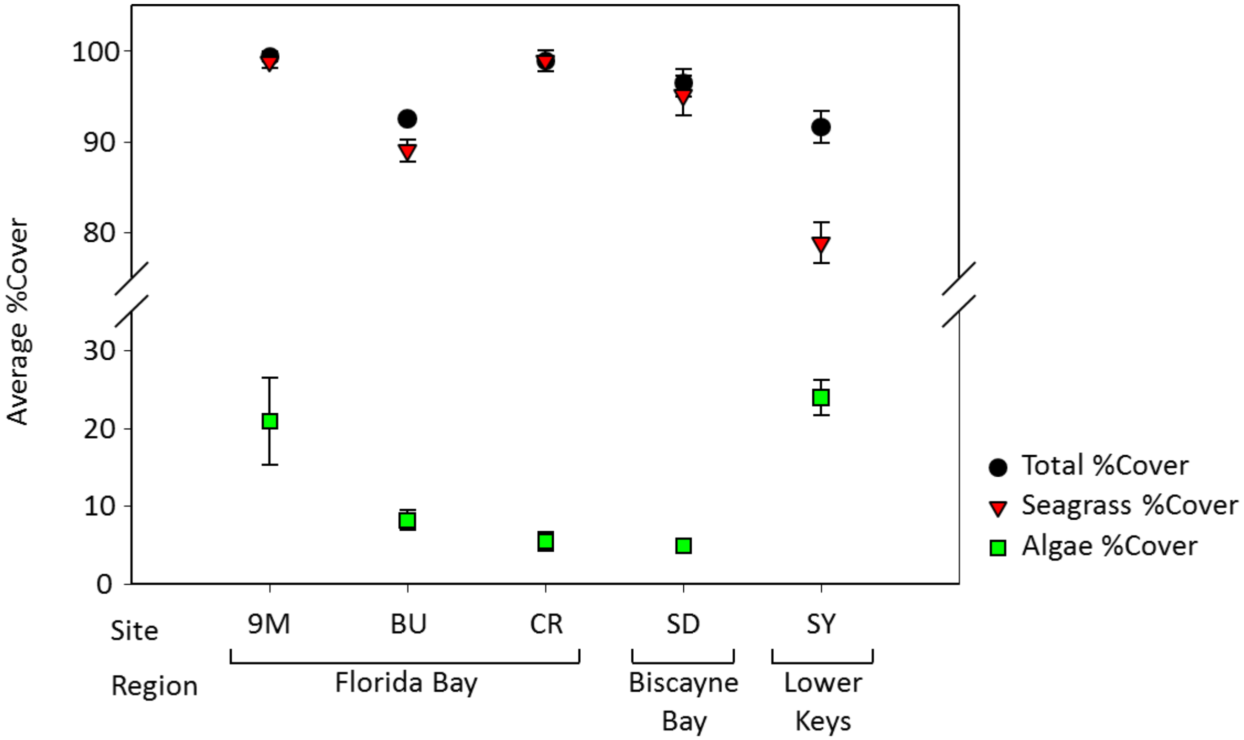

Fig. 13. Average %cover of seagrass, algae, and total %cover recorded within throw traps at each site (9M=9-Mile, BU=Buchanan, CR=Cross, SD=Sands, SY=Sawyer) in this study. Error bars represent ±1 SE.

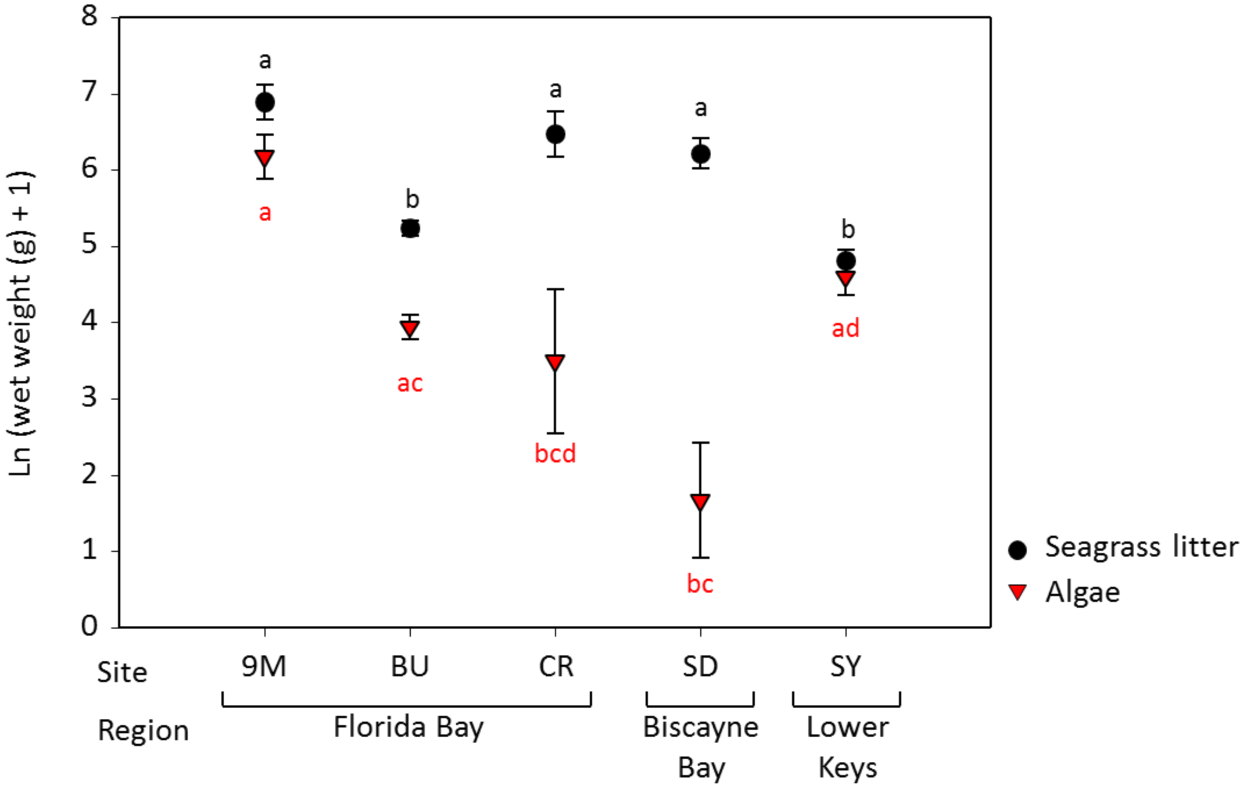

Fig. 14. Average wet weight (g; ln(y+1)-transformed) of seagrass litter and algae (drift & calcareous) collected from throw traps at each site (9M=9-Mile, BU=Buchanan, CR=Cross, SD=Sands, SY=Sawyer) in this study. For each metric, different letters indicate significant pairwise differences (Tukey P≤0.05). Error bars represent ±1 SE.

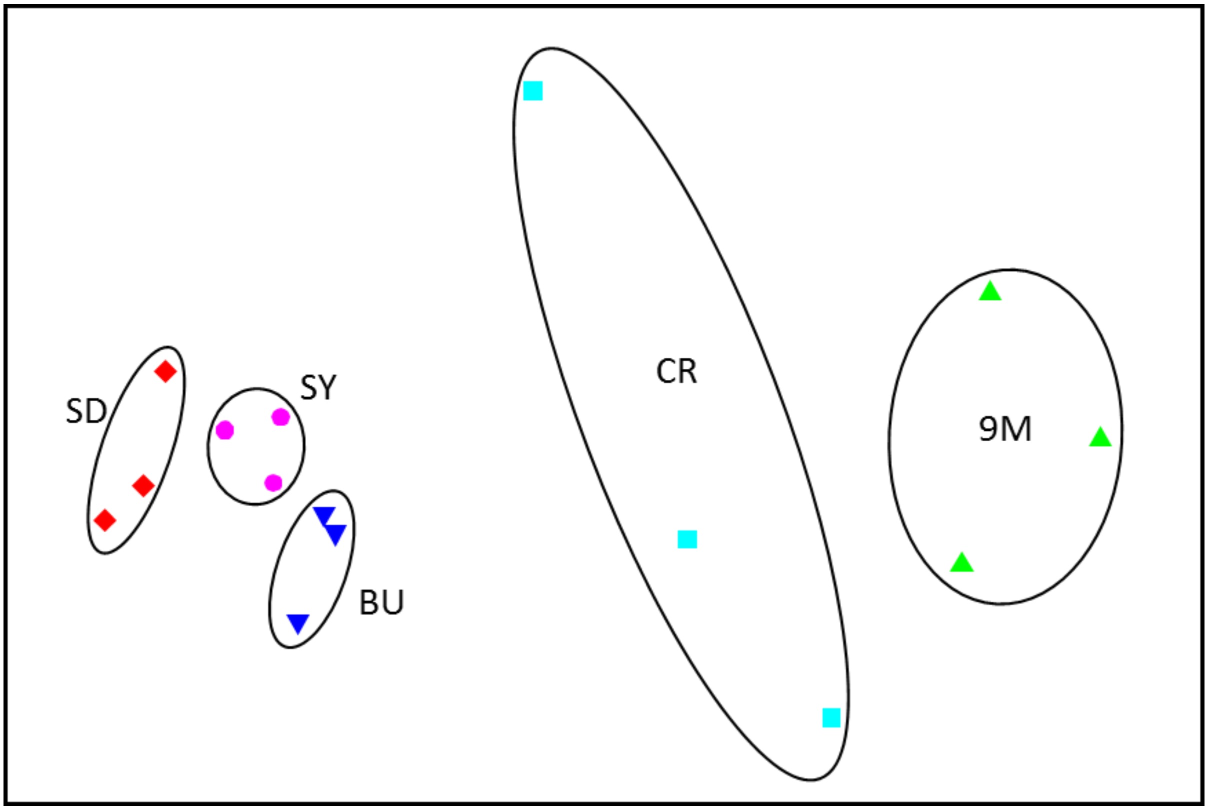

Fig. 15. NMDS of invertebrate communities at each site (9M=9-Mile, BU=Buchanan, CR=Cross, SD=Sands, SY=Sawyer) during each of three sampling events in this study (stress=0.07).

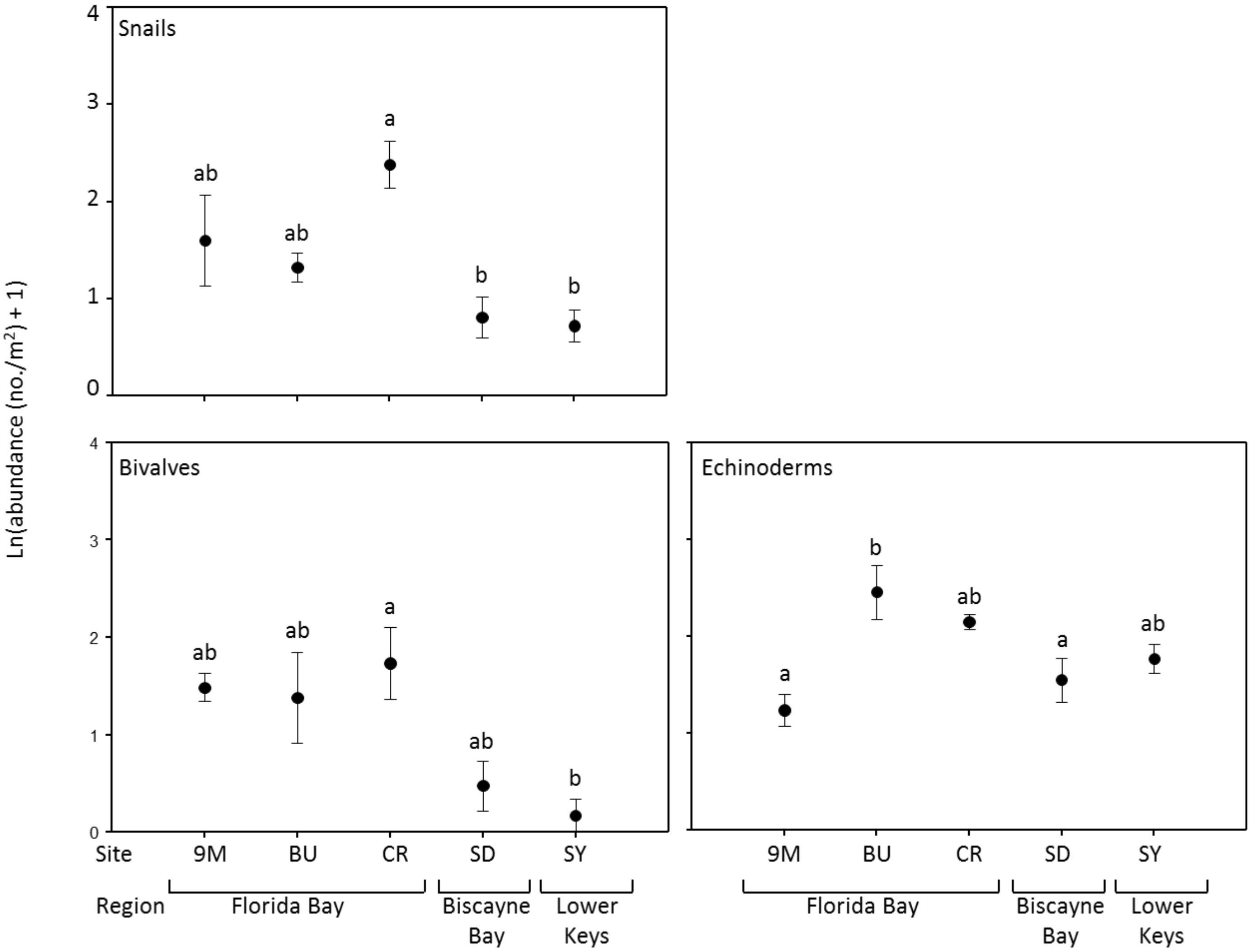

Fig. 16. Average abundance (no./m^2; ln(y+1)-transformed) of common non-crustacean invertebrates collected at each site (9M=9-Mile, BU=Buchanan, CR=Cross, SD=Sands, SY=Sawyer) in this study. For each taxon, different letters indicate significant pairwise differences (Tukey P≤0.05). Error bars represent ±1 SE.

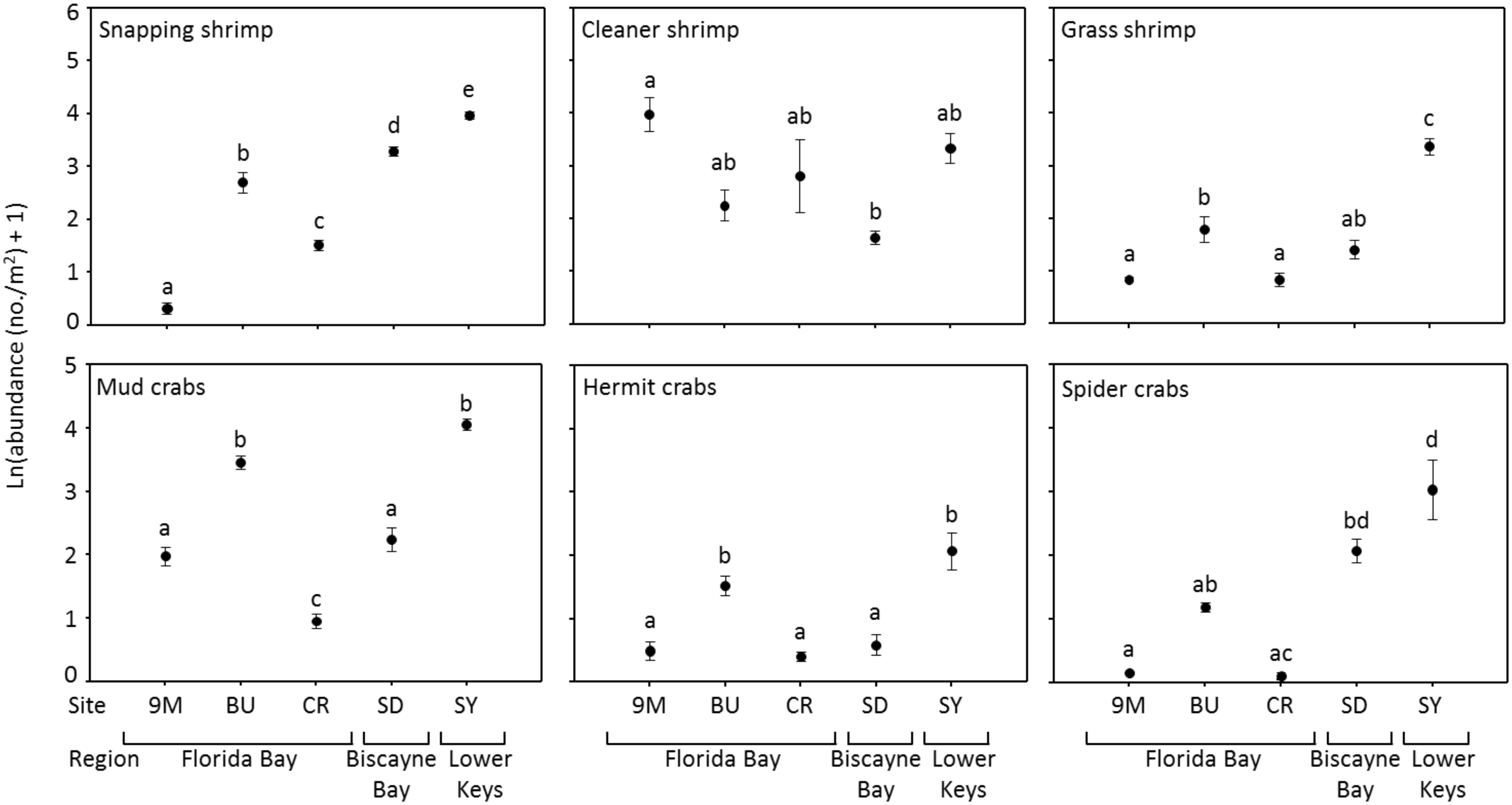

Fig. 17. Average abundance (no./m^2; ln(y+1)-transformed) of common crustacean taxa collected at each site (9M=9-Mile, BU=Buchanan, CR=Cross, SD=Sands, SY=Sawyer) in this study. For each taxon, different letters indicate significant pairwise differences (Tukey P≤0.05). Error bars represent ±1 SE.

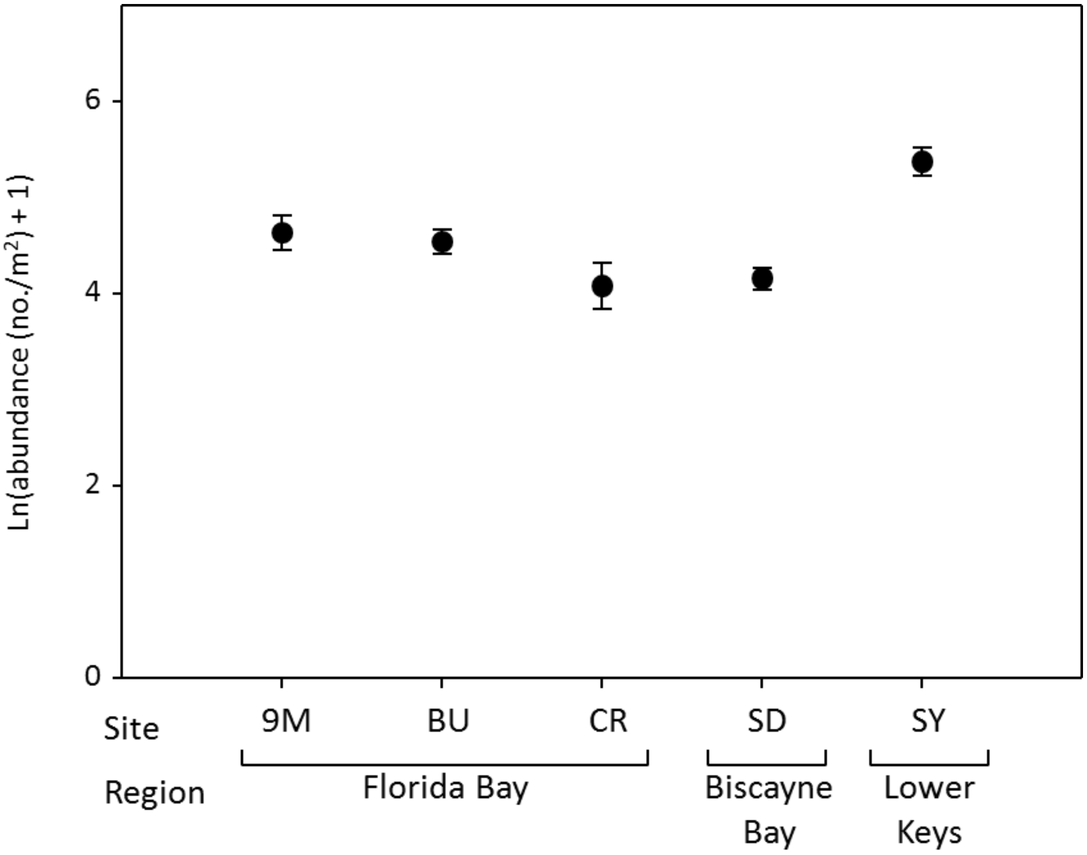

Fig. 18. Average abundance (no./m^2; ln(y+1)-transformed) of total invertebrates collected at each site (9M=9-Mile, BU=Buchanan, CR=Cross, SD=Sands, SY=Sawyer) in this study.

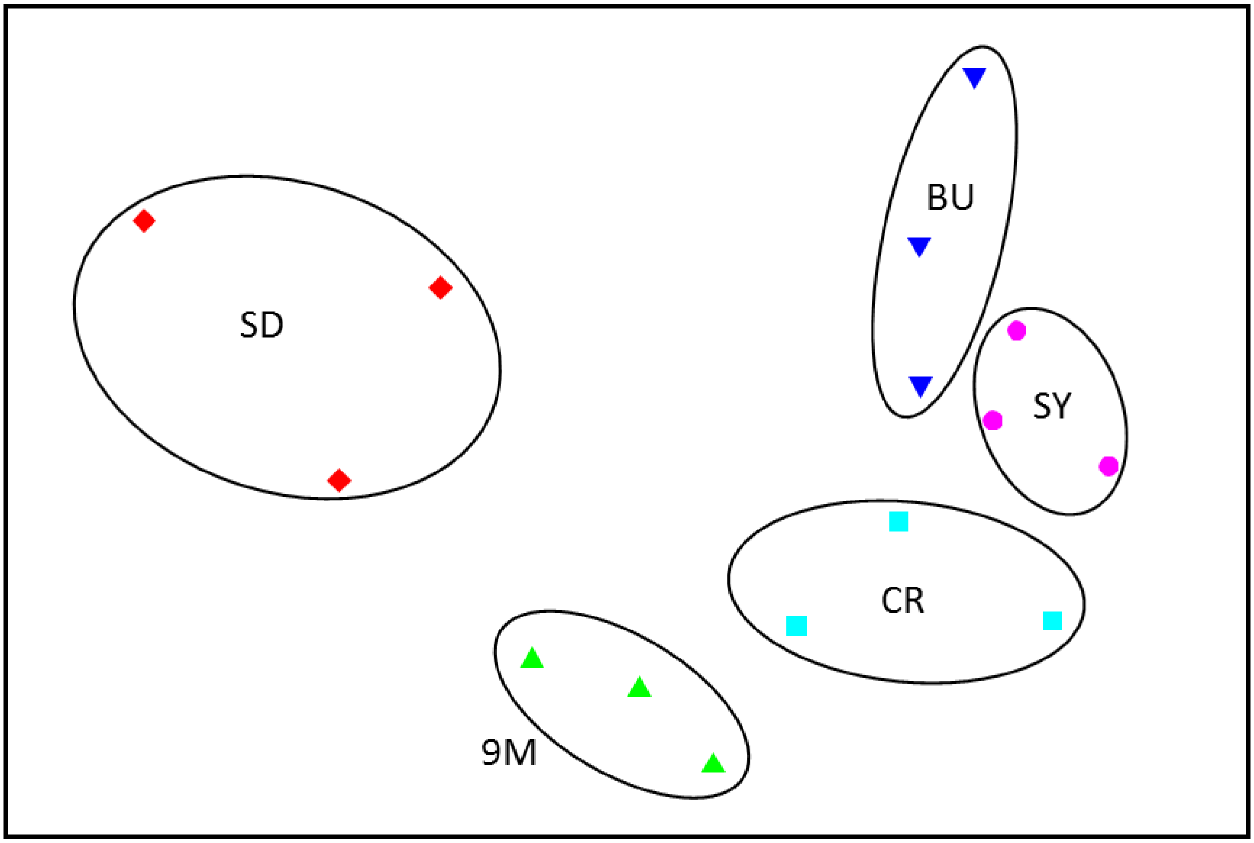

Fig. 19. NMDS of fish communities at each site (9M=9-Mile, BU=Buchanan, CR=Cross, SD=Sands, SY=Sawyer) during each of three sampling events in this study (stress=0.11).

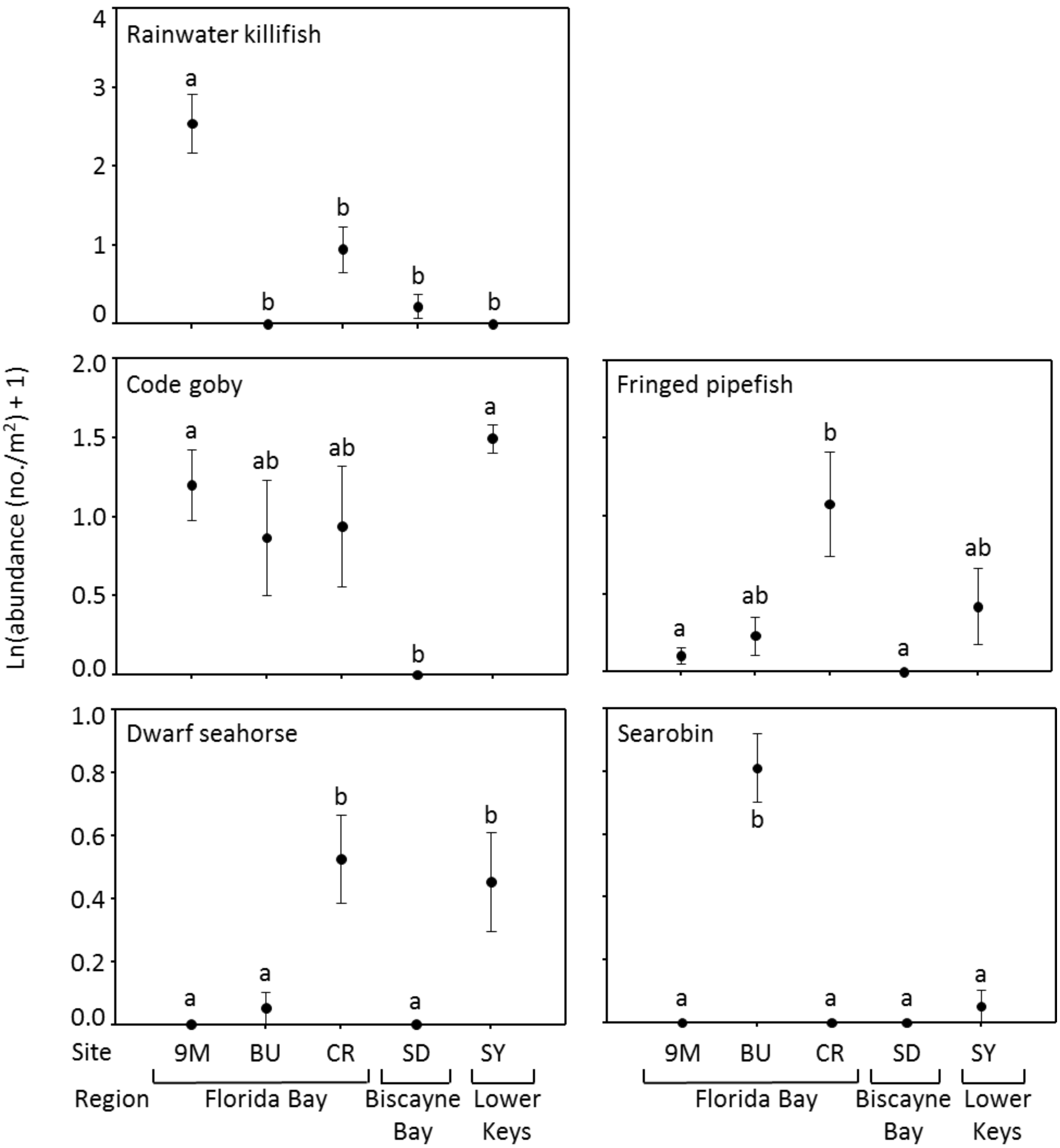

Fig. 20. Average abundance (no./m^2; ln(y+1)-transformed) of common fishes collected at each site (9M=9-Mile, BU=Buchanan, CR=Cross, SD=Sands, SY=Sawyer) in this study. For each taxon, different letters indicate significant pairwise differences (Tukey $P \leq 0.05$). Error bars represent ±1 SE.

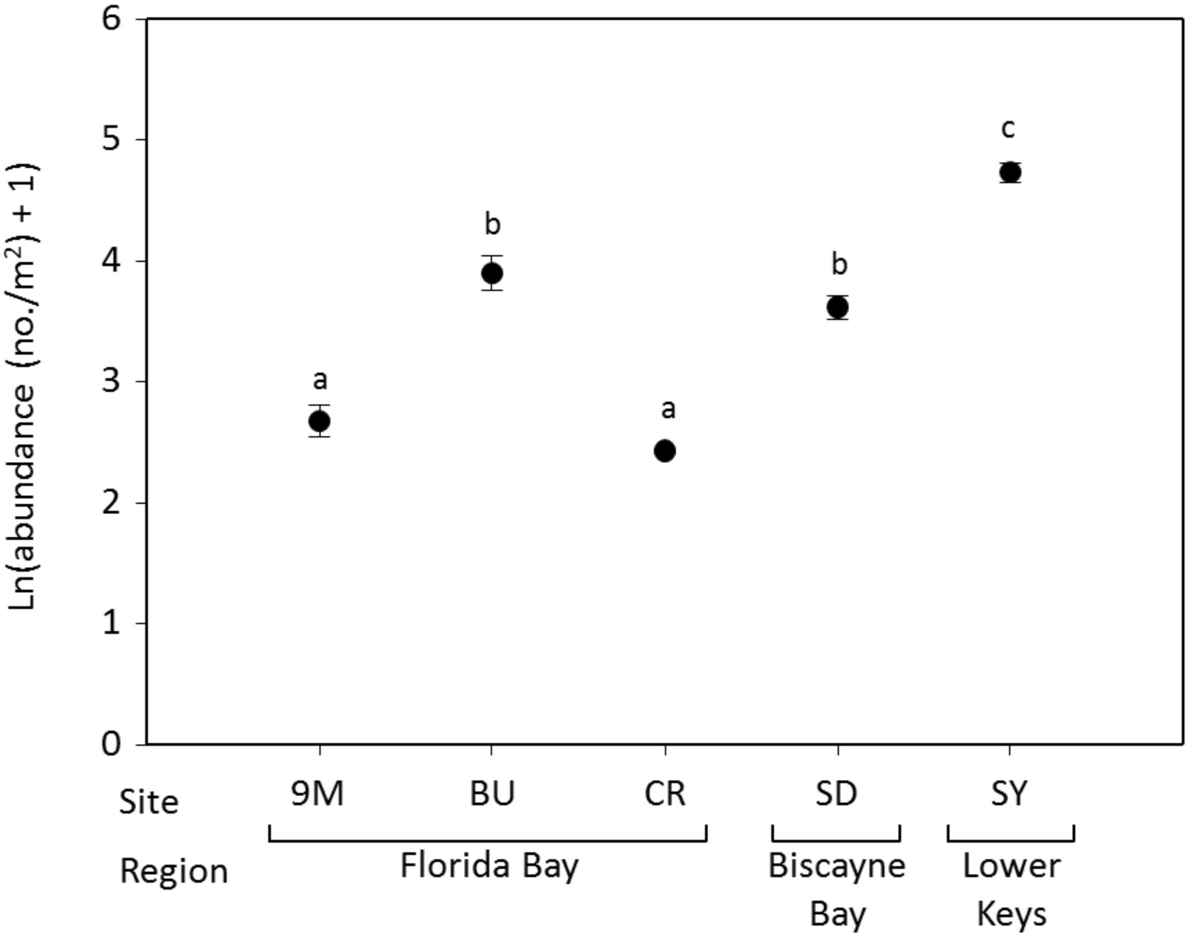

Fig. 21. Average abundance (no./m^2; ln(y+1)-transformed) of bonefish prey taxa (mud crabs, snapping shrimp, gulf toadfish, pink shrimp and blue crabs) collected at each site (9M=9-Mile, BU=Buchanan, CR=Cross, SD=Sands, SY=Sawyer) in this study. Different letters indicate significant pairwise differences (Tukey $P \leq 0.05$). Error bars represent ±1 SE.

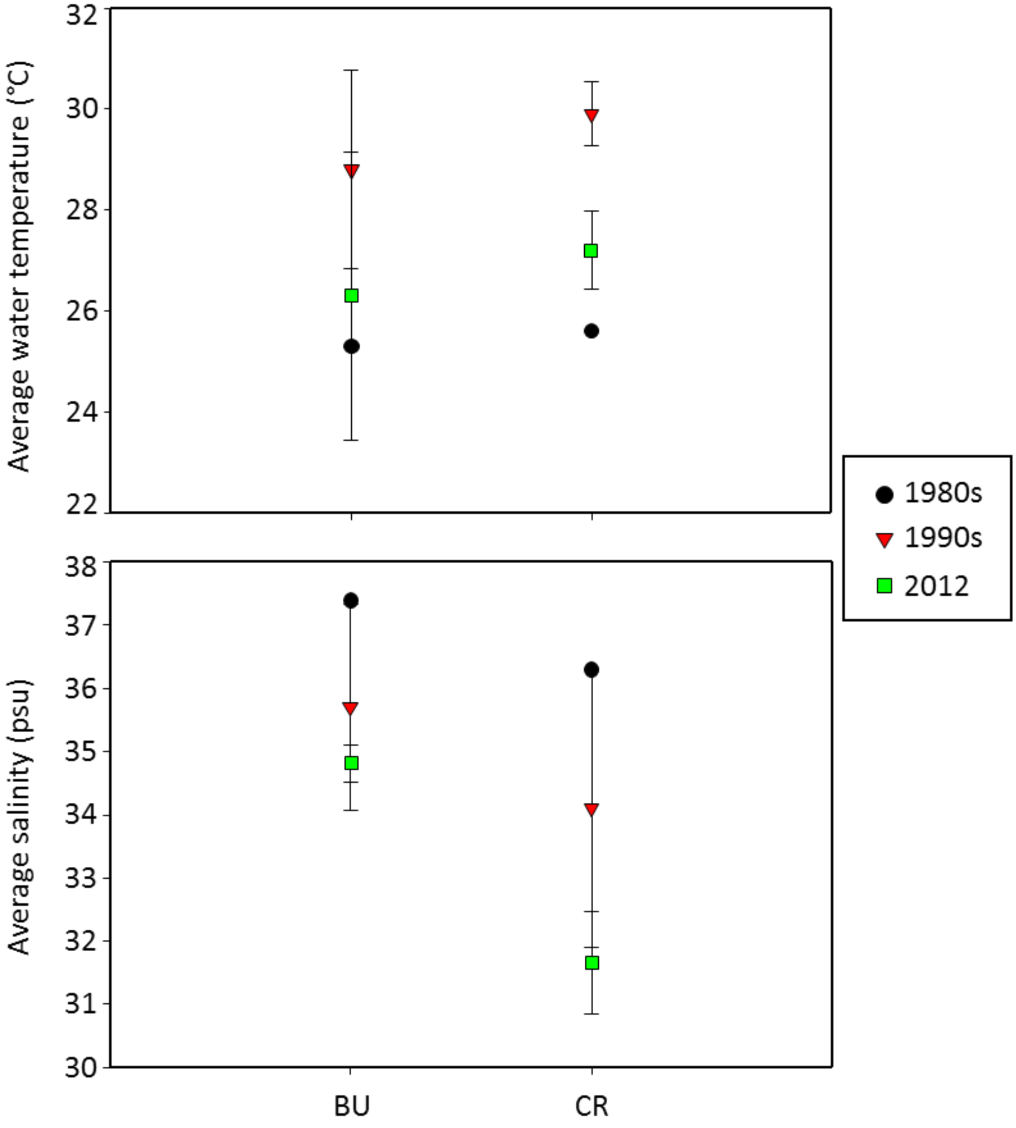

Fig. 22. Average water temperature (°C) and salinity (psu) at Buchanan (BU) and Cross (CR) during studies conducted in the 1980s (Powell et al. 1987), the 1990s (Matheson et al. 1999) and 2012 (this study). Error bars represent ±1 SE. No variance is reported for 1980s data points.

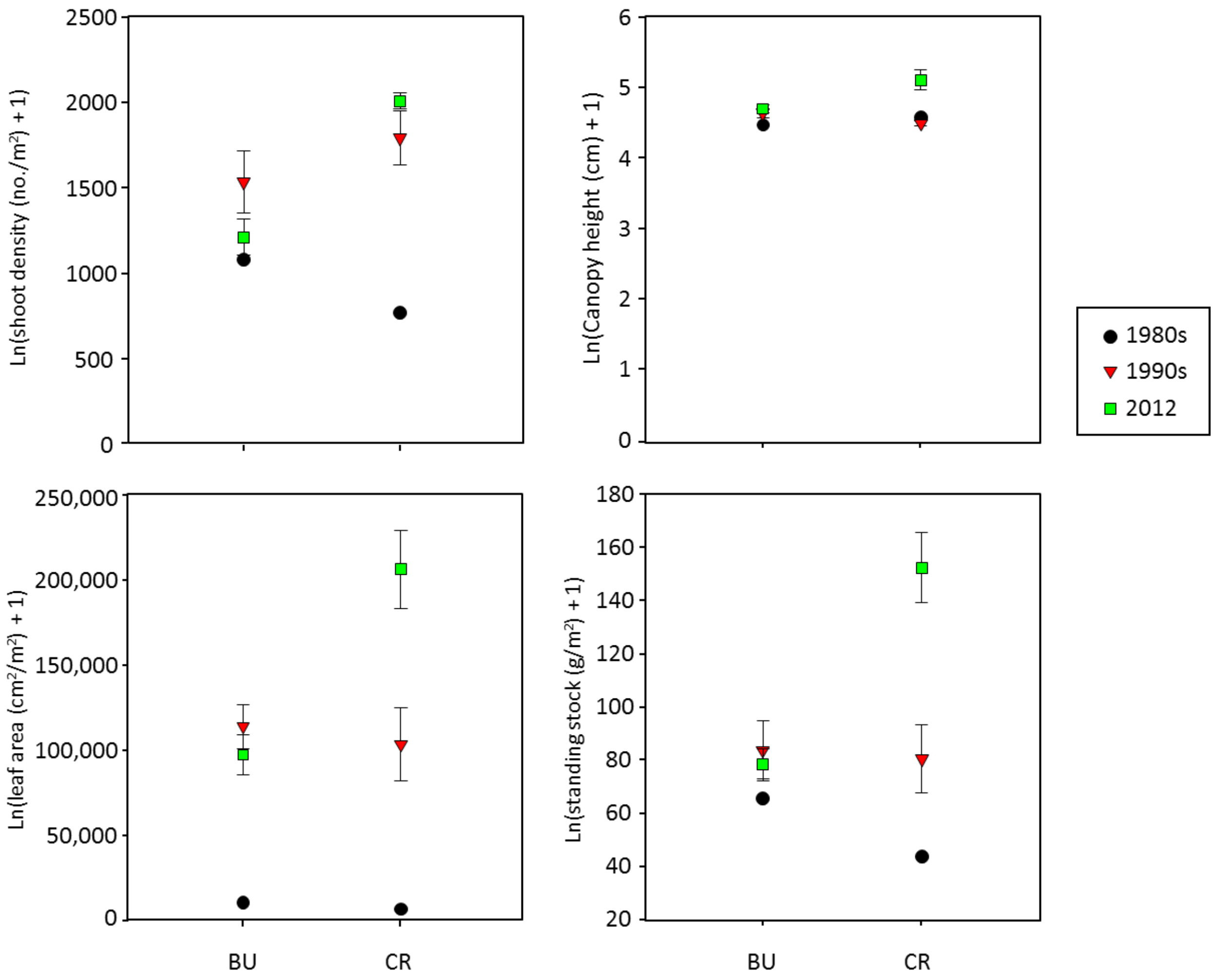

Fig. 23. Averages of seagrass metrics at Buchanan (BU) and Cross (CR) from seagrass cores collected in the 1980s (Powell et al. 1987), the 1990s (Matheson et al. 1999) and 2012 (this study). Error bars represent ±1 SE. No variance is reported for 1980s data points.

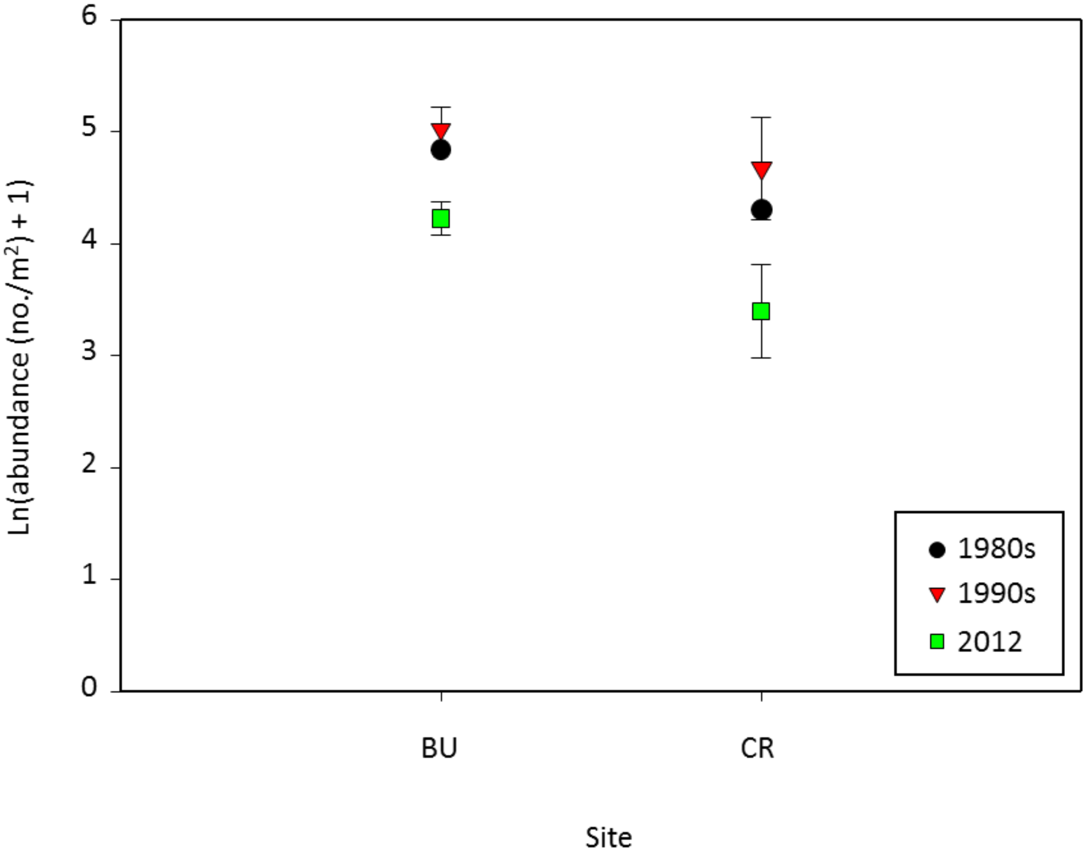

Fig. 24. Average abundance of crustaceans (no./m^2) at Buchanan (BU) and Cross (CR) during collections in the 1980s (Powell et al. 1987), the 1990s (Matheson et al. 1999) and 2012 (this study). Error bars represent ±1 SE. No variance is reported for 1980s data points.

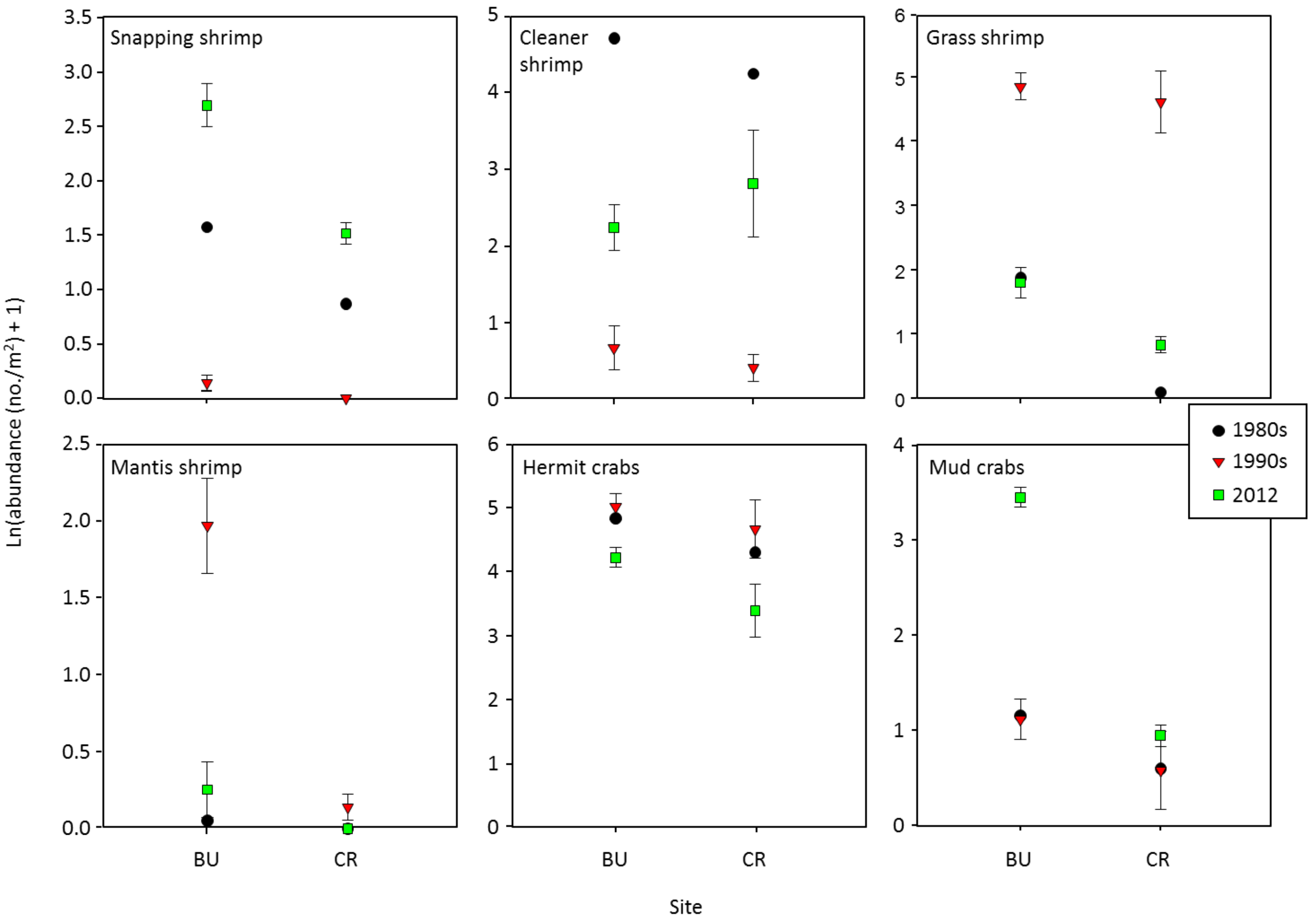

Fig. 25. Average abundance of common crustacean taxa (no./m^2) at Buchanan (BU) and Cross (CR) during collections in the 1980s (Powell et al. 1987), the 1990s (Matheson et al. 1999) and 2012 (this study). Error bars represent ±1 SE. No variance is reported for 1980s data points.

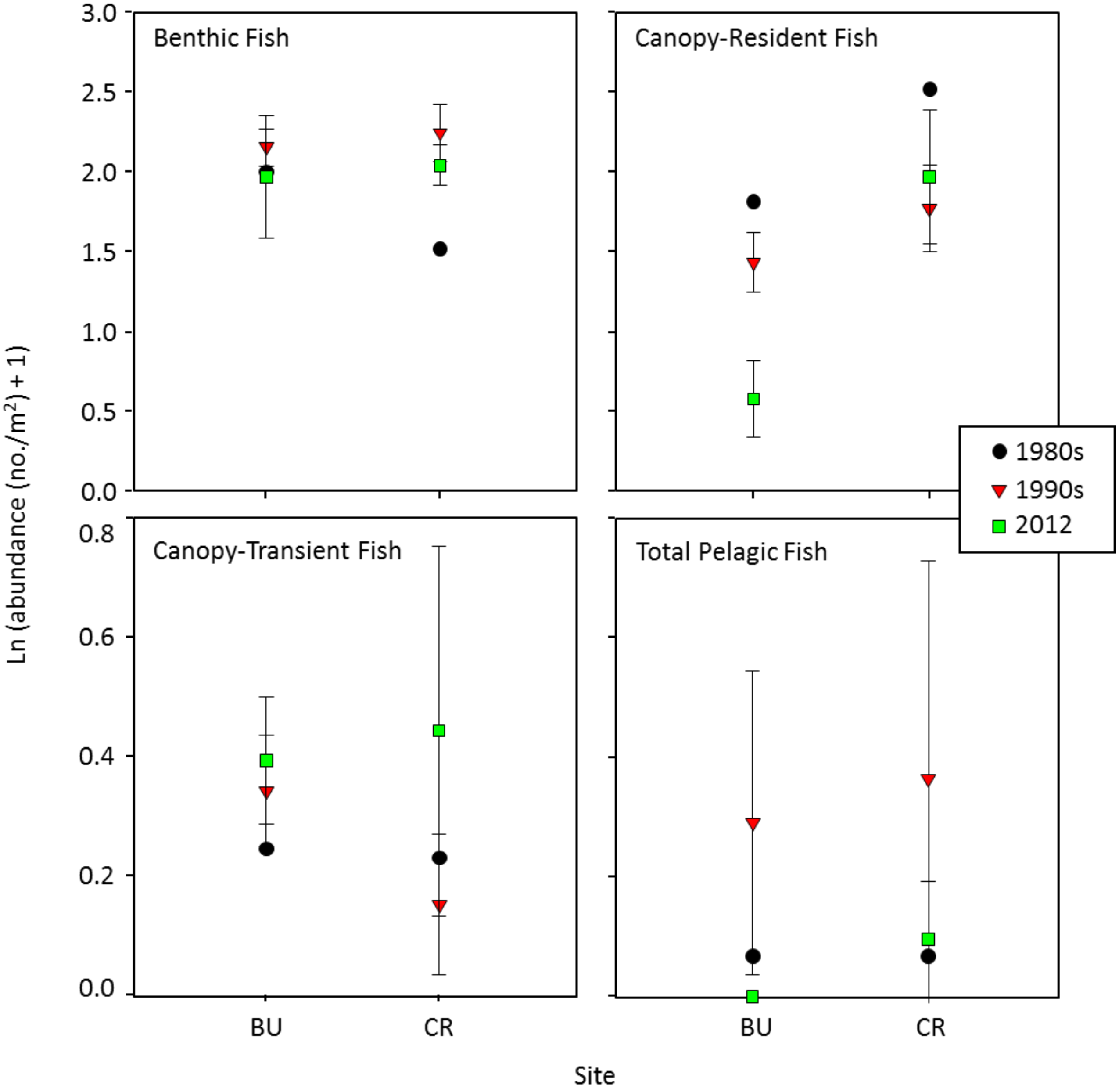

Fig. 26. Average abundance of fish (no./m^2) at Buchanan (BU) and Cross (CR) during collections in the 1980s (Powell et al. 1987), the 1990s (Matheson et al. 1999) and 2012 (this study). Ecological groupings follow those of and described by Matheson et al. (1999). Error bars represent ±1 SE. No variance is reported for 1980s data points.