# GRAZING EFFECTS OF HERBIVOROUS FISHES AND JUVENILE GREEN TURTLES (*CHELONIA MYDAS*) ON MACROALGAL COMMUNITIES

by

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A Dissertation Submitted to the Faculty of

The Charles E. Schmidt College of Science

in Partial Fulfillment of the Requirements for the Degree of

Doctor of Philosophy

Florida Atlantic University

Boca Raton, FL

May 2014

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This dissertation was prepared under the direction of the candidate's dissertation advisor, Dr. M. Dennis Hanisak, Department of Biological Sciences, and has been approved by the members of her supervisory committee. It was submitted to the faculty of the Charles E. Schmidt College of Science and was accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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ACKNOWLEDGEMENTS

I am in awe of the support and encouragement that has been given me while pursuing this most long and arduous journey to fulfilling my PhD. I was most fortunate to have an excellent advisor and committee team members, some I have known for many years. Each one of them was always willing to talk with me from their experiences both scientific and personal and I am deeply grateful to them all. Perhaps the most pleasant surprise was working with my advisor, Dennis Hanisak. He was generous with his time and I was constantly impressed by the breadth and depth of his scientific knowledge. All the while, he has given me the opportunity to meet my goals with support and encouragement while pushing me to move beyond my comfort zone.

The fieldwork would not have been possible without the support of my colleagues at IHA (formerly Dynamac): Carly Garreau, Eric Reyier, Doug Scheidt, Shanon Gann, and Russ Lowers. I'm also very appreciative of Dr. Eric Stolen (IHA) lending an ear to my internalized statistical debates and Dr. Carlton Hall for his encouragement to keep up the PhD pursuit. I am grateful for the opportunity that Don George and Angy Chambers (US Air Force - 45$^{th}$ Space Wing) afforded me to be able to carry out this study, their review of materials, and assistance with site accessibility. I found inputs from several phycologists most inspiring and helpful and really appreciate the time that Dr. Wilson Freshwater (University of North Carolina, Wilmington) assisted me in identifying difficult Gelidiales species and the insights and inspirations of Mark and Diane

Littler (previously at the Natural History Museum, Smithsonian Institution). My chelonid (turtle) friends from my alma mater (University of Central Florida - Marine Turtle Research Group) were the very best of companions and team of turtle researchers and I find myself indebted as much as inspired by them. I especially want to thank Bill Redfoot for sharing his green turtle population with me and helping me integrate UCF's work into my research. Thank you to Dean Bagley, Terry Williamson, Andrew Sterner, Jennifer Solis, Sheryl Sanchez and many others that have helped over this project's years and beyond.

I truly am rich with many, many friends and a great sister that have offered nothing but good will, love and patience for many years. I dedicate this work to all who love the marine world just for the sake of itself, especially my dear friend, Shannon Hackett. Most of all, the love and support of my husband, Daryl S. Adkins, was unending. He truly believed in me and reminded me that this was a worthwhile pursuit and I could do it!

ABSTRACT

Author: Karen Gayle Holloway-Adkins

Title: Grazing Effects of Herbivorous Fishes and Juvenile Green Turtles (*Chelonia mydas*) on Macroalgal Communities

Institution: Florida Atlantic University

Dissertation Advisor: Dr. M. Dennis Hanisak

Degree: Doctor of Philosophy

Year: 2014

The impact of grazers on the primary production of marine ecosystems has largely been explored in tropical environments. A number of studies support theories on the functional importance of grazers in the community structure of coral reefs. However, large-bodied grazers, like juvenile green turtles, co-occur with herbivorous fishes in subtropical and tropical regions throughout the world and we know little about their combined impact on macroalgal communities and whether they compete for macroalgal resources.

My dissertation research was composed of four studies that were conducted simultaneously to further our understanding of plant/herbivore interactions in marine ecosystems. Studies were conducted at the Trident Basin, a non-public military facility within the Port Canaveral Inlet at Cape Canaveral, Florida, USA. The macroalgal study (Chapter 1), determined the spatial and temporal distribution of the macroalgal

community. The foraging habits of juvenile green turtles were compared with the macroalgal abundance within the Basin and over time (Chapter 2). Selection 'for' specific macroalgal species (based on their availability in the macroalgae study) was used to determine the level of overlap and/or partitioning of resources among herbivorous fishes and juvenile green turtles (Chapter 3). The final empirical study (Chapter 4) measured the impact on thallus height, diameter and/or branching of macroalgae as well as the macroalgal community composition fro caging experiments that excluded herbivorous fishes and juvenile green turtles.

The algal community was predominantly composed of nine red and green macroalgal species that were persistent year-round. Grazer-resistant macroalgae were rarely observed. Green turtles foraged on many of these same macroalgae but also opportunistically foraged on flotsam, including anthropogenic debris (e.g., plastic). The gut content of the major herbivorous fishes in the community (*Abudefduf saxatilis*, *Archosargus probatocephalus*, *Diplodus holbrooki*, and *Lagodon rhomboides*) foraged as omnivores depending on where they were captured within the Basin area or their size. All herbivores showed selection for less abundant green algae (i.e., *Ulva* spp.). Results of the exclusion of juvenile green turtles and large herbivorous fishes in caging experiments suggest that grazing by these large-bodied herbivores had no impact on the composition of the macroalgal community and little impact on the morphological structure of the macroalgal species that were examined. Collectively these four studies contribute to a better understanding of how multiple grazers have evolved to forage in macroalgal communities without detrimental effects on their food resources.

DEDICATION

I dedicate this work to my father, Alan Travis Holloway,

my grandmother, Thelma Lee Holloway, and

my very dear friend, Robin Duqyn Rounds.

While you each passed-on before I could finish this chapter in my life,

I heard your words in my thoughts and your love

inspires me to this day.

And I dedicate this work to my husband, Daryl Adkins,

you are an integral part of my life and well-being;

you have shared my dreams, my love, and, been the best support team

I could ever hope for.

GRAZING EFFECTS OF HERBIVOROUS FISHES AND JUVENILE GREEN TURTLES (*CHELONIA MYDAS*) ON MACROALGAL COMMUNITIES

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# I. MACROALGAL COMMUNITY IN PORT CANAVERAL FLORIDA: A TEMPERATE/SUBTROPICAL TRANSITION ZONE


## Abstract

While Cape Canaveral, Florida is a recognized biogeographic transition zone for warm temperate/subtropical marine biota, little is known of the nearshore marine flora. The macroalgal community growing on rock revetments within the Trident Basin, a tidal-driven area of Port Canaveral, supports diverse and abundant herbivorous fish as well as endangered green turtle (*Chelonia mydas*, Linnaeus 1758) populations. Objectives of this study were to describe this previously unexplored macroalgal community and determine if the macroalgal composition significantly differed spatially or temporally based on the following factors: distance from the channel/inlet, water depth, rock surface, quarterly sampling period (n = 8), mean water temperature, and/or interactions among factors. Samples were collected from 13 randomly selected transects that ran perpendicular to the shoreline. Samples (n = 1181) were primarily composed of macroalgae, of which rhodophytes were the most dominant algal group (88.2%), followed by chlorophytes (11.7%). Thirty-five species of macroalgae were identified, 9 of which were the most common taxa that persisted regardless of spatial location, sampling period, or temperature. The macroalgal community composition was significantly different for temporal and spatial factors as well as interactions. Macroalgal groups and taxa associated with intense grazing (e.g., Ochrophyta, crustose rhodophytes, calcareous

chlorophytes) were absent or present in <1.0% of samples. This is the first study that examines the nearshore flora in a biogeographic transition zone on the east central coast of Florida and quantifies patterns in the spatial and temporal distribution of macroalgae, an important food resource for juvenile green turtles and herbivorous fishes.

## Introduction

Rock revetment and concrete seawalls are used to maintain shoreline integrity of dredged channels and basins throughout the world (Airoldi et al. 2005; Moschella et al. 2005). These structures provide substrate for the attachment of macroalgae and other epibiota. Little is known about the communities on these structures that act as artificial reefs or artificial hardbottom (AHB) habitat and in many cases introduce a new floral and faunal community to areas previously dominated by soft bottom assemblages (Bohnsack et al. 1991; Atilla et al. 2003).

The Cape Canaveral region has been recognized as a biogeographic transition zone for temperate/subtropical marine flora for several decades (Humm 1969). However, knowledge of the regional flora has been limited to qualitative sampling (Searles 1984) and deepwater algal communities (Hanisak and Blair 1988). The two areas closest to Cape Canaveral with natural substrate for macroalgae are the nearshore hardbottom habitat approximately 150 km north at the Marineland coquina outcroppings (29° 40’ N, 81° 13’ W) in St. Augustine Beach (Stephenson and Stephenson 1952) and sabellariid worm reefs on exposed Anastasia rock approximately 20 km south of Port Canaveral (28° 13’ N, 80° 35’ W. The introduction of granite rock for shoreline revetment (i.e., riprap) in the construction of Port Canaveral created artificial habitat that is recognized for its

importance to a diverse and abundant community of fishes (Reyier et al. 2010) and a large population of juvenile green turtles (*Chelonia mydas*) (Redfoot 1997).

Marine macroalgal communities are highly variable (Underwood 2000), and individual species are influenced by several factors or combinations of factors [(e.g., competition for space (Carpenter 1990), substrate type (Wells et al. 1989), available light (Wells et al. 1989; Markager and Sand-Jensen 1992), water temperature and salinity (Davison and Pearson 1996), nutrient availability (Kraufvelin et al. 2010), water depth (Whorff et al. 1995), wave energy (Hurd 2000), sedimentation (Eriksson and Johansson 2005), dispersal/recruitment distances (Kinlan and Gaines 2003), and herbivory (Huntly 1991)].

In many areas, riprap structures support rocky intertidal communities. Characteristics of boulder fields (e.g., vertical profile, porosity) provide microhabitat, potentially influencing the recruitment of sessile and mobile assemblages in natural and artificial hardbottom habitats (McGuinness and Underwood 1986; Chapman 2002). Macroalgal communities that established on new rock jetties in Texas exhibited patterns of higher composition of chlorophytes on wave-exposed areas vs. rhodophytes on quiet, less wave-exposed areas (Agan and Lehman 2001) with no significant seasonal change in the overall biomass of algae. In another study, Kapraun and Zechman (1982) found seasonality in the macroalgal community, a horizontal gradient with distance from high energy sources, but no clear "disjunction of the infralittoral algal community at mean low water (MLW) that portrayed a distinct intertidal community" (i.e., vertical zonation) in the macroalgae growing on rock jetties off the North Carolina coast.

The goal of this study was to characterize and explore patterns in the distribution and composition of the marine flora in a previously uninvestigated temperate/subtropical transition zone. Environmental (i.e., water temperature, salinity) and physical factors (e.g., distance from the inlet, water depth, rock surface) data were measured and/or documented during the study period to investigate their relationship to macroalgal distribution. Specific objectives were to: (1) describe the macroalgal composition, (2) determine if there were significant differences in macroalgal composition based on distance from the channel/inlet, depth of collection, and/or location on the rock surface, and (3) determine if there were significant differences in the temporal composition of macroalgae based on sampling period (June 2008 to April 2010; n = 8), mean water temperature, and salinity. In addition, combinations of environmental factors (e.g., temperature x distance from the inlet x water depth) were tested for significant interactions.

## Methods

### *Study Area and Methods*

The study was located at the Trident Submarine Basin, a non-public military facility immediately inside Port Canaveral Inlet at Cape Canaveral, Florida, USA (28° 24’ N, 80° 34’ W; Figure 1.1). The Basin was constructed in the mid-1970s. Granite boulders ranging from 20 to 60 cm in diameter were installed around the perimeter of the Basin to maintain the integrity of the shoreline. The area of study was predominantly along the western bank of the Basin where the rock-base and algae are most dense. Rocks extend approximately 5 m above the high tide line down to various depths ranging from 1 to 6 m below the surface of the water (Figure 1.2). Beyond the boulders, the bottom is a

sand-mud mixture. A narrow shelf extends approximately 5 m out from the base of the rocks and then the bottom sharply slopes to a depth of 14 m (Redfoot 1997). The number of samples per transect varied due to differences in the amount of rock present below MHW (Figure 1.3). Subtidally submerged rock was most dense near the channel/inlet and averaged 4-6 m below the surface. The number of samples per transect within the first 200 m ranged between 15 and 35 (mean 25.0 ± 5.7 SD). The density of submerged rock becomes progressively shallower along the western wall. The average number of samples per transect in the west and northwest portions of the study area, furthest from the channel/inlet, ranged between 2 and 15 (mean 7.3 ± 2.8 SD).

Water temperature and salinity were retrieved from downloads of a subtidally submerged YSI 6920 v2 sonde (YSI, Inc., Yellow Springs, Ohio) located in the central section of the study area (approximately 20 m east of the shoreline). Data were recorded hourly on a near-continuous basis from June 2008 through April 2010. A second source of water temperature and salinity was available online from the National Data Buoy Center (NDBC; US Dept of Commerce 2010) which has a permanent monitoring station located in the Basin. Daily mean temperature and salinity measurements from both sources were calculated and tested for differences (t-test, $p < 0.05$) for days when both instruments were operable. No significant differences in measurements from either instrument were found ($df = 26$, $t = -0.805$, $p = 0.428$) and a near-continuous database of temperature and salinity values was constructed using the sonde as a primary source and supplemented with NDBC data when the sonde was out of the water for maintenance or repair.

Macroalgae were collected within an approximately 3900-$m^2$ (3 x 1300 m) area of tidally submerged rock. Samples were collected quarterly from June 2008 until April 2010 (n = 8). Underwater sampling was conducted by SCUBA, and depths did not exceed 6 m. Granite rock boulders along the shoreline were marked with a number every 100 m starting from 0 at the channel/Basin interface (or southwest tip of the study area) and continuing around the perimeter of the Basin (Figure 1.1). To determine if the macroalgal community differed based on distance from the channel/inlet, samples were collected from a randomly-selected transect line within every 100-m section (n = 13) each quarter. Transects were set perpendicular to the shore from the high tide line to the deep edge of the boulders. As the sampling method involved the destructive harvesting of macroalgae, survey locations within each 100-m section were randomly selected without replacement and established at least 3 m from any previous transect.

Preliminary sampling and observations of the macroalgal composition prior to this study indicated that algae in the Basin were dominated by turf-forming species with mean thallus heights <20 mm and diameters <0.5 mm. *Hypnea* spp., *Polysiphonia* spp. and *Amphiroa fragilissima* (Linnaeus) Lamouroux, which were loosely attached with secondary rhizoids to the lower turf community, potentially represent "canopy" species during periods of high productivity. The collection and quantification methods for this study were selected based on techniques best suited for this 3-dimensional habitat-type and previously utilized in turf community analyses (Scheibling 1986; Schmidt and Scheibling 2007; Irving and Witman 2009; Thrush et al. 2011).

Due to the rugose nature of the rock boulder profile, a metal chain marked every 20 cm with pink flagging tape was deployed as a transect line (Witman et al. 1999). If an

entire transect line was located over sand, the line was not sampled. Samples were collected at 20-cm intervals along the transect chain, starting at the first 20-cm mark at the deep end of the transect line. When a 20-cm sample location on a transect fell in an area of sand or an inaccessible crevice between the rocks, no sample was taken and it was recorded on the datasheet as such. Designation of sample collection water depth (or tide level) was categorical and based on arbitrary distances from MHW (mean high water). Samples collected from MHW to 1 m (0-1 m) deep were "intertidal", samples below 1 m down to 2 m (1-2 m) were "upper subtidal", and samples from below 2 m (>2 m) were "lower subtidal." The surface of the rock (or side) where the sample was collected was categorized based on position. Side categories were "top" (horizontal surface), "face" (vertical surface) and "underhang" (exposed underside).

Because the macroalgae in this area were highly turfed, a 25-mm diameter sample was cut and scraped from the rock surface with a modified cork borer (Webster 1974) and a flat, thin stainless steel plate to lift and maintain the sample together. Each sample was plunged into an individual, pre-labeled compartment of a sample container. The quarter, transect number, location, estimated depth, and rock surface were recorded on a waterproof datasheet for each sample (Kingsford and Battershill 1998). Full sample containers were placed on ice to keep them fresh and were later refrigerated in the laboratory until examination.

In the laboratory, the macroalgal contents of each sample were identified to the lowest taxonomic level possible with the aid of several taxonomic keys (Schneider and Searles 1991; Littler and Littler 2000; Littler et al. 2008; Dawes and Mathieson 2009). In some cases verification assistance was necessary to confidently identify difficult species

of Gelidiales (W. Freshwater, University of North Carolina, pers. comm..). After identification, the sample was thoroughly mixed and spread across a gridded Petri dish into a single layer to allow light for quantification (Forbes 1999). Samples were examined with modified procedures of microstereology (Weibel et al. 1966). A stereoscope was fitted with a grid reticle (100 squares) in the ocular. The reticle was aligned within one of the 13-$mm^2$ grids on the Petri dish. The macroalga (or other material) located in the top left corner of odd-numbered squares in the reticle was recorded for calculation of percent composition data. Macroalgae or other materials observed during the initial identification process but not quantified during the enumeration process were recorded as "trace" in terms of composition. The contribution of organisms and inanimate objects (i.e., flotsam, rock, and sand), were based on the percent of all items enumerated in a sample (total sample = 100%). Further data analyses focused on the nine most abundant macroalgal species that were found in every sampling period and comprising >3% composition of the macroalgal community: *Amphiroa fragilissima*, *Centroceras clavulatum* (C. Agardh) Montagne, *Gelidiopsis planicaulis* (W. Taylor) W. Taylor, *Gelidium crinale* (Hare ex Turner) Guillon, *Grateloupia filicina* (J.V. Lamouroux) C. Agardh, *Hypnea spinella* (C. Agardh) Kützing, *Jania adhaerens* J.V. Lamouroux, *Cladophora catenata* (Linnaeus) Kützing, and *Ulva flexuosa* Wulfen. Samples containing <10 data points and/or no macroalgae were eliminated (n = 30) and the remaining analyses was based on 1151 samples.

*Data Analyses*

Non-parametric statistical methods were conducted using PRIMER and PERMANOVA 6+ package (Primer-E Ltd, Plymouth, UK) to display and examine

correlations between percent composition of the macroalgal community and environmental and physical factors among sampling periods. Permutational multivariate analysis of variance (PERMANOVA; Anderson et al. 2008) is appropriate for multivariate ecological data which are generally over-dispersed with heavily right-skewed distributions, contain a large number of zero values, and are unable to meet the multivariate normality assumptions of traditional MANOVA (Anderson 2001). First, data were fourth-root transformed to down-weight the contribution of the most abundant species and standardized. Second, samples were averaged by individual factors (e.g., sampling period, transect, etc.) and merged into a single datasheet. Next, a Bray-Curtis resemblance matrix (B-C matrix) was constructed with similarity coefficient calculations between averaged replicates within and among the sample 'groups' (Clarke and Green 1988; Clarke and Warwick 2001). Finally, MDS (multidimensional scaling) ordination plots were constructed to visually represent dissimilarities among groups in as few dimensions as possible (Clarke and Warwick 2001).

PERMANOVA procedure was used to test the hypothesis of no significant differences in the spatial and temporal distribution of the macroalgal community and to detect potential interactions (e.g., transect x water depth). The sampling design consisted of six factors: Qtr = quarterly sampling period (fixed, 8 levels; Jun-08, Sep-08, Dec-08, Mar-09, Jun-09, Sep-09, Feb-10, Apr-10), Tran = transect (fixed, 13 levels; 0 through 12), Depth = depth of sample collection (fixed, 3 levels; intertidal, upper subtidal, lower subtidal), Side = collection surface of the rock (fixed, 3 levels: top, face, underhang), and Temp = quarterly mean temperature (fixed, 8 levels ranging from 17.2-28.2°C). A PERMANOVA design file inclusive of all factors and interactions was created and run

on Type I (sequential), permutations = 9999, fixed effects sum to zero, and permutations of residuals under a reduced model. Effect sizes were considered low at F, t <4.0, P (perm) <0.05. Separate design files were created for significant main effects (e.g., depth) to conduct post hoc pairwise comparisons (e.g., intertidal vs. lower subtidal) as well as contrast comparisons of factors (e.g., intertidal vs. upper and lower subtidal combined) via univariate PERMANOVA (Anderson et al. 2008). In addition, principle coordinate analysis (PCO; Anderson and Willis 2003) was run on a B-C resemblance matrix to construct a two-dimensional PCO ordination plot. Vectors derived from Pearson's correlation of variables (i.e., macroalgal species) were superimposed onto the axes of the ordination plot to show the raw correlations between percent composition of macroalgal species and factors (e.g., water temperature, water depth zone) (Anderson et al. 2008). SIMPER (similarity percentage) routine was used to identify differences in macroalgal species compositions that contributed up to 90% of the dissimilarity among groups (Clarke and Warwick 2001). Linear regression analyses (SigmaPlot vs. 11.0; Systat Software, Inc.) were conducted to examine the potential relationship of abundant species with factors (e.g., temperature, transect). Analysis of variance (ANOVA) procedure was used to further explore and test for differences in the percent composition of individual species based on factors that were significantly different in the initial PERMANOVA analysis.

## Results

### *Community Composition*

Samples contained 109 different biotic and abiotic materials, including: macroalgae, cyanobacteria, invertebrate animals or parts, fish eggs, plastic, and bare

substrate (i.e., rock, sand). The composition of the samples was predominantly macroalgae (80.8%) and invertebrate animal/parts (17.9%). Overall, 36 different species of macroalgae (17 Rhodophyta, 15 Chlorophyta, 3 Ochrophyta, and 1 Cyanobacteria) were identified in samples (Table 1.1). The number of species present per sampling period ranged from 17 to 28 (mean = 21.1 ± 4.0 SD; Table 1.1). Macroalgal species richness was highest (28 species) in February 2010 (Table 1.1). Thirteen of 36 (36.1%) species were present during every sampling period and 9 of the 13 species occurred in >20.0% (≥245) of 1151 samples and made up 83.6% of the total composition of samples (Table 1.1). The most abundant species was *Gelidium crinale*. Three species of brown macroalgae (Ochrophyta) were found in only two sampling periods (March and June 2009) in <1.0% amounts in 7 samples. *Dictyota pulchella* Hörnig & Schnetter and *Rosenvingea sanctae-crucis* Børgesen were found in samples from transects within 100 m of the channel/inlet. *Sargassum platycarpum* Montagne (unattached species) was found in one sample from a central location within the study area (transect 7).

PERMANOVA procedure results were significant for differences among the macroalgal community composition based on all of the main factors tested during the study (i.e., water depth, water temperature, distance from the channel/inlet, and rock surface; Table 1.2).

*Water Depth*

The macroalgal community based on water depth was significantly different and had the largest effect size among all factors and interactions tested [PERMANOVA, df = 2, Psuedo F = 35.2, P (perm) <0.01; Table 1.2]. The MDS ordination plot shows distinct separation (dissimilarity) among macroalgal communities based on water depth zones

(MDS; stress = 0.03; Figure 1.4). Post hoc pairwise comparisons detected significant differences between the macroalgal community at intertidal (0-1 m) vs. lower subtidal (>2 m) water depth [PERMANOVA; df = 2, t = 4.1, P (perm) <0.01; Table 1.3a]. All of the contrast comparison tests for macroalgal communities using combined different water depth zones comparisons were all significant with much higher effect sizes than pairwise tests (PERMANOVA; Table 1.3b).

*Amphiroa fragilissima*, *G. planicaulis*, and *H. spinella* were among the top species that contributed >70% to the dissimilarity of the macroalgal community between the intertidal vs. both lower and upper subtidal water depth zones (SIMPER; Table 1.3a). Significant differences in the mean percent composition of 5 (*A. fragilissima*, *C. clavulatum*, *G. planicaulis*, *H. spinella*, and *C. catenata*) of the 9 most abundant macroalgae (Figure 1.5) were detected between intertidal and both (upper and lower) subtidal depth zones while the compositions of 2 species, *G. crinale* and *J. adhaerens*, were not significantly different among water depth zones (Figure 1.5).

*Temperature and Salinity (quarterly sampling period)*

Mean monthly salinity was 35.2 ± 1.02 SD and ranged from 31.9 (September 2008) to 36.6 (May 2008; Figure 1.6). From August 19 to August 22, 2008 two meteorological stations at Port Canaveral recorded 50 and 63 cm of rainfall from Tropical Storm Fay (NASA 2013). In addition, the locks at Port Canaveral were open for several hours to relieve residential areas of localized flooding along the Banana River Lagoon banks. For approximately 2 weeks, these freshwater inputs and pulses lowered salinity in the Trident Basin to as low as 21.1. However, the constant mixing with nearby (<150 m) oceanic waters quickly brought salinity back to normal (~35). The range of salinity

during the study period was not considered biologically significant for macroalgae (Kirst 1989, Lobban. and Harrison 1994, Larsen and Sand-Jensen 2006), and hypothesis tests for correlations with salinity were not conducted.

Average water temperatures within the Trident Basin ranged from 17.0 to 29.5°C (Figure 1.6). Extreme cold water temperatures in January 2010 occurred during the coldest winter on record for Brevard County since records were first kept (1937). During this time, water temperatures dropped to 12.4°C and daily air temperatures were below 10°C for several days.

The MDS ordination plot indicates dissimilarity among sampling periods (Figure 1.7) but while macroalgal community composition among sampling periods was significantly different, these differences were clearly correlated with the mean monthly water temperature of the sampling period [MDS; Figure 1.7; PERMANOVA, df = 7, Psuedo F = 28.1, P (perm) <0.01; Table 1.2). Dissimilarity in the macroalgal community present in June and September of 2008 and 2009 vs. April and February of 2010 corresponded to sampling periods when temperatures were ≥25.3°C vs. ≤18.4°C (Figure 1.7). All post hoc pairwise comparisons of the macroalgal community based on mean water temperature were significant; however, only comparisons of the community when temperatures were ≥25.3°C vs. ≤18.4°C had effect sizes ≥4.0 (Table 1.4); these groups were designated 'warmer' vs. 'cooler' groups; respectively. The higher percent composition of *A. fragilissima, J. adhaerens,* and *H. spinella* in 'warmer' vs. 'cooler' groups were the species that most frequently contributed to differences (dissimilarities) among groups (SIMPER; Table 1.4). Regression analyses detected significant positive relationships with temperature for the abundance of *A. fragilissima*, *H. spinella*, and *J.*

*adhaerens* ($R^2$>0.5, p <0.05; Figure 1.8) and a significant negative relationship for temperature and the abundance of *G. filicina* ($R^2$ = 0.588, p = 0.026; Figure 1.8).

*Distance from the Channel/Inlet (transect)*

Significant differences were detected in the macroalgal community compositions at different distances (transect) from the channel/inlet [PERMANOVA; df = 12, Psuedo F = 7.17, P (perm) = <0.01; Table 1.2]. The trajectory overlaid on the MDS plot indicates a "gradient" correlated with distance from the channel/inlet (Figure 1.9). Post hoc analysis were significant among all pairwise comparisons of the macroalgal community based on transect; however, effect sizes were low (t ≤4.0; data not shown). Transect data were pooled based on their proximity to the channel/inlet: "close" = transects 0-2, "mid" = transects 3-7, and "far" = transects 8-12. Data were re-analyzed based on these new groups and pairwise tests were significant for close vs, both mid and far groups with low effect sizes [PERMANOVA; t <4.0, P (perm) <0.0; Table 1.5a). Contrast comparisons of close vs. combined mid and far groups as well as far vs. mid and close groups resulted in comparatively higher effect sizes than the pairwise tests [PERMANOVA; t 11.0 and 6.47, respectively, P (perm) <0.01; Table 1.5b]. At the species level, the higher composition of *A. fragilissima*, *H. spinella*, and *G. filicina* were among the top species that contributed >70% to the dissimilarity of the macroalgal community between the close vs. far and mid groups which had higher percent compositions of *C. clavulatum* and *C. catenata* (SIMPER, Table 1.5a). Regression analyses detected a significant relationship with the abundance of *A. fragilissima, G. filicina, C. clavulatum*, and *U. flexuosa,* and distances from the channel/inlet ($R^2$ ≥0.50, p <0.05; Figure 1.10).

*Rock Surface*

Sample sizes based on macroalgal communities collected from rock surfaces were substantially uneven given that 644 samples (56.0%) were collected from the top, 390 (33.9%) from the face, and 117 (10.1%) from underhang surfaces of boulders. The macroalgal community composition was significantly different based on rock surface [PERMANOVA, n = 2, Psuedo F = 4.5, P (perm) <0.01; Table 1.2]; post hoc pairwise comparisons were statistically significant for "top" vs. "underhang" rock surface, but the effect size was low [PERMANOVA; t = 1.99, P (perm) <0.01; Table 1.6a]. Post hoc contrast comparison tests were significant for only the face vs. combined top and underhang comparison of the macroalgal community composition [PERMANOVA; t = 3.63, P (perm) <0.01; Table 1.6a]. Contrast comparison results were significant for differences in the macroalgal community of face vs. combined top and underhang surfaces but the effect size was low [PERMANOVA; t =3.63, P (perm) <0.01; Table 1.6b]. All significant post hoc tests had low effect sizes (t <4.0; Table 1.6).

At the species level, the higher percent composition of *C. clavulatum*, *G. crinale*, and *A. fragilissima* were among the top species that contributed >70% dissimilarity between the macroalgal communities from top vs. face and underhang rock surfaces (SIMPER; Table 1.6a). The higher percent composition of *G. filicina*, *H. spinella*, and *J. adhaerens* were species that contributed >70% dissimilarity of the community on face vs. top and underhang surfaces (SIMPER; Table 1.6a). The macroalgal species compositions of *A. fragilissima* and *G. planicaulis* from samples collected from the top, face, or underhang surfaces of rocks were significantly different among intertidal vs. upper and lower subtidal water depths regardless of collection side (ANOVA; p <0.05; Figure 1.11). The

compositions of *C. clavulatum*, *H. spinella*, *C. catenata*, and *U. flexuosa* were significantly different between inter- vs. both subtidal water zones for samples collected from top and face surfaces but not from samples collected from the underhang surface in any water depth zone. The percent composition of *G. crinale* exhibited the least variability with only a significant difference in the composition of samples collected from the top surface of rocks in intertidal and upper subtidal vs. lower subtidal water depths (Figure 1.11).

*Interactions of Factors*

The interaction test for temperature x depth was significant with an effect size >4.0 [PERMANOVA; t = 4.16; P (perm) <0.01; Table 1.2]. The PCO ordination plot indicates a distinct separation of the macroalgal community at different water temperatures where the split of *J. adhaerens*. *H. spinella*, and *A. fragilissima* from *C. catenata, G. filicina,* and *G. crinale* on PC01 explains 46.1% of total variation and PCO2 explains 24.3% of total variation where the separation among water depth zones splits *U. flexuosa*, *C. clavulatum*, and *J. adhaerens* from *G. crinale, G. planicaulis*, and *A. fragilissima* (Figure 1.12).

No further analyses of the remaining interaction tests were conducted since initial results were either non-significant [P (perm) >0.05] or effect sizes were comparatively low [PERMANOVA; t <4.0; P (perm) <0.01; Table 1.2].

Discussion

*Community Composition*

The macroalgal community composition within the Trident Basin was primarily rhodophytes and secondarily chlorophytes. Ochrophyta and cyanobacteria were present in

unexpectedly low levels. Crustose macroalgae were not present at any time nor were species of chemically-defended rhodophytes (e.g., *Laurencia* spp.) found in samples. The relatively shallow depth and/or competition among macroalgal species most likely played a role in the presence and exclusion of several macroalgal species (Lubchenco 1980; Kapraun and Zechman 1982; Markager and Sand-Jensen 1992). Altogether, 9 species were consistently present and abundant throughout the 2-year study period with subtle, but discernible, spatial and temporal patterns in the distribution of the macroalgal assemblage. During this study, the greatest differences in the macroalgal community were detected based on water depth, mean water temperature, and distance from the channel/inlet.

*Water Depth*

Vertical zonation in shallow rocky intertidal systems has been described extensively (Lubchenco 1980; Markager and Sand-Jensen 1992). Light attenuation, exposure to air (desiccation), wave activity, sedimentation, and other factors typically differ in intensity and/or duration between intertidal and subtidal zones of rocky intertidal. Differences are oftentimes important in shaping the marine community of shallow nearshore waters. While the Trident Basin "intertidal" zone was relatively shallow (1-1.2 m tidal difference year-round), significant differences in the macroalgal community composition between intertidal and subtidal zones were still detectable, in some cases, at 1-m increments. Some unusual patterns in the algal community were found during this study. For example, chlorophytes (green macroalgae) which typically dominate the intertidal (Stephenson and Stephenson 1952; Lobban and Harrison 1994; Guinda et al. 2012) were found in relatively low percent composition in the intertidal as

well as subtidal zones. The percent compositions of *J. adhaerens* and *A. fragilissima,* which are slightly brittle, jointed-calcareous species, differed based on water depth. *Jania adhaerens* was found in high percent composition in the intertidal zone while the highest percent composition of *A. fragilissima* was present in the lower subtidal zone. Another interesting distribution pattern was the comparatively high percent composition of *G. filicina* in samples from the underhang surface of rocks within all water depths. Several species showed similar distribution patterns between intertidal and subtidal (upper and lower combined) water depth zones regardless of the surface (side) of collection (e.g., *A. fragilissima*, *G. planicaulis*) suggesting that adequate light resources were available through reflective or refractive light attenuation for these species (Häder and Figueroa 1997; Schubert et al. 2001). The crevices and underhangs of boulder fields may provide escape from predation, desiccation, mechanical damage, and competition for space as well as facilitate the growth of some macroalgal species even in lower-light areas of rock revetment (Underwood and Jernakoff 1984; Klöser et al. 1996).

*Salinity and Temperature*

Macroalgae in the Basin were tolerant of freshwater pulses that temporarily lowered salinity (Tropical Storm Fay in 2008) and an extreme dip in water temperatures that lasted for several weeks (January 2010) without deleterious effects. Others report similar response to freshwater pulses in marine macroalgae (Kirst 1989; Kirst 1996) and wide-range tolerances to temperature fluctuations for many of the same species discussed here (Breeman and Pakker 1994). Dawes (1989) found a much wider tolerance to fluctuations in salinity and water temperature in macroalgae species in subtropical Florida vs. tropical Caribbean waters. Shifts in the percent composition of macroalgal

species with subtropical/tropical distributions (e.g., *A. fragilissima*, *J. adhaerens*, and *H. spinella*) and species that are more cold-tolerant (e.g., *G. filicina*) (De Clerck et al. 2005) as well as 'annual' species (e.g., *C. catenata*) drove the differences detected among the macroalgal community based on temperature (Valiela et al. 1997). Species diversity was highest in the Trident Basin during cooler sampling periods and unseasonably cooler temperatures (<15°C). The presence of some filamentous species (e.g., *Griffithsia globulifera* Harvey ex Kützing and *Dasya abbottiana* D.L. Ballantine & N.E. Aponte), may indicate their ability to successfully colonize areas of disturbance but are quickly outcompeted by more robust turf species under warmer, more favorable conditions (Kain 1975; Sousa 1979a; Bulleri and Benedetti-Cecchi 2006) and/or are readily consumed by grazers (Benedetti-Cecchi 2000; Dayton 1971). During the study, the community appeared to "de-stabilize" under the extreme cold water temperatures. In the future, the application of controlled experiments, regulating temperature, simulating the "de-stabilization", and then measuring the resilience or recovery of the community would lend greater insight into how quickly these ecological systems equilibrate or if they remain in early-succession (Sousa 1979b; Allison 2004).

*Distance from Channel/Inlet*

Differences in wave energy exposure generated from natural and anthropogenic sources (boat traffic) likely contributed to the horizontal gradient observed in the macroalgal community with distance from the channel/inlet (Coutinho and Seeliger 1984). As aforementioned, high-energy wave activity plays a role in the vertical distribution of macroalgae; in this study, the profile of the Basin with close proximity to the channel/inlet appeared to influence macroalgal community composition. While the

Basin is tidally flushed, wave energy is attenuated at the mouth of the Basin where the rock density is highest and dampened before reaching the area furthest from the channel/inlet at the back of the Basin. In the calmer region, furthest from the inlet, the macroalgal percent composition was highest for *C. clavulatum* and *U. flexuosa*. In areas where wave energy was highest (near the channel/inlet), *A. fragilissima* and *G. filicina* had the highest percent composition of the macroalgal community.

*Rock Surface*

Patterns in the macroalgal species composition of samples collected from the 3 different rock surfaces (sides) within all 3 water depth zones suggest that for some species, growth and distribution patterns persist regardless of water depth or microhabitat features. Certainly, turf-forming species exhibit both morphological plasticity as well as physicochemical adaptations that include maximizing photosynthesis and respiration processes under short-term or in some cases, long term sub-optimal conditions (Archambault and Bourget 1996; Pérez-Lloréns et al. 2004).

*Additional Factors to Consider*

Herbivores have been identified as important contributors in shaping and maintaining the existing algal community in the form of cropping, selective foraging, and farming macroalgae (Ceccarelli et al. 2005). While not examined here, significant changes in macroalgal community composition based on fluctuations in grazing pressure during different time periods or under various conditions potentially influence the community (Huntly 1991; Wright et al. 2005; Bulleri et al. 2012) as well as fluctuations in available nutrient sources (Worm and Sommer 2000). Experiments designed to explore the impacts of both herbivore and nutrient resources on the macroalgal community within

the Trident Basin warrant investigation for their impact on species abundance, diversity, as well as zonation patterns.

Rock revetment and other artificial hardbottom structures for breakwaters and shoreline retention are circumglobally present in the marine environment (Airoldi et al. 2005). In Florida alone, there are 119 coastal inlets and jetties (Dept of Interior - US Geological Service 2013). These structures inadvertently provide habitat for marine flora and fauna (Hay and Sutherland 1988; Bohnsack et al. 1991). In some cases, researchers found that artificial habitats supported the same or many of the same species found on natural hardbottom habitat (Prekel et al. 2008) while others found significant differences in the macroalgal assemblage on artificial vs. natural hardbottom (Moschella et al. 2005). Many macroalgal species documented during this study have also been found growing on jetties and inlets in the southeastern Atlantic (Richardson 1987; Hay and Sutherland 1988) and Gulf of Mexico (Kaldy et al. 1995). While some species observed on the nearshore hardbottom (NHB) habitat approximately 20 km south of Port Canaveral (pers. observ.) were also identified in the Trident Basin (e.g., *Gelidium crinale*, *Caulerpa racemosa*, *Ulva* spp.), several species frequently observed on nearby NHB were absent from the Basin during this study (e.g., *Bryocladia cuspidata*, *Padina* spp., *Caulerpa prolifera*, *Laurencia* spp.).

*Conclusion*

The data presented here represent the first quantification of the macroalgal community within the Cape Canaveral region. Patterns in the temporal and spatial distribution of macroalgae were detected during this study. Species that exhibited significant changes with decreased water temperatures were likely near the northern

extent of their subtropical range (i.e. *A. fragilissima*, *J. adhaerens*, and *H. spinella*). Vertical zonation of the macroalgal community measured during this study has been similarly described for natural as well as artificial rocky intertidal systems along Atlantic coastal shorelines (Stephenson and Stephenson 1952; Zaneveld 1972). Less studied were the horizontal gradient differences in the macroalgal composition detected during this study. Small-scale spatial patterns in the macroalgal composition that were detected for rock surface have rarely been quantified and likely deserve greater attention for their ecological value in artificial reef construction.

The mechanisms contributing to and/or responsible for patterns in the macroalgal distribution within the Basin were not determined during this study; however, the identification of patterns in spatial and temporal variability within the study area establishes a premise for future manipulative experiments to isolate factors important in shaping these resultant communities present on rock rubble and other artificial structures. This study provides baseline data for future experiments that aid in modeling global climate change impacts to areas established as biogeographic transition zones, such as this region, that support diverse and abundant flora and fauna.

Tables

Table 1.1. The total number of samples (n), mean percent composition (± SD), and quarterly sampling period in which macroalgal species were present in samples collected from June 2008 through April 2010 (n = 8) off shoreline rock revetment in the Trident Basin at Port Canaveral Inlet, Cape Canaveral, Florida. + = species present during that sampling period, tr = species present but not detected in the percent composition analysis (trace), Frequency = total number of sampling periods when a species was present.

| Macroalgae (including Cyanobacteria) | Samples Present (n) | Composition (%) Mean | SD | Jun 2008 | Sep 2008 | Dec 2008 | Mar 2009 | Jun 2009 | Sep 2009 | Feb 2010 | Apr 2010 | Frequency Occurrence |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| RHODOPHYTA | | | | | | | | | | | | |
| *Agardhiella subulata* | 1 | 0.01 | 0.47 | | | | | + | | tr | | 2 |
| *Amphiroa fragilissima* ** | 504 | 10.28 | 53.79 | + | + | + | + | + | + | + | + | 8 |
| *Centroceras clavulatum* ** | 486 | 10.82 | 32.80 | + | + | + | + | + | + | + | + | 8 |
| *Ceramium floridanum* | 76 | 0.60 | 3.73 | + | + | + | + | + | + | | + | 7 |
| *Chrysymenia enteromorpha* | 16 | 0.25 | 3.55 | | | + | | | | + | + | 3 |
| *Dasya abbottiana* | 14 | 0.23 | 3.95 | | | tr | | + | | + | | 3 |
| *Gelidiopsis planicaulis* ** | 419 | 9.82 | 28.66 | + | + | + | + | + | + | + | + | 8 |
| *Gelidium crinale* ** | 830 | 18.11 | 58.20 | + | + | + | + | + | + | + | + | 8 |
| *Gracilaria mammillaris* | | | | | tr | | | tr | | | | 2 |
| *Grateloupia filicina* ** | 340 | 10.69 | 38.94 | + | + | + | + | + | + | + | + | 8 |
| *Griffithsia globulifera* | 4 | 0.04 | 0.74 | | + | + | + | tr | tr | | | 5 |
| *Hypnea spinella* ** | 473 | 9.18 | 62.77 | + | + | + | + | + | + | + | + | 8 |
| *Hypnea valentiae* | 2 | 0.08 | 2.05 | | | | | + | | tr | | 2 |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Jania adhaerens* ** | 426 | 6.19 | 37.27 | + | + | + | + | + | + | + | + | 8 |
| *Polysiphonia denudata* * | 217 | 5.06 | 26.69 | + | + | + | + | + | + | + | + | 8 |
| *Polysiphonia subtilissima* | 88 | 3.06 | 26.93 | | | | + | | | + | + | 3 |
| *Spyridia filamentosa* | 1 | 0.02 | 0.60 | | | | + | | | + | | 2 |
| CHLOROPHYTA | | | | | | | | | | | | |
| *Bryobesia johannae* | 1 | 0.01 | 0.23 | | tr | | | | tr | + | | 3 |
| *Bryopsis plumosa* * | 27 | 0.39 | 3.98 | + | + | + | + | + | + | tr | + | 8 |
| *Caulerpa racemosa* | 20 | 0.58 | 11.98 | + | | | + | + | + | tr | | 5 |
| *Chaetomorpha aerea* | 2 | 0.01 | 0.16 | | | | | tr | + | + | | 3 |
| *Chaetomorpha crassa* | 2 | 0.02 | 0.47 | | | | + | | | + | | 2 |
| *Chaetomorpha gracilis* * | 236 | 1.67 | 6.63 | + | + | + | + | + | + | + | + | 8 |
| *Cladophora catenata* ** | 370 | 4.29 | 21.92 | + | + | + | + | + | + | + | + | 8 |
| *Cladophora laetevirens* | 3 | 0.01 | 0.35 | | + | | | | | + | | 2 |
| *Cladophora liniformis* | 46 | 0.85 | 11.77 | | + | + | + | + | + | + | | 6 |
| *Cladophora prolifera* | 1 | 0.01 | 0.30 | | | | | | | + | | 1 |
| *Cladophora vagabunda* | 1 | 0.01 | 0.29 | + | | | | | | | | 1 |
| *Ulva chaetomorphoides* | 4 | 0.01 | 0.36 | | | | | + | | | + | 2 |
| *Ulva flexuosa* ** | 245 | 3.76 | 13.03 | + | + | + | + | + | + | + | + | 8 |
| *Ulva lactuca* * | 133 | 1.59 | 8.89 | + | + | + | + | + | + | + | + | 8 |
| *Ulva prolifera* | 22 | 0.31 | 3.59 | tr | | | | + | + | + | + | 5 |
| OCHROPHYTA | | | | | | | | | | | | |
| *Dictyota pulchella* | 2 | 0.03 | 2 | | | | + | | | | | 1 |
| *Rosenvingea sanctae-crucis* | 3 | 0.05 | 3 | | | | tr | + | | | | 2 |
| *Sargassum platycarpum* | 1 | 0.00 | 1 | | | | | + | | | | 1 |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CYANOBACTERIA | | | | | | | | | | | | |
| *Schizothrix* sp. | 3 | 0.09 | 3 | | + | | | | | + | | 2 |
| Number of species by quarter (includes trace) | 2 | 0.03 | 2 | 17 | 20 | 18 | 22 | 26 | 20 | 28 | 18 | |

*species present in every sampling period
**species present in ≥245 of 1151 (>20.0%) samples

Table 1.2. Dissimilarity of the macroalgal community composition based on the 9 most abundant macroalgae for the factors: Temp (mean water temperature), Tran (transect number which corresponds to the distance from the channel/inlet), Depth (water depth of sample collection), Side (rock surface of collection), and interactions among factors. Samples were collected quarterly from June 2008-April 2010 from rock revetment structures in the Trident Basin at Port Canaveral Inlet, Cape Canaveral, Florida.

| Source | df | MS | *F* | P(perm) |
|---|---|---|---|---|
| Depth | 2 | 34980.0 | 35.17 | <0.01 |
| Temp | 7 | 29203.0 | 29.37 | <0.01 |
| Tran | 12 | 7133.2 | 7.17 | <0.01 |
| Side | 2 | 4501.2 | 4.53 | <0.01 |
| Temp x Depth | 14 | 4139.5 | 4.16 | <0.01 |
| Temp x Tran** | 80 | 2756.9 | 2.78 | <0.01 |
| Tran x Depth** | 16 | 2591.1 | 2.61 | <0.01 |
| Temp x Side | 14 | 2163.5 | 2.18 | 0.07 |
| Depth x Side | 4 | 2105.4 | 2.12 | 0.01 |
| Tran x Side** | 23 | 1595.3 | 1.60 | <0.01 |
| Temp x Tran x Depth ** | 70 | 1832.6 | 1.84 | <0.01 |
| Temp x Tran x Side** | 105 | 1314.6 | 1.32 | 0.01 |
| Temp x Depth x Side | 26 | 1272.4 | 1.28 | 0.06 |
| Tran x Depth x Side** | 20 | 1233.7 | 1.24 | 0.11 |
| Residual | 45 | 994.5 | | |
| Total | 440 | | | |

** Term has one or more empty cells (uneven sample size)

Table 1.3. Pairwise comparison (a) and contrast comparison (b) results for the macroalgal community present in samples collected at different water depths. Comparisons of groups were significant at P (perms) <0.05; however, effect sizes were considered low at t ≤4.0. Species that were higher in percent composition and contributed to dissimilarity between pairwise comparisons of groups are listed in descending order (SIMPER). Rhodophyte species are: *Af = Amphiroa fragilissima*, *Cc = Centroceras clavulatum*, *Gp = Gelidiopsis planicaulis*, *Gc = Gelidium crinale*, *Gf = Grateloupia filicina*, *Hs = Hypnea spinella*, *Ja = Jania adhaerens*. Chlorophyte species are: *Cl = Cladophora catenata*, *Uf = Ulva flexuosa*.

(a)

| Group 1 | Group 2 | t | P (perm) | SIMPER (%) | Species in higher composition (Group 1) | Species in higher composition (Group 2) |
|---|---|---|---|---|---|---|
| Intertidal | Upper subtidal | 3.72* | <0.01 | 71.7 | *Gf, Cc, Gc, Ja, Uf* | *Af, Gp, Hs* |
| Upper subtidal | Lower subtidal | 1.85* | <0.01 | 66.1 | *Gf, Hs, Cc, Ja* | *Af, Gp, Gc,* |
| Intertidal | Lower subtidal | 4.06** | <0.01 | 69.3 | *Cc, Gf, Ja* | *Gc, Af, Gp, Hs* |

(b)

| | | | | | | |
|---|---|---|---|---|---|---|
| Intertidal | (Upper subtidal, Lower subtidal) | 20.71** | <0.01 | | | |
| Upper subtidal | (Intertidal, Lower subtidal) | 8.12** | <0.01 | | | |
| Lower subtidal | (Intertidal, Upper subtidal) | 9.54** | <0.01 | | | |

* significantly different [P (perm) <0.05] with effect sizes <4.0

** significantly different [P (perms) <0.05] with effect sizes ≥4.0

Table 1.4. Pairwise comparisons for the macroalgal community present at different mean temperatures during the 2-year study (n = 8, June 2008-April 2010). Sampling period temperature means were June 2008 = 25.3°C, June 2009 = 25.4°C, September 2008 = 26.8°C, September 2009 = 28.2°C, December 2008 = 22.0°C, February 2010 = 17.2°C, March 2009 = 19.3°C, and April 18.4°C. All comparisons were significant [P (perms) <0.01]; however, effect sizes that were considered low (t <4.0) are not shown here. Species that were higher in percent composition and contributed to dissimilarity between pairwise comparisons of macroalgal communities present in the relative warmer vs. cooler temperature groups are listed in descending order (SIMPER). Rhodophyte species are: *Af = Amphiroa fragilissima*, *Cc = Centroceras clavulatum*, *Gp = Gelidiopsis planicaulis*, *Gc = Gelidium crinale*, *Gf = Grateloupia filicina*, *Hs = Hypnea spinella*, *Ja = Jania adhaerens*. Chlorophyte species are: *Cl = Cladophora catenata*, *Uf = Ulva flexuosa*.

| Warmer group | Cooler group | t** | SIMPER (%) | Species higher composition (warmer group) | Species in higher composition (cooler group) |
|---|---|---|---|---|---|
| 28.2°C | 18.4°C | 5.25 | 79.7 | *Af, Hs, Gp, Ja* | *Gf, Cc, Gc* |
| 26.8°C | 18.4°C | 4.71 | 78.2 | *Af, Gc, Hs, Ja* | *Gf, Cc, Gp* |
| 28.2°C | 17.2°C | 4.66 | 76.3 | *Af, Hs, Gp, Ja, Cc* | *Gf, Gc* |
| 26.8°C | 19.3°C | 4.33 | 72.6 | *Af, Gc, Hs, Ja* | *Cc, Gp, Gf, Uf* |
| 26.8°C | 17.2°C | 4.31 | 75.4 | *Af, Gc, Hs, Ja, Cc* | *Gf, Gp, Cl* |
| 28.2°C | 25.3°C | 4.15 | 58.8 | *Ja, Af, Gp, Cl, Cc* | *Gc, Hs* |
| 28.2°C | 19.3°C | 4.06 | 71.2 | *Af, Hs, Ja, Gc* | *Cc, Gp, Gf, Uf* |
| 25.3°C | 18.4°C | 4.05 | 74.4 | *Gc, Hs, Ja, Uf* | *Gf, Cc, Gp* |

** significantly different [P (perm) <0.05] with effect sizes ≥4.0

Table 1.5. Pairwise comparisons for the macroalgal community present in samples collected from transects located at different distances based on 100-m increments (e.g., 1 = 100 m) from the channel/inlet (a). Transect data were pooled into 3 groups (Close = transects 0-2, Mid = transects 3-7, Far = transects 8-12) for contrast comparisons of groups (b). Comparisons were significant at P (perms) <0.05; however, effect sizes <4.0 were considered low. Species that were higher in percent composition and contributed to dissimilarity between pairwise comparisons of groups are listed in descending order (SIMPER). Rhodophyte species are: *Af = Amphiroa fragilissima*, *Cc = Centroceras clavulatum*, *Gp = Gelidiopsis planicaulis*, *Gc = Gelidium crinale*, *Gf = Grateloupia filicina*, *Hs = Hypnea spinella*, Ja = *Jania adhaerens*. Chlorophyte species are: *Cl = Cladophora catenata*, *Uf = Ulva flexuosa*.

(a)

| Group 1 | Group 2 | t | P (perm) | SIMPER (%) | Species in higher composition (Group 1) | Species in higher composition (Group 2) |
|---|---|---|---|---|---|---|
| Close | Mid | 2.56* | <0.01 | 67.0 | *Gf, Af, Hs, Ja* | *Gc, Cc, Gp, Cl* |
| Close | Far | 3.27* | <0.01 | 69.0 | *Gc, Af, Gf, Hs, Gp* | *Cc, Uf, Cl* |
| Mid | Far | 1.37 | 0.08 | 65.4 | *Gc, Gp, Hs, Af, Cl, Ja* | *Cc, Uf,* |
| (b) | | | | | | |
| Close | (Mid, Far) | 11.00** | <0.01 | | | |
| Mid | (Close, Far) | 2.37* | 0.03 | | | |
| Far | (Close, Mid) | 6.47** | <0.01 | | | |

*significantly different [P (perm) <0.05] with effect sizes >4.0
**significantly different[P (perm) <0.05] with effect size ≥4.0

Table 1.6. Pairwise comparisons of the macroalgal community present on different rock surfaces (sides; a) and contrast comparisons of combined rock surface groups (b). Comparisons of groups were significantly different at P (perms) <0.05; however, effect sizes <4.0 were considered low. Species that were higher in percent composition and contributed to dissimilarity between pairwise comparisons of groups are listed in descending order (SIMPER). Rhodophyte species are: *Af = Amphiroa fragilissima*, *Cc = Centroceras clavulatum*, *Gp = Gelidiopsis planicaulis*, *Gc = Gelidium crinale*, *Gf = Grateloupia filicina*, *Hs = Hypnea spinella*, *Ja = Jania adhaerens*. Chlorophyte species are: *Cl = Cladophora catenata*, *Uf = Ulva flexuosa*.

(a)

| Group 1 | Group 2 | t | P (perm) | SIMPER (%) | Species in higher composition (Group 1) | Species in higher composition (Group 2) |
|---|---|---|---|---|---|---|
| Top | Face | 1.18 | 0.23 | 67.3 | *Cc, Gc, Af* | *Gf, Gp, Hs, Ja* |
| Top | Underhang | 1.99* | <0.01 | 72.3 | *Cc, Gc, Af, Gp,* | *Gf, Hs, Ja, Uf* |
| Face | Underhang | 1.15 | 0.26 | 74.2 | *Cc, Gc, Gp, Af* | *Gf, Hs, Ja, Cl* |

(b)

| | | | | | | |
|---|---|---|---|---|---|---|
| Top | Face, Underhang | 1.39 | 0.20 | | | |
| Face | Top, Underhang | 3.63* | <0.01 | | | |

*significantly different [P (perm) <0.05] with effect sizes <4.0

**F**igures

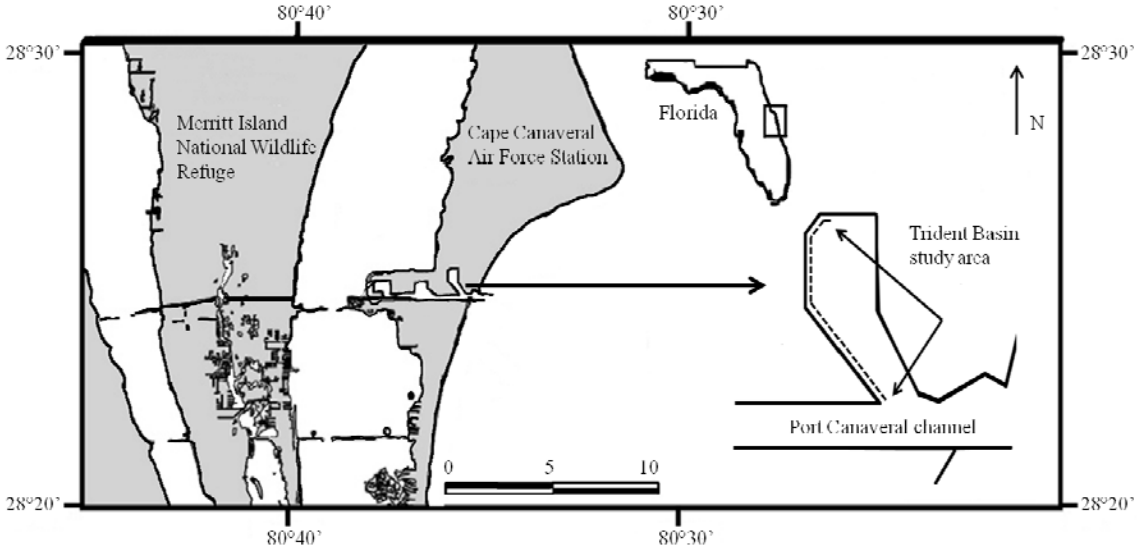


Figure 1.1. The study area within the Trident Basin located just inside Port Canaveral Inlet in Cape Canaveral on the east coast of Florida, USA. Transects to collect macroalgal samples were placed perpendicular to the shoreline over the rock revetment on the west wall of the Basin (study area inlay; diagram is not to scale).

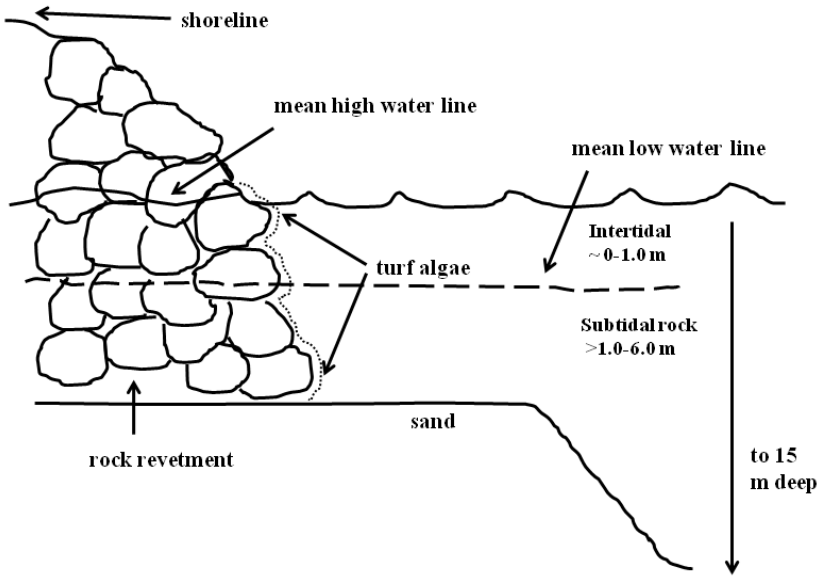


Figure 1.2. Bathymetric profile of the Trident Basin (diagram not to scale). Samples were collected every 20 cm along a transect chain (not shown) that extended from the mean high water line to the rock/sand interface that ranged between 1-6 m below mean high water depending on the location within the Basin.

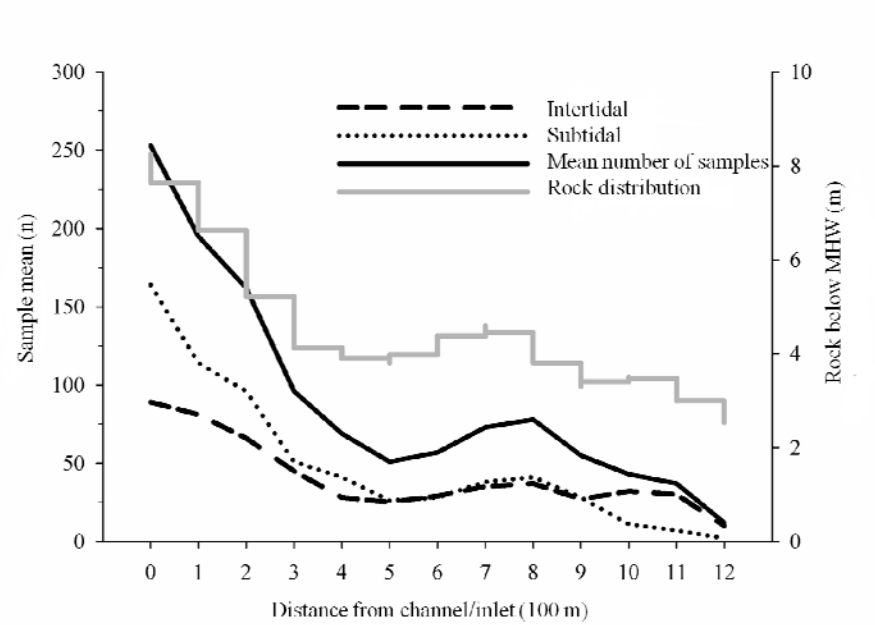


Figure 1.3. Mean number of samples collected per transect and rock distribution. Samples were collected every 20 cm from transects set perpendicular to shore and were documented as intertidal (long dashes) or subtidal (dotted line) based on their relative distance from the mean low water line. The total numbers of samples (n) per transect are indicated by the solid black line. The distribution of inter- and subtidal rock (below mean high water) is shown by the solid gray line. Sampling areas closest to the channel/inlet were deeper, with more rock below mean low water while sampling areas furthest from the channel were shallow with limited submerged rock.

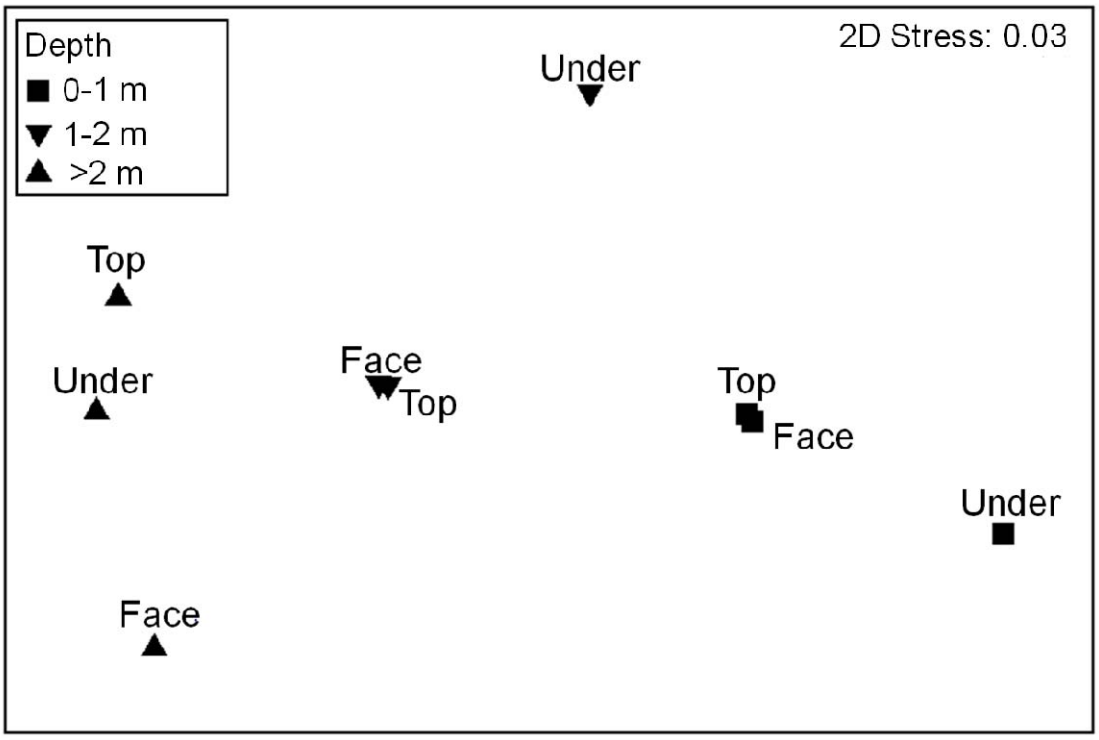


Figure 1.4. Multidimensional scaling (MDS) ordination plot visually representing dissimilarities (differences) among macroalgal species composition based on depth of collection [■ = intertidal (0-1 m), ▼= upper subtidal (1-2 m), ▲ = lower subtidal (>2 m)] and rock surface (top, face, under).

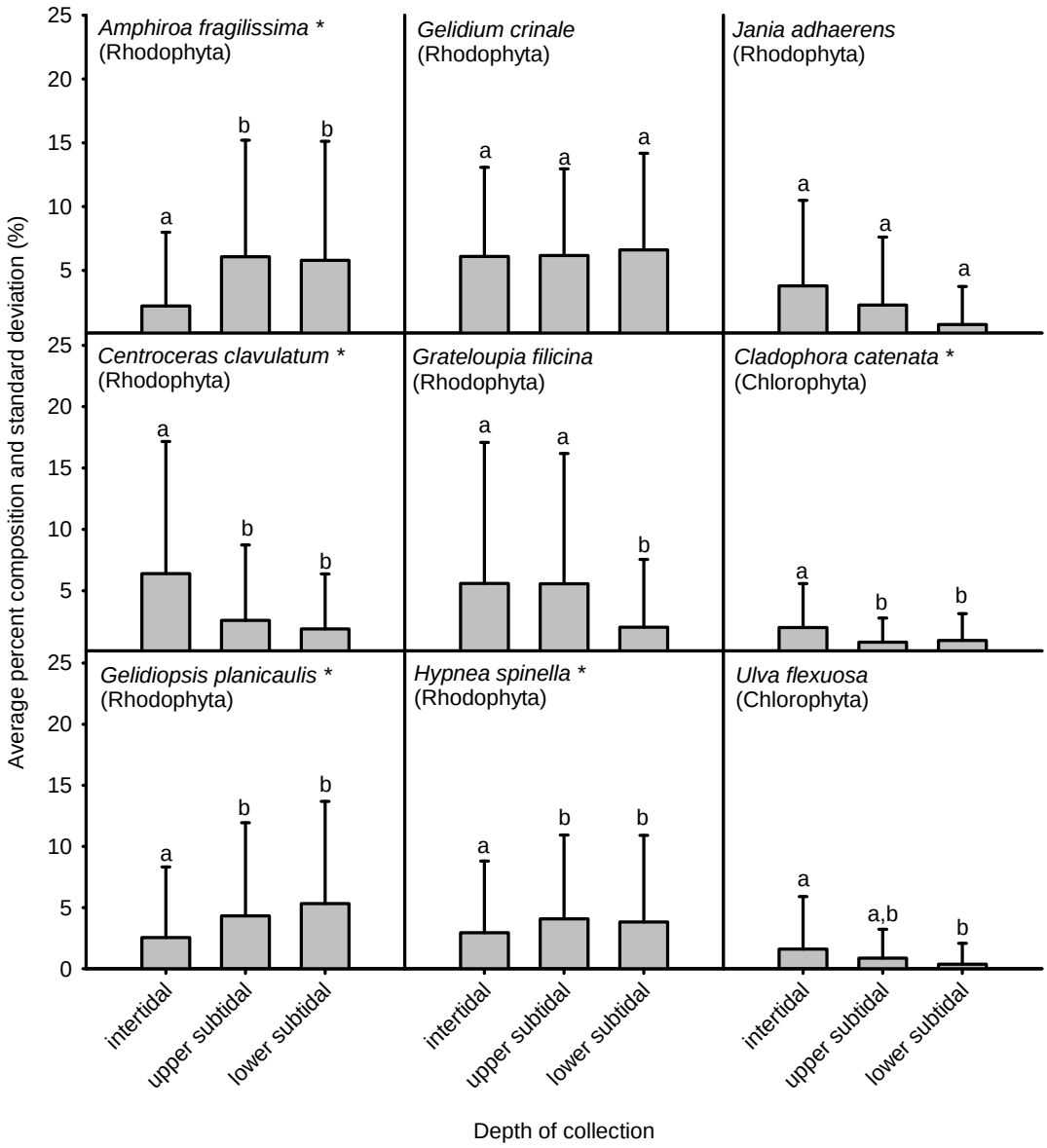


Figure. 1.5. Percent composition of the nine most abundant macroalgae based on depth of collection (intertidal = 0-1 m, upper subtidal = 1-2 m, lower subtidal = >2 m). Unmatched letters among the graph bars indicate significant differences among groups. An asterisk (*) indicates the percent composition of a species was significantly different between intertidal and both subtidal (upper and lower) water depth zones.

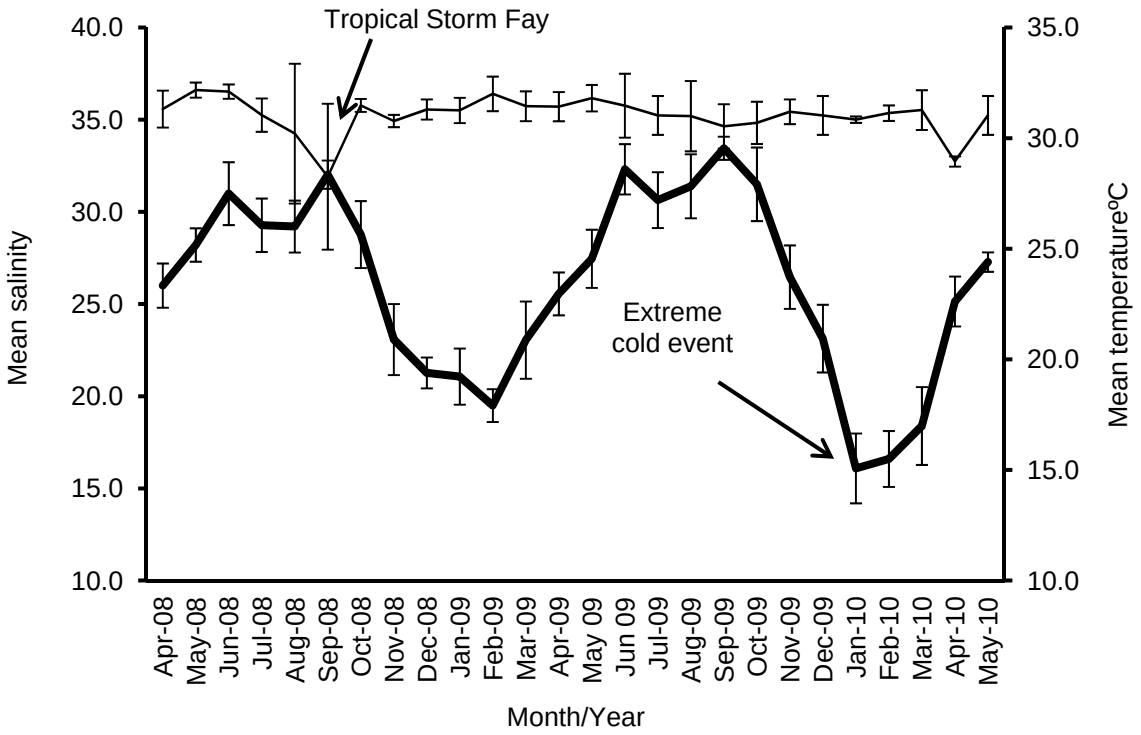


Figure 1.6. Monthly mean salinity (thin line) and temperature (thick line) values in the Trident Basin (June 2008-April 2010). Salinity values were unavailable for July 2009 and December 2009 due to instrument failure. Episodic events were excessive rainfall from Tropical Storm Fay during August 2008 and extreme cold water temperatures during January 2010.

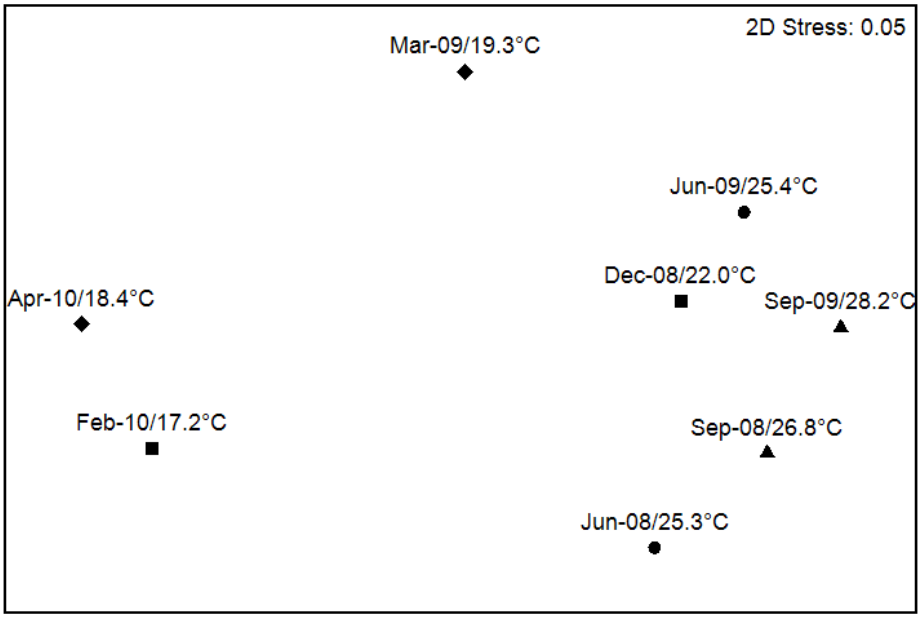


Figure 1.7. Multidimensional scaling (MDS) ordination plot visually representing dissimilarities (differences) among macroalgal communities based on the mean water temperature for the month that macroalgae were sampled. Symbols represent the season in which a sampling period occurred: ● = summer, ▲ = fall, ■ = winter, ◆ = spring.

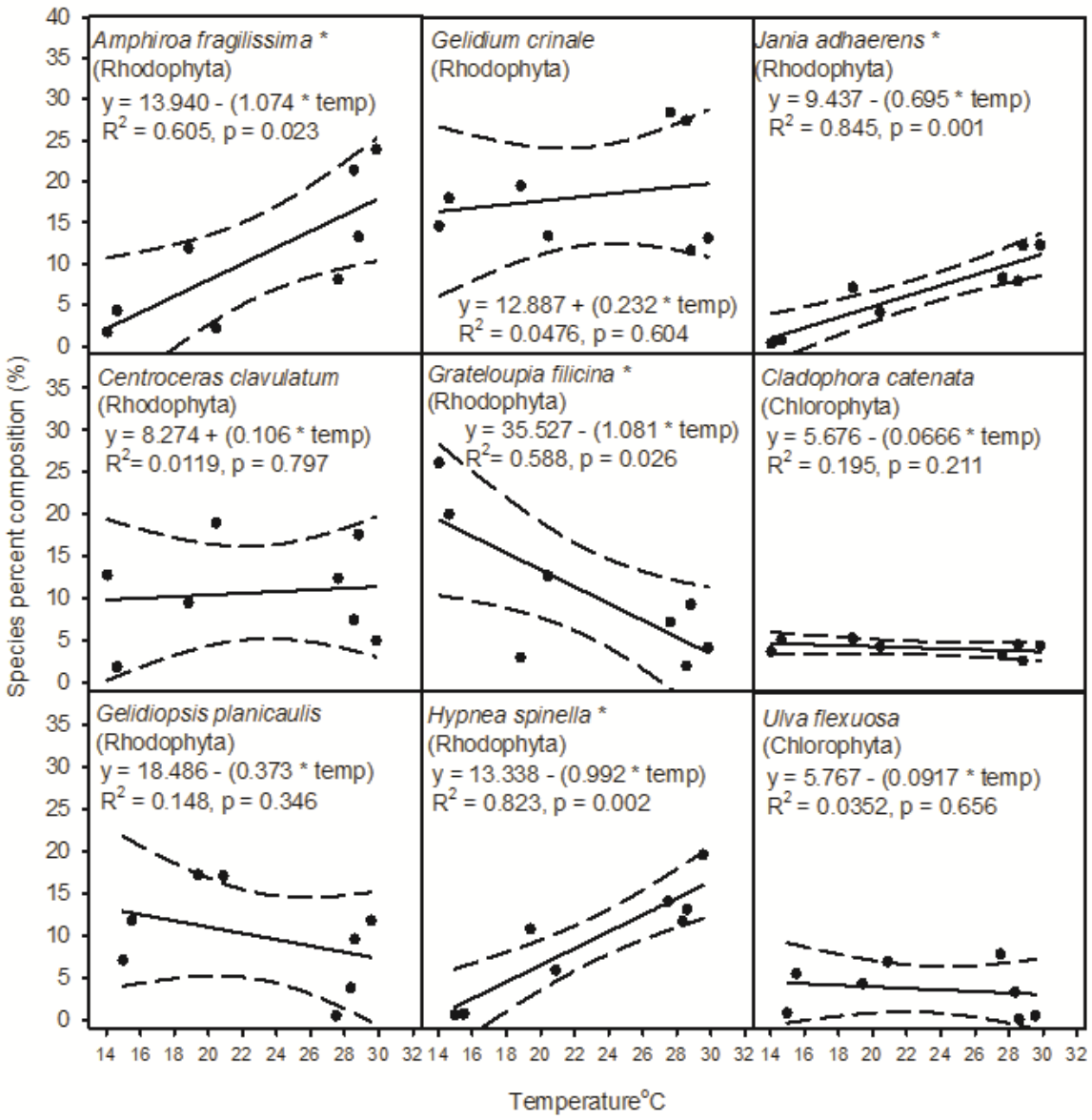


Figure 1.8. Linear regression analyses of percent compositions of the 9 most abundant macroalgal species as a function of temperature.

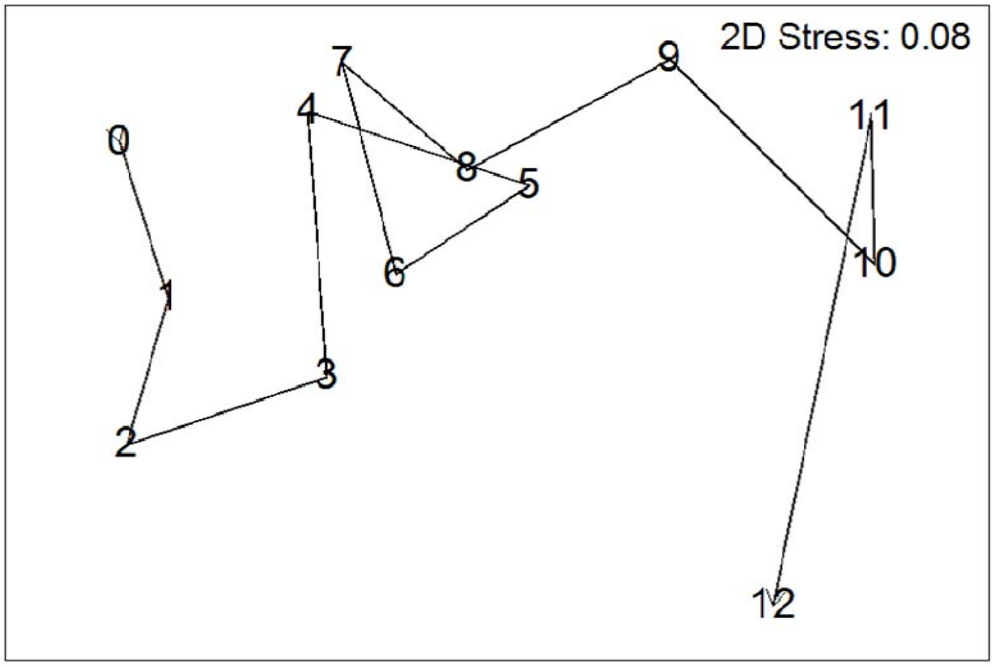


Figure 1.9. Multidimensional scaling (MDS) ordination plot visually representing dissimilarities (differences) among macroalgal species composition at different distances from the channel/inlet (or transect). The transect number is the relative distance from the channel/inlet by 100's of meter [(i.e., transect 0 is between 0-99 m from the channel/inlet, transect 12 (the most distant transect) is located between 1200-1299 m from the channel/inlet)] within the study area.

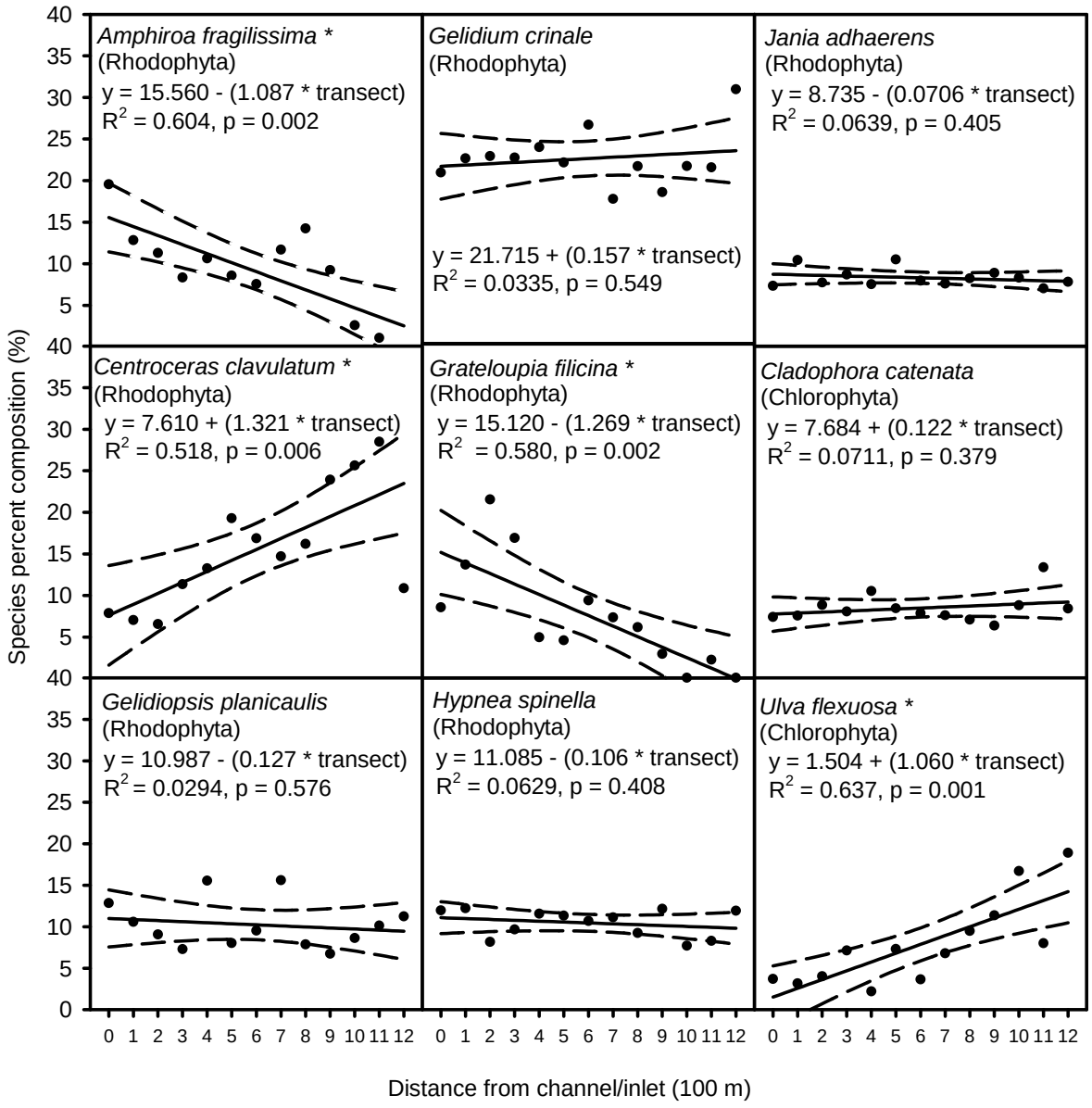


Figure 1.10. Linear regression analyses of macroalgal species as a function of distance from the channel/inlet (or transect). The transect number is the relative distance from the channel/inlet by 100's of meter [(i.e., transect 0 is between 0-99 m from the channel/inlet, transect 12 (the most distant transect) is located between 1200-1299 m from the channel/inlet)] within the study area.

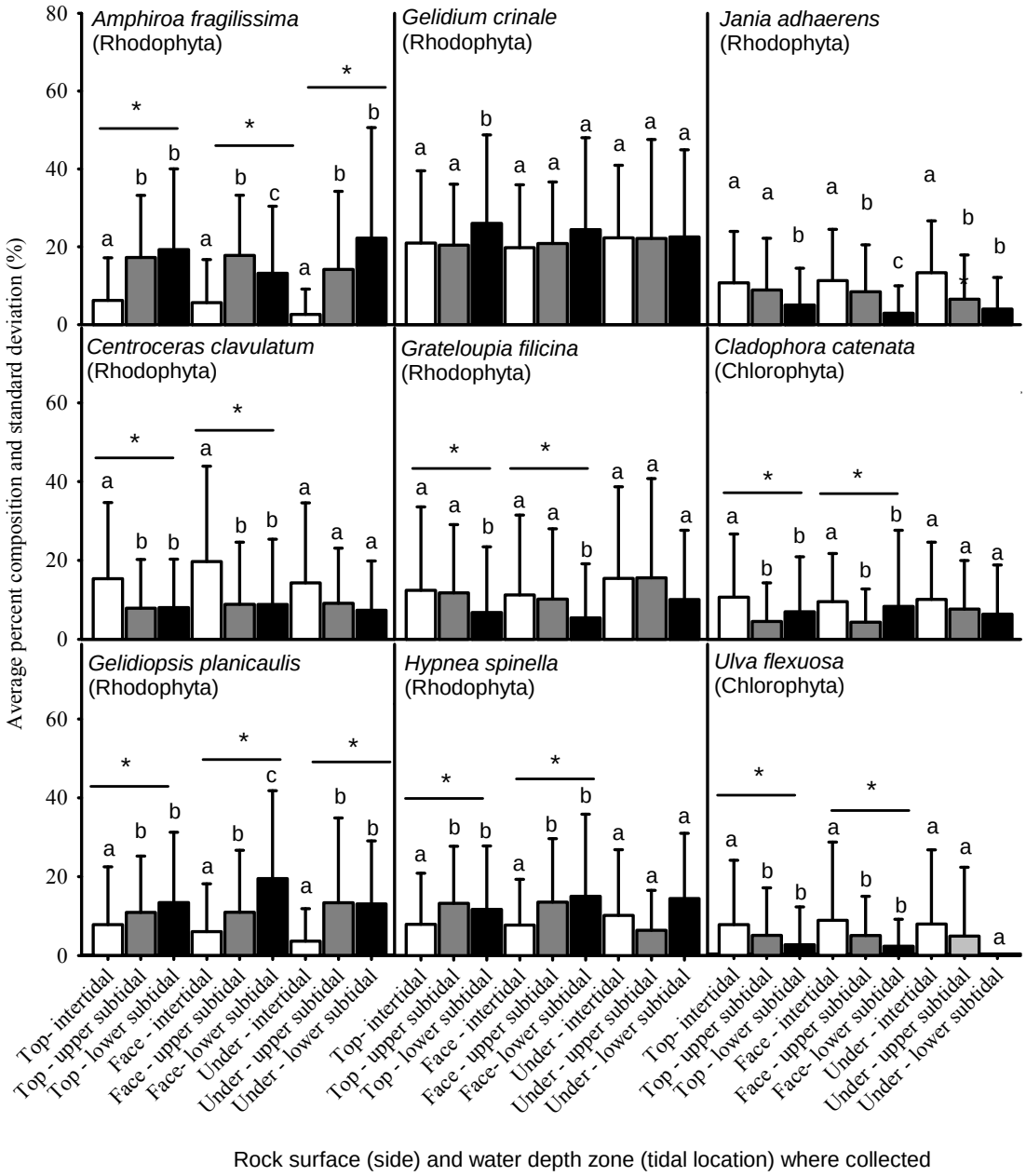


Figure 1.11. Percent composition of the nine most abundant macroalgae in samples collected from different rock surfaces (sides) within different water depth zones. Sides were designated: top (horizontal surface), face (vertical surface), under (underhang) and were grouped for water depth zones [(i.e., intertidal (white bars; 0-1 m), upper subtidal (gray bars; 1-2 m), lower subtidal (black bars; >2 m)]. Unmatched letters among the graph bars indicate significant differences within a side group based on the water depth zone. Horizontal bars with asterisks (*) indicate a species had similar patterns in their composition between intertidal vs both subtidal water depth zones or between intertidal and upper subtidal vs; lower subtidal zones for 2 or more side (surface) groups.

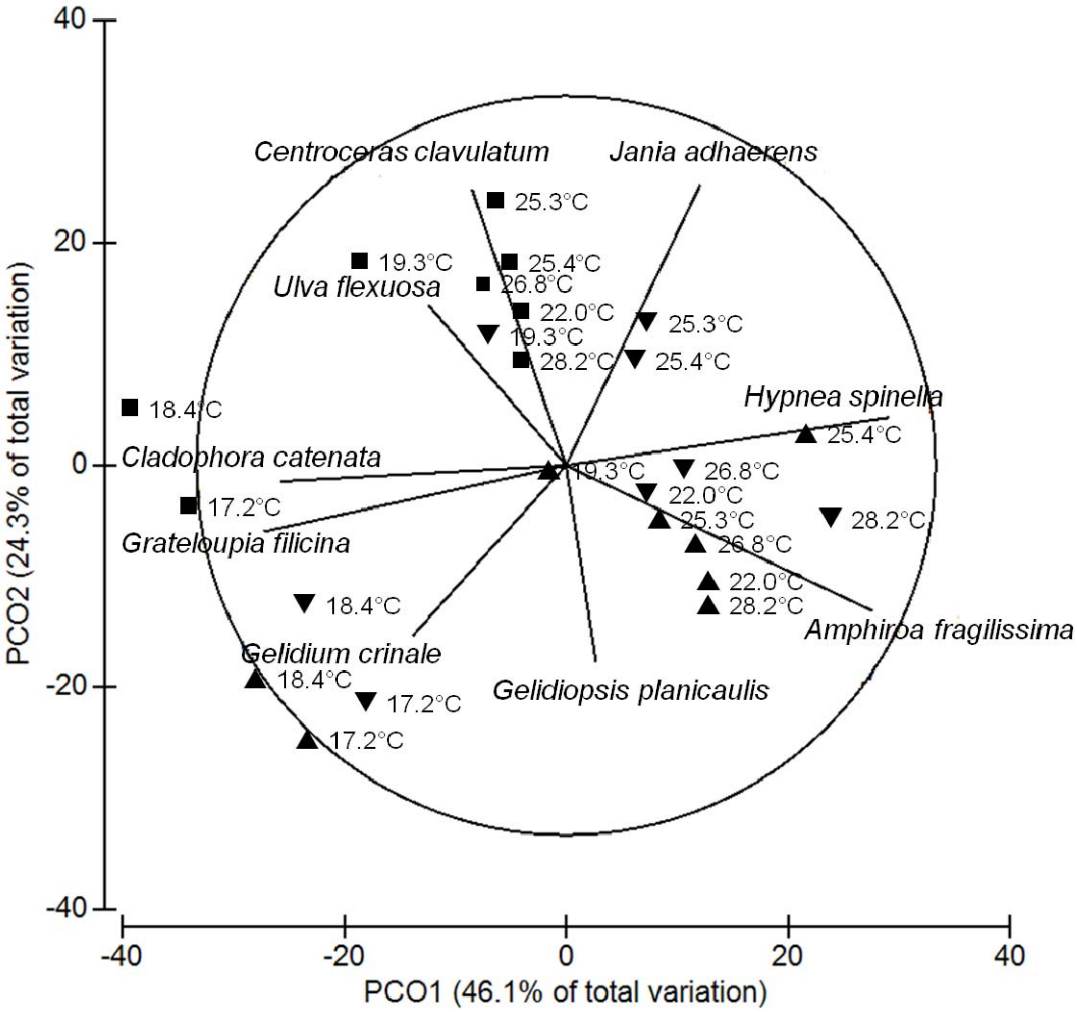


Figure 1.12. Unconstrained PCO (principle coordinate analysis) ordination plot indicating separation of the macroalgal community at different water temperatures (PCO1) and water depth zones (PCO2) as shown by splits in the plot among species. Water depthzones were: ■ = intertidal (0-1 m), ▼= upper subtidal (1-2 m), ▲ = lower subtidal (>2 m). Vector projections indicate the distributions of the sign of individual species.

Acknowledgements

All diving activities were conducted in accordance with the American Association of Underwater Scientists diving and safety operating standards. Access to publicly restricted areas of CCAFS and Trident Basin was granted by US NAVY and US Air Force - 45th Space Wing. Special thanks to D. George and A. Chambers for their reviews of materials and assistance with site accessibility. I would like to thank the following persons for their assistance in sampling, underwater photography, and diving activities: C. Garreau, E. Reyier, D. Scheidt, S. Gann, R. Lowers, and C. Hall. Dynamac and IHA provided time and materials for this project. Thank you to my dissertation committee members, M.D. Hanisak, L.M. Ehrhart, C. Hughes, C.E. Proffitt, T. Sutton, and R. Virnstein for their guidance and contributions to both the proposed project and final manuscript review. I would also like to thank K.R. Clarke and P. Somerfield (Plymouth Marine Laboratory, UK) for their comments and assistance in reviewing statistical analyses. We very much appreciate the assistance of W. Freshwater (University of North Carolina, Wilmington) in identifying difficult Gelidiales species, and extend a gracious thank you to M. and D. Littler for their algal insights and inspiration.

References

Agan, J.C., and R.L. Lehman. 2001. Seaweed abundance and diversity in high energy and low energy areas at Port Aransas, Texas jetties. Journal of Phycology, 37:4.

Airoldi, L., M. Abbiati, M.W. Beck, S.J. Hawkins, P.R. Jonsson, D. Martin, P.S. Moschella, A. Sundelof, R.C. Thompson, P. Åberg. 2005. An ecological perspective on the deployment and design of low-crested and other hard coastal defence structures. Coastal Engineering, 52:1073-1087.

Allison, G. 2004. The influence of species diversity and stress intensity on community resistance and resilience. Ecological Monographs, 74:117-134.

Anderson, M., R. Gorley, and K.R. Clarke. 2008. PERMANOVA+ for PRIMER. Plymouth: PRIMER-E.

Anderson, M.J. 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecology, 26:32-46.

Anderson, M.J., and T.J. Willis. 2003. Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology. Ecology, 84:511-525.

Astronomical Applications Department. 2013. Duration of Daylight/Darkness. United States Naval Observatory. Available from: http://aa.usno.navy.mil/data/docs/Dur_OneYear.php.

Atilla, N., M.A. Wetzel, and J.W. Fleeger. 2003. Abundance and colonization potential of artificial hard substrate-associated meiofauna. Journal of Experimental Marine Biology and Ecology, 287:273-287.

Bohnsack, J.A., D.L. Johnson, and R.G. Ambrose. 1991. Ecology of artificial reef habitats and fishes. P. 61-107 in Artificial habitats for marine and freshwater

fisheries, Seaman, J.W., and L.M. Sprague (Eds.). Academic Press, San Diego, California.

Breeman, A.M., and H. Pakker 1994. Temperature ecotypes in seaweeds: adaptive significance and biogeographic implications. Botanica Marina, 37:171-180.

Bulleri, F., and L. Benedetti-Cecchi. 2006. Mechanisms of recovery and resilience of different components of mosaics of habitats on shallow rocky reefs. Oecologia, 149:482-492.

Bulleri, F., B. Russell, and S. Connell. 2012. Context-dependency in the effects of nutrient loading and consumers on the availability of space in marine rocky environments. PLoS ONE, 7: P. e33825.

Carpenter, R.C. 1990. Competition among marine macroalgae: a physiological perspective. Journal of Phycology, 26:6-12.

Ceccarelli, D.M., G.P. Jones, and L.J. McCook. 2005. Foragers versus farmers: contrasting effects of two behavioural groups of herbivores on coral reefs. Oecologia, 145:445-453.

Chapman, M.G. 2002. Early colonization of shallow subtidal boulders in two habitats. Journal of Experimental Marine Biology and Ecology, 275:95-116.

Clarke, K.R., and R.H. Green. 1988. Statistical design and analyses for a 'biological effects' study. Marine Ecology Progress Series, 46:213-226.

Clarke, K.R., and R.M. Warwick. 2001. Change in marine communities: an approach to statistical analysis and interpretation, 2nd edition. Plymouth PL: PRIMER-E Ltd.

Coutinho, R., and U. Seeliger. 1984. The horizontal distribution of the benthic algal flora in the Patos Lagoon estuary, Brazil, in relation to salinity, substratum and wave exposure. Journal of Experimental Marine Biology and Ecology, 80:247-257.

Davison, I.R., and G.A. Pearson. 1996. Stress tolerance in intertidal seaweeds. Journal of Phycology, 32:197-211.

Dawes, C.J. 1989. Temperature acclimation in cultured *Eucheuma isiforme* from Florida and *E. alvarezii* from the Philippines. Journal of Applied Phycology, 1:59-65.

Dawes, C.J., and A.C. Mathieson. 2009. The Seaweeds of Florida. University Press of Florida, Gainesville, Florida. 592 p.

De Clerck, O., B. Gavio, S. Fredericq, I. Barbara, and E. Coppejans. 2005. Systematics of *Grateloupia filicina* (Halymeniaceae, Rhodophyta), based on rbcL sequence analyses and morphological evidence, including the reinstatement of G-minima and the description of G-capensis sp nov. Journal of Phycology, 41:391-410.

Dept of Interior-US Geological Service. 2013. Coastal Marine & Geology Program: Coastal Classification Mapping. USGS. Available from: http://pubs.usgs.gov/of/2003/of03-322/mapintro.html.

Eriksson, B.K., and E.G. Johansson. 2005. Effects of sedimentation on macroalgae: species-specific responses are related to reproductive traits. Oecologia, 143:439-448.

Forbes, G.A. 1999. Diet sampling and diet component analysis. P. 144-148 in Research and management techniques for the conservation of sea turtles, Eckert, K.L., K.A. Bjorndal, F.A. Abreu-Grobois, and M. Donnelly (Eds.). SSC/IUCCN Marine Turtle Specialist Group, Washington, D.C.

Guinda, X., J.A. Juanes, A. Puente, and B. Echavarri-Erasun. 2012. Spatial distribution pattern analysis of subtidal macroalgae assemblages by a non-destructive rapid assessment method. Journal of Sea Research, 67:34-43.

Häder, D.P., and F.L. Figueroa. 1997. Photoecophysiology of marine macroalgae. Photochemistry and Photobiology, 66:1-14.

Hanisak, M.D., and S.M. Blair. 1988. The deep-water macroalgal community of the East Florida continental shelf (U.S.A.). Helgoland Marine Research, 42:133-163

Hay, M.E., and J.P. Sutherland. 1988. The ecology of rubble structures of the South Atlantic Bight: a community profile. Washington, D.C. No. U.S. Fish and Wildlife Service Biological Report 85 (7.20). 67 p.

Humm, H.J. 1969. Distribution of marine algae along the Atlantic coast of North America. Phycologia, 7:43-53.

Huntly, N. 1991. Herbivores and the dynamics of communities and ecosystems. Annual Review of Ecology and Systematics, 22:477-503.

Hurd, C.L. 2000. Water motion, marine macroalgal physiology, and production. Journal of Phycology, 36:453-472.

Irving, A.D., and J.D.Witman. 2009. Positive effects of damselfish override negative effects of urchins to prevent an algal habitat switch. Journal of Ecology, 97:337–347.

Kain, J.M. 1975. Algal recolonization of some cleared subtidal areas. Journal of Ecology, 63:739-765.

Kaldy, J.E., K.H. Dunton, and A.B. Czerny. 1995. Variation in macroalgal species composition and abundance on a rock jetty in the northwest Gulf of Mexico. Botanica Marina, 38:519-528.

Kapraun, D.F., and F.W. Zechman. 1982. Seasonality and vertical zonation of benthic marine algae on a North Carolina coastal jetty. Bulletin of Marine Science, 32:702-714.

Kingsford, M.J., and C.N. Battershill. 1998. Studying Temperate Marine Environments: A Handbook for Ecologists. Canterbury University Press, Christchurch, New Zealand. 335 p.

Kinlan, B.P., and S.D. Gaines. 2003. Propagule dispersal in marine and terrestrial environments: A community perspective. Ecology, 84:2007-2020.

Kirst, G.O. 1989. Salinity tolerance of eukaryotic marine algae. Annual Review of Plant Physiology and Plant Molecular Biology, 41:21-53.

Kirst, G.O. 1996. Osmotic adjustment in phytoplankton and macroalgae. P. 121-129 in Biological and environmental chemistry of DMSP and related sulfonium compounds, Keller, M.D., R.P. Kiene, G.O. Kirst, and P.T. Visscher (Eds.). Springer, New York, New York.

Klöser, H., M.L. Quartino, and C. Wiencke. 1996. Distribution of macroalgae and macroalgal communities in gradients of physical conditions in Potter Cove, King George Island, Antarctica. Hydrobiologia, 333:1-17.

Kraufvelin, P., A. Lindholm, M.F. Pedersen, L.A. Kirkerud, and E. Bonsdorff . 2010. Biomass, diversity and production of rocky shore macroalgae at two nutrient enrichment and wave action levels. Marine Biology, 157:29-47.

Larsen, A. and K. Sand-Jensen. 2006. Salt tolerance and distribution of estuarine benthic macroalgae in the Kattegat - Baltic Sea area. Phycologia, 45:13-23.

Littler, D.S., and M.M. Littler. 2000. Caribbean Reef Plants. OffShore Graphics, Inc.,Washington, D.C. 542 p.

Littler, D.S., M.M. Littler, and M.D. Hanisak. 2008. Submersed Plants of the Indian River Lagoon. OffShore Graphics, Inc.,Washington, D.C. 286 p.

Lobban, C.S., and P.J. Harrison. 1994. Seaweed Ecology and Physiology. Cambridge University Press, Cambridge, United Kingdom. 360 p.

Lubchenco, J. 1980. Algal zonation in the New England rocky intertidal community: an experimental analysis. Ecology, 61:333-344.

Markager ,S., and K. Sand-Jensen. 1992. Light requirements and depth zonation of marine macroalgae. Marine Ecology Progress Series, 88:83-92.

McGuinness, K.A., and A.J. Underwood. 1986. Habitat structure and the nature of communities on intertidal boulders. Journal of Experimental Marine Biology and Ecology, 104:97-123.

Moschella, P.S., M. Abbiati, P. Åberg, L. Airoldi, J.M. Anderson, F. Bacchiocchi, F. Bulleri, G.E. Dinesen, M. Frost, E. Gacia E, et al. 2005. Low-crested coastal defence structures as artificial habitats for marine life: Using ecological criteria in design. Coastal Engineering, 52:1053-1071.

NASA. 2013. Spaceport Weather Data Archive. National Aeronautics and Space Administration.

Prekel, S., L. Fisher, and S. Higgins. 2008. P. 135-1138 in Habitat similarity between an artificial reef and the surrounding natural hardbottom in Broward County, FL,

U.S.A., ReefBase, (Ed.). 11th International Coral Reef Symposium; Ft. Lauderdale, Florida.

Redfoot, W.E. 1997. Population structure and feeding ecology of green turtles utilizing the Trident Submarine Basin, Cape Canaveral, Florida as developmental habitat. Master's thesis, University of Central Florida, Orlando. 72 p.

Reyier, E.A., D.M. Scheidt, K.G. Holloway-Adkins, C.M. Garreau, R.H. Lowers, and S.L. Gann. 2010. A characterization of biological resources within the Cape Canaveral Air Force Station Trident Submarine Basin, and adjacent marine waters of Port Canaveral, Florida (May 2008-April 2010). Patrick Air Force Base: 45 CES/CEAN.60 p.

Richardson, J.P. 1987. Floristic and seasonal characteristics of inshore Georgia macroalgae. Bulletin of Marine Science, 40:210-219.

Scheibling, R. 1986. Increased macroalgal abundance following mass mortalities of sea urchins (*Strongylocentrotus droebachiensis*) along the Atlantic coast of Nova Scotia. Oecologia, 68:186-198.

Schmidt, A.L., R.E. Scheibling. 2007. Effects of native and invasive macroalgal canopies on composition and abundance of mobile benthic macrofauna and turf-forming algae. Journal of Experimental Marine Biology and Ecology, 341:110-130.

Schneider, C.W., and R.B. Searles. 1991. Seaweeds of the Southeastern United States: Cape Hatteras to Cape Canaveral. Duke University Press, Durham, North Carolina. 553 p.

Schubert, H., S. Sagert, and R.M. Forster. 2001. Evaluation of the different levels of variability in the underwater light field of a shallow estuary. Helgoland Marine Research, 55:12-22.

Searles, R.B. 1984. Seaweed biogeography of the mid-Atlantic coast of the United States. Helgoland Marine Research, 38:259-271.

Sousa, W.P. 1979a. Disturbance in marine inter-tidal boulder fields: the non-equilibrium maintenance of species-diversity. Ecology, 60:1225-1239.

Sousa, W.P. 1979b. Experimental investigations of disturbance and ecological succession in a rocky inter-tidal algal community. Ecological Monographs, 49:227-254.

Stephenson, T.A., and A. Stephenson. 1952. Life between tide-marks in North America: II. Northern Florida and the Carolinas. Journal of Ecology, 40:1-49.

Thrush, S.F., M. Chiantore, V. Asnaghi, J. Hewitt, D. Fiorentino, and R.Cattaneo-Vietti. 2011. Habitat-diversity relationships in rocky shore algal turf infaunal communities. Marine Ecology Progress Series, 424:119-132.

Underwood, A., P. Jernakoff. 1984. The effects of tidal height, wave-exposure, seasonality and rock-pools on grazing and the distribution of intertidal macroalgae in New South Wales. Journal of Experimental Marine Biology and Ecology, 75:71-96.

U.S. Dept of Commerce NOAA. 2010. National Data Buoy Center - Station TRDF1 - 8721604 - Trident Pier, Florida. Available from: http://www.ndbc.noaa.gov/station_page.php?station=TRDF1.

Valiela, I., J. McClelland, J. Hauxwell, P.J. Behr, D. Hersh, and K. Foreman. 1997. Macroalgal blooms in shallow estuaries: Controls and ecophysiological and ecosystem consequences. Limnology and Oceanography, 42:1105-1118.

Webster, R.M. 1974. An inexpensive sampler for studying the microbiology of river mud. Limnology and Oceanography, 19:159-161.

Weibel, E.R., Kistler GS, F. W. 1966. Practical stereological methods for morphometric cytology. Journal of Cell Biology, 30:23-38.

Wells, J., E.J. Moll, and J.J. Bolton. 1989. Substrate as a determinant of marine intertidal algal communities at Smitswinkel Bay, False Bay, Cape. Botanica Marina, 32:499-502.

Whorff, J.S., L.L.Whorff, and M.H. Sweet. 1995. Spatial variation in an algal turf community with respect to substratum slope and wave height. Journal of the Marine Biological Association of the United Kingdom, 75:429-444.

Witman, J., D. Steller, and J.Coyer. 1999. A Guide to Methods in Underwater Research: The Underwater Catalog. Shoals Marine Laboratory, Ithaca, New York.

Worm, B., and U. Sommer. 2000. Rapid direct and indirect effects of a single nutrient pulse in a seaweed-epiphyte-grazer system. Marine Ecology Progress Series, 202:283-288.

Wright, J.T., S.A. Dworjanyn, C.N. Rogers, P.D. Steinberg, J.E. Williamson, A.G.B. Poore. 2005. Density-dependent sea urchin grazing: differential removal of species, changes in community composition and alternative community states. Marine Ecology Progress Series, 298:143-156.

Zaneveld, J.S. 1972. The benthic marine algae of Delaware, USA. Chesapeake Science, 13:120-138.

# II. MACROALGAL FORAGING PREFERENCES OF JUVENILE GREEN TURTLES (CHELONIA MYDAS) IN A WARM TEMPERATE/SUBTROPICAL TRANSITION ZONE


## Abstract

The juvenile green turtle (*Chelonia mydas*) population at the Trident Basin at Port Canaveral, Cape Canaveral, Florida (28.41ºN, 80.59ºW) has historically exhibited strong site fidelity based on high recapture rates. Macroalgae growing on rock revetment provide the primary food resource for turtles within the Basin. The purpose of this study was to compare the foraging of juvenile green turtles (*Chelonia mydas*) with the availability of macroalgal resources. Foraging (lavage) samples from 94 juvenile green turtles during a 2-year study period from September 2008 through April 2010 were analyzed with data from two previous studies to determine patterns of foraging habits through time. Turtles predominantly foraged on species of Rhodophyta and Chlorophyta; however, opportunistic foraging on flotsam and invertebrates was common. Electivity indices indicated that selection for certain rhodophytes (i.e., *Gelidiopsis planicaulis*, *Grateloupia filicina*, and *Hypnea spinella*) and chlorophytes (i.e., *Cladophora liniformis*, *Ulva flexuosa*, *U. lactuca*, and *U. prolifera*) varied by sampling period. In addition, after an extended cold event, foraging samples from several turtles contained macroalgae not present in the Basin which suggests that turtles moved out of the Basin to forage during this time or newly immigrated. Establishing baseline resource utilization is instrumental

for identifying the quality and function of natural and artificial habitats supporting juvenile green turtles, as their populations continue to recover around the globe.

## Introduction

After *Chelonia mydas* (green turtles) emerge from a sandy nest, they will make four different ontogenetic habitat shifts during their lifetime: (1) post-hatchling and early juvenile stages in oceanic waters, (2) early juvenile stage in neritic waters, (3) adults in neritic feeding grounds, and (4) adults in inter-nesting and/or breeding habitat (Musick and Limpus 1997). On a finer scale, there is increasing evidence that green turtles occupy different geographic and neritic habitat-types (e.g., estuarine, rocky intertidal, coral reef, inlet) at different stages of their juvenile years. In Florida, long-term capture studies show that the mean size-class of juvenile green turtles differs in ecologically dissimilar habitats (Ehrhart et al. 1996; Bresette et al. 1998; Holloway-Adkins and Provancha 2005). Recruitment patterns in two Florida locations suggest a seasonal immigration of the smallest post-pelagic, juvenile size-class animals in winter/spring (Bresette et al. 1998; Redfoot and Ehrhart 2013).

A handful of studies have identified and characterized juvenile green turtles associated with inlet and jetty areas and examined the foraging of turtles in these developmental habitats (Coyne 1994; Shaver 1994; Metz and Landry 2013). The Trident Basin at Port Canaveral in Cape Canaveral, Florida has been recognized as juvenile green turtle habitat since 1993. Researchers estimate that the Basin is a roughly 0.5 $km^2$ body of water that is occupied by 27-224 (mean 61 ± 10 SD) juvenile green turtles at any one time (Redfoot and Ehrhart 2013). The Trident Basin population represents the largest

aggregation of the smallest size-class of juvenile green turtles currently found on the east coast of Florida (Redfoot and Ehrhart 2013). Their small size-class indicates that many are newly post-pelagic animals undergoing ontogenetic shifts from oceanic to neritic waters (Hirth 1997). This shift entails a transition from a characteristically carnivorous to a predominantly herbivorous diet (Reich et al. 2007; Arthur and Balazs 2008). Many juvenile green turtles captured in the Trident Basin are measurably thinner than the norm, and their growth rates are slower than green turtles in adjacent estuarine and nearshore developmental habitats (Kubis 2003). Researchers have suggested that the macroalgal resources within the Basin drive the size-class and recruitment status of green turtles within this habitat (Redfoot and Ehrhart 2013).

The foraging habits of green turtles in seagrass habitats have been well-documented (Bjorndal 1980; Mortimer 1981; Bjorndal 1985; Garnett et al. 1985; Bjorndal et al. 1991) as has the role and impact of green turtles grazing in seagrass communities (Williams 1988; Moran and Bjorndal 2005, 2007; Kuiper-Linley et al. 2007). These studies have contributed to a greater understanding of the ability of seagrass ecosystems to support green turtles (Moran and Bjorndal 2005). However, in many areas green turtles primarily forage on macroalgae (Brand-Gardner et al. 1999; Holloway-Adkins 2001; Gilbert 2005; Makowski et al. 2006; Arthur and Balazs 2008), and little is currently known of the impacts of grazing on macroalgal communities. As green turtle populations begin to recover, it is important to understand the habitat requirements for survival at all life stages. Marine turtle populations exceeding carrying capacity have already been recognized in some areas (Lal et al. 2010), necessitating research to

understand present and future challenges for managing resources for humans and wildlife.

The purpose of this study was to compare the foraging habits of juvenile green turtles with the availability of macroalgal resources within the Trident Basin. The specific research objectives were: (1) determine the foraging ecology of juvenile green turtles in the Trident Basin in a recent 2-year study period (September 2008-April 2010), (2) compare foraging data with concurrent macroalgal availability to determine if foraging is based on selection or availability for individual species, and (3) compare the present foraging data with two previous studies conducted in the Basin to determine if foraging content differs temporally (over periods of years, as well as seasons).

## Material and Methods

### *Study site*

The study was located at the Trident Submarine Basin, a non-public military facility at Port Canaveral, Cape Canaveral, Florida (28.41°N, 80.59ºW). The mouth of the Basin is located approximately 150 m west of the inlet mouth (Figure 2.1). The Basin was dug out of the existing land mass, with a shallow shelf along the perimeter that extends towards the center approximately 10 m and then drops sharply towards the 15-m deep center (Redfoot 1997). Concrete walls and sloped rock revetments reduce soil runoff and erosion along the shoreline, and a large concrete wharf supports ship activities. Imported granite boulders line the north, west, and part of the northeast side of the Basin while the concrete wharf and seawall encompass an area approximately 375 x 50 m on the east wall (Figure 2.2). Boulder and seawall areas were previously marked to delineate 100-m linear distances around the Basin with the 0 point located at the

southwest-most Basin area (Figure 2.2). Boulders on the west wall and approximately 100 m of the north wall were subtidally submerged, supporting a diversity of macroalgae and invertebrate epibiota (see Chapter 1). Macroalgal cover within the 1300-m long study area was estimated at 5.93 $km^2$ (or 593 ha) based on sampling conducted for algal abundance and distribution (see Chapter 1).

Tangle nets and long-handled dip nets were used to capture juvenile green turtles in and adjacent to the Trident Basin. Sampling was conducted during five 2-day sampling events (September 13-14, 2008, March 7-8 and August 8-9, 2009, February 27-28 and April 17-18, 2010). Turtle captures ranged from 11-40 turtles per sampling event. Capture and handling methods for marine turtles followed techniques outlined in Ehrhart and Ogren (1999). Two tangle nets approximately 220-m long and 4-m high with 30- and 40-cm stretch (knot to knot) mesh sizes were typically set in approximately 2-m water depth over sand adjacent to the rock revetment. Nets were tended continuously from a small boat and entangled turtles were quickly retrieved by the researchers and brought to shore for processing.

*Foraging sample collection and processing*

Foraging samples were collected via lavage, which is a modified veterinary stomach pump procedure (Balazs 1980; Forbes and Limpus 1993). Clean, flexible tubing was pre-lubricated with cooking oil spray and a small, sturdy prying tool was used to keep the jaws open prior to inserting the tube into the turtle's mouth. Seawater was pumped through the tubing and the lubricated tube was slowly inserted into the lower esophageal area. The tube was moved slowly and gently back and forth to dislodge food particles for approximately 20 s. An 8-L bucket was placed beneath the turtle's head to

receive the lavage sample contents. Sample contents from the receiving bucket were filtered from the seawater with 0.5-mm size mesh netting material (e.g., paint strainer, fish net). The sample was placed into a Nalgene 250-ml smoke-tinted plastic jar to reduce cell destruction caused by UV radiation, and a 5% formalin/seawater mix was added to the sample. The formalin preserved the food items, and the seawater helped maintain cellular osmotic pressure, which is important in the identification phase.

Foraging samples were quantified by a modified procedure from Channells and Morrissey (1981) and Forbes (1999). In the laboratory, samples were strained through a 0.1-mm filter. Stereo and light microscopes were used to identify the sample contents, including cross-sections to reveal the internal structure and cell size. After all items in the foraging sample were identified to the lowest taxonomic level possible, the sample was spread over a Petri dish marked with a grid system composed of 16 1-$cm^2$ grids and viewed through a stereoscope set at 0.79 x power and fitted with a 100-count gradicule in the ocular. One of the 16 squares on the Petri dish was aligned within the ocular gradicule, and the foraging item located in the apex of the left corner was recorded for odd-numbered squares in the ocular grid. Each 1- x 1-cm Petri dish square potentially contained 50 counts of foraging items. The Petri dish was aligned with the next square until the foraging items that covered all squares of the Petri dish were counted. If a foraging sample covered all 16 grid squares on the Petri dish, there were potentially 800 foraging items per sample for data analysis. Percent composition (based on counts of each item in a foraging sample divided by the total counts in the sample) and standard deviation (± SD) were calculated for individual foraging samples. The frequency of occurrence was the number of foraging samples that contained a macroalgal species.

*Foraging data*

A reference list of all foraging items found in lavage samples, their frequency of occurrence (i.e., the number of lavage samples a foraging item was present in), and their average percent composition (± SD) in lavage samples was constructed for the 2008-2010 (herein referred to as the recent or "2010") foraging study. Ivlev's electivity indices were calculated for the 10 most abundant macroalgae in the 2010 foraging study. The comparative foraging study analyses was conducted on algal and non-algal content in the lavage samples; some items were identified as individual species while others were grouped by morphological similarity (e.g., *Amphiroa* spp. and *Jania adhaerens*) or abiotic or biotic characteristics (e.g., flotsam associated invertebrates). Ultimately, 16 foraging items belonging to one of 9 different categories [i.e., Rhodophyta, Chlorophyta, Ochrophyta, Cyanobacteria, seagrass, flotsam-associated invertebrates (e.g., *Sargassum* nudibranchs, jellyfish), benthic-associated invertebrates (e.g., tunicates, hydroids, tubeworms), substrate/detritus (e.g., rock, sand, decomposed matter), and plastic/paint and metal flakes] were used to conduct comparative analyses of foraging studies.

*Ivlev's Electivity Index*

Ivlev's Electivity Index (Krebs 1989), which is a method for measuring foraging selection based on relative prey abundance was used to determine if juvenile green turtles foraged selectively or based on abundance on macroalgae within the Basin. The percent composition of the 10 most frequently encountered macroalgae in green turtle foraging samples for each sampling period (n = 5) was compared with the average percent composition of the macroalgal species from transects (n = 13) within the Trident Basin during the same time period (see Chapter 1).

Ivlev's Electivity Index $E = \frac{r_i - p_i}{r_i + p_i}$

The measure of electivity (E) is based on the relative abundance (percentage or proportion) of a prey item ($r_i$) in foraging samples and the relative abundance (percent or proportion) of that prey item in the environment ($p_i$) (Strauss 1979). Measurements between 0 and +1 represent selection based on relative abundance, and measurements between -1 and 0 represent avoidance or inaccessible prey items (Jacobs 1974; Krebs 1989). For the purpose of this study, $E \geq 0.50$ was considered selection 'for' and $\leq -0.50$ was considered 'avoidance' or selection against a macroalga in relation to its availability in the environment.

*Foraging study comparison*

The present foraging data were compared with two previous foraging studies conducted in the Basin to determine if foraging content differed over periods of years, as well as seasons. The first study was from 1993-1996 (Redfoot 1997) and the second study was from 1999-2002 (Ehrhart et al. 2002, unpubl. data) herein referred to as the "1997" and "2002" studies (respectively). No macroalgal abundance data for the 1997 and 2002 studies were available due to security restrictions on diving imposed by the U.S. Navy; therefore, electivity indices could not be calculated for these earlier study periods.

Non-parametric multivariate statistical procedures (Primer-E software, Plymouth, UK), useful in the analyses of community data which are characteristically non-normal, right-skewed, and contain an abundance of zero values, were used to test for differences in foraging samples within and among studies and seasons. Data were standardized and

square root-transformed to down-weight the contribution of the most abundant species (Clarke and Green 1988; Mumby et al. 1996). For comparisons among foraging studies, data were averaged by season and study period and merged into a single datasheet to further reduce variability. A Bray-Curtis (B-C) similarity matrix was constructed with similarity coefficient calculations being computed between every pair of replicates within and among the studies (and/or seasons) (Clarke and Warwick 2001). MDS (multidimensional scaling) ordination plots were constructed to visually represent dissimilarities among groups in as few dimensions as possible (Clarke and Warwick 2001). Plotted points that are close together are more similar while points further away are less similar. The "stress" value of a plot is a measure of the distortion that was required to represent the data in the 2D plot. A stress value of 0 indicates a perfect representation of the data. A stress value $\leq 0.2$ is considered a useful representation for data interpretation. Ordination plots resulting in stress values >0.2 should be interpreted with caution, as the distortion is considerably high. Values >0.3 indicate a high level of distortion was created to display the data and are considered unreliable to generate inferences from the configuration (Clarke and Warwick 2001).

ANOSIM procedure (Primer-E routine; Clarke and Warwick 2001) was used to test the null hypotheses of no significant differences in juvenile green turtle foraging samples among studies (n = 3), among studies within seasons (n = 12), and among seasons within each study (n=4). When there are a large number of samples, as was the case in this study, ANOSIM R values can be substantially close to 0 but be "significant" ($p < 0.05$). For interpretation purposes, significant values (p) were considered both biologically and statistically significant at R values $\geq 0.45$, indicating that samples within

groups (i.e., sampling periods) were more similar than among group replicates (Clarke and Warwick 2001). R values near 0 occur when similarities among and within groups on average are the same. SIMPER (similarity percentage) routine was used to identify the foraging items that contributed up to 90% of the differences among and within studies and seasons that were significantly different (criteria $R \geq 0.45$, $p < 0.5$) in composition (Clarke and Warwick 2001).

## Results

### *Recent foraging study*

Foraging samples were obtained from 94 juvenile green turtles during five 2-day capture-and-release events between September 2008 and April 2010 (i.e., 2010 present study). Turtle capture locations were not specific to any one area of the Basin, but were instead distributed around the Basin between the 0-2100 m marks and included deeper water adjacent to the wharf (1800-2100-m) and shipwalk (south of 1400-1500 m) structures (Figure 2.2). Straight carapace lengths (SCL) ranged from 24.3 to 44.5 cm (average 29.4 ± 3.4 cm SD). Foraging samples contained over 32 macroalgal species, one cyanobacterium species, and 17 non-algal food items (e.g., seagrass, invertebrates, rock, etc.; Table 2.1). Four rhodophytes (*Gelidium crinale*, *Grateloupia filicina*, *Hypnea spinella*, and *Centroceras clavulatum*) were found in >50.0% of samples (66, 53, 52, 48, respectively, out of 94; Table 2.1). The combined average percent composition of six rhodophytes (*G. filicina*, *H. spinella*, *G. crinale*, *G. planicaulis*, *P. denudata*, and *C. clavulatum*) and two chlorophyte species (*U. lactuca* and *U. prolifera*) amounted to >58% of the total macroalgal composition (Table 2.1).

### *Ivlev's Electivity Index*

Green turtles selected several macroalgal species beyond what would be expected based on their availability (E $\geq$0.5): *G. planicaulis* (September 2008), *G. filicina* (September 2008 and March 2009), *H. spinella* (August 2009 and April 2010), *Cladophora liniformis* (August 2009 and February 2010), *U. flexuosa* (August 2009 and February 2010), *U. lactuca* (August 2009, February 2010, and April 2010), and *U. prolifera* (September 2008, August 2009, and February 2010) (Table 2.2). During all sampling periods green turtles selected against or "avoided" *Centroceras clavulatum* beyond what would be expected based on its availability (E $\leq$-0.5). Other species which were at times selected against were *G. planicaulis* (March 2009), *P. denudata* (March 2009 and February 2010), *C. liniformis* (September 2008 and March 2009), *U. flexuosa* (September 2008 and March 2009), and *U. lactuca* (September 2008).

*Foraging study comparison*

Overall, rhodophytes were the most frequently consumed macroalgae (Figure 2.3) and had the highest percent composition of foraging items for all 3 studies (Figure 2.4). Categorically, the Gelidiales (i.e., *G. planicaulis* and *G. crinale*) were the most frequently consumed (77.7-98.6% of the samples in studies; Figure 2.3) and had the highest percent composition in lavage samples, averaging between 21.1-54.0% of percent composition (Figure 2.4). While the frequency of occurrence of chlorophytes *Cladophora* spp. and *U. lactuca* in lavage samples ranged between 36.1-68.4% and 11.1-41.5%, respectively, the percent compositions were comparatively lower (0.4-2.3% and 0.6-5.1%; respectively) than many rhodophyte species (Figs. 3-4). Among all three studies, the frequency of occurrence of substrate/detritus in foraging samples was high (87.0-89.9%; Figure 2.3) and the percent composition was relatively moderate (6.5-13.4%; Figure 2.4).

*Comparisons among and within foraging studies*

The MDS ordination plot indicated low dissimilarity for the percent composition of foraging samples among studies based on season (Figure 2.5a) and ANOSIM tests were non-significant (n = 12, Global R = 0.235, p = 0.068). However, comparisons of foraging samples of the three different studies significantly differed between the 2002 and 2010 studies (ANOSIM; R = 0.750, p = 0.029; Table 2.3). Higher compositions of *Hypnea* spp., combined *Gelidiopsis* and *Gelidium*, and *Polysiphonia* spp. in 2002 and higher compositions of *G. filicina*, *U. flexuosa*, *U. lactuca*, and *Cladophora* spp. in 2010 contributed to >90% of differences between the two studies (SIMPER; Table 2.4).

MDS ordination plots for each of the foraging studies showed little separation (dissimilarity) among foraging samples based on season (Figure 2.5b-d) and ANOSIM results were considered biologically non-significant (R <0.45, p <0.05; Table 2.5). However, a pairwise comparison was significant for summer vs. winter of 2010 study (ANOSIM; R = 0.483, p <0.001; Table 2.5). Nine foraging items contributed approximately 90% to differences in the percent composition of foraging samples between summer and winter (SIMPER; Table 2.6). Foraging items that contributed to differences among lavage samples were the higher abundance of *H. spinella*, Gelidiales (*G. planicaulis* and *G. crinale*) in summer and the higher percent composition of *C. catenata* and *U. flexuosa* in winter (Table 2.6).

Discussion

*Foraging content*

Juvenile green turtles foraged as generalists on many of the relatively abundant macroalgal species present within the Trident Basin. Lavage samples were dominated by

red (e.g., *Gelidium* spp., *Hypnea* spp.) and green (e.g., *Ulva* spp. and *Cladophora* spp.) macroalgae. Attached species of brown macroalgae (e.g., *Dictyota* spp., *Padina* spp.) were rarely encountered in algal transects (see Chapter 1) and only drift species of *Sargassum* (e.g., *S. natans*, *S. fluitans*) were found in lavage samples (Table 2.1). Opportunistic foraging on flotsam-associated invertebrates (e.g., *Sargassum* nudibranchs, jellyfish, etc.) was common among all three foraging studies, as was the consumption of substrate and detritus (e.g., sand, rock, decomposed plant). Anthropogenic debris (i.e., plastic, paint, and metal flakes) was found in 15% (14 of 94) of samples.

*Ivlev's Electivity Index*

Selection "for" certain macroalgae varied among sampling periods and may have been a result of changes in the food resource availability caused by changes in temperature, pressure on resources via herbivore competition, and/or the presence of alternate foodstuffs (e.g. flotsam). The latter case, possibly a vestige of epipelagic foraging strategies prior to ontogenetic changes to benthic feeding (Arthur and Balazs 2008), was unexpected and not accounted for during this study. Following the extreme cold period in January 2010 (NOAA-NCDC 2013), 'non-local' macroalgae [e.g., *Bryocladia cuspidata*, *Gracilaria mammillaris*, and *Caulerpa prolifera*] were found in the foraging samples of turtles captured in April 2010 (spring). These 'non-local' macroalgae are abundant as attached species on nearshore hardbottom reefs approximately 20 km south of the Trident Basin (pers. observ.) and were frequently found in the foraging samples of juvenile green turtles captured over nearshore reefs in southern Brevard County (Holloway-Adkins 2006). Some of the juvenile green turtles that typically reside within the Trident Basin (recaptured animals) may have sought

warmer waters during the extreme cold period and returned to the Basin in April as temperatures began to warm while others may have recently emigrated.

*Foraging study comparison*

Differences in the average percent composition of *Hypnea* spp. and *G. filicina* contributed to the dissimilarity between the 2002 and 2010 foraging studies and were associated with changes in the macroalgal composition after the extreme cold period that occurred in January 2010. As a result of the extreme cold, the percent compositions of subtropical species such as *Hypnea* spp., *Amphiroa fragilissima*, and *Jania adhaerens* declined with decreasing temperature whereas the percent composition of *G. filicina* increased with decreased temperature (see Chapter 1). Among all three foraging studies, few changes in the seasonal composition of foraging items were interpreted as biologically significant. The impact of large or small variations in the presence and abundance of nutritiously superior macroalgae (e.g., *Hypnea* spp., *G. crinale;* McDermid et al. 2007) are unknown at this time.

Green turtle foraging on invertebrate prey items, especially foraging items associated with pelagic drift lines or surface water convergence zones, has been previously described (Seminoff et al. 2002). Based on isotope foraging study analysis conducted by Vander-Zanden et al. (2013), pelagic and neritic juvenile green turtles have a comparatively wide niche breadth encompassing multiple trophic level feeding habits. As green turtles mature, they become more specialized feeders on seagrass (Vander-Zanden et al. 2013). Our current understanding of juvenile green turtle foraging ecology would benefit from studies that address prey encounter rates and selection criteria of green turtles in the wild. The opportunistic foraging of flotsam-associated organisms

leaves turtles vulnerable to non-discriminate ingestion of anthropogenic debris and surfactant toxins which have negative effects on green turtle health and survival (Bjorndal et al. 1994; McCauley and Bjorndal 1999; Cserháti et al. 2002; Roark et al. 2009).

*Significance of this study*

Habitats essential to managed species are regulated by the South Atlantic Fishery Management Council (SAFMC 1998) under both Essential Fish Habitat (EFH) and Habitat of Particular Concern (HAPC) plans. Coastal inlets are designated EFH-HAPC for several federally managed fishes (e.g., snapper-grouper, migratory, and demersal fishes). Recovery plans for marine turtles, in combination with fishery management regulation of ecologically and economically important fishes, directly and/or indirectly benefit both fish and sea turtle populations through habitat conservation, water quality monitoring, marine debris reduction, as well as the restriction and reduction on harvesting. One example in the Trident Basin has been the recommendation of both sea turtle and fishery biologists to expand the existing habitat by deploying additional boulders in subtidal waters of the Basin where little or no rock currently exists (Redfoot 1997; Nelson 2001; Reyier et al. 2010), a plan that would potentially benefit both sea turtles and fishes.

This is the first study to compare the content of juvenile green turtle foraging samples with the macroalgal community present within the Trident Basin. Previous foraging studies (Redfoot 1997, Ehrhart et al. 2002, unpub data) provided the opportunity to explore a near-continuous examination of the foraging habits of juvenile green turtles within this developmental habitat for nearly two decades. Altogether, these studies

provide critical baseline data about the green turtles that reside in this warm temperate/subtropical transition zone. Biogeographic transition zones are key areas to monitor shifts in the distribution of flora and fauna in response to changes at environmental and community levels (Beier et al. 2012). Expanding our current knowledge of the role of green turtles in algal-based communities, both the impact (e.g., cropping, grazing) and contribution of turtles (e.g., nutrient cycling, substrate clearing), is important to the long-term recovery and protection of habitats important to marine turtles and other ecologically important species.

Marine turtles are increasingly utilizing man-made inlet and jetty habitats; sites of growing industrial and recreational vessel activity. Monitoring anthropogenic impacts (e.g., stormwater runoff, monofilament fishing line, trash, etc.) is critical in the maintenance of quality habitat for a number of species and, in this case, the endangered green turtle. Equally important are the challenges in assessing the functional role of artificial vs. natural hardbottom types. The quality of habitat, regardless if it is natural or artificial, plays a significant role in the pace and path of the recovery of green turtle populations. The selection, site-fidelity, and function of these areas as developmental habitat for marine turtles are unknown as well as the long-term consequences and evolutionary significance. Future researchers are encouraged to take these points into consideration.

Tables

Table 2.1. Foraging sample content from juvenile green turtles captured in the Trident Basin during the sampling periods between September 2008-April 2010 (n = 94). Frequency = total number of samples that contained a particular foraging item. Mean (%)

= average percent composition of a foraging item in all samples and standard deviation (± SD).

| Foraging item | Frequency | Composition Mean % | Composition ±SD |
|---|---|---|---|
| RHODOPHYTA | | | |
| *Agardhiella subulata* | 1 | 0.10 | 0.96 |
| *Amphiroa fragilissima* | 27 | 1.86 | 6.35 |
| *Bryocladia cuspidata* | 4 | 0.32 | 1.78 |
| *Centroceras clavulatum* | 48 | 2.77 | 5.52 |
| *Ceramium floridanum* | 3 | 0.02 | 0.16 |
| *Chrysemenia enteromorpha* | 3 | 0.03 | 0.24 |
| *Dasya abbottiana* | 1 | 0.02 | 0.15 |
| *Gelidiopsis planicaulis* | 43 | 6.93 | 14.56 |
| *Gelidium crinale* | 66 | 9.46 | 15.90 |
| *Gracilaria mammillaris* | 2 | 1.60 | 11.25 |
| *Grateloupia filicina* | 53 | 15.33 | 26.50 |
| *Halymenia floresii* | 1 | 0.38 | 3.65 |
| *Hypnea spinella* | 52 | 12.75 | 23.02 |
| *Jania adhaerens* | 8 | 0.11 | 0.59 |
| *Lomentaria baileyana* | 1 | 0.01 | 0.09 |
| *Polysiphonia denudata* | 33 | 2.86 | 8.81 |
| *Polysiphonia subtilissima* | 1 | 0.09 | 0.92 |
| CHLOROPHYTA | | | |
| *Bryopsis plumosa* | 6 | 0.06 | 0.31 |
| *Caulerpa prolifera* | 3 | 0.33 | 2.86 |
| *Caulerpa racemosa* | 4 | 1.43 | 7.66 |
| *Chaetomorpha aerea* | 1 | 0.24 | 2.30 |
| *Chaetomorpha gracilis* | 10 | 0.09 | 0.44 |
| *Cladophora catenata* | 29 | 1.22 | 7.20 |
| *Cladophora liniformis* | 12 | 1.06 | 5.53 |
| *Ulva flexuosa* | 20 | 1.36 | 4.77 |
| *Ulva intestinalis* | 1 | 0.99 | 9.64 |
| *Ulva lactuca* | 39 | 4.09 | 9.76 |
| *Ulva prolifera* | 12 | 4.20 | 17.60 |
| OCHROPHYTA | | | |
| *Sargassum fluitans* | 3 | 0.09 | 0.81 |
| *Sargassum hystrix* var. *buxifolium* | 9 | 1.26 | 5.51 |
| *Sargassum natans* | 1 | 0.17 | 1.68 |
| CYANOBACTERIA | | | |
| cyanobacteria (unidentified) | 3 | 0.08 | 0.62 |
| SEAGRASS | | | |
| seagrass/other plant | 18 | 2.85 | 9.70 |
| FLOTSAM-ASSOCIATED INVERTEBRATES | | | |
| *Scyllaea pelagica* (*Sargassum* nudibranch) | 7 | 5.71 | 20.87 |
| *Stomolophus* sp. (cannonball jellyfish) and fish eggs | 5 | 2.5 | 49.49 |
| BENTHIC-ASSOCIATED INVERTEBRATES | | | |
| Polychaeta (tubed, calcareous worms, segmented worms) | 11 | 0.46 | 1.85 |
| Demospongia (e.g., *Cliona* sp.) | 2 | 0.04 | 0.30 |
| Ascidiacea (sea squirts) | 8 | 1.54 | 8.14 |
| Gymnolaemata-bryozoans (*Bugula neritina*) | 7 | 0.27 | 1.57 |
| Hydrozoa (*Hydroides* sp.) | 13 | 0.44 | 1.84 |
| *Balanus* sp. (barnacles) | 8 | 0.19 | 0.93 |

| | | | |
|---|---|---|---|
| Malacostraca (*Cymadusa* sp., *Caprella* sp., *Pagurus* sp.) | 6 | 0.06 | 0.35 |
| Gastropoda (e.g., *Cerithium* sp.) | 17 | 18.1 | 2.96 |
| SUBSTRATE/DETRITUS | | | |
| rock | 7 | 0.68 | 4.33 |
| mollusk shell pieces | 66 | 6.8 | 12.43 |
| detritus | 32 | 5.54 | 15.53 |
| PLASTIC/PAINT AND METAL FLAKES | | | |
| paint and metal flakes | 4 | 0.01 | 0.08 |
| plastic | 14 | 1.08 | 4.02 |

Table 2.2. Ivlev's Electivity Index (IEI) calculations based on percent composition data for the ten most abundant macroalgae in transect surveys (Trans) and percent composition of algae found in the lavage samples (Lav) of green turtles (*Chelonia mydas*; n = 94). Indices characterize the degree of prey selection based on its relative abundance in the environment (Strauss 1979). Values range between -1 to +1; values close to +1, -1 , and 0 indicate animals are respectively selecting for, against, or based on availability of a particular prey item (i.e., a macroalgal species). Numbers in bold are Ivlev's Electivity indices ≥0.5, that indicate turtles were selecting 'for' a macroalgal species. Bold values for indices ≤-0.5 indicate turtles' selection 'against' or avoidance of a macroalgal species.

| Species | Sep-08 Trans | Sep-08 Lav | IEI | Mar-09 Trans | Mar-09 Lav | IEI | Jun -09 Trans | Aug-09 Lav | IEI | Feb-10 Trans | Feb-10 Lav | IEI | Apr-10 Trans | Apr-10 Lav | IEI |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Centroceras clavulatum* | 7.9 | 2.3 | **-0.6** | 18.7 | 3.4 | **-0.7** | 18.0 | 8.6 | -0.4 | 2.1 | 0.1 | **-0.9** | 12.7 | 2.1 | **-0.7** |
| *Gelidiopsis planicaulis* | 4.3 | 23.0 | **0.7** | 17.7 | 4.4 | **-0.6** | 10.0 | 10.4 | 0.0 | 11.5 | 7.4 | -0.2 | 6.5 | 0.1 | **-1.0** |
| *Gelidium crinale* | 27.0 | 26.3 | 0.0 | 12.6 | 6.3 | -0.3 | 11.1 | 9.7 | -0.1 | 17.5 | 20.1 | 0.1 | 15.3 | 11.7 | -0.1 |
| *Grateloupia filicina* | 2.0 | 11.1 | **0.7** | 12.8 | 36.7 | **0.5** | 8.9 | 9.3 | 0.0 | 19.9 | 10.6 | -0.3 | 25.8 | 25.0 | 0.0 |
| *Hypnea spinella* | 11.5 | 6.2 | -0.3 | 6.8 | 7.4 | 0.1 | 12.9 | 40.2 | **0.5** | 1.1 | 0.6 | -0.3 | 0.6 | 16.6 | **0.9** |
| *Polysiphonia denudata* | 0.3 | 0.3 | 0.1 | 5.4 | 1.2 | **-0.6** | 1.7 | 2.2 | 0.2 | 19.3 | 6.8 | **-0.5** | 5.0 | 10.3 | 0.3 |
| *Cladophora liniformis* | 1.7 | 0 | **-1.0** | 2.8 | 0.1 | **-0.9** | 0.1 | 0.3 | **0.5** | 0.6 | 19.5 | **0.9** | 0.0 | 0.0 | – |
| *Ulva flexuosa* | 3.5 | 0 | **-1.0** | 6.6 | 0.9 | **-0.8** | 0.1 | 1.5 | **0.9** | 5.4 | 14.2 | **0.5** | 0.8 | 1.5 | 0.3 |
| *U. lactuca* | 1.5 | 0.3 | **-0.6** | 2.8 | 5.7 | 0.3 | 0.7 | 5.1 | **0.8** | 3.8 | 10.5 | **0.5** | 1.0 | 9.3 | **0.8** |
| *U. prolifera* | 0.0 | 17.5 | **1.0** | 0.0 | 0.0 | – | 0.3 | 1.6 | **0.7** | 0.1 | 5.9 | **1.0** | 0.1 | 0.0 | 0.0 |

Table 2.3. Pairwise comparisons of the percent composition of juvenile green turtle foraging samples among three foraging studies that were conducted within the Trident Basin. The most recent study (2010) was conducted from 2008-2010. The first study was conducted by Redfoot (1997) followed by a second study in 2002 (b; Ehrhart et al. 2002, unpub data). Data were averaged by season within study (ANOSIM; Global R value = 0.391, p = 0.007, permutations 5775).

| Pairwise tests | R | p |
|---|---|---|
| 1997, 2002 | 0.135 | 0.257 |
| 1997, 2010 | 0.260 | 0.114 |
| 2002, 2010 * | 0.750 | 0.029 |

*****results were significant based on R ≥0.45, p <0.05.

Table 2.4.Foraging items that contributed 90% or more to the dissimilarity between lavage samples of juvenile green turtles in 2002 vs. 2010 foraging studies (a; SIMPER; average dissimilarity = 43.2%). Foraging items are listed in descending order of dissimilarity contribution. Asterisks (*) indicate foraging item(s) were identified in previous studies under alternate name(s) and/or were combined for the analyses.



| Foraging item(s) | 2002 Abundance Average | 2010 Abundance Average | Dissimilarity Average | Dissimilarity ± SD | Contribution Percent | Cumulative Percent |
|---|---|---|---|---|---|---|
| *Hypnea* spp. | 19.72 | 9.00 | 5.68 | 1.5 | 13.13 | 13.13 |
| *Gelidiopsis* and *Gelidium** | 25.12 | 13.94 | 5.59 | 2.28 | 12.94 | 26.06 |
| *Grateloupia filicina* * | - | 10.70 | 5.35 | 8.23 | 12.37 | 38.43 |
| Seagrass/other plant | 10.76 | 4.67 | 3.54 | 1.55 | 8.19 | 46.62 |
| *Ulva flexuosa** | 6.64 | 8.13 | 2.74 | 1.45 | 6.35 | 52.96 |
| *Ulva lactuca** | 2.18 | 6.96 | 2.74 | 1.76 | 6.33 | 59.29 |
| *Polysiphonia* spp. * | 9.79 | 4.70 | 2.69 | 1.37 | 6.22 | 65.52 |
| Flotsam-associated invertebrates | 1.39 | 5.25 | 2.45 | 1.24 | 5.67 | 71.19 |
| *Centroceras clavulatum* | 4.87 | 4.47 | 2.35 | 1.39 | 5.44 | 76.63 |
| Benthic-associated invertebrates | 0.78 | 5.26 | 2.24 | 1.94 | 5.18 | 81.81 |

| | | | | | | |
|---|---|---|---|---|---|---|
| *Cladophora* spp. | 1.64 | 4.96 | 1.86 | 0.93 | 4.31 | 86.12 |
| Substrate/detritus | 12.71 | 12.37 | 1.84 | 1.43 | 4.26 | 90.38 |

Table 2.5. Pairwise comparisons of the percent composition of juvenile green turtle foraging samples among three foraging studies based on season. Foraging samples were retrieved (non-lethally) from juvenile green turtles captured within the Trident Basin. The most recent study (2010) was conducted from 2008-2010. The first study was conducted by Redfoot (1997) followed by a second study conducted in 2002 (Ehrhart et al. 2002, unpub data). ANOSIM Global R and significance results were: R = 0.157, p <0.001, R = 0.069, p <0.007, R = 0.186, P <0.001, respectively.

| | 2010 | | 2002 | | 1997 | |
|---|---|---|---|---|---|---|
| Pairwise Tests | R | p | R | p | R | p |
| Fall, Spring | 0.206 | 0.20 | 0.129 | <0.01 | 0.393 | <0.01 |
| Fall, Summer | 0.197 | 0.01 | -0.082 | 0.70 | 0.322 | <0.01 |
| Fall, Winter | 0.221 | 0.90 | 0.017 | 0.15 | 0.306 | <0.01 |
| Spring, Summer | 0.081 | 0.78 | 0.063 | 0.29 | 0.176 | <0.01 |
| Spring, Winter | 0.079 | 0.15 | 0.08 | <0.01 | 0.08 | <0.01 |
| Summer, Winter | 0.483 * | <0.01 | -0.081 | 0.70 | 0.103 | 0.02 |

*****results were significant based on R ≥0.45, p <0.05).

Table 2.6. Foraging items that contributed 90% or more to the dissimilarity between lavage samples of juvenile green turtles in August 2009 vs. February 2010 during the recent (2010) foraging study (b; SIMPER; average dissimilarity = 69.1%). Foraging items are listed in descending order of dissimilarity contribution and % contribution. Asterisks (*) indicate foraging item(s) were identified in previous studies under alternate name(s) and/or were combined for the analyses.

| Foraging item(s) | Summer Abundance Average | Winter Abundance Average | Dissimilarity Average | Dissimilarity ± SD | Contribution Percent | Cumulative Percent |
|---|---|---|---|---|---|---|
| *Hypnea* spp. | 24.38 | 1.67 | 11.52 | 1.57 | 17.21 | 17.21 |
| Substrate/detritus | 12.01 | 28.71 | 10.03 | 1.38 | 14.98 | 32.19 |
| *Cladophora* spp. | 2.18 | 14.14 | 6.40 | 1.62 | 9.56 | 41.75 |
| *Gelidiopsis*, *Gelidium** | 15.15 | 13.89 | 6.19 | 1.14 | 9.25 | 51.00 |
| *Ulva flexuosa** | 4.05 | 12.24 | 5.70 | 1.34 | 8.51 | 59.51 |
| *Ulva lactuca** | 10.39 | 7.29 | 5.63 | 0.82 | 8.41 | 67.92 |
| *Centroceras clavulatum* | 10.77 | 0.34 | 5.30 | 1.33 | 7.91 | 75.84 |
| *Grateloupia filicina* * | 8.55 | 6.84 | 4.79 | 1.14 | 7.16 | 83.00 |
| *Polysiphonia* spp. | 1.84 | 4.85 | 2.81 | 0.83 | 4.20 | 87.20 |

Figures

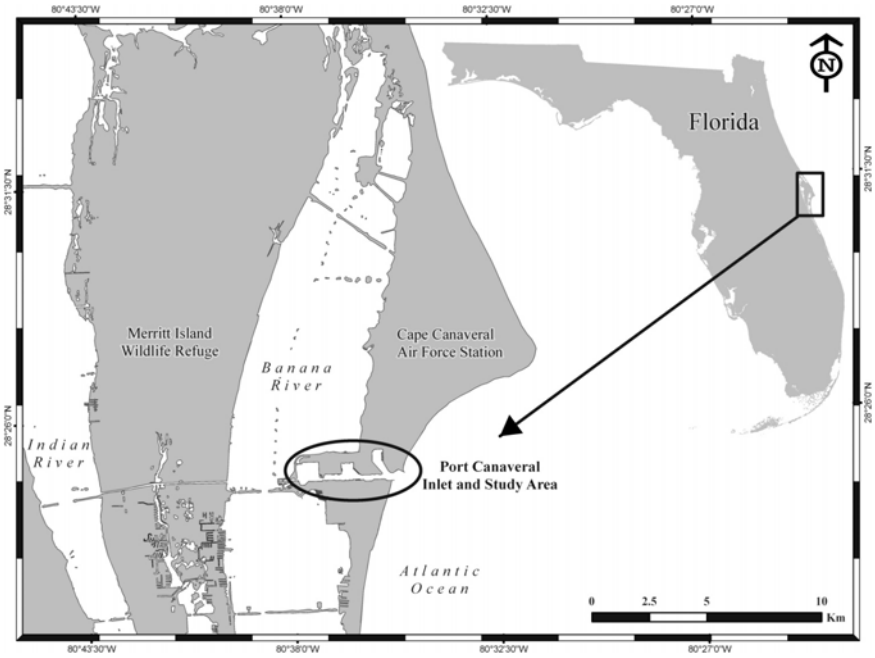


Figure 2.1. The study area (circled) within the Trident Basin located just inside Port Canaveral Inlet in Cape Canaveral on the east coast of Florida (28o24´N, 80o35´W). Map source: LABINS 2010.


Figure 2.2. Trident Basin at Port Canaveral, Cape Canaveral, Florida. White circles represent the marker locations for all of the 100-m delineated distances around the Basin (0-2800) used for recording the juvenile green turtle capture locations during the two-year study of green turtle foraging habits. Areas with both inter- and subtidally submerged rocks were surveyed for macroalgae (0-1300) in a concurrent study (see Chapter 1) to determine if turtles were foraging based on macroalgal resource availability or preferential selection. Map source: Google Earth 2010.

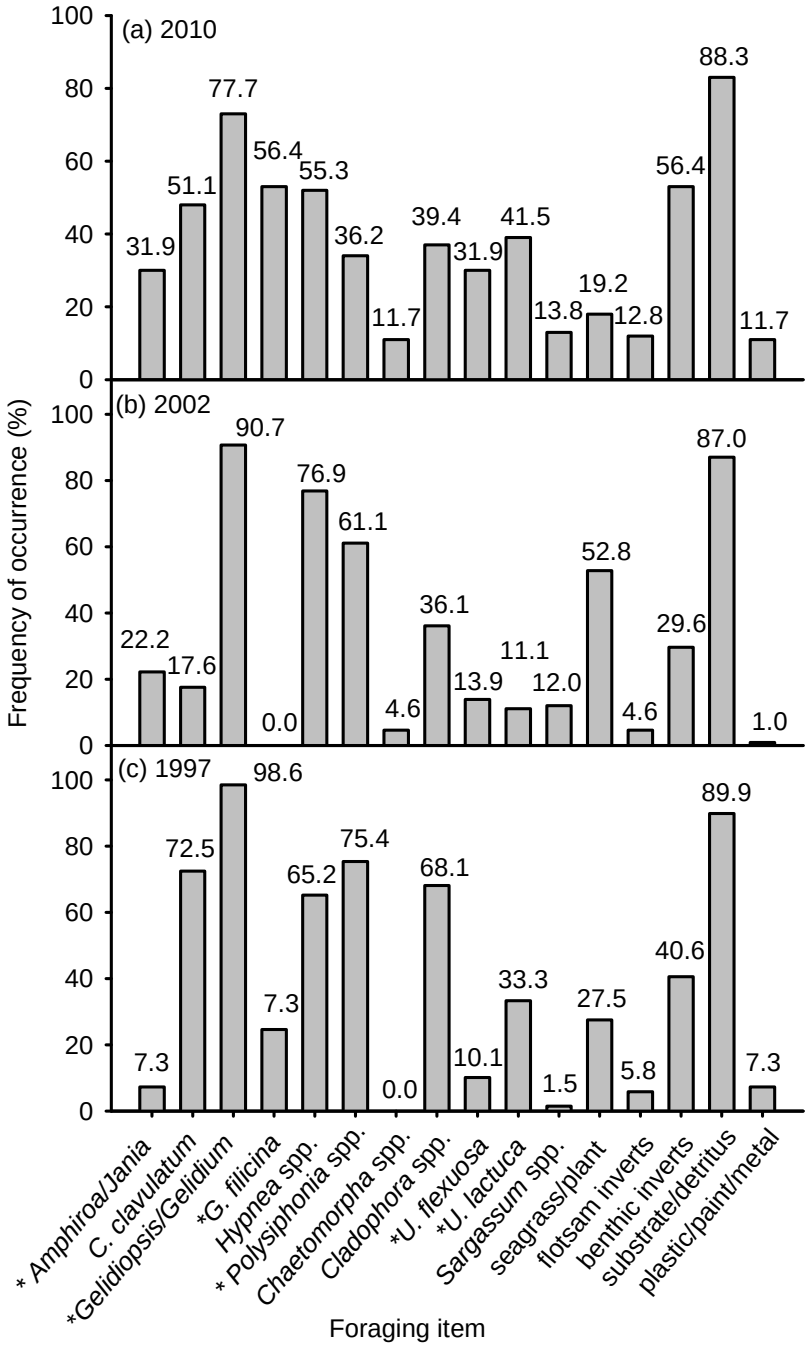


Figure 2.3. Frequency of occurrence of foraging items found in the lavage samples of juvenile green turtles from the 2010 (a; n = 94; recent), 2002 (b; n = 108; Ehrhart et al. 2002, unpub. data), and 1997 (c; n = 69; Redfoot 1997) studies. Asterisks (*) indicate foraging item(s) were previously identified under alternate name(s) and/or were combined for the analyses.

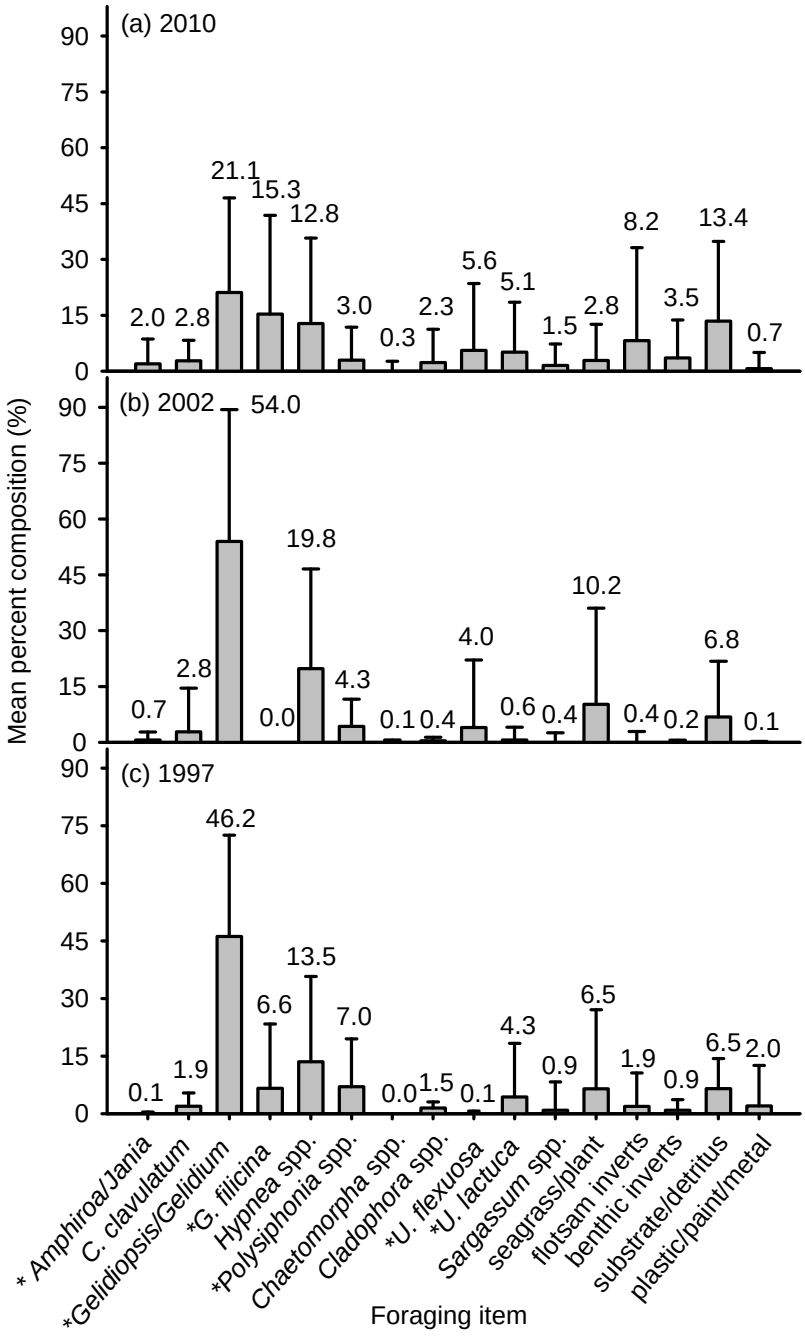


Figure 2.4. Percent composition (± SD) of foraging categories in juvenile green turtle (*Chelonia mydas*) lavage samples from 2010 (a; n = 94; recent), 2002 (b; n = 108; Ehrhart et al. 2002, unpub data), and 1997 (c; n = 69; Redfoot 1997) studies. Asterisks (*) indicate foraging item(s) were previously identified under alternate name(s) and/or were combined for the analyses.

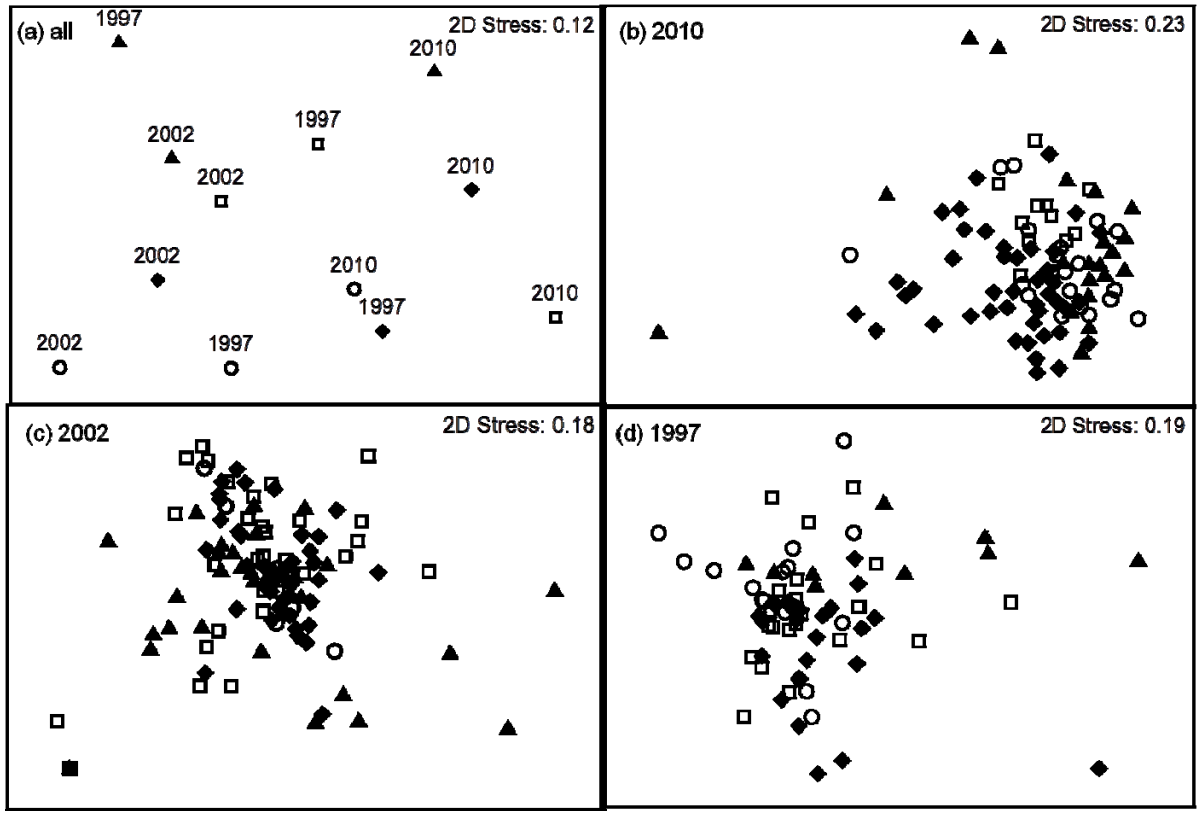


Figure 2.5. Non-metric multidimensional scaling (*n*MDS) ordination plot of juvenile green turtle lavage samples analyzed by season (○ = summer, ▲ = fall, □ = winter, ◆ = spring) for three separate foraging studies (a; summarized by study), the 2010 study (b; recent), the 2002 study (c; 2002, Ehrhart et al. 2002, unpubl. data), and the 1997 study [d; (Redfoot 1997)]. Distances between points represent similarity/dissimilarity of the percent composition among samples (Clarke and Warwick 2001). Data were the percent composition of foraging items in lavage samples during green turtle studies at the Trident Basin in Port Canaveral, Cape Canaveral, Florida over the past two decades.

Acknowledgements

Access to publicly restricted areas of CCAFS and Trident Basin were granted by US Air Force - 45th Space Wing and US NAVY. Special thanks to D. George and A. Chambers for their reviews of materials and M. Carroll and M. O'Quinn for assistance with site accessibility. Research activities were conducted under Marine Turtle permit # 25 (FWC) and # 14506 (NMFS) and approved under University of Central Florida IACUC # 08-51W. Many thanks to L. Ehrhart, W. Redfoot, and UCF's Marine Turtle Research group for many hours of netting turtles in all conditions. My work colleagues were instrumental in data collection and field support during this project and I especially want to thank C. Garreau, E. Reyier, D. Scheidt, S. Gann, R. Lowers, and C. Hall for the generosity of their time and effort. Dynamac and IHA provided time and materials for this project. I am appreciative of the assistance of W. Freshwater (University of North Carolina, Wilmington) in identification of difficult Gelidiales species. Thank you to L. Herren for help with map creation and supporting my efforts in this project. I owe a great deal to my advisor, M.D. Hanisak whose contributions to this manuscript and my work was invaluable. His patience, editing, and contributions to this manuscript were invaluable. Thank you to dissertation committee members, M.D. Hanisak, L. Ehrhart, C.E. Proffitt, T. Sutton, and R. Virnstein, for their guidance and contributions to both the proposed project and the final manuscript review.

References

Arthur, K.E., and G.H. Balazs. 2008. A comparison of immature green turtles (*Chelonia mydas*) diets among seven sites in the main Hawaiian Islands. Pacific Science, 62:205-217.

Balazs, G.H. 1980. Field methods for sampling the dietary components of green turtles *Chelonia mydas*. Herpetological Review, 11:5-6.

Beier, C.M., J.C. Stella, M. Dovčiak, and S.A.McNulty. 2012. Local climatic drivers of changes in phenology at a boreal-temperate ecotone in eastern North America. Climate Change, 115:399-417.

Bjorndal, K.A. 1980. Nutrition and grazing behavior of the green turtle *Chelonia mydas*. Marine Biology, 56:147-154.

Bjorndal, K.A. 1985. Nutritional ecology of sea turtles. Copeia, 1985:736-751.

Bjorndal, K.A., A.B. Bolten, and C.J. Lagueux. 1994. Ingestion of marine debris by juvenile sea turtles in coastal Florida habitats. Marine Pollution Bulletin, 28:154-158.

Bjorndal, K.A., H. Suganuma, and A.B. Bolten. 1991. Digestive fermentation in green turtles, *Chelonia mydas*, feeding on algae. Bulletin of Marine Science, 48:166-171.

Brand-Gardner, S.J., J.M. Lanyon, and C.J. Limpus. 1999. Diet selection by immature green turtles, *Chelonia mydas*, in subtropical Moreton Bay, south-east Queensland. Australian Journal of Zoology, 47:181-191.

Bresette, M., J. Gorham, and B. Peery. 1998. Site fidelity and size frequencies of juvenile green turtles (*Chelonia mydas*) utilizing near shore reefs in St. Lucie County, Florida. Marine Turtle Newsletter, 82:5-7.

Channells, P.W., and J. Morrissey. 1981. Technique for analysis of seagrass genera present in dugong stomachs, including a key to north Queensland seagrasses based on cell details. P. 176-179 *in* The Dugong, Marsh, H. (Ed.). James Cook University, Townsville.

Clarke, K.R., and R.H. Green. 1988. Statistical design and analyses for a 'biological effects' study. Marine Ecology Progress Series, 46:213-226.

Clarke, K.R., and R.M. Warwick. 2001. Change in marine communities: an approach to statistical analysis and interpretation, 2nd edition. PRIMER-E Ltd., Plymouth PL.

Coyne, M.S. 1994. Feeding ecology of subadult green sea turtles in south Texas waters. Master's, Texas A & M University, College Station. 76 p.

Cserháti, T., E. Forgács, G. Oros. 2002. Biological activity and environmental impact of anionic surfactants. Environmental International, 28:337-348.

Ehrhart, L.M., and L.H. Ogren. 1999. Studies in foraging habitats: capturing and handling turtles. P. 61-64 in Research and management techniques for the conservation of sea turtles, Eckert, K.L., K.A. Bjorndal, F.A. Abreu-Grobois, and M. Donnelly (Eds.). SSC/IUCCN Marine Turtle Specialist Group, Washington, D.C.

Ehrhart, L.M., W.E. Redfoot, and D.A. Bagley. 1996. A study of the population ecology of the in-water marine turtle populations on the east-central Florida coast from 1982-96. NOAA/NMFS/SEFC. 164.

Forbes, G.A. 1999. Diet sampling and diet component analysis. P. 144-148 in Research and management techniques for the conservation of sea turtles, Eckert, K.L., K.A. Bjorndal, F.A. Abreu-Grobois, and M. Donnelly (Eds.). SSC/IUCCN Marine Turtle Specialist Group, Washington, D.C.

Forbes, G.A., and L.J. Limpus. 1993. A non-lethal method for retrieving stomach contents from sea turtles. Australian Wildlife Research, 20:339-343.

Garnett, S.T., I.R. Price, and F.J. Scott. 1985. The diet of the green turtle, *Chelonia mydas* (L.), in Torres Strait. Australian Wildlife Research, 12:103-112.

Gilbert, E.I. 2005. Juvenile green turtle (*Chelonia mydas*) foraging ecology: feeding selectivity and forage nutrient analysis. Master's thesis, University of Central Florida, Orlando. 47 p.

Hirth, H.F. 1997. Synopsis of the biological data on the green turtle *Chelonia mydas* (Linnaeus 1758). Fish and Wildlife Service, U.S. DOI. Biological Report 120.

Holloway-Adkins, K. 2006. Juvenile green turtle (*Chelonia mydas*) foraging on a high-energy, shallow reef on the east coast of Florida. P. 193 in Twenty-sixth annual symposium on sea turtle biology and conservation. Frick, M., A. Panagopoulou, A.F. Rees, and K. Williams (Eds.). International Sea Turtle Society, Athens.

Holloway-Adkins, K.G. 2001. A comparative study of the feeding ecology of *Chelonia mydas* (green turtle) and the incidental ingestion of *Prorocentrum* spp. Master's thesis, University of Central Florida, Orlando. 168 p.

Holloway-Adkins, K.G., and J.A. Provancha. 2005. Abundance and foraging activity of marine turtles using nearshore rock resources along the Mid Reach of Brevard County, Florida. Brevard County. 45.

Jacobs, J. 1974. Quantitative measurement of food selection: a modification of the forage ratio and Ivlev's Electivity Index. Oecologia, 14:413-417.

Krebs, C.J. 1989. Ecological Methodology. Harper-Collins Publishers, New York. 654 p.

Kubis, S.A. 2003. Growth rates of juvenile green turtles, *Chelonia mydas*, from three developmental habitats along the east central coast of Florida. Master's thesis, University of Central Florida, Orlando. 60 p.

Kuiper-Linley, M., C.R. Johnson, and J.M. Lanyon. 2007. Effects of simulated green turtle regrazing on seagrass abundance, growth and nutritional status in Moreton Bay, south-east Queensland, Australia Marine and Freshwater Research, 58:492-503.

Lal, A., R. Arthur, N. Marbà, A.W.T. Lill, and T. Alcoverro. 2010. Implications of conserving an ecosystem modifier: Increasing green turtle (*Chelonia mydas*) densities substantially alters seagrass meadows Biological Conservation, 143:2730-2738.

Makowski, C., J.A. Seminoff, and M. Salmon. 2006. Home range and habitat use of juvenile Atlantic green turtles (*Chelonia mydas* L.) on shallow reef habitats in Palm Beach, Florida, USA. Marine Biology, 148:1167-1179.

McCauley, S.J., and K.A. Bjorndal. 1999. Conservation implications of dietary dilution from debris ingestion: sublethal effects in post-hatchling loggerhead sea turtles. Conservation Biology, 13:925-929.

McDermid, K.J., B. Stuercke, and G.H. Balazs. 2007. Nutritional composition of marine plants in the diet of the green sea turtle (*Chelonia mydas*) in the Hawaiian Islands. Bulletin of Marine Science, 81:55-71.

Metz, T.L., and A.M. Landry, Jr. 2013. An Assessment of green turtle (*Chelonia mydas*) stocks along the Texas Coast, with emphasis on the Lower Laguna Madre. Chelonian Conservation and Biology, 12:293-302.

Moran, K.L., and K.A. Bjorndal. 2005. Simulated green turtle grazing affects structure and productivity of seagrass pastures. Marine Ecology-Progress Series, 305:235-247.

Moran, K.L., and K.A. Bjorndal. 2007. Simulated green turtle grazing affects nutrient composition of the seagrass *Thalassia testudinum*. Marine Biology, 150:1083-1092.

Mortimer, J.A. 1981. The feeding ecology of the west Caribbean green turtle (*Chelonia mydas*) in Nicaragua. Biotropica, 13:59-58.

Mumby, P.J., K.R. Clarke, and A.R. Harbone. 1996. Weighting species abundance estimates for marine resource assessment. Aquatic Conservation: Marine and Freshwater Ecosystems, 6:115-120.

Musick, J.A., and C.J. Limpus. 1997. Habitat utilization and migration in juvenile sea turtles. P. 137-163 in The biology of sea turtles, Lutz, P., and J. Musick (Eds.). CRC Press, Boca Raton.

Nelson, D.A. 2001. Habitat use and movements of juvenile green turtles (*Chelonia mydas*) in Cape Canaveral Air Station, Trident Submarine Basin, Florida. Army Corps of Engineers. 38+ p.

NOAA-NCDC. 2013. 2009/2010 Cold season significant events. NOAA, Asheville.

Redfoot, W.E. 1997. Population structure and feeding ecology of green turtles utilizing the Trident Submarine Basin, Cape Canaveral, Florida as developmental habitat. Master's thesis, University of Central Florida, Orlando. 72 p.

Redfoot, W.E., and L.M. Ehrhart. 2013. Trends in size class distribution, recaptures, and abundance of juvenile green turtles (*Chelonia mydas*) utilizing a rock riprap lined embayment at Port Canaveral, Florida, U.S.A. as developmental habitat. Chelonian Conservation and Biology, 12:252-261.

Reich, K.J., K.A. Bjorndal, and A.B. Bolten. 2007. The 'lost years' of green turtles: Using stable isotopes to study cryptic lifestages. Biology Letters, 2007:712-714.

Reyier, E.A., D.M. Scheidt, K.G. Holloway-Adkins, C.M. Garreau, R.H. Lowers, and S.L. Gann. 2010. A characterization of biological resources within the Cape Canaveral Air Force Station Trident Submarine Basin, and adjacent marine waters of Port Canaveral, Florida (May 2008-April 2010). 45 CES/CEAN. 60.

Roark, A.M., K.A. Bjorndal, and A.B. Bolten. 2009. Compensatory responses to food restriction in juvenile green turtles (*Chelonia mydas*). Ecology, 90:2524-2534.

Seminoff, J.A., A. Resendiz, and W.J. Nichols. 2002. Diet of East Pacific green turtles (*Chelonia mydas*) in the Central Gulf of California, Mexico. Journal of Herpetology, 36:447-453.

Shaver, D.J. 1994. Relative abundance, temporal patterns, and growth of sea turtles at the Mansfield Channel, Texas. Journal of Herpetology, 28:491-497.

South Atlantic Fisheries Management Council. 1998. Final habitat plan for the South Atlantic region. P. 457, Council, S.A.F.M. (Ed.).

Strauss, R.E. 1979. Reliability estimates for Ivlev's Electivity Index, the forage ratio, and a proposed linear index of food selection. Transactions of the American Fisheries Society, 108:344-352.

Williams, S.L. 1988. *Thalassia testudinum* productivity and grazing by green turtles in a highly disturbed seagrass bed. Marine Biology, 98:447-455.

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# III. OVERLAP AND PARTITIONING OF FORAGING RESOURCES AMONG AN HERBIVORUS FISH COMMUNITY AND A JUVENILE GREEN TURTLE POPULATION


## Abstract

Distribution patterns and foraging habits of co-occurring marine herbivorous fishes and juvenile green turtles in a zoogeographic transition zone (Cape Canaveral, Florida; 28º24´N, 80º35´W) were examined to determine the relative overlap or partitioning of available resources. Foraging samples were obtained from juvenile green turtles (*Chelonia mydas*) and herbivorous fishes [*Abudefduf saxatilis* (sergeant major), *Archosargus probatocephalus* (sheepshead), *Diplodus holbrooki* (spottail pinfish), *Lagodon rhomboides* (pinfish porgy)] which were the most abundant macroalgal consumers. Collectively herbivores foraged on 32 species of macroalgae; however, only 10 species made up ≥80% of foraging samples from abundant fishes and green turtles. While *A. probatocephalus* and *C. mydas* were generalists in their feeding habits and present year-round, *A. saxatilis*, *D. holbrooki*, and *L. rhomboides* selectively fed more on foliose and filamentous macroalgae and their presence and abundance were related to season and water temperature. Based on Ivlev's electivity indices, both generalist and specialist herbivores frequently selected for less abundant macroalgae (e.g., *Ulva* spp.). During an extreme cold period (<20°C), that lasted 12 consecutive days in January 2010, most herbivorous fishes were absent or present in relatively low numbers. Overlaps in the

foraging composition among herbivores more frequently occurred when water temperatures were >26°C and the macroalgal community composition was highest for the subtropical species *Hypnea spinella* and *Amphiroa fragilissima*. This is the first study to determine the foraging selections of co-occurring herbivorous fishes and green turtles, and explore the potential impact on available macroalgal resources.

## Introduction

The ecological role and impact of grazing in marine macroalgal systems have largely focused on coral reef and kelp-based ecosystems (Carpenter 1986; Lewis 1986; Huntly 1991; Gagnon et al. 2005; Wismer et al. 2009). Although rocky intertidal communities in warm temperate/subtropical ecosystems in the Mediterranean (Benedetti-Cecchi 2000; Sala et al. 2012) and Pacific coastal waters (Lubchenco 1978; Barry and Ehret 1993) have been well-examined, warm temperature/subtropical marine communities of the southeastern Atlantic are less well understood. A better understanding of herbivore-grazer interactions requires exploring beyond single-species impacts and integrating grazer density and diversity, as well as selection effects on the macroalgal community (Bruno et al. 2008).

Juvenile and adult green turtles (*Chelonia mydas*), which are listed as an endangered species (USFWS and NOAA Fisheries 1978), are herbivores that primarily forage on seagrass and macroalgae (Hirth 1997). Green turtles co-occur with herbivorous fishes throughout their range in warm temperate to tropical estuarine and nearshore habitats (Musick and Limpus 1997; Bolten 2003); however, only recently has the

potential foraging overlap between herbivorous fishes and juvenile green turtles in macroalgal-dominated systems been considered (Wabnitz et al. 2010).

Researchers have documented a number of strategies organisms engage in when feeding at the same trophic-level, including: resource partitioning (Klumpp and Polunin 1989), prey-switching, and/or changing the trophic-level in which they feed (Jennings et al. 1997; Siddon and Witman 2004). In some cases, however, the exclusion or restricted access to available resources results in compromised growth, increased predation, lowered fecundity, and/or reduced survival rate of one or more species examined (Schoener 1983; Grand 2002). In addition, experiments that excluded or reduced herbivore biomass in coral reef systems resulted in a decline or altered coral community composition (de Ruyter van Steveninck and Bak 1986; Duffy 2002; Burkepile and Hay 2008; Rasher et al. 2012).

Inlets and jetties are typically situated between oceanic and estuarine habitats and provide access for a number of species exhibiting ocean-estuary coupling where their life history involves movement(s) between the two systems (Gilmore 1977; Gillanders et al. 2003). Most inlet areas are reinforced with structures of rock boulders that result in artificial hard bottom habitat (AHB) for a large number of marine species (Lindquist et al. 1985; Hay and Sutherland 1988; Pister 2009). More recently, Atlantic coastal inlets from Virginia to Key West, Florida (USA) were designated Habitats of Particular Concern (HAPC) and Essential Fish Habitat (South Atlantic Fisheries Management Council 1998; 2003) for their importance in the sustainability of commercially and recreationally important fishes.

The Cape Canaveral region has been recognized as a zoogeographic transition zone for macroalgae (Searles 1984) as well as icthyofauna (Gilmore 1995). The region has also been identified as endangered sea turtle habitat for subadult and adult stage loggerhead (*Caretta caretta*) and Kemp's ridley (*Lepidochelys kempi*) turtles, which have been discovered overwintering in Port Canaveral channel (Henwood 1987). In 1993, the University of Central Florida began investigating frequent sightings of juvenile green turtles within the Trident Basin (located within Port Canaveral) and discovered a relatively large population of juvenile green turtles utilizing this area as developmental habitat (Ehrhart and Redfoot 1996; Redfoot and Ehrhart 2013). During the past two decades, researchers have learned that turtles in the Basin primarily forage on macroalgae growing on rock revetments lining the perimeter of the Basin (Redfoot 1997; see Chapter 2). Researchers have suggested that the Basin's predominantly turf macroalgal community is the result of overgrazing and that this community is a limited resource that restricts the carrying capacity and size class of turtles that utilize this habitat (Redfoot and Ehrhart 2013; Kubis 2003). Long-term capture data indicated that turtles recruiting to the area were the smallest size-class of juvenile green turtles on the east coast of Florida (Hirth 1997) and exhibited high site-fidelity to the Basin (Redfoot and Ehrhart 2013). Recaptured juvenile green turtles grew at significantly slower growth rates when compared to juvenile green turtle populations in nearby estuarine and nearshore reef habitats, and many turtles exhibited poor body condition (e.g., sunken plastron, lower body mass; Kubis et al. 2009).

While Persson (1983) and Svanbäck et al. (2008) found that co-evolved fish species partition resources or have relatively low or no competition for the same

resources, current and future anthropogenic influences threaten to alter resource availability and have the capacity to facilitate ecological rates of change (trophic cascades) with unexpected consequences (Eklöf et al. 2012). Steep declines in herbivore populations, the introduction of ecologically-destructive non-native species (e.g., lionfish) and climate change pose threats to local food resources. Organisms may be limited in their ability to accelerate adaptations to survive the rates of change in competition, predators, habitat, and/or community structures (Sala et al. 2012).

Latitudinal gradients in the distribution of herbivorous fishes indicate that the presence and impact of grazers decrease with increasing latitude (Ferreira et al. 2004; Floeter et al. 2004). The abundance and co-occurrence of herbivores and their role in the development and maintenance of hard coral reef systems have been well-documented (Burkepile and Hay 2008; Francini et al. 2013). While it has been suggested that temperate marine communities incur less impact from grazers due to a lower abundance and diversity of herbivorous fishes (Horn 1989; Choat 1991), the mechanisms of herbivore/plant interactions in warm temperate/subtropical regions of the southeastern U.S. have been little documented. In this region, temperate herbivore abundance is estimated to be <75-80% than in tropical marine systems (Meekan and Choat 1997).

Juvenile green turtles are the most conspicuous and abundant grazers of macroalgae within the Trident Basin (see Chapter 2) and may overlap and/or partition available resources of macroalgae with the herbivorous fish community. The purpose of this study was to: (1) determine spatial and temporal patterns in the distributions of herbivorous fish species and juvenile green turtles over a 2-year period, (2) analyze the foraging habits of herbivorous fishes and juvenile green turtles, (3) determine if herbivore

grazing was based on availability or selection of local macroalgal resources, and (4) determine the degree of diet overlap among herbivores that would indicate competition and/or partitioning of food resources.

## Methods

This study was conducted within the Port Canaveral Inlet on the east coast of Florida, at the Navy's Trident Turning Basin (28°24´N, 80°35´W), approximately 150 m west of the oceanic port entrance (Figure 3.1). Rock revetments constructed of large granite boulders line ~80% of the perimeter and were installed to reduce shoreline erosion in the Basin. Approximately 46% of the rock is inter- or subtidally submerged, providing substratum for a diverse community of macroalgae and invertebrates. The entire length of the Basin was previously delineated into 100-m sections and numbered from 0-27 around the basin. The 0 mark for the 1$^{st}$ 100-m section started at the southwest section of the Basin closest to the inlet. Sections 0-13 (1,300 m total length; Figure 3.1) were selected for the study area because these areas contained the only rock with macroalgal growth.

Temperature and salinity data were recorded hourly on a near-continuous basis from April 2008 through April 2010 by a YSI 6920 v2 sonde (YSI, Inc., Yellow Springs, Ohio) installed approximately 20 m east of the shoreline and 1.5 m deep within the study area. The YSI served as the primary data source. When the YSI was out of the water for maintenance or repair, data were supplemented with National Data Buoy Center (NOAA-NDBC 2013) sources online from a permanent monitoring station also located within the Basin.

### Distribution of herbivorous fishes and turtles

Two complementary methods outlined in Bohnsack and Bannerot (1986) were used to determine the relative spatial and temporal abundance and distribution of the herbivorous fish assemblage: (a) underwater (UW) video transect, better at detecting more mobile fishes, and (b) a modified stationary sampling method, better for detecting smaller and/or less cryptic fishes. Fish surveys were targeted to occur mid-day, during flood tide of quarter moon phases. Surveys occurred quarterly for 2 years from June 2008-May 2010 (n = 8). Comparisons of the herbivore community composition in the two sampling periods following a relatively mild winter (December 2008 and March 2009, collectively referred to as "mild winter") were compared with the herbivore composition in the sampling periods that followed the episodic cold event in January 2010 (February and April 2010, collectively referred to as "cold winter").

*Video transect surveys for fishes and green turtles*

Continuous UW video transect surveys were conducted across the entire 1,300-m study area, originating from the 0 or 13 marker end points. Surveys were conducted parallel to shore at approximately 1-2 m water depth, 2.5 m off the shoreline. A diver carrying a high-definition digital video camera (Sony HDR-SR5 Handycam) in an Ikelite® UW housing swam the length of the study area parallel to the shoreline revetment. The camera was positioned approximately 45° to the rock face. The diver swam at a speed of approximately 1.2 km/h for the entire length of the study area, positioned in the water column at the relative intertidal/subtidal convergence. A 100-m shoreline marker or hand signal was recorded during the video recording to indicate the start of each 100-m section during the review process.

*Stationary sampling for fishes and boat transects for turtles*

Temporal abundance and distribution data for less-conspicuous fish species were determined with modified techniques from the stationary sampling method (Bohnsack and Bannerot 1986). Areas to be sampled were randomly selected (without replacement) for coordinates within 100-m sections of the study area. Sampling was conducted when visibility was ≥1.5 m. For the purposes of determining fish recruitment periods and estimate the sizes among fish species, the total lengths (TL) of fishes in inches (later converted to millimeters) were recorded during surveys. Prior to sampling, researchers visually reviewed size lengths and utilized ruler marks on the underwater datasheet clipboards to estimate accuracy for fish size assessment. Researchers on SCUBA settled facing the rock revetment at the relative subtidal/intertidal interface (~1.2 m depth). The researchers sat side-by-side and arranged themselves in two $45^{o}$ visual radii areas for fish observation. The researchers maintained minimal movement and disturbance throughout the sampling time period (10 min). During the initial 5-min settling period, divers recorded the different species present within the designated survey area. During the last 5 minutes, divers recorded fish species, number of fishes, and their relative size on waterproof datasheets.

Boat transect surveys to estimate juvenile green turtle density within the study area were conducted quarterly with techniques similarly employed for other marine animals (Anderson et al. 1979). Three surveys were conducted within a quarterly survey day under the best available conditions during the sampling periods (i.e., water clarity >2.0 m deep, clear skies, light wind, low to no glare). Water conditions were documented and ranked between 1 (excellent >3.0 m visibility) and 4 (poor ≤1.0 m). Three persons (a boat driver and two observers) experienced in onwater survey methods conducted

surveys aboard a 7.3-m Carolina Skiff watercraft equipped with a 2.5-m sighting tower. Surveys began at either end of the study area (0 or 13 m marker). The starting positions for the 2nd and 3rd surveys were haphazardly alternated. The driver entered a waypoint on a GPS unit (Garmin 76X) to record the start and end times and locations for each survey. Observers positioned in the boat tower announced when a turtle was sighted and the boat driver would enter a waypoint for the animal's location. Additional data that were manually collected were the turtle's position in the water column (surface, middle, or bottom), position on transect (inside, outside, or on), and behavior (swimming, diving, feeding, resting, or breathing).

Survey data and statistical analyses

Data were square-root transformed to down-weight less abundant species and analyzed with Primer-E (Plymouth, UK) software routines. CLUSTER was used for hierarchical graphing. MDS (multi-dimensional scaling) ordination plots were generated from Bray-Curtis correlation matrices (Clarke and Green 1988) to spatially represent similarity among samples (e.g., among quarterly sampling events or transects). The reported "stress" value of a constructed plot is the measure of distortion required to represent the data in the 2D plot (Clarke and Warwick 2001). A stress value of 0 indicates a perfect representation of the data. A stress value $\leq 0.2$ is also considered a useful representation for interpreting the data. Ordination plots resulting in stress values $>0.2$ should be interpreted with caution, as the distortion is considerably high at this level. Stress values $>0.3$ result from a very high level of distortion created in order to display the data and are considered unreliable to generate inferences (Clarke and Warwick 2001). Another Primer-E routine, Analysis of Similarity (ANOSIM), was used

to test the hypothesis of no significant differences in the spatial distribution of herbivorous fishes and juvenile green turtles based on 100-m sections of the study area (n = 13). ANOSIM was also conducted to test the hypotheses of no significance differences in the temporal distribution of herbivorous fishes and turtles based on: (1) quarterly sampling period (n = 8), (2) season (n = 4), and (3) sampling periods following a mild vs. cold winter (n = 4). Confidence intervals were set at $\alpha = 0.05$. R values near 0 occurred when similarities between and within sites on average were the same. When there were a large number of replicates, as was the case in some of the datasets in this study, R can be substantially close to 0 but be "significant" ($P < 0.05$). For interpretation purposes, significant values (P) were considered both biologically and statistically significant at $R \geq 0.50$, indicating that within site replicates were more similar than among site replicates (Clarke and Warwick 2001).

In addition, the Primer-E routine SIMPER (similarity percentage) was used to elicit the species (fish or alga) that contributed up to 90% to the differences between groups that were significantly different (criteria $R \geq 0.50$, $P < 0.05$) in composition (Clarke and Warwick 2001). Linear regression analyses were conducted with SigmaPlot v. 11.0 (SYSTAT 2008) to determine if there was a significant ($P < 0.05$) correlation between fish abundance (dependent variable) and temperature (°C; independent variable).

UW videos were reviewed to document the abundance of fishes and marine turtles within each 100-m section. Marine turtle abundance data from waypoints taken during boat surveys were downloaded from the GPS via MapSource v 6.13.7 (Garmin Ltd.) software and exported to Excel (Microsoft Office). The mean number of turtles per boat survey day from transects (n = 3) for each sampling period was calculated per 100-m

section. While data from boat and stationary transect surveys were presented together in the analyses, the UW video and stationary (including boat) survey datasets were used independently to calculate herbivore density and spatial distribution.

Foraging content collection

Fishes for foraging sample analyses were obtained from a concurrent monthly ichythofaunal demographics study conducted in the Port Canaveral region (Reyier et al. 2010). Fishes were captured using a variety of techniques and fishing hardware, including: otter trawl, small-mesh gillnet, Hawaiian sling, and cast net. Only fishes captured within the Trident Basin were used in the foraging analysis. When available, approximately 20 fish from each relatively abundant taxa (e.g., Sparids and Pomacentrids) were examined per quarterly sampling period. Scarids and other less-abundant herbivorous fishes were sampled more conservatively (n <5) (Randall 1967; West et al. 2003). The date of capture, straight length (SL; tip to caudal crease in mm), and gut content of potentially herbivorous fishes were recorded for each fish.

Juvenile green turtle foraging samples were obtained from an ongoing, concurrent study in the Trident Basin by the University of Central Florida Marine Turtle Research group (Redfoot and Ehrhart 2013). Turtles were captured with long-handled dip nets or within one of two 180-m long, 4-m deep large-mesh (30 and 40-cm stretch) tangle nets. The capture and handling of turtles followed methods outlined in Ehrhart and Ogren (1999). Researchers recorded straight carapace length (SCL) measurements which were used to calculate mean population size. Foraging samples from juvenile green turtles were collected via a non-lethal procedure called “lavage” described in Redfoot (1997) and Forbes (1999). Samples were preserved in a 5% formalin/seawater mix.

Forage sampling and enumeration

In the laboratory, digestive tracts of fishes were removed from preservative for examination. Stomach fullness was ranked between 0 and 5. An empty stomach was ranked '0' and a very full or over-stuffed stomach was ranked '5' (Pike and Lindquist 1994; Rissik and Suthers 2000). The condition of the sample contents based on the relative level of digestion was ranked on a 0 to 4 scale where '0' was a fresh sample with little evidence of digestion and '4' was a sample in the late stage of digestion (i.e., the content was completely indiscernible or "mush"). In addition, a cursory examination of upper and lower intestinal tracts was conducted to document if contents within the stomach differed substantially from the rest of the digestive tract. The stomach content of each fish was removed and placed in individual Petri dishes. The green turtle lavage samples were rinsed over a 0.5-mm mesh filter and placed in individual Petri dishes. Both fish and turtle foraging samples were quantified with a modified procedure adapted from Channells and Morrissey (1981) and Forbes (1999). Each sample was thoroughly mixed and spread across a gridded Petri dish into a single layer to allow light for quantification (Forbes 1999). Samples were examined with modified procedures of microstereology (Weibel et al. 1966). A stereoscope was fitted with a grid reticle (100 squares) in the ocular. The reticle was aligned within one of the 1.3-$cm^2$ grids on the Petri dish. The macroalga (or other material) located in the top left corner of each odd-numbered square in the reticle was recorded for calculation of percent composition data. A maximum of 16 1-$cm^2$ grids were quantified (16 x 50 = 800 maximum data points) per foraging sample. The contribution of organisms and inanimate objects (i.e., flotsam, rock, and

sand) was based on the percent of all items enumerated in a sample (total sample = 100%).

Statistical analyses of foraging samples

A fish whose gut contained ≥50% macroalgae was considered an herbivore following Randall (1967); further data analyses focused on samples with ≥50% plant material and excluded any non-macroalgal content in the samples. Individual foraging samples were standardized to percent composition, square-root transformed, and a Bray-Curtis similarity matrix was generated for data analyses (Clarke and Green 1988). Multi-dimensional scaling (MDS) ordination plots were generated for interpreting relative similarity among the foraging habits of different herbivores (Clarke and Green 1988). ANOSIM procedure was used to determine if foraging samples of different grazers significantly differed or overlapped. Significant differences (criteria of $R \geq 0.50$, $P < 0.05$) in post hoc pairwise comparisons of grazer groups (i.e., *A. probatocephalus* vs. *L. rhomboides*) indicated the foraging composition of the grazer groups had no to relatively low overlap in composition. Low R values and/or non-significant pairwise results ($R < 0.5$, $P > 0.05$) indicated moderate to high levels of overlap in the foraging composition between herbivore species. SIMPER routines calculated the percent that macroalgal species contributed to the dissimilarity of foraging samples between herbivore species.

Ivlev's Electivity Index

Ivlev's electivity indices were calculated to determine if herbivores foraged selectively or based on available macroalgal resources (Krebs 1989):

Ivlev's electivity index $$E = \frac{r_i - p_i}{r_i + p_i}$$

The measure of electivity (E) was based on the relative abundance (percentage or proportion) of a prey item ($r_i$) in foraging samples and the relative abundance of that prey item in the environment ($p_i$) (Strauss 1979). A concurrent macroalgal study (see Chapter 1) provided the necessary data to calculate available resources of macroalgae ($p_i$) within the Basin. Electivity indices ranged between -1 to +1 where values between -1 and 0 represent avoidance or inaccessible prey (macroalgae) items and values between 0 and +1 represent selection based on relative abundance (Jacobs 1974; Krebs 1989).

Tests for significant differences in the mean size of herbivorous fishes from stationary surveys, as well as fish and turtles from the foraging sample analysis, were conducted using either a One-way ANOVA or the Kruskal-Wallis test if data did not fit assumptions of normality and equal variance (SigmaPlot v. 11.0; Systat Software, Inc.). All tests were considered significant at $P < 0.05$.

## Results

### Environmental conditions

Two major weather events occurred over the course of the 2-year study period. The first event was Tropical Storm Fay (TS Fay) that began 19 August 2008. This storm delivered the highest rainfall documented in recorded history over a 3-day period in Brevard County (Verdi and Holt 2010; NOAA 2013). Two meteorological stations at Port Canaveral recorded 50 and 63 cm of rainfall from 19 August to 22 August 2008 (NASA 2013). Monthly mean salinity ranged between 33-37 during the 2-year study period except for approximately 2 weeks during and after TS Fay when freshwater inputs and pulses lowered salinity values in the Basin (Figure 3.2). The Port Canaveral locks were opened for several hours to relieve residential areas of localized flooding along the

Banana River lagoon banks and contributed to salinities as low as 21.1 during this period. However, constant mixing with nearby (<150 m) oceanic waters, quickly brought salinity levels back to normal values (~35; Figure 3.2). Even though sampling was delayed for several weeks after the storm, survey conditions for UW video and boat surveys during this period were less than optimal due to residual water quality impacts from substantial stormwater run-off. All other surveys were conducted in water clarity ≥2 m.

The second major weather event occurred in January 2010 when air temperatures on Florida's central east coast dropped below 16°C for 12 consecutive days (NOAA-NCDC 2013). During these 12 days the water temperatures in the Basin averaged 15.1°C (±1.6 SD; Figure 3.2). In the past, tropical fishes and juvenile green turtles in shallow estuaries on the east coast of Florida succumbed to hypothermic (or cold) stunning when water temperatures abruptly declined below10°C and persisted for 4 to 5 days (Witherington and Ehrhart 1989; Gilmore 1995). In January 2010, >3000 green turtles stranded from the extreme cold in inland waters on the central east coast of Florida (Florida Fish and Wildlife Conservation Commission, unpubl. data). As poikolotherms, green turtles' hindgut fermentation, digestive efficiency, and retention time are correlated with temperature (Bjorndal 1980; O'Toole 2008). While temperatures in the Trident Basin were 5 to 10°C warmer than adjacent Indian and Banana River lagoons, turtles in the Basin were less-active following the January cold event and during February 2010 survey and foraging sampling periods (pers. observ.).

Fish surveys

Fishes from 27 families were observed during UW video and stationary surveys conducted during the 2-year study period (Table 3.1). Forty-three different fish species

were identified, and four additional fishes were assigned to family level [i.e., Anchovidae, Gobiidae, Mugilidae (larval-stage), Scianidae (larval-stage)] due to the difficulty of identifying them with the unaided eye. Both of the juvenile and adult life-stages of *Sphyraena barracuda*, *Anisotremus virginicus*, *Lagodon rhomboides*, *Pomacanthus arcuatus*, *Lutjanus* spp., and *Caranx* spp. were observed in surveys (Table 3.1). Species richness was higher for fishes in UW video (43 out of 45 species or 95.0%) vs. stationary surveys (21 out of 45 species or 46.7.0%); however, 42.2% (19 out of 45) of fish species were documented from both survey methods (Appendix Table 3.1). Ten out of the total 45 fish species (22.2%) previously identified as herbivores based on Randall (1967) were present in at least one quarterly survey (Table 3.1).

*Herbivorous fish distribution*

The four most abundant herbivorous fish species in UW video and stationary surveys were *Abudefduf saxatilis* (sergeant major), *Archosargus probatocephalus* (sheepshead), *Diplodus holbrooki* (spottail pinfish), and *Lagodon rhomboides* (pinfish porgy) (Figure 3.3, 4). Other herbivorous fish species present but infrequently encountered (≤3 times) in surveys were *Abudefduf taurus* (night sergeant), *Acanthurus bahianus* (surgeonfish), *A. chirurgus* (doctorfish), *Nicolsina usta usta* (emerald parrotfish), *Labrisomus nuchipinnis* (hairy blenny), *Pomacanthus arcuatus* (gray angelfish), *Scartella cristata* (molly miller), *Stegastes leucostictus* (beaugregory), and *S. variabilis* (cocoa damselfish). No significant differences were detected for the spatial distribution of the abundant herbivorous fish community composition (n = 4) within the Basin based on 100-m sections (n = 13) from quarterly UW video or stationary surveys (ANOSIM, Global R = -0.04, P = 0.99, and R = 0.01, P = 0.29; respectively).

Hierarchical relationships generated from the Primer-E CLUSTER routine indicated the quarterly percent composition of herbivore fishes was >80% similar for the June 2009 and September 2009 sampling periods based on data from UW video and stationary surveys (Figure 3.5a, b). However, similarity between fish compositions was <40% vs. >80% for UW video vs. stationary survey in June 2008 and September 2008 (Figure 3.5a, b). Overall differences of fish compositions among survey periods were biologically significant for UW video but not stationary surveys (ANOSIM, R = 0.672, P = 0.001; R = 0.366, P = 0.001, n = 8, respectively; Table 3.2). *Post hoc* analysis of the quarterly compositions of fishes from UW video surveys indicated biologically significant differences (R ≥0.50, P <0.05) for 75% (21 out of 28) of the pairwise comparisons (Table 3.3a).

The MDS ordination plot of the percent compositions of herbivorous fishes from the mild vs. cold winter surveys indicated distinct separation in community compositions from UW video survey data (stress = 0.09; Figure 3.6). Significant differences were detected between fish compositions during these time periods (ANOSIM R = 0.634, P = 0.0001; Table 3.3b). However, no significant differences in the fish composition from stationary surveys were detected for the mild vs. cold winter comparisons (ANOSIM, R = 0.239, P = 0.001). *Post hoc* pairwise comparisons of fish composition based on UW video surveys in April 2010 surveys were significantly different from December 2008, March 2009, and February 2010 surveys (Table 3.3b).

The average percent dissimilarity among six pairwise comparisons of seasonal fish abundance from UW video surveys ranged between 49.9% (summer vs. fall) to 94.6% (winter vs. spring) (SIMPER; Appendix Table 3.2a). The average abundance of *L.*

*rhomboides* from spring surveys contributed 43.5-54.1% dissimilarity in pairwise comparisons of seasonal fish abundances. The large schools of *L. rhomboides* in April 2010 contributed between 56.4-89.3% dissimilarity among pairwise comparisons of all quarterly surveys (Appendix Table 3.2b). Pairwise comparisons of the abundance of *D. holbrooki* in summer vs. fall and winter, as well as fall vs. winter, indicate the species contributed >40% to the average dissimilarity among the seasonal fish compositions. Among quarterly surveys, the dissimilarity in the percent composition of *D. holbrooki* was highest for comparisons between June 2008 and 2009 vs. September 2008 and 2009 surveys. Dissimilarity among the summer and fall sampling periods ranged between 32.6-52.8%. Altogether, the contributions of *D. holbrooki* and *A. saxatilis* contributed the highest percentage to the dissimilarity of fish compositions for summer and fall while the abundance of *L. rhomboides* in spring contributed to the largest percentage of dissimilarities among other seasons (Appendix Table 3.2a). Differences detected between the quarterly sampling periods that corresponded to each season (e.g., March 2009 and April 2010) indicate that variability existed at finer temporal scales (Appendix Table 3.2b).

The abundances of *A. saxatilis* and *D. holbrooki* were both positively related to temperature based on survey data from UW video and stationary surveys (Figure 3.7-8). The strength of the relationship was greater for fish abundance in stationary vs. UW video surveys (SigmaPlot; $r^2 = 0.86$, $P < 0.0001$ and $r^2 = 0.75$, $P < 0.006$; respectively; Figure 3.7-8). No significant correlation between temperature and the abundance of *A. probatocephalus*, *L. rhomboides*, or *C. mydas* was detected based on UW video or stationary surveys.

The estimated mean sizes of herbivorous fish were significantly different among stationary surveys for all four fishes (*A. saxatilis*, *A. probatocephalus*, *D. holbrooki*, and *L. rhomboides*; Dunn's; H = 88.9, 37.0, 567.4, 168.3, P = <0.001, respectively; Figure 3.9). *Abudefduf saxatilis* were most abundant in June and September stationary surveys in 2008 and 2009 (Figure 3.9). Differences in the size of fishes in stationary surveys were most conspicuous in February 2010 and April 2010 for *L. rhomboides* (Figure 3.9). While schools of *L. rhomboides* were relatively abundant in March 2009 and February 2010 surveys, in April 2010, the schools were larger and their estimated mean size was smaller than all previous surveys (Figure 3.9). *Diplodus holbrooki* and *L. rhomboides* were absent in December 2008, and *A. saxatilis*, *A. probatocephalus*, and *D. holbrooki* were absent in the February 2010 stationary surveys (Figure 3.9). The smallest sized fishes were potential new recruits, transient schools, and/or newly-settled fishes and were most abundant in spring surveys (March 2009 and April 2010) for *A. saxatilis*, *D. holbrooki*, and *L. rhomboides* (Figure 3.9).

*Juvenile green turtle distribution*

While turtles were more frequently observed within the first 500 m of the port channel (transect areas 0-4; Figure 3.10a), significant differences were not detected for the spatial distribution of turtles based on 100-m sections of the study area in UW video (Kruskal-Wallis, H = 15.291, P = 0.170) or boat surveys (ANOVA, F = 1.85, P = 0.051). No significant differences in the temporal distribution of juvenile green turtles were detected in UW video (Kruskal-Wallis, H = 8.723, P = 0.273). However, the mean number of turtles sighted during boat surveys ranged between 0-43 and the average abundance of turtles in quarterly surveys were significantly different (ANOVA, F = 4.72,

P <0.001; Figure 3.10b). Turtles were most frequently observed in the mid- or bottom sections of the water column (71.4-98.9%; Figure 3.10c) except during the October 2008 surveys (post Tropical Storm Fay) when visibility was less than optimal (Rank = 4; ~1.5 m visibility). Significant differences were detected for the number of turtles present based on different water column categories (ANOVA, $F = 9.94$, $P<0.001$). Post hoc comparisons were significant for turtle observed at the bottom vs. surface and mid-water categories (Holm-Sidak, $t = 4.4$ and 2.8, $p \leq 0.01$; respectively). Researchers observed turtles resting (38.4%), swimming (35.5%), feeding (16.3%) or breathing at the surface (9.8%) during initial survey sightings (Figure 3.10d). Resting and feeding activities which occur at or near the bottom of the water column were not observed during the October 2008 surveys due to poor water quality post Tropical Storm Fay (Figure 3.10d). Significant differences were detected for the number of turtles present based on behavior categories (ANOVA, $F = 6.19$, $P<0.002$). Post hoc comparisons were significant for turtles observed resting vs. breathing and feeding (Holm-Sidak, $t = 3.57$ and 2.76, $p \leq 0.01$; respectively) and swimming vs. breathing (Holm-Sidak, $t = 3.21$, $P<0.003$).

Foraging samples

Initially, 308 fishes from 16 species were obtained from a concurrent ichythofaunal study at the Trident Basin (Reyier et al. 2010). The stomach contents of fish species previously recognized as herbivores (Randall 1967) were examined (n = 265) and 165 of these fishes from nine different species were considered herbivores. The most abundant fishes (*A. saxatilis*, *A. probatocephalus*, *D. holbrooki*, and *L. rhomboides*) were used for the foraging data analysis while species that were spatially and temporally less abundant (*A. taurus*, *A. bahianus*, *A. chirurgus*, *P. arcuatus*, and *S. cristata*) were not

included in the foraging analysis. The presence and mean size distributions of fishes varied among sampling quarters and were significantly different for all species examined except *L. rhomboides* that were only foraging as herbivores in samples from fish collected in March 2009 (Figure 3.11).

The gut contents of fishes were in relatively low states of decomposition at the time of analyses and the majority of samples (83.6%) ranked 'fresh' to 'partially-digested.' One sample (*D. holbrooki*) was not discernible and could not be used in the analysis. Only three of 265 stomachs examined were empty, whereas 73.9% of stomachs were ≥50% full, indicating fish had recently foraged before they were captured.

Lavage samples were obtained from 94 juvenile green turtles captured during five 2-day sampling periods (September 13-14, 2008, March 7-8 and August 8-9, 2009, February 27-28 and April 17-18, 2010) in the Trident Basin (see Chapter 2). The straight carapace lengths of juvenile green turtles ranged from 24.3 to 44.5 cm SCL (mean 29.6 cm ± 3.7 SD; Figure 3.12) and were not significantly different among sampling periods (ANOVA, df = 4, F = 2.74, P = 0.05).

Biotic and abiotic foraging items (n = 66) were found in the sample contents of herbivorous fishes (n = 165) and juvenile green turtles (n = 94). Grazers foraged collectively on 32 different species of macroalgae and cyanobacteria. Nine macroalgae found in the foraging samples were not present in samples collected in the concurrent macroalgal study (see Chapter 2).

Selection vs. availability of macroalgal resources

Of the 10 most abundant macroalgae observed in foraging samples (Figure 3.14-20), *Centroceras clavulatum* (fine filamentous alga), was the only species that was never

selected 'for' (Ivlev's electivity index, E ≥0.50) by abundant herbivorous fishes or juvenile green turtles during any of the quarterly sampling periods (Figure 3.14). *Abudefduf saxatilis*, *D. holbrooki*, and *L. rhomboides* displayed specialist foraging habits, feeding most on macroalgae that were present in low percent compositions (e.g., *Ulva* spp.). *Archosargus probatocephalus* and *C. mydas* exhibited generalist feeding habits, eating between 8 and 10 species that were present in relatively high percent compositions in the Basin. Foraging data for *A. saxatilis* (n = 19) captured in June 2008 and September 2009 indicate macroalgal consumption levels were highest for *Gelidium crinale*, *Hypnea spinella*, *Ulva flexuosa*, and *U. prolifera* (Figure 3.16, 18, 20, 22) and selective (E ≥0.5) for all species except *G. crinale*. Low percentages (<12%) of the relatively more abundant macroalgae, *G. planicaulis*, *G. crinale*, *H. spinella*, and *P. denudata* (Figure 3.15-16, 18-19) were foraged by *D. holbrooki* (n = 62) while selective foraging for less abundant *Ulva* was more frequent among quarterly sampling periods (Figure 3.20-22). Herbivorous *L. rhomboides* (n = 16) captured in April 2009 consumed *H. spinella*, *P. denudata*, and three species of *Ulva* (Figure 3.18-22) and selected for all species except *H. spinella* based on electivity indices.

While it occurred infrequently, there were sampling periods where an herbivore selected for a macroalgal species and avoided (selected against) that same species in another sampling period. For example, *A. probatocephalus* selected for *A. fragilissima* in June 2008 but avoided the species in February and April 2010 (Figure 3.13).

*Archosargus probatocephalus* (n = 79) was the only fish species that foraged as generalists and fed primarily on macroalgae available in the highest percent compositions in the environment (e.g., *A. fragilissima*, *G. crinale*, *G. filicina*) (Figure 3.13, 16-17).

*Chelonia mydas* (n = 94) foraged as generalists and consumed 8 of the 10 macroalgal species, with percent compositions ≥10% of their foraging samples during at least one sampling period (Figure 3.15-22). In addition, *C. mydas* selectively foraged on *H. spinella* and *U. lactuca* in June 2009 and April 2010 (Figure 3.18, 21).

Foraging overlap and partitioning

Overall, the comparisons of herbivorous fishes and juvenile green turtle foraging samples for the 2-year study period indicate that the generalist species, *A. probatocephalus,* overlapped with all of the other herbivores, and *C. mydas* overlapped with all herbivores except *L. rhomboides. Diplodus holbrooki* and *A. saxatilis*, specialist foragers, overlapped in foraging sample compositions while *L. rhomboides* and *A. saxatilis* significantly differed (Table 3.5). Dissimilarity within the foraging samples of *L. rhomboides* were greater than differences with *D. holbrooki* foraging samples (R = -0.04, p = 0.88). Comparisons of *L. rhomboides* vs. *A. saxatilis and C. mydas*, however, indicated there were overlaps in foraging composition among species (R <0.50; Table 3.5). Overlaps in the macroalgal species of foraging samples favored less-abundant species of *U. flexuosa*, *U. lactuca* and *U. prolifera* (Figure 3.20-22) that were frequently selected 'for' based on Ivlev's electivity index calculations. Foraging overlap for more abundant macroalgae (i.e., *G. planicaulis*, *G. crinale*; Figure 3.15-16) was infrequent and occurred most between the generalist species (*A. probatocephalus* and *C. mydas*).

*Temporal partitioning*

Analyses of foraging samples by season and quarterly sampling period further suggest herbivores partitioned macroalgal resources (Table 3.6-7) during some periods and fluctuated in their selection of some macroalgae (Figure 3.23). Not all herbivore

species were present and/or abundant during every season or sampling period, and the foraging habits of some species differed as a function of life history stage. For example, *L. rhomboides* stomach contents in the spring (March 2009) indicated selective foraging on species with relatively low availability, such as *Ulva* spp. (Figure 3.20-22). However, *A. saxatilis*, which was abundant in summer and fall, also selectively foraged on *Ulva* spp. (Figure 3.20-22, Table 3.6-7a, c, d). *Chelonia mydas* and *A. probatocephalus* both foraged as generalists but frequently selected macroalgae present in low available percent compositions (e.g., *P. denudata* and *Ulva* spp.) during winter and spring sampling periods (Figure 3.19-22; Table 3.6-7b). These periods coincided with the absence or relatively low abundance of *D. holbrooki* and *A. saxatilis* that targeted the same macroalgal species.

Selection was most frequent for comparatively less-abundant species (i.e., *P. denudata* and *Ulva* spp.; Figure 3.19-22; Table 3.7). Generalist species, *A. probatocephalus* and *C. mydas*, also selectively foraged on these less abundant species in relatively small percentages of their foraging compositions (Figure 3.20-22). However, high electivity indices for several of the same macroalgae (e.g., *H. spinella*, *P. denudata*, *U. flexuosa*, *U. lactuca*, *U. prolifera*) occurred frequently in the foraging samples of *D. holbrooki, A. saxatilis* and *L. rhomboides* during different time periods (Figure 3.18-22; Table 3.7). In addition, the percent composition of chlorophytes was highest in the foraging samples of generalists (*C. mydas* and *A. probatocephalus*) in sampling periods where *A. saxatilis*, *D. holbrooki*, and *L. rhomboides* (specialists) were absent or present in low abundance (e.g., February and April 2010; Figure 3.20-22). MDS ordination plots and pairwise comparisons based on the percent composition of species' foraging samples

indicate that the highest degree of overlap occurred in June 2008 and September 2009). During this time, *A. saxatilis* and *D. holbrooki* were comparatively more abundant within the Basin, the macroalgal community composition was greater for subtropical macroalgae (i.e., *H. spinella*, *A. fragilissima*), and water temperatures were >26°C (Figure 3.7-8, 13, 18, 25; Table 3.7).

## Discussion

### Herbivore distribution

The herbivorous fish community consisted of 10 fishes; this study focused on the most abundant four fishes. These included *A. saxatilis*, *A. probatocephalus*, *D. holbrooki*, and *L. rhomboides*, as well as *C. mydas* (green turtle). The presence and abundance of the four fish species examined in this study have previously been identified in association with both artificial hardbottom (AHB) and natural hardbottom habitats in the southeastern U.S. (Hastings 1979; Hay and Sutherland 1988; Parker 1990). In addition, aggregations of juvenile green turtles are frequently found in AHB and natural hardbottom habitats in the Gulf of Mexico and southeastern U.S. (Shaver 1990; Coyne 1994; Redfoot 1997; Bresette et al. 1998; Makowski et al. 2006).

#### *Spatial distribution*

The spatial distribution of herbivorous fishes based on transect distance from the channel/inlet was not significantly different within the Trident Basin. However, herbivores exhibited conspicuous vertical distribution within the water column (pers. observ.). Sergeant majors (*A. saxatilis*) occupied inter- and upper-subtidal zones, while spottail pinfish (*D. holbrooki*) and pinfish porgies (*L. rhomboides*) occupied mainly upper and mid-subtidal zones. Sheepshead browsed and grazed the mid- and lower

subtidal zone and were photodocumented in summer and spring foraging and/or winnowing in thick mats of *A. fragilissima*. Green turtles were observed foraging on macroalgae that were more difficult to access in rock crevices (e.g., *G. planicaulis*, *B. hypnoides*) in both inter- and subtidal regions.

*Temporal distribution*

Temporal patterns of recruitment and/or fluxes in species abundance, indicative of pre-settlement life stage of fish stocks (Hastings 1979), were most evident for *L. rhomboides*. Schooling small *L. rhomboides* were abundant in spring periods and low or absent during other or seasonal sampling periods. Sergeant major (*A. saxatilis*) and spottail pinfish (*D. holbrooki*) were most abundant in summer and fall, which correlated with the warmest water temperatures. Lower abundance of *A. saxatilis* between the fall sampling periods (September 2008 and 2009) may have been due to relatively poor water conditions (i.e., low water clarity) that persisted post Tropical Storm Fay. The absence and/or decline of *A. saxatilis* and *D. holbrooki* abundance correlated with cooler water temperatures in winter, especially following the extreme cold period that began in January 2010. Sheepshead (*A. probatocephalus*) and green turtles (*C. mydas*) were present in all surveys throughout the 2-year study period. Temporal patterns in the abundance and size class of juvenile green turtles in the Basin during this study indicate a seasonal influx of new recruits of smaller juvenile turtles occurring in winter/spring periods. This phenomenon was previously documented by Redfoot and Ehrhart (2013) for the Trident Basin green turtle population. Bresette et al. (1998) also documented this phenomenon for juvenile green turtle aggregations at the St. Lucie power plant, which is approximately 120 km south of the Port Canaveral. Stochastic events (i.e., T.S. Fay and

the extreme cold in January 2010) may be responsible for much of the variation found in the distribution of species during this study, especially between sampling periods of the same season.

Foraging

*Abudefduf saxatilis, D. holbrooki, and L. rhomboides* foraged as specialists, targeting less-abundant macroalgae (e.g., *Ulva* spp.) while sheepshead (*A. probatocephalus*) and green turtles (*C. mydas*) foraged as generalists (consuming a wide range of macroalgal species). The diets of *D. holbrooki* (spottail pinfish) and *L. rhomboides* (pinfish porgy), which are typically recognized as warm temperate and subtropical species (Lindquist et al. 1985; Hay and Fenical 1988; Pike and Lindquist 1994), vary based on location, life history stage, size-class, resource availability, and can also be influenced by anti-predator based behavior (Conover and Schultz 1997). In this study, similar-sized 'herbivorous' fishes were sometimes found foraging as omnivores or carnivores. Site-specific foraging behavior was evident in similar-sized fishes of *L. rhomboides* captured over the rock revetment compared to fishes captured below the Trident wharf or in mid-water otter trawls. The gut contents of *L. rhomboides* captured over revetment were predominantly composed of macroalgae while the gut contents from fishes captured from other locations in the Basin contained only invertebrates. In addition, *L. rhomboides* only foraged as herbivores during spring sampling periods. The foraging contents of *D. holbrooki* and *A. saxatilis* contained >50% macroalgae regardless of size. Similar-sized fishes of *A. probatocephalus* exhibited site-specific foraging behavior similar to *L. rhomboides*, where the gut content of fishes captured over rock revetment contained >50% macroalgae vs. the gut content of fishes captured below the

Trident wharf, which consisted primarily of invertebrates (e.g., calcareous tube worms, barnacles, crab pieces).

The largest percent composition of juvenile green turtle lavage samples was red algae which is characteristic of previous foraging studies of juvenile green turtles over nearshore reefs (Holloway-Adkins 2001; Gilbert 2005) and was previously documented for turtles in the Trident Basin (Redfoot 1997). Consumption of *G. crinale*, *G. filicina*, and highly-turfed *H. spinella* made up the largest portion of green turtle foraging samples. Opportunistic foraging by juvenile green turtles on flotsam species of *Sargassum*, jellyfish, and other floating invertebrates and plastic frequently occurred, a phenomenon documented by others (Bjorndal et al. 1994, Seminoff et al. 2002).

Overlap and partitioning of resources

Patterns in the presence (or absence) of abundant fishes documented during this study support resource partitioning theory through foraging selection, temporal abundance of algae and/or herbivore conspecifics (Carothers and Jaksić 1984). In this study, grazing pressure by specialist herbivores appears to have been ameloriated by temporal partitioning. *Lagodon rhomboides* were abundant and feeding as herbivores in spring (March 2009) prior to the migration of *A. saxatilis* and *D. holbrooki* to the Basin in summer and fall (June and September 2008, 2009). The influx of the latter species coincided with warm water temperatures and an increase in subtropical macroalgae (i.e., *Hypnea spinella*, *Amphiroa fragilissima*). However, the selection for *Ulva* spp. by generalists and specialist may indicate pressure on a potentially limited resource. Juvenile green turtles were observed to forage on species of *U. lactuca* and *intestinalis* growing on ships that entered the Basin (pers. observ.). Opportunistic foraging on flotsam by juvenile

green turtles was most common in fall foraging samples. For turtles, feeding on drift species of jellyfish, nudibranchs, and other non-algal food resources may be an attempt to supplement their macroalgal diet, gain necessary nutrients, and/or maintain digestive flexibility (Bjorndal 1980).

Inlets and jetties constructed of rock boulders (a.k.a. rock riprap) are circumglobally distributed with applications in structuring inlets (i.e., breakwater and retainer walls) and have been widely used to enhance recreational fishing and/or mitigate disturbances to natural hardbottom habitat. These man-made structures appear to attract relatively large populations of endangered loggerhead, Kemp's ridley, and green sea turtles (Dickerson et al. 1995; Schmid 1995) and are documented to be juvenile green turtle developmental habitat in the Gulf of Mexico and southeastern U.S. Atlantic (Coyne 1994; Shaver 1994; Dickerson et al. 1995; Redfoot 1997; Fonferek 2003; USACE 2007; Howell et al. 2011). These artificial hardbottom (AHB) habitats are typically set in soft sediment areas and offer settlement space, shelter, and ultimately, food resources for a diverse but different community than previously existed. However, attraction to these areas tells us little about whether these structures serve as source or sink areas for the flora and fauna that inhabit them and the functional role AHB play in the life history of fishes and sea turtles.

Species and/or taxa examined during this study are found in association with nearshore natural and artificial reef systems throughout temperate and subtropical regions. While this study focused on a single location, the results can be cautiously extrapolated to rocky intertidal systems within this latitudinal range and used to further identify the impact of co-occurring herbivores on resources. Studies that target

plant/herbivore responses to alterations in the existing macroalgal resource including the introduction of non-native species are key to modeling future impacts among herbivores under increased coastal development and global climate change.

The foraging analysis presented here is the first *in situ* examination of the potential overlap in the foraging niches of green turtles and herbivorous fishes. During this study the presence, abundance, and foraging selections of an unprecedented number of co-occurring herbivore species were surveyed and sampled. Five different co-occurring relatively large and abundant vertebrate herbivores and their foraging selections with respect to available macroalgal resources were examined. These data are important to advance our understanding of the role of different herbivores, individually and collectively, in marine communities. More specifically, this research allows us to continue to uncover mechanisms that have evolved to allow multiple grazers to forage in macroalgal communities without detrimental effects on their food resources.

Tables

Table 3.1. Analysis of similarities (ANOSIM; $\alpha = 0.05$) results for the temporal distribution of the four most abundant herbivorous fishes (*Abudefduf saxatilis*, *Archosargus probatocephalus*, *Diplodus holbrooki*, and *Lagodon rhomboides*) from UW video and stationary sampling surveys. Results are for quarterly surveys and sampling periods that occurred during or following a "mild" winter (Dec-08 and Mar-09) vs. an extremely "cold" winter (Feb and Apr-10).

| Temporal variable | Survey method | (n) | Global R | Significance (*P*) |
|---|---|---|---|---|
| Quarter | video | 8 | 0.672* | 0.001 |
| | stationary | 8 | 0.366 | 0.001 |
| Mild vs. cold winter | video | 4 | 0.634* | 0.001 |
| | stationary | 4 | 0.239 | 0.001 |

* significant at R>0.50, P <0.05.

Table 3.2. *Post hoc* pairwise comparisons of quarterly (a) percent compositions of the herbivorous fish community based on UW video surveys (ANOSIM, Global R = 0.672, P = 0.001, N = 8) and for sampling periods that occurred during or following a "mild" winter (Dec-08 and Mar-09) vs. an extremely "cold" winter (Feb and Apr-10) (ANOSIM, Global R = 0.634, P = 0.001).

(a)

| Sample period(s) | Jun-08 | Sep-08 | Dec-08 | Mar-09 | Jun-09 | Sep-09 | Feb-10 |
|---|---|---|---|---|---|---|---|
| Apr-10 | 0.831* | 0.943* | 0.918* | 0.801* | 0.903* | 0.936* | 0.901* |
| Feb-10 | 0.932* | 0.862* | 0.125 | 0.416 | 0.929* | 0.935* | |
| Sep-09 | 0.550* | 0.947* | 0.946* | 0.772* | 0.145 | | |
| Jun-09 | 0.338 | 0.818* | 0.924* | 0.662* | | | |
| Mar-09 | 0.266 | 0.424 | 0.334 | | | | |
| Dec-08 | 0.790* | 0.844* | | | | | |
| Sep-08 | 0.528* | | | | | | |

(b)

| Sample period(s) | Mild: Dec-08 | Mild: Mar-09 | Cold: Feb-10 |
|---|---|---|---|
| Cold:Apr-10 | 0.956* | 0.698* | 0.942* |
| Cold:Feb-10 | -0.031 | 0.168 | |
| Mild:Mar-09 | 0.187 | | |

* significant at R >0.50, P <0.05

Table 3.3. Analysis of similarities (ANOSIM) results for foraging samples from herbivorous fishes and juvenile green turtles (*Chelonia mydas*). R values ≥0.50 indicate a moderate to high level of difference in the foraging composition between herbivores (e.g., *L. rhomboides* vs. *C. mydas*). Low R values (<0.50) indicate there was an overlap in the composition of foraging samples between herbivores. Negative R values indicate that foraging samples within species were more dissimilar than samples among species. Not all herbivore species were present during every sampling period.

| Species | *Archosargus probatocephalus* | *Abudefduf saxatilis* | *Diplodus holbrooki* | *Lagodon rhomboides* |
|---|---|---|---|---|
| *Chelonia mydas* | 0.20 | 0.05 | 0.30 | **0.50** |
| *Lagodon rhomboides* | 0.41 | **0.60** | -0.04 | |
| *Diplodus holbrooki* | 0.39 | 0.09 | | |
| *Abudeduf saxatilis* | 0.29 | | | |

Table 3.4. Analysis of similarities (ANOSIM) results for foraging samples from *Archosargus probatocephalus* (*Ap*), *Chelonia mydas* (*Cm*), *Abudefduf saxatilis* (*As*), *Diplodus holbrooki* (*Dh*), and *Lagodon rhomboides* (*Lr*) during seasons where three or more different species were present [summer (a), fall (b), winter (c)]. R values ≥0.50 indicate a moderate to high level of difference in the foraging composition between herbivores (e.g., in fall, *D. holbrooki* vs. *A. probatocephalus*; in bold). Low R values (<0.50) indicate there was an overlap in the composition of foraging samples between herbivores (e.g, in summer, *C. mydas* and *A. saxatilis*). Negative R values indicate that foraging samples within species were more dissimilar than samples among species.

| Summer Species | *Archosargus probatocephalus* | *Abudefduf saxatilis* | *Diplodus holbrooki* |
|---|---|---|---|
| *Chelonia mydas* | 0.32 | 0.16 | 0.25 |
| *Diplodus holbrooki* | 0.28 | 0.16 | |
| *Abudefduf saxatilis* | 0.47 | | |
| Fall | *Archosargus probatocephalus* | *Abudefduf saxatilis* | *Diplodus holbrooki* |
| *Chelonia mydas* | 0.23 | 0.25 | **0.50** |
| *Diplodus holbrooki* | **0.57** | 0.18 | |
| *Abudefduf saxatilis* | 0.31 | | |
| Spring | *Archosargus probatocephalus* | *Diplodus holbrooki* | *Lagodon rhomboides* |
| *Chelonia mydas* | 0.41 | **0.59** | **0.63** |
| *Lagodon rhomboides* | **0.61** | -0.07 | |
| *Diplodus holbrooki* | **0.52** | | |

Table 3.5. Analysis of similarities (ANOSIM) for foraging samples from *Archosargus probatocephalus* (*Ap*), *Chelonia mydas* (*Cm*), *Abudefduf saxatilis* (*As*), *Diplodus holbrooki* (*Dh*), and *Lagodon rhomboides* (*Lr*) during quarterly periods where three or more different species were present [Jun-08 (a), Mar-09 (b), Jun-09 (c), Sep-09 (d)]. R values ≥0.50 indicate a moderate to high level of difference in the foraging composition between herbivores (e.g., in March 2009, *L. rhomboides* vs. *C. mydas*; in bold). Low R values (<0.50) indicate there was an overlap in the composition of foraging samples between herbivores (e.g, in June 2008, *D. holbrooki* and *A. probatocephalus*). Negative R values indicate that foraging samples within species were more dissimilar than samples among species.

(a)

| Jun-08 Species | *Archosargus probatocephalus* | *Abudefduf saxatilis* |
|---|---|---|
| *Diplodus holbrooki* | 0.24 | 0.30 |
| *Abudefduf saxatilis* | 0.29 | |

(b)

| Mar-09 Species | *Archosargus probatocephalus* | *Lagodon rhomboides* | *Diplodus holbrooki* |
|---|---|---|---|

| | | | |
|---|---|---|---|
| *Chelonia mydas* | 0.45 | **0.79** | **0.80** |
| *Diplodus holbrooki* | **0.79** | -0.07 | |
| *Lagodon rhomboides* | **0.72** | | |
| (c) | | | |
| Jun-09 | *Archosargus* | *Abudefduf* | *Diplodus* |
| Species | *probatocephalus* | *saxatilis* | *holbrooki* |
| *Chelonia mydas* | 0.43 | 0.41 | 0.30 |
| *Diplodus holbrooki* | **0.75** | -1.0 | |
| *Abudefduf saxatilis* | **1.00** | | |
| (d) | | | |
| Sep-09 | *Archosargus* | *Abudefduf* | |
| Species | *probatocephalus* | *saxatilis* | |
| *Diplodus holbrooki* | **0.76** | 0.18 | |
| *Abudefduf saxatilis* | **0.78** | | |

Table 3.6. Selection pressure by season and quarterly sampling period on abundant macroalgae by abundant herbivorous fishes and juvenile green turtles (based on Ivlev's electivity indices calculations >0.50). Herbivores were As = *Abudefduf saxatilis*, Ap = *Archosargus probatocephalus*, Dh = *Diplodus holbrooki*, Lr = *Lagodon rhomboides*, and Cm = *Chelonia mydas* (green turtles).

| | Summer | | Fall | | Winter | | Spring | |
|---|---|---|---|---|---|---|---|---|
| Macroalgal species | Jun-08 | Jun-09 | Sep-08 | Sep-09 | Dec-08 | Feb-10 | Mar-09 | Apr-10 |
| *Amphiroa fragilissima* | Ap | Ap | - | - | - | - | Ap | - |
| *Centroceras clavulatum* | - | - | - | - | - | - | - | - |
| *Gelidiopsis planicaulis* | Ap | - | Cm | Ap | - | - | - | - |
| *Gelidium crinale* | - | Dh | - | - | - | Cm | - | - |
| *Grateloupia filicina* | - | - | Cm | - | - | - | - | - |
| *Hypnea spinella* | As | Cm | Ap | - | - | - | - | Cm |
| *Polysiphonia denudata* | Ap, Dh | - | Ap | Ap, Dh | - | - | Ap, Lr | Ap |
| *Ulva flexuosa* | - | As, Cm | - | As, Dh | - | - | Lr, Cm | Ap |
| *U. lactuca* | As, Ap | Cm | - | Dh | Ap | Ap, Cm | Dh, Lr | Ap, Cm |
| *U. prolifera* | As, Ap, Dh | As, Dh | Ap, Cm | As, Dh | Ap | Ap, Cm | Dh, Lr | - |

Figures

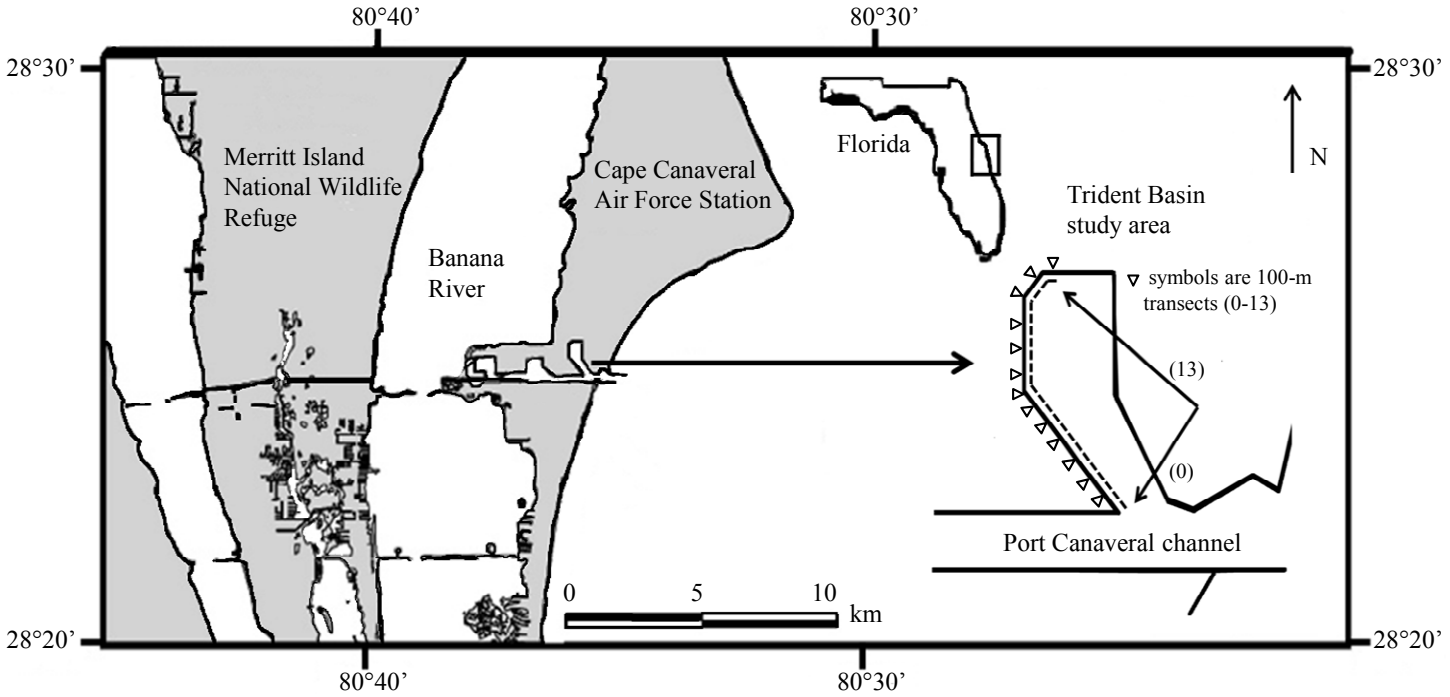


Figure 3.1. The study area within the Trident Basin located just inside Port Canaveral Inlet in Cape Canaveral on the east coast of Florida, USA. Fish and turtle surveys were conducted along a 1300-m long area of the rock revetment on the north, west, and south walls (dashed line within the study area inlay). Transects (n = 13) within the survey area were parallel to shore and were each 100-m long between the 0-13 marks (diagram is not to scale).

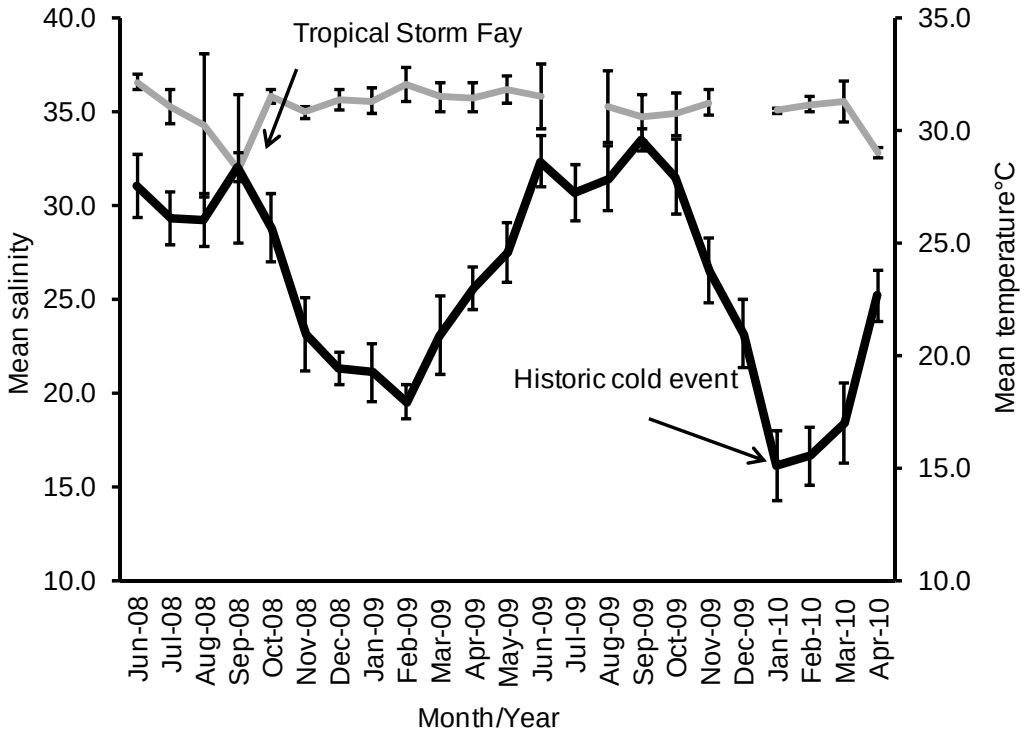


Figure 3.2. Mean monthly salinity (gray line) and temperature (black thick line) values in the Trident Basin (June 2008-April 2010). Episodic events were excessive rainfall from Tropical Storm Fay during August 2008 and extreme cold water temperatures during January 2010.

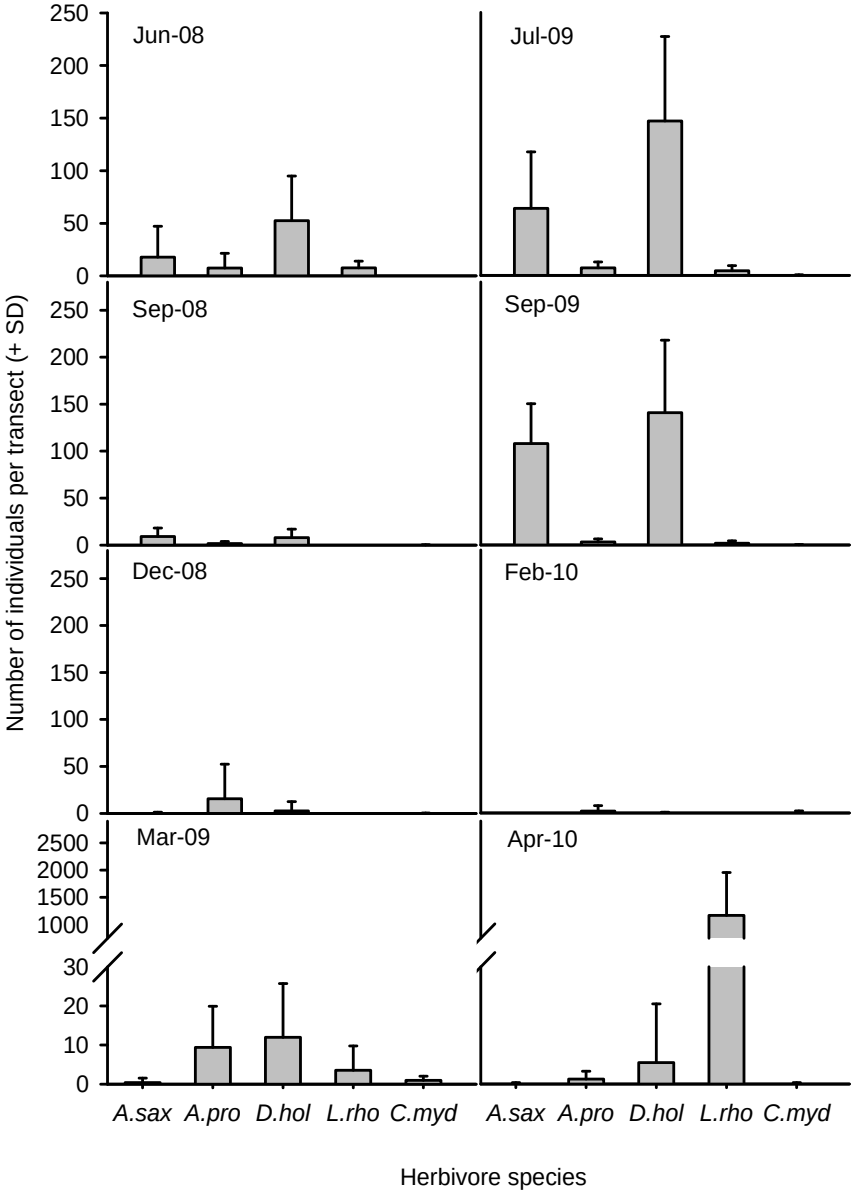


Figure 3.3. Mean number of the four most abundant herbivorous fishes [*Abudefduf saxatilis* (*A sax*), *Archosargus probatocephalus* (*A pro*), *Diplodus holbrooki* (*D hol*), *Lagodon rhomboides* (*L rho*)] and juvenile green turtles (*Chelonia mydas; C myd*) in 100-m transects (n = 13) from UW video surveys conducted quarterly between June 2008 and April 2010 (n = 8) in the Trident Basin at Port Canaveral in Cape Canaveral, Florida. Error bars are standard deviation.

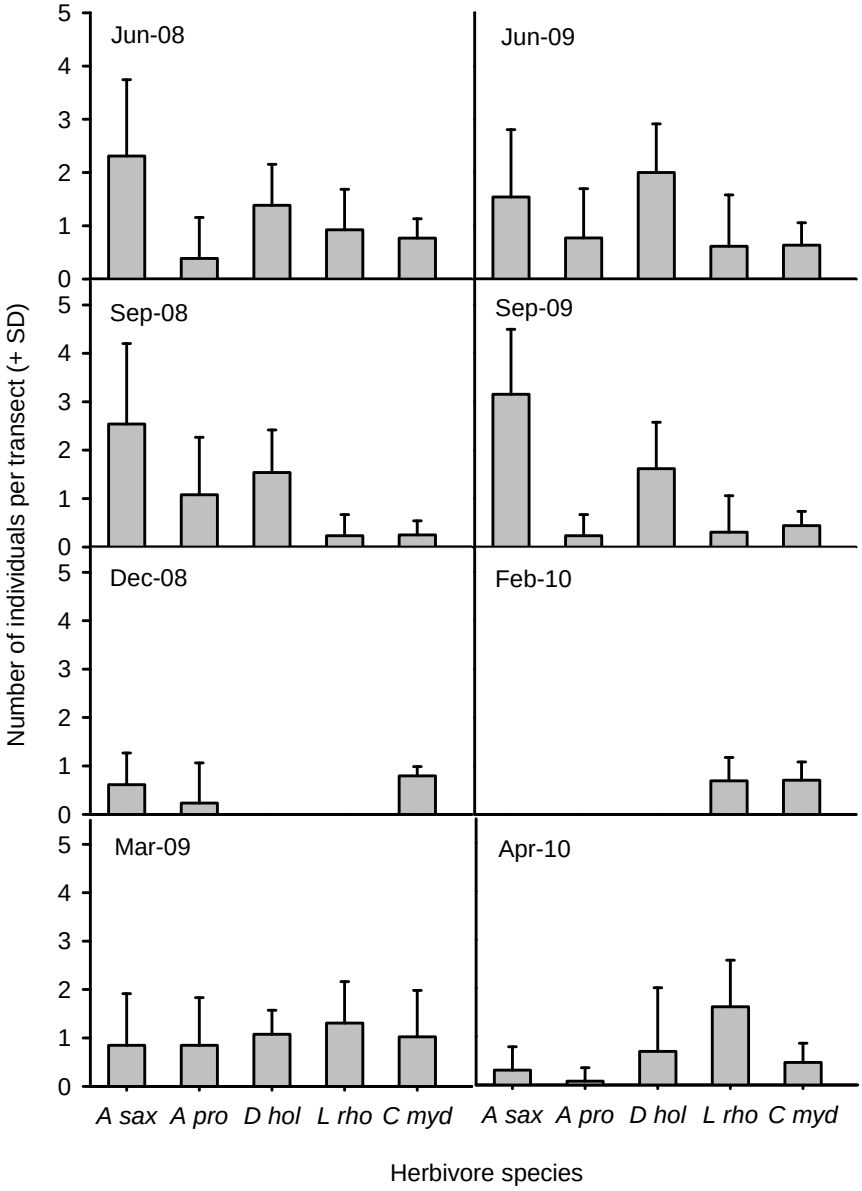


Figure 3.4. Mean number of the four most abundant herbivorous fishes [*Abudefduf saxatilis* (*A sax*), *Archosargus probatocephalus* (*A pro*), *Diplodus holbrooki* (*D hol*), *Lagodon rhomboides* (*L rho*)] observed during stationary surveys and juvenile green turtles (*Chelonia mydas*; *C myd*) based on onwater boat surveys conducted quarterly between June 2008-April 2010 (n = 8) in the Trident Basin at Port Canaveral in Cape Canaveral, Florida. Error bars are standard deviation.

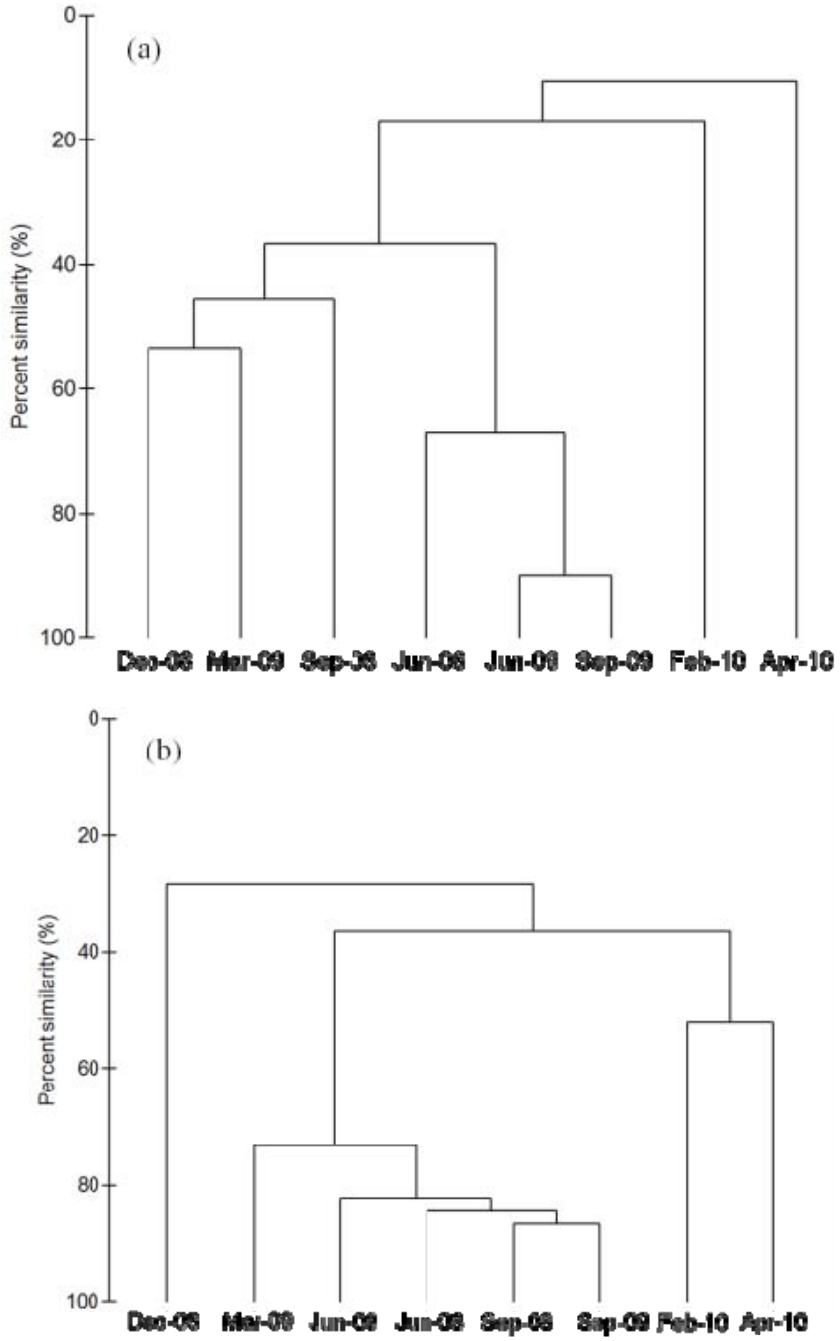


Figure 3.5. Cluster analysis of percent compositions for temporal distribution of the four most abundant herbivorous fishes (*Abudefduf saxatilis*, *Archosargus probatocephalus*, *Diplodus holbrooki*, *Lagodon rhomboides*) observed in UW video surveys (a) and stationary surveys (b) conducted quarterly between June 2008-April 2010.

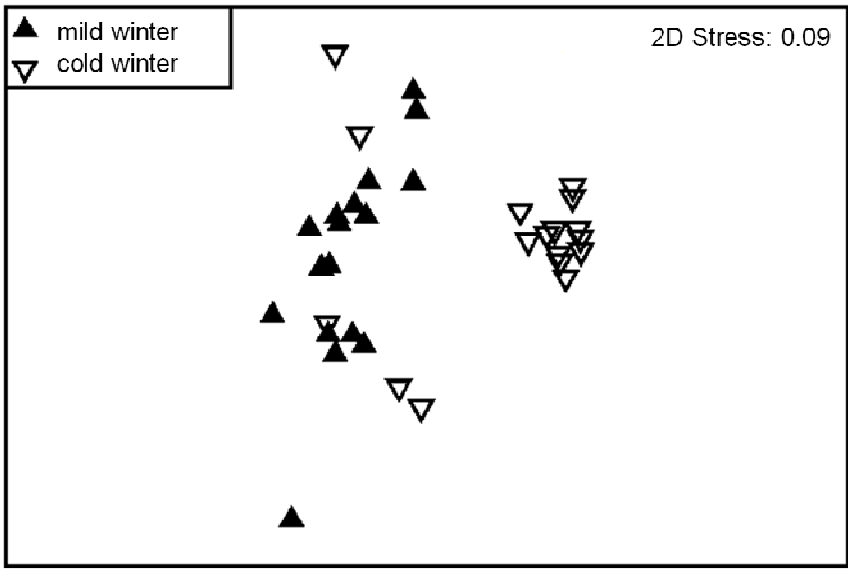


Figure 3.6. MDS plot comparing the herbivore community composition from UW video surveys for the two quarterly surveys that occurred during or following a relatively mild winter (December 2008 and March 2009, collectively referred to as "mild-winter"; solid triangle) vs. the quarterly surveys that followed an episodic cold event in January 2010 (February and April 2010, collectively referred to as "cold winter"; inverted open triangle).

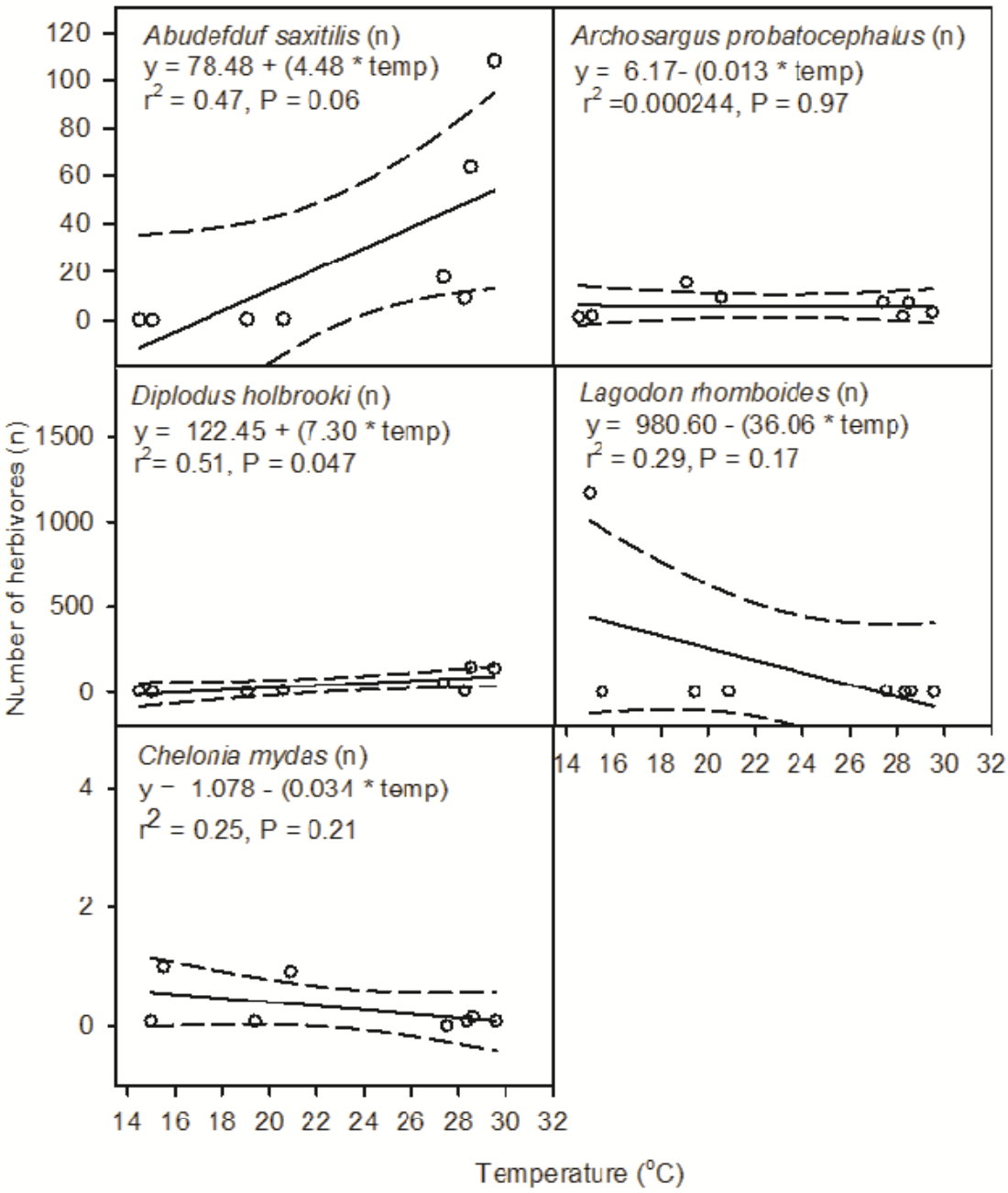


Figure 3.7. Distribution of the four-most abundant herbivorous fishes and juvenile green turtles as a function of temperature. Data were from UW video surveys conducted quarterly between June 2008-April 2010 (n = 8) in the Trident Basin at Port Canaveral in Cape Canaveral, Florida.

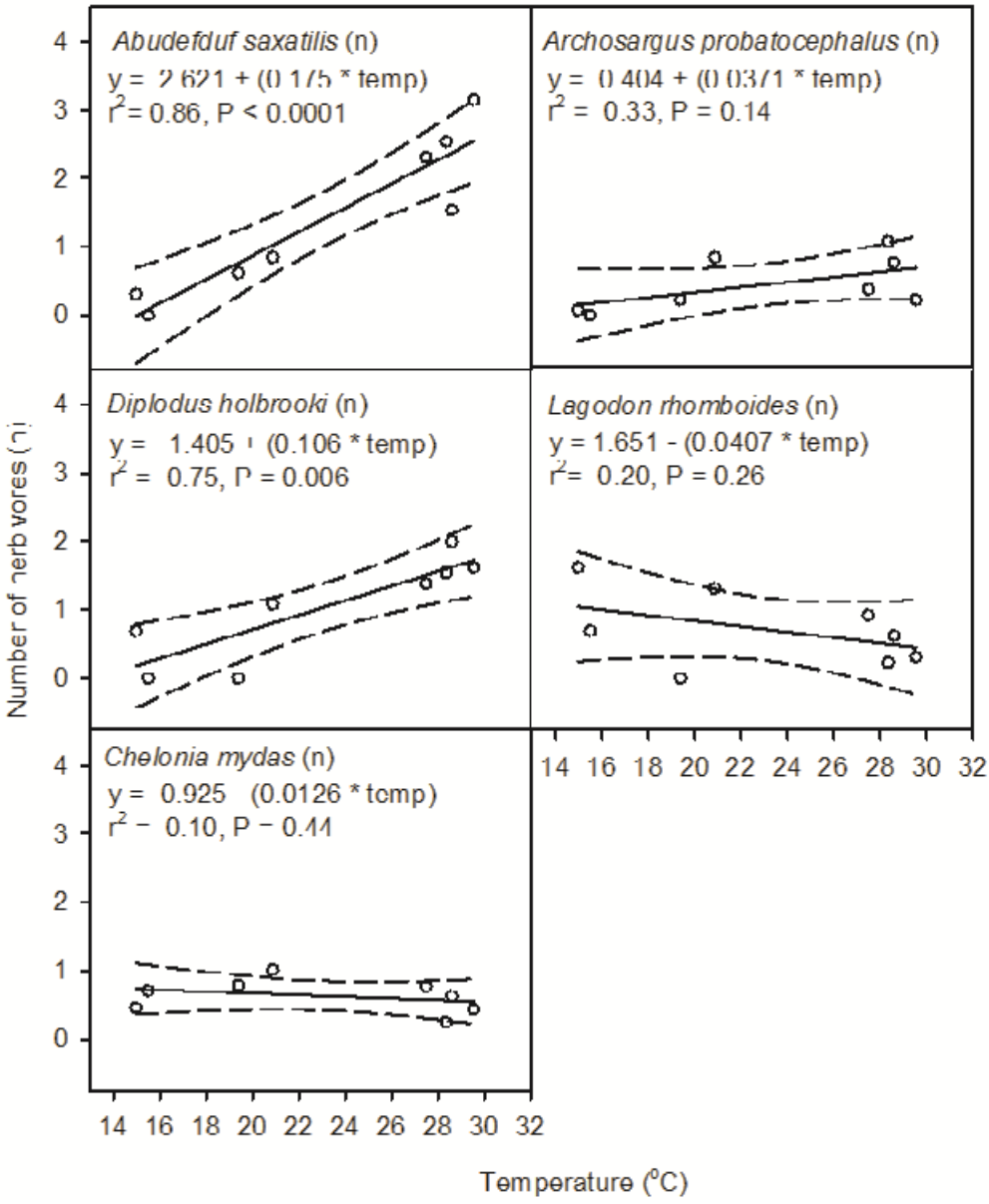


Figure 3.8. Distribution of the four-most abundant herbivorous fishes and juvenile green turtles as a function of temperature. Fish abundance data were from stationary surveys and green turtle data were from boat surveys.

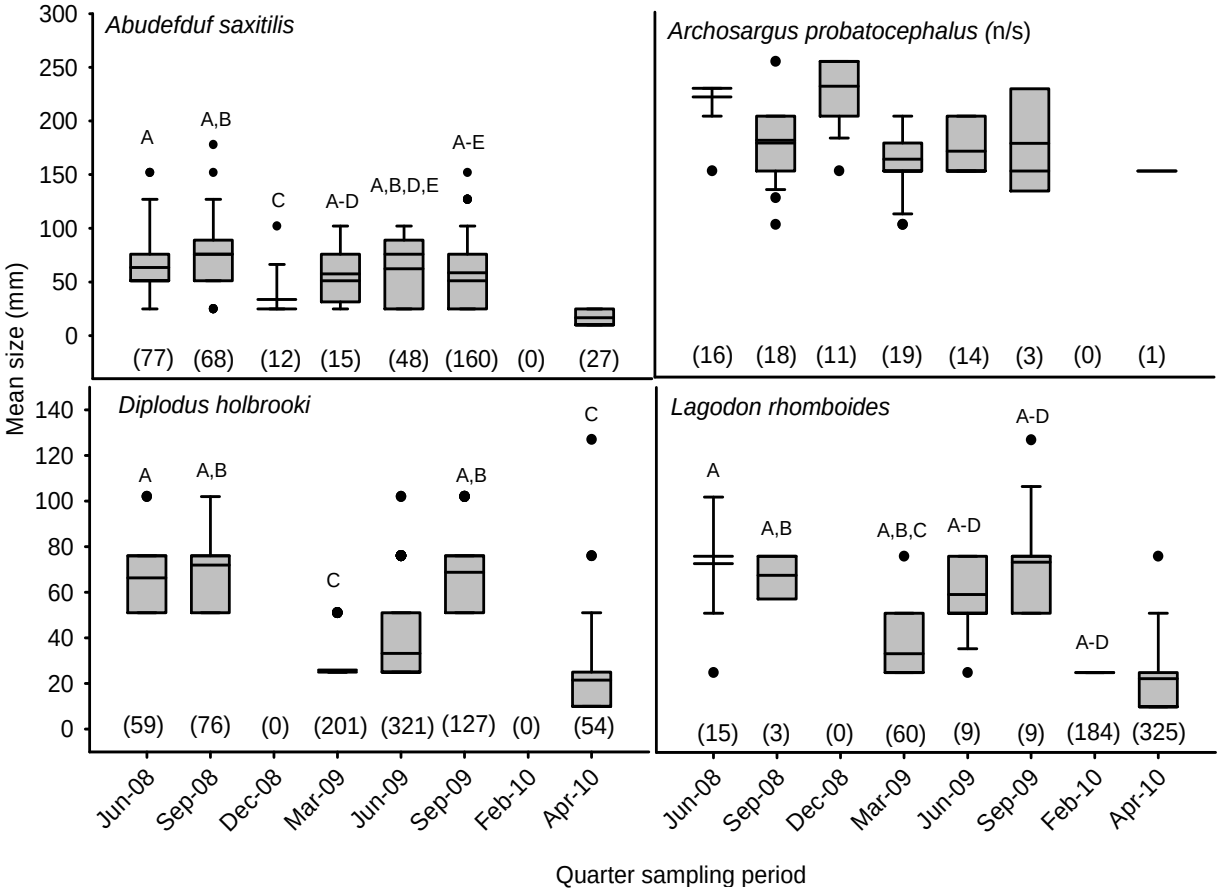


Figure 3.9. The mean, median, and distribution of size of herbivorous fishes in the quarterly stationary surveys. Matching letters (e.g., "A") indicate similarity in mean size among fishes from these surveys. Values in parentheses = n.

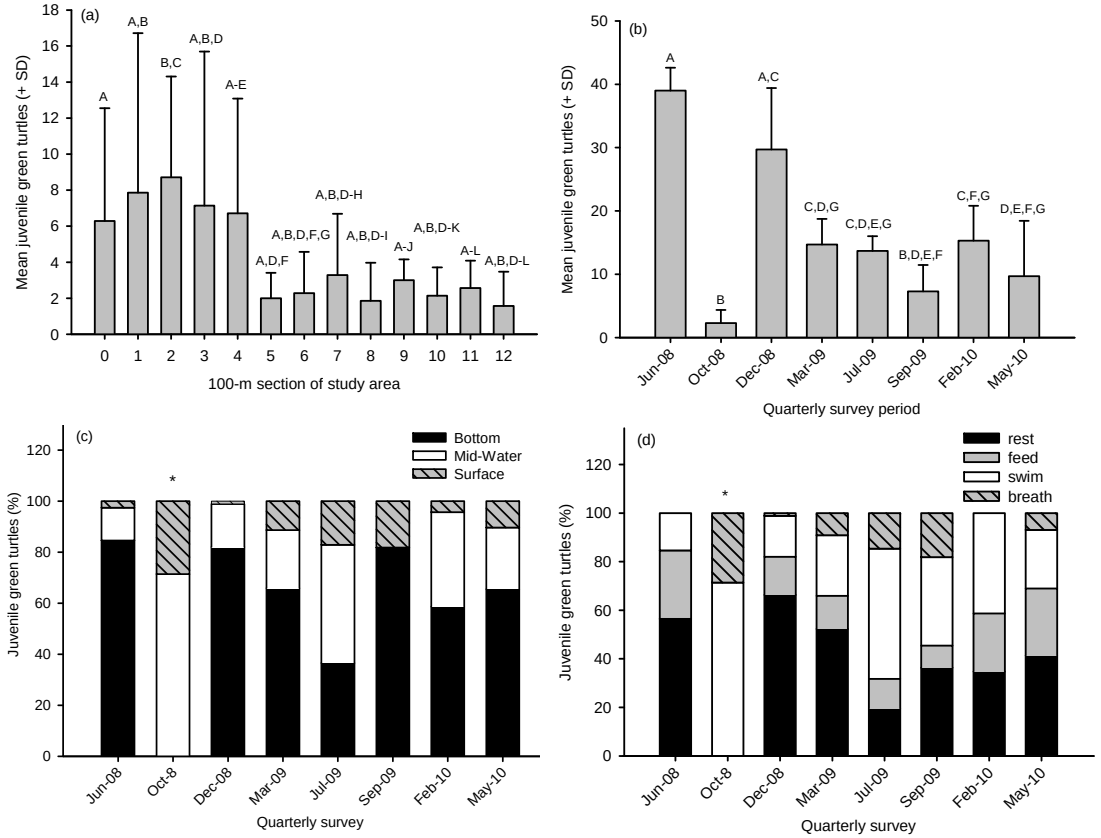


Figure 3.10. Juvenile green turtle spatial distribution (a), temporal distribution (b), water column position (c), and activity (d) from quarterly boat surveys. Matching letters (e.g., "A") indicate similarity among the mean number of juvenile green turtles present (top graphs). * period of limited water clarity (October 2008) due to excessive stormwater runoff from Tropical Storm Fay.

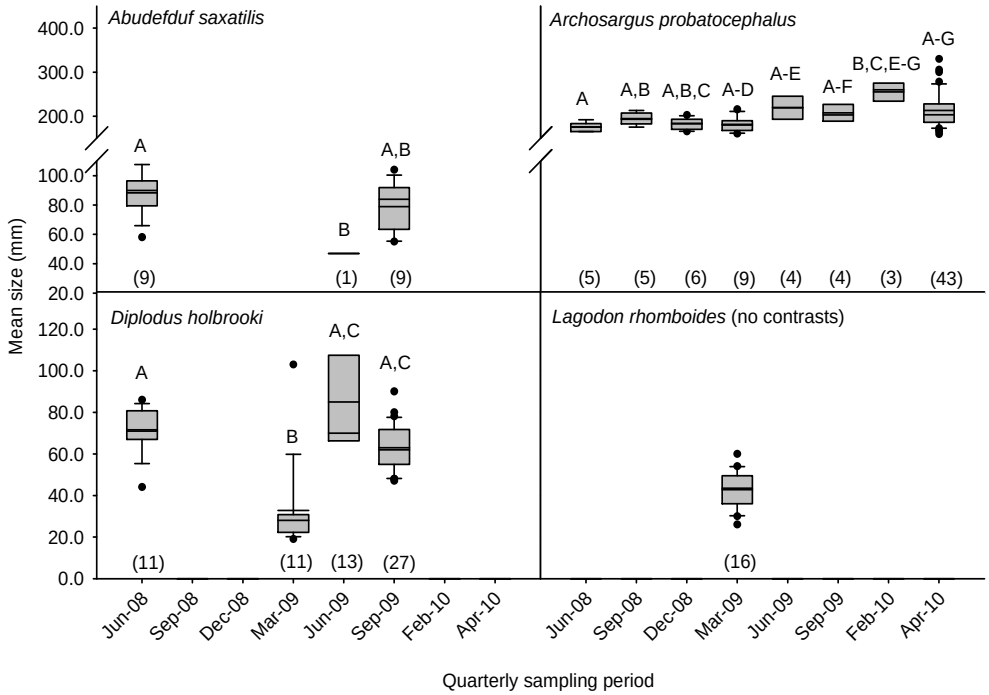


Figure 3.11. The mean, median, and distribution of fishes in the quarterly foraging surveys. Matching letters (e.g., "A") indicate similarity in mean size among fishes from these quarterly sampling periods. Values in parentheses = n.

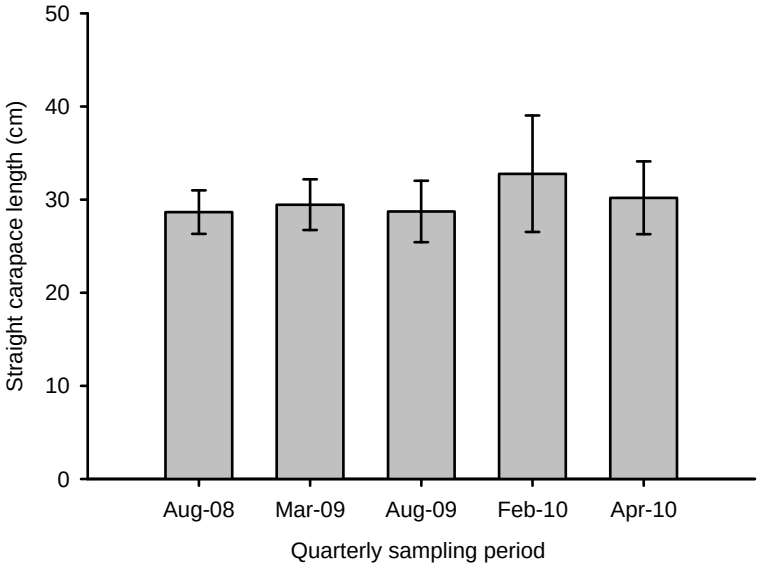


Figure 3.12. Size (straight carapace length) of juvenile green turtles captured during 5 two-day sampling events between June 2008 and April 2010**.**

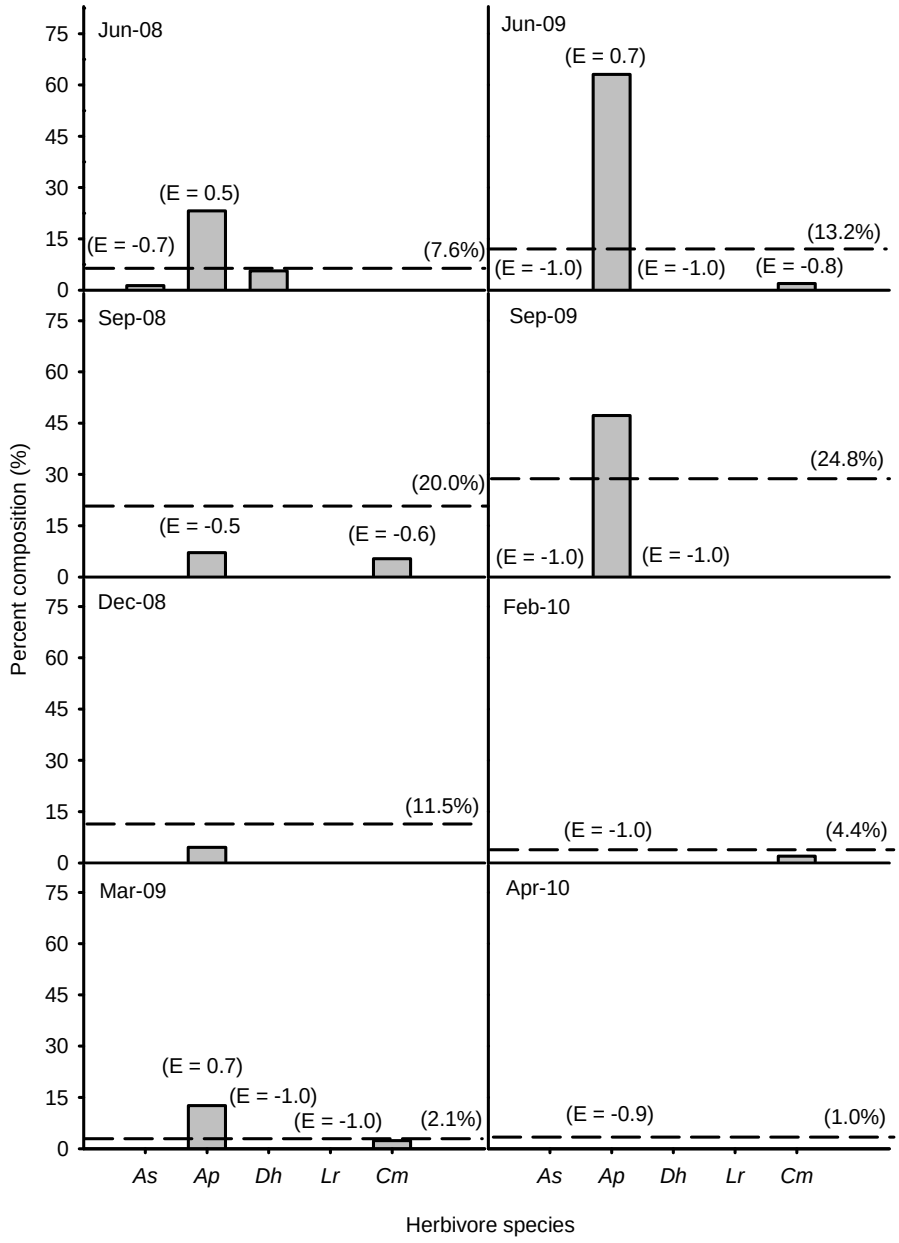


Figure 3.13. Quarterly average consumption of the jointed calcareous alga *Amphiroa fragilissima* based on foraging samples from the four most abundant herbivorous fish species (As = *Abudefduf saxatilis*, Ap = *Archosargus probatocephalus*, Dh = *Diplodus holbrooki*, Lr = *Lagodon rhomboides*) and juvenile green turtles (Cm = *Chelonia mydas*). Dashed horizontal lines represent the average presence of *A. fragilissima* from concurrent algal surveys. Ivlev's electivity indices ≥0.5 (E) indicate herbivores were selecting 'for' *A. fragilissima* in June 2008, March 2009 and June 2009.

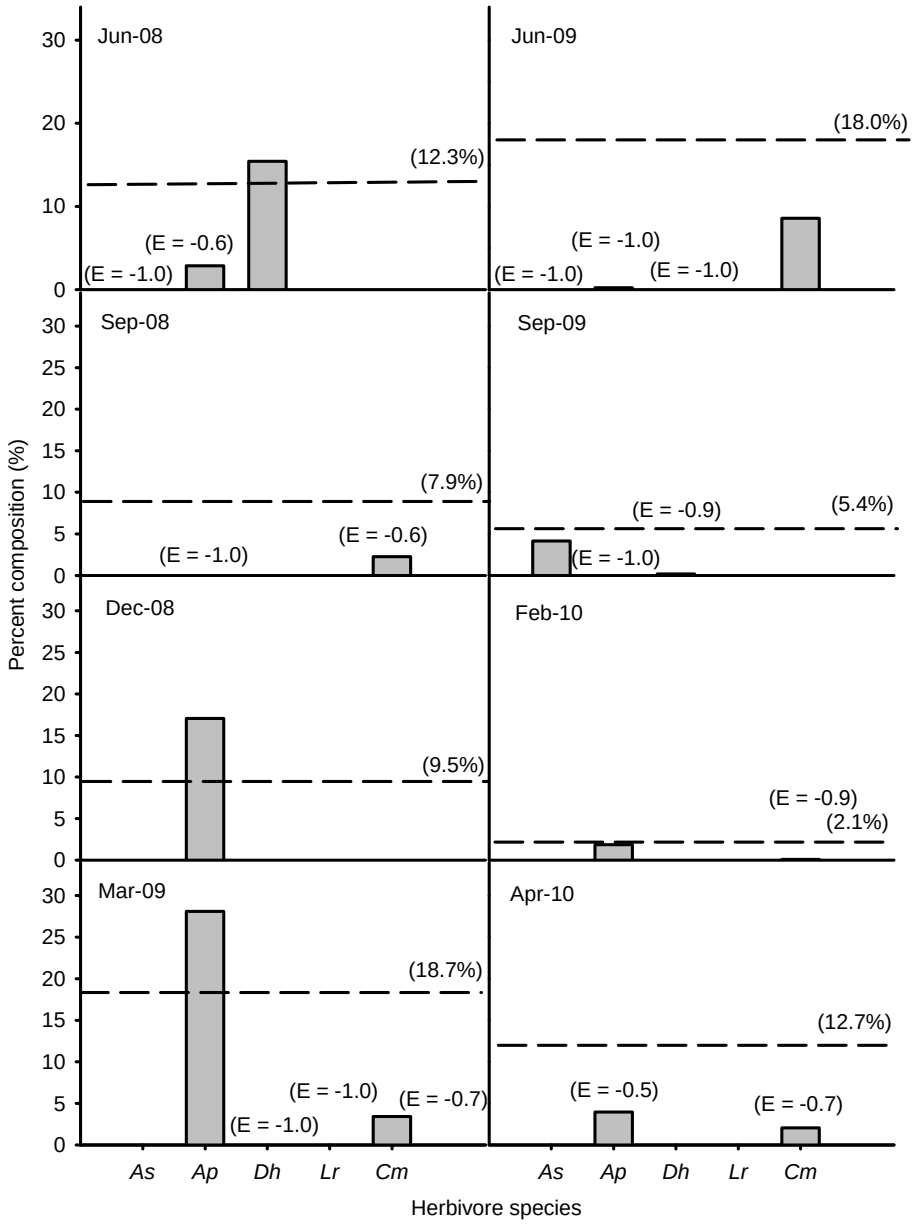


Figure 3.14. Quarterly average consumption of the filamentous alga *Centroceras clavulatum* based on foraging samples from the four most abundant herbivorous fish species (As = *Abudefduf saxatilis*, Ap = *Archosargus probatocephalus*, Dh = *Diplodus holbrooki*, Lr = *Lagodon rhomboides*) and juvenile green turtles (Cm = *Chelonia mydas*). Dashed horizontal lines represent average presence of *C. clavulatum* from concurrent algal surveys. Herbivores present in all quarterly sampling periods except December 2008, selected against *C. clavulatum* [or avoided; Ivlev's electively indices ≤-0.5 (E)]

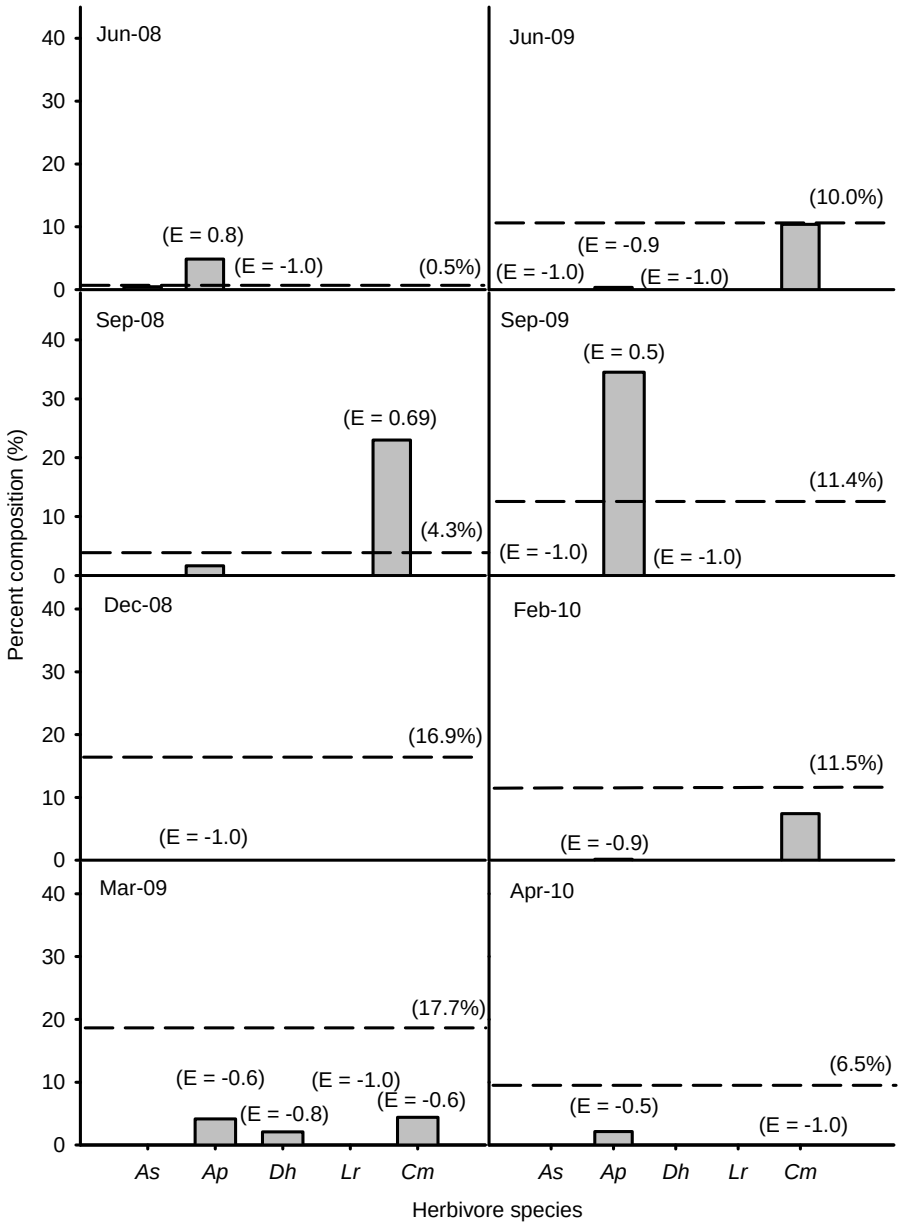


Figure 3.15. Quarterly average consumption of *Gelidiopsis planicaulis* based on foraging samples from the four most abundant herbivorous fish species (As = *Abudefduf saxatilis*, Ap = *Archosargus probatocephalus*, Dh = *Diplodus holbrooki*, Lr = *Lagodon rhomboides*) and juvenile green turtles (Cm = *Chelonia mydas*). Dashed horizontal lines represent the average presence of *G. planicaulis* from concurrent algal surveys. Ivlev's electivity indices ≥0.5 (E) indicate herbivores were selecting 'for' *G. planicaulis* in June 2008, September 2008 and 2009.

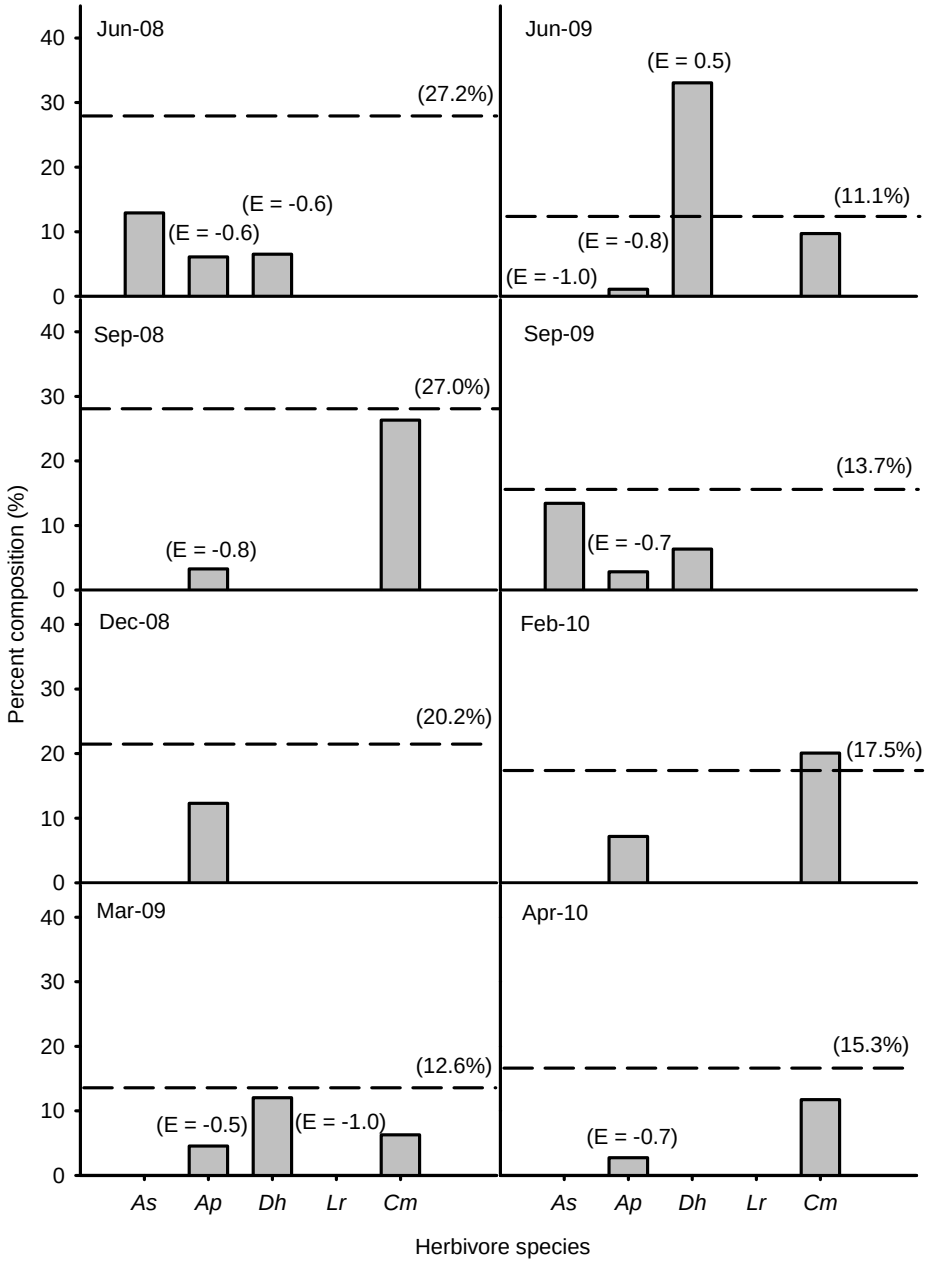


Figure 3.16. Quarterly average consumption of *Gelidium crinale* based on foraging samples from the four most abundant herbivorous fish species (As = *Abudefduf saxatilis*, Ap = *Archosargus probatocephalus*, Dh = *Diplodus holbrooki*, Lr = *Lagodon rhomboides*) and juvenile green turtles (Cm = *Chelonia mydas*). Dashed horizontal lines represent the average presence of *G. crinale* from concurrent algal surveys. Ivlev's electivity indices ≥0.5 (E) indicate herbivores were selecting 'for' *G. crinale* in June 2009.

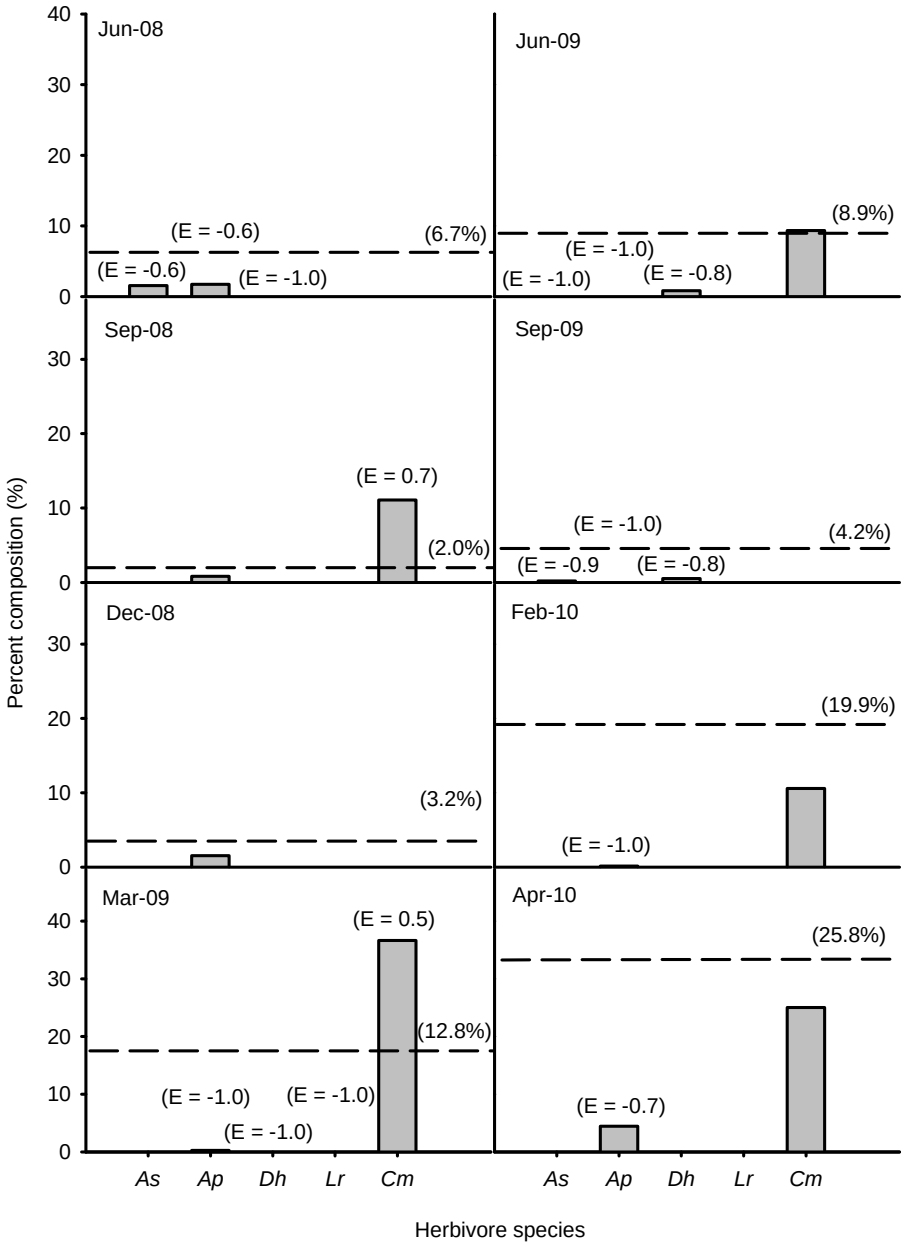


Figure 3.17. Quarterly average consumption of *Grateloupia filicina* based on the results of quarterly foraging samples from the four most abundant herbivorous fish species (As = *Abudefduf saxatilis*, Ap = *Archosargus probatocephalus*, Dh = *Diplodus holbrooki*, Lr = *Lagodon rhomboides*) and juvenile green turtles (Cm = *Chelonia mydas*). Dashed horizontal lines represent the average presence of *G. filicina* from concurrent algal surveys. Ivlev's electivity indices ≥0.5 (E) indicate *C. mydas* selected 'for' *G. filicina* in September 2008 and March 2009.

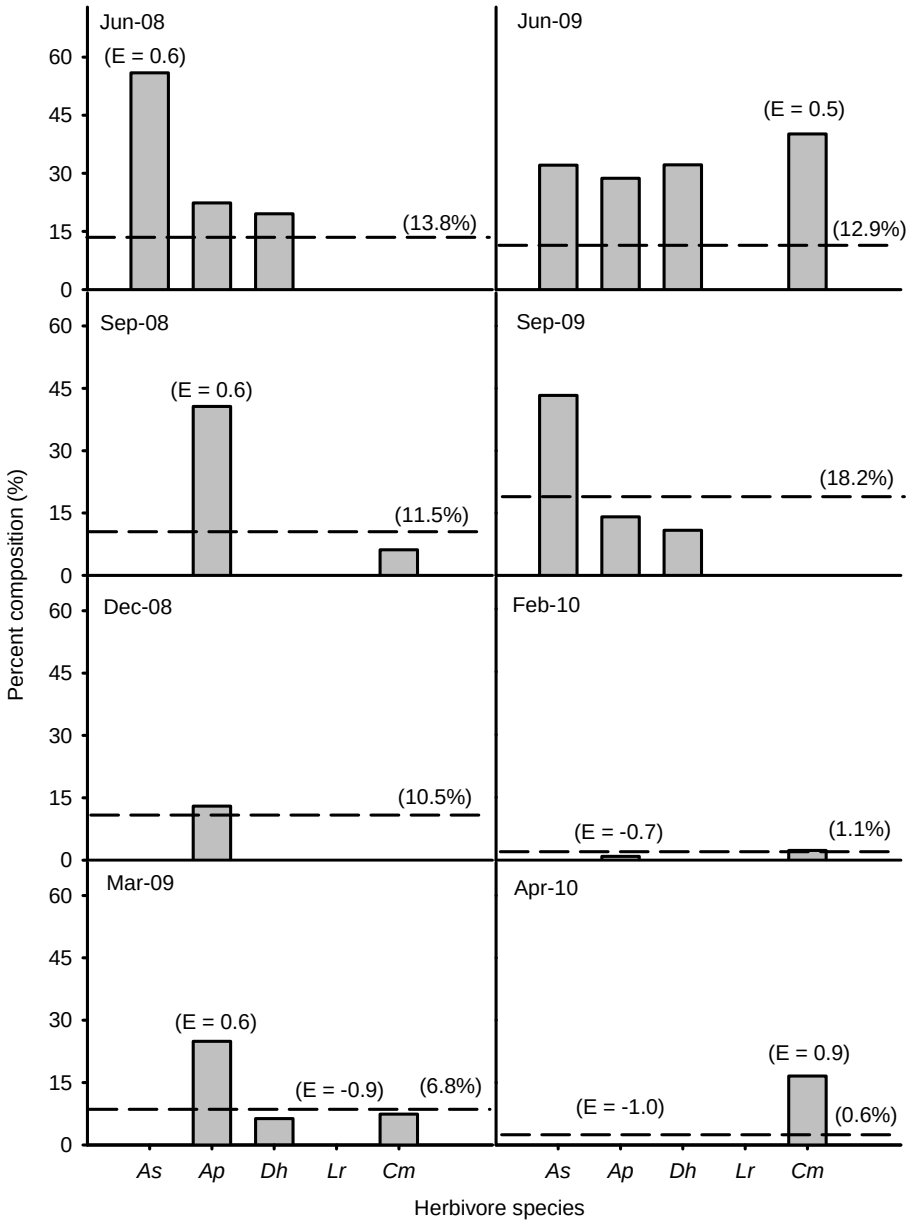


Figure 3.18. Quarterly average consumption of *Hypnea spinella* based on foraging samples from the four most abundant herbivorous fish species (As = *Abudefduf saxatilis*, Ap = *Archosargus probatocephalus*, Dh = *Diplodus holbrooki*, Lr = *Lagodon rhomboides*) and juvenile green turtles (Cm = *Chelonia mydas*). Dashed horizontal lines represent the average presence of *H. spinella* from concurrent algal surveys. Ivlev's electivity indices ≥0.5 (E) indicate herbivores were selecting 'for' *H. spinella* except in December 2008, September 2009, and February 2010.

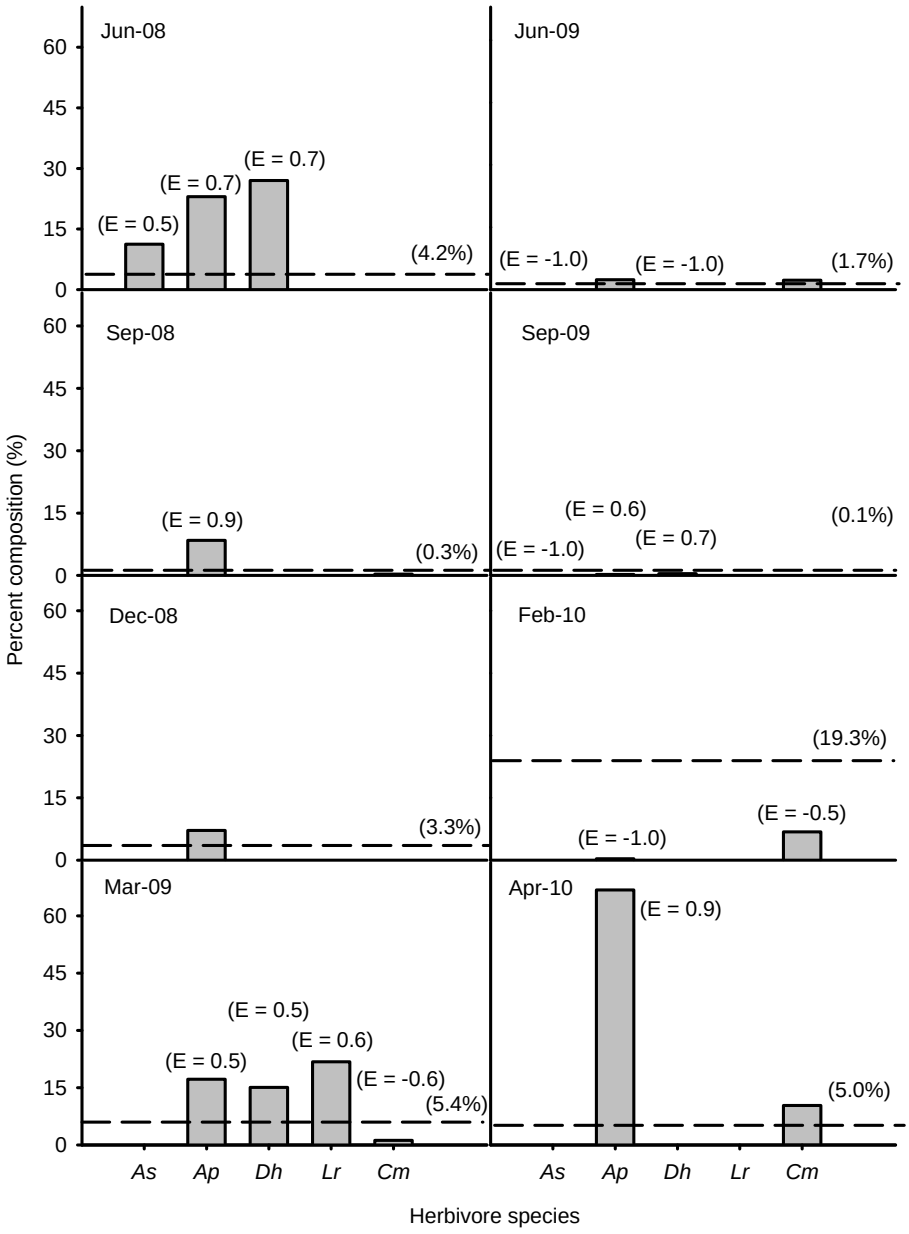


Figure 3.19. Quarterly average consumption of *Polysiphonia denudata* based on foraging samples from the four most abundant herbivorous fish species (As = *Abudefduf saxatilis*, Ap = *Archosargus probatocephalus*, Dh = *Diplodus holbrooki*, Lr = *Lagodon rhomboides*) and juvenile green turtles (Cm = *Chelonia mydas*). Dashed horizontal lines represent the average presence of *P. denudata* from concurrent algal surveys. Ivlev's electivity indices ≥0.5 (E) indicate herbivores were selecting 'for' *P. denudata* except in June 2008, December 2008, and February 2010.

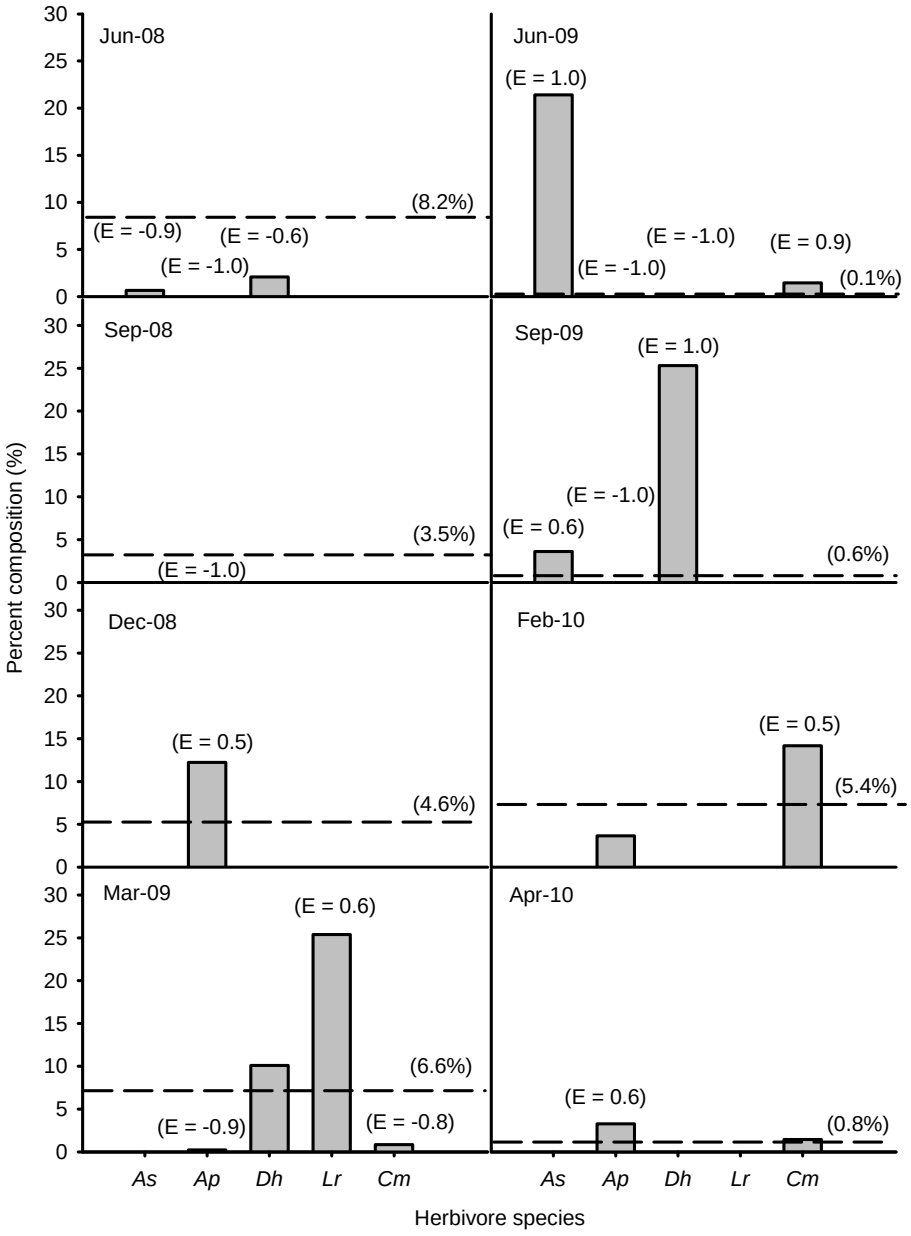


Figure 3.20. Quarterly average consumption of *Ulva flexuosa* based on foraging samples from the four most abundant herbivorous fish species (As = *Abudefduf saxatilis*, Ap = *Archosargus probatocephalus*, Dh = *Diplodus holbrooki*, Lr = *Lagodon rhomboides*) and juvenile green turtles (Cm = *Chelonia mydas*). Dashed horizontal lines represent the average presence of *U. flexuosa* from concurrent algal surveys. Ivlev's electivity indices ≥0.5 (E) indicate herbivores were selecting 'for' *U. flexuosa* except in June and September 2008.

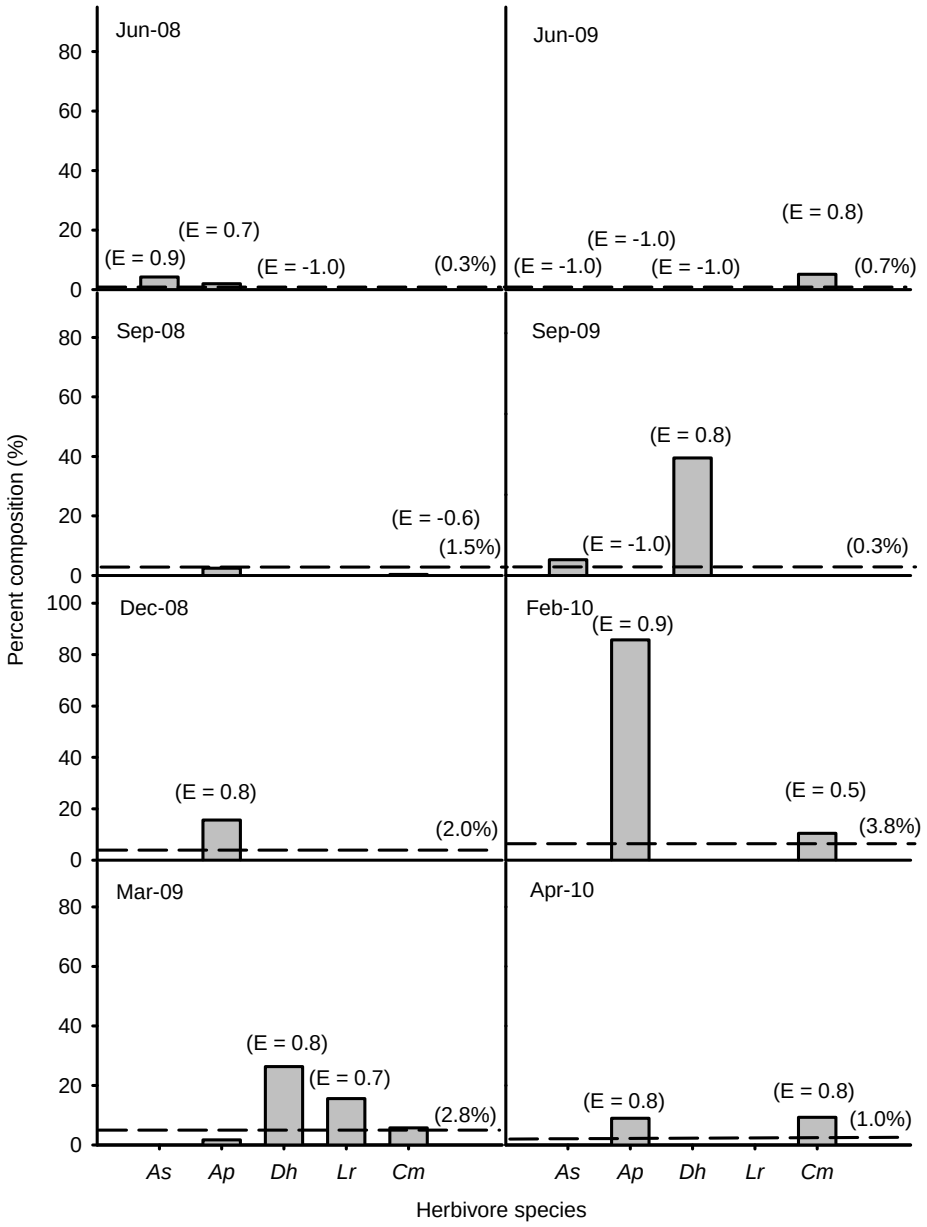


Figure 3.21. Quarterly average consumption of *Ulva lactuca* based on foraging samples from the four most abundant herbivorous fish species (As = *Abudefduf saxatilis*, Ap = *Archosargus probatocephalus*, Dh = *Diplodus holbrooki*, Lr = *Lagodon rhomboides*) and juvenile green turtles (Cm = *Chelonia mydas*). Dashed horizontal lines represent the average presence of *U. lactuca* from concurrent algal surveys. Ivlev's electivity indices ≥0.5 (E) indicate herbivores were selecting 'for' *U. lactuca* except in September 2008.

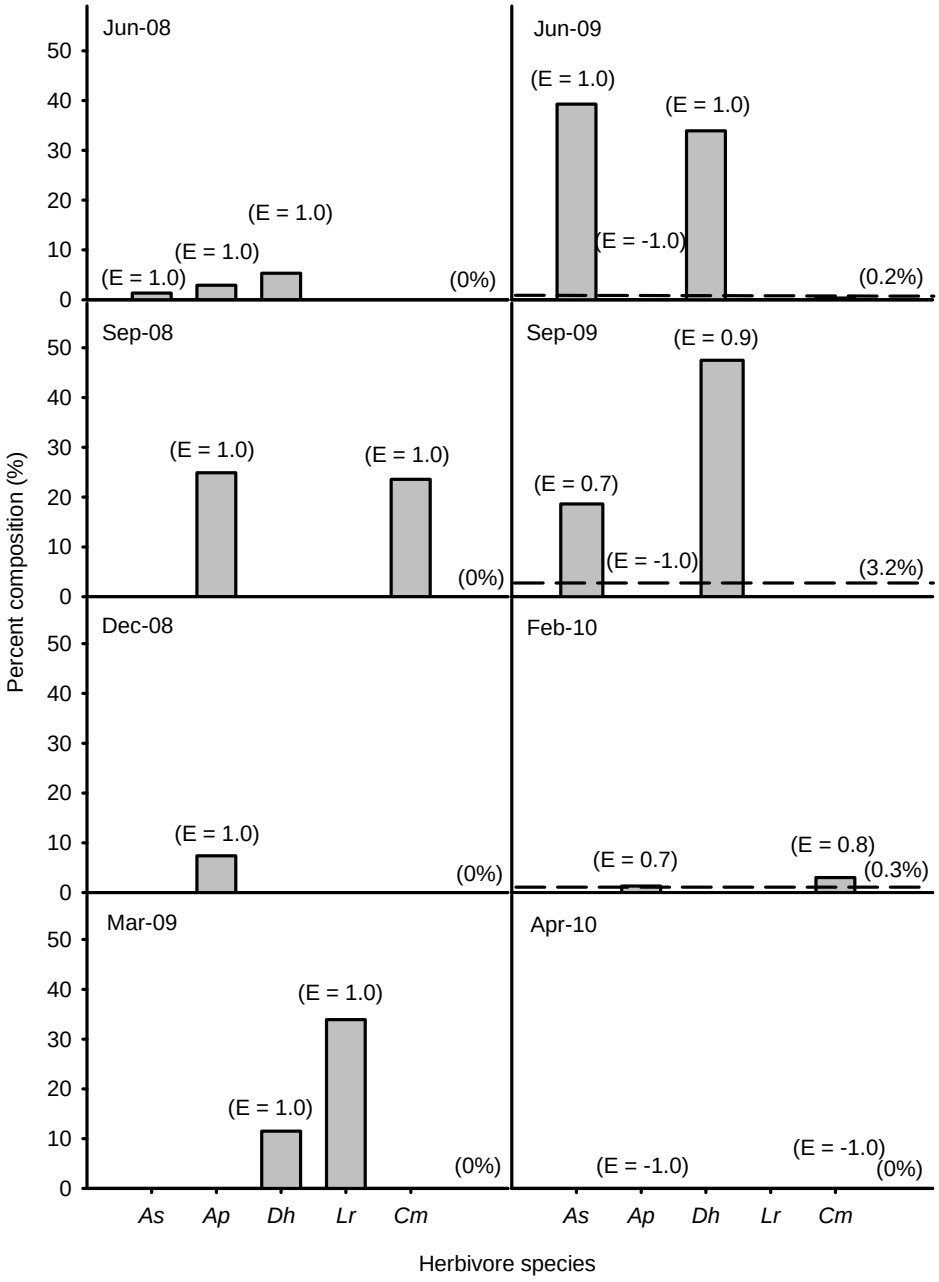


Figure 3.22. Quarterly average consumption of *Ulva prolifera* based on foraging samples from the four most abundant herbivorous fish species (As = *Abudefduf saxatilis*, Ap = *Archosargus probatocephalus*, Dh = *Diplodus holbrooki*, Lr = *Lagodon rhomboides*) and juvenile green turtles (Cm = *Chelonia mydas*). Dashed horizontal lines represent the average presence of *U. prolifera* from concurrent algal surveys. Ivlev's electivity indices ≥0.5 (E) indicate herbivores were selecting 'for' *U. prolifera* except in April 2010.

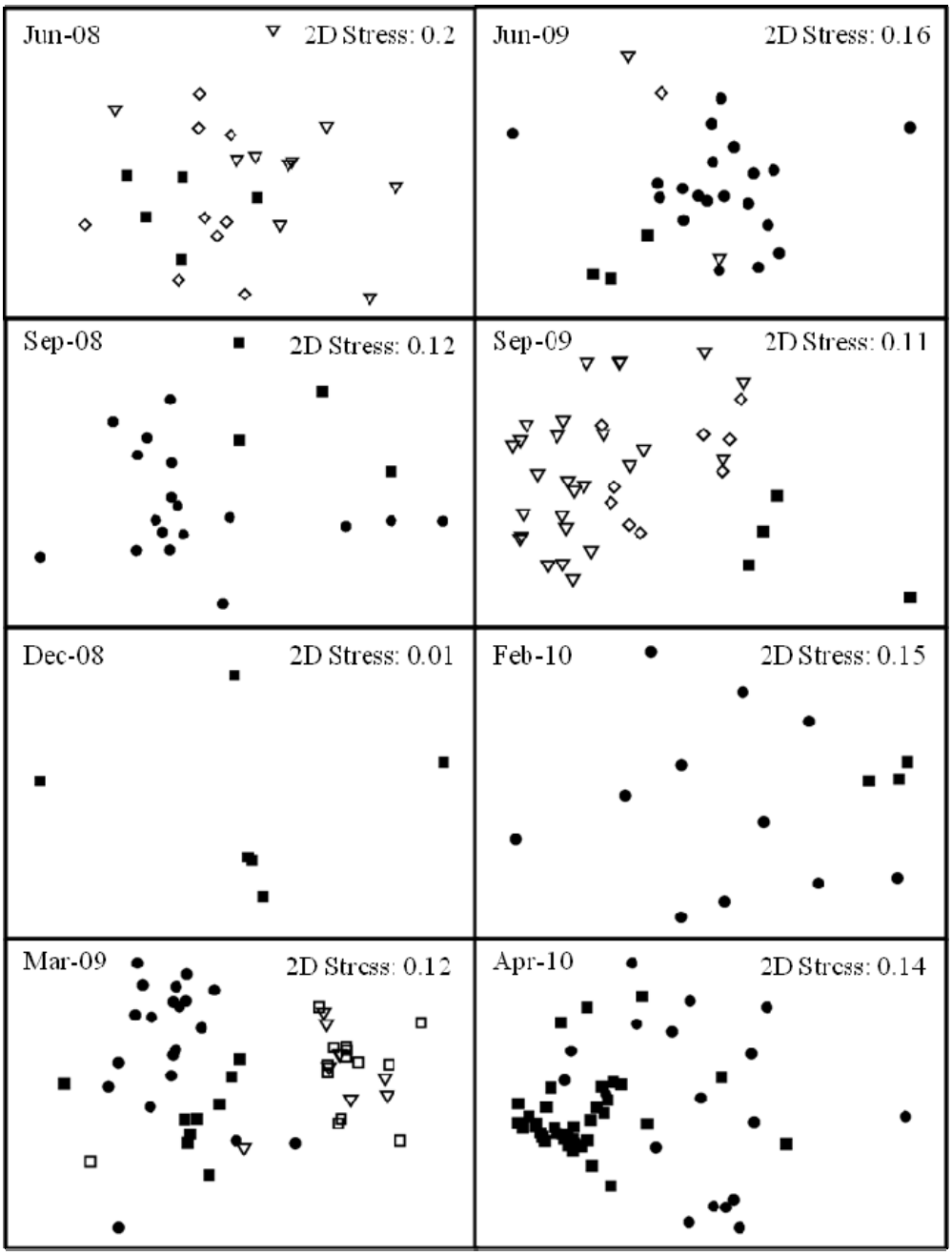


Figure 3.23. MDS 2D plot comparing the foraging data of the four most abundant herbivorous fish species and juvenile green turtles (*Chelonia mydas*) by quarterly sampling period. Data were based on the 10 macroalgal species in foraging samples among herbivores. Symbols for herbivores are: *Abudefduf saxatilis* = open diamond, *Archosargus probatocephalus* = solid box, *Diplodus holbrooki* = inverted triangle, *Lagodon rhomboides* = open square, and *Chelonia mydas* (green turtle) = solid circle.

Acknowledgements

I would like to acknowledge the long hours of fieldwork contributed by: C. Garreau, E. Reyier, and D. Scheidt. Committee members M. D. Hanisak, L. Ehrhart, C. Proffitt, T. Sutton, and R. Virnstein contributed constructive comments on the project proposal and review of manuscripts. Cape Canaveral Air Force Station's 45$^{th}$ Space Wing Environmental Management Department facilitated access and approval for the study and greatly appreciate A. Chambers and D. George for their assistance. Aquatic biologists at Dynamac Corporation and InoMedic, Health Applications, Inc. provided fish for foraging samples and the University of Central Florida Marine Turtle Research Group under the direction of L. Ehrhart and W. Redfoot facilitated access to green turtle foraging samples. All portions of this study were conducted under the appropriate federal and state permits, and in compliance with International Animal Care and Use Committee regulations (IACUC) at NASA (Kennedy Space Center) and the University of Central Florida.

References

Anderson, D.R., J.L. Laake, B.R. Crain, and K.P. Burnham. 1979. Guidelines for line transect sampling of biological populations. Journal of Wildlife Management, 43:70-78.

Barry, J.P., and M.J. Ehret. 1993. Diet, food preference, and algal availability for fishes and crabs on intertidal reef communities in southern California. Environmental Biology of Fishes, 37:75-95.

Benedetti-Cecchi, L. 2000. Predicting direct and indirect interactions during succession in a mid-littoral rocky shore assemblage. Ecological Monographs, 70:45-72.

Bjorndal, K.A. 1980. Nutrition and grazing behavior of the green turtle *Chelonia mydas*. Marine Biology, 56:147-154.

Bjorndal, K.A., A.B. Bolten, and C.J. Lagueux. 1994. Ingestion of marine debris by juvenile sea turtles in coastal Florida habitats. Marine Pollution Bulletin, 28:154-158.

Bohnsack, J.A., and S.P. Bannerot. 1986. A stationary visual census technique for quantitatively assessing community structure of coral reef fishes. NOAA-NMFS. NOAA Technical Report NMFS-41. 15.

Bolten, A.B. 2003. Variation in sea turtle life history patterns: neritic vs. oceanic developmental stages. P. 243-257 in The biology of sea turtles, Lutz, P.L., J.A. Musick, and J. Wyneken (Eds.). CRC Press LLC, Boca Raton.

Bonaldo, R.M,, J.P. Krajewski, C, Sazima, and I. Sazima. 2006. Foraging activity and resource use by three parrotfish species at Fernando de Noronha Archipelago, tropical West Atlantic. Marine Biology, 149:423-433.

Bresette, M., J. Gorham, and B. Peery. 1998. Site fidelity and size frequencies of juvenile green turtles (*Chelonia mydas*) utilizing near shore reefs in St. Lucie County, Florida. Marine Turtle Newsletter, 82:5-7.

Bruno, J.F., K.E. Boyer, J.E. Duffy, and S.C. Lee. 2008. Relative and interactive effects of plant and grazer richness in a benthic marine community. Ecology, 89:2518-2528.

Burkepile, D.E., and M.E. Hay. 2008. Herbivore species richness and feeding complementarity affect community structure and function on a coral reef. Proceedings of the National Academy of Sciences of the United States of America, 105:16201-16206.

Carothers, J.H., and F.M. Jaksić. 1984. Time as a niche difference: the role of interference competition. Oikos, 42:403-406.

Carpenter, R.C. 1986. Partitioning herbivory and its effects on coral reef algal communities. Ecological Monographs, 56:345-364.

Channells, P.W., and J. Morrissey. 1981. Technique for analysis of seagrass genera present in dugong stomachs, including a key to north Queensland seagrasses based on cell details. P. 176-179 *in* The Dugong, Marsh, H. (Ed.). James Cook University, Townsville.

Choat, J.H. 1991. The biology of herbivorous fishes on coral reefs. P. 120-155 in The ecology of fishes on coral reefs, Sale, P. (Ed.). Academic Press, San Diego.

Clarke, K.R., and R.H. Green. 1988. Statistical design and analyses for a 'biological effects' study. Marine Ecology Progress Series, 46:213-226.

Clarke, K.R., and R.M. Warwick. 2001. Change in marine communities: an approach to statistical analysis and interpretation, 2nd edition. PRIMER-E Ltd., Plymouth PL.

Conover, D.O., and E.T. Schultz. 1997. Natural selection and the evolution of growth rate in the early life history: What are the trade-offs? P. 305-332 in Early life history and recruitment in fish populations, Chambers, C., and E.A. Trippel (Eds.). Chapman & Hall, London.

Coyne, M.S. 1994. Feeding ecology of subadult green sea turtles in south Texas waters. Master's thesis, Texas A & M University, College Station. 76 p.

de Ruyter van Steveninck, E.D., and R.P.M. Bak. 1986. Changes in abundance of coral-reef bottom components related to mass mortality of the sea urchin *Diadema antillarum*. Marine Ecology Progress Series, 34:87-94.

Dickerson, D.D., K.J. Reine, D.A. Nelson, and C.E. Dickerson. 1995. Assessment of sea turtle abundance in six south Atlantic U.S. channels. USACE. Miscellaneous Paper EL-95-5. 138.

Duffy, J.E. 2002. Biodiversity and ecosystem function: the consumer connection. Oikos, 99:201-219.

Ehrhart, L.M., and L.H. Ogren. 1999. Studies in foraging habitats: capturing and handling turtles. P. 61-64 in Research and management techniques for the conservation of sea turtles, Eckert, K.L., K.A. Bjorndal, F.A. Abreu-Grobois, and M. Donnelly (Eds.). SSC/IUCCN Marine Turtle Specialist Group, Washington, D.C.

Ehrhart, L.M., and W.E. Redfoot. 1996. Assessment of green turtle relative abundance in the Cape Canaveral AFS Port area, Trident Submarine Basin. USAE Waterways Experiment Station, Vicksburg.

Eklöf, J.S., C. Alsterberg, J. N.Havenhand, K. Sundbäck, H.L. Wood, and L. Gamfeldt. 2012. Experimental climate change weakens the insurance effect of biodiversity. Ecology Letters, 15:861-872.

Ferreira, C.E.L., S.R. Floeter, J.L. Gasparini, B.P. Ferreira, and J.C. Joyeux. 2004. Trophic structure patterns of Brazilian reef fishes: a latitudinal comparison. Journal of Biogeography, 31:1093-1106.

Floeter, S.R., M.D. Behrens, C.E.L. Ferreira, M.J. Paddack, and M.H. Horn. 2005. Geographical gradients of marine herbivorous fishes: patterns and processes. Marine Biology, 147:1435–1447.

Floeter, S.R., C. Ferreira, A. Dominici-Arosemena, I.R. Zalmon, and C.E. Ferreira. 2004. Latitudinal gradients in Atlantic reef fish communities: trophic structure and spatial use patterns. Journal of Fish Biology, 64:1680-1699.

Fonferek, B. 2003. Point survey of sea turtles in entrance channels. USACE (Ed.). USACE, Jacksonville.

Forbes, G.A. 1999. Diet sampling and diet component analysis. P. 144-148 in Research and management techniques for the conservation of sea turtles, Eckert, K.L., K.A. Bjorndal, F.A. Abreu-Grobois, and M. Donnelly (Eds.). SSC/IUCCN Marine Turtle Specialist Group, Washington, D.C.

Francini, R.B., E.O.C. Coni, P.M. Meirelles, G.M. Amado, F.L. Thompson, G.H. Pereira, A.C. Bastos, D.P. Abrantes, C.M. Ferreira, F.Z. Gibran, A.Z. Guth, P.Y.G. Sumida, N.L. Oliveira, L. Kaufman, C.V. Minte-Vera, and R.L. Moura. 2013. Dynamics of coral reef benthic assemblages of the Abrolhos Bank, Eastern Brazil: inferences on natural and anthropogenic drivers. PLoS ONE, 8:e54260.

Frutchey, K.P. 2004. Plasma levels of vitamins A and E in marine turtles (*Chelonia mydas* and *Caretta caretta*). Master's thesis, University of Central Florida, Orlando. 82 p.

Gagnon, P., L.E. Johnson, and J.H. Himmelman. 2005. Kelp patch dynamics in the face of intense herbivory: Stability of *Agarum clathratum* (Phaeophyta) stands and associated flora on urchin barrens. Journal of Phycology, 41:498-505.

Gilbert, E.I. 2005. Juvenile green turtle (*Chelonia mydas*) foraging ecology: feeding selectivity and forage nutrient analysis. Master's thesis, University of Central Florida, Orlando. 47 p.

Gillanders, B.M., K.W. Able, J.A. Brown, D.B. Eggleston, and P.F. Sheridan. 2003. Evidence of connectivity between juvenile and adult habitats for mobile marine fauna: an important component of nurseries. Marine Ecology Progress Series, 247:281-295.

Gilmore, R.G. 1977. Fishes of the Indian River Lagoon and adjacent waters, Florida. Bulletin of Florida State Museum, Biological Sciences, 22:101-148.

Gilmore, R.G. 1995. Environmental and biogeographical factors influencing icthyofaunal diversity: Indian River Lagoon. Bulletin of Marine Science, 57:153-170.

Grand, T.C. 2002. Alternative forms of competition and predation dramatically affect habitat selection under foraging--predation-risk trade-offs. Behavioral Ecology, 13:280-290.

Hastings, R.W. 1979. The origin and seasonality of the fish fauna on a new jetty in the northeastern Gulf of Mexico. Bulletin of Florida State Museum: Biological Sciences, 24:1-122.

Hay, M.E., and J.P. Sutherland. 1988. The ecology of rubble structures of the South Atlantic Bight: a community profile. U.S. Fish and Wildlife Service Biological Report 85 (7.20). 67.

Henwood, T.A. 1987. Movements and seasonal changes in loggerhead turtle *Caretta caretta* aggregations in the vicinity of Cape Canaveral, Florida (1978-1984). Biological Conservation, 40:191-202.

Hirth, H.F. 1997. Synopsis of the biological data on the green turtle *Chelonia mydas* (Linnaeus 1758). Fish and Wildlife Service, U.S. DOI. Biological Report 120.

Holloway-Adkins, K. 2001. A comparative study of the feeding ecology of *Chelonia mydas* (green turtle) and the incidental ingestion of *Prorocentrum* spp. Master's thesis. University of Central Florida, Orlando. 168 p.

Horn, M.H. 1989. Biology of marine herbivorous fishes. P. 167-272 in Oceanography and Marine Biology: An Annual Review, Barnes, M. (Ed.). Aberdeen University Press, Aberdeen.

Howell, L.N., K.J. Reich, D.J. Shaver, and A.M. Landry. 2011. Evidence of multiple ontogenetic shifts of green turtles along the lower Texas coast. P. 139-140 in Thirty-first annual symposium on sea turtle biology and conservation, Jones, T.T., and B.P. Wallace (Eds.). Sea Turtle Society, San Diego.

Huntly, N. 1991. Herbivores and the dynamics of communities and ecosystems. Annual Review of Ecology and Systematics, 22:477-503.

Jennings, S., O. Reňones, B. Morales-Nin, N.V.C. Polunin, J. Moranta, and J. Coll. 1997. Spatial variation in the 15N and 13C stable isotope composition of plants,

invertebrates and fishes on Mediterranean reefs: implications for the study of trophic pathways. Marine Ecology Progress Series, 146:109-116.

Krebs, C.J. 1989. Ecological Methodology. Harper-Collins Publishers, New York. 654 p.

Kubis, S.A. 2003. Growth rates of juvenile green turtles, *Chelonia mydas*, from three developmental habitats along the east central coast of Florida. Master's thesis, University of Central Florida, Orlando. 60 p.

Kubis, S., M. Chaloupka, L.M. Ehrhart, and M.J. Bresette. 2009. Growth rates of juvenile green turtles *Chelonia mydas* from three ecologically distinct foraging habitats along the east central coast of Florida, USA. Marine Ecology Progress Series, 389:257-269.

Lewis, S.M. 1986. The role of herbivorous fishes in the organization of a Caribbean reef community. Ecological Monographs, 56:183-200.

Lindquist, D.G., M.V. Ogburn, W.B. Stanley, H.L. Troutman, and S.M. Pereira. 1985. Fish utilization patterns on temperate rubble-mound jetties in North Carolina. Bulletin of Marine Science, 37:244-251.

Lubchenco, J. 1978. Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. The American Naturalist, 112:23-39.

Makowski, C., J.A. Seminoff, and M. Salmon. 2006. Home range and habitat use of juvenile Atlantic green turtles (*Chelonia mydas* L.) on shallow reef habitats in Palm Beach, Florida, USA. Marine Biology, 148:1167-1179.

Meekan, M.G., and J.H. Choat. 1997. Latitudinal variation in abundance of herbivorous fishes: A comparison of temperate and tropical reefs. Marine Biology, 128:373-383.

Musick, J.A., and C.J. Limpus. 1997. Habitat utilization and migration in juvenile sea turtles. P. 137-163 in The biology of sea turtles, Lutz, P., and J. Musick (Eds.). CRC Press, Boca Raton.

NASA. 2013. Spaceport Weather Data Archive. National Aeronautics and Space Administration. Available from http://kscwxarchive.ksc.nasa.gov/. NASA, Kennedy Space Center.

NOAA-NDBC (2013) Station TRDF1 - 8721604 - Trident Pier, FL. Available from: http://www.ndbc.noaa.gov/station_page.php?station=trdf1.

NOAA-NCDC. 2013. 2009/2010 Cold season significant events. Available from: http://www.ncdc.noaa.gov/special-reports/2009-2010-cold-season.html#jan. NOAA, Asheville.

O'Toole, T. 2008. Effect of water temperature on the digestive physiology of juvenile green turtles (*Chelonia mydas*) in a temperate feeding ground, Moreton Bay, Australia, University of Queensland, Brisbane.

Parker, R., Jr. 1990. Tagging studies and diver observations of fish populations on live-bottom reefs of the US southeastern coast. Bulletin of Marine Science, 46:749-760.

Persson, L. 1983. Effects of intra- and interspecific competition on dynamics and size structure of a perch *Perca fluviatilis* and a roach *Rutilus rutilus* population. Oikos, 41:126-132.

Pike, L.A., and D.G. Lindquist. 1994. Feeding ecology of spottail pinfish (*Diplodus holbrooki*) from an artificial and natural reef in Onslow Bay, North Carolina. Bulletin of Marine Science, 55:363-374.

Pister, B. 2009. Urban marine ecology in southern California: the ability of riprap structures to serve as rocky intertidal habitat. Marine Biology, 156:861–873.

Randall, J.E. 1967. Food habits of reef fishes of the West Indies. University of Miami, Coral Gables. 94 p.

Rasher, D.B., S. Engel, V. Bonito, G.J. Fraser, J.P. Montoya, and M.E. Hay. 2012. Effects of herbivory, nutrients, and reef protection on algal proliferation and coral growth on a tropical reef. Oecologia, 169:187-198.

Redfoot, W.E. 1997. Population structure and feeding ecology of green turtles utilizing the Trident Submarine Basin, Cape Canaveral, Florida as developmental habitat. Master's, University of Central Florida, Orlando. 72 p.

Redfoot, W.E., and L.M. Ehrhart. 2013. Trends in size class distribution, recaptures, and abundance of juvenile green turtles (*Chelonia mydas*) utilizing a rock riprap lined embayment at Port Canaveral, Florida, U.S.A. as developmental habitat. Chelonian Conservation and Biology, 12:252-261.

Reyier, E.A., D.M. Scheidt, K.G. Holloway-Adkins, C.M. Garreau, R.H. Lowers, and S.L. Gann. 2010. A characterization of biological resources within the Cape Canaveral Air Force Station Trident Submarine Basin, and adjacent marine waters of Port Canaveral, Florida (May 2008-April 2010). 45 CES/CEAN. 60 p.

Rissik, D., and I.M. Suthers. 2000. Enhanced feeding by pelagic juvenile myctophid fishes within a region of island-induced flow disturbance in the Coral Sea. Marine Ecology Progress Series, 203:263–273.

Sala, E., E. Ballesteros, P. Dendrinos, A.D. Franco, F. Ferretti, D. Foley, S. Fraschetti, A. Friedlander, J. Garrabou, H.G.c.l. soy, P. Guidetti, B.S. Halpern, B. Hereu, A.A. Karamanlidis, Z. Kizilkaya, E. Macpherson, L. Mangialajo, S. Mariani, F. Micheli, A. Pais, K. Riser, A.A. Rosenberg, M. Sales, K.A. Selkoe, R. Starr, F. Tomas, and M. Zabala. 2012. The structure of Mediterranean rocky reef ecosystems across environmental and human gradients, and conservation implications. PLoS ONE, 7:e32742.

Schmid, J.R. 1995. Marine turtle populations on the east-central coast of Florida: results of tagging studies at Cape Canaveral, Florida, 1986-1991. Fishery Bulletin, 98:139-151.

Schoener, T.W. 1983. Field experiments on interspecific competition. The American Naturalist, 122:240-285.

Searles, R.B. 1984. Seaweed biogeography of the mid-Atlantic coast of the United States. Helgoland Marine Research, 38:259-271.

Seminoff, J.A., A. Resendiz, and W.J. Nichols. 2002. Diet of east Pacific green turtles (*Chelonia mydas*) in the central Gulf of California, México. Journal of Herpetology, 36:447-453.

Shaver, D.J. 1990. Sea turtle in south Texas inshore waters. P. 131-132 in Tenth Annual Workshop on Sea Turtle Biology and Conservation, Richardson, T.H., J.I.

Richardson, and M. Donnelly (Eds.). NOAA Technical Memorandum NMFS-SEFC-278, Hilton Head.

Shaver, D.J. 1994. Relative abundance, temporal patterns, and growth of sea turtles at the Mansfield Channel, Texas. Journal of Herpetology, 28:491-497.

Siddon, C.E., and J.D. Witman. 2004. Behavioral indirect interactions: Multiple predator effects and prey switching in the rocky subtidal. Ecology, 85:2938-2945.

South Atlantic Fisheries Management Council. 1998. Final habitat plan for the South Atlantic region. P. 457, Council, S.A.F.M. (Ed.).

South Atlantic Fisheries Management Council. 2003. Policies for the Protection and Restoration of Essential Fish Habitats from Beach Dredging and Filling and Large-Scale Coastal Engineering. P. 7, SAFMC (Ed.).

Strauss, R.E. 1979. Reliability estimates for Ivlev's Electivity Index, the forage ratio, and a proposed linear index of food selection. Transactions of the American Fisheries Society, 108:344-352.

Svanbäck, R., P. Eklöv, R. Fransson, and K. Holmgren. 2008. Intraspecific competition drives multiple species resource polymorphism in fish communities. Oikos, 117:114-124.

SYSTAT. 2008. SigmaPlot for Windows version 11.0. Systat Software, San Jose, CA.

USACE. 2007. USACE sea turtle data warehouse. Available from: http://el.erdc.usace.army.mil/seaturtles. Accessed 18, May, 2013. USACE, Vicksburg.

USFWS and NOAA Fisheries. 1978. Endangered Species Act 1973 | 1978 ESA Amendment. Environmental Conservation Online System, Washington, D.C.

Verdi, R.J., and S.L. Holt. 2010. Floods in Florida due to Tropical Storm Fay, August 15 through September 26, 2008: U.S. Geological Survey Open-File Report 2010-1142, 18 p. Available from: http://pubs.usgs.gov/of/2010/1142/pdf/ofr2010-1142.pdf

Wabnitz, C.C.C., G. Balazs, S. Beavers, K.A. Bjorndal, A.B. Bolten, V. Christensen, S. Hargrove, and D. Pauly. 2010. Ecosystem structure and processes at Kaloko Honokōhau, focusing on the role of herbivores, including the green sea turtle *Chelonia mydas*, in reef resilience. Marine Ecology Progress Series, 420:27-44.

Weibel, E.R., G.S. Kistler, and W. F. 1966. Practical stereological methods for morphometric cytology. The Journal of Cell Biology, 30:23-38.

West, J.M., G.D. Williams, S.P. Madon, and J.B. Zedler. 2003. Integrating spatial and temporal variability into the analysis of fish food web linkages in Tijuana Estuary. Environmental Biology of Fishes, 67:297-309.

Wismer, S., A.S. Hoey, and D.R. Bellwood. 2009. Cross-shelf benthic community structure on the Great Barrier Reef: relationships between macroalgal cover and herbivore biomass. Marine Ecology Progress Series, 376:45-54.

Witherington, B.E., and L.M. Ehrhart. 1989. Hypothermic stunning and mortality of marine turtles in the Indian River Lagoon System, Florida. Copeia, 1989:696-703.

Appendix

Table A3.1. Fishes observed in underwater video and stationary sampling surveys and their trophic level foraging habits. Fish foraging habits noted here are from Randall (1967).

| Family | Common name | Genus/species | UW video (1300 m) | stationary surveys | algae/ seagrass (%) | fishes (%) | inverte-brates (%) |
|---|---|---|---|---|---|---|---|
| Orectolobidae (Nurse Sharks) | Nurse shark | *Ginglymostoma cirratum* | 1 | | | 89 | |
| Carcharhinidae (Requiem Sharks) | Lemon shark | *Negaprion brevirostris* | 1 | | | 100 | |
| Sphyraenidae (Barracudas) | Great barracuda | *Sphyraena barracuda* | 1 | | | 96 | 4 |
| | Great barracuda (juv) | *Sphyraena barracuda* (juv) | | | | 100 | |
| Serranidae (Groupers and Sea Basses) | Black seabass | *Centropristis striata* | 1 | | | | 100 |
| | Black grouper | *Mycteroperca bonaci* | 1 | | | 100 | |
| | Belted sandfish | *Serranus subligarius* | 1 | 1 | | | |
| Lutjanidae (Snappers) | Snapper | *Lutjanus* sp. | | | | 60 | 40 |
| | Snapper (juv) | *Lutjanus* sp. (juv) | | | | 40 | 60 |
| | Schoolmaster | *Lutjanus apodus* | 1 | 1 | | | 100 |
| | Gray snapper | *Lutjanus griseus* | 1 | 1 | | 40 | 60 |
| | Lane snapper | *Lutjanus synagris* | 1 | 1 | | | 100 |
| | Yellowtail snapper | *Ocyurus chrysurus* | 1 | | | 15 | 85 |
| Haemulidae (Grunts) | Grunt (juv) | *Haemulon* spp. | | | | 3 | 97 |
| | White grunt | *Haemulon plumierii* | 1 | 1 | | 2 | 98 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| | Black margate (juv) | *Anisotremus surinamensis* (juv) | 1 | | | | 100 |
| | Porkfish | *Anisotremus virginicus* | 1 | 1 | | | 100 |
| | Porkfish (juv) | *Anisotremus virginicus* (juv) | | | | | 100 |
| | Pigfish | *Orthopristis chrysoptera* | 1 | 1 | | | 100 |
| Sparidae | Sheepshead | *Archosargus probatocephalus*[*] | 1 | 1 | 90 | | 10 |
| (Porgies) | Spottail (porgy) seabream | *Diplodus holbrooki*[*] | 1 | 1 | 80 | 10 | 10 |
| | Pinfish | *Lagodon rhomboides* | 1 | 1 | 19 | | 82 |
| | Pinfish (juv) | *Lagodon rhomboides* (juv)[*] | | | 97 | | 3 |
| Sciaenidae | Highhat (striped drum) | *Pareques acuminatus* | 1 | 1 | | | 100 |
| (Croakers) | scianid larval-stage | scianid larval-stage | | | | | |
| Gerreidae | Mojarra | *Eucinostomus* spp. | | | | | 100 |
| (Mojarras) | Flagfin mojarra | *Eucinostomus melanopterus* | 1 | 1 | | | |
| | Mojarra school | *Eucinostomus* spp. (school) | | | | | |
| Carangidae | Jack (juv) | *Caranx* sp. (juv) | | | | 91 | 9 |
| (Jacks) | Blue runner | *Caranx crysos* | 1 | | | 87 | 12 |
| | Lookdown | *Selene vomer* | 1 | | | | 100 |
| Pomacentridae | Sergeant-major | *Abudefduf saxatilis*[*] | 1 | 1 | 9 | | 91 |
| (Damselfishes) | Night sergeant | *Abudefduf taurus*[*] | 1 | 1 | 94 | | 6 |
| | Beaugregory | *Stegastes leucostictus* | 1 | | 22 | | 78 |
| | Cocoa damsel (juv) | *Stegastes variabilis* (juv) | 1 | | 57 | | 43 |
| Labridae | Slippery dick | *Halichoeres bivittatus* | 1 | 1 | | | 100 |
| (Wrasses) | Puddingwife wrasse | *Halichoeres radiatus* | 1 | | | | 100 |
| Scaridae | Yellow tail parrotfish | *Sparisoma rubripinne* | 1 | | 100 | | |
| (Parrotfishes) | Emerald parrotfish | *Nicolsina usta usta* | 1 | | 100 | | |

| | | | | | | |
|---|---|---|---|---|---|---|
| Bothidae (Lefteye Flounders) | Flounder | *Paralichthys* spp. | 1 | 1 | | 100 |
| Gobiidae (Gobies) | Goby (unid) | Goby (unid) | | | | |
| Blennidae (Blennies) | Barred blenny | *Hypleurochilus bermudensis* | 1 | | | |
| | Hairy blenny | *Labrisomus nuchipinnis*[*] | 1 | | | |
| | Molly miller | *Scartella cristata*[*] | 1 | 1 | 99 | |
| Ephippidae (Spadefishes) | Atlantic spadefish | *Chaetodipterus faber* | 1 | | 5 | 95 |
| Pomacanthidae | Gray angelfish | *Pomacanthus arcuatus* | 1 | 1 | 8 | 92 |
| Angelfishes) | Gray angelfish (juv) | *Pomacanthus arcuatus* (juv)[*] | | | | |
| Chaetodontidae | Spotfin butterflyfish | *Chaetodon ocellatus* | 1 | | | 100 |
| (Butterflyfishes) | Banded butterflyfish | *Chaetodon striatus* | 1 | | | 100 |
| | Four-eye butterflyfish | *Chaetodon capistratus* | 1 | 1 | | 100 |
| Acanthuridae | Doctorfish | *Acanthurus chirurgus*[*] | | 1 | 100 | |
| (Surgeonfishes) | Surgeonfish | *Acanthurus bahianus* | | 1 | 100 | |
| Tetraodontidae (Puffers) | Bandtail puffer | *Sphoeroides spengleri* | 1 | | 3 | 97 |
| Diodontidae (Porcupinefishes) | Striped burrfish | *Chilomycterus schoepfii* | 1 | | | 100 |

| | | | | | | |
|---|---|---|---|---|---|---|
| Ariidae (Sea catfishes) | Gafftopsail sea catfish | *Bagre marinus* | 1 | | | 100 |
| Syngnathidae (Pipefishes and seahorses) | Gulf pipefish | *Syngnathus scovelli* | 1 | | | 100 |
| Engraulidae (Anchovies) | Anchovie school | Anchovie school | | | | |
| Centropomidae (Snooks) | Common snook | *Centropomus undecimalis* | 1 | | 25 | 75 |
| Mugilidae (Mullet) | mullet (larval) | | | | | |
| Total | | | 43 | 21 | | |

* >50.0% plant material in the gut content of these fishes in the current foraging study.



Table A3.2. Similarity percentage (SIMPER) of seasonal (a) and quarterly (b) fish abundances from UW video surveys conducted between June 2008 and April 2010 at the Trident Basin.

(a)

| Pairwise comparison, Average dissimilarity (%), Species | Average abundance | Average abundance | Average dissimilarity | Dissimilarity ± SD | Contribution (%) | Cumulative (%) |
|---|---|---|---|---|---|---|
| Summer and Fall<br>Average dissimilarity = 49.93<br>Species | | | | | | |
| *Diplodus holbrooki* | 9.18 | 6.80 | 21.12 | 1.24 | 42.29 | 42.29 |
| *Abudefduf saxatilis* | 5.16 | 6.26 | 15.85 | 1.39 | 31.74 | 74.03 |
| *Lagodon rhomboides* | 2.03 | 0.41 | 7.17 | 0.97 | 14.36 | 88.39 |

| | | | | | | |
|---|---|---|---|---|---|---|
| *Archosargus probatocephalus* | 2.09 | 1.12 | 5.80 | 1.02 | 11.61 | 100.00 |
| Summer and Winter<br>Average dissimilarity = 94.11<br>Species | | | | | | |
| *Diplodus holbrooki* | 9.18 | 0.28 | 46.33 | 3.38 | 49.23 | 49.23 |
| *Abudefduf saxatilis* | 5.16 | 0.11 | 22.89 | 1.57 | 24.32 | 73.56 |
| *Lagodon rhomboides* | 2.03 | 0.00 | 12.61 | 1.12 | 13.40 | 86.96 |
| *Archosargus probatocephalus* | 2.09 | 1.16 | 12.27 | 1.25 | 13.04 | 100.00 |
| Fall and Winter<br>Average dissimilarity = 94.49<br>Species | | | | | | |
| *Diplodus holbrooki* | 6.80 | 0.28 | 39.77 | 2.30 | 42.09 | 42.09 |
| *Abudefduf saxatilis* | 6.26 | 0.11 | 38.52 | 2.49 | 40.77 | 82.86 |
| *Archosargus probatocephalus* | 1.12 | 1.16 | 14.41 | 0.74 | 15.25 | 98.11 |
| Summer and Spring<br>Average dissimilarity = 72.18<br>Species | | | | | | |
| *Lagodon rhomboides* | 2.03 | 16.36 | 31.42 | 1.15 | 43.53 | 43.53 |
| *Diplodus holbrooki* | 9.18 | 1.85 | 20.87 | 1.72 | 28.92 | 72.45 |
| *Abudefduf saxatilis* | 5.16 | 0.15 | 13.86 | 1.31 | 19.21 | 91.66 |
| Fall and Spring<br>Average dissimilarity = 82.52<br>Species | | | | | | |
| *Lagodon rhomboides* | 0.41 | 16.36 | 36.17 | 1.06 | 43.83 | 43.83 |
| *Diplodus holbrooki* | 6.80 | 1.85 | 19.33 | 1.25 | 23.42 | 67.25 |
| *Abudefduf saxatilis* | 6.26 | 0.15 | 18.56 | 1.47 | 22.50 | 89.75 |

| | | | | | | |
|---|---|---|---|---|---|---|
| *Archosargus probatocephalus* | 1.12 | 1.64 | 8.46 | 0.55 | 10.25 | 100.00 |
| Winter and Spring<br>Average dissimilarity = 94.61<br>Species | | | | | | |
| *Lagodon rhomboides* | 0.00 | 16.36 | 51.17 | 1.22 | 54.08 | 54.08 |
| *Archosargus probatocephalus* | 1.16 | 1.64 | 21.57 | 0.77 | 22.79 | 76.88 |
| *Diplodus holbrooki* | 0.28 | 1.85 | 19.60 | 0.80 | 20.71 | 97.59 |

(b)

| Pairwise comparison, Average dissimilarity (%), Species | Average abundance | Average abundance | Average dissimilarity | Dissimilarity ± SD | Contribution (%) | Cumulative (%) |
|---|---|---|---|---|---|---|
| Jun-08 and Sep-08<br>Average dissimilarity = 65.55<br>Species | | | | | | |
| *Diplodus holbrooki* | 6.70 | 2.13 | 26.97 | 1.44 | 41.15 | 41.15 |
| *Lagodon rhomboides* | 2.44 | 0.00 | 15.02 | 1.53 | 22.91 | 64.06 |
| *Abudefduf saxatilis* | 2.98 | 2.36 | 14.73 | 1.23 | 22.48 | 86.53 |
| *Archosargus probatocephalus* | 1.74 | 0.81 | 8.83 | 1.05 | 13.47 | 100.00 |
| Jun-08 and Dec-08<br>Average dissimilarity = 92.45<br>Species | | | | | | |
| *Diplodus holbrooki* | 6.70 | 0.46 | 42.81 | 2.69 | 46.31 | 46.31 |
| *Lagodon rhomboides* | 2.44 | 0.00 | 18.45 | 1.55 | 19.96 | 66.27 |
| *Abudefduf saxatilis* | 2.98 | 0.21 | 16.14 | 1.08 | 17.46 | 83.73 |
| *Archosargus probatocephalus* | 1.74 | 1.78 | 15.04 | 1.09 | 16.27 | 100.00 |
| Sep-08 and Mar-09<br>Average dissimilarity = 91.79<br>Species | | | | | | |
| *Abudefduf saxatilis* | 2.36 | 0.21 | 35.96 | 1.58 | 39.18 | 39.18 |
| *Diplodus holbrooki* | 2.13 | 0.46 | 31.53 | 1.67 | 34.35 | 73.53 |
| *Archosargus probatocephalus* | 0.81 | 1.78 | 24.30 | 1.01 | 26.47 | 100.00 |

| | | | | | | |
|---|---|---|---|---|---|---|
| Jun-08 and Mar-09<br>Average dissimilarity = 55.17<br>Species | | | | | | |
| *Diplodus holbrooki* | 6.70 | 2.76 | 21.04 | 1.51 | 38.15 | 38.15 |
| *Abudefduf saxatilis* | 2.98 | 0.23 | 12.58 | 1.08 | 22.81 | 60.96 |
| *Archosargus probatocephalus* | 1.74 | 2.58 | 11.30 | 1.30 | 20.48 | 81.44 |
| *Lagodon rhomboides* | 2.44 | 1.18 | 10.24 | 1.35 | 18.56 | 100.00 |
| Sep-08 and Mar-09<br>Average dissimilarity = 72.38<br>Species | | | | | | |
| *Archosargus probatocephalus* | 0.81 | 2.58 | 22.94 | 0.92 | 31.69 | 31.69 |
| *Diplodus holbrooki* | 2.13 | 2.76 | 21.51 | 1.15 | 29.71 | 61.40 |
| *Abudefduf saxatilis* | 2.36 | 0.23 | 16.85 | 1.28 | 23.27 | 84.68 |
| *Lagodon rhomboides* | 0.00 | 1.18 | 11.09 | 0.68 | 15.32 | 100.00 |
| Dec-08 and Mar-09<br>Average dissimilarity = 90.26<br>Species | | | | | | |
| *Archosargus probatocephalus* | 1.78 | 2.58 | 39.57 | 1.31 | 43.84 | 43.84 |
| *Diplodus holbrooki* | 0.46 | 2.76 | 30.83 | 1.38 | 34.15 | 77.99 |
| *Lagodon rhomboides* | 0.00 | 1.18 | 14.99 | 0.71 | 16.60 | 94.60 |
| Jun-08 and Jun-09<br>Average dissimilarity = 40.00<br>Species | | | | | | |
| *Diplodus holbrooki* | 6.70 | 11.66 | 15.33 | 1.53 | 38.32 | 38.32 |
| *Abudefduf saxatilis* | 2.98 | 7.35 | 14.44 | 1.51 | 36.11 | 74.43 |
| *Archosargus probatocephalus* | 1.74 | 2.45 | 5.37 | 1.56 | 13.43 | 87.86 |
| *Lagodon rhomboides* | 2.44 | 1.61 | 4.85 | 1.17 | 12.14 | 100.00 |
| Sep-08 and Jun-09<br>Average dissimilarity = 66.58<br>Species | | | | | | |
| *Diplodus holbrooki* | 2.13 | 11.66 | 35.13 | 2.30 | 52.76 | 52.76 |
| *Abudefduf saxatilis* | 2.36 | 7.35 | 19.27 | 1.62 | 28.95 | 81.71 |

| | | | | | | |
|---|---|---|---|---|---|---|
| *Archosargus probatocephalus* | 0.81 | 2.45 | 6.85 | 1.42 | 10.29 | 92.00 |
| Jun-08 and Jun-09<br>Average dissimilarity = 92.27<br>Species | | | | | | |
| *Diplodus holbrooki* | 0.46 | 11.66 | 46.36 | 3.19 | 50.24 | 50.24 |
| *Abudefduf saxatilis* | 0.21 | 7.35 | 27.83 | 2.54 | 30.16 | 80.40 |
| *Archosargus probatocephalus* | 1.78 | 2.45 | 12.19 | 1.88 | 13.21 | 93.61 |
| Mar-09 and Jun-09<br>Average dissimilarity = 64.41<br>Species | | | | | | |
| *Diplodus holbrooki* | 2.76 | 11.66 | 30.28 | 2.38 | 47.01 | 47.01 |
| *Abudefduf saxatilis* | 0.23 | 7.35 | 23.26 | 2.52 | 36.11 | 83.12 |
| *Archosargus probatocephalus* | 2.58 | 2.45 | 5.47 | 1.20 | 8.49 | 91.61 |
| Jun-08 and Sep-09<br>Average dissimilarity = 44.69<br>Species | | | | | | |
| *Abudefduf saxatilis* | 2.98 | 10.15 | 20.35 | 1.95 | 45.52 | 45.52 |
| *Diplodus holbrooki* | 6.70 | 11.48 | 14.55 | 1.49 | 32.56 | 78.08 |
| *Lagodon rhomboides* | 2.44 | 0.81 | 5.27 | 1.43 | 11.79 | 89.87 |
| *Archosargus probatocephalus* | 1.74 | 1.43 | 4.53 | 1.27 | 10.13 | 100.00 |
| Sep-08 and Sep-09<br>Average dissimilarity = 68.45<br>Species | | | | | | |
| *Diplodus holbrooki* | 2.13 | 11.48 | 33.31 | 2.37 | 48.67 | 48.67 |
| *Abudefduf saxatilis* | 2.36 | 10.15 | 27.91 | 2.25 | 40.78 | 89.45 |
| *Archosargus probatocephalus* | 0.81 | 1.43 | 4.42 | 1.20 | 6.46 | 95.90 |
| Dec-08 and Sep-09<br>Average dissimilarity = 93.96<br>Species | | | | | | |
| *Diplodus holbrooki* | 0.46 | 11.48 | 43.36 | 3.22 | 46.14 | 46.14 |
| *Abudefduf saxatilis* | 0.21 | 10.15 | 38.61 | 4.35 | 41.09 | 87.23 |
| *Archosargus probatocephalus* | 1.78 | 1.43 | 8.88 | 1.16 | 9.45 | 96.68 |

| | | | | | | |
|---|---|---|---|---|---|---|
| Mar-09 and Sep-09<br>Average dissimilarity = 71.66<br>Species | | | | | | |
| *Abudefduf saxatilis* | 0.23 | 10.15 | 32.51 | 4.85 | 45.37 | 45.37 |
| *Diplodus holbrooki* | 2.76 | 11.48 | 28.93 | 2.35 | 40.38 | 85.75 |
| *Archosargus probatocephalus* | 2.58 | 1.43 | 5.91 | 1.26 | 8.24 | 93.99 |
| Jun-09 and Sep-09<br>Average dissimilarity = 22.89<br>Species | | | | | | |
| *Abudefduf saxatilis* | 7.35 | 10.15 | 9.04 | 1.27 | 39.48 | 39.48 |
| *Diplodus holbrooki* | 11.66 | 11.48 | 7.81 | 1.30 | 34.11 | 73.59 |
| *Lagodon rhomboides* | 1.61 | 0.81 | 3.06 | 1.27 | 13.39 | 86.97 |
| *Archosargus probatocephalus* | 2.45 | 1.43 | 2.98 | 1.36 | 13.03 | 100.00 |
| Jun-08 and Feb-10<br>Average dissimilarity = 95.73<br>Species | | | | | | |
| *Diplodus holbrooki* | 6.70 | 0.11 | 46.44 | 3.90 | 48.52 | 48.52 |
| *Lagodon rhomboides* | 2.44 | 0.00 | 19.91 | 1.67 | 20.80 | 69.31 |
| *Abudefduf saxatilis* | 2.98 | 0.00 | 17.39 | 1.09 | 18.17 | 87.48 |
| *Archosargus probatocephalus* | 1.74 | 0.54 | 11.98 | 1.10 | 12.52 | 100.00 |
| Sep-09 and Feb-10<br>Average dissimilarity = 94.35<br>Species | | | | | | |
| *Abudefduf saxatilis* | 2.36 | 0.00 | 37.27 | 1.88 | 39.50 | 39.50 |
| *Diplodus holbrooki* | 2.13 | 0.11 | 34.98 | 1.61 | 37.07 | 76.57 |
| *Archosargus probatocephalus* | 0.81 | 0.54 | 22.11 | 0.81 | 23.43 | 100.00 |
| Dec-08 and Feb-10<br>Average dissimilarity = 95.91<br>Species | | | | | | |
| *Archosargus probatocephalus* | 1.78 | 0.54 | 63.66 | 1.60 | 66.38 | 66.38 |
| *Diplodus holbrooki* | 0.46 | 0.11 | 17.15 | 0.54 | 17.88 | 84.26 |
| *Abudefduf saxatilis* | 0.21 | 0.00 | 15.10 | 0.48 | 15.74 | 100.00 |

| | | | | | | |
|---|---|---|---|---|---|---|
| Mar-09 and Feb-10<br>Average dissimilarity = 90.40<br>Species | | | | | | |
| *Archosargus probatocephalus* | 2.58 | 0.54 | 37.92 | 1.24 | 41.94 | 41.94 |
| *Diplodus holbrooki* | 2.76 | 0.11 | 32.77 | 1.47 | 36.25 | 78.19 |
| *Lagodon rhomboides* | 1.18 | 0.00 | 16.42 | 0.74 | 18.16 | 96.35 |
| Jun-09 and Feb-10<br>Average dissimilarity = 96.00<br>Species | | | | | | |
| *Diplodus holbrooki* | 11.66 | 0.11 | 49.72 | 4.49 | 51.80 | 51.80 |
| *Abudefduf saxatilis* | 7.35 | 0.00 | 30.20 | 2.98 | 31.46 | 83.26 |
| *Archosargus probatocephalus* | 2.45 | 0.54 | 9.88 | 2.06 | 10.30 | 93.55 |
| Sep-09 and Feb-10<br>Average dissimilarity = 97.24<br>Species | | | | | | |
| *Diplodus holbrooki* | 11.48 | 0.11 | 46.44 | 4.50 | 47.76 | 47.76 |
| *Abudefduf saxatilis* | 10.15 | 0.00 | 41.44 | 5.83 | 42.61 | 90.37 |
| Jun-08 and Apr-10<br>Average dissimilarity = 82.07<br>Species | | | | | | |
| *Lagodon rhomboides* | 2.44 | 31.55 | 59.03 | 3.20 | 71.92 | 71.92 |
| *Diplodus holbrooki* | 6.70 | 0.95 | 12.98 | 2.17 | 15.81 | 87.73 |
| *Abudefduf saxatilis* | 2.98 | 0.08 | 6.29 | 0.96 | 7.67 | 95.40 |
| Sep-08 and Apr-10<br>Average dissimilarity = 95.53<br>Species | | | | | | |
| *Lagodon rhomboides* | 0.00 | 31.55 | 78.21 | 3.54 | 81.87 | 81.87 |
| *Diplodus holbrooki* | 2.13 | 0.95 | 8.26 | 0.60 | 8.64 | 90.51 |
| Dec-08 and Apr-10<br>Average dissimilarity = 98.77<br>Species | | | | | | |

| | | | | | | |
|---|---|---|---|---|---|---|
| *Lagodon rhomboides* | 0.00 | 31.55 | 84.90 | 3.68 | 85.96 | 85.96 |
| *Diplodus holbrooki* | 0.46 | 0.95 | 7.36 | 0.37 | 7.45 | 93.41 |
| Mar-09 and Apr-10 | | | | | | |
| Average dissimilarity = 87.41 | | | | | | |
| Species | | | | | | |
| *Lagodon rhomboides* | 1.18 | 31.55 | 71.95 | 3.49 | 82.31 | 82.31 |
| *Diplodus holbrooki* | 2.76 | 0.95 | 8.49 | 0.85 | 9.71 | 92.02 |
| Jun-09 and Apr-10 | | | | | | |
| Average dissimilarity = 87.07 | | | | | | |
| Species | | | | | | |
| *Lagodon rhomboides* | 1.61 | 31.55 | 51.02 | 2.89 | 58.60 | 58.60 |
| *Diplodus holbrooki* | 11.66 | 0.95 | 19.19 | 2.97 | 22.04 | 80.63 |
| *Abudefduf saxatilis* | 7.35 | 0.08 | 13.32 | 2.08 | 15.30 | 95.93 |
| *Sep-09 and Apr-10* | | | | | | |
| Average dissimilarity = 90.49 | | | | | | |
| Species | | | | | | |
| *Lagodon rhomboides* | 0.81 | 31.55 | 51.06 | 3.12 | 56.42 | 56.42 |
| *Diplodus holbrooki* | 11.48 | 0.95 | 18.62 | 2.84 | 20.57 | 77.00 |
| *Abudefduf saxatilis* | 10.15 | 0.08 | 18.52 | 3.10 | 20.47 | 97.47 |
| Feb-10 and Apr-10 | | | | | | |
| Average dissimilarity = 99.02 | | | | | | |
| Species | | | | | | |
| *Lagodon rhomboides* | 0.00 | 31.55 | 88.38 | 4.03 | 89.25 | 89.25 |
| *Diplodus holbrooki* | 0.11 | 0.95 | 7.43 | 0.36 | 7.50 | 96.75 |

# IV. DO VERTEBRATE GRAZERS ALWAYS MAKE THE DIFFERENCE? A STUDY OF HERBIVOROUS FISHES AND JUVENILE GREEN TURTLES (*CHELONIA MYDAS*) GRAZING ON AN ARTIFICIAL ROCKY SHORELINE


## Abstract

While inlet and jetty habitats exist worldwide, little is known about the structure, ecological processes, and carrying capacity of these marine ecosystems. The Trident Basin at Port Canaveral in Cape Canaveral, Florida (28º24´N, 80º35´W) is located within a recognized biological transition zone for temperate/subtropical species. Revetments constructed of large granite boulders line the perimeter of the Basin to retain shoreline integrity in this high-energy environment. The macroalgal community, consisting of predominantly red and green macroalgal of filamentous and foliose form, is characteristically turfed and is foraged by a relatively diverse and abundant assemblage of herbivorous fishes and juvenile green turtles. Exclusion experiments were conducted to test the hypothesis that grazing by these large herbivores impacts the structure and abundance of the macroalgal community growing on the rock boulders. Cages designed to exclude large herbivorous fishes and juvenile green turtles were deployed during four replicated experiments over one year. Macroalgal samples collected from small-mesh and large-mesh exclusion treatments and controls were examined at the end of each experiment for differences in macroalgal community composition, thallus height or

number of branches per length, and diameter of abundant species. Differences in the community composition of macroalgae between treatments and controls were low and detected only within fall and winter experiments. Few biologically significant differences were detected for thallus height and/or diameter measurements, and detections varied for algal species and sampling period. Observations of the macroalgal community during this study are more consistent with bottom-up (high-energy and nutrient) processes and not top-down herbivory.

## Introduction

Little is known about the complex interactions of organisms living on rock rubble structures. These types of structures, usually in the form of jetties to maintain deepwater ports, are present throughout the United States (Rosati and Kraus 2009) and are used for other varying purposes including mitigation, habitat restoration, and even aesthetic purposes (Salahuddin 2006). There is a paucity of knowledge concerning the communities that settle on these introduced structures and their ecological role. The construction of jetties and inlets typically includes the installation of granite boulders to maintain port profiles, stabilize shorelines, and provide buffers to high-energy wave activity. Over the last several decades, an increasing number of marine turtles have been identified as resident organisms in these areas (Dickerson et al. 1995). Of particular interest is the occurrence of juvenile green turtles, a federally-listed endangered species, that has been documented utilizing inlet jetties as developmental habitat, grazing the macroalgae on rock rubble structures as their primary food resource (Coyne 1994, Shaver 1994, Redfoot 1997). These areas also provide food and shelter for populations of

resident and migratory, ecologically and economically important fish populations (Anderson and Gehringer 1965, Hay and Sutherland 1988, Reyier et al. 2010).

The influence of large marine herbivores on macroalgal morphology (e.g., turf-forming vs. foliar) and community composition have largely been demonstrated in the tropics (Randall 1965, Hay 1981, Littler et al. 1983, Lewis et al. 1987). Substantial changes in macroalgal morphology have been documented to occur in as little as 96 hrs (Lewis 1985) or 2 to 4 weeks (Randall 1961) of reduced grazing pressure. The impact of megavertebrates on the composition and productivity (i.e., growth) of temperate/subtropical macroalgae is little understood. Even less known is the potential role that juvenile green turtles (*Chelonia mydas*) play in the structure and ecology of macroalgal communities or the potential pressure on resources when populations of herbivorous fish and green turtles coexist.

The Trident Basin at Port Canaveral in Cape Canaveral, Florida provided an excellent opportunity to investigate the impact of large herbivorous fishes and juvenile green turtles on the macroalgal community. The Cape Canaveral region is a zoogeographic transition zone (Briggs 1974) that supports a rich assemblage of cool subtropical and warm temperate marine biota (Briggs 1958, Searles 1984). Mean monthly water temperatures range between 18.0-28.0°C and mean monthly salinity range from 34.3 to 36.0 (US Dept of Commerce 2010). While appearing bay-like in its profile (i.e., a semi-enclosed, slow-moving body of water), the Basin's proximity to the Atlantic Ocean (within 150 m of the inlet; Figure 4.1) makes it more characteristically oceanic, being heavily influenced by tidal exchange as well as ocean surge and wave energy. The macroalgae in this area are characteristically turfed with the height of most species

typically <2.0 cm (Redfoot 1997, see Chapter 1). The abundance of fishes have previously (Anderson and Gehringer 1965) and recently (Reyier et al. 2010) been documented in the Trident Basin and adjacent harbor areas of Port Canaveral. The herbivore fish composition was generally composed of Sparids (warm temperate-ranging species) and frequented seasonally by several tropical-ranging species (Pomacanthidae, Acanthuridae, and Pomacentridae). In addition, the juvenile green turtle (*Chelonia mydas*) population has been documented as present within this area since 1993 (Redfoot 1997, Redfoot and Ehrhart 2013). Comparatively low growth rates and generally poor body conditions of many turtles in the area (Kubis et al. 2009) have been previously suggested as a result of a marginal or sub-quality foraging habitat. Expectations were that foraging habitat resources were limited for the large aggregation of juvenile green turtles and relatively abundant herbivorous fish population residing within the Basin (see Chapter 3). The nearest natural hard bottom habitat is located >10 km from this site. Low connectivity and limited hard substratum for macroalgal growth suggests that the Basin might provide sub-quality and/or inadequate quantities of food for algal herbivores.

The purpose of this study was to measure changes in macroalgae when juvenile green turtles and relatively large herbivorous fishes were excluded from areas they typically graze. *In situ* experiments were conducted using a stratified random block design. Sets of cages were constructed from two different mesh sizes to exclude green turtles (large-mesh, 5 x 10 cm openings) and large herbivorous fishes (small-mesh, 2.5 cm x 2.5 cm openings). Associated cage controls (open top and open side cages) were constructed from the two different mesh sizes and deployed within each experiment block to control for the effects of reduced light and water flow in full cages. Experiments (n =

4) were repeated for 7 weeks at a time and designed to test the hypotheses that excluding large herbivorous fishes (>2.5 cm) and juvenile green turtles would not significantly alter (1) macroalgal community composition, (2) thallus height or the number of branches per thallus height), or (3) thallus diameter of abundant macroalgae. Samples from all treatments and controls were contrasted at the end of each experiment to measure changes in macroalgal community composition and morphological structure of abundant macroalgal species. Comparisons among experiments (n = 4) were conducted to determine if the macroalgal community differed based on experimental period (season), block (replicate), treatment (all cages and uncaged controls), disturbance (e.g., invertebrates in cages), or interactions among factors (e.g., treatment x disturbance). Comparisons within experiments were used to detect for differences in the macroalgal community based on block, treatment, disturbance, or interactions among factors. Data from experiments were expected to provide evidence that both the macroalgal community composition and morphological structure of abundant macroalgal species were influenced by grazing from herbivorous fishes and green turtles. In addition, foraging selection by abundant fishes and juvenile green turtles identified during this same study period (see Chapter 3) were contrasted with detections in changes to the macroalgal community.

## Methods

### *Study site*

Experiments were conducted within the Trident Basin at Port Canaveral in Cape Canaveral, Florida (28º24´N, 80º35´W) along the southwest wall of the Basin within 150 m of the inlet channel (Figure 4.1). The Basin is subjected to a regular oceanic microtidal exchange (1.03 m, spring tide = 1.19 m) (McBride and Moslow 1991), as well as surge

from boat traffic and wave energy. Local water quality data were available during the experiment periods from a YSI 6920 (Yellow Springs Instrument Company, Yellow Springs, OH) water quality datasonde and the Trident NDBC (National Data Buoy Center; US Dept of Commerce 2010) located in the southeast region of the Basin (28°24'57", 80°35'35"). The primary source of temperature and salinity data was from the YSI, which was deployed within 20 m of the shoreline, 400 m north (28°24'56.8"N, 80°35'51.8"W) of the experiment site in approximately 1.5 m water depth.

*Experiment design*

A complete randomized block design (Krebs 1999) was used to measure changes in community composition and macroalgal morphology under different treatment factors (i.e., large-mesh exclusion, small-mesh exclusion, etc.). The experimental design was balanced with equal replicates (n = 42). Six blocks were randomly arranged within the study area, and treatments were interspersed within blocks by restricted randomization (i.e., random placement of cages within blocks) (see Hurlbert 1984, Kingsford and Battershill 1998). Each block contained treatments that were constructed of large and small-mesh (n = 2, full; n = 2, sides only; n = 2, top only cages), and a control (n = 1; Figure 4.2). Blocks were randomly dispersed over a linear distance of approximately 50 m within the upper subtidal zone and spaced a minimum of 4 m apart. Treatments and controls within blocks were spaced a minimum of 2 m apart.

Experiments were conducted between October 2008 and August 2009 on four separate occasions. The length of experiments varied between 48 to 70 days (average 54.5 days ± 10.5 SD; Table 4.1) due to weather and/or security restrictions extending or shortening access to the study area. Cages were designed to exclude grazing by juvenile

green turtles (*C. mydas*) and large herbivorous fishes [sergeant majors (*Abudefduf saxatilis*), sheepshead (*Archosargus probatocephalus*), spottail pinfish (*Diplodus holbrooki*), and pinfish (*Lagodon rhomboides*)]. To avoid cumulative local effects of the experiment, cage installations were offset within the 100-m experimental area for each sampling period.

Large-mesh treatment cages with 5.0 cm x 10.0 cm openings (Figure 4.3A) were designed to allow relatively large fishes access to the cages' interior while excluding juvenile green turtles based on the median and mode of straight length head widths (5.1 and 5.4 cm, respectively) of juvenile green turtles previously documented in the Trident Basin (Redfoot and Ehrhart 2013). The small-mesh (2.5 x 2.5 cm openings) treatment cages were intended to exclude juvenile green turtles and relatively large herbivorous fishes (>2.5 cm; Figure 4.3B). All cages measured 26 cm height x 26 cm long x 26 cm deep and were constructed from 12-gauge, vinyl coated, galvanized wire. In addition, cages made from large- and small-mesh material were constructed to control for the effects of reduced water flow (open sides, Figure 4.3C-D) and reduced light penetration (open top, Figure 4.3E-F). Control sites (rocks) were marked with a 5-mm diameter elastic bungee cord wrapped around a rock to identify the location for sampling. All treatments and cage controls had a stainless steel identification tag (2.7 x 5.0 x 0.02 cm) affixed to the outside bottom edge of the cage with a small cable tie. Tags were labeled with block number (1-6) and treatment type [i.e., A = Full-L (full cage, large-mesh), B = Full-S (full cage, small-mesh), C = Side-L (cage with sides only, large-mesh), D = Side-S (cage with sides only, small-mesh), E = Top-L (cage with top only, large-mesh), F = Top-S (cage with top only, small-mesh)]. Cages were secured to boulders with two bungee

cords that were clipped to the bottom of the cage and wrapped around a boulder. The uncaged control, which in this instance was a rock boulder, was identified by a labeled tag (G = control) that was attached to a 0.5-mm diameter bungee cord. The cord was placed near the edge of the boulder and wrapped in a vertical direction around the boulder.

*Addressing exclusion experiment challenges*

Exclusion experiments are inherently difficult under field conditions and biofouling has been identified as a serious challenge in the success of caging experiments (Virnstein 1978, van Blaricom 1982). To avoid excessive fouling which potentially alters light penetration and water flow, cages in the field were exchanged weekly with a clean tagged duplicate (n = 36). The removed cages were brought back to the lab, pressure-washed clean with fresh water, and re-deployed the following week when cages were exchanged.

While infrequent, the presence or activity of a "disturbance" within cages was documented for each site visit. Disturbance categories were herbivorous invertebrates (e.g., gastropod or crab), resident herbivorous fish (e.g., *Scartella cristata*, molly miller), and coverage disruption (i.e., cage partially knocked off the rock). Very small invertebrate grazers (e.g., *Ampithoe* spp., *Idotea* spp.) found in samples at the end of the experiment were also categorized as a disturbance for the analysis. Each disturbance was recorded as a single incident in one of the categories. The percentage of disturbances encountered during each experiment was calculated as:

$$\text{Disturbance rate per treatment} = \frac{\sum \text{treatment disturbances}}{\text{block x visits}} \text{ x } 100$$

Disturbances were treated as a random factor and addressed in the final analysis to test for variability in the macroalgal community that could have been attributed to disturbance that occurred during the experiment.

*Field sampling of macroalgae*

Macroalgal samples were collected from treatment and control areas when the cages were initially installed and approximately every 2 weeks during the experiment. Sampling was conducted in the center 10 x 10 cm area of the cages to avoid any halo effect created by the bottom edge of the cage contacting the substratum. Since the macroalgae in this area are highly turfed, a 2.5-cm diameter sample was cut and scraped from the rock surface with a modified cork borer (Webster 1974). A removable template was used to identify the sampling location each time to prevent coring from a previously sampled area. Each sample was plunged into an individual, pre-labeled compartment of a sample container. Sample containers were kept in a cooler of ice until transferred to refrigeration. The samples taken at the conclusion of each experiment were analyzed, while the initial and bi-weekly samples were retained to ascertain a timeline of change in the event that significant changes were detected in the morphology and/or macroalgal community from treatment and control samples.

*Macroalgal community composition*

Macroalgae in samples were identified to the lowest taxonomic level possible with the aid of microscopy and several taxonomic keys (Dawes 1974, Schneider and Searles 1991, Littler and Littler 2000, Littler et al. 2008, Dawes and Mathieson 2009). Gelidiales were difficult to identify and voucher samples were sent to University of North Carolina (W. Freshwater, pers comm) for molecular analysis.

Quantification of the percent composition of the macroalgal community followed Forbes (1999) where samples were thoroughly mixed and spread across a gridded Petri dish into a single layer and examined with modified procedures of microstereology (Weibel et al. 1966). A stereoscope was fitted with a grid reticle (100 squares) in the ocular. The reticle was aligned within one of the 1.3-$cm^2$ grids of the Petri dish. Calculations for percent composition data were generated from equidistant counts of the macroalga within the gridded reticle (n = 50 potential points). The count of individual species was divided by the sum of all species counts and standardized to 100% for the macroalgal community composition data.

*Morphological structure: height (or branching) and diameter*

The height of approximately 6 thalli (or branch counts per thallus) from temporally abundant macroalgae (i.e., *A. fragilissima*, *C. clavulatum*, *G. planicaulis*, *G. crinale*, *G. filicina*, and *Hypnea spinella*) were measured under stereomicroscopy. Individual thalli were spread onto the grid area of a Petri dish and measured under stereoscopy at 7.9x with a 1.25-cm ocular micrometer (0.1-mm scale). Thallus diameters of the same specimens were measured under microscopy with a 1.0-mm ocular micrometer at 100x (0.01-µm scale). The number of branches per cm thallus length of *Hypnea spinella* samples was calculated in lieu of a thallus height measurement due to *Hypnea*'s prostrate growth habit.

*Statistical analysis of macroalgal community data*

Data were analyzed with Primer-E software (Clarke and Gorley 2006) with multidimensional scaling (MDS) and permutational multivariate analysis of variance (PERMANOVA) procedure. Percent composition data from treatment and controls (n =

42) in each experiment (n = 4) were square root transformed to down-weight the contribution of the most abundant species (Clarke and Green 1988, Mumby et al. 1996). Similarity coefficients were generated from Bray-Curtis resemblance matrix calculations of the data between every pair of replicates, within and among the sample groups to interpret the relative values of similarity among groups (Clarke and Warwick 2001). The 2D ordination plots were used to spatially represent similarity among samples (e.g., treatments, blocks). The reported "stress" value of a constructed plot is the measure of distortion required to represent the data in the 2D plot (Clarke and Warwick 2001). A stress value of 0 indicates a perfect representation of the data. A stress value ≤0.2 is also considered a useful representation for interpreting the data. Ordination plots resulting in stress values >0.2 should be interpreted with caution, as the distortion is considerably high at this level. Stress values >0.3 result from a very high level of distortion created in order to display the data and are considered unreliable to generate inferences (Clarke and Warwick 2001).

A PERMANOVA design file inclusive of all factors and interactions was created and run on the Bray-Curtis resemblance matrix of macroalgal percent composition data to test the hypothesis that there were no significant differences in the macroalgal community composition of samples collected from treatments, cage controls, and controls. Analytic factors among experiments were season (n = 4, fixed), block (n = 6, random), mesh (n = 2, fixed), treatment (n = 7, fixed), and disturbance (n = 4, random). Factors for comparisons within experiments were block (n = 6, random), mesh (n = 2, fixed), treatment (n = 7, fixed), and disturbance (n = 4, random). Selections for the analyses were Type I (sequential), permutations = 9999, fixed effects sum to zero, and permutations of

residuals under a reduced model. Effect sizes were relatively low (<3.0) for tests between treatments due to low replication but were considered significant at P (perm) <0.05 and marginally significant at ≤0.10 levels. Separate design files were created for significant main effects (e.g., treatment) to conduct post hoc pairwise comparisons (e.g., full large-mesh cages vs. controls) via univariate PERMANOVA (Anderson 2001).

*Morphological structure analyses*

Thallus height (or branches-per-thallus length) and diameter measurements of macroalgae were contrasted among treatments, cage controls, and uncaged controls using ANOVA (Sigma Plot 2008) to test the hypothesis of no significant differences in morphological structure of abundant macroalgal species. Post hoc pairwise comparisons were conducted using Holm-Sidak procedure (with adjusted critical p-levels for multiple tests). Differences in the mean height of macroalgae from treatment (full cages) vs. control (uncaged) samples were considered biologically significant at a 5 mm or ± 40% difference. A ± 25% difference in thallus diameter measurements from macroalgae in treatments vs. controls was considered biologically significant. These *a priori* criteria were established based on grazing experiments conducted by Randall (1961) and Lewis (1987). Results of contrasts between all treatments, cage controls, and controls were used to explore potential anomalies within cages (e.g., enhanced abundance of mesograzers).

*Herbivore selection on macroalgae*

The relationship of changes observed in the macroalgal community due to the foraging selections of abundant herbivorous fishes and juvenile green turtles (see Chapter 3) was determined in a series of field experiments. Seasonally abundant herbivores were *Chelonia mydas* (green turtle), *Abudefduf saxatilis* (sergeant major), *Archosargus*

*probatocephalus* (sheepshead), *Diplodus holbrooki* (spottail pinfish), and *Lagodon rhomboides* (pinfish). Significant differences in the macroalgal species composition in cages that excluded some or all of these herbivores were compared with the relative abundance and macroalgal selections of these grazers in experiments.

## Results

### *Experiment conditions*

Experiments were conducted between October 2008 and August 2009 on four separate occasions. The length of experiments varied between 48 to 70 days (average 54.5 days ± 10.5 SD; Table 4.1) due to weather and/or security restrictions extending or shortening access to the study area. Temperature and salinity measurements were collected primarily from downloads of the YSI data sonde; however, missing data were supplemented with Trident NDBC data. Temperature and salinity data between the two sources were not significantly different when compared for the same time periods (t-test; $t_{1,10} = -0.805$, $P = 0.428$). Mean monthly water temperatures ranged from 17.9 $^{o}$C (± 0.7 SD) in February to 27.8 $^{o}$C (± 1.4 SD) in August (Figure 4.4). Water temperatures were coolest during the winter experiment and warmest during summer (Table 4.1). Monthly salinity averages were between 34.9 (± 0.3 SD) and 36.4 (± 0.9 SD; Figure 4.4). Salinity measurements were lowest during the summer experiment (Table 4.1).

### *Macroalgal community*

Fourteen species of macroalgae (9 rhodophytes and 5 chlorophytes) were identified from exclusion experiments (Table 4.2). The number of species present per experiment (n = 4) ranged from 10-13. Nine species, predominantly rhodophytes, were found in samples during all four experiments, while four of the five chlorophytes (i.e.,

*Bryopsis plumosa*, *Chaetomorpha gracilis*, *Ulva flexuosa*, *U. lactuca*) and *Ceramium floridanum* (rhodophyte) were absent from one or more sampling periods. Macroalgae found within cages but absent in control samples were *Grateloupia filicina* in the fall, *Bryopsis plumosa* in the winter, *Gelidiopsis planicaulis* in the spring, and *Cladophora catenata* in the summer experiment. Likewise, there were control samples that contained macroalgae that were not found in treatment samples (e.g., *Polysiphonia denudata* in fall and *Ulva lactuca* in spring; Table 4.2). No species of brown (Ochrophyta) macroalgae or Cyanobacteria were found in samples during any of the experiments.

*Among-experiment comparisons*

Dissimilarity in the macroalgal community among experiments were visually evident in the MDS ordination plot (Figure 4.6), and significant differences were detected among all four experiments (PERMANOVA, Psuedo F = 12.606, P (perm) - 0.007; Table 4.3). Post hoc pairwise comparisons were significant for all contrasts, and dissimilarity in the percent composition of macroalgae ranged from 56.4-70.7% among comparisons (SIMPER; Table 4.4). The overall composition of macroalgal was most dissimilar (70.7%) in contrasts for fall vs. spring experiments. The percent compositions *G. crinale*, *P. planicaulis*, *A. fragilissima*, and *H. spinella* were higher in the fall experiment, and *G. filicina*, *C. clavulatum*, and *J. adhaerens* were higher in spring. This contributed >90% of the dissimilarity between the experiments (Appendix Table 4.1a-f). No significant differences in the macroalgal community were detected among experiments for treatment, block, disturbance, or interactions of these factors (Table 4.3).

*Within-experiment comparisons*

Significant differences in the macroalgal composition based on treatment were detected for the fall experiment only [PERMANOVA; Psuedo-F = 1.424, P (perm) = 0.067; Table 4.5a-d]. Differences in the macroalgal community were detected in full large-mesh cages vs. uncaged controls [univariate PERMANOVA, t = 1.605, P (perm) = 0.021; Table 4.5a]. The higher percent composition of *G. crinale*, *G. filicina*, *C. clavulatum*, and *A. fragilissima* in full-large-mesh cages and higher percent composition of *H. spinella*, *G. planicaulis*, *Polysiphonia denudata* in controls contributed >90% of differences between the two treatments (SIMPER; Table 4.6a).

In some cases, significant differences were detected in the comparisons of the macroalgal composition for one or more cage controls (sides or top-only cages; Table 4.6a, d). Both fall and summer experiments had significantly different macroalgal compositions for comparisons between sides-only cages, tops-only vs. controls or full cage treatments (Figure 4.9-10, Table 4.6d).

*Morphological structure comparisons*

There were no significant differences in the mean thallus height of 6 abundant macroalgal species measured for differences in full cage treatment vs. uncaged control fall and winter experiments (Figure 4.7-10, Table 4.6a-b). In spring, mean thallus height of *G. planicaulis* was significantly taller in full large-and small-mesh treatment cages vs. controls (Figure 4.9, Table 4.6c). In summer, *G. planicaulis* mean thallus height was also greater in full treatment vs. controls (Figure 4.10, Table 4.6d). Mean thallus height of *C. clavulatum* was greater in both full mesh treatments vs. controls but less for *A. fragilissima* from full small-mesh cages vs. controls (Figure 4.10, Table 4.6d). *Gelidium*

*crinale* was significantly greater in full small-mesh cages vs. full large-mesh cages and controls (Figure 4.10, Table 4.6d). Significant differences were also detected in the comparisons of thallus height for one or more cage controls (sides or top-only cages; Appendix Table 4.2). All contrasts of the branch per cm length of *H. spinella* were non-significant.

Significant difference in the mean thallus diameter between full cage treatments and controls were detected for one or more species measured during experiments except in spring. Thallus diameter of *G. crinale* was significantly greater in full-mesh treatment cages vs. controls (Figure 4.11-14, Table 4.6a-d). The mean diameter of *G. planicaulis* in winter and summer experiments was less in full large-mesh cages vs. controls, and in summer *G. planicaulis* was also less in full large vs. small-mesh cages (Figure 4.12, 14, Table 4.6b, d). While differences in the diameter of *A. fragilissima* and *H. spinella* met statistical significance tests for the winter experiment comparisons (Figure 4.12, Table 4.6b), they failed to meet *a priori* criteria ($\Delta \pm 25\%$) as differences ranged between 14.0-18.1% (Appendix Table 4.3). Significant differences were also detected in the comparisons of thallus diameter for one or more cage controls (e.g., sides or top-only cages) (Figure 4.12, 13, Appendix Table 4.3).

*Herbivore selection on macroalgae: summarizing results*

For the fall experiment, *G. planicaulis*, *G. crinale*, *G. filicina*, *H. spinella*, and *P. denudata* were species identified as selectively foraged or made up >10% of composition of the foraging samples for herbivorous fishes or juvenile green turtles (see Chapter 3). The percent composition of the species (*H. spinella* and *P. denudata*) selected by *A. probatocephalus* was significantly lower in full large-mesh cages vs. controls (Table

4.6a). Two species (*G. crinale* and *G. filicina*) selected for by *C. mydas* were found in higher percent compositions in full large-mesh cages vs. controls, while one species (*G. planicaulis*) had higher composition in control samples (Table 4.6a). *Gelidium crinale* was the only species that had a significantly larger mean thallus diameter in plants from full large-mesh cages vs. full small-mesh cages and controls.

Several species were selectively foraged by *A. probatocephalus* in winter; however, the percent composition and height of species were not significantly different between full cage treatments vs. controls. Differences detected for the thallus diameter of *A. fragilissima*, *G. planicaulis*, and *H. spinella* were considered biologically non-significant, and *H. spinella* was the only species of the three to be selectively foraged by *A. probatocephalus* during this time period.

*Chelonia mydas* selectively foraged on *G. filicina*, and *A. probatocephalus* selectively foraged on *H. spinella* and *P. denudata* in spring. *Diplodus holbrooki* and *L. rhomboides* selectively foraged on *P. denudata* and *Ulva lactuca*. While no differences were detected in contrasts of the percent composition of macroalgae in full cage treatments vs. controls, the mean thallus height for *G. planicaulis* was significantly higher in full cage treatments (Table 4.6c).

In summer, the mean thallus height of four macroalgal species in full cage treatments significantly differed from controls. The mean thallus height of *A. fragilissima* which was selectively foraged by *A. probatocephalus* in summer was significantly less in full small-mesh treatment cages vs. controls during this time period (Table 4.6d). *Gelidium crinale* was selectively foraged by *Diplodus holbrooki* in summer, and the thallus height of this species in full small-mesh treatment cages was significantly greater

than thalli from full large-mesh cages or the control. No selective foraging was recognized for *G. planicaulis*; however the height of *G. planicaulis* was greater in full cage treatments vs. controls and mean thallus diameter was less in full large-mesh cages vs. small-mesh cages and controls (Table 4.6d). *Hypnea spinella* was selectively foraged by *Abudefduf saxatilis* and *D. holbrooki* and made up >10% of foraging sample compositions of *C. mydas* and *A. probatocephalus* in summer; there were no significant differences detected in the percent composition, thallus branching or diameter of *H. spinella* during the summer experiment (Table 4.6d).

Discussion

*Macroalgal community*

While there were shifts in the percent composition of dominant macroalgal species, the macroalgal community consisted of the same species throughout the study period. Dissimilarity for the percent composition of macroalgal species among experiments revealed few distribution patterns that were correlated with season (i.e., temperature). The relationship of individual species abundance and temperature previously identified (see Chapter 1) were not consistent with the percent composition of macroalgae from treatment or controls. For example, *A. fragilissima* and *H. spinella* were positively correlated with temperature; however, these macroalgae were present in comparatively higher percent compositions in one or more of the 6 contrasts among the experiments that occurred during periods of warm and cool water temperatures. Few significant changes in the abundance of most macroalgae in relationship with water temperature support previous work in subtropical latitudes where macroalgae tend to have greater tolerance to a wide range of temperatures and salinities than the same

species from tropical latitudes (Rueness and Tananger 1984, Smith and Berry 1986, Lobban. and Harrison 1994).

*Herbivore presence and influence on macroalgal community and morphological structure*

Herbivorous fishes and juvenile green turtles were observed grazing in and around the area where the exclusion experiments were conducted. Estimated encounter rates of grazers (based on UW video and boat transect surveys) suggest that 40.1 (±17.8) grazers [i.e., 1.8 (± 2.4 SD) *A. saxatilis*, 17.8 (±14.1 SD) *A. probatocephalus*, 38.5 (± 57.9), 0.5 (± 1.0 SD) *L. rhomboides*, and 0.9 (± 0.3 SD) *C. mydas*] were present at any one time within the 100-m area where exclusion experiments were conducted. However, the composition of the macroalgal community was not significantly altered under exclusion cages and relatively few changes in the structures of individual macroalgal species were impacted by the exclusion of fishes and/or juvenile green turtles, even when foraging selection pressure was considered (see Chapter 3). Results of the experiments indicate that large herbivorous fishes and juvenile green turtles may play a very small role in influencing the macroalgal composition or altering the morphological structure of abundant macroalgae within the study area. Green turtles (*C. mydas*) and large sheepshead (*A. probatocephalus*), which forage as generalists, were excluded from the large- and small-mesh cage treatments. These grazers were present year-round within the Basin, and they selectively foraged or consumed in relatively high percent compositions of their diet one or more of the species that were present in every experiment period. However, relatively few relationships between foraging exclusion and grazing selection correlated with significant differences in the macroalgae under exclusion vs. non-

exclusion conditions and appeared inconsistent among experiments. In some cases, a macroalga responded as expected and increased in percent composition and/or morphological structure in exclusion vs. control treatments. For example, the percent composition and thallus diameter of *G. crinale* increased in cages that excluded juvenile green turtles and large sheepshead fishes in fall. In summer, the mean thallus height of *G. planicaulis* and *G. crinale* from cages that excluded herbivores >2.5 cm (full small-mesh cages) were significantly taller than controls during a period where *D. holbrooki* selectively foraged on *G. crinale* and the grazer abundance and diversity was highest (see Chapter 3). Likewise, a decline in the mean thallus measurements between treatments and controls in the absence of foraging selection pressure for some species (e.g., *A. fragilissima* and *G. planicaulis* in summer and others) were also detected, which suggests that some macroalgal species may respond positively to grazing. Future experiments would benefit from simulated cropping over time under different grazer and grazing regimes to isolate individual algal species response to grazing. In addition, experiments that examine the viability of macroalgal fragments and spores that have passed through the gut of fishes and green turtles would provide insight to nutrient cycling paths and turf algal production in these habitats.

Macroalgae were extremely turfed and maintained similar profiles throughout all four seasonal experiments and, in nearly all cases, regardless of grazer abundance. The relatively few changes detected during experiments suggest that other factors play a more significant role in shaping the macroalgal community within the Basin and/or the turf nature of macroalgae in this habitat-type. The macroalgal community in the Trident Basin was very similar to highly productive algal communities found in low-shore, high energy

environments. The turf communities in these areas are highly resilient and re-vegetate quickly in response to disturbance (i.e., scouring, damage) (Airoldi 2000, Hurd 2000, Copertino et al. 2005, Copertino et al. 2006). Areas where macroalgae were cored to the bare rock (under treatment cages and control areas) were sometimes re-vegetated in <1 week, and bare patches were uncommon on submerged rock outside of the experiment area (pers. observ.).

Airoldi (1998) found seasonal thicknesses of turf species fluctuated in response to changes in weather conditions as well as associated intensity of sediment deposition. Composition and structure of turf assemblages, however, remained rather constant and maintained relatively low diversity (Airoldi 1998). Positive responses to herbivory have been documented in terrestrial and freshwater ecosystems; that said, few studies address this in marine systems. Results of this study indicate a lack of measurable response of the macroalgal community to grazing by *C. mydas* and large herbivorous fishes in this high-energy environment at <80 day time-scales, suggesting that alternative characteristics or features of this habitat direct primary production.

*Conclusions*

Many of the same macroalgal taxa (e.g., *Gelidium*, *Hypnea* spp.) in this study have been identified in foraging samples from juvenile green turtles in Hawaii (McDermid et al. 2007, Arthur and Balazs 2008), Gulf of Mexico (Seminoff et al. 2002), Brazil (Reisser et al. 2013), and Australia (Garnett et al. 1985). Although researchers have speculated that macroalgal resources within the Basin were sub-quality and incapable of supporting the foraging requirements of larger size-class (40-60 cm SCL) juvenile green turtles (Redfoot 1997, Kubis et al. 2009), results of this study suggest that

may not be the case. During this study, the growth and composition of very few macroalgae within this habitat were measurably impacted by the current level of grazing. The well-documented nutrient composition responses to green turtle grazing on seagrasses (Moran and Bjorndal 2005, 2007) warrant investigating if similar response mechanisms exist in frequently consumed species of macroalgae. As populations of green turtles in parts of the world appear to be increasing, important recovery measures require the inclusion of examining both habitat quantity and quality to support their continued survival in the future (Witherington et al. 2006). Studies that investigate preferences of developmental habitat by juvenile green turtles (e.g., shelter, perceived predation levels) could shed light on characteristics that attract turtles to these inlet/ jetty habitats.

While extrapolating the results of this study to other areas is respectfully cautioned, similarly-structured habitats have been identified across the South Atlantic Bight (Hay and Sutherland 1988) and the Gulf of Mexico (Hastings 1979, Renaud et al. 1995, Agan and Lehman 2001). Many of these areas share similar features and characteristics of flora and fauna, and their macroalgal communities support ecologically and economically important fish stocks as well as aggregations of federally endangered juvenile green turtle populations. As anthropogenic activities continue to impact coastal areas and the introduction of artificial structures as tools for mitigation and restoration continue, further research is warranted to determine the function and carrying capacity of these habitat-types.

Tables

Table 4.1. Dates of exclusion experiments (n = 4), experiment length in days, and average (± SD) of temperature ($^{o}$C) and salinity during the entire study period from October 2, 2008 through August 10, 2009.

| Experiment period | Start date | End date | Duration (days) | Temperature °C (average ± SD) | Salinity (average ± SD) |
|---|---|---|---|---|---|
| Fall | Oct 2, 2008 | Nov 23, 2008 | 52 | 23.7 ± 2.5 | 35.0 ± 0.4 |
| Winter | Dec 19, 2008 | Feb 5, 2009 | 48 | 19.4 ± 1.2 | 35.4 ± 0.7 |
| Spring | Mar 31, 2009 | Jun 8, 2009 | 70 | 23.7 ± 1.4 | 36.0 ± 0.9 |
| Summer | Jun 23, 2009 | Aug 10, 2009 | 48 | 27.5 ± 0.3 | 34.3 ± 2.0 |

Table 4.2. Species of macroalgae found in samples from exclusion experiments that were conducted four times (seasonally) from October 2008-August 2009. '*' indicates species was found in treatment and control samples, '+' found in treatment only, 'cc' found in cage controls only, 'c' found in control only, '–' not found in any samples for that experiment period.

| Macroalgae | October '08 | December '08 | March '09 | August '09 |
|---|---|---|---|---|
| RHODOPHYTA | | | | |
| *Amphiroa fragilissima* | * | * | * | * |
| *Centroceras clavulatum* | * | * | * | * |
| *Ceramium floridanum* | – | – | * | * |
| *Gelidiopsis planicaulis* | * | * | + | * |
| *Gelidium crinale* | * | * | * | * |
| *Grateloupia filicina* | + | * | * | * |
| *Hypnea spinella* | * | * | * | * |
| *Jania adhaerens* | * | * | * | * |
| *Polysiphonia denudata* | c | + | * | cc |
| CHLOROPHYTA | | | | |
| *Bryopsis plumosa* | – | * | * | * |
| *Chaetomorpha gracilis* | * | – | * | * |
| *Cladophora catenata* | * | * | * | + |
| *Ulva flexuosa* | * | * | * | – |
| *Ulva lactuca* | – | * | c | – |
| Total species present in treatment/control samples for exclusion experiments | 10/10 | 12/11 | 13/13 | 11/10 |

Table 4.3. Results of comparisons for the macroalgal percent composition from four exclusion experiments that were conducted for approximately 7 weeks each between October 2008-August 2009. Factor comparisons were for experiment (n = 4, fixed; season), block (n = 6, random; design replicate), treatment (n = 7, fixed; cages, cage controls, and uncaged controls), disturbance (n = 2, random; yes or no). Incidents that were considered disturbances were invertebrate grazers found inside cages, herbivorous fishes (i.e., *Scartella cristata*) that took up residence in cages, cage coverage disruption (cage shifted on the boulder), and invertebrate grazers found in samples. Tests were also conducted for interactions among factors (e.g., experiment x block x treatment). Data were analyzed using permutational multivariate analysis of variance (PERMANOVA; Anderson 2001).

| Factors (df) | Psuedo-F | P (perm) |
|---|---|---|
| Experiment (3) | 12.606 | 0.007 |
| Treatment (6) | 1.249 | 0.265 |
| Disturbance (1) | 0.481 | 0.783 |
| Experiment x Treatment (18) | 0.936 | 0.577 |
| Experiment x Disturbance (3) | 0.461 | 0.950 |
| Treatment x Disturbance (6) | 0.723 | 0.849 |

Table 4.4. Results for comparisons of the macroalgal community among experiments (n = 4; season) using permutational multivariate analysis of variance (PERMANOVA; Anderson 2001). Experiments were conducted for approximately 7 weeks each between October 2008-August 2009. Species that were higher in percent composition and contributed to dissimilarity between pairwise comparisons of groups are listed in descending order (SIMPER). Abbreviations of macroalgal species are: *Af* (*Amphiroa fragilissima*), *Cc* (*Centroceras clavulatum)*, *Gp* (*Gelidiopsis planicaulis*), *Gc* (*Gelidium crinale*), *Gf* (*Grateloupia filicina*), *Hs* (*Hypnea spinella*), *Ja* (*Jania adhaerens*).

| Group 1 | Group 2 | t | P (perm) | SIMPER (%) | Species in higher composition (Group 1) | Selectively foraged species (Group 1)[A] | Species in higher composition (Group 2) | Selectively foraged species (Group 2)[A] |
|---|---|---|---|---|---|---|---|---|
| Fall | Winter | 2.361 | 0.019 | 62.0 | *Gc, Gp, Hs, Af* | $Gp^{cm}$, $Gf^{cm}$, $Hs^{ap}$ | *Gf, Ja, Cc* | $*Cc^{ap}$, $Hs^{ap}$ |
| Fall | Spring | 2.599 | 0.016 | 70.7 | *Gc, Gp, Af, Hs* | $Gp^{cm}$, $Gf^{cm}$, $Hs^{ap}$ | *Gf, Cc, Ja* | $Af^{ap,cm}$, $Cc^{ap}$, ,$Gf^{cm}$, $Hs^{ap}$ |
| Fall | Summer | 2.900 | 0.004 | 56.4 | *Gp, Gc, Hs* | $Gp^{cm}$, $Gf^{cm}$, $Hs^{ap}$ | *Af , Gf, Cc, Ja* | $Af^{ap}$, $Gp^{ap,cm}$, $Gc^{dh}$,$Gf^{cm}$, $Hs^{all}$ |
| Winter | Spring | 2.529 | 0.011 | 68.7 | *Gp, Gc, Af, Hs, Ja* | $*Cc^{ap}$, $Hs^{ap}$ | *Gf, Cc* | $Af^{ap,cm}$, $Cc^{ap}$, ,$Gf^{cm}$, $Hs^{ap}$ |
| Winter | Summer | 2.735 | 0.007 | 61.1 | *Gp, Gc, Cc, Ja* | $*Cc^{ap}$, $Hs^{ap}$ | *Gf, Af , Hs* | $Af^{ap}$, $Gp^{ap,cm}$, $Gc^{dh}$,$Gf^{cm}$, $Hs^{all}$ |
| Spring | Summer | 2.585 | 0.016 | 60.6 | *Gf, Cc, Ja, Gp* | $Af^{ap,cm}$, $Cc^{ap}$, $Gf^{cm}$, $Hs^{ap}$ | *Af , Hs, Gc* | $Af^{ap}$, $Gp^{ap,cm}$, $Gc^{dh}$,$Gf^{cm}$, $Hs^{all}$ |

[A]Herbivores previously identified as selectively foraging on certain macroalgal species (see Chapter 3) during the same seasonal time period as the experiment are denoted by subscripts as: $^{cm}$ = green turtle (*Chelonia mydas*), $^{ap}$ = sheepshead (*Archosargus probatocephalus*), $^{as}$ = sergeant major (*Abudefduf saxatilis*), $^{dh}$ = spottail pinfish (*Diplodus holbrooki*), or $^{all}$ = all species.

*indicates green turtles (*C. mydas*) were present but no foraging selection data were available for winter.

Table 4.5. Results of comparisons for the macroalgal percent composition from exclusion experiments (n = 4, seasons) conducted during October 2008-August 2009 based on the factors. season (n = 4, fixed; season), block (n = 6, random; design replicate), treatment (n = 7, fixed; cages, cage controls, uncaged controls), disturbance [(n = 2, random; invertebrate grazer, resident fish (i.e., *Scartella cristata*), and/or coverage disruption in any treatments or controls areas, and invertebrate grazers found in samples)]. Tests were also conducted for interactions among factors (e.g., experiment x block x treatment). Data were analyzed with permutational multivariate analysis of variance (PERMANOVA; Anderson 2001).

(a)

| Fall - Factors (df) | Psuedo-F | P (perm) | Comparisons | t | P (perm) |
|---|---|---|---|---|---|
| Block(5)$^R$ | 30.448 | 0.042 | | | |
| Treatment (1) | 1.424 | 0.067 | Full-L, contrast | 1.605 | 0.021 |
| | | | Sides-L, Top-L | 1.583 | 0.039 |
| | | | Sides-L, control | 1.905 | 0.031 |
| | | | Top-L, control | 2.138 | 0.001 |
| | | | Top-S, control | 1.813 | 0.002 |
| Invertebrates in cage (1) | 288.02 | 0.368 | | | |
| Coverage disruption (1) | 4.297 | 0.775 | | | |
| Invertebrates in samples (0) | No test | | | | |

(b)

| Winter - Factors (df) | Psuedo-F | P (perm) | Comparisons | t | P (perm) |
|---|---|---|---|---|---|
| Block(5)$^R$ | 2.551 | 0.428 | | | |
| Treatment (1) | 0.665 | 0.726 | | | |
| Invertebrates in cages(1) | 2.121 | 0.247 | | | |
| Fish in cage (1) | 70.001 | 0.100 | | | |
| Invertebrates in samples (1) | 5.206 | 0.484 | | | |

(c)

| Spring - Factors (df) | Psuedo-F | P (perm) | Comparisons | t | P (perm) |
|---|---|---|---|---|---|
| Block(5)$^R$ | 18.24 | 0.010 | | | |
| Treatment (1) | 0.448 | 0.969 | | | |
| Invertebrate in cage (1) | 5.853 | 0.493 | | | |

(d)

| Summer - Factors (df) | Psuedo-F | P (perm) | Comparisons | t | P (perm) |
|---|---|---|---|---|---|
| Block(5)$^R$ | 31.675 | 0.096 | | | |
| Treatment (1) | 1.083 | 0.254 | Full-L, Sides-S | 1.975 | 0.013 |
| | | | Full-S- Sides S | 1.330 | 0.045 |
| Invertebrate in cage (1) | 16.835 | 0.742 | | | |

*significance for block$^R$ (n = 6, random factor) was attributed to the statistical artifact of running multiple comparisons and, in nearly all cases, *post hoc* pairwise comparisons were non-significant for block.

Table 4.6. Summary results of comparisons that were significantly different for percent composition or morphological structure of abundant macroalgae in exclusion experiments (n = 4). Results are listed for differences between full cage treatments (large- vs. small-mesh) and/or controls. Experiments were conducted for 7 weeks in fall (A; October 2 - November 23, 2008), winter (B; December 19, 2008 - February 5, 2009), spring (C; March 31- June 8, 2009), and summer (D; June 23, 2009 - August 10, 2009).

(a)

| Fall - Macroalgal species | Species in higher percent composition in full cage treatments or control | Thallus height (or branch per length; mm) comparisons between full cage treatments and/or control | Thallus diameter (μm ) comparisons between full cage treatments and/or control | Herbivore(s) that selectively foraged or consumed in >10%*of foraging composition |
|---|---|---|---|---|
| *Amphiroa* | Full-L | n/s | n/s | – |
| *Centroceras* | Full-L | n/s | n/s | – |
| *Gelidiopsis* | control | n/s | ns | *Cm* |
| *Gelidium* | Full-L | n/s | Full-L > control<br>Full-L > Full-S | *Cm** |
| *Grateloupia* | Full-L | n/s | n/s | *Cm* |
| *Hypnea* | control | n/s | n/s | *Ap* |
| *Polysiphonia* | control | n/a | n/a | *Ap* |
| *Ulva lactuca* | – | n/a | n/a | – |

(b)

| Winter - Macroalgal species | Species in higher percent composition in full cage treatments or control | Thallus height (or branch per length; mm) comparisons between full cage treatments and/or control | Thallus diameter (μm ) comparisons between full cage treatments and/or control | Herbivore(s) that selectively foraged or consumed in >10%*of foraging composition |
|---|---|---|---|---|
| *Amphiroa* | Full-L | n/s | [A]Full-S > control | – |
| *Centroceras* | – | n/s | n/s | *Ap** |
| *Gelidiopsis* | Full-L | n/s | [A]Full-L < control | – |
| *Gelidium* | control | n/s | n/s | – |
| *Grateloupia* | Full-L | n/s | n/s | – |
| *Hypnea* | Full-L | n/s | [A]Full-L > control | *Ap* |
| *Polysiphonia* | – | n/a | n/a | *Ap* |
| *Ulva lactuca* | – | n/a | n/a | *Ap* |

(c)

| Spring - Macroalgal species | Species in higher percent composition in full cage treatments or control | Thallus height (or branch per length; mm) comparisons between full cage treatments and/or control | Thallus diameter (μm ) comparisons between full cage treatments and/or control | Herbivore(s) that selectively foraged |
|---|---|---|---|---|
| *Amphiroa* | n/s | n/s | n/s | – |
| *Centroceras* | n/s | n/s | n/s | – |
| *Gelidiopsis* | n/s | Full-L > control<br>Full-S > control | n/s | – |
| *Gelidium* | n/s | n/s | n/s | – |
| *Grateloupia* | n/s | n/s | n/s | *Cm* |
| *Hypnea* | n/s | n/s | n/s | *Ap* |
| *Polysiphonia* | n/s | n/a | n/a | *Ap, Dh. lr* |
| *Ulva lactuca* | n/s | n/a | n/a | *Dh. Lr* |

(d)

| Summer- | Species in higher | Thallus height (or | Thallus diameter | Herbivore(s) that |
|---|---|---|---|---|

| Macroalgal species | percent composition in full cage treatments or control | branch per length; mm) comparisons between full cage treatments and/or control | (μm ) comparisons between full cage treatments and/or control | selectively foraged or consumed in >10%*of foraging composition[+] |
|---|---|---|---|---|
| *Amphiroa* | n/s | Full-S < control | n/s | *Ap* |
| *Centroceras* | n/s | Full-L > control | n/s | – |
| | | Full-L > Full-S | | |
| *Gelidiopsis* | n/s | Full-L > control | Full-L < control | – |
| | | Full-S > control | Full-L < Full-S | |
| *Gelidium* | n/s | Full-S > control | n/s | *Dh* |
| | | Full-L < Full-S | | |
| *Grateloupia* | n/s | n/s | n/s | *Cm** |
| *Hypnea* | n/s | n/s | n/s | *As, Dh, Cm*, Ap** |
| *Polysiphonia* | n/s | n/a | n/a | – |
| *Ulva lactuca* | n/s | n/a | n/a | *Cm** |

[A]Significant but did not meet *a prior* criteria

[+]Herbivore species were *Cm = Chelonia mydas* (green turtle), *As = Abudefduf saxatilis* (sergeant major), *Ap = Archosargus probatocephalus* (sheepshead), *Dh = Diplodus holbrooki* (spottail pinfish), and *Lr = Lagodon rhomboides* (pinfish). Grazing selection data were based on a concurrent study (Chapter 3).

Figures

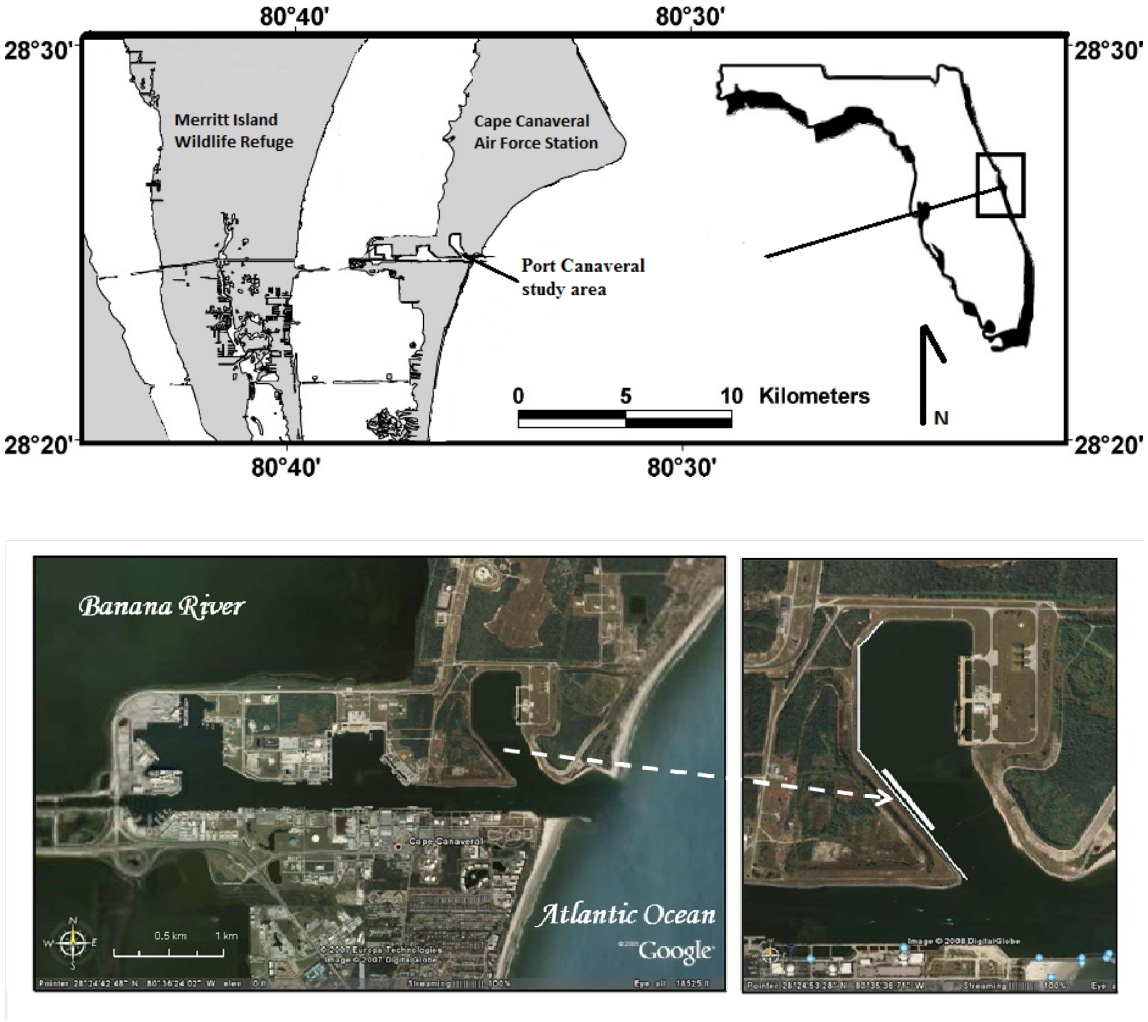


Figure 4.1. Map of the general location of the study (top) with respect to the east coast of Florida, USA. Experiments were conducted within an approximately 100-m area of the southwest wall of the Trident Basin (bottom right). The Basin is located approximately 150 m northwest of the mouth of Port Canaveral Inlet in Cape Canaveral, Florida (bottom left; 28°24´N, 80°35´W). Image from ©2013 Google earth.

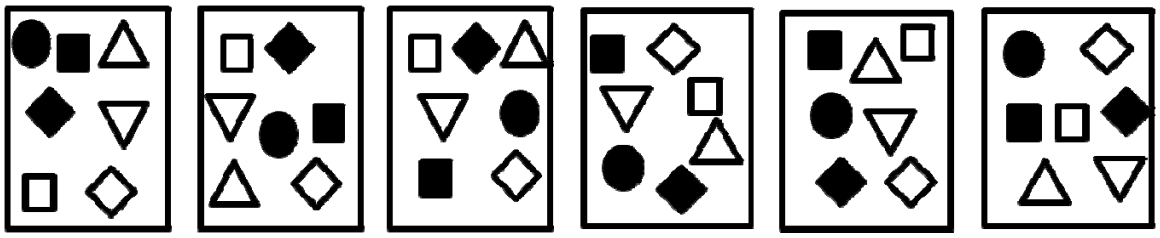

Figure 4.2. Example of the randomized block design for exclusion experiments. Each block (n = 6) contained a large-mesh treatment cage (■) and small-mesh treatment cage (◆), controls for treatment effects of reduced light for large- and small-mesh sizes (□, ◇; respectively), controls for the treatment effects of reduced water flow for large and small-mesh sizes (△ and▽; respectively), and a control (●).

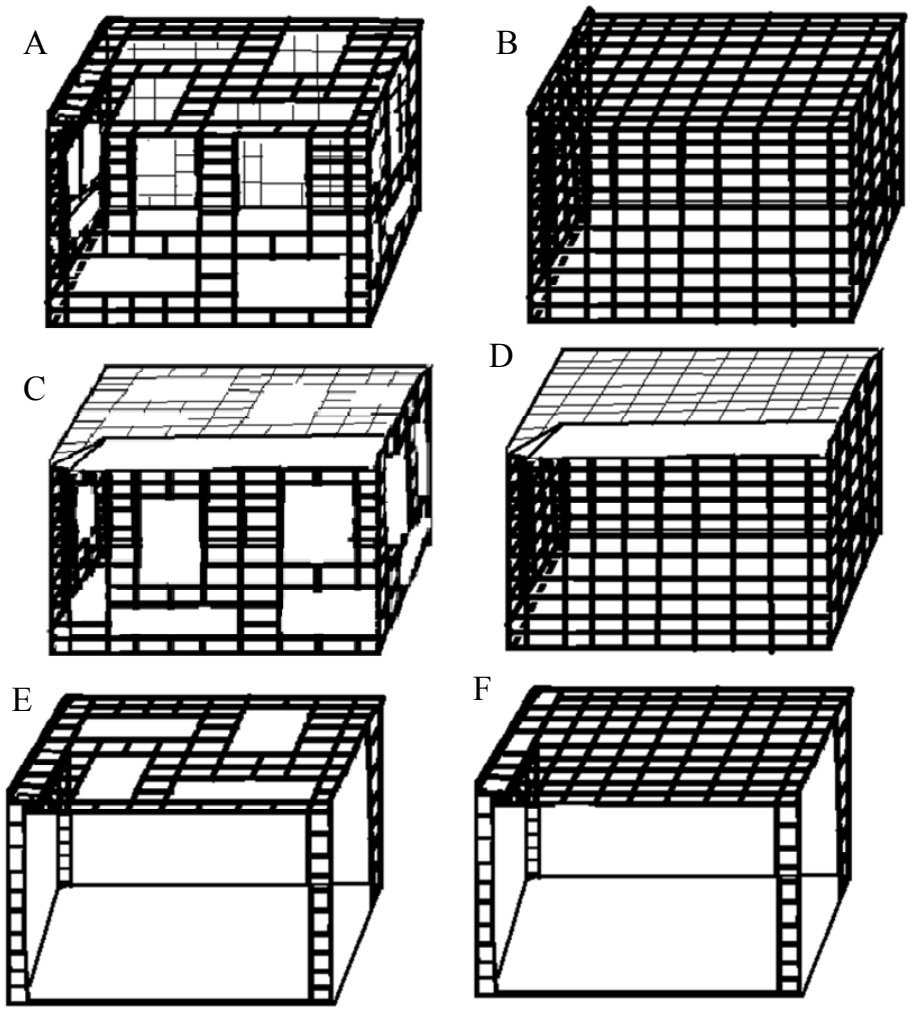


Figure 4.3. Cage designs of the treatment (A, B, full cages) and cage controls (C-F, partial cages) for exclusion experiments. Large-mesh cages (A) were designed to exclude

juvenile green turtles. Small-mesh cages (B) were designed to exclude large fish (>2.5 cm) and juvenile green turtles. Cages to control for treatment effects of light reduction were large-mesh (C) and small-mesh (D) cages. Cages to control for treatment effects of reduced water flow were large-mesh (E) and small-mesh (F). For the uncaged control, a rock boulder was marked with a labeled tag that was attached to a 0.5-mm bungee cord. The cord was placed near the edge of the boulder and wrapped in a vertical direction around the boulder.

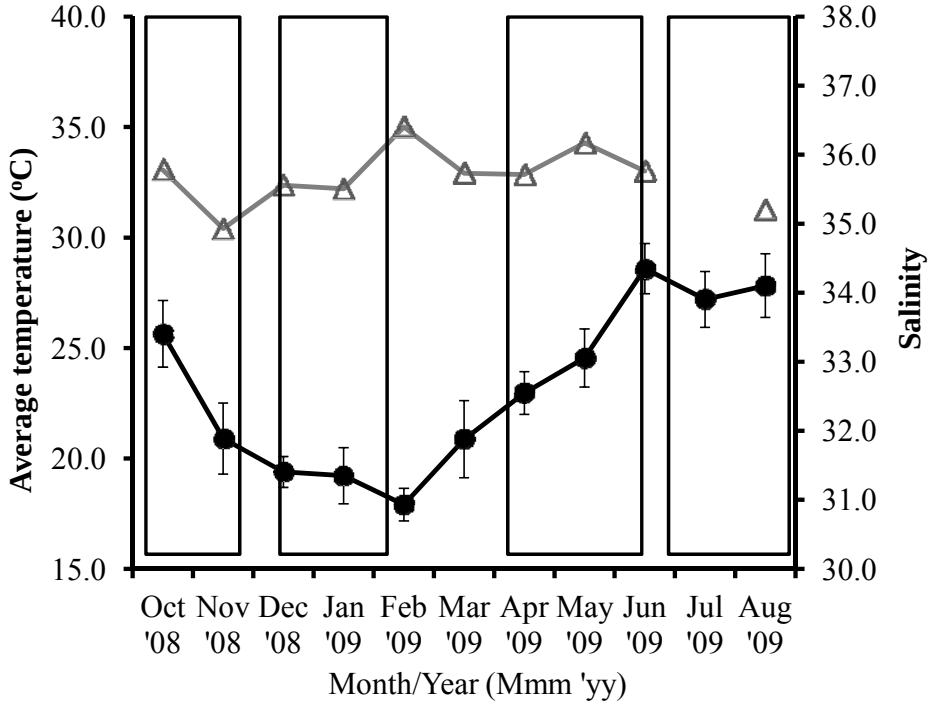


Figure 4.4. Temperature (black circles and line) and salinity (open triangles and gray line) averages (± SD) during experiments conducted from October 2008-August 2009 at the Trident Basin in Port Canaveral, Cape Canaveral, Florida. The super-imposed rectangles indicate the approximate time period experiments were conducted (n = 4; fall = October 2-November 23, winter = December 5-February 5, spring = March 31-June 8, summer = June 23-August 10).

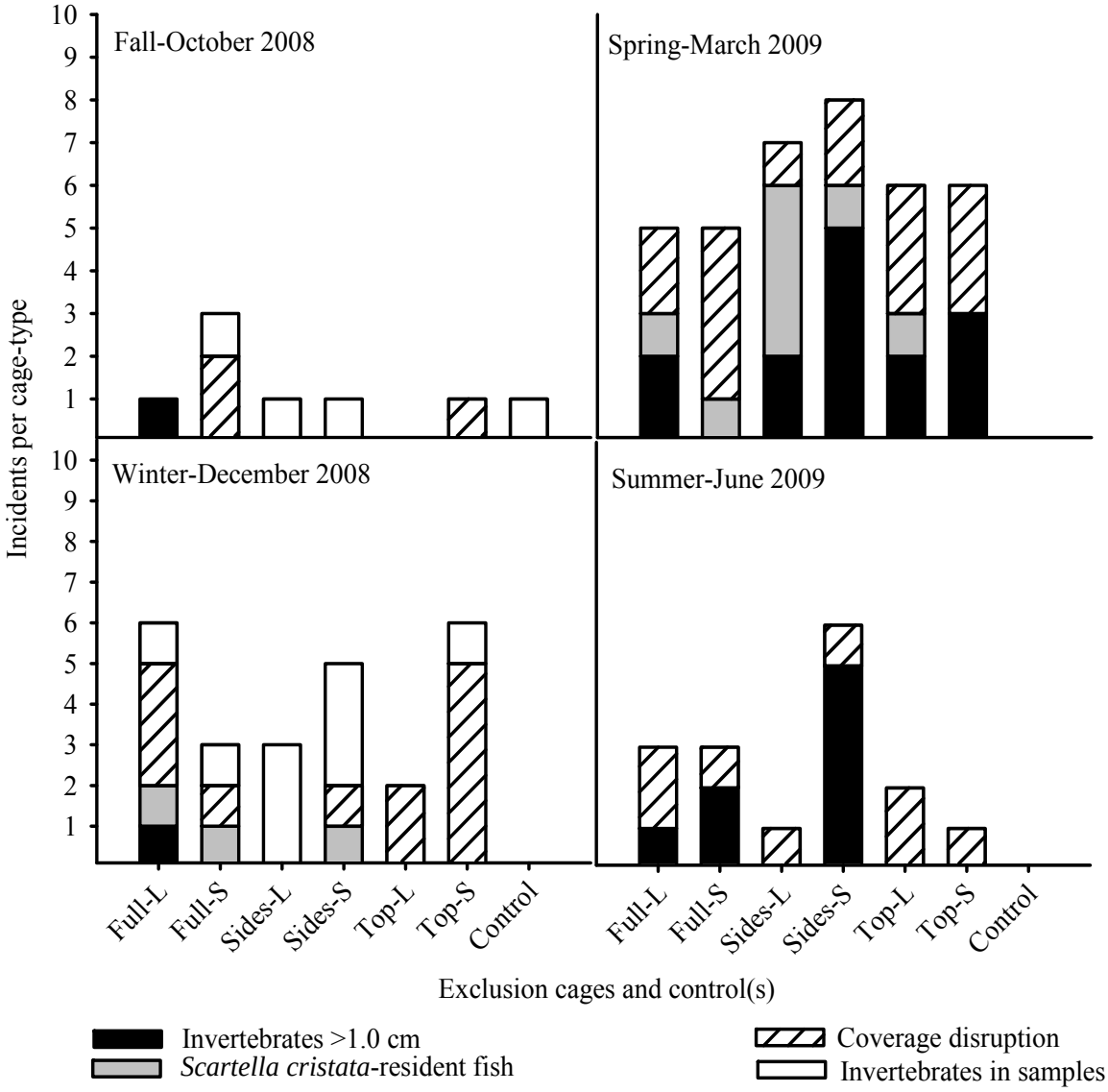


Figure 4.5. The number and types of disturbances in exclusion experiments conducted for four separate periods (or season) for approximately 7 weeks at a time from October 2008-August 2009 in the Trident Basin in Port Canaveral, Cape Canaveral, Florida. "Full-L" (L = large-mesh) treatment cages excluded juvenile green turtles. "Full-S" (S = small-mesh) treatment cages excluded large herbivorous fishes (>2.5cm) and juvenile green turtles. "Sides" and "top" cages were cage controls to measure potential impacts of light reduction and reduced water flow (respectively) in full cages.

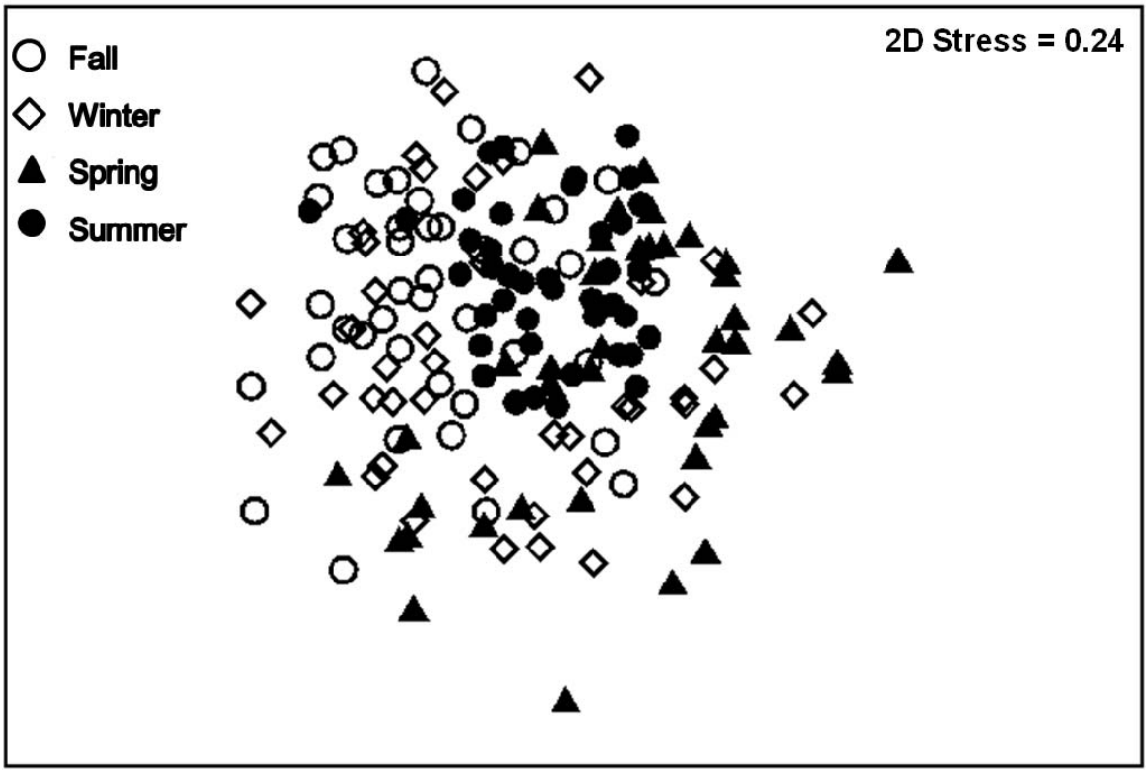


Figure 4.6. Multidimensional scaling (MDS) ordination plot visually representing dissimilarities (differences) among macroalgal species composition among experiments (n = 4) conducted during four seasons from October 2008-August 2009.

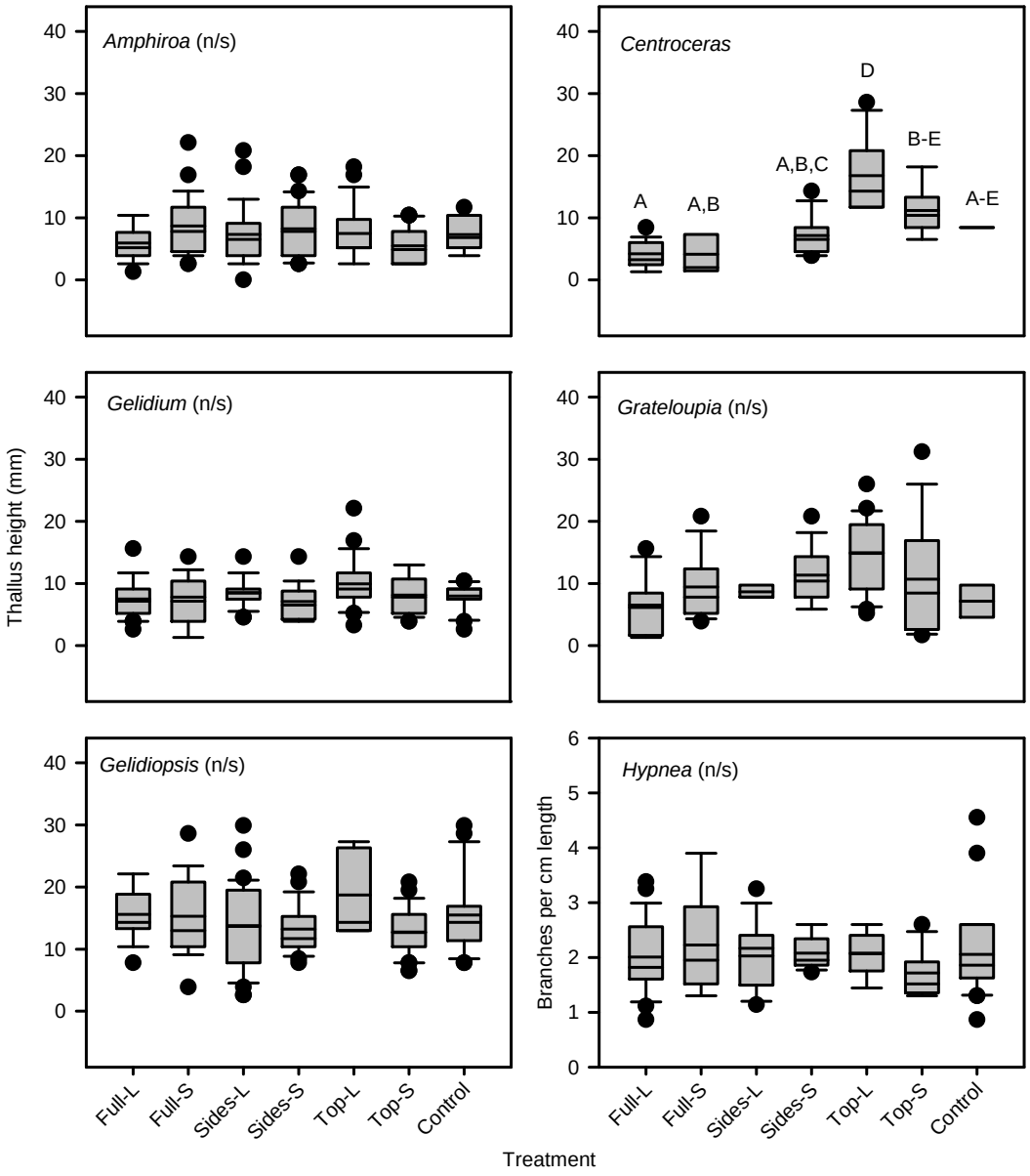


Figure 4.7. Fall (October 3 through November 23, 2008) mean, median, and distribution of thallus height measurements (*Amphiroa fragilissima, Centroceras clavulatum*, *Gelidium crinale*, *Grateloupia filicina, Gelidiopsis planicaulis*, and the number of branches per cm thallus length for *Hypnea spinella* from exclusion experiments. "Full-L" (L = large-mesh) treatment cages excluded juvenile green turtles. "Full-S" (S = small-mesh) treatment cages excluded large herbivorous fishes (>2.5cm) and juvenile green turtles. "Sides" and "Top" cages were cage controls to measure potential impacts of light reduction and reduced water flow (respectively) in full cages. All treatments and control (uncaged) were contrasted using ANOVA. Pairwise comparisons were conducted using Holm-Sidak (critical p-adjusted for multiple tests). n/s = non-significant for all contrasts.

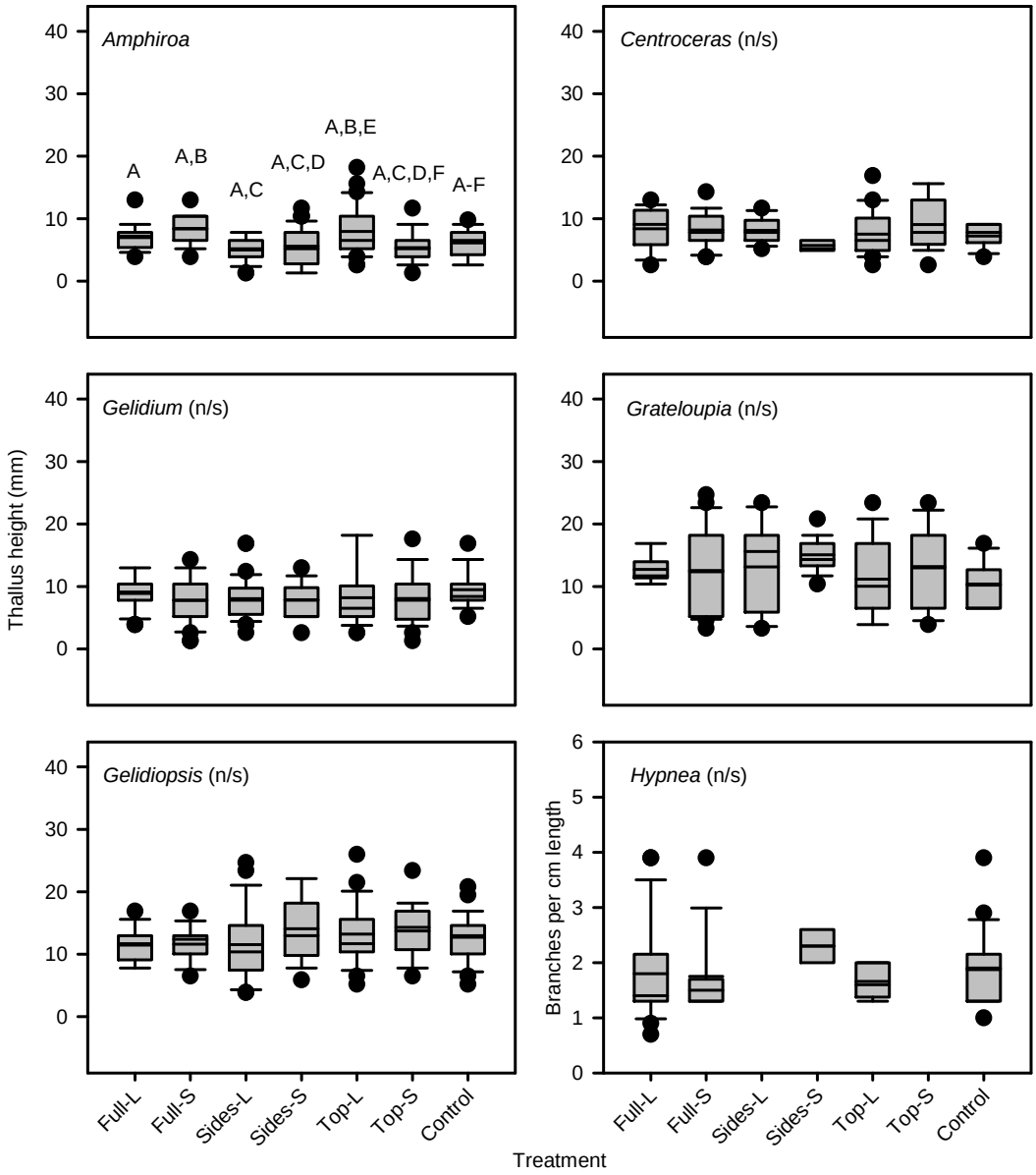


Figure 4.8. Winter (December 2008 through February 2009), mean, median, and distribution of thallus height measurements for *Amphiroa fragilissima, Centroceras clavulatum*, *Gelidium crinale*, *Grateloupia filicina, Gelidiopsis planicaulis*, and the number of branches per cm thallus length of *Hypnea spinella* from exclusion experiments. "Full-L" (L = large-mesh) treatment cages excluded juvenile green turtles. "Full-S" (S = small-mesh) treatment cages excluded large herbivorous fishes (>2.5cm) and juvenile green turtles. "Sides" and "Top" cages were cage controls to measure potential impacts of light reduction and reduced water flow (respectively) in full cages. All treatments and control (uncaged) were contrasted using ANOVA. Pairwise comparisons were conducted using Holm-Sidak (critical p-adjusted for multiple tests). n/s = non-significant for all contrasts.

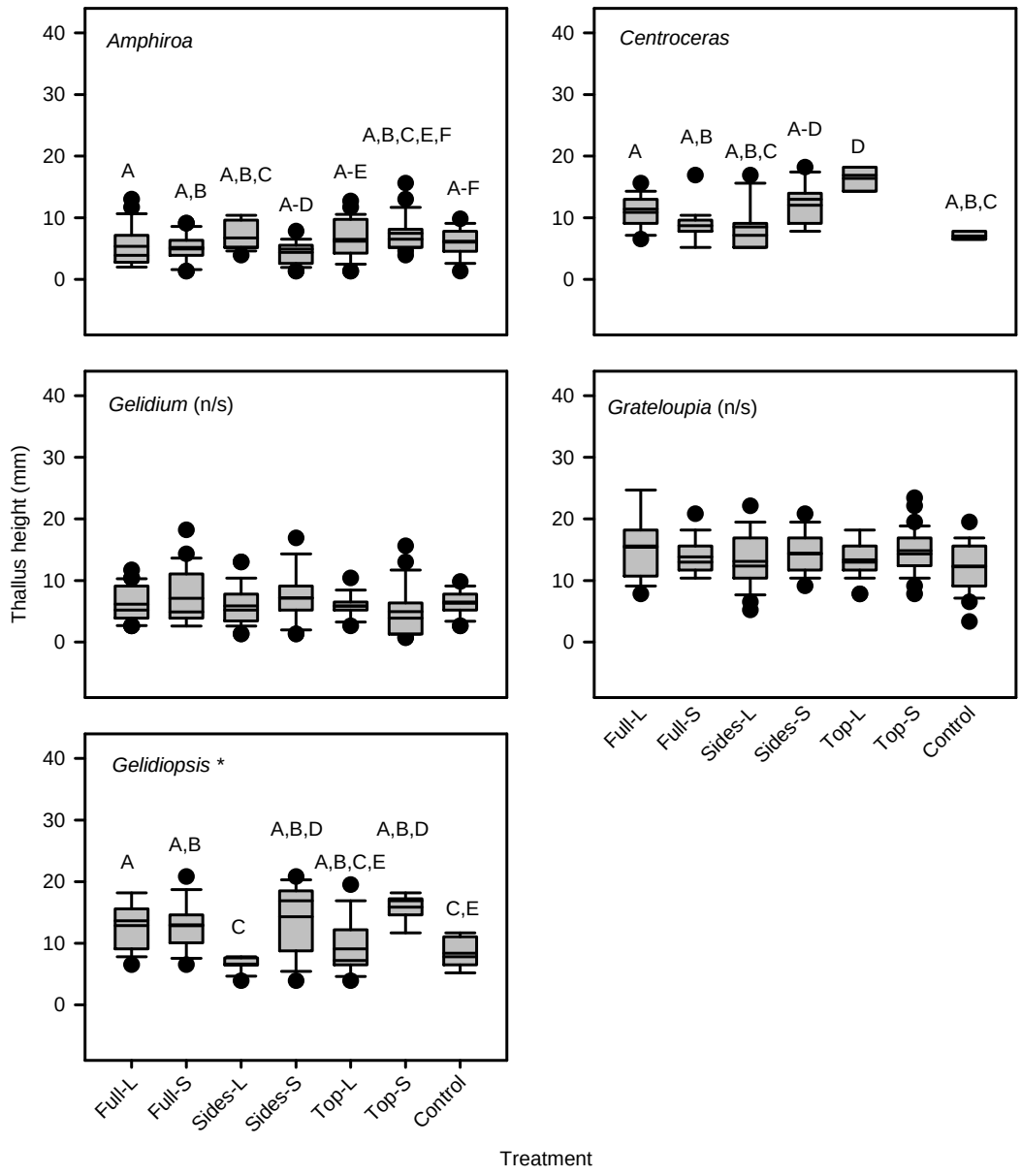


Figure 4.9. Spring (March through May 2009) mean, median, and distribution of thallus height measurements for *Amphiroa fragilissima, Centroceras clavulatum*, *Gelidium crinale*, *Grateloupia filicina,* and *Gelidiopsis planicaulis* from exclusion experiments. "Full-L" (L = large-mesh) treatment cages were designed to exclude juvenile green turtles."Full-S" (S = small-mesh) treatment cages excluded large herbivorous fishes (>2.5cm) and juvenile green turtles. "Sides" and "Top" cages were cage controls to measure potential impacts of light reduction and reduced water flow (respectively) in full cages. All treatments and control (uncaged) were contrasted using ANOVA. Pairwise comparisons were conducted using Holm-Sidak (critical p-adjusted for multiple tests). n/s = non-significant for all contrasts. * = significant differences were detected between full treatment cages and controls.

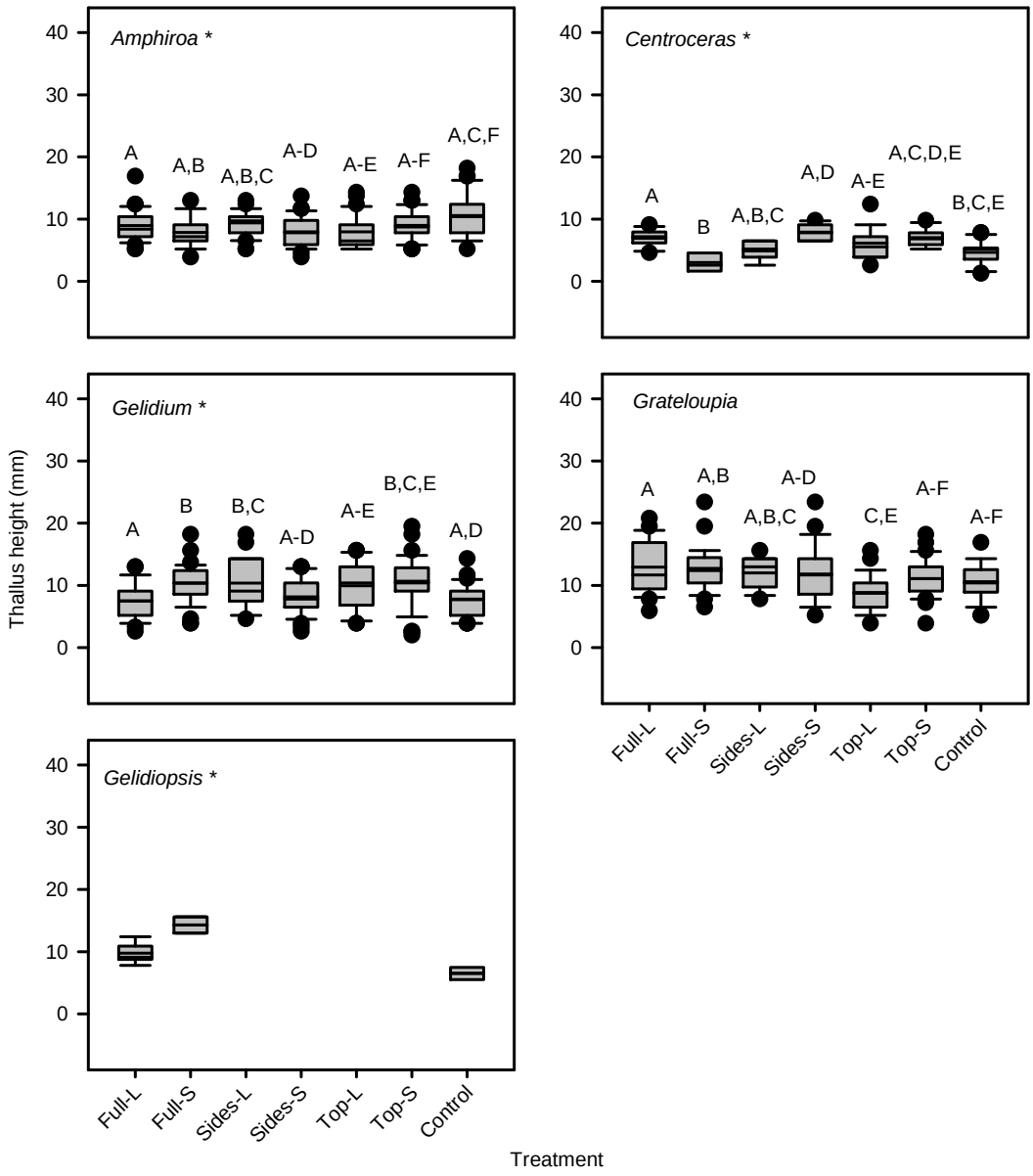


Figure 4.10. Summer (June 2008- August 2008) mean, median, and distribution of thallus height measurements for *Amphiroa fragilissima, Centroceras clavulatum*, *Gelidium crinale*, *Grateloupia filicina,* and *Gelidiopsis planicaulis* from exclusion experiments. "Full-L" (L = large-mesh) treatment cages excluded juvenile green turtles. "Full-S" (S = small-mesh) treatment cages excluded large herbivorous fishes (>2.5cm) and juvenile green turtles. "Sides" and "Top" cages were cage controls to measure potential impacts of light reduction and reduced water flow (respectively) in full cages. All treatments and control (uncaged) were contrasted using ANOVA. Pairwise comparisons were conducted using Holm-Sidak (critical p-adjusted for multiple tests). * = significant differences were detected between full treatment cages and controls.

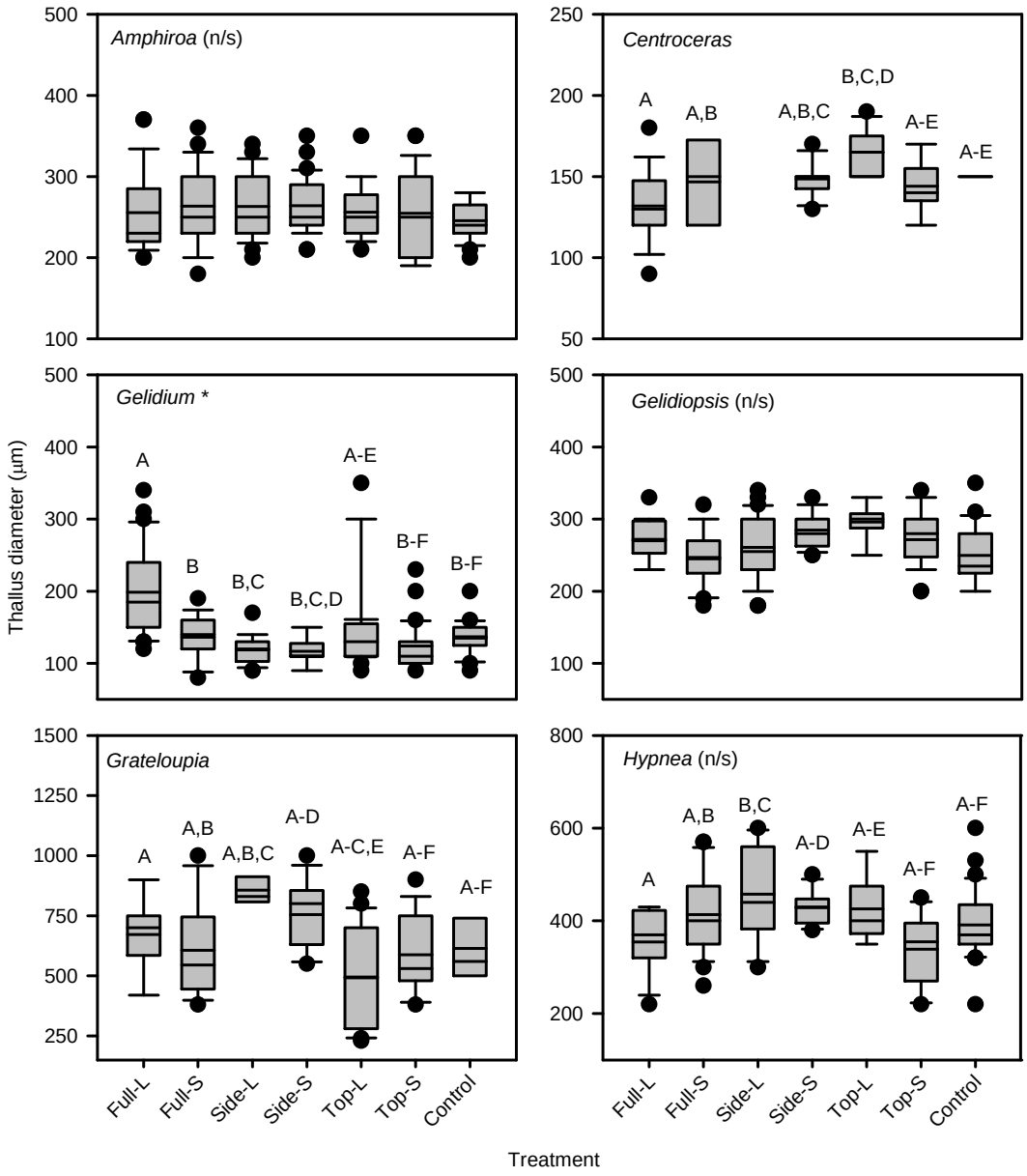


Figure 4.11. Fall (October 3 through November 23, 2008) mean, median, and distribution of thallus diameter measurements for *Amphiroa fragilissima, Centroceras clavulatum*, *Gelidium crinale*, *Grateloupia filicina, Gelidiopsis planicaulis*, and *Hypnea spinella* from exclusion experiments. "Full-L" (L = large-mesh) treatment cages excluded juvenile green turtles. "Full-S" (S = small-mesh) treatment cages excluded large herbivorous fishes (>2.5cm) and juvenile green turtles. "Sides" and "Top" cages were controls to measure potential impacts of light reduction and reduced water flow (respectively) in full cages. All treatments and control (uncaged) were contrasted using ANOVA. Pairwise comparisons were conducted using Holm-Sidak (critical p-adjusted for multiple tests). n/s = non-significant for all contrasts. * = significant differences were detected between full treatment cages and controls.

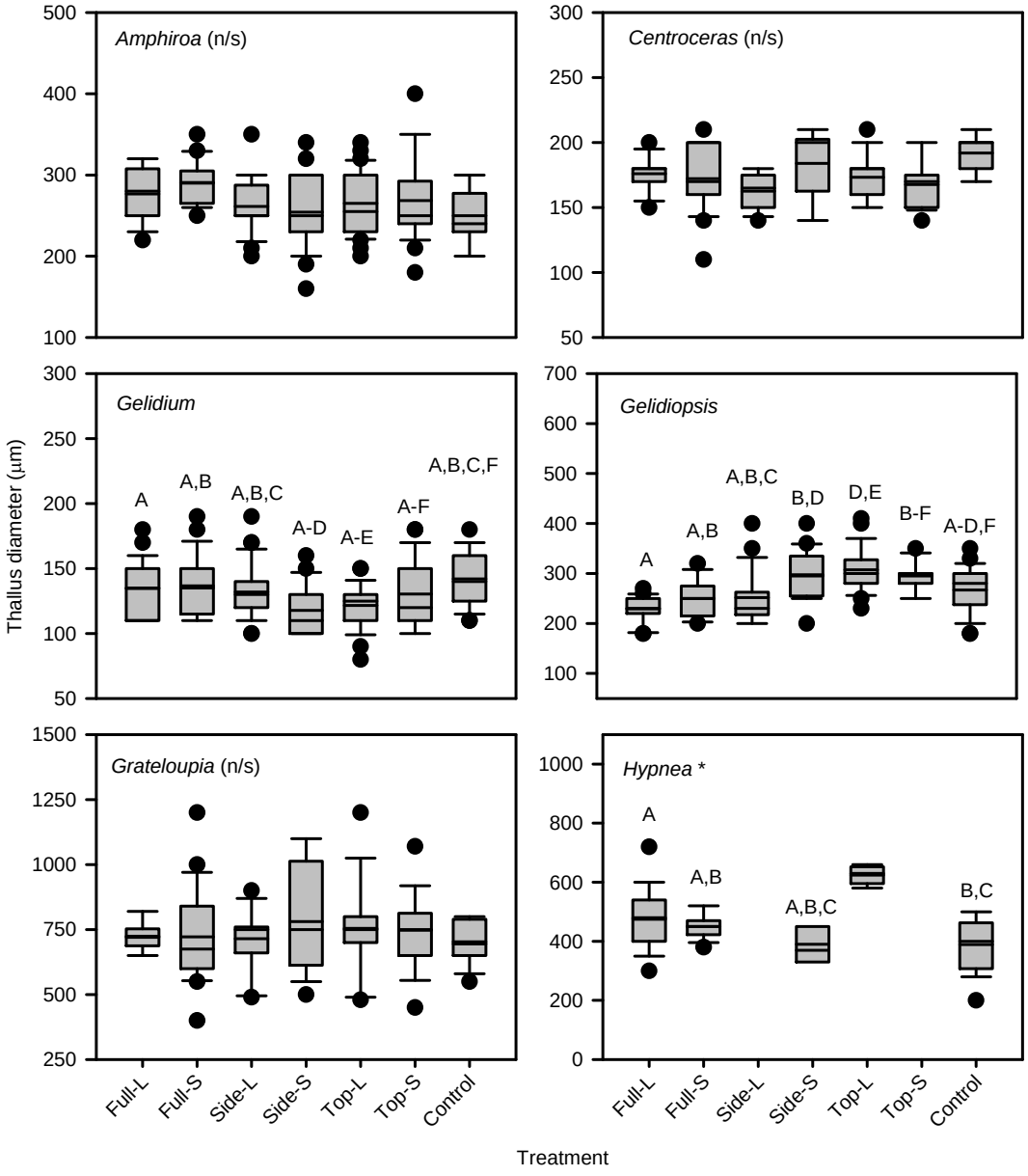


Figure 4.12. Winter (December 2008 - February 2009) mean, median, and distribution of thallus diameter measurements for *Amphiroa fragilissima, Centroceras clavulatum*, *Gelidium crinale*, *Grateloupia filicina, Gelidiopsis planicaulis*, and *Hypnea spinella* from exclusion experiments. "Full-L" (L = large-mesh) treatment cages excluded juvenile green turtles. "Full-S" (S = small-mesh) treatment cages excluded large herbivorous fishes (>2.5cm) and juvenile green turtles. "Sides" and "Top" cages were cage controls to measure potential impacts of light reduction and reduced water flow (respectively) in full cages. All treatments and control (uncaged) were contrasted using ANOVA. Pairwise comparisons were conducted using Holm-Sidak (critical p-adjusted for multiple tests). n/s = non-significant for all contrasts. * = significant differences were detected between full treatment cages and controls.

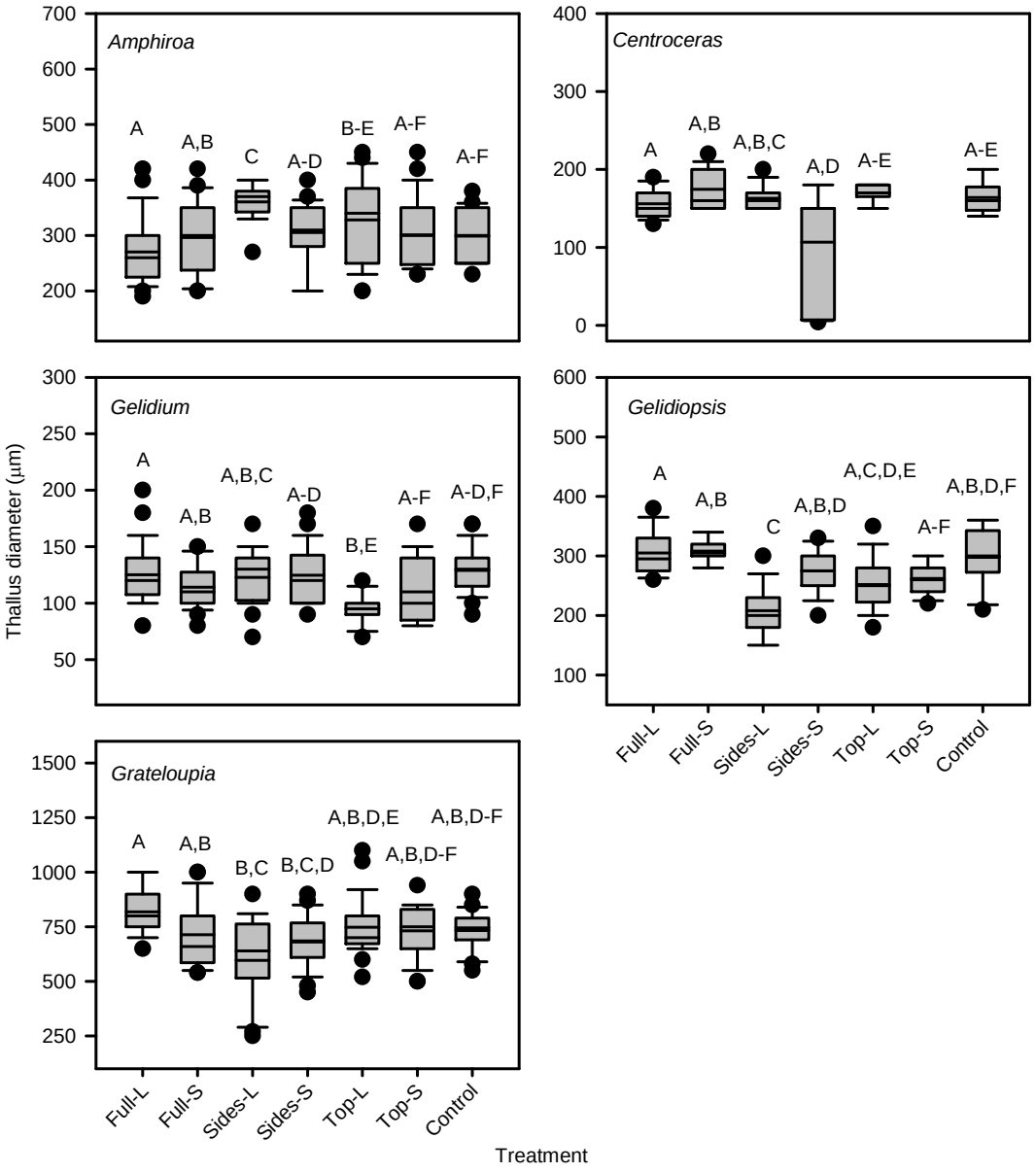


Figure 4.13. Spring (March through May 2009) mean, median, and distribution of thallus diameter measurements for *Amphiroa fragilissima, Centroceras clavulatum*, *Gelidium crinale*, *Grateloupia filicina,* and *Gelidiopsis planicaulis* from exclusion experiments. "Full-L" (L = large-mesh) treatment cages excluded juvenile green turtles. "Full-S" (S = small-mesh) treatment cages excluded large herbivorous fishes (>2.5cm) and juvenile green turtles. "Sides" and "Top" cages were cage controls to measure potential impacts of light reduction and reduced water flow (respectively) in full cages. All treatments and control (uncaged) were contrasted using ANOVA. Pairwise comparisons were conducted using Holm-Sidak (critical p-adjusted for multiple tests).

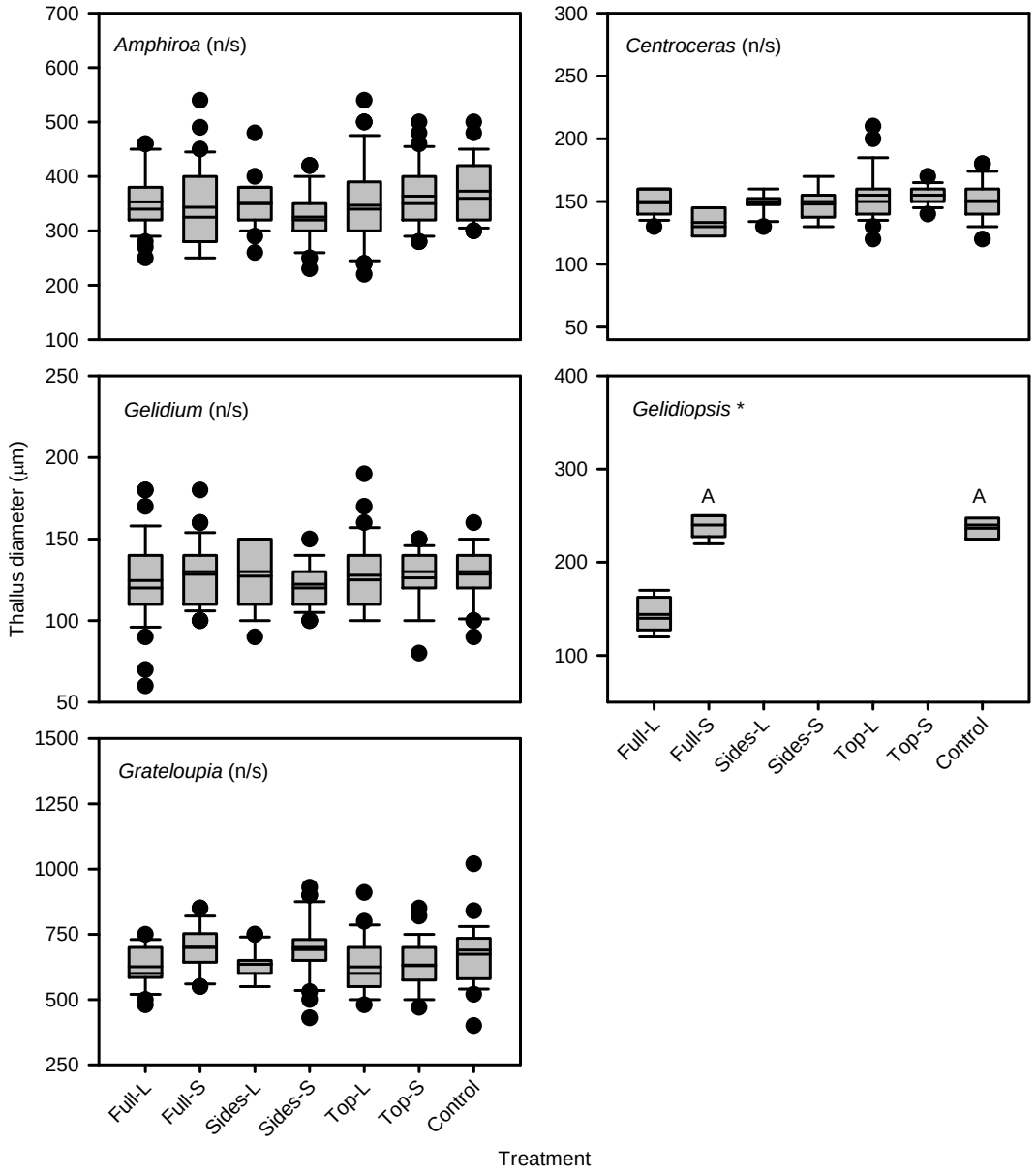


Figure 4.14. Summer (June 2008- August 2008) mean, median, and distribution of thallus diameter measurements for *Amphiroa fragilissima*, *Centroceras clavulatum*, *Gelidium crinale*, *Grateloupia filicina,* and *Gelidiopsis planicaulis* from exclusion experiments. "Full-L" (L = large-mesh) treatment cages excluded juvenile green turtles. "Full-S" (S = small-mesh) treatment cages excluded large herbivorous fishes (>2.5cm) and juvenile green turtles. "Sides" and "Top" cages were cage controls to measure potential impacts of light reduction and reduced water flow (respectively) in full cages. All treatments and control (uncaged) were contrasted using ANOVA. Pairwise comparisons were conducted using Holm-Sidak (critical p-adjusted for multiple tests). n/s = non-significant for all contrasts. * = significant differences were detected between full treatment cages and controls.

Acknowledgements

Access to publicly restricted areas of CCAFS and Trident Basin were granted by US Air Force - 45th Space Wing and US NAVY. Special thanks to D. George and A. Chambers for their reviews of materials and M. Carroll and M. O'Quinn for assistance with site accessibility. Many thanks to L. Ehrhart, W. Redfoot and UCF's Marine Turtle Research Group for their camaraderie and support with the juvenile green turtle aspect of this work and the many hours spent netting turtles in all kinds of weather conditions. Field support for this project was generously supported by D. Scheidt and C. Garreau as well as E. Reyier, S. Gann, R. Lowers, and C. Hall. Dynamac and IHA provided time and materials for this project. I appreciate the assistance of W. Freshwater (University of North Carolina, Wilmington) in identification of difficult Gelidiales species and L. Jennings for taking the time to help identify invertebrate species. Thank you to my dissertation committee members, M.D. Hanisak, L. Ehrhart, C.E. Proffitt, T. Sutton, C. Hughes, and R. Virnstein, for their guidance and contributions to both the proposed project and final manuscript review.

References

Agan, J.C., and R.L. Lehman. 2001. Seaweed abundance and diversity in high energy and low energy areas at Port Aransas, Texas jetties. Journal of Phycology, 37:4.

Airoldi, L. 1998. Roles of disturbance, sediment stress, and substratum retention of spatial dominance in algal turf. Ecology, 79:2759-2770.

Airoldi, L. 2000. Effects of disturbance, life histories, and overgrowth on coexistence of algal crusts and turfs. Ecology, 8:798-814.

Anderson, M.J. 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecology, 26:32-46.

Anderson, W.W., and J.W. Gehringer. 1965. Biological-statistical census of the species entering fisheries in the Cape Canaveral area. United States Fish and Wildlife Service. USDOI Technical Report. Special Scientific Report - Fisheries No. 514. 79.

Arthur, K.E., and G.H. Balazs. 2008. A comparison of immature green turtles (*Chelonia mydas*) diets among seven sites in the main Hawaiian Islands. Pacific Science, 62:205-217.

Briggs, J.C. 1958. A list of Florida fishes and their distribution. Bulletin of the Florida State Museum Biological Sciences, 2:223-319.

Briggs, J.C. 1974. Marine Zoogeography. McGraw-Hill, NewYork, NY. 475 p.

Clarke, K.R., and R.N. Gorley. 2006. Primer v6: user manual and tutorial. Primer-E Ltd, Plymouth Place, UK.

Clarke, K.R., and R.H. Green. 1988. Statistical design and analyses for a 'biological effects' study. Marine Ecology Progress Series, 46:213-226.

Clarke, K.R., and R.M. Warwick. 2001. Change in marine communities: an approach to statistical analysis and interpretation, 2nd edition. PRIMER-E Ltd., Plymouth PL.

Copertino, M., S.D. Connell, and A. Cheshire. 2005. The prevalence and production of turf-forming algae on a temperate subtidal coast. Phycologia, 44:241-248.

Copertino, M.S., A. Cheshire, and J. Watling. 2006. Photoinhibition and photoacclimation of turf algal communities on a temperate reef, after *in situ* transplantation experiments. Journal of Phycology, 42:580-592.

Coyne, M.S. 1994. Feeding ecology of subadult green sea turtles in south Texas waters. Master's, Texas A & M University, College Station. 76 p.

Dawes, C.J. 1974. Marine Algae of the West Coast of Florida. University of Miami Press, Coral Gables, Florida. 201 p.

Dawes, C.J., and A.C. Mathieson. 2009. The Seaweeds of Florida. University Press of Florida, Gainesville, Florida. 591 p.

Forbes, G.A. 1999. Diet sampling and diet component analysis. P. 144-148 in Research and management techniques for the conservation of sea turtles, Eckert, K.L., K.A. Bjorndal, F.A. Abreu-Grobois, and M. Donnelly (Eds.). SSC/IUCCN Marine Turtle Specialist Group, Washington, D.C.

Goatley, C.H.R., A.S. Hoey, and D.R. Bellwood. 2012. The role of turtles as coral reef macroherbivores. PLoS ONE, 7:e39979.

Hastings, R.W. 1979. The origin and seasonality of the fish fauna on a new jetty in the northeastern Gulf of Mexico. Bulletin of Florida State Museum: BioIogical Sciences, 24:1-122.

Hay, M.E. 1981. The functional morphology of turf-forming seaweeds: persistence in stressful marine habitats. Ecology, 62:739-750.

Hay, M.E., and J.P. Sutherland. 1988. The ecology of rubble structures of the South Atlantic Bight: a community profile. U.S. Fish and Wildlife Service Biological Report 85 (7.20). 67.

Hurd, C.L. 2000. Water motion, marine macroalgal physiology, and production. Journal of Phycology, 36:453-472.

Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs, 54:187-211.

Kingsford, M.J., and C.N. Battershill. 1998. Studying Temperate Marine Environments: A Handbook for Ecologists. Canterbury University Press, Christchurch, New Zealand. 335 p.

Krebs, C.J. 1989. Ecological Methodology. Harper-Collins Publishers, New York. 654 p.

Krebs, C.J. 1999. Ecological Methodology: second edition. Benjamin/Cummings, Menlo Park. 620 p.

Kubis, S., M. Chaloupka, L. Ehrhart, and M. Bresette. 2009. Growth rates of juvenile green turtles *Chelonia mydas* from three ecologically distinct foraging habitats along the east central coast of Florida, USA. Marine Ecology Progress Series, 389:257–269.

Lewis, S. 1985. Herbivory on coral reefs: algal susceptibility to herbivorous fishes. Oecologia, 65:370-375.

Lewis, S.M., J.N. Norris, and R.B. Searles. 1987. The regulation of morphological plasticity in tropical reef algae by herbivory. Ecology, 68:636-641.

Littler, D.S., and M.M. Littler. 2000. Caribbean Reef Plants. OffShore Graphics, Inc., Washington, D.C. 542 p.

Littler, D.S., M.M. Littler, and M.D. Hanisak. 2008. Submersed Plants of the Indian River Lagoon. OffShore Graphics, Inc., Washington, D.C. 286 p.

Littler, M.M., D.S. Littler, and P.R. Taylor. 1983. Evolutionary strategies in a tropical barrier reef system: functional-form groups of marine macroalgae. Journal of Phycology, 19:229-237.

Lobban., C.S., and P.J. Harrison. 1994. Seaweed ecology and physiology. Cambridge University Press, Cambridge, UK. 366 p.

McBride, R.A., and T.F. Moslow. 1991. Origin, evolution, and distribution of shoreface sand ridges, Atlantic inner shelf, USA. Marine Geology, 97:57-85.

McCauley, S.J., and K.A. Bjorndal. 1999. Conservation implications of dietary dilution from debris ingestion: sublethal effects in post-hatchling loggerhead sea turtles. Conservation Biology, 13:925-929.

McDermid, K.J., B. Stuercke, and G.H. Balazs. 2007. Nutritional composition of marine plants in the diet of the green sea turtle (*Chelonia mydas*) in the Hawaiian Islands. Bulletin of Marine Science, 81:55-71.

Moran, K.L., and K.A. Bjorndal. 2005. Simulated green turtle grazing affects structure and productivity of seagrass pastures. Marine Ecology-Progress Series, 305:235-247.

Moran, K.L., and K.A. Bjorndal. 2007. Simulated green turtle grazing affects nutrient composition of the seagrass *Thalassia testudinum*. Marine Biology, 150:1083-1092.

Mumby, P.J., K.R. Clarke, and A.R. Harbone. 1996. Weighting species abundance estimates for marine resource assessment. Aquatic Conservation: Marine and Freshwater Ecosystems, 6:115-120.

Randall, J.E. 1961. Overgrazing of algae by herbivorous marine fishes. Ecology, 42:812.

Randall, J.E. 1965. Grazing effect on seagrasses by herbivorous reef fishes in the West Indies. Ecology, 46:255-260.

Redfoot, W.E. 1997. Population structure and feeding ecology of green turtles utilizing the Trident Submarine Basin, Cape Canaveral, Florida as developmental habitat. Master's, University of Central Florida, Orlando. 72 p.

Redfoot, W.E., and L.M. Ehrhart. 2013. Trends in size class distribution, recaptures, and abundance of juvenile green turtles (*Chelonia mydas*) utilizing a rock riprap lined embayment at Port Canaveral, Florida, U.S.A. as developmental habitat. Chelonian Conservation and Biology, 12:252-261.

Reisser, J., M. Proietti, I. Sazima, P. Kinas, P, Horta, and E. Secchi. 2013. Feeding ecology of the green turtle (*Chelonia mydas*) at rocky reefs in western South Atlantic. Marine Biology 160:3169-3179.

Renaud, M.L., J.A. Carpenter, J.A. Williams, and S.A. Manzella-Tirpak. 1995. Activities of juvenile green turtles, *Chelonia mydas*, at a jettied pass. Fishery Bulletin, 93:586-593.

Reyier, E.A., D.M. Scheidt, K.G. Holloway-Adkins, C.M. Garreau, R.H. Lowers, and S.L. Gann. 2010. A characterization of biological resources within the Cape Canaveral Air Force Station Trident Submarine Basin, and adjacent marine waters of Port Canaveral, Florida (May 2008-April 2010). 45 CES/CEAN. 60.

Rosati, J.D., and N.C. Kraus. 2009. Sea level rise and consequences for navigable coastal inlets. Shore & Beach, 77:1-7.

Rueness, J., and T. Tananger. 1984. Growth in culture of four red algae from Norway with potential for mariculture. Hydrobiologia, 116-117:303-307.

Salahuddin, B. 2006. The Marine Environmental Impacts of Artificial Island Construction, Dubai, UAE, Duke, Durham, NC. 96 p.

Schneider, C.W., and R.B. Searles. 1991. Seaweeds of the Southeastern United States: Cape Hatteras to Cape Canaveral. Duke University Press, Durham, North Carolina. 553 p.

Searles, R.B. 1984. Seaweed biogeography of the mid-Atlantic coast of the United States. Helgoland Marine Research, 38:259-271.

Seminoff, J.A., A. Resendiz, and W.J. Nichols. 2002. Diet of east Pacific green turtles (*Chelonia mydas*) in the central Gulf of California, México. Journal of Herpetology, 36:447-453.

Shaver, D.J. 1994. Relative abundance, temporal patterns, and growth of sea turtles at the Mansfield Channel, Texas. Journal of Herpetology, 28:491-497.

Smith, C.M., and J.A. Berry. 1986. Recovery of photosynthesis after exposure of intertidal algae to osmotic and temperature stresses - comparative-studies of species with differing distributional limits. Oecologia, 70:6-12.

SYSTAT. 2008. SigmaPlot for Windows version 11.0. Systat Software, San Jose, CA.

US Dept of Commerce N. National Data Buoy Center-Station TRDF1-8721604-Trident Pier, FL [Internet]. weather.gov. Available from: http://www.ndbc.noaa.gov/station_page.php?station=TRDF1.

van Blaricom, G.R. 1982. Experimental analyses of structural regulation in a marine sand community exposed to oceanic swell. Ecological Monographs, 52:283-305.

Virnstein, R.W. 1978. Predator caging experiments in soft sediments: caution advised. P. 261-273 in Estuarine Interactions, Wiley, M.L. (Ed.). Academic Press, Inc., New York, NY.

Webster, R.M. 1974. An inexpensive sampler for studying the microbiology of river mud. Limnology and Oceanography, 19:159-161.

Weibel, E.R., G.S. Kistler, and W. F. 1966. Practical stereological methods for morphometric cytology. The Journal of Cell Biology, 30:23-38.

Witherington, B., M.J. Bresette, and R.M. Herren. 2006. *Chelonia mydas* - Green Turtle. P. 90-104 in Chelonian Research Monographs, Meylan, P.A. (Ed.). Chelonian Research Monographs.

Appendix

Table A4.1. Similarity percentage (SIMPER) procedure results for contrasts (n = 6; a-f) among experiments (n = 4). Species listed are ones that contributed >70% to differences in the percent composition of macroalgae among experiments conducted at the Trident Basin at Port Canaveral, Cape Canaveral, Florida. Experiments were conducted for approximately 7 weeks each in fall (October 2008), winter (December 2008), spring (March 2009), and summer (June 2009).

(a)

| Fall vs. Winter | | | | | |
|---|---|---|---|---|---|
| Mean dissimilarity = 62.02 | Mean Percent Composition | | Dissimilarity | | Contribution |
| Species | Fall | Winter | Mean | SD | (%) |
| *Gelidium crinale* | 20.92 | 15.06 | 10.99 | 1.22 | 17.73 |
| *Gelidiopsis planicaulis* | 19.36 | 19.23 | 10.26 | 1.24 | 16.55 |
| *Hypnea spinella* | 18.22 | 9.27 | 9.3 | 1.04 | 15.00 |
| *Amphiroa fragilissima* | 22.97 | 18.12 | 8.67 | 1.36 | 13.99 |
| *Grateloupia filicina* | 7.26 | 12.26 | 7.5 | 0.84 | 12.09 |
| *Jania adhaerens* | 3.28 | 9.28 | 4.87 | 1.07 | 7.85 |
| *Centroceras clavulatum* | 4.18 | 8.32 | 4.79 | 0.83 | 7.72 |

(b)

| Fall vs. Spring | | | | | |
|---|---|---|---|---|---|
| Mean dissimilarity = 70.67 | Mean Percent Composition | | Dissimilarity | | Contribution |
| Species | Fall | Spring | Mean | SD | (%) |
| *Grateloupia filicina* | 7.26 | 33.88 | 15.37 | 1.2 | 21.74 |
| *Gelidium crinale* | 20.92 | 9.51 | 9.67 | 1.26 | 13.68 |
| *Gelidiopsis planicaulis* | 19.36 | 5.79 | 9.63 | 1.05 | 13.62 |
| *Amphiroa fragilissima* | 22.97 | 13.03 | 9.31 | 1.35 | 13.18 |
| *Hypnea spinella* | 18.22 | 6.57 | 8.86 | 1.03 | 12.54 |
| *Centroceras clavulatum* | 4.18 | 17.29 | 8.78 | 0.84 | 12.42 |
| *Jania adhaerens* | 3.28 | 8.04 | 4.65 | 0.76 | 6.58 |

(c)

| Winter vs. Spring | | | | | |
|---|---|---|---|---|---|
| Mean dissimilarity = 68.70 | Mean Percent Composition | | Dissimilarity | | Contribution |
| Species | Winter | Spring | Mean | SD | (%) |
| *Grateloupia filicina* | 12.26 | 33.88 | 15.49 | 1.23 | 22.54 |
| *Gelidiopsis planicaulis* | 19.23 | 5.79 | 9.37 | 1.13 | 13.63 |
| *Centroceras clavulatum* | 8.32 | 17.29 | 9.13 | 0.92 | 13.29 |
| *Gelidium crinale* | 15.06 | 9.51 | 8.73 | 0.94 | 12.7 |
| *Amphiroa fragilissima* | 18.12 | 13.03 | 8.12 | 1.22 | 11.82 |
| *Hypnea spinella* | 9.27 | 6.57 | 5.97 | 0.83 | 8.68 |
| *Jania adhaerens* | 9.28 | 8.04 | 5.73 | 1.06 | 8.35 |

(d)

| Fall vs. Summer | | | | | |
|---|---|---|---|---|---|
| Mean dissimilarity = 56.40 | Mean Percent Composition | | Dissimilarity | | Contribution |
| Species | Fall | Summer | Mean | SD | (%) |
| *Gelidiopsis planicaulis* | 19.36 | 4.38 | 9.96 | 1.02 | 17.66 |
| *Amphiroa fragilissima* | 22.97 | 29.97 | 8.88 | 1.29 | 15.75 |
| *Gelidium crinale* | 20.92 | 12.82 | 8.8 | 1.36 | 15.6 |
| *Hypnea spinella* | 18.22 | 16.55 | 8.61 | 1.2 | 15.27 |
| *Grateloupia filicina* | 7.26 | 18.29 | 8.3 | 1.44 | 14.72 |
| *Centroceras clavulatum* | 4.18 | 6.76 | 4.05 | 1.04 | 7.18 |
| *Jania adhaerens* | 3.28 | 6.23 | 3.77 | 0.9 | 6.68 |

(e)

Winter vs. Spring

| Mean dissimilarity = 61.14 | Mean Percent Composition | | Dissimilarity | | Contribution |
|---|---|---|---|---|---|
| Species | Winter | Spring | Mean | SD | (%) |
| *Gelidiopsis planicaulis* | 19.23 | 4.38 | 9.84 | 1.12 | 16.09 |
| *Grateloupia filicina* | 12.26 | 18.29 | 9.52 | 1.37 | 15.57 |
| *Amphiroa fragilissima* | 18.12 | 29.97 | 9.51 | 1.3 | 15.55 |
| *Gelidium crinale* | 15.06 | 12.82 | 8.75 | 1.11 | 14.32 |
| *Hypnea spinella* | 9.27 | 16.55 | 8.01 | 1.26 | 13.1 |
| *Centroceras clavulatum* | 8.32 | 6.76 | 4.95 | 0.98 | 8.1 |
| *Jania adhaerens* | 9.28 | 6.23 | 4.83 | 1.19 | 7.9 |

(f)

| Spring vs. Summer<br>Mean dissimilarity = 60.59 | Mean Percent Composition | | Dissimilarity | | Contribution |
|---|---|---|---|---|---|
| Species | Spring | Summer | Mean | SD | (%) |
| *Grateloupia filicina* | 33.88 | 18.29 | 12.83 | 1.18 | 21.17 |
| *Amphiroa fragilissima* | 13.03 | 29.97 | 10.91 | 1.4 | 18.01 |
| *Centroceras clavulatum* | 17.29 | 6.76 | 8.65 | 0.9 | 14.28 |
| *Hypnea spinella* | 6.57 | 16.55 | 7.61 | 1.37 | 12.56 |
| *Gelidium crinale* | 9.51 | 12.82 | 6.43 | 1.28 | 10.62 |
| *Jania adhaerens* | 8.04 | 6.23 | 5.07 | 0.91 | 8.38 |
| *Gelidiopsis planicaulis* | 5.79 | 4.38 | 4.43 | 0.59 | 7.31 |

Table A4.2. Differences detected in ANOVA tests of the height of abundant macroalgal species from seasonal exclusion experiments (n = 4, a-d) conducted on the upper subtidal rock boulders at the Trident Basin in Port Canaveral, Cape Canaveral, Florida. Measurements were considered biologically significant (*) if the contrast of a macroalga from a treatment, cage control or control (uncaged) differed ± 5mm or ± 40.0% (p <0.05). Comparisons for *Hypnea spinella* were based on the number of branches per thallus height. Abbreviation of treatments (trtmt) were FL = full large-mesh cage, FS = full small-mesh cage, SL = sides large-mesh cage control, SS = sides small-mesh cage control, TL = top large-mesh control, TS - top small mesh control, and C = controls (uncaged).

(a)

| FALL | met *a priori*? | trtmt 1 | trtmt 2 | Mean trtmt 1 | Mean trtmt 2 | ±SD trtmt 1 | ± SD trtmt 2 | difference in means | % diff trtmt 1 | % diff trtmt 2 | t | un-adjusted p | critical level |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Centroceras* | yes | FL | TL | 4.2 | 16.77 | 2.308 | 6.323 | -12.57 | -299.3% | -75.0% | 7.007 | <0.001 | 0.003 |
| *Centroceras* | yes | FL | TS | 4.2 | 11.18 | 2.308 | 4.37 | -6.98 | -166.2% | -62.4% | 3.11 | 0.004 | 0.004 |
| *Centroceras* | yes | FS | TL | 4.133 | 16.77 | 4.315 | 6.323 | -12.64 | -305.8% | -75.4% | 4.501 | <0.001 | 0.004 |
| *Centroceras* | yes | SS | TL | 7.15 | 16.77 | 3.404 | 6.323 | -9.62 | -134.5% | -57.4% | 4.755 | <0.001 | 0.004 |

(b)

| WINTER | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Amphiroa* | yes | FS | SL | 8.369 | 4.983 | 2.465 | 1.946 | 3.39 | 40.5% | 68.0% | 3.654 | <0.001 | 0.002 |
| *Amphiroa* | yes | FS | SS | 8.369 | 5.603 | 2.465 | 3.018 | 2.77 | 33.1% | 49.4% | 3.156 | 0.002 | 0.003 |
| *Amphiroa* | yes | FS | TS | 8.369 | 5.362 | 2.465 | 2.494 | 3.01 | 35.9% | 56.1% | 3.272 | 0.001 | 0.003 |
| *Amphiroa* | yes | SL | TL | 4.983 | 7.95 | 1.946 | 4.121 | -2.97 | -59.5% | -37.3% | 3.641 | <0.001 | 0.003 |
| *Amphiroa* | yes | SS | TL | 5.603 | 7.95 | 3.018 | 4.121 | -2.35 | -41.9% | -29.5% | 3.1 | 0.002 | 0.003 |
| *Amphiroa* | yes | TL | TS | 7.95 | 5.362 | 4.121 | 2.494 | 2.59 | 32.6% | 48.3% | 3.211 | 0.002 | 0.003 |

(c)

| SPRING | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Amphiroa* | yes | SS | TS | 4.395 | 7.468 | 1.864 | 2.903 | -3.07 | -69.9% | -41.1% | 3.744 | <0.001 | 0.002 |
| *Centroceras* | yes | FL | TL | 10.86 | 16.38 | 2.742 | 1.972 | -5.52 | -50.8% | -33.7% | 3.296 | 0.002 | 0.004 |
| *Centroceras* | yes | FS | TL | 8.713 | 16.38 | 2.779 | 1.972 | -7.67 | -88.0% | -46.8% | 4.855 | <0.001 | 0.003 |
| *Centroceras* | yes | SL | TL | 8.52 | 16.38 | 4.067 | 1.972 | -7.86 | -92.3% | -48.0% | 4.693 | <0.001 | 0.004 |
| *Centroceras* | yes | SS | C | 12.055 | 7.02 | 3.541 | 0.712 | 5.04 | 41.8% | 71.7% | 3.053 | 0.004 | 0.005 |
| *Centroceras* | yes | TL | C | 16.38 | 7.02 | 1.972 | 0.712 | 9.36 | 57.1% | 133.3% | 4.84 | <0.001 | 0.004 |
| *Gelidiopsis* | yes | FL | C | 12.87 | 8.4 | 4.177 | 2.468 | 4.47 | 34.7% | 53.2% | 2.665 | 0.01 | 0.004 |
| *Gelidiopsis* | yes | FL | SL | 12.87 | 6.627 | 4.177 | 1.197 | 6.24 | 48.5% | 94.2% | 3.647 | <0.001 | 0.003 |
| *Gelidiopsis* | yes | FS | C | 12.856 | 8.4 | 4.082 | 2.468 | 4.46 | 34.7% | 53.0% | 2.579 | 0.012 | 0.004 |
| *Gelidiopsis* | yes | FS | SL | 12.856 | 6.627 | 4.082 | 1.197 | 6.23 | 48.5% | 94.0% | 3.537 | <0.001 | 0.003 |
| *Gelidiopsis* | yes | SL | SS | 6.627 | 14.3 | 1.197 | 5.886 | -7.67 | -115.8% | -53.7% | 4.357 | <0.001 | 0.003 |
| *Gelidiopsis* | yes | SL | TS | 6.627 | 15.86 | 1.197 | 2.501 | -9.23 | -139.3% | -58.2% | 4.369 | <0.001 | 0.002 |
| *Gelidiopsis* | yes | SS | C | 14.3 | 8.4 | 5.886 | 2.468 | 5.90 | 41.3% | 70.2% | 3.415 | 0.001 | 0.003 |
| *Gelidiopsis* | yes | SS | TL | 14.3 | 9.113 | 5.886 | 4.694 | 5.19 | 36.3% | 56.9% | 3.14 | 0.003 | 0.004 |
| *Gelidiopsis* | yes | TL | TS | 9.113 | 15.86 | 4.694 | 2.501 | -6.75 | -74.0% | -42.5% | 3.335 | 0.001 | 0.003 |

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Gelidiopsis* | yes | TS | C | 15.86 | 8.4 | 2.501 | 2.468 | 7.46 | 47.0% | 88.8% | 3.577 | <0.001 | 0.003 |
| (d) | | | | | | | | | | | | | |
| SUMMER | | | | | | | | | | | | | |
| *Amphiroa* | yes | FS | C | 7.845 | 10.583 | 2.264 | 3.54 | -2.74 | -34.9% | -25.9% | 4.088 | <0.001 | 0.002 |
| *Amphiroa* | yes | SS | C | 7.965 | 10.583 | 2.45 | 3.54 | -2.62 | -32.9% | -24.7% | 3.91 | <0.001 | 0.003 |
| *Amphiroa* | yes | TL | C | 7.98 | 10.583 | 2.75 | 3.54 | -2.60 | -32.6% | -24.6% | 3.856 | <0.001 | 0.003 |
| *Amphiroa* | no | TS | C | 8.973 | 10.583 | 2.326 | 3.54 | -1.61 | -17.9% | -15.2% | 2.384 | 0.018 | 0.003 |
| *Centroceras* | yes | FL | C | 6.944 | 4.671 | 1.439 | 1.914 | 2.27 | 32.7% | 48.7% | 2.902 | 0.005 | 0.003 |
| *Centroceras* | yes | FL | FS | 6.944 | 3.033 | 1.439 | 1.986 | 3.91 | 56.3% | 128.9% | 3.087 | 0.003 | 0.003 |
| *Centroceras* | yes | FS | SS | 3.033 | 7.917 | 1.986 | 1.573 | -4.88 | -161.0% | -61.7% | 3.634 | <0.001 | 0.002 |
| *Centroceras* | yes | FS | TS | 3.033 | 7.04 | 1.986 | 1.588 | -4.01 | -132.1% | -56.9% | 3.203 | 0.002 | 0.003 |
| *Centroceras* | yes | SL | SS | 4.88 | 7.917 | 1.476 | 1.573 | -3.04 | -62.2% | -38.4% | 3.094 | 0.003 | 0.003 |
| *Centroceras* | yes | SS | C | 7.917 | 4.671 | 1.573 | 1.914 | 3.25 | 41.0% | 69.5% | 3.597 | <0.001 | 0.003 |
| *Centroceras* | yes | TS | C | 7.04 | 4.671 | 1.588 | 1.914 | 2.37 | 33.7% | 50.7% | 3.128 | 0.003 | 0.003 |
| *Gelidiopsis* | yes | FL | C | 9.76 | 6.5 | 1.739 | 1.3 | 3.26 | 33.4% | 50.2% | 2.994 | 0.013 | 0.05 |
| *Gelidiopsis* | yes | FL | FS | 9.76 | 14.3 | 1.739 | 1.3 | -4.54 | -46.5% | -31.7% | 4.814 | <0.001 | 0.025 |
| *Gelidiopsis* | yes | FS | C | 14.3 | 6.5 | 1.3 | 1.3 | 7.80 | 54.5% | 120.0% | 7.163 | <0.001 | 0.017 |
| *Gelidium* | yes | FL | FS | 7.503 | 10.348 | 2.745 | 3.115 | -2.85 | -37.9% | -27.5% | 3.438 | <0.001 | 0.003 |
| *Gelidium* | yes | FL | SL | 7.503 | 10.376 | 2.745 | 3.868 | -2.87 | -38.3% | -27.7% | 3.277 | 0.001 | 0.003 |
| *Gelidium* | yes | FL | TS | 7.503 | 10.681 | 2.745 | 3.3966 | -3.18 | -42.4% | -29.8% | 3.84 | <0.001 | 0.002 |
| *Gelidium* | yes | FS | C | 10.348 | 7.708 | 3.115 | 2.646 | 2.64 | 25.5% | 34.3% | 3.024 | 0.003 | 0.003 |
| *Gelidium* | yes | SL | C | 10.376 | 7.708 | 3.868 | 2.646 | 2.67 | 25.7% | 34.6% | 2.901 | 0.004 | 0.003 |
| *Gelidium* | yes | SS | TS | 8.17 | 10.681 | 2.829 | 3.966 | -2.51 | -30.7% | -23.5% | 2.985 | 0.003 | 0.003 |
| *Gelidium* | yes | TL | C | 9.944 | 7.708 | 3.617 | 2.646 | 2.24 | 22.5% | 29.0% | 2.479 | 0.014 | 0.005 |
| *Gelidium* | yes | TS | C | 10.681 | 7.708 | 3.966 | 2.646 | 2.97 | 27.8% | 38.6% | 3.404 | <0.001 | 0.003 |
| *Grateloupia* | yes | FL | TL | 12.94 | 8.859 | 4.213 | 2.867 | 4.08 | 31.5% | 46.1% | 3.793 | <0.001 | 0.003 |
| *Grateloupia* | yes | FS | TL | 12.748 | 8.859 | 3.712 | 2.867 | 3.89 | 30.5% | 43.9% | 3.82 | <0.001 | 0.002 |
| *Grateloupia* | yes | SS | TL | 11.826 | 8.859 | 4.334 | 2.867 | 2.97 | 25.1% | 33.5% | 3.056 | 0.003 | 0.003 |

Table A4.3. Differences detected in ANOVA tests of the thallus diameter of abundant macroalgal species from seasonal exclusion experiments (n = 4, a-d) conducted on the upper subtidal rock boulders at the Trident Basin in Port Canaveral, Cape Canaveral, Florida. Measurements were considered biologically significant (*) if the contrast of a macroalga from a treatment, cage control or control (uncaged) differed ± 25.0% (p <0.05).

(a)

| FALL | met *a priori*? | trtmt 1 | trtmt 2 | Mean trtmt 1 | Mean trtmt 2 | ±SD trtmt 1 | ± SD trtmt 2 | differences in mean | % diff trtmt 1 | % diff trtmt 2 | t | un-adjusted-p | critical level |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Centroceras* | yes | TL | FL | 165 | 131.82 | 15.12 | 24.01 | 33.18 | 20.1% | 25.2% | 3.505 | 0.002 | 0.003 |
| *Gelidiopsis* | no | SS | C | 284.74 | 249.50 | 24.35 | 40.84 | 35.24 | 12.4% | 14.1% | 2.933 | 0.004 | 0.003 |
| *Gelidium* | yes | FL | FS | 198.46 | 136.15 | 25.22 | 33.05 | 62.31 | 31.4% | 45.8% | 3.935 | <0.001 | 0.003 |
| *Gelidium* | yes | FL | SL | 198.46 | 118.42 | 25.22 | 19.51 | 80.04 | 40.3% | 67.6% | 5.690 | <0.001 | 0.003 |
| *Gelidium* | yes | FL | SS | 198.46 | 116.67 | 25.22 | 18.00 | 81.80 | 41.2% | 70.1% | 5.412 | <0.001 | 0.003 |
| *Gelidium* | yes | FL | TS | 198.46 | 123.85 | 25.22 | 32.63 | 74.62 | 37.6% | 60.2% | 5.772 | <0.001 | 0.002 |
| *Gelidium* | yes | FL | C | 198.46 | 136.88 | 25.22 | 25.22 | 61.59 | 31.0% | 45.0% | 4.158 | <0.001 | 0.003 |
| *Grateloupia* | yes | SS | TL | 754.44 | 491.94 | 155.81 | 216.46 | 262.50 | 34.8% | 53.4% | 3.385 | 0.001 | 0.002 |
| *Hypnea* | yes | SL | FL | 457.78 | 354.74 | 109.06 | 69.07 | 103.04 | 22.5% | 29.0% | 3.197 | 0.002 | 0.002 |

(b)

| WINTER | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Amphiroa* | no | FS | C | 290.63 | 250.00 | 28.16 | 33.38 | 40.63 | 14.0% | 16.3% | 2.884 | 0.005 | 0.003 |
| *Centroceras* | no | SL | C | 162.5 | 192.00 | 14.88 | 15.49 | -29.50 | -18.2% | -15.4% | 3.091 | 0.003 | 0.002 |
| *Centroceras* | no | TS | C | 167.96 | 192.00 | 19.22 | 15.49 | -24.04 | -14.3% | -12.5% | 2.872 | 0.005 | 0.003 |
| *Gelidiopsis* | no | FL | C | 229.38 | 266.80 | 26.20 | 47.06 | -37.43 | -16.3% | -14.0% | 2.626 | 0.01 | 0.004 |
| *Gelidiopsis* | yes | FL | SS | 229.38 | 297.50 | 26.20 | 51.19 | -68.13 | -29.7% | -22.9% | 4.329 | <0.001 | 0.003 |
| *Gelidiopsis* | yes | FL | TL | 229.38 | 307.14 | 26.20 | 45.51 | -77.77 | -33.9% | -25.3% | 5.265 | <0.001 | 0.002 |
| *Gelidiopsis* | yes | FL | TS | 229.38 | 295.00 | 26.20 | 47.06 | -65.63 | -28.6% | -22.2% | 4.029 | <0.001 | 0.003 |
| *Gelidiopsis* | no | FS | TL | 250 | 307.14 | 41.40 | 45.51 | -57.14 | -22.9% | -18.6% | 3.090 | 0.003 | 0.003 |
| *Gelidiopsis* | no | SL | TL | 251.91 | 307.14 | 54.55 | 45.51 | -55.24 | -21.9% | -18.0% | 4.021 | <0.001 | 0.003 |
| *Gelidiopsis* | no | SL | SS | 251.91 | 297.50 | 54.55 | 51.19 | -45.60 | -18.1% | -15.3% | 3.087 | 0.003 | 0.003 |
| *Gelidiopsis* | no | TL | C | 307.14 | 266.80 | 45.51 | 47.06 | 40.34 | 13.1% | 15.1% | 3.062 | 0.003 | 0.003 |
| *Gelidium* | no | SS | C | 117.78 | 142.00 | 18.01 | 21.18 | -24.22 | -20.6% | -17.1% | 3.519 | <0.001 | 0.002 |
| *Gelidium* | no | TL | C | 121.67 | 142.00 | 17.86 | 21.18 | -20.33 | -16.7% | -14.3% | 3.170 | 0.002 | 0.003 |
| *Hypnea* | no | FL | C | 475 | 389.05 | 104.50 | 90.93 | 85.95 | 18.1% | 22.1% | 3.232 | 0.002 | 0.009 |
| *Hypnea* | yes | FL | TL | 475 | 624.00 | 104.50 | 33.62 | -149.00 | -31.4% | -23.9% | 3.501 | <0.001 | 0.007 |
| *Hypnea* | yes | FS | TL | 450 | 624.00 | 43.97 | 33.62 | -174.00 | -38.7% | -27.9% | 3.885 | <0.001 | 0.006 |
| *Hypnea* | yes | SS | TL | 390 | 624.00 | 80.83 | 33.62 | -234.00 | -60.0% | -37.5% | 4.098 | <0.001 | 0.006 |
| *Hypnea* | yes | TL | C | 624 | 389.05 | 33.62 | 90.93 | 234.95 | 37.7% | 60.4% | 5.547 | <0.001 | 0.005 |

(c)

| SPRING | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Amphiroa* | yes | FL | SL | 270.44 | 360.67 | 60.49 | 32.83 | -90.23 | -33.4% | -25.0% | 4.479 | <0.001 | 0.002 |

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Amphiroa* | no | FS | SL | 293.32 | 360.67 | 66.93 | 32.83 | -67.35 | -23.0% | -18.7% | 3.069 | 0.003 | 0.003 |
| *Amphiroa* | no | FL | TL | 270.44 | 328.00 | 60.49 | 75.72 | -57.57 | -21.3% | -17.6% | 3.282 | 0.001 | 0.003 |
| *Centroceras* | yes | FS | SS | 174.67 | 106.67 | 26.15 | 74.36 | 68.00 | 38.9% | 63.7% | 4.431 | <0.001 | 0.003 |
| *Centroceras* | yes | SL | SS | 163 | 106.67 | 16.36 | 74.36 | 56.33 | 34.6% | 52.8% | 3.284 | 0.002 | 0.004 |
| *Gelidiopsis* | yes | SL | C | 208 | 297.69 | 44.92 | 49.52 | -89.69 | -43.1% | -30.1% | 5.237 | <0.001 | 0.003 |
| *Gelidiopsis* | yes | FL | SL | 305 | 208.00 | 39.64 | 44.92 | 97.00 | 31.8% | 46.6% | 5.022 | <0.001 | 0.003 |
| *Gelidiopsis* | yes | FS | SL | 308 | 208.00 | 20.98 | 44.92 | 100.00 | 32.5% | 48.1% | 5.492 | <0.001 | 0.002 |
| *Gelidiopsis* | yes | SL | SS | 208 | 275.00 | 44.92 | 39.23 | -67.00 | -32.2% | -24.4% | 3.679 | <0.001 | 0.003 |
| *Gelidiopsis* | no | FS | TL | 308 | 252.00 | 20.98 | 46.94 | 56.00 | 18.2% | 22.2% | 3.369 | 0.001 | 0.003 |
| *Gelidium* | yes | TL | C | 95 | 129.00 | 14.34 | 20.24 | -34.00 | -35.8% | -26.4% | 3.670 | <0.001 | 0.002 |
| *Gelidium* | yes | FL | TL | 125.2 | 95.00 | 27.40 | 14.34 | 30.20 | 24.1% | 31.8% | 3.375 | <0.001 | 0.003 |
| *Gelidium* | yes | SL | TL | 122.9 | 95.00 | 22.24 | 14.34 | 27.90 | 22.7% | 29.4% | 3.208 | 0.002 | 0.003 |
| *Gelidium* | yes | SS | TL | 124.8 | 95.00 | 25.02 | 14.34 | 29.80 | 23.9% | 31.4% | 3.330 | 0.001 | 0.003 |
| *Grateloupia* | no | SL | C | 596 | 732.50 | 190.20 | 90.43 | -136.50 | -22.9% | -18.6% | 3.364 | <0.001 | 0.003 |
| *Grateloupia* | yes | FL | SL | 818.67 | 596.00 | 107.56 | 190.20 | 222.67 | 27.2% | 37.4% | 5.041 | <0.001 | 0.002 |
| *Grateloupia* | no | FL | SS | 818.67 | 685.20 | 107.56 | 125.47 | 133.47 | 16.3% | 19.5% | 3.021 | 0.003 | 0.003 |
| *Grateloupia* | yes | SL | TL | 596 | 748.00 | 190.20 | 131.80 | -152.00 | -25.5% | -20.3% | 3.973 | <0.001 | 0.003 |
| *Grateloupia* | no | SL | TS | 596 | 731.00 | 190.20 | 116.36 | -135.00 | -22.7% | -18.5% | 3.686 | <0.001 | 0.003 |

(d)

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| SUMMER | | | | | | | | | | | | | |
| *Amphiroa* | no | SS | C | 325.16 | 373.00 | 50.26 | 56.46 | -47.84 | -14.7% | -12.8% | 3.023 | 0.003 | 0.009 |
| *Gelidiopsis* | yes | FL | FS | 144 | 240.00 | 20.74 | 14.14 | -96.00 | -66.7% | -40.0% | 8.783 | <0.001 | 0.017 |
| *Gelidiopsis* | yes | FL | C | 144 | 236.67 | 20.74 | 15.28 | -92.67 | -64.4% | -39.2% | 7.342 | <0.001 | 0.025 |