An Investigation into the Habitat, Behavior and Opportunistic Feeding Strategies of the Protected Goliath Grouper (*Epinephelus itajara*)

by

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DEDICATION

To my parents, for passing down their passion for learning, providing examples of an incredible work ethic, and for keeping my cheering section filled through decades of school; to my husband, for his perspective, patience, and gentle humor; to my committee, for challenging me and providing continued guidance and support; and of course, to all of the fish in the sea, for an inspiring source of never-ending questions.

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ABSTRACT

Groupers (Epinephelidae: Epinephelinae) are apex predators within many reef communities worldwide. Grouper landings contribute significantly to global fisheries, and many populations are suffering from unsustainable levels of exploitation. The large size, site specificity and catchability of most groupers increase susceptibility to fishing pressure, and a large number of grouper species throughout the world are currently overfished. Multiple species are listed as endangered or threatened, and many have suffered local extirpations across their range. Removal of these upper level predators can significantly alter community structure and result in second order effects that may have critical ecological implications. The economic and ecological value of groupers is significant, and data regarding the abundance, habitat and behavior of these exploited species are necessary in order to implement realistic and effective management strategies.

Atlantic Goliath Grouper (*Epinephelus itajara*) historically occurred in tropical and subtropical waters from the west coast of Africa to the east coast of Florida, south to Brazil, and throughout the Caribbean Sea and Gulf of Mexico. As one of the world's largest groupers, individuals are known to reach at least 37 years of age, and may grow to sizes exceeding 2.5 meters and 400 kilograms. The life history and behavioral characteristics of this species amplify vulnerability to exploitation, and Atlantic Goliath

Grouper harvest was banned in U.S. waters in 1990 after a noted sharp decline in population numbers. The species has responded encouragingly to protective measures; however, the population's recovery and present status with U.S. waters should be thoroughly evaluated before altering regulatory guidelines. Traditional fishery-dependent data are not available (i.e., landings data); thus estimates of population demographics and recovery are dependent upon directed, fishery independent research efforts. It was the goal of this project to provide information regarding demographics, movement patterns, effects of catch and release angling, and feeding behavior of Atlantic Goliath Grouper within the central eastern Gulf of Mexico.

The majority of research involving Atlantic Goliath Grouper began after the stock was already overfished, resulting in the absence of an existing "baseline" with which to compare current population parameters. Replication of visual surveys over a range of depths and habitat types provided an index of abundance for specific sites, and allowed for quantification of the size distribution of individuals. Atlantic Goliath Grouper were most abundant at high relief, high volume artificial reefs within the study area, and the majority of individuals observed were 80 – 160 cm in total length. Knowledge of fish movement, behavior and habitat associations has been used to exploit many species of fish; thus, this knowledge is critical for the creation of regulatory guidelines regarding conservation.

Protection from harvest does not immediately imply that fishing mortality is negligible. As opportunistic ambush predators, Atlantic Goliath Grouper are relatively easy to catch

on hook and line, and the species is often targeted for sport or caught incidentally during angling efforts for other reef fish species. Acoustic tracking allowed for continuous monitoring of individuals for several years after catch and release events. Barotrauma severity increased with capture depth, but immediate mortality was not observed during this study. Additionally, the length of total monitoring period was not affected by the severity of barotrauma, which suggests that with proper handling, Atlantic Goliath Grouper are not subject to high levels of release mortality in the study area (at depths < 40 m). However, strong site fidelity of Atlantic Goliath Grouper to artificial reefs increases susceptibility to fishing pressure and amplifies interactions with anglers, so the chronic effects of repeated capture remain unclear.

Description and quantification of goliath grouper feeding behavior may allow for innovative suggestions to decrease the probability of catch and release mortality, and potentially offer new tactics to reduce opportunistic predation upon hooked fish. Kinematic analysis of Atlantic Goliath Grouper feeding sequences demonstrated that they are capable of modulating feeding behavior based upon prey activity level and position within the water column. Individuals exhibited larger maximum gapes and more rapid feeding sequences when presented with mobile live food. Immobile (dead) food was primarily consumed through suction, and strikes upon these items were characterized by slower, closer approaches, smaller maximum gapes and longer bite durations. It is hopeful that the information presented herein will provide insight regarding the ecology of Atlantic Goliath Grouper and can be applied to future management efforts involving this protected species.

CHAPTER ONE

GENERAL INTRODUCTION

Groupers (Epinephelidae) are important upper level predators within reef communities throughout the world. There are over 150 species included within the subfamily Epinephelinae (Nelson, 1994), and representatives are found within tropical and subtropical waters worldwide (Heemstra and Randall, 1993; Craig et al., 2011). Groupers are typically associated with complex benthic habitats (Heemstra and Randall, 1993; Craig et al., 2011), and many species occupy an important ecological role within these communities (Parrish, 1987; Randall, 1998; Brule et al., 2004; Gobert et al., 2005; Coleman et al., 2010). The large size, site specificity and catchability of most groupers increase their fisheries value, and indeed, grouper landings contribute significantly to the world's commercial fish catch (approximately 100,000 – 300,000 tons annually; Heemstra and Randall, 1993; Craig et al., 2011).

Groupers are highly susceptible to fishing pressure (Bannerot et al., 1987; Shapiro, 1987; Russ, 1991; Huntsman et al., 1999; Coleman et al., 2000), and a large number of grouper species throughout the world are currently overfished or are undergoing overfishing (Sadovy, 1994; Bohnsack et al., 1994; Sadovy de Mitcheson et al., 2013). Multiple species are listed as endangered or threatened, and many have suffered local extirpations across their range. Removal

of these predators can significantly alter community structure (Goeden, 1982; Bohnsack, 1982; Sluka et al. 1998; Stallings, 2009) and result in second order effects (Thompson and Munroe, 1978; Bohnsack, 1982; Stallings, 2008) that may have critical ecological implications. The economic and ecological value of groupers is significant, and data regarding the abundance, habitat and behavior of these exploited species are necessary in order to implement realistic and effective management strategies.

Study Species: Atlantic Goliath Grouper *Epinephelus itajara*

Geographic distribution

The Atlantic Goliath Grouper (*Epinephelus itajara* Lichtenstein 1822) historically occurred in tropical and subtropical waters from the west coast of Africa to the east coast of Florida, south to Brazil, and throughout the Caribbean Sea and Gulf of Mexico (Craig et al., 2011). They have been reported in the Gulf of Mexico as far north as Mississippi and Louisiana (Franks, 2005), but the center of abundance for this species has historically been described as the southwestern coast of Florida in the southeastern Gulf of Mexico (Bullock et al., 1992; Sadovy and Eklund, 1999).

Life history

As one of the world's largest groupers, individuals may reach 2.5 m in length and exceed 400 kg (Bullock et al., 1992; Craig et al., 2011). Atlantic Goliath Grouper are relatively long-lived, and have been aged to 37 years (Bullock et al., 1992). After a planktonic larval period, juveniles settle within inshore estuaries, where growth rates may exceed 100 mm per year during the first 6 years of life (Bullock et al., 1992).

Atlantic Goliath Grouper do not reach maturity until they are between 4 and 7 years of age, at approximately 110 – 140 cm total length (TL) (Bullock et al., 1992). Similar to other groupers (Bullock and Smith, 1991; Ross and Moser, 1995), an ontogenetic shift to deeper water is suspected around the time of maturation (Bullock et al., 1992; Gerhardinger et al., 2006; Koenig et al., 2007). Adults have been recorded at depths to 100 m (Craig et al., 2011); however, they occur most commonly at depths < 50 m (Bullock et al., 1992). Size-based offshore migration does not appear to be obligatory, however, as large adults are still caught inside channels and around bridges within nearshore waters (Eklund and Schull 2001; Gerhardinger et al., 2006).

Atlantic Goliath Grouper spawn during the late summer and early fall (June – December), and peak activity in Florida waters has been noted July through September (Bullock et al., 1992). Several spawning aggregations have been identified along both coasts of Florida, as well as in waters off central and South America (Sadovy and Eklund, 1999; Porch and Eklund, 2004; Gerhardinger et al., 2006; Pusack and Graham 2009). Spawning aggregation sites identified to date are in deeper waters offshore (30 – 45 m) and are typically associated with high relief artificial or natural reefs (Sadovy and Eklund, 1999; Eklund and Schull, 2001; Porch and Eklund, 2004; Phelan, 2008; Mann et al., 2009). At least one quarter of all Atlantic Goliath Grouper spawning aggregations were believed to be extirpated in the year 2000 (Musick et al., 2000). No conclusive evidence exists regarding the sexual pattern of Atlantic Goliath Grouper (Bullock et al., 1992; Sadovy and Eklund, 1999). Protogynous hermaphroditism is suspected (Smith, 1959; 1971) and recent research has demonstrated the capacity for hermaphroditism in some individuals (Koenig and Coleman, 2013). This is noteworthy, as the regulation of protogynous species involves more precaution than gonochoristic species because preferential fishing pressure

can significantly skew the sex ratio of the population and rapidly reduce reproductive potential to critically low levels (Musick, 1999; Heppell et al., 2006; Brooks et al., 2008; Ellis and Powers 2012).

Habitat and behavior

Juveniles are typically associated with structural overhangs that provide cover (primarily mangrove habitat, limestone solution holes or eroded shoreline; Frias-Torres, 2006; Frias-Torres et al., 2007; Koenig et al., 2007). Mangrove habitats are especially important nursery areas for Atlantic Goliath Grouper, and increasing coastal development throughout their range has been suggested as a bottleneck to the recovery of this species (Koenig et al., 2007). Atlantic Goliath Grouper are one of the few grouper species that can withstand brackish conditions, and has been observed to tolerate salinities as low as 4.5 (Garcia-Tellez, 2002; Botero and Ospina, 2003). Juveniles have also been noted to withstand hypoxic conditions (dissolved oxygen ≥ 0.9 mg/l; Sadovy and Eklund, 1999; Botero and Ospina, 2003); however, mortality for both juveniles and adults is observed during extended periods of low temperatures (< 15˚ C; Gilmore et al., 1978; FWC/FWRI unpublished data) and during toxic algal blooms (specifically red tide *Karenia brevis*; Smith, 1976; FWC/FWRI unpublished data).

Adults, like juveniles, maintain association with structurally complex habitat including bridge pilings, shipwrecks, natural and artificial reefs (Eklund and Schull 2001; Garcia-Tellez et al., 2002; Gerhardinger et al., 2006; Collins, 2009; Koenig et al., 2011). The behavioral data that exist for Atlantic Goliath Grouper indicate high site fidelity. Eklund and Schull (2001) performed a tagging study on adult Atlantic Goliath Grouper and reported individual fish at the

same location for up to three years. Similarly, tagged juveniles remained within small defined areas of the Ten Thousand Islands for many months (Frias-Torres et al., 2007; Koenig et al., 2007). These data indicate relatively low movement rates; however, fish have been reported to travel distances exceeding 100 km (Koenig and Coleman 2009; Pina-Amargos and Gonzalez-Sanson 2009), and it has been demonstrated that some individuals will travel even longer distances (> 400 km) to reach spawning aggregation sites (Koenig and Coleman 2013).

Diet and feeding behavior

Crustaceans contribute significantly to the diet of both juvenile and adult Atlantic Goliath Grouper (Longley and Hildebrand, 1941; Randall, 1967; Randall, 1983; Bullock and Smith, 1991; Koenig and Coleman, 2009). However, fish are not uncommon prey (Randall, 1983; Bullock and Smith, 1991), and sea turtles (Randall, 1967; Yeiser et al., 2008) and octopus (Bullock and Smith, 1991) have also been discovered within stomach contents. The majority of fish prey identified to date consists of slow-moving, benthic associated species (i.e. cowfish, catfish, stingray), supporting contentions that Atlantic Goliath Grouper are typically slow-moving and sedentary predators (Sadovy and Eklund, 1999). However, feeding in the water column on schools of baitfish (e.g., Clupeidae, Carangidae) has also been observed (Gerhardinger et al., 2006; Phelan et al., 2008; A. Collins pers. obs.).

Most groupers are opportunistic ambush predators (Burnett-Herkes, 1975; Parrish, 1987; Bullock and Smith, 1991; Weaver 1996) that are believed to engulf prey through suction feeding (Thompson and Monroe, 1978, Viladiu et al., 1999; Ouifero et al., 2012). Reports from anglers and divers have established that Atlantic Goliath Grouper will feed opportunistically on fish shot

by spearfishers, and will readily prey upon other fish being reeled in by anglers or being released after an angling event (L. Barbieri, FWC, pers. com.; A. Collins, pers. obs.). These anecdotes indicate that Atlantic Goliath Grouper modify their behavior to feed upon easily captured prey.

Management

Fisheries for the Atlantic Goliath Grouper have existed for centuries, both for food value as well as recreational "trophy" fishing (McClenachan, 2008). The life history and behavioral characteristics of this species amplify their vulnerability to exploitation and extend the time required for population recovery (Sadovy and Eklund, 1999; Musick et al., 2000; Porch et al., 2006). Indeed, Atlantic Goliath Grouper suffered significant overfishing throughout the last half of the 20th century and harvest of Atlantic Goliath Grouper was banned in U.S. waters in 1990 after a sharp decline in population numbers (GMFMC, 1990; SAFMC, 1990). The population decline was evidenced through reports from the public as well as fishery landings data (Sadovy and Eklund, 1999; Porch et al., 2006). In 1994, the species was listed as critically endangered on the International Union for the Conservation of Nature (IUCN) World Conservation Union's Red List of Threatened Species (Pusack and Graham, 2009). The species has since been protected in Brazil (2002), Puerto Rico (2004) and the US Virgin Islands (2004; NMFS 2006). However, fisheries for Atlantic Goliath Grouper persist in other areas and the status of the species throughout its entire geographic range remains unclear.

After nearly 16 years of protection in the United States, a National Marine Fisheries Service (NMFS) status report showed a significant increase in Atlantic Goliath Grouper abundance throughout U.S. waters, and the National Oceanic and Atmospheric Administration (NOAA)

removed Atlantic Goliath Grouper from the Species of Concern list in February 2006 (NMFS, 2006). The species remains protected from harvest at this time. However, the growing public perception that the species is rebounding has created a push among several fishing sectors within the state of Florida for a re-evaluation of state and federal management strategy [Luiz Barbieri, FWC, personal communication]. However, because the life history and behavioral characteristics of Atlantic Goliath Grouper significantly increase susceptibility to exploitation, additional data regarding the population's recovery and present status with U.S. waters are necessary prior to any changes in management (SEDAR 6, 2005; SEDAR 23, 2011).

Project goals

The majority of research involving Atlantic Goliath Grouper began after the stock was already overfished, resulting in the absence of an existing "baseline" with which to compare current population parameters. This lack of information has confounded recent stock assessments (SEDAR 6, 2004; SEDAR 23, 2011), highlighting the need for additional data regarding this species throughout its geographic range. The primary objective of this project was therefore to gather previously unavailable information regarding Atlantic Goliath Grouper within the central eastern Gulf of Mexico. Specific goals included the following: (1) to assess abundance, size distribution and habitat association of Atlantic Goliath Grouper within the study area; (2) to identify catch and release mortality and characterize behavior immediately following catch and release events; (3) to quantify site fidelity and fine-scale movement patterns of individuals over extended time frames (months – years); and (4) to describe the prey capture behavior and feeding kinematics of individuals during simulated angling events in order to better understand the feeding behavior of this species.

Abundance, size distribution and habitat association

During this study, abundance, size distribution and habitat association of Atlantic Goliath Grouper were assessed during visual surveys over a range of depths and habitat types throughout the central eastern Gulf of Mexico. Assessments of population distribution and stock status are better informed when measures of habitat association and suitability are well defined (Jones and Syms 1998). In the case of a protected species such as the Atlantic Goliath Grouper, identification of the parameters that influence habitat selection is critical to ensure proper management of essential habitats and to more efficiently target monitoring efforts during attempts to assess recovery or disturbance (MacCall 1990; Jones and Syms 1998). Additionally, abundance and density estimates, combined with length and age composition of a stock, may be used to assess the status of species and allows scientists to track changes in stock size over time (Jennings et al., 2001). Fisheries landings are typically the primary source for these types of data; however, Atlantic Goliath Grouper are protected from harvest and landings data are unavailable. Fishery-independent surveys are therefore necessary to provide an alternative to the fishery-dependent methods typically used to assess the population (Jennings et al., 2001; Ehrhardt and Deleveaux, 2007; Ault et al., 2008).

Catch and release mortality, site fidelity and movement patterns

Protection from harvest does not immediately imply that fishing mortality is zero. Atlantic Goliath Grouper are targeted for sport catch and release angling, and are also caught incidentally during angling efforts for other reef fish species. Atlantic Goliath Grouper that are caught may be subject to barotrauma and extensive boat-side handling that may result mortality or injury (Burns

and Restrepo, 2002; Lucy and Studholme, 2002); however, this subject has not previously been addressed for Atlantic Goliath Grouper. Acoustic telemetry and continuous passive monitoring were used to identify the survival of Atlantic Goliath Grouper after catch and release events, and also provided long-term (> 2 years) data regarding site fidelity and fine-scale movement patterns of individuals. Most fish populations are not dispersed evenly throughout the environment and instead occur in patchy, clumped distributions based on behavior (MacCall, 1990; Sale, 1991; Walters and Martell, 2004). Knowledge regarding habitat associations and behavior of fishes has historically been used as a tool for efficient exploitation (e.g., Sadovy 1994; Kurlanski, 1997; Parrish, 1999; Koenig et al., 2000; Sadovy and Domeier, 2005), and species with high site fidelity and predictable movement or migration patterns are more vulnerable than those that exhibit irregular or random behavior (Huntsman et al., 1999). Behavioral patterns of fishes are therefore key pieces of information used during the development of fishing regulations (Walters and Martell, 2004; Lowe and Bray, 2006).

Feeding behavior

Underwater videography and subsequent kinematic analyses of adult Atlantic Goliath Grouper *Epinephelus itajara* feeding events upon a variety of 'prey' situations allowed for a description of feeding behavior and demonstrated the capacity of individuals to modulate feeding behavior based upon the mobility and position of food items. Analysis of the morphological components and mechanisms of prey capture can provide insight to the interaction between fishery species and anglers; therefore a description of Atlantic Goliath Grouper feeding behavior may eventually allow for innovative suggestions to decrease the probability of incidental catch and release, as well as offer new tactics to reduce opportunistic predation upon hooked fish.

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CHAPTER TWO

SIZING UP THE PLACE: HABITAT TYPE, RELIEF AND VOLUME ARE PREDICTORS OF ATLANTIC GOLIATH GROUPER *EPINEPHELUS ITAJARA* PRESENCE AND DENSITY IN THE EASTERN GULF OF MEXICO

Abstract

Atlantic Goliath Grouper (*Epinephelus itajara*) habitat association, abundance, and size distribution in the central eastern Gulf of Mexico were assessed during monthly underwater visual surveys performed October 2007 through May 2010. Surveys were completed at natural and artificial reefs ranging in depth from 7 to 48 m. Atlantic Goliath Grouper were present during all months of the year and for 74% of all surveys (256/349 surveys). The number of Atlantic Goliath Grouper observed during surveys ranged from 0 to 24 individuals. Presence and abundance were significantly related to habitat type, and Atlantic Goliath Grouper were most likely to be observed at artificial reefs. Atlantic Goliath Grouper were present for over 90% of surveys at artificial reefs (mean number observed = 4.5), but for less than 40% of surveys at natural reefs (mean number observed < 1). The largest numbers of fish were recorded at high relief, high volume artificial reefs (all shipwrecks) in deeper water (>20 m). Atlantic Goliath Grouper measured via underwater video ranged in size from 37 to 214 cm total length (TL), and the majority of individuals were 80 to 160 cm TL. Average size of individuals was not related to site depth, except during August and September, when there were significantly more large

individuals at the deepest sites (> 20 m). A total of 172 Atlantic Goliath Grouper were tagged *in situ* with external conventional identification tags, and 27 individuals have been resighted or recaptured to date (16%). Tag return data indicate high site fidelity, with 82% (22/27) of the resighted fish recorded at the same site as the initial tagging up to 958 days later (the mean number of days at large = 117). Individuals were also documented to move between sites, and travelled distances ranging from 10 – 203 km from their initial tagging site (mean distance travelled = 50 km; median = 22 km). The strong site fidelity of Atlantic Goliath Grouper combined with their continuous and predictable association with high relief, high volume artificial reefs allows for relatively efficient monitoring of individuals within a given region; however, these traits also increase vulnerability to exploitation, underlining the need for cautious management.

Introduction

The spatial distribution of marine fish populations is rarely uniform. Whether or not a species is present within a given area is influenced by an extensive suite of factors, including habitat suitability, individual movement and the presence of conspecifics (Sinclair 1988; MacCall 1990). Numerous studies have demonstrated the influence of habitat upon fish presence, especially for reef fishes (Sale and Douglas 1984; Jones 1991; Hixon and Beets 1993; Sale et al., 1994; Nagelkerken et al., 2000; Wilson et al., 2010), and assessments of population distribution, stock status and levels of abundance are better informed when measures of habitat association and suitability are well defined (Jones and Syms 1998). In the case of exploited or protected species, identification of the parameters that influence habitat selection is critical to ensure proper

management of essential habitats and to more efficiently target monitoring efforts during attempts to assess recovery or disturbance (MacCall 1990; Jones and Syms 1998).

Atlantic Goliath Grouper (Epinephelidae: *Epinephelus itajara* Lichtenstein, 1822) are one of the world's largest groupers, and may attain 2.5 m in total length (TL), weigh up to 400 kg, and live at least 37 years (Bullock et al., 1992; Craig et al., 2011). Although the species historically occurred throughout subtropical and tropical waters of the Atlantic Ocean and Gulf of Mexico (Bullock et al., 1992; Craig et al., 2011), a significant population decline was observed through the latter part of the 20th century after intense fishing pressure at aggregation sites (Sadovy and Eklund 1999). In 1990, Atlantic Goliath Grouper were protected from all harvest in US waters (GMFMC, 1990; SAFMC, 1990) and in 1994 the species was listed as critically endangered on the IUCN World Conservation Union's Red List of Threatened Species (Craig et al., 2011). At least one quarter of all Atlantic Goliath Grouper spawning aggregations were believed to be extirpated in 2000 (Musick et al., 2000). The species remains protected in US waters and is also protected in some parts of the Caribbean and South Atlantic (Craig et al., 2011) but fisheries persist in other areas and the status of Atlantic Goliath Grouper throughout its geographic range remains unclear.

Within the United States, Atlantic Goliath Grouper have responded well to protection and are showing signs of recovery (Cass-Calay and Schmidt 2009; Koenig et al., 2011). However, the life history characteristics of the species make them especially susceptible to overfishing (Musick 1999; Sadovy and Eklund 1999), so any changes in management should proceed with caution. After a planktonic larval stage, juvenile Atlantic Goliath Grouper settle in shallow,

nearshore estuaries, commonly near mangroves (Eklund and Schull, 2001; Koenig et al., 2007; Lara et al., 2009). They do not reach maturity until they are between 4 and 7 years of age and at least 110 cm TL (Bullock et al., 1992), and they gradually move to offshore marine habitats with growth (Smith 1976; Koenig et al., 2007). Adults are reef associated, and may occur in depths to 100 m (Craig et al., 2011), but they are most commonly found at natural and artificial reefs < 50 m (Bullock et al., 1992; Heemstra and Randall, 1993; Gerhardinger et al. 2006). This predictable and continuous association with reef habitats relatively close to shore further increases Atlantic Goliath Grouper vulnerability to exploitation (Huntsman et al., 1999). Individuals are believed to be relatively sedentary with high site fidelity through most of the year, except during spawning periods (August – September), when they may travel hundreds of kilometers to reach spawning aggregations (Sadovy and Eklund 1999; C. Koenig, pers. comm.). The majority of spawning aggregations that have been identified to date within the eastern Gulf of Mexico are at moderate to high relief artificial reefs between 30 – 50 m deep (Sadovy and Eklund 1999; Eklund and Schull, 2001; Porch and Eklund 2004).

Future success of the Atlantic Goliath Grouper population depends upon responsible management as well as the identification and availability of suitable habitat and resources throughout ontogeny. The southwest coast of Florida has historically been a center of abundance for Atlantic Goliath Grouper (Bullock and Smith, 1991), yet Atlantic Goliath Grouper distribution and size structure within the region have been relatively undocumented (but see Koenig et al., 2011). Based on what is known regarding the life history of this species, it was predicted that Atlantic Goliath Grouper would be most common at reef habitats with enough structural complexity to accommodate their preference for cover (Bullock and Smith, 1991;

Sadovy and Eklund 1999, Koenig et al., 2011) and that there would be a positive relationship between fish size and depth, since they settle in estuaries and are expected to recruit to offshore reefs with growth. In the absence of landings data and the associated life history information (e.g., length and age composition), quantification of size structure through visual surveys can provide a proxy for age distribution that should inform stock assessments. Thus, this research aimed to describe the presence and abundance of Atlantic Goliath Grouper throughout the study area in order to identify specific characteristics of preferred habitat, and to characterize the size distribution of the species in the central eastern Gulf of Mexico. This information should advance the ability to monitor population changes through time, and assist with predictions of population dynamics for a species currently in a period of stock recovery.

Methods

Selection and evaluation of survey sites

Visual census and underwater video were used to quantify the abundance and size distribution of Atlantic Goliath Grouper within the study area. Dive surveys were conducted in all months of the year during daylight hours. Since adult Atlantic Goliath Grouper are reef associated (Bullock and Smith 1991; Craig et al., 2011) and typically inhabit artificial or natural habitat in relatively shallow water (< 50 m) (Bullock et al., 1992; Heemstra and Randall 1993), dive sites were distributed as evenly as possible across a range of depths to 50 m to include both artificial and natural habitats (Fig. 2.1). Artificial habitat was defined as any man-made structure and included mostly shipwrecks, but also incorporated other debris consisting of concrete pilings and concrete rubble fields. Natural sites included limestone ledges, pinnacles, and offshore freshwater spring openings, which comprise the typical hard-bottom within the study area (Smith, 1976). Effort

was made to survey a diverse distribution of natural and artificial habitats with varying levels of structural complexity and relief, and sites were chosen based upon published numbers of reef habitat as well as upon recommendations by local veteran divers with extensive knowledge of the study area.

Although Atlantic Goliath Grouper are protected from harvest, there is still a targeted catch and release fishery and the species is also caught incidentally by anglers fishing for other reef fish. Since barotrauma effects after catch and release have the potential to contribute to mortality (Wilde 2009; Sumpton et al., 2010), sites were classified as "shallow" (≤ 20 m) or "deep" (> 20 m), based on the depth at which pressure related fishing trauma becomes more likely to occur for this species (C. Koenig, pers. comm.; Collins, unpublished data). To assess seasonal effects upon presence and size distribution, 18 sites were designated for quarterly sampling and included 12 artificial sites and 6 natural sites (Fig. 2.1). To better define seasonal patterns in the size distribution of fish, more artificial reefs than natural reefs (12 vs. 6) were targeted for repeat surveys because they had larger number of individuals present (A. Collins, personal observation) and presented an increased opportunity to observe and measure Atlantic Goliath Grouper. These 18 sites were surveyed at least once per season, defined as winter (January – March), spring (April - June), summer (July – September), and fall (October – December). Additional sites (24 artificial and 38 natural; Fig. 2.1) surrounding the designated 18 quarterly sites were surveyed opportunistically throughout the study period. Site relief was recorded as the maximum height of the site (straight vertical distance from the seafloor to the top of the habitat structure). Site volume was estimated for artificial habitats by separating the site into manageable, measurable units and summing unit volumes (length*width*height) to obtain a total volume of

the structure. The structure was also assessed for internal cavities and the presence of openings > 1 m^2. For natural habitats, site volume could not be calculated but the vertical relief, presence of undercuts, and length of the ledge were recorded.

Assessing Atlantic Goliath Grouper abundance and size distribution

Atlantic Goliath Grouper presence and abundance were assessed by swimming in a single direction from one end of the site to the other. All crevices and holes were visually inspected, and then the process was repeated in reverse so that all sites were visually surveyed in their entirety at least twice. Total survey time was positively related to the total area of the site, but required a minimum search time of 15 minutes. Only sites that could be completely surveyed during a single dive were considered for the data analyses. Due to the large size and high visibility of Atlantic Goliath Grouper, all fish observed were included in the survey and restrictive underwater visual census methods (e.g., counting only individuals within 5 m of the midline of the transect tape or within a defined cylinder; Colvocoresses and Acosta, 2007) were not applied. Surveys performed in visibilities less than 5 m or lasting less than 15 minutes were excluded from statistical analyses. Water-quality parameters (surface and bottom water temperature, dissolved oxygen, and salinity) were recorded prior to each survey using a YSI multi-probe meter (Yellow Springs Instruments, Model 85).

Atlantic Goliath Grouper were considered present if at least one individual was observed during the survey. To reduce the error associated with the potential of double-counting, abundance values are minimum estimates defined as the number of Atlantic Goliath Grouper encountered during a systematic one-way survey of the area. All attempts were made to identify characteristic

marks of individual fish to further reduce the chance of double-counting, and since fish were filmed during the survey, subsequent underwater video analysis assisted with differentiation between specific individuals and provided confirmation of counts recorded in the field. A custom made laser apparatus fitted to the video camera permitted total length (TL) estimates (to the nearest cm) of fish filmed perpendicular to the optical axis of the camera.

Conventional tagging of Atlantic Goliath Grouper

Following the visual census, Atlantic Goliath Grouper were tagged *in situ* using a modified speargun to shoot the tag into the musculature directly beneath the dorsal fin. External tags were constructed of a nylon dart (Floy BFIM96 Billfish tag) modified to display an oversized plastic ID tag (6.5 x 3 cm) with enlarged text (2 cm font height) (Fig. 2.2). A telephone number on the tag encouraged anglers and divers to report fish. Prior to deployment, tags were sprayed with clear anti-foul paint (Aquagard Alumi-Koat, Flexdel Corp., NJ) to inhibit biofouling. Atlantic Goliath Grouper less than 100 cm TL were not tagged to reduce the potential for injury.

Statistics

Data did not meet the assumptions of normality, so non-parametric tests were necessary to identify the relationships between habitat characteristics and Atlantic Goliath Grouper presence, abundance and size distribution. A generalized linear mixed model (Proc Glimmix, SAS version 9.2, SAS Institute, Inc., Cary, NC USA) was used to identify relationships between Atlantic Goliath Grouper presence and abundance and the following parameters: habitat (artificial or natural), depth (deep, > 20 m, or shallow, ≤ 20 m), season, site relief ("low," < 1.5m, or "high," > 1.5 m), and site volume ("low,"< 1000 m^3, "moderate," 1000-10,000 m^3, or "high," > 10000

m^3; volume could be calculated for artificial habitats only). Presence was modeled as a binomial distribution; abundance was modeled as a negative binomial distribution. A Mann-Whitney Rank sum test was used to determine if fish size was related to habitat type (artificial versus natural), and to examine the correlation between size distribution and site parameters (depth, relief and season), a mixed model General Additive Model (GAM) was applied (using the gamm4 package in R).

Results

Research dives (n=378 total) occurred between October 11, 2007 and May 8, 2010. Of these surveys, 349 were performed in adequate visibility (> 5 m), resulting in an assessment of 44 natural (6 of which were seasonally assessed; total survey n = 104) and 36 artificial sites (12 of which were seasonally assessed; total survey n = 245) (Fig. 2.1). Natural reefs ranged in relief from 0.5 – 5.5 m (median = 1.2 m) and artificial reefs ranged in relief from 1.2 – 11.8 m (median = 3.7) and in volume from 10 – 13,716 m^3. All of the natural sites surveyed had undercuts, restricted in height by the vertical relief of the outcropping. All artificial reefs surveyed had multiple openings of at least 1 m^2. The mean survey time was 36 minutes (range 15 – 125 min). Site depths ranged 7 – 50 m. Bottom temperature during the study period ranged 14.1 – 31.7 °C. The frequency of surveys for each site was dependent upon environmental conditions, and ranged 1 – 29 surveys per site.

Presence

Atlantic Goliath Grouper were most likely to be present at high relief, artificial habitat. At least one individual was present during 90% of surveys at artificial reefs (221/245 surveys; 34/36

sites), but only during 40% of surveys at natural reefs (35/104 surveys; 17/44 sites) (Fig. 2.3). During all seasons of the year and across all depths sampled, Atlantic Goliath Grouper were present significantly less at natural habitat than at artificial habitat ($p < 0.0001$, Proc Glimmix, df = 340). Presence was lower during the winter than any other season (Table 1), especially in shallow water (Fig. 2.3). Presence increased with habitat relief for both habitat types ($p = 0.0314$; Table 1, Fig. 2.4). Atlantic Goliath Grouper presence was not related to depth ($p = 0.2268$), or site volume (volume could be calculated for artificial sites only; $p=0.9273$) (Table 2.1).

Abundance

Greatest numbers of Atlantic Goliath Grouper were observed at high relief artificial reefs in deep (> 20 m) water (Table 1). Abundance values per artificial reef survey ranged from 0 – 24 (mean = 4.77). Deep artificial reefs had larger numbers of Atlantic Goliath Grouper than shallow artificial reefs ($p<0.0001$; Table 1) and this pattern was evident through all seasons (Fig. 2.5, Fig. 2.6), with the highest numbers observed during the summer (Fig. 2.6, Table 2.1). Natural reefs had consistently low abundances of Atlantic Goliath Grouper throughout the year, and often none were observed at all (range 0 – 3 individuals; mean = 0.43; Fig. 2.6.) Higher relief reefs, both artificial and natural, were most likely to have larger numbers of Atlantic Goliath Grouper (Fig. 2.7; Table 2.1).

For artificial sites there was a positive relationship between artificial reef relief and site depth ($r^2 = 0.14$; ANOVA $p=0.03$, Fig. 2.8.) The largest artificial sites (highest relief and greatest volume) occurred in deeper water and had the greatest number of fish (Fig. 2.9), with a significant

positive relationship between Atlantic Goliath Grouper abundance and site relief ($r^2 = 0.31$, ANOVA $p = 0.0094$) as well as site volume (Fig. 2.9).

Size distribution

Underwater videography and subsequent image analyses yielded total length measurements for 65% (823/1270) of Atlantic Goliath Grouper that were filmed during surveys. Lengths verified through video image analysis ranged from 36 to 214 cm TL. Throughout the study, the majority of individuals observed were 80 – 160 cm TL (Fig. 2.10). There was no significant relationship between fish size and depth zone (Proc Glimmix; $p = 0.8171$, df = 817). Individuals as small as 67 cm TL were verified from sites as far as 80 km from shore and as deep as 36 m (Fig. 2.11). The size of fish observed in shallow (≤ 20 m) water ranged 36 – 204 cm TL, and fish measured in deep (> 20 m) water ranged 54 – 214 cm TL. Only 18 individuals were measured at natural sites, but they were significantly smaller (mean TL = 99 cm) than those observed at artificial sites (mean TL = 121 cm, n = 805; Mann-Whitney Rank Sum test: $p = 0.002$).The GAM model with repeated measures indicated no relationship between fish TL and site depth ($p = 0.790$) or site relief ($p = 0.227$), but there was a significant effect of season ($p < 0.01$), where larger fish were observed during July – September (Fig. 2.12).

Site fidelity and movement based on conventional tags

A total of 172 Atlantic Goliath Grouper were identified by unique markings or tagged *in situ* with external identification tags during surveys performed between November 9, 2007 and May 8, 2010. Re-sightings were verified for 27/172 (16%) tagged fish (Table 2.2). Most re-sightings were witnessed by the author (ABC), with only four recaptures reported by anglers. Time at

large ranged 1 – 958 days, and eight individuals were re-sighted multiple times (2 – 5 re-sightings per fish). Re-captures were reported as far as 203 km away from the initial tagging site, but most (83%) re-sightings or re-captures occurred in the same location as the initial tagging event. The majority of fish were tagged at artificial habitats (166/172 tagged fish), and all re-sightings occurred at artificial habitats. There were no re-sightings of the individuals tagged at natural sites. Only six individuals were verified at locations other than their initial tagging site, five of which provided evidence for movement between artificial reefs within the study area and one which showed movement out of the study area (Fig. 2.13; Table 2.2).

Discussion

Presence and abundance

Atlantic Goliath Grouper were present during almost all surveys at artificial reefs, but were rarely observed at natural hard bottom habitats during the study period (2007 – 2010). Within the surveyed area, artificial reefs had higher relief and offered more cover than natural reefs, and Atlantic Goliath Grouper abundance increased with vertical relief and site volume, indicating that habitat preference is driven by ample refuge opportunities. This has been observed for other groupers including gag *Mycteroperca microlepis* and scamp *M. phenax*, which have been shown to exhibit a positive relationship between abundance and vertical height of ledge undercuts (Kendall et al., 2008). In areas of limited natural structure, artificial reefs provide complex habitat that can attract and aggregate fishes (Bohnsack 1989; Hackradt et al., 2011). In the central eastern Gulf of Mexico, most of the benthic hard bottom habitat consists of low relief limestone outcroppings (Smith, 1976; Parker et al., 1983), so artificial reefs provide considerable structure in a geographic region relatively devoid of comparable high relief natural habitat.

There are over 2400 artificial reefs documented off of the Florida coast (FWC artificial reef program: myfwc.com/conservation/saltwater/artificial-reefs/), and the role that these reefs – especially the large, high volume structures (shipwrecks) – play in the distribution of Atlantic Goliath Grouper is becoming evident as the population recovers. The habitat preference of Atlantic Goliath Grouper for artificial reefs suggests that fish become more aggregated than they would be under natural conditions within this region. Alternatively, artificial reefs may increase abundance of Atlantic Goliath Grouper for a geographic range previously low in numbers by creating additional habitat opportunities. Whether or not the artificial reefs are a benefit to the population by increasing production (i.e., "source"), or are simply aggregating fish by providing a behaviorally preferred habitat type (i.e., "sink") remains open for investigation.

Before the harvest moratorium, the majority of commercially harvested Atlantic Goliath Grouper were landed along Florida's southwest coast (Bullock et al. 1992), an area believed to be a center of abundance for this species due to the extensive mangrove nursery habitat that exists south of Naples (Bullock and Smith, 1991; Sadovy and Eklund 1999; Koenig et al. 2007). The species was recorded periodically along the central and northwest coast of Florida (Smith, 1976; Gilmore et al., 1978; Bullock and Smith 1991) and as far north as Mississippi and Louisiana (Franks 2005), but limited information is available pertaining to the current status of the species within the current study area (but see Koenig et al., 2011). As the Atlantic Goliath Grouper population recovers, it should be expected that individuals will begin to occur farther from the population center of abundance in southwest Florida and into areas of less "optimal" habitat (MacCall 1990). Density dependent habitat selection states that as abundance (and

therefore competition) increases, individuals should overflow into less and less “optimal” habitat (Rosenzweig 1981; MacCall, 1990; Lindberg et al., 2006). In the same light, densities over the best habitat often will not reflect population decline until significant reductions have already occurred (Rose and Kulka, 1999). This is due to the shift of individuals into optimal habitat from surrounding, less favorable habitat as overall population decline occurs (Fretwell and Lucas, 1970; Jennings et al., 2001.)

Most populations are assumed to preferentially occupy habitats that allow individuals to maximize growth and reproduction while minimizing predation risk (Walters and Martell, 2004), and animal abundance and distribution have traditionally been considered to be limited in part by available resources (i.e, shelter, food; Solomon, 1949; Hairston et al., 1960; Fretwell and Lucas, 1970; Bohnsack, 1989). The positive relationship between hard bottom habitat and the diversity and abundance of temperate and tropical reef fishes has been well demonstrated (Connell and Jones, 1991; Hixon and Beets, 1993; McCormick 1994; Knowlton, 2001; Almany 2004). Fish association with complex habitat may also be a function of predator avoidance (e.g., White, 2007; Piko and Szedlmayer 2007) and/or feeding strategy (i.e., reduced detection by prey; Helfman, 1979). Predatory fishes may move into shade in order to better detect prey in more illuminated areas (Helfman, 1981) and to decrease the odds of being detected (e.g., Horinouchi et al., 2009). Additionally, structural complexity may also serve to concentrate prey (Jones, 1991; Almany, 2004; Arena et al., 2007). Atlantic Goliath Grouper are opportunistic ambush predators, so large artificial reefs should provide enhanced cover and increase ambush success.

In some cases the availability of shelter and refuge may be a more important factor in habitat selection than competition for food. For example, Gag grouper (*Mycteroperca microlepis*) have

been observed to occur in higher densities at larger artificial reefs, and were found to sacrifice growth for shelter (Lindberg et al., 2006). The number of Atlantic Goliath Grouper observed during this study was positively associated with site size (relief and volume), and although high abundances (>20) were noted, the average number recorded was only between 4 and 5 individuals at artificial reefs (and less than 1 for natural reefs). Data regarding the metabolic needs of Atlantic Goliath Grouper in the wild are not available, but an adult Atlantic Goliath Grouper (weighing approximately 82 kg) in an aquarium was observed to consume only 3.5 – 5 kg of food per month (4 – 6% of total body weight; Kittell and Ratte 2008). Consistent numbers of Atlantic Goliath Grouper observed at sites surveyed seasonally suggest that these areas maintained approximately the same number of individuals throughout the year. Whether or not the density of Atlantic Goliath Grouper at a particular reef is constrained by prey availability, refuge space or current population levels remains open for further investigation and continued research should be directed at addressing this issue as the stock recovers.

Atlantic Goliath Grouper are sensitive to low temperatures (< 15° C; Gilmore et al., 1978; FWC unpublished data), so even as the population recovers, the northern range should remain restricted by the thermal tolerance of the species. Although individuals have been reported in the Gulf of Mexico as far north as the Florida Panhandle and the mouth of the Mississippi River (Franks, 2005; E. Chesney pers. comm.; A. Collins, pers. obs.) these individuals are likely present only seasonally and will move south or to deeper water during the colder months of the year when bottom water temperatures are regularly below 15° C. Within the current study area, Atlantic Goliath Grouper were present during surveys throughout all months of the year. There were less fish observed at shallow sites during the winter months, which may have been a result

of lower water temperatures during the coldest months of the year (<15 ° C; Appendix 1) or alternatively, lower detection capability by divers since Atlantic Goliath Grouper become less active when the water is cold (Collins, pers. obs.). Regardless, multiple individuals were still recorded at most sites within the study area during all seasons (Fig. 2.3; Fig. 2.5) which suggests year round residence of the species within the study region.

Size distribution

This study aimed to document the sizes of Atlantic Goliath Grouper at natural and artificial reef habitats in the central eastern Gulf of Mexico in order to estimate the general size distribution of individuals within this region. Length (and by proxy, age) composition of a stock can be correlated with population size and indicate stock status (Ricker, 1963; Jennings et al., 2001); thus, quantifying the size distribution of Atlantic Goliath Grouper is an important component when attempting to assess population recovery.

Most individuals recorded during visual surveys for the current study were between 100 and 150 cm TL, corresponding with an age distribution of approximately 5 – 15 years (Bullock et al., 1992). For a fish that can live to at least 37 years of age and exceed 200 cm TL (Bullock et al., 1992), the majority of fish observed during this study were relatively young and many were likely immature (length at maturity = 110 – 135 cm TL; Bullock et al., 1992). Life history theory predicts the size and age distribution of most marine fish populations will be typically skewed to the left (older fish are ultimately less numerous than younger ones; Walters and Martell 2004), so the size distribution reported herein is not necessarily surprising. The current study observed a median TL of 121 cm (range 35 – 213 cm), based upon visual surveys that were

restricted to a relatively defined region of the eastern Gulf of Mexico. In the only study regarding size and age distribution of Atlantic Goliath Grouper in Florida, Bullock et al. (1992) collected data mostly from fisheries landings throughout the state of Florida, and observed a median TL and age of 168 cm (range = 8 – 216 cm) and 13 years (range = 0 – 37 y). However, their data were collected after the population had already suffered significant declines and size and age truncation. There is therefore no existing "healthy" baseline with which to compare current population parameters. The life history characteristics of Atlantic Goliath Grouper make them especially vulnerable to overharvest and removal of the largest and oldest individuals has the potential to further increase population fluctuation and volatility (Anderson et al., 2008); thus any change in fishing regulations should be approached as cautiously as possible.

After a planktonic larval period, juvenile Atlantic Goliath Grouper settle within shallow, inshore estuaries and bays. Similar to other groupers (Bullock and Smith, 1991; Ross and Moser, 1995), an ontogenetic shift to deeper water occurs around the size at which Atlantic Goliath Grouper approach maturity (> 1 meter TL) (Bullock et al., 1992; Gerhardinger et al., 2006). Other fished reef fish species in the Gulf of Mexico (i.e., hogfish *Lachnolaimus maximus*, Collins and McBride, 2011; gag *M. microlepis*, Coleman et al., 1996) show a significant increase in size with increasing depth, and it was initially expected that the largest Atlantic Goliath Grouper would be observed the farthest from shore. Size-based offshore migration of Atlantic Goliath Grouper did not appear to be obligatory, however, as large adults (> 150 cm) were observed throughout the depth range sampled and there was no relationship between depth or distance from shore and the size distribution of fish observed. Interestingly, smaller (< 1 m TL), presumably sub-adult fish, were also observed throughout the surveyed area, including offshore sites, suggesting that the

species may disperse offshore at earlier ages than previously believed. It is also possible that a proportion of the population has always displayed this strategy and simply went unnoticed due to reduced population numbers and the absence of regular surveys and directed research activities.

Although large adults were observed throughout the depths surveyed, the largest sizes and numbers of Atlantic Goliath Grouper occurred at deep artificial reefs during the summer. Atlantic Goliath Grouper in Florida aggregate to spawn July through September (Bullock et al., 1992; Sadovy and Eklund 1999) and will migrate long distances to reach spawning aggregation sites (Eklund and Schull, 2001; Koenig and Coleman, 2009, 2013; Collins unpublished data). Previously documented spawning aggregations in the southeastern Gulf of Mexico were deep artificial reefs (35 – 45 m; Porch and Eklund 2004; Sadovy and Eklund 1999; Mann et al., 2009; D. DeMaria, pers. comm.), but there have been no confirmed spawning aggregations identified within the study area. It is possible that the peak in large individuals during the summer at the deepest artificial reefs was related to spawning, but this was not verified and requires additional investigation.

Site fidelity and movement based on conventional tags

Most groupers are typically sedentary and have been characterized as spending a high proportion of their time "resting" (Donaldson, 1995; Sluka et al., 1998). High site fidelity has been observed for multiple grouper species (i.e. gag *Mycteroperca microlepis*, Kiel, 2004; dusky grouper *E. marginatus*, Lembo et al., 2002; and Nassau grouper *E. striatus*, Sadovy and Eklund, 1999). Individual adult Atlantic Goliath Grouper off the southwest coast of Florida have been resighted at the same location for up to three years (Eklund and Schull, 2001). Similarly, acoustically

monitored juveniles remained within small defined areas of nursery habitat in the Ten Thousand Islands region of Florida for many months (Frias-Torres et al., 2007; Koenig et al., 2007). Thus, site fidelity of tagged Atlantic Goliath Grouper during this study was not unexpected and almost all individuals resighted were in fact reported at their initial location up to 958 days after tagging. This high site fidelity, combined with the tendency to aggregate over structure that is relatively accessible to anglers, makes Atlantic Goliath Grouper particularly vulnerable to overfishing, and repeated catch and release events may lead to decreased fitness of fish at frequently visited sites due to jaw damage, handling stress or potential barotrauma effects (Huntsman et al., 1999).

Although it appears that most Atlantic Goliath Grouper maintain residence at specific sites for extended periods, the recapture data herein demonstrated that long distance movements are possible. Movements reported for six of the tagged fish ranged 10 to 203 km from the initial site of tagging. Similar findings were reported by Koenig and Coleman (2009) who confirmed Atlantic Goliath Grouper movements exceeding 200 km. These observations are important when creating management and protection guidelines, since areas of vulnerability range temporally from relatively small daily activity spaces to lifetime ranges that have the potential to encompass hundreds of kilometers.

Conclusions

Artificial reefs were the preferred habitat for Atlantic Goliath Grouper within the study area in the central eastern Gulf of Mexico. Individuals were present during almost all surveys at artificial reefs, where average abundances were typically between four and five individuals but increased with site relief and site volume. Atlantic Goliath Grouper were present less than half of

the time and in very low abundances at natural reefs (mean abundance < 1), and this is likely due to the fact that most of the natural hard bottom in the study region consists of low relief limestone outcroppings that offer minimal cover for large-bodied fish. Fish ranged in size from 36 to 214 cm TL, demonstrating the occurrence juvenile and large adult individuals at offshore habitat, but most individuals were between 80 and 160 cm TL. There was no relationship between fish size and distance from shore. Conventional tags indicated high site fidelity, but also demonstrated the ability of individuals to travel distances as far as 203 km. Interpretations of conventional tagging data are limited since the location of individuals between recapture or resighting events is unknown. Future studies that utilize acoustic monitoring of individuals to better define residence times and fine scale movement patterns within the region are warranted.

Advances in technology (e.g., depth sounders, side-scan sonar, underwater video cameras) continue to increase human ability to locate marine hard bottom habitats, which assists with monitoring and management efforts but also increases fish susceptibility to harvest by making them easier to find. The tendency for Atlantic Goliath Grouper to gather predictably around high relief structure escalates the interaction between Atlantic Goliath Grouper and anglers and increases vulnerability to intense fishing pressure. The findings reported herein provide information regarding spatial and temporal habitat associations of a protected species in the central eastern Gulf of Mexico, and should inform regulatory guidelines and management efforts regarding conservation.

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Table 2.1. Results of PROC GLIMMIX test for effects of habitat type (artificial vs. natural), depth zone (deep vs. shallow), relief (high vs. low), seasonal quarter (where 1 is winter Jan – Mar, 2 is spring Apr – Jun, etc.) and volume (low, moderate or high) on the presence and abundance of Atlantic Goliath Grouper *Epinephelus itajara* observed during underwater visual surveys within the central eastern Gulf of Mexico. Presence was modeled as a binomial distribution; abundance was modeled as a negative binomial distribution. Significant differences ($p < 0.05$) are indicated in bold.

	Presence				Abundance		
	DF	F	P	Diff of LS means (p-value)	F	P	Diff of LS means (p-value)
Habitat (artificial v. natural)	1/342	17.23	**<0.0001**		38.12	**<0.0001**	
Depth zone (deep v. shallow)	1/342	1.47	0.2268		9.10	**0.0027**	
Relief (high v. low)	1/342	4.67	**0.0314**		8.10	**0.0047**	
Season	3/342	3.17	**0.0244**		2.32	0.0748	
Winter v. spring				**0.0056**			0.3521
Winter v. summer				**0.0146**			**0.0255**
Winter v. fall				**0.0127**			0.7468
Spring v. summer				0.7513			0.1062
Spring v. fall				0.9625			0.5231
Summer v. fall				0.7576			**0.0382**
Volume (low, moderate or high; artificial habitats only)	2/215	0.08	0.9273		16.09	**<0.0001**	

Table 2.2. Tag/recapture data for Atlantic Goliath Grouper *Epinephelus itajara* that have been re-sighted since their initial tagging date. Days at large indicates number of days between sightings (* = recaptured and reported by angler; ** = caught by author [AC] via hook and line as part of another study). Distance moved is the straight line distance between sites of tagging and resighting. Individual IDs correspond to their tag ID; individuals HK and YS were not tagged but had distinctive features that allowed for easy recognition.

Individual	Tag date	Resight date	Days at large	Distance moved from tagging location (km)	Size at tagging (TL, cm)	Depth of site at tagging, depth of site at resighting (m), if different
1	11/9/2007	11/29/2007	20	0	152	26
11	12/1/2007	6/22/2008*	204	203	122	19, 9
18	12/29/2007	7/20/2008	204	29	140	28, 34
31	2/4/2008	5/30/2008	116	0	100	18
55	4/2/2008	4/3/2008	1	0	181	28
57	4/2/2008	4/3/2008	1	0	178	28
67	4/18/2008	6/3/2008	46	0	133	19
87	6/3/2008	7/10/2008	37	0	142	19
90	6/3/2008	6/11/2008*	8	16	153	34, 26
		7/10/2008	37	16		
93	6/4/2008	7/4/2008	30	0	155	9
103	7/10/2008	7/23/2008	13	0	135	25
107	7/18/2008	7/27/2008	9	0	143	29
112	7/20/2008	7/23/2008	3	0	118	34
113	7/20/2008	7/23/2008	3	0	135	34
136	8/8/2008	9/4/2008	27	0	100	21
		9/28/2008	51	0		
137	8/8/08	7/22/10*	713	10	170	21, 19
159	10/10/2008	8/28/2009	322	28	129	31, 30
184	5/8/2009	5/9/2009	1	0	139	32
		6/1/2009	24	0		
188	5/11/2009	8/11/2009	92	0	110	19
HK	5/15/2009	5/25/2009	10	0	190	21
		6/25/2009	41	0		
190	6/8/2009	6/20/2009	12	0	137	30
		7/10/2009	32	0		
		7/21/2009	43	0		
		8/28/2009	81	0		
		10/7/2009	121	0		
194	6/9/2009	8/4/2009	56	0	114	26
		9/1/2009	84	0		
		10/13/2009	126	0		
YS	6/17/2009	6/25/2009	8	0	80	19
197	7/3/2009	7/10/2009	7	0	179	19, 26
		8/15/2009	43	15		
200	6/1/2009	6/25/2009	24	0	149	19
		7/9/2009	38	0		
		8/11/2009	71	0		
		10/1/2009	122	0		
206	11/17/09	11/24/10*	372	0	150	26
208	11/17/09	4/14/11**	513	0	182	26
		7/2/12**	958	0	190	

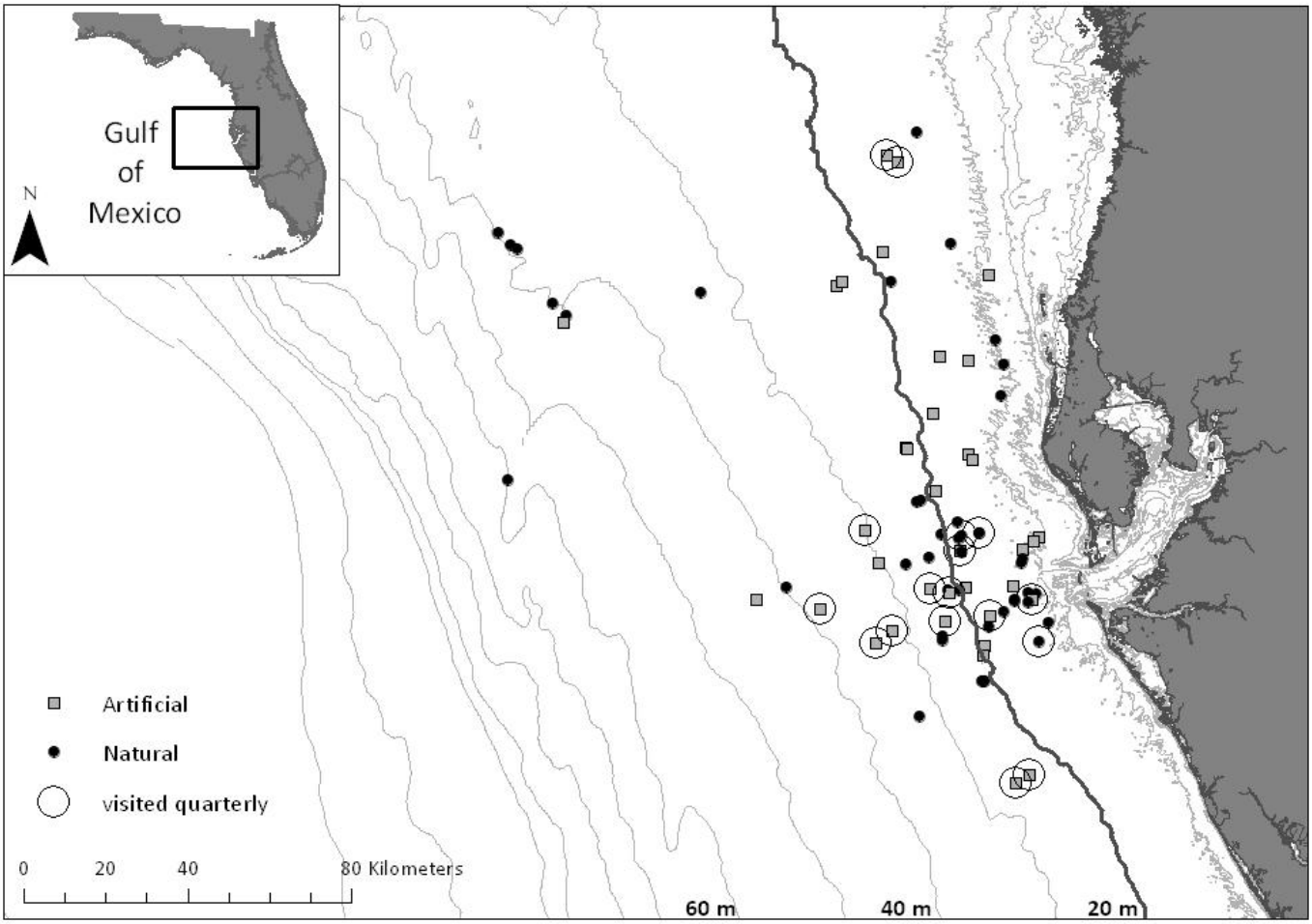

Fig. 2.1. Study area within the central eastern Gulf of Mexico. A total of 349 surveys were performed at 80 different sites classified as artificial (n=36) or natural (n=44) habitat between November 2007 and May 2010. Sites visited at least quarterly (n=18) are circled. Offshore bathymetry contours are displayed by 10 m intervals; shallow sites are inside 20 m as indicated by the bold contour line.

Fig. 2.2. An Atlantic Goliath Grouper *Epinephelus itajara* fitted with an external ID tag. Large print assists divers with resighting and individual identification, and a telephone number directs anglers to report tagged fish to the Florida Fish and Wildlife Conservation Commission tagged fish hotline.

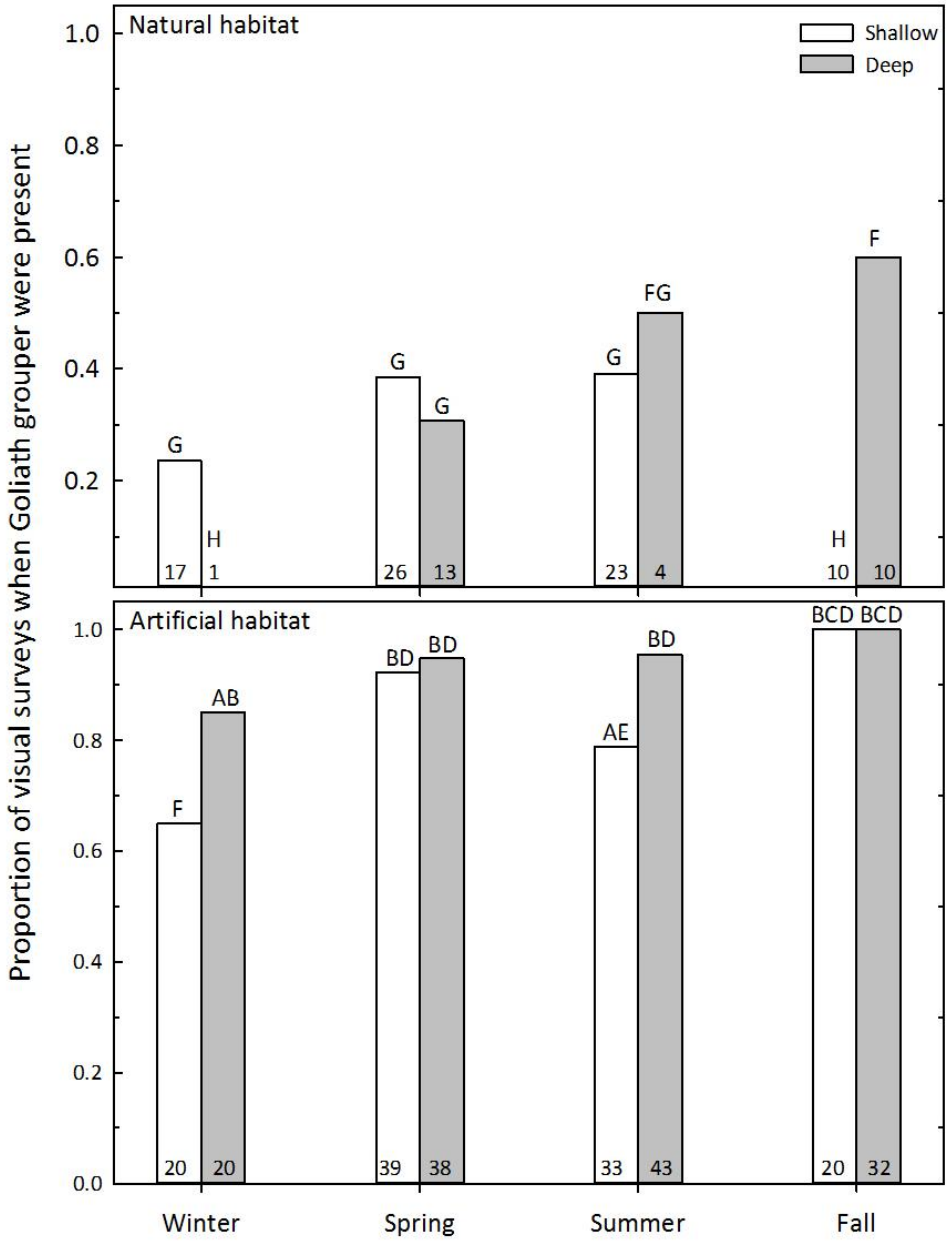

Fig. 2.3. The proportion of surveys performed where at least one Atlantic Goliath Grouper *Epinephelus itajara* was observed. Data are grouped by habitat type (natural, top panel or artificial, bottom panel), depth (shallow, ≤ 20 m, or deep, > 20 m) and season (winter is January - March, spring is April - June, summer is July - September and fall is October – December). The total number of surveys performed for each season/depth combination is displayed within each bar. Atlantic Goliath Grouper were observed more at artificial habitats than natural habitats in all depths and all seasons. Statistical differences between seasons and depth zones at artificial habitats are indicted by letter groups above each bar. Groups with the same letter are not statistically different (e.g., AC and AB are not different but AE and BD are.)

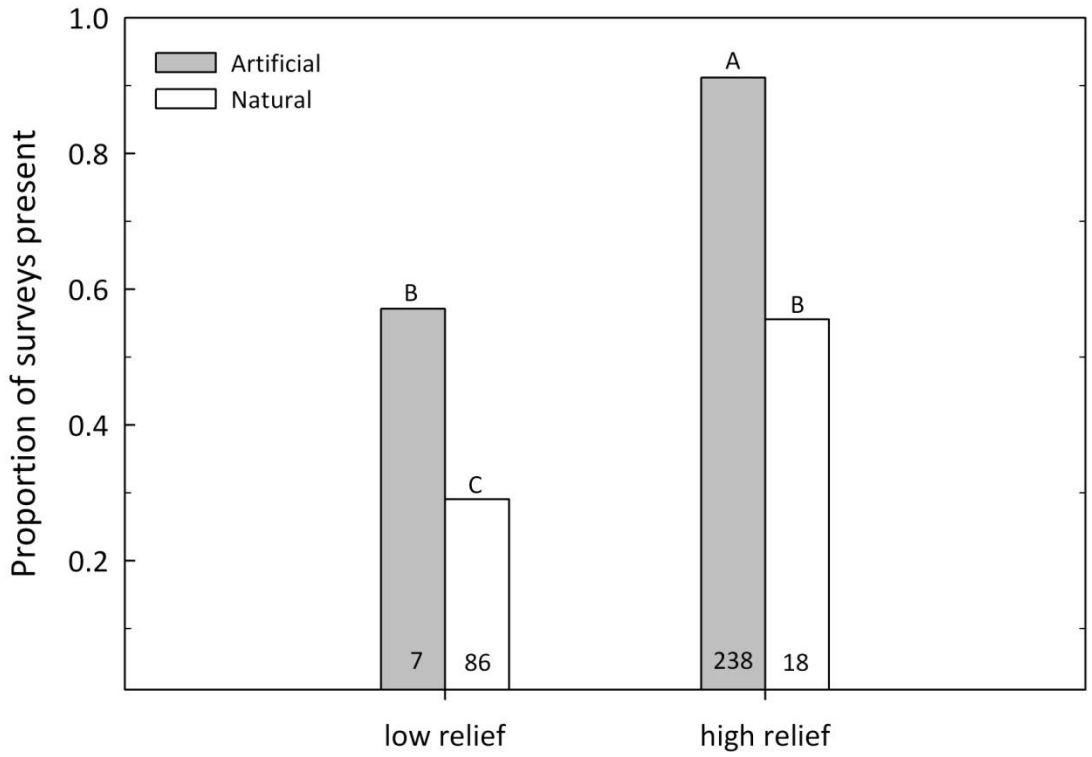

Fig. 2.4. The proportion of surveys performed where at least one Atlantic Goliath Grouper *Epinephelus itajara* was observed, by habitat type and relief, where low relief sites are < 1.5 m and high relief sites are ≥1.5 m. The total number of surveys performed for each habitat/relief combination is displayed within each bar. Statistical differences between groups are indicted by letters above each bar.

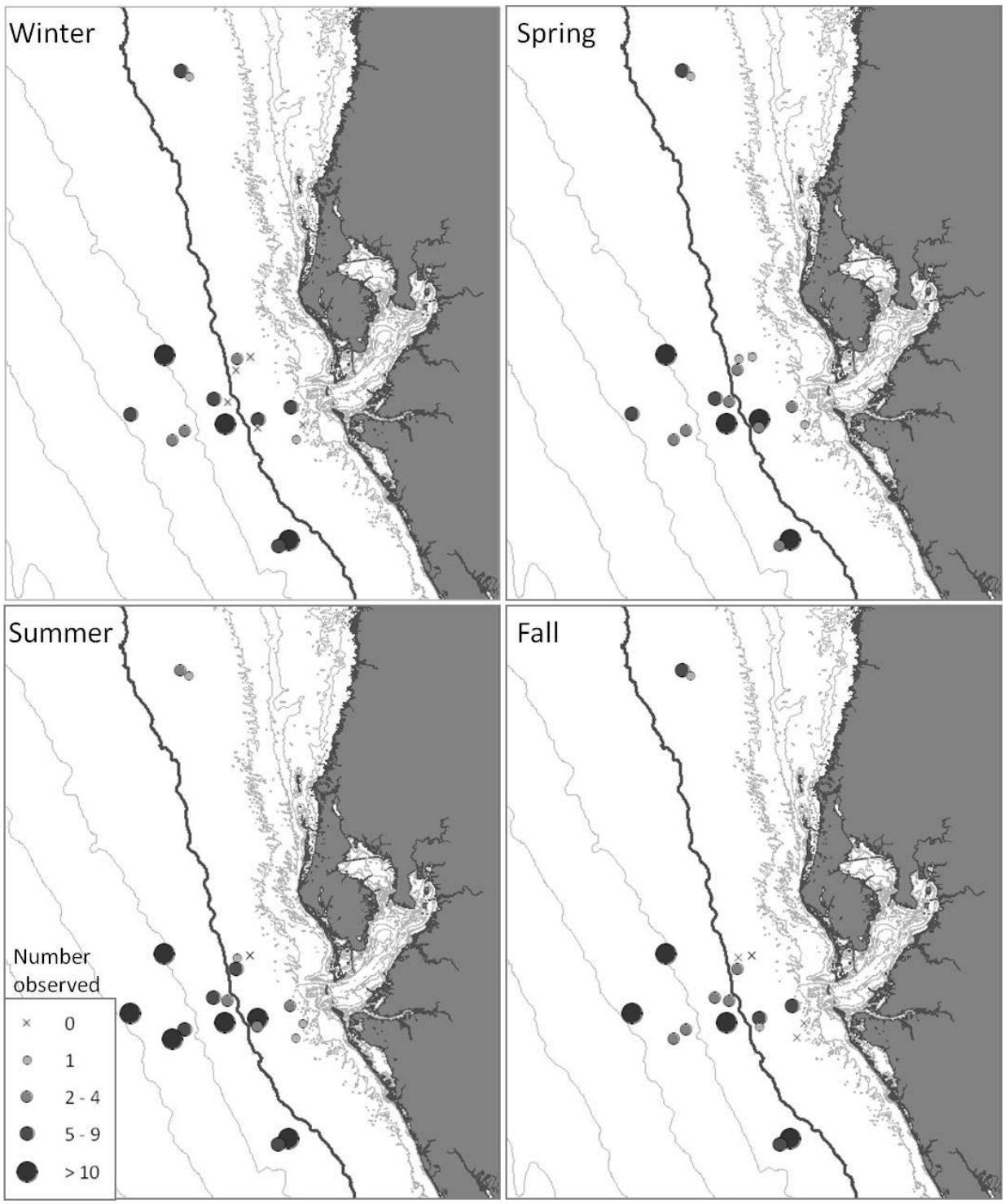

Fig. 2.5. Mean number of Atlantic Goliath Grouper *Epinephelus itajara* by season for sites surveyed quarterly.

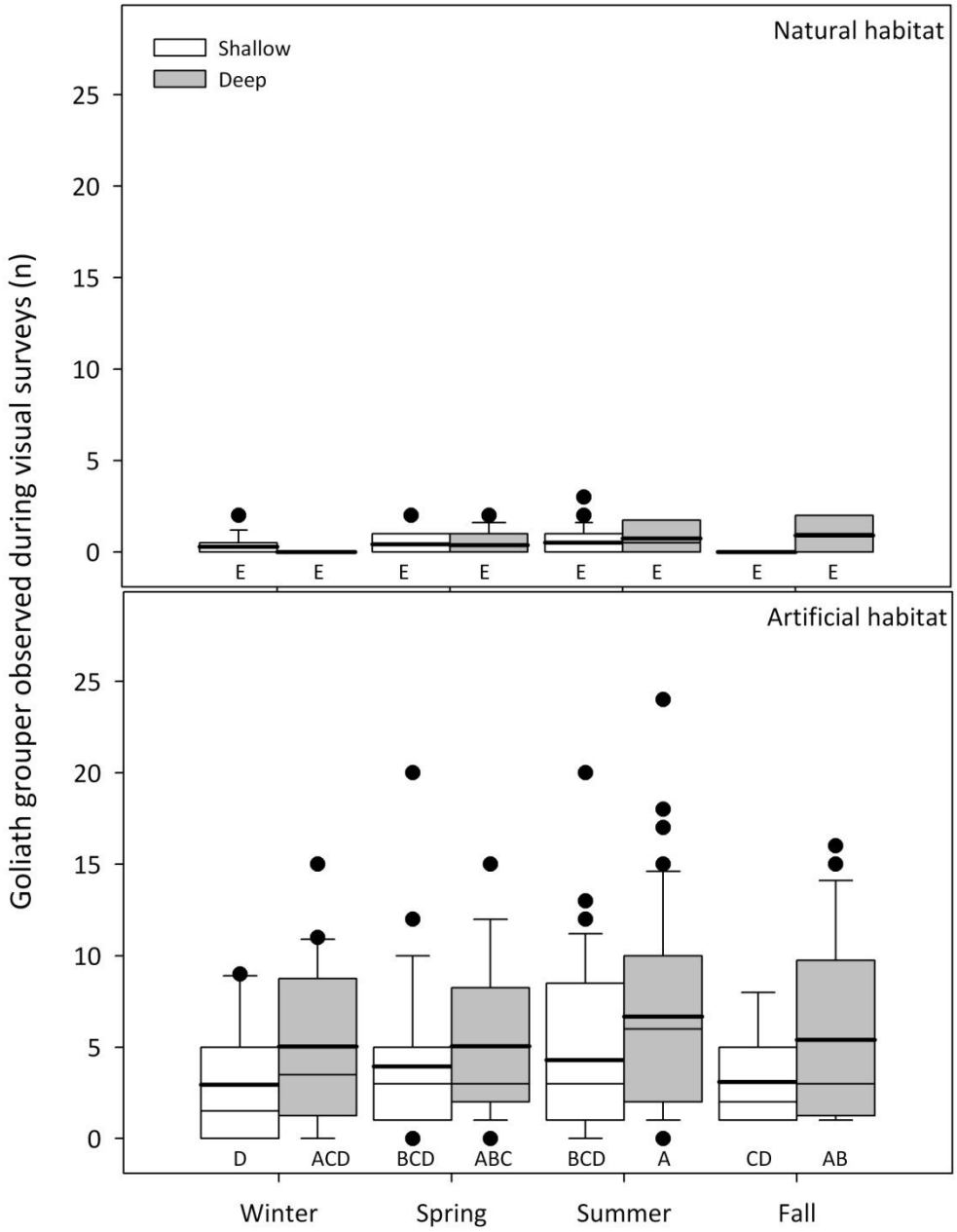

Fig. 2.6. The number of Atlantic Goliath Grouper *Epinephelus itajara* observed per season during surveys of natural and artificial habitats within shallow (≤ 20m) and deep (> 20 m) water. The mean of each data set is represented by the bold solid line, the median by the thin line, the boxes indicate the interquartile range, and 95% confidence intervals are contained within the error bars. The bold dots indicate observations that fall outside the confidence intervals. Letter groups indicate significant differences among groups.

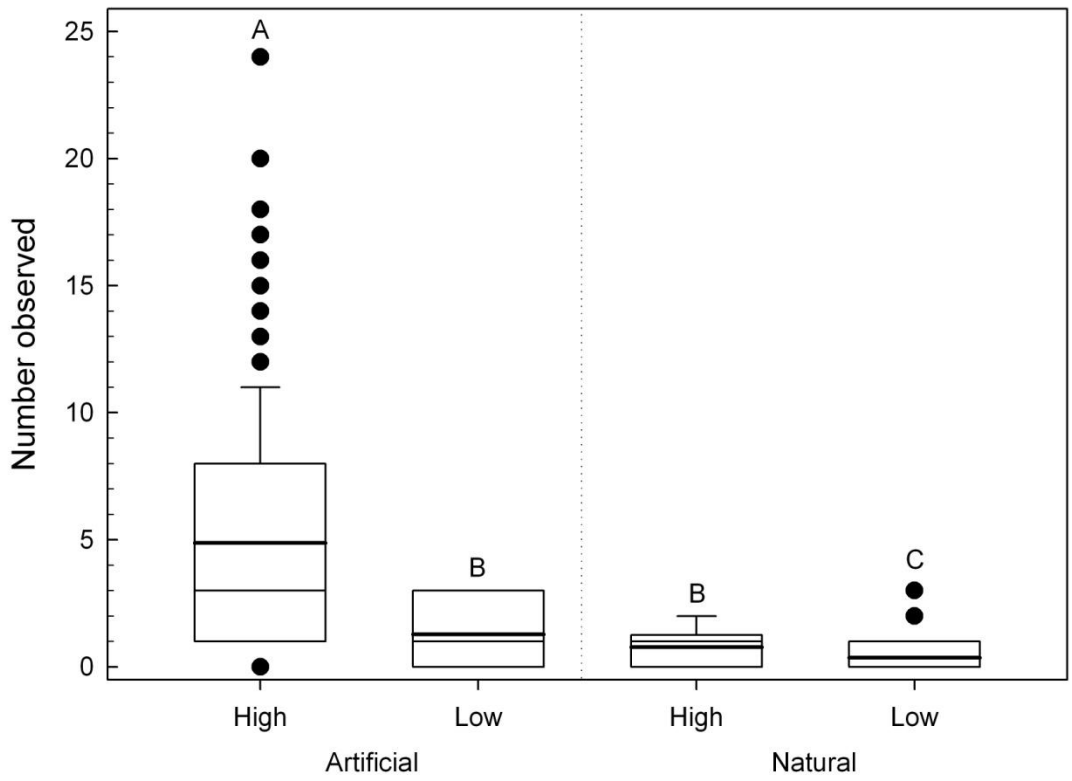

Fig. 2.7. The number of Atlantic Goliath Grouper *Epinephelus itajara* observed at high (≥1.5 m) and low relief (< 1.5 m) artificial and natural reefs. The mean of each data set is represented by the bold solid line, the median by the thin line, the boxes indicate the interquartile range, and 95% confidence intervals are contained within the error bars. The bold dots indicate observations that fall outside the confidence intervals. Letters denote significant differences in the number of Atlantic Goliath Grouper observed.

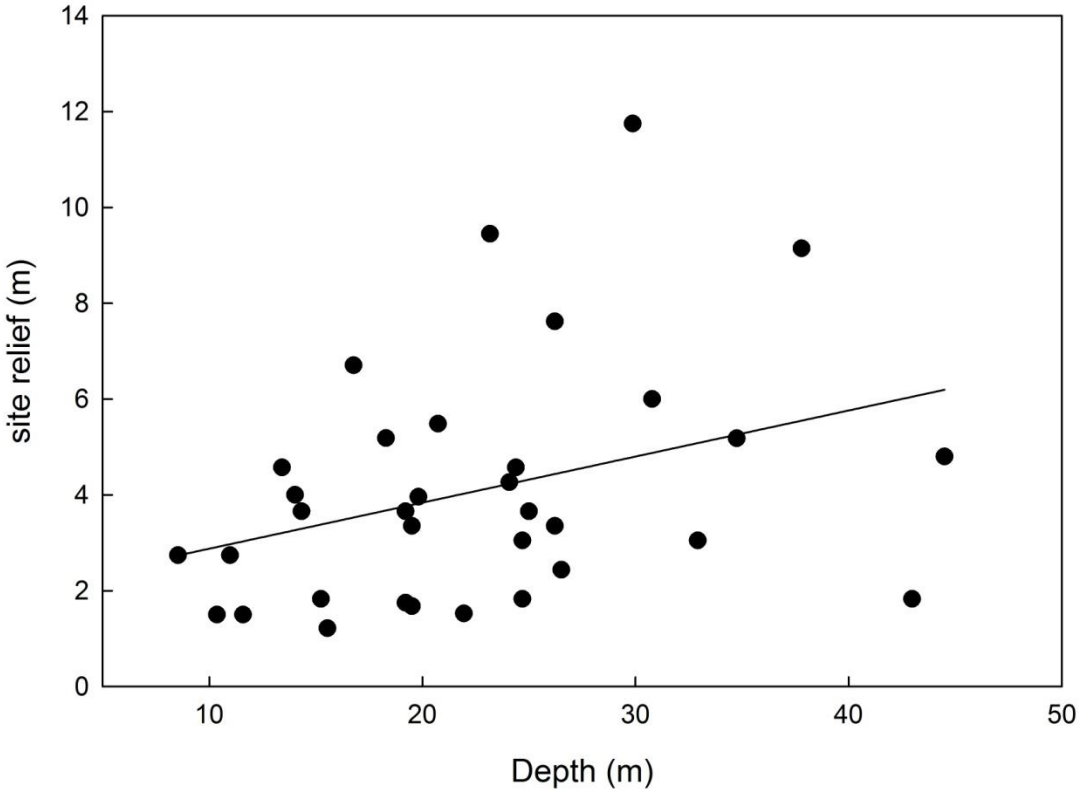

Fig. 2.8. Site relief versus site depth for artificial habitats surveyed during this study. Data were log transformed and assessed for a relationship using linear regression ($r^2 = 0.14$; $p = 0.029$).

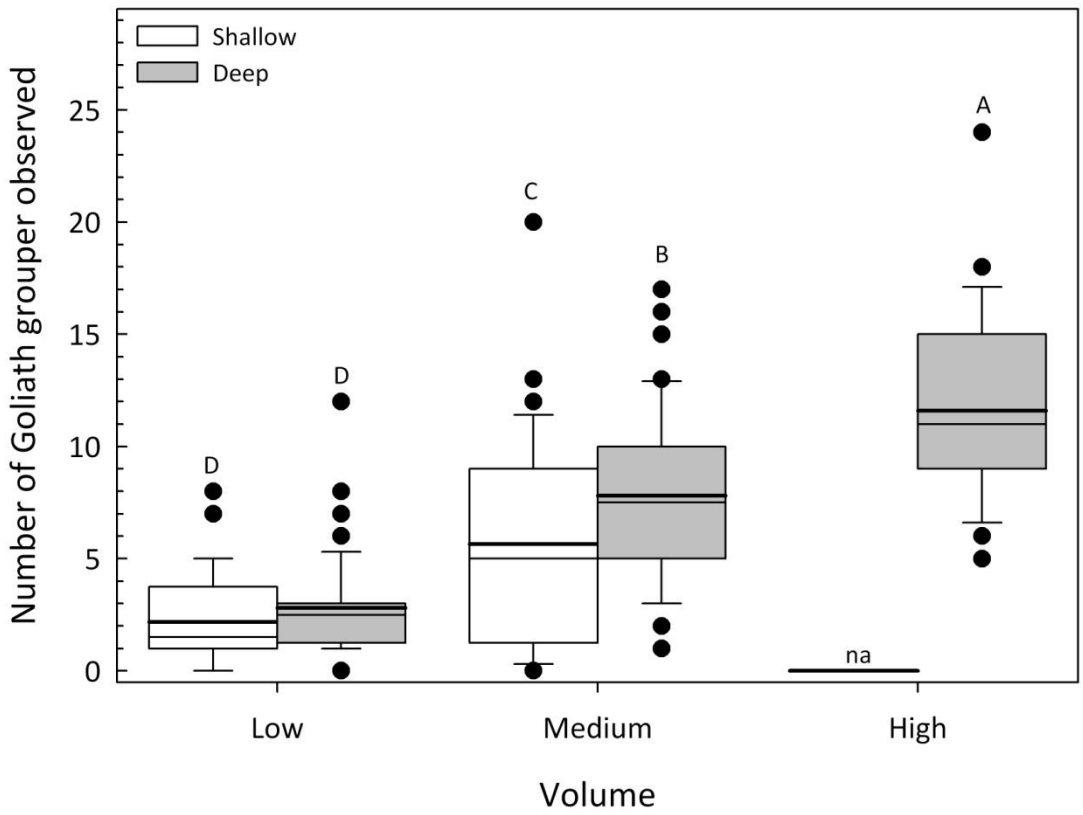

Fig. 2.9. Box plots represent the number of Atlantic Goliath Grouper *Epinephelus itajara* observed by volume of site at deep (> 20 m) and shallow (≤20 m) artificial reefs. There were no high volume artificial reefs surveyed in shallow water (na). Volume is characterized as low (< 1000m^3), medium (1000 – 10,000 m^3) or high (>10,000 m^3). The mean of each data set is represented by the bold solid line, the median by the thin line, the boxes indicate the interquartile range, and 95% confidence intervals are contained within the error bars. The bold dots indicate observations that fall outside the confidence intervals. Letter groups indicate significant differences among groups.

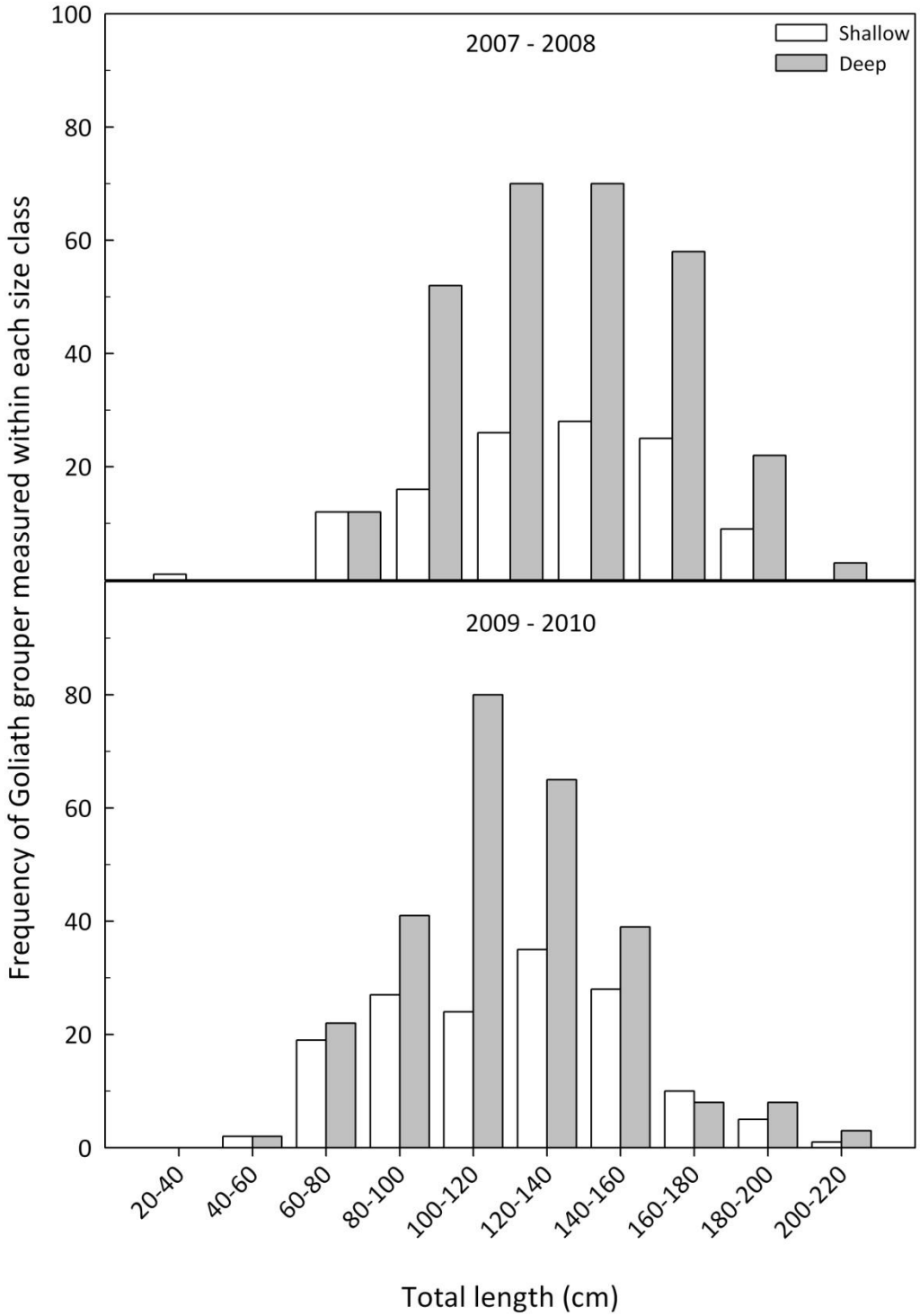

Fig. 2.10. Size distribution of Atlantic Goliath Grouper *Epinephelus itajara* measured during the study period (November 2007 – May 2010). Frequency distributions are split into time frames (October 2007 – December 2008, top panel, and January 2009 – May 2010, bottom panel). There were no significant differences in size frequencies across years.

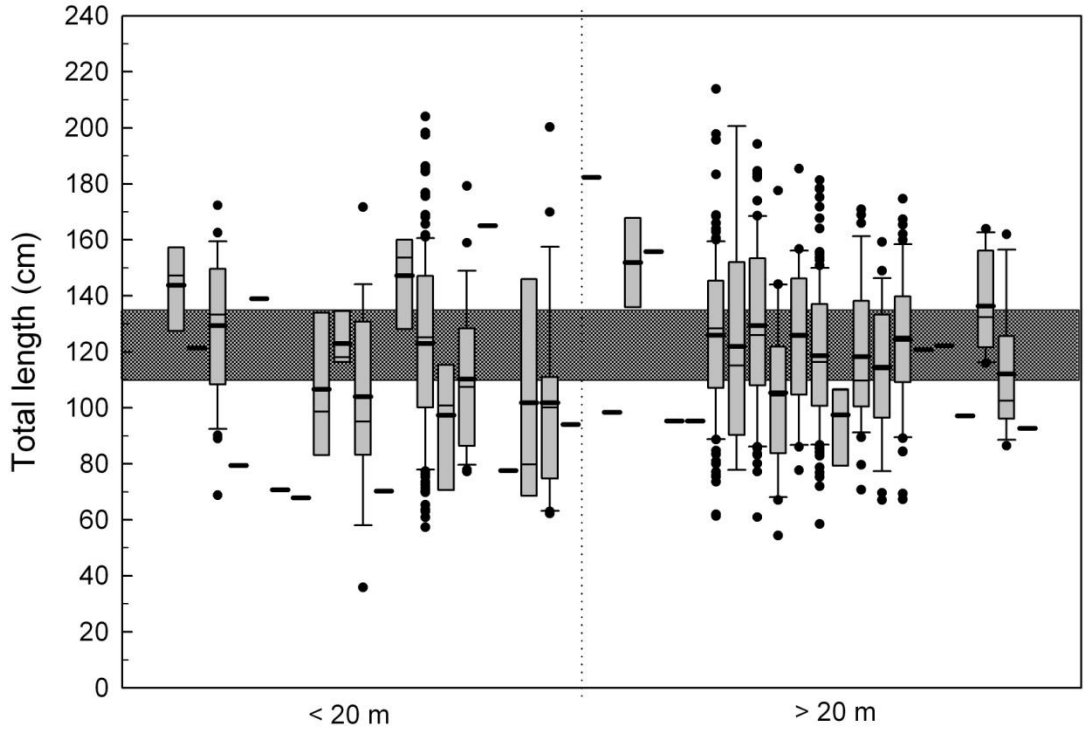

Fig. 2.11. Size distribution of Atlantic Goliath Grouper *Epinephelus itajara* observed at each site surveyed between November 2007 and May 2010. Sites (n = 42) are arranged in order of depth from left to right (7- 48 m) and include all sites for which Atlantic Goliath Grouper were observed and measured. The shaded horizontal bar represents the size range at which Atlantic Goliath Grouper mature (110 – 135 cm TL; Bullock et al., 1992).The dotted line indicates the 20 m break. The mean of each data set is represented by the bold solid line, the median by the thin line, the boxes indicate the interquartile range, and 95% confidence intervals are contained within the error bars. Sites that only show the mean value (bold solid line) indicate that < 3 fish were measured.

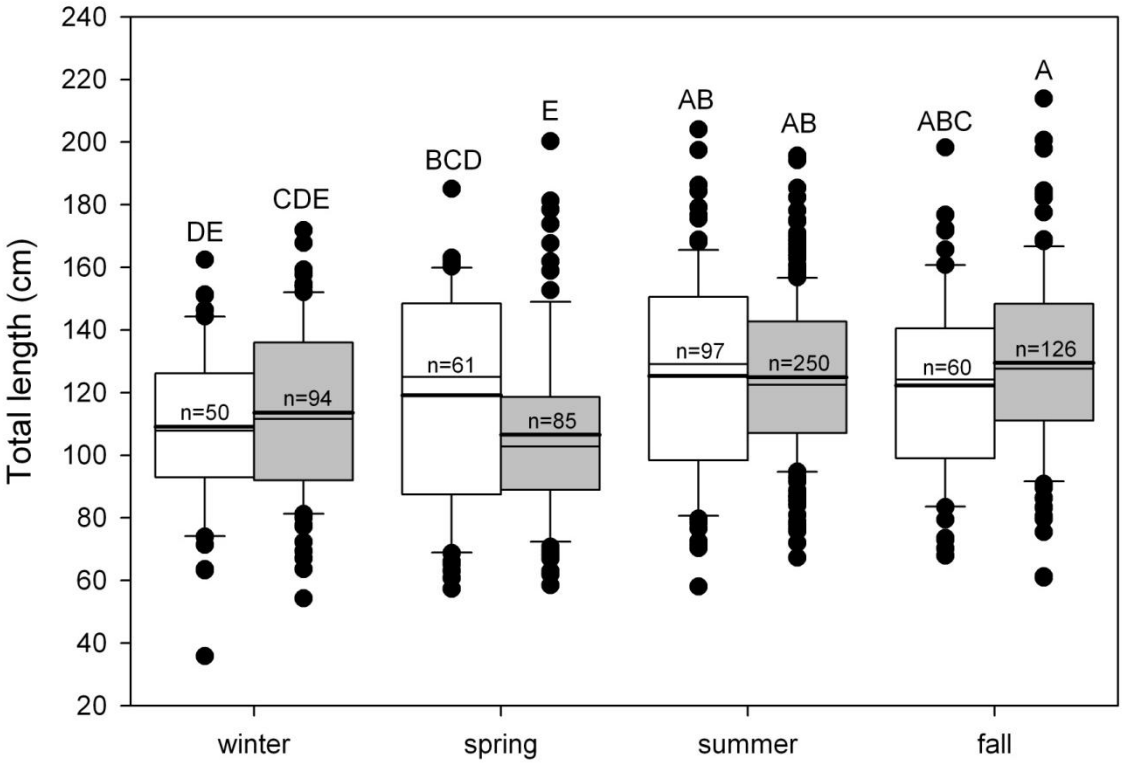

Fig. 2.12. Size range of Atlantic Goliath Grouper *Epinephelus itajara* observed by season for shallow (white boxes) and deep (shaded boxes) surveys. Numbers of measured fish are denoted inside each box. The mean of each data set is represented by the bold solid line, the median by the thin line, the boxes indicate the interquartile range, and 95% confidence intervals are contained within the error bars. Letters denote significant differences in size among seasons and/or depth zones (i.e., ABC and BCD are not statistically different but AB and DE are.)

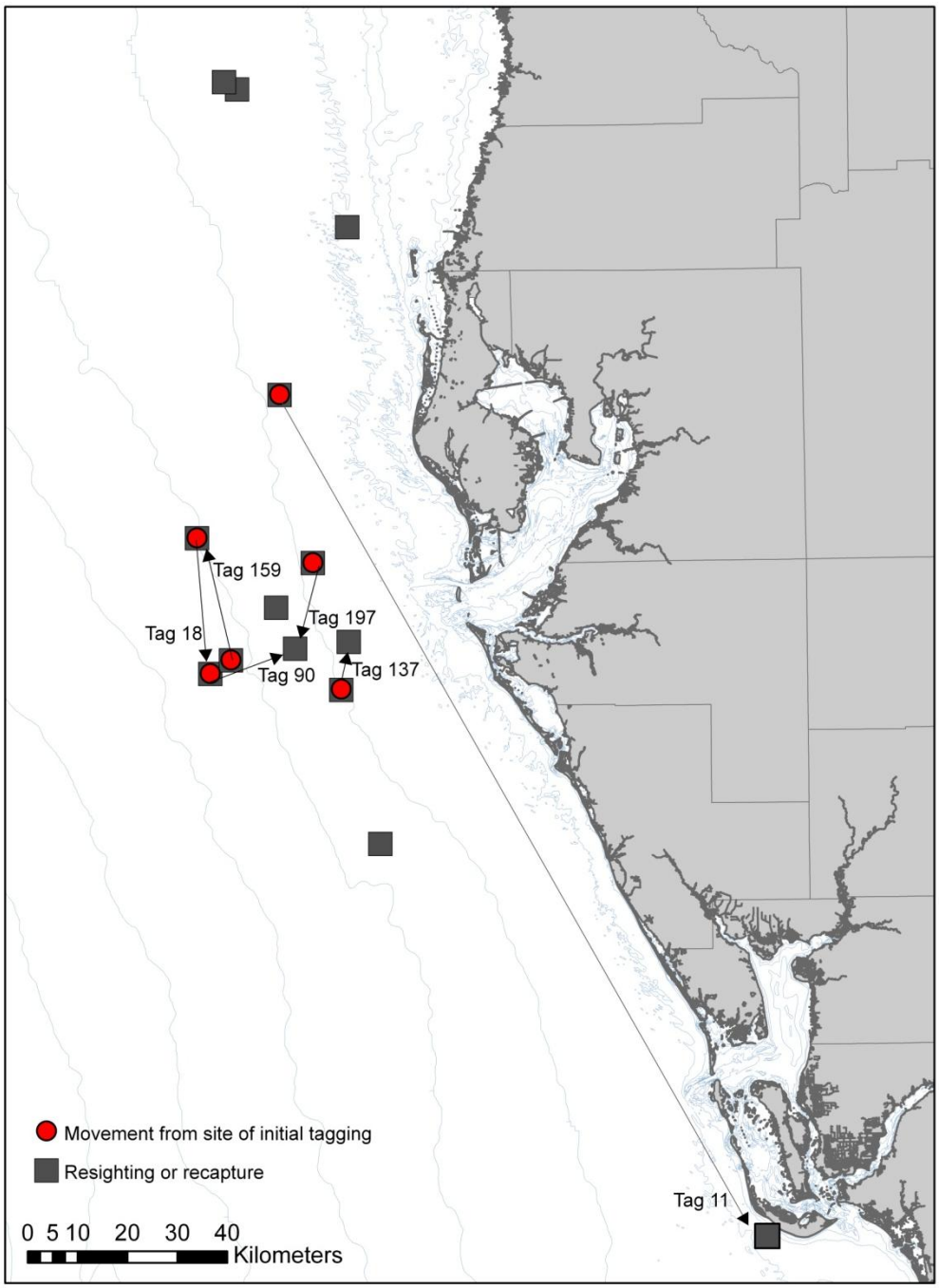

Fig. 2.13. Movement of conventionally tagged Atlantic Goliath Grouper *Epinephelus itajara*. The majority of individuals were resighted at the same location as the initial tagging event. Grey squares indicate sites where fish were recaptured by anglers or resighted during visual surveys. Movements (up to 203 km) were verified for six individuals. Movement directions are indicated by arrows; red circles indicate the sites of initial tagging.

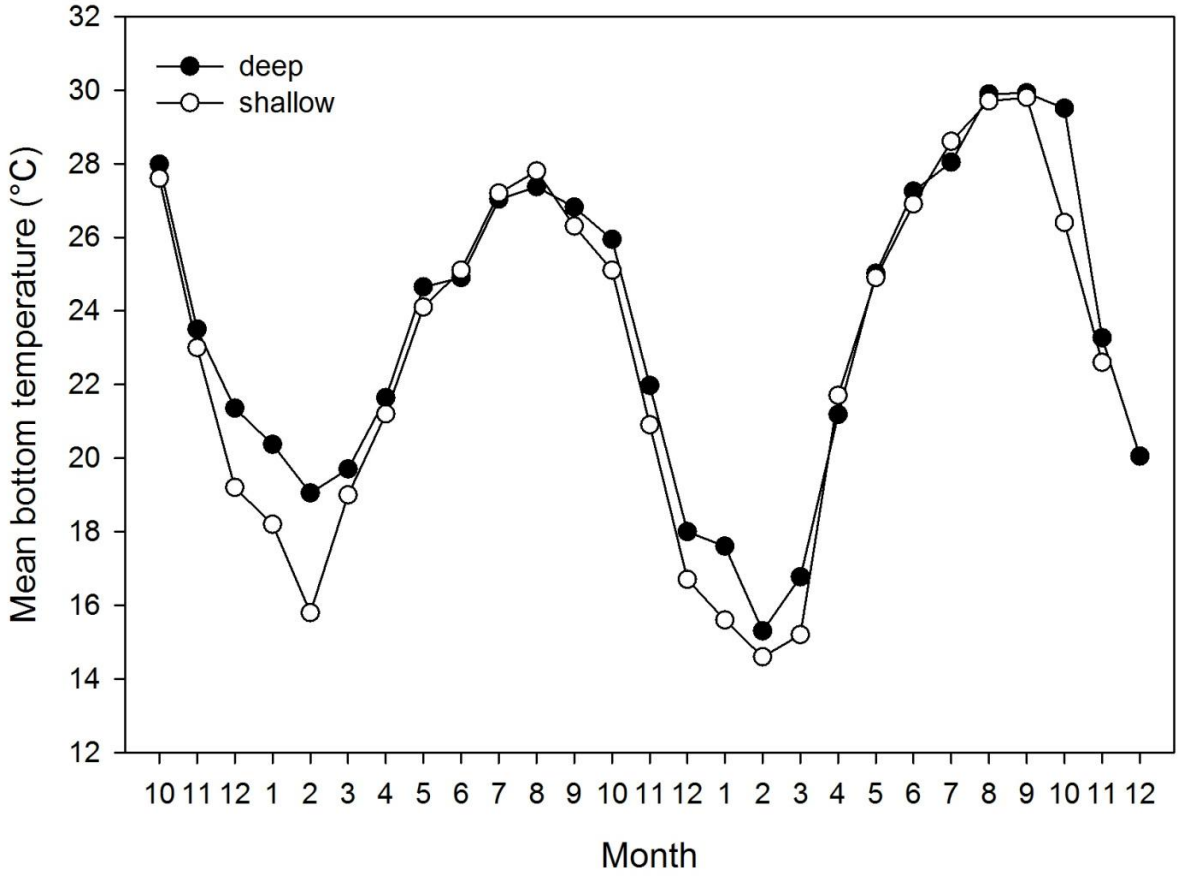

Fig. 2.14. Mean bottom water temperatures recorded at the bottom during research trips performed between October 2007 and December 2009. Site depth is indicated as deep (> 20 m; ●) or shallow (≤ 20m; ○).

CHAPTER THREE

BAROTRAUMA, SITE FIDELITY, AND LONG TERM MOVEMENT PATTERNS OF ATLANTIC GOLIATH GROUPER *EPINEPHELUS ITAJARA* AFTER CATCH AND RELEASE

Abstract

Atlantic Goliath Grouper *Epinephelus itajara* are the world's second largest grouper and have suffered significant overfishing throughout their range. Although protected from direct harvest within US waters since 1990, interaction between Atlantic Goliath Grouper and anglers persists through a directed catch and release fishery and incidental capture during angling efforts for other reef species. To assess the immediate effects of catch and release upon survival, Atlantic Goliath Grouper (105 – 206 cm TL; n = 39) were caught at artificial reefs across a range of depths (8 – 40 m) and tagged with pressure-sensitive acoustic transmitters. Barotrauma increased with capture depth and was the most severe at fishing depths > 30 m. Immediate mortality was not observed after a catch and release event, although Atlantic Goliath Grouper did exhibit reduced vertical movement and activity during the first 4 – 6 hours after release. Individuals were monitored for 18 – 950 days (mean = 443 d) after tagging, and monitoring period had no relationship with the level of barotrauma, the length of handling time or the length of fight time. Atlantic Goliath Grouper maintained consistent daily presence at specific artificial reefs for 18 –

737 days (mean = 241 d). Pressure sensors within acoustic tags allowed for a description of fine scale movement of individuals within the water column, and revealed a distinct diel and seasonal pattern in behavior. Atlantic Goliath Grouper exhibited more expansive vertical movements within the water column during the daylight hours, especially during crepuscular periods. Further, reduced vertical activity was associated with the coldest months of the year. A distinct seasonal departure of mature-sized Atlantic Goliath Grouper (> 140 cm TL) occurred during their spawning season (June – September). The majority of these fish returned within three months, including one fish that travelled to an artificial reef located 174 km away from the study area. Forays during the rest of the year were sporadic among individuals, but continued to demonstrate site fidelity and the ability to return to home sites after extended absences of up to 16 months.

Introduction

Atlantic Goliath Grouper (Epinephelidae: *Epinephelus itajara* Lichtenstein 1822) are the world's second largest grouper, and occupy tropical and subtropical waters of the South Atlantic Ocean and Gulf of Mexico (Craig et al., 2011). They can achieve sizes exceeding 200 cm in total length (TL) and 400 kg, and live at least 37 years (Bullock et al., 1992). Like many large, long lived marine species, Atlantic Goliath Grouper have experienced overfishing throughout their range and suffered significant population declines (Sadovy and Eklund, 1999; Musick et al., 2000). The species has been protected from all harvest within the United States since 1990 (GMFMC, 1990; SAFMC, 1990) and is listed internationally as critically endangered on the IUCN Red List (Pusack and Graham 2009). The population within the US has responded encouragingly to protection, and has shown signs of recovery in recent years (Cass-Calay and Schmidt, 2009;

Koenig et al., 2011). Their comeback is especially evident along the southwest coast of Florida, an historical center of abundance for this species, and one of the few areas that has been able to sustain an undeveloped stretch of critical nursery habitat (Koenig et al., 2007).

The impressive size and charismatic reef presence of Atlantic Goliath Grouper make them a favorite of the underwater tourism industry, and their economic impact has been argued to be greater as a protected species than a harvested one (Frias-Torres, 2012). Conversely, pressure from other sectors to re-open the fishery is escalating as the population rebuilds and interaction with anglers increases. The life history characteristics of Atlantic Goliath Grouper make the species especially vulnerable to exploitation, so any changes in regulation should proceed cautiously (Musick et al., 2000; Rhodes and Graham, 2009). The need for additional data has become clear during recent attempts for stock assessment that have failed due to a lack of information (SEDAR 6, 2004; SEDAR 23, 2011). For example, total mortality estimates are uncertain since protection from harvest does not immediately imply that fishing mortality (F) is negligible (Casey, 1996; Porch et al., 2006). Recreational fishing charters that operate throughout the eastern Gulf of Mexico advertise Atlantic Goliath Grouper as a prime target species for catch and release fishing. The species is also regularly caught unintentionally during both recreational and commercial fishing efforts for other reef species (SEDAR 23, 2011) and Atlantic Goliath Grouper are repeatedly reported to prey upon caught fish being reeled in by anglers [Florida Fish and Wildlife Conservation Commission (FWC), unpublished data]. Atlantic Goliath Grouper are a shallow water species (typically < 50 m) that aggregate at high relief, artificial habitats (Sadovy and Eklund, 1999; Coleman and Koenig 2010; Koenig et al., 2011; Collins et al., *in review*), the locations of which are often publicly available and relatively easy for anglers and divers to

locate. Thus, these artificial reefs receive a disproportionate amount of anthropogenic pressure than surrounding natural habitats, increasing the potential for interaction between resident fish and humans (Huntsman et al., 1999). Previous indications of high site fidelity (Eklund and Schull, 2001; Koenig et al., 2011) suggest that Atlantic Goliath Grouper remain resident at predictable locations and therefore would be subject to repeated catch and release at sites with high fishing activity. The impact upon the behavior and survival of Atlantic Goliath Grouper after these interactions has not been previously described.

The first goal of this study was to identify the immediate effects of catch and release angling on the behavior and survival of Atlantic Goliath Grouper. Immediate mortality after catch and release is difficult to quantify through conventional tagging, which depends upon recapture reports that may take months to years (Sumpton et al., 2010). Monitoring survival in holding bins or cages post-release (e.g., Jarvis and Lowe, 2008; Brown et al., 2010), or through experimental procedures in the laboratory (e.g., Rogers et al., 2008; Campbell et al, 2010) are not practical for adult Atlantic Goliath Grouper considering their large size. Acoustic telemetry was therefore employed to monitor fish survival and behavior directly after catch and release, which allowed for a realistic mimic of fishing activity and provided fine scale information that conventional tags or other experimental techniques could not (Afonso et al., 2012; Bryars et al., 2012).,

The second goal of this study was to characterize the site fidelity and residence time of tagged Atlantic Goliath Grouper over extended time frames (1 – 2 years), and to identify seasonal and diel patterns in movement of individuals within the study area. Continuous tracking of individuals over extended periods can provide fine scale information regarding the long-term

survival and behavior of protected species that may otherwise be unavailable (Wearmouth and Sims 2009; Simpfendorfer et al., 2011; Bryars et al., 2012). For instance, monitoring seasonal patterns in movement allow for a description of an animal's home range over varying temporal scales that can assist in the identification of essential fish habitats and inform fishing regulations (Botsford et al., 2003; Topping et al., 2006; DeCelles and Cadrin 2010; Kneebone et al., 2012). Additionally, residence time and site fidelity as they relate to particular variables (habitat type, habitat size, and presence of conspecifics) can provide information regarding the ecological importance of specific areas to a given species (Matthews, 1990; Heupel et al., 2007; Meyer et al., 2007; Botsford et al., 2009; Lowe et al., 2009). Atlantic Goliath Grouper are relatively easy to catch, which, when combined with life history characteristics that make them especially vulnerable to overharvest (Musick et al., 2000), the quantification of release mortality, site fidelity and movement patterns are especially important concerns in the development of future management strategies for this species.

Methods

Study area

Sites for catch and release were chosen based upon habitat type, as well as depth and location within the central eastern Gulf of Mexico. Previous work (Collins et al., *in review*) demonstrated Atlantic Goliath Grouper preference for artificial reefs within the study area, and six primary sites (P1 – P6) were selected from previously characterized sites for which Atlantic Goliath Grouper abundance data were already available (Fig. 3.1; Table 3.1). An additional six accessory sites (A1 – A6; Fig. 3.2; Table 3.1) were opportunistically monitored as time and weather conditions allowed throughout the study period. Sites were chosen to represent a range of

artificial reef sizes, varying in relief, area (total length × total width) and volume (Table 3.1). In order to assess the effects of potential barotrauma with increasing capture depth, sites were distributed from 12 to 39 m (10 – 70 km from shore), representing the general depth range for Atlantic Goliath Grouper (Bullock et al. 1992; Sadovy and Eklund 1999; Gerhardinger et al., 2006) and also the typical range of recreational fishing effort for this species in the eastern Gulf of Mexico (FWC, Fisheries-Dependent Monitoring Program, pers. comm.). Finally, sites were picked based upon relative proximity to each other in order to maximize the odds of detecting fish moving between sites (Fig. 3.2).

Acoustic array

Detection tests were performed at each of the six primary sites to ensure acoustic receivers were placed properly for optimum (> 90 %) detection of acoustic tags (McWhorter and Collins, 2011). In order to maximize detection capability of fish on any side of the artificial reef, multiple acoustic receivers (two to four Vemco VR2Ws, depending on site size) were positioned 50 – 100 m from the center of each site as these receivers have a listening radius of approximately 150 – 750 m, depending upon environmental conditions (Pincock 2008). Single receivers were also deployed in the same fashion at the six accessory sites to extend acoustic coverage within the study area (Table 3.1; Fig. 3.2). Detection tests were not performed at the accessory sites; however, the depth range and habitat characteristics of these sites were similar to primary sites (Table 3.1). Prior to deployment, receivers were coated with a copper based antifouling paint to prevent biofouling and the associated reduction in detection capability (Heupel et al., 2008). All receivers were maintained and downloaded quarterly.

Acoustic tagging

Atlantic Goliath Grouper were caught between April 2011 and December 2012 using either rod and reel or hand-lines and 12-0 circle hooks baited with dead fish, typical methods utilized by recreational anglers who target this species. Gear type, fight and handling time (HT; time from bite until release), hook position, and fish total length (TL, cm) were recorded. Fish were inspected visually and the level of barotrauma (BT) was assigned a qualitative value of 1, 2 or 3, where (1): minimal with no external signs of trauma and descent occurred immediately and independently upon release without venting; (2): moderate with signs of gas bladder expansion (bloated body cavity) but no other signs of trauma; venting was required for independent descent; and (3): severe; external signs of trauma included an everted stomach, intestinal protrusion from the anus, or evidence of exophthalmia; multiple venting procedures required before the fish was capable of independent descent. Fish were vented behind the pectoral fin with a large stainless steel hollow needle (300 mm x 5 mm), which is custom made for a local bait shop (Fisherman's Ideal Supply House, Saint Petersburg, FL USA). Whether or not fish were required to be hauled on board the vessel to achieve an adequate vent (versus vented boat-side and in the water) was also recorded and given a 'yes' or 'no' value.

All captured fish were fitted with a pressure sensitive acoustic transmitter (Vemco V13P-1L 69kHz; ping rate 60 – 180 s; estimated battery life = 684 d) and a conventional identification (ID) tag (Fig. 3.3). Although there was some concern about tag retention of externally attached transmitters, it was necessary to mimic catch and release as closely as possible to recreational angling events. For this reason as well as the large size of the study animals, transmitters were attached externally to avoid the additional stress associated with surgery and internal

implantation. Transmitters were anchored between the 1st and 4th soft dorsal fin rays. Conventional ID tags were attached on the same side of the animal anterior to the transmitter and displayed a unique ID number large enough to read underwater, as well as the FWC tagging hotline phone number to facilitate diver and angler reports of tagged fish. Both tags were sprayed with clear antifouling paint (AquaGard Alumi-Koat, Flexdel Corporation, Lakewood, NJ, USA) to discourage invertebrate and algal growth.

Visual surveys

To assess Atlantic Goliath Grouper abundance and size distribution at acoustically monitored sites, visual SCUBA surveys were performed approximately every other month (2011 – 2013) at each of the six primary sites. The six accessory sites were also surveyed opportunistically throughout this period (Table 3.1). During each survey, the same researcher (ABC) swam methodically from one end of the site to the other, checking all holes, crevices and the surrounding perimeter for Atlantic Goliath Grouper. This process was then repeated in reverse so that the entire site was surveyed at least twice. Abundance estimates were recorded as the number of fish encountered during a one way survey of the site. All fish within the field of view of the diver, regardless of their distance from the diver, were recorded and filmed using a high definition digital video camera (Sony HDR Handycam CX550) within an underwater housing (Light and Motion Bluefin housing) fitted with a custom made laser measuring device that projected equidistant green laser points (20 cm apart) onto the fish. Still image frames from the video in which fish were filmed perpendicular to the camera were assessed using image analysis software (Image Pro Plus, Media Cybernetics Inc., Rockville MD, USA) and analyzed to obtain total length estimates of Atlantic Goliath Grouper (+/- 1 cm total length, TL). Video analysis also

allowed for confirmation of abundance estimates recorded in the field. Surveys performed in visibilities less than 5 m or lasting less than 15 minutes were not considered in the results.

Data analysis

Acoustic data were analyzed to determine short term survival after catch and release, to assess site fidelity and behavioral patterns of fish at each monitored site, and to describe movements among sites within the study area. Duplicate and spurious detections were removed from the data prior to analysis. Acute survival and subsequent behavior after catch and release were monitored by assessing fish movement within the water column, as indicated by pressure sensors within acoustic tags, which transmitted a depth position approximately every 1 – 3 minutes. Total monitoring period (TMP) for each individual was calculated as the number of days between tagging and the last detection recorded. Residence indices (RI) were calculated for fish at their tagging site (RI_{TS} = total days detected at tagging site/TMP) as well as within the entire study array (RI_A = total days detected within array/TMP) to identify residence times and site fidelity. The relationship between TMP and RI to the site of tagging and level of barotrauma were compared using the Kruskal-Wallis One-Way ANOVA. TMP and RIs were compared to site depth and fish total length using the Pearson Correlation.

When fish were observed to move between sites within 24 hours, a general rate of movement (ROM) was calculated by dividing the distance between sites by the travel time (the time between the last detection at one site and the first detection at another). ROMs were compared to fish TL using linear regression.

To identify seasonal, diel or site-specific patterns in fish movement within the water column, depth data from pressure sensors were standardized across all fish to indicate fish depth position as a proportion of the water column (POS). Fish depth was divided by the maximum water depth at the site of detection, such that POS at the bottom = 1.0 and position at the surface = 0.0. To identify patterns in fish vertical activity, the relationship between POS and month, time of day and site were compared using generalized linear mixed models (Proc Glimmix in SAS). Finally, data from visual surveys were examined to identify whether RIs were related to Atlantic Goliath Grouper abundance or size distribution at that site (Kruskal-Wallis one-way ANOVA). All statistical analyses were performed using either SigmaPlot 12.5 (Systat Software Inc., San Jose CA, USA) or SAS Enterprise (SAS Institute Inc., Cary NC USA).

Results

Acoustic tagging

Acoustic tags were deployed on 39 Atlantic Goliath Grouper between April 11, 2011 and December 20, 2012 (Table 3.2; Fig. 3.4). The total number of detections per individual (after the removal of duplicate and spurious detections) ranged from 2,232 – 721,263 (mean = 156,615), with an average number of 569 detections per day for each fish (range 20 – 1,463 detections per day). Tagged individuals ranged in size from 105 – 206 cm TL.

Catch and release mortality and barotrauma

No immediate or delayed mortality was observed for any of the Atlantic Goliath Grouper caught during this study. Barotrauma increased at capture depths greater than 30 m (Fig. 3.5; $p < 0.001$; Kruskal Wallis one-way ANOVA), but was not related to fish TL ($p=0.288$) or total monitoring

period (TMP; p= 0.536; Kruskal Wallis 1-way ANOVA; Fig. 3.6). Handling time ranged 3 – 62 minutes (mean HT = 10 min), and immediately after release, the majority of individuals descended to the bottom and displayed limited movement for several hours (Fig. 3.7). Average depth of released individuals was significantly deeper for the first 24 hours of monitoring than for the following 2 days ($p < 0.001$; Proc Glimmix). One fish provided no data during the first 24 hours because it went undetected for almost 4 months after release (118 days; tag 5766), but eventually this individual returned to the initial tag site, providing evidence of survival. All other fish (n = 38) resumed movement within the water column at their tagging site within 24 hours, providing evidence of no immediate or delayed mortality after catch and release.

Monitoring periods and residence time

Total monitoring periods (TMP, the length of time between the first and last detections) ranged 18 – 950 days (mean = 444 d). The total number of days for which individuals were positively detected (> 5 detections within 24 hours) ranged 18 – 736 days (mean = 253 d). Atlantic Goliath Grouper displayed strong site fidelity, and individuals were detected daily at their sites of tagging for continuous periods as long as 736 days (mean = 242 d; Fig. 3.8b). Most detections for fish occurred at their initial site of tagging (mean RI_{TS} = 0.61, range 0.02 – 1.0; Fig. 3.8c), but individuals were observed to move around the study area and 22/39 (56%) were detected sporadically at other sites within the array. Total proportion of time unaccounted for ($1 – RI_A$) ranged from 0 – 0.98 (mean = 0.34; Fig. 3.8d). Site of capture did not affect TMP (p=0.440), RI_{TS} (p=0.815) or time unaccounted for ($1 – RI_A$; p=0.534) (Fig. 3.8b – 3.8d). There was no relationship between the site of capture and Atlantic Goliath Grouper TL (p = 0.06; Fig 3.8a),

and Pearson correlations indicated that fish size (TL) was also not related to TMP ($p = 0.733$), RI_{TS} ($p = 0.713$), or RI_A ($p = 0.449$) (Fig. 3.9).

Forays and seasonal movements

Although relatively faithful to a single reef throughout much of the study, periods of absence exceeding 7 days, termed hereafter as 'forays,' occurred for 28/39 (72%) individuals. Forays as long as 487 days (mean = 41 d) and as far away as 174 km (mean = 23.9 km) were observed, after which fish either returned to their initial site or appeared at another monitored site within the study array (Fig. 3.4). Almost all individuals (23/28, 82%) eventually returned to their initial tagging site, although 5 (18%) were detected elsewhere in the study array but did not return to their original site during the study period. Forays occurred sporadically throughout the year and timing and length of forays varied among individuals, with the exception of a concerted departure of tagged fish that occurred during the spawning season (June – September; Bullock et al., 1992). Over the three summers for which Atlantic Goliath Grouper were tracked, over 65% of tagged individuals present departed their resident sites between June 1 and September 15, typically within one week of each other, regardless of their location (Table 3.3; Fig. 3.4). This seasonal departure was significantly related to total length (Fig. 3.10; $p < 0.001$), and departures were observed only for individuals that were > 140 cm TL at tagging. Interestingly, three smaller fish (134, 148 and 150 cm TL at tagging) that did not depart during their first year of monitoring did exhibit a seasonal departure the following year (Fig. 3.11); however, because sizes were only measured at initial tagging, exact sizes in following years are unavailable. The destinations of fish during this seasonal departure are unknown, with the exception of two individuals. Tag ID 91 (202 cm TL, BT =3) appeared 174 km south of the study array at a shipwreck being

monitored by another researcher (C. Koenig, pers.comm.). This individual exhibited daily presence at this site for two weeks before returning to the study area. Tag ID 81 (149 cm TL; BT = 2) left its tag site (P4) and appeared to the northwest at another site within our study array (P5), where it remained for one month before tag transmissions ended entirely (Fig. 3.4).

Rates of movement

Eleven Atlantic Goliath Grouper (122 – 202 cm TL; mean = 164 cm TL) swam between monitored sites within a single day (< 24 hours). Data from these fish were examined to assess general rates of movement (ROM). Estimated ROMs ranged 0.52 – 2.87 km/h (mean = 1.49 km/h). There was no difference in ROM between individuals (One way ANOVA; $p = 0.248$), nor was there any relationship between ROM and TL (Proc Glimmix $p = 0.896$) (Fig. 3.11).

Fine scale diel and seasonal patterns in vertical activity

Individuals spent the majority of their time associated with the structure near the bottom, in the lower quarter of the water column (Fig. 3.12). Atlantic Goliath Grouper were present at their resident sites during all hours, and vertical movement was higher during the day for all months of the year (Fig. 3.12a; $p< 0.0001$, Proc Glimmix POS vs. Diel). Atlantic Goliath Grouper exhibited the highest breadth of vertical activity during the early morning and early evening hours (Fig. 3.12b; $p<0.001$ Proc Glimmix POS vs. hour). Seasonal patterns in water column position were apparent, and fish position at each site was significantly higher during the Spring and Summer (April – September; $p< 0.001$, Proc Glimmix POS vs. month, season; Fig. 3.12a). The smallest breadth of vertical movement was observed during January and February, when bottom water temperatures were the lowest (14 – 20°C; mean = 18°C). There was also a

significant difference between sites and POS ($p<0.001$, Proc Glimmix, POS vs. site), where POS exhibited a positive relationship with volume (ANOVA, $p = 0.025$) and vertical relief (ANOVA, $p = 0.028$) of the site (Fig. 3.13). Although the majority of time was spent in the lowest quarter of the water column, individuals did make extreme vertical movements and were recorded throughout the entire water column to some extent during all months of the year (Fig. 3.14). Analysis of all depth data showed that the final detection for each tagged individual occurred in the bottom quarter of the water column, except for one fish that was last detected at 0.0 m and then disappeared from the study array (Fig. 3.15a).

Recaptures

Multiple individuals (7/39, 18%) were recaptured by the authors at three different sites (depths of 19, 25 and 40 m) 13 – 445 days after initial tagging. Two of these individuals had lost their acoustic tags but were recaptured at their original site of tagging (372 and 445 days later). Recaptured fish often had new hooks in their mouths (5/7) and were trailing fishing leaders (2/7) or lead weights (1/7), providing further evidence of periodic interactions with anglers. Acoustic data (depth positions) were assessed and compared with known recapture times to identify whether catch and release events were detectable. For the five fish that still had acoustic tags attached during recapture, ascent to the surface was visible for only two individuals (e.g., Fig 3.15b).

Visual Surveys

Underwater visual surveys were performed at least every other month from April 2011 until November 2013 at each of the six main sites (Fig. 3.16) and opportunistically at the six accessory

sites (Table 3.1) in order to assess *in situ* Atlantic Goliath Grouper abundance and size distribution at monitored areas throughout the study period.

As expected from related work (Collins et al., *in review*), the highest numbers of Atlantic Goliath Grouper were observed at the largest artificial reefs. However, residence times of individual fish (RI_{TS}) were not related to site size or to the mean number of other Atlantic Goliath Grouper present throughout the study period. Size distributions of Atlantic Goliath Grouper were not dependent upon site, depth or season, and were relatively consistent at each site throughout the year, even during spawning season (Fig. 3.16).

Discussion

Catch and release mortality and barotrauma

Species with high site fidelity and predictable movement or migration patterns are more vulnerable to exploitation because they are easier to locate than those that exhibit irregular or random behavior (Polunin and Roberts 1996; Huntsman et al., 1999; Cheung et al., 2007). Although Atlantic Goliath Grouper are prohibited from harvest within the U.S., their high site fidelity and tendency to aggregate at artificial reefs in nearshore waters make them susceptible to relatively high levels of capture, either through directed catch and release efforts or incidental fishing pressure by anglers targeting other species (SEDAR 23, 2011). Mortality due to catch and release has not previously been quantified for Atlantic Goliath Grouper, but it is an important consideration during stock assessment and management of marine species (e.g., Bartholomew and Bohnsack 2005; Arlinghaus et al., 2007; Campbell et al., 2010).

Barotrauma of Atlantic Goliath Grouper increased with capture depth, but was not related to fish size, and immediate mortality following catch and release was not observed during this study. Pressure related fishing trauma typically increases with capture depth (Feathers and Knable, 1983; Gitschlag and Renauld, 1994; Arlinghaus et al., 2007; Jarvis and Lowe, 2008; Campbell et al., 2010), and the most extreme cases of barotrauma for Atlantic Goliath Grouper occurred at sites deeper than 30 m. These fish exhibited stomach eversion, intestinal protrusion from the anus and gas bladder expansion, although exophthalmia was not observed. Extreme cases required lengthy and multiple venting procedures before fish were able to descend independently. It should be noted here that all of the fish suffering from moderate or extreme barotrauma were vented so that they could descend independently, a procedure that has been identified to significantly reduce mortality in other species (e.g., Feathers and Knable 1983; Wilson and Burns, 1996; Collins et al., 1999; Alos, 2008; Butcher et al., 2012). Atlantic Goliath Grouper suffering moderate – extreme barotrauma often were required to be hauled on board in order to release enough gas for the fish to descend, and handling times associated with tagging lasted up to 62 minutes (from capture to release), which may not always be practical or possible for recreational catch and release anglers.

Pressure sensitive acoustic tags provided a depth data point every 90 – 180 seconds, and allowed for a detailed description of behavior immediately after catch and release. Although most fish descended directly to the bottom and remained relatively immobile for the first few hours following release, all resumed movement in the water column within 24 hours and provided data for at least two weeks and up to almost three years after release. These data suggest minimal immediate or delayed mortality and indicate that Atlantic Goliath Grouper are able to handle

catch and release relatively well if they are vented, at least for the depths fished during this research (to 40 m). Since this species is rarely observed at depths > 50 m (Sadovy and Eklund 1999; Gerhardinger et al., 2006; Craig et al., 2011) and most recreational fishing on the west Florida shelf occurs inside of this depth range (FWC Fisheries-Dependent Monitoring Program, pers. comm.), interactions between anglers and Atlantic Goliath Grouper at depths greater than 40 m are expected to be minimal. Evidence of residual fishing gear in recaptured Atlantic Goliath Grouper included new hooks and trailing fishing leaders, confirming that periodic interactions between this species and anglers within the study area are common. Fish that everted their stomachs during barotrauma exhibited fishing gear lodged within the stomach (monofilament fishing line, hooks, fishing lures, lead weights). Ingested fishing tackle is likely due to Atlantic Goliath Grouper predation upon other fish being reeled in by anglers rather than targeted catch and release activities. Although the repeat interval on the acoustic tags was not rapid enough to detect all recapture events, the telemetry data did reveal one fish that ascended from the bottom to the surface within 3 minutes, and then disappeared entirely from the study array (Fig. 3.14). This could potentially be indicative of catch and release mortality, illegal harvest, tag malfunction or tag removal by the angler. Further investigation into this area is required, but even so, the extended monitoring periods observed for most individuals suggest that illegal harvest is not an overwhelming issue within the study area. Acute mortality due to catch and release appears to be minimal, but the chronic effects of repeated capture and ingestion or entanglement in residual fishing gear are not clear.

Residence time and site fidelity

Knowledge regarding habitat associations and movement patterns of fishes has historically been used as a tool for efficient exploitation (e.g.,Parrish, 1999; Sadovy and Domeier, 2005; Sadovy de Mitcheson 2008).The majority of tracking work performed on Atlantic Goliath Grouper to date has utilized conventional tags (Eklund and Schull, 2001; Pina-Amargós and González-Sansón 2009; Koenig et al. 2011; Collins et al., *in review*). Previous acoustic monitoring studies have had restricted time frames, a low number of acoustically tagged individuals or a small number of monitored sites (Eklund and Schull, 2001; Frias-Torres et al., 2007; Mann et al., 2009). Although the nature of these studies limited the ability to detect fine scale behavioral patterns, all indicated high site fidelity for this species throughout its ontogeny (Eklund and Schull 2001; Frias-Torres et al., 2007; Koenig et al., 2007).

Benthic reef fishes are often sedentary with restricted home ranges (Sale 1978, Topping et al. 2005; Bryars et al., 2012), and this has been noted repeatedly among groupers (e.g., *Epinephelus striatus*, Bardach 1958; *E. guttatus*, Shapiro et al., 1994; *Plectropomus leopardus*; Zeller 1997; *E. tauvina*, Kaunda and Rose, 2004; *Mycteroperca microlepis*, Kiel 2004; *E. marginatus*, Afonso et al., 2011), so the high residence of Atlantic Goliath Grouper observed during this study was not surprising. Individuals maintained consistent daily presence at the same site for up to 737 days (mean = 242 days). Consistent association with home sites by mobile fishes may be maintained for access to shelter (Samoilys, 1997; Arendt et al., 2001), potential mates (Colin, 1982; Munoz et al., 2010) and foraging opportunities (Afonso et al., 2012).

Atlantic Goliath Grouper juveniles emigrate from inshore nurseries after reaching approximately ~ 1 m TL (Koenig et al., 2007), and maturation occurs between 110 and 140 cm TL (Bullock et al., 1992). The length of time between leaving the estuary and recruiting to offshore reef habitats is not known, but it appears that once settled, Atlantic Goliath Grouper maintain strong site fidelity as adults. Typical daily behavior was consistent with that of a site-attached, relatively sedentary organism inhabiting a small core area; however, individuals did exhibit forays away from home sites that lasted for up to 16 months. Foray destinations were generally unidentified (although there were multiple observations of individuals moving between monitored sites), but it is possible that animals perform excursions to assess surrounding habitat quality or resource availability (Zeller, 1997; Lowe et al., 2009; Lowe 2009). Forays showed no relationship to season or fish size, except for a concerted seasonal departure that occurred during the spawning season.

Large groupers present an interesting management challenge (Sadovy and Domeier 2005; Sadovy de Mitcheson et al., 2008) as many species form large spawning aggregations far from their typical residence (gag *Mycteroperca microlepis*, McGovern et al., 2005; Coleman et al., 2012; Nassau grouper *E. striatus*, Starr et al., 2007; squaretail grouper *Plectropomus areolatus*, Hutchinson and Rhodes 2010). Atlantic Goliath Grouper also form spawning aggregations (Sadovy and Eklund, 1999; Bullock et al., 1992), and individuals have been reported to travel hundreds of kilometers to reach aggregation sites (Koenig et al., 2011). The capacity to move extensive distances has implications for the consideration of marine reserves or protected areas as management tools for such mobile species, if individuals are unlikely to maintain residence within refuges throughout the year (Coleman et al., 2011; Sadovy deMitcheson et al., 2013).

Further data is needed regarding the genetic structure of the population in order to determine extent of connectivity between regions, but long distance movements of even a small number of adults may facilitate genetic exchange within the population, as has been suggested for other reef species (e.g., mutton snapper *Lutjanus analis* Shulzitski et al 2009).

During this study, there was a concerted seasonal departure of mature-sized individuals during the spawning season (July – September). Although the destination and activities of individuals during this period could not be positively identified (with the exception of one individual that travelled to a suspected spawning site 175 km south of the study array and another that travelled 26 km between sites within the study array), the timing coincidence with the reproductive period (Bullock et al., 1992) is strongly indicative of a spawning migration. Eklund and Schull (2001) also noted a departure of adult Atlantic Goliath Grouper from a nearshore site in southwest Florida during the spawning season. As part of another study offshore, they reported that although some tagged fish left in September or October, the majority of fish acoustically tagged on a verified spawning aggregation site remained at that site past the end of the spawning season, suggesting permanent residence at the spawning site for some individuals. These individuals were all classified as adults but total lengths were not reported so it is not known whether the same size-specific pattern was observed. These mixed observations are similar to the data reported herein and indicate that some fish may remain present year round at aggregation sites while others are transient and travel from elsewhere to reach spawning aggregations.

Interestingly, size distributions of fish recorded during visual surveys in the current study did not demonstrate a lack of large individuals within the study array during the spawning months. It is

possible that the visual surveys simply did not occur often enough to capture significant differences in size across months. Alternatively, some large fish may stay where they are to spawn or simply may not spawn every year. This has also been observed for cod *Gadhus morhua* (Nielsen et al., 2013) and winter flounder *Pseudopleuronectes americanus* (DeCelles and Cadrin, 2010). Behavioral plasticity in reproduction related movement likely is an adaptive strategy and individual variability in movement should increase mixing of fishes typically segregated throughout the rest of the year (e.g., Colin, 1992; Zeller 1998, Bolden 2000, Marino et al. 2001; Afonso et al., 2009).

Distances moved and rates of movement

Home range of an organism was first defined by Burt (1943) and included the space required for feeding, reproduction and the care of young. Numerous authors have adjusted this definition since (e.g., Morris 1988; Kernohan et al., 2001), and the concept of a home range can shift over spatial and temporal scales (Jacoby et al., 2012). Home ranges of fishes have been related to fish sex (Samoilys 1997; Kaunda-Arara and Rose 2004), size (Larson 1980; Leum and Choat 1980; Jones 1984), season (Jones 1981), habitat (Matthews 1990; Lowe et al., 2003) and geographic region (Moser and Shepherd 2009). Information regarding overall spatial and temporal changes in habitat use is critical in the understanding of fish population dynamics (Alos et al., 2011; Jacoby et al., 2012).

Most Atlantic Goliath Grouper maintained very small core activity spaces, but long distance movements were also recorded (up to 175 km). Eklund and Schull (2001) also reported Atlantic Goliath Grouper recaptures 16 – 153 km from the tagging site, and Pina-Armagos & Gonzalz-

Sanson (2009) reported movements up to 168 km for two large individuals (150 – 180 cm TL) in Cuba. Recent work by Koenig and Coleman (2013) has demonstrated that individuals along the east coast of Florida will travel over 400 km to reach spawning aggregation sites. These data are important considerations in the development of protective measures, since fish are capable of moving between regions and thus have relatively large home ranges overall, which might indicate the potential for mixing between stocks.

Individuals (122 – 202 cm; mean = 164 cm TL) were observed to move between artificial reefs at rates as high as 3 km/h (range = 0.52 – 2.87 k/h) (0.8m/s), and average rates of movement observed for individuals moving between sites was approximately 1.5 km/h (0.42 m/s). Fish total length did not have an effect on ROM. Since the direct path and behavior of an individual while travelling between sites was unknown, ROMs were calculated based on the assumption that fish moved in a straight horizontal line and did not stop. Therefore the ROMs calculated herein are likely an underestimate of actual swimming speed. The theoretical formula for the most energy efficient swimming speed in fishes (U_0=0.503$L^{0.43}$; Wiehs, 1977) predicts that a fish of 164 cm would move at approximately 0.62 m/s (2.23 km/h), and for the size range of Atlantic Goliath Grouper for which ROM was estimated (0.54 – 0.68 m/s or 1.9 – 2.5 km/h). The ROMs calculated herein are well within the range of energy efficient swimming speeds for a fish of this size (Weihs, 1977) and although a bit slower than the predicted energy efficient speed, still suggest that most fish are taking a relatively direct path to move between sites.

Direct movements between sites suggest that fish are not moving randomly (Papastamatiou et al., 2011) and are using visual, chemical or acoustic cues to orient to specific sites, or potentially

operating on memory based on previous experience. Direct movements between marine habitats allows for an efficient use of energy and reduces the potential of predation, and has been noted previously for multiple species (e.g., yellowfin tuna *Thunnus albacares*, dolphinfish *Coryphaena hippurus* and vermillion rockfish *Sebastes miniatus*,and lingcod *Ophiodon elongatus*; Girard, Benhamou & Dagorn 2004; Girard et al. 2007; Lowe et al., 2009).

Diel and seasonal patterns in vertical movements

Atlantic Goliath Grouper maintained close association with the structure and bottom of the water column throughout the study. As opportunistic ambush predators, many groupers are typically observed under the cover of structure which provides an increased opportunity for capture of exposed prey (Thompson and Munroe 1978; Stallings, 2008). However, the extent of vertical movements within the water column corresponded with the diel period, and fish exhibited greater movement and shallower position during the daylight hours. Higher activity levels during the day are normal for diurnal species (e.g., tautog *Tautoga onitis* Arendt 2001; Californai sheephead *Semicossyphus pulcher* Topping et al., 2006; painted comber *Serranus scriba* March et al., 2010). Vertical activity of Atlantic Goliath Grouper was especially evident during crepuscular periods, which may correspond with increased feeding activity at dawn and dusk (Zeller 1997; Lowe et al., 2003; Meyer and Holland 2005; Gibran, 2007; March et al. 2010; Afonso et al 2012; Masuda et al., 2012).

A distinct seasonal pattern was also observed, with the lowest frequency of vertical movements during the coldest months of the year, and average depths of individuals were the deepest during January and February. The average bottom temperature during these months was 18°C (range 14

– 20°C for all 3 years of the study), while temps during the warmest months (July – September) ranged 27 - 30°C (mean = 29°C). The thermal range of the species is generally restricted to temperatures > 14°C (Gilmore et al. 1978), and the winter months are assumed to be a period of reduced feeding because the species becomes visibly lethargic (Collins, pers. obs) and is also more difficult to catch on hook and line (Eklund and Schull 2001; Collins pers. obs.). Lower temperatures are likely to reduce metabolism of marine fishes and seasonally reduced activity during periods of low temperatures has also been noted for multiple species (e.g., tautog *Tautoga onitis*, Arendt et al., 2001; California sheephead *Semicossyphus pulcher*, Topping et al., 2006). As water temperatures began to increase in the spring (~ April), Atlantic Goliath Grouper vertical movement within the water column increased and average depth became shallower.

Extreme vertical movements to upper portions of the water column were observed during all months, and were most common during the spring and summer (April – September). It is hypothesized that these events may be related to feeding, either upon natural prey (baitfish) or as orientation and predation upon hooked fish being reeled in by anglers. Atlantic Goliath Grouper have been observed to chase hooked fish to the surface during angling activities (Collins, pers. obs.), so the detection of Atlantic Goliath Grouper presence in the upper portions of the water column could very likely be related to this behavior since all monitoring sites are well within the reach of recreational and commercial fishers in the area. Alternately, extreme movements within the water column may be indicative of catch and release events. Additionally, mean fish position was related to site characteristics, and higher average positions within the water column were observed at sites with higher vertical relief. This further supports the idea that Atlantic Goliath Grouper prefer to maintain consistent association with shelter and that movement within the

water column is most likely influenced by a behavioral preference to maintain contact with benthic structure.

Conclusions

No immediate or delayed mortality was observed for any of the Atlantic Goliath Grouper that were caught and released during this study. Additionally, monitoring period was not affected by the severity of barotrauma or the length of handling time, which suggests that with proper handling, Atlantic Goliath Grouper are not subject to high levels of release mortality in the eastern Gulf of Mexico (at depths < 40 m). However, strong site fidelity of Atlantic Goliath Grouper to artificial reefs increases susceptibility to fishing pressure and amplifies interactions with anglers, so the chronic effects of repeated capture remain unclear. Acoustically tagged Atlantic Goliath Grouper displayed small core areas of use, maintaining consistent daily presence at specific artificial reefs for up to 736 days, but long distance movements (>175 km) demonstrated the capacity of individuals to move over broader geographic scales. The concerted departure of mature sized fish (>140 cm) during the reproductive period is suggestive of a spawning migration, although the destinations of departed individuals during this period remain unknown. Future efforts to identify spawning aggregation sites within the eastern Gulf of Mexico are warranted. The high numbers of conspecifics and the persistent long-term presence of individuals at high relief artificial reefs further demonstrated the importance of these habitats for Atlantic Goliath Grouper in the eastern Gulf of Mexico.

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Table 3.1. Characteristics of artificial reef sites (shipwrecks; Fig.2) acoustically monitored 2011 through 2013. The depth, maximum vertical relief, volume, and area are listed for each reef, as well as the number of deployed acoustic receivers (VR2s) and number of acoustically tagged Atlantic Goliath Grouper (tags) at each site. The mean number of Atlantic Goliath Grouper *Epinephelus itajara* observed during visual surveys over a 5 year period is indicated seasonally for each site (number of surveys per season for each site is indicated in parentheses). The primary six primary sites are indicated by asterisks (P1 – P6), and were surveyed seasonally 2008 – 2009, sporadically in 2010, and at least every other month 2011 – 2013. The remaining accessory sites (A1 – A6) were surveyed opportunistically throughout the study period.

							Mean number of Goliath Grouper observed 2008 – 2013 (*survey n*)			
Site	Depth (m)	Relief (m)	Vol (m^3)	Area (m^2)	VR2 (n)	Tag (n)	winter	spring	summer	fall
P1*	13	4.57	432	95	2	3	4.2 (11)	2.4 (14)	2.3 (8)	3.2 (9)
P2*	19	1.68	854	510	4	11	6.5 (11)	9.9 (18)	9.2 (18)	6.8 (12)
P3*	19	3.05	3853	1264	3	0	1.5 (6)	1.5 (16)	1.3 (14)	1.5 (8)
P4*	26	7.62	10401	1365	4	9	10.1 (8)	12 (14)	13.9 (17)	11.4 (13)
P5*	30	11.75	1670	142	3	8	9.0 (7)	9.9 (14)	11.9 (13)	9.9 (8)
P6*	32	3.05	507	166	2	1	4.3 (8)	4.5 (10)	7.1 (10)	3.73 (11)
A1	12	2.74	765	279	1	1	Na (0)	3 (2)	Na (0)	1 (1)
A2	21	4.88	4828	990	1	2	Na (0)	3.8 (4)	4 (1)	3 (2)
A3	24	3.66	413	113	1	0	0 (1)	1.7 (3)	1.8 (4)	2.3 (4)
A4	26	2.44	1554	638	1	0	4.33 (3)	3.25 (4)	5 (5)	2 (3)
A5	34	5.18	881	170	1	2	3.3 (4)	4.5 (6)	11.2 (10)	4.5 (4)
A6	39	10.25	18288	2000	2	2	9.7 (3)	9 (1)	23.4 (5)	12 (2)

Table 3.2. Acoustically monitored Atlantic Goliath Grouper *Epinephelus itajara*. Headings indicate tagging site depth, fish ID, total length (TL), barotrauma (BT), handling time (HT), tag date, date of last detection, total monitoring period (TMP), total days detected at tagging site (DTS), total days detected at other sites (DOS), number of sites detected, number of absences exceeding 7 days (Sites/forays), maximum distance between sites of detection (Max dist), and whether there was a departure during spawning season (Yes indicates a departure each spawning season that the fish was within the array; Year 2 indicates a departure only during the second year of monitoring but not during the first year; NA indicates the fish was not in the array).

Tag Site (m)	ID	TL (cm)	BT	HT (min)	Tag date	Last detection	TMP (days)	DTS (days)	DOS (days)	Sites/ forays	Max dist (km)	Seasonal depart?
A1	5779	192	1	10	5/3/12	11/18/13	565	227	9	2/4		Yes
(10)												
P1	85	172	1	11	4/26/11	4/15/13	721	14	4	3/0		NA
(13)	5766	122	1	3	6/29/11	1/22/13	574	112	1	2/5	11.4	No
	5775	130	1	7	8/16/11	9/22/11	38	32	0	1/0	0	No
P2	79	150	2	14, 1	4/13/11	3/25/13	713	467	3	2/5	11.4	Yes
(19)	80	181	2	14, 7	4/13/11	8/1/12	477	354	2	3/9	11.4	Yes
	86	157	2	8	4/26/11	4/14/13	720	170	7	3/10	17.3	Yes
	87	180	1	6	4/27/11	4/25/13	730	318	4	3/6	148.5	Yes
	88	150	1	6, 7	4/27/11	1/12/13	627	487	0	1/0	0	Year 2
	90	205	1	9	4/27/11	6/15/11	50	50	0	1/0	0	NA
	5768	141	1	3	7/6/11	3/13/13	617	188	38	3/4	41.3	No
	5769	134	2	5	7/6/11	6/18/13	714	532	26	5/6	25.8	Year 2
	5770	148	2	5	7/6/11	7/12/13	738	490	3	5/12	11.4	Year 2
	5771	150	2	9	7/6/11	7/5/12	366	48	47	2/1	7.4	Yes
	5773	105	2	5	8/12/11	8/17/13	737	737	0	1/0	0	No
A2	139	146	1	12	9/20/12	3/7/13	169	12	97	2/4	7.4	NA
(20)	5785	141	1	5	9/20/12	11/7/13	414	414	0	1/0	0	No
P4	81	149	2	11	4/14/11	9/17/11	157	111	26	2/1	29.6	Yes
(25)	82	182	2	10,12	4/14/11	11/18/13	950	461	0	1/2	U	Yes
	89	150	1	5	4/14/11	7/2/11	80	80	0	1/0	0	NA
	5761	196	2	16	6/9/11	7/9/11	31	31	0	1/0	0	Yes
	5762	186	2	7	6/9/11	6/15/13	738	550	8	4/6	29.6	Yes
	5763	174	2	8	6/9/11	3/14/13	645	271	1	2/2	11.3	Yes
	5764	196	2	5,10	6/9/11	6/15/13	738	577	2	2/3		Yes
	5774	206	2	10	8/16/11	5/14/12	273	226	0	1/1	U	Yes
	138	176	2	13	8/9/12	12/5/12	119	7	45	2/1	7.1	Yes
P5	83	175	2	12	4/19/11	5/6/11	18	18	0	1/0	0	NA
(30)	84	181	2	14	4/19/11	5/3/12	381	336	0	1/1	U	Yes
	91	202	3	32	5/10/11	1/9/13	611	119	22	3/9	173.5	Yes
	92	155	1	5	5/10/11	8/20/11	104	103	1	2/1	26.3	Yes
	93	134	1	4	5/10/11	2/28/12	295	183	67	2/3	22.1	No
	5765	145	2	6	6/16/11	10/20/11	127	127	0	1/0	0	No
	5782	175	3	12	7/3/12	6/11/13	344	192	6	3/3	26.3	Yes
	5783	163	2	9	7/3/12	11/18/13	504	280	9	3/11	27.3	Yes
P6	140	195	3	62	12/6/12	11/18/13	348	180	12	4/8	19.2	Yes
(32)												
A5	5777	135	3	8	9/29/11	9/2/12	340	339	0	1/0	0	Year 2
(34)	5778	146	3	11	9/29/11	9/24/13	727	168	1	2/4	4.9	No
A6	5767	188	3	9	7/20/11	8/11/12	389	141	0	1/5		Yes
(39)	5772	168	3	9,19	7/20/11	8/29/12	407	275	0	1/1		Yes

Table 3.3. Seasonal departures of acoustically tagged Atlantic Goliath Grouper *Epinephelus itajara* observed during their spawning season (June – September) for all three years of the study. The number of Atlantic Goliath Grouper that departed is displayed as a percentage of the total number of acoustically tagged present within the array during this period. The date range of departure indicates the time frame during which individuals departed; days at large indicates the number of days that the individuals were gone from their 'home' sites, and the number of fish that returned is indicated as a percentage of the total number of fish that departed.

Year	*n* departed/ *n* present (% departed)	Date range of departure (mean)	Days at large (mean)	*n* returned/ *n* departed (% return)
2011	18/26 (69%)	6/15/11 – 9/15/11 (8/11/11)	18 – 304 (94)	14/18 (78%) to array; 13/18 (72%) to original tag site
2012	20/22 (91%)	6/1/12 – 9/2/12 (8/1/12)	18 – 183 (93)	14/22 (64%) to array; 12/22 (55%) to original tag site
2013	7/9 (78%)	7/12/13 – 8/29/13 (8/3/13)	70 – 119 (95)	4/7 (57%) to original tag site

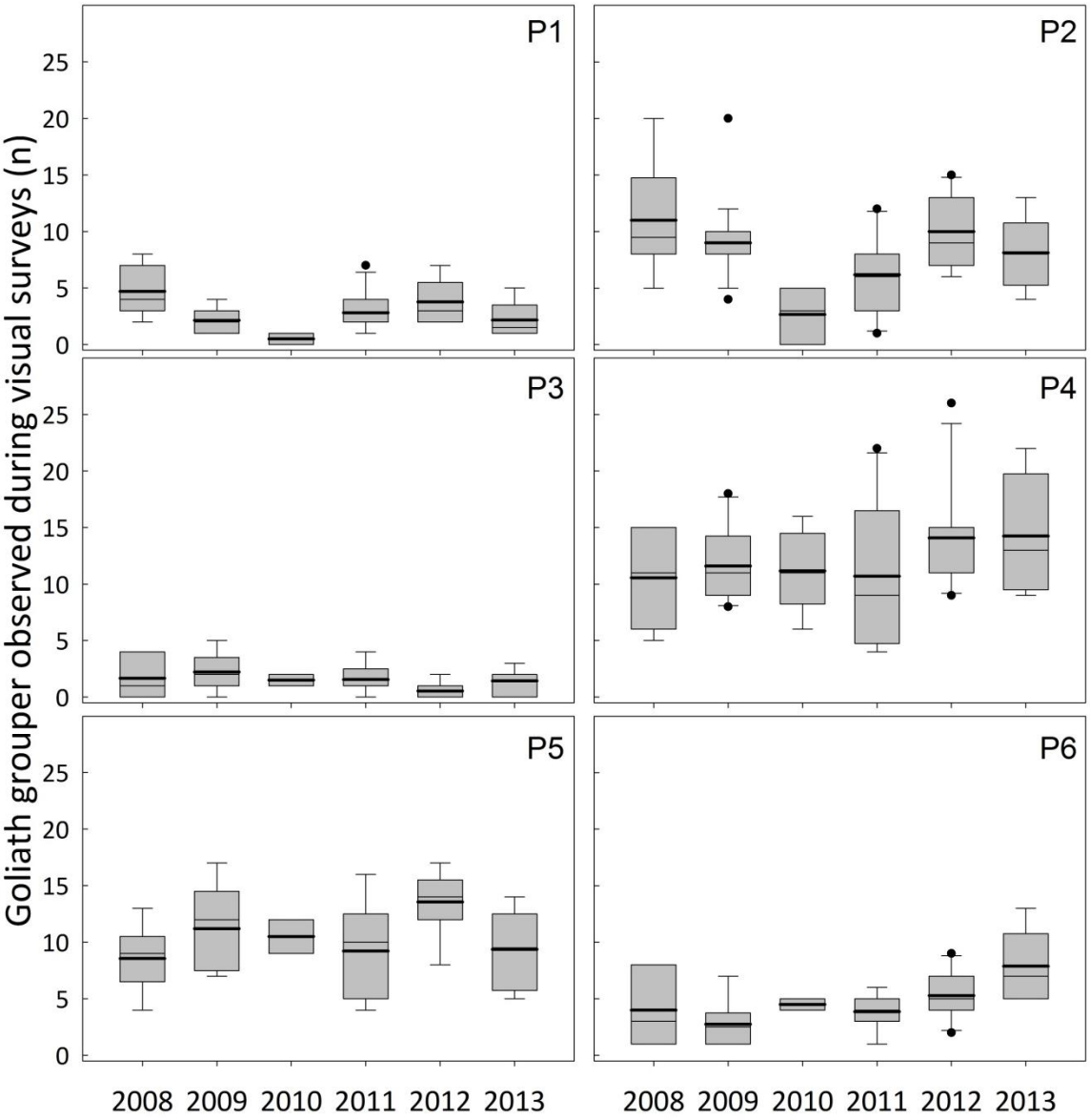

Fig. 3.1. Number of Atlantic Goliath Grouper *Epinephelus itajara* observed at each of the six primary sites (site characteristics are described in Table 3.1) during visual surveys from 2008 – 2013 (adjusted from Collins et al., *in review*). Box plots indicate the 25 – 75 quartiles, whiskers indicate 95% confidence intervals, and observations falling outside of the 95% confidence intervals are indicated by (●). The mean and median are indicated by the bold and thin horizontal lines, respectively.

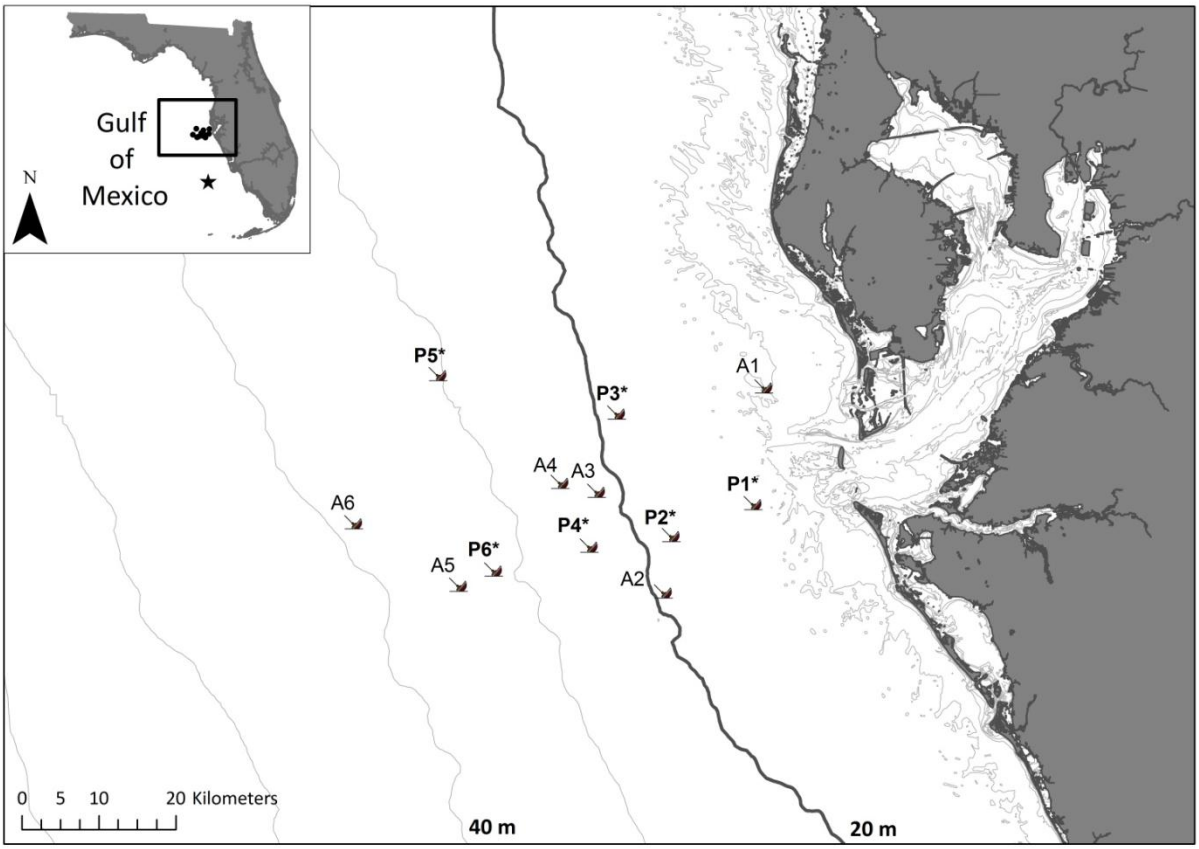

Fig. 3.2. Map of study area and sites of receiver (Vemco VR2W) deployment. Inset indicates the study array as well as an additional receiver (star) deployed briefly by another research group approximately 175 km south of the study area that detected 2 tagged individuals in 2011. Primary sites are in bold and indicated by asterisks.

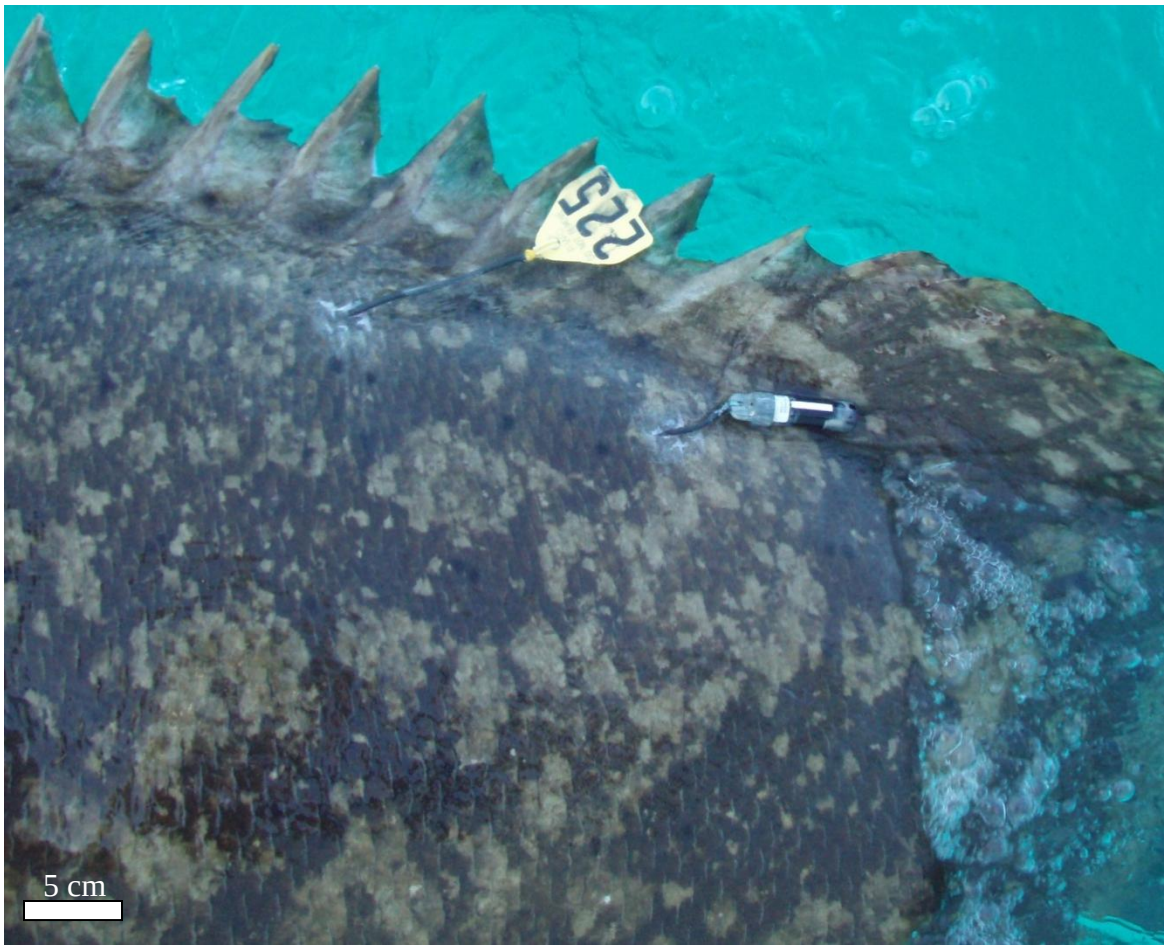

Fig. 3.3. Conventional identification tag (anterior) and acoustic transmitter (posterior) externally attached beneath the dorsal fin of an Atlantic Goliath Grouper *Epinephelus itajara* prior to release.

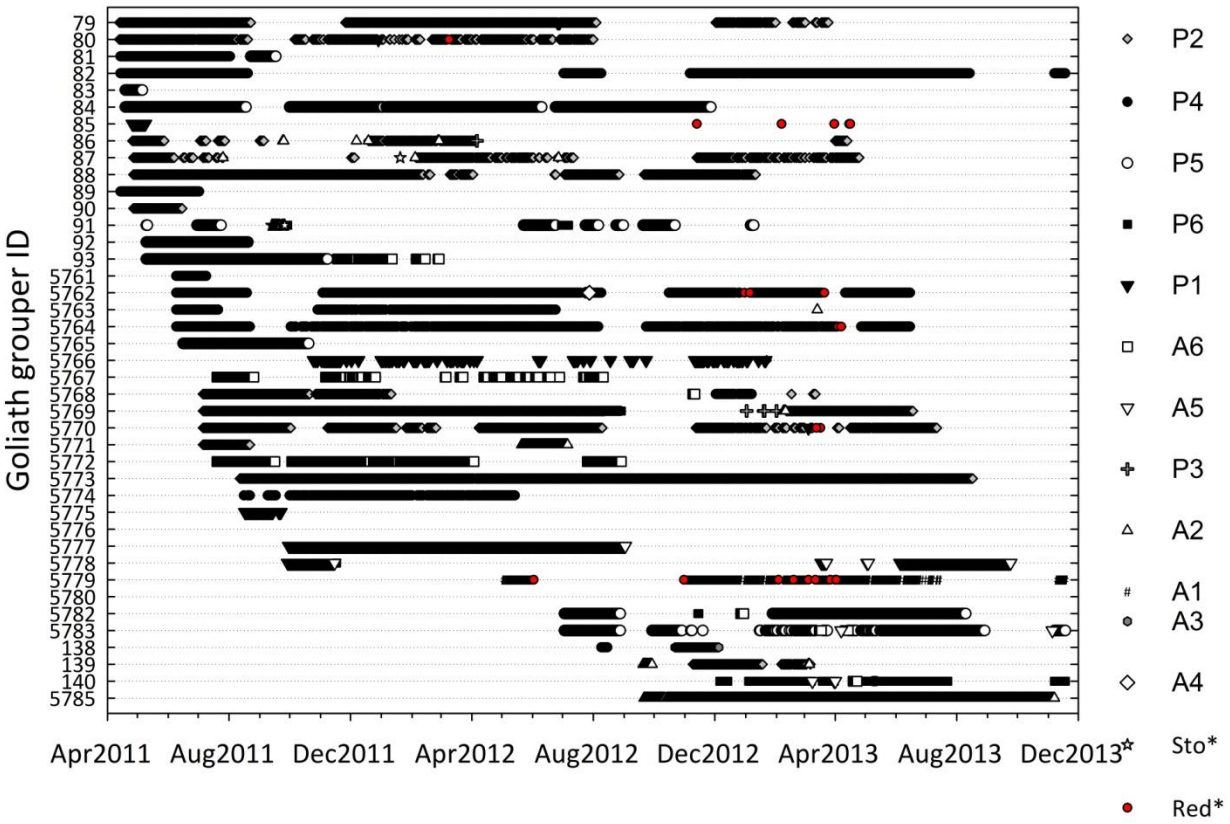

Fig. 3.4. Daily presence at monitored sites within the study area for 39 acoustically tagged Atlantic Goliath Grouper *Epinephelus itajara* between April 2011 and December 2013. Atlantic Goliath Grouper tag ID is indicated along the y-axis. Symbols represent presence at specific artificial reefs monitored during this study (as described in Table 3.1) plus 2 additional sites (*) being monitored by different research groups within the study area.

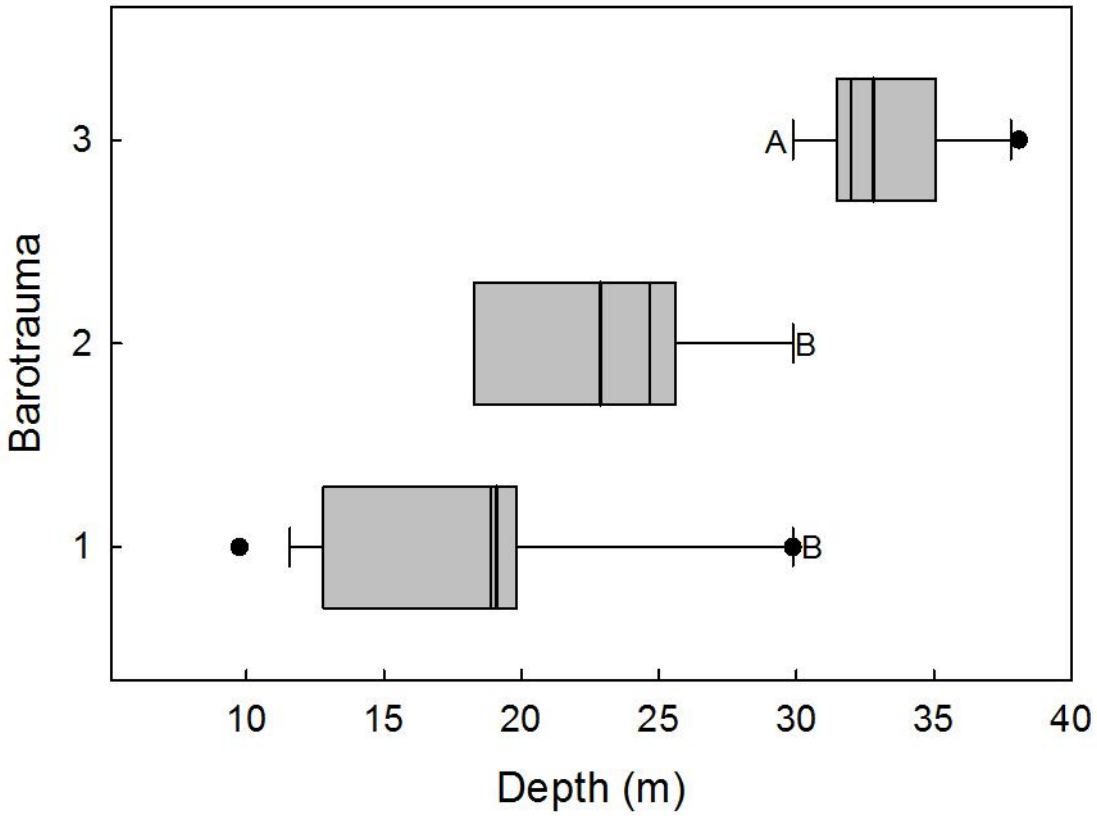

Fig. 3.5. Barotrauma (BT) values for Atlantic Goliath Grouper, *Epinephelus itajara*, by depth of capture. BT values were assigned qualitatively after a visual inspection as minimal (1), moderate (2) or severe (3). Severity was significantly higher ($p < 0.001$; Kruskal-Wallis One Way Anova) at capture depths greater than 30 m. Box plots indicate the 25 – 75 quartiles, whiskers indicate 95% confidence intervals, and observations falling outside of the 95% confidence intervals are indicated by (●). The mean and median are indicated by the bold and thin horizontal lines, respectively. Letters denote significant differences between groups.

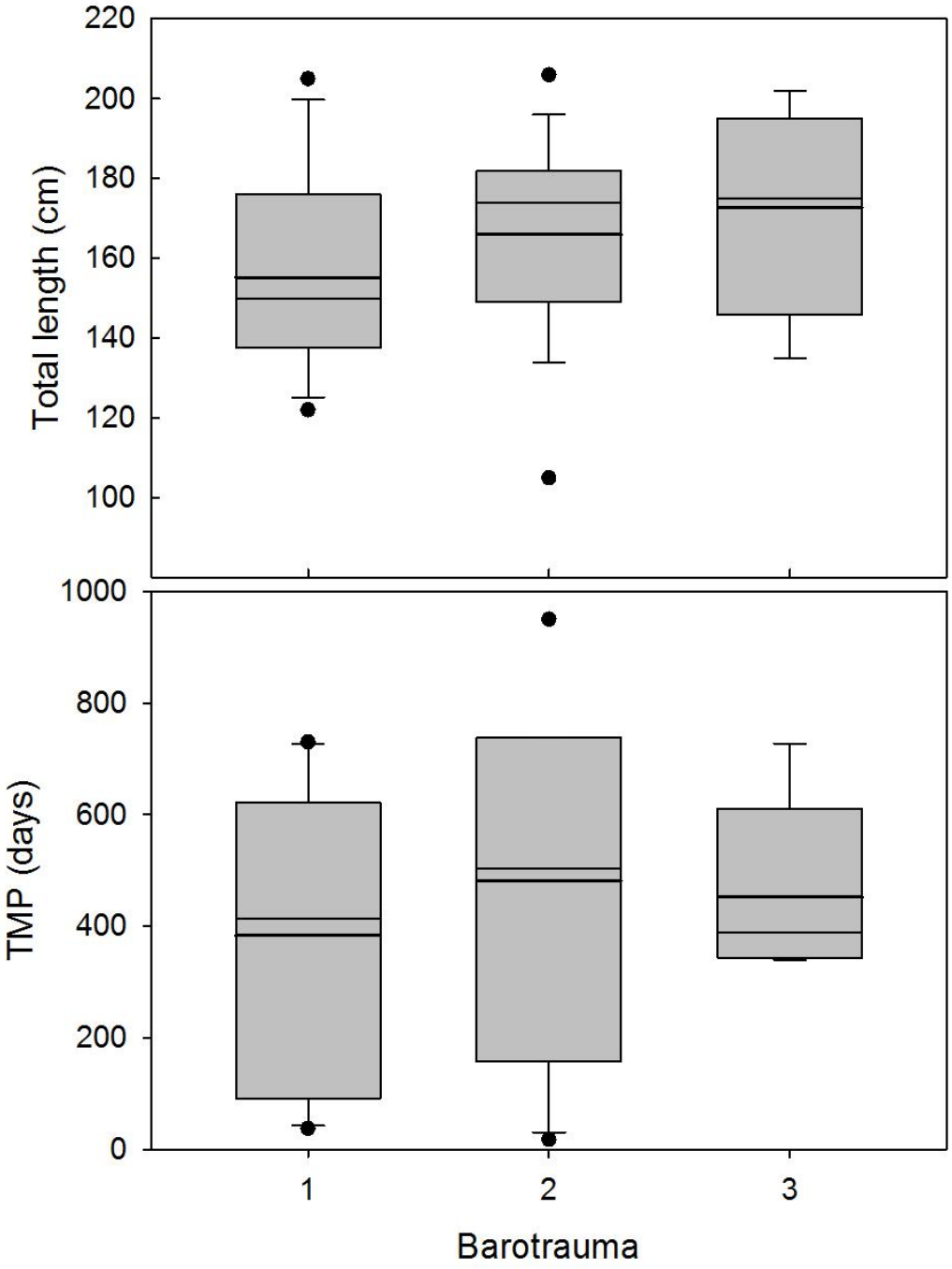

Fig. 3.6. Total length (top) and total monitoring period (TMP, bottom) of Atlantic Goliath Grouper, *Epinephelus itajara,* experiencing minimal (n=13), moderate (n=19) or extreme (n=7) barotrauma (1 – 3, respectively). There was no relationship between TL (p = 0.288) or TMP (p = 0.536) between barotrauma groups (Kruskal-Wallis One Way ANOVA). Box plots indicate the 25 – 75 quartiles, whiskers indicate 95% confidence intervals, and observations falling outside of the 95% confidence intervals are indicated by (●). The mean and median are indicated by the bold and thin horizontal lines, respectively.

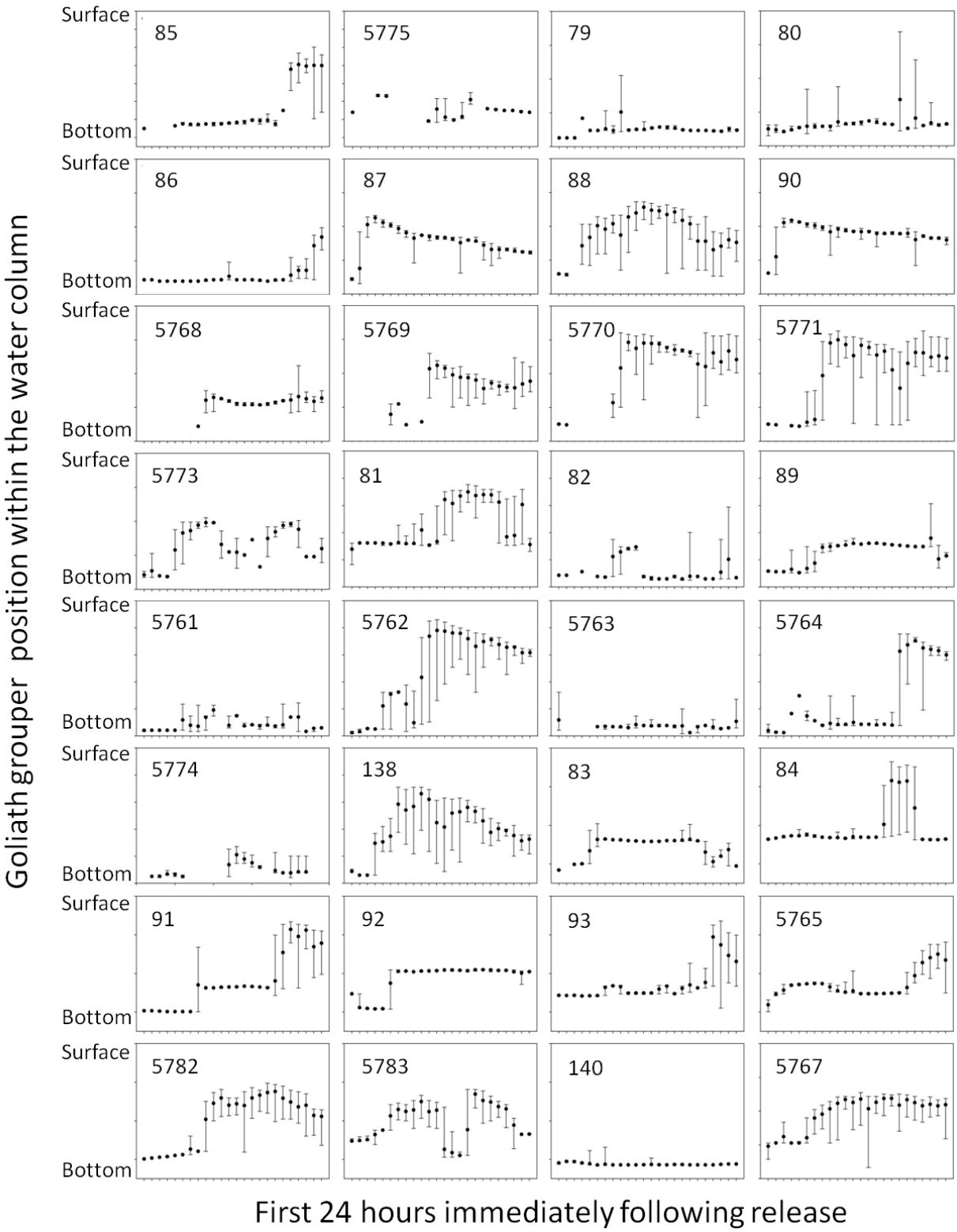
Goliath grouper position within the water column
Surface
Bottom
85
5775
79
80
86
87
88
90
5768
5769
5770
5771
5773
81
82
89
5761
5762
5763
5764
5774
138
83
84
91
92
93
5765
5782
5783
140
5767
First 24 hours immediately following release

Fig. 3.7. Hourly depth position (y-axes) of each individual Atlantic Goliath Grouper, *Epinephelus itajara*, tagged at one of the 6 main sites for the first 24 hours (x-axes) after catch and release. Error bars indicate the minimum and maximum depth of the fish for that hour. Individuals are arranged in order of increasing capture depth. Details for each individual are available in Table 3.2.

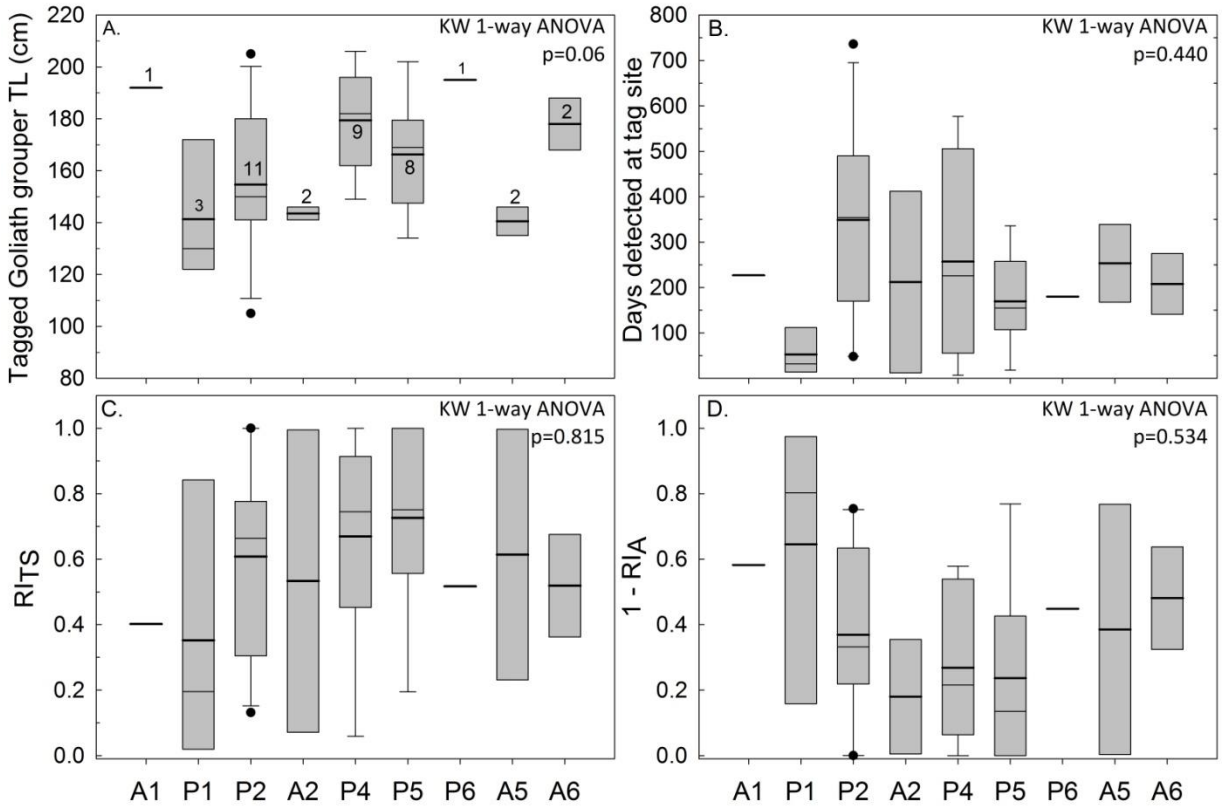

Fig. 3.8. Data for acoustically tagged Atlantic Goliath Grouper, *Epinephelus itajara*, for each tagging site within the study array by (A) total length (the number of fish tagged per site is indicated for each box), (B) the total number of days detected at the site of tagging, (C) the residence index at tag site (RI_{TS}) and (D) the total time fish were unaccounted for (1 – residence index within the array, RI_A where 1 = 100% presence). Sites are listed in order of increasing depth (10 – 40 m) along the x-axis. There were no significant differences among sites for any of these 4 variables (Kruskal-Wallis one-way ANOVA). Box plots indicate the 25 – 75 quartiles, whiskers indicate 95% confidence intervals, and observations falling outside of the 95% confidence intervals are indicated by (●). The mean and median are indicated by the bold and thin horizontal lines, respectively.

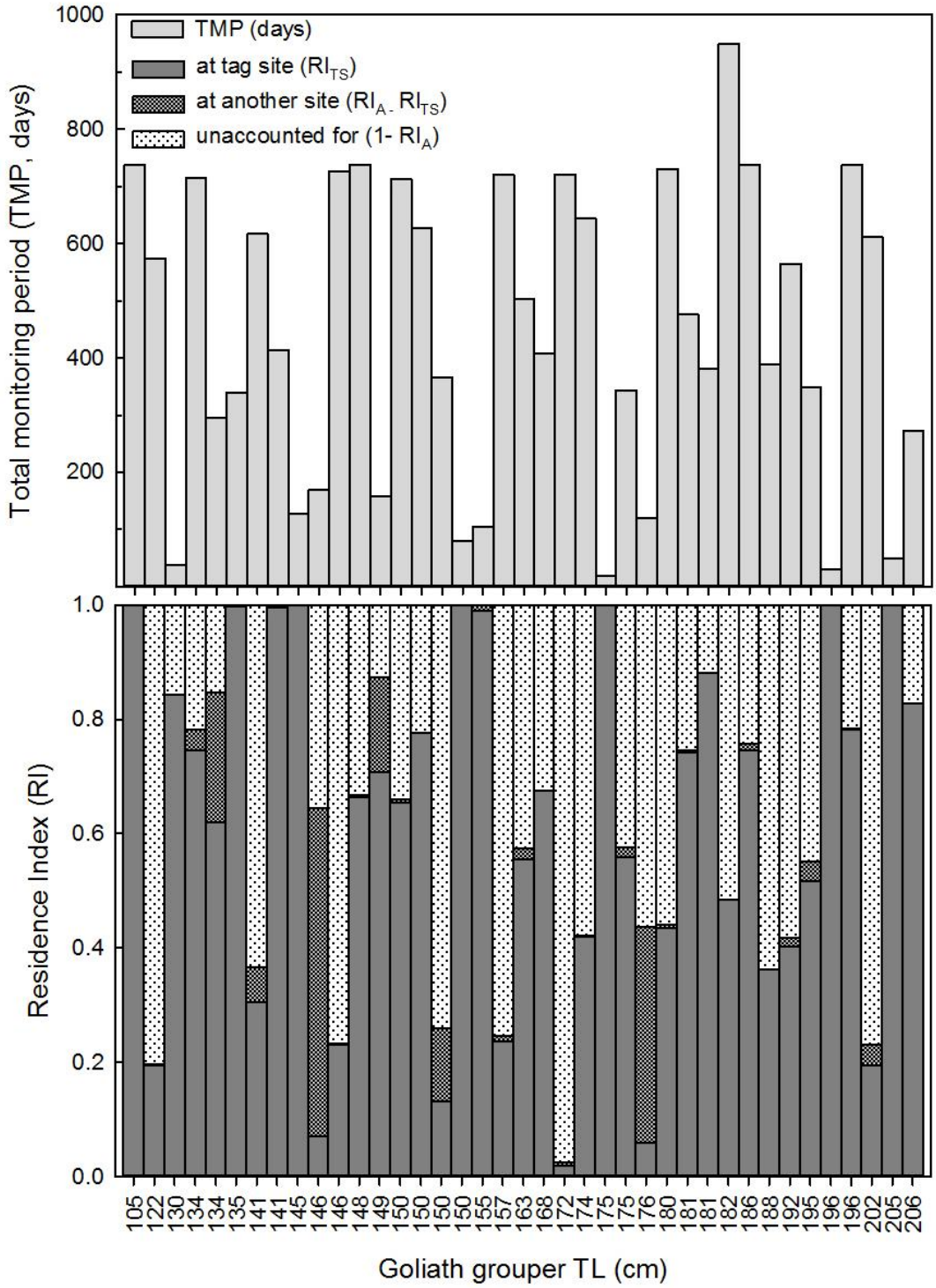

Fig. 3.9. Total monitoring period and residence indices for 39 acoustically tagged Atlantic Goliath Grouper *Epinephelus itajara*. Individuals are arranged by total length, as indicated on the x-axis. Pearson correlation indicated that TL did not affect TMP ($p = 0.773$), RI_{TS} ($p = 0.713$) or time unaccounted for ($1 – RI_A$; $p = 0.449$).

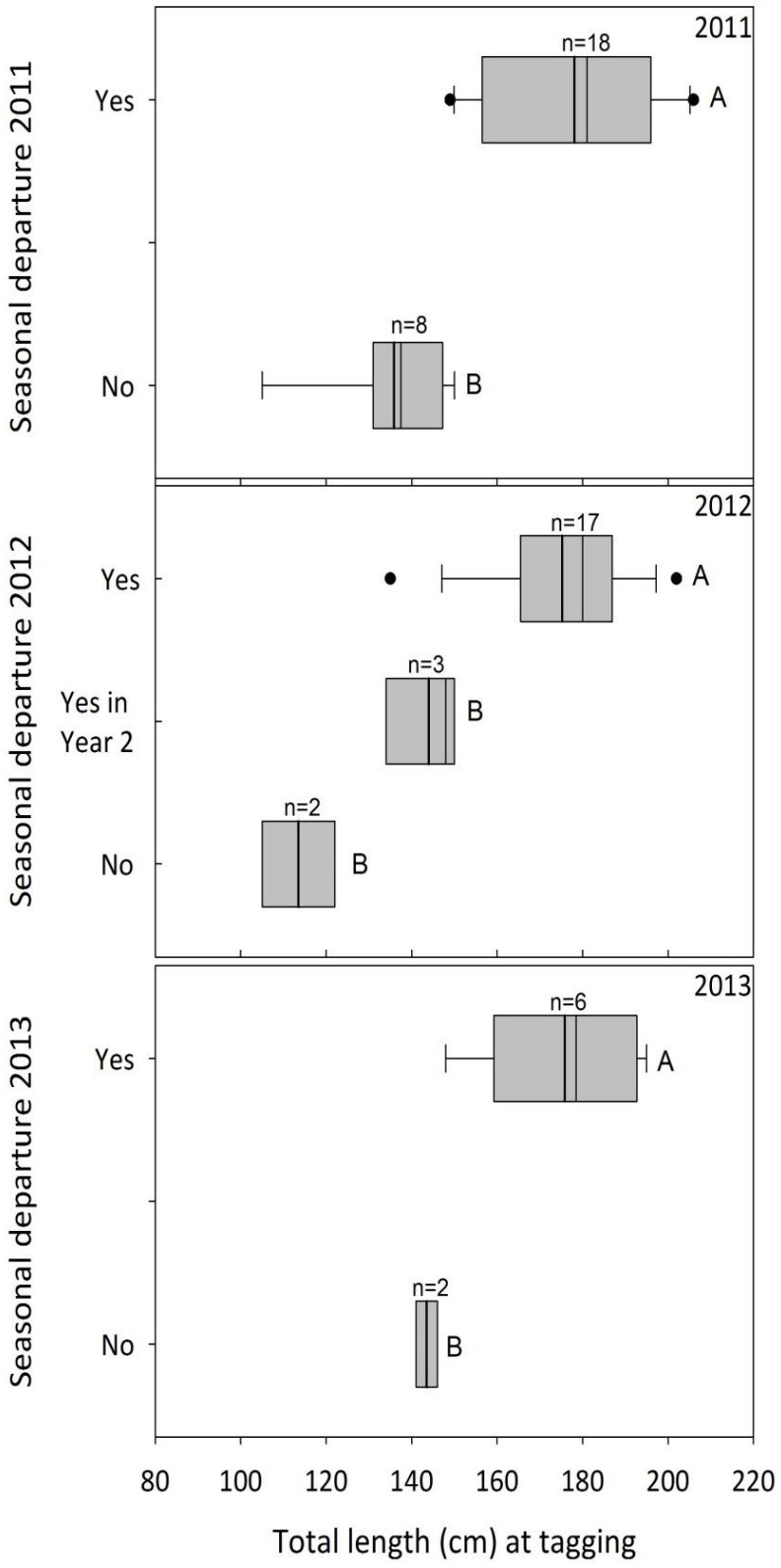
2011
n=18
Yes
A
n=8
No
B
Seasonal departure 2011
2012
n=17
Yes
A
n=3
Yes in
Year 2
B
n=2
No
B
Seasonal departure 2012
2013
n=6
Yes
A
n=2
No
B
Seasonal departure 2013
80
100
120
140
160
180
200
220
Total length (cm) at tagging

Fig. 3.10. Size distribution of Atlantic Goliath Grouper *Epinephelus itajara* that exhibited a seasonal departure during spawning season ('Yes') or maintained continuous presence at resident sites ('No'). Total lengths were measured at initial capture. Letters denote significant differences ($p<0.001$, ANOVA) between groups and the number of individuals within each group is indicated above each box. Box plots indicate the 25 – 75 quartiles, whiskers indicate 95% confidence intervals, and observations falling outside of the 95% confidence intervals are indicated by (●). The mean and median are indicated by the bold and thin horizontal lines, respectively.

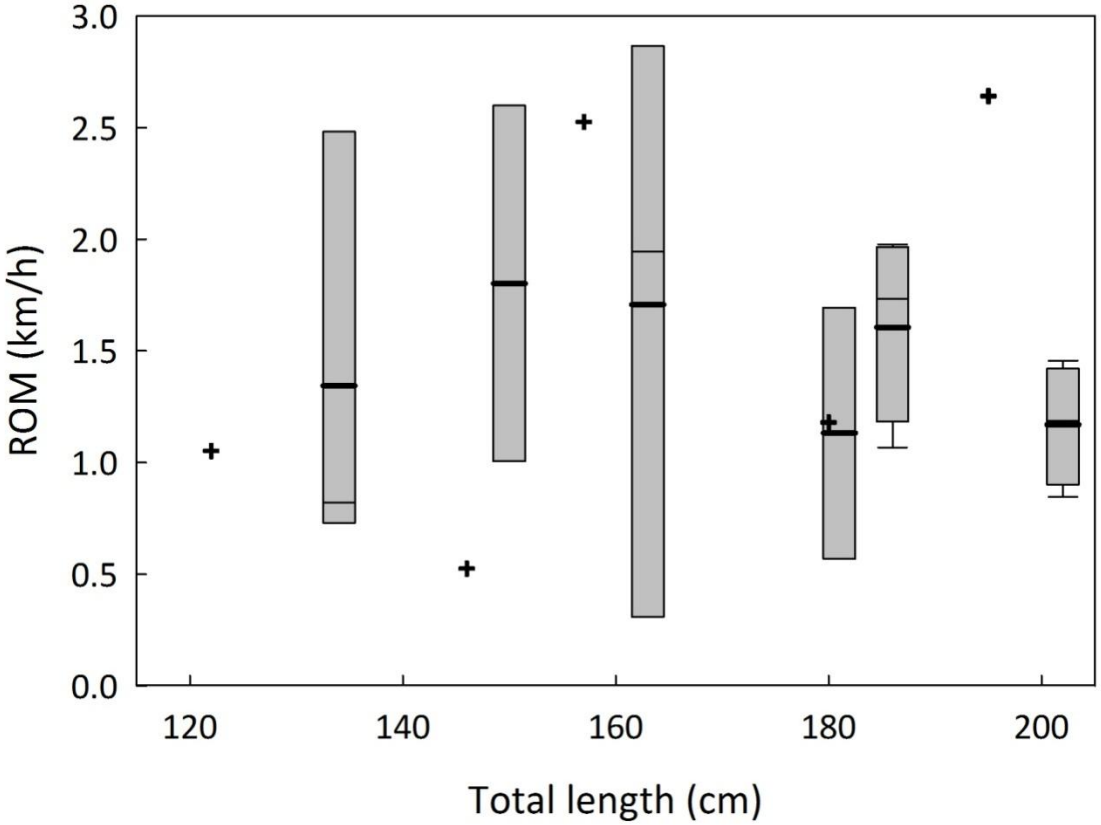

Fig. 3.11. Rates of movement (ROM) for Atlantic Goliath Grouper *Epinephelus itajara*, moving between sites within the study array inside of a 24 hour period (n=11 individuals). Individuals that exhibited multiple movements that allowed for ROM calculations are indicated by boxes (mean and median values are displayed as the bold and thin horizontal lines within each box). Individuals for which only one ROM was calculated are indicated by (+) ROMs are reported by fish total length (TL, cm). There was no significant difference among individual ROMs (p = 0.248), and ROM was not related to fish TL (p = 0.896). Box plots indicate the 25 – 75 quartiles, whiskers indicate 95% confidence intervals, and observations falling outside of the 95% confidence intervals are indicated by (●). The mean and median are indicated by the bold and thin horizontal lines, respectively.

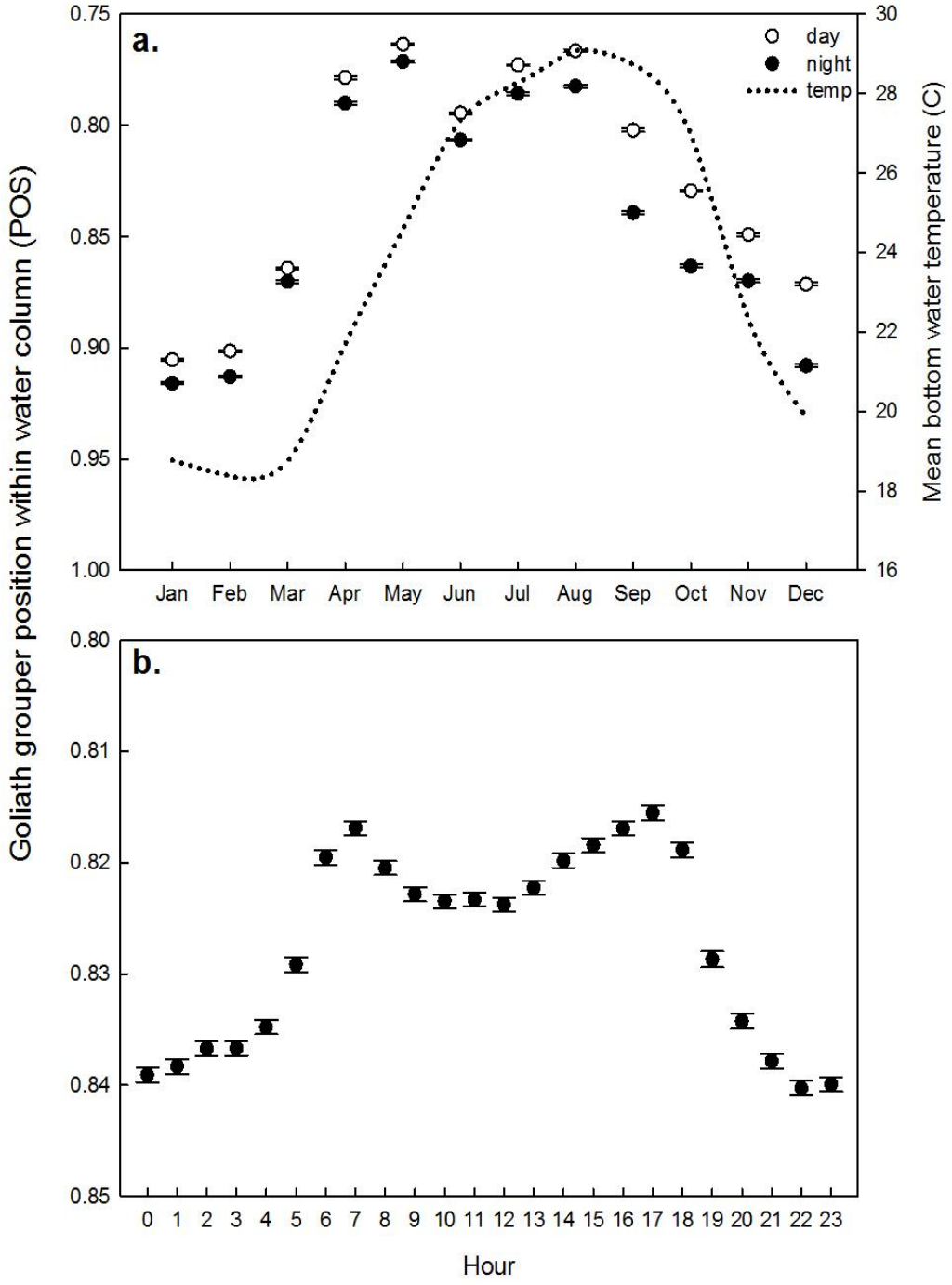

Fig. 3.12. (a.) Mean monthly position within the water column during the day (05:01 – 18:59 EST) and night (19:00 – 05:00 EST) and (b.) mean hourly position over all months (EST) of acoustically monitored. Atlantic Goliath Grouper *Epinephelus itajara* (n=39). Position is standardized across sites by dividing fish depth by the maximum depth of the site, such that a position of 1.00 corresponds to the bottom and 0.0 corresponds to the surface. Error bars indicate 95% confidence limits.

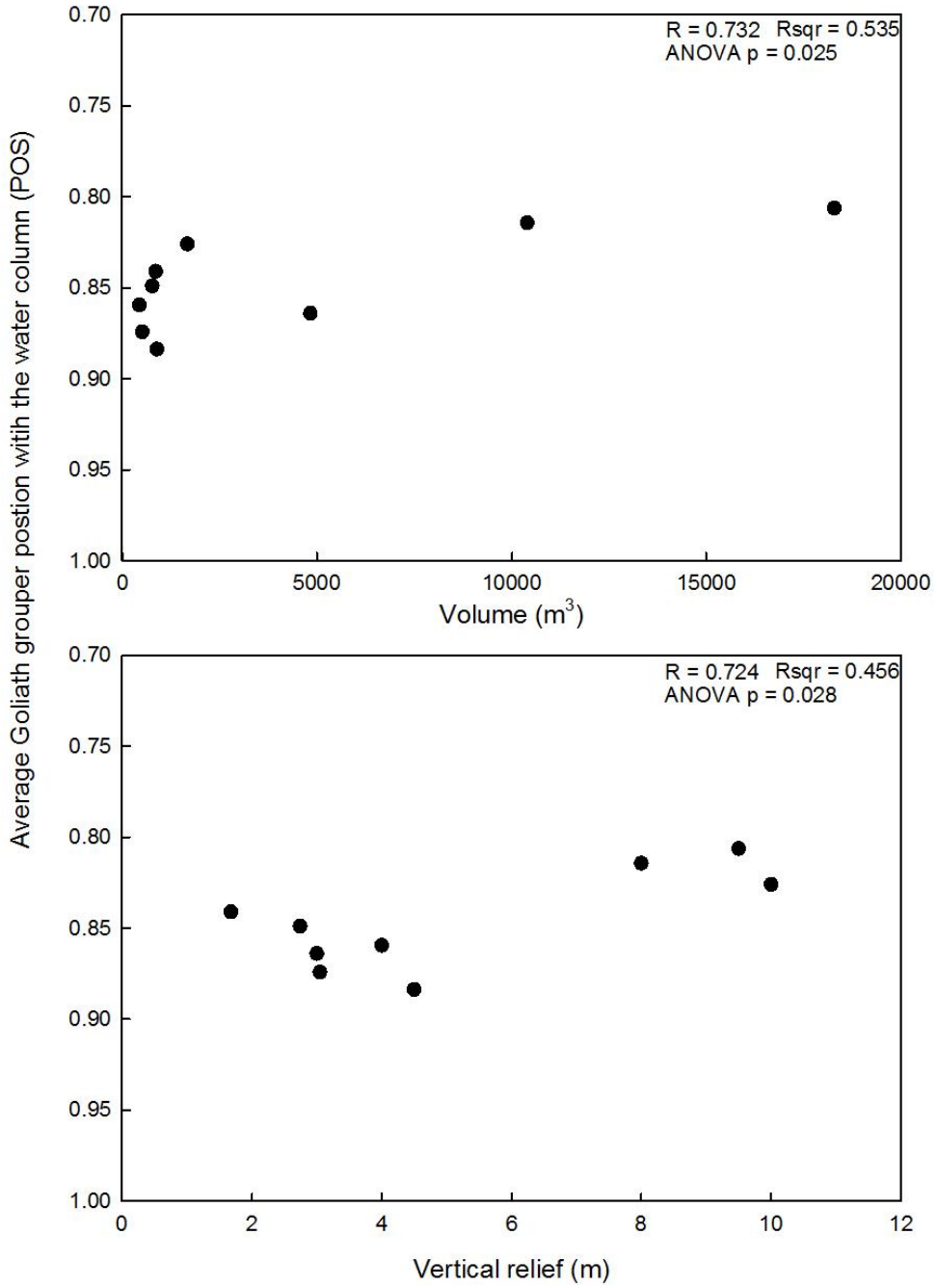

Fig. 3.13. Atlantic Goliath Grouper *Epinephelus itajara* position within the water column, as related to the volume and vertical relief of the site. Position is standardized across sites by dividing fish depth by the maximum depth of the site, such that 1.0 corresponds to the bottom and 0.0 corresponds to the surface.

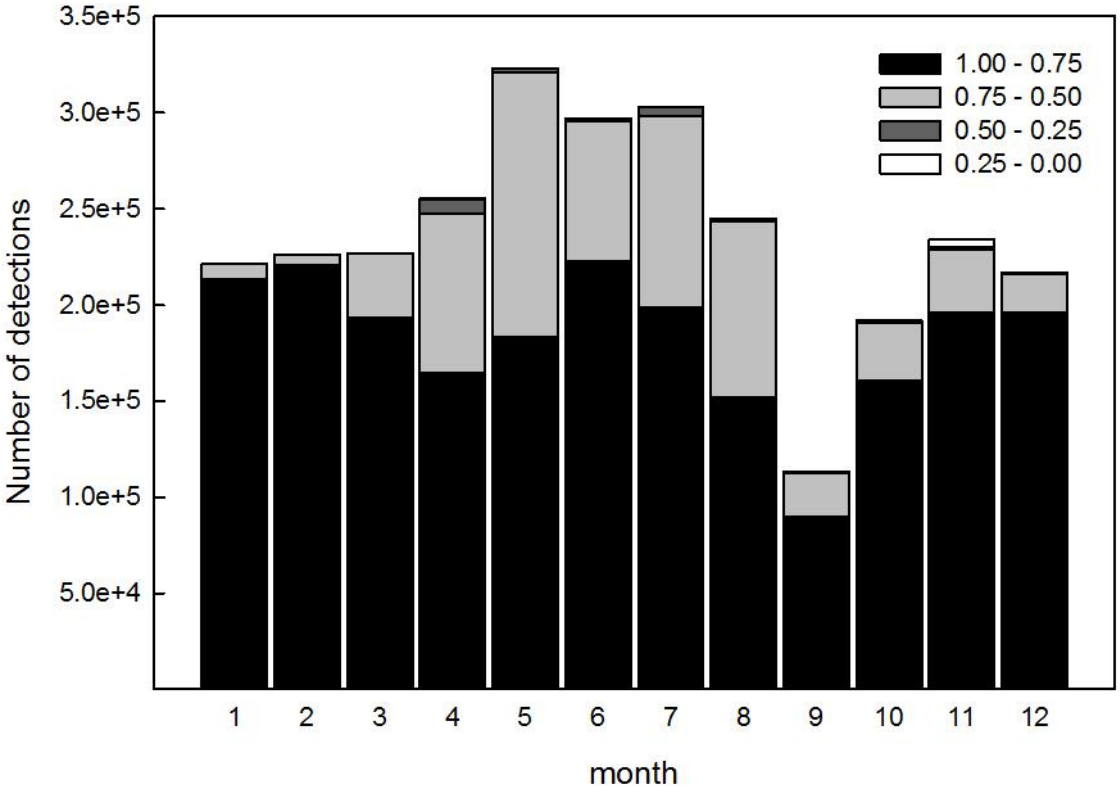

Fig. 3.14. The number of detections of Atlantic Goliath Grouper *Epinephelus itajara* during each month within each quarter of the water column. Position is standardized by dividing fish depth by the maximum depth of the site, such that 1.0 corresponds to the bottom and 0.0 corresponds to the surface (i.e., 1.00 – 0.75 is the bottom quarter of the water column.)

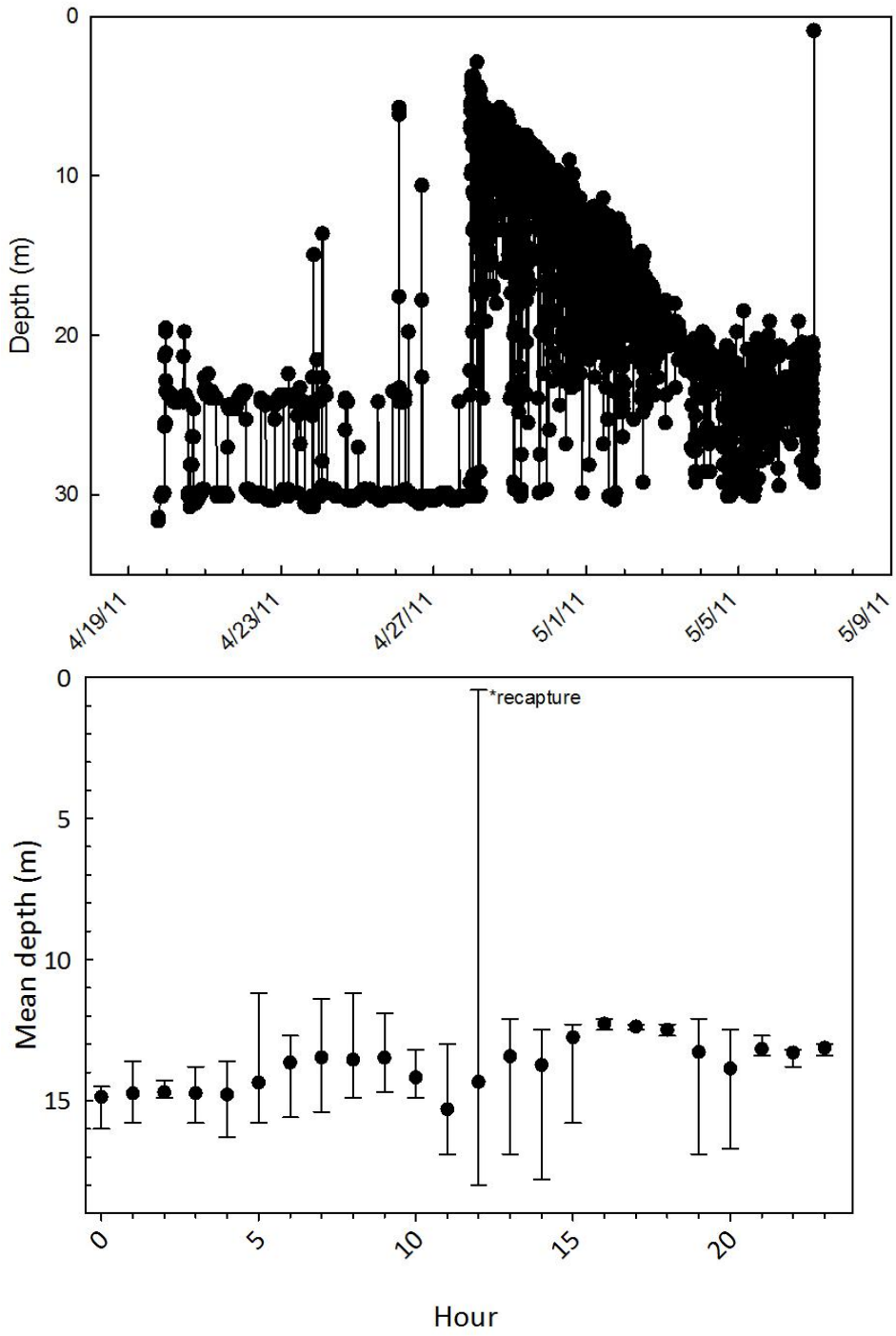

Fig. 3.15. Example of potential catch and release mortality, illegal harvest or tag removal (top graph). Raw depth position data through time is indicated by symbols, with the last detection at 0 m. Example of catch and release event of Atlantic Goliath Grouper, *Epinephelus itajara*, recaptured by the authors (bottom graph). Mean hourly position before and after catch and release is indicated by symbols; minimum and maximum depth per hour are identified by error bars.

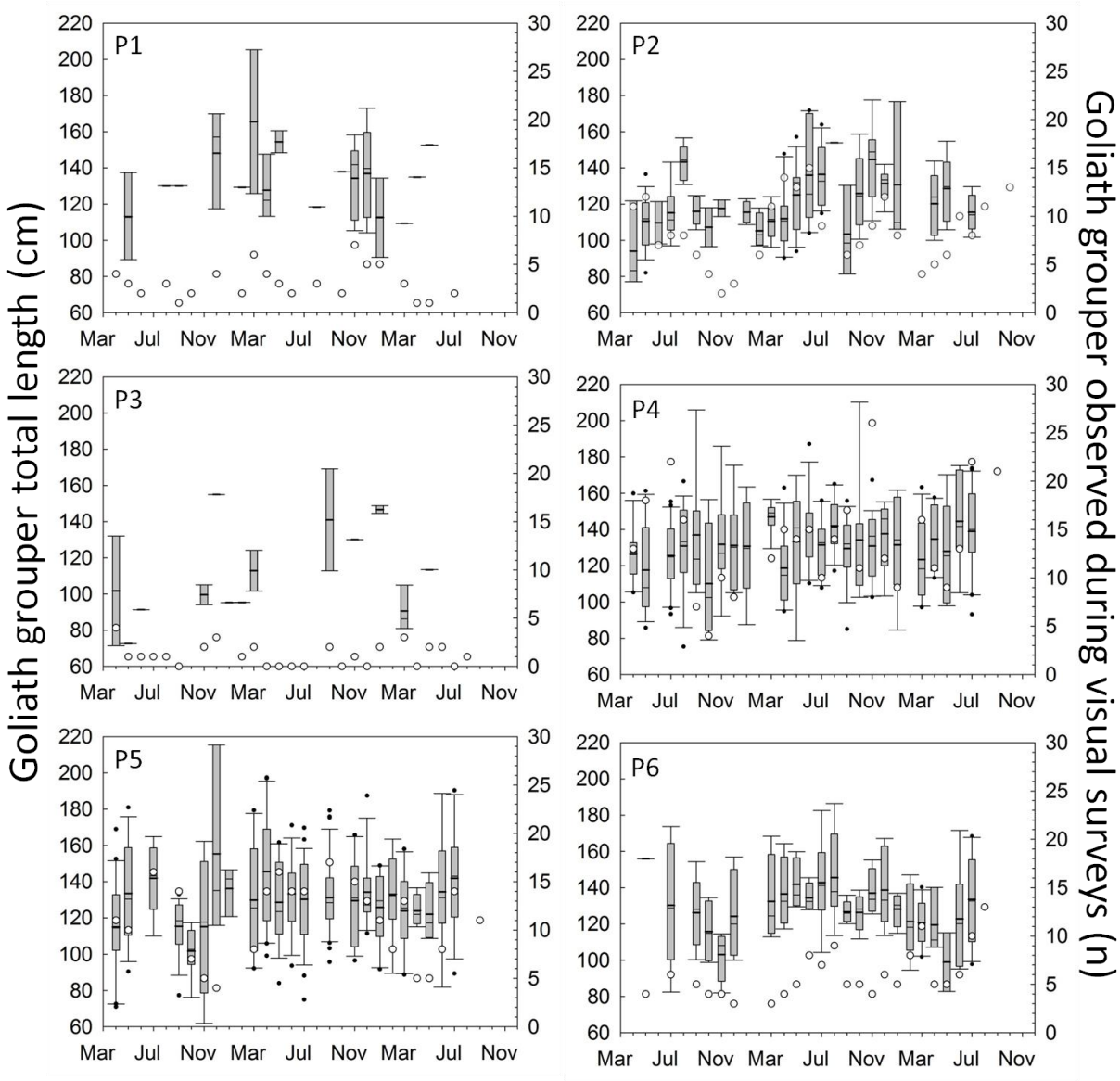

Fig. 3.16. The size distribution (box plots) and number (○) of Atlantic Goliath Grouper, *Epinephelus itajara*, observed during visual surveys at each of the six main study sites during the study period (April 2011 – November 2013). Box plots indicate the 25 – 75 quartiles, whiskers indicate 95% confidence intervals, and observations falling outside of the 95% confidence intervals are indicated by (●). The mean and median are indicated by the bold and thin horizontal lines, respectively.

CHAPTER FOUR

A KINEMATIC INVESTIGATION INTO THE FEEDING BEHAVIOR OF THE ATLANTIC GOLIATH GROUPER *EPINEPHELUS ITAJARA*

Abstract

Atlantic Goliath Grouper *Epinephelus itajara* were overfished within United States waters until their protection from harvest in 1990. As the population recovers, increasing interactions between Atlantic Goliath Grouper and anglers are being reported, often as a result of grouper predation upon hooked fish. Atlantic Goliath Grouper are generally characterized as opportunistic predators capable of consuming a wide variety of prey types; however, minimal data are available regarding the prey capture behavior of this species. Kinematic analyses of adult Atlantic Goliath Grouper feeding events demonstrated the capacity of individuals to modulate feeding behavior based upon the mobility and position of 'prey' items. Mobile food (i.e., tethered swimming fish) elicited larger maximum gapes, faster times to food capture, shorter times to mouth closing, and more rapid total bite durations than food items that were not moving (i.e., dead bait). Feeding sequences involving these mobile, more 'elusive' food items were characterized by a significantly higher degree of 'ram' feeding behavior, while immobile food elicited primarily suction feeding from Atlantic Goliath Grouper. Strikes upon immobile food were preceded by a slower and closer approach to the food item prior to the onset of mouth opening (mean distance to immobile food at onset of mouth opening = 54 mm vs. 221 mm for

mobile food). Additionally, immobile food that was suspended within the water column elicited shorter times to maximum gape, faster mouth closing and more rapid bite durations than immobile food that was positioned on the substrate. These findings demonstrate the ability of Atlantic Goliath Grouper to adjust their feeding strategy based upon prey type and condition, which likely allows for the exploitation of a wide variety of prey and provides an expansive dietary berth for these opportunistic predators.

Introduction

Fish feeding has been the focus of a large body of research over the past century due to the ecological, evolutionary and economic implications of prey selection and capture behavior. Understanding what and how fish eat is of critical importance when describing community structure, trophic relationships and population dynamics within aquatic systems (Hixon, 1991; Beukers-Stewart and Jones, 2004; Matich et al., 2011). Analysis of the morphological components and mechanisms of prey capture can also provide insight regarding phylogenetic relationships among species and the success and performance of particular taxa over evolutionary time (Wiens 1977; Liem, 1980; Wimberger 1991; Motta and Kotrshal, 1992; Liem 1993; Ferry-Graham et al., 2002). For economically important species, predator-prey relationships and feeding behavior can be translated and applied to enhance aquaculture (Wintzer and Motta 2005; Mahjoub et al. 2008) or facilitate commercial and recreational fishing efforts (Wolf and Chislett 1974; High 1980; Wraith et al. 2013).

The mechanism of prey capture among fishes is typically categorized as biting, ram or suction, and most species can utilize a combination of these tactics to capture prey (Liem 1980; Van

Leeuwen and Muller 1984; Norton 1991; Ferry-Graham et al., 2002; Motta 2004). Biting involves using the jaws and teeth to rip prey from the substrate or a larger item (Norton, 1995; Clifton and Motta; 1998). Ram feeding occurs when a predator rapidly approaches and engulfs a prey item (Liem 1980; Norton, 1991; Nemeth 1997; Wainwright, 2001). Suction feeding is characterized by rapid opening of the mouth that creates a significant subambient pressure within the buccal cavity, sucking prey into the predator's mouth with relatively little forward motion by the predator (Lauder 1980; Muller et al., 1982; Van Leeuwen 1984; Carroll et al., 2004; Higham et al., 2006; Wainwright and Day 2007). The majority of teleost fishes utilize suction to capture prey (Liem 1980; Muller and Osse 1984; Carroll et al., 2004), but modulation of feeding behavior is not uncommon and many predators will adjust their prey capture technique in response to prey type, prey size or environmental conditions. For example, faster mouth opening may occur when feeding upon elusive, mobile prey (Coughlin and Strickler, 1990; Wainwright et al., 2001; Holzman et al., 2007), and wider maximum gapes may be achieved if the predator is presented with larger prey (Wainwright et al., 2001). Additionally, fish may locate prey faster and feed more rapidly when competition is perceived to be high (Stoner and Ottmar 2004; Pfeiffenberger and Motta 2011). The capacity to alter feeding behavior in response to varying conditions likely influences fitness at the individual level by expanding dietary breadth and increasing feeding opportunities (Liem 1978; Sanderson 1991).

Atlantic Goliath Grouper (*Epinephelus itajara*, Lichtenstein 1822) are one of the world's largest groupers (Craig et al., 2011), and can attain sizes exceeding 400 kg and two meters in total length (Bullock et al., 1992). Like many large, long lived species, Atlantic Goliath Grouper have suffered significant population declines throughout their geographic range (Musick 2000) and

are currently listed as critically endangered on the IUCN Red List (Pusack and Graham 2009). The species was protected from all harvest within United States waters in 1990 (GMFMC, 1990; SAFMC, 1990). The population responded encouragingly to these protective measures and is beginning to exhibit signs of recovery, especially along the southwest coast of Florida (Cass-Calay and Schmidt 2009; Koenig et al., 2011), where increasing interactions between Atlantic Goliath Groupers and anglers have become a source of contention among some groups. Anglers report that Atlantic Goliath Groupers are becoming a 'nuisance' species in some areas due to their propensity to take anglers' bait and 'steal' hooked fish (Fleshler 2011; Kelly, 2011; Frias-Torres 2012).

The expansive buccal cavity of Atlantic Goliath Grouper appears specialized for volume suction feeding (Lauder, 1980; Weaver, 1996; Wainwright et al., 2001; Carroll et al, 2004; Westneat, 2005); however, the feeding mechanics of this species have not previously been described. Atlantic Goliath Grouper are reported to feed primarily upon benthic crustaceans (Longley and Hildebrand, 1941; Randall, 1967; Randall, 1983; Bullock and Smith, 1991; Heemstra and Randall, 1993; Koenig and Coleman, 2009) but fish are not uncommon prey (Randall, 1983; Bullock and Smith, 1991) and both teleost and elasmobranch species have been identified within their stomachs (Randall 1967), as well as sea turtles (Yeiser et al., 2008) and octopus (Bullock and Smith, 1991). The majority of fish prey identified to date consists of slower moving or benthic associated species (i.e. cowfish *Acanthostracion* spp., pufferfish *Sphoeroides* spp., catfish *Bagridae marinus* and stingrays *Dasyatis* spp.), which supports contentions that Atlantic Goliath Grouper are typically relatively sedentary ambush predators (Sadovy and Eklund, 1999). However, feeding in the water column upon schools of baitfish (e.g., Clupeidae, Carangidae) as

well as upon hooked fish being reeled in by anglers or shot by spearfishers is often observed (Gerhardinger et al., 2006; Phelan et al., 2008; Collins pers. obs.).

Although Atlantic Goliath Grouper are generally characterized as suction feeders (Gerhardinger et al., 2006; Koenig and Coleman 2009), their wide dietary berth and aggressive attacks upon hooked fish suggest that they are capable of modifying their feeding behavior to take advantage of alternate prey opportunities. The goal of this study was to provide a general baseline description of Atlantic Goliath Grouper prey capture behavior and to assess whether Atlantic Goliath Grouper modulated feeding behavior in response to varied prey types and presentations. We hypothesized that immobile and benthic prey would elicit suction feeding, and that more mobile and elevated prey would result in a behavioral shift toward ram feeding. A description of Atlantic Goliath Grouper feeding behavior may allow for future innovative suggestions to decrease the probability of catching this species and reduce predation upon hooked fish, and should assist with better understanding the interaction between Atlantic Goliath Grouper and anglers.

Methods

Experimental trials took place *in situ* at artificial reefs in the central eastern Gulf of Mexico that exhibited consistent Atlantic Goliath Grouper presence throughout the year (Collins et al., in review). Site depths ranged between 20 and 30 meters. Feeding trials took place during the summer (June – August) when bottom water temperatures were between 27 – 30 °C, and were only attempted when horizontal visibility was greater than five meters.

Feeding trials

A thick monofilament line (225 kg test), hereafter referred to as the 'mainline,' was attached to a concrete weight positioned on the bottom. The main line was marked in 200 mm increments (to provide scale) and connected to a subsurface buoy that kept it suspended vertically. Prey items were measured (length and width, mm) and threaded with a short piece (10 – 20 cm) of cotton line through their approximate center of mass that provided an easy "break-away" component so that Atlantic Goliath Grouper would not ingest anything other than the attached prey item. The cotton thread was connected to a 20 cm section of lightweight monofilament (5 kg test) secured to a stainless steel gangion that could be snapped on to the mainline.

Prey items, hereafter referred to as 'food' for consistency, were classified as 'mobile' (live grunt *Haemulon* spp.) or 'immobile' (cut dead bait; either *Euthynnus alletteratus* or *Sphyraena barracuda*). Mobile food was attached to the main line at least 2 meters from the bottom in order to keep the fish swimming. Immobile food was also attached to the main line and was presented either on the substrate (benthic) or suspended from the main line at least two meters above the bottom (elevated). All food items (mobile and immobile) were generally the same size and ranged from 100×100 mm to 100×330 mm (width×length; mean = 219×100 mm; Table 4.1).

Atlantic Goliath Grouper ranged in size from 1100 – 2070 mm TL (n = 26; mean ± S.E. = 1475 ± 39 mm). Only one feeding strike was evaluated for each individual, resulting in a total of 11 individual feeding sequences upon mobile food, and 15 individual feeding sequences upon immobile food (9 individuals fed upon elevated immobile items and 6 fed upon benthic immobile items; Table 4.1). Atlantic Goliath Grouper mature between 1100 – 1350 mm (Bullock

et al., 1992), so it is assumed that all feeding trials were performed by adult fish. Atlantic Goliath Grouper were recorded and measured prior to presenting the food item using a custom-made laser apparatus that was attached to an underwater video camera (Sony Handycam, HDR-550 CX, 60 frames per second) that was operated by an underwater observer. The lasers projected equidistant points (200 mm apart) onto the body of the Atlantic Goliath Grouper and still frames in which the fish was perpendicular to the optical axis of the camera were used to calculate TL to the nearest cm. Furthermore, head length for each individual was calculated as the distance between the anterior tip of the premaxilla and the posterior edge of the operculum.

Two high definition video cameras (GoPro HD HeroII) were placed orthogonal to each other and positioned four meters from the main line by divers. Cameras recorded at 60 fields per second and were positioned so that the food was centered within the field of view. When possible, a third high definition camera (Sony Handycam, HDR-550 CX, 60 fields per second) held by an underwater observer approximately four meters from the food was also used to film feeding sequences. This additional videography was not always feasible, however, since Atlantic Goliath Grouper would not feed consistently in the presence of divers. Videos from each camera were assessed and only sequences in which feeding occurred perpendicular to the camera (so that a lateral view of the predator was visible) were selected for analysis of feeding kinematics. All experimental procedures were performed with the approval of the University of South Florida Institutional Animal Care and Use Committee (permits #3210 and #3887).

Kinematics

Feeding sequences were analyzed using the program Tracker (version 4.84, © 2014, www.cabrillo.edu/~dbrown/tracker). For each feeding sequence, the following landmarks were tracked from the field before the onset of mouth opening until the field after the mouth closed: (1) estimated geometric center of mass of the food item (COM), (2) anterior tip of the predator's premaxilla (APM), (3) anterior tip of the predator's lower jaw (ALJ), and (4) center of the eye of the predator (COE) (Fig. 4.1). Using these landmarks, the following kinematic variables were assessed: (1) maximum gape (MG): the maximum distance between the anterior tip of the premaxilla and the anterior tip of the lower jaw during food capture; (2) time to maximum gape (TTMG): the length of time from onset of mouth opening until maximum gape was obtained; (3) time to food capture (TTFC): the time between the onset of mouth opening and the point at which the center of mass of the food item passed through the anterior gape of the predator; (4) time to close mouth (TTCM): the time between the end of maximum gape and the jaws returning to a closed position; and (5) total bite duration (TBD): the time from the onset of mouth opening until the mouth closed. Stalking duration (StD) was calculated as the time between orientation of the predator to the food item (the point at which the head oriented to the food item and began approach) and the onset of mouth opening.

Food distance from the predator at the onset of mouth opening (FDMO) was calculated as the distance between the center of mass of the food item and the anterior tip of the premaxilla. Distance moved by the predator (D_{pred}) was calculated as the total distance travelled by the predator (measured at the center of the eye) from the onset of jaw opening until the center of mass of the food passed through the anterior gape. Distance moved by the food (D_{food}) was

calculated as the total distance travelled by the estimated center of mass of the food from the onset of predator jaw opening until passing through the anterior gape of the predator (vertical line between the anterior tip of the premaxilla and the lower jaw). For feeding events upon immobile food, suction distance was calculated as the distance between the center of mass of the food and the anterior tip of the premaxilla for the frame in which the food item began to move toward the predator.

Data Analysis

The distances moved by the predator were plotted against the distances moved by the food item for all feeding sequences. In addition, these distances were used to calculate a value of "ram-suction" index (I_{RS}; Norton and Brainerd 1993), where

$I_{RS} = (D_{predator} - D_{food})/(D_{predator} + D_{food})$.

Calculation of I_{RS} allowed for a description of the strike mode and designation of individual feeding behavior along the 'ram-suction' continuum (Norton and Brainerd 1993; Sass and Motta 2002; Ouifiero et al., 2012), where an I_{RS} value = +1.0 is indicative of complete ram feeding and alternately, an I_{RS} value = -1.0 designates pure suction. For feeding events upon immobile food, suction distance was expressed as a percentage of total length, head length, and maximum vertical gape. Kinematic variable data were assessed for equality of variance (using Levene's test) and for normality (using the Shapiro-Wilk test) and were log-transformed when necessary to meet the assumptions of normality and equal variance. Linear regressions were performed to test for relationships between predator total length and the variables as defined above: StD, MG, TTMG, TTFC, TTCM, and TBD (Table 4.2). To assess whether these variables exhibited a relationship to food type (mobile vs. immobile) or food position (benthic vs. elevated; for

immobile food only), t-tests were performed to identify differences between groups. All statistical analyses were performed using the program SigmaPlot (version 12.5, Systat Software, San Jose, CA).

Results

Total length of the predator did not affect the stalking duration (StD), maximum gape (MG), time to food capture (TTFC), time to maximum gape (TTMG), time to close mouth (TTCM), or total bite duration (TBD) ($p > 0.05$; see Table 4.2 for exact p - values). Consequently, all individuals were grouped together for the remaining analyses. Feeding behavior of Atlantic Goliath Grouper was significantly affected by the activity level of the food (Table 4.1). Stalking durations (time between orientation to food and the onset of mouth opening) lasted up to 50 seconds, and were generally shorter when approaching mobile food (range 3 – 25 s; Fig. 4.2), although there was not a significant statistical difference ($p = 0.064$, $df = 24$). Mobile food elicited significantly larger maximum gapes, shorter capture times, shorter times to maximum gape, faster mouth closing and more rapid bite durations overall than those involving immobile food ($p < 0.05$; $df = 24$; Fig.4.2). All feeding sequences on mobile food were more characteristic of ram feeding (Fig. 4.3a) and I_{RS} ranged +0.46 to +1.0 (Fig. 4.3b). When presented with immobile food, Atlantic Goliath Grouper approached more slowly, exhibited smaller maximum gapes, longer capture times and greater bite durations, and almost all feeding sequences upon immobile food demonstrated suction feeding (Fig. 4.3). All Atlantic Goliath Grouper attacks upon mobile food involved continuous forward motion by the grouper through the feeding sequence, while attacks upon immobile food typically involved an initial approach to the food item, followed by an abrupt stop in front of the food before the onset of mouth opening.

Additionally, Atlantic Goliath Grouper began to open their mouth from farther away when feeding upon mobile food (range: 122 – 262 mm; mean = 221 mm), but minimized the distance between their mouth and the food prior to suction feeding upon immobile items (range: 1 – 120 mm; mean = 54 mm; $p < 0.001$, df = 24; Fig. 4.4a). During feeding events upon immobile food, mouth opening was initiated at a distance which corresponded to 0.001 – 29% of head length (mean distance at onset of mouth opening = 12.6%). This was in contrast to feeding events upon mobile food, where mouth opening was initiated at a distance of 25 – 68% of predator head length (mean distance = 57%).

Suction distances for feeding sequences upon immobile food ranged from 0 – 120 mm (mean = 53.5 ± 12.3 S.E.), corresponding with a mean of 3.4% of total length (± 0.1% S.E.; range = 0 – 7.9%), 12.2% of head length (± 2.8% S.E.; range = 0 – 28.6%) and 29.4% of maximum gape (± 7.7% S.E.; range = 0 – 65.4%). Feeding sequences upon immobile, elevated food elicited faster times to maximum gape, faster times to close the mouth and shorter bite durations than food that was positioned on the substrate ($p < 0.05$, df = 13); however, there were no significant differences in predator distance from the food at the onset of mouth opening (Fig. 4.4b), stalking period, maximum gape, or food capture time (Fig. 4.5). Both elevated and benthic immobile food elicited feeding that was typically characteristic of suction feeding (Fig. 4.6a), with I_{RS} values that ranged from –1.0 to +0.16 for elevated immobile food, and from –1.0 to –0.37 for benthic immobile food (Fig. 4.6b).There was not a significant difference in I_{RS} values between these two groups ($p = 0.094$, df = 13).

Discussion

Most groupers are ambush predators (Burnett-Herkes, 1975; Parrish, 1987; Bullock and Smith, 1991) that often engulf prey through suction feeding (Thompson and Monroe, 1978, Viladiu et al., 1999; Burns 2009); however, this family is ecologically diverse and there are many grouper species that actively chase down prey and exhibit prey capture behavior that is characteristic of ram feeding (Wainwright and Bellwood 2002; Ouifiero et al., 2012). Atlantic Goliath Groupers have been characterized as ambush suction feeders that prey predominantly upon slow moving benthic fishes and crustaceans (Sadovy and Eklund, 1999; Koenig and Coleman, 2009), but increasing reports of predation by Atlantic Goliath Grouper upon hooked fish during angling events indicate that they are capable of modulating their feeding behavior to take advantage of scavenging opportunities. During this study, mobile food elicited faster approaches, wider maximum gapes, and more rapid capture than immobile food. Furthermore, for strikes upon immobile food, feeding behavior shifted with food position, and elevated items elicited faster strikes and shorter bite durations than food positioned on the ground.

Flexibility in feeding behavior is indicative of a diverse diet (Liem 1980; McKaye and Marsh 1983; Norton 1991), and the capacity to modulate prey capture strategy may significantly influence growth and survival at the individual level by expanding dietary breadth and increasing feeding opportunities (Liem 1978; Sanderson 1991). Modulation of feeding behavior as a response to differing prey conditions has been demonstrated for multiple species. For example, largemouth bass (*Micropterus salmoides*) switch from ram to suction feeding when visibility is inhibited (Gardiner and Motta 2012), and also will increase ram feeding behavior when presented with elusive prey (Wintzer and Motta 2005). Elusive prey has also been shown to elicit

increased ram behavior in sculpins (Cottidae; Norton 1991), larger gape width and increased ram distance in cichlids (Wainwright et al., 2001), and faster approach and strike velocities in the kelp greenling *Hexagrammos decagrammus* (Nemeth 1997). Wider gapes and faster mouth closing times reduce the chance of prey escaping (Motta et al. 2002), so the most effective predation strategies upon evasive prey should include exhibit rapid approaches, shorter bite times and larger maximum gapes.

Categorizing prey capture behavior as either ram or suction has long been used to describe fish feeding strategies (Alexander 1967; Nyberg 1971; Van Leeuwen and Muller, 1984; Wainwright and Lauder 1986; Norton 1991). Most fishes utilize a combination of both ram and suction, placing them somewhere along a 'ram-suction' continuum (e.g., Norton and Brainerd, 1993; Wainwright and Richard 1995; Nemeth 1997; Van Damme and Aerts, 1997; Higham et al., 2005; Flammang et al., 2009). The ram suction index (Norton and Brainerd 1993) provides a relatively easy way to compare feeding behaviors, both among and within species (Gibb, 1997; Nemeth, 1997; Ferry-Graham, 1998; Sass and Motta 2002; Wintzer and Motta 2005). Calculated I_{RS} values for Atlantic Goliath Grouper spanned the full ram-suction continuum during this study, providing evidence of their ability to adjust their prey capture strategy based upon the situation. When presented with live, active food, all Atlantic Goliath Grouper demonstrated I_{RS} values characteristic of ram feeding (i.e., $I_{RS} > 0.0$), and exhibited forward movement to engulf the swimming fish. In contrast, non-moving food items, regardless of their position within the water column (elevated vs. benthic), typically elicited I_{RS} values indicative of suction feeding (< 0.0). While estimates of I_{RS} provide an index value and thus are not meant to provide an exact measure of feeding performance on their own (Wainwright et al., 2001), the index can be

especially useful during attempts to demonstrate how fish adjust their feeding behavior in response to differing prey opportunities. The I_{RS} values calculated herein were supported by an assessment of the actual distances moved by food and predator during alternate scenarios: distances moved by the food items were much greater than distances moved by the Atlantic Goliath Grouper when presented with immobile food, while the opposite was true for mobile food.

Atlantic Goliath Grouper suction feeding was preempted by slow approaches and often, a complete halt in forward motion prior to mouth opening, which was directly followed by the food being rapidly sucked into the mouth. Additionally, suction feeding sequences exhibited significantly shorter distances between predator's mouth and the food at the onset of mouth opening (mean distance = 3.5% of total length versus 16% of total length during ram feeding). Similarly, largemouth bass (mean standard length = 235 mm) initiated suction feeding at small distances of 0.4 – 26.6 mm (mean = 10.1 mm versus 44.8 mm for ram feeding; Svanback et al., 2002), which corresponded to < 1 – 11% (mean ~ 4.3%) of predator standard length. Slow approaches during suction feeding are likely an attempt to reduce the "bow wave" created by forward motion of the head – the reduction of which should allow for greater suction pressure (Ferry-Graham et al., 2003; Wintzer and Motta, 2005). Furthermore, the capacity for effective suction decreases with distance from the target (Muller et al., 1982; Norton and Brainerd 1993; Wainwright et al. 2001; Day et al., 2005), so suction feeding at close range should increase efficiency (Gibb and Ferry-Graham 2005), especially for non-elusive prey that is unlikely to escape (Higham et al. 2006). Suction distances during feeding sequences upon immobile food ranged between 0 and 120 mm (mean = 53.5 mm), corresponding to < 1 – 8% of predator total

length (mean =3.4%), < 1 – 29% of predator head length (mean = 12.2%), and <1 – 65.4% of maximum gape (mean = 29.4%). Bluegill sunfish *Lepomis macrochirus*, are specialized suction feeders (Gillis and Lauder, 1995; Carroll et al., 2004), and Holzman et al. (2007) demonstrated that individuals (156 – 178 mm SL) would initiate strikes upon tethered shrimp from an average of ~10 mm away (~6% of predator SL). Perch (*Perca fluviatilis* L.) between 60 – 200 mm TL displayed suction distances ~ 7 – 12 mm (6 – 11% of predator TL), and larger perch had longer suction distances than smaller perch (Svanback and Eklov 2003). Similarly, Van Wassenberg et al. (2006) showed that theoretical suction distance generally increased with catfish *Clarius gariepinus* head size, at least up to a suction distance of 100 mm (catfish ranged in size from 111 – 923 mm TL). In contrast, suction distances for nurse sharks (*Ginglymostoma cirratum*) were not affected by the total length of the shark (1000 – 1720 mm TL; Motta et al., 2008) and were typically only ~ 30 mm (1.7 – 3% of TL). The suction distances observed within this study (1 – 120 mm) are relatively small compared to the large size of Atlantic Goliath Grouper (> 1000 mm TL), but are comparable to those observed for other large and small fishes (Svanback and Eklov, 2003; Van Wassenberg et al., 2006; Motta et al., 2008). This is likely due to the hydrodynamic restrictions imposed during aquatic suction feeding, which limit the effectiveness of suction to relatively short distances from the mouth (Muller et al., 1982; Norton and Brainerd 1993; Wainwright et al. 2001; Day et al., 2005; Gibb and Ferry-Graham 2005).

Due to the forward motion required for ram feeding, benthic prey is most effectively captured through suction (Day et al., 2005; Nauwelaerts et al., 2007; Carroll et al., 2004; Gibb and Ferry-Graham, 2005), and Atlantic Goliath Grouper exhibited suction for all benthic food items during this study. When immobile food items were elevated off of the bottom, Atlantic Goliath Grouper

continued to exhibit suction feeding behavior but exhibited shorter times to maximum gape and mouth closing and shorter bite durations. Similar differences in feeding kinematics between benthic and midwater feeding have been observed for other fishes such as the European ruff *Gymnocephalus cernua* (Elshoud-Oldenhave and Osse 1976) and the Malawi cichlid *Petrotilapia tridentiger* (Liem 1980). The longer times to maximum gape, mouth closing and total bite durations during benthic feeding may be explained by an increased need to properly orient the mouth for good suction in order to work around substrate interference, or alternately, because the substrate may facilitate prey capture by providing an additional barrier to prey escape, the urgency to close the mouth may be reduced.

The morphology of specialized suction feeding teleosts [e.g., butterflyfishes (Motta 1988), seahorses (Bergert and Wainwright 1997), bluegill sunfish (Carroll et al., 2004)] is typically exemplified by small mouths, reduced dentition and deep bodies (Muller and Osse 1984; Norton and Brainerd 1993; Clifton and Motta 1998). In contrast, specialized 'ram' feeders are characterized by large mouths, relatively large teeth and more streamlined bodies that are efficient at rapidly overtaking prey (Rand and Lauder 1981; Webb, 1984; Porter and Motta, 2004; Grubich et al., 2008). Atlantic Goliath Grouper have large mouths, exhibiting a maximum vertical gape at least 15% of total body length, but possess small villiform teeth and have bodies that are not suggestive of high cruising speed. A large mouth increases the size range of potential prey (Keast, 1985; Werner, 1974; Wainwright and Richard, 1995) but may also decrease suction performance (Muller at al., 1982; Van Leeuwen and Muller 1984; Liem, 1990). Ouifero et al. (2012) suggested that species with low morphological potential for suction may exhibit a range of attack behaviors. Feeding behavior by Atlantic Goliath Grouper demonstrated that they are

capable of exhibiting a range of prey capture strategies and will adapt prey capture mechanisms in response to different situations. While their morphology is not predictive of a specialized ram feeder, they are capable of short explosive bursts of speed (Bullock and Smith, 1991) and will overtake fish struggling on a line that presents allows for easy capture and provides an additional food opportunity.

Groupers are generally classified as opportunistic and 'generalist' predators (Parish, 1987; Nakai et al., 2001; Gibran 2007) and will consume a variety of prey based upon availability and likely, ease of capture (Randall and Brock, 1960; Brule et al., 1994; St. John, 1999; Beukers-Stewart and Jones 2004). The dietary data available for Atlantic Goliath Grouper (Longley and Hildebrand, 1941; Randall, 1967; Randall, 1983; Bullock and Smith, 1991; Heemstra and Randall, 1993; Koenig and Coleman, 2009) indicate that they most commonly consume benthic prey (crustaceans and slow benthic-associated fishes). Based upon the results herein, we suspect that these types of prey items are likely consumed primarily through suction feeding. However, more elusive, mobile prey is still represented within their diet and they are likely consumed during short bursts of ram-dominated feeding.

The ability to modulate feeding behavior, combined with their large gape, allow Atlantic Goliath Grouper to consume a wide variety of prey. Along the west coast of Florida, Atlantic Goliath Grouper are most commonly associated with artificial reefs (Koenig et al, 2011; Collins et al., in review). Artificial reefs are favored fishing areas for many anglers, and as the Atlantic Goliath Grouper population recovers, the interaction between this species and anglers is likely to increase. Angled fish that are struggling on a hook and line immediately above resident habitat

present a readily exploitable food opportunity. Predation upon these items increases the potential for incidental catch and release of Atlantic Goliath Grouper, and attacks upon hooked prey may also result in fishing gear entanglement or ingestion. Burns (2009) demonstrated a difference in survival after hooking (using circle hooks) for two species of reef fish (Red Grouper *E. morio* and Red Snapper, *Lutjanus campechanus*) and based this upon their feeding mechanism. Specifically, Red Grouper fed primarily through suction, followed by a period of prey manipulation within the buccal cavity that resulted in a higher proportion of mouth hooks, a lower incidence of gut hooking, and reduced the overall catch and release mortality for this species. Conversely, Red Snapper displayed fast biting behavior that resulted in a higher incidence of gut hooking because they swallowed prey more rapidly. For Atlantic Goliath Grouper, we have identified that prey capture strategy shifts with prey type, so the effects of interaction with anglers are not as easily defined. Rapid ram-based predation upon struggling fish that are being reeled in may increase the incidence of gut hooking as well as the ingestion of hooks and the associated fishing gear. Predation upon dead bait is likely more suction-based, which should increase the chance of being hooked in mouth or jaw rather than in the esophagus or stomach. However, further investigation is warranted to better define these interactions as well as the chronic health effects and levels of Atlantic Goliath Grouper mortality that are related to their escalating predation upon fish hooked by anglers.

Conclusions

'Elusive' food elicited an increased capacity for ram feeding, and Atlantic Goliath Grouper exhibited larger maximum gapes and more rapid feeding sequences when presented with mobile food. Immobile food was primarily consumed through suction, and strikes upon these items were

characterized by slower, closer approaches, smaller maximum gapes and longer bite durations. The results reported herein demonstrate that Atlantic Goliath Grouper are capable of modulating feeding behavior based upon prey activity level and position within the water column.

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Table 4.1. Kinematic and timing variables assessed through video analysis of feeding sequences for 26 individual Atlantic Goliath Grouper *Epinephelus itajara*, separated by food type (mobile or immobile). The *Immobile* food group was additionally split further and separated by position within the water column (elevated or benthic) and these results are presented within the shaded columns. Variable abbreviations indicate predator total length (TL), stalking duration (StD), food distance at the onset of predator mouth opening (FDMO), maximum gape (MG), distance moved by the predator (D_{pred}), distance moved by the food (D_{food}), time to food capture (TTFC), time to maximum gape (TTMG), time to close mouth (TTCM) and total bite duration (TBD).

Kinematic or timing variable	Mobile Mean ± S.E.	Immobile Mean ± S.E.	*Immobile Elevated Mean ± S.E.*	*Immobile Benthic Mean ± S.E.*
Predator TL (mm)	1422 ± 63	1501 ± 50.1	*1485 ± 94.1*	*1630 ± 39.6*
Food length (mm)	281 ± 10.4	163 ± 13.9	*152 ± 19.3*	*205 ± 36*
StD (s)	8.1 ± 1.9	12.3 ± 2.3	*14.2 ± 4.9*	*16.4 ± 4.7*
FDMO (mm)	221 ± 12.2	54 ± 12.6	*71.9 ± 17.7*	*38 ± 17*
MG (mm)	317 ± 32	161 ± 6.5	*156 ± 10.4*	*176 ± 21*
D_{pred} (mm)	273 ± 15	33 ± 10.4	*52.6 ± 16.4*	*13.8 ± 8.8*
D_{food} (mm)	52 ± 11	96 ± 11.1	*100 ± 6.9*	*90 ± 27.2*
TTFC (ms)	77 ± 7.5	137 ± 12.6	*123 ± 16.7*	*180 ± 39*
TTMG (ms)	121 ± 6.7	173 ± 13.3	*148 ± 21.7*	*227 ± 26*
TTCM (ms)	124 ± 9.8	265 ± 58.3	*200 ± 15.7*	*494 ± 23*
TBD (ms)	246 ± 15.9	442 ± 60.2	*349 ± 30.0*	*667 ± 21*
Number of individual bites (n)	11	15	*9*	*6*

Table 4.2. Results from regression analyses to identify whether a relationship existed between predator total length and the following variables for all individual bites: (1) stalking distance (StD); (2) maximum gape (MG); (3) time to food capture (TTFC); (4) time to maximum gape (TTMG); (5) time to close mouth (TTCM); and (6) total bite duration (TBD).

Kinematic variable	Mean ± S.E.	Minimum	Maximum	df	F	P - value
StD (s)	11.9 ± 2.2	2.7	49.7	24	0.10	0.76
MG (mm)	223.1 ± 21.1	114	460	24	0.257	0.62
TTFC (ms)	114 ± 13	34	300	24	0.01	0.98
TTMG (ms)	152 ± 12	70	300	24	0.03	0.95
TTCM (ms)	226 ± 51	67	1370	24	1.37	0.25
TBD (ms)	379 ± 57	134	1635	24	1.03	0.32

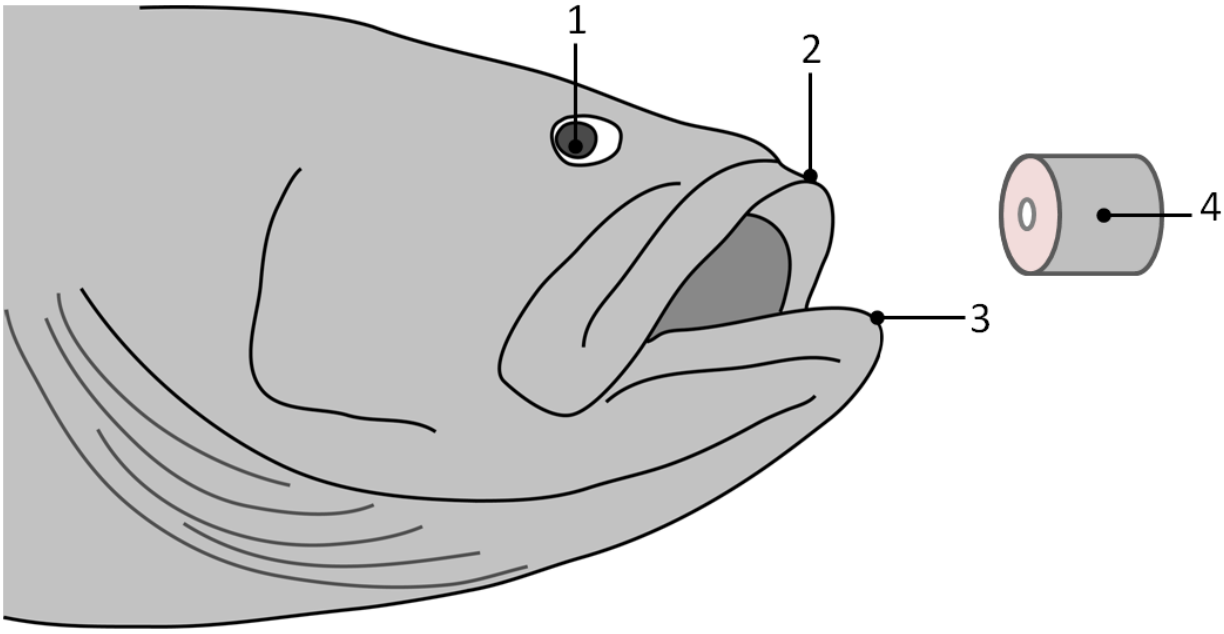

Fig. 4.1. Kinematic analyses of feeding sequences for Atlantic Goliath Grouper *Epinephelus itajara* were performed by tracking the following landmarks: (1) midpoint of the eye; (2) anterior point of the premaxilla; (3) anterior point of the lower jaw; and (4) estimated center of mass of the food item.

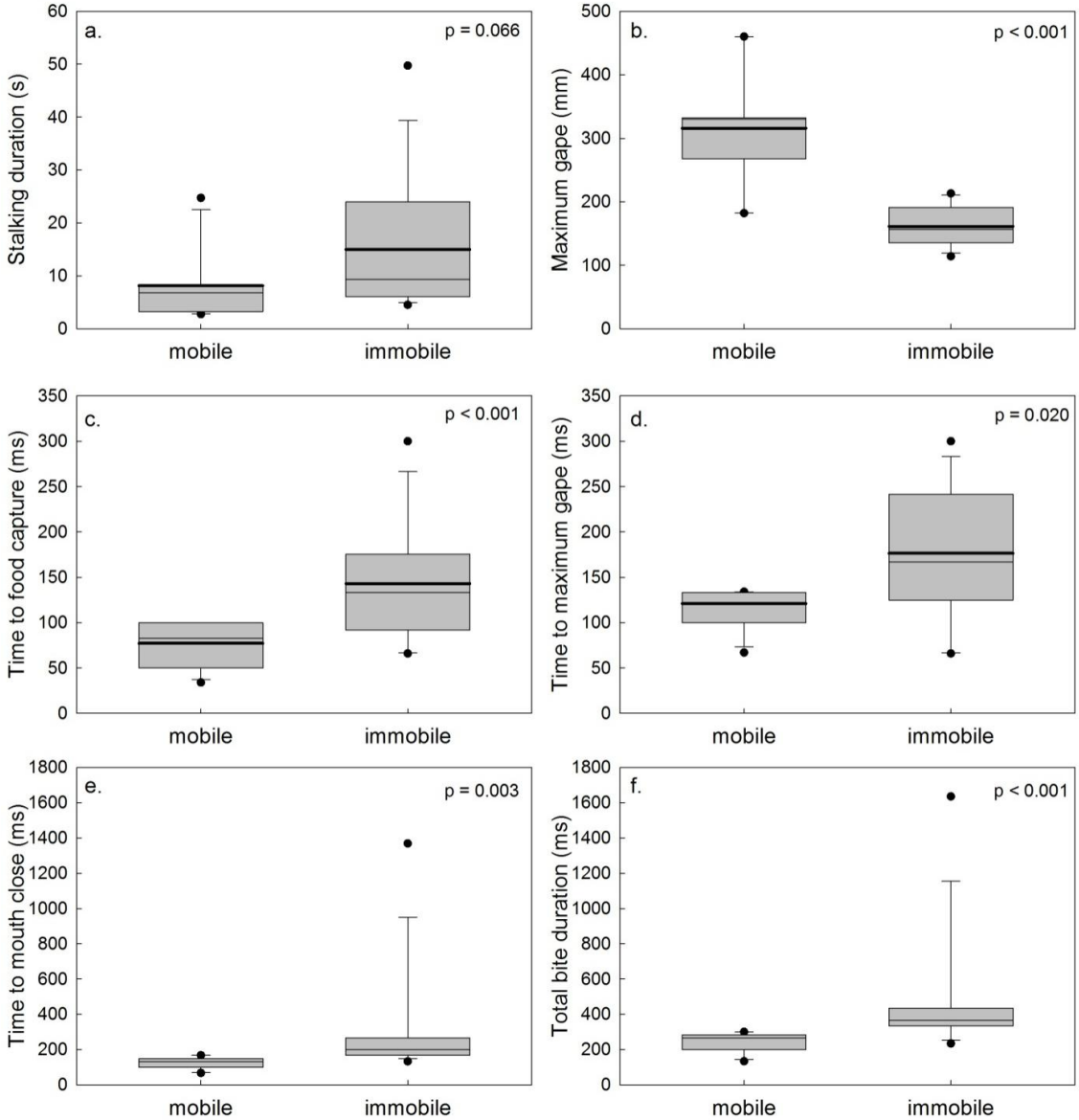

Fig. 4.2. Kinematic variables recorded during Atlantic Goliath Grouper *Epinephelus itajara* feeding events on mobile (n = 11) and immobile (n = 15) food: (a) stalking period, the time between orientation to food and onset of mouth opening (t = 1.9, df = 24); (b) maximum gape, the maximum distance between the anterior tip of the premaxilla and the anterior tip of the lower jaw(t = 2.44, df = 24); (c) time to food capture, the time between the onset of mouth opening and the center of mass passing through the jaws (t = 2.90, df = 24); (d) time to maximum gape, the time between the onset of mouth opening and achieving maximum gape(t = 2.28, df = 24); (e) time to mouth close, the time between the end of maximum gape and the jaws returning to a closed position(t = 2.13, df = 24); and (f) total bite duration, the time between the onset of mouth opening and the jaws returning to the closed position (t = 2.86, df = 24). The mean of each data set is represented by the bold solid line, the median by the thin line, the boxes indicate the interquartile range, and 95% confidence intervals are contained within the error bars. The bold dots indicate observations that fall outside of the 95% confidence intervals. Results of t-test comparisons are displayed in the upper right corner of each graph.

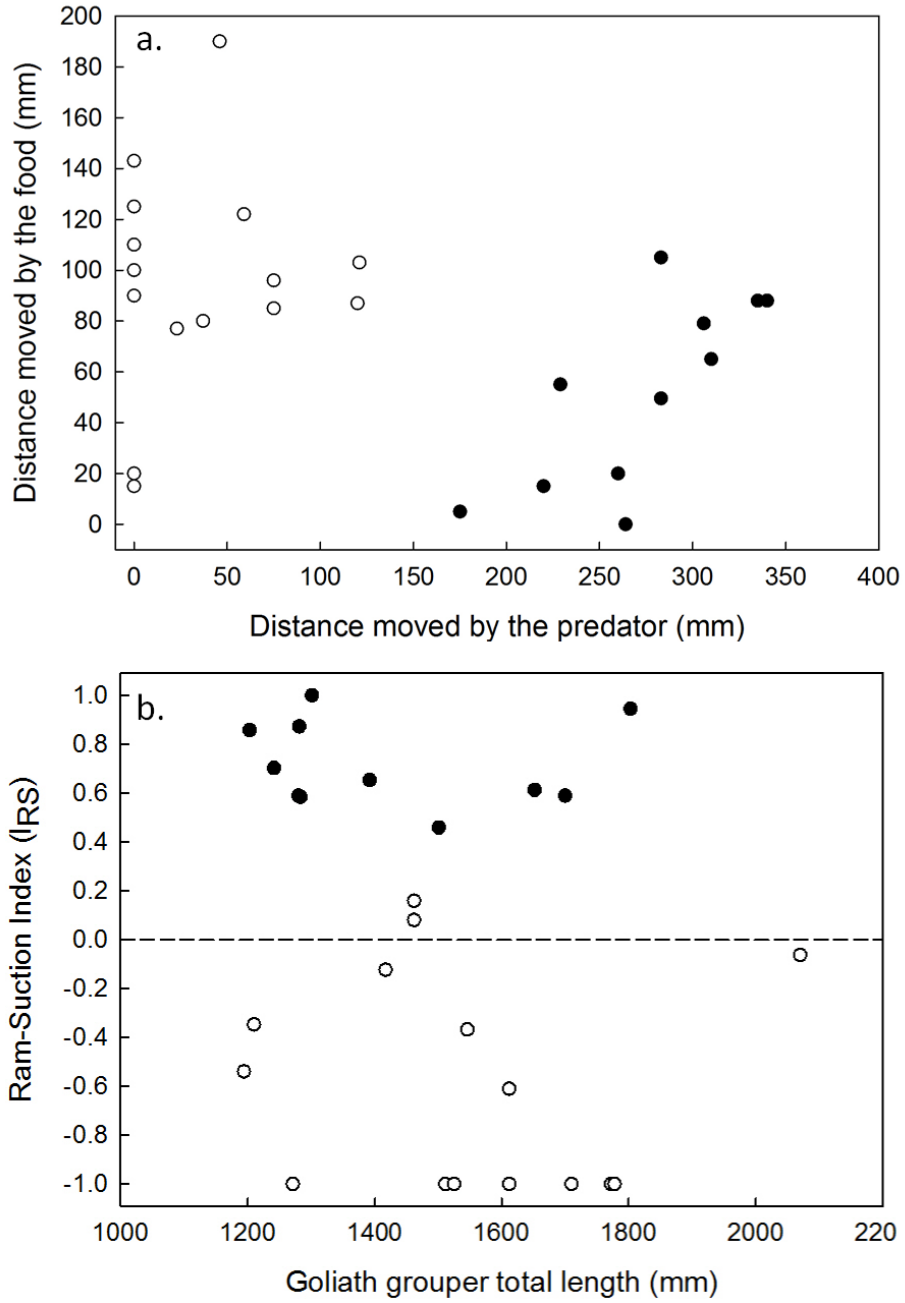

Fig. 4.3. (a) Distances moved by Atlantic Goliath Grouper *Epinephelus itajara* plotted against distances moved by food items during feeding events upon mobile (●; live grunt *Haemulon* spp.) or immobile (○; dead bait; white symbols) food, and (b) Ram-suction index (I_{RS}) values calculated for these feeding events. There was a significant difference in I_{RS} between groups ($p < 0.001$, df = 24).

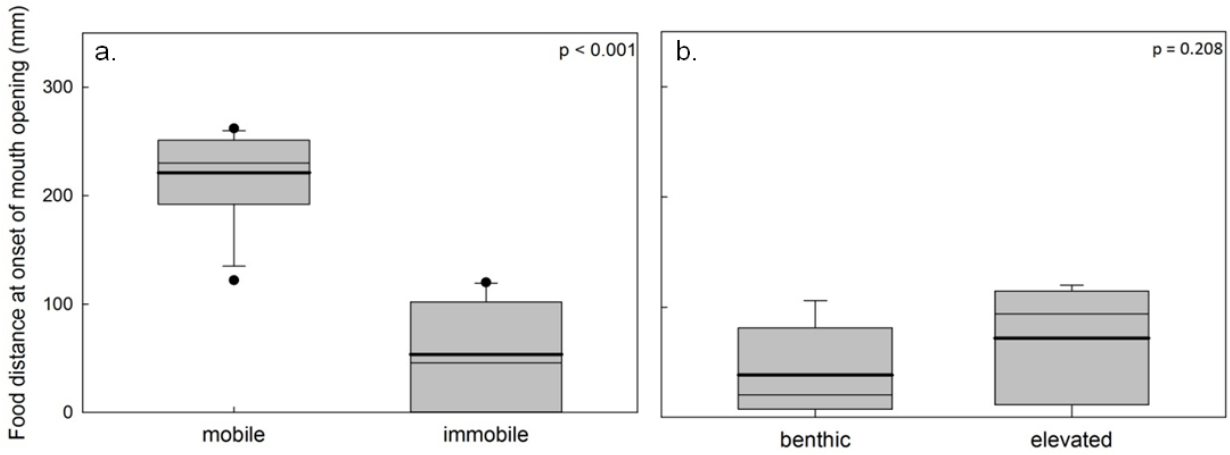

Fig. 4.4. The distance of the food from the anterior tip of the premaxilla of the Atlantic Goliath Grouper *Epinephelus itajara* at the onset of mouth opening for (a), mobile food versus immobile food (t= 9.3; df = 24), and (b), for immobile food that were presented on the ground (benthic) or within the water column (elevated) (t = 1.3; df = 13). The mean of each data set is represented by the bold solid line, the median by the thin line, the boxes indicate the interquartile range, and 95% confidence intervals are contained within the error bars. The bold dots indicate observations that fall outside of the 95% confidence intervals. Results of t-test comparisons are listed in the upper right corner of each graph.

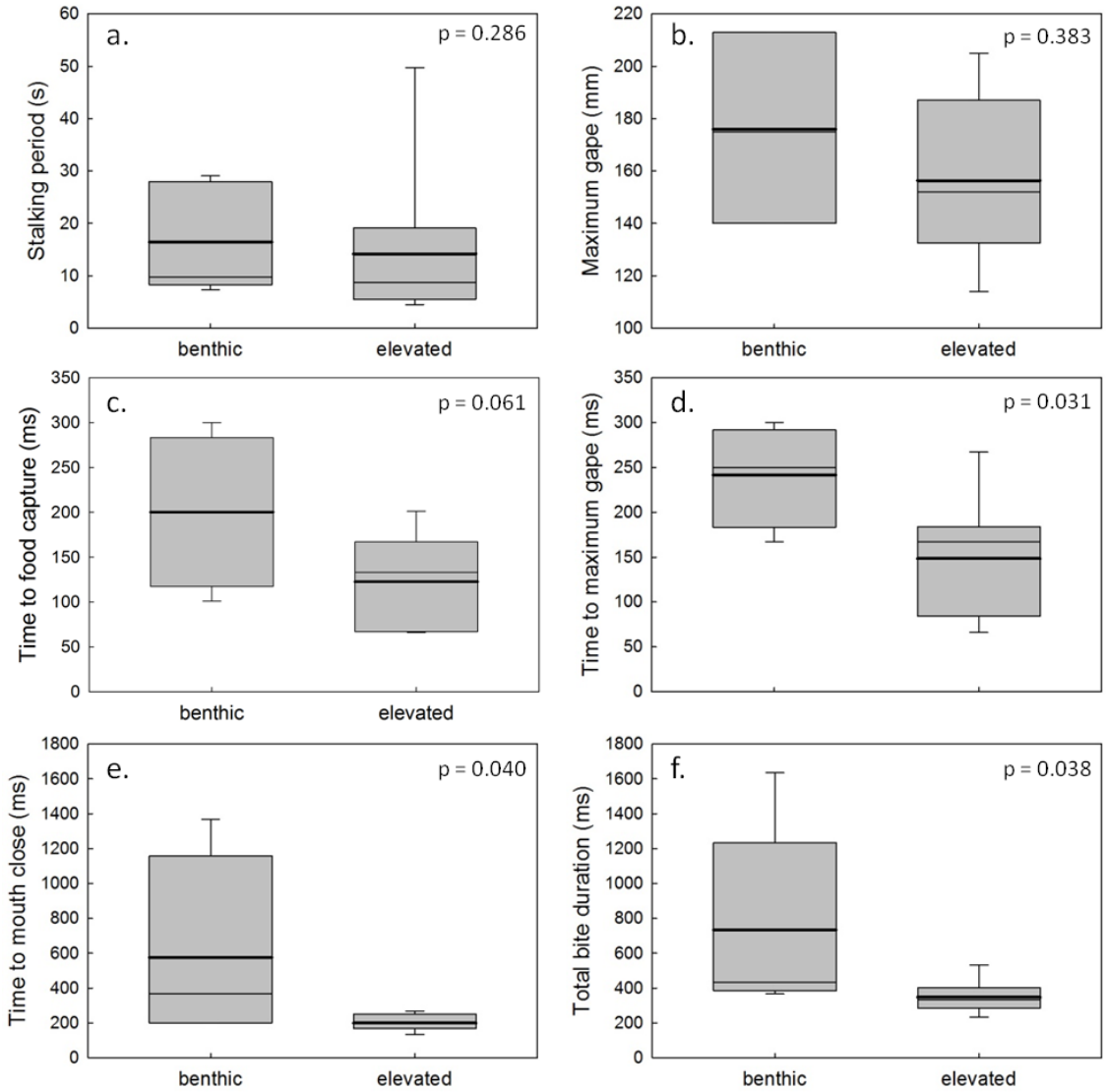

Fig. 4.5. Kinematic variables recorded during Atlantic Goliath Grouper *Epinephelus itajara* feeding events on immobile food that were positioned on the ground (benthic, n = 6) or in the water column (elevated; n = 9): (a) stalking period, the time between orientation to food and onset of mouth opening (t = 1.46, df = 13); (b) maximum gape, the maximum distance between the anterior tip of the premaxilla and the anterior tip of the lower jaw(t = 0.91, df = 13); (c) time to food capture, the time between the onset of mouth opening and the center of mass passing through the jaws (t = 2.08, df = 13); (d) time to maximum gape, the time between the onset of mouth opening and achieving maximum gape(t = 2.47, df = 13); (e) time to mouth close, the time between the end of maximum gape and the jaws returning to a closed position(t = 2.37, df = 13); and (f) total bite duration, the time between the onset of mouth opening and the jaws returning to the closed position (t = 2.53, df = 13). The mean of each data set is represented by the bold solid line, the median by the thin line, the boxes indicate the interquartile range, and 95% confidence intervals are contained within the error bars. The bold dots indicate observations that fall outside of the 95% confidence intervals. Results of t-test comparisons are listed in the upper right corner of each graph.

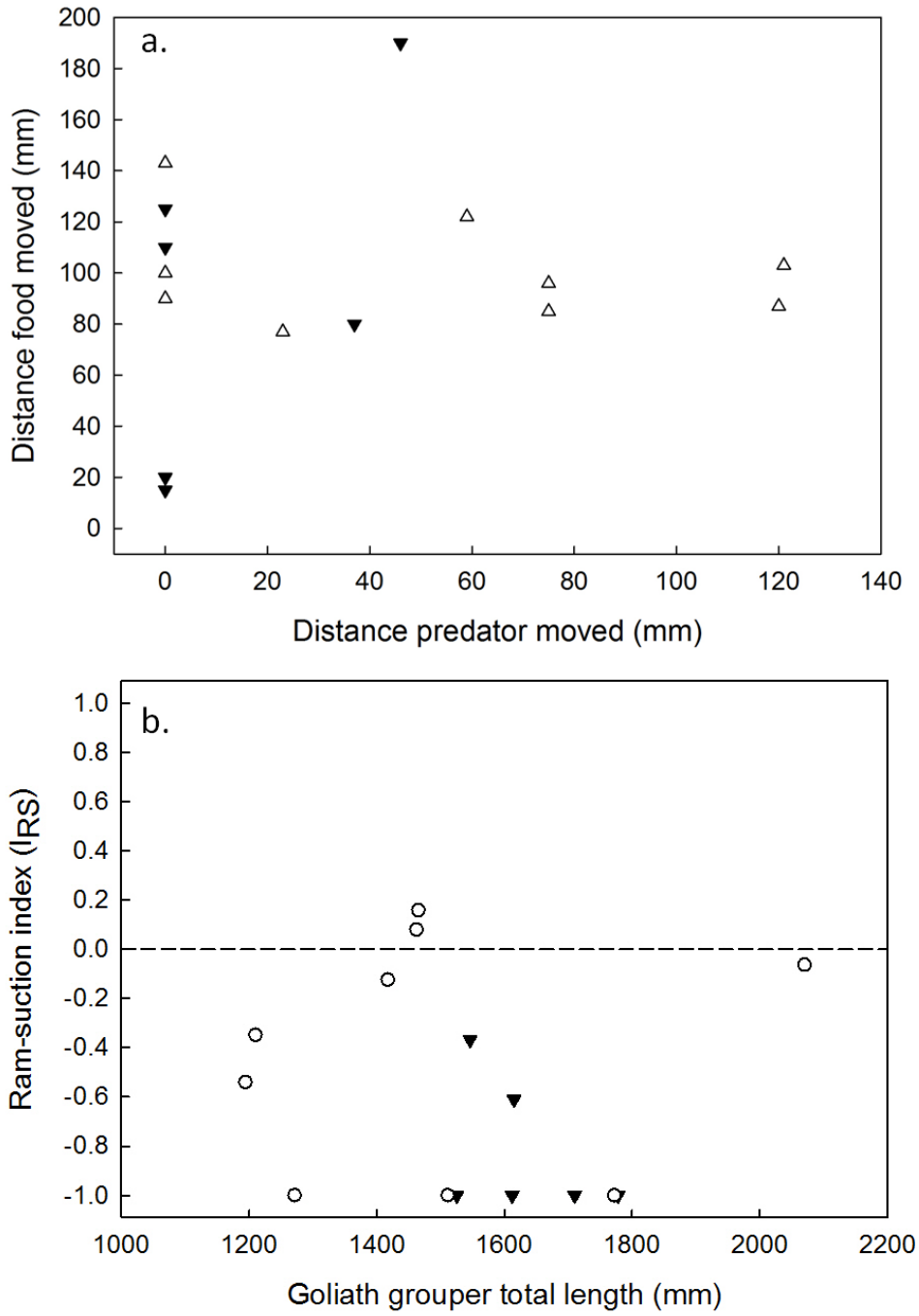

Fig. 4.6. (a) Distances moved by Atlantic Goliath Grouper *Epinephelus itajara* plotted against distances moved by food items during feeding events upon immobile benthic (●) or elevated (○) food, and (b) Ram-suction index (I_{RS}) values calculated for these feeding events. There was not a significant difference in I_{RS} between groups (df = 13; p = 0.094).

CHAPTER FIVE

GENERAL CONCLUSIONS

Abundance, size distribution and habitat association

Artificial reefs were by far the preferred habitat for Atlantic Goliath Grouper within the study area in the central eastern Gulf of Mexico. Individuals were present throughout all months of the year and during almost all surveys at artificial reefs. Abundance exhibited a positive relationship with site relief and site volume, demonstrating the preference of this species for structural cover. Overall mean abundance at artificial reefs was between 4 – 5 individuals (range: 0 – 25). Natural reefs within the study area exhibited significantly lower presence and abundance levels (mean abundance < 1; range: 0 – 4), which was likely due to the fact that most of the natural hard bottom in the study region consists of low relief limestone outcroppings that offer minimal cover for large-bodied fish. The majority of individuals recorded were between 80 and 160 cm TL, but both juveniles and adults were observed within the study area and sizes ranged 36 – 214 cm TL. Mean Atlantic Goliath Grouper size exhibited no relationship with depth or distance from shore. Conventional tags indicated high site fidelity, but also demonstrated the ability of individuals to travel distances as far as 203 km; however, interpretations of conventional tagging data were limited since the location of individuals between recapture events was unknown.

Acoustic tracking: Catch and release mortality, site fidelity and movement patterns

Acoustic tracking allowed for continuous monitoring of individual Atlantic Goliath Grouper for over two years after catch and release events. Barotrauma severity increased with capture depth, but immediate mortality was not observed for any of the Atlantic Goliath Grouper that were caught and released during this study. Additionally, the length of total monitoring period was not affected by the severity of barotrauma or the length of handling time, which suggests that with proper handling, Atlantic Goliath Grouper are not subject to high levels of release mortality in the eastern Gulf of Mexico (at depths < 40 m). However, strong site fidelity of Atlantic Goliath Grouper to artificial reefs increases susceptibility to fishing pressure and amplifies interactions with anglers, so the chronic effects of repeated capture remain unclear.

Acoustically tagged Atlantic Goliath Grouper displayed small core areas of use, maintaining consistent presence at specific artificial reefs for up to 736 days. Vertical movement and activity within the water column was higher during daylight hours for all months of the year, with the widest range of activity observed during crepuscular periods. Additionally, fine-scale seasonal patterns became evident, and all individuals demonstrated reduced activity during the coldest months of the year. Although relatively sedentary and faithful to a specific site throughout most of the study, long distance movements (>175 km) were also observed and demonstrated the capacity of some individuals to move over broader geographic scales. The concerted departure of mature sized fish (>140 cm) during the reproductive period is suggestive of a spawning migration, although the actual activity and destinations of departed individuals during this period remains unknown. Future efforts to identify spawning aggregation sites within the eastern Gulf of Mexico are warranted.

Feeding behavior

‘Elusive’ food elicited an increased capacity for ram feeding, and Atlantic Goliath Grouper exhibited larger maximum gapes and more rapid feeding sequences when presented with mobile live food. Immobile (dead) food was primarily consumed through suction, and strikes upon these items were characterized by slower, closer approaches, smaller maximum gapes and longer bite durations. The results reported herein demonstrate that Atlantic Goliath Grouper are capable of modulating feeding behavior based upon prey activity level and position within the water column.

Advances in technology (e.g., depth sounders, side-scan sonar, underwater video cameras) continue to increase human ability to locate marine hard bottom habitats, which assists with monitoring and management efforts but also increases fish susceptibility to harvest by making them easier to find. The high numbers of conspecifics and the persistent long-term presence of individuals at high relief artificial reefs further demonstrated the importance of these habitats for Atlantic Goliath Grouper in the eastern Gulf of Mexico. The tendency for Atlantic Goliath Grouper to readily feed upon struggling hooked fish escalates the interaction between Atlantic Goliath Grouper and anglers and may further increase susceptibility to hooking or entanglement in fishing gear. The findings reported herein provide information regarding spatial and temporal habitat associations of a protected species in the central eastern Gulf of Mexico, and should help to inform regulatory guidelines and management efforts regarding conservation.

APPENDICES

Appendix A: IACUC Protocol approval letters applicable to this dissertation research.

UNIVERSITY OF SOUTH FLORIDA

DIVISION OF RESEARCH INTEGRITY AND COMPLIANCE
INSTITUTIONAL ANIMAL CARE USE COMMITTEE

MEMORANDUM

TO:	Philip Motta, Ph.D. Dept. of Biology SCA110	
FROM:	William R. Gower, Ph.D., Chairperson Institutional Animal Care & Use Committee Division of Research Integrity and Compliance	William R. Gower
DATE:	10/1/2007	
PROJECT TITLE:	Behavior, Habitat and Abundance of the Goliath Grouper, Epinephelus itajara, in the Central Eastern Gulf of Mexico	
AGENCY/SOURCE OF SUPPORT:	NOAA/NMFS	NA07NMF4540
IACUC PROTOCOL#:	3210	
PROTOCOL STATUS:	**APPROVED**	

The Institutional Animal Care and Use Committee (IACUC) reviewed your application requesting the use of animals in research for the above-entitled study. The IACUC **APPROVED** your request to use the following animals in your protocol for a one-year period **beginning 9/28/2007 :**

- 500 grouper

Please reference the above IACUC protocol number in all correspondence regarding this project with the IACUC, Comparative Medicine, or the Division of Research Integrity and Compliance. In addition, please take note of the following:

- **IACUC approval is granted for a one-year period at the end of which, an annual renewal form must be submitted for years two (2) and three (3) of the protocol.** After three years all continuing studies must be completely re-described in a new application and submitted to IACUC for review.
- **All Comparative Medicine pre-performance safety and logistic meetings must occur prior to implementation of this protocol** [IACUC policy V.10]. Please contact the program coordinator at compmed@research.usf.edu to schedule a pre-performance meeting.
- **All changes to the IACUC-Approved Protocol must be pre-approved by the IACUC [IACUC policyIII.11].** Minor changes can be submitted to the IACUC for review and approval as an amendment or procedural change, whereas major changes to the protocol require submission of a new IACUC application. Minor changes are changes considered to be within the scope of the original research hypothesis or involve the original species and are submitted to the IACUC as an Amendment or Procedural change. Any change in the IACUC–approved protocol that does not meet the latter definition is considered a major protocol change and requires the submission of a new application. More information on what constitutes a minor versus major protocol change and procedural steps necessary for IACUC review and approval are available on the Comparative Medicine web site at http://www.research.usf.edu/cm/amendments.htm
- **All costs invoiced to a grant account must be allocable to the purpose of the grant [IACUC policies IV.5 and V.10].** allocable to one protocol may not be shifted to another in order to meet deficiencies caused by overruns, or for other reasons of convenience. Rotation of charges among protocols by month without establishing that the rotation schedule credibly reflects the relative benefit to each protocol is unacceptable.
- **The PI must assist the IACUC with tracking wild animal field research activities [IACUC policy XXIII.24].** The PI must report episodes of wild animal use, the approximate range of taxa, and the approximate numbers of animals encountered or used at intervals appropriate to the study but at least once a year.

For more IACUC information, please visit the Comparative Medicine web site at http://www.research.usf.edu/cm/default.htm .

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INSTITUTIONAL ANIMAL CARE AND USE COMMITTEE
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University of South Florida · 12901 Bruce B. Downs Blvd., MDC35 · Tampa, FL 33612-4799
(813) 974-7106 · FAX (813) 974-7091

UNIVERSITY OF SOUTH FLORIDA

DIVISION OF RESEARCH INTEGRITY AND COMPLIANCE
INSTITUTIONAL ANIMAL CARE_USE COMMITTEE

MEMORANDUM

TO:	Philip Motta, Ph.D. Dept. of Biology SCA110
FROM:	Jay B. Dean, Ph.D, Chairperson Institutional Animal Care & Use Committee Division of Research Integrity and Compliance
DATE:	10/27/2010
PROJECT TITLE:	An Evaluation of the Effects of Catch and Release Angling on Survival and Behavior of Goliath Grouper (Epinephelus itajara) with additional Investigation into Long-Term Residence and Movement Patterns
AGENCY/SOURCE OF SUPPORT:	NOAA/NMFS Marfin Program NA10NMF4330
IACUC PROTOCOL#:	**W 3887**
PROTOCOL STATUS:	**APPROVED**

The Institutional Animal Care and Use Committee (IACUC) reviewed your application requesting the use of animals in research for the above-entitled study. The IACUC **APPROVED** your request to use the following animals in your protocol for a one-year period **beginning 10/27/2010 :**

- 500 Goliath Grouper
- 50 Grunts

Please reference the above IACUC protocol number in all correspondence regarding this project with the IACUC, Comparative Medicine, or the Division of Research Integrity and Compliance. In addition, please take note of the following:

- **IACUC approval is granted for a one-year period at the end of which, an annual renewal form must be submitted for years two (2) and three (3) of the protocol.** After three years all continuing studies must be completely re-described in a new application and submitted to IACUC for review.
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