Horizontal and Vertical Movement, Residency and Mortality of Gray Triggerfish (*Balistes capriscus*) on Artificial Reefs in the Northern Gulf of Mexico

by

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Abstract

The present telemetry study evaluated movements of gray triggerfish (*Balistes capriscus*) on artificial reefs in the northern Gulf of Mexico from 23 January 2013 through 5 September 2017. Five Vemco Positioning System (VPS) acoustic receiver arrays assessed the fine-scale (m) horizontal and vertical movement, volume use, residency, site fidelity and mortality (*F* and *M*) of transmitter tagged gray triggerfish (*n* = 49). Additional single, surrounding receivers (*n* = 21) recorded presence-absence data to validate emigrations, document large-scale movements (km) and confirm mortality events. All VPS arrays and single receivers were associated with small steel cage artificial reefs (2.5 x 1.3 x 2.4 m) each positioned 1.4 – 1.6 km apart at depths of 18 – 35 m, encompassing a 64 km^2 area. Tracked gray triggerfish had a mean residency time of 7 weeks and an annual site fidelity of 18% $year^{-1}$. Fish remained closely associated with artificial reef structures (mean ± SD = 18 ± 41 m) and used much of the water column with a mean distance from the seafloor = 4.2 ± 4.2 m. Fish displayed seasonal and diel patterns of behavior with home range areas (95% kernel density estimates, KDE) smaller in the spring from March through May and larger in fall and winter from September through February. Gray triggerfish were closer to the seafloor from November through March and were higher up in the water column from April through October. Fish used smaller home range volumes (95% three-dimensional KDE) during winter and spring from December through May and the larger volumes during summer from June through

August. Area use was greater at higher mean bottom water temperatures and dissolved oxygen (DO) concentrations. Fish were closer to the seafloor when temperatures were lower and shallower when DO was lower. Home range volumes increased with higher bottom water temperature and with lower DO. Gray triggerfish made fewer movements and remained significantly closer to the seafloor and reef habitat at night than during the day, transitioning during crepuscular periods. Most ($n = 41$, 84%) of the transmitter tagged gray triggerfish emigrated away from their VPS site during their tracking period. However, patterns differed among fish, where some fish emigrated and did not return ($n = 25$, 51%), some fish emigrated once and then returned ($n = 3$, 6%), while others emigrated and returned multiple times ($n = 13$, 27%). High emigration from VPS sites (97% of the fish present, $n = 28$) occurred during two tropical storms, after which 32% ($n = 9$) returned. Gray triggerfish movement patterns were most likely related to foraging and resting behaviors, spawning and associated competitive interactions and predator evasion. For all years combined, annual fishing mortality $F = 0.23$ (95% CI = 0.07 – 0.50), natural mortality $M = 0.25$ (0.07 – 0.57) and total mortality $Z = 0.48$ (0.18 – 0.85). Present instantaneous mortality estimates suggest that while past management efforts were likely successful, the gray triggerfish stock may still be experiencing overfishing and values support the Gulf of Mexico Fishery Management Council’s decision for increased fishery restrictions in 2018.

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Abstract

Gray triggerfish (*Balistes capriscus*) is an ecologically and economically valuable species that inhabits natural and artificial reefs in the northern Gulf of Mexico. Regional populations support both sport and commercial fisheries that have grown in importance in recent decades. Recent stock assessments indicated that the stock was overfished but is no longer experiencing overfishing. A new 9-yr rebuilding plan was initiated in 2018 to promote stock recovery and reduce the potential for recreational quote overages. Concern over stock status has prompted numerous studies into the life history, movement patterns and habitat use of gray triggerfish. They are epibenthic predators that feed diurnally and prey primarily upon hard-shelled invertebrates and reef encrusting organisms, but will also consume soft-bottom and pelagic species. Based on previous conventional tagging studies and one telemetry study, gray triggerfish remain closely associated with reef structures, have high site fidelity (37 – 67%) and remain within 10 km from their home reef. They also show diel and seasonal patterns of area use; however, little is known about their vertical movement patterns. Gray triggerfish have moderately fast growth rates and reach sexual maturity relatively early by age 3. Males

and females are 100% sexually mature by 250 mm fork-length (FL). They are moderately long-lived, reaching ages of 15 years and sizes of 725 mm FL for males and 567 mm FL for females. Gray triggerfish are benthic, multiple batch spawners that show elaborate courtship and mating displays, territoriality, nest building, harem spawning and parental care. Peak spawning occurs in June and lasts for approximately 86 days.

Distribution and Range

Gray triggerfish (*Balistes capriscus*) are an important member of natural and artificial reef communities in temperate and sub-tropical waters throughout the Atlantic basin. They inhabit coastal regions of the western Atlantic from Nova Scotia, Canada, to Argentina, including the Gulf of Mexico and waters off Bermuda (Briggs 1958; Moore 1967; Bernardes 2002; Harper and McClellan 2014). In the eastern Atlantic, they extend from Norway to southwestern Africa (Caveriviere 1982; Ofori-Danson 1989). Throughout their range, gray triggerfish remain closely associated with structured habitats at depths less than 100 m. Within the Gulf of Mexico, they are common at depths between 12 and 42 m (Smith 1975; Harper and McClellan 2014), except during their first few months of life, when they are planktonic and associated with communities of drifting *Sargassum* spp. (Wells and Rooker 2004; Ballard and Rakocinski 2012), after which they settle directly to benthic habitat (Simmons and Szedlmayer 2011).

Assessment and Management History

Gray triggerfish are exploited by sport and commercial fishers within the northern Gulf of Mexico and southeastern United States (SEDAR 43 2015). Historically, gray triggerfish were not heavily targeted nor considered an important food resource. However, as fishing restrictions on other high-value fisheries, such as red snapper (*Lutjanus campechanus*), have intensified gray triggerfish have become increasingly valued (Valle et al. 2001;SEDAR 31 2013; Harper and McClellan 2014; SEDAR 43 2015). As a result, landings of gray triggerfish increased through the mid-1980s, peaking at 1.5 million kg in 1990. Landings have since gradually declined to less than 0.2 million kg, annually (SEDAR 43 2015). Since the development of the gray triggerfish fishery is relatively recent, so are efforts to assess and manage this species.

Fishery assessments of gray triggerfish are carried out by the Gulf of Mexico and South Atlantic Fishery Management Councils. The management area in the northern Gulf of Mexico includes federal waters off Texas, Louisiana, Mississippi, Alabama and the eastern side of Florida from 16.6 km out to 370 km offshore, which is the exclusive economic zone boundary. Stock assessments are conducted to establish the current stock status (e.g., overfished or in process of overfishing), quantify the current rate of exploitation (e.g., fishing mortality) and examine relevant life history data such as age structure, sex ratio, spawning stock biomass and recruitment. These assessments are then used to generate fishery management plans, set current harvest strategies (e.g., quotas), and implement catch and effort controls and technical measures (e.g., size and bag limits; Jennings et al. 2001).

Presently, there are no subdivisions in geographic stock either within or between the Gulf of Mexico or South Atlantic management zones (Antoni et al. 2011; Antoni and Saillant 2012; SEDAR 43 2015). Recent DNA analyses confirm that gray triggerfish populations in the northern Gulf of Mexico and western Atlantic waters are comprised of a single stock and are appropriately managed as such (Antoni et al. 2011; Antoni and Saillant 2012). However, development of additional DNA markers is needed to increase the resolution of genetic analyses necessary to evaluate fine-scale genetic stock structure and identify potential subunits in the region (Antoni et al. 2011).

Early attempts by the National Marine Fisheries Service (NMFS) to estimate Gulf of Mexico gray triggerfish stock status used surplus production modeling (Goodyear and Thompson 1993; Harper and McClellan 1997; Valle et al. 2001). During the 2006 Southeast Data Assessment and Review (SEDAR) benchmark assessment and the 2012 stock reevaluation, age-structured models were applied along with a non-aged based aggregated stock production model (SEDAR 9 2006; SEDAR 43 2015). Age-based models are typically preferred over non-aged based models, because they allow for life history parameters, such as age at maturity, age at recruitment, growth rates and age-specific mortalities to be modeled as part of the assessment (Fioramonti 2014). However, aging techniques and model parameters must be validated, which has only recently begun despite their inclusion in past stock assessment models (Kolmos et al. 2013; Fioramonti 2014; Allman et al. 2015; Burton et al. 2015).

Since 2015, the Gulf Council has used an integrated statistical catch at age model to assess the status of the gray triggerfish stock. Data input into the assessment includes life history data (age, growth parameters, natural mortality, maturity, fecundity and the

Beverton-Holt stock-recruitment relation), landings data (commercial and sport catch and effort), estimates of discard mortality (commercial and sport = 5%, shrimp trawl bycatch = 100%), the length composition of landings data converted into an age-based composition, indices of abundance based on fishery dependent and fishery independent data, gear selectivity (hook selectivity) and correction factors (current circle hook catch per unit effort [CPUE] * 2.14 = past j-hook CPUE; SEDAR 43 2015; Amendment 46 2017).

Fishery dependent commercial landings and effort data are obtained from the NMFS accumulated landings system. Sport landings data are estimated from three sampling programs: 1) the marine recreational information program, 2) the Texas parks & wildlife survey and 3) the southeast regional headboat survey. Fishery independent sampling is also conducted to collect relevant life history data and abundance estimates via three surveys: 1) the Southeast Area Monitoring and Assessment Program (SEAMAP) trawl survey, 2) the SEAMAP larval survey and 3) the combined video/ROV survey (SEDAR 43 2015; Amendment 46 2017).

The most recent benchmark gray triggerfish stock assessment was completed in 2015 and includes data from 1986 – 2013 (SEDAR 43 2015). However, a recent stock reevaluation was released in April 2017, as part of the newly proposed Amendment 46: the gray triggerfish rebuilding plan that includes data through 2016. The next benchmark stock assessment was expected to be released in June 2018, but at the time of writing was not yet available (Amendment 46 2017).

These past stock assessments have resulted in continually shifting management goals and objectives. This process has caused new amendments to be added to the original 1984 Reef Fish Fishery Management Plan (RFFMP) to improve stock status, ensure sustainability of the fishery and reduce the potential for growth or recruitment overfishing. In Amendment 1 (1990), the primary objective was to update the list of managed species to include gray triggerfish and maintain a spawning potential ratio (SPR) of 20% for all species included in the management unit. Amendment 12 to the RFFMP (1997) established an aggregate sport daily bag limit of 20 fish in federal waters for all reef fish species including gray triggerfish. Amendment 16b (1999) introduced a minimum size limit of 305 mm fork length (FL). Also, in 1999 the Generic Sustainable Fisheries Act Amendment was implemented, which set the maximum fishing mortality threshold for gray triggerfish at F = 30% SPR. In 2006, a benchmark stock assessment concluded that gray triggerfish were experiencing overfishing but was unable to assess overfished status (SEDAR 9 2006). In response, Amendment 27 (2008) required the use of circle hooks, venting tools and de-hooking devices, while Amendment 30A (2008) increased the size limit from 305 to 356 mm FL. It also aimed to reduced harvest levels by 60% through introducing a total allowable catch (TAC) based system with a catch quota (231,785 kg), with the fishery set to remain open until TAC is reached. In addition, it changed allocations to 21% for commercial and 79% for sport sectors with the intent of ending overfishing and rebuilding the Gulf of Mexico Stock. In 2013, Amendment 37 further reduced annual catch limits from 231,785 to 126,100 kg due to the 2012 assessment that indicated the stock was not rebuilding, still overfished and experiencing overfishing. In addition, a fixed spawning season closure from 1 June through 31 July was implemented, along with a commercial trip limit of 12 gray triggerfish and a sport bag limit of 2 individuals. Accountability measures were also put into place that would require sport quota overages to be deducted from the following year's TAC. For example, the sport fishery was closed for all of 2017 due to landing at 245% greater than TAC during the 2016 season. The commercial fishery remained open and was allocated its normal quota of 27,624 kg for the 2017 season (SEDAR 43 2015; Amendment 46 2017).

Based on the most recent 2017 stock reevaluation, the gray triggerfish stock is still considered overfished, but no longer experiencing overfishing. The 2017 assessment also indicated that total population size and the spawning stock biomass (SSB) have generally declined since the start of assessment in 1986 and are presently at or near the lowest recorded annual level. Although the SSB did show signs of recovery between 1995 and 2002, the SSB has since continued to decline. Low SSB is potentially due to the stock showing signs of depensation (i.e., recruitment below what is predicted by the Beverton-Holt stock-recruitment relation). These declines in recruitment and the SSB are occurring despite a general trend of decreased fishing mortality and effort in both the commercial and sport sectors, which should promote some stock recovery. It has also been suggested that stock recovery may be impeded by different state and federal sport fishing seasons. Many state sport fisheries for gray triggerfish remain open past the federal in season closure, causing annual landing to be well above TAC. This adds further ambiguity to the stock assessment model (SEDAR 43 2015; Amendment 46 2017).

The general trend of declining SSB, causing slow recovery despite management effort and reductions in fishing mortality, has led the Gulf Council to a new 9-year rebuilding plan (2017 – 2025). The newly established 2018 regulations (Amendment 46

2017) retained the current annual catch limit of 126,100 kg, but reduced the sport bag limit to 1 fish, increased the commercial trip limit to 16 fish, increased the size limit to 381 mm and added an additional January and February seasonal closure (15 Jan – 28 Feb) to the existing spawning season closure (1 June – 31 July). These combined measures were expected to reduce the sport sector's annual catch to 91,247 kg, which is below its quota limit of 98,475 kg. Increasing the bag limit from 12 to 16 fish within the commercial sector is not estimated to cause an excess in landings, because the commercial sector rarely reaches is current quota of 27,625 kg. However, it may provide for increased profits for some commercial fisherman if they are occasionally able to land higher catches of gray triggerfish (SEDAR 43 2015; Amendment 46 2017).

Life History

Increased interest about stock status has resulted in numerous studies of gray triggerfish life history, behavior and movement patterns. Gray triggerfish are a moderately long-lived member of the Gulf of Mexico reef fish community, reaching ages of 15 years and achieving maximum reported lengths of up to 725 mm fork length (FL) for males and 567 mm FL for females (Johnson and Saloman 1984; Wilson et al. 1995; Hood and Johnson 1997; Fioramonti 2014; Allman et al. 2015, Burton et al. 2015). Gray triggerfish grow moderately fast, attaining an average observed size of 353 mm FL by age 3, when growth slows, thereby reaching 496 mm FL by age 5 and then averaging annual size increment increases of 21 mm through age 10 (Burton et al. 2015). This estimate was consistent with an earlier Gulf of Mexico study that reported gray triggerfish grew moderately fast at early ages and reached 357 mm FL by age 3, then growth decreased to 50 mm per year through age 5, followed by slower growth at 15 mm per year for ages 6 – 13 (Johnson and Saloman 1984). Based on observed age-growth parameters and catch curve analyses, gray triggerfish are fully recruited to the sport fishery by age 3 – 4 and the commercial fishery by age 5 (Johnson and Salmon 1984; Moore 2001; Burton et al. 2015).

Recent oxytetracycline (OTC) marking and laboratory rearing experiments confirm annual growth ring formation in gray triggerfish dorsal spines, fin rays and vertebrae. A translucent zone is formed in the winter and an opaque zone in spring and summer (Fioramonti 2014; Allman et al. 2015; Burton et al. 2015). It has been suggested that dorsal spines are the most reliable ageing structure, due to the ability of readers to easily identify the first translucent zone and distinguish between subsequent banding patterns, which has resulted in significantly lower reader error. It is also apparent that fish aged with fin rays are about one year older than fish aged with dorsal spines. Vertebrae are recommended only as a complimentary aging structure, due to high reader variance (Fioramonti 2014; Allman et al. 2015; Burton et al. 2015). Otoliths are not recommended for aging in triggerfish, because they are difficult to locate, extract and process due to their small size (< 5mm) and irregular shape (Moore 2001; Bernardes 2002).

Gray triggerfish sexually mature soon after they recruit to benthic, hard-bottom structures and reef habitats. Histological and microscopic gonadal observations indicate that male and female gray triggerfish can first reach sexual maturity by age 1, with 100%

of individuals mature by age 3 (Ofori-Danson 1990; Wilson et al.1995; Hood and Johnson 1997; Moore 2001; Ingram 2001; Kolmos et al. 2013; Fitzhugh et al 2015). Estimated length at the time of first spawning is also highly variable but has been reported to range between 130 to 250 mm FL (Ofori-Danson 1989, 1990; Manooch 1984; Hood and Johnson 1997; Kolmos et al. 2013; Fitzhugh et al. 2015). No evidence of sex change has been reported (Wilson et al. 1995; Lang and Fitzhugh 2015).

Spawning in gray triggerfish begins in May, peaks in June, then decreases by late July and August (Dooley 1972; Wilson et al. 1995; Ingram 2001; Simmons and Szedlmayer 2012; Lang and Fitzhugh 2015). In the Gulf, spawning has been observed at depths of 14.6 – 31.1 m, and at temperatures ranging from 21.9 – 29.9 °C, with a salinity of 29.8 – 36.8 ppm and dissolved oxygen concentrations of 4.8 – 6.8 mg l^{-1} (Simmons and Szedlmayer 2012).

Gray triggerfish show spawning behaviors that are atypical of other aggregate spawning reef fish (e.g., pelagic broadcast spawning), but are representative of Balistids worldwide (Fricke 1980; Gladstone 1994; Ishihara and Kuwamura 1996; Kuwamura 1997). They are benthic, multiple batch spawners that show elaborate courtship and mating displays, territoriality, nest building, harem spawning and bi-parental care of eggs (Simmons and Szedlmayer 2012). During the spawning season, gray triggerfish are sexually dimorphic. Males are typically larger than females, have dark coloration and black fins. Females are smaller and show distinct banding patterns of white and black vertical bars when actively guarding a nest or engaging in courtship and mating displays. Outside of spawning, both males and females show typical plain gray coloration (Simmons and Szedlmayer 2012). At the onset of spawning, dominant males establish territories, building between 1 and 13 nests within a 9 m radius from the reef. Nests consist of mainly fine-grain sand (≤ 250 µm) with average diameters of 0.53 m and depths of 0.24 m. Nests are aggressively guarded against other males and reef fish. Pre-fertilization females observe males and inspect nests prior to initiation of courtship displays. Male courtship behaviors include elaborate circling of a female, color changes and leading a female to the nest. Once on the nest, courtship continues for several minutes as both male and females circle each other and rapidly change color, before the release of demersal gametes. Once fertilized, females continue to guard and defend the nest for 24 – 48 hours, while fanning and blowing on the eggs. Males move off the nest (≤ 15 m) but continue to defend the territory immediately surrounding active nests, by chasing off other fish. Observations of aggressive male behavior toward smaller submissive males, as well as female-dominated sex ratios with up to five females per male, suggest that gray triggerfish have harem-like spawning behavior (Simmons and Szedlmayer 2012). It is possible the gray triggerfish demonstrate lekking behaviors, however this has not been confirmed through field-based studies. Lek-like spawning behavior has been observed in the yellowmargin triggerfish (*Pseudobalistes flavmarginatus*) and the crosshatch triggerfish (*Xanthichthys mento*; Gladstone 1994; Kawase 2003).

Gray triggerfish have been described as capital breeders (Lang and Fitzhugh 2015). Their gonadosomatic index (GSI), hepatosomatic index (HSI) and Fulton's condition factor (K) indicate that liver and somatic energy stores increase prior to spawning and are depleted throughout the spawning period. These indices peak in May, one month prior to peak spawning (peak GSI) then decrease sharply from May through

September, after which they began to increase again (Lang and Fitzhugh 2015). In contrast, income-breeding species lack seasonal patterns in condition indices or show only weak seasonal patterns (Dominguez-Petit et al. 2010). The liver in gray triggerfish appears to be important for energy storage and mobilization, emphasized by the fact that HSI exceeds GSI in all months (Lang and Fitzhugh 2015). However, gray triggerfish still likely feed during the spawning season, as in the present study fish were easily captured throughout the spring and summer (Chapter 2) and reproductively active females have been observed searching for food by blowing in the sand within a 1 m radius of their nests (Simmons and Szedlmayer 2012).

Gray triggerfish have an indeterminate fecundity type, with mixed reproductive traits characteristic of species with female parental care. Throughout the spawning season, the number of vitellogenic oocytes does not decrease nor does their diameter increase, which suggests that de novo vitellogenesis is occurring. This violates the assumptions of determinate fecundity, despite the presence of group-synchronous secondary oocyte development (Lang and Fitzhugh 2015). Histological examination of ovaries suggests that gray triggerfish are iteroparous gonochorists, with females producing between 8 – 11 batches of eggs per year and spawning on average every 8 – 11 days over the course of an approximately 86-day breeding period (Lang and Fitzhugh 2015). The number of batches does not vary significantly with age, but fecundity is correlated to length and gonad weight (Manooch 1984; Caveriviere et al. 1981; Ofori-Danson 1990; Lang and Fitzhugh 2015). Simmons and Szedlmayer (2012) estimated fecundity from counts of eggs collected from nests and estimated a mean of 772,415 eggs nest^{-1} (range: 420,286 – 1,371,409) for females averaging 261 mm FL. Ingram (2001) also showed high fecundity for gray triggerfish, ranging from 96,379 to 2,649,027 oocytes for a mean fish size of 326 mm FL. These estimates were consistent with a more recently published study which concluded that fecundity ranged from 0.34 – 1.99 million eggs in 266 – 386 mm FL specimens (Lang and Fitzhugh 2015). Mean egg diameter was determined to be 0.62 mm (Simmons and Szedlmayer 2013).

Based on laboratory reared samples, eggs hatched from 24 to 48 hours after fertilization (Simmons and Szedlmayer 2013). This was shorter than previous incubation period estimates of 50 – 55 hrs (Caveriviere 1982; Lyczkowi-Shultz and Ingram 2005). At which time, larvae are reported to be between 1.7 and 2.2 mm notochord length (NT) (Lyczkowi-Shultz and Ingram 2005; Simmons and Szedlmayer 2013). After hatching, larval gray triggerfish are believed to inhabit the pelagic zone for 4 – 7 months (Simmons and Szedlmayer 2011). This is inferred from their occurrence in pelagic ichthyoplankton tows (Caveriviere 1982; Lyczkowi-Shultz and Ingram 2005) and from laboratory rearing experiments that observed larvae suspended throughout the tank water column (Simmons and Szedlmayer 2013). Seasonal peaks in the pelagic stage of gray triggerfish were similar among studies, for example, July through August (Fahay 1975), August through October (Dooley 1972) and May through August (Wells and Rooker 2004). During the pelagic stage, larval and juvenile gray triggerfish (≤ 175 mm standard length, SL) are associated with drifting mats of seaweed (mostly *Sargassum* spp.) and other flotsam (Dooley 1972; Fahay 1975; Bortone et al. 1977; Wells and Rooker 2004).

Juvenile gray triggerfish typically rank among the top 3 most abundant fish associated with *Sargassum* spp (Dooley 1072). They are often observed co-occurring with other ichthyofaunal species, such as the planehead filefish (*Stephanolepis hispidus*;

Dooley 1972; Bortone et al. 1977; Coston-Clements et al. 1991; Casazza and Ross 2008; Ballard and Rakocinski 2012). Previous studies have reported that the diets of both species contain *Sargassum*-associated epifauna and pelagic species (Dooley 1972; Coston-Clements et al. 1991; Harper and McClellan 1997; Turner and Rooker 2006; Casazza and Ross 2008; Ballard and Rakocinski 2012). Triggerfish can feed exogenously by four days post hatch, coinciding with the disappearance of their yolk sack and the development of their lower jaw (Simmons and Szedlmayer 2013). The feeding strategies of even small juvenile gray triggerfish are highly adaptable. When triggerfish occur with planehead filefish, they employ a pelagic feeding strategy, preying primarily upon zooplankton (e.g., pelagic copepods, hyperiid amphipods and fish eggs), while in contrast the filefish feed almost exclusively upon *Sargassum*-associated epifauna. When gray triggerfish are segregated from other species, they consume almost excessively epifaunal prey items, such as bryozoans, portunid crabs and hippolytid shrimp (Ballard and Rakocinski 2012). It has been argued that their fusiform shape and independently undulating paired and medial fins may allow for increased maneuverability and rapid movements needed to capture zooplankton and evade predators when making forays away from refuge of the *Sargassum*, as opposed to the laterally compressed body shape of planehead filefish (Alexander 1974; Arreola and Westneat 1996). This derived body design combined with a nimble but strong oral-jaw apparatus and dentition may also promote feeding plasticity in the benthic adults as well (Kotrschal 1989; Turingan and Wainwright 1993; Turingan 1994; Vose and Nelson 1994).

At approximately 80 – 175 mm SL, gray triggerfish settle out of the pelagic zone to natural and artificial reef habitats (Vose and Nelson 1994; Wells and Rooker 2004;

Franks et al. 2007). Recruitment of age-0 fish to benthic structured habitat occurs from September through December, peaking in October (Simmons and Szedlmayer 2011). It has been suggested that decreasing water temperatures in fall and winter may be a cue for triggerfish to settle out to the benthos (Simmons and Szedlmayer 2011). Reef type and complexity may also affect annual recruitment rates (Shulman 1984; Lingo and Szedlmayer 2006; Piko and Szedlmayer 2007). Once settled on newly recruited substrate, juvenile triggerfish use territories of 61 – 162 m^2 (Chen et al. 2001), where they feed primarily on algae, hydroids, barnacles and polychaetes (Dooley 1972).

Adult gray triggerfish feed diurnally and are particularly adapted to prey upon hard-shelled invertebrates that are consumed by few other reef dwelling fish (Aiken 1983; Frazer et al. 1991; Vose and Nelson 1994; Kurz 1995). Gray triggerfish are well suited to feed on armored prey, but they are also opportunistic feeders and will consume unarmored, soft-bottom and planktonic species (Turingan and Wainwright 1993; Turingan 1994; Blitch 2000). Vose and Nelson (1994) concluded that attached, epifaunal biota were the primary food sources for gray triggerfish residing on both natural and artificial reefs. However, greater amounts of bivalves were consumed on natural reefs and more barnacles were consumed on artificial structures (Vose and Nelson 1994). They also feed on sand dollars, sea urchins, crabs, gastropods, chitons, corals and algae (Aiken 1983; Reinthal et al. 1984; Nelson et al. 1986; Frazer et al. 1991; Vose and Nelson 1994; Kurz 1995). In contrast to earlier diet studies, Blitch (2000) reported that pelagic mollusks and crustacean larvae were the most important prey item in gray triggerfish diets, followed by decapod crustaceans. The ecological versatility of gray triggerfish may allow them to gain access to a greater range of resources and enhance their distribution among local habitats (Bean et al. 2002).

Gray triggerfish sampled in the Gulf of Mexico have a skewed sex ratio. Fitzhugh et al. (2015) observed a female to male sex ratio of 1.3:1 (56%) based upon histology and a ratio of 1.8:1 (64%) based upon microscopic observations. Fioramonti (2014), attained a female to male ratio of 1.6 to 1. An earlier study reported a female to male sex ratio at study sites outside the spawning season to be 1.7:1, and sex ratios of 1:1, 2:1 and 4:1 at sites where active spawning was observed (Mackichan and Szedlmayer 2007). Gray triggerfish sampled from commercial fisheries in the Gulf of Mexico indicated male to female ratios of 2:1 and 2.1:1, as well as reported larger fish sizes compared to the above ecological studies (Wilson et al. 1995; Hood and Johnson 1997). These commercial fishery samples were likely biased by sampling depth and gear type and may not be representative of the stock. The fact that females typically outnumber males may be a result of the polygynous reproductive strategy employed by the species and/or the accompanying aggressiveness of the males during the spawning season, leading to higher total mortality for males (Fioramonti 2014). Males and females may also have different natural mortality as indicated by sex ratios and longevity (Johnson and Saloman 1984; Hood and Johnson 1997). It is also possible that males and females experience differential fishing mortalities due to higher aggressiveness observed in males, however this has yet to be confirmed with direct field-based studies.

Movement Patterns and Habitat Use

Natural and artificial reef habitats provide gray triggerfish with a variety of resources including access to mates, food and refuge (Frazer and Lindberg 1994; Vose and Nelson 1994; Redman and Szedlmayer 2009; Simmons and Szedlmayer 2011, 2012). However, little is known about how triggerfish use these habitats in terms of movement patterns (vertical and horizontal), area use, emigration frequency, site fidelity or residency periods. Conventional mark-recapture studies indicate that gray triggerfish display limited horizontal movement and high site fidelity to reef structures (Beaumariage 1969; Ingram and Patterson 2001; Addis et al. 2013). However, estimates of annual site fidelity from conventional tag returns at the site of release are highly variable, for example, 37% (Beaumariage 1969), 55% (Addis et al. 2013) and 67% (Ingram and Patterson 2001). Most tagged fish have been recaptured within 10 km of their tagging site (Ingram and Patterson 2001), but one study reported greater movements of up to 60 km (Addis et al .2013).

A more recent study demonstrated that gray triggerfish could be successfully tagged with acoustic transmitters with high survival (76%) and tracked for extended periods due to high residency (> 57 weeks; Herbig and Szedlmayer 2016). These fish showed high annual site fidelity (64%) and used larger areas during the day than at night, and larger areas during the late summer and fall compared to winter and spring. Seasonal movement patterns were positively correlated with mean bottom water temperature. Throughout the study, tagged gray triggerfish remained closely associated with their release site reef (mean distance = 36 m, Herbig and Szedlmayer 2016). This was consistent with other studies that reported a mean daily dispersal distances of 56 m (Addis et al. 2013) and a mean foraging radius of 20 – 30 m (Frazer et al. 1991; Kurz 1995).

Diver (SCUBA) and video surveys provide some insight into patterns of vertical movement for Balistids (Hobson 1965; Fricke 1980; Kavanagh and Olney 2006). The redtoothed triggerfish (*Odonus niger*) has been described as living in open water, but substrate bonded by hiding and sleeping holes. Throughout the day, individuals were seen congregating in open water approximately 2 m above the seafloor, moving to nearby sleeping holes 30 min after sunset for the night, and then moving back out of their holes the following morning an hour before sunrise (Fricke 1980). The fine-scale triggerfish (*Balistes polylepis*), the orangeside triggerfish (*Sufflamen verres*) and the black triggerfish (*Melichthys niger*) have also been observed retiring to sleeping holes at night (Hobson 1965; Kavanagh and Olney 2006). Vertical movement patterns have not been examined in gray triggerfish but are an important aspect of their biology.

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Chapter 2:

Movement patterns, residency and site fidelity of gray triggerfish (*Balistes capriscus*) on artificial reefs in the northern Gulf of Mexico

Abstract

The present telemetry study evaluated horizontal movement patterns of gray triggerfish (*Balistes capriscus*) on artificial reefs in the northern Gulf of Mexico, using the Vemco Positioning System (VPS). Tagged fish (*n* = 49) were monitored for up to 662 d, from 23 January 2013 through 5 September 2017. Gray triggerfish had a mean residency time of 7 weeks and an annual site fidelity of 18% year^{-1}. When fish were active at their VPS site, they remained closely associated with reef structures (95% of positions were within 18 ± 41 m). Home range areas (95% kernel density estimates, KDE) varied significantly with season and diel period. Gray triggerfish showed the smallest area use in spring, increased area use in summer and the largest area use during fall and winter. Gray triggerfish used larger areas during the day (0700 to 1600) than at night (2000 to 2300 and 0000 to 0400), transitioning during crepuscular periods. These diel patterns were consistent across seasons. Seasonal area use was positively correlated with mean bottom water temperature and dissolved oxygen concentration. Most (*n* = 41, 84%) of the transmitter tagged gray triggerfish emigrated away from their VPS site during their tracking period. However, patterns differed among fish, in which some fish emigrated and did not return (*n* = 25, 51%), some emigrated once and then returned (*n* = 3, 6%), and others emigrated and returned multiple times (*n* = 13, 27%). High emigration from VPS sites (*n* = 28, 97% of the fish present) occurred during two tropical storms, after which 32% (*n* = 9) returned 2 to 15 d later. Based on the present study, gray triggerfish maintained a close association with artificial reefs and showed localized (≤ 7 km) frequent movements from reef to reef, with returns to release sites. Due to this close association with artificial reef habitat, the Gulf of Mexico gray triggerfish stock would likely benefit from alternative management strategies such as habitat enhancement programs, development of reef building zones or establishment of marine protected areas.

Introduction

Gray triggerfish (*Balistes capriscus*) is an ecologically and economically valuable species that inhabits natural and artificial reefs in the northern Gulf of Mexico and southeastern United States, typically at depths between 12 and 42 m (Smith 1975; Harper and McClellan 2014). Regional populations support both sport and commercial fisheries (SEDAR 43 2015). Historically, gray triggerfish were not heavily targeted nor considered an important food resource. In recent decades however, they have grown in value as fishing restrictions on other reef fish, such as red snapper (*Lutjanus campechanus*), have increased (Valle et al. 2001; SEDAR 31 2013; Harper and McClellan 2014; SEDAR 43 2015). Thus, landings of gray triggerfish increased through the mid-1980s, peaking at 1.5 million kg in 1990. Landings have since gradually declined to less than 0.2 million kg annually (SEDAR 43 2015; Amendment 46 2017).

The development of the gray triggerfish fishery was relatively recent, as were efforts to assess and manage this species. At the time of the present study, gray triggerfish were managed independently by both the Gulf of Mexico and south Atlantic regional councils. No subdivisions in geographic stock were recognized within either management zone (Antoni et al. 2011; Antoni and Saillant 2012; SEDAR 43 2015). The most recent Gulf of Mexico stock assessment indicated that the species was overfished, but no longer experiencing overfishing (Amendment 46 2017). However, the most recent estimates of population size and spawning stock biomass indicated that the stock was at or near historic lows and since 2014 showed signs of depensation (i.e., recruitment was below what was predicted by its stock-recruitment relation; SEDAR 43 2015; Amendment 46 2017). In addition, frequent sport catches were above the allocated total allowable catch (TAC), which led to a new 9-year rebuilding plan that went into effect 15 January 2018 (Amendment 46 2017). These new regulations permitted an annual harvest level of 126,100 kg (sport = 98,475 kg and commercial = 27,625 kg), but reduced the sport bag limit to 1 fish, changed the commercial limit to 16 fish, increased the size limit to 381 mm fork length (FL), and added in an additional January and February seasonal closure to the existing June and July spawning season closure (Amendment 46 2017).

Despite the increasing value of gray triggerfish and the new management plan, many life history parameters remain unclear. While natural and artificial reef habitats provide gray triggerfish with a variety of resources including access to mates, food and refuge (Frazer and Lindberg 1994; Vose and Nelson 1994; Redman and Szedlmayer

2009; Simmons and Szedlmayer 2011, 2012), little was known about how gray triggerfish use these habitats in terms of movement patterns, area use, site fidelity or residency periods (Herbig and Szedlmayer 2016). Conventional mark-recapture studies indicate that gray triggerfish display limited horizontal movement and high site fidelity to reef structures (Beaumariage 1969; Ingram and Patterson 2001; Addis et al. 2013). However, estimates of annual site fidelity from conventional tag returns have been variable, ranging from 37 to 67% (Beaumariage 1969; Ingram and Patterson 2001; Addis et al. 2013). Most externally tagged fish have been recaptured within 10 km of their tagging site (Ingram and Patterson 2001), but one study reported movements up to 60 km (Addis et al. 2013).

Conventional tagging studies are frequently used to assess movement patterns, site fidelity and residency, however they have several inherent difficulties. Conventional tagging studies are fishery dependent, fishing effort may not be consistent over areas or across seasons, recapture rates are typically low and tagging artifact mortality can be high (Parker 1990; Appledoorn 1997; Kohler and Turner 2001; Denson et al. 2002; Miranda et al. 2002). In addition, recaptures typically provide poor temporal and spatial resolution of site fidelity, degree of movement or actual timing of large-scale migrations (Appeldoorn 1997; Eristhee and Oxenford 2001; Kohler and Turner 2001). For example, conventional tag studies can provide only a straight-line distance from the site of tagging to the site of recapture. These studies also assume the recognition of tagged fish, reliable reporting of tagged fish and accurate reporting of recapture date and location (Matlock 1981; Parker 1990; Appeldoorn 1997; Schwartz 2000; Jenkins et al. 2000; Eristhee and Oxenford 2001; Kohler and Turner 2001; Denson et al. 2002; Miranda et al. 2002). In fact, false reporting of recapture location has been documented at least 56 km from actual capture location, based on telemetry (Szedlmayer and Schroepfer 2005; Williams-Grove and Szedlmayer 2016b). In contrast, acoustic telemetry methods are fishery-independent and eliminate many of the difficulties of conventional mark-recapture studies. Telemetry can allow researchers to continuously monitor the presence or absence of tagged fish over the course of several months to years, and determine movement patterns on temporal and spatial scales that are more relevant to ecological studies and management efforts (Hussey et al. 2015; Crossin et al. 2017). While several acoustic telemetry studies have successfully defined movement patterns and site fidelity of red snapper in the northern Gulf of Mexico (Szedlmayer and Schroepfer 2005; Topping and Szedlmayer 2011a, 2011b; Piraino and Szedlmayer 2014; Williams-Grove and Szedlmayer 2016a, 2016b), at the present time only one study has applied these methods to gray triggerfish (Herbig and Szedlmayer 2016).

Herbig and Szedlmayer (2016) successfully tagged gray triggerfish with internal acoustic transmitters and reported high survival (76%) and the ability to track fish for extended periods due to high residency (> 57 weeks). Transmitter tagged gray triggerfish showed high annual site fidelity (64%) and their movement patterns indicated diel and seasonal periodicity. Tracked individuals remained close to their release site reef (mean distance = 36 m), used larger areas during the day than at night and larger areas during the late summer and fall compared to winter and spring. Movements were positively correlated with water temperature (Herbig and Szedlmayer 2016).

Two additional studies have used acoustic telemetry to determine Balistids movement patterns. In the first study, six ocean triggerfish (*Canthidermis sufflamen*) were tagged with transmitters and their movements monitored around a fish aggregation device (FAD) in the Indian Ocean. Tagged ocean triggerfish showed short 15-d residency times, but due to their short residency, other patterns could not be evaluated (Dagorn et al. 2007). In the second study, three queen triggerfish (*Balistes vetula*) were tagged with transmitters and movements monitored in the U.S. Virgin Islands. These fish also had short mean residency times (29 d) and remained within 1.2 km of their release site (Friedlander et al. 2013).

The primary objective of the present study was to evaluate fine-scale (m) horizontal movement patterns of gray triggerfish captured near artificial reefs (0.32 km^2 area) in the northern Gulf of Mexico, using the Vemco Positioning System (VPS), and to document large-scale (km) movements and emigrations using a surrounding 64 km^2 array of single acoustic receivers. The present study quantified area use, diel and seasonal movement patterns, emigration frequency, site fidelity and residency. Movement and behavior patterns were compared to fish size, temperature and dissolved oxygen levels. Estimates of movement patterns will better enable management decisions on alternative management strategies, such as the establishment of marine protected areas and deployment of artificial reef habitats, in efforts to sustain the gray triggerfish stock in the northern Gulf of Mexico.

Methods

Study location

The study site (64 km^2) was located 23 – 35 km south of Dauphin Island, Alabama, USA, within the Hugh Swingle General Permit Area, in the northeastern Gulf of Mexico. The site contained 26 steel cage artificial reefs (2.5 x 1.3 x 2.4 m) each positioned 1.4 – 1.6 km apart at depths of 18 – 35 m. The artificial reefs were deployed at unpublished locations from 2006 – 2010 (Syc and Szedlmayer 2012). An array of Vemco acoustic receivers were previously deployed to monitor movement patterns of transmitter tagged fish (Piraino and Szedlmayer 2014; Herbig and Szedlmayer 2016; Williams-Grove and Szedlmayer 2016a, 2016b; Fig. 2-1).

Detection efficiency, range validation and positional accuracy

Detection efficiency, range and accuracy of Vemco Positioning System (VPS) derived positions have been previously determined for the larger V16-6x transmitters used to tag red snapper (Topping and Szedlmayer 2011a; Piraino and Szedlmayer 2014), but these measures have not been evaluated for the smaller, lower power V13-1L tags used in the present study. Range and detection frequency were evaluated by placing a control V13-1L (69 kHz, transmission delay: 40 – 80 sec) transmitter at a fixed location within the study site, along with a single VR2W acoustic receiver. Two additional receivers were placed at 100 m intervals out to 600 m distance from the control transmitter. Transmitter detections on each receiver were recorded at each distance for 5 h. Detection frequency was plotted against distance and a nonlinear four parameter logistic regression was fitted to the data ($F_{[3,9]} = 3.2$, $P = 0.008$, $r^2 = 0.72$). Detection frequency was then calculated at 5 m intervals out to 1,000 m, based on the logistic regression: $y = \min + (\max - \min)/(1 + [x/EC50]^{[-hillslope]})$, where min = asymptotic minimum of the curve, max = asymptotic maximum of the curve, x = distance (m), EC50 = the x-value for 50% of the y-range and hillslope = slope of the curve at its midpoint (McKinzie et al. 2014). Then the maximum detection distance was plotted in ArcGIS (ESRI ArcMap 10.1, Redlands, CA) to calculate the large-scale detection area and identify any gaps in receiver coverage.

The maximum number of V13-1L transmitters that can be deployed at a single VPS site was determined to reduce data loss due to signal collision. To make this evaluation, a single transmitter (V13-1L; 69 kHz, transmission delay: 40 – 80 sec) was placed 10 cm from a VR2W receiver (in air) and detections recorded for 1 h. Then another transmitter was added, and detections recorded for 1 h. This process was repeated until a total of 15 transmitters were simultaneously being recorded. The maximum number of transmitters that could be deployed at a single VPS site at any one time would then correspond to the number of transmitters at which total detections per hour begins to decline (Topping and Szedlmayer 2011a).

Placement of a stationary control transmitter (V13-1L or V13P-1L, 69 kHz, transmission delay: 40 – 80 sec) at each VPS site allowed for analysis of changes in detection frequency due to changing environmental conditions (e.g., seasonal storms) and environmental noise (e.g., boat traffic) that may influence fish detection patterns (Topping and Szedlmayer 2011a). The positional accuracy of the VPS system was validated by comparing the known latitude and longitude positions of the control transmitters with the VPS positions. The distance between the known and VPS-calculated positions of the control transmitters was calculated by the haversine formula (Sinnott 1984; Piraino and Szedlmayer 2014).

Fish tagging and cage-release method

Prior to tagging, dissolved oxygen concentration (DO) and temperature were measured throughout the water column (YSI Model 6920, YSI Incorporated). Fish were tagged and released if bottom water DO levels were > 2.5 mg l^{-1}. If water temperatures at the surface exceeded 27 °C, ice was added to the holding tanks during anesthetization and recovery to reduce high temperature stress (Williams-Grove and Szedlmayer 2016b).

Gray triggerfish were caught with hook and line baited with squid (*Loligo* or *Lolliguncula* spp.) at each of the five VPS sites (Fig. 2-1). Once captured, fish ≥ 250 mm fork length (FL) were anesthetized in a 70-l container with 150 mg MS-222 l^{-1} seawater (tricaine methanesulfonate; Munday and Wilson 1997; Cho and Heath 2000) for 80 sec to level four (Summerfelt and Smith 1990). After anesthesia, fish were weighed (nearest 0.1 kg) and measured (mm SL, FL and TL). An acoustic transmitter (Vemco, V13-1L or V13P-1L, 69 kHz, transmission delay = 40 – 80 s, battery life = 566 – 991 d) was surgically implanted within the peritoneal cavity through a 1 – 2 cm vertical incision on the ventral left side. The incision was then closed with 2 – 3 discontinuous, dissolvable sutures (Ethicon Inc., Chromic Gut). Betadine was spread over the wound to reduce the risk of infection. Fish were also injected with oxytetracycline (OTC). Fish were then tagged with an external anchor tag (Floy® FM-95W) inserted 1 – 2 cm posterior to the incision, with a unique identification number, contact information and reward notice for later identification by fishers or SCUBA divers.

After tagging, fish were transferred to a 185-l recovery tank with aerated seawater. During the recovery period, fish were monitored for increased opercular pumping, control of body orientation and resumption of normal swimming motion. Recovered fish were then placed into a weighted rectangular cage (46 x 61 x 61 cm) constructed of 13-gauge plastic covered wire and lowered to the seafloor (19 – 31 m) within 10 m of the capture site. Once the cage reached the seafloor, a door automatically opened, allowing the tagged fish to leave on its own initiative (Williams et al. 2015). Any tagged fish that did not leave the cage after 20 min on the seafloor were not released and were euthanized for transmitter recovery.

Fine-scale tracking

Each VPS site consisted of five Vemco VR2W acoustic receivers (Vemco Ltd., Nova Scotia) moored 4.5 m above the seafloor. A center receiver was placed 10 – 20 m north of the reef site, with four additional receivers placed 300 m north, south, east and west of the center receiver. Synchronization transmitters (sync tags; Vemco V16-6x, 69 kHz, transmission delay = 540 – 720 s) were attached 1 m above each receiver to standardize the internal receiver clocks (Piraino and Szedlmayer 2014). All receivers and mooring floats were coated with a copper-based antifouling paint to reduce the potential of signal occlusion due to biofouling (Topping and Szedlmayer 2011a). Each of the VPS array receivers were exchanged and downloaded every 4 to 6 mo. Data from the VPS receivers were post-processed by Vemco for fish positions. Fish positions (latitude, longitude) were derived from the time differential of signal arrival at three to five receivers.

Large-scale tracking

Large-scale movements of tagged gray triggerfish were monitored by a network of single VR2W acoustic receivers (*n* = 21; Vemco Ltd., Nova Scotia) placed approximately 1.6 km apart at locations surrounding the VPS arrays (Fig. 2-1). Each of these single receivers were also associated with an unpublished steel cage artificial reef (Syc and Szedlmayer 2012; Herbig and Szedlmayer 2016; Williams-Grove and Szedlmayer 2016b). The outside receivers were exchanged and downloaded every 6 to 12 months. The combination of VPS and surrounding site receivers allowed continuous monitoring of gray triggerfish movements over a large 64 km^2 area.

Environmental monitoring

A YSI EX02 environmental recorder (YSI Inc., Yellow Spring, Ohio) was deployed 3 m above the seafloor 38 m north of the R4 VPS site, to continuously monitor temperature, salinity, dissolved oxygen (DO) and turbidity from 7 May 2015 through 3 November 2015 and from 23 May 2016 through 7 December 2016. In addition, a HOBO temperature and DO data logger (Onset HOBO® U26-001) was attached to the R4 center receiver mooring line, 0.5 m above the seafloor starting 7 December 2016 through the end of the study period on 5 September 2017. Additional HOBO temperature loggers (Onset HOBO® U22 Water Temp Pro v2) were placed at each of the VPS sites center receivers over the entire study period (January 2013 through September 2017). One temperature logger was attached at the seafloor and one was attached 4 m above the seafloor. Temperature and DO loggers recorded at 1-hour intervals, with loggers exchanged and downloaded at 4 to 6 month intervals.

Residency and site fidelity

The VPS arrays were used to categorize tagged fish as active (continuously swimming), caught (sudden disappearance from a VPS reef), emigrated (progressively moving farther away from a VPS reef and then lost or detected on a surrounding, single receiver) or deceased (tag became stationary; Topping and Szedlmayer 2011a; Williams-Grove and Szedlmayer 2016b). For all five years combined (2013 – 2017), a known fate model (Kaplan-Meier) was applied in the MARK program to estimate conditional survivals, total survivals, standard error and 95% confidence limits (Edwards 1992; Topping and Szedlmayer 2013). Median residence time was defined as the period when 50% of the tagged gray triggerfish were still present, while site fidelity was the percentage of tagged fish remaining at their VPS site one year after release (Schroepfer and Szedlmayer 2006; Topping and Szedlmayer 2011a; Herbig and Szedlmayer 2016; Williams-Grove and Szedlmayer 2016b). Residency and site fidelity estimates were based on survival analyses from conditional probabilities of surviving specified events (e.g., emigration). Fish were removed from the analysis (right censored) if they showed other events not under consideration. For example, when estimating residency or site fidelity, a fish that was caught or experienced a natural mortality event was removed from subsequent estimates in the following time intervals under analysis.

Fine-scale area use analyses

Habitat use patterns were compared with kernel density estimates (KDE) of VPS derived positions. This analysis is a probabilistic approach to estimating area use with respect to other factors, for example different time intervals (Hooge et al. 2001). Home range was defined as the area within the 95% KDE (Piraino and Szedlmayer 2014; Herbig and Szedlmayer 2016; Williams-Grove and Szedlmayer 2016b) and was calculated using the *MASS* package in R (Calenge 2006). Home range area was estimated for each fish by hour and season (winter = December, January, February; spring = March, April, May; summer = June, July, August; fall = September, October, November). Home range areas were compared over time periods with a one-way mixed model repeated measures analysis of variance (rmANOVA), with individual gray triggerfish areas measured repeatedly over time. A Tukey-Kramer test was used to show specific differences, after rmANOVA detected a significant difference (Zar 2010). Home range areas were compared to environmental factors using rmANOVA, with temperature and DO as continuous predictor variables. Home range area was also compared to fish size (FL) with a linear regression (Herbig and Szedlmayer 2016; Williams-Grove and Szedlmayer 2016b, 2017). Mean distance fish traveled while resident at their release site was calculated with the haversine formula (Sinnott 1984; Herbig and Szedlmayer 2016; Williams-Grove and Szedlmayer 2016b). The use of secondary reef sites located within the VPS arrays was analyzed by site, fish and season with the proximity tool "near" (ESRI ArcMap 10.1, Redlands, CA; McKinzie et al 2014). Fish were considered resident to a reef site (either VPS release site or secondary reef site) if positions occurred within 59 m from the corresponding reef. This 59 m distance was based on the mean distance of all positions within the home range area plus one SD. If positions were located ≥ 59 m from a reef, they were assumed to have occurred over open habitat (Williams-Grove and Szedlmayer 2016b). Times of sunrise and sunset were determined from the US Naval Observatory website (http://aa.usno.navy.mil/data/docs/RS_OneYear.php). All statistical analyses were carried out in SAS (Statistical Analysis Software, Cary, NC).

Large-scale movement analysis

Large-scale movements of tagged gray triggerfish were detected by an array of surrounding, single VR2W receivers (n = 21). The amount of time a fish spent near a surrounding reef site was measured by these individual surrounding receivers. A false detection analysis was applied to single receiver detections to filter out false detections. False detections can result from incomplete transmission due to interference (i.e., noise) or collision of signals when two or more transmitters simultaneously reach a receiver (Pincock 2012). Transmitter detections were accepted as valid if there were at least two detections per transmitter with less than 30 min (short interval) between detections. If multiple detections were recorded, they were considered valid if there were more short intervals (30 min) than long intervals (12 h) between individual detections. The short interval was based on 30 times the nominal ping interval of 60 sec, and the long interval was based on 720 times the 60 sec nominal ping interval (Pincock 2012). All false detections were removed from analysis (Pincock 2012; Williams-Grove and Szedlmayer 2016b).

Results

Detection efficiency, range and positional accuracy

As the number of V13-1L transmitters next to a VR2W receiver was increased, mean detections per transmitter per hour significantly decreased ($r^2 = 0.93$, $P < 0.001$; Fig. 2-2). Detections per transmitter decreased from 55 detections per hour with one transmitter to eight detections per hour with 15 transmitters. Total detections increased to a maximum of 170 per hour with seven transmitters and decreased with greater than nine transmitters ($r^2 = 0.87$, $P = 0.0002$; Fig. 2-2). Thus, active transmitters were limited to ≤ 10 at individual reef sites at any one time. Active transmitters included tagged gray triggerfish, controls (details below) and other transmitter tagged species that were not part of the present study.

Stationary control transmitters placed within each VPS array showed that detections ($n = 785{,}912$) were continuous (no interruptions in data collection) over the five-year study period. The mean difference (± SD) between the known position of these control transmitters and the VPS derived positions was 3.1 ± 1.5 m. Detection frequency was 88% out to 300 m (extent of VPS array) and the maximum detection radius around each receiver was estimated to be 770 m (Fig 2-3). Therefore, within the larger 64 km^2 array, coverage was approximately 82% of the array area (53 km^2; Fig. 2-1). Thus, there was an ~11 km^2 cumulative area (18%), which had little coverage. These areas of low to no coverage occurred in 100 – 300 m corridors between single receiver coverage areas (Fig. 2-1).

Tagging and tracking

A total of 60 gray triggerfish were tagged with acoustic transmitters. Four fish (7%) failed to exit their release cage, were euthanized and removed from the study. The remaining 56 tagged individuals were successfully released at one of five VPS sites (Fig. 2-1) and were tracked for up to 662 d, from 23 January 2013 through 5 September 2017. Mean ± SD size of tagged fish was 395 ± 52 mm FL, and ranged from 276 to 535 mm FL. All tagged fish were above the estimated size (> 250 mm FL) of 100% sexual maturity for both males and females (Fitzhugh et al. 2015).

There were 390,476 accurate positions (± 3.1 m) used to assess gray triggerfish ($n = 56$) fine-scale movement and behavior. The number of positions per fish ranged from 59 to 97,765. Five fish (10%) had low numbers of positions ($n < 85$) and were removed from all area use analyses but were included in large-scale and survival analyses. All other fish had high numbers of positions with n = 118 to 1000 (18%), 1,000 to 10,000 (55%), 10,000 to 20,000 (16%) and 20,000 to 97,765 (11%). Gray triggerfish that left (9%, $n = 5$) their VPS site within 3 d post tagging were categorized as lost and removed from all subsequent analyses. Two fish (3%) showed no movement after exiting their release cage and were also removed from analysis. Fish that remained after 3 d (88%, $n = 49$) were categorized as active, caught, emigrated or deceased and were included in all subsequent movement analyses.

Fine-scale (m) and large-scale (km) movements of tagged gray triggerfish ($n = 49$) were monitored for 4 to 662 d. Among these tagged and tracked gray triggerfish, 30 fish had a final event status as an emigration, four were caught by fishers, four suffered natural mortality and 11 fish were active until either their transmitter battery died ($n = 8$)

or the study period ended (*n* = 3; Fig. 2-4). The four fish (8%) which were caught by fishers were active for 73 to 164 d before capture. All of these four VPS identified fishing mortalities (*F*) were verified by fisher reporting. Two additional fish were reported as captured by fishers after they ceased to be detected due to emigration from their VPS site (T20 and T28). Fish T20 was active for 443 d at its release site, then emigrated and was caught after 693 d at liberty 2.2 km to the northwest. Fish T28 was active for 237 d at its release site, then emigrated and was caught after 249 d at liberty 0.9 km to the west. Four fish (8%) showed tracking patterns that indicated natural mortalities (regular movements followed by stationary positions), most likely from predation 15 to 362 d after released. Four fish (8%) were active on their VPS site for their entire tracking period, until their transmitter battery expired (284 – 508 d) and did not emigrate. Another four fish were active when their transmitter battery died (386 – 622 d post-release) but did periodically emigrate. At the end of the study on 5 September 2017, four fish (8%) were still active on their VPS sites after being tracked for 119 to 146 d.

Storm events

A high percentage of tagged gray triggerfish (60%, *n* = 29) were active at their VPS site during major tropical storms. These storm events included hurricane Patricia (26 October 2015) and tropical storm Cindy (20 – 21 June 2017). High emigration (97% of the fish present, *n* = 28) from VPS sites occurred during storm events, after which 32% (*n* = 9) returned 2 to 15 d later (mean ± SD = 6 ± 4 d). Most (89%) of the fish that emigrated during storm events were detected moving outside the large-scale array during their time of absence. Tagged fish needed to travel ~ 2 km to exit the large-scale array via the most direct route, but once outside the array, their movements could not be determined. Three fish (11%) that had emigrated from their tagging site, but stayed within the large-scale array, moved on average 4.7 ± 2.4 km (range: 1.9 – 6.1 km) and were detected at 1 to 3 sites for 1 to 7 d. These fish then returned to their tagging sites (after 9 d) or left the large-scale array after 4 to 6 d. Emigrations and large-scale movements associated with storm events occurred throughout the 24 h diel period. Continuous detections of the control transmitters during storm events confirmed that these emigrations were not due to loss of detections from storm sea conditions. In addition, 71% of the emigrations were verified by detection on surrounding receiver sites, or by fish returns to a VPS site following emigration.

Hurricane Patricia entered the Gulf of Mexico on 25 October 2015 and passed just northwest of the present study site on 26 October 2015. Wave heights reached 4.5 m, winds occurred up to 80 km h^{-1} (www.ndbc.noaa.gov), bottom water temperature was 24.5 ± 0.1 °C (mean ± SD) and dissolved oxygen concentration was 6.1 ± 0.3 mg l^{-1}. There were seven fish active when the storm passed and 86% ($n = 6$) emigrated from their VPS site, and then 57% ($n = 4$) returned after 2 – 15 d (mean ± SD = 9 ± 5 d).

Tropical storm Cindy passed directly over the study site on 20 – 21 June 2017, with wave heights reaching 3.5 m and winds up to 70 km h^{-1} (www.ndbc.noaa.gov). Mean bottom water temperature was 26.1 ± 0.9 °C. Dissolved oxygen concentration was 3.2 ± 0.4 mg l^{-1} prior to the storm event, but during the storm DO concentration increased to a mean of 6.7 ± 0.3 mg l^{-1}. During this storm, all tagged gray triggerfish ($n = 22$) emigrated from their VPS site and 23% ($n = 5$) returned to their VPS site 2 to 8 d (5 ± 2

d) after the storm. One additional fish (T51) also returned to its VPS site 3 d after the storm, but this fish had emigrated 33 d prior to tropical storm Cindy.

Residency and site fidelity

In the present residency analysis, more fish emigrated (*n* = 40, 82%) than were right censored due to fishing mortality (*n* = 1, 2%), natural mortality (*n* = 3, 6%) or transmitter battery failure (*n* = 5, 10%). Based on a combined analysis from all 5 years, median residence time = 7 weeks , total survival *S* = 0.09 (confidence interval [CI]: 0.03 – 0.25) and annual site fidelity = 18% $year^{-1}$ (Fig. 2-5).

Fine-scale area use

The 390,476 gray triggerfish positions analyzed indicated a mean ± SD seasonal home range area of 5284 ± 4641 m^2 (range: 156 – 20,866 m^2). While active within their VPS array, tagged individuals remained in close association with their tagging reef (VPS site), with a mean ± SD distance from the reef = 40.2 ± 83.0 m. Home range showed no significant variation with site ($F_{[4,100]}$ = 2.1, P = 0.09), year ($F_{[4,100]}$ = 1.3, P = 0.28) or fish size ($F_{[1,103]}$ = 1.3, P = 0.23, r^2 = 0.01).

Gray triggerfish movement patterns varied significantly with season ($F_{[3,84.4]}$ = 5.5, P = 0.002). Fall and winter (September through February) area use (mean ± SD = 7246 ± 4662 m^2) was significantly larger than spring (March through May = 3097 ± 3671 m^2), but not significantly different from summer (June through August) area use (4982 ± 4555 m^2; Fig. 2-6). Home range areas were greater when mean bottom water temperatures were higher ($F_{[1,63]}$ = 5.3, P = 0.03, r^2 = 0.49). Home range areas were also greater when bottom DO levels were higher, at the VPS site where DO was measured (R4; $F_{[1,12]} = 20.1$, $P = 0.0008$, $r^2 = 0.31$).

Gray triggerfish showed distinct diel patterns of movement and behavior. Home range area was significantly larger during the day from 0700 to 1600 h (mean ± SD = 3242 ± 2989 m^2) than at night from 2000 to 2300 and 0000 to 0400 (309 ± 315 m^2), but not significantly different from that at dawn 0500 to 0600 and dusk 1700 to 1900 (1893 ± 2279 m^2; $F_{[23,1241]} = 16.7$, $P < 0.001$ for both dawn and dusk grouped together). The time of day that diel patterns changed between the day and night periods varied with season ($F_{[23, 1169]} = 21.2$, $P < 0.001$) and coincided with the changing times of sunrise and sunset. During all four seasons, the increase in area use occurred at sunrise, while the decrease in area use occurred at sunset (Fig. 2-7). Tagged gray triggerfish also remained significantly farther from reef habitats during the day (24.1 ± 46.1 m) than at night (6.7 ± 30.4 m) or crepuscular periods (15.5 ± 36.5 m; $F_{[23, 4E5]} = 602.6$, $P < 0.001$).

Secondary reef sites were present within four of the five VPS arrays (R2, R3, R4, R5) that were used to monitor gray triggerfish fine-scale movement patterns. The presence of these secondary reef sites was unknown at the start of the present study, but their locations became apparent based on gray triggerfish movement patterns, as the fish positions were concentrated at locations away from their release site reefs. Surveys by SCUBA divers confirmed the presence of these secondary reef sites. Site R2 had one secondary reef (concrete pyramid) located 289 m (225 degrees) from the VPS reef. Site R3 had two secondary reefs: one was present (steel cage) for the entire study period and located 144 m (45 degrees) from the VPS reef and the second (steel cage) was located 277 m (315 degrees) from the VPS reef, but used only in 2017. Site R4 had three secondary reefs: a concrete pipe that was located 115 m (180 degrees), a concrete pyramid 156 m (315 degrees) and another concrete pyramid 302 m (200 degrees) from the VPS reef. Site R5 had one secondary reef site (steel cage) that was present for only part of the study (2017) and was located 83 m (135 degrees) from its VPS site reef. Site R6 did not contain any secondary reef sites. Most (95%) of the tagged gray triggerfish that had access to these secondary reef sites visited them at one time or another. Fish resided on these secondary reefs for 1% to 98% of their tracking periods. For all sites and years combined, fish that had access to secondary reefs (*n* = 37, 76%) spent 81% of their time on their primary VPS site reef, 15% of the time on secondary reefs and 4% over open habitat. Gray triggerfish that did not have access to secondary reefs (*n* = 12, 24%) spent most (94%) of their time on their VPS reef site and 6% over open habitat. When distance from both the tagging and secondary reefs was considered, fish mean distance from a reef structure was substantially reduced to 17.6 ± 41.1 m.

Gray triggerfish residing on VPS sites with secondary reefs showed seasonal patterns in reef use (Table 2-1). Seasonal movements to secondary reefs were evaluated for fish that were released at R3 (*n* = 12) and R4 (*n* = 12). At other sites, seasonal patterns of secondary reef site use could not be evaluated, because at site R2 there was only one tagged fish, at site R5 a secondary reef site was available for only part of 2017, and at site R6 no secondary reef sites were present. Fish showed the highest use of VPS reef sites in the spring, decreased use in the summer and fall, then increased use again in the winter. In contrast, fish use of secondary reef sites showed the opposite trend and was lowest in the spring, increased in summer and fall, and then decreased again in winter (Table 2-1). Fish distance to reef habitat (both VPS reef and secondary reef) was significantly reduced during the spring compared to all other seasons (mean ± SD = 12.4 ± 26.6 m), increased during the summer (19.7 ± 43.3 m) and fall (19.9 ± 52.4 m), and was significantly greater during the winter than during all other seasons (21.4 ± 48.5; $F_{[3,4E5]} = 1025.9$, $P < 0.001$).

Emigrations and large-scale area use

The surrounding receiver array (*n* = 21; 64 km^2) was used to confirm emigrations from the five VPS sites and to estimate large-scale (km) movement patterns (Fig. 2-1). Across all sites and years, 84% (*n* = 41) of all tagged gray triggerfish emigrated from their VPS site at least once, with a total of 151 emigration events detected (Fig. 2-4). Most (91%) of these VPS determined emigrations were verified by detection on surrounding receiver sites or by fish returns to VPS sites following an emigration. In the present study, gray triggerfish showed three emigration patterns: one-time emigrants (*n* = 3, 6%), permanent emigrants (*n* = 25, 51%) and multiple emigrants (*n* = 13, 21%). One-time emigrants moved away from their VPS site after being resident for 42 – 60 d, left for 2 – 4 d, and then returned to their VPS site where they remained until the end of the study (*n* = 1), were caught by fishers (*n* = 1; 9 d after return) or died naturally (*n* = 1; 50 d after return). All one-time emigrations coincided with tropical storm events. For example, fish T36 resided on R6 for 47 d, emigrated to an unknown location on 26 October 2015 as hurricane Patricia passed through, and then 2 d later returned and resided on R6 for 50 d, then died of natural causes.

Permanent emigrants (*n* = 25) were classified as individuals that moved away from their VPS site after being resident for 4 to 335 d (mean ± SD = 82 ± 109 d) and did not return. Most (72%) permanent emigrations occurred during tropical storms. Two gray triggerfish left on 26 October 2015 (hurricane Patricia) and 16 fish left between 20 – 21 June 2017 (tropical storm Cindy; Fig. 2-4). Permanent emigrants were detected at up to seven surrounding reef sites before exiting the acoustic array < 1 to 7 d after emigration from their VPS site. For example, fish T40 resided at R4 for 306 d then emigrated on 20 June 2017 (tropical storm Cindy) and was detected at a single surrounding reef site (R12) before leaving the large-scale receiver array after < 1 day.

Multiple emigrants were individuals that showed homing behavior, in that they made more than one movement away followed by subsequent returns to their VPS site. These individuals (n = 13) made 10 ± 12 (mean ±SD) emigrations (range: 2 – 42) and stayed away for 13 ± 34 d (range: < 1 – 232 d) at intervals of 18 ± 49 d (range: < 1 – 339 d), during which they visited up to four surrounding reef sites. These repeated emigrations were not significantly related to seasonal changes, in that they occurred throughout the year during all seasons (likelihood ratio: $\chi^2 = 4.8$, P = 0.57). For example, fish T17 emigrated from its VPS site three times over its 622 d tracking period. This fish was active for 399 d at its release site R3, then emigrated initially to S40 for 3 h, and returned to R3 for 2 d. It then emigrated a second time to S40 for 5 d, moved to an unknown location for 3 d, returned to S40 for 29 d, moved to an unknown location for 117 d, and subsequently returned to R3 for 8d. It then emigrated a third time to an unknown location for 54 d, returned to R3 for 4 d and finally was lost due its battery life being exceeded.

Discussion

Movement patterns of gray triggerfish *(n* = 49) captured and released on artificial reefs in the northern Gulf of Mexico were investigated for extended periods (up to 622 d) over a five-year study period. The present telemetry study expanded upon a previous study (*n* = 13; 399 d) that validated the feasibility of internal transmitter implantation, detection of subsequent long-term survival of tagged gray triggerfish and the use of VPS telemetry methods (Herbig and Szedlmayer 2016). Accurate positions (3.1 ± 1.5 m, *n* = 390,476) collected over short intervals (mean detection time < 10 min) were analyzed to document diel and seasonal area use patterns, emigration events, annual site fidelity and residency periods.

Residency and site fidelity

The present study estimate of gray triggerfish mean residency was 7 weeks and annual site fidelity was 18% year^{-1}. These estimates were lower than previous VPS telemetry estimates of > 57 weeks and 64% year^{-1} (Herbig and Szedlmayer 2016). Higher emigrations (*n* = 151) by tagged individuals from their VPS site likely caused the differences from the earlier study (*n* = 5; Herbig and Szedlmayer 2016). Emigrations were observed in 84% (*n* = 41) of the presently tagged gray triggerfish, compared to only 23% (*n* = 3) in the previous study (Herbig and Szedlmayer 2016).

Importantly, two major storm events (hurricane Patricia and tropical storm Cindy) passed over the study site during the present study period, but no large-scale storms occurred during the previous study (Herbig and Szedlmayer 2016). Most (97%) of the tagged gray triggerfish that were active during these storm events emigrated from their VPS site and 32% returned 2 to 15 d later. Similarly, blacktip shark (*Carcharhinus limbatus*) were shown to leave shallow bays for deeper water just prior to arrival of tropical storm Gabrielle and returned after 5 to 13 d (Heupel et al. 2003). Previous telemetry studies on red snapper have also reported emigrations in association with cold fronts and tropical storm activity, however most red snapper remained resident at their reef site during storm events (Szedlmayer and Schroepfer 2005; Topping and Szedlmayer 2011a).

Conventional tagging studies have also suggested that tropical storms may influence reef fish movement patterns and reduce residency times (Watterson et al. 1998; Ingram and Patterson 2001; Patterson et al. 2001; Addis et al. 2013). For example, one study reported that tagged gray triggerfish and red snapper exposed to storms showed larger and more rapid emigrations than did individuals not exposed to storms (Ingram and Patterson 2001). Addis et al. (2013) also reported that hurricane exposure significantly affected the probability that gray triggerfish and red snapper would emigrate from tagging sites, but not their distance traveled. In addition, two previous red snapper studies reported that hurricane exposure not only affected the likelihood and magnitude of movement, but also the distance traveled (Watterson et al. 1998; Patterson et al. 2001). Discrepancies in hurricane related movements among studies may be due to differences in reef type, size, location or depth, and also differences in storm intensity, duration or proximity to tagging site (Watterson et al. 1998; Ingram and Patterson 2001; Patterson et al. 2001; Szedlmayer and Schroepfer 2005; Topping and Szedlmayer 2011a; Addis et al. 2013).

The present telemetry study estimate of site fidelity (18% year^{-1}) was lower than previous conventional tagging study estimates (37 – 67% year^{-1}; Beaumarige 1969; Ingram and Patterson 2001; Addis et al. 2013). Conventional tagging study estimates were based on fisher reported recaptures at release sites verses non-release sites (Ingram and Patterson 2001; Addis et al. 2013). In contrast, VPS telemetry estimates of site fidelity were more precise, because they were based on measured events (emigrations and mortalities) from accurate positional data and the identification of these events did not depend on fisher reports (Topping and Szedlmayer 2011a; Williams-Grove and Szedlmayer 2016a). It is possible that conventional methods overestimated site fidelity of gray triggerfish in comparison to telemetry estimates, because short duration movements away from their reef site could not be detected. For example, conventionally tagged fish would be considered as resident at their tagging reef for their entire time at liberty, even if they emigrated and returned before recapture. In contrast, all emigrations were detected in the present telemetry study.

Gray triggerfish showed homing behavior (Herbig and Szedlmayer 2016). In the present study, many tagged fish (33%, n = 16, one-time and multiple emigrants) left their VPS site at least once, visited up to four surrounding reef sites as far as 7 km away and then returned to their original VPS site after 1 to 232 d. In a previous gray triggerfish telemetry study, a single fish left its VPS site on two separate occasions, visited up to seven surrounding reef sites up to 7 km away and then returned after 9 to 11 d. Other reef fish such as red snapper have also shown homing behavior, with individuals emigrating up to 8 km and returning after as long as 336 d (Topping and Szedlmayer 2011a; Piraino and Szedlmayer 2014; Williams-Grove and Szedlmayer 2016a). Gray triggerfish emigrations were identified as valid movements of transmitter tagged fish rather than misidentified natural mortality events (i.e., shark predation; Williams-Grove and Szedlmayer 2016a, 2016b), because the observed large-scale movement patterns of one-time and multiple emigrant fish did not mimic the large-scale movement patterns of bull shark (*Carcharhinus leucas*) or sandbar shark (*C. plumbeus*; Altobelli and Szedlmayer In Prep). In addition, several (*n* = 4) of the presently tagged one-time and multiple emigrant gray triggerfish were later caught and returned by fishers.

Previous telemetry studies have also described the use of secondary reef sites within the VPS array as evidence of homing behavior and suggested that tagged fish knew their habitat as indicated by the long residence periods on these secondary reef sites, with regular returns to their tagging reef (Piraino and Szedlmayer 2014; Williams-Grove and Szedlmayer 2016). In the present study, most (94%) tagged gray triggerfish that had access to secondary reef sites within their VPS array used them for 1% up to 98% of their tracking periods. Movement to and from different reef sites both inside and outside the VPS arrays may provide benefits in the form of increased access to prey, mates or shelter, that may account for the expenditure of energy associated with these excursions (Wakeman et al. 1979; Hays et al., 2016).

Diel patterns

Similar to the present study, previously described gray triggerfish area use was related to diel periodicity, with home range area significantly larger during the day than at night (Herbig and Szedlmayer 2016). Nighttime area use was so substantially reduced that fish were most likely taking refuge or resting in available reef habitat. In addition, the presently observed movement patterns indicated that tracked gray triggerfish remained significantly closer to reefs at night compared to day time periods. These diel patterns were tied to sunrise and sunset, as area use shifted with seasonal changes in daylight hours. Other Balistids have shown similar diel patterns. For example, black triggerfish (*Melichthys niger*), fine-scale triggerfish (*Balistes polylepis*) and orangeside triggerfish (*Sufflamen verres*) are known to rest in small holes during the night (Hobson 1965; Kavanagh and Olney 2006).

Predation pressure may play an important role in the observed diel patterns of gray triggerfish. Visual observations by scuba divers of large sandbar shark and bull shark on VPS and surrounding reef sites were common throughout the study period (McKinzie and Szedlmayer, personal observation). Both shark species increase their feeding activity at night (Driggers et al. 2012) and a previous study reported direct observations of a sandbar shark chasing a female gray triggerfish off its nest (Simmonds and Szedlmayer 2012). Greatly diminished nocturnal movements and resting within reef shelter would reduce the vulnerability of gray triggerfish to predation (Werner et al. 1983; Piraino and Szedlmayer 2014; Herbig and Szedlmayer 2016).

Diel patterns may also relate to foraging, as gray triggerfish have been observed to forage away from reef structures only during the daytime, and stomach content analyses indicate daytime foraging (Frazer and Lindberg 1994; Vose and Nelson 1994). In addition, the presently tagged gray triggerfish that showed multiple emigrations not related to storms, did so only during the day.

Another possible cause for these emigrations may have been aggressive interactions during spawning. Dominant male gray triggerfish aggressively defend a territory around a reef structure and actively chase away other male gray triggerfish from the site (Simmons and Szedlmayer 2012). Similarly, male redtail triggerfish (*Xanthichthys mento*) chase other males off nests during spawning (Kawase 2003), female blue triggerfish (*Pseudobalistes fuscus*) routinely display agnostic behaviors during spawning (Fricke 1980) and female-female aggressive encounters are common during the breeding season for red-toothed triggerfish (*Odonus niger*; Fricke 1980). While it is difficult to identify the actual reasons for daytime emigrations and diel movement patterns, they most likely involve a combination of behaviors related to feeding, spawning, shelter and competitive exclusion (Simmons and Szedlmayer 2018).

Seasonal patterns

In the present study, gray triggerfish home range area was significantly reduced in spring (March – May), increased during the summer (June – August), and was largest during fall (September– November) and winter (September – February). Herbig and Szedlmayer (2016) also showed significantly reduced springtime area use with significantly larger fall areas, however, in contrast to this previous study, the present area use was also significantly larger in winter (Herbig and Szedlmayer 2016). Low sample size (*n* = 13) in the previous study (Herbig and Szedlmayer 2016) most likely contributed to the observed differences in seasonal area use patterns compared to the present study (*n* = 49), as sample size has been shown to influence home range estimates (Seaman et al. 1999; Girard et al. 2002; Börger et al. 2006). Another difference between the two telemetry studies was that gray triggerfish in the present study had greater access to secondary reef sites due to more VPS tagging sites. Gray triggerfish may simply show expanded area use and different seasonal patterns due to the increased reef habitats observed here, in comparison to the previous study (Herbig and Szedlmayer 2016).

Despite larger winter areas, seasonal area use patterns correlated positively with bottom water temperature in the present study. This was similar to previous reef fish studies that also showed a significant positive correlation between temperature and area use in gray triggerfish and red snapper (Piraino and Szedlmayer 2014; Herbig and Szedlmayer 2016; Williams-Grove and Szedlmayer 2016b). Previous studies have shown that seasonal hypoxia events in the Gulf of Mexico influence fish movement and behavior, with fish moving away from hypoxic environments either vertically or horizontally (Kramer 1987; Chesney et al. 2000; Huenenmann et al. 2012; Szedlmayer and Mudrak 2014; Everett 2018). In the present study, seasonal area use correlated positively with bottom water dissolved oxygen (DO) concentration, but this was measured only at site R4. Gray triggerfish decreased their area use during periods of low summer DO, in contrast to patterns reported for red snapper (Szedlmayer and Mudrak 2014; Everett 2018). However, gray triggerfish likely respond to low bottom DO by vertical movement up into the water column, as indicated by a significant vertical response to low DO ($r^2 = 0.47$; Chapter 3). In addition, gray triggerfish horizontal movement patterns may be relatively limited by spawning and foraging activities that tend to keep gray triggerfish close to reef structures (Frazer and Lindberg 1994; Vose and Nelson 1994; Redman and Szedlmayer 2009; Simmons and Szedlmayer 2011, 2012). For example, spawning in gray triggerfish begins in May, peaks in June and ends by late July and August (Dooley 1972; Wilson et al. 1995; Simmons and Szedlmayer 2012; Lang and Fitzhugh 2015).

It is possible that gray triggerfish go through pre-spawning lekking behavior in the spring that may reduce area use. Most likely territoriality and intraspecific aggression begin in the spring before actual spawning, as gray triggerfish establish their summer dominance hierarchies and territories. As spawning decreases in late July and August, territoriality decreases allowing greater movements among reefs during the late summer. Lek-like spawning behaviors have been observed in the yellowmargin triggerfish (*P. flavmarginatus*) and the crosshatch triggerfish (*X. mento*; Gladstone 1994; Kawase 2003).

In the fall and winter, gray triggerfish maximized their area use by increasing secondary reef site use and foraging farther from VPS reef sites. During these seasons, movement patterns may no longer be restricted by low summer DO and spawning behaviors, and fish may expand their foraging area to replenish depleted energy reserves and potentially take advantage of open habitat prey sources (Vose and Nelson 1994; Kurz 1995; Blitch 2000; Lang and Fitzhugh 2015; Herbig and Szedlmayer 2016). This fall to winter increase in foraging activity is accompanied by post-spawning increases in both the hepatosomatic index (HSI) and Fulton's condition factor (K, g cm^{-3}; Lang and Fitzhugh 2015).

Diet studies have shown the importance of reef associated epibenthic prey communities as well as unarmored, soft-bottom and planktonic species for gray triggerfish (Aiken 1983; Frazer et al. 1991; Turingan and Wainwright 1993; Turingan 1994; Vose and Nelson 1994; Kurz 1995; Blitch 2000; Durie and Turingan 2001). The importance of reef associated prey species was apparent in the presently observed movement patterns, in that tracked gray triggerfish remained closely associated with available reef habitat (95% of all positions within 18 ± 41 m). Similarly, a previous study also reported that gray triggerfish remained closely associated (36 m) with their VPS reef habitat (Herbig and Szedlmayer 2016). These patterns were consistent with other studies that reported a mean daily dispersal distances of 56 m (Addis et al. 2013) and a mean foraging radius of 20 to 30 m (Frazer et al. 1991; Kurz 1995).

Management implications and conclusions

The present study may have implications for reef fish management in the northern Gulf of Mexico, particularly regarding the use of alternative management strategies such as the deployment of artificial reefs and establishment of marine protected areas (MPA). An important ecological factor to consider when proposing artificial reef or MPA design as a management tool is the site fidelity and movement of associated reef fish (Bohnsack 1989; Bortone 1998; Patterson and Cowan, 2003; Shipp 2003; Addis et al. 2013). It has been hypothesized that fish which show low site fidelity and only partial reef dependence would be less likely to benefit from these alternative management strategies, compared to those with high site fidelity and strong reef dependence (Bohnsack 1989; Ingram and Patterson 2001; Shipp 2003 Addis et al. 2013). In addition, fish that display greater movement may have increased exposure to fishing mortality when moving between areas of lower and higher fishing pressure (Crowder et al. 2000; Ingram and Patterson 2001; Shipp 2003; Kaunda-Arara and Rose 2004).

In the present study, gray triggerfish showed high dependency on artificial reef habitat. They remained closely associated with reef structures throughout their tracking period, displayed seasonal and diel patterns in fine-scale area use and showed homing behavior. Annual site fidelity and mean residency time were lower than previous telemetry and conventional tagging study estimates (Beaumarige 1969; Ingram and Patterson 2001; Addis et al. 2013; Herbig and Szedlmayer 2016). However, the present estimates were specific to the time that fish spent on small, single artificial reef or reef patches within their VPS array area (0.32 km^2) and were affected by increased emigration and tropical storm events. No seasonal storm events occurred during the previous telemetry study (Herbig and Szedlmayer 2016) and conventional tagging studies cannot account for emigrations and returns (Beaumarige 1969; Ingram and Patterson 2001; Addis et al. 2013). In addition, large-scale movements that were documented by surrounding site receivers showed that movements between reef sites were quick and direct (little time over open habitat) and confirmed high association with reef habitats despite frequent emigrations away from VPS sites.

Based on the observed fine-scale and large-scale movement patterns of presently tagged gray triggerfish, it is likely that regional Gulf of Mexico stock would benefit from alternative managements strategies (e.g., artificial reefs, MPAs) in conjunction with traditional management plans (e.g., size limits, bag limits, seasonal closures) if areas are planned and carefully selected. Periodic seasonal storm events may help to export adult biomass away from any protected or alternative management zones, thus contributing to surrounding areas. However, summer storms may also disrupt spawning-related dominance hierarchies and territories, potentially reducing reproductive success and recruitment. Caution is also warranted, in that high association of gray triggerfish to reef structures and frequent large-scale movements among reef patches, may increase their susceptibility to fishing mortality; thus, management should continue to assess the stock to ensure the long-term sustainability of this species.

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Table 2-1: Variation with season (Winter, Spring, Summer, Fall) and VPS reef site (R2, R3, R4, R5 or R6), in the percent time that gray triggerfish (*Balistes capriscus*) resided on each VPS reef site, secondary reefs (2nd), or open habitat within the VPS detection area, based on detections within 59 m of the reefs. Seasons and sites with dashed lines indicate periods when tracking data were not available (R2 and R5) or secondary reef sites were not available (R5 and R6).

Season	R2			R3			R4			R5			R5			R6		
	VPS	2nd	open	VPS	2nd	Open	VPS	2nd	open	VPS	2nd	open	VPS	2nd	open	VPS	2nd	open
Winter	--	--	--	80.3	16.9	2.8	79.2	16.6	4.2	95.3	--	4.7	--	--	--	95.5	--	4.5
Spring	--	--	--	89.1	9	1.9	90.3	8.4	1.3	92.8	--	7.2	75.5	24	0.5	96.8	--	3.2
Summer	99.6	0	0.4	81.8	14.1	4.1	87.6	10.4	2	99.5	--	0.5	75.9	20.4	3.7	84	--	16
Fall	69.8	0	30.2	68.6	26.1	5.3	71.6	22.7	5.7	97.4	--	2.6	--	--	--	96.6	--	3.4
Mean	84.7	0	15.3	80	16.5	3.5	82.2	14.5	3.3	96.2	--	3.8	75.7	22.2	2.1	93.2	--	6.8
SD	21.1	0	21.1	8.5	7.2	1.5	8.5	6.5	2	2.9	--	2.9	0.3	2.5	2.3	6.2	--	6.2

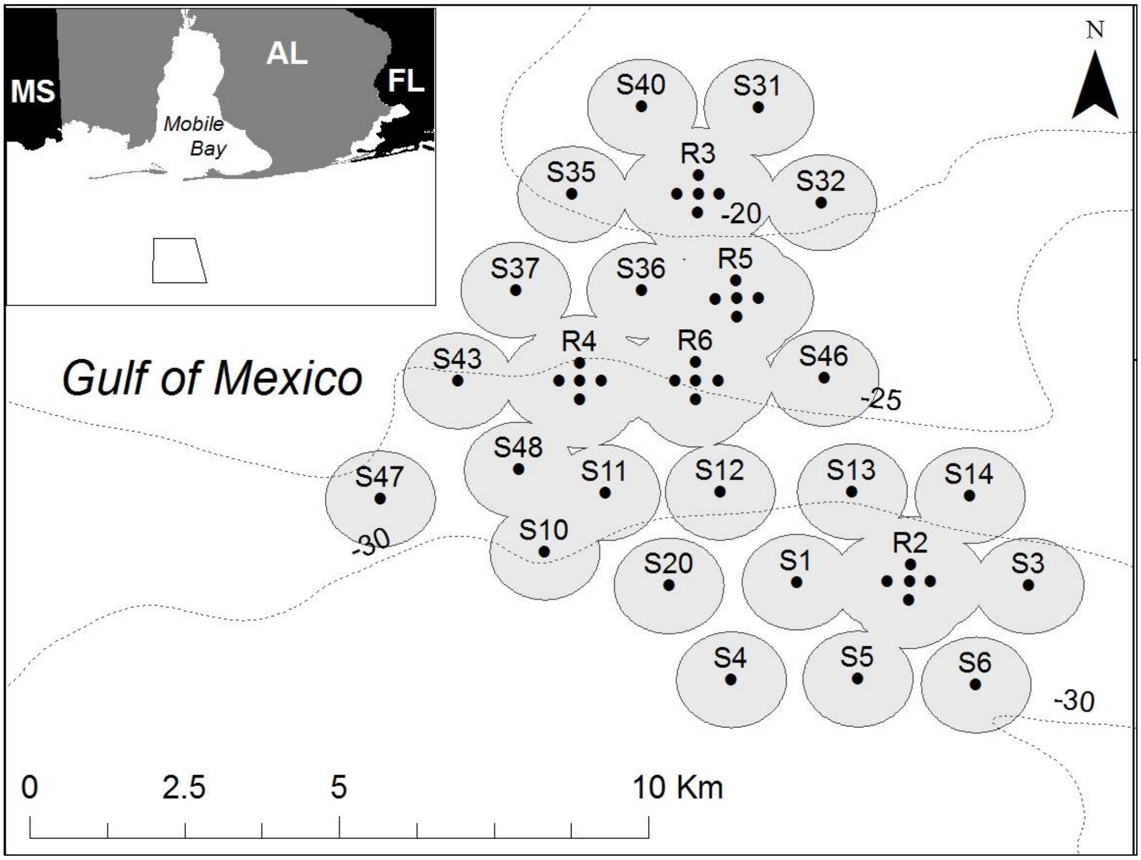


Figure 2-1: Location of receivers (area = 64 km^2) used to track movement patterns of gray triggerfish (*Balistes capriscus*). The map insert shows the Hugh Swingle General Permit Area (black polygon). Black dots represent receiver positions, VPS sites are R2, R3, R4, R5 and R6, and S1 to S48 are surrounding reef site single receivers. Gray shaded circles are receiver detection areas. Wavy lines represent depth contours in meters.

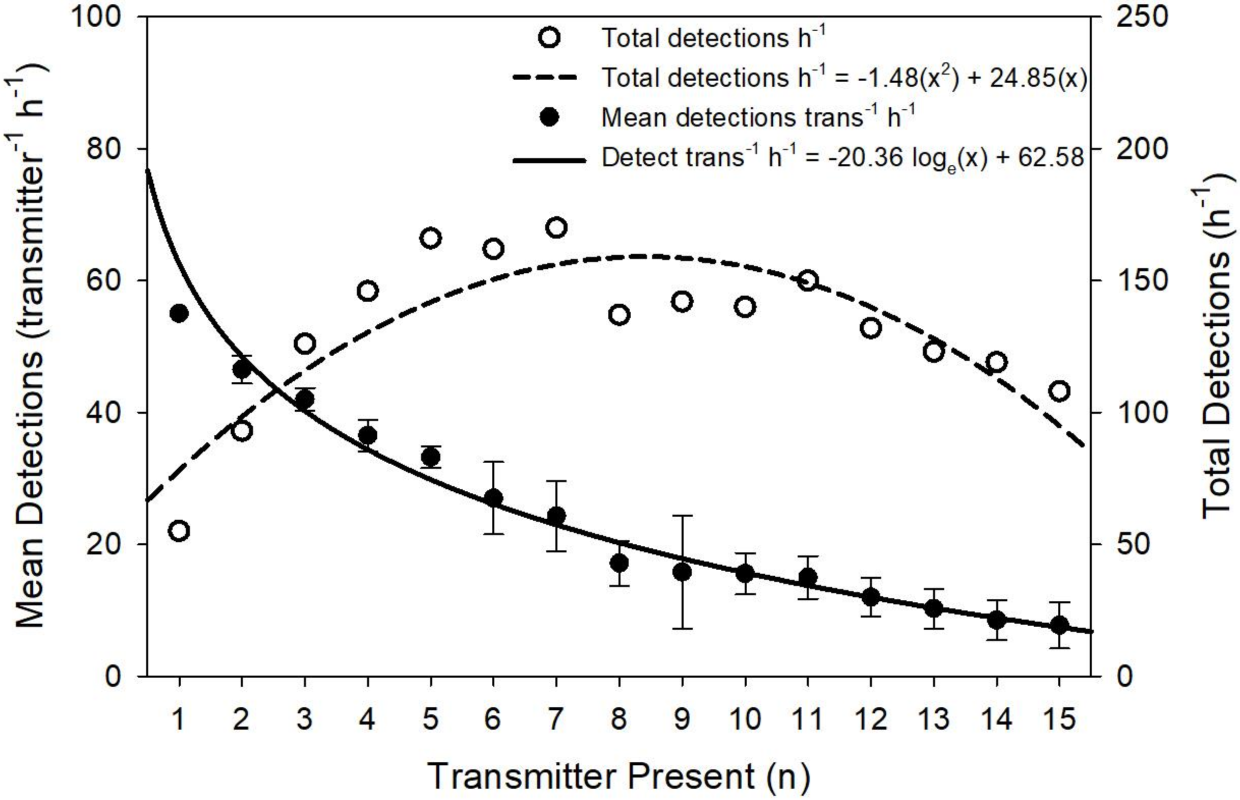


Figure 2-2: Comparison of mean detections per transmitter per hour (± SD) to number of transmitters present and the logarithmic negative relation (solid line; $r^2 = 0.93$, $P < 0.001$). Comparison of total detections per hour to transmitter number showed a quadratic relation (dotted line; $r^2 = 0.87$, $P = 0.0002$).

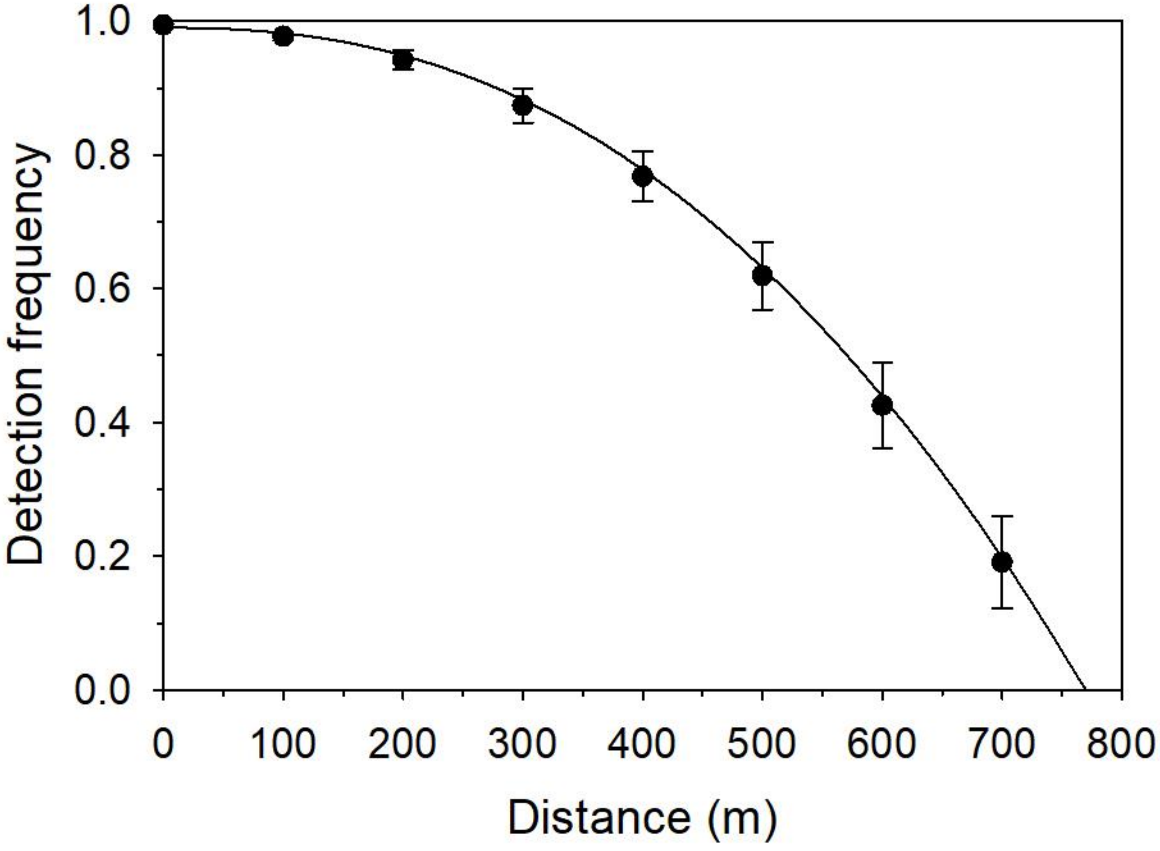
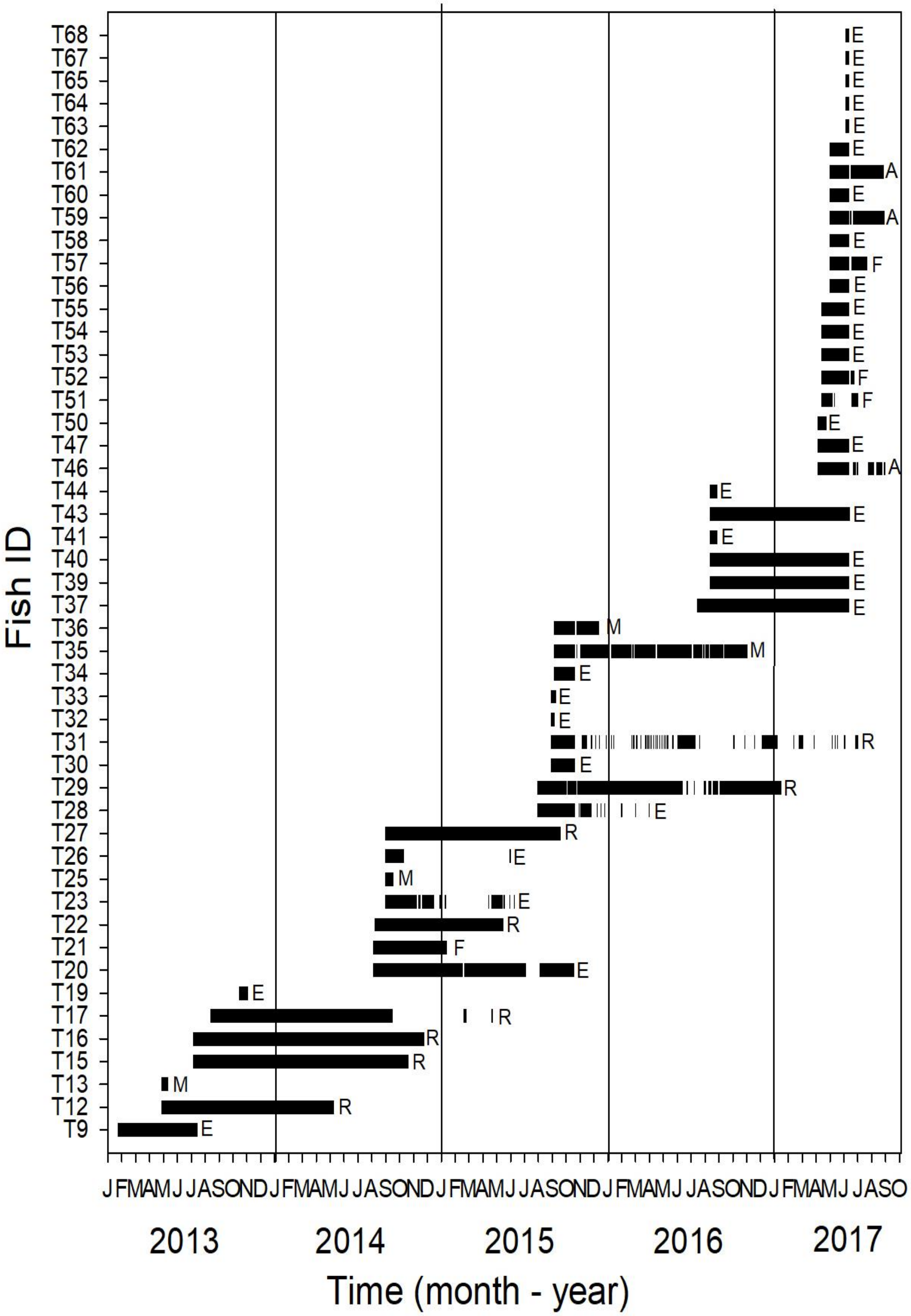


Figure 2-3: Comparison of transmitter (Vemco; V13-1L) detection frequency (mean + SD) to distance from receiver.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2013
2014
2015
2016
2017
Time (month - year)

Figure 2-4: Time periods of detections for transmitter tagged (*n* = 49) gray triggerfish (*Balistes capriscus*) at artificial reef sites, for all fish tracked > 3 d. Black bars = active on VPS site. Letters denote final fate of fish on VPS sites: E = emigration, F = caught, M = natural mortality, R = resident with a dead battery, and A= active as of end of study 5 September 2017.

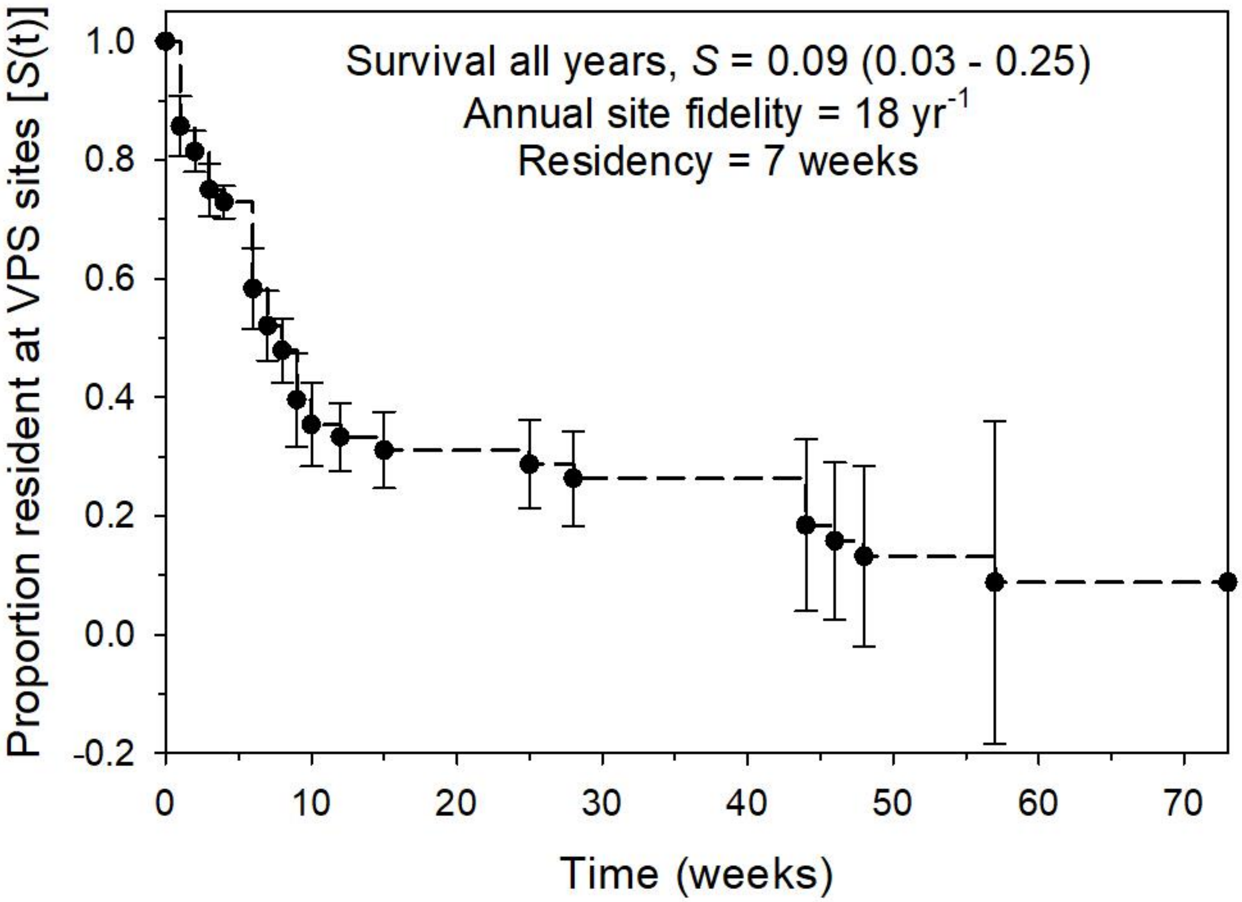

Figure 2-5: Survival (*S*) of gray triggerfish (*Balistes capriscus*) at artificial reef sites. Dashed line shows proportion of fish that remained resident after each weekly interval. Points and standard error bars were conditional estimates of *S* for time interval at each emigration or mortality event.

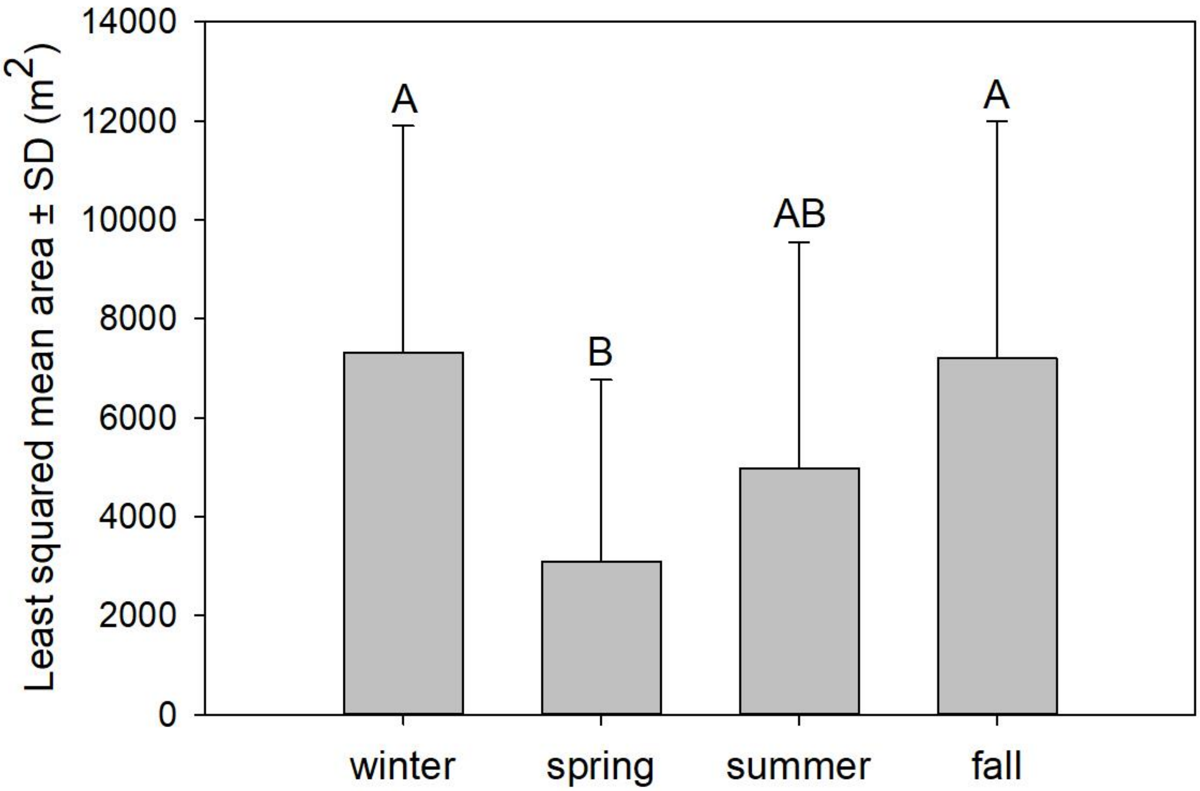

Figure 2-6: Variation in area use of tagged gray triggerfish (*Balistes capriscus*) with season on artificial reefs in the northern Gulf of Mexico. Gray bars indicate home range area (95% KDE) Letters above bars denote significant differences among seasons ($P \leq 0.05$).

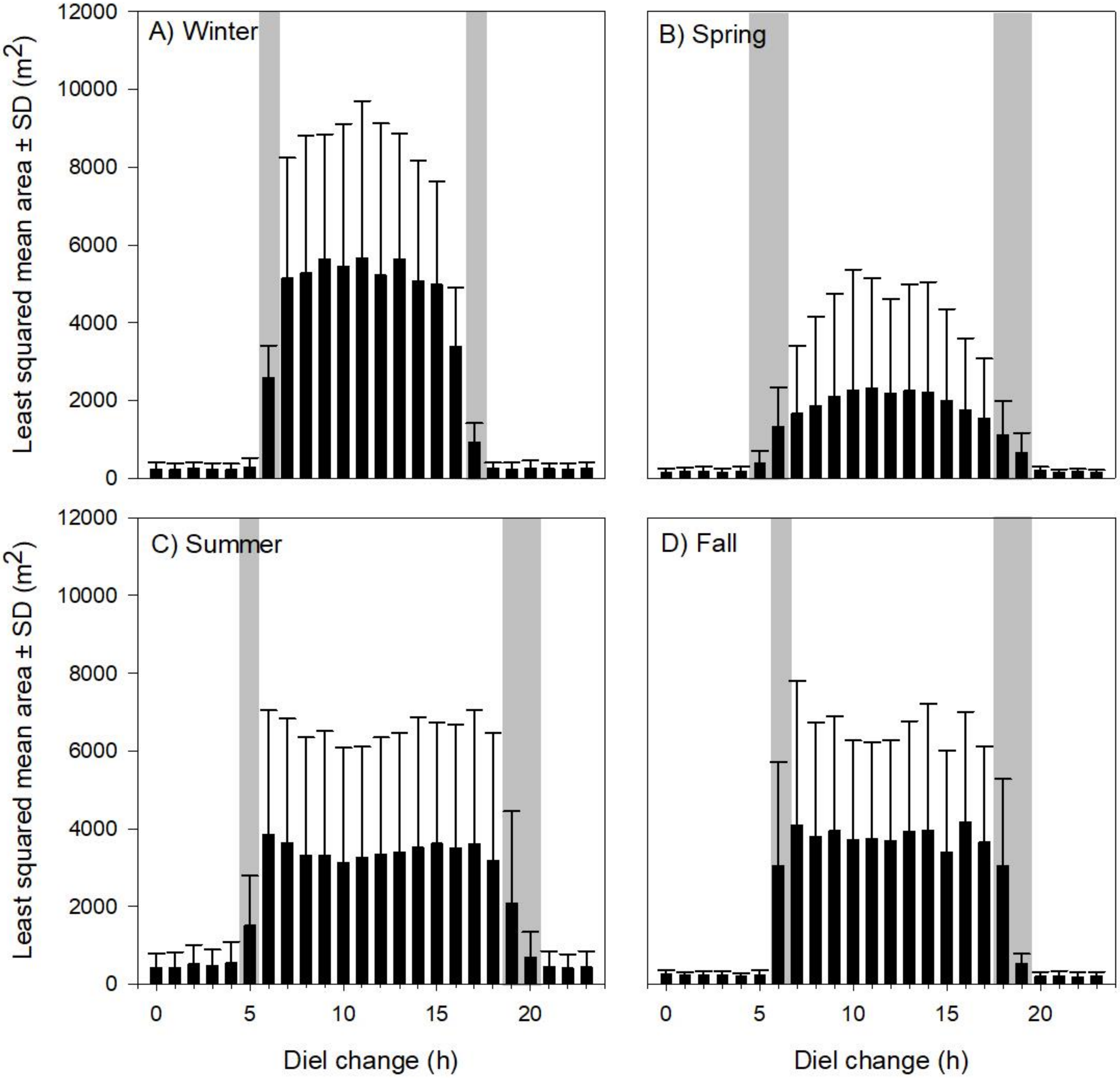

Figure 2-7: Variation in diel patterns of gray triggerfish (*Balistes capriscus*) area use (95% KDE; black bars) with season. Gray bars indicate crepuscular periods around sunrise and sunset.

Chapter 3:

Vertical movement and volume use estimates in gray triggerfish (*Balistes capriscus*) on artificial reefs in the northern Gulf of Mexico

Abstract

The present study examined fine-scale vertical movement and volume use patterns of gray triggerfish (*Balistes capriscus*) on artificial reefs in the northern Gulf of Mexico. Tagged fish (n = 18) were monitored for up to 308 d from 18 August 2016 through 5 September 2017 with the Vemco Positioning System (VPS). Depth preferences and home range volumes (95% kernel density estimate; KDE) were compared over hourly and monthly time periods, and to temperature and dissolved oxygen (DO). Mean vertical distance above the seafloor and home range volume varied significantly by month, and with changes in temperature and DO. Gray triggerfish were closest to the seafloor from November through March, with a minimum mean distance from seafloor observed in January, and higher up in the water column from April through October, with the highest mean maximum distance from the seafloor observed in April and June. Gray triggerfish used the smallest volumes during winter and spring from December through May with a minimum in January and the largest volumes during the summer from June through August with a maximum in August. Fish were significantly

higher up in the water column and used larger volumes when temperatures were higher and when DO was lower. These seasonal vertical movements and volume use patterns were likely related to foraging and spawning behaviors. Gray triggerfish made fewer movements and remained significantly closer to the seafloor at night (2000 to 2300 and 0000 to 0500) than during the day (0700 to 1700), transitioning during crepuscular periods based on depth and home range volume. These diel patterns were consistent with previous horizontal movement patterns and were likely driven by foraging, resting and predator avoidance, while seasonal patterns were not consistent with previously reported horizontal movements. Thus, to fully understand marine fish habitat use, studies need to examine movement patterns in all dimensions. In addition, vertical movements may have contributed to lack of stock recovery in gray triggerfish as fish moved off the seafloor away from benthic nests, when periods of low DO concentrations coincided with their spawning season.

Introduction

Advances in acoustic telemetry techniques have provided increasingly improved methods to study the behavior and ecology of marine organisms at varying temporal and spatial scales (Huessey et al. 2015). Telemetry can be used to define a species home range or core areas of use (Piraino and Szedlmayer 2014; Herbig and Szedlmayer 2016; Williams-Gove and Szedlmayer 2016a), document depth preferences (McKinzie et al. 2014; Williams-Grove and Szedlmayer 2017) and residency times (Topping and

Szedlmayer 2011; Williams-Grove and Szedlmayer 2016). These methods can help define fish movement patterns over time (Pittman and McAlpine 2003) or in relation to environmental parameters (Avgar et al. 2013; Bestley et al. 2013; Dudgeon et al. 2013; Udyawer et al. 2015). Movement studies have also been used to assess interactions with conspecifics (Jacoby et al. 2012; Stehfest et al. 2013), spawning behaviors (McKinzie et al. 2014; Lee et al. 2017), foraging strategies (Priede et al. 1990; Weimerskirch et al. 1993; Harcourt et al. 2002, 2007; Bestley et al. 2015; Berejikian et al. 2016) and territoriality (Parson et al. 2003; Righton and Mills 2006; Pastor et al. 2009).

Most telemetry studies restrict analysis of habitat use and behavior to either horizontal or vertical movement even though fish live in a three-dimensional (3D) habitat and must employ 3D movements to fully exploit the resources of their environment. To date, comparatively few fish telemetry studies have examined movement patterns in three dimensions. For example, 3D movements have been used to study coastal habitat use by the European eel (*Anguilla Anguilla*; Simpfendorfer et al. 2012), spawning versus non-spawning behaviors of barred sand bass (*Paralabrax nebulifer*; McKinzie et al. 2014), artificial reef use by red snapper (*Lutjanus campechanus* (Williams-Grove and Szedlmayer 2017), long-term movements patterns of grey reef sharks (*Carcharhinus amblyrhynchos*; Heupel and Simpendorfer 2014, 2015) and the effects of sex on seasonal movements of eastern blue groper (*Achoerodus viridis*; Lee et al. 2017).

Gray triggerfish (*Balistes capriscus*) is an economically important species that support sport and commercial fisheries in the Gulf of Mexico (SEDAR 43 2015). In recent years, gray triggerfish importance to fishers has grown as catch restrictions on other reef fish such as red snapper have increased (Valle et al. 2001; SEDAR 31 2013;

Harper and McClellan 2014; SEDAR 43 2015). Despite their heightened value and new management strategies (Amendment 46 2017), few studies have examined their movement patterns and many life history parameters remain unclear. Conventional mark-recapture indicates that gray triggerfish display limited horizontal movements and high site fidelity to reef structures (Beaumariage 1969; Ingram and Patterson 2001; Addis et al. 2013). However, estimates of annual site fidelity from conventional tag returns have been variable and ranged from 37 to 67% year^{-1} (Beaumariage 1969; Ingram and Patterson 2001; Addis et al. 2013). Most tagged fish were recaptured within 10 km of their tagging site (Ingram and Patterson 2001), but one study reported greater movements of up to 60 km (Addis et al. 2013).

Similarly, previous telemetry studies report wide ranging site fidelity and residency periods. For example, Herbig and Szedlmayer (2016) observed high annual site fidelity (64%) and high residency (> 57 weeks), while McKinzie (2018; Chapter 2) observed lower site fidelity (18% year^{-1}) and residency (7 weeks). Differences between the two studies were attributed to the occurrence of major tropical storms and increased emigration frequency (Chapter 2). Both telemetry studies indicated increased daytime area use and decreased movements at night, however seasonal patterns differed. In Herbig and Szedlmayer (2016) temperature was a significant predictor of seasonal movements with larger area use during late summer and fall compared to winter and spring. In contrast, McKinzie (2018; Chapter 2) observed the largest area use in fall and winter and the smallest area use in spring, but temperature was still a significant predictor of seasonal movement patterns.

There are few previous studies on the vertical or three-dimensional movement patterns of Balistids, but SCUBA diver and video surveys have provided limited information (Hobson 1965; Fricke 1980; Caveriviere 1982; Kavanagh and Olney 2006). The redtoothed triggerfish (*Odonus niger*) has been described as free-water living, but substrate bonded by hiding and sleeping holes. Throughout the day, redtoothed triggerfish were observed congregating in open-water about 2 m above the substratum, moving to nearby sleeping holes 30 min after sunset, and then moving out of their holes the following morning an hour before sunrise (Fricke 1980). The fine-scale triggerfish (*Balistes polylepis*), the orangeside triggerfish (*Sufflamen verres*) and the black triggerfish (*Melichthys niger*) have also been observed retiring to sleeping holes at night (Hobson 1965; Kavanagh and Olney 2006).

The objectives of the present study were to use the Vemco Positioning System (VPS) to document fine-scale vertical and three-dimensional movement patterns of gray triggerfish that were captured and released on artificial reefs in the northern Gulf of Mexico. Movement and behavior patterns were compared to fish size (mm fork length, FL), temperature and dissolved oxygen, over diel and monthly periods. The present study provides new ecological information about the habitat use patterns of gray triggerfish and their relations to artificial reefs in the northern Gulf of Mexico.

Methods

Study site and array design

The study area was located 23 – 35 km south of Dauphin Island, Alabama, USA, within the Hugh Swingle General Permit Area, in the northeastern Gulf of Mexico. Tagging sites consisted of three steel cage artificial reefs (2.5 x 1.3 x 2.4 m), spaced 1.5 – 3.0 km apart, at depths of 18.9 m (R3), 22.9 m (R5) and 26.5 m (R4; Fig. 3-1). A Vemco VPS array was deployed at each of the three tagging sites to monitor fine-scale movement patterns of transmitter-tagged gray triggerfish. Each VPS site consisted of five Vemco VR2W acoustic receivers moored 4.5 m above the seafloor. A center receiver was placed 10 – 20 m north of the reef site, with four additional receivers placed 300 m north, south, east and west of the center receiver. Synchronization transmitters (sync tags; Vemco V16-6x, 69 kHz, transmission delay: 540 – 720 s; $n = 3$) were attached 1 m above each receiver to standardize the internal receiver clocks (Piraino and Szedlmayer 2014). The VPS array design permitted high detection efficiency of transmitter-tagged gray triggerfish (≥ 88%; Chapter 2). Each of the VPS array receivers were exchanged and downloaded every 4 to 6 months. Data from the VPS receivers were sent to Vemco for post-processing and determination of fish positions (Vemco, Ltd., Nova Scotia). A stationary control transmitter (V13P-1L, 69 kHz, transmission delay: 40 – 80 sec) was placed at a known location within each of the VPS arrays, to validate the accuracy of Vemco derived positions and to confirm continuous transmitter detections during the study.

An additional array of single VR2W acoustic receivers (*n* = 23) were placed 1.4 – 1.6 km apart, around each VPS site, to help document emigrations away from the VPS arrays (Fig. 3-1). Each of these single receivers were also associated with a steel cage artificial reef. The single receivers were exchanged and downloaded every 6 to 12 months. Within this surrounding large scale receiver array, the detection coverage area was 82% of the total area (53 km^2), leaving 18% (~11 km^2) of the array area with little to no coverage. These areas of low detection potential were narrow paths approximately 100 – 300 m wide between single receiver coverage areas (Chapter 2). All receivers and mooring floats were coated with a copper-based antifouling paint to reduce the potential of signal detection loss due to biofouling (Topping and Szedlmayer 2011). All artificial reefs were deployed at unpublished locations from 2006 – 2010 and encompassed a 64 km^2 area (Syc and Szedlmayer 2012).

Fish tagging and cage-release method

Gray triggerfish (*n* = 18) were tagged and released from 18 August 2016 to 16 June 2017, and movements monitored until 5 September 2017 (Table 3-1). No more than 10 transmitters were active at individual VPS sites at the same time. These active transmitters included tagged red snapper (not part of the present study, Mudrak and Szedlmayer In Review) and control transmitters, in addition to presently tagged gray triggerfish. The 10-transmitter limit reduced the potential for data loss due to signal collision (Topping and Szedlmayer 2011; Piraino and Szedlmayer 2014; Chapter 2). Prior to tagging, dissolved oxygen concentration (DO) and temperature were measured throughout the water column (YSI Model 6920, YSI Inc., Yellow Springs, Ohio). Fish were tagged and released only if DO levels were > 2.5 mg l^{-1}. If water temperatures at the surface exceeded 27 °C, ice was added to the holding tanks during anesthetization and recovery to reduce high temperature stress.

Gray triggerfish were captured with hook-and-line baited with squid (*Loligo* or *Lolliguncula* spp.) at each VPS site (n = 3; Fig. 3-1). After capture, adult fish ≥ 250 mm fork length (FL) were anesthetized in a 70-l container with 150 mg MS-222 l^{-1} seawater (tricaine methanesulfonate; Munday and Wilson 1997; Cho and Heath 2000) for 80 sec to level four (Summerfelt and Smith 1990). After sedation, fish were weighed (nearest 0.1 kg) and measured (mm SL, FL and TL). An acoustic transmitter (Vemco, V13P-1L, 69 kHz, transmission delay 40 to 80 s, battery life 566 d) was surgically implanted within the peritoneal cavity through a 1 to 2 cm vertical incision on the ventral left side. The incision was closed with 2 to 3 discontinuous, dissolvable sutures (Ethicon Inc., Chromic Gut). Betadine was spread over the incision to reduce the risk of infection. Fish were also injected with oxytetracycline (OTC). Fish were then tagged with an external anchor tag (Floy® FM-95W) inserted 1 to 2 cm posterior to the incision, with a unique identification number, contact information and reward notice for later identification by fishers or SCUBA divers (Herbig and Szedlmayer 2016).

After tagging, fish were transferred to a 185-l recovery tank with aerated seawater. During the recovery period, fish were monitored for increased opercular pumping, control of body orientation and resumption of normal swimming motion. Recovered fish then were placed into a weighted rectangular cage (46 x 61 x 61 cm, 13-gauge vinyl coated wire) and lowered to the seafloor (19 – 27 m) within 10 m of the capture site. Once the cage reached the seafloor, a door automatically opened, allowing the tagged fish to leave on its own initiative (Williams et al. 2015). Any tagged fish that did not leave the cage after 20 min on the seafloor were not released.

Environmental monitoring

A YSI EX02 environmental recorder (YSI Inc., Yellow Spring, Ohio) was deployed 3 m above the seafloor 38 m north of the R4 VPS site to continuously monitor temperature, salinity, dissolved oxygen (DO) and turbidity from 18 August 2016 through 7 December 2016. A HOBO temperature and DO data logger (Onset HOBO® U26-001) also was attached to the R4 center receiver mooring line, 0.5 m above the seafloor from 7 December 2016 through 5 September 2017. At each VPS site ($n = 3$), two HOBO temperature loggers (Onset HOBO® U22 Water Temp Pro v2) were also attached to the receiver mooring line, with one at the seafloor and one just below the receiver (4 m above seafloor) throughout the study (18 August 2016 through 5 September 2017). Temperature and DO data loggers recorded environmental parameters at 1-hour intervals and were downloaded every 4 to 6 months.

Depth preferences

Depth data were downloaded from each of the five VR2W VPS receivers and exported from the VUE software (Vemco Ltd., Nova Scotia). To analyze patterns in vertical movement, depth data were filtered to remove negative depths and values deeper than actual seafloor depth. Depth data were then converted to distance from seafloor (m) by subtracting the fish depth from the seafloor depth to account for different bottom depths (18.9 – 26.5 m) among study sites (McKinzie et al. 2014). Fish depths were compared over hourly and monthly time periods with a one-way, mixed model repeated measure analysis of variance (rmANOVA) with individual fish depths measured repeatedly over time. Fish depths were compared to environmental measures using rmANOVA, with temperature and DO as continuous predictor variables. A Tukey-Kramer test was used to show specific differences after significant differences were detected with rmANOVA. Fish depths were compared to fish size (FL) using a linear regression (Zar 2010). All fish depths were reported as mean ± standard deviation (SD). Times of sunrise and sunset were determined from the US Naval Observatory website (http://aa.usno.navy.mil/data/docs/RS_OneYear.php).

Three-dimensional kernel density estimates

Volume kernel density estimates (KDE) were based on horizontal and vertical movement data obtained from Vemco post-processing. Prior to volume KDE estimates, all positional data (latitude and longitude) were converted to Universal Transverse Mercator (UTM) projections. Volume KDEs were calculated in R with the *ks* package (Duong 2007). Home range (95% KDE) volume was estimated by determining the number of voxels contained within the 95% probability contour and multiplying it by the volume of each voxel (Simpfendorfer et al. 2012; McKinzie et al. 2014; Williams-Grove and Szedlmayer 2017). Home range volume was compared among time-periods (hour and month) using a one-way mixed-model repeated measures analysis of variance (rmANOVA), with individual fish volumes measured repeatedly over time. A Tukey-Kramer test was used to show specific differences, after significant differences were detected with rmANOVA. Fish volumes were compared to environmental measures by employing rmANOVA, with temperature and DO as continuous predictor variables. Fish monthly volumes were compared to fish size (FL) with a linear regression (Zar 2010). Fish volume (95% KDE) was reported as least square mean ± standard deviation (SD). All statistical analyses were completed with the statistical analysis software SAS (SAS Institute Inc., Cary, North Carolina).

Results

Tagging and fish status

All tagged gray triggerfish (*n* = 18) were > 250 mm FL, which is the estimated size of 100% sexual maturity for both males and females (Fitzhugh et al. 2015). Fish mean size ± SD was 399 ± 55 mm FL and ranged from 333 to 528 mm FL. One fish (6%; T45) permanently left its VPS site 2 d after release, was detected (< 1 d later) at an outside reef site (S46), then left the large-scale receiver array and was removed from all statistical analysis. Fine-scale vertical and volume use patterns of the remaining gray triggerfish (*n* = 17; 94%) were monitored for 4 to 308 d over the 383 d study period, from 18 August 2016 through 5 September 2017 (Table 3-1). Among these tagged and tracked gray triggerfish, 12 fish had a final event status that was an emigration, three were caught by fishers and two fish were still active at the end of the study (Fig. 3-2; for further information of residency and site fidelity, see Chapter 2; for mortality, see Chapter 4).

Depth preferences

Depth positions (n = 969,516) were determined for 17 gray triggerfish over the 383 d study period. Based on depth determinations from the stationary control transmitters within each VPS site, depths were accurate to 1.5 ± 2.1 m. Gray triggerfish were positioned at a mean depth ± SD of 4.2 ± 4.2 m from the seafloor. Fish occurred over most of the water column, from the seafloor at 18.9 to 26.5 m depth, up to within 3.1 ± 1.3 m from the sea surface. Fish were significantly closer to the seafloor during late fall through the early spring months, with the mean (± SD) distance from the seafloor during November through March at 1.9 ± 0.9 m (minimum = 1.2 ± 0.5 m, in January 2017). Fish were significantly higher up in the water column during late spring through early fall, with a distance from the seafloor for April through October of 4.8 ± 1.9 m (maximum = 5.6 ± 1.7 m in April 2017 and 5.8 ± 2.9 m in June 2017; $F_{[13,42.2]} = 13.8$, $P < 0.0001$). Fish were significantly closer to the seafloor when temperatures were lower ($F_{[1,53]} = 4.7$, $P = 0.03$, $r^2 = 0.19$, Fig. 3-3), and significantly higher up when bottom water dissolved oxygen (DO) concentration was lower ($F_{[1,53]} = 35.6$, $P < 0.0001$, $r^2 = 0.47$, Fig. 3-4). No fish length effects were detected ($F_{[1,67]} = 0.07$, $P = 0.80$, $r^2 < 0.01$).

Gray triggerfish showed distinct diel patterns of vertical movement and behavior ($F_{[23,1582]} = 32.8$, $P < 0.0001$). Fish remained significantly closer to the seafloor at night (mean ± SD = 2.1 ± 1.9 m distance from the seafloor, during 2000 to 2300 and 0100 to 0400 h) than during the day (5.6 ± 2.9 m, during 0700 to 1700 h) and were observed at intermediate depths (3.6 ± 2.7 m distance from the seafloor) during both dawn (0500 to 0600 h) and dusk (1800 to 1900 h). The time of day that gray triggerfish changed from more benthic-oriented movements to a wider range of vertical movements coincided with the seasonal time change of sunrise and sunset. Although gray triggerfish were closer to the seafloor in the winter, diel patterns were consistent over all seasons, with fish higher up during the day compared to at night and transitioning during the crepuscular periods (Fig. 3-5).

Three-dimensional kernel density estimations

The present study analyzed 100,840 VPS derived positions (latitude, longitude and depth) to estimate diel and monthly patterns in volume use. Control stationary transmitters showed that these derived positions had a mean horizontal accuracy of 3.1 ± 1.5 m and a vertical (depth) positional accuracy of 1.4 ± 2.0 m. Home range volume was not affected by fish size ($F_{[1,64]} = 0.56$, $P = 0.46$, $r^2 < 0.01$), but varied significantly by month ($F_{[13,41.8]} = 2.3$, $P = 0.02$, Fig. 3-6). Home range volume was smallest during the winter and spring from December through May (mean ± SD = 48,650 ± 53,195 m^3, minimum = 22,569 ± 614 m^3 in January 2017) and largest during the summer from June through August (mean = 148,991 ± 161,961 m^3, maximum = 186,535 ± 36,097 m^3 in August 2017), with intermediate volume use observed during the Fall from September through November (mean = 113,513 ± 49,457). Monthly home range volumes increased with higher bottom water temperature ($F_{[1,50]} = 4.8$, $P = 0.03$, $r^2 = 0.37$, Fig. 3-7) and lower bottom water DO ($F_{[1,50]} = 8.7$, $P = 0.005$, $r^2 = 0.41$, Fig. 3-8).

Significant diel changes were detected in gray triggerfish volume use ($F_{[23,1244]} = 11.9$, $P < 0.0001$, Fig. 3-9). Gray triggerfish showed less movement and activity at night, from 2000 to 2300 and 0000 to 0500 (mean ± SD = 2,116 ± 7,624 m^3) and larger movement and activity during the day, from 0700 to 1700 h (73,000 ± 105,916 m^3), with transition values during crepuscular periods (0600 and 1800 – 1900 h; 31,803 ± 78,574 m^3).

Discussion

Seasonal depth preferences

The present study examined annual depth preferences in gray triggerfish and showed significant vertical differences across months. Tracked fish were closer to the seafloor from November through March and were higher up in the water column from April through October. Vertical patterns varied significantly with abiotic factors (temperature and DO). Previous studies have indicated that seasonal (April through October) hypoxia events in the northern Gulf of Mexico correlate with changes in fish movement and behavior, with fish leaving hypoxic areas either vertically or horizontally (Kramer 1987; Chesney et al. 2000; Huenenmann et al. 2012; Szedlmayer and Mudrak 2014; Everett 2018). In the present study, periods of low (2 – 3 mg l^{-1}), hypoxic (1 – 2 mg l^{-1}) and anoxic (< 1 mg l^{-1}) conditions were observed during summer and early fall over three separate time intervals: 19 – 27 August 2016, 30 September to 4 October 2016 and 27 June to 31 August 2017 (21% of tracking days). During these periods of low (< 3 mg l^{-1}) bottom water DO, gray triggerfish were significantly higher up in the water column. A recent telemetry study on red snapper vertical movement also observed fish moving off the seafloor and away from artificial reef structures during periods of low bottom DO (Williams-Grove and Szedlmayer 2017).

Low summer DO may contribute to the slower than expected recovery of the Gulf of Mexico gray triggerfish stock, despite increased fishing restrictions and reduced effort in recent years (SEDAR 43 2015; Amendment 46 2017). The 2017 stock assessment indicated that the present population size and spawning stock biomass were near an historic low and the stock was showing signs of depensation (i.e., recruitment was below what was predicted by its Beverton-Holt stock recruitment curve; Amendment 46 2017). Spawning in gray triggerfish begins in May, peaks in June, and ends by late July and August (Dooley 1972; Wilson et al. 1995; Lang and Fitzhugh 2015), and has been observed when dissolved oxygen levels were 4.8 to 6.8 mg l^{-1} (Simmons and Szedlmayer 2012). Only 20% of the 2017 spawning season (1 May – 31 August) had mean daily DO concentrations > 4.8 mg l^{-1}. If low bottom DO was forcing individuals away from the seafloor for extended periods of time, as present vertical movement patterns suggest, summer spawning frequency and egg survival may have been affected. Gray triggerfish are benthic, multiple batch spawners that have elaborate courtship and mating displays, territoriality, nest building, harem spawning and bi-parental care of eggs (Simmons and Szedlmayer 2012). In addition, periodic seasonal storm events have been shown to increase emigration rates and reduce residency (Ingram and Patterson 2001; Addis et al. 2013; Chapter 2). If summer spawning hierarchies and territories were also disrupted by tropical storms, further reduction of reproductive success and recruitment might be expected (Chapter 2).

Spawning behavior may also contribute to vertical movement patterns, as gray triggerfish are benthic spawners and show elaborate courtship and aggressive territoriality (Simmons and Szedlmayer 2012). In the late spring, it is possible that gray triggerfish go through pre-spawning lekking behaviors that may increase their range of vertical positions. For example, dominance hierarchies and territories were just becoming established and gray triggerfish were showing higher vertical movements as male fish aggressively chased other males up into the water column (Simmons and Szedlmayer 2012; Simmons and Szedlmayer 2018). As the season progressed and territories became well established, chasing behavior decreased and the mean height of vertical positions decreased in July. Lek-like spawning behaviors have also been observed in the yellowmargin triggerfish (*P. flavmarginatus*) and the crosshatch triggerfish (*X. mento*; Gladstone 1994; Kawase 2003).

Another potential biotic factor that could influence vertical movement patterns of gray triggerfish is prey availability. Gray triggerfish are opportunistic feeders that are highly adaptable due to their fusiform shape and independently undulating paired and medial fins, combined with a strong oral-jaw apparatus and dentition (Turingan and Wainwright 1993; Turingan 1994). This may promote feeding plasticity and allow individuals to take advantage of a range of prey sources consumed by few other reef dwelling fish (i.e., hard shelled invertebrates) as well as seasonally available pelagic prey sources (Frazer et al. 1991; Turingan and Wainwright 1993; Turingan 1994; Vose and Nelson 1994; Kurz 1995; Blitch 2000). One study reported that pelagic mollusks and crustacean larvae were the most important prey items in gray triggerfish diets, followed by decapod crustaceans (Blitch 2000). In addition, gray triggerfish are known to switch between prey sources due to changes in the relative abundance of prey organisms across time and space (Frazer et al. 1991; Vose and Nelson 1994; Kurz 1995; Durie and Turingan 2001). Queen triggerfish (*Balistes vetula*) also showed prey-switching during time periods when their primary prey item (*Diadema antillarum*) was absent from reef habitats (Reinthal et al. 1984). It is also possible that increased metabolic rates in warmer months may increase foraging activity, while decreased temperatures in cooler months may reduce foraging activity (Helfman 1986; Hidalgo et al. 1987; Johnston and Dunn 1987; Avgar et al. 2013; Williams-Grove and Szedlmayer 2017). At the time of the present study, there were no reports on the seasonality of pelagic invertebrates on the continental shelf in the northern Gulf of Mexico (Bjorndal 2011), but it might be expected that seasonal differences would occur. Thus, it is likely that gray triggerfish move up into the water column in part to take advantage of increased pelagic prey during the warmer months, in addition to potentially being impacted directly by low DO near the bottom at those times.

Seasonal volume use patterns

Similar to vertical patterns, gray triggerfish showed the greatest volume use from June through August when mean bottom water temperatures were higher and the smallest volume use from December through May when mean bottom water temperatures were lower. Volume use also increased as DO decreased, so fish may have moved up and down in the water column to escape hypoxic conditions, or as an indirect response to their prey or other related factors being affected by DO, as indicated by their vertical movement patterns. Consistent with the present study, European eels from Norwegian coastal waters and red snapper off Alabama both showed increased volume use in summer and decreased volume use in winter, corresponding to seasonal changes in water temperature (Simpfendorfer et al. 2012; Williams-Grove et al. 2017). As discussed for vertical patterns, it is likely that spawning behavior and feeding activity were contributing factors to volume use patterns. There was one important difference, in that vertical positions were highest in April, but volumes were lowest in April and May. This again might be related to male spawning behaviors, as territories are still being established in the spring. For example, subordinate males repeatedly returned to reef sites and had reduced horizontal movements and reduced volume, until they finally gave up and moved away as spawning groups became established in June (Simmons and Szedlmayer 2012; Simmons and Szedlmayer 2018). Increased volume use during the spawning seasons has also been documented in barred sand bass, red snapper, eastern blue gropers, European eels and gray reef sharks (Heupel and Simpfendorfer 2014; 2015; McKinzie et al. 2014; Lee et al. 2017; Williams-Grove and Szedlmayer 2017).

Diel patterns of movement

Gray triggerfish were higher up in the water column and showed greater volume use during the day and were closer to the seafloor with smaller volume use at night. Changes in depth preferences and volume use were consistent with previous horizontal movement studies, where gray triggerfish used larger areas and were farther from the reef during the day and used smaller areas and were closer to the reef at night (Herbig and Szedlmayer 2016; Chapter 2). Both vertical and horizontal diel movement patterns and volume use were linked to dawn and dusk time periods that shifted seasonally with changes in daylight hours (Herbig and Szedlmayer 2016; Chapter 2). Other Balistids also showed similar patterns of diel movement. For example, black triggerfish, fine-scale triggerfish, orangeside triggerfish and redthoothed triggerfish all congregate in open water during the day, show reduced movement at night when they rest in holes and crevasses and transition between these two areas during crepuscular periods (Hobson 1965; Fricke 1980; Kavanagh and Olney 2006).

Diel patterns of activity are common for many reef-associated species, and the use of different habitats during different times of day may help to fulfill biological and ecological needs such as foraging, predator avoidance and resting (Willis et al. 2006; Fox and Bellwood 2011; McKinzie et al. 2014; Currey et al. 2015; Herbig and Szedlmayer 2016; Lee et al. 2017; Williams-Grove and Szedlmayer 2016, 2017). For nocturnal species, foraging typically occurs during crepuscular and nighttime periods, while daylight hours are spent resting or patrolling (Hobson 1972, 1975; Helfman 1986). For example, the redthroat emperor, a nocturnal predator, uses significantly larger areas during dawn, dusk and night compared to during the day (Currey et al. 2015). Reef-associated Caribbean reef shark (*Carcharhinus perezi*) and whitetip reef shark (*Triaenodon obesus*) tagged with depth transmitters have also been shown to increase their movement and use shallower depths at night, which indicates nocturnal foraging tactics (Chapman et al. 2007; Whitney et al. 2007; Fitzpatrick et al. 2011). In contrast, diurnally active species typically leave night-time refuges at dawn to forage and return at sunset to rest (Helfman 1986; Howard et al. 2013; McKinzie et al. 2014; Herbig and Szedlmayer 2016; Lee et al. 2017). For example, eastern blue groper movement patterns show a clear increase in volume use during the day when individuals are foraging, with decreased volumes and acoustic detections at night suggesting refuge behaviors (Lee et al. 2017). Similarly, barred sand bass, a diurnal predator that rests over sand habitat along ecotone edges at night has increased vertical movement and volume use during the day, with decreased movement and volume use at night during both spawning and non-spawning seasons (McKinzie et al. 2014). The presently observed diel patterns of gray triggerfish vertical movement and volume use were similar to other reef-associated diurnally active species. Therefore, the significantly reduced nighttime movement and close association with reef habitat indicated resting or refuge behavior, while increased daytime movements were likely related to foraging. Diver surveys have also observed that gray triggerfish forage away from reef structures only during the day, which has been further supported by stomach content analyses (Frazer and Lindberg 1994; Vose and Nelson 1994; Kurz 1995; Blitch 2000).

Observed diel patterns may also be related to predator avoidance (Simmons and Szedlmayer 2012; Herbig and Szedlmayer 2016). Visual observations in the present study by SCUBA divers of sandbar shark (*C. plumbeus*) and bull shark (*C. leucas*) on VPS and outside reef sites were common throughout the study period (McKinzie and Szedlmayer, personal observation). Both shark species increase their feeding activity at night (Driggers et al. 2012) and have been documented chasing female gray triggerfish off their nests and toward reef structures (Simmons and Szedlmayer 2012). Greatly diminished nocturnal movements and resting within reef structure would reduce gray triggerfish vulnerability to predation (Werner et al. 1983; Piraino and Szedlmayer 2014; Herbig and Szedlmayer 2016).

Two-dimensional and three-dimensional comparisons

Diel trends were consistent for both vertical and horizontal movement patterns (Herbig and Szedlmayer 2016; Chapter 2). However, seasonal depth preferences and volume use patterns were not consistent with previously reported horizontal area use patterns (Herbig and Szedlmayer 2016;Chapter 2). Therefore, seasonal changes in gray triggerfish volume use were associated with significant seasonal changes in both horizontal and vertical movements. For example, winter and spring (December through May) volume use were similar, but during the winter tracked gray triggerfish had significantly depressed vertical movement, with increased lateral movement. In contrast, in the spring vertical movement increased while lateral movement was significantly reduced. Differences between horizontal and vertical movements, and volume use patterns, have also been detected in the European eel and the eastern blue groper. However, these studies indicated that volume analyses were better able to detect significant trends than area or vertical analyses (Simpfendorfer et al. 2012; Lee et al. 2017). Lee et al. (2017) reported that volume analyses were able to detect significant seasonal differences by sex, as well as differences between fished and protected areas that were undetectable in area analyses. In addition, Simpfendorfer et al. (2012) indicated that area use analyses overestimated overlap in home range of European eels by as much as 20% compared to home range volume estimates, due to individuals using different water depths within the same geographic location. These previous studies and the present detection of distinct seasonal horizontal and vertical movement, as well as volume use patterns, in gray triggerfish indicated that to fully understand its habitat requirements, future studies must examine movements in the 3D environment (Simpfendorfer et al. 2012; Lee et al. 2017; Williams-Grove and Szedlmayer 2017).

Conclusions

Presently observed vertical movement and volume use confirmed that gray triggerfish were highly reef dependent and displayed diel and seasonal patterns of behavior. Tracked fish used more of the water column and remained higher off the seafloor during the day, with significantly larger volume use, while they used smaller volumes and remained significantly closer to the seafloor and reef habitat at night, transitioning during crepuscular periods. Observed diel patterns were consistent with the movement patterns of other diurnally active, reef associated species and were likely driven by foraging and resting behaviors along with predator avoidance. Seasonal patterns indicated that gray triggerfish used the smallest activity space volumes during winter and spring, with the largest volume use during summer. Vertical movement indicated that gray triggerfish were significantly closer to the seafloor from November through March and significantly higher off the seafloor from April through October. Seasonal patterns of movement correlated with seasonally changing temperatures and DO and likely were influenced by foraging strategies, prey availability and spawning behavior. In addition, sustained periods of low summer DO conditions may have contributed to a lack of recovery in this economically important species, even after restrictive management efforts.

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Table 3-1: Gray triggerfish (*Balistes capriscus*) tagged with depth transmitters on artificial reefs in the northeastern Gulf of Mexico to assess patterns in vertical movement and volume use over diel and monthly periods.

Fish ID	FL (mm)	Weight (kg)	Date Tagged	VPS Site	Days VPS Tracked	Final VPS Status	Outside Site	Days Tracked
T38	407	1.6	18-Aug-16	R4	59	Active	Yes	157
T39	413	1.5	18-Aug-16	R4	306	Emigration	Yes	5
T40	367	1.2	18-Aug-16	R4	306	Emigration	Yes	1
T41	407	1.5	18-Aug-16	R4	16	Emigration	No	-
T43	427	1.5	18-Aug-16	R4	308	Emigration	No	-
T44	429	1.6	18-Aug-16	R5	16	Emigration	Yes	3
T45	528	3.2	18-Aug-16	R5	2	Lost	Yes	1
T46	521	3.2	12-Apr-17	R5	109	Active	Yes	2
T47	377	1.3	12-Apr-17	R5	70	Emigration	No	-
T50	424	1.6	12-Apr-17	R4	19	Emigration	No	-
T51	333	0.9	21-Apr-17	R5	42	Caught	No	-
T52	360	1.1	21-Apr-17	R4	69	Caught	No	-
T53	359	1.1	21-Apr-17	R5	61	Emigration	No	-
T56	393	1.2	9-May-17	R3	42	Emigration	No	-
T57	397	1.4	9-May-17	R3	77	Caught	Yes	5
T58	335	0.8	9-May-17	R3	42	Emigration	No	-
T63	372	1.1	16-Jun-17	R4	4	Emigration	Yes	1
T65	337	1.0	16-Jun-17	R4	4	Emigration	Yes	1

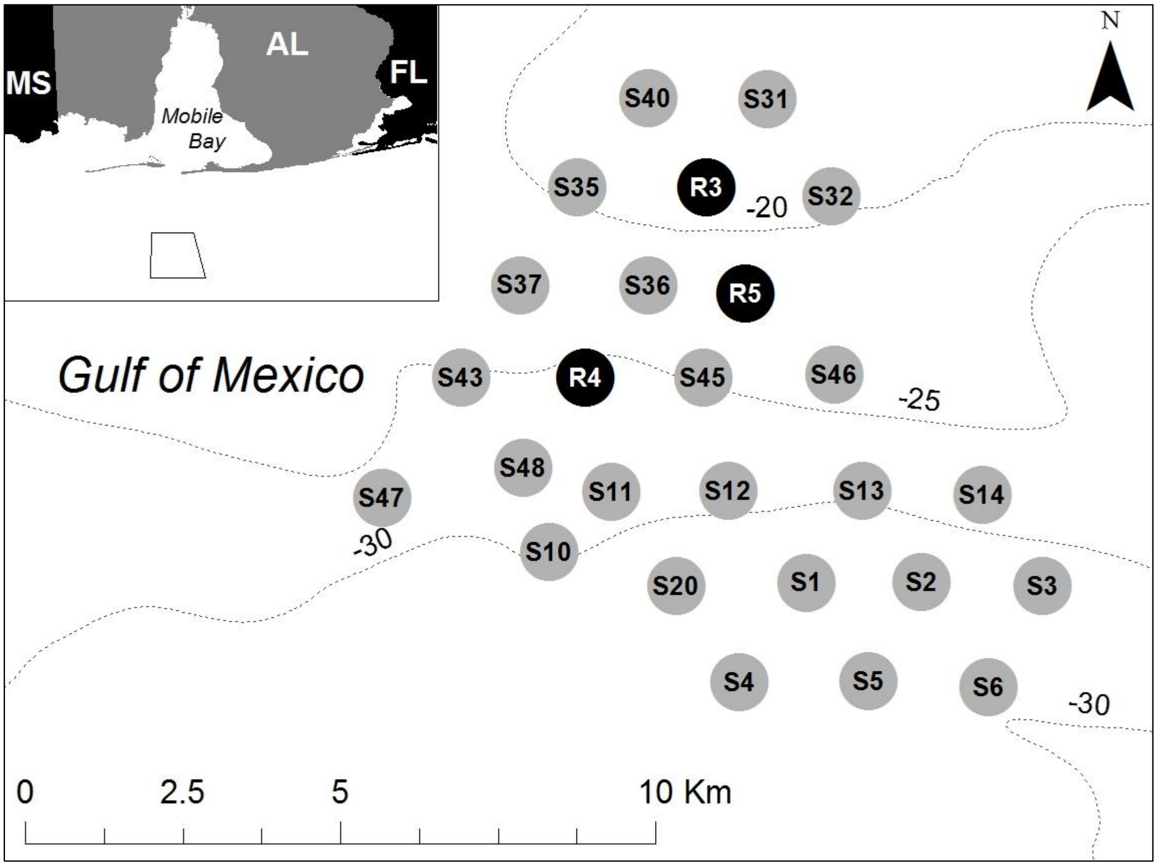

Figure 3-1: Location of Vemco Positioning System (VPS) artificial reef sites (black circles; *n* = 3) and surrounding reef site receivers (gray circles; *n* = 23) used to track fine-scale vertical movements and volume use of gray triggerfish (*Balistes capriscus*) within the Hugh Swingle General Permit Area (black polygon; insert map) in the northern Gulf of Mexico. Numbers along depth contour lines indicate depth below sea level in meters.

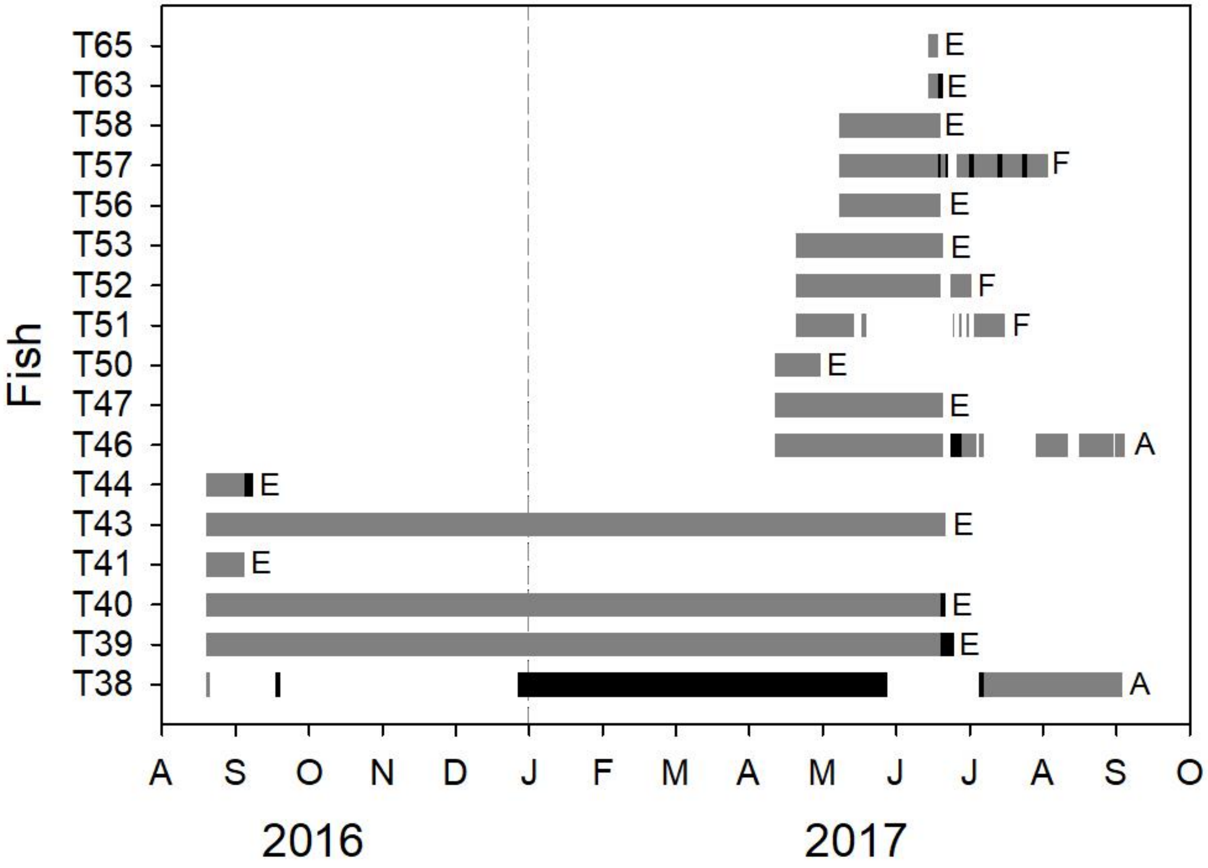

Figure 3-2: Tracking periods for transmitter tagged (*n* = 17) gray triggerfish (*Balistes capriscus*) at VPS and surrounding reef sites to monitor depth preferences and volume use. Gray bars = active on VPS site, black bars = active on outside reef site. Letters denote final fate of fish on VPS sites: E = emigration, F = caught and A = active at the end of study on 5 September 2017.

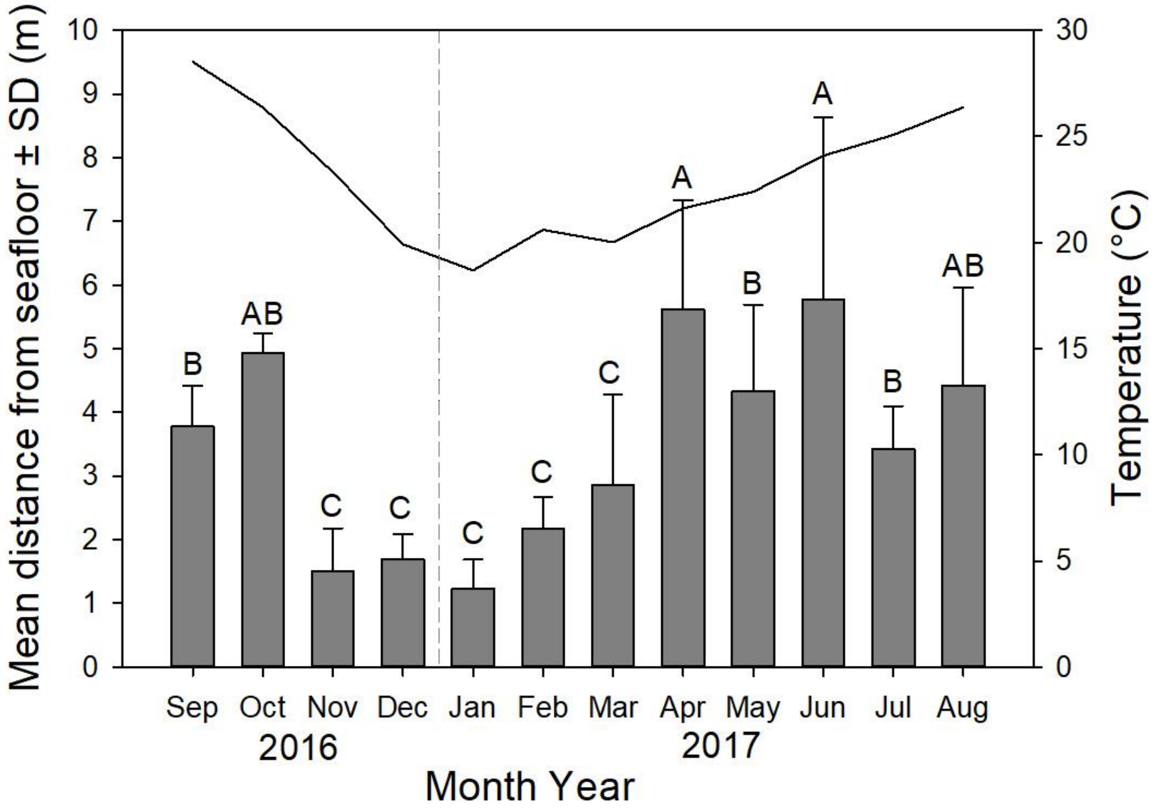

Figure 3-3: Mean monthly distance (± SD) from seafloor for gray triggerfish (*Balistes capriscus*) on artificial reefs in the northern Gulf of Mexico and monthly mean bottom water temperature. Gray bars = mean distance from the seafloor and solid line = mean temperature. Months with different letters denote significance ($P \leq 0.05$).

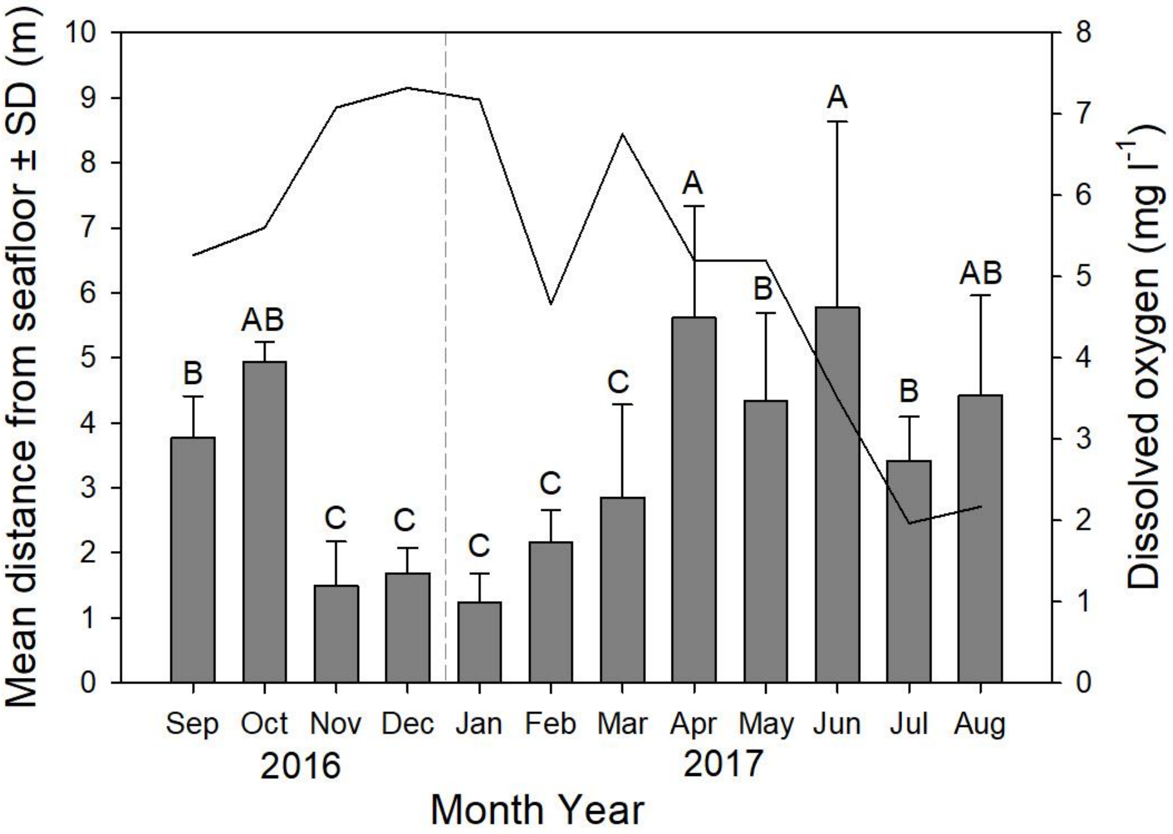

Figure 3-4: Mean monthly distance (± SD) from the seafloor for gray triggerfish (*Balistes capriscus*) on artificial reefs in the northern Gulf of Mexico and monthly mean bottom water dissolved oxygen (DO) concentration. Gray bars = mean distance from the seafloor and solid line = mean DO. Months with different letters denote significance ($P \leq 0.05$).

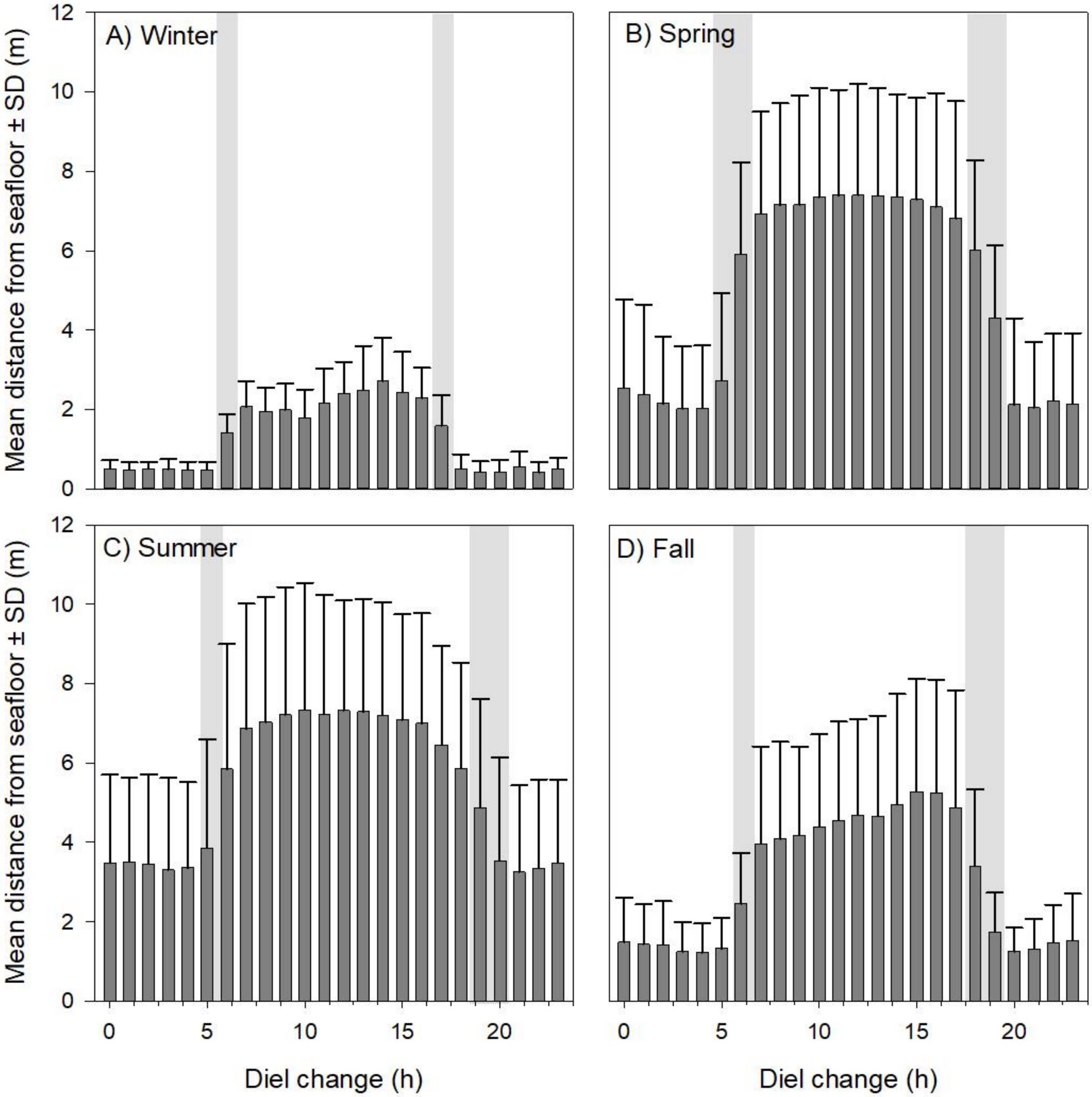

Figure 3-5: Diel depth preferences (mean distance from the seafloor ± SD) for gray triggerfish (*Balistes capriscus*) at artificial reef sites in the northern Gulf of Mexico by season (Winter = December to February; Spring = March to May; Summer = June to August; Fall = September to November). Gray bars show the range in times for sunrise and sunset.

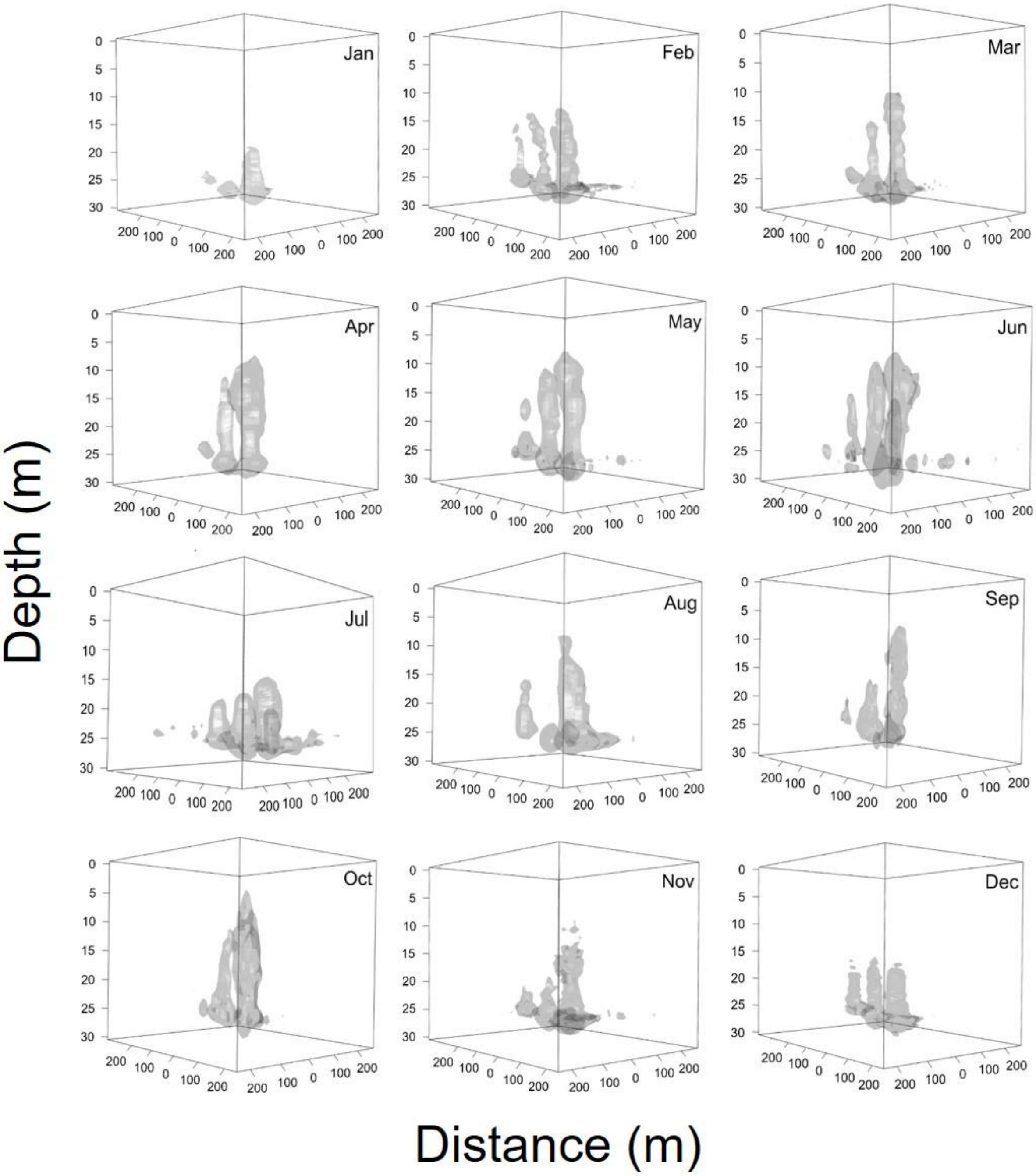

Figure 3-6: Monthly comparison of volume (m^3) use for all tagged gray triggerfish (*Balistes capriscus*) at VPS site R4. Home range (95% kernel density estimate, KDE) = gray, horizontal position (latitude and longitude) = range of 500 m (0 m at reef to 250 m away) and vertical position (depth) = 0 – 30 m, actual seafloor depth = 26.5 m.

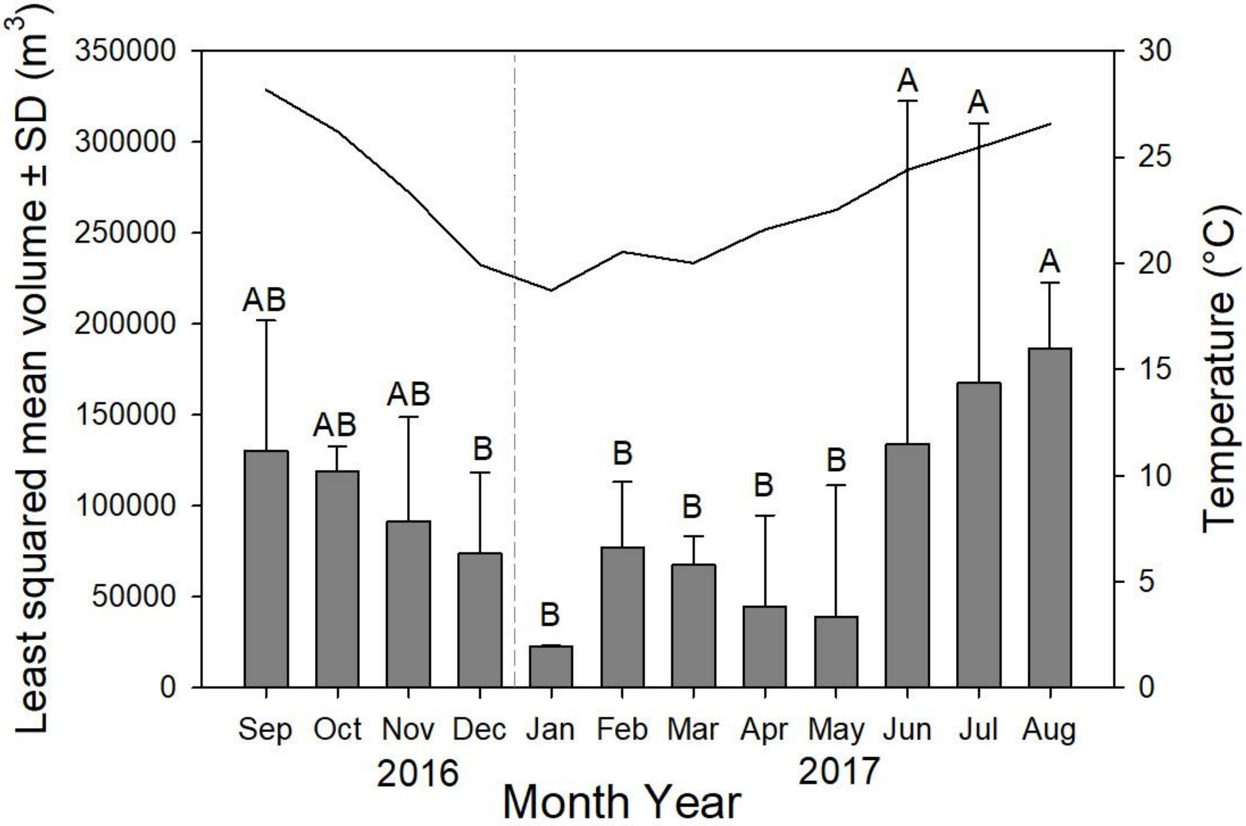

Figure 3-7: Mean monthly home range volume (95% kernel density estimate, KDE) for gray triggerfish (*Balistes capriscus*) on artificial reefs in the northern Gulf of Mexico and mean bottom water temperature. Gray bars = mean volume, error bars = standard deviation, and solid line = mean DO. Months with different letters denote significance ($P \leq 0.05$).

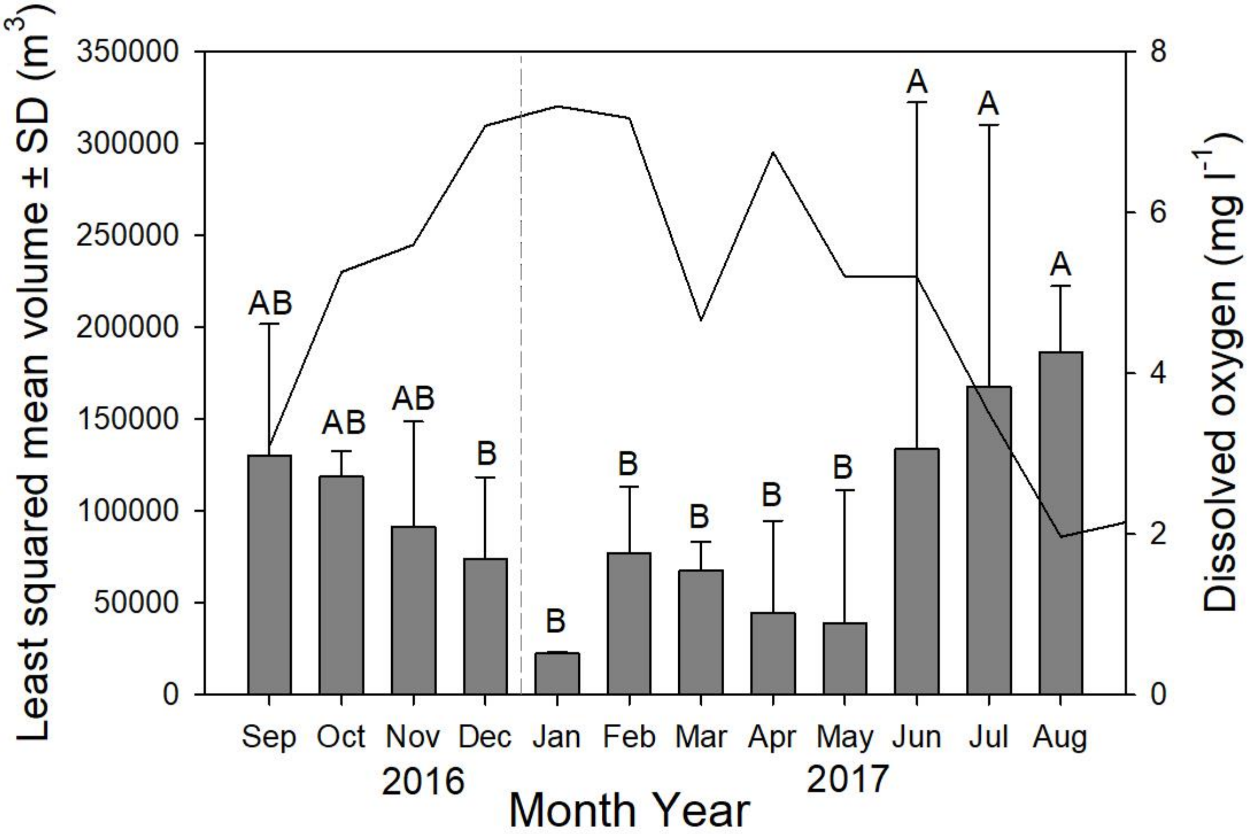

Figure 3-8: Mean monthly home range volume (95% kernel density estimate, KDE) for gray triggerfish (*Balistes capriscus*) on artificial reefs in the northern Gulf of Mexico and mean bottom water dissolved oxygen (DO) concentration. Gray bars = mean volume, error bars = standard deviation, and solid line = mean DO. Months with different letters denote significance ($P \leq 0.05$).

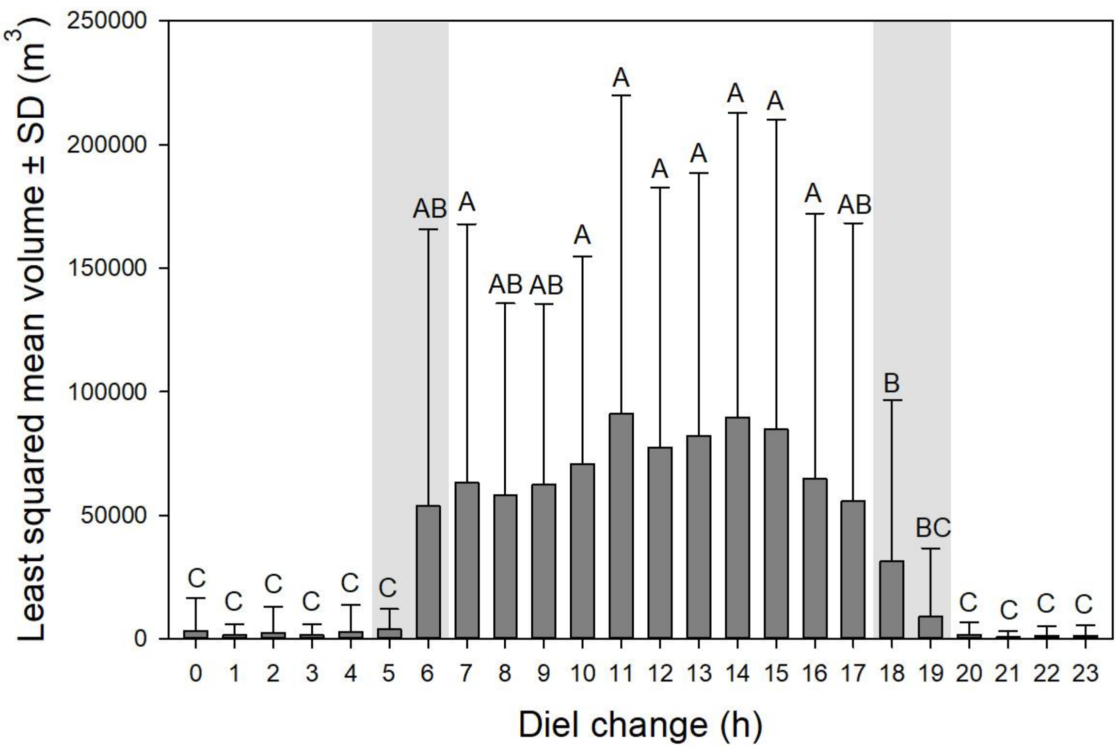

Figure 3-9: Diel patterns of home range volume (m^3 ± SD) for gray triggerfish (*Balistes capriscus*) at artificial reefs in the northern Gulf of Mexico. Hours with different letters denote significance ($P \leq 0.05$). Light gray bars show the range in times for sunrise and sunset.

Chapter 4:

Mortality estimates of gray triggerfish (*Balistes capriscus*) in the northern Gulf of Mexico based on acoustic telemetry

Abstract

Instantaneous rates of mortality (*F*, *M* and *Z*) for gray triggerfish (*Balistes capriscus*; *n* = 49) residing on artificial reefs in the northern Gulf of Mexico were estimated using Vemco Positioning System (VPS) acoustic receiver arrays (*n* = 5). Additional telemetry receivers (*n* = 21) recorded presence-absence data, to validate emigrations away from VPS sites and further confirm mortality events. The VPS array design enabled the determination of fish status as either active, emigrated, caught (*F*) or deceased (*M*) at weekly intervals from 23 January 2013 to 5 September 2017. At the end of the study, 30 fish had emigrated, four fish were caught by fishers, four suffered natural mortality events and 11 fish were still active when either their transmitter battery failed (*n* = 8) or the study period ended (*n* = 3). For all years combined, annual fishing mortality *F* = 0.23 (0.07 – 0.50, 95% CI). This present *F* estimate was lower than past stock assessment values and indicated that previous management efforts were successful. However, the present *F* was still greater than the management goal of reducing *F* to 0.17

based on a 30% spawning potential ratio. Thus, gray triggerfish stocks were still likely experiencing overfishing. In the present study, natural mortality $M = 0.25$ (0.07 – 0.57) for all years and supported the management applied value of $M = 0.28$. Present telemetry based total mortality $Z = 0.48$ (0.18 – 0.85) was not considered sustainable under the most recent stock assessment model and supports the Gulf of Mexico Fishery Management Council's decision for increased fishery restrictions.

Introduction

Gray triggerfish (*Balistes capriscus*) are exploited by sport and commercial fishers throughout the northern Gulf of Mexico and southeastern United States (SEDAR 43 2015). Historically, gray triggerfish were not heavily targeted nor considered an important food resource. However, their value has increased in recent years as fishing restrictions on other regionally important reef fish, such as red snapper (*Lutjanus campechanus*) have tightened and season lengths have substantially decreased (Valle et al. 2001; SEDAR 31 2013; Harper and McClellan 2014; SEDAR 43 2015). The most recent 2017 gray triggerfish stock assessment indicated that the Gulf of Mexico stock was overfished (stock abundance was too low), but not experiencing overfishing (rate of removal was not too high; Amendment 46 2017).

Stock assessment indicated that gray triggerfish stock depletion resulted from prior overfishing, unsustainably high mortality rates and recent prolonged periods of low recruitment (SEDAR 43 2015; Amendment 46 2017). Prior to the implementation of the

Reef Fish Fishery Management Plan in 1984 (GMFMC 1981) and federal management for the Gulf of Mexico gray triggerfish stock in 1990 (Amendment 1 1989), total mortality (Z) was estimated to range from 0.40 to 0.67 (1979 – 1982; Johnson and Salomon 1984). More recent estimates (1986 – 2011) based on catch curve analyses indicated a mean $Z = 0.95$ (Burton et al. 2015), which exceeded the estimated sustainable level of $Z = 0.45$ based on the stock assessment model (Amendment 46 2017). The most recent management goals set a target $F = 0.13$ and a maximum $F = 0.17$ (Amendment 46 2017). The latest assessment estimated $F = 0.12$ (2013 – 2016; Amendment 46 2017), while previous estimates of F exceeded sustainable levels and ranged from 0.35 to 0.67 (SEDAR 9 update 2011; Burton et al. 2015). Natural mortality (M) estimates have remained constant over time and ranged from 0.27 to 0.28 (SEDAR 9 update 2011; SEDAR 43 2015; Burton et al. 2015; Amendment 46 2017).

Gray triggerfish mortality estimates (F, M and Z) are critical for management, but previous values were based on equations that were theoretically or empirically derived from fishery-dependent data. For management, it is relatively easy to estimate total mortality (Z) from age-frequency analyses, but more difficult to separate Z into fishing (F) and natural (M) mortality for an exploited stock. Most previous methods to estimate M were based on derived equations that attempt to relate M to life history parameters such as maximum size (L_∞), maximum age ($T_{\max}$) or growth rate (K). For example, one method suggested that $M = 4.22/T_{\max}$ (Hewitt and Hoeing 2005), while another age-specific method suggested that $M = (L/L_\infty)^{-1.5} \times K$, where L_∞ and K were the stock specific von Bertalanffy growth equation parameters and L was equal to fish length at age (Charnov et al. 2013).

Mortality can also be estimated through mark-recapture studies based on the number of tagged fish that are caught and reported by fishers (Pine et al. 2013). However, there are inherent difficulties with conventional mark-recapture studies; for example, fisher non-reporting, tag shedding and emigrations (Schwartz 2000; Pollock et al. 2001; Denson et al. 2002; Pine et al. 2003; 2013).

Telemetry methods provide more direct estimates of mortality and have been used in terrestrial animals for some time (Trent and Rongstad 1974; Pollock et al. 1995). These methods have recently been applied to aquatic organisms (Hightower et al. 2001; Heupel and Simpfendorfer 2002; Pollock et al. 2004; Starr et al. 2005; Melnychuk et al. 2007; Karam et al. 2008; Knip et al. 2012). In the northern Gulf of Mexico, telemetry methods have been successfully employed to estimate fishing (F) and natural mortality (M) of red snapper residing at natural and artificial reefs, independent of fisher returns (Topping and Szedlmayer 2013; Williams-Grove and Szedlmayer 2016a). Telemetry methods can also estimate fisher non-reporting and tagging effect mortality (Hightower et al. 2001; Topping and Szedlmayer 2013; Williams-Grove and Szedlmayer 2016a). The present study applied telemetry methods to gray triggerfish. Mortalities (M, F and Z) were estimated with a known-fate model (Kaplan-Meier staggered entry method; Kaplan and Meier 1958; Pollock et al. 1989) based on fine-scale positions obtained from the Vemco Positioning System (VPS). Mortality rates were estimated for all years combined (2013 – 2017) and also compared among years.

Methods

Study site and array design

The study area (64 km^2) was located 23 – 35 km south of Dauphin Island, Alabama, USA in the northeastern Gulf of Mexico. The study site contained 26 steel cage artificial reefs (2.5 x 1.3 x 2.4 m), each positioned 1.4 – 1.6 km apart at depths of 18 – 35 m (Fig. 4-1). The artificial reefs were deployed at unpublished locations from 2006 to 2010 within a designated reef building zone, the Hugh Swingle General Permit Area (Syc and Szedlmayer 2012). Vemco positioning system (VPS) receiver arrays were deployed at five reef sites (R2, R3, R4, R5 and R6) to monitor fine-scale movement (m) patterns and mortality of transmitter tagged gray triggerfish. In addition, single Vemco acoustic receivers were placed on surrounding reef sites (*n* = 21) to detect large-scale movements (km) and emigrations away from VPS tagging sites (Fig. 4-1).

Each VPS site consisted of five receivers: a center receiver placed 10 – 20 m north of the reef site and four additional receivers placed 300 m north, south, east and west of the center receiver (Piraino and Szedlmayer 2014). Synchronization transmitters (sync tags; Vemco V16-6x, 69 kHz, transmission delay: 540 – 720 s; *n* = 5) were attach 1 m above each receiver to standardize the internal receiver clocks (Piraino and Szedlmayer 2014). The VPS array design permitted high detection efficiency of tagged gray triggerfish (≥ 88%; Chapter 2). Each of the VPS array receivers were exchanged and downloaded every 4 to 6 months. Data from the VPS receivers were sent to Vemco for post-processing after every download (Vemco, Ltd., Nova Scotia). A stationary control transmitter (V13-1L, 69 kHz, transmission delay: 40 – 80 sec) was placed at a known location within each VPS array to validate the accuracy of Vemco derived positions and to ensure continuous data collection throughout the study period.

Each of the surrounding reef sites (*n* = 21) contained a single VR2W acoustic receiver that detected presence and absence data. These single receivers were exchanged and downloaded every 6 to 12 months. Maximum detection radius around each receiver was estimated to be 770 m (Chapter 2). Thus, transmitter tagged gray triggerfish were detected in 82% (53 km^2) of the area, leaving 18% (11 km^2) of the area with little to no coverage within the large-scale surrounding receiver array. These areas of low detection occurred over 100 – 300 m wide paths between single receiver coverage areas (Chapter 2).

Fish tagging and cage-release method

Adult gray triggerfish were tagged and released (*n* = 56) on from 23 January 2013 through 16 June 2017. Movements were monitored until 5 September 2017. Prior to tagging, dissolved oxygen concentration and temperature were measured throughout the water column (YSI Model 6920, YSI Inc., Yellow Springs, Ohio). Fish were tagged and released if dissolved oxygen levels were > 2.5 mg l^{-1}. If water temperatures at the surface exceed 27 °C, ice was added to the holding tanks during sedation and recovery to reduce high temperature stress.

Gray triggerfish were captured with hook-and-line baited with squid (*Loligo* or *Lolliguncula* spp.) at one of five VPS sites (Fig. 4-1). On the research vessel, adult fish ≥ 250 mm fork length (FL; Fitzhugh et al. 2015) were anesthetized in 70-l containers with 150 mg MS-222 l^{-1} seawater (tricaine methanesulfonate; Munday and Wilson 1997; Cho and Heath 2000) for 80 sec to level 4 (Summerfelt and Smith 1990). After anesthesia, fish were weighed (nearest 0.1 kg) and measured (mm SL, FL and TL). An acoustic transmitter (Vemco, V13-1L or V13P-1L, 69 kHz, transmission delay: 40 – 80 s, battery life: 566 – 991 d) was surgically implanted within the peritoneal cavity through a 1 – 2 cm vertical incision on the ventral left side. The incision was then closed with 2 – 3 discontinuous, dissolvable sutures (Ethicon Inc., Chromic Gut). Betadine was spread over the wound to reduce the risk of infection. Fish were also injected with oxytetracycline (OTC). Fish were then tagged with an external anchor tag (Floy® FM-95W) inserted 1 – 2 cm posterior to the incision, with a unique identification number, contact information and reward notice for later identification by fishers or SCUBA divers (Herbig and Szedlmayer 2016).

After tagging, fish were transferred to a 185-l recovery tank with aerated seawater. During the recovery period, fish were monitored for increased opercular pumping, control of body orientation and resumption of normal swimming motion. Recovered fish were then placed into a weighted rectangular cage (46 x 61 x 61 cm) constructed out of 13-gauge vinyl covered wire and slowly lowered to the seafloor (19 – 31 m) within 10 m of the capture site. Once the cage reached the seafloor a door automatically opened, allowing the tagged fish to leave on its own initiative (Williams et al. 2015). Any tagged fish that did not leave the cage after 20 min on the seafloor were not released.

Validating detection data

Acoustic receivers can generate false detections that are not from valid transmitter tagged fish (Pincock 2012). False detections can result from incomplete transmission due to interference (noise) or collision of signals when two or more transmitters simultaneously reach a receiver (Pincock 2012). To reduce the potential for data loss due to signal collision no more than 10 transmitters (tagged fish + control) were deployed at any individual VPS reef site at any one-time (Chapter 2; Topping and Szedlmayer 2011a; Piraino and Szedlmayer 2014). False detections that produced unknown tag IDs were removed from all subsequent analyses. Transmitter detections of known tags were screened before accepted as valid. Transmitter detections were accepted as valid if there were a minimum of two detections for a single transmitter ID and there was at least one short interval between detections and more short intervals than long intervals. The short interval time was set at 30 min (30 times the nominal ping interval of 60 sec). The long interval was set at 12 hours (720 times 60 sec nominal ping interval). All false detections of valid transmitters were removed from analysis (Pincock 2012).

Survival and mortality estimates

Fish positions (latitude, longitude and depth) were calculated by Vemco from the time differential of signal arrival at three to five receivers. Status of transmitter tagged fish were based on positions along with the time interval between detections after a 3 d post-tagging recovery period. Any fish that remained stationary after exiting their release cage or that permanently emigrated away from their VPS tagging site within the 3 d recovery period were consider lost and removed from analyses. After 3 d, tagged gray triggerfish were categorized as active (continuously swimming around VPS site), emigrated (progressively moving farther away from VPS reef and then lost or movement to a surrounding reef site), natural mortality (tag becomes stationary or undergoes erratic large-scale movements) and fishing mortality (sudden disappearance near reef center). Fish that emigrated were frequently detected on surrounding reef site receivers, while fish that experienced a mortality event lacked detections on surrounding sites. Fishing mortalities were also confirmed by fisher returns. To increase the probability of fisher returns, a high monetary reward was offered ($150). Posters describing the present study and reward offer were posted at marinas, bait-shops, and other public sites, and an Auburn University fish tagging web-site was maintained to reach a larger audience. All fish were also tagged with external anchor tags marked with a reward notice and reporting phone number. It was assumed that tagged gray triggerfish active within their VPS array experienced similar mortality rates to untagged fish outside of these VPS arrays (Topping and Szedlmayer 2013; Williams-Grove and Szedlmayer 2016a).

A known fate model (Kaplan-Meier staggered entry method) was applied in the MARK program to estimate conditional survivals, total survivals, standard error (SE) and 95% confidence intervals (CI; Schroepfer and Szedlmayer 2006; Topping and Szedlmayer 2013; Williams-Grove and Szedlmayer 2016a, 2016b; Herbig and Szedlmayer 2016). Annual estimates were based on weekly time intervals for each year of the study (2013 – 2017). The MARK program calculated survival estimates based on the maximum likelihood binomial (MLE; Edwards 1992). The probability of surviving a mortality event was determined by calculating the number of individuals at risk of dying and the number of individuals that survived for that time interval. Fish that emigrated or suffered a mortality event not under consideration were removed (right censored). For example, when fishing mortality (*F*) was estimated all emigrations and natural mortalities (*M*) were removed (for detailed equation see: Williams-Grove and Szedlmayer 2016a).

Instantaneous annual mortality rates were based on total survival throughout the entire study period (241 weeks) adjusted to 52 weeks (annual S = total $S^{(52/241)}$) for each mortality type. For example, annual $F = -\log_e S^{(52/241)}$ for fishing mortality, annual $M = -\log_e S^{(52/241)}$ for natural mortality and annual $Z = -\log_e S^{(52/241)}$ for total mortality (Starr et al. 2005). Confidence limits for instantaneous mortality rates were calculated from the 95% confidence intervals estimated from the MLE of the survival functions at 1 year (52 weeks; Klein and Moeschberger 2003; Topping and Szedlmayer 2013; Williams-Grove and Szedlmayer 2016a). The reported sample sizes for the mortality estimates were the number of tagged gray triggerfish at risk during the time interval under analysis (Krebs 2014).

Results

Fine-scale movement patterns of transmitter tagged gray triggerfish (n = 56) were monitored from 23 January 2013 through 5 September 2017. All tagged fish were above the estimated size of 100% sexual maturity for both males and females (250 mm fork length, FL; Fitzhugh et al. 2015). Mean ± SD fish size = 395 ± 52 mm and ranged from 276 to 535 mm FL. Most tagged gray triggerfish (86%) were above the legal sport and commercial size limit (356 mm FL) at the time of release. Five fish (9%) left their VPS site within 3 d post-release and two additional fish (3%) showed no movement after exiting their release cage. These individuals were removed from all analyses. The remaining individuals (88%, *n* = 49) were categorized as active, caught, emigrated or deceased at weekly time intervals and were included in all subsequent mortality estimates.

Movement patterns of gray triggerfish that remained after the 3 d recovery period (*n* = 49) were monitored for 4 to 622 d. Among these tracked individuals, 30 fish had a final event status as an emigration, four fish were caught by fishers, four had natural mortalities, and 11 fish were active when either their transmitter battery failed (*n* = 8) or the study period ended (*n* = 3; Fig. 4-2). Most tagged gray triggerfish (84%, *n* = 41) emigrated away from their VPS site at least once and 33% of these fish (*n* = 16) showed homing behavior (for further information on residency, site fidelity and horizontal movements see Chapter 2). Emigrant fish (*n* = 41) were considered active while on their VPS site and right-censored from the data set when they emigrated away from their VPS site.

Fishing mortality occurred in four (8%) tagged gray triggerfish while they resided on their VPS release site (Fig. 4-2). Detection patterns on individual receivers and VPS positional data were used to identify fishing mortality (*F*). All telemetry identified *F* mortalities were verified by fisher-reported recaptures (100% reporting rate). Two additional fish (T20 and T28) were reported as captured by fishers in 2016 after they ceased to be detected due to emigration from their VPS site. Fish T20 was caught 693 d after release, and reported 2.2 km northwest of its last known location, after it had emigrated from its release site, where it had been detected and tracked intermittently for 443 d. Fish T28 was caught 249 d after release and was reported 0.9 km west of its release site, 12 d after it had emigrated from its VPS site, where it had been active on and off for 237 d. Total survival from all fishing mortality within the VPS arrays over the 241-week study period was $S_F = 0.35$ (0.10 – 0.73, 95% CI). Total survival adjusted to annual survival was $S_F{}^{(52/241)} = 0.35^{(52/241)} = 0.80$, thus annual $F = -\log_e 0.80 = 0.23$ (0.07 – 0.50; Fig 4-3). Fishing mortalities rates varied across years. Fishing mortalities ($n = 4$) occurred in 2015 and 2017. In 2015, there was one gray triggerfish caught among 15 fish available for recapture at VPS sites, and $F = 0.29$ (0.03 – 1.44; Table 4-1). In 2017, three gray triggerfish were caught among 26 fish available for recapture and $F = 1.13$ (0.29 – 2.87; Table 4-1). No fishing mortalities were detected in 2013 (seven at liberty), 2014 (11 at liberty) or 2016 (nine at liberty; Table 4-1).

During the present study, natural mortalities (M) were detected in four fish (8%), while they were active on their VPS site (Fig. 4-2). One additional M was detected in fish T34 outside the VPS array 199 d after emigrating, but this fish had been removed from analysis. Total survival from all M over the entire study was $S_M = 0.32$ (0.07 – 0.74, 95% CI). Total survival adjusted to annual survival $S_M{}^{(52/241)} = 0.32^{(52/241)} = 0.78$, thus annual $M = -\log_e 0.78 = 0.25$ (0.07 – 0.57; Fig 4-4). One M occurred in 2013, $M = 0.42$ (0.05 – 1.95); one in 2014, $M = 0.12$ (0.02 – 0.69); one in 2015, $M = 0.41$ (0.04 – 1.87) and one in 2016, $M = 0.22$ (0.03 – 1.17). No natural mortalities were detected in 2017 (Table 4-1).

Total survival for all years was $S_Z = 0.11$ (0.02 – 0.44, 95% CI). Total survival adjusted to annual survival was $S_Z{}^{(52/241)} = 0.11^{(52/241)} = 0.62$, with annual $Z = -\log_e 0.62 = 0.48$ (0.18 – 0.85; Fig 4-5). Total mortality (Z) varied by year and ranged from 0.12 (2014) to 1.13 (2017; Table 4-1). No false detections were recorded on VPS or surrounding reef site receivers after mortalities occurred. Lack of false detections along with fisher reported recaptures verified all VPS determined mortalities (*F* and *M*).

Discussion

The present study applied acoustic telemetry techniques to directly estimate instantaneous rates of mortality (*F*, *M* and *Z*) for gray triggerfish. The VPS arrays allowed for continuous, long term (up to 662 d), highly accurate (≤ 3 m) tracking of transmitter tagged gray triggerfish residing at artificial reefs in the northern Gulf of Mexico (Chapter 2; Piraino and Szedlmayer 2014; Herbig and Szedlmayer 2016; Williams-Groves and Szedlmayer 2016a, 2016b). Importantly, mortalities were estimated directly, independent of fisher returns, because the fate of tagged individuals was known while they resided on VPS monitored reef sites (Hightower et al. 2001; Heupel and Simpfendorfer 2002; Bacheler et al. 2009; Topping and Szedlmayer 2013; Williams-Grove and Szedlmayer 2016a).

In 2012, the Gulf of Mexico Fishery Management Council (Gulf Council) modified the gray triggerfish rebuilding plan through Reef Fish Amendment 37 (2012), which took effect 10 June 2013 (SEDAR 43 2015). This amendment reduced the annual harvest limit from 231,786 kg (sport = 183,705 kg, commercial = 48,081 kg) to 126,100 kg (sport = 98,475 kg and commercial = 27,625 kg), set a spawning season closure from 1 June through 31 July, a sport bag limit of 2 fish and a commercial trip limit of 12 individuals. It also established sport accountability measures (AMs) to allow for in-season closures if target harvest levels were reached (SEDAR 43 2013). A 356 mm fork length (FL) size limit had previously been established in 2008 (Amendment 30A 2008); SEDAR 43 2015). Prior to Amendment 37, estimated F = 0.44 (2008 – 2010) and the stock was considered overfished and experiencing overfishing (SEDAR 9 updated 2011). The present study annual estimate of F = 0.23 (2013 – 2017) was substantially lower than the previous SEDAR 9 assessment value (F = 0.44) and indicated that Amendment 37 management efforts were successful in reducing F (Amendment 37 2012). However, the present study F = 0.23 was greater than the F = 0.12 (2013 – 2016) estimated in a 2017 stock assessment (Amendment 46 2017). This greater F estimate in the present study indicated that the Gulf of Mexico gray triggerfish stock may still be experiencing overfishing (rate of removal is too high), as it was greater than the 2017 stock assessment maximum fishing mortality threshold (F_{MFMT}) = 0.17, based on a spawning potential ratio (SPR) of 30% (Amendment 46 2017). The 2017 assessment also indicated that the Gulf of Mexico gray triggerfish stock was not rebuilding on target, likely due to sport catch often exceeding catch limits, incompatibilities between the federal and state fishing seasons and low annual recruitment (Amendment 46 2017). This rebuilding failure led to the establishment of an updated 9-year gray triggerfish rebuilding plan that went into effect on 15 January 2018 (Amendment 46 2017). Amendment 46 (2017) maintained the annual harvest limit at 126,100 kg, but reduced the sport bag limit to one fish, increased the commercial limit to 16 fish, increased the size limit to 381 mm FL and added in a January and February seasonal closure to the existing June and July closure. Continued acoustic monitoring of transmitter tagged gray triggerfish may help evaluate the effects on F of this more recent 2018 management plan.

Gray triggerfish fishery regulations were the same over the present study period (2013 –2017). However, sport fishery accountability measures led to varying season lengths (from 37 to 236 d) for the years 2013 – 2016, with a complete closure in 2017 due to 2016 landings exceeding the harvest limit by 245% (Amendment 46 2017). Previous telemetry studies on red snapper have shown that changes in season length can influence annual fishing mortality rates (Topping and Szedlmayer 2013; Williams-Grove and Szedlmayer 2016a). One study determined that annual *F* decreased (0.22 to 0.14) when the season length decreased from 194 d to 65 d (2007-2008; Topping and Szedlmayer 2013). However, another study showed that when the red snapper season was further reduced to a 9 d from a 42 d season (2013 – 2014) *F* increased (0.18 to 0.42) as fishers concentrated their effort (Williams-Grove and Szedlmayer 2016a). In the present study, changes in season length did not appear to influence annual *F*. It is possible that no trends were observed, because fishers were unaware of season length and closure dates prior to the start of the annual fishing season as they were announced mid-season once annual harvest limits were estimated to be reached (SEDAR 43 2015). This contrasts with the red snapper fishery, where annual season lengths were set and announced prior to the start of the annual sport fishing season in June (SEDAR 31 2013). However, as with most telemetry tagging studies sample sizes were low in the present study. Therefore, inter-annual comparisons in *F* should be treated with caution due to the limited number of tagged fish that were available for recapture each year (Topping and Szedlmayer 2013; Williams-Grove and Szedlmayer 2016a).

Different fishery regulations for target and non-target species may have unexpected consequences (Northridge 1991; Gislason 2003; Walters et al. 2005). In the present study, the highest annual $F = 1.13$ was in 2017. Surprisingly, this occurred when the sport fishery for gray triggerfish was completely closed, because fishers exceeded the 2016 quota (Amendment 46 2017). All 2017 gray triggerfish F occurred in July during the extended sport fishery season for red snapper (NMFS 2017). Thus, the red snapper sport fishery affected a non-target species, gray triggerfish, due to their shared dependence on natural and artificial reef habitats (Ingram and Patterson 2001; Patterson and Cowen 2003; Addis et al. 2013). Previous telemetry studies confirm that both species were reef dependent, maintained long-term residencies and often displayed high site-fidelity to individual reef structures (Chapter 2; Szedlmayer and Schroepfer 2005; Topping and Szedlmayer 2011a, 2011b; Piraino and Szedlmayer 2014; Herbig and Szedlmayer 2016; Williams-Grove and Szedlmayer 2016b, 2017). Increased F has also been linked to fish species that congregate at predictable or known locations (Roughgarden and Smith 1996; Hutchings 2000; Worm et al. 2009; Jaxion-Harm and Szedlmayer 2015; Williams-Grove and Szedlmayer 2016a). At the time of the present study, the Gulf of Mexico gray triggerfish stock was overfished and not rebuilding on target. In addition, the present population size and spawning stock biomass were near an historic low (Amendment 46 2017). Any additional fishing pressure on gray triggerfish, particularly during critical time-periods such as spawning when the fishery is closed could further slow stock recovery (van Overzee and Rijnsdorp 2015).

One of the advantages of telemetry-based mortality studies is that they allow for the direct determination of fisher reporting rates (Hightower et al. 2001; Topping and Szedlmayer 2013; Williams-Grove and Szedlmayer 2016a). Historically, fisher reporting rates were indirectly measured with secretly implanted tags, port or processor surveys, landings data and multiple-tag studies (Pollock et al. 2001; Pine et al. 2003). In multiple tag studies, high-reward tags were assumed to be 100% reported and the relative difference between the standard tag reporting and the high-reward reporting was considered the true reporting rate (Pollock et al. 2001; Bacheler et al. 2009, Hightower and Pollock 2013). In the present high-reward ($150) tagging study, reporting rates were 100%, however, these results should be interpreted with caution due to low sample sizes. Always assuming 100% return rates of high-reward tags may be inaccurate and can cause underestimates of *F* (Pollock et al. 2001; Pine et al. 2003). Previous telemetry studies that directly estimated tag reporting indicated that rates were < 100% (17%, Hightower et al. 2001; 89% Topping and Szedlmayer 2013; 63%, Williams-Grove and Szedlmayer 2016a). Lower than 100% reporting rates were attributed to tag shedding, unintentional noncompliance or intentional non-reporting due to disagreements over management restrictions (Schwartz 2000; Pollock et al. 2001; Denson et al. 2002; Gaertner and Hallier 2015; Williams-Grove and Szedlmayer 2016a). Another advantage of telemetry studies is that they provide fisher-independent estimates of *F* and *M*, but fisher-reported recaptures are still important for validating the telemetry-based estimates (Hightower and Pollock 2013; Topping and Szedlmayer 2013; Williams-Grove and Szedlmayer 2016a). In addition, fisher returns can provide a unique opportunity to understand fisher behavior (Pine et al. 2003) and generate species-specific reporting rates (Williams-Grove and Szedlmayer 2016a).

In the present study, one natural mortality event was observed during each year of the study except 2017. Annual *M* = 0.25 for all years of the study (2013 – 2017), but varied from 0.12 to 0.42 across years, but sample sizes were low. In 2017, *M* = 0 possibly due to increased emigrations during tropical storm Cindy (Chapter 2), followed by low number of returns and high rates of *F* during the remainder of the study. The present long-term estimate of *M* = 0.25 (0.07 – 0.57, 95% CI), was similar to the *M* = 0.28 used in the 2017 stock assessment model and provides justification for its use by management (Burton et al. 2017; Amendment 46 2017).

Interestingly, one gray triggerfish (T35) was identified as *M* rather than an emigration based on detections patterns on surrounding reef site receivers. Detections of fish T35 were recorded on 15 single surrounding receiver sites after leaving its VPS site. However, these T35 detections showed 38 directed movements occurring over the next 5 d covering a distance of 91 km. This substantially increased horizontal movement matched movement patterns of acoustically tagged sandbar shark (*Carcharhinus plumbeus*) and bull shark (*C. leucas*) in the same present study area (Altobelli and Szedlmayer, In Prep). Thus, these T35 detections likely showed the movements of a predator rather than a gray triggerfish.

In conclusion, the present study successfully identified the fates of 100% of transmitter tagged gray triggerfish residing on artificial reefs in the northern Gulf of Mexico, independent of fisher return and allowed for direct estimates of *F*, *M* and *Z* based on VPS telemetry methods. Surrounding reef site receivers were successful in verifying emigrations based on valid detections on individual receivers. Mortalities were confirmed by fisher returns and the lack of detections on single receivers after being caught, or detection patterns that indicated predator movements. The present study estimate of *M* supported management applied values, and present *F* indicated that previous management efforts were successful in reducing *F*, but the stock may still be experiencing overfishing. The present study also illuminated the importance of bycatch on gray triggerfish, especially during critical closed spawning periods, when other fisheries such as red snapper were still open. Continued acoustic tracking and development of direct mortality estimates based on telemetry methods will be essential in monitoring the success of management efforts for gray triggerfish.

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Table 4-1: Gray triggerfish (*Balistes capriscus*) instantaneous annual mortality rates estimated from VPS telemetry methods (*Z* = total, *F* = fishing, *M* = natural mortalities). Mortalities were estimated for each year and for all 5 years combined. Values in parentheses are 95% confidence intervals (CI), *n* = the number of tagged fish available for recapture during each time-interval and days were the duration of the fishing season for each year.

Year	*n*	*Z*	*F*	*M*	Season dates	Days
2013	7	0.42 (0.05-1.95)	0	0.42 (0.05-1.95)	1 Jan to 9 Jun; 1 Aug to 15 Oct	236
2014	12	0.12 (0.02-0.69)	0	0.12 (0.02-0.69)	1 Jan to 30 Apr	120
2015	15	0.69 (0.13-2.09)	0.29 (0.03-1.44)	0.41 (0.04-1.87)	1 Jan to 6 Feb	37
2016	9	0.22 (0.03-1.17)	0	0.22 (0.03-1.17)	1 Jan to 31 May	152
2017	26	1.13 (0.29-2.87)	1.13 (0.29-2.87)	0	Closed	0
Total	49	0.48 (0.18-0.85)	0.23 (0.07-0.50)	0.25 (0.07-0.57)	--	545

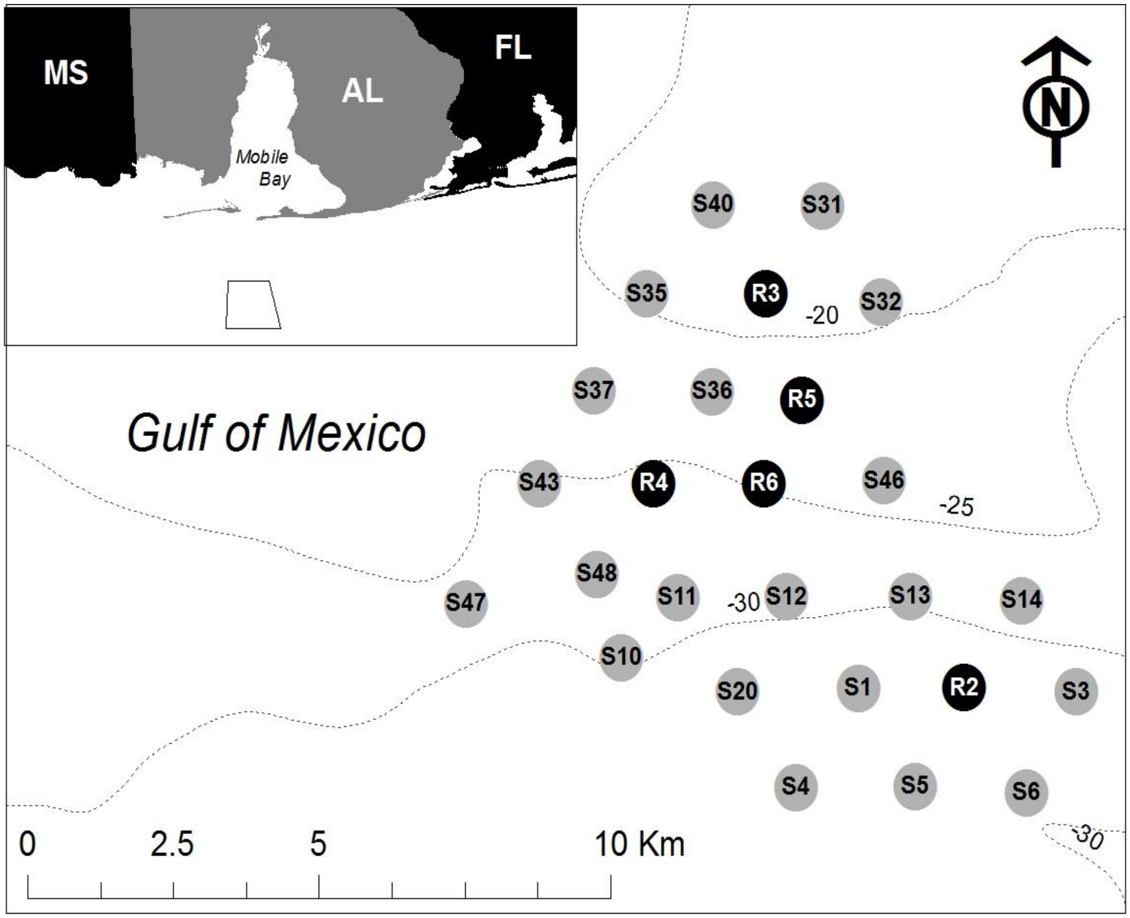
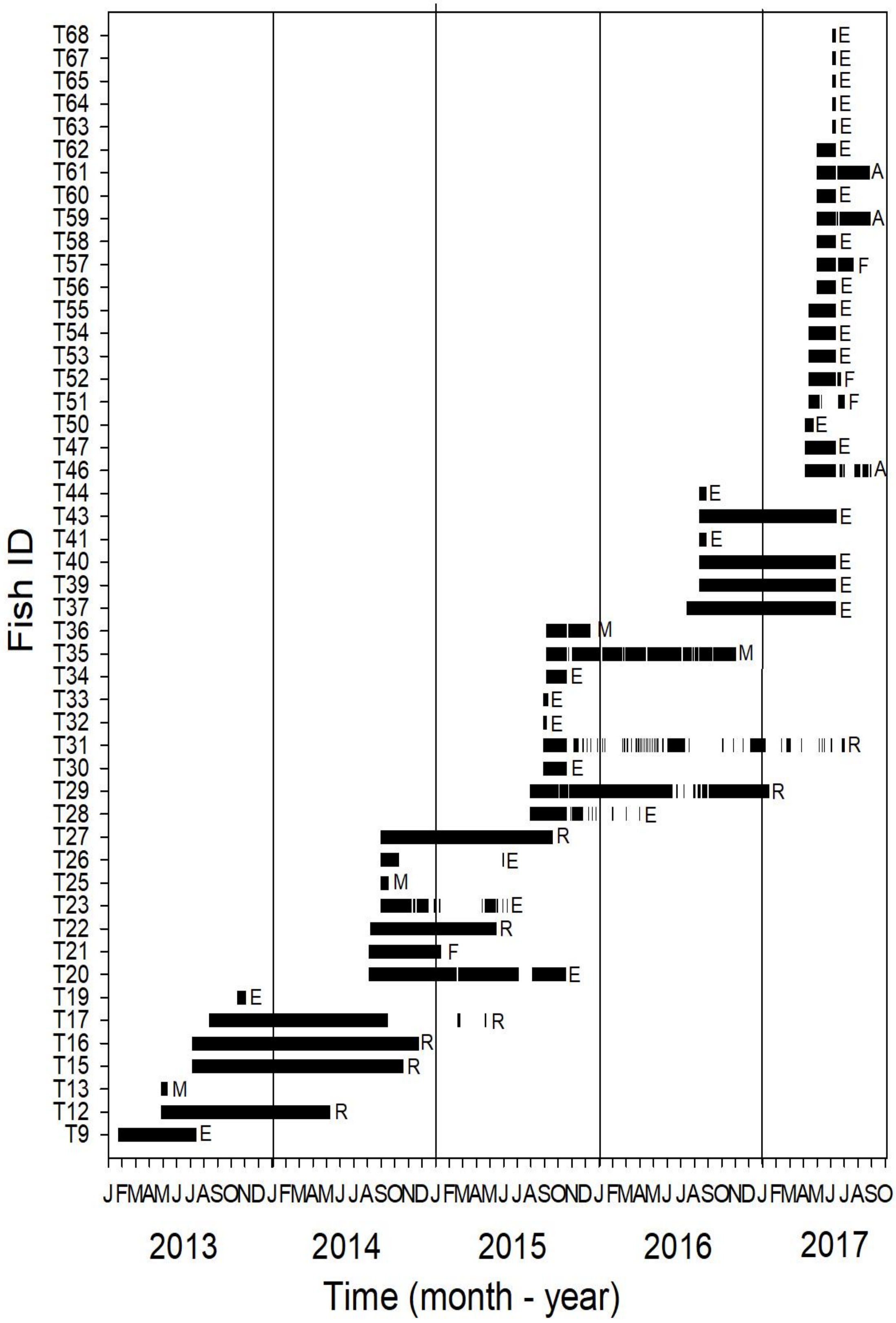


Figure 4-1: Location of Vemco Positioning System (VPS) artificial reef sites (black circles, *n* = 5) and surrounding reef site receivers (gray circles, *n* = 21) within the Hugh Swingle General Permit Area (black polygon; insert map), northeastern Gulf of Mexico. Dotted lines are 5 m depth contours.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2013
2014
2015
2016
2017
Time (month - year)

Figure 4-2: Detection duration of transmitter tagged (*n* = 49) gray triggerfish (*Balistes capriscus*) tracked at artificial reef sites in the northern Gulf of Mexico. Black bars = active on VPS reef sites. Letters denote final fate of fish on VPS site: E = emigration, F = fishing mortality, M = natural mortality, A = active as of the end of study (5 September 2017), R = resident at VPS site when transmitter battery failed.

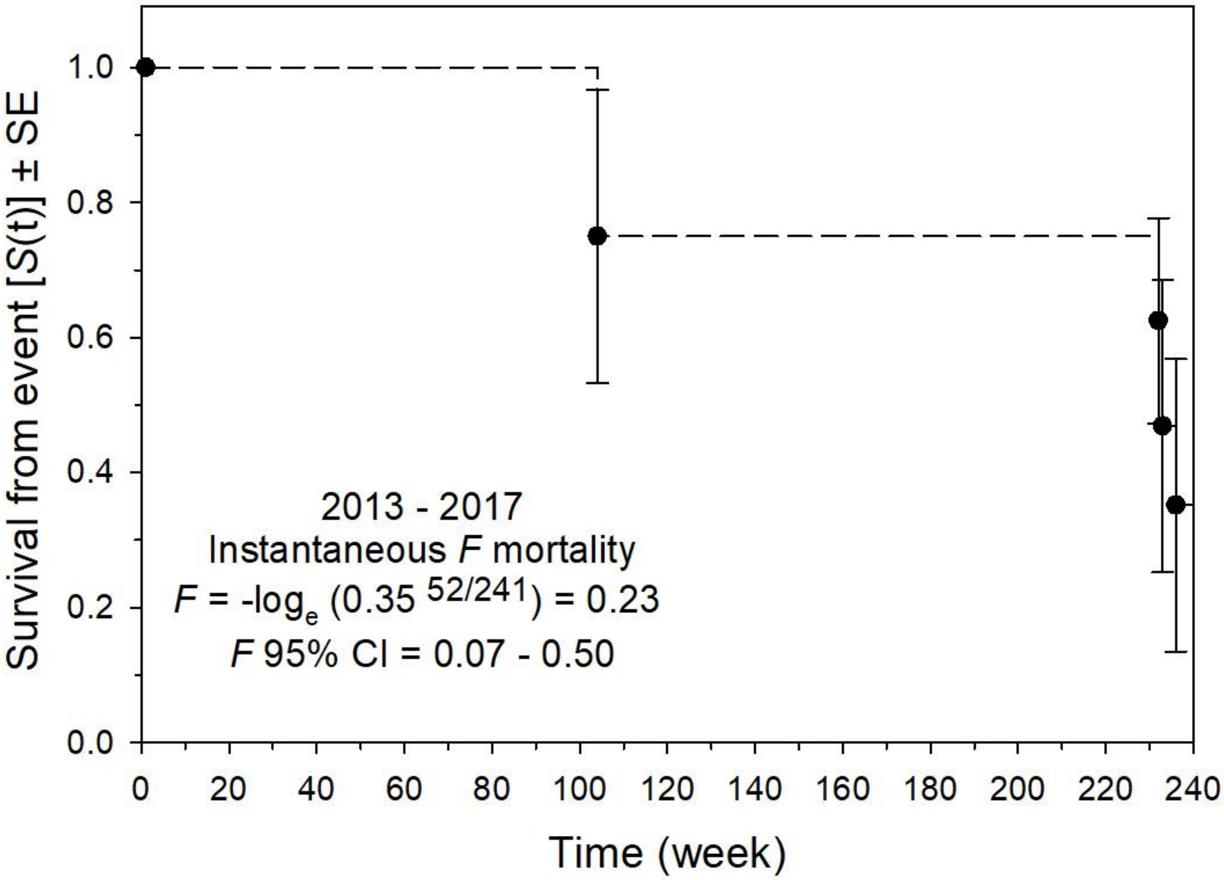

Figure 4-3: Survival (*S*) of gray triggerfish (*Balistes capriscus*) from fishing mortality for 2013 – 2017. Dashed line shows proportion of fish surviving fishing mortality after each weekly interval. Instantaneous fishing mortality rates (*F*) were calculated from *S* at 52 weeks. Points and error bars (SE) were conditional estimates of *S* for weekly time intervals with a mortality event.

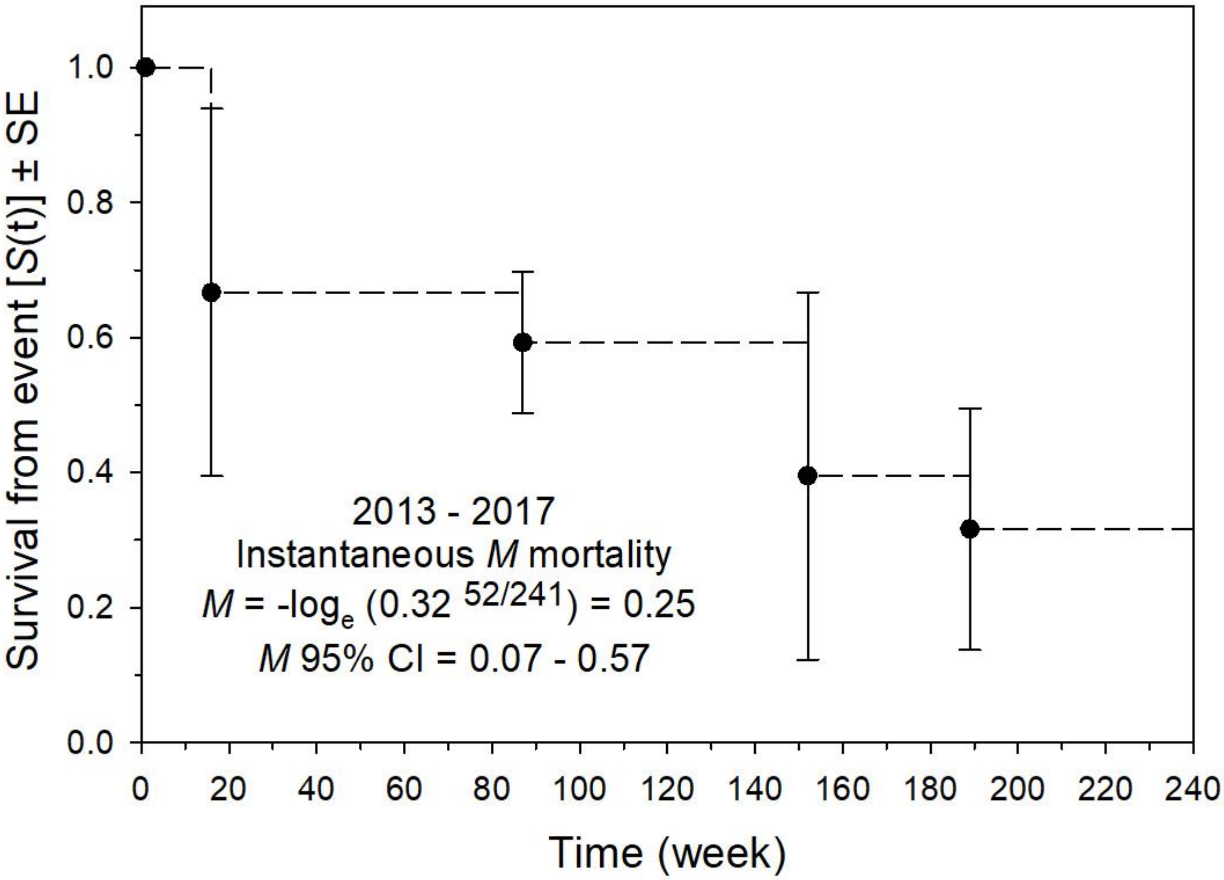

Figure 4-4: Survival (*S*) of gray triggerfish (*Balistes capriscus*) from natural mortality (*M*) for 2013 – 2017. Dashed line shows proportion of fish surviving after each weekly interval. Instantaneous natural mortality rates (*M*) were calculated from *S* at 52 weeks. Points and error bars (SE) were conditional estimates of *S* for weekly time intervals with a mortality event.

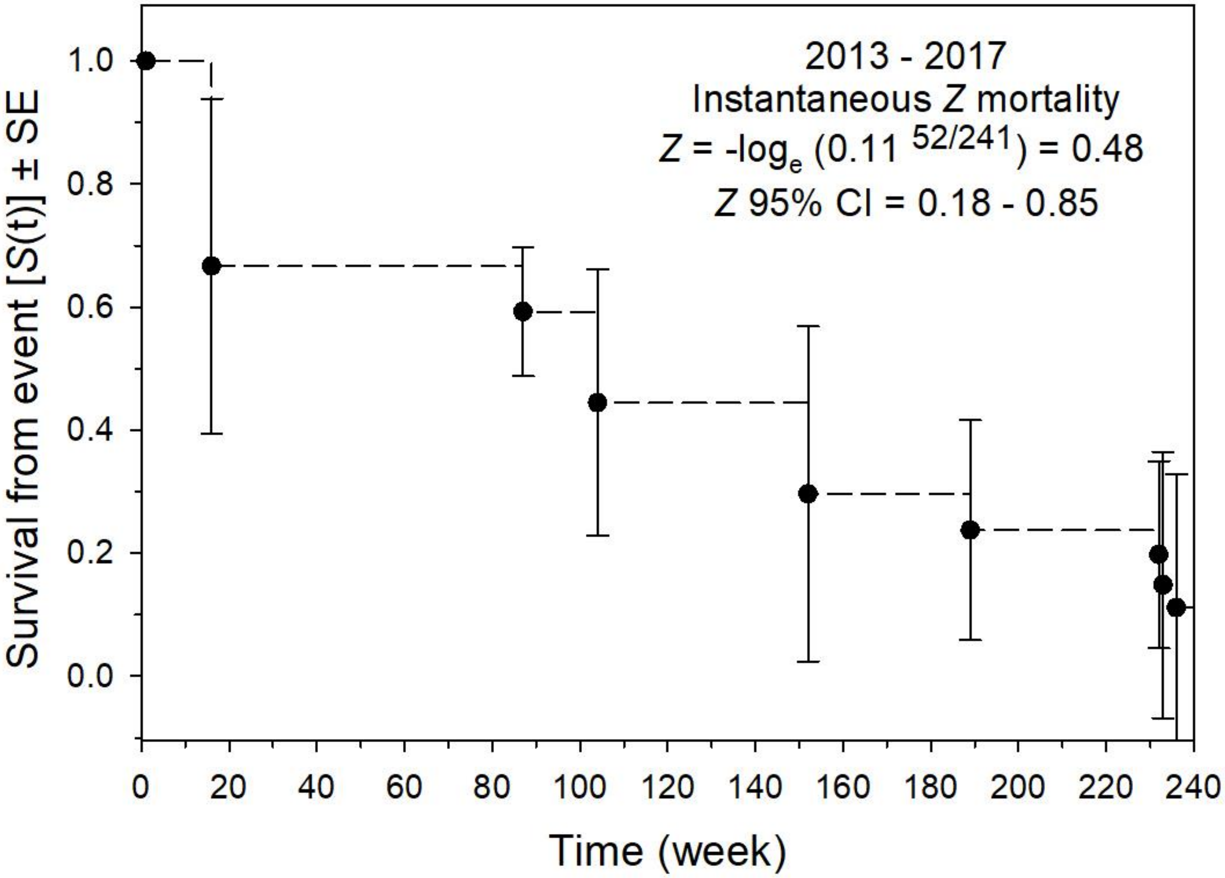

Figure 4-5: Survival (*S*) of gray triggerfish (*Balistes capriscus*) from all mortality for 2013 – 2017. Dashed line shows proportion of fish surviving after each weekly interval. Instantaneous total mortality rates (*Z*) were calculated from *S* at 52 weeks. Points and error bars (SE) were conditional estimates of *S* for weekly time intervals with a mortality event.