DUSK TRANSITION IN SUB-TROPICAL REEF FISH COMMUNITIES OFF OF NORTH AND SOUTH CAROLINA

A thesis submitted in partial fulfillment of the requirements for the degree

MASTER OF SCIENCE

in

MARINE BIOLOGY

by

DAVID P. COLES
AUGUST 2014

at

THE GRADUATE SCHOOL OF THE COLLEGE OF CHARLESTON

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ABSTRACT

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Although dawn and dusk periods comprise a relatively small part of the day, their importance as key ecological transition periods has been recognized for some time. Previous marine investigations into this transition have focused on tropical locations and have mostly been qualitative in nature. This project focused on the dusk period in sub-tropical reef fish communities off the coasts of North and South Carolina. High-definition underwater video was collected in 2013 and 2014 at a variety of sites featuring natural live-bottom habitat. Independent samples (43 videos) were obtained on 17 sampling dates. Fishes were tallied by time relative to sunset (TRTS) in an effort to identify temporal abundance patterns and categorize taxa by temporal niche. Sufficient data were collected for statistical analysis of 27 taxa, representing 15 families. Analyses explored whether there was a relationship between time and abundance. Of the taxa analyzed, ten showed no temporal pattern during the dusk period, seven showed abundance peaks during dusk, and ten showed declines in abundance during dusk. Patterns were not always consistent within families. In particular, the Serranidae and Sparidae families featured a variety of patterns. Uncommon species and ephemeral behavioral events were also noted and described.

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INTRODUCTION

Ecological theory holds that fishes divide most of their time between two basic activities: foraging and predator avoidance (Hobson, 1973; Helfman, 1978). Selection pressure over the millennia has resulted in ichthyofauna being adapted to maximize foraging efficiency, while minimizing risk of predation (McFarland *et al.*, 1979; Burrows *et al.*, 1994; Arrington and Winemiller, 2003; McCauley *et al.*, 2012). Predator avoidance most often takes the form of either schooling behavior or individuals seeking refuge (Hobson, 1972; Rooker and Dennis, 1991; Rooker *et al.*, 1997).

Numerous authors have documented temporal niche partitioning in fishes, with some primarily active by day, others by night, and a smaller number during "crepuscular" or twilight periods (Hobson, 1968, 1972; Collette and Talbot, 1972; Sbikin, 1977; Piet and Guruge, 1997). The selective forces at work in shaping this temporal community architecture are both biotic (competitors, predators, prey) and abiotic (light intensity, water temperature, etc.) (Piet and Guruge, 1997; Arrington and Winemiller, 2003). This diel rhythm is likely a product of both exogenous and endogenous cues, and possession of a circadian rhythm that syncs with external cues is thought to be adaptive (Payne *et al.*, 2012). Perhaps the most classic example of diel turnover was documented by Collette and Talbot (1972), with diurnal pomacentrids (damselfishes and clownfishes) trading hiding places with nocturnal apogonids (cardinalfishes). Diel replacement may be evidence of resource partitioning and avoidance of interference (i.e. direct) competition for space and other resources (Helfman, 1978; Piet and Guruge, 1997). Sbikin (1977) suggested that diurnal turnover in fish communities was evidence of efficient resource partitioning, enabling taxa to occupy a wide diversity of ecological niches.

Early observers noted peaks in abundance of piscivorous predators during twilight (Starck and Davis, 1966; Hobson, 1968; Collette and Talbot, 1972; Helfman, 1981). Multiple theories exist for why piscivorous predation may peak during twilight, and most of these have focused on ocular morphology of prey and predator fishes (Munz and McFarland, 1973; Helfman, 1978, 1993; McFarland *et al.*, 1979; Danilowicz and Sale, 1999). Piscivorous predators may see best under twilight conditions (Rickel and Genin, 2005). Twilight conditions backlight prey from below, giving crepuscular predators an advantage they can use to strike at their prey (Helfman, 1981; McFarland, 1991). Presumably, this phenomenon would become steadily less relevant with increasing depth, especially in turbid water (Helfman, 1981). Another factor explaining crepuscular predation peaks is an apparent loss of the protective qualities of schools under twilight conditions (Hobson, 1972). Early researchers noticed an apparent "quiet period," when there is an elevated threat of predation and neither diurnal nor nocturnal fishes are active (Collette and Talbot, 1972; Hobson, 1972; McFarland *et al.*, 1979; Danilowicz and Sale, 1999). Authors have variously described this period as falling between sunset and civil twilight (when the center of the sun falls 6 degrees below the horizon), which is a 10- to 15-min period (Collette and Talbot, 1972), and between sunset and 25-30 min after sunset (Hobson, 1972).

Exceptions to the pattern of twilight peaks in piscivory have been found (Danilowicz and Sale, 1999; Sancho *et al.*, 2000). If predation does not exhibit a crepuscular peak, then additional selective forces may be at play to explain changeover patterns (Danilowicz and Sale, 1999). For example, various authors have proposed that foraging, rather than predator avoidance, is actually the primary force dictating temporal niche, noting that nocturnal fishes have numerous adaptations for low-light foraging activity (Hobson *et al.*, 1981; Rooker and Dennis, 1991; Rooker *et al.*, 1997). Another reason it has been difficult to conclusively state that predation peaks during twilight is that observations of piscivorous predation have been so infrequent that statistical analyses comparing time periods have usually not been possible (Helfman, 1993). One challenge in collecting large amounts of predation data in live-bottom reefs is that, because of limited visibility, the spatial scale at which predator/prey interactions occur is often greater than the scale at which making observations is possible (Auster *et al.*, 2013).

Several researchers have found evidence of sequential turnover based on size, with the smallest diurnal species retreating first as night falls, and the largest crepuscular/nocturnal species emerging first as night falls (Sbikin, 1977; Potts, 1981; Rickel and Genin, 2005). This sequence has been speculated to reflect relative vulnerabilities (Hobson, 1972). At some point, the marginal benefit of adding another minute or two to a 10-14 h foraging period is simply outweighed by the cost of added predation risk (Rickel and Genin, 2005). Domm and Domm (1973) demonstrated an exception to this pattern, noting that intraspecific size differences do not correlate with differences in time of emergence/retreat, highlighting the need for further research on this topic. While turnover is generally believed to occur in mirror image at dawn/dusk (Hobson, 1972), some level of asymmetry has been demonstrated, perhaps owing to asymmetries in predation risk, hunger, and competition (Rickel and Genin, 2005).

Early researchers noted that, remarkably, temporal patterns are essentially the same around the world and therefore must be a result of universal selective pressures (Sbikin, 1977; Helfman, 1978). Investigators asserted that patterns found in the tropics, where the first studies were conducted, result from a long evolutionary history, and thus were likely to converge broadly across geographic regions, irrespective of community composition (Hobson, 1972; Sbikin, 1977). Helfman (1993) suggested that diel activity patterns may be vestiges of historic forces, and do not necessarily reflect current environmental and biological conditions. For example, even in systems lacking piscivorous predators, prey fishes tend to adhere to temporal niches that would seem adaptive for predator avoidance (Hobson, 1972).

A growing body of evidence is casting doubt on early theories regarding universal temporal niche architecture, suggesting greater levels of temporal plasticity than previously known (Reebs, 2002). Diel plasticity in fishes has been linked with differences in habitat (Fox and Bellwood, 2011), storm-caused turbidity (Collette and Talbot, 1972), in response to nutrition/hunger (Metcalfe and Steele, 2001), predator abundance (McCauley *et al.*, 2012), rainfall (Payne *et al.*, 2012), ontogeny (Helfman, 1978; Annese and Kingsford, 2005), reproductive seasonality (Helfman, 1981), and temperature (Fraser *et al.*, 1993). It is worth noting that the majority of these examples are correlative, and direct causation of diel plasticity has not typically been demonstrated. While conscious of the perils of over-generalizing the world's extremely diverse ichthyofauna, Reebs (2002) drew a rough dichotomy between marine fishes (sleeping, more rigidly circadian, and less plastic) and freshwater fishes (non-sleeping, less rigidly circadian, and more plastic); he attributed this phenomenon to the relatively stable conditions of marine waters, and resultant higher degree of specialization among marine fishes.

One factor complicating efforts to classify fish families by temporal niche is the diversity of ways various investigators have defined and measured activity. Typically, activity is defined as feeding, and inactivity is defined as resting or predator avoidance behavior (Helfman, 1978). School formation has been described by some authors as “inactive” behavior (Hobson, 1972; Ogden and Ehrlich, 1977; Helfman, 1978; Rooker and Dennis, 1991; Pereira and Ferreira, 2013). Times of peak feeding may not correspond to times of other “active” behavior, such as locomotion, reproductive, and other social activities (Helfman, 1978). When conducting direct observational surveys, before patterns of activity/abundance can be interpreted, it is important to note the various reasons why a given fish may not appear at any moment (having been observed at some other point during the same sample). If a fish is not seen at a given time, likely explanations are that it is (1) hiding – either in shelter, or via camouflage and/or inactivity, or (2) removed laterally or vertically from the habitat in question. The latter would not necessarily suggest inactivity, but rather a different type of activity, possibly including feeding migrations. Indeed we have a poor understanding of the importance of reefs vs. water column vs. adjacent soft-bottom habitats as feeding grounds for numerous fish species (Sedberry and Cuellar, 1993). Further complicating temporal categorization efforts is the fact that fishes lack eyelids, making it difficult to definitively determine whether they are sleeping (Reebs, 2002). Many fishes appear to be alert and active twenty-four hours a day.

Several investigators (Collette and Talbot, 1972; Gushima *et al*., 1977; Helfman, 1978, 1993; Nagelkerken *et al*., 2000) found that the time of day when fishes are active is a family-level characteristic, and listed which families are active at which times. Hobson (1974) found that those families active during crepuscular and nighttime periods tend to be carnivorous, while diurnal fishes tend to be herbivorous. Temporal categories are admittedly arbitrary, as most fishes are at least somewhat opportunistic and can occasionally be active outside of expected time periods (Helfman, 1978). Still, general trends in relative abundance are apparent and useful. According to several researchers, roughly two thirds of fishes globally are diurnal and one third nocturnal, with a small fraction crepuscular or cathemeral (active at all times) (Helfman, 1978; Piet and Guruge, 1997). Helfman (1993) stated that the ratio of diurnal:crepuscular:nocturnal species is remarkably similar between assemblages, with crepuscular species composing about 10% of the assemblage. It is worth cautioning that data for peak times of feeding may actually reflect temporal niche of their prey, as many fishes are opportunistic feeders (Helfman, 1978).

More recently, McCauley *et al*. (2012) reviewed diel classifications for a diverse suite of fish taxa, drawing from a broad variety of sources. Notably, this review does not include the category "crepuscular," so it is impossible to infer whether certain cathemeral or even "diurnal" species may demonstrate a crepuscular peak in activity. While the authors made no comment on whether diel niche is a family-level attribute, examination of the taxa described reveals some noteworthy patterns: Of 15 Pomacentridae species reviewed, representing seven genera, all were classified as diurnal (McCauley *et al*., 2012). This echoes characterizations made by a previous generation of ecologists, who also described damselfishes as diurnal (Gushima *et al*., 1977; Helfman, 1978). Of 39 Labridae species reviewed, representing 20 genera, all were described as diurnal (McCauley *et al*., 2012).

Two families reviewed by McCauley *et al*. (2012) included species from multiple temporal niches: Of six Lutjanidae species reviewed, representing three genera, two were described as diurnal, and four (all *Lutjanus* spp.) were described as cathemeral. Meanwhile, numerous researchers (e.g. Hobson, 1965, 1968; Starck and Davis, 1966; Randall, 1967; Helfman, 1978; McFarland *et al*., 1979; Rooker and Dennis, 1991; Nagelkerken *et al*., 2000; Zapata, 2013) suggested that lutjanids feed mainly at night, consistent with a cathemeral lifestyle featuring twilight feeding migrations. Of 15 Serranidae species reviewed by McCauley *et al*. (2012), representing four genera, 13 were described as cathemeral, one was described as diurnal, and one was described as nocturnal. This inconsistency may not be surprising, given that other authors have variously described serranids as mostly-crepuscular/mixed/unclear (Gushima *et al*., 1977; Helfman, 1978). While McCauley *et al*. (2012) did not review any Haemulidae taxa, several early researchers reported conflicting results, as Gushima *et al*. (1977) suggested haemulids (formerly Pomadasyidae) are diurnal, while Helfman (1978) suggested they are nocturnal.

Aims and Importance of Present Study

The present study is an investigation of sub-tropical reef fish communities during the dusk period, which, to my knowledge, has not previously been explored. To truly sample the fish community, sampling should be conducted throughout the diel period, as limiting sampling to daytime will give an incomplete assessment of stocks (Arrington and Winemiller, 2003; Carpentieri *et al.*, 2005; Roach and Winemiller, 2011; Harvey *et al.*, 2012a). Increasing our understanding of temporal patterns in fish behavior can improve management practices, for example by informing the design of sampling regimes used to monitor stocks. Expansion of this type of investigation into understudied habitats is a critical research need (Helfman, 1993; Harvey *et al*., 2012a). Gaining a better understanding of temporal partitioning in fish communities will be increasingly important in light of growing human impact; in many systems, fishing activity may drastically reduce abundance of top piscivores, and it will be important to be able to predict how fish communities may respond to these disruptions (McCauley *et al.*, 2012). While many studies have compared daytime vs. nighttime community composition (e.g. Nagelkerken *et al*., 2000; Azzurro *et al.*, 2007; Roach and Winemiller, 2011; Haley, 2012), studies including examination of dawn and dusk periods have been far more rare, and mostly qualitative (Collette and Talbot, 1972; Gushima *et al*., 1977; Sbikin, 1977; Rickel and Genin, 2005; Zapata, 2013). This study aims to provide quantitative information on a previously unstudied diel period and region.

I examined the dusk period at a variety of natural, live-bottom reef sites in the shelf region off of North and South Carolina. My objectives were to: (1) provide data on diel trends in habitat use by reef-associated fishes, (2) determine independent variables influencing diel patterns, (3) assign taxa to diel niche categories, including diurnal, nocturnal, crepuscular, and cathemeral, (4) determine if diel trends are consistent within fish families, (5) determine if diurnal taxa retreat sequentially by size, with smallest taxa retreating earliest, and (6) determine if piscivore abundance demonstrates a dusk peak.

My primary hypothesis was that, for many taxa, time of day would have a significant relationship with abundance levels.

METHODS

Sampling

The study area is within an area known as the Southeast U.S. Continental Shelf Large Marine Ecosystem, or SUSLME. The region is dominated by soft benthos, interspersed with patchy areas of hard-bottom (aka live-bottom) substrate, including ledges. Ledges cover between 1-5% of the shelf (Kendall *et al*., 2009). Hard substrates harbor a great diversity of epifauna, which in turn attract many reef-associated fishes. Notably, the region receives a warming influence from the Florida Current, making it habitable for some tropical fishes (Sedberry and Cuellar, 1993). This research was performed in a variety of natural, live-bottom reef habitats off North and South Carolina (Figure 1). It was decided that selecting sampling sites off the Carolina coasts, targeting live-bottom habitat, would provide an appropriate dataset for this investigation of local, reef fish community ecology. While known live-bottom sites were targeted for sampling, approximately 30% of sampling ended up occurring in adjacent sand-flats. The Marine Resources Monitoring, Assessment, and Prediction (MARMAP) program's sampling regime also includes some sampling of sand-flats near live-bottom reefs, taking into consideration the fact that there is some spillover of reef populations.

Data were collected by lowering video cameras onto the seafloor before sunset and retrieving them approximately 40 min later. The sampling period began 30 min before sunset and ended 10 min after sunset. Cameras were deployed ≥40 min before sunset, under the assumption that fishes would resume natural behavior by the beginning of the dusk sampling period, 30 min before sunset. Thus, while most videos obtained are well over one hour in length, only 40 min were thoroughly analyzed. (Note: On several occasions, logistical constraints prevented camera deployment at the desired time, resulting in an abbreviated observation period.) Canon™ Vixia HF SF200 and GoPro™ Hero2 cameras were used, recording continuous high-definition video. GoPro™ cameras were set to record footage at a video resolution of 960p - 30fps. The Canon™ footage was excluded from the analysis, based on the desire to avoid potential biases resulting from the use of two different aspect ratios and video resolution levels. However, the Canon™ footage was archived and is available for future analyses. For the present study, each GoPro™ camera from a given date was treated as an independent sample.

Sampling was conducted opportunistically using three vessels: the R/V *Palmetto* and R/V *Silver Crescent* (both owned by SCDNR), and a private SCUBA diving boat (Table 1). Sampling aboard the R/V *Palmetto* was conducted during MARMAP cruises on six dates from May – October of 2013. MARMAP uses baited chevron traps to sample fishes at a variety of live-bottom sites throughout the region. Locations for trap deployments are chosen randomly from a list of 2,500 stations at known, live-bottom habitat locations. MARMAP sampling occurs during daylight hours. For my research, this same, randomized approach was deemed appropriate, as the project aimed to assess community turnover for the broad region. In this case, traps were un-baited, and a GoPro™ camera was mounted on the front, top edge of each, with a Canon™ camera pointing 180° from the other (Figure 2). Three camera/trap combinations were deployed at each study site. Video was recorded continuously until trap retrieval. For most deployments, trap openings were also sealed with mesh, to prohibit fishes from entering the traps.

Sampling via private charter was conducted on five dates from July 2013 – January 2014. Each of three GoPro™ cameras was mounted on a custom-made, milk-crate camera stand weighted with 16 lbs of lead dive-weights (Figure 3). Video was recorded continuously until retrieval. The stands were dropped overboard on live-bottom sites indicating medium- to high-relief ledges on the vessel's sonar recorder. Some of these camera stands were subsequently maneuvered by SCUBA divers, who descended the tether line and moved the stand to point it toward structure, completing this action prior to the sampling period in most cases. Cameras were moved in order to point the camera toward reef features conducive to fish activity (e.g. high-relief ledges). Locations were selected based on recommendations from SCDNR employees and the captain's database of sites with high-quality live-bottom habitat and an abundance of fishes. The divers surfaced immediately after maneuvering the camera stands, and used the buoy lines to retrieve the cameras after dark. Sampling via the SCDNR's R/V *Silver Crescent* was conducted on six dates from October 2013 – January 2014. The methodology used on the private charter was replicated exactly, although SCUBA diving was not conducted.

Depth, date, season, water temperature, salinity, GPS coordinates of sampling locations, qualitative visibility ("good," i.e. clear water, or "bad," i.e. turbid water), and qualitative habitat type ("sand-flat" or "live-bottom") were recorded for each deployment. "Live-bottom" was defined as habitat featuring substantial presence of hard substrate, while "sand-flat" was defined as habitat featuring soft substrate largely free of structure. Visibility and habitat were determined during video analysis. Seasons were defined as spring (March – April), summer (May – August), fall (September – November), and winter (December – February). Temperature and salinity were recorded using a CTD sensor (Seabird Electronics, Inc. Model #19-03), a YSI sensor (YSI, Inc. Model #Pro 2030, length - 10 m), and a personal dive computer (Oceanic™ Veo 3.0), sometimes in concert.

Pre-dusk Sampling

On several occasions “pre-dusk” periods were also sampled, as part of a preliminary, sub-investigation, undertaken in the interest of exploring the possibility that ecological turnover was already underway by the beginning of the standard dusk sampling period. This sampling was conducted via the R/V *Silver Crescent* using the milk crate camera stand methodology described above. On three dates, 28-30 October, 2013, footage was collected in two waves, one well before the dusk sampling period and one covering the standard dusk sampling period, in approximately the same locations; because of currents, it was not possible to successively deploy cameras in the exact same location. Beyond cursory viewing, the “pre-dusk” samples were not analyzed, because the deployment locations and associated habitat differences between the day and dusk samples were sufficient to make comparisons impossible. A method of “extended dusk” sampling was conducted on two dates: 19-20 December, 2013. Cameras were deployed ≥70 min before sunset, and left in place throughout the duration of the standard dusk sampling period. Full video analysis was conducted for the four “extended dusk” samples obtained, providing continuous data from -70 TRTS to +10 TRTS. In addition to focused sampling efforts, substantial amounts of pre-dusk footage were recorded merely by deploying cameras a bit early. All of this was subjected to at least a cursory viewing, though not a thorough analysis. All uncommon taxa were noted.

Video Analysis

Footage was analyzed using QuickTime™ Player software. The cameras imprint time stamps, and the time is visible when using media players. For the purposes of this study, time relative to sunset (TRTS) was the relevant metric, and all times were converted to TRTS. Sunset time was determined using a NOAA calculator, (www.esrl.noaa.gov/gmd/grad/solcalc/), based on GPS location of sample, and ground-truthed by recording the time of the sun's complete disappearance beneath the horizon during sampling. Times prior to sunset were listed as negative TRTS values, and times after sunset as positive TRTS values, with sunset being time zero. The sampling period was divided into 1-min intervals, with each interval described by its TRTS. For example, the time period from 10 min prior to sunset to 9 min prior to sunset is listed as -10 TRTS. This approach enabled the analysis to treat time as an effectively continuous variable – a key consideration for quantitative study of temporal transitions. All samples were analyzed in their entirety; no subsampling was undertaken.

Fishes were identified, enumerated, and marked as present for each 1-min interval during which they appear on screen; a fish lingering on screen during successive intervals would be tallied for both intervals. However, to avoid repeat counts of the same individual, the conservative MaxN metric was used (Burge *et al*., 2012; Harvey *et al*., 2012b). MaxN is defined as the highest number of conspecifics visible on screen in a given time interval; in this case, a MaxN value was recorded for each minute of the sampling period. Fishes were identified to lowest taxonomic level possible. Unidentifiable fishes were tallied as well, to test for temporal differences in visibility. No attempt was made to estimate size of individual fishes, other than for the purpose of species identification. On average, video analysis took four-to-five times as long as the real-time duration.

In addition to analyzing the data on a taxon-by-taxon basis, I also pooled data for six taxa that can be classified as large, pelagic, piscivorous predators. All of these are fast-swimming, midwater species that are known to cruise above reefs and prey on smaller reef fishes. As higher trophic species, they are less abundant, making observations rare and reducing statistical power of species-specific analyses. To assess systemic patterns during the dusk period, aggregate abundance numbers for all taxa pooled (including unidentifiable fishes) were also tallied by time increment.

In addition to presence/absence data, other information was recorded from the video footage for use in a qualitative, descriptive component. For example, ephemeral events such as predation and reproductive activity were noted and described. Additionally, species that occur only rarely in the videos (fewer than eight observations) are listed (Table 2), but were omitted from further analyses.

As sampling was conducted from three different vessels using slightly different methodologies, an assumption was made that data from the different methodologies are comparable, as the deployments are identical at their essence. Trap effect, (e.g. chevron traps, being much larger than milk crates, and thus potentially "creating" structure), was assumed to be negligible.

Statistical Analysis

Statistical analyses were conducted to ascertain if there is a relationship between abundance (MaxN) and time (TRTS). Other covariates used in the analyses included habitat, depth, season, latitude, and (bottom) water temperature. Habitat and season were treated as discrete variables, while depth, latitude, and water temperature were treated as continuous variables. Covariates were included in order to standardize for their potential effect on abundance, i.e. to remove their effect. A Generalized Additive Mixed Model (GAMM) was used to analyze the data for each taxon, assuming a Poisson distribution for residuals around MaxN, and with TRTS nested within “sample” (i.e. video). A random effect of sample on the intercept was estimated. This analysis was performed using the mgcv package (Wood, 2011) in R (R Core Team, 2012). GAMM analysis was deemed appropriate because count data, such as temporal abundance patterns, are typically non-linear, and because data from individual samples (videos) are non-independent. In other words, data from within samples are expected to be more similar than data from across samples; this model allows data to be nested within individual samples. Based on an ANOVA table for the fixed effects of the GAMM, a backwards selection technique was used to sequentially remove the least significant covariate from the model until all remaining covariates were significant for each taxon. In some cases a non-significant covariate was retained in the model, as removal led to convergence problems within the GAMM model. A covariate was considered significant if $p<0.05$ for that term or for its smoother.

If a taxon did not appear at all in a given sample, that sample was excluded from the analysis. The rationale behind this decision was that if a taxon was not present at any point in a video, that sample would contribute no information about temporal trends for the taxon. Rather, it may simply reflect the fact that the taxon in question was not found in that location at all. If any individuals from the taxon in question were observed either before or after, but not during the dusk sampling period, zeros were inputted for all time increments of the dusk sampling period. Pooling at genus level was conducted either to increase sample size or based on inability to confidently distinguish similar congenerics in videos. For each taxon, plots were generated depicting raw MaxN vs. TRTS, mean (across samples) MaxN vs. TRTS, smoothed TRTS effect on MaxN, and predicted MaxN values for each time increment. The latter two plots were generated by GAMM analyses, and it is the smoothed TRTS effect on MaxN to which p-levels apply. Pseudo-confidence intervals around predicted MaxN were generated by bootstrapping.

Each fish taxon was categorized by its temporal abundance trend and its apparent temporal niche, and in certain cases, the niche assigned may not match the temporal pattern identified. For example, while it may be tempting to affix the label “diurnal” to all fish taxa showing declines in abundance after sunset, this approach would be overly simplistic. Fishes can be absent for a number of reasons, not all of which suggest inactivity, but rather a change in activity and/or location of activity. Beyond results from GAMM analyses, (which only indicate if there is a significant relationship between time and abundance), categorizations were also informed by visual examination of the various data plots, as well as life history characteristics of each taxon. P-levels were interpreted cautiously, as sample sizes were relatively small, and statistical theory suggests applying caution when interpreting p-levels from GAMM model results, as they are approximate in nature. In some cases, significant results were viewed skeptically, either because of p-levels close to the 0.05 threshold, or because of the disproportionate influence of isolated data points. In others, small sample size may explain lack of statistical significance, and I still comment on probable temporal niche for the taxon in question, based on visual examination of data plots.

RESULTS

In total, 43 independent samples (videos) were collected, representing 17 dates from May, 2013 through January, 2014 (Table 1). Sampling depths ranged from 20.6 – 32.2 m (Figure 1, Table 1). As noted, not every sample covered the complete 40-min sampling period; thus $n<43$ for certain time increments. Over 100 h of footage were recorded during the study, including dusk, pre-dusk, post-dusk, and archived Canon™ footage. The final amount of footage analyzed was approximately 30 h.

Information for 77 distinct taxa, representing 41 families, was gathered in this study (Table 2). Statistical analyses were conducted on all taxa observed in ≥8 samples (videos). Sufficient data were obtained for analysis of 27 taxa, 17 at the species level and 10 at the genus level (Table 3). Significance of abiotic parameters varied by taxon, and covariates included in the final GAMM model for each taxon are listed in Table 3. The following results are presented alphabetically by family, with brief reference to observed temporal patterns in abundance. Temporal abundance patterns refer to those observed during the dusk period (minutes scale) rather than over the temporal span of the study (months scale). Three basic patterns emerged: a decline in abundance, a dusk peak in abundance, and no change in abundance. Increasing abundance was not observed for any fishes.

Balistidae (one species). Gray Triggerfish (*Balistes capriscus*) displayed a temporal decline in abundance ($p=0.006$) (Figure 4).

Carangidae (one taxon). Banded Rudderfish (*Seriola zonata*), Almaco Jack (*S. rivoliana*), Greater Amberjack (*S. dumerili*), and Lesser Amberjack (*S. fasciata*) were pooled by genus to increase statistical power and because of difficulty distinguishing congenerics in videos, particularly *S. dumerili* vs. *S. fasciata*. *Seriola* spp. displayed a general temporal decline in abundance (p=0.0002), though there is some indication of a dusk abundance peak between -25 TRTS and -15 TRTS (Figure 5).

Carcharhinidae (one species). Atlantic Sharpnose Shark (*Rhizoprionodon terraenovae*) displayed no significant temporal abundance pattern (Figure 6).

Chaetodontidae (one taxon). Reef Butterflyfish (*Chaetodon sedentarius*) and Spotfin Butterflyfish (*C. ocellatus*) were pooled to increase statistical power. *Chaetodon* spp. displayed no significant temporal abundance pattern (Figure 7).

Haemulidae (two species). Tomtate (*Haemulon aurolineatum*) displayed a dusk abundance peak (p=9.11e-05) (Figure 8), while White Grunt (*H. plumierii*) showed no significant temporal abundance pattern (Figure 9).

Labridae (one taxon). Data were pooled by the genus *Halichoeres* because of difficulty distinguishing between several congenerics found in the region. *Halichoeres* spp. displayed a strong temporal decline in abundance (p=9.94e-13), with these wrasses disappearing entirely around sunset (Figure 10).

Lutjanidae (two species). Vermilion Snapper (*Rhomboplites aurorubens*) displayed a dusk abundance peak (p=1.18e-10) (Figure 11). Red Snapper (*Lutjanus campechanus*) exhibited a temporal decline in abundance (p=4.74e-09) (Figure 12).

Monacanthidae (two taxa). Orange Filefish (*Aluterus schoepfi*) and Unicorn Filefish (*A. monoceros*) were pooled to increase statistical power. *Aluterus* spp. exhibited a dusk peak in abundance (p=0.003) (Figure 13). Planehead Filefish (*Stephanolepis hispidus*) also exhibited a dusk peak in abundance (p=0.0253) (Figure 14).

Paralichthyidae (one taxon). Data were pooled by the genus *Paralichthys* because of difficulty distinguishing between several congenerics (e.g. Gulf Flounder (*P. albiguttata*), Southern Flounder (*P. lethostigma*), and Summer Flounder (*P. dentatus*)) found in the region. *Paralichthys* spp. displayed no significant temporal abundance pattern (Figure 15). However, it is worth noting that this taxon was never observed post-sunset.

Pomacanthidae (one species). Blue Angelfish (*Holacanthus bermudensis*) exhibited no significant temporal abundance pattern (Figure 16).

Pomacentridae (two taxa). Bicolor Damselfish (*Stegastes partitus*), Beaugregory (*S. leucostictus*), and Cocoa Damselfish (*S. variabilis*), were pooled to increase statistical power and because of the virtual impossibility of distinguishing between the latter two species in videos. *Stegastes* spp. exhibited a strong temporal decline in abundance ($p<2e-16$) (Figure 17). Yellowtail Reeffish (*Chromis enchrysura*) and Sunshinefish (*C. insolata*) were pooled to increase statistical power. *Chromis* spp. exhibited a strong temporal decline in abundance ($p<2e-16$) (Figure 18). There is some indication that *Chromis* spp. began disappearing from the environment prior to *Stegastes* spp.

Rhinobatidae (one species). Atlantic Guitarfish (*Rhinobatos lentiginosus*) displayed no significant temporal abundance pattern (Figure 19). However, this taxon was never observed post-sunset.

Serranidae (five taxa). Both Black Sea Bass (*Centropristis striata*) and Bank Sea Bass (*C. ocyurus*) displayed no significant temporal abundance pattern (Figures 20 and 21). Sand Perch (*Diplectrum formosum*) exhibited a weak temporal decline in abundance beginning around -15 TRTS ($p=0.046$) (Figure 22). Gag (*Mycteroperca microlepis*) and

Scamp (*M. phenax*) were pooled to increase statistical power. *Mycteroperca* spp. exhibited a temporal decline in abundance (p=8.43e-05) (Figure 23). Belted Sandfish (*Serranus subligarius*) also exhibited a temporal decline in abundance (p=0.019) (Figure 24).

Sparidae (five taxa). Scup (*Stenotomus chrysops*) and Longspine Porgy (*S. caprinus*) were pooled because of difficulty definitively distinguishing between the two species on videos. The majority of the specimens categorized as *Stenotomus* spp. are expected to be Scup, given their prevalence in the region compared to Longspine Porgy. *Stenotomus* spp. displayed no significant temporal abundance pattern (Figure 25). Sheepshead (*Archosargus probatocephalus*) also displayed no significant temporal abundance pattern (Figure 26). Red Porgy (*Pagrus pagrus*) exhibited a temporal decline in abundance (p=0.017) (Figure 27). Data from several congenerics (primarily Knobbed Porgy (*Calamus nodusus*)) were pooled because of difficulty identifying the congenerics to the species level. *Calamus* spp. exhibited a dusk peak in abundance, from approximately -10 TRTS to sunset (p=0.001) (Figure 28). Spottail Pinfish (*Diplodus holbrookii*) also exhibited a dusk peak in abundance, from approximately -15 TRTS to -10 TRTS (p=4.02e-15) (Figure 29).

Tetraodontidae (one taxon). Goldface Toby (*Canthigaster jamestyleri*) and Sharpnose Puffer (*C. rostrata*) were pooled because of difficulty distinguishing between the two species in videos. *Canthigaster* spp. displayed a temporal decline in abundance (p=0.002) (Figure 30).

Pooled predators. Pooled predators [Atlantic Sharpnose Shark (*R. terraenovae*), Common Thresher Shark (*Alopias vulpinus*), Cobia (*Rachycentron canadum*), Great

Barracuda (*Sphyraena barracuda*), mackerel (*Scomberomorus* spp.), and jacks (*Seriola* spp.)] exhibited a temporal decline in abundance (p=0.0001) (Figure 31).

Unclassified Fishes and All Fishes Pooled. The abundance of unidentifiable fishes showed no significant temporal trends (Figure 32). The abundance of all taxa pooled, including rare and unidentifiable fishes, had a significant relationship with TRTS, declining slightly during the dusk sampling period (p=1.05e-04) (Figure 33).

Pre-dusk Observations

In the four “extended dusk” samples, MaxN counts showed noticeable declines between -70 TRTS and -30 TRTS for *Halichoeres* wrasses, *Chromis* damselfishes, and *Stegastes* damselfishes, with most of the decline occurring between -40 TRTS and -30 TRTS. No decline was apparent for any other taxa. Statistical analysis was not conducted, given the small sample size. There were seven taxa observed exclusively before the dusk sampling period, including “pre-dusk” samples, “extended dusk” samples, and footage recorded merely by deploying cameras a bit early (Table 2): juvenile African Pompano (Carangidae – *Alectis ciliaris*), Scrawled Filefish (Monacanthidae – *Aluterus scriptus*), Bullnose Ray (Myliobatidae – *Myliobatis freminvillei*), Smooth Dogfish (Triakidae – *Mustelus canis*), Great Hammerhead Shark (Sphyrnidae – *Sphyrna mokarran*), Sea Lamprey (Petromyzontidae – *Petromyzon marinus*, which were attached to the hammerhead shark), and a lone squirrelfish (*Holocentrus* sp.).

DISCUSSION

Experimental Design

In the present study, absent the use of artificial lights, the video in almost all cases becomes unreadable by 12 min after sunset, dictating the duration of the sampling period, somewhat. This falls roughly, though not perfectly, in line with the ideal dusk sampling period; other authors have variously suggested that the dusk turnover period covers 30 min around sunset (Rickel and Genin, 2005), from 30 min before sunset to 10-15 min after sunset (Sbikin, 1977), or until 45 min after sunset (Hobson, 1972). Thus, the scope of the present research focuses on the earlier segment of the dusk transition and does not include data collection for the emergence of nocturnal fishes from daytime shelter. The decision to tally fish abundance by 1-min increments allows time to be treated as an effectively continuous variable, which I felt was important for studying temporal transitions. This stands in marked contrast to previous studies (Powles and Barans, 1980; Nagelkerken *et al*., 2000; Carpentieri *et al*., 2005; Azzurro *et al*., 2007; Roach and Winemiller, 2011; Haley, 2012; Harvey *et al*., 2012a) which have treated time as a categorical variable and compared community composition in day *vs.* night.

Subsampling, which has been employed by numerous researchers using video to collect data (e.g. Burge *et al*., 2012; Bacheler *et al*., 2013), is a means of optimizing data collection given limited resources. While it would have saved considerable time in this study, video analyses entailing subsampling have drawbacks, as key moments may fall just outside the sampled segment (Bacheler *et al*., 2013; D. Glasgow, pers. comm.), and this tradeoff was deemed unacceptable.

While numerous observational studies have used bait to attract fishes (Sbikin, 1977; Burge *et al.*, 2012; Harvey *et al.*, 2012a), there are also pros and cons to this practice, which have been debated (Powles and Barans, 1980; Posey and Ambrose, 1994). For the present study, the choice of un-baited traps was made in an effort to minimize affecting normal fish behavior.

Checks Against Potential Biases

As a check against potential diel biases in visibility and fish identification, I analyzed temporal abundance data for unclassified fishes and for all fishes aggregated. The flat trend found for unclassified fishes bolsters confidence levels in the overall findings, as it suggests there was no significant reduction in the ability to identify fishes later in the dusk sampling period. The dusk period pattern of declining abundance for all taxa aggregated is not surprising, as this dataset pools together fishes exhibiting three basic patterns: decline, dusk peak, and flat line. Despite the statistically significant decline, examination of the mean MaxN values over time shows that overall numbers do not differ greatly. This observation, viewed in concert with the aforementioned lack of a relationship between TRTS and MaxN for unclassified fishes, helps alleviate concerns that temporally declining numbers of observations might actually reflect reduced visibility. On a related note, given that there is no reason to expect all species to behave identically, had all taxa analyzed demonstrated declines in abundance as dusk proceeded, that would be strong evidence of a diel visibility bias. That this pattern was not observed, coupled with the measurements mentioned above, leads me to conclude that there was no diel bias in my study. The fairly steady overall levels are also evidence of temporal resource partitioning; there are fishes active at all times of the day, but during any given time period, different fishes are active. There was no evidence of the so-called "quiet period" described by other authors, after diurnal fishes have retreated but before nocturnal fishes have emerged.

While video censuses have their own biases when compared to other census methodologies, these biases should not be problematic in studies of intra-specific relative abundance, as long as the methodology is consistent throughout the experiment. As a metric, MaxN also has its own biases, but is an effective tool for measuring relative abundance in video analyses (Harvey *et al.*, 2012a). Burge *et al.* (2012) argued that MaxN may lead to underestimates of solitary species. In contrast, Schobernd *et al.* (2013) found that MaxN may underestimate abundant species, and proposed that an alternative metric known as MeanCount (i.e. the average number of conspecifics observed in a series of snapshots over a viewing period) may be superior.

Temporal Niches

Several temporal niche utilization patterns were inferred, based on observed abundance patterns as well as knowledge of diet and life history characteristics. Some exhibited notable temporal patterns:

Diurnal Fishes

Eight of the taxa analyzed appear to be diurnal. Six of these exhibited significant declines in abundance during the dusk period: *Halichoeres* spp., *Stegastes* spp., *Chromis* spp., Belted Sandfish, Red Porgy, and *Canthigaster* spp. For two others, *Paralichthys* spp.

and Atlantic Guitarfish, while there was no statistically significant pattern, there was some indication of a decline in abundance during dusk.

Halichoeres spp. wrasses (family Labridae) exhibited a strong temporal decline in abundance and disappeared entirely around sunset. Wrasses are visual, planktivorous feeders (Hobson, 1975). Given this, the diurnal lifestyle observed in this study is not surprising. Like many labrids, wrassses are known to sleep (Reebs, 2002) and thus probably have a strict temporal niche. They are also small and vulnerable, and appear to seek shelter in which to safely sleep. Pomacentrids are small, vulnerable, strongly reef-dependent fishes, and the diurnal pattern observed in *Stegastes* spp. and *Chromis* spp. is consistent with findings from other systems around the world (Rooker and Dennis, 1991; Al-Zibdah and Kan'an, 2009; McCauley *et al.*, 2012). Pomacentrids are visual feeders (Hobson, 1975); most are herbivorous or omnivorous midwater planktivores, though some feed on benthic algae or invertebrates (Hobson, 1975; Al-Zibdah and Kan'an, 2009). Of the pomacentrids observed in the present study, Yellowtail Reeffish swam farthest above the reef at the beginning of the dusk sampling period, eventually retreating to safety as darkness fell. Belted Sandfish (family Serranidae), which exhibited a decline in abundance toward the end of the dusk sampling period, is behaviorally quite different from many of the other serranids observed in the present study. Their behavior is much more similar to that typical of pomacentrid fishes; they demonstrate strong reef association, and dart in and out of crevices. They are small and vulnerable, and their disappearance toward the end of the dusk period makes intuitive sense, as they are likely taking shelter in reef crevices. Similarly, the *Canthigaster* spp. (puffers) are small, slow-swimming fishes that have a strong reef association and likely take shelter at night.

While *Paralichthys* spp. flounders and Atlantic Guitarfish displayed no significant diel change in abundance, they were never observed post-sunset, leading me to suspect that these are diurnal taxa. That the temporal patterns were not statistically significant, despite the complete disappearance after sunset, most likely reflects the small sample size. Flounder appeared in only ten videos, and Atlantic Guitarfish appeared in only eight, and MaxN was never an integer other than one or zero, making statistical analyses challenging. While the reduction in observations after sunset may fairly be explained by these taxa's cryptic attributes, making it impossible to detect these fishes on videos, that does not necessarily negate the notion that they taxa may be "inactive" at night. If they were actively feeding, their locomotion would make them visible; only when resting on the substrate is their behavior cryptic.

Cathemeral Fishes

Twelve of the taxa analyzed appear to be cathemeral. Seven of these exhibited no significant diel abundance pattern: *Chaetodon* spp., White Grunt, Blue Angelfish, *Stenotomus* spp., Sheepshead, and two congenerics from the Serranidae family, Black Sea Bass, and Bank Sea Bass. For three other taxa, *Mycteroperca* spp. groupers, Red Snapper, and Gray Triggerfish, the declining abundance observed during the dusk period in all likelihood does not reflect diurnalism, and is probably explained by feeding migrations away from the reef. For two taxa, Tomtate and Sand Perch, statistical significance was weak, and does not provide convincing evidence of a diel abundance pattern.

Black Sea Bass was the most commonly encountered species in terms of number of samples in which they were observed, and this is consistent with MARMAP's findings (SEDAR, 2011). Black Sea Bass abundance was steady through all periods, and they were often observed well after the dusk sampling period, in videos where water clarity was high enough to allow fish identification beyond +9 TRTS. They have a generalized diet, but it is strongly associated with hard-bottom habitat (Sedberry, 1988). Black Sea Bass mostly consume motile, epibenthic invertebrates, including amphipods, decapods, and small fishes, but they also consume some sessile ascidians. While Sedberry (1988) reported Black Sea Bass to have a strong dependence on hard-bottom habitats, in the present study they were widely observed on sand-flats as well. No evidence of a diel migration to/from reefs was observed, as Black Sea Bass abundance remained steady throughout the sampling period in both habitat types. However, given that hard-bottom habitats were targeted, even videos from sand-flats are presumably quite close to hard-bottom habitat.

Scup, [for the purposes of this discussion, all *Stenotomus* spp. observed are assumed to be Scup (*S. chrysops*)], are schooling fish known to be benthic feeders, preying on a diverse suite of primarily invertebrate taxa, both epifaunal and infaunal, and especially in soft benthos (Steimle *et al*., 1999). In the present study, Scup were observed rooting prey out of the sand in many of the videos; similar behavior was also observed for another genus of sparids – the *Calamus* spp. Scup is a demersal species, using both structured and unstructured areas for feeding (Steimle *et al*., 1999); this matches observations here, as Scup were abundant in both hard-bottom and sand-flat habitats. Sedberry and Cuellar (1993) reported that Scup feed diurnally, and have the same prey noted for Vermilion Snapper. That Scup forage diurnally and Vermilion Snapper nocturnally suggests temporal resource partitioning (Sedberry and Cuellar, 1993). However, I observed no decrease in activity in Scup as dusk proceeded, an indication that this species is not strictly diurnal. Chaetodontids (butterflyfishes) and Blue Angelfish both exhibit strong reef association and may have been expected to take cover at night. However, I found no indication of such behavior; if they do take cover, it may occur later in the dusk period, after the conclusion of the dusk sampling period used here.

Mycteroperca spp. groupers and Red Snapper both exhibited a decline in abundance during the dusk period. However, these are relatively large fishes that would be unable to take shelter in most reef structure found in this region, and would only be susceptible to predation by the very largest top predators. I suggest that both taxa are cathemeral, as this declining abundance may merely reflect a change in activity; they may be heading away from the reef either laterally or vertically in order to feed. While many authors have suggested that lutjanids feed mainly at night, (Hobson, 1965, 1968; Starck and Davis, 1966; Randall, 1967; McFarland *et al*., 1979; Rooker and Dennis, 1991; Nagelkerken *et al*., 2000; Zapata, 2013), Red Snapper may be an exception. Ouzts and Szedlmayer (2003) reported that Gulf of Mexico Red Snapper fed during all diel periods, although gut fullness was lower at dusk vs. daytime. While they have long been known to be piscivorous (Randall, 1967), in the northern Gulf of Mexico they also eat tunicates and crabs, and feed over a mixture of sand, reef, and mixed habitats (Ouzts and Szedlmayer, 2003). The same study found that fishes were the most important prey during all diel periods, but, of secondary prey sources, crabs dominated dusk (the 30 min after sunset) and night periods. Thus, it is possible that Red Snapper are migrating away from reefs to feed on nocturnally active crabs, which commonly are found on soft substrates (Ouzts and Szedlmayer, 2003). More recent MARMAP studies have suggested that Red Snapper also prey on swimming crabs and rock shrimp, both of which migrate vertically at night; it is possible that Red Snapper swim up in the water column to feed on these crustaceans at night (S. Goldman, pers. comm.).

Gray Triggerfish were observed only over reef habitats and showed a temporal decline, disappearing from the reef after sunset. Details of their diet and life history offer clues as to where they may have gone. Gray Triggerfish are opportunistic predators; while they are morphologically specialized for armored invertebrate prey, they also eat un-armored prey, and among their main prey are barnacles, bivalves, polychaetes, decapod crabs, and echinoderms, including sand dollars (Vose and Nelson, 1994). They have been described as diurnally active, based on day- and night SCUBA observations and gut contents of specimens collected nocturnally (Vose and Nelson, 1994). I suggest that Gray Triggerfish may actually be cathemeral, leaving the reef around sunset to feed on nocturnally active decapods. Decapods are only a secondary prey source, so the relatively low gut contents at night may reflect the lesser importance of this feeding period. Additional work needs to be undertaken to understand nocturnal behavior of Gray Triggerfish.

Tomtate (family Haemulidae) displayed higher abundances during diurnal periods, with a slight dusk abundance peak. However, this appears to be driven by activity of large schools in a handful of samples. Indeed, the removal of data from a single video resulted in loss of statistical significance (results not shown). Thus, I suggest that Tomtate are actually cathemeral. Tomtate are known to feed in soft substrates near reef areas, on infaunal invertebrates (Randall, 1967; Sedberry, 1985; Zapata, 2013). Haemulids rest near hard substrates by day, and conduct twilight migrations to/from soft-bottom foraging grounds – behavior some authors have characterized as nocturnal (Hobson, 1965, 1968, 1973; Starck and Davis, 1966; Ogden and Ehrlich, 1977; McFarland *et al*., 1979; Rooker and Dennis, 1991; Nagelkerken *et al*., 2000; Zapata, 2013). Exceptions exist, as certain *Haemulon* species have been shown to feed actively by day (Pereira and Ferreira, 2013). In the southeast US Atlantic shelf, Tomtate demonstrate the more typical lifestyle, foraging on adjacent soft-bottom habitats at night (Sedberry, 1985; Zapata, 2013). Given what we know about this species, and that in the present study they were widely observed on both hard and soft substrates, it was imperative to compare temporal trends by habitat type. While habitat was a significant covariate, Tomtate showed fairly steady abundance levels throughout the sampling period on each habitat type. It is possible that the dusk migration to soft-bottom habitats is imperceptibly subtle in the SUSLME; as all hard-bottom zones are patchy, Tomtate may not need to migrate laterally to find suitable foraging grounds. It is worth noting that pooling by genus was conducted for numerous taxa, under the assumption that congenerics would have similar behavior and diel pattern. The differences in diel abundance patterns observed for the two *Haemulon* spp. serves as a cautionary example that this might not always be an appropriate assumption. Among other behavioral differences, Tomtate (*H. aurolineatum*) form schools, while White Grunt (*H. plumierii*) were usually observed alone or in pairs. As with Tomtate, the diel pattern shown for Sand Perch is not convincing. Sand Perch exhibited a decline in abundance beginning around

-15 TRTS, but this decline is extremely weakly significant (p=0.046), and I suggest that this is actually a cathemeral species.

Dusk Peak

Seven of the taxa analyzed appear to have dusk peaks in activity. Five of these exhibited significant dusk peaks in abundance: Vermilion Snapper, *Aluterus* spp., Planehead Filefish, *Calamus* spp., and Spottail Pinfish. For two others, Atlantic Sharpnose and *Seriola* spp., plus the group formed by pooling data from large, midwater piscivores, the data showed either a lack of a diel pattern or a decline in abundance; however, there is some indication of a dusk peak in abundance.

Of the taxa displaying significant dusk peaks in abundance, none are large piscivores, the group for which such a pattern would have been predicted. The patterns observed may be explained by dusk planktivory and/or feeding migrations between reefs and soft substrates. One example is Vermilion Snapper, for which the observed pattern of increased abundance around sunset is consistent with the life history patterns of the species. They prey on small nekton and zooplankton (Grimes, 1979), and on soft-benthos, infaunal invertebrates that swarm in the water column at night (Sedberry and Cuellar, 1993). Vermilion Snapper feed most actively during dusk and at night (Grimes, 1979; Sedberry and Cuellar, 1993). They are relatively inactive by day, moving slowly in large schools near the bottom (Sedberry and Cuellar, 1993). The signal shown in the present study is influenced by the result of a single sample in which a school of ~100 small Vermilion Snapper was observed from -21 TRTS to -4 TRTS. It is likely that added sampling effort would produce further evidence of dusk activity, even if the data from the large school were exclude from analyses.

While Atlantic Sharpnose Shark displayed no significant change in abundance during the dusk period, they were most abundant from -20 TRTS to -10 TRTS. Though this dusk abundance spike was not statistically significant, this pattern is consistent with expectations for large, midwater piscivores, and may reflect the relatively low sample size. Curiously, most other fishes, including potential prey fishes, appeared to ignore these sharks. *Seriola* spp., which showed a general temporal decline in abundance, also exhibited some indication of a spike in abundance levels from -25 TRTS to -15 TRTS. This is a taxon for which little is known about diel activity patterns, and the pattern found is intriguing. These jacks feed on fishes, cephalopods, and decapod crustacea (Manooch and Haimovici, 1983). While feeding excursions over reef areas are known (Randall, 1967; Manooch and Haimovici, 1983), feeding is not limited to areas over reefs, as they also feed in the water column, including near the surface. It is possible that the dusk spike observed in the present study reflects heightened twilight vulnerability of prey fishes, although one might predict such a spike to occur later in the dusk period, i.e. near sunset. Interestingly, one of this study's only observations of piscivorous predation occurred well before dusk, on 10/30/13, when a school of Greater Amberjack (*S. dumerili*) ambushed a school of scad (*Decapterus* sp.). The timing of a second observation of predation, on 11/10/13, was more in line with expectations, however, when a single *Seriola* sp. individual was seen attacking a mixed school of Tomtate and Vermilion Snapper at -3 TRTS. Contrary to expectations, the pooled data for large, midwater predators showed a steady temporal decline during the dusk period, rather than the crepuscular peak that was predicted. However, there is some indication of a peak in abundance from -25 TRTS to -15 TRTS, which may reflect cruising behavior related to heightened vulnerability of prey under twilight conditions. As with the *Seriola* spp., one might have expected this peak to occur closer to sunset. Despite the lack of clear evidence found in this study, midwater piscivores can still fairly be described as having dusk activity peaks.

Pre-dusk Observations

The preliminary, pre-dusk sampling experiment was conducted after analyzing early samples, as it became apparent that light levels probably drop sooner in this region vs. in the tropics. Thus, I began to question whether turnover may have already commenced by the beginning of the sampling period, and if some diurnal taxa may already be inactive/absent by this time. The small sample size for this secondary investigation precluded rigorous, quantitative analysis, but offers some preliminary insights and pathways for future research efforts. As noted in the results, there was limited evidence of a reduction in abundance between -40 TRTS and -30 TRTS for several taxa. To err on the side of caution, future studies may consider beginning the sampling period ten minutes earlier, at -40 TRTS, but it is debatable whether the benefits of such an extension would outweigh the costs of the additional analysis effort. Additionally, seven taxa were observed exclusively before the sampling period. Two interpretations of these results are possible: (1) they are not seen in dusk samples because they are already inactive or absent from the given habitat by -30 TRTS, or (2) they are not seen in dusk samples simply because they are rare taxa that are less likely to be observed at any time. The latter explanation seems more plausible, but further work would need to be performed to answer this question.

Behavioral Observations

Predation: In one pre-dusk sample (12/20/13), a school of Yellowtail Reeffish reacted synchronously to an unseen, apparent threat, darting down toward the shelter of the reef for a moment, and rising again once the threat had apparently passed. In one sample (8/8/13), a Sheepshead sped away after a Great Barracuda appeared, around -11 TRTS. In a pre-dusk sample (12/19/13) a Tomtate was observed preying on a severed half of an unidentified fish. **Reproductive Behavior**: On 5/29/13, possible courtship behavior was observed for a pair of Planehead Filefish. This pair was swimming purposefully at an extremely rapid rate, a sharp contrast to the seemingly aimless, languorous movement pattern that this species typically displays. In two videos recorded on 5/29/13, pairs of Scamp displayed apparent courtship behavior, chasing each other back and forth throughout much of the observation period, while occasionally displaying different color morphs. Histological evidence from gonadal tissue suggests that Scamp, like many groupers, spawn around sunset (Harris *et al*., 2002), so the timing of this courtship is not surprising. Scamp in several color morphs were also observed in a sample from 11/10/13. **Symbioses**: In two pre-dusk samples from the same date (10/30/13), Cobia were observed closely trailing a Roughtail Stingray (*Dasyatis centroura*). Similar associations between Cobia and large rays have been reported elsewhere in the literature (Smith and Merriner, 1982). In one video (8/8/13), a school of seven Atlantic Bumper (*Chloroscombrus chrysurus*) was observed associating with a

Loggerhead Sea Turtle (*Caretta caretta*). The bumpers swam just above the turtle's head, perhaps gaining some protective advantage by associating with such a large animal. In a pre-dusk sample (10/30/13), two Gag were observed being cleaned by scad (*Decapterus* sp.). In a pre-dusk sample (10/29/13), a mixed school of about a dozen sharks was observed. While the school was mostly Atlantic Sharpnose, at least one Smooth Dogfish swam alongside the others. **Rare Sitings**: On 6/17/13, a school of post-larval (10-15 mm) fishes was observed swimming by the tether rope. Direct observations of such small fishes are uncommon in this system (D. Glasgow, pers. comm.). In one sample (10/29/13), an intermediate phase Hogfish (*Lachnolaimus maximus*) was observed at sunset.

Sequential Retreat

Results from this study offer limited support for the theory that diurnal fishes retreat sequentially, based on size, (and presumed vulnerability). In looking for evidence of a sequential retreat according to size, not all diurnal taxa are relevant. Only the five taxa that demonstrate strong reef association and obvious shelter taking as dusk proceeded are discussed here. The sequence of retreat, along with crude turning points (i.e. the TRTS when they begin to sharply decrease in abundance) are as follows: *Chromis* spp. (-15 TRTS), *Stegastes* spp. (-10 TRTS), *Halichoeres* spp. wrasses (-10 TRTS), Belted Sandfish (-5 TRTS), and *Canthigaster* spp. (+2 TRTS). This roughly corresponds with size, although size differences between the taxa are minimal.

Temporal Niche: A Family-Level Attribute?

The pattern of pomacentrid diurnalism noted by earlier authors (Gushima *et al*., 1977; Helfman, 1978; McCauley *et al*., 2012) also holds true in the present study. Likewise, the pattern of labrid diurnalism (McCauley *et al*., 2012) also matches observations made in the present study. While other authors have disagreed about the temporal niche of Haemulidae (Gushima *et al*., 1977; Helfman, 1978), in the present study, I found no convincing evidence of a diel pattern in the two haemulid species analyzed, suggesting a cathemeral lifestyle. As for lutjanids, in the present study, *L. campechanus* appears to be a cathemeral species, matching findings in McCauley *et al*. (2012), who describe all four *Lutjanus* spp. reviewed as cathemeral. In the present study, three of the five serranid taxa analyzed were found to be cathemeral, while two, *Mycteroperca* spp. and Belted Sandfish (*Serranus subligarius*), were found to be diurnal. This inconsistency matches earlier, conflicting findings (Gushima *et al*., 1977; Helfman, 1978; Sedberry and Cuellar, 1993; McCauley *et al*., 2012). Belted Sandfish is a clear example of a species with drastically different behavior than that of some other family members, suggesting that it may be too simplistic to call temporal niche a family-level characteristic, especially for large, diverse families. That said, family does seem to be a good predictor of temporal niche.

Directions for Future Research

Future extensions of this research would entail a methodology allowing examination of the latter stages of the dusk period, including the emergence of nocturnal fishes. Such a methodology would necessarily entail the use of some form of artificial lights, ideally one that is not perceived by fishes. Recently developed blue-light LED technology may permit nighttime sampling with minimal disturbance to fishes (Harvey *et al.*, 2012b). Given the impracticality of switching on lights in the middle of a sampling period, (at least while using remote cameras, as in the present study), cameras would have to be deployed before sunset with lights already turned on; whether this would reduce the footage quality for the relatively bright, pre-sunset portion of the dusk sampling period, is unclear. This would also require longer battery life and larger memory cards than those used in the present study. While cost and practical considerations precluded the use of such lighting here, at the rate technology is changing, such modifications to the methodology should be practical and affordable in the relatively near future.

Increasing the sampling effort may elucidate more details in behavioral patterns. The highly variable nature of both biotic and abiotic field conditions complicates efforts to draw conclusions, as any given observation could reflect a stochastic event. Only by scaling up the sampling effort could we increase the ratio of signal:noise. The labor-intensive nature of video analysis (at least four hours of analysis were required for each one hour of footage) means that any increase in sampling effort would have a multiplier effect on the scope of work necessary to complete an analysis.

Deepening the investigation beyond abundance counts would also be a worthwhile direction for future extensions of this research. Increased scrutiny over specific fish behaviors would provide insight into not only abundance trends, but also activity types, including temporal changes in behavior. While certain obvious behaviors cannot be missed, even while only concentrating on abundance tallies, many subtler activities inevitably escape the eye of the video analyst. Such an extension of the research would be impractical to pursue for the nearly one hundred taxa observed in this study, as often there is too much simultaneously happening on the screen to record all behavior observed. A targeted approach toward a handful of taxa, or even a single taxonomic group, would be feasible, though.

Qualitative observations in the present study made clear the fact that light levels at dusk vary seasonally; in winter samples, phytoplankton levels were lower and light attenuation was reduced accordingly. This begs the question: Do fishes respond more to external cues, (i.e. light level on a given day), or internal, programmed cues, (i.e. day length)? Incorporating light meters into future research efforts would help answer this question.

The “milk crate camera” methodology developed in this study proved extremely practical and effective for collecting data, and should be considered for future investigations. Among the favorable attributes of the setup are its light weight, and thus its ability to be deployed and retrieved by a single individual. The rig landed upright in nearly all deployments and was stable in all but the roughest seas. On several occasions, rough seas did drag the marker buoys enough to shift the camera stand, but adding weight (~2 kg) would probably solve this problem. Further benefits to the methodology used include the creation of permanent archives, which can be used for baseline data or mined for future research questions. Also, video sampling is non-extractive, providing data without the fish mortality that is inherent in so many sampling methodologies. This could be an especially advantageous approach when studying imperiled species.

This study is the first to detail dusk behavior of fishes associated with live-bottom habitat off the coast of North and South Carolina. The study of this behavior is important for a better overall understanding of this ecosystem and may aid in better ecosystem-based management.

LITERATURE CITED

Al-Zibdah, M. and N. Kan'an. 2009. Aspects of growth, reproduction, and feeding habit of three pomacentrid fish from Gulf of Aqaba, Jordan. *Jordan Journal of Biological Sciences*. 2:119-128.

Annese, D.M. and M.J. Kingsford. 2005. Distribution, movements and diet of nocturnal fishes on temperate reefs. *Environmental Biology of Fishes*. 72:161-174.

Arrington, D.A. and K.O. Winemiller. 2003. Diel changeover in sandbank fish assemblages in a neotropical floodplain river. *Journal of Fish Biology*. 63:442-459.

Azzurro, E., A. Pais, P. Consoli, and F. Andaloro. 2007. Evaluating day-night changes in shallow Mediterranean rocky reef fish assemblages by visual census. *Marine Biology.* 151:2245-2253.

Auster, P.J., L. Kracker, V. Price, E. Heupel, G. McFall, and D. Grenda. 2013. Behavior Webs of piscivores at subtropical live-bottom reefs. *Bulletin of Marine Science.* 89:377-396.

Bacheler, N.M., C.M. Schobernd, Z.H. Schobernd, W.A. Mitchell, D.J. Berrane, G.T. Kellison, and M.J.M. Reichert. 2013. Comparison of trap and underwater video gears for indexing reef fish presence and abundance in the southeast United States. *Fisheries Research*. 143:81-88.

Burge, E.J., J.D. Atack, C. Andrews, B.M. Binder, Z.D. Hart, A.C. Wood, L.E. Bohrer, and K. Jagannathan. 2012. Underwater video monitoring of groupers and the associated hard-bottom reef fish assemblage of North Carolina. *Bulletin of Marine Science.* 88:15-38.

Burrows, M.T., R.N. Gibson, L. Cobb, and C.A. Comely. 1994. Temporal patterns of movement in juvenile flatfishes and their predators: underwater television observations. *Journal of Experimental Marine Biology and Ecology*. 177:251-268.

Carpentieri, P., F. Colloca, and G.D. Ardizzone. 2005. Day-night variations in the demersal nekton assemblage on the Mediterranean shelf-break. *Estuarine, Coastal and Shelf Science*. 63:577-588.

Collette, B.B. and F.H. Talbot. 1972. Activity patterns of coral reef fishes with emphasis on nocturnal-diurnal changeover. *Bulletin of the Natural History Museum of Los Angeles County.*14:98-124.

Danilowicz, B.S. and P.F. Sale. 1999. Relative intensity of predation on the French grunts, *Haemulon flavolineatum*, during diurnal, dusk, and nocturnal periods on a coral reef. *Marine Biology*. 133:337-343.

Domm, S.B. and A.J. Domm. 1973. The sequence of appearance at dawn and disappearance at dusk of some coral reef fishes. *Pacific Science*. 27:128-135.

Fox, R.J. and D.R. Bellwood. 2011. Unconstrained by the clock? Plasticity of diel activity rhythm in a tropical reef fish, *Siganus lineatus*. *Functional Ecology*. 25:1096-1105.

Fraser, N.H.C., N.B. Metcalfe, and J.E. Thorpe. 1993 Temperature-dependent switch between diurnal and nocturnal foraging in salmon. *Proceedings of the Royal Society B*. 252:135-139.

Grimes, C. B. 1979. Diet and feeding ecology of the vermilion snapper, *Rhomboplites aurorubens* (Cuvier) from North Carolina and South Carolina waters. *Bulletin of Marine Science.* 29:53-61.

Gushima, K., K. Kondou, and Y. Murakami. 1977. Diel change in family composition of reef fishes. *Journal of the Faculty of Fisheries and Animal Husbandry, Hiroshima University.* 16:151-156.

Haley, T.H. 2012. Persistence of fish assemblages on sand and gravel bar habitat in the Alabama River, Alabama. Master's Thesis. University of Auburn, Auburn, AL.

Harris, P.J., D.M. Wyanski, D.B. White, and J.L. Moore. 2002. Age, growth, and reproduction of scamp, *Mycteroperca phenax*, in the southwestern North Atlantic, 1979-1997. *Bulletin of Marine Science.* 70:113-132.

Harvey E.S., J.J. Butler, D.L. McLean, and J. Shand. 2012a. Contrasting habitat use of diurnal and nocturnal fish assemblages in temperate Western Australia. *Journal of Experimental Marine Biology and Ecology.* 426-427:78-86.

Harvey E.S., S.R. Dorman, C. Fitzpatrick, S.J. Newman, and D.L. McLean. 2012b. Response of diurnal and nocturnal coral reef fish to protection from fishing: an assessment using baited remote underwater video. *Coral Reefs*. 31:939-950.

Helfman, G.S. 1978. Patterns of community structure in fishes: summary and overview. *Environmental Biology of Fishes* 3:129-148.

Helfman, G.S. 1981. Twilight activities and temporal structure in a freshwater fish community. *Canadian Journal of Fisheries and Aquatic Sciences.* 38:1405-1420.

Helfman, G.S. 1993. Fish behaviour by day, night, and twilight. In: Pitcher, T.J. (ed.), Behaviour of Teleost Fishes, 2nd edn. Chapman and Hall, London, pp. 479-512.

Hobson, E.S. 1965. Diurnal-nocturnal activity of some inshore fishes in the Gulf of California. *Copeia*. 1965:291-301.

Hobson, E.S. 1968. Predatory behavior of some shore fishes in the Gulf of California. *U.S. Fish and Wildlife Service, Research Report*. 73, 92 p.

Hobson, E.S. 1972. Activity of Hawaiian reef fishes during the evening and morning transitions between daylight and darkness. *Fishery Bulletin* 70:715-740.

Hobson, E.S. 1973. Diel feeding migrations in tropical reef fishes. *Helgoländer Wissenschaftliche Meeresunters.* 24:361-370.

Hobson, E.S. 1975. Feeding patterns among tropical reef fishes. *American Scientist*. 63:382-392.

Hobson, E.S., W.N. McFarland, and J.R. Chess. 1981. Crepuscular and nocturnal activities of Californian nearshore fishes, with consideration of their scotopic visual pigments and the photic environment. *Fishery Bulletin* 79:1-30.

Kendall, M.S., L.J. Bauer, and C.F.G. Jeffrey. 2009. Influence of hard bottom morphology on fish assemblages of the continental shelf off Georgia, southeastern USA. *Bulletin of Marine Science.* 84:265-286.

Manooch, C.S. and M. Haimovici. 1983. Foods of greater amberjack, *Seriola dumerili*, and almaco jack, *Seriola rivoliana* (Pisces: Carangidae), from the south Atlantic bight. *The Journal of the Elisha Mitchell Scientific Society*. 99:1-9.

McCauley, D.J., E. Hoffmann, H.S. Young, and F. Micheli. 2012. Night Shift: Expansion of temporal niche use following reductions in predator density. *PlosOne* 7: e38871.

McFarland, W.N., J.C. Ogden, and J.N. Lythgoe. 1979. The influence of light on the twilight migrations of grunts. *Environmental Biology of Fishes* 4:9-22.

McFarland, W.N. 1991. The visual world of coral reef fishes. In: Sale, P.F. (ed.). The ecology of fishes on coral reefs. Academic Press, San Diego, pp 16-38.

Metcalfe, N.B. and G.I. Steele. 2001. Changing nutritional status causes a shift in the balance of nocturnal to diurnal activity in European Minnows. *Functional Ecology.* 15:304-309.

Munz, F.W. and W.N. McFarland. 1973. The significance of spectral position in the rodopsins of tropical marine fishes. *Vision Research*. 13:1829-1874.

Nagelkerken, I., M. Dorenbosch, W.C.E.P. Verberk, E. Cocheret de la Morinière, and G. van der Velde. 2000. Day-night shifts of fishes between shallow-water biotopes of a Caribbean bay, with emphasis on the nocturnal feeding of Haemulidae and Lutjanidae. *Marine Ecological Progress Series* 194:55-64.

Ogden, J.C. and P.R. Ehrlich. 1977. The behavior of heterotypic resting schools of juvenile grunts (Pomadasyidae). *Marine Biology* 273-280.

Ouzts, A.C. and S.T. Szedlmayer. 2003. Diel feeding patterns of red snapper on artificial reefs in the north-central Gulf of Mexico. *Transactions of the American Fisheries Society*. 132:1186-1193.

Payne, N.L., D.E. van der Meulen, R. Gannon, J.M Semmens, I.M. Suthers, C.A. Gray, and M.D. Taylor. 2012. Rain reverses diel activity rhythms in an estuarine teleost. *Proceedings of the Royal Society B.* 280: 20122363.

Pereira, P.H.C. and B.P. Ferreira. 2013. Effects of life phase and schooling patterns on the foraging behaviour of coral-reef fishes from the genus *Haemulon*. *Journal of Fish Biology.* 82:1226-1238.

Piet, G.J. and W.A.H.P. Guruge. 1997. Diel variation in feeding and vertical distribution of ten co-occurring fish species: consequences for resource partitioning. *Environmental Biology of Fishes* 50:293-307.

Posey, M.H., and W.G. Ambrose. 1994. Effects of proximity to an offshore hard-bottom reef on infaunal abundances. *Marine Biology* 118:745-753.

Potts, G.W. 1981. Behavioural interactions between the Carangidae (Pisces) and their prey on the fore-reef slope of Aldabra, with notes on other predators. *Journal of Zoology, London*. 195:385-404.

Powles, H., and C.A. Barans. 1980. Groundfish monitoring in sponge-coral areas off the southeastern United States. *Marine Fisheries Review*. 42:21-35.

R Core Team. 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/.

Randall, J.E. 1967. Food habits of reef fishes of the West Indies. *Studies in Tropical Oceanography, Miami.* 5:665-847.

Reebs, S.G. 2002. Plasticity of diel and circadian activity rhythms in fishes. *Reviews in Fish Biology and Fisheries*. 12:349-371.

Rickel, S. and A. Genin. 2005. Twilight transitions in coral reef fish: the input of light-induced changes in foraging behavior. *Animal Behaviour.* 70:133-144.

Roach, K.A. and K.O. Winemiller. 2011. Diel turnover of assemblages of fish and shrimp on sandbanks in a temperate floodplain river. *Transactions of the American Fisheries Society*. 140:1, 84-90.

Rooker, J.R., and G.D. Dennis. 1991. Diel, lunar and seasonal changes in a mangrove fish assemblage off southwestern Puerto Rico. *Bulletin of Marine Science.* 49:684-698.

Rooker J.R., Q.R. Dokken, C.V. Pattengill, and G.J. Holt. 1997. Fish assemblages on artificial and natural reefs in the Flower Garden Banks National Marine Sanctuary, USA. *Coral Reefs*. 16:83-92.

Sancho, G., C.W. Petersen, and P.S. Lobel. 2000. Predator-prey relations at a spawning aggregation site of coral reef fishes. *Marine Ecological Progress Series* 203:275-288.

Sbikin, Y.N. 1977. Changes in the behavior of some fish from the Cuban shelf during morning and evening twilight. *Journal of Ichthyology.* 17:785-790.

Schobernd, Z.H., N.M. Bacheler, and P.B. Conn. 2013. Examining the utility of alternative video monitoring metrics for indexing reef fish abundance. *Canadian Journal of Fisheries and Aquatic Sciences.* 71**:**464–471.

SEDAR. 2011. SEDAR 25 – South Atlantic Black Sea Bass Stock Assessment Report. SEDAR, North Charleston, SC. Available online at: http://www.sefsc.noaa.gov/sedar/

Sedberry, G.R. 1985. Food and feeding of the tomtate, *Haemulon aurolineatum* (Pisces, Haemulidae), in the south Atlantic bight. *Fishery Bulletin* 83:461-466.

Sedberry, G.R. 1988. Food and feeding of black sea bass, Centropristis striata, in live bottom habitats in the south Atlantic bight. *The Journal of the Elisha Mitchell Scientific Society*. 104:35-50.

Sedberry, G.R. and N. Cuellar. 1993. Planktonic and benthic feeding by the reef-associated vermilion snapper, *Rhomboplites aurobens* (Teleostei, Lutjanidae). *Fishery Bulletin* 91:699-709.

Smith, J.W. and J.V. Merriner. 1982. Association of cobia, *Rachycentron canadum*, with cownose ray, *Rhinoptera bonasus*. *Estuaries*. 5:240-242.

Starck, W.A. II and W.P. Davis. 1966. Night habits of fishes of Alligator Reef, Florida. *Ichthyologica: The Aquarium Journal.* 38:313-356.

Steimle, F.W., C.A. Zetlin, P.L. Berrien, D.L. Johnson, and S. Chang. 1999. Scup, *Stenotomus chrysops*, life history and habitat characteristics. *NOAA Technical Report.* NMFS 149. 48 p.

Vose, F.E. and W.G. Nelson. 1994. Gray triggerfish (*Balistes capriscus* Gmelin) feeding from artificial and natural substrates in shallow Atlantic waters of Florida. *Bulletin of Marine Science.* 55:1316-1323.

Wood, S.N. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society*. (B) 73:3-36.

Zapata, M.J. 2013. Diel Patterns of Patch Reef Community Dynamics in a Caribbean Back-Reef System. Department of Biological Sciences - Undergraduate Honors Theses. Paper 49. Florida International University, Miami, FL.

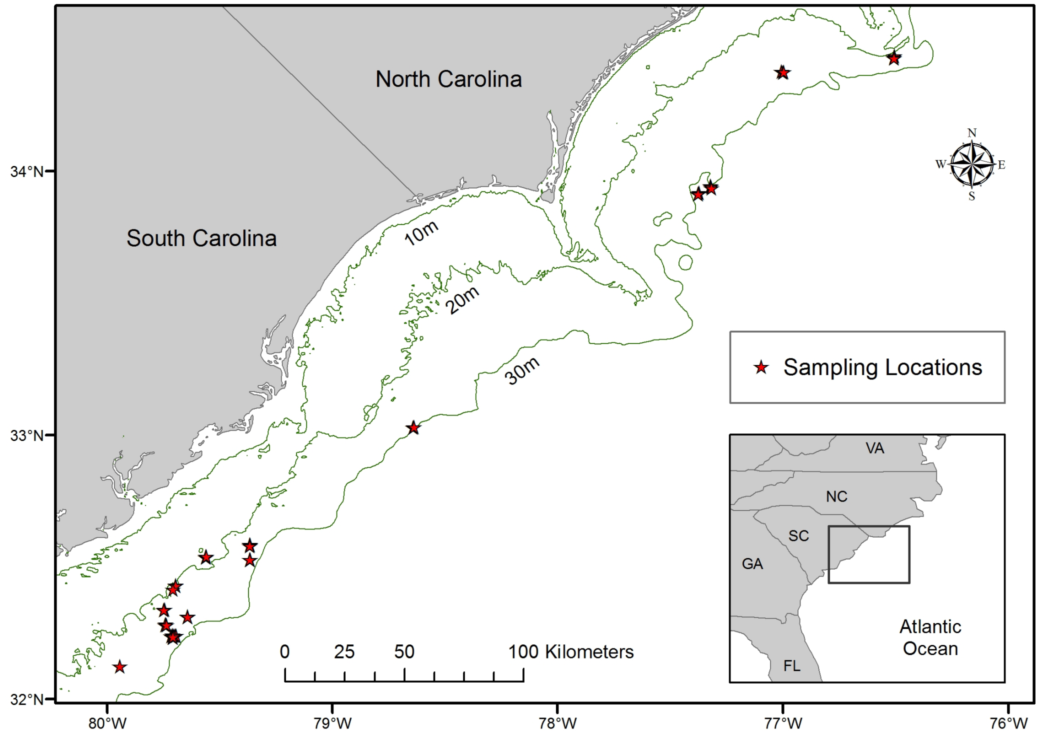

Figure 1. Sampling locations (n=43). Collections from individual dates are clustered and symbols may overlap.

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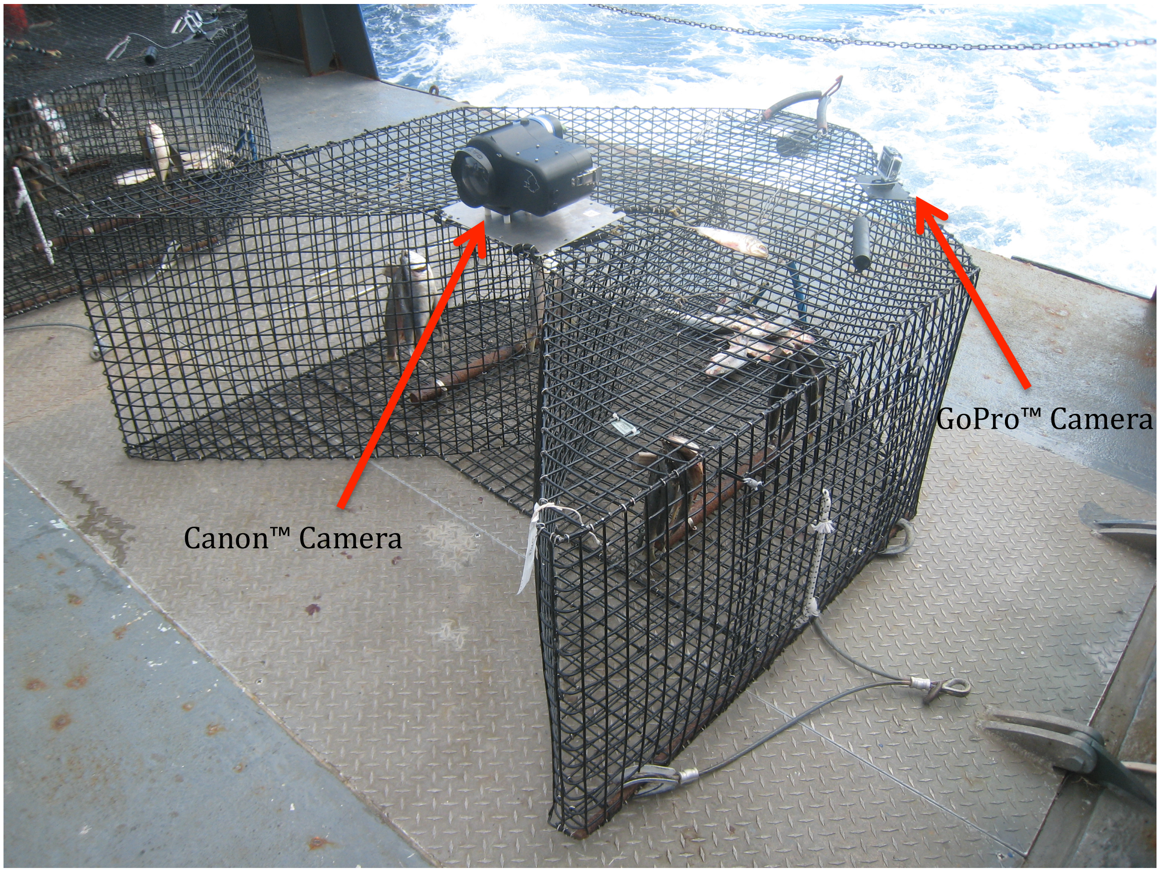

Figure 2. Chevron trap with cameras mounted. Note: Un-baited traps were used in the present study

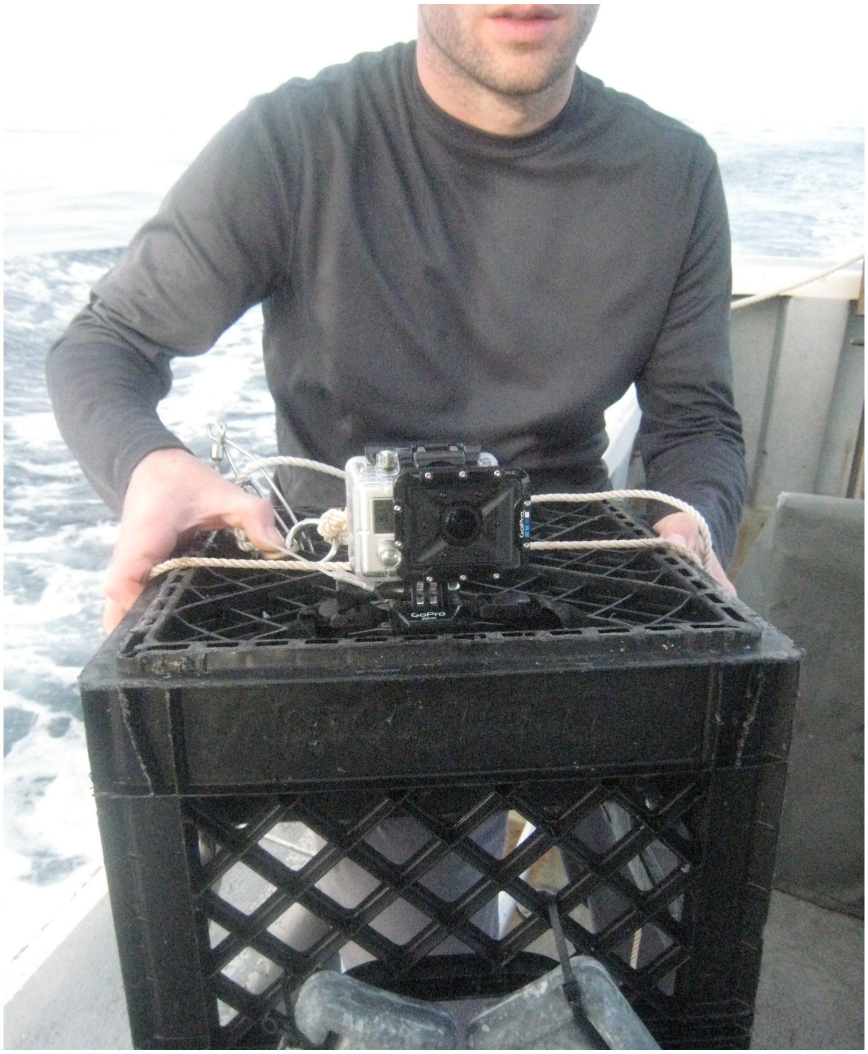

Figure 3. Custom-made camera stand: a weighted milk crate mounted with a GoPro™ camera.

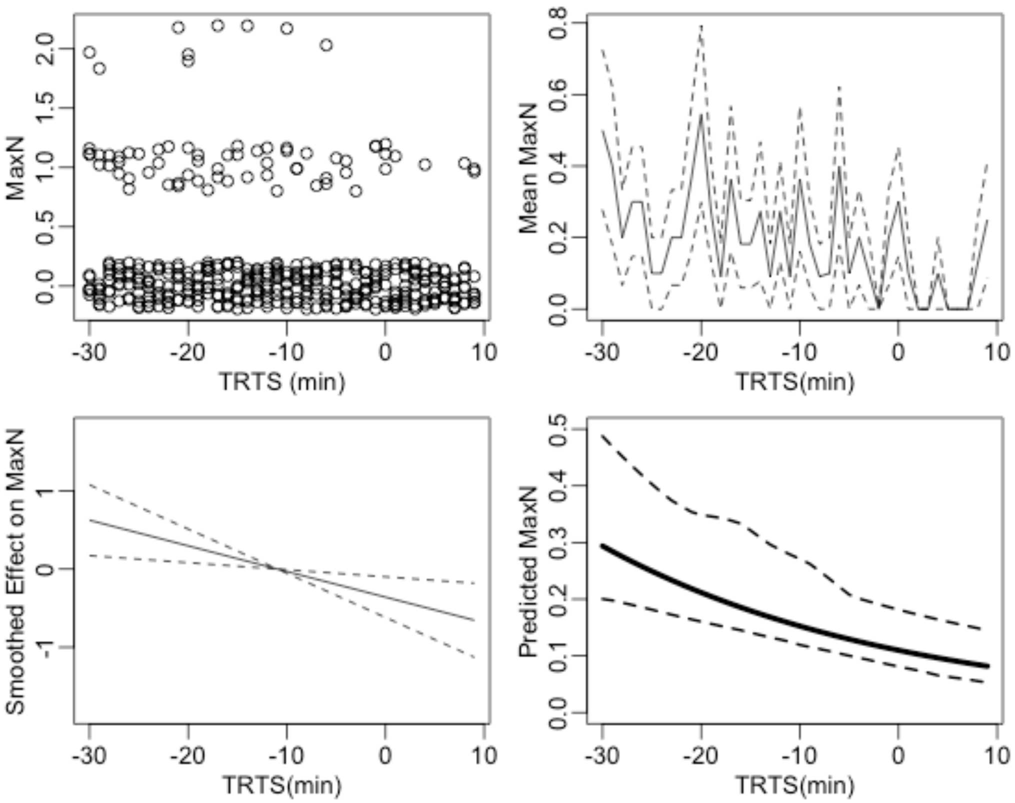

Figure 4. Gray Triggerfish temporal abundance patterns in videos (n=11). Top left panel shows jittered raw MaxN values vs. time relative to sunset (TRTS). MaxN is defined as maximum number of conspecifics visible on screen at same time. Top right panel shows mean (across videos) MaxN vs. TRTS. Lower left panel shows the smoothed TRTS effect on MaxN, based on generalized additive mixed model (GAMM) analysis. Lower right panel shows predicted MaxN values, based on GAMM analysis. Dotted lines represent 95% confidence intervals.

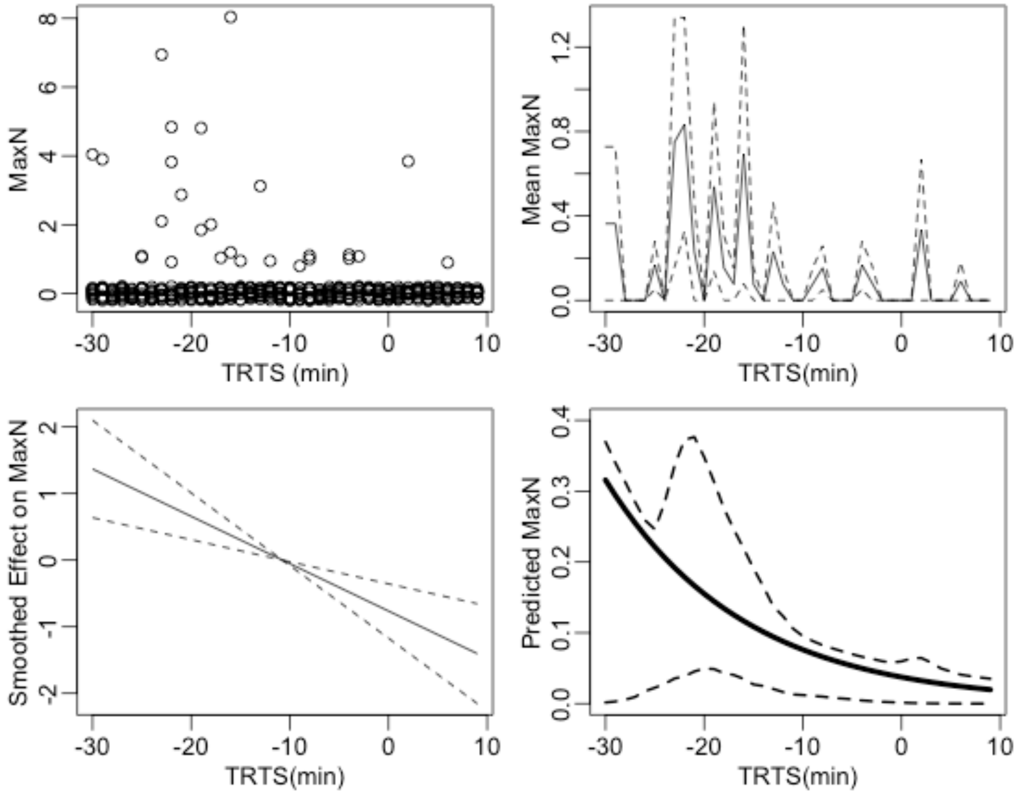

Figure 5. *Seriola* spp. temporal abundance patterns in videos (n=13). Panels are defined as in Fig. 4.

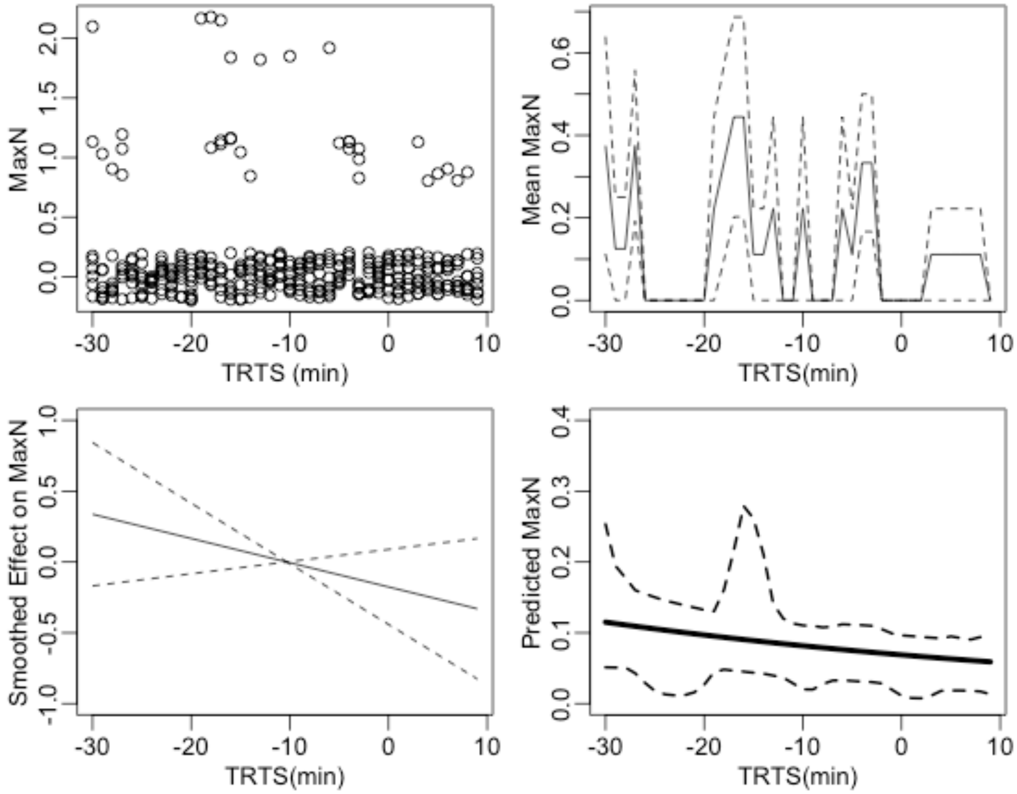

Figure 6. Atlantic Sharpnose temporal abundance patterns in videos (n=9). Panels are defined as in Fig. 4

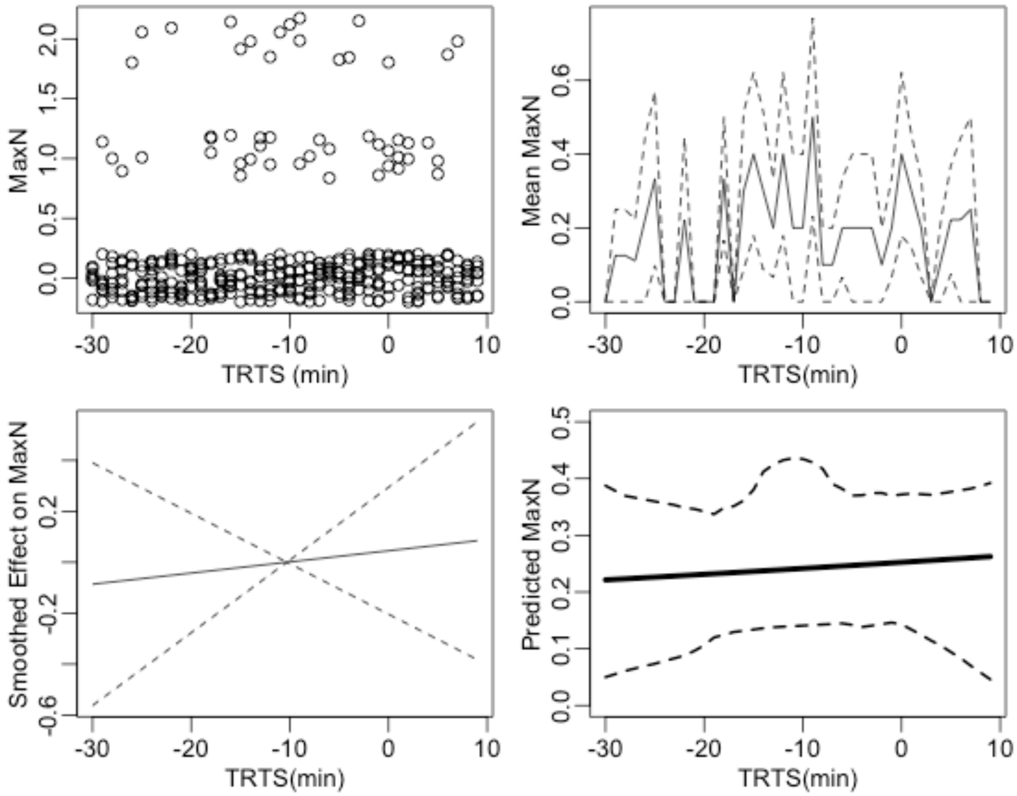

Figure 7. *Chaetodon* spp. temporal abundance patterns in videos (n=12). Panels are defined as in Fig. 4.

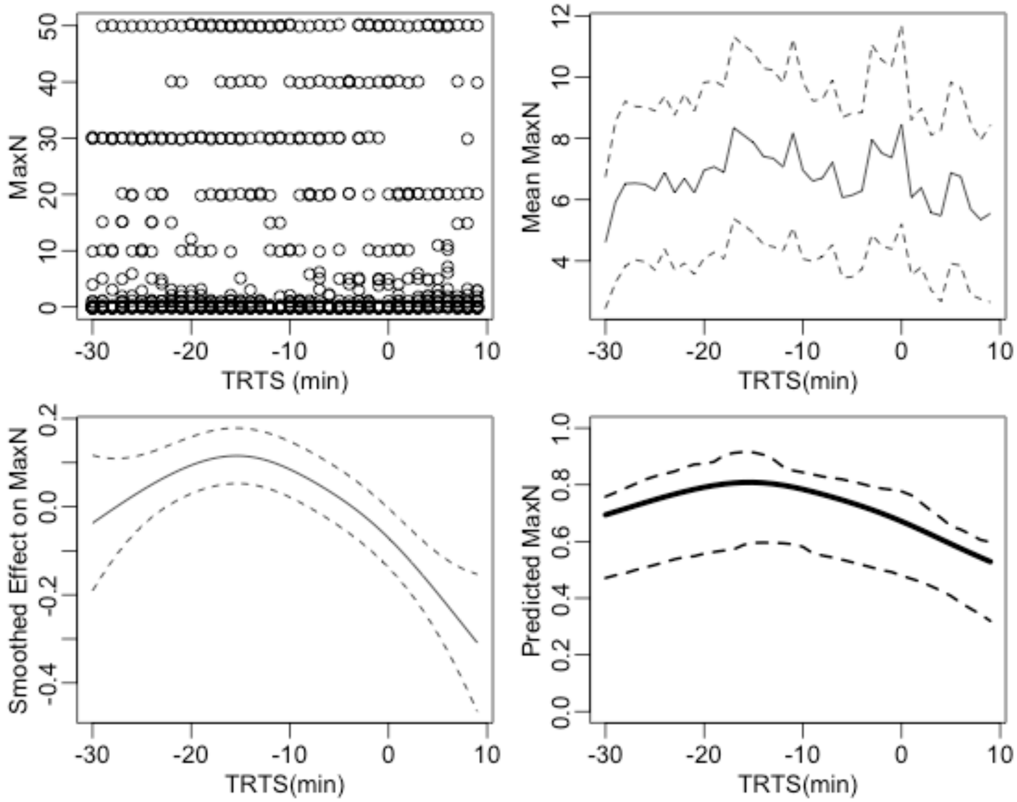

Figure 8. Tomtate temporal abundance patterns in videos (n=29). Panels are defined as in Fig. 4.

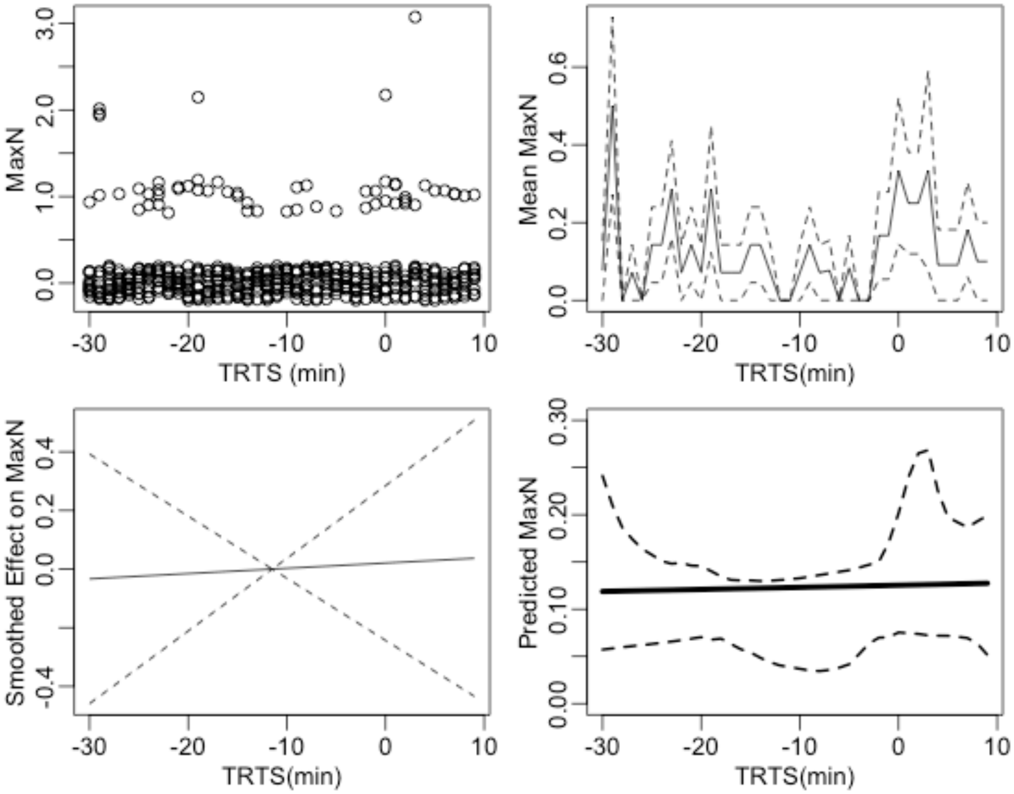

Figure 9. White Grunt temporal abundance patterns in videos (n=14). Panels are defined as in Fig. 4.

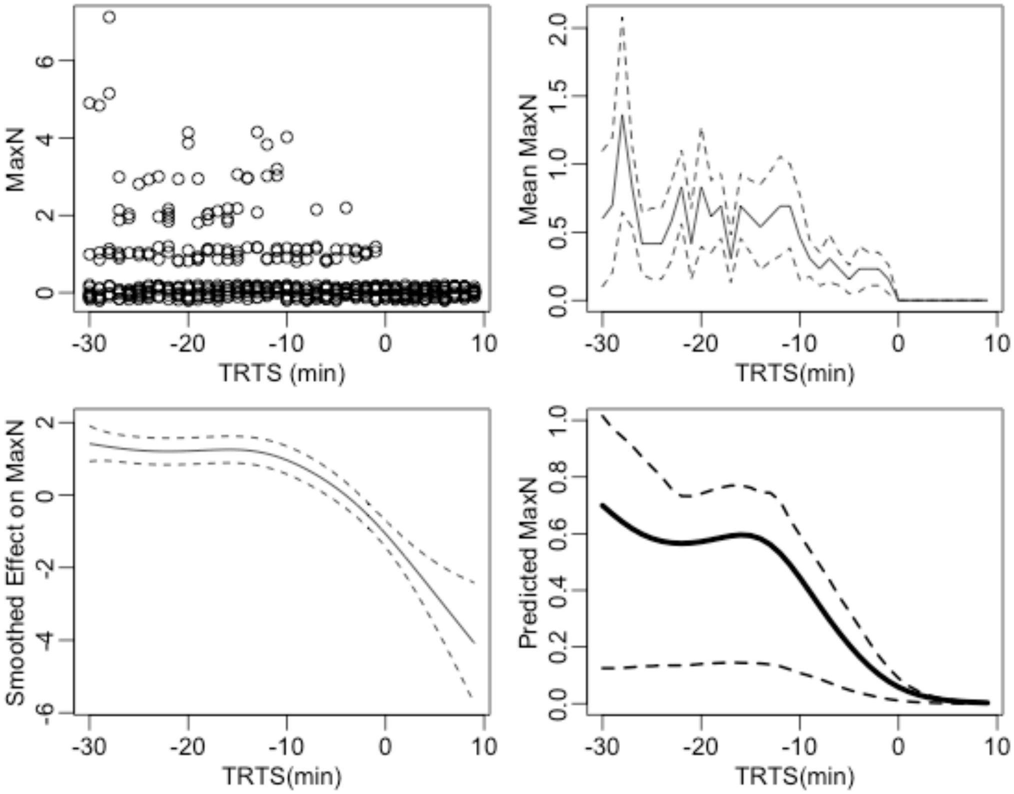

Figure 10. *Halichoeres* spp. temporal abundance patterns in videos (n=13). Panels are defined as in Fig. 4.

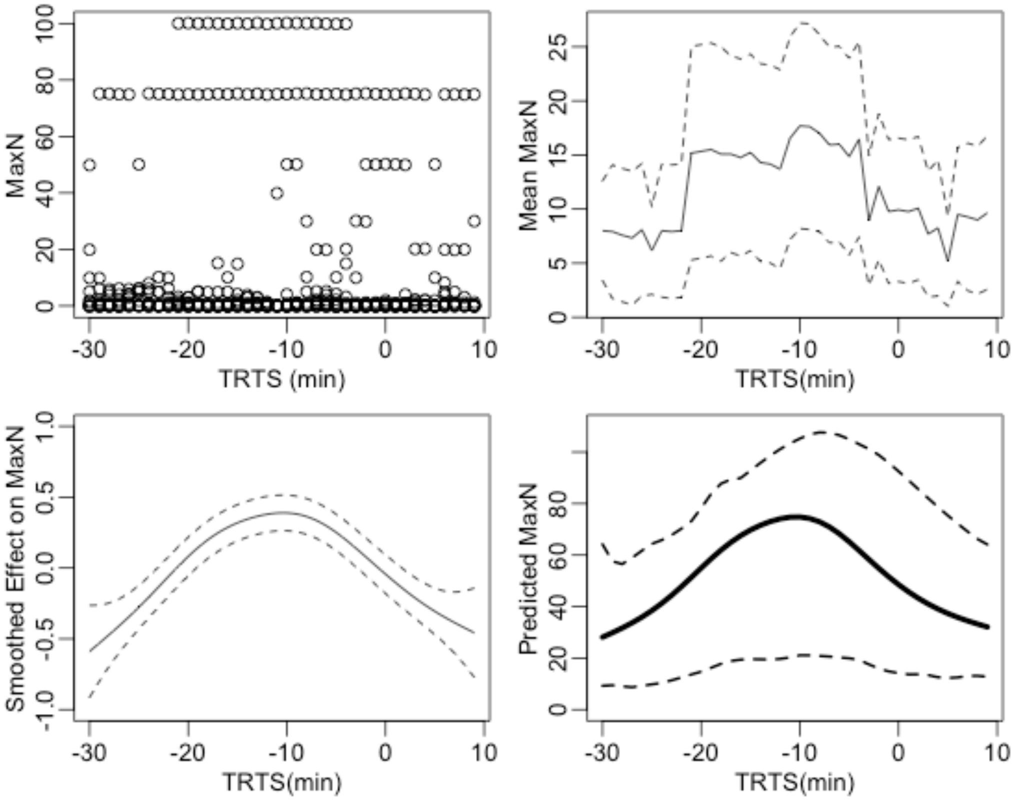

Figure 11. Vermilion Snapper temporal abundance patterns in videos (n=13). Panels are defined as in Fig. 4.

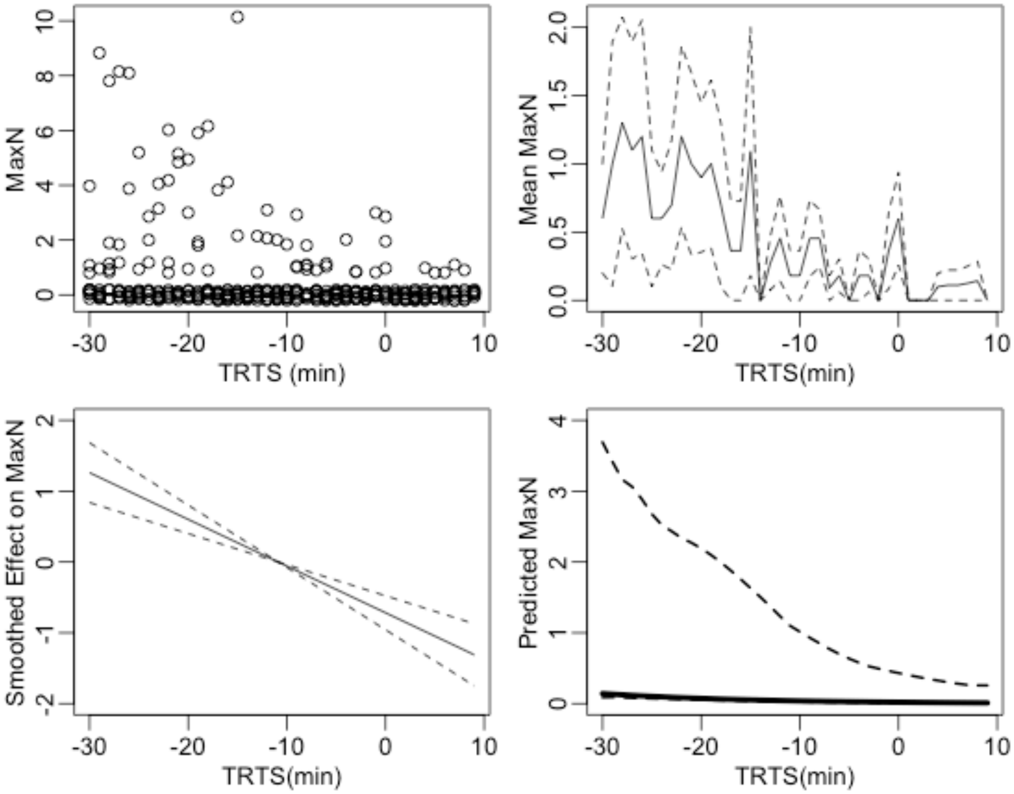

Figure 12. Red Snapper temporal abundance patterns in videos (n=11). Panels are defined as in Fig. 4.

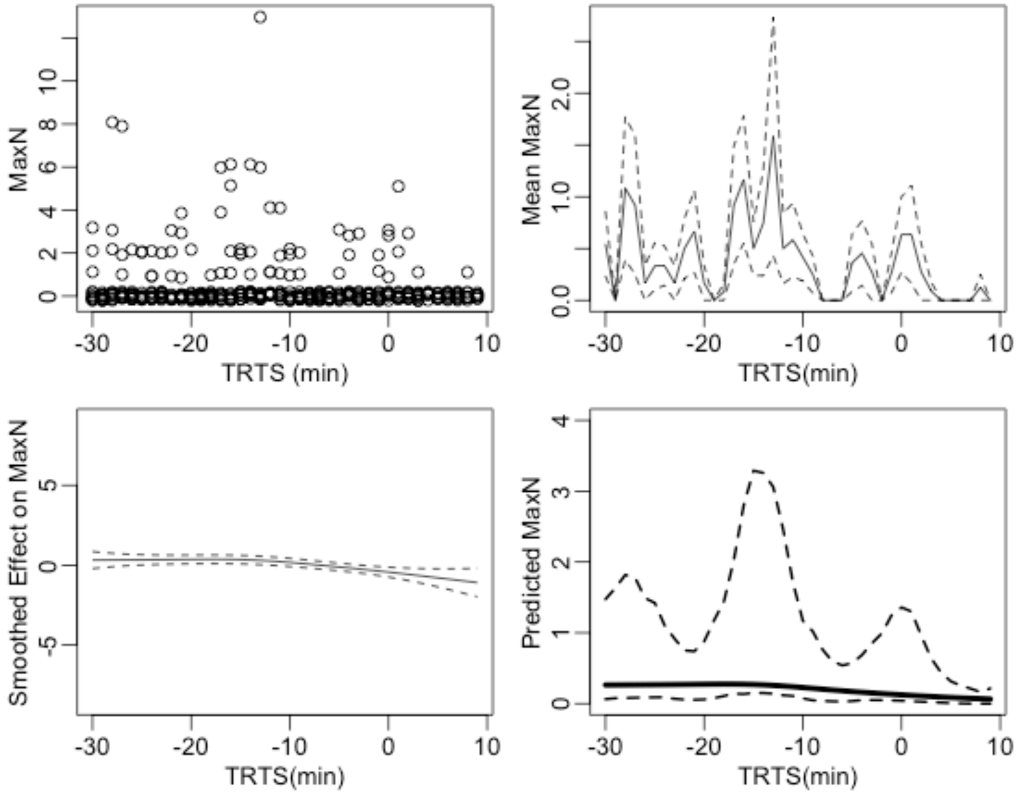

Fig. 13. *Aluterus* spp. temporal abundance patterns in videos (n=12). Panels are defined as in Fig. 4.

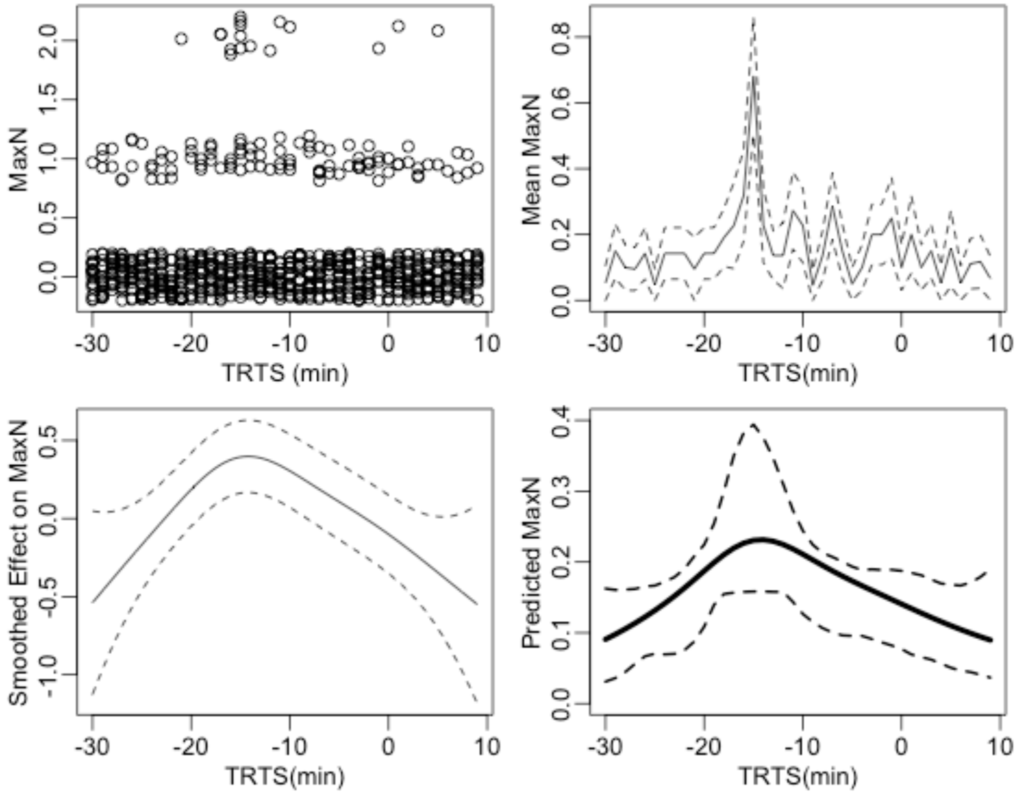

Figure 14. Planehead Filefish temporal abundance patterns in videos (n=22). Panels are defined as in Fig. 4.

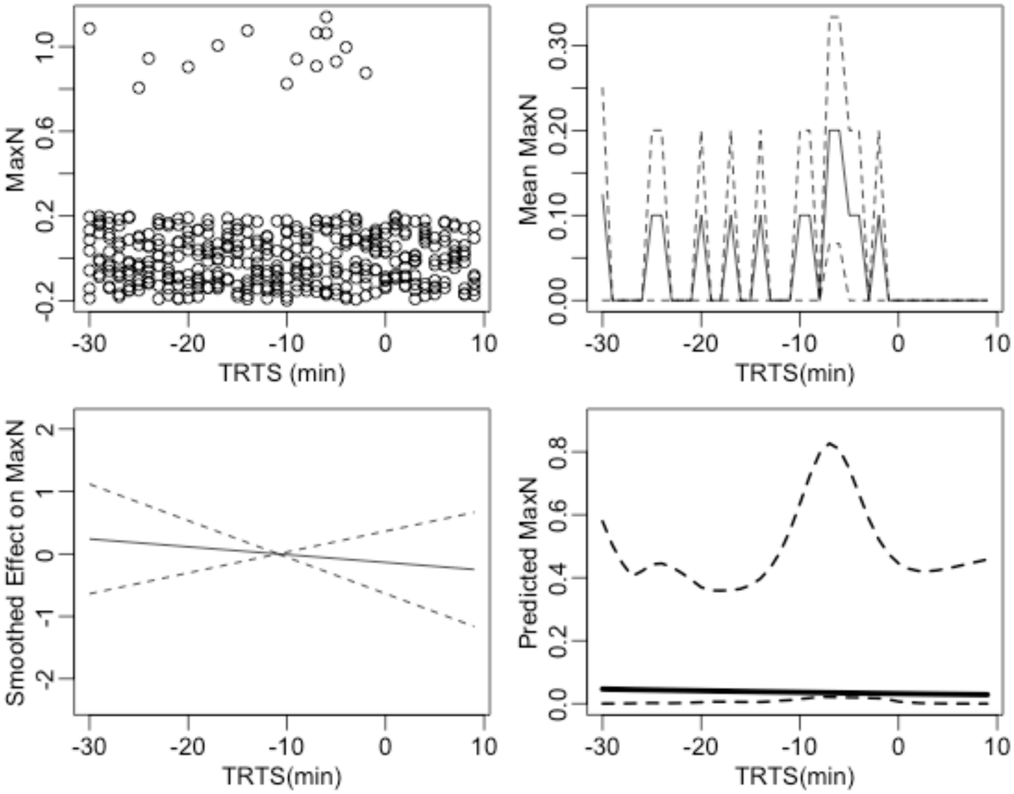

Figure 15. *Paralichthys* spp. temporal abundance patterns in videos (n=10). Panels are defined as in Fig. 4.

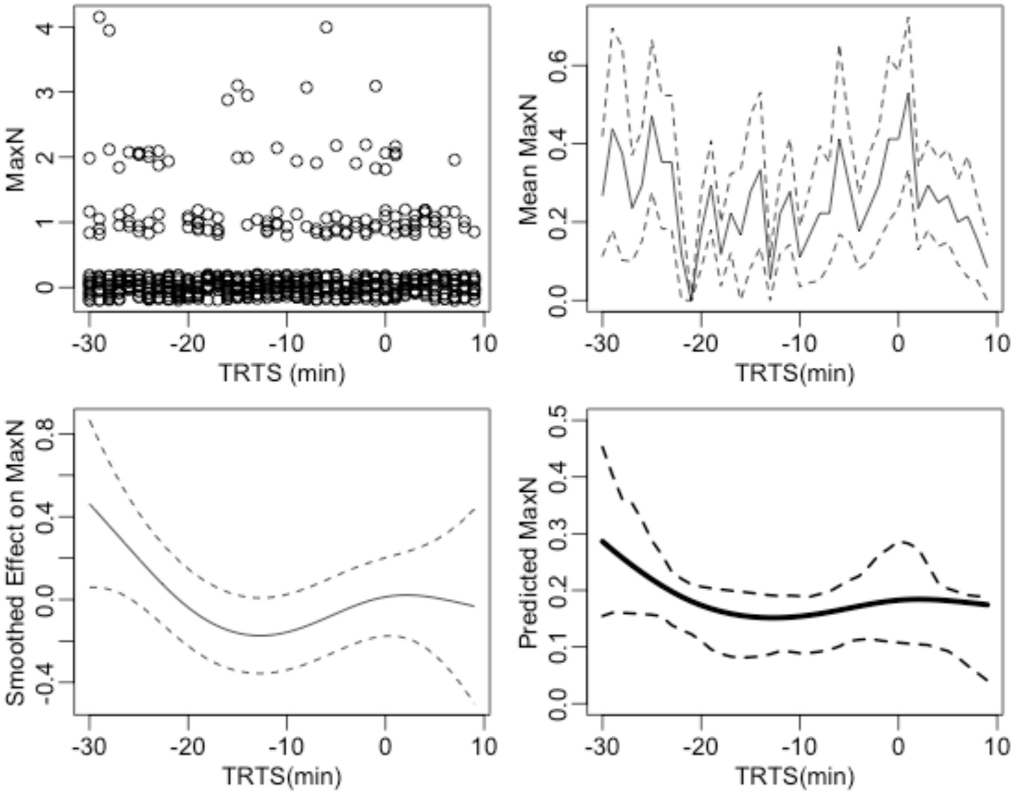

Figure 16. Blue Angelfish temporal abundance patterns in videos (n=18). Panels are defined as in Fig. 4.

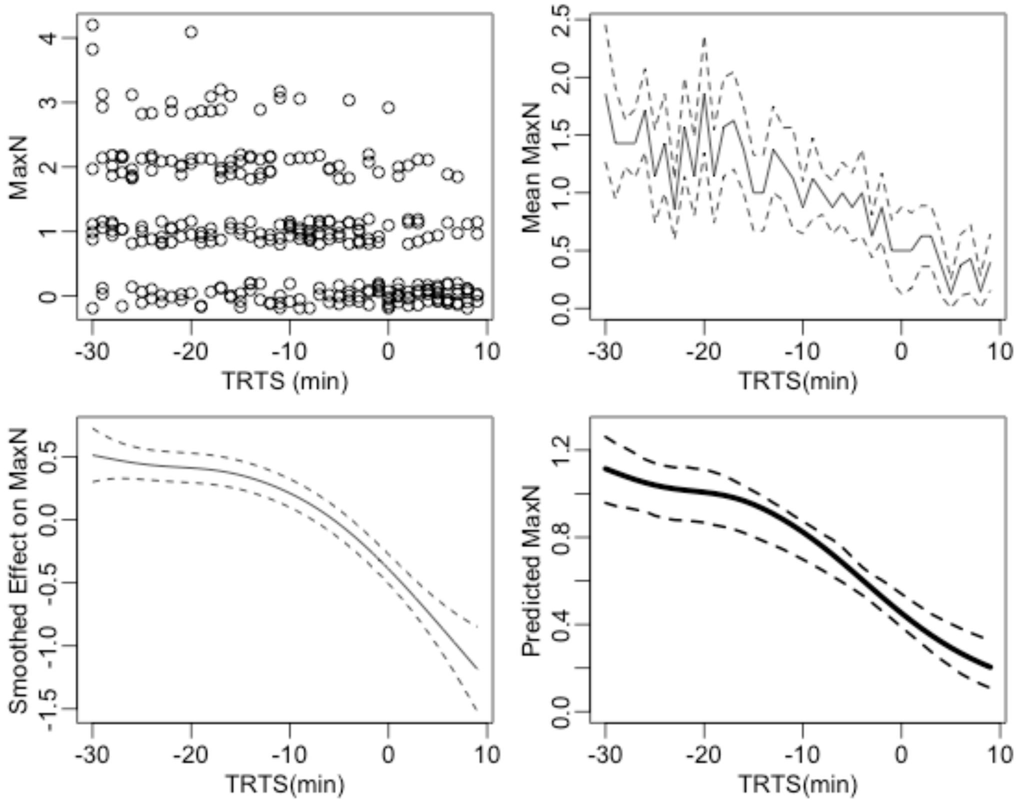

Figure 17. *Stegastes* spp. temporal abundance patterns in videos (n=8). Panels are defined as in Fig. 4.

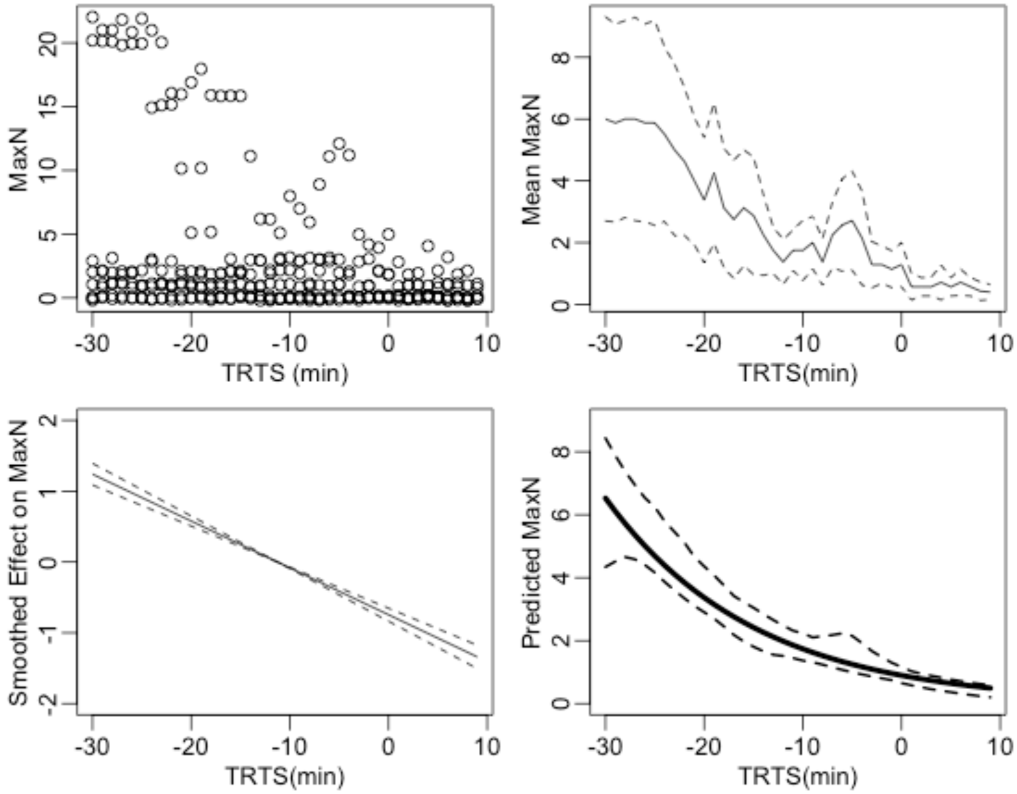

Figure 18. *Chromis* spp. temporal abundance patterns in videos (n=8). Panels are defined as in Fig. 4.

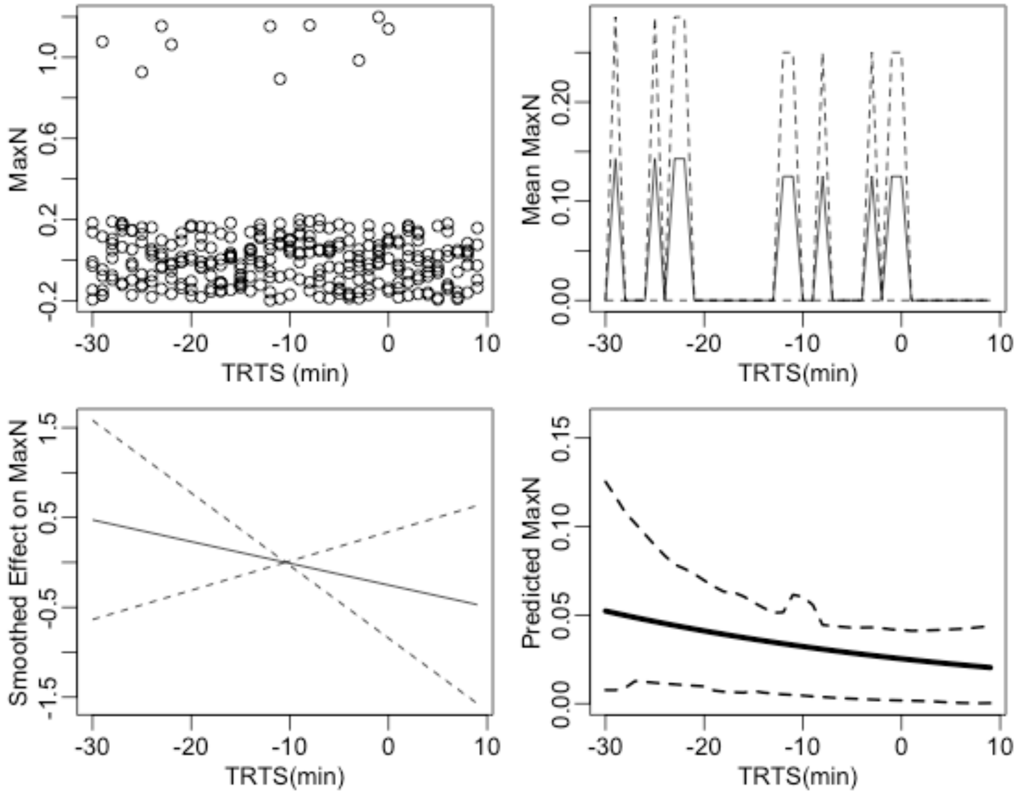

Figure 19. Atlantic Guitarfish temporal abundance patterns in videos (n=8). Panels are defined as in Fig. 4.

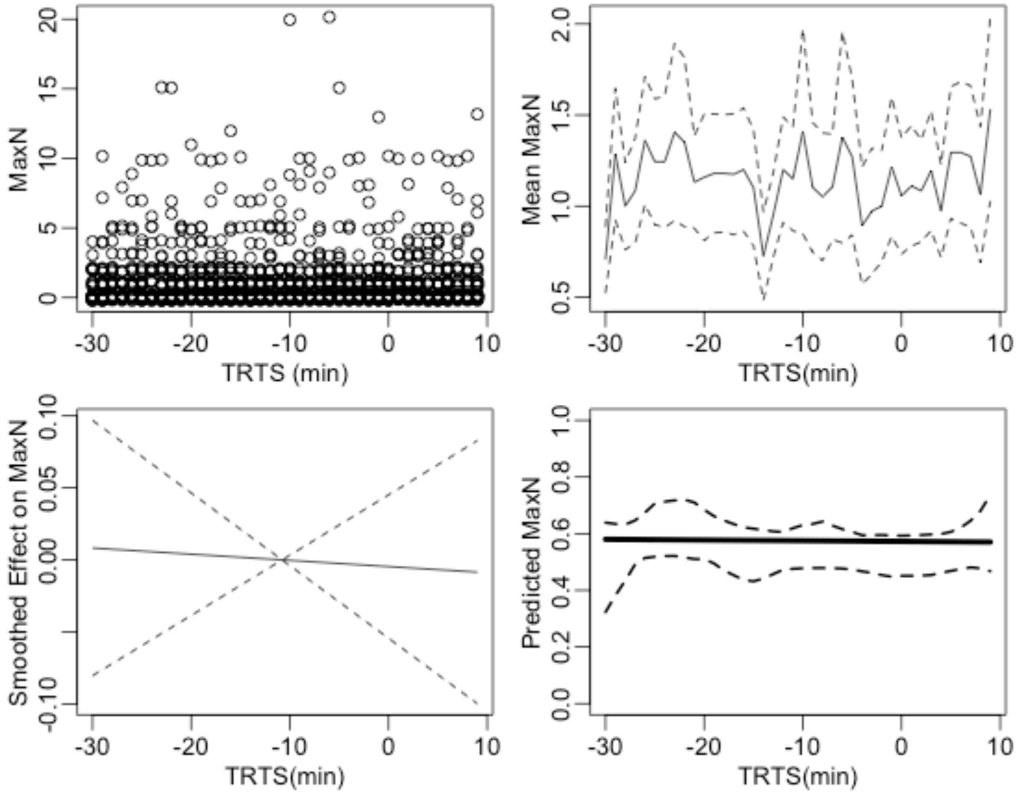

Figure 20. Black Sea Bass temporal abundance patterns in videos (n=40). Panels are defined as in Fig. 4.

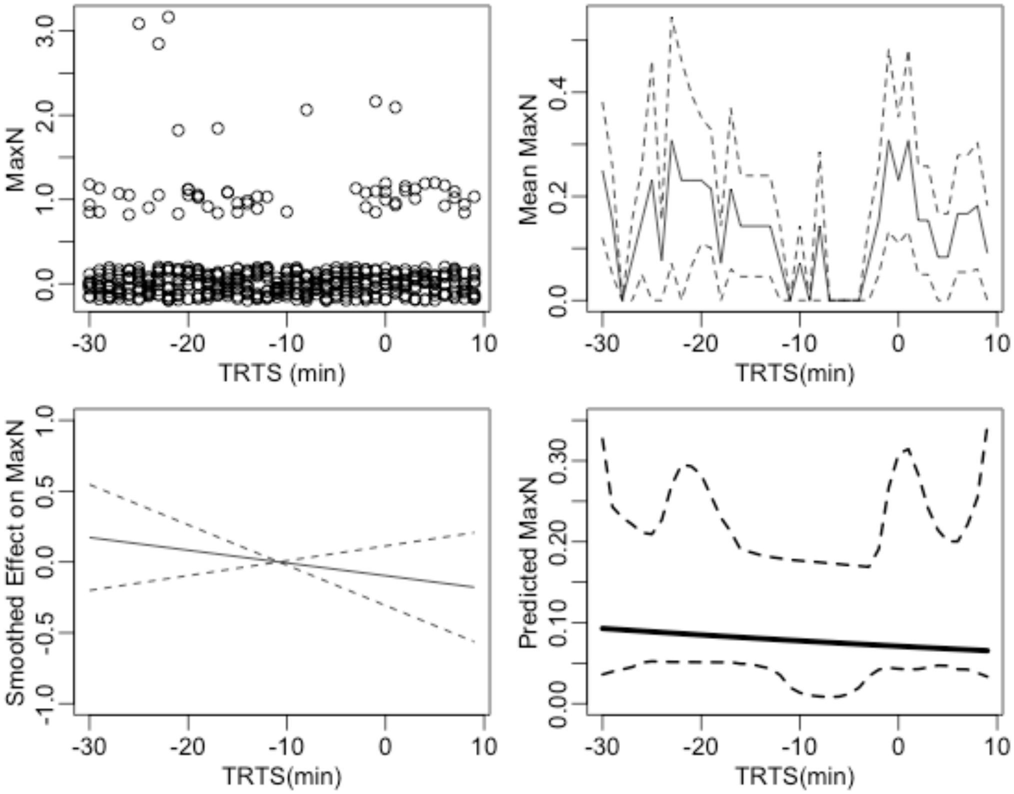

Figure 21. Bank Sea Bass temporal abundance patterns in videos (n=14). Panels are defined as in Fig. 4.

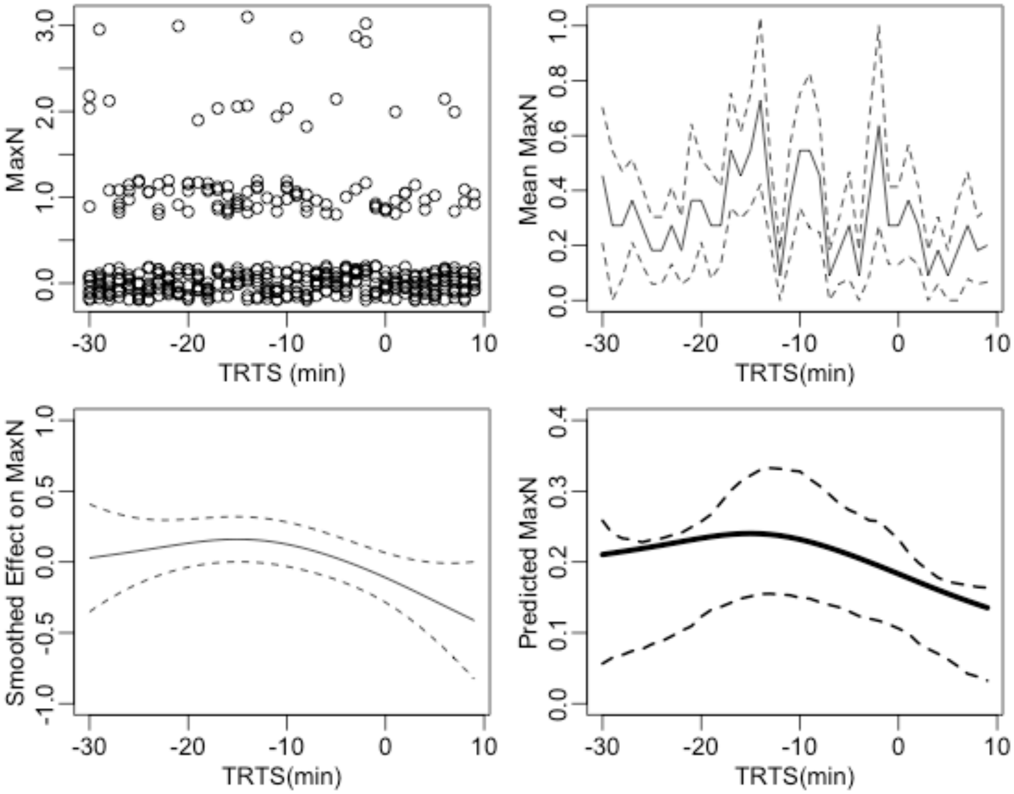

Figure 22. Sand Perch temporal abundance patterns in videos (n=11). Panels are defined as in Fig. 4.

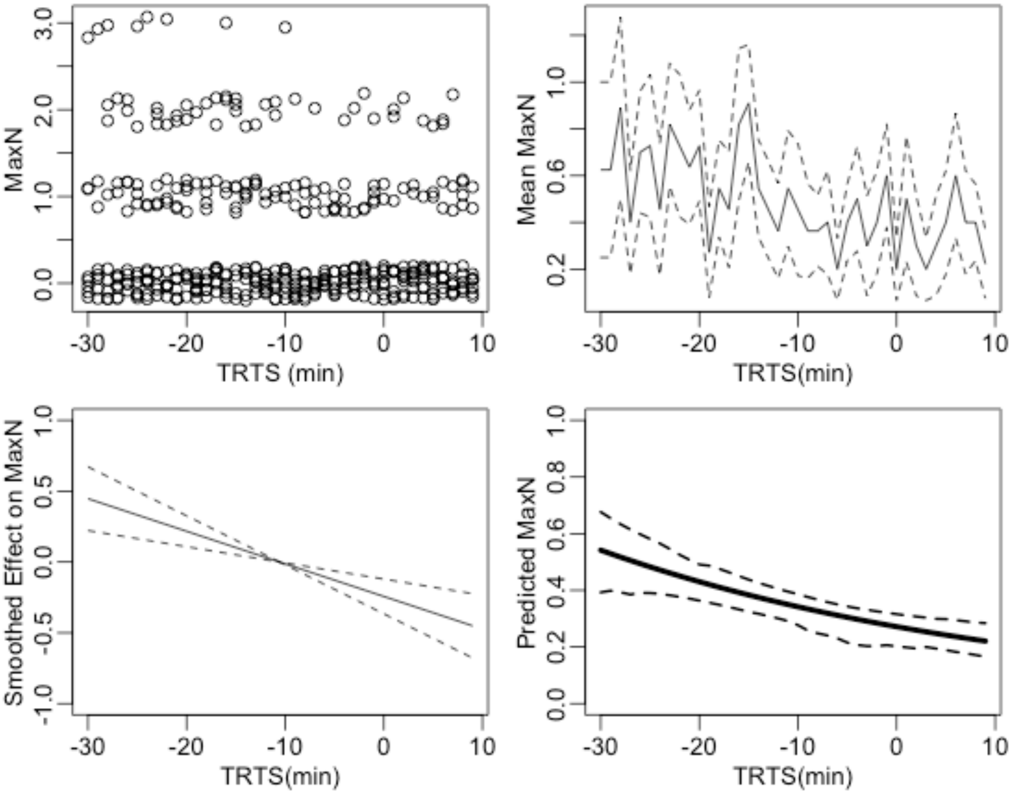

Figure 23. *Mycteroperca* spp. temporal abundance patterns in videos (n=11). Panels are defined as in Fig. 4.

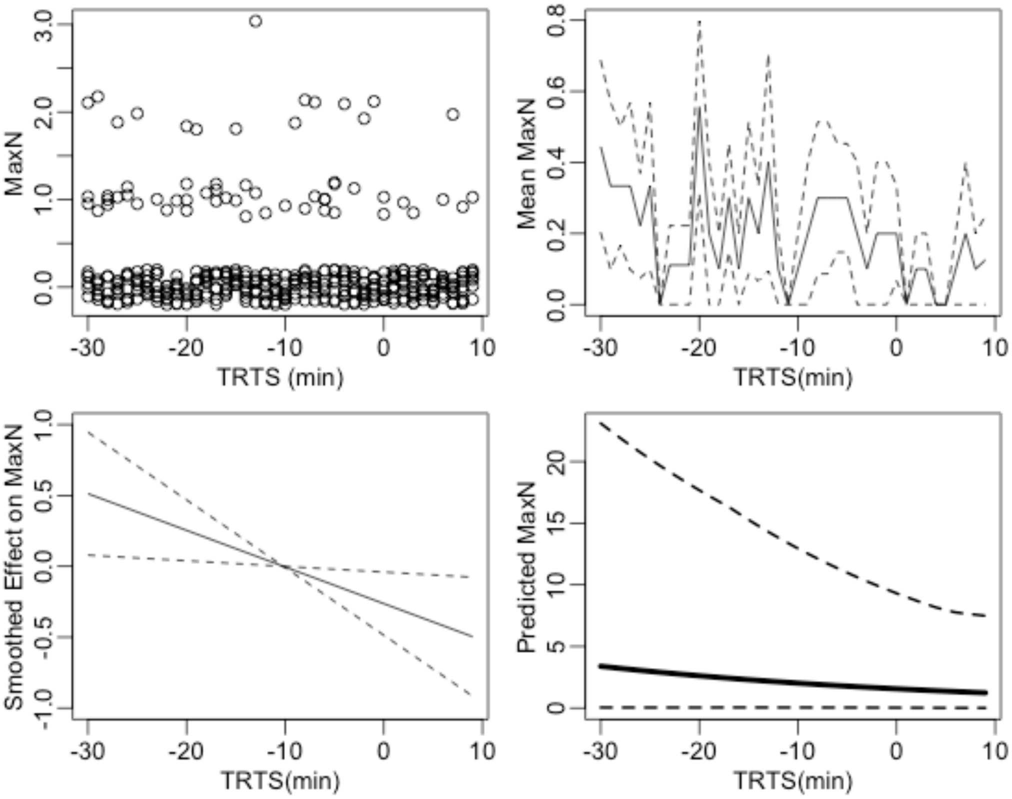

Figure 24. Belted Sandfish temporal abundance patterns in videos (n=10). Panels are defined as in Fig. 4.

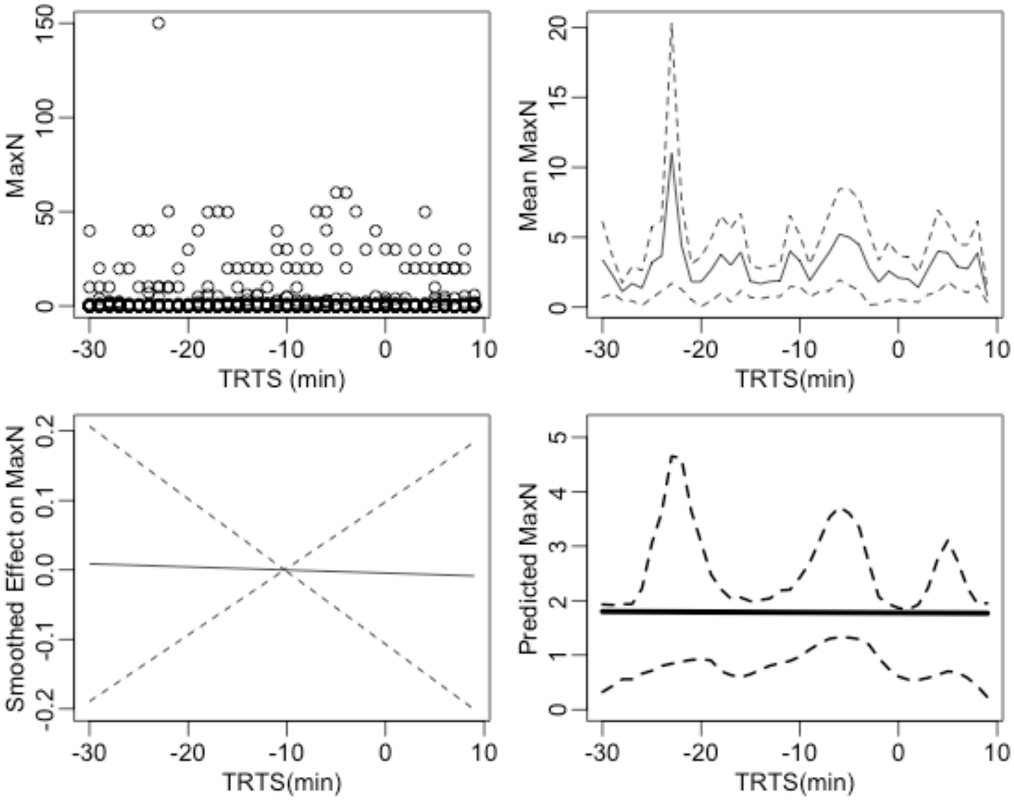

Figure 25. *Stenotomus* spp. temporal abundance patterns in videos (n=19). Panels are defined as in Fig. 4.

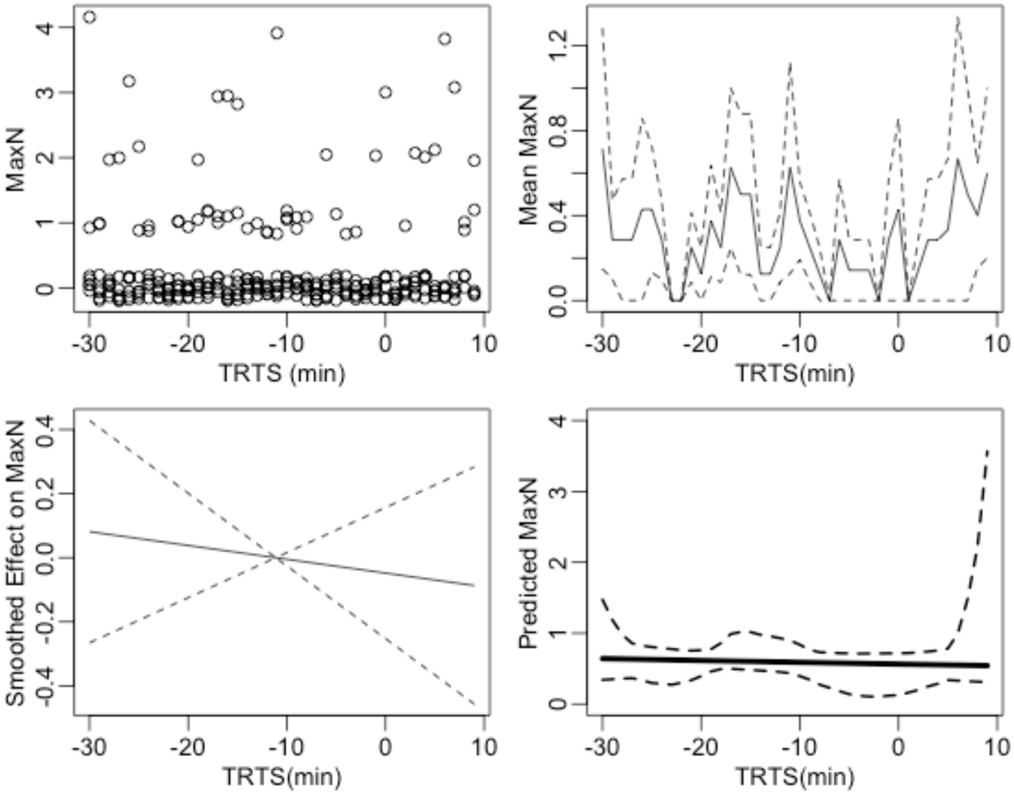

Figure 26. Sheepshead temporal abundance patterns in videos (n=8). Panels are defined as in Fig. 4.

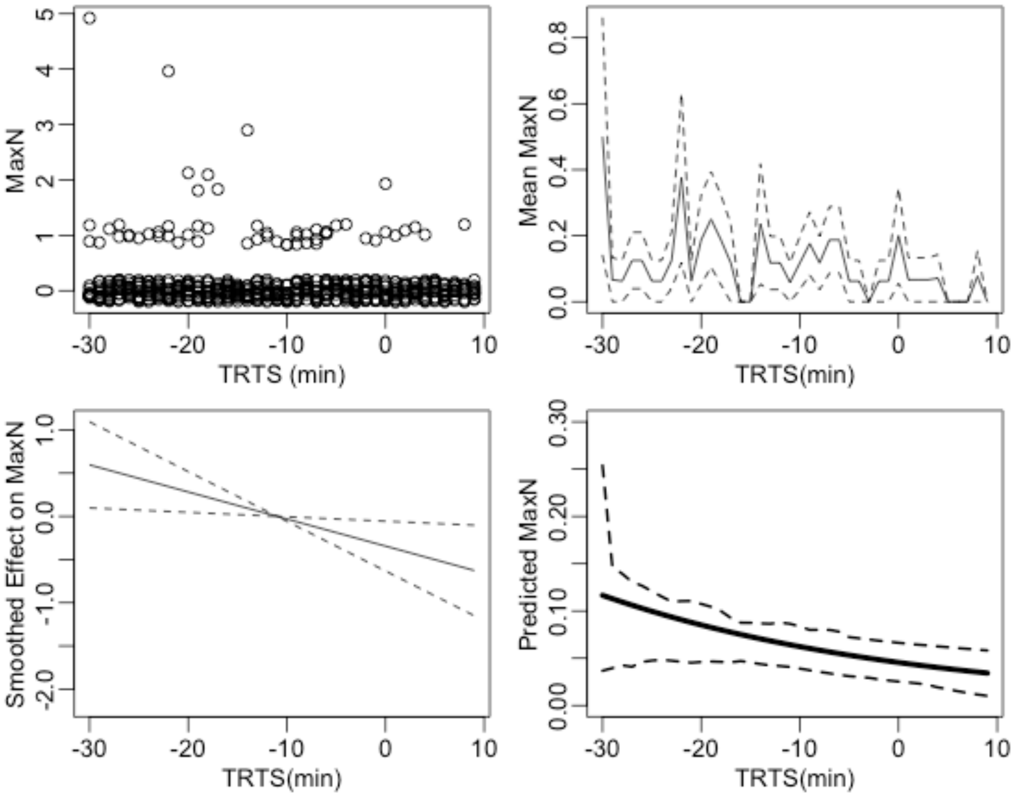

Figure 27. Red Porgy temporal abundance patterns in videos (n=17). Panels are defined as in Fig. 4.

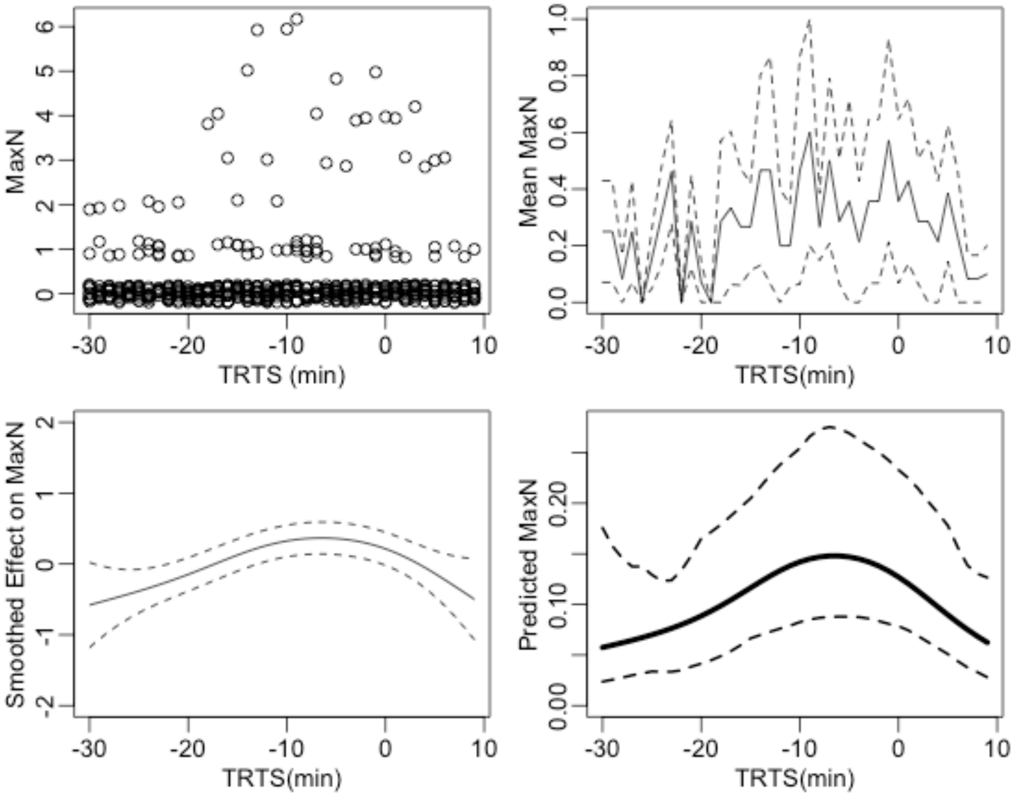

Fig. 28. *Calamus* spp. temporal abundance patterns in videos (n=15). Panels are defined as in Fig. 4.

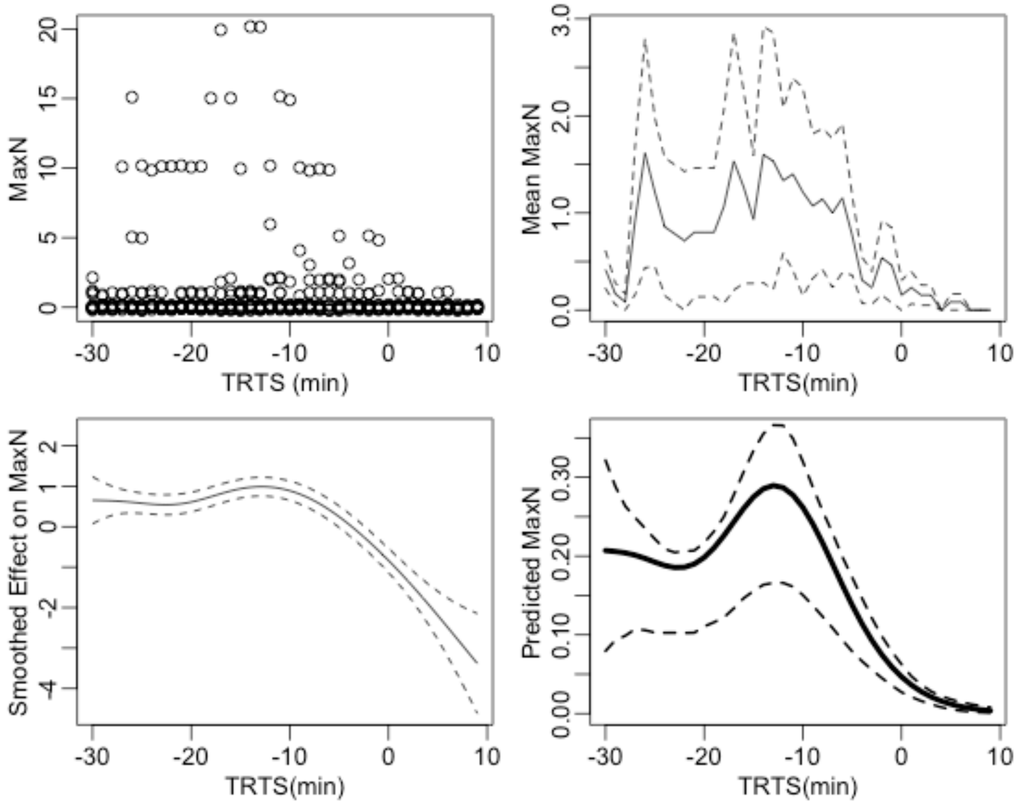

Figure 29. Spottail Pinfish temporal abundance patterns in videos (n=15). Panels are defined as in Fig. 4.

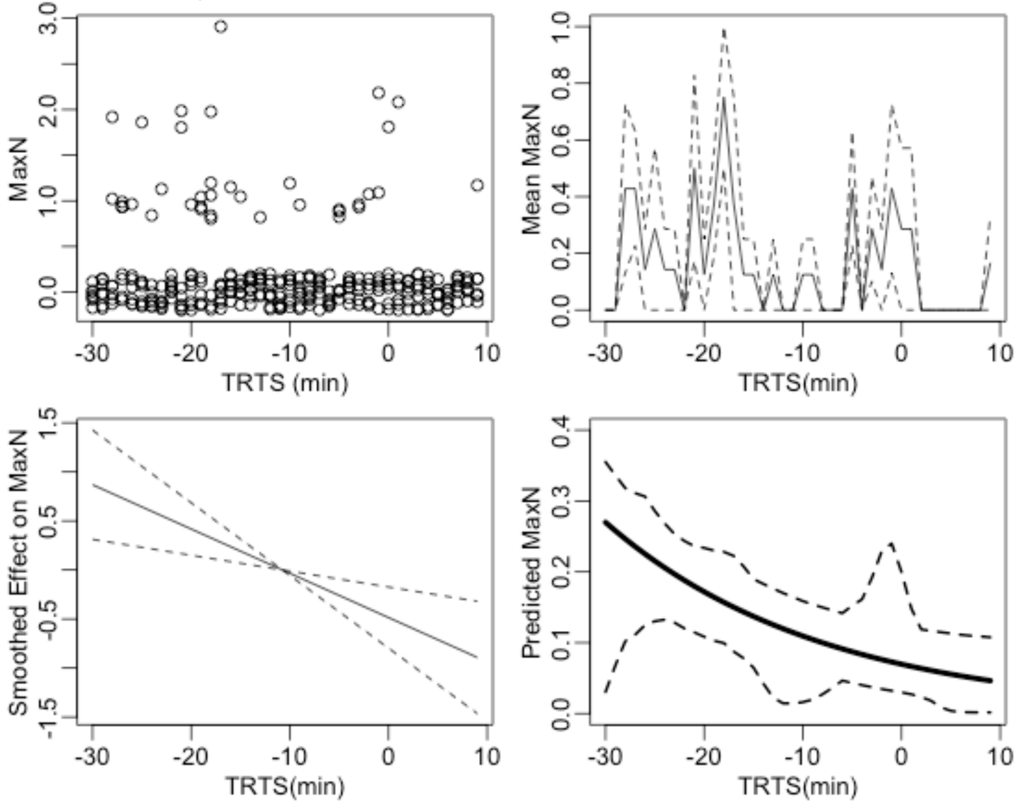

Figure 30. *Canthigaster* spp. temporal abundance patterns in videos (n=8). Panels are defined as in Fig. 4.

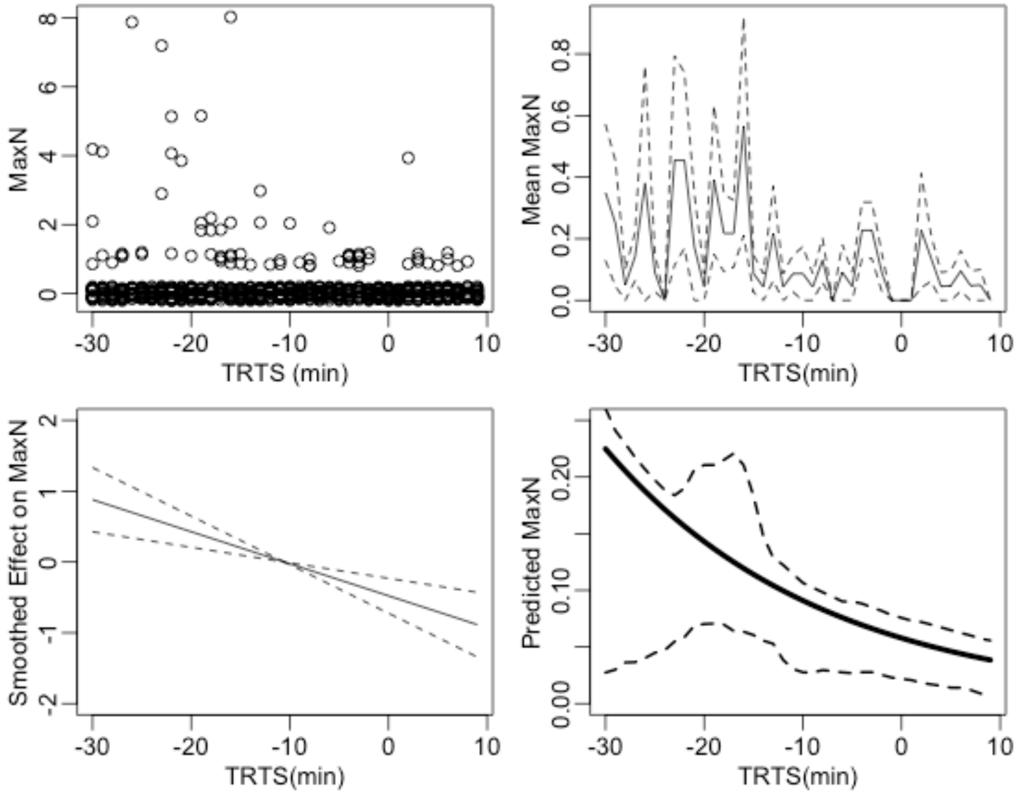

Figure 31. Pooled predators temporal abundance patterns in videos (n=23). Panels are defined as in Fig. 4.

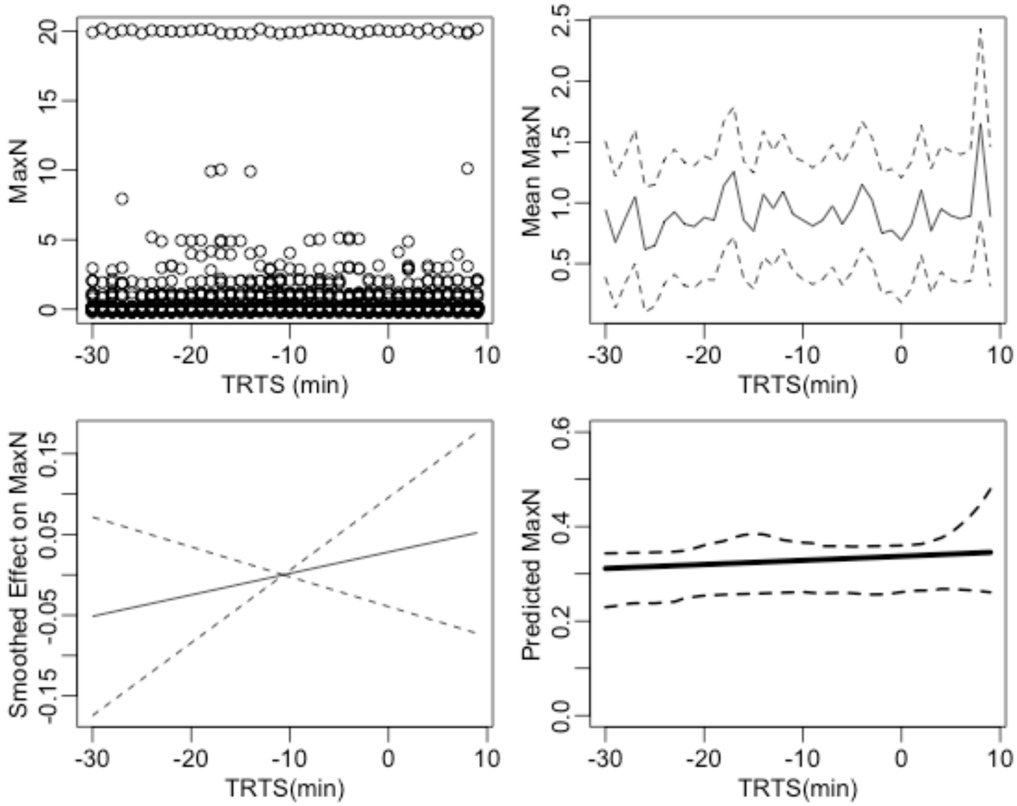

Figure 32. Unclassified fishes temporal abundance patterns in videos (n=43). Panels are defined as in Fig. 4.

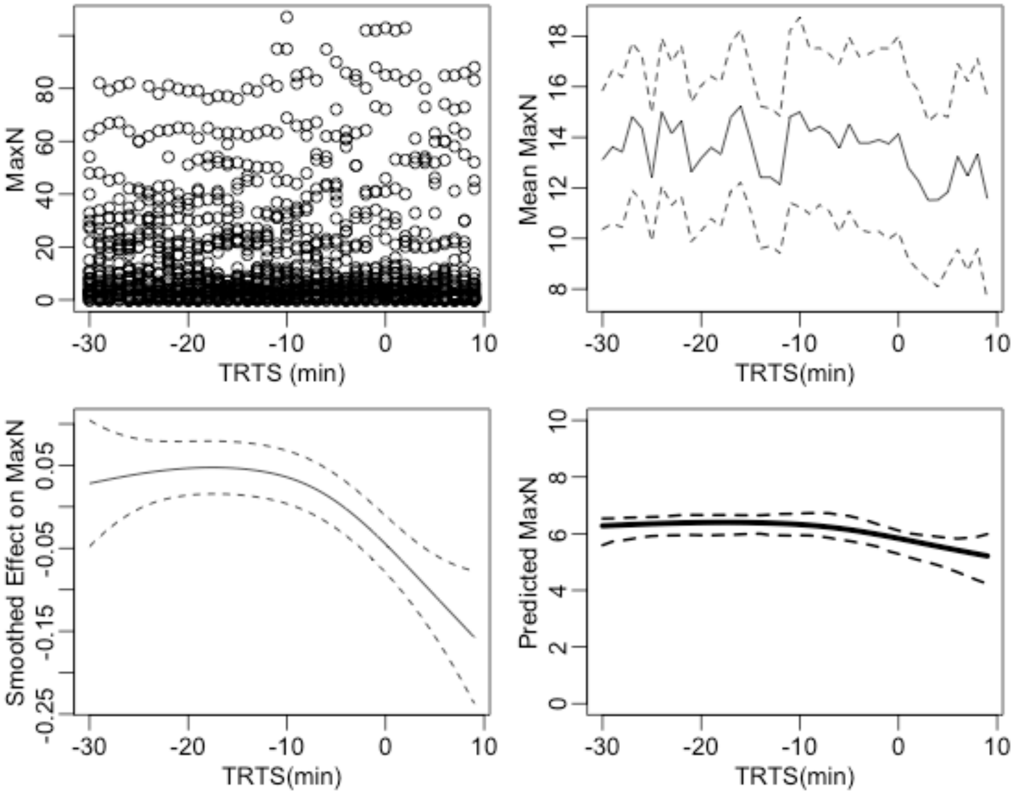

Fig. 33. Temporal abundance patterns across all taxa, including unclassified fishes. Note: Data from scad (*Decapterus* sp.) and from two large schools of Vermilion Snapper are excluded to avoid skewing data with isolated observations of large schools of these taxa. Panels are defined as in Fig. 4.

Table 1. Sampling effort. 43 independent samples (videos) were collected on 17 dates.

Date	Vessel	Latitude (°N)	Longitude (°W)	Depth (m)	Temperature (°C)	Habitat
5/29/13	R/V *Palmetto*	33.86	-77.29	28.3	21.7	hard-bottom
5/29/13	R/V *Palmetto*	33.86	-77.29	32.2	21.7	hard-bottom
5/29/13	R/V *Palmetto*	33.86	-77.29	31.4	21.7	sand-flat
5/30/13	R/V *Palmetto*	33.01	-78.61	30.8	22.7	sand-flat
5/30/13	R/V *Palmetto*	33.01	-78.61	28.4	22.7	sand-flat
6/17/13	R/V *Palmetto*	32.28	-79.73	24.4	23.7	hard-bottom
6/17/13	R/V *Palmetto*	32.28	-79.74	25.2	23.7	hard-bottom
6/17/13	R/V *Palmetto*	32.28	-79.73	24.3	23.7	sand-flat
7/10/13	private charter	32.24	-79.69	29.6	22.7	hard-bottom
7/10/13	private charter	32.24	-79.69	29.5	22.7	hard-bottom
7/16/13	R/V *Palmetto*	33.89	-77.24	30.5	23.2	sand-flat
7/16/13	R/V *Palmetto*	33.89	-77.24	27.0	23.2	hard-bottom
7/16/13	R/V *Palmetto*	33.88	-77.24	28.1	23.2	hard-bottom
8/8/13	private charter	32.31	-79.64	29.5	24.0	sand-flat
8/8/13	private charter	32.31	-79.64	29.5	24.0	hard-bottom
8/8/13	private charter	32.31	-79.64	29.5	24.0	hard-bottom
8/11/13	private charter	32.12	-79.94	28.8	25.0	sand-flat
10/1/13	R/V *Palmetto*	34.31	-76.90	24.4	24.5	hard-bottom
10/1/13	R/V *Palmetto*	34.31	-76.89	25.0	24.5	hard-bottom
10/1/13	R/V *Palmetto*	34.31	-76.88	25.3	24.5	hard-bottom
10/2/13	R/V *Palmetto*	34.35	-76.38	21.3	25.1	hard-bottom
10/2/13	R/V *Palmetto*	34.35	-76.38	21.9	25.1	hard-bottom
10/2/13	R/V *Palmetto*	34.34	-76.38	20.6	25.1	hard-bottom
10/28/13	R/V *Silver Crescent*	32.23	-79.71	30.8	24.6	hard-bottom
10/28/13	R/V *Silver Crescent*	32.24	-79.71	30.8	24.6	sand-flat
10/29/13	R/V *Silver Crescent*	32.23	-79.71	30.8	24.7	hard-bottom
10/29/13	R/V *Silver Crescent*	32.23	-79.70	31.3	24.7	hard-bottom
10/29/13	R/V *Silver Crescent*	32.24	-79.70	30.9	24.7	hard-bottom
10/30/13	R/V *Silver Crescent*	32.53	-79.55	21.9	22.3	hard-bottom
10/30/13	R/V *Silver Crescent*	32.53	-79.55	21.9	22.3	sand-flat
10/30/13	R/V *Silver Crescent*	32.53	-79.55	22.3	22.3	hard-bottom
11/10/13	private charter	32.58	-79.35	25.9	16.7	hard-bottom
11/10/13	private charter	32.58	-79.35	25.9	16.7	hard-bottom
11/10/13	private charter	32.57	-79.35	25.9	16.7	hard-bottom
12/19/13	R/V *Silver Crescent*	32.52	-79.35	26.2	20.5	sand-flat
12/19/13	R/V *Silver Crescent*	32.52	-79.35	26.2	20.5	sand-flat
12/19/13	R/V *Silver Crescent*	32.52	-79.35	26.2	20.5	sand-flat
12/20/13	R/V *Silver Crescent*	32.23	-79.70	29.0	20.5	hard-bottom

Date	**Vessel**	**Latitude (°N)**	**Longitude (°W)**	**Depth (m)**	**Temperature (°C)**	**Habitat**
12/20/13	R/V *Silver Crescent*	32.23	-79.70	29.0	20.5	hard-bottom
12/20/13	R/V *Silver Crescent*	32.23	-79.70	29.0	20.5	hard-bottom
1/26/14	private charter	32.33	-79.74	25.6	10.6	sand-flat
1/26/14	private charter	32.33	-79.74	25.7	10.6	hard-bottom
1/27/14	R/V *Silver Crescent*	32.41	-79.70	22.6	11.9	hard-bottom

Table 2. Complete list of all taxa observed. Number of videos in which a given taxon was observed is described as "n."
* – taxon was observed in ≥8 samples, and thus included in the statistical analysis.
** – taxon was observed exclusively before the dusk sampling period (n=0, as no observations were made during the dusk sampling period).

Family	**Genus**	**Species**	**Common Name**	**n**
Acanthuridae	*Acanthurus*	*chirurgus*	Doctorfish	1
Alopiidae	*Alopias*	*vulpinus*	Common Thresher Shark	1
Antennariidae	*Antennarius*	*ocellatus*	Ocellated Frogfish	1
Balistidae	*Balistes*	*capriscus*	Gray Triggerfish	10*
Carangidae	*Alectis*	*ciliaris*	African Pompano	0**
Carangidae	*Chloroscombrus*	*chrysurus*	Atlantic Bumper	2
Carangidae	*Decapterus*	sp.	scad	4
Carangidae	*Selene*	*vomer*	Lookdown	3
Carangidae	*Seriola*	sp.	Greater Amberjack Lesser Amberjack Almaco Jack Banded Rudderfish	13*
Carcharhinidae	*Rhizoprionodon*	*terraenovae*	Atlantic Sharpnose	9*
Chaetodontidae	*Chaetodon*	*ocellatus*	Spotfin Butterflyfish	4*
Chaetodontidae	*Chaetodon*	*sedentarius*	Reef Butterflyfish	7*
Dasyatidae	*Dasyatis*	*centroura*	Roughtail Stingray	1
Diodontidae	*Chilomycterus*	*reticulatus*	Spotted Burrfish	2
Echeneidae		sp.	remora sharksucker	2
Ephippidae	*Chaetodipterus*	*faber*	Atlantic Spadefish	5
Fistulariidae	*Fistularia*	sp.	cornetfish	2
Haemulidae	*Haemulon*	*aurolineatum*	Tomtate	29*
Haemulidae	*Haemulon*	*plumierii*	White Grunt	14*
Haemulidae	*Orthopristis*	*chrysoptera*	Pigfish	1
Holocentridae	*Holocentrus*	sp.	squirrelfish	0**
Labridae	*Halichoeres*	sp.	wrasse	13*
Labridae	*Lachnolaimus*	*maximus*	Hogfish	5
Lutjanidae	*Lutjanus*	*campechanus*	Red Snapper	11*
Lutjanidae	*Rhomboplites*	*aurorubens*	Vermilion Snapper	13*
Molidae	*Mola*	*mola*	Ocean Sunfish	1
Monacanthidae	*Aluterus*	*monoceros*	Unicorn Filefish	8*
Monacanthidae	*Aluterus*	*schoepfi*	Orange Filefish	4
Monacanthidae	*Aluterus*	*scriptus*	Scrawled Filefish	0**
Monacanthidae	*Stephanolepis*	*hispidus*	Planehead Filefish	22*
Mullidae	*Pseudupeneus*	*maculatus*	Spotted Goatfish	2
Muraenidae	*Gymnothorax*	*saxicola*	Honeycomb Moray Eel	1
Muraenidae		sp.	moray eel	3

Family	**Genus**	**Species**	**Common Name**	**n**
Myliobatidae	*Myliobatis*	*freminvillei*	Bullnose Ray	0**
Ostraciidae	*Acanthostracion*	*quadricornis*	Scrawled Cowfish	0**
Ostraciidae		sp.	unidentified beyond family	3
Paralichthyidae	*Paralichthys*	sp.	Gulf Flounder & other congenerics	10*
Petromyzontidae	*Petromyzon*	*marinus*	Sea Lamprey	0**
Phycidae	*Urophycis*	sp.	hake	1
Pomacanthidae	*Holacanthus*	*bermudensis*	Blue Angelfish	18*
Pomacentridae	*Chromis*	*enchrysura*	Yellowtail Reeffish	7*
Pomacentridae	*Chromis*	sp.	Sunshinefish Purple Reeffish	3*
Pomacentridae	*Stegastes*	*partitus*	Bicolor Damselfish	5*
Pomacentridae	*Stegastes*	sp.	Beaugregory Cocoa Damselfish	8*
Rachycentridae	*Rachycentron*	*canadum*	Cobia	2
Rajidae	*Raja*	*eglanteria*	Clearnose Skate	1
Rhinobatidae	*Rhinobatos*	*lentiginosus*	Atlantic Guitarfish	8*
Sciaenidae	*Equetus*	*lanceolatus*	Jackknife Fish	3
Sciaenidae	*Pareques*	*umbrosus*	Cubbyu	2
Scombridae	*Scomberomorus*	*cavalla*	King Mackerel	1
Scombridae	*Scomberomorus*	sp.	Spanish or King Mackerel	2
Scorpaenidae	*Pterois*	*volitans*	Red Lionfish	4
Serranidae	*Centropristis*	*ocyurus*	Bank Sea Bass	14*
Serranidae	*Centropristis*	*striata*	Black Sea Bass	40*
Serranidae	*Cephalopholis*	*cruentata*	Graysby	1
Serranidae	*Diplectrum*	*bivattatum*	Dwarf Sand Perch	3
Serranidae	*Diplectrum*	*formosum*	Sand Perch	11*
Serranidae	*Epinephelus*	*adscensionis*	Rock Hind	2
Serranidae	*Mycteroperca*	*microlepis*	Gag	4*
Serranidae	*Mycteroperca*	*phenax*	Scamp	9*
Serranidae	*Rypticus*	*maculatus*	Whitespotted Soapfish	7
Serranidae	*Serranus*	*phoebe*	Tattler	1
Serranidae	*Serranus*	*subligarius*	Belted Sandfish	10*
Sparidae	*Archosargus*	*probatocephalus*	Sheepshead	8*
Sparidae	*Calamus*	*arctifrons*	Grass Porgy	1*
Sparidae	*Calamus*	sp.	Knobbed Porgy & other congenerics	15*
Sparidae	*Diplodus*	*holbrookii*	Spottail Pinfish	15*
Sparidae	*Lagodon*	*rhomboides*	Pinfish	3
Sparidae	*Pagrus*	*pagrus*	Red Porgy	17*

Family	**Genus**	**Species**	**Common Name**	**n**
Sparidae	*Stenotomus*	sp.	Scup Longspine Porgy	19*
Sphyraenidae	*Sphyraena*	*barracuda*	Great Barracuda	4
Sphyrnidae	*Sphyrna*	*mokarran*	Great Hammerhead	0**
Synodontidae	*Synodus*	sp.	lizardfish	4
Tetraodontidae	*Canthigaster*	sp.	Sharpnose Puffer Goldface Toby	8*
Tetraodontidae	*Sphoeroides*	*spengleri*	Bandtail Puffer	5
Triakidae	*Mustelus*	*canis*	Smooth Dogfish	0**
Trichiuridae	*Trichiurus*	*lepturus*	Atlantic Cutlassfish	1

Table 3. List of all taxa subjected to statistical analyses via GAMM, including covariates used in the model for each taxon, estimated degrees of freedom (EDF) for TRTS smoother, and p-level of smoother. Covariates were included if they had a significant relationship with abundance, or if the model failed to converge without their inclusion. The observed temporal trend and inferred temporal niche based on life history and statistical analyses are listed.

								TRTS			
Family	**Scientific Name**	**Common Name**	**Lat**	**Depth**	**Temp**	**Season**	**Habitat**	**EDF**	**p-level**	**Trend**	**Niche**
Balistidae	*Balistes capriscus*	Gray Triggerfish	–	✓	✓	✓	–	1	0.006	Decline	Cathemeral
Carangidae	*Seriola* spp.	amberjacks	–	–	–	–	–	1	0.0002	Decline	Dusk Peak
Carcharhinidae	*Rhizoprionodon terraenovae*	Atlantic Sharpnose	–	–	–	–	–	1	0.184	None	Dusk Peak
Chaetodontidae	*Chaetodon* spp.	butterflyfishes	–	–	–	✓	–	1	0.718	None	Cathemeral
Haemulidae	*Haemulon aurolineatum*	Tomtate	✓	–	✓	–	✓	2.548	9.11E-05	Dusk Peak	Cathemeral
Haemulidae	*Haemulon plumierii*	White Grunt	–	–	–	–	–	1	0.876	None	Cathemeral
Labridae	*Halichoeres* spp.	wrasses	✓	–	✓	✓	–	3.894	9.94E-13	Decline	Diurnal
Lutjanidae	*Rhomboplites aurorubens*	Vermilion Snapper	–	–	✓	–	✓	3.717	1.18E-10	Dusk Peak	Dusk Peak
Lutjanidae	*Lutjanus campechanus*	Red Snapper	✓	–	✓	✓	✓	1	4.74E-09	Decline	Cathemeral
Monacanthidae	*Stephanolepis hispidus*	Planehead Filefish	–	–	–	✓	–	2.744	0.025	Dusk Peak	Dusk Peak
Monacanthidae	*Aluterus* spp.	*Aluterus* filefishes	✓	✓	✓	✓	✓	5.887	0.003	Dusk Peak	Dusk Peak
Paralichthyidae	*Paralichthys* spp.	flounders	✓	✓	✓	✓	–	1	0.586	None	Diurnal
Pomacanthidae	*Holacanthus bermudensis*	Blue Angelfish	–	–	–	–	–	2.393	0.267	None	Cathemeral

								TRTS			
Family	**Scientific Name**	**Common Name**	**Lat**	**Depth**	**Temp**	**Season**	**Habitat**	**EDF**	**p-level**	**Trend**	**Niche**
Pomacentridae	*Chromis* spp.	reeffishes	–	–	✓	✓	–	1	<2e-16	Decline	Diurnal
Pomacentridae	*Stegastes* spp.	damselfishes	–	–	–	✓	–	2.964	<2e-16	Decline	Diurnal
Rhinobatidae	*Rhinobatos lentiginosus*	Atlantic Guitarfish	–	–	–	–	–	1	0.384	None	Diurnal
Serranidae	*Centropristis ocyurus*	Bank Sea Bass	–	✓	✓	–	–	1	0.355	None	Cathemeral
Serranidae	*Centropristis striata*	Black Sea Bass	–	–	–	–	–	1	0.852	None	Cathemeral
Serranidae	*Diplectrum formosum*	Sand Perch	✓	✓	–	–	✓	1.739	0.046	Dusk Peak	Cathemeral
Serranidae	*Mycteroperca* spp.	Gag and Scamp Grouper	–	–	✓	✓	–	1	8.43E-05	Decline	Cathemeral
Serranidae	*Serranus subligarius*	Belted Sandfish	✓	✓	–	✓	–	1	0.019	Decline	Diurnal
Sparidae	*Stenotomus* spp.	Scup and Longspine Porgy	–	–	–	–	✓	1	0.930	None	Cathemeral
Sparidae	*Pagrus pagrus*	Red Porgy	✓	–	–	✓	✓	1	0.017	Decline	Diurnal
Sparidae	*Calamus* spp.	porgies	–	✓	✓	✓	–	2.7048	0.001	Dusk Peak	Dusk Peak
Sparidae	*Diplodus holbrookii*	Spottail Pinfish	–	✓	–	–	–	4.449	4.02E-15	Dusk Peak	Dusk Peak
Sparidae	*Archosargus probatocephalus*	Sheepshead	–	–	–	✓	–	1	0.639	None	Cathemeral
Tetraodontidae	*Canthigaster* spp.	puffers	–	–	–	–	–	1	0.002	Decline	Diurnal
pooled predators	various	various	–	–	✓	–	–	1	0.0001	Decline	Dusk Peak
unclassified fishes	various	various	–	–	–	–	✓	1	0.403	None	NA