Diel patterns of depth use and swimming activity of post-release greater amberjack (*Seriola dumerili*) in the northern Gulf of Mexico

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Abstract Greater amberjack are active swimmers that occur over a range of depths around reefs and artificial structures. In this study, we describe overall diel patterns of depth use and swimming activity for greater amberjack. We tested for impacts of fishing-related stress on diel patterns, and we describe the potential influence of cyclonic storms on diel behavior and site attachment. Fifty-five fish were tagged with depth and accelerometer tags off coastal Alabama, USA, in three field efforts (FEs): FE1, summer–fall 2018; FE2, spring 2019; and FE3, summer–fall 2020. Fish displayed diel depth patterns that varied among individuals: fish that occupied a narrow depth range midway within the water column, fish that spent time both at mid-water and near bottom, and fish with more generalized patterns. Diel depth use was best predicted by both site depth and field effort, while swimming patterns were best predicted by field effort among tested factors: legal or sublegal sizes, field effort, site, and use of a descender device vs. surface release. Swimming activity was elevated on post-release days 1–5, consistent with predicted impacts of fishing stress. For most fish, however, depth use did not vary appreciably following release. Release with a descender did not prevent altered diel patterns, and thus, barotrauma was not likely a factor. Fish occupied shallower depths when Hurricane Laura (2020) passed south of the study area, and swimming activity was elevated during Hurricane Sally (2020). Our study highlights that depth use and swimming activity of greater amberjack are influenced by multiple factors and recreational fishing discards may impart sublethal stress that results in elevated swimming activity.

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Introduction

The greater amberjack (*Seriola dumerili* [Risso]) is a large piscivorous species with a circumglobal distribution in warm temperate and tropical waters (Smith-Vaniz 2002; Fishbase 2022). Greater amberjack occur at a broad range of depths across the water column

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and are found on natural and artificial reefs over a range of depths along continental shelves and oceanic islands (Smith-Vaniz 2002; Jackson et al. 2018; Tone et al. 2021). This species supports important recreational and commercial fisheries in the northern Gulf of Mexico. In a recent assessment, greater amberjack in the Gulf of Mexico were considered overfished and currently experiencing overfishing (SEDAR, 2020). Recreational fishery management of this species involves seasonal closures and size limits (SEDAR, 2020) that result in release of sublegal sized fish during the open season and release of fish of all sizes during closures. Fish release involves the potential for both discard mortality (Curtis et al. 2015; Runde and Buckel 2018; Runde et al. 2021; Boyle et al. 2022) as well as sublethal impacts from stress and exhaustion (Hoolihan et al. 2011; Dolton et al. 2022; Iosilevskii et al. 2022). Thus, there is a need to better understand how greater amberjack utilize depth and vary swimming activity following capture and release and after longer periods of recovery. Further, active fish like greater amberjack may be expected to vary their use of water column habitat depending on bottom depth and seasonal oceanographic conditions.

Greater amberjack may also be predicted to vary swimming speed and depth associations over the course of a day. Diel patterns of habitat use and activity in fishes may be influenced by foraging behavior, predator avoidance, and sensory limitations such as light availability for vision (Helfman 1993; Volpato and Trajano 2005). Habitat and depth utilization may also be shaped by physiological optima or constraints for temperature and dissolved oxygen that vary with depth because of stratification (Aspillaga et al. 2017; Nimit et al. 2020). Released fish that experience stress from capture may be predicted to deviate from their typical diel patterns in activity and habitat use.

Stress and exhaustion from fishing is predicted to temporarily alter fish behavior following release, such as changes in swimming behavior and increased time spent immobile and vulnerable to predation (Raby et al. 2018) and changes in equilibrium (Danylchuk et al. 2007).

For greater amberjack, barotrauma of the swim bladder, a factor that can increase discard mortality in released fishes (Curtis et al. 2015; Runde and Buckel, 2018), may also be a present sublethal stress. Potential stress-related impacts on discarded animals include decreases in daily vertical depth movement in sharks

and increased vertical movement in large pelagic teleost fish (Hoolihan et al. 2011). Monitoring post-release behavior in fisheries is important because altered behavior may provide an estimate of sublethal impacts (Whitney et al. 2016). For greater amberjack, however, such sublethal impacts remain unknown.

Depth use by greater amberjack may be predicted to be influenced by a combination of abiotic and biotic factors. Certain depth ranges may present foraging opportunities, reduce or increase risk of encounters with predators, and can vary in terms of abiotic conditions like temperature, dissolved oxygen, and salinity (Zhang et al. 2009; Aspillaga et al. 2017; Nimit et al. 2020). If sublethal stress is present in discarded greater amberjack, then fish may be expected to have altered behavior, such as lowered swimming activity or differences in diel depth movements. Sublethal barotrauma, for example, could prevent the swim bladder from producing enough luminal pressure to generate sufficient volume, requiring additional thrust from swimming to produce lift to offset sinking.

The use of acoustic sensor telemetry can provide information on fish depth and swimming activity estimated from acceleration, as well as the general location of the fish. Together, these data can be used to describe general patterns of behavior and allow for inference on post-release survival, impacted behavior, and recovery following release from capture (Whitney et al. 2016). Biotelemetry sensor tags can be used to monitor diel patterns of fish depth use, swimming activity, or both (Thiem et al. 2018; Shipley et al. 2018; Noda et al. 2019; Freitas et al. 2021). These data have the potential to reveal variation in behavior among individuals, to show changes over time, and to determine if fish activity is disrupted following release and recovers over time.

This study examined the post-release behavior of greater amberjack around artificial reefs using acoustic telemetry sensor tags. The four main objectives of our study were (1) to describe the overall diel patterns of depth use and swimming activity and (2) to examine factors associated with diel patterns. (3) In addition, we tested for capture-related impacts on diel depth use and swimming activity that would be predicted from fishing stress and determined if descender devices designed to alleviate barotrauma mitigate these impacts. (4) We describe impacts of cyclonic storms on diel behavior and site attachment of greater amberjack.

Methods

We examined post-release behavior in 55 greater amberjack off coastal Alabama that were acoustically tagged as part of another study (Boyle et al. 2022) that estimated the contribution of several factors on post-release mortality from recreational fishing.

Sampling periods and study sites

Acoustic monitoring of tagged fish occurred during three study field efforts (FE1, FE2, FE3): FE1, late summer 2018 (August 16–September 12); FE2, late spring–early summer 2019 (April 30–June 25); and FE3, late summer to early fall 2020 (August 17–October 1). Over the three sampling periods, receiver deployment and fishing occurred at 16 acoustic receiver sites: steel and concrete pyramids (abbreviated Py1–8), sunken boats (Bt1–3),

a sunken barge (Bg), a sunken oil rig jacket (Jk), a sunken fuel tank (FT), a sunken grain hopper (Hp), and a submarine (Su) (Fig. 1).

Acoustic receiver deployment and retrieval

Vemco VR2AR receivers (www.innovasea.com) were deployed near artificial reefs, with one or two receivers per site (Fig. 1). Receivers were anchored to cement moorings and suspended from a line below two non-compressible 8-in. trawl floats, approximately 2 m above cement moorings. The receiver, anchor, and mooring assemblies were deployed from the surface and the receiver, and trawl floats were recovered at the end of each study period using the manufacturer's acoustic release function with a VHTx-100 transponding hydrophone and VR100 receiver.
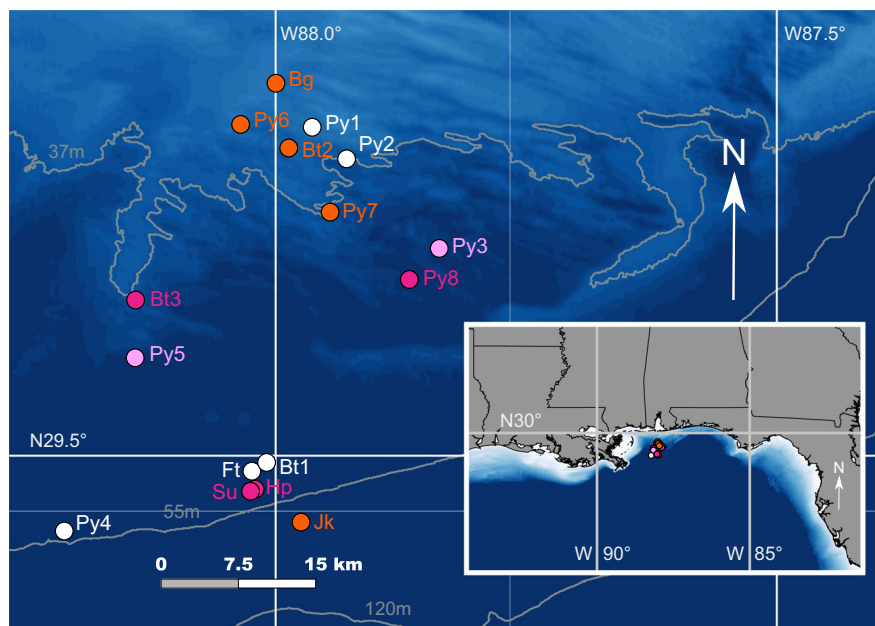

Fig. 1 Artificial reef locations of greater amberjack tagging and acoustic monitoring. Sites monitored in 2018 (FE1) are shown in white, 2019 (FE2) in orange, 2020 (FE3) in dark pink, and sites used in both 2018 and 2019 in light pink. Sites are indicated on the close-up view of the inset (right). Fish were tagged at all sites except site Su. Artificial reef site abbreviations: Py1–8, steel or concrete pyramids; Bt1–3, sunken boats; Bg, sunken barge; Jk, sunken oil rig jacket; FT, sunken fuel tank; Hp, sunken grain hopper; and Su, submarine. Number of receivers present at each reef: Py1 (2 receivers, 2018), Py2 (1 receiver, 2018), Py3 (2 receivers, 2018; 1 receiver, 2020), Py4 (2 receivers, 2018), Py5 (2 receivers, 2018; 1 receiver, 2020), Py6 (1 receiver, 2019), Py7 (2 receivers, 2019), Py8 (1 receiver, 2020), Bt1 (1 receiver, 2018), Bt2 (2 receivers, 2019), Bt3 (1 receiver, 2020), Bg (2 receivers, 2019), FT (2 receivers, 2018), Jk (2 receivers, 2019), Hp (1 receiver, 2020), and Su (1 receiver, 2020)

Fish collection, tagging, and data collection

Greater amberjack were caught and tagged following common recreational fishing methods on chartered boats (*F/V* Lady Ann and *F/V* Escape). Fish were tagged in 2018 (August 16–17 and 23–24), 2019 (April 30 and May 13–14), and 2020 (August 17–18 and 21–22). Tagging dates were chosen based on personnel and vessel availability. Fish were tagged at all sites except for site Su (Fig. 1). Abiotic data were collected on the day of fishing and tagging at each site prior to fishing. A Hydrolab sonde was used to obtain temperature in °C, salinity in practical salinity units (psu), and dissolved oxygen (DO) in mg L^{-1}. Measurements were taken at the surface and mid-depth and on the bottom. The sonde was not available on May 14 and 15, 2019, and thus, we did not have salinity, DO, and mid-depth data on release dates for FE2 for 14 fish (70% of FE2 fish) for which diel behavior was analyzed. Bottom temperature data were available from VR2AR receivers for each day. Surface temperature on these dates was obtained from the fishing vessel's depth finder. Fish were caught with live bait on 11/0 or 12/0 circle hooks and 12–16 oz weights on an 80–100-lb test monofilament leader with a swivel tied to the mainline or with artificial lures (5–6 oz jig heads with soft plastic lures). Immediately after landing, fish were measured on a board (fork length to the nearest mm) and ventilated with a saltwater hose during tagging.

Acoustic sensor tags (Vemco v9AP) were coded with the following parameters: 20–40-s delay, accelerometer range of ±4.9 m s^{-2}, high power setting, slope (resolution) of 0.3032 m for depth, depth range of 68 m, and acceleration/depth transmit ratio of 1:1. The v9AP accelerometer used the *activity algorithm*, which measures a triaxial root mean square value of acceleration, and data were sampled at 5 samples s^{-1}. In 2018, acoustic tags were attached to the fish on an external dart tag, Floy FH-69 stainless steel dart tag (www.floytag.com), with the tag attached to the dart via a 150-lb monofilament line. Prior to tagging, Vemco v9AP tags were attached to the FH-69 dart tag with marine epoxy and two zip ties, with the longitudinal axis of the cylindrical transmitter parallel to the external tag. During tagging, FH-60 dart tags were inserted and locked to interneural bones, also known as dorsal fin pterygiophores, below the spiny dorsal fin on the left side of the fish. A second dart

tag (FIM-96 nylon dart tag, www.floytag.com) with a unique tag ID number, phone number, and website was placed caudally to the stainless dart tag on the left side of the fish. Because of tag shedding in 2018, we switched to internal acoustic tag implantation in 2019 and 2020.

V9AP transmitters were placed in the peritoneal cavity with a small incision in the abdomen on the left side of the fish, 1–2 cm dorsal and 1–2 cm anterior to the anus, and incisions were closed with two interrupted sutures using a monofilament suture thread. In addition to the acoustic transmitter, fish received a dart tag with ID and contact information (FIM-96 tags were used in 2019 and FH-69 tags in 2020).

Data analyses

Fish that succumbed to post-release mortality, were not detected, or were detected <1 day were not included in the current study. Our study on post-release mortality examined acceleration and depth data from acoustic transmissions to interpret mortality, which was determined by a rapid and consistent drop in acceleration data and depth values corresponding with site depth (Boyle et al. 2022). One mortality event involved a rapid rise in depth that was consistent with either a predation event of a wounded fish or scavenging of a carcass (Boyle et al. 2022). No other events of suspected predation, i.e., rapid change in depth and consistent increase in acceleration values, were observed during the study (Boyle et al. 2022). In the present study, we examine data from fish that were inferred to be alive until the last received acoustic transmission, either when fish emigrated away from receiver sites or at the end of transmitter battery life.

Telemetry data from receivers was downloaded and arranged using VUE 2.7.0 software (Innovasea. com). We used the false detection analyzer in VUE software to look for potential erroneous detections from collisions. Obvious false detections were not observed among our data. Data analyzed in this study represent hourly and daily means of replicate observations. Erroneous detections from collisions usually result in the production of an unknown tag code (type A collision), and such events are rare (<0.05% of detections) (Simpendorfer et al. 2015) and thus unlikely to contribute substantial error in our study.

Fish movement among reefs

Fish movement was not an original focus of acoustic receiver deployment in the study design but was examined because several fish were found to have emigrated to other reef locations where receivers happened to be located. We reported the number of these observations and the minimum distance between reefs. With these methods, it was not possible to determine precise fish locations and we did not test the detection range of acoustic tags. However, range testing and modeling in another study conducted near our field sites but with larger 16-mm Vemco transmitters indicated substantial drop-off in detections at 1 km from the site (Topping and Szedlmayer 2011). In our study, we report the minimum distance between tagging site and recapture site of recaptured fish.

Abiotic conditions at the time of tagging

We tested for differences in abiotic conditions (temperature, salinity, DO at each depth: surface, mid, bottom) among the three field seasons (FE1, FE2, FE3). With the exception of bottom time, these data were taken from sonde measurements at each site visit on each day of tagging. Though these data are only the start of the study period, they describe a potential variation between the three field efforts, with FE2 occurring in late spring and FE1 and FE2 beginning in summer that may impact behavior. Bottom temperature data were available for all days during the tracking period from VR2AR receivers. For each fish, we calculated the mean bottom temperature among days examined for diel behavior (see below) from values obtained from receivers from the corresponding artificial reef site of each fish's location on each day. Data for each abiotic variate were tested for homogeneity of variance using Levene's test in the R package "car," version 3.1-1. In cases when the null hypothesis of equal variances was violated ($p < 0.05$), differences were tested with the Kruskal-Wallis test and Holm's post hoc test. Otherwise, differences were assessed with one-way ANOVA and the Tukey HSD post hoc test. We report the means of abiotic data from each field season, except for cases when Kruskal-Wallis tests were conducted, in which we report medians.

Overall diel patterns of depth use and swimming activity

We conducted an analysis of diel depth and activity patterns for all fish in which multiple complete days of depth and acceleration transmissions were available. Acceleration was standardized as a percent of the maximum tag value, 4.9 m s^{-2}, and binned in whole percentages. Depth was binned in 1-m values. For each complete 24-h activity period, an hourly mean of depth and acceleration values was calculated. The overall activity of each fish was then calculated by determining mean depth and acceleration for each hour from among the daily means of each fish. These data were used to produce two activity matrices (depth and acceleration) for each fish, with rows of depth or acceleration values and columns for 0–23 h. These calculations were conducted with Microsoft Excel. Subsequent analyses were conducted in R software, version 4.1.1 (R Core Team, 2021).

We assessed the similarity of activity patterns among fish to determine potential associations with the following predictors: reef, depth, fish size (legal or sublegal), descender device, and year of effort. Separate analyses were conducted for both depth and acceleration. Similarity among fish was assessed by calculating the pairwise similarity of activity matrices among all fish ($n = 55$) using the similarity of matrices index (SMI) (Indahl et al. 2018) with the R package "MatrixCorrelation" (Liland 2021). These pairwise SMI values were then used to produce a 54×54 similarity matrix containing SMI values for all pairs of individuals. Patterns of depth and swimming activity among fish were visualized with classical metric multidimensional scaling (MDS) using the "cmdscale" function in R. We examined the association of depth use and swimming activity using a series of permutational multivariate analysis of variance (PERMANOVA) models. PERMANOVA was performed using the "adonis2" function in the R package "Vegan" (Oksanen et al. 2022). We began with a saturated model including all possible predictor terms and interactions. For each PERMANOVA model, we calculated the Akaike information criterion corrected for small sample sizes using the "AICc_PERMANOVA.R" function (AICc) (kdyson, 2022). We tested simpler models by first removing non-significant (term p value > 0.05) interactions followed by removal of non-significant main effects.

We then removed interactions and main effects that had the lowest R^2 value, one at a time. We proceeded until observing the lowest AICc value. Models with the best support were considered to have the lowest AICc or ≤ 2 ΔAICc units from a model with the lowest AICc with an additional parameter (Burnham and Anderson, 2002). For significant terms ($p < 0.05$) within the best supported model, differences were assessed with Bonferroni post hoc tests using the "pairwise.perm.manova" function of the R package "RVAideMemoire" (Hervé, 2022).

We determined the predicted sunrise and sunset times over the date ranges of the three study periods. Sunrise and sunset times were determined with the NOAA Earth System Research Lab sunrise and sunset calculator (https://gml.noaa.gov/grad/solcalc/sunrise.html) using a latitude and longitude corresponding to a location central among our study sites. For most of each study period, sunrise and sunset occurred during hours 6 and 19 CST daylight savings time, respectively. The earliest observed sunrise during our study period was 5:56, and the earliest observed sunset was 18:28. Because our analyses of fish diel patterns were binned hourly, in our qualitative descriptions of activity patterns, we refer to activity from 6:00 to 19:00 hours as diurnal and from 20:00 to 5:00 hours as nocturnal. All times reported in our study correspond to the local time during the study period, CST daylight savings time.

Capture-related impacts on fish detection, depth use, and swimming activity

We developed a novel method to test for altered diel patterns of depth use and swimming activity that we expected could occur as the result of fishing stress. We predicted that if capture stress impacts post-release behavior, such effects would be most pronounced immediately following release. Thus, we examined depth use and swimming activity in post-release days 1–7 relative to the overall post-release pattern. For each fish, we calculated the mean depth and acceleration value for each hour per day. We then assessed the diel similarity among all complete days of data for each fish by calculating a correlation value between each pair of days, which was done using the cross-correlation function (CCF) in R with zero lags. This analysis was done for fish depth and swimming activity separately, and correlations between days were conducted only on days with data available for all 24 h. The resulting cross-correlation values between each day ranged from -1 to 1, with -1 being the complete negative correlation (out of phase), zero as randomly associated, and 1 as the maximum positive correlation.

For each fish, we then used these correlation values among days to examine post-release changes in depth use and swimming activity. We expected that if fish show strong diel cycles for depth use and swimming activity, then days that were similar to the overall mean pattern across the study period would express higher correlation coefficients than days with atypical patterns. Thus, for each day, separately for depth and swimming activity, we calculated the median correlation value among all other days, i.e., that row or column in a similarity matrix, to examine how diel patterns changed over time. We termed this median correlation value the "daily similarity value." This analysis was conducted on all fish that had complete 24-h data for post-release days 1–7 and had at least 14 days of complete observations, though not necessarily contiguous days.

We predicted that early post-release behavior would differ most from the overall pattern of diel similarity because of potential stress resulting from fishing effort, e.g., fight duration and handling time. To assess differences over time, we ranked the daily similarity values and normalized the ranks to a common 0–100 scale, with the most dissimilar day expressed as $100/(n$ ranks$)$ and the day most similar to the overall pattern equal to 100. The common scale allowed for comparisons among fish with differences in the number of complete days of observation. We performed resampling tests to determine if diel depth and swimming activity patterns of the first 7 days post release differed more from the overall pattern than would be expected by chance. For each fish with ≥ 14 complete observation days and observations during days 1 through 7, we shuffled the order of potential daily similarity values (shuffling without replacement) 10,000 times. For each iteration, we sampled seven values (representing post-release days 1–7). We then examined the distribution of median and mean resampled values for each day and considered values below the lower 5th percentile (resampled $p < 0.05$) as unlikely to have happened by chance. Separate resampling procedures were done for depth and acceleration data.

We examined the length, site depth, and release treatment (surface or descender) of fish with altered diel depth profiles or swimming activity relative to fish that did not appear affected. We considered individual fish to have altered post-release behavior in the first week based on the following criteria: having at least one of the first three post-release days with a daily similarity value in the lowest 5th percentile and having the mean rank of daily similarity value for post-release days 1–3 and 1–7 both in the lower half of correlation values for all days. We tested for size differences between lengths of affected fish and unaffected test using Welch's t test. To determine if site depth and release treatment were associated with higher proportions of affected fish than would be expected by chance, we used Fisher's exact tests.

Cyclonic storm impacts on depth use and swimming activity

Four cyclonic storms were present in the northern Gulf of Mexico during this study: 2018 Tropical Storm Gordon (Brown et al. 2018), 2020 Hurricane Marco (Beven and Berg 2021a), 2020 Hurricane Laura (Pasch et al. 2021), 2020 Hurricane Sally (Berg and Reinhart 2021), and 2020 Tropical Storm Beta (Beven and Berg 2021b). We examined the daily similarity values of fish on days when tropical storms and hurricanes were present in the region relative to other days to determine if fish exhibited atypical behavior on these days. As described above, we quantified the relative rank (0–100) of daily similarity values. We used similar resampling procedures as described above to determine if daily similarity values were atypical ($<5^{th}$ percentile of resampled data). For fish that were present on any of the examined cyclonic storm days, we shuffled the possible relative ranks (n = number of complete days) 10,000 times without replacement. At each iteration, we sampled reshuffled rank values on each analyzed storm day for all fish that had complete observations on that date. For example, three resampled ranks were drawn if a fish was observed on three separate storm days for each iteration of the resampling procedure. We examined the distribution of median and mean resampled values for each storm day. A separate resampling procedure was performed for depth and swimming profile data of Hurricane Sally because complete (24 h) accelerometer data were available for fish 118 on September

13, 2020, but depth data were not available at all hours on the same date for fish 118.

Results

We analyzed acoustic telemetry records from greater amberjack at 15 artificial reef sites that ranged from 29 to 64 m deep during separate efforts in 2018 (FE1), 2019 (FE2), and 2020 (FE3) (Table 1, Fig. 1). Fifty-five greater amberjack were tagged between 2018 and 2020 and tracked for a range of 2–56 days (mean ± SD = 31.4 d ± 16.5). Sizes of tagged fish ranged from 491 to 1100 mm fork length (mean ± SD = 794 mm ± 125). Within the observation period, eight of the acoustically tagged fish from the current study (14%) were detected on receivers at reefs where they were not originally tagged (Table 2, Fig. 1). In addition, four fish that were tagged as part of this study effort but not included in the analysis of post-release behavior because of few detections ($\leq$26 total detections, <1 complete day) were also observed at different reefs after leaving their tagging location (Table 2). Fish tagged at the hopper reef (Hp) in 2020 (n = 4) were detected at the submarine reef (S), 0.5 km away, throughout their detection periods (Fig. 1, Table 2). One of these fish (fish 121) was not included in the post-release behavior analyses because of few detections (22 total detections, <1 complete day). The receivers at Hp and Su were likely within detection range most of the time, while in this area and consistent with this observation, an acoustic tag from a fish tagged at the hopper that died following release was detected on both reefs throughout the life of the tag. Detection patterns from the remaining fish observed on receivers from multiple reefs were consistent with fish movement, and distances between the second reef location ranged from 4.5 to 18.6 km (Table 2). One fish was detected at a third reef an additional 31.7 km from the second reef, and three fish returned to their original reef (Table 2).

Several emigrations from artificial reef sites coincided with the presence of cyclonic storms. Eight emigrations occurred on September 14, 2020, when Hurricane Sally was present and five of these fish were detected at different reefs several days later (Tables 1 and 2). In addition, fish 115 emigrated on August 24, 2020, during Hurricane Marco (Table 2) and fish 113 emigrated on August 26, 2020, during

Table 1 Summary of greater amberjack tagging effort, location, and fates

Fish[1]	Site[2]	Depth (m)	Tag date (M/D/Y)	1st detection (M/D/Y)	Last detection[3] (M/D/Y)	No. of complete diel dates[4]	Range of complete diel dates (M/D–M/D)[5]	Size cat.[6]	FL (mm)	Release treatment[7]	Fate[8]
01*	Py1	30.5	8/16/18	8/16/18	8/23/18ST	6	8/17–8/22	L	950	s	A
03*	Py2	33.2	8/16/18	8/16/18	8/23/18[ST,†]	6	8/17–8/22	S	750	s	R
04*	Py3	37.0	8/16/18	8/16/18	8/23/18[ST,†]	6	8/17–8/22	L	995	dc	R
05*	Py3	37.0	8/16/18	8/16/18	9/17/18ST	23	8/17–9/17	S	630	s	A
06*	Py3	37.0	8/16/18	8/16/18	9/12/18ST	25	8/17–9/11	S	527	dc	A
07*	Py3	37.0	8/16/18	8/16/18	8/23/18ST	6	8/17–8/22	L	1100	s	A
08*	Bt1	45.0	8/16/18	8/16/18	8/21/18ST	4	8/17–8/20	L	895	dc	A
10*	Bt1	45.0	8/16/18	8/16/18	8/20/18[ST,†]	3	8/17–8/19	L	940	dc	R
11*	Bt1	45.0	8/16/18	8/16/18	8/16/18ST	6	8/17–8/24	L	900	s	A
12*	FT	49.0	8/16/18	8/16/18	10/8/18	50	8/17–10/8	S	855	dc	A
13*	Py4	52.4	8/17/18	8/17/18	8/17/18	9	8/18–8/26	L	984	s	A, E
16*	Py5	38.0	8/17/18	8/17/18	8/17/18	5	8/18–8/22	L	896	dc	A, E
17*	Py5	38.0	8/17/18	8/17/18	8/17/18ST	2	8/18–8/19	L	917	s	A
19*	Py5	38.0	8/17/18	8/17/18	8/17/18ST	7	8/18–8/26	L	966	s	A, E
20*	Py5	38.0	8/17/18	8/17/18	8/17/18ST	5	8/18–8/22	L	919	dc	A
21*	Py2	33.2	8/23/18	8/23/18	8/25/18[ST,†]	1	8/24–8/24	L	836	s	R
24	Bg	29.1	4/30/19	4/30/19	6/25/19	11	5/1–6/9	S	835	dc	A
25	Bg	29.1	4/30/19	4/30/19	5/23/19	20	5/1–5/20	S	736	s	A, E
26	Bg	29.1	4/30/19	4/30/19	6/25/19[†]	34	5/1–6/23	S	730	dc	R
27	Bg	29.1	4/30/19	4/30/19	6/5/19	20	5/1–6/2	S	730	s	A, E
28	Jk	64.0	4/30/19	4/30/19	6/25/19[†]	51	5/1–6/24	S	829	dc	R
29	Jk	64.0	4/30/19	4/30/19	5/23/19	22	5/1–5/22	S	825	s	A, E
32	Py6	32.3	5/13/19	5/13/19	6/25/19	27	5/14–6/23	S	718	dc	A, M
33	Py6	32.3	5/13/19	5/13/19	6/25/19	22	5/14–6/21	S	735	s	A
34	Bt2	32.3	5/13/19	5/13/19	5/31/19	17	5/14–5/23	S	707	dc	A, E
35	Bt2	32.3	5/13/19	5/13/19	6/25/19	30	5/14–6/22	S	720	s	A, M
36	Py7	36.9	5/13/19	5/13/19	6/25/19	35	5/14–6/24	S	634	dc	A
37	Py7	36.9	5/13/19	5/13/19	6/25/19	41	5/14–6/24	S	703	s	A
38	Jk	64.0	5/14/19	5/14/19	6/22/19	35	5/15–6/21	S	650	dc	A, E
39	Jk	64.0	5/14/19	5/14/19	6/22/19	35	5/15–6/21	S	809	s	A, E
40	Jk	64.0	5/14/19	5/14/19	6/22/19[†]	22	5/15–6/21	S	705	dc	R
41	Jk	64.0	5/14/19	5/14/19	6/25/219	38	5/15–6/24	S	800	s	A
42	Jk	64.0	5/14/19	5/14/19	6/22/19	33	5/15–6/21	S	734	dc	A, E
43	Bg	29.1	5/14/19	5/14/19	6/25/19	13	5/15–6/20	S	656	s	A
44	Bg	29.1	5/14/19	5/14/19	5/27/19	11	5/15–5/26	S	716	dc	A, E
45	Bg	29.1	5/14/19	5/14/19	5/27/19	13	5/15–6/20	S	705	s	A

Table 1 (continued)

Fish[1]	Site[2]	Depth (m)	Tag date (M/D/Y)	1st detection (M/D/Y)	Last detection[3] (M/D/Y)	No. of complete diel dates[4]	Range of complete diel dates (M/D–M/D)[5]	Size cat.[6]	FL (mm)	Release treatment[7]	Fate[8]
49	Py3	37.0	8/17/20	8/17/20	9/14/20	8	8/19–9/6	L	1050	dc	A, M, E
52	Bt3	34.8	8/18/20	8/18/20	10/1/20	7	8/30–9/30	S	785	s	A
53	Bt3	34.8	8/18/20	8/25/20	9/23/20	7	8/29–9/13	S	804	dc	A, M, E
56	Bt3	34.8	8/18/20	8/30/20	10/1/20	4	8/31–9/30	S	780	s	A
57	Bt3	34.8	8/18/20	8/18/20	10/1/20	11	9/4–9/30	S	773	dc	A
58	Bt3	34.8	8/18/20	8/28/20	10/1/20	7	8/30–9/30	S	715	s	A
59	Bt3	34.8	8/18/20	8/18/20	10/1/20	11	9/3–9/30	S	810	dc	A
104	Bt3	34.8	8/18/20	8/28/20	9/14/20	11	8/29–9/13	S	845	dc	A, E
105	Bt3	34.8	8/18/20	8/30/20	10/1/20	2	9/4–9/7	S	785	s	A
106	Bt3	34.8	8/18/20	8/18/20	10/1/20	4	9/1–9/26	S	787	dc	A
107	Py5	38.0	8/18/20	8/29/20	9/26/20	4	8/30–9/3	S	800	s	A, E
108	Py5	38.0	8/18/20	8/18/20	10/1/20	12	8/19–9/8	S	515	dc	A, M
109	Py5	38.0	8/18/20	8/18/20	10/1/20	24	8/19–9/30	S	751	s	A, M
111	Py5	38.0	8/18/20	8/18/20	9/15/20	14	8/19–9/13	S	491	s	A, M, E
113	Py5	38.0	8/18/20	8/18/20	8/26/20	7	8/19–8/25	S	824	s	A, E
114	Py5	38.0	8/18/20	8/18/20	10/1/20	16	8/19–9/13	S	750	dc	A, M
116	Py8	36.1	8/21/20	8/21/20	9/14/20	6	8/23–9/13	L	1004	s	A, E
118	Hp	47.8	8/22/20	8/22/20	9/25/20	30	8/23–9/24	S	774	dc	A, E
120	Hp	47.8	8/22/20	8/22/20	10/1/20	34	8/23–9/28	L	865	dc	A

Acoustically tagged fish were alternately released at the surface or with a descender based on the order of landing. We randomized the start of the alternating release sequence each fishing day

FL fork length, *No.* number, *D* day, *M* month, *Y* year

[1]Single asterisk (*) indicates acoustic tags placed externally on external dart tags

[2]Artificial reef sites: Py1–8, concrete or steel pyramid modules; Bt1–3, sunken boats; Bg, a sunken barge; FT, a sunken fuel tank; Jk, sunken oil rig jacket; Hp, sunken grain hopper

[3]Last detection date or shed tag date (ST, presented in superscript); dagger (†) indicates being recaptured later (see Table 3)

[4]Number of complete diel dates: days with depth and acceleration data available from all 24-h bins

[5]Date range of complete diel dates used to examine overall patterns of diel activity

[6]Size category: L, legal; S, sublegal

[7]Release treatment: s, surface; dc, descender device used

[8]Fate: A, alive; D, died; R, lived until recapture; E, emigrated outside of detection range during the life of the transmitter and prior to receiver retrieval; M, moved between sites with receivers

Table 2 Summary of greater amberjack fish that were detected on two or more reefs throughout the acoustic telemetry period

Fish	Location #1, site tagged			Location #2				Location #3			
	Reef	Date tagged	Last detection	Reef	Date of 1st detection at location #2	Distance to reef #1 (km)	Last detection at location #2	Reef	Date of 1st detection at location #3	Distance to reef #2 (km)	Last detection
32	Py6	5/13/19	6/6/19	Bg	6/6/19	5.7	6/11/19	Py6 (returned)	6/11/19	5.7	6/25/19
35	Bt2	5/13/19	6/1/19	Py6	6/1/19	5.3	6/25/19				
48*	Py3	8/17/20	8/17/20	Py8	8/17/20	4.5	8/18/20				
49	Py3	8/17/20	8/17/20	Py8	8/18/20	4.5	9/14/20				
50*	Py8	8/17/20	8/18/20	Py3	8/18/20	4.5	8/18/20	Py8 (returned)	8/19/20	4.5	8/21/20
53	Bt3	8/18/20	9/14/20	Py6	9/23/20	6.5	9/23/20				
108	Py5	8/18/20	9/14/20	Bt3	9/23/20	6.4	10/1/20				
109	Py5	8/18/20	9/14/20	Bt3	9/18/20	6.4	9/20/20	Py5 (returned)	9/21/20	6.4	10/1/20
111	Py5	8/18/20	9/14/20	Hp & Su[1]	9/15/20	18.6	9/15/20				
114	Py5	8/18/20	9/14/20	Bt3	9/30/20	6.4	10/1/20				
115*	Py8	8/21/20	8/23/20	Py3	8/23/20	4.5	8/24/20	Py5	8/24/20	31.7	8/24/20
118	Hp	8/22/20	8/22/20	Hp & Su[2]	8/22/20	0.5	8/22/20				
120	Hp	8/22/20	10/1/20	Hp & Su[2]	8/22/20	0.5	10/1/20				
121*	Hp	8/22/20	8/22/20	Hp & Su[2]	8/22/20	0.5	8/22/20				

Fish were detected on up to three reefs, with some fish returning to the original site of tagging (reef #1). Fish at the hopper and submarine sites were detected at both reefs (0.5 km apart) throughout their presence at either site. Artificial reef sites: Py1–8, concrete or steel pyramid modules; Bt1–3, sunken boats; Bg, a sunken barge; FT, a sunken fuel tank; Jk, sunken oil rig jacket; Hp, sunken grain hopper

[1] Fish emigrated to an area within detection range of the hopper and submarine reefs. The fish was detected on both reefs during the same time period, and the reefs are within 0.5 km

[2] Fish was tagged near the hopper reef but detected on receivers at both the hopper and submarine reefs (0.5 km) over the same time period

*Fish that were not included in post-release behavior analyses because of few detections and without a full day with at least one detection per hour

Hurricane Laura (Table 1). In total, 42% of observed emigrations, including both movements to reefs with receivers and emigrations of unknown fate, were associated with cyclonic storm events.

Data on location of recaptured fish were provided by anglers for five of seven acoustically tagged fish (Table 3). Distances of the recaptured location after liberty ranged from 0 to 63 km (Table 3).

Overall diel patterns

During the 2018 field effort (FE1), days with depth and swimming activity data from each hour, in most cases, were only available during August (Table 1), in part because fish shed external tags. In FE3, complete diel data were available over a similar period: August to September (Table 1). In FE2, complete diel data was available in most cases from May to June (Table 1). Notably, all fish from FE2 had sublegal length, while fish from FE1 and FE2 had both sublegal and legal sizes.

Fish from FE2 in spring 2019 were released at sites with significantly cooler surface and mid-depth temperatures in April and May than fish from FE1 and FE3 (Table 4). Bottom temperatures were also cooler throughout the tracking period in FE2. On tagging days, salinity was lower at mid and bottom depths in FE2 relative to FE1 and FE3 (Table 4). Fish in FE2 were released at sites with higher bottom DO than

fish from FE1 (mean 5.8 vs. 4.1 and 4.5 O_2 mg L^{-1}, respectively). FE3 and FE1 tracking periods occurred at a similar time, beginning in August. However, in FE3, surface, mid-depth, and bottom temperatures were highest; surface salinity was lowest; mid-depth and bottom depth salinities were lower than those in FE1; surface DO was higher than that in FE1; and mid-depth DO was lower than that in FE1 (Table 4).

Overall diel patterns of depth use

Several patterns of diel depth use measured over the course of the study were revealed among fish (Fig. 2). An assessment of diel depth use among fish in multi-dimensional space identified several patterns among fish (Fig. 3). Some fish (e.g., fish 07, 04, 21, and 20) typically occupied a narrow depth range (19–25 m) approximately midway between the bottom and surface that varied little over the course of a day, while others (e.g., fish 44 and 45) showed slightly shallower depth preferences (10–20 m) that varied over the day to a slightly shallower profile during diurnal hours (Figs. 2 and 3A). Another observed pattern was seen for fish (e.g., fish 36 and 37) that occupied two narrow regions of depth: one near the bottom (30–36 m) and one mid-depth (12–15 m). Broad variation in depth use was observed for some fish (e.g., 104, 106), while other fish (e.g., 42, 39, 3) also displayed a wide depth range but spent some time within a narrow

Table 3 Summary of recaptured greater amberjack

Fish	Tagging			Recapture	
	Reef name	Date tagged	Last detection	Date recaptured	Distance to location of last acoustic detection (km)
03	Py2	8/16/18	8/23/18*	8/1/19	63
04	Py3	8/16/18	8/23/18*	6/5/19	12
10	Bt1	8/16/18	8/20/18*	9/19/18	15
21	Py2	8/23/18	8/24/18*	6/5/19	Unknown recapture location
26	Bg	4/30/19	6/25/19	1/6/20	Unknown recapture location
27	Bg	4/30/19	6/5/19	10/15/21	77
28	Jk	4/30/19	6/25/19	8/2/19	0
40	Jk	5/14/19	6/22/19	5/24/20	25
120	Hp	8/22/20	10/1/20	4/21/22	960

Tagging reef site, tagging date, last acoustic detection at tagging site and recapture location if name known, date recaptured, and distance to tagging location when recaptured coordinates were provided by anglers. Artificial reefs: Py2 and 3, pyramid reefs; Bt1, sunken boat; Bg, sunken barge; Jk, sunken oil rig jacket

*External tag with acoustic transmitter was shed on this date

Table 4 Summary and comparison among field efforts (FE1, FE2, FE3) of abiotic conditions taken at the site of tag and release for 55 greater amberjack fish for which telemetry data were used to track depth use and swimming activity

	Test	Test statistic	df	p value	Value, units	Values			Post hoc tests		
						FE1	FE2	FE3	FE1 vs. FE2	FE1 vs. FE3	FE2 vs. FE3
Surface temp.	ANOVA	$F = 417.1$	52, 2	**<0.001**	Mean °C	29.6	24.5	30.9	**<0.001**	**<0.001**	**<0.001**
Mid temp.	ANOVA	$F = 44.5$	38, 2	**<0.001**	Mean °C	24.3	22.2	25.8	**<0.001**	**<0.001**	**<0.001**
Bottom temp.*	Kruskal-Wallis	$\chi^2 = 44.5$	2	**<0.001**	Median °C	22.9	20.7	24.8	**<0.001**	**0.008**	**<0.001**
Surface salinity	Kruskal-Wallis	$\chi^2 = 12.0$	2	**0.002**	Median PSU	31.9	28.4	25.1	0.819	**0.011**	**0.005**
Mid salinity	ANOVA	$F = 84.1$	38, 2	**<0.001**	Mean PSU	36.7	35.3	35.8	**<0.001**	**<0.001**	**<0.001**
Bottom salinity	ANOVA	$F = 898.3$	38, 2	**<0.001**	Mean PSU	37.0	35.6	36.1	**<0.001**	**<0.001**	**<0.001**
Surface DO	ANOVA	$F = 54.7$	38, 2	**<0.001**	Mean O_2 Mg L^{-1}	6.1	7.9	7.5	**<0.001**	**<0.001**	0.203
Mid DO	Kruskal-Wallis	$\chi^2 = 10.0$	2	**0.007**	Mean O_2 mg L^{-1}	6.0	5.9	5.8	0.583	**0.023**	**0.025**
Bottom DO	ANOVA	$F = 31.6$	38, 2	**<0.001**	Mean O_2 mg L^{-1}	4.1	5.8	4.5	**<0.001**	0.060	**<0.001**

Bold text indicates p values ≤ 0.05

Tagging in FE1 occurred on August 16, 17, and 23, 2018; tagging in FE2 occurred on April 30, May 13, and May 14, 2019; tagging in FE3 occurred in August 17, 18, 21, and 22, 2020. Differences in abiotic features among field efforts (FE1, summer to fall 2018; FE2, spring 2019; FE3, summer to fall 2020) were tested with one-way ANOVA, except when assumptions of homogeneity of variance were not met, in which case the Kruskal-Wallis test was used. Summary data are presented as means when ANOVA was used and medians when the Kruskal-Wallis test was employed

DO dissolved oxygen, *temp.* temperature

*Bottom temp. was determined from temperature readings from acoustic receivers. Mean average daily bottom temperature was calculated for each fish replicate from receivers present at each fish's location on that day
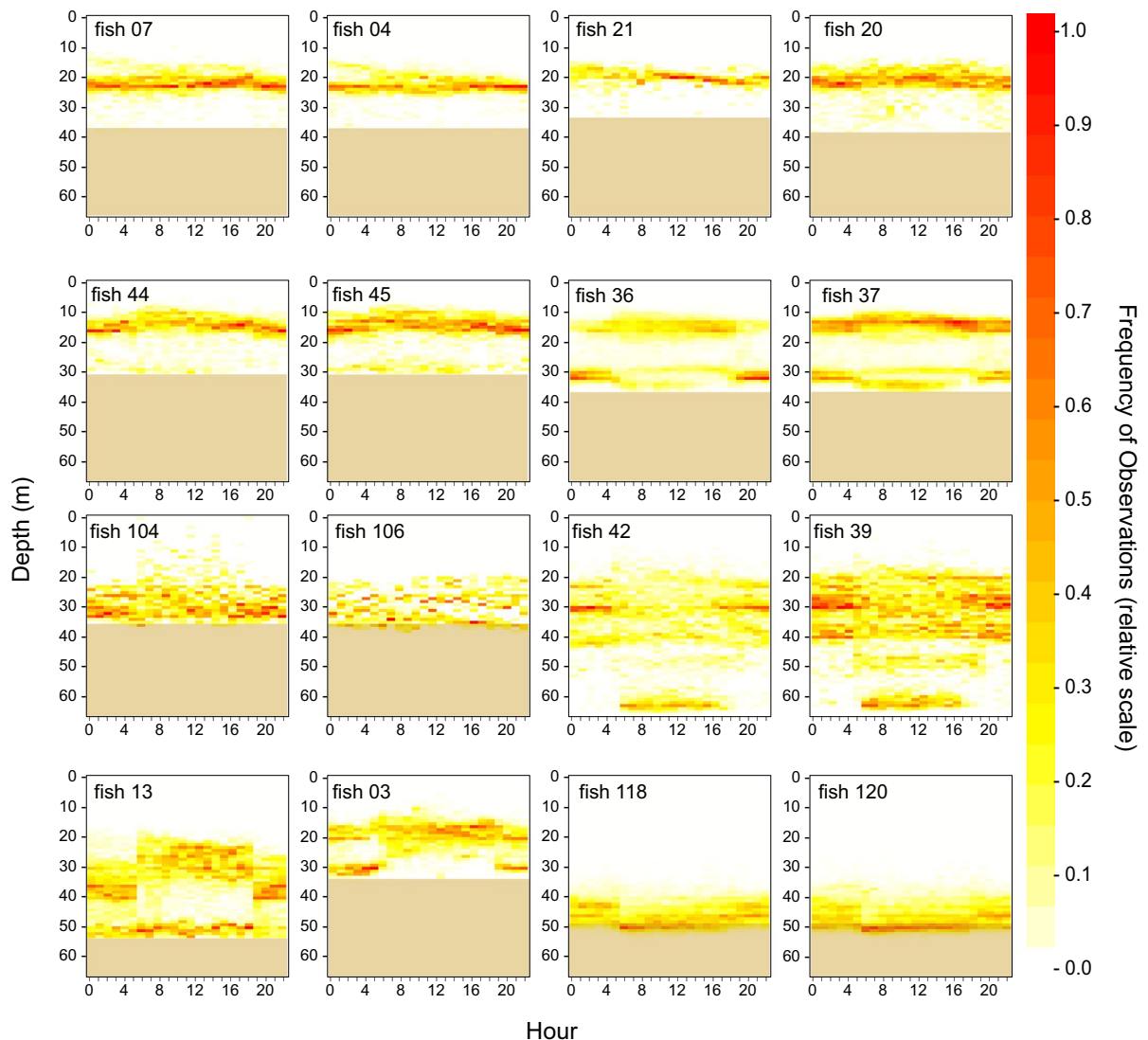
Fig. 2 Heatmap plots of mean diel depth associations for 16 fish. Warmer colors indicate higher frequency of observations averaged in hourly depth bins. Tan shading indicates non-available depth habitat for fish tagged at shallower depths

depth range near the bottom. Fish 03 occupied two distinct depth zones in evening hours, near 20 m and 30 m, and avoided deeper depths (> 25 m) during the day (Fig. 2). Fish 118 and 120 used a relatively narrow range of depth near the bottom (40–53 m) with deepest depths occurring from 6 to 19 h, during diurnal hours (Figs. 2 and 3A).

Variation in depth use patterns among legal and sublegal length fish was not strongly associated with fish size (legal vs. sublegal) (Fig. 3A) Fish of legal and sublegal sizes appear throughout most of the

observed multidimensional space of diel depth use, except for sublegal fish with low scores on MDS axes I and II; however, these fish were all tracked within FE2 (Fig. 3A). Artificial reef site and release treatment (descender or surface) were also not clear influences on diel depth use patterns (Fig. 3C, E). The observed patterns of depth use among fish in this study were mainly associated with two factors: site depth and field effort (Fig. 3B, D). Among PER-MANOVA models examining factors associated with greater amberjack diel depth, a model including field

Fig. 3 Patterns of mean diel depth use among released greater amberjack with respect to legal and sublegal fish sizes (**A**), field effort (FE1, summer–fall 2018; FE2, spring 2019; FE3, summer–fall 2020) (**B**), associated reef (**C**), depth of associated reef (**D**), and whether a descender device was used (**E**). Similarity of the mean diel depth use is displayed on a classical multidimensional scaling plot. Groups in each plot are shown with different colors and labeled on each plot. Individual fish are labeled in **A**. Circles around data points in **A**–**E** indicate fish with depth profiles shown as heatmaps in Fig. 2. Depths in **D** are in groups after rounding to the nearest 5 m. Abbreviations for artificial reefs in **C**: Py1–8, steel or concrete pyramids; Bt1–3, sunken boats; Bg, sunken barge; Jk, sunken oil rig jacket; FT, sunken fuel tank; Bt2–Py6, fish tagged at B-2 that traveled and stayed at Py6; Hp and Su, fish that stayed at sunken grain hopper and submarine reefs, which were 0.5 km apart
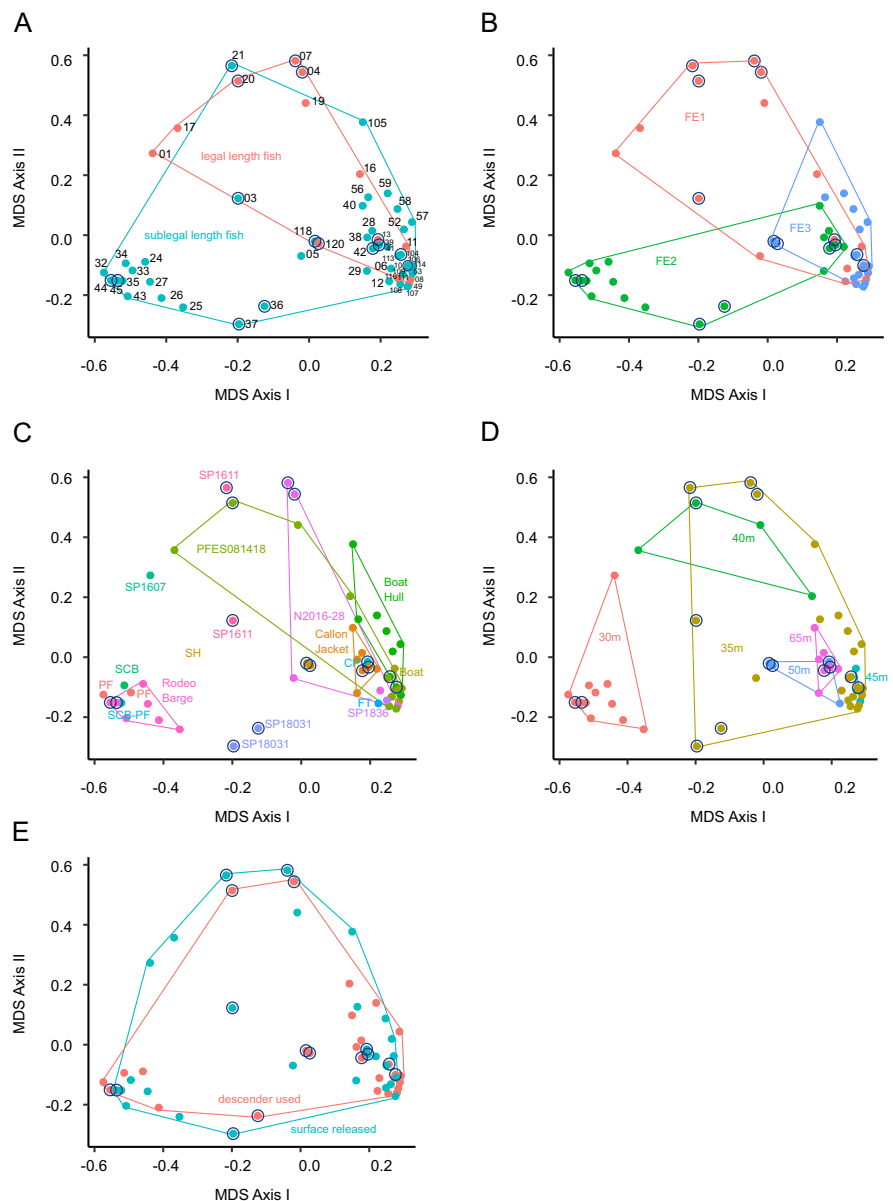
effort and depth as factors, without any interactions, was best supported (ΔAICc units = 1.308, Online Resource 1; $R^2 = 0.184$, $p = 0.001$, $R^2 = 0.282$).

Post hoc analyses indicated that diel depth patterns differed among fish from all three field efforts (Table 5). Some FE2 fish differed in multidimensional space from fish in other years in having low scores on MDS axis I and axis II. These distinctive patterns from FE2, which occurred in late spring, involve a concentration of activity at two separate depths: one at approximately 15 m throughout the 24-h cycle and a second concentration of activity at approximately 30 m, with slightly increased variability during diurnal hours. These two bands of activity correspond to a period when, at least at the time of tag and release, water temperatures were cooler (bottom temperatures were cooler throughout the tracked period of diel activity), mid-depth and bottom salinities were lower, and bottom DO was higher relative to the summertime tag and release period of FE1 and FE2 (Table 4). Some FE1 fish were distinguished in depth use from fish from other field efforts in having

Table 5 Post hoc analysis of the PERMANOVA model examining patterns of diel depth use of fish from six depth groups and between field efforts from 2018 to 2020 (FE1, FE2, FE30)

	30 m	35 m	40 m	45 m	50 m
35 m	**0.018**				
40 m	**0.036**	0.108			
45 m	0.072	1.000	0.918		
50 m	**0.018**	**0.018**	0.576	1.000	
65 m	**0.018**	0.090	0.054	0.288	0.180
	FE1	FE2			
FE2	**0.018**				
FE3	**0.018**	**0.018**			

p values for depth groups adjusted for multiple comparisons

modest scores on MDS axis I and high scores on MDS axis II. These FE1 fish were characterized by having depth use concentrated along a narrow depth range, at approximately 20 m. This narrow band of depth use occurred after a period of higher temperatures (surface, mid, bottom) relative to FE2, higher surface salinity relative to FE3, and higher mid-depth and bottom salinities than both years at the time of tagging (Table 4). Notably, in FE1, DO was lower at the surface compared to the other field efforts and lower on the bottom compared to FE2 (Table 4).

Post hoc tests indicated that diel depth patterns of fish at 30-m sites differed greater than would be expected by chance ($p < 0.05$) from 35 m, 40 m, 50 m, and 65 m (Table 5). In addition, fish from 35-m sites differed ($p < 0.05$) in diel depth use compared to fish from 50-m sites (Table 5). These differences among depth groups appear to be associated with a general trend of fish from deeper sites spending more time at greater depths.

Overall diel patterns of swimming activity

In general, swimming activity patterns were slightly elevated during diurnal hours and diel patterns varied among fish (Fig. 4). Some fish showed relatively stronger swimming activity during diurnal hours (fish 05, 118, 07, and 38) (Fig. 4). Other fish showed a narrow range of activity across the diel cycle (fish 37, 43, 49, 10, and 44) (Fig. 4). In addition, moderate to variable diel swimming patterns were observed (fish 104, 106, 53, and 58) (Fig. 4).

In contrast to observations of diel depth profiles, swimming activity among fish was less distinguished

by legal size, field effort, associated reef, and associated reef depth (Fig. 5). Multidimensional scaling plots indicated extensive overlap among fish of legal and sublegal sizes, field effort, artificial reef site, site depth, and release treatment (Fig. 5). The PERMANOVA model examining factors associated with greater amberjack swimming activity that was best supported included only field effort as a factor (Online Resource 2; $R^2 = 0.068$, $p = 0.001$). This model had better support (ΔAICc units = 0.105) than the model with an additional term, fish size (legal/sublegal). Post hoc tests indicated differences ($p < 0.05$) in swimming patterns among all three field efforts (Table 6).

High scores on MDS axis I were associated with concentrations of swimming activity higher than 10% and more variation among observed swimming activity levels, while low scores on MDS axis I were associated with more consistent, low ($< 10\%$) swimming activity levels (Fig. 5). High scores on MDS axis I were associated with lower variation in swimming activity levels across the diel cycle, while low scores on MDS axis II were associated with more variation in swimming activity at all hours of the day (Fig. 5). Fish from FE2 tended to have low scores on MDS axis I and high scores on MDS axis II, with the most dissimilar fish showing pronounced activity between 5 and 10% of maximum across the diel cycle with a marginal increase associated at 5 h and 20 h. Notably, fish exhibiting this pattern were tagged and released at a time with the coolest observed temperatures (surface, mid-depth, and bottom) (Table 4). Fish from FE3 displayed diel swimming activities that displayed more variation on MDS axis I than fish from FE1 and less variation on MDS axis II than fish from FE2. Fish from FE3 displayed wide variation on both MDS axes.

Capture-related impacts on depth use and swimming activity

Only four of fourteen fish appeared to have altered patterns of depth use following release based on our predefined criteria (Table 7). The resampling procedure indicated that median and mean daily similarity values on post-release days 1–7 did not differ substantially (resampled $p > 0.05$ for all days) from later observations. The most dissimilar days to overall depth use patterns often occurred variably among
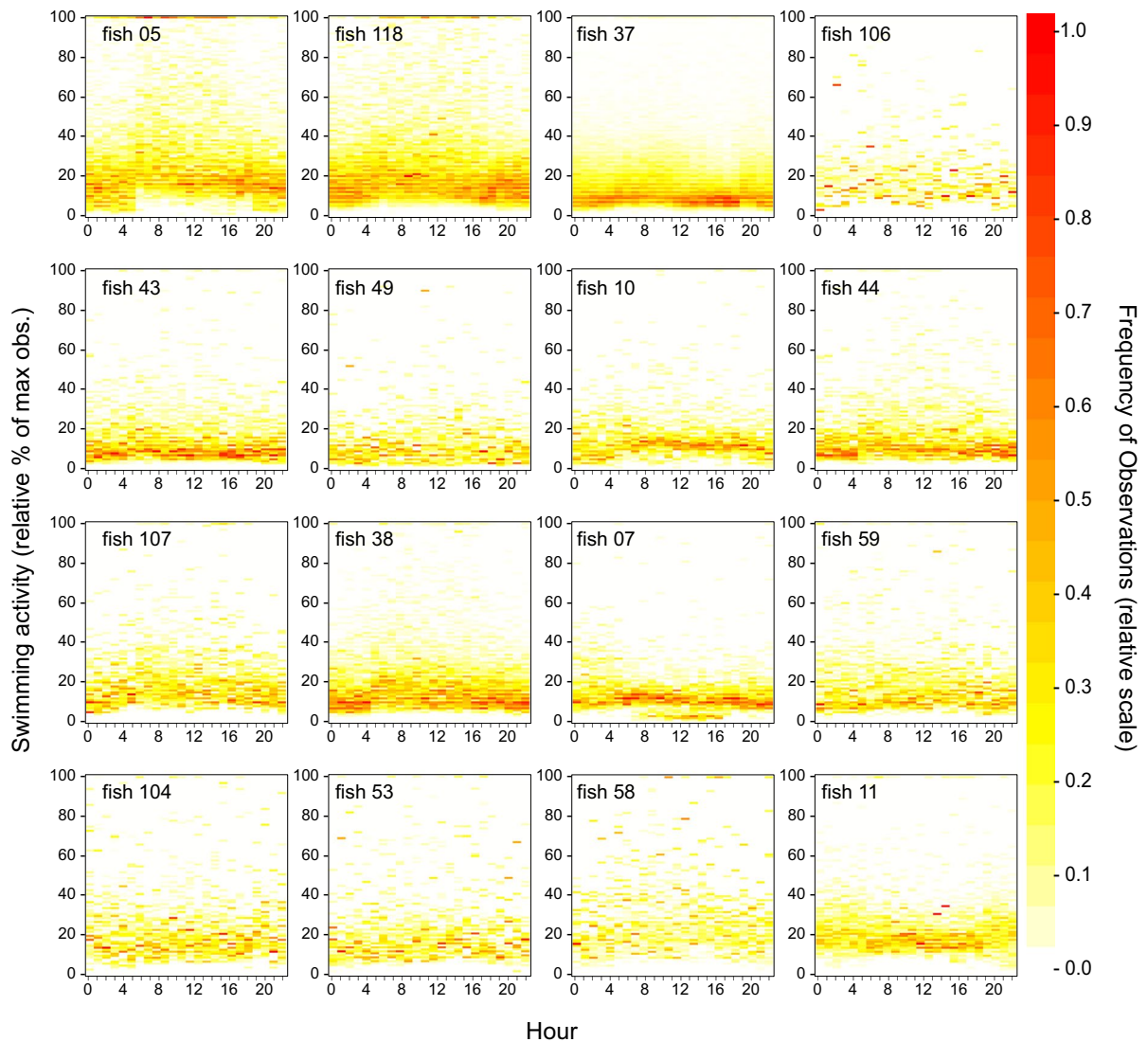
Fig. 4 Heatmap plots of swimming activity patterns for 16 fish. Warmer colors indicate higher frequency of observations averaged in hourly depth bins. Swimming activity represents accelerometry data binned among 100 values between 0 and 4.9 m s^{-2}

fish and after initial post-release days (Table 7). For example, fish 25 showed a strongly diel cycle of depth use from post-release days 0–4 and the greatest deviation from the overall pattern existed on post-release day 13, as shown by the hourly position data over time and higher daily similarity values immediately following post release (Fig. 6). Thus, in this fish, the biggest evident deviation in diel behavior appeared to occur well after release and is not consistent with an immediate impact from fishing and release. Some fish lacked strong cyclical patterns, e.g., fish 28 (Table 7,

Fig. 6). Several fish, however, showed a pattern consistent with altered depth use in the days immediately following release (Table 7). For example, fish 12 and 42 showed more consistent and pronounced diel depth migration beginning around day 10 post release and higher daily similarity values on these days (Fig. 6). Fish with altered post-release depth use tended to be longer than fish that did not appear affected (mean fork length 800 mm vs. 709 mm, Welch's t test, $df =$ 9.75, $p = 0.032$). The proportion of fish from deep reef sites (>45 m) with altered depth patterns was

Fig. 5 Patterns of mean swimming activity among released greater amberjack with respect to legal and sublegal fish sizes (**A**), field effort (FE1, summer–fall 2018; FE2, spring 2019; FE3, summer–fall 2020) (**B**), associated reef (**C**), depth of associated reef (**D**), and whether a descender device was used (**E**). Similarity of the mean diel depth use is displayed on a classical multidimensional scaling plot. Groups in each plot are shown with different colors and labeled on each plot. Individual fish are labeled in **A**. Circles around data points in **A**–**E** indicate fish with swimming activity profiles shown as heatmaps in Fig. 4. Depths in **D** are in groups after rounding to the nearest 5 m. Abbreviations for reefs are the same as in Fig. 3
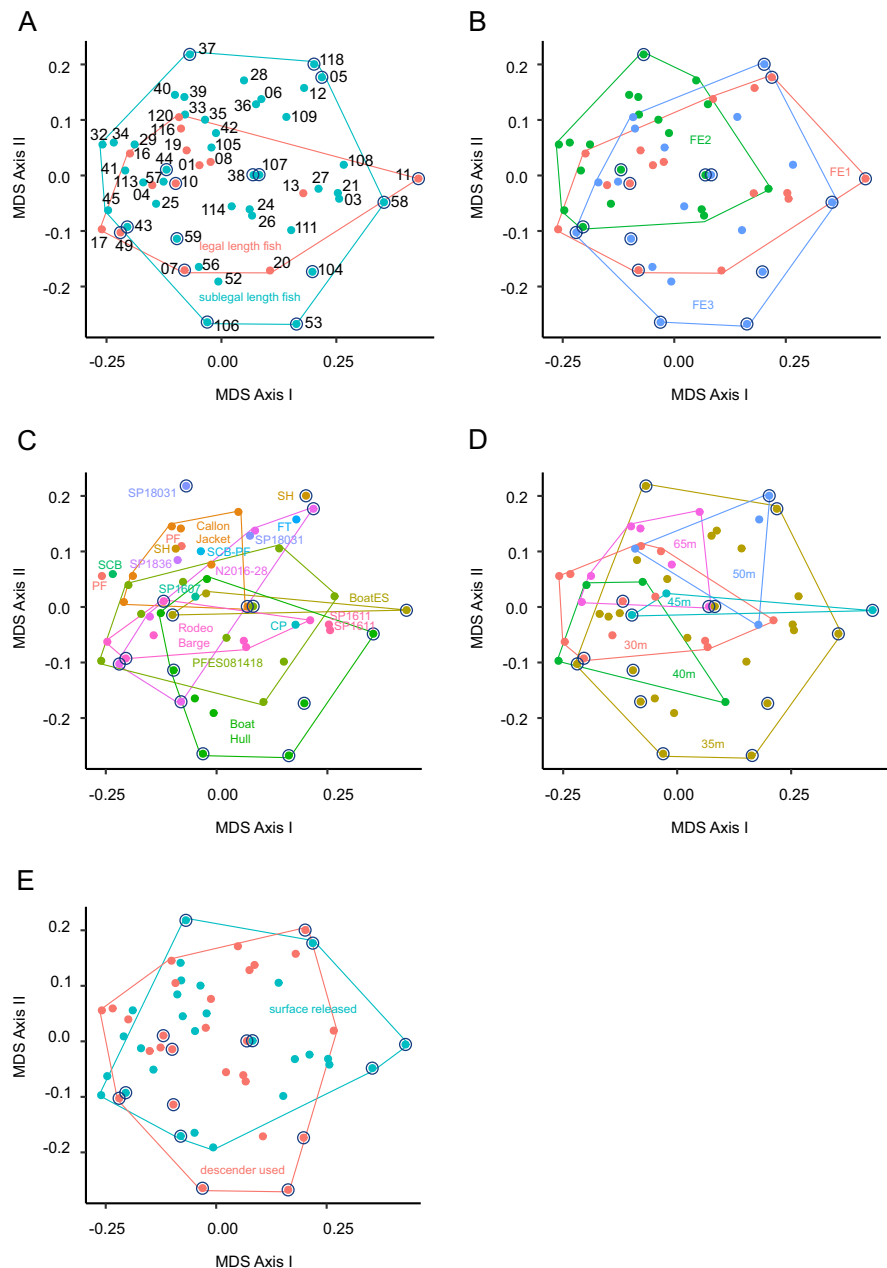
Table 6 Post hoc analysis of the PERMANOVA model examining patterns of diel swimming activity of fish among field efforts from 2018 to 2020 (FE1, FE2, FE3)

	FE1	FE2
FE2	0.003	
FE3	0.048	0.018

p values for depth groups adjusted for multiple comparisons

greater than the proportion of fish with altered depth patterns following release observed from shallower sites (0.5 vs. 0.07, respectively), and this difference exceeded expectations by chance (Fisher's exact test: odds ratio 12.11, $p = 0.033$). The proportion of fish with altered depth patterns following release, however, did not differ between fish released at the surface or by descender device (Fisher's exact test: odds ratio 0.607, $p > 0.999$).

Table 7 Early post-release diel depth association patterns relative to overall post-release diel depth behavior for fish with 14 or more complete days ($\geq$ 1 detections each daily hour) after release and with observations on the first complete post-release day

Fish	Depth (m) at site caught	Descender device used?[1]	Dissimilar post-release days ($\leq 5^{th}$ percentile)	Average rank of daily similarity values among post-release days 1–3 (relative scale 0–100)[2]			Average rank of daily similarity values among post-release days 1–7 (relative scale 0–100)[2]		
				Avg	95% CI	Max	Avg	95% CI	Max
6	< 45	desc.	6, 7	45	0–91	92	27	5–49	92
26	< 45	desc.	36, 37	34	16–53	50	53	31–75	97
32	< 45	desc.	27, 28	80	70–90	89	85	77–92	100
34	< 45	desc.	16	65	41–89	82	73	60–87	94
36	< 45	desc.	29, 41	42	14–69	66	42	29–55	66
114	< 45	desc.	15	35	2–68	68	31	12–50	68
5	< 45	su	1, 31	65	9–122	100	63	38–87	100
25	< 45	su	13	70	38–102	95	74	57–90	100
27	< 45	su	33	85	68–102	100	69	47–92	100
33	< 45	su	4, 6	35	2–68	68	31	12–50	68
35	< 45	su	5, 7	27	19–34	33	22	10–35	53
37	< 45	su	6, 16, 33	54	17–91	90	43	19–66	90
109	< 45	su	4, 5	67	42–92	92	42	18–67	92
111	< 45	su	20	79	54–103	100	67	50–85	100
12*	> 45	desc.	1, 7, 53	17	2–31	25	14	7–21	25
28	> 45	desc.	27, 38, 50	62	34–90	86	62	44–79	94
42*	> 45	desc.	3, 4	11	1–22	21	13	7–19	24
118	> 45	desc.	4, 33	58	19–97	97	45	24–66	97
120*	> 45	desc.	1, 12	19	− 2 to 39	38	34	13–54	79
29	> 45	su	13, 14	73	46–100	100	72	55–90	100
39*	> 45	su	1, 4	14	5–24	23	18	9–26	34
41	> 45	su	26, 32	46	7–84	47	47	28–66	82

[1] Abbreviations: desc., fish released with a descender device; su, fish released at the surface

[2] Ranks of post-release daily similarity values were expressed on a relative scale (0–100) because the number of full post-release day observations (all 24 h) varied among fish

*Fish with potentially altered depth use patterns during the first post-release week. These four fish also appear to have altered activity patterns (see Table 7)

Capture-related impacts on depth use and swimming activity

In contrast to observations of diel depth use, most fish tended to alter their swimming activity patterns in the first several days following release (Table 8). The resampling procedure indicated that the median and mean ranks among fish were lower than expected by chance (< 5% of resampled data) for post-release days 1–5 (Table 9). This was evident in the low daily similarity value ranks in the first few days following release: for most fish, post-release day 1 was below the 5th percentile of daily similarity values (Table 8). Altered post-release swimming behavior was evident in mean hourly acceleration values in fish with high swimming activity in the first hours following release and several days until regular and pronounced diel cycles of swimming activity were evident (e.g., fish 12, 25, 28, 33, and 42) (Fig. 7, Online Resource 3). In addition, these fish showed low daily similarity values on post-release day 1 that increased over the first week (fish 25 and 42) or, in some cases, more quickly (fish 28) (Fig. 7). While most fish displayed this altered pattern, diel swimming patterns of several

Fig. 6 Post-release diel depth associations for five fish. Depth profiles (left) and associated daily similarity of each day relative to all days (right). Plots on the left are from hourly depth transmission means from acoustic telemetry tags. Day 0 represents the day of capture. Plots on the right show the daily similarity values (see "Methods" for details) of each post-release day (beginning day 1) relative to all other days. Lower daily similarity values are associated with greater dissimilarity relative to other days. Fish 12, 38, and 42 exhibit patterns consistent with altered depth associations following capture followed by correlated diel cyclical depth associations, while fish 25 and 28 do not show this pattern
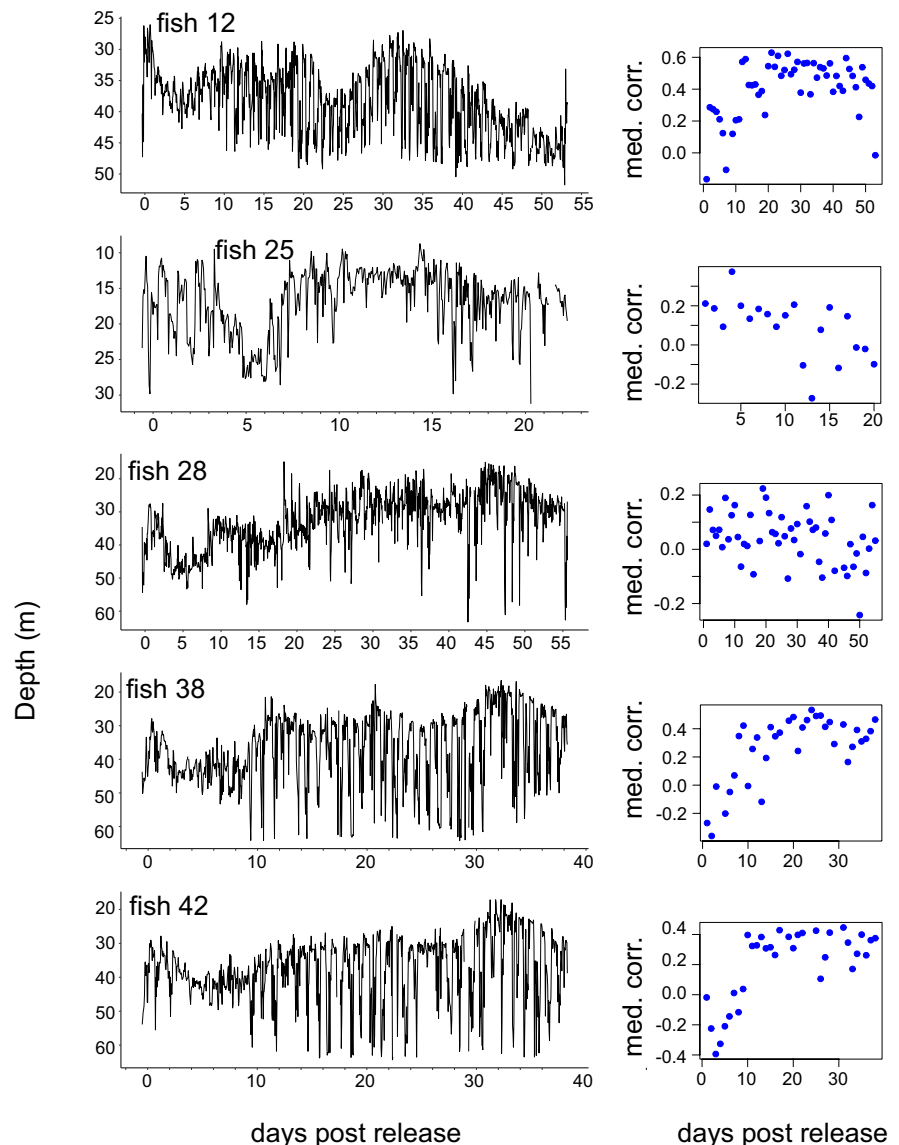
fish did not appear altered following release (fish 36 and 114) (Fig. 7). Fish with altered swimming behavior did not differ in length (Welch's *t* test, $df = 7.03$, $p = 0.308$). The proportions of fish from deep reef sites (> 45 m) between fish with and without altered swimming did not vary greater than would be expected by chance (Fisher's exact test: odds ratio 0.196, $p = 0.189$). In addition, differences in the proportions of fish with early post-release altered swimming patterns released by descender and at the surface were not observed (Fisher's exact test: odds ratio 0.893, $p > 0.999$).

Cyclonic storm impacts on depth use and swimming activity

Five named cyclonic storms passed through the northern Gulf of Mexico during the study period (Online Resources 4 and 5). Detection rates of fish on storm dates were estimated as the percentage of fish detected during a storm out of the total number of fish known to have remained in the area with active transmitters (i.e., fish detected on the storm day or at a later date). Detection rates ranged from 89 to 21%. The three lowest detection rates occurred during Hurricane Laura on August 27, 2020 (22%), and

Table 8 Early post-release diel swimming activity association patterns relative to overall post-release diel swimming behavior for fish with 14 or more complete days (≥1 detection each daily hour) after release and with observations on the first complete post-release day

Fish	Depth (m) at site caught	Descender device used?[1]	Dissimilar post-release days (≤5th percentile)	Average rank of daily similarity values among post-release days 1–3 (relative scale 0–100)[2]			Average rank of daily similarity values among post-release days 1–7 (relative scale 0–100)[2]		
				Avg	95% CI	Max	Avg	95% CI	Max
6*	<45	desc.	1, 10	19	2–36	36	45	19–70	96
26	<45	desc.	2, 53	23	0–46	44	39	12–67	100
32*	<45	desc.	1, 2	19	−8 to 46	46	38	15–60	86
34	<45	desc.	16	49	12–86	71	55	30–79	100
36	<45	desc.	5, 29	51	26–77	77	39	22–56	77
114	<45	desc.	15	67	30–103	94	71	52–90	100
5*	<45	su	2, 4	14	2–27	26	24	12–35	43
25*	<45	su	1	17	2–31	30	28	7–49	90
27*	<45	su	1	17	−2 to 35	35	42	18–66	85
33*	<45	su	1, 2	12	1–23	23	19	11–28	36
35*	<45	su	1, 2	13	−3 to 30	30	16	8–23	30
37	<45	su	14, 26, 33	12	9–15	15	39	17–60	76
109*	<45	su	1, 18	24	1–46	46	34	18–50	63
111	<45	su	26	50	7–93	93	45	23–67	93
12**	>45	desc.	1, 3, 4	5	1–8	8	9	5–13	18
28*	>45	desc.	1, 20, 23	16	−3 to 35	34	49	23–74	96
38*	>45	desc.	1, 2	10	−2 to 23	23	19	6–32	54
42**	>45	desc.	1, 2	5	2–7	6	12	6–18	25
118*	<45	desc.	1, 23	29	3–55	48	37	18–57	74
120**	>45	desc.	1, 23	28	7–50	41	43	22–63	81
29	>45	su	5	45	23–68	68	40	16–64	100
39**	>45	su	1, 4	13	3–23	21	20	4–35	65
41*	>45	su	1, 2	19	−11 to 49	50	26	8–43	55

[1]Abbreviations: desc., fish released with a descender device; su, fish released at the surface

[2]Ranks of post-release daily similarity values were expressed on a relative scale (0–100) because the number of full post-release day observations (all 24 h) varied among fish

*Fish with potentially altered swimming activity patterns during the first post-release week

**Fish in which both swimming patterns and depth use (see Table 6) appear altered

Table 9 Mean and median ranks of daily similarity values of swimming activity profiles for the first 7 days post release of 23 fish

Fish	Day 1	Day 2	Day 3	Day 4	Day 5	Day 6	Day 7
Mean	15	24	35	31	**29**	56	51
Resampled p	<0.001	0.002	0.002	<0.001	<0.001	>0.05	>0.05
Median	7	12	33	25	**18**	63	54
Resampled p	<0.001	<0.001	0.022	0.0014	<0.001	>0.05	>0.05

Bold text indicates p values ≤ 0.05. Ranks are on a common scale (0–100). Lower values are more dissimilar from the overall pattern of swimming activity among days with 24 h of observation. Resampled p indicates probabilities of observing means and median ranks this low from a resampling procedure

Fig. 7 Post-release swimming activity patterns for five fish. Swimming activity data (left) and associated daily similarity of each day relative to all days (right). Plots on the left are from hourly accelerometry transmission means from acoustic telemetry tags. Day 0 represents the day of capture. Plots on the right show the daily similarity value (see "Methods" for details) of each post-release day (beginning day 1) relative to all other days. Lower daily similarity values are associated with greater dissimilarity relative to other days. Fish 25, 28, and 42 exhibit patterns consistent with altered swimming behavior following capture followed by correlated diel swimming activity (elevated swimming activity during diurnal hours), while fish 36 and 114 do not show this pattern
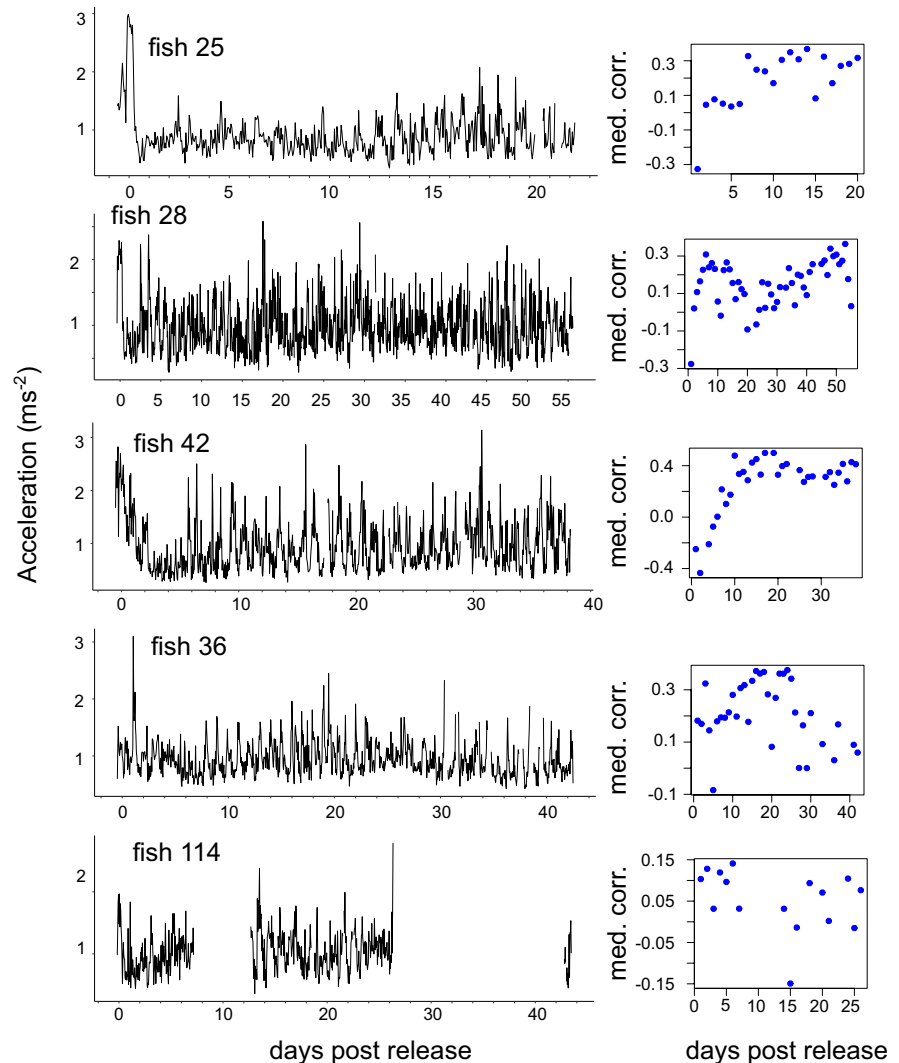
Hurricane Sally on September 15 and 16, 2020 (25% and 21%, respectively) (Online Resources 4 and 5) when several fish emigrated. A resampling test indicated that daily similarity profiles among fish differed from the overall diel depth pattern on August 26, 2020, during Hurricane Laura ($n = 4$, daily similarity value rank mean = 25.5, $p = 0.023$, median = 16.0, $p = 0.012$) (Online Resource 4). On this date, fish 118 and 120 tended to occur at slightly shallower depths during hours 6–18, fish 111 tended to occur at shallower depths in the early hours (0–4) and across a broader depth range from 20 to 24 h, while fish 108 occupied depths similar to the fish's overall diel pattern (Online Resource 6). Depth patterns on other storm dates did not differ from overall patterns

($p > 0.05$ for all dates). Resampling tests indicated that diel swimming profiles differed on 2 days during Hurricane Sally on September 14, 2020 ($n = 2$, daily similarity value rank mean and median = 9.5, $p = 0.009$) (Online Resource 5). Fish 118 and 120 tended to have more instances of elevated swimming activity on September 14 and 16 (Online Resource 7). Swimming profiles on other storm dates did not differ from overall patterns ($p > 0.05$ for all dates).

Discussion

This study revealed broad variation in greater amberjack depth associations and swimming activity. Our

results indicate that there are diel patterns in depth use and activity levels, but also notable variation exists among fish. In a previous study, greater amberjack at two sites in the same area were usually observed slightly deeper than mid-depth, with smaller fish found at 30–40 m and larger individuals found more often at depths > 45 m (Jackson et al. 2018). In the current study, however, we found greater amberjack depth use to be quite variable, with some fish mainly occupying a narrow range of depth habitat, some fish occupying several narrow bands of depth habitat, and other fish showing a wider breadth of depth use. A recent study on greater amberjack in eastern Taiwan found that daily depth migrations were associated with female fish during the spawning season after warming ocean temperatures (Tone et al. 2021). Diel depth movement was evident for many fish in the current study; however, the sex of individual fish was not known.

In our study, site depth was the factor most strongly correlated with diel depth use patterns. This relationship was not simply because of differences in available depth among sites. Depth profiles of fish on some artificial reef sites showed much more variation than others, and some depth profile patterns were uniquely observed in certain years (2018 and 2019). Clusters of similar fish depth profiles observed at some reefs within the same field effort (e.g., Bg) may result from concerted behaviors of fish present in the same school. Further, variation seen at some reefs within a single field effort could result if there are multiple schools of fish that behave differently. This prediction is consistent with the distinct patterns of some legal and sublegal fish tagged at Py3 in the same year, legal sized fish 07 and fish 04, and sublegal fish 05.

Greater amberjack in this study also showed broad variation in diel swimming activity patterns. However, in contrast to diel depth patterns, diel swimming activity patterns had weaker associations with features we examined in this study. In general, fish activity increased in the early morning and remained elevated during diurnal hours. Variation among fish also seemed to be associated with the diversity of observed acceleration values across all hours, with some fish exhibiting a narrow range of swimming activity relative to others. Diel variation in swimming activity has been observed in other taxa observed with accelerometer tags, such as Caribbean reef sharks (*Carcharhinus perezi*) that showed increased evening activity

peaking at 12 am (Shipley et al. 2018), Japanese eels (*Anguilla japonica*) which showed increased nocturnal activity (Noda et al. 2019), and increased activity in crepuscular and nocturnal periods in Murray cod (*Maccullochella peelii*), a large freshwater fish (Thiem et al. 2018). Differences in the timing of peak activity among taxa may reflect differences related to ecology, such as when these species feed and the type of prey eaten.

Fish size was not a strong predictor of diel depth use or swimming activity patterns. Legal and some sublegal sized fish appeared to maintain relatively consistent levels of swimming activity, with only modest differences between diurnal and nocturnal hours. Some sublegal fish, however, showed more variable diel patterns and more instances of intense swimming activity. Further research is needed to determine if such observations of higher swimming activity present substantial energetic costs. In a concurrent study estimating sources of greater amberjack recreational fishing discard mortality, which included fish in the present study and fish observed to succumb to post-release mortality, we found that smaller fish were far less likely to experience post-release mortality (Boyle et al. 2022). Therefore, even if high swimming activity of sublegal fish puts fish closer to their physiological limits, these smaller individuals do not appear to be at greater risk of post-release mortality.

Field effort was a predictor of diel depth and swimming activity patterns. It is possible that some of this variation is associated with oceanographic conditions varying among years and months of sampling effort. In agreement with this prediction, fish tagged at the same reef in different years (e.g., Py5) showed different depth profiles between FE1 and FE2. Differences among field efforts may be predicted in part because of differences in abiotic conditions associated with the time of each effort. FE2 occurred during spring, when water temperatures were likely cooler, as was observed at the time of tagging for surface and mid-water depths, and throughout the period of diel observations for bottom temperatures. In addition, the temperature differential between the surface, mid, and bottom depths was smaller. Such conditions may be predicted to allow the fish to occupy more depths without physiological challenges related to thermal stress. In agreement with this prediction, some fish in FE2 were observed to occupy a substantial portion of each hour at shallower depths (10–20 m) than

most fish observed in the study. Diel pattern observations for most fish from FE1 and FE2 were largely over a comparable period (August–September) within each year, yet depth use patterns of many FE1 fish differed from FE2 fish in occupying a narrow band of depth near 20 m, while many FE3 fish occupied a broader range of depth from 20 to 40 m. FE1 fish that displayed the 20-m depth use pattern were from shallower sites (35–40 m), and DO measurements at the time of tagging indicated lower bottom DO than conditions during FE2. Thus, it is possible that fish were avoiding areas with lower dissolved oxygen. Day length differences between fish observed during FE2 in spring and FE1 and FE3 in summer may also contribute to the slight variation in activity patterns observed among field efforts, as well as differences in oceanographic conditions at the time of each study period. Lastly, cyclonic storms showed measurable differences in depth use for 1 day for four fish and on swimming activity on 2 days for two fish in FE3. The influence of these days on the overall diel pattern of depth use and swimming activity, however, seems small because multidimensional scaling plots indicate that the overall depth use and swimming activity patterns were similar to other fish from the same 2020 field effort (FE3) for which diel data were not available on cyclonic storm days.

Variation in diel depth use and swimming activity among field efforts may be influenced by the reproductive season on fish behavior, as has been observed in greater amberjack off eastern Taiwan (Tone et al. 2021). In the present study, however, fish were not observed during the peak spawning season. In the Gulf of Mexico, greater amberjack peak spawning period occurs from March to May (Murie and Parkyn, 2008) and thus FE1 and FE3 of this study occurred outside of the greater amberjack spawning period, while FE1 occurred at the end of spawning season. Sex of fish was not determined in the present study; however, assuming tagged fish included a similar proportion of males and females, it is likely that at least most females tracked from FE2 were immature. All tracked fish from FE2 examined in this study were sublegal (< 864 mm fork length (FL)), their mean size was 734 mm FL, and 80% of FE 2019 fish were < 800 mm FL. Murie and Parkyn (2008) observed that 50% maturity for female greater amberjack in the Gulf of Mexico occurs around 900 mm FL, between 3 and 4 years of age, and less than 10% maturity for females

under 800 mm FL. Murie and Parkyn (2008) did not assess 50% maturity for male fish in the Gulf of Mexico, but in the southeastern U.S. Atlantic coast, where females were observed to reach 50% maturity at a smaller size (733 mm FL), 50% maturity for male was observed at 644 FL (Harris et al. 2007), which is smaller than all but one fish from FE2. Thus, it is likely that male fish from FE 2019 would be more likely to have reached maturity. Most fish caught during FE2 were sublegal (Boyle et al. 2022), and the spawning condition and history of these fishes is unknown. Thus, in the present study, it seems unlikely that spawning period had a direct influence on the observed depth use patterns and swimming activity for most fish during FE2.

Capture-related impacts on depth use and swimming activity

We observed evidence that greater amberjack show altered diel patterns following release that is consistent with the prediction that fishing stress may impact their behavior. In general, depth use appeared less impacted than swimming activity. Depth use patterns only appeared to affect several fish, and these affected fish tended to be longer and from deeper sites. However, as only five fish appeared to have potentially impacted depth use, fish length and reef depth do not appear to have a major impact on post-release depth use. By contrast, swimming activity appeared altered for most fish for up to 5 days post release. Fish with altered swimming activity patterns did not differ in length, and reef depth was not associated with altered patterns. Thus, our data indicate that discarded greater amberjack that survive release from recreational fishing are likely to exhibit higher swimming activity in the days following release regardless of reef depth, fish size, or use of a descender device. Increased swimming activity has been observed in other species; several species of sharks and Atlantic bluefin tuna (*Thunnus thynnus*) exhibit elevated swimming speeds up to 6 h post release (Iosilevskii et al. 2022). Atlantic bluefin tuna also exhibit elevated tail beat frequency for 5–10 h post release (Dolton et al. 2022). Our data indicate that elevated swimming activity can occur substantially longer (up to 5 days) in greater amberjack.

Factors associated with post-release mortality risk may be expected to also correlate with observations

of sublethal impacts in released fish. Barotrauma, which results from swim bladder expansion when fish are rapidly ascended from fishing, can impact post-release survivorship of reef fishes (Curtis et al. 2015; Runde and Buckel 2018; Bellquist et al. 2019). Damage to the swim bladder may be predicted to impact a fish's ability to maintain neutral buoyancy (Rankin et al. 2017), which could affect swimming efficiency and depth profiles. Elevated swimming activity in the days immediately following release could be consistent with this prediction. Notably, however, impacts of barotrauma would be predicted to be more severe at deeper sites, assuming capture depth correlated with reef depth, which was not observed in this study. In addition, use of a descender device did not appear to reduce incidents of altered post-release swimming behavior. Further, several carangid species, including greater amberjack, have a thin pharyngo-cleithral membrane that permits the formation of small holes in tissue when fish ascend rapidly that allow swim bladder gas to vent without causing major trauma (Hughes et al. 2016). In a companion study that included fish tagged in this study as well as fish determined to have suffered post-release mortality, factors predicted to influence likelihood of barotrauma (reef depth, descender use) were not associated with mortality risk (Boyle et al. 2022). Thus, there does not appear to be strong evidence for barotrauma as a causal factor in elevated swimming activity in the first days following release from fishing. It is notable, however, that no altered behavior or mortality risk was associated with descender use and thus the use of a descender to release greater amberjack was not associated with negative impacts and may have utility at deeper sites than the sites and the artificial reefs in the current study.

Our study observed individual variability in depth use and swimming activity among fish. Variation among individuals in spatial resource use was reported for another carangid, *Caranx latus* (Novak et al. 2020). We are not aware, however, of studies explicitly examining inter-individual variation in swimming activity and depth use in carangid fishes. Our research indicates the some of the apparent inter-individual variation in depth use and swimming activity patterns among individual greater amberjack is driven by the maximum depth of the habitat. In the first several days following release, depth use and swimming activity of some fish diverged strongly

from diel patterns observed overall. This observation suggests that some, but not all fish, appear to have sublethal impacts from fishing. Previous research in another species has found high individual variability in post-release behavior that does not always follow a simple relationship with capture parameters and indicators of stress (Eberts et al. 2018). In contrast, some species have shown no obvious impacts on diel depth migration behavior following release. For example, in a species of shark, the big-eye thresher *Alopias superciliosus*, depth migration immediately resumed following release (Sepulveda et al. 2019). Post-release mortality has been a focus of reef-associated game fishes (Curtis et al. 2015; Runde and Buckel 2018; Bohaboy et al. 2020, Runde et al. 2021), including greater amberjack (Jackson et al. 2018). Post-release behavior of fish that have not succumbed to discard morality, however, has received less attention (Wegner et al. 2021).

For greater amberjack, observations of high swimming activity following release suggest that fishing discards may impart energetic costs and potential stress for fish.

It is not yet known if such putative impacts have measurable consequences for growth or reproductive output for greater amberjack. Sublethal impacts from fishing on released fish are difficult to assess, though a modeling approach is possible (Watson et al. 2020). Such information, in conjunction with annual estimates of fishing effort, discard rate, and size structure could be valuable for management of the greater amberjack fishery in the northern Gulf of Mexico.

Fish movement from tagging locations

In our study, a relatively high percentage (14%) of fish was found to have moved among artificial reef locations over the relatively brief period of observation. In a mark-recapture study on greater amberjack in a nearby location over a 6-year period, most recaptures occurred near (within ~30 km) the point of capture (Ingram and Patterson 2001). Ingram and Patterson (2001) concluded that greater amberjack exhibit fidelity to an area but that emigration probability increases over time. In support of this conclusion, in a tag-recapture study of greater amberjack in the northern Gulf of Mexico from 2007 to 2011, half of all recaptured fish were caught within 8.0 km of their site of capture, but the mean recapture distance was much

greater (~70 km) (Murie et al. 2011). Greater amberjack off Taiwan were observed to migrate broadly southward in early winter (Tone et al. 2021).

Of the 14% of fish that were detected on multiple artificial reefs, 37.5% returned to their original tagging location before the end of the study period. Movement of greater amberjack was not an initial goal of this study, but because some fish happened to emigrate to sites within the detection range of other receivers, we were able to quantify the minimum number of emigration events. An additional 16 fish (29%) were observed to have emigrated away from any receivers (3 of 8 fish that were confirmed to have moved between reef sites emigrated outside of the array before the end of the observation period). Thus, 43% of all fish in the study appeared to have moved at least once over the observation period (31.9–55.9 days). A substantial portion (16.9%) of acoustically tagged fish as part of this study and analyzed in a companion study on post-release mortality (Boyle et al. 2022) were detected <4 h. The current study indicates that movement between reef sites is quite common, and thus, many greater amberjack that are briefly detected in studies examining post-release mortality may have survived but moved to locations outside of acoustic detection. In a study on discard mortality in the northern Gulf of Mexico, Jackson et al. (2018) estimated that 22% of released fish emigrated over a 30-day observation period. Emigration events are common in many acoustic telemetry studies (Topping and Szedlemayer 2011; Curtis et al. 2015) but pose a challenge for interpretation of post-release fish fate. It is possible that sublethal fishing stress following release increases the likelihood of emigration, but further investigation is warranted. These observations underscore the benefit of having receivers at multiple locations in studying post-release mortality of greater amberjack to decrease the probability of unknown classifications resulting from emigration.

Some of the emigration of fish observed in this study coincided with cyclonic storms in the northern Gulf of Mexico, which has been seen in other studies of reef fishes in this area. Emigration events following cyclonic storms have been observed for red snapper in the northern Gulf of Mexico (Topping and Szedlmayer 2011; Addis et al. 2013). Gray triggerfish (*Balistes capriscus*) off North Carolina were found to emigrate following hurricanes and, in many cases, to return later (Bacheler et al. 2019). Large fish with a cruising body morphology like greater amberjack (Webb 1984) may be expected to face fewer negative impacts from surge and currents produced by storms than smaller reef fishes that have a higher drag-to-body mass ratio. Previous mark-recapture work with greater amberjack, in Panama City, FL, found no effects of tropical cyclones on movement, but the storm paths were not very close to the study site (Ingram and Patterson 2001). Our study, however, indicates that at least in severe storms, greater amberjack movement appears associated with cyclonic events in the Gulf of Mexico. Researchers using acoustic telemetry to monitor greater amberjack during hurricane season should consider the potential of site emigration for study design and receiver placement.

We observed some altered activity of greater amberjack during cyclonic storms: fish occupied shallower depths on 1 day during Hurricane Laura, and swimming activity was elevated on 2 days during Hurricane Sally. Most fish were not detected during all hours of these storms, which may result in part from decreased signal noise because of ambient noise from wind and waves during the storm. Though the sample size of fish detected for complete 24-h periods was low during these storms, this altered activity and the observed emigration events that coincided with these weather events suggest that severe storms impact the daily activity of greater amberjack. Hurricane Laura was a major hurricane but passed well south of our study site (Pasch et al. 2021). Nevertheless, such a storm would produce high seas at our study sites. Hurricane Sally passed very close to our study sites as a hurricane (Berg and Reinhart 2021). Storms, for which we did not observe apparent effects on depth use and swimming activity, were weaker and, in some cases, did not pass close to our study sites (Brown et al. 2019; Beven and Berg 2021a, b). Further study is needed to determine if there are negative impacts like increased energy expenditure and decreased foraging opportunities as a direct consequence of storms. Given that greater amberjack appear to show moderate site fidelity (Ingram and Patterson 2001; Murie et al. 2011), movement of fish between suitable habitat following storms may have additional consequences.

Conclusions

Our study showed that greater amberjack exhibit diel patterns of depth use and swimming activity. Swimming activity is elevated during diurnal hours, but depth use patterns vary among fish, with some fish venturing shallower during the day and others occurring deeper during daytime. These diel patterns appear disrupted during intense storms and when fish are caught and released. Release following capture from recreational fishing gear did not alter depth use patterns for most fish, but fish that appeared to have altered diel depth patterns tended to be longer and from deep sites. In our companion study, larger fish were more likely to succumb to post-release mortality (Boyle et al. 2022) and the current study indicates there may be some addition risk of sublethal impacts on behavior for larger fish. Swimming activity following capture was more evidently impacted, with fish displaying elevated swimming activity following release for up to 5 days. Thus, in addition to post-release mortality risk, greater amberjack discarded from the recreational fishery face potential energetic costs from elevated swimming effort for up to 5 days post release that may negatively impact growth and reproductive investment.

Declarations

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