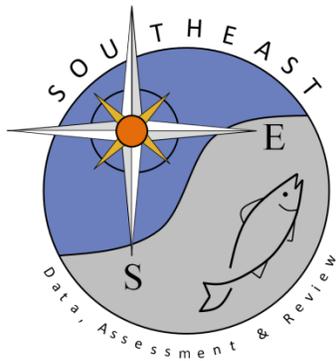


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Fine-scale movement patterns and behavioral states of gray triggerfish *Balistes capriscus* determined from acoustic telemetry and hidden Markov models



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ABSTRACT

Movement is a central feature of the ecology of fish, yet the study of fish movement has been inhibited due to its multidimensional nature and technological and analytical limitations. We used a relatively new fine-scale acoustic tracking system to quantify movements of an economically valuable, demersal marine fish species (gray triggerfish *Balistes capriscus*) on a natural hardbottom reef on the continental shelf of North Carolina, USA. Overall, 30 fish were tagged and released, and 104,170 highly precise (~1–3 m) spatial positions were estimated during the 43-d study. To quantify gray triggerfish movements, we used a combination of exploratory data analyses and hidden Markov models (HMM), the latter of which can identify and elucidate normally hidden behavioral states. Both methods suggested gray triggerfish movements varied by diel period and among individuals, and that some of the variation among individuals could be explained by fish size. Depending on model specification, HMMs identified two or three behavioral states, one of which was likely resting that occurred mostly at night and another was likely foraging or transit that occurred mostly during the day. Moreover, resting at night occurred in small, discrete patches within the study area, whereas foraging or transit behaviors occurred broadly throughout the study area. We encourage a wider use of acoustic telemetry and HMMs to shed light on the normally hidden behaviors of demersal fishes.

1. Introduction

Movement is a fundamental, organizing feature of animal ecology, influencing gene flow, colonization and extinction rates, disease spread, intraspecific interactions, and population and community dynamics (Nathan et al., 2008). Despite its importance, methodologies for quantifying movement have received less attention than methods for measuring population density and survival, in part because movement is inherently a multidimensional (spatial and temporal) phenomenon (Turchin, 1998). Elucidating movement is also challenging because it varies widely based on an animal's physiological demands, internal state, and their biotic and abiotic environment (Gurarie et al., 2009).

Quantifying the movements of marine organisms has tended to lag behind those in terrestrial environments due to various logistical and technical challenges imposed by the open ocean. It is difficult to find and tag marine organisms that spend most of their time underwater, far offshore, or in deep seafloor habitats. Moreover, animals in terrestrial

environments are most commonly tracked using devices based on the global positioning system (Kays et al., 2015), but these tags cannot be spatially located while underwater, so they are only useful for tracking marine organisms that regularly come to the surface (e.g., Michelot et al., 2017; Quick et al., 2017). Most fish species do not break the water's surface, so traditional tracking methods cannot be used for this diverse group of marine organisms. Some tags can estimate an animal's position while underwater, but these tags typically use sunrise and sunset times and perhaps water temperature for geolocation, and they are therefore useful only for fish moving across broad spatial scales (e.g., bluefin tuna *Thunnus thynnus*; Block et al., 2005). Very recently, novel tracking systems have been developed that can provide meters-level spatial resolution of a wide variety of marine fishes using arrays of underwater receivers (e.g., Espinoza et al., 2011), allowing for fine-scale relocations of many animal species that were previously untrackable.

Although recent technological advances in tracking devices have

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resulted in an abundance of tracking studies (Kays et al., 2015), approaches for analyzing these datasets have been a bottleneck (Calabrese et al., 2016). Traditionally, animal movement data have been analyzed empirically to determine temporal movement patterns across space, home range size, and diurnal or seasonal movement rates (see review by White and Garrott 1990). Yet an animal's movement path is composed of a mixture of different behavioral states (e.g., resting, feeding, transiting) that may leave statistically unique signatures. Recent movement models have been developed that can be used to identify behavioral states of individually tracked organisms using information such as distance moved over time, turning angle, acceleration or deceleration, and depth or elevation (Langrock et al., 2012; Leos-Barajas et al., 2017). Most of these movement models are hidden Markov models (HMMs; Franke et al., 2006), which are time series models that use an observation model derived from relocation data to make inferences about an animal's "hidden" or non-observable behavioral states (Langrock et al., 2012). Hidden Markov models have been rarely applied to fish telemetry data.

Here we use exploratory data analyses and HMMs to describe the movement patterns and identify behavioral states of a marine fish species, gray triggerfish (*Balistes capriscus*), on a natural temperate reef in the western North Atlantic Ocean. Gray triggerfish is a demersal reef-associated fish species (asymptotic length = 457 mm fork length; Burton et al. 2015) that is targeted by recreational and commercial fishers along the southeast United States Atlantic coast (hereafter, SEUS), and occurs in 15–100 m water depth (Bacheler et al., 2016a, 2016b). Movements of gray triggerfish have been elucidated in relation to hurricanes (Bacheler et al., 2019) and around artificial reefs (Herbig and Szedlmayer, 2016), but their movements around natural reefs, and their associated behavioral states, are unknown.

We tested four hypotheses about triggerfish movement. First, we hypothesized that movements would vary among individual gray triggerfish. Many animal populations exhibit leptokurtic movements, whereby most individuals remain in relatively small areas while others move long distances (Fraser et al., 2001), but this topic has received little attention for marine fishes. Second, we hypothesized that some of the individual differences in movements could be explained by fish size. This question has important implications for the ecology of the species, size-based fisheries management practices, and the efficacy of marine protected areas across the species ontogeny, but to the best of our knowledge has not been previously examined in gray triggerfish. Third, we hypothesized that gray triggerfish would exhibit diurnal movements, given that Herbig and Szedlmayer (2016) documented highly diurnal movements of gray triggerfish around artificial reefs in the Gulf of Mexico, with fish moving substantially more during the day than at night. Last, we hypothesized that gray triggerfish would display different movement behaviors in distinct areas within the study area. Each of these hypotheses has importance for applied fisheries management (e.g., design of marine protected areas), as well as for a broad, ecological understanding given the relative dearth of information about demersal marine fishes whose natural behavior is rarely observed.

2. Material and methods

2.1. Study site

This study was conducted at an area of mixed low-relief hardbottom reef and sand habitats covering approximately 0.5 km² on the continental shelf of North Carolina, USA (Fig. 1). The specific site was located about 35 km east of Cape Lookout, North Carolina, in 37 m of water and was chosen for three reasons. First, gray triggerfish have been tagged at this location by Runde (2017), who documented high abundance and site fidelity of the species. Second, a high-resolution bathymetric seafloor map was available for the study area (C. Taylor, unpublished data). Third, the bathymetric relief across the study area was low, which eliminated acoustic signal dead zones that can

complicate fish telemetry studies in high-relief habitats (Bacheler et al., 2015).

2.2. Data collection

We quantified the movements of gray triggerfish using a Vemco positioning system (VPS). In VPS, an array of underwater receivers are used to acoustically triangulate coded transmitters within the array, providing meters-level precision of spatial positions each time the transmitter emits a signal (Espinoza et al., 2011; Piraino and Szedlmayer, 2014). Several previous studies have successfully used VPS to quantify demersal marine fish movements (e.g., Espinoza et al., 2011; Furey et al., 2013; Piraino and Szedlmayer, 2014; Herbig and Szedlmayer, 2016; Williams-Grove and Szedlmayer, 2017).

The process by which receivers were deployed and retrieved and fish were tagged was previously described in detail by Bacheler et al. (2018), so we only provide a brief summary here. We deployed 20 submersible Vemco VR2AR receivers on 31 August 2017 in a 4 × 5 grid at the study area (Fig. 1). Receivers were separated by ~200 m from one another based on the detection range estimates of Bacheler et al. (2015) using smaller (V9) transmitters. Thus, our receivers covered an area that was 600 × 800 m in size.

Gray triggerfish were captured, tagged, and released in the study area on 15 September 2017. After capture in baited traps, gray triggerfish were immediately placed in a holding tank and then tagged externally with Vemco V13-1x transmitters. We attached transmitters externally to maximize the detection range of transmitters (Dance et al., 2016) and minimize the time it took to attach transmitters to reduce barotrauma effects (Burns et al., 2002; Jepsen et al., 2015). Transmitters emitted unique acoustic signals every 110–250 sec on a frequency of 69 kHz, weighed 11 g in air, and had a battery life of approximately 2.5 years. Gray triggerfish were tracked for 43 d (until 27 October 2017), at which point receivers were retrieved and detection data were downloaded.

We also deployed a separate reference transmitter in the study area to estimate water temperature and horizontal positional error of transmitters (Fig. 1). This reference transmitter (Vemco V13T-1x; ping rate = 9–11 min) was attached to a 4-m line connected to a buoy on one end and weight on the other. The reference transmitter was used to calculate horizontal positional error as the difference in distance between the reference tag's known location and its estimated position each time it emitted a signal. Daily horizontal position estimates from the reference tag were used to make inferences about the accuracy and precision of gray triggerfish positions.

2.3. Analyses

We tested our four hypotheses using two quantitative approaches – exploratory data analyses and HMMs. These two analytical approaches were analyzed independently from one another but were based on the same raw acoustic data. When used in combination, these two approaches are more powerful and informative than either approach alone, especially if there is strong agreement between the two. For the exploratory data analyses, movement rate of gray triggerfish was the response variable used for all calculations. Movement rates (m/s) for each fish in the study area were calculated as the distance moved (m) between each successive pair of spatial positions divided by the time between detections (s). The downside of using movement rates is that it assumes straight-line movements between detections, when in fact fish may not move in straight lines. Given that gray triggerfish were detected on average every 2–4 min, this issue is less critical in our study compared to studies with longer time intervals between detections (Alós et al., 2016), but it does imply that our movement rates should be interpreted as minimum estimates.

Specific exploratory data analyses were used to provide an initial evaluation of each of our hypotheses. First, we tested for differences in

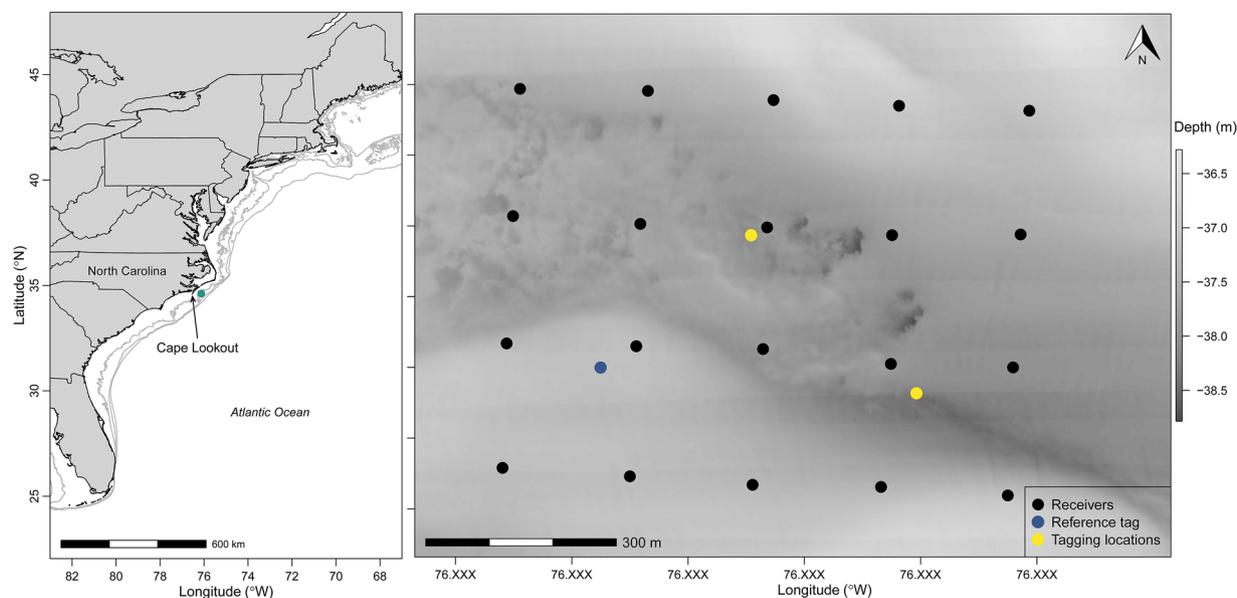


Fig. 1. Left panel: location of the study (green filled circle) east of Cape Lookout along the coast of North Carolina, USA, in 2017. Right panel: close-up view of the study area where a Vemco positioning system was used to estimate fine-scale positions of telemetered gray triggerfish (*Balistes capriscus*). The background of the right panel is a multibeam sonar map showing the bathymetry (depth) of the study area, submersible receivers are represented by black filled circles, the reference tag location is represented by the blue filled circle, and tagging locations are represented by yellow filled circles. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

movement rates across individuals using a linear model, treating fish as a categorical variable. This and all subsequent analyses were conducted in R (R Core Team, 2017). Second, we tested for size-dependent movement rates of gray triggerfish by relating mean movement rates of each fish across the entire study to their fork length using a linear model. For this analysis, we weighted points based on the available sample size for each fish. And last, we tested for diel differences in movement rates for gray triggerfish using a linear model; hour of the day was binned into 24 hourly bins and treated as a categorical variable in the model. Observations that straddled two adjacent hourly bins were assigned to the first bin. For all linear models, model effects were considered fixed effects. We used Akaike information criterion (AIC) to test whether the above linear models were better or worse when including the variable of interest compared to excluding that variable (Burnham and Anderson, 2002). We compared the AICs of fitted models to select the most parsimonious formulations, and models with the lowest AIC values ($\Delta\text{AIC} = 0$) were considered the best model in the set.

We also described the movement behaviors of gray triggerfish using HMMs. These models have recently become a popular method to analyze animal movements (e.g., Langrock et al., 2014; DeRuiter et al., 2017; Michelot et al., 2017), and in a few cases have been applied to marine fishes (e.g., Patterson et al., 2009; Phillips et al., 2015; Heerah et al., 2017; Papastamatiou et al., 2018). We used HMMs to classify gray triggerfish movement behaviors into the most likely underlying (hidden) behavioral states that give rise to our empirical, observed data. In our case, observed data included in the HMMs were step length, which was the distance moved during each time interval, and turning angle, which was the change in direction between time intervals t and $t + 1$. A fish continuing in exactly the same direction across two time intervals would have a turning angle of 0° , whereas a fish turning in the opposite direction would have a turning angle of 180° .

The HMMs require that telemetry data are provided on a consistent time interval, but our telemetry data occurred on an irregular time interval to reduce the likelihood of acoustic signal collision among individuals. We regularized our telemetry data by interpolating the animals' locations on a regular time grid using package *crawl* (Johnson et al., 2008) in R (R Core Team, 2017), which implements continuous-time correlated random walk models to provide a consistent time

interval for the HMMs. We explored a variety of time intervals for regularization, but ultimately chose a 4-min interval because most time intervals in the data were between 2 and 4 min. Regardless of the time interval used for regularization, output from the HMMs were nearly identical.

There were also instances where longer gaps between acoustic detections were apparent due to, for instance, temporary emigration of individual fish from the study area. Regularizing telemetry data across these longer time gaps was problematic because it introduced substantial regularization uncertainty. Therefore, we split tracks for individual fish when there were temporal gaps in detections longer than 20 min, which removed the temporal gap from further analyses. Multiple split tracks were then treated as independent time series arising from the same underlying statistical model. Because a common set of parameters was fitted to all tracks, the same behavioral states govern the movement before and after the gap, and they can therefore capture any existing correlation. Moreover, individual tracks for fish that included fewer than 100 detections were also removed from analyses because a continuous-time model needs to be fitted to each track for the regularization, and numerical issues arose for short tracks. Short tracks also provide very little information about the dynamics of switching between behavioral states. We also ran HMMs with different values for the time of temporal gaps and minimum sample sizes for detections and all HMM outputs were very similar, suggesting insensitivity of HMMs to our choice of threshold values. If telemetered gray triggerfish did not have any tracks with more than 100 detections, they were excluded from our HMM analyses.

A primary strength of HMMs is the ability to identify underlying behavioral states of animals that are not easily observed (i.e., unsupervised), which is particularly useful for demersal marine fishes. For instance, marine fishes may exhibit resting, foraging, and traveling states. A key challenge, however, is determining how many behavioral states should be included in HMMs (Pohle et al., 2017). Traditional model selection approaches like Akaike information criterion appear to select a much larger number of states than is expected or meaningful based on *a priori* knowledge (DeRuiter et al., 2017; Li and Bolker, 2017). Pohle et al. (2017) argue that the number of states in HMMs should be chosen pragmatically using a combination of statistical and

biological inferences. Given we have very limited inference about the behavioral states of gray triggerfish, we focused our analyses on two- and three-state HMMs, by far the most common in the movement ecology literature. We refrain from presenting more complicated models because (1) we lack biological justification that more than three behavioral states exist for gray triggerfish, (2) increasing the number of behavioral states results in a quadratic increase in the number of parameters to estimate, and (3) the goodness-of-fit improved little with additional states.

We fitted the models using the R package *momentuHMM* v1.4.1 (McClintock and Michelot, 2018). In all models, we used gamma distributions to model the step lengths and von Mises distributions for the turning angles. The von Mises distribution is a continuous probability distribution on the circle and has a concentration parameter, which measures how concentrated the turning angles are around their mean. An angle concentration of 0 indicates random turning angles, while values ~ 1 indicate highly correlated turning angles. The package *momentuHMM* uses numerical optimization to obtain maximum likelihood estimates of all model parameters. Initial parameter values must be provided to begin optimization, and poorly-chosen starting values can lead to failure to identify the global maximum of the likelihood function (Michelot et al., 2016). To ensure that we correctly estimated the parameters, we ran the fitting procedure 25 times with randomly selected starting parameters, and kept the models with highest maximum likelihood. There were no signs of convergence issues for the selected fits, even for the more complex models.

We modeled the transition probabilities of the HMM as functions of fish length and time (hour) of day to address our specific hypotheses. A multinomial logit link function was used to ensure that the transition probabilities were between 0 and 1, and that rows of the transition probability matrix summed to 1 (Michelot et al., 2016). The effect of the time of day should be cyclic over 24-hour periods to capture the circadian rhythm of the fish. This was implemented with the inclusion of the periodic covariates $\cos(2\pi t/24)$ and $\sin(2\pi t/24)$, where t is the time of the observation as a number between 0 and 24 (Towner et al., 2016). We considered five 2-state and five 3-state models with the following covariate dependencies: (1) no covariates (hereafter, “base” model), (2) fish length only (“length”), (3) time of day only (“tod”), (4) fish length and time of day (“tod + length”), and (5) fish length and time of day with interaction (“full”). We again used AIC for HMM covariate selection (Burnham and Anderson, 2002). For the selected models, we estimated the unobserved behavioral states using the Viterbi algorithm, which is the standard method to derive the most likely sequence of states of a HMM given the observations and the fitted model (Zucchini et al., 2016). From the Viterbi algorithm, we obtained an estimated behavioral state for each observed location.

Last, we estimated the probability of state persistence and state switching for fish in each of the HMMs. High state transition probabilities would indicate switching among behavioral states was common for gray triggerfish, while low transition and high persistence probabilities would indicate gray triggerfish movement behaviors occurred in bouts and were correlated. All transition probabilities were obtained by fixing each covariate to its mean value.

3. Results

Thirty adult gray triggerfish tagged in our study ranged in size from 250 to 335 mm fork length (Table 1). Using observed positional data for each fish (Appendix A), we determined that six gray triggerfish either died in the study area or lost their transmitter, 13 fish permanently emigrated from the study area during the study, and 11 fish were alive, retained their transmitter, and remained in the study area at the end of the study (Table 1). We censored all fish that stopped moving due to tag loss or death from all analyses after their movement ceased. Overall, 104,170 spatial positions were determined for the 30 telemetered gray

Table 1

Information for individual gray triggerfish (*Balistes capriscus*) in North Carolina, USA, in 2017. A Vemco positioning system was used to estimate spatial positions for telemetered gray triggerfish, and fish were tagged on 15 September 2017. An asterisk next to the fish tag number indicates that fish was excluded from hidden Markov models due to insufficient estimated positions.

Tag	Fork length (mm)	Number of estimated positions	Last day detected	Fate
30	335	1764	27-Sep	Emigrated
31	270	4321	10-Oct	Lost tag or died
32	290	235	29-Sep	Emigrated
33	265	1668	02-Oct	Lost tag or died
34	275	2002	29-Sep	Lost tag or died
35	335	982	01-Oct	Emigrated
36	310	7884	27-Oct	Alive in array
37	280	6992	27-Oct	Alive in array
38	250	8491	27-Oct	Alive in array
39	273	1263	23-Sep	Lost tag or died
40	325	1079	01-Oct	Lost tag or died
41*	275	178	18-Sep	Emigrated
42*	268	242	15-Oct	Emigrated
43	320	661	26-Sep	Emigrated
44	295	8223	27-Oct	Alive in array
45*	312	92	15-Sep	Emigrated
46	285	4345	27-Oct	Alive in array
47	268	8881	27-Oct	Alive in array
48	315	837	22-Sep	Lost tag or died
49	285	5061	27-Oct	Alive in array
50*	305	204	18-Sep	Emigrated
51	318	1320	24-Sep	Emigrated
52	275	10912	27-Oct	Alive in array
53*	250	167	27-Sep	Emigrated
54	270	9018	27-Oct	Alive in array
55*	308	63	16-Sep	Emigrated
56	312	5028	27-Oct	Alive in array
57	305	370	20-Sep	Emigrated
58	255	11789	27-Oct	Alive in array
59*	315	98	17-Sep	Emigrated

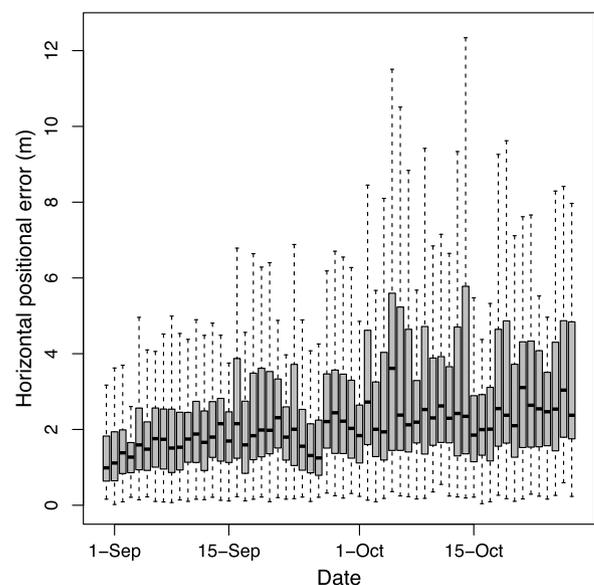


Fig. 2. Daily horizontal positional error (m) estimates of a reference transmitter deployed in North Carolina, USA, in 2017. The estimated position of the reference tag each time it emitted an acoustic signal was compared to its actual, known position to determine the horizontal positional error on each day of the study. Daily boxes show median horizontal positional error rates by the thick horizontal black line, bottom and top of boxes provide 25th and 75th percentiles, respectively, and whiskers are 1.5 times the interquartile range.

Table 2

Model selection of 2-state and 3-state hidden Markov models fit to gray triggerfish (*Balistes capricus*) telemetry data from North Carolina, USA, in 2017. Models are defined in the *Methods* section, K is the number of parameters in the model, and ΔAIC is the Akaike information criterion of that model relative to the best model in the set. The full models included tod, length, and their interaction, while base models did not include any predictor variables.

Model	K	ΔAIC
2-state model		
full	21	0
tod + length	17	49
tod	15	110
length	13	1549
base	11	1579
3-state model		
full	50	0
tod	32	301
tod + length	38	470
length	26	1988
base	20	2110

triggerfish during the 43-d study (mean = 3,472 detections per fish; range = 63 – 11,789; Table 1).

Using the reference transmitter, we estimated median daily horizontal positional error at approximately 1–3 m (Fig. 2). Median horizontal positional error of the reference transmitter appeared to increase slightly throughout the study, from around 1 m early in the study to 2–3 m near the end of the study (Fig. 2). Rarely, some individual horizontal positional error estimates were as high as 10 m. In general, these results suggest that spatial precision of telemetered gray triggerfish in the study area was quite high over the same time frame.

Seven telemetered gray triggerfish did not meet minimum sample size requirements of the HMMs (i.e., at least 100 spatial positions with no more than a 20-min temporal interruption; Table 1). These seven fish were excluded from all HMM analyses, leaving 23 fish that were included in HMMs.

Model selection for the 2- and 3-state HMMs indicated that full models including fish size, time of day, and their interaction were preferred over various reduced models (Table 2). The 2-state full model that included tod and length effects, as well as their interaction, was 49 AIC points lower than the second-best model that excluded the tod \times length interaction. Similarly, the 3-state full model was 301 AIC points lower than the next best model that only included tod (Table 2). Thus, it appears that, regardless of the number of assumed behavioral states, gray triggerfish movement behavior varied by time of day, fish length, and their interaction. All subsequent results focus on 2- and 3-state full models that were preferred based on AIC.

The 2- and 3-state gray triggerfish HMMs identified behavioral states that differed in their step lengths and turning angles (Fig. 3, Table 3). In the 2-state model, state 1 was characterized by a short step length, with fish only moving a mean of 2.7 m every min, and a lack of concentrated turning angles (angle concentration = 0.18), suggesting frequent change of direction (Table 3). In contrast, state 2 was characterized by a much longer step length (mean = 21.7 m) and turning angles concentrated around 0° (angle concentration = 0.78), suggesting movement direction was often similar (correlated) among successive positions (Table 3). In the 3-state HMM, state 1 was similar to the 2-state model in that step length was short (mean = 1.6 m) and turning angles were diffuse (angle concentration = 0.33). State 3 in the 3-state model was similar to state 2 in the 2-state model, typified by a longer step length (mean = 27.5 m) and a high turning angle concentration (1.08) around 0° (Fig. 3, Table 3). State 2 in the 3-state model had a moderate step length (mean = 6.4 m), but the least concentrated turning angle of all behavioral states (angle concentration = 0.02), suggesting frequent turning.

There were significant individual differences in movement rates and

state behaviors among gray triggerfish in our study. Mean movement rates varied among individuals, ranging from a minimum of 0.028 m/s for fish #45 to 0.127 m/s for fish #55, with an overall mean of 0.061 m/s (Fig. 4A). In the 2-state HMM, individual fish spent 24 to 97% of their total time in state 1 (low movement state) and their remaining time (3–76%) in state 2 (Fig. 4B). Results for the 3-state model were similarly variable among individuals. Time spent by individual fish in state 1 was the most variable, ranging from 10 to 86% among individuals (Fig. 4C), but the time spent by gray triggerfish in state 2 (12–62%) and state 3 (2–59%) was also quite variable (Fig. 4C).

Exploratory data analyses and HMMs indicated that some of the variability in gray triggerfish movement could be explained by fish size. Exploratory data analyses indicated that movement rates for larger fish were about twice as high than for smaller fish ($P < 0.0001$), increasing from a mean of approximately 0.04 m/s at 250 mm fork length to 0.08 m/s at 335 mm (Fig. 5A). The 2-state HMM showed that larger gray triggerfish tended to spend more time in State 2, which was typified by higher movement rates, compared to smaller gray triggerfish that spent more time in state 1 (Fig. 5C). Similarly, in the 3-state model, larger gray triggerfish spent about twice as much time in state 3 and less time in state 2 compared to smaller gray triggerfish (Fig. 5E). However, there did not appear to be a size effect on the time spent in state 1 for the 3-state HMM (Fig. 5E).

Strongly diel movement rates and state probabilities for gray triggerfish were also observed using exploratory data analyses and HMMs. Mean movement rates of gray triggerfish were significantly lower (0.03 m/s) at night and higher (0.07–0.10 m/s) during the day ($F = 1122$, $P < 0.0001$; Fig. 5B, Appendix B1, B2), and median movement rates followed the same general pattern. These results were obvious from the both 2- and 3-state HMMs. At night, the 2-state HMM suggested gray triggerfish spent most (> 90%) of their time in state 1 (low movement state), while most of their time during the day (~ 70%) was spent in state 2, the high movement state (Fig. 5D). The 3-state HMM results were very similar to the 2-state model, indicating gray triggerfish spent most of their time in state 1 at night (~ 60%) and state 3 during the day (~ 50%; Fig. 5F). State 2 was exhibited by gray triggerfish similarly (~ 30%) both day and night (Fig. 5F).

The spatial distribution of locations where gray triggerfish exhibited various behavioral states in the HMMs were nonrandom and spatially distinct. Gray triggerfish exhibited state 1 behaviors in 15 or 20 small (< 100 m diameter) patches that were associated with low-relief hardbottom throughout the study area (Fig. 6). In contrast, state 2 (in the 2-state model) and state 3 (in the 3-state model) behaviors occurred more broadly across the study region. State 2 in the 3-state model occurred in distinct patches, but these patches tended to be much larger (up to 200 m in diameter) than locations where state 1 behaviors were exhibited by gray triggerfish (Fig. 6B).

Gray triggerfish displayed highly correlated state behaviors. Gray triggerfish remained in their current behavioral state with a probability greater than 0.80 across all states and models, and in the 2-state model, the probability of state persistence was at least 0.96 for both states (Table 4). The lowest probability of staying in the current state was observed for state 2 of the 3-state model (0.83). The probability of switching to a different state was always less than 0.10 across all models and states (Table 4).

4. Discussion

Gray triggerfish inhabit demersal seafloor habitats where they are rarely observed directly, yet understanding their movement behavior is important for their sustainable management and conservation. During summer and fall months, we found that gray triggerfish movements and behavioral states varied greatly across the diel period (higher during the day than at night) and among individuals, the latter of which could partially be explained by fish size. Gray triggerfish also exhibited strong persistence in each behavioral state identified by the HMMs, suggesting

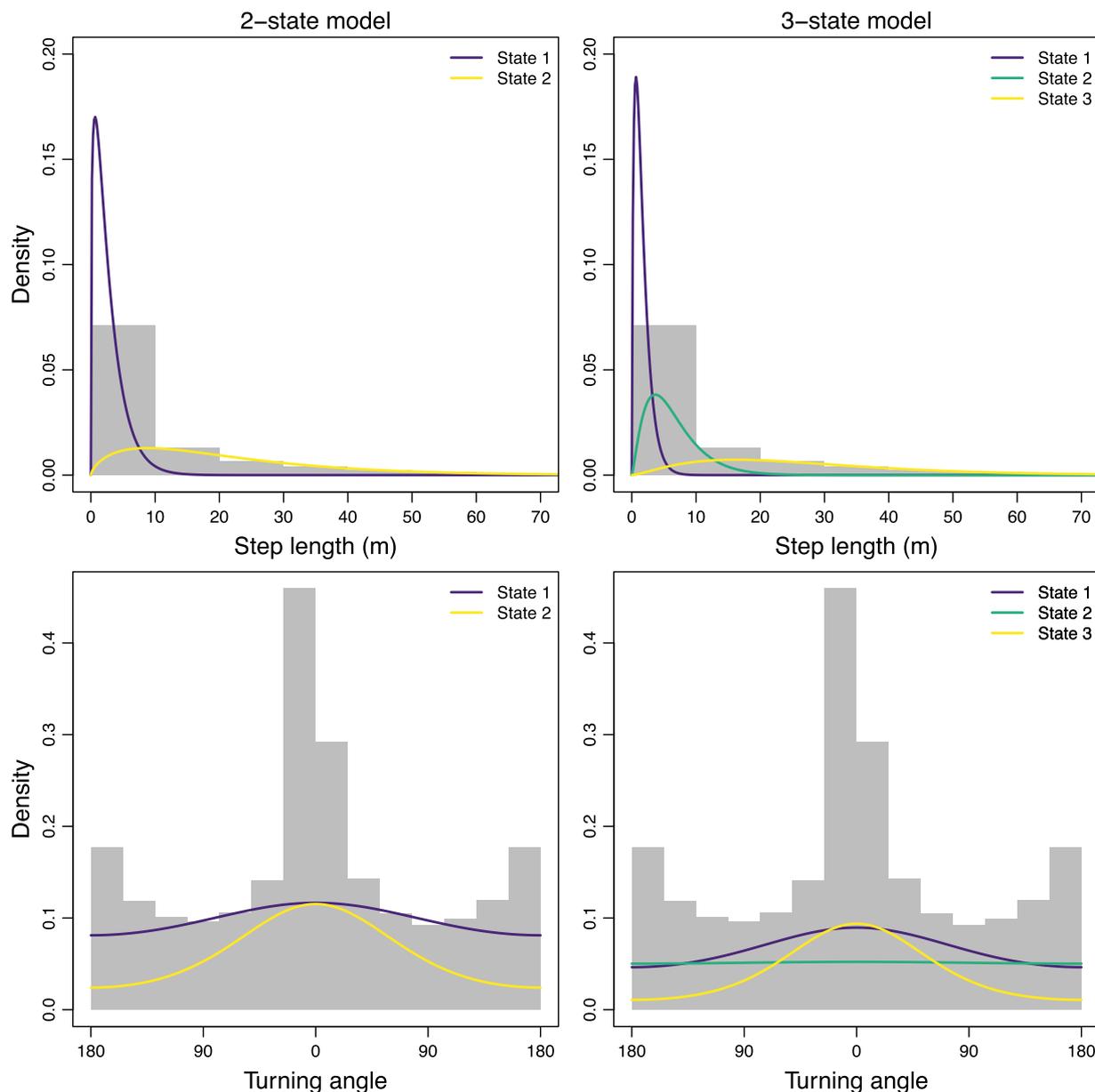


Fig. 3. Distributions (lines) and histograms (gray bars) of step lengths (m) and turning angles for 2-state (left column) and 3-state (right column) hidden Markov models developed for telemetered gray triggerfish (*Balistes caprisicus*) in North Carolina, USA, in 2017. A fish continuing in exactly the same direction across two time intervals would have a turning angle of 0°, whereas a fish turning in the opposite direction would have a turning angle of 180°.

Table 3

Estimates of telemetered gray triggerfish (*Balistes caprisicus*) step length (m) and turning angle distributions in the 2-state and 3-state hidden Markov models at 4-min intervals in North Carolina, USA, in 2017. Step length is the mean distance moved in each state during each time interval, and “Step SD” is the standard deviation of step length. The angle concentration is a measure of how concentrated the distribution is around its mean.

	State 1	State 2	State 3
2-state model			
Step mean (m)	2.7	21.7	–
Step SD	2.4	16.7	–
Angle concentration	0.18	0.78	–
3-state model			
Step mean (m)	1.6	6.4	27.5
Step SD	1.2	4.2	17.7
Angle concentration	0.33	0.02	1.08

serially correlated behaviors. Strong agreement between our exploratory data analyses and HMMs indicated that our results are robust.

The main benefit of HMMs is the ability to identify behavioral states of animals that are not easily observed. However, it can be challenging to interpret each behavioral state from the HMMs for a species such as gray triggerfish with little supporting biological information. It is likely that state 1 of both the 2- and 3-state models is resting behavior; fish moved very little and was similar in magnitude to our estimated median horizontal position error, had a low turning angle concentration, and mostly exhibited this behavioral state at night when gray triggerfish are thought to rest on the bottom (Herbig and Szedlmayer, 2016). State 2 of the 2-state model and state 3 of the 3-state model were characterized by faster movement mostly in a correlated direction, so those states are likely transit or foraging. State 2 of the 3-state model is more difficult to interpret because it was characterized by moderate movement rates, frequent turning, and occurred both day (when they are active) and night (when they typically rest). More research is needed to determine

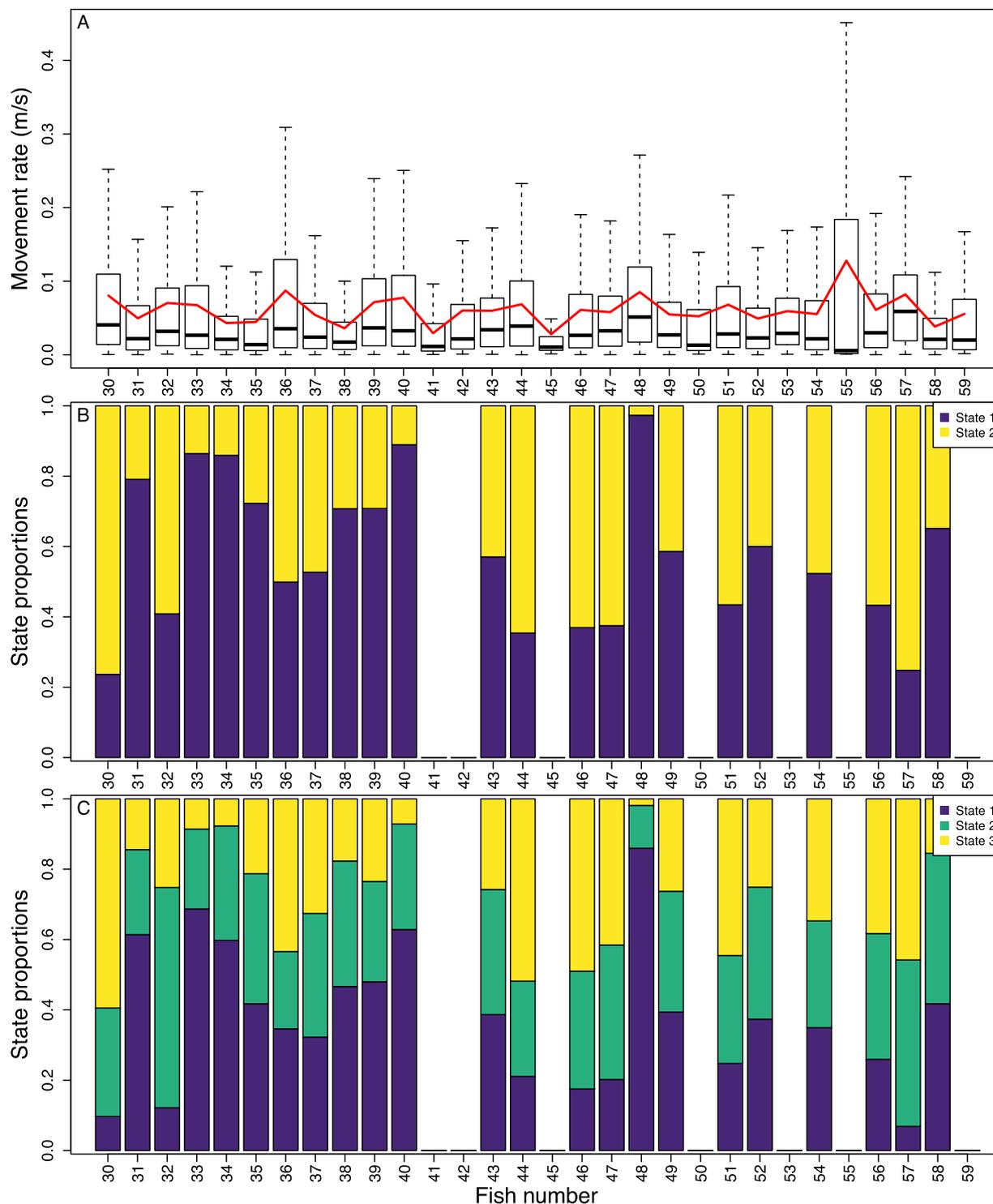


Fig. 4. Individual-level variability in movement rates and state probabilities among telemetered gray triggerfish (*Balistes capricus*) in North Carolina, USA, in 2017. (A) Boxplot of observed movement rates of telemetered gray triggerfish, also showing mean movement rates (red line). (B) The amount of time each individual telemetered gray triggerfish spent in each of the two states of the 2-state hidden Markov model. (C) The amount of time each individual telemetered gray triggerfish spent in each of the three states of the 3-state hidden Markov model. Empty columns of B and C indicate fish that were excluded from hidden Markov models due to limited sample sizes. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

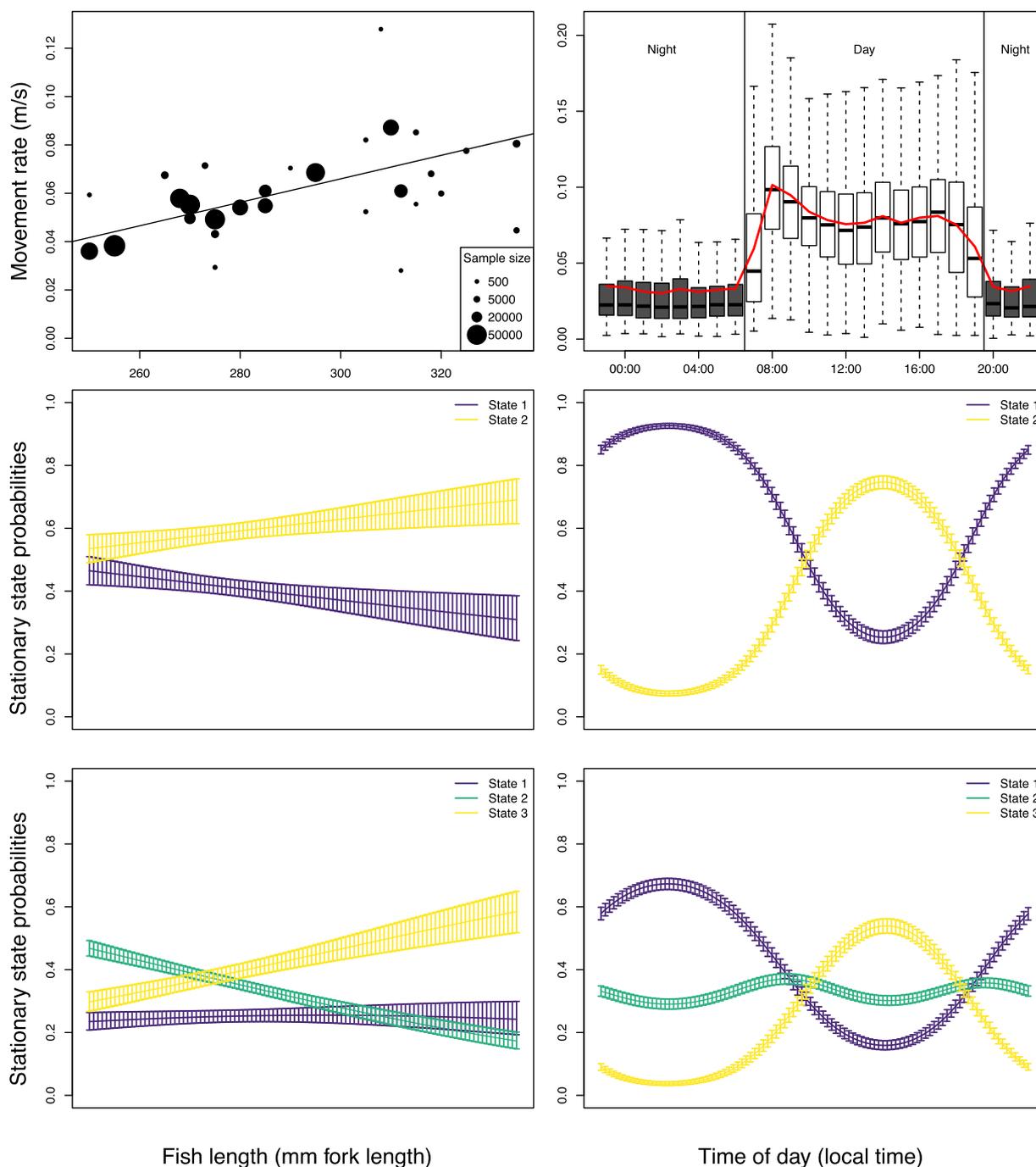


Fig. 5. (A) Relationship between movement rate and length of telemetered gray triggerfish (*Balistes capriscus*), weighted by the total number of positions available for each fish in North Carolina, USA, in 2017. (B) Diel movement rates of telemetered gray triggerfish in our study; boxes show median (thick horizontal black line), 25th, and 75th percentiles of movement rate; whiskers are 1.5 times the interquartile range; and red line is mean movement rate by hour of the day. (C) Size-dependent and (D) time-of-day-dependent stationary state probabilities for two behavioral states of gray triggerfish using hidden Markov models. (E) Size-dependent and (F) time-of-day-dependent stationary state probabilities for three behavioral states of gray triggerfish using hidden Markov models. Solid lines show mean stationary state probabilities, and error bars indicate 95% confidence intervals. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

if this was a true behavioral state (and not just a blending of other behavioral states), and if so, what behaviors gray triggerfish are exhibiting while in this state.

Gray triggerfish exhibited highly variable movement behaviors

across individuals. For instance, there was a ~350% difference in movement rates between individuals moving the least and most in our study, which was similar to the substantial differences among individuals in the time they spent in resting and transit behavioral states

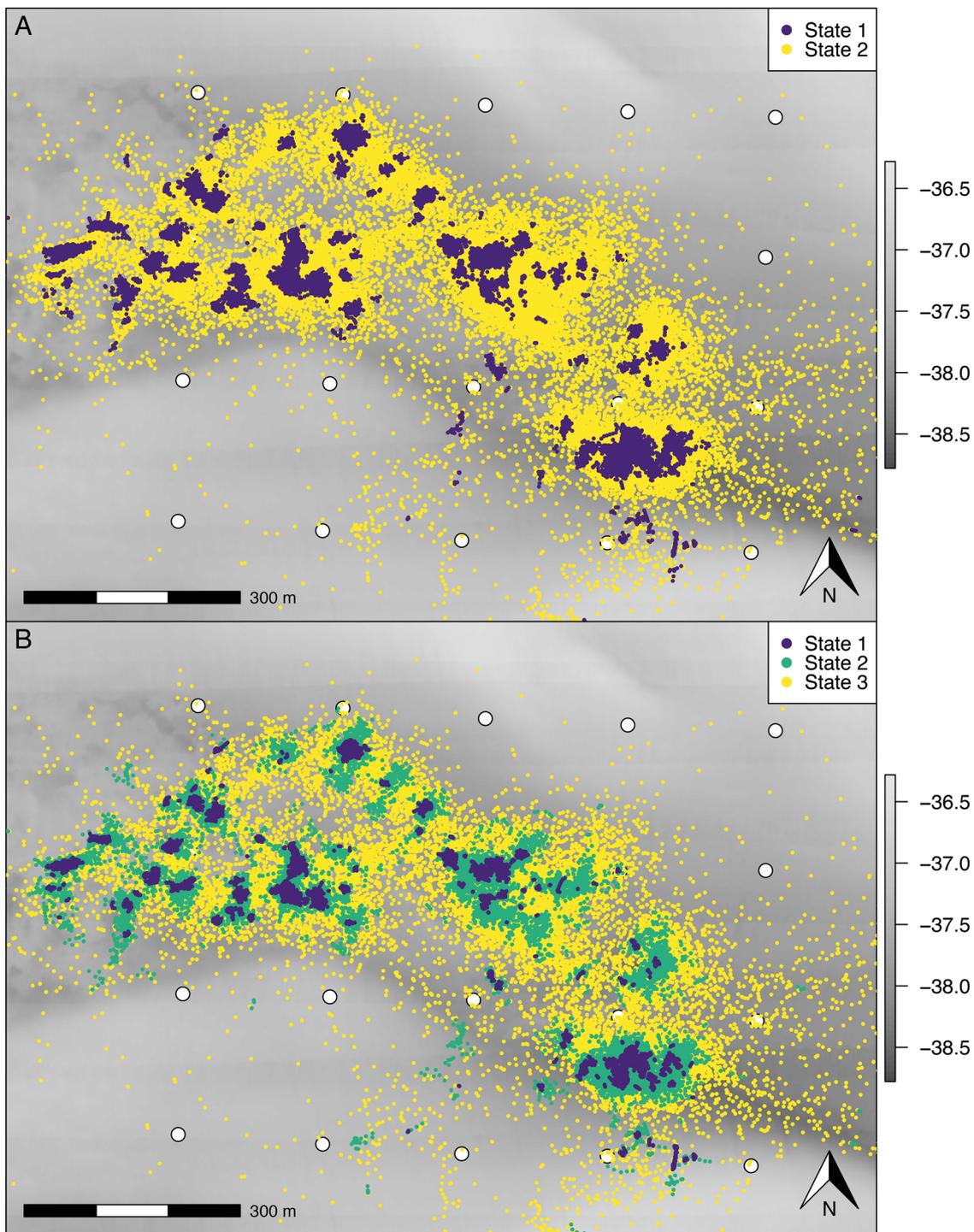


Fig. 6. Locations where telemetered gray triggerfish (*Balistes capriscus*) exhibited various behavioral states in the 2-state (A) or 3-state (B) hidden Markov models in North Carolina, USA, in 2017. Note that points overlap, and state 1 is plotted on top of states 2 or 3. Receiver locations are noted by the filled white circles.

in our HMMs. A portion of the variation in gray triggerfish movement rates was explained by fish size, which is consistent with most studies finding a positive relationship between movement rates and animal size (Ware, 1978; Swihart et al., 1988). However, the size range of fish

examined in our study (250–335 mm fork length) was fairly narrow, so our analyses may not represent gray triggerfish of a broader size range. For instance, larval and juvenile gray triggerfish are pelagic and associate with floating debris while likely circling the Atlantic Ocean

Table 4

State transition probabilities of telemetered gray triggerfish (*Balistes capricus*) among behavioral states estimated by the 2-state and 3-state hidden Markov models in North Carolina, USA, in 2017. Since transition probabilities depended somewhat on time of day, they are provided here for 12:00 local time, and all transition probabilities were obtained by fixing each covariate to its mean value.

Current state	Next state		
	State 1	State 2	State 3
2-state model			
State 1	0.96	0.04	–
State 2	0.03	0.97	–
3-state model			
State 1	0.91	0.08	0.01
State 2	0.08	0.83	0.09
State 3	0.00	0.06	0.94

(Harper and McClellan, 1997), suggesting fish of that smaller size move or drift much more than the larger sizes examined in our study. Movement rates of gray triggerfish larger than the sizes examined in our study (i.e., > 335 mm fork length) are also unknown.

While size explained some of the observed behavioral differences among gray triggerfish in our study, other factors such as sex or personality may have contributed to the substantial differences in movements among individuals. Externally determining sex is not possible for gray triggerfish, so we were unable to examine potential differences in movement rates between males and females. Recent research suggests variability in animal personalities like boldness or shyness can explain individual differences in movement behaviors (Villegas-Ríos et al., 2018). Heterogeneity in movement rates can also produce leptokurtic distributions, where most individuals move small distances (“stayers”) and some move very large distances (“movers”; Gilliam and Fraser, 2001). Gray triggerfish superficially appeared to display leptokurtic movements in our study, but it is unclear if this is due to differences among the sexes (i.e., one sex moving much more than the other), personality, or some other trait. Whether movement distributions are leptokurtic or not has important implications for marine protected area design, predator-prey interactions, and the genetic consequences of fishery harvests (Fraser et al., 2001; Grüss et al., 2011).

In addition to identifying distinct behavioral states, our analyses also characterized locations where gray triggerfish displayed each of the states. Resting behavior only occurred in small areas around low-relief hardbottom (i.e., ledges), whereas foraging or transit behaviors occurred broadly throughout the study area over a variety of sand and hardbottom areas. In a similar study, blacktip reef sharks (*Carcharhinus melanopterus*) and grey reef sharks (*Carcharhinus amblyrhynchos*) used relatively small deep areas when they were less active and broad, shallow areas for feeding (Papastamatiou et al., 2018); the main difference was that sharks were much more active during the night than at day, the opposite of gray triggerfish. Being able to determine specific locations where gray triggerfish or other species display behaviors can be used to identify habitats that require protection and optimally design marine protected areas for specific behavioral states.

Gray triggerfish movements and behavioral states were highly variable across the diel period. Movement rates were over 200% higher during daylight hours than at night, and fish spent much more time in a resting state at night than during the day. Similarly, Herbig and Szedlmayer (2016) showed that, on average, gray triggerfish ranged

over a much larger area during the day (~ 2000 m²) than at night (~ 200 m²) around artificial reefs in the Gulf of Mexico. Other closely related species such as fine-scale triggerfish (*Balistes polylepis*), orangeside triggerfish (*Sufflamen verres*), and black triggerfish (*Melichthys niger*) show similar diel patterns of resting at night and being active during the day (Hobson, 1965; Kavanagh and Olney, 2006). Herbig and Szedlmayer (2016) posit that inactivity of gray triggerfish at night may be a strategy to reduce predation from nocturnal predators like sharks, or perhaps their prey are not active at night.

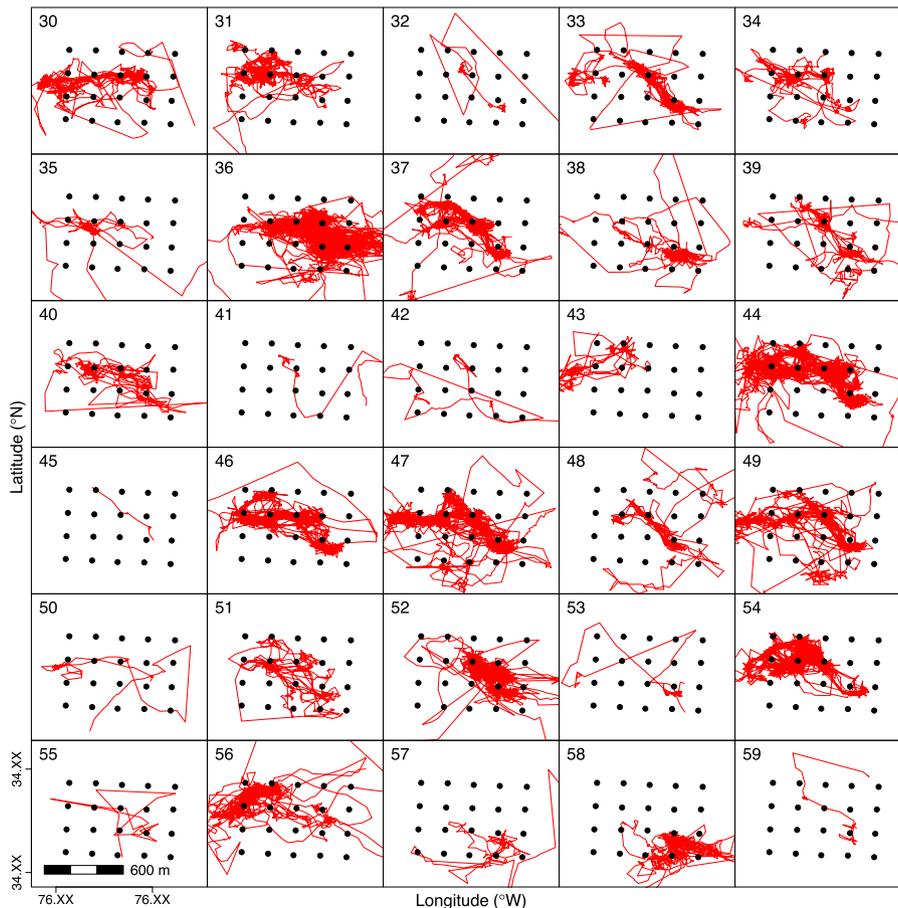
There were some shortcomings of our study. First, since we focused on a demersal marine species, we mostly lacked biological information that could be used to help develop our HMMs (i.e., choosing the number of HMM states, verification that each HMM state is an actual behavioral state), as recommended by Pohle et al. (2017). Anecdotal information from fishers and SCUBA divers suggests gray triggerfish rest on the bottom at night without foraging, consistent with the resting behavioral state we identified that mostly occurred at night. However, similar biological information does not exist for other behavioral states of gray triggerfish. Second, we used two characteristics of gray triggerfish movement behavior – step length and turning angles – to parameterize our HMMs, but additional concurrent information on such factors as depth or acceleration would have helped to refine and classify behavioral states of gray triggerfish and should be used in future studies where possible (Leos-Barajas et al., 2017). Last, gray triggerfish have been shown to display highly seasonal movements (Herbig and Szedlmayer, 2016), yet our study occurred over a relatively short (43-d) period in September–October 2017. Thus, it would be imprudent to assume that the gray triggerfish movement behaviors quantified in our study would be static year-round.

With recent advances in tracking technologies and new analytical approaches such as HMMs, some believe we have entered a golden age of animal tracking science (Kays et al., 2015). Tags are becoming more reliable, smaller, and less invasive, allowing for the tracking of more animal species than ever before, including relatively small marine fish like gray triggerfish that display relatively high site fidelity in the open ocean. Data from fish tracking studies are being used by scientists and managers to determine optimal marine protected area design (Meyer et al., 2007), identify essential fish habitats (Simpfendorfer et al., 2010), and quantify fish mortality rates (Bacheler et al., 2009). Thus, we encourage a wider use of VPS systems combined with HMMs to shed light on the normally hidden behaviors of demersal marine fishes.

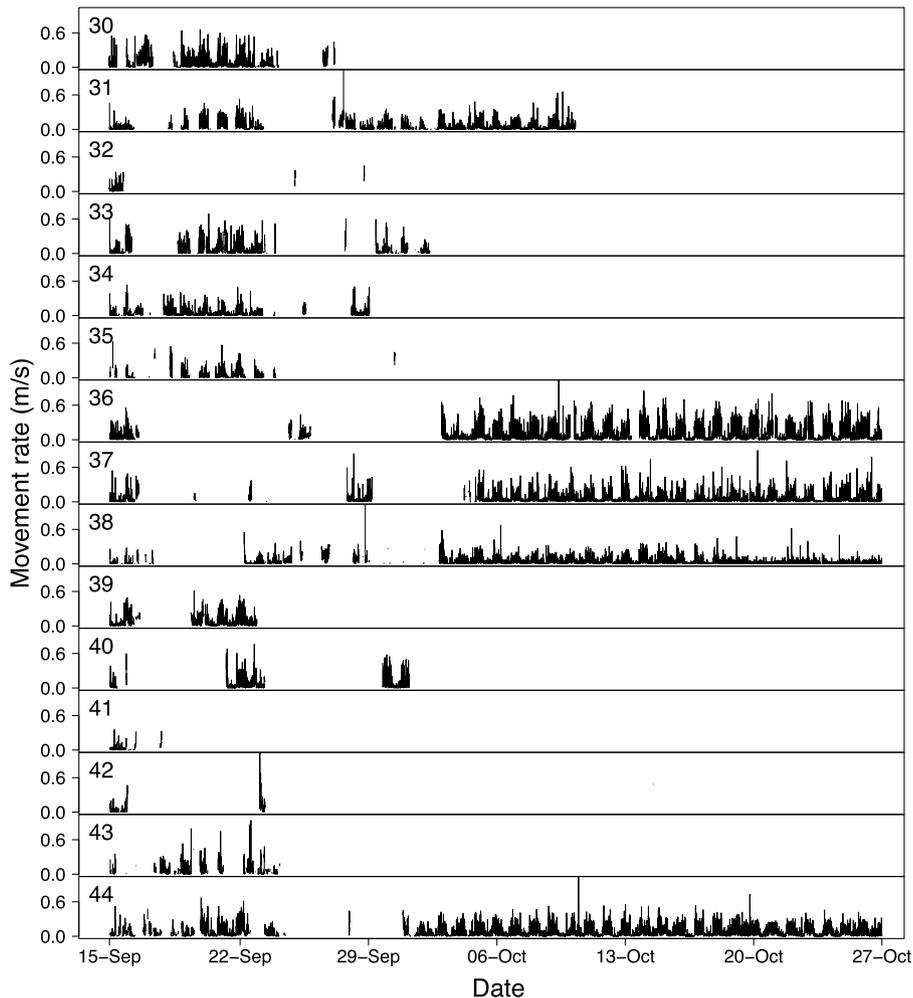
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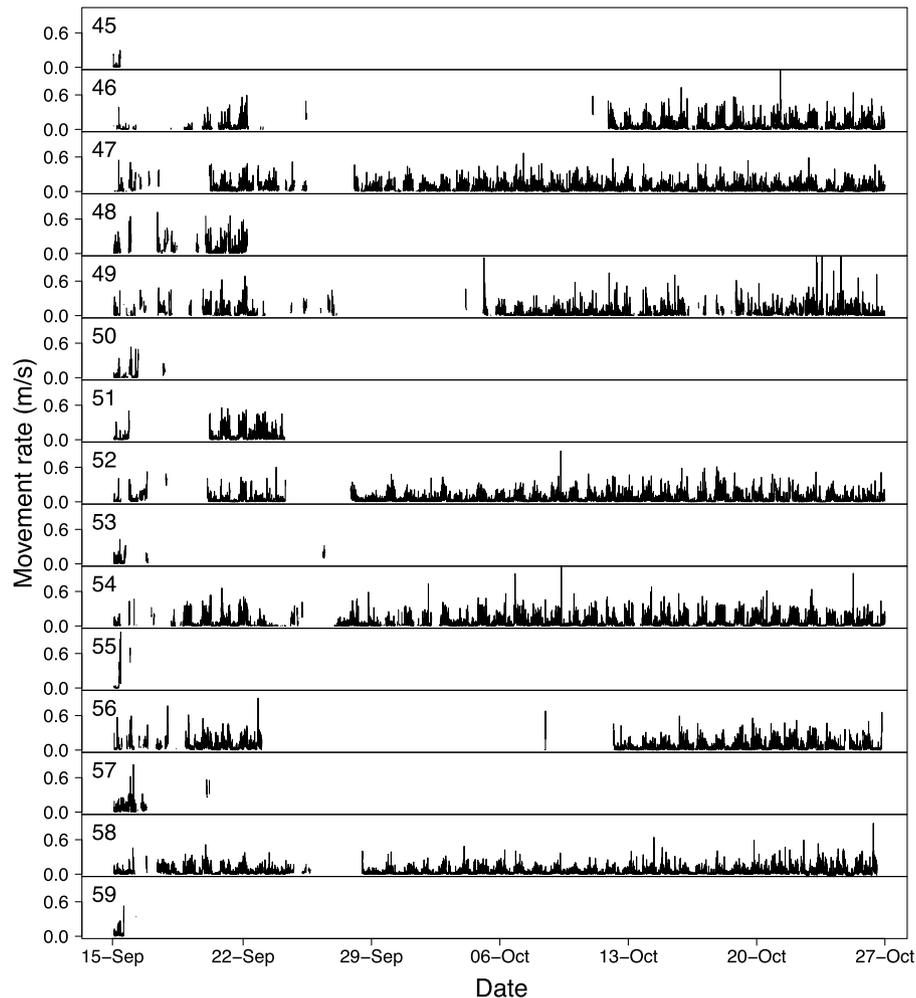
Appendix A. Movement paths of each telemetered gray triggerfish (*Balistes capriscus*) in this study, 15 September – 27 October 2017, in North Carolina, USA. The grid of submersible receivers used to estimate gray triggerfish positions are shown by black dots. Note that lines representing gray triggerfish movement paths overlap often



Appendix B1 Time series of movement rates estimated for telemetered gray triggerfish (*Balistes capricus*) over the course of the study, 15 September – 27 October 2017, in North Carolina, USA. Missing data for fish in certain time periods was due to those fish being absent from the study area. Only fish 30 through 44 are shown in this plot



Appendix B2 Time series of movement rates estimated for telemetered gray triggerfish (*Balistes capriscus*) over the course of the study, 15 September–27 October 2017, in North Carolina, USA. Missing data for fish in certain time periods was due to those fish being absent from the study area. Only fish 45 through 59 are shown in this plot



References

- Alós, J., Palmer, M., Balle, S., Arlinghaus, R., 2016. Bayesian state-space modelling of conventional acoustic tracking provides accurate descriptors of home range behavior in a small-bodied coastal fish species. *PLoS One* 11, e0154089. <https://doi.org/10.1371/journal.pone.0154089>.
- Bacheler, N.M., Buckel, J.A., Hightower, J.E., Paramore, L.M., Pollock, K.H., 2009. A combined telemetry-tag return approach to estimate fishing and natural mortality rates of an estuarine fish. *Can. J. Fish. Aquat. Sci.* 66, 1230–1244. <https://doi.org/10.1139/F09-076>.
- Bacheler, N.M., Whitfield, P.E., Muñoz, R.C., Harrison, B.B., Harms, C.A., Buckel, C.A., 2015. Movement of invasive adult lionfish *Pterois volitans* using telemetry: importance of controls to estimate and explain variable detection probabilities. *Mar. Ecol. Prog. Ser.* 527, 205–220. <https://doi.org/10.3354/meps11241>.
- Bacheler, N.M., Schobernd, Z.H., Berrane, D.J., Schobernd, C.M., Mitchell, W.A., Teer, B.Z., Gregalis, K.C., Glasgow, D.M., 2016a. Spatial distribution of reef fish species along the southeast US Atlantic coast inferred from underwater video survey data. *PLoS One* 11, e0162653. <https://doi.org/10.1371/journal.pone.0162653>.
- Bacheler, N.M., Schobernd, C.M., Harter, S.L., David, A.W., Sedberry, G.R., Kellison, G.T., 2016b. No evidence of increased demersal fish abundance six years after creation of marine protected areas along the southeast United States Atlantic coast. *Bull. Mar. Sci.* 92, 447–471. <https://doi.org/10.5343/bms.2016.1053>.
- Bacheler, N.M., Shertzer, K.W., Buckel, J.A., Rudershausen, P.J., Runde, B.J., 2018. Behavior of gray triggerfish *Balistes capriscus* around baited fish traps determined from fine-scale acoustic tracking. *Mar. Ecol. Prog. Ser.* 606, 133–150. <https://doi.org/10.3354/meps12780>.
- Bacheler, N.M., Shertzer, K.W., Cheshire, R.T., MacMahan, J.H., 2019. Tropical storms influence the movement behavior of a demersal oceanic fish species. *Sci. Rep.* 9, 1481. <https://doi.org/10.1038/s41598-018-37527-1>.
- Block, B.A., Teo, S.L.H., Walli, A., Boustany, A., Stokesbury, M.J.W., Farwell, C.J., Weng, K.C., Dewar, H., Williams, T.D., 2005. Electronic tagging and population structure of Atlantic bluefin tuna. *Nature* 434, 1121–1127. <https://doi.org/10.1038/nature03463>.
- Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Multimodel Inference: a Practical Information-Theoretic Approach*, 2nd ed. Springer, New York.
- Burns, K.M., Koenig, C.C., Coleman, F.C., 2002. Evaluation of Multiple Factors Involved in Release Mortality of Undersized Red Grouper, Gag, Red Snapper and Vermilion Snapper. Mote Marine Laboratory Technical Report No. 790. Accessed on 18 May 2018 at: <https://dspace.mote.org:8443/bitstream/2075/294/3/MTR%20790.pdf>.
- Calabrese, J.M., Fleming, C.H., Gurarie, E., 2016. ctmm: an R package for analyzing animal relocation data as a continuous-time stochastic process. *Meth. Ecol. Evol.* 7, 1124–1132. <https://doi.org/10.1111/2041-210X.12559>.
- Dance, M.A., Moulton, D.L., Furey, N.B., Rooker, J.R., 2016. Does transmitter placement or species affect detection efficiency of tagged animals in biotelemetry research? *Fish. Res.* 183, 80–85. <https://doi.org/10.1016/j.fishres.2016.05.009>.
- DeRuiter, S.L., Langrock, R., Skirbutas, T., Goldbogen, T.A., Calambokidis, J., Friedlaender, A.S., Southall, B.L., 2017. A multivariate mixed hidden Markov model for blue whale behaviour and responses to sound exposure. *Ann. Appl. Stat.* 11, 362–392. <https://doi.org/10.1214/16-aos1008>.
- Espinoza, M., Farrugia, T.J., Webber, D.M., Smith, F., Lowe, C.G., 2011. Testing a new aquatic telemetry technique to quantify long-term, fine-scale movements of aquatic animals. *Fish. Res.* 108, 364–371. <https://doi.org/10.1016/j.fishres.2011.01.011>.
- Franke, A., Caelli, T., Kuzyk, G., Hudson, R.J., 2006. Prediction of wolf (*Canis lupus*) kill-sites using hidden Markov models. *Ecol. Mod.* 197, 237–246. <https://doi.org/10.1016/j.ecolmodel.2006.02.043>.
- Fraser, D.F., Gilliam, J.F., Daley, M.J., Le, A.N., Skalski, G.T., 2001. Explaining leptokurtic movement distributions: intrapopulation variation in boldness and

- exploration. *Am. Nat.* 158, 124–135. <https://doi.org/10.1086/321307>.
- Furey, N.M., Dance, M.A., Rooker, J.R., 2013. Fine-scale movements and habitat use of juvenile southern flounder *Paralichthys lethostigma* in an estuarine seascape. *J. Fish. Biol.* 82, 1469–1483. <https://doi.org/10.1111/jfb.12074>.
- Gilliam, F.J., Fraser, D.F., 2001. Corridor movement: enhancement by predation threat, habitat structure and disturbance. *Ecol.* 82, 258–273. [https://doi.org/10.1890/0012-9658\(2001\)082\[0258:MICEBP\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082[0258:MICEBP]2.0.CO;2).
- Grüss, A., Kaplan, D.M., Guenette, S., Roberts, C.M., Botsford, L.W., 2011. Consequences of adult and juvenile movement for marine protected areas. *Biol. Conserv.* 144, 692–702. <https://doi.org/10.1016/j.biocon.2010.12.015>.
- Gurarie, E., Andrews, R.D., Laidre, K.L., 2009. A novel method for identifying behavioural changes in animal movement data. *Ecol. Lett.* 12, 395–408. <https://doi.org/10.1111/j.1461-0248.2009.01293.x>.
- Harper, D.E., McClellan, D.B., 1997. A Review of the Biology and Fishery for Gray Triggerfish, *Balistes capricus*, in the Gulf of Mexico. MIA-96/97-52. National Marine Fisheries Service, Miami. http://aquaticcommons.org/13452/1/gcfi_52-58.pdf.
- Heerah, K., Woillez, M., Fablet, R., Garren, F., Martin, S., De Pontual, H., 2017. Coupling spectral analysis and hidden Markov models for the segmentation of behavioural patterns. *Mov. Ecol.* 5, 20. <https://doi.org/10.1186/s40462-017-0111-3>.
- Herbig, J.L., Szedlmayer, S.T., 2016. Movement patterns of gray triggerfish, *Balistes capricus*, around artificial reefs in the northern Gulf of Mexico. *Fish. Manag. Ecol.* 23, 418–427. <https://doi.org/10.1111/fme.12190>.
- Hobson, E.S., 1965. Diurnal-nocturnal activity of some inshore fishes in the Gulf of California. *Copeia* 1965, 291–302. <https://doi.org/10.2307/1440790>.
- Jepsen, N., Thorstad, E.B., Havn, T., Lucas, M.C., 2015. The use of external electronic tags on fish: an evaluation of tag retention and tagging effects. *Anim. Biotelem.* 3, 49. <https://doi.org/10.1186/s40317-015-0086-z>.
- Johnson, D., London, J., Lea, M.A., Durban, J., 2008. Continuous-time correlated random walk model for animal telemetry data. *Ecology* 89, 1208–1215. <https://doi.org/10.1890/07-1032.1>.
- Kavanagh, K.D., Olney, J.E., 2006. Ecological correlates of population density and behavior in the circumtropical black triggerfish *Melichthys niger* (Balistidae). *Environ. Biol. Fish.* 76, 387–398. <https://doi.org/10.1007/s10641-006-9044-1>.
- Kays, R., Crofoot, M.C., Jetz, W., Wikelski, M., 2015. Terrestrial animal tracking as an eye on life and planet. *Science* 348. <https://doi.org/10.1126/science.aaa2478>. aaa2478.
- Langrock, R., King, R., Matthiopoulos, J., Thomas, L., Fortin, D., Morales, J.M., 2012. Flexible and practical modeling of animal telemetry data: hidden Markov models and extensions. *Ecology* 93, 2336–2342. <https://doi.org/10.1890/11-2241.1>.
- Langrock, R., Hopcraft, J.G.C., Blackwell, P.G., Goodall, V., King, R., Niu, M., Patterson, T.A., Pedersen, M.W., Skarin, A., Schick, R.S., 2014. Modeling group dynamic animal movements. *Meth. Ecol. Evol.* 5, 190–199. <https://doi.org/10.1111/2041-210X.12155>.
- Leos-Barajas, V., Photopoulou, T., Langrock, R., Patterson, T.A., Watanabe, Y.Y., Murgatroyd, M., Papastamatiou, Y.P., 2017. Analysis of animal accelerometer data using hidden Markov models. *Meth. Ecol. Evol.* 8, 161–173. <https://doi.org/10.1111/2041-210X.12657>.
- Li, M., Bolker, B.M., 2017. Incorporating periodic variability in hidden Markov models for animal movement. *Mov. Ecol.* 5, 1. <https://doi.org/10.1186/s40462-016-0093-6>.
- McClintock, B.T., Michelot, T., 2018. momentuHMM: R package for generalized hidden Markov models of animal movement. *Meth. Ecol. Evol.* 9, 1518–1530. <https://doi.org/10.1111/2041-210X.12995>.
- Meyer, C.G., Holland, K.N., Papastamatiou, Y.P., 2007. Seasonal and diel movements of giant trevally *Caranx ignobilis* at remote Hawaiian atolls: implications for the design of marine protected areas. *Mar. Ecol. Prog. Ser.* 333, 13–25. <https://doi.org/10.3354/meps333013>.
- Michelot, T., Langrock, R., Patterson, T.A., 2016. moveHMM: an R package for the statistical modelling of animal movement data using hidden Markov models. *Meth. Ecol. Evol.* 7, 1308–1315. <https://doi.org/10.1111/2041-210X.12578>.
- Michelot, T., Langrock, R., Bestley, S., Jonsen, I.D., Photopoulou, T., Patterson, T.A., 2017. Estimation and simulation of foraging trips in land-based marine predators. *Ecology* 98, 1932–1944. <https://doi.org/10.1002/ecy.1880>.
- Nathan, R., Getz, W.M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., Smouse, P.E., 2008. A movement ecology paradigm for unifying organismal movement research. *Proc. Nat. Acad. Sci. U. S. A.* 105, 19052–19059. <https://doi.org/10.1073/pnas.0800375105>.
- Papastamatiou, Y.P., Watanabe, Y.Y., Demšar, U., Leos-Barajas, V., Bradley, D., Langrock, R., Weng, K., Lowe, C.G., Friedlander, A.M., Caselle, J.E., 2018. Activity seascapes highlight central place foraging strategies in marine predators that never stop swimming. *Mov. Ecol.* 6, 9. <https://doi.org/10.1186/s40462-018-0127-3>.
- Patterson, T.A., Basson, M., Bravington, M.V., Gunn, J.S., 2009. Classifying movement behaviour in relation to environmental conditions using hidden Markov models. *J. Anim. Ecol.* 78, 1113–1123. <https://doi.org/10.1111/j.1365-2656.2009.01583.x>.
- Phillips, J.S., Patterson, T.A., Leroy, B., Pilling, G.M., Nicol, S.J., 2015. Objective classification of latent behavioral states in bio-logging data using multivariate-normal hidden Markov models. *Ecol. Appl.* 25, 1244–1258. <https://doi.org/10.1890/14-0862.1>.
- Piraino, M.N., Szedlmayer, S.T., 2014. Fine-scale movements and home ranges of red snapper around artificial reefs in the northern Gulf of Mexico. *Trans. Am. Fish. Soc.* 143, 988–998. <https://doi.org/10.1080/00028487.2014.901249>.
- Pohle, J., Langrock, R., van Beest, F.M., Schmidt, N.M., 2017. Selecting the number of states in hidden Markov models: pragmatic solutions illustrated using animal movement. *J. Agric. Biol. Env. Stats.* 22, 270–293. <https://doi.org/10.1007/s13253-017-0283-8>.
- Quick, N.J., Isojunno, S., Sadykova, D., Bowers, M., Nowacek, D.P., Read, A.J., 2017. Hidden Markov models reveal complexity in the diving behaviour of short-finned pilot whales. *Sci. Rep.* 7, 45765. <https://doi.org/10.1038/srep45765>.
- R Core Team, 2017. R: A Language and Environment for Statistical Computing. URL: R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Runde, B.J., 2017. Estimating and Mitigating Discard Mortality of Reef Fishes. Master'S Thesis, Department of Applied Ecology. North Carolina State University. <http://www.lib.ncsu.edu/resolver/1840.20/34369>.
- Simpfendorfer, C.A., Wiley, T.R., Yeiser, B.G., 2010. Improving conservation planning for an endangered sawfish using data from acoustic telemetry. *Biol. Conserv.* 143, 1460–1469. <https://doi.org/10.1016/j.biocon.2010.03.021>.
- Swihart, R.K., Slade, N.A., Bergstrom, B.J., 1988. Relating body size to the rate of home range use in mammals. *Ecology* 69, 393–399. <https://doi.org/10.2307/1940437>.
- Towner, A.V., Leos-Barajas, V., Langrock, R., Schick, R.S., Smale, M.J., Kaschke, T., Jewell, O.J.D., Papastamatiou, Y.P., 2016. Sex-specific and individual preferences for hunting strategies in white sharks. *Funct. Ecol.* 30, 1397–1407. <https://doi.org/10.1111/1365-2435.12613>.
- Turchin, P., 1998. *Quantitative Analysis of Movement: Measuring and Modeling Population Redistribution in Animals and Plants*. Sinauer Associates, Inc, Sunderland, Massachusetts.
- Villegas-Ríos, D., Réale, D., Freitas, C., Moland, E., Olsen, E.M., 2018. Personalities influence spatial responses to environmental fluctuations in wild fish. *J. Anim. Ecol.* 87, 1309–1319. <https://doi.org/10.1111/1365-2656.12872>.
- Ware, D.M., 1978. Bioenergetics of pelagic fish: theoretical change in swimming speed and ration with body size. *J. Fish. Res. Board Can.* 35, 220–228. <https://doi.org/10.1139/f78-036>.
- White, G.C., Garrott, R.A., 1990. *Analysis of Wildlife Radio-Tracking Data*. Academic Press, San Diego.
- Williams-Grove, L.J., Szedlmayer, S.T., 2017. Depth preferences and three-dimensional movements of red snapper, *Lutjanus campechanus*, on an artificial reef in the northern Gulf of Mexico. *Fish. Res.* 190, 61–70. <https://doi.org/10.1016/j.fishres.2017.01.003>.
- Zucchini, W., MacDonald, I.L., Langrock, R., 2016. *Hidden Markov Models for Time Series: an Introduction Using R*, 2nd ed. Chapman and Hall/CRC.