

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

3

4 Nathan M Bachelor<sup>a,\*</sup>, Théo Michelot<sup>b</sup>, Rob Cheshire<sup>a</sup>, Kyle Shertzer<sup>a</sup>

5

6 <sup>a</sup> Southeast Fisheries Science Center, National Marine Fisheries Service, 101 Pivers Island Road,  
7 Beaufort, North Carolina 28516, USA.

8

9 <sup>b</sup> School of Mathematics and Statistics, University of Sheffield, Sheffield S3 7RH, United  
10 Kingdom.

11

12 \* Corresponding author. Email address: [nate.bachelor@noaa.gov](mailto:nate.bachelor@noaa.gov) (N.M. Bachelor)

13

14

15

16

17

18

19

20

## 21 ABSTRACT

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

38

39 Keywords: Movement rate, Behavior, Marine, Tracking, VPS

## 40 **1. Introduction**

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

49 Quantifying the movements of marine organisms has tended to lag behind those in  
50 terrestrial environments due to various logistical and technical challenges imposed by the open  
51 ocean. It is difficult to find and tag marine organisms that spend most of their time underwater,  
52 far offshore, or in deep seafloor habitats. Moreover, animals in terrestrial environments are most  
53 commonly tracked using devices based on the global positioning system (Kays et al. 2015), but  
54 these tags cannot be spatially located while underwater, so they are only useful for tracking  
55 marine organisms that regularly come to the surface (e.g., Michelot et al., 2017; Quick et al.,  
56 2017). Most fish species do not break the water's surface, so traditional tracking methods cannot  
57 be used for this diverse group of marine organisms. Some tags can estimate an animal's position  
58 while underwater, but these tags typically use sunrise and sunset times and perhaps water  
59 temperature for geolocation, and they are therefore useful only for fish moving across broad  
60 spatial scales (e.g., bluefin tuna *Thunnus thynnus*; Block et al., 2005). Very recently, novel  
61 tracking systems have been developed that can provide meters-level spatial resolution of a wide

62 variety of marine fishes using arrays of underwater receivers (e.g., Espinoza et al., 2011),  
63 allowing for fine-scale relocations of many animal species that were previously untrackable.

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

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

85 artificial reefs (Herbig and Szedlmayer, 2016), but their movements around natural reefs, and  
86 their associated behavioral states, are unknown.

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

103

## 104 **2. Material and methods**

### 105 *2.1. Study site*

106         This study was conducted at an area of mixed low-relief hardbottom reef and sand  
107 habitats covering approximately 0.5 km<sup>2</sup> on the continental shelf of North Carolina, USA (Fig.

108 1). The specific site was located about 35 km east of Cape Lookout, North Carolina, in 37 m of  
109 water and was chosen for three reasons. First, gray triggerfish have been tagged at this location  
110 by Runde (2017), who documented high abundance and site fidelity of the species. Second, a  
111 high-resolution bathymetric seafloor map was available for the study area (C. Taylor,  
112 unpublished data). Third, the bathymetric relief across the study area was low, which eliminated  
113 acoustic signal dead zones that can complicate fish telemetry studies in high-relief habitats  
114 (Bacheler et al., 2015).

115

## 116 2.2. Data collection

117 We quantified the movements of gray triggerfish using a Vemco positioning system  
118 (VPS). In VPS, an array of underwater receivers are used to acoustically triangulate coded  
119 transmitters within the array, providing meters-level precision of spatial positions each time the  
120 transmitter emits a signal (Espinoza et al., 2011; Piraino and Szedlmayer, 2014). Several  
121 previous studies have successfully used VPS to quantify demersal marine fish movements (e.g.,  
122 Espinoza et al., 2011; Furey et al., 2013; Piraino and Szedlmayer, 2014; Herbig and Szedlmayer,  
123 2016; Williams-Grove and Szedlmayer, 2017).

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

130 Gray triggerfish were captured, tagged, and released in the study area on 15 September  
131 2017. After capture in baited traps, gray triggerfish were immediately placed in a holding tank  
132 and then tagged externally with Vemco V13-1x transmitters. We attached transmitters externally  
133 to maximize the detection range of transmitters (Dance et al., 2016) and minimize the time it  
134 took to attach transmitters to reduce barotrauma effects (Burns et al., 2002; Jepsen et al., 2015).  
135 Transmitters emitted unique acoustic signals every 110 – 250 sec on a frequency of 69 kHz,  
136 weighed 11 g in air, and had a battery life of approximately 2.5 years. Gray triggerfish were  
137 tracked for 43 d (until 27 October 2017), at which point receivers were retrieved and detection  
138 data were downloaded.

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

147

### 148 2.3. Analyses

149 We tested our four hypotheses using two quantitative approaches – exploratory data  
150 analyses and HMMs. These two analytical approaches were analyzed independently from one  
151 another but were based on the same raw acoustic data. When used in combination, these two  
152 approaches are more powerful and informative than either approach alone, especially if there is

153 strong agreement between the two. For the exploratory data analyses, movement rate of gray  
154 triggerfish was the response variable used for all calculations. Movement rates (m/s) for each  
155 fish in the study area were calculated as the distance moved (m) between each successive pair of  
156 spatial positions divided by the time between detections (s). The downside of using movement  
157 rates is that it assumes straight-line movements between detections, when in fact fish may not  
158 move in straight lines. Given that gray triggerfish were detected on average every 2–4 minutes,  
159 this issue is less critical in our study compared to studies with longer time intervals between  
160 detections (Alós et al., 2016), but it does imply that our movement rates should be interpreted as  
161 minimum estimates.

162       Specific exploratory data analyses were used to provide an initial evaluation of each of  
163 our hypotheses. First, we tested for differences in movement rates across individuals using a  
164 linear model, treating fish as a categorical variable. This and all subsequent analyses were  
165 conducted in R (R Core Team, 2017). Second, we tested for size-dependent movement rates of  
166 gray triggerfish by relating mean movement rates of each fish across the entire study to their fork  
167 length using a linear model. For this analysis, we weighted points based on the available sample  
168 size for each fish. And last, we tested for diel differences in movement rates for gray triggerfish  
169 using a linear model; hour of the day was binned into 24 hourly bins and treated as a categorical  
170 variable in the model. Observations that straddled two adjacent hourly bins were assigned to the  
171 first bin. For all linear models, model effects were considered fixed effects. We used Akaike  
172 information criterion (AIC) to test whether the above linear models were better or worse when  
173 including the variable of interest compared to excluding that variable (Burnham and Anderson,  
174 2002). We compared the AICs of fitted models to select the most parsimonious formulations,  
175 and models with the lowest AIC values ( $\Delta\text{AIC} = 0$ ) were considered the best model in the set.



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

187 The HMMs require that telemetry data are provided on a consistent time interval, but our  
188 telemetry data occurred on an irregular time interval to reduce the likelihood of acoustic signal  
189 collision among individuals. We regularized our telemetry data by interpolating the animals'  
190 locations on a regular time grid using package *crawl* (Johnson et al., 2008) in R (R Core Team,  
191 2017), which implements continuous-time correlated random walk models to provide a  
192 consistent time interval for the HMMs. We explored a variety of time intervals for  
193 regularization, but ultimately chose a 4-min interval because most time intervals in the data were  
194 between 2 and 4 min. Regardless of the time interval used for regularization, output from the  
195 HMMs were nearly identical.

196 There were also instances where longer gaps between acoustic detections were apparent  
197 due to, for instance, temporary emigration of individual fish from the study area. Regularizing  
198 telemetry data across these longer time gaps was problematic because it introduced substantial

199 regularization uncertainty. Therefore, we split tracks for individual fish when there were  
200 temporal gaps in detections longer than 20 min, which removed the temporal gap from further  
201 analyses. Multiple split tracks were then treated as independent time series arising from the  
202 same underlying statistical model. Because a common set of parameters is fitted to all tracks, the  
203 same behavioral states govern the movement before and after the gap, and they can therefore  
204 capture any existing correlation. Moreover, individual tracks for fish that included fewer than  
205 100 detections were also removed from analyses because a continuous-time model needs to be  
206 fitted to each track for the regularization, and numerical issues arose for short tracks. Short  
207 tracks also provide very little information about the dynamics of switching between behavioral  
208 states. We also ran HMMs with different values for the time of temporal gaps and minimum  
209 sample sizes for detections and all HMM outputs were very similar, suggesting insensitivity of  
210 HMMs to our choice of threshold values. If telemetered gray triggerfish did not have any tracks  
211 with more than 100 detections, they were excluded from our HMM analyses.

212         A primary strength of HMMs is the ability to identify underlying behavioral states of  
213 animals that are not easily observed (i.e., unsupervised), which is particularly useful for demersal  
214 marine fishes. For instance, marine fishes may exhibit resting, foraging, and traveling states. A  
215 key challenge, however, is determining how many behavioral states should be included in  
216 HMMs (Pohle et al., 2017). Traditional model selection approaches like Akaike information  
217 criterion appear to select a much larger number of states than is expected or meaningful based on  
218 *a priori* knowledge (DeRuiter et al., 2017; Li and Bolker, 2017). Pohle et al. (2017) argue that  
219 the number of states in HMMs should be chosen pragmatically using a combination of statistical  
220 and biological inferences. Given we have very limited inference about the behavioral states of  
221 gray triggerfish, we focused our analyses on two- and three-state HMMs, by far the most

222 common in the movement ecology literature. We refrain from presenting more complicated  
223 models because (1) we lack biological justification that more than three behavioral states exist  
224 for gray triggerfish, (2) increasing the number of behavioral states results in a quadratic increase  
225 in the number of parameters to estimate, and (3) the goodness-of-fit improved little with  
226 additional states.

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

240         We modeled the transition probabilities of the HMM as functions of fish length and time  
241 (hour) of day to address our specific hypotheses. A multinomial logit link function was used to  
242 ensure that the transition probabilities were between 0 and 1, and that rows of the transition  
243 probability matrix summed to 1 (Michelot et al., 2016). The effect of the time of day should be  
244 cyclic over 24-hour periods to capture the circadian rhythm of the fish. This was implemented

245 with the inclusion of the periodic covariates  $\cos(2\pi t/24)$  and  $\sin(2\pi t/24)$ , where  $t$  is the time  
246 of the observation as a number between 0 and 24 (Towner et al., 2016). We considered five 2-  
247 state and five 3-state models with the following covariate dependencies: (1) no covariates  
248 (hereafter, “base” model, (2) fish length only (“length”), (3) time of day only (“tod”), (4) fish  
249 length and time of day (“tod + length”), and (5) fish length and time of day with interaction  
250 (“full”). We again used AIC for HMM covariate selection (Burnham and Anderson, 2002). For  
251 the selected models, we estimated the unobserved behavioral states using the Viterbi algorithm,  
252 which is the standard method to derive the most likely sequence of states of a HMM given the  
253 observations and the fitted model (Zucchini et al., 2016). From the Viterbi algorithm, we  
254 obtained an estimated behavioral state for each observed location.

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

260

### 261 **3. Results**

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

268 104,170 spatial positions were determined for the 30 telemetered gray triggerfish during the 43-d  
269 study (mean = 3,472 detections per fish; range = 63 – 11,789; Table 1).

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

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

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

289 The 2- and 3-state gray triggerfish HMMs identified behavioral states that differed in  
290 their step lengths and turning angles (Fig. 3, Table 3). In the 2-state model, state 1 was

291 characterized by a short step length, with fish only moving a mean of 2.7 m every min, and a  
292 lack of concentrated turning angles (angle concentration = 0.18), suggesting frequent change of  
293 direction (Table 3). In contrast, state 2 was characterized by a much longer step length (mean =  
294 21.7 m) and turning angles concentrated around 0° (angle concentration = 0.78), suggesting  
295 movement direction was often similar (correlated) among successive positions (Table 3). In the  
296 3-state HMM, state 1 was similar to the 2-state model in that step length was short (mean = 1.6  
297 m) and turning angles were diffuse (angle concentration = 0.33). State 3 in the 3-state model  
298 was similar to state 2 in the 2-state model, typified by a longer step length (mean = 27.5 m) and a  
299 high turning angle concentration (1.08) around 0° (Fig. 3, Table 3). State 2 in the 3-state model  
300 had a moderate step length (mean = 6.4 m), but the least concentrated turning angle of all  
301 behavioral states (angle concentration = 0.02), suggesting frequent turning.

302         There were significant individual differences in movement rates and state behaviors  
303 among gray triggerfish in our study. Mean movement rates varied among individuals, ranging  
304 from a minimum of 0.028 m/s for fish #45 to 0.127 m/s for fish #55, with an overall mean of  
305 0.061 m/s (Fig. 4A). In the 2-state HMM, individual fish spent 24 to 97% of their total time in  
306 state 1 (low movement state) and their remaining time (3 – 76%) in state 2 (Fig. 4B). Results for  
307 the 3-state model were similarly variable among individuals. Time spent by individual fish in  
308 state 1 was the most variable, ranging from 10 to 86% among individuals (Fig. 4C), but the time  
309 spent by gray triggerfish in state 2 (12 – 62%) and state 3 (2 – 59%) was also quite variable (Fig.  
310 4C).

311         Exploratory data analyses and HMMs indicated that some of the variability in gray  
312 triggerfish movement could be explained by fish size. Exploratory data analyses indicated that  
313 movement rates for larger fish were about twice as high than for smaller fish ( $P < 0.0001$ ),

314 increasing from a mean of approximately 0.04 m/s at 250 mm fork length to 0.08 m/s at 335 mm  
315 (Fig. 5A). The 2-state HMM showed that larger gray triggerfish tended to spend more time in  
316 State 2, which was typified by higher movement rates, compared to smaller gray triggerfish that  
317 spent more time in state 1 (Fig. 5C). Similarly, in the 3-state model, larger gray triggerfish spent  
318 about twice as much time in state 3 and less time in state 2 compared to smaller gray triggerfish  
319 (Fig. 5E). However, there did not appear to be a size effect on the time spent in state 1 for the 3-  
320 state HMM (Fig. 5E).

321 Strongly diel movement rates and state probabilities for gray triggerfish were also  
322 observed using exploratory data analyses and HMMs. Mean movement rates of gray triggerfish  
323 were significantly lower ( $\sim 0.03$  m/s) at night and higher (0.07–0.10 m/s) during the day ( $F =$   
324 1122,  $P < 0.0001$ ; Fig. 5B, Appendix B1, B2), and median movement rates followed the same  
325 general pattern. These results were obvious from the both 2- and 3-state HMMs. At night, the 2-  
326 state HMM suggested gray triggerfish spent most ( $> 90\%$ ) of their time in state 1 (low movement  
327 state), while most of their time during the day ( $\sim 70\%$ ) was spent in state 2, the high movement  
328 state (Fig. 5D). The 3-state HMM results were very similar to the 2-state model, indicating gray  
329 triggerfish spent most of their time in state 1 at night ( $\sim 60\%$ ) and state 3 during the day ( $\sim 50\%$ ;  
330 Fig. 5F). State 2 was exhibited by gray triggerfish similarly ( $\sim 30\%$ ) both day and night (Fig.  
331 5F).

332 The spatial distribution of locations where gray triggerfish exhibited various behavioral  
333 states in the HMMs were nonrandom and spatially distinct. Gray triggerfish exhibited state 1  
334 behaviors in 15 or 20 small ( $< 100$  m diameter) patches that were associated with low-relief  
335 hardbottom throughout the study area (Fig. 6). In contrast, state 2 (in the 2-state model) and state  
336 3 (in the 3-state model) behaviors occurred more broadly across the study region. State 2 in the

337 3-state model occurred in distinct patches, but these patches tended to be much larger (up to 200  
338 m in diameter) than locations where state 1 behaviors were exhibited by gray triggerfish (Fig.  
339 6B).

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

346

#### 347 **4. Discussion**

348 Gray triggerfish inhabit demersal seafloor habitats where they are rarely observed  
349 directly, yet understanding their movement behavior is important for their sustainable  
350 management and conservation. During summer and fall months, we found that gray triggerfish  
351 movements and behavioral states varied greatly across the diel period (higher during the day than  
352 at night) and among individuals, the latter of which could partially be explained by fish size.  
353 Gray triggerfish also exhibited strong persistence in each behavioral state identified by the  
354 HMMs, suggesting serially correlated behaviors. Strong agreement between our exploratory  
355 data analyses and HMMs indicated that our results are robust.

356 The main benefit of HMMs is the ability to identify behavioral states of animals that are  
357 not easily observed. However, it can be challenging to interpret each behavioral state from the  
358 HMMs for a species such as gray triggerfish with little supporting biological information. It is  
359 likely that state 1 of both the 2- and 3-state models is resting behavior; fish moved very little and



360 was similar in magnitude to our estimated median horizontal position error, had a low turning  
361 angle concentration, and mostly exhibited this behavioral state at night when gray triggerfish are  
362 thought to rest on the bottom (Herbig and Szedlmayer, 2016). State 2 of the 2-state model and  
363 state 3 of the 3-state model were characterized by faster movement mostly in a correlated  
364 direction, so those states are likely transit or foraging. State 2 of the 3-state model is more  
365 difficult to interpret because it was characterized by moderate movement rates, frequent turning,  
366 and occurred both day (when they are active) and night (when they typically rest). More  
367 research is needed to determine if this was a true behavioral state (and not just a blending of  
368 other behavioral states), and if so, what behaviors gray triggerfish are exhibiting while in this  
369 state.

370         Gray triggerfish exhibited highly variable movement behaviors across individuals. For  
371 instance, there was a ~350% difference in movement rates between individuals moving the least  
372 and most in our study, which was similar to the substantial differences among individuals in the  
373 time they spent in resting and transit behavioral states in our HMMs. A portion of the variation  
374 in gray triggerfish movement rates was explained by fish size, which is consistent with most  
375 studies finding a positive relationship between movement rates and animal size (Ware, 1987;  
376 Swihart et al., 1988). However, the size range of fish examined in our study (250 – 335 mm fork  
377 length) was fairly narrow, so our analyses likely do not represent gray triggerfish of a broader  
378 size range. For instance, larval and juvenile gray triggerfish are pelagic and associate with  
379 floating debris while likely circling the Atlantic Ocean (Harper and McClellan, 1997), suggesting  
380 fish of that smaller size move or drift much more than the larger sizes examined in our study.  
381 Movement rates of gray triggerfish larger than the sizes examined in our study (i.e., > 335 mm  
382 fork length) are also unknown.

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

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

406 used to identify habitats that require protection and optimally design marine protected areas for  
407 specific behavioral states.

408         Gray triggerfish movements and behavioral states were highly variable across the diel  
409 period. Movement rates were over 200% higher during daylight hours than at night, and fish  
410 spent much more time in a resting state at night than during the day. Similarly, Herbig and  
411 Szedlmayer (2016) showed that, on average, gray triggerfish ranged over a much larger area  
412 during the day (~ 2,000 m<sup>2</sup>) than at night (~ 200 m<sup>2</sup>) around artificial reefs in the Gulf of Mexico.  
413 Other closely related species such as fine-scale triggerfish (*Balistes polylepis*), orangeside  
414 triggerfish (*Sufflamen verres*), and black triggerfish (*Melichthys niger*) show similar diel patterns  
415 of resting at night and being active during the day (Hobson 1965, Kavanagh and Olney 2006).  
416 Herbig and Szedlmayer (2016) posit that inactivity of gray triggerfish at night may be a strategy  
417 to reduce predation from nocturnal predators like sharks, or perhaps their prey are not active at  
418 night.

419         There were some shortcomings of our study. First, since we focused on a demersal  
420 marine species, we mostly lacked biological information that could be used to help develop our  
421 HMMs (i.e., choosing the number of HMM states, verification that each HMM state is an actual  
422 behavioral state), as recommended by Pohle et al. (2017). Anecdotal information from fishers  
423 and SCUBA divers suggests gray triggerfish rest on the bottom at night without foraging,  
424 consistent with the resting behavioral state we identified that mostly occurred at night. However,  
425 similar biological information does not exist for other behavioral states of gray triggerfish.  
426 Second, we used two characteristics of gray triggerfish movement behavior – step length and  
427 turning angles – to parameterize our HMMs, but additional concurrent information on such  
428 factors as depth or acceleration would have helped to refine and classify behavioral states of gray

429 triggerfish and should be used in future studies where possible (Leos-Barajas et al., 2017). Last,  
430 gray triggerfish have been shown to display highly seasonal movements (Herbig and  
431 Szedlmayer, 2016), yet our study occurred over a relatively short (43-d) period in September–  
432 October 2017. Thus, it would be imprudent to assume that the gray triggerfish movement  
433 behaviors quantified in our study would be static year-round.

434         With recent advances in tracking technologies and new analytical approaches such as  
435 HMMs, some believe we have entered a golden age of animal tracking science (Kays et al.,  
436 2015). Tags are becoming more reliable, smaller, and less invasive, allowing for the tracking of  
437 more animal species than ever before, including relatively small marine fish like gray triggerfish  
438 that display relatively high site fidelity in the open ocean. Data from fish tracking studies are  
439 being used by scientists and managers to determine optimal marine protected area design (Meyer  
440 et al., 2007), identify essential fish habitats (Simpfendorfer et al., 2010), and quantify fish  
441 mortality rates (Bacheler et al., 2009). Thus, we encourage a wider use of VPS systems  
442 combined with HMMs to shed light on the normally hidden behaviors of demersal marine fishes.

443

#### 444 **Acknowledgements**

445         We acknowledge D. Berrane, J. Buckel, E. Ebert, K. Egan, A. Gorgone, K. Gregalis, C.  
446 Harms, J. Krause, S. Lombardo, J. Potts, W. Rogers, T. Rezek, B. Runde, P. Rudershausen, C.  
447 Schobernd, Z. Schobernd, C. Taylor, T. Tears, and B. Teer for help with this study. We thank  
448 A. Chester, A. Hohn, T. Kellison, and K. Siegfried for reviewing previous versions of this  
449 manuscript. This work was supported by the Marine Fisheries Initiative program of the U.S.  
450 National Marine Fisheries Service. Mention of trade names or commercial companies is for  
451 identification purposes only and does not imply endorsement by the National Marine Fisheries

452 Service, NOAA. The scientific results and conclusions, as well as any views and opinions  
453 expressed herein, are those of the authors and do not necessarily reflect those of any government  
454 agency.

455

456

457 **References**

- 458 Alós, J., Palmer, M., Balle, S., Arlinghaus, R., 2016. Bayesian state-space modelling of  
459 conventional acoustic tracking provides accurate descriptors of home range behavior in a  
460 small-bodied coastal fish species. PLoS ONE 11, e0154089.  
461 <https://doi.org/10.1371/journal.pone.0154089>
- 462 Bacheler, N.M., Buckel, J.A., Hightower, J.E., Paramore, L.M., Pollock, K.H., 2009. A  
463 combined telemetry-tag return approach to estimate fishing and natural mortality rates of  
464 an estuarine fish. Can. J. Fish. Aquat. Sci. 66, 1230–1244. <https://doi.org/10.1139/F09-076>
- 465
- 466 Bacheler, N.M., Schobernd, C.M., Harter, S.L., David, A.W., Sedberry, G.R., Kellison, G.T.,  
467 2016b. No evidence of increased demersal fish abundance six years after creation of  
468 marine protected areas along the southeast United States Atlantic coast. Bull. Mar. Sci.  
469 92, 447–471. <https://doi.org/10.5343/bms.2016.1053>
- 470 Bacheler, N.M., Schobernd, Z.H., Berrane, D.J., Schobernd, C.M., Mitchell, W.A., Teer, B.Z.,  
471 Gregalis, K.C., Glasgow, D.M., 2016a. Spatial distribution of reef fish species along the  
472 southeast US Atlantic coast inferred from underwater video survey data. PLoS ONE 11,  
473 e0162653. <https://doi.org/10.1371/journal.pone.0162653>
- 474 Bacheler, N.M., Shertzer, K.W., Buckel, J.A., Rudershausen, P.J., Runde, B.J., 2018. Behavior  
475 of gray triggerfish *Balistes capriscus* around baited fish traps determined from fine-scale  
476 acoustic tracking. Mar. Ecol. Prog. Ser. 606, 133–150.  
477 <https://doi.org/10.3354/meps12780>

478

479

- 480 Bacheler, N.M., Shertzer, K.W., Cheshire, R.T., MacMahan, J.H., 2019. Tropical storms  
481 influence the movement behavior of a demersal oceanic fish species. *Sci. Rep.* 9:1481.  
482 <https://doi.org/10.1038/s41598-018-37527-1>
- 483 Bacheler, N.M., Whitfield, P.E., Muñoz, R.C., Harrison, B.B., Harms, C.A., Buckel, C.A., 2015.  
484 Movement of invasive adult lionfish *Pterois volitans* using telemetry: importance of  
485 controls to estimate and explain variable detection probabilities. *Mar. Ecol. Prog. Ser.*  
486 527, 205–220. <https://doi.org/10.3354/meps11241>
- 487 Block, B.A., Teo, S.L.H., Walli, A., Boustany, A., Stokesbury, M.J.W., Farwell, C.J., Weng,  
488 K.C., Dewar, H., Williams, T.D., 2005. Electronic tagging and population structure of  
489 Atlantic bluefin tuna. *Nature* 434, 1121–1127. <https://doi.org/10.1038/nature03463>
- 490 Burnham, K.P., Anderson, D.R., 2002. Model selection and multimodel inference: a practical  
491 information-theoretic approach, 2<sup>nd</sup> edition. Springer, New York.
- 492 Burns, K.M., Koenig, C.C., Coleman, F.C., 2002. Evaluation of multiple factors involved in  
493 release mortality of undersized red grouper, gag, red snapper and vermilion snapper.  
494 Mote Marine Laboratory Technical Report No. 790. Accessed on 18 May 2018 at:  
495 <https://dspace.mote.org:8443/bitstream/2075/294/3/MTR%20790.pdf>
- 496 Calabrese, J.M., Fleming, C.H., Gurarie, E., 2016. ctmm: an R package for analyzing animal  
497 relocation data as a continuous-time stochastic process. *Meth. Ecol. Evol.* 7, 1124–1132.  
498 <https://doi.org/10.1111/2041-210X.12559>
- 499 Dance, M.A., Moulton, D.L., Furey, N.B., Rooker, J.R., 2016. Does transmitter placement or  
500 species affect detection efficiency of tagged animals in biotelemetry research? *Fish. Res.*  
501 183, 80–85. <https://doi.org/10.1016/j.fishres.2016.05.009>  
502

- 503 DeRuiter, S.L., Langrock, R., Skirbutas, T., Goldbogen, T.A., Calambokidis, J., Friedlaender,  
504 A.S., Southall, B.L., 2017. A multivariate mixed hidden Markov model for blue whale  
505 behaviour and responses to sound exposure. *Ann. Appl. Stat.* 11, 362–392.  
506 <https://doi.org/10.1214/16-aos1008>
- 507 Espinoza, M., Farrugia, T.J., Webber, D.M., Smith, F., Lowe, C.G., 2011. Testing a new aquatic  
508 telemetry technique to quantify long-term, fine-scale movements of aquatic animals.  
509 *Fish. Res.* 108, 364–371. <https://doi.org/10.1016/j.fishres.2011.01.011>
- 510 Franke, A., Caelli, T., Kuzyk, G., Hudson, R.J., 2006. Prediction of wolf (*Canis lupus*) kill-sites  
511 using hidden Markov models. *Ecol. Mod.* 197, 237–246.  
512 <https://doi.org/10.1016/j.ecolmodel.2006.02.043>
- 513 Fraser, D.F., Gilliam, J.F., Daley, M.J., Le, A.N., Skalski, G.T., 2001. Explaining leptokurtic  
514 movement distributions: intrapopulation variation in boldness and exploration. *Am. Nat.*  
515 158, 124–135. <https://doi.org/10.1086/321307>
- 516 Furey, N.M., Dance, M.A., Rooker, J.R., 2013. Fine-scale movements and habitat use of juvenile  
517 southern flounder *Paralichthys lethostigma* in an estuarine seascape. *J. Fish. Biol.* 82,  
518 1469–1483. <https://doi.org/10.1111/jfb.12074>
- 519 Gilliam, F.J., Fraser, D.F., 2001. Corridor movement: enhancement by predation threat, habitat  
520 structure and disturbance. *Ecol.* 82, 258–273. [https://doi.org/10.1890/0012-  
521 9658\(2001\)082\[0258:MICEBP\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082[0258:MICEBP]2.0.CO;2)
- 522 Grüss, A., Kaplan, D.M., Guenette, S., Roberts, C.M., Botsford, L.W., 2011. Consequences of  
523 adult and juvenile movement for marine protected areas. *Biol. Conserv.* 144, 692–702.  
524 <https://doi.org/10.1016/j.biocon.2010.12.015>  
525



- 526 Gurarie, E., Andrews, R.D., Laidre, K.L., 2009. A novel method for identifying behavioural  
527 changes in animal movement data. *Ecol. Lett.* 12, 395–408.  
528 <https://doi.org/10.1111/j.1461-0248.2009.01293.x>
- 529 Harper, D.E., McClellan, D.B., 1997. A review of the biology and fishery for gray triggerfish,  
530 *Balistes capriscus*, in the Gulf of Mexico. National Marine Fisheries Service, Miami.  
531 MIA-96/97-52. [http://aquaticcommons.org/13452/1/gcfi\\_52-58.pdf](http://aquaticcommons.org/13452/1/gcfi_52-58.pdf)
- 532 Heerah, K., Woillez, M., Fablet, R., Garren, F., Martin, S., De Pontual, H., 2017. Coupling  
533 spectral analysis and hidden Markov models for the segmentation of behavioural patterns.  
534 *Mov. Ecol.* 5, 20. <https://doi.org/10.1186/s40462-017-0111-3>
- 535 Herbig, J.L., Szedlmayer, S.T., 2016. Movement patterns of gray triggerfish, *Balistes capriscus*,  
536 around artificial reefs in the northern Gulf of Mexico. *Fish. Manag. Ecol.* 23, 418–427.  
537 <https://doi.org/10.1111/fme.12190>
- 538 Hobson, E.S., 1965. Diurnal-nocturnal activity of some inshore fishes in the Gulf of California.  
539 *Copeia* 1965, 291–302. <https://doi.org/10.2307/1440790>
- 540 Jepsen, N., Thorstad, E.B., Havn, T., Lucas, M.C., 2015. The use of external electronic tags on  
541 fish: an evaluation of tag retention and tagging effects. *Anim. Biotelem.* 3, 49.  
542 <https://doi.org/10.1186/s40317-015-0086-z>
- 543 Johnson, D., London, J., Lea, M.A., Durban, J., 2008. Continuous-time correlated random  
544 walk model for animal telemetry data. *Ecol.* 89, 1208–1215. <https://doi.org/10.1890/07-1032.1>
- 546 Kays, R., Crofoot, M.C., Jetz, W., Wikelski, M., 2015. Terrestrial animal tracking as an eye on  
547 life and planet. *Science* 348, aaa2478. <https://doi.org/10.1126/science.aaa2478>
- 548

- 549 Kavanagh, K.D., Olney, J.E., 2006. Ecological correlates of population density and behavior in  
550 the circumtropical black triggerfish *Melichthys niger* (Balistidae). *Env. Biol. Fish.* 76,  
551 387–398. <https://doi.org/10.1007/s10641-006-9044-1>
- 552 Langrock, R., King, R., Matthiopoulos, J., Thomas, L., Fortin, D., Morales, J.M., 2012. Flexible  
553 and practical modeling of animal telemetry data: hidden Markov models and extensions.  
554 *Ecol.* 93, 2336–2342. <https://doi.org/10.1890/11-2241.1>
- 555 Langrock, R., Hopcraft, J.G.C., Blackwell, P.G., Goodall, V., King, R., Niu, M., Patterson, T.A.,  
556 Pedersen, M.W., Skarin, A., Schick, R.S., 2014. Modeling group dynamic animal  
557 movements. *Meth. Ecol. Evol.* 5, 190–199. <https://doi.org/10.1111/2041-210X.12155>
- 558 Leos-Barajas, V., Photopoulou, T., Langrock, R., Patterson, T.A., Watanabe, Y.Y., Murgatroyd  
559 M., Papastamatiou, Y.P., 2017. Analysis of animal accelerometer data using hidden  
560 Markov models. *Meth. Ecol. Evol.* 8, 161–173. <https://doi.org/10.1111/2041-210X.12657>
- 561 Li, M., Bolker, B.M., 2017. Incorporating periodic variability in hidden Markov models for  
562 animal movement. *Mov. Ecol.* 5, 1. <https://doi.org/10.1186/s40462-016-0093-6>
- 563 McClintock, B.T., Michelot, T., 2018. momentuHMM: R package for generalized hidden  
564 Markov models of animal movement. *Meth. Ecol. Evol.* 9, 1518–1530.  
565 <https://doi.org/10.1111/2041-210X.12995>
- 566 Meyer, C.G., Holland, K.N., Papastamatiou, Y.P., 2007. Seasonal and diel movements of giant  
567 trevally *Caranx ignobilis* at remote Hawaiian atolls: implications for the design of marine  
568 protected areas. *Mar. Ecol. Prog. Ser.* 333, 13–25. <https://doi.org/10.3354/meps333013>
- 569 Michelot, T., Langrock, R., Bestley, S., Jonsen, I.D., Photopoulou, T., Patterson, T.A., 2017.  
570 Estimation and simulation of foraging trips in land-based marine predators. *Ecol.* 98,  
571 1932–1944. <https://doi.org/10.1002/ecy.1880>

- 572 Michelot, T., Langrock, R., Patterson, T.A., 2016. moveHMM: an R package for the statistical  
573 modelling of animal movement data using hidden Markov models. *Meth. Ecol. Evol.* 7,  
574 1308–1315. <https://doi.org/10.1111/2041-210X.12578>
- 575 Nathan, R., Getz, W.M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., Smouse, P.E., 2008. A  
576 movement ecology paradigm for unifying organismal movement research. *Proc. Nat.  
577 Acad. Sci. USA* 105, 19052–19059. <https://doi.org/10.1073/pnas.0800375105>
- 578 Papastamatiou, Y.P., Watanabe, Y.Y., Demšar, U., Leos-Barajas, V., Bradley, D., Langrock, R.,  
579 Weng, K., Lowe, C.G., Friedlander, A.M., Caselle, J.E., 2018. Activity seascapes  
580 highlight central place foraging strategies in marine predators that never stop swimming.  
581 *Mov. Ecol.* 6, 9. <https://doi.org/10.1186/s40462-018-0127-3>
- 582 Patterson, T.A., Basson, M., Bravington, M.V., Gunn, J.S., 2009. Classifying movement  
583 behaviour in relation to environmental conditions using hidden Markov models. *J. Anim.  
584 Ecol.* 78, 1113–1123. <https://doi.org/10.1111/j.1365-2656.2009.01583.x>
- 585 Phillips, J.S., Patterson, T.A., Leroy, B., Pilling, G.M., Nicol, S.J., 2015. Objective classification  
586 of latent behavioral states in bio-logging data using multivariate-normal hidden Markov  
587 models. *Ecol. Appl.* 25, 1244–1258. <https://doi.org/10.1890/14-0862.1>
- 588 Piraino, M.N., Szedlmayer, S.T., 2014. Fine-scale movements and home ranges of red snapper  
589 around artificial reefs in the northern Gulf of Mexico. *Trans. Am. Fish. Soc.* 143, 988–  
590 998. <https://doi.org/10.1080/00028487.2014.901249>
- 591 Pohle, J., Langrock, R., van Beest, F.M., Schmidt, N.M., 2017. Selecting the number of states in  
592 hidden Markov models: pragmatic solutions illustrated using animal movement. *J. Agr.  
593 Biol. Env. Stat.* 22, 270–293. <https://doi.org/10.1007/s13253-017-0283-8>
- 594

- 595 Quick, N.J., Isojunno, S., Sadykova, D., Bowers, M., Nowacek, D.P., Read, A.J., 2017. Hidden  
596 Markov models reveal complexity in the diving behaviour of short-finned pilot whales.  
597 *Sci. Rep.* 7, 45765. <https://doi.org/10.1038/srep45765>
- 598 R Core Team, 2017. R: a language and environment for statistical computing. R Foundation for  
599 Statistical Computing, Vienna, Austria. URL: <https://www.R-project.org/>
- 600 Runde, B.J., 2017. Estimating and mitigating discard mortality of reef fishes. Master's Thesis,  
601 Department of Applied Ecology, North Carolina State University.  
602 <http://www.lib.ncsu.edu/resolver/1840.20/34369>
- 603 Simpfendorfer, C.A., Wiley, T.R., Yeiser, B.G., 2010. Improving conservation planning for an  
604 endangered sawfish using data from acoustic telemetry. *Biol. Cons.* 143, 1460–1469.  
605 <https://doi.org/10.1016/j.biocon.2010.03.021>
- 606 Swihart, R.K., Slade, N.A., Bergstrom, B.J., 1988. Relating body size to the rate of home range  
607 use in mammals. *Ecol.* 69, 393–399. <https://doi.org/10.2307/1940437>
- 608 Towner, A.V., Leos- Barajas, V., Langrock, R., Schick, R.S., Smale, M.J., Kaschke, T., Jewell,  
609 O.J.D., Papastamatiou, Y.P., 2016. Sex- specific and individual preferences for hunting  
610 strategies in white sharks. *Funct. Ecol.* 30, 1397–1407. [https://doi.org/10.1111/1365-](https://doi.org/10.1111/1365-2435.12613)  
611 [2435.12613](https://doi.org/10.1111/1365-2435.12613)
- 612 Turchin, P., 1998. Quantitative analysis of movement: measuring and modeling population  
613 redistribution in animals and plants. Sinauer Associates, Inc, Sunderland, Massachusetts.
- 614 Villegas-Ríos, D., Réale, D., Freitas, C., Moland, E., Olsen, E.M., 2018. Personalities influence  
615 spatial responses to environmental fluctuations in wild fish. *J. Anim. Ecol.* 87, 1309–  
616 1319. <https://doi.org/10.1111/1365-2656.12872>
- 617

- 618 Ware, D.M., 1978. Bioenergetics of pelagic fish: theoretical change in swimming speed and  
619 ration with body size. *J. Fish. Res. Board Can.* 35, 220–228. [https://doi.org/10.1139/f78-](https://doi.org/10.1139/f78-036)  
620 036
- 621 White, G.C., Garrott, R.A., 1990. Analysis of wildlife radio-tracking data. Academic Press, San  
622 Diego.
- 623 Williams-Grove, L.J., Szedlmayer, S.T., 2017. Depth preferences and three-dimensional  
624 movements of red snapper, *Lutjanus campechanus*, on an artificial reef in the northern  
625 Gulf of Mexico. *Fish. Res.* 190, 61–70. <https://doi.org/10.1016/j.fishres.2017.01.003>
- 626 Zucchini, W., MacDonald, I.L., Langrock, R., 2016. Hidden Markov models for time series:  
627 an introduction using R, 2<sup>nd</sup> edition. Chapman and Hall/CRC.
- 628

629 **Table 1**630 Information for individual gray triggerfish (*Balistes caprisкус*) in North Carolina, USA, in 2017.

631 A Vemco positioning system was used to estimate spatial positions for telemetered gray

632 triggerfish, and fish were tagged on 15 September 2017. An asterisk next to the fish tag number

633 indicates that fish was excluded from hidden Markov models due to insufficient estimated

634 positions.

635

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

636

637 **Table 2**

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

643

Model	$K$	$\Delta\text{AIC}$
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

644

645

646

647

648

649

650

651

652

653 **Table 3**

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

659

	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

660

661

662

663

664

665

666

667

668

669

670

671



672 **Table 4**

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

678

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

679

680

681

682

683

684

685

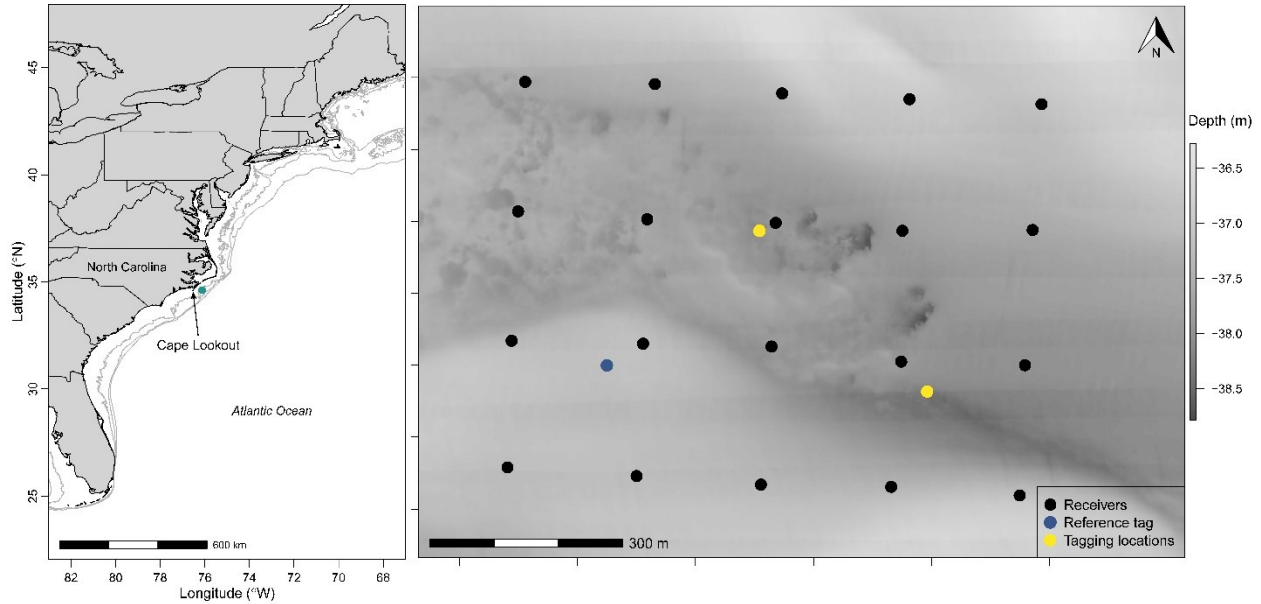
686

687

688

689

690



691

692

693 **Fig. 1.** Left panel: location of the study (green filled circle) east of Cape Lookout along the coast

694 of North Carolina, USA, in 2017. Right panel: close-up view of the study area where a Vemco

695 positioning system was used to estimate fine-scale positions of telemetered gray triggerfish

696 (*Balistes capriscus*). The background of the right panel is a multibeam sonar map showing the

697 bathymetry (depth) of the study area, submersible receivers are represented by black filled

698 circles, the reference tag location is represented by the blue filled circle, and tagging locations

699 are represented by yellow filled circles.

700

701

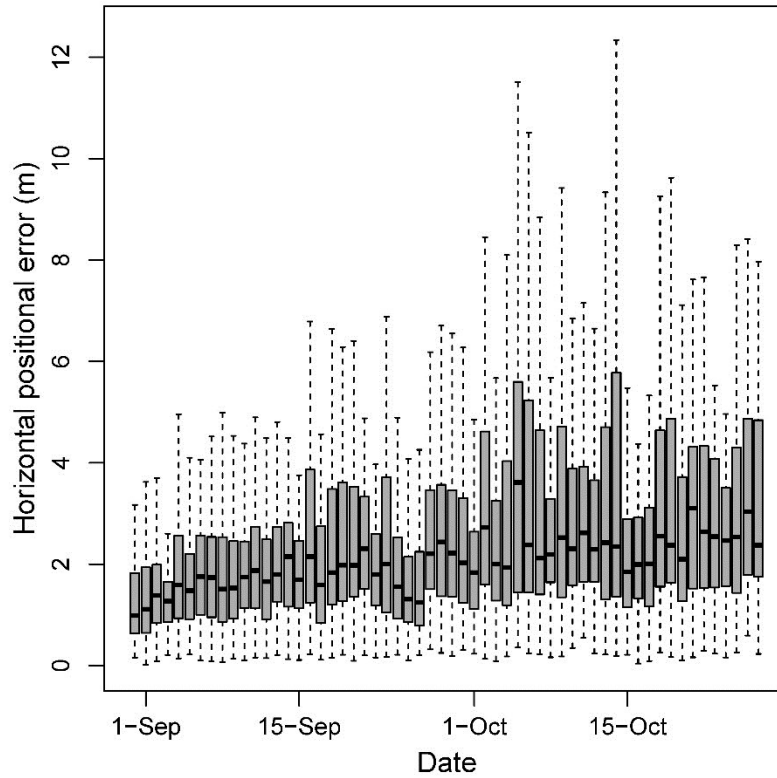
702

703

704

705

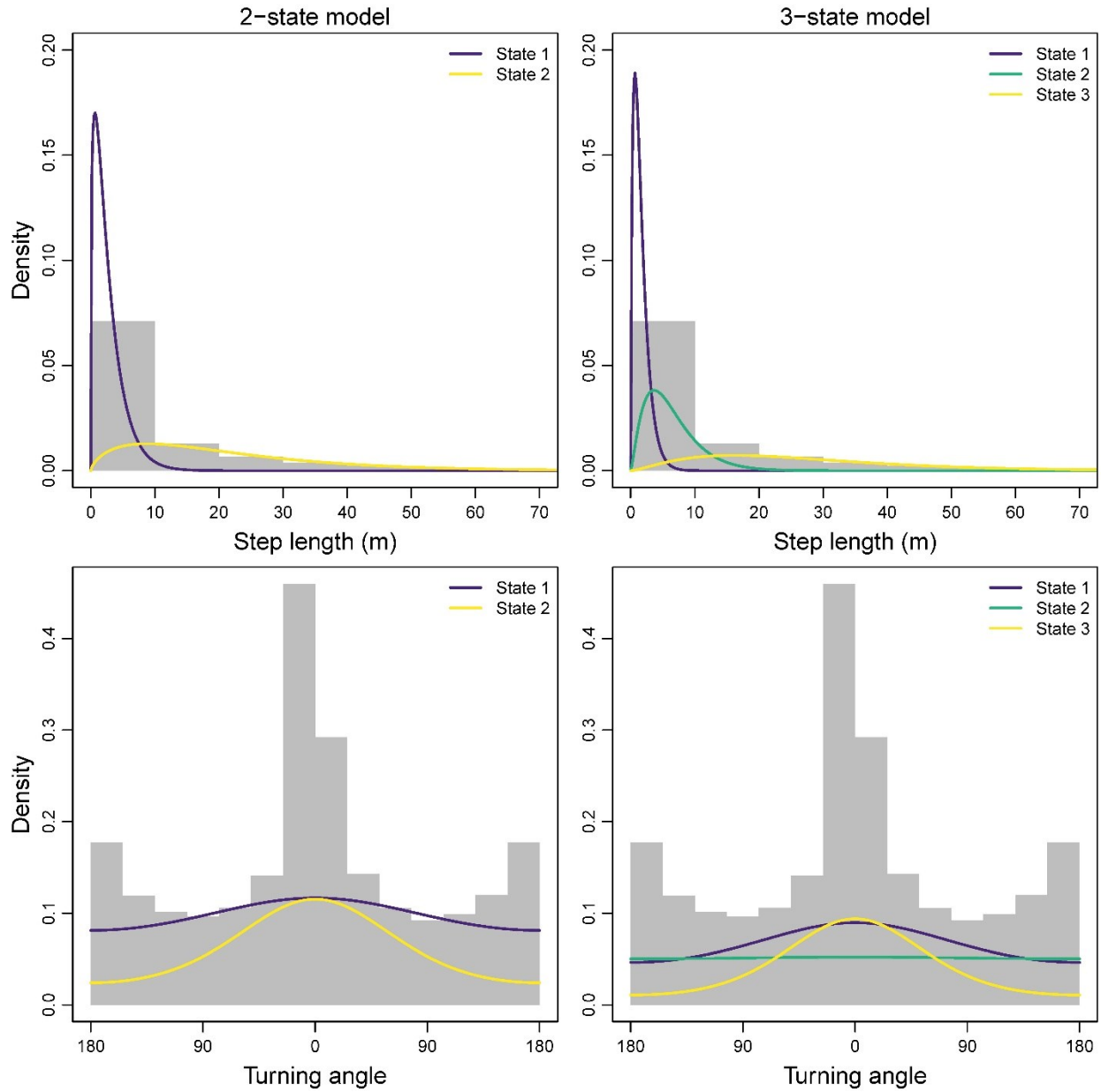
706



707

708

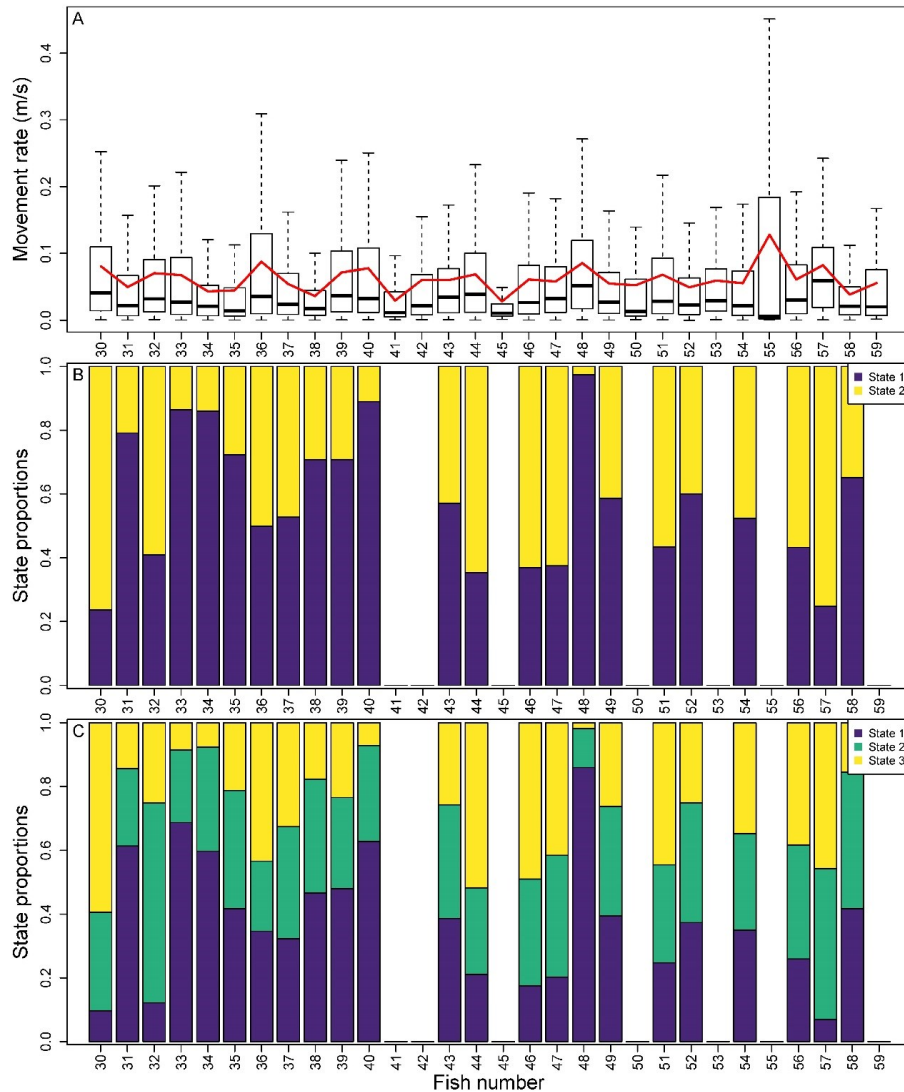
709 **Fig. 2.** Daily horizontal positional error (m) estimates of a reference transmitter deployed in  
710 North Carolina, USA, in 2017. The estimated position of the reference tag each time it emitted  
711 an acoustic signal was compared to its actual, known position to determine the horizontal 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



715

716

717 **Fig. 3.** Distributions (lines) and histograms (gray bars) of step lengths (m) and turning angles for  
 718 2-state (left column) and 3-state (right column) hidden Markov models developed for  
 719 telemetered gray triggerfish (*Balistes capriscus*) in North Carolina, USA, in 2017. A fish  
 720 continuing in exactly the same direction across two time intervals would have a turning angle of  
 721 0°, whereas a fish turning in the opposite direction would have a turning angle of 180°.



722

723 **Fig. 4.** Individual-level variability in movement rates and state probabilities among telemetered724 gray triggerfish (*Balistes capriscus*) in North Carolina, USA, in 2017. (A) Boxplot of observed

725 movement rates of telemetered gray triggerfish, also showing mean movement rates (red line).

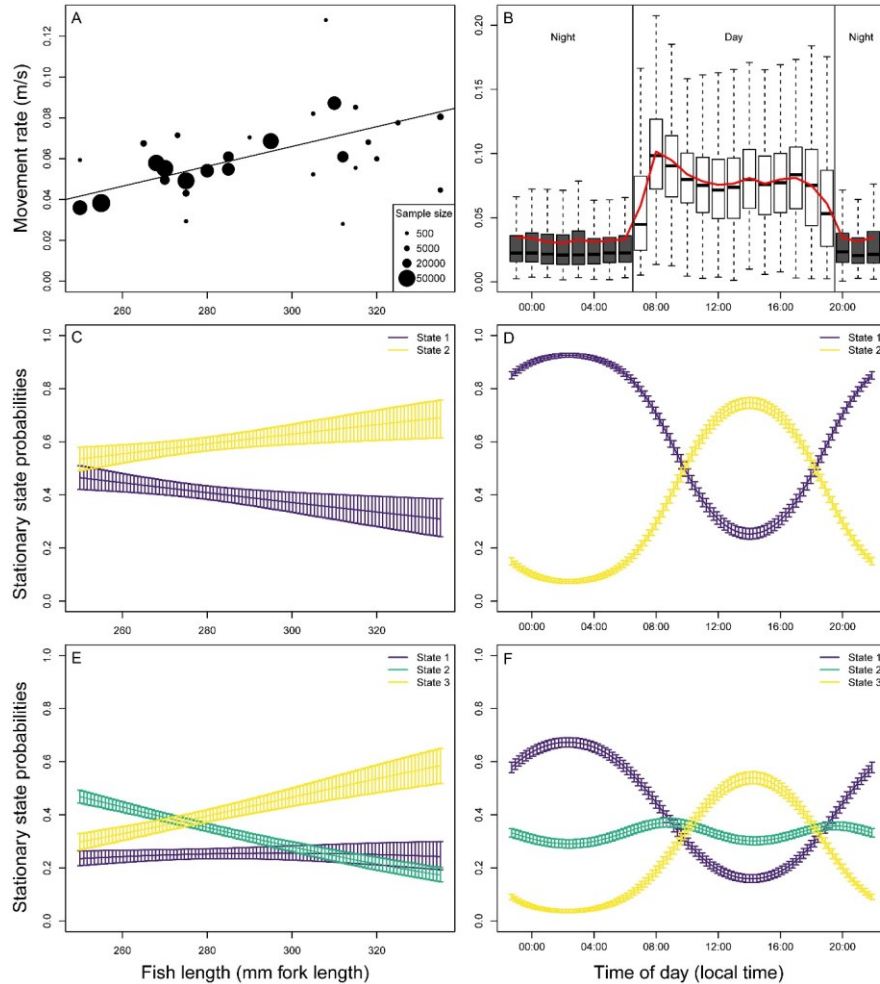
726 (B) The amount of time each individual telemetered gray triggerfish spent in each of the two

727 states of the 2-state hidden Markov model. (C) The amount of time each individual telemetered

728 gray triggerfish spent in each of the three states of the 3-state hidden Markov model. Empty

729 columns of B and C indicate fish that were excluded from hidden Markov models due to limited

730 sample sizes.



731

732 **Fig. 5.** (A) Relationship between movement rate and length of telemetered gray triggerfish733 (*Balistes capriscus*), weighted by the total number of positions available for each fish in North

734 Carolina, USA, in 2017. (B) Diel movement rates of telemetered gray triggerfish in our study;

735 boxes show median (thick horizontal black line), 25<sup>th</sup>, and 75<sup>th</sup> percentiles of movement rate;

736 whiskers are 1.5 times the interquartile range; and red line is mean movement rate by hour of the

737 day. (C) Size-dependent and (D) time-of-day-dependent stationary state probabilities for two

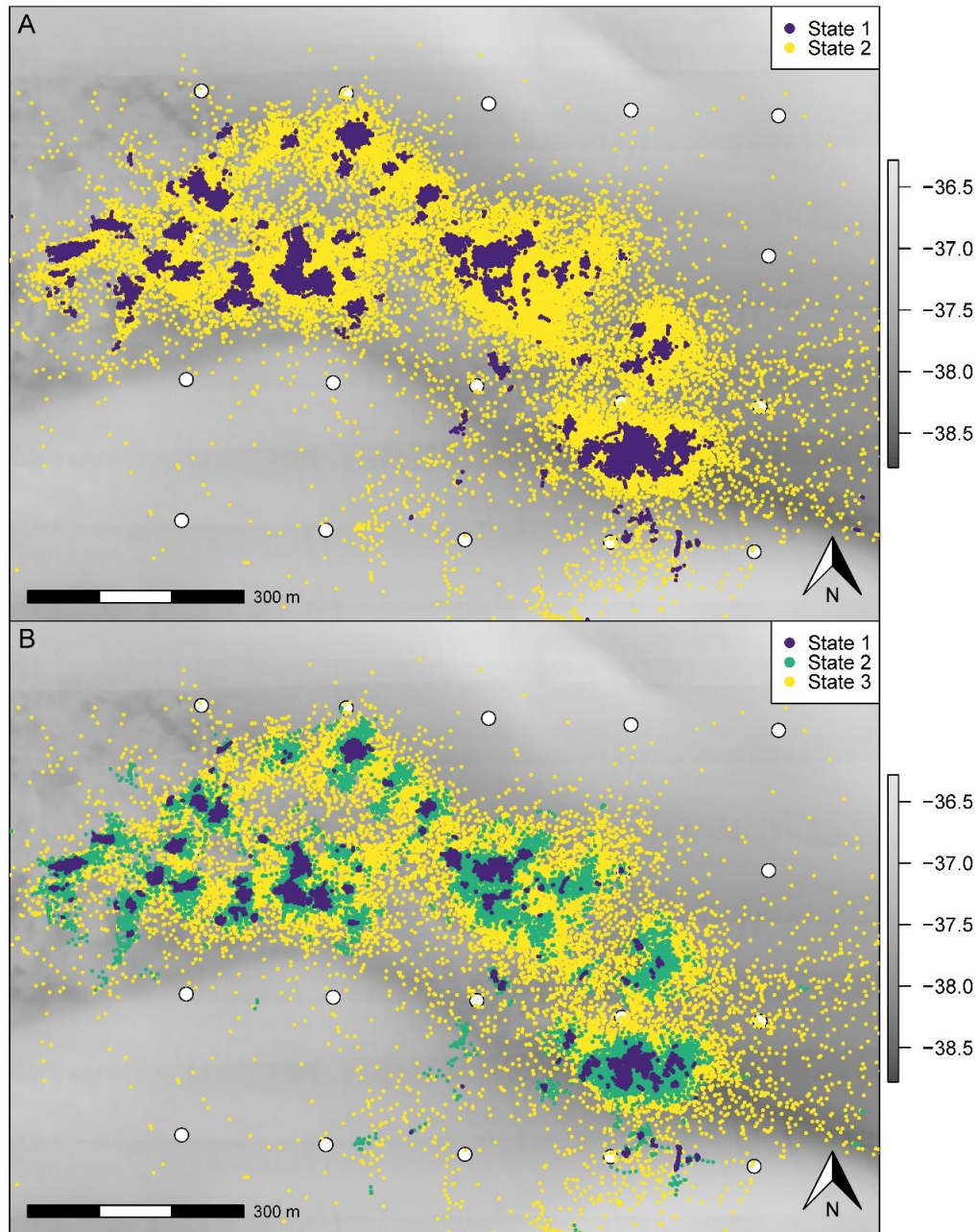
738 behavioral states of gray triggerfish using hidden Markov models. (E) Size-dependent and (F)

739 time-of-day-dependent stationary state probabilities for three behavioral states of gray triggerfish

740 using hidden Markov models. Solid lines show mean stationary state probabilities, and error bars

741 indicate 95% confidence intervals.





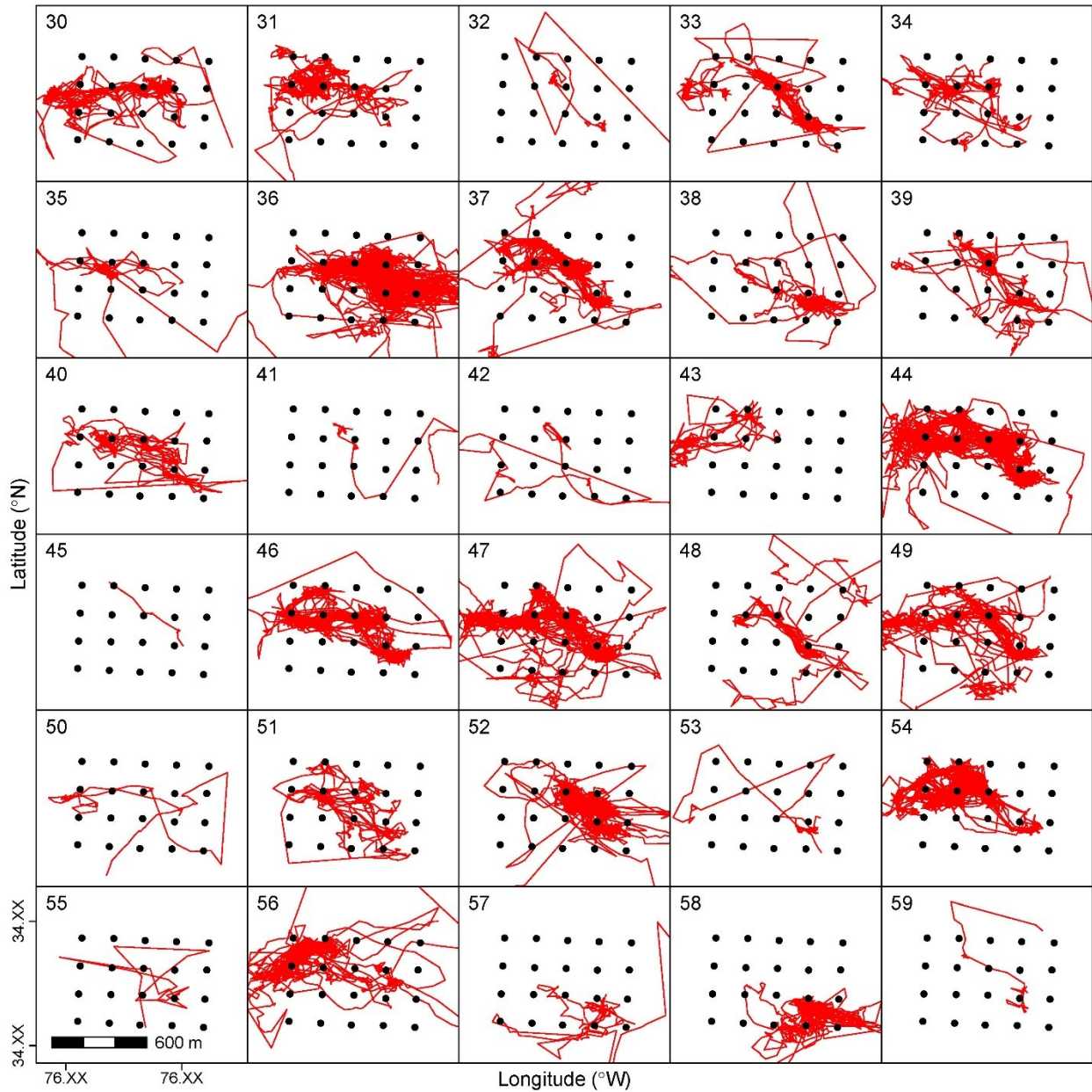
742

743

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

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

752

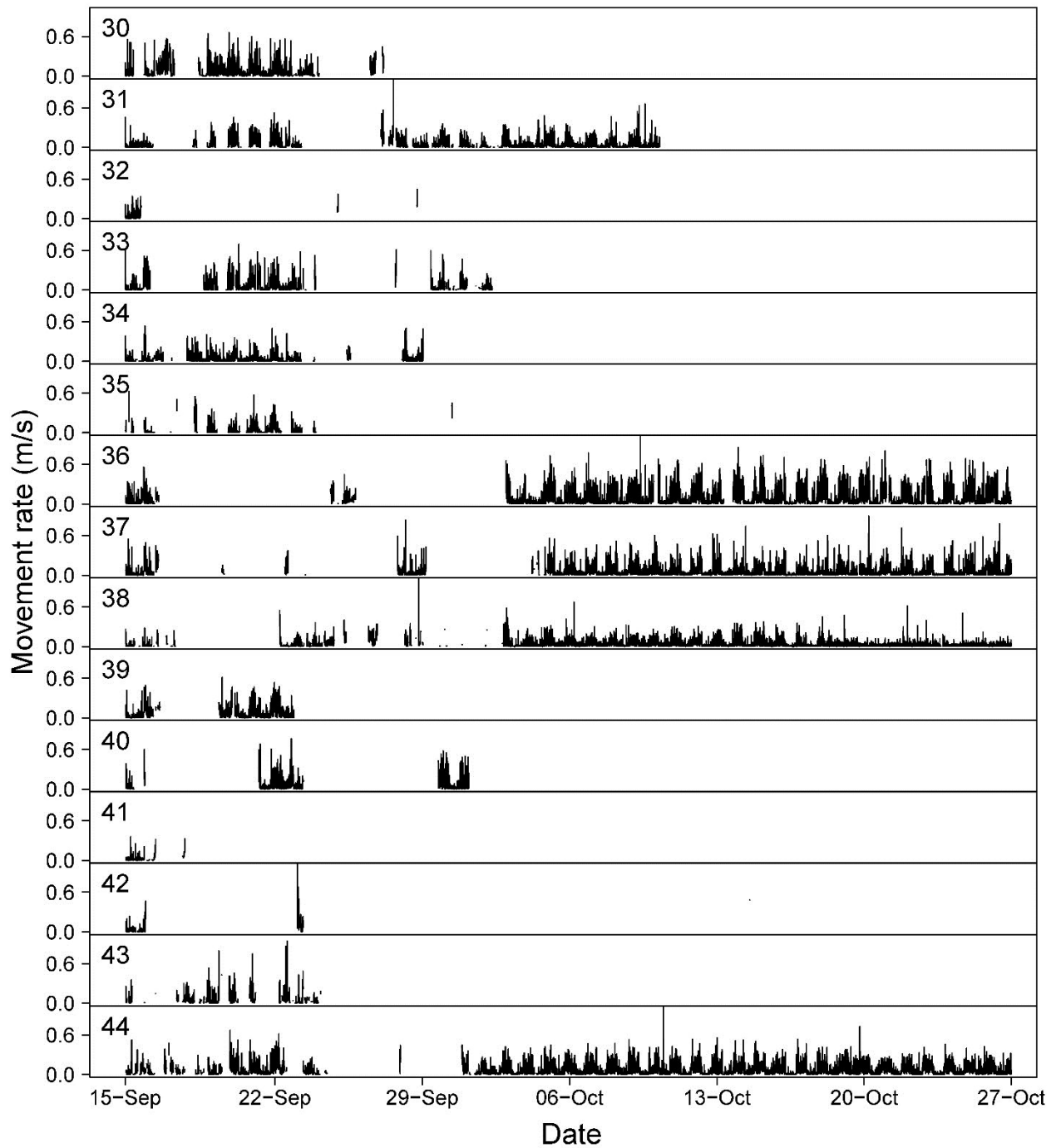


753

754

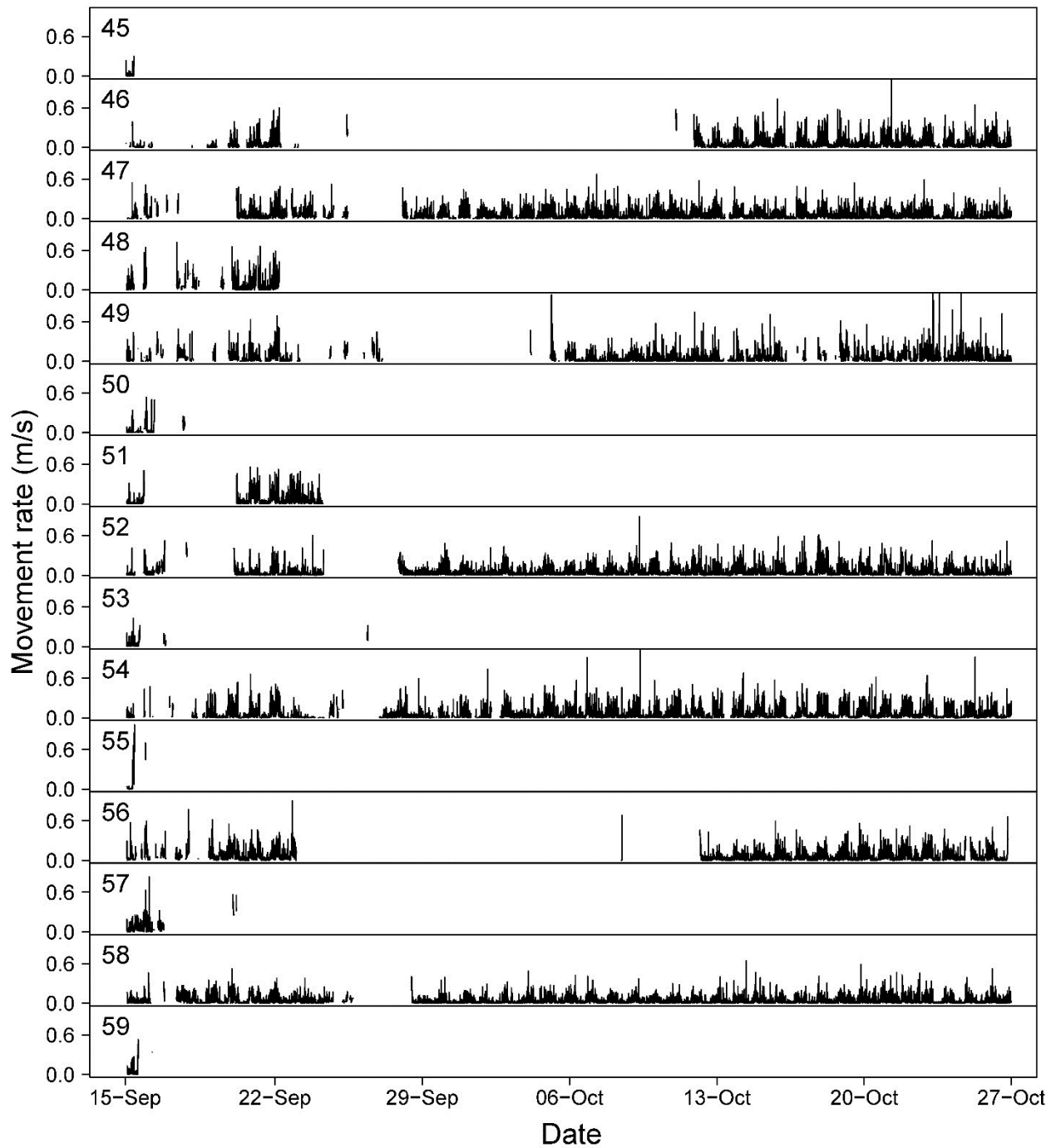


755 **Appendix B1.** Time series of movement rates estimated for telemetered gray triggerfish  
 756 (*Balistes capriscus*) over the course of the study, 15 September – 27 October 2017, in North  
 757 Carolina, USA. Missing data for fish in certain time periods was due to those fish being absent  
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



759

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



764