

1 **Title:** The influence of blue crab movement on mark-recapture estimates of recreational  
2 harvest and exploitation

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29

**30 Abstract**

31 Despite the need to quantify total catch to support sustainable fisheries management, estimating  
32 harvests of recreational fishers remains a challenge. Harvest estimates from mark-recapture  
33 studies have proven valuable, yet animal movements and migrations may bias some of these  
34 estimates. To improve recreational harvest estimates, explore seasonal and spatial harvest  
35 patterns, and understand the influence of animal movement on exploitation rates, a mark-  
36 recapture experiment was conducted for the blue crab fishery in Maryland waters of Chesapeake  
37 Bay, USA. Data were analyzed with standard tag-return methods and with revised equations that  
38 accounted for crab movement between reporting areas. Using standard calculations, state-wide  
39 recreational harvest was estimated to be 4.04 million crabs. When movement was included in the  
40 calculations, the estimate was 5.39 million, an increase of 34%. With crab movement,  
41 recreational harvest in Maryland was estimated to be 6.5% of commercial harvest, a finding  
42 consistent with previous effort surveys. The new methods presented herein are broadly  
43 applicable for estimating recreational harvest in fisheries that target mobile species and for which  
44 spatial variation in commercial harvest is known.

## 45 **Introduction**

46           Mark-recapture experiments are valuable tools for obtaining information on individuals,  
47 populations, and harvest regimes. Mark-recapture data have been modeled for closed and open  
48 populations, and models have increased in complexity to include multiple stages, multi-model  
49 comparisons, and new statistical techniques (Pollock 2000). For fishery species, mark-recapture  
50 experiments have been designed to investigate local population sizes and sources of mortality  
51 like fishery exploitation rates (Seber 1986, Pine et al. 2003). Models for analyzing mark-  
52 recapture data have been adapted to address various sources of uncertainty, including unequal  
53 catchability (Chao 1987, Agresti 1994), mixed stocks (Michielsens et al. 2006), and tag loss  
54 (Kremers 1988, Conn et al. 2004). Mark-recapture studies also have been used to study animal  
55 movements (Dorazio et al. 1994, Aguilar et al. 2005, Trudel et al. 2009). However, animal  
56 movements can influence mark-recapture-based estimates of exploitation rates (Nichols et al.  
57 1995, Munro and Kimball 1982), especially in cases where the harvest areas are small enough  
58 that there is substantial movement of tagged individuals among them.

59           Blue crabs (*Callinectes sapidus*) can make extensive movements during the open season  
60 of the blue crab fishery in Maryland waters of the Chesapeake Bay. The fishery targets this  
61 highly mobile species which is known to make short-duration movements as well as long-  
62 distance ontogenetic migrations (McConaughy et al. 1983, Walcott and Hines 1990, Hines 2007).  
63 For crabs of harvestable size (>127 mm carapace width in Maryland), this movement can be as  
64 much as 569 m per day; far enough to allow movement between harvest areas (Walcott and  
65 Hines 1990). Crabs in Maryland are targeted by two fishery sectors: commercial fishers which  
66 are required to report their harvest and recreational fishers which are not. Fishers in both sectors  
67 use multiple gear types (e.g. crab pot, trotline, hand-line, crab scrape) (Cargo 1954, Van Engel

68 1962, Kennedy et al. 2007). Knowledge of crab movement is important for understanding the  
69 dynamics of the crab population (Hines 2007) and spatiotemporal patterns of harvest effort  
70 (Slacum et al. 2012).

71 Management of the blue crab fishery in Chesapeake Bay is based on integrated targets  
72 and thresholds for the abundance and exploitation of female crabs (Miller et al. 2011). These are  
73 jointly estimated within the stock assessment model so both sets of indices are fully compatible.  
74 Additionally, there is an empirically determined trigger for management of male crabs, based on  
75 their exploitation. Abundance and exploitation are calculated based on commercial harvest  
76 reporting data, estimated recreational harvest from effort surveys (Miller et al. 2011), and three  
77 annual fishery-independent surveys: a dredge survey of overwintering crabs (Sharov et al. 2003),  
78 a trawl survey in MD (Davis et al. 2001, Miller et al. 2011), and a trawl survey in Virginia  
79 (Tuckey and Fabrizio 2019). In Maryland, the fishery is divided into 29 commercial harvest  
80 reporting areas which range from large areas of the mainstem bay to small tributaries (Fig. 1,  
81 Table 1). Recreational harvest of females was banned in Maryland in 2008 as one of several  
82 measures to address recruitment overfishing, potentially shifting fishing effort onto males (Miller  
83 et al. 2011) and altering sex ratios which can have negative consequences for population  
84 reproductive output (Ogburn 2019). Recreational crabbers are not required to report their male  
85 crab harvest, which is instead estimated by effort surveys to be 8% of commercial harvest  
86 (Ashford et al. 2009, 2010a,b, 2013a,b). Fishery managers and stakeholders have expressed  
87 concern that the effort surveys may underestimate recreational harvest (Fogarty and Lipcius  
88 2007, Miller et al. 2011), although substantial efforts to minimize bias have been undertaken  
89 (Ashford et al. 2009, 2013a,b). We conducted a mark-recapture study to provide an independent  
90 estimate of recreational harvest in Maryland for comparison with effort surveys and evaluated

91 the potential influence of crab movement among harvest areas on estimates of harvest and sector-  
92 specific exploitation rates.

93

#### 94 **Methods**

95 A large-scale mark-recapture study was conducted to study harvest patterns in the blue  
96 crab fishery in Maryland waters of Chesapeake Bay. Detailed below are 1) the tagging methods  
97 and experimental setup for the mark-recapture study, 2) methods used to estimate recreational  
98 harvest and exploitation from the tagging results without taking into account crab movement, and  
99 3) the adjusted equations used to include the influence of crab movement on these estimates.

100 Using mark-recapture data to answer these questions relies on an important set of assumptions;  
101 namely that marked animals 1) are well-mixed within the population, 2) behave in a similar  
102 manner as unmarked individuals, and 3) do not vary in catchability (Schwarz and Taylor 1998).  
103 Evidence from prior studies indicates that crabs tagged using the method described below  
104 undergo full spawning migrations and otherwise behave similarly to unmarked individuals  
105 (Turner et al. 2003, Aguilar et al. 2005) and are healthy and thus unlikely to have reduced  
106 catchability (Turner et al. 2003). Several characteristics of the blue crab fishery in Maryland –  
107 especially the continuous fishery during the time of year when crabs are available for tagging,  
108 the large spatial scale of the study area, and expected strong spatial and temporal variation in  
109 fishing effort – prevented us from meeting the assumption that tagged crabs were well-mixed  
110 within the state-wide population. Instead we estimated spatial and temporal variation directly in  
111 smaller regions and then aggregated estimates up to the state-wide level as detailed below.

112 The primary goal of this mark-recapture experiment was to estimate the level of  
113 recreational harvest by multiplying reported commercial harvests with the ratio of recreational to  
114 commercial harvest determined from reported tag recaptures, as follows:

$$115 \quad H_R = \frac{nR}{nC} * H_C \quad (1)$$

116 where  $H_R$  was the total estimated recreational harvest,  $\frac{nR}{nC}$  was the ratio of the number of  
117 recreational recaptures ( $nR$ ) to commercial recaptures ( $nC$ ) observed from the tagging  
118 experiment, hereafter referred to as the “recapture ratio”, and  $H_C$  and was the total reported  
119 commercial harvest. A similar method is employed in the management of striped bass (*Morone*  
120 *saxatilis*) fishery, whereby commercial discards are estimated based on known recreational  
121 discards, and the ratio of tags reported from discarded fish in the commercial sector to the  
122 recreational sector (NFSC 2019).

123 Because we were unable to ensure that tagged crabs were well-mixed in the population,  
124 we designed the mark-recapture experiment to directly estimate variability in recapture ratio over  
125 the course of the crabbing season (section 2.2) and spatial variability in recapture ratio across  
126 harvest reporting areas (section 2.3). In addition, unequal tag reporting between the two sectors  
127 was accounted for (section 2.1). Finally, the calculation of recapture ratio by harvest area could  
128 have been influenced by crab movement, so the analyses were conducted both with and without  
129 information on crab movement, making it possible to identify the effects of movement on  
130 estimates of harvest and exploitation rates (section 3.1).

131 Although population-level estimates of exploitation can be calculated from the estimate  
132 of total recreational harvest plus commercial harvest and population data from the stock  
133 assessment, our secondary goal was to explore variation in sector-specific exploitation rates

134 among harvest reporting areas. This was calculated by dividing the number of crabs recaptured  
135 by each sector by the number of crabs initially released, as follows:

$$136 \quad u_{Sector} = \frac{RP_{Sector}}{RL} \quad (2)$$

137 where  $u_{Sector}$  was the exploitation rate (proportion of crabs caught per month) of either the  
138 recreational or commercial sector,  $RP_{Sector}$  was the number of tagged crabs that were captured by  
139 that sector, and  $RL$  was the number of tagged crabs initially released. As before, potentially  
140 influential factors were accounted for in these calculations, including: unequal reporting  
141 between the two sectors (section 2.4), various sources of tag loss (section 2.4), and effects of  
142 crab movement (section 3.2).

### 143 ***1. Mark-Recapture Experiments***

144 A total of 6,800 adult male blue crabs were tagged and released to study the blue crab  
145 fishery in Maryland waters of the Chesapeake Bay over two consecutive summers, 2014 and  
146 2015. During the first summer (2014), 2,261 crabs were tagged and released during early  
147 summer (June/July), late summer (August), and fall (September) in four representative harvest  
148 reporting areas to determine seasonal trends in the recapture ratio (Table 2). During the second  
149 summer (June – August 2015), 4,539 crabs were tagged and released in 15 representative harvest  
150 reporting areas to investigate spatial patterns in recapture ratio and sector-specific exploitation  
151 rates (Table 1).

152 Crabs were tagged with 2.5 cm x 5 cm vinyl discs attached to their dorsal surface with  
153 stainless steel wire wrapped around the lateral spines (Turner et al. 2003, Aguilar et al. 2005).  
154 The front of each tag used for this study had a unique identification number, the word “Reward”,  
155 and contact information for reporting recaptures either by phone or web form. Standard rewards

156 were \$5. Five percent of tags were randomly assigned high value tags for estimating reporting  
157 rates. The high value tags had \$50 written in black ink on the front and back. On the reverse side,  
158 all tags listed information for fishers to record and report (tag number, date, GPS coordinates,  
159 capture depth, gear type and crab sex). Within each reporting area, all tagging was conducted on  
160 the same day. Crabs were tagged at given site over the course of day and were released as they  
161 were tagged while drifting across the tributary. This helped disperse crabs across the tagging  
162 area. Although tagged crabs were occasionally recaptured more than once, only the initial  
163 recapture was used in analyses. Some crabs that were released in Maryland were recaptured in  
164 Virginia (n = 44 of 2,039 total returns in 2015). Nearly 90% of crabs recaptured in Virginia were  
165 captured by commercial fishers. While these returns were included in harvest calculations when  
166 movement was not considered, tag returns from these crabs were excluded when making  
167 estimates that accounted for crab movement. We follow the Guide for Care and Use of  
168 Laboratory Animals in our crab tagging protocol.

## 169 ***2. Estimating Recreational Harvest and Exploitation without Animal Movement***

### 170 *2.1 Estimating statewide recreational harvest*

171 The statewide recreational harvest of crabs in 2015 ( $H_R$ ) was estimated using crabs that  
172 were tagged and released in 15 representative harvest reporting areas in 2015 (n = 4,539). Our  
173 multiple harvest area approach was similar to that of the first year of release and year of first  
174 recapture for multi-stratum capture-recapture models of an open population as described in  
175 Brownie et al. (1993) except that we also accounted for two harvest sectors, seasonal variation in  
176 harvest, and tag reporting rates.  $H_R$  was computed by taking the ratio of recreational to  
177 commercial recaptures from the mark-recapture experiment and then multiplying this ratio by the  
178 reported commercial landings:



$$H_R = \sum_{l=1}^{29} \sum_{m=1}^9 \frac{nR_{l,m}}{nC_{l,m}} * H_C_{l,m} \quad (3)$$

179 where  $H_C$  was the total reported commercial harvest of male hard crabs in 2015 in each of the 29  
 180 harvest areas ( $l$ ) for each of the 9 months ( $m$ ) of crab harvest season, and  $nR$  and  $nC$  were the  
 181 number of recreational and commercial recaptures, respectively, estimated from tagging data for  
 182 each area.  $H_C$  values for each area and month were obtained from the Maryland Department of  
 183 Natural Resources (MD DNR 2015a,b). For these calculations, all crab recaptures from a  
 184 particular release, regardless of their eventual recapture area were used (e.g., Fig. 2a).  
 185

186 The number of recreational and commercial recaptures from each release were adjusted  
 187 with sector-specific tag-reporting rates, as follows:

$$\frac{nR_{l,m}}{nC_{l,m}} = \frac{RP_{R,l,m}}{RP_{C,l,m}} * \frac{RR_R}{RR_C} \quad (4)$$

188 where  $nR$  and  $nC$  were the number of recreational and commercial recaptures, estimated from  
 189 tagging data for each area ( $l$ ) and month ( $m$ ),  $RP_{R,l,m}$  and  $RP_{C,l,m}$  were the raw number of  
 190 recaptures for each sector reported by crabbers in the given area and month, and  $RR_R$  and  
 191  $RR_C$  (equation 5) were the tag-reporting rates for recreational and commercial crabbers in 2015.  
 192 A single reporting rate was calculated for each sector in each year. These were calculated across  
 193 all harvest reporting areas, using standard and high-value tags as follows:  
 194  
 195

$$RR_{Sector} = (R_s/N_s) / (R_r/N_r) = R_s N_r / R_r N_s \quad (5)$$

196 where  $RR$  represents the proportion of caught crabs which were reported,  $N_s$  was the number of  
 197 standard tags released,  $N_r$  was the number of high-value tags released,  $R_s$  was the number of  
 198 standard tags returned,  $R_r$  was the number of high-value tags returned, and sector was either  
 199 commercial or recreational (Pollock et al. 2001). These reporting rates were calculated including  
 200

201 both male and female crabs released in 2014 because there were not sufficient crabs recaptured  
202 to determine reporting rates for each crab sex within each fishery sector. Budgetary limitations  
203 on tagging prevented calculation of sector-specific reporting rates for each harvest reporting area  
204 or for each month of the crabbing season. While significant spatial or seasonal variation in tag  
205 reporting could affect the accuracy of these values, a single value was used for each sector to  
206 best focus on differences in reporting between the two sectors.

207 Similarly, it was not feasible within our budget to determine the recapture ratio ( $\frac{nR}{nC}$ ) for  
208 all 29 reporting areas directly through releases of tagged crabs. For areas where tagging was not  
209 conducted ( $n = 14$ ), the ratio of recreational to commercial recaptures for nearby reporting area  
210 was used (Table 1). For example, crabs were not tagged in the Manokin River so the recapture  
211 ratio from the nearby Nanticoke River was used in calculations. Decisions about these data  
212 substitutions were based on our best professional judgement and took into account discussions  
213 with fishery managers, characteristics such as proximity to other sites, and visual comparisons of  
214 the level of residential development in satellite imagery.

## 215 *2.2 Seasonal variation in recapture ratios*

216 Monthly commercial harvest data were available for each reporting area and tagging data  
217 provided reliable estimates of recreational recapture rates for a single month, which allowed  
218 calculation of monthly ratios of recreational to commercial recaptures ( $\frac{nR_{Season}}{nC_{Season}}$ ) across the  
219 harvest season. Recapture data from 2014 and 2015 were used to calculate these monthly  
220 recapture ratios. In 2014, a total of 2,261 crabs were tagged in early summer, late summer, and  
221 fall in four harvest areas representative of the Eastern and Western Shore tributaries of  
222 Maryland's Chesapeake Bay (South River, Rhode River, Eastern Bay, Little Choptank River)

223 (Table 2). In 2015, 1,368 crabs were tagged in these areas (Table 1). Hence, a total of 3,629  
 224 tagged crabs were used to identify monthly variations in recapture ratios.

225 Using releases from both 2014 and 2015, recreational and commercial recaptures from  
 226 the four harvest areas above were summed across these regions for each month. Then  
 227 recreational recaptures for each month ( $m$ ) were divided by commercial recaptures to determine  
 228 a statewide ratio of recreational to commercial harvest for each month:

$$229 \quad \frac{nR_{Season,m}}{nC_{Season,m}} = \frac{\sum_{l=1}^4 RP_{R,l,m}}{\sum_{l=1}^4 RP_{C,l,m}} \quad (6)$$

230 where  $RP_{R,l,m}$  and  $RP_{C,l,m}$  represented the number of tagged crabs reported ( $RP$ ) that were  
 231 captured by recreational crabbers ( $R$ ) or commercial crabbers ( $C$ ) in the given month ( $m$ ) in one  
 232 of the four harvest areas ( $l$ ) where crabs were tagged in both 2014 and 2015.

233 Without tagging in the months of April, May, and November, the recapture ratio for these  
 234 months at the beginning and end of the crabbing season could not be empirically determined.  
 235 Compared to the mid-season peak, the recapture ratios in these months were expected to be quite  
 236 low. Recapture ratios for the months of April, May, and November were assigned values of 0 to  
 237 generate a more conservative estimate of recreational harvest. The sensitivity to this assumption  
 238 was gauged by performing a separate calculation where the recapture ratios were constant during  
 239 these months ( $\frac{nR_{Season}}{nR_{Season}}$  in April = June, May = June, November = October). This second  
 240 calculation served as an upper bound for recapture ratios.

### 241 2.3 Spatial variation in recapture ratios

242 To characterize spatial variation in the ratio of recreational to commercial recaptures,  
 243 records of the 4,539 crabs that were tagged in 15 harvest reporting areas in 2015 were analyzed

244 (Table 1). These releases occurred during the middle of the harvest season (July-September),  
 245 when recreational harvests were expected to be at their peak. The exact date of each tagging  
 246 event was dependent on weather and the availability of commercial fishermen to assist with  
 247 capturing crabs in each of the 15 locations. Recreational and commercial recaptures occurring  
 248 within 60 days of release were tallied. The sixty-day timeframe for recaptures was used because  
 249 it accounted for 98% of recaptures reported by the end of the fishing season.

250 When calculating monthly ratios of recreational to commercial harvest for each reporting  
 251 area in 2015, additional estimates were necessary because tagging occurred only once at each  
 252 site in 2015, either in July, August, or September (Table 1). The ratios of recreational to  
 253 commercial recaptures were estimated for all months of the harvest season with no available data  
 254 using the seasonal relationship developed above (equation 6). To calculate the recapture ratio  
 255 ( $nR_{l,m} / nC_{l,m}$ ) for a given month ( $m$ ) in a specific harvest area ( $l$ ), it was necessary to determine  
 256 how recapture ratios in that month ( $m$ ) compared to those in the month the release occurred ( $o$ ).  
 257 Specifically, we divided the recapture ratio for that month of the seasonal relationship  
 258 ( $\frac{nR_{Season,m}}{nC_{Season,m}}$ ) by the recapture ratio of the seasonal relationship in the month when the release  
 259 occurred ( $\frac{nR_{Season,o}}{nC_{Season,o}}$ ). This was then multiplied by the recapture ratio observed at that site in 2015  
 260 ( $\frac{nR_{2015l,o}}{nC_{2015l,o}}$ ) following the equation:

$$261 \quad \frac{nR_{l,m}}{nC_{l,m}} = \frac{\frac{nR_{Season,m}}{nC_{Season,m}}}{\frac{nR_{Season,o}}{nC_{Season,o}}} * \frac{nR_{2015l,o}}{nC_{2015l,o}} \quad (7)$$

262

263 *2.4. Spatial variation in exploitation*

264 To determine spatial variation in exploitation, exploitation rates for each fishery sector  
 265 were calculated for each of the first two months (standardized as two 30-day periods) after each  
 266 release in each of the harvest areas in 2015. Monthly exploitation rates were calculated by  
 267 comparing the number of crabs that were caught within the month and the number of crabs  
 268 available to be caught at the beginning of the month. All tagged crabs were assumed to be  
 269 available for harvest in the first month. In the second month, a tagged crab was considered to be  
 270 unavailable for recapture if it had died, molted, or otherwise lost its tag.

271 Exploitation (proportion of crabs caught per month) in each area was calculated as  
 272 follows:

$$273 \quad u_{Sector,l,m} = \frac{RP_{Sector,l,m} / RR_{Sector}}{RL_{l,m}} \quad (8)$$

274 where  $RP_{Sector,m}$  was the number of tagged crabs reported as captured by the given sector in the  
 275 first month ( $m = 1$ ),  $RR$  was the reporting rate of tags caught by that sector over the crabbing  
 276 season (equation 5), and  $RL$  was the number of tagged crabs released in each area ( $l$ ) at the  
 277 beginning of the first month. In the second month, crabs were removed from the number of  
 278 released crabs if they were caught in the first month, or were predicted to have died, molted or  
 279 lost their tag during the first month. Exploitation in the second month was calculated as follows:

$$280 \quad u_{Sector,l,m} = \frac{RP_{Sector,l,m} / RR_{Sector}}{(RL_{l,m} - (C_{l,m-1} + M_{l,m-1} + D_{l,m-1} + L_{l,m-1}))} \quad (9)$$

281 where  $RP_{Sector,m,l}$  was the number of tagged crabs reported as captured by the given sector in the  
 282 second month ( $m = 2$ ) in each area ( $l$ ),  $RR_{Sector,l}$  was the reporting rate of tags caught by that  
 283 sector,  $RL_l$  was the number of tagged crabs released in each area ( $l$ ), and  
 284  $C_{m-1,l}$ ,  $M_{m-1,l}$ ,  $D_{m-1,l}$ , and  $L_{m-1,l}$  were the number of tagged crabs caught ( $C$ ) or expected to  
 285 have molted ( $M$ ), died ( $D$ ), or lost their tag ( $L$ ) in the time leading up to month  $m$ .

286 In this analysis, natural mortality was set at a rate of  $0.075 \text{ month}^{-1}$  based on the  
287 instantaneous rate of natural mortality ( $M = 0.9$ ) used in the stock assessment (Miller et al.  
288 2011). The proportion of crabs that had molted prior to the given month was based on a  
289 probabilistic model, using published data on the time to molting for tank-held crabs in degree-  
290 days (Tagatz 1968), as well as average monthly water temperatures for the mainstem Chesapeake  
291 Bay obtained from the Maryland Department of Natural Resources. This resulted in a molting  
292 rate ranging from  $0.107 \text{ month}^{-1}$  (June 18, 2015 release in the Little Choptank River) to  $0.199$   
293  $\text{month}^{-1}$  (July 11, 2015 release in the Patuxent River) which corresponded to 492 and 556 degree-  
294 days passing at these sites, respectively. Physical tag loss was estimated as thirty times the daily  
295 rate of tag loss ( $0.00067 \text{ d}^{-1}$ ), previously estimated from tank-holding studies (Hines,  
296 unpublished data). Given that the number of tagged crabs remaining at large decreased with time,  
297 exploitation calculations for both months were then somewhat conservative. This is due to the  
298 fact that calculations only accounted for recaptures, tag loss, molting or mortality which occurred  
299 prior to each month, ignoring any losses which occurred during the period of calculation.

### 300 ***3. Revised Estimates Accounting for Crab Movement***

#### 301 *3.1 Revised estimates of recreational harvest*

302 Our basic approach for evaluating the effect of movement was to multiply reported  
303 commercial harvest ( $H_C$ ) by two estimates of recapture ratio calculated either with or without  
304 accounting for movement and then comparing the two resulting sets of recreational harvest  
305 estimates. Without crab movement,  $H_R$  was calculated using equations 3-7 above, which were  
306 based on crabs released in each reporting area and recaptured in all areas (Fig. 2a). To  
307 incorporate crab movement,  $H_R$  was calculated for each area based on crabs released in any  
308 reporting area and only those recaptured in the reporting area of interest (Fig. 2b). These

309 methods yield identical results when no movement occurs among reporting areas. Comparing  
 310 their results allowed us to estimate the effect of crabs moving from the release area into a  
 311 different area before recapture on area-specific recapture ratios.

### 312 3.2 Revised estimates of exploitation

313 The influence of movement on exploitation in each harvest area was also evaluated by  
 314 incorporating information about the movements of tagged individuals among harvest reporting  
 315 areas into area-specific exploitation rate calculations. As illustrated above (eqs: 8-9),  
 316 traditionally exploitation rate ( $u$ , proportion of crabs caught per month) is calculated as the  
 317 number of tagged individuals caught and reported ( $RP$ ) divided by the number of tagged  
 318 individuals released and available to be caught ( $RL$ ) in a given amount of time (Ricker 1975).  
 319 Both the catch and availability components of each exploitation rate in each region and each  
 320 month were adjusted to reflect crab movements. Movement-adjusted exploitation in the first  
 321 (equation 10) and second (equation 11) month were calculated as follows:

$$322 \quad u_{Sector,l,m}^* = \frac{RP_{Sector,l,m}^* / RR_{Sector}}{RL_{l,m}^*} \quad (10)$$

$$323 \quad u_{Sector,l,m}^* = \frac{RP_{Sector,l,m}^* / RR_{Sector}}{(RL_{l,m}^* - (C_{m-1,l} + M_{m-1,l} + D_{m-1,l} + L_{m-1,l}))} \quad (11)$$

324 using adapted versions of equations 8 and 9, where  $RP_{Sector,l,m}^*$  indicated the number of tagged  
 325 crabs recaptured from the release during that month, after accounting for crab movement (see  
 326 equation 12), and  $RL_{l,m}^*$  indicated the number of crabs available to be caught during that period  
 327 after accounting for movement (see equation 13).

328 When implementing equations 10 and 11, the number of recaptures ( $RP_{Sector,m,l}^*$ ) was  
 329 adjusted to reflect crab movement during the month by 1) removing crabs that were released in

330 the reporting area and were captured in other reporting areas and 2) adding crabs that were  
 331 released in other reporting areas and were captured in the reporting area (Fig. 2c). This recapture  
 332 adjustment was calculated as follows:

$$333 \quad RP_{Sector,l,m}^* = RP_{Sector,l,m} + \left(\sum_{b=1}^{14} RP_{Sector,b,l}\right) - \left(\sum_{c=1}^{28} RP_{Sector,l,c}\right) \quad (12)$$

334 Where  $RP_{Sector,l,m}$  was the total number of recaptures in the reporting area ( $l$ ) and month ( $m$ ) and  
 335 the first sum represented the number of crabs released at each of the 14 other release areas and  
 336 were caught in the given reporting area during the given month (moving from any of the 14 other  
 337 reporting areas where crabs were released ( $b$ ) to the given reporting area ( $l$ )). The second sum  
 338 indicated the number of crabs released within the given reporting area which were captured  
 339 within each of the 28 other harvest reporting area during the given month (moving from the  
 340 given reporting area ( $l$ ) to any of the 28 other reporting areas used in this study ( $c$ )).

341 The number of crabs that were available to be caught within the harvest reporting area in  
 342 a given month was adjusted with conditional probabilities of crab movement, in two steps: First,  
 343 the total number of tagged crabs predicted to have left the reporting area were subtracted off.  
 344 Then the total number of tagged crabs predicted to arrive in the harvest reporting area from other  
 345 areas was added in (Fig. 2c). The availability adjustment was calculated as follows:

$$346 \quad RL_{l,m}^* = RL_{l,m} + \left(\sum_{b=1}^{14} RL_{b,m} * P_{b,l}\right) - \left(\sum_{c=1}^{28} RL_{l,m} * P_{l,c}\right) \quad (13)$$

347 where  $RL_{l,m}$  was the total number of available crabs in the reporting area ( $l$ ) and month  
 348 ( $m$ ) and the first sum was the predicted number of tagged crabs moving into the given reporting  
 349 area during the given month from the 14 other release areas. This sum was a function of the  
 350 crabs available in the given month ( $m$ ) at each of the 14 sites ( $b$ ) where crabs were released  
 351 ( $RL_{b,m}$ ) and the proportion of crabs ( $P_{b,l}$ ) at each of those sites which moved to the given



352 reporting area ( $l$ ). The second sum indicated the number of crabs predicted to move from the  
353 given reporting area to each of the 28 other harvest reporting areas in the given month. The  
354 second sum was a function of the crabs available in the given month ( $m$ ) at the given reporting  
355 area ( $l$ ) ( $RL_{l,m}$ ) and the proportion of crabs ( $P_{l,c}$ ) in the given reporting area ( $l$ ) which moved to  
356 each of the 28 other harvest reporting areas ( $c$ ). It was assumed that the proportion of tagged  
357 crabs moving out of each harvest reporting area was equivalent to the proportion of tagged crabs  
358 caught within or outside the release location. We also gauged the reliability of movement  
359 probabilities by evaluating their consistency between years. To assess this, we compared  
360 movement probability matrices for the four reporting areas which were tagged in both 2014 and  
361 2015 and calculated the overall level of correlation between them.

## 362 **Results**

### 363 *Tag return rates*

364 Of the 6,800 tagged crabs released in 2014 and 2015, a total of 1,891 tags were returned  
365 (Tables 2 and 3) for an overall return rate of 27.8%. This rate is higher than prior studies on  
366 female blue crabs (Aguilar et al. 2005 (4-17%), Turner et al. 2003 (5-21%), Rittschof et al. 2011  
367 (15.6%). This can be expected because males are the primary target of the fishery. A similar  
368 return rate for tagged female crabs (8.6%) was seen from a separate but concurrent study  
369 performed by our lab, with an overall exploitation rate of 10.5% (Corrick 2018).

370 When examining seasonal variations in recapture ratios, the analysis included 1,211  
371 recaptures from 3,629 crabs which were tagged during 16 releases (12 releases in 2014 and 4  
372 releases in 2015) (Table 2). Of the 2,261 male crabs released in 2014, 728 (32.2%) were  
373 recaptured and reported (Table 2). Of these, 527 (72.4%) were captured by commercial crabbers,

374 195 (26.8%) by recreational crabbers, and 5 (0.7%) by unidentified crabbers. Of the 3,085 \$5  
375 tags (male and female) released in 2014, 786 (25.5%) were recaptured. Of the 163 \$50 tags  
376 released, 47 (28.8%) were recaptured. This resulted in an overall reporting rate of 88.4% across  
377 the fishery in 2014 with sector-specific reporting rates of 93.3% and 75.1% for the commercial  
378 fishery and recreational fisheries, respectively. Area-specific reporting rates in 2014 ranged from  
379 80.2% in South River to 98.5% in Eastern Bay. Of the additional 1,368 male crabs released in  
380 the 4 reporting areas in 2015, 483 (35.3%) were recaptured and reported (Table 1). Of these, 360  
381 (74.5%) were captured by commercial crabbers, 110 (22.7%) by recreational crabbers and 13  
382 (2.7%) by unidentified crabbers.

383       When examining spatial variations in recapture ratios in 2015, the analysis included  
384 1,163 recaptures (25.6%) from the 4,539 male crabs tagged and released during all 15 releases in  
385 2015 (Table 1, Fig. 3). Of these, 897 (77.1%) were captured by commercial crabbers, 235  
386 (20.2%) by recreational crabbers, and 31 (2.7%) by unidentified crabbers. Of the 5,244 \$5 tags  
387 (male and female) released in 2015, 1,159 (22.1%) were recaptured. Of the 276 \$50 tags  
388 released, 84 (30.4%) were recaptured. This resulted in an overall reporting rate of 72.6% across  
389 the fishery. Sector-specific reporting rates in 2015 were 67.2% for the commercial fishery and  
390 85.3% for the recreational fishery. There were insufficient recaptures in individual harvest  
391 reporting areas to produce reliable area-specific reporting rates. Of the 1,147 male crabs released  
392 in 2015 that were recaptured and reported with sufficient spatial information, 220 (19.2%) were  
393 recaptured in a different reporting area from where they were released. Of these, 157 (71.4%)  
394 were crabs that moved from tributaries into the mainstem Bay.

395       There was notable consistency in recapture and reporting of crabs between the two years  
396 of the analysis. The overall reporting rate of across the fishery was 88.4% and 72.6% in 2015. In

397 2014 the reporting rate for male crabs was 93.0%. When all crabs (male and female) were  
398 included that number decreased slightly to 88.4%. In 2015, the reporting rate for males was  
399 (71.5%), however, when all crabs (male and female) were included this increased slightly to  
400 (72.6%).

#### 401 *Seasonal variation in recapture ratios*

402 The ratio of recreational to commercial recaptures ( $\frac{nR}{nC}$ ) exhibited a domed relationship  
403 over time, increasing during June and July to a similar high values in August (0.50) and  
404 September (0.52) followed by a sharp drop in October (Fig. 4a).

405 This seasonal trend in recapture ratio likely stemmed from a strong seasonal trend in  
406 recreational fishing effort. It should be noted that commercial harvests showed a domed  
407 relationship, with a peak in July/August (MD DNR 2015). If the seasonal variation in  
408 recreational effort was proportional to that of commercial effort, there would have been little  
409 change in recapture ratios across the harvest season. Because the recapture ratios showed a  
410 seasonal trend on top of changing commercial harvest, the seasonality of recreational effort was  
411 likely much greater than that of commercial effort.

#### 412 *Spatial variation in recapture ratios*

413 There were spatial variations in the ratio of recreational to commercial recaptures in  
414 2015, with the highest values on Maryland's Western Shore and middle Eastern Shore (Fig. 4b)  
415 indicating higher proportions of recaptures in those regions. When animal movement was  
416 included in the calculations, there were substantial changes in the recapture ratios (Table 4),  
417 especially in the regions with high recreational recaptures.

#### 418 *Estimates of recreational harvest*

419 Statewide recreational crab harvest in 2015 was estimated to be 4.04 million crabs  
420 without crab movements and 5.39 million crabs when accounting for crab movement (Table 3).  
421 These levels of harvest were 4.9% or 6.5% of total commercial crab harvests (all male and  
422 female harvests), or 8.4% or 11.2% of male hard crab harvests, when crab movement was not, or  
423 was, included (higher values included movement information). When movement was included,  
424 the estimate of Maryland-wide recreational harvest increased by 33.5%. These harvest values  
425 were computed with recapture ratios equal to zero for the months of April, May, and November.  
426 When using constant values instead of zero (i.e., the value for April and May = June, and  
427 November = October), recreational harvest calculated with movement was 5.46 million crabs  
428 (11.3% of male hard crab harvests), a value very similar to the estimate when ratios in these  
429 months were set to zero.

430 Estimated recreational harvest of crabs varied substantially across the different harvest  
431 reporting areas, with most landings occurring in tributaries (Fig. 5c). In particular, incorporating  
432 data on movement increased the estimate of recreational harvest in tributaries (Fig. 5d) because  
433 many crabs moved from tributaries that had greater recreational harvest to mainstem bay areas  
434 that had almost exclusively commercial harvest. Using data that accounted for movement,  
435 recreational harvest estimates ranged from 0 crabs in Fishing Bay and the Honga River to 1.91  
436 million crabs in the Patuxent River (Fig. 5c). The spatial pattern was substantially different from  
437 reported commercial harvest (Fig. 5b), which was characterized by high harvests in the Choptank  
438 River and the mainstem bay. Tributaries with high recreational landings included the Patuxent  
439 (1.91 million crabs), Severn (0.52 million crabs), and Miles rivers (0.40 million crabs).

#### 440 *Spatial variation in exploitation*

441 There were marked differences in recreational and commercial exploitation rates among

442 the 15 harvest reporting areas in which crabs were tagged (Table 5). The most noticeable  
443 differences were observed between sites in tributaries along the Western Shore of the Bay,  
444 Eastern Bay, and the Miles and Wye rivers, where recreational fishing was greatest, and areas of  
445 the Bay Mainstem, where recreational harvest was negligible. Mean commercial exploitation per  
446 month (calculated using movement information) ranged from 0.04 month<sup>-1</sup> in the Patuxent River  
447 to 0.48 month<sup>-1</sup> in the Wicomico River tributary of the Potomac River. Notably high rates of  
448 commercial exploitation were observed in the Wicomico River (0.48 month<sup>-1</sup>), Magothy River  
449 (0.34 month<sup>-1</sup>), and West River (0.29 month<sup>-1</sup>). Mean recreational exploitation per month ranged  
450 from 0 month<sup>-1</sup> in both the Honga River and Fishing Bay to 0.34 month<sup>-1</sup> in the Magothy River.  
451 Notably high rates of recreational exploitation were observed in the Magothy River and in South  
452 River (0.288 month<sup>-1</sup>).

453 Accounting for movement resulted in substantial differences in sector-specific  
454 exploitation rates. Estimates of commercial exploitation increased by 37.0% in the Magothy  
455 River and by 246.4% in the Bay Mainstem S region after movements were considered (Fig. 6a).  
456 For the Magothy River, this increase was a result of decreases in the number of crabs available to  
457 be caught, because many left the area. In the case of the Bay Mainstem S, however, the large  
458 increase in commercial exploitation was due to a large number of crabs leaving other areas and  
459 subsequently being caught by commercial fishers in the Bay Mainstem S. Commercial  
460 exploitation decreased by 30.0% in the South River and by 36.5% in the West River because of  
461 the large number of crabs from these releases that were caught by commercial fishers in the Bay  
462 Mainstem (Fig. 6a). Recreational exploitation rates increased by 283.4% in the Magothy River,  
463 by 48.3% in the South River, and by 186.5% in the Severn River due to reductions in the number  
464 of crabs available to be caught in these systems (Fig. 6b). These differences are underpinned by a

465 great degree of consistency in movement probabilities between years. For the four sites tagged in  
466 both 2014 and 2015, there was a strong degree of correlation in movement probabilities between  
467 years ( $r = 0.99$ ,  $t = 36.72$ ,  $p < 0.01$ ).

468

## 469 **Discussion**

470 The movement of tagged individuals strongly influenced the results of a mark-recapture  
471 study of the blue crab fishery in Maryland waters of the Chesapeake Bay. Tag return data  
472 revealed strong variation in the ratio of recreational to commercial recaptures among adjacent  
473 harvest reporting areas that set the stage for movement to influence estimates of area-specific  
474 recreational harvest and exploitation. In the most extreme case (Severn River), a crab could  
475 move from an area where it is 2.5 times more likely to be caught by a recreational fisher than a  
476 commercial fisher, to one with 100% commercial harvest, by moving only a few km. Adult blue  
477 crabs are easily capable of traveling this distance in a few days (Souza et al. 1980, Wolcott and  
478 Hines 1990) and commercial fishing effort is concentrated at tributary mouths to intercept crabs  
479 moving out of shallow nursery habitats (Slacum et al. 2012). Overall, the resulting estimate of  
480 statewide recreational harvest was 34% higher when movement was taken into account  
481 compared to the estimated based on the release location of tagged crabs only. The results of this  
482 study highlight the importance of incorporating movement into mark-recapture studies focused  
483 on exploring spatial variation in exploitation among harvest areas when the target species  
484 commonly moves among them.

485 Although mark-recapture studies are often used to address fishery management questions  
486 at the population level when the effect of individual movements may be negligible, there are a  
487 few examples that incorporate movement data into calculations of exploitation rates. In a study

488 of snapper, site-by-site estimates of density and exploitation were used to standardize movement  
489 patterns of snapper that were determined from recapture locations in New Zealand (Parsons et al.  
490 2011). The method used by Parsons et al. (2011) is in some sense the inverse of the technique  
491 employed in the present study. In other examples, exploitation calculations are conducted for  
492 each release area but did not account for movement between release areas (e.g. Rudd et al. 2014,  
493 Whitlock et al. 2016). Analyses of waterfowl data provide examples for incorporating  
494 information on movement among multiple harvest areas into harvest and exploitation rate  
495 calculations (Munro and Kimball 1982, Nichols et al 1995). Our methods expand on this to  
496 incorporate within-year temporal variation and multiple harvest sectors which was needed to  
497 estimate recreational harvest based on reported commercial harvest.

498         The present study represents the first quantitative, statewide assessment of recreational  
499 exploitation and harvest for a blue crab fishery using mark-recapture information. Recreational  
500 harvest was highest in tributaries near population centers along Maryland's Western Shore, and  
501 in the Miles and Wye Rivers on the Eastern Shore. These areas also had some of the highest  
502 recreational and total exploitation rates. The extremely high total exploitation rates in the  
503 Patuxent (0.71) and Magothy (0.68) rivers indicate that total exploitation was high enough in  
504 some tributaries to remove the majority of male crabs large enough to recruit to the fishery each  
505 month. If these removals substantially reduce the operational sex ratio (the ratio of mature males  
506 to reproductively active females), they could potentially lead to sperm limitation (the reduction  
507 in lifetime reproductive output) of females maturing in these locations (Ogburn et al. 2014,  
508 2019). In contrast, recreational exploitation made up a smaller proportion of total exploitation,  
509 and recreational harvest was smaller, at sites along the southern portion of the Eastern Shore and  
510 in the mainstem bay.

511 One reason for the difference in commercial reporting rate between 2014 and 2015 could  
512 be the effect of prior crab tagging efforts by our lab (Turner et al. 2003, Aguilar et al. 2005,  
513 Corrick 2018). We have a good working relationship with a number of crabbers in the areas  
514 tagged in 2014 (Eastern Bay, Little Choptank River, Rhode River, South River) but have not had  
515 as much outreach within other areas of the Bay tagged less frequently. This could have led to  
516 greater reporting in 2014 when tagging was concentrated in these areas. However, the 2015  
517 commercial reporting rate is more accurate on a bay-wide scale because of the broader spatial  
518 distribution of tagging, and these data were used in harvest ratio calculations herein.  
519 Investigating possible spatial variations in reporting would be particularly valuable if this type of  
520 mark recapture study were used on a regular basis to inform stock assessments. While there also  
521 were slight differences in reporting rates among sex (males vs males and females), the direction  
522 of this difference changed by year and could reflect variations in high-value captures, gear types,  
523 and effort between years.

524 Information on the size of the recreational blue crab harvest in Maryland has regularly  
525 been identified as a critical management need. Prior studies in 2001, 2002, 2005, and 2009 using  
526 effort survey methods (Ashford and Jones 2002a, 2002b, 2005, 2011) estimated that the ratio of  
527 recreational to commercial harvest within Maryland remained close to the 8% estimate chosen in  
528 the stock assessment. Estimates of recreational harvest from effort surveys averaged 11.6% of  
529 commercial male hard crab harvests and 5.8% of total commercial harvests. In the present study,  
530 recreational harvest of male hard crabs in 2015 was estimated at 11.2% the size of commercial  
531 male hard crab harvests and 6.5% of total commercial harvests (male and female) when  
532 movement was included. Although comparison of effort surveys and a Maryland-wide mark-  
533 recapture experiment conducted in the same year would be preferable, the similarity between



534 recreational harvest fraction estimates suggests that the methods proposed herein are consistent  
535 with effort surveys.

536         With data for only a single statewide recreational harvest estimate, it is difficult to  
537 quantify uncertainty, but the sensitivity of the estimate to potential sources of uncertainty can be  
538 discussed (Semmler 2016). In terms of uncertainty related to underreporting, the underreporting  
539 of high value tags by the commercial sector would increase the estimated recreational harvest an  
540 equivalent amount (e.g. 5% underreporting would yield a 5% increase in the recreational harvest  
541 estimate). In addition, underreporting of regular value tags by the commercial sector would also  
542 inflate recreational harvest estimates, with the magnitude of the increase depending on whether  
543 underreporting occurred in areas with only commercial recaptures (no effect), a high fraction of  
544 commercial recaptures (minimal effect), or a relatively high fraction of recreational recaptures  
545 (larger effect). The regions where commercial underreporting could have occurred were in areas  
546 with only commercial recaptures, so underreporting would not have substantially inflated the  
547 estimate of recreational harvest.

548         Other sources of uncertainty include the focus on a single year and the lack of tagging  
549 data during the first and last months of the harvest season within that year. Between years, when  
550 replacing the 2015 commercial harvest data with the previous 5 years of data, the ratios of  
551 recreational to total commercial harvest were 10.4% – 13.1% (11.2 % in 2015), suggesting that  
552 our estimate was not very sensitive to annual variation in commercial harvest. Within 2015,  
553 setting the recapture ratios in April, May, and November to the June and October values instead  
554 of assuming a value of 0 increased the percent of recreational harvest from 11.2% to 11.3%,  
555 suggesting that recreational harvest in these months was negligible. Repeating the mark-

556 recapture study in one or more years in combination with effort surveys or recreational harvest  
557 reporting would help assess the validity of this approach.

558         Additionally, uncertainty in conditional movement probabilities themselves are important  
559 to consider. While we do not have a means of assessing error in these estimates, consistency in  
560 movement probabilities between years may serve as some indication of their reliability. To  
561 assess this, we compare movement probabilities matrices for the four reporting areas which were  
562 tagged in both 2014 and 2015. There was a strong degree of correlation between the movement  
563 probabilities ( $r = 0.99$ ,  $t = 36.72$ ,  $p < 0.01$ ), supporting the expectation that the probabilities were  
564 reliably determined.

565         Our method of calculating recreational harvest based on commercial harvest assumes that  
566 the level of commercial harvest is reliably known. Commercial crabbers in Maryland are  
567 required to report their daily harvest under penalty of license suspension/revocation and the state  
568 has an electronic reporting system coupled with a check point program to evaluate compliance  
569 with reporting, although we do not know the degree of compliance in 2014 and 2015. While  
570 these measures help ensure reliable harvest estimates, an analysis of the possibility of random  
571 error and potential differences in harvest reporting across the state would further strengthen  
572 confidence in this method of calculating recreational harvest estimates.

573         The proportion of recreational to total commercial harvest (8%) used in the stock  
574 assessment was set prior to the moratorium on recreational harvest of female crabs in Maryland  
575 in 2008 (Miller et al. 2011). However, after 2008, recreational harvest was thought to be better  
576 calculated as 8.0% of male harvests (CBSAC 2016). While recreational harvest could have been  
577 8.0% of male harvests in 2011, our estimated harvest in 2015 equates to 11.2% of male harvests,  
578 representing a 40% increase over the 8% guideline. It's unclear whether this increase resulted

579 from the shifting of recreational fishing effort from female onto male crabs, or simply from  
580 increased recreational fishing effort targeting male crabs.

581         The estimated contribution of the recreational fishery to total harvest in this study was at  
582 the lower end of recreational harvest fractions for temperate or subtropical crab fisheries and is  
583 comparable to other blue crab fisheries within the US. In Maryland, recreational crabbers take  
584 roughly 6.5% percent of the commercial harvest of male and female blue crabs. In Louisiana,  
585 which has the second largest commercial blue crab fishery by state in the US, recreational  
586 crabbers take in roughly 5% of all blue crabs (Guillory 1999b, LDWF 2011). Similar results  
587 were observed for recreational blue crab fishers in Galveston Bay, Texas (5.6% of harvest)  
588 (TPW 2007). In Oregon, 5.6% of landings in the Dungeness crab *Metacarcinus magister* fishery  
589 are taken by recreational crabbers (ODFW 2014). In contrast, some crab fisheries have a much  
590 higher proportion of recreational harvest including the mud crab *Scylla serrata* fishery in  
591 Queensland, Australia (~50% recreational harvest) (Ryan 2003), the Dungeness crab fishery in  
592 Washington (41% of harvest) (WDFW 2016) and the blue swimming crab *Portunus pelagicus*  
593 fishery in South Australia (29.8% of harvest) (Jones 2009). Other crab fisheries, such as those for  
594 Atlantic Jonah crabs *Cancer borealis* and California Dungeness crabs, do not have sufficiently  
595 reliable recreational harvest data to make similar comparisons (ASMFC 2015, CA OPC 2014).  
596 Understanding the contribution of recreational fisheries to total harvests, estimated at 12%  
597 globally, is a critical issue in conservation of fishery resources (Cooke and Cowx 2004). The  
598 methods used here could be applied to blue crab fisheries in other regions or used as a model for  
599 crab fisheries for which recreational harvest estimates are needed and commercial harvests are  
600 known.

601           The present study illustrates clear influence of animal movement when mark-recapture  
602 methods are used to estimate harvest and exploitation rates for multiple harvest areas. Results of  
603 the study reduce uncertainty in recreational harvest estimates by complementing results of effort  
604 surveys and could be useful for refining stock assessments of the blue crab fishery in Chesapeake  
605 Bay. In addition, these new methods for including animal movement could be useful for other  
606 fisheries for which variation in sector-specific harvest or exploitation rates among harvest areas  
607 is of interest and the scale of movement of the target species exceeds that of harvest area  
608 boundaries. These methods were applied to a two-sector fishery, but could be modified for one to  
609 several fishery sectors for blue crabs in other regions or for other species and fisheries with  
610 similar characteristics.

611

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Table 1. Harvest reporting areas and unique site codes in Maryland for which the ratio of recreational to commercial blue crab *Callinectes sapidus* captures was assessed. Site codes preceded by a M or T represent reporting areas which were split into portions spanning the bay mainstem (M) and adjacent tributaries (T). All male crabs were released on the date listed (see Fig. 1 for map), as is the number of crabs recaptured within the end of the 2015 crabbing season. Tagging was not possible in all areas. For areas where tagging was not conducted (bold type), data from a similar area was used to estimate results. Finally, the recapture ratio is listed, scaled to the late-summer peak (August).

Site Code	Site	Date	Released	Recaptured	Estimated As	Peak Recapture Ratio (August)
<b>005</b>	<b>Big Ammenesex</b>	----	----	----	<b>Nanticoke River</b>	<b>0.046</b>
<b>M014</b>	<b>Mainstem NN</b>	----	----	----	<b>Mainstem N</b>	<b>0.009</b>
<b>T014</b>	<b>Tribs NN</b>	----	----	----	<b>Magothy River</b>	<b>0.703</b>
M025	Mainstem N	8/05/2015	385	52	----	0.009
<b>T025</b>	<b>Tribs N</b>	7/21/2015	----	----	<b>Magothy River</b>	<b>0.703</b>
M027	Mainstem S	7/31/2015	357	23	----	0.007
T027	Tribs S		387	187	----	0.304
<b>M029</b>	<b>Mainstem SS</b>	----	----	----	<b>Mainstem S</b>	<b>0.007</b>
<b>T029</b>	<b>Tribs SS</b>	----	----	----	<b>Patuxent River</b>	<b>1.273</b>
<b>031</b>	<b>Chester River</b>	----	----	----	<b>Eastern Bay</b>	<b>0.310</b>
037	Choptank River	7/30/2015	343	91	----	0.269
039	Eastern Bay	7/17/2015	381	80	----	0.310
043	Fishing Bay	6/25/2015	220	22	----	0.000
047	Honga River	6/19/2015	277	32	----	0.000
053	Little Choptank River	6/18/2015	259	56	----	0.046
055	Magothy River	7/29/2015	350	123	----	0.703
<b>057</b>	<b>Manokin River</b>	----	----	----	<b>Nanticoke River</b>	<b>0.046</b>
060	Miles River	8/04/2015	181	46	----	0.670
062	Nanticoke River	8/25/2015	376	80	----	0.042
<b>066</b>	<b>Patapsco River</b>	----	----	----	<b>Magothy River</b>	<b>0.703</b>
068	Patuxent River	7/15/2015	182	21	----	1.273
<b>072</b>	<b>Pocomoke Sound</b>	----	----	----	<b>Nanticoke River</b>	<b>0.046</b>
074	Potomac (MD Tribs)	7/20/2015	305	150	----	0.239
082	Severn River	8/10/2015	195	40	----	2.363
088	South River	7/22/2015	341	160	----	0.471
<b>M092</b>	<b>Tangier Sound</b>	----	----	----	<b>Nanticoke River</b>	<b>0.046</b>
<b>T092</b>	<b>Tangier Sound Tribs</b>	----	----	----	<b>Nanticoke River</b>	<b>0.046</b>
<b>096</b>	<b>Wicomico River</b>	----	----	----	<b>Nanticoke River</b>	<b>0.046</b>
<b>099</b>	<b>Wye River</b>	----	----	----	<b>Miles River</b>	<b>0.670</b>
<b>Total</b>			<b>4,539</b>	<b>1,163</b>		

Table 2. The number of male blue crabs *Callinectes sapidus* which were released and recaptured in 2014 to evaluate seasonal patterns in the fishery. Releases occurred during early (June/July), middle (August), and late (September) periods of the fishing season on the date indicated. The number of crabs recaptured by the end of the 2014 fishing season is also reported. The small crab population in 2014 resulted in low numbers tagged in some seasons.

<b>Site</b>	<b>Release</b>	<b>Date</b>	<b>Released</b>	<b>Recaptured</b>
South River	Early	7/14/2014	102	54
South River	Middle	8/11/2014	233	126
South River	Late	9/10/2014	108	14
Rhode River	Early	6/24/2014	53	22
Rhode River	Middle	8/4/2014	333	201
Rhode River	Late	9/8/2014	135	38
Eastern Bay	Early	6/23/2014	61	16
Eastern Bay	Middle	8/13/2014	343	123
Eastern Bay	Late	9/16/2014	185	31
Little Choptank River	Early	7/16/2014	338	66
Little Choptank River	Middle	8/6/2014	312	35
Little Choptank River	Late	9/17/2014	58	2
<b>Total</b>			<b>2,261</b>	<b>728</b>

Table 3. Estimates of recreational harvest of blue crabs *Callinectes sapidus* calculated based on release location (standard method) or recapture location (movement-adjusted method). Data reported include estimated size of the recreational harvest, recreational catch as a percentage of commercial male hard crab harvest, and recreational catch as a percentage of total commercial harvest of male and female crabs.

	<b>Standard Method</b>	<b>Movement Adjusted</b>
Total recreational harvest (million crabs)	4.04	5.39
Percent recreational harvest of male commercial harvest	8.36%	11.17%
Percent recreational harvest of total commercial harvest	4.88%	6.52%

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Table 4. Recapture ratio ( $nR/nC$ ) and overall recreational harvest (in thousands) for blue crabs *Callinectes sapidus* in the 15 harvest reporting areas where tagging was conducted. These are reported with and without movement-adjustment. Site codes preceded by a M or T, represent reporting areas which were split into portions spanning the bay mainstem (M) and adjacent tributaries (T)

Reporting Area	Site Code	Recapture Ratio		Recreational Harvest	
		No Movement	Movement-Adjusted	No Movement	Movement-Adjusted
Choptank River	037	0.04	0.03	244.99	177.48
Eastern Bay	039	0.29	0.31	248.14	262.39
Fishing Bay	043	0.00	0.00	0.00	0.00
Honga River	047	0.00	0.00	0.00	0.00
Little Choptank River	053	0.01	0.03	19.37	42.27
Magothy River	055	0.30	0.70	24.27	56.66
Mainstem N	M025	0.03	0.01	97.80	27.23
Mainstem S	M027	0.08	0.01	314.85	28.36
Miles River	068	0.43	0.67	259.10	399.17
Nanticoke River	062	0.04	0.05	17.55	18.58
Patuxent River	068	0.48	0.79	1169.24	1913.30
Severn River	082	0.64	2.36	143.01	524.38
South River	088	0.37	0.47	94.56	118.78
Tribs S	T027	0.20	0.30	214.58	333.68
Wicomico River (Potomac)	074	0.20	0.24	181.33	215.28

Table 5. Estimated monthly exploitation rate (month<sup>-1</sup>) for blue crabs *Callinectes sapidus* in the 15 harvest reporting areas where tagging was conducted. Commercial, recreational and total exploitation rates were calculated after accounting for crab movement among harvest reporting areas. Site codes preceded by a M or T, represent reporting areas which were split into portions spanning the bay mainstem (M) and adjacent tributaries (T)

<b>Reporting Area</b>	<b>Site Code</b>	<b>Commercial</b>	<b>Recreational</b>	<b>Total</b>
Choptank River	037	0.221	0.005	0.226
Eastern Bay	039	0.161	0.037	0.198
Fishing Bay	043	0.076	0.000	0.076
Honga River	047	0.093	0.000	0.093
Little Choptank River	053	0.152	0.020	0.172
Magothy River	055	0.338	0.338	0.675
Mainstem N	M025	0.160	0.001	0.161
Mainstem S	M027	0.172	0.003	0.175
Miles River	068	0.140	0.126	0.266
Nanticoke River	062	0.146	0.006	0.153
Patuxent River	068	0.041	0.039	0.080
Severn River	082	0.100	0.213	0.313
South River	088	0.205	0.288	0.492
Tribs S	T027	0.292	0.065	0.357
Wicomico River (Potomac)	074	0.479	0.226	0.705

Figure 1. Boundaries of the 29 commercial harvest reporting areas in Maryland waters of the Chesapeake Bay. Three-digit numerical designations assigned for reporting data (i.e., site codes) for each reporting area are shown within or adjacent to their boundaries. Site codes preceded by a M or T, represent reporting areas which were split into portions spanning the bay mainstem (M) and adjacent tributaries (T). Note that reporting area names are listed in Table 1.

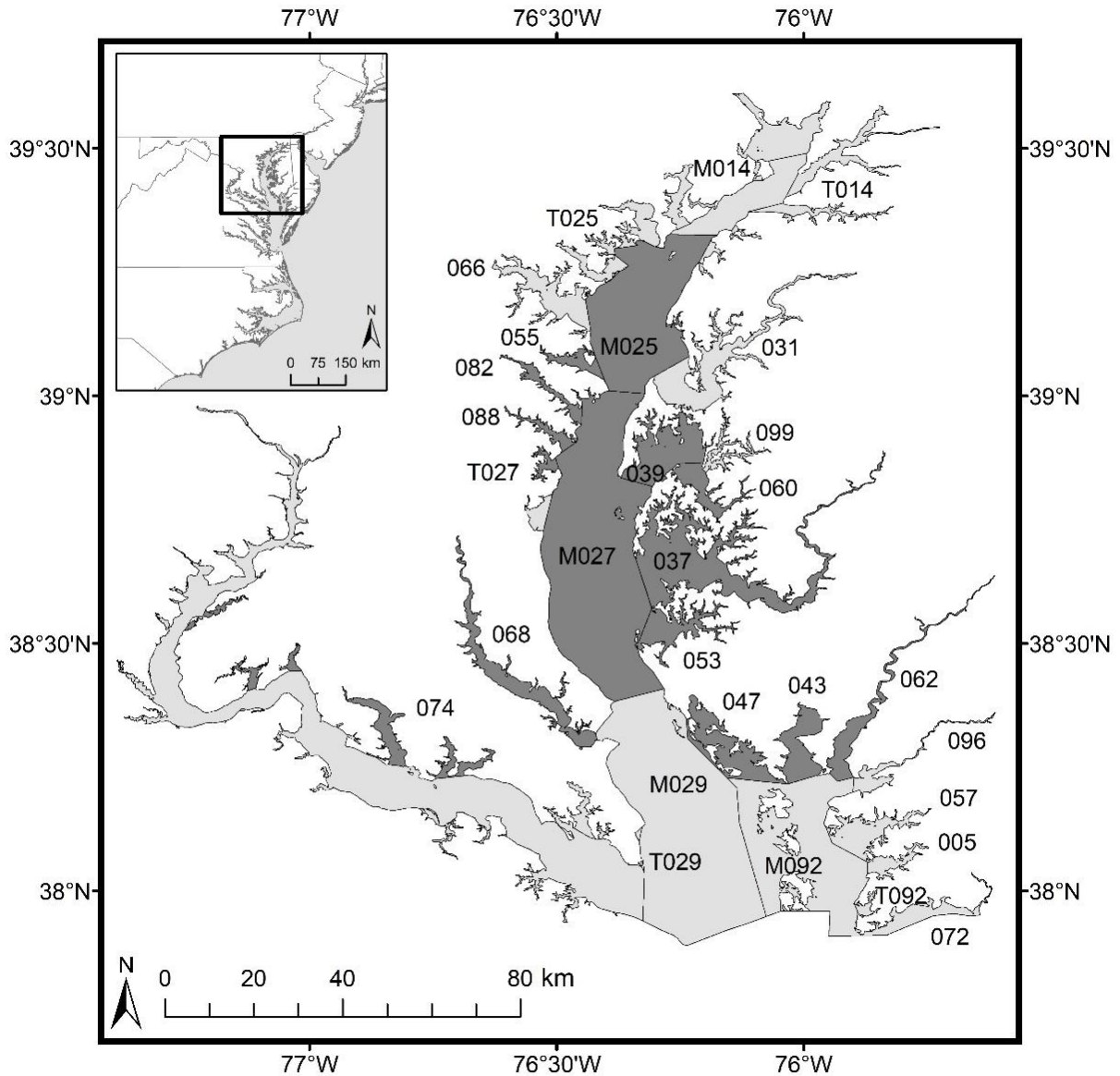


Figure 2. Example illustrating two types of recapture data that were used to calculate recreational harvest and sector-specific exploitation of blue crabs *Callinectes sapidus* for the Magothy River, Maryland: a) data used for calculation based on crabs released in the Magothy and recaptured anywhere in Maryland's reporting areas, and b) data used for calculation based on crabs released anywhere in Maryland's reporting areas and recaptured in the Magothy River. Also pictured c) are arrows that depict the movement of crabs into or out of the harvest area with the arrow weight indicating the relative magnitude of animal movement. These subsidies were used to adjust local exploitation rates in the analysis that included movement.

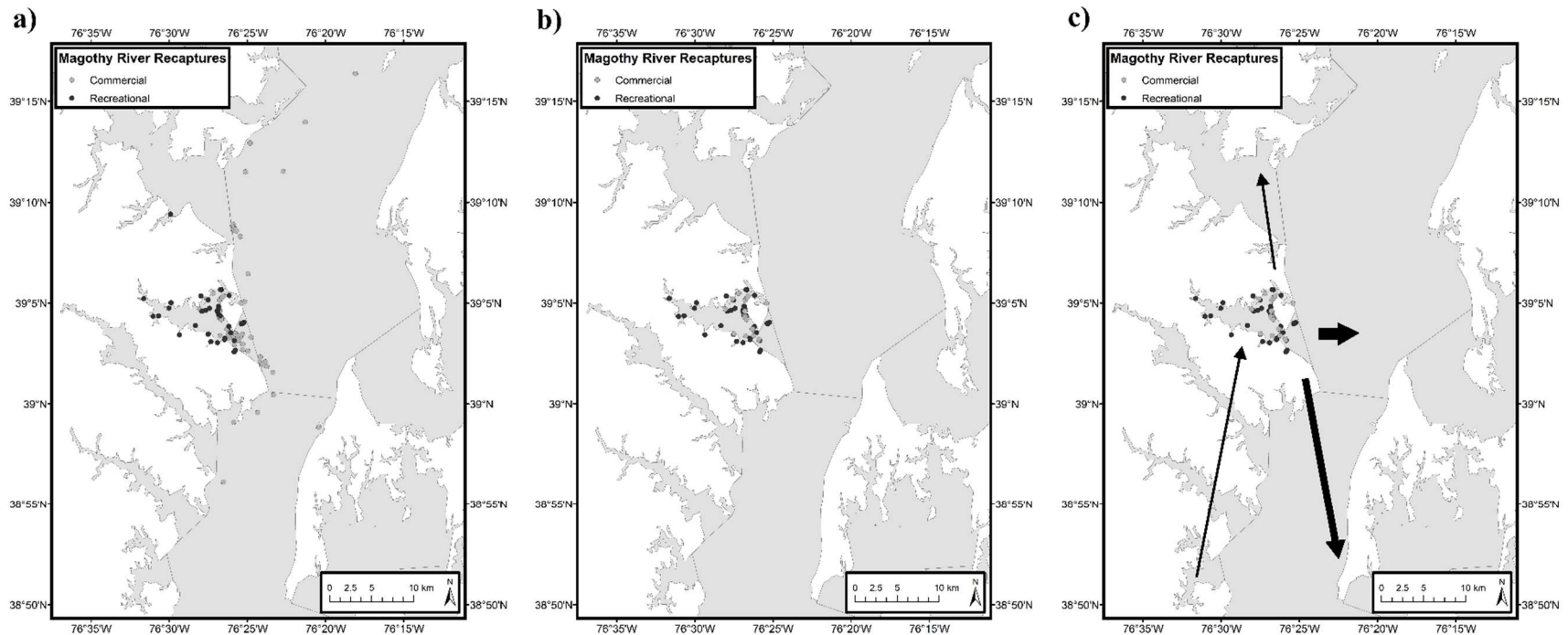


Figure 3. Release and recapture locations for blue crabs *Callinectes sapidus* tagged in 2015 to evaluate spatial patterns. White dots with Xs represent the 15 sites where crabs were tagged and released. a) Crabs caught by recreational crabbers (dark gray, N = 230). b) Crabs caught by commercial crabbers (light gray, N = 883). Many recapture locations are overlapping.

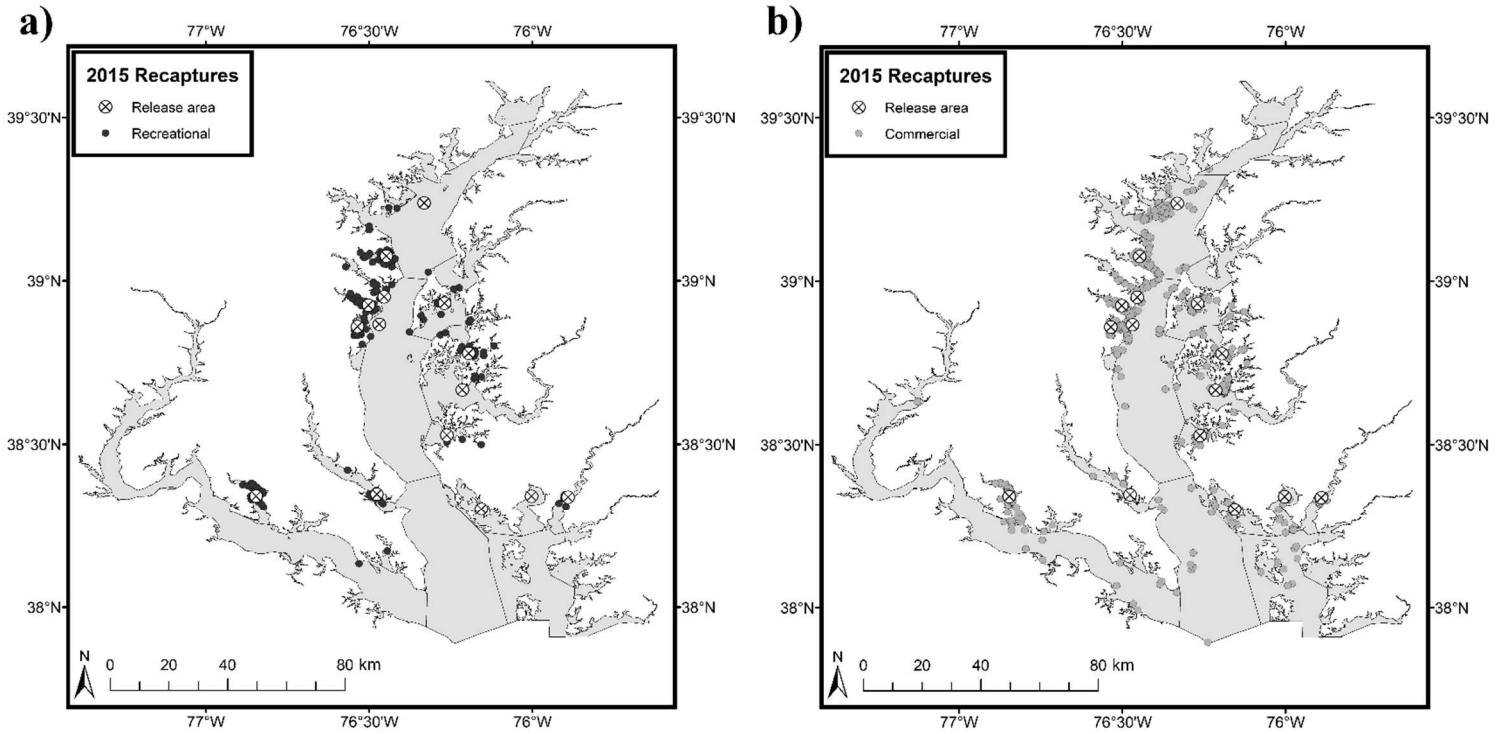


Figure 4. Seasonal and spatial variation in the ratio of recreational to commercial recaptures of tagged blue crab *Callinectes sapidus*. a) Ratio of recreational to commercial recaptures ( $\frac{nR}{nC}$ ) by month in 2014 and 2015 for tagged crabs released from four representative sites (listed in Table 2). b) Proportion of recreational (dark gray) to commercial (light gray) recaptures for each harvest reporting area where crabs were tagged at 15 sites (listed in Table 3) in 2015.

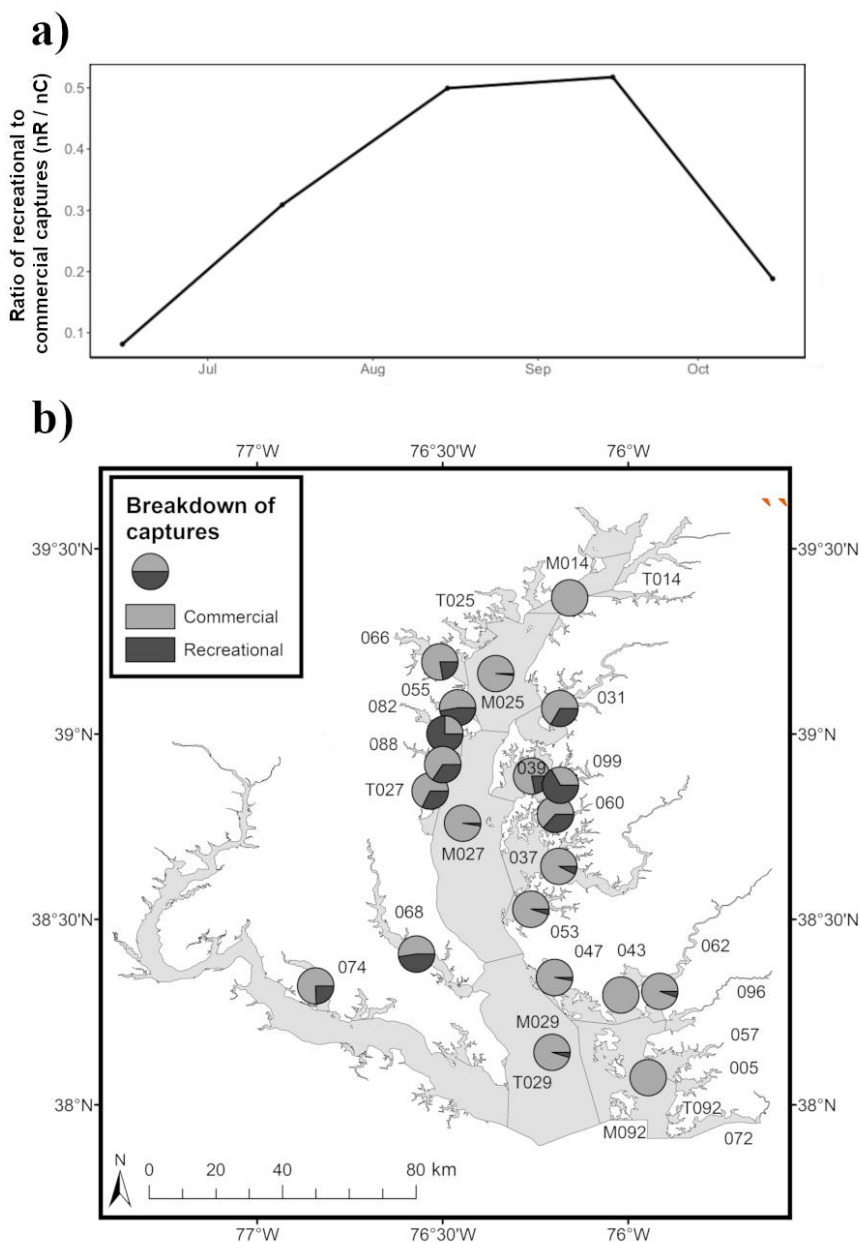


Figure 5. Estimated recreational harvest (a, c) and reported commercial harvest (b) of male hard blue crabs *Callinectes sapidus* in each harvest reporting area of Maryland in 2015. (a) Recreational harvests (number of crabs, dark gray circles) were estimated based on standard methods and the tagged crabs recaptured from each release area, ignoring crab movement. (b) Reported commercial harvests (number of crabs) are shown in light gray. (c) Recreational harvests (number of crabs, dark gray circles) were estimated based on the method which adjusted for crab movement and the tagged crabs which were recaptured within each reporting area, accounting for animal movement. (d) Difference between recreational harvest in each reporting area between the standard and adjusted approaches. A greater estimate for the movement approach is shown in black, and a greater estimate for the standard approach is shown in white. Numbers indicate harvest reporting area site codes.

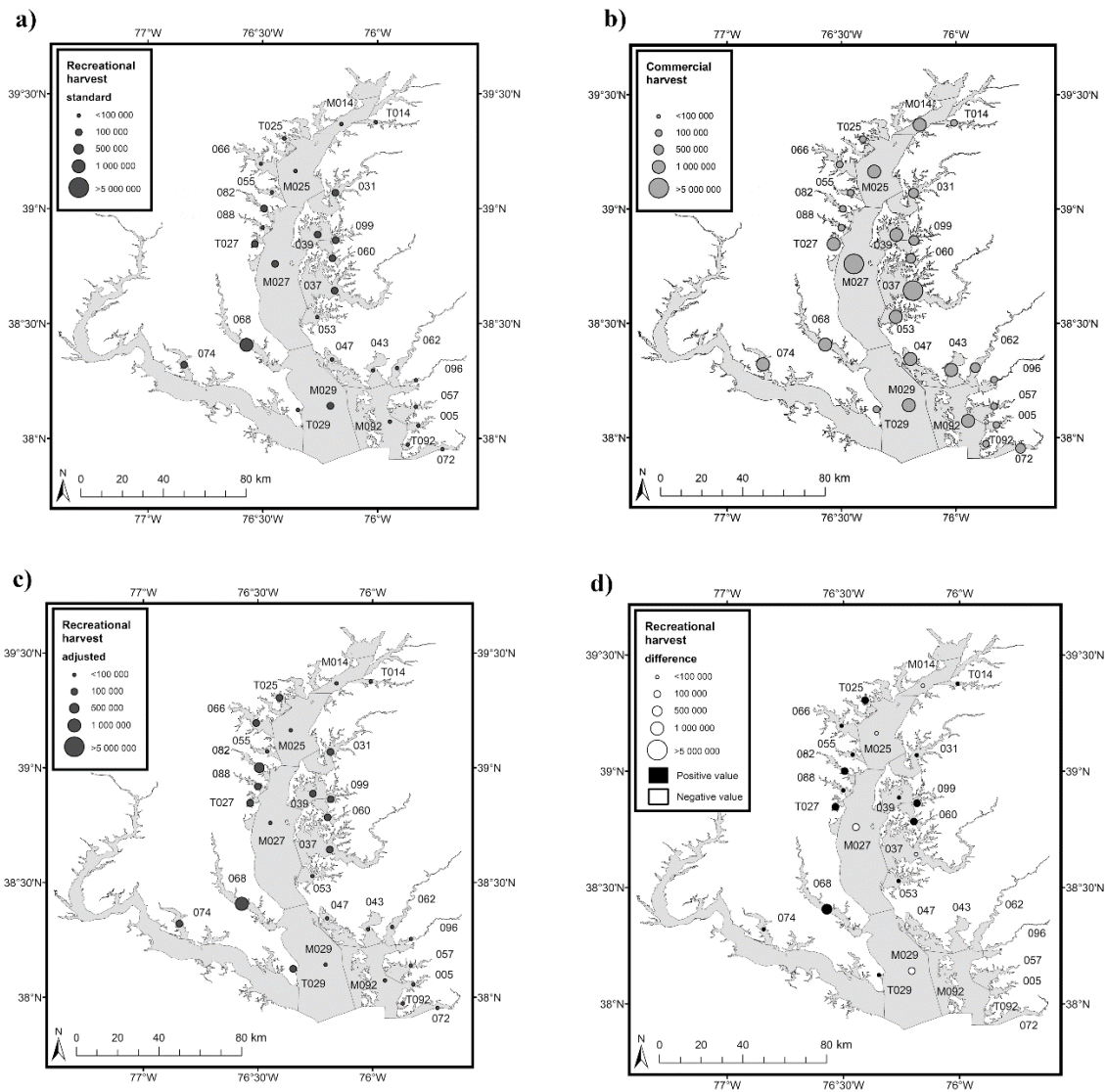
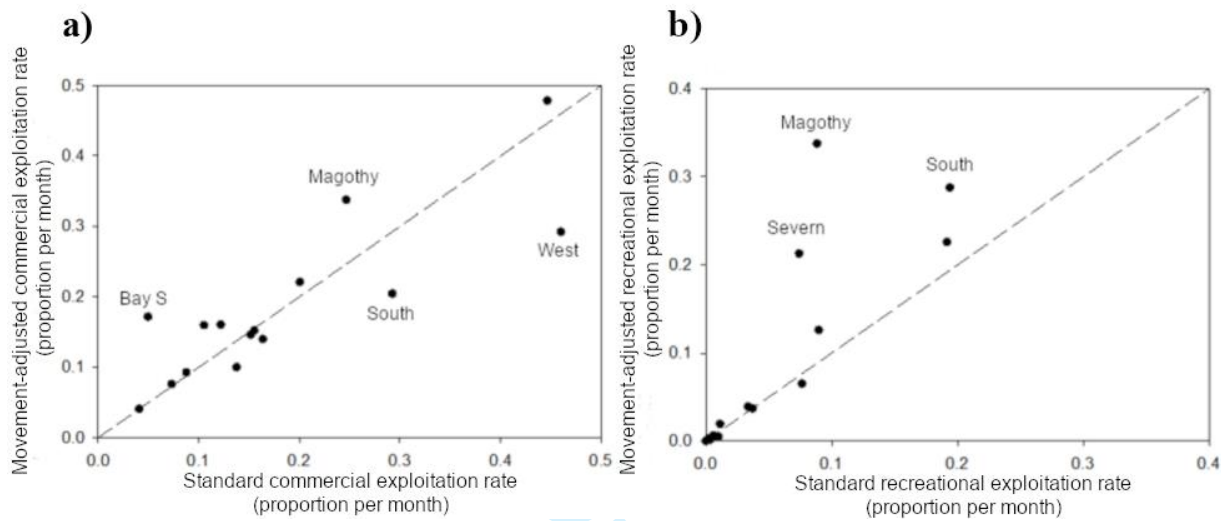


Figure 6. Comparison of (a) commercial exploitation rates and (b) recreational exploitation rates for blue crabs *Callinectes sapidus* when using standard calculation methods (X-axes) and when incorporating movement information (Y-axes) for each harvest reporting area where tagging occurred in 2015. The dashed line is the 1:1 line. Values for reporting areas (black dots) falling along this line did not differ when movement was considered. Labeled data points are examples noted in the text.





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25 Movement

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29

## 30 **Abstract**

31 Despite the need to quantify total catch to support sustainable fisheries management, estimating  
32 harvests of recreational fishers remains a challenge. Harvest estimates from mark-recapture  
33 studies have proven valuable, yet animal movements and migrations may bias some of these  
34 estimates. To improve recreational harvest estimates, explore seasonal and spatial harvest  
35 patterns, and understand the influence of animal movement on exploitation rates, a mark-  
36 recapture experiment was conducted for the blue crab fishery in Maryland waters of Chesapeake  
37 Bay, USA. Data were analyzed with standard tag-return methods and with revised equations that  
38 accounted for crab movement between reporting areas. Using standard calculations, state-wide  
39 recreational harvest was estimated to be 4.04 million crabs. When movement was included in the  
40 calculations, the estimate was 5.39 million, an increase of 34%. With crab movement,  
41 recreational harvest in Maryland was estimated to be 6.5% of commercial harvest, a finding  
42 consistent with previous effort surveys. The new methods presented herein are broadly  
43 applicable for estimating recreational harvest in fisheries that target mobile species and for which  
44 spatial variation in commercial harvest is known.

## 45 Introduction

46 Mark-recapture experiments are valuable tools for obtaining information on individuals,  
47 populations, and harvest regimes. [Mark-recapture data have been modeled for closed and open](#)  
48 [populations, and models have increased in complexity to include multiple stages, multi-model](#)  
49 [comparisons, and new statistical techniques \(Pollock 2000\)](#). For fishery species, mark-recapture  
50 experiments have been designed to investigate local population sizes and sources of mortality  
51 like fishery exploitation rates (Seber 1986, Pine et al. 2003). Models for analyzing mark-  
52 recapture data have been adapted to address various sources of uncertainty, including unequal  
53 catchability (Chao 1987, Agresti 1994), mixed stocks (Michielsens et al. 2006), and tag loss  
54 (Kremers 1988, Conn et al. 2004). Mark-recapture studies also have been used to study animal  
55 movements (Dorazio et al. 1994, Aguilar et al. 2005, Trudel et al. 2009). However, animal  
56 movements can influence mark-recapture-based estimates of exploitation rates (Nichols et al.  
57 1995, Munro and Kimball 1982), especially in cases where the harvest areas are small enough  
58 that there is substantial movement of tagged individuals among them.

59 Blue crabs (*Callinectes sapidus*) can make extensive movements during the open season  
60 of the blue crab fishery in Maryland waters of the Chesapeake Bay. The fishery targets this  
61 highly mobile species which is known to make short-duration movements as well as long-  
62 distance ontogenetic migrations (McConaughy et al. 1983, [Walcott and Hines 1990](#), Hines 2007).  
63 For crabs of harvestable size (>127 mm carapace width in Maryland), this movement can be [as](#)  
64 [much as 569](#) m per day; far enough to allow movement between harvest areas ([Walcott and](#)  
65 [Hines 1990](#)). [Crabs in Maryland are targeted by two fishery sectors: commercial fishers which](#)  
66 [are required to report their harvest and recreational fishers which are not. Fishers in both sectors](#)  
67 [use multiple gear types \(e.g. crab pot, trotline, hand-line, crab scrape\) \(Cargo 1954, Van Engel](#)

68 [1962, Kennedy et al. 2007](#)). Knowledge of crab movement is important for understanding the  
69 dynamics of the crab population (Hines 2007) and spatiotemporal patterns of harvest effort  
70 (Slacum et al. 2012).

71 Management of the blue crab fishery in Chesapeake Bay is based on [integrated targets](#)  
72 [and thresholds for the abundance and exploitation of](#) female crabs (Miller et al. 2011). [These are](#)  
73 [jointly estimated within the stock assessment model so both sets of indices are fully compatible.](#)  
74 [Additionally, there is an empirically determined trigger for management of male crabs, based on](#)  
75 [their exploitation. Abundance and exploitation are calculated based on commercial harvest](#)  
76 [reporting data, estimated recreational harvest from effort surveys \(Miller et al. 2011\), and three](#)  
77 [annual fishery-independent surveys: a dredge survey of overwintering crabs \(Sharov et al. 2003\),](#)  
78 [a trawl survey in MD \(Davis et al. 2001, Miller et al. 2011\), and a trawl survey in Virginia](#)  
79 [\(Tuckey and Fabrizio 2019\). In Maryland, the fishery is divided into](#) 29 commercial harvest  
80 reporting areas [which](#) range from large areas of the mainstem bay to small tributaries (Fig. 1,  
81 Table 1). Recreational harvest of females was banned in Maryland in 2008 as one of several  
82 measures to address recruitment overfishing, potentially shifting fishing effort onto males (Miller  
83 et al. 2011) [and altering sex ratios which can have negative consequences for population](#)  
84 [reproductive output \(Ogburn 2019\)](#). Recreational crabbers are not required to report their male  
85 crab harvest, which is instead estimated by [effort](#) surveys to be 8% of commercial harvest  
86 (Ashford et al. 2009, 2010a,b, 2013a,b). Fishery managers and stakeholders have expressed  
87 concern that the [effort](#) surveys may underestimate recreational harvest (Fogarty and Lipcius  
88 2007, Miller et al. 2011), although substantial efforts to minimize bias have been undertaken  
89 (Ashford et al. 2009, 2013a,b). We conducted a mark-recapture study to provide an independent  
90 estimate of recreational harvest in Maryland for comparison with [effort](#) surveys and evaluated

91 the potential influence of crab movement among harvest areas on estimates of harvest and sector-  
92 specific exploitation rates.

93

## 94 **Methods**

95 A large-scale mark-recapture study was conducted to study harvest patterns in the blue  
96 crab fishery in Maryland waters of Chesapeake Bay. Detailed below are 1) the tagging methods  
97 and experimental setup for the mark-recapture study, 2) methods used to estimate recreational  
98 harvest and exploitation from the tagging results without taking into account crab movement, and  
99 3) the adjusted equations used to include the influence of crab movement on these estimates.

100 Using mark-recapture data to answer these questions relies on an important set of assumptions;  
101 namely that marked animals 1) are well-mixed within the population, 2) behave in a similar  
102 manner as unmarked individuals , and 3) do not vary in catchability (Schwarz and Taylor 1998).  
103 Evidence from prior studies ~~does suggest~~ indicates that crabs tagged using ~~our~~ the method  
104 described below undergo full spawning migrations and otherwise behave similarly to unmarked  
105 individuals (Turner et al. 2003, Aguilar et al. 2005) and are healthy and thus unlikely to have  
106 reduced catchability (Turner et al. 2003). Several characteristics of the blue crab fishery in  
107 Maryland – especially the continuous fishery during the time of year when crabs are available for  
108 tagging, the large spatial scale of the study area, and expected strong spatial and temporal  
109 variation in fishing effort – prevented us from meeting the assumption that tagged crabs were  
110 well-mixed within the state-wide population. Instead we estimated spatial and temporal variation  
111 directly in ~~specifies~~ smaller regions and then aggregated estimates up to the state-wide level as  
112 detailed below. ~~We also tagged a given site over the course of day, releasing crabs as they were~~

113 ~~tagged. We did so while drifting across the tributary where tagging took place. This helped to~~  
114 ~~disperse crabs across the tagging area.~~

115 The primary goal [of this mark-recapture experiment](#) was to estimate the level of  
116 recreational harvest by multiplying reported commercial harvests with the ratio of recreational to  
117 commercial harvest determined from reported tag recaptures, as follows:

$$118 \quad H_R = \frac{nR}{nC} * H_C \quad (1)$$

119 where  $H_R$  was the total estimated recreational harvest,  $\frac{nR}{nC}$  was the ratio of the number of  
120 recreational recaptures ( $nR$ ) to commercial recaptures ( $nC$ ) observed from the tagging  
121 experiment, hereafter referred to as the “recapture ratio”, and  $H_C$  and was the total reported  
122 commercial harvest. [A similar method is employed in the management of striped bass \(\*Morone\*](#)  
123 [saxatilis\) fishery, whereby commercial discards are estimated based on known recreational](#)  
124 [discards, and the ratio of tags reported from discarded fish in the commercial sector to the](#)  
125 [recreational sector \(NFSC 2019\). Our method of calculating recreational harvest based on](#)  
126 [commercial harvest assumes that the level of commercial harvest is reliably known. Commercial](#)  
127 [crabbers in Maryland are required to timely report their harvest under penalty of license](#)  
128 [suspension/revocation and the state has an electronic reporting system. While these measures](#)  
129 [help ensure reliable harvest estimates, an analysis of the possibility of random error or](#)  
130 [differences in reporting across the state would further strengthen confidence in recreational](#)  
131 [harvest estimates.](#)

132 [Because we were unable to ensure that tagged crabs were well-mixed in the population,](#)  
133 [we designed the mark-recapture experiment to directly estimate](#) variability in recapture ratio over  
134 the course of the crabbing season (section 2.2) and spatial variability in recapture ratio across



135 harvest reporting areas (section 2.3). In addition, unequal tag reporting between the two sectors  
136 was [accounted for](#) (section 2.12). Finally, the calculation of recapture ratio [by harvest area](#) could  
137 have been influenced by crab movement, so the analyses were conducted both with and without  
138 information on crab movement, making it possible to identify the effects of movement on  
139 estimates of harvest and exploitation rates (section 3.1).

140 [Although population-level estimates of exploitation can be calculated from the estimate](#)  
141 [of total recreational harvest plus commercial harvest and population data from the stock](#)  
142 [assessment, our](#) secondary goal was to [explore variation in](#) sector-specific exploitation rates  
143 [among harvest reporting areas. This was](#) calculated by dividing the number of crabs recaptured  
144 by each sector by the number of crabs initially released, as follows:

$$145 \quad u_{Sector} = \frac{RP_{Sector}}{RL} \quad (2)$$

146 where  $u_{Sector}$  was the exploitation rate (proportion of crabs caught per month) of either the  
147 recreational or commercial sector,  $RP_{Sector}$  was the number of tagged crabs that were captured by  
148 that sector, and  $RL$  was the number of tagged crabs initially released. As before, potentially  
149 influential factors were accounted for in these calculations, including: unequal reporting  
150 between the two sectors (section 2.42), various sources of tag loss (section 2.4), and effects of  
151 crab movement (section 3.2).

### 152 ***1. Mark-Recapture Experiments***

153 A total of 6,800 adult male blue crabs were tagged and released to study the blue crab  
154 fishery in Maryland waters of the Chesapeake Bay over two consecutive summers, 2014 and  
155 2015. During the first summer (2014), 2,261 crabs were tagged and released during early  
156 summer (June/July), late summer (August), and fall (September) in four representative harvest

157 reporting areas to determine seasonal trends in the recapture ratio (Table 2). During the second  
158 summer (June – August 2015), 4,539 crabs were tagged and released in 15 representative harvest  
159 reporting areas to investigate spatial patterns in recapture ratio and sector-specific exploitation  
160 rates (Table 1).

161 Crabs were tagged with 2.5 cm x 5 cm vinyl discs attached to their dorsal surface with  
162 stainless steel wire wrapped around the lateral spines (Turner et al. 2003, Aguilar et al. 2005).  
163 The front of each tag used for this study had a unique identification number, the word “Reward”,  
164 and contact information for reporting recaptures either by phone or web form. Standard rewards  
165 were \$5. Five percent of tags were randomly assigned high value tags for estimating reporting  
166 rates. The high value tags had \$50 written in black ink on the front and back. On the reverse side,  
167 all tags listed information for fishers to record and report (tag number, date, GPS coordinates,  
168 capture depth, gear type and crab sex). Within each reporting area, all tagging was conducted on  
169 the same day. We also Crabs were tagged at given site over the course of day, releasing crabs  
170 and were released as they were tagged. We did so while drifting across the tributary where  
171 tagging took place. This helped to disperse crabs across the tagging area. Although tagged crabs  
172 were occasionally recaptured more than once, only the initial recapture was used in analyses.  
173 Some crabs that were released in Maryland were recaptured in Virginia (n = 44 of 2,039 total  
174 returns in 2015). Nearly 90% of crabs recaptured in Virginia were captured by commercial  
175 fishers. While these returns were included in harvest calculations when movement was not  
176 considered, tag returns from these crabs were excluded when making estimates that accounted  
177 for crab movement. We follow the Guide for Care and Use of Laboratory Animals in our crab  
178 tagging protocol.

## 179 ***2. Estimating Recreational Harvest and Exploitation without Animal Movement***

## 180 2.1 Estimating statewide recreational harvest

181 The statewide recreational harvest of crabs in 2015 ( $H_R$ ) was estimated using crabs that  
 182 were tagged and released in 15 representative harvest reporting areas in 2015 ( $n = 4,539$ ). [Our](#)  
 183 [multiple harvest area approach was similar to that of the first year of release and year of first](#)  
 184 [recapture for multi-stratum capture-recapture models of an open population as described in](#)  
 185 [Brownie et al. \(1993\) except that we also accounted for two harvest sectors, seasonal variation in](#)  
 186 [harvest, and tag reporting rates.](#)  $H_R$  was computed by taking the ratio of recreational to  
 187 commercial recaptures from the mark-recapture experiment and then multiplying this ratio by the  
 188 reported commercial landings:

$$189 \quad H_R = \sum_{l=1}^{29} \sum_{m=1}^9 \frac{nR_{l,m}}{nC_{l,m}} * H_{C_{l,m}} \quad (3)$$

190 where  $H_C$  was the total reported commercial harvest of male hard crabs in 2015 in each of the 29  
 191 harvest areas ( $l$ ) for each of the 9 months ( $m$ ) of crab harvest season, and  $nR$  and  $nC$  were the  
 192 number of recreational and commercial recaptures, respectively, estimated from tagging data for  
 193 each area. [H<sub>C</sub> values for each area and month were obtained from the Maryland Department of](#)  
 194 [Natural Resources \(MD DNR 2015a,b\).](#) For these calculations, all crab recaptures from a  
 195 particular release, regardless of their eventual recapture area were used (e.g., Fig. 2aA).

196 [The number of recreational and commercial recaptures from each release were adjusted](#)  
 197 [with sector-specific tag-reporting rates, as follows:](#)

$$198 \quad \frac{nR_{l,m}}{nC_{l,m}} = \frac{RP_{R,l,m}}{RP_{C,l,m}} * \frac{RR_R}{RR_C} \quad (4)$$

199  
 200 [where  \$nR\$  and  \$nC\$  were the number of recreational and commercial recaptures, estimated from](#)  
 201 [tagging data for each area \( \$l\$ \) and month \( \$m\$ \),  \$RP\_{R,l,m}\$  and  \$RP\_{C,l,m}\$  were the raw number of](#)

202 recaptures for each sector reported by crabbers in the given area and month, and  $RR_R$  and  $RR_C$   
 203 (equation- 5) were the tag-reporting rates for recreational and commercial crabbers in 2015. A  
 204 single reporting rate was calculated for each sector in each year. These were calculated across all  
 205 harvest reporting areas, using standard and high-value tags as follows:

$$206 \quad RR_{Sector} = (R_s/N_s) / (R_r/N_r) = R_s N_r / R_r N_s \quad (5)$$

207 where  $RR$  represents the proportion of caught crabs which were reported,  $N_s$  was the number of  
 208 standard tags released,  $N_r$  was the number of high-value tags released,  $R_s$  was the number of  
 209 standard tags returned,  $R_r$  was the number of high-value tags returned, and sector was either  
 210 commercial or recreational (Pollock et al. 2001). These reporting rates were calculated including  
 211 both male and female crabs released in 2014 because there were not sufficient crabs recaptured  
 212 to determine reporting rates for each crab sex within each fishery sector. Budgetary limitations  
 213 on tagging prevented us from calculating of sector-specific reporting rates for each harvest  
 214 reporting area or for each month of the crabbing season. While significant spatial or seasonal  
 215 variation in tag reporting could affect the accuracy of these values, a single value was used for  
 216 each sector to best focus on differences in reporting between the two sectors.

217 Similarly, it was not feasible within our budget to determine the recapture ratio ( $\frac{nR}{nC}$ ) for  
 218 all 29 reporting areas directly through releases of tagged crabs. For areas where tagging was not  
 219 conducted ( $n = 14$ ), the ratio of recreational to commercial recaptures for nearby reporting area  
 220 was used (Table 1). For example, crabs were not tagged in the Manokin River so the recapture  
 221 ratio from the nearby Nanticoke River was used in calculations. Decisions about these data  
 222 substitutions were based on our best professional judgement and took into account discussions  
 223 with fishery managers, characteristics such as proximity to other sites, and visual comparisons of  
 224 the level of residential development in satellite imagery.

## 225 2.2 Seasonal variation in recapture ratios

226 ~~€Monthly commercial harvest data were available for each reporting area at monthly~~  
 227 ~~intervals but and tagging releases data themselves would only reliably estimate the recapture~~  
 228 ~~ratio provided reliable estimates of recreational recapture rates for a single month, which allowed~~  
 229 ~~calculation of. This required the calculation of monthly ratios of recreational to commercial~~  
 230 ~~recaptures ( $\frac{nR_{Season}}{nC_{Season}}$  - ) for each reporting area across the harvest season. ~~to~~ Recapture data from~~  
 231 ~~2014 and 2015 were used to characterize calculate these variation- monthly recapture~~  
 232 ~~ratios throughout the harvest season. In 2014, a total of 2,261 crabs were tagged in early summer,~~  
 233 ~~late summer, and fall of 2014 in four harvest areas representative of the Eastern and Western~~  
 234 ~~Shore tributaries of Maryland's Chesapeake Bay (South River, Rhode River, Eastern Bay, Little~~  
 235 ~~Choptank River) (Table 2). An In 2015, additional 1,368 crabs were tagged in these areas in~~  
 236 ~~summer 2015 (Table 1) and used in this analysis, for Hence, a total of 3,629 tagged crabs~~  
 237 ~~tagged were used to identify seasonal-monthly variations in recapture ratios ( $\frac{nR}{nC}$ ).~~

238 ~~Including Using~~ releases from both 2014 and 2015, recreational and commercial  
 239 ~~recaptures from the four harvest areas above were summed across these regions for each month.~~  
 240 ~~Then~~ recreational recaptures for each month ( $m$ ) were divided by commercial recaptures to  
 241 determine a statewide ratio of recreational to commercial harvest for each month:

$$242 \frac{nR_{Season,m}}{nC_{Season,m}} = \frac{\sum_{l=1}^4 RP_{R,l,m}}{\sum_{l=1}^4 RP_{C,l,m}} \quad (6)$$

243 where  $RP_{R,l,m}$  and  $RP_{C,l,m}$  represented the number of tagged crabs reported ( $RP$ ) that were  
 244 captured by recreational crabbers ( $R$ ) or commercial crabbers ( $C$ ) in the given month ( $m$ ) in one  
 245 of the four harvest areas ( $l$ ) where crabs were tagged in both 2014 and 2015.

246 Without tagging in the months of April, May, and November, the recapture ratio for these  
247 months at the beginning and end of the crabbing season could not be empirically determined.  
248 Compared to the mid-season peak, the recapture ratios in these months were expected to be quite  
249 low. Recapture ratios for the months of April, May, and November were assigned values of 0 to  
250 generate a more conservative estimate of recreational harvest. The sensitivity to this assumption  
251 was gauged by performing a separate calculation where the recapture ratios ~~were~~ constant  
252 during these months ( $\frac{nR_{Season}}{nR_{Season}}$  in April = June, May = June, November = October). This second  
253 calculation served as an upper bound for recapture ratios.

### 254 *2.3 Spatial variation in recapture ratios*

255 To characterize spatial variation in the ratio of recreational to commercial recaptures,  
256 records of the 4,539 crabs that were tagged in 15 harvest reporting areas in 2015 were analyzed  
257 (Table 1). These releases occurred during the middle of the harvest season (July-September),  
258 when recreational harvests were expected to be at their peak. The exact date of each tagging  
259 event was dependent on weather and the availability of commercial fishermen to assist with  
260 capturing crabs in each of the 15 locations. Recreational and commercial recaptures occurring  
261 within 60 days of release were tallied. The sixty-day timeframe for recaptures was used because  
262 it accounted for 98% of recaptures reported by the end of the fishing season.

263 When calculating monthly ratios of recreational to commercial harvest for each reporting  
264 area in 2015, additional estimates were necessary because tagging occurred only once at each  
265 site in 2015, either in July, August, or September (Table 1). The ratios of recreational to  
266 commercial recaptures were estimated for all months of the harvest season with no available data  
267 using the seasonal relationship developed above (equation 6). To calculate the recapture ratio (

268  $nR_{l,m} / nC_{l,m}$  for a given month ( $m$ ) in a specific harvest area ( $l$ ), ~~we had to~~ it was necessary to  
 269 determine how recapture ratios in that month ( $m$ ) compared to those in the month the release  
 270 occurred ( $o$ ). Specifically, we divided the recapture ratio for that month of the seasonal  
 271 relationship ( $\frac{nR_{Season,m}}{nC_{Season,m}}$ ) by the recapture ratio of the seasonal relationship in the month when the  
 272 release occurred ( $\frac{nR_{Season,o}}{nC_{Season,o}}$ ). This was then multiplied by the recapture ratio observed at that site in  
 273 2015 ( $\frac{nR_{2015,o}}{nC_{2015,o}}$ ) following the equation:

$$274 \frac{nR_{l,m}}{nC_{l,m}} = \frac{\frac{nR_{Season,m}}{nC_{Season,m}}}{\frac{nR_{Season,o}}{nC_{Season,o}}} * \frac{nR_{2015,o}}{nC_{2015,o}} \quad (7)$$

#### 276 2.4. Spatial variation in exploitation

277 To determine spatial variation in exploitation, exploitation rates for each fishery sector  
 278 were calculated for each of the first two months (standardized as two 30-day periods) after each  
 279 release in each of the harvest areas in 2015. Monthly exploitation rates were calculated by  
 280 comparing the number of crabs that were caught within the month and the number of crabs  
 281 available to be caught at the beginning of the month. All tagged crabs were assumed to be  
 282 available for harvest in the first month. In the second month, a tagged crab was considered to be  
 283 unavailable for recapture if it had died, molted, or otherwise lost its tag.

284 Exploitation (proportion of crabs caught per month) in each area was calculated as  
 285 follows:

$$286 u_{Sector,l,m} = \frac{RP_{Sector,l,m} / RR_{Sector}}{RL_{l,m}} \quad (8)$$

287 where  $RP_{Sector,m}$  was the number of tagged crabs reported as captured by the given sector in the  
 288 first month ( $m = 1$ ),  $RR$  was the reporting rate of tags caught by that sector over the crabbing

289 season (equation 5), and  $RL$  was the number of tagged crabs released in each area ( $I$ ) at the  
 290 beginning of the first month. In the second month, crabs were removed from the number of  
 291 released crabs if they were caught in the first month, or were predicted to have died, molted or  
 292 lost their tag during the first month. Exploitation in the second month was calculated as follows:

$$293 \quad u_{Sector,l,m} = \frac{RP_{Sector,l,m} / RR_{Sector}}{(RL_{l,m} - (C_{l,m-1} + M_{l,m-1} + D_{l,m-1} + L_{l,m-1}))} \quad (9)$$

294 where  $RP_{Sector,m,l}$  was the number of tagged crabs reported as captured by the given sector in the  
 295 second month ( $m = 2$ ) in each area ( $I$ ),  $RR_{Sector,l}$  was the reporting rate of tags caught by that  
 296 sector,  $RL_l$  was the number of tagged crabs released in each area ( $I$ ), and  $C_{m-1,l}$ ,  $M_{m-1,l}$ ,  $D_{m-1,l}$   
 297 and  $L_{m-1,l}$  were the number of tagged crabs caught ( $C$ ) or expected to have molted ( $M$ ), died  
 298 ( $D$ ), or lost their tag ( $L$ ) in the time leading up to month  $m$ .

299 In this analysis, natural mortality was set at a rate of  $0.075 \text{ month}^{-1}$  based on the  
 300 instantaneous rate of natural mortality ( $M = 0.9$ ) used in the stock assessment (Miller et al.  
 301 2011). The proportion of crabs that had molted prior to the given month was based on a  
 302 probabilistic model, using published data on the time to molting for tank-held crabs in degree-  
 303 days (Tagatz 1968), as well as average monthly water temperatures for the mainstem Chesapeake  
 304 Bay obtained from the Maryland Department of Natural Resources. This resulted in a molting  
 305 rate ranging from  $0.107 \text{ month}^{-1}$  for the (June 18, 2015<sup>th</sup> release in the Little Choptank River) to  
 306  $0.199 \text{ month}^{-1}$  for the (July 11, 2015<sup>th</sup> release in the Patuxent River) which corresponded to (492  
 307 and 556 degree-days passing at these sites, respectively). Physical tag loss was estimated as  
 308 thirty times the daily rate of tag loss ( $0.00067 \text{ d}^{-1}$ ), previously estimated from tank-holding  
 309 studies (Hines, unpublished data). Given that the number of tagged crabs remaining at large  
 310 decreased with time, exploitation calculations for both months were then somewhat conservative.  
 311 This is due to the fact that calculations only accounted for recaptures, tag loss, molting or



312 mortality which occurred prior to each month, ignoring any losses which occurred during the  
313 period of calculation.

### 314 **3. Revised Estimates Accounting for Crab Movement**

#### 315 *3.1 Revised estimates of recreational harvest*

316 Our basic approach for evaluating the effect of movement was to multiply reported  
317 commercial harvest ( $H_C$ ) by two estimates of recapture ratio calculated either with or without  
318 accounting for movement and then comparing the two resulting sets of recreational harvest  
319 estimates. Without crab movement,  $H_R$  was calculated using equations 3-7 above, which were  
320 based on crabs released in each reporting area and recaptured in all areas (Fig. 2aA). To  
321 incorporate crab movement,  $H_R$  was calculated [for each area](#) based on crabs released in any  
322 reporting area [and](#) only those recaptured in the reporting area of interest (Fig. 2bB). These  
323 methods yield identical results when no movement occurs among reporting areas. [Comparing](#)  
324 [their results allowed us to estimate the effect of](#) crabs mov~~ing~~[ing](#) from the release area into a  
325 different area before recapture [on area-specific recapture ratios](#).

#### 326 *3.2 Revised estimates of exploitation*

327 The influence of movement on exploitation [in each harvest area](#) was [also evaluated](#) by  
328 incorporating information about the movements of tagged individuals among harvest reporting  
329 areas into [area-specific](#) exploitation rate calculations. As illustrated above (eqs: [8-9](#)),  
330 traditionally exploitation rate ( $u$ , proportion of crabs caught per month) is calculated as the  
331 number of tagged individuals caught and reported ( $RP$ ) divided by the number of tagged  
332 individuals released and available to be caught ( $RL$ ) in a given amount of time (Ricker 1975).  
333 Both the catch and availability components of each exploitation rate in each region and each

334 month were adjusted to reflect crab movements. Movement-adjusted exploitation in the first  
 335 (equation 10) and second (equation 11) month were calculated as follows:

$$336 \quad u_{Sector,l,m}^* = \frac{RP_{Sector,l,m}^* / RR_{Sector}}{RL_{l,m}^*} \quad (10)$$

$$337 \quad u_{Sector,l,m}^* = \frac{RP_{Sector,l,m}^* / RR_{Sector}}{(RL_{l,m}^* - (C_{m-1,l} + M_{m-1,l} + D_{m-1,l} + L_{m-1,l}))} \quad (11)$$

338 using adapted versions of equations 8 and 9, where  $RP_{Sector,l,m}^*$  indicated the number of tagged  
 339 crabs recaptured from the release during that month, after accounting for crab movement (see  
 340 equation 12), and  $RL_l^*$  indicated the number of crabs available to be caught during that period  
 341 after accounting for movement (see equation 13).

342 When implementing equations 10 and 11, the number of recaptures ( $RP_{Sector,m,l}^*$ ) was  
 343 adjusted to reflect crab movement during the month by 1) removing crabs that were released in  
 344 the reporting area and were captured in other reporting areas and 2) adding crabs that were  
 345 released in other reporting areas and were captured in the reporting area (Fig. 2c). This  
 346 recapture adjustment was calculated as follows:

$$347 \quad RP_{Sector,l,m}^* = RP_{Sector,l,m} + \left( \sum_{b=1}^{14} RP_{Sector,b,l} \right) - \left( \sum_{c=1}^{28} RP_{Sector,l,c} \right) \quad (12)$$

348 Where  $RP_{Sector,l,m}$  was the total number of recaptures in the reporting area ( $l$ ) and month ( $m$ ) and  
 349 the first sum represented the number of crabs released at each of the 14 other release areas and  
 350 were caught in the given reporting area during the given month (moving from any of the 14 other  
 351 reporting areas where crabs were released ( $b$ ) to the given reporting area ( $l$ )). The second sum  
 352 indicated the number of crabs released within the given reporting area which were captured  
 353 within each of the 28 other harvest reporting area during the given month (moving from the  
 354 given reporting area ( $l$ ) to any of the 28 other reporting areas used in this study ( $c$ )).

355 The number of crabs that were available to be caught within the harvest reporting area in  
 356 a given month was adjusted with conditional probabilities of crab movement, in two steps: First,  
 357 the total number of tagged crabs predicted to have left the reporting area were subtracted off.  
 358 Then the total number of tagged crabs predicted to arrive in the harvest reporting area from other  
 359 areas was added in (Fig. 2c). The availability adjustment was calculated as follows:

$$360 \quad RL_{l,m}^* = RL_{l,m} + \left( \sum_{b=1}^{14} RL_{b,m} * P_{b,l} \right) - \left( \sum_{c=1}^{28} RL_{l,m} * P_{l,c} \right) \quad (13)$$

361 where  $RL_{l,m}$  was the total number of available crabs in the reporting area ( $l$ ) and month  
 362 ( $m$ ) and the first sum was the predicted number of tagged crabs moving into the given reporting  
 363 area during the given month from the 14 other release areas. This sum was a function of the  
 364 crabs available in the given month ( $m$ ) at each of the 14 sites ( $b$ ) where crabs were released ( $RL_{b,m}$ )  
 365 and the proportion of crabs ( $P_{b,l}$ ) at each of those sites which moved to the given  
 366 reporting area ( $l$ ). The second sum indicated the number of crabs predicted to move from the  
 367 given reporting area to each of the 28 other harvest reporting areas in the given month. The  
 368 second sum was a function of the crabs available in the given month ( $m$ ) at the given reporting  
 369 area ( $l$ ) ( $RL_{l,m}$ ) and the proportion of crabs ( $P_{l,c}$ ) in the given reporting area ( $l$ ) which moved to  
 370 each of the 28 other harvest reporting areas ( $c$ ). It was assumed that the proportion of tagged  
 371 crabs moving out of each harvest reporting area was equivalent to the proportion of tagged crabs  
 372 caught within or outside the release location. We also gauged the reliability of movement  
 373 probabilities by evaluating their consistency between years. To assess this, we compared  
 374 movement probability matrices for the four reporting areas which were tagged in both 2014 and  
 375 2015 and calculated the overall level of correlation between them.

## 376 Results

377 *Tag return rates*

378 Of the 6,800 tagged crabs released in 2014 and 2015, a total of 1,891 tags were returned  
379 (Tables 2 and 3) for an overall return rate of 27.8%. This rate is higher than prior studies on  
380 female blue crabs (Aguilar et al. 2005 (4-17%), Turner et al. 2003 (5-21%), Rittschof et al. 2011  
381 (15.6%). This can be expected because males are the primary target of the fishery. A similar  
382 return rates for tagged female crabs (8.6%) was seen from a separate but concurrent study  
383 performed by our lab, with an overall exploitation rate of 10.5% (Corrick 2018).

384 When examining seasonal variations in recapture ratios, the analysis included 1,211  
385 recaptures from 3,629 crabs which were tagged during 16 releases (12 releases in 2014 and 4  
386 releases in 2015) (Table 2). Of the 2,261 male crabs released in 2014, 728 (32.2%) were  
387 recaptured and reported (Table 2). Of these, 527 (72.4%) were captured by commercial crabbers,  
388 195 (26.8%) by recreational crabbers, and 5 (0.7%) by unidentified crabbers. Of the 3,085 \$5  
389 tags (male and female) released in 2014, 786 (25.5%) were recaptured. Of the 163 \$50 tags  
390 released, 47 (28.8%) were recaptured. This resulted in an overall reporting rate of 88.4% across  
391 the fishery in 2014 with sector-specific reporting rates of 93.3% and 75.1% for the commercial  
392 fishery and recreational fisheries, respectively. In 2014 the reporting rate for male crabs was  
393 0.930. When all crabs (male and female) were included that number decreased slightly to 0.884.  
394 Area-specific reporting rates in 2014 ranged from 80.2% in South River to 98.5% in Eastern  
395 Bay. Of the additional 1,368 male crabs released in the 4 reporting areas in 2015, 483 (35.3%)  
396 were recaptured and reported (Table 1). Of these, 360 (74.5%) were captured by commercial  
397 crabbers, 110 (22.7%) by recreational crabbers and 13 (2.7%) by unidentified crabbers.

398 There was notable consistency in recapture and reporting of crabs between the two years  
399 of the analysis. When examining spatial variations in recapture ratios in 2015, the analysis

400 included 1,163 recaptures (25.6%) from the 4,539 male crabs tagged and released during all 15  
401 releases in 2015 (Table 1, Fig. 3). Of these, 897 (77.1%) were captured by commercial crabbers,  
402 235 (20.2%) by recreational crabbers, and 31 (2.7%) by unidentified crabbers. Of the 5,244 \$5  
403 tags (male and female) released in 2015, 1,159 (22.1%) were recaptured. Of the 276 \$50 tags  
404 released, 84 (30.4%) were recaptured. This resulted in an overall reporting rate of 72.6% across  
405 the fishery. Sector-specific reporting rates in 2015 were 67.2% for the commercial fishery and  
406 85.3% for the recreational fishery. ~~In 2015, the reporting rate for males was (0.715), however,~~  
407 ~~when all crabs (male and female) were included this increased slightly to (0.726).~~ There were  
408 insufficient recaptures in individual harvest reporting areas to produce reliable area-specific  
409 reporting rates. Of the 1,147 male crabs released in 2015 that were recaptured and reported with  
410 sufficient spatial information, 220 (19.2%) were recaptured in a different reporting area from  
411 where they were released. Of these, 157 (71.4%) were crabs that moved from tributaries into the  
412 mainstem Bay.

413 ~~There was notable consistency in recapture and reporting of crabs between the two years~~  
414 ~~of the analysis. The overall reporting rate of across the fishery was 88.4% and 72.6% in 2015. In~~  
415 ~~2014, the reporting rate for male crabs was 0.93.0%. When all crabs (male and female) were~~  
416 ~~included that number decreased slightly to 0.88.4%. In 2015, the reporting rate for males was~~  
417 ~~(0.71.5%), however, when all crabs (male and female) were included this increased slightly to~~  
418 ~~(0.72.6%).~~

#### 419 *Seasonal variation in recapture ratios*

420 The ratio of recreational to commercial recaptures ( $\frac{nR}{nC}$ ) exhibited a domed relationship  
421 over time, increasing during June and July to a similar high values in August (0.50) and  
422 September (0.52) followed by a sharp drop in October (Fig. 4a). ~~Without tagging in the months~~

423 ~~of April, May, and November, we could not empirically determine the recapture ratio for these~~  
424 ~~months at the beginning and end of the crabbing season. Compared to the mid-season peak, these~~  
425 ~~are expected to be quite low. Recapture ratio for the months of April, May, and November were~~  
426 ~~assigned values of 0 to generate a more conservative estimate of harvest. We also gauged the~~  
427 ~~sensitivity to this, by performing a separate calculation where the recapture ratio remains~~  
428 ~~constant through these months (nR/nC for April / May = June, nR/nC for November = October).~~  
429 ~~This serves as an important upper bound, as the domed seasonal relationship is expected to~~  
430 ~~continue into these months.~~

431 ~~This seasonal trend in recapture ratio clearly likely stems from a strong seasonal trend~~  
432 ~~in recreational fishing effort. It should be noted that commercial harvests already showed a~~  
433 ~~domed relationship of their own, with a peak in July/August (MD DNR 2015). If the seasonal~~  
434 ~~variation in recreational effort was proportional to that of commercial effort, we would see there~~  
435 ~~would have been little change in recapture ratios across the harvest season. As Because the~~  
436 ~~recapture ratios showed a seasonal trend on top of changing commercial harvest, we can see that~~  
437 ~~the seasonality of recreational effort is was likely much greater than that of commercial effort.~~

#### 438 *Spatial variation in recapture ratios*

439 There were spatial variations in the ratio of recreational to commercial recaptures in  
440 2015, with the highest values on Maryland's Western Shore and middle Eastern Shore (Fig. 4b)  
441 indicating higher proportions of recaptures in those regions.

442 When animal movement was included in the calculations, there were substantial changes  
443 in the recapture ratios (Table 4), especially in the regions with high recreational recaptures.

#### 444 *Estimates of recreational harvest*

445 Statewide recreational crab harvest in 2015 was estimated to be 4.04 million crabs  
446 without crab movements and 5.39 million crabs when accounting for crab movement (Table 3).  
447 These levels of harvest were 4.9% or 6.5% of total commercial crab harvests (all male and  
448 female harvests), or 8.4% or 11.2% of male hard crab harvests, when crab movement was not, or  
449 was, included (higher values included movement information). When movement was included,  
450 the estimate of Maryland-wide recreational harvest increased by 33.5%. These harvest values  
451 were computed with recapture ratios equal to zero for the months of April, May, and November.  
452 When using the alternate constant values seasonal estimate instead of zero (i.e., the value for April  
453 and May = June, and November = October), recreational harvest was calculated with movement  
454 was 5.46 million crabs (11.293% of male hard crab harvests), a value very similar to the estimate  
455 when ratios in these months were set to zero.

456 Estimated recreational harvest of crabs varied substantially across the different harvest  
457 reporting areas, with most landings occurring in tributaries (Fig. 5c). In particular, incorporating  
458 data on movement increased the estimate of recreational harvest in tributaries (Fig. 5d) because  
459 many crabs moved from tributaries that had greater recreational harvest to mainstem bay areas  
460 that had almost exclusively commercial harvest. Using data that accounted for movement,  
461 recreational harvest estimates ranged from 0 crabs in Fishing Bay and the Honga River to 1.91  
462 million crabs in the Patuxent River (Fig. 5c). The spatial pattern was substantially different from  
463 reported commercial harvest (Fig. 5b), which was characterized by high harvests in the Choptank  
464 River and the mainstem bay. Tributaries with high recreational landings included the Patuxent  
465 (1.91 million crabs), Severn (0.52 million crabs), and Miles rivers (0.40 million crabs).

#### 466 *Spatial variation in exploitation*

467 There were marked differences in recreational and commercial exploitation rates among

468 the 15 harvest reporting areas in which crabs were tagged (Table 54). The most noticeable  
469 differences were observed between sites in tributaries along the Western Shore of the Bay,  
470 Eastern Bay, and the Miles and Wye rivers, where recreational fishing was greatest, and areas of  
471 the Bay Mainstem, where recreational harvest was negligible. Mean commercial exploitation per  
472 month (calculated using movement information) ranged from 0.04 month<sup>-1</sup> in the Patuxent River  
473 to 0.48 month<sup>-1</sup> in the Wicomico River tributary of the Potomac River. Notably high rates of  
474 commercial exploitation were observed in the Wicomico River (0.48 month<sup>-1</sup>), Magothy River  
475 (0.34 month<sup>-1</sup>), and West River (0.29 month<sup>-1</sup>). Mean recreational exploitation per month ranged  
476 from 0 month<sup>-1</sup> in both the Honga River and Fishing Bay to 0.3438 month<sup>-1</sup> in the Magothy  
477 River. Notably high rates of recreational exploitation were observed in the Magothy River and in  
478 South River (0.288 month<sup>-1</sup>).

479 Accounting for movement resulted in substantial differences in sector-specific  
480 exploitation rates. Estimates of commercial exploitation increased by 37.0% in the Magothy  
481 River and by 246.4% in the Bay Mainstem S region after movements were considered (Fig. 6a).  
482 For the Magothy River, this increase was a result of decreases in the number of crabs available to  
483 be caught, because many left the area. In the case of the Bay Mainstem S, however, the large  
484 increase in commercial exploitation was due to a large number of crabs leaving other areas and  
485 subsequently being caught by commercial fishers in the Bay Mainstem S. Commercial  
486 exploitation decreased by 30.0% in the South River and by 36.5% in the West River because of  
487 the large number of crabs from these releases that were caught by commercial fishers in the Bay  
488 Mainstem (Fig. 6a). Recreational exploitation rates increased by 283.4% in the Magothy River,  
489 by 48.3% in the South River, and by 186.5% in the Severn River due to reductions in the number  
490 of crabs available to be caught in these systems (Fig. 6b). These differences are underpinned by a



491 [great degree of consistency in movement probabilities between years. For the four sites tagged in](#)  
492 [both 2014 and 2015, there was a strong degree of correlation in movement probabilities between](#)  
493 [years \( \$r = 0.99\$ ,  \$t = 36.72\$ ,  \$p < 0.01\$ \).](#)

494

## 495 **Discussion**

496 The movement of tagged individuals strongly influenced the results of a mark-recapture  
497 study of the blue crab fishery in Maryland waters of the Chesapeake Bay. Tag return data  
498 revealed strong variation in the ratio of recreational to commercial recaptures among adjacent  
499 harvest reporting areas that set the stage for movement to influence estimates of [area-specific](#)  
500 recreational harvest and exploitation. In the most extreme case (Severn River), a crab could  
501 move from an area where it is 2.5 times more likely to be caught by a recreational fisher than a  
502 commercial fisher, to one with 100% commercial harvest, by moving only a few km. Adult blue  
503 crabs are easily capable of traveling this distance in a few days (Souza et al. 1980, Wolcott and  
504 Hines 1990) and commercial fishing effort is concentrated at tributary mouths to intercept crabs  
505 moving out of shallow nursery habitats (Slacum et al. 2012). Overall, the resulting estimate of  
506 statewide recreational harvest was 34% higher when movement was taken into account  
507 compared to the estimated based on the release location of tagged crabs only. The results of this  
508 study highlight the importance of incorporating movement into mark-recapture studies [focused](#)  
509 [on exploring](#) spatial variation in exploitation [among harvest areas when](#) the target species  
510 commonly moves among [them](#).

511 Although mark-recapture studies are often used to address fishery management questions  
512 [at the population level when the effect of individual movements may be negligible, there are a](#)  
513 [few examples that](#) incorporate movement data into calculations of exploitation rates. [I](#)n a study

514 of snapper, site-by-site estimates of density and exploitation were used to standardize movement  
515 patterns of snapper that were determined from recapture locations in New Zealand (Parsons et al.  
516 2011). The method used by Parsons et al. (2011) is in some sense the inverse of the technique  
517 employed in the present study. In other [examples](#), exploitation calculations are conducted for  
518 each release area but [did not account for movement](#) between release areas (e.g. Rudd et al. 2014,  
519 Whitlock et al. 2016). [Analyses of waterfowl data provide examples for incorporating  
520 information on movement among multiple harvest areas into harvest and exploitation rate  
521 calculations \(Munro and Kimball 1982, Nichols et al 1995\). Our methods expand on this to  
522 incorporate within-year temporal variation and multiple harvest sectors which was needed to  
523 estimate recreational harvest based on reported commercial harvest.](#)

524 The present study represents the first quantitative, statewide assessment of recreational  
525 exploitation and harvest for a blue crab fishery using mark-recapture information. Recreational  
526 harvest was highest in tributaries near population centers along Maryland's Western Shore, and  
527 in the Miles and Wye Rivers on the Eastern Shore. These areas also had some of the highest  
528 recreational and total exploitation rates. The extremely high total exploitation rates in the  
529 Patuxent (0.71) and Magothy (0.68) rivers indicate that total exploitation was high enough in  
530 some tributaries to remove the majority of male crabs large enough to recruit to the fishery each  
531 month. If these removals substantially reduce the operational sex ratio (the ratio of mature males  
532 to reproductively active females), they could potentially lead to sperm limitation (the reduction  
533 in lifetime reproductive output) of females maturing in these locations (Ogburn et al. 2014,  
534 [2019](#)). In contrast, recreational exploitation made up a smaller proportion of total exploitation,  
535 and recreational harvest was smaller, at sites along the southern portion of the Eastern Shore and  
536 in the mainstem bay.

537

538 One reason for the difference in commercial reporting rate between 2014 and 2015 could  
539 be the effect of prior crab tagging efforts by our lab (Turner et al. 2003, Aguilar et al. 2005,  
540 Corrick 2018). We have a ~~close~~ good working relationship with a number of crabbers in the areas  
541 tagged in 2014 (Rhode River, South River, Eastern Bay, Little Choptank River, Rhode River,  
542 South River) but have not had as much outreach within other areas of the Bay tagged less  
543 frequently. This could have leading to greater reporting in 2014 when tagging was concentrated  
544 in these areas. However, the 2015 commercial reporting rate is more accurate on a bay-wide  
545 scale because of the broader spatial distribution of tagging, and this was the one these data were  
546 used in harvest ratio calculations herein. Investigating possible spatial variations in reporting  
547 would be particularly valuable if this type of mark recapture study is were used on a regular basis  
548 in the future to inform the stock assessments. While there also were also slight differences in  
549 reporting rates among sex (males vs males and females), the direction of their difference  
550 changed by year and could reflect variations in high-value captures, gear types, and effort  
551 between years differences are unlikely to be significant given the stochasticity of high-value  
552 captures. For example: single additional high-value capture of a male in 2014 would change the  
553 male reporting rate from 0.930 to 0.906, well in line with the rate for males and females  
554 combined (0.884).

555 Information on the size of the recreational blue crab harvest in Maryland has regularly  
556 been identified as a critical management need. Prior studies in 2001, 2002, 2005, and 2009 using  
557 effort survey methods (Ashford and Jones 2002a, 2002b, 2005, 2011) estimated that the ratio of  
558 recreational to commercial harvest within Maryland remained close to the 8% estimate chosen in  
559 the stock assessment. Estimates of recreational harvest from effort surveys averaged 11.6% of

560 commercial male hard crab harvests and 5.8% of total commercial harvests. In the present study,  
561 recreational harvest of male hard crabs in 2015 was estimated at 11.2% the size of commercial  
562 male hard crab harvests and 6.5% of total commercial harvests (male and female) when  
563 movement was included. ~~€Although comparison of effort surveys and a Maryland-wide mark-~~  
564 ~~recapture experiments conducted in the same year would be preferable, but the~~  
565 ~~consistency similarity between of recreational harvest fraction estimates hints that they likely are~~  
566 ~~reasonable estimates of the true values suggests that the methods proposed herein are consistent~~  
567 ~~with effort surveys.~~

568 ~~With data for only a single statewide recreational harvest estimate using mark-recapture~~  
569 ~~methods, it is difficult to quantify uncertainty, but the sensitivity of the estimate to some~~  
570 ~~potential sources of uncertainty can be evaluated discussed (Semmler 2016). In terms of~~  
571 ~~uncertainty related to underreporting, 1) the underreporting of high value tags by the~~  
572 ~~commercial sector would increase the estimated recreational harvest an equivalent amount (e.g.~~  
573 ~~5% underreporting would yield a 5% increase in the recreational harvest estimate). 2) In~~  
574 ~~addition, underreporting of regular value tags by the commercial sector would also inflate~~  
575 ~~recreational harvest estimates, with the magnitude of the increase depending on whether~~  
576 ~~underreporting it occurred in areas with only commercial recaptures (no effect), a high fraction of~~  
577 ~~commercial recaptures (minimal effect), or a relatively high fraction of recreational recaptures~~  
578 ~~(larger effect). The regions where commercial underreporting could have occurred were in areas~~  
579 ~~with only commercial recaptures, so underreporting would not have substantially inflated the~~  
580 ~~estimate of recreational harvest. The only cases of commercial reporting we are aware of were in~~  
581 ~~areas with only commercial recaptures, so we do not think underreporting substantially inflated~~  
582 ~~the estimate of recreational harvest. 3) R~~

583 Other sources of uncertainty include the focus on a single year and the lack of tagging  
584 data during the first and last months of the harvest season within that year. Between years, when  
585 replacing the 2015 commercial harvest data with the previous 5 years of data, yields the ratios of  
586 recreational to total commercial harvest of were 10.4% – 13.1% (11.2 % in 2015), suggesting that  
587 our estimate was not very sensitive to annual variation in commercial harvest. 4) Within 2015,  
588 setting the recapture ratios in April, May, and November to the June and October values instead  
589 of assuming a value of 0 increased the percent of recreational harvest from 11.2% to 11.3%,  
590 suggesting that recreational harvest in these months was negligible. Setting the recapture ratio flat  
591 across the early and late season (April / May = June, November = October), did not substantially  
592 alter harvest estimates (11.29% vs 11.17% ) and this is bound to be an overestimate. Repeating  
593 the mark-recapture study in one or more years- in combination with effort surveys or recreational  
594 harvest reporting would help assess the validity of this approach- would provide additional  
595 information for estimating uncertainty. If these mark-recapture methods, or the effort surveys,  
596 were implemented annually at the baywide scale, either or both could improve stock assessments  
597 by replacing the constant 8% value currently used.

598 Additionally, uncertainty in conditional movement probabilities themselves are important  
599 to consider. While we do not have a means of assessing error in these estimates, consistency in  
600 movement probabilities between years may serve as some indication of their reliability. To  
601 assess this, we compare movement probabilities matrices for the four reporting areas which were  
602 tagged in both 2014 and 2015. There was a strong degree of correlation between the movement  
603 probabilities ( $r = 0.99$ ,  $t = 36.72$ ,  $p < 0.01$ ), supporting the expectation that these probabilities  
604 were reliably determined.

605 Our method of calculating recreational harvest based on commercial harvest assumes that  
606 the level of commercial harvest is reliably known. Commercial crabbers in Maryland are  
607 required to report their daily harvest under penalty of license suspension/revocation and the state  
608 has an electronic reporting system coupled with a check point program to evaluate compliance  
609 with reporting, although we do not know the degree of compliance in 2014 and 2015. While  
610 these measures help ensure reliable harvest estimates, an analysis of the possibility of random  
611 error and potential differences in harvest reporting across the state would further strengthen  
612 confidence in this method of calculating recreational harvest estimates.

613 The proportion of recreational to total commercial harvest (8%) used in the stock  
614 assessment was set prior to the moratorium on recreational harvest of female crabs in Maryland  
615 in 2008 (Miller et al. 2011). However, after 2008, recreational harvest was thought to be better  
616 calculated as 8.0% of male harvests (CBSAC 2016). While recreational harvest could have been  
617 8.0% of male harvests in 2011, our estimated harvest in 2015 equates to 11.2% of male harvests,  
618 representing a 40% increase over the 8% guideline. It's unclear whether this increase resulted  
619 from the shifting of recreational fishing effort from female onto male crabs, or simply from  
620 increased recreational fishing effort targeting male crabs.

621 The estimated contribution of the recreational fishery to total harvest we observed in this  
622 study was at the lower end of recreational harvest fractions for comparable to many other  
623 temperate or subtropical crab fisheries, and is comparable to other blue crab fisheries within the  
624 US. In Maryland, recreational crabbers take roughly 6.5% percent of the commercial harvest of  
625 male and female blue crabs. In Louisiana, which has the second largest commercial blue crab  
626 fishery by state in the US, recreational crabbers take in roughly 5% of all blue crabs (Guillory  
627 1999b, LDWF 2011). Similar results were observed for recreational blue crab fishers in

628 Galveston Bay, Texas (5.6% of harvest) (TPW 2007). In Oregon, 5.6% of landings in the  
629 Dungeness crab *Metacarcinus magister* fishery are taken by recreational crabbers (ODFW 2014).  
630 In contrast, some crab fisheries have a much higher proportion of recreational harvest including  
631 the mud crab *Scylla serrata* fishery in Queensland, Australia (~50% recreational harvest) (Ryan  
632 2003), the Dungeness crab fishery in Washington (41% of harvest) (WDFW 2016) and the blue  
633 swimming crab *Portunus pelagicus* fishery in South Australia (29.8% of harvest) (Jones 2009).  
634 ~~Many other~~ Other crab fisheries, such as those for Atlantic Jonah crabs *Cancer borealis* and  
635 California Dungeness crabs, do not have sufficiently reliable recreational harvest data to make  
636 similar comparisons (ASMFC 2015, CA OPC 2014). Understanding the contribution of  
637 recreational fisheries to total harvests, estimated at 12% globally, is a critical issue in  
638 conservation of fishery resources (Cooke and Cowx 2004). The methods used here could be  
639 applied to blue crab fisheries in other regions or used as a model for crab fisheries for which  
640 recreational harvest estimates are needed and commercial harvests are known.

641 ~~In Maryland, recreational harvest of male crabs was 11.2% of commercial male harvest, a~~  
642 ~~40% increase over the 8% expected after recreational harvest of females was banned in 2008.~~  
643 ~~These updated harvest values should be incorporated into future blue crab stock assessments.~~  
644 ~~Recreational harvests remain small in comparison to the commercial sector, and this difference,~~  
645 ~~while notable, likely did not have a large effect on the overall exploitation of male crabs.~~  
646 ~~Nonetheless, accurate and timely estimates of harvest and exploitation are required to reliably~~  
647 ~~make management decisions. For example, the exploitation fraction of adult males has not~~  
648 ~~exceeded 33% in recent history, the threshold level triggering male harvest restrictions (CBSAC~~  
649 ~~2015). The exploitation fraction of males has often been as low as 21.6–22.2% (CBSAC 2015).~~  
650 ~~However, in 2011 male exploitation was estimated to be 32% (CBSAC 2015). If recreational~~

651 ~~male harvests were similar in 2011 to those seen here, then exploitation would have been even~~  
652 ~~closer to that trigger. However, one caveat to this possibility is that the 33% trigger is calculated~~  
653 ~~for the Chesapeake Bay as a whole. While it makes sense that banning recreational harvest of~~  
654 ~~females might have shifted fishing effort onto male crabs in Maryland, no such ban occurred in~~  
655 ~~Virginia.~~

656 The present study illustrates clear influence of animal movement when mark-recapture  
657 [methods](#) are used to estimate harvest and exploitation rates [for multiple harvest areas](#). Results of  
658 the study reduce uncertainty in recreational harvest estimates by [complementing](#) results of [effort](#)  
659 surveys and could be useful for refining stock assessments of the [blue crab](#) fishery in Chesapeake  
660 Bay. In addition, these new methods for including animal movement could be useful for other  
661 fisheries for which [variation in](#) sector-specific [harvest or](#) exploitation rates among harvest areas  
662 [is of interest](#) and the scale of movement of the target species exceeds that of harvest area  
663 boundaries. These methods were applied to a two-sector fishery, but could be modified for one to  
664 several fishery sectors for blue crabs in other regions or for other species and fisheries with  
665 similar characteristics.

666

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