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ARTICLE

The influence of blue crab movement on mark–recapture estimates of recreational harvest and exploitation

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

Résumé : S'il est nécessaire de quantifier les prises totales pour appuyer une gestion durable des pêches, l'estimation des prises des pêcheurs sportifs constitue toujours un défi. Les estimations de prises issues d'études de marquage–recapture se sont avérées utiles, mais les déplacements et migrations des animaux peuvent biaiser certaines de ces estimations. Afin d'améliorer les estimations des prises de pêche sportive, d'explorer les motifs saisonniers et spatiaux des prises et de comprendre l'influence des déplacements des animaux sur les taux d'exploitation, une expérience de marquage–recapture a été menée pour la pêche au crabe bleu (*Callinectes sapidus*) dans les eaux du Maryland de la baie de Chesapeake (États-Unis). Les données ont été analysées par des méthodes standards de retour d'étiquettes et en utilisant des équations révisées qui tiennent compte des déplacements des crabes entre les différents secteurs de signalement. Les prises de pêche sportive estimées en utilisant des calculs normalisés sont de 4,04 millions de crabes. Si les déplacements sont inclus dans les calculs, le chiffre estimé s'élève à 5,39 millions, soit une augmentation de 34 %. En incluant les déplacements des crabes, les prises de pêche sportive au Maryland sont estimées s'élever à 6,5 % des prises commerciales, un résultat qui concorde avec ceux d'évaluations de l'effort passées. Les nouvelles méthodes présentées sont largement applicables à l'estimation des prises de pêche sportive dans les pêches qui ciblent des espèces mobiles et pour lesquelles les variations spatiales des prises commerciales sont. [Traduit par la Rédaction]

1. Introduction

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

Blue crabs (*Callinectes sapidus*) can make extensive movements during the open season of the blue crab fishery in Maryland waters of the Chesapeake Bay. The fishery targets this highly mobile species, which is known to make short-duration movements as well as long-distance ontogenetic migrations (McConaugha et al. 1983; Wolcott and Hines 1990; Hines 2007). For crabs of harvestable size (>127 mm carapace width in Maryland), this movement can be as much as 569 $m\cdot day^{-1}$, far enough to allow movement between harvest areas (Wolcott and Hines 1990). Crabs in Maryland are targeted by two fishery sectors: commercial fishers, which are required to report their harvest, and recreational fishers, which are not. Fishers in both sectors use

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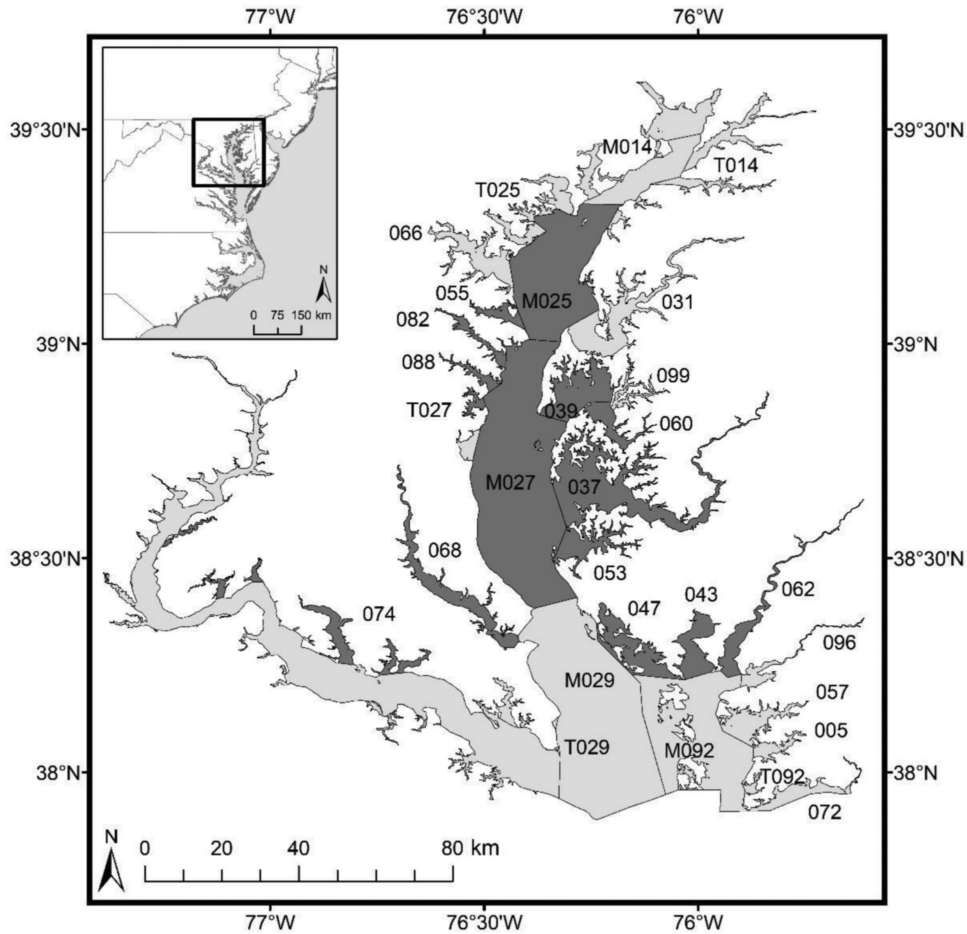
Fig. 1. Boundaries of the 29 commercial harvest reporting areas in Maryland waters of the Chesapeake Bay. Three-digit numerical designations assigned for reporting data (i.e., site codes) for each reporting area are shown within or adjacent to their boundaries. Site codes preceded by M or T represent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



multiple gear types (e.g., crab pot, trotline, handline, crab scrape; Cargo 1954; Van Engel 1962; Kennedy et al. 2007). Knowledge of crab movement is important for understanding the dynamics of the crab population (Hines 2007) and spatiotemporal patterns of harvest effort (Slacum et al. 2012).

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

2. Methods

A large-scale mark–recapture study was conducted to study harvest patterns in the blue crab fishery in Maryland waters of Chesapeake Bay. Detailed below are (*i*) the tagging methods and experimental setup for the mark–recapture study, (*ii*) methods used to estimate recreational harvest and exploitation from the tagging results without accounting for crab movement, and (*iii*) the adjusted equations used to include the influence of crab movement on these estimates. Using mark–recapture data to answer these questions relies on an important set of assumptions, namely that marked animals (*i*) are well-mixed within the population, (*ii*) behave in a similar manner as unmarked individuals, and (*iii*) do not vary in catchability (Schwarz and Taylor 1998). Evidence from prior studies indicates that crabs tagged using the

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 code	Site	Date	Released	Recaptured	Estimated as	Peak recapture ratio (August)
005	**Big Ammenesex**	—	—	—	**Nanticoke River**	**0.046**
M014	**Mainstem NN**	—	—	—	**Mainstem N**	**0.009**
T014	**Tribs. NN**	—	—	—	**Magothy River**	**0.703**
M025	Mainstem N	5 Aug. 2015	385	52	—	0.009
T025	**Tribs. N**	—	—	—	**Magothy River**	**0.703**
M027	Mainstem S	31 July 2015	357	23	—	0.007
T027	Tribs. S	21 July 2015	387	187	—	0.304
M029	**Mainstem SS**	—	—	—	**Mainstem S**	**0.007**
T029	**Tribs. SS**	—	—	—	**Patuxent River**	**1.273**
031	**Chester River**	—	—	—	**Eastern Bay**	**0.310**
037	Choptank River	30 July 2015	343	91	—	0.269
039	Eastern Bay	17 July 2015	381	80	—	0.310
043	Fishing Bay	25 June 2015	220	22	—	0.000
047	Honga River	19 June 2015	277	32	—	0.000
053	Little Choptank River	18 June 2015	259	56	—	0.046
055	Magothy River	29 July 2015	350	123	—	0.703
057	**Manokin River**	—	—	—	**Nanticoke River**	**0.046**
060	Miles River	4 Aug. 2015	181	46	—	0.670
062	Nanticoke River	25 Aug. 2015	376	80	—	0.042
066	**Patapsco River**	—	—	—	**Magothy River**	**0.703**
068	Patuxent River	15 July 2015	182	21	—	1.273
072	**Pocomoke Sound**	—	—	—	**Nanticoke River**	**0.046**
074	Potomac (Maryland tribs.)	20 July 2015	305	150	—	0.239
082	Severn River	10 Aug. 2015	195	40	—	2.363
088	South River	22 July 2015	341	160	—	0.471
M092	**Tangier Sound**	—	—	—	**Nanticoke River**	**0.046**
T092	**Tangier Sound tribs.**	—	—	—	**Nanticoke River**	**0.046**
096	**Wicomico River**	—	—	—	**Nanticoke River**	**0.046**
099	**Wye River**	—	—	—	**Miles River**	**0.670**
Total			4539	1163		

Note: Site codes preceded by M or T represent reporting areas that were split into portions spanning the mainstem bay (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).

method described below undergo full spawning migrations and otherwise behave similarly to unmarked individuals (Turner et al. 2003; Aguilar et al. 2005) and are healthy and thus unlikely to have reduced catchability (Turner et al. 2003). Several characteristics of the blue crab fishery in Maryland — especially the continuous fishery during the time of year when crabs are available for tagging, the large spatial scale of the study area, and expected strong spatial and temporal variation in fishing effort — prevented us from meeting the assumption that tagged crabs were well-mixed within the state-wide population. Instead we estimated spatial and temporal variation directly in smaller regions and then aggregated estimates up to the state-wide level as detailed below.

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

$$(1)\qquad H_R = \frac{nR}{nC} \cdot H_C$$

where H_R was the total estimated recreational harvest, nR/nC was the ratio of the number of recreational recaptures (nR) to commercial recaptures (nC) observed from the tagging experiment, hereinafter referred to as the “recapture ratio”, and H_C was the total reported commercial harvest. A similar method is employed in the management of striped bass (*Morone saxatilis*) fishery, whereby commercial discards are estimated based on known recreational discards and the ratio of tags reported from discarded fish in the commercial sector to the recreational sector (NFSC 2019).

Because we were unable to ensure that tagged crabs were well-mixed in the population, we designed the mark–recapture experiment to directly estimate variability in recapture ratio over the course of the crabbing season (section 2.2.2) and spatial variability in recapture ratio across harvest reporting areas (section 2.2.3). In addition, unequal tag reporting between the two sectors was accounted for (section 2.2.1). Finally, the calculation of recapture ratio by harvest area could have been influenced by crab movement, so the analyses were conducted both with and without information on crab movement, making it possible to identify the effects of movement on estimates of harvest and exploitation rates (section 2.3.1).

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

$$(2)\qquad \text{uSector} = \frac{RP_{\text{Sector}}}{RL}$$

where uSector was the exploitation rate (proportion of crabs caught per month) of either the recreational or commercial

Table 2. The number of male blue crabs (*Callinectes sapidus*) that 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.

Site	Release	Date	Released	Recaptured
South River	Early	14 July 2014	102	54
	Middle	11 Aug. 2014	233	126
	Late	10 Sept. 2014	108	14
Rhode River	Early	24 June 2014	53	22
	Middle	4 Aug. 2014	333	201
	Late	8 Sept. 2014	135	38
Eastern Bay	Early	23 June 2014	61	16
	Middle	13 Aug. 2014	343	123
	Late	16 Sept. 2014	185	31
Little Choptank River	Early	16 July 2014	338	66
	Middle	6 Aug. 014	312	35
	Late	17 Sept. 2014	58	2
Total			2261	728

Note: 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.

sector, RP_{Sector} was the number of tagged crabs that were captured by that sector, and RL was the number of tagged crabs initially released. As before, potentially influential factors were accounted for in these calculations, including unequal reporting between the two sectors (section 2.2.4), various sources of tag loss (section 2.2.4), and effects of crab movement (section 2.3.2).

2.1. Mark–recapture experiments

A total of 6800 adult male blue crabs were tagged and released to study the blue crab fishery in Maryland waters of the Chesapeake Bay over two consecutive summers of 2014 and 2015. During the first summer (2014), 2261 crabs were tagged and released during early summer (June–July), late summer (August), and fall (September) in four representative harvest reporting areas to determine seasonal trends in the recapture ratio (Table 2). During the second summer (June–August 2015), 4539 crabs were tagged and released in 15 representative harvest reporting areas to investigate spatial patterns in recapture ratio and sector-specific exploitation rates (Table 1).

Crabs were tagged with 2.5 cm × 5 cm vinyl discs attached to their dorsal surface with stainless steel wire wrapped around the lateral spines (Turner et al. 2003; Aguilar et al. 2005). The front of each tag used for this study had a unique identification number, the word "Reward", and contact information for reporting recaptures either by phone or web form. Standard rewards were \$5 (all money is in US dollars). Five percent of tags were randomly assigned high-value tags for estimating reporting rates. The high value tags had \$50 written in black ink on the front and back. On the reverse side, all tags listed information for fishers to record and report (tag number, date, GPS coordinates, capture depth, gear type, and crab sex). Within each reporting area, all tagging was conducted on the same day. Crabs were tagged at given sites over the course of day and were released as they were tagged while drifting across the tributary. This helped disperse crabs across the tagging area. Although tagged crabs were occasionally recaptured more than once, only the initial recapture was used in analyses. Some crabs that were released in Maryland were recaptured in Virginia (n = 44 of 2039 total returns in 2015). Nearly 90% of crabs recaptured in Virginia were captured by commercial fishers. While these returns were included in harvest calculations when movement was not considered, tag returns from these crabs were excluded when making estimates that accounted for crab movement. We followed the Guide for Care and Use of Laboratory Animals in our crab tagging protocol.

2.2. Estimating recreational harvest and exploitation without animal movement

2.2.1. Estimating statewide recreational harvest

The statewide recreational harvest of crabs in 2015 (H_R) was estimated using crabs that were tagged and released in 15 representative harvest reporting areas in 2015 (n = 4539). Our multiple harvest area approach was similar to that of the first year of release and year of first recapture for multistratum capture–recapture models of an open population as described in Brownie et al. (1993) except that we also accounted for two harvest sectors, seasonal variation in harvest, and tag reporting rates. H_R was computed by taking the ratio of recreational to commercial recaptures from the mark–recapture experiment and then multiplying this ratio by the reported commercial landings:

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

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

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

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

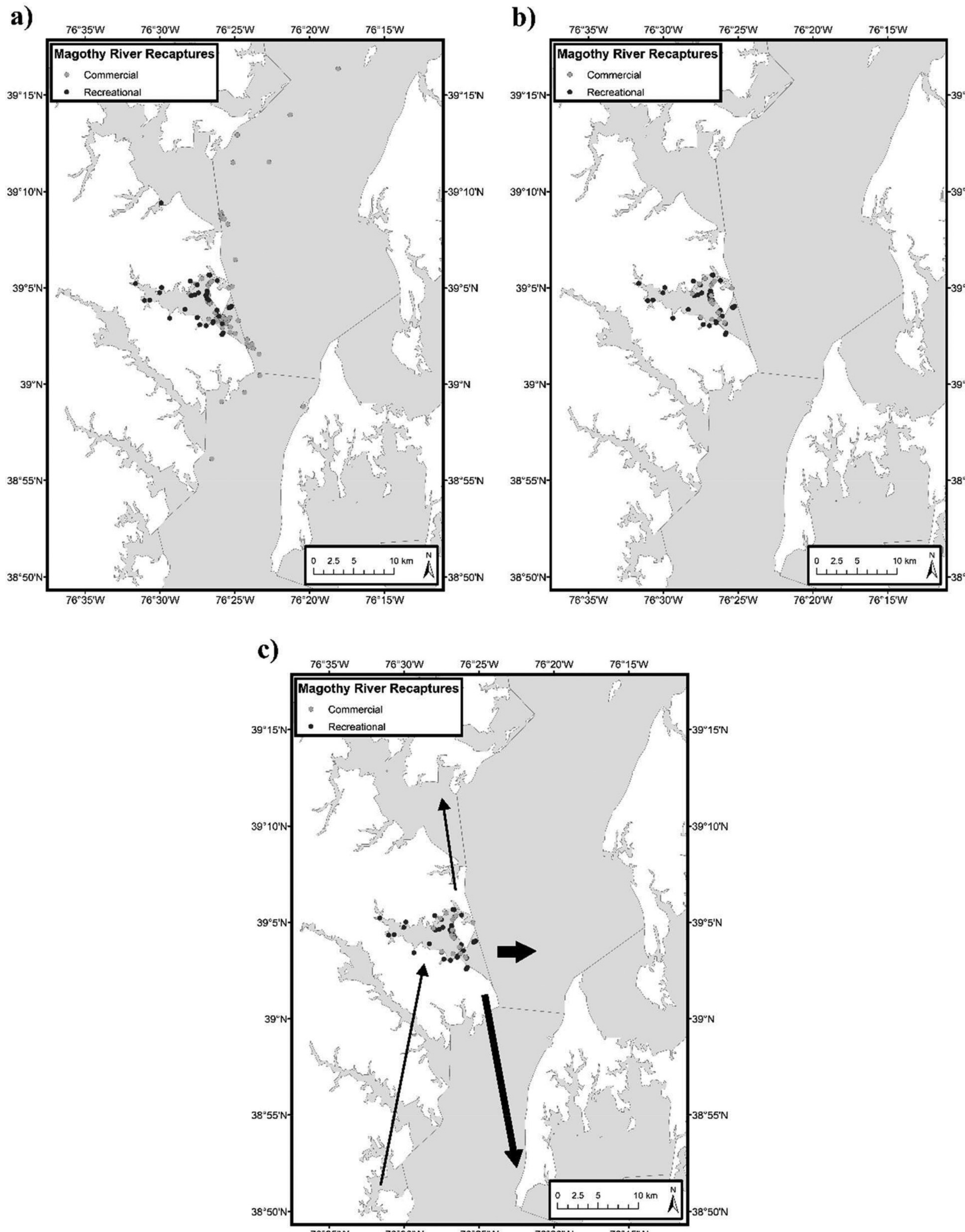
where $RP_{R,l,m}$ and $RP_{C,l,m}$ were the raw number of recaptures for each sector reported by crabbers in the given area and month, and RR_R and RR_C (eq. 5) were the tag-reporting rates for recreational and commercial crabbers in 2015; other terms are as defined previously. A single reporting rate was calculated for each sector in each year. These were calculated across all harvest reporting areas, using standard and high-value tags as follows:

$$(5) \qquad RR_{Sector} = (R_s/N_s)/(R_r/N_r) = R_sN_r/R_rN_s$$

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

Similarly, it was not feasible within our budget to determine the recapture ratio (nR/nC) for all 29 reporting areas directly through releases of tagged crabs. For areas where tagging was not conducted (n = 14), the ratio of recreational to commercial

Fig. 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 River 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.



recaptures for nearby reporting area was used (Table 1). For example, crabs were not tagged in the Manokin River, so the recapture ratio from the nearby Nanticoke River was used in calculations. Decisions about these data substitutions were based on our best professional judgement and took into account discussions with fishery managers, characteristics such as proximity to other sites, and visual comparisons of the level of residential development in satellite imagery.

2.2.2. Seasonal variation in recapture ratios

Monthly commercial harvest data were available for each reporting area, and tagging data provided reliable estimates of recreational recapture rates for a single month, which allowed calculation of monthly ratios of recreational to commercial recaptures (nR_{Season}/nC_{Season}) across the harvest season. Recapture data from 2014 and 2015 were used to calculate these monthly recapture ratios. In 2014, a total of 2261 crabs were tagged in early summer, late summer, and fall in four harvest areas representative of the Eastern and Western Shore tributaries of Maryland's Chesapeake Bay (South River, Rhode River, Eastern Bay, Little Choptank River; Table 2). In 2015, 1368 crabs were tagged in these areas (Table 1). Hence, a total of 3629 tagged crabs were used to identify monthly variations in recapture ratios.

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

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

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

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

2.2.3. Spatial variation in recapture ratios

To characterize spatial variation in the ratio of recreational to commercial recaptures, records of the 4539 crabs that were tagged in 15 harvest reporting areas in 2015 were analyzed (Table 1). These releases occurred during the middle of the harvest season (July–September), when recreational harvests were expected to be at their peak. The exact date of each tagging event was dependent on weather and the availability of commercial fishermen to assist with capturing crabs in each of the 15 locations. Recreational and commercial recaptures occurring within 60 days of release were tallied. The 60-day time frame for recaptures was used because it accounted for 98% of recaptures reported by the end of the fishing season.

When calculating monthly ratios of recreational to commercial harvest for each reporting area in 2015, additional estimates were necessary because tagging occurred only once at each site in 2015, in July, August, or September (Table 1). The ratios of recreational to commercial recaptures were estimated for all months of the harvest season with no available data using the seasonal relationship developed above (eq. 6). To calculate the recapture ratio ($nR_{l,m}/nC_{l,m}$) for a given month (m) in a specific harvest area (l), it was necessary to determine how recapture ratios in that month (m) compared with those in the month the release occurred (o). Specifically, we divided the recapture ratio for that month of the seasonal relationship ($nR_{Season,m}/nC_{Season,m}$) by the recapture ratio of the seasonal relationship in the month when the release occurred ($nR_{Season,o}/nC_{Season,o}$). This was then multiplied by the recapture ratio observed at that site in 2015 ($nR_{2015l,o}/nC_{2015l,o}$) following eq. 7:

$$\text{(7)} \qquad \frac{nR_{l,m}}{nC_{l,m}} = \frac{\left(\frac{nR_{Season,m}}{nC_{Season,m}}\right)}{\left(\frac{nR_{Season,o}}{nC_{Season,o}}\right)} \cdot \frac{nR_{2015l,o}}{nC_{2015l,o}}$$

2.2.4. Spatial variation in exploitation

To determine spatial variation in exploitation, we calculated exploitation rates for each fishery sector for each of the first 2 months (standardized as two 30-day periods) after each release in each of the harvest areas in 2015. Monthly exploitation rates were calculated by comparing the number of crabs that were caught within the month and the number of crabs available to be caught at the beginning of the month. All tagged crabs were assumed to be available for harvest in the first month. In the second month, a tagged crab was considered to be unavailable for recapture if it had died, molted, or otherwise lost its tag.

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

$$\text{(8)} \qquad uSector_{l,m} = \frac{RP_{Sector,l,m}/RR_{Sector}}{RL_{l,m}}$$

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

$$\text{(9)} \qquad uSector_{l,m} = \frac{RP_{Sector,l,m}/RR_{Sector}}{[RL_{l,m-1} - (C_{l,m-1} + M_{l,m-1} + D_{l,m-1} + L_{l,m-1})]}$$

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

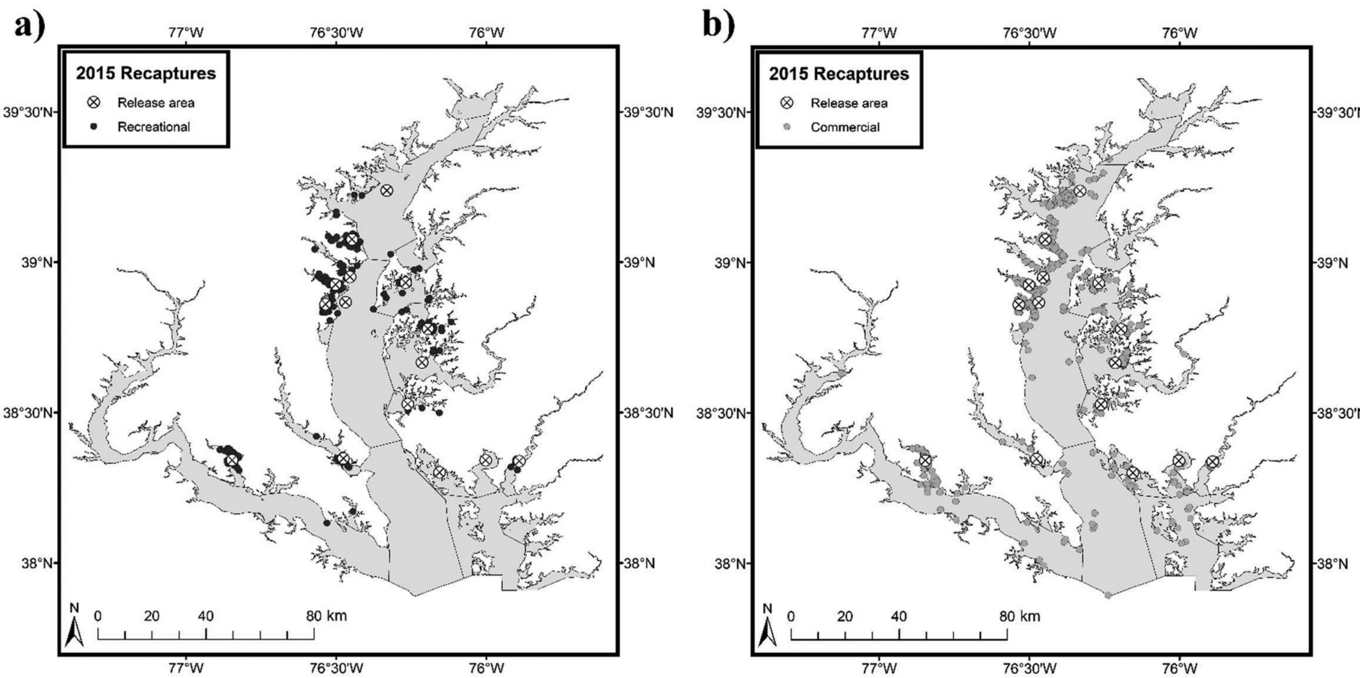
In this analysis, natural mortality was set at a rate of 0.075 $month^{-1}$ based on the instantaneous rate of natural mortality (M = 0.9) used in the stock assessment (Miller et al. 2011). The proportion of crabs that had molted prior to the given month was based on a probabilistic model, using published data on the time to molting for tank-held crabs in degree-days (Tagatz 1968), as well as average monthly water temperatures for the mainstem

Table 3. Estimates of recreational harvest of blue crabs (*Callinectes sapidus*) calculated based on release location (standard method) or recapture location (movement-adjusted method).

	Standard method	Movement-adjusted
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%

Note: 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.

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



Chesapeake Bay obtained from the Maryland Department of Natural Resources. This resulted in a molting rate ranging from 0.107 month^{-1} (18 June 2015 release in the Little Choptank River) to 0.199 month^{-1} (11 July 2015 release in the Patuxent River), which corresponded to 492 and 556 degree-days passing at these sites, respectively. Physical tag loss was estimated as 30 times the daily rate of tag loss (0.00067 day^{-1}), previously estimated from tank-holding studies (A. Hines, E. Johnson, R. Aguilar, and P. Roberts, unpublished data). Given that the number of tagged crabs remaining at large decreased with time, exploitation calculations for both months were then somewhat conservative. This is due to the fact that calculations only accounted for recaptures, tag loss, molting, or mortality that occurred prior to each month, ignoring any losses that occurred during the period of calculation.

2.3. Revised estimates accounting for crab movement

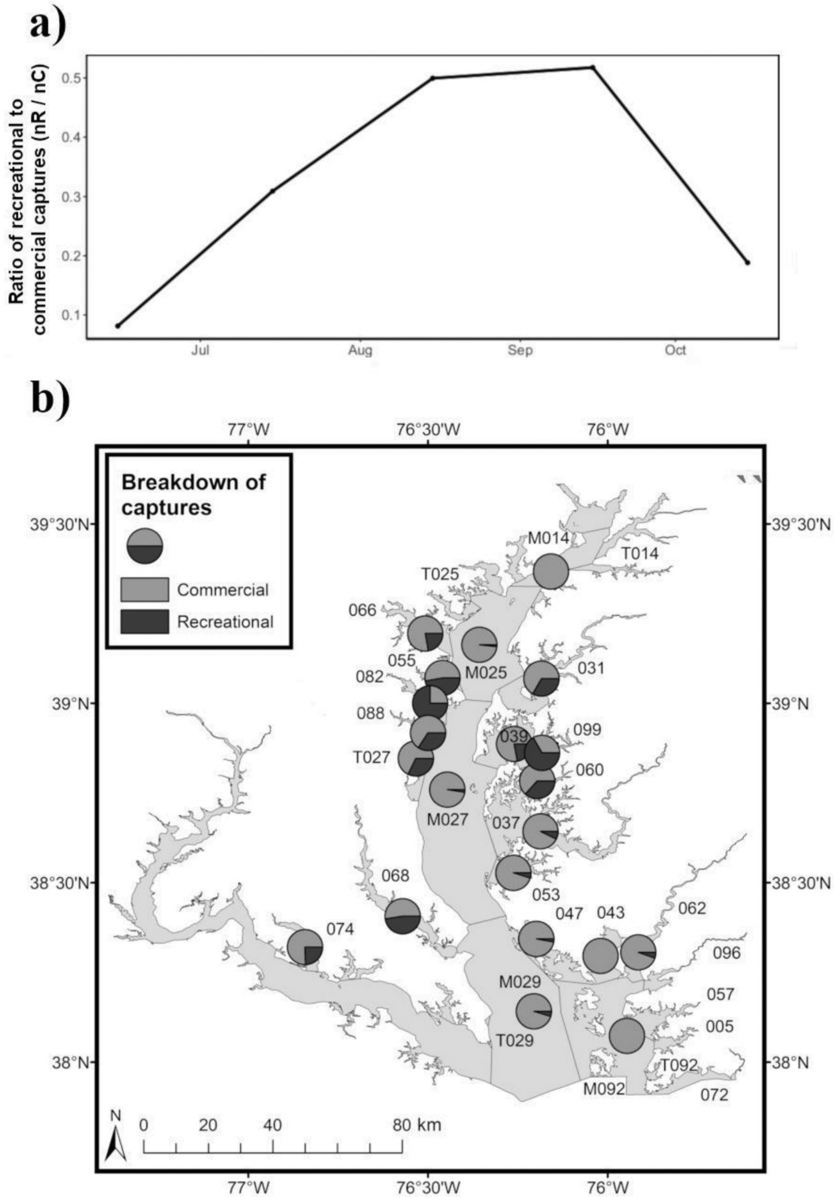
2.3.1. Revised estimates of recreational harvest

Our basic approach for evaluating the effect of movement was to multiply reported commercial harvest (H_C) by two estimates of recapture ratio calculated either with or without accounting for movement and then comparing the two resulting sets of recreational harvest estimates. Without crab movement, H_R was calculated using eqs. 3–7 above, which were based on crabs released in each reporting area and recaptured in all areas (Fig. 2*a*). To incorporate crab movement, we calculated H_R for each area based on crabs released in any reporting area and only those recaptured in the reporting area of interest (Fig. 2*b*). These methods yield identical results when no movement occurs among reporting areas. Comparing their results allowed us to estimate the effect of crabs moving from the release area into a different area before recapture on area-specific recapture ratios.

2.3.2. Revised estimates of exploitation

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

Fig. 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 (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.



adjusted exploitation in the first (eq. 10) and second (eq. 11) month were calculated as follows:

$$(10) \qquad \mathrm{uSector}^*_{l,m} = \frac{\mathrm{RP}^*_{\mathrm{Sector},l,m}/\mathrm{RR}_{\mathrm{Sector}}}{\mathrm{RL}^*_{l,m}}$$

$$(11) \qquad \mathrm{uSector}^*_{l,m} = \frac{\mathrm{RP}^*_{\mathrm{Sector},l,m}/\mathrm{RR}_{\mathrm{Sector}}}{\left[\mathrm{RL}^*_{l,m-1} - (C_{l,m-1} + M_{l,m-1} + D_{l,m-1} + L_{l,m-1})\right]}$$

using adapted versions of eqs. 8 and 9, where $\mathrm{RP}^*_{\mathrm{Sector},l,m}$ indicated the number of tagged crabs recaptured from the release during that month, after accounting for crab movement (see eq. 12), and $\mathrm{RL}^*_{l,m-1}$ indicated the number of crabs available to be caught during that period after accounting for movement (see eq. 13).

When implementing eqs. 10 and 11, the number of recaptures ($\mathrm{RP}^*_{\mathrm{Sector},l,m}$) was adjusted to reflect crab movement during the month by (*i*) removing crabs that were released in the reporting area and were captured in other reporting areas and (*ii*) adding crabs that were released in other reporting areas and were captured in the reporting area (Fig. 2*c*). This recapture adjustment was calculated as follows:

$$(12) \qquad \mathrm{RP}^*_{\mathrm{Sector},l,m} = \mathrm{RP}_{\mathrm{Sector},l,m} + \left(\sum_{b=1}^{14} \mathrm{RP}_{\mathrm{Sector},b,l}\right) - \left(\sum_{c=1}^{28} \mathrm{RP}_{\mathrm{Sector},l,c}\right)$$

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.

		Recapture ratio		Recreational harvest	
Reporting area	Site code	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

Note: Data are reported with and without movement-adjustment. Site codes preceded by M or T represent reporting areas that were split into portions spanning the mainstem bay (M) and adjacent tributaries (T).

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

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

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

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

3. Results

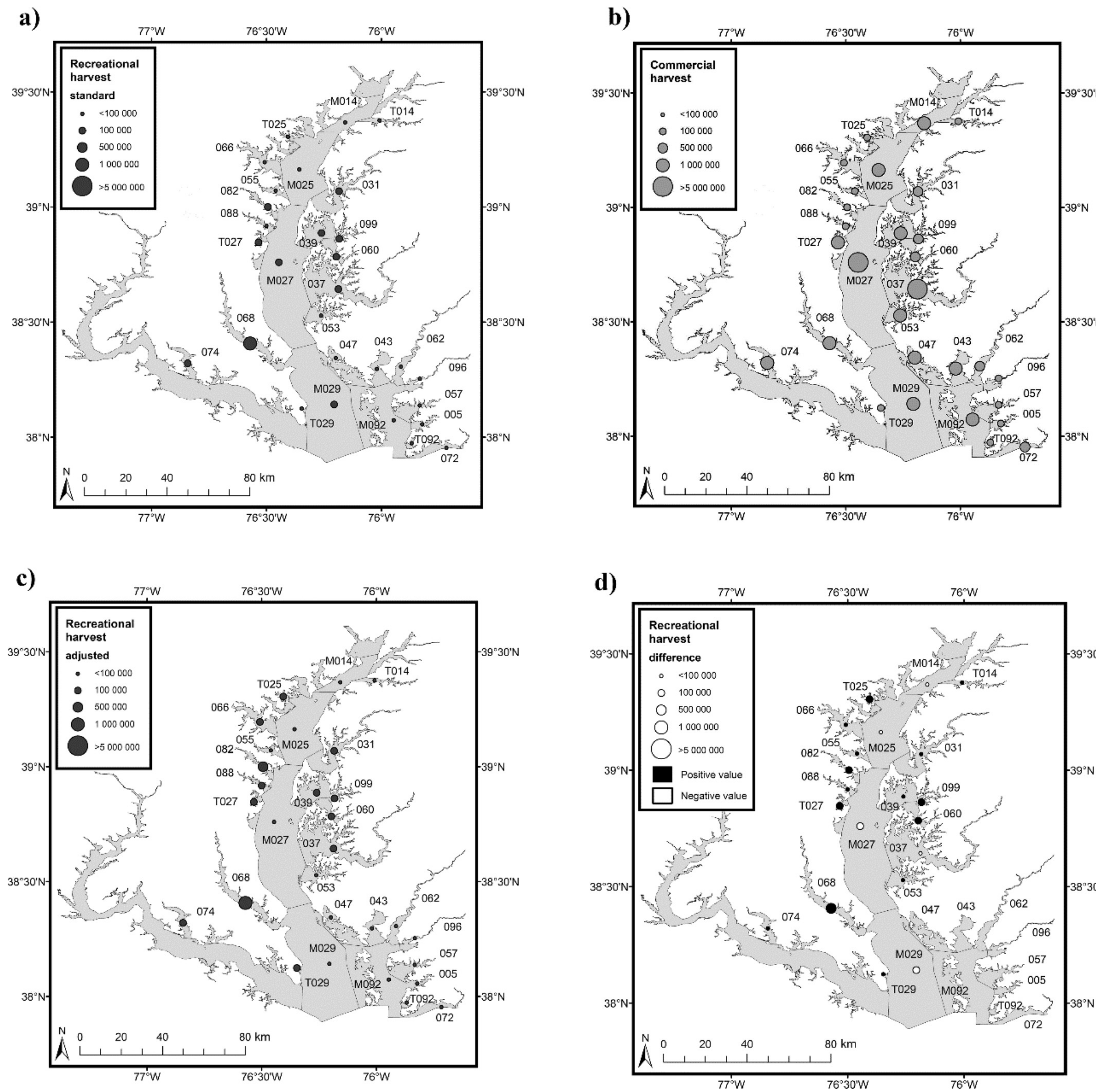
3.1. Tag return rates

Of the 6800 tagged crabs released in 2014 and 2015, a total of 1891 tags were returned (Tables 2 and 3) for an overall return rate of 27.8%. This rate is higher than prior studies on female blue crabs (Aguilar et al. 2005: 4%–17%; Turner et al. 2003: 5%–21%; Rittschof et al. 2010: 15.6%). This can be expected because males are the primary target of the fishery. A similar return rate for tagged female crabs (8.6%) was seen from a separate but concurrent study performed by our lab, with an overall exploitation rate of 10.5% (Corrick 2018).

When examining seasonal variations in recapture ratios, the analysis included 1211 recaptures from 3629 crabs that were tagged during 16 releases (12 releases in 2104 and four releases in 2015; Table 2). Of the 2261 male crabs released in 2014, 728 (32.2%) were recaptured and reported (Table 2). Of these, 527 (72.4%) were captured by commercial crabbers, 195 (26.8%) by recreational crabbers, and 5 (0.7%) by unidentified crabbers. Of the 3085 \$5 tags (male and female) released in 2014, 786 (25.5%) were recaptured. Of the 163 \$50 tags released, 47 (28.8%) were recaptured. This resulted in an overall reporting rate of 88.4% across the fishery in 2014, with sector-specific reporting rates of 93.3% and 75.1% for the commercial and recreational fisheries, respectively. Area-specific reporting rates in 2014 ranged from 80.2% in South River to 98.5% in Eastern Bay. Of the additional 1368 male crabs released in the four reporting areas in 2015, 483 (35.3%) were recaptured and reported (Table 1). Of these, 360 (74.5%) were captured by commercial crabbers, 110 (22.7%) by recreational crabbers, and 13 (2.7%) by unidentified crabbers.

When examining spatial variations in recapture ratios in 2015, the analysis included 1163 recaptures (25.6%) from the 4539 male crabs tagged and released during all 15 releases in 2015 (Table 1; Fig. 3). Of these, 897 (77.1%) were captured by commercial crabbers, 235 (20.2%) by recreational crabbers, and 31 (2.7%) by unidentified crabbers. Of the 5244 \$5 tags (male and female) released in 2015, 1159 (22.1%) were recaptured. Of the 276 \$50 tags released, 84 (30.4%) were recaptured. This resulted in an overall reporting rate of 72.6% across the fishery. Sector-specific reporting rates in 2015 were 67.2% for the commercial fishery and 85.3% for the recreational fishery. There were insufficient recaptures in individual harvest reporting areas to produce reliable area-specific reporting

Fig. 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 that adjusted for crab movement and the tagged crabs that 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.



rates. Of the 1147 male crabs released in 2015 that were recaptured and reported with sufficient spatial information, 220 (19.2%) were recaptured in a different reporting area from where they were released. Of these, 157 (71.4%) were crabs that moved from tributaries into the mainstem bay.

There was notable consistency in recapture and reporting of crabs between the 2 years of the analysis. The overall reporting rate of across the fishery was 88.4% and 72.6% in 2015. In 2014, the reporting rate for male crabs was 93.0%. When all crabs (male and female) were included, that number decreased slightly to

Table 5. Estimated monthly exploitation rate ($month^{-1}$) for blue crabs (*Callinectes sapidus*) in the 15 harvest reporting areas where tagging was conducted.

Reporting area	Site code	Commercial	Recreational	Total
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

Note: Commercial, recreational, and total exploitation rates were calculated after accounting for crab movement among harvest reporting areas. Site codes preceded by M or T represent reporting areas that were split into portions spanning the mainstem bay (M) and adjacent tributaries (T).

88.4%. In 2015, the reporting rate for males was (71.5%); however, when all crabs (male and female) were included this increased slightly to (72.6%).

3.2. Seasonal variation in recapture ratios

The ratio of recreational to commercial recaptures (nR/nC) exhibited a domed relationship over time, increasing during June and July to similar high values in August (0.50) and September (0.52) followed by a sharp drop in October (Fig. 4*a*).

This seasonal trend in recapture ratio likely stemmed from a strong seasonal trend in recreational fishing effort. It should be noted that commercial harvests showed a domed relationship, with a peak in July–August (Maryland Department of Natural Resources 2015*a*, 2015*b*). If the seasonal variation in recreational effort was proportional to that of commercial effort, there would have been little change in recapture ratios across the harvest season. Because the recapture ratios showed a seasonal trend on top of changing commercial harvest, the seasonality of recreational effort was likely much greater than that of commercial effort.

3.3. Spatial variation in recapture ratios

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

3.4. Estimates of recreational harvest

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

Estimated recreational harvest of crabs varied substantially across the different harvest reporting areas, with most landings occurring in tributaries (Fig. 5*c*). In particular, incorporating data on movement increased the estimate of recreational harvest in tributaries (Fig. 5*d*) because many crabs moved from tributaries that had greater recreational harvest to mainstem bay areas that had almost exclusively commercial harvest. Using data that accounted for movement, recreational harvest estimates ranged from no crabs in Fishing Bay and the Honga River to 1.91 million crabs in the Patuxent River (Fig. 5*c*). The spatial pattern was substantially different from reported commercial harvest (Fig. 5*b*), which was characterized by high harvests in the Choptank River and the mainstem bay. Tributaries with high recreational landings included the Patuxent (1.91 million crabs), Severn (0.52 million crabs), and Miles rivers (0.40 million crabs).

3.5. Spatial variation in exploitation

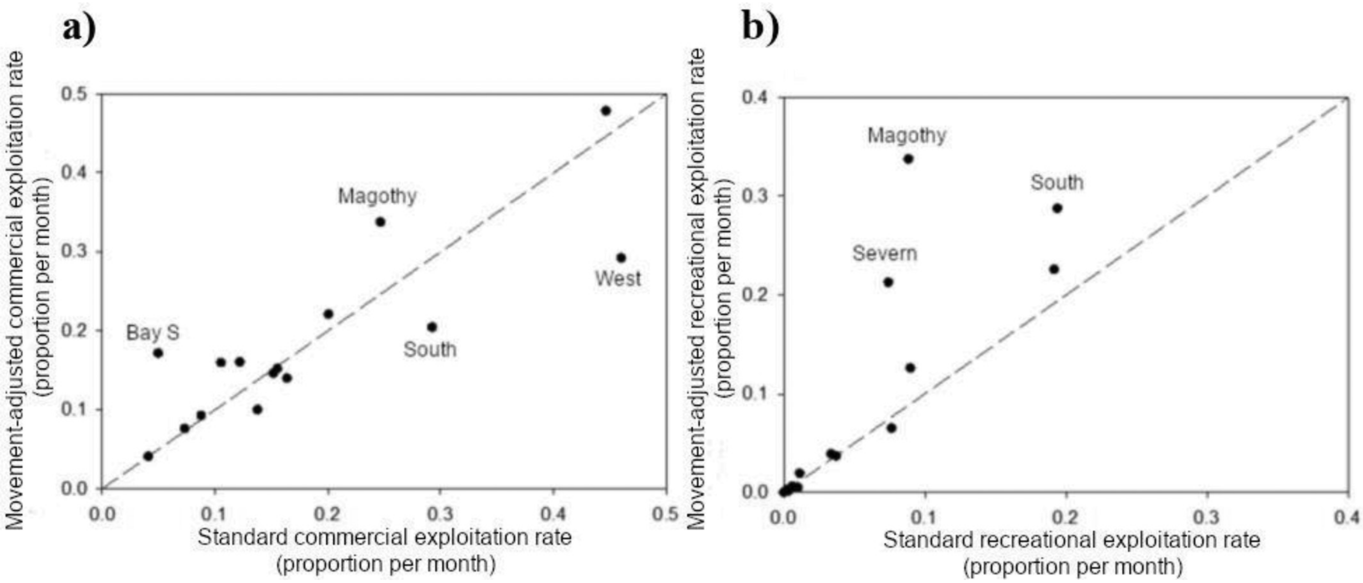
There were marked differences in recreational and commercial exploitation rates among the 15 harvest reporting areas in which crabs were tagged (Table 5). The most noticeable differences were observed between sites in tributaries along the Western Shore of the bay, Eastern Bay, and the Miles and Wye rivers, where recreational fishing was greatest, and areas of the mainstem bay, where recreational harvest was negligible. Mean commercial exploitation per month (calculated using movement information) ranged from 0.04 $month^{-1}$ in the Patuxent River to 0.48 $month^{-1}$ in the Wicomico River tributary of the Potomac River. Notably high rates of commercial exploitation were observed in the Wicomico River (0.48 $month^{-1}$), Magothy River (0.34 $month^{-1}$), and West River (0.29 $month^{-1}$). Mean recreational exploitation per month ranged from 0 $month^{-1}$ in both the Honga River and Fishing Bay to 0.34 $month^{-1}$ in the Magothy River. Notably high rates of recreational exploitation were observed in the Magothy River and in South River (0.288 $month^{-1}$).

Accounting for movement resulted in substantial differences in sector-specific exploitation rates. Estimates of commercial exploitation increased by 37.0% in the Magothy River and by 246.4% in the bay's Mainstem S region after movements were considered (Fig. 6*a*). For the Magothy River, this increase was a result of decreases in the number of crabs available to be caught, because many left the area. In the case of the Mainstem S area, however, the large increase in commercial exploitation was due to a large number of crabs leaving other areas and subsequently being caught by commercial fishers in Mainstem S. Commercial exploitation decreased by 30.0% in the South River and by 36.5% in the West River because of the large number of crabs from these releases that were caught by commercial fishers in the mainstem bay (Fig. 6*a*). Recreational exploitation rates increased by 283.4% in the Magothy River, by 48.3% in the South River, and by 186.5% in the Severn River due to reductions in the number of crabs available to be caught in these systems (Fig. 6*b*). These differences are underpinned by a great degree of consistency in movement probabilities between years. For the four sites tagged in both 2014 and 2015, there was a strong degree of correlation in movement probabilities between years ($r = 0.99$, $t = 36.72$, $p < 0.01$).

4. Discussion

The movement of tagged individuals strongly influenced the results of a mark–recapture study of the blue crab fishery in Maryland waters of the Chesapeake Bay. Tag return data revealed strong variation in the ratio of recreational to commercial recaptures among adjacent harvest reporting areas that set the stage for movement to influence estimates of area-specific recreational harvest and exploitation. In the most extreme case (Severn River), a crab could move from an area where it is 2.5 times more likely to be caught by a recreational fisher than a commercial fisher to an area

Fig. 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.



with 100% commercial harvest by moving only a few kilometres. Adult blue crabs are easily capable of traveling this distance in a few days (Souza et al. 1980; Wolcott and Hines 1990), and commercial fishing effort is concentrated at tributary mouths to intercept crabs moving out of shallow nursery habitats (Slacum et al. 2012). Overall, the resulting estimate of statewide recreational harvest was 34% higher when movement was accounted for compared with the estimate based on the release location of tagged crabs only. The results of this study highlight the importance of incorporating movement into mark–recapture studies focused on exploring spatial variation in exploitation among harvest areas when the target species commonly moves among them.

Although mark–recapture studies are often used to address fishery management questions at the population level when the effect of individual movements may be negligible, there are a few examples that incorporate movement data into calculations of exploitation rates. In a study of snapper (*Pagrus auratus*), site-by-site estimates of density and exploitation were used to standardize movement patterns of snapper that were determined from recapture locations in New Zealand (Parsons et al. 2011). The method used by Parsons et al. (2011) is in some sense the inverse of the technique employed in the present study. In other examples, exploitation calculations are conducted for each release area but did not account for movement between release areas (e.g., Rudd et al. 2014; Whitlock et al. 2017). Analyses of waterfowl data provide examples for incorporating information on movement among multiple harvest areas into harvest and exploitation rate calculations (Munro and Kimball 1982; Nichols et al. 1995). Our methods expand on this to incorporate within-year temporal variation and multiple harvest sectors, which was needed to estimate recreational harvest based on reported commercial harvest.

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

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

Information on the size of the recreational blue crab harvest in Maryland has regularly been identified as a critical management need. Prior studies in 2001, 2002, 2005, and 2009 using effort survey methods (Ashford et al. 2009, 2010*a*, 2010*b*, 2013*a*, 2013*b*) estimated that the ratio of recreational to commercial harvest within Maryland remained close to the 8% estimate chosen in the stock assessment. Estimates of recreational harvest from effort surveys averaged 11.6% of commercial male hard crab harvests and 5.8% of total commercial harvests. In the present study, recreational harvest of male hard crabs in 2015 was estimated at 11.2% of commercial male hard crab harvests and 6.5% of total commercial harvests (male and female) when movement was included. Although comparison of effort surveys and a Maryland-wide recapture experiment conducted in the same year would be preferable, the similarity between recreational harvest fraction estimates suggests that the methods proposed herein are consistent with effort surveys.

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

Other sources of uncertainty include the focus on a single year and the lack of tagging data during the first and last months of the harvest season within that year. Between years, when replacing the 2015 commercial harvest data with the previous 5 years of data, the ratios of recreational to total commercial harvest were 10.4%–13.1% (11.2% in 2015), suggesting that our estimate was not very sensitive to annual variation in commercial harvest. Within 2015, setting the recapture ratios in April, May, and November to the June and October values instead of assuming a value of 0 increased the percentage of recreational harvest from 11.2% to 11.3%, suggesting that recreational harvest in these months was negligible. Repeating the mark–recapture study in 1 or more years in combination with effort surveys or recreational harvest reporting would help assess the validity of this approach.

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

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

The proportion of recreational to total commercial harvest (8%) used in the stock assessment was set prior to the moratorium on recreational harvest of female crabs in Maryland in 2008 (Miller et al. 2011). However, after 2008, recreational harvest was thought to be better calculated as 8.0% of male harvests (Chesapeake Bay Stock Assessment Committee 2016). While recreational harvest could have been 8.0% of male harvests in 2011, our estimated harvest in 2015 equates to 11.2% of male harvests, representing a 40% increase over the 8% guideline. It is unclear whether this increase resulted from the shifting of recreational fishing effort from female to male crabs or simply from increased recreational fishing effort targeting male crabs.

The estimated contribution of the recreational fishery to total harvest in this study was at the lower end of recreational harvest fractions for temperate or subtropical crab fisheries and is comparable to other blue crab fisheries within the US. In Maryland, recreational crabbers take roughly 6.5% of the commercial harvest of male and female blue crabs. In Louisiana, which has the second largest commercial blue crab fishery by state in the US, recreational crabbers take in roughly 5% of all blue crabs (Guillory 1998; Louisiana Department of Wildlife and Fisheries 2011). Similar results were observed for recreational blue crab fishers in Galveston Bay, Texas (5.6% of harvest; Texas Parks and Wildlife 2007). In Oregon, 5.5% of landings in the Dungeness crab (*Metacarcinus magister*) fishery are taken by recreational crabbers (Oregon Department of Fish and Wildlife 2014). In contrast, some crab fisheries have a much higher proportion of recreational harvest including the mud crab (*Scylla serrata*) fishery in Queensland, Australia (~50% recreational harvest; Ryan 2003) and the blue swimming crab (*Portunus pelagicus*) fishery in South Australia (29.8% of harvest; Jones 2009). Other crab fisheries, such as those for Atlantic Jonah crabs (*Cancer borealis*) and California Dungeness crabs, do not have sufficiently reliable recreational harvest data to make similar comparisons (Atlantic States Marine Fisheries Commission 2015; California Ocean Protection Council 2014). Understanding the contribution of recreational fisheries to total harvests, estimated at 12% globally, is a critical issue in conservation of fishery resources (Cooke and Cowx 2004). The methods used here could be applied to blue crab fisheries in other regions or used as a model for crab fisheries for which recreational harvest estimates are needed and commercial harvests are known.

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

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