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Assessing Risks from Harbor Dredging to the Northernmost Population of Diamondback Terrapins Using Acoustic Telemetry

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Abstract
The northern diamondback terrapin (*Malaclemys terrapin terrapin*) is a saltmarsh-dependent turtle that occupies coastal habitats throughout much of the Atlantic coast of North America. We used a novel application of acoustic telemetry to quantify both mobility and occupancy of terrapins within a dredged harbor and surrounding habitats, and used these metrics to quantify relative risk to individuals posed by harbor dredging. Terrapins showed strong fidelity to brumating areas within subdrainages, but extensive movements between these zones during the active period. Activity was greatest in late spring and early summer, declining to near zero by December. Occupancy of the dredge zone was also greatest during spring and summer and declined throughout the autumn months to an annual minimum during winter. Taken together, these data indicate that risks from harbor dredging are minimized during the autumn and early winter months.

Keywords Terrapin · Telemetry · Dredging · Brumation · Hibernation · Movement · Modeling · Risk · Assessment

Introduction

Coastal and estuarine environments accommodate a range of human activities, including fisheries, aquaculture, recreation, and transportation. These activities are supported by infrastructure, the maintenance of which can affect sensitive species that inhabit these zones (Culloch et al. 2016; Moser and Ross 1995). One such activity is harbor dredging. Harbors are typically located in sheltered waterways, often with additional armoring to protect anchorages and ports. This sheltered quality creates an opportunity for sediments to accumulate, and harbors must be dredged periodically to maintain navigability. Dredging requires heavy equipment and the removal of large volumes of sediment. It is highly disruptive to the environment and esthetically unpleasant, interfering with economically and culturally important activities such as boating, aquaculture, and tourism. To minimize these effects, dredging is often undertaken during winter months, when human activities are reduced.

Dredging also poses several potential threats to wildlife, including suspension of sediments (which may contain toxic chemicals) and direct mechanical contact with the dredge equipment (O'Donnell et al. 2007; Wilkens et al. 2015). One species that is vulnerable to harbor dredging is the northern diamondback terrapin (*Malaclemys terrapin terrapin*, hereafter referred to as "terrapin"), a saltmarsh-adapted species that occupies nearshore habitats along the East Coast of North America (Brennessel 2006). Historic overharvest, combined with fishery bycatch and habitat destruction, has caused many populations to be extirpated, and the species is listed for protection in many states throughout its range (Butler et al. 2006; Hart and Lee 2006). During winter months, terrapins enter a period of dormancy known as brumation, during which they aggregate and remain essentially immobile, buried in the benthos (Brennessel 2006; Haramis et al. 2011; Yearicks et al. 1981). Given that coastal dredging also often occurs during this period, there is the potential for considerable mortality of terrapins that brumate within the dredge zone, prompting management agencies to restrict dredging to summer months,

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when the high level of activity presumably confers ability to volitionally avoid dredging equipment.

The most northerly terrapin population resides in Wellfleet Harbor, Massachusetts (USA), where the species is listed as threatened under the Massachusetts Endangered Species Act (MESA, MGL c131A). The harbor is a federal waterway and municipal anchorage, both subject to periodic dredging, and terrapins are regularly observed throughout the dredge zone. Large breeding aggregations occur each spring in a cove adjacent to the harbor, indicating that this is vital habitat for this population, and raising concerns that brumation may be occurring within the dredge zone.

While any mortality holds the potential to affect the population, the magnitude of the threat posed by dredging depends in part on which portion of the population is at risk. If dredging is performed during brumation, and if the dredge zone comprises preferred brumation habitat, then dredging will likely pose serious risks, both to individuals and to the local population. The objective of this study was to use acoustic telemetry to assess seasonality of risk from dredging by quantifying rates of movement and occupancy of terrapins within the dredge zone of Wellfleet Harbor. Our observations can inform decisions on timing of dredging activity to minimize risk to this threatened coastal species.

Methods

Study Area

Wellfleet Harbor is a protected harbor in Cape Cod Bay located in the Town of Wellfleet, MA, USA (41° 55′ 48″ N, 70° 01′ 30″ W; Fig. 1). It is a *Spartina* spp. grass-dominated marsh system, comprising several subdrainages with a mix of inlets, rivers, and creeks. It has an extensive intertidal zone, with regular tidal fluctuations of 3–4 m. The area of primary concern was the harbor proper, which consists of the federal and town anchorages (hereafter called the anchorage) and the main navigation channel, all of which are dredged (Fig. 1). In addition to the anchorage, the study area also included each of the primary subdrainages within the Wellfleet Harbor watershed.

Capture and Handling

Mature terrapins were collected during three distinct time periods to ensure that we characterized movement behaviors of a representative sample of the population. We focused on mature individuals, both to ensure that they were of sufficient size to bear the mass of the tag, and also because impacts on mature individuals are more likely to affect the population (Heppell et al. 2000). The first and third collections were performed during the mating aggregation in Chipman's Cove (Duck Creek, adjacent to the dredge zone) shortly after terrapins emerged from brumation (April–May, 2011 and 2012). These individuals were intended to provide information on whether and to what extent terrapins brumated nearby, and to maximize the likelihood of identifying individuals at risk if the dredge zone proved to include important brumation habitat.

The second collection was performed during July, 2011, and was intended to be representative of the entire population. To that end, terrapins were captured in the tributaries (South of Lt. Island (hereafter termed "WBWS" or "sanctuary"), Blackfish Creek, Herring River, and Duck Creek). The July collection occurred after their reproductive period, when terrapins were dispersed throughout the watershed. The purpose of this group was to help us to identify other brumation sites, in the event that dispersal rates were low.

Transmitters and Tag Lots

Terrapins were tagged with acoustic transmitters (V9 coded tags, 69 kHz; VEMCO Division, AMIRIX Systems Inc., Halifax, Nova Scotia, Canada). Tags were purchased in two separate groups ("tag lots"). Each group had a distinct programming scheme, intended to ensure maximum longevity, and in particular to allow for documentation of onset of brumation in each of 2 years for each tag. To achieve this, they were programmed to transmit every 50–180 s (randomly distributed), and to have a dormant period during the first winter following tagging. These were originally intended to be applied during 2010 and 2011. However, owing to permitting restrictions, all tags were deployed during 2011 and 2012. This meant that the first tag lot became dormant and re-activated later than the initial study design intended, and only one brumation onset event was observed for this tag lot (Tables 2 and 3).

Collection Methods and Transmitter Attachment

Terrapins were collected manually using dip nets. Transmitters were attached to the first and second marginal scutes to the left of the supracaudal scute (Fig. S1). Two small holes were drilled through the scutes and the supporting dermal plate, through which were inserted small cable ties. Each transmitter was secured with the cable ties and embedded in epoxy (ACE Quick Set epoxy, Henkel AG & Co. KGaA, 40191 Düsseldorf, Germany). The epoxy was thickened with colloidal silica (West Systems 406 Colloidal Silica Adhesive Filler, West Systems, Bay City, MI, USA) and mixed with black pigment (Evercoat Coloring Agent, Evercoat, Cincinnati, OH, USA). This produced a smooth finished product with no sharp edges to snag on vegetation and fishing gear, and cryptic coloration which we hoped would reduce risk of predation. To avoid biofouling on the transmitters and potential adverse effects on the animals, we coated the entire transmitter package with anti-fouling paint (Interlux Micron CSC, International Paint LLC, Union, NJ, USA). The tagging

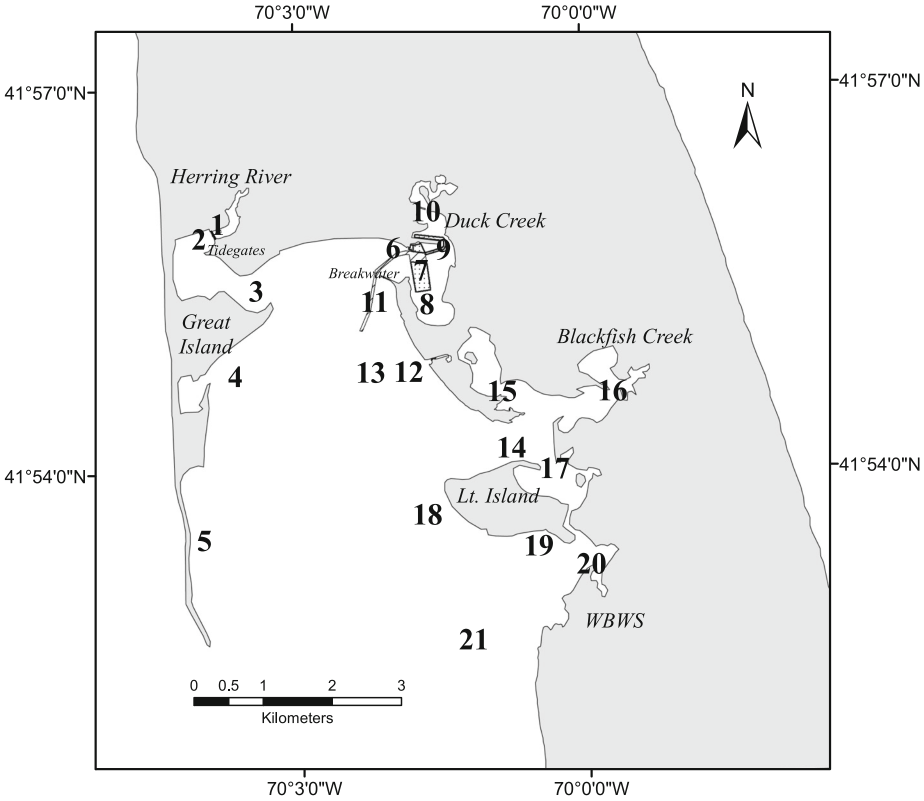

Fig. 1 Receiver deployment locations in Wellfleet Harbor, Wellfleet, MA (white area indicates water). The map shows the proposed dredging project (stippled and striped area near the breakwater), subdrainages (labeled according to either the legend or body of Table 1), and receiver locations (numerals). Receiver numbers are sized to approximate the typical detection range at each site

procedure was approved by the University of Massachusetts Amherst IACUC (protocol 2011-0009). All captured terrapins were sexed (Brennessel 2006), measured, weighed, and released at their point of capture.

Fixed-Receiver Array

We used an array of fixed-station receivers to monitor broad-scale movements and distribution of terrapins. We deployed 20 submersible receivers (VR2W, VEMCO Division, AMIRIX Systems Inc., Halifax, Nova Scotia Canada) throughout Wellfleet Harbor during 2011, and 21 during 2012 and 2013 (Fig. 1; Tables 1 and 2). Receivers were placed to optimize our ability to test key hypotheses regarding movement of terrapins in Wellfleet Harbor, and placement was consistent across years. The most important metrics concerned rates of occupancy within the anchorage throughout the year, seasonal changes in mobility (including onset of brumation), and fidelity to brumation sites among years. The array was deployed in March and retrieved in January, which ensured complete coverage during the active phase of the transmitters (Table 2).

Each receiver was attached to a 40-kg concrete mooring using a buoy system that optimized its ability to detect passing terrapins at any phase of the tidal cycle (Fig. S2). Receivers were deployed in a series of "gates" (channel constrictions where a swimming terrapin would have to pass through the detection zone in order to pass the receiver) and "nodes" (distributed sites within an area of interest) so that movement among detection zones as well as residency at key locations (e.g., brumation sites) was documented. Maximum receiver detection ranges were measured by deploying a range testing transmitter (V9, coded tag range testing transmitter emitting at a 69 kHz signal, battery life = 14 days, VEMCO Division, AMIRIX Systems Inc., Halifax, Nova Scotia, Canada) concentrically in all four cardinal directions in 50-m increments (max = 600 m) from each receiver location (Selby et al. 2016). The maximum range at which a tag was detected was assumed to represent the maximum detection range for that receiver. Receivers were downloaded biweekly, and on each download, clocks were synchronized with official US Naval time, and any clock drift was corrected assuming a linear rate of drift between downloads.

Temperature loggers (HOBO Pendant Temperature/Light Data Logger 64 bit—UA-002-64, Onset, Pocasset, MA, USA) were also deployed on four receivers (one each at the mouths of Blackfish Creek (receiver 14), Herring River (receiver 3), and Duck Creek (receiver 9) as well as in the Main Channel (receiver 11; Fig. 1). Loggers were configured to record water temperature every 15 min.

Manual Tracking

We performed manual tracking from a variety of vessel types to verify fixed-station observations and to identify exact locations of brumation sites of those terrapins we were able to detect. Terrapins that remained stationary during multiple scanning events were assumed to be brumating. Surveys

Table 1 Locations of the 21 acoustic telemetry receivers (latitude and longitude in decimal degrees). Map ID refers to numbers shown on Fig. 1; station names are referred to throughout the text. Subdrainages refer to the four primary drainage areas in the system (Herring River (HR), Duck Creek (DC), Blackfish Creek (BFC), Wellfleet Bay Wildlife Sanctuary (WBWS)) or various locations outside of these drainages within Wellfleet Harbor (WH). Receivers marked with an asterisk (*) were affixed with a temperature logger

Map ID	Station name	Subdrainage	Intertidal	Latitude	Longitude
1	Herring River 3	HR	Yes	41.931394	−70.063555
2	Herring River 2	HR	Yes	41.930683	−70.066383
3*	Herring River 1	HR	Yes	41.92375	−70.056983
4	Great Island	WH	No	41.912694	−70.060944
5	Jeremy Point	WH	No	41.89137	−70.06682
6	Mooring Basin	DC	No	41.9284	−70.033016
7	Anchorage	DC	No	41.926194	−70.028194
8	The Cove	DC	Yes	41.922138	−70.027277
9*	Duck Creek	DC	Yes	41.930133	−70.024166
10	Railroad Bridge	DC	Yes	41.933861	−70.027194
11	Channel 1	WH	No	41.922166	−70.036388
12	Indian Neck 1	WH	No	41.91295	−70.030616
13	Indian Neck 2	WH	No	41.912950	−70.037236
14*	Blackfish 1	BFC	Yes	41.9029	−70.012916
15	Fox Island	BFC	Yes	41.910277	−70.014416
16	Pleasant Point	BFC	Yes	41.910116	−69.995183
17	Loagy Bay	BFC	Yes	41.900111	−70.005527
18	Lt. Island	WH	No	41.894333	−70.02780
19	Sanctuary 2	WBWS	Yes	41.890055	−70.00850
20	Sanctuary	WBWS	Yes	41.8876	−69.99936
21	Eastham	WH	No	41.877983	−70.020041

began in October and were performed weekly as weather and tides permitted. We used two receiver types for this: a Vemco VR-100 (VEMCO Division, AMIRIX Systems Inc., Halifax, Nova Scotia, Canada) and a Sonotronics USR-08 (Sonotronics, Tucson, AZ, USA). Both receiver types were outfitted with directional and omni-directional hydrophones and were able to decode all tags.

We established density of scanning transects based on detection ranges of known brumating terrapins. Wind and tide made it impossible to follow planned transects exactly, but this detection range was used to establish a grid that was covered throughout the dredge zone during each manual tracking session. Thus, the individual transects scanned varied by session, but were always designed to ensure a strong likelihood of detecting tags that were present anywhere within the surveyed zone. Similar methods were used outside the dredge zone, but because of the importance of identifying any brumating terrapins within that zone, we concentrated our efforts there.

Data Management and Analysis

All data for this study were compiled in a relational Microsoft Access database and analyzed using R statistical software (R 3.2.3; R Core Team 2014).

Occupancy and Movement

Vulnerability of terrapins was assessed by measuring both occupancy of the dredge zone and mobility. Occupancy addresses when animals were present within the dredge zone,

Table 2 Period of coverage for fixed receivers (Rx coverage) and tags. Date on and Date off indicate expected on-off cycles, based on manufacturer's programming. First detection and Last detection indicate actual observations, and are presented as median (range). Note that some tags were detected before their programmed activation date—evidently arising from a manufacturing defect in programmed on/off times

Tag lot	Date on	Date off	First detection	Last detection	Rx coverage
1	02 Jun 2011	3 Jan 2012	25 May 2011 (24 May–15 Jun)	18 Oct 2011 (13 Jul–25 Dec)	18 Mar 2011–10 Jan 2012
2	04 Jul 2011	18 Dec 2012	19 Jul 2011 (5 July–14 Aug)	05 Oct 2011 (12 Sep–15 Nov)	
1	01 Jun 2012	06 Aug 2012 (expired)	23 May 2012 (16 Apr–24 May)	05 Aug 2012 (15 Jun–27 Aug)	20 Mar 2012–07 Jan 2013
2	18 Apr 2012	18 Dec 2012	25 Apr 2012 (18 Apr–13 May)	09 Oct 2012 (01 Jun–18 Dec)	
2	19 Apr 2013	13 Jul 2013 (expired)	29 Apr 2013 (9 Apr–25 Jul)	01 Jul 2013 (28 Apr–02 Aug)	19 Mar 2013–02 Aug 2013

and so vulnerable to equipment; mobility addresses the ability of terrapins to actively avoid the dredge, given that they be present during operations.

Occupancy of the anchorage and dredge zone was measured as the proportion of available active tags detected within the Duck Creek subarray. This included all receivers deployed from the mouth of Duck Creek (receiver 10) out to the breakwater, including the entire dredge zone (Fig. 1) on each day of the study.

Movement was considered an indicator of each animal's "mobility" (and by association its ability to avoid dredge equipment), and was measured by identifying transitions in detections between receivers within the Duck Creek system. Transitions were determined based on occupancy events within the detection zone of each receiver. We applied time-to-event techniques, whereby the log density function of interval durations between detections at each receiver were used to identify times when terrapins entered and left each detection zone (Castro-Santos and Perry 2012).

The density of receivers within the Duck Creek subarray meant that it was possible to discern movements throughout the subdrainage. Data from all receivers were combined, and any detections occurring within 20 s of each other on two or more receivers were identified, retaining only the first of these detections and assigning the location to that receiver. These simultaneous detections were very rare, comprising < 0.1% of the total detections. More commonly, there was a gap between detections as terrapins moved around the harbor, passing among the detection zones of the array; > 95% of all new detections were separated by > 1 transmission interval. Taken together, the low incidence of simultaneous detections combined with successive receivers typically being separated by more than one transmission interval suggests that any error associated with animals occupying overlapping zones must be trivial, and that successive detections at distinct receivers represented actual movements of animals among the receivers in the array. Distance between receivers was known, and at each transition, an individual animal was assigned this distance minus 300 m (the average radius of one receiver's detection range). This provided a conservative estimate of movement distance, balancing considerations of detection range, detection probability, transmission rate, and rate of movement of the turtles, and assuming a straight-line path between receivers. In reality, movement paths are rarely truly straight, and so, actual movement was probably greater that what we estimate using this method. The transition distances were then summed for each detected terrapin on each day, and median daily values were then calculated based on all detected animals. Note that by using only receivers within the Duck Creek drainage, this also provides a conservative measure of mobility. Since most movements occurred within drainages, however, and because we used the median value, influence of extreme values was minimized, providing a conservative but realistic index of movement.

Loess smooth functions were fitted to both the occupancy and movement data, providing a continuous estimate of average occupancy and movement by terrapins throughout the year. Means and 95% confidence intervals were calculated for both metrics.

Combined Risk

The exposure risk was assumed to be directly proportional to the probability of being present within the dredge zone on a given date. We therefore used the untransformed occupancy metric described above as a direct index of risk (R_o):

$$R_o = P(Occupancy) \tag{1}$$

where $P\ (Occupancy) \in [0, 1]$ is the proportion of the population present in the dredge zone on a given day of the year as estimated by the loess smooth.

Next, we produced an index of relative mobility risk (R_m):

$$R_m = 1 - \frac{M_d}{M_{max}} \tag{2}$$

where M_d is the median observed movement on a given day and M_{max} is the annual maximum of these values. Values for R_m range from 0 to 1, with 0 being associated with the day of greatest mobility and 1 associated with the day of least mobility within a given year. Thus, brumating terrapins experience the greatest mobility-related risk, and this risk is minimized on the day of greatest activity.

Values used for calculating both R_o and R_m were taken from the among-years loess smooth. Combined risk exposure (R_T) was then calculated as the product of occupancy and mobility risks:

$$R_T = R_o \times R_m \tag{3}$$

Results

Capture and Handling

Seventy-five terrapins (56 females and 19 males) were tagged during the 2011 field season (Table 3). Of these, 30 females and 19 males comprised the spring collection from the proposed dredging area (Table 2; Fig. 1). Twenty-six terrapins were also tagged, distributed throughout Wellfleet Harbor during July (Table 3). During this second period, no males were captured that were large enough to tag. Instead, all transmitters were attached to mature females.

An additional 25 terrapins (13 females and 12 males) were tagged during the 2012 mating aggregation (Table 3). Thus, 74 of 100 terrapins were captured within the anchorage area.

Table 3 Numbers and location of terrapin captures. Capture locations are abbreviated as CC (Chipman's Cove), BFC (Blackfish Creek), DC (Duck Creek), WBWS (Wellfleet Bay Wildlife Sanctuary—actually includes marshes and beaches south of Lt. Island), and HR (Herring River). Anchorage refers to the federal and town dredge zones, adjacent to Chipman's Cove

Date	Tag lot	Capture location	Females	Males	Total
May 2011	1	CC, anchorage	30	19	49
July 2011	2	WBWS	8	0	8
	2	HR	8	0	8
	2	BFC	8	0	8
	2	CC, anchorage	2	0	2
May 2012	2	CC, anchorage	13	12	25
Total			69	31	100

By concentrating our collections near the dredge zone, we expected the observed proportion of brumating terrapins within this zone to overestimate their representation in the larger population. In this way, we ensured that assessments of occupancy risk were conservative, i.e., biased in favor of detecting occupancy when it occurred.

Females were larger and more variable in size than males. Mean and standard deviations of straight carapace length and in-air mass of females were 18.4 ± 1.3 cm and 1071 ± 224 g; of males, they were 12.3 ± 0.4 cm and 280 ± 27 g. There was no difference in size or mass between years within sexes ($p > t > 0.3$ in all cases). All terrapins were held overnight and released within 18–30 h of capture. They all swam away once released; no abnormal or disoriented behavior was observed.

The total transmitter package weighed 9 g in air, or 0.84% ± 18% of the average body mass of females and 3.21% ± 0.31% of the average body mass of males; on no individual did it exceed 3.7% of the body mass. Most tags activated and deactivated within a day of their programmed dates. Some drift in these settings did occur, however with at least one tag activating at least 10 days before its programmed date (Table 2; Fig. S3).

Receiver Array

Receivers performed well throughout the deployment period (Table 2). Tested detection ranges ranged from 117 to 602 m (mean = 421 m), and varied with tide and bathymetry. Range testing was typically performed within 2 h of high tide, and so, these represent maximum values. At low tide and shallow conditions, these ranges were reduced, with periods (< 2 h) of zero efficiency for receivers in the intertidal zone (Table 1). Thus, the 300-m detection ranges used for calculating relative movement over the course of the study were appropriate, given the available information.

Mobility

Terrapins were active during the entire period of telemetry coverage (April–December: Fig. 2). Total movement had little relationship to water temperature (Figs. 2 and S4; Kendall's tau = 0.056). Instead, activity was greatest in mid-May, with median movement values of about 2 km/day. This corresponded with the breeding period of this population.

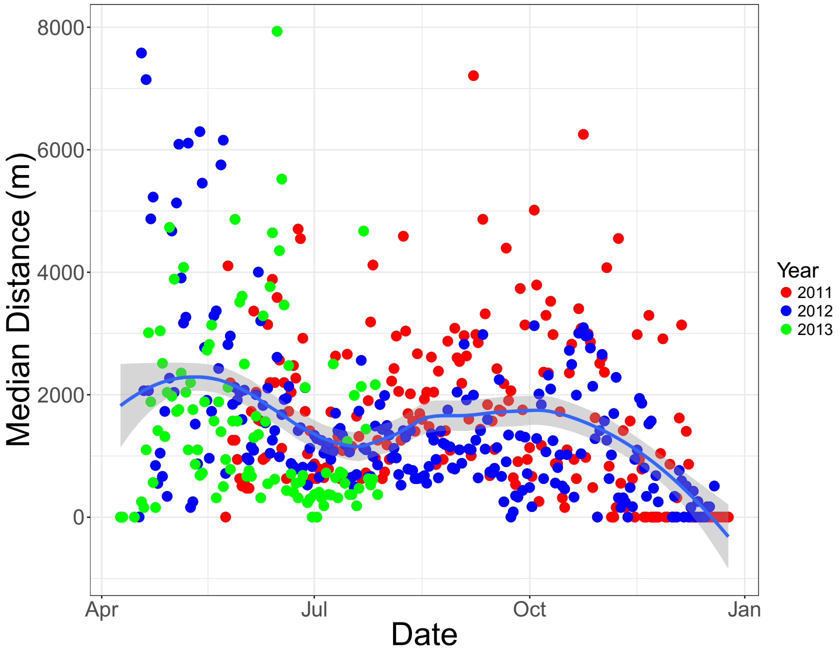

Fig. 2 Median known distance traveled per day by detected terrapins. Points represent median for a given day on a given year. The loess smooth averages across years

There was a slight decrease in movement in mid-summer, which corresponded with the female nesting season, followed by another broad peak from August to October, where the median movement was about 1.8 km/day. Movement then began to decrease until reaching a minimum in December, shortly before the tags shut down for the winter. By December 1, it became common for entire days to pass without any observed movement between receivers (Fig. 2).

Occupancy and Brumation

Because the tags became active in late April or later (Table 2), it is not possible to estimate actual dates of emergence and onset of activity. The fixed array, however, provides some insights into this. In both 2012 and 2013, many terrapins were already active on the date that the tags turned on (Fig. S3). Dates of last detection in the fall do not correspond with reduced activity. Median dates of last detection were 30 September (2011) and 3 October (2012), with no difference between sexes (Kruskal-Wallis, $p > 0.57$ in both years). Although it is tempting to infer from this that brumation had begun, those terrapins that were detected after these dates continued to be highly active, and it is likely that the absence of detections instead indicates that the terrapins had moved elsewhere in the system, away from the anchorage and the rest of the fixed-receiver array.

This "departure hypothesis" is supported by the occupancy data (Fig. 3; Table 4). Occupancy in the anchorage was greatest during the May breeding aggregation (58% of tagged terrapins being present on any given day (%/day)), with another strong plateau in midsummer, with about 45%/day. Occupancy declined rapidly from late August– to September. By October 1, only about 20% of the population occupied the dredge zone, and this proportion continued to decline until most movement ceased in December. It is possible that as movement declined, some terrapins might have been present but undetected because they occupied zones outside the detection radius of the receivers. Any associated error in the occupancy estimate appears to be negligible, however: in each year, eight individuals were detected in the anchorage using manual tracking, corresponding to 11% of tagged terrapins in 2011 and 8% in 2012. This is consistent with the smoothed occupancy estimate (Fig. 3).

Data from the larger receiver array supports the interpretation that most terrapins left the anchorage for the winter. Of 128 last fixed-receiver detections in 2011 and 2012, 97% were within creeks, with only four at open water receivers (Table 4, Fig. S5; see also Table 1 and Fig. 1). The distribution of the last date of detection was broadly distributed among the four major drainages within the Wellfleet Harbor estuary (mean ± SD number of individuals per drainage were 18 ± 3 in 2011 and 12 ± 2 in 2012), suggesting a pattern of dispersal, rather than aggregation.

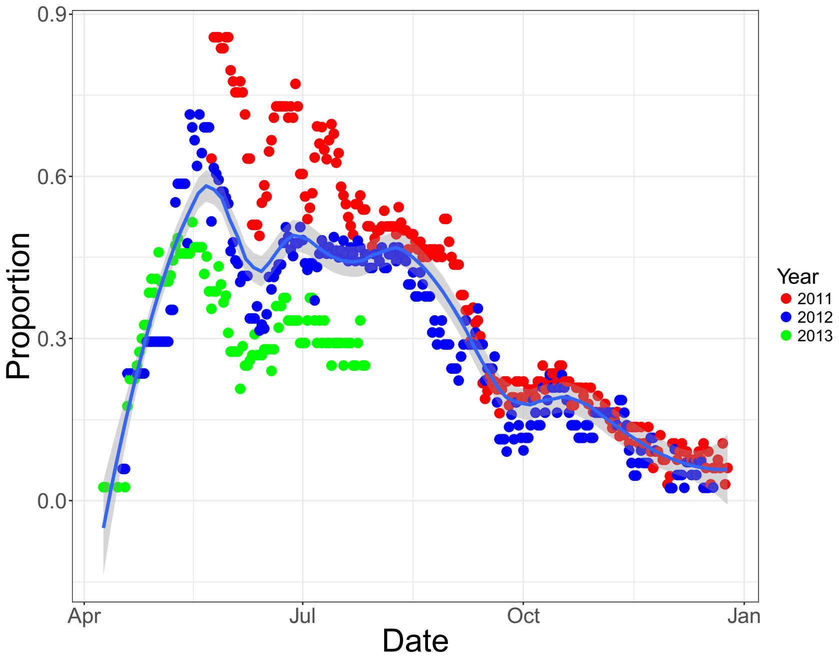

Fig. 3 Mean proportion of tagged terrapins detected within the dredge zone. Data from each year are indicated by dots. The loess smooth represents the mean across years. The shaded area is the 95% confidence interval for this mean. Note the consistent aggregation that occurs in May of each year. This appears to correspond with the known mating aggregation that occurs at that time. This is followed in each year by a departure (perhaps reflecting nesting activity) but then by a subsequent return to the dredge zone in late June, which persists until mid-August. From mid-August through September, there is a dramatic exodus, with about half of the terrapins leaving the Duck Creek subdrainage. The remaining terrapins stay within the subdrainage until early November, when they also begin to leave. By December, nearly all of the terrapins have left the subdrainage, with only about 5% detected on any given day

Table 4 Relationship between capture and brumation sites in 2011 and 2012. Data are presented as *n* (proportion of population captured within that subdrainage). Subdrainage labels are defined in Table 1. Note that a substantial proportion of terrapins captured within the Duck Creek watershed distribute throughout the harbor, while those caught outside of Duck Creek tend to brumate within the subdrainage where they were captured

Subdrainage		Year			
Capture	Brumation	2011		2012	
BFC	BFC	5	(0.63)	4	(0.67)
	DC	0	(0.00)	0	(0.00)
	HR	0	(0.00)	1	(0.17)
	WBWS	3	(0.38)	1	(0.17)
	WH	0	(0.00)	0	(0.00)
DC	BFC	11	(0.22)	6	(0.23)
	DC	23	(0.45)	14	(0.54)
	HR	8	(0.16)	2	(0.08)
	WBWS	6	(0.12)	1	(0.04)
	WH	3	(0.06)	3	(0.12)
HR	BFC	0	(0.00)	0	(0.00)
	DC	0	(0.00)	0	(0.00)
	HR	8	(1.00)	7	(1.00)
	WBWS	0	(0.00)	0	(0.00)
	WH	0	(0.00)	0	(0.00)
WBWS	BFC	1	(0.13)	1	(0.13)
	DC	0	(0.00)	0	(0.00)
	HR	0	(0.00)	0	(0.00)
	WBWS	7	(0.88)	7	(0.88)
	WH	0	(0.00)	0	(0.00)

We also observed evidence of interannual, creek-specific fidelity in selection of fall and winter habitat. Of the 26 terrapins that carried active tags through December of both 2011 and 2012 (Table 2), 23 individuals (88%) were last detected by fixed receivers after September 1 in both years. Of these, all but one were last detected in the same subdrainage in both years, most of them being detected on the same receiver as on the previous year (Fig. 4). We observed a similar pattern with emergence. During the spring emergence events of 2012 and 2013, terrapins were typically detected in the same drainage as their last detection (Fig. S6). Notably, however, there were several first detections outside of the drainages where they had been last detected the previous fall, and nearly all of these occurred within the zone between the breakwater and Duck Creek. Because tags from tag lot 1 were dormant from January to May, and from December to April for tag lot 2 (Tables 2 and 3), it was not possible to determine with certainty when this movement occurred. By comparing the distributions of last vs. first detections, however, it is possible to infer that activity had already begun by mid-April, making it more likely that those movements that were observed occurred in the early spring, before tag re-activation (Fig. S3).

Most terrapins occupied habitat outside the anchorage during the fall and winter periods. Combined risk from occupancy and mobility restrictions was calculated by multiplying occupancy (Fig. 3; Eq. 1) by the transformed mobility risk (Fig. 2, Eqs. 2 and 3). The results indicate that a tradeoff exists between the two risk metrics: Occupancy is greatest at the same time that mobility is near its peak, resulting in a minimum combined risk occurring both during the spring period and again during the fall (Fig. 5). The low risk in spring is

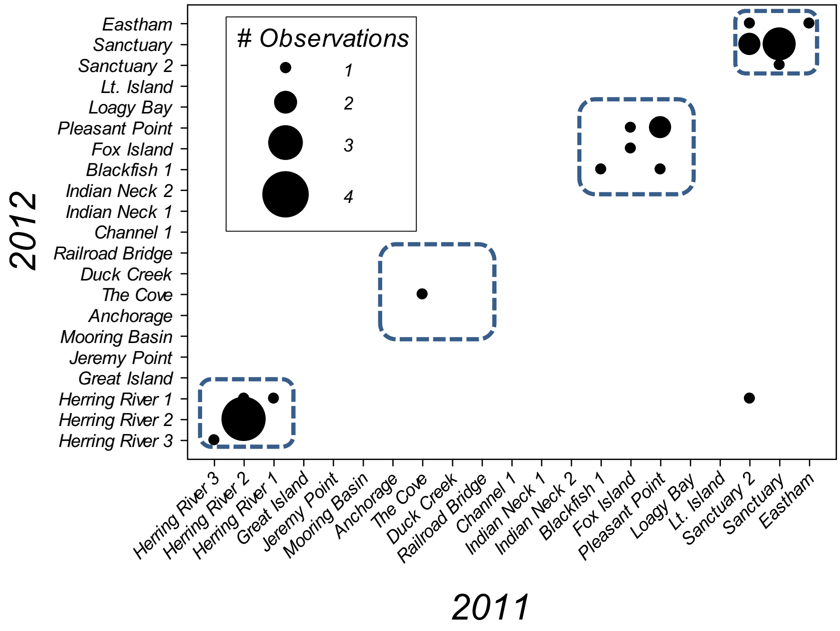

Fig. 4 Correlation between years of last receiver detection locations. Dashed rectangles delineate the four primary subdrainages (Fig. 1)

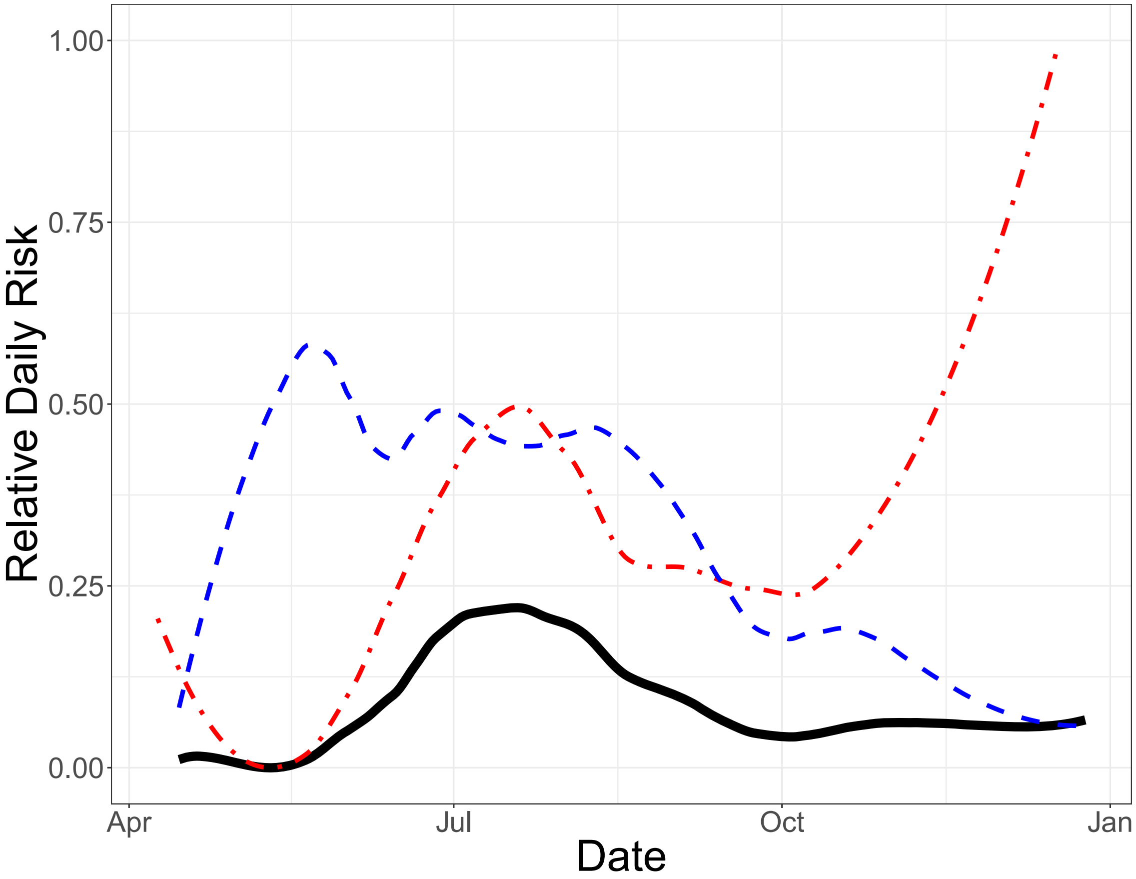

Fig. 5 Three risk components, showing total risk scale. Occupancy risk (R_o. Eq. 1; dashed curve) is the proportion of known terrapins in the dredge zone and is on the same scale as in Fig. 3. Mobility risk (R_m Eq. 2; dash-dot) was calculated from the loess smooths for each year of data shown in Fig. 2 (M_{max} = 2416 m/day; Eq. 2). Combined risk (R_T Eq. 3) is the product of occupancy and mobility components, and is shown by a solid black curve

driven by mobility, and in the fall by reduced occupancy. Any terrapins that remain in the anchorage after late November are assumed to be at high mortality risk, owing to their limited mobility. Although a small proportion of the population did remain near the anchorage at this time in both years, their locations fell primarily outside of the dredge zone (Fig. S7). Nevertheless, across the 2 years, three individuals were last detected within the dredge zone. The combined data thus indicate that a prolonged period of reduced risk exists from September to December, and probably through much of the winter. Nevertheless, there is a small but significant risk to individuals during the winter months.

Discussion

Data from this study provide a useful gauge to infer risk from harbor dredging, but the implications go beyond this. Risks from other activities can also be inferred, along with associated seasonality, etc. The study has also shown some interesting patterns that shed light more generally on the movement ecology of this species. The tagged terrapins were highly mobile, in some cases traveling several kilometers in a single day. They actively moved between creeks, although this movement appeared to be primarily restricted to spring and summer months, and they exhibited strong fidelity to wintering habitat. This fidelity puts them at some risk from catastrophic events (e.g., severe weather, chemical spills, etc.)—a brumating population that is locally extirpated may take considerable time to recover (Tucker et al. 2001). The evidence suggests, however, that the Wellfleet population is widely distributed throughout the available habitat, and there does not appear to be a single site that would render the population vulnerable to such an event. These observations differ from previous studies in that although other authors have described strong within-creek site fidelity, movements among creeks have been thought to be rare (Muehlbauer 1987; Gibbons et al. 2001; Tucker et al. 2001; Harden et al. 2007). Some of this difference, however, may be an artifact of the techniques used. By continuously monitoring movement with a fixed-receiver array, we were able to identify movements that can be missed using other mark-recapture techniques, and our observations may just be the result of improved resolution offered by acoustic telemetry. Regardless, we did observe strong between-year fidelity to creeks during the fall months, which is consistent with other studies.

In other ways, however, our observations were similar to previous studies. For example, we were unable to find and capture males during the summer months. Roosenburg et al. (1999) described within-creek habitat partitioning by sex and size, with larger mature females using more open, deep water habitats in contrast to the males and juvenile females using upper marsh habitats. Such sex-based partitioning might explain our inability to capture males in summer. The fixed-station data did not show clear evidence of this, however; in our study, both sexes occupied open water areas, moving to the upper intertidal zones in late summer and early fall. Other authors have described age-dependent variability in location of brumacula (brumation sites), with adults remaining in the intertidal zone, either on top of the substrate, under scarred-out banks, or buried in mud, frequently in aggregations of several individuals (Haramis et al. 2011; Yearicks et al. 1981). Hatchlings, juveniles, and subadult terrapins often overwinter terrestrially, buried under the soil or dense vegetation above mean high water line (Lawler and Musick 1972; Muldoon and Burke 2012; Pitler 1985). We did not observe these patterns; however, we specifically targeted adult individuals in this study. If demographic segregation is occurring, it is likely to be happening primarily within the upper intertidal zone or above, in locations where we were unable to monitor.

High levels of gene flow are common among terrapin populations. Published data suggest that there is a tendency towards male-biased dispersal, with limited genetic separation by distance (Hauswaldt and Glenn 2005; Sheridan et al. 2010). Our collection data suggest that some sex-based habitat partitioning did occur. More work is needed to determine the extent of this partitioning, and whether this is typical of the species or if it reflects a unique characteristic of this population.

It is unclear why the terrapins congregate in the harbor during summer months. Interestingly, this is the period of greatest human activity within the harbor. Also during this period, ground tackle (moorings, floats, etc.) is deployed throughout the anchorage. This gear creates a reef effect, with abundant invertebrate communities that may serve as forage for terrapins (Tucker et al. 1995). This equipment is removed in the winter to prevent ice damage—if terrapins are attracted to this structure in summer, its absence in winter might help to explain the timing of the fall exodus. Comparable studies performed at lower latitudes where ground tackle remains in place throughout the year might yield different results. In any event, it is evident that activity within the harbor does not repel terrapins, which calls into question the assumption that they would actively avoid a dredge should that activity occur during summer (Brennessel 2006; Cecala et al. 2009). Further, the summer occupancy of this zone suggests that any activity that did repel them might constitute harm to the population through deprivation of access to vital resources.

Adequacy of the Approach

We applied a movement-theoretic approach to quantifying movement and occupancy. By analyzing the log-linear relationship between the density function of the intervals between detections, we were able to differentiate between departures from receivers and the missed detections associated with imperfect detection efficiency and movements near the periphery of receiver detection zones (Castro-Santos and Perry 2012). This approach recognizes the mixed distribution nature of movement data (Langton et al. 1995), and is an improvement over techniques that apply arbitrary thresholds to these intervals (e.g., Andrews and Quinn 2012; Chamberlin et al. 2011; Rohde et al. 2013). This approach, combined with a dense array of receivers, provided near-continuous monitoring of movements within the system of interest.

By combining occupancy and mobility, we were able to produce a reasoned estimate of how these two factors combine to produce total risk. The occupancy component of the model is robust, biased only by the deliberately disproportionate number of terrapins collected within the zone of interest. The interannual fidelity raises concerns that portions of the population that are impacted might be slow to re-colonize (Tucker et al. 2001). These data were for last observations on fixed receivers, however, which we have shown did not correspond with cessation of movement or actual locations of brumation. Instead, brumation appears to occur further up the intertidal zone within the creeks. Furthermore, the anchorage had the lowest level of interannual fidelity, suggesting that any disturbance in this area would represent low risk to the population. A less biased study would have selected terrapins from throughout the harbor. However, given that the aggregation appears to draw from the entire population, the actual bias may be small, and the results are conservative.

The other source of bias in our risk assessment comes from the assumption that there is zero risk when terrapins are maximally mobile and 100% risk when they are dormant. While it is likely true that a dormant terrapin would not be able to avoid a dredge, the dredge would have to be at the same site, and if the brumation location does not co-occur with the dredge, then the risk to the dormant animal is overestimated using our approach. Conversely, the risk may be underestimated to the extent that terrapins are unable to avoid the dredge when maximally active. Furthermore, we assume that the greatest distance traveled corresponds with greatest ability to avoid the dredge. At the time of greatest movement in late May, the water temperature ranged from 15 to 20 °C. Mean daily temperatures reached as high as 25 °C in the summer, however. Terrapins are ectotherms, and performance tends to increase with temperature. This relationship is not linear though, and for many species, the greatest scope for activity occurs at temperatures below the maximum environmental temperature that they are likely to encounter (Brett and Glass 1973;

Peterson et al. 1990). More work is needed to better understand the relationship between temperature and avoidance performance of terrapins. Still, it is important to recognize that the increased metabolic costs associated with activity during elevated temperatures often induce a state of reduced activity, meaning that it is possible for terrapins to be at greater risk from both exposure and mobility during the summer months.

Given the data, it is possible to gauge the effect of any error that might exist in our approach. First, if some vulnerability exists even during maximum activity, then the combined outcome would increase the expected risk during spring and summer. The fall/winter predictions would be relatively unaffected, indicating that the same period would still constitute the optimum period for risk minimization. This same logic applies to any reduction in protection from avoidance performance: If we are willing to assume that a dormant terrapin has zero avoidance ability, the general shape of the relationship will remain unchanged, with increased benefits accruing to performing dredging during fall and winter.

In conclusion, the data compiled in this study provide strong evidence that risk to the Wellfleet Harbor population of diamondback terrapins is minimized during late fall through early winter. The approach described here could readily be applied to other species and environments, and holds promise as a conservation tool for sensitive populations.

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