Individual Movement Behaviors of New York Harbor Striped Bass and Their Response to Extreme Events

Final Report to the Hudson River Foundation

Grant number: 002/13A

Principal Investigators:
Helen Bailey
University of Maryland Center for Environmental Science
Chesapeake Biological Laboratory
Solomons, MD 20688
Phone: 410-326-7284, E-mail: hbailey@umces.edu

David Secor
University of Maryland Center for Environmental Science
Chesapeake Biological Laboratory
Solomons, MD 20688
Phone: 410-326-7229, E-mail: secor@umces.edu

February 2017

Table of Contents

Abstract

Striped bass are a signature fished species of the Hudson River and have important foraging habitats in the lower Hudson River Estuary. Partial migration occurs in this species: seasonal migrations that persist throughout the lifespan, but differ between population components (aka contingents). The upper estuary (UEC) and lower estuary contingents (LEC) are known to occupy the estuary throughout most of the year, but with some movement into the surrounding coastal areas during the winter months. In this study we examined the movement patterns of acoustically tagged LEC and UEC striped bass to determine their swimming speeds and residency patterns in New York (NY) Harbor. The mean speed across NY Harbor was similar for the LEC (0.55 m s^{-1}, SE = 0.06 m s^{-1}) and the UEC tagged fish (0.52 m s^{-1}, SE = 0.06 m s^{-1}) and equated to approximately 1 body length s^{-1} (mean = 0.94 and 1.10 body lengths s^{-1} for the LEC and UEC tagged fish respectively). However, there was significant seasonal variation with swimming speeds peaking in April and May as they moved through the harbor to their spawning grounds upriver. After the spawning period, striped bass, particularly the LEC, returned to NY Harbor and many remained there during the period June to October with some fish remaining there over the winter months. The mean duration in NY Harbor was 57 days, but ranged up to 312 days.

The environmental conditions, for example temperature, are known to be an important determinant of fish movements and spatial distribution. We examined the relationship between the environmental variables water temperature, salinity, water level and the phase of the moon and the daily presence of tagged striped bass in NY Harbor. During the spawning period, water level was significantly and negatively related to the presence of striped bass in NY Harbor indicating that fish tended to occur there when the water level was lower. There was no significant difference in occurrence between the UEC and LEC contingents during the spawning period. However, during the non-spawning period, contingent membership was significantly related to presence in NY Harbor with the LEC contingent being present in New York Harbor more frequently than the UEC contingent. The phase of the moon was significantly and negatively related to the presence of striped bass in NY Harbor, indicating that fish were more likely to be present around the new moon when night light levels are lower and there are spring tides, which may facilitate foraging.

An increase in the intensity and frequency of extreme events is predicted to occur as a result of climate change. In this study we identified coastal evacuations by striped bass caused by an intense period of tropical storms in autumn 2011. These storms produced record rainfall and high water discharges into the Hudson River Estuary that increased the water level and reduced the water temperature, salinity and dissolved oxygen levels. Striped bass moved out of the estuary, exhibiting novel migration behaviors, that may have been in response to the strong flow and unsuitable conditions. In the months following the storms, some fish demonstrated exploratory trips back to the estuary, which may have been to assess the conditions before returning for the remainder of the winter. Behavioural adaptions to weather events by striped bass and other coastal fishes will depend on maintenance of key population segments and unimpeded evacuation routes.

Summaries

Striped bass movement and residency patterns

In past research (Gahagan et al. 2015), a total of 75 striped bass were implanted with transmitter tags during autumn 2009 and spring 2010 in New York (NY) Harbor and the Hudson River. Fifteen acoustic receivers were moored in and around NY Harbor in a "gates" design (Heupel et al. 2006, Wingate and Secor 2007) that allowed all tagged individuals to be monitored when they passed through any of the channels to the harbor. Tag battery life greatly exceeded expectations with transmissions received up to 2.5 years after deployment. Data sharing through the Atlantic Coastal Telemetry (ACT) Network also provided additional acoustic detections and from a much larger area in coastal waters.

The database of acoustic detections included 548,732 records with information on the date and time of detection, the transmitter number to identify the individual fish, and the name, latitude and longitude of the receiver station. An additional 30,849 acoustic detections from 30 of our tagged striped bass were received from collaborators through the ACT Network extending the period of detection to July 2012. These acoustic detections were integrated into our database. The data were then formatted for individual movement analysis. Since we were focusing on NY Harbor, individual tracks were selected that had at least one detection in this area. This resulted in a total of 43 individual tracks, of which 26 were from the Lower Estuary Contingent (LEC), 10 from the Ocean Contingent (OC) and 7 from the Upper Estuary Contingent (UEC). These data are summarized in Table 1. The overall mean tracking duration was 708 days (mean duration 770, 753 and 548 days for the UEC, LEC and OC respectively) and the mean number of detections per track was 8,515 (mean detections 18,213, 7,847, 3,461 for the UEC, LEC and OC respectively). There were a total of 1,417 days with detections in NY Harbor.

Swimming speeds

The time-series of detections at known receiver locations allowed us to reconstruct the approximate movement paths of the tagged striped bass. We focused on the LEC and UEC contingents because they spent the most time in NY Harbor. Entry of an individual into NY Harbor was confirmed by detection at a receiver site in NY Harbor. The speed of the tagged fish as it moved across NY Harbor was calculated using the in-water distance and time interval between detections at different entry or egress receiver locations around NY Harbor (Table 2). We did not include movement between receivers less than 2 km apart since the detection range of the receivers is approximately 1 km and detection at nearby receivers could have occurred as a result of a fish moving between them at the periphery of their detection range. The mean speed across NY Harbor was similar for the LEC (0.55 m s^{-1}, SE = 0.06 m s^{-1}) and the UEC tagged fish (0.52 m s^{-1}, SE = 0.06 m s^{-1}) and equated to approximately 1 body length s^{-1} (mean = 0.94 and 1.10 body lengths s^{-1} for the LEC and UEC tagged fish respectively). There was no significant relationship between fish total length and swimming speed (linear regression: $F_{1,24}$ = 1.425 and 0.942, p=0.244 and 0.342 for speed in m s^{-1} and body length s^{-1} respectively). However, there was significant seasonal variation with swimming speeds peaking in April and May (Mean speeds 0.81 and 0.62 m s^{-1} respectively, generalized additive mixed model with the individual fish as a random effect: F = 3.03, edf = 3.67, p < 0.01). For example, Study ID 11 swam at its maximum speed (1.61 m s^{-1}, 2.68 body length s^{-1}) in May 2011 (Figure 1 and Table 3). The striped bass generally moved northwards through NY Harbor to the spawning grounds up the Hudson River in April and southwards downriver into the harbor in May.

Table 1: Summary of individually tracked striped bass. These fish were all detected at least once within New York Harbor between spring 2010 and 2012. LEC=lower estuarine contingent; OC=ocean contingent; UEC=upper estuary contingent.

Transmitter (Study ID)	Contingent	Tag date	Last detection date	Track duration (days)	Total number of detections	Average number of detections per day
62479 (11)	LEC	10/17/2009	11/29/2011	773	5,002	6.5
62480 (12)	LEC	10/17/2009	12/9/2011	783	10,925	14.0
62481 (13)	LEC	10/17/2009	12/8/2011	782	6,844	8.8
62483 (15)	LEC	10/17/2009	10/4/2010	352	1,779	5.1
62484 (16)	LEC	10/18/2009	11/5/2011	749	16,081	21.5
62485 (17)	LEC	10/17/2009	10/29/2011	741	9,513	12.9
62487 (18)	LEC	10/17/2009	1/9/2012	814	5,181	6.4
62489 (19)	LEC	10/17/2009	10/29/2011	742	4,197	5.7
62490 (20)	LEC	10/17/2009	12/13/2011	787	8,262	10.5
62492 (21)	LEC	10/17/2009	9/25/2011	708	284	0.4
62494 (22)	LEC	10/18/2009	12/5/2011	778	10,294	13.2
62496 (23)	LEC	10/17/2009	1/9/2012	814	15,971	19.7
62497 (24)	LEC	10/17/2009	1/3/2012	808	17,532	21.7
62500 (25)	LEC	10/17/2009	1/9/2012	814	886	1.1
62503 (27)	LEC	10/17/2009	10/27/2011	740	1,538	2.1
62506 (29)	LEC	10/17/2009	11/27/2011	771	26,521	34.4
62509 (30)	LEC	10/17/2009	12/9/2011	783	3,213	4.2
62510 (31)	LEC	10/18/2009	8/14/2011	665	3,452	5.2

62512 (32)	LEC	10/17/2009	10/31/2011	744	7,093	9.5
62514 (33)	LEC	10/17/2009	11/14/2011	758	2,949	3.9
62515 (34)	LEC	10/17/2009	1/11/2012	816	9,312	11.4
62517 (35)	LEC	10/17/2009	11/18/2011	762	26,471	35.1
62518 (36)	LEC	10/18/2009	11/9/2011	752	5,220	6.9
62523 (37)	LEC	10/18/2009	12/18/2011	791	3,215	4.1
62527 (38)	LEC	10/18/2009	12/3/2011	776	1,461	1.9
62530 (39)	LEC	10/18/2009	12/1/2011	774	832	1.1
47952 (41)	OC	5/16/2010	10/23/2010	160	465	2.9
47954 (42)	OC	5/18/2010	6/5/2012	749	4,065	5.4
47956 (43)	OC	5/18/2010	6/5/2012	749	4,959	6.6
47958 (44)	OC	5/18/2010	1/11/2012	603	1,463	2.4
47959 (45)	OC	5/18/2010	4/12/2011	329	248	0.8
47960 (46)	OC	5/18/2010	8/1/2011	440	16,741	38.0
47961 (47)	OC	5/18/2010	7/8/2011	416	1,071	2.6
47962 (48)	OC	5/18/2010	11/14/2011	545	376	0.7
47963 (49)	OC	5/18/2010	6/6/2012	750	3,379	4.5
47967 (50)	OC	5/18/2010	5/22/2012	735	1,846	2.5
62491 (1)	UEC	10/21/2009	10/15/2011	724	22,845	31.6
62495 (3)	UEC	10/21/2009	1/15/2012	816	15,725	19.3
62499 (4)	UEC	10/19/2009	12/30/2011	802	26,015	32.5
62507 (5)	UEC	10/19/2009	11/5/2011	747	32,943	44.2
62516 (6)	UEC	10/26/2009	1/10/2012	806	10,759	13.4
62521 (7)	UEC	10/21/2009	9/19/2011	698	13,342	19.1
62531 (10)	UEC	10/19/2009	12/22/2011	794	5,863	7.4

Table 2: Swimming speeds of tagged striped bass across New York Harbor. These fish were all detected at two or more entry or egress receiver locations within New York Harbor. LEC=lower estuarine contingent, and UEC=upper estuary contingent.

Study ID	Contingent	Total length (mm)	Mean speed	
			m s^{-1}	body lengths s^{-1}
3	UEC	0.483	0.24	0.50
4	UEC	0.410	1.01	2.47
6	UEC	0.533	0.66	1.23
7	UEC	0.483	0.30	0.61
10	UEC	0.540	0.38	0.70
11	LEC	0.600	0.49	0.81
13	LEC	0.500	0.09	0.19
16	LEC	0.590	0.43	0.73
17	LEC	0.435	0.16	0.37
18	LEC	0.560	0.37	0.65
19	LEC	0.960	0.85	0.88
20	LEC	0.480	0.46	0.95
22	LEC	0.475	0.80	1.67
23	LEC	0.525	0.29	0.55
24	LEC	0.850	0.69	0.81
25	LEC	0.850	0.67	0.79
27	LEC	0.460	0.99	2.16
29	LEC	0.710	1.08	1.52
30	LEC	0.620	0.79	1.28
32	LEC	0.660	0.30	0.46
33	LEC	0.620	0.05	0.08
34	LEC	0.540	0.45	0.83

35	LEC	0.490	0.43	0.88
36	LEC	0.540	0.79	1.47
37	LEC	0.490	0.56	1.14
38	LEC	0.550	0.89	1.61
MEAN		**0.575**	**0.55**	**0.97**

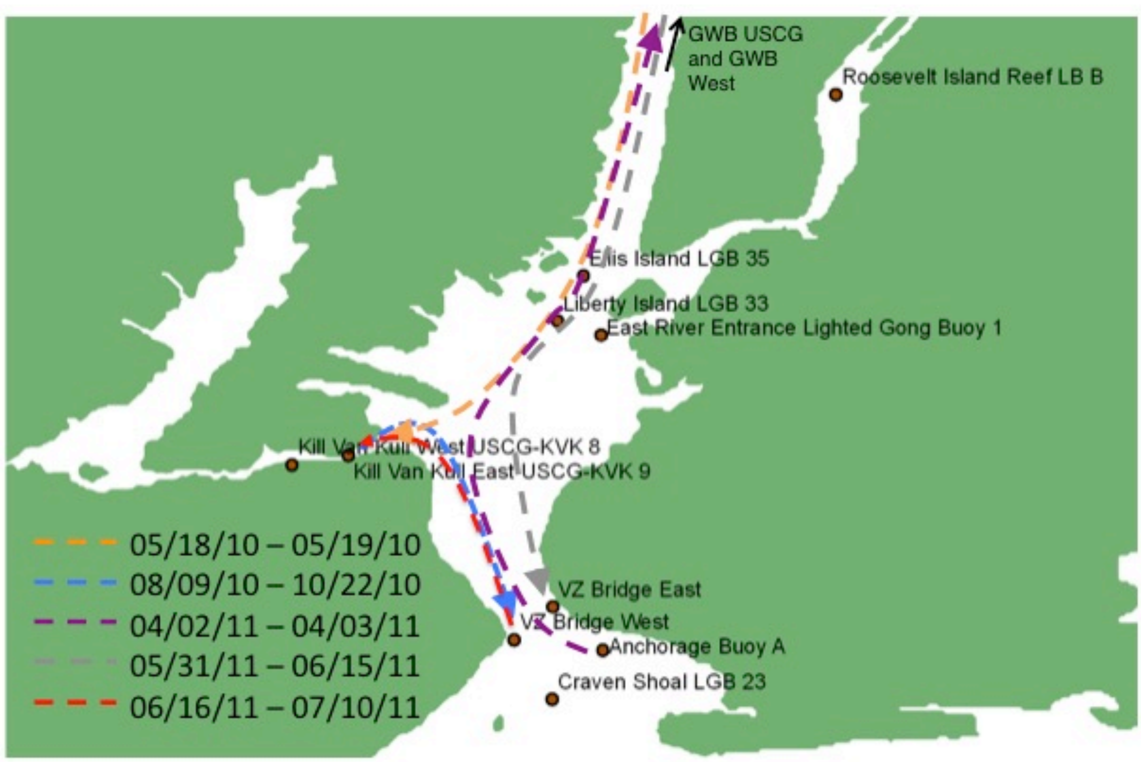


Figure 1: Map of NY Harbor receiver locations (dark red circles) and reconstructed movement paths for Study ID 11 when it passed through NY Harbor (lines connect chronological receiver detections, but may not represent the actual path taken).

Table 3: Detection and movement metrics for Study ID 11 when there were consecutive detections at different receiver locations around NY Harbor and it is established that the animal was within NY Harbor during that period. The station names correspond to those in Figure 1.

Dates of detections at different egress sites	Station Names	Time elapsed (days)	In-water distance (km)	Speed m/s (km/day)	Direction
05/18/10 09:31:39 to 05/19/10 00:27:48	GWB USCG to Kill Van Kull East	0.62	26.36	0.49 (42.36)	Southwards
8/9/10 1:13:00 to 10/22/10 5:47:00	Kill Van Kull East to VZ Bridge West	74.17	9.22	0.00 (0.12)	Southwards
04/02/11 21:51:42 to 04/03/11 02:24:38	Anchorage Buoy A to Liberty Island	0.19	9.61	0.59 (50.70)	Northwards
04/03/11 07:14:51 to 04/03/11 14:27:59	Ellis Island to GWB West	0.30	18.69	0.72 (62.14)	Northwards
05/31/11 14:53:11 to 05/31/11 18:06:54	GWB West to Ellis Island	0.13	18.69	1.61 (138.93)	Southwards
05/31/11 18:30:02 to 06/15/11 04:38:48	Liberty Island to VZ Bridge East	14.42	10.91	0.01 (0.76)	Southwards
06/16/11 02:29:02 to 07/10/11 02:35:54	VZ Bridge West to Kill Van Kull East	24.00	9.22	0.00 (0.38)	Northwards

Quantifying residency patterns

Analysis of the receiver detections in the NY Harbor region revealed that the greatest number occurred in November (n= 33,477). There were differences in occurrence in this region amongst the three contingents (Figure 2). The OC fish only occurred in NY Harbor in February to August, with the majority of detections during April to July. These fish moved northwards up the Hudson River in April and May to spawn, and moved out to the coastal waters in June and July.

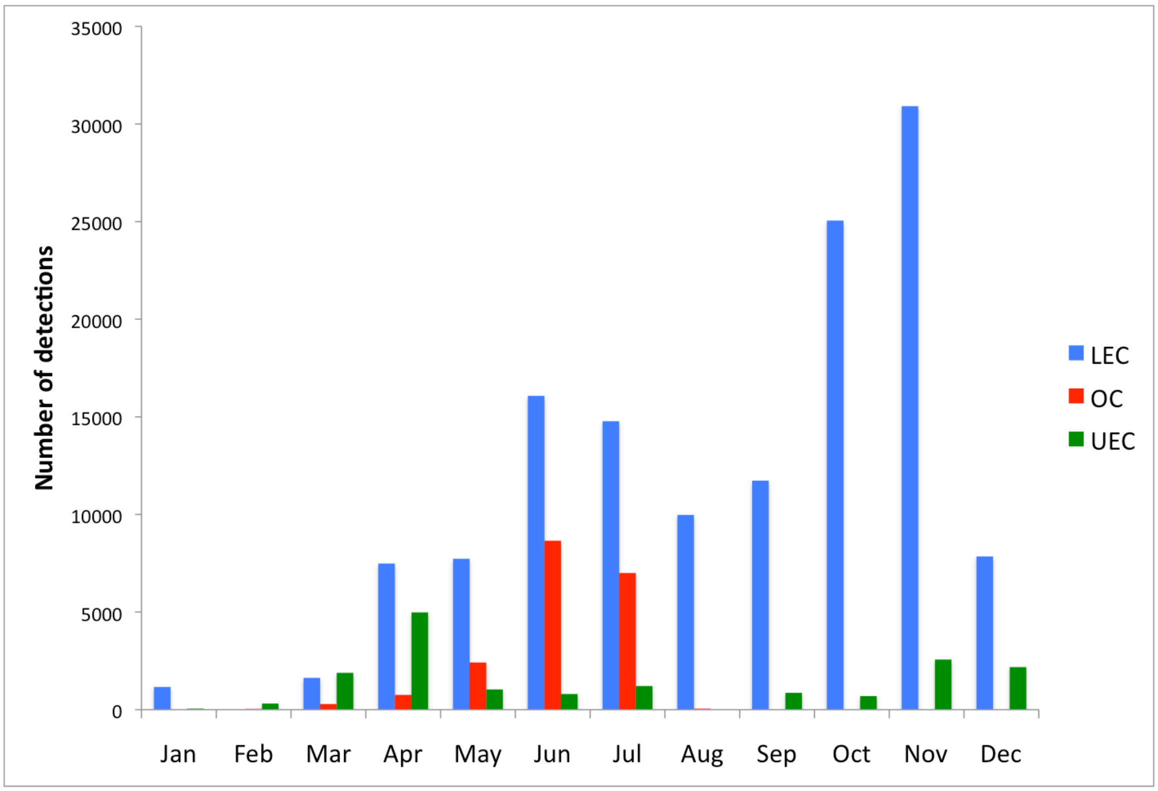


Figure 2: Number of detections per month in NY Harbor for the three striped bass contingents (LEC, OC and UEC).

The LEC and UEC fish were detected year-round and therefore these contingents were the focus of our further analysis into the residency patterns of striped bass in NY Harbor. The time series of detections at known egress locations around NY Harbor allowed us to infer when tagged striped bass were in the harbor, even when they were not specifically detected by a receiver. For example a detection at Liberty Island followed 14 days later by a detection at VZ Bridge East (Table 3) indicates the fish was in NY Harbor during that 14 day time period. In this way we were able to determine daily whether a tagged fish was present or absent in NY Harbor (Figure 3a). We analyzed the presence/absence of striped bass in NY Harbor for the period 1 June 2010 – 27 August 2011. Movements after 27 August 2011 were not included in this residency pattern analysis because of the confounding effect of the Storms Irene and Lee, which led to evacuation into the coastal environment (see section "Evaluating the response of striped bass to extreme storm events").

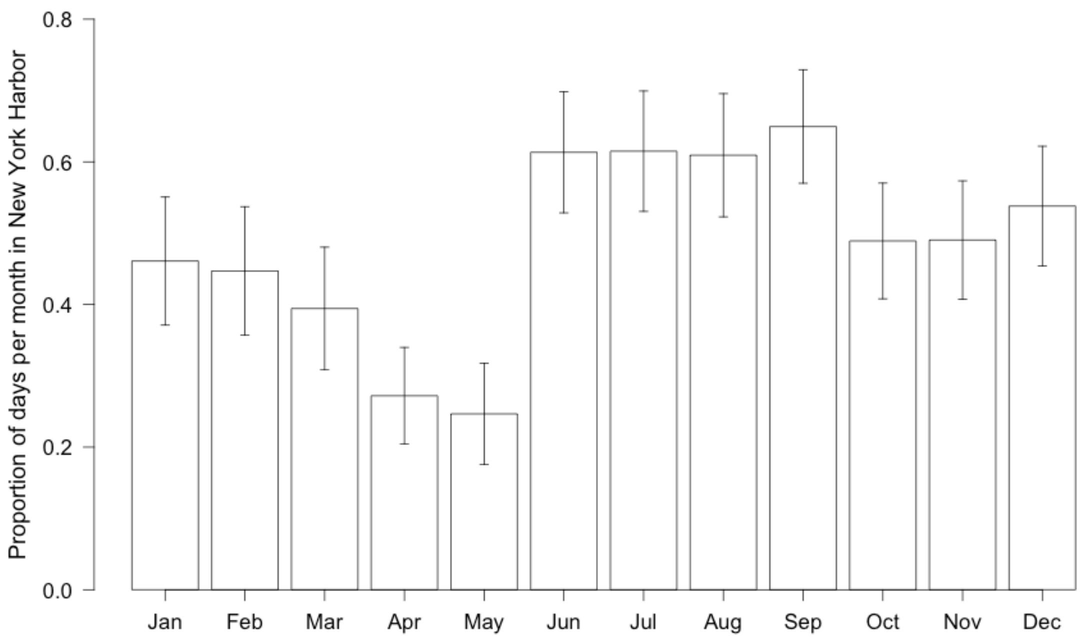
There were occasionally extended periods when there were no detections during the study period. If this occurred at the egress sites nearest the coast (receiver sites VZ Bridge East, VZ Bridge West, Anchorage Buoy A and Craven Shoal), it is possible that the fish may have moved into coastal waters during this time. A current study on ocean migrations of striped bass (HRF Award No. 011/15A to David Secor, Helen Bailey, Kathryn Hattala and Amanda Higgs) will help to elucidate the coastal movements of striped bass. In order to identify periods when striped bass may have moved out of the harbor into coastal areas, we analyzed the distribution of the time between detections for all of the LEC and UEC tagged fish. The median time between detections was 7 days (range = 1 – 191 days). During gaps in detections at the egress sites nearest the coast that were greater than 7 days, the tagged fish was considered as not being present in NY Harbor on those days. This is a conservative assumption as lack of detection could alternatively indicate a period of relative immobility away from the range of receiver detections within the Harbor. The extended gaps in detections occurred most frequently during November to March leading to a reduction in the estimated proportion of days per month that striped bass occurred in NY Harbor during the winter (Figure 3b). Striped bass tended to occur in NY Harbor on the greatest proportion of days per month in June to October (Figure 3b).

Movement through NY Harbor during the spawning migration was relatively rapid and generally took only 1-2 days. This led to a relatively low mean number of days that striped bass were present in NY Harbor during April and May, although it serves as a critical route during the spawning migration (Gahagan et al. 2015). During the spawning migration in April and May 2011, the majority (20 out of 31 fish that occurred at least once in NY Harbor) of the tagged LEC and UEC fish were detected in NY Harbor. However, they did not occur there simultaneously. The fish moved rapidly across the Harbor resulting in a maximum of 8 tagged fish occurring in NY Harbor (Figure 4) on any particular day during April and May (assuming the 7 day gap limit criteria described above). The UEC fish tended to move through the Harbor (mean date = 5th April, SD = 16 days) slightly earlier than the LEC (mean date = 17th April, SD = 17 days).

The number of tagged fish in NY Harbor peaked in June to October 2010 (Figure 4). Although there was also an increase during the summer in 2011, the number was lower than in 2010 most likely due to mortality or attrition of the tags. The maximum number of tagged fish in NY Harbor was 19 on 11th July 2010 and lowest at 2 fish on 20th – 27th November 2010 and 4th December 2010. There was no occasion during the study period when none of the tagged striped bass occurred in NY Harbor. The year-round occurrence of striped bass suggests that NY Harbor is not only a migratory route, but also an important foraging habitat.

The residency time and number of visits were calculated individually for each tagged LEC and UEC striped bass and then averaged across these individuals (Table 4). The mean total residency time for a tagged striped bass in NY Harbor over the study period (total 453 days) was 144 days (SD = 91 days, range = 2 – 385 days). The mean number of visits for each track during the study period was 3 (range = 1 – 7) corresponding to 6 excursions into and out of NY Harbor, with a mean visit duration of 57 days (SD = 48 days, range = 1 – 312 days). The number and duration of visits was similar for the LEC and UEC fish (mean number of visits = 3.4 and 2.6, mean visit duration = 59 and 53 days, respectively).

a)



b)

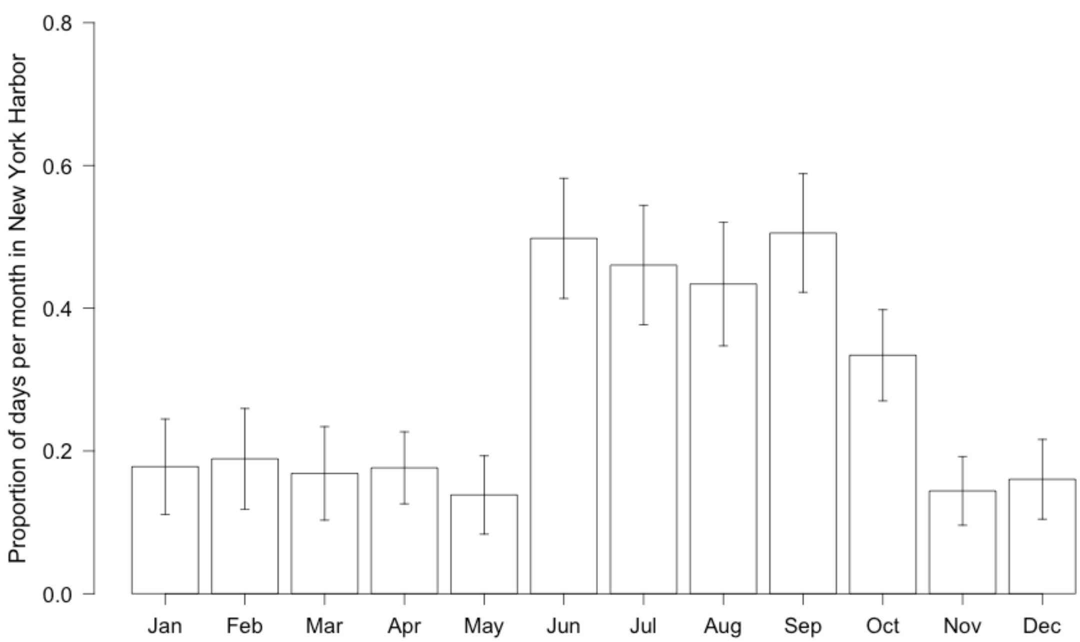


Figure 3: Mean (±SE) proportion of days per month striped bass were present in New York assuming a) continuous inhabitance in NY Harbor between receiver detections, and b) inhabitance limited to gaps in detections of 7 days at the egress sites nearest the coast.

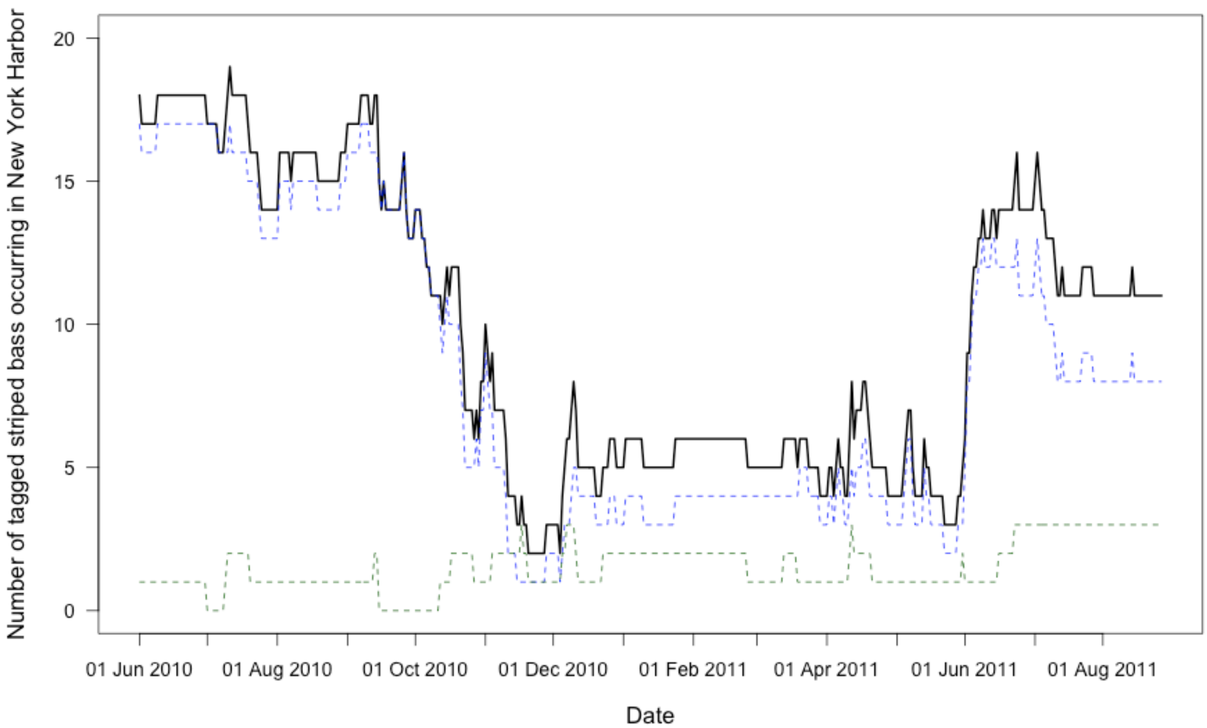


Figure 4: Number of tagged LEC and UEC striped bass (black solid line) occurring in New York Harbor during the study period 1 June 2010 – 27 August 2011. The individual contingents are shown as dashed lines where the LEC is in blue and the UEC in green.

Table 4: The residency time and number of visits to New York Harbor by tagged striped bass during the study period 1 June 2010 – 27 August 2011.

Study ID	Contingent	Mean total residence time (days)	Number of visits	Mean residence time per visit (days)	Period of longest visit
1	UEC	164	1	164	Nov 2010-Apr 2011
3	UEC	74	2	37	Dec 2010-Feb 2011
4	UEC	178	2	89	Apr 2011-Aug 2011
5	UEC	11	2	6	Dec 2010
6	UEC	10	4	3	Mar 2011
7	UEC	115	4	29	Jun 2011–Aug 2011

10	UEC	137	3	46	Jul 2010-Sep 2010
11	LEC	235	3	78	Jun 2010-Oct 2010
12	LEC	2	2	1	Jun 2010
13	LEC	134	1	134	Jun 2010-Oct 2010
16	LEC	385	3	128	Jun 2010-Apr 2011
17	LEC	170	6	28	Jun 2011–Aug 2011
18	LEC	243	3	81	Jun 2010-Nov 2010
19	LEC	15	33	5	Oct 2010-Nov 2010
20	LEC	222	4	56	Jun 2010-Oct 2010
22	LEC	78	44	20	Aug 2010-Sep 2010
23	LEC	134	5	27	Jul 2010-Sep 2010
24	LEC	87	4	22	Jun 2010-Jul 2010
25	LEC	24	3	11	Oct 2010-Nov 2010
27	LEC	134	3	45	Dec 2010-Apr 2011
29	LEC	294	3	98	Jun 2010-Oct 2010
30	LEC	44	5	9	Apr 2011-May 2011
31	LEC	131	3	44	Jun 2010-Oct 2010
32	LEC	162	4	41	Aug 2010-Nov 2010
33	LEC	229	2	115	Jun 2010-Oct 2010
34	LEC	171	7	24	Jun 2010-Jul 2010
35	LEC	188	6	31	Jun 2011–Aug 2011
36	LEC	293	3	98	Jun 2010-Oct 2010
37	LEC	144	1	144	Dec 2010-Apr 2011
38	LEC	120	4	30	Jun 2010-Sep 2010
39	LEC	136	1	136	Jun 2010-Oct 2010
MEAN		**144**	**3**	**57**	**June-October**

Evaluating the response of striped bass to extreme storm events

Published paper: Bailey, H. and Secor, D.H. (2016) Coastal evacuations by fish during extreme weather events. Scientific Reports, 6: 30280

An increase in the intensity and frequency of extreme events is predicted to occur as a result of climate change. In coastal ecosystems, hurricanes and flooding can cause dramatic changes in water quality resulting in large mortality events in estuarine fauna. Facultative migration behaviors represent a key adaptation by which animals can evacuate ecological catastrophes, but remain poorly studied in marine systems. In this study we identified coastal evacuations by otherwise resident riverine striped bass in the Hudson River Estuary, New York, USA, caused by an intense period of tropical storms in autumn 2011. These storms produced record rainfall and high water discharges into the Hudson River Estuary that increased the water level and reduced the water temperature, salinity and dissolved oxygen levels. Striped bass moved out of the estuary, exhibiting novel migration behaviors, that may have been in response to the strong flow and unsuitable conditions. In the months following the storms, some fish demonstrated exploratory trips back to the estuary, which may have been to assess the conditions before returning for the remainder of the winter. Behavioral adaptions to weather events by striped bass and other coastal fishes will depend on maintenance of key population segments and unimpeded evacuation routes.

Striped bass habitat preference model for NY Harbor

The environmental conditions, for example temperature, are known to be an important determinant of fish movements and spatial distribution (Nelson et al. 2010). Identifying the environmental preferences of species allows us to coarsely predict their spatial distribution based on knowledge of the environmental conditions (Elith and Leathwick 2009). For example, the occurrence and densities of satellite tracked blue whales has been modeled and is predicted monthly in near real-time based on the latest environmental data (Hazen et al. 2016). In order to understand the habitat preferences of striped bass we combined the acoustic detections of the tagged fish with environmental data from the Hudson River Environmental Conditions Observing System (HRECOS, www.hrecos.org) and other sources.

We reviewed all of the acoustic detections and considered fish to be within NY Harbor at and between times they were detected at receiver stations at entry and egress locations to the harbor (see "Quantifying residency patterns" section). Presence or absence within NY Harbor was then assigned for each fish to each day within the study period of 1 June 2010 to 27 August 2011 (movements after this time were affected by the Storm Events Irene and Lee and were therefore not included in this analysis). Corresponding daily environmental data were obtained for water level, temperature, salinity and fraction of the moon illuminated (a quantitative measure of the moon's phase). Water level data were obtained from the U.S. Geological Survey (USGS) daily statistics (available at: http://waterdata.usgs.gov/usa/nwis/dvstat/?referred_module=sw) for the station in the lower Hudson River Estuary at the south dock at West Point, NY (USGS Station 01374019 at 41.386°N, 73.955°W). Water temperature and salinity data were obtained from HRECOS for the Castle Point Buoy Station (40.743°N, 74.023°W) and the George Washington Bridge Station (40.852°N, 73.959°W). These data were recorded every 15 minutes and a daily mean was calculated. Data were collected during the study period at both of these stations. The

George Washington Bridge Station became inactive and data collection ceased on 1st October 2012. In order to incorporate water temperature and salinity values into the model that would allow predictions to be made with current environmental conditions, a station that is currently actively collecting data is preferable. However, the Castle Point Buoy Station had several periods with salinity data gaps during July to September 2010. We therefore used the salinity data from the George Washington Bridge Station to fill these gaps. This station is upriver of the Castle Point Buoy Station and the data from both stations were first compared to determine the appropriate conversion factor necessary to provide salinity values that would be comparable to the location of the Castle Point Buoy Station. This involved performing a linear regression ($F_{1,370} = 1924$, $p<0.01$, $r^2 = 0.84$) that resulted in the conversion equation (where CPB refers to the Castle Point Buoy and GWB to the George Washington Bridge Station):

$$\text{CPB (salinity)} = 2.513 + 1.098 \times \text{GWB (salinity)} \qquad \text{(eqn 1)}$$

This conversion equation was applied to the salinity data from the George Washington Bridge Station for the days during the study period that data were missing from the Castle Point Buoy Station. We used the daily fraction of the moon illuminated as an index of the amplitude of the tides, with the amplitude, and consequently current speed, being greatest when the moon is full or new (spring tides) and lowest during the moon's quarter phases (neap tides). The moon illumination also affects night light levels, which could affect striped bass foraging behavior and their prey. Data on the fraction of the moon illuminated for each night (values ranging from 0 during a new moon to 1 during a full moon) were obtained from the Astronomical Applications Department of the US Naval Observatory (http://aa.usno.navy.mil/data/docs/MoonFraction.php).

We used generalized estimating equations (GEE) to model the marginal means, which averages across individuals in a population-averaged approach (Fieberg et al. 2009). GEEs are an extension of generalized linear models (GLM), but unlike GLMs do not assume an identity covariance structure and instead explicitly model the correlation structure (Zeger and Liang 1986, Bailey et al. 2013). GEEs are highly flexible in terms of the distribution of response variables that can be accommodated and are becoming increasingly popular as a tool for modeling resource selection (Koper and Manseau 2009). We fit a GEE model with the response variable as the daily presence/absence of each tagged striped bass within NY harbor. As in the analysis of residency time, during gaps in detections at the egress sites nearest the coast that were greater than 7 days, the tagged fish were considered as no longer being present in NY Harbor. The explanatory variables in the model were water level, temperature, salinity, and fraction of the moon illuminated. The size and contingent classification for each individual were included as covariates. An autoregressive correlation structure was implemented in the GEE as the observations for each individual form a time series. However, a benefit of GEEs is that they yield consistent estimates even with misspecification of the working correlation matrix (Liang and Zeger 1986, Bailey et al. 2013). We separated the data set into the spawning (April and May) and non-spawning (June to March) periods because the movements were different with significantly higher speeds as the fish migrated through NY to their spawning habitats. Such different seasonal behavior can result in different relationships with environmental variables and sub-setting the data can improve model fit (Hazen et al. 2016, Roberts et al. 2016).

During the spawning season, water level was significantly negatively related to the presence of striped bass in NY Harbor indicating that fish tended to occur there when the water level was lower (Table 5). There was no significant difference between the UEC and LEC contingents, presumably as both move upriver to spawn during this period. In contrast, during the non-spawning period, contingent membership was significantly related to presence in NY Harbor with the LEC contingent being present in NY Harbor more frequently than the UEC contingent as expected (Table 6). Also, instead of water level, it was the fraction of the moon illuminated that was significantly and negatively related to the presence of striped bass in NY Harbor (Table 6), although the effect size was relatively small (Figure 5). This indicates that fish were more likely to be present nearer the new moon when light levels at night were lower. The new moon is also when there are spring tides and the tidal amplitude (up to 1.5 m), and consequently current strength, will be greater. The low night light and stronger tides may facilitate foraging for striped bass. Tidal currents may potentially aid movement from the river and/or coast into the harbor.

The correlation estimate from the GEE model for the presence of striped bass between two sequential days was extremely high at 0.98, which corresponds to a correlation in a week of 0.87, suggesting striped bass are likely to remain within NY Harbor once they enter it (outside of the spawning season). The persistence of striped bass within NY Harbor likely reflects their generalist feeding behavior. This allows them to switch amongst prey species depending on what is available and predate across multiple species (Hartman and Brandt 1995, Hartman 2003). None of the environmental variables studied had consistent values over the long time period striped bass were generally in NY Harbor with environmental variability occurring on much shorter time scales. Consequently, although statistically significant, the environmental conditions did not appear to have a large effect on striped bass occurrence in NY Harbor. The storm events during the fall of 2011, which caused many striped bass to evacuate the Hudson River Estuary, meant that we had to truncate our data set for the habitat preference model leaving only had 14 months of data for each tagged fish. Telemetry data from multiple years with continued receiver coverage in and around the Harbor would help to determine the degree of interannual variation in striped bass occurrence and how this is affected by the environmental conditions. It would also allow a more detailed analysis of the timing of entry and exit into NY Harbor, which could help to determine how strongly environmental cues play a role in striped bass movements. Mobile tracking of striped bass may help to elucidate finer scale movement and foraging patterns, particularly if concurrent surveys of prey species could be conducted. Comparison with the coastal movements of striped bass may also help to determine the factors influencing movement in and out of the Harbor.

Table 5: Results from the generalized estimating equations (GEE) model for the spawning season (April and May). Variables with $P < 0.05$ are indicated by an asterisk. Contingent was specified as a categorical variable where the reference level was the UEC contingent.

Parameter	Coefficient estimate	Standard error	Wald	*P*
Intercept	-1.509	1.665	0.821	0.365
Water level	-0.640	0.322	3.958	0.047*
Water temperature	0.012	0.043	0.081	0.776
Salinity	0.012	0.018	0.416	0.519
Fraction of the moon illuminated	0.344	0.298	1.329	0.249
Fish size	-0.000	0.003	0.020	0.888
Contingent	-0.006	0.721	0.000	0.993

Table 6: Results from the GEE model for the non-spawning period (June to March). Variables with $P < 0.05$ are indicated by an asterisk. Contingent was specified as a categorical variable where the reference level was the UEC contingent.

Parameter	Coefficient estimate	Standard error	Wald	*P*
Intercept	-0.323	0.892	0.130	0.718
Water level	-0.055	0.035	2.550	0.110
Water temperature	0.015	0.025	0.380	0.535
Salinity	0.002	0.003	0.450	0.503
Fraction of the moon illuminated	-0.127	0.048	6.850	0.009*
Fish size	-0.002	0.002	2.560	0.110
Contingent	1.183	0.506	5.460	0.020*

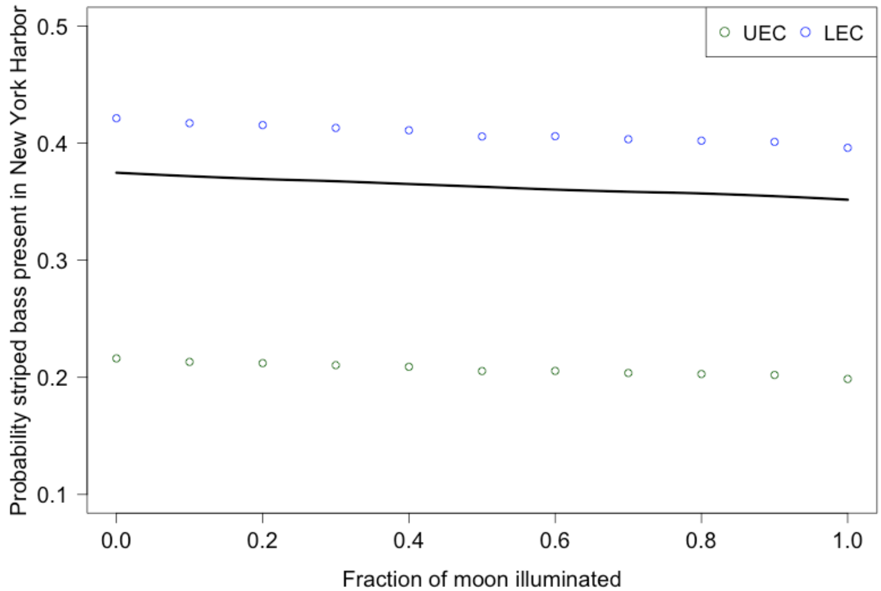


Figure 5: Best-fit line for the fitted values from the GEE model of the probability of striped bass being present in New York Harbor during the non-spawning period (June to March) in relation to the fraction of the moon illuminated. The mean proportion of days in which striped bass were present for the two contingents (UEC and LEC) are shown as circles (calculated in 0.1 moon fraction bins).

List of papers, manuscripts and presentations

Papers:
Bailey, H. and Secor, D.H. (2016) Coastal evacuations by fish during extreme weather events. *Scientific Reports*, 6: 30280

Manuscripts:
Bailey, H. and Secor, D.H. (in preparation) Habitat preferences of striped bass in New York Harbor.

Presentations:
Helen Bailey and David Secor. Movement Ecology. Chesapeake Biological Laboratory, Solomons, MD. 8th April 2014.
David Secor. Migration Ecology of NY Harbor Striped Bass: Fish of Gotham. Hudson River Foundation, New York, NY. 14th March 2014.
Helen Bailey. Going with the flow? Movement ecology of mobile marine species. Horn Point Laboratory, Cambridge, MD. 20th January 2016.
Helen Bailey and David Secor. Movements of striped bass in response to extreme weather events. Hudson River Foundation, New York. 24th October 2016.

Bibliography

Bailey, H., R. Corkrey, B. Cheney, and P. M. Thompson. 2013. Analyzing temporally correlated dolphin sightings data using generalized estimating equations Marine Mammal Science 29:123-141.

Elith, J., and J. R. Leathwick. 2009. Species distribution models: Ecological explanation and prediction across space and time. Annual Review of Ecology, Evolution, and Systematics 40:677-697.

Fieberg, J., R. H. Rieger, M. C. Zicus, and J. S. Schildcrout. 2009. Regression modelling of correlated data in ecology: subject-specific and population averaged response patterns. Journal of Applied Ecology 46:1018-1025.

Gahagan, B. I., D. A. Fox, and D. H. Secor. 2015. Partial migration of striped bass: revisiting the contingent hypothesis. Marine Ecology Progress Series 525:185-197.

Hartman, K. J., and S. B. Brandt. 1995. Trophic resource partitioning, diets, and growth of sympatric estuarine predators. Transactions of the American Fisheries Society 124:520-537.

Hartman, K. J. 2003. Population-level consumption by Atlantic coastal striped bass and the influence of population recovery upon prey communities. Fisheries Management and Ecology 10:281-288.

Hazen, E. L., D. Palacios, K. A. Forney, E. A. Howell, E. A. Becker, A. Hoover, L. Irvine, M. DeAngelis, S. J. Bograd, B. R. Mate, and H. Bailey. 2016. WhaleWatch: a dynamic management tool for predicting blue whale density in the California Current. Journal of Applied Ecology doi: 10.1111/1365-2664.12820.

Heupel, M. R., J. M. Semmens, and A. J. Hobday. 2006. Automated acoustic tracking of aquatic animals: scales, design and deployment of listening station arrays. Marine and Freshwater Research 57:1-13.

Koper, N., and M. Manseau. 2009. Generalized estimating equations and generalized linear mixed-effects models for modelling resource selection. Journal of Applied Ecology 46:590-599.

Liang, K. Y., and S. L. Zeger. 1986. Longitudinal data analysis using generalized linear models. Biometrika 73:13-22.

Nelson, G. A., M. P. Armstrong, J. Strizel-Thomson, and K. D. Friedland. 2010. Thermal habitat of striped bass (*Morone saxatilis*) in coastal waters of northern Massachusetts, USA, during summer. Fisheries Oceanography 19:370-381.

Roberts, J. J., B. D. Best, L. Mannocci, E. Fujioka, P. N. Halpin, D. L. Palka, L. P. Garrison, K. D. Mullin, T. V. N. Cole, C. B. Khan, W. A. McLellan, D. A. Pabst, and G. G. Lockhart. 2016. Habitat-based cetacean density models for the U.S. Atlantic and Gulf of Mexico. Scientific Reports 6:22615.

Wingate, R. L., and D. H. Secor. 2007. Intercept telemetry of the Hudson River Striped Bass resident contingent: migration and homing patterns. Transactions of the American Fisheries Society 136:95-104.

Zeger, S. L., and K. Y. Liang. 1986. Longitudinal data analysis for discrete and continuous outcomes. Biometrics 42:121-130.

www.nature.com/scientificreports

SCIENTIFIC REPORTS

OPEN

Coastal evacuations by fish during extreme weather events

Helen Bailey & David H. Secor

Received: 08 March 2016
Accepted: 21 June 2016
Published: 26 July 2016

An increase in the intensity and frequency of extreme events is predicted to occur as a result of climate change. In coastal ecosystems, hurricanes and flooding can cause dramatic changes in water quality resulting in large mortality events in estuarine fauna. Facultative migration behaviors represent a key adaptation by which animals can evacuate ecological catastrophes, but remain poorly studied in marine systems. Here we identify coastal evacuations by otherwise resident riverine striped bass in the Hudson River Estuary, New York, USA, caused by an intense period of tropical storms in autumn 2011. These storms produced record rainfall and high water discharges into the Hudson River Estuary that increased the water level and reduced the water temperature, salinity and dissolved oxygen levels. Striped bass moved out of the estuary, exhibiting novel migration behaviours, that may have been in response to the strong flow and unsuitable conditions. In the months following the storms, some fish demonstrated exploratory trips back to the estuary, which may have been to assess the conditions before returning for the remainder of the winter. Behavioural adaptions to weather events by striped bass and other coastal fishes will depend on maintenance of key population segments and unimpeded evacuation routes.

Climate extremes have important impacts on society and ecosystems[1–3]. These extreme events are by definition rare, although they may become more common in the future as a result of climate change[4]. Evacuations are a principal means by which humans and animals react to ecological catastrophes, but behavioural and environmental impediments can intervene. Populations and communities that are less mobile or obligatory in their migration behaviours are more vulnerable than those that can conditionally respond to extreme events. Among the most migratory animals, birds and fishes, evacuations likely represent a central adaptation to frequent events, but remain poorly documented. The majority of these studies have been on terrestrial ecosystems[1,5] and there are far fewer examples for the aquatic environment[6,7]. Studying fish and bird evacuations to weather events has largely relied on serendipity, which precludes strong design elements owing to investigator hazards, unpredictability in timing, and exclusion of experimental controls.

Coastal ecosystems, which receive large inputs from upstream watersheds, are particularly vulnerable to catastrophic change due to hurricanes and other storm events. Sudden delivery of upstream nutrients and sediments and resultant increases in system respiration and hypoxia can result in large mortalities in estuarine fauna that cannot evade such events[8]. How fishes evade such events remains unknown.

Studies of storm events have indicated that sharks and sea snakes can detect changes in barometric pressure associated with the approach of a storm and they respond by taking refuge[9,10]. The American lobster (*Homarus americanus*) exhibited increased movement down an estuary towards the coast in association with a storm event[11]. Movements of teleost fish[12] and elasmobranchs[13] similarly support the hypothesis that storms can induce movements and shifts in distribution. This in turn alters food webs. For example, changes in reproductive rates and foraging behaviour of marine mammals were observed after a storm, likely in response to changes in prey distribution[14,15].

In many cases our understanding of the effect of extreme events on aquatic organisms has been based on surveys before and after the event. However, relevant ecological responses that are likely behavioural and dynamic, are coarsely represented in surveyed changes in spatial density. Characterizing the movements of highly mobile species during these events provides important information on their behavioural response and may help to predict and mitigate the impacts of future and more frequent events with climate change[13]. Telemetry has been used to determine the habitat use of aquatic species[16], but only rarely to record detailed movements during extreme events[13,17].

Here, our objective was to determine the response of a key predatory fish species, striped bass (*Morone saxtilis*), to two tropical storm events by examining their individual movements using acoustic telemetry and a

Chesapeake Biological Laboratory, University of Maryland Center for Environmental Science, P.O. Box 38, Solomons, MD 20688, USA. Correspondence and requests for materials should be addressed to H.B. (email: hbailey@umces.edu)

before-during-after-control-impact approach. Partial migration occurs in this species: seasonal migrations that persist throughout the lifespan, but differ between population components (aka contingents)[18]. Overlapping migration pathways by contingents occur in the Hudson River Estuary, which harbours one of the largest populations of this species[19–21]. The upper estuary (UEC) and lower estuary contingents (LEC) occupy the estuary throughout most of the year, but with some movement into the surrounding coastal areas during the winter months[19]. In 2011, there were two extreme events beginning with Hurricane Irene, which had weakened to a tropical storm by the time it made landfall at New York City (28th August). This was followed just over a week later by Tropical Storm Lee (6th–7th September). How these striped bass contingents respond to extreme events was the focus of this study. We also analyzed survey data for white perch (*Morone americana*) to determine if a similar pattern was detected for another coastal fish species. White perch occur year-round throughout the Hudson River, but are less abundant in the lower estuary[22,23]. Although the survey data do not provide information on individual movements, these biweekly surveys provide distribution and abundance data that could indicate whether white perch were displaced as a result of the storm events and the high discharge rates that occurred in the Hudson River[24]. An increase in abundance in the lower estuary after the storms would indicate that the fish had been displaced downriver.

Results

Environmental conditions. The annual mean water level in the Hudson River at Albany, New York (NY), in 2010 was 0.65 m and the mean water level in August 2010 was 1.98 m, which were similar to the averages for the decade 2002–2012 (mean $\pm$ s.d.: Annual 0.66 ± 0.08 m; August 1.97 ± 0.38 m). The water temperature at this site was also close to the average for the decade. The mean temperature in 2010 was 12.60 °C (Annual mean for 2002–2012: 12.46 ± 1.76 °C) and the mean in August 2010 was 24.74 °C (August monthly mean for 2002–2012: 24.84 ± 1.46 °C). The year 2010 was therefore considered a suitable control in our study based on the environmental conditions in the Hudson River being close to average.

In 2011, much more extreme conditions in the Hudson River occurred as a result of the two tropical storms in late August and early September. The water level in the Hudson River rose rapidly because of the rainfall from the storms. It was significantly higher in 2011 during the storms in the upper estuary at Albany, NY, compared to preceding levels and those for the corresponding period in 2010 ($F_{2,83} = 20.2$, $p < 0.001$). The water temperature also decreased during the storm events and was significantly lower compared to the same time period in 2010 ($F_{2,83} = 16.9$, $p < 0.001$). Data on dissolved oxygen and salinity were not available for this site in 2010, but increases in dissolved oxygen and decreases in salinity were observed following each storm event in 2011 (Supplementary Figure S1). In the lower estuary, higher water levels were similarly recorded during the storms compared to preceding levels or those in 2010 ($F_{2,83} = 28.4$, $p < 0.001$), although the change in water level was not as great as in the upper estuary (Fig. 1 and Supplementary Figure S1). There were significant decreases in water temperature ($F_{2,83} = 68.1$, $p < 0.001$), salinity ($F_{1,55} = 66.4$, $p < 0.001$) and dissolved oxygen ($F_{1,55} = 68.0$, $p < 0.001$) in the lower estuary (Fig. 1).

The monthly mean discharge rate measured at the gauge at Green Island, NY, was 269 $m^3 s^{-1}$ in August and 263 $m^3 s^{-1}$ in September (averaged over the period 2002–2012). On 29th August 2011 following Tropical Storm Irene, the daily mean discharge rate at this station reached 4,471 $m^3 s^{-1}$. At a cross-sectional channel area of 2,212 m^2 (at stage 20)[25], the water flow velocity would be up to 2.0 m s^{-1}. After the Tropical Storm Lee, the daily mean discharge rate reached 3,028 $m^3 s^{-1}$ on 8th September 2011 (estimated water velocity 1.4 m s^{-1}).

Striped bass movements. Individual fish were tagged in October 2009 and May 2010 and acoustically tracked for a mean of 708 days (range = 160–816 days, individual fish n = 43). We identified a significant interaction between the time period (before-during-after) and event (control-impact) for the location of the fish indicating that displacement occurred after the storms with movement southwards out of the Hudson River Estuary and into the coastal environment (Supplementary Table S1). Although striped bass also moved southwards in the autumn of 2010 resulting in a decrease in mean latitude from late August to mid-September, this pattern was much more pronounced in the year of the storms (Fig. 2). When the analysis was repeated for the LEC subset only, individuals demonstrated a more dramatic southwards movement both during and after the storms in 2011 compared to the corresponding time period in 2010 (Supplementary Table S2 and Figure S2).

Examination of the movement pathways indicated that initial location played a role in the response of striped bass. Fish that were in the Hudson River before the storms tended to move rapidly downstream and into the coastal environment during the storms, whereas those in the harbour either remained there or moved into the coastal environment and headed southwards (Fig. 3). In particular, three fish were detected at the same or nearby (within 2 km) receiver sites during the storm period in 2011 (n = 2 and 1 from the LEC and UEC respectively). The UEC fish (Study ID 1) was acoustically detected in the two-week period before and after the storms in the Hudson River near Catskill, NY, a site 184 river km from the mouth of the river. The two LEC fish (Study IDs 16 and 29) were detected almost daily (and often with multiple detections per day) during the entire before-during-after period of the storms at the three receiver sites in the northern part of New York Harbor (Fig. 3c). The UEC fish had a total length of 0.48 m (mean UEC tagged fish length = 0.49 m) and the LEC fish were 0.59 m and 0.71 m in length (mean LEC tagged fish length = 0.61 m). The water flow velocity of 2.0 m s^{-1} after storm Irene would correspond to a swimming speed of 4.2, 3.4 and 2.8 body lengths s^{-1} respectively for these fish.

We also analysed the effect of the storms on the residency time of fish within New York Harbor. The tagged striped bass spent significantly more time in the harbour in 2011 compared to 2010 (Supplementary Table S3). Contingent membership significantly influenced harbour occupancy, with a greater number of days spent in the harbour by the LEC than the UEC fish. There was no significant interaction between the time period and year variables indicating that the amount of time spent in New York Harbor did not significantly change during the period of the storms. Examination of the movement pathways indicated that changes in residency in the harbour

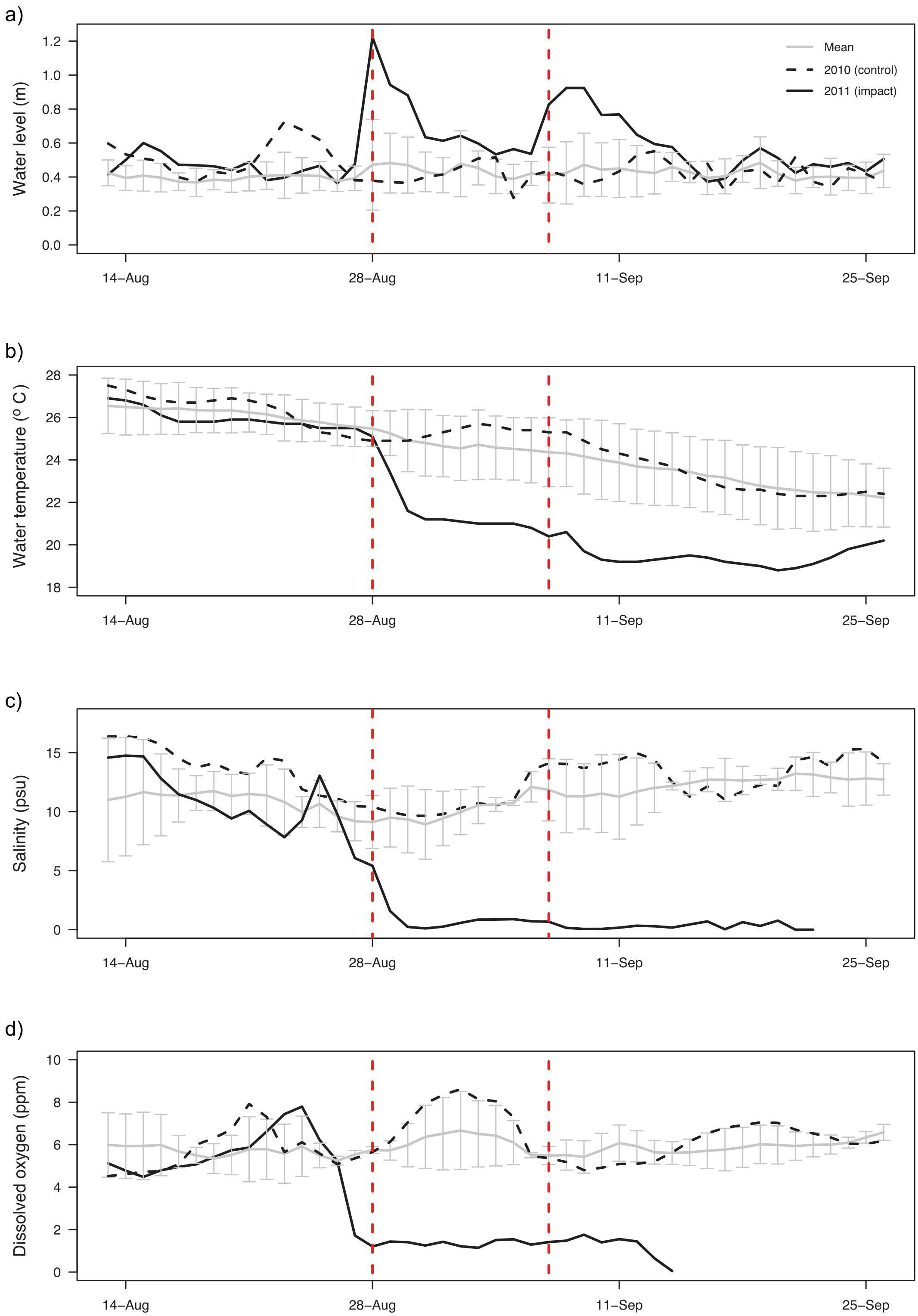


Figure 1. Environmental conditions during August to September in the Lower Hudson River Estuary in 2010 and 2011. Water quality parameters (**a**), water level, (**b**), water temperature, (**c**), salinity, and (**d**), dissolved oxygen. The mean (±SD) daily values are for the period 2002–2012 for water level and water temperature, and for the period 2008–2011 for salinity and dissolved oxygen. The vertical dashed red lines indicate the timing of the Tropical Storms Irene and Lee in 2011.

occurred over longer time-scales than the two week before-during-after periods. We therefore also tested whether there was any difference in the proportion of days per month spent in the harbour from July to October in 2010 and 2011 (Supplementary Table S4). There was a significant interaction between the month of October and the

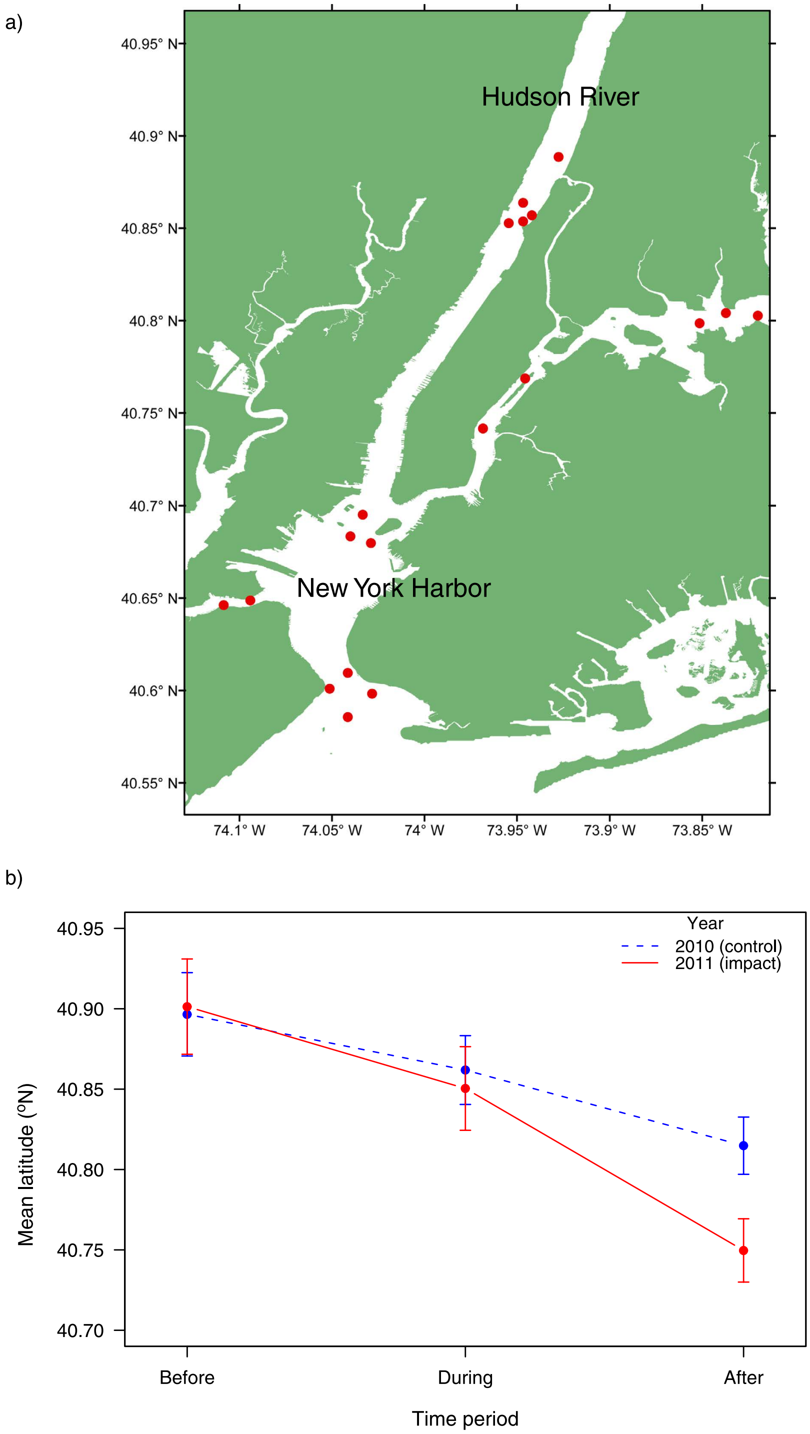


Figure 2. Coastal evacuation of fish in response to the storm events. (**a**) Map of Hudson River Estuary with acoustic receiver locations (red circles). The map was created in ESRI ArcMap version 9.3.1 (http://desktop.arcgis.com/en/arcmap). (**b**) Mean (±SE) latitude of tagged striped bass in the time period before (13th–27th August), during (28th August–11th September), and after (12th–26th September) the storms in 2011 and for the control year 2010.

year indicating that the amount of time spent in New York Harbor by tagged striped bass was significantly lower in October 2011, after the storms, than in 2010. This effect was even more pronounced in the LEC striped bass (Supplementary Table S5). In 2010, the proportion of time spent in the harbour was similar in July and August and increased in September, remaining high in October. In contrast, in 2011 there was a marginal increase in September, but a dramatic reduction in October (Fig. 4).

White perch abundance. The adult standing stock of white perch in the Hudson River rose rapidly after the first storm event and was approximately twice the mean abundance for 1997–2013 for the four weeks (weeks

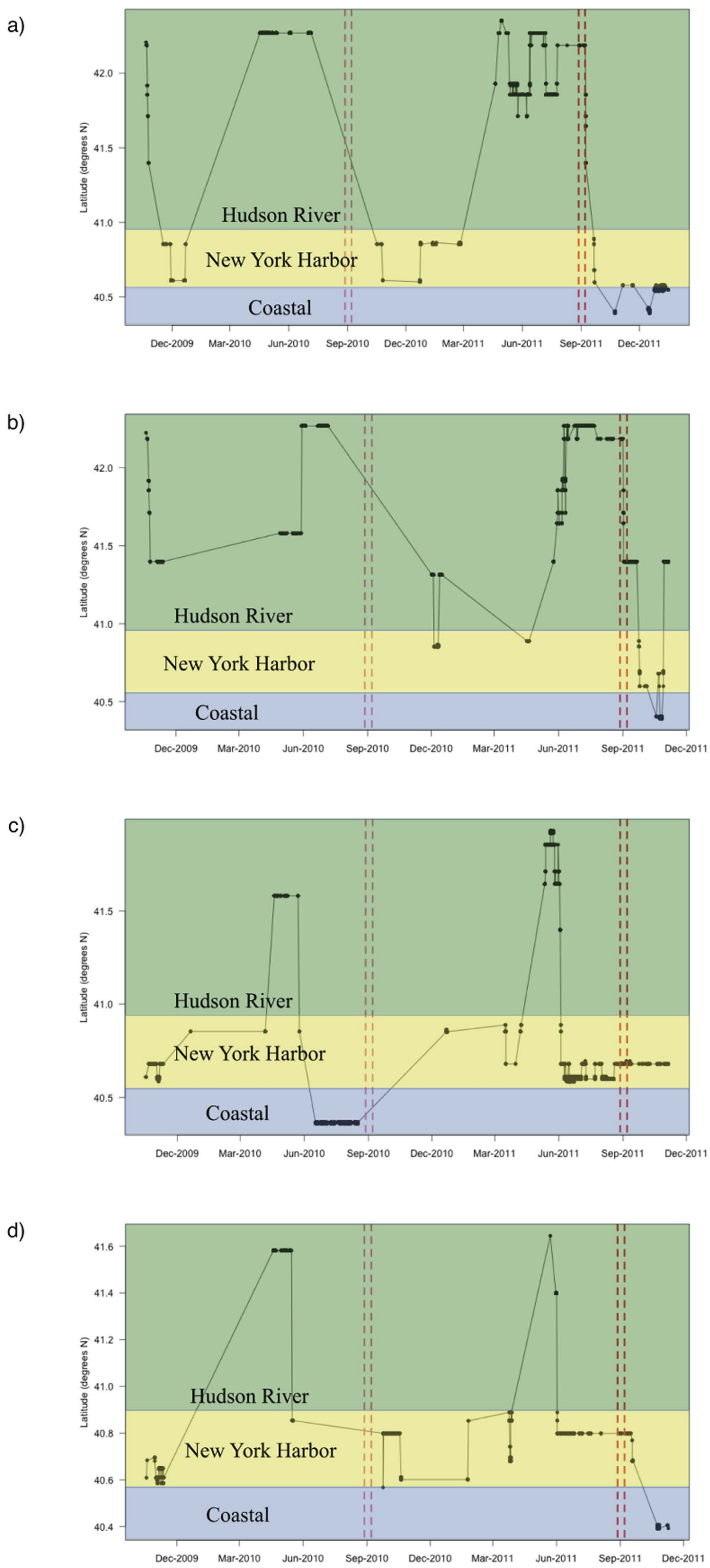


Figure 3. Individual movements of acoustically tagged striped bass in the Hudson River Estuary. Latitude of acoustic detections for the Upper Estuary Contingent (UEC) individuals (**a**), ID 3 and (**b**), ID 5, and for the Lower Estuary Contingent (LEC) individuals (**c**), ID 16 and (**d**), ID 36. The black circles represent dates of receiver detections, the bold vertical red lines indicate the timing of the Tropical Storms Irene and Lee in 2011, and the pale vertical red lines are the same time periods in 2010 for comparison.

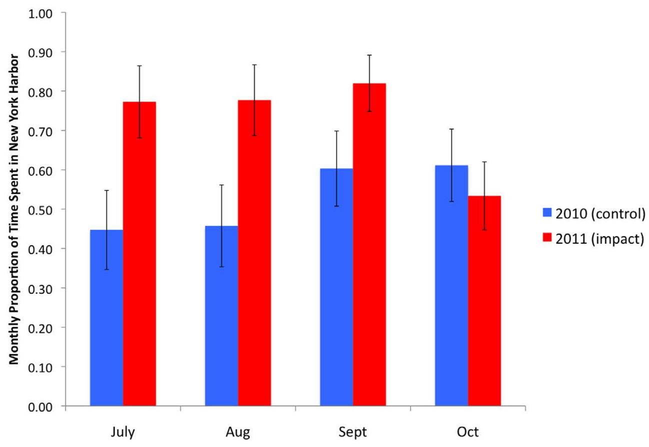


Figure 4. Residency time in New York Harbor in relation to the storm events. Monthly proportion of days spent in New York Harbor (±SE) by tagged striped bass from the Lower Estuary Contingent (LEC) in July to October of the control year 2010 and the year of the storms 2011.

37–41) after the storms (Supplementary Figure S3). The geographic regions within the Hudson River Estuary did not have any data recorded for the sites upriver of Poughkeepsie (100–122 river km) for week 35 (30th August 2011) following Storm Irene. However, the standing stock for older-than-yearling for the regions Battery (0–18 river km) and Yonkers (19–38 river km) in the lower Hudson River Estuary rose rapidly from 81,000 and 73,000 in week 35 to 380,000 and 831,000 in week 37 (12th September 2011) respectively, and then declined again in weeks 39 (26th September 2011) and 41 (10th October 2011) (Supplementary Figure S3).

Discussion

Evacuation behaviour may be triggered by environmental cues that indicate unsuitable conditions, inadequate resources, or unfavourable interactions with competitors and/or predators in the occupied habitat[26]. In our study, the behaviour was most likely initiated in response to the unsuitable conditions that arose in the Hudson River Estuary as a result of the extreme storm events. Tropical Storms Irene and Lee in 2011 caused heavy rainfall and major flooding in New York[24] that resulted in high freshwater discharges and a rapid decline in water temperature. The strong water flows may have displaced white perch downriver into the lower estuary. It may also have potentially displaced striped bass out of the Hudson River and New York Harbor where the less suitable conditions, particularly the lower dissolved oxygen[27], may have triggered the behaviour to evacuate into the coastal environment.

The detection of striped bass fully evacuating the Hudson River, rapidly moving downstream into the coastal environment, is noteworthy as a particularly unusual behaviour for the UEC fish, and suggests that the high discharge within the narrower river portion may have been sufficient to displace them. The extended movement into the coastal environment and even farther south than recorded in the previous year could also indicate evidence of initiation of the migratory syndrome, where movement behaviour continues despite resource-based stimuli that ordinarily stop further movement[18].

Striped bass is a relatively large, long-lived anadromous species. Although many of the tagged fish had left the estuary and moved into coastal waters, there were three tagged fish that were detected throughout the storms and maintained their position in the Hudson River and New York Harbor. A swimming speed of 2.8–4.2 body lengths s^{-1} would have been necessary to swim against the peak daily mean water velocity. Speeds of up to 3.7 body lengths s^{-1} have been recorded over a distance of 5 km, but generally striped bass move at slower rates[20]. The maximum sustainable swimming speed recorded for striped bass is 2.9–3.3 body lengths s^{-1} during a 30–45 minute swimming bout[28]. It therefore seems unlikely the fish were continuously swimming at high speed during the period of the storms, which lasted several days[24]. They may have instead sought refuge within the estuary. Small-scale movements to refuge locations with cover or lower velocities has been observed in stream-dwelling fish during high discharge events[17].

Contingent membership significantly influenced occupancy within New York Harbor, with a greater number of days spent in the harbour by the striped bass LEC than the UEC fish, which is consistent with what is known about these contingents' movements[19,20]. The southward movement during the fall and winter in 2010 is also consistent with previous studies on their seasonal movements within the Hudson River Estuary[20] and Chesapeake Bay[29]. However, the increased occurrence in the harbour in September followed by the rapid decline in October 2011 compared to 2010 supports the hypothesis that lower estuarine striped bass were displaced southwards by the storms into the harbour and had moved into the coastal environment by October.

White perch are generally most abundant in the upper estuary and more sparsely distributed in the lower estuary[30]. As expected, the abundance of white perch was relatively low in the lower Hudson River Estuary prior to the storms in 2011. However, there was a rapid increase in abundance of white perch in the lower Hudson River Estuary after the storms. The standing stock for older-than-yearling fish was 11 times greater in the week after the storms at Yonkers (19–38 river km) than it had been in the previous bi-weekly survey. This suggests that white perch moved out of the streams and upriver segments, with a downriver shift in their distribution after the storm, similar to that observed in striped bass. There was also an overall increase in abundance of white perch in the Hudson River Estuary for the four weeks after the storms indicating movement out of the streams and nontidal river segments.

A few of the tags transmitted long enough to enable the detection of three striped bass returning to New York Harbor during late October and November for short periods after the storm. This was then followed by a return to the harbour for the remainder of the winter and in some instances a continued movement northwards up the Hudson River. Seasonal site fidelity is well known for striped bass[20], and these excursions may have served to re-establish regular movement patterns. Alternatively, this behavior could represent exploratory movements. Such movements would be expected to be sustained until suitable conditions are perceived[26].

Although many of the striped bass LEC fish remained in coastal waters, two of the UEC fish for which we had longer tracking durations returned to the harbour and eventually to the Hudson River indicating the response to the storms lasted only a few months. However, if extreme events become more frequent in the future such changes could potentially become more severe or longer term. The timing of the extreme events is also likely to affect the strength and duration of the response and consequent impact on the fish community and ecosystem[31–33]. As extreme events become more frequent, telemetry will provide a valuable tool for linking event-scale forcing to migration responses. The estuaries and harbours that form important habitat for fish species are likely to experience more extreme conditions in the future as a result of climate change. Responses of fish species to extreme weather events should be considered when planning management strategies to ensure efforts are appropriately targeted to maintain key population segments and critical evacuation routes.

Methods

Ethics statement. This research was approved by the Institutional Animal Care and Use Committees (IACUC) of the University of Maryland Center for Environmental Science (Research Protocol No. 09C02) and was carried out in accordance with the approved guidelines.

Environmental data. Water level and water temperature data were obtained from the U.S. Geological Survey (USGS) daily, monthly and annual statistics (available at: http://waterdata.usgs.gov/usa/nwis/dvstat/?referred_module=sw) for the station in the Hudson River at Albany, NY (USGS Station 01359139 at 42.646°N, 73.748°W), and in the lower estuary at the south dock at West Point, NY (USGS Station 01374019 at 41.386°N, 73.955°W) for the period 2002 to 2012. Salinity and dissolved oxygen data were obtained from the Hudson River Environmental Conditions Observing System (HRECOS, www.hrecos.org, accessed 20th April 2016) for the Port of Albany Hydrologic Station (42.620°N, 73.759°W) and the lower estuary George Washington Bridge Station (40.852°N, 73.959°W). These data were recorded every 15 minutes and a daily mean was calculated. Data were available for 2008 to 2011 from the George Washington Bridge Station, but data collection only began on 4th January 2011 at the Port of Albany Hydrologic Station. A before-during-after-control-impact design was applied with a repeated measures analysis of variance (ANOVA) to determine whether there were changes in water quality as a result of the storms. The time period was defined as the two weeks before (13th–27th August), during (28th August–11th September), and after (12th–26th September) the Tropical Storms Irene and Lee occurred in New York, USA. Sensor malfunctions as a result of the storms led to some missing data for salinity and dissolved oxygen. Only the before and during periods in the two years were therefore compared for these parameters.

Water discharge rates were obtained for the station in the Hudson River at Green Island, NY (USGS Station 01358000 at 42.752°N, 73.689°W) from the U.S. Geological Survey (USGS) daily and monthly statistics (available at: http://nwis.waterdata.usgs.gov/ny/nwis/inventory/?site_no=01358000&agency_cd=USGS). The water flow velocity was calculated by dividing the discharge rate by the cross-sectional area of the channel. The channel area at this site corresponding to the highest available stage value was used (stage 20)[25].

Striped bass acoustic telemetry data. In October 2009 to May 2010, 75 striped bass were tagged with individually coded ultrasonic transmitters (Vemco V16-4H-R64k; 67 mm, 10 g, 2.5 year expected battery life) in the Hudson River and New York Harbor[19]. These fish ranged in size approximately 400–1000 mm total length, and included three contingents called the upper estuary (UEC), lower estuary (LEC), and ocean contingents (OC)[20,21], which were assigned on the basis of the location and season of capture[19,34]. Fifteen acoustic receivers were moored in and around New York Harbor in a "gates" design[20] that allowed all tagged individuals to be monitored when they passed through any of the channels to the harbour. There were also additional receivers within the Hudson River and surrounding coastal environment (Fig. 2a). None of the tagged fish from the OC were present in the Hudson River or New York Harbor during the autumn of 2010 or 2011, and they were therefore not included in the analysis.

Striped bass data analysis. We used the prior year, 2010, as our baseline control and compared it to the anomalous year with the extreme events, 2011. This is necessary as there is likely to be non-event related seasonal variation in striped bass use of the area that could act as a confounding factor if it is not taken into account. We determined if there were any changes in the location or behaviour of striped bass resulting from these events using a generalized linear mixed model (GLMM) with a before-during-after-control-impact design. The same time periods were used as in the analysis of the environmental data.

In the first model, our response variable was the latitude of the striped bass locations. The explanatory variables were the time period (before, during, after) and year (control, impact) and the interaction between these two categorical variables. We also included the contingent the fish belonged to as a covariate to account for seasonal differences in latitude that are generally found amongst the contingents. We calculated the mean daily location for each individual and interpolated daily positions between receiver sites to reconstruct the movement paths.

This resulted in a daily latitude value for every day during the entire time period of interest for each individual. We excluded any movement paths that did not occur within the Hudson River Estuary or New York Harbor during the period of interest or that ceased transmitting before 26th September 2011, which was the end of the study period. This resulted in a sample size of 22 individuals movement paths ($n = 17$ and 5 from the LEC and UEC respectively). There were 90 daily latitude values for each individual resulting in a total of 1,980 observations in the analysis. The track section in August to September each year was nested within the individual as a random effect in the GLMM to account for serial correlation in the movements of each individual tagged fish. We also repeated the analysis for the LEC fish only because of the larger sample size.

In the second model, we examined changes in residency patterns within New York Harbor. We used the same approach as in the previous model, but our response variable was the proportion of days per time period that fish were present in New York Harbor. We used the daily interpolated positions to include when the fish were within New York Harbor as well as detected by the acoustic receivers at its boundaries. We defined the New York Harbor area as within 1 km of our boundary acoustic receivers based on their expected detection range (Latitude: 40.575 to 40.898°N, Longitude: 73.810 to 74.120°W). Examination of the tracks indicated that changes in occurrence of striped bass in New York Harbor may have occurred over a longer time-scale and we therefore also tested whether there was any significant difference in the proportion of days per month from July to October between the control year 2010 and the year of the storms 2011.

White perch data analysis. Adult white perch standing stock estimates were obtained for the period 1997–2013[35]. A mean standing stock for the Hudson River was calculated and compared to that for 2011 for the weeks 27 (5th July 2011) to 47 (28th November 2011), which included the storm events. The standing stock of older-than-yearling white perch was also compared for this period within specific geographic regions[35].

References

1. Jentsch, A., Kreyling, J. & Beierkuhnlein, C. A new generation of climate-change experiments: Events, not trends. *Frontiers in Ecology and the Environment* **5,** 365–374 (2007).
2. Greenough, G. *et al.* The potential impacts of climate variability and change on health impacts of extreme weather events in the United States. *Environmental Health Perpectives* **109,** 191–198 (2001).
3. Easterling, D. R. *et al.* Climate extremes: Observations, modeling, and impacts. *Science* **289,** 2068–2074 (2000).
4. Hegerl, G. C., Hanlon, H. & Beierkuhnlein, C. Climate science: Elusive extremes. *Nature Geoscience* **4,** 142–143 (2011).
5. Streby, H. M. *et al.* Tornadic storm avoidance behavior in breeding songbirds. *Current Biology* **25,** 1–5 (2015).
6. Davis, S. E. *et al.* Importance of storm events in controlling ecosystem structure and function in a Florida Gulf Coast Estuary. *Journal of Coastal Research* **20,** 1198–1208 (2004).
7. Wernberg, T. *et al.* An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot. *Nature Climate Change* **3,** 78–82 (2013).
8. Paerl, H. W., Pinckney, J. L., Fear, J. M. & Peierls, B. L. Ecosystem responses to internal and watershed organic matter loading: consequences for hypoxia in the eutrophying Neuse River Estuary, North Carolina, USA. *Marine Ecology Progress Series* **166,** 17–25 (1998).
9. Heupel, M. R., Simpfendorfer, C. A. & Hueter, R. E. Running before the storm: blacktip sharks respond to falling barometric pressure assoicated with Tropical Storm Gabrielle. *Journal of Fish Biology* **63,** 1357–1363 (2003).
10. Liu, Y. L., Lillywhite, H. B. & Tu, M. C. Sea snakes anticipate tropical cyclone. *Marine Biology* **157,** 2369–2373 (2010).
11. Jury, S. H., Howell, W. H. & Watson, W. H. Lobster movements in response to a hurricane. *Marine Ecology Progress Series* **119,** 305–310 (1995).
12. Patterson, W. F., Watterson, J. C., Shipp, R. L. & Cowan, J. H. Movement of tagged red snapper in the Northern Gulf of Mexico. *Transactions of the American Fisheries Society* **130,** 533–545 (2001).
13. Udyawer, V., Chin, A., Knip, D. M., Simpfendorfer, C. A. & Heupel, M. R. Variable response of coastal sharks to severe tropical storms: environmental cues and changes in space use. *Marine Ecology Progress Series* **480,** 171–183 (2013).
14. Smith, C. E. *et al.* Hurricane impacts on the foraging patterns of bottlenose dolphins *Tursiops truncatus* in Mississippi Sound. *Marine Ecology Progress Series* **487,** 231–244 (2013).
15. Miller, L. J., Mackey, A. D., Hoffland, T., Solangi, M. & Kuczaj, S. A. Potential effects of a major hurricane on Atlantic bottlenose dolphin (*Tursiops truncatus*) reproduction in the Mississippi Sound. *Marine Mammal Science* **26,** 707–715 (2010).
16. Hazen, E. L. *et al.* Predicted habitat shifts of Pacific top predators in a changing climate. *Nature Climate Change* **3,** 234–238, doi: 10.1038/NCLIMATE1686 (2012).
17. David, B. O. & Closs, G. P. Behavior of a stream-dwelling fish before, during, and after high-discharge events. *Transactions of the American Fisheries Society* **131,** 762–771 (2002).
18. Secor, D. H. *Migration ecology of marine fishes.* (Johns Hopkins University Press, 2015).
19. Gahagan, B. I., Fox, D. A. & Secor, D. H. Partial migration of striped bass: revisiting the contingent hypothesis. *Marine Ecology Progress Series* **525,** 185–197 (2015).
20. Wingate, R. L. & Secor, D. H. Intercept telemetry of the Hudson River Striped Bass resident contingent: migration and homing patterns. *Transactions of the American Fisheries Society* **136,** 95–104 (2007).
21. Secor, D. H. Specifying divergent migrations in the concept of stock: the contingent hypothesis. *Fisheries Research* **43,** 13–34 (1999).
22. Kraus, R. T. & Secor, D. H. Dynamics of white perch *Morone americana* population contingents in the Patuxent River estuary, Maryland, USA. *Marine Ecology Progress Series* **279,** 247–259 (2004).
23. Klauda, R. J., McLaren, J. B., Schmidt, R. E. & Dey, W. P. Life history of white perch in the Hudson River Estuary. *American Fisheries Society Monograph* **4,** 69–88 (1988).
24. Lumia, R., Firda, G. D. & Smith, T. L. Floods of 2011 in New York. (US Geological Survey Scientific Investigations Report 2014-5058, 2014).
25. de Vries, M. P. & Weiss, L. A. Salt-front movement in the Hudson River Estuary, New York - Simulations by one-dimensional flow and solute-transport models. 69 (US Geological Survey, Water-Resources Investigations Report 99-4024, 2001).
26. McMahon, T. E. & Matter, W. J. Linking habitat selection, emigration and population dynamics of freshwater fishes: a synthesis of ideas and approaches. *Ecology of Freshwater Fish* **15,** 200–210 (2006).
27. Kraus, R. T., Secor, D. H. & Wingate, R. L. Testing the thermal-niche oxygen-squeeze hypothesis for estuarine striped bass. *Environmental Biology of Fishes* **98,** 2083–2092 (2015).
28. Freadman, M. A. Swimming energetics of striped bass (*Morone saxatilis*) and bluefish (*Pomatomus saltatrix*): gill ventilation and swimming metabolism. *Journal of Experimental Biology* **83,** 217–230 (1979).

29. Wingate, R. L., Secor, D. H. & Kraus, R. T. Seasonal patterns of movement and residency by striped bass within a subestuary of the Chesapeake Bay. *Transactions of the American Fisheries Society* **140,** 1441–1450 (2011).
30. ASA Analysis & Communication. 2011 Year class report for the Hudson River Estuary monitoring program. (Washingtonville, NY, 2013).
31. Matthews, W. J., Marsh-Matthews, E., Adams, G. L. & Adams, S. R. Two catastrophic floods: Similarities and differences in effects on an Ozark stream fish community. *Copeia* **2014,** 682–693 (2014).
32. McConnaughey, R. A. & Syrjala, S. E. Short-term effects of bottom trawling and a storm event on soft-bottom benthos in the eastern Bering Sea. *ICES Journal of Marine Science* **71,** 2469–2483 (2014).
33. Dunning, D. J., Ross, Q. E., Blumberg, A. F. & Heimbuch, D. G. Transport of striped bass larvae out of the lower Hudson River Estuary. *American Fisheries Society Symposium* 51, 273–286 (2006).
34. Secor, D. H., Rooker, J. R., Zlokovitz, E. & Zdanowicz, V. S. Identification of riverine, estuarine, and coastal contingents of Hudson River striped bass based upon otolith elemental fingerprints. *Marine Ecology Progress Series* **211,** 245–253 (2001).
35. Applied Science Associates. 2013 Year class report for the Hudson River Estuary monitoring program and Central Hudson Gas and Electrical Corporation. (New Hampton, NY, 2014).

Acknowledgements

This research was supported by a Hudson River Foundation grant to H.B. and D.S. (Grant No. 002/13A). We thank Dewayne Fox and Lori Brown (ACT Network), Mike Frisk and Keith Dunton (Stony Brook University), Amanda Higgs (NYSDEC), John Manderson (NOAA Sandy Hook) and Mary Fabrizio and Mark Henderson (VIMS) who all supplied vital equipment. Steve Nack provided key technical field support for our Hudson River studies. Rebecca Wingate, Mike O'Brien, Sean Harding, Ben Gahagan, and Matt Breece all made important contributions to field research. Ben Gahagan and Mike O'Brien contributed to the acoustic telemetry data analysis. Brian Gallagher assisted with the analysis of the white perch data.

Author Contributions

H.B. and D.H.S. conceived and designed the study. D.H.S. tagged the fish and collected the data. H.B. analysed the data. H.B. and D.H.S. co-wrote the paper.

Additional Information

Supplementary information accompanies this paper at http://www.nature.com/srep

Competing financial interests: The authors declare no competing financial interests.

How to cite this article: Bailey, H. and Secor, D. H. Coastal evacuations by fish during extreme weather events. *Sci. Rep.* **6**, 30280; doi: 10.1038/srep30280 (2016).

Supplementary Information

Coastal evacuations by fish during extreme weather events

Helen Bailey and David H. Secor

Table S1: Results of the generalized linear mixed model (GLMM) for the location (latitude) of the tagged striped bass in relation to the categorical variables time period ("Before" given as the reference level) and Year (2010 given as the reference level) and their interaction. Contingent (Upper Estuary Contingent (UEC) given as the reference level) was also included as a covariate. An asterisk indicates where a P-value is less than 0.05 and is considered statistically significant.

Factor	**Estimate**	**SE**	**P-value**
Intercept	41.458	0.113	<0.001*
Contingent: LEC	-0.727	0.123	<0.001*
Time Period: During	-0.035	0.010	<0.001*
After	-0.082	0.010	<0.001*
Year: 2011	0.005	0.068	0.945
Interaction: During x 2011	-0.016	0.014	0.252
After x 2011	-0.070	0.014	<0.001*

Table S2: Results of the generalized linear mixed model (GLMM) for the location (latitude) of the Lower Estuary Contingent (LEC) tagged striped bass in relation to the categorical variables time period ("Before" given as the reference level) and Year (2010 given as the reference level) and their interaction. An asterisk indicates where a P-value is less than 0.05 and is considered statistically significant.

Factor	Estimate	SE	P-value
Intercept	40.699	0.041	<0.001*
Time Period: During	-0.004	0.006	0.476
After	-0.026	0.006	<0.001*
Year: 2011	0.006	0.058	0.921
Interaction: During x 2011	-0.023	0.008	0.004*
After x 2011	-0.044	0.008	<0.001*

Table S3: Results of the generalized linear mixed model (GLMM) for the proportion of days per 2-week time period that tagged striped bass were present in New York Harbour in relation to the categorical variables time period ("Before" given as the reference level) and Year (2010 given as the reference level) and their interaction. Contingent (UEC given as the reference level) was also included as a covariate. An asterisk indicates where a P-value is less than 0.05 and is considered statistically significant.

Factor	**Estimate**	**SE**	**P-value**
Intercept	-5.407	1.999	0.007*
Contingent: LEC	6.126	1.978	0.002*
Time Period: During	1.612	1.047	0.124
After	1.836	1.069	0.086
Year: 2011	4.192	1.712	0.014*
Interaction: During x 2011	-1.194	1.701	0.483
After x 2011	-0.553	1.767	0.754

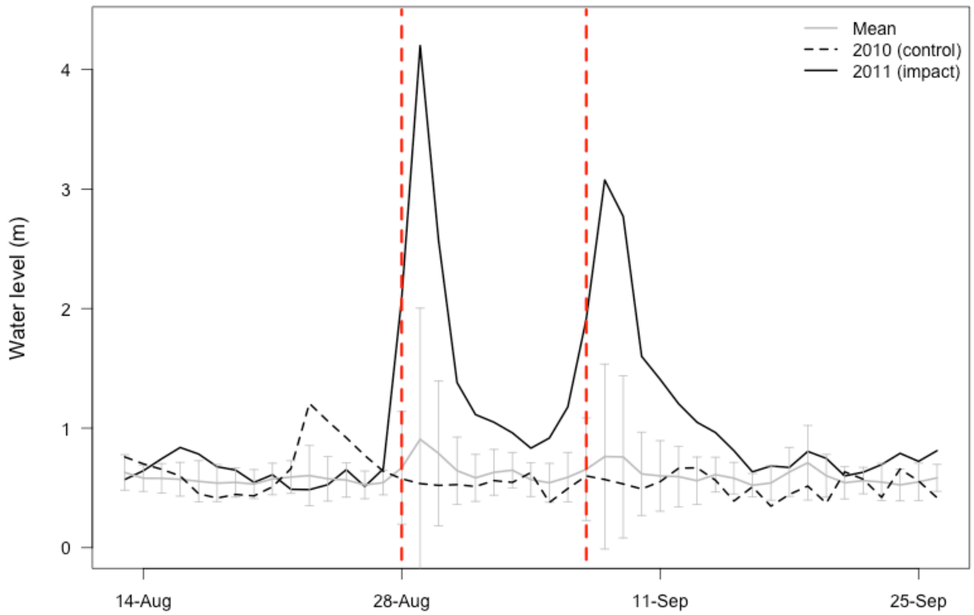
Table S4: Results of the generalized linear mixed model (GLMM) for the proportion of days per month that tagged striped bass were present in New York Harbour in relation to the categorical variables month ("July" given as the reference level) and Year (2010 given as the reference level) and their interaction. Contingent (UEC given as the reference level) was also included as a covariate. An asterisk indicates where a P-value is less than 0.05 and is considered statistically significant.

Factor	Estimate	SE	P-value
Intercept	-2.476	0.894	0.006*
Contingent: LEC	2.666	0.816	0.001*
Month: August	0.064	0.709	0.928
September	0.984	0.730	0.178
October	1.039	0.732	0.156
Year: 2011	2.268	0.888	0.011*
Interaction: August x 2011	-0.023	1.165	0.984
September x 2011	-0.511	1.208	0.672
October x 2011	-2.797	1.120	0.013*

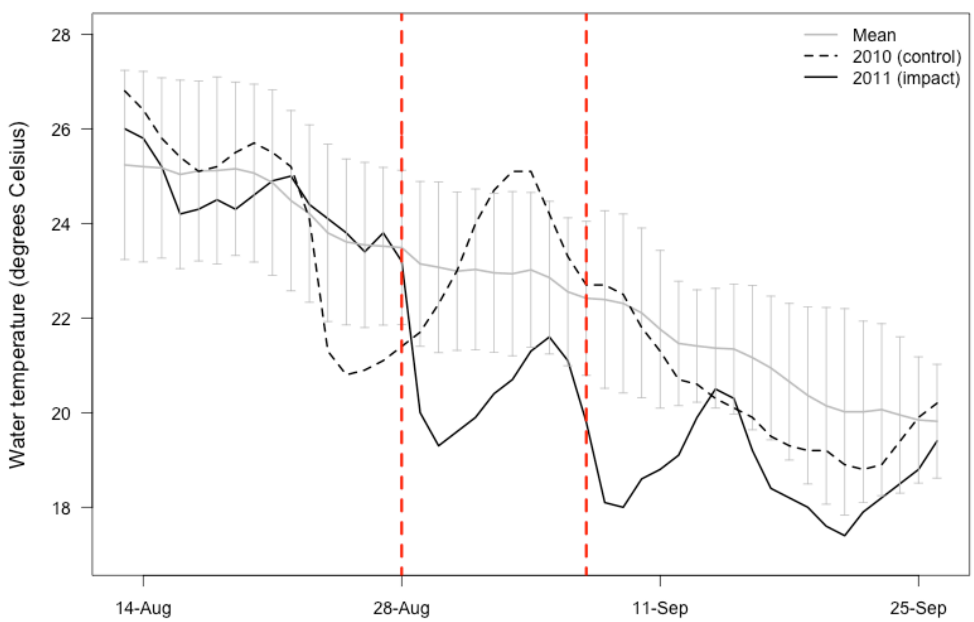
Table S5: Results of the generalized linear mixed model (GLMM) for the proportion of days per month that the Lower Estuary Contingent (LEC) tagged striped bass were present in New York Harbour in relation to the categorical variables month ("July" given as the reference level) and Year (2010 given as the reference level) and their interaction. An asterisk indicates where a P-value is less than 0.05 and is considered statistically significant.

Factor	**Estimate**	**SE**	**P-value**
Intercept	0.205	0.636	0.747
Month: August	-0.021	0.759	0.978
September	1.225	0.821	0.136
October	1.014	0.803	0.207
Year: 2011	2.504	1.125	0.026*
Interaction: August x 2011	0.091	1.465	0.950
September x 2011	-0.768	1.575	0.626
October x 2011	-3.392	1.324	0.010*

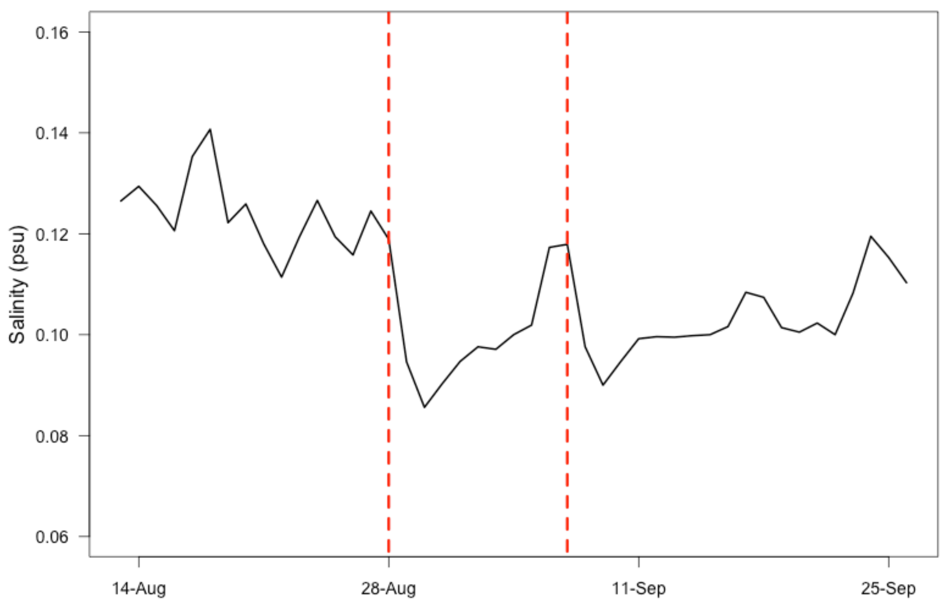
a)


Mean
2010 (control)
2011 (impact)
Water level (m)
0
1
2
3
4
14-Aug
28-Aug
11-Sep
25-Sep

b)


Mean
2010 (control)
2011 (impact)
Water temperature (degrees Celsius)
18
20
22
24
26
28
14-Aug
28-Aug
11-Sep
25-Sep

c)



d)

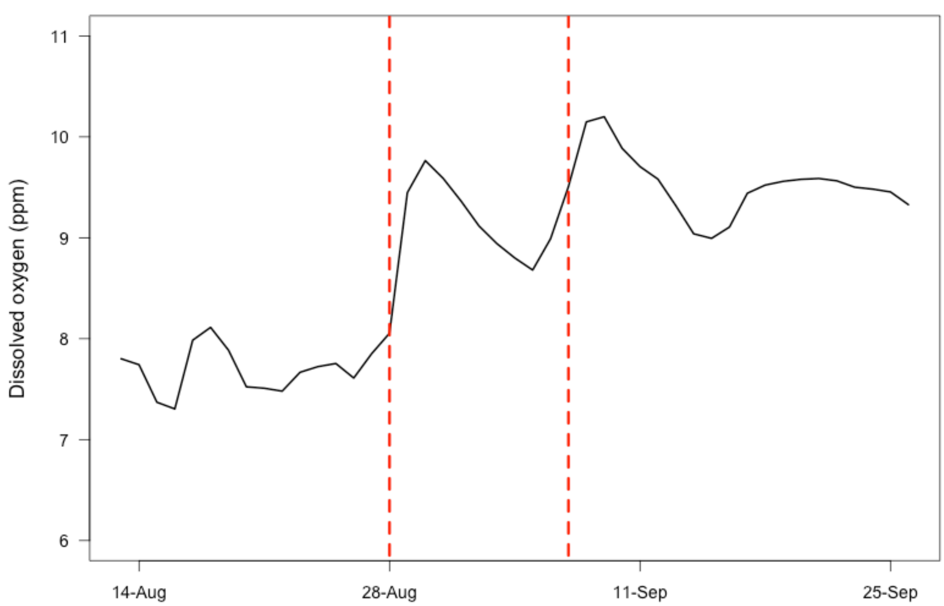


Figure S1: Environmental conditions in the Upper Hudson River Estuary. Water quality parameters in the Hudson River at Albany, NY, **a**, water level, **b**, water temperature, **c**, salinity, and **d**, dissolved oxygen. The mean (±SD) daily values are for the period 2002-2012 for water level and water temperature (data for salinity and dissolved oxygen were not available prior to 2011 for this station). The vertical dashed red lines indicate the timing of the Tropical Storms Irene and Lee in 2011.

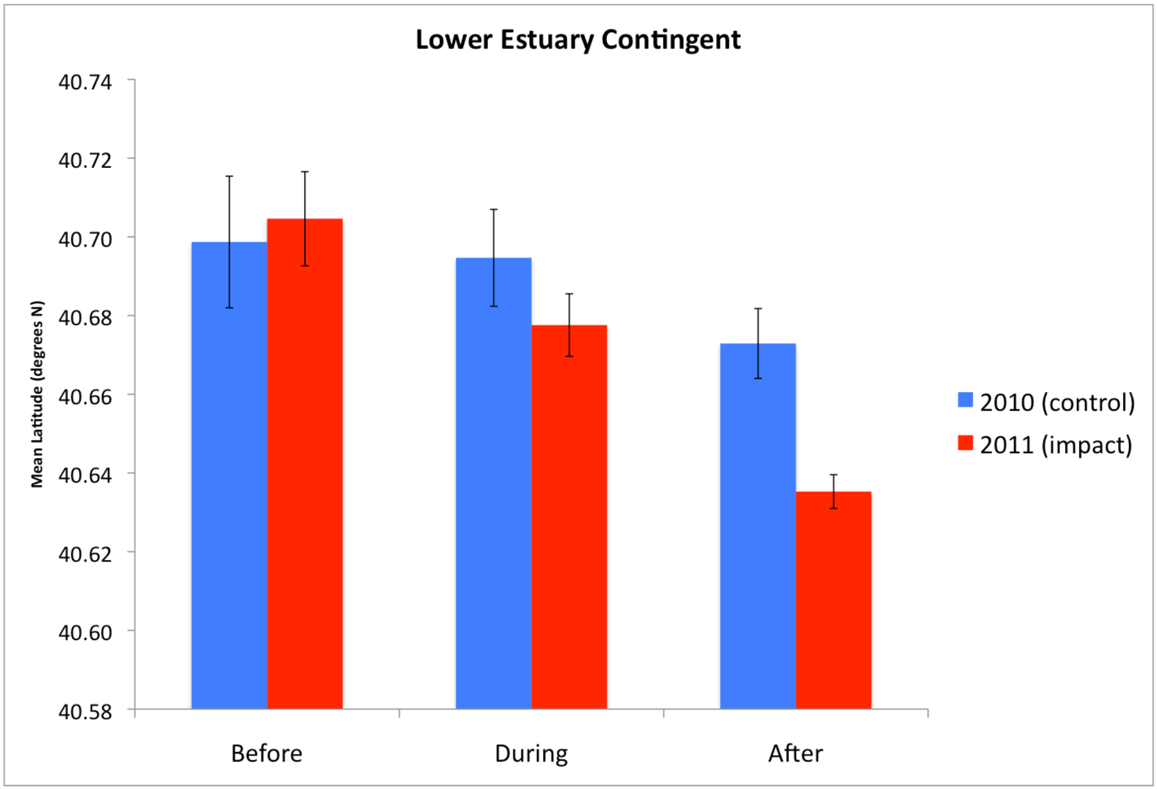
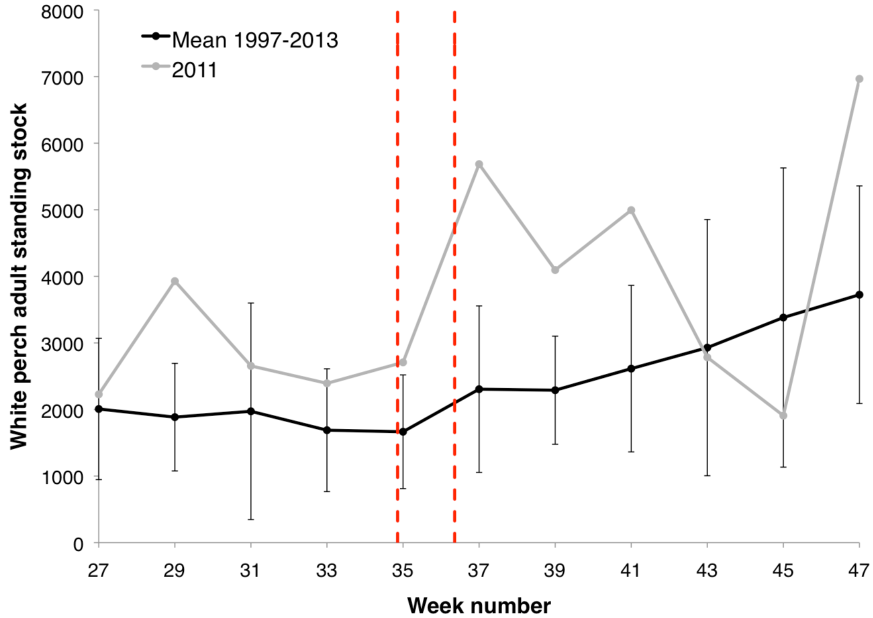


Figure S2: Movement of fish in response to the storm events. Mean (±SE) latitude of the Lower Estuary Contingent (LEC) striped bass in the time period before (13^{th} - 27^{th} August), during (28^{th} August – 11^{th} September), and after (12^{th}-26^{th} September) the storms in 2011 and for the control year 2010.

a)



b)

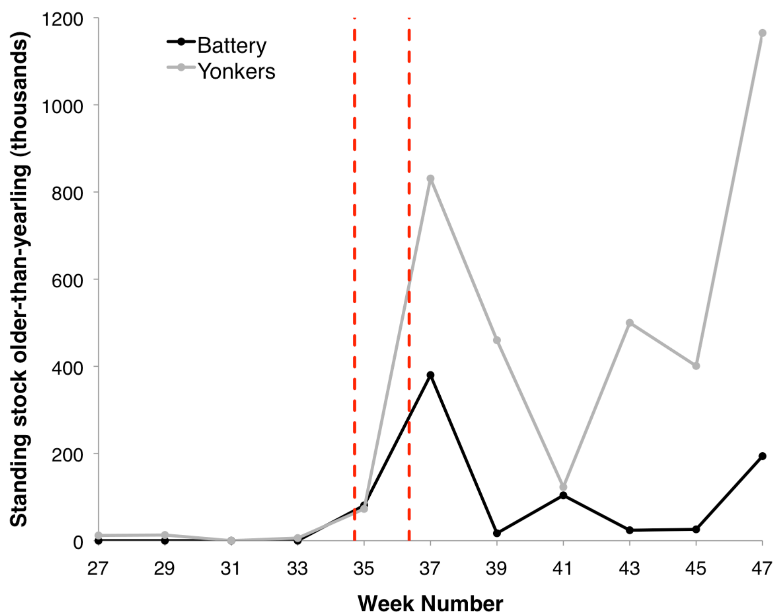


Figure S3: Abundance of white perch during the storm events. a) Adult standing stock of white perch in the Hudson River in 2011 and the mean for 1997-2013 (±SD), and b) Standing stock of older-than-yearling white perch in the Battery and Yonkers region in the lower Hudson River. The vertical dashed red lines indicate the timing of the Tropical Storms Irene and Lee in 2011.