

Research Article

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Site fidelity, population identity and demographic characteristics of humpback whales in the New York Bight apex

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Abstract

Humpback whales (*Megaptera novaeangliae*) exhibit maternally driven fidelity to feeding grounds, and yet occasionally occupy new areas. Humpback whale sightings and mortalities in the New York Bight apex (NYBA) have been increasing over the last decade, providing an opportunity to study this phenomenon in an urban habitat. Whales in this area overlap with human activities, including busy shipping traffic leading into the Port of New York and New Jersey. The site fidelity, population composition and demographics of individual whales were analysed to better inform management in this high-risk area. Whale watching and other opportunistic data collections were used to identify 101 individual humpback whales in the NYBA from spring through autumn, 2012–2018. Although mean occurrence was low (2.5 days), mean occupancy was 37.6 days, and 31.3% of whales returned from one year to the next. Individuals compared with other regional and ocean-basin-wide photo-identification catalogues (N=52) were primarily resighted at other sites along the US East Coast, including the Gulf of Maine feeding ground. Sightings of mother-calf pairs were rare in the NYBA, suggesting that maternally directed fidelity may not be responsible for the presence of young whales in this area. Other factors including shifts in prey species distribution or changes in population structure more broadly should be investigated.

Introduction

North Atlantic humpback whales were heavily targeted by commercial whalers as early as the 1600s (Mitchell & Reeves, 1983). Overexploitation led to a ban on commercial humpback whaling in the North Atlantic by the International Whaling Commission in 1955 (NMFS, 1991). In the USA, they were protected under the Marine Mammal Protection Act in 1972, and under the Endangered Species Act in 1973 (NMFS, 1991). Due to their wide-ranging movements and complex population dynamics, the recovery of humpback whales following the ban on whaling has been difficult to assess (Punt *et al.*, 2006; Smith & Pike, 2009). However, humpback whales that feed in the western North Atlantic are part of the West Indies Distinct Population Segment that is thought to no longer be in danger of extinction (Bettridge *et al.*, 2015).

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Humpback whales typically migrate annually to specific mid- to high-latitude summer feeding grounds where they were first brought as calves (Martin *et al.*, 1984; Baker *et al.*, 1985; Clapham & Mayo, 1987). In the North Atlantic, this maternally directed fidelity has resulted in significant population structure across relatively discrete feeding grounds off the Gulf of Maine (GoM), eastern Canada, west Greenland and the eastern North Atlantic (Iceland and Norway) (Katona & Beard, 1990; Palsbøll *et al.*, 1995; Stevick *et al.*, 2006). However, North Atlantic humpback whales have also been documented outside of these primary areas (e.g. Barco *et al.*, 2002; Ryan *et al.*, 2016). For example, four decades ago, humpback whales were infrequently sighted off the US mid-Atlantic states (USMA, New York, New Jersey, Delaware, Maryland, Virginia and North Carolina, CeTAP, 1982), but they are now regular visitors to coastal Virginia in winter when most North Atlantic humpback whales are on their breeding grounds (Swingle *et al.*, 1993; Barco *et al.*, 2002; Aschettino *et al.*, 2020). Barco *et al.* (2002) used photo-identification techniques to determine that these individuals were primarily juveniles from multiple summer feeding grounds, including the GoM, the Gulf of St. Lawrence and Newfoundland/Labrador. Humpback whales were also once uncommon off New York City, but they are now frequently seen inside the New York–New Jersey harbor estuary and in the greater New York Bight apex (NYBA, Brown *et al.*, 2018, 2019; King *et al.*, 2021; Zoidis *et al.*, 2021; Smith *et al.*, 2022), located at the northernmost portion of the USMA. Sightings occur year-round in the NYBA but appear to be most common during summer and autumn (Brown *et al.*, 2018; King *et al.*, 2021; Zoidis *et al.*, 2021). It remains to be determined whether humpback whales in the NYBA represent a northern expansion of individuals that had wintered off Virginia, a southern expansion of individuals from the adjacent GoM, or is the result of another phenomenon. It is also unclear how long individual humpback whales remain in the NYBA. This is of particular interest due to the region's urban location, and the potential for extended exposure to high levels of commercial and recreational vessel activity (Brown *et al.*, 2019; King *et al.*, 2021; Zoidis *et al.*, 2021), and other human interactions. For example, an Unusual Mortality Event for humpback whales along the Atlantic Coast of the USA has been ongoing since January 2016, with 50% of the examined carcasses showing signs of human interaction and 30% of documented strandings occurring off New York and New Jersey.¹ A better understanding of individual humpback whales in the NYBA area may help to clarify the factors involved and associated population impacts.

This study uses photo-identification techniques to investigate how individual humpback whales use the waters in and adjacent to the NYBA and to determine their relationship to other feeding areas of the western North Atlantic. The results provide information to better understand the presence of humpback whales off a major US city, as well as details on the characteristics of a humpback whale aggregation outside of its traditional range in the North Atlantic.

Materials and methods

Study area

The New York Bight is located at the northern extent of the USMA on the east coast of the USA. The New York Bight apex (NYBA; Figure 1) is the term typically used to describe the area of water adjacent to Manhattan, New York, at the north-west corner of the triangular-shaped New York Bight (i.e. Duedall *et al.*, 1977; Edenborn & Litchfield, 1987; Brown *et al.*, 2018). In

addition to a history of contamination and coastline alteration (Mahoney & McLaughlin, 1977; Waldhauer *et al.*, 1978; Lodge *et al.*, 2015), the NYBA is home to the largest port on the east coast of the USA (Gibb, 1997). The data used in this study were collected within a ~900 km² area extending east to Fire Island, New York and south to Manasquan Inlet, New Jersey and included the New York–New Jersey harbor estuary (Figure 1).

Data collection

Gotham Whale is a non-profit research organization that operates out of Staten Island, New York. From 2012–2018, they collected data on cetaceans from whale-watching platforms and solicited sightings reports from the public. The whale-watching data used in this study were collected aboard the 'American Princess', a 29-m commercial passenger vessel. The 'American Princess' made 413 whale-watch trips during the study period that ranged from 3–4.5 h. Trips in 2012 took place during spring and summer, while trips from 2013–2018 took place during spring, summer and autumn (Table 1). During each trip, Gotham Whale staff members scanned the horizon using either binoculars or the unaided eye and recorded the date, time, GPS location and general behaviour of sighted humpback whales. Staff members also attempted to photograph the flukes, left and right sides of the dorsal fin, and any other identifying markings of the individuals encountered (Katona *et al.*, 1979). Sightings from the general public were submitted to Gotham Whale through an online submission form, email or social media platform. These were independent of Gotham Whale trip effort on-board the 'American Princess', and most often came from recreational vessels or shore-based sightings of live or stranded animals. These submissions were reviewed by Gotham Whale staff and were only accepted if they included a photograph, sighting date and GPS location.

Gotham Whale staff manually compared photographs from both the whale-watching platform and the public using standard photo-identification techniques (Katona *et al.*, 1979) and synthesized the data to form the New York City Humpback Whale Catalog. When an individual was new to the catalogue, the best photo of the ventral flukes and associated dorsal fin images were added with a unique identification number. Occasionally, when the flukes were not photographed, unique dorsal fins were entered into the catalogue. Dorsal fins were included in the analysis of sighting characteristics within the NYBA but were excluded from inter-regional matching because individuals without fluke documentation were less likely to be successfully matched across years and to other areas of the North Atlantic.

Sighting characteristics in the NYBA

Sighting histories were collated for whales identified in the NYBA from 2012–2018. These were analysed for occurrence (number of days each whale was sighted within a year), occupancy (number of days between the first and last sighting for each whale, calculated only for whales seen more than once in a year), annual return (percentage that returned in the next consecutive year), and the number of years seen during the study period. Mean occupancy, occurrence and annual return were reported with their standard deviations using R software (R Core Team, 2020). Only whales with at least one identifying photo, an associated sighting date and GPS position were included in the analysis of sighting characteristics. For the purposes of this study, seasons were defined as: Winter (January–March), Spring (April–June), Summer (July–September) and Autumn (October–December).

¹<https://www.fisheries.noaa.gov/national/marine-life-distress/2016-2021-humpback-whale-unusual-mortality-event-along-atlantic-coast>.

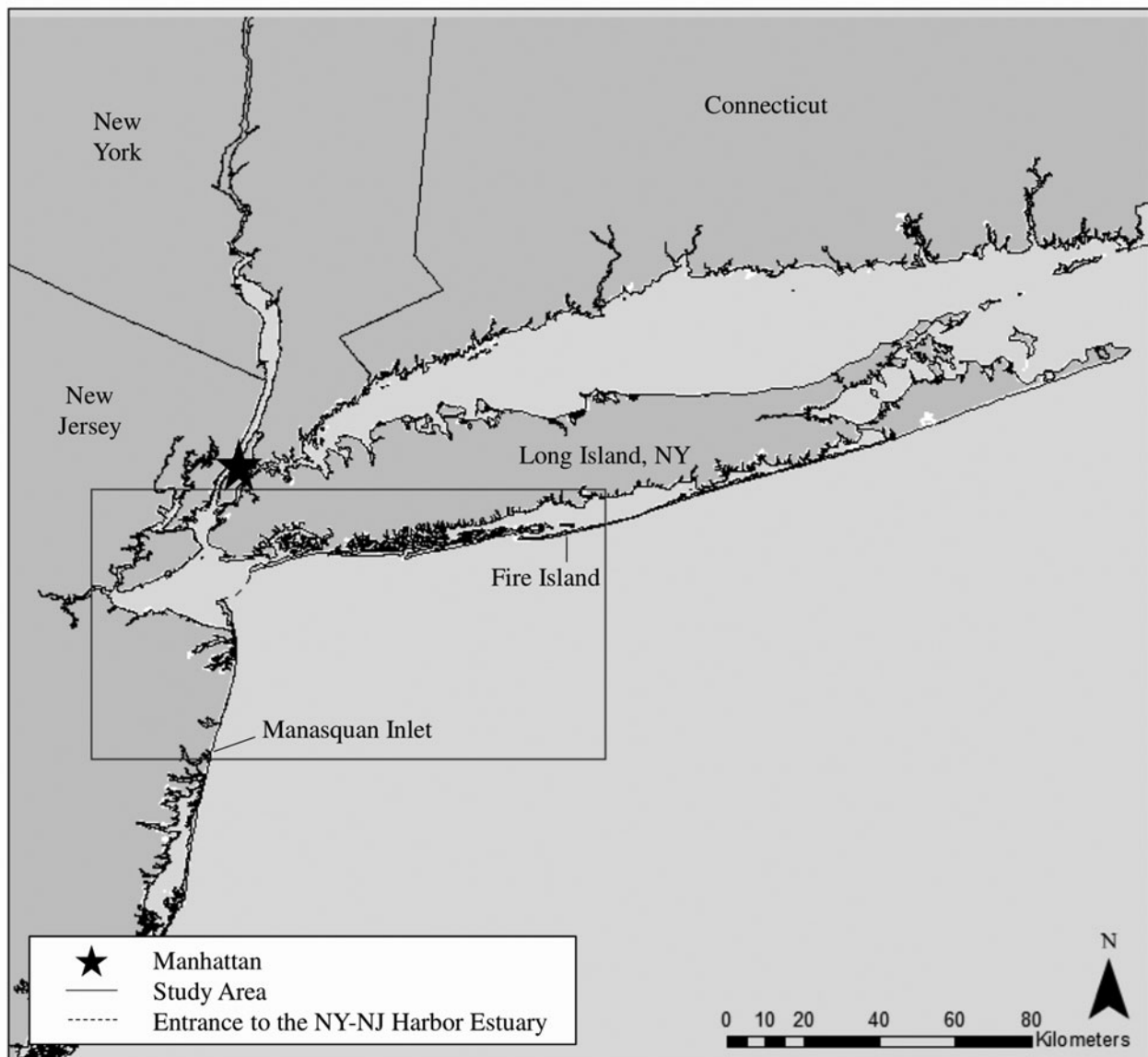


Fig. 1. Map of the study area within the New York Bight. The box outlines the New York Bight apex (NYBA) where humpback whale sightings were collected by Gotham Whale from 2011–2018.

Table 1. The frequency and seasonal extent of whale-watching trips during the study period

Year	2012	2013	2014	2015	2016	2017	2018
No. of Trips	31	36	54	60	72	74	86
Seasons	Jun–Sep	Jun–Nov	Jun–Oct	Jun–Oct	Apr–Dec	May–Nov	May–Nov

Population identity and exchange

To determine population identity and exchange with other North Atlantic areas, a subset of individuals observed in the NYBA through 2016 ($N = 52$) were compared with both ocean-scale and regional catalogues. This subset represents the most complete photographic data available at the time of analysis. Comparisons were made with the ocean-basin-wide North Atlantic Humpback Whale Catalog (curated by Allied Whale, College of the Atlantic) to investigate movement of individuals to all North Atlantic feeding areas. To obtain more detailed sighting histories and examine individual movement between the NYBA and primary feeding grounds in the western North Atlantic (Figure 2), fluke photographs were also compared directly with the Gulf of Maine

Humpback Whale Catalog (curated by the Center for Coastal Studies), two catalogues in eastern Canada (the Gulf of St. Lawrence, curated by Mingan Island Cetacean Study, and Newfoundland, curated by the Davoren Lab at the University of Manitoba) and west and east Greenland (curated by Greenland Institute of Natural Resources). Intensive research effort in the GoM resulted in the largest regional sample size for comparison, including many individuals first documented in their calf year. Photographs from the NYBA were also compared with whales seen off Delaware, Maryland, Virginia and North Carolina through a regional catalogue for the USMA (curated by the Virginia Aquarium and Marine Science Center and hosted on OBIS-SEAMAP). To investigate movements within the broader New York Bight, identified individuals were compared with



Fig. 2. Map of the western North Atlantic, including specific areas mentioned in this study. The box denotes the New York Bight apex (NYBA) where humpback whale sightings were collected by Gotham Whale from 2011–2018.

collections from off eastern Long Island, New York (separately curated by the Wildlife Conservation Society, Coastal Research and Education Society of Long Island (CRESLI), and the Thorne Lab at Stony Brook University) and the southern portion of New Jersey (curated jointly by Whale and Dolphin

Conservation and the Cape May Whale Watch and Research Center).

To make the comparisons, Gotham Whale shared fluke photographs from the NYBA with each of the regional catalogues. Each organization compared these photographs with their own

Table 2. Number of NYBA individuals matched to other feeding sites in the western North Atlantic, and the percentage of matched whales that comprised all whales sighted in each region from 2012–2018

Region		Total matches (#)	Percentage of catalogued individuals seen from 2012–2018	Data sources ^a
US Mid-Atlantic	• North Carolina, Virginia, Maryland, Delaware	10	9.3	1, 10
	• Cape May (New Jersey)	15	23.8	1, 9
	• Eastern Long Island (New York)	9	9.3	1, 6, 7, 8
Gulf of Maine Primary Feeding Ground	• Massachusetts to Nova Scotia (Canada)	20	1.3	1, 5
Other Primary Western NA Feeding Grounds	• Gulf of St. Lawrence	1	<1	1, 4
	• Newfoundland	2	<1	1, 3
	• Greenland ^b	0	0	1, 2

Some individuals were seen in more than one location. NYBA individuals made up a higher frequency of individuals observed off the US East Coast, including the Gulf of Maine, than other areas.

^a1. North Atlantic Humpback Whale Catalog, 2. Greenland Institute of Natural Resources, 3. Davoren Lab at the University of Manitoba, 4. Mingan Island Cetacean Study, 5. Gulf of Maine Humpback Whale Catalog, 6. Wildlife Conservation Society, 7. Coastal Research and Education Society of Long Island, 8. Stony Brook University, 9. Whale and Dolphin Conservation/Cape May Whale Watch and Research Center, 10. Mid-Atlantic Humpback Whale Catalog/Virginia Aquarium and Marine Science Center.

^bData for Greenland were only available through 2014.

catalogue holdings through 2018 with the exception of the Davoren Lab, which only had data through 2017. All matches were made manually, using standard photo-identification techniques (Katona *et al.*, 1979), with the exception of CRESLI, which used computer-aided matching via the program Flukebook (Levenson *et al.*, 2015). Matches were verified by multiple staff members within each organization. Table 2 summarizes the number of NYBA individuals successfully matched to each region and the percentage of matched whales out of all individuals documented in those areas during the study period.

Demographic categorization

Data to assess age-class were available for individuals that were successfully matched to multi-decade population studies in other parts of the North Atlantic (the GoM and the Gulf of St. Lawrence). Individuals were defined as juvenile if they had a known year of birth and were less than five years old, the earliest age of first calving (Clapham, 1992; Robbins, 2007). Any whale with a North Atlantic sighting history of five or more years was

considered potentially adult. We also used data from NOAA's Greater Atlantic and Southeast Region Marine Mammal Stranding Networks to assess the age class of stranded whales. Stranded individuals were categorized as juvenile if their total length was no longer than 11.6 m (male) or 12.0 m (female) (Nishiwaki, 1959; Rice, 1963) and/or their reproductive organs were assessed as being immature.

Results

Sighting characteristics in the NYBA

There were 323 sightings of 101 individual humpback whales, including 272 sightings from whale-watch trips and 51 sightings from public reports. The majority of whales were seen during summer (July–September, 62.5%), followed by autumn (October–December, 23.5%) and spring (April–June, 13.9%). Less than half of individuals (41.6%, $N = 42$) were seen only once in the NYBA. The rest (58.4%, $N = 59$) were seen on multiple occasions, either within the same year or between years. Occurrence across

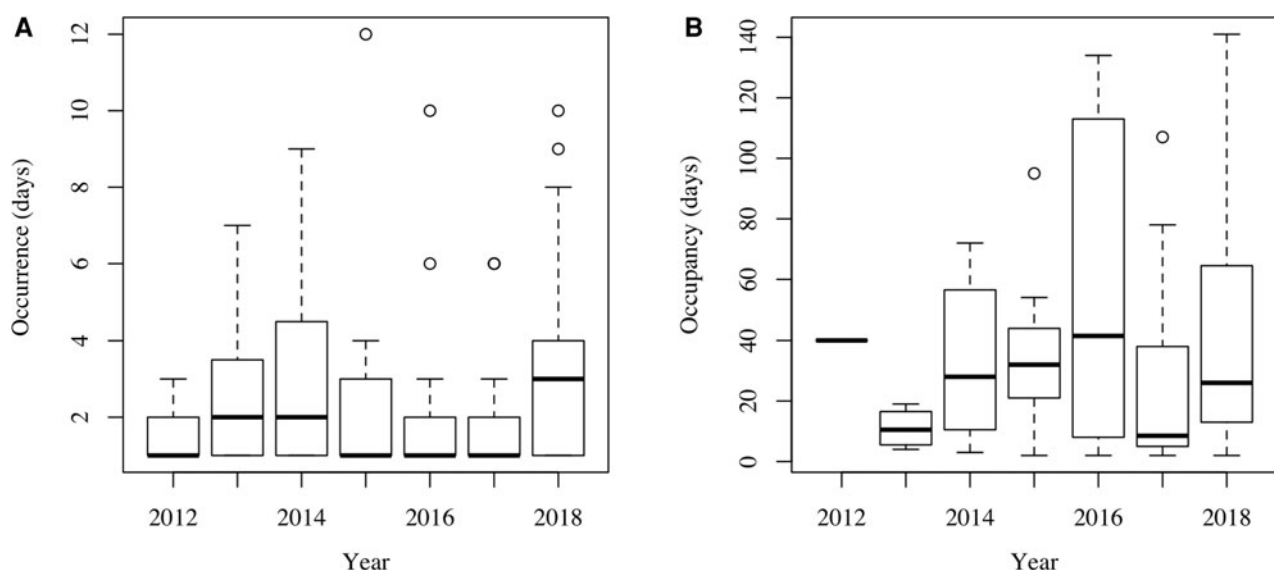


Fig. 3. Boxplot of (A) occurrence (number of days each whale was sighted within a season) and (B) occupancy (number of days between the first and last sighting for whales sighted multiple times in a year) by year. The boxes represent the interquartile range (IQR), with the median represented by the dark horizontal line. Whiskers are calculated as 1.5 times the IQR, and open circles indicate values outside of the whisker range.

all seven years ranged from 1–12 days, with a mean of 2.5 days (SD = 2.2). The year with the greatest mean occurrence (number of days sighted within a year) was in 2018 (mean = 3.3, SD = 2.66), and the fewest was in 2012 (mean = 1.5, SD = 1.0; [Figure 3](#)). Overall occupancy length ranged from 2–141 days, with a mean of 37.6 days (SD = 36.9). The year with the greatest occupancy length was in 2016 (mean = 55.2, SD = 50.5), and the lowest was in 2013 (mean = 11, SD = 6.8; [Figure 3](#)). Of the whales seen on more than one occasion (N = 59), most sightings took place in only one (N = 41) or two (N = 13) years. However, there was evidence of extended use of the NYBA by a few individuals involving return in 3 (N = 3) or 5 (N = 2) different years. The percentage that returned in the next consecutive year was 31.3% (SD = 25.5%).

Population identity and exchange

Of the 52 whales compared with regional catalogues, 25 (48.1%) were documented in other parts of the New York Bight (Eastern Long Island and Cape May) or off Virginia. Nine (36.0%) of these whales were seen in more than one other location. The majority of matches within the New York Bight involved within-year sightings; 73.3% of matches to Cape May were within the same year and 55.6% of matches to Eastern Long Island were within the same year. Of these within-year matches, most individuals were seen in Eastern Long Island (72.7%) or Cape May (60.0%) prior to being seen in the NYBA. Only 20.0% (N = 2) of individuals matched between the NYBA and Virginia were seen in both locations in the same year. In both cases, the Virginia sightings were in winter and the NYBA sightings were either in spring or autumn.

Twenty whales (38.5%) had sighting histories in the adjacent GoM, of which one also had a history in the Gulf of St. Lawrence. Six of these individuals (30.0%) were seen in both the GoM and the NYBA in the same year. Of these, two (33.3%) were seen in the NYBA first and three (50.0%) were seen in the GoM first. One whale was seen in both areas in two different years; in 2016 it was seen in the GoM first, and then in 2017 it was seen in the NYBA first.

Two (3.8%) individuals from the NYBA also had sighting histories in Newfoundland. Both were seen in the NYBA in the autumn of 2016. They were seen in Newfoundland within a year of their NYBA sighting (one in August 2015 and one in August 2017). There were no matches to other primary North Atlantic feeding grounds.

Demography

Only six whales in the NYBA had been catalogued by long-term studies on primary feeding grounds prior to 2012. When data were available to evaluate age, most individuals were either confirmed or suspected juveniles, including four whales known to be 2–4 years old based on known birth year, and 13 whales with sighting histories of two years or less on primary feeding grounds. Three individuals were considered adults based on North Atlantic sighting records, including two females with calving histories. One of the adult females was seen with her first calf in the NYBA in the autumn of 2016. The calf was subsequently documented in the GoM in 2017 and 2018. Six deceased whales, including three of the above catalogued whales with short sighting histories, had body lengths ranging from 8.43–10.96 m, and were therefore classified as juveniles.

Discussion

This study is the first attempt to investigate the site fidelity, population identity and demographic characteristics of humpback whales in the NYBA. The results suggest that humpback whales exhibit extended occupancy (mean 37.6 days) in the NYBA and

were likely to return from one year to the next (mean 31.3%). Whales were also seen at a variety of other sites in the New York Bight within the same year, suggesting that they may occupy this broader area throughout the feeding season. This study shows that while many humpback whales found in the NYBA originated in the GoM or eastern Canada, the feeding population for many others remains unknown.

The GoM is the closest primary feeding ground and has the largest regional catalogue in this study. Therefore, a small number of whales travelling to the NYBA to feed would be consistent with previous findings of a greater frequency of short-distance movements and a higher rate of exchange with nearby areas than more distant ones (Stevick *et al.*, 2006; Heide-Jørgensen & Laidre, 2007; Dalla Rosa *et al.*, 2008; Kennedy *et al.*, 2014). Barco *et al.* (2002) found similar exchange between whales seen in a portion of the USMA (New Jersey to North Carolina) and other oceanic areas, with the majority of whales having sighting histories in the GoM, and a small number with histories in eastern Canada. For the limited number of whales for which age class could be inferred, the majority were either confirmed or suspected juveniles. Thus, it is conceivable that the young age of individuals in the NYBA may have biased matches toward the GoM considering the extensive effort employed there to catalogue whales from the year of birth. The young age structure in the nearshore waters of the NYBA is consistent with recent work by Stepanuk *et al.* (2021) in the greater New York Bight, and as described by Swingle *et al.* (1993), Barco *et al.* (2002) and Aschettino *et al.* (2020) for live whales from the USMA. It is also consistent with the primary age-class of stranded humpback whales found in the USMA from 1985–2000 (Wiley *et al.*, 1995; Barco *et al.*, 2002) and whales catalogued in the NYBA that were found stranded. However, this age structure differs from what is found in the primary feeding ground with the most exchange (GoM, Robbins, 2007), suggesting that there is preferential exchange by younger whales. It remains to be determined how and why individual humpback whales are finding the nearshore waters of the NYBA, but sightings of adults (and especially mother-calf pairs) have thus far been rare. The only dependent calf documented in the study period returned consistently to the GoM and has not yet been resighted in the NYBA. Since that time, only one additional mother was observed in the NYBA (in 2021), totalling just two in 10 years of observation (Gotham Whale, unpublished data). Long-term population research will be needed to determine the degree to which catalogued NYBA whales continue to use the area as adults, and whether their own calves return to this area.

It is not clear if and how humpback whales used the NYBA before this study began, but there were acoustic detections outside New York harbor and the NYBA in 2008–2009 (Davis *et al.*, 2020; Zeh *et al.*, 2020). In the greater New York Bight, there are historical records of sporadic sightings off western Long Island in the 1980s and 1990s (Sadove & Cardinale, 1993) and off southern New Jersey in the 1990s and 2000s (Barco *et al.*, 2002; Whitt *et al.*, 2015). Due to limited data on humpback whales prior to the 1980s, it cannot be ascertained whether the NYBA was consistently occupied habitat in earlier years. Therefore, it is currently difficult to draw conclusions regarding the relationship between the recent increase in NYBA sightings and the recovery trends in the West Indies Distinct Population Segment. Until recently, there was considerable uncertainty in trends of population abundance and growth along the US East Coast (Bettridge *et al.*, 2015; Hayes *et al.*, 2019, 2020), but on-going research on abundance trends in the GoM during the past two decades (e.g. Robbins & Pace, 2018) will likely lead to greater insight into the role that large-scale population dynamics may play in the results reported here. However, there may also be factors unrelated to population growth that are attracting younger animals to the NYBA.

Changes in prey availability are a common cause of changes in the distribution of humpback whales at high latitudes (Payne *et al.*, 1986, 1990; Piatt *et al.*, 1989; Stevick *et al.*, 2006). The prey species of humpback whales in the NYBA have not been well-established. However, Brown *et al.* (2018) and King *et al.* (2021) described visual observations of humpback whales feeding on Atlantic menhaden (*Brevoortia tyrannus*), and eDNA metabarcoding detected menhaden in most water samples collected near whales in the NYB (Alter *et al.*, 2022). Aschettino *et al.* (2020) also found that increasing numbers of humpback whales wintering off coastal Virginia appeared to be feeding on Atlantic menhaden. Lucca & Warren (2019) detected large schools of Atlantic menhaden in the NYBA during the summers of 2014–2015, and the most recent Atlantic menhaden stock assessment found that the rate of fishing mortality has been below the single species target since the 1990s (SEDAR, 2020). Therefore, increased or more consistent availability of this prey species may be driving the increase in sightings of humpback whales in the NYBA.

Our results are in contrast to previous studies in the USMA that found humpback whales to occur primarily during the winter (Swingle *et al.*, 1993; Barco *et al.*, 2002; Aschettino *et al.*, 2020). However, the majority of whales documented by Swingle *et al.* (1993), Barco *et al.* (2002) and Aschettino *et al.* (2020) were seen off Virginia, ~430 km south of the NYBA, in an area now known as a supplemental wintering ground. It is possible that whales wintering off Virginia are extending their range north to the NYBA during the feeding season. However, the present study found few (N = 2) whales seen in both areas in the same year.

Gotham Whale did not have any vessel-based effort during winter in any year but did not receive any humpback whale sighting reports from the public during this season. The carcass of one whale catalogued in this study was discovered in the area in February 2018, although it is not known where it died. Other studies detected humpback whales in the NYBA and the greater New York Bight during winter (e.g. Whitt *et al.*, 2015; Davis *et al.*, 2020; Zeh *et al.*, 2020; Zoidis *et al.*, 2021). Aerial surveys conducted by Zoidis *et al.* (2021) found lower sighting rates for humpback whales in the New York Bight during winter and spring than the rest of the year, which would be consistent with small numbers of humpback whales found wintering on primary feeding grounds (Clapham *et al.*, 1993; Robbins, 2007). Thus, the lack of public sighting reports to Gotham Whale during winter may be due to a lower number of humpback whales in the area, lower presence of observers, or both. However, an earlier study by Whitt *et al.* (2015) documented a small number (N = 17) of humpback whales off southern New Jersey from 2008–2009, and they were mainly seen from December–April. The degree to which individuals are using the NYBA in winter requires further examination.

This study was based largely on opportunistic effort. Sightings collected from whale-watching boats are limited to the seasonality and spatial distribution of the effort within the NYBA. There is currently no reason to assume that the individuals sampled are not representative of the NYBA with respect to feeding ground origin and general sighting characteristics. However, it is not necessarily representative of the greater New York Bight. Future studies, including those that compare datasets from 2017 onward, along with continued opportunistic and systematic efforts, will allow greater understanding of habitat use in this area.

This study provides new information on the characteristics of humpback whales in the NYBA and adds to existing knowledge of the distribution of western North Atlantic feeding populations. Extended occupancy in the NYBA has the potential to increase individual overlap with human activities. Increasing sightings in

and around shipping lanes in the New York Bight and greater USMA (Brown *et al.*, 2019; Aschettino *et al.*, 2020; King *et al.*, 2021; Stepanuk *et al.*, 2021; Zoidis *et al.*, 2021; Smith *et al.*, 2022) may be a significant factor in the latest Unusual Mortality Event for humpback whales along the Atlantic Coast. The recent designation of several Wind Energy Areas within the New York Bight (BOEM, 2021) will inevitably lead to an increase in vessel traffic (Dolman & Simmonds, 2010). Additional work is therefore recommended to continue to monitor humpback whale use of the NYBA and the greater New York Bight, including overlap with human activities and changes in humpback whale population structure more broadly along the US East Coast.

Data. The data that support the findings of this study are available from the corresponding author, DMB, upon reasonable request.

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