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A decade of humpback whale abundance estimates at Bermuda, an oceanic migratory stopover site

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We constructed annual abundance of a migratory baleen whale at an oceanic stopover site to elucidate temporal changes in Bermuda, an area with increasing anthropogenic activity. The annual abundance of North Atlantic humpback whales visiting Bermuda between 2011 and 2020 was estimated using photo-identification capture-recapture data for 1,204 whales, collected between December 2009 and May 2020. Owing to a sparse data set, we combined a Cormack-Jolly-Seber (CJS) model, fit through maximum likelihood estimation, with a Horvitz-Thompson estimator to calculate abundance and used stratified bootstrap resampling to derive 95% confidence intervals (CI). We accounted for temporal heterogeneity in detection and sighting rates *via* a catch-effort model and, guided by goodness-of-fit testing, considered models that accounted for transience. A model incorporating modified sighting effort and time-varying transience was selected using (corrected) Akaike's Information Criterion (AICc). The survival probability of non-transient animals was 0.97 (95% CI 0.91-0.98), which is comparable with other studies. The rate of transience increased gradually from 2011 to 2018, before a large drop in 2019. Abundance varied from 786 individuals (95% CI 593-964) in 2016 to 1,434 (95% CI 924-1,908) in 2020, with a non-significant linear increase across the period and interannual fluctuations. These abundance estimates confirm the importance of Bermuda for migrating North Atlantic humpback whales and should encourage a review of cetacean conservation measures in Bermudian waters, including area-based management tools. Moreover, in line with the time series presented here, regional abundance estimates should be updated across the North Atlantic to facilitate population monitoring over the entire migratory range.

KEYWORDS

baleen whale, humpback whale, *Megaptera novaeangliae*, abundance, capture-recapture, migratory stopover

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1 Introduction

Abundance time series are critical to wildlife management as they can inform conservation status and determine underlying drivers of observed trends (Lawton, 1993; Taylor and Gerrodette, 1993; Mace et al., 2008). As a population metric, abundance is relatively easy to understand and interpret, and values can be compared across different time periods (Moore and Barlow, 2011), populations (Barlow et al., 2011), and species (Víkingsson et al., 2015). Further, variation in abundance may relate to other population-scale changes (Madon et al., 2013). For example, temporal trends in baleen whale abundance have been related to variation in mortality, body condition, reproductive rates, and species range shifts (Moore, 2005; Patrician and Kenney, 2010; Ramp et al., 2014; Becker et al., 2019; Simard et al., 2019; Kügler et al., 2020). Combined, such indices allow an integrated assessment of population responses to environmental change and stressors (Hazen et al., 2019), and inform local-regional marine management (Gabriele et al., 2017).

The abundance of baleen whales is frequently estimated through capture-recapture (CR) methods (Hammond et al., 2021). Applied to humpback whales (*Megaptera novaeangliae* [Borowski 1781]), this typically involves photo-identification of naturally occurring markings on tail flukes to determine individual sighting histories over time (e.g., Katona and Whitehead, 1981; Franklin et al., 2020). Values for parameters including survival, detection and abundance are then estimated. To minimize bias of abundance estimates, analyses may account for heterogeneity in survival and detection, including features such as: transient animals, which are only available within the study system once across the study period (Pradel et al., 1997; Madon et al., 2013); temporal heterogeneity due to variable sighting effort (Marucco et al., 2009; Monnahan et al., 2019); and individual detection heterogeneity (IDH), where detection varies as a function of individual attributes and habitat features (Hammond, 1990; Cubaynes et al., 2010). CR methods have been used to construct humpback whale abundance time series at local, regional, and basin scales (e.g., Barlow et al., 2011; Madon et al., 2013; Monnahan et al., 2019). These have been used to inform conservation status for the global and regional populations (Bettridge et al., 2015; Cooke, 2018) and to inform species management (International Whaling Commission, 2009).

Abundance estimates for humpback whales rarely incorporate all parts of a population's range. Like other mysticetes, humpback whales are capital breeders, undertaking long-distance annual migrations between low-latitude winter breeding grounds and high-latitude summer feeding grounds (Mackintosh, 1946; Carwardine, 2019). During this migration, animals may use stopover sites as transitory stops, from days to weeks, for activities such as feeding, resting, socializing or information gathering (Linscott and Senner, 2021). Stopover sites can be coastal, such as Hervey Bay in East Australia (Franklin et al., 2021), but are often oceanic, such as the Kermadec Islands in Oceania (Owen et al., 2019) and the Rio Grande Rise in the Southwest Atlantic (Horton et al., 2020). To date, whale abundance time series have been largely derived for the 'end points' of migration – feeding and breeding grounds (e.g., Chaloupka et al., 1999; Schleimer et al., 2019). These abundance estimates are crucial to monitor population size (Stevick et al., 2003; Punt et al., 2006). In contrast, there are few abundance estimates or time series for stopover sites, particularly mid-ocean areas, which may provide more information about migratory patterns in space and time (Findlay et al., 2011).

In the present study, we investigate humpback whale abundance around Bermuda, a North Atlantic mid-ocean stopover site (Figure 1; Payne and McVay, 1971; Stevenson, 2011). The North Atlantic is considered to be a discrete population of humpback whales (Cooke, 2018) with two distinct population segments (DPS), listed as 'not at risk' in the Caribbean breeding area and 'endangered' at Cape Verde (NOAA, 2016). The Caribbean DPS is subdivided into northern and southeastern Caribbean breeding grounds; and the principal feeding grounds are the Gulf of Maine, eastern Canada, West Greenland, Iceland, and north of Norway (Smith et al., 1999; Reeves et al., 2002; Stevick et al., 2003; Stevick et al., 2018; Wenzel et al., 2020), with each feeding ground considered as a separate management unit (International Whaling Commission, 2002; Hayes et al., 2019). Long-distance migration routes in the North Atlantic are not coastal (Stevick et al., 2006; Kennedy et al., 2014) and there are few mid-ocean migratory stopovers, including Bermuda and the Azores (Visser et al., 2011; Cucuzza et al., 2015). Following extensive commercial hunting in the 19th and 20th centuries (Smith and Reeves, 2010) and a commercial whaling ban in 1955 (Best, 1993), the population size of North Atlantic humpback whales steadily increased through the end of the 20th century (Punt et al., 2006). From CR analysis, modeled annual increase ranged from 1.2% to 3.1% in the principal breeding ground in the northern Caribbean, 1979-1992 (Stevick et al., 2003; Punt et al., 2006). Rates of annual increase varied widely across feeding grounds, from 3% in the Gulf of Maine, 2009-2016, determined by CR (Robbins and Pace, 2018); to ~15% in Icelandic waters, 1987-2001 (Pike et al., 2005), and a sharp decline in the West Greenland feeding ground, 2007-2015 (Heide-Jørgensen and Laidre, 2015; Hansen et al., 2018), determined by line transect sampling. Total abundance in the North Atlantic is still thought to be far below pre-exploitation population size (Punt et al., 2006; Ruegg et al., 2013), although the carrying capacity may have changed due to environmental shifts (Tulloch et al., 2019). To our knowledge, abundance estimates have not been provided for any part of this population more recently than 2016 (Robbins and Pace, 2018). Moreover, in 2018, the International Whaling Commission (IWC) recommended a range-wide, in-depth assessment for North Atlantic humpback whales, including abundance (International Whaling Commission, 2019).

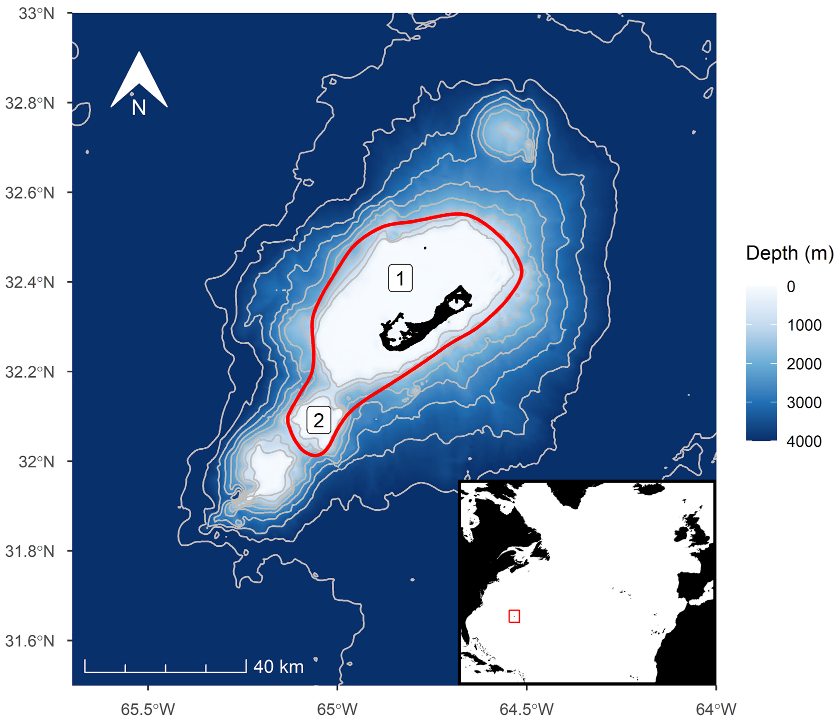

FIGURE 1
Map of the study area, the waters around Bermuda, and its position within the North Atlantic (inset). The approximate search area is denoted by the red line. The study area encompasses two major bathymetric features, 1) the Bermuda Platform and 2) Challenger Bank.

Bermuda has strong migratory connections to other parts of the North Atlantic, with evidence of stopover behavior. Using photo-identification, individuals sighted in Bermuda have been matched to all major feeding grounds, in addition to North Carolina (USA) and Franz Josef Land (Russia); and both Caribbean breeding grounds (Katona and Whitehead, 1981; Stone et al., 1987; A. S., unpublished data; Happywhale[1]). Re-sighting rates suggest that Bermuda is primarily a stopover between the northwest Caribbean and western feeding grounds (Beaudette et al., 2009). Meanwhile, breeding behavior in the form of extensive seasonal singing activity has been recorded at the Bermuda stopover site (Homfeldt et al., 2022), as well as preliminary evidence of foraging (Stone et al., 1987; Hamilton et al., 1997; Stevenson, 2011), aggregation and competitive (Stevenson, pers. comm.) behaviors, during south- and northbound migration.

Due to Bermuda's position along the humpback whale migratory route, the exclusive economic zone was declared a Marine Mammal Sanctuary in 2012, as part of a 'Sister Sanctuary Agreement' with western North Atlantic feeding and breeding areas (NOAA and Government of Bermuda, 2012). However, this designation confers no additional legal protection to humpback whales, and the importance of these waters as a stopover site has not been confirmed through abundance estimates until the present study. With persistent and increasing levels of regional human activity, particularly large vessel traffic (Roberts, 2011; Halpern et al., 2015; Širović et al., 2016), and the announcement of a Blue Economy Strategy for Bermuda (Bermuda Ocean Prosperity Programme, 2021), such evidence could underpin future designations that do carry legally binding management measures, such as Particularly Sensitive Sea Areas (PSSAs; Kachel, 2008), to mitigate risks to humpback whales posed by these activities.

Here, we use a CR framework to model the seasonal abundance of humpback whales around Bermuda from 2011 to 2020 using photo-identification sightings. The data set exhibits low inter-seasonal resighting rates and the resulting model framework does not provide an abundance estimate for the first season of data collection (2010). To reduce bias in our abundance estimates, we account for temporal heterogeneity in sighting effort and whale occurrence, and formally test for both transience and IDH in our data to guide subsequent model fitting and selection. We discuss the potential of this time series to inform marine management in Bermudian waters and establish new baselines to monitor changes through the migratory range of North Atlantic humpback whales.

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[1] Happywhale, https://www.happewhale.com [last accessed 12 September, 2022]

2 Materials and methods

2.1 Data collection

Between December 2009 and May 2020, annual humpback whale photo-identification surveys were conducted from a small vessel (6.5-10 m length) in coastal and offshore waters around Bermuda (Figure 1). Surveys took place between December and May, the period during which humpback whales typically occur (A. S., unpublished data), and were daily whenever possible. In 2020, survey effort was limited by Covid-19 restrictions in Bermuda (Table 1). All surveys were conducted in calm weather (Beaufort Sea State<3, no precipitation, swell<2 m) with good visibility, and typically spanned daylight hours. Surveys followed a haphazard regime to maximize encounters with whales and focused spatially on the southwestern Bermuda Platform and the Challenger Bank seamount (Figure 1; Vogt and Jung, 2007), although survey routes and sighting locations were not consistently recorded. Surveys were conducted in closing mode; whales were approached on detection and a focal follow of variable duration was conducted at each encounter (Altmann, 1974), which generally lasted 20-30 minutes and up to 2 hours. When possible, the ventral side of the tail flukes of each encountered animal was photographed with a digital SLR camera (Nikon D200, 2010-2017; Nikon D700, 2018-2020; 70-300 mm lens).

Images were used for individual photo-identification *via* scarring patterns and coloration, following Calambokidis et al. (2001). Briefly, two trained researchers independently assigned each image a score of highest quality (1) to lowest quality (5) for five variables against photographic archetypes: proportion of fluke visible, fluke angle (relative to the water), lateral angle of the photographer, sharpness, and lighting. Scores from both researchers were then compared: where there was a discrepancy, the lowest quality (highest score) was retained. We adopted a conservative approach wherein photographs with a score of ≥4 in any category were rejected. Photographs were analyzed independently by two teams and matches detected by only one team were verified by the other.

Data were processed in two ways. For simplicity, each December-May season was named according to the January-May calendar year (e.g., the 2010 season refers to the period December 2009-May 2010). First, to explore residency and support existing evidence that Bermuda is used as a stopover site (a transitory stop, used by whales during long-distance migration for days to weeks), we determined the number of animals that were re-sighted within each season. We calculated the duration (in days) between first and last sightings for each animal within each season, which can be used to infer the minimum residence time in Bermuda. Because Bermuda is thought to encompass south- and north-bound migrations, we removed any durations greater than 20 days. Second, for capture-recapture modeling, each animal was recorded as present or absent for each season, resulting in a summary record of seasonal sighting histories. This was used to determine the number of inter-seasonal re-sights each season (from all previous seasons within the study period) and estimate abundance.

2.2 Model construction

Abundance trends were derived from annual sighting histories using capture-recapture (CR) methods (for example:

TABLE 1 Survey effort (absolute and standardized), sightings, inter-seasonal re-sights (from all previous years within the period) and intra-seasonal re-sights for each season (December-May, e.g., the 2010 season corresponds to December 2009-May 2010), determined through photo-identification.

Season	Effort (days)	Standardized effort	No. whales	No. inter-seasonal re-sights	Intra-seasonal re-sights	
					No. whales	Days between sightings
2010	18	4.35	78		6	1-2
2011	25	7.01	104	4	9	1-7
2012	32	8.60	165	16	21	1-7
2013	33	8.37	158	27	21	1-8
2014	29	6.37	103	20	6	1-5
2015	33	8.38	180	26	13	1-6
2016	31	6.81	88	19	10	1-7
2017	27	7.29	122	28	1	1-1
2018	25	6.59	148	22	17	1-11
2019	38	9.81	218	49	26	1-14
2020	13	3.01	71	20	6	1-14

King, 2014; McCrea and Morgan, 2015; Seber and Schofield, 2019; Hammond et al., 2021). Annual abundance was defined as the total number of animals passing through the approximate search area in a single December-May season. All model construction and analyses were performed in *R* (R Core Team, 2020), and outputs were visualized with the *ggplot2* package (Wickham, 2016). CR models were fitted using *MARK* (White and Burnham, 1999), accessed through *R* using the *RMark* package (Laake and Rexstad, 2012).

With the majority of whales only sighted in one season across all survey years, the data set is information-poor, increasing the risk of over-parameterization and limiting the complexity of suitable CR frameworks (Lebreton et al., 1992; Forster, 2000). Therefore, using a two-step approach, we initially fit a modified Cormack-Jolly-Seber (CJS; Lebreton et al., 1992) model to the data, and then used the fitted model estimates to calculate annual abundance (Cubaynes et al., 2010 season). We also investigated the use of the more complex Jolly-Seber-Schwarz-Arnason (JSSA; Jolly, 1965; Seber, 1965; Schwarz and Arnason, 1996) and Pollock's closed robust design (Pollock, 1982) models. However, for these data, both models led to identifiability issues in the estimation of model parameters (associated with boundary estimates) and thus were not investigated further.

The CJS framework provides estimates of apparent survival and detection, from which abundance can be subsequently derived. The model can be modified to account for variable survey effort, transience, and IDH. We defined each year as a single capture occasion. CJS conditions on the first sighting of each animal, so that we are not able to estimate the associated capture probabilities for the first season of the study, which consequently means that abundance estimates cannot be produced for the first capture occasion (i.e., 2010; Cubaynes et al., 2010). Capture histories were modeled as a function of two parameters: apparent survival rate, Φ, and per-animal detection probability, p. Parameters were linked to covariates with an inverse logit function and values were estimated from observed data using a maximum likelihood estimation (MLE) approach. To estimate total annual abundance, we followed Cubaynes et al. (2010) and used a Horvitz-Thompson estimator (Borchers et al, 2002; Horvitz and Thompson, 1952; McDonald and Amstrup, 2001) such that:

$$\hat{N}_i = \frac{n_i}{\hat{p}_i};$$

where $\hat{N}_i$ denotes the estimated annual total abundance, $\hat{p}_i$ the estimated detection probability and n_i the number of sighted animals at occasion *i*. A stratified bootstrap approach (1000 replicates) was used to calculate 95% confidence intervals for p, Φ and N (Morgan, 2008; King and McCrea, 2019; Worthington et al., 2021). For each bootstrap replicate, the number of animals first sighted in a given year was set equal to the observed value.

Core CJS model assumptions include that each animal has an independent fate; that identifying marks are retained and recorded correctly; and that all emigration is permanent (Lebreton et al., 1992). Calves were excluded from the present study and humpback whales are thought to form only loose, temporary associations (Valsecchi et al., 2002), suggesting that individuals behave independently from one another. The long-term reliability of humpback whale fluke photo-identification has been exhaustively demonstrated (Katona et al., 1979; Katona and Whitehead, 1981; Carlson et al., 1990; Stevick et al., 2001; Franklin et al., 2020). Temporary emigration in this system was defined as animals that did not visit Bermuda for one or more seasons (years). Despite limited information, temporary emigration is thought to occur in humpback whale breeding grounds (Brown et al., 1995; Madon et al., 2013; Kowarski et al., 2018) and may occur at the Bermuda stopover site, which would violate a model assumption and could contribute to a transience signal.

Within the basic CJS framework, Φ and p can be constant or time dependent. Modifications to this framework were considered to account for heterogeneous detection and survival, based on system knowledge and goodness-of-fit testing, to minimize bias of abundance estimates.

2.2.1 Capture effort

Detection probability p is likely to vary between years as a function of seasonal survey effort (Marucco et al., 2009; Monnahan et al., 2019). However, in terms of explaining detection probabilities, the number of survey days is a coarse and perhaps naïve estimate of effort, given that a) the number of whales present changes during a season, with a consistent peak in sightings in March and April across all years; and b) the temporal distribution of effort varies between seasons (Figure 2). To account for this, we derived a standardized effort value for each season i ($effort_{s,i}$). First, we calculated the mean number of whales seen per day (WPD) for a given calendar month m over all seasons (WPD_m), defined as:

$$WPD_m = \frac{sightings_m}{days_m};$$

where $sightings_m$ is the total number of sightings (one sighting is equal to one identifiable whale seen at least once on one day) and $days_m$ is the total number of effort days, for calendar month m across all seasons. We then derived an associated correction factor for each month (cor_m) as:

$$cor_m = \frac{WPD_m}{\sum_m WPD_m}.$$

This correction factor is an empirical distribution of the average WPD across months, and thus takes into account differences over time relating to whale presence in the area.

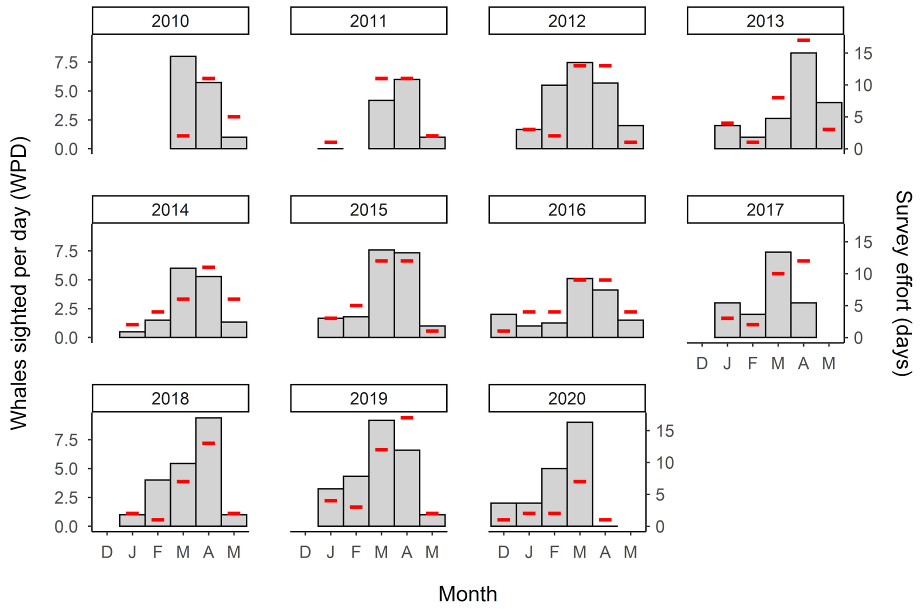

FIGURE 2
Whales sighted per day (WPD; gray bars, left-hand y-axis) and number of days of survey effort (red lines, right-hand y-axis) for each survey month and season.

Finally, we defined the standardized effort ($effort_s$) for season i as:

$$\text{effort}_{s,i} = \sum_{m} effort_{i,m} \times cor_m \ ;$$

where $effort_{i,m}$ denotes the number of days of effort for month m in season i. In this way, our standardized effort accounts for intra-seasonal patterns in whale occurrence and the heterogeneous temporal distribution of effort between seasons (years). We considered models in which standardized effort was included as a covariate with p *via* logistic regression.

2.2.2 Transience

We considered the presence of transients, defined as animals that visited Bermuda in only one season during the study period. By definition, transients cannot be observed again and are unavailable for recapture within the study (i.e., have zero "survival" probability; Pradel et al., 1997). Transience has been detected in humpback whale breeding grounds (Constantine et al., 2012; Madon et al., 2013; Chero et al., 2020), although the source of the signal is uncertain. Failure to account for this feature will typically lead to an overestimation of abundance (Madon et al., 2013; Genovart and Pradel, 2019), due to an associated underestimation of capture probability.

We used goodness-of-fit (GoF) testing, implemented through the *R2ucare* package (Choquet et al., 2009; Gimenez et al., 2018), to investigate the presence of transient animals. A significant chi-squared test result (χ^2 = 121, df = 44, p< 0.0001) suggested a poor fit of the basic CJS model to sighting histories. This test was decomposed to four interpretable components using contingency tables; the TEST 3.SR (Pradel et al., 2005) component yielded a significant result (Z = 89, p< 0.0001), indicating that newly encountered and previously encountered animals have different probabilities of subsequent re-sighting. This is typically interpreted as a strong signal for transience and removing this component improved goodness of fit considerably (χ^2 = 32, df = 35, p = 0.60). To account for transience, we followed Pradel et al. (1997) and structured Φ into two age classes ($\Phi \sim transient$), 0 and 1+ years, where 'age' is the time elapsed since first capture and not the actual age of the animal. Φ_0 (model age 0) can be interpreted as the combined apparent survival of 'transient' animals (zero survival probability) and 'resident' animals, and Φ_{1+} (model age 1+) as the survival of residents alone. The proportion of transients among newly sighted animals, τ, was estimated using:

$$\hat{\tau} = 1 - \frac{\hat{\Phi}_0}{\hat{\Phi}_{1+}}.$$

The proportion of transients in the population, T, was then estimated via,

$$\hat{T} = \frac{E(u_i) \times \ \hat{\tau}}{E(u_i + \ m_i)},$$

where $E(u_i)$ is the expected number of newly sighted animals and $E(m_i)$ the expected number of re-sighted animals. Following

Perret et al. (2003), we used observed u_i and m_i as estimates for expected values.

We considered models in which Φ_0 and Φ_{1+} were constant (single value) or time-varying in an additive way ($\Phi \sim time + transient$). Additionally, to account for the possibility that temporal variation in Φ was driven by variable transience and not survival, we considered models in which Φ_0 varied over time but Φ_{1+} was constant by using age class as a dummy variable ($\Phi \sim time{:}transient$; Laake and Rexstad, 2012).

2.2.3 Individual detection heterogeneity

Detectability may also vary between animals as a function of individual attributes, including fluke-up behavior for humpback whales (Barendse et al., 2011) and habitat features, such that each animal within the study system has a unique sighting probability (Cubaynes et al., 2010; Gimenez and Choquet, 2010). Failing to account for individual detection heterogeneity (IDH) can lead to an underestimation of abundance (Hammond, 1990; Hwang and Huggins, 2005; Cubaynes et al., 2010). To test for this feature, following Jeyam et al. (2018), we applied tests of positive association between previous and future encounters using Goodman-Kruskal's gamma. A global version of the test (all capture occasions pooled) was only marginally significant ($\gamma = 0.47$, $p = 0.03$). From occasion-specific tests, only 2013, 2015 and 2016 were (marginally) significant. Therefore, modifications of the detection process p to account for IDH were not included. Of note, in a preliminary analysis, including IDH had little effect on parameter estimates but did lead to some additional identifiability issues.

2.2.4 Model selection

In total, we fitted and compared 16 CJS models, constructed from combinations of the different parameter specifications: three for p (constant, time, standardized effort) and five for Φ (constant, time, transient, time + transient, time:transient). Selection of the final, best-fitting model was achieved with Akaike's Information Criterion corrected for small sample size (AICc; Burnham and Anderson, 2004), where a low score indicates improved model fit offset against model complexity, supplemented with visual inspection of parameter values and associated confidence intervals. The final annual abundance estimates were linearly regressed against time to detect a significant temporal trend. The regression was weighted by the inverse of the variance of each abundance estimate to account for varying precision (Stevick et al., 2003; Kutner et al., 2005; Somerford et al., 2022).

3 Results

In total, 304 days of surveys were conducted between December 2009 and May 2020. Seasonal survey effort ranged from 13 days (2020 season) to 38 days (2019 season; Table 1), with a mean of 27 days (SD = 7.2 days). Seasonal standardized effort, which accounted for intra-seasonal variation in whale sighting rates, varied from 3.01 (2020) to 9.81 (2019), with a mean of 6.96 (SD = 1.95). Out of 2,038 sightings with fluke images, 1,594 sightings on 276 days had images of sufficient quality (a score of ≤3 in all five variables). From these filtered sightings, 1,204 individual whales were identified (Figure 3). The number of identifiable whales per season ranged from 71 (2020) to 218 (2019; Table 1, Figure 3), with a mean of 130 whales (SD = 47 whales). The majority of whales (1,042, 87%) were sighted in only one year, with whales sighted in up to seven different seasons (one whale). The number of animals that were re-sighted between years ranged from 4 (2011) to 49 (2019; Table 1) for each year of re-sighting. Between 1 (2017) and 26 (2019) animals were re-sighted within each season, with a maximum duration of 14 days between first and last sightings (after removing durations >20 days; Table 1).

Candidate CJS models were compared with AICc values (Table 2). The top two models represented 95% of the weight of evidence, had similar AICc values (ΔAICc = 0.6 for second model) and both contained detection p linked to standardized effort and transient Φ. The only difference in model structure was the time dependence of Φ (apparent survival): in the best-fitting model, Φ_0 was time-varying and Φ_{1+} was constant (the apparent survival of non-transient animals did not vary with time), whereas both were time-varying in an additive way in the second best-fitting model. In this way, the best-fitting model, with constant survival following re-sighting, can be regarded as a simpler version of the second best-fitting model. In both these models, the CJS model parameters and associated estimates of abundance are all very similar (Table S1, Figure S1), including substantially overlapping 95% CIs. Thus, in this case we did not compute weighted averages (which would be similar).

From the best-fitting CJS model (constant Φ_{1+}; Figure 4), detection probabilities, p, ranged from 0.05 (95% CI 0.03-0.08) in 2020 to 0.20 (95% CI 0.15-0.28) in 2019. The survival of non-transients, Φ_{1+},was 0.97 (95% CI 0.91-0.98) and the proportion of transients, T, ranged from 0.2 (95% CI 0.04-0.64) in 2019 to 0.8 (95% CI 0.69-0.86) in 2018. The number of transient (N_T) and non-transient (N_R) animals showed differing trends, particularly towards the end of the period, with non-transients increasing and transients decreasing considerably from 2018 to 2019 (Figure 4). Total abundance, N_{tot}, ranged from 786 (95% CI 593-964) in 2016 to 1,434 (95% CI 924-1,908) in 2020, with a non-significant increasing linear trend across the period determined by weighted linear regression ($R^2 = 0.28$, $F = 4.43$, $p = 0.07$). Full model results are available at Grove et al. (2022). Abundance estimates from CJS models with alternative specifications of p (time-varying or linked to unmodified effort) showed similar trends and overlapping confidence intervals (Figure S2).

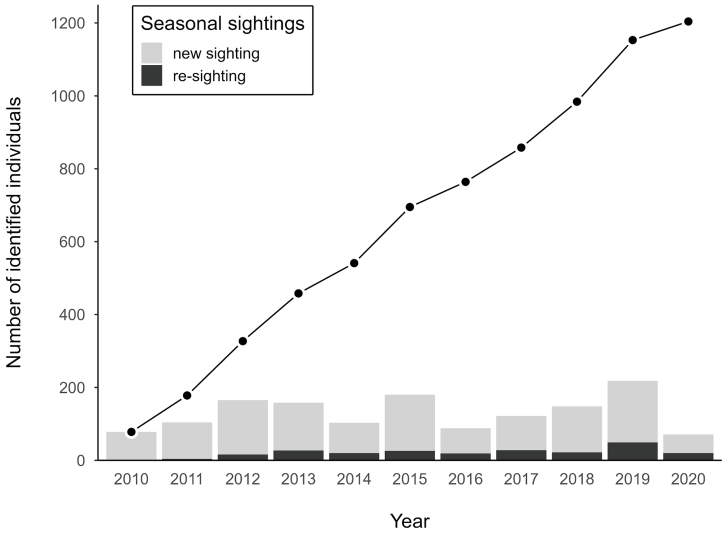

FIGURE 3
Discovery curve of the cumulative number of photo-identified individuals from 2010 to 2020 (points), with bar plots showing the number of new and previously identified (re-sighted) individuals seen each year.

4 Discussion

Abundance estimates for mysticetes are usually derived for feeding and breeding grounds, the endpoints of migration. Here, we provide a ten-year abundance time series at an oceanic, migratory stopover site. According to our best-fitting CR model, up to 1,434 North Atlantic humpback whales (95% CI 924-1,908) visited Bermuda annually between 2011 and 2020, with fluctuations between consecutive years and a slight increase overall. These abundances are comparable with some

TABLE 2 Parameter specification and summary of each candidate CJS model, including AICc score used for model selection.

Apparent survival (Φ)	Detection (p)	Parameters	AICc	ΔAICc	Weight	Deviance
time:transient	**effort**	**13**	**1855.3**	**0**	**0.55**	**300.3**
time + transient	effort	13	1855.9	0.6	0.4	300.9
transient	effort	4	1861	5.8	0.03	324.3
time + transient	time	21	1862.3	7.1	0.02	290.9
time:transient	constant	12	1884.3	29	0	331.3
time + transient	constant	12	1886.5	31.2	0	333.5
transient	constant	3	1890.6	35.4	0	355.9
time:transient	time	20	1891.3	36.1	0	322
constant	effort	3	1921.5	66.3	0	386.8
constant	time	11	1926.1	70.8	0	375.2
transient	time	11	1931	75.7	0	380.1
time	effort	12	1934.1	78.8	0	381.1
time	constant	8	1936.5	81.3	0	391.8
time	time	20	1938.6	83.3	0	369.3
constant	constant	2	1947.7	92.4	0	415

The best-fitting model is in bold. For apparent survival, *transient* denotes that survival is split into two model age classes to account for transient animals; *transient+time* denotes that the two survival values are time-varying; and *time:transient* denotes that Φ_0 is time-varying and Φ_{1+} is constant.

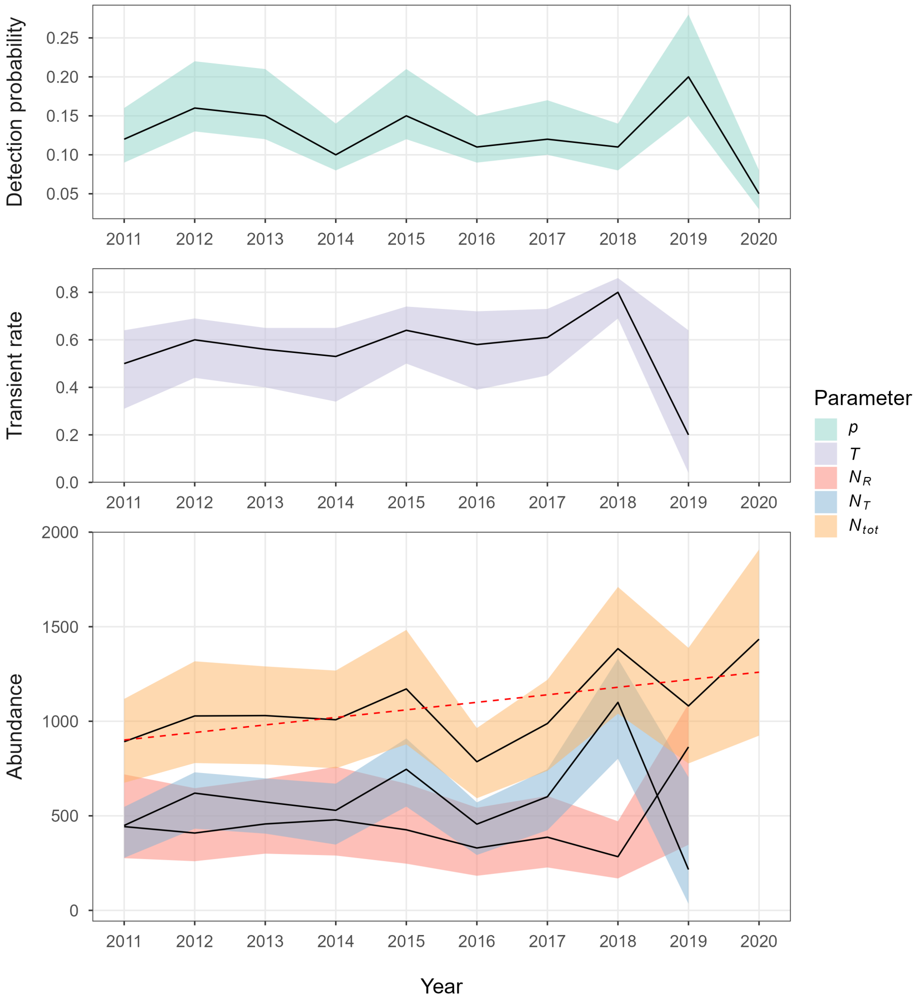

FIGURE 4
Annual estimates for detection probability (p), transient rate (T), abundance of non-transients (N_R), abundance of transients (N_T), and total abundance (N_{tot}), with 95% confidence intervals (CI, shaded regions), for the best-fitting model (effort-dependent p, transient Φ, time-dependent Φ_0, constant Φ_{1+}). The weighted linear trend (non-significant) for total abundance is denoted by the dashed red line.

destination feeding grounds and confirm the contemporary importance of this Marine Mammal Sanctuary as a stopover site. Given the limited protection afforded to humpback whales in Bermudian waters, these estimates should encourage the implementation of area-based management tools to mitigate risks from increasing human activities such as shipping, commercial fishing, and marine wildlife tourism in the waters around Bermuda. Moreover, with Bermuda's migratory connections to both feeding and breeding grounds across the entire North Atlantic, this time series may facilitate population monitoring at a basin scale.

The capture-recapture data set used here is relatively information-poor, with only 13% of whales re-sighted between seasons across the decade. This is unsurprising, given the challenges of monitoring migratory humpback whales around the Bermuda stopover site: inclement weather frequently prevented survey effort, with the number of survey days per December-May season ranging from 13 in 2020 to 38 in 2019 (out of 182 days); Challenger Bank, a major geographical focus of this study, is 15-20 km offshore; and it was often not possible to survey the entire area of interest within a single day. Furthermore, satellite tagging (Kennedy et al., 2014) and historical sightings from whaling ships (Reeves et al., 2004) suggest that North Atlantic humpback whales follow diffuse, poorly defined migration routes from the Caribbean to northern feeding grounds, over several months. The general migration route passing Bermuda may, therefore, be a very wide corridor (hundreds to thousands of kilometers), and the full extent of the stopover site may be greater than the surveyed area, further limiting detectability.

The resulting sparseness of individual sighting histories limits the complexity (number of parameters) of suitable CR models (Lebreton et al., 1992). We derived abundance estimates with a modified CJS model of detection and apparent survival, and a modified Horvitz-Thompson estimator. Using a combination of system knowledge, goodness-of-fit testing, and information criterion, we identified time dependence on detection probabilities, modeled as a function of modified survey effort; as well a considerable time-varying proportion of transients in the population (Figure 4). Strictly, in this study, a transient animal is only present in the study area (waters around Bermuda) for one occasion (season). We acknowledge that sightings data were used twice for model fitting, in terms of capture-recapture data and applying an availability weighting to the catch-effort covariate. However, the latter may be considered a 'long-term average' of monthly sighting rates over the duration of the study period, that is then applied to all years individually. Sensitivity analyses demonstrated that, in practice, the impact of this effort modification on abundance estimates was negligible (Figure S2). Furthermore, a comparable (simple) JSSA model yielded parameter estimates that are broadly similar to those derived from the best-fitting CJS model (Table S2, Figure S3), lending further confidence to our abundance estimates, but the use of JSSA models for these data was strictly limited as a result of associated identifiability issues due to the additional model complexity and parameters to be estimated. Future research could explore the suitability of other CR modeling approaches, such as a recently developed integrated stopover model (Worthington et al., 2019), for this data set.

From the best-fitting CJS model, apparent survival was high (Φ_{1+} = 0.97, 95% CI 0.92-0.98), yet comparable with estimates obtained from other studies, both within and outside the North Atlantic, with such values ranging from 0.9 to 0.99 (Barlow and Clapham, 1997; Mizroch et al., 2004; Ramp et al., 2010; Félix et al., 2011; Hendrix et al., 2012). The modeled proportion of transients, T, was also high between 2011 and 2018 (Figure 4); this was unsurprising, given the high percentage of animals sighted in only one season (87%). However, T declined steeply to 0.2 (95% CI 0.04-0.64) in 2019, which matches a higher inter-seasonal re-sighting rate (Table 1, Figure 3). A transience signal, as defined in this study, has previously been detected at humpback whale breeding grounds (Chero et al., 2020), but, to our knowledge, not feeding grounds or migratory stopovers (Bertulli et al., 2018). Madon et al. (2013) quantified transience using a similar method at a South Pacific breeding ground (New Caledonia), using both photographic and genetic CR. Whilst the values of T were lower from photographic CR (0.19-0.3), values from genetic CR were similar to our results (0.39-0.66; Madon et al., 2013).

The cause of this 'transience' signal and its temporal variability have not been determined for humpback whales (including this study), may not meet the definition of biological transients, and are likely to differ between study systems. The CJS framework is relatively simple and specifies two parameters, p and Φ; therefore, it is unable to distinguish transience from other processes such as temporary emigration. In addition, transience may be confounded with low re-capture probabilities (Genovart and Pradel, 2019), but this is considered unlikely in our model due to the estimation of both low values for p (0.05-0.2) and high transient rates. Alternatively, the 'transience' signal may be driven by several factors. First, animals may not use the same migration route every year. For example, animals may switch breeding or feeding ground and shift migration route in the process (Katona, 1986; Kennedy et al., 2014). However, this is unlikely to be prevalent because exchange rates are very low between breeding grounds (Mattila et al., 1989; Stevick et al., 1999; Stevick et al., 2016) and feeding grounds (Palsbøll et al., 1995; Stevick et al., 2006), particularly between the western and eastern Atlantic. Alternatively, animals may use the same general migration route but be transient in their localized use of Bermuda. Whilst multidecadal route fidelity has been demonstrated for Southwest Atlantic humpback whales (Horton et al., 2020), migratory corridors in the North Atlantic appear to be wide and diffuse between the Caribbean and northern feeding grounds (Reeves et al., 2004; Kennedy et al., 2014). Therefore, animals may follow this corridor annually but be transient in their use of Bermuda as a stopover.

Second, animals may faithfully use the migration route, but not annually. For example, females may take 'rest years' after giving birth, during which they remain in high latitudes and do not visit breeding grounds (Craig et al., 2003). This is supported by a large discrepancy between sex ratios in humpback whale breeding grounds (1.5-2.5 males for every female) and feeding grounds (near to 1:1) around the world (Brown et al., 1995; Craig and Herman, 1997; Chero et al., 2020), including the North Atlantic (Palsbøll et al., 1997; Smith et al., 1999). Furthermore, persistent humpback whale occurrence in North Atlantic feeding grounds in the winter (Kowarski et al., 2018; Martin et al., 2021) suggests that possibly not all animals migrate south every year. This non-annual visitation would constitute temporary 'emigration' from the migration route and not true transience. Temporary emigration can be investigated and characterized using a robust design framework (Pollock, 1982), which structures capture occasions into primary and secondary periods (e.g., Boys et al., 2019). However, this model is more complex, in terms of additional parameters compared to CJS and JSSA, and was unsuitable for our data set, given the low intra- and inter-seasonal re-sighting rates.

To our knowledge, the results presented here provide the most recent abundance time series (2011-2020) for humpback whales within the North Atlantic (Robbins and Pace (2018) provided estimates for the Gulf of Maine up to 2016). From the best-fitting model, annual abundance showed a weak, non-significant, positive linear trend across the decade (Figure 4). Fluctuations in total abundance were sometimes large between years, with a 34% decrease from 2015 to 2016, and a 40% increase from 2018 to 2019 (Figure 4, Table S1). However, our abundance estimates are imprecise, with largely overlapping confidence intervals (Figure 4), so true inter-annual changes may be far smaller. Nevertheless, these fluctuations may have obscured an underlying temporal trend in abundance (Legendre & Legendre, 2012), and are far greater than the maximum plausible rate of increase in population size for humpback whales (11.8% annually; Zerbini et al., 2010). As such, abundance trends at Bermuda alone should not be used as a proxy for variation in the size of the entire North Atlantic population.

Beyond population size, fluctuations may additionally be explained by (1) annual changes in the number of animals undertaking migration (Gabriele et al., 2017; Cartwright et al., 2019); or (2) annual changes in the migration route itself (Zerbini et al., 2016). The potential drivers of migratory changes are unknown for this stopover site but could include variability in oceanographic conditions and, therefore, habitat suitability, either at distant feeding grounds or Bermuda itself. Prey availability at feeding grounds may influence the likelihood of migration to breeding grounds (Frankel et al., 2022), and there is evidence of both foraging and breeding behavior at the Bermuda stopover (Payne and McVay, 1971; Hamilton et al., 1997; Stevenson, 2011; Homfeldt et al., 2022). Studies in Hawai'i, the principal North Pacific breeding ground, found interannual changes of similar magnitude in humpback whale abundance (Frankel et al., 2022), reproductive rates (Cartwright et al., 2019), and male singing activity (Kügler et al., 2020) in response to the North Pacific Marine Heatwave of 2014-2016. Meanwhile, in North Atlantic feeding grounds, a sharp decline in baleen whale abundance in West Greenland was attributed to species range shifts driven by climate-induced changes in pelagic productivity (Heide-Jørgensen and Laidre, 2015; Hansen et al., 2018); and phenological shifts related to increasing water temperature in the Gulf of Maine (Pendleton et al., 2022). In the Azores, a foraging stopover site in the eastern Atlantic, the seasonal timing of baleen whale sightings (including humpback whales) during northbound migration was related to the timing of the regional spring phytoplankton bloom (Visser et al., 2011). Future work should relate local and regional variation in dynamic oceanography to a Bermuda abundance time series, preferably extended to improve statistical power.

Despite these potential fluctuations, our abundance time series suggests that up to 1,434 whales (95% CI 924-1,908) visited the study area each year, with intra-seasonal sightings demonstrating stopover residency (Table 1). Together, these results confirm the use and importance of Bermuda as a migratory stopover for humpback whales. Due to the lack of recent abundance estimates for North Atlantic feeding and breeding grounds (Kennedy and Clapham, 2017), it is challenging to place these results in the context of the wider North Atlantic and comparisons with outdated abundance estimates should be made cautiously. Total abundance in the primary Caribbean breeding ground was estimated to be 10,752 in 1992-93 (CV = 0.068, Stevick et al., 2003), and it is plausible that the growth rate of 3% has continued (Punt et al., 2006). Abundances for Bermuda are smaller than estimates from some feeding areas, including Iceland (>10,000 during 1995-2007; Víkingsson et al., 2015), and Norway (4,695 during 1996-2001; Øien, 2009), but are comparable with other feeding grounds such as the Gulf of Maine (1,317 in 2016; Robbins and Pace, 2018) and eastern Canada (1,903 in 1982; Katona and Beard, 1990). Therefore, whilst Bermuda is apparently visited by a small proportion of the total North Atlantic population, the island may serve as an important migratory stopover site for individual feeding grounds, particularly in western areas (Beaudette et al., 2009). These feeding grounds are treated as distinct management units at a basin scale (Hayes et al., 2019). Further analysis of the migratory connectivity between Bermuda and other parts of North Atlantic will improve our understanding of Bermuda's role within the wider population.

These results are timely, given the recent announcement of a draft Blue Economy Strategy for Bermuda (Bermuda Ocean Prosperity Programme, 2021) and the lack of specific protection afforded to humpback whales in these waters. The declaration of Bermuda's exclusive economic zone as a Marine Mammal Sanctuary in 2012 formed part of a transboundary network of 'protected areas' (Wenzel et al., 2019) but provided no management measures (NOAA and Government of Bermuda, 2012); the inclusion of humpback whales in Bermuda's Protected Species Act of 2003 broadly prohibits disturbance, harassment and injury (Government of Bermuda, 2003; Government of Bermuda, 2016); and existing whale-watching guidelines are voluntary (Department of Environment and Natural Resources, 2017). Moreover, around Bermuda and the wider Sargasso Sea, anthropogenic activity, particularly large vessel traffic, has increased in recent years and this growth is forecast to continue (Roberts, 2011; Halpern et al., 2015; Širović et al., 2016). As a result, ocean ambient sound is now dominated by shipping in Bermudian waters (Širović et al., 2016). Combined with possible increases in commercial fishing activity and whale-watching tourism (Bermuda Tourism Authority, 2019), any resulting mortality or disturbance may impact whales across the North Atlantic, particularly western feeding grounds and northern Caribbean breeding grounds. Our time series should encourage consideration of area-based management tools to mitigate risks from human activities around Bermuda, such as PSSAs and marine protected areas, as well as a review of existing whale-watching guidelines (Department of Environment and Natural Resources, 2017). Abundance estimates can be combined with current acoustic monitoring (Homfeldt et al., 2022) and behavioral observation to provide evidence of spatiotemporal patterns in habitat use to guide specific policies (Minton et al., 2011; Rossi-Santos, 2015; Stepanuk et al., 2021). Moreover, such evidence may determine whether Bermuda constitutes critical habitat, defined as areas that are regularly used by a population to perform essential tasks for survival and reproduction (Hoyt, 2011), and may require special consideration for species conservation (Endangered Species Act, 1973).

Beyond Bermuda, the large sightings database (1,204 whales) and ten-year abundance time series may facilitate wider population monitoring on a basin scale (Moore, 2008; Hazen et al., 2019), in conjunction with comparable time series in breeding and feeding grounds (e.g., Robbins and Pace, 2018). Due to Bermuda's unique migratory connections (Katona, 1986) and its role as a stopover site (Payne and McVay, 1971; Stevenson, 2011), changes in abundance around Bermuda may reflect shifts in migratory patterns and population dynamics in distant feeding or breeding grounds across the North Atlantic, and provide extra information on population-level processes. Therefore, we encourage the construction of contemporary, separate abundance time series in other parts of the North Atlantic (especially feeding and breeding grounds), for example, by using existing photo-identification databases, e.g., Happywhale (https://happywhale.com) and the North Atlantic Humpback Whale Catalogue (Katona and Beard, 1990). This aligns with the IWC's recommendation for a range-wide assessment of abundance to replace outdated estimates (International Whaling Commission, 2019). Furthermore, humpback whales are a cosmopolitan marine predator and sensitive to ecosystem change (Cartwright et al., 2019). Better understanding basin-scale population processes, including migratory patterns over space and time, will facilitate assessing the response to environmental change, which may be used as a sentinel for ecosystem monitoring (Simmons et al., 2017; Miloslavich et al., 2018).

Using a capture-recapture framework, guided by goodness-of-fit-testing, we provide an abundance time series for a baleen whale migratory stopover site. Accounting for heterogeneity in survival and detection, we generate robust abundance estimates across a decade and demonstrate the importance of Bermuda for migrating North Atlantic humpback whales. Future marine spatial planning around Bermuda should consider the potential impact that growing anthropogenic pressures, such as vessel traffic and marine wildlife tourism, may have on thousands of humpback whales within potential critical habitat. Furthermore, with Bermuda's migratory connections to feeding and breeding grounds, this time series may facilitate monitoring of population-level processes across the North Atlantic. More generally, we encourage the investigation of whale abundance across a species' range as a potential sentinel for basin-scale ecosystem change. As marine environmental change accelerates across the North Atlantic, sustained photo-identification survey effort in Bermudian waters should be supported to extend this time series.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: The model outputs generated from this study are available at: https://doi.pangaea.de/10.1594/PANGAEA.945442.

Ethics statement

Ethical review and approval was not required for the animal study because Humpback whales were photographed from a vessel, which did not require any contact or close approach. Nevertheless, WhalesBermuda (Andrew Stevenson) obtained an annual research from the Department of Environmental and Natural Resources, Government of Bermuda, for each year of the study.

Author contributions

L-AH conceptualized the study and acquired funding for analysis and submission. AS conducted all fieldwork and provided resources for data collection. TG and RK designed the study methodology. AS and TG conducted image quality filtering and photo-identification. TG subsequently processed the data, performed analyses, created graphics and led manuscript writing. L-AH and RK supervised the project. RK, AS, and L-AH provided regular feedback; and contributed to and reviewed the manuscript. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2022.971801/full#supplementary-material

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