Abundance estimates of humpback whales (*Megaptera novaeangliae*) in Irish coastal waters using mark-recapture and citizen science

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ABSTRACT

Abundance estimates are crucial for implementing effective conservation measures for large marine megafauna – particularly cetaceans. When combined with robust research methodologies, citizen science can provide a very useful tool to monitor large baleen whale populations, especially given their migratory nature, with individuals covering large areas typically exceeding the capacity of single research teams. The Irish Whale and Dolphin Group has been collecting humpback whale photo-ID data in the inshore waters of Ireland since 1999. The Group curates a catalogue that contained 120 individual humpback whales up to 2022. Most of these data were obtained through citizen science and the catalogue was built following robust methodologies and strict data-quality protocols. We used this photo-ID catalogue to derive the first comprehensive abundance estimates for the species in Irish waters using mark-recapture modelling techniques. We applied two approaches: (1) open population maximum likelihood mark-recapture models based on the POPAN formulation; (2) a multi-site mark-recapture model selection framework based on Bayesian inference. The first method yielded a humpback whale superpopulation size of 154 ± 9 (95% CI = 138–172, CV = 0.06) between 1999–2022, with annual abundance ranging between 2 ± 1 and 77 ± 8 individuals. The second approach provided annual abundance estimates from 3 ± 2 to 76 ± 11 for the same period. This study supports the idea of an increased presence of humpback whales in inshore Irish waters, especially during the last decade. Despite this increase, results also highlight the apparently very small size of the North Atlantic humpback whale subgroup occurring in the inshore waters of Ireland.

KEYWORDS: HUMPBACK WHALE; ABUNDANCE; POPULATION SIZE; MARK-RECAPTURE; CITIZEN SCIENCE; CONSERVATION; IRELAND

INTRODUCTION

The humpback whale (*Megaptera novaeangliae*) is a cosmopolitan species present in all ocean basins. This species generally undertakes long seasonal migrations between low-latitude breeding grounds and high-latitude feeding areas in both hemispheres (Mittermeier and Wilson, 2014). In the North Atlantic Ocean, the breeding season occurs during winter months in the West Indies, including Silver and Navidad Banks in Dominican Republic, Guadeloupe (Clapham and Mead, 1999; Stevick *et al.*, 1999a; 2016; 2018; Whitehead and Moore, 1982), and in the Cabo Verde archipelago, c.500km off the coast of Senegal (West Africa), particularly around the island of Boa Vista (Berrow *et al.*, 2021; Punt *et al.*, 2006; Reiner *et al.*, 1996; Ryan *et al.*, 2013a; 2014; Wenzel *et al.*, 2009;

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2020). Humpback whales are also known to regularly visit high-latitude feeding grounds in the western North Atlantic (US, Gulf of Maine; Eastern Canada, including Nova Scotia, Labrador, Newfoundland and Gulf of Saint Lawrence and West Greenland) and eastern North Atlantic (Iceland, Norway and Svalbard) during the summer (Katona and Beard, 1990; Larsen *et al.*, 1996; Palsbøll *et al.*, 1997; Smith *et al.*, 1999; Stevick *et al.*, 1998; 1999b).

Individual humpback whales can be recognised using natural markings and pigmentation patterns present on their bodies, primarily those on the ventral side of the fluke (tail) and secondarily on the dorsal fin (Katona and Whitehead, 1981). Hence, photo-identification techniques can be used to record the presence of individual whales, providing essential information that can be used to track movements, estimate population size, residency patterns and site fidelity and forms an integral part of humpback whale population monitoring (Berrow *et al.*, 2021; Constantine *et al.*, 2012; Félix *et al.*, 2011; Punt *et al.*, 2006; Ryan *et al.*, 2014; Smith *et al.*, 1999; Wenzel *et al.*, 2020). Understanding population size and structure as well as movement patterns is essential for the conservation of large whales, like the humpback, as they still face many anthropogenic threats that can jeopardise the health and recovery of their populations, especially those that are particularly small or isolated. Incidental interactions with the fishing industry (entanglements) or maritime traffic (ship strikes), chemical or acoustic pollution, habitat degradation, food scarcity and uncontrolled pressure from the ecotourism industry are just a few examples of these threats (Thomas *et al*., 2016). In the case of migratory species like the humpback whale, the establishment of long-term population monitoring programmes must go hand in hand with collaboration and integration of monitoring programmes carried out by different research groups throughout the distribution range to gain a clearer understanding of their structure, dynamics and health. A good example is the North Atlantic Humpback Whale Catalogue (NAHWC, College of the Atlantic, Bar Harbor, ME, USA), the oldest and largest collection of individual humpback whale photo-ID data available in the North Atlantic. This catalogue was first set up in 1976 as a collaborative photo-ID catalogue encompassing the entire North Atlantic Ocean. Today, the NAHWC has received photographs from more than 750 international contributors and contains more than 11,000 individual animals (L. Jones, NAHWC, pers. comm.). There are also a number of regional humpback whale photo-ID databases throughout the North Atlantic Ocean, such as the ÍSland Megaptera Novaeangliae (ISMN) catalogue curated by the Marine and Freshwater Research Institute (MFRI, Hafnarfjörður, Iceland), the North Norwegian Humpback Whale Catalogue (NNHWC) and the Gulf of Maine Humpback Whale Catalogue (Centre for Coastal Studies). In Ireland, the Irish Whale and Dolphin Group (IWDG) has been collecting baleen whale photo-ID data since 1999 under the Whale Track Ireland project, including humpback whales. Thanks to this data collection scheme, which is predominantly based on citizen science, the IWDG catalogue contained 120 individual humpback whales as of December 2022, with most of them regularly sighted off the coasts of Counties Kerry and Cork in southwest Ireland (Berrow *et al.*, 2021; Berrow and Whooley, 2022; Ryan *et al.*, 2016).

During the first quarter of the 20th Century, there were substantial whaling operations in Ireland based on the Mullet Peninsula, Co. Mayo. During this period, 125 blue whales (*Balaenoptera musculus*) and 600 fin whales (*Balaenoptera physalus*) were captured, whereas only six humpback whales were reported landed (Fairley, 1981). This suggests humpback whales were quite rare in Ireland during this period. Sightings of humpback whales were still uncommon during the second half of the 20th Century and even as recently as the first decade of the 21st century, with only modest numbers reported each year (Berrow *et al.*, 2010). This trend changed dramatically during the 2010s, particularly in 2015, when the number of humpback whales in the IWDG catalogue increased by 120%, including 36 new individuals, many of them sighted off the southwest coast of Ireland (Berrow and Whooley, 2022). Since then, the number of annual sightings, newly photo-identified individuals and resighting rates have been sufficiently and consistently high. It is possible that part of this increase may have been due to intensified observation effort, driven in turn by the presence of this species near the coast where the animals are easily accessible, together with the expanded use of digital and social media, especially during the last decade. However, it should be noted that under a similar search effort since 1999, information collected by the IWDG on the presence of other baleen whales in Ireland's inshore waters, such as the common minke whale (*Balaenoptera acutorostrata*) and fin whale, indicates that the presence of the latter species in the same area was historically higher than the humpback whale, whereas humpback whale sightings in this area are now almost as frequent as fin whale sightings (IWDG, unpub. data), suggesting that the presence of this species in these inshore waters has indeed increased over the last two decades. There is also evidence that the coastal waters of Ireland are not just a mere stopover along the species' migration routes in the NE Atlantic but provides feeding opportunities as they are usually observed feeding on small schooling fish in different coastal areas around Ireland (Berrow *et al*., 2021). In addition, an average minimum residency time of 48 days has been reported in Ireland, with one individual being observed in the area for up to 186 days within the same year (Berrow and Whooley, 2022). Connectivity to other areas in the North Atlantic is also well supported as some humpback whales reported in Ireland have been photographed on feeding grounds off Iceland and Norway, as well as in breeding grounds off Dominican Republic in the Caribbean and Boa Vista in Cabo Verde (Berrow *et al.*, 2021; IWDG, unpub. data).

Photo-ID data can also be used to create sighting histories of individual whales identified in a given area during a given period of time, and thus used to estimate population parameters, such as abundance or survival rates using mark-recapture modelling (Hammond, 1986; 2010; 2018; Hammond *et al.*, 2021). Mark-recapture abundance estimation is a well-established methodology and has been widely used to monitor a range of marine mammal populations all over the world, including bottlenose dolphins (Arso Civil *et al.*, 2019; Balmer *et al.*, 2008; Berrow *et al.*, 2012a; Blázquez *et al.*, 2020; Read *et al.*, 2003), killer whales (Beck *et al.*, 2014; Durban *et al.*, 2010; Kuningas *et al.*, 2014), humpback whales (Calambokidis and Barlow, 2004; Constantine *et al.*, 2012; Félix *et al.*, 2011; Ryan *et al.*, 2014; Smith *et al.*, 1999; Stevick *et al.*, 2003; Wenzel *et al.*, 2020), fin whales (Ramp *et al.*, 2014) and pinnipeds (Baker *et al.*, 2016; Forcada and Aguilar, 2000; Gerondeau *et al.*, 2007). There are no previously published humpback whale abundance estimates in inshore Irish waters and thus, the main objective of this study was to present the first abundance estimates for the species in this area using a +20y humpback whale photo-ID catalogue curated by the IWDG and mark-recapture modelling techniques. We used two approaches: one based on open population mark-recapture analysis; a second based on a closed population multi-site mark-recapture model selection framework. This allowed us to test if dissimilar modelling methodologies provided consistent estimates which would indicate robust results.

MATERIALS AND METHODS

Photo-identification data collection and analysis

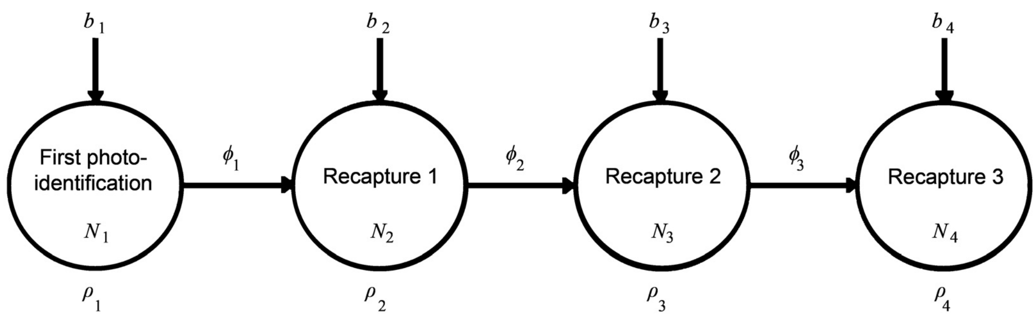
Since 1999, the Irish Whale and Dolphin Group (IWDG) has collected sightings and photo-ID data on humpback whales in Irish waters within the framework of the Whale Track Ireland project. The project's data collection is strongly supported by citizen science, which means data are mostly opportunistic, obtained from whale watching vessels, private boats and members of the public interested in contributing to the project. Usually, the images and associated metadata (coordinates, time, date, observers, animal's behaviour, etc.) are submitted to the IWDG via the IWDG website or through a dedicated smartphone application. The IWDG validates each sighting record and match images where possible to the IWDG Humpback Whale Photo-ID Catalogue, after which the data are added to an Excel spreadsheet. Photographs are included in the catalogue following strict and robust methodologies to ensure data quality. More details about photographic data handling and catalogue management can be found in Whooley *et al.* (2011) and Ryan *et al.* (2016). For humpback whales, where photographs of any part of the body (particularly fluke and dorsal fin) that enable the identification of individual animals are available, these are cross-matched and added to the catalogue. If no match is possible, a new individual is added to the catalogue, although this decision may be reassessed if better pictures are obtained of the same individual in future. This catalogue of individual humpback whales is also shared with the NAHWC. For mark-recapture analyses, individual sighting histories were derived from the catalogue using both fluke and dorsal fin images. Matching mistakes were highly unlikely in our dataset, since a large majority of the animals identified (c.80%) had good quality photographs of their distinctive fluke pigmentation patterns and dorsal fins (both right and left sides) (Blázquez *et al*., 2020; Friday *et al*., 2000; 2008; Yoshizaki *et al.*, 2009). Observation effort data associated with this photo-ID catalogue were not available.

Open population mark-recapture analysis

We created a sighting history that included all the 120 individual humpback whales photo-identified in Ireland between 1999 and 2022. Year of sighting was used as capture occasion. This sighting history consisted of a binary matrix in which rows represented a single humpback whale sighting history and columns represented years.

Here, 1 means a given whale was sighted in a given year, whereas 0 means there was no sighting of that individual in a given year. No other covariates – such as sex or age class – were included as there was insufficient information available for the vast majority (> 90%) of animals included in the catalogue.

The open population mark-recapture analysis was performed in the software MARK, version 6.2 (White and Burnham, 1999). MARK applies maximum likelihood models to estimate population parameters such as abundance and includes several types of parameterisations with different assumptions (Cooch and White, 2014). Given the length of the study period (22 years) and the inter-capture intervals (one year), closure of the population could not be assumed since animals may enter (via birth/immigration) or leave (death/emigration) the study area in such periods of time (Hammond, 2018). Therefore, we chose the open population POPAN parameterisation (Schwarz and Arnason, 1996; 2006) available in MARK (Figure 1). This parameterisation, which is a development of the classic Jolly-Seber models (Jolly, 1965; Seber, 1965), includes the parameter *N*, or super-population size, which can be expressed as the estimated total number of animals available for capture during the whole length of the study (Crosbie and Manly, 1985; Nichols, 2005). It also includes three other parameters: ϕ (apparent survival rate), *p* (probability of capture) and *b* (or *PENT,* the probability of entrance of an animal into the study area via birth and immigration). These three parameters can be held constant (.) or allowed to vary over time (*t*). See Cooch and White (2014) for more details.



ϕ_i Probability of a whale surviving between occasion *i* and *i* + 1

p_i Probability of capture at occasion *i*

b_i Probability of a whale entering the population from the super-population at occasion *i*

N_i Population size at occasion *i*

Figure 1: Conceptual representation of the open population Jolly-Seber model under the POPAN parameterisation.

As for other Jolly-Seber models, the POPAN parameterisation involves a series of assumptions that should not be violated in order to avoid biased estimates of the parameters of interest. These assumptions are:

1. Unmarked (non-photo-identified) animals have the same probability of capture as marked (photo-identified) animals in the population;
2. Animals retain their marks throughout the length of the experiment;
3. Marks are unmistakable and correctly noted at each sampling occasion;
4. Apparent survival probabilities are the same for all animals between each pair of sampling occasions;
5. Study area is constant throughout the whole study.

The first step when fitting open population models using the POPAN formulation was running the saturated, fully time-dependent model *ϕ(t), p(t), b(t)* (Cooch and White, 2014). Then, the goodness-of-fit of this model to the data was tested using TEST 2 and TEST 3 of the programme RELEASE available in MARK. These are Chi-Square tests used to validate assumptions of equal catchability (TEST 2) and equal apparent survival (TEST 3). More specifically, TEST 2 evaluates if the recapture of an animal seen at occasion *i*, but not captured at *i + 1*, depends or not on whether it was captured at occasion *i*. TEST 3 includes two components: TEST 3.SR and TEST 3.Sm. The first component tests if the probability that an individual (known to be alive at occasion *i*) to be seen again depends on whether it was captured at or before occasion *i*. Component TEST 3.Sm addresses if – among recaptured individuals (seen again) – when they are recaptured depends or not on whether they were captured at occasion *i*. More details about these tests are available in Cooch and White (2014). Assumptions 2 and 3 were probably met thanks to photo-ID data quality thresholds and catalogue management.

Further steps involved running other models using all possible combinations of time-dependent or constant parameters of the POPAN formulation. Thus, eight models were fitted in total (Table 2). These models were ranked according to the resulting Akaike Information Criterion value and the model with the lowest AIC value was selected as the most appropriate one (Akaike, 1987).

Bayesian multisite mark-recapture approach

As discussed previously, Jolly-Seber mark-recapture models such as the POPAN parameterisation rely on a series of assumptions that should not be violated in order to yield unbiased estimates of the parameters of interest. Given that most of the data were gathered under a citizen science scheme, not following standardised survey protocols or sampling over well-defined areas, it might be expected that some violations have occurred. Our data were mainly provided by citizen scientists with a clear geographic bias (Figure 2). Over 80% of sightings occurred off counties Kerry and Cork, although humpback whales have also been recorded in other areas around Ireland (Figure 2). Furthermore, the lack of a standardised sampling design conflicts with Assumption 5 (constant study area) which means population size estimates may be negatively biased by the changing size of the study area throughout the study period, since, in those years when effort was lower, a proportion of the individuals present in the area may have remained unavailable for capture.

Due to these facts, we wanted to compare the abundance estimate yielded by maximum likelihood mark-recapture models with an estimate derived from an alternative estimation method. Durban *et al.* (2005) presented an abundance estimation method based on Bayesian model selection that was designed to handle data obtained beyond a single defined study area (multi-site experiment) and models the dependence between

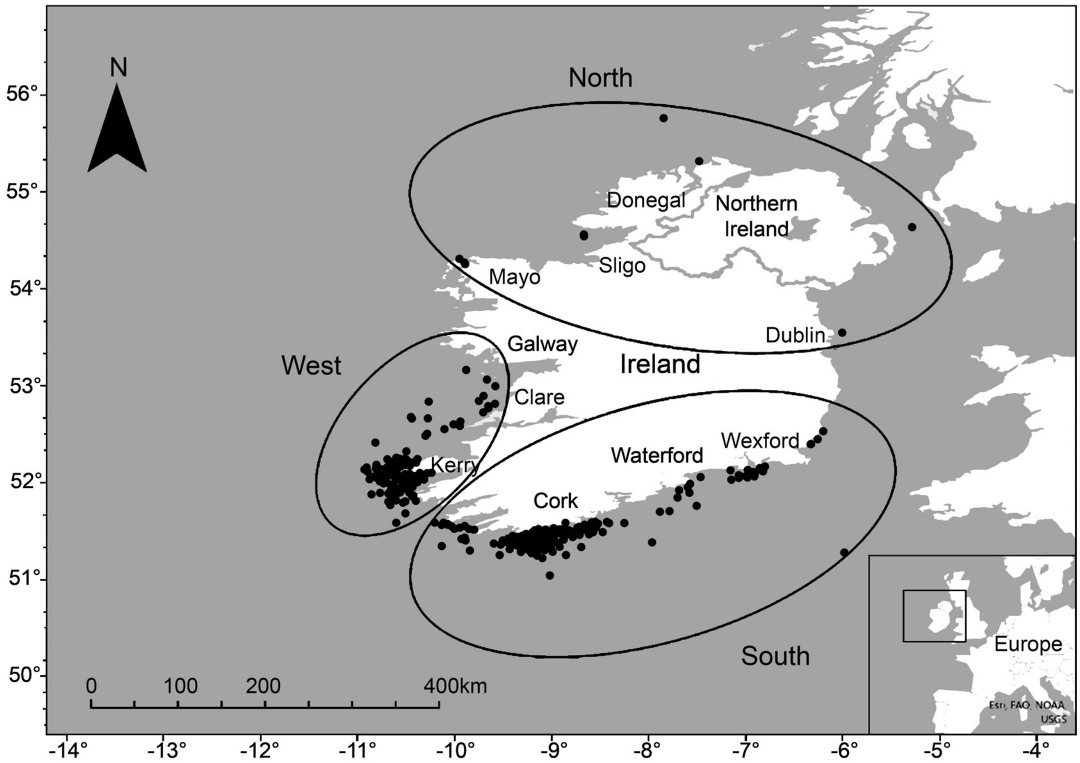


Figure 2: Photo-identified humpback whale sightings in Ireland between 1999–2022. Ellipses indicate Bayesian multisite mark-recapture sampling areas (see Tables 1 and 2).

areas in order to account for heterogenous capture probabilities across individuals (Nykänen *et al.*, 2020). This multi-site modelling approach has been successfully applied in other cetacean population studies (Beck *et al.*, 2014; Cheney *et al.*, 2013; Durban *et al.*, 2005; Durban *et al.*, 2010; Fearnbach *et al.*, 2012; Moore and Barlow, 2011; Nykänen *et al.*, 2020). The method was originally designed to address the problematic capture heterogeneity induced by the movement of individuals beyond single sampling areas or individual movement preferences which violates typical assumptions of mark-recapture models such as POPAN. This approach means we can combine data gathered at distant geographical sampling areas within a wider distribution range of the population whose size is to be estimated, so the whole population range is not required to be consistently surveyed. Another characteristic of this method is that data do not need to have been obtained following the same sampling protocols in each sampling site, nor requires pre-defined sampling designs. This is particularly relevant when the survey protocol was not designed to suit a specific model, as when data were mostly collected in an opportunistic manner.

Following Durban *et al.* (2005) and subsequent studies by Cheney *et al.* (2013) and Nykänen *et al.* (2020), our study area was divided *post hoc* into three sampling regions that encompassed sighting locations of all individual humpback whales identified between 1999 and 2022 (Figure 2). These three regions were designated as West (Kerry, Clare and Galway), South (Cork, Waterford and Wexford) and North (Mayo, Donegal and Dublin and all Northern Ireland). Using these three regions, we built contingency tables of sightings based on the presence or absence of whales within each discrete category formed by the combination of the three regions (Table 1). The overlap of individual whales between sites represents recaptures in a mark-recapture framework and the lists of each region represent sampling occasions defined by space instead of time (Durban *et al*., 2005). In contrast with POPAN models, this multi-site mark-recapture approach assumes the population is closed: i.e., no individuals are gained or lost during the study period. Humpback whale counts were therefore done within each year to derive annual abundance estimates since population closure can be assumed as valid in such a time period.

These matrices were then introduced into WinBUGS Version 1.4.3 to perform the Bayesian estimation analysis (Lunn *et al*., 2000). The software was fitted to assume the cell counts (n_i) of the contingency matrix as independent Poisson random variables with mean μ_i (Tables 1 and 2). The logarithm of the Poisson mean (μ_i) of

Table 1

Example of the contingency table of the counts (n_i) of humpback whales per sampling area combination.
1 = present, –1 = absent. N = abundance estimate.

Cell (i)	Counts (n_i)	West (x_{i1})	South (x_{i2})	North (x_{i3})
1	n_1	1	1	1
2	n_2	1	1	–1
3	n_3	1	–1	1
4	n_4	–1	1	1
5	n_5	1	–1	–1
6	n_6	–1	1	–1
7	n_7	–1	–1	1
8	n_8	–1	–1	–1
	$N = \sum n_i$			

Table 2

Contingency table of the counts of humpback whales per sampling area combination within each year of the study period.
? = number of animals that were not present in any of the study regions. Dashes indicate no individual was available for a given category.

West	South	North	1999	2001	2002	2003	2004	2005	2007	2008	2009	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021	2022
1	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
1	1	–1	–	–	–	–	–	–	–	–	–	–	1	1	–	8	5	5	11	11	12	5	1
1	–1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	3
–1	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
1	–1	–1	–	–	–	–	1	–	–	–	1	3	2	9	9	32	26	12	10	13	18	14	13
–1	1	–1	2	2	1	1	5	1	2	10	1	2	7	1	1	5	5	13	14	12	12	15	4
–1	–1	1	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	1	–	1	–
–1	–1	–1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

those counts was modelled as an additive regression function of the effect of each study region and their possible interactions, obtaining eight possible candidate log-linear models (Table 3). The saturated model is formulated as following:

$$\log(\mu_i) = \beta_0 x_{i0} + \beta_1 x_{i1} + \beta_2 x_{i2} + \beta_3 x_{i3} + \delta_1 \beta_4 x_{i1} x_{i2} + \delta_2 \beta_5 x_{i1} x_{i3} + \delta_3 \beta_6 x_{i2} x_{i3}$$

Where x_{i0} is 1 for all *i*, and β_0 is an overall mean of the counts on the log-scale. β_1, β_2 and β_3 represent the effect of each study region on β_0. Elements x_{i1}, x_{i2} and x_{i3} are indicators that take values 1 or –1 according to each category presented in the contingency table. x_{i1} was the indicator of the West sampling region and x_{i2}, x_{i3} were the indicators of the South and North areas, respectively. The last three terms of this equation describe the possible two-way interaction effects, with β_4, β_5 and β_6 indicating the strength and direction of effects of pairs of study regions. These interactions were included or excluded to build all the candidate models by the addition of three binary indicator variables δ_1, δ_2 and δ_3 in the interaction terms. These indicator variables take values 1 or 0 according to Table 3. Bayesian inference was applied to estimate model parameters and their associated uncertainties. Prior probability distributions of model parameters were assigned as in Durban *et al.* (2005). In addition, we used the number of identified humpbacks as of December 2022 (120) as a realistic maximum value to the prior for abundance. Once priors were specified, the estimation was performed using the Gibbs sampling Markov Chain Monte Carlo (MCMC) method (Casella and George, 1992), implemented in WinBUGS with 100,000 burn-ins followed by 100,000 iterations (Cheney *et al.*, 2013; Durban *et al.*, 2005; Nykänen *et al.,* 2020). This method produced a sequence of sampled values from the posterior distribution of log-linear parameters and derived population size estimates for each of the eight candidate models. Each model likelihood was estimated in turn before the final population size estimate was model averaged using these likelihood values as weights (Table 6).

Table 3

Candidate multisite mark-recapture model selection process and meaning.

δ_1	δ_2	δ_3	Candidate model selected	Meaning
0	0	0	M1 $\log(\mu_i) = \beta_0 x_{i0} + \beta_1 x_{i1} + \beta_2 x_{i2} + \beta_3 x_{i3}$	No interaction
1	0	0	M2 $\log(\mu_i) = \beta_0 x_{i0} + \beta_1 x_{i1} + \beta_2 x_{i2} + \beta_3 x_{i3} + \delta_1 \beta_4 x_{i1} x_{i2}$	West:South interaction only
0	1	0	M3 $\log(\mu_i) = \beta_0 x_{i0} + \beta_1 x_{i1} + \beta_2 x_{i2} + \beta_3 x_{i3} + \delta_2 \beta_5 x_{i1} x_{i3}$	West:North interaction only
0	0	1	M4 $\log(\mu_i) = \beta_0 x_{i0} + \beta_1 x_{i1} + \beta_2 x_{i2} + \beta_3 x_{i3} + \delta_3 \beta_6 x_{i2} x_{i3}$	South:North interaction only
1	1	0	M5 $\log(\mu_i) = \beta_0 x_{i0} + \beta_1 x_{i1} + \beta_2 x_{i2} + \beta_3 x_{i3} + \delta_1 \beta_4 x_{i1} x_{i2} + \delta_2 \beta_5 x_{i1} x_{i3}$	West:South + West:North interactions
1	0	1	M6 $\log(\mu_i) = \beta_0 x_{i0} + \beta_1 x_{i1} + \beta_2 x_{i2} + \beta_3 x_{i3} + \delta_1 \beta_4 x_{i1} x_{i2} + \delta_3 \beta_6 x_{i2} x_{i3}$	West:South + South:North interactions
0	1	1	M7 $\log(\mu_i) = \beta_0 x_{i0} + \beta_1 x_{i1} + \beta_2 x_{i2} + \beta_3 x_{i3} + \delta_2 \beta_5 x_{i1} x_{i3} + \delta_3 \beta_6 x_{i2} x_{i3}$	West:North + South:North interactions
1	1	1	M8 $\log(\mu_i) = \beta_0 x_{i0} + \beta_1 x_{i1} + \beta_2 x_{i2} + \beta_3 x_{i3} + \delta_1 \beta_4 x_{i1} x_{i2} + \delta_2 \beta_5 x_{i1} x_{i3} + \delta_3 \beta_6 x_{i2} x_{i3}$	West:South + West:North + South:North interactions

RESULTS

Photo-identification data analysis

Between 1999–2022, a total of 1,030 sightings of individual humpback whales were made with images suitable for photo-identification. This resulted in a total of 120 individual humpback whales being identified and included in the IWDG Irish Humpback Whale Photo-ID catalogue. The catalogue includes images of 92 (77%) humpback whale flukes as well as images of the right and left sides of the dorsal fin. Fifteen (12.5%) animals were missing images of their fluke, whereas 12 animals with identified flukes (10%) lacked any sides of the dorsal fin. Two (1.7%) whales were included using photographs of only one side of the dorsal fin.

Resighting rates were high and consistent, reaching over 80% in some years, while the mean resighting rate over the period 1999 to 2020 was 63% (Berrow and Whooley, 2022). Site fidelity was also relatively high. Slightly less than one-half of all whales in the catalogue (54, 45%) were sighted in only one year (Figure 3B), whereas some individuals (e.g., HBIRL003 and HBIRL017) have been resighted in 17 and 12 different years, respectively. Most sightings (773, 75%) occurred during late spring and summer months, between May and September, reaching a peak in August with 197 individual sightings between 1999 -2022. On the other hand, winter months produced fewer humpback whale sightings with a minimum of only two individual sightings obtained in March

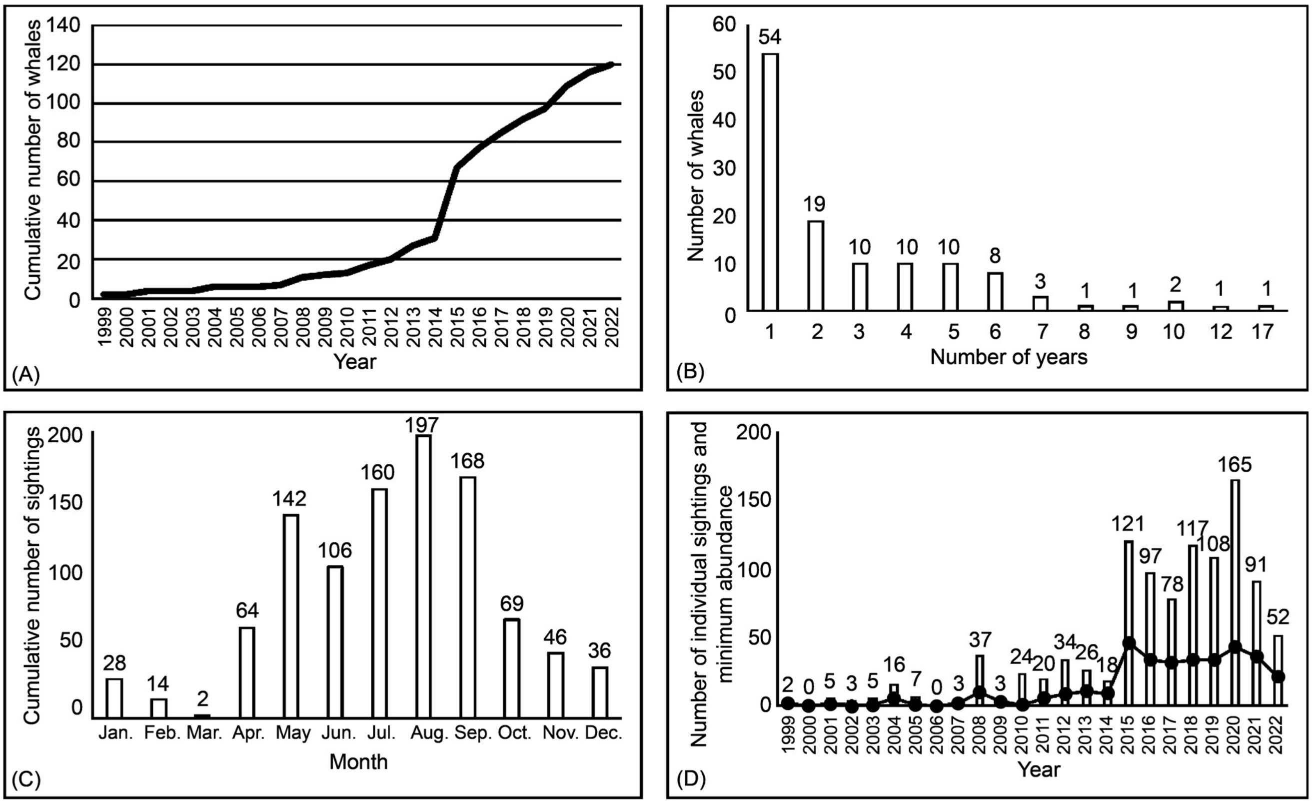


Figure 3: Panels show data for Ireland between 1999–2022: A) discovery curve of the total number of photo-identified humpback whales; B) number of years different humpback whales have been sighted; C) monthly total number of individual humpback whales; D) number of humpback whale sightings (white bars and numbers) and number of individuals photo-identified (black dots).

(Figure 3C). No whales were photo-identified in 2000 and 2006. Only 30 individual whales were included in the catalogue prior to 2014. In contrast, 90 new individuals were photo-identified between 2015–2022, an increase of 300% compared to the previous 15 years. A discovery curve presenting the cumulative number of identifications (Figure 3A) did not reach a clear asymptote, suggesting there are still new individuals to identify in the study area. The number of identified individuals ranged between 0 animals identified in 2000 and 2006 and 46 individuals identified in 2015. The highest number of sightings and individual whale IDs occurred in 2015 and 2020. In addition, 2022 produced the lowest number of sightings and whale IDs since 2014 (Figure 3D).

From a geographic point of view, most sightings (895, 87%) occurred in only two areas off west County Cork (418, 40.6%) and west County Kerry (477, 46.3%), along the south and south-west coasts of Ireland (Figure 2).

Open population maximum likelihood mark-recapture analysis

A total of eight models were fitted to the humpback whale sighting data. Goodness-of-fit tests were performed for the fully time-dependent model $\phi(t)$, $p(t)$, $b(t)$. TEST 2 + TEST 3 did not indicate any lack of fit ($\hat{c}$ = 1.040; *p-value* = 0.40). Separately, neither TEST 2 (equal catchability test) nor TEST 3 (equal apparent survival test) indicated lack of fit (TEST 2: $\hat{c}$ = 0.69; *p-value* = 0.81. TEST 3: $\hat{c}$ = 1.28; *p-value* = 0.16). However, it is worth noting that, in a deeper examination of TEST 3, component TEST 3.SR manifested some possible effect of transient animals ($\hat{c}$ = 2.08; *p-value* = 0.01); i.e., those animals only seen in a single year. Since this effect was weak enough not to affect overall tests, no correction of the AIC model ranking was undertaken and assumptions of equal probability of capture and apparent survival across individuals were considered fulfilled (Reisinger and Karczmarski, 2010).

According to the AIC model ranking (Table 2), the model that best fitted the data was $\phi(.)$, $p(t)$, $b(t)$. For this model, apparent survival probability (ϕ) was constant, whereas probabilities of capture (p) and entry (b) were allowed to vary annually. This model yielded a super-population size (the number of humpback whales that have ever been present in Irish waters) of 154 ± 9 animals (95% CI = 138–172, CV = 0.06). Apparent survival probability

Table 4

Maximum likelihood model selection criteria and abundance estimates of humpback whale in Irish waters between 1999 and 2022 using the open population POPAN formulation. AIC = Akaike Information Criterion, NP = number of parameters, N = super-population size, SE = standard error, CV = coefficient of variation. ϕ = apparent survival probability, p = capture probability, b = probability of entry. (t) = time-dependent parameter. (.) = constant parameter.

	Model selection criteria					Super-population size estimates			
Model	AIC	ΔAIC	AIC weight	NP	Deviance	N	SE	95% CI	CV
$\phi(.),p(t),b(t)$	939.268	0	0.99620	45	−98.662	154	9	138–172	0.06
$\phi(.),p(.),b(t)$	950.431	11.162	0.00375	24	−31.941	148	7	136–161	0.05
$\phi(t),p(.),b(t)$	959.006	19.738	0	44	−51.341	146	7	133–161	0.05
$\phi(t),p(t),b(t)$	977.222	37.954	0	65	−116.333	145	7	128–154	0.05
$\phi(t),p(t),b(.)$	3,085.251	2,145.983	0	45	2,079.712	625	58	444–672	0.09
$\phi(.),p(.),b(.)$	3,516.608	2,577.340	0	4	2,566.443	801	65	684–938	0.08
$\phi(t),p(.),b(.)$	6,010.473	5,071.206	0	24	5,023.582	340	57	245–472	0.18
$\phi(.),p(t),b(.)$	–	–	–	25	–	No numerical convergence			

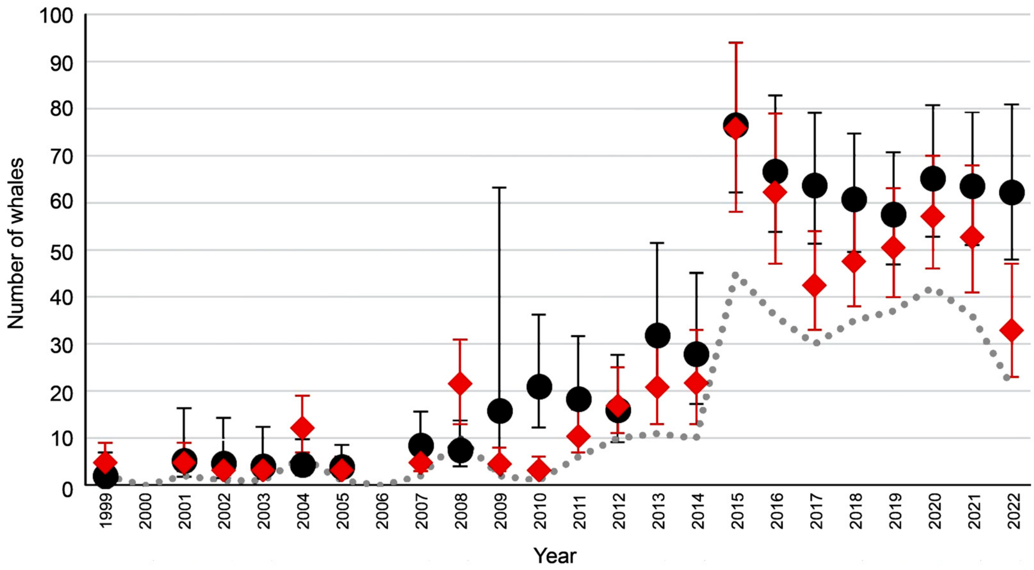


Figure 4: Number of individual humpback whales identified (dashed line), abundance estimates (black dots) of humpback whale in Ireland between 1999–2022 yielded by the best ranked POPAN formulation model ϕ(.), p(t), b(t), and model-averaged estimates computed by the multi-site mark-recapture analysis (red diamonds). Error bars indicate 95% Confidence Intervals (black) and 95% Highest Posterior Density Intervals (red).

was 0.87 (SE = 0.02), average probability of capture equalled 0.46 (SD = 0.28) and average probability of entrance resulted in 0.05 (SD = 0.08). Annual abundance estimates ranged between 2 ± 1 (1999) and 77 ± 8 (2015) individuals. The lowest estimate for the 2015–22 period was 58 in 2019, and while 2022 produced the lowest number of individuals identified for this period, the model still yielded an estimated abundance of 62 individuals for that year (Figure 4; Table 5).

Bayesian multi-site mark-recapture analysis

Overlapping between sampling regions varied greatly throughout the study period. Between 1999 and 2008, whales were only present in more than one region in 2004. On the other hand, between 2009 and 2022, individual whales were always present in at least two of the three sampling regions. Whales were present in all three areas only in 2011, 2019, 2021 and 2022, but no individual overlapped between all three regions in any single year. No individual whale overlapped between South and North sampling regions, but they did between South and West and between West and North areas, suggesting that within-year movements mainly occurred along the western seaboard of Ireland. On average, the West area had the highest number of individuals available each year (10.81 ± 12.66), followed by the South (8.38 ± 8.62) and North (0.33 ± 0.80).

Table 5

Humpback whale abundance estimates in Irish waters between 1999 and 2022 from both mark-recapture methods. SD = standard deviation, HPDI = high posterior density interval, CI = confidence interval, CV = coefficient of variation.

	Multisite				POPAN			
Year	Abundance	SD	95%HPDI	CV	Abundance	SD	95%CI	CV
1999	5	2.79	3–8	0.58	2	1.40	1–7	0.70
2001	5	2.79	3–8	0.58	5	3.31	2–16	0.63
2002	3	2.01	2–6	0.64	5	2.89	1–14	0.63
2003	3	2.01	2–6	0.64	4	2.52	1–12	0.63
2004	12	5.82	7–19	0.49	4	1.85	2–10	0.42
2005	3	2.01	2–6	0.64	4	1.62	2–8	0.42
2007	5	2.79	3–8	0.58	9	2.71	5–16	0.32
2008	21	6.51	14–30	0.31	7	2.37	4–14	0.32
2009	4	2.00	3–8	0.45	16	12.74	4–63	0.81
2010	3	2.01	2–6	0.64	21	5.97	12–36	0.28
2011	10	4.22	7–16	0.41	18	5.22	11–32	0.28
2012	17	4.96	11–25	0.30	16	4.59	9–28	0.29
2013	21	7.41	13–31	0.36	32	7.88	20–51	0.25
2014	21	9.74	13–32	0.46	28	6.94	17–45	0.25
2015	76	10.84	60–94	0.14	77	8.14	62–94	0.11
2016	62	10.61	46–79	0.17	67	7.38	54–83	0.11
2017	42	6.56	33–54	0.15	64	7.10	51–79	0.11
2018	48	6.71	38–60	0.14	61	6.39	50–75	0.11
2019	50	6.96	40–63	0.14	58	6.07	47–71	0.11
2020	57	7.53	46–70	0.13	65	7.09	53–81	0.11
2021	53	9.00	41–68	0.17	64	7.19	51–79	0.11
2022	33	8.95	23–46	0.28	62	8.36	48–81	0.13

Abundance estimates yielded by the multi-site mark-recapture models were generally similar to those provided by the maximum-likelihood open population model, with highly overlapping uncertainty intervals for most of the estimates (Figure 4; Table 5). The greatest discrepancies between both approaches occurred in 2008, 2010, 2017 and 2022, when the open population model generated larger abundances than the multi-site mark-recapture models with little or no overlap between the intervals. Moreover, multi-site models consistently yielded lower estimates than the open population model, except in 1999, 2004, 2008 and 2012. Multi-site model estimates also tended to be more influenced by the sample size of individual whales available each year since they tracked the line of minimum abundance in a clearer way than the open population model estimates.

The coefficients of variation suggested that the ability of both modelling approaches to derive precise estimates was greatly impacted by the number of individuals identified each year with higher estimate variability happening between 1999 and 2014, whereas lower coefficients of variation occurred between 2015 and 2022, when sample sizes were markedly larger than in the previous period (Table 5).

Regarding the estimated multi-site model parameters (Table 6), sampling site effect values reflected the number of individual whales observed in each region, with β_3 (North effect) consistently presenting the most negative values and β_2 (South effect) presenting the most positive values during the first half of the study period, approximately. The interaction effects showed various relationships between the sampling regions. During the first half of the study period, between 1999 and 2010, β_5 (West:North interaction) was generally the most positive interaction term, whereas β_4 (West:South interaction) and β_6 (North:South interaction) were generally negative, suggesting whale movements between West and North regions, although these West-North exchanges were not observed (Table 2). In the second half of the study period, interactions between sampling regions were more variable. Between 2013 and 2016, the South:North interaction was estimated to be very positive whereas the other interaction effects were predicted to be weak (close to zero). Moreover, when whales were observed in all three regions (2011, 2019, 2021 and 2022), different interactions were also predicted by the models. In 2011, the West:South interaction was negative, suggesting no movements between these areas occurred, whereas, in 2019, this interaction was positive while the other two were negative, indicating an exchange of animals between West and South regions which reflects their geographical proximity. In contrast, West:North interaction was the most positive in 2021 and 2022, which also reflected the proximity of these two regions.

Table 6

Estimated parameters of the annual multisite mark-recapture models. PM = candidate model probability, this is, the weights used to compute the model-averaged abundance estimate (N). For β values and model formulation, see Table 3 in Materials and Methods.

Year	β_0	β_1	β_2	β_3	β_4	β_5	β_6	PM1	PM2	PM3	PM4	PM5	PM6	PM7	PM8	N
1999	−0.50	−3.77	0.96	−3.77	−0.41	2.11	−0.47	0.13	0.11	0.17	0.11	0.14	0.10	0.14	0.12	5
2001	−0.50	−3.77	0.96	−3.77	−0.41	2.11	−0.47	0.13	0.11	0.17	0.11	0.14	0.10	0.14	0.12	5
2002	−0.06	−2.88	1.08	−2.86	−0.52	1.38	−0.62	0.13	0.12	0.14	0.12	0.13	0.11	0.13	0.12	3
2003	−0.06	−2.88	1.08	−2.86	−0.52	1.38	−0.62	0.13	0.12	0.14	0.12	0.13	0.11	0.13	0.12	3
2004	−1.46	−3.39	−1.66	−7.09	−0.91	2.32	0.67	0.14	0.10	0.23	0.08	0.14	0.07	0.14	0.10	12
2005	−0.06	−2.88	1.08	−2.86	−0.52	1.38	−0.62	0.13	0.12	0.14	0.12	0.13	0.11	0.13	0.12	3
2007	−0.50	−3.77	0.96	−3.77	−0.41	2.11	−0.47	0.13	0.11	0.17	0.11	0.14	0.10	0.14	0.12	5
2008	−2.29	−7.27	0.02	−7.23	0.02	7.16	0.00	0.03	0.01	0.46	0.01	0.19	0.01	0.20	0.09	21
2009	0.05	−0.80	−0.74	−4.76	−1.32	0.27	0.31	0.15	0.14	0.12	0.12	0.12	0.12	0.11	0.11	4
2010	−0.06	−2.88	1.08	−2.86	−0.52	1.38	−0.62	0.13	0.12	0.14	0.12	0.13	0.11	0.13	0.12	3
2011	−0.14	−4.94	−5.23	−5.90	−0.34	−0.06	0.01	0.28	0.13	0.13	0.14	0.08	0.09	0.08	0.06	10
2012	−1.12	−1.55	−0.31	−8.44	−0.27	0.94	0.06	0.24	0.12	0.21	0.11	0.11	0.07	0.09	0.06	17
2013	−2.20	0.12	−2.87	−5.82	−0.10	0.00	2.13	0.19	0.06	0.06	0.35	0.03	0.14	0.11	0.06	21
2014	−2.31	−1.38	−4.64	−6.68	−0.30	0.52	4.06	0.09	0.04	0.03	0.37	0.02	0.17	0.18	0.10	21
2015	−2.27	0.28	−3.46	−7.13	−0.04	0.02	2.84	0.20	0.04	0.04	0.40	0.01	0.17	0.08	0.06	76
2016	−2.58	−0.01	−2.74	−5.67	−0.01	0.02	1.96	0.22	0.05	0.05	0.38	0.02	0.13	0.10	0.04	62
2017	−0.69	−1.10	−1.04	−11.73	−0.47	0.43	0.37	0.26	0.15	0.15	0.15	0.09	0.08	0.08	0.05	42
2018	−0.34	0.06	0.47	−13.03	−0.12	−0.07	−0.17	0.30	0.14	0.15	0.14	0.07	0.08	0.08	0.04	48
2019	0.13	−2.15	−2.08	−9.12	0.51	−0.58	−0.49	0.33	0.13	0.14	0.14	0.07	0.07	0.08	0.04	50
2020	−0.39	0.34	−0.18	−12.84	−0.13	−0.13	0.13	0.30	0.14	0.15	0.15	0.08	0.07	0.07	0.04	57
2021	−0.62	−1.07	−2.47	−5.05	−0.26	0.51	−0.11	0.28	0.16	0.22	0.09	0.09	0.06	0.07	0.03	53
2022	−1.69	0.70	−2.84	−4.17	−1.39	0.99	0.27	0.05	0.27	0.17	0.02	0.16	0.15	0.08	0.09	33

With respect to the model probabilities, which were used to weight the final model-averaged multi-site abundance estimates, these were generally similar when yearly sample size and resulting abundance estimate were low (approx. 1999–2010). In contrast, when the number of observed individuals was larger, if one of the interaction effects were estimated to be very positive, the model that included this interaction term was generally the most weighted one. In general, the heaviest model in this part of the study period (2011–2022) was M1 – the model with no interaction terms.

DISCUSSION

Humpback whale abundance in Ireland

This study provides the first abundance estimates of humpback whales in Irish waters based on mark-recapture modelling techniques. With 120 individuals photo-identified as of December 2022, the best-ranked maximum likelihood open population model estimated the number of humpback whales that have ever been present in these waters to be 154 individuals between 1999 and 2022. It also provided annual estimates that indicated a positive trend in abundance since the beginning of the study period. However, the constant study area assumption of the open population model was likely violated. Inconsistency regarding the study area, within which images were collected each year, may have led to negatively biased abundance estimates since the presence of transient individuals, i.e., those only seen in one single year (54 of 120 identified individuals (45%), Figure 3B) can produce underestimated apparent survival values (0.87) as the model may confound these individuals with dead animals and remove them from the population. Low apparent survival probability might be consistent with some negative effect of migration to other areas around Ireland where sampling effort was low. It could also indicate that a fraction of the individuals ever present in Irish inshore waters were transient animals just passing through during their migration to more favourable feeding grounds in other areas of the NE Atlantic. This is well supported by photo-ID data since some individuals have been observed in other feeding grounds in the NE Atlantic (Berrow *et al*., 2021). A wider study design, including photo-ID data from these further feeding grounds (e.g., Scotland, Iceland or Norway) would be useful to test this hypothesis.

The data used in this study were mostly collected via citizen science and opportunistic sampling onboard whale watching and private vessels without standardised methodologies or experimental designs. This means our study area was diffuse and variable between years, with most data collected from two hotspots (Figure 2), primarily due to the presence of two whale watching boats providing extra sampling effort in those areas (Berrow *et al.*, 2021). The open population model also provided a high average recapture probability (0.46) which, in addition to high resighting rates of some individuals (Berrow *et al*., 2021), would support the existence of a small group of humpback whales with high site fidelity to coastal Irish waters that use this area as a feeding ground.

The combination of undefined study areas, through time and space, and high mobility of the humpback whales within or beyond the study area, would produce negatively biased abundance estimates, since some individuals visited the inshore areas without being observed before moving on to other areas. An apparent northward expansion of humpback whale sightings along the west coast of Ireland has been observed (IWDG, unpub. data). Thus, it is possible that increased observer effort in other areas around Ireland may have provided more re-sightings of known individuals.

Annual estimates were also derived using an alternative method based on closed multi-site mark-recapture models in order to compare and test the results provided by the open population model. While not identical, both estimation approaches provided similar numbers, with low abundance and precision during the first half of the study period, and higher abundance and precision during the second half of the study, especially since 2015 when the number of sightings and identified individuals were consistently higher than in the previous period (Figure 4; Table 5). Moreover, the estimates yielded by the multi-site mark-recapture models were consistently lower or very similar to the open population model, which would suggest that the effect of transient (not recaptured) animals did not result in an underestimation of humpback whale abundance in Irish coastal waters by the open population model. This was also supported by the goodness-of-fit tests of the fully time-dependent open population model (see Results). It is also reassuring that estimates derived using very different modelling approaches have resulted in abundance numbers within the same order of magnitude and with greatly overlapping uncertainty intervals. Durban *et al.* (2005) found similar results when comparing abundance estimates for bottlenose dolphins in Scotland collected through standardised survey-based mark-recapture models presented by Wilson *et al.* (1999).

Results from the open population maximum likelihood model and the closed multi-site mark-recapture models indicate an apparent increase of humpback whale abundance since the beginning of the study, with annual abundance estimates tracking the minimum abundance line (Figure 4). Part of this increase in abundance may be attributed to an increase in observation and reporting effort, especially when comparing the beginning and end of the time series. However, this cannot completely explain the increase in abundance. The number of sightings reported to the IWDG of other frequently recorded baleen whales in inshore Irish waters such as fin whales and common minke whales has been historically higher than humpbacks despite similar observation effort. However, in the last decade, the number of humpback whale sightings have been approaching and almost surpassing the number of fin whale sightings, (IWDG, unpub. data), suggesting either that the presence of humpback whales in inshore Irish waters is increasing, as suggested by Berrow and Whooley (2022), or fin whale occurrence is decreasing. The reasons behind this increase in humpback whales remain unknown. A possible population recovery after the IWC moratorium in 1982 (Bortolotto *et al*., 2016) and the subsequent utilisation of new (and previously used) migration routes and feeding grounds (O'Neill *et al*., 2019) may explain why humpback whale presence is increasing in Ireland. However, it is also possible that this increase may be driven by climate change. Global changes in ocean dynamics may alter the timing and distribution of prey at regional levels, and, as a result, its present and future availability in certain areas. These drifts in temporal and spatial distribution of prey may in turn drive changes in the presence and/or density of marine apex predators such as baleen whales (Ramp *et al*., 2015), leading to previously undocumented sightings and aggregations in some areas (Askin *et al.*, 2017; Findlay *et al.*, 2017; Giardino *et al.*, 2022; Insley *et al.*, 2021; Zein and Haugum, 2018). These range-shifts in humpback whales may lead to a local increase in whale presence over time, although this may not necessarily be linked to an increase in population size (O'Brien *et al.*, 2022). Population monitoring at regional levels should be maintained, in addition to joint efforts and international collaboration between research groups, environmental NGOs and citizen scientists in order to monitor humpback population trends in the North Atlantic Ocean. The NAHWC and Happy Whale are good examples of these initiatives.

Irish inshore regions within the wider North Atlantic humpback whale distribution

In a wider geographical context, these abundance estimates are notably modest when compared to other areas in the eastern North Atlantic Ocean. The NAHWC currently includes more than 11,000 individual humpback whales photo-identified which are similar numbers to those presented by Smith *et al.* (1999) who derived a basin-wide humpback whale abundance estimate in the North Atlantic of 10,600 individuals (95% CI = 9,300–12,100, CV = 0.07) using photographic and genetic data. The sub-group of humpback whales regularly visiting Irish waters represents no more than around 1% of the estimated North Atlantic population. Other studies have provided larger abundance estimates based on aerial and vessel-based line-transect surveys (see Hammond *et al*. (2021) for more details on cetacean abundance estimation methods). More than 18,000 (CV = 0.43) individuals were estimated by Pike *et al.* (2019) in 2007 as part of the large-scale Trans-North Sighting Survey (T-NASS) for Iceland and the Faroe Islands. Around 5,000 (CV = 0.44) humpback whales were estimated in Greenland in 2015 by Hansen *et al.* (2018). More than 10,000 (CV = 0.38) humpback whales were estimated in Norwegian waters (including the Barents Sea) between 2014–18 by Leonard and Øien (2020). It should be noted that these studies were not based on photo-ID but distance sampling techniques, usually covering much wider study areas, and thus providing larger population sizes. It is also worth mentioning that some humpbacks photo-identified in Ireland have also been photographed in other feeding grounds in the eastern North Atlantic, including Iceland and Norway (Berrow *et al*., 2021). Some individuals have also been recorded in areas off the UK, such as the Hebrides (Scotland) and Scilly Islands (England), so it is possible that a wider regional study including photo-ID data from UK waters would provide more accurate abundance estimates for this geographical area of the NE Atlantic Ocean.

The number of humpback whales estimated to occur in inshore Irish waters by the present study is below the estimates derived for the western North Atlantic and the main feeding grounds off the Nordic countries, although they are comparable to those obtained in other areas of the eastern North Atlantic, such as Cabo Verde. To date, seven individual humpback whales in the IWDG catalogue have been matched to this breeding ground (Berrow *et al*., 2021). This makes Cabo Verde the known breeding ground where most individual Irish humpbacks have been matched to date in the North Atlantic Ocean. Humpback whales using this breeding ground were considered as a Distinct Population Segment (DPS) under the US Endangered Species Act (Bettridge *et al.*, 2015); i.e., a population or group of animals that are 'discrete from and significant to the remainder of the taxon to which it belongs', according to information on 'distribution, ecological situation [and] genetics'. Reported abundance estimates in Cabo Verde are also low compared to estimates derived in other areas of the North Atlantic. Ryan *et al.* (2014) estimated abundances of 260 (CV = 0.02) between 2010–13 from mark-recapture modelling and Wenzel *et al.* (2020) estimated 272 (SE = 10) individuals between 2010–18. Similar to Ireland, these estimates were based on photo-ID data collected from opportunistic platforms such as whale watching boats, so the extent of the waters used by humpback whales in the archipelago remains understudied (Berrow *et al*., 2021; Ryan *et al*., 2014; Wenzel *et al.*, 2020). In addition, these studies also reported high resighting rates and site fidelity to the study area. Given the small population sizes estimated and high site fidelity for Ireland and Cabo Verde, in addition to the potentially strong link between Irish humpback whales to this breeding ground, we might expect to find more photo-ID recaptures between these two areas, especially sexually mature individuals and young calves. It is not clear what proportion of sexually active humpback whales occur in Ireland as well as their male/female ratio, which is relevant to understanding their migratory behaviours. To date, only 11 humpbacks identified in Ireland are of known sex – six males and five females (Berrow *et al*., 2012b). Hence, we recommend that further research effort focus on increasing current knowledge on Irish humpbacks demography including age class and sex group distributions. Moreover, sighting and photo-ID effort should be maintained and increased in order to identify new matches to Cabo Verde and other areas. This task would benefit from recent developments of automated photo-ID data management tools (e.g., Cheeseman *et al*., 2021), accelerating the usually tedious cross-matching process of different photo-ID catalogues collected all over the North Atlantic. This will help improve our understanding of humpback whale population structure and dynamics in an ocean basin where current knowledge of the species is still limited in some areas, especially in the eastern side of the basin.

CONCLUSION

We present here the first robust humpback whale abundance estimates for inshore Irish waters using photo-ID data mainly sourced by citizen scientists over a 20-year period. This dataset with over 1,000 photo-ID encounters with humpback whales demonstrates the benefits of collaborating with citizen scientists and adhering to robust data management protocols when researching and monitoring marine megafauna, including large baleen whales. This also highlights the need to maintain and improve current monitoring programmes of large megafauna and their habitats in the interest of conservation.

This study also provides evidence that the presence of humpback whales in Irish coastal waters has been consistently increasing, particularly in the last decade. However, the number of whales using inshore Irish waters is still relatively small. In addition, these waters seem to provide important feeding areas, especially for forage fish such as clupeids, which are known to be important in the diet of humpback whales (Ryan *et al*., 2013b). We encourage more participation in the IWDG Whale Track Ireland project to maintain and increase photo-ID data collection, especially in other areas, such as the Irish northwest and Northern Ireland. Moreover, passive acoustic monitoring techniques along with habitat suitability modelling could also help identify other areas throughout Ireland where humpback whales are present on a regular basis but remain undetected because of low sighting effort. As a very charismatic species, exhibiting an extensive behavioural repertoire, humpback whales are a highly valuable attraction for marine tourism. While whale watching may provide useful and cost-effective platforms for data collection under citizen science schemes, given the small number of humpback whales in inshore Irish waters, it is essential for this activity to be made as responsible and sensitive as possible. We recommend a Code of Conduct, enforceable by law, to ensure whale-watching pressures are sustainable and minimise disturbance. A better understanding of the habitat use by humpback whales in Ireland would help wildlife managers and policymakers make informed decisions about conservation management within a Marine Spatial Planning framework.

ACKNOWLEDGEMENTS

First of all, the authors express their gratitude to all IWDG members, Whale Watch/Marine Tourism boats and crew in Counties Cork, Kerry, Clare, Galway, Mayo and Donegal, for sharing their Photo-ID images with the Irish Humpback Whale Catalogue, which is curated by the IWDG. Many thanks to Dr Barbara Cheney and Dr Milaja Nykänen who provided valuable advice regarding the Bayesian mark-recapture analysis as well as instructions and code scripts necessary to perform this analysis on WinBUGS. We also highly appreciate code access permission granted by the original author, Dr John W. Durban. This study was made possible thanks to the financial support provided by Fundación Mutua Madrileña.

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