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Abundance of fin whales (*Balaenoptera physalus*) in the north-western Mediterranean Sea, using photo-identification and microsatellite genotyping

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Abstract

The Mediterranean fin whale population, *Balaenoptera physalus*, is resident, with almost no exchanges with the Atlantic population. The entire population was estimated at 1300 or 13,300 individuals by a recent project depending on the platform used. This disparity shows the importance of long-term monitoring with a unique protocol of survey. Capture-recapture approaches using dorsal photographs and genetic identity collections over a 10 years period were used to estimate the abundance of the north-western Mediterranean fin whale. We identified 332 individuals using photographs and 470 using genotypes, with a total of 546 individuals identified between 2008 and 2019, when some whales were double-marked. The inter-annual percentage of recapture varied between 15% and 17% respectively for genotypes and photographs methods. Using Cormack-Jolly-Seber models, the abundance of fin whales in the north-western Mediterranean is estimated at 1295 individuals (95% CI: 1116–1474) with a survival probability of 0.945 (95% CI: 0.690–0.993) from genotypes. Abundance estimates from combined collections (photographs and genotypes) and corrected photograph estimates were similar to the genetic ones. Future studies might prioritize the genetic approach which is the least biased and with a narrower confidence interval. The genetic abundance estimates show relative stability over time, when compared to 1990 estimates, and should be included in future conservation actions.

KEYWORDS
abundance, capture-recapture, fin-whale, microsatellite, photo-identification

1 | INTRODUCTION

Abundance, the number of individuals in a population, is a fundamental parameter in evolution, ecology and conservation. To protect endangered populations, estimates of abundance and survival probability over extended study periods are needed to determine temporal trends (Childerhouse et al., 2008) and infer the causes of observed trends in population dynamics (Pace et al., 2017). We consider a population as a set of individuals that mix together (Evans & Hammond, 2004) and, that may share some characteristics such as genetic, habitat, dietary, behavioural, etc. Interactions and exchanges between individuals of the same population are more important than amongst individuals of different populations (Palsbøll et al., 2007).

The type of method used for abundance estimation may depend on the nature of the population investigated, namely whether it is 'closed' or 'open'. A closed population refers to a population that remains unchanged during the investigation, whilst an open population refers to a dynamic population that will change through the import and export of individuals via migration processes and, the birth and

death of individuals. Several methods are commonly used to estimate abundance (e.g. Lebreton et al., 1992; Lukacs & Burnham, 2005; Schwarz & Seber, 1999), in particular, some are based on statistics from capture-recapture data (Schwarz & Seber, 1999).

In capture-recapture protocols, individuals are first captured and then marked with a unique identifier, and then released back into their natural habitat. As the sampling protocol continues, new individuals are caught along with individuals that were previously caught, now considered 'recaptures'. From these data (recapture vs new first capture), it is possible to provide robust estimates of abundance and survival probability, which are required to determine population status, though they remain difficult to obtain for wide-ranging, mobile species that make recaptures more unlikely. The capture-recapture approach allows for the estimation of demographic parameters (e.g. abundance, survival), group structure, site fidelity and movement patterns (Hammond, 1986; Hammond et al., 1990).

For cetaceans, most capture-recapture approaches require individual identification that is undertaken by one of three methods: satellite telemetry (Panigada et al., 2015), genotyping (Palsbøll, Allen, et al., 1997) and photo-identification (Photo-ID; Hammond, 1990). Photo-ID and genetic tools are the most commonly used methods because they rely on permanent characteristics, in contrast to satellite telemetry, which can be deployed for only a few months at most.

Photo-ID is a useful tool to study free-ranging species, like cetaceans. It is a widely-used method based on stable markings (i.e. which do not vary through time; Blackmer et al., 2000), and allows for the distinction of individuals (Hammond et al., 1990). Some marks are the result of injuries that have affected the dermis, such as nicks and notches in the trailing edges of dorsal fins and scars on the body, although the shape of the dorsal fin and pigmentation patterns are also used to identify individuals (Urian et al., 2015).

Genetic analyses are less frequently used than photo-identification to estimate abundance because they require sampling tissue from the animals, but both methods can be used for the same analysis. The use of microsatellite markers allows individuals to be identified, by reconstructing their genotypes and by producing a unique and stable through-time identification tag for each organism (Lamb et al., 2019). However, the assignment of duplicate individuals depends highly on the variability of the markers. This technique is widely used in biology, medicine and forensics, to track the movement of individuals and for population and conservation genetics (Chistiakov et al., 2006; Palsbøll, Allen, et al., 1997).

Based on individual and recapture identification, it is possible to estimate abundance for a given species and to derive certain characteristics of population dynamics (Hammond et al., 1990). A census can be done when all the individuals of a population resident inside a limited area can be counted (Shane et al., 1986), opposite to an estimation when only a sample of the population can be identified (Notarbartolo-di-Sciara et al., 2003; Wilson et al., 1999). The estimation approach by capture-recapture is often used to estimate the abundance of cetaceans over a long-term study period

(Hammond, 1986) and when the detection of individuals is heterogeneous, i.e. detection depends on covariates like offshore distance and visibility. Comparison of data sources (photographs and genotypes) was conducted for the humpback whale in Oceania, *Megaptera novaeangliae*, where the photograph estimate was lower than the genotype estimate due to several factors (different levels of effort and/or data collection strategies; Constantine et al., 2012), yet for the right whale, *Eubalaena australis*, abundance estimates from photographs and genotypes were comparable due to a similar data collection strategy (datasets collected at the same time in the same surveys) and a high overlap (~16%) between the two datasets (Carroll et al., 2011).

Whaling during the 19th and 20th centuries significantly reduced the abundance of whale populations across the globe (Reeves & Smith, 2006), as for southern right whales (Jackson et al., 2008) and humpback whales in the Southern Ocean (Jackson et al., 2015). However, the degree of the reduction in abundance caused by whaling and current human activities remains unknown for some species, such as fin whales. Human activities are the greatest threat to large whales (ship-strikes, bycatch, noise and chemical pollution; Harwood, 2001, Peel et al., 2018) and these activities are steadily increasing. Today, most countries recognize that it is important to have a precise estimate of abundance for each population that is threatened to understand the severity of these impacts and to take action to mitigate them. Further, regular estimates of abundance should be acquired to detect changes in these populations. Populations are also the unit of management internationally and the IUCN red list has for instance separate listings for certain populations (e.g. Mediterranean Cuvier's beaked whale, Oceania humpback whales, etc.).

The fin whale, *Balaenoptera physalus* (Linnaeus, 1758), the second-largest species in the world, has seen its worldwide population decrease by more than 70% over the last three generations (1927–2007; Reilly et al., 2013). In 2018, global world abundance was roughly estimated at 100,000 individuals (Cooke, 2018), and the species remains 'vulnerable' with regard to the global population on the IUCN Red List of Threatened Species (Cooke, 2018). The fin whale is present throughout the Mediterranean basin (Notarbartolo-Di-Sciara et al., 2016) with a population that is considered as a resident, displaying a significant level of differentiation in the mitochondrial DNA from the north Atlantic population (Bérubé et al., 1998). However, limited gene flow exists between the North Atlantic and the Mediterranean populations (Palsbøll et al., 2004). Observations and bioacoustics studies also suggest a spatial and temporal overlap between the North Atlantic and Mediterranean populations (Castellote et al., 2012; Gauffier et al., 2018). Breeding and feeding areas are different between these two populations (Aguilar et al., 2002; Giménez et al., 2013), further reinforcing the isolation of the Mediterranean population, and increasing its vulnerability. The fin whale occurrence is conspicuously uneven in the Mediterranean basin. The species is more abundant in the north-western part in summer, when concentrated due to the high

densities of its principal prey, krill *Meganyctiphanes norvegica* (Druon et al., 2012; Notarbartolo-Di-Sciara et al., 2016). The northwestern part is known to be one of the main feeding grounds for fin whales. During the rest of the year, the fin whale occurs at lower rates in the Mediterranean basin, notably close to Sicily (Druon et al., 2012). The most recent estimates of total abundance for the entire basin come from the ACCOBAMS Survey Initiative project led by ACCOBAMS (Agreement on the Conservation of Cetaceans of the Black Sea, Mediterranean Sea and Contiguous Atlantic Area), which have estimated at 1700 and 13,300 individuals (model-based analysis from aerial and vessel surveys respectively; ACCOBAMS, 2021). In the western basin, the estimate was 3500 fin whales (distance sampling method: 95% CI: 2130–6027; Forcada et al., 1996) and 1800 individuals in the north-western basin (data collection of publications; Notarbartolo-di-Sciara et al., 2003). However, these estimates were made from different types of data and platforms. A comparison between ship and aerial surveys suggested an appreciable decrease in abundance by a factor of six between 1990 and 2009 (Panigada et al., 2011). As such, temporal monitoring is required to follow trends over the years.

In the present study, we used a Cormack-Jolly-Seber (CJS) model to estimate apparent survival and recapture probabilities. We applied a Horvitz-Thompson estimator (McDonald & Amstrup, 2001) to derive the abundance of fin whales in the north-western Mediterranean Sea based on long-term monitoring conducted in summer over the last 10 years. We applied a CJS model to individuals identified separately from photographs and/or genotypes. Estimates calculated here will be compared with previous estimates for the species in the area and elsewhere to assess their relative importance and temporal trends, both of which (survival and abundance) will be essential for future conservation planning efforts.

2 | MATERIALS AND METHODS

2.1 | Data collection

The target study area of approximately 91,000 km² is located in the north-western Mediterranean Sea (~27.5% of the Mediterranean Sea surface), including a major part of the Pelagos Sanctuary (an International Sanctuary for Marine Mammals, Figure 1). Whale sightings were collected from sailboats, each of which had trained observers on board, who continuously scanned the sea with binoculars. When a fin whale was sighted, photographs and skin biopsies were taken from an inflatable dinghy for identification and its position was recorded. Only adult fin whales were identified, as calves are unmarked and were not sampled. Images were taken with a Canon 30D digital camera from 2008 to 2016 and from 2017 to 2019, a Canon 80D digital camera fitted with a Canon 70 to 200 mm lens was used. Skin samples were collected using biopsy darts fired from a crossbow (Lambertsen, 1987). In the field, samples were stored in 70% ethanol. However, the survey effort was weather-dependent, and when sea conditions were worse than Beaufort scale 3, the effort was stopped. In total, approximately 27,400 km were surveyed (Figure 1), between 2008 and 2019 during the summer season (between June and September), except in 2015 when no sampling campaign was conducted.

2.2 | Microsatellite loci genotyping

DNA was extracted from skin biopsies using the Gentra PureGene tissue kit (Qiagen, Hilden, Germany). A total of 32 microsatellite markers were used in six multiplexes PCRs (Table S1; Bérubé
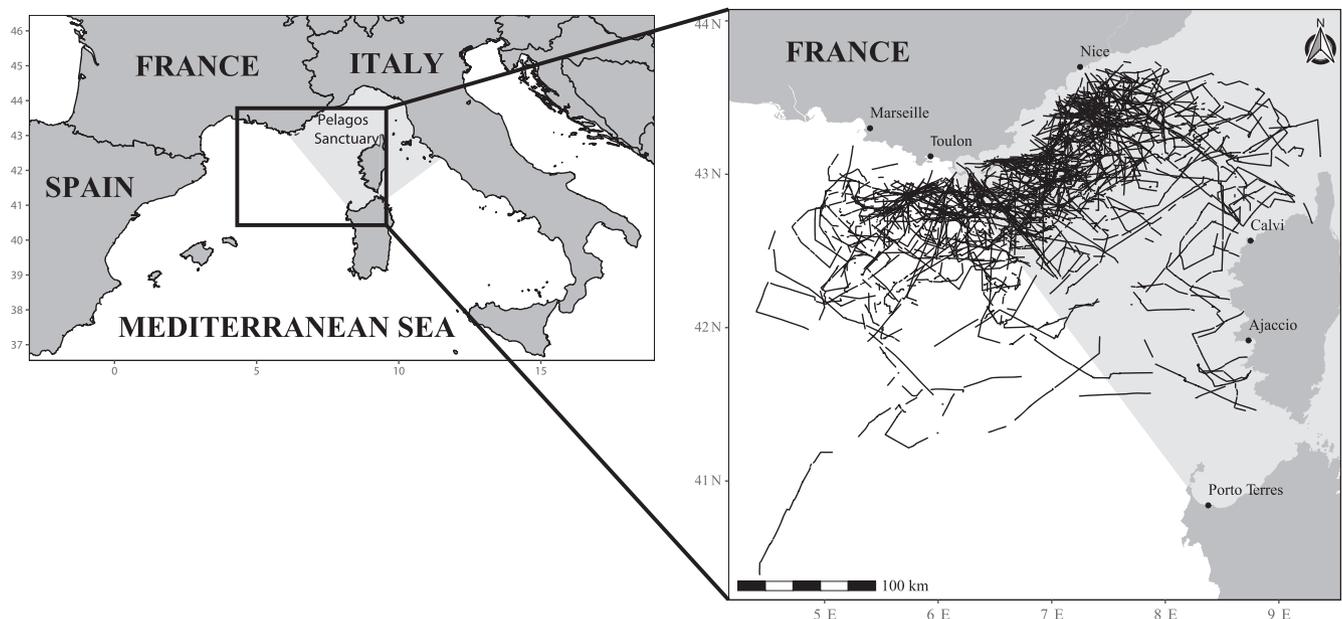
FIGURE 1 North-western Mediterranean Sea, including track effort (black lines) obtained whilst conducting boat surveys between 2008 and 2019, and Pelagos sanctuary (light-grey in the background).

et al., 1998, 2000, 2005; Palsbøll, Bérubé, et al., 1997; Tardy et al., 2020; Valsecchi & Amos, 1996). PCR amplifications were performed using Type-it Microsatellite PCR kits (Qiagen, Hilden, Germany) in 12.5 μL total volume reactions containing 4 μL Type-it Multiplex PCR Master Mix, 6 μL RNase-free water, 1 μL of primers (2 μM forward and reverse primers diluted in TE pH 8 buffer) and 1.5 μL of DNA template at 50 ng/μL. Amplifications were carried out for 5 min at 95°C, followed by 40 cycles of 30 s at 95°C, 1 min 30 s at annealing temperature (53–63°C, depending on the locus), 30 s at 72°C and a final extension for 30 min at 60°C. PCR products were sent to the GenoScreen platform (Lille, France) for fragment analysis and allele sizes were visualized using an Applied Biosystems 3730 Sequencer. For accurate sizing, an internal size ladder (GeneScan 500 LIZ, Applied Biosystems) was included. Allele sizes were scored and checked manually using GENEMAPPER software v.5 (Applied Biosystems). All ambiguous peak profiles were considered as missing data. For one genotype, a maximum of eight missing data was allowed on 32 microsatellite markers. The sex of individuals was genetically identified by amplifying fragments of the ZFX and ZFY genes (Bérubé & Palsbøll, 1996). Sequencing of the mtDNA control region (465 bp) was performed using primers TRO (Archer et al., 2013) and D (Rosel et al., 1994).

Controls for the presence of null alleles and large allele dropout were performed with MICRO-CHECKER v.2.2.3 (Van Oosterhout et al., 2004). Repeated genotypes were identified and estimated in GenAlex v.6.503 (Peakall & Smouse, 2012). Two samples are considered as belonging to the same individual when all alleles are identical, supported by control region haplotypes and sex. Lastly, in situations where between 1 and 10 differences were detected between the two genotypes, all PCR amplifications were performed again to remove possible contamination or genotyping errors to verify the individual's identity or difference. In the microsatellite analysis, different individuals could have identical profiles with 99% certainty when an insufficient number of loci was used. We estimated by computing the probability of identity (P_{ID}), and we estimated the P_{ID} amongst siblings if there is the potential for relatives to be present in samples. These were estimated following (Paetkau et al., 1995) and using the R package PopGenUtils (Tourvas, 2021).

2.3 | Photo-identification

Photo-ID was done on the right side for each observed individual, with a focus on two parts: the dorsal fin and the chevron (a light 'V' shaped pigmentation pattern behind the head; Agler et al., 1990). For each individual and each encounter, the best photograph was selected and scored, as (3) poor, (2) fair and (1) good or excellent, based on the lighting, focus, size and angle of the body relative to the photographic frame. Then, each individual was scored with respect to its markings, as (3) not distinctive with superficial lesions, (2) slightly distinctive with deep scars and minor lesions, (1) distinctive or very distinctive with a damaged fin or important scars on the fin. To minimize heterogeneity in captures due to the misidentification

of non-distinctive fins, both scores were added, and only photographs with a score inferior or equal to 3 were kept for a standardized comparison between individuals. This type of quality control reduces error rates due to false positives and/or false negatives (type 1 and type 2 errors; Barendse et al., 2011; Friday et al., 2008; Urian et al., 2015). Following these steps, photographs allowed individuals to be identified and for re-sightings to be determined. As recommended by Friday et al. (2000), the quality control review of all catalogues was conducted by a single researcher (the first author) to ensure consistency.

2.4 | Capture-recapture modelling and abundance estimation

To allow for the comparison of abundance estimates over time, biases due to variation in sampling effort were reduced by creating a grid of 5 km per 5 km in our spatial area and by selecting per year cells where the total effort (km) exceeded the surface area (km^2) of the same zone ($km/km^2 > 1\ km^{-1}$; Gnone et al., 2011). Only the data present in these cells were included in this study. After this step, photo-ID and genotype data were treated separately, to compare estimates from both data sources. The last step was to combine both collections to increase the number of individuals sighted and to estimate the abundance of fin whales occurring in the north-western Mediterranean. Several individuals were both photo-identified and sampled for genotyping, whilst others were either photo-identified or sampled. All concordances of data are known from sampling surveys.

In this study, each capture occasion (1 year of the survey) spanned the summer season (June to September) to avoid sparseness in the data due to non-detections (Cooch & White, 2011), and yielded a total of 11 capture occasions, corresponding to 11 years of effort with one field season per year. A matrix was then constructed, which included the detection/non-detection of each fin whale for each capture occasion.

The CJS model is commonly used in the modelling of capture-recapture data (Lebreton et al., 1992). In open populations, the CJS model is suitable for the estimation of population parameters when birth, death and emigration are stochastic between sampling periods, and is thus widely used for cetaceans (e.g. Schleimer et al., 2019; Wierucka et al., 2014). Furthermore, the CJS model is more appropriate than the POPAN model in view of our target species (the fin whale), and our study area (one of the major feeding grounds for this species). The POPAN model assumes equal catchability between marked and unmarked individuals in the survey areas (Schwarz & Arnason, 1996). However, the fin whale is less marked than the right whale, which is concerned by the studies using the POPAN model (Carroll et al., 2011, 2013; Constantine et al., 2012). From there, the CJS model is better suited than the POPAN model. To determine which CJS model best fits our data, goodness-of-fit tests (GOF; Pradel et al., 2005) were conducted using the R package R2ucare (Gimenez et al., 2018). The GOF tests assess for any violations of the

assumptions of homogeneity of capture and apparent survival probabilities, transience and trap-dependence. Unequal apparent survival or recapture probabilities could be due to biological factors, such as a transient effect or trap-dependence phenomena. Transience could reflect the behaviour of some individuals that passed by the study area only once and therefore had a low probability of being re-sighted (Madon et al., 2013; Pradel et al., 1997). This is due to the limited spatial size of the area compared to the total area used by a population. Trap dependence refers to the effect of previous detections on the recapture probability due to, for example, animal behaviour or the observers' protocol (Pradel & Sanz-Aguilar, 2012). Furthermore, to quantify over-dispersion in the data, we estimated the variance inflation factor, $\hat{c}$, which equates to the ratio of residual deviance to degrees of freedom (values close to 1 indicating a well-fitting model; Burnham & Anderson, 2002).

Following GOF tests, the estimation of abundance and apparent survival probability was conducted using the R package RMark (Laake, 2013). The study population was considered demographically open (i.e. births and deaths are possible). The standard model of CJS for open populations was used to estimate recapture probabilities (p) and apparent survival (φ) for each season (Lebreton et al., 1992). Capture-recapture models for open populations, such as CJS, rely on a series of assumptions: (a) the mark (or the recognition system) should be reliable during the study period; (b) the capture of an animal should not modify the probability of being recaptured; (c) all of the individuals of the population should have the same apparent survival probability at each sampling event; (d) capture occasions are short in time compared to the interval between two successive occasions (Hammond, 1990; Lebreton et al., 1992). Recaptures are possible over long time periods due to the permanent markings present on fin whales, as in this study or others (Agler et al., 1990, 1993), Moreover, each photograph was quality controlled to avoid misidentification, and only unambiguous individual identifications were retained (Assumption 'a'). We considered that assumptions 'b' and 'c' were respected by the results of the GOF tests. Initial monitoring of fin whales was conducted in 2006 and 2007 but for these 2 years, the spatial effort was more limited and as such, we did not include these 2 years in the global analysis. In addition, the use of a grid system led to the deletion of two sightings (corresponding to two individuals in total), which were present in cells where the effort was heterogeneous. We, therefore, removed important geographic extent changes from the study over time. The geographic range of the fin whale and their movements are not completely known. However, one of the advantages of the Cormack-Jolly-Seber model is that it does not assume a closed population, it allows for the possibility of inward and/or outward random temporary migration (Schaub et al., 2004). Assumption 'd' was certified by grouping all of the summer months to form one capture occasion per year and to have a larger and constant interval between occasions.

We built several models based on different combinations of effects on recapture probabilities and survival following the notation: constant over capture occasions (c) and fully time-dependent (t; Lebreton et al., 1992). Moreover, heterogeneity in the recapture

probabilities may be expected due to individual attributes (e.g. age, body mass, social status) and habitat features (home-range location and composition; Cubaynes et al., 2010). To address heterogeneity, a finite mixture model was tested to account for this parameter by assuming the presence of unobserved individuals (Pledger et al., 2003) with two groups of individuals, one with a high probability of recapture (p_{high}) and the other one with a low probability of recapture (p_{low}). Furthermore, a chi-squared test was used to test for independence in recapture related to sex.

In total, six models were tested on both matrices (photo-ID and genotypes) and the combined collection, which is the matrix combining individual identification by photo-ID and/or by genotypes. To find the best-fitting model, models were compared under Akaike's Information Criterion (AIC; Akaike, 1973), which helped to select the most parsimonious model (penalising maximum likelihood with the number of parameters used) amongst the tested models. Therefore, when $\hat{c}$ parameters were ≠ 1, we have chosen to apply the relevant corrections to the given model to obtain the Quasi-likelihood AIC (Richards, 2007), because the way to treat the result is not a consensus in the scientific community. The model with the lowest QAIC was selected. Abundance estimates were derived from the CJS model and obtained as a ratio of captured individuals per season by their associated probabilities. The global abundance estimate was obtained by averaging the estimates for each season. The bootstrap technique was used to calculate a confidence interval for abundance, whereby we resampled individuals with replacement to get 1000 bootstrapped samples (Cubaynes et al., 2010).

Abundance estimates obtained from photo-identification were corrected by the proportion of marked individuals for each capture occasion since all the whales did not exhibit enough marks for individual identification. The proportion of marked individuals corresponds to the number of individuals which was kept after the quality control divided by the total number of identified individuals per year. A different proportion was applied for each year because the proportion of marked/unmarked individuals varied by year. Total abundance was estimated as the abundance of marked fin whales on the proportion of marked fin whales for each capture occasion. Log-normal confidence intervals for the total abundance were obtained (Burnham, 1987).

3 | RESULTS

3.1 | Genotype collection

During the study period, 612 skin biopsies were collected and 547 were correctly genotyped. All 32 microsatellite markers were successfully amplified. However, three loci revealed the presence of null alleles (Bp1430262, Bp747752 and Bp1003953) and were removed in further analyses to remove any potential miss-scoring. All samples available from 2008 to 2019 were then analysed with 29 microsatellite markers. The genotyping error rate was estimated <0.01 from the recaptures. The P_{ID} values amongst the 29 microsatellite loci

were lower than 0.01 ($P_{ID} = 5.87 \times 10^{-33}$; P_{ID}-sibs $= 1.89 \times 10^{-12}$), and ranged from 0.02 to 0.55 for the P_{ID}, and from 0.30 to 0.74 for the P_{ID}-sibs indicating that this microsatellite panel is accurate for individual identification. The panel power comes from the combination of microsatellite markers. The average number that each sample was genotyped, was 28 microsatellite markers with a variance of 1.08. The average number of matching loci per genotype replicates was 29.

From the 547 genotypes, 470 individuals with unique genotypes were identified. All matching genotypes matched at sex and mtDNA haplotype. The inter-annual percentage of recapture was 15.3%, where a total of 72 individuals were recaptured with 67 captured twice, and with 5 captured three times. The chi-squared test showed no heterogeneity in recapture linked to sex ($p \approx 1$). The number of identified individuals increased steadily from 2008 to 2019. Each year, most of the samples were composed of new individuals and only a small portion of intra-annual recapture (average at 1.9% per year; Table 1). Within-year sample sizes ranged from 9 (in 2008) to 69 (in 2011), with an average of 50 samples per year.

Parallel to the development of the genetic collection, the photo-identification collection was created in the same way, with data processing and quality control.

3.2 | Photograph collection

Seven hundred and one individuals were identified via photo-identification. However, 308 photo-identified individuals could not be used due to quality limitations. The total proportion of marked individuals was 58%. After quality control of the photographs, 393 remained for the analysis with 332 single individuals identified and used to build the catalogue of photo-identification. Noticeably, for these 332 individuals, 11 presented marks from ship strike, representing 3.3% of individuals. Through an analysis of inter-annual re-captures, a total of 54 individuals were re-sighted, with 49 sighted twice, three individuals recaptured three times and two recaptured four times. The chi-squared test showed no heterogeneity in recapture linked to sex ($p \approx 1$). The inter-annual percentage of recapture was 16.3%, with a small portion of intra-annual recapture (3.8%). Over the years, the number of identified individuals increased progressively (Table 1). The mean number of individuals identified by photo-ID per year was 36 with a range from 10 (in 2008) to 67 (in 2017).

3.3 | Combined collection

When genotype and photograph collections were combined, a total of 546 individuals were identified by one or both methods in the study area between 2008 and 2019. A total of 249 individuals were both photo-identified and sampled, corresponding to 45.6% of the total identified individuals. In contrast, 84 fin whales (15.4%) were only photo-identified, and 213 (39%) were only DNA sampled.

3.4 | Goodness-of-fit tests

Once the three collections were obtained, the presence/absence matrices could be constructed, and the goodness-of-fit tests carried out.

For the two collections, the global GOF test was not significant (photographs: $\chi^2 = 11.779$, df $= 27$, $p = .995$; genotypes: $\chi^2 = 23.438$, df $= 31$, $p = .833$). None of the tests showed a significant departure from transient effect or trap-dependence assumptions (Table 2). When the two datasets were combined, the results did not indicate a lack of fit ($\chi^2 = 40.402$, df $= 32$, $p = .146$). Over-dispersion was accommodated by modifying the $\hat{c}$ (genotype collection: $\hat{c} = 0.756$; photograph collection: $\hat{c} = 0.436$; combined collection: $\hat{c} = 1.263$).

3.5 | Best-fitted model and estimated abundance

Each collection was treated separately before combining the two to test the best-fitting model and estimate abundance.

For the genotype collection, a comparison of the six models showed that the model that best fitted the data was model 2 (Table 3) with time-dependent recapture probabilities (p) and a constant survival (φ). The three models with constant survival had more support than those with time effect. The apparent survival probability was 0.945 (95% CI: 0.690–0.993) for the best model. The recapture probability between years had low estimate values under 0.2 with a slightly declining trend over the years (Figure 2), ranging from 0.116 in 2009 to 0.009 in 2018. Using this model, the abundance of fin whales in the north-western Mediterranean Sea was estimated at 1295 individuals from all samples collected from 2008 to 2019 (95% CI: 1116–1474). Annual abundance estimates varied from 326 (95% CI: 232–429) in 2009 to 2256 (95% CI: 1397–3331) in 2018 (Figure 3).

For the photograph collection, the best model was model 2 (Table 3) with time-dependent recapture probability and a constant survival. The apparent survival probability was 0.990 (95% CI: 0.001–0.999). The recapture probability between years had low estimate values under 0.1 with a slightly declining trend over the years (Figure 2), ranging from 0.095 in 2010 to 0.015 in 2018. This collection provided an abundance of 911 individuals during the entire period surveyed (95% CI: 777–1046). Annual abundance estimates varied from 401 (95% CI: 274–517) in 2010 to 1466 (95% CI: 866–2066) in 2018 (Figure 3). Those values were corrected from the proportion of marked individuals each year for the total population abundance, which ranged from 958 (95% CI: 618–1487) in 2009 to 1946 (95% CI: 1254–3020) in 2010. The total corrected abundance for the north-western Mediterranean fin whale was estimated at 1549 individuals from all samples collected from 2008 to 2019 (95% CI: 1174–1923).

For combined collections, a comparison of the six models indicated that the model that best fit the data was model 2 (Table 3), with time-dependent recapture probabilities between years (p) and a constant survival (φ). Similar to the genotype collection, the

TABLE 1 Summary of fin whales (*Balaenoptera physalus*) identified from 2008 to 2019 in the north-western Mediterranean Sea, by (a) microsatellite genotypes and (b) photographs.

	Year										
	2008	**2009**	**2010**	**2011**	**2012**	**2013**	**2014**	**2016**	**2017**	**2018**	**2019**
a. Genotypes											
Ind. Captured	9	38	64	69	57	61	49	64	62	21	53
Cumul. Ind. captured	9	46	106	169	220	273	316	370	416	434	470
Effort (km)	2274	2389	2963	4411	3046	2946	3281	1975	1407	731	1950
Year of initial capture	**Year of recapture**										
	2008	**2009**	**2010**	**2011**	**2012**	**2013**	**2014**	**2016**	**2017**	**2018**	**2019**
2008	–	1	1					1	1		1
2009		–	3	5				2	2	1	1
2010			–	2	2	1		1	3		2
2011				–	4	3	1	2	4	1	1
2012					–	4	3		1		5
2013						–	2	1			2
2014							–	4			1
2016								–	5	1	2
2017									–	1	3
2018										–	1
2019											–

	Recaptures			
	1X	**2X**	**3X**	**Total Ind.**
Number of Ind.	398	67	5	470

	2008	2009	2010	2011	2012	2013	2014	2016	2017	2018	2019
b. Photographs											
Ind. Captured	10	22	38	39	32	27	26	60	67	22	50
Cumul. Ind. captured	10	32	67	100	128	148	171	222	278	296	332
Effort (km)	2274	2389	2963	4411	3046	2946	3281	1975	1407	731	1950
Year of initial capture	**Year of recapture**										
	2008	**2009**	**2010**	**2011**	**2012**	**2013**	**2014**	**2016**	**2017**	**2018**	**2019**
2008	–		1	2	1	1		2	1		1
2009		–	2	3		1		2	2	1	1
2010			–	2	1	3	1	1	2		
2011				–	2	1		3	3	1	1
2012					–	2	1				3
2013						–	2	2			2
2014							–	2			
2016								–	3	2	1
2017									–	2	4
2018										–	2
2019											–

	Recaptures				
	1X	**2X**	**3X**	**4X**	**Total Ind.**
Number of Ind.	278	49	3	2	332

three models with constant survival had more support than those with time effect. The apparent survival probability was 0.958 (95% CI: 0.711–0.995). The recapture probability between years had low estimate values under 0.1 with a slightly declining trend over the years (Figure 2), ranging from 0.079 in 2009 to 0.010 in 2018. The abundance of fin whales in the study area was estimated at 1383

individuals (95% CI: 1168–1597) and estimates varied from 517 (95% CI: 365–680) in 2009 to 2932 (95% CI: 1955–3909) in 2018 (Figure 3).

TABLE 2 Summary of goodness-of-fit test results for a study on the fin whale, for photo-identification and microsatellite genotype collections.

Collection	Tests	χ^2	df	p-value
Photo-identification	3sr	0.822	8	.999
	3sm	0.585	5	.989
	2ct	5.400	8	.714
	2cl	4.972	6	.547
	Goodness-of-fit	11.779	27	.995
Microsatellite genotype	3sr	1.848	9	.994
	3sm	0.787	5	.978
	2ct	1.644	6	.949
	2cl	0.000	0	1.000
	Goodness-of-fit	23.438	31	.833
Both collections	3sr	5.063	9	.829
	3sm	4.418	5	.491
	2ct	0.000	5	1.000
	2cl	0.000	0	1.000
	Goodness-of-fit	40.402	32	.146

4 | DISCUSSION

In this study, we used the CJS model based on an extensive dataset, allowing access to a large catalogue of genotypes and photographs, with a total of 470 individuals that were clearly differentiated and identified by genotypes and 332 by photographs. A large number of individuals is only DNA sampled (39%) because of the quality control which removes photos for numerous sampled individuals. In total, 546 fin whales were identified in the north-western Mediterranean Sea.
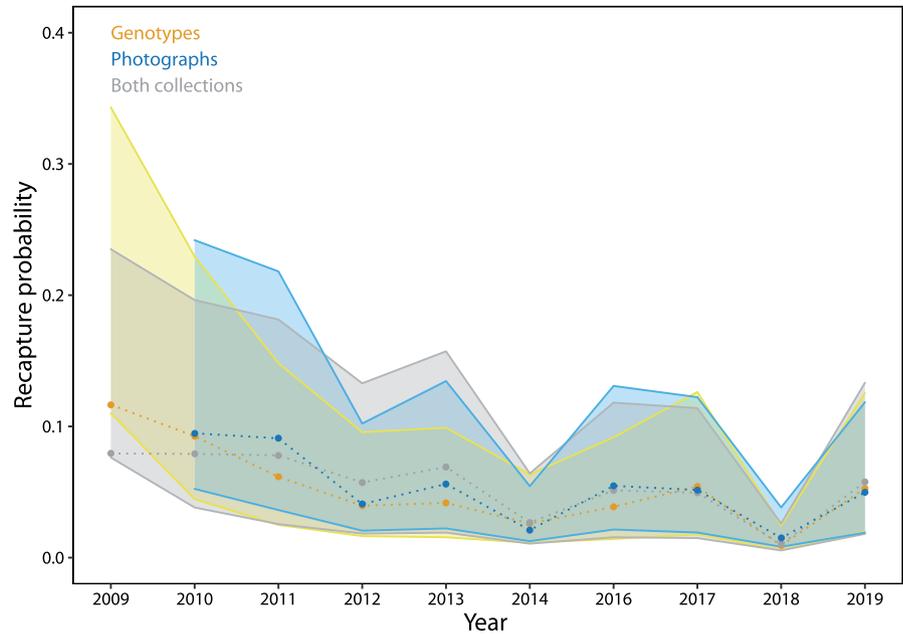
For each collection (photographs and genotypes) a minimum of 15% recapture was recorded, meaning that approximatively 85% of individuals were only seen once. A large number of unseen individuals and constant growth of the cumulative number of identified individuals (Table 1) suggest that the entire population was far from being observed, even with 10 years of recurrent monitoring. Likely, our sampling corresponds to a fraction of the range of the Mediterranean fin whale population. Moreover, new individuals joined this population every year (births, immigration) yet the percentage is unknown. However, the existence of inter-annual recaptures may indicate that some individuals are either sedentary or return regularly to this area. Nevertheless, these recaptures only concerned a minor part of the fin whales when considering the total number of individuals identified (546 fin whales) and the highest abundance estimate (~1500 individuals) in a single area, representing only 3.6% of the surface of the Mediterranean. If site fidelity existed, it would imply more recaptures. Even so, site fidelity was

Collection	Models	Npar	AICc	QAICc	ΔQAICc
Photo-identification	2. φc Pt	11	513.0	1146.3	0
	4. φt Pt	20	530.5	1159.0	12.7
	1. φc Pc	2	509.6	1163.7	17.4
	5. φc Pm	4	513.6	1167.4	21.1
	3. φt Pc	11	523.5	1170.4	24.1
	6. φt Pm	13	527.8	1174.4	28.1
Microsatellite genotype	2. φc Pt	11	678.7	889.9	0
	1. φc Pc	2	679.5	897.5	7.6
	5. φc Pm	4	683.6	901.5	11.6
	4. φt Pt	20	695.4	904.6	14.7
	3. φt Pc	11	692.2	907.8	17.9
	6. φt Pm	13	696.4	911.8	21.9
Both collections	2. φc Pt	11	875.7	697.6	0
	1. φc Pc	2	883.2	700.1	2.5
	5. φc Pm	4	887.3	704.1	6.5
	3. φt Pc	11	892.8	711.1	13.5
	4. φt Pt	20	892.3	713.6	16.0
	6. φt Pm	13	897.0	715.1	17.5

TABLE 3 Cormack-Jolly-Seber models fitted to data from 2008 to 2019 for photo-identification and microsatellite genotype collections.

Abbreviations: ΔQAICc, difference in QAICc with the best-fitting model; φ, survival probability; AICc, Akaike Information Criterion; c, parameter is constant over time; m, parameter is heterogeneous; Npar, number of parameters; P, recapture probability; QAICc, Quasi-likelihood AICc; t, parameter varies with capture occasion.

FIGURE 2 Recapture probability of the fin whale (*Balaenoptera physalus*) estimated from CJS model (model 2 in Table 2) on genotype, photograph, and both collections, with associated 95% confidence intervals.

FIGURE 3 Abundance estimation for the fin whale (*Balaenoptera physalus*) with associated 95% confidence intervals, for photo-identification, microsatellite genotype, both collections, and corrected estimates from photographs.
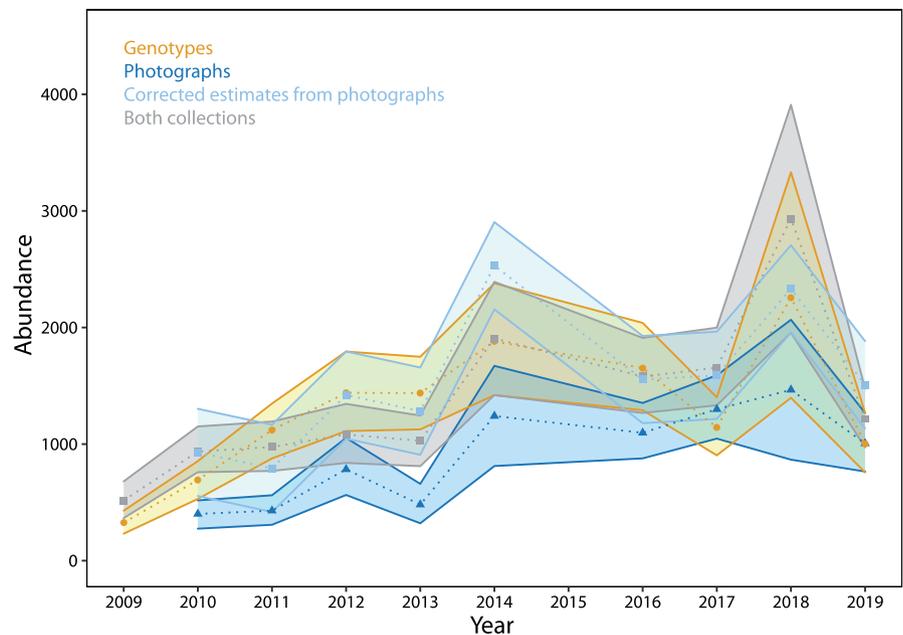
already confirmed (Forcada et al., 1995; Laran & Gannier, 2008; Tardy et al., 2016) and justified by a remarkable primary production during the summer when all Mediterranean become mostly oligotrophic, inducing a large abundance of krill *M. norvegica* (Labat & Cuzin-Roudy, 1996).

From the capture-recapture model, the total abundance obtained from the genotype collection, the combined collections and the photographs were similar, with estimates varying between 1200 and 1500 individuals. The estimate from the photograph collection was lower than the three others. This difference is due to the quality control applied to the photographs which considerably reduces the size of the final collection (Friday et al., 2008); by half in our case. With quality control, animals with no permanent marks and no distinguishable characteristics are excluded from the collection and subsequently in the estimate of total population size (Urian

et al., 2015). For this reason, the abundance was corrected to take into account unmarked individuals. The estimate from the genotype collection has a narrower confidence interval than the other estimates. Concerning the combined collections, we might expect to have a higher abundance, or at least a more precise estimate, than those from the two separate collections (Madon et al., 2011). Surprisingly, this was not the case. A method was developed by Madon et al. (2011) to estimate abundance from two sources of data, but they found that the abundance may be underestimated due to heterogeneity in recapture probability and due to the difficulty to obtain a correct adjustment factor, which is the 'Probability of true identity' (Bonner, 2013). For these reasons, we did not use this model.

It is not surprising that similar abundance estimates resulted from models which used the genotype collection and corrected

photograph estimates, as the data were collected at the same time and because the overlap between the two collections was high (45.6%). Another study presented similar abundance estimates and overlap at 16% for the New Zealand right whale population, between photograph and genotype collections (Carroll et al., 2011) due to data collected from the same platform. In another study which estimated the abundance of humpback whales in New Caledonia, the estimate from the genotype collection was higher than those yielded from the photograph collection (Constantine et al., 2012; Madon et al., 2011), and the inverse for a similar study conducted for the west South African population (Barendse et al., 2011) and likely dependent on the sampling effort regionally dedicated to each method. Indeed, by increasing the sampling effort, the number of recaptures will also increase and the abundance estimate will be more precise. Constantine et al. (2012) also mentioned the inclusion of transients in the genotype collection, which has important consequences on the estimation of abundance, especially for males. Our results indicate that independent of the best-fit model if the sampling effort is similar and estimates from photographs are corrected, the abundance estimates are similar.

In our case, slightly more precise abundance estimates were obtained from the genotype collection, equating to 1295 fin whales (95% CI: 1116–1474) which visit the north-western Mediterranean Sea during the summer season. Our estimates contribute to the knowledge about this species. The total number of fin whales present in the entire Mediterranean Sea was estimated at 1700 individuals from aerial survey and 13,300 from vessel survey (ACCOBAMS, 2021). The authors explained the high disparity by a lower level of coverage and number of sightings during the vessel survey than during the aerial survey. Their vessel estimate seems to be overestimated. However, other estimates exist at different spatial scales. At the occidental basin scale, 3500 individuals were estimated (95% CI: 2130–6027; Forcada et al., 1996), 2500 and 1800 in the northern part of this basin (Laran et al., 2017; Notarbartolo-di-Sciara et al., 2003) and 901 individuals (95% CI: 591–1374) in the Ligurian-Corsican-Provencal basin (north-eastern part of occidental basin; Forcada et al., 1995). Our spatial scale falls within the limits established by the two previously defined spatial scales, and the estimate we obtained from the genotype collection is congruent with previous ones, but rests in the low range. A recent estimate was done for the Pelagos sanctuary between 900 and 1200 individuals depending on the approach used for the model (Zanardelli et al., 2022) from a study period between 1990 and 2007. Our study area corresponds to the latter study but our estimate is higher and with more recent data. The slight difference may come from the different models used between the two studies.

The advantages and disadvantages of the two methodologies have already been previously addressed in detail (Friday et al., 2008; Lukacs & Burnham, 2005; Smith et al., 1999; Wilson & Delahay, 2001; Wright et al., 2009); for this reason, it will only be discussed briefly. We chose to use the estimates from the genotype collection for the reliability of the genetic identification of individuals. In this study, a large number of microsatellite markers were used (29) and a maximum

of eight missing data in the genotype were considered. Given that 14 markers are enough to identify an individual (Rew et al., 2011) and the probability of identity is low (Paetkau et al., 1995), we have considerably reduced the number of errors in the genotype due to mis-identification of microsatellites which would lead to an upward bias in abundance estimates by classifying recaptures as new captures (Lukacs & Burnham, 2005; Wright et al., 2009). Obtaining a biopsy is technically more complicated and invasive than taking a photo. However, biopsy sampling is considered minimally invasive as it does not involve capturing or handling the animal (Carroll et al., 2018), and a review study suggests it only has a short-term impact on the animal (Noren & Mocklin, 2012). Furthermore, the biopsy can also be used for many other research purposes (e.g. genetic structure, contamination loads, foraging ecology, etc.). A biopsy requires the person sampling to be much closer to the whale than what is required for the photographic approach, and may also introduce some individual heterogeneity in recapture probability. This could be a result of individuals responding differently to being approached by boats. Two different studies tested this hypothesis with datasets and analyses similar to those used in this study and found no evidence that whales avoided boats after the biopsy (Carroll et al., 2013; Constantine et al., 2012). Conversely, a study revealed that for 20% of re-sighted humpback whales, no biopsy was collected, suggesting that the whales seem to avoid the boat (Barendse et al., 2011). However, if this percentage is confirmed, we should observe a difference between the estimate from genotypes and the corrected estimate from photographs, but it is not the case. Furthermore, a potential heterogeneity in recapture probability was thus assessed in our analyses and was found to be negligible.

The CJS model used to estimate the abundance of the fin whale generated an individual apparent survival probability, that it is a product of true survival and permanent emigration/death. Apparent survival probabilities varied between 0.924 and 0.969 for the three models. These values are consistent with the estimated value for a whale population which is homogenously structured, with sexual parity (Buckland, 1990) and, are similar to that obtained from a fin whale study in the same study area (0.916 95% CI = 0.773–0.972; Zanardelli et al., 2022). These survival probabilities are also typical for a long-lived species (Bloch et al., 1993; Verborgh et al., 2009). These probabilities represent the survival probability of mature and immature individuals because they were indistinguishable from photographs and genotypes. Immature survival is typically lower than mature survival and survival probability tends to increase as the animal approaches maturity (Gaillard et al., 1998). It is thus likely that the actual value for mature individuals alone will be higher than those estimated in this study. This high probability of survival could also be less precise due to the short length of the study relative to the long generation time of the fin whale (25.9 years; Taylor, Chivers, et al., 2007), which is more than twice as long as the study period.

Our updated estimate of abundance and its trends will be useful for future fin whale conservation and management planning efforts in this area. The Mediterranean Sea is a biodiversity hotspot and includes a large number of cetaceans (Viale, 1985). The fin whale

is the second most commonly observed species after the striped dolphin, and migrates to the north-western part for feeding during summer, whilst the vessel traffic is high (Notarbartolo-di-Sciara et al., 2003; Panigada et al., 2006). Collisions with large vessels present a major conservation issue for the fin whale because they represent the primary fatal threat (David et al., 2022; Pace et al., 2015). The number of stranded fin whales from 1990 to 2009 was constant over time with an average of 2.5 individuals per year (Dhermain et al., 2015). Our photograph collection revealed that 3.3% of fin whales displayed marks from ship-strikes. This rate is higher than the rate that was estimated between 1990 and 2001 for the same region (2.4%; Panigada et al., 2006). The number of ship-strikes is underestimated for the fin whale because generally not all ship-strikes are reported. The percentage of scarred fin whales only represents the incidence of non-lethal ship-strikes and that the incidence of lethal ship-strikes is unknown. Estimates of abundance did not show a significant declining trend. Some slight variations are visible from 1 year to another, and as researchers previously explained, these variations could reflect the overall trend in the fin whale population (e.g. Gauffier et al., 2018; Laran et al., 2017; Laran & Gannier, 2008), or artefacts within the variability of inter-annual recaptures. The dataset in this study corresponds to a fraction of the Mediterranean population, and the Mediterranean fin whale migration seems to be complex with seasonal and annual variability (e.g. Geijer et al., 2016; Tepsich et al., 2020). Furthermore, detecting changes in abundance from abundance estimates is notoriously difficult for cetaceans as discussed by Taylor, Martinez, et al. (2007) and by Authier et al. (2020). Taylor, Martinez, et al. (2007) recommend annual surveys, over a minimum period of at least 15 years and the use of models that include covariates to remove some of the 'noise', which we did. However, to demonstrate these variations and the underlying reasons for them (anthropogenic or natural threats), ecosystem models and demographic parameters such as recruitment, immigration rate and birth interval, are needed.

AUTHOR CONTRIBUTIONS

Céline Tardy: Conceptualization; data curation; formal analysis; investigation; methodology; visualization; writing—original draft; writing—review and editing. **Denis Ody**: Conceptualization; data curation; supervision; writing—review and editing. **Olivier Gimenez**: Methodology; writing—review and editing. **Serge Planes**: Conceptualization; resources; supervision; writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

The datasets generated during and/or analysed during the current study are provided in the Supporting Information section.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.