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RESEARCH ARTICLE

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Long-term photo-identification study of fin whales in the Pelagos Sanctuary (NW Mediterranean) as a baseline for targeted conservation and mitigation measures

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Abstract

1. Historical abundance estimates are important for establishing baselines from which trends can be determined using more recent data. Long-term studies based on photo-identification were merged and used to estimate population size, survival rate and sex ratio (biopsy sampling) of fin whales in the North-western Mediterranean.
2. Merging four existing photo-id catalogues yielded a Mediterranean catalogue with 507 individually identified fin whales. Ninety-five (18.7%) individuals were resighted at least once during the study period (1990–2007): 71 whales were resighted in different years, 24 within the same season and 13 both in the same season and in different years. The number of resightings within-season ranged from one to four, over periods from 1 to 90 days.
3. Capture histories from these individuals were used in the capture–recapture analyses. Estimates of the animals present in the area each year between 1991 and 1995 through different modelling approaches were consistent: 900–1,000 from a POPAN open population model; 1,200 from a multi-sample closed population model; and 900–1,100 from simple two-sample closed population models for pairs of consecutive years, all with heavily overlapping 95% confidence intervals.
4. The estimated apparent survival rate of 0.916 (95% CI = 0.773–0.972) was lower than expected, which may be linked to temporary or permanent emigration, or mortality possibly owing to ship strikes.
5. Conservation and mitigation measures such as Important Marine Mammal Areas and Particularly Sensitive Sea Areas are presented and discussed.

Giuseppe Notarbartolo di Sciara and Simone Panigada should be considered joint senior authors.

KEYWORDS
abundance estimate, conservation management plans (CMP), fin whale *Balaenoptera physalus*, Important Marine Mammal Areas, mark–recapture, Mediterranean Sea, Particularly Sensitive Sea Area, photo-identification, survival rate

1 | INTRODUCTION

Fin whales (*Balaenoptera physalus*) are classified as Vulnerable worldwide (Cooke, 2018), while they are listed as Endangered in the Mediterranean Sea on the IUCN Red List of Threatened Species (Panigada, Gauffier & Notarbartolo di Sciara, 2021). The species is also listed in Appendices I and II of the Convention on the Conservation of Migratory Species, in Appendix II of the Bern Convention, in Appendix I of CITES, and in Annex 2 to the Protocol on Specially Protected Areas and the Biological Diversity in the Mediterranean of the Barcelona Convention.

Based on high cetacean density, the Pelagos Sanctuary for Mediterranean Marine Mammals (hereafter 'Pelagos Sanctuary') in the Corso-Ligurian-Provençal Basin was established in 1999 by Italy, France and the Principality of Monaco. This was the first marine protected area for marine mammals established in large part in the high seas (Hoyt, 2011; approximately 90,000 km^2) and in 2001 it was listed among the Specially Protected Areas of Mediterranean Importance under the framework of the Barcelona Convention (Notarbartolo di Sciara et al., 2008; Notarbartolo di Sciara & Agardy, 2016).

When compared with the rest of the Mediterranean, the Corso-Ligurian-Provençal Basin and the Gulf of Lion are characterized by high levels of offshore primary productivity, with a large biomass of highly diversified zooplankton (Astraldi, Gasparini & Sparnocchia, 1994; Astraldi et al., 1995), which attracts large marine vertebrates (Coll et al., 2012), including eight cetacean species (Notarbartolo di Sciara et al., 1993). Fin whales, the most common mysticete in the Mediterranean Sea, congregate to feed on the abundant euphausiid *Meganyctiphanes norvegica* in this area during summer (Notarbartolo di Sciara et al., 2003; Notarbartolo di Sciara et al., 2016).

Genetic evidence based on both mitochondrial and nuclear DNA indicates that fin whales sampled from the Pelagos Sanctuary are distinct from those in North Atlantic coastal waters of Canada, Greenland, Iceland and Spain (Bérubé et al., 1998; Archer et al., 2013). Further genetic analyses (Palsbøll et al., 2004) indicated that the same Pelagos Sanctuary fin whales may be largely resident in the basin, although limited but recurrent gene flow was detected in the data. However, evidence based on acoustic (Castellote, Clark & Lammers, 2012; Pereira et al., 2020) and stable isotope studies (Bentaleb et al., 2011; Giménez et al., 2013) revealed that two distinct populations of fin whales coexist in the Mediterranean Sea: the so called north-eastern North Atlantic population, and the true Mediterranean population (Notarbartolo di Sciara et al., 2016). The North-eastern North Atlantic fin whales apparently travel between the North Atlantic Ocean and the Balearic Region south of Spain through the Strait of Gibraltar (Pereira et al., 2020), while the true Mediterranean fin whales spend their entire lives in the basin, with moderate exchanges with the North Atlantic Ocean conspecifics (Gauffier et al., 2018; Gauffier et al., 2020). Palsbøll et al. (2004) estimated the effective number of migrant females between the Mediterranean Sea (Ligurian Sea or Pelagos Sanctuary) and the Eastern North Atlantic to be 0.33 migrants/year, a value that is consistent with the IUCN definition for a subpopulation (i.e. less than about 1 migrant/year).

Fin whales in the Mediterranean Sea face a number of anthropogenic pressures and threats. Ship strikes represent the major cause of non-natural mortality (Panigada et al., 2006). High levels of contamination by organochlorines, trace elements, DDT metabolites and endocrine-disrupting chemicals are likely to negatively influence the population's reproductive success (Fossi et al., 2003; Fossi, Casini & Marsili, 2007). Moreover, the recent recognition of high levels of microplastics in the main fin whale summer feeding habitat (Fossi et al., 2012; Cózar et al., 2015; Fossi et al., 2016) is causing additional ingestion of persistent, bio-accumulative and toxic compounds, with endocrine-disruption effects potentially affecting population viability (Fossi et al., 2012; Fossi et al., 2016). The potential effects of global climate change on this population are currently unknown, but cannot be ignored and need further investigation (Simmonds, Gambaiani & Notarbartolo di Sciara, 2012). For example, Mediterranean fin whales are largely dependent on euphausiid species such as *M. norvegica* and *Nyctiphanes couchii* (Panigada et al., 1999; Astruc, 2005; Canese et al., 2006) that are possibly susceptible to climate change effects (Tarling et al., 2010). Although each separate pressure may not be considered a major threat by itself, the cumulative effects (Crain, Kroeker & Halpern, 2008) in this heavily impacted semi-enclosed basin require the consideration of a precautionary approach for the conservation measures; indeed, there may be potentially large and detrimental effects on both birth and death rates.

Between 1992 and 2017 several surveys of fin whales were conducted across the North-western Mediterranean, with an emphasis over the Pelagos Sanctuary area: the results were often inconsistent with different abundances and density estimates provided. The first abundance estimate of Mediterranean fin whales, limited to the Pelagos Sanctuary area, was 901 individuals (CV = 22%, 95% CI = 591–1,374) in summer 1992 from a ship-based line transect survey (Forcada, Notarbartolo di Sciara & Fabbri, 1995). Additional ship-based line transect surveys, between 1991 and 1994 (Gannier, 1997) and in 2001 (Gannier, 2006), produced similar results (715 individuals (CV = 31%, 95% CI = 421–1,215)). In contrast, aerial line-transect surveys conducted during winter and summer 2009 over the entire area of the Pelagos Sanctuary estimated only 147 fin whales (CV = 27%; 95% CI = 86–250), a significant reduction in estimated numbers compared with previous surveys (Panigada et al., 2011). Additional aerial surveys conducted in summer 2010 estimated 330 fin whales (CV = 34%; 95% CI = 172–633) in the Pelagos Sanctuary area and 665 individuals (CV = 33%; 95% CI = 350–1,260) over a wider area that included the Pelagos Sanctuary, the Central Tyrrhenian Sea and waters west of Sardinia (Panigada et al., 2017a). Aerial surveys over the North-western Mediterranean Sea in winter 2011–2012 and summer 2012 (the French Exclusive Economic Zone, including the whole Pelagos Sanctuary and Spanish waters in the west) estimated fin whale abundance as 1,000 individuals (95% CI = 500–2,500) in winter and 2,500 individuals (95% CI = 1,500–4,300) in summer (Laran et al., 2017).

In summer 2018, the first synoptic survey was carried out across the Mediterranean Sea and contiguous Atlantic area, combining aerial and ship line-transect surveys and passive acoustic monitoring from vessels. Fin whale abundance, uncorrected for animals missed on the transect line, was estimated as 1,765 (CV = 27.9%; 95% CI = 1,028–3,031) in the Western Mediterranean Sea and 191 (CV = 82.2%; 95% CI = 46–790) in the Central Mediterranean Sea (ACCOBAMS, 2021). Bauer et al. (2015) calculated Mediterranean fin whales' availability at the surface as 0.245 (bootstrapped CV = 0.53), while Mannocci et al. (2018) calculated a similar value of 0.311, after Carretta et al. (2000). A specific correction factor for availability was calculated for this synoptic survey, resulting in a value of 0.538 for an average group size of 1.6 whales. The corrected estimate for fin whales in the Western Mediterranean Sea – between the western coast of Italy and the Strait of Gibraltar – therefore is 3,282 (CV = 30.85%) individuals (Panigada, Gauffier & Notarbartolo di Sciara, 2021).

Obtaining robust data on distribution, abundance and population dynamics are amongst the most important and challenging tasks for ecologists (Freckleton et al., 2006; Taylor et al., 2007). This knowledge is crucial for conservation purposes, for example as required by the European Union under the Habitats and the Marine Strategy Framework Directives (MSFD, 2017), as well as the Ecosystem Approach under the framework of the Barcelona Convention (UNEP-MAP, 2012). Such data are also needed to improve knowledge on cetacean status through trend analysis to facilitate the development of targeted conservation and mitigation measures.

For the purpose of this paper, photo-identification data for Mediterranean fin whales from 1990 to 2007 were used to estimate the population size, which was then compared with estimates obtained through line-transect surveys. In addition, photo-id data provided information for the investigation of survival rate, site fidelity and seasonal residence. The sex ratio was assessed through the genetic results obtained by biopsy sampling of free-ranging individuals. The merging of the photo-identification catalogues of four organizations (Tethys, GREC (Groupe de Recherche sur les Cétacés), EPHE (Ecole Pratique des Hautes Etudes)/EcoOcéan Institut and CEBC (Centre d'Études Biologiques de Chizé)) increased the sample sizes, which improved the fitting of mark–recapture models. The results obtained include robust baseline estimates of abundance from which trends over time can be assessed, thus providing valuable information to help conservation efforts focused on this Mediterranean fin whale subpopulation in the Pelagos Sanctuary area and beyond.

2 | METHODS

2.1 | Study area and field effort

The study area, data collection protocols and photographic/survey effort varied among the different research groups over the years in terms of platform used, study period and field-work area, with each research group working independently.

Tethys research cruises were conducted in the summer season, mainly between June and September, onboard auxiliary sailing vessels 15–20 m long, during 18 consecutive years (1990–2007). The research campaigns covered two different study areas, one in the offshore waters of the Western Ligurian Sea, between Sanremo, the French Riviera and North-west Corsica, and the second around Asinara Island (north-western Sardinia), mainly within the borders of the Pelagos Sanctuary (Figure 1). The survey effort was directed to maximize whale encounters within the study area and systematic tracks were not followed. Details regarding the study area and data collection protocols are available in Panigada et al. (2005), Panigada et al. (2008) and Lauriano et al. (2003).

GREC surveys were carried out on a 10 m sailboat from 1990 to 1994, and from a 12 m motor-sailer from 1995 to 2007. Surveys from both platforms were not dedicated to fin whale photo-identification, and therefore photographic data collection took place opportunistically. Fin whale summer distribution data were collected mainly within the Pelagos Sanctuary area (Gannier, 2002; Figure 1).

The EPHE/EcoOcéan Institut surveys were conducted from different sailing vessels ranging between 25 and 32 m in 1994 and 1995, mainly between June and September. These research campaigns were carried out in the North-western Mediterranean, within the Pelagos Sanctuary and adjacent waters. The study area lies between the French–Spanish border and the Island of Asinara, and between Cape Corse and Sanremo (David, Di-Meglio & Beaubrun, 2001; Figure 1). Photographic data collection for fin whale photo-identification was conducted opportunistically during the research surveys.

The CEBC provided pictures of a few individuals collected opportunistically in the Ligurian Sea during 2001 and during a satellite tagging project carried out in August 2003 (Cotté et al., 2009).

For photo-identification purposes, different SLR 35 mm cameras were initially used (e.g. a Canon EOS 100 and a Nikon F 90X), equipped with zoom lenses with different focal lengths, ranging from 70 to 300 mm, motor drive and data-back. The films used were black and white Ilford HP5, 400 ISO and Kodachrome slides. Digital cameras were used once they became available, using similar zoom lenses.

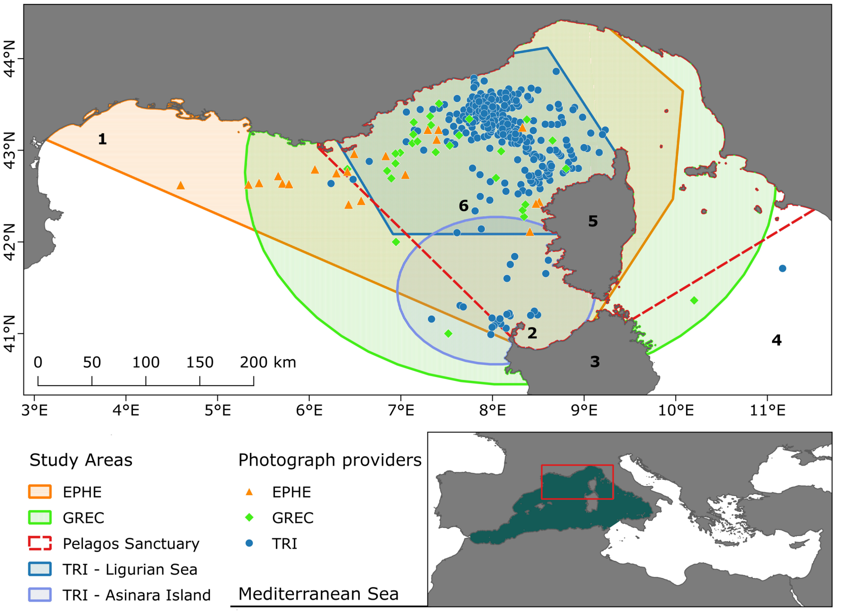

FIGURE 1 The study area in the Mediterranean Sea with the boundaries of the Pelagos Sanctuary and the areas covered by the different research groups (TRI A, Tethys Research Institute Asinara; TRI L, Tethys Research Institute Ligurian Sea; EPHE, Ecole Pratique des Hautes Etudes/EcoOcéan Institut; GREC, Groupe de Recherche sur les Cétacés). The dots represent all fin whales photo-identified by the four research organizations. Numbers on the main map represent toponyms: (1) Gulf of Lion; (2) Asinara Island; (3) Sardinia Island; (4) Central Tyrrhenian Sea; (5) Island of Corsica; and (6) Corso-Ligurian-Provençal Basin (formerly 'Ligurian Sea', centred at 42.5° N 7.8° E; https://www.marineregions.org/gazetteer.php?p=details&id=3983). The boundaries of the Pelagos Sanctuary are shown as a red dashed line. The green shaded area in the map inset represents the Western Mediterranean Sea subregion (sensu MSFD; https://dd.eionet.europa.eu/vocabularyconcept/msfd/regions/MWE/view?facet=HTML+Representation).

To define a fin whale as properly identified for photo-identification purposes, pictures of the dorsal fin, and of the right side (including both blaze and chevron) were taken, following the protocols developed by Agler et al. (1990) and widely used for this species (e.g. Whooley, Berrow & Barnes, 2011; Ramp et al., 2014).

2.2 | Photo-identification image processing and matching

The Tethys photo-id catalogue was considered the main one, with the largest number of individuals ($n = 437$) and covering a longer time interval; the three other contributing catalogues were defined as 'external'.

All of the images of photo-identified fin whales received from the three external research institutes were first reviewed to unify the format for data consistency. The matching process followed four steps: (1) matching within each single catalogue; (2) matching within the three external partners' catalogues; (3) matching with the main Tethys catalogue; and (4) merging into a single catalogue.

Each set of images of an individual was scored based on the presence of the different features (e.g. dorsal fin, blaze and chevron), allowing the identification of the single animal, combined with the photographic quality. Determination of photographic quality took into account focus, light conditions, distance and angle between photographer and animal, and the presence of water or spray on the body. This scoring system does not include the distinctiveness of a single individual (i.e. how nicks and scars may facilitate identification). As a result, a whale in a set of images was categorized as: (a) identified, first choice (when all the physical characteristics were captured with high photographic standards); (b) identified, second choice (when all the physical characteristics were captured but with not all photographic requirements satisfied); and (c) not identified.

A unique catalogue number was assigned to each individual whale categorized in the matching process as identified, both of first and second choice. Photographic matching was conducted using the naked eye using photographic prints and/or digital images on screen. To confirm re-sightings, photographic matches had to comply with criteria specified and applied by the North Atlantic Fin Whale Catalogue (Agler et al., 1990).

To ensure consistency, the lead author conducted the review of all catalogues.

2.3 | Estimation of apparent survival and population size

2.3.1 | Annual apparent survival

The annual apparent survival probability, incorporating mortality and any permanent emigration from the study area, was estimated based on the Cormack–Jolly–Seber (CJS) open population model (see, e.g. Amstrup, McDonald & Manly, 2005), which is the most robust capture–recapture model framework for estimating survival, and more robust than the POPAN model used below to estimate the superpopulation size. Prior to running models, goodness of fit (GoF) tests for the CJS model were conducted using the software U-CARE with the library R2ucare (Gimenez et al., 2018) in software R version 4.1.0 (R Core Team, 2021). The results of these tests showed no departure from the model assumptions tested. In particular, for Test 3.SR (newly encountered individuals have the same probability of being recaptured as previously encountered individuals), $\chi^2 = 15.4$, degrees of freedom = 11, $P = 0.163$; and for Test 2.CT (on any sampling occasion, missed individuals and captured individuals have the same probability of being recaptured in the next occasion), $\chi^2 = 8.3$, degrees of freedom = 11, $P = 0.686$.

Test 3.SR is often interpreted as a test of so-called 'transience', where a 'transient' individual is defined as an animal that is seen only once. If 'transience' is present in the data and is not taken into account in analysis, survival probabilities will be underestimated. Although this GoF test was not significant at the 5% probability level ($P = 0.163$), the sparseness of the data may have limited the power of the test to identify a significant effect and thus CJS models were investigated in which survival was modelled as two time-since-marking classes for (a) the first year after first capture (marking) and (b) for all subsequent years. These models are referred to as 'transient-class' models.

The sparseness of the data led us to model apparent survival probability, *ø*, as constant over time. The varying research effort across years led us to model the recapture probability, *c*, as varying over time.

The models considered were thus:

- *ø*(.)*c*(*t*) – constant apparent survival; recapture probability varying by time;
- *ø* (transient-class)*c*(*t*) – apparent survival varying by 'transient-class'; recapture probability varying by time.

Modelling was conducted using package RMark version 2.2.7 (Laake & Rexstad, 2008) in R.

Model selection was based on the small sample size formulation of Akaike's information criterion (AICc). To account for the impact of overdispersion in the data, from the result of the overall GoF test of the CJS model the value of '*c*-hat' = χ^2/degrees of freedom was calculated and used to adjust the AICc to the Quasi-Akaike's information criterion (QAICc), which was used for model selection (Burnham & Anderson, 2010).

2.3.2 | Population size

Because of the sparseness of the data, and because the different methods available make different assumptions that cannot be fully substantiated, several approaches were investigated for estimating the population size with the aim of using the results to draw the most supportable conclusions about the number of fin whales inhabiting the Pelagos Sanctuary during the study period.

To analyse the whole time series of data (1990–2007), the POPAN open population model was used (Arnason & Schwarz, 1995), which estimates a 'superpopulation', defined as the number of individuals that ever used the study area during the study period.

The POPAN model has four parameters: apparent survival probability, *ø*; capture probability, *p*; probability of entry into the study area, *pent*; and superpopulation size, *N*. As for the CJS survival models, *ø* was modelled as constant over time, and *p* was modelled as varying over time. The parameter *pent* was modelled as constant over time because of the sparseness of the data. Estimates of the number of animals in the study area in each year were derived from these estimates. The modelling was conducted using RMark in R.

Open population models cannot allow for capture probability to vary among individuals within a sampling occasion (year). Such heterogeneity is a common feature of cetacean photo-id capture–recapture datasets and can cause bias in estimates of population size if present but not accounted for (Hammond, 1986; Hammond, 2018; Hammond et al., 2021). To investigate the impact of heterogeneity of capture probabilities, multi-sample closed population models to estimate population size for the period in which the data were most plentiful – 1991–1995 – were used. Estimates were made using models in which annual capture probability was (a) assumed constant, model M_0; (b) varied over time, model M_t; and (c) varied over both time and among individuals, as modelled using the Pledger model formulation (Pledger, 2005), assuming a mixture of two groups of animals, model M_{th}. Recapture probability was assumed to be equal to capture probability in all models. Model selection was based on the AICc.

Applying closed population models to data from an open population leads to positive bias in estimates of population size and the magnitude of the bias depends on the period of time covered by the data (Hammond, 1986). To minimize this time period, a two-sample Chapman-modified Petersen estimator (see, e.g. Hammond, 2018) was also applied to consecutive pairs of years for the period 1991–1995. These simple estimates were calculated in a spreadsheet; 95% confidence intervals were calculated assuming that estimated population size was log-normally distributed (Burnham & Anderson, 2010). These models provide estimates for 'snapshots' in time that should be unbiased in this respect. However, they cannot model the heterogeneity of capture probabilities and so may generate negatively biased estimates of population size if this is a feature of the data.

2.3.3 | Biopsy sampling and genetic analysis

Biopsy samples were collected from free-ranging fin whales in the Pelagos Sanctuary only by the Tethys Research Institute between 1990 and 2007, using a modified biopsy dart with a stainless-steel tip and a crossbow (Palsbøll, Larsen & Sigurd-Hansen, 1991). Biopsy samples were taken from the dorsal area between the dorsal fin and the upper part of the caudal peduncle (Fossi et al., 2000) and were preserved in a saturated NaCl solution with 20% dimethylsulphoxide (Amos & Hoelzel, 1991). All samples were stored at either −20 or −80°C pending analysis.

Total cell DNA was extracted from all fin whale tissue samples using standard procedures with cell lysis by addition of sodium dodecyllauryl sulphate and Proteinase K digestion, followed by phenol/chloroform/isoamyl alcohol extractions and finally precipitation with ethanol (Sambrook & Russell, 2001). Sex was determined for all individuals as described by Bérubé & Palsbøll (1996a); Bérubé & Palsbøll (1996b). A chi-square (χ^2) test (Lindgren, 1975) for goodness of fit of the proportion of males to females against the 1:1 ratio observed in other areas was performed.

3 | RESULTS

3.1 | Survey effort

Research effort in the Pelagos Sanctuary and adjacent waters was mainly concentrated during the summer months – between June and September - characterized by calmer seas and lighter winds, compared with winter months, when strong north-westerly winds are predominant.

Figure 1 presents the different study areas of the four contributing partners. Tethys survey effort ranged between 1990 and 2007, with 78,000 km spent in favourable conditions and 2940 cetacean sightings. GREC data collection spanned the period 1990–2007, with 54,458 km covered on effort, resulting in 3,465 cetacean sightings of all of the eight species regularly present in the Pelagos Sanctuary (Gannier, 2006), including 841 encounters of fin whales.

The EPHE/EcoOcéan Institut collected data on cetaceans during different summer surveys in the North-western Mediterranean Sea between 1994 and 1995. In total, 9,693 km were surveyed on effort, with 778 cetacean sightings, including 240 encounters of fin whales.

The CEBC provided pictures of fin whales observed in the Ligurian Sea and Gulf of Lion in the summers of 2001 and 2003.

3.2 | Photo-identification effort

The Tethys photo-identification catalogue, updated to 2007, comprised 437 identified fin whales, including 32 individuals from the North-western Sardinian Sea (off Asinara Island; Figure 1). The collaborating research groups provided altogether pictures of 103 photo-identified whales. At the end of the photographic analysis, 507 fin whales had been individually identified and included in the Mediterranean fin whale catalogue (Table 1). Capture histories from these individuals were used in the capture–recapture analyses.

3.3 | Site fidelity and seasonal residence

Of the 95 (18.7%) fin whales resighted in the study period, 24 were observed in the same year, 71 in different years and 13 in both the same and different years. The 71 individual fin whales observed in multiple years presented a frequency of sighting from 2 to 6 times; the large majority, however, were observed in only two (80%) or three (14.5%) different years.

The dataset contains 37 fin whales resighted during the same field season, with animals observed up to four times over the whole summer. Intervals between sightings of at least 30 days for six fin whales were recorded, while one animal was first sighted in June and encountered again in September, 90 days later.

Different time spans were recorded between the first and the last sightings of individuals, with several individuals observed at multi-year intervals (Figure 2); the maximum time span between two sightings of the same individual was 17 years (1991–2007). A detailed table presenting the capture histories of all resighted individuals between 1990 and 2007 is available as Table S1 in the Supplementary Material.

TABLE 1 Summary of photo-identification effort for each research group, indicating the data collection time period, the number of identified fin whales, the number of resightings within catalogues and matches between groups, and finally the number of individuals included in the Mediterranean fin whale catalogue

Partner	Years	Identified whales	Resightings within catalogues and matches between groups	MED catalogue
Tethys	1990–2007	529	92 internal	437
GREC (Groupe de Recherche sur les Cétacés)	1990–1997	53	4 internal 12 with Tethys	37
EPHE (Ecole Pratique des Hautes Etudes)/ EcoOcéan Institut	1994–1995	43	13 with Tethys, 4 with GREC	26
CEBC (Centre d'Études Biologiques de Chizé)	2001, 2003	7	0	7
				507 individuals in total

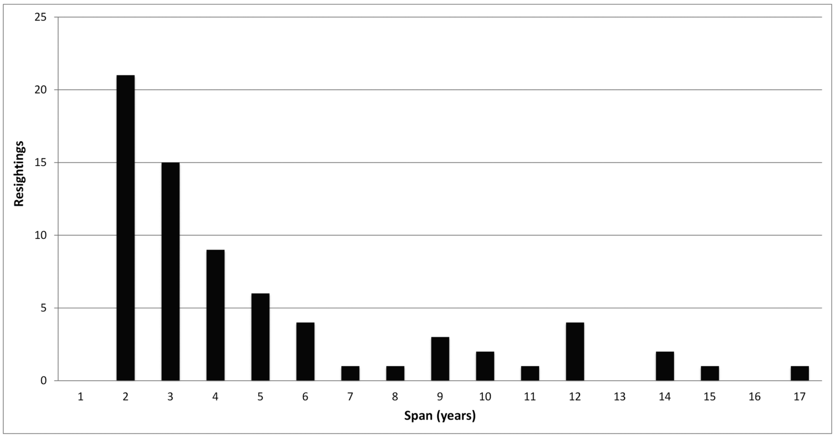

FIGURE 2 Histogram presenting the different time spans between the first and the last sightings of individuals.

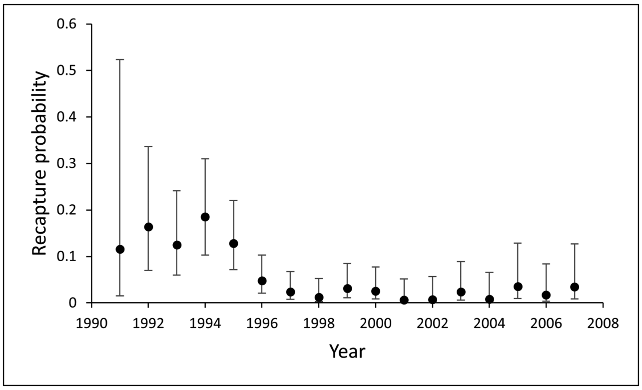

FIGURE 3 Recapture probability estimated from the CJS model ø (transient-class)*c*(*t*).

The temporal interval between resightings within the same season indicates that at least some individuals might spend the entire summer in the Pelagos Sanctuary, and points to a marked seasonal residence in the major summer feeding area in the Mediterranean Sea.

3.4 | Estimates of apparent survival probability and population size

3.4.1 | Apparent survival probability

From the overall goodness of fit test of the CJS model, *c*-hat was estimated as 1.165, indicating only mild overdispersion in the data. Using this value of *c*-hat, model ø (transient-class)*p*(*t*) had the most support from the data with the lowest QAICc and 70% of the QAICc weight. From this model, the annual apparent survival probability was estimated as ø = 0.916 (SE = 0.0457; 95% CI = 0.773–0.972) for non-transients (individuals seen more than once). For transients (individuals seen only once), the survival probability was estimated as ø = 0.555 (SE = 0.113; 95% CI = 0.336–0.754). Estimates of recapture probability, *c*, were highest in the early years of the study (1991–1995) but very low over most of the time series (Figure 3).

Model ø(.)*c*(*t*) had a delta-QAICc of 1.725 and 30% of the QAICc weight. The estimated survival probability from this model was ø = 0.883 (SE = 0.0415; 5% CI = 0.775–0.943).

Although the model that ignored the effects of transience had some support from the data, the model incorporating the effects of transience showed a clear effect and the estimate of annual apparent survival probability for fin whales in the Pelagos Sanctuary of ø = 0.916 (95% CI = 0.773–0.972) was selected as the best estimate.

3.4.2 | Population size

The estimate of superpopulation size from the POPAN model was *N* = 2,875 (SE = 434; CV = 0.15; 95% CI = 2,141–3,859). POPAN models incorporating the transient class were unable to estimate the survival probability adequately, but in the model without the transient class, the estimated survival probability was ø = 0.905 (95% CI = 0.790–0.960), similar to that from the selected CJS model. Estimates of capture probability, *p*, showed a similar pattern to the recapture probabilities estimated using the CJS model.

Estimates of the number of animals in the Pelagos Sanctuary study area for each year derived from the POPAN model are shown in Figure 4. The estimates increase slightly from 873 (SE = 337) in 1990 to 1,120 (SE = 519) in 2007 but they are very imprecise, so it is not possible to draw inferences about changes in the number of animals using this area from these results.

The best-fitting closed population model to estimate population size for the years 1991–1995 was model M_t, in which capture probability varied over time. Population size was estimated as *N* = 1,212 (SE = 154; CV = 0.13; 95% CI = 956–1,570). Estimates of capture probability for the 5 years were 0.040, 0.062, 0.055, 0.103 and 0.066. Model M_{th} was unable to distinguish an estimate of the mixture parameter from the null value of 0.5, indicating that the modelling of heterogeneity in this way was not supported. Model M_0 had a delta-AICc of 33.8 and thus had no support from the data.

Two-sample Chapman-modified Petersen estimates of population size for pairs of consecutive years are shown in Table 2. The number of recaptures is small but greatest for 1993–1994 and 1994–1995; estimates for these years are therefore the most precise. These estimates are consistent with those from model M_t, but considerably less precise.

3.5 | Test for sexual segregation

During the study period, 154 biopsy samples were collected in the Pelagos Sanctuary by Tethys between 1990 and 2007. Sex determination analysis revealed that 66 individuals (43%) were males and 88 specimens (57%) were females, which did not significantly differ from parity ($\chi^2 = 3.14$, 1 degree of freedom, $0.05 < P < 0.10$). Of those 154 biopsied samples, 47 individuals were apparently isolated and 76 individuals were encountered in groups of one to seven whales (33 sampling events). The sex ratio was compared in groups where a minimum of two biopsies were collected from the same aggregation. In all cases, no significant difference from a sex-ratio of 1:1 was found except between male–male pairs vs. female–female pairs (Table 3).

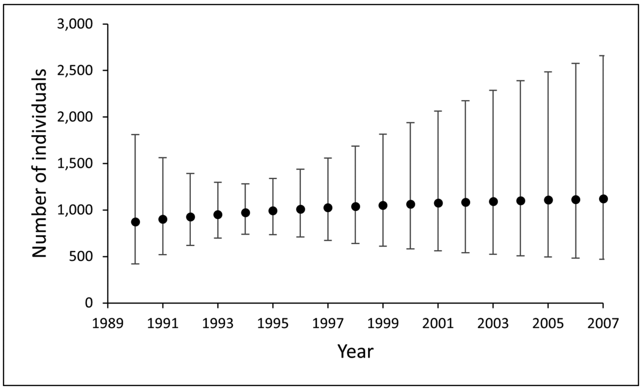

FIGURE 4 Number of individuals estimated to be in the study area each year, derived from the POPAN model.

4 | DISCUSSION

The results obtained provide valuable information to help conservation efforts focused on this Mediterranean subpopulation, in the Pelagos Sanctuary area and in the entire Basin.

4.1 | Site fidelity and seasonal residence

The resighting data point to the existence of a persistent site fidelity by whales to this feeding ground, with some individuals been re-sighted up to seven times, across time-intervals of up to 17 years.

Resightings also showed evidence of long-range movements of fin whales inside the Pelagos Sanctuary, with recaptures of whales sighted in different years in the Ligurian Sea and in the waters surrounding Asinara Island, on the south-western border of the Sanctuary. These movements over the years point to a wide use of the Pelagos area, where whales move around in search of prey and feeding where biomass is more abundant (Notarbartolo di Sciara et al., 2016; Panigada et al., 2017b). Seeing the same whales in different years, in the Ligurian Sea and off Asinara Island, which are around 170 nm distant, suggests a widespread use of a broader feeding area (Druon et al., 2012).

Fin whales' local occurence decreases substantially during the winter months (Laran & Drouot-Dulau, 2007; Panigada et al., 2011; Notarbartolo di Sciara et al., 2016; Laran et al., 2017). It is still unclear where fin whales go when they are not in the Pelagos Sanctuary. Some have been observed in late winter/early spring off the Island of Lampedusa in the Strait of Sicily, where a winter feeding ground was

TABLE 2 Number of captures in the first (n_1) and second (n_2) year, number of recaptures between years (m_2) and Chapman-modified Petersen estimates of population size (*N*) for pairs of consecutive years

Years	n_1	n_2	m_2	N	SE	CV	95% CI
1991–1992	48	75	3	930	388	0.42	424–2,041
1992–1993	75	67	5	860	298	0.35	444–1,665
1993–1994	67	125	7	1,070	325	0.30	598–1,914
1994–1995	125	80	8	1,133	326	0.29	652–1,969

TABLE 3 Summary of sex ratio analysis. Significant difference from a sex-ratio of 1:1 was only found in male–male pairs vs. female–female pairs (NS, non-significant, $P < 0.05$; S, significant, $P > 0.01$)

	Male individuals	Female individuals	χ^2 d.f.: 1	Total
Pairs (♂/♀)	8	16	2.66, NS	24 (12 pairs)
Pairs (♂♂/♀♀)	2	10	4.33, S	12 (6 pairs)
Single	18	29	2.57, NS	47

described (Canese et al., 2006). This was further corroborated by sightings of one whale (showing evidence of a collision with a ship), observed near Lampedusa in February 2005, and later twice in the Pelagos Sanctuary in May and September 2005 (Aïssi et al., 2008). Satellite transmitters deployed on fin whales off Lampedusa in March 2015 revealed the same migratory patterns (Panigada et al., 2017b). A reduced number of fin whales are found in the Pelagos Sanctuary also in winter (Clark, Borsani & Notarbartolo di Sciara, 2002; Lauriano et al., 2003; Notarbartolo di Sciara et al., 2003; Notarbartolo di Sciara et al., 2016), suggesting a permanence in the area throughout the year. Geijer, Notarbartolo di Sciara & Panigada (2016) analysed in detail the migratory patterns of Mediterranean fin whales, suggesting that the population in this area has adapted to a broad spectrum of feeding and breeding behaviours throughout the year and across the basin.

4.2 | Population size and survival

Capture–recapture estimates of population size and apparent survival probability for fin whales summering in the Pelagos Sanctuary are presented here for the first time. Merging existing photo-identification catalogues from different research groups operating in adjacent study areas in the North-western Mediterranean Sea provided a combined dataset that made this possible. The rationale for this *a posteriori* collaborative effort was that survey effort by each of the different research groups varied in time and area coverage and only by combining the data was it possible to obtain a reasonably comprehensive dataset. Nevertheless, estimated (re)capture probabilities were very low, less than 0.05, except for in the first few years of the study (1990–1995).

Considering all of the results from the modelling of population size, it can be inferred that the number of fin whales summering in the Pelagos Sanctuary was around 1,000 animals each year, from a larger population of 2,000–4,000 animals. In 1991–1995, the period with the most data available for analysis, estimates of the number of animals present each year were 900–1,000 from the POPAN model, 1,200 from the multi-sample closed model and 900–1,100 from the two-sample estimates for pairs of consecutive years. Analyses found no evidence of heterogeneity in capture probabilities, which is commonly a feature of cetacean photo-id capture–recapture studies. This result may have occurred because the diverse coverage of the multiple datasets provided more equal probability of capture over the study area than is typically the case.

Closed population models fitted to data from dynamically open populations generate estimates of population size that are positively biased. The size of the bias increases with the length of the time series and can be approximated by $1 - \phi^{s-1}$, where ϕ is annual survival probability and s is the number of study years (Hammond, 1986). Applying our estimate of survival probability of 0.916, it might therefore be expected that the multi-sample closed population model estimate of 1,212 is positively biased by approximately $1–0.916^4$, or around 30%. This would suggest an estimate of around 900–1,000, which is very similar to the estimates from the other methods that are not subject to such a bias.

These results compare very well with the line transect survey estimate of 901 (95% CI = 591–1,374) for 1992 (Forcada, Notarbartolo di Sciara & Fabbri, 1995) and are consistent with the estimated 715 individuals in the Pelagos Sanctuary from a ship-based survey in 2001 (Gannier, 2006). The consistency of these line-transect and mark–recapture estimates confer some confidence that a summering population of around 1,000 fin whales can be considered as a baseline from which to assess future trends in population size over time. An appropriate year for this baseline is 1995, because the closed population models use data from 1991–1995 and the estimates for subsequent years from the open population POPAN model are increasingly imprecise because of the sparseness of the data.

The very small number of recaptures in the data after 1995 probably reflects the reduced effort by Tethys Research Institute in offshore areas, resulting from a shift in focus towards more coastal and slope cetacean species (Azzellino et al., 2008). However, it may also reflect lower concentrations of fin whales in the areas covered by the research vessels, in agreement with data on fin whale distribution in the Ligurian Sea and adjacent waters (Panigada et al., 2005; Azzellino et al., 2012).

The low number of sightings in recent years (after 2010) supports the hypothesis of a more dispersed feeding area with fin whales distributed outside the study area, as observed over the last few years and discussed above (Lauriano et al., 2010; Druon et al., 2012; Arcangeli, Marini & Crosti, 2013; Arcangeli et al., 2014; Laran et al., 2017).

The estimates of population size presented here are derived from data collected in the western portion of the Pelagos Sanctuary only. However, considering the uneven distribution of fin whales (Panigada et al., 2011), with a marked preference for the western portion and very few sightings in the eastern part (Notarbartolo di Sciara et al., 2003; Notarbartolo di Sciara et al., 2016), the estimate may be taken as representative of the entire Sanctuary area. This is reinforced by satellite tracking data of fin whales tagged in the Western Ligurian Sea that remained in the western part of the Sanctuary, without moving eastwards (Cotté et al., 2009; Panigada et al., 2017b).

Our estimates of a ‘superpopulation’ of 2,000–4,000 fin whales, with the fraction summering in the Pelagos Sanctuary consisting of approximately 1,000 animals, implies that there is movement of fin whales between the Pelagos Sanctuary and contiguous areas, such as the Southern Gulf of Lion and Provençal Basin (Laran & Gannier, 2008). Forcada, Notarbartolo di Sciara & Fabbri (1995) and Forcada et al. (1996) found that only approximately one-third of the Mediterranean fin whale population was in the Ligurian Sea. The size of the annual estimates as a proportion of the estimated superpopulation compare very well with this.

A first estimate of annual apparent survival probability for Mediterranean fin whales for the period 1990–2007 is also presented. The point estimate of 0.916 (SE = 0.0457; 95% CI = 0.773–0.972) is lower than estimates for fin whales in the Gulf of St Lawrence of 0.955 (95% CI = 0.94–0.97) (Ramp et al., 2014) and 0.946 (95% CI = 0.910–0.967) (Schleimer et al., 2019), but the confidence intervals overlap.

Reasons for a lower-than-expected survival probability may include: (a) negative bias because of 'transient' animals; (b) permanent emigration; (c) temporary emigration/immigration if the pattern is not random; and (d) anthropogenic mortality additional to natural mortality. Our model took account of transient animals, so our estimate should not be biased in that respect. It is possible that animals could be emigrating permanently from the Pelagos Sanctuary but there is no information to confirm this. If this were the case, reasons could include disturbance from shipping and recreational boats or a reduction in available prey, as also suggested as possible explanations for a decline in fin whale survival and abundance in the Gulf of St Lawrence (Schleimer et al., 2019). Ship strikes are known to be a cause of additional mortality (Panigada et al., 2006); if the low estimate of survival rate is partly a result of additional mortality, it could be the reason behind the observed decline in abundance in the Pelagos Sanctuary (Panigada et al., 2011).

Indeed, ship strikes do represent one of the main human-induced causes of mortality for fin whales in the Mediterranean Sea (Panigada et al., 2006). The reported percentage of free-ranging whales presenting evidence of a ship strike argues in favour of the urgent need for appropriate mitigation measures within the framework of the International Maritime Organization to reduce lethal and non-lethal incidents, such as speed reduction and re-routing (Panigada et al., 2006; Panigada, Gauffier & Notarbartolo di Sciara, 2021).

4.3 | Sex ratio and group sizes

The molecular sex determination of individuals sampled in the Pelagos Sanctuary revealed the presence of 88 females and 66 males, which does not differ significantly from the expected parity, suggesting that no sampling bias occurred. This result corresponds to data reported earlier in the same locality but with a smaller sample size and from the estimates calculated from whaling logbook data which yielded a 1:1 ratio of males to females (Aguilar & Lockyer, 1987; Bérubé et al., 1998).

The group size of fin whales in this study ranged from single individuals to groups of a maximum of seven individuals. The comparison of the sex ratio in pairs and solitary individuals did not reveal any significant differences, except in groups of two individuals of the same gender, where female-only groups were more abundant than male-only groups (male–male, n = 1; female–female, n = 5). The reasons for this disparity are not clear at the moment; they could be related to the small sample size. A previous study on the analysis of 109 skin biopsies collected from free-ranging fin whales in the Gulf of St Lawrence detected a significant biased sex ratio, but towards males. That analysis, also based on a small dataset, suggests that the observed male-biased sex ratio could be due to group structure segregation where pods (groups of more than three whales) are mainly composed of males (Bérubé, Berchok & Sears, 2001).

4.4 | Collaborations

This paper demonstrates the positive outputs deriving from the establishment of collaborations between different research groups. In this particular case, only by merging existing datasets was it possible to perform robust analysis and estimate population parameters for the first time for this subpopulation. This long-term collaboration between different research groups has been an innovative and unprecedented initiative within the Mediterranean community of cetacean researchers.

4.5 | Management and conservation implications

This paper represents a contribution to an already rich body of information on the ecology of fin whales summering in the Pelagos Sanctuary, which was gained through several research efforts undertaken in recent years by a variety of research groups. This knowledge stands in stark contrast with our understanding of fin whale ecology in other parts of the Mediterranean and in other seasons, including their reproductive habits, which is still very fragmentary and hampers the implementation of regional conservation actions which would greatly benefit from a more complete overview of fin whale movement patterns and habitat choice.

Data on site fidelity within the study area revealed by the repeated successive sightings of individually recognizable whales reaffirm the importance of the Pelagos Sanctuary as a major feeding ground and critical habitat for the Mediterranean fin whale subpopulation. However, the data also confirm that the fin whale feeding habitat significantly extends westwards, as reflected by the boundaries of the 'North-western Mediterranean Sea Slope and Canyon System' Important Marine Mammal Area (https://www.marinemammalhabitat.org/portfolio-item/north-western-mediterranean-sea-slope-canyon-system/).

The site fidelity data, coupled with the reported evidence of ship strikes in the Pelagos Sanctuary and adjacent waters (Panigada et al., 2006; Panigada, Gauffier & Notarbartolo di Sciara, 2021), further corroborate the need for the designation of a Particularly Sensitive Sea Area under the International Maritime Organization framework, at a scale that includes the North-western Mediterranean Sea, Slope and Canyon Important Marine Mammal Area, plus the eastern portion of the Pelagos Sanctuary and the Spanish Cetacean Migration corridor, to take into account whale population movements and distribution. Zoning within the area with ship strike mitigation measures, such as speed restrictions and routing measures, would be essential as part of the Associated Protective Measures within the Particularly Sensitive Sea Area.

The mark–recapture population estimates presented here, by confirming estimates from the 1990s obtained from line-transect surveys, point to a decrease of fin whale numbers within the Sanctuary at present: summer aerial surveys carried out in 2009 and 2010 resulted in abundance estimates of 148 (CV = 27.4%) and

330 (CV = 33.9%) individuals, respectively (Panigada et al., 2011; Panigada et al., 2017a), compared with 860–1,133 whales as proposed by the present study for 1991–1995. This leaves the question open as to whether such a decrease is due only to the whales' redistribution, within the Mediterranean or elsewhere, or is indicative of a real population reduction. Further research is needed to understand why the Central Ligurian Sea has apparently lost part of its trophic interest for fin whales, to better describe the future patterns of the species' feeding habitats in the Mediterranean Sea. We suggest that the observed decrease in fin whale numbers within the Sanctuary in recent years (i.e. after 2010, Panigada et al., 2011; Panigada et al., 2017a) should raise concern for the species' conservation in the region. On such a basis, a recent reassessment of the Mediterranean subpopulation Red List status, previously assessed as Vulnerable (Panigada & Notarbartolo di Sciara, 2012), has resulted in a new listing as Endangered (Panigada, Gauffier & Notarbartolo di Sciara, 2021).

The International Whaling Commission (IWC) and the Agreement on the Conservation of Cetaceans of the Black Sea, Mediterranean Sea and contiguous Atlantic area (ACCOBAMS) have started to draft a Conservation and Management Plan (CMP) for Mediterranean fin whales. The overall goal of this CMP is to manage human activities that affect fin whales in the Mediterranean Sea in order to maintain a favourable conservation status throughout their historical range, based on the best available scientific knowledge. One of the necessary actions in the CMP consists of the creation and maintenance of a single, centralized photo-identification catalogue – in conjunction with a genetic-ID catalogue – to improve information on population structure and movements, abundance and trends, population parameters, scarring and threats.

This study represents the best cooperative effort on photo-identification for fin whales in the Mediterranean and future activities will stem from this joint conservation endeavour. The integration of information on Mediterranean fin whales from all areas where they are observed is of substantial value in understanding patterns of habitat use and the links between geographic areas, as well as in determining migration routes and wintering area location(s), where conservation and mitigation measures should be improved.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

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

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SUPPORTING INFORMATION

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

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