

Population estimation and survival rate
of
long-finned pilot whales (*Globicephala melas*)
in
the Strait of Gibraltar

By

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Abstract

The distribution of long-finned pilot whales in the Strait of Gibraltar is situated on the routes of cargos and ferries which expose them to risks of collisions and probably also acoustic and physical disturbances. They are also the main target of the whale watching companies. The aim of this study is to estimate the population and survival rate of long-finned pilot whales using photo-identification. Closed population models were applied using the program CAPTURE to estimate the population and the Cormack-Jolly-Seber model was used to estimate survival rate with the program MARK. A total of 5319 pictures representing 9865 individual pilot whales were analysed. Between 1999 and 2004, 192 marked pilot whales have been identified in the catalogue. Corrected population estimations during summer for 2002 is 259 (95% CI: 202-380), 2003 is 270 (95% CI: 206-415) and 2004 is 267 (95% CI: 238-330). The survival rate of adults between 1999 and 2004 is estimated at 0.976 (95% CI: 0.691-1.000; SE: 0.043). The same individuals have been observed all year round and from year to year which strongly suggests that there is a resident population formed by the same individuals of long-finned pilot whales in the Strait of Gibraltar. So far, the adult population does not seem to suffer great mortality. However, it is important to follow the population in the long term as a new important harbour is in construction on the Moroccan coast which will increase the passage of ferries and fast-ferries on the distribution area of the long-finned pilot whales. This offers the opportunity to follow the population on the long term and study the possible impacts on long-finned pilot whales.

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Declaration

This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree.

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STATEMENT 1

This dissertation is being submitted in partial fulfilment of the requirements for the degree of

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Date

STATEMENT 2

This dissertation is the result of my own independent work/investigation, except where otherwise stated. Other sources are acknowledged by footnotes giving explicit references. A bibliography is appended.

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1. Introduction

1.1. Cetaceans in the Strait of Gibraltar

Cetaceans are reported to occur regularly in the Strait of Gibraltar, however until recently, the distribution and abundance of cetaceans in the Strait of Gibraltar have been poorly described and is limited to a few references. One of them comes from data on commercial whaling activities that took place between 1921 and 1954 from land whaling stations based in Getares in Spain and Benzou in Morocco and from factory boats. It has been calculated that 826 sperm whales (*Physeter macrocephalus*), 4516 fin whales (*Balaenoptera physalus*) and 189 sei whales (*Balaenoptera borealis*) were captured during this period (Aloncle 1964, Aguilar and Lens 1981, Bayed and Beaubrun 1987, Sanpera and Aguilar 1992). Another study carried out from ferries uniting Spain to Ceuta, from March to May 1999, shows that most of the species found in the Eastern part of the Strait were striped dolphins (*Stenella coeruleoalba*), common dolphins (*Delphinus delphis*) and occasionally bottlenose dolphins (*Tursiops truncatus*), long-finned pilot whales (*Globicephala melas*) and sperm whales (*Physeter macrocephalus*) (Roussel 1999). Silvani et al 1999, in a study on incidental catches in driftnets in the western Mediterranean showed the abundant presence of common dolphins and striped dolphins in the Strait. However, none of these studies made references to the relative density, residence or absolute abundance of the cetacean species. The first study on relative density and distribution of cetaceans in the Strait of Gibraltar was carried out by de Stephanis et al (2005a) who showed that 7 species of cetaceans can be observed in summer and 6 of them on a regular basis. These are the striped, common and bottlenose dolphins, long-finned pilot whales, sperm whales and killer whales. The fin whale is the only species observed passing through the Strait (Salazar Sierra et al 2004), while the 6 other species are using it as a feeding ground (Laplanche et al 2004, de Stephanis et al 2005a and de Stephanis et al 2005b). The distribution of pilot whales occurs over significantly deeper depths and on the southern side of the Strait of Gibraltar (de Stephanis et al, 2005a).

The Strait of Gibraltar is also important for whale watching companies and the industry has been ever growing since 1982 (Pérez-Gimeno et al., 2002). It started with one boat and increased to 13 in 2001. Although the capacity of the boat has increased exponentially over the last years, the number of boats is now decreasing with only 4 whale watching boats going regularly to watch pilot whales in 2005. Pilot whales are the main target species of whale watching companies with bottlenose dolphins which made up 54% of the sightings, then striped and common dolphins (37% of the sightings) and occasionally sperm whales (6% of the sightings), killer whales and fin whales (1% each of the sightings) (Fernández-Casado, 2000).

1.2. The Strait of Gibraltar

The ecological importance of the Strait of Gibraltar for cetaceans is most likely to be related to the high productivity of this area induced by the oceanographic conditions of the Strait. The Strait of Gibraltar, is the only connection between the Mediterranean Sea and the Atlantic Ocean. The water mass circulation is characterised by a system of West-East currents. The Mediterranean Sea has a negative water balance due to the high loss through evaporation which exceeds the gains from precipitations and rivers. The currents in the Strait of Gibraltar are therefore the only regulation to this unbalance. The currents are formed by a surface flux of Atlantic waters entering the Mediterranean Sea and a deep counter-current of Mediterranean waters going to the Atlantic, each one with its own salinity (Lacombe and Richez, 1982). Water mixing also occurs through upwellings the force of which will depend on tides and bathymetry (Echevarria et al, 2002). This creates a nutrient rich environment in which cetaceans are abundant (de Stephanis et al., 2005).

The Strait of Gibraltar is also very important in terms of maritime traffic as it is the second most used natural navigation channel in the world (de Stephanis et al., 2000). Every year more than 80 000 vessels cross the Strait of Gibraltar. They consist mainly of cargos that use defined and controlled entrance and exit navigation routes of the Mediterranean Sea. They use West-East routes while ferries uniting Spain and Morocco travel on North-South routes. The distribution of pilot whales, sperm whales and killer whales is on these routes which exposes them to risks of collisions and probably also acoustic and physical disturbances (de Stephanis et al., 2003). Furthermore a new large

commercial harbor is under construction on the Moroccan coast of the Strait (Oued Rmel Harbor). In relation to this new harbour which will be completed in 2007, shipping traffic is expected to increase and new ferry lines, including fast ferry ones, will be crossing the main foraging habitat of the pilot whales.

1.3. Aims and Objectives

The aim of this study was using the photo-identification technique (i.e. the identification of each individual using the natural marking of their dorsal fin) to assess 1) the degree of residency of the pilot whale population in the strait from one year to the next and 2) the population size and 3) possible change in survival rate of pilot whales occurring in the strait of Gibraltar and their possible inter-annual variation. This information is critical if we want to be in position to assess the possible impact of the anthropogenic activity on the pilot whale population occurring in the strait, particularly in relation to i) the expected increase of maritime traffic and change of the shipping route associated with the creation of the new Tanger commercial harbor and ii) the increase of whale watching activity.

2. Material and methods

2.1. The study animal

2.1.1. Taxonomy of the long-finned pilot whale

Phylum: Chordate

Subphylum: Vertebrae

Class: Mammal

Subclass: Theria

Infraclass: Eutheria

Order: Cetacea

Suborder: Odontoceti

Family: Delphinidae

Subfamily Globicephalinae

Genus: *Globicephala*

Species: *Globicephala melas* (Traill, 1809)

Common name: long-finned pilot whales, blackfish, pothead, northern pilot whale, Atlantic pilot whale, caa'ing whale, and grindehval (Abend and Smith, 1999).

Long-finned pilot whales are a species closely related to short-finned pilot whales (*Globicephala macrorhynchus* Gray, 1846). However, the latter species lives in more tropical regions even though their distribution overlap in the Bay of Biscay. They have nevertheless never been observed in the Mediterranean Sea.

2.1.2. Morphology

Pilot whales have been well described from whaling in the Faeroe's Islands, Greenland and Japan and from the massive strandings occurring throughout the the world. Adult

males measure around 6 to 6.5m while adult females 4 to 5.5m. They can weigh over 2 tons. As well as differences in size, sexual dimorphism also occurs in other morphological characteristic such as the head which is more round for males. The dorsal fin is situated on the middle front of the body. Its shape and size also depend on the age and sex of the individual. Adult males have large and concave dorsal fins. Females have smaller and straighter dorsal fins than males. The pectoral fins, situated close to the head are very large (from 18 to 27% of the total body size) and have a pointed end (Figure 1.1 C) (Bloch et al., 1993c). The coloration is also characteristic and depends on the age of the individual: the younger are light grey while the adults are black or dark grey (Figure 1.1 A). Neonates and young calves can easily be recognised from natal folds (Figure 1.1 A). Pilot whales have an anchor-shaped white patch on the throat and the belly that can be seen when they spy-hop (Figure 1.1 B).

A.



B.



C.



Figure 1.1. Morphology of the pilot whale: A. Adult and calf with its natal folds. B. Juvenile spy-hopping with anchor-shaped white patch. C. Long pectoral fin characteristic of long-finned pilot whales.

2.1.3. General biology

They are gregarious animals that can sometimes form pods of more than hundreds of individuals; however they are mostly seen in groups of less than 50 individuals (Leatherwood et al., 1976). We often find them in company of other odontocetes such as bottlenose dolphins (Kraus and Gahr, 1971).

Squid are the preferred prey in all locations where information is available, although Atlantic mackerel and Atlantic cod may also be significant prey items on occasion. Pilot whales may change their distribution patterns as preferred prey species change in abundance (Abend and Smith, 1999).

Their reproductive cycle is rather long. Gestation lasts about 12 months and lactation (or nursing?) at least 20 months (Martin and Rothery, 1993), which represents the longest parental dependence period known for cetaceans! Females attain sexual maturity around 8-9 years old while males attain it only at the age of 12 to 17. The reproduction interval can reach 5 years. Females live longer than males and can attain more than 60 years while males live to 46-47 years old (Bloch *et al.*, 1993b).

2.1.4. Status

Long-finned pilot whales (*Globicephala melas*) are classed by the Cetacean Specialist Group on the CITES (Convention International on Trades of Endangered Species) and IUCN (International Union for the Conservation of Nature) red list as a species with lower risk and least concerns (CITES website, 2005). However, the North and Baltic Sea populations are classed in the Annex II of the CMS (Convention on Migratory Species) which defines a species that have an unfavourable conservation status or would benefit significantly from international co-operation organised by tailored

agreements are listed in Appendix II to the Convention (CMS website, 2005). For this reason, the Convention encourages the Range States to conclude global or regional Agreements for the conservation and management of individual species or, more often, of a group of species listed on Appendix II.

2.2. Distribution and population estimations

Pilot whales live in temperate and subpolar waters of varying depths, sometimes in pelagic waters and others in coastal waters (Abend and Smith, 1999; Van Canneyt et al., 1999). They can also be found on the edge of the continental shelf (Payne and Heinemann, 1993) and on some occasions they have been observed going up rivers looking for food. Some groups migrate from the coast to the open sea for feeding purposes (Abend and Smith, 1999). Long-finned pilot whales are present in the North-East Atlantic with a population estimated at 778 000 individuals (CV=0.30, Buckland et al., 1993). In the North-West Atlantic some surveys partially covered the area and showed that a population of 10 000 to 12 000 pilot whales were present between the Gulf of Maine and Hatteras Cape (Winn, 1982; Payne and Heinemann, 1993) and another population of 13 167 individuals live between Labrador and Newfoundland (Hay, 1982). Morphometric segregations have been shown between long-finned pilot whales living in eastern and western North Atlantic (Bloch et al. 1989b; Bloch and Lastein, 1993). They are also present in the Mediterranean Sea although few populations have been studied (Abend and Smith 1999; Baird et al. 2002). The importance of the Alboran Sea as a breeding and feeding ground has been documented (Cañadas and Sagarminaga, 2000). However, until now, no population estimation has been based on photo-identification and mark-recapture models. Photo-identification has been used to study social structure of long-finned pilot whales in Newfoundland (Ottensmeyer and Whitehead, 2003).

2.3. Photo-identification

2.3.1. Origin

Since several decades, biologists have needed to go further than simple species identification. Whether it is to study migration, social structure or behaviour, there is a need to identify each individual. In that aim, an incredible number of markings have been designed, such as rings for bird's legs or stickers on butterfly wings. Unfortunately, all these systems almost always need a physical recapture of the animal, which is far from easy and devoid of risk. To avoid these problems, the idea came to put markings that could be read from a distance. Thereafter, all sorts of colourful markings appeared on wings of large bird of prey, fluorescent rings on flamingo's legs, swan's necks and different kinds of marks on dolphin's fins.

If the recapture problem was partly solved, there were still some uncertainties about the reliability of the method. These marks may disturb the animals' life: a colourful patch on the immaculate wing of an aigrette may change its seduction advantages and therefore its reproduction success. A sticker on a butterfly wing could attract predators. In other words, are these animals still representative of the species?

At that time, some biologists that were following groups of animals such as gorillas or elephants pointed out that they were able to recognise each individual from particular external signs, scars, patches, deformities, etc. First sceptical on the validity on the long term and at a large scale of such a rule-of-thumb method, the scientific community had to come to the fact that it was working for many species once the right criterion was found. If a certain specific character was found on an individual it could be photographed and looked after in later pictures. Photo-identification was born.

This new method revolutionised many studies by offering unsuspected perspectives and research sectors inaccessible until now. Since then, there have been countless numbers of individual recognition files: African elephant ears, Scotian vipers cephalic scales, humpback whales flukes from all the oceans and Mediterranean Sea grouper patches are at the centre of all the attentions. To recognise an individual, it only needs to be captured on photographic films. Physical recapture disturbances or flashy markings are now a thing of the past. This procedure not only allows to monitor the movements of the animals but can also point out important life-histories events (births, reproduction, accidents, etc) and many other relevant biological aspects.

2.3.2. Applications

First, photo-identification consists of finding a character which is sufficiently variable within a species so that each individual has its own characteristics that has to be as stable as possible over time (at least during the time of the study) and that it can be easily photographed. It is for this reason that the characters chosen concern either the back of the cetaceans (e.g. the dorsal fin of bottlenose dolphins), or certain parts that are exposed at a precise moment (e.g. humpback whale's fluke when it is diving).

Once at sea, other challenges can arise: in South Africa for example, scientists often come across large groups of hundreds of bottlenose dolphins travelling at high speed. It is impossible to take good pictures of all the individual dorsal fins so they use high speed video cameras and later select the images to be archived, sorted out and analysed. There is not one photo-identification technique but a general principle with all its variants and tricks necessary to adapt it to the situation and the species studied.

Once the pictures are taken, the most fastidious step begins: sort out and match all the pictures with preceding ones in order to recognise an individual already identified. When there are only a few pictures of a few individuals it is rather easy. However, it soon becomes a daunting challenge when there are hundreds of individual files and thousands of pictures. Despite all the progress in computer science, it is still by eye and hands that most of the large photo-identification files are classified and compared.

Other aspects are taken into account: since we know the number of individuals identified and the re-contacts rate, we can deduce the population size. This method enabled to determine with great precision how many right whales were still present in Atlantic (International Whaling Commission, 2001). Bottlenose dolphin populations have also been largely studied in the world through this mark-recapture method (Wilson et al., 1999).

Many cetacean species have been studied using photo-identification and some populations are now entirely identified. The best examples are probably the resident killer whales of the Northeast Pacific where almost every individual is known. This

allowed the understanding of social structure and dynamics of the population and moreover of the species. Long term datasets of this population have been analysed extensively in order to understand what factors may influence their survival.

Bottlenose dolphins of Sarasota in Florida, USA have also been studied for long time through photo-identification. Population dynamics of the species could be understood by looking at index of associations between identified individuals. I showed that they have a fusion-fission dynamic in the population where individuals form group or association for short period of times then separate themselves to later form other groups with other individuals.

To estimate survival parameters in the field under natural conditions, one must follow individually marked animals through time. As early as the 1930's marked animals were used in the study of survival and other parameters (Jackson 1933, 1939). The emphasis in statistical methodology for such capture-recapture data was on the estimation of population size more than on estimation or comparisons of survival rates, whereas ecologists and evolutionists emphasised the structure of survival processes (Stearns, 1976, Charlesworth, 1980).

2.3.3. Pictures at sea

Since 1999, pictures of pilot whale's dorsal fin have been taken in the Strait of Gibraltar. From 1999 until 2000, pictures were taken from a whale watching boat (Fundación Firmm) with a Nikon camera equipped with a 100-300mm objective. From 2001 until 2002, pictures were taken from the research boat ELSA, a 10 m motorboat, of the research association CIRCE (Conservation, Information and Research on Cetaceans) with the same camera. From 2002 to 2004 a Canon EF100-400mm objective with image stabilizer was used on a Canon EOS-3 camera. In 2004, this objective was mounted on digital camera Canon 10D.

To photograph the dorsal fin, the animals are approached as close as possible to take pictures of the left side of the dorsal fin. The left side is the most accessible as they are

swimming most of the time against the predominant east current in order to stay on the same location. Therefore, the left side is facing south where it is best lit by the sun to take good pictures. A catalogue is made for the left side as analyses are using only one side. All the individuals in the sighting were photographed irrespective of their level of marking in order to have the same probability of captures for all individuals. Many pictures have more than one individual or dorsal fin on it because pilot whales are often in very compact groups and do not all have their dorsal fin above the surface at the same time. The term fin image will be used to talk about the representation of a single dorsal fin in a picture that can contain many others. The same method has been used since 1999 therefore all the pictures can be used and analysed in the same way.

2.3.4. Analyses of pictures on land

All pictures taken from 1999 to 2003 were revealed as colour slides named with the sighting number, group name, roll number and picture number. In 2004 all pictures were digital and renamed with the sighting number, group name and picture number. All the slides were looked at with an 8x magnifying eyepiece on a light table. Each picture was analysed and data entered in a Microsoft EXCEL database. Data consist of general information with sighting number, group name, roll number, picture number, total number of individuals in the picture, number of the individual analysed on the picture (starting from the closest individual to the furthest and from left to right in case of confusion when two animals are at the same distance); and of information on each individual with exposure of the fin (out of the water or not), angle, individual quality, code name of the individual, proportion of the back exposed and behaviour.

The angle starts from 0° when the animal is seen directly in front and goes around the animal every 30° (Fig. 1). This allows a selection of only the animals seen on the left side (from 240° to 300°) for the analyses.

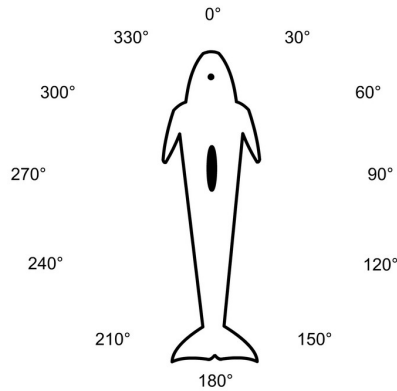


Figure 2.1. Angle description around the dorsal fin. The angle number is the position of the photographer.

A quality rating (Q) on a scale of 0 to 2 (poor to excellent) is assigned to each fin image based on image suitability in terms of five characteristics: focus, size, orientation, exposure, and the percentage of the fin that was visible in the frame:

Q 0: unusable individual dorsal fin when its representation is blurred, too far away or if the angle is between 330 and 30° or 150° and 210° (see fig. 1).

Q 1: medium quality representation of part of or the entire dorsal fin

Q 2: high quality representation of the entire dorsal fin

A code name is given to each individual identified in the catalogue under the following form: GM_GIB_XXX where GM stands for *Globicephala melas*, GIB for Gibraltar and XXX for the number assigned to each identified individual in the catalogue. Matches with previously identified individuals were made by comparing each new photograph, taken of the left side, with all the others in the catalogue. Animals that could not be matched were given a new identification number. The best slide of each individual for each sighting was scanned with a Nikon Coolscan III, in a 2700 dpi resolution which allows easier future matching with digital pictures.

The proportion of the back exposed is classed in 4 different categories:

0 when none of the back is exposed;

1 when 1/3 of the back is exposed behind the dorsal fin;

2 when 2/3 of the back is exposed behind the dorsal fin;

3 when the entire back is exposed behind the dorsal fin.

It can be used later to find certain individuals that have white fringes on the back e.g. individuals identified in M0 (Figure 2.3).

The behaviour is applied to individuals that don't show their dorsal fin and is classed under different categories: jump, caudal, underwater, on the side, on the back, spy-hopping and seen from above. This is only used to search for pictures of certain behaviours.

Each individual in the catalogue received a marking level (M) going from 0 to 3:

M0: individuals without any marks on the dorsal fin but with a specific shape and a white fringe on the back.

M1: individuals with small nicks that can only be seen on very high quality pictures.

M2: individuals with medium size nicks or many small ones

M3: individuals with characteristic nicks i.e. very deep or amputation of part or whole of the dorsal fin. They can be recognised on very low quality pictures.

The individuals not included in the catalogue will be named unmarked (Figure 2.2) while the individuals in the catalogue (from M0 to M3) will be called marked individuals. The individuals with marking level M0 and M1 will be called lightly marked and those with marking level M2 and M3 will be called well marked.



Figure 2.2. Unmarked individual not included in the catalogue



Figure 2.3. Individual with a marking level 0 (M0): it has no marks but a specific dorsal shape and a white fringe behind the dorsal fin on the back.



Figure 2.4. Individual with a marking level 1 (M1): 2 small nicks are shown by the black arrows.



Figure 2.5. Individual with a marking level 2 (M2): two medium size nicks are shown by the black arrows.



Figure 2.6. Individual with a marking level 3 (M3): deep and easily recognisable nicks.

2.4. Analyses

2.4.1. Population estimation

Mark-recapture models only estimate the size of marked individuals in the population (\hat{N}). Therefore, the total population size (\hat{N}') has been corrected by the correction factor \hat{c} or \hat{c}_{M2+M3} (see Equation 4, 5 and 6):

Equation 1:

$$\hat{N}' = \hat{N} \times \hat{c}$$

The same has been applied to the 95% Confidence Interval (CI) limits estimated by the program CAPTURE:

Equation 2:

$$L.CI(\hat{N}') = L.CI(\hat{N}) \times \hat{c}$$

$$U.CI(\hat{N}') = U.CI(\hat{N}) \times \hat{c}$$

where *L.CI* is the lower 95% CI and *U.CI* is the upper 95% CI.

The proportion of all marked individuals (M0, M1, M2 and M3) in the population is estimated in order to correct the estimation made by mark-recapture models in the program CAPTURE. A correction factor (\hat{c}) is calculated for each year:

Equation 3:

$$\hat{c} = \frac{\text{number of good quality fin images (Q2) of unmarked and marked individual s}}{\text{number of good quality fin images (Q2) of marked individual s (M0, M1, M2, M3)}}$$

This estimate assumes that, on average, the same numbers of best quality photographs (Q2) were taken of well-marked individuals as of lightly marked or unmarked ones (Ottensmeyer and Whitehead, 2003).

The proportion of well marked individuals (M2 and M3) over lightly marked individuals (M1 and M0) and unmarked individuals was also calculated for each year:

First the total number of unmarked individual was estimated through the correction factor calculated in Eq. 1:

Equation 4:

Total number of unmarked individuals=

Total number of marked individual identified $\times \hat{c} \times$ Proportion of unmarked individual s

Then the proportion of individuals M2 and M3 (\hat{c}_{M2+M3}) can be calculated:

Equation 5:

$$\hat{c}_{M2+M3} = \frac{\text{Total n}^\circ \text{ of marked (M0, M1, M2, M3) and unmarked individual s}}{\text{Total n}^\circ \text{ of individual identified in M2 and M3}}$$

Discovery curves of all marked (M0; M1, M2 and M3) and well marked (M2 and M3) individuals are produced to estimate how close we are to identifying most of the individuals in the population. Polynomial tendency curves of order 2 can produce a first rough estimation of the marked population at the inflexion point. This technique is only used to have an idea of how far we are from identifying most of the individuals in the population. A polynomial tendency curve will decrease after the inflexion point which will not be the case for the real discovery curve. A logarithmic tendency curve would be more realistic considering the kind of curve expected but would not give a specific value that could be used.

Two different estimations were then made for each year using mark-recapture models. First using all marked individual (M0, M1, M2 and M3), secondly using only well marked

individuals (M2 and M3). The latter estimation was done in order to decrease problems of recapture of less marked individual. All identifications of fin images in Q0 were not used in the analyses in order to decrease the highest probability of M3 individual being captured.

Within each year, different recapture histories were tested to see the influence of time and number of recapture histories on the estimations. Grouping of data was then applied at the level of 2 weeks, 1 week, 2 days, 1 day and a grouping where the number of individual captured was more or less equal for each session. Another session was done with all the sightings ungrouped.

Mark-recapture models for closed populations are used to estimate the number of pilot whales present in the population in the Strait of Gibraltar. These models are derived from the model M_0 that relies on four strong hypotheses (Otis et al., 1978; Pollock et al., 1990):

- H1.* The population is demographically and geographically closed;
- H2.* All the individuals have the same probability of recapture on each capture occasion;
- H3.* All the marks are clearly seen and recorded on each occasion;
- H4.* The marks are not lost;

H1. We assumed that the population was approximately closed, i.e. without mortality, births, emigration and immigration during the period studied i.e. only sighting during summer months were used for each year. From the study by de Stephanis et al (2005a) it can be seen that the distribution of pilot whales is mainly limited to the central deep channel of the Strait. Therefore, their geographical distribution is most probably closed as well.

H2. The hypothesis on same probability of capture can be overcome by three types of variation of the M_0 model:

- time variation (t)
- heterogeneity between individuals (h)
- behavioural response of the individuals to their first capture (b)

These models can be taken alone or combined as: M_b , M_t , M_h , M_b , M_{th} , M_{tb} , M_{bh} and M_{tbh} .

The program MARK has integrated the program CAPTURE that allows the selection of all the models and gives model criteria to assist in the choice of the right model. These models are then classified on a scale from 0 to 1, 1 being the best model to use. However, these criteria are not absolute and it is recommended to consider only the models coherent with observation conditions and the biology of the species studied (Pollock et al., 1990).

The behavioural response concerns the behaviour after the first capture in a trap i.e. the animal will either be attracted, indifferent or avoiding it. "Trap shy" behaviour (lower probability of capture following marking) will result in overestimation of population size; "trap happy" behaviour (higher probability of capture following marking) will result in underestimation (Wilson et al., 1999). As photo-identification uses existing marks it involves no physical interaction between animal and researcher in relation to the marking event and so behavioural responses of this type cannot occur (Wilson et al., 1999). Therefore, all the models with the effect of behaviour (M_b , M_{bh} , M_{tb} and M_{tbh}) have not been considered.

H3. All the individuals in the sighting are photographed irrespective of their level of marking. An effort is also made to make sure that all the individuals have been well photographed so that there is at least one good picture of each individual. Marking histories of each individual have also been created in order to follow the evolution of the marks. Nicks on the dorsal fin are conserved for years but can evolve for example when new nicks appear around an older one.

H4. Nicks are not lost over the study period as individuals identified in 1999 still have the same nicks in 2004.

All fin images of quality Q0 were not used in the analyses in order to decrease the highest probability of M3 individual being captured.

2.4.2. Survival rate

Annual capture-recapture data is analysed with Cormack Jolly Seber (CJS) model in the program MARK in order to estimate survival and recapture probability. This model stands on the following hypothesis (Pollock et al. 1990):

H1. All the individuals have the same capture probability p at the occasion t ;

H2. All the individuals have the same survival probability F between the occasions t and $t+1$;

H3. Marks are not lost;

H4. Capture occasions are short in time compared to the interval between two successive occasions.

The CJS model considers a survival probability F and a capture probability p that can both vary with time which is noted as model $F_t p_t$.

H1 and *H2*. First the goodness of fit of the model $F_t p_t$ is tested in the program U-care (Choquet et al., 2003) developed by the University of Montpellier (France) which tests the assumptions made by the model $F_t p_t$ i.e. the first and second hypothesis mentioned above (*H1* and *H2*). This program looks for the effects of transience and trapping dependence of certain individuals in the population. Transient individuals would be individuals captured in a certain year and not seen afterwards while trap dependent individuals would have different capture probabilities over time. They can be either trap-happy or trap-shy. Trap-happy individuals have a higher capture probability after the first capture while trap-shy individuals would have a lower capture probability after the first capture. The program does X^2 tests to see which factor would influence the model between each occasion and for all the occasions.

Then two possibilities arise from these results:

1. The data can be changed to get rid of the transients. Then all the first captures of all the individuals are deleted which has the effect of removing all the individuals with a single capture between 1999 and 2004 from the dataset. This means that data is lost and the estimation is from 2000 to 2004 but it maintains the CJS model hypotheses.

2. The models can be adapted to take into account the effects of the two factors. In the program MARK it is possible to adapt the parameters used to estimate the survival probability or the capture probability so that each factor is analysed independently. If the survival probability changes between transient and resident individuals the model is able to make the distinction between the two and give survival estimations for both. The same is true for trap-dependent individual for which capture probability can change. The model will then give capture probability estimations for trap-dependent individuals and non-trap-dependent individuals.

Capture probability can also be adjusted with the photographic effort per year. Here, the total number of fin pictures in quality Q1 and Q2 (the only one taken into account for the analysis) per year (see Figure 3.2) has been used. All the models have been adjusted in MARK (White and Burnham, 1999) that enables the choice of the most parsimonious models i.e. the one explaining a maximum of variability with a minimum of internal parameters. This is done by the calculation of the Akaike's Information Criterion (AICc) adjusted to the sample size (Hurvich and Tsai, 1989):

Equation 6:

$$AICc = -2 \log(L) + 2K \left(\frac{n}{n - K - 1} \right)$$

where L is the model likelihood, K is the number of parameter and n the sample size. The program also gives the number of estimable parameters in the model, its deviance and the AICc weight (a measure of the model likelihood in the presence of other models, Williams et al., 2002). Finally it can estimate the parameters following the method of maximum likelihood and integrates a model averaging which does a mean of the models conserved weighted by the AICc weights.

H3. The marks were not lost over the study period as explained in *H4* for closed population estimations.

H4. The capture occasion was only the summer months grouped as one occasion while the interval between occasions is one year. Therefore we considered that this hypothesis was respected.

Survival probability is function of the capture probability. The latter is given in the model and through the logit (p) function we can find the intercept and the slope of the function (β_0 is the intercept and β_1 the slope). These values are given by the program MARK as the beta functions of the parameters used for the capture probability function. Because the capture probability is corrected by the photographic effort, we can derive the annual photographic effort needed to obtain a certain capture probability that would give good estimation of the survival:

Equation 7:

$$p = \frac{e^{\beta_0 + \beta_1 x}}{1 + e^{\beta_0 + \beta_1 x}}$$

Where p is the capture probability, β_0 is the intercept, β_1 the slope and x the number of pictures.

3. Results

3.1. Photo-identification

A total of 5319 pictures representing 9865 pilot whales, i.e. a given picture can include several individuals, of which 6723 individual dorsal fins have been analysed for a total of 107 sightings realized over 76 days in the Strait of Gibraltar. From these, 3142 were fin images of quality Q0, 1864 of Q1 and 1717 of Q2. From 1999 to 2004, a total of 192 individuals have been identified in the catalogue (Appendix 4) with 1 individual marked M0, 108 marked M1, 58 marked M2 and 25 marked M3.

Only individuals with nicks were used in the catalogue as scars tend to disappear over weeks or months and completely disappear over a year (Figure 3.1) (unpublished data). This was observed on well marked individuals (M2 and M3) which were observed regularly. Although some deep scars could still be observed after 4 months, it was not the case for all scars (unpublished data). Only 6 individuals, which represents 3.1% of the individuals identified, gained new nicks between 1999 and 2004. This shows that it is a good marker to be used in long term studies.

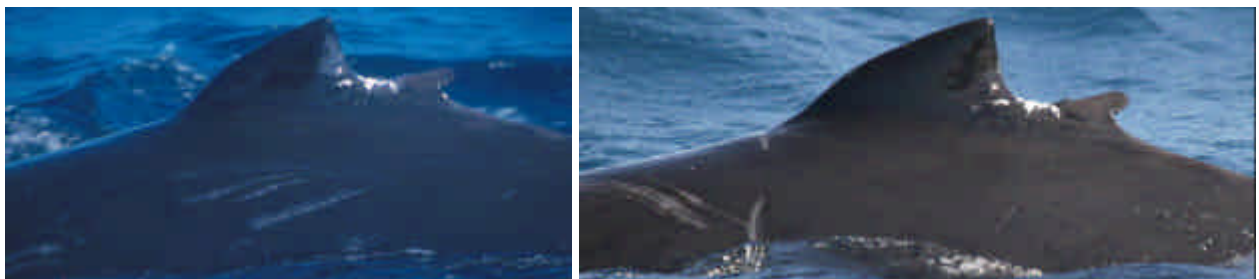


Figure 3.1. The same individual (GM_GIB_011) observed on the 28th of July 2003 and on the 7th of July 2004 with different scars on the back around the dorsal fin.

The correction factor \hat{c} is estimated at 1.53 for the entire dataset (Table 3.1). This corresponds to 65% of marked individuals in the population. However, different \hat{c} and \hat{c}_{M2M3} are calculated for each year as the ratio of marked individuals changes (Table 3.1). This ratio varied greatly between years.

Table 3.1. Estimation of the correction factors \hat{c} and \hat{c}_{M2M3} per year and mean for all years.

	1999	2000	2001	2002	2003	2004	All years
\hat{c}	1.90	2.47	2.18	1.90	1.71	1.37	1.53
\hat{c}_{M2M3}	3	3.6	3.6	3.13	2.91	3.17	3.54

Each year has a different photographic effort that is reflected by the total number of individuals identified (Figure 3.2). The curve of total individual identified follows the number of fin analysed in quality Q1 and Q2 and not the total number of fin analysed. As fins in Q0 were most of the times not identified this was expected. The ratio between the total number of fin analysed and the fin in Q1 and Q2 has a mean of 2.53 (SD: 0.83) from 1999 to 2003 while the ratio was only 1.17 for 2004.

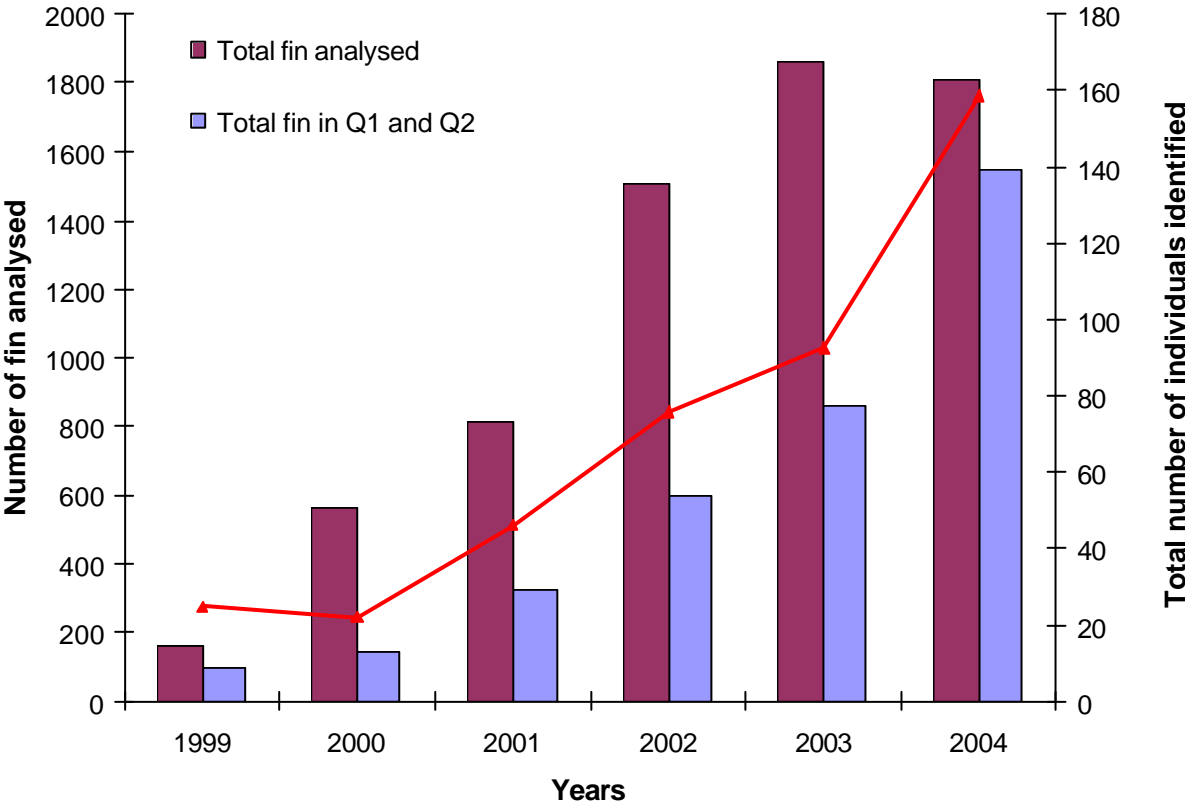


Figure 3.2. Photographic effort and total number of individuals analysed per year

The curve of total individuals identified can be broken into new individuals identified and recaptured individuals (Figure 3.3). It can be seen that the discovery rate of new individual is quite constant from 1999 to 2003 with a mean of 26 individuals newly identified per year (95% CI: 20-32) and increases greatly in 2004 with 60 individuals newly identified. On the other side the number of individual recaptured is increasing almost linearly since 1999 to 2004.

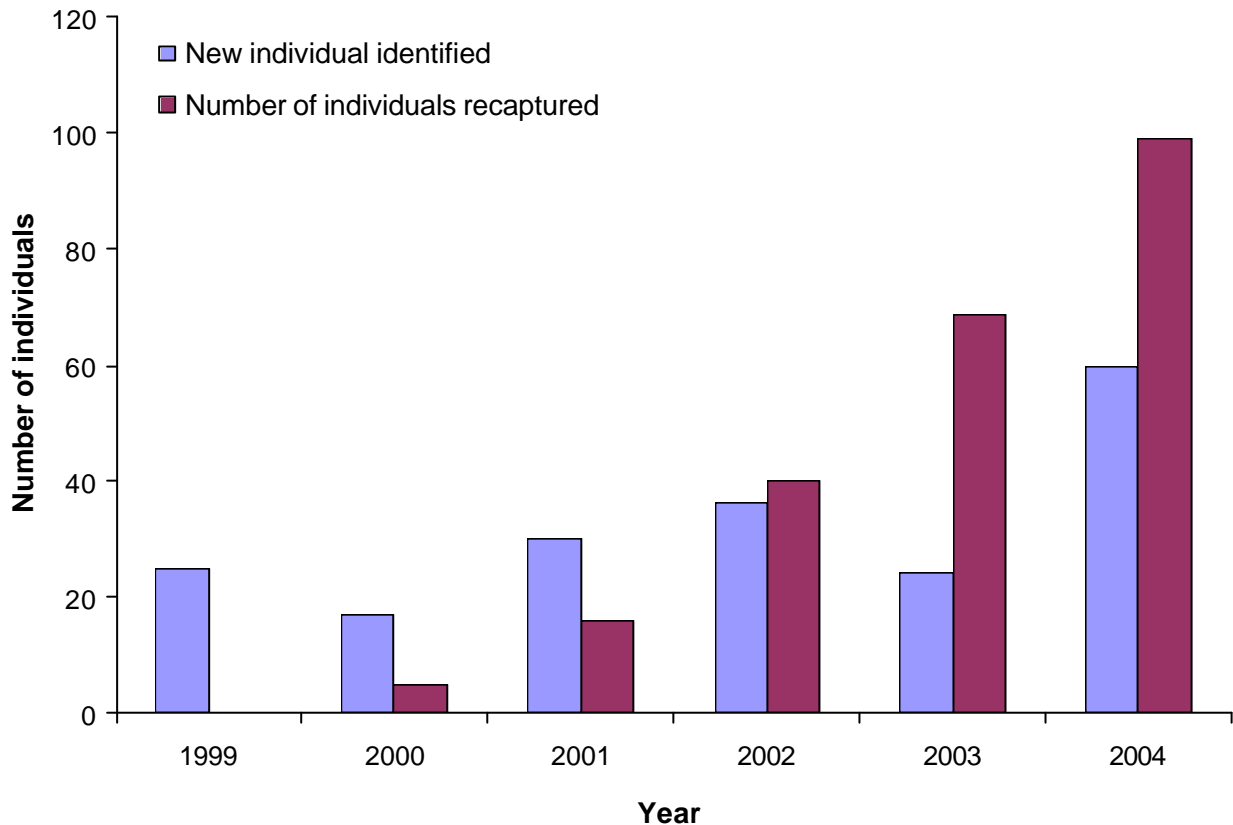


Figure 3.3. Comparison between the number of new individuals identified and the number of individuals recaptured per year.

3.2. Population estimation

3.2.1. Discovery curves

As shown in Figure 3.4, the discovery curve of all individuals indicates that we should still identify new individuals because the asymptote has not been reached yet. The

tendency curve of all individuals $y = -0.0066x^2 + 2.4119x$ ($R^2 = 0.9921$) estimates that 220 individuals should be identified in the population after 185 sightings which is where the polynomial tendency curve makes the inflection. If we correct this number with the correction factor \hat{c} for all years (Table 3.1), we can make a first rough estimation of most of the individual of the population of **337 pilot whales**. However, the tendency curve ($y = -0.0074x^2 + 1.5361x$; $R^2 = 0.9908$) for animals marked M2 and M3 made the inflection before even reaching the maximum number of pilot whales identified (Figure 3.4). This suggests that for this category of animals most of individuals have been identified. With 83 pilot whales identified as M2 and M3 corrected by the correction factor \hat{c}_{M2M3} for all years (Table 3.1) the second rough population size estimation is around **294 pilot whales**.

The percentage of previously identified individuals that have been recaptured in a year has also increased over the years, with only 20% in 2000, 38% in 2001, 55.6% in 2002, 63.8%, in 2003 and 75% in 2004. This increase also suggests that we are reaching the identification of most of the population.

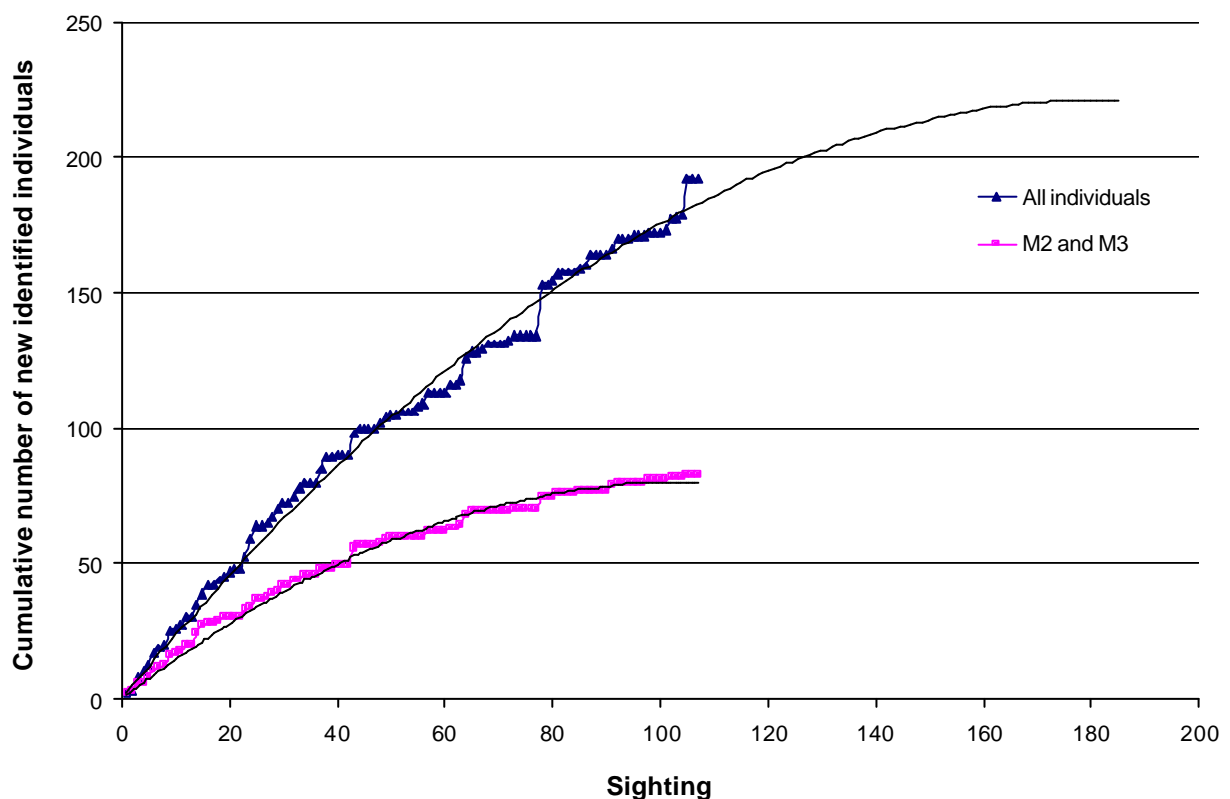


Figure 3.4. Discovery curve of all identified and marked M2 and M3 pilot whales with their tendency curve.

3.2.2. Mark-recapture models

The models M of Darroch (Darroch, 1958) and M of Chao (Chao, 1989) have been chosen for the population estimations of 1999, 2000 and 2001 where very few recaptures took place and therefore heterogeneity is very unlikely to occur (Chao et al., 1992). As the number of captures were greater than the number of recapture it is recommended to use the estimator of Chao (1989): capture frequency for 1999 (f_1 to $f_9 = 21, 4, 0, 0, 0, 0, 0, 0, 0$), for 2000 (f_1 to $f_7 = 20, 2, 0, 0, 0, 0, 0$) and for 2001 (f_1 to $f_{13} = 43, 3, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0$). The following year, 2002, 2003 and 2004 had many recaptures and both time and heterogeneity were most likely to affect capture probabilities. Therefore the model M_{th} (Chao et al., 1992) has been used to estimate the population.

As seen in Figure 3.2, the number of pilot whales identified is not the same for each year. From 1999 to 2001, the effort is not considered to be good enough to make realistic population estimation. All three years have large coefficient of variation ($CV(\hat{N}) > 0.43$). The estimation produced for 1999 do not come close to the number of individuals already identified. The estimation for 2000 is close to the other estimations made in 2002 and after however the 95% confidence interval is very large (from 111 to 953 individuals) which means that it has very little power. Finally the estimation for 2001 is well over all the other estimations. Therefore, these years will not be considered any further for the analyses of mark-recapture and no analyses for well marked individuals have been done as it would reduce even more the already small dataset which would give even more biased estimations.

The estimations for 2002, 2003 and 2004 are all close to each other whether all marked individuals or only well marked ones were used in the analyses varying from 259 (95% CI: 202-380) in 2002 to 298 (95% CI: 231-429) pilot whales in 2003. All the estimations for these three years fall within the 95% confidence interval of the others. The most precise estimations is given by the year 2004 that had a low coefficient of variation (0.08 for well marked and 0.07 for all marked individuals). It can be observed that the 95% CI

for the estimations using well marked individuals is each time larger than when all the marked individuals are used to make estimations.

Table 3.2. Population estimations corrected (\hat{N}') per year for all marked individuals (M0, M1, M2 and M3) and well marked individuals (M2 and M3) with the model used: M_t C. = model M_t of Chao (Chao, 1989), M_{th} = model M_{th} of Chao (Chao et al., 1992); coefficient of variation (CV) and 95% confidence interval (95% CI).

Year	Marking level used	Number of occasion	Model used	CV	Population estimation corrected	95% CI corrected
1999*	All marked	9	M_t C.	0.38	118*	70-268
2000*	All marked	7	M_t C.	0.53	191*	92-550
2001*	All marked	13	M_t C.	0.47	440*	210-1113
2002	All marked	16	M_{th}	0.17	259	202-380
	Well marked	15	M_{th}	0.17	260	194-423
2003	All marked	10	M_{th}	0.16	298	231-429
	Well marked	10	M_{th}	0.18	270	206-415
2004	All marked	18	M_{th}	0.07	273	246-323
	Well marked	18	M_{th}	0.08	267	238-330

*Estimation unrealistic and not considered due to lack of data for the year.

Different grouping of data have been tested in order to see the influence of occasion number. However, no great changes occurred between the different grouping of occasion (Appendix 1 and 2). The results presented in Table 3.2 are on a daily occasion which is the most in accordance with the different hypotheses of the mark-recapture models.

3.3. Survival rate

The goodness of fit for the model $F_t p_t$ showed that there was transience and trap-dependence in the dataset (*Quadratic* $X^2=20.51$, $p=0.0117$ for transience and $p=0.0306$ for trap-dependence).

Therefore both approaches were tested:

1. Integration of transience and trap-dependence in the model;
2. All first captures deleted.

3.3.1. Transience and trap-dependence models

The AICc of model 4 is smaller than model 5 which shows that capture probability (p) varies with time. Models 2 and 3 are better than model 4 which shows that there is an effect of the photographic effort on the capture probability. Model 1 is better than model 2 and 3 which means that the survival rate is constant over time. The results from the best model taking into account the variables made a **survival estimate of 1 for the “residents” and 0.8362 (SE: 0.0341) for the “transients”**. These results would imply that “transients” would have a very low survival rate while the residents would “never” die. Therefore, another method was used which consists of a model averaging the first three models that have a delta AICc less than 2 which means that they have an equal weight in the data (Anderson and Burnham, 1999). However the model averaging of the program MARK does take into account the AICc weight. Only the parameters for “resident” group have been averaged in order to have more realistic survival rate estimation. A mean **estimate of all the survival rate parameters used in the three different models gave an estimation of 0.976 (SE: 0.043; 95% CI: 0.691-1.000)** (see Appendix 3 for full results).

Table 3.3. Selection of survival model taking into account transience (F_{a2}) and trap-dependence (p_m) for pilot whales between 1999 and 2004. The most parsimonious model is the one with the smallest AICc value. N.P. is the number of parameters used in the model.

N°	Model	AICc	Delta AICc	AICc weights	Model likelihood	N. P.	Deviance
1	$F_{a2} p_{effort+m}$	306.726	0.000	0.4141	1	4	132.543
2	$F_{t^*a2} p_{effort+m}$	307.366	0.640	0.3006	0.726	8	124.335
3	$F_{t+a2} p_{effort+m}$	308.086	1.359	0.2098	0.507	8	125.054
4	$F_{t^*a2} p_{t+m}$	310.133	3.407	0.0754	0.182	10	122.459
5	$F_{t^*a2} p_m$	323.748	17.02	0.0001	0.001	5	147.405

3.3.2. Models with first capture deleted

As all the first captures are deleted, we are losing the estimations between 1999 and 2000. However, the effect would not be very important considering the little data available for both years (see Figure 3.2). Once the first capture deleted, neither transience nor trap-dependence could be detected in the dataset by the goodness-of-fit (*Quadratic* $X^2=2.6395$, $p=0.68122$ for transience and $p=0.65972$ for trap-dependence). Therefore, only the effect of time and photographic effort could influence the models. The AICc of model 2 is inferior to model 3 and 4 which shows that there is an influence of the photographic effort on the capture probability. The model 1 is preferred to all the other models which indicate that the survival rate is constant over the years. Therefore, the model used is $F p_{effort}$ which means that the survival probability does not change over time and that the capture probability is corrected by the effort. **The survival rate is estimated at 0.965 (SE: 0.029; 95% CI: 0.835-0.993)** between 2000 and 2004. The photographic effort varied greatly from one year to the next, therefore the capture probability was most probably influenced by this factor. This is reflected in the results with p increasing over the years (Figure 3.5).

Table 3.4. Selection of survival model for pilot whales between 2000 and 2004. The most parsimonious model is the one with the smallest AICc value. N.P. is the number of parameters used in the model.

N°	Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Num. Par	Deviance
1	$F p_{effort}$	144.5774	0	0.7299	1	3	20.2148
2	$F_t p_{effort}$	147.9004	3.323	0.1386	0.1899	5	19.2419
3	$F_t p_t$	149.3124	4.735	0.0684	0.0937	6	18.4532
4	$F_t p$	149.4769	4.899	0.0630	0.0863	3	25.1143

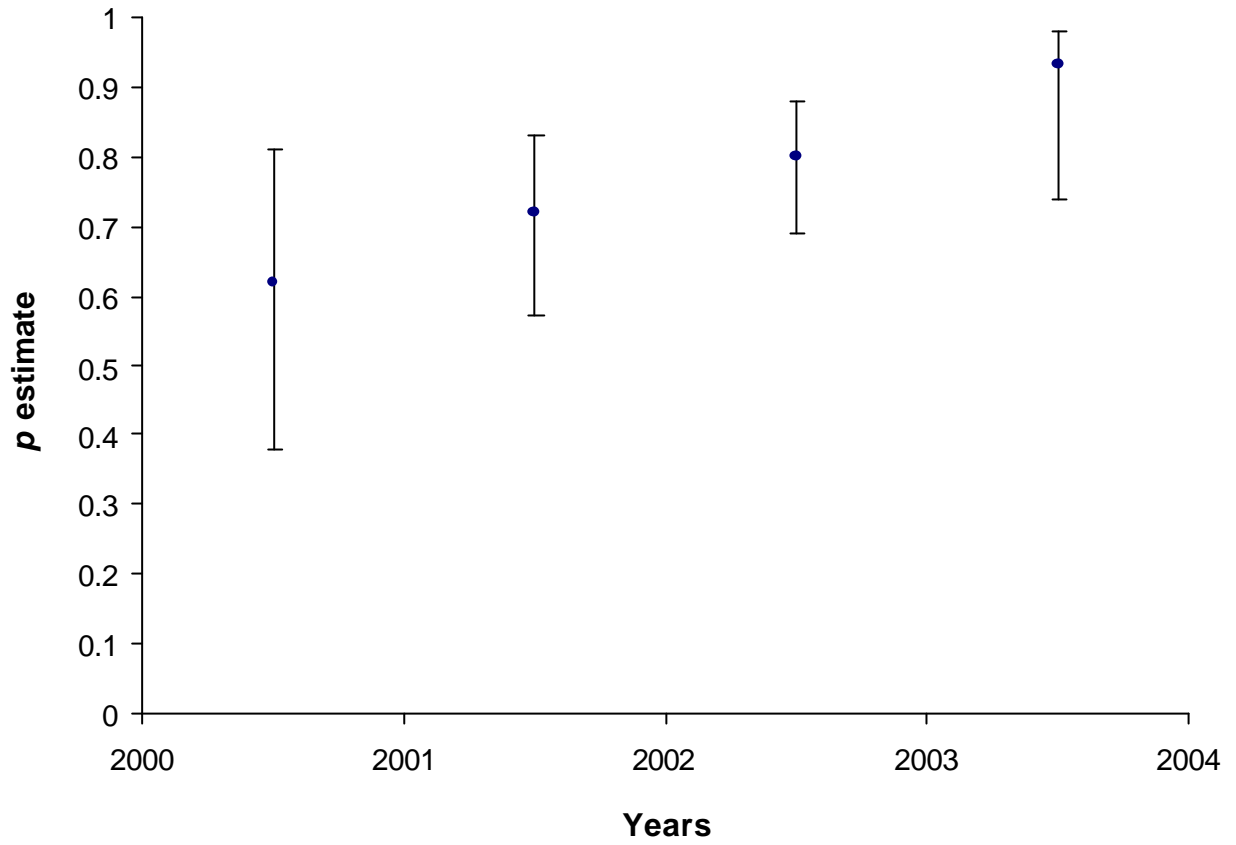


Figure 3.5. Inter-annual capture probability (p) with 95% confidence interval bars.

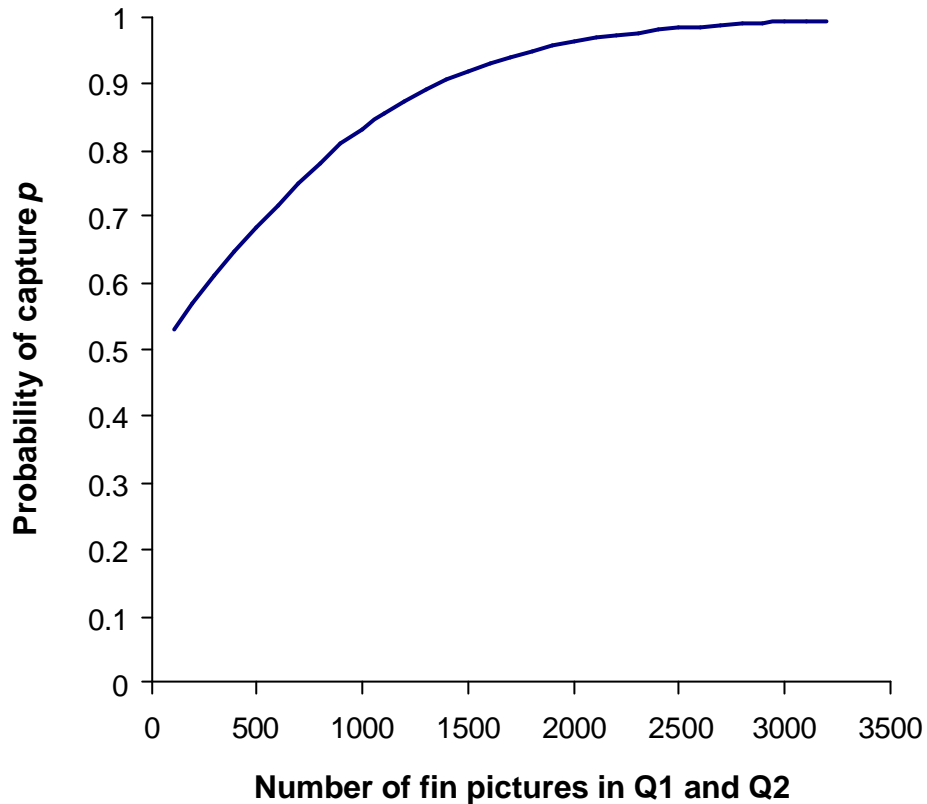


Figure 3.6. Probability of capture in function of the photographic effort from the model F
 p_{effort}

Figure 3.6 shows that the probability of capture (p) is already quite high with 500 fin pictures in Q1 and Q2 taken in a year ($p=0.69$). It also shows why 2004 is such a good year in terms of data collection and confirms that the data before 2002 (less than 330 fin pictures in Q1 and Q2) had a lower capture probability ($p<0.61$). This shows that to have good estimations ($p>0.8$) of the inter-annual survival rate, around 900 fin pictures should be taken in quality Q1 and Q2 each year. This represents more total pictures because some pictures missed the fin or are of quality Q0.

4. Discussion

4.1. Photo-identification

As shown in Figure 3.2, the number of identified individuals has increased over the years. This is due to two major factors. First the quality of the camera increased over the years which is reflected by the number of fins analysed in Q1 and Q2 and second the total number of pictures (all fins analysed) also increased. Until 2003, the number of pictures taken on films within a day and the costs of development were limiting factors. However, in 2004 the digital camera erased those factors and further increased the image quality. Furthermore, the experience of the photographer also increased over the years.

Before 2004, individuals further away from the boat were photographed however their quality were not as good. Therefore, most of the individual taken close to the boat would be the ones either interested in the boat or the closest. As juveniles are usually the ones most attracted by the boat they would be the ones captured most of the time with the best quality. This would influence the correction factor because they are generally lightly or not marked.

The ratio between total fins analysed and fins in Q1 and Q2 is very different for 2004. This is simply due to the way pictures are sorted. More slides of Q0 have been kept and analysed than digital pictures. In 2004, almost all pictures in Q0 have been directly erased as many pictures in Q1 and Q2 were taken of all the individuals. Now that picture development budget is no longer a limiting factor, we can almost take as many pictures as we want.

4.2. Population estimation

The discovery curve for all identified individuals continues to increase and does not seem to reach a plateau so far unlike the one for marked individuals M2 and M3 which has a slower discovery rate (Figure 3.4). Although the tendency curve for M2 and M3 individuals made the inflection before even reaching the top of the curve, it is still increasing. These increases could be explained by different factors:

- most of the population is still not identified;
- newly marked individuals are being captured such as juveniles
- some of the individuals that were previously marked and gained new marks that did not allow for positive identification were misidentified. Incorrect identification may involve falsely identifying two sightings of different individuals as the same (a false positive error) or two sightings of the same individual as different (a false negative error) (Stevick et al., 2001).
- Very small nicks can now be seen and recaptured thanks to the digital camera that allows great zooming into the picture. Therefore previously unidentified individuals are now in the catalogue.

The two large increases in the all individuals curve are the reflections of the effort increase of 2004. It happened in two different ways. The first is that many more pictures were taken for every sighting and second the quality of the pictures was higher. Therefore, the poorly marked individuals are now easy to identify and have higher capture and recapture probabilities.

The estimation made from the tendency curves are probably overestimated because the correction factor is influenced by the number of good pictures. If we use the correction factor for 2004 and apply it to the estimations made from the tendency curves, we found closer estimates to the ones made by the capture-recapture analysis. For all individuals we then have an estimation of 301 individuals and for the individuals marked M2 and M3 we have an estimation of 263 individual pilot whales. These estimations are probably more realistic as they are less biased by the highest proportion of unmarked individuals in Q2 found for the other years. This technique shows that using well marked individuals can make good estimations as long as the correction factor is realistic. However care

must be taken as they are only rough estimations and it is not possible to know the 95% Confidence Interval.

The population estimation from mark-recapture models will be biased by the effort difference over the years. This is partly observed in Table 3.2, even though the estimation themselves do not vary greatly between 2002 and 2004 (from 259 to 298 individuals), the 95% CI decreased substantially in 2004. This can be explained by the quantity and the quality of the data in 2004. Therefore, the estimation of **273 individuals (95% CI 246-323)** and **267 (95% CI: 238-330)** in 2004 are the most accurate and probably closer to reality. However, it is still interesting to see that very close estimations were done for 2002 and 2003 where fewer individuals were identified.

The estimation made for different groupings did not differ greatly and all fell within the 95% CI of the others. This shows that the number of occasion does not influence greatly the estimations. However, by grouping different sightings, days or weeks, some recaptures are lost and the accuracy of the estimation decreased. Therefore, the situation of 2004 on a daily basis is more favourable where many sightings were made with many recaptures. This has the advantage that recaptures will be less influenced by grouping of sightings.

The estimations found for all individuals and for individuals marked M2 and M3 are quite similar and all fall within the 95% CI of the others. This means that for future estimations individuals marked M2 and M3 can be used on their own to make the estimations. This has the advantage of using easier identifiable individuals and therefore decreases the risks of mistakes in identification. However it also decreases the number of recaptures that are still possible with poorly marked individuals, especially now that we are using the high quality digital camera that allows small details to be seen. Furthermore, the precision also decreased with well marked individuals as the 95% CI was larger for these estimations.

4.3. Survival rate

Transience was detected in the dataset which means that either there are transient individuals that are not present in the resident population and may come from another population or that they were only seen in a single year and were missed on the other years. The trap-dependency is probably due to individuals that were more attracted to the boat than others or to the marking level of individuals where the well marked individuals have higher probabilities of being re-identified. Both of these factors may also be found due to the poor dataset before 2002 which would influence them. The survival estimation of the best model taking into account transience and trap-dependence is probably true as it is probable that all the “resident” individuals stayed alive during the study period. However the mean survival rate estimation of 0.976 (SE: 0.043; 95% CI: 0.691-1.000) from the model averaging is more realistic and close to the estimation expected. The survival rate estimation for the model with first capture deleted of 0.965 (SE: 0.029; 95% CI: 0.835-0.993) is close to the model averaging results. It is probably underestimated due to the great changes in photographic effort over the years. Although the model has been adapted to take these changes into account, there is still a great difference in number of individual identified which bias the estimation downward. As noted by Lebreton et al (1992), when survival rate is constant, it is not valid to infer that true annual survival rates in the population are strictly constant. Rather, given the data, the single “average” value of survival rate, is being recommended as a better (smaller mean square error) estimate of survival in any given year than would a separate estimate of survival F_i for that year from a more general model allowing year-dependent survival.

These survival rates estimates are superior to the ones found for resident southern killer whales of the Northeast Pacific which had a mean survival rate of 0.961 for juveniles and adults of both sexes between 1974 and 2000 (Krahn et al., 2002). Pilot whales have often been compared to killer whales in term of their biology and social structure which suggests that the adult population of the Strait of Gibraltar does not suffer from a high death rate. No newborns and few calves have marks that allow their identification. Therefore, these estimates concern only the adult population. Data on sex and age class are not available yet for pilot whales in the Strait of Gibraltar but it would be

important to have them in order to better understand demographic parameters of the population.

4.4. Residence of the population

The fact that more or less the same population estimations were found over the years, that the same individuals have been observed from year to year and the high survival rate strongly suggests that pilot whales are at least seasonally resident in summer in the Strait of Gibraltar. Furthermore the same individuals encountered in summer have been identified all year round which suggests that at least some individuals are resident in the Strait of Gibraltar. This is in accordance with Cañadas et al. (2005) who found that the long-finned pilot whale was encountered in all seasons and everywhere in the Alboran Sea and the Strait of Gibraltar. This could imply that the population in the Strait of Gibraltar could be part of a larger population of the Alboran Sea. Comparisons of the catalogue from the Strait of the Gibraltar and the Alboran Sea will be carried out in the future in order to see if there are any individuals that have been observed out of the Strait of Gibraltar. Genetic work on the different populations of long-finned pilot whales around the Strait of Gibraltar is also necessary to truly understand the gene flows that may occur between the different populations. Ottensmeyer and Whitehead (2003) studied social structure of long-finned pilot whales off northern Nova Scotia, Canada and there did not appear to be a resident population that uses the study area exclusively.

Residency of pilot whales has already been observed by Mussi et al. (2000) who photo-identified the same 6 pilot whales over 5 years in Italy. They seemed to be resident off the Ventotene Island and showed very strong social bond. The population of the Strait of Gibraltar is much larger but it does indicate that if they can find food and reproduce in the same place, they do not need to migrate and can stay in the same location.

5. Conclusion

These results show how important it is to use high quality material and increase the quantity of data to have more precise population estimations from mark-recapture models. The direct effect is observed on the precision of the 95% CI and the number of individual identified over the years (from 22 in 2000 to 159 in 2004).

There are very few strandings of pilot whales in the area probably due to continuous strong currents. Therefore, the population estimation of living individual is crucial to detect any trends in the population. Furthermore, account of births i.e. observation of newborns at sea is also very important to make estimations of birth rates and reproductive success.

This study is the first step to better understand long-finned pilot whales living in the Strait of Gibraltar. As it most probably is a resident population that can easily be accessed by boat (about 30 minutes from the harbour of Tarifa, Spain), it is a unique opportunity to further understand the biology of the species. Now that many individuals have been identified, social structure can be studied as well as the role of whistles and calls in certain groups or individuals. Future work on differentiation of sex and age status of the individuals identified will also be carried out to better understand the social structure and demographic parameters of the species. It is also a unique opportunity to study long-term effects of anthropogenic impacts such as maritime traffic and whale watching.

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7. Appendices

Appendix 1. Results of population estimation corrected (\hat{N}') for all marked individuals (M0, M1, M2 and M3) and 95% confidence interval (95% CI) per session and per year with model used: M_t D. = model M_t of Darroch; M_t C. = model M_t of Chao; M_{th} = model M_{th} of Chao; M_h J. = model M_h of Jackknife.

Session	2002			2003			2004		
	Model	\hat{N}'	95% CI	Model	\hat{N}'	95% CI	Model	\hat{N}'	95% CI
2 weeks	M _t D.	260	203-374	M _t D.	250	210-322	M _t C.	264	240-308
1 week	M _t D.	264	209-367	M _t D.	256	213-330	M _t C.	261	237-303
2 days	M _t D.	260	192-414*	M _t D.	226	192-321*	M _{th}	284	253-340
All sightings	M _{th}	272	209-401	M _{th}	290	228-407	M _{th}	278	249-328
Equal capture	M _h J.	259	218-319	M _t D.	226	192-321*	M _{th}	269	243-320
Mean		263	206-375		250	207-340		271	244-320

*All estimations of the lower 95% CI that are under the number of individual identified (192) have been changed to 192 in order to have more realistic estimation.

Appendix 2. Results of population estimation corrected (\hat{N}') for marked individuals M2 and M3 and 95% confidence interval (95% CI) per session and per year with model used: M_t D. = model M_t of Darroch; M_h J. = model M_h of Jackknife.

Session	2002			2003			2004		
	Model	\hat{N}'	95% CI	Model	\hat{N}'	95% CI	Model	\hat{N}'	95% CI
2 weeks	M _h J.	276	226-363	M _t D.	227	192-305	M _h J.	270	241-324
1 week	M _h J.	263	213-348	M _t D.	233	195-314	M _h J.	260	235-314
2 days	M _h J.	232	192-329*	M _h J.	241	198-320	M _h J.	264	238-330
All sightings	M _h J.	263	207-382	M _h J.	279	221-390	M _h J.	267	238-330
Equal capture	M _h J.	238	194-320	M _h J.	250	203-328	M _h J.	260	235-317
Mean		254	206-348		246	202-331		264	237-323

*All estimations of the lower 95% CI that are under the number of individual identified (192) have been changed to 192 in order to have more realistic estimation.

Appendix 3. Estimations of survival rate per parameter from the model averaging

Estimates only for data type Live Recaptures (CJS)

Apparent Survival Parameter (Phi) Group 1 Parameter 2

Model	Weight	Estimate	Standard Error	
{phi(a2) p(Effort+m)}	0.44790	1.0000000	0.0000000	Invalid parameter estimate with zero SE?
{phi(t*a2) p(Effort+m)}	0.32518	1.0000000	0.0000000	Invalid parameter estimate with zero SE?
{phi(t+a2) p(Effort+m)}	0.22692	0.9896096	0.0124824	

Weighted Average		0.9976422	0.0028326	
Unconditional SE			0.0051912	
95% CI for Weighted Average Estimate is 0.9874675 to 1.0078168				
Percent of Variation Attributable to Model Variation is 70.23%				

Apparent Survival Parameter (Phi) Group 1 Parameter 3

Model	Weight	Estimate	Standard Error	
{phi(a2) p(Effort+m)}	0.44790	1.0000000	0.0000000	Invalid parameter estimate with zero SE?
{phi(t*a2) p(Effort+m)}	0.32518	1.0000000	0.0000000	Invalid parameter estimate with zero SE?
{phi(t+a2) p(Effort+m)}	0.22692	0.9527415	0.0561062	

Weighted Average		0.9892759	0.0127319	
Unconditional SE			0.0234838	
95% CI for Wgt. Ave. Est. (logit trans.) is 0.5463477 to 0.9998585				
Percent of Variation Attributable to Model Variation is 70.61%				

Apparent Survival Parameter (Phi) Group 1 Parameter 4

Model	Weight	Estimate	Standard Error	
{phi(a2) p(Effort+m)}	0.44790	1.0000000	0.0000000	Invalid parameter estimate with zero SE?
{phi(t*a2) p(Effort+m)}	0.32518	0.8123870	0.1613691	
{phi(t+a2) p(Effort+m)}	0.22692	0.9778521	0.0291849	

Weighted Average		0.9339668	0.0590962	
Unconditional SE			0.1072358	
95% CI for Wgt. Ave. Est. (logit trans.) is 0.3189208 to 0.9976648				
Percent of Variation Attributable to Model Variation is 69.63%				

Apparent Survival Parameter (Phi) Group 1 Parameter 5

Model	Weight	Estimate	Standard Error	
{phi(a2) p(Effort+m)}	0.44790	1.0000000	0.0000000	Invalid parameter estimate with zero SE?
{phi(t*a2) p(Effort+m)}	0.32518	1.0000000	0.0000000	Invalid parameter estimate with zero SE?
{phi(t+a2) p(Effort+m)}	0.22692	0.9746128	0.0346468	

Weighted Average		0.9942390	0.0078622	
Unconditional SE			0.0134897	
95% CI for Weighted Average Estimate is 0.9677992 to 1.0206788				
Percent of Variation Attributable to Model Variation is 66.03%				

Apparent Survival Parameter (Phi) Group 1 Parameter 7

Model	Weight	Estimate	Standard Error	
{phi(a2) p(Effort+m)}	0.44790	1.0000000	0.0000000	Invalid parameter estimate with zero SE?
{phi(t*a2) p(Effort+m)}	0.32518	1.0000000	0.0000000	Invalid parameter estimate with zero SE?
{phi(t+a2) p(Effort+m)}	0.22692	0.9527415	0.0561062	

Weighted Average		0.9892759	0.0127319	
Unconditional SE			0.0234838	
95% CI for Wgt. Ave. Est. (logit trans.) is 0.5463477 to 0.9998585				
Percent of Variation Attributable to Model Variation is 70.61%				

Apparent Survival Parameter (Phi) Group 1 Parameter 8

Model	Weight	Estimate	Standard Error	
{phi(a2) p(Effort+m)}	0.44790	1.0000000	0.0000000	Invalid parameter estimate with zero SE?
{phi(t*a2) p(Effort+m)}	0.32518	0.8123870	0.1613691	
{phi(t+a2) p(Effort+m)}	0.22692	0.9778521	0.0291849	

Weighted Average		0.9339668	0.0590962	
Unconditional SE			0.1072358	
95% CI for Wgt. Ave. Est. (logit trans.) is 0.3189208 to 0.9976648				
Percent of Variation Attributable to Model Variation is 69.63%				

Apparent Survival Parameter (Phi) Group 1 Parameter 9

Model	Weight	Estimate	Standard Error	
{phi(a2) p(Effort+m)}	0.44790	1.0000000	0.0000000	Invalid parameter estimate with zero SE?
{phi(t*a2) p(Effort+m)}	0.32518	1.0000000	0.0000000	Invalid parameter estimate with zero SE?

{phi(t+a2) p(Effort+m)} 0.22692 0.9746128 0.0346468

Weighted Average 0.9942390 0.0078622
Unconditional SE 0.0134897
95% CI for Weighted Average Estimate is 0.9677992 to 1.0206788
Percent of Variation Attributable to Model Variation is 66.03%

Apparent Survival Parameter (Phi) Group 1 Parameter 11

Model Weight Estimate Standard Error

{phi(a2) p(Effort+m)} 0.44790 1.0000000 0.0000000 Invalid parameter estimate with zero SE?
{phi(t*a2) p(Effort+m)} 0.32518 0.8123870 0.1613691
{phi(t+a2) p(Effort+m)} 0.22692 0.9778521 0.0291849

Weighted Average 0.9339668 0.0590962
Unconditional SE 0.1072358
95% CI for Wgt. Ave. Est. (logit trans.) is 0.3189208 to 0.9976648
Percent of Variation Attributable to Model Variation is 69.63%

Apparent Survival Parameter (Phi) Group 1 Parameter 12

Model Weight Estimate Standard Error

{phi(a2) p(Effort+m)} 0.44790 1.0000000 0.0000000 Invalid parameter estimate with zero SE?
{phi(t*a2) p(Effort+m)} 0.32518 1.0000000 0.0000000 Invalid parameter estimate with zero SE?
{phi(t+a2) p(Effort+m)} 0.22692 0.9746128 0.0346468

Weighted Average 0.9942390 0.0078622
Unconditional SE 0.0134897
95% CI for Weighted Average Estimate is 0.9677992 to 1.0206788
Percent of Variation Attributable to Model Variation is 66.03%

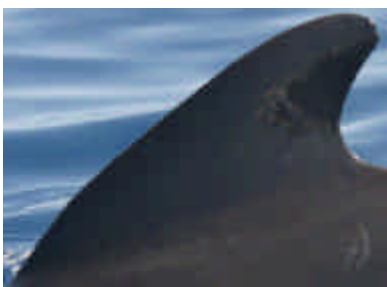








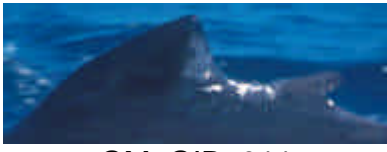





Apparent Survival Parameter (Phi) Group 1 Parameter 14













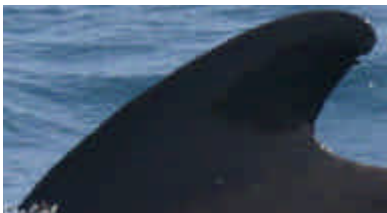





Model Weight Estimate Standard Error

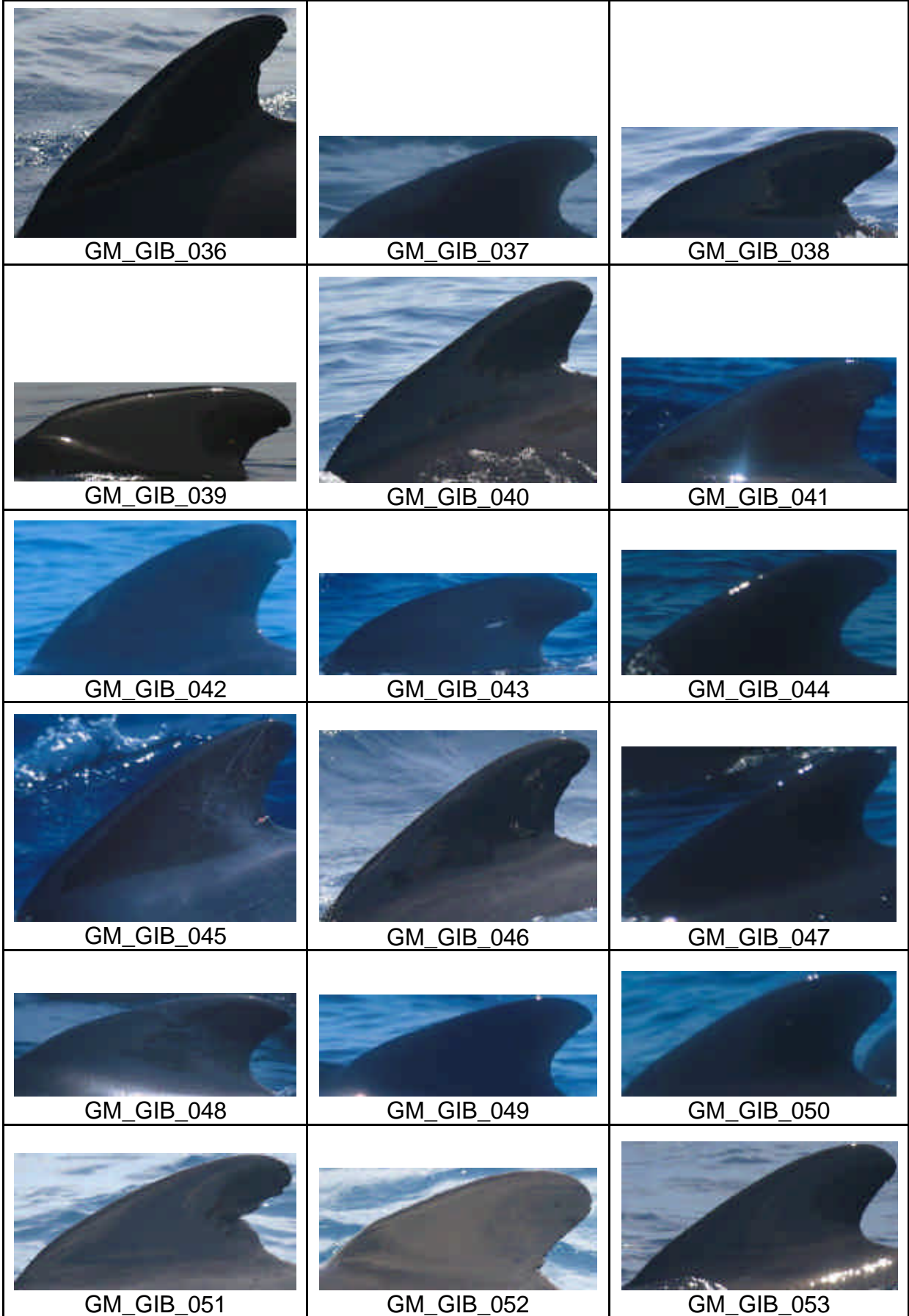
{phi(a2) p(Effort+m)} 0.44790 1.0000000 0.0000000 Invalid parameter estimate with zero SE?
{phi(t*a2) p(Effort+m)} 0.32518 1.0000000 0.0000000 Invalid parameter estimate with zero SE?
{phi(t+a2) p(Effort+m)} 0.22692 0.9746128 0.0346468

Weighted Average 0.9942390 0.0078622
Unconditional SE 0.0134897
95% CI for Weighted Average Estimate is 0.9677992 to 1.0206788
Percent of Variation Attributable to Model Variation is 66.03%

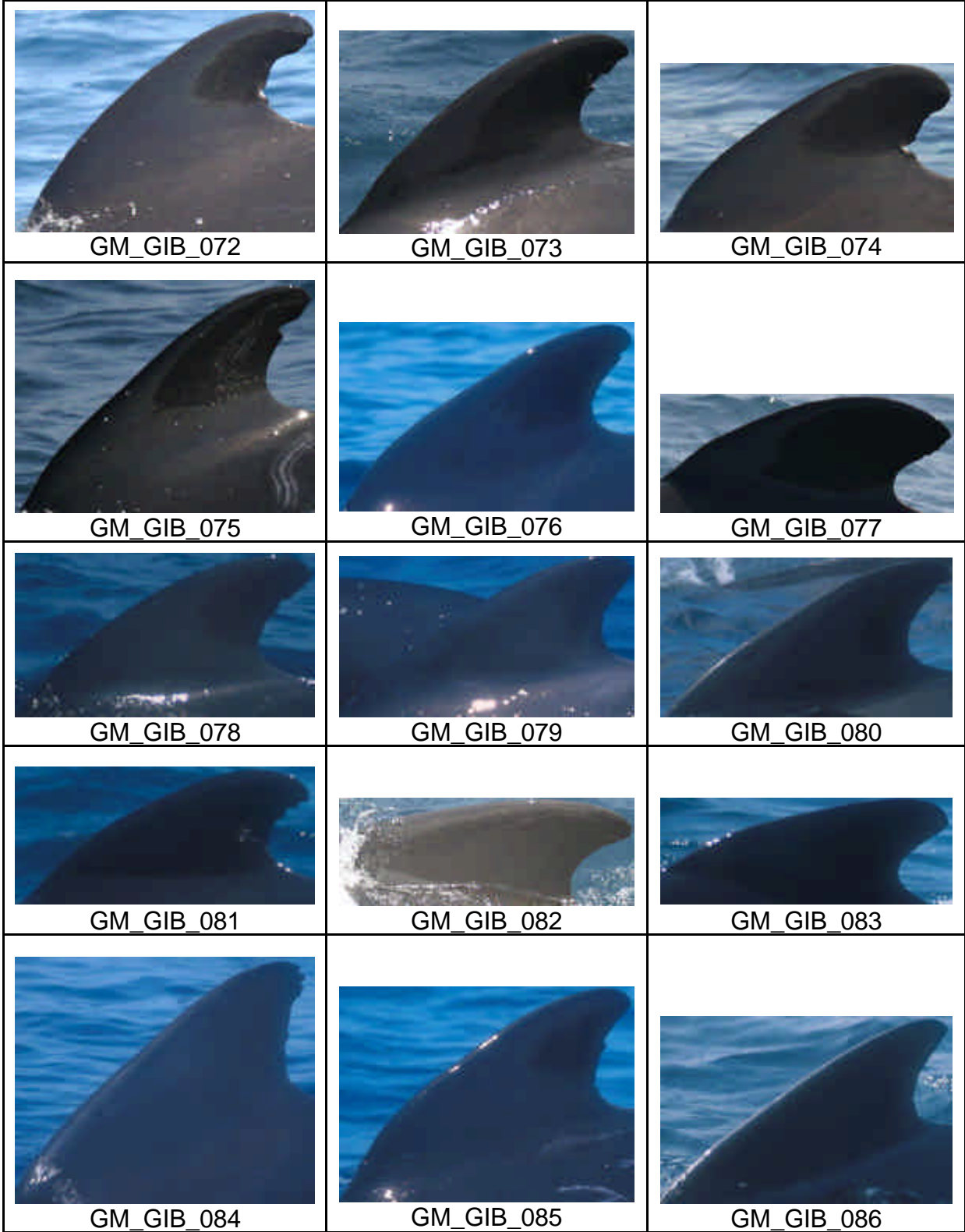
Appendix 4. Photo-identification catalogue of the long-finned pilot whales from the Strait of Gibraltar between 1999 and 2004.

 <p>GM_GIB_001</p>	 <p>GM_GIB_002</p>	 <p>GM_GIB_003</p>
 <p>GM_GIB_004</p>	 <p>GM_GIB_005</p>	 <p>GM_GIB_007</p>
 <p>GM_GIB_008</p>	 <p>GM_GIB_009</p>	 <p>GM_GIB_010</p>
 <p>GM_GIB_011</p>	 <p>GM_GIB_012</p>	 <p>GM_GIB_013</p>
 <p>GM_GIB_014</p>	 <p>GM_GIB_015</p>	 <p>GM_GIB_016</p>



 GM_GIB_017	 GM_GIB_018	 GM_GIB_019
 GM_GIB_020	 GM_GIB_021	 GM_GIB_022
 GM_GIB_023	 GM_GIB_024	 GM_GIB_025
 GM_GIB_026	 GM_GIB_027	 GM_GIB_028
 GM_GIB_029	 GM_GIB_030	 GM_GIB_031
 GM_GIB_032	 GM_GIB_033	 GM_GIB_034










































 GM_GIB_106	 GM_GIB_107	 GM_GIB_109
 GM_GIB_110	 GM_GIB_111	 GM_GIB_112
 GM_GIB_113	 GM_GIB_115	 GM_GIB_116
 GM_GIB_117	 GM_GIB_118	 GM_GIB_120
 GM_GIB_121	 GM_GIB_122	 GM_GIB_124
 GM_GIB_125	 GM_GIB_126	 GM_GIB_127

 GM_GIB_129	 GM_GIB_130	 GM_GIB_131
 GM_GIB_132	 GM_GIB_133	 GM_GIB_134
 GM_GIB_135	 GM_GIB_136	 GM_GIB_137
 GM_GIB_138	 GM_GIB_139	 GM_GIB_140
 GM_GIB_141	 GM_GIB_142	 GM_GIB_143

 GM_GIB_144	 GM_GIB_145	 GM_GIB_146
 GM_GIB_147	 GM_GIB_148	 GM_GIB_150
 GM_GIB_151	 GM_GIB_152	 GM_GIB_153
 GM_GIB_154	 GM_GIB_155	 GM_GIB_157
 GM_GIB_158	 GM_GIB_159	 GM_GIB_160

 GM_GIB_161	 GM_GIB_162	 GM_GIB_163
 GM_GIB_164	 GM_GIB_165	 GM_GIB_166
 GM_GIB_167	 GM_GIB_168	 GM_GIB_169
 GM_GIB_170	 GM_GIB_171	 GM_GIB_173
 GM_GIB_174	 GM_GIB_175	 GM_GIB_176
 GM_GIB_177	 GM_GIB_178	 GM_GIB_179

 GM_GIB_180	 GM_GIB_181	 GM_GIB_182
 GM_GIB_183	 GM_GIB_184	 GM_GIB_185
 GM_GIB_186	 GM_GIB_187	 GM_GIB_188
 GM_GIB_189	 GM_GIB_190	 GM_GIB_191
 GM_GIB_192	 GM_GIB_193	 GM_GIB_194

