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Survival rate, abundance, and residency of long-finned pilot whales in the Strait of Gibraltar

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ABSTRACT

Long-finned pilot whales in the Strait of Gibraltar are distributed over the main shipping routes. This exposes them to risks of collisions and probable acoustic and physical disturbance. This species is also the target of whale-watching operations. The aim of this study was to estimate the annual population size, survival rate, and population growth rate of pilot whales occurring in the Strait and their inter-annual variation using photo-identification. A robust design was used to estimate all three parameters. A total of 10,784 individual pilot whale fins were photographed and analyzed. The population size estimation in summer ranged from a low of 147 individuals in 1999 to a high of 265 individuals in 2003. The annual population growth rate was estimated from mark recapture models to be 5.5%. The survival rate of adults was estimated at 0.982 (95% CI: 0.955–0.993). The same individuals have been observed between years. This suggests that this population is resident in the Strait, at least during summer. This study provides baseline knowledge prior to a predicted increase in shipping traffic throughout the main foraging area due to the opening in 2007 of a major shipping harbor along the Moroccan coast of the Strait.

Key words: long-finned pilot whales, population estimation, survival rate, population growth rate, Strait of Gibraltar, anthropogenic impact.

The long-finned pilot whale is widely distributed in the western Mediterranean Sea and is among the most commonly encountered cetacean species in the Strait of Gibraltar (Roussel 1999), where it occurs mainly in the central and deeper part of the Strait (de Stephanis *et al.* 2008). However, the abundance and residency status of long-finned pilot whales in the Strait of Gibraltar remains unknown.

The Strait of Gibraltar is a narrow, shallow connection between the Mediterranean Sea and the Atlantic Ocean (Fig. 1). This area is also characterized by having one of the highest levels of human activity in a maritime environment. Every year over 90,000 cargo ships and ferries cross the Strait (de Stephanis *et al.* 2005). Fishing and motor and sailing boats are not taken into account in these statistics. Pilot whales are also the focus of whale-watching boats operating in this area. Anthropogenic pressure due to shipping activity is expected to further increase due to the opening in 2007 of a major shipping and ferry (including fast ferries) harbor (Oued Rmel Harbor) on the Moroccan coastline of the Strait of Gibraltar. The new shipping lines to this harbor will cross the main foraging and resting area of pilot whales within the Strait (de Stephanis *et al.* 2005, 2008).

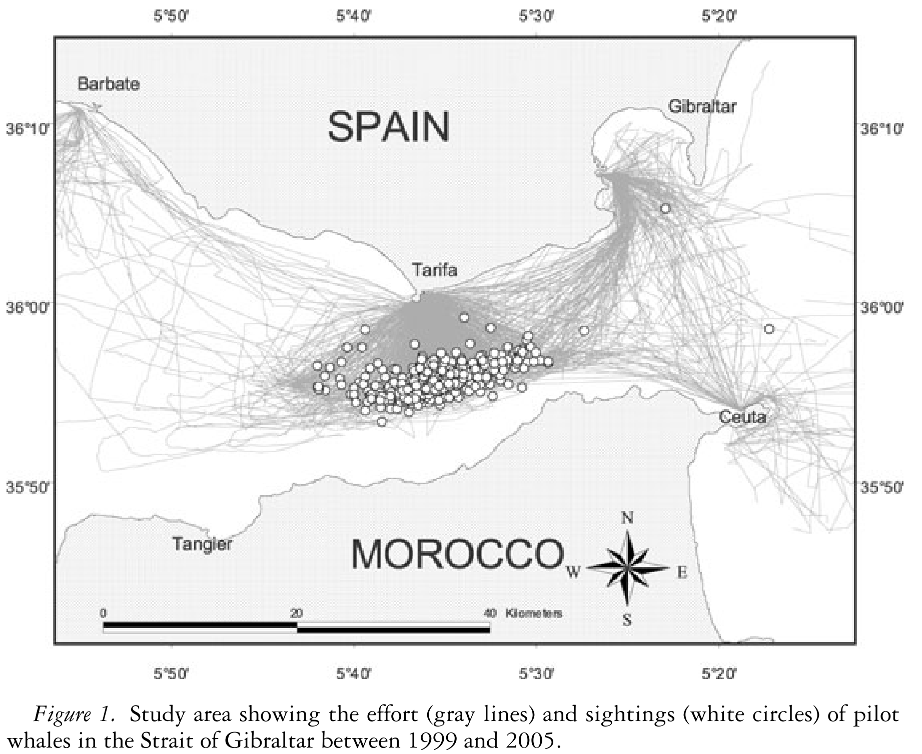

Figure 1. Study area showing the effort (gray lines) and sightings (white circles) of pilot whales in the Strait of Gibraltar between 1999 and 2005.

Abundance and vital rates of naturally marked cetacean species, including pilot whales, can be estimated using mark recapture methods applied to photo-identified individuals (Hammond 1986, Wilson *et al.* 1999, Williams *et al.* 2002,). The aim of this study was to provide baseline knowledge on the status of the pilot whales occurring in the Strait of Gibraltar using photo-identification techniques. First, the degree of residency of the pilot whale population from one summer to the next was assessed. Second, the summer population size of pilot whales was estimated during consecutive years. Finally, information on the annual survival rate and population growth rate of pilot whales occurring in the Strait of Gibraltar and how these values compare with studies conducted on pilot whales elsewhere is provided. A further aim of this study was to assess how long-term monitoring of pilot whales within the Strait of Gibraltar can be efficiently conducted either from dedicated research vessels or platforms of opportunities (*i.e.,* whale-watching vessels) with dedicated observers that could constitute a suitable and less expensive alternative to estimate abundance of pilot whales in the Strait.

These data are critical if we want to be in a position to assess the possible impact of human activity on pilot whale populations occurring in the Strait. It has particular significance in relation to the expected increase of maritime traffic and change of the shipping route associated with the creation of the Oued Rmel commercial harbor and ii) the expected increase of whale-watching activities in the coming years.

Materials and Methods

Study Area and Surveys

The study area is the Strait of Gibraltar and contiguous waters, located between 5°W and 6°W, and covering all areas outside Moroccan waters. The Strait of Gibraltar is nearly 60 km long (Fig. 1).

Survey transects were conducted from whale-watching boats between 1999 and 2000, and from the CIRCE research motorboat, Elsa (10 m) between 2001 and 2005, sampling the study area throughout the months of June, July, August, and September. Transects were conducted randomly for each of these surveys but were designed to cover the whole range of bathymetry of the Strait every month. The sampling strategy was identical throughout the survey period and onboard the different boats (SEC 1999). The area was surveyed at an average speed of 5.3 kn. Searching effort stopped when cetaceans were first sighted and started again when the sighting ended, with a return to the course previously established. Two trained observers occupied an observation platform, 4 m above sea level, in 1-h shifts during daylight with visibility over 3 nmi (5.6 km), assisted by 8 × 50 binoculars, covering 180° ahead of the vessel.

Photo-identification

Following a sighting of pilot whales, pictures of their dorsal fins were taken. The photographers took pictures of completely exposed dorsal fins of all pilot whales surfacing in the vicinity of the research vessel with the best possible magnification. Animals were approached as closely 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 easterly current. Therefore, the left side is facing south where it is best lit by the sun. A catalog was made only for the left side, as analyses were restricted to only one side. 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. The dorsal fin close-ups allowed individuals to be identified based on the natural features or "marks" of the dorsal fins (shape, notches, and nicks) (Bigg 1982, Ottensmeyer and Whitehead 2003) that were used in a mark-recapture analysis (Hammond 1986). From 1999 to 2002, pictures were taken with a Nikon F-810 camera (Nikon Corporation, Chiyoda-ku, Tokyo, Japan) equipped with a 100–300-mm lens. The films used were Fujichrome Sensia 100 ASA color slides (Fujifilm S.A., Aragón, Barcelona, Spain). From 2002 to 2004, a Canon EF100–400-mm lens (Canon España S.A., Madrid, Spain) with image stabilizer was used on a Canon EOS-3 camera (Canon España S.A., Madrid, Spain). From 2004 onward, this lens was mounted on a Canon 10D (Canon España S.A., Madrid, Spain) 6.3 mega pixel digital camera.

Because pilot whales are often in very compact groups, many pictures include more than one individual. 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 analyzed in the same way.

All the slides taken from 1999 to 2003 were examined with an 8× magnifying eyepiece on a light table. Since 2004, digital pictures were examined on a computer screen. Information on each individual in the picture was noted with exposure of the fin (out of the water or not), angle of the fin (every 30° starting from 0° when the animal is facing the camera), individual fin image quality (named Q on a scale from 0 [worst] to 2 [best]), identification number of the individual in the catalog, proportion of dorsal surface exposed, and behavior.

The individual fin image quality (Q) was assigned to each fin image based on image suitability in terms of five characteristics: focus, size, orientation, exposure, and percentage of the fin that was visible in the frame:

- Q0: unusable individual dorsal fin because its representation is blurred, too far away or the angle is between 330° and 30° or 150° and 210°,
- Q1: medium quality representation of part of or the entire dorsal fin,
- Q2: high quality representation of the entire dorsal fin.

An identification number is given to each individual identified in the catalog. Matches with previously identified individuals were made by comparing each new photograph, taken of the left side, with all the others in the catalog. Animals that could not be matched and positively identified on more than two high quality pictures were given a new identification number. The best slide of each individual for each sighting was scanned with a Nikon Coolscan III scanner (Nikon Corporation, Chiyoda-ku, Tokyo, Japan) at a resolution of 2,700 dpi, which allowed easier matching with digital pictures.

Each individual in the catalog received a marking level (M) from 0 (few marks) to 3 (highly marked). Individuals not included in the catalog were categorized as unmarked while individuals in the catalog (from M0 to M3) were considered marked. The individuals with marking level M0 and M1 were lightly marked and those with marking level M2 and M3 were well marked.

Survival Rate and Population Growth Rate

Pollock's robust design (Pollock 1982) with Pradel's population growth estimator (Pradel 1996) was used to calculate annual survival rates, population growth rate,

Table 1. Well-marked population estimates ($\hat{N}$) per year using the robust design model with heterogeneity; 95% confidence interval (95% CI) and coefficient of variation (CV). Estimate of the percentage of marked individuals per year is the inverse of $\bar{\hat{c}}$, with the 95% CI. The session numbers are those used in the robust design analysis as secondary sessions.

Year	Well-marked population estimate	95% CI	CV	% well-marked individuals (95% CI)	Sighting number	Session number
1999	59	54–70	0.07	40.2 (34.0–49.1)	49	7
2000	69	61–85	0.08	33.5 (28.6–40.5)	33	7
2001	75	51–122	0.23	35.3 (29.3–44.5)	15	4
2002	73	61–96	0.12	36.5 (31.8–42.8)	24	6
2003	80	68–101	0.10	30.2 (26.9–34.3)	17	4
2004	78	73–90	0.05	33.1 (30.8–35.7)	30	5
2005	83	71–107	0.11	36.4 (34.2–38.8)	13	5

and abundance estimates based on 7 yr of capture–resighting data. Each primary period (June–September of each year) was divided into multiple secondary periods, each consisting of 15 consecutive days of sampling. All sightings of an individual within a secondary period were considered as one sighting. The number of secondary sessions varied among years (Table 1). For the intervals between primary periods the following parameters were estimated:

- Φ_T, the probability that a member of the population in period T survives and is still a member of the population in period $T + 1$;
- λ_T, the population growth rate based on both survival parameters and recruitment in the population between primary periods.

During secondary sampling occasions, a closed population model was used to estimate the capture probabilities. Because we suspected some heterogeneity of capture between individuals, models with heterogeneity were used. Heterogeneity was modeled using a finite mixture model (Pledger 2000) with two groups of individuals, one with high probability of capture (P_{high}) and the other with low probability of capture (P_{low}). The mixing parameter π indicated the proportion of the population in one of the two groups of individuals. It implies having only two probabilities of capture for each year. The mixing parameter either differed between years or did not.

We started our model selection with the model ($\Phi_T\ \lambda_T\ \pi_T\ P_T$) where survival, population growth rate, heterogeneity, and capture probability varied between primary periods. We tested the effect of using slide (1999–2003) or digital pictures (2004–2005) on the capture probability ($\Phi_T\ \lambda_T\ \pi_T\ P_{\text{Slide+Digital}}$) and the effect of working from whale-watching boats in 1999 and 2000 and a research boat 2001 to 2005 ($\Phi_T\ \lambda_T\ \pi_T\ P_{\text{WW+Research}}$). We also integrated a constraint on the capture probability using the standardized number of fin images analyzed in Q1 and Q2 per year as a covariate named effort ($\Phi_T\ \lambda_T\ \pi_T\ P_{(\text{effort})T}$). We then fitted more parsimonious models by constraining parameters to be constant.

The following assumptions were made for the robust design (Kendall *et al.* 1995):

(1) The population is assumed closed to immigration, emigration, births, and deaths within primary periods.
(2) Naturally marked individuals are "captured" in secondary sample occasions and assumed identified without errors.

(3) All individuals used the area within the study period, but not necessarily every year (allowing for random temporary emigration).

Discovery curves of all marked and well-marked individuals were produced to examine population closure.

All mark-recapture analyses were run on Mark 4.3 (White and Burnham 1999). Models were compared and selected using the Akaike (1974) Information Criterion, adjusted for small sample size (AICc, Sugiura 1978), an index of model fit (Buckland *et al.* 2001). The difference in AICc between any given model and the most supported model (ΔAICc) was used to evaluate relative model fit. Models within a $\Delta\text{AICc} \leq 2$ were considered to be well supported by the data (Burnham and Anderson 1998).

Population Estimation

The robust design models also permitted estimating the number of well-marked individuals (M2 and M3) in the population ($\hat{N}$) for each year. Therefore, the total population size ($\hat{N}'$) was obtained from $\hat{N} \times \bar{\hat{c}}$, where $\bar{\hat{c}}$ is defined below.

The proportion of well-marked individuals in the population was estimated for each year. A program in R 2.4.1 (R Development Core Team 2006) was made to calculate the correction factor (c) which was the total number of fin images divided by the number of fin images of well-marked individuals with medium (Q1) and high quality (Q2) fin images. Since only well-marked individuals were used in the analyses, it was decided to also use medium-quality fin images (Q1) in order to increase sample sizes, particularly for the first years of the study. Well-marked individuals can always be identified on Q1 fin images. This method assumes that, on average, the same numbers of photographs were taken for all individuals independently of their marking levels (Ottensmeyer and Whitehead 2003). To estimate the precision of c for each year, the data set of fin images was resampled by parametric bootstrap. To estimate the number of iterations (i) necessary to minimize the variance of c we first obtained a set of $\hat{c}_i$ from a number of i bootstrap iterations. The samples of $\hat{c}$ were then characterized by their CV calculated by the bootstrap. We then estimated an i value where $\hat{c}$ would have a precision defined as when 95% of the $CV(\hat{c}_i)$ did not vary above the $\overline{CV(\hat{c}_i)} \pm 5\%$. That is to say, the number of bootstrap iteration (i) was the smallest i verifying the following equation: $0.01 \times \overline{CV(\hat{c}_i)} \geq 2 \times 1.96 \times SD(CV(\hat{c}_i))$. Once the number of bootstrap iteration was estimated, we used that number to obtain the value of $\bar{\hat{c}}$ and its CV for each year, which was then used to correct the population estimation, the CV and the 95% CI given by the robust design models for each year. Finally, the correction factor was expressed as a percentage of marked individuals in Table 1.

The limits of the confidence interval of $\hat{N}'$ were corrected according to the formula used by Whitehead *et al.* (1997):

$$\text{LCI}(\hat{N}') = \hat{N}^{\times}\bar{\hat{c}} \times \left(1 - 2 \times \sqrt{\left(\frac{\hat{N} - \text{LCI}(\hat{N})}{2 \times \hat{N}}\right)^2 + CV(\bar{\hat{c}})^2}\right)$$

$$\text{UCI}(\hat{N}') = \hat{N} \times \bar{\hat{c}} \times \left(1 + 2 \times \sqrt{\left(\frac{\text{UCI}(\hat{N}) - \hat{N}}{2 \times \hat{N}}\right)^2 + CV(\bar{\hat{c}})^2}\right)$$

where LCI is the lower 95% CI and UCI is the upper 95% CI.

The coefficient of variation for the total population estimate also took into account the variation of the correction factor as follows:

$$CV(\hat{N}') = \bar{\hat{c}}^2 CV(\hat{N}) + \hat{N}^2 CV(\bar{\hat{c}}) - CV(\hat{N})CV(\bar{\hat{c}})$$

where $CV(X)$ is the coefficient of variation of X and $\bar{\hat{c}}$ the correction factor of abundance estimates (Goodman 1960). The CV was calculated as the ratio of the SE to the mean in order to be compared with other studies (*e.g.*, Wilson *et al.* 1999). The rate of increase was also calculated according to the change in the number of well-marked individuals over the study period by fitting the data to an exponential function (Caughley 1977).

Results

Surveys and Sightings

In Figure 1, the effort carried out between June and September 1999–2005 is plotted (18,158 km) together with pilot whale sightings realized during the period (611 sightings). Photographs could be used for photo-identification purposes from 181 of the total sightings.

Photo-identification

The 181 sightings realized over 107 field days yielded a total of 8,111 pictures representing 15,178 pilot whale individuals (*i.e.,* a given picture can include several individuals), of which 10,784 individual dorsal fins were analyzed. From these, 4,579 were fin images of quality Q0, 3,140 of Q1 and 3,065 of Q2. From 1999 to 2005, 209 individuals were identified and included in the catalogue with one individual marked M0, 119 marked M1, 64 marked M2, and 25 marked M3 (*i.e.*, there were 89 well-marked individuals that were used to produce the estimations).

The photographic effort has varied and mainly increased over the study period along with the number of individuals identified (Fig. 2).

Correction factors were calculated for each year because the ratio of well-marked individuals varied among years (Table 1). We used 1,000 (*i*) bootstrap for each year to calculate the correction factor and its variation. The lowest percentage found was in 2003 with 30.2% (95% CI: 26.9%–34.3%) well-marked individuals in the population and the highest in 1999 with 40.2% (95% CI: 34.0%–49.1%).

As shown in Figure 3, the discovery rate of new individuals was low for well-marked individuals and increased constantly for poor and well-marked individuals from 1999 to 2005 with a mean of 21 individuals newly identified per year (SE: 10; 95% CI: 14–29). The increase appears to start in 2004, when the digital camera was introduced to the study. The number of known individuals recaptured in a year increased from 1999 to 2005 with a mean of 76 known individuals recaptured per year (SE: 33; 95% CI: 51–100). Over the study period, 45 well-marked individuals were recaptured per year, with a mean of 51 well-marked individuals identified per year. On average, well-marked individual pilot whales were recaptured in 3.8 yr (range 1–7 yr).

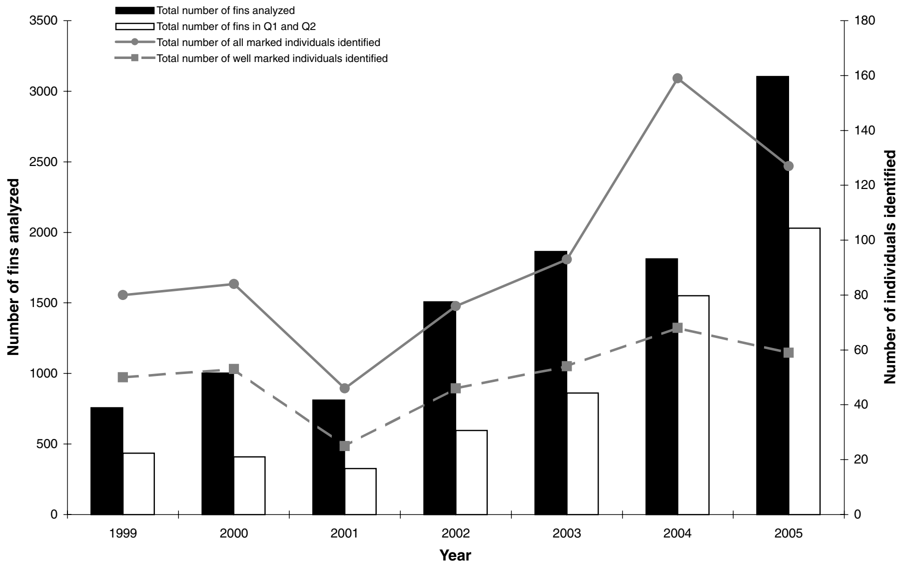

Figure 2. Photographic effort and number of well-marked (M2 and M3) and all marked (M0, M1, M2, and M3) individuals identified per year.

Survival Rate and Population Growth Rate

The first model considered was $\Phi_T\ \lambda_T\ \pi_T\ P_T$ (Table 2, model 7). First, we tested the hypothesis that the capture probability P does not change over time (Table 2, model 19). We found that when P is time-dependent, the model provides a better fit. Then we tested the hypothesis that there was an effect in the use of whale-watching boats (in 1999 and 2000) and of a research boat (2001–2005) on P (Table 2, model 16). The model is not a better fit than when P is time dependent; therefore, we reject the hypothesis that different boat use had an effect on P. Then we tested whether the use of slide *vs.* digital pictures had an effect on P (Table 2, model 12). The model is not a better fit than when P is time-dependent; therefore, we reject the hypothesis that different camera use had an effect on P. Then we tested whether a combination of whale-watching boat and the use of slide *vs.* digital pictures had an effect on P (Table 2, model 5). This gave a better model. Finally we tested the effect of photographic effort on P; first on the best model ($\Phi_T\ \lambda_T\ \pi_T\ P_{\text{(effort)WW+Slide+Digital}}$), which provided exact same fit (Table 2, model 4), then on the second best model ($\Phi_T\ \lambda_T\ \pi_T\ P_{\text{(effort)}T}$), which provided a similar fit (Table 2, delta AICc of 2.1 for model 8). From these four models, we tried to constrain π to be constant over time. However, all the models had a poor fit (Table 2, model 10, 17, 22, and 23). Therefore, only the four best models (Table 2, models 4, 5, 7, and 8) were used to look for the effect of time on survival rate and population growth rate (Table 2, models 1, 2, 3, 6, 9, 11, 13, 14, 15, 18, 20, and 21). The best model ($\Phi.\ \lambda.\ \pi_T\ P_{\text{(effort)}T}$) was used for all the estimates of survival rate, population growth rate, and population size estimations. This model gave an estimate of survival rate of 0.982 (SE: 0.008; 95% CI: 0.955–0.993) between 1999 and 2005.

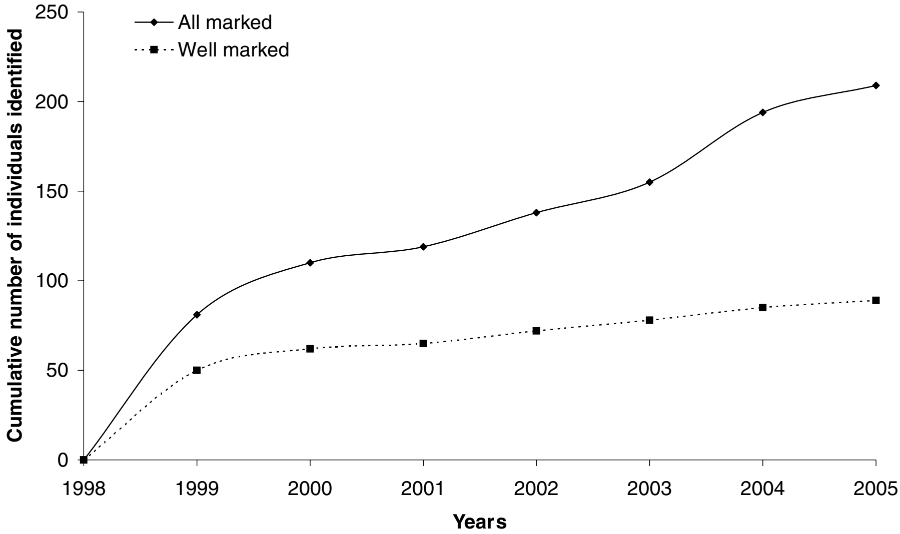

Figure 3. Discovery curve of all marked (M0–M3) and well-marked (M2 and M3) identified pilot whales in the Strait of Gibraltar.

The annual population growth rate (λ) was estimated at 1.055 (SE: 0.017; 95% CI: 1.021–1.089), indicating an increase in the population during the study period of approximately 5.5% per year. A linear trend was detected between years in the proportion of well-marked individuals $r^2 = 0.17$, $n = 7$, $P < 0.05$). However, the population estimate of well-marked individuals increased from 59 to 83 between 1999 and 2005 (Table 1) with an estimated mean annual rate of increase of 6.8%.

Population Estimation

Using the correction factors presented in Table 1, all total population size estimates fell within the 95% confidence interval of the others, except for 1999, which was below the estimates of 2003, 2004, and 2005 (Fig. 4). Although there was slight inter-annual variation, the mean estimated number of total individuals in the Strait of Gibraltar was 213 between 1999 and 2005.

Discussion

As noted by Chao *et al*. (1992), when population estimates made by a model with heterogeneity are larger than the ones produced by a model without, it indicates that heterogeneity of capture probabilities is present within the data. This was the case for all years; therefore, the robust design Pradel's model (1996) with heterogeneity was used to estimate the population size for each year.

A number of assumptions were required by the robust design. Given the life span, reproductive rate, and social organization of pilot whales we assumed that the population was effectively closed, (*i.e.*, without mortality, births, emigration, and immigration within primary periods) because only sightings during summer months

Table 2. Selection of model for pilot whales between 1999 and 2005. The most parsimonious model is the one with the smallest AICc value. N.P. is the number of parameters used in the model.

	Model	AICc	Delta AICc	AICc weights	Model likelihood	N.P.	Deviance
1	$\Phi.\ \lambda.\ \pi_T\ P_{(effort)T}$	891.05	0.00	0.56	1.00	17	856
2	$\Phi.\ \lambda.\ \pi_T\ P_T$	894.74	3.69	0.09	0.16	22	849
3	$\Phi_T\ \lambda.\ \pi_T\ P_T$	895.13	4.09	0.07	0.13	24	845
4	$\Phi_T\ \lambda_T\ \pi_T\ P_{(effort)WW+Slide+Digital}$	895.23	4.19	0.07	0.12	24	845
5	$\Phi_T\ \lambda_T\ \pi_T\ P_{WW+Slide+Digital}$	895.23	4.19	0.07	0.12	24	845
6	$\Phi.\ \lambda.\ \pi_T\ P_{WW+Slide+Digital}$	896.40	5.35	0.04	0.07	17	861
7	$\Phi_T\ \lambda_T\ \pi_T\ P_T$	896.66	5.62	0.03	0.06	26	842
8	$\Phi_T\ \lambda_T\ \pi_T\ P_{(effort)T}$	897.33	6.28	0.02	0.04	23	849
9	$\Phi_T\ \lambda.\ \pi_T\ P_{WW+Slide+Digital}$	897.40	6.35	0.02	0.04	18	860
10	$\Phi_T\ \lambda_T\ \pi.\ P_{(effort)T}$	899.88	8.83	0.01	0.01	25	848
11	$\Phi_T\ \lambda.\ \pi_T\ P_{(effort)T}$	899.99	8.95	0.01	0.01	20	859
12	$\Phi_T\ \lambda_T\ \pi_T\ P_{Slide+Digital}$	902.33	11.29	0.00	0.00	22	857
13	$\Phi.\ \lambda_T\ \pi_T\ P_T$	902.50	11.46	0.00	0.00	26	848
14	$\Phi_T\ \lambda.\ \pi_T\ P_{(effort)WW+Slide+Digital}$	902.86	11.81	0.00	0.00	20	861
15	$\Phi.\ \lambda_T\ \pi_T\ P_{(effort)T}$	905.05	14.01	0.00	0.00	24	855
16	$\Phi_T\ \lambda_T\ \pi_T\ P_{WW+Research}$	906.10	15.05	0.00	0.00	23	858
17	$\Phi_T\ \lambda_T\ \pi.\ P_T$	906.42	15.38	0.00	0.00	28	848
18	$\Phi.\ \lambda_T\ \pi_T\ P_{(effort)WW+Slide+Digital}$	906.77	15.72	0.00	0.00	22	861
19	$\Phi_T\ \lambda_T\ \pi_T\ P$	909.25	18.20	0.00	0.00	20	868
20	$\Phi.\ \lambda.\ \pi_T\ P_{(effort)WW+Slide+Digital}$	910.67	19.63	0.00	0.00	17	876
21	$\Phi.\ \lambda_T\ \pi_T\ P_{WW+Slide+Digital}$	921.64	30.60	0.00	0.00	21	878
22	$\Phi_T\ \lambda_T\ \pi.\ P_{(effort)WW+Slide+Digital}$	925.50	34.45	0.00	0.00	22	880
23	$\Phi_T\ \lambda_T\ \pi.\ P_{WW+Slide+Digital}$	932.60	41.55	0.00	0.00	24	883

were used for each year. A study by de Stephanis *et al.* (2008) (see Fig. 1) demonstrated that the distribution of pilot whales is restricted to the central deep channel of the Strait. Therefore, their geographical distribution is most likely closed as well. Second, we assumed that all the individuals in each sighting were photographed irrespective of their level of marking. An effort was also made to make sure that all the individuals were well photographed so that there was at least one good picture of each individual. Nicks were not lost over the study period as individuals identified in 1999 still had the same nicks in 2005. No trends in the proportion of well-marked individuals were detected during the study period suggesting that no major changes in marking level took place throughout the study. However, new nicks occasionally appeared and a long-term track of the marking changes on the fin was therefore undertaken. Finally, all individuals used in the study were identified and resighted in the study area during the study period.

The annual population growth rate (λ) of 1.055 estimated from mark recapture models and 1.068 from the change in the estimated number of well-marked individuals suggests that this population of pilot whale was growing rapidly over the study period. These estimated growth rates are high for cetaceans (Reilly and Barlow 1986). Our high-growth rate values are likely explained by a combination of high recruitment in the population, possibly some immigration, and an increase in the photographic effort over the years (*e.g.*, model 1, Table 2).

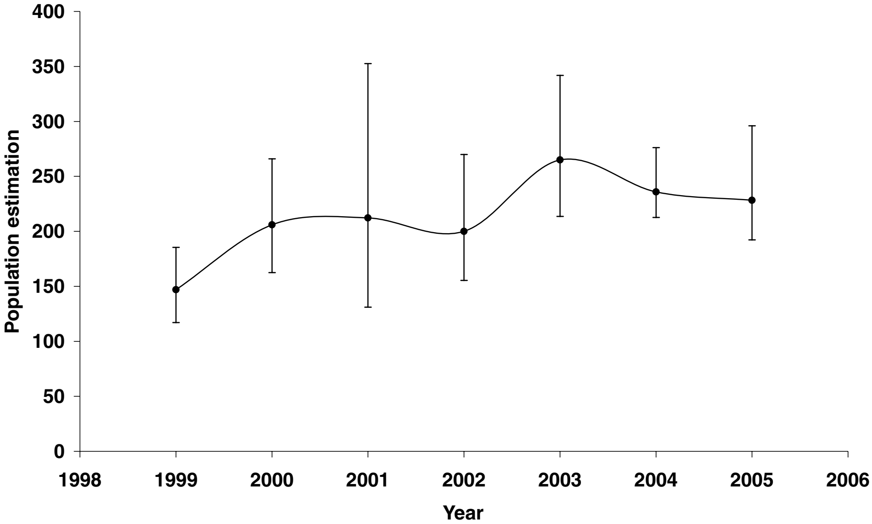

Figure 4. Absolute abundance estimates with 95% confidence interval bars.

No newborns and few calves have marks that allow for their identification. Therefore, the survival rate, population growth rate, and lifespan estimates apply only to the adult population. A rough estimate of lifespan can be calculated as inverse of the mortality (1 − survival rate) (Charnov 1993). This provides a mean lifespan for the well-marked population of approximately 56 yr (95% CI: 22–143 yr), which is similar to the maximum longevity found for long-finned pilot whales in the Faroe Islands of 46 yr for males and 59 yr for females (Bloch *et al.* 1993). Data on sex and age class are not yet available for pilot whales in the Strait of Gibraltar.

The increase in population size estimates between years may be the reflection of the cumulative number of identified individuals increase over the years (Fig. 3). This may be due to both an increase in the photo-identification effort and an increase in the photo-identification quality over the scope of this study (Fig. 2). Very small nicks can now be seen so that previously unidentified individuals have been added to the catalog and lightly marked individuals are now easy to identify. Increasing experience of the photographer may also have contributed to the increased number of photo-identified pilot whales.

Our major findings are that approximately 213 long-finned pilot whales are present every summer in the central part of the Strait of Gibraltar. The fact that similar population estimates were obtained over the 7-yr period of study and that the same individuals have been observed from year to year strongly suggests that some pilot whales are seasonally resident. Indeed, most photo-identified individuals are resighted through the summer of a given year and from year to year. These findings tend to oppose the hypothesis of a continuous flux of animals migrating through the Strait between the Mediterranean Sea and the Atlantic Ocean as described by Hashmi and Adloff (1992). Residency of pilot whales has also been documented by Mussi *et al.* (2000) who photo-identified the same six pilot whales over 5 yr in Italy. Conversely, Ottensmeyer and Whitehead (2003) studied long-finned pilot whales off northern Nova Scotia, Canada, and no resident populations appear to use that area exclusively.

Data which was exclusively collected from whale-watching boats, with a dedicated observer in 1999 and 2000, gave more or less similar population estimations to that of the following years from dedicated photo-identification surveys from a research boat (Fig. 4). This can be explained by the fact that the summer distribution of long-finned pilot whales in the Strait of Gibraltar is restricted to only 12% of the central deep areas of the Strait, an area that is almost entirely covered by whale-watching boats (de Stephanis *et al.* 2005). Furthermore, most of the population can be captured and recaptured within a summer if the photographic effort is high enough. These findings suggest that the long-term monitoring of this population could possibly be undertaken from these whale-watching platforms.

We stress the need for long-term monitoring as the anthropogenic pressures are expected to increase significantly over the next few years. Specifically, whale-watching activity, the rapidly increasing number of fast ferries in the area and the major increase of shipping activity expected with the opening of the Oued Rmel harbor in 2007 (Fig. 1).

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