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Project Report:

Understanding harbour porpoise (*Phocoena phocoena*) and fisheries interactions in the north-west Iberian Peninsula

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Understanding harbour porpoise (*Phocoena phocoena*) and fishery interactions in the north-west Iberian Peninsula

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Introduction

The North West Iberian Peninsula (NWIP), as defined for the present project, consists of Galicia (north-west Spain), and north-central Portugal as far south as Peniche (Figure 1). Due to seasonal upwelling (Fraga, 1981), the NWIP sustains high productivity and high biodiversity, including almost 300 species of fish (Solørzano *et al*., 1988) and over 75 species of cephalopods (Guerra, 1992). At least 19 species of marine mammals (16 cetaceans and 3 pinnipeds) have been recorded in Galicia (Penas-Patiño and Piñeriro-Seage, 1989; Fernández de la Cigoña, 1990; López *el al*., 2003) and 13 species of cetaceans in Portugal (Brito *et al*., 2009). The area is also an important nursery ground for several commercially important fish species including hake (*Merluccius merluccius*), sardine (*Sardina pilchardus*), scad (*Trachurus* spp.) and blue whiting (*Micromesistius poutassou*) (Pereiro *et al*., 1980; Fariña *et al*., 1985).

Spain and Portugal are traditionally fishing countries, with the largest and fifth largest fishing fleets within the European Community respectively (http://ec.europa.eu/fisheries/index_en.htm), and over half of the Spanish fishing fleet is based in Galicia. The NWIP is one of the world's main fishing areas, with an estimated 1.5 million fishing trips per annum from over 120 fishing harbours. Fisheries in the NWIP are highly diverse, exploiting a large number of species and using a large variety of fishing gears including traps, purse-seines, beach seines (Portugal only), single and pair trawls and several different types of gillnets.

Several European and international agreements and directives require EU Member States to carry out monitoring of small cetaceans and take steps to ensure that good conservation status is achieved and maintained, while mitigating effects of specific threats such as fishery by-catches (e.g. EU Habitats Directive, EU Common Fisheries Policy, Directive 812/2004, EU Marine Strategy Framework Directive; Convention on Migratory Species and its daughter agreements ASCOBANS and ACCOBAMS). However, implementation of marine mammal monitoring by Member States is patchy and the vast majority of current monitoring in the NWIP is conducted by two non-governmental organizations (NGOs) 'Coordinadora para o Estudio dos Mamiferos Mariños' (CEMMA) and the 'Sociedade Portuguesa de Vida Selvagem' (SPVS), in Galicia and Portugal, respectively.

In a recent study covering the entire range of east Atlantic harbour porpoises (*Phocoena phocoena*) (Figure 2), the Iberian harbour porpoise population was found to be genetically distinct from porpoises in the rest of Europe (Fontaine *et al*., 2007). As a consequence of this, in 2009, the ICES Working Group on Marine Mammal Ecology recommended treating it as a separate management unit and strongly advised immediate action by the Spanish and Portuguese governments to monitor and ensure the conservation the Iberian porpoise population (ICES, 2009).

The harbour porpoise is generally found in waters of less than 30 m depth in Portugal (Sequeira, 1996) but, although most sightings in Galicia are in coastal waters (López *et al.*, 2004; Pierce *et al.*, 2010; CEMMA, unpublished data), it has been recorded in waters of up to around 150 m depth in Galicia (Spyrakos *et al.*, 2011). Although porpoise is often considered to be a coastal species, this is a misconception since it is, for example, found throughout the North Sea.

In Portugal, harbour porpoises are mostly sighted around Averio and Figueria da Foz (Sequeira, 1996). Coastal sightings data from Galicia suggest the highest abundances are found in the Ría de Pontevedra (Martínez *et al.*, 1995), near the Asturian and Portuguese borders and around Cape Fisterra, the most westerly point in Galicia (Pierce *et al.*, 2010). These are all areas with high fishing activity.

Porpoises were said to be a very common species in the NWIP in the 19th Century and were reported to enter rías, rivers and estuaries in large groups (Bocage, 1863; Norbre, 1895; 1935; Sequeira, 1996). Several recent surveys have recorded porpoise sightings. Aguilar (1997) reports that observers placed on fishing boats in Galician waters saw harbour porpoises on twenty-three occasions (around 7% of sightings). During opportunistic surveys on-board fishing vessels, López *et al*. (2004) observed porpoises on three occasions (2.8% of sightings). Harbour porpoises made up 1.6% of coastal sightings of cetaceans in Galicia during 2003–2007 (Pierce *et al*., 2010). Finally, boat-based opportunistic surveys during 2001 and 2003 (reported in Spyrakos *et al.*, 2011) recorded porpoises on five occasions, all in waters of 100-160 m depth. The low frequency of sightings of harbour porpoises relates at least in part to their small size and short surfacing intervals, which make them easy to miss except in the calmest sea states.

To date, the only abundance estimate for the Iberian harbour porpoise was obtained by the SCANS-II project, which estimated the population to be 2600 individuals (SCANS-II, 2008). Although this is the only existing population estimate, in the 1990s several authors noted a decreasing trend in harbour porpoise numbers in Portugal (Silva *et al*., 1999) and the northern Atlantic coast of Spain (Perez *et al*., 1990; Lens, 1997) over the period during which observations had been recorded. It is also thought that the range of porpoise within the NWIP has contracted (Pérez *et al*., 1990), as seen in stranding records by CEMMA and SPVS.

Harbour porpoises are one of the smallest cetaceans although their body size varies with geographic location. They are sexually dimorphic, with females exhibiting larger sizes than males (Gaskin, 1984; Read, 1999). In general, there appears to be an increase in size with a decrease in latitude or increased water temperature (Learmonth, 2006). Several previous studies have found harbour porpoises to have a life expectancy of over 20 years (Lockyer, 1995, 2003; Lockyer and Kinze, 2003; Ólafsdóttir *et al*., 2003; Learmonth, 2006) although the majority of individuals do not reach physical maturity (Lockyer, 2003).

Very limited published information exists for the Iberian harbour porpoise population although Sequeira (1996), Lens (1997) and López (2003) have all suggested that harbour porpoises in the Iberian Peninsula are considerably larger than harbour porpoises studied in more northern Atlantic waters including the British Isles (Lockyer, 1995; 2003), West Greenland (Lockyer *et al*. 2003) and Scotland (Learmonth, 2006). Based on analysis of life history samples of harbour porpoises stranded in Galicia during the 1990s, López (2003) estimated sexual maturity to occur at 155 cm length and 5 years old in males, and at 166 cm and 3 years old in females. However, the analysis was based on very few samples. Additional data were collected during the BIOCET project during 2001-2003 but, again due to small sample size (N=10), only the range of age and body length of sexually mature animals was reported (Pierce *et al*., 2004).

The NWIP has one of the highest rates of marine mammal strandings in Europe and, due to the high intensity of fishing activity, a high number of by-catches is reported (López *et al*., 2003). Harbour porpoises make up 7% of strandings in Galicia (López *et al*., 2002) and 13% of strandings in central-north Portugal (Ferreira, 2007). During 1990-1999, 22% of harbour porpoise strandings in Galicia showed evidence of fisheries interactions (López *et al*., 2002), whilst in central-north Portugal, 58% of porpoise strandings between 2000-2005 showed evidence of fisheries interactions. In more recent years, when only stranded animals with a diagnosed cause of death are included, over 40% of porpoise strandings in Galicia have shown indications of fisheries interactions, compared to almost 60% in central-north Portugal (CEMMA and SPVS, unpublished data). Although these figures clearly suggest that by-catch could be an increasing problem, some care in interpretations is needed as methods for diagnosing by-catches have been refined over the years and the improved efficiency of the strandings networks means that more carcases are reported and examined while still relatively fresh than in former times.

ASCOBANS (1997) and the International Whaling Commission (IWC) (1995) respectively state that an anthropogenic removal of more than 1.7 or 2% of the best available population estimate, or more than half the net growth rate of a population, represents an '*unacceptable interaction*'. Based on available information (e.g. López *et al.*, 2002, 2003), harbour porpoise by-catch in the NWIP is likely to substantially exceed these limits.

For conservation management measures to be successful it is necessary to have sound knowledge of population status (e.g. Murphy *et al*. 2009). Monitoring of life-history traits (e.g. age at sexual maturity, pregnancy rate) is increasingly recognised as a means to provide important information on population status. Provided that possible biases are taken into account, life history data from stranded and by-caught cetaceans can be used to estimate overall mortality and fishery mortality rates. Diet analysis provides information on feeding ecology and can indicate potential competition for resources with fisheries. Although diets of several other small cetacean species in the NWIP are relatively well-known (e.g. Silva, 1999; Santos *et al*., 2004, 2007), there is little published information for porpoises in the area. The generation of this baseline data will provide context for information on interactions between fisheries and harbour porpoises in the NWIP.

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The proposed project aims to:

1) Quantify life history parameters (age structure, age and length at sexual and physical maturity, pregnancy rate, etc) in harbour porpoises for the NWIP.
2) Use age-at-death data to estimate total and fisheries mortality rate for porpoises in the NWIP.
3) Examine evidence for temporal trends in age at sexual maturity, reproductive output and mortality rates.
4) Compare life history parameters for Iberian porpoises with those from northern Europe.
5) Investigate seasonal, geographic, annual and ontogenetic variation in the diet of NWIP in relation to prey abundance and thus define their trophic role in the area. In addition we evaluate possible biases and limitations in the data.
6) Provide recommendations on conservation of porpoises along the north-west Iberian Peninsula.

Materials and Methods

Necropsies and sample collection

Monitoring of cetacean strandings is coordinated by Coordinadora para o Estudio dos Mamíferos Mariños (CEMMA) in Galicia and the Sociedade Portuguesa de Vida Selvagem (SPVS) in cooperation with Instituto de Conservação da Natureza e Biodiversidade in north-central Portugal. The strandings monitoring networks, run by CEMMA and SPVS, have been operational since 1990 and 2000, respectively. In addition to stranded animals, the networks receive some carcases of by-caught animals from fishers.

Stranded and by-caught harbour porpoises were necropsied following the standard European Cetacean Society (ECS) necropsy protocol (Kuiken and Hartmann, 1991). Basic biometric data were recorded, females were examined for evidence of pregnancy and lactation, and samples were collected for life history and diet analysis (among other studies). Samples of teeth and stomach contents were stored in 70% alcohol and reproductive tracts (ovaries and testes) were stored in 10% buffered formalin until further analysis. Cause of death and evidence of fisheries interactions were recorded, when possible, for carcasses with a state of decomposition 1-3, in compliance with the ECS protocol for evidence of fisheries interactions (Kuiken, 1994). For the present project, we have classified causes of death as follows:

1. known by-catch (carcass handed over by fishermen or observed being caught)
2. evidence of fisheries interactions
3. no evidence of fisheries interactions
4. cause of death not determined.

Age estimation

Teeth were prepared following a protocol adapted from Hohn and Lockyer (1995). After being formalin-fixed for 24 hours and then thoroughly rinsed in water, teeth were decalcified using the commercial decalcifying agent *Rapid Decalcifier* (RDO©) until they were slightly pliable. Decalcification times ranged from 1 hour for teeth of neonates to around 8-10 hours for those of adults. Once decalcified, the teeth were rinsed thoroughly in water for at least 8 hours. One tooth from each individual was sectioned parallel to the mandible (the 'porpoise cut') and a second was sectioned perpendicular to the mandible (the 'dolphin cut'). Sections of 25 µm thickness were cut using a cryostat set at -12°C. Sections were stained with Mayer's haematoxylin (modified by Grue) and 'blued' in a weak ammonia solution. For both dolphin and porpoise cuts, the best sections (those cut through the centre point of the crown and pulp cavity) were selected and mounted on glass slides using DPX. Age was estimated by counting growth layer groups (GLGs) in the dentine of the tooth sections, using a binocular microscope (x10-50 magnification). Duplicate age estimates were obtained, by two independent readers, without reference to biological data. If the age estimates obtained by the two readers differed by more than 1 year, readings were repeated. If the increments were difficult to count, both readers discussed the interpretation and either reached an agreed age or judged the tooth to be unreadable. Individual porpoises for which age could not be determined or for which estimated age was considered to be unreliable were excluded from further analysis.

Female reproductive status

Females were examined at the time of necropsy for evidence of pregnancy and/or lactation. Formalin-fixed ovaries were weighed, measured and sectioned at 5 mm intervals along the broad ligament. The presence of mature follicles, *corpora lutea* and *corpora albicantia* was recorded and these structures were measured, to determine individual reproductive status and history. Females were classified into 5 reproductive status classes based on recommendations by the IWC (Perrin *et al*., 1984): 1) sexually immature, 2) pregnant with foetus, 3) pregnant and lactating, 4) lactating and recently pregnant, and 5) resting mature. Microscopic examination was conducted to confirm macroscopic findings. Portions of ovary were paraffin-embedded and cut into 5-8 µm sections, which were then stained with Mayer's hematoxylin and eosin.

Male reproductive status

Testes with attached epididymis were measured and weighed, and a central cross-section was formalin-fixed. Standard histological analysis of paraffin-embedded sections was conducted. Sections were cut at 5-8 µm and stained with Mayer's haematoxylin and eosin. Microscopic analysis was conducted to measure the diameter of seminiferous tubules and to record cell activity (sertoli cells, interstitial tissue, and germinal cells such as spermatogonia, spermatocytes, spermatids and spermatozoa). Males were classified into 4 reproductive status classes based on Murphy *et al*. (2005): 1) immature, 2) pubescent, (3) active mature and (4) resting mature.

Diet analysis

Diet analysis was only conducted for porpoises stranded and by-caught in Galicia. Analysis was conducted following a standard protocol (Santos *et al.*, 2001) whereby stomach contents were rinsed in water and all prey remains initially stored in 70% alcohol. Fish otoliths and bones were subsequently air dried and stored dry while other prey remains such as crustacean exoskeletons, eyes and cephalopod beaks were retained in 70% alcohol. Prey remains consisted mainly of fish (sagittal) otoliths, bones and lenses, and cephalopod mandibles (beaks). Few crustacean remains were present and these could not always be further identified, due to the poor state of preservation. Fish otoliths and bones were identified using reference material and published guides (e.g. Härkönen, 1986; Watt *et al.*, 1997; Tuset *et al.*, 2008). Cephalopods beaks were also identified using reference material and guides (Clarke, 1986; Pérez-Gándaras, 1986).

Data analysis

Age at sexual maturity (ASM)

Females were considered sexually mature when the ovaries contained at least one *corpus luteum* or *albicans*. Active and resting sexually mature males were considered mature based on cellular activity and seminiferous tubule diameter from histological analysis of the testes. Age at sexual maturity for males and females was estimated by fitting binominal generalised linear models (GLM) for maturity versus age in *Brodgar* 2.6.6 (Highland Statistics Ltd).

Annual pregnancy rate (APR)

The presence of a foetus was used to determine pregnancy. Samples collected during June, July and August were initially eliminated from the analysis of pregnancy rate to avoid any bias due to undetected pregnancies around the time of conception and implantation, assuming that these occur around the same time as in harbour porpoises in the north Atlantic (Lockyer, 2003 and references therein). Annual pregnancy rate was determined by the following equation:

$$APR = \frac{\text{Number of mature females with foetus during September to May}}{\text{Number of mature females during September to May}}$$

Since sample size was relatively small, a second estimate was derived using all mature females.

Calving Interval (CI)

The calving interval is an estimate of the period between parturition in mature females. CI was calculated as the inverse of the annual pregnancy rate, i.e. CI = 1/APR

Life tables and estimated mortality rate

Age data were used to construct life tables and survivorship curves in *Microsoft Excel*. The methodology essentially follows the non-parametric Kaplan-Meier approach to estimating survivorship and is described in Krebs (1989). In order to examine possible differences in

survivorship of sub-groups, life tables were created separately for (1) males and females (2) for by-caught and non by-caught animals, and (3) strandings from different time periods. The reliability/survivorship routines in *Minitab* (Minitab Inc.) were used for statistical comparison of survivorship in different sub-sets of data, based on log-rank and Wilcoxon tests. In addition, age distributions of sub-groups were compared using Chi-square (χ^2) tests in *Minitab*. For these comparisons, age classes were grouped as: <1 year, 1-5 years, 6-10 years and 11+ years old.

Population simulations to test life table methodology
The validity of the non-parametric life table methodology depends on the age distribution being static (so that cohort and static life tables would be identical). In practice this is unlikely and the behaviour of the mortality rate metric under different circumstances was investigated using simple age-structured population models implemented in *Excel*. The models assumed a 1:1 sex ratio, achievement of sexual maturity at 4 years old, and a maximum lifespan of 20 years. Pregnancy rate in mature females was set to 0.8 (in line with results from some other studies), with all pregnancies assumed to lead to birth. Mortality rate was initially set to be equal at all ages, with a realistic initial value of 0.17.

Numbers alive in each age class in each calendar year were then calculated by allowing the previous year's population to age by one year, adding the estimated number of births based on the number of mature females alive the previous year, and applying mortality to each age class. The animals dying each year were assumed to be stranded and a life table was fitted to the age data from each year's strandings to derive the observed mortality rate. The mortality rate that would generate a stable age distribution was then found using *Solver*: with the setting described, it is 0.177. The model was also run by setting mortality equal to the observed value and seeking the pregnancy rate needed to achieve a stable population size. When the age structure is static, underlying and observed mortality rates are identical. The effect on observed mortality of a step or gradual change in underlying mortality rate was then investigated.

In addition, a version of the population model was developed in which there were three mortality components (i.e. similar to the Siler (1979) model): (a) juvenile (decreasing exponentially with increasing age), (b) constant (applied equally to all age classes) and (c) senescent (increasing exponentially to reach 1.0 at 20 years old). Again, mortality rate values which would result in a stable age structure were found using *Solver*. Effects of increasing or decreasing each mortality component separately were then examined.

Diet composition
The number of fish in the stomachs was estimated from the number of otoliths or (for species with fragile otoliths, e.g. sardines) specific jaw bones (e.g. premaxilla, dentary), whichever was higher. Fish sizes were estimated by measuring the otoliths, using callipers or a binocular microscope fitted with an eyepiece graticule. For stomachs in which one fish species was represented by >30 otoliths, a random sample of 30-60 otoliths was measured. Usually otolith

length was measured, except for the otoliths of sardine and Gobiidae, for which width is the standard measurement (Härkönen, 1986), and any identifiable otolith that was broken lengthways. Fish length and weight were calculated from standard regressions (e.g. Härkönen, 1986). For otoliths not identifiable to species but identifiable to genus, family or other grouping of species, regressions based on combined data from all the species in the group were used. To reconstruct total prey weight, each otolith was assumed to represent 0.5 fishes.

For cephalopod remains, standard measurements (rostral length for squid and hood length for octopods and sepiolids; Clarke, 1986) were taken on both upper and lower beaks, using a binocular microscope fitted with an eyepiece graticule. Dorsal mantle length (DML) and body weight of the animals were estimated using standard regressions (Clarke, 1986). Complete pairs of cephalopod beaks were rarely present and in all cases DML and weight was estimated from either the upper or the lower beak. The importance of individual prey species/taxa in each stomach was evaluated by presence/absence, number and summed estimated weight. For overall (population) diet, relative importance of each prey taxon was estimated as (a) percentage frequency of occurrence, (b) proportion of the total number of prey and (c) proportion of total prey weight.

Diet variation
Generalised Additive Models (GAMs) were used to investigate dietary variation. Response variables were numbers of the main prey (*Trsiopterus* spp., blue whiting, *Trachurus* spp., hake and sardine) in the stomachs while the following explanatory variables were considered: year of stranding, month, (estimated) porpoise length and porpoise sex. All variables except sex were treated as continuous and fitted as smoothers. Although year and month are discrete rather than continuous variables (and month is a circular variable), this approach is convenient to visualize temporal variation. For response variables which showed significant interannual variation, we additionally investigated effects of annual prey abundance series, these being annual estimates of the Iberian sardine stock and southern hake stock spawning biomass, and of Iberian sardine stock recruitment, obtained from the assessment of the stocks as reported by the International Council for the Exploration of the Sea (ICES, 2011).

All data series were explored for outliers, collinearity, interactions, etc. following the protocol proposed by Zuur *et al*. (2010). Numbers of each prey species in porpoise stomachs were generally characterized by very right skewed distributions. Count data would normally be expected to follow a Poisson or negative binomial distribution but these distributions were all overdispersed. One possible approach is to use zero-inflated models but large data sets are needed to reliably distinguish between "true" and "false" zeros. Another approach is to use prey presence and fit binomial models but this means a substantial proportion of available information is not included in the models. However, we found that square-root transformation of the count data reduced dispersion to a level appropriate for using Poisson or negative binomial models. Since the theoretical basis for this transformation is debatable, results should be treated with caution.

We fitted GAMs with a Poisson or negative binomial distribution assumed for the (transformed) response variables, depending on the dispersion of the distribution (negative binomial distributions have a longer right tail). For all GAMs, a backwards selection procedure was used. At each step, the least important non-significant variable was dropped and the model was re-run. In all cases, relationships with continuous explanatory variables (i.e. everything except dolphin sex) were fitted using loess smoothers. For length, month and annual stock abundance, the maximum number of degrees of freedom of smoothers was restricted to 3 (k=4), since relationships of prey numbers with these variables are not expected to be complex and restricting k prevents overfitting. For the variable year there is no clear theoretical basis for expecting simple relationships and k was initially unrestricted. However, in the case of models of sardine numbers, overfitting was apparent and therefore k for year was restricted (k=4). If "final" models contained non-significant terms, the consequence of removing these was tested using an *F*-test; such terms were retained if they significantly improved the model fit. Once "final" models were obtained, residuals were checked for patterns and the absence of highly influential data points was checked based on "hat" values. All statistical analyses were carried out in *Brodgar*.

Results

Strandings
Between 1990-2010 a total of 319 harbour porpoises were recorded as stranded in the NWIP, an annual mean of 20 harbour porpoises per year (Figure 3). During the study period, only 8 porpoise carcasses were known by-catches (handed in by fishermen or observed being by-caught). Between 1990-1999 only the Galician network was operational and although some older data exist for Portugal they are not strictly comparable and so have not been included in the present project.

Size, Age and Sex Ratio
Harbour porpoises in the NWIP are considerable larger than in other studied areas (Table 1). Body length ranged from 81-202 cm for females (N=127) and 82-189 cm for males (N=136). The sex ratio of stranded and by-caught porpoises was 1:1.07 females to males, which is not significantly different from 1:1. Age was estimated for 151 harbour porpoises, 71 females, 77 males and 3 of undetermined sex. Age estimates ranged from 0-18 years old for females and 0-19 years old for males. The three animals of undetermined sex were aged 3, 15 and 21 years old (Figure 4). Over 85% of the porpoises in the present study were 10 years old or younger and over 60% were 3 years old or younger. There was no significant difference in the age structure of females and males (χ^2=2.169; df=3; P=0.538) as might be expected from the very similar survivorship curves (Figure 5). Although there is obviously wide variation in individual age, the fitted smoother suggests that average age was higher at the start and end of the study period than in the middle (Figure 6).

Based on applying life table methodology to age-at-death data, there is an estimated annual mortality rate of 18% for the population. Survivorship curves for different time periods differed (Figure 7), and differences were significant when the data were divided into 5-year periods (log rank test, P=0.002 and Wilcoxon test, P=0.027). This reflects the above-mentioned lower average age in the middle decade of the series. Also as expected from examining the raw age data, the difference in survivorship between males and females was not significant (log rank test P=0.055; Wilcoxon test P=0.208) while the difference in survivorship between by-caught and non-by-caught animals was marginally significant (log rank test P=0.057; Wilcoxon test P=0.021). Survivorship was higher in by-caught animals, probably because few age-zero animals are by-caught.

Reproduction and maturity status
Maturity status was obtained for a total of 60 females and 47 male harbour porpoises in the NWIP. Immature females (N=43) ranged from 0-6 years old (N=37) and 84.5-172 cm (N=43). Mature females (N=17) ranged from 6-18 years old (N=11) and 161-202 cm (N=16). Maturity and age data were available for 48 females. Results from the maturity ogive result in an estimated age at sexual maturity of around 5.5 years old for females (Figure 8).

No females were found to be lactating. Pregnancy, based on the presence of a foetus in animals stranded between September and May, was detected in 7 out of 13 mature females. APR was thus estimated to be 0.54. As the sample size of mature females in September to May is very small (N=13), we also estimated the APR including animals stranded during June, July and August. The APR for all mature females (N=17) was estimated to be 0.53 (9 of 17 mature females had a foetus in the uterus). Pregnant porpoises ranged in length from 176-202 cm (N=8) and were aged from 6 to over 16 years old (only a minimum age could be determined in the oldest pregnant female). Foetuses were detected from August to July, ranging from 10 cm to 85 cm in length (with both largest and smallest foetuses recorded in August). No further analysis was conducted on the foetuses due to the limited data available. The calving interval, during which gestation, lactation and reproductive resting occur, was estimated to be 1.89 years (22.7 months).

Corpora lutea and *corpora albicantia* were detected in both left and right ovaries, although only one ovary was active (contained *corpora*) in any one individual. However, it should be noted that both ovaries were available for only 9 mature females. The maximum number of *corpora albicantia* seen in one individual was 15. There was no evidence of senescence in the mature females although the oldest mature female, 18 years old and 192 cm long, was determined as 'resting mature' as there was no evidence of a foetus or recent pregnancy.

Seminiferious tubule diameter ranged from 32.50-53.80 µm in immature males, 41.30-68.50 µm in pubertal males, 126.80-247.90 µm for active mature males and 93.20-154.80 µm for resting mature males. Immature males (N=28) ranged from 0-5 years old (N=25) and 86-154 cm (N=28). Mature males (N=17) ranged from 3-19 years old (N=14) and 154-171 cm (N=17). Maturity and

age data were available for 40 males and results from the maturity ogive give an estimated age at sexual maturity of around 3.8 years old for males (Figure 9). Results from the Gompertz growth model indicated physical length to be 185 cm and 162 cm for females and males respectively, which is achieved at around 10 years of age (Figure 10). Given that over 60% of stranded animals for which age was established were 3 years old or younger, the majority of porpoises die before attainment of sexual maturity.

Causes of mortality and importance of fisheries interactions

Cause of death could be determined for around 40% of harbour porpoise strandings (including known by-caught animals) in the NWIP. Among these animals, around 60% of mortality is attributed to fisheries interactions (Figure 11). Therefore, if we assume unbiased sampling, 18% (annual mortality rate) × 60% (fisheries interactions) = 11% of the Iberian harbour porpoise population dies annually due to fisheries interactions. If we assume that none of the undiagnosed deaths were due to by-catch, the mortality rate due to fisheries interactions is 18% × 60% × 40% = 4.3%.

No overall age difference was observed between by-caught and non-by-caught porpoises (χ^2=4.487, df= 3, P=0.213) (Figure 12) (although as noted above, survivorship curves are marginally significantly different) and males and females were equally likely to be by-caught (χ^2=4.159; df=3; P=0.245).

Population modelling

Assuming a stable age structure and age-independent mortality rate, a pregnancy rate of at least 0.824 is needed to balance an annual mortality rate of 18%.

The simulation models showed that strandings mortality rate is rather insensitive to changes in overall mortality rate, essentially because the estimated mortality rates depend on relative numbers of deaths in each age class and are insensitive to population size changes. Here we illustrate two scenarios. In scenario 1, a 50% increase in real mortality leads to a much smaller increase in estimated (strandings) mortality (Figure 13). Ten years after the increase in mortality rate, the previously stable population has dropped to 50% of its former size even though estimated mortality rate from strandings increased by only 7%.

Scenario 2 is based on the model with three different mortality components. Of these components, strandings mortality is sensitive only to juvenile mortality. If juvenile mortality is doubled, both real average mortality and strandings mortality show sharp increases (the former by 27%, the latter by 18%). However, while maintaining an elevated juvenile mortality rate results in a continued slow increase in true overall mortality rate (after 10 years it has increased to 32% of its initial value), mortality estimated from strandings actually declines again; after 10 years it is only 5.5% above its initial value). The proportion of young deaths in strandings remains consistently higher than before the increase in mortality. The actual population size in

this simulation dropped to around 60% of its original value 10 years after increased juvenile mortality was introduced (Figure 14).

In both scenarios, the increase in mortality rate results in a sharp increase in the annual number of strandings but the number of strandings then drops as the population size falls (Figure 15), emphasizing that data on absolute numbers of strandings are needed to help interpret strandings mortality rates.

Diet

Remains of at least 1958 individual fish were recovered from the 56 stomachs together with remains of 49 cephalopods, 28 crustaceans and 4 other molluscs. Eighteen fish taxa and four cephalopod taxa were identified from these remains (Table 2). Crustacean remains were found in twenty stomachs but consisted of very digested remains. In some cases these were identified as parasitic isopods.

Trisopterus spp. were the main prey, making up 32.2% of reconstructed weight. There are three species in the area, *T. luscus*, *T. minutus* and *T. esmarkii*, the otoliths of which are very similar, especially if eroded. Blue whiting was the second most important prey by weight and the most numerous prey group followed by silvery pout (*Gadiculus argenteus*) and *Trisopterus*. The family Gadidae together represented more than half of the diet of porpoises in reconstructed weight (Table 2). The third most important prey taxon by weight was *Trachurus* sp. (17.6%). Of the cephalopod prey, the species identified were all neritic species (cuttlefishes, small loliginid squid, and sepiolids). Overall, cephalopods contributed little to the porpoise diet either by weight or number even if they were found in around 1/3 of the stomachs analysed.

The estimated length of blue whiting eaten by porpoises in Iberian Galician waters ranged from 4 to 31 cm total length, with a mode at 17.5 cm, while sardine eaten ranged from 7.5 to 25.5 cm total length with a mode at 17.5 cm. *Trisopterus* spp. ranged from 2.5 to 38.5 cm with several cohorts apparent in the sample. Scad ranged from 6.5 to 38.5 cm with a mode at 20.5 cm, while hake ranged from 2.5 to 38.5 cm with several modes (Figure 16). These results, however, were not corrected for otolith erosion due to digestion, so fish lengths are likely to be under-estimated.

Results from the GAM models for numbers of main prey in porpoise stomachs (N=56) (Table 3) showed a significant seasonal pattern, with numbers of hake increasing towards the end of the year (P=< 0.01) (Figure 17a). Porpoise length had a significant effect on numbers of blue whiting, *Trachurus* spp. and hake in the stomachs, with bigger porpoises eating larger numbers of these prey (Figure 17b). There was an increase in the number of hake in the stomachs over the study period, while sardine numbers have fluctuated widely (but with no clear trend) over the same period (Figure 17c). There were also small differences between diets of males and females.

When year is substituted in the models by a measure of prey abundance (spawning stock biomass (SSB) or recruitment), SSB of the southern hake stock was seen to have a significant positive effect on numbers of hake in porpoise stomachs (Figure 18a). Sardine numbers in the stomachs were positively related to the recruitment of the Iberian sardine stock, although not to the SSB, the shape the smoother indicating that fewer sardine were eaten in years of very poor sardine recruitment (Figure 18b).

Discussion

Strandings data
Information from stranded animals is subject to various possible biases, most notably in relation to the fate of carcases of animals which die at sea and if the strandings are representative of the living population. Studies in the Bay of Biscay (Peltier *et al*., 2012) and Galicia (CEMMA, unpublished data) have examined the likelihood of carcases arriving on the shore based on tagging experiments and, in the former study, on current modelling. Based on Peltier *et al*. (2012), it can be assumed that a relatively small proportion of carcases arrive on the shore and that there will be some northwards movement related to the upwelling system and prevailing currents. Ideally, modelling of carcass drift is needed to interpret spatial trends in by-catch and strandings in the NWIP especially given the likelihood of transport between countries because it is thought that due to the upwelling system, some of the strandings in Galicia are by-caught in Portugal. Nevertheless, the value of strandings data should not be underestimated as it potentially offers real insights into the nature and underlying causes of trends in population status.

No long-term trend in the number of strandings could be detected in the NWIP. Considering the extension of the study area to include north-central Portugal from 2000 and the increase in public awareness of marine mammals and strandings in the last 20 years, an upward trend in reported strandings might have been expected. Thus one could speculate that there is an underlying decline in the number of porpoise strandings, perhaps related to the suspected contraction of their range. However, the relatively low number of strandings (N=319) in 21 years means that only strong trends would be likely to be detected.

Size, age, mortality rate
Results from the present study are consistent with previous observations by Sequeira (1996), Lens (1997) and López (2003) that harbour porpoises in the Iberian Peninsula are considerably larger than harbour porpoises in northern Atlantic waters (e.g. Lockyer, 1995, 2003; Lockyer *et al*., 2003; Learmonth, 2006; Read and Hohn, 1995).

Age was estimated by two experienced readers. One reader also conducted the age estimations for López (2003) thus helping to control the potential biases associated with using age data generated by different laboratories and people. However, it should be noted that Iberian harbour

porpoise teeth are difficult to age and contain a large number of anomalies, such as accessory lines, which can make accurate reading difficult. Although it is not fully understood what causes such anomalies to occur, their presence has been associated with stresses due to environmental variation e.g. El Niño (Manzanilla, 1988) or climate change (Boyd and Roberts, 1993) as well as life history events (Klevezal and Myrick, 1984; Medill *et al*., 2009; Luque *et al*., 2009).

In the NWIP, the majority of harbour porpoises that died were estimated to be 3 years old and younger. Assuming these animals are representative of the population, our results suggest that there are few older animals in the Iberian population, something also seen in other studied populations (e.g. Hohn and Brownell, 1990; Read and Hohn, 1995; Lockyer, 1995; Lockyer and Kinze 2003; Learmonth, 2006). The young age at which harbour porpoises become sexually mature may be related to (as cause or consequence of) their short life span in comparison to other cetacean species.

Based on age-at-death data, we estimated an annual mortality rate of 18% of the population. The validity of this estimate depends on the representativeness of the strandings data and on a stable age structure but it is similar to results obtained for Scotland (Pierce *et al*., unpublished data). The long term trend in average age indicates a dip around 1995-2000 which could be interpreted as an increase in mortality while the strongest pattern seems to be a recent increase in average age and this was also evident from the life table/survivorship analysis. The associated variation in survivorship was statistically significant.

Population simulations show that mortality rate derived from strandings can be insensitive to changes in underlying mortality rate, except in the case of juvenile mortality. Large changes in mortality rate would also be expected to impact on the numbers stranded, with population decline accompanied by a falling number of strandings. In the NWIP, total numbers of porpoises stranded annually do not show any clear trend. It should also be noted though that numbers of strandings will be influenced by any shifts in porpoise distribution.

Reproduction, age at sexual maturity, pregnancy rate
Corpora lutea (CL) and *corpora albicantia* (CA) were detected in both left and right ovaries (although not in the same individual animals), as also recorded by Learmonth (2006) for porpoises in Scotland, whereas Read and Hohn (1995) found that CL and CAs were usually present only on the left ovary in porpoises from the western Atlantic.

The estimates of age at sexual maturity (ASM) obtained in the present study differ from those of López (2003) but the latter study was based on a smaller sample size. Hohn (1989) indicated that a sample size of <50 individuals was too small to estimate ASM. In the present study, data on both age and maturity status were available for 60 females and 47 males. The sample size was too small to investigate whether any temporal patterns existed in ASM.

Results on pregnancy rate (54%) and calving interval (22.7 months) indicate that porpoises in the NWIP give birth every second year as also suggested for Scotland (Learmonth, 2006), although these values are lower than estimates for porpoises in the Bay of Fundy (Read, 1990), Denmark (Sørensen and Kinze, 1994) and West Greenland (Lockyer *et al.*, 2003). APR in the NWIP was similar to Scotland (Learmonth, 2006) but lower than in Denmark (Sørensen and Kinze, 1994) and the Bay of Fundy (Read, 1990). However, estimates of APR based on stranded animals are sensitive to the general health status of a population and in particular to the proportion of disease mortalities in the strandings: pregnancy rate is likely to be lower in unhealthy animals and in such cases pregnancy rate estimates from strandings are likely to be biased downwards. The pregnancy rate that would be needed to maintain a stable population size when annual mortality is 18% would be at least 82.4% (assuming 100% survival of foetuses).

Diet and fishery interactions

Several commercially important species were found in the diet of the porpoises stranded in Galicia. The diet comprised pelagic and demersal species with members of the family Gadidae dominating the diet, specially *Trisopterus* spp. and blue whiting. Sizes of prey eaten indicate that fish eaten by harbour porpoises were mainly above the minimum landing sizes, established for hake at 27 cm, for scad (*Trachurus trachurus*) and *Trisopterus luscus* at 15 cm and for sardine at 11 cm. Around half of the blue whiting was below the minimum landing size (18 cm). It should be noted that sizes may be underestimated since no correction was applied for otolith erosion. In other areas of the NE Atlantic where the diet of the species has been studied, porpoises were also found to feed on a mixture of demersal and pelagic species. For example in Scotland, Santos *et al.* (2004) described the diet as dominated by sandeels and whiting. In Ireland, Rogan and Berrow (1996) also found *Trisopterus* to be the main prey of by-caught and stranded porpoises.

The trends identified in diet variation must be treated with caution since the count data were not a good fit to expected distributions and an ad-hoc transformation was therefore applied. There were clear ontogenetic trends in numbers of prey eaten, with larger porpoises having higher numbers of prey in the stomachs – this may simply be a consequence of larger animals eating larger meals but the trend was not evident for all prey species suggesting that there is also an element of changing dietary preference and/or habitat use. There was a seasonal pattern in predation on hake. Predation on hake and sardine appeared to be related to the abundance of these species (at least on an annual basis at a large spatial scale). Numbers of hake eaten were strongly positively correlated with hake abundance while numbers of sardine eaten were related to sardine recruitment, although the relationship reached a plateau at relatively low recruitment levels.

These results make clear that commercially exploited fish species are a major part of the diet. While porpoises may sometimes take smaller fish than typically targeted by fisheries (as in the case of blue whiting), interaction with fisheries seems to be an inevitable consequence of their feeding habits.

By-catch mortality

By-catch is apparently a significant cause of death for porpoises in the NWIP. Although caution is obviously needed in interpretation, the figure of 18% derive from the strandings data seems to be a plausible figure for annual mortality rate. A high proportion of stranded animals died from by-catch and, taken together, the two figures suggest that the rate of by-catch mortality is unacceptably high. By comparison, in Scotland, fishery by-catch is a relatively minor cause of porpoise deaths. There is a relatively high proportion of pathological modes of death (i.e. death due to diseases and parasites, starvation and condition loss (Learmonth *et al*., submitted). Another of the main causes of death for the harbour porpoise is fatal attacks by bottlenose dolphins (*Tursiops truncatus*) which, although noted in Galicia (López and Rodriguez, 1995; Alonso *et al*., 2000), are relatively scarce in the NWIP.

The Iberian harbour porpoise is particularly vulnerable in heavily fished areas (Sequeira, 1996) and is frequently observed close to fishing nets (Silva *et al*., 1999) although carcasses are rarely handed-in by fishermen. Diagnosis of fisheries interactions on stranded animals is not possible for heavily decomposed individuals (state of decomposition >3), in which evidence used to determine fisheries interactions (e.g. twine marks on the skin) might not be detected. In the present study, over 45% of harbour porpoise strandings were significantly decomposed, meaning that our sample size was limited. Among animals in which evidence of fisheries interactions could be evaluated, 60% of harbour porpoises had evidence of fisheries interactions. Males and females and most age classes appear to be equally susceptible to mortality due to fisheries interactions (except that age 0 animals are under-represented among by-catches). There was however an apparent area difference: slightly over 40% of porpoise strandings in Galicia have indications of by-catch, whilst by-catch accounts for almost 60% of strandings in central-northern Portugal.

A possible reason for the higher recorded by-catch rate in Portugal is the continued use of beach seines. Beach-seines are commonly used in north-central Portugal and are often up to 5 km long. They are an unselective gear with a mesh size similar to that of a pelagic trawl. Beach-seines are illegal in most other European countries and their use stopped in Galicia over 50 years ago. A study on fisheries interactions in Portugal in the 1990s found no porpoises to be by-caught in beach-seines (Sequeira, 1996). However, five individuals were observed to be by-caught in a single beach seine in 2007 (SPVS, unpublished data) and they are thought to be one of the gears to which harbour porpoises are most vulnerable (Ferreira, 2007). Beach-seines are most commonly used in Aveiro and Figueria do Foz, coinciding with the area of highest harbour porpoise abundance in Portugal (Sequeira, 1996). Gillnets are one of the gears with the highest cetacean by-catch rate in Galicia and are also problematic in Portugal (Sequeira and Inacio, 1992; Silva, 1996; López and Valeiras, 1997; López *et al*., 2003; Silva and Sequiera, 2003).

Conservation

While eliminating fisheries interactions and by-catch of harbour porpoises in the NWIP is unlikely to be realistic, given social and economic importance of the fishing industry, there is a need to explore ways to reduce by-catch. Thus, a reduction in the use of beach-seines or restricting their use to areas with lower densities of harbour porpoises is potentially achievable. Time-area closures for problematic gears, e.g. limiting the use of gillnets during the reproductive season, could also be effective in reducing by-catch.

In recent years several marine mammal-fisheries interactions 'feed-back' projects have been conducted in the NWIP e.g. LIFE-INDEMARES and DIVULGANDO A PE DE MAR projects in Galicia and SAFESEA in Portugal. These projects have worked in collaboration with the fisheries sector, with the aim to improve environmental education and awareness of fisheries stakeholders whilst emphasising the scientific importance of by-caught samples. The projects have promoted the collaboration of scientists, fishermen and other stakeholders to devise ways to reduce/avoid interactions.

Conclusions and future work

In conclusion, the relative stability of numbers of strandings could indicate that numbers are currently stable, while the recent increase in average age could indicate that juvenile mortality has declined since the early 2000s. However, the small resident population size, low longevity, low reproductive output and apparent high by-catch rate, especially in northern Portugal, suggest that some conservation action is still necessary.

Following discussions about strandings monitoring protocols at the recent meeting of ICES WGMME (ICES, 2011), we note the need for greater consistency in recording evidence pertaining to cause of death. Both for assessing health status, bearing in mind that the proximate cause of death may not reflect an animal's general health, and to provide further information and quality control in relation to by-catch diagnosis, it is important to know which signs were checked and which were seen. Thus it is recommended that the recording of all relevant evidence is itemised, e.g. the necropsy report should note whether the carcass was checked for net marks and whether they were present.

We would like to recommend that cetacean monitoring under ASCOBANS makes full use of available life history and dietary data. Age, maturity and diet studies are not funded within core monitoring programmes and this has been recognised by ICES WGMME (ICES, 2009) as representing an important gap in coverage.

Dissemination of Results

Data generated from the present project were presented at both the European Cetacean Society and Society for Marine Mammalogy conferences and at the SAFESEA project conference during 2011.

Iberian harbour porpoise ages will also be used for studying age-related patterns in stable isotope signatures and contaminant bioaccumulation as part of the PhD of Paula Méndez Fernandez from the University of La Rochelle, France and the University of Minho, Portugal.

Conference presentations
By-catch mortality and conservation of the Iberian harbour porpoise population. Fiona L. Read, Ángel F. González, Marisa Ferreira, Alfredo López, José Vingada, M. Begoña Santos and Graham J. Pierce. 19th Biennial Conference on the Biology of Marine Mammals, Tampa, USA. December 2011. Oral presentation.

Life History data from harbour porpoises stranded in the Iberian Peninsula. Fiona L. Read, Ángel F. González, Marisa Ferreira, Alfredo López, José Vingada, M. Begoña Santos and Graham J. Pierce. 'Sustainability of local fishing arts and the promotion of a safer sea for cetaceans' SAFESEA conference, Figueira do Foz, Portugal. April 2011. Invited oral presentation.

The importance of long-term datasets for conserving the Iberian harbour porpoise population. Fiona L. Read, Ángel F. González, Marisa Ferreira, Alfredo López, José Vingada, M. Begoña Santos and Graham J. Pierce. 25th European Cetacean Society Conference, Cadiz, Spain, March 2011. Oral presentation.

Collaborative projects
Long term ecological segregation among the NW Iberian Peninsula odontocete species as evidence using ecological tracers. Paula Méndez Fernandez, Paco Bustamante, Tiphaine Chouvelon, Marisa Ferreira, Ángel González, Alfredo López, Graham Pierce, Fiona Read, M. Begoña Santos, Jérôme Spitz, José Vingada and Florence Caurant. 'Sustainability of local fishing arts and the promotion of a safer sea for cetaceans' SAFESEA conference, Figueira do Foz, Portugal. April 2011. Invited oral presentation. (Extended version of the latter presentation).

Long-term ecological segregation among the NW Iberian Peninsula odontocete species as evidenced using ecological tracers. Paula Méndez Fernandez, Paco Bustamante, Tiphaine Chouvelon, Marisa Ferreira, Ángel González, Alfredo López, Graham Pierce, Fiona Read, M. Begoña Santos, Jérôme Spitz, José Vingada and Florence Caurant. 25th European Cetacean Society Conference, Cadiz, Spain, March 2011. Oral presentation.

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Figure 1. The north-west Iberian Peninsula (NWIP).

Figure 2. Harbour porpoise abundance in the north-east Atlantic. Fontaine *et al*., 2007.
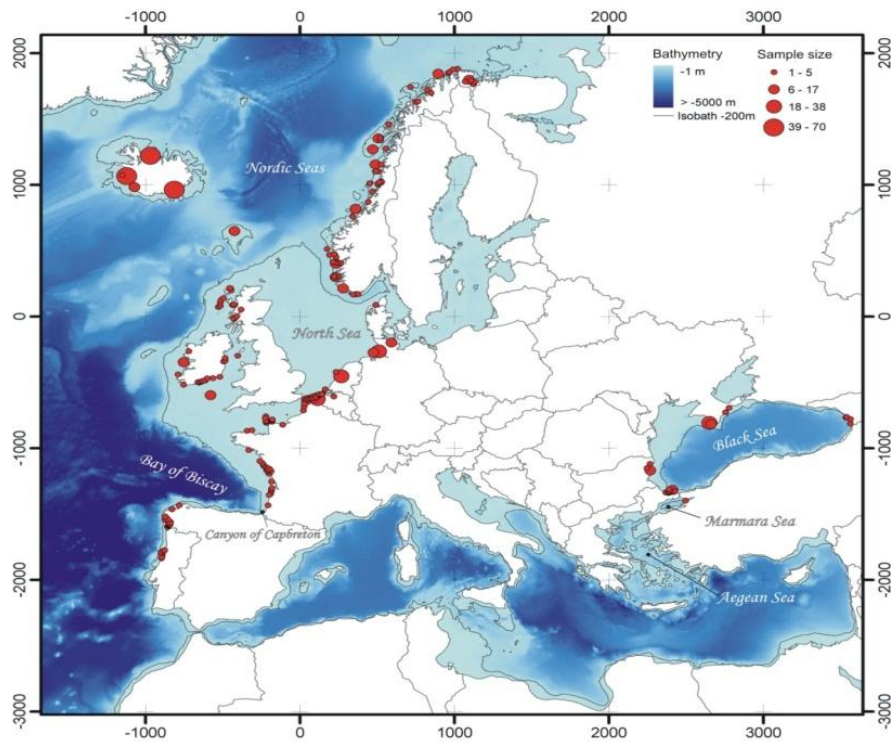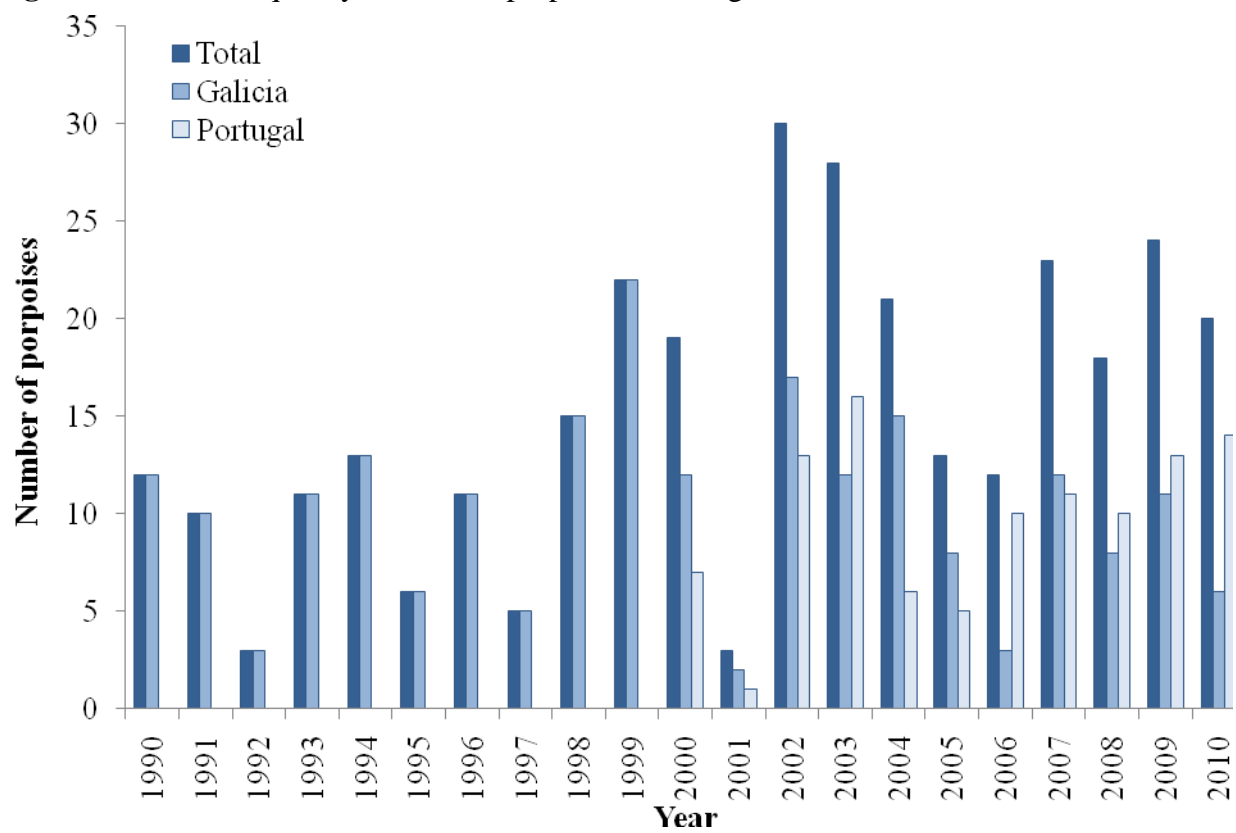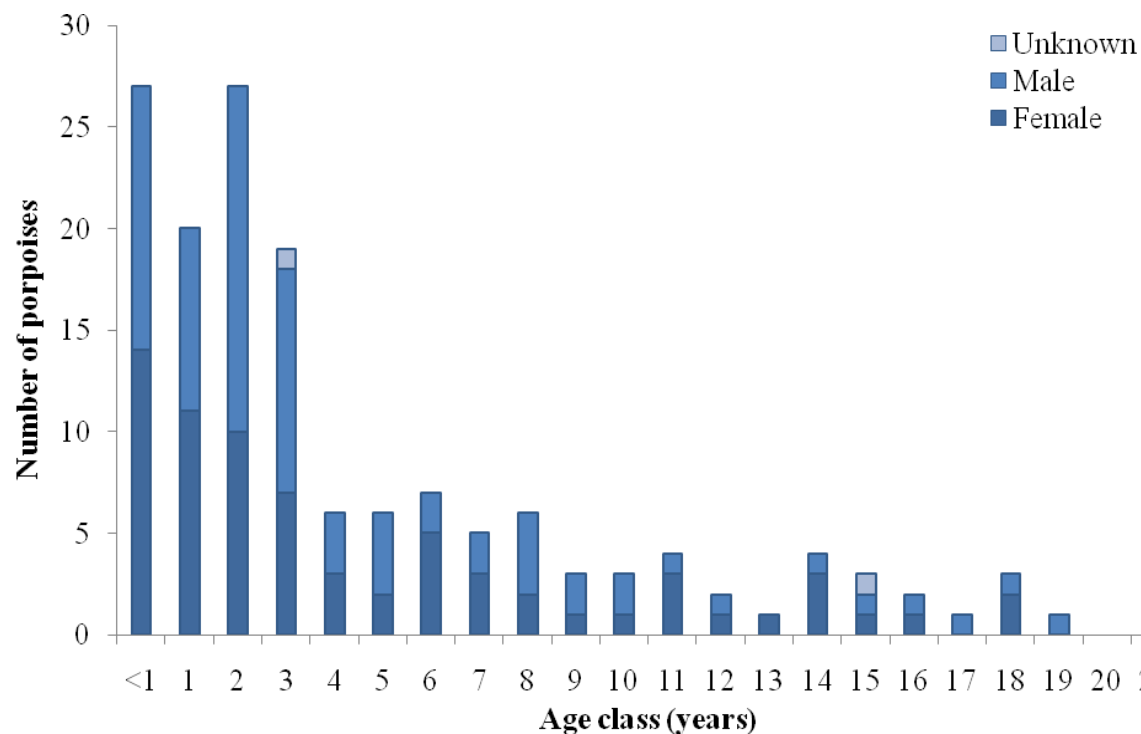
Figure 3. Annual frequency of harbour porpoise strandings in the NWIP.

Figure 4. Frequency of estimated age of stranded harbour porpoises in the NWIP.

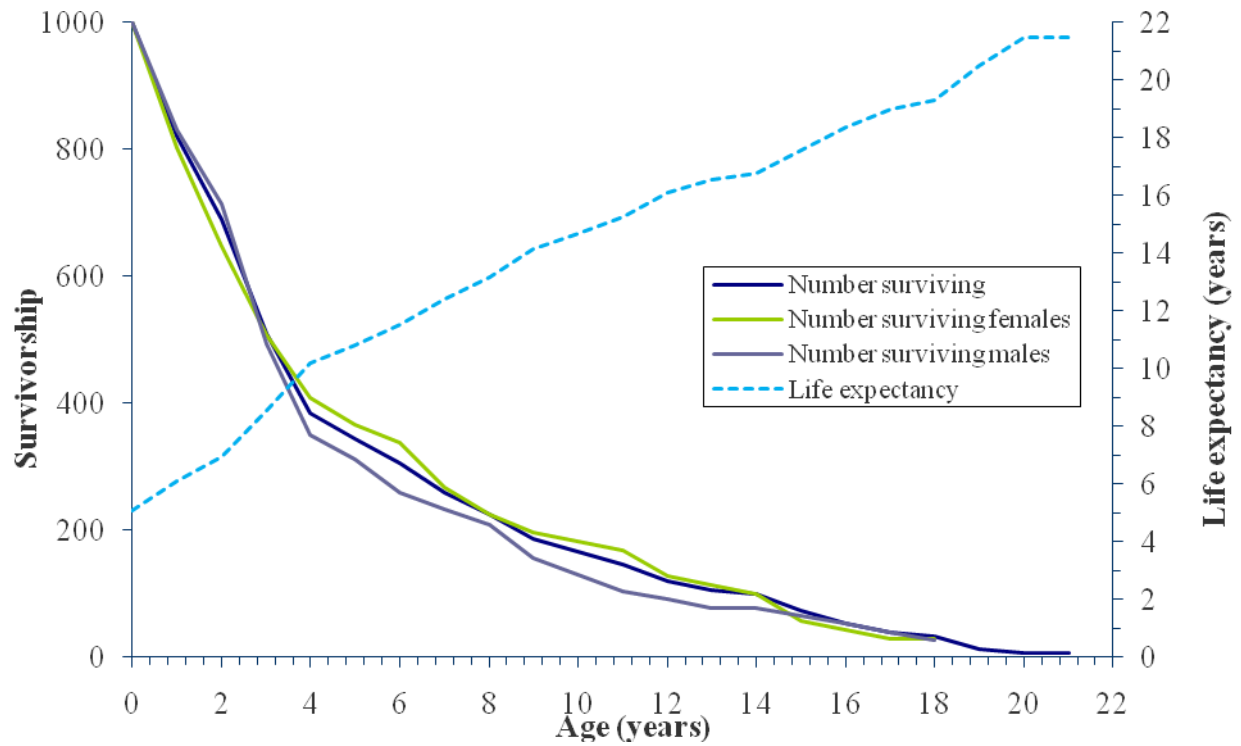**Figure 5.** Survivorship curve for all harbour porpoises stranded between 1990-2010.

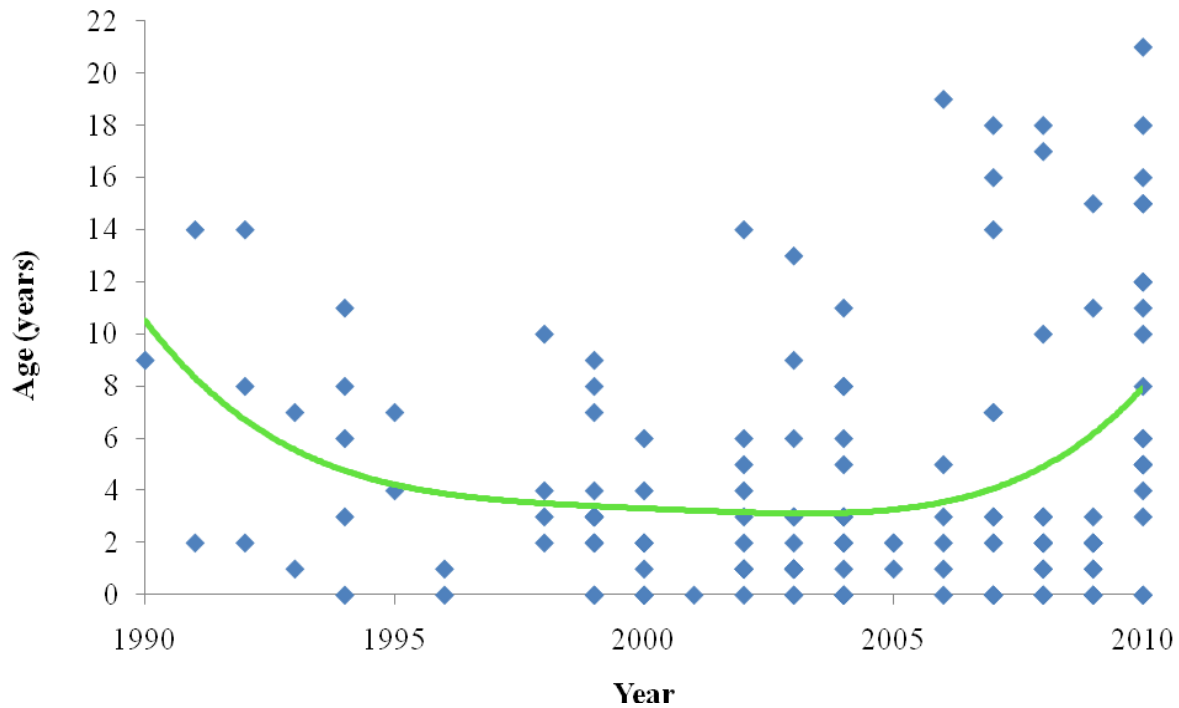**Figure 6.** Estimated age of stranded and by-caught harbour porpoises in each year.

Figure 7. Fitted non-parametric survivorship curves and 95% confidence limits for four 5-year periods (1990-95, 1996-2000, 2001-05, 2006-10). Also shown is mean age for each group.

Figure 8. The predicted age at which 50% of the female porpoises are sexually mature.

Figure 9. The predicted age at which 50% of the male porpoises are sexually mature.

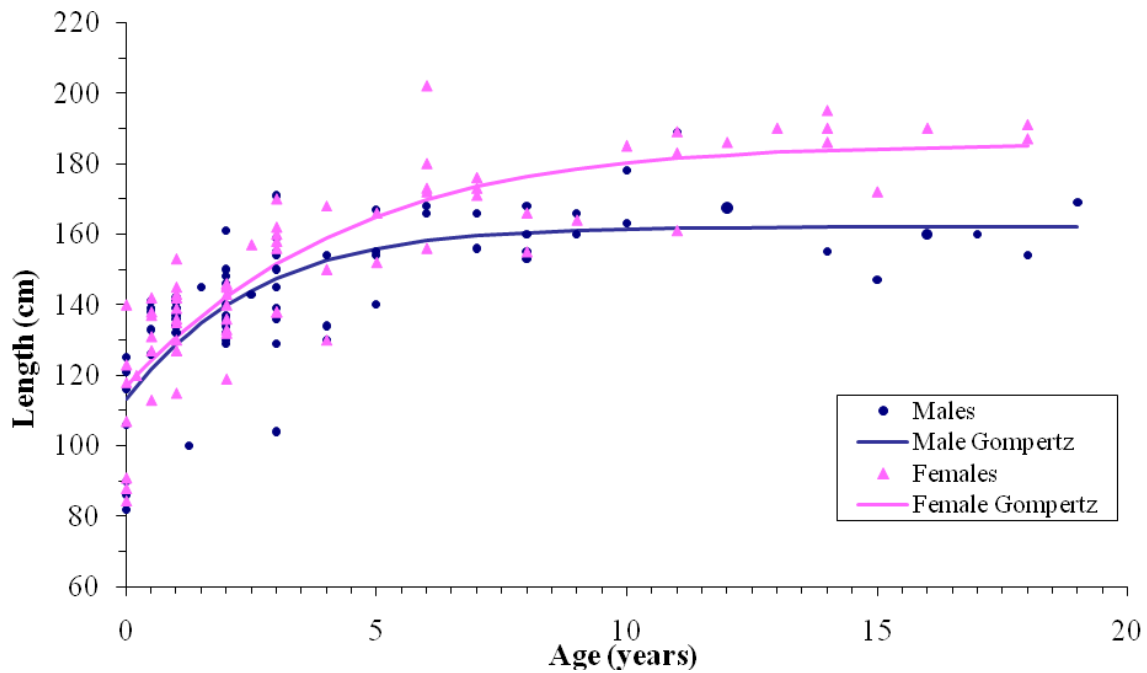**Figure 10.** Gompertz growth curve for male and female harbour porpoises in the NWIP.

Figure 11. Fisheries interactions versus non-fisheries interactions for porpoises with a known cause of death.
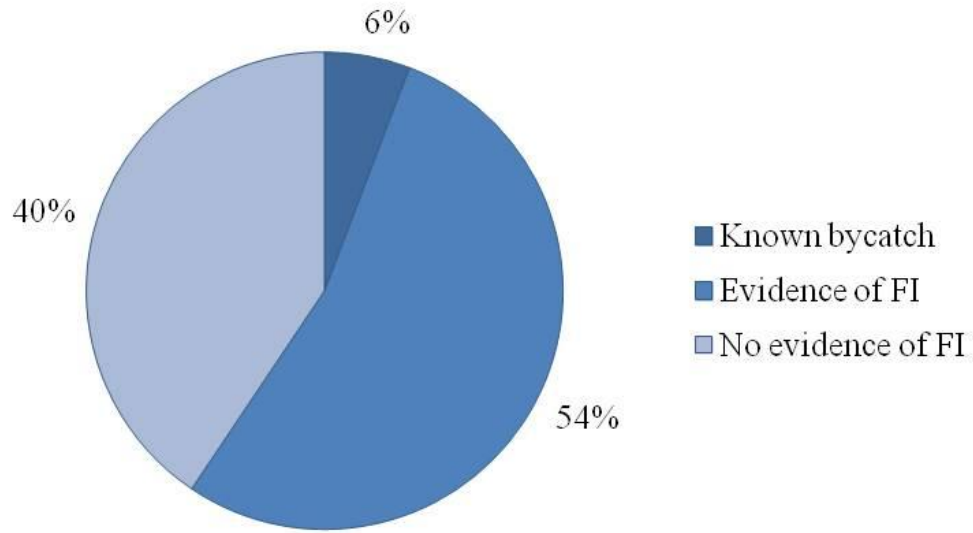

Figure 12. Survivorship curve for all by-caught versus non by-caught harbour porpoises.
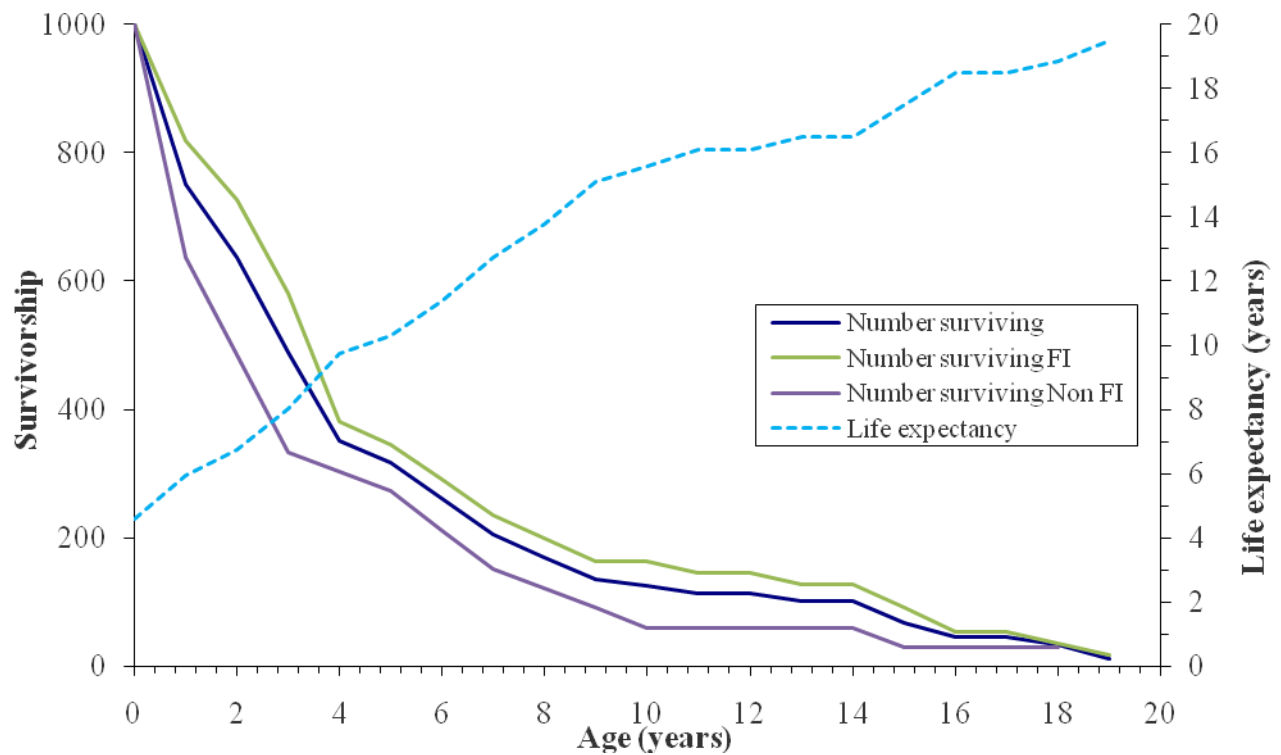
Figure 13. Response of a simulated population to a sustained 50% increase in real mortality rate (M), from 0.177 to 0.265. The graph shows true mortality rate, strandings mortality rate and the proportion of strandings in young (<5) and old (>10) porpoises.
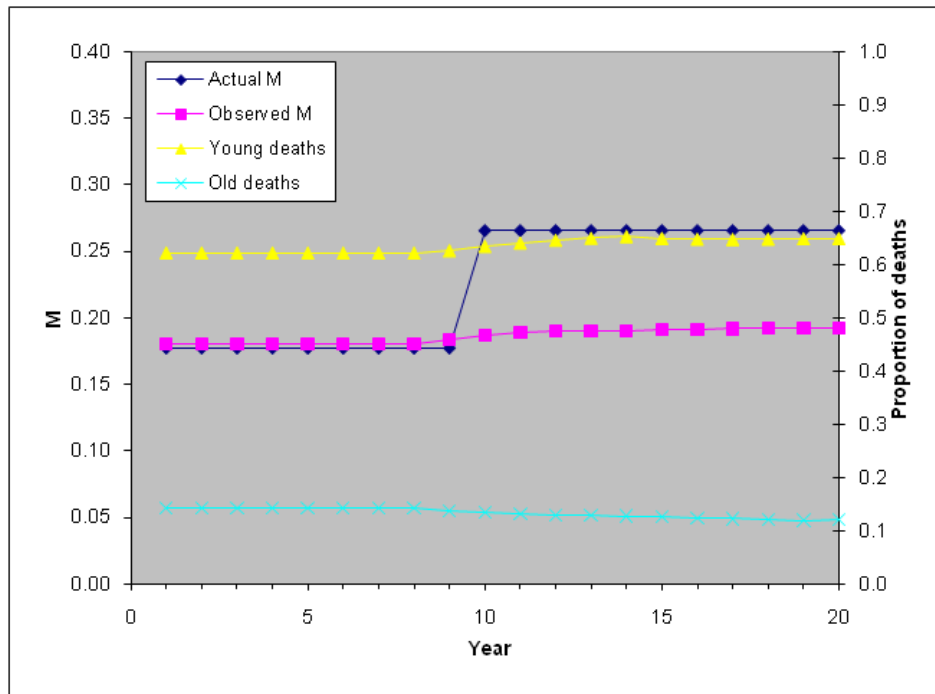

Figure 14. Response of a simulated population to a sustained doubling of juvenile mortality rate. The graph shows true average mortality rate, strandings mortality rate and the proportion of strandings in young (<5) and old (>10) porpoises.
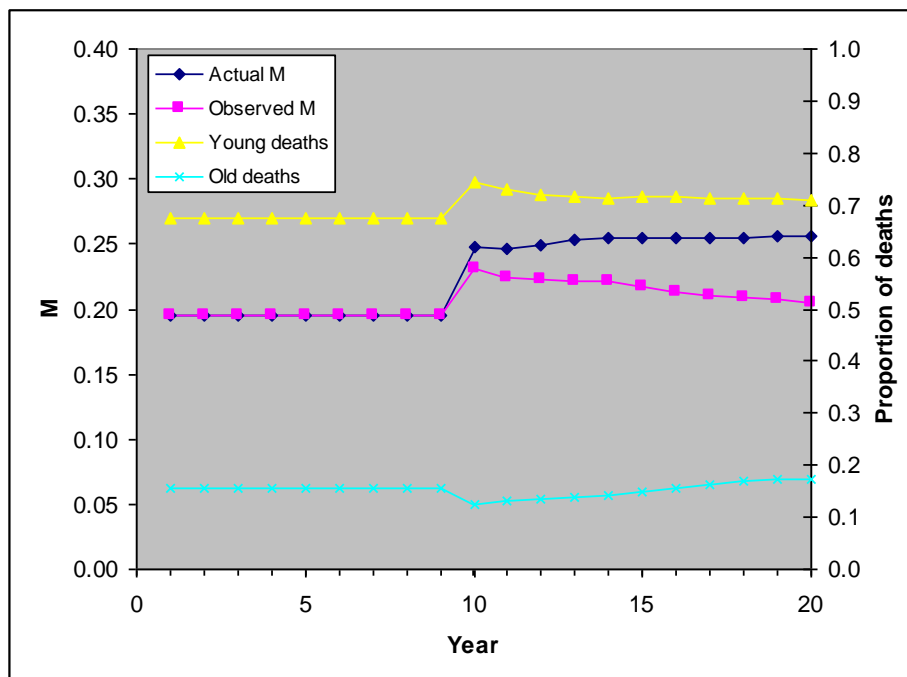
Figure 15. Response of a simulated population to increases in (1) total mortality and (2) juvenile mortality. The number of strandings recorded initially shows a sharp increase but then falls as population size falls.
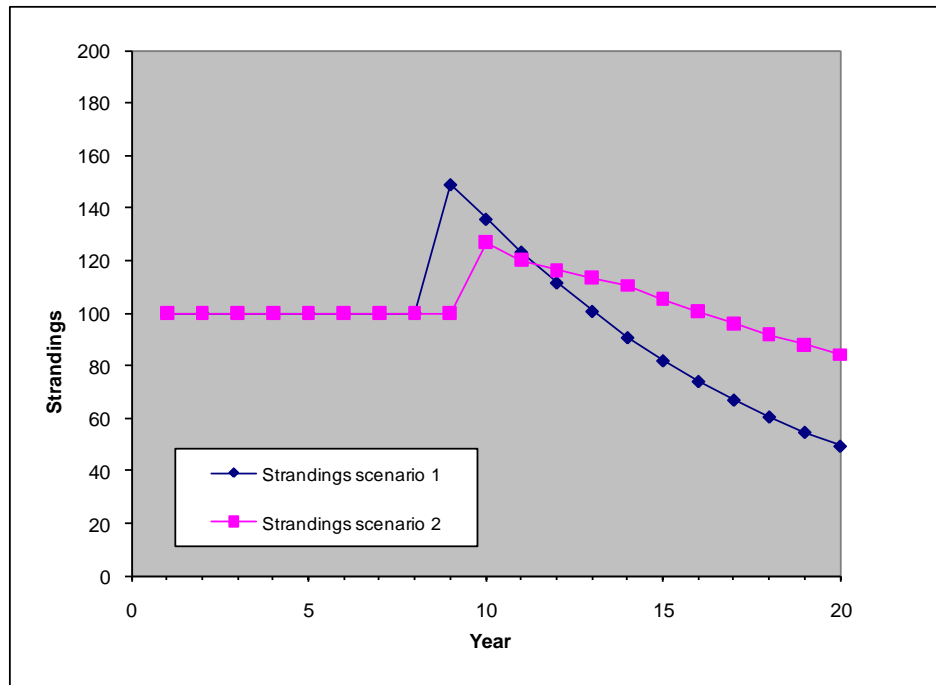
Figure 16. Percentage frequency distributions of estimated size (fish length in mm) of *Trisopterus* spp., blue whiting, hake, *Trachurus* spp. (scad) and sardine eaten by harbour porpoises in Galician waters. The vertical lines represent the minimum landing size established for the species (colour coded by species).
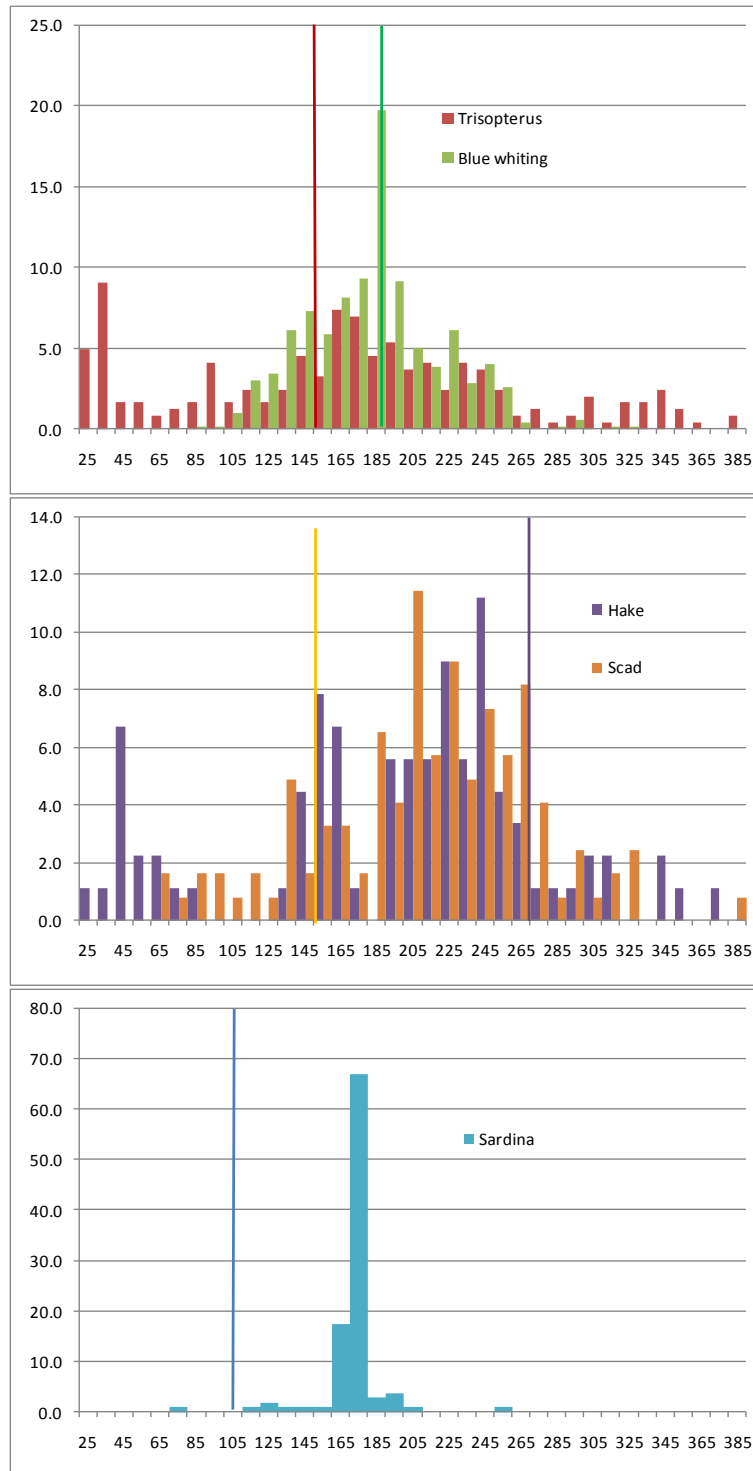
Figure 17. Final GAM models for number of main prey in porpoise stomachs in relation to explanatory variables: smoothers for significant effects of (a) month on hake numbers in the stomachs, (b) estimated porpoise length on blue whiting numbers (left), on *Trachurus* numbers (middle) and on hake numbers (right) and (c) year on hake numbers (left) and on sardine numbers (right).
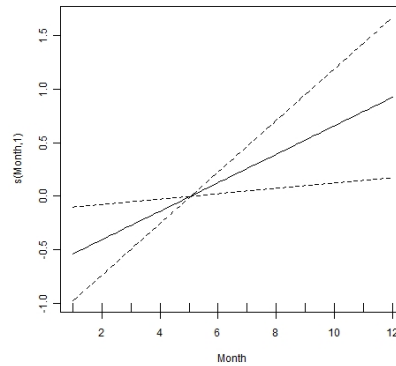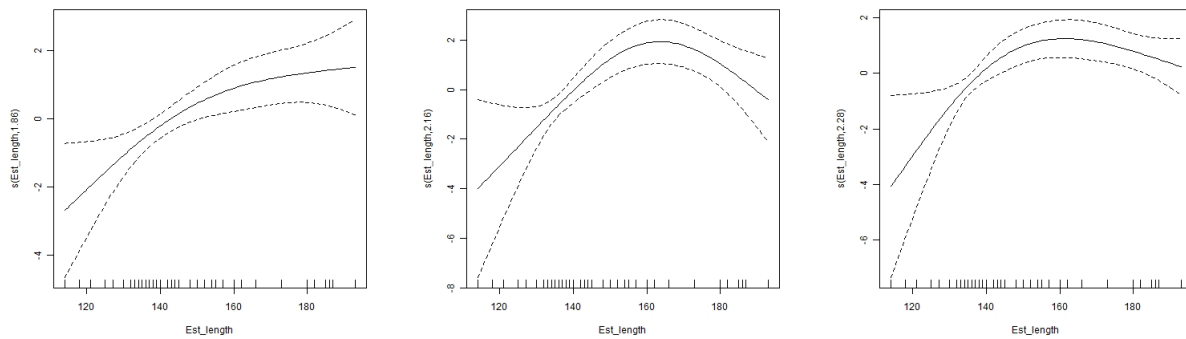
(a)

(b)

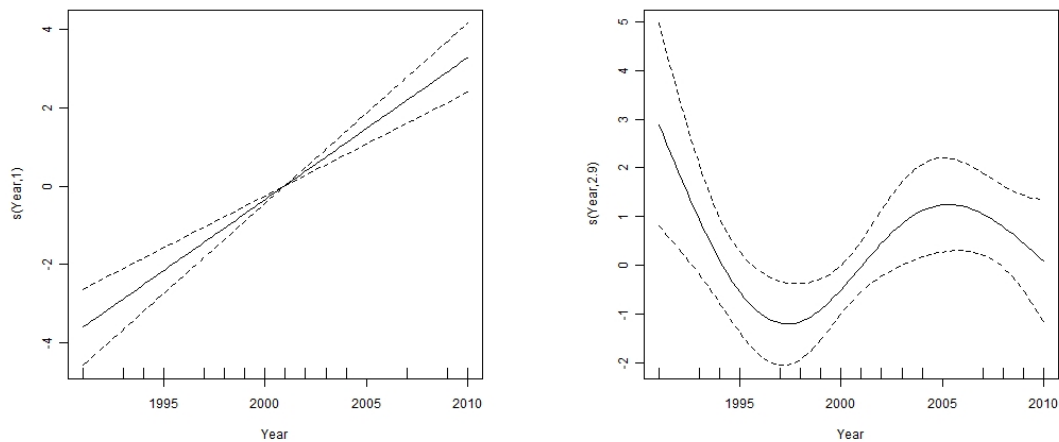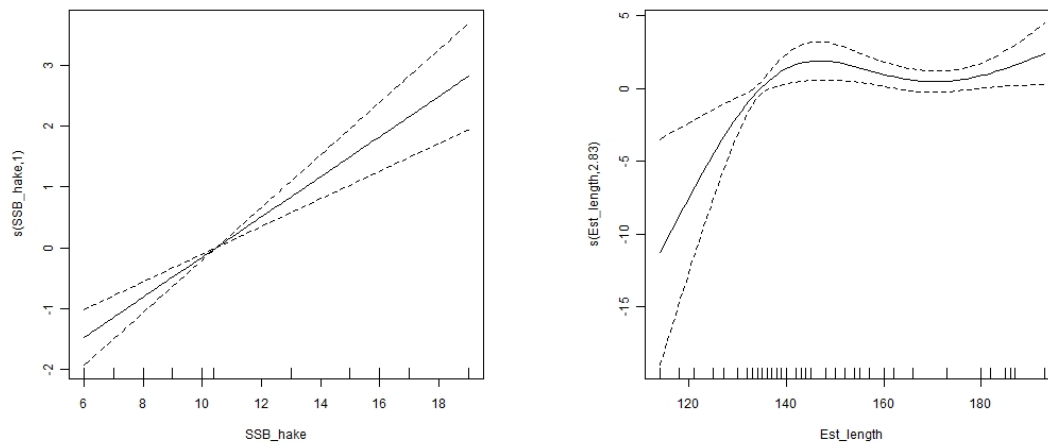
(c)

Figure 18. Final GAM models for number of main prey in porpoise stomachs in relation to explanatory variables: smoothers for significant effects of (a) SSB (SSB_Hake) of the southern hake stock (left graph) and porpoise estimated length (right graph) on hake numbers in the stomachs and (b) Recruitment (R_Sar) of the Iberian sardine stock on sardine numbers in the stomachs.
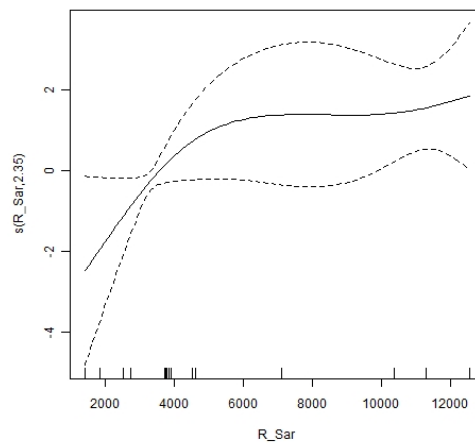
(a)

(b)

Table 1. Comparison of harbour porpoise biological parameters.

Area	Females							Males						Reference
	Maximum length (cm)	Maximum age (yrs)	Sexual maturity length (cm)	Sexual maturity age (yrs)	Physical maturity length (cm)	Physical maturity age (yrs)	Pregnancy rate (Presence of foetus)	Maximum length (cm)	Maximum age (yrs)	Sexual maturity length (cm)	Sexual maturity age (yrs)	Physical maturity length (cm)	Physical maturity age (yrs)	
NWIP	202 (N=127)	18 (N=71)	161-202 (N=60)	5.5 (N=60)	185 (N=60)	10 (N=60)	0.54 (N=13)	189 (N=136)	19 (N=77)	154-171 (N=47)	3.8 (N=47)	162 (N=47)	10 (N=47)	Present study
Atlantic Spain	202 cm (N=31*)	n/a	n/a	n/a	n/a	n/a	n/a	176 (N=27)	n/a	n/a	n/a	n/a	n/a	Lens (1997)
Galicia, north-west Spain	202 (N=38)	9	166	3	n/a	n/a	n/a	n/a	9	155	5	n/a	n/a	Lopez (2003)
Portugal (1981-1994)	208 (N=22)	n/a	n/a	n/a	n/a	n/a	n/a	175 (N=15)	n/a	n/a	n/a	n/a	n/a	Sequeira (1996)
Scotland (1992-2004)	173 (N=227)	20 (N=132)	119-148 (N=111)	4.6 (2-5) (N=111)	164 (157-171)	~5	0.42 (N=33)	170 (N=252)	20 (N=138)	116-144 (N=64)	5.7 (3-6) (N=64)	151 (147-155)	~5	Learmouth, (2006)
British Isles (1985-1994)	189 (N=96)	22 (N=96)	n/a	n/a	160	n/a	n/a	163 (N=114)	24 (N=114)	>130 (N=114)	>3 (N=114)	145	n/a	Lockyer (1995; 2003)
Ireland (2001-2003)	175 (N=27)	11 (N=21)	n/a	n/a	n/a	n/a	n/a	157 (N=19)	n/a	n/a	n/a	7.5 (N=14)	n/a	Pierce et al. (2004)
Denmark (1938-1998)	189	23	136-151 (N=59)	3.6 (2-5) (N=59)	160	n/a	n/a	167	23	130-135.5 (N=96)	2.93 (2-3) (N=96)	145	n/a	Lockyer and Kinze (2003)
The Netherlands	160 (N=19)	12 (N=14)	n/a	n/a	n/a	n/a	n/a	147 (N=5)	12.5 (N=2)	n/a	n/a	n/a	n/a	Pierce et al. (2004)
France (2001-2003)	192 (N=14)	24 (N=9)	n/a	n/a	n/a	n/a	n/a	165 (N=17)	14 (N=12)	n/a	n/a	n/a	n/a	Pierce et al. (2004)
West Greenland (1988-89, 1995)	166 (N=85)	14 (N=85)	138-142 (N=85)	3.6 (N=84)	154 ± 2.6	n/a	n/a	158 (N=91)	17 (N=91)	127 (123-130)(N=91)	2.45 (N=94)	142 ± 1.7	n/a	Lockyer et al. (2003)
Iceland (1991-1997)	174 (N=474)	20 (N=354)	~138-147	~3.2 (2-6) (N=293)	160	n/a	n/a	165 (N=794)	16 (N=615)	~135 (N=526)	~1.9-2.9 (2-5) (N=526)	150	n/a	Ólafsdóttir et al. (2003)
Gulf of Maine (1989-93)	168	17*	n/a	3.4 (2.4) (N=99)	158 ±1.56	~7	0.93 (N=14)	157	15*	n/a	>3 (3-4) (N=31)	143 ±1.25	~5*	Read and Hohn (1995)

Table 2. Overall importance of prey species identified from Galician harbour dolphins (N=56). The first estimate (%F) indicates the percentage of stomachs containing each prey category. The estimates for total number of individuals (N) are based on all prey remains. Measurements on otoliths and beaks were used to derive the first estimate of total prey weight (W, g). The latter two estimates are also expressed as percentages.

PREY SPECIES	% F	N	%N	W	%W
Fish	**96.2**	**1958**	**96.0**	**74338.4**	**98.7**
Sardine (*Sardina pilchardus*)	20.8	156	7.7	4411.2	5.9
All Clupeoids	*20.8*	*156*	*7.7*	*4411.2*	*5.9*
Argentine (*Argentina* sp.)	7.5	11	0.5	269.5	0.4
Blue whiting (*Micromesistius poutassou*)	43.4	493	24.2	15677.1	20.8
Trisopterus spp. (*T. esmarkii*, *T. minutus*, *T. luscus*)	47.2	239	11.7	24267.6	32.2
Silvery pout (*Gadiculus argenteus thori*)	15.1	236	11.6	1186.1	1.6
All Gadidae	*52.8*	*972*	*47.7*	*41394.2*	*54.9*
Hake (*Merluccius merluccius*)	24.5	87	4.3	6454.6	8.6
Snipefish (*Macroramphosus scolopax*)	5.7	108	5.3		
Garfish (*Belone belone*)	9.4	21	1.0	1484.8	2.0
Scad (*Trachurus* sp.)	26.4	142	7.0	13242.9	17.6
Sparidae	13.2	24	1.2	2261.6	3.0
Cottidae	1.9	2	0.1	167.2	0.2
Labridae	3.8	2	0.1	24.1	<0.01
Sandeel (*Ammodytes* spp.)	7.5	71	3.5	1955.9	2.6
Dragonet (Callyonymidae)	13.2	47	2.3	2264.0	3.0
Gobiidae	24.5	219	10.7	217.9	0.3
Atherina sp.	1.9	1	<0.1	7.0	<0.1
Sole (*Solea solea*)	3.8	2	0.1	183.3	0.2
Other flatfish	*1.9*	*1*	*<0.1*	*0.4*	*<0.1*
Unidentified Fish	*47.2*	*91*	*4.5*	*-*	*-*
	32.0	**49**	**2.4**	**1016.7**	**1.3**
Cuttlefish (*Sepia* spp.)	9.4	12	0.6	410.4	0.5
Sepiolid (*Sepiola atlantica*)	1.9	1	<0.1	0.8	<0.1
All Sepiolidae	*18.9*	*17*	*0.7*	*62.0*	*0.1*
Squid (*Loligo sp.*)	5.8	6	0.2	392.5	0.5
Squid (*Alloteuthis sp.*)	17.0	13	0.6	147.1	0.2
	37.7	**28**	**1.4**	**-**	**-**
	7.6	**4**	**0.2**		

Table 3. Results of the GAM models for the main prey in harbour porpoise stomachs stranded and by-caught in the Northwest Iberian Peninsula.

Species	Type of Model	Type of data	Variable	P-value	% Dev
Blue whiting	Negative binomial	Number	Estimated length Year	** ns	45.8
Trachurus spp.	Negative binomial	Number	Estimated length	**	40.3
Hake	Poisson	Number	Estimated length Year Month	** *** *	73.4
			Estimated length Hake SSB Sex	* *** *	65.4
Sardine	Negative binomial	Number	Year Sex	** ns	17.3
			Sardine recruitment	**	20.8

*** <0.001, ** <0.01, * <0.05, ns (no significant)