STATUS OF THE RESIDENT BOTTLENOSE DOLPHIN POPULATION IN THE SADO ESTUARY: PAST, PRESENT AND FUTURE

Raquel Gaspar

A Thesis Submitted for the Degree of PhD
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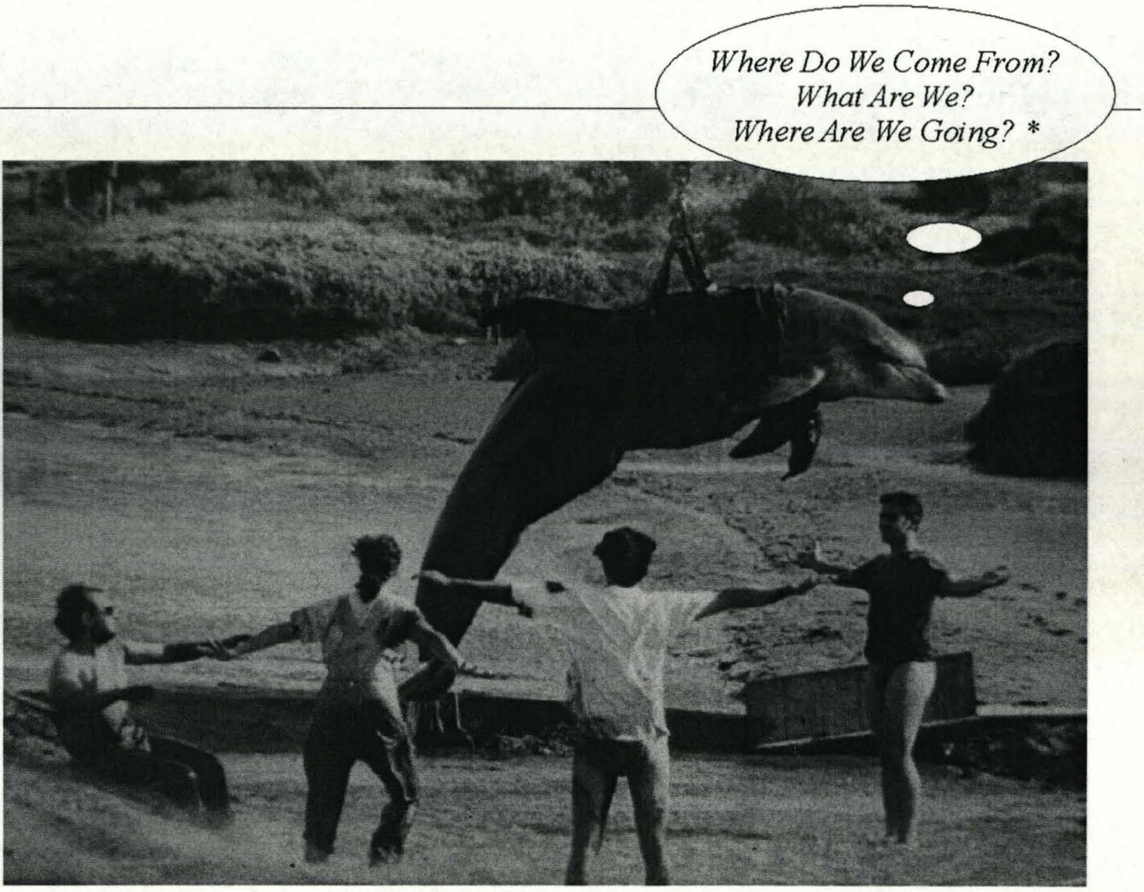
RAQUEL GASPAR

A thesis submitted in partial fulfilment of the requirements for the degree of Doctor of Philosophy

University of St. Andrews

August 2003



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* Paul Gauguin (1848-1903)

TO VITOR ALMADA

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When I was about to give up doing my graduation thesis on the Sado bottlenose dolphins, Vitor Almada maintained my interest and with him the monitoring programme and the core questions for this PhD were born. By dedicating this work to him, I would like to acknowledge the confidence placed in me by this giant man of knowledge and friendship.

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I will always remember St. Andrews as the coldest place I have ever been.
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Throughout these six years I met wonderful human beings, who are now spread over the world, who helped me to grow.
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To Isabel, the quickest thinking friend I ever had,
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To Ben Wilson, the smart, intelligent and "important scientist" but so much a friend
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And last,

deep in my life, I wish that this work can contribute to the welfare of the resident bottlenose dolphins from the Sado estuary.

And…

For those I here forgot, a big acknowledgement from my heart.

DECLARATIONS

i. I, RAQUEL GASPAR, hereby certify that this thesis, which is approximately 40 000 words in length, has been written by me, that it is the record of work carried out by me and that it has not been submitted in any previous application for a higher degree.

date .11.08.03... signature of candidate ... [redacted]

ii. I was admitted as a research student in September 1997 and as a candidate for the degree of PhD. In September 1998; the higher study for which this is a record was carried out in the University of St Andrews between 1997 to July 1999 and from February 2000 to 2003.

date .11.08.03.. signature of candidate ..... [redacted]

iii. I hereby certify that the candidate has fulfilled the conditions of the Resolution and Regulations appropriate for the degree of PhD in the University of St Andrews and that the candidate is qualified to submit this thesis in application for that degree.

date .13|8|03.. signature of supervisor ..... [redacted]

iv. In submitting this thesis to the University of St Andrews I understand that I am giving permission for it to be made available for use in accordance with the regulations of the University Library for the time being in force, subject to any copyright vested in the work not being affected thereby. I also understand that the title and abstract will be published, and that a copy of the work may be made and supplied to any bona fide library or research worker.

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ABSTRACT

The main aim of this work was to determine the past, present and future conservation status of the bottlenose dolphin population inhabiting the Sado estuary region, Portugal, using a long term (photo ID) data set. Resident animals, identified from their strong resighting pattern, were confined to the estuary region. There is little evidence of social interchange with other coastal bottlenose dolphins and the role of emigration and immigration is unclear. This is a very small population. Numbers of animals have decreased in the past but now seem to be increasing. A mark-recapture analysis of individual capture histories showed that time changes in age-specific survival explained the observed changes in number of animals. Survival was lower, particularly in young animals, in earlier years which have resulted in a long period of lack of recruitment to adulthood. In the most recent years survival has increased, especially for calves in their second and third years. Fecundity has also been higher. Protected areas and proposed marine SACs reflect the importance of the Sado estuary region; this is also an area of intense anthropogenic activities that threaten the dolphin population. Population viability analysis was conducted using the software VORTEX incorporating estimates of past or current vital rates. The likely future of the resident population is for it to decline, especially during the next few decades. A viable population was only predicted if maximum values of vital rates were used or if regular immigration occurred. A number of proposals for management action are discussed. This work constitutes an example in conservation biology where life history parameters were estimated, and used to predict future viability and thus to indicate management actions that could increase the chance of saving a very small marine mammal population.

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CHAPTER 1. GENERAL INTRODUCTION

1.1. CONSERVATION BIOLOGY

During the past decades, the Earth's biodiversity has been challenged by a very high rate of extinctions and a declining rate of speciation. If this is not avoided, our children and grand children may live through a period of species extinction comparable to the mass extinctions evident in geological record (Townsend et al. 2003).

The human population is now more than 5.4 x 10^9 persons and is growing by 95 x 10^6 a year and its per-capita consumption of unrenewable energies is unsustainable. The impact of this expansion is generating the worldwide destruction of biodiversity and degradation of natural ecosystems. It is the urgent challenge of conservation biology to try to prevent this negative feedback mechanism coming into play (Brussard and Ehrlich 1992). To achieve that goal, conservation biologists need to provide scientific concepts and information on life history dynamics of species and on the functional structure of ecological systems to inform the design of effective management actions towards the maintenance of the Earth's biodiversity (Orians and Soulé 2001). The success of the implementation of such conservation actions depends on the social and economic value of biodiversity, which is culturally sensitive (Possingham et al. 2002).

1.1.1. The dynamics of small populations

Much of the focus of conservation biology has been on small populations of rare and endangered species. This is because 1) classic rare species have a limited distribution and restricted habitats (Rabinowitz 1981) and for this reason they are more likely to be endangered; and 2) the smaller the population, the greater the risk of it being driven to extinction (Soulé 1987). In general, the dynamics of large populations are governed by the "law of averages", whereas small populations are governed by the specific fate of its few individuals (Caughley 1994). What factors make a small population susceptible to be driven to extinction due to its smallness?

Caughley (1994) pointed out several stochastic causes that reflect the effect of population size on the viability of small populations (the small population paradigm). Environmental stochasticity (May 1973), unpredictable fluctuations in environmental factors (such as floods, droughts and storms) and catastrophes can perturb population growth rate. This can affect both small and large populations if the resulting variance on population growth is higher than the population growth itself (Lande 1993). The problem of small populations is that when subjected to such perturbations, the possible resulting increase in mortality or reduced births due to severe conditions has a more serious impact due to the low numbers. In addition, the capacity of small populations to recover is low or impossible before extinction occurs. On the other hand, as the size of a large population grows, the range of environments occupied by individual organisms can increase (Stacey and Taper 1992). Whereas environmental stochasticity affects the background variation of the population growth rate, demographic stochasticity reflects the uncertainty of individual fortunes. Demographic stochasticity results from the random variation in the number of animals that are born male or female, or in how many animals die or reproduce in a given year. In general, demographic variability is critical to extinction when populations are less then 30-50 individuals. One serious affect of very small population size can be the low chance of mating opportunities or group defence and foraging (Allee effect).

Environmental variability is more likely to affect small mammals with a large number of offspring and a short lifespan than demographic stochasticity. Whereas the resulting lack of food may affect key elements of their life history strategy such as their capacity to reproduce and the survival of their offspring (Heppell et al. 2000), their large number of offspring can buffer the effect of demographic variation. On the contrary, large long lived mammal species are more buffered to environmental variation (Morris and Doack 2002).

Another factor to consider is the genetic quality of the individuals. In general, the higher the heterozygosity of the individuals from the same cohort, the fitter they are (Keller and Waller 2002). When the population is small and isolated for many generations, the genetic variation necessary for adaptative evolution tends to be scarcer, as the alleles are randomly fixed or lost from the population by drift. In addition, deleterious mutations will tend to accumulate because selection is less effective in small populations. These processes tend to be gradual and do not threaten populations in the short term (Keller and Waller 2002). By contrast, inbreeding can act more quickly. When population size is small, mating between close relatives may happen frequently, although many species have behavioural mechanisms to prevent mating between close relatives (Ingvarsson 2002). As a result, as the population size decreases, the level of heterozygosity will tend to be lower. Additionally, inbreeding creates the exposure of recessive alleles which can decrease individual fitness if some of those recessives are deleterious (Caughley 1994). For this double effect, inbreeding depression poses a more immediate risk of extinction compared to the other genetic mechanisms (Keller and Waller 2002). Although inbreeding depression may be a key factor in the extinction of small populations, it is not well understood the mechanisms by which it affects the life history and persistence of natural populations (Caughley 1994, Beissinger 2002, Keller and Waller 2002).

The extinction process resulting from environmental, demographic and genetic stochasticity is likely to act as an “extinction vortex” produced by a positive feedback loop between population size and fitness of its members (Caughley 1994). Although in small natural populations, all these factors may play pivotal roles in causing extinction, in captive populations the small size and the genetic quality of the individuals are probably the most critical elements since population fluctuations caused by external factors such as lack of food, predators and disease can be avoided (Hedrick and Miller 1992).

How big should population size be for a population to be not driven to extinction by its smallness? There are two ways of addressing the minimum viable population size. The demographic way considers the total number of animals as population size. The minimum viable population size (MVP) is given by the number of animals that ensures at some acceptable probability of risk that the population will persist for a specified time (Gilpin and Soulé 1986, Shaffer and Samson 1985). The genetic criteria concerns the genetic population that is the number of animals that reproduce and thus contribute genes to the next generation; the effective population size (N_e.). Franklin (1980) provided a general rule of thumb in which a population with 50 reproducing animals could keep a low level of inbreeding depression and a population with 500 animals would be necessary to avoid genetic drift. However, as shown below other factors than population size itself may play a pivotal role in the recovering of small populations from extinction.

The recovery of the Scandinavian population of the grey wolf (*Canis lupis*) from a very small population size was triggered by the immigration of a single male wolf of Finnish or Siberian origin. The lack of genetic diversity once limiting the size of the population was restored (Vilà et al. 2003) and natural selection has driven a rapid increase in numbers (Ingvarsson and Whitlock 2000). This example suggests that low levels of migration (natural or artificial) between small populations of endangered species can be extremely successful in restoring genetic diversity and reducing inbreeding depression (Ingvarsson 2002).

Another example is the dynamics of extinctions and recolonizations in subpopulations that occur in more or less discrete patches of habitat (metapopulations). Demographic and genetic stochasticity factors are likely to differ among these subpopulations and so the environmental stochasticity acting on the patches they live in. For example, the Acorn Woodpecker (*Melanerpes formicivorus*) subpopulations in New Mexico, may be regularly rescued from extinction triggered by environmental stochasticity by immigration from other, independently varying subpopulations (Stacey and Taper 1992).

1.1.2. Threats to the species and communities and solutions

Although a positive feedback between several stochastic causes may be established, the cause of the decline of small populations is much more likely to be an extrinsic factor than the small size itself. Many of these factors are due to the unsustainable expansion of the human population, which has major impacts on the natural habitats, especially in the tropics (Brussard and Ehrlich 1992). Habitats can be destroyed due to conversion of natural ecosystems into agricultural, urban or industrial uses. Naturally, habitats can also be destroyed by fires. More commonly the habitat becomes fragmented. Although this is likely to be a major problem for species with naturally low dispersal rates, it may result in lower carrying capacity for species to survive and reproduce. In addition, habitats have been degradated due to pollution of all kinds or disturbed due to the role of activities to which species are sensitive. Another way to destroy or degradate a habitat is by introducing exotic species. These may have more success than local ones (which may be endemic species) resulting in their elimination. This change in the community may give origin to a chain of extinctions, which can be also achieved independently by the elimination of a key species of a trophic chain, for example by overdepletion. Ultimately, these deterministic causes of extinction (Shaffer and Samson

1985) result in the loss of biodiversity for which action has to be taken to halt the decline.

Whereas the small population paradigm relies on the theoretical causes of smallness in the persistence of small populations making generalizations across species, empirical investigations of declining populations tend to be case specific and aim to provide the solution to stop the decline (the declining population paradigm) Caughley (1994). However, resolution of the conservation problems requires an integration of both approaches. We cannot rely in theoretical models, which may have no relevance to a particular population, but we gain little general understanding of how best to approach conservation if each case is different (Boyce 2002). Population viability analysis (PVA) (see chapters 5 and 6) reconciles both methods by using theoretical models of the extinction mechanisms that plague small populations in order to predict their viability and the effect of specific conservation actions (Beissinger 2002, Boyce 2002). Although PVA is not a process to determine the cause of the decline, sensitivity analysis can be a useful tool in defining conservation objectives and management plans to avoid the decline.

Conservation actions can involve the protection of natural habitats by the creation of protected areas. On a broad scale, the Habitats Directive (92/43/EEC) is the contribution of the European Union (EU) to the Biodiversity Convention by encouraging the future conservation of biodiversity in Europe. The Directive aims to ensure that biodiversity is maintained through the conservation of important, rare or threatened habitats and animal and plant species, taking into account economic, social, cultural, and regional requirements. To achieve that, a network of areas (Natura 2000) within the European community is being designated to enable the habitats and species to be maintained, or restored to a favourable conservation status over their natural range. These areas are called Special Areas of Conservation (SACs) which, together with Special Protection Areas (SPAs) from the Birds Directive, constitute the Natura 2000 network. Each EU country has a role to play by proposing candidate Special Areas of Conservation (cSACs) for species and habitats identified as having special status. Management of SACs may involve the restoration of habitats and *ex situ* conservation through captive breeding in zoos and botanical gardens. These can be used as demographic and genetic reservoirs for enhancing existing natural populations or the establishment of new ones.

1.2. CONSERVATION ISSUES OF MARINE MAMMAL SPECIES AND POPULATIONS

The conservation of marine mammals started early in the last century as a legacy of their past unsustainable exploitation (Reeves and Reijnders 2002). Whaling, sealing, intensive exploitation of sirenians and sea otters, and Eskimo "subsistence" hunting of polar bears provided markets with oil, fur, food, carving, ivory and contributed to the subsistence of local populations (Reeves 2002). However, marine mammals have relatively low intrinsic rates of increase due to their long maturation, low reproductive rates and long life spans, which prevents them compensating quickly for overexploitation (Evans and Stirling 2002). One consequence was the extinction of the Steller sea cow (*Hydrodamalis gigas*) (Reeves and Reijnders 2002). Of major current concern is the critical status of many exploited populations because they were reduced to very low levels, such as the Svalbard population of bowhead whales listed as critically endangered (IUCN/CSG 2003). In addition, some populations have been exterminated and many others remain at extremely low levels and whose prospects of recovery are uncertain (IUCN/CSG 2003).

The depletion of the stocks and the increasing demand for alternative products, and restrictions on the international trade under the Convention of International Trade of Endangered Species of Wild Fauna and Flora (CITES) and under the International Whaling Commission (IWC) contributed to a reduction of the intensity of commercial exploitation. Nowadays, some populations are still harvested directly (e.g. the long finned pilot whales (*Globicephala melaena*) at the Faroe Islands and the beluga whales (*Delphinapterus leucas*) in Canada). Many populations of pinnipeds are controlled by deliberate killing in order to avoid competition for food or damage of fishing gear or private land use (Northridge and Hoffman 1999). However, the sustainability of these captures is subject to discussion due to the lack of data in some cases and also to non-scientific issues.

The greatest current threats to marine mammals are habitat degradation and especially incidental mortality in fisheries. Habitat degradation is most likely to affect freshwater and coastal species but pelagic species can also be affected. Rivers and coastal environments tend to be exploited due to their high productivity but also to absorb increasing amounts of waste (IUCN/CSG 2003). As a result, overfishing, chemical and noise pollution, disturbance and vessel collisions can contribute to, changes in distribution and possibly depletion of populations of marine mammals.

Decreasing carrying capacity due to overfishing has been suggested to be linked with the decrease in sub-adult survival of the Hawaiian monk seal (Ragen and Lavigne 1999). Chemical pollution, particularly from organochlorines, may contribute to reproductive (O'Shea et al. 1999) and immunocompetence (Reijnders et al. 1999) failure. Acoustic pollution due to vessel traffic, oil exploration, high-energy sounds from seismic and drilling noise could be especially damaging to cetaceans since many species rely on sound to explore their environment, for foraging and communication

(Gordon and Tyack 2002). Disturbance from vessel traffic but also from seal, dolphin and whale watching may cause short term negative impacts (Williams et al. 2002) and concern, exists in a few cases, for the long term impact on population dynamics. Mortality or injury due to vessel collisions is most likely to affect coastal species that rely on areas heavily used by watercraft such as the Florida manatee (*Trichechus manatus latirostris*) (Marmontel et al.1997). Ship strikes have been responsible for additional mortality in the very small population of North Atlantic right whales (*Eubalaena glacialis*) (Fujiwara and Caswell 2001). Climate change can affect the distribution and availability of prey of marine mammals, especially otariid species (Harwood 2001), or loss of habitat such as ice which is a critical breeding habitat for Artic seals and exposing them to predation by polar bears (Hansel et al. 1998).

Passive fishery gear (drift nets, gillnets and anti shark nets) is generally responsible for mortality of more marine mammals than active gear (purse seine and trawling nets). This is especially true in the case of gillnets (Perrin et al. 1994, Hofman 1990) (see below). In the recent past, pelagic drift nets were responsible for the death of thousands of dolphins, whales, porpoises and pinnipeds a year (Northridge 1990, Reeves 2002). Anti shark nets threaten the Indo Pacific bottlenose (*Tursiops truncatus*) and humpbacked (*Sousa chinensis*) dolphins in southern Africa (Cockcroft 1990, 1992), and dugongs (*Dugong dugon*) in Australia (Marsh 2000). Entanglement in fishing gear has been a major cause of mortality for Hawaiian monk seals (Ragen and Lavigne 1999). This includes entanglement in discarded fishing gear (and other marine debris) which is also a problem for dolphins (Hall 1998). Tuna purse seine nets have been an important cause of mortality of pelagic dolphins (Gosliner 1999). Trawling nets affect some dolphins, such as common dolphins (*Delphinus delphis*) in English Channel waters

(UK) (Northridge 2003), and some species of seals, sea lions, and fur seals (Northridge and Hofman 1999).

Combined habitat degradation and mortality in active and passive fishing gear or fishing related marine debris is driving some cetacean species and populations to extinction. The only existing population of the river dolphin baiji (*Lipotes vexillifer*), inhabiting the Yangtze River basin in China, is listed as critically endangered in the IUCN red list. The population is thought to be in the tens due to habitat degradation (construction of dams) and due to fishery bycatch in illegal "rolling hooks" and electrofishing (IUCN/CSG 2003). Another example is the vaquita (*Phocoena sinus*) in Mexico, which has an extremely high mortality in gillnets (IUCN/CSG 2003). The North Island population of Hector's dolphin (*Cephalorhynchus hectori*) in New Zealand is mainly threatened by mortality in gillnet fisheries and is also listed as critically endangered (IUCN/CSG 2003).

The resolution of the conservation problems of marine mammal species has a long way to run and, in many cases, substantial management actions are needed. The recommended conservation measures for the recovery of the Baiji constitute a good example. Because resources have to be managed, efforts should concentrate on action and not in further surveys. Due to the very small population size and past failure (e.g. captive breeding) in conservation actions, the urgency to act is clearly evident. However, it implies the construction of a "semi natural reserve" with the consequent catch and translocation of the individuals into that area, the translocation of finless porpoises (*Neophocaena phocaenoides*) from the reserve in order to avoid disadvantageous ecological interactions, the monitoring of the water of the reserve, the full enforcement of a ban on the use of fishing techniques causing mortality and the parallel improvement of economic activities of the locals (IUCN/CSG 2003).

Smaller steps however can be made to avoid increased mortality in fishing gear, such as deterrence programmes using pingers and similar devices (Kraus et al. 1997), although concern exists because this may cause habituation (Cox et al. 2001), among other issues. At a regional scale, international agreements under the Convention on the Conservation of Migratory Species of Wild Animals (Bonn Convention), such as the Agreement on the Conservation of Small Cetaceans of the Baltic and North Seas (ASCOBANS) and the Agreement on the Conservation of Small Cetaceans in the Black Sea, Mediterranean Sea and Contiguous Atlantic Area (ACCOBAMS) provide a focus for conservation efforts and can provide political support for scientific work, such as estimates of abundance of small cetaceans (Hammond et al. 2002) or bycatch. Reserves focused on the protection of marine mammals may also involve the commitment of several countries. The International Ligurian Sea Cetacean Sanctuary is an example. This reserve is located in an unusually high productive region in the Mediterranean Sea which constitutes an important feeding area for fin whales (*Balaenoptera physalus*) and other cetacean species. Conservation actions are aimed at the elimination of a number of threats including mortality in drift nets, habitat degradation and disturbance. Candidate Special Areas of Conservation for marine mammal species under the Habitats Directive are also good examples of area based conservation, although how well they will achieve their conservation objectives remains to be seen. At a broader scale, the UN banned the use of drift nets at distances greater than 200 nautical miles from the coastline, reducing marine mammal mortality on the high seas, although not affecting coastal species. But still much has to be achieved not only in determining the conservation status of the species but also the implementation, enforcement and compliance of specific legislation to protect populations or species when necessary.

Acute mortality events such as the die offs of thousands of seals and dolphins (Aguilar and Raga 1993, Kennedy 1998) from morbilivirus infection and those resulting from oil spills (e.g. Exxon Valdez and, more recently, the Prestige) are also a cause of mass mortality of marine mammals. Rescue and rehabilitation programmes, although not appropriate in every case, may help to save individuals (and perhaps populations). The image seen at the front of this thesis shows the rescue of a resident bottlenose dolphin from the study population in the Sado Estuary in April 1999. This adult male (LUA) live-stranded in the inner estuary channels and was translocated by helicopter to a deeper area in the south channel. It is still alive at the time of writing. When kept in captive facilities, opportunities arise for learning about the life history of the species (Geraci and Lounsbury 1993). Additionally it may provide an opportunity to monitor the individual animals. A satellite-linked transmitter was deployed on one injured bottlenose dolphin "Gulliver" in Florida and information gathered after its release gave new insight into previous assumptions about the extent of movements of dolphins and definition of stock boundaries (Wells *at el.* 1999).

1.3. THE LIFE HISTORY AND SOCIAL BEHAVIOUR OF THE BOTTLENOSE DOLPHIN

The bottlenose dolphin is a "slow"mammal (Heppell et al. 2000) species. After a twelve-month gestation period (Perrin and Reilly 1984, Schroeder 1990) female bottlenose dolphins have a single, precocious, large (usually between 90 and 120 cm) (Leatherwood and Reeves 1983) calf with well developed sensory and locomotion abilities (Derrickson 1992). Growth rates during early life are very high (Cockcroft and Ross 1989, Read et al. 1993, Fernandez and Hohn 1998). Lactation provides most of the energy during the early stages through the fat rich milk. Although calves may successfully catch and consume small fish by four to six months old, bottlenose dolphins rely on milk as the main source of food in their first year, nursing (Mann and Smuts 1998). This makes them vulnerable to fluctuations in their mothers' body condition. Milk nutrients can also contribute to disease resistance and improve future survival of the calf (Whitehead and Mann 2000). During lactation mothers have a high increase in their food consumption (Cheal and Gales 1991, Urian et al. 1996, Kastelein et al. 2002).

If they are in poor body condition, mothers may have to decide between their own survival and that of their offspring (Monson et al. 2000). To capture prey mothers may need to accelerate rapidly and dive deeply. Since newborns are less competent swimmers and divers (Whitehead and Mann 2000), separations between mother and calf are likely to occur. Calves have little physical protection nor are there specific protected places in the marine environment where a mother can raise its calf. Thus separations represent a significant risk for newborn survival due to natural dangers, such as predation (Herzing 1997), and anthropogenic dangers, such as incidental captures (Cockcroft 1992). Although protection is gained from group living (e.g. babysitting Connor et al. 2000, Whitehead and Mann 2000) newborn bottlenose dolphins may suffer aggression from conspecifics (Patterson et al. 1998).

During the second and third years, calves gain fitness from dependence to their mothers and the protection and learning from group living. They can also rely on their more successful and reliable acquired techniques to feed themselves and the learned skills to explore the environment and communicate with conspecifics. Bottlenose dolphins exhibit a prolonged dependence on their mother due to a prolonged lactation (about 18 months) (Cockcroft and Ross 1989). Separation from the mother is most likely to occur after the third year (Wells and Scott 1990, Mann et al. 2000). Such a strategy of life may be necessary since bottlenose dolphin prey distribution may require special foraging skills (Whitehead and Mann 2000). Thus infants need to develop the necessary foraging skills before they are completely dependent on solid food. Foraging activity increases throughout the life of the calf (Mann and Smuts 1998). While feeding themselves, additional food intake through nursing may provide specific nutrients for their still high growth rates (Cockcroft and Ross 1989, Read et al. 1993, Fernandez and Hohn 1998).

In the bottlenose dolphin and in other large long-lived mammals, such as primates (Walters 1987) and elephants (Moss 2001), the sub-adult phase is a relatively long period compared to the life span (Whitehead and Mann 2000). Despite this phase being twice as long as the infancy period, little is known about it (Connor et al. 2000). The long period of immaturity results from a trade-off between early reproduction and an extended period of growing, learning and development of locomotive, social and foraging skills (Norris 1994, Connor et al. 2000). Sub-adults are active, exploratory growing animals. After weaning, both male and female sub-adult bottlenose dolphins disperse from their natal groups (social dispersion) (Wells 1993) but remain within the local population (Connor et al. 2000) associating with other inexperienced peers (Wells et al. 1987, Wells 1993). During this phase, adults may play a minor role in their instruction and protection compared to when they were calves. Further, infection of infant diseases can successfully develop in such sub-adult schools where frequent close contact occurs (Van Bressem and Van Waerebeek 1996).

Sexual maturity is attained late: females become sexually mature between age 5 and 12 and males between 8 and 14 years old (Perrin and Reilly, 1984, Cockcroft and Ross 1989, Wells et al. 1987, Kasuya et al. 1997). Females cease their growth near sexual maturity. Males continue to grow, particularly in girth and mass, for some years more. This additional growth in males may also represent an investment in future reproduction

(Read et al. 1993) since bottlenose dolphins have a promiscuous mating system (Wells et al. 1987, Connor et al. 1996, 1998). The bottlenose dolphin is a large dolphin species. Total length in adults ranges from 238 cm to 390 cm, depending on the geographic origin (Cockcroft and Ross 1989, Leatherwood and Reeves 1983). Maximum longevity varies between 35 and over 50 years (Cockcroft and Ross 1989, Hohn et al. 1989, Fernandez and Hohn 1997, Kasuya et al. 1997, Wells and Scott 1990, Stolen and Barlow in press). As in other large long lived mammal species (Heppel et al. 2000), the bottlenose dolphin has a low reproductive rate. Calving intervals in wild populations are long (2 to 6 years) and annual crude birth rates are low (0.031 to 0.068) (see chapter 2). Reproductive senescence does not seem to exist in the bottlenose dolphin (Cockcroft and Ross 1989; Marsh and Kasuya 1986). For such a large, long-lived and slow reproducting mammal species, survival in adult bottlenose dolphins is expected to be high (see chapter 4).

1.4. BOTTLENOSE DOLPHINS IN THE SADO ESTUARY, PORTUGAL

The bottlenose dolphin population inhabiting the Sado estuary region (Figs.1.1 and 1.2) is one of the few resident populations of this species in Europe (chapter 2). Like many other coastal marine mammal populations, this small population (Teixeira 1981, Hussenot 1982, Dos Santos and Lacerda 1987, Gaspar 1994) inhabits a degraded marine environment due to untreated urban, agriculture and industrial sewage, shipping and port activities, and recreational watercraft (Fig. 1.2). Since 1980 a reserve (the Sado Estuary Natural Reserve) was created in the upper and middle parts of the estuary and since 1998 a Marine Park was created (the Arrábida Marine Park) nearby.This includes part of the marine area near the estuary entrance. Recently, two areas have been proposed by the Portuguese Nature Conservation Institute (ICN) to be Special Areas of Conservation under the EU Natura 2000 network: the Sado cSAC, which enlarges the existing borders of the reserve and covers the interior and middle part of the estuary; and the Arrábida cSAC, whose limits overlap with those from the marine park (see chapter 3, Fig. 3.1).

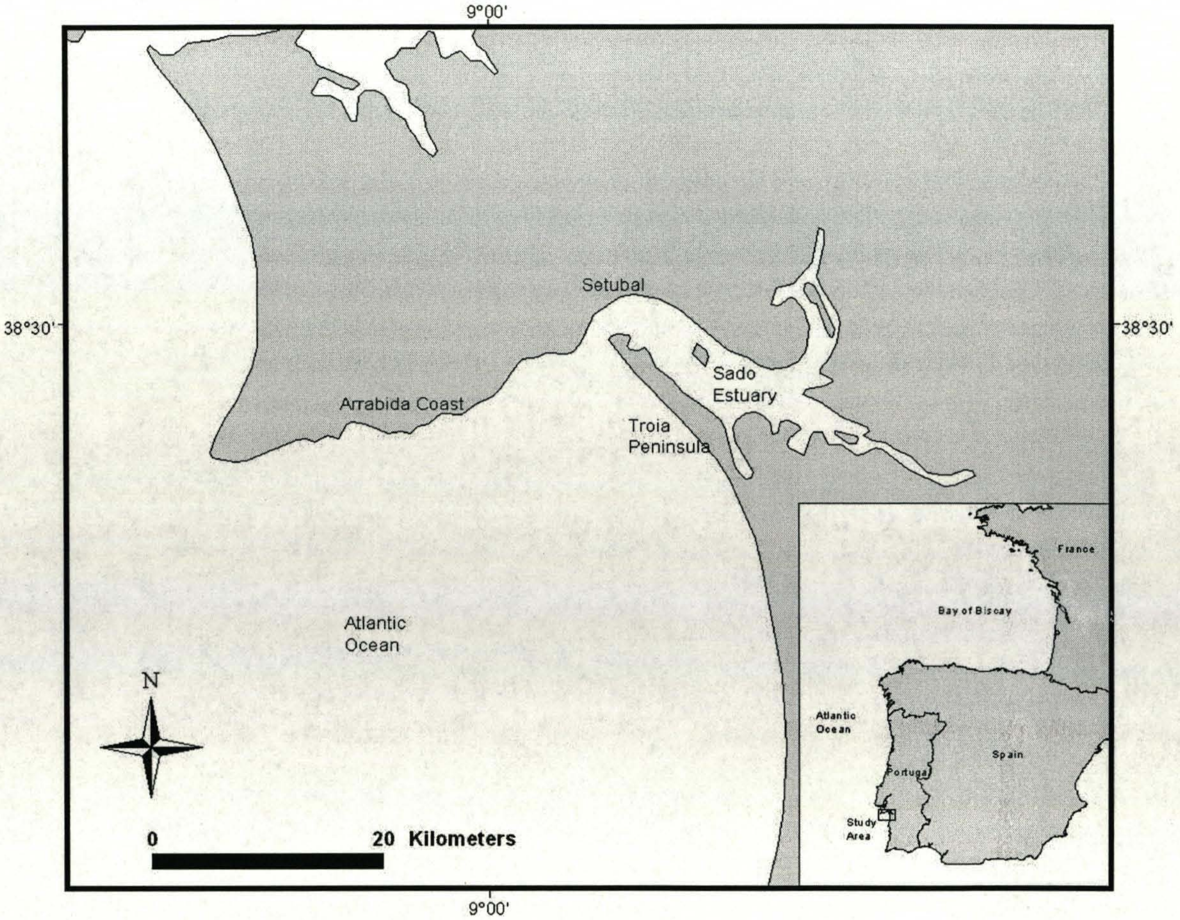

Figure 1.1. Location of the Sado estuary region.

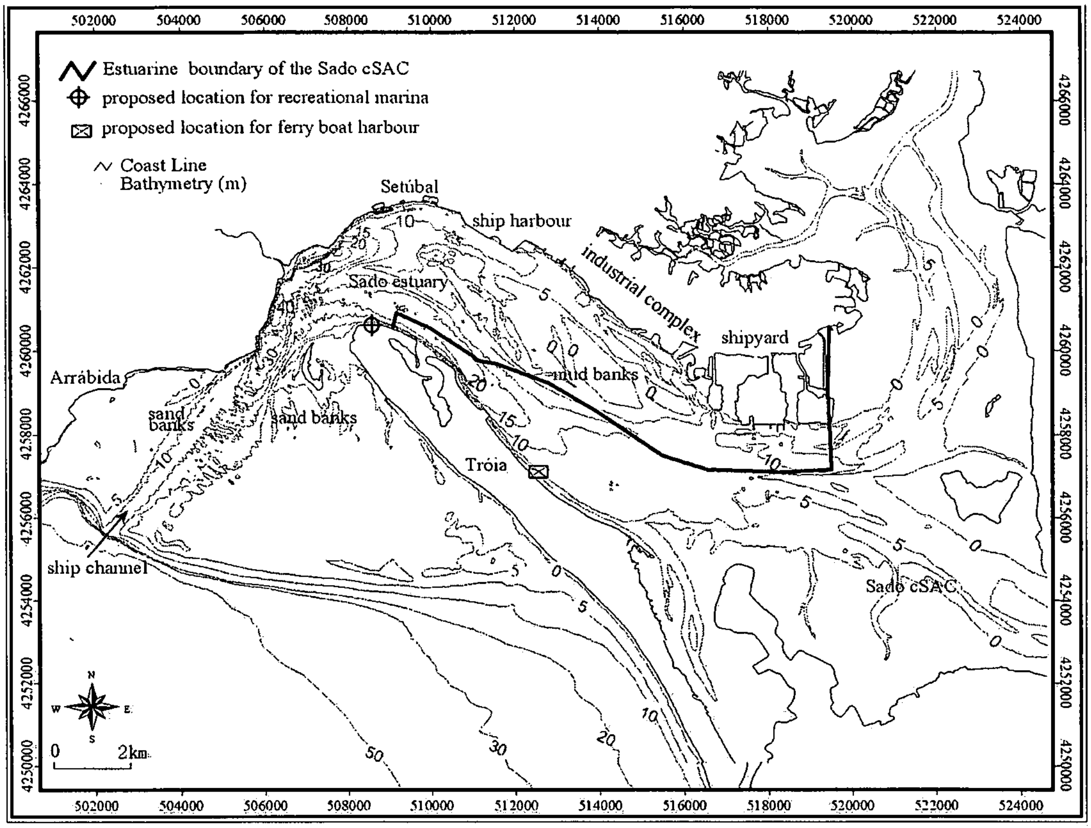

Figure 1.2. Sado estuary region.

The Sado estuary is located on the west coast of Portugal (Fig. 1.1) and is the second largest Portuguese estuary and one of the largest estuaries in Europe. The tidal influence reaches 45km upstream; the tidal range is approximately 4m. The Sado river main flow is approximately $7m^3 s^{-1}$ although it is seasonally variable (Cabral 1999). In the upper part of the estuary, mean values of water temperature range from 16.5°C (SD=3.9°C) to 17.5°C (SD=6°C) and those from salinity range from 35.3ppt (SD=1.7) to 32.5ppt (SD=2.6). Temperature and salinity amplitudes are higher in the inner estuary (Cabral 2000). Sand and mud are the more common sediment types of the estuary bottom. The estuary can be divided into three parts. The upper estuary is shallow (generally less than 5m deep) and comprises a main channel and several smaller channels, which border mainly rice and aquaculture fields and a few small local villages. In the middle part, the estuary is dived into two channels separated by mud banks. The north channel is approximately 5-10m deep and is limited by the city and harbour of Setúbal and by an industrial and shipyard complex. The south channel is deeper (generally 10-20m) and wider and is limited by the sandy peninsula of Tróia. Water circulation and currents are higher in this channel (Ambar et al. 1982). At the estuary mouth there is one main deep (around 20-40m) channel. The estuarine water flow is mainly towards the south-east along the marine coast of Tróia.

Bottlenose dolphins from the Sado resident population have been studied since 1976 (Teixeira 1981) although with more detail since 1986. Much of what is known about this population relates to its habitat use, behaviour (including acoustic signals and social structure), disease and contaminant load. The estuary is an important feeding ground for the resident dolphins (Dos Santos and Lacerda 1987, Harzen 1998, Dos Santos 1998, Nunes 2001). Within the estuary, dolphins seem to spend more time in less contaminated and high prey diversity areas such as the south channel (Freitas 1995, Dos Santos 1998, Harzen 1998, Nunes 2001). They are also frequently seen at the estuary entrance, which they have to use to enter or leave the estuary (Gaspar 1994, Dos Santos 1998, Vieira 1998). These apparently preferred areas are partly covered by the protected areas mentioned above. Behaviour of the resident dolphins has been categorised as travelling, travelling with foraging, disperse foraging, surface feeding, social interactions at the surface and resting (Freitas 1995, Dos Santos 1998, Louro 2001, Brito 2001, Carvalho 2000, Nunes 2001). Behaviour indicative of short term disturbance has been observed during interactions with recreational and dolphin watching boats, and jetskis (Cascão 2002). In general, the production of the types of sounds does not seem to depend on the estuary area, water visibility nor depth (Lourenço 2003). However, echolocation signals tend to increase with a increase in water turbidity (Brito 2001). The production of whistles in a group of dolphins was lowest during travelling and highest during social interaction (Couchinho 1999, Louro 2001). Acoustic background noise may impede passive listening for prey (Dos Santos 1998). Dolphins whistle frequently in the presence of background noise (Lourenço 2003, Picanço 2003). Dolphins seem to enter the estuary during the morning with the flood tide and leave during late afternoon during the ebb tide (Harzen 1998, Vieira 1998). Group size varies according to definitions: 4 to 7 animals (Teixeira 1981), 7 to 12 animals (Nunes 2001), and 1 to 40 (Dos Santos and Lacerda 1987). On several occasions, resident bottlenose dolphins were seen carrying dead calves (Harzen and Dos Santos 1992). The majority of the individuals show high site fidelity (Gaspar 1994, Harzen 1995).Observations of interactions among individuals have led to the suggestion that the association between individuals is typical of a fission-fusion society (Picanço 2003). Harzen (1995) has suggested that the Sado resident dolphins may be a breeding unit of a larger population. Dolphins inhabiting this temperate estuarine and marine system are large, reaching 300-330m length (Dos Santos 1985, R. Gaspar, personal observation).

Most of the resident animals have skin lesions (Gaspar 1994, Harzen 1997, Wilson et al. 1999a) and many of these lesions were identified as being tattoo lesions from dolphin pox virus, which affected mostly sub-adults (Van Bressem et al. in press). Levels of heavy metals found in stranded resident dolphins were not high compared to those found in bottlenose dolphins living elsewhere, except inorganic mercury in the liver of a sub-adult dolphin (Barreiros et al. 1996). Although resident dolphins have been studied for a long period, the demographic trend of this small resident population was unknown.

1.5. AIM AND OBJECTIVES OF THE PRESENT STUDY

In 1994, I established the basis for a monitoring programme of the resident population as part of my graduation theses under the supervision of Professor Vitor Almada and Professor Jorge Palmeirim (Gaspar 1994). Dolphins were individually identified through photo identification, population size enumerated as being 34-36 animals, and the number of animals per category of age class and their identity was determined. This programme continued until 2001, under the auspices of the Natural Reserve, and until 2002 as part of this PhD.

The overall aim of this study was to determine the status of the resident bottlenose dolphin population inhabiting the Sado estuary region. The objectives of this thesis are:

1. To define the resident population and investigate trends in vital rates and population size;
2. To investigate the distribution of the resident animals in the marine area adjacent to the estuary and their interaction with other bottlenose dolphin populations;
3. To estimate the viability of the resident population;
4. To suggest management actions for the conservation of the resident population.

In chapter 2 photographic records from other authors (M.E. Dos Santos, M.Lacerda, S. Harzen) collected prior to the monitoring program were added to data collected before the beginning of this PhD and analysed to determine the past trend of the population. For this reason, this chapter is multi-authored (R. Gaspar, S. Harzen, A.Silva and M.E. dos Santos). The resulting long term data set (1981-1997) was analysed to investigate residency, social interactions with other coastal bottlenose dolphins, and changes in population size and reproductive parameters over the past years.

Additional boat surveys were carried out during 1998 and extended to 2001. In chapter 3, data from these surveys were used to investigate the distribution of the resident dolphins at sea and social interactions between the resident population and other coastal bottlenose dolphins. Sightings of these and other cetacean species were used to justify their inclusion in the candidature of the Arrábida SAC and the enlargement of its limits. In chapter 4, current and past life history traits, such as fecundity and age and time specific survival, are estimated. This allowed the trend in the number of animals observed over the period 1986-2001 to be explained. In chapter 5, the future viability of the resident population is addressed under several different biological scenarios. In the final chapter 6, information from all other chapters is brought together. This is used to discuss the implications of the population projections for determining conservation objectives and management actions.

CHAPTER 2. LONG-TERM PHOTO-IDENTIFICATION STUDY OF BOTTLENOSE DOLPHINS IN THE SADO ESTUARY: RESIDENCY, POPULATION SIZE AND REPRODUCTIVE PARAMETERS

Can the existing long term data set reveal the past trend of the resident population?

2.1. INTRODUCTION

Cetaceans are long-lived mammals and in general have low reproductive rates. For these reasons, long term studies of wild cetacean populations based on individual identification are required in order to learn about population dynamics. Because individual animals can be followed throughout most of their lives, such longitudinal studies provide unique opportunities to gather the least biased information on demographic parameters (Whitehead and Mann 2000).

Species that occur in near shore waters and which may constitute resident populations, such as the bottlenose dolphin, provide a good opportunity to accumulate long term data since access to their habitat is relatively easy. Demographic parameters are key features in the management and conservation of these species and their habitats. Although several coastal resident populations of this species are known to exist worldwide, very few studies were able to present demographic parameters (Wells and Scott 1990, Mann et al. 2000, Haase and Schneider 2001).

One of these known resident populations of bottlenose dolphins inhabits the Sado estuary and adjacent coastal waters on the west coast of Portugal. Although part of the estuary is already designated as a protected area and an estuarine cSAC is planned (the Sado cSAC) certain human activities are a cause of concern to the viability of this population. Since the late 1970's several studies have focused on different aspects of this resident population, including photo-identification (photo ID), socio-ecology, behavior and acoustics (Teixeira 1981, Hussenot 1982, dos Santos and Lacerda 1987, Harzen 1989, 1995, dos Santos et al. 1990, 1995). However, data collection was irregular and in general did not focus on demographic parameters. In 1994, a monitoring program of the resident population based on photo-ID was initiated under the auspices of the local nature protection agency (RNES) (Gaspar 1994). Here we present data on residence patterns, population size and reproductive rates, based on the analysis of the photo-ID record for the time period 1981-1997.

2.2. METHODS

2.2.1. Study area

The study site is located on the West Coast of Portugal and is centered on the Sado estuary (38° 29'N, 8° 55W). It covers approximately 213 km^2 and includes the outer estuary and the nearby marine waters (Fig. 1.1 and 1.2). The Sado estuary is the second largest estuarine system on the Portuguese coast and carries the highest species diversity (Cabral 2000). Detailed information about this region can be found in dos Santos and Lacerda (1987), Cunha (1994), Harzen (1998) and Cabral (2000) (see also chapter 1).

2.2.2. Data collection

Data reported here were collected during boat surveys between 1981 and 1997. From 1981 to 1993 dolphins were searched for in the estuary region mainly through combined systematic boat surveys and land observations, but opportunistic boat surveys were also used (dos Santos and Lacerda 1987, Harzen 1995, dos Santos 1998). From 1994 dolphins were searched for through systematic boat surveys along pre-defined transects within the estuary and in the marine adjacent waters. In addition, some observations were also made from a tower located in the mouth of the estuary (Gaspar 1994). Field observations started in the morning and typically lasted at least 5 hours, but ceased when sea state exceeded Beaufort 3, or if animals were lost and could not be found after 30min of searching. Once encountered, dolphins were photographed from the boat while idling, or at speeds up to 5.5 km.h^{-1} (3 knots), at ranges of less than 150m. Photographs were taken using motor-driven 35mm auto and manual focus cameras with lenses ranging from 50 to 600mm, using Kodak and Fuji colour films of 64, 100, 200 and 400 ISO. Black and white negative film (Ilford 400) was also used in the earlier years (1981-1987).

2.2.2. Data analysis

2.2.2.1. Individual identification from photographs

Prints and slides were analysed to determine the identity of the individual animals based on their natural marks (Würsig and Jefferson 1990). The natural marks used were distinctive nicks and subtle notches in the dorsal fin, shape of the dorsal fin, natural pigmentation patterns, and scratches, scars, and skin lesions in the dorsal fin and dorsum (Scott et al. 1990, Slooten and Dawson 1992, Harzen and Brunnick 1997, Wilson et al. 1999a).

The primary criteria for the selection of photo ID pictures to be analyzed were if they were well lit, taken as perpendicular to the body axis as possible, and the dorsal fin of at least one animal was in focus to be distinguished (Wilson et al. 1999b). Of the total record, more than 12, 250 prints and slides met these quality criteria and were included in the analysis. These images were analyzed by naked eye, optical amplifying loupes (3x or 8x) using a light table, or slide projectors.

The photographic record obtained during the 1981-1987 and 1992-1994 periods had already been described in previous works (dos Santos and Lacerda 1987, Gaspar 1994, Harzen 1995) resulting in different catalogues in which the ID codification used was not always the same. In a first step, these existing catalogues of left or right pictures were reanalysed to a) clear possible errors in individual identification and b) establish consistency between different ID codes. When identification errors were found, either a new animal was added to the catalogue to correct the false negative error, or an erroneously identified individual was eliminated to correct the false positive error. The ID codification used in the present work is based on three capital letters that mostly correspond to the first letters of the name given to each individual (dos Santos and Lacerda 1987). Secondly, each dolphin present in the remaining selected photo ID pictures obtained during the entire study period was matched with the previously identified individuals by comparing every new picture to all others from the reanalyzed catalogue. Animals that could not be matched were given a new identification code or were considered as nonidentifiable. The identity of stranded dolphins was determined based on the natural marks found on the carcass.

2.2.2.2. Age category and sex

Each individual dolphin was categorized into one of the three age classes in the year it was first identified. The adult class corresponds to large and robust animals (Félix 1997, Wilson et al. 1999b) that are assumed to be mature (see also below in the case of females). Dolphins whose body size is smaller than that of adults (Wilson et al. 1999b) and which do not regularly associate with a particular adult (Wells 1991) were considered to be sub-adults. Small animals with foetal folds or with a pronounced paler skin than adults (Wilson et al. 1999b) and which showed a consistent association with an adult (Shane 1990, Wells and Scott 1990, Smolker et al. 1992, Félix 1997) were classified as calves. Because this is a long-term study, dolphins first sighted as a calf or sub-adult, may reach another age class over time. The age of maturity is a particular interesting reproductive parameter (see below), especially for females. Because there is no extensive evidence regarding the age at which female dolphins in the Sado estuary reach sexual maturity, assumptions were made based on the available information in the literature. Age at sexual maturity of female bottlenose dolphins ranges from 5 to 12 years (Perrin and Reilly 1984, Cockcroft and Ross 1990, Read et al. 1993). For the purpose of this study, it is assumed that on average females reach sexual maturity by age 10, the mode of the described ranges. Individual adults were assumed to be females if repeated field observations and photographic records showed them consistently with a small calf (Wilson et al. 1997, Scott et al. 1990). An individual was identified as a male through direct observation of an erect penis during behavior at the surface. In dead stranded animals, both genders were identified through examination of the genital area and mammary slits.

2.2.2.3. Occurrence pattern

A monthly sighting rate was calculated for all animals first identified as an adult or sub-adult, by dividing the number of months the individual was encountered by the number of months surveyed in the years that animal was seen. Only years in which the number of months surveyed were three or more were used in this analysis. These data were then used to classify individuals as either non-resident or resident. Year-round residence was examined for the years 1994-1997 only, when surveys were conducted during 9 or more months per year. For that, the proportion of resident animals seen per total months surveyed in each year was calculated.

2.2.2.4. Age distribution and proportion of calves

The age distribution of animals age 1 through 6 is presented for the last year of the study (1997). This year was chosen because it potentially contained a wider age distribution and the maximum number of known age calves. In addition, the age distribution of calves in the year 1995 is also presented. Not all calves were identified prior to 1994. The proportion of calves within the resident population was estimated for each year between 1994 (the first year in which all calves were identified) and 1997. A weighted average for that period was also determined.

2.2.2.5. Seasonality of reproduction

Seasonality of reproduction was analyzed based on the month of birth of identified new born calves and still born dead calves. The date of birth of identified newborn calves was estimated as the midpoint between the last sighting of the presumed mother without newborn and the first sighting with the calf, alive or dead (Urian et al. 1996). The period between these sightings did not exceed 20 days.

2.2.2.6. Adult sex ratio

There are no reliable data on age specific sex ratios for wild bottlenose dolphins in the literature. Sex ratio in this species is often considered as being 1:1, but in delphinid populations the ratio of males to females appears to decline with age (Perrin and Reilly 1984). This also seems to be the case in bottlenose dolphins, for which Wells et al. (1987), based on a rather small sample size, reported an adult sex ratio of 1:2.3 (males to females). In this study, these sex ratios were used to encompass the likely range.

2.2.2.7. Crude birth rate, fecundity rate, calving interval and inter-births interval of individual females

Reproductive parameters were estimated at the population level and also from observed individual data. Because information on the total number of births is less reliable during the early years of this study (there was less effort, not all calves were identified and some births could have been missed), population parameters were estimated from 1992 throughout 1997 only. Estimates of the following reproductive parameters were determined pooled over years: 1) crude birth rate, obtained by dividing the total number of live births by the total number of animals (excluding newborns), 2) fecundity rate, determined by dividing the total number of live births by the total number of adult females, and 3) calving interval, calculated as the reciprocal of the fecundity rate.

For the purpose of comparison with the values obtained for the Sado (Sad) resident population, we estimated the same reproductive parameters for three other resident bottlenose dolphin populations. Crude birth rate from resident bottlenose dolphins living in Doubtful Sound (DS), New Zealand, was calculated with data from the years 1994-1997 and 1999, (Figure 1 and Table 2, Haase and Schneider 2001). Reproductive estimates from the Sarasota (Sar) community were obtained using data from 1980 to 1987 (Table 2A, Wells and Scott 1990). Estimates of fecundity rate and calving interval were based on the 1:2.3 adult sex ratio observed in the Sarasota population. Reproductive estimates from the Moray Firth (M-F) population were calculated using data from 1990 to 1997 provided by Carol Sanders Reed (personal communication). Fecundity rate and calving interval were based on a joint number of adult and sub-adult females assuming an even sex ratio. Similar estimates of these parameters were also calculated for the Sado resident population, for comparison. Statistical comparison of reproductive rates between populations was made using the formula for comparison of two percentages based on two large samples (Bailey 1972).

Inter-births intervals of individual females from the Sado resident population were also calculated using the overall data set. In addition to the uncertainty regarding the number of births per female, the year of birth remained unknown for most of the calves born during the earlier years (1986 to 1991). For these calves, the year of birth was allocated assuming that the animal had at least one year of age when first seen and no more than 6 years when last seen close to its presumed mother. In this way, the range of calving intervals (2 to 6 years) observed in other resident bottlenose dolphin populations (see Connor et al. 2000, Wells and Scott 1990, Mann et al. 2000, Haase and Schneider 2001, Wilson 1995) was included. If the resulting allocated years of birth overlapped with a year in which the identified mother was still with a previous calf, the following year was chosen as year of birth.

2.3. RESULTS

Over the 16-year study period, 330 surveys were conducted. In 1992 and 1993 surveys were conducted during 6 months of the year and between 10 and 12 months since then (Table 2.1). Dolphins were sighted in all surveys.

2.3.1. Individual identification

Eighty animals were individually identified: 57 were first seen as adults, 4 as sub-adults and 19 as calves (Fig.2.1). Additionally, at least 8 different calves were born but not identified from photographs during the period 1981-1992. By the end of this study, none of the sub-adults is known to have reached the adult class (Fig.2.1). Sex was determined in only a small number of animals: 4 males and 8 females (Fig.2.1). Two of the known adult females had no distinctive nicks whereas all known males had at least one distinctive nick on the trailing edge of their dorsal fin.

Table 2.1. Number of months surveyed and number of surveys per month during the study period (1981-1997).

year	number of months surveyed	number of surveys
1981	1	1
1983	2	2
1984	4	5
1985	3	5
1986	6	26
1987	3	19
1988	5	25
1989	7	25
1990	3	7
1991	3	6
1992	6	22
1993	6	26
1994	9	48
1995	10	47
1996	11	31
1997	12	35
total	91	330

2.3.2. Non-resident and resident dolphins

The distribution of the monthly sighting ratio for animals identified as sub-adults and adults at the time of their first encounter shows a clear discontinuity that we use to define resident and non-resident animals (Fig. 2.2). Animals with a monthly sighting ratio less than or equal to 0.2 were seen only once (n=18) or twice (n=2) during the 13 years period considered (1984-1997). Those seen twice were seen in only one survey per year. Due to their low sighting regularity in the study area, these 19 adults and one sub-adult are considered non-resident animals (Fig.2.2). Non-resident dolphins were exclusively encountered at the mouth of the estuary and along the coast of Tróia, between May and October. In all but one of these encounters, resident dolphins were present as well.

			Year															
	ID name	sex	81	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97
Adults	**AGU**	f	●	●	○	●	●	●	●	●	●	●	●	●	●	●	●	●
	ALC		●	●	●	●	●	●	●	●	○	●	○	○	○	○	○	○
	BRO													◍	○	○	○	○
	BUM	f	●	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●
	CAR	m					●	●	●	●	●	●	●	●	●	●d		
	CHI			○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
	COV				●	●	●	●	●	●	●	●	●	●	●	●	●	●
	CUR						●	●	○	●	●	●	●	○	●	●	●	●
	DEN	f					●	●	●	●	●	●	○	○	○	○	○	○
	DUE																	◍
	ELE	f	●	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●
	EST						●	●	●	●	●	●	○	○	○	○	○	○
	FAC			●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
	FAR	f			●	●	●	○	●	●	●	●	●	●	●	●	●	●
	FUG				●	○	●	●	●	●	●	●	●	●	●	●	●	○
	GEM						●	●	●	●	●	●	●	●	●	○	○	○
	GOD														◍	○	○	○
	GOR				●	●	●	●	●	●	●	●	●	●	●	●	●	●
	HEN																	◍
	HIP																	◍
	HUB				●	○	●	●	●	●	●	●	●	●	●	●	●	●
	INC		◊	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
	ISA																	◍
	JAN						●	●	●	●	●	●	●	●	●	●	●	●
	JOL					●	●	●	●	●	○	○	○	○	○	○	○	○
	KAP																	◍
	KIT																	◍
	LIS	m		●	○	●	●	●	●	●	●	●	●	●	●	●	●d	
	LUA				●	○	●	●	●	●	●	●	●	●	●	●	●	●
	MAM	f			●	○	●	●	●	●	●d							
	MED																	◍
	MIL						●	●	●	●	●	●	●	●	●	●	●	●
	MUR	m	●	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●
	NEO													◍	○	○	○	○
	OSG																	◍
	OUT																	◍
	PAR												◍	◍	○	○	○	○
	PIN				●	●	○	○	○	○	○	○	○	○	○	○	○	○

Figure 2.1. Annual occurrence pattern, age class and sex of the 80 individually identified bottlenose dolphins [dark circle = resident dolphins, grey circle = non-resident dolphins; grey diamond= not considered for residence pattern analysis, m = male, f = female; d = recovered carcasses].

			Year															
	ID name	sex	81	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97
Adults	**PLU**													◍	○	○	○	○
	QUA				●	○	●	●	●	●	●	●	●	●	●	●	●	●
	RED				●	●	●	●	●	●	●	●	●	●	●	●	●	●
	RIB														◍	○	○	◍
	SER													◍	○	○	○	○
	TAL			●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
	THO			●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
	TIP		●	●	●	○	●	●	●	●	●	●	●	●	●	●	●	●
	TOQ				●	●	●	●	●	●	●	●	●	●	●	●	●	●
	TOZ														◍	○	○	○
	TRU	f				●	●	●	●	●	●	●	●	●	●	●	●	●
	TUB					●	●	○	●	●	●	●	●	●	●	●	●	●
	UMM		●	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●
	UNO														◍	○	○	○
	VEL		●	○	●	●	●	●	○	○	○	○	○	●	○	○	○	◍
	VIT	f					●	●	●	●	●	●	●	○	○	○	○	○
	WWW		◊	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
	YAG																	◍
	ZIG		◊	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
Subadults	**DIS**						●	●	●	●	●	●	○	○	○	○	○	○
	ORL	f											●	●	●	●d		
	SUP												●	●	●	●	●	●
	XAD																	◍
Calves	**APA**										●	●	●	●	●	●	●	●
	BOL															●	●	●
	CAA											●	○	○	○	○	○	○
	CAC						●	○	○	○	○	○	○	○	○	○	○	○
	CAG						●	●	●	○	○	●	○	○	○	○	○	○
	CBU						●	●	○	○	○	○	○	○	○	○	○	○
	CDE						●	●	●	●	○	○	○	○	○	○	○	○
	CMA						●	○	○	○	○	○	○	○	○	○	○	○
	CVI						●	●	●	●	○	○	○	○	○	○	○	○
	CVT								●	●	○	○	○	○	○	○	○	○
	EAG												●	●	●	●	●	●
	ECL																●	●
	ESC																●	●
	ESP															●	●	●
	NBC							●	○	○	○	○	○	○	○	○	○	○
	NIC											●	●	○	○	○	○	○
	RUS											●	●	●	○	○	○	○
	SIC	m						●	○	●	●	●	●	●	●	●	●d	
	ZOE													●	●	●	●	●

Figure 2.1. (continued)

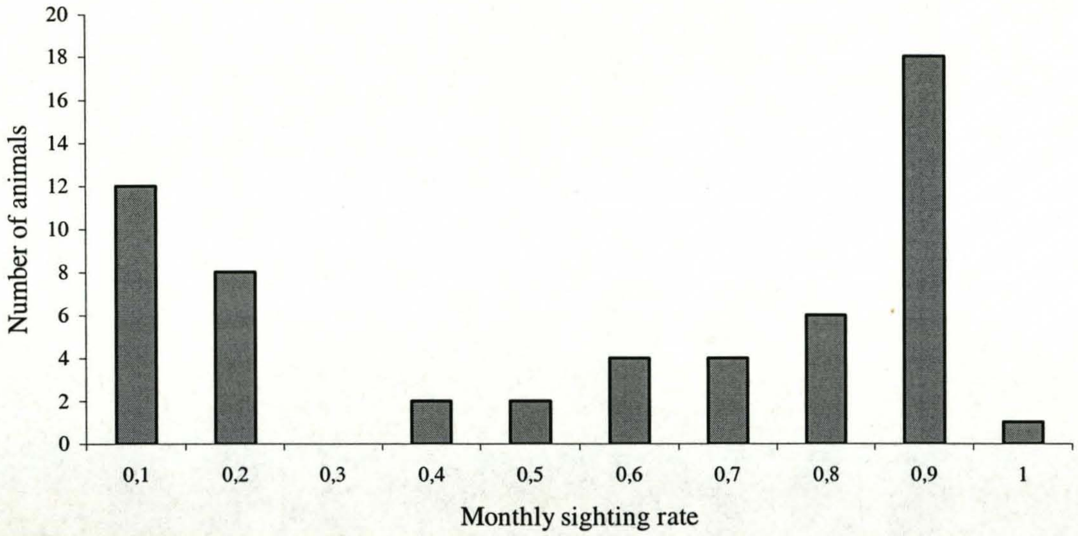

Figure 2.2. Frequency distribution of the monthly sighting rate of non resident and resident dolphins, first seen as adults and sub-adults, over the period 1984-1997. Numbers along the horizontal axis represent the upper limit of the interval.

Animals with a monthly sighting rate greater than, or equal to 0.4, were seen several months in each year of the period they were present (Fig.2.2). These 34 adults and 3 sub-adults are considered resident animals due to their high sighting regularity. Together with calves presumed, or known to be born to resident females, these animals are defined as the resident population of bottlenose dolphins in the Sado estuary region. All resident animals except two sub-adults, were first seen before 1987. In general, resident animals were seen over a long period in the study area. Although the number of months these dolphins were encountered varied from 4 to 82 over a period of 2 to 15 years, the great majority (74%) of adults was seen in at least 10 years, and the sub-adults in at least 4 years (Fig.2.1). During the period 1984-1997, resident animals were seen nearly every year: 70% were seen during consecutive years and 27% were seen in all but one year. Exceptionally, resident animals were not seen for a long period between consecutive sightings. This is the case of only one adult (VEL) that was not sighted from 1988 through 1992 and was then seen again from 1994 through 1996. In 1997, it was seen as part of the non-resident population of visiting dolphins. Because of its atypical occurrence pattern, this adult was excluded when analyzing population size and reproductive parameters concerning the year 1997.

During 1994 through 1997, the majority of the resident animals were year round residents in the study area. Resident animals first identified as adults and sub-adults were seen in nearly every month surveyed: 83% in 1994, 86% in 1995 and 100% in 1996 and 1997 (Table 2.2).

Table 2.2. Proportion of resident dolphins, first seen as adults and sub-adults, according to the number of months surveyed in which they were seen in each year (1994-1997).

	year			
Number of months seen	1994	1995	1996	1997
all	0.79	0.79	0.62	0.78
all but one	0.07	0.04	0.38	0.22
all but two	0.00	0.14		
less	0.13	0.04		

In addition to non-resident and resident animals, 4 adults (diamonds, Fig.2.1) were not considered in the residence pattern analysis since they were only sighted prior to 1984. These animals were seen on only one occasion during the entire study period.

2.3.3. Resident population: population size and reproductive parameters

Since nearly every animal was seen every year, population size was calculated as annual counts of the resident animals known to be alive, that is, counting animals that were not seen in a particular year(s) but were seen later during the study period (1986-1997). Population size decreased from 40 animals in 1986 to around 30 in the latest years, with a minimum in 1997 (Fig. 2.3).

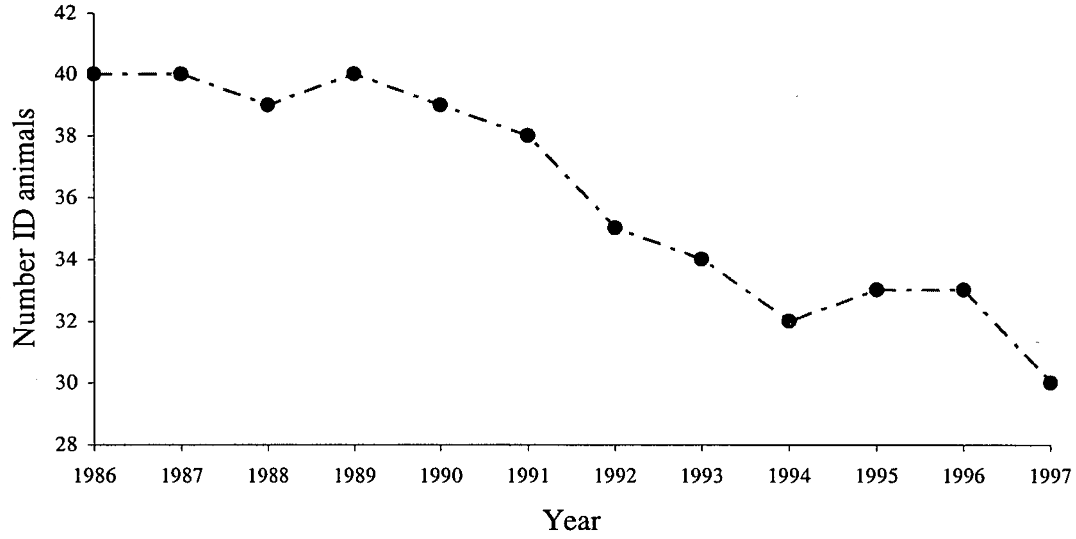

Figure 2.3. Annual counts of the individually identified resident bottlenose dolphins alive in the study area during the period 1986-1997.

The age distribution of calves in 1995 and 1997 is presented in Table 2.3. Calves from the Sado resident population remain close to their mothers during the first 3 or 4 years. The estimated proportion of calves in the population during the period 1994-1997 increased from 0.06 to 0.17 (0.06 in 1994, 0.09 in 1995, 0.15 in 1996 and 0.17 in 1997) with an average of 0.12 (SD=0.049).

Table 2.3. Number of calves at each age in 1995 and 1997.

	Age in years						
	<1	1	2	3	4	5	6
1995	2	0	1	1	0	0	0
1997	0	2	2	0	1	0	0

In most of the cases (84%) the mother of known calves was identified by association. Five of the nine identified mothers gave birth to two or three calves (Table 2.4). Most of the calves whose date of birth is known to the nearest month were born during late summer. Two calves were born during the period March-May and a stillborn dead calf was observed in March 1995 (Table 2.4). Thus, the distribution of births indicates these occur from March to September with a peak in August.

Table 2.4. Date of birth of known calves and range of inter-birth intervals of presumed mothers. In only one case did this interval result from the period elapsed between known date of births from two consecutive calves (*).

Presumed mother ID	Calf ID	Date of birth		Inter-birth interval
		Month	Year	
AGU	CAG		1982 to 1985	
	APA		1985 to 1989	3 to 7
	ZOE	September	1993	4 to 8
ALC	CAC		1980 to 1985	
BUM	CBU		1981 to 1985	
	EAG	August	1992	7 to 11
	ESP	August	1995	3*
DEN	CDE		1982 to 1985	
ELE	ESC	May	1996	
FAR	RUS		1986 to 1990	
	BOL	August	1995	11 to 5
MAM	CMA		1980 to 1985	
	SIC		1987	2 to 7
TRU	ECL	March	1996	
VIT	CVI		1981 to 1985	
	CVT		1988	3 to 7

On average, at least one calf was born each year (1992-1997) in the Sado estuary resident population: the estimate of crude birth rate is 0.032 (SE=0.0128) (Table 2.5). Estimates of fecundity rate ranged from 0.080 (SE=0.0313) assuming a sex ratio of 1:1, to 0.057 (SE= 0.0227) assuming a sex ratio of 1:2.3. The corresponding calving intervals ranged from 12.5 to 17.5 years, respectively (Table 2.5). Estimated calving intervals are clearly longer than the inter-birth intervals calculated from data on individual female reproductive history, which ranged from 3 to 11 years (Table 2.4). Estimated reproductive rates, in the Sado resident population are lower than in other bottlenose dolphin populations elsewhere (Table 2.5), but these differences are not significant at the 5% probability level (DS-Sad P=0.091; MF-Sad P=1.174; Sar-Sad P=0.145). Estimated fecundity rate and calving interval from the Sado are much lower than those observed in the Sarasota and Moray Firth resident populations. Differences between fecundity rates are significant at the 0.01 (Sar-Sad P=0.004) and 0.05 (MF-Sad P=0.042) probability levels, respectively.

Table 2.5. Comparison of reproductive estimates between the Sado, Doubtfull Sound, Moray Firth and Sarasota bottlenose dolphin populations. Numbers in brackets are standard errors.

	Sado	Doubtfull Sound	d	*P*	Moray Firth	d	*P*	Sarasota	d	*P*
Crude birth rate	0.032 (0.0128)	0.068 (0.0154)	1.689	0.091	0.056 (0.0086)	1.360	1.174	0.059 (0.0094)	1.459	0.145
fecundity rate										
sex ratio 1:1										
Adults	0.080 (0.0313)									
adults + subadults	0.075 (0.0294)				0.167 (0.0241)	2.036	0.042			
sex ratio 1:2.3										
Adults	0.057 (0.0227)							0.178 (0.0265)	2.918	0.004
Calving interval										
sex ratio 1:1										
Adults	12.5									
adults + subadults	13.3				6					
sex ratio 1:2.3										
Adults	17.54							5.6		

2.4. DISCUSSION

2.4.1. Resighting rate

The resident population of the Sado estuary constitutes an uncommon example in photo-ID studies of marine mammals. Usually it is not possible to enumerate an entire population in order to estimate population size (Hammond 2001). But resident animals were seen nearly every year and for this reason population size was assessed as a census rather than from a sample.

Since 1994, almost all resident animals were seen every or nearly every month, indicating that most are year round residents. In many other resident bottlenose dolphin populations, the majority of the animals are not seen every month (Würsig 1978, Shane 1980, Wilson 1995).

The high resighting rate was critical in the ability to distinguish between resident and non-resident animals. Other studies of bottlenose dolphin populations have attempted to categorize residency using quantitative measures of sighting rates (see Ballance 1990). Typically, however, the distribution of resightings does not show a clear cut off point between categories (Ballance 1990, Williams et al. 1993, Wilson 1995, Möller et al. in press).

2.4.2. The resident population

The bottlenose dolphin is a cosmopolitan species whose distribution only excludes very high latitudes. Within this range, coastal bottlenose dolphins typically have limited but overlapping home ranges (Leatherwoood and Reeves 1983, Wells et al. 1987, Félix 1997). The Portuguese coast is located in temperate waters and coastal bottlenose dolphins are known to occur along most of its extent (Teixeira 1979, Sequeira et al.

1992, 1996). This work provides evidence that resident dolphins in the Sado estuary region encounter other non-resident conspecifics. It is not known, however, if mating occurs during these encounters. In the Sado resident population, births occur during spring and summer months. The few encounters between resident and non-resident bottlenose dolphins observed occurred from May to October when bottlenose dolphin prey abundance and diversity is highest in the estuary (Cunha 1994, Cabral 1999, Costa et al. 2000). This seasonality in prey availability may affect resident female (pregnant or lactating) condition (see Urian et al. 1996). However, there is no information about the distribution of the prey and births from other Portuguese coastal bottlenose dolphin populations.

Evidence has been presented of emigration from the Sado resident population, but whether or not immigration occurs remains unclear. Adults seen only once or twice before 1986 could have been emigrants, immigrants or non-resident animals. The two sub-adults first sighted in the resident population in 1992 could have been immigrants, but could also have been young resident animals not identified when calves. The Sado resident population of bottlenose dolphins is not geographically nor socially isolated, but it remains unclear if it is a discrete biological unit.

2.4.3. Long term residency

Bottlenose dolphins were sighted in the Sado estuary 140 years ago (Bacage 1863). Although it is unclear for how long a resident population has inhabited the Sado estuary, this work shows that since 1984, it has been mainly composed of long-term, year round, resident dolphins. Most of the adult animals described here have lived in the Sado estuary region for more than a decade. Why should this small group of bottlenose dolphins have such a strong residency pattern? Their long term residency may result from a trade-off between obtaining food and protection and facing natural and anthropogenic threats. The Sado estuary region is a relatively large embayment along the Portuguese coast with abundant and diverse prey species (Cabral 1999, Costa et al. 2000). Although it is an open system, it is a relatively predator-free environment. Marine mammal eating sharks have not been reported in the estuarine waters (Cabral 1999, Costa et al. 2000) and killer whales were only once observed at the estuary mouth (dos Santos and Lacerta 1987). However, the estuary water is turbid and tide flux can be crucial for movement of dolphins in the interior estuary channels. Anthropogenic background noise (Ferreira et al. 1996) and by-catch in local trawling nets represent constant risks.

Why don't the identified non-resident coastal bottlenose dolphins join the resident population? In other resident bottlenose dolphin populations, resident and non-resident animals were seen mixing for hours or days (Félix 1997) but immigration rate seems to be very low (Wells and Scott 1990). Tracking of the afore mentioned local features and developing appropriate responses requires great behavioral flexibility. Cultural transmission between individuals and generations (Norris 1994) can evolve through social learning in long lived species such as the bottlenose dolphin (see Rendell and Whitehead 2001a,b). Although the question of immigration into the resident population remains open, non-resident dolphins have rarely been seen socializing with resident animals. In addition to the very low level of social contact, behavioral, ecological and other social mechanisms may also account for differences in the observed residency patterns in the study area. These mechanisms may also explain the existence of distinct communities (*sensu* Wells and Scott 1990) of bottlenose dolphins with overlapping home ranges, elsewhere (Wells et al. 1987, Félix 1997). However, a striking phenomenon reported here, is the lack of recruitment to the adult stage during 11 years.

Young animals from the Sado may have died or emigrated. However, it has been shown that sub-adult resident bottlenose dolphins from other populations tend to be philopatric (Connor et al. 2000). This lack of recruitment may compromise the maintenance of such local knowledge and therefore the viability of this resident population in the Sado estuary. In addition, the population has declined 25% over the study period and survival has been shown to have been low until the early-mid 1990s, especially for the young animals (chapter 4).

2.4.4. Very small population size

The Sado estuary resident population is very small (30 to 40 animals). It is one of the smallest coastal resident populations of bottlenose dolphins recorded in the literature. Apart from the resident population of 14 to 17 animals bottlenose dolphins in Sein Island, France(Liret 2001), other small populations that have been studied elsewhere are larger: 56 to 68 dolphins in the Shannon estuary, Ireland (Berrow et al. 1996); 65 animals in Doubtful Sound, New Zealand (Haase and Schneider 2001); 100 in Sarasota, Florida (Wells and Scott 1990); 61 to 108 dolphins (*Tursiops aduncus*), in Jervis Bay, Australia, (Möller et al. in press); 113 animals in Croatia (Fortuna et al. 2001); 129 in the Moray Firth, Scotland (Wilson et al. 1999b); 143 to 160 dolphins (*Tursiops aduncus*) in Port Stephens, Australia (Möller et al. in press); and 152 to 287 in Cardigan Bay, Wales (Baines et al. 2002).

2.4.4.1. Population size and reproductive rates

As observed in other bottlenose dolphin populations, calves were seen with their mothers during 3 and 4 years (Wells and Scott 1990, Wilson 1995, Connor et al. 2000, Mann et al. 2000, Haase and Schneider 2001). However, estimated reproductive rates in the Sado resident population are lower than in any other studied bottlenose dolphin populations elsewhere. This is especially the case in the estimates of fecundity rate. In addition, estimated calving intervals, are much higher than the calculated range of inter-birth intervals of individual females. The very small population size could account for these differences for several reasons.

Minor variations in the number of recorded births have greater effects on reproductive parameter estimates in very small populations (Brault 1999).This can result from inadequate sampling effort. In order to avoid such a bias, reproductive estimates were made from the later period of the study when surveys occurred at least during half of the year. These constitute our best estimates. Inter-birth intervals of individual females, calculated for the earlier years when sampling effort was lower, are likely to be biased because not all calves were identified, and the mothers of some identified calves could not be identified.

Besides differences in the sampling effort, reported discrepancies concerning reproductive estimates may also reflect the variability in the number and condition of adult females (Brault 1999). For example, the number of adult animals (and known females) was higher during the earlier years. Further, there has been no recruitment of adults in the period 1986-1997. As a result, adult females during the later years, may be old, with possibly lower reproductive rates (Marsh and Kasuya 1986). This would be of especial relevance because reproductive estimates were obtained in the later years of the study. If this were the case, it could account for the lower reproductive rates of the Sado resident population compared to other populations. However, a wide variability was recorded in the annual proportion of calves, suggesting that some females may be reproducing well and but others are not.

Being a small population, the sex ratio may be atypical and thus the number of adult females may be even lower than that of the assumed sex ratios. In fact, only a small number of females were seen to reproduce during the overall period compared to the expected number of existing mature (and thus calving) females if assuming a 1:1 or a 1:2.3 sex ratios.

Finally, reproductive rates may be responding to changes in the environment such as availability of food (Fowler 1984), pollution and disease causing agents (Lockyer 2001, Reeves and Reijnders 2002). Anecdotal information suggests that during recent decades, food resources in the estuary have decreased and certain pollutant levels decreased whereas others increased. Quantitative measurements of the pollutant levels in the tissues of the resident dolphins were, in general, inconclusive (Barreiros et al. 1996). Several skin disorders (Harzen and Brunick 1997, Wilson et al. 1999a) and pox virus infection (Van Bressem and Gaspar 1999) were identified in the resident dolphins. But any synergistic effect these factors may have on the reproductive parameters of this resident population of dolphins is unknown.

2.4.5. Conservation issues

Very small populations are particularly vulnerable to extinction and avoiding a single death may have an important impact on population trend (Fujiwara and Caswell 2001). Being such a small group of long term, year round resident animals, cumulative exposure to anthropogenic threats such as pollutants, shipping and recreational boat traffic, habitat destruction and harassment from dolphin watching boats, may be particularly high in this situation and may act to reduce individual fitness.

Intrinsic individual and population characteristics such as condition and health, sex ratio and age structure, can influence population trend, so it is difficult to distinguish between external and intrinsic causes. In future work, the viability of this very small bottlenose dolphin population will be modeled. Although it remains unclear if the Sado bottlenose dolphin resident population is a biological distinct group, the very small population size shown in the present work, suggests that management and conservation actions must not neglect factors affecting individual dolphins. Further, the strong residency reinforces the importance for protection of the Sado estuary which has been proposed to be designated and managed as a "special area of conservation" under the European Community's Habitats Directive.

CHAPTER 3. DISTRIBUTION AND HABITAT USE IN THE MARINE AREA ADJACENT TO THE SADO ESTUARY

In order to provide more information to clarify the past status obtained from the long term data base presented in chapter 2, in this chapter we try to address the following question: are the Sado resident animals restricted to the estuary region and what is their degree of mixing with non-resident animals?

3.1. INTRODUCTION

The distribution of the resident bottlenose dolphins at sea is poorly known. Distribution at sea is difficult to access for logistic and financial reasons. For this reason, apart from the few marine surveys described in chapter 1, knowledge about the distribution of the resident dolphins is restricted to opportunistic observations in the marine area adjacent to the estuary mouth (Hussenot 1982, Gaspar 1994, Freitas 1995). Although resident dolphins have a strong residency pattern some adults are more likely not to be seen on a daily basis in the core area of the estuary. These animals could be either in the inner estuary or outside the estuary at sea (Gaspar 1994).

Anecdotal evidence from beach users suggests that bottlenose dolphins travel along the coastline of Tróia during the summer. Dolphins have been seen from several beaches located approximately 21km to 29km from the estuary mouth. According to fishermen, bottlenose dolphins (and other cetacean species) are also seen in the marine area outside the estuary entrance. If these observations were of resident bottlenose dolphins, the photo-ID surveys used to monitor the resident population should be designed to cover both near shore and offshore waters. These marine areas adjacent to the estuary may be suitable habitat for the resident population but, because of their strong residency pattern, it is likely that observations in these areas refer to other coastal bottlenose dolphins.

Another reason for surveying the marine area exterior to the estuary is to address the question of how small and isolated is the resident population. In chapter 2 it was shown that the resident population is neither geographically nor socially isolated although mixed encounters were rare. However, this statement is based on opportunistic observations. It was also shown (in chapter 2) that one resident adult emigrated to a coastal group. It may be hypothesised that adults that are not found on a daily basis may be at sea further away from the estuary mouth, and possibly joining other coastal groups.

Previous studies have shown the presence of harbour porpoises (*Phoceona phocoena*) near the estuary mouth, (Gaspar 1994, Martins 1998, Vieira 1998). Although simultaneous observations had never occurred this area is also used by the resident bottlenose dolphins (Hussenot 1982, Gaspar 1994, Freitas 1995, Harzen 1997, Dos Santos 1998, Nunes 2001). Other species such as the common dolphin were also observed (Teixeira and Duguy 1981) along the coast of Arrábida.

The known distribution of the resident population of bottlenose dolphins at sea is partly covered by the Arrábida Marine Park and the Arrábida cSAC. This extends along the Arrábida coastline from the marine area at the estuary entrance to Cape Espichel and northwards (Fig.3.1). The Sado cSAC, does not include the marine area along the coast of Tróia (Fig.3.1). Information on the distribution of this (and other species) is a useful tool in defining boundaries of marine protected areas (Hastie et al. in press). If we are to justify management actions based on the home range of this population, such as alterations of the limits of these special areas for conservation , the distribution of the resident population at sea has to be known. Further, the definition of the status of the resident population is critical for the extent of management actions. If the Sado bottlenose dolphins rarely mix with other bottlenose dolphins, then conservation efforts should focus primarily on the resident animals, whereas if they constitute a breeding unit from a larger population (Harzen 1995), conservation efforts may be relaxed and have a broader extent. In addition, the assessment of the distribution of other cetacean species within the Arrábida marine cSAC could serve as a basis for debate on the inclusion of these other cetacean species.

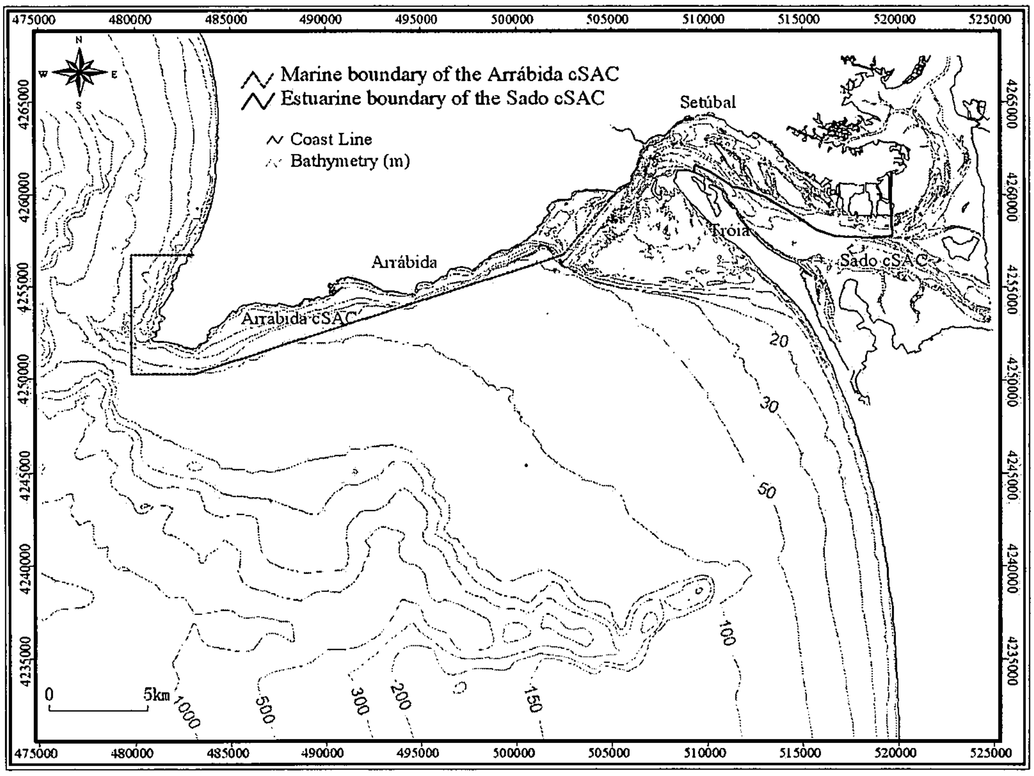

Figure 3.1. Marine boundaries of Arrábida and Sado cSACs.

3.2. METHODS

3.2.1. Study area

In order to investigate the distribution at sea of the resident bottlenose dolphins and their interaction with other coastal bottlenose dolphin populations, the marine area outside the estuary was surveyed, along the coast of Arrábida and Tróia.

The bottom topography in waters along these coasts is very distinct (Fig. 3.1.). Along the coast of Arrábida, water depth decreases sharply close to shore. At 3 nautical miles

(5,6 km) from this coastline depths are from 50 to more than 100m. This area faces south and is protected from the prevailing north and north-west winds by the adjacent mountain chain of Arrábida. This area is located near the northern limit of the main north-east Atlantic upwelling events (Wooster et al. 1976). For that reason, during the summer nearshore water temperature is frequently lower than offshore water temperature (Henriques et al. 1999). The coast of Tróia is shallower. At 3 nautical miles (5,6 km) from the coast maximum depths is only 50m. This is a result of the southwards flow of the estuary efflux. For this reason, sand is carried to and along the Tróia coast making the depth gradient along this coast smoother. Maximum depths in most parts of the estuary are no more than 20 m; more similar to the coast of Tróia. At the estuary mouth, there is a shipping channel (around 10 m in depth) that artificially deepens the shallow sandbank area at the entrance of the estuary (around 5m). In between these coasts there is a submarine canyon, which is closer to the Arrábida coast.

3.2.2. Survey design

For logistic and safety reasons surveys only covered the marine area close to the coastline. Between June 1998 and September 2001, ninety-four boat surveys were carried out along the coastline of Arrábida and Tróia. Surveys were initiated and ended at a buoy located in the ship channel and extended for 29 km along the coast of Arrábida (Fig.3.2) and for 21 to27 km along the coast of Tróia (Fig.3.3). Initially, transect lines were fixed at 1.5 nautical miles (2,8 km) and 3 nautical miles (5,6 km) from the coastline. However, this survey track didn't allow dolphins to be sighted if they were very close to shore. In addition, it was believed to be too far away from the coast for logistic reasons. Accordingly, the survey track was changed to be 2

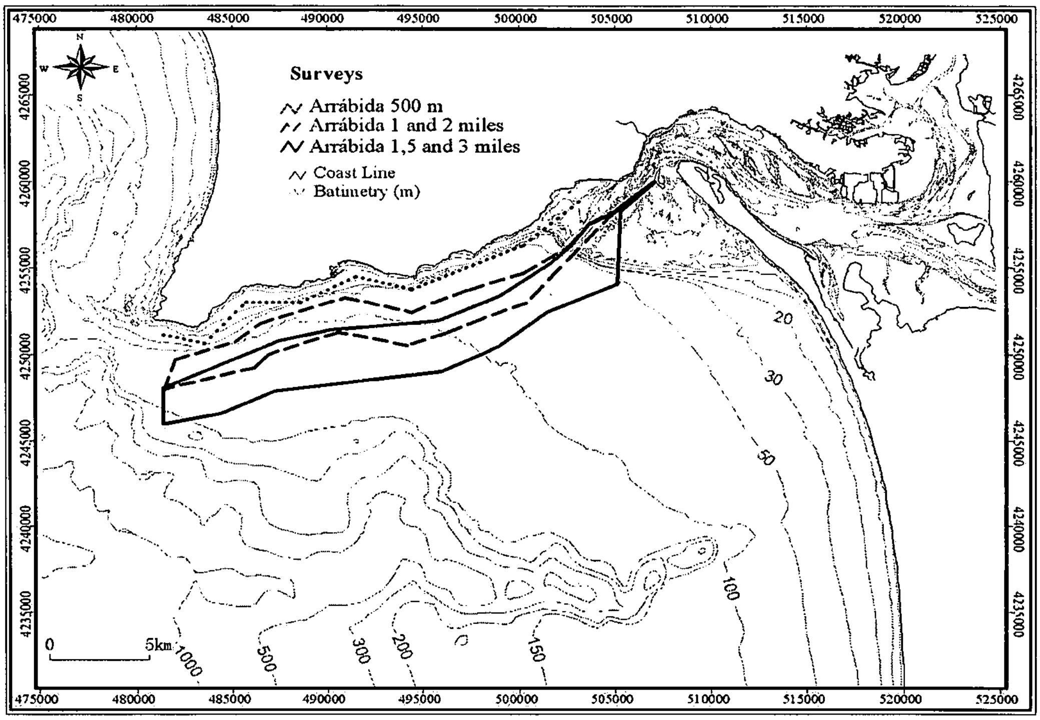

Figure 3.2. Transect lines of the boat surveys conducted along the coast of Arrábida.

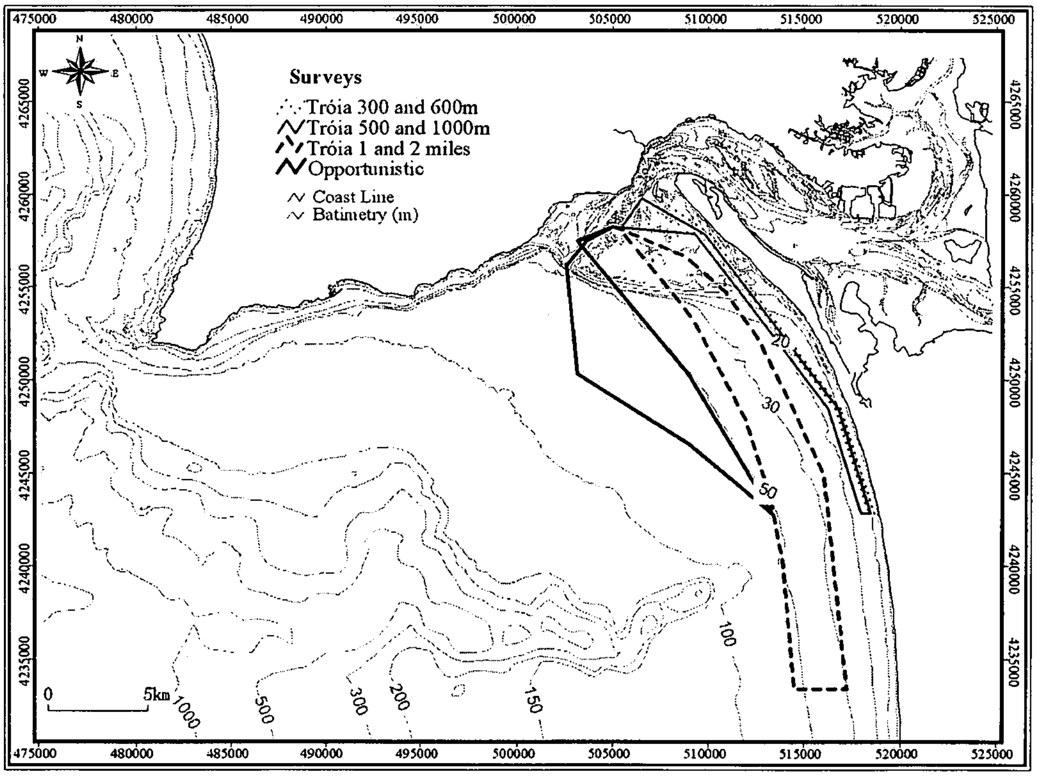

Figure 3.3. Transect lines of the boat surveys conducted along the coast of Tróia.

nautical miles (3,7 km) and 1 nautical mile (1,9 km) from the coastline. Because resident bottlenose dolphins were not encountered at those distances along the Tróia survey track, distance from shore was further reduced to 1000m and 500m in 1999 and to 600m and 300m in 2000. When Beaufort sea state was 3 and greater and wave height did not permit the survey to be conducted in safety, an alternative survey track was designed along the coast of Arrábida at 500m from shore. Opportunistically, when sea conditions were extremely favourable, part of the area in between survey tracks was also covered ("opportunistic surveys") (Fig.3.3). Data from 94% of the surveys conducted in 1999 were collected by I. Cascão, under my supervision.

Previous studies indicate that resident dolphins tend to leave the estuary during the afternoon (Harzen 1997). Empirical observations suggest that during the summer, this is most likely to occur around 18:00, when surveys typically ended. Thus another strategy to access the distribution of the resident dolphins at sea would be to initiate a survey before sunset and follow dolphins when they leave the estuary mouth. However, this poses several logistic problems because after sunset dolphins cannot be seen. Dolphins could be followed acoustically (Gordon and Tyack 2002) but a hydrophone was not available. However, if dolphins were kept close to the boat and there was no wind they could be followed by listening to their breathing (blows). Three "night surveys" were carried out in the summer of 2000 using this strategy. Table 3.1 presents the number of surveys for each type conducted in each year and the months they covered.

Data collection followed the protocol described in chapter 2 for any cetacean species encountered. Photographs were taken to individually identify bottlenose dolphins. GPS positions were recorded every 10 min. Group size, was based on the maximum number of dolphins that were visually counted by crew members.

Table 3.1. Survey effort.

Survey type	1998		1999		2000		2001		total	
	month	number surveys	month	number surveys	month	number surveys	month	number surveys	with sightings	No sightings
Arrábida 1,5 and 3 miles	6	1								1
Arrábida 1 and 2 miles	7-10	20	2-6, 8-11	19			1, 4-9, 11	15	49	5
Arrábida 500m	7,11	2	2	1			2,7,11	3	6	
Tróia 1,5 and 3 miles	7	1							1	
Tróia 1 and 2 miles	7-11	5							5	
Tróia 100 and 500m			4-12	16					16	
Tróia 300 and 600m					3		1-3	3	5	1
Oportunistic							8,9	2	2	
Night					8,9	3			3	

3.3. RESULTS

Figure 3.4 presents the location of the sightings of resident bottlenose dolphins in the marine area. Locations refer to all 10 min positions recorded during encounters made in "day surveys" and "night surveys". Only encounters from the year 1998 (13 encounters from June to October), were included as "day surveys" for simplicity. This year was chosen because it is representative of the locations of the sightings that occurred in the other years. During these surveys, dolphins were encountered either at the beginning (between 8:20 and 10:13) or at the end (between 15:20 and 17:13) of the survey track. The distribution of the resident dolphins seems to be concentrated in the estuary entrance (Fig. 3.4). Resident bottlenose dolphins were observed within the 10m depth contour no further than 5 to 7.8 Km from the tip of the Tróia peninsula at the estuary mouth. The furthest sightings from the estuary mouth towards the west and southwest were obtained during "night surveys". In these cases, dolphins were moving away from the estuary mouth. The furthest sightings from the estuary mouth towards the south were made during "day surveys". In June 1998, resident bottlenose dolphins were encountered with non-resident bottlenose dolphins as identified in chapter 2. This encounter occurred at the shallow sandbanks near the estuary entrance. No other mixed encounter was observed. Most of these observations occurred near the limits of the Arrábida marine cSAC (Fig. 3.4).

During the marine surveys along the Arrábida coastline other bottlenose dolphins were encountered. These animals were not individually identified, although their dorsal fins were photographed. However, adults found in these groups, were not any adult known to be part of the population during the years surveys were carried, since these are visually identified. Thus it is assumed that if a resident adult was present in the encounter, it would be visually identified as such. For this reason these were considered to be non-resident bottlenose dolphins.

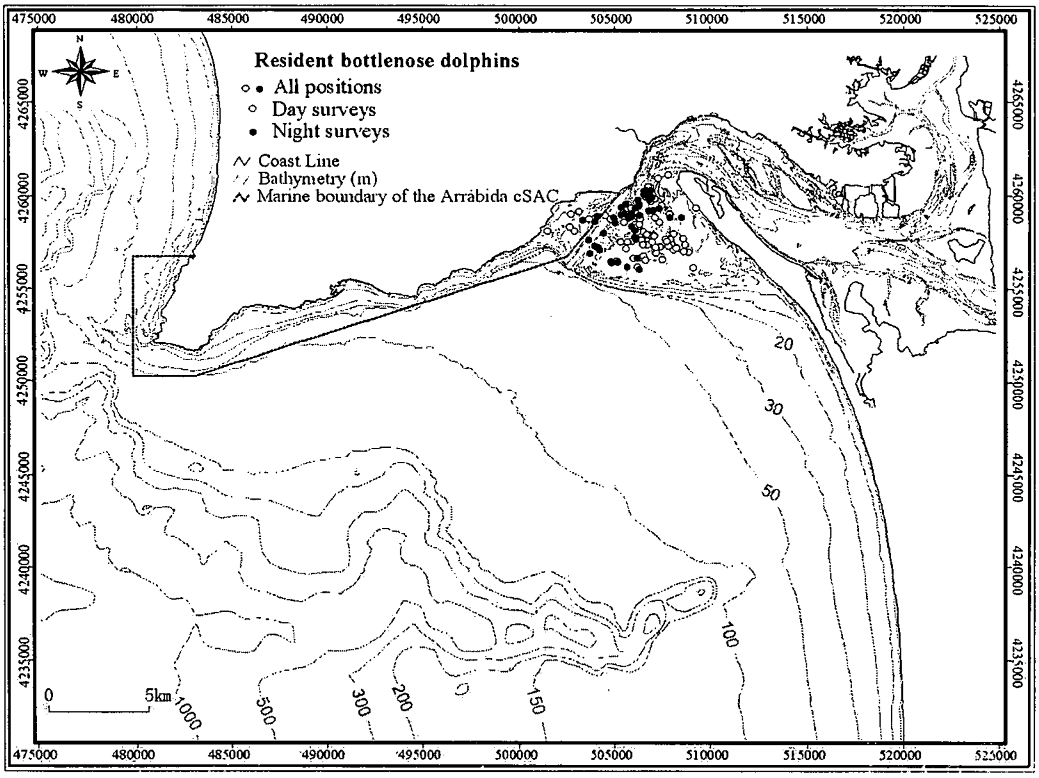

Figure 3.4. Location of all positions of encounters with resident bottlenose dolphins in the marine area adjacent to the Sado estuary during boat surveys in the year 1998.

Encounters with non-resident bottlenose dolphins were located at a wide range of depths, as indicated by the first position (Fig.3.5) and all positions of the observations (Fig 3.6). In addition to the above reported mixed encounter located in the sandbanks at the estuary entrance (Fig.3.5), non-resident bottlenose dolphins were followed at shallow depths (below 30m) near Cape Espichel. Only observations in shallower waters along the Arrábida coast were within the boundaries of the marine Arrábida cSAC (Fig. 3.6). Most of the encounters with non-resident bottlenose dolphins occurred near the 50m and 100m depth contours and up to 150m. These observations were outside the boundaries of the Arrábida cSAC (Fig. 3.6). Most of the groups encountered were moving parallel to the depth contours towards the west and southwest (Fig. 3.6). Group size varied between 2 and a maximum of 40 animals, but most often, less then 10 or

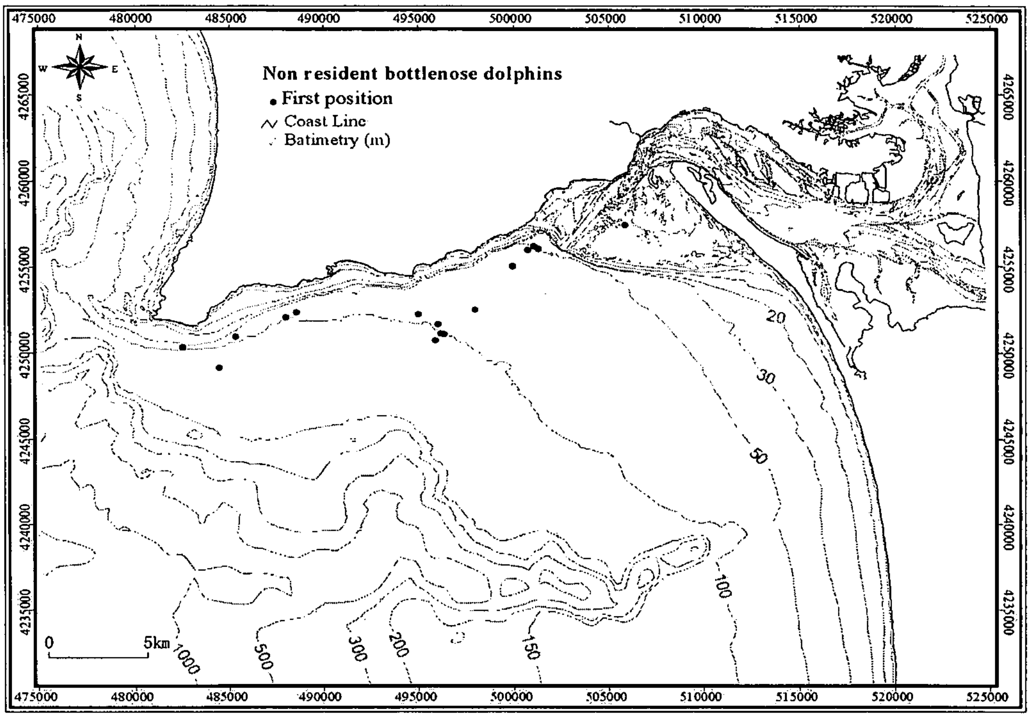

Figure 3.5. Location of the first position of encounters with non-resident bottlenose dolphins during boat surveys conducted along the marine area adjacent to the Sado estuary.

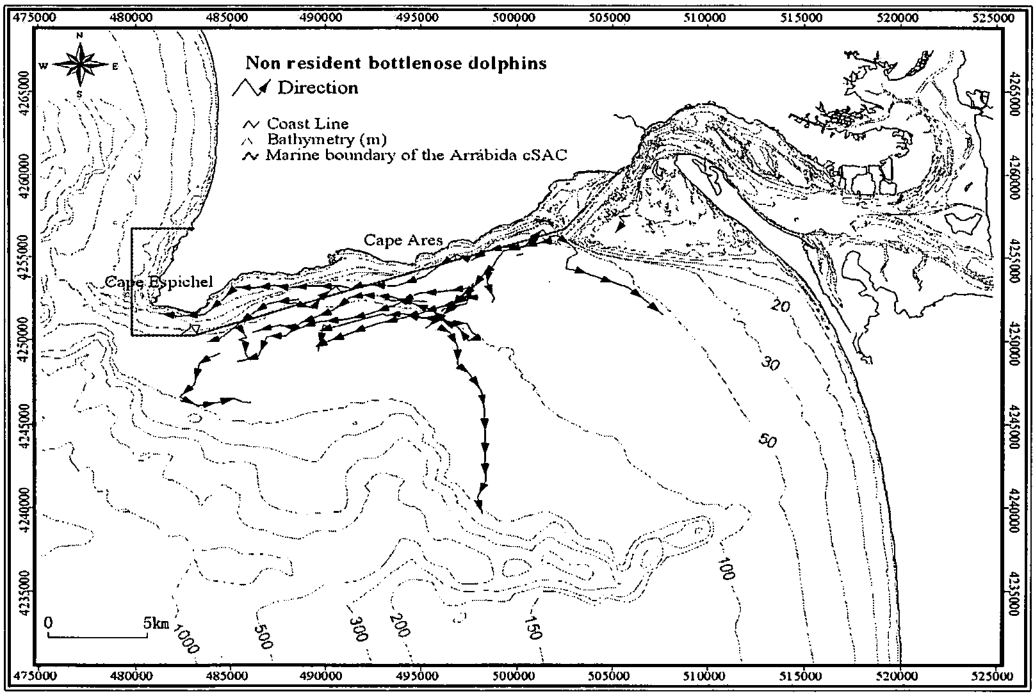

Figure 3.6. Movements of non-resident bottlenose dolphins during encounters along the marine area adjacent to the Sado estuary.

between 15 and 30 individuals. Non-resident bottlenose dolphins were not encountered every year. Most of the seventeen reported encounters occurred in 1998 and 1999, no encounters occurred in 2000 and only one in 2001. Non-resident bottlenose dolphins were seen from March to November.

Harbour porpoises were mainly encountered in one area, around the ship channel (Fig. 3.7). The first position of the 41 encounters with this species was chosen for display because encounters with harbour porpoises were short and the animals did not move far from the initial sighting position. Other observations occurred in the vicinity of the channel, at shallow waters nearby or on the sandbanks and at the estuary entrance. A few observations occurred in deeper waters, (between 30m and over 50m). The locations of the observations of this species are mostly adjacent to the boundary of the Arrábida cSAC (Fig. 3.7). Harbour porpoises were observed in very year, and encounters occurred from May to November. Maximum group size varied from 1 to 11 animals. One animal had a deformed dorsal fin and was seen every year of these surveys. Calves were also seen during the summer and autumn months.

Observations of common dolphins occurred mainly along the coast of Arrábida (Fig. 3.8 and 3.9). From the 38 encounters with this species, only 2 occurred along the coast of Tróia at shallow areas, between 10 and 20 meters. Observations along the coast of Arrábida were located near and along the 100m depth contour from Cape Ares to Cape Espichel and within 50-100m depth between Cape Ares and the ship channel. Most of these observations at the vicinity of limits of the Arrábida cSAC (Fig. 3.8). Common dolphins were encountered from January to October but were not sighted in 2001. Group size varied from 1 individual to a maximum of 200 animals, but most frequently a few tens of animals.

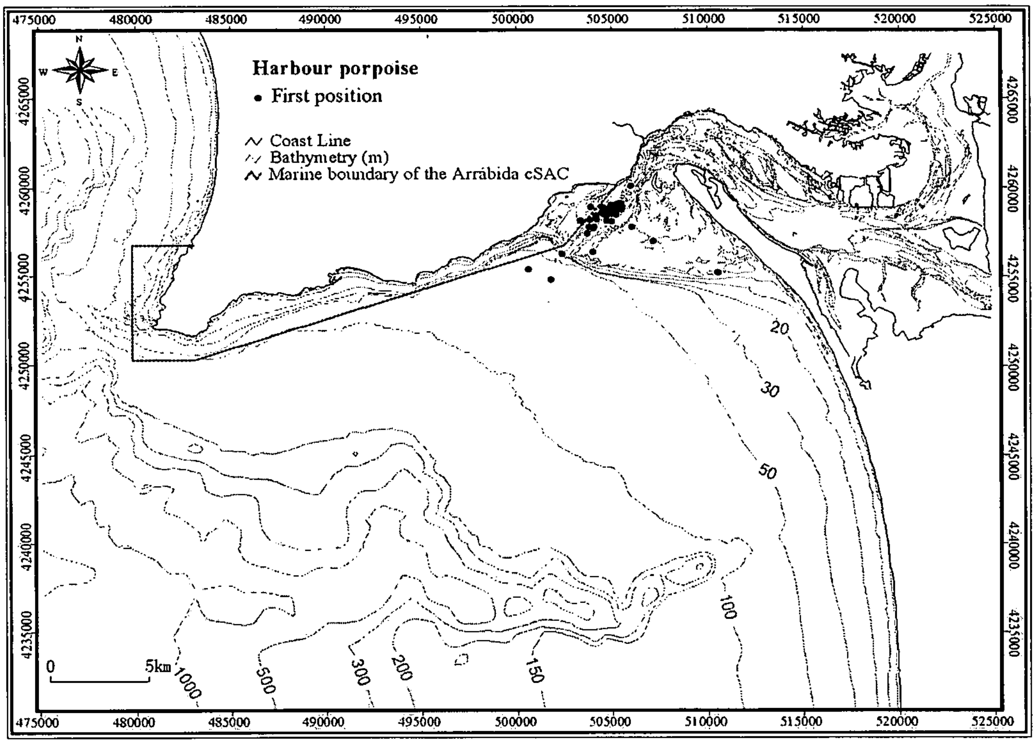

Figure 3.7. Location of the first position of encounters with harbour porpoises during boat surveys in the marine area adjacent to the Sado estuary.

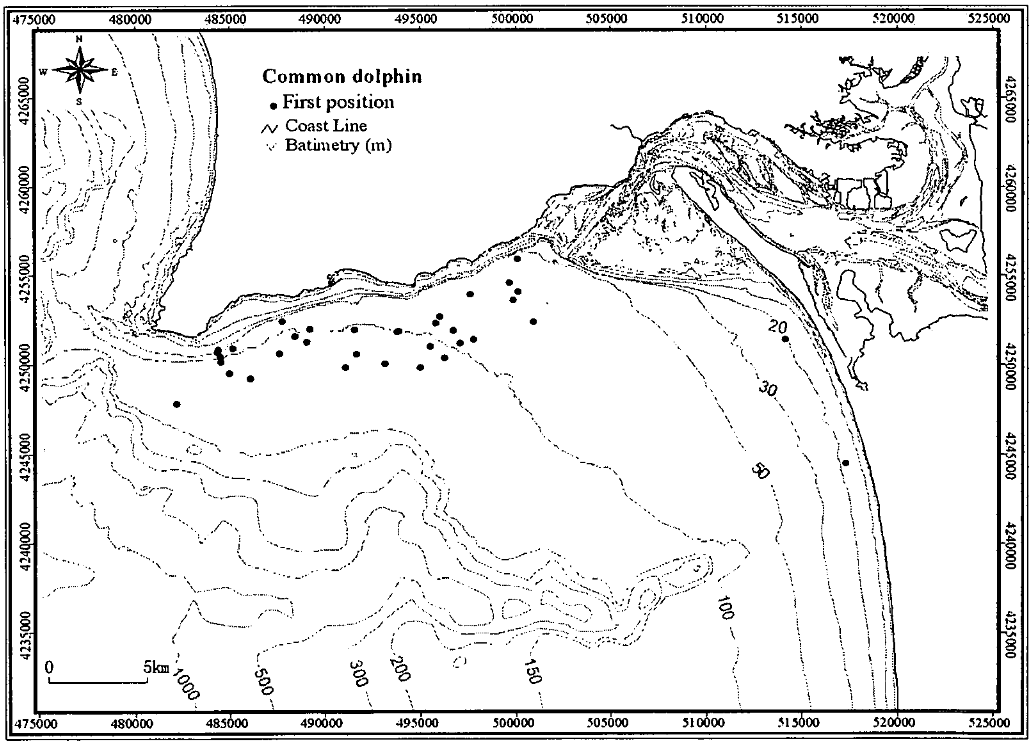

Figure 3.8. Location of the first position of the encounters with common dolphins during surveys in the marine region of the adjacent to the Sado estuary.

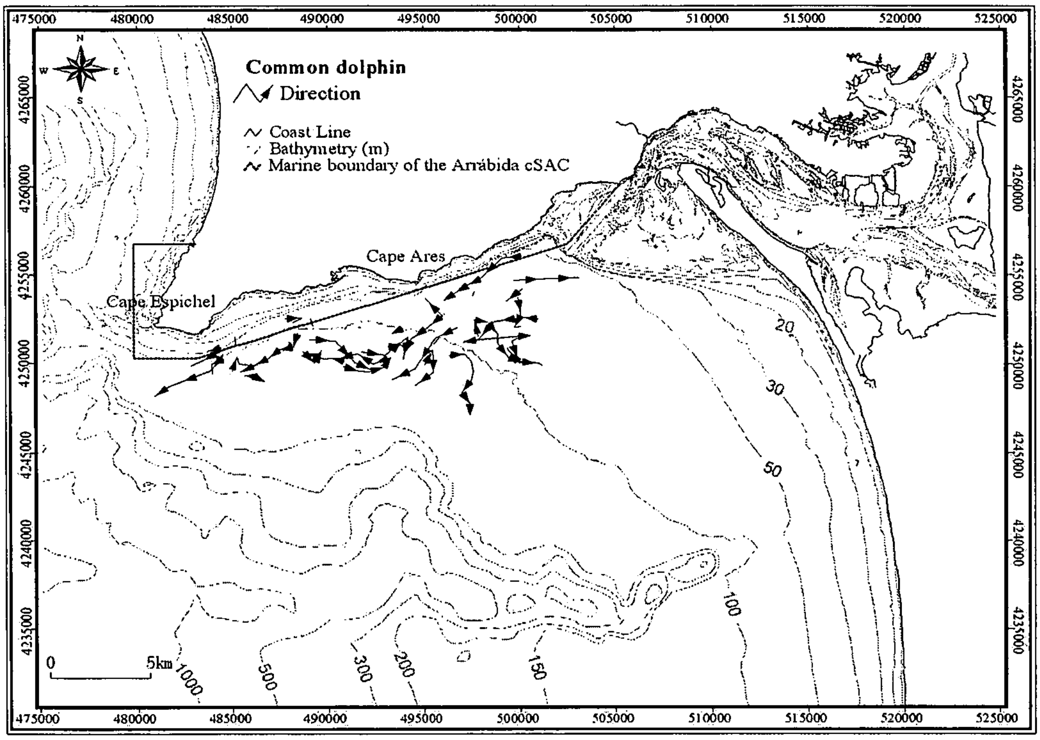

Figure 3.9. Movement of common dolphins during encounters in the marine area adjacent to the Sado estuary.

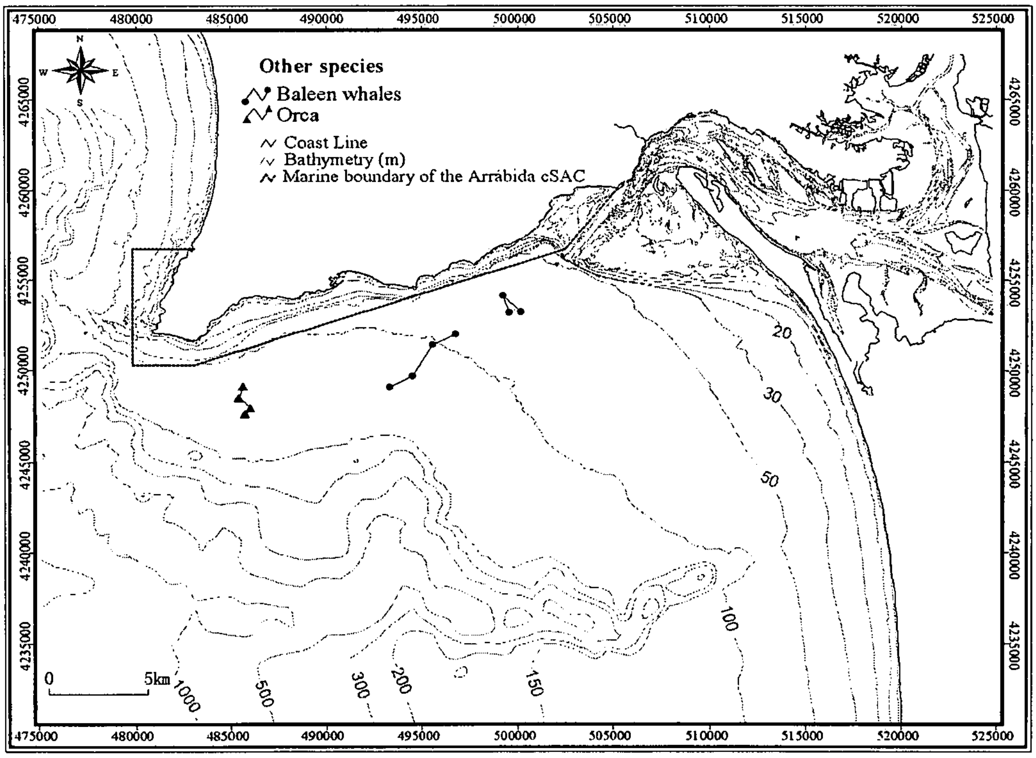

Figure 3.10. Location of sightings of baleen whales and killer whales during surveys in the marine area adjacent to the Sado estuary.

Two other species were encountered occasionally along the Arrábida coast mainly at depths greater than 100m (Fig.3.10). Baleen whales and killer whales were encountered in waters between 50 and 150m depth. These sightings occurred outside the limits of the Arrábida marine cSAC .

3.4. DISCUSSION

Although not all of the marine area outside the estuary was surveyed, the distribution of resident dolphins at sea seems to be very restricted and confined to shallow waters near the estuary entrance. This is in agreement with their high level of residency in the estuary area (Harzen 1995 and this study) and indicates the importance of the estuary as a feeding ground (Dos Santos and Lacerda 1987, Harzen 1998, Dos Santos 1998, Nunes 2001). Resident dolphins may not need to move further away from the estuary if this habitat provides them with the necessary prey.

Adult resident bottlenose dolphins were not seen with non-resident dolphins away from the estuary region. In contrast, non-resident bottlenose dolphins were found to cover a wider range of habitats. These were found from shallow water to deep water but mainly in depths around 50m or more. Encounters between resident and non-resident dolphins observed throughout the study period (see also chapter 2) occurred only in the shallow waters near the estuary. Of the total, only 6 encounters between resident and non-resident dolphins were observed during the period 1992 to 2001. Thus additional marine surveys presented in this chapter confirm the lack of evidence that resident dolphins frequently mix with non-resident ones. Further, they do not provide information about the dispersal of the resident adults which have been not observed on a daily basis (Gaspar 1994). If this is the case, the Sado bottlenose dolphins may not be a breeding unit from a larger population as suggested by Harzen (1997). This resident population could constitute a small and relatively closed breeding group. However the role of emigration and immigration, if they exist, (see chapter 2) between resident and non-resident bottlenose dolphins is not clear. These results indicate that the resident dolphins have a similar residency behavioural pattern to the community of resident bottlenose dolphins in Sarasota (Wells and Scott 1990) and Shark Bay (Smolker et al. 1992). However, it is not clear if some resident Sado animals regularly interchange with nearby coastal bottlenose dolphin groups, as happens in those communities. On the other side, the Sado resident population is not geographically isolated as the Moray Firth resident population of bottlenose dolphins appears to be (Wilson et al. 1995). The relationship between the resident bottlenose dolphins in the Shannon estuary in Western Ireland (Ingram & Rogan 2002) and coastal animals to the north and south of the estuary is unclear as is the case for the bottlenose Sado resident population. Implications for management of the residence status of the Sado dolphins are discussed in chapter 6.

Because bottlenose dolphins were not seen along the coast of Tróia near the locations where beach users claim to have seen this species, the present findings cannot clarify the origin of these observations. It is worth pointing out that in the year 2000, when no sightings of non-resident bottlenose dolphins occurred, the beach sightings were made from an elevated point located at the Arrábida coast on three occasions (A. Martins personal communication). If this information is correct, a higher frequency of surveys may be needed to study the distribution of non-resident bottlenose dolphins at sea. Observations from land with binoculars can only be also used in a complementary way because this method does not always allow dolphins to be individually identified.

Harbour porpoises were found to be sympatric with resident bottlenose dolphins at sea. However, mixed encounters were never observed in this study nor in previous studies

(Gaspar 1994, Martins 1998, Vieira 1998). If agonistic encounters between these species could occur as described in the Moray Firth (Ross and Wilson 1996), the present finding may be indicative that porpoises avoid encounters with resident dolphins.

The distribution of the harbour porpoises was centred in the ship channel at the estuary entrance. Harbour porpoises show affinity for shallow waters (Hammond et al.1995, Skov et al. 1995) and were also found in shipping lanes in other areas (Hammond et al.1995). Because the ship channel is at the entrance to an estuary, these animals may find in this area abundant prey that moves with the tide into and out of the estuary. Harbour porpoises were also seen with calves in this area, including calves with foetal folds. The ship channel and the surrounding area may be an important feeding and calving area of this species in the Sado estuary region. Further, the observation of groups containing several animals and the sighting of the same animal over the 4 years study period in the area may reinforce the importance of this confined, partly artificial habitat to harbour porpoises.

Bottlenose dolphins, common dolphins and harbour porpoises were observed along the coast of Arrábida over a 2-3 year period and during several months of the year. Most of the distribution of these species extended to outside the boundaries of the Arrábida cSAC. These findings may support the inclusion of these three species in the candidature of this area to the Natura 2000 network and provide a framework for future monitoring the distribution of these species and the identification of important habitats within and at the vicinity of the marine Arrábida cSAC. In particular, this work supports the importance of extending the existing limits to cover the distribution at sea of the resident bottlenose dolphin population and harbour porpoises. These populations were confined to an area that is heavily used by recreational boats during the summer. As mentioned above, for the harbour porpoise, this may be a feeding and calving area. For the resident bottlenose dolphins this may be a feeding, resting and socializing area (Hussenot 1982, Nunes 2001) but is also a mandatory passage area to enter and leave the estuary. A growing literature shows that dolphin-boat interactions may disturb dolphins (Bejder et al. 1999, Acevedo 1991, Janik and Thompson 1996). Calves from both species were observed during the summer and these are particularly susceptible to collision (Wells and Scot 1997). The implications of these findings for the conservation of the resident population will be further addressed in chapter 6.

CHAPTER 4. ESTIMATED VITAL RATES EXPLAIN TRENDS IN NUMBERS IN A SMALL RESIDENT DOLPHIN POPULATION

Up to 1997, numbers of resident animals are known to have declined and recruitment to the adult stage was nule. Further, reproductive rates may be particularly low in this resident population, compared to other resident populations of this species (chapter 2). Can life history traits explain the trend in the number of animals?

4.1. INTRODUCTION

Vital rates, such as survival and reproductive rates, are descriptors of life history strategies and population dynamics. For example, in long lived species that mature late and have few offspring, juvenile survival is critical to maturity and population growth is more sensitive to adult survival (Brault and Caswell 1993, Heppell et al. 2000). Perturbations produced by ecological variations on vital rates are important determinants of population dynamics, from both evolutionary and management viewpoints (Gaillard et al. 1993, Monson et al. 2000). In small populations however, especially long-lived species, natural demographic variability may also influence perturbations in vital rates (Brault 1999).

Despite their theoretical and practical relevance, obtaining robust estimates of vital rates, particularly age specific survival, poses many difficulties in long lived wild animals (Lebreton et al. 1993). Methods used to estimate survival, include age-at-death life-tables and mark recapture. Transversal life table methods are widely used (Spinage 1972, Gaillard et al. 1993, Richard et al. 2002). These assume that the age structure is stable (Caughley 1966); estimates of survival in younger and older age-classes are often imprecise due to small sample size (Spinage 1972) and don't generally allow analysis of variability (Buckland 1990). Longitudinal sampling of individually marked animals provides one of the most effective ways of estimating this parameter. Although these methods require a considerable number of animals to be marked and recovered over time, they allow the application of statistical models to estimate and compare survival probabilities (Lebreton et al. 1993) and can potentially provide robust and precise estimates of survival (Lebreton 1992, Buckland 1990). Marks can be artificial, such as in radio-telemetry (Sorensen and Powell 1998) and bands (Brownie et al. 1985). But natural marks such as those used in photo- (Fujiwara and Caswell 2001) and visual- (Moss 2001) identification studies, can be used providing that assumptions are carefully considered (Hammond 1986).

Cetaceans are long lived animals that spend their entire life in water and thus are difficult to study (Samuels and Tyack 2000). Survival rates have generally been estimated from the age structure of harvested, incidentally killed or stranded animals [Commerson's dolphins *Cephalorhynchus commersonii*, Lockyer et al. (1988); killer whales, Olesuik et al. (1990); harbour porpoise and spotted dolphins, Barlow and Boveng (1991); pilot whales from the Faroe Islands, Bloch and Lockyer (1993); beluga whales, from the St. Lawrence River, Lesage and Kingsley (1998); bottlenose dolphins, Stolen and Barlow in press). However, in many species, animals can be identified individually from their naturally occurring marks and "recaptured" through photo-identification (photo ID) (Hammond 1990). Long term photo ID studies and mark recapture methods provided stage specific survival rates for the Florida manatee (Langtimm et al. 1998), humpback whales from the Gulf of Maine (Buckland 1990; Barlow and Clapham 1997) and the Central North Pacific (Mizroch et al. in preparation), the killer whale (Wade et al. 2001), the North Pacific grey whale (Bradford et al. 2001) and the North Atlantic right whale (Fujiwara and Caswell 2001).

Among dolphins, available age specific survival estimates have been mainly obtained from long-term photo-ID studies. These estimates are either restricted to the first (Wells and Scott 1990, Slooten and Lad 1991, Herzing 1997, Fifas et al. 1998) or early years of life (Mann et al. 2000, Haase and Schneider 2001), and assume that mortality rates are constant over a wide range of ages (Wells and Scott 1990, Slooten and Lad 1991, Fifas et al. 1998, Sanders-Reed et al. submitted). Because typical mammalian mortality rate patterns show distinct age-related phases (Caughley 1966, Spinage 1972, Siler 1979) such survival parameters may lack biological meaning (Barlow and Boveng 1991).

In this work we aim to explain the trend in number of animals of the resident population, by analysing births and age and time specific survival rates. The long term data set based on individual identification makes this small group exceptionally suitable to apply mark recapture methods.

4.2. METHODS

4.2.1. Data collection

Data analysed here were collected as part of a long term study of the resident bottlenose dolphin group inhabiting the Sado estuary region, on the west coast of Portugal (Fig.1.1 and 1.2). The study area covers approximately 213 km^2 and includes the outer estuary waters and adjacent marine waters. Resident dolphins were rarely seen in contact with non resident bottlenose dolphins (chapters 2 and 3); here we focus only on the resident animals.

Photographs from the dorsal fin and dorsum of surfacing dolphins were taken during 353 systematic boat surveys between 1986 and 2001, in the study area. In each year, surveys were conducted over at least 3 months but usually 6 or greater. Up to 1997, several boat survey designs were used, covering mainly the Sado estuary and the marine waters nearby. These were described in chapter 2. Since then, only estuary and coastal boat surveys were conducted. Estuary surveys were carried out along the estuary and in the marine zone nearby, when appropriate. Coastal surveys were systematic surveys carried out along the marine coast of Arrábida and Tróia but always included the estuary mouth (Fig. 3.2 and 3.3). Pictures were taken with manual and autofocus cameras, 50-400mm zoom lenses and 64 to 400 ISO colour prints and slides and black and white prints. Left and right side good quality pictures (Wilson et al. 1999b) were inspected to identify individual dolphins using the unique combination of their natural marks (Wursig and Jefferson, 1990), such as shape of the dorsal fin, scars, nicks, skin lesions and natural pigmentation patterns (Scott et al. 1990, Slooten and Dawson 1992, Wilson et al. 1999b). Annual sighting histories of each individually identified dolphin were obtained by comparing all selected photographs taken within and between years. Part of this photographic record, from 1986 to 1997, has been described in chapter 2.

4.2.2. Data definition

Each individually identified dolphin was first categorised into one of three age classes: adults, sub-adults and calves. Adults were the large and robust dolphins (Wilson et al. 1999b), which are assumed to be mature. Sub-adults were dolphins whose body size was smaller than that of adults (Wilson et al. 1999b) and which did not regularly associate with a particular adult (Wells et al. 1987). Calves were identified as small dolphins with foetal folds or with a pronounced paler skin than the adults (Wilson et al. 1999b) and which showed a consistent association with an adult (Smolker et al. 1992, Shane 1990, Wells and Scott 1990).

Calves were assumed to become sub-adults after their 3rd year because most calves from the Sado resident group were observed to leave their mothers after this time (RG, personal observation). This is also the case in other bottlenose dolphin populations (Connor et al. 2000). There is little information about the age at which Sado dolphins reach sexual maturity. Further, the sex of the animals is mostly unknown. The age at which sub-adults became adults was taken as the mode at which female bottlenose dolphins become sexually mature elsewhere; in the tenth year of life (chapter 2).

For the purpose of estimating survival probabilities, the encounter histories of the identified dolphins were initially used to construct two data sets: the adults and young animal's data sets. The adult data set comprised 35 animals whose age was mostly unknown. All except two of these animals were already adults at the beginning of the study, in 1986.

The young animals data set included only dolphins first seen as a calf (n=29). This data set included all identified calves and most of the known sub-adult animals. The exact year of birth was known for most of the animals (66%). Animals not seen in their year of birth could have been in either their second or third year when first seen (see above). For these unknown age calves, the year of birth was allocated based on their size and degree of darker pigmentation. Capture histories were "backfilled" to accommodate this and we consider this as the "base case data set" for the young animals.

Although this may be the best data set to estimate stage specific survival of young animals because their age is either known or can be allocated with reasonable accuracy, it does not include 3 animals first seen as sub-adults. Two of these sub-adults were first seen in 1992 and the other at the beginning of the study (1986). Neither the origin nor the age of these sub-adult animals is known.

If there were no differences between annual survival rates of these 3 animals and of sub-adults included in the young animal data set, there would be no problem in excluding them from the analysis. However, these sub-adults lived longer than most of the known age young animals and thus a biased estimate of the population sub-adult survival rate may result by excluding them.

Thus another data set was created to include only the encounter histories of the sub-adults (n=18). This comprised known age sub-adults, from their 3rd year, and these 3 other sub-adult animals from the year they were first seen.

4.2.3. Population numbers and births

Because nearly every animal was seen in every year, the total number of animals known to be alive counted each year was taken as the size of the population for that particular year (chapter 2). The annual number of births was calculated as the sum of the number of identified calves with foetal folds (newborn calves) seen in each year. Annual fecundity rate was measured as the number of births divided by number of adults in a year since sex ratio was not known.

During the earlier years of this study, photo identification effort did not focus on identifying every individual calf. As a result, fewer and poorer quality pictures were available for the analysis relating to those years. Because not all calves may have been photographed prior to 1992, the number of births presented for that period is believed to be underestimated and should be regarded as a minimum estimate. Conversely, since 1992, and particularly since 1994, monitoring surveys aimed to identify every individual animal (chapter 2) and since 1999, additional sighting effort provided by dolphin watching boats also helped to identify newborn calves.

4.2.4. Survival analysis

Because animals were individually identified (marked) and resighted (recaptured and released alive) during successive boat surveys within each year and between years (encounter occasions), estimation of survival probability was based on the Cormack-

Jolly-Seber (CJS) mark-recapture model. Program MARK [1] (White and Burnham 2001) was used to estimate survival (noted as S) and capture probabilities (noted as p). This program computes these model parameters via maximum likelihood techniques and allows them to be constrained according to biological questions to be addressed. In order to investigate the effect of age and time in the survival of the Sado resident dolphins, each data set (encounter history file) was modelled separately as "live recaptures". The encounter history of each individual animal was coded as "1" (sighted alive) or "0" (not sighted). In the CJS model, permanent emigration is treated as death, meaning not available for further recapture. A logit link function was used to link the design matrix to the parameters of the model.

4.2.4.1. Model selection

The quasi-likelihood Akaike's Information Criterion (AIC_c) was used as a measure of the fit of the model to the data penalised by the number of estimable parameters. Where competing models had a difference in AIC_c of less than or equal to two (Burnham and Anderson 1998), results were compared to investigate their robustness to model choice. When this difference was bigger, models with greater AIC_c values were not considered.

4.2.4.2. Time related changes

The three data sets were too small to support models with year-specific survival or capture probabilities. Consequently, changes over time were examined by investigating models in which survival (and capture probability) was constant during the overall study period, or during two or three distinct periods. The best number of periods and the

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[1] Available from www.cnr.colostate.edu/~gwhite/mark/mark.htm, version September 2002

best change point year between periods was found using the model selection criteria described above. Investigation of change point years was limited to 1990-1999 for the adult data set, 1987-1999 for the young animals data set and to 1989-1999 for the sub-adult data set, in order to ensure sufficient data for the first or last period.

4.2.4.3. Stage related changes

In the young animal data set, survival was estimated for calves in their first, second and third years of life. A single survival estimate for sub-adults in their fourth year and greater was also estimated from the young animals data set. However it was believed that the equivalent estimate provided by the sub-adult data set should be more representative of the population.

4.2.4.4. Sensitivity analysis to the allocation of year of birth

Analyses were conducted to investigate the sensitivity of survival estimates from the young animal data set to alternative choices of allocating age to calves of unknown age. Alternative data sets were constructed in which the ages of unknown-age calves was assigned (a) based on the best information (see above, "base case data set"), (b) all as one year, and (c) all as two years. In constructing the data for (c), there is a choice of backfilling the capture history with '1 0' or '1 1'; both alternatives were investigated. Analyses were based on a simple model with a single parameter for calf survival and a single parameter for sub-adult survival.

4.2.5. Survivorship of calves

Because the resulting sub-adult survival estimates represent an average of annual survival over seven years, the proportion of calves surviving from year to year and the cumulative proportion of calves surviving through adulthood, was also calculated pooled from 1984 to 2001, using the "base case" data set.

4.3. RESULTS

4.3.1. Population numbers and births

Over the 15-year period of this study, population size declined by 15%. Total number of animals was fairly stable during the late eighties, declined to a minimum of 30 animals in 1997 but appears to have been increasing since then (Fig. 4.1). A similar but steeper (30%) decline was seen for the annual number of adults (Fig. 4.1). Two new adults recruited in 1999. The number of young animals did not change much during the earlier

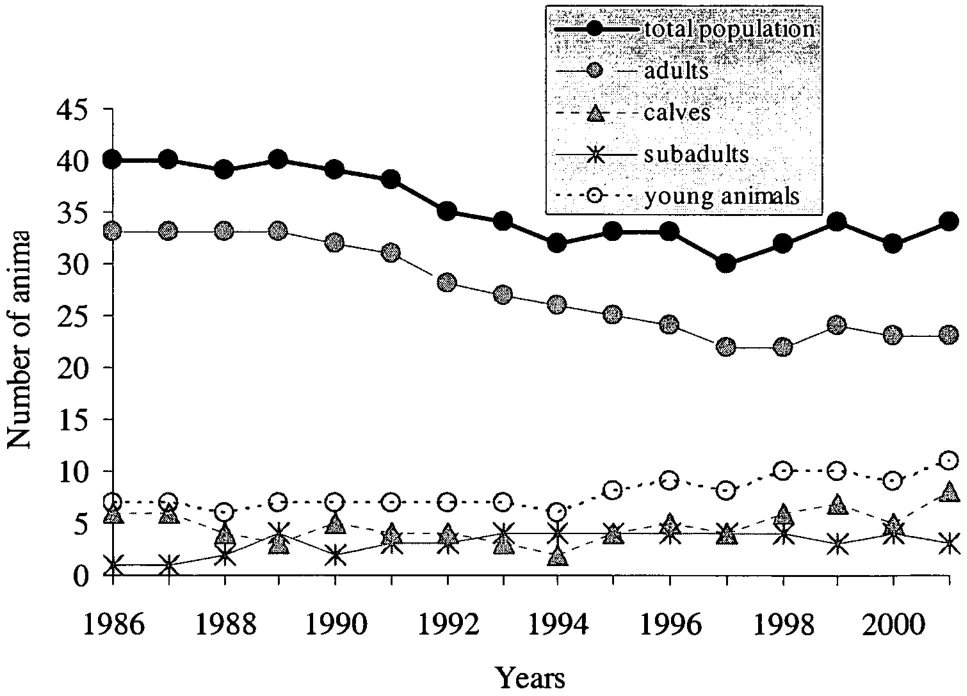

Figure 4.1. Number of animals known to be alive.

years but increased steeply after 1994 due to an increase in the number of calves during the later years. The number of calves varied between 2 and 8 per year. The number of sub-adults was in general relatively low, particularly during the earlier years and remained relatively constant around 3-4 animals during the later period (Fig. 4.1).

Births occurred in most of the years; no more than 3 per year were recorded (Fig. 4.2). Fecundity, as shown by the 3 year moving average, has been increasing during the later years (when records are believed to be complete) and was apparently lower during the earlier years (Fig. 4.2).

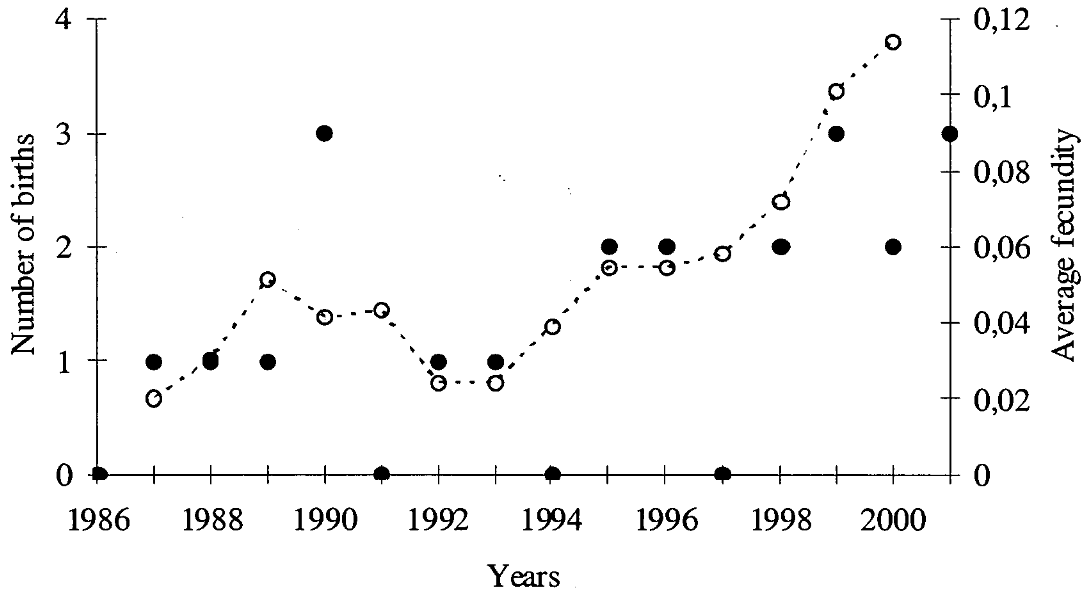

Figure 4.2. Number of births (•) and average fecundity (○).

4.3.2. Survival analysis

4.3.2.1. Adults

4.3.2.1.1. Model selection

Eight models with three different structures fell within 2 AIC_c units (Table 4.1). These results indicate that survival of adult dolphins changed during the study period. The model structures differ in number of change point years in survival and capture probabilities. The best model structure was obtained with only one change point in adult survival (1990) and capture probabilities (1995). However, very similar support was obtained from the data for the second model (delta AIC_c =0.26), according to which, adult survival changed again in 1998.

Table 4.1. Model fits to the adult data set. The best model of each different structure are in bold; S*t* and p are time-related survival and capture parameters, respectively. Note - the number of parameters estimated is always one less than the number of parameters in the model because p=1 from 1995 onwards.

Model		AIC_c	Δ AIC_c	No. parameters	Deviance
1	**S*t*(1986-1990) S*t*(1991-2001) p(1986-1995) p(1996-2000)**	**216.724**	**0.00**	**3**	**1**
2	**S*t*(1986-1990) S*t*(1991-1998) S*t*(1999-2001) p(1986-1995) p(1996-2000)**	**216.986**	**0.26**	**4**	**2**
3	S*t*(1986-1990) S*t*(1991-1997) S*t*(1998-2001) p(1986-1995) p(1996-2000)	217.569	0.84	4	3
4	**S*t*(1986-1990) S*t*(1991-2001) p(1986-1991) p(1992-1995) p(1996-2000)**	**217.699**	**0.98**	**4**	**4**
5	S*t*(1986-1991) S*t*(1992-2001) p(1986-1995) p(1996-2000)	217.797	1.07	3	5
6	**S*t*(1986-1990) S*t*(1991-1998) S*t*(1999-2001) p(1986-1991) p(1992-1995) p(1996-2000)**	**217.949**	**1.23**	**5**	**6**
7	S*t*(1986-1990) S*t*(1991-1997) S*t*(1998-2001) p(1986-1991) p(1992-1995) p(1996-2000)	218.532	1.81	5	7
8	S*t*(1986-1990) S*t*(1991-2001) p(1986-1996) p(1997-2000)	218.638	1.91	3	8

4.3.2.1.2. Survival estimates

Estimates of survival and capture probabilities obtained from the best model of each different structure were highly consistent (Table 4.2), indicating that survival estimates were robust to the number of survival (post-1990) and capture probability parameters. The best model (model 1, Table 4.2) shows a decrease in adult survival around 1990/91 (S86-90 = 0.995 and S91-2001 = 0.961). However, the second best model shows that survival was lower during the period 1991-1998 and increased again after 1998 (S99-2001=0.986). Capture probabilities were very high (0.94 to 0.99).

Table 4.2. Estimates of adult survival and capture probabilities obtained from the best models of each structure. S*t* and p are time-related survival and capture parameters, respectively.

Model	Parameter	Estimate	Standard error
1	S*t*(1986-1990)	0.994	0.0076
	S*t*(1991-2001)	0.961	0.0115
	p(1986-1995)	0.954	0.0124
	p(1996-2000)	1	(-)
2	S*t*(1986-1990)	0.995	0.0076
	S*t*(1991-1998)	0.953	0.0145
	S*t*(1999-2001)	0.986	0.0144
	p(1986-1995)	0.954	0.0124
	p(1996-2000)	1	(-)
4	S*t*(1986-1990)	0.995	0.0076
	S*t*(1991-2001)	0.961	0.0116
	p(1986-1991)	0.945	0.0170
	p(1992-1995)	0.971	0.0167
	p(1996-2000)	1	(-)
6	S*t*(1986-1990)	0.995	0.0077
	S*t*(1991-1998)	0.953	0.0146
	S*t*(1999-2001)	0.986	0.0144
	p(1986-1991)	0.944	0.0171
	p(1992-1995)	0.971	0.0167
	p(1996-2000)	1	(-)

4.3.2.2. Young animals

4.3.2.2.1. Sensitivity to the allocation of year of birth

Results from the sensitivity analysis show that the estimates of survival obtained from the young animals "base case data set" were insensitive to the allocation of the year of birth and to the method of backfilling the data with respect to capture probabilities (Table 4.3). Relative differences were no more than ±4% (calf survival) or ±1% (sub-adult survival) even when the most extreme assumptions about age and capture history were made.

Table 4.3. Effect of the allocation of year of birth and the method of backfilling the data on average calf survival during the first three years Sa(1-3), sub-adult survival Sa(4-10) and constant capture probability p(1984-2000). Standard errors of the estimates are in brackets. The percentages refer to the relative difference between the estimates obtained from the "Base case" model and those obtained from models where assumptions about the age (models A and B) and capture history (models C and D) or both (model D) were made. Model A assumes that calves whose year of birth is not known were one year old when first sighted, models B and C assumed they were two years old, models C and D assume they were not seen during the second year.

	Model				
Parameter	Base case	A	B	C	D
S(1984-2001) a(1-3)	0.878 (0.0414)	-1.82%	2.16%	0.34%	4.21%
S(1984-2001) a(4-10)	0.802 (0.06)	1.25%	-0.12%	0.25%	-0.12%
p(1984-2000)	0.959 (0.0232)	-0.21%	0.13%	-4.28%	-13.24%

4.3.2.2.2. Model selection

Table 4.4. Model fits to the young animals data set. The best models of each different structure are in bold. S*t* and p are time-related survival and capture parameters, respectively, and S*a* are age-related survival parameters. Note - two fewer parameters were estimated because S2-3 and p=1 after the change point year.

Model		AIC_c	$\Delta\ AIC_c$	No. parameters	Deviance
1	**S*t*(1984-1993)*a*(1, 2-3) S*t*(1994-2001)*a*(1, 2-3) S*t*(1984-2001)*a*(4-10) p(1984-1989) p(1990-2000)**	**112.730**	**0.00**	**5**	**1**
2	S*t*(1984-1994)*a*(1, 2-3) S*t*(1995-2001)*a*(1, 2-3) S*t*(1984-2001)*a*(4-10) p(1984-1989) p(1990-2000)	112.958	0.23	5	2
3	**S*t*(1984-1993)*a*(1, 2-3) S*t*(1994-2001)*a*(1, 2-3) S*t*(1984-1992)*a*(4-10) S*t*(1993-2001)*a*(4-10) p(1984-1989) p(1990-2000)**	**113,286**	**0.54**	**6**	**3**
4	S*t*(1984-1994)*a*(1, 2-3) S*t*(1995-2001)*a*(1, 2-3) S*t*(1984-1992)*a*(4-10) S*t*(1993-2001)*a*(4-10) p(1984-1989) p(1990-2000)	113.487	0.76	6	4
5	S*t*(1984-1993)*a*(1, 2-3) S*t*(1994-2001)*a*(1, 2-3) S*t*(1984-1994)*a*(4-10) S*t*(1995-2001)*a*(4-10) p(1984-1989) p(1990-2000)	113.489	0.76	6	5
6	S*t*(1984-1993)*a*(1, 2-3) S*t*(1994-2001)*a*(1, 2-3) S*t*(1984-1990)*a*(4-10) S*t*(1991-2001)*a*(4-10) p(1984-1989) p(1990-2000)	113.540	0.81	6	6
7	S*t*(1984-1994)*a*(1, 2-3) S*t*(1995-2001)*a*(1, 2-3) S*t*(1984-2001)*a*(4-10) p(1984-1989) p(1990-2000)	113.710	0.98	6	7
8	**S*t*(1984-1994)*a*(1, 2-3, 4-10) S*t*(1995-2001)*a*(1, 2-3, 4-10) p(1984-1989) p(1990-2000)**	**113.761**	**1.03**	**6**	**8**
9	S*t*(1984-1995)*a*(1, 2-3) S*t*(1996-2001)*a*(1, 2-3) S*t*(1984-2001)*a*(4-10) p(1984-1989) p(1990-2000)	114.005	1.27	5	9
10	S*t*(1984-1993)*a*(1, 2-3, 4-10) S*t*(1994-2001)*a*(1, 2-3, 4-10) p(1984-1989) p(1990-2000)	114.070	1.34	6	10

Table 4.4. Continued

Model	AIC$_c$	Δ AIC$_c$	No. parameters	Deviance
11 S*t*(1984-1993)*a*(1, 2-3) S*t*(1994-2001)*a*(1, 2-3) S*t*(1984-1991)*a*(4-10) S*t*(1992-2001)*a*(4-10) p(1984-1989) p(1990-2000)	114.212	1.48	6	11
12 S*t*(1984-1994)*a*(1, 2-3) S*t*(1995-2001)*a*(1, 2-3) S*t*(1984-1993)*a*(4-10) S*t*(1994-2001)*a*(4-10) p(1984-1989) p(1990-2000)	114.292	1.56	6	12
13 S*t*(1984-1994)*a*(1, 2-3) S*t*(1995-2001)*a*(1, 2-3) S*t*(1984-1991)*a*(4-10) S*t*(1992-2001)*a*(4-10) p(1984-1989) p(1990-2000)	114.433	1.70	6	13
14 S*t*(1984-1995)*a*(1, 2-3) S*t*(1996-2001)*a*(1, 2-3) S*t*(1984-1992)*a*(4-10) S*t*(1993-2001)*a*(4-10) p(1984-1989) p(1990-2000)	114.516	1.79	6	14

Forteen models with two distinct structures fell within 2 AIC$_c$ units (Table 4.4). Differences between model structures were characterised by either time varying or constant sub-adult survival. For models with the same structure, the change point year for survival probabilities varied over several years whereas the change point year in capture probabilities was consistently the same in all models (1989). These most supported models indicate that calf and also sub-adult survival, changed over the study period. Calf survival was consistently estimated as two stage specific parameters: survival during the first year and survival during both second and third years. These parameters changed at the same change point years (1993/1994). Differences between model structures were characterised by either time varying or constant sub-adult survival. The best model based on AIC$_c$ was obtained with constant sub-adult survival. However, the model where sub-adult survival changes in 1992 (model 3) had a small delta AIC$_c$ (0.54). This model also had the lowest deviance.

4.3.2.2.3. Survival estimates

Estimates of survival and capture probabilities obtained from models with the same structure were very similar. For this reason, only estimates from the best model of each structure are presented (Table 4.5). In addition, age specific calf survival estimates, obtained from different model structures were not affected by changing model structure. Survival during the first year was very high before the change point year (S=0.98), decreasing thereafter (S=0.82-0.83). On the contrary, survival of animals from age 1 to age 3 was low before the change point year (S=0.75-0.76) and maximum thereafter (S=1).

Table 4.5. Estimates of survival and capture probabilities obtained from the best model of each structure for young animals. S*t* and p are time-related survival and capture parameters, respectively; S*a* are age-related survival parameters.

Model	Parameter	Estimate	Standard error
1	S*t*(1984-1993)*a*(1)	0.977	0.0812
	S*t*(1994-2001)*a*(1)	0.833	0.1076
	S*t*(1984-1993)*a*(2-3)	0.748	0.099
	S*t*(1994-2001)*a*(2-3)	1	(-)
	S*t*(1984-2001)*a*(4-10)	0.80	0.060
	p(1984-1989)	0.829	0.090
	p(1990-2000)	1	(-)
3	S*t*(1984-1993)*a*(1)	0.977	0.0813
	S*t*(1994-2001)*a*(1)	0.833	0.1076
	S*t*(1984-1993)*a*(2-3)	0.751	0.0993
4	S*t*(1994-2001)*a*(2-3)	1	(-)
	S*t*(1984-1992)*a*(4-10)	0.666	0.1358
	S*t*(1993-2001)*a*(4-10)	0.848	0.0624
	p(1984-1989)	0.828	0.0902
	p(1990-2000)	1	(-)
8	S*t*(1984-1994)*a*(1)	0.980	0.0768
	S*t*(1995-2001)*a*(1)	0.818	0.1163
	S*t*(1984-1994)*a*(2-3)	0.761	0.960
	S*t*(1995-2001)*a*(2-3)	1	(-)
	S*t*(1984-1994)*a*(4-10)	0.7046	0.1105
	S*t*(1995-2001)*a*(4-10)	0.857	0.0661
	p(1984-1989)	0.826	0.0911
	p(1990-2000)	1	(-)

The estimate of constant sub-adult survival was 0.80. For the best model in which sub-adult survival changed (in 1994) survival before the change point year was very low (S=0.66) and increased thereafter (S=0.85). Capture probabilities were lower before 1989 (p=0.83) but after that period, every marked animal estimated to be alive was sighted every year (p=1).

4.3.2.3. Sub-adults

4.3.2.3.1. Model selection

Eight models were obtained within two AIC_c units with constant or time varying sub-adult survival and capture probabilities (Table 4.6). The best model was obtained with constant survival. However, the second best model (smaller deviance and a small delta AIC_c =0.53) shows a change in sub-adult survival. The best change point year was 1992, although good support was also obtained for 1993, 1994 and 1997. The change point in capture probabilities was consistently the same in all models (1989).

Table 4.6. Model fits to the sub-adult data set. S*t* and p are time-related survival and capture parameters, respectively. The number of estimable parameters is one fewer because p=1 after the change point year.

	Model	$\mathrm{AIC_c}$	$\Delta\ \mathrm{AIC_c}$	No. parameters	Deviance
1	**S*t*(1984-2001) p(1984-1989) p(1990-2000)**	**71.268**	**0.00**	**2**	**1**
2	**S*t*(1984-1992) S*t*(1993-2001) p(1984-1989) p(1990-2000)**	**71.801**	**0.53**	**3**	**2**
3	S*t*(1984-2001) p(1984-1991) p(1992-2000)	72.578	1.31	2	3
4	S*t*(1984-1994) S*t*(1995-2001) p(1984-1989) p(1990-2000)	72.734	1.47	3	4
5	S*t*(1984-2001) p(1984-1990) p(1991-2000)	72.766	1.50	2	5
6	S*t*(1984-1993) S*t*(1994-2001) p(1984-1989) p(1990-2000)	72.862	1.59	3	6
7	S*t*(1984-1997) S*t*(1998-2001) p(1984-1989) p(1990-2000)	73.066	1.80	3	7
8	S*t*(1984-1989) S*t*(1990-2001) p(1984-1989) p(1990-2000)	73.241	1.97	3	8

4.3.2.3.2. Survival estimates

Estimates of survival obtained from models with the same structure as the best model were very similar: constant sub-adult survival was 0.83 (Table 4.7). However, models supporting time varying sub-adult survival probabilities showed some differences during the earlier years (S84-93=0.78, SE=0.0877; S84-94=0.78, SE=0.0788; S84-97=0.81, SE=0.0612). This is indicative of survival changing over a number of years. Sub-adult survival probabilities after the change point year were higher and similar between models (S=0.86-0.87). Capture probabilities were lower during the earlier period (p=0.72-0.73) and the maximum since 1990 (p=1) (Table 4.7).

Table 4.7. Estimates of sub-adult survival and capture probabilities obtained from the best model of each structure. S*t* and p are time-related survival and capture parameters, respectively.

Model	Parameter	Estimate	Standard error
1	S*t*(1984-2001)	0.830	0.0468
	p(1984-1989)	0.723	0.1583
	p(1990-2000)	1	(-)
2	S*t*(1984-1992)	0.731	0.1036
	S*t*(1993-2001)	0.870	0.0497
	p(1984-1989)	0.732	0.1563
	p(1990-2000)	1	(-)

4.3. 3. Survivorship of calves

The proportion of sub-adults surviving from year to year (Fig 4.3) decreased during the first four years after weaning, being higher since then, until age 10, when it decreases again. Cumulative proportion of calves surviving, shows that 47% of calves disappears from weaning (age 3) to age 7 and that only a very small proportion (6%) will reach maturity (age 10).

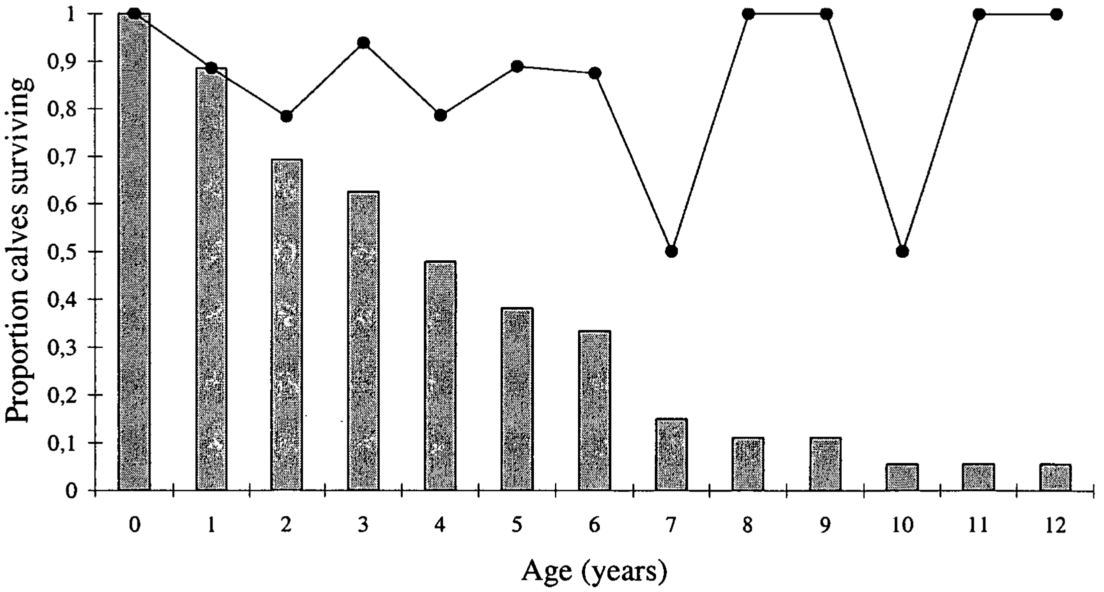

Figure 4.3. Survivorship of calves from the resident population: cumulative proportion surviving (bars) and annual proportion surviving (line)

4.4. DISCUSSION

4.4.1. Data and methodological constraints

Although in general, estimates of survival from models such as the Cormack-Jolly-Seber are robust to violations of assumptions (Lebreton 1992) it is nevertheless important to assess the degree to which assumptions have been met if results are to be viewed as unbiased.

By using photo-identification as the marking technique two advantages generally emerge. Marking does not affect future catchability because there is no physical contact when marking (photographing) an animal. In this study, the boat was manoeuvred to not approach closer than 50m in order to prevent dolphin harassment. Secondly, appropriate chosen marks should be unique and should not get lost (Hammond 1986, Wilson et al. 1999b). But animals may have not the same probability of being captured within a sampling occasion as a result of different probabilities of being encountered, photographed or recognised (Hammond 1986, Wilson et al. 1999b). However, in this study, most animals were seen in almost all years and estimated capture probabilities were high (p=.72) to very high (p=1). Bias resulting from heterogeneity of capture probabilities is therefore likely to be negligible because the feasible variations about average capture probabilities is small (Carothers 1973, Gilbert 1973).

Recognition may be affected by quality of the photographs, the rate of change and distinctiveness of marks (Wilson et al. 1999b). In this study, only good quality pictures were used in the process of identification. Permanent and distinctive marks such as nicks in the dorsal fin, dorsal fin shape and natural pigmentation patterns were used for identifying individual dolphins. But temporary features, such as subtle notches in the dorsal fin, scratches, scars and skin lesions were also used (chapter 2). These temporary marks were used particularly for identifying young animals, which are fast growing animals, and their marks may change as a result. In particular, temporary marks may change within and between years. Because animals could be encountered and photographed several times per year (surveys covered at least 3 months, but usually 6 months or greater), a regular track of mark change throughout the year allowed the update of temporary identification marks between sampling occasions (years).

However this may have not been the case of two animals first seen in 1992 as sub-adults. Three hypotheses are viable for the origin of these animals. First, they could result from immigrant sub-adult animals. If that were the case, sub-adult survival should be the only parameter affected, as accommodated in the sub-adult data set (see methods). Migration rates in resident bottlenose dolphin population are poorly documented. In the Sarasota resident bottlenose dolphin population, annual rates of immigration and emigration are very low, no more than 2-3% (Wells and Scott 1990). But there is no information to infer these rates in the Sado estuary. Secondly, these animals could result from non identified resident calves. If this were the case they would have had to live for several years before being first seen. Given the high capture probabilities this hypothesis seems to be unlikely. Finally, they could result from calves that were initially identified and than lost track of later on, either because of temporary emigration or because of mark change. This hypothesis is acceptable since less effort in identifying every individual calf was made during the earlier years; if true, the exclusion of the two unknown origin sub-adults from the young animal data set can bias the estimates of calf survival downwards during the earlier years. This also means that the sub-adults in the young animal data set were not representative of the population.

In order to explore the possible bias in calf survival for that time period, several modified “base case” data sets were created. Changes in the original “base case” data set were made by linking the capture history of each of the two unknown origin sub-adults with the capture history of any two calves that could feasibly be the same animal. All possible combinations of different calves were considered. Each modified data set was modelled using the simpler (and most likely) model structures obtained previously for the "base case" data set (models 1 and 3, table 4.4). Estimates of calf survival during the second and third years were obtained and compared with the earlier years. Resulting calf survival estimates obtained from models within 2 AIC_c units, were higher (6.7% to 14.1%) than those obtained from the "base case" data set. These ranged from 0.80 (SE=0.086) to 0.86 (SE=0.076).

In conclusion, although estimates of survival of young animals may have been greater during the earlier years, the previous obtained pattern of higher survival rates for young animals during the later years is not affected, at least for calves during their second and third years.

Since there was less effort in identifying every individual calf during the earlier years, survival during the early life, reproductive parameters and numbers of animals during that period could be affected. In mark recapture studies, it is likely that new-born calves may die before being first marked (Wells and Scott 1990). New-born calves are difficult to photograph and identify: they are generally hidden by the adults and are poorly marked (Grellier 2000). In addition, because less effort was put into their identification, not all calves encountered, especially new-born calves, may have been photographed and/or identified. A likely consequence is that, during the earlier period, the estimate of survival for the first year of life is biased upwards, perhaps by a considerable amount. In addition, population size was larger during the earlier years and more reproductive females were alive. In fact, four known calving females died or disappeared before 1992. Thus the number of births (and possibly, fecundity) is likely to have been higher than that reported. Finally, as an overall consequence, the decline in population size would be steeper and the difference between the number of young animals in the earlier and later years would be less. In summary, it is clear that the lower sampling effort during the earlier years affected the estimation of several population parameters but it cannot account for the lack of recruitment to the adult stage, later in the study period. A plausible explanation of that is the low survival of the young animals during the earlier years.

In long-lived species, variation in population dynamics due to environmental variation is usually very little (Morris and Doak 2002) compared to variation caused by demographic variability, especially in very small populations (Brault 1999) as was the case in this study (see chapter 5). The high demographic variability means that there is an important advantage in including as many individuals as possible to reduce uncertainty. In this study, all individuals from the population were included in the survival analysis. In addition, the small population size limits the extent of the analysis. For instance, to obtain a larger sample, more years of sampling effort are required. But, if changes in survival are occurring with time, it will be difficult to detect them, due to small sample size. In addition, sampling variation (capture probability) must also be considered. Because capture probabilities were high over many years, estimated variation is most likely due to demographic variability. Such high capture probabilities over such a long time period have been found in few other studies (Langtimm et al. 1998). The Sado estuary resident group of bottlenose dolphins constitutes a most unusual case in mark recapture studies.

4.4.2. Change in numbers of animals

The Sado estuary resident group of dolphins is very small and overall numbers of animals have declined 15% during the last 15 years (1986-2001). However, population size seems to be increasing after 1997. Results from age structure, reproductive parameters and time and stage specific survival analysis explain the observed pattern of population size.

The decline in total number of animals can be explained by the low survival of the young animals (first year excluded, see above) before 1994 and by the low adult survival during the early nineties. The way reproductive parameters and sub-adult survival affected this decline during the earlier years is not very clear because not all births nor calves may have been recorded before 1992 and the sighting history of a few sub-adults was incomplete.

The recent increase in total number of animals is consistent with greater survival at least in calf (first year excluded, see above) and adult age classes and number of births and fecundity rate during the recent years. The increase in the annual number of calves in particular, contributed to the increase in population size, since the number of sub-adults remained relatively constant and the number of adults decreased.

The low survival of young animals during the earlier years has greatly affected the age structure of the resident group through a long period (12 years) of lack of recruitment to the adult stage. Based on the available estimates, the probability of a one year old calf reaching maturity is very low (0.06). As a result, the age structure is composed predominantly of adults over 25 years, whose reproductive rates will tend to decrease during the coming years (Marsh and Kasuya 1986). Although an increase in survival of the young animals was observed during the later years (38% of the weaned calves could reach maturity) the ageing of the adults and the delay in future recruitment of young adults, may compromise future viability of this very small resident population (see chapter 5).

4.4.3.Stage specific survival patterns

Stage specific survival patterns were consistent during the study period: adults have highest survival, sub-adults have lower survival than calves during their second and third years (survival during the first year is very likely biased). Stage specific survival also varied with time. These empirically obtained survival patterns do not however always corroborate predicted survival patterns for large mammals by contemporary life history theory.

4.4.3.1. Adult survival

For a large, long lived and slow reproducing mammal species such as the bottlenose dolphin, adult survival is expected to be high, as observed in other mammals (Ngog Nje 1988, Moss 2001), including other marine mammals (Harwood and Prime 1978, Olesiuk et al. 1990, Langtimm et al. 1998). The high adult survival rate observed throughout this study (0.95 to 0.99) is consistent with this general pattern and with a high longevity, even if adult emigration has occurred as shown in the second chapter. High survival rates have also been reported for adult stranded bottlenose dolphins from Indian River Lagoon, Florida, before senescence (Stolen and Barlow in press). However, these survival rates were lower than those here reported and are indicative of a lower longevity; Indian River Lagoon bottlenose dolphins live only to age 35 and some of the Sado resident adults may be close or older than that.

Constant adult survival over time is a life history characteristic common to large long lived mammals (Fowler 1981) and thus very small variability is expected. The change over time, in adult survival reported in this study is therefore not according to this general pattern. This variation may be due to demographic variability caused by the age structure of a small number of adults. There is some evidence that in older age classes sex ratio in dolphin populations is close to unity or biased towards females (Perrin and Reilly 1984); adult males experiencing lower survival, as is the case of the bottlenose dolphins from Indian River Lagoon (Stolen and Barlow in press). However, the sex ratio over the study period is unknown (but see next chapter). The ageing of the adult class resulting from the long period of lack of recruitment (see chapter 2), could also influence adult survival patterns. As in other large mammal species (Caughley 1966), older bottlenose dolphins experience lower survival after age 30 (Stolen and Barlow in press). Because resident adults are believed to have lived in a contaminated area such as the Sado estuary, it is reasonable to expect that certain contaminants may affect their survival, especially of males, whose burdens accumulate with age (Weisbrod et al. 2001). However, the role of contaminants in the survival of dolphins is not clear (Aguilar and Raga 1993, Ross 2002). In addition, there is no evidence that resident adult male survival is biased since the sex ratio of disappearing or dead known sex adults was close to parity (1:1.3). Finally, although adults are experienced animals, ageing may affect their physical capabilities. This factor may have accounted for two recent (1999 and 2002, respectively) live strandings of male adults aged close or over 30 years, in the margins of the interior estuary channels.

4.4.3.2. First year survival

In bottlenose dolphins, as in other large mammals, the probability of surviving to the first year is often low (Caughley 1966, Clutton-Brock et al. 1987, Ngog Nje 1988).

Newborn bottlenose dolphins are particularly vulnerable when their mothers have to separate from them to feed (Mann and Smuts 1998). Although protection may be gained from group living (Connor 2000, Whitehead and Mann 2000) they may suffer aggression from other conspecifics (Patterson et al. 1998). Further, because newborn bottlenose dolphins are less competent swimmers and divers and have less developed sensory abilities than adults, they are more vulnerable to natural and anthropogenic dangers (Whitehead and Mann 2000). Risk of stillbirth and neonatal mortality may be higher for primiparous females which may be affected by their PCBs load (Schwacke et al. 2002).

When more effort was put into identifying every individual calf, during the later period of the study, survival during the first year (S = 0.82-0.83) is low, which is consistent with contemporary life history theory. The estimate of first year survival obtained for the later period is close to that observed in wild cetaceans (Herzing 1997, Whitehead and Mann 2000) and in other bottlenose dolphin populations(S=0.76 in Shark Bay (Mann et al. 2000); S=0.80 in Doubtfull Sound (Haase and Schneider 2001) and S=0.81 in Sarasota (Wells and Scott 1990)).

Causes of mortality of newborn calves may differ among study sites. Predators are often referred to as a main cause of mortality of newborn dolphins (Cockcroft et al. 1989a, Herzing 1997, Mann and Barnett 1999). However, predators may not constitute a real threat inside the Sado estuary. There are no records of shark attacks on the resident dolphins. The known shark species in the estuary (Cabral 1999, Costa et al. 2000) do not eat marine mammals. Killer whales may constitute a potential but very rare predator pressure. Over twenty years, they were once observed at the estuary mouth (dos Santos and Lacerda 1987). Killer whales (chapter 3) and hammer head sharks were seen several miles away from the estuary mouth, where resident dolphins were never observed (R.

Gaspar, personal observation). Infanticide (Patterson et al. 1998) was a possible cause of the death of one newborn calf from the Sado (R Gaspar, personal observation). Anthropogenic dangers may play an important role since the estuary water is turbid. Due to their inexperience and curiosity, younger dolphins have greater susceptibility to entanglement in active (Wells et al. 1998, Noke and Odell 2002) and lost or discharged (Hall 1998) fishing gear and may be more vulnerable to collisions with boats (Wells and Scott 1997).

4.4.3.3. Calf survival

After a period of low survival during the early life of a large mammal, survival tends to increase (Caughley 1966). Typically, bottlenose dolphins remain close to their mothers during their second and third years of life (Connor et al. 2000). In this way, they gain from dependence to their mothers and from protection and learning in group living. In addition, they can rely on their more successful and reliable acquired techniques to feed themselves and on learned skills to explore the environment and communicate with their conspecifics (Connor et al. 2000).

The typical mammalian survival pattern was observed during the later period of the present study, when estimates of calf survival are believed to be less biased. During that period, survival increased from the first to the second and third years. Although in many studies, estimates of survival during the first year are often biased upwards (Wells and Scott 1990), this pattern was also observed in another wild bottlenose dolphin population (Mann et al. 2000) and in captive animals (Small and DeMaster 1995).

However the magnitude of increase in the probability of survival from the second to the third years of life of a bottlenose dolphin remains unclear. In this study, calf survival during the second and third years was estimated as constant, according to the best models (within 2 AIC_c units). In captive animals, little variation was also recorded (Small and DeMaster 1995), but this refers to artificial conditions. In other wild bottlenose dolphins, calf survival increased from the second (S=0.82) to the third (S=0.97) years (Mann et al. 2000). Differences in ecological features between study sites may account for variation in survival estimates. Estimates of second and third year calf survival from the Sado resident dolphins during the early period (S=0.75 to 0.86) are close to survival estimates during the second year (S=0.83) reported for the small bottlenose dolphin population from Doubtful Sound, New Zealand (Haase and Shneider 2001) and to the large population of Shark Bay, Australia (S=0.82). The estimate obtained for the later period (S=1), is closer to survival estimates obtained in captive animals and during the third year of life of bottlenose dolphins from Shark Bay, Australia (see above).

4.4.3.4. Sub-adult survival

Although uncertainty exists around the sub-adult survival estimate during the earlier years, sub-adult survival in the population was lower than survival of calves completing their second and third years, during the most recent period. However, the low sub-adult survival estimates here obtained were pooled over a life time period of seven years. This estimate seems to be most sensitive to the very low survivorship after separation from the mother, in particular from age 4 to 7. Thus survival of the resident bottlenose dolphins from the Sado estuary seems to be higher while young animals remain in close association with their mothers (during the second and third years of life) and to decrease during the first few years after separation from the mother. This pattern is also observed in some terrestrial mammals, particularly in younger males (see Ralls et al. 1980) and does not conform to the typical "U" shape curve of mortality patterns from large mammals, where survival of young animals tends to increase as they get older

(Caughley 1966). Can this difference be explained by the current knowledge of life history and social organization of the bottlenose dolphin or can it be a consequence of the Sado estuary features and of the small size of the resident group? Both factors could account for the observed pattern.

Sub-adult bottlenose dolphins are active, inexperienced, exploratory, growing animals. After weaning, both males and females disperse (sensu Isbell and Van Vuren 1996) from their natal groups (Wells 1991) and tend to associate with other inexperienced peers (Wells et al. 1987, Wells 1991). This behaviour may also occur in other dolphin species such as the spinner dolphin (Norris 1994), the striped dolphin (Perryman and Lynn 1994), the spotted dolphin (Pryor and Shallenberger 1994), the Atlantic white sided dolphin (Seargent et al. 1980, Rogan et al. 1997) and the common dolphin (Waring et al. 1990, Silva and Sequeira 2003) for which segregated schools of young (immature) animals from both (or mainly one) sexes have been reported. During the sub-adult phase, adults may play a minor role in their instruction and protection, compared to when they were calves (Norris 1994). Because of the more frequent close contact between peers, infection from young animals' diseases can successfully develop more at this phase (Van Bressem and Van Waerebeek 1996). This may explain the higher prevalence of tattoo skin disease among Sado sub-adult resident dolphins (Van Bressem et al. in press), although only a few sub-adults composed sample size (n=5). Under these conditions, sub-adult bottlenose dolphins may be more exposed to mortality risk factors than calves during their second and third years. This may be especially the case during the first period after separation when in addition, animals have less experience (Walters 1987). In fact, survival of bottlenose dolphins seems to be particularly low at weaning (Stolen and Barlow in press) and during four years thereafter, as shown in the present study.

In addition to the above life history features of the bottlenose dolphin, natural and anthropogenic features of the Sado estuary for which extended learning may be required can enhance the risk of mortality. The turbidity of the interior estuary water and the strong tidal flux in narrow channels may constitute natural dangers. Whereas fishing gear (Noke and Odell 2002) and the high levels of boat traffic (Wells and Scott 1997) during the peak of the summer months may constitute anthropogenic threats. In addition, young inexperienced animals may be more susceptible to acoustic masking resulting from background noise due to human activities occurring in the estuary and along its margins (Ferreira et al. 1996). This in turn may adversely affect dolphin communication, and detection of faint natural sounds or echolocation signals (Richardson et al. 1995) necessary to detect anthropogenic perils, such as abandoned or active nets.

In addition to factors related to experience, the Sado estuary contains several sources of pollutants resulting from agriculture, mining, urban, industrial and shipyard sewage (Bruxelas et al. 1992). It is known that certain pollutants may accumulate in sub-adult dolphins (Jefferson et al. 2002). However, it is not clear if survival of these fast growing animals is differentially affected.

Another cause to consider for the low sub-adult survival, is the possibility of emigration of young animals, because mortality is not distinguished from permanent emigration in the CJS model. In polygynous or promiscuous large mammal species, young males usually disperse and females tend to be philopatric (Greenwood 1980, Dobson 1982, Clutton-Brock 1989, Pusey and Packer 1987, Tiedemann et al. 2000). Although the bottlenose dolphin is a promiscuous large mammal species (Wells et al.1987), evidence from resident bottlenose dolphin populations elsewhere suggests that young animals of both sexes tend to be philopatric (Connor et al. 2000). In addition, one must also consider temporary dispersal from the natal area and social group. This could also affect survival of the resident sub-adults, if they immigrated later into their natal group, as was hypothesized for the two unknown origin sub-adults first seen in 1992. Dispersing (social or locational) young animals may experience fitness costs resulting in differential survival, as is the case of some terrestrial mammals (Jarman and Jarman 1973, Dittus 1977; Isbell and Van Vuren 1996, Monard and Duncan 1996) and the sperm whale (Best 1979, Ralls et al. 1980). However, evidence does not exist for temporary emigration of sub-adult bottlenose dolphins.

Although in large long lived mammals, the sub-adult phase is long comparative to infancy, little is known about survival during this life stage in dolphins (Barlow and Boveng 1990) including the bottlenose dolphin (Connor et al. 2000). Immature dolphins comprise a large percentage of incidentally caught animals in fishing gear (Silva and Sequeira 2003). However, it is not clear if this human caused mortality shapes the species age specific survival patterns. Existing estimates of survival patterns of sub-adult bottlenose dolphins rely on information from stranded animals (Hersh et al. 1990, Stolen and Barlow in press) and younger animals may be under represented since these may be more apt to sink (Lesage and Kingsley 1998).

Small populations, such as the Sado estuary resident group, may present atypical vital rates (Lacy 1993) due to demographic variability such as a biased sex ratio. Furthermore, sample size was small, especially among the oldest sub-adult animals due to the very small number of known age resident sub-adult dolphins that reached maturity. There is some evidence that in delphinid populations, the ratio of males to females appears to decline with age (Perrin and Reilly 1984). In the bottlenose dolphins from Indian River Lagoon, sub-adult males have lower survival than females (Stolen and Barlow in press). If differential mortality among sexes occurs during the sub-adult phase, as is also the case in other mammalian species (see above), the sex ratio of this small population could also affect the estimates of sub-adult survival.

Although several factors can account for the lower survival of young animals after weaning, the uniqueness of the Sado bottlenose dolphin population may mean that patterns here observed may have no parallel. On-going similar long term studies based on individual identification should investigate the pattern of sub-adult survival.

4.4.4. Time related changes in survival patterns

Time related changes in survival were greatest for calves. Survival of young animals is more sensitive to changes in the environment (Clutton-Brock et al. 1987, Gaillard et al. 1993, Sæther 1997, Ragen and Lavigne 1999, Hall et al. 2001) due to their higher growth rates (Read et al. 1993). Maternal body condition can also affect their survival by the amount of energy (Clutton-Brock et al. 1987, Monson et al. 2000), pollutant loads (Cockcroft et al. 1989b) and immune profile (Hall et al. 2002) they receive from the mother through lactation. Further, young dolphins have little experience which makes them more exposed to risks in their environment. This can also be affected by maternal body condition through the amount of maternal social and physiological care received that is necessary for its development (Monson et al. 2000) and for learning skills. In this study the highest changes in survival were from calves during their second and third years.

The observed time related changes in survival may be due to changes in the environment triggered by density dependent and density independent factors. These can operate through a common effect on the resource availability (Sæther 1997) or through other mechanisms. Density independent factors such as anthropogenic activities (e.g.

accidental catches) (Read 1996) may also operate directly on survival or indirectly, at the individual toxicity level (e.g. pollutants) (Aguilar and Raga 1993).

Which factors occurring in the Sado estuary could have accounted for the observed time related changes in survival, in particular, that of young animals? Climatic changes in the marine environment may have a quick impact on food availability (Ragen and Lavigne 1999). However, little information exists on time related changes in resource availability. Another aspect to consider is changes in pollutant levels, although these may have a slower effect due to the need of bioaccumulation through the food chain (Reijnders 1988). Pollutant discharges from the industrial complex along the estuary North margin were particularly important during its early development, in the 1970s but their diffuse origin and the lack of systematic records mask evidence of any trend. As a consequence, carrying capacity may have been reached before this study had begun, when anecdotical evidence suggests that population size was higher (n=50, M.E. dos Santos, personal communication). Although no long term records of fish captures within the estuary exist, fishing activity could have also contributed to a lower survival during the earlier years through a decrease of food resources in the estuary which could force dolphins to emigrate from the estuary region or by causing dolphin mortality due to entanglement.

In conclusion, the cause(s) for the observed time related changes in survival are not clear and as a result it is not possible to relate causes with particular change point years suggested by the models.

4.4.5. Final considerations

Population growth in large mammals is more sensitive to adult survival (Brault and Caswell 1993, Heppell et al. 2000). In small populations however, saving the life of any animal may have an important impact on population growth rate (Fujiwara and Caswell 2001, Sanders-Reed et al. submitted). In this particular population, survival of young animals may have a critical role in the viability of this small resident group of dolphins. To investigate the effect of the reported lack of recruitment to the adult age on the viability of this population, several population models will be addressed in chapter 5 in the context of a population viability analysis.

Year-round coastal resident populations of dolphins constitute ideal opportunities to develop longitudinal studies based on individual identification since animals spend most of their lives in a definable area close to shore. Long-term data sets such as this, where nearly every individual is seen every year, are unusual. The build-up of such data set, particularly in such a small resident group, will permit the impact of survival and reproductive rates on population dynamics of small populations to be monitored and also allow the effect of management strategies to be assessed. Further, it will permit hypothesis related to the life history and social organization of dolphins to be tested.

CHAPTER 5. VIABILITY OF A SMALL POPULATION OF BOTTLENOSE DOLPHINS

As found in previous chapters the Sado resident group of bottlenose dolphins has a very small population size, an unstable age structure and a changeable past population dynamic. What plausible perspectives can we predict for its future?

5.1. INTRODUCTION

The characteristics of the Sado resident population of bottlenose dolphins and the questions concerning its conservation are typical of the issues dealt within the field of conservation biology which deals with small populations and endangered species in the wild and in captivity (Orians and Soulé 2001). Small populations are more likely to go extinct than large populations (Gilpin and Soulé 1986). They can easily move towards extinction due to natural variation in individual reproductive and survival rates (demographic stochasticity) and their greater vulnerability to genetic problems (inbreeding and genetic drift) and natural and anthropogenic caused fluctuations in the environment (environmental stochasticity) (Keller and Waller 2002).

Quantitative analysis of extinction risk is necessary to define population status and is one of the criteria for risk categorization used by the International Union of Conservation of Nature (IUCN 1994). This issue may also be of interest in the management of Special Areas for Conservation for a particular classified species under the European Union Habitats 2000 Directive.

Population viability analysis (PVA) is a controversial tool (Brook et al. 2000, Coulson et al. 2001, Beissinger 2002) that uses quantitative methods to estimate future size and risk of extinction of populations of animals and plants (Morris and Doak 2002). Several approaches can be used to assess the future status of populations of conservation concern.

Endangered species are rare and in most cases demographic information is poor. In the absence of such information, long term studies from similar species can portray useful demographic patterns. For example, Heppell et al. (2000) used data from 44 mammal species in order to classify the elasticity of mammalian life history traits. As mentioned in chapter 4, population dynamics of mammals that mature late and have few offspring are more sensitive to changes in adult survival and also in sub-adult survival but less sensitive to changes in fertility. In contrast, mammals that mature early and have a short lifespan, have relatively high fertility elasticities and lower adult survival elasticities. Information such as this may provide a guide to research and management of poorly known species. These can be incorporated in decision trees complementing expert subjective knowledge (Begon et al. 1996).

When enough demographic data are available, models can be developed that encapsulate these life history parameters or simply counts, in age or stage structured populations. Population projections based on matrix models have been widely used (Heppell et al. 1996, Brault and Caswell 1993, Fujiwara and Caswell 2001). These simple models cannot consider random processes that affect very small populations (Lacy et al. 1995) but this can be avoided by setting the extinction threshold at a high enough level (Morris and Doak 2002). Alternatively, simulation models that implicitly deal with the interacting deterministic and stochastic events that affect persistence of the population can be used (Gilpin and Soulé 1986).

Demographic stochasticity is simulated by performing a Monte Carlo alogorithm, in which the fate of each individual is decided by a set of independent random choices, based on the distribution of the mean of vital rates (Morris and Doak 2002). Environmental stochasticity is modelled from additional variance around mean vital rates. Computer software to simulate population viability such as ALEX, GAPPS, INMAT, the RAMAS series and VORTEX is readily available (Brook et al.1999).

All of these models can include density dependence by making the vital rates respond to a certain level of population size specified. This effect is not likely to happen in very small populations, but it can be used to simulate food or habitat shortage. Simulation programs can offer other scenarios such as the effect of catastrophic events (GAPS, RAMAS and VORTEX), supplementation and harvesting (VORTEX). Some PVA software incorporates the interaction between genetic and demographic effects (GAPS, INMAT and VORTEX), although much debate exists on how to model these effects (Beissinger 2002, Keller and Waller 2002). Additional complexity of the models can be achieved by incorporating the dispersion of animals through the landscape using spatially structured population models. Spatially explicit models (ALEX) require a large number of parameters to be estimated, this can rarely be achieved in endangered species (Lindenmayer and Possingham 1996).

Population viability analysis can be used in two main issues of conservation concern: assessment of extinction risk and guiding management (Lindenmayer and Possingham 1996). A classic example covering both concepts is the population of grizzly bears living in the area of the Yellowstone National Park. Shaffer and Samson (1985) used a simulation model to ask whether that bear population was large enough to have at least 95% chance of surviving for different specified times. Their findings suggested that a larger protected area would be necessary to guarantee that level of extinction avoidance in the long term. Another well known example is from the loggerhead sea turtle (*Caretta caretta*), a species threatened by the trampling of eggs and hatchlings and by the drowning of older turtles. Deterministic models from Crouse et al. (1987) and Crowder et al. (1994) identified the key life stage as being the survival of the older animals and not that of the hatchings. Their models were able to provide a quantitative projection of the population growth under different scenarios and concluded that installing turtle excluder devices in shrimp nets would be more efficient than protection of the early stages.

Population viability analysis has been also used for marine mammal species. Examples are the simulation model of the Florida manatee (Marmontel et al. 1997) which identified changes in adult mortality as being a key vital rate. This scientific finding will be very useful in supporting unpopular management polices to reduce manatee mortality and protection of its habitat such as reduction of boating activity, speed and zoning of manatee occupied areas. Population viability analysis in the small and isolated population of bottlenose dolphins from the Moray Firth, Scotland, show how PVA can be influential to stake holders so that precautionary management actions are put in place (Thompson et al. 2000, Sanders-Reed et al. submitted).

Matrix models were used to examine the causes of the more recent decline of the small population of the North Atlantic right whale and showed that management action which prevented the death of two females a year would result in a population growth rate that was close to replacement level (Fujiwara and Caswell 2001). The long term data from the eastern North Pacific grey whale (*Eschrichtius robustus*) was analysed in a retrospective way to estimate the amount of monitoring years needed to support the decision of delisting the species from the U.S. endangered species act (Gerber et al. 1998). Brault and Caswell (1993) examined the effect of social structure of killer whales in pod specific demography using matrix models. They concluded that there is no evidence that older, post reproductive females enhance the fitness of their pod members and thus pod specific population growth rate. A theoretical application of a PVA was done with data from Steller Sea Lion (*Eumetopias jubatus*) showing how extinction probabilities can be influenced by how accurately the models portray population dynamics and how accurately parameters are estimated (Taylor 1995).

Although PVA can have an easy and wide application in conservation biology (Brook et al. 2000, Ellner et al. 2002) caveats about its predictive accuracy must be taken into account (Coulson et al. 2001, McCarthy et al. 2001). Predictions will only be useful if the distributions of growth rate and vital rates will not change in the future (Coulson et al. 2001, Fieberg and Ellner 2000). Further, as mentioned above, predictive accuracy is influenced by the accuracy in parameter estimates and how the model adjusts to the life history of the species (Taylor 1995). Precision of risk estimates decreases with the time length being projected. Thus PVAs should be used in a relative rather than in an absolute perspective (Beissinger and Westphal 1998) and projections should only be made over the appropriate time length of data (Fieber and Ellner 2000). Population viability analysis works in a “what if?” scenario and does not reveal what causes underlie the imperilment of small populations. Although simpler models are usually most appropriate (Fieber and Ellner 2000), forecasts predicted by this methodology are restricted to the factors that were incorporated in the model. However, ecological systems are complex and dynamic. For this reason, PVAs need be adaptative (Coulson et al. 2001, Beissinger 2002). Finally, testing the reliability of PVA’s extinction prediction would require comparison with the distribution of the fate of many replicate populations (Lacy et al. 1995). Although this is a situation most likely to occur in the laboratory rather in the wild, testing its secondary predictions may be a useful approach to evaluate its reliability (Beissinger 2002).

In this chapter a population viability analysis is used to predict the future status of the Sado resident group and to identify the life history parameters to which the model is most sensitive.

5.2. METHODS

5.2.1. Past growth rate

In order to compare the population's historic growth rate (see chapter 4) with the predictions from the simulations described in the next sections, an instantaneous annual growth rate (r) was calculated as:

$$r = \ln\left(\frac{N_{t+1}}{N_t}\right)$$

where, N_t is the observed population size at year t.

5.2.2. Population viability analysis

Population viability analysis of the resident group of bottlenose dolphins from the Sado estuary was conducted using the simulation program VORTEX version 8.41[2] (Lacy 1993, Lacy et al. 1995). VORTEX was chosen because it is a widely used age specific simulation model designated for long-lived species with low fecundity (Lacy et al. 1993), such as marine mammals (Marmontel et al. 1997) including the bottlenose dolphin (Sanders-Reed et al. submitted).

This program is based on a Monte Carlo simulation of the effects of deterministic and stochastic factors (demographic, environmental and genetic) on populations. In the present work genetic factors were not considered. VORTEX simulates variability in life history events on an annual basis using a pseudo-random generator. Annual fluctuations in probabilities of demographic factors (such as reproduction, survival and sex ratio) are modelled as binomial distributions whereas environmental variation and carrying

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[2] Available from http://pw1.netcom.com/~rlacy/vortex.html

capacity are modelled as normal distributions. Each simulation was replicated 1000 times in order to ensure statistical reliability. Internal consistency of the program was conducted by comparing deterministic with stochastic results.

5.2.2.1. Model structures

Two model structures were created. These share the same general input parameters as described in the following section, except in relation to vital rates. Differences in their structure refer to how adult mortality is modelled. In the first and simpler model, adult mortality is constant. In the second model, an age specific adult mortality function was entered in order to reflect a more realistic adult mortality age specific pattern for a bottlenose dolphin. In long lived species, including cetaceans, adult survival (Caughley 1966, Barlow and Boveng 1991) is known to be initially relatively constant and then to decline, especially after mid adult life. There is little information about age specific adult survival in the bottlenose dolphin (Small and De Master 1995, Sanders-Reed et al. submitted, Stolen and Barlow in press). The most complete information refers to bottlenose dolphins from Indian River Lagoon (Stolen and Barlow in press). However their survival rates are lower than those observed in the Sado resident group (see chapter 4), particularly during the adult stage. As a result, longevity of those bottlenose dolphins is shorter (35 years) than that of individuals from the Sado estuary. Information about adult age specific survival does not exist for many other cetacean species; exceptions are the common dolphin (Fifas et al. 1998), the beluga whale (Lesage and Kingsley 1998), the killer whale (Olesiuk et al. 1990) and the long finned pilot whale from the Faroe Islands (Bloch and Lockyer 1993). However, existing information is not built from real data, except in the last two examples. Killer whales have particularly high survival rates and thus a longer longevity than the bottlenose dolphin, whose maximum longevity is about 50 years (see below). Because long finned pilot whales are known to live for about 50 years, the adult age specific mortality pattern from the more realistic model was based on existing data on adult age specific survival for this species. The resulting function that approximates the age-specific adult mortality for long-finned pilot whales has a constant mortality until age 30 and a linear rate of increase of 0.01793 per year thereafter.

Besides this difference in the complexity of the two model structures, they also differ in respect to the data used to estimate survival and fecundity rates. In the simple model, the most recent estimates of fecundity and survival rates were used. In the more realistic model, average estimates of fecundity and survival over the maximum available time length of study period were used. However, in this model, the most recent estimates of first year survival and not the long term average were used since the estimate obtained during the earlier years of the study is certainly biased upwards (see chapter 4). The long term average values of vital rates incorporate the long term behaviour of the population whereas the most recent values are more likely to describe the current situation. Because current values of vital rates are higher (see chapter 4), the more realistic model will generate a more pessimistic scenario. For this reason the simpler model was named the "current" model and the more realistic model, the "pessimistic" model. In addition to these two models, the most optimistic scenario for the population was created by running a model in which the maximum values of the vital rates were introduced. This is the "optimistic" model. Altogether, these models were chosen to bound the future viability of the population. A model with the lowest values of the estimates of vital rates was not used because these refer to the earlier years, when uncertainty about the data existed.

For the age specific mortality relationship, mid adult life survival was adjusted to 0.988 (maintaining the slope in the increase in mortality after mid-life obtained from the pilot whale data) so that the population growth rate was the same as for the constant mortality model. The same adult age specific mortality schedule could not be used in the "current" model nor in the "optimistic" model without changing the slope of the increase in mortality, due to the very high values of adult survival.

5.2.2.2 Inputs to VORTEX

The following choices and parameter values were used:

5.2.2.2.1. Number years simulation to run

In order to examine population behaviour over the short and the long term, simulations were run over several decades, with results examined each decade.

5.2.2.2.2. Extinction definition

Extinction was defined as no animals or only animals of one sex.

5.2.2.2.3. Inbreeding depression

Data on the inbreeding level of this very small population are not available and for this reason the effect of genetic factors on the viability of the resident group was not considered.

5.2.2.2.4. Type of breeding

The promiscuous mating system was chosen since in the bottlenose dolphin, females can mate with several males (Wells et al. 1987, Connor et al. 1996).

5.2.2.2.5. Longevity and maximum breeding age

Reproductive senescence does not seem to exist in the bottlenose dolphin (Cockcroft and Ross 1989; Marsh and Kasuya 1986) suggesting that in this species, maximum breeding age corresponds to maximum longevity which varies between age 35 and over 50 years (Cockcroft and Ross 1989, Hohn et al. 1989, Fernandez and Hohn 1998, Kasuya et al. 1997, Wells and Scott 1990), Stolen and Barlow in press). A maximum value of longevity and thus breeding age was chosen as 50 years. Although there is indication that female bottlenose dolphins live longer than males (Stolen and Barlow in press), longevity is constrained to be the same in both sexes in VORTEX.

5.2.2.2.6. Gestation length and litter size

Bottlenose dolphins give birth to a single calf (Connor et al. 2000) after a twelve-month gestation period (Perrin and Reilly 1984, Schroeder 1990).

5.2.2.2.7. Age at first offspring

Female bottlenose dolphins attain sexual maturity between 5 and 12 years old (Perrin and Reilly, 1984, Cockcroft and Ross 1989, Read et al. 1993). Males attain sexual maturity two or three years later, between 8 and 14 years old (Perrin and Reilly, 1984, Cockcroft and Ross 1989, Wells et al. 1987, Kasuya et al. 1997, Connor et al. 2000). A modal age from the range recorded in the literature was chosen as the age at sexual maturity, being 10 years for females (see chapter 2) and 12 years for males. Female and male age at first offspring entered were 11 and 13 years old, respectively.

5.2.2.2.8.. Sex ratio at birth

The sex ratio in juveniles seems to be biased towards males (Perrin and Reilly 1984); but no information is available on sex ratio at birth. A 1:1 sex ratio was entered.

5.2.2.2.9. Age (and sex) distribution

Age structure was based on the composition of the resident population alive at the end of 2002, when the population size was 30. Because VORTEX simulates life history events on an annual basis and starts the simulation before the breeding season, only animals aged one or more years old were considered in the starting population.

The age of individually identified animals is only known from year one to thirteen which includes calves (n=4, from age one to three), sub-adults (n=4, from age four to age seven) and young adults (n=2, age thirteen). The remaining adults (n=20), were assumed to be 26 or more years old because of the lack of recruitment to the adult stage during the study period (see chapter 2). As there is no indication of the range of ages of these older adults, their age distribution was based on a stable age structure predicted by the deterministic model presented in VORTEX output (see below). Note the gap existing between sub-adults and young adults and especially from these and older adults. As reported in previous chapters (chapters 2 and 4), these reflect the lack of recruitment to the adult stage. For this reason, the initial population does not have a stable age structure.

The sex of all calves and sub-adults and many (55%) adults is unknown. For young animals, the sex ratio was defined as 1:1 by alternating arbitrarily chosen individuals as males or females along the existing age range (one to seven years old). Similarly, adult sex ratio was also chosen to be 1:1. Individual adults were identified to be females or males, according to field observations and photographic records, as defined in chapter 2. For those adults whose sex was unknown, assumptions were made based on the frequency that animals were seen in close proximity of calves whose mothers a) were not identified during the time length the calf was alive or b) were identified to be another animal. An individual adult was assumed to be a male if it was seen only rarely with a calf. If it was frequently seen with a calf, it was categorized as a female. The resulting adult sex ratio was 11 males and 11 females. If the contrary of this last assumption was made, sex ratio would be 14 males and 8 females. The previous assumption was chosen because as described in chapter 2, there is indication in the literature that the adult sex ratio in the bottlenose dolphin is parity or skewed towards females (Perrin and Reilly 1984, Hohn et al. 1989, Wells and Scott 1990, Fernandez and Hohn 1998, Stolen and Barlow in press).

5.2.2.2.10. Carrying capacity

The maximum population size (n=50) recorded in the Sado estuary based on visual counts (M. E. dos Santos, personal communication), was used as the maximum carrying capacity. Although population size has declined 15% since 1986 (see chapter 2), no trend in carrying capacity was chosen because the underlying causes of such a reduction in numbers are unknown.

5.2.2.2.11. Density dependence in reproduction

Reproduction was chosen not to be density dependent since no evidence exists showing this effect.

5.2.2.2.12. Fecundity and annual percent of males in the breeding pool

Age specific patterns in fecundity are characteristic of long lived mammalian species (Packer et al. 1998). However, evidence of such patterns in the bottlenose dolphin is unclear (Kasuya et al. 1997, Marsh and Kasuya 1986) and some information is based in a small sample size (Kasuya et al. 1997). For this reason, fecundity was modelled as constant. VORTEX assumes equal probability of breeding of all animals of reproductive age. Fecundity was calculated by dividing the number of births by the number of females pooled over different combinations of years. Sex ratio was based on the assumption that dubious sex adult animals were females. Values entered in the "current", "pessimistic" and "optimistic" models are presented in Table 5.1. Information is not available on annual percentage of breeding males and for this reason, all males were assumed to be in the breeding pool.

5.2.2.2.13. Annual mortality

Age specific annual mortality rate was based on stage specific survival probability estimates obtained with the Cormack-Jolly-Seber mark-recapture model as estimated by program MARK in chapter 4. Although sex differences in survival have been reported for the bottlenose dolphin (Kasuya et al. 1997, Stolen and Barlow in press), estimates obtained here were not sex specific and for this reason male and female mortality rates were assumed to be the same. The probability of survival was not density dependent.

Table 5.1. Input values of fecundity and survival estimates to the "current", "pessimistic" and "optimistic" models.

Model	Value
"Current" model	
mortality during the 1st year (1994-2001)	16.67%
mortality during the 2^{nd} and 3^{rd} years (1994-2001)	0%
mortality of sub adults (1993-2001)	13.04%
mortality of adults (1999-2001)	1.45%
fecundity (1997-2002)	18.75%
"Pessimistic" model	
mortality during the 1st year (1994-2001)	16.67%
mortality during the 2^{nd} and 3^{rd} years (1984-2001)	12.82%
mortality of sub adults (1984-2001)	17.01%
mortality of adults (1986-2001)	1.243% + [(A>30)*(A-30)*(1.793%)]
fecundity (1992-2002)	14.52%
"Optimistic" model	
mortality during the 1st year (1994-2001)	16.67%
mortality during the 2^{nd} and 3^{rd} years (1984-2001)	0%
mortality of sub adults (1984-2001)	13.04%
mortality of adults (1986-2001)	0.53%
fecundity (1998-2002)	22.22%

However, if population size is higher than carrying capacity, additional mortality is generated by VORTEX affecting all age classes and sexes equally. Values entered in the "current", "pessimistic" and in the "optimistic" models are also presented in Table 5.1.

5.2.2.2.14. Environmentally caused variation

Following Lacy et al. (1995), environmentally caused variation (EV) associated with demographic estimates (fecundity and survival) was calculated by subtracting the mean theoretical binomial variance from the observed inter year variance, assuming that data refer not to a sample but to the population because all animals have been observed. EV in reproduction was chosen not to be correlated with EV in mortality since such variation around the percentage of females that breed was not detected. No available information exists concerning environmentally caused variation in carrying capacity and for this reason no additional variation was entered.

5.2.2.2.15. Harvest and supplementation

Harvest and supplementation were not considered in most of the models.

5.2.2.3. Output parameters

In order to describe the simulated fate of the populations under each scenario three outputs from VORTEX are considered below: mean population size (N), the stochastic mean population growth rate (r) and probability of extinction (PE). Mean population size is the arithmetic mean of the total population size, averaged across all iteration years and refers to all populations (extinct and extant). If population size exceeds the carrying capacity (K) in a particular year, additional mortality is imposed in all age classes. Stochastic population growth rate was obtained as:

$$r = ln\left(\frac{N_{t+1}}{N_t}\right)$$

in which N_{t+1} is the size at year t+1, before any reduction that is needed to keep the population below carrying capacity (K). The mean population growth rate is the arithmetic mean of r, across iterations and across all years. Probability of extinction is calculated from the number of simulations that became extinct from a total of 1000. Standard Errors of these estimates were taken as the Standard Deviations of the 1000 replicate estimates.

VORTEX also provides the deterministic value of population growth rate (r_d) which was used for comparison with stochastic mean population growth rate (r). The deterministic growth rate may provide an accurate long term average if stochastic variation is minimal (Lacy et al. 1995)

5.2.2.4. Sensitivity analysis

A sensitivity analysis was conducted to measure how sensitive mean population growth rate is to changes in vital rates and other parameters for which data were not collected. This analysis was based on the "current" model because of its simpler structure. Two sensitivity indices were used: sensitivity and elasticity. Sensitivity (S_x) of stochastic mean population growth rate (λ) to changes in a particular vital rate or other parameter (X) was calculated as the slope of the tangent line describing the population growth rate as a function of the parameter (Morris and Doak 2002):

$$S_x = \frac{\lambda_{new} - \lambda_{current}}{X_{new} - X_{current}} = \frac{\Delta\lambda}{\Delta X}$$

where stochastic mean growth rate is presented as lambda (λ) which results from the transformation of r as follows:

$$\lambda = e^r$$

The new value of the parameter was obtained by changing by a certain amount the current value of a vital rate or the default value of a parameter for which data were not available. The new value of mean population growth rate was then obtained by the simulation of the "current" model using the changed value of the parameter.

Elasticity measures the proportional change in the current mean population growth rate ($\delta\lambda_{current} / \lambda_{current}$) resulting from a proportional change in the current parameter of interest ($\delta X_{current} / X_{current}$) (De Kroon et al. 1986, Morris and Doak 2002)

$$E_x = \frac{X_{current}}{\lambda_{current}} \frac{\delta\lambda_{current}}{\delta X_{current}} = \frac{\delta\lambda_{current} / \lambda_{current}}{\delta X_{current} / X_{current}}$$

Elasticity is the standard way to recalibrate sensitivity analysis to account for differences in the scale of measurement of different parameters. However, comparisons based in elasticity values will always have the tendency to identify vital rates with higher means as being the most important. This is because the elasticity of a parameter is its sensitivity value ($\delta\lambda_{current} / \delta X_{current}$) times its current value (and divided by the current population growth) (Morris and Doak 2002). Sensitivity is not affected by this problem and for this reason both measures are reported. The present sensitivity analysis was based on survival estimates and not on mortality rates because the first is the scale that has more biological meaning.

To get accurate sensitivity (and elasticity) values using the above method, the estimate of λ values should be precise (Morris and Doak 2002) and ΔX should be small (less than 5%) (Crowder et al. 1994, Heppell et al. 1996, Mills et al. 1999). To meet the first condition, the default number of replicate simulations (n=1000) seems to be enough to guarantee statistical reliability. As to the second condition, sensitivity analysis was based in a -1% change of vital rates (fecundity and survival) and in other parameters for which data were not available (longevity, female and male age at first reproduction, sex ratio at birth and carrying capacity). However, in most of these parameters, the minimum change possible was higher than 5%. Results from this small change sensitivity analysis should indicate to which vital rates and other parameters mean population growth rate is more sensitive and thus for which parameters uncertainty is most likely to effect the PVA results.

Elasticity and sensitivity values assume a linear relationship between the change in the vital rate and the change in population growth rate. However, this linearity is only guaranteed for small changes. Because maximum and minimum observed values of vital rates may cover a wide range of values, their ability to change population growth rate may not be accounted for by the small change sensitivity analysis. For this reason, a second sensitivity analysis was conducted incorporating the largest changes observed in those vital rates for which the sensitivity indices were the highest in the previous analysis. This large change sensitivity analysis was also extended to probability of extinction.

5.2.2.5. Additional scenarios

Three additional scenarios were created based on the "current" model. A model was created in which the starting population had a stable age structure. The comparison of the results from this scenario with those from the "current" model aimed to quantify the effect of the lack of recruitment in the present age structure on the future viability of the population. Secondly, the effect of regular immigration of sub-adult animals into the population was also modelled. This scenario was created to cover the possibility exposed in chapters 2 and 4 about the origin of the two sub-adults first seen in 1992. Two sub-adults, one male and one female, with mid sub-adult age (7 years old), were added every 16 years to the resident group using the supplementation function of the program. The conditions of this supplementation aimed to mimic the past possible observed sub-adult immigration.

The third scenario aimed to quantify the effect of a decrease in current adult survival resulting from the hypothetical loss of the adult male LUA during the live stranding in 1999 (see chapters 1, 4 and cover image). PVA results from the "current" model were compared with those resulting from a model in which adult survival (1999-2001) was 0.9706 (mortality = 2.94%). Fecundity was not changed because this adult is a male and thus the number of females would remain the same.

5.3. RESULTS

5.3.1. Past growth rate

Figure 5.1 presents the instantaneous growth rate of the Sado resident group of bottlenose dolphins observed each year from 1986 to 2002. The fluctuating pattern resulting from the plot of the original data was smoothed by a three year moving average. Growth rates were negative during the earlier years and positive mainly since the late nineties. As a result, population growth rate decreased during the early nineties (until around 1993), and has been increasing since then. This result is expected since growth rate is calculated from the annual number of animals. As shown in chapter 4, population size declined mainly during the mid-earlier years and seems to be increasing after 1997. Maximum and minimum average growth rates were 2% and -5%, respectively.

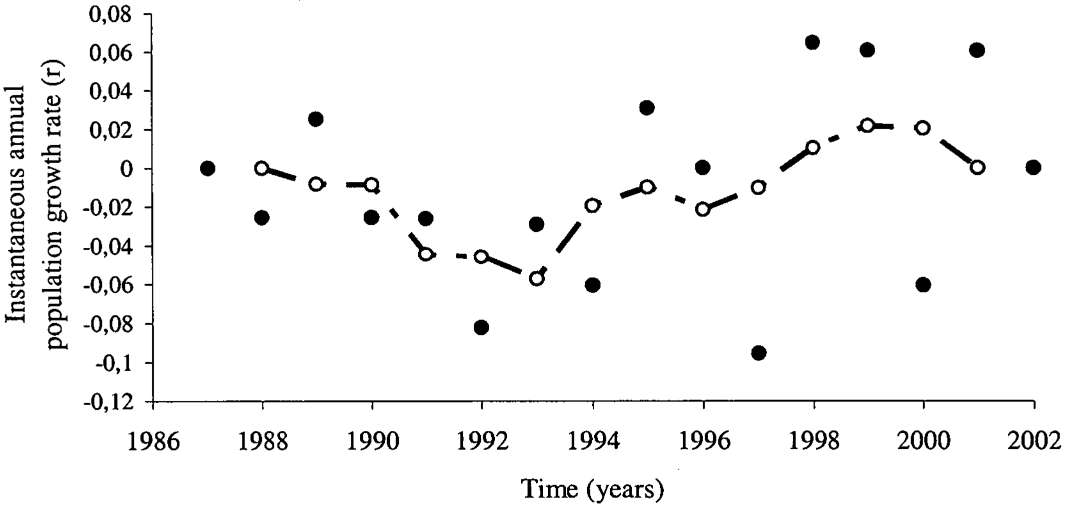

Figure 5.1. Instantaneous annual population growth rate. Original data (●) and three year moving average (—o — —).

5.3.2. PVA incorporating current values of vital rates

Results from the simulation of the simplest model using the current values of vital rates over 200 years are shown in Figure 5.2. Mean population size is predicted to decline (Fig. 5.2 A). As a result, mean annual growth rate (Fig. 5.2 B) is negative and probability of extinction increases over time (Fig. 5.2 C). The decrease in population size is more evident during the next 30 years (33%), in particular during the second decade, as a result of the unstable age structure of the starting population. This results in a decrease (50%) in mean population growth rate during that time period (Fig. 5.2 B). Mean growth rate then increases over the next 50 years, stabilizing at an annual rate of -0,9% in aproximately 80 years. By the end of the simulation period, population size is very small (n≈10-15 animals) but does not become extinct (Fig. 5.2 A).

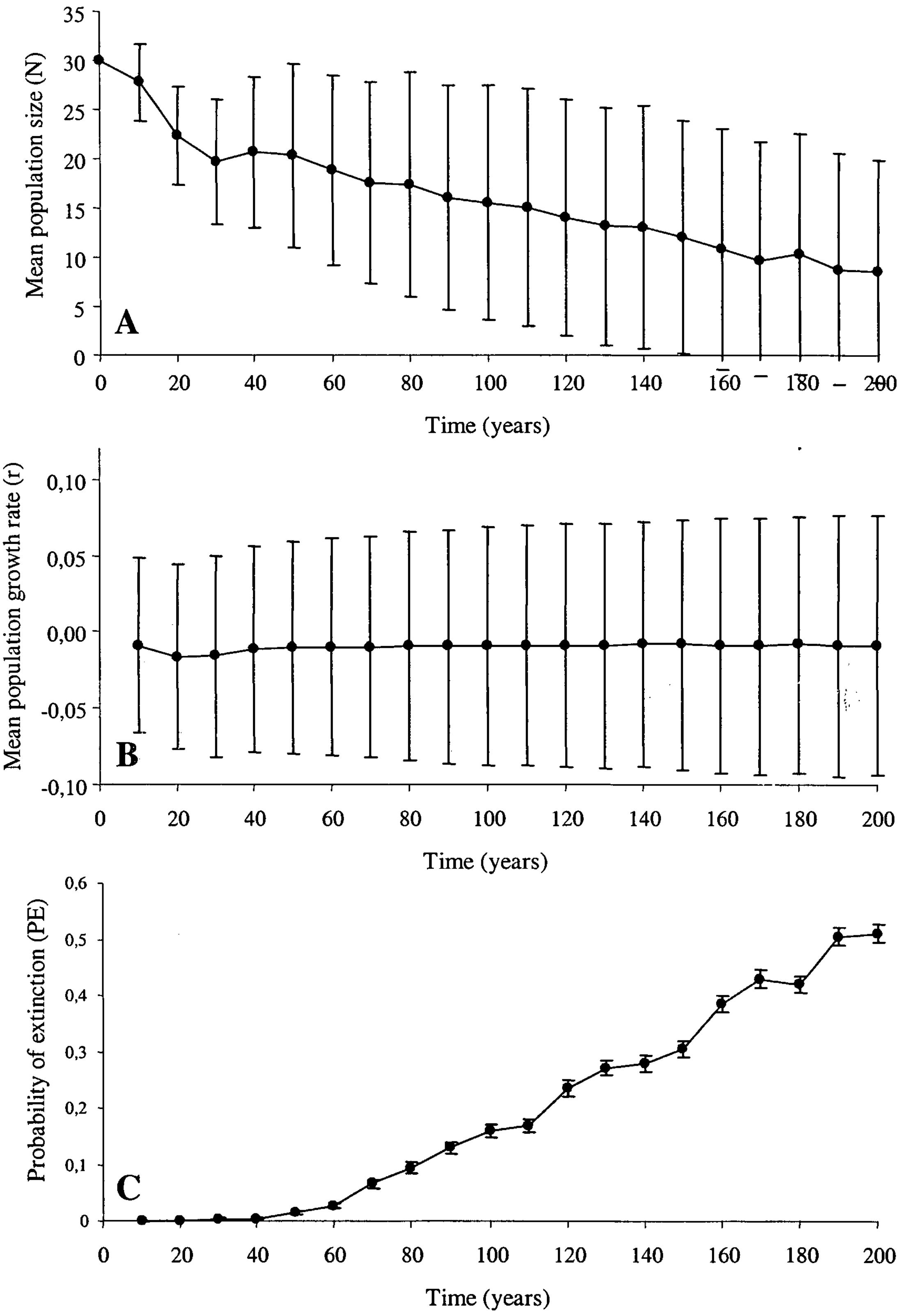

Figure 5.2. PVA predictions for the "current" model (error bars are plus/minus one standard error). **A** -Mean population size; **B** - Mean population growth rate; **C** - Probability of extinction.

Maximum probability of extinction is around 50% within 200 years (Fig.5.2 C). Deterministic growth rate (r_d = -0.004) and the long term stochastic mean population growth rate (r= -0.009) are close to zero. This is consistent with the predicted long term stabilization of the population. Stochastic growth rate is less negative due to demographic randomness caused by the very small population size.

Because of these changes driving mean population growth rate, the following analysis takes into consideration three different time scales: a) a phase during the next 20 years representing the short term behaviour of the resident group, marked by a decreasing growth rate, b) a middle phase up to 40 years incorporating the increase in growth rate and, c) a long term phase, over 120 years, when mean population growth rate will have stabilized.

5.3.3. PVA incorporating long term average values of vital rates and age specific adult mortality

Results from PVA incorporating average values of vital rates over the maximum period of time for which data are available, predicts a pessimistic scenario for the Sado resident group of bottlenose dolphins (Figs. 5.3). According to this model, the resident group will have a sharp decline in number of animals (Fig. 5.3 A), resulting in high negative growth rates (-9.3% to -5.3% a year) (Fig.5.3 B) and consequently, it will become extinct within the next 80 years (Fig. 5.3 C). It is worth pointing out that mean population growth rates predicted by the "pessimistic" scenario are within the lower values observed in the past. Although the SE around mean values of predicted growth rate from these two models overlap, the same is not true for mean population size and probability of extinction. This "pessimistic" scenario is partly due to the lower average value of vital rates compared to the current values. In addition, by incorporating an age

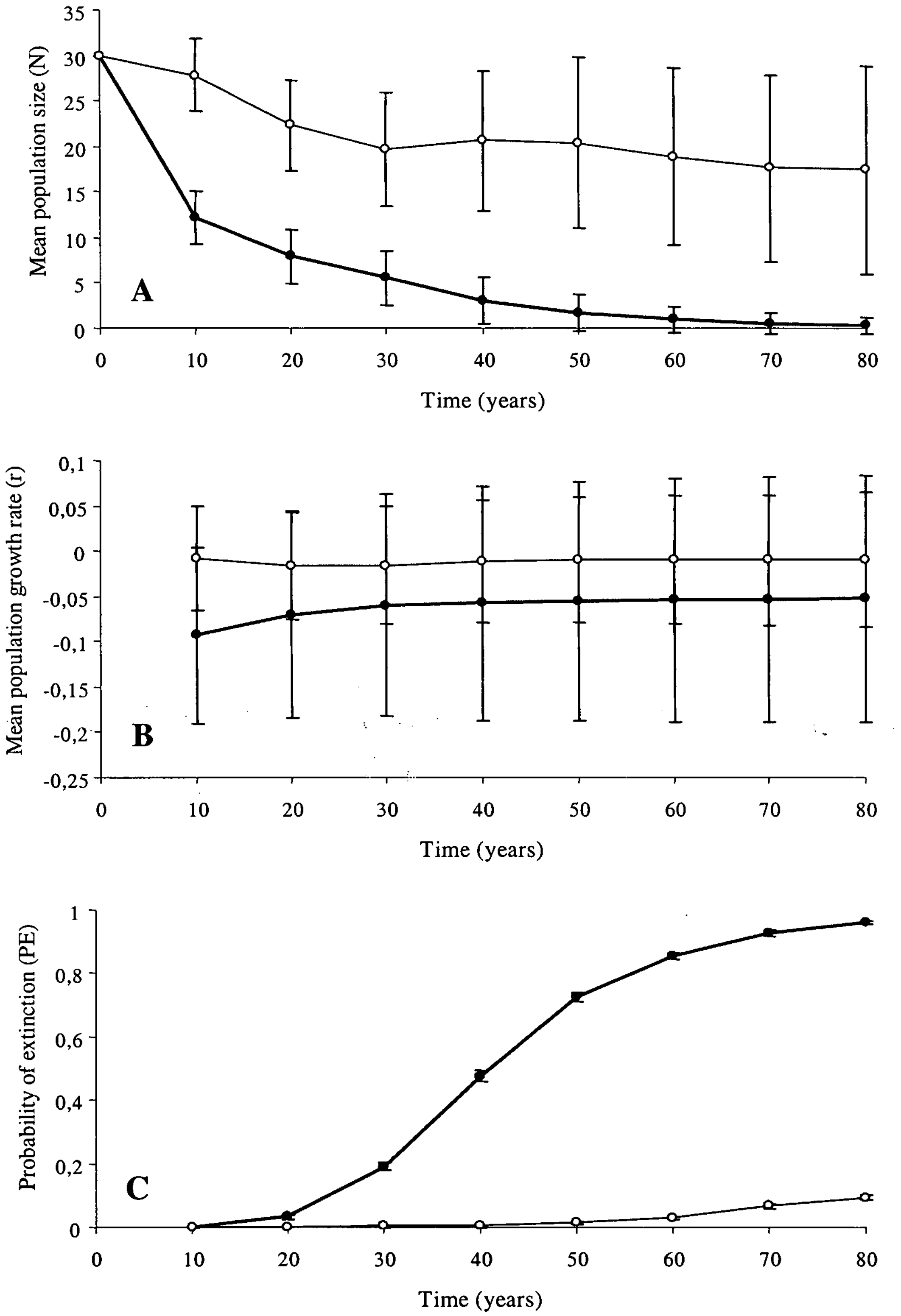

Figure 5.3. PVA predictions for the "pessimistic" model (●) (error bars are plus/minus one standard error), and that of the "current model" (○); **A** -Mean population size; **B** - Mean population growth rate; **C** - Probability of extinction.

specific adult mortality function, the loss of adults older than 30 years (mid adult life) is higher. As a result, the decrease in population size is initially more rapid due to the unstable age structure of the starting population (Fig. 5.3 A). This explains the difference in the initial pattern of the predicted mean population growth rate (Fig. 5.3 B) between the "current" and "pessimistic" scenarios. Demographic stochasticity due to the very small population size in the long term, when population growth has stabilized, may account for the higher growth rate given by the deterministic model ($r_d = -0.031$) compared with the long term stochastic growth rate ($r \approx -0.05$).

5.3.4. PVA incorporating maximum values of vital rates

As expected, results from PVA incorporating the maximum values of vital rates observed over the study period ("optimistic" model), predicted the most optimistic scenario over the simulated long term period (120 years) (Fig. 5.4). After the effect of the unstable age structure has passed, population size is predicted to increase above the current level (Fig. 5.4 A). Mean population growth rate predicted by this model has the same shape as predicted by previous models. After stabilization, the growth rate levels out at positive values around 0.004 (Fig. 5.4 B). This value is close to the deterministic mean population growth rate ($r_d = 0.008$) and to the highest past values of annual growth rates. The probability of extinction is very low (Fig. 5.4 C). The population projection given by the "optimistic" model is however more similar to the projection predicted by the "current" model than to the "pessimistic" model. This is shown by the higher level of overlap of the SE around mean population size and growth rate given by these two models which is caused by their similarity in the input vital rates. Overall, predictions made by these three models ("current", "pessimistic" and "optimistic") should encompass the future viability of the Sado resident group.

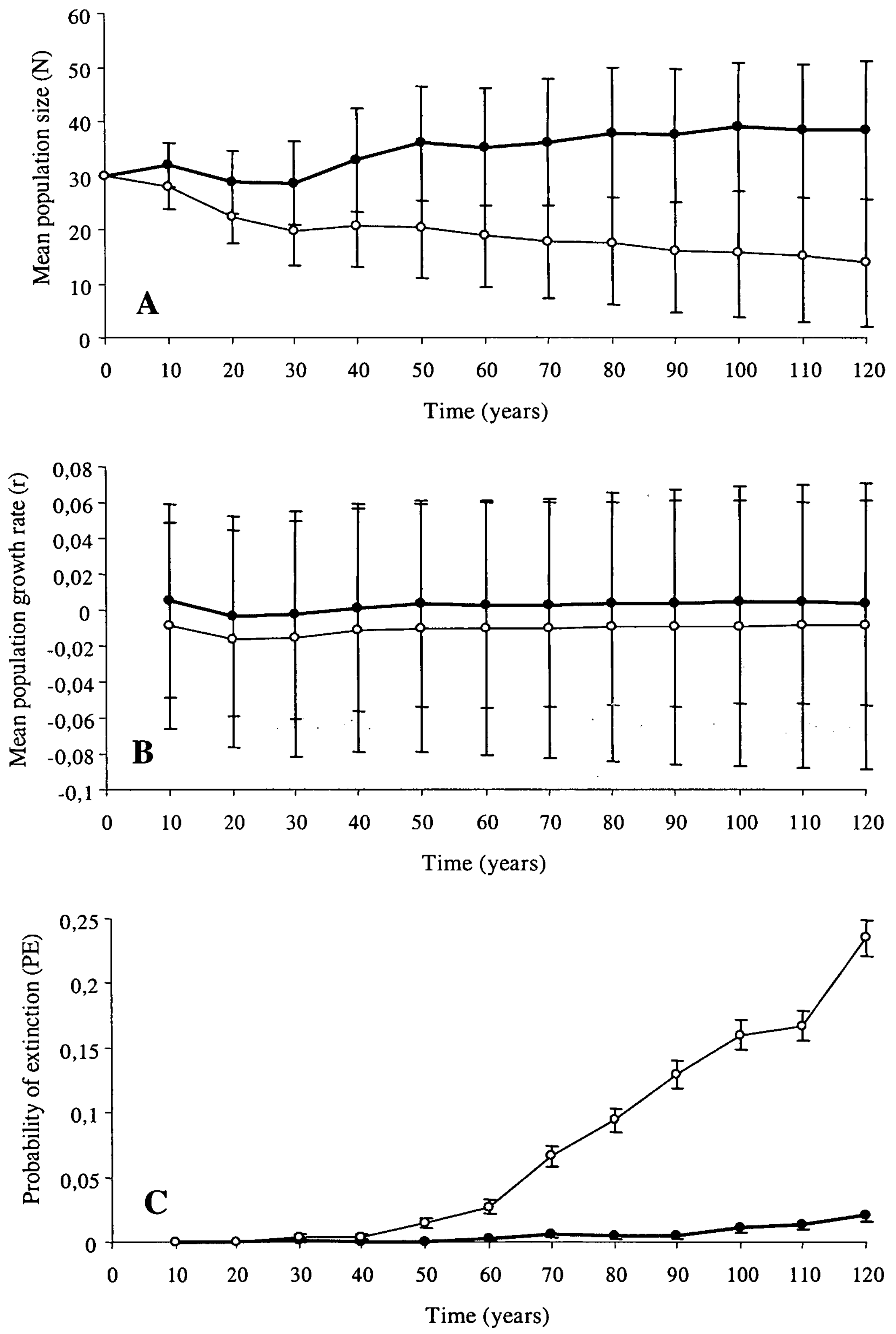

Figure 5.4. PVA predictions for the "optimistic" model (●) (error bars are plus/minus one standard error), and that of the "current model" (○); **A** -Mean population size; **B** - Mean population growth rate; **C** - Probability of extinction.

5.3.5. Small change sensitivity analysis

The absolute magnitude of change in elasticity and sensitivity values of vital rates towards population growth (Table 5.2) varies with the time scale considered (20, 40 and 120 years). For example, the elasticity and sensitivity values of calf survival during the first year are higher (by over 50%) in the long term, when population size is predicted to be smaller, whereas those of fecundity are higher (by over 25%) in the short and middle term when number of adults would be higher.

Table 5.2. Sensitivity and elasticity of population growth to small perturbations (-1%) in life history traits.

		-1% change	
	parameter	sensitivity	elasticity
20 years			
	fecundity	0.2623	0.0500
	adult survival	0.7472	0.7460
	sub-adult survival	0.2712	0.2397
	calf survival (2nd and 3rd years)	0.0197	0.0200
	calf survival (1st year)	0.0354	0.0300
40 years			
	fecundity	0.2109	0.0400
	adult survival	0.7174	0.7198
	sub-adult survival	0.2272	0.1998
	calf survival (2nd and 3rd years)	0.0198	0.0200
	calf survival (1st year)	0.0237	0.0200
120 years			
	fecundity	0.1585	0.0300
	adult survival	0.7869	0.7913
	sub-adult survival	0.2618	0.2297
	calf survival (2nd and 3rd years)	0.0198	0.0200
	calf survival (1st year)	0.0713	0.0600

However, the relative magnitude of these sensitivity indices is independent of the time scale considered. Adult survival is the vital rate with highest sensitivity and elasticity values, followed by sub-adult survival (around three times lower). Fecundity has a similar sensitivity to that of sub-adult survival but a much lower elasticity. Calf survival (survival during the first year and survival during the second and third years) has low sensitivity and elasticity values, which indicates that the model is insensitive to small changes in these parameters.

Table 5.3. Sensitivity and elasticity of population growth rate to small populations in input parameters based on values from the literature.

	parameter	minimum change	sensitivity	elasticity
20 years				
	longevity	-2%	0.0023	0.1149
	female age at first reproduction	-9%	0.0008	0.0088
	male age at first reproduction	-8%	0.0001	0.0013
	sex ratio at birth	-2%	-0.0001	-0.0050
	carrying capacity	-2%	-0.0001	-0.0050
40 years				
	longevity	-2%	-0.0005	-0.0250
	female age at first reproduction	-9%	0.0007	0.0077
	male age at first reproduction	-8%	0.0000	0.0000
	sex ratio at birth	-2%	-0.0001	-0.0050
	carrying capacity	-2%	-0.0003	-0.0150
120 years				
	longevity	-2%	0.0006	0.0300
	female age at first reproduction	-9%	0.0006	0.0066
	male age at first reproduction	-8%	0.0001	0.0013
	sex ratio at birth	-2%	-0.0004	-0.0200
	carrying capacity	-2%	0.0002	0.0100

Results from the sensitivity analysis of parameters for which data were not available (Table 5.3) indicate that small changes around the selected value of these parameters produced low sensitivity indices, among which longevity had the highest values (Table 5.3). Because uncertainty around these parameters is likely to produce small changes in the chosen value, this result means that the model is robust to the lack of information about these parameters. Variation in the absolute value of sensitivity and elasticity was also found to exist according to the time scale. For example, longevity has higher (by around 70%) sensitivity and elasticity values during the first twenty years, when most of the adults would be near or over mid adult life; sex ratio at birth has higher (by 75%) sensitivity indices in the longer term, when population size is very small and carrying capacity has higher elasticity values in the middle term, when population growth rate is predicted to increase and a lower elasticity during the short term phase, when population growth is predicted to decrease sharply.

Contrary to what was observed in the sensitivity analysis of vital rates, the relative ranking in the ability of these parameters to produce changes in population growth rate varies according to the time scale considered. This scattered pattern may however, be unimportant. As sensitivity indices are very small, resulting changes in the mean population growth rate are likely to be very small. The reported variation may be due to the chosen number of simulations (n=1000). The variation around the mean estimate of population growth rate due to stochasticity may be not precise enough to distinguish between very small changes in growth rate, as indicated by the large standard errors around the estimate of mean population size (see Fig. 5.2).

5.3.6. Sensitivity analysis incorporating the ability of vital rates to change as indicated by their past observed range

When larger changes are incorporated in the sensitivity analysis of the vital rates towards population growth rate (Table 5.4), the ranking pattern of the sensitivity and elasticity values of the vital rates considered as in the previous sensitivity analysis is maintained. Adult survival has the highest elasticity value, followed by sub-adult survival and fecundity. The sensitivity value of adult survival is the highest; fecundity and sub-adult survival have similar sensitivity values. Similarly, the absolute values of elasticity and sensitivity of the vital rates do not vary much with the time scale considered. The concordance of the results from the sensitivity analyses incorporating small and large changes in recent vital rate values is indicative of a linear relation between changes in vital rates and the resulting changes in the population growth rate.

Table 5.5 presents the sensitivity and elasticity values of maximum and minimum values of vital rates towards probability of extinction. These sensitivity indices are negative because an increase or a decrease in the recent value of the vital rate has a contrary effect on probability of extinction.

The ranking of sensitivity and elasticity values of vital rates to probability of extinction is the same as previously observed for growth rate but these values are much higher. This indicates that the same variation in the current value of the vital rate produces a stronger effect in probability of extinction than in population growth rate. Another aspect to consider is that sensitivity and elasticity values change markedly with the time scale considered in the probability of extinction. This is because probability of extinction is in itself time dependent. Very high elasticity values were obtained from minimum values of the vital rates during the first 40 years, when growth rate is increasing. Lower, but still high, elasticity values were obtained in the long term, when population growth has stabilized. The opposite pattern was observed for sensitivity values where higher values were observed in the long term.

Table 5.4. Sensitivity and elasticity of mean population growth rate (λ) to changes in current and past minimum and maximum values of vital rates.

	recent lambda	vital rate	recent value	minimum value (% change)	lambda	elasticity	sensitivity	maximum value (% change)	lambda	elasticity	sensitivity
20 y	0.984										
		adult survival	0.986	0.953 (-3.29)	0.960	0.748	0.747	0.995 (0.93)	0.990	0.701	0.700
		sub-adult survival	0.870	0.731 (-15.97)	0.956	0.181	0.205	0.870 (0)	0.984		
		fecundity	0.188	0.0857 (-54.29)	0.962	0.0403	0.211	0.222 (15.62)	0.990	0.0358	0.188
40 y	0.989										
		adult survival	0.986	0.953 (-3.29)	0.965	0.722	0.724	0.995 (0.93)	0.995	0.690	0.693
		sub-adult survival	0.870	0.731 (-15.97)	0.954	0.218	0.248	0.870 (0)	0.989		
		fecundity	0.188	0.0857 (-54.29)	0.994	0.0298	0.157	0.222 (15.62)	0.966	0.0417	0.220
120 y	0.991										
		adult survival	0.986	0.953 (-3.29)	0.968	0.719	0.723	0.995 (0.93)	0.998	0.777	0.781
		sub-adult survival	0.870	0.731 (-15.97)	0.958	0.208	0.237	0.870 (0)	0.991		
		fecundity	0.188	0.0857 (-54.29)	0.969	0.0410	0.217	0.222 (15.62)	0.998	0.0358	0.189

Table 5.5. Sensitivity and elasticity of probability of extinction (PE) to changes in current and past minimum and maximum values of vital rates.

	recent PE	vital rate	recent value	minimum value (% change)	PE	elasticity	sensitivity	maximum value (% change)	PE	elasticity	sensitivity
40 y	0.004	adult survival	0.986	0.953 (-3.29)	0.152	-1125.77	-4.57	0.995 (0.93)	0.003	-26.88	-0.109
		sub-adult survival	0.870	0.731 (-15.97)	0.274	-422.63	-1.94	0.870 (0)	0.004		
		fecundity	0.188	0.086 (-54.29)	0.0560	-23.94	-0.511	0.222 (15.62)	0.004	0	0
120 y	0.235	adult survival	0.986	0.953 (-3.29)	0.950	-92.57	-22.07	0.995 (0.93)	0.060	-80.07	-19.09
		sub-adult survival	0.870	0.731 (-15.97)	0.995	-20.25	-5.47	0.870 (0)	0.235		
		fecundity	0.188	0.086 (-54.29)	0.930	-5.45	-6.83	0.222 (15.62)	0.083	-3.50	-4.38

The past observed range between the maximum and minimum values of the vital rates was smaller for adult survival (+1% to -3%) and larger for fecundity (+19% to -54%). Sub-adult survival also presented a considerable variation (-16%; note that the current value of sub-adult survival is also the maximum observed value). The effect of past variation in vital rates on the mean population growth rate and probability of extinction does not follow the ranking pattern in elasticity and sensitivity values previously described. Although adult survival had the highest elasticity values, sub-adult survival is the vital rate with the largest potential to change growth rate and particularly, probability of extinction. Finally, maximum values of adult survival and fecundity result in a minimum decrease in population growth rate and minimum values of probability of extinction in the long term.

5.3.7. Effect of the initial age structure

The unstable age structure at the starting population generates a more pessimistic scenario at any time scale than that caused by the same number of animals in the starting population with a stable age structure (Table 5.6): mean population size and growth rate are lower and probability of extinction is higher. Major differences are observed during the first 20 years.

The effect of the past lack of recruitment to the adult stage found in chapter 2 due to the very low survival of young animals (chapter 4), resulted in an unstable age structure. As a result, 90% of the adult class in the starting population is composed of animals near or older than mid adult life. In the long term, the age structure will tend to stabilise and similar results are obtained. Overall, these results indicate that although the major effect of the unstable age structure is temporary, it will have an effect in the long term by reducing the viability of the population.

Table 5.6. Mean population size, mean population growth rate and mean probability of extinction predicted from the stable age structure model.

	age structure	N (SE)	r (SE)	PE (SE)
20 years				
	unstable	22.3 (4.97)	-0.0162 (0.0604)	0
	stable	28.37 (5.56)	-0.0038 (0.0596)	0
40 years				
	unstable	20.59 (7.67)	-0.0113 (0.0675)	0.004 (0.002)
	stable	24.93 (8.14)	-0.006 (0.0625)	0
120 years				
	unstable	14 (12.05)	-0.009 (0.0795)	0.235 (0.0134)
	stable	16.68 (12.47)	-0.0072 (0.0734)	0.15 (0.0113)

It is also worth pointing out from these results that even if this very small starting population had a stable age structure, the most recent vital rates will generate a declining population. Resulting mean population growth rates although very small (less than 1% a year) are still negative.

5.3.8. Effect of immigration of sub-adults

The effect of a possible regular sub-adult immigration feeds population size so that in the middle and long term, the size of the population (around 26 animals) is similar to that of the starting population (Table 5.7). Consequently, probability of extinction is very low in the long term. Although mean population growth rate is still negative, in the middle and long term it is very close to zero.

Table 5.7. Mean population size, mean population growth rate and mean probability of extinction predicted from the model simulating regular immigration of sub-adults.

	subadult immigration	N (SE)	r (SE)	PE (SE)
20 years				
	no immigration	22.3	-0.0162	0
		(4.97)	(0.0604)	
	with immigration	23.76	-0.013	0
		(5.43)	(0.0628)	
40 years				
	no immigration	20.59	-0.0113	0.004
		(7.67)	(0.0675)	(0.002)
	with immigration	26.14	-0.0048	0.001
		(8.27)	(0.0625)	(0.001)
120 years				
	no immigration	14	-0.009	0.235
		(12.05)	(0.0795)	(0.0134)
	with immigration	26.65	-0.0017	0.0020
		(12.06)	(0.0709)	(0.0014)

5.4. DISCUSSION

5.4.1. Future viability of the Sado dolphins

Although the number of animals and thus population growth rate has increased recently, the population is likely to decline in the short term. This predicted change in current status is characteristic of the typical fluctuating dynamics of small populations (Lacy et al. 1993 Coulson et al. 2001). The effect of the lack of recruitment to the adult stage in the past has resulted in the current unstable age structure in which the great majority of the adults are near or older than mid adult life. Even if adult survival was constant ("current" model) and maximum observed values of adult survival and/or fecundity were used in the model, these adults will die within 20-30 years. The consequent reduction in population size has the most impact on population growth rate in the short term, and to some extent, in the long term. Sensitivity and elasticity analysis from the present study showed that the model is most sensitive to adult survival. This is because in long lived mammals the adult class groups many ages which are responsible for the production of new animals. The impact of this loss in the short term population growth rate may be worsened by the very small number of young animals.

When most of the older adults have died, there will be an increase in population growth rate in the medium term because the loss in number of animals will be slower. In the long term, all models predict that population growth rate will stabilize at a declining rate, except the "optimistic" model, which predicts that the population will increase in size. It is worth noticing however that when maximum values of adult survival or fecundity are used, or when sub-adult immigration is considered, population growth rates (lambda) are very close to one. This may indicate that apart from the effect of the unstable age structure, current sub-adult survival may contribute to a long term decline. The current value of sub-adult survival is the maximum observed value and, as shown in the chapter 4, only a small percentage of sub-adults will reach adult age. It may be that this vital rate is still currently depressed.

In conclusion, the future status of the Sado resident group given by the selected input model parameters is most likely to be a declining population. Only in extreme conditions (maximum observed values of all vital rates, very high adult survival rate and regular immigration of sub-adults) may the current population be considered to be a minimum viable population size, that is, which guarantees less than 5% probability of extinction within 100 years (Shaffer and Samson 1985). Caution should be made in interpreting long term extinction risks because precision in the estimate of this parameter decreases over time (Beissinger and Westphal 1998).

5.4.2. Accuracy and reliability of the PVA

PVA is inherently speculative and predictions are probabilistic (Beissinger 2002). The small change sensitivity and elasticity values of the model parameters for which data were not collected were very low, indicating that the model is robust to uncertainty in these assumptions. Apart from these, two main factors are critical for the predictive accuracy of the model: how accurate the estimates of vital rates are and how well the model describes the life history patterns of the bottlenose dolphin (Taylor 1995).

As seen in the small change perturbation analysis, uncertainty in the vital rates, particularly adult and sub-adult survival and fecundity, is likely to affect population projections,. The accuracy of these estimates relies on how long the time series of data is (Fieber and Ellner 2000) and on the methods used. The data set from the Sado resident group is unusual because it involves a long time series of data (1986-2002) of all the individuals. With the exception of first year survival, average estimates of survival and fecundity used in the "pessimistic" model were obtained from most of the data available. These average values incorporate the widest variation observed in the past behaviour of the Sado dolphins. On the other hand, estimates used in the "current" and partly in the "optimistic" models cover only a short period. Because shifts in population numbers were observed in the past, estimates from the "current" model are more likely to represent the present status of the population.

Estimates of survival presented in chapter 4, were obtained using mark-recapture methods. In general, very high capture probabilities were obtained which is a good indication of their accuracy. However, first year survival and fecundity may be biased downwards. As explained in chapter 4, this may also be the case for the sub-adult and calf survival estimates during the earlier years. As a result, average estimates of survival obtained over the study period may be biased downwards. The "pessimistic" model may be too pessimistic. On the contrary, current estimates of survival should not be biased, except the estimate of first year survival (and thus fecundity). The differences between the pessimistic and "current"scenarios may be less than seen in the results presented.

Another factor affecting the accuracy of the estimates is the unknown sex ratio. Age and sex specific patterns in adult survival, fecundity and percentage of males in the breeding pool used in the model are based on the most appropriate available information but may be not the most realistic functions describing these vital rates. (Fujiwara and Caswell 2001), including in the bottlenose dolphin (Sander-Reed et al. submitted), have shown the positive effect of adding a few adult females to the long term viability of the populations.

Environmentally caused variation was only found in first year survival. In general, long lived mammals species are well buffered against environmental variation (Morris and Doak 2002). However, as mentioned in chapter 4, there is also evidence that the early stages of life are more sensitive to environmental variation, which is consistent with this result.

Apart from uncertainty around age and sex specific vital rates, other factors may account for the inadequacy of the model in describing the life history of the bottlenose dolphin. VORTEX simulates reproduction as discrete events on an annual basis and assumes that all animals of reproductive age have an equal probability of reproducing. However, subsequent reproduction of female bottlenose dolphins is dependent on the survivorship of its calf (Thompson et al. 2000). If the calf is lost, females may become attractive to males within 1-2 weeks. If the calf survives, females may only become attractive when its calf is about 2-2.5 years old (Connor et al. 1996). It was shown in chapter 2 that calving intervals can be very long (between 2 to 11 years). In addition, as mentioned in chapter 2, some females of the resident group were not seen with a newborn calf for many years whereas others were seen regularly with calves during the study period. One explanation is that some females may be reproducing at a lower rate then others. Under these modelled circumstances of life history patterns, more animals will be added to the population than the actual socio-biological potential of females to reproduce. In this way, by constraining the life history of the bottlenose dolphin to this assumption, stochasticity and extinction risk will be underestimated. This issue will be of particular relevance when population size is very small and when fecundity is higher (models using maximum values of fecundity). This assumption is also inadequate for adult males. Although the option that all males are in the breeding pool is consistent with this assumption, the impact of such an unrealistic condition may be of minor importance.

The use of the simplest model containing the least uncertainty could be the best model to use (Beissinger 2002, Fieber and Ellner 2000); however, the simplest model is usually not the most comprehensive (Beissinger 2002). Having this constraint, the simplest model ("current" model) was used in the perturbation analysis and was chosen to be the base for alternative scenarios based on observed data, including the "optimistic" model. Additional scenarios such as inbreeding depression, catastrophes, bonanzas, density dependence and covariation among environmentally caused variance in vital rates due to trade-offs, would increase the complexity of the model. However because no data exist to quantify such processes, an increase in the uncertainty of the model output would result. The conducted alternative scenarios and perturbation analysis based on data may portray the likely effect of some of these processes in the fate of the Sado dolphins.

Another useful approach would be to test internal model consistency by comparing the deterministic r with the stochastic one when population growth rate would be in a stabilized phase. The "current" and the "optimistic" models provide the most feasible comparisons, whereas the "pessimistic" model is affected by the very small size predicted in the long term. Inherent stochastic demography may account for the small differences found between these parameters given by the "current" and "optimistic" models.

One way of testing the inadequacy of model assumptions to the life history patterns of the bottlenose dolphin would be to run the same model inputs using different but similar simulation software (Brook et al.1997, 1999). This exercise could give evidence that a particular pattern was obtained solely based on model choice. However, simple models like we used, from different software packages are usually congruent (Brook et al. 1999)

Finally, the reliability of the predicted population projections could be evaluated either in such a prospective analysis, as the above mentioned small change perturbation analysis, or through a retrospective analysis (Benton and Grant 1999). This kind of analysis uses some part of the data set to predict the fate of the population in the subsequent period (Gerber et al. 1998, Brook et al. 1997, 2000, Fieberg and Ellner 2000). Fieber and Ellner (2000) showed that a precise estimate of probability of extinction over a horizon of t years would require between 5t and 10t years of data. Although the present data set has a long time series, and the "pessimistic" model could fit this requirement, future predictions would be limited to a few years. In addition, uncertainty in vital rates from the earlier years would make this exercise obsolete.

Another aspect worth mentioning is the questionable reliability of the "optimistic" model. This model assumes that all vital rates are maintained at their maximum observed values. This is unlikely to be biologically feasible overt a long time period due to trade-offs between vital rates or due to density dependent factors.

5.4.3. Sensitivity analysis of population projections to biological bounds in life history traits

The tendency of vital rates to fluctuate depends on the life history pattern of a species. As seen in the previous chapter, in long lived mammal species, such as the bottlenose dolphin, adult survival is usually close to one, which allows little variation (Benton and Grant 1999). Fecundity and survival of young animals may present considerable fluctuations due to the vulnerability of these rates to density dependent and density independent factors. The observed range in the biological potential of life history traits is consistent with life history patterns typical of large and long lived mammal species (Fowler 1981, Paker et al. 1998).

However, this range may also be influenced by uncertainty in the mean estimates. As mentioned above, adult survival estimates are accurate but the same may not be true for fecundity and sub-adult survival. If this bias was corrected, a narrower range of values for fecundity and sub-adult survival would be obtained.

Accuracy in the estimates is more likely to be influential if their elasticity is high (Benton and Grant 1999, Morris and Doak 2002). Adult survival is the vital rate with highest sensitivity and elasticity values, which is consistent with findings in other long lived mammal species (Heppell et al. 2000). However, it was found that the potential to change population growth rate and probability of extinction was higher when the minimum value of sub-adult survival was modelled. This result is also consistent with the high sensitivity and elasticity values of sub-adult survival. Although the implications of these results on the reliability of future models would be to consider maintaining accurate estimates of adult and sub-adult survival, the past depression of this last vital rate may be artificial.

The elasticity analysis here conducted considers the impact of each vital rate as independent. This is likely to be a simplification of reality because variation in one vital rate may be correlated through physiological trade offs with other vital rates (Van Tienderen 1995, Benton and Grant 1999). Similarly, because not all factors were considered, the interaction of the various forces may be more than additive (Morris and Doak 2002).

Another lesson from perturbation analysis is that the fate of the population is most critically influenced by minimum values of vital rates during the next 10-30 years in particular, when population growth rate will be increasing. The implications for management of these and other results are discussed in chapter 6.

CHAPTER 6. TOWARDS CONSERVATION OF THE RESIDENT BOTTLENOSE DOLPHINS IN THE SADO ESTUARY

In the future, the Sado bottlenose dolphin population is likely to decline and its status is likely to worsen. In order to preserve this small population in the long term, the main conservation objective should be to avoid deepening its decline and secondly to create appropriate conditions for the population to stabilize. Thirdly, a broad scale management action should be to maintain a sustainable environment. Which evidence from this work can support the necessary management actions to achieve these aims?

6.1. WHY SHOULD CONSERVATION EFFORTS BE DIRECTED TO A SMALL DECLINING RESIDENT BOTTLENOSE DOLPHIN POPULATION LIVING IN AN ANTHROPOGENIC STRESSED ENVIRONMENT?

Although the distribution of the resident bottlenose dolphin population is partly enclosed within the local Sado Estuary Natural Reserve and in the Arrábida Marine Park, these protected areas are not subject to specific legislation in practice towards the conservation of this species. However, as long as there is one wild bottlenose dolphin, the Portuguese authorities are mandated to protect it through national legislation. For this reason, extinction in the population viability analysis was defined as the minimum number of animals allowed by the simulation program.

In a wider context, under the Natura 2000 network, two local Special Areas of Conservation (SACs) were proposed to the European Union by the Portuguese Institute of Nature Conservation (ICN). The Sado site was proposed for a number of habitats and species, both terrestrial and marine, including the bottlenose dolphin. The Arrábida site does not include any cetacean species. The selection of a SAC for a particular habitat or species depends, among other criteria, on how representative and how well conserved the site is from the local and from the European perspective. However, even though these local sites may not meet the quantitative representativeness criteria for the bottlenose dolphin, the conservation of this species is required towards the overall sustainable conservation of the SAC. To achieve sustainable conservation under such a high anthropogenic level of pressure as found in the Sado estuary will not be an easy task. But if other actions are not taken, the key features of these ecologically rich estuarine and marine environments may be lost.

The context of Natura 2000 is based on global biodiversity, and for this reason, it focuses directly on species rather than on populations. However, some populations may gather learned behaviours, as resident populations, which may or may not be shared by other populations of the same species. If SACs aimed at preserving the bottlenose dolphin do not take into account residency patterns, this learned behaviour may be lost in cases of population declines.

6.2. WHERE TO ACT?

Resident animals are year round residents and nearly every animal was seen every month in the estuary region (chapter 2). On the other hand, as seen in chapter 3, resident animals have not been seen away from that region. Another important aspect to consider is the lack of evidence of frequent encounters between resident and non-resident bottlenose dolphins (chapter 3). This high level of residency in a restricted area and the possible closure of this small resident populations makes these animals highly exposed to the environmental conditions of the estuary region. For this reason, broad scale management actions towards the conservation objectives should focus on the estuary region. However, due to the dynamic nature of the estuarine environment, efforts should also consider key components beyond its boundaries. For example, if fisheries outside the estuary are not managed to guarantee a certain recruitment level in the estuary, dolphin prey may decrease. Implementing conservation policy outside the estuary region may face a favourable context due to the existence of the Marine Park of Arrábida, which is also a candidate for a Special Area of Conservation. On which areas should fall the focus of specific management actions with direct effects on the resident dolphin? Two approaches must be taken into account: the importance of these areas for the dolphins and the anthropogenic negative impacts on the dolphins at these areas.

Several studies describe or quantify observations of the resident dolphins along the estuary region as well as describing their behaviour (Hussenot 1982, Dos Santos and Lacerda 1997, Freitas 1995, Dos Santos 1998, Harzen 1998, Louro 2001, Brito 2001, Carvalho 2000, Nunes 2001). However these studies share several common caveats. Results were obtained by following groups of dolphins that were not individually identified. Effort was not designed in order to search distinct areas, and interior estuary areas where dolphins feed mainly during the spring (R. Gaspar, personal observation) were not searched. As a result, habitat use patterns obtained may not be representative of the whole population. Data collection did not cover the whole year but seasonal changes occur in the diversity of the marine fauna within the estuary (Cunha 1994, Cabral 1999, Costa et al. 2000). This last point is also important because dolphins are known to shift their distribution and habitat preferences (Shane 1980, Ballance 1990) by following their prey (Irvine et al. 1981). Consequently, it is not possible to identify year round preferential areas of the resident dolphins.

However results from most of these studies are useful since they are consistent in their main conclusion: the south channel is the estuarine area where most of the observations have occurred. Figure 6.1 shows the results from the study of Nunes (2001) and is illustrative of the available information. As seen in Figure 1.2, this channel is much less impacted by human activities compared to the north channel. Naturally, it presents a stronger water circulation (Ambar et al. 1982) and a higher diversity in bottom topography, compared to the northern channel and to the interior of the estuary.

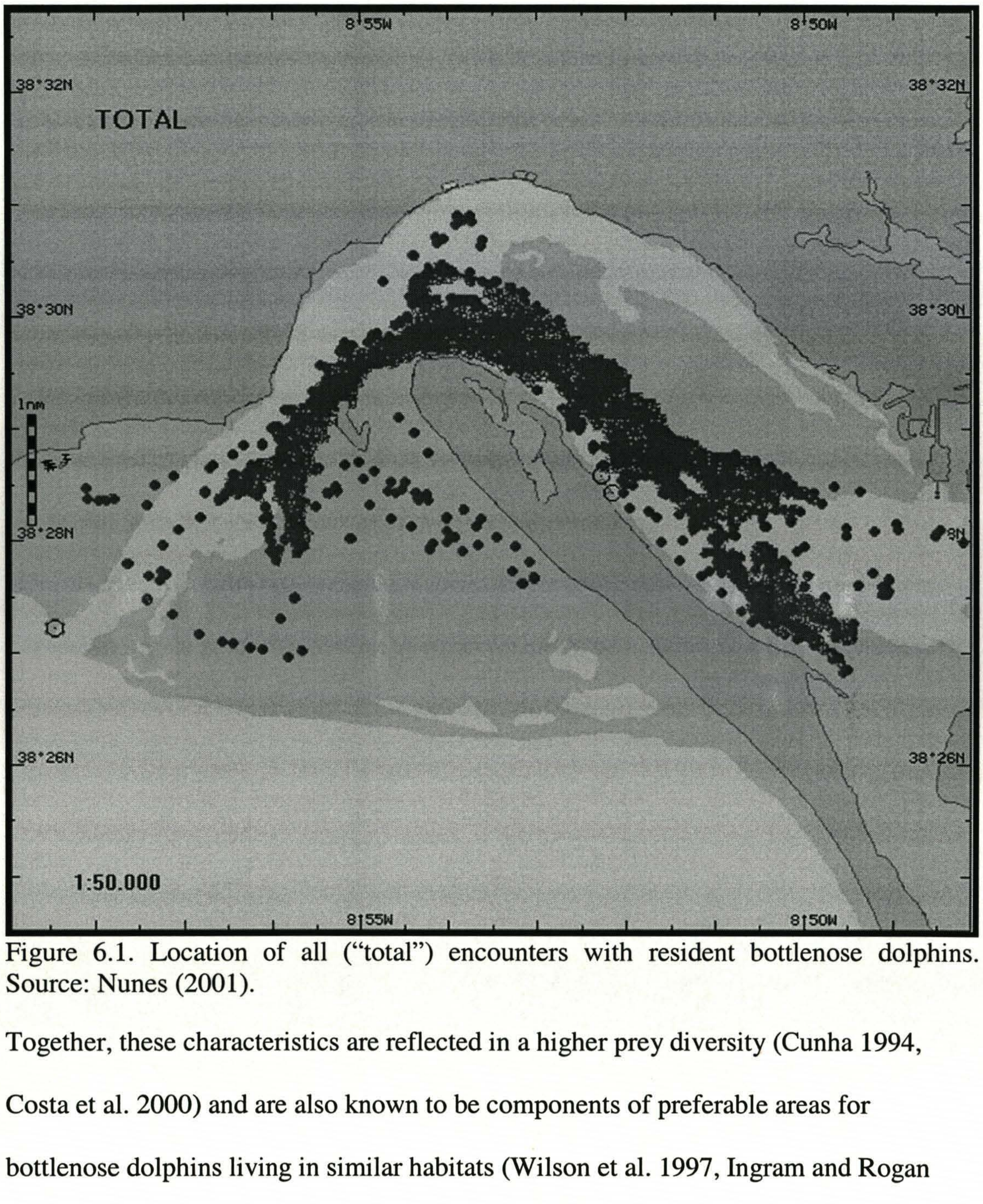

Figure 6.1. Location of all ("total") encounters with resident bottlenose dolphins. Source: Nunes (2001).

Together, these characteristics are reflected in a higher prey diversity (Cunha 1994, Costa et al. 2000) and are also known to be components of preferable areas for bottlenose dolphins living in similar habitats (Wilson et al. 1997, Ingram and Rogan 2002). It is not surprising that most of these studies (Dos Santos and Lacerda 1997, Freitas 1995, Dos Santos 1998, Harzen 1998, Nunes 2001) conclude that a greater percentage of feeding and feeding related behaviour occurred along this channel compared to the north channel.

The south channel is also mostly used by recreational boats and jetskis during the summer months to access the beaches and anchor points along the coast of the Tróia Península. During the summer of 2002 there was in the estuary region an average of 578 recreational boats and jetskis per day anchored or parked in the marinas, whereas during the autumn/winter this number was reduced to 156 (I. Cascão, personal communication). Along the South channel, boats can take any course and may travel at speeds above the allowed limit. Dolphins cannot predict the course of these boats and disruption of their behaviours may result (Janick and Thompson 1996). Because of the high speed of the jetskis, collisions with inexperienced young animals may occur which could result in injuries and possibly mortality (Wells and Scott 1997). In addition, many boats and jetskis try to approach dolphins. In 1999, dolphin-boat interactions involved between 2 and 10 boats and the number of boat-dolphin encounters per day varied between 2 and 22. These encounters were mainly located in the south channel and estuary entrance. In most of these interactions, the resident dolphins clearly showed behaviour indicative of disturbance, such as repetitive tail slaps, increasing diving time, decreasing surfacing time, and alteration in course and activity (Cascão 2001).

As part of the tourist development of the Tróia Península, the ferry boat harbour presently located at the west tip of the Tróia peninsula is proposed to be relocated up river near the Naval Base (Fig 1.2). At present, dolphin and ferry-boat interactions seem to be harmless (Freitas 1995). If relocation does occur, these animals may learn the new route of the ferry-boats (Janick and Thompson 1996). However it must also be considered that a new harbour also means that other boats will be able to use it. This could result in prolonging boat traffic up river, although recreational boats are more likely to use it during the summer months. It is not possible to predict if dolphins would shift their habitat to less appropriate feeding areas or if dolphins would remain in that area and, in any of these circumstances, to what extent would it affect the population fecundity and survival. It is worth remembering from chapter 5 that individual changes may have a considerable impact on population trend.

As seen in chapter 3, another important area seems to be the narrow estuary mouth and the sandbanks nearby (Figs.1.2 and 3.4). The justification is that this is a mandatory narrow passage area for both dolphins and boats (fishing, commercial, recreational and jetskis) entering or leaving the estuary. On a much smaller scale, dolphins and boats are able to pass over the sand banks during the flow tide (Gaspar 1994, Vieira 1997). No quantification exists on simultaneous dolphin and boat encounters in this area, but this may be critical during the summer months. Dolphins can travel through the estuary entrance several times a day (Gaspar 1994). They may not move out of the estuary every day during the spring, but they frequently travel in that area during the summer and autumn months (R. Gaspar personal observation). Recreational boats and jetskis use this area mainly during the summer to travel from the estuary to the beaches (including the sand banks at the estuary entrance) and anchorages nearby, as well as from the beaches to the gas station, anchorages or locations from where they leave the water to reach land. Boats may also enter from land or from other marinas away from the estuary region. The problem of such a high density of boats at that narrow area when dolphins need to travel through it is that dolphin and boat encounters may result in collisions (Wells and Scott 1997) or impede or disturb their natural behaviour (Baker and Macgibbon 1991, Hastie et al. 2003). It also been shown that dolphin's natural behaviour is more affected in shallow waters (Nowacek et al. 2001) which is the case of the sandbanks at the estuary entrance.

Special attention should be also devoted to the interior estuary area. Field observations (R. Gaspar personal observation) and the location of the live strandings are consistent with a higher abundance of prey species (Cunha 1994, Costa et al. 2000) and higher fishing effort in the interior estuary during the spring. The reason for conservation policies to act in this area is in part precautionary since no records exist on resident dolphin mortality in trammel fishing nets mainly used in this fishing area.

If the first two conservation objectives are to be achieved, the south channel, the estuary entrance and the interior estuary area should be the focus of conservation management for dolphins. The Sado cSAC includes most of the south channel and the Arrábida cSAC part of the estuary entrance (Fig. 3.1). Precautionary management is highly justified when the level of decline of a small population is high (Thompson et al. 2000). This is particular important if the population has a low level of contact with conspecifics. For these reasons, additional factors that may decrease individual fitness should be addressed.

6.3. WHEN TO ACT?

In an ideal situation, precautionary management actions should be put in place before the decline of a population reaches serious levels (Thompson et al. 2000; Dawson et al. 2001). It may seem that the present time is right since a deep decline of the population size and growth is likely to happen in the near future (10-30 years). However, it should be kept in mind that the population is already reduced to low levels, below the minimum viable population size, due to a past decline. Thus further delaying management actions may result in not achieving the conservation objectives. As seen in the chapter 5, management actions in the near future should aim not to let vital rates decrease, especially those of the adults.

Another reason for urgent action is that the loss of adults in the near future will result in a loss of unique and unrecoverable information (see below in Section 6.4.1). The call for urgency in action is also justified by the fact that it is very unusual to recover a carcass of a dead animal in sufficiently good condition to be analysed.

Finally, management actions should maintain their effectiveness during the medium to long term. As predicted in chapter 5, population size could be even lower than at the present time, which means that the population will be even more vulnerable to stochastic events.

6.4. HOW TO ACT?

6.4.1.Towards determining the causes of the decline

One of the underlying issues of the decline of this small resident population is that the cause of the past low survival of young animals is unknown. And if current sub-adult survival is still depressed we have not learned how to stop it. Thus it is essential to determine the causes for this lowered vital rate.

It may be argued that these causes may be out of date, for example because current fecundity and survival rates are higher. But it is worth remembering that small populations typically have changeable dynamics. It may also be that the same causes that acted in the past are no longer prevalent. For example, until 1981 resident dolphins could be intentionally captured for food. If smaller animals were preferentially captured, this could have caused an age structure with lack of sub-adults as seen at the beginning of the study. As in other similar situations elsewhere (for example after the ban of the sperm whale hunting industry in the Azores, Portugal) illegal capture could have continued for a few years after the ban and been the cause of mortality of young animals during the initial period of the study. Gathering this information from friendly fishermen's is one possible way to obtain this information.

Although some sources of contaminants may have been eliminated, their effects extend, into the present time. An illustrative example is the past application of the insecticide DDT in the rice fields along the basin of the Sado river. In addition, PCBs from industrial run-off over the years, which may represent a factor that facilitates disease emergence. Because marine mammals occupy high trophic levels, they can be highly contaminated with persistent organic pollutants (Ross 2002), especially adult males (Weisbrod et al. 2001). Young bottlenose dolphins, especially primiparous calves (Schwacke et al. 2002), also face a particularly high risk of exposure to organochlorines. As mentioned in chapter 4, there is no time series of pollutant records within the estuary. A database on pollutant levels in the Sado estuary will be available in the near future. However, a comprehensive monitoring scheme of the pollutant levels in the food chain and in the physical environment would be a step forward from the current uncertainty about the pollutant levels in the Sado estuary region.

To obtain more information about the role of pollutants in the decline, animals could be biopsied. Biopsying animals from a very small and declining population may be controversial. One opinion is that there is a risk of deepening the decline by decreasing survival of a few individuals. This is a justifiable matter of concern since the estuary water is polluted with untreated urban and hospital sewage. In addition, a preliminary analysis showed that healing rates from tooth rakes of the Sado bottlenose dolphins are lower than elsewhere (Wilson et al. 1999c). However, biopsy sampling with darts is a common technique used in large (Hooker et al. 2001, Gauthier and Sears 1999) and small cetaceans (Parsons et al. 2003). Usually animals resume their activities and do not avoid the boat after being sampled. In the bottlenose dolphin, healing time of the wound resulting from the biopsy can take about twenty days (Krützen et al. 2002). In order to monitor the reaction of the resident dolphins to this technique and its effects, a few animals may be chosen and followed before application of this technique to the whole population. Attempts were made during this study to biopsy the bottlenose dolphins with a purpose-built metallic scraper that was deployed from a small rubber boat. These experiments were unsuccessful because as soon as the cable was hung out of the boat, bow riding dolphins would move further away.

If animals are to be biopsied, this should began as soon as possible so that changes in pollutant levels of adult males can be monitored. Pollutant profiles of females with known reproductive histories could also be compared. If young animals, especially calves, are contaminated this may be indicative that high levels of pollutants are present in the food chain, since previous calves from the same adult females would have received the past pollutant burden accumulated by the mother during infancy and adulthood.

Biopsy samples could have a second purpose: genetic analysis. One basic result from this analysis would be sex determination of individually identified animals. This would clear the uncertainty about sex ratios and, more importantly, part of the uncertainty in fecundity estimates, an important parameter in population viability analysis. More importantly it would permit sex specific survival rates to be estimated which are a cause of uncertainty in the PVA models. Genetic analysis could also be used to determine the pedigrees of individual calves. It could also clarify if resident dolphins mate with outside groups. This information would clarify the lack of evidence of frequent encounters between resident and non-resident animals and possibly the role of immigration, if it exists, in the genetic quality of the offspring. Finally, this technique could be used to assess the level of inbreeding within the population.

Another possible cause of the low survival of young animals, and maybe the current sub-adult survival, may be mortality in fishing nets. It would be worth investigating the possible impact of fisheries in the survival of young animals within the distribution area of the resident population. As mentioned above, fisheries that occur during the spring at the interior estuary should be a particular focus. An onboard observer scheme and inquires to friendly fishermen should be put in place.

Finally, if the low sub-adult survival is due to sub-adult emigration, the way forward to investigate this cause would be to remotely track individual resident sub-adults over several years using radio telemetry. Photo identification is not the technique to be used because these are growing animals whose natural marks can quickly change. A more limiting factor is the small chance of finding the group to which animals could emigrate. However, there have been successful attempts using this technique in wild bottlenose dolphins (Scott et al. 1990, Wells et al. 1999). Applying radio telemetry to young resident sub-adult dolphins would require the development of an immobilization technique adapted to these larger animals and their habitat. This procedure is potentially much more hazardous than biopsy sampling. An easier way would be if a sub-adult animal had been naturally immobilized during a live stranding, as occurred recently with two adults. This would be an ideal situation if the animal survived. Appropriate transmitters should be acquired and personnel trained to deploy them should an occasion arise. This technique could be also applied to any live stranded dolphin.

6.4.2. Towards the conservation objectives

Broad scale management actions are applied to the environment dolphins live in and should envision a sustainable environment. As seen in chapter 5, if conditions existed for vital rates, namely adult survival or fecundity, to achieve their maximum values population growth rate would decline at a much slower rate and would stabilize at a rate close to zero. If the mean value of most vital rates could be improved then a stronger positive effect could be obtained towards the determined conservation objectives, as suggested by the "optimistic" model.

Management should act to minimise the negative indirect effects of anthropogenic activities on individual performance. For example, certain pollutants accumulate in the food chain. Because dolphins are top predators, the effect of pollutant offloads is not immediate in these animals. High levels of certain pollutants may affect survival (Reijnders 1986) and reproduction of marine mammals (O'Shea et al. 1999). If management actions towards reducing the pollutant levels in the estuary environment are delayed, there may be no time for a positive effect in the dolphin population towards the conservation objectives. Furthermore, habitat degradation can cause a decline in food availability. Although reduction in carrying capacity has shown to have little effect on the population projection, if a shortage of food occurred, young resident animals could emigrate. Maintaining abundant and diverse prey in the estuary should be another aim towards a sustainable environment. A realistic problem that this type of action will face is the large amount of agricultural runoff into the estuary basin due to the new Alqueva dam.

As seen in chapter 5, adult survival is the vital rate with highest elasticity and sub-adult survival is the vital rate with most potential to change the population projection into the future. The good news about the small scale sensitivity and elasticity results is that a very small change in these vital rates will have a positive effect in the future viability of the population. However, caution must be taken, because the same small change if negative will also have an effect. Thus specific management actions should be primarily directed towards these vital rates.

In recent years, two adult males stranded alive in the interior estuary mud banks. Both strandings occurred during the month of April, which is when dolphins are known to travel to the most interior estuary areas. If this is likely to happen again, saving adult animals should be the aim of a specific management action. In particular, as mentioned in chapter 5, if saved adults were to be females, a slower rate of loss of reproductive animals would result and potentially, more calves would be born (Fujiwara and Caswell 2001, Sander-Reed et al. submitted). In order to illustrate this effect, a model was constructed assuming that two adults were saved each nine years. Figure 6.2 A, B and C shows the results of that simulation. As expected, if adult survival is regularly artificially increased, conservation objectives would be met: population size will recover to present levels, growth rate will stabilise at almost no decline and extinction probability will be insignificant. These results are consistent with those obtained by using the maximum value of adult survival.

In practice, a dolphin stranding watch scheme could survey the interior estuary channels during the low tide period, especially during full and new moon when the tidal amplitude is higher. Surveys should focus on the spring months when dolphins are using the interior estuary areas. This scheme should involve local fishermen because fisheries are more intensive in the interior estuary during the spring. A network of trained personnel, equipment and logistic means should be on alert during that particular period. Simulation of such an event in the field should be conducted to achieve the high level of success of such stranding operation.

Management actions towards increasing survival of sub-adults may be constrained by the natural variability of this vital rate, since the maximum value observed is the current one. If that is the case, conservation actions should focus on not allowing a decrease in

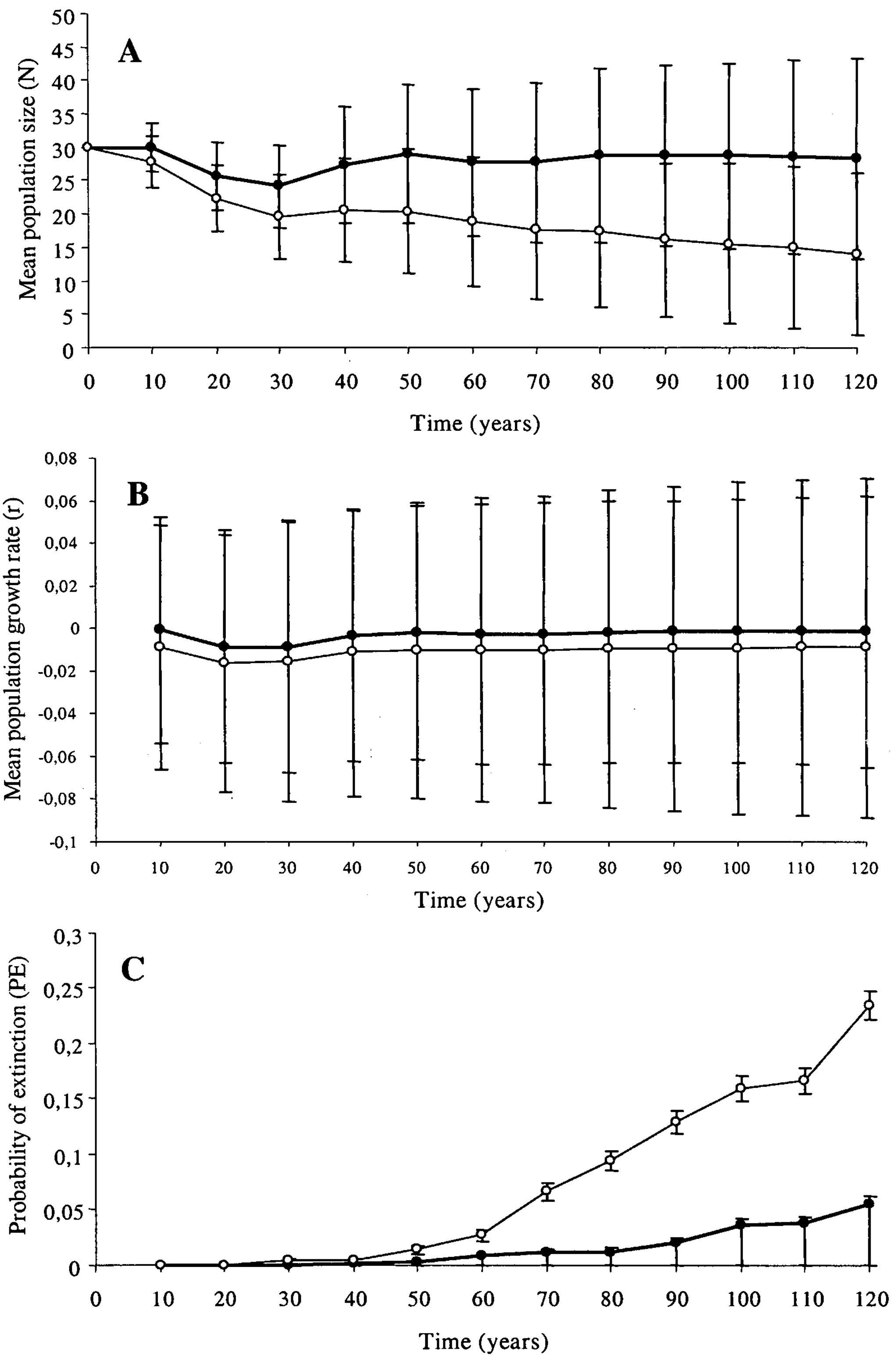

Figure 6.2. PVA predictions for the model simulating that 2 adults would be saved in every 9 years (●) (error bars are plus/minus one standard error), and that of the "current model" (○); **A** -Mean population size; **B** - Mean population growth rate; **C** - Probability of extinction.

this vital rate. However, if the current value is still depressed, then management actions should also aim at increasing it.

The model run simulating sub-adult immigration (chapter 5, table 5.7) is illustrative of a positive effect of management actions towards the increase of sub-adult survival. Stakeholders have suggested the translocation of sub-adult bottlenose dolphins from other coastal groups in order for the population to recover. This seems to be inappropriate because bottlenose dolphins have complex social systems. Another reason is that inexperienced dolphins living in another habitat may face a reduction in their survival when moving into a different habitat. The cost of such an operation would be more worthwhile if it were applicable to monitoring sub-adult bycatches in the fishery nets, to remotely tracking individual sub-adults, and at a much broader scale, or acting towards a sustainable environment. It is of no use to make efforts in the translocation of young animals into the resident population if the problems of their low survival are not identified and solved.

Another way to establish priorities of actions is to look for factors that in the future are most likely to affect the population. Dolphin-boat interaction can be one of them. It seems clear that in the future the number of recreational boats and jetskis will increase in the estuary region.

As an example, the construction of a new marina for another 150 recreational boats is foreseen as part of the tourist development of the Tróia peninsula. The location of this marina, at the tip of the Tróia peninsula (Fig. 1.2) may facilitate an unprecedented movement of recreational boats through the south margin into the estuary water. In addition, for boats to enter or leave the new marina, they will have to cross one of the most frequently used passage areas for dolphins (Gaspar 1994, Vieira 1998).

This situation will be particularly critical during the summer months because the number of recreational boats in the water is highest. In addition, as shown in chapter 2, births usually also occur during the summer months. Females with calves are particularly susceptible to disturbance due to their higher energetic requirements (Kastelein et al. 2002, Cheal and Gales 1991, Urian et al. 1996) and possibly inexperience (Nowacek et al. 1999). Newborn calves are inexperienced animals and mortality can be caused due to collisions (Wells and Scott 1997).

In order to illustrate the possible impact of this additional mortality in future viability of the population, a model was created in which two calves died in every four years. As figure 6.3, A, B and C shows, this would lower the population size and the decline in population size would be deeper. Note that the negative impact of this simulation is much weaker than the impact of reducing adult survival at a similar rate (chapter 5) which is consistent with the lower sensitivity and elasticity values of first year survival. In both models of suggested management actions, the SEs are large because of the demographic variability due to small population size. However, the value of these management actions is accounted by the difference in the extinction risk.

A specific management action should address the regulation of the movement (course and speed) of recreational boats and jetskis in critical areas previously identified for this purpose (south channel and estuary entrance). The creation of corridors for the boat traffic could be a practical solution. They should be placed in appropriate navigational areas that have the least interference with dolphin habitat use. The advantages of this action would be avoiding dolphin and boat collisions by allowing the boats to take the same course in these critical areas. By maintaining the course, boats would then become predictable for the dolphins. Another advantage of these corridors would be to avoid

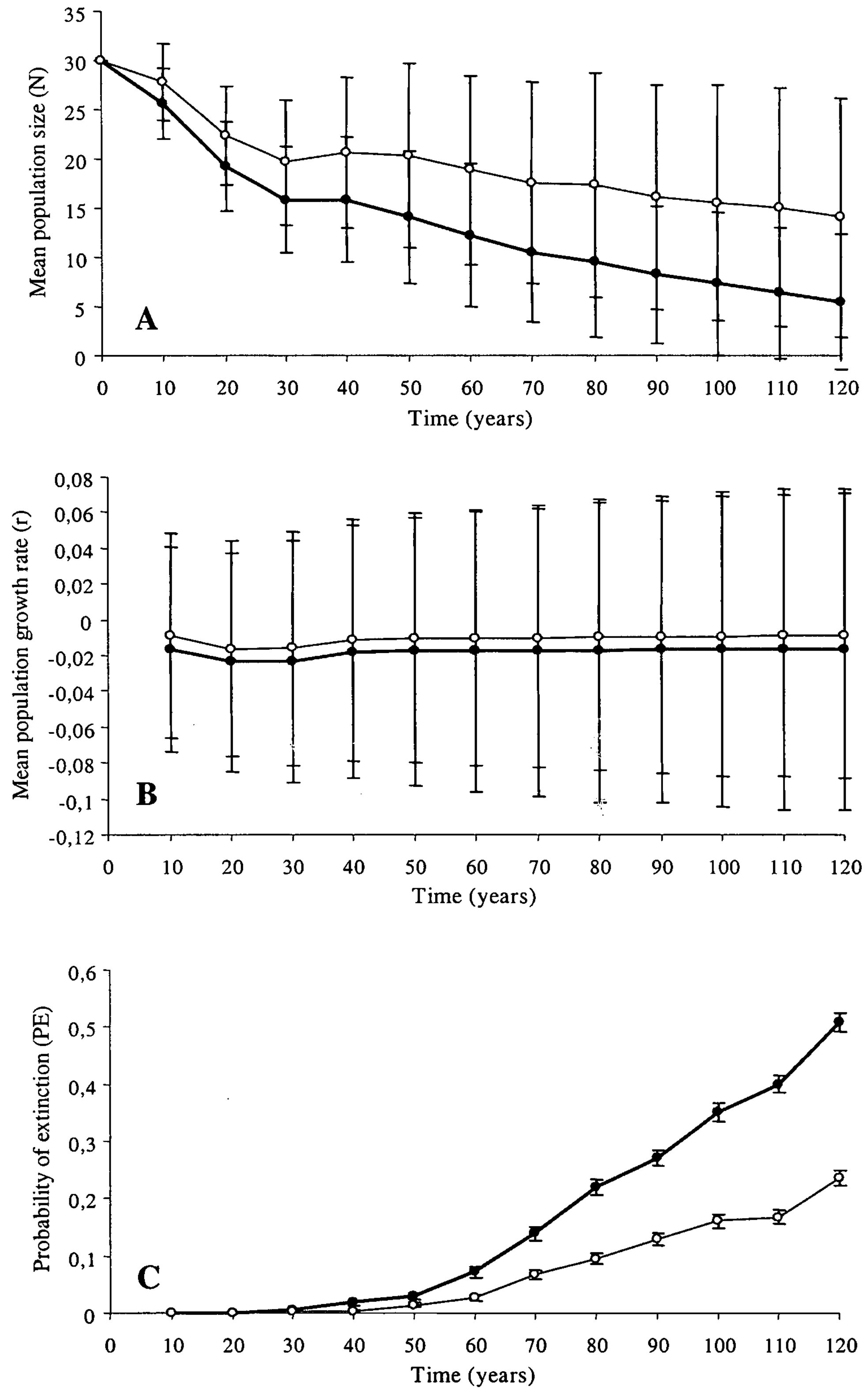

Figure 6.3. PVA predictions for the model which simulates the death of 2 calves each 4 years due to collisions with recreational watercraft (●) (error bars are plus/minus one standard error), and that of the "current model" (○); **A** -Mean population size; **B** - Mean population growth rate; **C** - Probability of extinction.

disturbance due to dolphin-watching in critical areas. Outside these areas, a code of conduct is also urgently necessary.

6.4.3. Monitoring

If we are to document the results of the management actions towards the conservation objectives, a monitoring scheme must be implemented. Because the bottlenose dolphin is a long-lived animal and the conservation objectives are also long term, a long term monitoring scheme will be necessary. Acquiring data regularly over a long time period may be an economic problem for local agencies. A long term monitoring scheme, such as the one described in this study, is also valuable because of the biological information it generates, as it has been seen in other studies (Gerber et al. 1998), and it will help to ensure that further declines are detected quickly (Thompson et al. 2000).

Special requirements would be: a) maintaining the ability to generate accurate estimates of life history traits, particularly of adult and sub-adult survival, b) to improve the accuracy of the first year survival estimate and thus fecundity estimates. Our past experience suggests that the level of survey effort should guarantee that animals have been photographed on both sides in each month. This may be unnecessary for adults whose marks do not change very much. However this level is particularly critical for being able to keep track of the high rate of change of temporary marks used to identify newborn and older calves (chapters 2 and 4).

A final point is that the PVA results presented here should not be seen as fixed over time. This is not only because conservation objectives aim to change the status of the population, but also because, if that is the case, changes should be incorporated to update the predictions so that management actions can be reviewed (Beissinger 2002).

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