

Dolphins in a bottle: abundance, residency patterns and conservation of bottlenose dolphins *Tursiops truncatus* in the semi-closed eutrophic Amvrakikos Gulf, Greece

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ABSTRACT

1. Boat surveys were conducted between 2002 and 2005 to study bottlenose dolphins living in the 400 km² Amvrakikos Gulf, western Greece. During 116 survey days, 4705 km of total effort resulted in the individual photo-identification of 106 animals, through long-term natural markings on their dorsal fins.

2. Mark–recapture analyses based on the M_{th} model provided estimates of 82 marked individuals in 2003 (95% CI = 80–91), 92 in 2004 (95% CI = 86–108) and 98 in 2005 (95% CI = 94–110). To include the unmarked portion of the population, the proportion of unmarked individuals was computed based on the number of photographs of marked and unmarked dorsal fins. The mean proportion of unmarked animals in the population was 0.338 (95% CI = 0.288–0.389). By adding this to the estimate for marked animals in 2005, considered as the most robust, a total population estimate of 148 individuals (95% CI = 132–180) was obtained.

3. Dolphin encounter rates in 2003–2005 did not show significant variations, and averaged 7.2 groups per 100 km or 72.5 individuals per 100 km. Encounter rates within the Gulf were about one order of magnitude greater than those found for bottlenose dolphins in nearby eastern Ionian Sea coastal waters.

4. Mean dolphin density in the Gulf was 0.37 animals km⁻². This relatively high density, together with high levels of site fidelity shown by most individuals, was thought to be related primarily to prey availability, particularly of epipelagic schooling fish.

5. The importance of the semi-closed Amvrakikos Gulf for bottlenose dolphins and other threatened species encourages the adoption of measures aimed to conserve its valuable ecosystems and raise the naturalistic profile of the area, while promoting environment-conscious development. Meaningful action includes restoring natural hydrology (e.g. freshwater input from rivers), curtailing pollution from various sources, responsible fisheries and aquaculture management, and control of illegal fishing. Interactions between dolphins and fisheries also deserve careful quantitative investigation.

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INTRODUCTION

The common bottlenose dolphin *Tursiops truncatus* (hereafter ‘bottlenose dolphin’) has been studied intensively in numerous locations around the world, and today is one of the best known of the 85+ living cetacean species (Leatherwood and Reeves, 1990; Reynolds *et al.*, 2000). In the Mediterranean Sea, field studies on cetaceans started only in the late 1980s (Notarbartolo di Sciara and Bearzi, 2005) and still relatively little is known about bottlenose dolphins in this basin. In 2006, the Mediterranean ‘subpopulation’ of bottlenose dolphins was assessed by an IUCN/ACCOBAMS Red List Workshop and considered to qualify as ‘Vulnerable’ according to the IUCN Red List criteria (Bearzi and Fortuna, 2006). This assessment was based on suspected population declines caused by intentional killing and extermination campaigns conducted in portions of the basin until at least the early 1960s (Bearzi *et al.*, 2004), and by recent and ongoing incidental mortality in fishing gear. The proposed classification also took into consideration the ongoing threats from habitat degradation (including environmental contamination by chemical pollutants and disturbance by marine traffic) and from overfishing of prey populations. These latter factors were suspected of contributing to generalized declines in abundance of bottlenose dolphins in the Mediterranean.

Estimating population sizes and determining trends in abundance is an integral part of any management strategy. This study focuses on a resident, largely isolated population of bottlenose dolphins living in the murky and eutrophic waters of a semi-closed shallow enclosure, the Amvrakikos Gulf, connected to open sea waters by a single narrow channel.

The Amvrakikos Gulf—which comprises a series of marshes and lagoons and is one of the most important wetland systems in Greece—has been designated as a Ramsar site in 1975, as a Special Protection Area (EC Directive 79/409 on the conservation of wild birds) and as a Specially Protected Area (SPA) under Protocol 4 of the Barcelona Convention. In 2006 the Amvrakikos Gulf was proposed as a National Park.

High dolphin density in a virtually closed ecosystem makes the Gulf an important ‘natural laboratory’ for dolphin research and food-web studies (Bearzi, 2004), and further highlights the need for protecting this unique and vulnerable area through the adoption of substantial management measures informed by scientific evidence.

METHODS

Study area

The Amvrakikos Gulf is a semi-closed sea situated in north-western Greece, stretching over about 35 km and covering an area of approximately 400 km² (excluding its enclosed marshes and lagoons). It is virtually a closed basin as its only link to the open Ionian Sea is a narrow strait, the Preveza channel, 370 m wide and 5 m deep in its narrowest and shallowest points (Figure 1). The sea floor is mostly 30 m deep (maximum depth 60 m) and covered with mud or sand. The waters are murky (Secchi disk readings ranging between 2 and 12 m), eutrophic and strongly affected by runoff from the two rivers Louros and Arachthos. The Gulf acts as a typical dilution basin from winter to early summer; evaporation during summer and early autumn becomes more important than freshwater input from rivers, but not enough to raise salinity values above

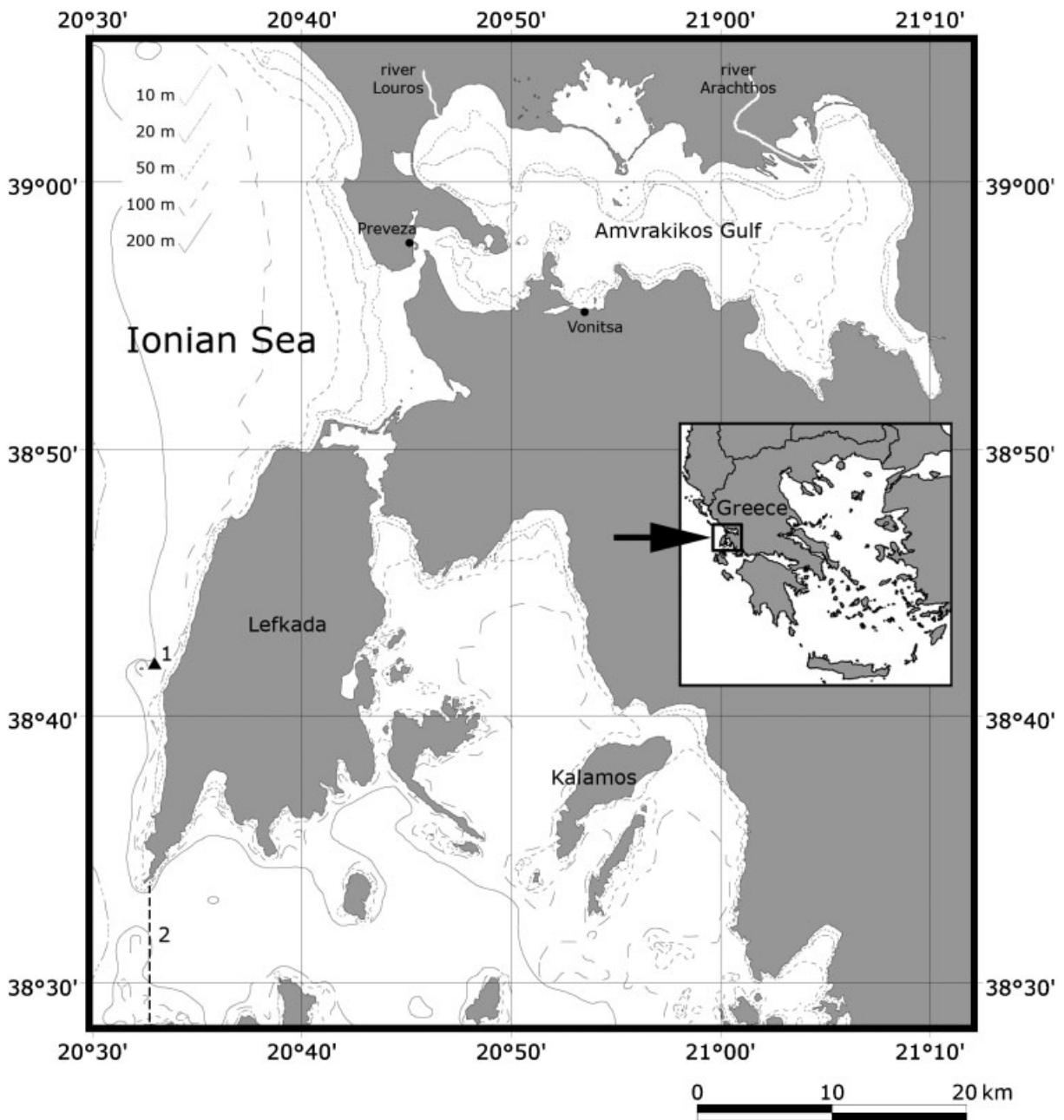


Figure 1. The Amvrakikos Gulf and surrounding eastern Ionian Sea coastal waters with the bathymetry and the locations cited in the text. (1) The black triangle shows the position where eight bottlenose dolphins were individually identified in 2003. (2) East of the dashed line 85 bottlenose dolphins were individually identified between 1993 and 2004 (see 'Discussion').

those of the open sea (Panayotidis *et al.*, 1994; Friligos *et al.*, 1997). Surface salinity fluctuates widely but remains low throughout the year (17–35‰: Friligos *et al.*, 1997), resulting in strong stratification of the upper layer. Sea-surface temperatures measured between February and September throughout this study ranged between 9.0 and 30.5°C.

Survey effort and encounter rates

A total of 116 surveys were conducted from 4.7 to 5.8 m inflatable craft with rigid hulls powered by 50–80 HP four-stroke outboard engines in years 2002–2005, between February and September. Different portions of the study area were covered on different days during *ad libitum* navigation. Bottlenose dolphins were the only cetacean species observed in the Gulf. The survey coverage totalled 4705 km. Of these, 1477 km of survey met the following conditions ('on effort': Bearzi *et al.*, 2005, 2006): (1) daylight and long-distance visibility; (2) sea state ≤ 1 Douglas with no swell (including either completely flat sea, flat sea with capillary waves or wavelets less than 10 cm high with no foam or breaking crests); (3) at least two experienced observers scanning the sea surface; (4) eye elevation of approximately 2 m for both observers; and (5) survey speeds between 28 and 36 km h⁻¹. Binoculars were not used during navigation. All daily surveys started from the port of Vonitsa (Figure 1), and ended there. A daily survey was interrupted and navigation went off effort if (1) dolphins were sighted; (2) sea or weather conditions deteriorated; or (3) other factors forced the crew to return to the port (e.g. late hour, running out of fuel, etc.). Survey routes varied depending

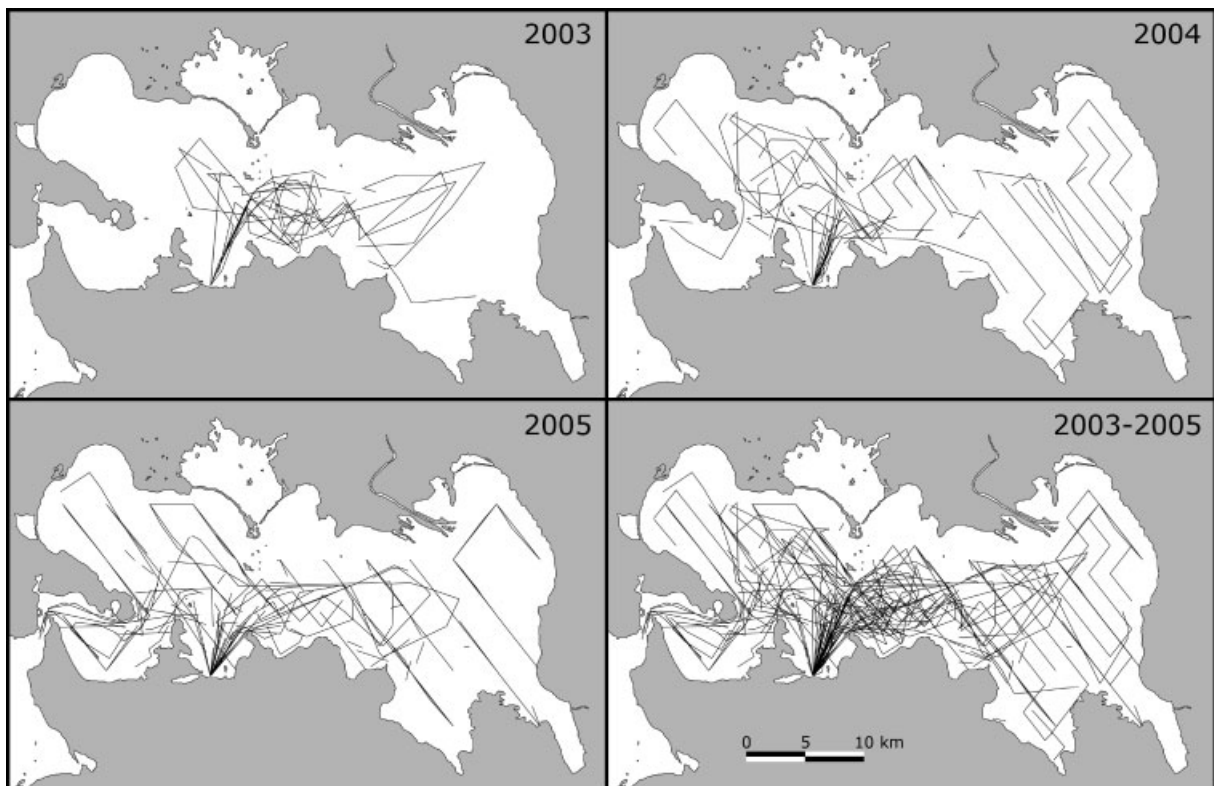


Figure 2. Survey coverage 'on effort' in years 2003–2005.

primarily on weather conditions (Figure 2). To account for the uneven geographical distribution of the survey effort, the study area was subdivided into cells of 2' latitude by 2' longitude (3704 × 2889 m). Cells with a total survey effort lower than a cell's diagonal (4697 m) were excluded from the analysis of encounter rates, resulting in a set of 28 cells used for the analyses. Encounter rates were calculated for each year by the ratio n/L , where n is the total number of sightings and L is the total number of kilometres spent on effort (Bearzi *et al.*, 2005). As several cells contained variable portions of land, encounter rates in individual cells including portions of land were weighed on the relative proportion of land within the cell, based on the simple formula:

$$\text{weight}_i = \frac{\text{sea area within cell}_i}{\text{total area cell}_i}$$

Weighted estimators were then used in every step of the analysis involving the 28 cells instead of the usual unweighted central tendency estimators. A survey subset with consistent effort, totalling 870 km, was used to compare encounter rates in July–August 2003–2005 (Table 1). To test whether cells were spatially autocorrelated, and hence not independent, Moran's I index was computed for encounter rates in years 2003–2005 by using the MapStat extension to ArcView. Moran's I index was not significantly different from zero ($I = 0.12$, $p > 0.05$) showing that cells were not spatially autocorrelated.

Individual photo-identification

During 106 days it was possible to obtain colour photographs suitable for individual identification, based on long-term natural marks on the dolphins' dorsal fins (Würsig and Würsig, 1977). On each encounter with a group of dolphins the attempt was made to obtain as many good photographs as possible of all individuals present, throughout the duration of the observation. Photo-identification was performed following Würsig and Jefferson (1990), with cameras equipped with 70–200-mm f2.8 zoom lenses, using 100 ISO colour transparency film in August–September 2002 and February–April 2004, and digital photography in all the other months. Considering that digital photography substantially improves the efficiency of individual dolphin identification (Markowitz *et al.*, 2003), transparencies were scanned at high

Table 1. Number of daily surveys, number of bottlenose dolphin sightings and kilometres surveyed 'on effort' in years 2002–2005. The boxed areas show the survey subsets on which encounter rates were computed

Year	Feb	Apr	Jun	Jul	Aug	Sep	Subtotal	Sightings
2002					1	7	8	10
2003				9	6		15	20
2004	6	5	7	9	18	6	51	56
2005			8	10	14	18	50	91
Total	6	5	15	28	39	31	124	177
Kilometres surveyed 'on effort'								
Year	Feb	Apr	Jun	Jul	Aug	Sep	Subtotal	
2002					15.9	69.2	85.1	
2003				161.4	137.2		298.6	
2004	68.8	85.4	44.7	37.9	200.5	33.1	470.5	
2005			104.7	140.0	192.4	185.5	622.6	
Total	68.8	85.4	149.4	339.3	546.1	287.8	1476.8	

resolution and turned into digital images for consistency of evaluation and analysis. Both transparencies and digital photos were then cropped around the dorsal fin and visible part of the body and selected using consistent criteria (i.e. entire dorsal fin visible, fin perpendicular to camera, high sharpness and resolution, no water spray masking fin profile), based on recommendations provided by Read *et al.* (2003). Following such selection, the catalogue included 1213 transparencies and 11 140 digital photos, totalling 12 353 dorsal fin photos (Table 2). These images were then matched and the identified animals included in a database. Only individuals with distinctive dorsal fin profiles, carrying permanent marks suitable for reliable long-term identification from either side of the fin were used for mark–recapture analyses. Individuals with a single tiny nick on their dorsal fins' trailing edge, and individuals without nicks recognizable exclusively on the basis of dorsal fin shape and/or temporary scars were not used, as their inclusion could result in borderline or incorrect attributions of a match, that could bias the analyses (e.g. through violation of one or more mark–recapture assumptions, see below).

Mark–recapture analyses

Mark–recapture studies rely on the number of animals marked and their proportion in subsequent samples to estimate population parameters including abundance (Seber, 1982). Since the 1980s these methods have been used widely to assess the population abundance of several cetacean species, based on photographic records of naturally marked individuals (Hammond, 1990; Hammond *et al.*, 1990; Wilson *et al.*, 1999). Mark–recapture estimates based on model M_{th} (which allows capture probabilities to vary from one day to the next and between individual animals; Chao *et al.*, 1992), and based on the alternative model M_t (which allows capture probabilities to vary by time or sampling occasion; Darroch, 1958), were obtained by using program Capture (found in program Mark 4.3; <http://www.warnercnr.colostate.edu/~gwhite/mark/mark.htm>). Following a multisample recapture approach similar to that used by Read *et al.* (2003), we selected two consecutive sampling periods of 18–23 days having a maximum of photo-identification effort in years 2003–2005, separated by gaps of 7–13 days (Table 3). These intervals were a compromise between a sampling period short enough to meet the closed-population assumptions, and long enough to include a high photo-identification effort. The 7–13-day gaps were intended to allow for the remixing of animals in the population.

Mark–recapture models operate under assumptions about the nature of the studied population and the way it is sampled. As violation of these assumptions can lead to biased estimates, it is important that assumptions are explored, validated and carefully described (Williams *et al.*, 1993; Wilson *et al.*, 1999; Read *et al.*, 2003). Closed population mark–recapture analyses commonly assume the following: (1) marks are not lost during the study; (2) animals do not respond to being captured in a way that affects their subsequent probability of recapture; (3) births and deaths do not occur during the study; (4) immigration and/or emigration do not occur during the study; (5) marks are correctly recognized on

Table 2. Number of dorsal fins photographs obtained in years 2002–2005 following selection

Year	Feb	Apr	Jun	Jul	Aug	Sep	Subtotal
2002					27	437	464
2003				1030	739		739
2004	537	212	788	1747	1384	1100	5768
2005			645	520	1743	2474	5382
Total	537	212	1433	2267	3893	4011	12353

Table 3. Estimates obtained in years 2003–2005 based on a closed population model M_{th}

Year	1st	2nd	Sampling interval					Marked animals					Marked and unmarked animals				
			Time interval days	Days between samples	Days with photo-id. effort	Suitable photos	Marked animals identified	N	SE	95% CI low	95% CI high	N	95% CI low	95% CI high	N	95% CI low	95% CI high
2003	12–29 Jul.		18		9	819	71	84	6.36	77	103						
	6–27 Aug.		22		6	598	70	108	16.78	87	156						
	12–29 Jul.	6–27 Aug.	37	7	15	1417	78	82	2.84	80	91	124	112	149			
2004	6–24 Jul.		19		7	552	58	76	9.85	65	107						
	7–25 Aug.		19		12	1060	71	90	8.45	80	114						
	6–24 Jul.	7–25 Aug.	51	13	19	1612	81	92	5.42	86	108	138	121	177			
2005	4–26 Aug.		23		12	1700	74	87	6.67	80	107						
	8–30 Sep.		23		13	2191	82	100	7.62	90	121						
	4–26 Aug.	8–30 Sep.	58	12	25	3891	91	98	3.98	94	110	148	132	180			

recapture; and (6) within a sampling occasion all animals in the population have an equal probability of being captured. In the present study, the assumptions under which mark–recapture models operate were addressed as follows.

1. Mark loss. Nicks and other dorsal fin edge mutilations are long-lasting in bottlenose dolphins (Wilson *et al.*, 1999). The main problem is represented by the progressive addition of new dorsal fin nicks and notches over time, that occasionally make photographs of the same dorsal fins difficult to match. Experience of the person doing the matching and use of a combination of dorsal fin features can solve the problem in most cases. In addition, changes in dorsal fin marks are a relatively infrequent occurrence over short periods of time, such as the sampling intervals used here (Wilson *et al.*, 1999). It is therefore considered that mark loss or gain was negligible over the duration of this study.
2. Behavioural responses. The Amvrakikos Gulf population lives in a basin where encounters with boats are a relatively common occurrence and the animals do not normally avoid small boats that approach them at slow speed and manoeuvre carefully to minimize disturbance. It is improbable that the benign process of being photographically ‘captured’ could lead to changes in subsequent behaviour. As with other studies of this kind, violation of this assumption is considered to be unlikely (Hammond, 1990; Wilson *et al.*, 1999; Read *et al.*, 2003).
3. Demographic closure. Bottlenose dolphins are large mammals with low reproductive and high survival rates (Reynolds *et al.*, 2000). A limited number of births and deaths might have occurred during the study but their low probability of occurrence within the chosen sampling periods makes it unlikely that the assumption of demographic closure was violated.
4. Geographic closure. Indirect evidence of population closure — at least within periods as short as the sampling periods used here — was given by high levels of site fidelity (Figure 3), lack of observed dolphin movements across the narrow channel connecting the Amvrakikos Gulf to the open Ionian Sea waters, lack of re-sightings in nearby open waters of dolphins identified in the Gulf, and specialized behaviour shown by dolphins within the Gulf (see ‘Discussion’). Zafropoulos and Merlini (2001) recorded no bottlenose dolphin sightings during surveys in Ionian Sea waters west of the Gulf (340 km of total effort), and considered this as further evidence of population closure within the Gulf. Similarly, no sightings occurred west of the Gulf across 326 km surveyed under favourable conditions in June–December 2006 (Tethys Research Institute, unpublished data). Although movements between the Amvrakikos Gulf and the Ionian Sea may take place, their occurrence appears to be low, and it is unlikely that the assumption of geographic closure within the chosen sampling period is violated.
5. Mark recognition. Mark–recapture analyses assume that a marked animal will be recognized with certainty if recaptured. This assumption can be violated if poor quality photographs or ambiguous markings are used to identify individuals. In this study, photographs having a sub-optimal quality were not used and only dolphins with distinctive dorsal fin marks were considered. Therefore, violation of the mark recognition assumption was extremely unlikely.
6. Heterogeneity of capture probabilities. Standard mark–recapture methods assume that, within a sample, all individuals have the same probability of being captured. While ways of handling this problem may vary (e.g. compare Wilson *et al.* (1999) with Read *et al.* (2003)), this assumption is often violated in cetacean mark–recapture studies (Hammond, 2001). Individual preferences for certain areas may affect the probability of encountering an animal, and individual differences in surface activity, surfacing pattern or boat-avoidance behaviour may affect the probability of obtaining usable photographs (Hammond, 1986; Wilson *et al.*, 1999). Violation of the assumption of equal probability of capture would result in underestimation of population size. Although during the sampling periods an attempt was made to cover the whole study area homogeneously (in particular in 2004 and 2005; Figure 2 and see ‘Discussion’), truly equal probabilities of encountering each individual were unlikely to have been achieved. To minimize this problem, attempts were made to photograph every individual in a group and

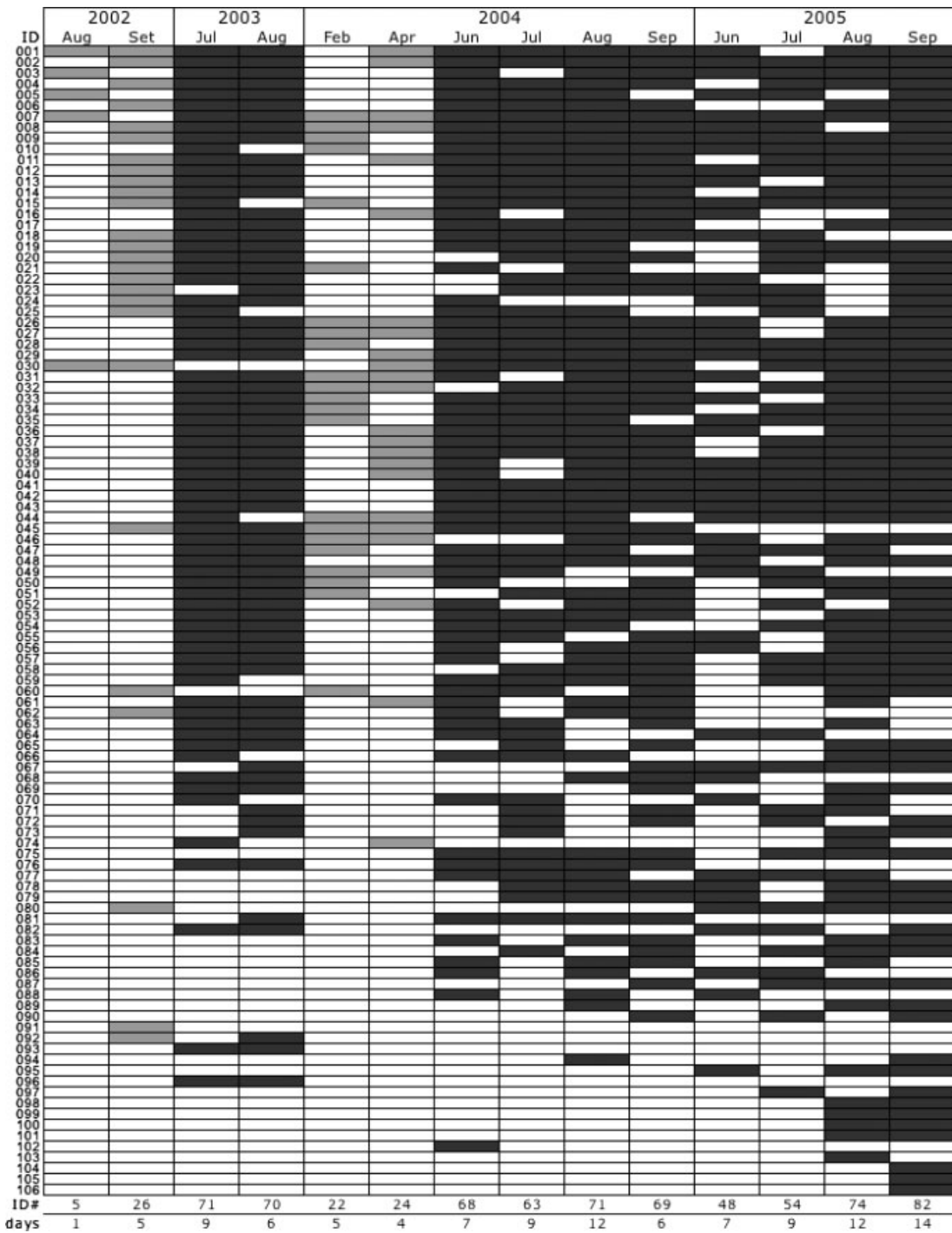


Figure 3. Residency pattern of 106 marked individuals in the Amvrakikos Gulf. Black and grey cells indicate presence documented through digital photo-identification and transparencies, respectively; 'ID' (001–106) are the individuals identified; 'ID#' indicates the number of individuals encountered in each month of the study; 'days' is the number of days with photo-identification effort in a given month.

avoid preferential photographing of any particular individual. Despite these attempts, heterogeneity of capture probabilities was unlikely to have been completely overcome, most notably owing to individual preferences for particular areas, and thus the use of the M_{th} model (which allows relaxation of this assumption; Chao *et al.*, 1992) was preferred over the alternative model M_t (Darroch, 1958).

Proportion of unmarked animals

Some mark–recapture studies disregard unmarked animals in final population estimates. The unmarked component, however, may be relevant. To include the unmarked portion of the population and obtain an estimate of the total population, the proportion of unmarked individuals (which also included sub-adult classes) was computed on the basis of the number of photographs of marked and unmarked dorsal fins obtained daily (Williams *et al.*, 1993). This method relies on (1) extensive photo-identification effort, making it likely that most if not all animals are photographed (Ballance, 1990); and (2) a consistent attempt to photograph as many animals as possible in a group, regardless of their dorsal fin markings and body size (or age class). Modern digital photography provides obvious advantages (fast focusing, sharpness etc.; Markowitz *et al.*, 2003) compared to methods used in the past, and is likely to reduce substantially the problem of sampling heterogeneity reported in studies relying on film and older cameras. The alternative method based on number of marked and unmarked animals in groups in which all members were photographed (e.g. Bearzi *et al.*, 1997) could not be reliably adopted in the study area, where groups were mostly extremely fluid, making it difficult to relate photo-identification data to any stable subgroup.

RESULTS

Encounter rates

Encounter rates in 2003–2005 (July–August) were computed for both groups and individuals. The former averaged 7.3 groups per 100 km (quartiles: 0.0, 0.0, 11.3; range 0.0–57.5, $n = 83$) and did not vary significantly among years (Kruskal–Wallis rank test $H = 0.451$, $df = 2$, $p > 0.05$). The latter averaged 72.5 individuals per 100 km (quartiles: 0.0, 0.0, 109.5; range 0.0–517.2, $n = 83$) and also did not vary significantly among years (Kruskal–Wallis rank test $H = 1.240$, $df = 2$, $p > 0.05$).

Individual photo-identification

A total of 106 marked individuals were photographically identified between 2002 and 2005. The residency pattern of all individuals identified during the study is shown in Figure 3. Changes in the monthly number of animals identified appeared to depend largely on photo-identification effort. Lower effort and the use of transparencies rather than digital photos in August–September 2002 and February–April 2004 resulted in few identifications. Conversely, 54–74 marked individuals could be identified in months of high photo-identification effort (6–12 days), with a peak of 82 animals in September 2005, when the effort was highest (14 days, 2474 photos: Table 2, Figure 3).

Mark–recapture and proportion of unmarked animals

Mark–recapture analyses based on closed population models resulted in different estimates for the chosen M_{th} model and for the alternative M_t model. Estimates obtained based on the M_{th} model were larger than the equivalent estimates based on the M_t model. This further confirmed that there was heterogeneity of capture probabilities within the data (Williams *et al.*, 1993; Wilson *et al.*, 1999). Population estimates obtained through the M_{th} model were therefore considered as the most reliable in this study.

Mark–recapture analyses provided different estimates for years 2003–2005 (Table 3). As these estimates relied on natural markings to identify individuals, mark–recapture estimates refer exclusively to the population of marked animals. To include the unmarked portion of the population and obtain estimates of the total population, the proportion of unmarked individuals (which also included sub-adult classes) was computed on the basis of the number of photographs of marked and unmarked dorsal fins obtained daily (Williams *et al.*, 1993). Across 42 survey days performed in June–September 2005 (when the photo-identification effort was greater: 5382 selected digital photos), a high correlation ($R^2 = 0.878$) was found between the number of photos of unmarked animals and the number of photos of marked and unmarked animals, suggesting that the proportion of marked and unmarked animals was relatively consistent. Based on the ratio of daily number of photos of marked and unmarked animals in year 2005, the mean proportion of unmarked animals in the population was 0.338 (95% CI = 0.288–0.389, $n = 42$). By adding this mean proportion of unmarked individuals to the mark–recapture estimate, total population estimates of 124 (95% CI = 112–149), 138 (95% CI = 121–177) and 148 (95% CI = 132–180) animals were obtained for years 2003, 2004 and 2005, respectively. The 2005 estimate should be considered as the most robust (see ‘Discussion’).

DISCUSSION

Following a study conducted in 1998–2000, resulting in the photographic identification of 48 individuals, Zafiroopoulos and Merlini (2001) suggested that about 90 dolphins could be living in the Amvrakikos Gulf. However, this figure was conjectural and cannot be compared with abundance estimates obtained in the present study, or used to infer trends in population abundance. The estimates presented here for years 2003–2005 were obtained following a methodology similar to that used by Read *et al.* (2003) to estimate bottlenose dolphin abundance in a much larger area off North Carolina, but choosing a different model that takes into account heterogeneity of capture probabilities (Williams *et al.*, 1993; Wilson *et al.*, 1999). Mark–recapture studies rely on extensive photo-identification effort and appropriate area coverage. Intensity of photo-identification effort and area coverage in year 2002 were inappropriate for a mark–recapture study. In year 2003, the geographic distribution of photo-identification effort (Figure 2) may have been insufficient to obtain mark–recapture estimates as reliable as those obtained in 2004 and particularly in 2005, when the effort was also higher. In addition, an interval of 7 days between sampling sessions in 2003 may not have allowed sufficient remixing of animals in the population. The geographic distribution of the effort in years 2004 and 2005 was similar, and the slight (about 6%) difference between central abundance estimates are likely to relate predominantly to differences in the intensity of the effort in terms of number of photos and sampling days (Table 3).

If significant immigration or emigration were to occur during the study, then sampling extending over longer time periods would result in larger estimates of abundance. In 2005, the estimate from the entire sampling period was greater than the estimate derived from the first sampling interval but smaller than the estimate from the second (Table 3). According to Read *et al.* (2003), this suggests that significant movement of animals into or out of the Amvrakikos Gulf did not occur during the course of the mark–recapture study. Conversely, in 2003 and 2004 the estimates from the entire sampling periods were smaller and greater, respectively, than those derived from the first and the second sampling intervals (Table 3). This also suggests a higher robustness of the 2005 estimate.

The alternative possibility of population fluctuations among years was further investigated through the analysis of encounter rates (Bearzi *et al.*, 2006). Although relatively small changes in population density could not be detected, owing to low statistical power, encounter rates in 2003–2005 did not show significant variations.

The estimated 148 dolphins that live in the 400 km² semi-closed Amvrakikos Gulf equate to a mean density of 0.37 animals km⁻². This is a relatively high value. Encounter rates in the Gulf, averaging 7.3 groups per 100 km, were much greater than those found for bottlenose dolphins in the nearby area of Kalamos (0.63 groups per 100 km), in eastern Ionian Sea coastal waters, where survey methods and analytical approach were consistent with those used in this study (Bearzi *et al.*, 2006). Comparisons with absolute and/or relative abundance estimates obtained in other portions of the Mediterranean are more difficult, as these are based on variable methods and expressed inconsistently. However, the available figures suggest that bottlenose dolphin density in the Amvrakikos Gulf is greater than that found in most other Mediterranean areas where mark-recapture or distance sampling studies have been conducted (Bearzi and Fortuna, 2006), with the exception of the Strait of Gibraltar (Pérez *et al.*, 2006). It should be stressed that as dolphin population estimates presented here are based on summer samples, absolute abundance and densities in other seasons cannot be inferred.

As a result of the high input of nutrients due to river runoff and from other sources, the Amvrakikos Gulf is amongst the most productive coastal areas of Greece. Biomass of phyto- and zooplankton is high and has probably increased in recent times (Panayotidis *et al.*, 1994; Pancucci and Panayotidis, 1994). Zooplankton abundance (particularly copepods, cladocerans and echinoderm larvae; Pancucci *et al.*, 1988; Panayotidis *et al.*, 1994) appears to support dense populations of small epipelagics (Conides and Papaconstantinou, 2001). Clupeids such as round sardinella *Sardinella aurita* and European pilchard *Sardina pilchardus* are abundant in the Gulf, and seem to represent important prey for local bottlenose dolphins (Zafiroopoulos and Merlini, 2001; Tethys Research Institute, unpublished data). High density of bottlenose dolphins within the Gulf seems to relate primarily to prey availability.

Predation by sharks is unlikely to affect dolphin population dynamics within the Gulf, as large sharks are rare in the region (Bearzi *et al.*, 2006) and evidence of shark attacks on dolphins has never been recorded either in eastern Ionian Sea waters or in the Amvrakikos Gulf.

Differences in prey type and availability appear to have resulted in diet and behavioural adaptations among dolphins living in the Amvrakikos Gulf, which show specialized feeding behaviour (Zafiroopoulos and Merlini, 2001; Tethys Research Institute, unpublished data). Dolphins in the Gulf consistently engage in obvious surface foraging and cooperatively target schooling epipelagic prey (particularly European pilchard and the locally abundant round sardinella). Conversely, bottlenose dolphins in the nearby open waters around the island of Kalamos feed predominantly on demersal prey, and occurrence of surface feeding is insignificant (Bearzi *et al.*, 2005).

Regular photographic recapture showed that bottlenose dolphins in the Amvrakikos Gulf have high levels of site fidelity, and most of the catalogued individuals could be predictably encountered whenever an appropriate photo-identification effort was in place (Figure 3). Although unknown levels of movements to and from the eastern Ionian Sea open waters may occur, dolphins living in the Gulf appear to be members of a population that is largely isolated. No matches were found between bottlenose dolphins photo-identified in the Amvrakikos Gulf and a total of 83 individuals identified in 1993–2006 in the waters surrounding the island of Kalamos and south of the island of Lefkada, approximately 40–60 km away from the Preveza channel (Bearzi *et al.*, 2005; Tethys Research Institute, unpublished data; Figure 1). A total of eight bottlenose dolphins identified in August 2003 west of the island of Lefkada, about 30 km from the Preveza channel (Figure 1), also provided no matches with animals identified within the Gulf. Dolphins encountered in the south-west portion of the Gulf, in proximity to the strait, were sometimes followed for periods of up to several hours, but they were never seen entering the narrow path leading to open waters. It must be noted, however, that this only represents indirect evidence from preliminary observations, and more focused research would be needed to evaluate the occurrence of crossings in and out of the Amvrakikos Gulf. Insightful studies to assess actual rates of immigration and emigration would include year-round visual and/or acoustic research in the channel linking the Gulf to the Ionian Sea, photo-identification effort in the open waters adjacent to the strait, and genetic comparisons.

The flexible social organization and opportunistic behaviour of bottlenose dolphins allow them to colonize various kinds of relatively small coastal systems. Many inshore 'communities' of bottlenose dolphins elsewhere in the world are known to live in relative isolation in semi-closed areas such as fiords (Williams *et al.*, 1993), large embayments, small bays and lagoons (Wells *et al.*, 1987; Ballance, 1990; Corkeron, 1990; Pryor *et al.*, 1990; Shane, 1990; Fertl, 1994; Wilson *et al.*, 1997; Read *et al.*, 2003), river systems and estuaries (Odell and Asper, 1990; Ingram, 2000; Harzen, 2002), or atolls (Campbell *et al.*, 2002). Under such circumstances, and particularly when philopatry is high, the dolphins tend to develop habitat-specific behaviour, social organization and diet patterns (Hoese, 1971; Pryor *et al.*, 1990; Barros and Wells, 1998; Connor *et al.*, 2000; Allen *et al.*, 2001; Gannon and Waples, 2004; Hastie *et al.*, 2004). Population structure and/or different 'ecotypes' may develop for isolated local groups that are habitat- or resource-dependent, as suggested by genetic, haematologic and morphometric studies (Duffield *et al.*, 1983; Hersh and Duffield, 1990; Van Waerebeek *et al.*, 1990; Hoelzel *et al.*, 1998; Natoli *et al.*, 2004, 2005), provided that segregation occurs for a sufficiently long time. Although philopatry within coastal systems varies among individuals, genders and populations, ranging from strict long-term residency within very small areas to long-distance movements (Connor *et al.*, 2000), complete isolation rarely or never occurs and genetic bottlenecks are eluded through variable levels of immigration/emigration. In the Amvrakikos Gulf, the extent and frequency of such exchanges remain to be documented, but movements of individuals to and from the adjacent Ionian Sea open waters are likely to occur.

However, the apparently high level of geographic isolation of bottlenose dolphins living in the Amvrakikos Gulf and the ongoing degradation of the Gulf's ecosystems raise concerns about their vulnerability. Water quality in the Amvrakikos Gulf has worsened owing to pollutants carried by the rivers Louros and Arachthos and waste waters from coastal cities and industrial/agricultural processes in the broader area (Albanis *et al.*, 1995; Kotti *et al.*, 2005). Hydroelectric power dams upstream of the rivers, use of the rivers' fresh water for agriculture irrigation and industry, and port construction that narrowed the width of the Preveza channel appear to have contributed to altering the Gulf's natural hydrology and hydrodynamics. Furthermore, agriculture, livestock, grazing and fish farming have affected nutrient flows into the Gulf, resulting in increased eutrophication (Panayotidis *et al.*, 1994; Nireus/NCMR, 2000; Kotti *et al.*, 2005). Anoxia in deep bottom waters, increased water temperatures, and illegal fishing were listed among the reasons behind the decline of economically valuable shrimps *Penaeus kerathurus* (Conides and Papaconstantinou, 2001). Other commercial fish species have declined considerably, and fishing is considered no longer economically viable, although the Amvrakikos Gulf was once one of the richest fishing areas of Greece (Nireus/NCMR, 2000; Conides and Papaconstantinou, 2001). Today, only a few fish species including European pilchard and round sardinella appear to be abundant, but market demand for the former is low, and the latter, often caught in large quantities, is regarded as bycatch and routinely discarded.

Claims of bottlenose dolphin immigration in the Amvrakikos Gulf driven by increased abundance of epipelagic schooling fish in recent times (e.g. Conides and Papaconstantinou, 2001) make a fascinating but at present unsupported hypothesis. It can equally be maintained that environment degradation having resulted in the decline of demersal species that represent typical prey for Mediterranean bottlenose dolphins (Blanco *et al.*, 2001) has forced these opportunistic and behaviourally flexible animals to switch diet and target epipelagic prey, with consequences at the population level that remain to be documented.

Gear damage and depredation caused by both dolphins and sea turtles is consistently lamented by artisanal fishermen operating in the Gulf (Conides and Papaconstantinou, 2001). However, this problem needs to be appropriately investigated and contextualized, e.g. by assessing the actual economic damage based on sound independent surveys, while refraining from using these animals as scapegoats for declining fishing yields and the remarkable anthropogenic impact suffered by the Gulf's ecosystems.

It has been suggested that the semi-closed Amvrakikos Gulf represents an ideal 'natural laboratory' for the investigation of food-web interactions and population dynamics of dolphins and fish that may increase

our understanding of marine trophodynamics (Bearzi, 2004). The Gulf's remarkable ecosystems and the valuable species living there, including the vulnerable Dalmatian pelican *Pelecanus crispus* and considerable numbers of endangered loggerhead sea turtle, *Caretta caretta*, are sustaining conservation efforts (Zogaris *et al.*, 2003). Basic conservation measures were outlined for the proposed National Park. Apart from improved management of the lagoons and marshes, however, the protection measures considered so far do not seem to be appropriate to solve the problems caused by reduced water exchange, increased eutrophication and pollution. The high local density of bottlenose dolphins documented by this study should be regarded as another reason to adopt management measures aimed to conserve the Gulf's valuable fauna and raise the naturalistic profile of the area, while promoting environmentally conscious development.

Actions that are likely to benefit water quality and marine biodiversity in the Amvrakikos Gulf include (1) measures aimed to restore water input from rivers and water exchange with the open sea; (2) curtailment of anthropogenic pollutants and nutrients from agriculture, industry and city waste waters; (3) efforts to prevent illegal fishing; and (4) monitoring and management of fish farming (both in the Gulf and in its tributaries Louros and Arachthos) which may contribute to eutrophication and cause other kinds of damage (Goldburg *et al.*, 2001), particularly in a semi-closed system such as the Amvrakikos Gulf. Environmental impact assessments should be conducted for works and activities that may alter (or may have altered) the Gulf's natural hydrology, particularly river dams, use of river water for irrigation, and constructions in the narrow Preveza channel. The existing prohibition of both trawling and purse-seining within the Gulf is a good example of insightful fishery management. However, patrolling is needed to make sure that existing regulations are fully respected, for example with regard to illegal trawling for shrimps. Navigation and pleasure boating in the Gulf, peaking in the summer, should be carefully regulated to reduce disturbance to dolphins and collision risk with sea turtles. Commercial nature trips organized in the Gulf, including dolphin-, turtle- and bird-watching, must be carefully managed based on strict codes of conduct that take into account the closed nature of the ecosystem, to prevent these activities from becoming yet another threat for the local fauna.

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