

Population biology, conservation threats and status of Mediterranean striped dolphins (*Stenella coeruleoalba*)

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ABSTRACT

The paper reviews the information available on those aspects of the biology, ecology and effects of human impact that are relevant to the management and conservation of striped dolphins in the Mediterranean Sea. The striped dolphin is common throughout the western Mediterranean, although it shows a preference for open waters beyond the continental shelf. In 1991, the western Mediterranean population was estimated as 117,880 (95% CI = 68,379-214,800), but no comparable estimates are available for the eastern basin. Geographical variation in body length, skull morphometrics and genetic analyses, as well as the geographic range and evolution of the 1990-1992 epizootic, suggest some degree of isolation between dolphins in different regions within the Mediterranean and independence from those in the Atlantic. Growth and reproductive parameters in the Mediterranean are, overall, similar to those of other populations, with the exception of age at sexual maturity, which in both sexes is extremely high (11-12 years). Tissue levels of organochlorine compounds, some heavy metals and selenium are high and exceed threshold levels above which detrimental effects commonly appear in mammals. However, apart from the indication that these levels may have acted as triggering factors in the 1990-1992 epizootic by depressing the immune system of diseased individuals and potential lesions in the ovaries, no information on pollutant-related effects is available. The 1990-1992 epizootic devastated the whole Mediterranean population; over one thousand corpses were examined in the western Mediterranean alone, but the toll was probably much higher. The causative agent of the die-off was a morbillivirus, but the effect of some pollutants and decreased food availability were suggested as triggering factors. Depletion of fish and cephalopod resources is widespread in the Mediterranean and, given that the diet of striped dolphins includes commercial species, this undoubtedly has a potential for limiting population numbers. A number of fishing activities produce an associated striped dolphin bycatch. In particular, the pelagic driftnet fishery for tuna and swordfish, carried out by boats from Italy, Spain and Morocco, produces a significant kill in various locations. Variation in sighting and stranding frequency suggests that striped dolphins may have increased their numbers in recent decades. However, this progressive increase may have run parallel to a reduction in carrying capacity of its habitat. This suggestion is supported by the late age at attainment of sexual maturity observed in the Mediterranean population as compared to other conspecific or even congeneric populations.

KEYWORDS: STRIPED DOLPHIN; FEEDING; REPRODUCTION; LONG-TERM CHANGE; ECOSYSTEM; POLLUTANTS; HEAVY METALS; ORGANOCHLORINES; EPIZOOTIC; HABITAT; TRENDS; FISHERIES; GILLNETS; INCIDENTAL CAPTURES; PURSE-SEINES; FOOD/PREY; MEDITERRANEAN; ATLANTIC OCEAN; EUROPE; AFRICA; DISEASE; CONSERVATION; ABUNDANCE ESTIMATE; SURVEY-VESSEL; GROWTH; DISTRIBUTION; GENETICS; AGE AT SEXUAL MATURITY

INTRODUCTION

Among the various cetacean species that inhabit the Mediterranean Sea, the striped dolphin (*Stenella coeruleoalba*) is generally considered to be the most abundant. However, the potential impact of fishing interactions, high levels of pollution and the drastic toll of an epizootic that afflicted the population during 1990-1992 have recently raised concerns about the capacity of the species to maintain its initial levels of abundance. The striped dolphin inhabits both the eastern and the western basins of the Mediterranean Sea and, although mainly an offshore species, it is also found in inshore waters when conditions are favourable.

This paper reviews the information available on those aspects of biology, ecology and effects of human impact relevant to the management and conservation of striped dolphins in the Mediterranean Sea.

DISTRIBUTION AND ABUNDANCE

The striped dolphin is present throughout the Mediterranean Sea but not at uniform densities. It is common in the western and central Mediterranean and is generally considered to be the most abundant cetacean (Forcada *et al.*, 1994). It is less common in the eastern basin, particularly in the easternmost part, where it is considered rare (Kinzelbach, 1997).

In all areas it shows a preference for highly productive, open waters beyond the continental shelf (Gannier and Gannier, 1993; Notarbartolo di Sciara *et al.*, 1993; Pulcini *et*

al., 1993a; Boutiba, 1994; Forcada *et al.*, 1994; Forcada and Hammond, 1998; Gannier, 1998; Cañadas and Sagarminaga, 1999). Thus, it is particularly abundant in the Ligurian Sea, the Gulf of Lions and the Alboran Sea (see Fig. 1).

Reliable population or density estimates are only available for the western basin and unfortunately they only refer to the period after the 1990-1992 die-off. Thus, in 1991, one year after the main epizootic outbreak in the western Mediterranean, striped dolphin numbers in the whole region (excluding the Tyrrhenian Sea) were estimated as 117,880 individuals (95% CI = 68,379-214,800; Forcada *et al.*, 1994).

Additionally, sightings cruises to estimate numbers and density for particular regions within the western Mediterranean were carried out during 1991-1992 (Forcada *et al.*, 1995; Forcada and Hammond, 1998). The results of these surveys are summarised in Table 1. The highest densities were found in the Ligurian Sea, with 0.2359 dolphins/km² (CV = 0.26; 95% CI = 0.1382-0.4026), and in the Alboran Sea, with 0.1955 dolphins/km² (CV = 0.33; 95% CI = 0.1048-0.3646). These two areas are generally considered to be the most productive in the western Mediterranean (Forcada and Hammond, 1998). Overall, striped dolphins were found to be more abundant in the northern rather than the southern regions, where they share the habitat with common (*Delphinus delphis*) and bottlenose (*Tursiops truncatus*) dolphins, which are also abundant in this region, particularly in inshore waters (e.g. Bayed and Beaubrun, 1987; Boutiba, 1994).

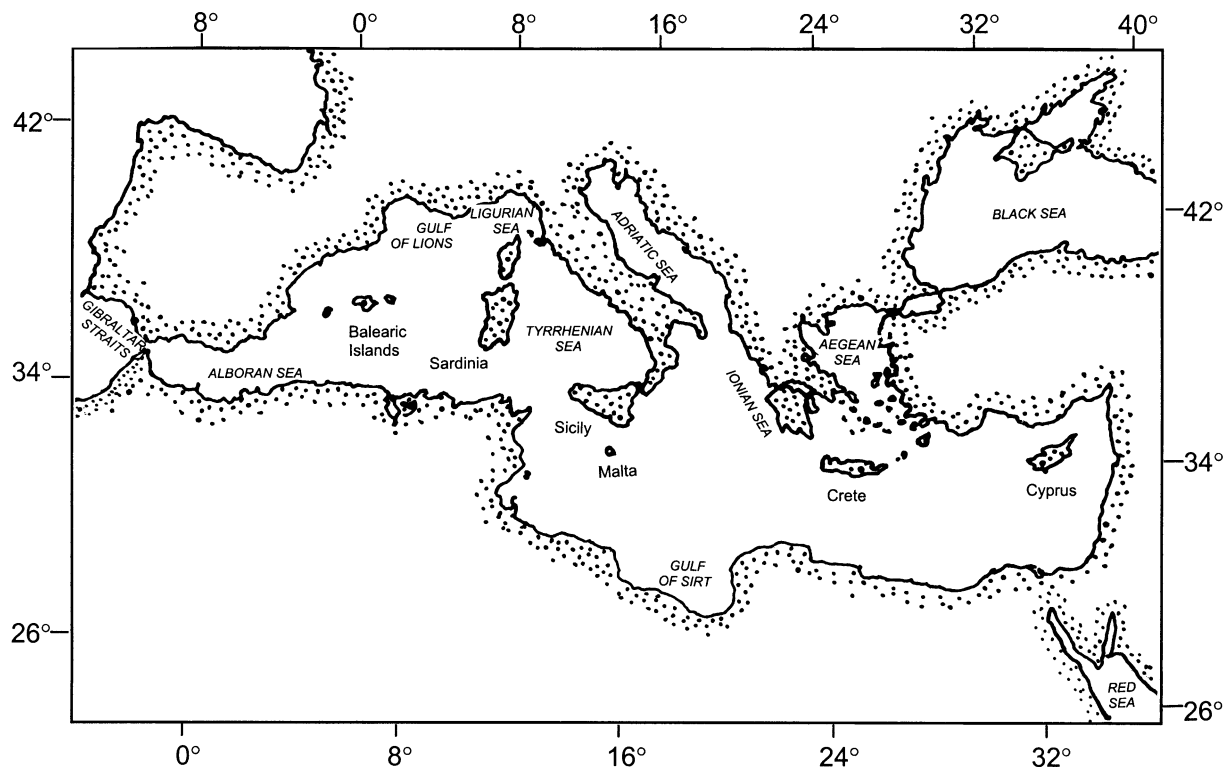


Fig. 1. Map of the Mediterranean Sea showing the locations cited in the text.

No abundance estimates are available for the Tyrrhenian Sea or the eastern Mediterranean. Although striped dolphins are also frequently seen in these areas, their density appears to be lower than in the western region (Marchessaux, 1980; Payne and Selzer, 1986; Marini *et al.*, 1993; 1996; Notarbartolo di Sciara *et al.*, 1993; Öztürk, 1995). The species has not been reported in the Black Sea.

Table 1

Population estimates of striped dolphins from various regions of the western Mediterranean (Forcada and Hammond, 1998).

Area	Point estimate	CV	95% confidence interval
Balearic Sea	5,826	0.36	2,193-15,476
Gulf of Lions	30,774	0.25	17,433-54,323
Ligurian Sea	14,003	0.35	6,305-31,101
South Balearic area	18,810	0.34	8,825-35,940
Alboran Sea	17,728	0.33	9,507-33,059

STOCK IDENTITY

Morphological and genetic studies strongly suggest that the Mediterranean and eastern North Atlantic populations of striped dolphins are isolated from each other, with little or no gene flow across the Gibraltar Straits. Calzada and Aguilar (1995) compared length distributions of stranded striped dolphins from the western Mediterranean and the eastern Atlantic and found that individuals from the two regions differ in maximum body length, with those from the Atlantic being 5-8cm longer. Di Mèglio and Romero-Alvarez (1996) compared growth curves from the two regions and although they only found significant differences in asymptotic length for males, the female sample size was probably too small ($n = 18$ in the Atlantic and $n = 22$ in the Mediterranean) to

reveal differences. Similarly, Archer (1997) found that skull size is significantly smaller in Mediterranean striped dolphins than in their neighbouring Atlantic counterparts. Genetic isolation between the two areas was confirmed by García-Martínez *et al.* (1995), who compared the mitochondrial DNA of striped dolphins from the Mediterranean Sea and from the eastern North Atlantic using restriction analysis. The analysis yielded 27 haplotypes, none of which was shared between the two areas. In addition, it should be noted that when the 1990-92 morbillivirus epizootic affected the Mediterranean population (see below), no cases of affected individuals were reported in the neighbouring North Atlantic waters (Aguilar and Raga, 1993).

However, the stock structure of striped dolphins within the Mediterranean Sea is not yet clearly understood. Calzada and Aguilar (1995) showed that in the western Mediterranean, animals from the southern edge of the range are about 3cm longer than their northern conspecifics. The authors attributed this to differences in the intensity of seasonality and population density between the two regions and believed that it probably reflected some restriction in gene flow between sub-populations. In addition, Monaci *et al.* (1998) found that the mercury tissue content differed between dolphins from the Spanish and Italian coasts, again suggesting some degree of isolation between regions. However, García-Martínez *et al.* (1995) analysed mitochondrial DNA variability in a sample of striped dolphins collected along a wide latitudinal range off the Mediterranean coast of Spain and found no evidence of correlation between haplotype frequencies and geographic distribution or other population subdivision.

Information from the eastern Mediterranean is much more limited. Besides the usual *S. coerulealba* morph, Mörzner-Bruyns (1971; 1974) proposed the existence of a

coastal form which had a smaller body, shorter beak and lacked the lateral black stripe. According to the author, this form of 'striped' dolphin inhabited waters around Greece (for which reason he named it the Greek dolphin), southern Italy and east of Sardinia. However, apart from a rather ambiguous morphological description, the author provided no appropriate data to support the existence of such a coastal form. No studies on geographical variation in body length, morphology or genetic composition are available for eastern Mediterranean striped dolphins.

BIOLOGY

Table 2 summarises the biological parameter data available for the western Mediterranean striped dolphin.

Growth and physical maturation

Mediterranean striped dolphins are the smallest of that species in the world. The difference between individuals from the western Pacific population, in which the largest individuals have been identified, and those from the Mediterranean Sea is about 10-11% (Archer, 1997). This is consistent with the previous finding that dolphins living in enclosed, relatively small bodies of water are smaller in body size than their conspecifics inhabiting large oceanic regions (Perrin *et al.*, 1989).

Information on growth and physical maturation parameters (Table 2) is only available for striped dolphins from the northern fringe of the western Mediterranean basin. Aguilar (1991) estimated length at birth at 90-95cm, which corresponds to an average weight of 11.3kg (SD = 5.6kg). Calzada *et al.* (1997) studied patterns of growth in a sample of 152 stranded striped dolphins from northern Spain and found that whilst females grow faster than males when they are young, their growth ceases and asymptotic length is attained earlier than in males. However, sex-related differences are small and a smaller sample (*n* = 44) from the neighbouring coast of southern France studied by Di-Mèglio and Romero-Alvarez (1996) did not reveal significant differences associated with sex.

The equations obtained by fitting a Gompertz growth curve to the length-age data by Calzada *et al.* (1997) were:

Males: length = 199.9 (exp(-0.513 exp(-0.258 age))) $r^2 = 0.79$
 Females: length = 194.4 (exp(0.575 exp(-0.376 age))) $r^2 = 0.72$

They also found that the asymptotic body length was significantly larger in males (200cm) than in females (194cm), which is consistent with the comparison of body length distributions of 208 stranded dolphins from the northwestern Mediterranean, which also indicated a larger maximum body length in males than in females (Calzada and Aguilar, 1995). Again, no sexual differences in asymptotic body length were observed by Di Mèglio and Romero-Alvarez (1996), but this negative result may be a result of the small sample size used (*n* = 44).

Calzada *et al.* (1997) estimated the age at attainment of physical maturity as 13-18 years in females and 15-20 years in males (*n* = 121). This was based on the assumption that the complete fusion of epiphyses to their centra in mid-thoracic vertebrae is indicative of physical maturation of the vertebral column and, therefore, the end of growth. Cranial maturity, as determined by the fusion of the nasal bones and the condition of the distal portion of the premaxillar-maxillar suture, was estimated to be achieved at a similar age, although the sample size was limited (*n* = 15). In the flipper, the ossification of epiphyses shows a decreasing gradient in the proximodistal direction, as is usual in odontocetes. Primary ossification centres are present at birth, while secondary centres generally appear within the first few months after birth. The proximal epiphysis of the humerus becomes evident when the animals are about 100cm long, and the two centres fuse when animals reach about 150cm. Phalangeal epiphyses do not appear to be useful as indicators of skeletal maturity. Physical maturation of the flipper, as assessed by the age and length at which the distal epiphyseal ossification centre fuses to the metaphysis in the radius and ulna, was established at 5-6 years and 160-175cm in females (Table 2) and 8-9 years and 170-181cm in males (Calzada and Aguilar, 1996; Calzada *et al.*, 1997; Di Giancamillo *et al.*, 1998).

Thus available information on sexual dimorphism in maximum body length, growth curves and patterns of physical maturation of the skeleton indicate that females grow faster and reach their asymptotic size earlier than males. This is consistent with comparable parameters determined for striped dolphins from Japanese waters (Miyazaki, 1977; Ito and Miyazaki, 1990) as well as those

Table 2
 Summary of biological parameters for the western Mediterranean striped dolphin.
 * = data calculated for males and females combined.

Parameter	Male	Female	<i>n</i>	Reference	
Asymptotic body length (cm)	200		75	Calzada <i>et al.</i> , 1997	
	191		22	Di-Mèglio and Romero-Alvarez, 1996	
		194	77	Calzada <i>et al.</i> , 1997	
		194	22	Di-Mèglio and Romero-Alvarez, 1996	
Neonatal length (cm)	90-95*	90-95*	401	Aguilar, 1991	
Neonatal weight (kg)	11.3*	11.3*	4	Aguilar, 1991	
Age at physical maturation of the vertebral column (years)	15-20		43	Calzada <i>et al.</i> , 1997	
			13-18	42	Calzada <i>et al.</i> , 1997
Age at physical maturation of skull (years)	13-20*	13-20*	15	Calzada <i>et al.</i> , 1997	
Age at physical maturation of flipper (years)	8-9		54	Calzada and Aguilar, 1996	
				44	Calzada <i>et al.</i> , 1997
		5-6	44	Calzada and Aguilar, 1996	
Length at sexual maturity (cm)	190.4		61	Calzada, 1996	
			187	84	Calzada <i>et al.</i> , 1996
Age at sexual maturity (years)	11.3		61	Calzada, 1996	
			12	84	Calzada <i>et al.</i> , 1996

for other delphinids (Calzada *et al.*, 1997) and is associated with a higher, more prolonged investment in building a competitive body mass in males than in females (Read *et al.*, 1993).

Reproduction

The only information available is from the northern part of the western basin. In this region, births occur during a single season, extending from late summer to autumn. Calving has been estimated from strandings to peak in mid-October, although it may take place somewhat earlier because of the delay between the death of the dolphin and the report of the stranding (Aguilar, 1991). This coincides with the time of the year in the western Mediterranean when waters are warmest and precedes a peak of productivity (Estrada *et al.*, 1985), therefore providing optimum conditions for lactation.

During the reproductive season, about 25% of the schools carry calves. However, calving appears to take place mainly in the larger dolphin aggregations. Thus, calves are not usually present in schools of less than 10 individuals, while schools of over 30 individuals showed the highest presence of calves (Forcada *et al.*, 1994). This is consistent with the reproductive behaviour observed in striped dolphins from Japan, where calving also takes place in large aggregations known as 'reproductive' schools, which are composed of sexually mature individuals, calves and a few immatures (Miyazaki and Nishiwaki, 1978).

The sex ratio in the adult population is estimated to be 1:1. However, males are more abundant at the foetal stage (1.4:1, $n = 12$). The male mortality rate appears to be higher than that of females, because the ratio in calves is 1.11 ($n = 95$) and numbers approach unity (1.03, $n = 294$) soon after weaning (Aguilar, 1991). This is consistent with the generally observed mammalian pattern (Ralls *et al.*, 1980). The frequency distribution of strandings of calves, with a peak in September-November, suggests that neonatal or early-lactation mortality is much higher than that during the mid or late phases of lactation or at the juvenile stage (Aguilar, 1991).

The attainment of sexual maturity has been estimated to occur when females are about 12 years old and measure about 187cm (Calzada *et al.*, 1996). Comparable figures for males are 11.3 years and 190cm (Calzada, 1996). These estimates (Table 2) are much higher than those for the striped dolphin population from Japanese waters (Kasuya, 1972; 1985) or those of other members of the *Stenella* genus from other areas (Perrin and Reilly, 1984). This may reflect density-dependent variation between populations subject to dissimilar demographic histories as is discussed further below.

Information on seasonal variation in testis weight suggests that mating peaks in August (Calzada, 1996). Considering that births also peak in late summer (Aguilar, 1991), the gestation period is estimated to be about, or slightly over, 12 months.

Feeding

The striped dolphin is an opportunistic feeder, generally exploiting a wide variety of oceanic, pelagic and bathypelagic prey species which form large, dense shoals in the water column. Stomach content analysis of Mediterranean specimens has shown that bony fishes are dominant in numbers, but cephalopods appear to represent an equally, or possibly more, important dietary item because they are of larger size when consumed. Preferred prey include muscular and gelatinous body cephalopods of the families Histioteuthidae, Ommastrephidae,

Enoploteuthidae and Onychoteuthidae, and bony fishes of the families Gadidae, Sparidae and Gonostomiidae. A number of species of shrimp-like crustaceans are also occasionally consumed, but they represent a small proportion of the diet. The size of preferred prey is < 130mm body length for fish and < 200mm dorsal mantle length for cephalopods (Würtz and Marrale, 1991; Pulcini *et al.*, 1993b; Blanco *et al.*, 1995; Meotti and Podestà, 1997).

POPULATION THREATS

Pollution

The Mediterranean is an enclosed sea surrounded by heavily industrialised countries to the north and predominantly agricultural countries to the south and east. The concentration of a variety of chemical pollutants is known to be high in all trophic levels of the ecosystem (e.g. Ramade, 1993), and since the early 1970s, high heavy metal and organochlorine levels have been recorded in a number of species of small cetaceans inhabiting the region. Research on this subject in Mediterranean striped dolphins has been extensive (Table 3), although mostly restricted to the western basin, where they have been found to carry extremely high levels of DDTs and PCBs (Alzieu and Duguy, 1979; Kannan *et al.*, 1993; Aguilar and Borrell, 1994; Arnoux *et al.*, 1994; Corsolini *et al.*, 1995; Borrell *et al.*, 1996a; b; Marsili and Focardi, 1996; 1997; Marsili *et al.*, 1997) and moderate to high levels of heavy metals, particularly mercury, and selenium (Viale, 1978; Carlini and Fabbri, 1990; André *et al.*, 1991a; b; Di Guardo *et al.*, 1992; Leonzio *et al.*, 1992; Augier *et al.*, 1993; Palmisano *et al.*, 1995; Monaci *et al.*, 1998; Storelli *et al.*, 1998). Recent surveys suggest that DDT and PCB levels in striped dolphins were slowly, but steadily, decreasing during the period 1987-1993 (Borrell *et al.*, 1996b). In the eastern Mediterranean, PCB blubber concentrations are also high, although the limited data available indicate that they are lower than those in the western Mediterranean (Troisi *et al.*, 1998).

The effects of pollutants on marine mammals, particularly in the wild, are not well understood (Reijnders *et al.*, 1999). High levels of organochlorine compounds have been associated with a number of physiological disruptions and pathologies mainly affecting growth (e.g. Zakharov and Yablokov, 1990), reproduction (e.g. Reijnders, 1986; Addison, 1989; Baker, 1989) and the immune system (e.g. Brouwer *et al.*, 1989; De Swart *et al.*, 1995; Ross *et al.*, 1995). Although most of these effects have been shown in pinnipeds, they have been assumed to also occur in cetaceans given the fact that the two taxonomic groups share similar pollutant levels as well as their main biological and ecological traits. Indeed, it has been suggested that these effects may be even more intense in cetaceans given their inability to degrade certain highly toxic forms of PCBs (Tanabe *et al.*, 1988; Tanabe and Tatsukawa, 1992).

Levels of organochlorine compounds and some heavy metals commonly found in Mediterranean striped dolphins (Table 3) far exceed thresholds usually associated with detrimental effects. Indeed, for DDTs and PCBs they are among the highest ever recorded in a living wild mammal and their potential impact on populations is a matter of serious concern. Guitart *et al.* (1996) have suggested that fatty acid composition in the blubber of Mediterranean striped dolphins may have been altered by the high concentrations of PCBs to which this population is exposed. PCBs, sometimes reaching blubber concentrations over 1,000 ppm, have also been suggested to have triggered the

onset and development of the 1990-92 Mediterranean morbillivirus epizootic either by debilitating the immune performance of individuals or by adversely affecting their liver function, in both scenarios making dolphins more susceptible to the infectious disease (Kannan *et al.*, 1993; Aguilar and Borrell, 1994; Borrell *et al.*, 1996a). It has also been proposed that high PCB exposure caused unusual luteinised cystic structures found in the ovaries which impede normal ovulation of striped dolphins from the western Mediterranean (Munson *et al.*, 1998). However, to date, lack of appropriate studies precludes confirmation of these potential cause-effect relationships (e.g. see Kennedy, 1999).

Fishing interactions

Fishing intensity is high in most parts of the Mediterranean and it is extremely diverse with respect to gear used, setting techniques and target species (e.g. Di Natale and Notarbartolo di Sciara, 1994). The potential for direct and indirect conflict between striped dolphins and fishing operations is thus very high. Depletion of fish and cephalopod resources is widespread in the Mediterranean and, given that the diet of striped dolphins includes commercial species (see above), this undoubtedly has the potential to affect population numbers. In addition, a number

of fishing activities are known to result in striped dolphin bycatches. However, most of the information available in this regard has been opportunistically collected and is fragmentary.

Undoubtedly, because of its potential for large bycatches, the fishery that has received most attention is the pelagic driftnet fishery for tuna and swordfish. This fishing is carried out by boats of at least three flags: Italy, Spain and Morocco. The Italian driftnetters, directed to albacore (*Thunnus alalunga*) and swordfish (*Xiphias gladius*), are the largest and best equipped. They number about 650-800, their length ranges from 5- >20m (although the majority range from 12-20m), and the nets they set range between 2.5-14km long. The fleet is based in over one hundred different ports located along the western Italian coast, Sicily and the Ionian coast of Calabria. Most boats operate in waters neighbouring Italy, but in recent years a significant part of the fleet has also been fishing off continental Spain, the Balearic Islands and western Greece. In various locations, the activity of this fleet has been associated with large cetacean bycatches, including striped dolphins. The fishery has been intermittently legal and outlawed, and the gear it uses quite often far exceeds the 2.5km limit set by European regulations (Di Natale and Notarbartolo di Sciara, 1994).

The Spanish driftnet fleet is mainly directed towards swordfish. The fishing grounds are restricted to a small area

Table 3
Tissue concentration of pollutants detected in Mediterranean striped dolphins.

Pollutant	Sampling area	Tissue	n	Mean	SD	Max.	Min.	Units	Reference
DDE	W. Italy	blubber	6			7.05	1.80	mg/kg ??	Di Guardo <i>et al.</i> , 1992
DDTs	N.E. Spain	blubber	142	135.00				mg/kg, lipid weight	Borrell <i>et al.</i> , 1996b
DDTs	N.E. Spain	blubber	10	436.70	378.07	1,200.00	62.00	mg/kg, lipid weight	Kannan <i>et al.</i> , 1993; Corsolini <i>et al.</i> , 1995
DDTs	Italy	blubber*	64	114.27		721.77	5.05	mg/kg, lipid weight	Marsili and Focardi, 1996; Marsili <i>et al.</i> , 1997
DDTs	Ligurian Sea	blubber*	61	45.45	24.32	72.16	26.82	mg/kg, lipid weight	Marsili and Focardi, 1996
PCB	N.E. Spain	blubber	142	240.00				mg/kg, lipid weight	Borrell <i>et al.</i> , 1996b
PCB	N.E. Spain	blubber	72	778.00**				mg/kg, lipid weight	Aguilar and Borrell, 1994
PCB	N.E. Spain	blubber	10	1,197.00	851.18	2,600.00	210.00	mg/kg, lipid weight	Kannan <i>et al.</i> , 1993; Corsolini <i>et al.</i> , 1995
PCB	Italy	blubber*	64	172.59		1,529.44	7.84	mg/kg, lipid weight	Marsili and Focardi, 1996; Marsili <i>et al.</i> , 1997
PCB	Ligurian Sea	blubber*	61	68.18	24.09	97.73	53.18	mg/kg, lipid weight	Marsili and Focardi, 1996
PCB	W. Italy	blubber	6			15.60	8.25	mg/kg ??	Di Guardo <i>et al.</i> , 1992
Cd	N.E. Spain	kidney	39	8.38	6.57			mg/kg, dry weight	Monaci <i>et al.</i> , 1998
Cd	Tyrrhenian Sea	kidney	19	44.80		98.8	10.8	mg/kg, dry weight	Leonzio <i>et al.</i> , 1992
Cd	W. Italy	kidney	86	27.51	31.29			mg/kg, dry weight	Monaci <i>et al.</i> , 1998
Cd	W. Italy	liver	6			0.66	0.55	mg/kg ??	Di Guardo <i>et al.</i> , 1992
Cu	N.E. Spain	liver	39	39.24	40.60			mg/kg, dry weight	Monaci <i>et al.</i> , 1998
Cu	W. Italy	liver	86	22.01	21.63			mg/kg, dry weight	Monaci <i>et al.</i> , 1998
Hg	France	liver	25	346.06	356.27	1,544.00	1.2	mg/kg, fresh weight	André <i>et al.</i> , 1991a,b
Hg	France	liver	13	668.40	588.19	2,271.6	396.8	mg/kg, dry weight	Augier <i>et al.</i> , 1993
Hg	N.E. Spain	liver	39	1,043.14	835.17			mg/kg, dry weight	Monaci <i>et al.</i> , 1998
Hg	Tyrrhenian Sea	liver	4	10.37	12.69	29.4	3.67	mg/kg, fresh weight	Carlini and Fabbri, 1990
Hg	Tyrrhenian Sea	liver	19	324.40		4,400.00	12.6	mg/kg, dry weight	Leonzio <i>et al.</i> , 1992
Hg	W. Italy	liver	86	592.97	1,120.01			mg/kg, dry weight	Monaci <i>et al.</i> , 1998
Hg	W. Italy	liver	6			112.00	85.00	mg/kg ??	Di Guardo <i>et al.</i> , 1992
Hg	Adriatic Sea	liver	1	827.60				mg/kg, fresh weight	Carlini and Fabbri, 1990
Hg	Adriatic Sea	liver	30	277.40	246.00	966.31	0.58	mg/kg, fresh weight	Storelli <i>et al.</i> , 1998
Pb	Tyrrhenian Sea	muscle	19	0.66		6.7	0.1	mg/kg, dry weight	Leonzio <i>et al.</i> , 1992
Pb	W. Italy	liver	6			0.31	0.27	mg/kg ??	Di Guardo <i>et al.</i> , 1992
Se	N.E. Spain	liver	39	100.82	220.21			mg/kg, dry weight	Monaci <i>et al.</i> , 1998
Se	Tyrrhenian Sea	liver	4	4.38	2.24	7.4	2.04	mg/kg, fresh weight	Carlini and Fabbri, 1990
Se	Tyrrhenian Sea	liver	19	106.00		960	2.00	mg/kg, dry weight	Leonzio <i>et al.</i> , 1992
Se	W. Italy	liver	86	265.95	316.45			mg/kg, dry weight	Monaci <i>et al.</i> , 1998
Se	Adriatic Sea	liver	30	141.65	104.00	423.98	0.89	mg/kg, fresh weight	Storelli <i>et al.</i> , 1998
Zn	N.E. Spain	liver	39	161.53	57.42			mg/kg, dry weight	Monaci <i>et al.</i> , 1998
Zn	Tyrrhenian Sea	liver	19	225.00		387.5	150.00	mg/kg, dry weight	Leonzio <i>et al.</i> , 1992
Zn	W. Italy	liver	86	111.06	58.87			mg/kg, dry weight	Monaci <i>et al.</i> , 1998

* recalculated from dry weight; ** median.

on both sides of the Gibraltar Straits. The fishery appears to have started in the early 1980s and, from 1988, the number of vessels increased markedly because of the high revenues obtained. In 1990, about 100 Spanish boats based in the harbours of southern Spain were involved in the fishery. In 1991, Spanish regulations outlawed the activity of this fleet, but a limited number of boats continued until 1994, when the fishery finally came to a halt. Given the unregulated nature of the operation in its later years of activity, no data on effort, landings or bycatch are available in the official Spanish fishing statistics. An observer programme developed during the 1993-1994 seasons showed that the fleet was comprised of 27 boats deploying nets 3.5-10.5km long. The bycatch rate of dolphins (common and striped dolphins in similar proportions) was established at about 0.1 individuals per km of net set. The total catch of striped dolphins was estimated at about 170 individuals for the 1993 fishing season and 148 for 1994; the catch was predominantly composed of juvenile males probably because of segregation of different components of the population in the fishing grounds and/or because of sex and age-related differences in behaviour or ability to avoid entanglement (Silvani *et al.*, 1999).

The Moroccan driftnet fishery is poorly understood, with most information arising from casual observations by Spanish observers (Silvani *et al.*, 1999). The fleet is estimated to comprise about 120 boats, most of which are of small tonnage and use shorter nets than the Spanish or the Italian fleets. They also target swordfish, and the fishing grounds appear to overlap those of the Spanish driftnetters.

Reports from other fishing activities are sparse and unsystematically collected. However, they suggest that the pelagic driftnet fishery is not an isolated case and that incidental catches, or even direct catches for human consumption or for use as bait, are widespread and therefore represent a serious toll for the local cetacean populations, including the striped dolphin (Collet, 1983; Duguy *et al.*, 1983; Troncone *et al.*, 1990; Di Natale and Notarbartolo di Sciarra, 1994; Mazzola *et al.*, 1995). In particular, purse-seine fishing for surface-schooling fish appears to be associated with significant bycatches in various locations (Di Natale and Notarbartolo di Sciarra, 1994; University of Barcelona, 1994).

The 1990-1992 epizootic

An epizootic of complex origin and development began in July 1990 and produced a massive mortality of striped dolphins in the Mediterranean Sea. The first affected dolphins were detected near Valencia (mid-Spain), but after a few months the die-off had extended to most of the western Mediterranean. This outbreak was followed by two subsequent outbreaks, the first in summer 1991, affecting at least southern Italy, Sicily and western Greece, and the second in summer 1992 affecting at least eastern Greece and Turkey (Aguilar and Raga, 1993; Cebrian, 1995).

The primary cause of the die-off was a morbillivirus infection (Domingo *et al.*, 1990) of unknown origin. It was similar, if not identical, to that isolated from harbour porpoises (*Phocoena phocoena*) from the Irish Sea in 1990, and distinct from that which caused the 1987 harbour seal epizootic (Bolt and Blixenkrone-Møller, 1994). The morbillivirus antigens were identical for different parts of the Mediterranean (Van Bresse *et al.*, 1993), indicating that the three outbreaks were caused by the same agent. Dolphins affected by the disease showed respiratory insufficiency and frequent nervous and locomotory

disorders. Pathological studies showed bronchiolo-interstitial pneumonia, non-suppurative meningoencephalitis, lymphoid depletion, necrosis of lymphocytes in spleen and lymph nodes, and formation of multinucleate syncytia in the cortex of lymph nodes (Van Bresse *et al.*, 1991; Domingo *et al.*, 1992; Duignan *et al.*, 1992). These lesions were similar to those caused by morbillivirus in seals and porpoises. After the 1990-92 outbreaks, the virus remained in the population and several later cases were reported. In these cases the systemic infection had apparently disappeared, giving way to chronic infection of the central nervous system. This mainly produced non-suppurative encephalitis, with diffuse gliosis and glial nodules and neuronophagia, and loss of neurons (Domingo *et al.*, 1995). The high mortality observed during the event was taken as an indication that in 1990 the morbillivirus had entered a naive population that had not been exposed to the virus before and therefore had no immunity (Van Bresse *et al.*, 1993).

The tissue concentration of PCBs and other organochlorine pollutants of recognised immunosuppressive effect in dolphins that were victims of the epizootic were found to be much higher than in the 'healthy' population sampled before or after the event. This difference could not be explained by the effect of nutritive condition or by differences in the age or sex composition of the samples (Kannan *et al.*, 1993; Aguilar and Borrell, 1994; Borrell *et al.*, 1996a). In addition, the population component that suffered the largest mortality was that of sexually mature individuals and calves, with juveniles apparently not affected. This mortality pattern is not consistent with the epidemiology of morbillivirus infections previously observed in other mammals (e.g. Calzada *et al.*, 1994).

A number of hypotheses on the key factors in the outbreak (other than pollutants) have been proposed, including:

- (1) behavioural factors increasing susceptibility to the disease in adults;
- (2) the existence of an allopatric geographical distribution of population components;
- (3) decreased food availability (as indicated by poor nutritive condition) and extensive epizootic infection in many of the diseased animals during the early phase of the 1990 outbreak (Aguilar *et al.*, 1991; Aznar *et al.*, 1994).

However, the abnormally high pollutant concentrations found in the stranded dolphins strongly support the hypothesis that pollutants played a role in the onset and spread of the morbillivirus infection and the associated high mortality (Aguilar and Borrell, 1994; Calzada *et al.*, 1994). Despite this, it will always be extremely difficult to identify the precise factors involved in such events (e.g. see Kennedy, 1999).

Although over 1,000 carcasses were recovered during 1990 and 1991 in the western Mediterranean alone (Bortolotto *et al.*, 1992; Aguilar and Raga, 1993), the toll caused by the epizootic could not be reliably assessed for two reasons. Firstly, an unknown proportion of dead dolphins sank before reaching the coast and were therefore not recorded in the statistics. The importance of this was undoubtedly enhanced by the offshore nature of striped dolphin distribution and numerous observations of dead dolphins far from shore were reported. Secondly, efficient monitoring of the shore for carcasses was only undertaken on the western European segment of the coastline, and no mortality numbers are available for the eastern Mediterranean basin or the western Mediterranean coast of

Africa, although substantial mortality of striped dolphins is also known to have occurred in these areas (Aguilar and Raga, 1993).

Forcada *et al.* (1994) found that the mean size of the dolphin schools observed in part of the western Mediterranean decreased from 25.3 (SE=4.7) before the event to only 7.0 (SE=2.3) during the outbreak. One interpretation of this is that at least in that area, the population decreased to less than one third of its initial level of abundance. However, (1) observations during the outbreak were restricted to the area around the Balearic Islands, northeastern Spain and the Gulf of Lions (the region that apparently suffered the greatest mortality), and (2) it is likely that the behaviour of the dolphins was altered by the process of the infectious disease. Thus the observed decrease in mean school size cannot be directly taken as a reliable indication of a parallel reduction in abundance. In 1991, mean school size appeared to return to usual levels, although this was not considered a sign of recovery but merely a regrouping of individuals into schools of a preferred size. It is likely that such regrouping was a response by surviving dolphins to facilitate social activities, foraging or reproduction (Forcada *et al.*, 1994). Reproductive parameters of females examined during the epizootic were profoundly altered, indicating a high frequency of abortions and abandonment of lactating calves. This will have had an extensive deleterious effect on recruitment to the population (Calzada *et al.*, 1996).

Other human-related threats

Given its offshore distribution, local effects of coastal development or human presence in coastal waters probably have limited impact on the striped dolphin. Boat traffic does not appear to represent a problem for this species, which is often attracted to boats, independently of their activity (Angradi *et al.*, 1993).

In January 1998, an abnormally high number of striped dolphins (more than 22 individuals in one a week) washed ashore on a small section of coastline on the French Gulf of Lions. The strandings included individuals of both sexes, adults as well as juveniles. Most dolphins had ulcers of uncertain origin on the lateral and ventral sides of the cephalic region. The cause of this mortality could not be established (Rigollet *et al.*, 1998).

CONCLUSIONS AND POPULATION STATUS

The pattern of the 1990-1992 epizootic, which through three successive outbreaks affected the whole Mediterranean Sea but did not extend to the eastern Atlantic, suggests that striped dolphins from the whole Mediterranean basin form an interconnected collective, separated from that from the Atlantic. The limited information available indicates that some degree of genetic subdivision or stratification occurs within the Mediterranean but considerably more work is required to elucidate stock structure. Therefore, biological parameters from one region should not be extrapolated directly to other regions, particularly if they relate to body size and growth, which have been shown to vary. Stock structure must be taken into account in a management context, particularly when assessing the effects of mortality associated with fishing operations, disease, pollution, habitat destruction or other factors.

Although no information on age-related parameters with respect to physical maturation and growth is available for the eastern Mediterranean, the parameters determined for the west (Calzada and Aguilar, 1996; Calzada *et al.*, 1997) are

similar to those for striped dolphins around Japan (Miyazaki, 1977; Ito and Miyazaki, 1990). The same is not true for reproductive parameters: western Mediterranean striped dolphins show a remarkably high age at attainment of sexual maturity in both sexes when compared to the striped dolphin population of Japan or to other congeneric populations (Miyazaki, 1984; Kasuya, 1985; 1999; Calzada *et al.*, 1996). This variation can be associated with differences in the demographic history of the populations, probably reflecting dissimilar density-dependent effects. Thus, while striped dolphins off Japan have been heavily exploited for a long time with numbers remaining well below the carrying capacity of the habitat (Miyazaki, 1984; Kasuya, 1985; 1999), the available information suggests that the Mediterranean population, at least in the western basin for which we have most information, may in fact have been increasing. Surveys in recent years indicate the presence, particularly in the western basin, of a large population. It is intriguing that until the end of the 1960s the striped dolphin was considered to be relatively rare in the Mediterranean, with most reports referring to the common dolphin as the most abundant small odontocete (Van Bree *et al.*, 1969). However, when in the early 1970s, trained cetologists began to collect strandings and sightings data in the region, the widespread presence of the striped dolphin was immediately recognised (e.g. Van Bree *et al.*, 1969; Duguy *et al.*, 1983). It is unclear whether the apparent scarcity of the species in the first half of the century was true, or whether it reflected the fact that striped dolphins were mistakenly identified as common dolphins (Casinos and Vericard, 1976; Viale, 1985).

Having said that, at least during the period 1970-1995, the common dolphin appears to have decreased throughout the northern part of the western Mediterranean. There has been some speculation that the striped dolphin began to occupy the ecological niche of the common dolphin and, thus, increased its numbers (Viale, 1985) although why competition between these two should have resulted in favour of the striped dolphin is unclear. Both species appear to share a common habitat in a wide portion of their distribution range (Sagarminaga and Cañadas, 1996; Forcada and Hammond, 1998), although no conclusive studies have been made to assess the extent of any competition between them, for example for food. However, data from a limited number of common dolphins do suggest at least a partial overlap in diet (Orsi Relini and Relini, 1993). Although the replacement of one species by another may have occurred to some extent, it is not clear whether the apparent increase in reports of strandings and sightings of striped dolphins was indeed significant, or whether it was partially a consequence of striped dolphins extending their range to the inshore waters traditionally inhabited by common dolphins.

In summary, there is some inconclusive evidence that striped dolphins may have increased in numbers in recent decades. However, this progressive increase may have occurred at a time when its available habitat is decreasing. Würtz and Marrale (1991) found that a single cephalopod species (the red squid, *Todarodes sagittatus*) and a single fish species, (the blue whiting, *Micromesistius poulassou*), comprised over 60% of the food items present in the stomachs of 23 striped dolphins stranded on the coasts of the Ligurian Sea; *Todarodes sagittatus* is also a significant food item of the striped dolphins found on the Spanish Mediterranean coast (Blanco *et al.*, 1995). Both of these species are of prime commercial interest and heavily exploited.

In this context, the extremely old age at attainment of sexual maturity observed in Mediterranean striped dolphins compared with those from Japan and other areas is suggestive of a population with stringent food limitations. Density-dependence theory suggests that in this situation, selection will induce compensatory responses resulting in low survival and pregnancy rates and high age at attainment of sexual maturity (Eberhardt and Siniff, 1977). Although opposite effects may indeed sometimes occur (Trites and York, 1993), it seems possible that the life-history parameters observed in Mediterranean striped dolphins do reflect a population that is at an abundance level close to if not beyond the carrying capacity of its environment. In such circumstances, the occurrence of the 1990-1992 epizootic might be considered more as a density-regulatory mechanism in a population at an excessive population level rather than an exceptional, isolated disaster (Harwood and Hall, 1990).

The implications of these scenarios for the management and conservation of the western Mediterranean population of striped dolphins are quite different and thus urgent research is required to assess: (1) long-term demographic changes in the population, mainly in its abundance and gross reproductive rates; (2) effects of chemical pollutants on reproductive rates and immunocompetence; (3) diet composition and potential overlapping with the catch of the main fishing activities in the region; and (4) the overall nutritive condition of the dolphins.

ACKNOWLEDGEMENTS

Assumpció Borrell (GRUMM, University of Barcelona, Spain) and Jaume Forcada (Southwest Fisheries Research Center, NMFS, NOAA, USA) reviewed the draft manuscript and contributed data and valuable comments, as did G.P. Donovan and two anonymous reviewers. This study was partially funded by project AMB99-0640 of the Spanish Comisión Interministerial de Ciencia y Tecnología (CICYT).

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