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Colour patterns and pigmentation variability on striped dolphin *Stenella coeruleoalba* in north-western Mediterranean Sea

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Studies on differences in external morphology and pigmentation patterns were historically carried out using stranded individuals or opportunistic sightings; few studies have involved sampling systematically free-ranging individuals. In order to investigate and describe main pigmentation characteristics, outlining 'typical' regional pigmentations, this work analysed systematic photographic information taken on free-ranging striped dolphins, Stenella coeruleoalba. *Photographs of dolphins in the Ligurian Sea were collected between May 2004 and December 2006. All individuals were described by the presence/absence of pigmentation variables and by differences in colour shades. The frequency of all the pigmentation variables analysed is stable in the population (10 'gene' variables, 19 'allele' variables), and remains similar between each different group of dolphins. But population presents widespread pigmentation variability between specimens, allowing identification even at single individual level. Cluster analysis also found that the majority of the pigmentations derive from two main colour patterns, called 'mat' and 'pale' patterns ($f_{mat} = 0.68$; $f_{pale} = 0.12$). The Bray–Curtis index showed a high variability of the intra-group pigmentation distance between groups. This resulted in a positive correlation between group size and 'intra-group' pigmentation distance: the distance increases rapidly up to a group size of 40 individuals. According to the results obtained, the striped dolphins seem to be concentrated in small groups in which there is a large phenotypic similarity among individuals. These small units could be associated between them to form temporary large groups observed only in pelagic waters.*

Keywords: colour pattern, striped dolphin, half-weight index, Bray–Curtis index, Mediterranean Sea

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INTRODUCTION

Pigmentation patterns in marine mammals may be very different, even at single species level, and in some cases they are driven to change the formal recognition of presupposed forms into new subspecies (Perrin *et al.*, 1991; Heyning & Perrin, 1994; Perrin, 1997). Often, in cetacean species, individuals belonging to different populations may also show variation in external morphology or colour patterns (Evans *et al.*, 1982; Jefferson, 1988; Perrin *et al.*, 1991; Amano & Miyazaki, 1996; Houck & Jefferson, 1999) and such differences might be an index of gene flow between populations (Herman *et al.*, 1980; Braham & Rice, 1984; Schaeff *et al.*, 1991; Schaeff & Hamilton, 1999). Variability in pigmentation pattern can also be observed among animals belonging to the same population. In fact, specimens may have distinctive natural variations which may reflect their individual genetic identity, allowing identification of single individuals through field photo-identification (Katona & Whitehead, 1981; Dorsey, 1983; Agler *et al.*, 1990; Hammond *et al.*, 1990; Sears *et al.*, 1990; Blackmer *et al.*, 2000).

Variations in colour patterns can be observed in most cetacean families, and significant dissimilarities among individuals are present in the Delphinidae family, especially in the *Stenella, Delphinus* and *Orcinus* genera (Evans *et al.*, 1982; Heyning & Perrin, 1994; Perrin, 1997).

The striped dolphin *Stenella coeruleoalba* (Meyen, 1833) is the only species belonging to the *Stenella* genus in the Mediterranean Sea. This species is a small cosmopolitan cetacean inhabiting pelagic tropical and warm-temperature waters where it is relatively abundant (Perrin, 1994). The striped dolphin is the most abundant cetacean species in the western Mediterranean, with an estimated population of 118,000 individuals (Forcada *et al.*, 1994). There is little information about striped dolphin feeding strategies, but its prey has been identified from stomach contents. The diet is mainly composed of mesopelagic fish and cephalopods but also planktonic crustaceans can be found (Würtz & Marrale, 1993; Ringelstein *et al.*, 2006).

Gaspari *et al.* (2007) found that all the Mediterranean striped dolphin populations considered in their study showed a high level of genetic variation. Microsatellite DNA analysis found genetic differences between Pacific, North

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Atlantic and Mediterranean populations (Archer, 1996); small genetic differences were also found among individuals in both eastern and western parts of the Mediterranean Sea, indicating a limited dispersal range between the two areas (Valsecchi *et al.*, 2006; Bourret *et al.*, 2007; Gaspari *et al.*, 2007). A large degree of variation in external size between Mediterranean and Atlantic populations was also detected (Archer, 1996). In addition, morphological studies based on stranding data pointed out that individuals inhabiting the southern area of the Mediterranean basin might be larger than those present in the northern area (Calzada & Aguilar, 1995).

Stenella coeruleoalba is boldly patterned in bluish grey and white with distinct diagnostic lateral stripes and spinal blaze that may vary between individuals, and possibly geographically (Perrin, 1994). Preliminary works, carried out in the western Mediterranean Sea, indicate that individuals seem to differ slightly in pigmentation at both the individual and group level (Acquarone & Notarbartolo di Sciara, 1992; Rosso *et al.*, 2006).

Although the striped dolphin is the most common cetacean species inhabiting the Mediterranean basin (Forcada *et al.*, 1994), there has been little information available on the variability of striped dolphin pigmentation patterns until now.

This work analysed systematic photographic data taken on free-ranging individuals in the Ligurian Sea. The aim of this research was to investigate and to describe the main pigmentation characteristics and their relative variability within the population (or populations) in the Ligurian Sea, outlining 'typical' regional pigmentations. Difference in colour patterns were investigated and used as an index of the phenotypic distance among animals within and between groups.

MATERIALS AND METHODS

Sampling

The study zone is located in the northern part of the *Pelagos* Sanctuary—Ligurian Sea—and it extends from the coast to the 43°10′ latitude N and between the 008°00′ and 009°52′ longitude E. This zone comprises both coastal and offshore waters including the Genoa Canyon and the Liguro–Provençal current.

Photographs have been collected during one-day scientific surveys, carried out all year round from May 2004 to December 2006, on board an 11 m semi-rigid inflatable vessel. Having recorded the positions, each sighted group was described *in situ* on the basis of the minimum, the maximum and the best estimation of the number of individuals. Also, group sizes were subdivided into three classes: 1, ≤20 individuals; 2, >20 and ≤40 individuals; 3, >40 individuals. The focal group was defined according to Shane (1990) as 'any group of dolphins observed in apparent association, moving in the same direction and often, but not always, engaged in the same activity'. Members of the focal group usually remained within approximately 100 m of each other.

Auto focus digital cameras equipped with 80–400 mm stabilized zoom lenses were used throughout the study. Photographs were shot randomly when porpoising behaviour was observed and were taken perpendicularly showing the exposed flank. The photographer was positioned just above sea level in order to increase the probability of taking images in the perfect profile. Photographs were taken throughout the encounter regardless of whether they had already been taken of a particular individual. Pictures collected during surveys ranged from 6 to 10 megapixel in size, and were converted into black and white. A quality index (Q) rating from 1 to 4 was assigned to all the photographs, based on focus, exposure, proportion of the frame filled by the body of the individual photographed and the degree of rotation on the three planes. Only quality 4 pictures inserted into the database were analysed for this study (Figure 1). The likelihood of all pigmentation patterns from one individual matching another individual is rare, and each individual was identified based on its pigmentation patterns and the presence/absence of notches, lesions or deformities.

Sample analysis

Photographs were analysed according to the animal side, left or right, but individual identification from different sides cannot be linked. To prevent pseudo-replication only photographs showing the most photographed side per group were selected, i.e. if, during a sighting, five photographs were taken of left sides and eight of right sides only the right side photographs were analysed.

The best picture of each individual was then used for the pigmentation pattern analysis. For the specimens description Fraser's pigmentation variables were used where possible (Fraser & Noble, 1970) with new ones indicated in Figure 2.

All individuals were described by the presence/absence of each pigmentation variable (10 'gene' variables) and by the presence/absence of pigmentation variables expressions (19 'allele' forms) represented in Figure 2. Specimens were also described by differences in colour shade among four pigmentation variables: dorsum, main Plimsoll line, branch Plimsoll line and shoulder band (a, darker; b, similar; c, lighter; see Table 1). Shade differences were measured by detecting grey degrees (GD) in the area from the eye to the origin of the flipper. Grey degrees of ten pixels per pigmentation variable *i* were measured and their mean value was the GD*i*. For this analysis we have used the software Corel Photo-Paint 12 to avoid systematic errors due to subjective valuations.

Photographs of individuals present in ≥4 photographs were utilized to determine the sensitivity of the method, applied to describe specimens. The bias was calculated by comparing results obtained from different pictures of the same specimens, B*p* (see later Bray–Curtis index).

At the same time morphometric data were collected although it was not possible to obtain any information on the total length of the specimens photographed. This study

Fig. 1. Typical Q = 4 picture: the animal is perfectly straight, perpendicular at the photographic axes, without pitching and rolling.

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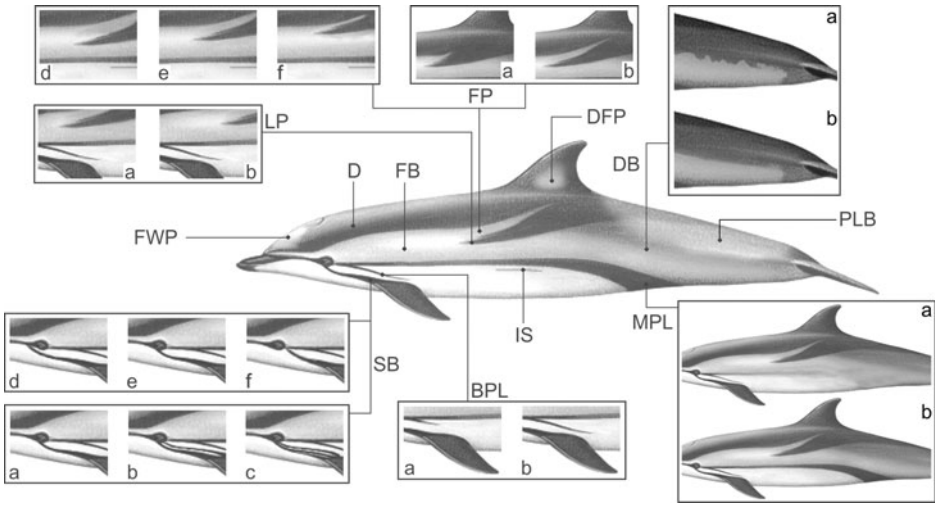

Fig. 2. Pigmentation variables used to characterize individuals. The presence/absence of each 10 'gene' variables (upper cases) and 19 'allele' variables (lower cases) was investigated: BPL, branch Plimsoll line, a, it stops before the flipper armpit, b, it stops after the flipper armpit; D, dorsum (it was not considered in the pigmentation variable group); DB, dorsum border, a, marked, b, unmarked; DFP, dorsal fin white patch; FB, flank belly (it was not considered in the pigmentation variable group); FP, flank pigmentation, a, it ends before the origin of the dorsal fin, b, it ends after the origin of the dorsal fin, d, the thickness ratio FB/FP ≤ 2, e, <2 FB/FP ≤ 3, f, FB/FP >3; FWP, forehead white patch; IS, intermediate streak; LP, lateral promontory, a, it ends before the flipper armpit, b, it ends after the flipper armpit; MPL, main Plimsoll line, a, it ends before the origin of the dorsal fin, b, after the origin of the dorsal fin; PLB, peduncle light blaze; SB, shoulder band, a, single, b, double, c, multiple, d, it starts before the eye, e, it starts on eye, f, it starts after eye.

describes only relative proportion among biometric parameters (RPB), following Cagnolaro and colleagues' (1986) descriptions. These parameters were measured using a tool of MapInfo Professional 7.8. Photographs of each individual present in ≥ 4 photographs were also compared to determine the bias in the method applied for measuring morphometric data, B*m*.

Pigmentation pattern

To define patterns in pigmentation minimizing bias, a cluster analysis using the half-weight index (HWI) was applied to quantify the frequency of association among pigmentation variables (Cairns & Schwager, 1987). The HWI was useful to measure the strength of each dyad of pigmentation variables:

$$\mathrm{HWI} = 2\mathrm{X}/(A + B)$$

where: X is the number of individuals where variable *A* and variable *B* were seen together, *A* is the number of individuals where variable *A* was sighted and *B* is the number of individuals where variable *B* was sighted. Pigmentation patterns, i.e. associations between pigmentation variables occurring more often than expected by chance, were defined when HWI was

Table 1. Morphometric matrix representing the relative proportion among different biometric data. For each pair mean value, in bold, and standard deviation were indicated. N, number of individuals for which the data were measured; B*m*, bias due to the experimental method used; n, number of individuals used to calculate the bias (sample size).

N		TL		Tdf		Dff		Lr		Tm		Tb		Te		Tf		Ldf		Hdf	
256	**TL**	–		**2.12**	*0.11*	**2.37**	*0.14*	**15.17**	*2.09*	**7.09**	*0.97*	**6.40**	*0.85*	**5.89**	*0.90*	**4.12**	*0.37*	**7.28**	*0.64*	**10.40**	*1.14*
256	**Tdf**	**0.47**	*0.02*	–		**1.12**	*0.11*	**7.22**	*0.81*	**3.34**	*0.36*	**3.02**	*0.29*	**2.77**	*0.34*	**1.94**	*0.12*	**3.43**	*0.36*	**4.91**	*0.57*
256	**Dff**	**0.42**	*0.02*	**0.90**	*0.08*	–		**6.48**	*1.09*	**3.03**	*0.52*	**2.73**	*0.46*	**2.51**	*0.46*	**1.76**	*0.22*	**3.10**	*0.33*	**4.44**	*0.57*
208	**Lr**	**0.07**	*0.01*	**0.14**	*0.02*	**0.16**	*0.03*	–		**0.46**	*0.04*	**0.42**	*0.04*	**0.38**	*0.04*	**0.27**	*0.03*	**0.48**	*0.08*	**0.69**	*0.10*
213	**Tm**	**0.14**	*0.03*	**0.30**	*0.05*	**0.33**	*0.07*	**2.15**	*0.31*	–		**0.90**	*0.11*	**0.82**	*0.10*	**0.58**	*0.08*	**1.03**	*0.21*	**1.46**	*0.28*
156	**Tb**	**0.16**	*0.02*	**0.33**	*0.03*	**0.38**	*0.06*	**2.39**	*0.22*	**1.10**	*0.06*	–		**0.91**	*0.06*	**0.64**	*0.05*	**1.15**	*0.19*	**1.64**	*0.25*
256	**Te**	**0.17**	*0.03*	**0.37**	*0.04*	**0.41**	*0.08*	**2.63**	*0.27*	**1.21**	*0.07*	**1.10**	*0.06*	–		**0.71**	*0.06*	**1.26**	*0.22*	**1.79**	*0.29*
213	**Tf**	**0.24**	*0.02*	**0.52**	*0.03*	**0.58**	*0.07*	**3.74**	*0.41*	**1.72**	*0.13*	**1.56**	*0.12*	**1.43**	*0.14*	–		**1.78**	*0.22*	**2.54**	*0.32*
256	**Ldf**	**0.14**	*0.01*	**0.29**	*0.03*	**0.33**	*0.04*	**2.13**	*0.35*	**0.99**	*0.17*	**0.89**	*0.15*	**0.82**	*0.15*	**0.57**	*0.07*	–		**1.44**	*0.13*
256	**Hdf**	**0.10**	*0.01*	**0.21**	*0.03*	**0.23**	*0.03*	**1.49**	*0.24*	**0.69**	*0.11*	**0.63**	*0.11*	**0.58**	*0.11*	**0.40**	*0.05*	**0.70**	*0.06*	–	

	Description	B*m*	n		Description	B*m*	n
TL	Total length	*0.02*	36	**Tb**	From tip of rostrum to anterior blowhole edge	*0.05*	36
Tdf	From tip of rostrum to origin of dorsal fin	*0.02*	36	**Te**	From tip of rostrum to anterior edge of eye	*0.04*	36
Dff	From insertion of the dorsal fin to fluke notch	*0.02*	36	**Tf**	From tip of rostrum to origin of flipper	*0.03*	36
Lr	Length of rostrum	*0.05*	36	**Ldf**	Length of dorsal fin base	*0.03*	36
Tm	From tip of rostrum to corner of mouth	*0.04*	36	**Hdf**	Height of dorsal fin	*0.03*	36

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greater than HWI_{null} (association index obtained if a variable associates randomly)

$$HWI_{null} = n_{associate}/(N-1)$$

$n_{associate}$ is the mean number of pigmentation variables shown by individuals and N the total number of individuals used for the analysis.

All associations which have a HWI value greater then HWI_{null} form a pattern.

Pigmentation dissimilarity among individuals

Dissimilarity in pigmentation between individuals may be an index of a 'phenotypic distance'. Any dolphin has a pigmentation defined by coordinates—presence/absence of each pigmentation variable—then it is possible to measure the distance (dissimilarity) among dolphins. For this analysis we used a normalization method of the Bray–Curtis index (Bray & Curtis, 1957) which helps to evaluate the amount of dissimilarity between the individual photographed:

$$d_{ij} = \frac{\sum_{k=1}^{n} |x_{ik} - x_{jk}|}{\sum_{k=1}^{n} (x_{ik} - x_{jk})}$$

where d_{ij} is the distance between individual i and individual j using as coordinates the n pigmentation variables (presence/absence of every pigmentation variable). d_{ij} value ranges between 0 (individual i is equal at individual j) and 1.

The Bray–Curtis distance was measured to calculate the bias obtained in the specimen description analysis, Bp, i.e. the pigmentation distance between different photographs of the same individual; the bias was calculated comparing photographs of each individual photographed ≥ 4 times.

RESULTS

During this study, 305 sightings of the striped dolphin were collected (7834 $Q \geq 1$ photographs). Class 1 represented the most common group size with a frequency $f = 0.68$ (204 groups) followed by Class 2, $f = 0.23$ (70 groups), and Class 3, $f = 0.09$ (31 groups). While Class 1 and Class 2 groups were sighted everywhere in the sampled area, Class 3 groups were not seen on the continental shelf (Figure 3).

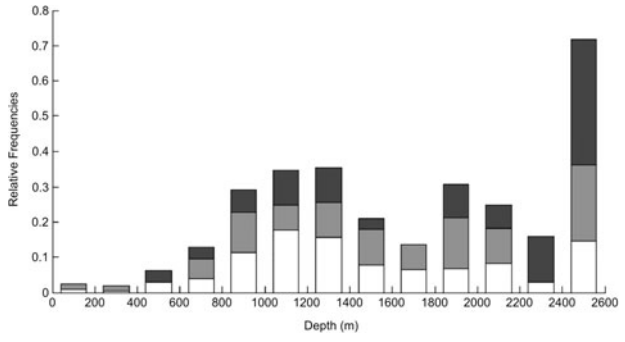

Fig. 3. Relative frequencies of the three group size-class, 1–20 individuals in white, 21–40 individuals in light grey and more than 40 individuals in dark grey. The histogram does not take into account the effort applied.

At least one $Q = 4$ photograph was taken during 86 encounters (mean = 12.54; SD = 8.21; range 1–26) for a total of 276 porpoising individuals identified (130 on right side, 146 on left side). A total of 884 $Q = 4$ photographs were analysed (476 left sides, 428 right sides). In 45 groups, 15% of total sightings, it was possible to collect photographs of more then three individuals in the same group (mean = 4.53; SD = 0.22; range 4–16). For 36 specimens more than three consecutive $Q = 4$ photographs were collected, during the same sighting (mean = 6.58; SD = 2.25; range 4–14).

Morphometric data

There is no important morphometric difference among the individuals (see Table 1). Biometric data are very similar to those measured by Cagnolaro and colleagues on a sample of ten stranded specimens (Cagnolaro *et al.*, 1986).

Photographs of the 36 individuals were used to determine the sensitivity of the method applied for measuring morphometric data. The mean bias Bm was 0.03 (SD = 0.01; range 0.02–0.05).

Pigmentation pattern

Frequencies of each variable analysed are listed in Table 2. Frequency of all variables is very stable in the population, being similar between each different group of dolphins. The main Plimsoll line and branch Plimsoll line were the most

Table 2. Frequencies in the population of the different variables analysed (N = 276 individuals). Variables marked with a* were the most frequent and were grouped to form the 'common' pattern.

Pigmentation variables			Colour shades	
'Gene'	**'Allele'**	**Frequency observed**	**Comparison**	**Frequency observed**
BPL	BPLa	0.13	D *vs* BPL a*	0.70
	BPLb*	0.87	D *vs* BPL b	0.26
			D *vs* BPL c	0.04
DB	DBa	0.26		
	DBb*	0.58	D *vs* MPL a*	0.66
			D *vs* MPL b	0.29
DFP		0.22	D *vs* MPL c	0.05
FP	Fpa	0.46	D *vs* SB a*	0.81
	FPb*	0.53	D *vs* SB b	0.12
	FPd	0.15	D *vs* SB c	0.06
	Fpe*	0.50		
	FPf	0.34	SB *vs* BPL a	0.10
			SB *vs* BPL b	0.40
FWP		0.30	SB *vs* BPL c*	0.51
IS		0.00	SB *vs* MPL a	0.09
			SB *vs* MPLb	0.34
LP	LPa	0.25	SB *vs* MPL c*	0.58
	LPb*	0.74		
			MPL *vs* BPL a	0.16
MPL	MPLa	0.13	MPL *vs* BPL b*	0.83
	MPLb*	0.87	MPL *vs* BPL c	0.01
PLB		0.27		
SB	Sba*	0.66		
	SBb	0.32		
	SBc	0.02		
	SBd	0.31		
	SBe*	0.63		
	SBf	0.06		

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common variables and the only ones consistently present on individuals of the population studied. The intermediate streak was not present in all of the individuals photographed.

Initially cluster analyses were made separately (Figure 4) for the pigmentation variables group (N = 276 individuals) and the colour shades group (N = 198 individuals). Results showed that 12 pigmentation variables were associated more often than expected, grouping them in three patterns (called from 1 to 3; $HWI_{null} = 0.468$). The difference in colour shades among the four features analysed form four different

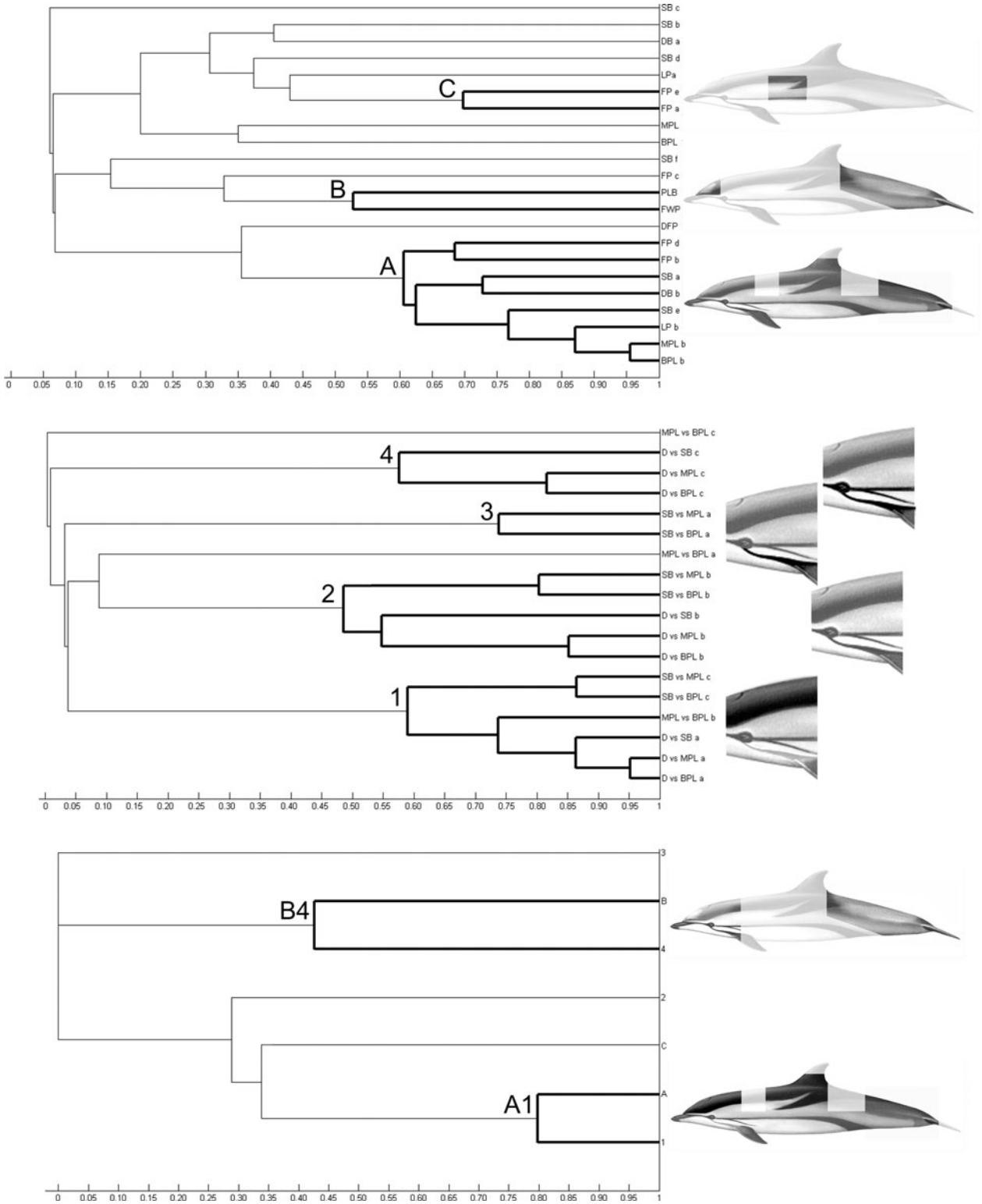

Fig. 4. Cluster analysis made to point out the presence of colour patterns. HWI is indicated on x axis while variables are indicated on the y axis. Patterns (bold lines) are represented and described by drawings on the right. The first drawing above shows cluster obtained from the pigmentation variables analysis: three patterns (A, B and C); the second drawing in the middle shows cluster obtained from the colour shade analysis: four patterns (1, 2, 3 and 4); the third drawing is the association result of the previous seven patterns. Two main patterns arise from the analysis, the 'mat' pattern (A1) and the 'pale' pattern (B4).

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patterns (called from A to D; $HWI_{null} = 0.423$). A third cluster analysis was made among the previous seven patterns (N = 198 individuals), and it showed preferred associations only between A-1 and B-4 patterns ($HWI_{null} = 0.387$). The pattern A-1, called 'mat' pattern, and the pattern B-4, called 'pale' pattern, were composed of 14 and five different variables respectively. Frequencies in the population of the two main patterns and an arbitrary 'common' pattern (composed of the most frequent characteristics, 14; see Table 2) were investigated, and the results show that the 'mat' pattern is the most common (f = 0.04) followed by the 'pale' pattern (f = 0.01), while the 'common' pattern was not present.

Also frequencies of patterns derived from the two main patterns were studied. In particular we calculated the frequency of patterns made by 75% of variables present in each main pattern ('mat family' patterns and 'pale family' patterns). These frequencies were f = 0.68 and f = 0.12 for the 'mat family' and 'pale family' patterns respectively.

Pigmentation dissimilarity among individuals

The Bray–Curtis index, or pigmentation distance, gave a B*p* = 0.009 (SD = 4.10^{-4}; range 0–0,02; calculated among the 36 specimens photographed ≥4 times).

The medium pigmentation distance among the individuals in the 'right side population' (130 individuals, 8385 pairs) was D = 0.450 (SD = 0.011; range 0–0.976), and in the 'left side population' (146 individuals, 10585 pairs) it was D =0.454 (SD = 0.013; range 0–0.946) with a frequency of 'twin' f < 1.10^{-3} (3 pairs) for both populations.

The medium pigmentation distance among individuals of the same group (45 groups, 204 individuals) was D =0.416 (SD = 0.088; range 0.161–0.571) showing a high variability of intra-group distance between groups. The *t*-test suggested that intra-group distances between the Class 1, 2 and 3 groups are statistically different ($P < 0.01$; Class 1 vs Class 2, $t = 4.024$, 33 df; Class 2 vs Class 3, $t = 6.266$, 34 df). If the pigmentation distance was a random variable in striped dolphins, for any dolphin group we consider the intra-group distance should not be statistically different (intra-group distance = pigmentation distance among dolphins of the same group) regardless of the number of dolphins forming the group. However, by looking at the real data collected, it is clear that dolphin herds formed by ≤20 individuals were characterized by a small inter-group distance. By investigating this issue a positive correlation between group size and pigmentation distance was found, i.e. the larger the group, the bigger the pigmentation distance within the group. The pigmentation distance increases quickly up to a group size value of ~40 individuals; within bigger group sizes the intra-group pigmentation distance remains stable (Figure 5). There is not a statistically supported difference in pigmentation between offshore versus inshore individuals (individuals sighted <500 m depth vs individuals sighted >2000 m depth), in fact this distance has a mean value D = 0.448 (SD = 0.0181; $t = 1.0593$, 12 df) which is very similar to the mean value observed among the individuals of the population.

DISCUSSION

Studies on the differences in external morphology and pigmentation patterns were historically carried out to assess variations within and between forms, subspecies and even among different species (Perrin *et al.*, 1991; Heyning & Perrin, 1994; Amano & Miyazaki, 1996; Perrin, 1997). This type of study was typically based on stranded individuals where post-mortem darkening of the skin may obscure or distort the colour pattern of the dead cetacean, compromising a part of the sample. Only a few studies have attempted to systematically sample free-ranging individuals (Stockin & Visser, 2005) to avoid post-mortem darkening. This study would also be a tool to test the effectiveness of this last approach.

In this work the 11% of the estimated number of dolphins sighted was represented by Q = 4 photographs (range 2–85% per group). Striped dolphins typically approach close to the boat during bow-riding behaviour, in small groups formed by a couple of individuals. Before they reach the bow, they show porpoising behaviour and it is possible

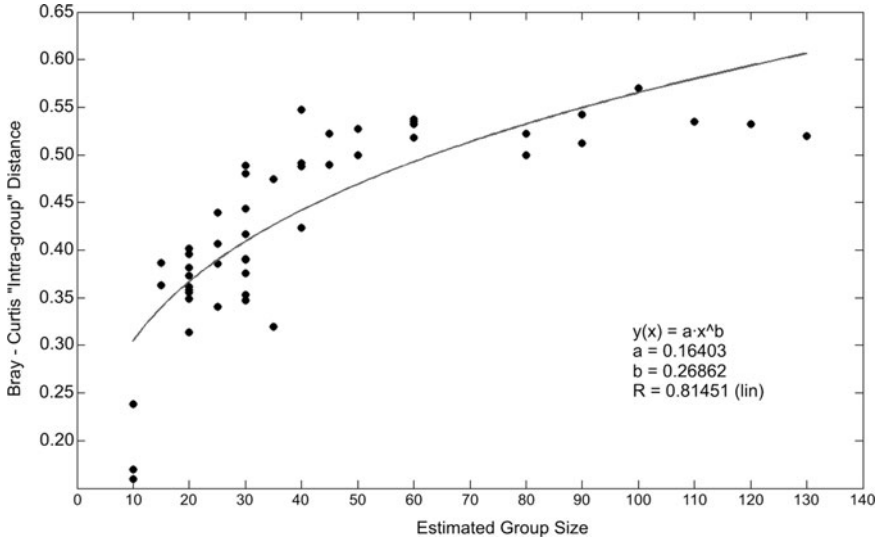

Fig. 5. Plot 'intra-group' pigmentation distance versus estimated group size. The best fit is shown by the black curve.

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to collect photographs of whole individuals. The sampling of bow-riding individuals may lead to an under-representation of mature females, since mothers rarely show this behaviour when accompanied by a calf.

Morphometric data

Although only relative proportions were measured, the comparisons between different photographs of the same individuals suggest that this approach has reliable results, due to a small bias ($Bm = 0.03$). The larger the morphological variable measured, the smaller is the Bm (see Table 1).

The biometric results are very similar to the ones relative to specimens stranded along the Ligurian coast (before the morbillivirus epizootic of 1990–1992; Cagnolaro *et al.*, 1986) which confirm that there is only a small variability among individuals and among different age-classes (excluding calves).

Pigmentation patterns

In this study of pigmentation patterns, the approach used gave reliable results and the bias observed was minimal (bias measured as Bray–Curtis distance, $Bp = 0.009$).

The frequency of all pigmentation variables is stable in the population and it remains similar among each different group of dolphins. The population presents widespread pigmentation variability among individuals: specimens usually differ in various pigmentation characteristics, and consequently this allows identification even at single individual level. The frequency of 'twin', i.e. the frequency of individuals that show the same pigmentation variables, is very rare within the sample studied ($f < 0.001$).

In the north-western Mediterranean Sea, the striped dolphin pigmentation is characterized by a constant presence and a low variability of the main Plimsoll line and the branch Plimsoll line. According to Fraser (1970) the two Plimsoll lines should be considered the more trenchant characteristics of the striped dolphin pigmentation.

Although the intermediate streak has not been found on the specimens analysed, this variable was found on specimens from the western Mediterranean Sea in past studies (Fraser & Noble, 1970) therefore it may not be completely absent in the population.

The most variable pigmentations are the flank pigment and the shoulder band which are usually present, although they may not appear on some individuals. The flank pigment varies considerably, mainly in thickness and in length; the shoulder band presents a high variability especially in shade, thickness and conformation (being composed of one to four bands).

Despite the general variability in pigmentation, the majority of the pigmentations photographed seem to derive from two main colour patterns. The primary, 'mat pattern', is the most common and it is mainly characterized by: (a) light contrast among the two lines (MPL and BPL) and the flank belly; (b) lighter single shoulder band; and (c) the dorsum colour is darker then the lines. The second colour pattern, 'pale pattern', is characterized by: (a) the presence of a lighter forehead and the peduncle light blaze; and (b) a visible contrast between the flank belly and both shoulder bands and the two lines.

Distance in pigmentation among individuals

There are no statistical differences in pigmentation between offshore and inshore individuals, even though a small genetic difference was pointed out in previous works (Gaspari *et al.*, 2007). By looking at the data collected, it is clear that small groups of dolphins (groups formed by ≤ 20 individuals) were characterized by a little difference in pigmentation among the individuals forming the heard (small 'intra-group' pigmentation distance). In these groups the pigmentation distance among individuals was always lower than the distance measured in larger groups, therefore the pigmentation distance was not random but it was biased by some factors. Although no genetic analysis was carried out during this work, we believe the pigmentation distance might be influenced by a higher kinship in the small groups. According to Gaspari *et al.* (2007), striped dolphins seem to be grouped in small kin groups that could be associated among them to form temporary larger groups. The similarity in pigmentation, among individuals forming the same group, decreased in group sizes of up to approximately 40 specimens. Above 40 it remained quite constant; therefore the enhancement of the 'intra-group' pigmentation distance may be caused by the overlapping of several small kin groups. The large phenotypic similarity in small groups could not be a sampling bias caused by mothers and their calves, because calves were not sampled.

In this study, large aggregations of dolphins were observed only in pelagic waters while smaller groups could be found in both pelagic and neritic waters. A preliminary work carried out by Gannier & David (1997) identified the presence of a daily migration cycle in which striped dolphins seemed to move offshore during the morning, before returning to the continental shelf during late afternoon. Dolphins might be dispersed on the continental shelf, in groups composed of some supposed kin units. In offshore waters they may form larger groups for various reasons including the need to defend themselves against possible predators which may be more common in pelagic waters.

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REFERENCES

Acquarone M. and Notarbartolo di Sciara G. (1992) Pigmentation patterns of the striped dolphin, *Stenella coeruleoalba*, (Meyen, 1833) in the Central Mediterranean Sea. In Evans P.G.H. (ed.) *Proceedings of the Sixth Annual Conference of the European Research on Cetaceans,*

https://doi.org/10.1017/S0025315408001641 Published online by Cambridge University Press

San Remo, Italy, 20–22 February, 1992. Cambridge: European Cetacean Society, pp. 203–205.

Agler B.A., Beard J.A., Bowman R.S., Corbett H.D., Frohock S.E., Hawvermale M.P., Katona S.E., Sadove S.S. and Seipt I.E. (1990) Finback whale, *Balaenoptera physalus*, photographic identification: methodology and preliminary results from the Western North Atlantic. *Report of the International Whaling Commission* 12 (Special Issue), 349–356.

Amano M. and Miyazaki N. (1996) Geographic variation in external morphology of Dall's porpoise, *Phocoenoides dalli*. *Aquatic Mammals* 22, 167–174.

Archer F.I. (1996) *Morphological and genetic variation of striped dolphins* (Stenella coeruleoalba, *Meyen 1833)*. PhD thesis, University of California, San Diego, USA.

Blackmer A.L., Anderson K. and Weinrich M.T. (2000) Temporal variability in features used to photo-identify humpback whales (*Megaptera novaeangliae*). *Marine Mammal Science* 16, 338–354.

Bourret V.J.R., Macé M.R.J.M. and Crouau-Roy B. (2007) Genetic variation and population structure of western Mediterranean and northern Atlantic *Stenella coeruleoalba* populations inferred from microsatellite data. *Journal of the Marine Biological Association of the United Kingdom* 87, 265–269.

Braham H.W. and Rice D.W. (1984) The right whale, *Balaena glacialis*. *Marine Fisheries Review* 46, 38–44.

Bray J.R. and Curtis J.T. (1957) An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs* 27, 325–349.

Cagnolaro L., Cozzi B., Magnaghi L., Podestà M., Poggi R. and Tangerini P. (1986) Su 18 cetacei piaggiati sulle coste italiane dal 1981 al 1985. Rilevamento biometrico ed osservazioni necroscopiche. *Atti della Società Italiana Scienze Naturale del Musec Civico di Storia Naturale di Milano* 127, 79–106.

Cairns J.S. and Schwager S.J. (1987) A comparison of association indices. *Animal Behaviour* 35, 1454–1469.

Calzada N. and Aguilar A. (1995) Geographic variation of body size in the Mediterranean striped dolphin. *Zeitschrift für Saeugetierkunde* 60, 257–264.

Dorsey E.M. (1983) Exclusive adjoining ranges in individually identified minke whales in Washington State. *Canadian Journal of Zoology* 61, 174–181.

Evans W.E., Yablokov A.V. and Bowles A.E. (1982) Geographic variation in the colour pattern of killer whales (*Orcinus orca*). *Report of the International Whaling Commission* 32, 687–694.

Forcada J., Aguilar A., Hammond P.S., Pastor X. and Aguilar R. (1994) Distribution and numbers of striped dolphin in the Western Mediterranean Sea after the 1990 epizootic outbreak. *Marine Mammal Science* 10, 137–150.

Fraser F.C. and Noble B.A. (1970) Variation of pigmentation pattern in Meyen's dolphin, *Stenella coeruleoalba* (Meyen). *Investigation on Cetacea* 2, 147–163.

Gannier A. and David L. (1997) Day and night distribution of the striped dolphin (*Stenella coeruleoalba*) in the area off Antibes (Ligurian Sea). In *Proceedings of the Eleventh Annual Conference of the European Research on Cetaceans, Stralsund, Germany, 10–12 March*. Cambridge: European Cetacean Society, pp. 160–163.

Gaspari S., Azzellino A., Airoldi S. and Hoelzel A.R. (2007) Social kin associations and genetic sctructuring of striped dolphin population (*Stenella coeruleoalba*) in the Mediterranean Sea. *Molecular Ecology* 16, 2922–2933.

Hammond P.S., Mizroch S.A. and Donovan G.P. (1990) Individual recognition of cetaceans: use of photo-identification and other techniques to estimate population parameters. *Report of the International Whaling Commission* 12 (Special Issue), 332–376.

Herman L.M., Baker C.S., Forestell P.H. and Antinoja R.C. (1980) Right whale, *Balaena glacialis*, sightings near Hawaii: a clue to wintering grounds? *Marine Ecology Progress Series* 2, 271–275.

Heyning J.E. and Perrin W.F. (1994) Two forms of common dolphin (genus *Delphinus*) from the Eastern Northern Pacific; evidence for two species. *Contribution in Science, Natural History Museum of the Los Angeles County* 442, 1–35.

Houck W.J. and Jefferson T.A. (1999) Dall's porpoise—*Phocoenoides dalli* (True, 1885). In Ridgway S.H. and Harrison S.R. (eds) *Handbook of marine mammals. Vol. 6: the second book of dolphins and porpoises*. London: Academic Press, pp. 443–472.

Jefferson T.A. (1988) *Phocoenoides dalli*. *Mammalian Species* 470, 319: 1–7.

Katona S.K. and Whitehead H.P. (1981). Identifying humpback whales using their natural markings. *Polar Record* 20, 439–444.

Perrin W.F., Akin P.A. and Kashiwada J.V. (1991) Geographic variation in external morphology of the spinner dolphin *Stenella longirostris* in the eastern Pacific and implications for conservation. *Fishery Bulletin* 89, 411–428.

Perrin W.F., Wilson C.E. and Archer F.I. II (1994) Striped dolphin *Stenella coeruleoalba* (Meyen, 1833). In Ridgway S.H. and Harrison R. (eds) *Handbook of marine mammals. Vol. 5: the first book of dolphins*. London: Academic Press, pp. 129–159.

Perrin W.F. (1997) Development and homologies of head stripes in the delphinoid cetaceans. *Marine Mammal Science* 13, 1–43.

Ringelstein J., Pusineri C., Hassani S., Meynier L., Nicolas R. and Ridoux V. (2006) Food and feeding ecology of the striped dolphin, *Stenella coeruleoalba*, in the oceanic waters of the north-east Atlantic. *Journal of the Marine Biological Association of the United Kingdom* 86, 909–918.

Rosso M., Siliceo Aznar I., Corsi A. and Würtz M. (2006) Pigmentation patterns variability of the striped dolphin *Stenella coeruleoalba* (Meyen, 1833) in the Ligurian Sea. In *Proceedings of the Eleventh Annual Conference of the European Research on Cetaceans, Gydnia, Poland 2–7 April, 2006*. Cambridge: European Cetacean society. In press.

Schaeff C.M. and Hamilton P.K. (1999) Genetic basis and evolutionary significance of ventral skin colour markings in North Atlantic right whales (*Eubalaena glacialis*). *Marine Mammal Science* 15, 701–711.

Schaeff C.M., Kraus S.D., Brown M.W., Gaskin D., Perkins J., Payne R., Boag B. and White B.N. (1991) Preliminary analysis of mitochondrial DNA variation within and between right whale species *Eubalaena glacialis* and *E. australis*. In Hoelzel A.R. (ed.) *Genetic ecology of whales and dolphins. International Whaling Commission* 13, 217–224.

Sears R., Williamson J.M., Wenzel F.W., Bérubé M., Gendron D. and Jones P. (1990) Photographic identification of the blue whale (*Balaenoptera musculus*) in the Gulf of St Lawrence, Canada. *Report of the International Whaling Commission* 12 (Special Issue), 335–348.

Shane S.H. (1990) Behavior and ecology of the bottlenose dolphin at Sanibel Island, Florida. In Leatherwood S. and Reeves R.R. (eds) *The bottlenose dolphin*. San Diego, CA: Academic Press, pp. 245–265.

Stockin K.A. and Visser I.N. (2005) Anomalously pigmented common dolphins (*Delphinus* sp.) off northern New Zealand. *Aquatic Mammals* 31, 43–51.

Valsecchi E., Amos W., Raga J.A., Podestà M. and Sherwin W. (2006) The effects of inbreeding on mortality during a morbillivirus outbreak

in the Mediterranean striped dolphins (*Stenella coeruleoalba*). *Animal Conservation* 7, 139–146.

and

Würtz M. and Marrale D. (1993) Food of striped dolphin *Stenella coeruleoalba* in the Ligurian Sea. *Journal of the Marine Biological Association of the United Kingdom* 73, 571–578.

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