

Abstract.— Examination of 95 Dall's porpoise specimens incidentally caught in gill nets, and 4 collected as beach strandings, indicate significant sexual dimorphism and developmental variation in several aspects of external morphology and coloration. The dorsal fins of males become extremely canted in adulthood, and mature males can be distinguished by this feature alone. Size of the post-anal hump of connective tissue and caudal peduncle depth also become exaggerated in adult males. The urogenital color pattern is highly variable, and frosting variations on the dorsal fin and flukes can be used to discern the general age of the individual. The strong sexual dimorphism and small testes of Dall's porpoise indicate a polygynous mating system. It is suggested that Dall's porpoise secondary sexual characteristics are used in male-male competition or female choice.

Sexual Dimorphism and Development of External Features in Dall's Porpoise *Phocoenoides dalli**

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Behavioral studies of many mammals have been greatly facilitated by the ability of researchers to distinguish different age and sex classes in the field (see Schaller 1963 for mountain gorillas *Gorilla gorilla beringei*; Geist 1968 for mountain sheep *Ovis dalli* and *O. canadensis*; Schaller 1972 for lions *Panthera leo*; Smith 1988 for mountain goats *Oreamnos americanus*). Knowledge of the behavior and social systems of cetaceans is not as advanced as that of terrestrial mammals, largely due to difficulties in studying these animals at sea and in identifying individuals and age/sex classes (but see Bigg 1982, Bigg et al. 1987 for killer whales *Orcinus orca*).

Dall's porpoise *Phocoenoides dalli* (True, 1885) presents particular problems for behavioral ecologists. It is generally an open-ocean species, seen most commonly several kilometers from shore; lives in small groups that are relatively hard to detect; and is extremely fast-swimming and unpredictable in its movements, often out-swimming or evading research vessels. In addition to these problems, detailed studies of sexual and age-related variation in external morphology of Dall's porpoise have not been conducted, and thus identification of different age/sex classes has been limited.

Although few quantitative studies have been done, comments in the

literature and my past observations led me to believe that there may be reliable external indicators of age and sex in this species. In particular, five features seemed promising: (1) dorsal fin shape (pers. observ.), (2) caudal peduncle shape (Mizue and Yoshida 1965, Houck 1976), (3) post-anal hump size (Scheffer 1949), (4) size of the thoracic epaxial muscle mass (Newby 1982), and (5) coloration patterns, especially the frosting variations of the dorsal fin and flukes (Mizue and Yoshida 1965, Morejohn et al. 1973, Morejohn 1979, Kasuya 1982).

These characteristics were chosen specifically for their potential use in identifying age/sex classes in the field. Another objective of this study was to quantify sexual, developmental, and individual variation in external morphology for use in population studies. Finally, it was hoped that this information, if combined with data on testis weight, would shed light on the type of social system possessed by Dall's porpoise.

Materials and methods

While working as a scientific observer in the U.S.-Japan Cooperative Research Program on Dall's Porpoise, between 12 June and 14 July 1986, I examined 95 Dall's porpoises aboard the mothership *Nojima Maru* of the Japanese high seas salmon driftnet fishery (see description of this fishery in Jones 1984). All of the animals died after becoming inciden-

tally entangled in gill nets set for salmon south of the Near Island group at the western end of the Aleutian Islands, Alaska. The capture locations of these specimens are plotted by 1-degree block in Figure 1. All specimens were of the *dalli*-type color morph (see Houck 1976) and were presumably from the northwestern North Pacific population that calves south of the western Aleutians (Kasuya and Ogi 1987). In addition to these specimens, four calves collected as beach strandings along the California coast in 1987 and 1988 were used in the analyses. Although these four specimens were from a separate population (Kasuya 1982, Kasuya and Ogi 1987), they were included because the sample size of calves was small, and geographic variation at the calf stage was assumed to be insignificant. Little work has been conducted on geographic variation in subadult animals. However, some differences in fin shapes between calves of different stocks of spinner dolphins *Stenella longirostris* have been identified, although these are minor compared with differences in adults (W.F. Perrin, Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, La Jolla, CA 92038, pers. commun., Aug. 1989).

Each porpoise was weighed and sexed, a specimen number was assigned, and black-and-white photographs were taken. A series of seven measurements were obtained to the nearest 0.5 cm (Fig. 2, Table 1), and the animal was dissected. The reproductive status of females was assessed as pregnant, lactating, resting, or immature, based on gross examination. The distribution of total lengths of the specimens is shown in Figure 3.

Each specimen was placed into one of seven age/sex classes (Table 2). Most of the classes were based on the total length of the porpoise, generally following the growth curve presented by Newby (1982). Because there was only one neonate male, and only one feature (Canting Index) was measured on it, it was pooled with the females. The assumption was made that there are no sexual differences at the neonate stage. The cutoff between immature and mature males was based on Jones et al. (1987), who gave 180 cm as the average length at sexual maturity. Attainment of sexual maturity in males is considered to be more strongly correlated with length than with age, and all males in this study over 180 cm had enlarged testes, indicative of maturity (Kasuya and Shiraga 1985). Female sexual maturity is not well correlated with length, so average length at maturity was not used to separate immature and mature females. If a female was pregnant, lactating, or had apparent corpora upon gross examination of the ovaries, it was classified as mature. If it fulfilled none of these criteria, but was ≥ 151 cm, it was placed into the immature class. Because over 95% of all mature females in the study area are pregnant or

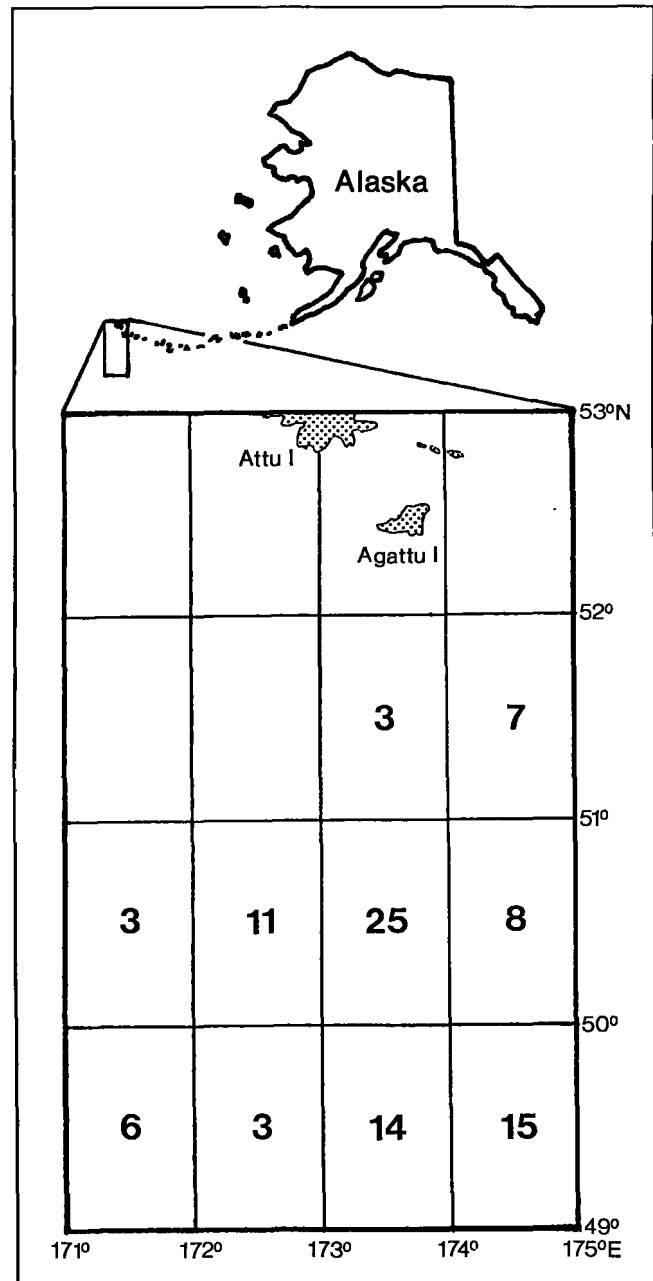


Figure 1

Capture locations of Dall's porpoise specimens from the northwestern North Pacific.

lactating during the fishing season, these are very good indicators of sexual maturity for this population (Jones et al. 1983).

In order to test quantitatively for variation in dorsal fin shape, a value similar to that used by Perrin (1975) for spinner dolphins was computed as the ratio a/b (where a is measurement 7 and b is measurement 6 in Table 1). This quantity is termed the Canting Index, and for Dall's porpoise will generally fall between

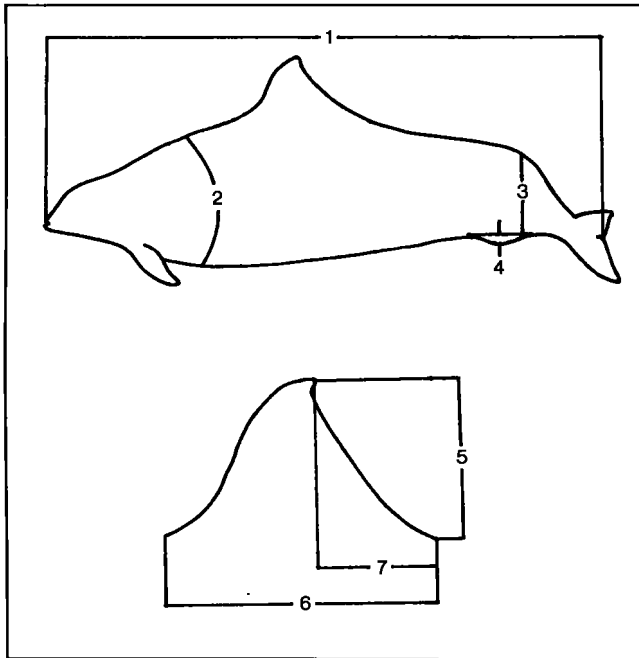


Figure 2

Measurements taken of Dall's porpoise specimens (see also Table 1).

Table 1

Measurements of Dall's porpoise specimens taken in this study, illustrated in Figure 2. Numbers in parentheses correspond to numbers of standard measurements in Norris (1961).

No. (Fig. 2)	Measurement
1	Total length (1)
2	Thoracic girth, midway between blowhole and dorsal fin
3	Depth of caudal peduncle, posterior to postanal hump
4	Depth of postanal hump
5	Height of dorsal fin (32)
6	Base of dorsal fin (33)
7	Length from posterior insertion of dorsal fin to a perpendicular from tip

Table 2

Summary of age/sex classes into which Dall's porpoise specimens were separated.

Age/sex class	Symbol	Criteria	n
Calf	N	≤ 130 cm	5
Juvenile female	JF	131-150 cm	2
Juvenile male	JM	131-150 cm	6
Immature female	IF	≥ 151 cm, not pregnant or lactating, no corpora	16
Immature male	IM	151-180 cm	12
Mature female	MF	≥ 151 cm, pregnant, lactating, or corpora present	44
Mature male	MM	≥ 181 cm	14
Total			99

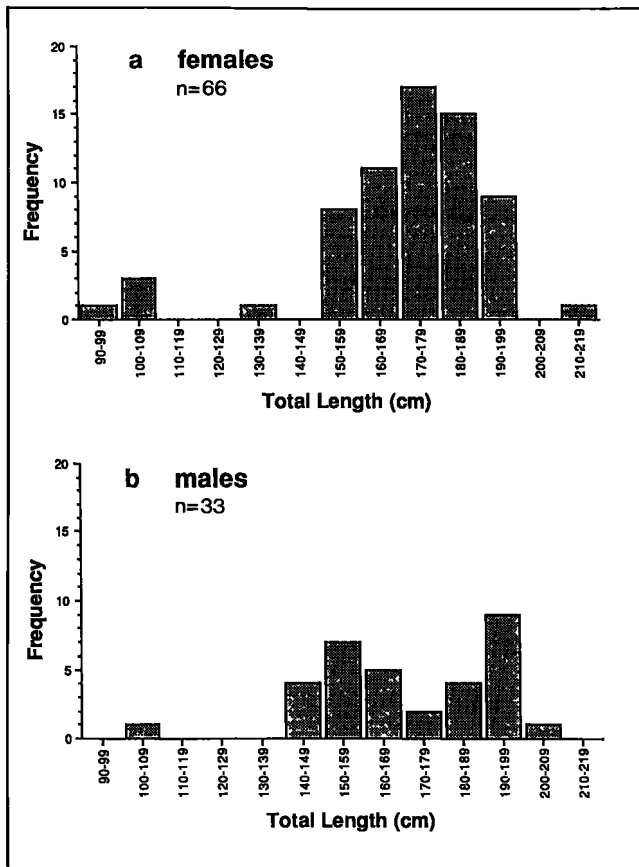


Figure 3

Frequency histograms of total lengths of Dall's porpoise specimens.

zero and one. The higher the Canting Index, the larger the degree of forward canting.

Sexual differences in morphology between immature males and females and between mature males and females were tested with a *t*-test, and age variation was tested separately for males and females with a one-way analysis of variance (ANOVA). Variation in dorsal fin coloration was tested with a chi-square test. Because proportions are known not to be normally distributed, an arc sine transformation was performed on all proportions for statistical analyses (the resulting data approached normality).

Results

External morphology

Dorsal fin shape The dorsal fins of Dall's porpoises cant forward to varying degrees (Fig. 4). The Canting Index of the dorsal fin shows a tendency to increase

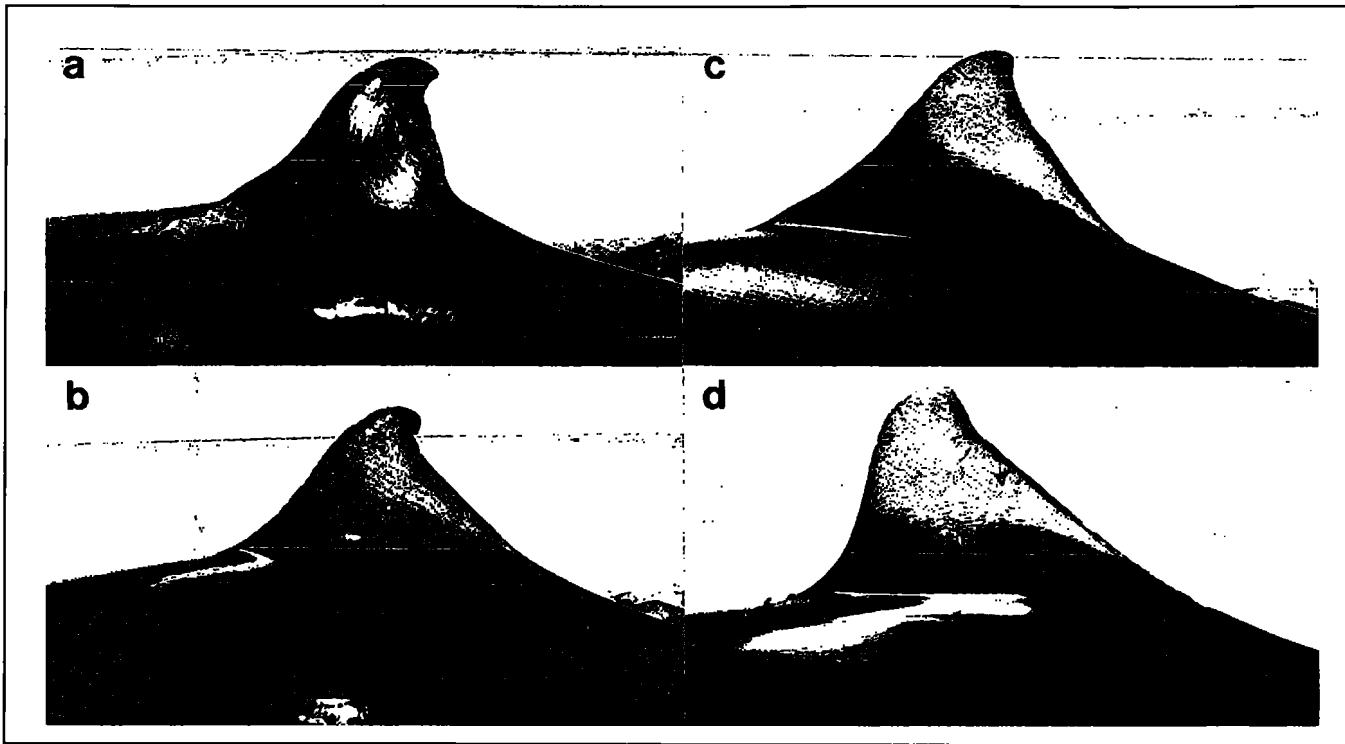


Figure 4

Dorsal fin shapes of Dall's porpoise specimens: (a) calf (TAJ 171), (b) immature male (TAJ 168), (c) mature female (TAJ 156), (d) mature male (TAJ 161).

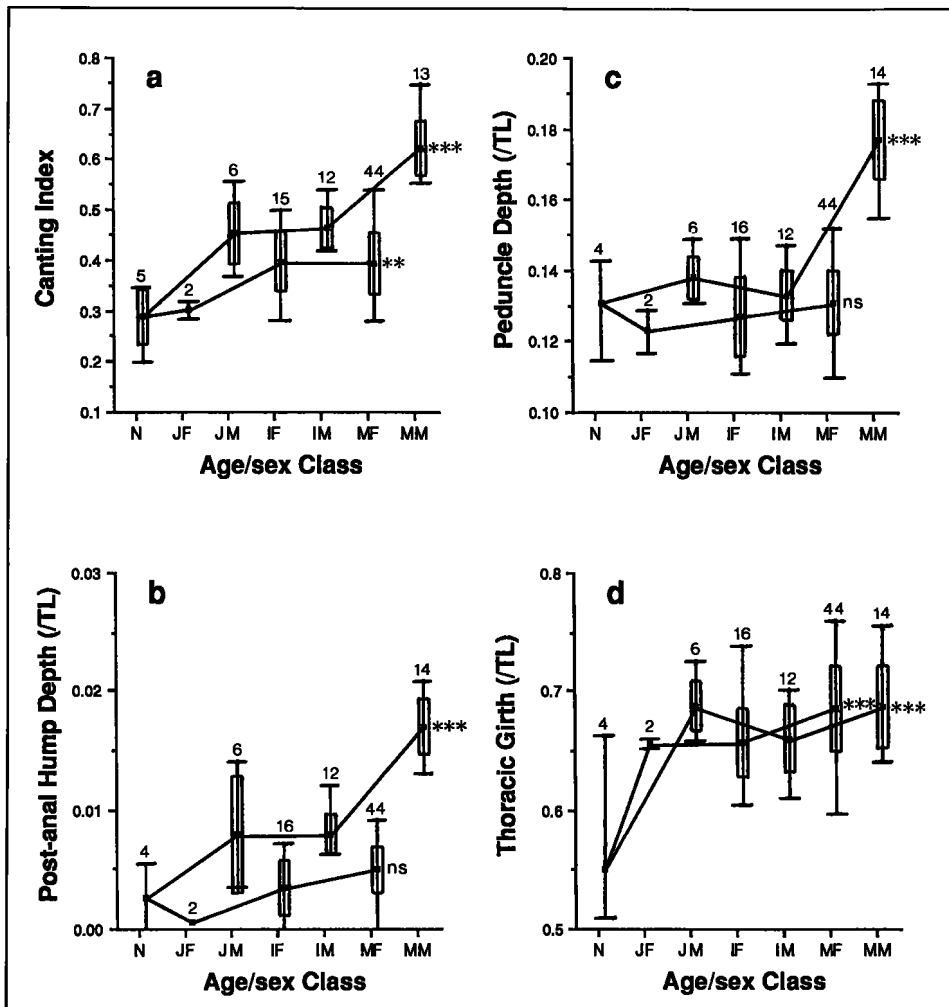


Figure 5

External features of Dall's porpoise specimens plotted by age/sex class. Points are mean, boxes are \pm 1SD, vertical bars are range, and numbers indicate sample size. ANOVAs test for developmental variation separately within each sex: significance *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, ns = not significant.

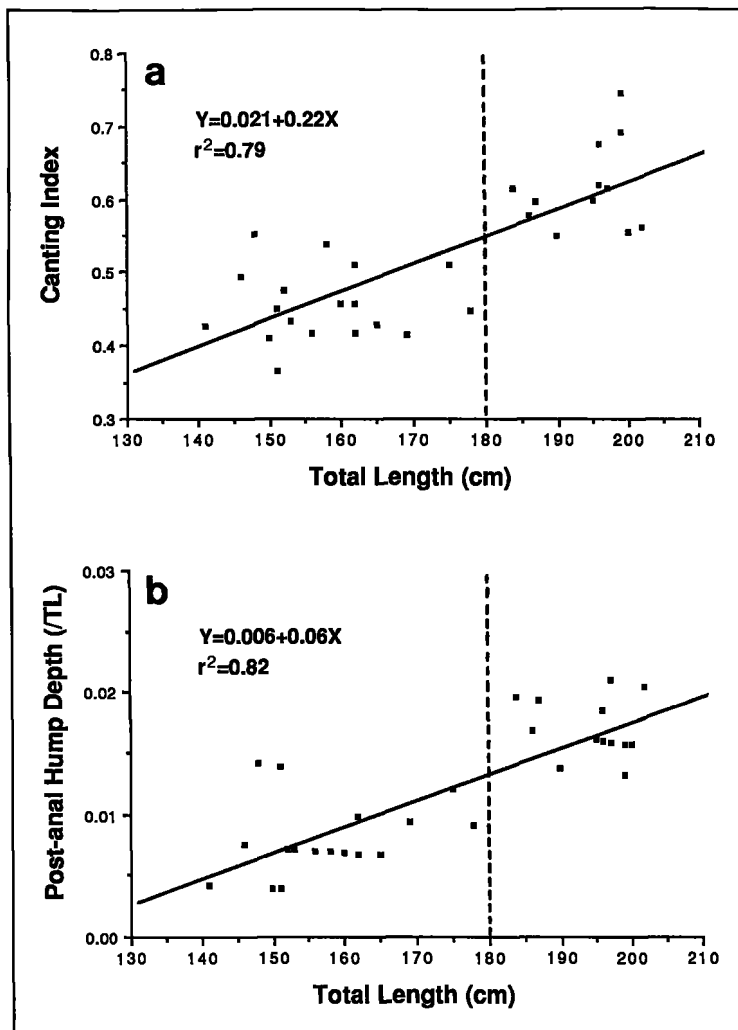


Figure 6

Development of external features in male Dall's porpoise specimens. Broken line represents average length at sexual maturity.

with age of the animal in males (Figs. 5a, 6a). In females, however, the dorsal fin apparently does not change shape once it reaches the immature stage. The difference between the mean Canting Indices for immature males and females was significant ($t=3.079$, $df=25$, $p<0.01$), and the difference between mature males and females was highly significant ($t=11.539$, $df=55$, $p<0.001$). In fact, there was little or no overlap between adult males and any other age/sex class, and individuals with a Canting Index of 0.55 or greater can be assumed to be adult males.

At a casual glance, it appears that the dorsal fins of adult males have a wider base than those of females. However, the mean base/height ratio for mature females was 2.15 (SD = 0.18, range = 1.83–2.57, $n=44$), and for mature males it was 2.16 (SD = 0.15, range = 1.94–2.41, $n=13$), a non-significant difference ($t=0.182$, $df=55$, $p>0.05$). The difference in appearance results from the more anterior position of the tip of the fin of adult males, not a wider base.

Postanal hump depth A small to moderate hump composed of connective tissue, just posterior to the anus, could be seen in nearly every Dall's porpoise, including newborn animals. This feature was even evident in most nearterm fetuses.

In some females of all female age classes, the hump was <0.5 cm, and thus not measurable (Fig. 5b). Immature and mature males all had significant postanal humps, but the feature was exaggerated only in adult males, in which it was $>1.2\%$ of the total length. Differences between immature males and females ($t=4.086$, $df=26$, $p<0.001$), and between mature males and females ($t=8.599$, $df=56$, $p<0.001$) were both highly significant. Postanal hump depth of males increases with increasing length (Fig. 6b), and is correlated with the degree of forward canting of the dorsal fin (Fig. 7).

Caudal peduncle depth Depth of the caudal peduncle (as a proportion of total length) showed a great deal

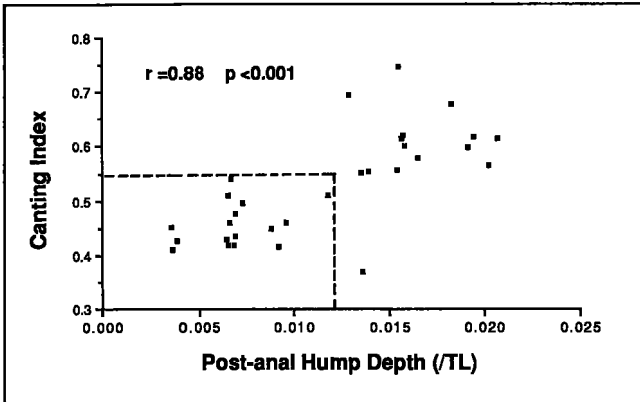


Figure 7

Canting Index vs. postanal hump depth for male Dall's porpoise specimens. Dashed box comprises juvenile and immature males.

of overlap for all age/sex classes, except mature males (Fig. 5c). There was no significant difference in this feature between sexes in immatures ($t = 1.683$, $df = 26$, $p > 0.05$), but the difference between mature males and females was highly significant ($t = 14.935$, $df = 56$, $p < 0.001$). The caudal peduncle only becomes greatly

deepened in adult males, and again this appears to be an absolute difference. Peduncle depth represents $>15\%$ of the total length in mature males, and $<15\%$ in all other age/sex classes.

Size of thoracic epaxial muscle mass There was a noticeable "hump" on the back of most adult males examined in this study (Fig. 8f). Dissections of this hump revealed that it resulted from an increase in the size of the thoracic epaxial muscle mass. It did not seem to be associated with an increase in the thickness of the blubber layer.

Measurement of the thoracic girth in Dall's porpoise was not a good indication of the size of this muscle mass. There was no difference in the size of the thoracic girth (relative to total length) either between immature males and females ($t = 0.245$, $df = 26$, $p > 0.05$) or between mature males and females ($t = 0.130$, $df = 56$, $p > 0.05$) (Fig. 5d). After an increase in thoracic girth from the neonate to the juvenile stage, it leveled off in both sexes.

Fluke shape Although no quantitative data were collected on this aspect of Dall's porpoise morphology,

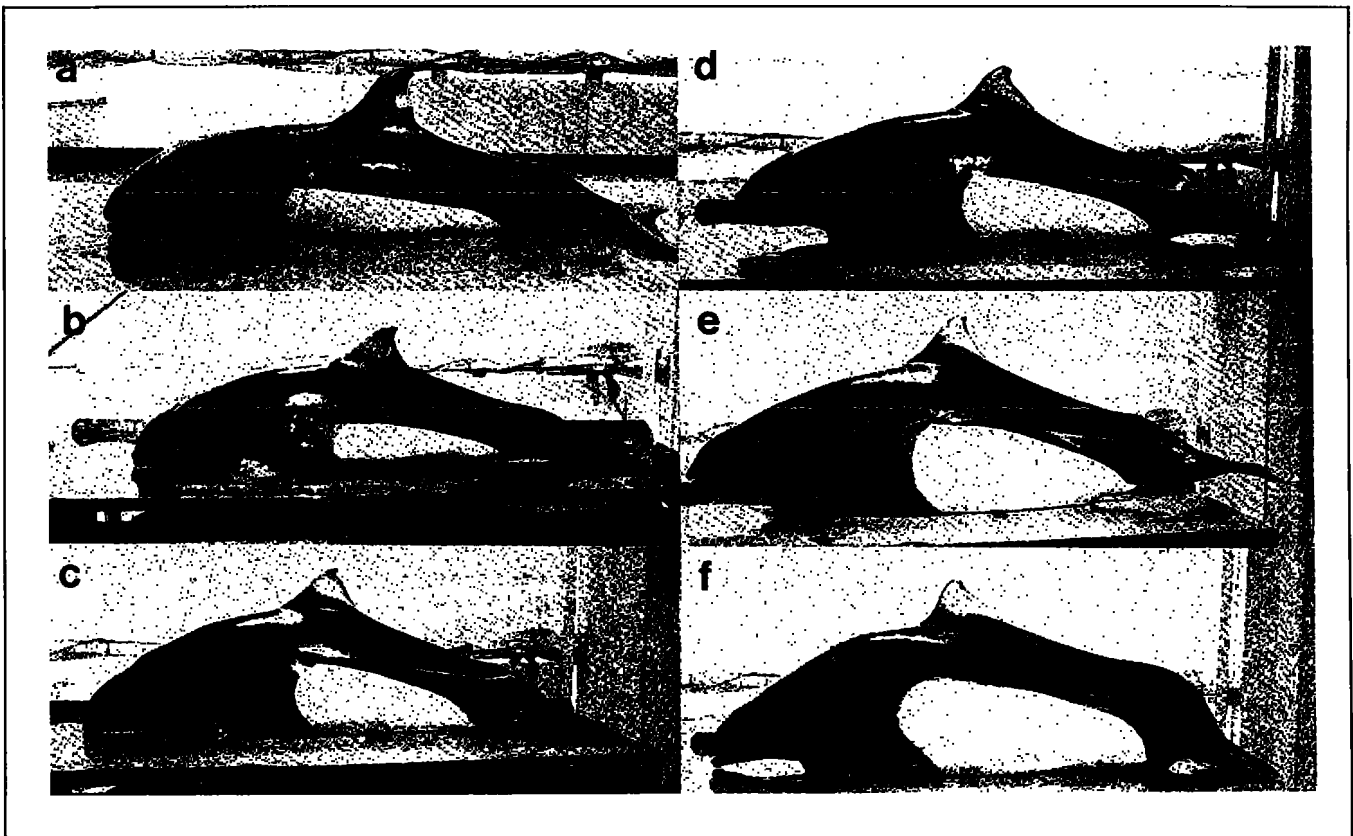


Figure 8

Dall's porpoise age/sex classes: (a) calf (TAJ 171), (b) juvenile female (TAJ 093), (c) immature female (TAJ 162), (d) immature male (TAJ 168), (e) mature female (TAJ 145), (f) mature male (TAJ 150).

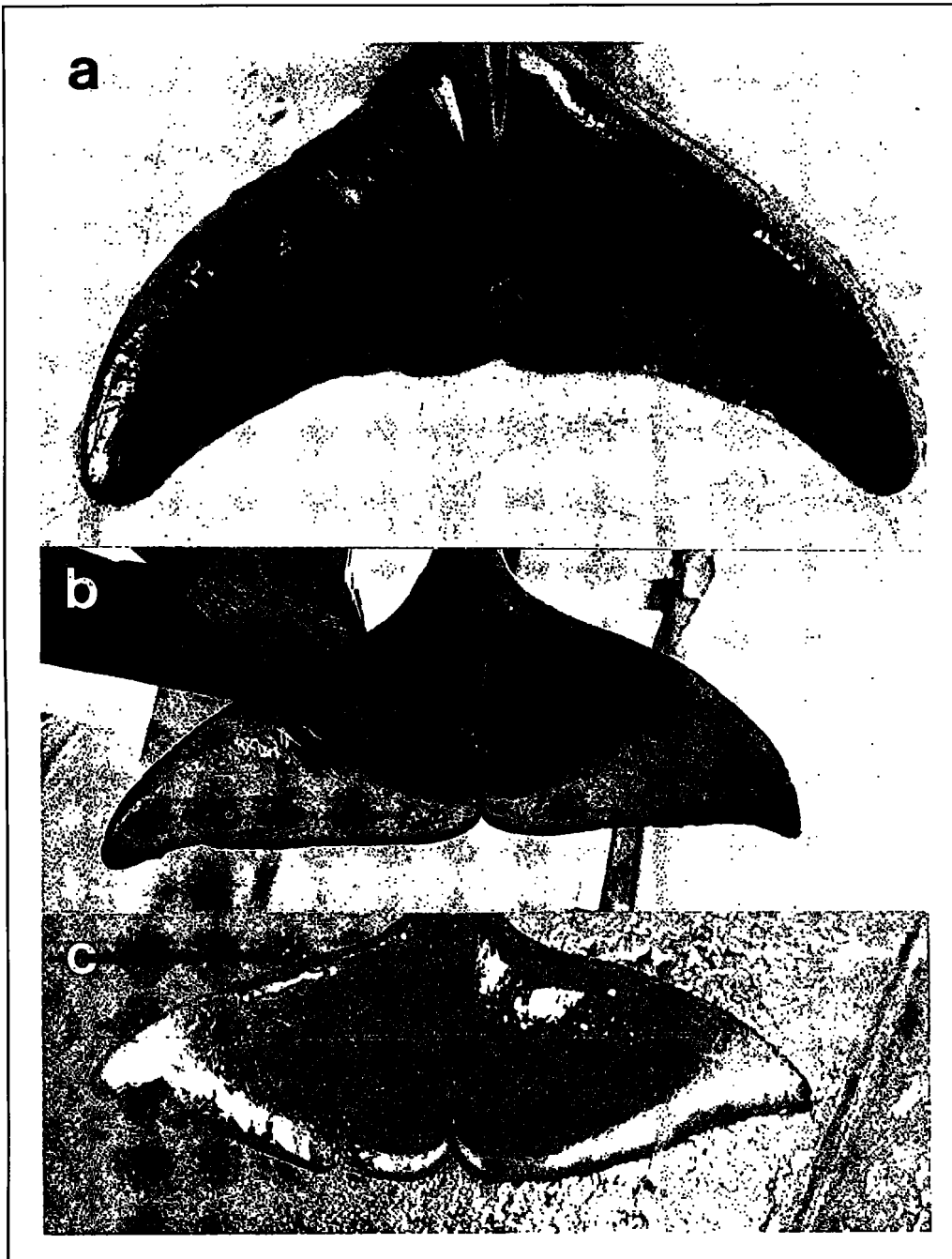


Figure 9
Shape of Dall's porpoise tail flukes: (a) calf (TAJ 171), (b) mature female (TAJ 121), (c) mature male (TAJ 090).

subjective observations suggested that there may be significant sexual dimorphism in the shape of the flukes (Fig. 9).

Newborn porpoises have flukes in which the trailing edge is more or less concave, and the tips are fairly rounded. As age increases, the trailing edge approaches a straight line, and the tips become more pointed and recurved. Some animals have flukes with a convex trailing edge, and these are almost always adult males (animals with extremely convex flukes are always

males). There seems to be much individual variability in this feature, however, as some mature males do not have convex flukes. Quantitative data are needed to further explore the relationship between fluke shape and age/sex class.

Coloration

Urogenital color pattern The coloration of the urogenital area of Dall's porpoise has been previously reported to be sexually-dimorphic (Morejohn et al.

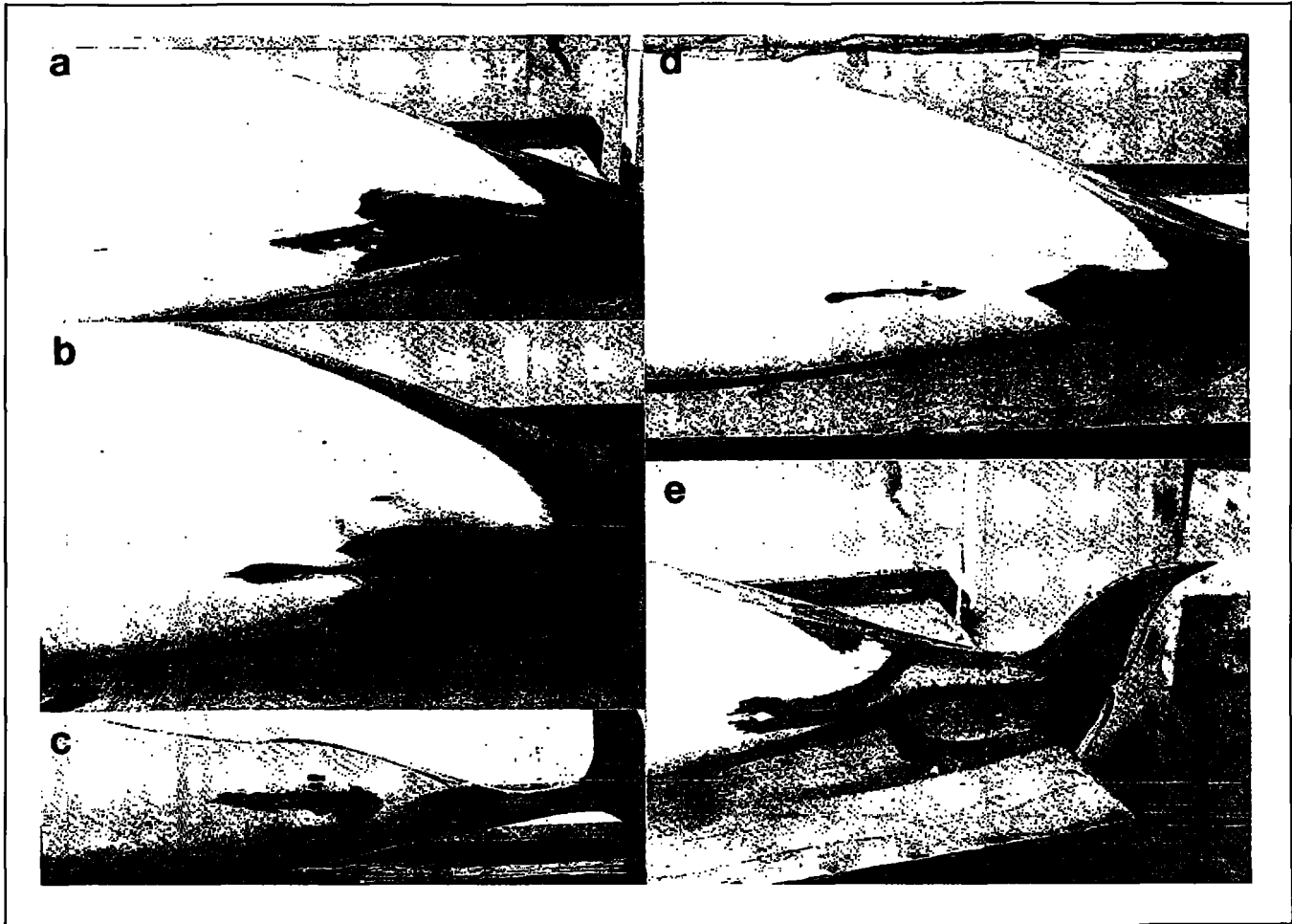


Figure 10

Urogenital color patterns of Dall's porpoise specimens: (a-c) females (TAJ 165, 104; SMB 060), (d-e) males (TAJ 172; WAA 053).

1973). Morejohn and his colleagues illustrated one female and two male patterns, but failed to recognize the large degree of individual variation exhibited by Dall's porpoises in this respect. Figure 10 shows only a few of the many observed patterns. Although most of the patterns can be recognized as more similar to the male or female type, the high degree of variability in this aspect of the color pattern makes sexing individuals by this characteristic alone somewhat risky.

Dorsal fin and fluke frosting A quantitative study of Dall's porpoise coloration may reveal significant sexual differences, but there seem to be no obvious differences between the sexes in any component of the pigmentation pattern, other than urogenital coloration. Analysis of photographs showed that there is, however, a high degree of developmental variation (Table 3). Newborn Dall's porpoises have a muted color pattern of gray tones with no frosting on the flukes or dorsal fin. As the animal ages, the colors apparently inten-

Table 3

Analysis of intensity of dorsal fin frosting coloration in various age/sex classes of Dall's porpoise (H_0 : the three categories occur with equal probability). Due to small sample sizes, calves (N), juvenile females (JF), and juvenile males (JM) were not tested.

Age/sex class	Color			Statistical test	
	No frosting	Gray	White	χ^2	Significance
N	5	0	0	—	—
JF	0	2	0	—	—
JM	0	4	0	—	—
IF	0	9	3	10.500	$p < 0.01$
IM	0	7	1	10.737	$p < 0.01$
MF	0	14	29	29.356	$p < 0.001$
MM	0	3	9	10.500	$p < 0.01$

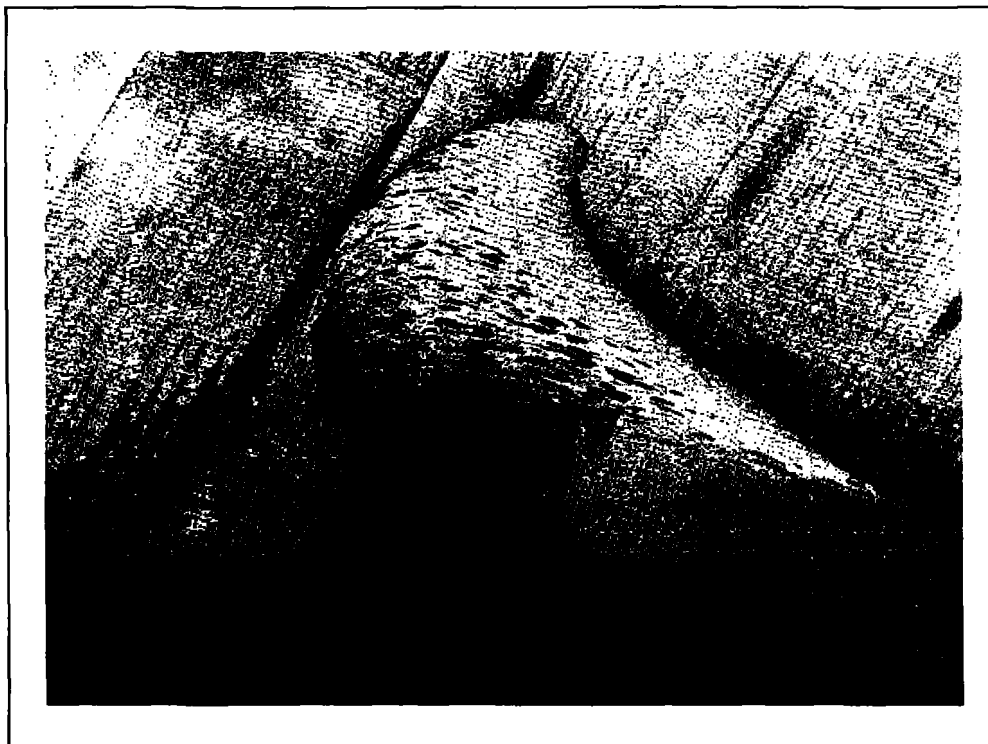


Figure 11

An example of the type of color pattern of the dorsal fin of Dall's porpoise specimens that can be used to identify individuals. Note the complex pattern of black flecking.

sify and approach the adult black-and-white pattern. Adults of both sexes have white to light-gray frosting on the dorsal fin and both surfaces of the flukes, and many also have light-colored areas on the peduncle, flippers, head, throat, and other areas (see Figs. 4, 8, and 9).

The color pattern of the dorsal fin, in addition to revealing something about the general age of the porpoise, may also be useful in distinguishing individuals. Most adults have an apparently unique pattern of black flecks on the white frosting, which are arranged in what Norris and Prescott (1961) called "flow patterns" (Fig. 11). These flecks tend to be absent or not as well developed in subadults.

Discussion

Identification of age/sex classes at sea

In this section, the results of this study are synthesized with other available information, and a description of how Dall's porpoise age/sex classes can be recognized in the field is given. Age and size ranges of the classes are derived from results of research by the National Marine Mammal Laboratory (Newby 1982; Jones et al. 1983, 1987, 1988). The Canting Index can be measured from a photograph taken perpendicular to the animal slow rolling at sea (Fig. 12).

Sexing Dall's porpoises by genital patch patterns is unreliable. More consistent genital pattern dimorphism apparently exists in killer whales (Bigg et al. 1987), northern right whale dolphins *Lissodelphis borealis* (Leatherwood and Walker 1979), Commerson's dolphins *Cephalorhynchus commersonii* (Robineau 1984, Goodall et al. 1988a), Heaviside's dolphins *C. heavisidii* (Best 1988), Hector's dolphins *C. hectori* (Slooten and Dawson 1988), and possibly Chilean dolphins *C. eutropia* (Goodall et al. 1988b). Despite the claim of Morejohn et al. (1973), using this method for Dall's porpoise would likely result in many incorrect classifications. However, most porpoises fitting the normal male and normal female patterns of Morejohn et al. could be sexed reliably. Those with more variable patterns should be sexed by other means.

Dall's porpoise calves (Fig. 8a) are between 85 and 130 cm in length and less than about 4 months old. Newborns are slate-gray in color, and the flank patch is lighter gray, often with an orangish tinge. Often the flank area just anterior to the flank patch is an intermediate gray. There is generally no frosting on the appendages. Hall (1981) reported that light-gray areas may be seen on the dorsal surface of the head and around the blowhole. The dorsal fin is not canted significantly (Canting Index < 0.35). The postanal hump is small to insignificant. The rear border of the flukes tends to be concave, and the head is relatively large compared with the body. Calves are usually in close

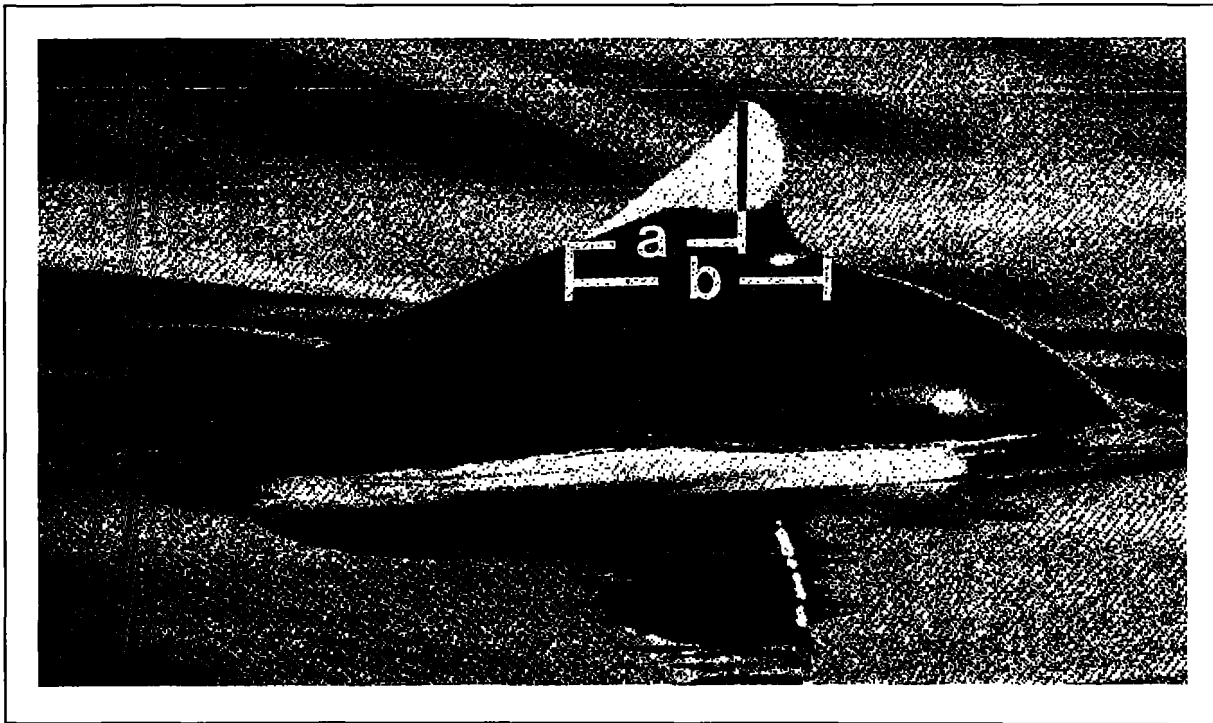


Figure 12

An example of how the Canting Index is measured from a photo of a live Dall's porpoise. In this case, the ratio equals 0.67, indicating that this is a sexually mature male.

proximity to an adult, but are rarely seen from boats because cow-calf pairs do not often ride bow waves.

Juveniles (Fig. 8b) are between 130 and 150 cm, and from 4 months to 1 year old. They are significantly lighter in color than adults, and the flank patch is still light-gray. Frosting has begun to develop on the dorsal fin and flukes, but is not extensive and is usually only a bit lighter than the rest of the body at this stage. The Canting Index is between 0.25 and 0.55. A slight to moderate postanal hump may be visible. These animals are most likely weaned, and independent of their mothers.

Immature males and females (Fig. 8c, d) range from about 150 to over 175 cm in females and to about 180 cm in males, but are nearly impossible to distinguish in the field. Females are 1-3 or 4 years old, and males are 1-5. Immatures are very difficult to distinguish from adult females. The color pattern has mostly reached black-and-white, although it may still be somewhat muted. There is usually prominent white to light-gray frosting, and little obvious sexual dimorphism (except that males may have a slightly more canted dorsal fin and a larger postanal hump). The Canting Index is between 0.25 and 0.55. Immatures appear to be the most common bow-riders in many areas.

Mature females (Fig. 8e) are from about 175 cm up to 215 cm long, and more than 3 or 4 years old. The

color pattern has reached the adult black-and-white stage, with extensive light frosting on the flukes and dorsal fin; but due to overlap adult females are difficult to distinguish from immatures. The dorsal fin is not strongly canted (Canting Index < 0.55). There is usually a small postanal hump. Adult females may be identified if closely accompanied by a small calf. Lactating females and those in late stages of pregnancy often appear to be of extremely large girth.

Adult males (Fig. 8f) are 180 to 225 cm long and greater than 4 years old. The coloration is black-and-white, and extensive white frosting is usually present on the fin and flukes. The dorsal fin is strongly canted (Canting Index > 0.55). There is almost always a large postanal hump ($> 1.2\%$ of the total length), and the peduncle is deepened ($> 15\%$ of the total length). Often, an enlargement of the thoracic epaxial muscle mass is apparent as a hump between the blowhole and the dorsal fin. Many (possibly older) adult males appear to have flukes with a convex rear border, and they are usually very robust (the head may look disproportionately small).

The assumption is made that results from animals of this northwestern North Pacific population are applicable to other Dall's porpoise populations as well. Growth characteristics of reproductively isolated, small cetacean populations are known to sometimes differ

widely (Perrin 1984, Kasuya and Shiraga 1985) however the same general trends seem to be apparent in photographs of animals from other populations. Only future studies of these features in other *P. dalli* populations will reveal if this assumption is justified.

Sexual dimorphism, testis weight, and mating system

The moderately extreme sexual dimorphism apparent in this species deserves some discussion. Not only are males significantly longer and heavier than females (Kasuya 1978, Morejohn 1979, Newby 1982), but several morphological features are exaggerated in adult males. The mating system of Dall's porpoise is unknown, but sexual dimorphism among mammals, in which the male is larger, is usually related to intra-sexual competition for females in a polygynous mating system. In fact, Ralls (1977) determined that extreme sexual dimorphism is a very good predictor of extreme polygyny.

Newby (1982) implied a polygynous system for *P. dalli*, and Landino (1985) suggested a unimale system (either polygyny or monogamy). Landino's prediction is based on the finding that the relative testes weights of various primate species are related to their breeding systems (Short 1979, Harcourt et al. 1981, Harvey and Harcourt 1984). Males with relatively large testes tend to have multimale systems (mostly promiscuity), while those with smaller testes have unimale systems. This is thought to be related to the need to deliver large loads of sperm in promiscuous species, in which the potential for sperm competition exists (see Trivers 1985 for a general description of sperm competition theory). Kenagy and Trombulak (1986) raised the question of whether mating system/testis size predictions apply to cetaceans, but Brownell and Ralls (1986) found sperm-competition theory to be quite useful in explaining mating systems in mysticete cetaceans.

Kenagy and Trombulak (1986) compared relative testis weights for 133 species of mammals, and found the harbor porpoise *Phocoena phocoena*, a closely related species, to have the highest value. This evidence points to extreme multimale (probably promiscuous) breeding for this species, which is consistent with morphological evidence. Harbor porpoises show reverse sexual dimorphism, with females larger than males (Gaskin et al. 1984), and males do not appear to possess any secondary sexual characteristics.

Unfortunately, Kenagy and Trombulak (1986) did not include data on testis weight in Dall's porpoise. In order to compare Dall's porpoise with their information on other species, data on nine adult males presented by Subramanian et al. (1986, 1987) were used in a manner consistent with that of Kenagy and Trombulak. Only

sexually mature males taken during the season of male sexual activity were used (August–September; Jones et al. 1988). When plotted on Figure 1 of Kenagy and Trombulak, the Dall's porpoise data point fell close to the regression line for all 133 mammalian species, and well below that of the other five species of small odontocete plotted. The testes of *P. dalli* comprise only about 0.22% of their body weight, as opposed to 4.00% in *P. phocoena*.

Small testes relative to body weight suggests a single-male system with low copulatory frequency (either monogamy or polygyny) for Dall's porpoise. Monogamy is rare in mammals (<3% of all mammal species are monogamous), and it is generally associated with sexual monomorphism (Kleiman 1977). Thus it is unlikely to be the case for *P. dalli*. This leaves polygyny, and this conclusion is further supported by the sexual dimorphism in size (males larger) and the striking secondary sexual characteristics of males in this species. Although some adult males are present, Kasuya and Jones (1984) and Kasuya and Ogi (1987) reported that the majority of mature males are segregated from mating areas during the mating season in the western Pacific. This finding is also more consistent with polygyny than with monogamy.

Several species of odontocete cetaceans show sexual dimorphism in these same characteristics. For instance, extremely canted dorsal fins are seen in adult male spinner dolphins, especially those of the eastern form of the eastern tropical Pacific (Perrin 1972, 1975). Killer whales and spectacled porpoises *Australophocaena dioptrica* have a significant degree of sexual dimorphism in both size and shape of the dorsal fin (Fraser 1968, Brownell 1975, Heimlich-Boran 1986, Leatherwood et al. 1982). Adult male long-finned pilot whales *Globicephala melas* have more rounded fins, with thicker leading edges than females and young (Sergeant 1962).

Postanal humps appear to be common in many species of odontocetes, although they have been properly described and correlated with age and sex in only a few (published photographs show them in several genera, including *Peponocephala*, *Lagenorhynchus*, and *Lagenodelphis*). Rough-toothed dolphin *Steno bredanensis*, spotted dolphin *Stenella attenuata*, spinner dolphin, and some common dolphin *Delphinus delphis* adult males exhibit prominent humps (Norris 1967; Perrin 1972, 1975; Evans 1975; Leatherwood et al. 1982). Again, this feature is most exaggerated in eastern spinners.

Deepened caudal peduncles (not including the post-anal hump) are apparent in photographs of adult male spinner dolphins (Perrin 1972), and Norris et al. (1985) were sometimes able to use this feature to distinguish adult male Hawaiian spinners in the field. To my

knowledge, thoracic humps of the extent seen in adult male Dall's porpoises have not been reported in other cetaceans, but they may exist in a more subtle form in some species. Sexual dimorphism in fluke shape similar to that in *P. dalli* has been reported by Nishiwaki et al. (1963) for sperm whales *Physeter macrocephalus*.

Overall, the dimorphism described here for Dall's porpoise most resembles that described for eastern and whitebelly spinner dolphins by Perrin (1972, 1975). Perrin (1972) proposed that the strikingly canted dorsal fins and enlarged postanal humps of adult male eastern Pacific spinners function as species-recognition signals within mixed schools of spinner dolphins and spotted dolphins. Norris et al. (1985) interpreted these secondary sexual characteristics as signals that make adult males easily recognizable, and possibly allow them to mimic gray reef sharks *Carcharhinus amblyrhynchos*. Subgroups of adult male spinners seem to play an ordering role in dolphin schools, and often achieve this by means of overt aggression. Thus their striking appearance would assist in this aggressive role.

Mating appears to be promiscuous in Hawaiian spinner dolphins (Norris et al. 1985), but understanding the functions of sexual dimorphism seems to be complicated by other social pressures than just mating system considerations. Sexual dimorphism may have originally evolved in association with a polygynous mating system. However, if Hawaiian spinners tended more toward promiscuity than other populations, the sexually dimorphic features might become reduced, but could still function in social ordering (as proposed by Norris et al. 1985). Perhaps eastern spinners have remained strongly polygynous and thus dimorphic, and Hawaiian spinners have moved more towards promiscuity, with whitebelly intermediate.

In this scenario, Hawaiian, whitebelly, and eastern spinner stocks would show a grade of increasing degrees of polygyny and sexual dimorphism, and decreasing testis size. In general, spinner dolphins have relatively large testes (Perrin et al. 1977, Perrin and Henderson 1984). However, eastern spinners have smaller testes than whitebelly spinners, and this is consistent with sperm competition predictions. There is little information on Hawaiian spinners (the form with the least pronounced dimorphism), but if this hypothesis is correct, one would expect them to have the least polygynous system and the largest testes of these three *S. longirostris* races.

I propose that despite the similarity in appearance, the sexual dimorphism in Dall's porpoise evolved and is used largely in polygynous mating. Dall's porpoises do not school with other species, and thus have no need for the type of species-recognition signals suggested by Perrin (1972). Also, Dall's live in small groups, and

the need for aggressive ordering of schools is probably nonexistent or very weak.

I have suggested above that *P. dalli* is polygynous, and I believe these sexually dimorphic features are mostly related to male-male competition for females in this species. Newby (1982) first suggested this after discovering that adult male Dall's taken closer to the "rutting season" were heavier, and had a larger thoracic girth, than those taken earlier. The relationship between androgen levels, social aggression, and neck girth has been well established in some polygynous mammals (Lincoln 1971, Bouissou 1983). It is easy to imagine how an increase in size of the thoracic musculature could benefit fighting males, but how the other features could relate to this requires some speculation. If canting of the dorsal fin increases its rigidity, this could aid males that use their dorsal fins in aggressive encounters. A large postanal hump may assist somehow in mating with the female. Of course, these features may not be used in fighting at all, but may instead function as visual signals, allowing males to gauge each other or in being attractive to females, and thus operating in terms of female choice.

It is not possible to evaluate the validity of these speculations at present, because almost nothing is known of the social behavior of Dall's porpoise. Long-term detailed observation of wild porpoises, especially including identification of individuals, is needed to understand how these features operate in wild Dall's porpoise groups.

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Citations

- Best, P.B.**
1988 The external appearance of Heaviside's dolphin, *Cephalorhynchus heavisidii* (Gray, 1828). Rep. Int. Whaling Comm. (Spec. Iss. 9):279-299.
- Bigg, M.**
1982 An assessment of killer whale (*Orcinus orca*) stocks off Vancouver Island, British Columbia. Rep. Int. Whaling Comm. 32:655-666.
- Bigg, M.A., G.M. Ellis, J.K.B. Ford, and K.C. Balcomb**
1987 Killer whales: A study of their identification, genealogy and natural history in British Columbia and Washington State. Phantom Press and Publishers, Nanaimo, B.C., 79 p.
- Bouissou, M.F.**
1983 Androgens, aggressive behaviour and social relationships in higher mammals. Horm. Res. (Basel) 18:43-61.
- Brownell, R.L., Jr.**
1975 *Phocoena dioptrica*. Mamm. Spec. 66:1-3.
- Brownell, R.L., Jr., and K.R. Ralls**
1986 Potential for sperm competition in baleen whales. Rep. Int. Whaling Comm. (Spec. Iss. 8):97-112.
- Evans, W.E.**
1975 Distribution, differentiation of populations, and other aspects of the natural history of *Delphinus delphis* Linnaeus in the northeastern Pacific. Ph.D. diss., Univ. Calif., Los Angeles, 145 p.
- Fraser, F.C.**
1968 Notes on a specimen of *Phocoena dioptrica* from South Georgia. Br. Antarct. Surv. Bull. 16:51-56.
- Gaskin, D.E., G.J.D. Smith, A.P. Watson, W.Y. Yasui, and D.B. Yurick**
1984 Reproduction in the porpoises (Phocoenidae): Implications for management. Rep. Int. Whaling Comm. (Spec. Iss. 6): 135-148.
- Geist, V.**
1968 On the interrelation of external appearance, social behaviour and social structure of mountain sheep. Z. Tierpsychol. 25:199-215.
- Goodall, R.N.P., A.R. Galeazzi, S. Leatherwood, K.W. Miller, I.S. Cameron, R.K. Kastelein, and A.P. Sobral**
1988a Studies of Commerson's dolphins, *Cephalorhynchus commersonii*, off Tierra del Fuego, 1976-1984, with a review of information on the species in the South Atlantic. Rep. Int. Whaling Comm. (Spec. Iss. 9):3-70.
- Goodall, R.N.P., K.S. Norris, A.R. Galeazzi, J.A. Oporto, and I.S. Cameron**
1988b On the Chilean dolphin, *Cephalorhynchus eutropia* (Gray, 1846). Rep. Int. Whaling Comm. (Spec. Iss. 9):197-257.
- Hall, J.D.**
1981 Aspects of the natural history of cetaceans of Prince William Sound, Alaska. Ph.D. diss., Univ. Calif., Santa Cruz, 148 p.
- Harcourt, A.R., P.H. Harvey, S.G. Larson, and R.V. Short**
1981 Testis weight, body weight and breeding system in primates. Nature (Lond.) 293:55-57.
- Harvey, P.H., and A.H. Harcourt**
1984 Sperm competition, testis size, and breeding systems in primates. In Smith, R.L. (ed.), Sperm competition and evolution of animal mating systems, p. 589-600. Acad. Press, NY.
- Heimlich-Boran, J.R.**
1986 Photogrammetric analysis of growth in Puget Sound *Orcinus orca*. In Kirkevold, B.C., and J.S. Lockard (eds.), Behavioral biology of killer whales, p. 97-111. Alan R. Liss, Inc., NY.
- Houck, W.J.**
1976 The taxonomic status of the species of the porpoise genus *Phocoenoides*. Unpubl. pap. ACMRR/MM/SC/114, presented to the Food Agric. Org. (FAO). Humboldt State Univ., Arcata, CA, 13 p.
- Jones, L.L.**
1984 Incidental take of the Dall's porpoise and the harbor porpoise by Japanese salmon driftnet fisheries in the western North Pacific. Rep. Int. Whaling Comm. 34:531-538.
- Jones, L.L., D.W. Rice, and A.A. Wolman**
1983 Biological studies of Dall's porpoise taken incidentally by the Japanese salmon mothership fishery. Unpubl. Rep. SC/35/Sm9, Int. Whaling Comm. Sci. Comm., The Red House, Station Rd., Histon, Cambridge, CB4 4NP, U.K., 21 p.
- Jones, L.L., G.C. Bouchet, and B.J. Turnock**
1987 Comprehensive report on the incidental take, biology and status of Dall's porpoise. Unpubl. Doc. 3156, Int. North Pac. Fish. Comm. Natl. Mar. Mammal Lab., Natl. Mar. Fish. Serv., NOAA, Seattle, WA 98115-0070, 78 p.
- Jones, L.L., M.E. Goshko, D.W. Rice, A.A. Wolman, M.M. Muto, and W.A. Walker**
1988 Report on biology of male Dall's porpoise in the western North Pacific and Bering Sea. Unpubl. Doc. 3289, Int. North Pac. Fish. Comm. Natl. Mar. Mammal Lab., Natl. Mar. Fish. Serv., NOAA, Seattle, WA 98115-0070, 25 p.
- Kasuya, T.**
1978 The life history of Dall's porpoise with special reference to the stock off the Pacific coast of Japan. Sci. Rep. Whales Res. Inst. Tokyo 30:1-63.
1982 Preliminary report of the biology, catch and populations of *Phocoenoides* in the western North Pacific. In Mammals of the seas, vol. 4: Small cetaceans and sirenians, p. 3-19. FAO Fish. Ser. 5.
- Kasuya, T., and L.L. Jones**
1984 Behavior and segregation of the Dall's porpoise in the northwestern North Pacific. Sci. Rep. Whales Res. Inst. Tokyo 35:107-128.
- Kasuya, T., and H. Ogi**
1987 Distribution of mother-calf Dall's porpoise pairs as an indication of calving grounds and stock identity. Sci. Rep. Whales Res. Inst. Tokyo 38:125-140.
- Kasuya, T., and S. Shiraga**
1985 Growth of Dall's porpoise in the western North Pacific and suggested geographical growth differentiation. Sci. Rep. Whales Res. Inst. Tokyo 36:139-152.
- Kenagy, G.J., and S.C. Trombulak**
1986 Size and function of mammalian testes in relation to body size. J. Mammal. 67:1-22.
- Kleiman, D.G.**
1977 Monogamy in mammals. Q. Rev. Biol. 52:39-69.
- Landino, S.W.**
1985 Cetacean breeding systems revealed by interspecific comparison [Abstr.] Sixth Bienn. Conf. Biol. Mar. Mammals, Vancouver, B.C., Canada. Soc. Mar. Mammal.
- Leatherwood, S., and W.A. Walker**
1979 The northern right whale dolphin, *Lissodelphis borealis* Peale in the eastern North Pacific. In Winn, H.E., and B.L. Olla (eds.), Behavior of marine animals, vol. 3: Cetaceans, p. 85-141. Plenum Press, NY.
- Leatherwood, S., R.R. Reeves, W.F. Perrin, and W.E. Evans**
1982 Whales, dolphins and porpoises of the eastern North Pacific and adjacent Arctic waters. NOAA Tech. Rep. NMFS Circ. 444, Natl. Oceanic Atmos. Adm., Natl. Mar. Fish. Serv., 245 p.

Lincoln, G.A.

1971 The seasonal reproductive changes in the red deer stag (*Cervus elaphus*). *J. Zool. (Lond.)* 163:105-123.

Mizue, K., and K. Yoshida

1965 On the porpoises caught by the salmon fishing gill-net in Bering Sea and the North Pacific Ocean. *Bull. Fac. Fish., Nagasaki Univ.* 19:1-36.

Morejohn, G.V.

1979 The natural history of Dall's porpoise in the North Pacific Ocean. In Winn, H.E., and B.L. Olla (eds.), *Behavior of marine animals*, vol. 3: Cetaceans, p. 45-83. Plenum Press, NY.

Morejohn, G.V., V. Loeb, and D.M. Baltz

1973 Coloration and sexual dimorphism in the Dall porpoise. *J. Mammal.* 54:977-982.

Newby, T.C.

1982 Life history of Dall porpoise (*Phocoenoides dalli*, True 1885) incidentally taken by the Japanese high seas salmon mothership fishery in the northwestern North Pacific and western Bering Sea, 1978 to 1980. Ph.D. diss., Univ. Wash., Seattle, 155 p.

Nishiwaki, M., S. Ohsumi, and Y. Maeda

1963 Change of form in the sperm whale accompanied with growth. *Sci. Rep. Whales Res. Inst. Tokyo* 17:1-14.

Norris, K.S.

1961 Standardized methods for measuring and recording data on the smaller cetaceans. *J. Mammal.* 42:471-476.

1967 Aggressive behavior in Cetacea. In Clemente, C.D., and D.B. Lindsley (eds.), *Aggression and defense*, p. 225-241. Univ. Calif. Press, Berkeley.

Norris, K.S., and J.H. Prescott

1961 Observations on Pacific cetaceans of Californian and Mexican waters. *Univ. Calif. Publ. Zool.* 63:291-402.

Norris, K.S., B. Würsig, R.S. Wells, M. Würsig, S.M. Brownlee, C. Johnson, and J. Solow

1985 The behavior of the Hawaiian spinner dolphin, *Stenella longirostris*. Unpubl. Admin. Rep. LJ-85-06C, Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, La Jolla, CA 92038, 213 p.

Perrin, W.F.

1972 Color patterns of spinner porpoises (*Stenella cf. S. longirostris*) of the eastern Pacific and Hawaii, with comments on delphinid pigmentation. *Fish. Bull., U.S.* 70:983-1003.

1975 Variation of spotted and spinner porpoise (genus *Stenella*) in the eastern tropical Pacific and Hawaii. *Bull. Scripps Inst. Oceanogr. Univ. Calif.* 21, 206 p.

1984 Patterns of geographical variation in small cetaceans. *Acta Zool. Fenn.* 172:137-140.

Perrin, W.F., and J.R. Henderson

1984 Growth and reproductive rates in two populations of spinner dolphins, *Stenella longirostris*, with different histories of exploitation. *Rep. Int. Whaling Comm. (Spec. Iss. 6)*:417-430.

Perrin, W.F., D.B. Holts, and R.B. Miller

1977 Growth and reproduction of the eastern spinner dolphin, a geographical form of *Stenella longirostris* in the eastern tropical Pacific. *Fish. Bull., U.S.* 75:725-750.

Ralls, K.

1977 Sexual dimorphism in mammals: Avian models and unanswered questions. *Am. Nat.* 111:917-938.

Robineau, D.

1984 Morphologie externe et pigmentation du dauphin de Commerson, *Cephalorhynchus commersonii* (Lacepede, 1804), en particulier celui des îles Kerguelen. *Can J. Zool.* 62: 2465-2475.

Schaller, G.B.

1963 The mountain gorilla: Ecology and behavior. Univ. Chicago Press, 429 p.

1972 The Serengeti lion: A study of predator-prey relations. Univ. Chicago Press, 480 p.

Scheffer, V.B.

1949 The Dall porpoise, *Phocoenoides dalli*, in Alaska. *J. Mammal.* 30:116-121.

Sergeant, D.E.

1962 On the external characters of the blackfish or pilot whales (genus *Globicephala*). *J. Mammal.* 43:394-413.

Short, R.V.

1979 Sexual selection and its component parts, somatic and genital selection, as illustrated by man and the great apes. *Adv. Study Behav.* 9:131-158.

Slouten, E., and S.M. Dawson

1988 Studies on Hector's dolphin, *Cephalorhynchus hectori*: A progress report. *Rep. Int. Whaling Comm. (Spec. Iss. 9)*:325-338.

Smith, B.L.

1988 Criteria for determining age and sex of American mountain goats in the field. *J. Mammal.* 69:395-402.

Subramanian, A., S. Tanabe, Y. Fujise, and R. Tatsukawa

1986 Organochlorine residues in Dall's and True's porpoises collected from northwestern Pacific and adjacent waters. *Mem. Natl. Inst. Polar Res., Ser. E. Biol. Med. Sci., Spec. Iss.* 44:167-173.

Subramanian, A. S. Tanabe, and R. Tatsukawa

1987 Age and size trends and male-female differences of PCBs and DDE in *dalli*-type Dall's porpoises, *Phocoenoides dalli* of northwestern North Pacific. *Proc., Natl. Inst. Polar Res. Symp. Polar Biol.* 1:205-216.

Trivers, R.L.

1985 Social evolution. Benjamin/Cummings Publ. Co., Menlo Park, CA, 462 p.