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Pseudorca crassidens.

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Pseudorca Reinhardt, 1862

Pseudorca Reinhardt, 1862. Type, *Phocaena crassidens* Owen.
Neorca Gray, 1871. Type, *Orca meridionalis* Flower.

CONTEXT AND CONTENT. Order Cetacea, Suborder Odontoceti, Superfamily Delphinoidea, Family Delphinidae. The genus *Pseudorca* has been placed in the subfamily Orcininae by several workers. However, membership of this taxon is far from agreed upon. Some workers consider it to include *Orcinus*, *Globicephala*, *Orcaella*, and *Feresa* in addition to *Pseudorca* (Fraser and Purves, 1960; Mead, 1975; Slijper, 1936); others argue it only contains *Orcinus* and *Pseudorca* (Heyning and Dahlheim, 1988; Kasuya, 1973).

Pseudorca crassidens (Owen, 1846)

False Killer Whale

Phocaena crassidens Owen, 1846:516. Type locality "Lincolnshire Fens, near Stanford, England" (subfossil).
Orca meridionalis Flower, 1864:420. Type locality "Tasmania."
Orca destructor Cope, 1866:293. Type locality "Paita, Peru."
Globicephalus grayi Burmeister, 1869:367. Type locality "Argentina."
Pseudorca? mediterranea Giglioli, 1882:268–289. Type locality "Mediterranean Sea."

CONTEXT AND CONTENT. Context as above. There are no subspecies recognized. The one subspecies proposed, *P. c. meridionalis* (Deraniyagala, 1945) was presented without adequate justification; so it is generally ignored. Flower, based on examination of adult skeletons, proposed and later abandoned a distinction between southern and northern forms of this animal (Flower, 1884 cited in Hector, 1885).

DIAGNOSIS. Externally, *P. crassidens* can be distinguished from the other large delphinids by some details of its sickle-shaped flippers: a broad hump on the front margin near the middle and a slight concavity to the distal extremity.

The dental formula is 7 to 11/7 to 12 (Purves and Pilleri, 1978; Ross, 1984). The skull (Fig. 1) of a large false killer whale can be distinguished from that of a killer whale, as the width across the premaxillaries of the former is >50% of the rostral width just anterior to the antorbital notches, and the lateral border of the premaxillaries is slightly less sigmoid in dorsal view and narrower distally (Heyning and Dahlheim, 1988). The tympanic bullae (Fig. 2) range from 47.7 mm to 50.5 mm in length, have an atrophied ventral keel, and lack bilateral compression (Kasuya, 1973).

GENERAL CHARACTERS. False killer whales (Figs. 3, 4) are almost entirely black on the dorsal surface, sides of the body, dorsal fin, pectoral flippers, and tail flukes. There may be an area of pale gray present on the sides of the head. There is also a blaze, varying from indistinct gray to nearly white, on the ventral surface; this occurs as an approximately anchor-shaped patch beginning on the throat and extending posteriorly between the flippers and occasionally to the genital slit (Norris and Prescott, 1961). The black coloration is occasionally marked by sparsely-scattered white star-shaped scars (Fraser, 1949), which may be attributable to bites from the cookie-cutter shark, *Isistius brasiliensis* (Porter, 1977).

Maximum recorded length is 5.96 m in a male from Denmark (Tomilin, 1957) and 5.06 m in a female from an unspecified location (Perrin and Reilly, 1984). Exact masses of full-grown animals are difficult to obtain, so estimates vary. Maximum body mass has been reported to be at least 1,360 kg (Leatherwood et al., 1988).

The falcate dorsal fin, which may be >40 cm tall, is pointed to rounded at the tip. The height is about 8% of the body length (Tomilin, 1957). The position of the dorsal fin relative to the midpoint of the back has been variously reported as: from slightly in front of, at, or slightly behind the midpoint (Fraser, 1949; Tomilin, 1957). The dorsal fin is located more anteriorly in males than in females, and in general in older animals of both genders (Tomilin, 1957). The pectoral flipper is distally narrow and pointed, slightly convex on the leading edge, and about 10% of the body length (Barnard, 1954). The tailstock is strongly keeled and the flukes are indistinguishable from those of most other delphinids. Nonfunctional accessory grooves are found distal to the mammary grooves in many animals of both genders (Comrie and Adam, 1938).

There is no demarcation between the head and beak. Slight

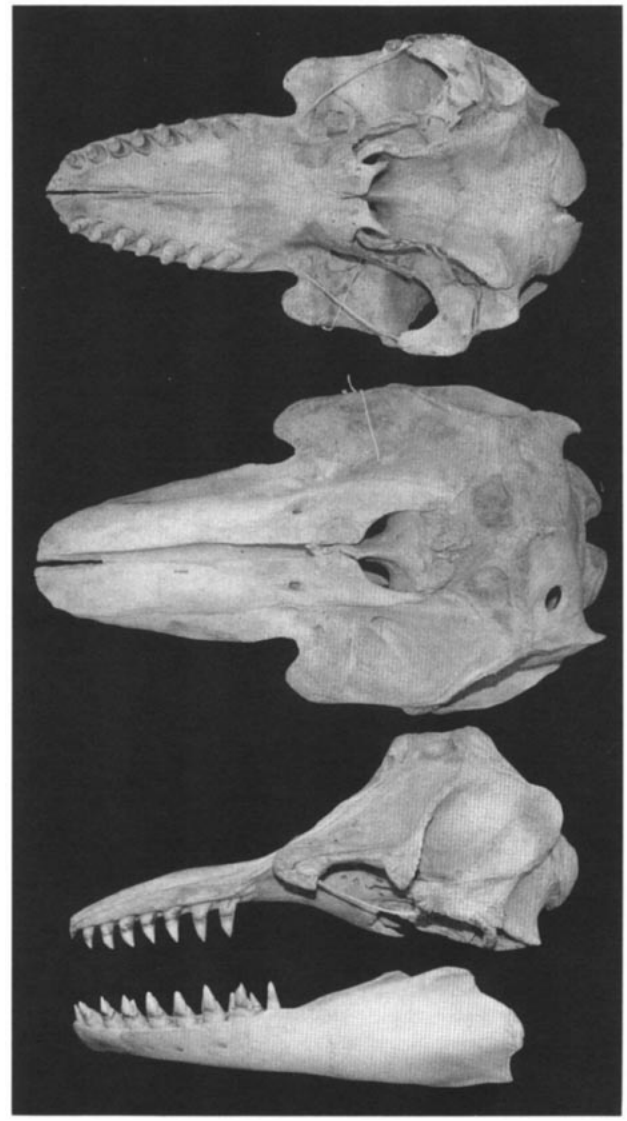

FIG. 1. Ventral, dorsal, and lateral views of the cranium, and lateral view of the left mandible of a male false killer whale (Los Angeles County Museum 84047). Greatest length of skull is 605 mm. Photos by John Heyning.

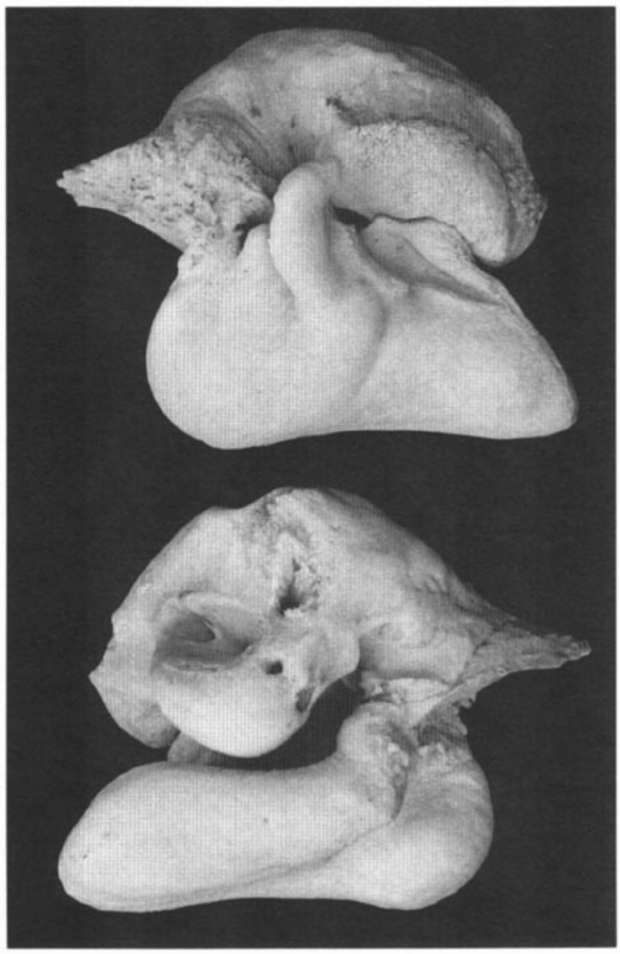

FIG. 2. Lateral (upper) and medial (lower) view of left tympanic bulla/periotic complex (Stranded Whale and Dolphin Program of British Columbia 89-21). The length of the tympanic bulla ranges from 47.7 to 50.5 mm.

sexual dimorphism in the external appearance of the head has been reported, with the overhang of the melon over the upper jaw in the male being greater than that in the female (Mead, 1975). There is a moderate degree of sexual dimorphism in the forehead, in that pre-melon connective tissue extends farther forward in males than in females. Skull and dentary measurements vary between genders, with those of males generally larger (Kitchener et al., 1990). The greatest skull length of 15 sexually mature female false killer whales in a stranded group in South Africa is 59 cm; for 16 males in the group the maximum skull length is 65 cm (Kitchener et al., 1990).

DISTRIBUTION. The false killer whale has been reported from all tropical, subtropical, and warm temperate seas (Fig. 5). The distribution of this species has been largely determined from stranding records; it has one of the largest continuous ranges among the cetaceans (Davies, 1963).

False killer whales are known from Prince William Sound, Alaska (Leatherwood et al., 1988), south to Chile (Brown et al., 1966; Miller, 1920; Mitchell, 1965; Oliver-Schneider, 1946; Sullivan and Houck, 1979; Van Gelder, 1960). The species has been reported from Hawaii and the Galapagos Islands (Donovan, 1984; Tomich, 1986). In the western Pacific, they are found around Japan and throughout the Indo-Australian Archipelago to New Zealand (Bryden, 1978; Cawthorn, 1984; Gaskin, 1968; Ohsumi, 1972; Zhou et al., 1982). False killer whales occur throughout the coastal rim of the Indian Ocean, from southwestern Australia to southern South Africa (Leatherwood et al., 1991).

In the eastern Atlantic, false killer whales have been recorded from the British Isles (Fraser, 1936), south to South Africa (Reinhardt, 1866), including the Mediterranean, where their presence is considered unusual (Duguy et al., 1983). They are common in the

FIG. 3. Head of a live, stranded false killer whale from Tofino, B.C., Canada. Photo by Mark Hobson.

western Atlantic and are known to range from Cape Hatteras, North Carolina (Brimley, 1937) to Tierra del Fuego at the southern tip of South America (Goodall, 1989; Langguth, 1977). A record based on a skull at the American Museum of Natural History, collected on the "northeast coast . . . probably . . . Davis' Strait", off Baffin Island, listed by True (1889:144), and subsequently reported by some authors as the northernmost record, is unsubstantiated (Miller, 1920). There is no evidence that false killer whales inhabit Antarctic waters as stated in Bellision (1966).

FOSSIL RECORD. Two fossil whale teeth from the Calabrian, lower Pliocene, Japan, are attributed to *P. yokoyamai*, a closely related species (Matsumoto, 1926). A subfossil skeleton from England in 1846 formed the basis of the false killer whale's description by Owen (1846).

FORM. The skin does not differ in any major respect from that of other cetaceans (Purves and Pilleri, 1978). In the epidermis, pigment is intense in the area of the caudal peduncle and fairly weak on the head (Sokolov, 1973). Coloration may already contain all elements at a very early stage of development, as evidenced by the advanced pigmentation of a 64.7-cm embryo (Tomilin, 1957).

There are 7 C, 9–11 T, 9–13 L, and 16-26 Ca, total 47–52 (Paulus, 1963; Purves and Pilleri, 1978). From 103 skeletons examined by Purves and Pilleri (1978), 82.5% had total vertebral counts of 48–50. Various degrees of fusion of the cervical vertebrae occur (Gray, 1864; Yamada, 1956). Of 82 skeletons, 67% had the first six cervical vertebrae fused, 23.8% had the first five fused, and the remaining 12.2% had all seven fused (Yamada, 1956). There is some evidence that the number of vertebrae fused increases with age (Yamada, 1956). There are 9–12 pairs of ribs (10 is the usual number), 6 of which are bicipital. The 11th and 12th pairs, when present, are floating (Purves and Pilleri, 1978). Unequal numbers of ribs on each side have been reported (Yamada, 1956). Four pairs of ribs attach directly to the sternum (Arvy and Pilleri, 1977). The sternum has four segments which fuse to varying degrees with age (Yamada, 1956). The skeleton of the pectoral flipper shows a great deal of variability, with a wide range in phalangeal formula. The first digit has from 0 to 1 phalanges, the second 4 to 8, the third 4 to 6, the fourth 1 to 3, and the fifth 0 to 2 (Gihr et al., 1982). The most common phalangeal formula from a sample of 93 flippers was: first digit, 0; second, 6; third, 4; fourth, 2; and the fifth, 1 (Gihr et al., 1982).

The skull is massive, with a short, broad rostrum (Fig. 1). The rostrum length is at least 1.5 times its width and increases in width with age (Elliot, 1901; Tomilin, 1957). The total length of the adult skull exceeds 500 mm (Glass, 1973). The rostral portion of the intermaxillaries are truncated at the distal end (Elliot, 1901). The intermaxillaries are rugose in front (Gray, 1846) and have developed laterally, occupying 60% of the rostrum's width (Tomilin, 1957). The pterygoid bones are nearly in contact and the intermaxillae are of equal breadth throughout (Dammerman, 1924). The presence of two ossa postinterparietalia has been noted in the fetus, but not in adults (Pilleri, 1987). A meckelian ossicle is present on the anterior margin of the narial aperture (Cave, 1987). The anatomy of the facial structure follows typical delphinid form and is most similar to

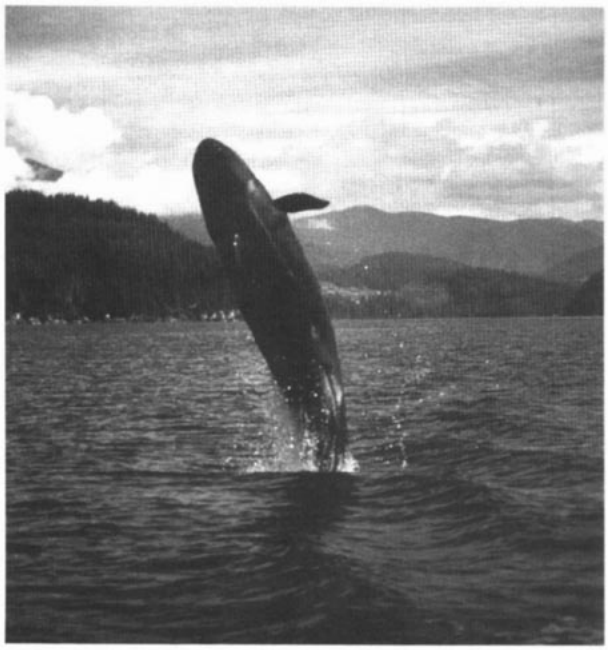

FIG. 4. Ventral view of false killer whale breaching, Barkley Sound, B.C., Canada. Photo by L. M. Barry/R. W. Baird.

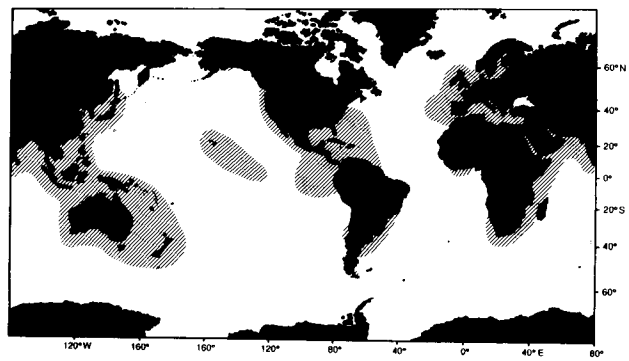

FIG. 5. Documented range of false killer whales in tropical to warm temperate seas (cross-hatched areas).

that of the bottlenose dolphin, *Tursiops truncatus* (Mead, 1975). Skull asymmetry and skew are similar to that in other delphinids (Ness, 1967).

The roots of the teeth may be up to 1.8 cm in diameter at the gum line (Fraser, 1949). Extensive wear on the teeth can occur; this wear includes lingual undercutting, which implies that false killer whales are capable of making small lateral and palinal jaw movements, related to the action of breaking up large prey (Ross, 1984).

In a captive animal, the body temperature ranged from 36.0 to 37.2°C, increasing with activity levels (Whittow et al., 1974). The mean body temperature was 36.6°C ($n = 83$). The normal heart rate of false killer whales ranges from 60 to 100 beats/min; the respiratory rate is 8 to 18 breaths/5 min (Walsh et al., 1990).

FUNCTION. Hematological values measured for 30 stranded false killer whales were similar to those of other small cetaceans (Odell et al., 1979). Red blood cell counts ranged from 3.58 to 4.81 $10^6/mm^3$ and white blood cell counts from 4,146 to 9,953 $10^6/mm^3$ (Odell et al., 1979). Hemoglobin ranged from 14.3 to 17.2 g/100 ml (Odell et al., 1979). Mean albumin and globulin values were 3.5 and 3.9 g/100 ml, respectively (Odell et al., 1979). There is 2.6 ng/ml angiotensin equivalent in the plasma, presumably produced in the kidney, which is similar to values obtained from other cetaceans (Arvy, 1971; Malvin and Vander, 1967). The absorption maxima for visual pigments in *P. crassidens* is 486.5 nm, similar to that of other delphinids (McFarland, 1971). The ductus arteriosus closes more slowly in this species than in other delphinids (Slijper, 1961). Heart and kidney masses of an animal from California were 1,743 and 1,051 g, respectively (Sullivan and Houck, 1979).

REPRODUCTION. The smallest size at which females were estimated to be reproductively mature was 334 cm in South Africa (Kitchener et al., 1990) and 336 cm in Scotland (Purves and Pilleri, 1978). Based on information from Japan, females mature at body lengths of 340–380 cm, corresponding to ages of 8–11 years, based on presumed annual deposition of growth layers in dentine and cementum (Kasuya, 1986). The proportion of females that were considered mature in this study was 75.3% (Kasuya, 1986).

Males from South Africa were estimated to be sexually mature at a shorter length (370–430 cm) than those from Scotland (396–457 cm—Kitchener et al., 1990). Fully mature males in Japan were >429 cm; the youngest mature males were 18.5 years old (Kasuya, 1986). Age at sexual maturity in both genders has also been estimated at 8–14 years (Purves and Pilleri, 1978), but Kasuya (1986) states that males attain sexual maturity 8–10 years later than females. If, as stated by Purves and Pilleri (1978), testes increase dramatically with attainment of reproductive maturity, males with a combined testes mass of 1,000 g are likely sexually mature (Kitchener et al., 1990). Other studies indicate that minimum mass of mature testis is about 1,700 g (Perrin and Reilly, 1984). Combined maximum testis mass has been reported at 8,200 g (Odell et al., 1980).

Ovulation rate is about once/year (Purves and Pilleri, 1978), and may be spontaneous (Harrison et al., 1972). One ovum is shed at a time (Comrie and Adam, 1938). Ovaries of the smallest adult females in one stranding were 7–10 cm in length (Comrie and Adam, 1938). The only estimate of gross annual reproductive rate is from a population off Japan; about 6.7%, with a net reproductive rate of about 1.4% (Kasuya, 1986). The proportion of females estimated to be pregnant annually is 14.5% (Kasuya, 1986). Data from Japan suggest that the interval between pregnancy and lactation increases with age and that females over 45 years of age may be post-reproductive (Kasuya, 1986). The average interval between births is 6.9 years (Kasuya, 1986). The calving, and thus presumably also the breeding season extends over several months (Fraser, 1949; Scott and Green, 1975) and may be year-round (Ross, 1984). Some seasonality has been found in Japan, with a parturition peak around March and a mating peak from December to January (Kasuya, 1986). Length of gestation ranges from 15.1 to 15.7 months (Kasuya, 1986; Perrin and Reilly, 1984; Purves and Pilleri, 1978). A single young is born.

Mean neonatal length in one study was estimated as 175 cm (Kasuya, 1986). Fetal growth rate is about 0.418 cm/day (Kasuya, 1986). The length of the umbilical cord in one case was 60 cm (Peacock et al., 1936). Lactation lasts from 18 to 24 months (Perrin and Reilly, 1984; Purves and Pilleri, 1978).

The sex ratio in both stranded and shore-driven herds is approximately equal (Fraser, 1949; Kasuya, 1986). Other studies have reported more females than males (Peacock et al., 1936; Yamada, 1956).

ECOLOGY. Longevity is estimated at 57.5 years for males and 62.5 years for females, based on presumed annual deposition of growth layers in teeth (Kasuya, 1986). There are insufficient data to estimate age-dependent mortality rates, but overall annual mortality was estimated to be 5–6% (Kasuya, 1986).

False killer whales prey mainly on a variety of fishes and squids. Prey items include various species of squids (*Oregoniateuthis* sp., *Todarodes* sp., *Phasmatopsis* sp.—Ross, 1984; *Gonatopsis borealis*, or *Berryteuthis magister*—Baird et al., 1989) and fish; cod (*Gadus callarias*—Peacock et al., 1936), bonito (*Sarda lineolata*), mahimahi (*Coryphaena hippurus*—Brown et al., 1966), yellowtail tuna (*Pseudosciaena* sp.), perch (*Lateolabrax japonicus*—Kasuya, 1985), salmon (*Oncorhynchus* sp.—Baird et al., 1989), and catfish (*Tachysurus* sp.). Food sharing has been observed in the wild (Connor and Norris, 1982). False killer whales feed during both day and night (Evans and Awbrey, 1988). In one study, food volume in the stomach was reported to have been highest in winter (Tsutsumi et al., 1961). A mean daily feeding rate of 4.7% (wet weight) of total body mass has been calculated for a captive animal (Sergeant, 1969).

Degenerative arthropathy of the cervical vertebrae may occur, with fusion of the first cervical vertebra to the skull (Baird et al., 1989; Yamada, 1956). Acute pneumonia has been reported in captive animals (Odell et al., 1980). While the effects of pollutants

are unknown, two stranded animals in British Columbia had levels of mercury among the highest reported in cetaceans (728 and >1,600 ppm in the liver), high levels of DDE (1,400 ppm in the blubber) and some measurable quantities of every contaminant analyzed (Baird et al., 1989; Stacey and Baird, 1991). Parasites recorded from the false killer whale include Nematoda [*Anisakis simplex, Anisakis typica, Stenurus auditivus* (Zam et al., 1971), *Stenurus globicephalus* (Odell et al., 1980)], Acanthocephala (*Bolbosoma capitatum*—Fraser, 1936), Trematoda (*Orthosplanchnus elongatus*—Zam et al., 1971; *Nasitrema attenuata, Nasitrema globicephalae*—Neiland et al., 1970; *Nasitrema gondo*—Morimitsu et al., 1987), Amphipoda (*Syncyamus pseudorcae, Isocyamus delphini*—Bowman, 1955), and Crustacea (*Xenobalanus globicipitus*—Caldwell et al., 1971).

False killer whales are not taken by standard whaling operations (Gaskin, 1967, 1968), but they are the object of some drive- and harpoon-fisheries (Miyazaki, 1983). There is some small scale incidental catch worldwide in a range of fisheries including gillnet and longline (Di Natale and Mangano, 1981; Harwood et al., 1984; Leatherwood et al., 1991). Blubber from a 4-m long animal of unknown gender yielded 45 l of oil (Reinhardt, 1866).

False killer whales occur in waters ranging in temperature from 9 to 30.8°C (Stacey and Baird, 1991; Miyazaki and Wada, 1978), but they are most common in water toward the higher end of this range (Kasuya, 1975). Inshore movements are occasionally associated with those of food resources or to shoreward flooding of warm ocean currents (Tomilin, 1957). Although the yellowtail tuna fishery off Iki Island, Japan, is year-round, kills of false killer whales associated with this fishery have been primarily from February through April (Kasuya, 1985); this possibly suggests a seasonal movement into the area. Kasuya (1971) notes that in winter, false killer whales reportedly migrate into the coastal waters near the north and west coasts of Kyushu, Japan.

False killer whales are sometimes seen in association with other cetaceans; at least 10 different species have been reported, most often bottlenose dolphins (Leatherwood et al., 1984; Miyazaki and Wada, 1978; Mizue and Yoshida, 1961; Tsutsumi et al., 1961; Zhou et al., 1982). Mixed herds with bottlenose dolphins occur off Japan only during winter months, as mixed feeding aggregations, but not in summer during the so-called breeding migrations (Tsutsumi et al., 1961).

Mean group size off Japan was 55 (n = 6, range = 2–200; Kasuya, 1971). It has been suggested, based on age composition and age at maturity, that males in the late maturing stage have been absent from schools studied in Japan (Kasuya, 1986). Mass and single strandings have been reported (Baird et al., 1989; Fraser, 1936; Mitchell, 1965; Odell et al., 1980; Ross, 1984). Group size from 14 mass strandings averaged 180 individuals ranging from 50 to 835 (Ross, 1984).

BEHAVIOR. False killer whales leap clear of the water (Fig. 4; Leatherwood et al., 1988). They have been recorded swimming at an estimated speed of at least 5 m/s (Brown et al., 1966). The relatively greater length than width of the lumbar vertebrae may facilitate rapid swimming (Wang, 1984). No scientific studies have been conducted on the diving behavior or actual depth of dives of false killer whales.

False killer whales make sounds with a dominant frequency around 28 kHz that last 60–75 ms and have a waveform similar to sounds of bottlenose dolphins, long sustained click trains, a whistle of 8 kHz, and occasional 2 component clicks around 100 kHz (Kamminga and van Velden, 1987). An underwater audiogram indicated false killer whales could hear sounds from 2 to 115 kHz, with a peak in sensitivity from 32 to 70 kHz, corresponding with peak frequencies of echolocation pulses (Thomas et al., 1988*a*). In experimental trials, a captive animal could detect the presence or absence of a 7.5-cm diameter water-filled steel sphere behind a visually opaque, acoustically-transparent screen (Thomas et al., 1988*b*). Vocalizations may be used for inter-individual communication and as grouping signals (Busnel and Dziedzic, 1968).

False killer whales have been captured for scientific study and have been successfully maintained in captivity. They are rated high for both observational learning and imitative behaviors (Defran and Pryor, 1980).

GENETICS. The false killer whale has the typical cetacean diploid chromosome number 2n = 44 (Kulu, 1972). Hybrids with bottlenose dolphins have been born in captivity in Japan and Hawaii (Sylvestre and Tasaka, 1985). These hybrids exhibited characters of both parents. False killer whales are more karyotypically conservative than killer whales (Duffield, 1986).

REMARKS. Many species of small to mid-sized odontocetes, including false killer whales, are known by the collective term blackfish (Leatherwood et al., 1991).

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LITERATURE CITED

ARVY, L. 1971. The enzymes of Cetacea. Investigations on Cetacea, 3:302–314.

ARVY, L., AND G. PILLERI. 1977. The sternum in Cetacea. Investigations on Cetacea, 8:123–148.

BAIRD, R. W., K. M. LANGELIER, AND P. J. STACEY. 1989. First records of false killer whales, *Pseudorca crassidens*, in Canada. The Canadian Field-Naturalist, 103:368–371.

BARNARD, K. H. 1954. A guide book to South African whales and dolphins. South African Museum Guide, Cape Town, 4:1–33.

BELLISION, N. B. 1966. Fauna marina Antarctica. Republica Argentina Secretaria de Marina, Servicio de Hidrografia Naval, Publico H. 907, Buenos Aires, 91 pp.

BOWMAN, T. E. 1955. A new genus and species of whale-louse (Amphipoda: Cyamidae) from the false killer whale. Bulletin of Marine Science of the Gulf and Caribbean, 5:315–320.

BRIMLEY, H. H. 1937. The false killer whale on the North Carolina coast. Journal of Mammalogy, 18:71–73.

BROWN, D. H., D. K. CALDWELL, AND M. C. CALDWELL. 1966. Observations on the behavior of wild and captive false killer whales, with notes on associated behavior of other genera of captive delphinids. Los Angeles County Museum Contributions in Science, 95:1–32.

BRYDEN, M. M. 1978. Whales and whaling in Queensland waters. Proceedings of the Royal Society of Queensland, 88:v–xvii, pls. 1–3.

BURMEISTER, H. 1869. Descripcion de cuatro especies de Delphinides. Anales Museo Publico Buenos Aires, 1:367–445.

BUSNEL, R.-G., AND A. DZIEDZIC. 1968. Caracteristiques physiques des signaux acoustiques de *Pseudorca crassidens* Owen (Cetace Odontocete). Mammalia, 32:1–5.

CALDWELL, D. K., M. C. CALDWELL, AND S. G. ZAM. 1971. A preliminary report on some ectoparasites and nasal-sac parasites from small odontocete cetaceans from Florida and Georgia. Marineland Research Laboratory Technical Report, 5:1–7.

CAVE, A. J. E. 1987. The meckelian ossicle of the Odontocete cranium. Investigations on Cetacea, 20:178–191.

CAWTHORN, M. W. 1984. New Zealand progress report on cetacean research May 1982 to May 1983. Reports of the International Whaling Commission, 34:213–215.

COMRIE, L. C., AND A. B. ADAM. 1938. The female reproductive system and corpora lutea of the false killer whale, *Pseudorca crassidens* Owen. Transactions of the Royal Society of Edinburgh, 59:521–532.

CONNOR, R. C., AND K. S. NORRIS. 1982. Are dolphins reciprocal altruists? The American Naturalist, 119:358–374.

COPE, E. D. 1866. Third contribution to the history of the Balaenidae and Delphinidae. Proceedings of the Academy of Natural Sciences of Philadelphia, 1866:293–300.

DAMMERMAN, K. W. 1924. On Globicephala and some other Delphinidae from the Indo-Australian Archipelago. Extrait de Treubia, 5:339–352.

DAVIES, J. L. 1963. The antitropical factor in cetacean speciation. Evolution, 17:107–116.

DEFRAN, R. H., AND K. PRYOR. 1980. The behavior and training of cetaceans in captivity. Pp. 319–362, *in* Cetacean behavior:

mechanisms and functions (L. M. Herman, ed.). John Wiley & Sons, New York, 463 pp.

DERANIYAGALA, P. 1945. Some odontoceti from Ceylon. Spoila Zeylanica, 24:113–120.

DI NATALE, A., AND A. MANGANO. 1981. Memorie di biologia marina e di oceanografia. Memorie di Biologia Marina e di Oceanografia Supplement Special, 11:1–49.

DONOVAN, G. P. 1984. Small cetaceans seen during the IWC/IDCR research cruise in the eastern tropical Pacific, and in particular off Peru. Reports of the International Whaling Commission, 34:561–567.

DUFFIELD, D. 1986. *Orcinus orca*: taxonomy, evolution, cytogenetics and population structure. Pp. 19–33, *in* Behavioral biology of killer whales (B. C. Kirkevold and J. S. Lockard, eds.). Alan R. Liss, Inc., New York, 457 pp.

DUGUY, R., ET AL. 1983. Repartition et frequence des mammiferes marins en Mediterranee. Rapport Commission Internationale pour la Mer Mediterranee, 28:223–230.

ELLIOT, D. G. 1901. Synopsis of the mammals of North America and the adjacent seas. Columbian Field Museum Zoological Series Publication 45, 2:1–471.

EVANS, W. E., AND F. T. AWBREY. 1988. Natural history aspects of marine mammal echolocation: feeding strategies and habitat. Pp. 521–534, *in* Animal sonar, processes and performance (P. E. Nachtigall and P. W. B. Moore, eds.). Plenum Press, New York, 862 pp.

FLOWER, W. H. 1864. On a new species of grampus (*Orca meridionalis*) from Tasmania. Proceedings of the Zoological Society of London, 1864:420–426.

FRASER, F. C. 1936. Recent strandings of the false killer whale, *Pseudorca crassidens*, with special reference to those found at Donna Nook, Lincolnshire. Scottish Naturalist July–Aug., 36:105–114.

———. 1949. Whales and dolphins. Pp. 201–349, *in* Field book of giant fishes (J. R. Norman and F. C. Fraser, eds.). G. Putnam's Sons, New York, 376 pp.

FRASER, F. C., AND P. E. PURVES. 1960. Hearing in cetaceans. Bulletin of the British Museum (Natural History), Zoology Series, 7:1–140.

GASKIN, D. E. 1967. The whaling potential of the New Zealand sub-region. New Zealand Marine Department Fisheries Technical Report, 16:1–28.

———. 1968. The New Zealand Cetacea. Fisheries Research Bulletin, 1:1–92.

GIGLIOLI, H. 1882. Note intorno un nuovo Cetaceo nel Mediterraneo da riferirsi probabilmente al genere *Pseudorca*. Zoologischer Anzeiger, 5(112):288–290.

GIHR, M., C. KRAUS, AND G. PILLERI. 1982. The manus of *Pseudorca crassidens* (Owen): a study of variability. Investigations on Cetacea, 13:101–124.

GLASS, B. P. 1973. A key to the skulls of North American mammals. Oklahoma State University, Stillwater, 59 pp.

GOODALL, R. N. P. 1989. The lost whales of Tierra del Fuego. Oceanus, 32:89–95.

GRAY, J. E. 1846. On the cetaceous animals. Pp. 13–53, *in* The zoology of the voyage of H. M. S. *Erebus* and *Terror* under the command of Captain Sir James Clarke Ross, R. N., F. R. S., during the years 1839 to 1843 (J. Richardson and J. E. Gray, eds.). 1:13–53 + 37 pls.

———. 1864. On the cetacea which have been observed in the seas surrounding the British Islands. Proceedings of the Zoological Society of London, 1864:195–248.

———. 1871. Supplement to the catalog of seals and whales in the British Museum. London, 103 pp.

HARRISON, R. J., R. L. BROWNELL, JR., AND R. C. BOICE. 1972. Reproduction and gonadal appearances in some odontocetes. Pp. 362–429, *in* Functional anatomy of marine mammals (R. J. Harrison, ed.). Academic Press, New York, 451 pp.

HARWOOD, M. B., K. J. MCNAMARA, G. R. V. ANDERSON, AND D. G. WALTER. 1984. Incidental catch of small cetaceans in a gillnet fishery in northern Australian waters. Reports of the International Whaling Commission, 34:555–559.

HECTOR, J. 1885. Notes on the dolphins of the New Zealand seas. Transactions and Proceedings of the New Zealand Institute, 1884, 17:15–23.

HEYNING, J. E., AND M. E. DAHLHEIM. 1988. Orcinus orca. Mammalian Species, 304:1–9.

KAMMINGA, C., AND J. G. VAN VELDEN. 1987. Investigations on cetacean sonar VIII—sonar signals of *Pseudorca crassidens* in comparison with *Tursiops truncatus*. Aquatic Mammals, 13: 43–49.

KASUYA, T. 1971. Consideration of distribution and migration of toothed whales off the Pacific coast of Japan based on aerial sighting records. Scientific Reports of the Whales Research Institute, 23:37–60.

———. 1973. Systematic consideration of recent toothed whales based on the morphology of tympano-periotic bone. Scientific Reports of the Whales Research Institute, 25:1–103.

———. 1975. Past occurrence of *Globicephala melaena* in the western north Pacific. Scientific Reports of the Whales Research Institute, 27:95–110.

———. 1985. The fishery-dolphin conflict in the Iki Island area of Japan. Pp. 253–272, *in* Marine mammals and fisheries (J. R. Beddington, R. J. H. Beverton, and D. M. Lavigne, eds.). George Allen & Unwin, London, 354 pp.

———. 1986. False killer whales. Pp. 178–187, *in* Report of investigation in search of solution for dolphin-fishery conflict in the Iki Island area (T. Tamura, S. Ohsumi, and S. Arai, eds.). Japan Fisheries Agency, 285 pp.

KITCHENER, D. J., G. J. B. ROSS, AND N. CAPUTI. 1990. Variation in skull and external morphology in the false killer whale, *Pseudorca crassidens*, from Australia, Scotland and South Africa. Mammalia, 54:119–135.

KULU, D. D. 1972. Evolution and cytogenetics. Pp. 503–527, *in* Mammals of the sea: biology and medicine (S. H. Ridgway, ed.). Charles C Thomas, Publisher, Springfield, Illinois, 812 pp.

LANGGUTH, A. 1977. Notas sobre la falsa orca "*Pseudorca crassidens*" (Owen) en el Atlantico sudoccidental. Revista Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (Zoologia), 12:59–68.

LEATHERWOOD, S., R. R. REEVES, W. F. PERRIN, AND W. E. EVANS. 1988. Whales, dolphins and porpoises of the eastern North Pacific and adjacent Arctic waters: a guide to their identification. Dover Publications, Inc., New York, 245 pp.

LEATHERWOOD, S., C. B. PETERS, R. SANTERRE, M. SANTERRE, AND J. T. CLARKE. 1984. Observations of cetaceans in the northern Indian Ocean sanctuary, November 1980–May 1983. Reports of the International Whaling Commission, 34:509–520.

LEATHERWOOD, S., D. MCDONALD, W. P. PREMATUNGA, P. GIRTON, A. ILANGAKOON, AND D. MCBREARTY. 1991. Records of the "blackfish" (killer, false killer, pilot, pygmy killer, and melon-headed whales) in the Indian Ocean, 1772–1986. Pp. 33–65, *in* Cetaceans and cetacean research in the Indian Ocean Sanctuary (S. Leatherwood and G. P. Donovan, eds.). Nairobi-United Nations Environment Programme, Marine Mammal Technical Report 3.

MALVIN, R. L., AND A. J. VANDER. 1967. Plasma renin activity in marine teleosts and cetacea. American Journal of Physiology, 213:1582–1584.

MATSUMOTO, H. 1926. On some fossil cetaceans of Japan. Scientific Reports of Tokoku Imperial University, Sendai, Japan, second series (geology), 10:17–27.

MCFARLAND, W. N. 1971. Cetacean visual pigments. Vision Research, 11:1065–1076.

MEAD, J. G. 1975. Anatomy of the external nasal passages and facial complex in the Delphinidae (Mammalia, Cetacea). Smithsonian Contributions to Zoology, 207:1–72.

MILLER, G. S., JR. 1920. American records of whales of the genus *Pseudorca*. Proceedings of the United States National Museum, 57:205–207.

MITCHELL, E. 1965. Evidence for mass strandings of the false killer whale (*Pseudorca crassidens*) in the eastern North Pacific Ocean. Norsk Hvalfangst-Tidende, 8:172–177.

MIYAZAKI, N. 1983. Catch statistics of small cetaceans taken in Japanese waters. Reports of the International Whaling Commission, 33:621–631.

MIYAZAKI, N., AND S. WADA. 1978. Observation on cetacea during whale marking cruise in the western tropical Pacific, 1976. Scientific Reports of the Whales Research Institute, 30:179–195.

MIZUE, K., AND K. YOSHIDA. 1961. Studies on the little toothed whales in the West Sea area of Kyushu-XVI—Underwater

sound of the false killer whale. Bulletin of the Faculty of Fisheries, Nagasaki University, 28:19–29.

MORIMITSU, T., T. NAGAI, M. IDE, H. KAWANO, A. NAICHUU, M. KOONO, AND A. ISHII. 1987. Mass stranding of odontoceti caused by parasitogenic eight cranial neuropathy. Journal of Wildlife Diseases, 23:586–590.

NEILAND, K. A., D. W. RICE, AND B. L. HOLDEN. 1970. Helminths of marine mammals, I. The genus Nasitrema, air sinus flukes of delphinid cetacea. The Journal of Parasitology, 56:305–316.

NESS, A. R. 1967. A measure of asymmetry of the skulls of odontocete whales. Journal of Zoology, 153:209–221.

NORRIS, K. S., AND J. H. PRESCOTT. 1961. Observations on Pacific cetaceans of Californian and Mexican waters. University of California Publications in Zoology, 63:291–402.

ODELL, D. K., E. D. ASPER, J. BAUCOM, AND L. H. CORNELL. 1979. A summary of information derived from the recurrent mass stranding of a herd of false killer whales, *Pseudorca crassidens* (Cetacea: Delphinidae). Pp. 207–222, *in* Biology of marine mammals: insights through strandings (J. R. Geraci and D. J. St. Aubin, eds.). U. S. Marine Mammal Commission Report No. MMC-77/13, 243 pp.

———. 1980. A recurrent mass stranding of the false killer whale, *Pseudorca crassidens*, in Florida. Fishery Bulletin, United States, 78:171–177.

OHSUMI, S. 1972. Catch of marine mammals, mainly of small cetaceans, by local fisheries along the coast of Japan. Bulletin of the Far Seas Fisheries Research Laboratory, 7:137–166.

OLIVER-SCHNEIDER, C. 1946. Catalogo de los Mamiferos de la provincia de Concepcion. Boletin de la Sociedad de Biologia de Concepcion, 21:67–83.

OWEN, R. A. 1846. A history of British fossil mammals and birds. London, 560 pp.

PAULUS, M. 1963. Etude osteographique et osteometrique sur un pseudorque (*Pseudorca crassidens* Owen, 1846) capture au large de Port-de-Bouc (Bouchesdu-Rhone) en Novembre 1948 (Collection du Museum de Marseille). Bulletin Musee d'Histoire Naturelle de Marseille, 23:29–67.

PEACOCK, A. D., L. COMRIE, AND F. GREENSHIELDS. 1936. The false killer whales stranded in the Tay Estuary. Scottish Naturalist, 36:93–104.

PERRIN, W. F., AND S. B. REILLY. 1984. Reproductive parameters of dolphins and small whales of the family Delphinidae. Pp. 97–134, *in* Reproduction in whales, dolphins, and porpoises (W. F. Perrin, R. L. Brownell, Jr., and D. P. DeMaster, eds.). Reports of the International Whaling Commission, Special Issue, 6:1–495.

PILLERI, G. 1987. Os interparietale and post-interparietal ossicles in a fetus of *Pseudorca crassidens* (Cetacea, Delphinidae). Investigations on Cetacea, 20:36–39.

PORTER, J. W. 1977. *Pseudorca* stranding. Oceans, 10(4):8–16.

PURVES, P. E., AND G. PILLERI. 1978. The functional anatomy and general biology of *Pseudorca crassidens* (Owen) with a review of the hydrodynamic and acoustics in Cetacea. Investigations on Cetacea, 9:67–230.

REINHARDT, J. 1862. Om en for den Danske Fauna ny Delphinart (*Pseudorca crassidens* Owen). Oversigt over det Konglige Danske Videnskabernes Selskabs Forhandlinger, 1862(November):103–152.

———. 1866. *Pseudorca crassidens*, a cetacean hitherto unknown in the Danish fauna. Pp. 189–218, *in* Recent memoirs on the Cetacea (W. H. Flower, ed.). Ray Society of London, 312 pp.

ROSS, G. J. B. 1984. The smaller cetaceans of the south east coast of southern Africa. Annals of the Cape Provincial Museums (Natural History), 15:173–410.

SCOTT, E. O. G., AND R. H. GREEN. 1975. Recent whale strandings in northern Tasmania. Papers and Proceedings of the Royal Society of Tasmania, 109:91–96.

SERGEANT, D. E. 1969. Feeding rates of cetacea. Fiskeridirektoratets Skrifter Serie Havundersokelser, 15:246–258.

SLIJPER, E. J. 1936. Die Cetaceen: Vergleichen-anatomisch und systematisch. (1973 reprint) A. Asher and Co., Amsterdam, 590 pp. (not seen, cited in Heyning and Dahlheim, 1988).

———. 1961. Foramen ovale and ductus arteriosus botalli in aquatic mammals. Mammalia, 5:528–570.

SOKOLOV, V. E. 1973. Structure of the skin cover in some cetacea. Pp. 102–118, *in* Morphology and ecology of marine mammals, seals, dolphins, porpoises (K. K. Chapskii and V. E. Sokolov, eds.). John Wiley & Sons, Inc., New York, 232 pp.

STACEY, P. J., AND R. W. BAIRD. 1991. Status of the false killer whale, *Pseudorca crassidens*, in Canada. The Canadian Field-Naturalist, 105:189–197.

SULLIVAN, R. M., AND W. J. HOUCK. 1979. Sightings and strandings of cetaceans from northern California. Journal of Mammalogy, 60:828–833.

SYLVESTRE, J.-P., AND S. TASAKA. 1985. On the intergeneric hybrids in cetaceans. Aquatic Mammals, 11:101–108.

THOMAS, J., N. CHUN, W. AU, AND K. PUGH. 1988*a*. Underwater audiogram of a false killer whale (*Pseudorca crassidens*). Journal of the Acoustical Society of America, 84:936–940.

THOMAS, J., M. STOERMER, C. BOWERS, L. ANDERSON, AND A. GARVER. 1988*b*. Detection abilities and signal characteristics of echolocating false killer whales (*Pseudorca crassidens*). Pp. 323–328, *in* Animal sonar, processes and performance (P. E. Nachtigall and P. W. B. Moore, eds.). Plenum Press, New York, 862 pp.

TOMICH, P. Q. 1986. Mammals in Hawaii, a synopsis and notational bibliography. Second ed. Bishop Museum Special Publication, 76:1–375.

TOMILIN, A. G. 1957. Mammals of the U.S.S.R. and adjacent countries. Vol 9: Cetacea. English translation 1967 by Israel Program for Scientific Translation, Jerusalem, 717 pp.

TRUE, F. W. 1889. A review of the family Delphinidae. Bulletin of the United States National Museum, 36:1–191.

TSUTSUMI, T., Z. KAMIMURA, AND K. MIZUE. 1961. Studies on the little toothed whales in the West Sea areas of Kyusyu-V. About the food of the little toothed whales. Bulletin of the Faculty of Fisheries, Nagasaki University, 11:19–28.

VAN GELDER, R. G. 1960. Results of the Puritan-American Museum of Natural History expedition to western Mexico 10. Marine mammals from the coasts of Baja California and the Tres Marias Islands, Mexico. American Museum Novitates, 1992:1–27.

WALSH, M. T., D. K. ODELL, G. YOUNG, E. D. ASPER, AND G. BOSSART. 1990. Mass strandings of cetaceans. Pp. 673–683, *in* CRC handbook of marine mammal medicine: health, disease, and rehabilitation (L. A. Dierauf, ed.). CRC Press, Boca Raton, Florida, 735 pp.

WANG, Z. 1984. The skeleton of the false killer whale *Pseudorca crassidens* (Owen) from the China Sea. Acta Zoologica Sinica, 30:286–294.

WHITTOW, G. C., I. F. C. HAMPTON, D. T. MATSUURA, C. A. OHATA, R. M. SMITH, AND J. F. ALLEN. 1974. Body temperature of three species of whales. Journal of Mammalogy, 55:653–656.

YAMADA, Y. 1956. An analysis in mass osteology of the false killer whale, *Pseudorca crassidens* (Owen) Part 1. Okajimas Folia Anatomica Japonica, 28:453–463.

ZAM, S. G., D. K. CALDWELL, AND M. C. CALDWELL. 1971. Some endoparasites from small odontocete cetaceans collected in Florida and Georgia. Cetology, 2:1–11.

ZHOU, K., W. QIAN, AND Y. LI. 1982. *Pseudorca crassidens* (Owen) from the coastal waters of China. Investigations on Cetacea, 13:264–269.

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