

*Phocoena phocoena*. By David E. Gaskin, Peter W. Arnold, and Barbara A. Blair

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*Phocoena phocoena* (Linnaeus, 1758)  
Harbor Porpoise

- Delphinus phocoena* Linnaeus, 1758:77. Type locality "Oceano Europaeo Balthico."  
*Phocaena fuscus* Kerr, 1792:363. Type locality St. Lawrence River.  
*Delphinus ventricosus* Lacépède, 1804:311. Type locality River Thames, England.  
*Phocaena communis* Lesson, 1827:413. New name for *phocoena*.  
*Phocaena tuberculifera* Gray, 1865:320. Type locality Margate, England.  
*Phocaena vomerina* Gill, 1865:178. Type locality Puget Sound, Washington.  
*Phocaena brachycium* Cope, 1865:279. Type locality Salem Harbor, Massachusetts.  
*Phocaena americana* J. A. Allen, 1869:206. Type locality Massachusetts.  
*Phocoena Rondeletii* Giglioli, 1870:78. Type locality European Coast.  
*Phocaena lineata* Cope, 1876:134. Type locality New York Harbor.  
*Phocaena relicta* Abel, 1905:387. Type locality Crimean Coast, Black Sea.

**CONTEXT AND CONTENT.** Order Cetacea, Suborder Odontoceti, Superfamily Delphinoidea, Family Phocoenidae. The genus *Phocoena* is currently thought to contain four species: *P. phocoena*, *P. spinipinnis*, *P. dioptrica*, and *P. sinus*. Two subspecies are recognized by many authors. The possible subspecific status of *vomerina* of the North Pacific needs further study (see Norris and McFarland, 1958). The synonymy below and that above follow Hershkovitz (1966), which see for citations not included in the Literature Cited of this account.

- P. p. phocoena* (Linnaeus, 1758:77), see above (*fuscus* Kerr, *ventricosus* Lacépède, *communis* Lesson, *tuberculifera* Gray, *vomerina* Gill, *brachycium* Cope, *americana* Allen, *Rondeletii* Giglioli, *lineata* Cope, *acuminata* Van Deinse, and *conidens* Van Deinse are synonyms).  
*P. p. relicta* Abel, 1905:387, see above (see discussion of this taxon by Zalkin, 1938, and Kirpichnikov, 1952).

**DIAGNOSIS.** Because the genus needs revision, a completely reliable specific diagnosis has not been written. *P. spinipinnis* and *P. dioptrica* at the time of writing are still best distinguished from *P. phocoena* by distribution and color pattern (Burmeister, 1865; Allen, 1925; Lahille, 1912; Hamilton, 1941).

Norris and McFarland (1958) compared cranial characters of the four recognized species of *Phocoena*. According to their data, *P. phocoena* can perhaps be distinguished, especially from *P. sinus*, by the following: coronoid border of mandible bends laterally to form a small flange; maxillary enters the orbit and covers the lateral margin of the frontal; width of exposure of frontal bones only about 8 to 9 mm in adults; adult ratio of skull width to length about 0.537; ratio of width of rostrum to length 0.470; mean zygomatic width across squamosal processes 149.5 mm; dental formula (including alveoli) 27 or 28 over 26 below. The measurements were taken by Norris and McFarland from 12 specimens judged to be adults by the degree of cranial ankylosis and fusion of postorbital processes. Unfortunately, their comparative material was limited. The skull is illustrated in Figure 1 and the tympanic and periotic bones in Figure 2.

**GENERAL CHARACTERS.** The smallest of the oceanic Cetacea (figure 3). Recorded maxima for length and weight are 1.86 m (Fischer, 1881) and 90 kg (Møhl-Hansen, 1954; Rice, 1967). However, average adult lengths and weights are much less, about 1.5 to 1.6 m and 45 to 60 kg. The body is robust, the snout blunt, and there is no externally delineated

rostrum. The mouth line slants slightly dorsad. The blowhole is single, central, and crescentic. The flippers are inserted about a fourth of the total body length posterior to the snout; they are relatively small in comparison to those of Delphinidae. The dorsal fin also is relatively small and triangular. A promi-

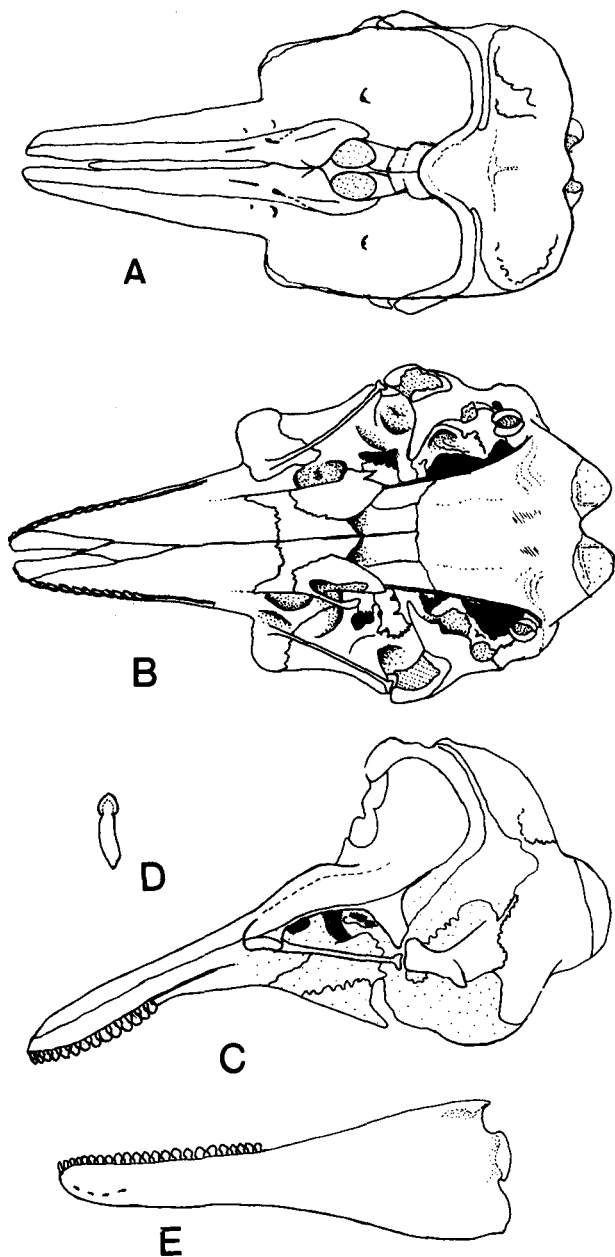


FIGURE 1. Skull of *Phocoena phocoena* (from a female 1.22 m long) in dorsal (A), ventral (B), and lateral (C) views, and lateral view (E) of mandible. The asymmetry of this skull in dorsal view is as shown. The auditory bullae are not present and some of the posterior teeth also are missing. An enlarged drawing of a tooth from mid-series of left maxillary of a female 1.43 m long is shown at D.

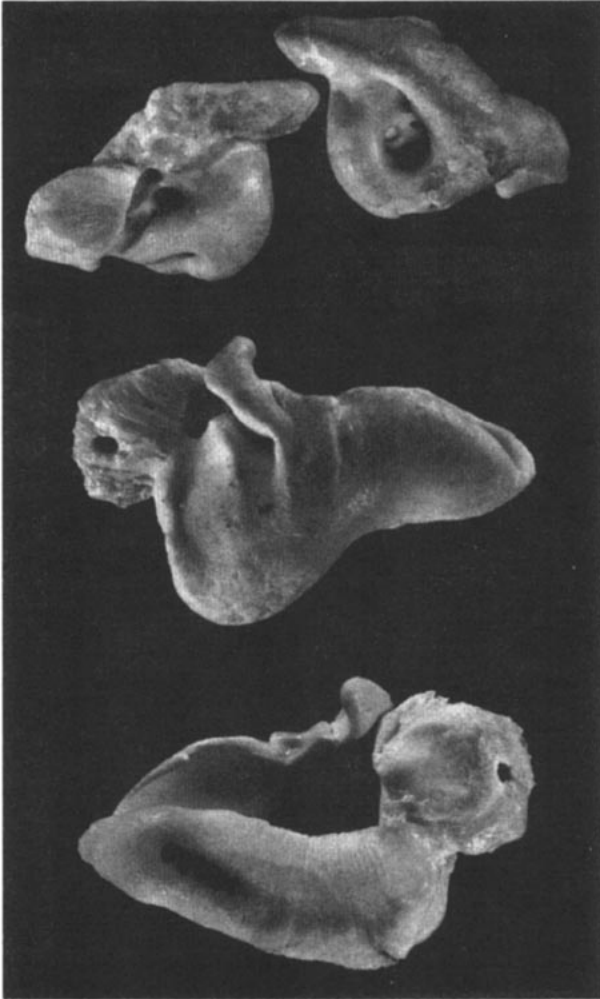


FIGURE 2. Right tympanic and periotic bones of *Phocoena phocoena* (AMNH 10200 from Holsteinborg, Greenland), from top right down views are approximately from medial side of periotic, lateral side of periotic, dorsolateral side of tympanic, and medial side of tympanic (dorsal at top in each view).

nent dorsal ridge extends from the dorsal fin to the point of fluke insertion. Color pattern is variable, possibly with age, within relatively narrow limits. The following is typical. Upper and lateral aspects of head dark gray, both jaws bordered with dark gray, throat pale gray adjacent to dark zones, giving way to white on the whole ventral surface save the caudal peduncle. Posterior to the eye the zone of dark gray is reduced in extent until the line of the dorsal fin. A line of dark gray, striking in adults, extends from the angle of the lower jaw to the anterior insertion of the flippers. There is often a thinner secondary streak parallel to the first. Posterior to the dorsal

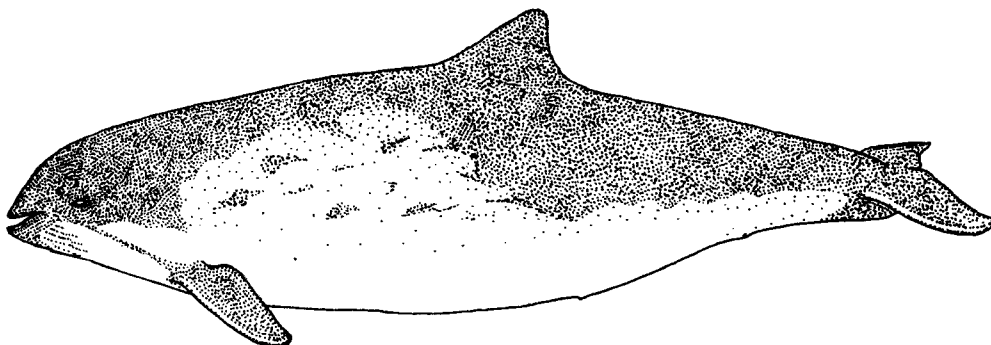


FIGURE 3. *Phocoena phocoena* L., common or harbor porpoise. The proportions and pattern shown are typical of an adult animal.

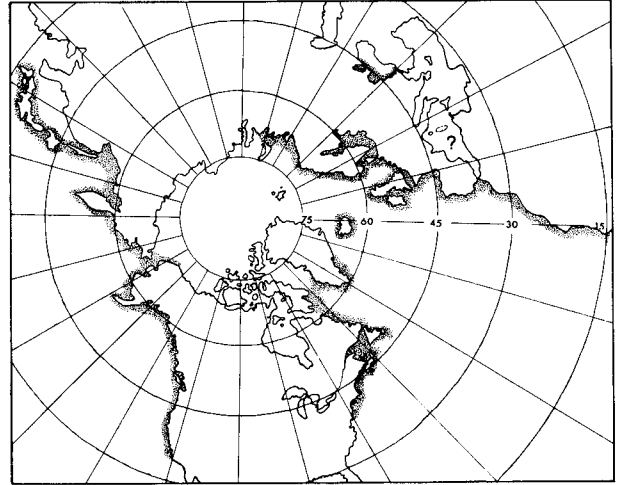


FIGURE 4. Distribution of *Phocoena phocoena* showing maximum range based on published records. No attempt has been made to differentiate areas of relative abundance; for more information see text.

fin the body is dark gray ventrad to the level of fluke insertion. Flippers, flukes, and dorsal fin are all dark gray to blackish. A variable pale gray zone extends posteriorly from the eye area in the lateral-sublateral line. Van Deirse (1935) recorded a case of pseudoalbinism from Holland, Kleinenberg (1936) an almost complete albino from the Black Sea, and Peters (1929) a partial albino from Germany. McIntosh (1927) recorded an albino from Scottish waters.

**DISTRIBUTION.** The range of this species is shown in Figure 4. Ecologically this can be defined as a boreal-temperate zone species, common in bays, estuaries, and tidal channels of the Atlantic coast of Europe, the east and west coasts of North America, and the Pacific coast of Asia (Rice, 1967). In Europe it is particularly common around Denmark (Møhl-Hansen, 1954), the British Isles (Rae, 1965), and in the Polish Baltic (Wolk, 1969).

Neave and Wright (1968) claimed that the species exhibited a north-south annual migratory pattern on the eastern coast of North America, moving northward in late May and southward in early October. However the extensive data of the present authors suggests an inshore-offshore movement of the same time scale, not a north-south movement. Sergeant *et al.* (1970) suggested wintering occurred near Sable Island.

In the summer months, the species has been recorded as far north as the southern coast of Baffin Island, although there are no records from Hudson's Strait and Hudson's Bay (Kumlien, 1879; Low, 1906, *in* Soper, 1944). At its northern limit of distribution the species appears to avoid truly polar seas, but is occasionally seen on the eastern coast of Greenland to Angmagssatik (Vahl *et al.*, 1928), and from April to November ranges northward along the coast of western Greenland between Cape Farewell and Upernivik (Brown, 1868). On the coast of Labrador the harbor porpoise has been taken as far north as Kaipokok Bay (Peterson, 1966).

The species is common from Trinity Bay, Newfoundland

(Sergeant and Fisher, 1957), to the Bay of Fundy (Neave and Wright, 1968). The latter authors reported a small overwintering population in the western part of the Bay of Fundy. Their methodology was strongly criticised by Schevill (1968), but their conclusions are in general agreement with recent and more adequate observations by the present authors. The species is plentiful along the southern shore of the St. Lawrence in summer (Vladykov, 1944), and has been taken at least 160 km from the mouth of that river (Peterson, 1966). Dr. H. D. Fisher (personal communication) recorded a school not far from Anticosti Island, and noted that the species was seasonally abundant around the Magdalen Islands. Seasonal concentrations also occur on the coast of Nova Scotia (Gilpin, 1875, and authors' observations). The harbor porpoise ranges southward at least to Cape May, New Jersey, and the Delaware River (True, 1889; Fowler, 1915), and is sometimes seen on the Connecticut coast (Goodwin, 1935). Ray and Ciampi (1956) listed the species as being "very rare" along the eastern seaboard of the United States, but being "occasionally seen in Maine." Dr. H. E. Winn (personal communication) reported a single small school from Narragansett Bay, Rhode Island, as well as a stranded specimen from Cape Cod, and concurred that the species was not common at that latitude. However, in the experience of the authors, the species is common off the coast of Maine in the Boothbay Harbor region during the summer months.

On the eastern side of the Atlantic the species ranges from the White Sea (Norman and Fraser, 1937) and Kara Sea (Tomilin, 1967), to Senegal in West Africa (Cadenat, 1949; 1959; Fraser, 1958), and on the west coast of North America from Point Barrow, Alaska (Hall and Bee, 1954) to Monterey, California (Booolootian, 1957), and Los Angeles harbor (Norris and Prescott, 1961). In the western Pacific it ranges from the Bering Sea, Kamchatka, and the Sea of Okhotsk to Hokkaido and Honshu in the coastal waters of Japan (Nishiwaki, 1967).

Zalkin (in Tomilin, 1967), reported *P. p. relicta* as being most abundant in the southern half of the Sea of Azov, Kersch Strait, and adjacent portions of the Black Sea. It ranges west commonly to Sevastopol and European Turkey, and is common as far east as Novorossiisk. It is observed all the year round near the mouths of the Bzyb and Kodor rivers (Zalkin, 1940; Tomilin, 1967).

**FOSSIL RECORD.** *Phocoena phocoena* has been reported from Pliocene strata of the USSR (Kirpichnikov, 1951). The geologic range of the family is from late Miocene in Europe to Recent (Rice, 1967). Three extinct genera conjecturally related to *Phocoena* are *Palaeophocaena* from the Crimean Tertiary, *Protophocaena* from the Belgian Tertiary, and *Phocaenopsis* from the New Zealand Pleistocene. These genera were all included in the Phocoenidae by Simpson (1945). However Miller (1921) had expressed the opinion that remains of *Palaeophocaena* were too fragmentary to classify beyond "delphinid," and that the shape of the intermaxillae anterior to the nares in *Protophocaena* indicated closer relationship to *Lagenorhynchus* or *Grampus* than *Phocoena*.

**FORM.** The pigmented region of the dermis is about 2 to 5 mm in depth, consisting of an outer stratum corneum and an inner stratum germinativum. Parry (1949) stated that the epidermis was not innervated, but later work (Palmer and Weddell, 1964, on *Tursiops truncatus*) makes this conclusion suspect. The nature of epidermal wounds and scars has been discussed by van Utrecht (1959). The hypodermal blubber layer is about 10 to 25 mm deep, and accounts for about 40% of the total body weight (Kanwisher and Sundnes, 1965). The oil composition was analyzed by Takaoka and Tuzino (1952). No detailed study of the mammary glands appears to have been made. Notes on the milk of a *Phocoena* caught in Scottish waters were given by McIntosh (1885).

Major elements of the skeletal system were shown by Fraser (1952: fig. 2). The species has from 62 to 66 vertebrae, of which seven are cervical (six fused), 12 to 14 thoracic, 14 to 17 lumbar, and 27 to 32 caudal (Nishiwaki, 1963). The same author cites the numbers of phalangeal bones, including metacarpals as: digit I, 1 to 3; II, 5 to 10; III, 5 to 8; IV, 2 to 6; V, 1 to 3. Supposed differences in length of the neonatal line in teeth of males and females were discussed by van Utrecht (1969) and the structure of the dentine and enamel by Keil and von Nolting (1969).

A short account of the musculature was given by Smirnowsky (1928), and more detailed accounts by Stannius (1849), Slijper (1936) and Browne (1971) who concentrated on functional aspects. The musculature of the head region, with

special reference to the cheeks and nasal sacs was discussed by Moris (1969).

The major vessels of the circulatory system were figured by Fraser (1952: figs. 2, 26, 27), an earlier general account was given by Stannius (1841). The arterial system of the head and neck region was described by MacKay (1886), DeKock (1959), and Moris (1969); MacKay also considered the rete mirabile. Harrison and Tomlinson (1956) described in detail the venous system while the hypophyseal portal system was outlined in Harris (1947). Van der Spoel (1963) discussed the renal vascular system, where there is a superficial plexus of veins, in addition to the renal vein, draining the organ. Red blood cell diameter has been reported as 6.6  $\mu$ m (Gulliver, 1875) and 9.5  $\mu$ m (Morimoto *et al.*, 1921). Zwillenberg (1959) described the spleen, of which about 30 per cent is white pulp.

Lymph nodes depart from the typical mammalian pattern: there is a central cortex with peripheral lymph tissue in cellular cordons (Moskov *et al.*, 1969).

The dorsal surface of an intact brain was figured by Fraser (1952: fig. 36). All aspects of the nervous system were discussed in comparative fashion by Jansen and Jansen (1969). They described the gross morphology, and noted a brain to body ratio of about 0.4%; the brain shows no remarkable unique features. The auditory region is highly developed as in most odontocetes; there are about 10 times as many cochlear nuclei in the harbor porpoise brain as in that of man. In earlier work Flatau and Jacobsohn (1899) studied the arrangement of fissures, Walberg (1952) the mesencephalon, Breathnach (1953, 1954) the olfactory region and the hippocampus and rhinencephalon. The cerebellum was described by Gierlich (1916) and the medulla by Rawitz (1903, 1908). Spinal cord structure and accessory nerves have been described (Cunningham, 1877; Hepburn and Waterston, 1904a; Pressey and Cobb, 1928; Fraser, 1952: fig. 37). An account of the basal ganglia was provided by Jelgersma (1934). Putter (1903) published on the density of rod cells in the retina, and various features of the retina were tabulated in Pilleri and Wandeler (1970). Boeninghaus (1903) described in detail the ear, whereas Dudok van Heel (1959), and Andersen (1970b) discussed audio-direction finding. Andersen (1970a) and Supin and Sukchoruchenko (1970) gave audiograms.

Anatomical features of the larynx were described by Rawitz (1900). Wislocki (1942) gave an account of the gross features of the respiratory system, a more detailed account of lung histology was given by Lacoste and Baudrimont (1933). The lungs have myoelastic sphincters in the bronchioles extending even to the alveoli, although these sphincters are less numerous and more delicate than in some other odontocete species. Also present are incomplete cartilaginous rings, not only lining the trachea, but even the smallest bronchioles. The diaphragm of this species is inserted obliquely, and lacks a restraining tendon (Fraser, 1952).

Observations on the alimentary canal have been made by Cleland (1884), Turner (1889), Hepburn and Waterston (1902), and Smith (1971). The stomach is composed of three morphologically and histologically distinct compartments. The first (forestomach), lacks digestive glands and possesses thick external muscles. It functions to store ingested food and facilitates mechanical breakdown of fish remains. Digestion is carried out in the glandular second compartment (main stomach) and the third compartment (pyloric stomach). These compartments are joined by a short connecting tube or channel. In the remainder of the alimentary canal little division is seen into small intestine and colon morphologically, but the anterior portion is pinkish in freshly killed specimens, and the posterior part of the canal greenish white. The liver is bilobate and lacks a gall bladder.

Many specimens are infected with the trematode *Campula oblonga*. The flukes are restricted to ducts of the liver and pancreas, while eggs may be spread throughout these organs, as well as to the lungs. Ridgway and Dailey (1972) reported campulid eggs in the brains of stranded *Delphinus* sp. and *Lagenorhynchus obliquidens*, and correlated the damage to nervous tissue with stranding. This is a possibility that should be investigated more fully. Other trematodes reported from *Phocoena* are *Opisthorchis tenuicollis* in "bile ducts" (Price, 1932) and *Lecithodesmus nipponicus* (Delyamure, 1972).

The urogenital system was described by Fraser (1952), and a more detailed account of the lobate kidneys given by van der Spoel (1963). Numerous authors have described the anatomy of the reproductive system of males (Hepburn and Waterston, 1904b; Braun, 1907; Meek, 1918; Möhl-Hansen, 1954; Fisher and Harrison, 1970) and of females (Klaatsch,

1886; Daudt, 1898; Wislocki, 1933; Fisher and Harrison, 1970). Systems of both sexes are typical for odontocetes except that mature testes are extremely large in relation to body size (up to 386 by 190 mm in a 1.5-m male, according to Fisher and Harrison). Morphology of spermatozoa was described by Ballowitz (1907).

Endocrine glands have been little studied. The basic histology of the thyroid was described by Turner (1862). The thymus was described by Petit and Buchet (1900); it is relatively large in immature animals (Harrison, 1969). The adrenal gland is a triangular lobate body immediately anterior to the kidney; its histology was described by Kolmer (1918).

General accounts of the anatomy and morphology of the harbor porpoise, without special reference to particular systems, have been provided by Braun (1905), Fraser (1952), and Slijper (1962), and of the systems of the head region by Moris (1969). Slijper (1958) discussed organ weights with respect to body symmetry; van Utrecht (1960) gave information on weight and length ratios.

**FUNCTION.** Thermal regulation through the blubber was discussed by Kanwisher and Sundnes (1965). The relatively small size of the species results in a ratio of surface area to body volume that does not favor retaining metabolic heat in a cold water environment. The periphery is in essence functionally poikilothermic; the temperature gradient through skin and blubber is from near ambient externally (0 to about 18°C) to about 37°C adjacent to the skeletal muscles. A capillary counter-current system appears to operate in the blubber, and most heat is lost at the extremities, where the blubber is thin and blood vessels lie close to the surface. The peripheral vascular system seems to function both in diving and thermoregulation (Kanwisher and Sundnes, 1965). The advantages of the retial system and the occurrence of bradycardia in diving were discussed by Scholander (1940). The anatomical lung modifications described in the previous section permit greater and more effective ventilation of the lungs than in most mammals (Lacoste and Baudrimont, 1933). The tidal volume of air of a 26 kg harbor porpoise is up to 1.85 litres compared with only about 0.4 litres in a 100 kg man (Kanwisher and Sundnes, 1965). Tachycardia occurs during inspiration, and the efficiency of oxygen extraction is increased. Expired air contains only 9% oxygen, compared with 16% in man. However these advantages are counterbalanced to some extent by the slow ventilation rate, which is about four times per minute (Parker, 1932). The respiratory function of the blood in this species was discussed by Green and Redfield (1933), the antibody formation by Lukyaneko (1964), aspects of haematology by Andersen (1966), blood chemistry by Andersen (1968), and electrocardiography by Andersen (1969a).

The harbor porpoise has a high metabolic rate, approximately three times that of a terrestrial mammal of comparable weight (Kanwisher and Sundnes, 1965). Correspondingly the feeding rate (food intake as percentage of body weight) is also high, ranging to about 10% per day (Sergeant, 1969). That author cited 4.2% as the equivalent for the larger bottle-nosed porpoise, *Tursiops truncatus*.

Van der Spoel (1963) discussed the function and blood circulation in the kidney, and the possible existence of a male sexual cycle was considered by Fraser (1953) and Fisher and Harrison (1970). Harrison (1969) found a slight decrease in the ratio of thyroid gland to total body weight with age, and noted that adrenal gland weights varied from 0.3-0.9 g/kg of body weight. This ratio is the highest known in Cetacea.

**ONTOGENY AND REPRODUCTION.** Information on the reproductive cycles of *P. phocoena* is inexact. Møhl-Hansen (1954) and Fisher and Harrison (1970) provided data to show that mating in the Baltic and North Atlantic occurred in July and August. Fraser (1953) reported it as taking place in June as well, and Slijper (1962) as occurring from July through to October. Implantation is almost immediate. Slijper (1962) considered gestation to last about 8 to 10 months. Fisher and Harrison (1970) indicated that 11 months was more realistic. Some early observations on the gestation period were published by Grieg (1891), and placentation was described by Hoedemaker (1935) and Wislocki (1933). Births have been recorded in June and July (Harmer, 1927; Fraser, 1934, 1946, 1953) in seas around Britain; between May and June in the Baltic Sea (Møhl-Hansen, 1954), with some as late as July and August; May to July has also been reported for the North Atlantic (Guldberg and Nansen, 1894), with births off Norway as early as March (Grieg, 1890; Slijper, 1962). Gilpin (1875) reported calving in the Nova Scotia waters of the Bay of Fundy as early

as April and May; the present authors have recorded calves on the New Brunswick side of the Bay of Fundy no earlier than 19 June. The foetus has been described by Friant (1952) and Møhl-Hansen (1954), and additional description of a neonate was given by Scheffer and Slipp (1948). Vibrissae about 7 to 8 mm in length are present, in one to three rows on the dorso-lateral surface of the snout of the foetus. The length at birth has been given as 800 to 860 mm (Guldberg and Nansen, 1894), and 800 to 900 mm (Fisher and Harrison, 1970), although Harmer (1927) recorded a neonate of 710 mm and Slijper (1962) one of 700 mm. Fraser's records (1934, 1946, 1953) gave ranges of 762 to 991 mm for a series of neonates.

The growth increment in the first 6 months (200 mm) is 25% of the body length at birth, and in the first year 300 mm (37%). According to Fisher and Harrison (1970) full sexual maturity is probably attained at an age of 3 to 4 years, supposedly at body lengths of about 1.33 m in males and 1.45 m in females. They had insufficient data to show if this was the result of different growth rates, or whether sexual dimorphism occurs in the species. The duration of lactation is not known. Møhl-Hansen (1954) and Slijper (1962) suggested about 8 months. Estimates of age at sexual maturity as 14 to 15 months (Møhl-Hansen, 1954; Scheffer and Slipp, 1948; and Slijper, 1962) are almost certainly much too low. In a sample of 107 specimens from the Bay of Fundy area that were aged from dental growth layers, only three were more than 8 years old (9, 10, 13) according to B. A. Blair (unpublished data). The estrous cycle is not completely understood. Estimates of its duration are complicated by the presence of two types of corpora albicantia (Fisher and Harrison, 1970). Females almost certainly do not inevitably bear a foetus every year (Fisher and Harrison, *op. cit.*).

**ECOLOGY.** Harbor porpoises suffer an unknown degree of predation by Greenland sharks, *Somniosus microcephalus* (Williamson, 1963), by great white sharks, *Carcharodon carcharias* (Templeman, 1963; Arnold, in press), and by killer whales, *Orcinus orca* (Eschricht, 1866).

The diet and feeding habits of the harbor porpoise have been described (Scott, 1903; Stephen, 1926; Orr, 1937; Wilke and Kenyon, 1952; Svardsen, 1955; Sergeant and Fisher, 1957; Fink, 1959; Lindroth, 1962; Rae, 1965; Tomilin, 1967; Smith, 1971). Nutrition in the wild and in captivity was considered by Andersen (1965). The diet consists mostly of smooth, nonspiny rayed fish 100 to 250 mm long, especially gadoids and clupeoids. The major dietary items in the western Bay of Fundy are herring (*Clupea harengus*), pollack (*Pollachius virens*), and mackerel (*Scomber scombrus*). Hake, *Urophycis tenuis*; *Illex* sp.; and *Loligo* sp. are also taken (Sergeant and Fisher, 1957; Smith, 1971). The North Pacific population feeds extensively on sardines, *Sardinops caerulea* (Scheffer and Slipp, 1948). In British waters (Scott, 1903; Stephen, 1926; Rae, 1965) major food items are whiting (*Gadus merlangus*), mackerel, herring, sprat (*Clupea sprattus*), and sandeel (*Ammodytes lanceus*). In the Baltic Sea, porpoises feed on cod (*Gadus morhua*), herring, whiting, sandeel, and perhaps smolt and grilse of salmon (Svardson, 1955; Lindroth, 1962). The daily intake of captive specimens varied from 4.3 kg per day (Andersen, 1965) to 11.3 kg (Dudok van Heel, 1962) or 13.6 kg (Boulenger, 1925). Males apparently ate less than females, and the intake varied in both sexes with condition, and with other factors not ascertained. The Black Sea population feeds predominantly on benthic fishes (Tomilin, 1967).

The alimentary canal is regularly, sometimes heavily, parasitized. Lesions of the forestomach associated with anisakids were described by Vik (1964) and Young and Lowe (1969). Stomach nematodes recorded are *Anisakis simplex* and *A. typica* (Young and Lowe, 1969; Davey, 1971), *Teranovia decipiens* (Schmidt-Ries, 1939; Scott and Fisher, 1958), and *Contracaecum* sp. (Scott and Fisher, 1958). *Contracaecum aduncum*, reported by Young and Lowe (1969), is a parasite of fishes and should be considered of accidental occurrence in porpoises. Stomach trematodes reported are *Hadwenius nipponicus* (Ching and Robinson, 1959), *Pholeter gastrophilus* (Kossack, 1910), and *Braunina cordiformis* (Arnold, personal observation). There is confusion concerning cestodes parasitic in *Phocoena*, as discussed by Delyamure (1968); species listed are *Diphyllobothrium stemmacephalum* (Borcea, 1935), *D. latum* (Schmidt-Ries, 1939), and *D. lanceolatum* (Schmidt-Ries, 1939). Rausch and Hilliard (1970) reported plerocercoids of *Pyramicocephalus phocarum*, a parasite of pinnipeds, from a porpoise caught in Alaska. Acanthocephalans *Corynosoma strumosum* (Delyamure, 1968; Schmidt-Ries, 1939) and *C. alaskensis* (Golvan, 1959) also have been recorded.

Helminth parasites of the respiratory system are common, approaching 100% infection rates in several series of specimens examined (Andersen, 1966; Delyamure, 1968; Møhl-Hansen, 1954). The following Nematoda (Pseudaliidae) have been recorded: *Pseudalius inflexus* in the pulmonary arteries and bronchial tubes (Abeloos, 1932; Møhl-Hansen, 1954; Schmidt-Ries, 1939); *Torynurus* (= *Pharurus*) *convolutus* in the bronchial tubes (Abeloos, 1932; Dougherty, 1943; Hsü and Chow, 1938; Schmidt-Ries, 1939); *Halocercus invaginatus* in nodules in lung parenchyma (Dougherty, 1943; Schmidt-Ries, 1939); *H. ponticus* within elastic capsules in lung parenchyma (Delyamure, 1946); *H. taurica* in bronchial tubes and lung parenchyma (Delyamure, 1946); *Stenurus minor* in bronchial tubes and cranial sinuses (Delyamure, 1968; Dougherty, 1943; Møhl-Hansen, 1954; Schmidt-Ries, 1939). Further studies on the systematics of this group are in progress by Arnold.

No detailed studies on the population dynamics of the species exist. The extent and duration of its migrations and the homogeneity of its populations in various parts of the Northern Hemisphere are unknown. Although generally considered to be coastal dwellers, the species seems to leave coastal waters during the winter months. Movements have been discussed for the Baltic population (Møhl-Hansen, 1954; Ropelowski, 1957; Wołk, 1969); for the population in British seas (Fraser, 1946, 1953); and for the Bay of Fundy population (Sergeant and Fisher, 1957; Fisher and Harrison, 1970; Neave and Wright, 1968). Our observations in the Passamaquoddy Bay region suggest some territoriality among groups, but many more observations and preferably tagging are necessary to substantiate this. We find no account of taggings and recapture in the literature.

While the species is difficult to maintain in captivity for any length of time, some have been held for periods of several months in Europe (Dudok van Heel, 1962; Andersen and Dziedzic, 1964; Andersen, 1965). The harbor porpoise is most difficult to obtain in the open sea, where Indian hunters (Fisher and Harrison, 1970) and the present authors, found that specimens could only be obtained by patient stalking and skillful use of shotguns. The animals rarely ride the bow waves of boats and are in fact so wary of them that nets or harpoons are useless. However, they occasionally become trapped in herring weirs, seines, and smaller fish traps, and specimens may be obtained in this manner alive (Schevill *et al.*, 1969). Harbor porpoises were killed for meat and oil by Indians on the coast of Nova Scotia (Gilpin, 1875; Leighton, 1937; Fisher and Harrison, 1970) and still are eaten when available on the coasts of New Brunswick and in parts of northern Maine by fishing families. They are still taken in the Baltic (Wołk, 1969) where they appear to be decreasing in numbers. They were taken in Denmark during the Second World War (Møhl-Hansen, 1954), and more recently by Russian fishermen during migrations between the Black Sea and the Sea of Azov from November to April (Tomilin, 1967). In economic terms, however, the species is of quite negligible importance at present.

Significant residues of chlorinated hydrocarbon insecticides were reported in the fat of harbor porpoises from the Baltic and seas around the United Kingdom (Holden and Marsden, 1967). However, much higher levels, ranging to 520 parts per million of extractable fat in the blubber, have been recorded recently by Gaskin *et al.* (1971) from animals in and near the Bay of Fundy. High levels of PCBs (polychlorinated biphenyls) also were recorded by these workers, together with up to 12 ppm of dieldrin.

**BEHAVIOR.** Little is known of breeding behavior in the wild, whether there is a single dominant male in a school, whether promiscuous mating is the rule, or whether long-term pairing occurs (Fisher and Harrison, 1970).

Kellogg (1940) reported the species to be highly gregarious. In our experience, however, large schools must be quite exceptional in the Bay of Fundy; the largest school seen by us contained only nine animals. Several smaller schools may be separated by only a few hundred yards, but the discrete identity of these units is rarely in doubt. Fink (1959) and Rae (1965) reported aggregations of several hundred animals in the North Pacific and near Britain.

Neave and Wright (1968) reported that two or three harbor porpoises usually were seen together early in the season in the Bay of Fundy, but in larger groups in June or July. We have observed this also.

Observations on swimming of *Phocoena* have been provided by Scheffer and Slipp (1948), Scholander (1940), Millais (1906), Walker *et al.* (1964), Dudok van Heel (1962), Klein-

enberg (*in* Slijper, 1962), and Andersen and Dziedzic (1964). Surfacing and diving were described in detail by Scheffer and Slipp (1948). Dive times of up to 6 min were recorded by Kleinenberg, dubiously to 12 min by Scholander (1940). Four min was about average for score of dives by wild animals timed by us. Scheffer and Slipp (1948) recorded a specimen taken in a fish trap 44 fathoms (79 m) below the surface. Porpoises are frequently seen resting at the surface, in some cases observation soon reveals that such an animal is a female suckling a calf, but immature animals also lie at the surface for up to 90 seconds, especially in calm water in sunny weather. The authors noted this behavior in April off New Brunswick, when the water temperature was less than 3°C, and attributed it to basking; however, the same behavior later was noted in August with water temperatures close to 16°C.

Generally, the activity of the species is constant. Andersen and Dziedzic (1964) reported captive animals showed neither diurnal nor nocturnal activity peaks. Maximum swimming speed recorded by Kanwisher and Sundnes (1965) was 9 knots (16.6 km/hr), but we have pursued physically mature animals over known distances in Passamaquoddy Bay at speeds close to 12 knots (22.2 km/hr) on numerous occasions. Play has been infrequently observed. However, Rae (1965) noted that Scottish fishermen claimed to have seen individuals play with salmon, and Aflalo *et al.* (1906) noted play with a conger eel. Common behavior among captive animals includes picking up objects such as starfish or pieces of *Fucus* and carrying the object in midwater for hours at a time, sometimes trying to balance it on a flipper or on the flukes (Andersen and Dziedzic, 1964). Dudok van Heel (1962) noted that his captive animals became much more active at times when bad weather was approaching. Seemingly succorant behavior was reported by Caldwell and Caldwell (1966), Møhl-Hansen (1954), and Andersen (1969b). At Chester, Nova Scotia, in July 1971, we saw clear succorant behavior by a mother while we were trying to capture a calf. The mother repeatedly swam across the bow of the boat, apparently attempting to divert attention from the calf. Later the same animal succeeded in joining with the calf and led it into a series of quite long dives, up to 3 minutes at a time, eventually resulting in the boat losing contact with them completely. Prior to this the calf swam at the surface, breathing every 8 to 10 seconds.

Sound production, including echolocation, has been studied (Busnel *et al.*, 1963; Busnel and Dziedzic, 1966; and Schevill *et al.*, 1969) and was well summarized by the last paper cited. The phonation of *P. phocaena* is of low intensity (less than 1 dyne per cm<sup>2</sup> at 1 m), consisting of narrow-band clicks generally close to 2000 Hz. The clicks are produced singly or in bursts of up to 1000 clicks per sec.

**REMARKS.** Many national or regional vernacular names are used for this animal. Among the most frequently cited are: harbo(u)r porpoise (Canada and United States), common porpoise (Britain), puffing pig (eastern Canada), poucil (French Canada), marsouin (France), and Braunfisch (Germany). Murray *et al.* (1931) published a list of vernacular names used in Britain from the time of the Roman occupation (78 A.D.) to the present day; Hershkovitz (1966) gave a list of names in 17 languages other than English. Scheffer and Slipp (1948) listed several amerindian names.

*Phocaena* is a variant spelling used for both the generic name and the name of this species (see Husson, 1968, and Schevill *et al.*, 1969, for discussion).

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