The effects of POLLUTION and contaminants on right whale dolphins in general are currently unknown. Given the nature of the pelagic habitat of the northern species, the effects of pollution are probably minimal. However, seasonal shifts in migration and distribution could possibly have a negative impact on these species. Minh *et al*. (2000) estimated the concentrations of polychlorinated biphenyls (PBCs) in cetaceans in the North Pacific. They found that in one northern right whale dolphin individual in their study contained high concentrations of PCBs such that the exceeded levels were associated with immunosuppresion in harbor seals. In another study, Jones *et al*. (1999) found that concentrations of halogenated aromatic hydrocarbons (HAHs) in open ocean cetaceans (southern right whale dolphins) had intermediate levels whereas coastal species had the highest levels of contaminants. So while research shows that *Lissodelphis* species are susceptible to marine pollutants, more research in ecotoxicology is needed.

See Also the Following Articles

Delphinids, Overview ■ North Pacific Marine Mammals

References

Aguayo, L. A. (1975). Progress report on small cetacean research in Chile. *J. Fish. Res. Board. Can.* **32**, 1123–1143.

Corvetto, A., Lamilla, J., and Pequeno, G. (1992). *Lissodelphis peronii* Lacépède 1804 (Delphinidae, Cetacea) within the stomach contents of a sleeping shark, *Somniosus* cf. *pacificus*, Bigelow and Schroeder 1944, in Chilean waters. *Mar. Mamm. Sci.* **8**, 312–314.

Ferrero, R. C., and Walker, W. A. (1993). Growth and reproduction of the northern right whale dolphin, *Lissodelphis borealis*, in the offshore waters of the North Pacific Ocean. *Can. J. Zool.* **71**(12), 2335–2344.

Fish, J. F., and Turl, C. W. (1976). Acoustic source levels of four species of small whales. *Naval Undersea Center Tech. Rep., TP* **547**, 1–14.

Forney, K. A., and Barlow, J. (1998). Seasonal patterns in the abundance and distribution of California cetaceans, 1991–1992. *Mar. Mamm. Sci.* **14**(3), 460–489.

Fraser, F. C. (1955). The southern right whale dolphin, *Lissodelphis peronii* (Lacépède) external characteristics and distribution. *Bull. Brit. Mus. (Nat. Hist.) Zool.* **2**(2), 339–346.

Gaskin, D. E. (1968). The New Zealand Cetacea. *Fish. Res. Bull. New Zealand* **1**, 1–92.

International Whaling Commission (1983). Report of the sub-committee on small cetaceans, Annex H. *Rep. Int. Whal. Commn.* **33**, 152–170.

Jefferson, T. A., and Newcomer, M. W. (1993). *Lissodelphis borealis*. *Mamm. Spec.* **425**, 1–6.

Jefferson, T. A., Newcomer, M. W., Leatherwood, S., and Van Waerebeek, K. (1994). Right whale dolphins *Lissodelphis borealis* (Peale, 1848) and *Lissodelphis peronii* (Lacépède, 1804). *In* “Handbook of Marine Mammals” (S. H. Ridgway, and R. Harrison, eds), Vol. 5, pp. 335–362. Academic Press, London.

Jones, P. D., *et al*. (9 authors) (1999). Polychlorinated dibenzo-p-dixions, dibenzofurans and polychlorinated biphenyls in New Zealand cetaceans. *J. Cetacean Res. Manag.*(Special Issue 1), 157–167.

Klumov, S. K. (1959). Commercial dolphins of the far east. *Pacific Sci. Res. Inst. Fish. Econ. Oceanogr. Rep.* **47**, 154–160 [Translated from Russian].

Leatherwood, S., and Reeves, R. R. (1983). “The Sierra Club Handbook of Whales and Dolphins.” Sierra Club Books, San Francisco.

Leatherwood, S., and Walker, W. A. (1979). The northern right whale dolphin *Lissodelphis borealis* Peale in the eastern North Pacific. *In* “Behavior of Marine Animals” (H. E. Winn, and B. L. Olla, eds), Vol. 3, pp. 85–141. Plenum Press, New York.

LeDuc, R. G., Perrin, W. F., and Dizon, A. E. (1999). Phylogenetic relationships among the delphinid cetaceans based on full cytochrome b sequences. *Mar. Mamm. Sci.* **15**(3), 619–648.

Mangel, M. (1993). Effects of high-seas driftnet fisheries on the northern right whale dolphin *Lissodelphis borealis*. *Ecol. Appl.* **3**, 221–229.

Martuscelli, P., Olmos, F., Silva e Silva, R., Mazzarella, I. P., Pino, F. V., and Raduan, E. N. (1996). Cetaceans of São Paulo, southeastern Brazil. *Mammalia* **60**(1), 125–139.

Minh, T. B., *et al*. (8 authors) (2000). Isomer-specific accumulation and toxic assessment of polychlorinated biphenyls, including coplanar congeners, in cetaceans from the North Pacific and Asian coastal waters. *Arch. Environ. Contam. Toxicol.* **39**, 398–410.

Newcomer, M. W., Jefferson, T. A., and Brownell, R. L., Jr. (1996). *Lissodelphis peronii*. *Mamm. Spec.* **531**, 1–5.

Rice, D. W. (1998). “Marine Mammals of the World: Systematics and Distribution.” *Soc. of Mar. Mamm.*, *Spec. Pub.* **4**. Allen Press. 231 p.

Rose, B., and Payne, A. I. L. (1991). Occurrence and behavior of the southern right whale dolphin *Lissodelphis peronii* off Namibia. *Mar. Mamm. Sci.* **7**(1), 25–34.

Van Waerebeek, K., Canto, J., Gonzalez, J., Oporto, J., and Brito, L. (1991). Southern right whale dolphins, *Lissodelphis peronii*, off the Pacific coast of South America. *Zeitsch. Säugetierk.* **56**, 284–295.

Visser, I. N., Fertl, D., and Pusser, L. T. (2004). Melantistic southern right-whale dolphins (*Lissodelphis peronii*) off Kaikoura, New Zealand, with records of other anomalously all-black cetaceans. *N. Z. J Mar. Fresh. Res.* **38**, 833–836.

Walker, W. A. (1975). Review of the live-capture fishery for smaller cetaceans taken in southern California waters for public display, 1966–73. *J. Fish. Res. Board Can.* **32**, 1197–1211.

Watson, L. (1981). “Sea Guide to Whales of the World.” London, Hutchinson & Co. Ltd, 302 p.

Yazdi, P. (2002). A possible hybrid between the dusky dolphin (*Lagenorhynchus obscurus*) and the southern right whale dolphin (*Lissodelphis peronii*). *Aquat. Mamm.* **28**(2), 211–217.

Right Whales
Eubalaena glacialis, E. japonica, and E. australis

ROBERT D. KENNEY

I. Characteristics and Taxonomy

A. Scientific and Common Names

Three species of right whales are currently recognized: North Atlantic right whale, *Eubalaena glacialis* (Müller, 1776); North Pacific right whale, *E. japonica* (Lacépède, 1818); and southern right whale, *E. australis* (Desmoulins, 1822). The generic name *Eubalaena* means “true whale;” the meanings of specific epithets are: *glacialis* = “of the ice,” *japonica* = “Japanese,” and *australis* = “southern.” Müller based his original description of *E. glacialis* on the “nördcaper” of Norwegian whalers. He did not specify a type locality; Eschricht and Reinhardt (1866) subsequently designated it as North Cape, Norway. Synonyms include *biscayensis* (Eschricht, 1860) and *nordcaper* (Lacépède, 1804). The type specimen of *E. australis* is a skeleton from Algoa Bay, Cape of Good Hope, South Africa in the Museum National d’Histoire Naturelle, Paris. Synonyms include *antarctica* (Lesson, 1828), *antipodarum* (Gray, 1843), and *temminckii* (Gray, 1864).

R

Lacépède's description of *E. japonica* was based upon an illustration by a Japanese artist; the type locality is Japan. A synonym is *sieboldii* (Gray, 1864) (Hershkovitz, 1966; Mead and Brownell, 2005).

Conventional wisdom holds that the common name "right whale" comes from English whalers, who designated this as the "right" (i.e., correct) whale to hunt because it occurred near shore, swam slowly enough to be caught from a small boat propelled by sails or oars, floated when dead, and yielded large amounts of valuable oil and BALEEN. Early writers, however (e.g. Eschricht and Reinhardt, 1866) considered "right" to mean "true" or "proper," meaning showing the characteristics typical of whales generally, as later formally recognized in the Latin generic name *Eubalaena.* Other common names in English include black right whale and black whale.

B. Systematics and Nomenclature

There has been disagreement on two questions of balaenid systematics and nomenclature—concerning the number of extant species of right whales and whether or not bowhead whales (*Balaena mysticetus*) and right whales are congeneric (see Reeves and Kenney, 2003 and Perrin and Reeves, 2004 for reviews). Northern and Southern Hemisphere right whales were long treated as distinct species (Cummings, 1985). Rice (1998) concluded that there was no evidence for consistent morphological differences and that only one globally distributed species should be recognized. Rosenbaum *et al*. (2000) showed clear, long-established mitochondrial DNA differences among right whale lineages in the North Atlantic, North Pacific, and Southern Hemisphere—concluding that three species should be recognized and that North Pacific and southern right whales are more closely related to one another than either is to North Atlantic right whales. Those results have been confirmed by both nuclear DNA markers (Gaines *et al*., 2005) and the genetics of whale lice on right whales (Kaliszewska *et al*., 2005). The conclusions have been accepted by the INTERNATIONAL WHALING COMMISSION'S scientific committee (IWC, 2001a) and broadly by marine mammalogists (Mead and Brownell, 2005), but not universally (Baker *et al*., 2003). The question is more a philosophical one, between phylogenetic and biological species concepts, but under either concept the two-species northern–southern classification is taxonomically invalid.

On the question of the correct generic name for right whales, Eschricht and Reinhardt (1866) published the first widely read, detailed comparison between bowheads and right whales, and maintained both species in the same genus. Rice (1998) reviewed the published comparisons and concluded that there was no scientific evidence from either morphology or genetics for recognizing the separate right whale genus *Eubalaena* (published by J. E. Gray; see Box 1), and that those differences that do exist are less than those between species of *Balaenoptera*. The consensus mitochondrial, nuclear, and combined phylogenetic trees (Gaines *et al*., 2005) appear to show little genetic divergence between bowheads and the three right whale species. Others (Schevill, 1986; Bannister *et al*., 1999; Rosenbaum *et al*., 2000) have argued that maintaining the generic-level separation was justified, in part, for reasons of nomenclatural stability. IWC (2001a), and Mead and Brownell (2005) have accepted that rationale and recognized the right whales as *Eubalaena* spp. That conclusion (although not the underlying justification) has been confirmed by a very recent study of balaenid systematics based on a detailed morphological analysis of all known species, both extant and fossil (Churchill, 2007). The results showed a crown Balaenidae containing two sister clades—one a monophyletic *Eubalaena* and the other containing *Balaena* and *Balaenella*.

BOX 1: Taxonomic Rules, J. E. Gray, and Right Whale Names

There is a set of very specific rules, the International Code of Zoological Nomenclature, for determining the correct scientific name to apply to any particular animal taxon. One important aspect of the Code is the rule of priority—when determining the valid name for any species (or genus or higher level category), the first published name applied should be used. For example, the original descriptions of all three right whale species included them in the genus *Balaena* (="whale"), a name published by Linnaeus in 1758. If biological evidence supports classifying right whales as a distinct genus from bowheads, the name *Eubalaena*, published by J. E. Gray in 1864, is the oldest name available applicable only to the right whales and therefore the valid name by the rule of priority.

John Edward Gray (1800–1875) was an English zoologist and an important figure in the history of cetacean taxonomy. He began his career at the British Museum at about age 15 as a volunteer insect collector, received a temporary appointment in 1824 to catalog reptiles, and was Keeper of Zoology from 1840 until his retirement only 2 months before his death 35 years later. In his years at the museum, he published well over 1000 papers, including half of the 200 catalogs issued by the museum during his time. *Eubalaena* is not the only cetacean name he coined; 15 or 16 of the currently accepted names of the 85–90 extant species and 40+ genera, 11 of the 14 family names (all except Eschrichtiidae, Kogiidae, and Lipotidae), and many of the subfamily names were authored by Gray. One might conclude that he was particularly knowledgeable about cetacean taxonomy. However, he worked at what was arguably the world's most influential museum of his day and apparently had a penchant for creating new species, genera, and higher taxa. He has been called one of the most notorious taxonomic "splitters" of all time. He also authored at least four other generic names for right whales, and in a single publication in 1871 he counted six genera and 14 species of right whales.

The rule of priority can be set aside under certain circumstances in order to maintain nomenclatural stability. If a taxonomic name is in common usage for a long period and then is discovered to be a junior synonym of an older published name, the International Committee on Zoological Nomenclature can be petitioned to suppress the senior synonym and conserve the junior synonym as the accepted name. For example, the binomial *Tursiops truncatus* (Montagu, 1821) for the common bottlenose dolphin has been conserved by suppression of the senior synonym *T. nesarnack* (Lacépède, 1804) (Rice, 1984, 1998). However, whether right whales and bowheads represent one or two genera is not simply a question of names, but of biological classification. The International Code of Zoological Nomenclature specifically "refrains from infringing upon taxonomic judgment, which must not be made subject to regulation or restraint" (Ride *et al*., 1985). Invoking the rule of stability in the case of the right whales' generic name is a misapplication of the Code, and rigorous application of the scientific method would suggest that the null hypothesis (i.e., there is no significant generic-level difference between bowhead and right whales) should stand until rejected by evidence. The study by Churchill (2007) now has provided the evidence to conclude that the three living right whale species do comprise a phylogenetic lineage distinct from the bowhead and are rightly classified into a separate genus. One must remember, however, that systematic classifications are scientific hypotheses, subject to revision after further study.

C. Description

Right whales have an extremely robust body form, bordering on rotund, with a thick blubber layer and the girth at times exceeding 60% of total body length (Omura *et al.*, 1969; Cummings, 1985; Reeves and Kenney, 2003; Fig. 1). The body is mostly black, sometimes with irregular white ventral patches. Some individuals may have a mottled appearance, and calves may sometimes be lighter colored. There is no dorsal fin. The pectoral flippers, which retain all five digits, are large, broad, and blunt. The flukes are very broad (up of 40% of body length), black on both dorsal and ventral surfaces, deeply notched, and smoothly tapered to the tips. Calves are 4.5–6 m long at birth; typical adults are 13–16 m. North Pacific right whales attain larger maximum sizes than the other species, up to 18 m and over 100 metric tons.

The head is relatively large, comprising about one-quarter to one-third of the total body length. The upper jaw is somewhat arched, and the margin of the lower lip forms a very pronounced curve. There are 200–270 baleen plates on each side of the upper jaw, and there is a gap between the two rows of plates at the anterior end of the upper jaw (Nemoto, 1970; Pivorunas, 1979). The baleen plates are relatively narrow and 2–2.8 m long, with very fine fringing hairs. The tongue is massive and solidly muscular.

The most conspicuous external characteristics of right whales are the callosities on the head (Payne and Dorsey, 1983). These are irregular patches of thickened, keratinized tissue, which are inhabited by dense populations of specialized amphipod crustaceans, known as cyamids or "whale lice" (see Box 2). At least three species of whale lice occur on right whales: *Cyamis gracilis*, *C. ovalis*, and *C. erraticus* (Rowntree, 1996; Kaliszewska *et al.*, 2005). In southern right whales the callosities are also inhabited by barnacles, *Tubicinella* sp. The callosities occur at the tip of the snout (called the "bonnet" by whalers), on the lower lips and chin, above the eyes, and in front of and behind the blowholes (Figs 1 and 2). The callosities are congenital and not caused externally, as their beginnings are present in fetuses and neonates, but the pattern is not fully developed and colonized by cyamids until the whale is at least several months old (Fig. 2). The callosity patterns are unique to individuals and are therefore extremely useful as a natural "tag," which allows repeated identification of individuals by photographs (Payne *et al.*, 1983; Kraus *et al.*, 1986).

BOX 2: Are Whale Lice Parasites?

Two species are said to be symbiotic when they live intimately associated with each other, with the exact nature of the relationship depending on the fitness costs and benefits incurred by each species (Townsend *et al.*, 2003). In the symbiosis involving right whales and cyamids, it can be assumed that the cyamid benefits from the relationship by having a place to live and a ready food supply. If the right whale also benefits, the association is defined as mutualism; if the whale receives neither benefits nor costs, the association is commensalism; and if the whale is harmed, the association is parasitism. Most sources refer to cyamids as parasites or ectoparasites. It is known that they do feed on the whale's skin (Schell *et al.*, 2000), however, there is scant evidence that their presence or feeding causes any harm to the whale. Leung (1976) concluded that "whale-lice cause certain damage to the whale skin when the young begin to maintain their livelihood, and the injury is a result of piercing the tissue in which they shelter for safety and for food," but did not actually show any harm to the whale. Similarly, while it is possible to construct various hypotheses for potential benefits provided to the whale by the cyamids, there is no evidence to test or confirm these theories. It therefore seems that the conservative course would be to consider cyamids as ectocommensals of right whales until convincing evidence demonstrating otherwise has been shown.

The closest relative of the right whale is the bowhead whale. Bowheads may be somewhat longer, are substantially stouter, have relatively larger heads (about 40% of body length) with a more arched appearance, have much longer baleen plates (up to 5.2 m long), and completely lack callosities.

D. Fossil Record and Evolution

Five fossil species of *Balaena* have been described from deposits of late Miocene, Pliocene, or Pleistocene age (2–10 million years old) from Europe and North America: *B. affinis*, *B. etrusca*, *B. montalionis*,

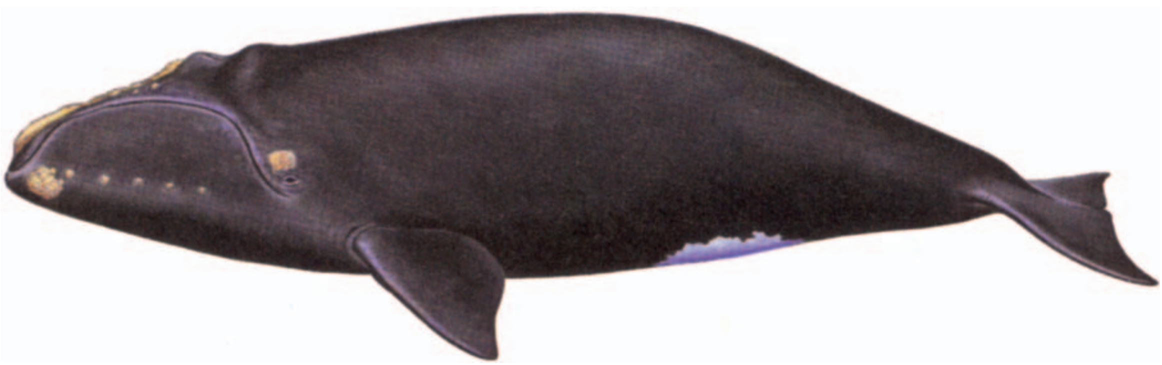

Figure 1 *The North Atlantic right whale (c. Brett Jarrett).*

Figure 2 *A mother–calf pair of North Atlantic right whales sighted off the coast of Florida on 9 January 1992. The mother, #1001 ("Fermata"), was the first animal included in the North Atlantic photoidentification catalog, from photographs taken in Cape Cod Bay by W. A. Watkins and W. E. Schevill in March 1978. This was her fifth known calf. A gray area on the calf's rostrum shows where the callosity will develop, and colonizing whale lice can be seen along the curved margin of its lips. "Fermata" was last seen in September of that same year in the Bay of Fundy, and is now presumed dead. Photograph by the author from Airship Shamu (courtesy of Sea World).*

B. primigenius, and *B. prisca* (Barnes and McLeod, 1984; McLeod *et al.*, 1993). The last of these is similar enough to modern bowheads (*B. mysticetus*) that it may, in fact, not be a separate species. There is then a long gap in the balaenid FOSSIL RECORD to *Morenocetus parvus*, the oldest known member of the family, found in early Miocene (23 million years old) deposits in South America. Molecular phylogenies generally agree that Balaenidae is the most primitive clade of extant mysticetes (Árnason *et al.*, 1992; Hatch *et al.*, 2006).

II. Distribution and Abundance

Right whales are found in the middle latitudes of both the Northern and the Southern Hemispheres, between approximately 20° and 60°S and N latitudes (Cummings, 1985; Reeves and Kenney, 2003; Fig. 3). There are three geographically isolated populations currently recognized as separate species: in the North Atlantic, North Pacific, and Southern Ocean. The populations are kept separated by Arctic ice and warm equatorial waters so that there is no interchange between populations, and apparently has not been for millions of years (Rosenbaum *et al.*, 2000; Gaines *et al.*, 2005; Kaliszewska *et al.*, 2005).

A. North Atlantic Right Whales

The historical range of North Atlantic right whales apparently extended as far south as Florida and northwestern Africa and as far north as Labrador, southern Greenland, Iceland, and Norway (Cummings, 1985; Reeves *et al.*, 2007). The traditional hypothesis has been that there were separate stocks with little interchange on the western and the eastern sides of the basin; however, analysis of some nineteenth century whaling specimens in European museums shows that they do not differ genetically from living western individuals (Rosenbaum *et al.*, 2000), and there have been one or two right whales seen in the eastern North Atlantic in recent years that were known individuals from the western stock (Jacobsen *et al.*, 2004). It is possible that the structure of a right whale population is that a particular ocean basin is inhabited by a single breeding population without long-term genetic isolation of stocks, but where return to traditional habitats learned from the mother (matrilineal habitat fidelity) maintains shorter-term separation between two or more subsets of the population.

The present range of western North Atlantic right whales, from Florida to Nova Scotia with very occasional occurrence beyond those limits, is much reduced from its historical extent (Winn *et al.*, 1986; Kenney *et al.*, 2001; Kraus and Rolland, 2007). The best estimate of present abundance is about 400 animals (NARWC, 2006). In the eastern North Atlantic, there have been only a handful of right whale sightings in the last few decades (reviewed in Reeves and Kenney, 2003). It is not known whether these represent a small remnant eastern stock or whether some or all of them are individuals from the known western population.

B. North Pacific Right Whales

The historical range in the North Pacific was similarly much more extensive than today. Right whales occurred from Japan and northern Mexico north to the Sea of Okhotsk, Bering Sea, and Gulf of Alaska (Scarff, 1986, 1991; Clapham *et al.*, 2004). Recent sightings are extremely rare, primarily in the Sea of Okhotsk (Brownell *et al.*, 2001) and eastern Bering Sea (Clapham *et al.*, 2004; Shelden *et al.*, 2005; Wade *et al.*, 2006). There are no reliable estimates of abundance, and there may be even fewer whales than in the North Atlantic. Wade *et al.* (2006) reported that 23 individuals had been identified so far in the southeastern Bering Sea. There are also insufficient genetic or resighting data to address whether there is support for the traditional separation into eastern and western stocks (Brownell *et al.*, 2001).

C. Southern Right Whales

Right whales are known from several areas of the Southern Ocean. Multiple stocks have been hypothesized, including Argentina/Brazil, South Africa, east Africa/Mozambique, western Australia, southeastern Australia, New Zealand, and Chile (Cummings, 1985; Best *et al.*, 2001; IWC, 2001b; Patenaude *et al.*, 2007). Additional stocks have been hypothesized for the central Indian Ocean, the Campbell and Auckland Islands in the southwestern Pacific, and Tristan da Cunha in the central South Atlantic. There have also been suggestions of even finer stock structuring, e.g., between Argentina and Brazil in the western South Atlantic or between Namibia and South Africa in the eastern South Atlantic. There is incomplete genetic isolation separation between stocks, especially between geographically adjacent stocks.

Right whale populations in Argentina, South Africa, and Australia are presently the largest and the best studied. The total abundance of southern right whales was estimated as of 1997 at 7571 animals, with the three well-studied stocks increasing at 7–8% annually (IWC, 2001b). Given that there were no estimates available for some stocks, and a population increasing at 7% doubles every 10 years, total abundance could currently exceed 15,000 animals.

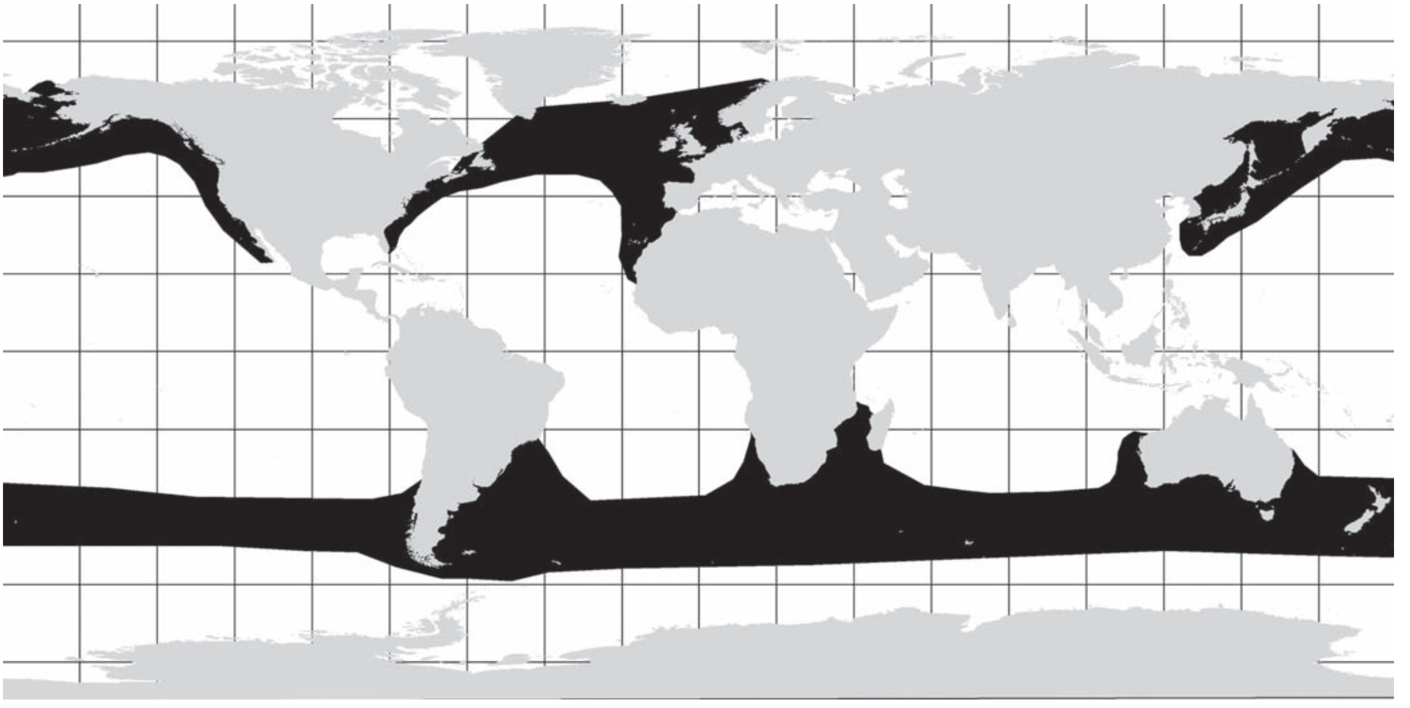

Figure 3 *Worldwide range of right whales* (Eubalaena glacialis, E. japonica, and E. australis). *Much of what is shown here is relatively speculative based on sparse historical records of whaling catches and the available recent sightings. Most recent data come from areas relatively nearshore, with few or no data for the pelagic areas between the known coastal habitats.*

III. Ecology

A. Diet

Right whales feed entirely on zooplankton, especially on large calanoid copepods (crustaceans approximately the size of a grain of rice) (Nemoto, 1970; Cummings, 1985; Baumgartner *et al*., 2007). At times they also feed on smaller copepods, krill (larger shrimp-like crustaceans), pteropods (tiny planktonic snails), or the planktonic larval stages of BARNACLES and other crustaceans. The details of their diet likely differ between regions, e.g., it is likely that krill comprise a higher proportion of the DIET in southern right whales. It is also likely that right whales can be somewhat opportunistic regarding prey species, FEEDING on any prey of a size that can be filtered efficiently by the baleen, which does not swim strongly enough to escape, and which is concentrated into sufficiently dense patches to trigger feeding behavior. For example, there have been observations of North Atlantic right whales in the Bay of Fundy feeding on aggregations of salps.

B. Habitat

R

Right whales migrate annually between high-latitude feeding grounds and low-latitude calving and breeding grounds (Cummings, 1985; Reeves and Kenney, 2003). There are substantial differences in the locations where most research has been conducted between the Northern and the Southern Hemispheres; therefore, there is often a lack of directly comparable information for different populations.

Feeding takes place in spring, summer, and fall in higher-latitude feeding grounds, where ocean temperatures are cooler and overall biological productivity is much higher. The best known right whale feeding grounds are in the western North Atlantic (Winn *et al*., 1986). These habitats are in nearshore and shelf waters, where some combination of bottom topography, water column structure and stratification, and currents acts to physically aggregate zooplankton into extremely dense concentrations (Kenney and Wishner, 1995; Baumgartner *et al*., 2007). The densest zooplankton concentrations measured in the North Atlantic were found by sampling near right whales. There are probably also offshore feeding grounds, in locations not yet known, based on historical whaling records and on the fact that some known whales are often missing from the known habitats for months or years at a time. There must also have been other feeding grounds in the past, when the range of North Atlantic right whales was more extensive.

Feeding grounds for the other species of right whales are much more poorly known. In the North Pacific, based on historical whaling records and the few recent sightings, the principal feeding grounds were most likely in the Sea of Okhotsk, central and eastern Bering Sea, and Gulf of Alaska (Clapham *et al*., 2004). All of these feeding areas are much more pelagic or offshore than the well-studied North Atlantic habitats. In the Southern Ocean, right whale feeding grounds also appear to be mostly in offshore, pelagic regions. Southern right whale feeding grounds are likely to be found associated with areas of extremely high productivity; limited sighting data available show most whales in the regions between the subtropical and Antarctic convergences (IWC, 2001b).

Calving in right whales occurs during winter. Where the calving grounds are known, they are in shallow coastal regions or bays. The only known current calving ground in the western North Atlantic is in coastal waters near Georgia and northeastern Florida (Winn *et al*., 1986; Kraus and Rolland, 2007). In that calving ground, right whales show a clear preference for waters in a relatively narrow depth and temperature range—13–19 m and 13–16°C (Keller *et al*., 2006). It has been speculated that other coastal areas, including Delaware Bay and Cape Cod Bay, may have been calving grounds before the population was depleted by whaling (Reeves *et al*., 1978). It has been noted, for example, that Cape Cod is similar topographically to Peninsula Valdés in Argentina and is located at about the same latitude (Payne, 1995). In the eastern North Atlantic, Cintra Bay in northwestern Africa is believed to have been a historical right whale calving ground (Reeves, 2001). It is possible that areas near the Azores and Madeira, as well as the Bay of Biscay, were also calving grounds. In the North Pacific, no right whale calving grounds have ever been discovered. In the Southern Hemisphere, shallow coastal waters and bays in many areas are currently known to be southern right whale calving areas or hypothesized to have been calving grounds historically, including Argentina, Brazil, Falkland Islands, Tristan de Cunha, Namibia, South Africa, Mozambique, Kerguelen Island, Australia, New Zealand, Auckland Islands, and Chile (IWC, 2001b).

Breeding or mating also occurs during the winter. Because of the 3-year female reproductive cycle, breeding can take place geographically distant from calving (Knowlton *et al*., 1994; Kraus *et al*., 2001, 2007). In the western North Atlantic, the location of the majority of the population during the winter is not known, and adult males are nearly absent from the calving ground (Brown *et al*., 2001). Breeding must occur wherever the adult population spends the winter, but it is not known whether there are specific, distinct winter habitats or whether the whales are broadly dispersed across wide regions of the North Atlantic.

In southern right whales, at least some mating behavior occurs in or near the calving grounds, although there may be small-scale segregation of breeding adults from females with calves (Payne, 1995). In Argentina, because females are observed infrequently in these breeding groups in the year prior to calving, it is possible either that the mating which actually leads to conception occurs in some other, unknown habitat or that receptive females only visit coastal waters for very brief periods.

Circumstantial evidence suggests that learning is an important component of habitat selection in right whales (Malik *et al*., 1999; Frasier *et al*., 2007). Calves apparently learn the locations of feeding grounds by accompanying their mothers during the first year of life and then return to those same habitats for the rest of their lives. This pattern of matrilineal habitat fidelity seems to be common in migratory whale species; resighting and genetic data demonstrate that it is responsible for population structuring in North Atlantic humpback whales (Clapham, 1996).

Figure 4 *A "skimming" North Atlantic right whale feeding on zooplankton near the surface. The rough black areas of the "bonnet" are the whale's skin, whereas the white areas are comprised of whale lice. Photograph by William Watkins.*

Figure 5 *Aerial view of a feeding North Atlantic right whale in the Gulf of Maine. Photograph by Peter Duley (courtesy of Northeast Fisheries Science Center).*

C. Predators

Potential predators of right whales include killer whales (*Orcinus orca*) and large sharks, and it is more likely that any predators would attack calves or juveniles. There have been few direct observations of killer whale attacks on right whales, and Mehta *et al*. (2007) concluded that the spacing of tooth rakes on the flukes of North Atlantic right whales was inconsistent with killer whales and more likely from smaller animals such as false killer whales. Reeves *et al.* (2006) reviewed the arguments for and against the hypothesis that migration in large baleen whales to low-latitude calving grounds evolved in response to killer predation on calves in higher latitudes. Predation by sharks similarly may have been one of the selective pressures leading to the evolution of right whales' use of cooler waters in very shallow coastal habitats for calving, since sharks prefer warmer waters and at least white sharks are known to often attack their prey from below (Klimley, 1994).

IV. Behavior and Physiology

Right whales are observed to frequently perform highly energetic behaviors at or above the surface of the water. These aerial behaviors include BREACHING (jumping partly or almost completely above the surface), LOBTAILING (violently slapping the surface with the flukes), and flippering (slapping the surface with a pectoral flipper). The functions of these behaviors are not known (Whitehead, 1985). They all produce very loud sounds, which may sometimes have a communicative and/or aggressive function. Right whales in Argentina and South Africa have been observed to lift their flukes above the surface, where the flukes act like a sail and allow the wind to push the whale horizontally (Payne, 1995). This "tail-sailing" behavior has not been reported in other habitats.

Right whales are "skimmers" (Nemoto, 1970; Pivorunas, 1979; Baumgartner *et al*., 2007; Figs 4 and 5). They feed by swimming forward with the mouth agape. Water flows into the opening at the front, and out through the baleen, straining their prey from the water. Feeding can occur at or just below the surface, where it can be observed easily, or at depth. At times, right whales apparently feed very close to the bottom, because they are observed to surface at the end of an extended dive with mud on the head. Typical feeding dives last for 10–20 min (Winn *et al*., 1995; Baumgartner *et al*., 2007).

Courtship in right whales often involves aggregations of whales termed "surface-active groups" (Donnelly, 1967; Payne and Dorsey, 1983; Kraus and Hatch, 2001; Kraus *et al*., 2007). These are usually centered around a single female and may involve large numbers of males; groups of more than 20 animals have been observed. Often the female is belly-up at the surface, whereas the males stroke her with their flippers or attempt to push her under. There is evidence that the female initiates the interaction by vocalizing. In the North Atlantic, surface-active groups are observed in all seasons, even though calving is highly synchronous and restricted to winter. Therefore much of the observed activity does not lead to fertilization and may serve a social function. The female may simply use the interactions to assess male quality for later mating. The interactions between males in the group generally involve very little of the violence and aggressiveness seen in humpback whales. One theory is that right whales engage in sperm competition (Brownell and Ralls, 1986), where the volume of semen is important in displacing the sperm of other males mating with the same female. Right whale testes may be the largest of any animal, at 2 m long and 500 kg each.

Right whale vocalizations are primarily low-frequency moans, groans, belches, and pulses (Cummings, 1985; Thomson and Richardson, 1995; Parks and Clark, 2007). Most acoustic energy produced is below 500 Hz, with some sounds up to 1500–2000 Hz. The functions of these sounds are not well understood. Hypothesized functions include maintenance of contact between separated individuals, threats or other aggressive signals, and social signals, including their possible involvement in surface-active group behavior.

V. Life History

Information on the age at maturity in right whales is not available from whaling data as it is for other whale species taken by twentieth century industrial whaling. The information must be derived from photoidentification studies that track known individuals from birth. The youngest mature female in the western North Atlantic was 4 at maturity and 5 at first calving (Knowlton *et al*., 1994). From both North Atlantic and Southern Hemisphere data, the average age at first calving is closer to 9 or 10 years (Best *et al*., 2001; Cooke *et al*., 2001; Kraus *et al*., 2001, 2007). Age at maturity is not yet known for males, as there is no external method for identifying paternity. Genetic studies may be better able to identify fathers of calves and begin to provide data for age of maturity in males (Frasier *et al*., 2007).

Growth is relatively rapid from birth to weaning at about age 1, by which time the calf approximately doubles in body length to 9–11 m (Brown *et al*., 2001). Available data on growth after age 1 are not entirely consistent. For example, in the North Atlantic, growth also can be relatively rapid in year 2, by which time total length may reach 12–13 m, and thereafter is much slower. However, South African right whales apparently grow little between ages 1 and 4 (Best and Schell, 1996). Growth after age 1 is likely to be dependent on feeding success. The western North Atlantic female that matured at age 4 remained with her mother well into her second year, possibly growing much faster than the typical rate by nursing for a longer period. Right whales are believed to reach sexual maturity at body lengths of 13–16 m.

There are very few data on longevity. Aging baleen whales is an extremely difficult problem. Japanese attempts to use the wax plug found in the auditory canal from the North Pacific right whales taken for research in 1956–1968 were not successful (Omura *et al*., 1969). The oldest known right whale to date was in the North Atlantic (Kraus and Rolland, 2007). A mother–calf pair near Fort Lauderdale, Florida, was pursued and shot at by fishermen on March 24, 1935. The calf was killed, but the mother escaped. A photograph of her published in the New York *Herald Tribune* at the time was later matched to photographs taken in Cape Cod Bay (by pioneering right whale researcher William E. Schevill) in April 1959. She was also photographed in 1980, 1985, and 1992. On August 13, 1995 she was photographed offshore, with a large, gaping wound on the head apparently caused by a ship strike. It is unlikely she could have survived that injury. Assuming she was at least 10 years old in 1935, she would have been at least 70 years old in 1995, and may have been substantially older. Research on bowhead whales suggests that they live substantially longer (George *et al*., 1999).

The typical reproductive cycle in mature females is 3 years between births (Kraus *et al*., 2007). The gestation period is approximately 1 year (Best, 1994), and weaning occurs at about 1 year of age (Hamilton *et al*., 1995). The female then takes a third year to replenish her energy stores, although it is possible for a female who has been especially successful at feeding to skip the resting year and calve after only a 2-year interval (one case observed in the North Atlantic, and at least one in Argentina). An alternative explanation for an observed 2-year interval is calf mortality soon after birth and subsequent avoidance by the mother of the high energetic demands of lactation; documented twice in Australia. This presumes that the mother–calf pair is sighted during the brief interval between birth and death of the calf. Otherwise what would be observed is an apparent 5-year interval, of which 25 were recorded in the North Atlantic between 1980 and 1998 (Kraus *et al*., 2001). Calving has been observed very rarely; in other instances, known females have been sighted in the calving ground both before and after the calf was born.

VI. Interactions with Humans

A. Whaling

North Atlantic right whales were the first whales to be harvested commercially by the Basques along the Atlantic coast of western Europe as early as the eleventh century (Aguilar, 1986; Reeves and Smith, 2006; Reeves *et al*., 2007). The whales were killed primarily for oil, which was sold across Europe, as the technology of the time did not permit preservation and widespread transportation of meat. As populations nearest shore were depleted, Basque whaling expanded to more distant waters, reaching eastern Canada by 1530. Basque whaling in Canada was centered in the Strait of Belle Isle between Labrador and Newfoundland and took 300–500 whales per year at its peak. Catches were declining by 1610–1620 and ended in 1713, by which time they had taken as many as 40,000 whales. Recent evidence from genetic sampling of whale bones from that era is that nearly all of the whales landed by the Basques in the Strait of Belle Isle were bowheads (Frasier *et al*., 2007). It is not clear whether or not Basque whaling beyond the Bay of Biscay impacted North Atlantic right whales, and if it did, where that occurred (Reeves *et al*., 2007).

Local shore-based right WHALING in North America began soon after the establishment of permanent colonies during the early seventeenth century (reviewed in Reeves *et al*., 2007). Peak catches were in the early eighteenth century (e.g., 86 in Nantucket, Massachusetts in 1726; 111 in Long Island, New York in 1707), and right whales in western North Atlantic waters may have been effectively extinct as a basis for a commercial fishery by the middle of the eighteenth century. The familiar Yankee whaling industry soon developed as a high-seas fishery targeting sperm whales; however, the whalers continued to opportunistically take any right whales encountered. Yankee whaling (including ships from several European nations) spread to the South Atlantic by 1775, into the South Pacific in 1789, and into the North Pacific by 1820. The Japanese had also begun their own shore-based fishery, which took some coastal migrant right whales, in the late sixteenth century.

The traditional high-seas Yankee whale fishery finally ended in the early twentieth century, when it was replaced by modern industrial whaling. Total right whale catches (although records are not complete) were at least 38,000 in the South Atlantic, 39,000 in the South Pacific, 1300 in the Indian Ocean, 15,000 in the North Pacific, and at least a few hundred in the North Atlantic. Some shore-based whaling in the eastern United States persisted into the 1920s, but it was minor, with only 8 taken in Long Island after 1900. In the North Atlantic, the last episode of intensive right whaling was in the late nineteenth and the early twentieth century off Norway, Iceland, and Scotland, and the last right whales taken were at Madeira, 1 in 1952 and 2 in 1967. All right whale populations worldwide were protected from commercial whaling in the 1930s by the first International Convention for the Regulation of Whaling. However, the Japanese took 23 North Pacific right whales in the 1940s and 13 more under special scientific research permits between 1956 and 1968, some illegal takes of right whales along the coast of Brazil were reported in the 1950s, there was a significant amount of illegal Soviet taking of right whales in the North Pacific and Southern Ocean into the 1960s (Brownell *et al*., 2001; Clapham *et al*., 2004), and it is possible that there has been illegal right whaling elsewhere in the world.

B. Ship Strikes

The most significant human-related source of mortality at present in western North Atlantic right whales is collision with large ships (Knowlton and Kraus, 2001; Kraus *et al*., 2005; Knowlton and Brown, 2007; Waring *et al*., 2007). Between 1970 and 2005, 24 right whales were known to have been killed by ships, and 3 others were last seen with serious and probably fatal injuries. There are probably additional mortalities that are never discovered because the carcasses are lost at sea. Ship collisions may be less of a mortality factor in other oceans, where right whales spend less time in nearshore habitats or where the level of industrial development is lower, although at least three probable ship-strike mortalities have been recorded in recent years off the Brazilian coast (Greig *et al*., 2001).

C. Entanglements

The second most important human-related mortality factor in western North Atlantic right whales is incidental capture in commercial fishing gear (Johnson, 2005; Johnson *et al*., 2007; Waring *et al*., 2007). The gear involved is fixed gear (set in one location rather than towed behind a vessel), including sink gill nets, drift nets, and a variety of pot and trap fisheries. In 1970–2005, 6 right whales are known to have been killed by ENTANGLEMENTS and 13 others were seriously injured but disappeared and probably died. It is not always known whether entanglements occur in actively fishing gear or in gear that has been lost, damaged, or moved by storms or vessels (often termed "ghost" gear). There are few data on entanglement mortalities in other populations.

Entanglement seems to be very common in right whales. Many entanglements involve the tail, where the leading edges of the flukes begin, and leave characteristic scars afterward. Over 75% of whales in the western North Atlantic carry such scars, and some individuals have been entangled two or three times (Hamilton *et al*., 2007). Entanglements are therefore often not lethal. They may be more dangerous in younger animals, who might grow into a relatively benign entanglement until it becomes life-threatening (Moore *et al*., 2007).

D. Climate Change

Right whales are feeding specialists, with a relatively narrow range of acceptable prey characteristics and requiring prey to be concentrated in exceptionally high densities. The development of right whale feeding grounds is closely linked to physical phenomena such as water structure, currents, and temperature (Kenney and Wishner, 1995; Baumgartner *et al*., 2007). This may make right whales more sensitive than other species to impacts from global climate change, with detectable environmentally induced variability in reproduction in recent years (Greene and Pershing, 2004; Leaper *et al*., 2006; Kenney, 2007). Any possible impacts may be increased because of matrilineal fidelity to their feeding grounds, and possibly a relatively low ability to locate new feeding grounds when conditions change.

E. Other Human Impacts

There are a number of other potential human impacts on right whales (reviewed by Katona and Kraus, 1999; Reeves and Kenney, 2003; Kraus and Rolland, 2007).

1. Habitat loss due to high levels of human activity is mentioned frequently as a possible impact. Right whales no longer occur in Delaware Bay, eastern United States; Table Bay, South Africa; Wellington Harbor, New Zealand; or Derwent River, Tasmania. However, a plausible alternative explanation is that they were extirpated by whaling and have never reoccupied the habitat due to matrilineal habitat fidelity.
2. Pollution is another potential impact that is mentioned frequently but where evidence is sparse. Oil spills may be a bigger threat to right whales than to other baleen whales because their very fine baleen might be fouled more easily. Blubber samples show a presence of toxic contaminants, but at lower levels than in cetaceans that feed at higher trophic levels (Woodley *et al.*, 1991; Weisbrod *et al*., 2000). A recent concern is that some contaminants may act as hormone mimics, affecting reproduction, or as immune system suppressants. They may be exposed via the food chain to naturally occurring biotoxins produced by phytoplankton, such as "red-tide" dinoflagellates (Durbin *et al.*, 2002).
3. Man-made noise may have the potential for interfering with acoustic communication, particularly since the major noise source, shipping, is also concentrated in the lower frequencies (Parks and Clark, 2007).
4. Effects of intensive commercial fisheries may alter ecosystem structure, increasing the abundance of other species that feed on zooplankton, particularly small fishes with lower economic value than the larger species harvested by FISHERIES.
5. The long-term effects of extreme population depletion by whaling might include reduced genetic diversity and associated health and reproductive problems (Frasier *et al*., 2007).

See Also the Following Articles

Bowhead Whale ■ Callosities ■ Filter Feeding ■ Species ■ Whale Lice ■ Baleen ■ Mysticetes

References

Aguilar, A. (1986). A review of old Basque whaling and its effect on the right whales (*Eubalaena glacialis*) of the North Atlantic. *Rep. Int. Whal. Comm., Spec. Iss.* **10**, 191–199.

Árnason, Ú., Grétarsdóttir, S., and Widegren, B. (1992). Mysticete (baleen whale) relationships based upon the sequence of the common cetacean DNA satellite. *Mol. Biol. Evol.* **9**, 1018–1028.

Baker, R. J., *et al*. (2003). Revised checklist of North American mammals north of Mexico, 2003. *Mus. Texas Tech Univ. Occas. Pap.* **229**, 1–23.

Bannister, J. L., Pastene, L. A., and Burnell, S. R. (1999). First record of movement of a southern right whale (*Eubalaena australis*) between warm water breeding grounds and the Antarctic Ocean, south of 60°S. *Mar. Mamm. Sci.* **15**, 1337–1342.

Barnes, L. G., and McLeod, S. A. (1984). The fossil record and phyletic relationships of gray whales. *In* "The Gray Whale, *Eschrichtius robustus*" (M. L. Jones, S. L. Swartz, and S. Leatherwood, eds), pp. 3–32. Academic Press, Orlando, FL.

Baumgartner, M. F., Mayo, C. A., and Kenney, R. D. (2007). Enormous carnivores, microscopic food, and a restaurant that's hard to find. *In*

"The Urban Whale: North Atlantic Right Whales at the Crossroads" (S. D. Kraus and R. M. Rolland, eds), pp. 138–171. Harvard University Press, Cambridge, MA.

Best, P. B. (1994). Seasonality of reproduction and the length of gestation in southern right whales *Eubalaena australis*. *J. Zool.* **232**, 175–189.

Best, P. B., and Schell, D. M. (1996). Stable isotopes in southern right whales (*Eubalaena australis*) baleen as indicators of seasonal movements, feeding and growth. *Mar. Biol.* **124**, 483–494.

Best, P. B., Brandão, A., and Butterworth, D. S. (2001). Demographic parameters of southern right whales off South Africa. *J. Cetacean Res. Manag., Spec. Iss.* **2**, 161–169.

Brown, M. W., *et al*. (2001). Sighting heterogeneity of right whales in the western North Atlantic: 1980–1992. *J. Cetacean Res. Manag., Spec. Iss.* **2**, 245–250.

Brownell, R. L., Jr., and Ralls, K. (1986). Potential for sperm competition in baleen whales. *Rep. Int. Whal. Comm., Spec. Iss.* **8**, 97–112.

Brownell, R. L., Jr., Clapham, P. J., Miyashita, T., and Kasuya, T. (2001). Conservation status of North Pacific right whales. *J. Cetacean Res. Manag., Spec. Iss.* **2**, 269–286.

Churchill, M. M. (2007). The systematics and biogeography of the Balaenidae (Cetacea: Mysticeti). M.S. Thesis, San Diego State University, San Diego, CA.

Clapham, P. J. (1996). The social and reproductive biology of humpback whales: An ecological perspective. *Mamm. Rev.* **26**, 27–49.

Clapham, P. J., Good, C., Quinn, S. E., Reeves, R. R., Scarff, J. E., and Brownell, R. L., Jr. (2004). Distribution of North Pacific right whales (*Eubalaena japonica*) as shown by 19th and 20th century whaling catch and sighting records. *J. Cetacean Res. Manag.* **6**, 1–6.

Cooke, J., Rowntree, V. J., and Payne, R. (2001). Estimates of demographic parameters for southern right whales (*Eubalaena australis*) observed off Peninsula Valdés, Argentina. *J. Cetacean Res. Manag., Spec. Iss.* **2**, 125–132.

Cummings, W. C. (1985). Right whales *Eubalaena glacialis* (Müller, 1776) and *Eubalaena australis* (Desmoulins, 1822). *In* "Handbook of Marine Mammals" (S. H. Ridgway, and R. Harrison, eds), Vol. 3, pp. 275–304. Academic Press, San Diego, CA.

Donnelly, B. G. (1967). Observations on the mating behaviour of the southern right whale *Eubalaena australis*. *S. Afr. J. Sci.* **63**, 176–181.

Durbin, E., Teegarden, G., Campbell, R., Cembella, A., Baumgartner, M. F., and Mate, B. R. (2002). North Atlantic right whales, *Eubalaena glacialis*, exposed to paralytic shellfish poisoning (PSP) toxins via a zooplankton vector, *Calanus finmarchicus*. *Harmful Algae* **1**, 243–251.

Eschricht, D. F., and Reinhardt, J. (1866). On the Greenland right whale (*Balaena mysticetus* Linn.); with especial reference to its geographical distribution and migrations in times past and present, and to its external and internal characteristics. *In* "Recent Memoirs on the Cetacea by Professors Eschricht, Reinhardt, and Lilljeborg." (W. H. Flower, ed.), pp. 1–150 and plates 1–6. Robert Hardwicke, London. [translated from the 1861 Danish original publication by J. Reinhardt].

Frasier, T. R., McLeod, B. A., Gillett, R. M., Brown, M. W., and White, B. N. (2007). Right whales past and present as revealed by their genes. *In* "The Urban Whale: North Atlantic Right Whales at the Crossroads" (S. D. Kraus and R. M. Rolland, eds), pp. 200–231. Harvard University Press, Cambridge, MA.

Gaines, C. A., Hare, M. P., Beck, S. E., and Rosenbaum, H. C. (2005). Nuclear markers confirm taxonomic status and relationships among highly endangered and closely related right whale species. *Proc R. Soc. B* **272**, 533–542.

George, J. C., Bada, J., Zeh, J., Scott, L., Brown, S. E., O'Hara, T., and Suydam, R. (1999). Age and growth estimates of bowhead whales (*Balaena mysticetus*) via aspartic acid racemization. *Can. J. Zool.* **77**, 571–580.

Greene, C. H., and Pershing, A. J. (2004). Climate and the conservation biology of North Atlantic right whales: The right whale at the wrong time? *Front. Ecol. Environ.* **2**, 29–34.

Greig, A. B., Secchi, E. R., Zerbini, A. N., and Dalla Rosa, L. (2001). Stranding events of southern right whales, *Eubalaena australis*, in southern Brazil. *J. Cetacean Res. Manag., Spec. Iss.* **2**, 157–160.

Hamilton, P. K., Marx, M. K., and Kraus, S. D. (1995). Weaning in North Atlantic right whales. *Mar. Mamm. Sci.* **11**, 386–390.

Hamilton, P. K., Knowlton, A. R., and Marx, M. K. (2007). Right whales tell their own stories: The photoidentification catalog. *In* "The Urban Whale: North Atlantic Right Whales at the Crossroads" (S. D. Kraus and R. M. Rolland, eds), pp. 75–104. Harvard University Press, Cambridge, MA.

Hatch, L. T., Dopman, E. B., and Harrison, R. G. (2006). Phylogenetic relationships among the baleen whales based on maternally and paternally inherited characters. *Mol. Phylogenet. Evol.* **41**, 12–27.

Hershkovitz, P. (1966). "Catalogue of Living Whales." U. S. National Museum, Washington, DC, Bulletin 246.

IWC (International Whaling Commission) (2001a). Annex U. Report of the working group on nomenclature. *J. Cetacean Res. Manag.* **3**(Supplement), 363–367.

IWC (2001b). Report of the workshop on the comprehensive assessment of right whales: A worldwide comparison. *J. Cetacean Res. Manag., Spec. Iss.* **2**, 1–60.

Jacobsen, K.-O., Marx, M., and Øien, N. (2004). Two-way trans-Atlantic migration of a North Atlantic right whale (*Eubalaena glacialis*). *Mar. Mamm. Sci.* **20**, 161–166.

Johnson, A. J., Kraus, S. D., Kenney, J. F., and Mayo, C. A. (2007). The entangled lives of right whales and fishermen: Can they coexist? *In* "The Urban Whale: North Atlantic Right Whales at the Crossroads" (S. D. Kraus and R. M. Rolland, eds), pp. 380–408. Harvard University Press, Cambridge, MA.

Johnson, T. (2005). "Entanglements: The Intertwined Fates of Whales and Fishermen." University Press of Florida, Gainesville, FL.

Kaliszewska, Z. A., *et al*. (2005). Population histories of right whales (Cetacea: *Eubalaena*) inferred from mitochondrial sequence diversities and divergences of their whale lice (Amphipoda: *Cyamus*). *Mol. Ecol.* **14**, 3439–3456.

Katona, S. K., and Kraus, S. D. (1999). Efforts to conserve the North Atlantic right whale. *In* "Conservation and Management of Marine Mammals" (J. R. Twiss and R. R. Reeves, eds), pp. 311–331. Smithsonian Institution Press, Washington, DC.

Keller, C. A., Ward-Geiger, L. I., Brooks, W. B., Slay, C. K., Taylor, C. R., and Zoodsma, B. J. (2006). North Atlantic right whale distribution in relation to sea surface temperature in the southeastern United States calving grounds. *Mar. Mamm. Sci.* **22**, 426–445.

Kenney, R. D. (2007). Right whales and climate change: Facing the prospect of a greenhouse future. *In* "The Urban Whale: North Atlantic Right Whales at the Crossroads" (S. D. Kraus and R. M. Rolland, eds), pp. 436–459. Harvard University Press, Cambridge, MA.

Kenney, R. D., and Wishner, K. F. (eds.) (1995). The South Channel Ocean Productivity Experiment: SCOPEX (special journal issue including ten papers). *Cont. Shelf Res.* **15**, 373–611.

Kenney, R. D., Mayo, C. A., and Winn, H. E. (2001). Migration and foraging strategies at varying spatial scales in western North Atlantic right whales: A review of hypotheses. *J. Cetacean Res. Manag., Spec. Iss.* **2**, 251–260.

Klimley, A. P. (1994). The predatory behavior of the white shark. *Am. Sci.* **82**, 122–133.

Knowlton, A. R., and Brown, M. W. (2007). Running the gauntlet: Right whales and vessel strikes. *In* "The Urban Whale: North Atlantic Right Whales at the Crossroads" (S. D. Kraus and R. M. Rolland, eds), pp. 409–435. Harvard University Press, Cambridge, MA.

Knowlton, A. R., Kraus, S. D., and Kenney, R. D. (1994). Reproduction in North Atlantic right whales (*Eubalaena glacialis*). *Can. J. Zool.* **72**, 1297–1305.

Kraus, S. D., and Hatch, J. J. (2001). Mating strategies in the North Atlantic right whale (*Eubalaena glacialis*). *J. Cetacean Res. Manag., Spec. Iss.* **2**, 237–244.

Kraus, S. D., and Rolland, R. M. (2007). Right whales in the urban ocean. *In* "The Urban Whale: North Atlantic Right Whales at the

Crossroads" (S. D. Kraus and R. M. Rolland, eds), pp. 1–38. Harvard University Press, Cambridge, MA.

Kraus, S. D., Moore, K. E., Price, C. A., Crone, M. J., Watkins, W. A., Winn, H. E., and Prescott, J. H. (1986). The use of photographs to identify individual North Atlantic right whales (*Eubalaena glacialis*). *Rep. Int. Whal. Commn., Spec. Iss.* **10**, 145–151.

Kraus, S. D., Hamilton, P. K., Kenney, R. D., Knowlton, A. R., and Slay, C. K. (2001). Reproductive parameters of the North Atlantic right whale. *J. Cetacean Res. Manag., Spec. Iss.* **2**, 231–236.

Kraus, S. D., *et al*. (2005). North Atlantic right whales in crisis. *Science* **309**, 561–562.

Kraus, S. D., Pace, R. M., III, and Frasier, T. R. (2007). High investment, low return: The strange case of reproduction in *Eubalaena glacialis*. *In* "The Urban Whale: North Atlantic Right Whales at the Crossroads" (S. D. Kraus and R. M. Rolland, eds), pp. 172–199. Harvard University Press, Cambridge, MA.

Leaper, R., Cooke, J., Trathan, P., Reid, K., Rowntree, V., and Payne, R. (2006). Global climate drives southern right whale (*Eubalaena australis*) population dynamics. *Biol. Lett.* **2**, 289–292.

Leung, Y. M. (1976). Life cycle of *Cyamus scammoni* (Amphipoda: Cyamidae), ectoparasite of gray whale, with a remark on the associated species. *Sci. Rep. Whales Res. Inst.* **28**, 153–160.

Malik, S., Brown, M. W., Kraus, S. D., Knowlton, A. R., Hamilton, P. K., and White, B. N. (1999). Assessment of mitochondrial DNA structuring and nursery use in the North Atlantic right whale (*Eubalaena glacialis*). *Can. J. Zool.* **77**, 1–6.

Mead, J. G., and Brownell, R. L., Jr. (2005). Order Cetacea. *In* "Mammal Species of the World, A Taxonomic and Geographic Reference, 3rd edition" (D. E. Wilson and D. M. Reeder, eds), Vol. 1, pp. 723–743. Johns Hopkins University Press, Baltimore, MD.

Mehta, A. V., *et al*. (2007). Baleen whales are not important as prey for killer whales *Orcinus orca* in high latitude regions. *Mar. Ecol. Prog. Ser.* **348**, 297–307.

McLeod, S. A., Whitmore, F. C., Jr., and Barnes, L. G. (1993). Evolutionary relationships and classification. *In* "The Bowhead Whale" (J. J. Burns, J. J. Montague, and C. J. Cowles, eds), pp. 45–70. Society for Marine Mammalogy, Lawrence, KS, Special Publication No. 2.

Moore, M. J., McLellan, W. A., Doust, P.-Y., Bonde, R. K., and Knowlton, A. R. (2007). Right whale mortality: A message from the dead to the living. *In* "The Urban Whale: North Atlantic Right Whales at the Crossroads" (S. D. Kraus and R. M. Rolland, eds), pp. 358–379. Harvard University Press, Cambridge, MA.

NARWC (North Atlantic Right Whale Consortium). (2006). "North Atlantic right whale report card: November 2005–October 2006." North Atlantic Right Whale Consortium, Boston, MA. http://www.rightwhaleweb.org/papers/pdf/NARWC_Report_Card2006.pdf

Nemoto, T. (1970). Feeding patterns of baleen whales in the ocean. *In* "Marine Food Chains" (J. H. Steele, ed.), pp. 241–252. University of California Press, Berkeley, CA.

Omura, H., Ohsumi, S., Nemoto, T., Nasu, K., and Kasuya, T. (1969). Black right whales in the North Pacific. *Sci. Rep. Whales Res. Inst.* **21**, 1–96.

Parks, S. E., and Clark, C. W. (2007). Acoustic communication: Social sounds and the potential impacts of noise. *In* "The Urban Whale: North Atlantic Right Whales at the Crossroads" (S. D. Kraus, and R. M. Rolland, eds), pp. 310–332. Harvard University Press, Cambridge, MA.

Patenaude, N. J., *et al*. (2007). Mitochondrial DNA diversity and population structure among southern right whales (*Eubalaena australis*). *J. Hered.* **98**, 147–157.

Payne, R. (1995). "Among Whales." Dell Publishing, New York.

Payne, R., and Dorsey, E. M. (1983). Sexual dimorphism and aggressive use of callosities in right whales (*Eubalaena australis*). *In* "Communication and Behavior of Whales" (R. Payne, ed.), pp. 295–329. Westview Press, Boulder, CO, AAAS Selected Symposium 76.

Payne, R., Brazier, O., Dorsey, E. M., Perkins, J. S., Rowntree, V. J., and Titus, A. (1983). External features in southern right whales (*Eubalaena australis*) and their use in identifying individuals. *In* "Communication and Behavior of Whales" (R. Payne, ed.), pp. 371–445. Westview Press, Boulder, CO, AAAS Selected Symposium 76.

Perrin, W. F., and Reeves, R. R. (eds.) (2004). Appendix 5. Report of the working group on species- and subspecies-level taxonomy. *In* "Report of the Workshop on Shortcomings of Cetacean Taxonomy in Relation to Needs of Conservation and Management, April 30–May 2, 2004, La Jolla, California" (R. R. Reeves, W. F. Perrin, B. L. Taylor, C. S. Baker, and S. L. Mesnick, eds.), NOAA Tech. Memo. NMFS-SWFSC-363, pp. 26–61. National Marine Fisheries Service, La Jolla, CA.

Pivorunas, A. (1979). The feeding mechanisms of baleen whales. *Am. Sci.* **67**, 432–440.

Reeves, R. R. (2001). Overview of catch history, historic abundance and distribution of right whales in the western North Atlantic and in Cintra Bay, West Africa. *J. Cetacean Res. Manag., Spec. Iss.* **2**, 187–192.

Reeves, R. R., and Kenney, R. D. (2003). Baleen whales, *Eubalaena* spp. and allies. *In* "Wild Mammals of North America: Biology, Management, and Economics" (G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, eds), 2nd Ed., pp. 425–453. Johns Hopkins University Press, Baltimore, MD.

Reeves, R. R., and Smith, T. D. (2006). A taxonomy of world whaling eras. *In* "Whales, Whaling, and Ocean Ecosystems" (J. A. Estes, D. P. DeMaster, D. F. Doak, T. M. Williams, and R. L. Brownell, Jr., eds), pp. 82–101. University of California Press, Berkeley, CA.

Reeves, R. R., Mead, J. G., and Katona, S. (1978). The right whale, *Eubalaena glacialis*, in the western North Atlantic. *Rep. Int. Whal. Commn.* **28**, 303–312.

Reeves, R. R., Berger, J., and Clapham, P. J. (2006). Killer whales as predators of large baleen whales and sperm whale. *In* "Whales, Whaling, and Ocean Ecosystems" (J. A. Estes, D. P. DeMaster, D. F. Doak, T. M. Williams, and R. L. Brownell, Jr., eds), pp. 174–187. University of California Press, Berkeley, CA.

Reeves, R. R., Smith, T. D., and Josephson, E. A. (2007). Near-annihilation of a species: Right whaling in the North Atlantic. *In* "The Urban Whale: North Atlantic Right Whales at the Crossroads" (S. D. Kraus and R. M. Rolland, eds), pp. 39–74. Harvard University Press, Cambridge, MA.

Rice, D. W. (1984). *Delphinus truncatus* Montagu, 1821, (Mammalia, Cetacea): Proposed conservation by suppression of *Delphinus nesarnack* Lacépède, 1804. Z. N. (S.) 2082. *Bull. Zool. Nomencl.* **43**, 256–257.

Rice, D. W. (1998). "Marine Mammals of the World: Systematics and Distribution." Society for Marine Mammalogy, Lawrence, KS, Special Publication Number 4.

Ride, W. D. L., *et al*. (1985). "International Code of Zoological Nomenclature," 3rd Ed. University of California Press, Berkeley, CA.

Rolland, R. M., Hunt, K. E., Doucette, G. J., Rickard, L. G., and Wasser, S. K. (2007). The inner whale: Hormones, biotoxins, and parasites. *In* "The Urban Whale: North Atlantic Right Whales at the Crossroads" (S. D. Kraus, and R. M. Rolland, eds), pp. 232–272. Harvard University Press, Cambridge, MA.

Rosenbaum, H. C., *et al*. (2000). World-wide genetic differentiation of *Eubalaena*: Questioning the number of right whale species. *Mol. Ecol.* **9**, 1793–1802.

Rowntree, V. (1996). Feeding, distribution, and reproductive behavior of cyamids (Crustacea: Amphipoda) living on humpback and right whales. *Can. J. Zool.* **74**, 103–109.

Scarff, J. E. (1986). Historic and present distribution of the right whale (*Eubalaena glacialis*) in the eastern North Pacific south of 50°N and east of 180°W. *Rep. Int. Whal. Commn., Spec. Iss.* **10**, 43–63.

Scarff, J. E. (1991). Historic distribution and abundance of the right whale (*Eubalaena glacialis*) in the North Pacific, Bering Sea, Sea of Okhotsk and Sea of Japan from the Maury whale charts. *Rep. Int. Whal. Commn.* **41**, 467–489.

Schell, D. M., Rowntree, V. J., and Pfeiffer, C. J. (2000). Stable-isotope and electron-microscopic evidence that cyamids (Crustacea: Amphipoda) feed on whale skin. *Can. J. Zool.* **78**, 721–727.

Schevill, W. E. (1986). Right whale nomenclature. *Rep. Int. Whal. Commn., Spec. Iss.* **10**, 19.

Shelden, K. E. W., Moore, S. E., Waite, J. M., Wade, P. R., and Rugh, D. J. (2005). Historic and current habitat use by North Pacific right whales *Eubalaena japonica* in the Bering Sea and Gulf of Alaska. *Mamm. Rev.* **35**, 129–155.

Thomson, D. H., and Richardson, W. J. (1995). Marine mammal sounds. *In* "Marine Mammals and Noise" (W. J. Richardson, C. R. Greene, C. I. Malme, and D. H. Thomson, eds), pp. 159–204. Academic Press, San Diego, CA.

Townsend, C. R., Begon, M., and Harper, J. L. (2003). "Essentials of Ecology," 2nd Ed. Blackwell, Malden, MA.

Wade, P. R., *et al*. (2006). Acoustic detection and satellite-tracking leads to discovery of rare concentration of endangered North Pacific right whales. *Biol. Lett.* **2**, 417–419.

Waring, G. T., Josephson, E., Fairfield, C. P., and Maze-Foley, K. (2007). "U.S. Atlantic and Gulf of Mexico Marine Mammal Stock Assessments—2006." NOAA Technical Memorandum NMFS-NE-201. National Marine Fisheries Service, Woods Hole, MA [Updated annually at http://www.nmfs.noaa.gov/pr/sars/].

Weisbrod, A. V., Shea, D., Moore, M. J., and Stegeman, J. J. (2000). Organochlorine exposure and bioaccumulation in the endangered northwest Atlantic right whale (*Eubalaena glacialis*) population. *Environ. Toxicol. Chem.* **19**, 654–666.

Whitehead, H. (1985). Why whales leap. *Sci. Am.* **252**(3), 84–93.

Winn, H. E., Price, C. A., and Sorensen, P. W. (1986). The distributional ecology of the right whale *Eubalaena glacialis* in the western North Atlantic. *Rep. Int. Whal. Commn., Spec. Iss.* **10**, 129–138.

Winn, H. E., Goodyear, J. D., Kenney, R. D., and Petricig, R. O. (1995). Dive patterns of tagged right whales in the Great South Channel. *Cont. Shelf Res.* **15**, 593–611.

Woodley, T. H., Brown, M. W., Kraus, S. D., and Gaskin, D. E. (1991). Organochlorine levels in North Atlantic right whale (*Eubalaena glacialis*) blubber. *Arch. Environ. Contam. Toxicol.* **21**, 141–145.

Ringed Seal
Pusa hispida

M.O. Hammill

I. Characteristics and Taxonomy

The ringed seal (Fig. 1) is among the smallest of pinnipeds, with adults reaching a maximum length of 1.3–1.5 m and weighing up to 100 kg prior to breeding. Males and females are similar in size, with males about 3% larger than females. Pelage descriptions vary slightly depending on the observer's perception. The ventral surface is normally light grey, whereas the dorsal area is variously described as being black with whitish-silvery rings, or silvery grey with black spots producing rings on its back. Its common name is derived from the characteristic ringed pattern on the pelage. The claws on the front flippers are quite rugged and are used to scratch open and maintain holes in the ice, which animals return to repeat to breathe and use to haul out on the ice. During the breeding season, the males emit a strong, pungent odor (Ryg *et al*., 1992). The odor is produced by modified sebaceous glands that are concentrated in the facial region of the males. On account of this odor, some early descriptions and engravings of ringed seals refer to them as *Pusa* (*Phoca*) *foetida*.

The ringed seal is a member of the subfamily Phocinae of the family Phocidae. Within this subfamily, *Pusa hispida*, along with four other genera, the *Phoca*, *Halichoerus*, *Histriophoca*, *and Pagophilus*

Figure 1 *An adult ringed seal (Pusa hispida) on Scalbard with a VHF transmitter on its back.*

constitute a well marked clade designated as tribe Phocini, which is distinguished from all other phocids by a unique karyotype ($2n = 32$), and a white lanugo (natal fur). Five subspecies are recognized, three are found in marine waters, whereas two subspecies are limited to freshwater areas.

P.h. hispida is the most widely distributed subspecies, occurring across northern regions of Canada, Alaska, Greenland, Svalbard, and Russia. This subspecies also includes animals found in freshwater areas in northern Canada such as in Lake Nettilling on Baffin Island and in Lake Melville in Labrador, but these animals have received little study.

P.h. botnica occurs throughout the northern Baltic Sea, primarily in the Gulf of Bothnia and Gulf of Finland; *P.h. ladogensis* is confined to the freshwater Lake Ladoga in western Russia. Some animals are thought to transit into the Gulf of Finland, and *P.h. saimensis* are found in southeast Finland in a series of landlocked interconnected lakes of Saimaa, Haukivesi, Orivesi, Puruvesi, and Pyhäselkä; *P.h. ochotensis* is found in the western, northern, and northeastern portions of the Sea of Okhotsk ranging south to the northern coast of Hokkaido on the west and to Mys Lopatka, Kamchatka in the east.

II. Distribution and Abundance

The ringed seal is northern circumpolar in distribution (Fig. 2). Although often considered as an inshore species, they have been observed at the North Pole and large numbers of animals are found in stable offshore pack-ice in polar regions. In North America they occur throughout the Arctic, extending as far south as the Labrador coast of Canada in the east. They are found throughout James and Hudson Bays, the Beaufort Sea, and extend as far south as Norton Sound along the Alaskan coast in the west. Ringed seals are found all along the coast of Greenland, but on the west coast are most abundant north of the Arctic circle. They are also common around Svalbard, but are rare around Iceland. Remnant populations are also found in the Baltic Sea, primarily in the Gulf of Bothnia, in Lake Saimaa in southeastern Finland and Lake Ladoga in western Russia, not far from the Gulf of Finland portion of the eastern Baltic Sea. They also occur along the northern coast of Russia, including the White Sea and are found in the Sea of Okhotsk off eastern Russia.

In general, seal ecology is characterized by marine feeding combined with a need to haul out on a solid substrate for reproduction or molting. Although hauled out under these conditions they are often concentrated in large numbers, which facilitates attempts to estimate abundance using aerial surveys. These surveys often attempt to count total numbers of hauled-out animals such as pups, then use a model incorporating information on haul-out patterns or a combination of

R