Environmental Adaptations of the Beluga Whale (*Delphinapterus leucas*)

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Abstract: This paper aims to analyze the physiological, perceptual, and behavioral adaptations in the Beluga Whale (*Delphinapterus leucas*) as a result of its arctic niche. The social implications of these adaptations will be examined by looking at each part as influential elements of each other. Lastly, the idea of defining culture in cetaceans will be addressed, including a proposal for examining culture in *Delphinapterus leucas*.

INTRODUCTION

It is unclear whether species adapt to a niche, or over time migrate towards a niche that best fits them; however it seems most probable that evolution is an ongoing compilation of both processes. More importantly, species adapt over time in a way that increases fitness. Processes of natural selection determine the best physiological adaptations; and in some species behavioral individuality may account for social adaptation. In order to attain behavioral individuality, a species must undergo physiological adaptations, which affect perceptual capabilities. These important adaptations influence the way an animal perceives its world; thus influence the way an animal behaves in its world. Lifespan, youth periods, and community types influence the animal during growth; and may sponsor individuality within a species. Greater individuality and social adaptation within a community may create species that are culturally distinct from one another. Therefore by analyzing physiological, perceptual, and behavioral evolution within a species such as the beluga whale (*Delphinapterus leucas*); it begins to be possible to analyze the possibility of culture within that species.

The beluga whale is a circumpolar species found in the coastal waters of Canada, Alaska, Russia, Norway, and Greenland (Smith, 1990). Group size within these populations range from 2-10 individuals to hundreds and thousands of individuals. As the ice melts, many of the belugas migrate north to summering grounds, which frequently include fresh water estuaries. As the water ices over again for the winter, belugas return to the southern Arctic. Some however, stay behind and spend the winter in ice leads and polynyas, or areas of open water surrounded by sea ice (O'Corry-Crowe, 2002). As ice forms rapidly over the cold arctic waters some belugas become trapped, while others seem to be especially good at navigating under an icy surface (Martin, 1996).

Recent satellite tracking data has indicated belugas moving up to 700km into areas in which ice coverage exceeds 90% of the surface (O'Corry-Crowe, 2002; see also Suydam *et al*., 2001). Belugas swim at an average speed of 6-9 km/hr (Brodie, 1989). Normal deep dives last 12-20 minutes, but have been recorded up to 25 minutes (Martin, 1996). This means that belugas must be exceptionally well adapted to find holes or air pockets at which to surface and breathe.

It has been suggested that the species' dorsal ridge may be used at times to break an icy surface, however a greater physiological adaptation is the morphology of the beluga melon. It is probable that the beluga's melon and specialized echolocation abilities play a large role in the location of cracks or polynyas to surface and breathe (O'Corry-Crowe, 2002). Also attributed to the specialization of the melon in *Delphinapterus leucas*, the beluga can propagate at least 50 different identifiable calls (O'Corry-Crowe, 2002) in variant social situations, giving ample reason for its common nickname, "Canary of the Sea."

As members of the same species, populations of beluga whales are physiologically similar. However there is substantial evidence for divergence in the migratory patterns, behavior, and vocal repertoire of the belugas. Though some information on social differences within the species is available, it is an intriguing area for future studies as we learn more about *Delphinapterus leucas*.

PHYSIOLOGY

The anatomy of the beluga whale differs in a few ways from the general anatomical characteristics of odontocetes. These adaptations have presumably occurred through process of natural selection to increase species fitness and allow the beluga to exploit an environmental niche less frequented amongst cetaceans. The features addressed in the following paragraphs result in behavioral and social modifications specific to the beluga whale.

If one were to observe a beluga, initial remarks would feature their pure white color, extra blubber, absence of a dorsal fin, motion of lateral flippers, range of head motion, and morphology of their large and bulbous melon. These are all adaptive structures of the beluga whale, and each play an important role in facilitating their existence in an arctic niche.

The beluga's white color and extra blubber are the most obvious adaptations to life in the arctic. Beluga whales are born a dark gray color and gradually attain their pure white color at maturity. Their coloration allows them to blend into their environment and presumably acts as camouflage from major predators; including the polar bear (*Ursus maritimus*) and the killer whale (*Orcinus orca*). Each year, the beluga undergoes a molting process that is facilitated by warmer summer waters. At this time their pure white color is regenerated (St. Aubin *et al.*, 1990). Belugas have a fat layer that extends over much of their body except for their head. This layer can become up to 15cm thick and accounts for 40% of their weight. It acts as insulation in water ranging from 0˚C to 18˚C, and functions as an energy reserve (Bonner, 1980; Culik, 2003).

The absence of a dorsal fin in *Delphinapterus leucas* is attributed to reduction in heat loss and adaptation to life under ice coverage. In its place, the beluga whale has a tough dorsal ridge, which, along with its head, can be used to break through sea ice up to 8 cm thick (St. Aubin *et al.*, 1989; *see also* Bel'kovich and Tarasevich, 1964; Sergeant, 1973).

The seven unfused cervical vertebrae characteristic of belugas is a fairly unique anatomical adaptation among cetaceans. Every other cetacean shows some sort of cervical fusion except for the rorquals, some river dolphins, and the Narwhal (*Monodon monoceros*) (Bonner, 1980). The subsequent lateral flexibility of head and neck enhances visual signaling, assists in pursuit of prey and predator evasion, and aids in maneuverability in waters only 1-3 meters deep (O'Corry-Crowe, 2002). This maneuverability is further enhanced by the mobility of lateral fins. Belugas can use their fins in a reverse motion, which helps in shallow waters and tidal changes (Brodie, 1989).

One of the most interesting and least studied aspects of the beluga whale is its characteristic melon. Unlike other cetaceans, the beluga can alter the shape of its large, bulbous melon. Presumably, it does this using peripheral muscles, resulting in a more focused and variable sonar output. There have been a few important studies that help to solidify this claim (see *Perception*) unfortunately there is not much direct information on the beluga melon.

Of these adaptations, the unique mobility of the head, body, and melon of the beluga play a large role in social interaction. The mobility of the head derived from the anatomically unfused cervical vertebrae allows the beluga accessibility to social interactions without necessarily altering its path. Furthermore, it provides the beluga greater control of its sonar beam. Many odontocetes display dualistic usage of their sonar in that it is utilized in both perceiving and influencing its physical and social environment.

PERCEPTION

The perceptual capabilities of the order *Odontoceti* are similar to most mammals and include vision, touch, chemoreception, and audition; however they have been adapted for an aquatic lifestyle. There are common similarities between the perceptual systems of cetaceans and more specifically odontocetes, however each species has undergone unique adaptations to increase fitness in different ecological niches.

Cetacean visual anatomy consists mostly of rods, which detect motion; and contain only one type of cone receptor for detail and contrast. Cetaceans see only in black and white. The retina contains two areas of high ganglion density; both of which are used in underwater vision, and only one of which is used in aerial vision. This insures a wide visual field and may play an important role in motion discrimination. The physiology of *Delphinapterus leucas* appears to be similar to that of most cetaceans, however it is noted that the beluga may have a slightly poorer visual acuity (Mass, 2001).

Chemoreception in cetaceans is differs from that of land mammals because the nares have undergone evolutionary migration to the top of the head. Though cetaceans exhibit evidence of taste receptors, there is no olfactory bulb or olfactory tract in odontocetes. There is further evidence of chemoreception in the mouth in some species including the beluga whale. Reports have suggested that belugas react to blood in the water by quickly retreating and showing unusual alarm. Furthermore, it has been proposed that belugas release a pheromone when alarmed (Dudzinski, 2002, *see also* Yablokov, 1961). This is something that should be investigated further as it may play a role in social communication of danger and perhaps other situations. It has also been discussed that chemoreception in cetaceans may include hormonal or pheromone analysis at mating time.

Little is known about touch in cetaceans except that it seems to play an important role in socialization, and that certain areas (face, jaw, blowhole, genital area) are more sensitive than others. It is also important to note that sound produces tactile stimulation. There is no further evidence of advancement of this sense in *Delphinapterus leucas*, except confirmation that belugas use touch in socialization.

Audition is the most evolved sense in cetaceans, and is additionally specialized in the beluga. Cetaceans produce sound by manipulation of air in the dorsal bursae of their nasal passageways. Nasal sacs reflect sound and direct it forward through a fatty melon. Manipulation of this process produces sound in the broad categories of echolocation, burst-pulse sounds, and whistles. These are emitted through the melon in a 'beam' of sound that can be analyzed by frequency and contour. Sound is perceived through a fat channel in the lower jaw, and packets of sound are assessed by their frequency, resonance, latency, and amplitude (Au, 1993).

In *Delphinapterus leucas*, the horizontal beam is pointed directly forward of the whale, parallel to the longitudinal axis defined by the whale's teeth. The vertical beam of the beluga whale is displaced five degrees above the horizontal axis. The 3-dB bandwidth is approximately 6.5° in both the horizontal and vertical direction of the beam; compared to a 9.8° – 10.7° horizontal and 10°-11.7° vertical 3-dB beamwidth in *Tursiops* (Au *et al.*, 1987; see also Au *et al.*, 1978; Au, 1980). Thus in comparison to *Tursiops*, *Delphinapterus leucas* demonstrate a much more focused beam that is offset 5° towards the surface. This is likely attributable to the specialized melon, and suggests that belugas use the muscles around the melon to direct a more focused beam. Furthermore, belugas are capable of transmitting and interpreting echolocation signals reflected off the icy surface of the water (Au *et al.*, 1987). It has been suggested this ability may enable the beluga to navigate through heavy pack ice and locate polynyas and air pockets under the ice (O'Corry-Crowe, 2002).

The beluga demonstrates good frequency discrimination and sensitivity to sounds at a lower frequency than *Tursiops truncatus.* They are also able to detect targets through backscatter (see Turl, 1990 for a thorough comparison of *T.truncatus* v. *D.leucas*), and can change the peak frequency and amplitude of echolocation signals depending on the range of ambient noise in the environment (Au *et al.*, 1985). Interestingly, the beluga transmits signals and receives echolocation signals simultaneously; assessing echoes and clicks in 'packets,' whereas *T.truncatus* will rapidly assess each returned echo before emitting another signal.

The perceptual adaptations of the beluga whale indicate that the species is exceptionally well adapted to its arctic niche. While noted that the beluga demonstrates a slightly worse visual acuity than that described in other cetaceans, they demonstrate very important adaptations in their environment. The lack of adaptation in vision suggests that there may be fewer demands in the arctic that can be assessed by vision. Au *et al.* (1985) demonstrate that the beluga whale can alter the range of its echolocation frequency depending on the ambient noise in the environment. This gives the beluga greater discriminatory ability in assessing its target. Increasing this ability further is evidence that belugas demonstrate great control over their sonar (Au *et al.*, 1987), and have the ability to echolocate and assess targets through backscatter (Turl, 1990) and surface reflections (Au *et al.*, 1987). These are important abilities that may assist in navigation and environmental perception through ice fields or pack ice.

In Old World Monkeys (*Cercopithecoidea*), the evolution of ischial callosities freed their limbs, and allowed them to use their hands for other things, such as social interactions. It may be possible that the physiological and perceptual adaptations in *Delphinapterus leucas* play a similar role. The easier it is for belugas (or any species) to perceive and interact with their environment, the less time they have to spend analyzing it. This allows time for the spawning of new types of environmental interaction, and may give rise to social novelties across populations.

BEHAVIOR & SOCIALIZATION

Sound production in cetaceans is a dualistic process, in that it functions in environmental analysis as well as socialization. There have been over 50 call types recognized in the beluga (O'Corry-Crowe, 2002) between which gradations, or sliding from one call structure to another, occur (Karlsen *et al.*, 2002). Many of these call types are common across the species; however there is exciting evidence of vocal novelties in different groups of belugas (Karlsen *et al.*, 2002). Furthermore, there are many common call types in the order *Odontoceti* that occur in similar contexts. This has been researched in a few species such as *Stenella frontalis* (Herzing, 2000), *Stenella longirostris* (Norris & Dohl, 1980, 1982; Brownlee, 1983), and in *Delphinapterus leucas* (Sjare and Smith, 1986b).

Analyzed calls include: whistles, signature whistles, blare type pulsed calls, squawk-type calls, clicks, and jaw claps. Among odontocetes, whistles have been suggested to function as contact calls used to facilitate coordinated group behaviors like feeding and pod movements (Norris & Dohl, 1980; 1982). Observations of the use of this call by *D. leucas* correspond with this evidence; the whistle call was observed during social interactions and directive swimming (Sjare & Smith, 1986b). Sjare and Smith define signature whistles as brief and sporadic outbursts of distinct stereotypic whistles produced during all behavioral activities. Signature whistles are emitted by certain odontocetes in announcement of presence, coalitions, and alarm. Beluga data coincides with this knowledge: signature whistles have been observed between close kin (O'Corry-Crowe, see also Bel'kovich and Sh'ekotov, 1990), and during all behavioral activities, but most commonly during periods of alarm (Sjare & Smith, 1986b). Blare-type pulsed calls were observed most often during periods of rest; squawk-type calls were commonly observed during times when the belugas were socially active. Clicks are generally described in odontocetes as fast broadband echolocation sounds used for environmental probing. In the beluga, these sounds were observed more often during social situations than alarm, and more during alarm than during rest. They were found to function in echolocation, but some deviated from normal definition. It has been proposed that those clicks that deviate from normal echolocation patterns of broad-band pulse and repetition may function as communicative (Sjare & Smith, 1986b; Watkins and Schevill, 1971). Jaw claps are loud and intense sounds produced in several cetaceans and are generally observed in accordance with alarm or threat. This was consistent in belugas as well, although it should be noted that the production of jaw claps was observed most commonly during social interaction and alarm, but varied very little with behavioral change.

The population of belugas studied by Sjare and Smith (1986b) was a transient population summering at Cunningham Inlet. While their study gives a general idea of the types and frequency of calls made by beluga whales, it is by no means a definitive study of calls made by belugas across populations. Karlsen *et al.* (2002) studied the population of male belugas off the coast of Svalbard, Norway, and found that the whales spent a surprisingly little amount of time vocalizing. They point out that vocal behavior in *Delphinapterus leucas* has also been studied in the St. Lawrence River Estuary, Bristol Bay, and the White Sea; and that correlations between calls and behavior vary between communities as well as with school size, structure, and geography.

The distribution of the beluga whale extends from 47°N to 49°N (St. Lawrence River in eastern Canada) to above 80°N in areas of the Arctic Ocean (O'Corry-Crowe, 2002). Within this great expanse belugas are distributed discontinuously, with five distinct populations of beluga whales identified as occurring in: St. Lawrence Estuary, North and West Sea of Okhotsk (including Tatarskyi Zaliv), Cook Inlet, and the Northern Gulf of Alaska (Rice, D.W., 1998, *See fig. 1)* Though informative, this number is inconclusive, as different numbers of populations have been recorded by different sources. For example, Martin (1996) recorded that there are 12-18 different populations. Regardless, it appears decisive that within the distribution both resident and transient populations of beluga whales occur.

The resident species of the White, Barants, and Kara seas have been recorded year round, and observed to remain in polynyas, deeper water, and ice leads during winter (Kleinenberg *et al*., 1964; O'Corry-Crowe, 2002). Other resident populations include belugas residing in the Cook Inlet, St. Lawrence estuary, and possibly in Cumberland Sound (Culik, 2003).

Transient populations of beluga whales generally follow the freeze and melt of the polar ice cap. These populations have specific summer and winter grounds that they return to annually. Though many of the specific dates and routes are poorly known, analysis of past studies provides a view of patterns that may continue to develop through future research. In general, transient populations of *Delphinapterus leucas* spend the winter in the southern offshore waters at the edge of ice packs or in polynyas, then travel thousands of kilometers to spend the summer in northern coastal waters and river estuaries. This migratory pattern is thought to be attributable to changes in ice and food, and possibly to more ideal calving grounds (Culik, 2003; *see also* Reyes, 1991). The breeding season in belugas is from late winter to early spring, and may occur at the winter grounds or during spring migration (O'Corry-Crowe, 2002). There is a 14-15 month gestation period, and births occur in late June to mid-July (Brodie, 1989) at the warmer summer locations. The beluga's adaptability to shallow, fresh-water, and food rich estuaries facilitates molting, and provides protection of newborn calves from killer whales (Brodie, 1989; O'Corry-Crowe, 2002; *see also* Smith *et al*., 1992). Mitochondrial DNA (mtDNA) analysis has shown limited movement between summering grounds, though certain groups appear to join together in the winter. This is demonstrated in the Northern Canadian populations where beluga pods from West Hudson Bay, East Hudson Bay, and Ungava Bay summer grounds overwinter together in the icy Hudson Strait (Culik, 2003; *see also* Reyes, 1991).

Group size and behavior varies between transient and resident belugas and within these large sub-groups (sometimes numbering in the thousands) as well. Most social behavior has been observed in the smaller groups containing a few hundred individuals. These are generally segregated into sub-groups including maternal or "nursery" groups, and male plus non-maternal female groups.

Maternal groups, often seen as a triad, are the most stable group and are generally composed of an adult female, a calf or juvenile, and an adolescent (immature beluga). This group remains stable for 2-3 years, and the nursing female does not breed again until the calf is around two years of age (Brodie, 1989). During this time, the calf stays close to its mother, and among other things learns the migratory path it will take for the rest of its life. Maternal groups are often seen as a part of a larger nursery group consisting of all females, calves, and juveniles. Within the nursery groups, babysitting behavior has been observed with the adolescents tending to the juveniles for 2-3 hours. During group hunting, juveniles follow females and separate only at the moment when females are catching fish (Bel'kovitch & Sh'ekotov, 1993). Alloparental behavior demonstrated by the babysitting adolescents and the behavior of juveniles during hunting indicates a longer period of youth; which may involve scaffolding, watching, and learning. This is an area for further study as a longer youth period is generally associated with greater individuality, intelligence, and opportunities for social deviation within a community. There is also some interesting evidence of reciprocal altruism in the nursery groups: Martin reports that at birth, calves are helped to the surface by surrounding adults, deemed "volunteer midwifes" (Martin, 1996). Reciprocal altruism generally indicates higher cognitive abilities in a species since it requires long-lived animals in a large group to be able to track debt, currency, and "cheaters"; and entails some sort of sanctioning of cheaters.

The existence of nursery groups leaves the males and adult females without calves to form another large group (Martin, 1996). A study of one specific group such as this found that the male dominated groups produced minor vocal novelties along with the general plethora of beluga calls. These novelties were hypothesized to represent either an anti-predator call or school type, or may have been due to the research boat or other influences produced by the research project (Karlsen *et al*., 2002). It is not unlikely that vocal novelties exist between groups, and may indicate group coherence or ecological schemes.

Further variation in the social behavior of *Delphinapterus leucas* occurs in hunting patterns between groups. The White Sea Beluga demonstrates individual hunting, though observations included stereotyped sequences of signals produced in the beginning of the hunt. The suggested interpretation was that these calls were used to maintain distant contact between individuals. When coupled with data that the beluga is able to conduct individual exchanges of acoustic signals or dialogue over distance (Bel'kovich & Sh'ekotov, 1993; 1990); this interpretation seems entirely plausible. It seems likely that the calls relate to prey location, but hopefully further research will confirm the purpose of coordinated individual hunting. The Amur Beluga is found in the Amur Estuary where fast moving prey such as salmon is a primary food source. In this area, the belugas demonstrate coordinated group hunts in which 6-8 individuals circle the prey while one darts in to feed. Close and remote communication between 2-3 individuals has been observed during this process, and is probably a method of coordination. The intensity of the social signals grows as the group size increases. Furthermore, it is suggested that this close communication may be associated with aggressive-subordinate hierarchical behavior (Bel'kovitch and Sh'ekotov, 1993).

Continuing to learn of the differences and similarities that exist between populations of beluga whales is a very important step in analysis of the species. Similarities among behaviors will likely show general survival activities; whereas dissimilarities may demonstrate traditions adapted through individual social behavior. Future analysis of subsets of specific behaviors across populations will allow for direct comparison. When viewed with analysis of environmental differences, access to different resources, and usage of different physiological capabilities; it may be possible to construct and analyze studies on the existence of culture in *Delphinapterus leucas.*

CONCLUSION

To fully discuss the social nature of a species, there must be analysis of the subsidiary parts that together form a social animal. In the beluga whale (*Delphinapterus leucas*), physiological evolution occurs in coordination with a specific arctic niche and specialized perceptual abilities have evolved to increase the species fitness in that niche. As in all species, perceptual abilities dictate the reality in which an animal resides. Manipulation of this reality is driven by perception, and in the order *Odontoceti*, specialized echolocation ability allows the animals to both gather from, and send information into their aquatic world. This ability is thus perceptual and physical; informative, behavioral, and social.

Physiological adaptations such as those discussed allocate specific behaviors. Flippers, head mobility, and chemoreception allow the beluga to maneuver in shallow estuaries where they can detect and escape from predators, nurse their newborn calves, and find an abundance of prey. Migration under icy surfaces and the ability to find polynyas and air pockets is possible because of the use of surface echolocation and a strong dorsal ridge, along with deep diving abilities and efficient oxygen usage.

While individual belugas demonstrate common abilities, they are a large and divergent species. Different groups demonstrate specific behavioral traits. These include migratory and non-migratory populations which demonstrate divergent social behaviors such as specialized group hunting, different types of social groupings, more or less proficient use of physiological adaptations, and unique or group-specific calls.

There is not yet enough evidence to argue for culture in *Delphinapterus leucas*, and responses to Rendall & Whitehead's article, "Culture in Whales and Dolphins" (2001) show that there is much work to be done in the cetacean field if an argument is going to be made for culture. However, the only reason that this argument exists is because studies of cetaceans are brimming with social behaviors that are all too similar to the rudiments of culture. The thought is simply irresistible, but must be examined properly if there is to be any serious argument.

Whiten *et al* (1999) defined culture as "behavior patterns …[that are] customary or habitual amongst some communities, yet are absent in others where ecological explanations have been discounted" (Whiten *et al.*, p. 682). They defined six behavior categories as follows:

> (1) Customary, for which the behaviour occurs in all or most able-bodied members of at least one age-sex class (e.g. adult males); (2) habitual, for which the behaviour is not customary but has occurred repeatedly in several individuals, consistent with some degree of social transmission; (3) present, for which the behaviour is neither customary nor habitual but is clearly identified; (4) absent, for which the behaviour has not been recorded and no ecological explanation is apparent; (5) ecological explanation, for which absence is explicable because of a local ecological feature; and (6) unknown, for which the behaviour has not been recorded, but this may be because of inadequacy of relevant observational opportunities.
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> Whiten *et al.*, 1999

These concise categories were used to analyze culture in chimpanzees across different communities. With more research in the right areas, it may be possible to analyze belugas as well as other cetaceans in a similar manner. The major difficulty is overcoming the fact that cetaceans, especially odontocetes, manipulate their environments through sound, whereas primates manipulate their environment with their hands. Analysis of culture in *Delphinapterus leucas* will have to begin with a full understanding of the repertoire of vocalizations produced by this species, and we are quite far from that. Social behaviors explored in this paper that may demonstrate rudiments of culture include: group specific behavior such as male-specific beluga calls, individual or group hunting, attention and involvement of juveniles in group hunting, and differences between resident and transient populations. These areas may provide a starting point for analysis of culture if studied across communities and prove ecologically independent divergence.

Figure 1: Circumpolar distribution of Beluga Whales. Not shown: St. Lawrence River (estuary), Canada; James Bay, Canada. Map adapted from University of Texas Libraries Map Collection, Arctic Region (Political) 2002. *See also* Rice, 1998.

REFERENCES:

Au, W. et al. 1987. Propagation of beluga echolocation signals. J.Acous. Society 82(3), 807-813.

Au W.W.L., D.A. Carder, R.H. Penner and B. Scronce. 1985. Demonstration of adaptation in Beluga whale echolocation signals. Journal of the Acoustical Society of America 772:726-730.

Au, W. W. L. 1993. The Sonar of dolphins. Springer-Verlag, New York, N.Y.

Bel'kovitch, V.M. & Sh'ekotov M.N. 1993. The Belukha Whale: Natural Behavior and Bioacoustics. Woods Hole Oceanographic Inst. Woods Hole, MA .

Bonner, W.N. 1980. Whales. Poole, England: Blandford Press, 1980, pp. 17, 23-24.

Brodie, Paul F. The White Whale *Delphinapterus leucas* (Pallas, 1776). 1989. *In* Handbook of Marine Mammals, Vol. 4: River Dolphins and Larger Toothed Whales. Ridgway S. H., and R. J. Harrison [ed.]. Academic Press, London.

Bryum, Jody. Beluga Whales. San Diego: Sea World Education Department Publication, 1995.

Culik, Boris. 2003. Review of small cetaceans: distribution, behaviour, migration and threats. CMS publication.

Dudzinski, K., Thomas, J.A., and E. Douaze. 2002. *In* “Encyclopedia of Marine Mammals.” William F. Perrin, Bernd Wursig and J.G.M. Thewissen, [ed.], pp. 248-268.

Frankel, A.S. 2002. Sound production. *In* “Encyclopedia of Marine Mammals.” William F. Perrin, Bernd Wursig and J.G.M. Thewissen, [ed.], pp. 1126-1138.

Herzing, D.L. 2000. Acoustics and social behavior of wild dolphins: implications for a sound society. *In* Hearing in Whales and Dolphins. Whitlow, W.L., Popper, A.N., and R.R. Fay [eds.]. New York, Springer. Pp. 225-272.

Karlsen, J., Bisther, A., Lydersen, C., Haug, T., and K. Kovacs. 2002. Summer vocalisations of adult male white whales (*Delphinapterus leucas)* in Svalbard, Norway, Polar Biology, Volume 25, Issue 11, pp. 808 – 817.

Kleinenberg, S.E., Yablokov, A.V., Bel’kovich, B.M., and Tarasevich, M.N. (1964). “Beluga (Delphinapterus leucas): Investigation of the Species.” Academy of Sciences of the USSR, Moscow. [Translated by Israel Program of Scientific Translations, 1969.]

L. R. Lukin, L. Yu. Vasil'ev, Distribution of White Whales (*Delphinapterus leucas*) in the White Sea and the Southeastern Region of the Barents Sea during the Ice Season, Russian Journal of Ecology, Volume 35, Issue 4, Jul 2004, Pages 236 – 241.

Norris, K.S. and T.P Dohl (1980) “The Structure and Functions of Cetacean Schools,” *Cetacean Behavior*, L.M. Herman ed., John Wiley and Sons, pp. 211-261.

Martin, T. (1996). Beluga Whales. Voyager Press, Stillwater MN.

O’Corry-Crowe, G.M. 2002. Beluga Whale: *Delphinapterus leucas*. *In* “Encyclopedia of Marine Mammals.” William F. Perrin, Bernd Wursig and J.G.M. Thewissen, [ed.], pp. 94-99.

Rendell, L. and H. Whitehead (2001) “Culture in Whales and Dolphins,” *Behavioral and Brain Science,* 24, Cambridge University Press, pp. 309-382.

Rice, D.W. 1998. Marine mammals of the world: systematics and distribution. Society for Marine Mammalogy, Special Publication Number 4. Wartzok, D, [ed.], pp. 96-97.

Sjare, B.L., and T.G. Smith. 1986a. The vocal repertoire of white whales, *Delphinapterus leucas*, summering in Cunningham Inlet, Northwest Territories. Canadian Journal of Zoology 64:407-415.

Sjare, B.L., and T.G. Smith. 1986b. The relationship between behavioral activity and underwater vocalizations of the white whale, *Delphinapterus leucas*. Canadian Journal of Zoology 64:2824-2831.

St. Aubin, D.J., Smith, T.Gl, and J.R. Geraci. 1990. Seasonal epidermal molt in beluga whales, *Delphinapterus leucas. Can. J. Zool.* 68, 359-367.

Turl, C.W. 1990. Echolocation abilities of the beluga, *Delphinapterus leucas*: a review and comparison with the bottlenose dolphin, *Tursiops truncatus*, p. 119-128. *In* T.G. Smith, D.J. St.Aubin, and J.R. Geraci [ed.] Advances in research on the beluga whale, Delphinapterus leucas. Can. Bull. Fish. Aquat. Sci. 224.

Watkins, W.A., and W.E. Schevill. 1971. Underwater sounds of *Monodon* (Narwhal). J. Acoust. Soc. Am. 49: 595-599.

Whiten, A., Goodall, J, McGew, W.C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, G.E.G., Wranghad, R.W. & Boesch, C. (1999). Cultures in chimpanzees, *Nature* 399, 682-5.