

A review of bowhead whale (*Balaena mysticetus*) stock identity

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ABSTRACT

For management purposes, the Scientific Committee of the International Whaling Commission has considered bowhead whales as having five stocks (geographically distinct segments of the population): Spitsbergen, Davis Strait, Hudson Bay, Okhotsk Sea and Bering-Chukchi-Beaufort Seas (B-C-B). These divisions are defined primarily by known distribution and seasonal movements. Historically, bowhead whales had a circumpolar distribution, with several periods of range expansion and contraction depending upon access through Arctic straits. Heavy exploitation by pre-20th century commercial whalers reduced bowhead whale abundance, further segregating stocks. A portion of the B-C-B stock escaped whalers by migrating into the pack ice each spring and summering in the Beaufort Sea. Few bowhead whales are now found in the summer in the Chukchi or Bering Seas. The distribution of this species should be considered labile, affected by sea ice and availability of prey, a factor that improves the likelihood of genetic mixing between stocks. Genetic variability has remained relatively high in spite of the severe depletion of the population, and there is no evidence of any recent genetic bottleneck. Besides geographic distribution and genetics, stock identity may be studied via morphological differences, reidentification of individuals between different stock areas, acoustic signatures, pollutant burdens, parasites and predators, feeding ecology and conception dates. Harpoon heads, research tags and lens racemisation indicate that bowhead whales are long-lived, can travel over large areas and may mix among stocks. Because conception occurs during or near the time of the spring migration, there are opportunities for genetic mixing among whales that might use different summering areas.

KEYWORDS: BOWHEAD WHALE; STOCK IDENTITY; DISTRIBUTION; GENETICS; ARCTIC; MOVEMENTS; WHALING-HISTORICAL

INTRODUCTION

As part of an ongoing process to develop a systematic approach to defining stocks within the management regime of the International Whaling Commission (IWC), this review was developed originally at the request of the Scientific Committee (IWC, 2000, p. 292).

Since 1984, the IWC Scientific Committee has considered the issue of bowhead stock structure many times (e.g. IWC, 1984; 1985; 1986; 1988; 1989; 1991; 1992b; 1995b; 1997). IWC (1984) concluded that the number of whales that fail to migrate past Pt Barrow in any one year is very small, and autumn sightings in the Chukchi Sea along the northeast Siberian coast were early returns from the Beaufort Sea, not a separate stock in the western Chukchi Sea. This view was reiterated in IWC (1985) supported by the recovery of a USSR discovery tag found in a bowhead taken off Wainwright, Alaska, in May 1983 (along the typical migratory route from the Bering Sea to the Beaufort Sea); the whale had been marked in October 1981 off Chukotka (Dronenburg *et al.*, 1984).

A major review took place in 1991 (IWC, 1992a). Although Fraker (1984) proposed that there had originally been two stocks, one of which was exterminated by commercial whalers, the Committee concluded that the present apparent absence of large numbers of bowhead whales in the summer in the Chukchi Sea relative to large takes in the summer during commercial whaling efforts is not evidence for two stocks. Subsequent discussions have not altered the Committee's conclusions (e.g. IWC, 2001a; b).

This review begins with definitions of stocks as presented by the IWC. This is followed by a description of each bowhead stock in terms of abundance (original and current), distribution and seasonal movements to give a context for the

detailed analysis of stock identity. Following this background information, a summary of IWC Scientific Committee assessments of the western Arctic stock is presented. Available methods applicable to discriminating whale stocks are presented. To conclude, a summary is given of historical findings regarding stock identity for bowhead whales, and a list of additional research that would be useful is provided.

BACKGROUND

IWC approach to stock identity

Hoelzel and Dover (1989) considered three types of stocks: (1) dynamic stock ('the fundamental unit described by a population model or assessment procedure'); (2) management unit ('a group of whales occurring within a specific geographical boundary which is actively or potentially exploited'); and (3) genetic stock ('a genetically differentiated population within a species'). Regarding existing IWC stock boundaries, Donovan (1991) noted that:

'Much of the data historically used to examine stock identity (examination of catch and sightings distributions, differences in biological parameters and length distributions, mark-recapture data) are not capable of being used to define biological stocks and provide equivocal information on 'management' units'.

In simple terms, he distinguished between management stocks ('population units that can be 'successfully' managed') and biological stocks ('based on genetic separation'). He noted that, for the IWC, management stocks are more important but that it may not be possible to define an appropriate management stock without some knowledge of the relevant biological stock(s).

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In practice, the IWC's operational definition of a stock (or population) has been the same as a management unit. That is, a management unit is defined such that specific management goals (e.g. harvesting does not reduce populations below a certain level or result in local extirpation, etc.) are met (Donovan, 1991). Prior to the development of molecular techniques, management units were sometimes coarsely defined on the basis of one or more of a number of factors including: discontinuities in the distribution of animals on their feeding and breeding grounds based on catch and sightings data; morphology; differences in life history parameters; and compatibility with models (Donovan, 1991). The rate of gene flow between putative stocks was unknown, nor was there any information on the degree to which an area could be 'recolonised'.

Throughout the 1980s and 1990s, however, putative stocks were defined based on inferences that gene flow was unlikely. More recently, Taylor and Dizon (1996) showed that the rate of interchange needed to maintain genetic diversity between populations is several orders of magnitude less than that needed to maintain demographic viability. Subsequently, others have incorporated these ideas; for example, Clapham and Hatch (2000) and Clapham and Palsbøll (1999) have suggested a definition of a large whale management unit (or stock) as a grouping of individuals that, if extirpated, would probably not be recolonised via immigration from other areas on a time scale relevant in management terms.

In 2001, the IWC Scientific Committee developed the following stock definitions (IWC, 2002):

- (1) Biological stock – all of the individuals in an area that are a part of the same reproductive process. They form a self-contained unit, with emigration/immigration rates far lower than the intrinsic rate of population growth.
- (2) Management stock/management unit – a human construct defined in the context of management, that may or may not be equivalent to a single biological stock. It refers to animals that happen to be present in a defined region and defined season where management is taking place or is contemplated.
- (3) Simulation stock/simulation sub-stock – a computational approximation denoting a homogenous group of animals, used to obtain inferences for management (as used in *Implementation Simulation Trials*, e.g. IWC, 1994).
- (4) Sub-stock – this deliberately vague term describes a group of animals with some degree of biological cohesion. There are circumstances (e.g. on a feeding ground where animals from two breeding stocks are mixed) where other terms might be more appropriate.
- (5) Closed sub-stock – this refers to a sub-stock which has negligible interchange with animals outside the sub-stock (i.e. at rates far lower than the intrinsic rate of population growth).

Review of bowhead stocks worldwide

Bowhead whales probably arose during the Pliocene in the Northern Hemisphere (McLeod *et al.*, 1993) and are endemic to Arctic and sub-Arctic waters (Moore and Reeves, 1993). These whales have an extremely thick epidermis of up to 25mm and a layer of blubber of up to 28cm (Haldiman and Tarpley, 1993), indicating their adaptation to the near-freezing temperatures of their environment. Historically, bowhead whales had a circumpolar distribution (Dyke *et al.*, 1996). More than

pelagic species, littoral species (like bowhead whales) tend to have a continuous, although dispersed, distribution (McLeod *et al.*, 1993). Dyke *et al.* (1996) and Savelle *et al.* (2000) used remains of bowhead whales found in the Canadian Arctic to demonstrate that over the past 10,500 years there were several periods of expansion and contraction of the east-west distribution of these whales. In particular, bowhead whales were able to cross from the Beaufort Sea to Baffin Bay 10,500-8,500 years ago and again 5,000-3,000 years ago. At times, the climate was warmer than at present, possibly allowing bowhead whales to travel north of even the northernmost Canadian Arctic islands (Bednarski, 1990). This would have been an avenue to genetic mixing among the stocks.

Bowhead whales are known to migrate long distances (Moore and Reeves, 1993), moving southward in the autumn with the advance of the pack ice and returning northward with break-up the following spring. They commonly travel along shallow inner-shelf waters when ice conditions are moderate and light, but they use deeper slope habitat in heavy ice (Moore, 2000). Bowhead whales can average 5km/hr over thousands of km, even through areas covered with >90% ice, and they are capable of diving for over an hour (Krutzikowsky and Mate, 2000). This complex behavioural relationship of bowhead whales to sea ice (a dynamic and changing feature) can lead to fragmentation or integration of populations (Reeves *et al.*, 1983). Although extreme ice fields can form a barrier to even large bowhead whales (Moore and Reeves, 1993) and ice entrapment is a cause of mortality (Savelle *et al.*, 2000), this species shows an attraction to ice fields possibly to avoid killer whales, *Orcinus orca* (George *et al.*, 1994; Finley, 2001) or to take advantage of prey concentrations near and under sea ice (Finley, 2001), such as *Calanus* (Lowry, 1993). When bowhead abundance was high, their range may have included most Arctic areas with seasonal sea ice. However, strong fidelity to essential habitats (Finley, 2001) may have limited mixing, and commercial whaling further segregated bowhead whales into what are currently described as five stocks (geographically distinct segments of the population): Spitsbergen, Davis Strait, Hudson Bay, Okhotsk and western Arctic (IWC, 1992a, p.27). The western Arctic stock is now usually referred to as the Bering-Chukchi-Beaufort Seas (B-C-B) stock (e.g. Zeh *et al.*, 1995a) although occasionally it is simply the Bering Sea stock (e.g. Burns, 1993). In this review the term B-C-B stock is used.

Spitsbergen stock

Bowhead whales in the eastern North Atlantic have been observed as far east as the Laptev Sea, Severnaya Zemlya, Novaya Zemlya, Zemlya Frantsa-Iosifa (Franz Josef Land), Svalbard, north of Norway and north of Iceland along the coast of Greenland (Fig. 1), but only 40 sightings have been made since 1940 (Belikov and Boltunov, In press; Born, in litt.; Moore and Reeves, 1993). Possibly now numbering only 'in the tens' (Christensen *et al.*, 1990), the Spitsbergen stock is thought to have originally been the largest of the bowhead whale stocks (Braham, 1984; Woodby and Botkin, 1993). From 1660-1912, commercial whalers took over 90,000 bowhead whales. There may have been roughly 25,000 bowhead whales in this stock prior to commercial whaling (Mitchell, 1977; Woodby and Botkin, 1993). Hacquebord (1999) reconstructed records of whaling activities in the 17th and 18th centuries and examined how a changing climate may have affected whaling productivity; this led to his proposal that it was not only human hunting

activities but changes in climate that may have caused the elimination of the Spitzbergen stock, or limited its ability to recover.

Jonsgård (1981; 1982) suggested that the historic Spitzbergen stock is extinct and that recent sightings may actually be immigrants circumventing Greenland (Davis Strait stock) or arriving via the East Siberian Sea (B-C-B stock). This was based on the lack of bowhead sightings in ice-covered waters of the northeast Atlantic in spite of many surveys. However, others (Reeves and Leatherwood, 1985; McQuaid, 1986; Moore and Reeves, 1993) believe that the present population between Greenland and Russia is probably a remnant of the severely depleted Spitzbergen stock. When bowhead whales were more plentiful, some overlap in ranges would have been more likely.

Movement patterns of bowhead whales within the Spitzbergen stock are not well known. Variations in the routes taken during the southbound migration have been attributed to the existence of separate 'tribes' (sub-species or species) of bowhead whales (Scoresby, 1820) or segregation of the population into age- or sex-specific groups (Southwell, 1898; de Jong, 1983).

Davis Strait stock

Bowhead whales west of Greenland and in northeastern Canada are recognised as two stocks (Moore and Reeves, 1993): the Davis Strait stock (centred in Davis Strait, Baffin Bay and waters of the Canadian Arctic Archipelago) and the Hudson Bay stock (found in Hudson Strait, Hudson Bay and Foxe Basin). The initial basis for defining these two stocks was the geographic separation of their summer feeding

distributions (Reeves *et al.*, 1983; Reeves and Mitchell, 1990). A recent genetic study (Maiers *et al.*, 2001) not only provides supporting evidence for genetic separation of these two stocks, but it indicates that the Hudson Bay stock is more closely related to the B-C-B stock than to the Davis Strait stock. This suggests that bowhead whales in Hudson Bay originally immigrated from (or mixed with) the B-C-B stock, and those in Davis Strait may have come from the Spitzbergen stock. The Spitzbergen stock became established >13,000 years ago (Dyke *et al.*, 1996). Regular intermingling of the B-C-B and Hudson Bay stocks could have occurred 10,000-8,500 years ago and 5,000-3,000 years ago (Dyke *et al.*, 1996; Savelle *et al.*, 2000). There is no direct evidence that the Davis Strait stock existed prior to 10,000 years ago, at a time when much of Baffin Bay was impenetrable, but by 9,500 years ago this stock had become established and could have intermixed with the B-C-B stock (Dyke *et al.*, 1996).

The reidentification of a whale photographed northeast of Baffin Island in September 1986 and again near Disko Bay, West Greenland, in April 1990 (Heide-Jorgensen and Finley, 1991) and the tracks of two bowhead whales with satellite transmitters showing travel from Disko Bay to northeastern Baffin Island (Heide-Jorgensen *et al.*, 2001) support the hypothesis that there is only one stock in Baffin Bay. Whalers did not attribute variations in body size and migration patterns to the existence of multiple stocks in Davis Strait, unlike the variations recognised in the Spitzbergen stock (Reeves *et al.*, 1983).

Almost 29,000 bowhead whales were harvested in Davis Strait between 1719 and the end of commercial whaling in 1915 (Ross, 1993) from an estimated original stock of over

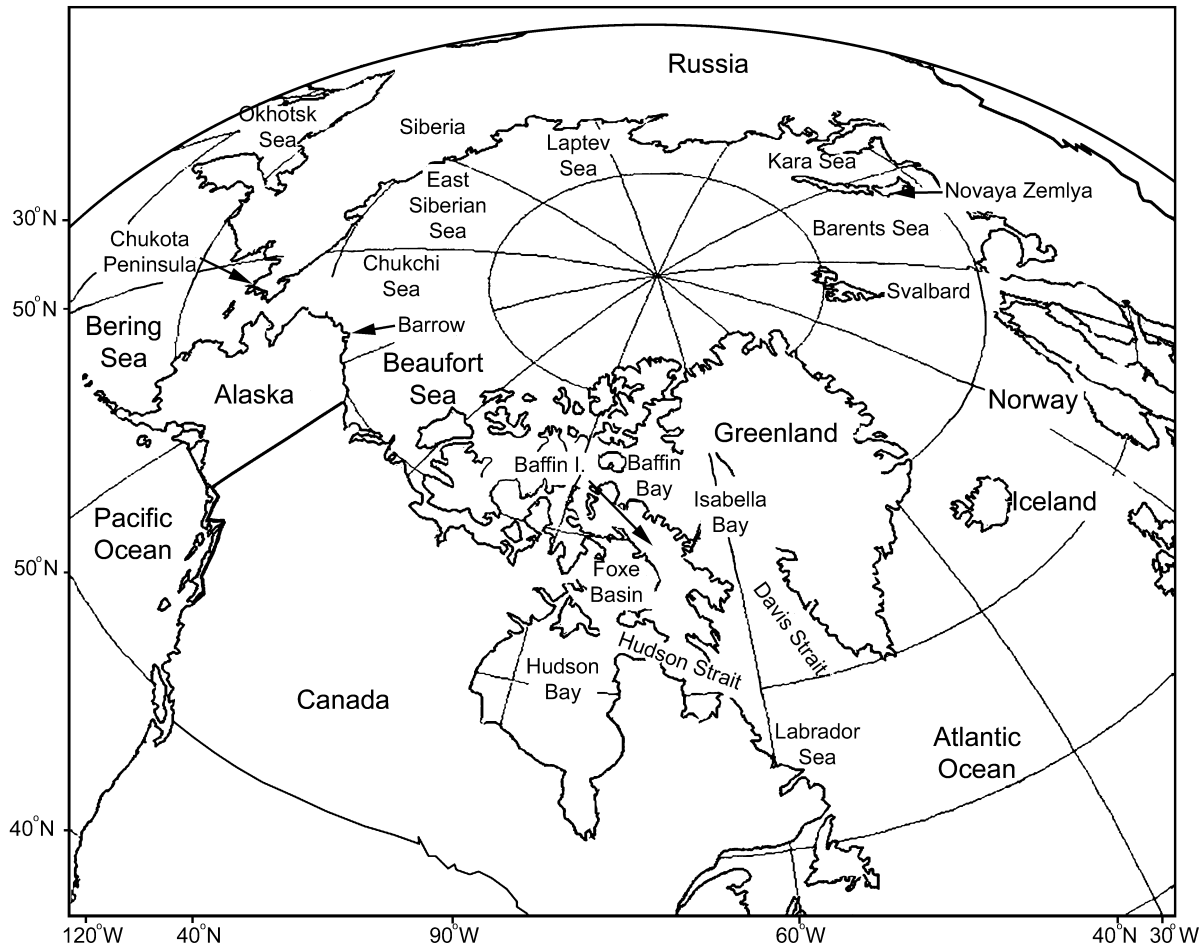


Fig. 1. Map of circumpolar area, including North Atlantic.

11,700 (Woodby and Botkin, 1993), although some whales were still being taken as recently as the 1970s (Reeves and Heide-Jorgensen, 1996). Current estimates of abundance are near 350 (Koski and Davis, 1980; Finley, 1990; Zeh *et al.*, 1993), and the viability of this stock is in doubt (Finley, 1990).

Hudson Bay stock

As mentioned in the preceding section, the Hudson Bay stock is not only genetically discrete from the Davis Strait stock but more closely related to B-C-B bowhead whales (Maiers *et al.*, 2001). Combining estimates from 1994 (Cosens *et al.*, 1997) and 1995 (Cosens and Innes, 2000) resulted in a minimum abundance of 345 (DFO, 1999), not including animals missed during the surveys. The original stock may have consisted of approximately 580 whales (Mitchell, 1977) as modified by Woodby and Botkin (1993).

Okhotsk Sea stock

There has been difficulty in assessing the historical distribution and abundance of bowhead whales in the Okhotsk Sea. North Pacific right whales (*Eubalaena japonica*) and gray whales (*Eschrichtius robustus*) were sometimes misidentified as bowhead whales, and whaling records collected during the short period of time (1848-57) this stock was hunted were incomplete (Bockstoce and Botkin, 1983; Bockstoce, 1986). In 1967-68, during a period of Soviet whaling, some of the misidentifications may have been deliberate to avoid laws protecting bowhead whales (Doroshenko, 2000). Pre-exploitation abundance was approximately 3,000 (Ross, 1993) or 6,500 (Mitchell, 1977).

Although Scammon (1874) stated that bowhead whales were hunted 'throughout the whole extent' of the Okhotsk Sea, certain areas were occupied by concentrations of animals during the summer months. In the northeastern Okhotsk Sea, whales were found in Penzhinskaya Gulf and Gizhiginskaya Gulf. The next area of concentration was to the southwest in Tauyskaya Bay. Farther south, the best whaling grounds were within the gulfs and bays south of the Shantarskiye Islands and west of Sakhalin Island (Moore and Reeves, 1993 provide additional details). Almost all of the areas where summer concentrations of bowhead whales occurred in the past are still occupied today, albeit in very low numbers.

In August 1995, during joint USA-Russian surveys, a few dozen bowhead whales were observed in a feeding aggregation south of the Shantarskiye Islands (Brownell *et al.*, 1997). Berzin *et al.* (1990) estimated the population in this area to be at least 250-300 animals. An estimate of abundance of 300-400 was made for the entire Okhotsk Sea based on data collected since 1979 (Vladimirov, 1994). However, 'no quantitative data are available to confirm' these estimates (Berzin *et al.*, 1995; Brownell *et al.*, 1997). There is some speculation as to whether animals found during the summer in the northeastern Okhotsk Sea form a distinct population separate from those in the Shantar region (Vladimirov, 2000). Doroshenko (2000) describes two routes used during the spring migration: some whales travelling to the Gulf of Shelikov, and others to the Shantar Islands. By July, these two groups appear to have joined in the Shantar Islands. The winter distribution is unknown because whalers left the Okhotsk Sea before the onset of winter storms in early November and did not return until June. Although some authors (e.g. Townsend, 1935;

Tomilin, 1957) suggest that originally there was a common stock between the Okhotsk and Bering Seas, others (e.g. Lindholm, 1863; Bockstoce and Botkin, 1983) have argued that the Okhotsk Sea stock has always been discrete from the B-C-B stock; recent genetic studies indicate a small but significant difference between these stocks (LeDuc *et al.*, 1998).

Bering-Chukchi-Beaufort Seas stock

The B-C-B stock is the only bowhead population showing appreciable recovery since the impact of commercial whaling over a century ago. An abundance estimate of 8,200 was derived from sightings and acoustic records made in 1993 at Barrow, Alaska (Zeh *et al.*, 1995b), indicating an annual increase of 3.2% since 1978 (IWC, 1995a; Zeh *et al.*, 1995b). George *et al.* (2003) presented the results of the 2001 survey, giving an abundance estimate of 10,020 (95% CI of 7,800 to 12,900) and an updated annual rate of increase of 3.4% (95% CI 2.1% to 4.8%). Despite this current increase, bowhead whales have not yet recovered large parts of their historic range; pre-exploitation feeding areas were much larger than at present (Bockstoce and Botkin, 1980). During the first decade of exploitation, 1848-58, bowhead whales were taken from April through October from the coast of Asia to 173°W and north to 69°N in the southern Chukchi Sea (Bockstoce and Botkin, 1980). The logbook data extracted by Bockstoce and Botkin (1980) indicate that during this decade, 105 whales were taken south of 60°N, and only 27 whales were taken here in the following decade (1859-68). In 1867, during an exceptionally light ice summer, several whaling ships went as far to the northwest as Wrangel Island, at the western edge of the Chukchi Sea, but no bowhead whales were encountered (Bockstoce and Burns, 1993). During the third decade, 1869-78, whales were only occasionally taken south of 60°N, and after 1878, whales were essentially eliminated from the area between 60°-63°N (Bockstoce and Botkin, 1980). As hunting continued and the population was reduced, the whalers travelled farther and farther north and east. The southern limit of the hunt retreated northward at a rate of about 3° latitude every 10 years (Bockstoce and Burns, 1993). Bockstoce and Burns (1993) noted the possibility that these whales responded to this intense hunting by leaving the accessible hunting areas, an observation made originally by both commercial and subsistence whalers. In 1889, steamships reached the summer feeding grounds off the Mackenzie River Delta in the Beaufort Sea, which remained the major focus of the industry until 1914, about the time that commercial whaling collapsed (Bockstoce and Botkin, 1980).

Stoker and Krupnik (1993) commented that early records from Siberia mention whaling as a summer activity (July-August), whereas commercial whaling in the late 1800s and early 1900s was carried out primarily during the spring and autumn migrations (April-early June and October-November). They contended that this difference in the timing of the hunt may support the hypothesis (e.g. Bogoslovskaya *et al.*, 1982; Bockstoce, 1986) of a separate bowhead stock which summered in the northern Bering Sea and Bering Strait before it was decimated by commercial whalers. Bockstoce and Botkin (1980) speculated (as did Fraker, 1984) that the bowhead population originally consisted of several discrete sub-populations, each with its own feeding area; however, these authors also recognised the possibility (as did Bockstoce and Burns, 1993) that there was originally only a single population that responded to

exploitation by moving farther north and east to safer areas near the ice or to areas that had not been previously exploited.

Burns (1993) supports the idea of a single stock. He has suggested that the records of relatively high numbers of bowhead whales summering in the Bering Sea prior to intense commercial whaling may reflect that: (1) some proportion of the commercially harvested whales in the Bering Sea may have actually been right whales, not bowhead whales; (2) commercial whaling in the North Pacific began after the 'Little Ice Age', and during colder periods, bowhead whales may have had a more southerly distribution than now; or (3) there have not been adequate surveys in the northwestern portion of the Bering Sea in summer. That is, the change in summer distribution may not be as dramatic as currently portrayed. Additionally, Burns (1993) points out that the documented increase in abundance of the B-C-B stock may lead to an expansion of its summer range. Indeed, the increase in sightings made in the Chukchi and Bering Seas in recent years (see below) may be an indication of a growing population expanding its range to refill former habitat (unless the increase in sightings is only the result of increased survey effort). Burns (1993) argued that the distribution of this species should be considered labile, affected easily by sea ice and availability of prey. In summary, then, the strongest evidence is for a continuous stock from the Bering to Beaufort Seas rather than multiple stocks summering in different areas.

Currently, the B-C-B stock is widely distributed in the central and western Bering Sea in winter (November-April), generally associated with the marginal ice front and found near the polynyas of St Matthew and St Lawrence Islands and the Gulf of Anadyr (Bogoslovskaya *et al.*, 1982; Brueggeman, 1982; Braham *et al.*, 1984; Ljungblad *et al.*, 1986; Brueggeman *et al.*, 1987; Bessonov *et al.*, 1990; Moore and Reeves, 1993; Mel'nikov *et al.*, 1998). From April to June, most of these whales migrate north and east, following leads in the sea ice in the eastern Chukchi Sea until they pass Pt Barrow where they travel east toward the southeastern Beaufort Sea (Braham *et al.*, 1980; 1984; Marko and Fraker, 1981). Most of the summer (June to September) bowhead whales range through the Beaufort Sea (Hazard and Cubbage, 1982; McLaren and Richardson, 1985; Richardson *et al.*, 1986; 1987a; b; Richardson, 1987; Moore and Clarke, 1991), predominately over outer continental shelf and slope habitats but independent of ice cover (Moore *et al.*, 2000). Distribution varies annually (Davis *et al.*, 1983; Thomson *et al.*, 1986; Richardson *et al.*, 1987a), affected in part by prey availability which is affected by surface temperature or turbidity fronts and anomalies (Borstad, 1985; Thomson *et al.*, 1986) and drilling rigs (Schick and Urban, 2000). During autumn (early September to mid-October), bowhead whales migrate across inner shelf waters (Moore *et al.*, 2000), moving west out of the Beaufort Sea, as evidenced during aerial surveys (Ljungblad *et al.*, 1987; Richardson, 1987; Moore *et al.*, 1989a; Moore and Clarke, 1992), radio-tracking (Wartzok *et al.*, 1990) and satellite-tracking (Mate *et al.*, 2000). From mid-September to mid-October bowhead whales are seen in the northeast Chukchi Sea, some as far north as 72°50'N (Moore and Clarke, 1993; Moore *et al.*, 2000). Whales migrate from Pt Barrow into the Chukchi Sea, with some whales turning southwest (247°True) along the axis of Barrow Canyon headed toward the Chukotka Peninsula (Moore and Reeves, 1993), while others head toward Wrangel Island (Mate *et al.*, 2000; Moore *et al.*, 2000), one group reaching the northern coast of the Chukotka Peninsula about the same time that

others arrive off the peninsula's eastern coast in the Bering Strait (Mel'nikov *et al.*, 1998). After reaching the coast, the whales follow it southeast to the Bering Strait (Bogoslovskaya *et al.*, 1982; Zelensky *et al.*, 1995). Autumn migrants begin arriving on the northern coast of the Chukotka in mid-September (Mel'nikov *et al.*, 1998), October (Mel'nikov *et al.*, 1997), November (Mel'nikov and Bobkov, 1994) or even December (Mel'nikov *et al.*, 1998) with large inter-year differences in the timing of the autumn migration through the Chukchi Sea (Mel'nikov *et al.*, 1998). By late October and November, many whales arrive in the Bering Sea (Kibal'chich *et al.*, 1986; Bessonov *et al.*, 1990), where they spend the winter.

Very few bowhead whales were found in the Bering or Chukchi seas in summer in the late 1970s and early 1980s (Dahlheim *et al.*, 1980; Miller *et al.*, 1986); however, there have been enough sightings to indicate that not all bowhead whales migrate to the Beaufort Sea. Mel'nikov *et al.* (1998) suggested that most bowhead whales make the Pt Barrow area the goal of their spring migration, and from there some continue east to the Beaufort Sea, some stay and others return to the west. Bowhead whales were consistently seen in the northeastern Chukchi Sea (near Pt Barrow) in summer from the mid-1980s to at least the early 1990s (Moore, 1992), and since then, summer sightings have included eight whales on 25 July 1999 near Pt Barrow (Moore, pers. obsv.) and 50 bowhead whales feeding off Cape Simpson on 19 August 2000 (C. George, pers. comm., North Slope Borough, Barrow, Alaska). In addition, small groups have been observed travelling northwest along the Chukotka Peninsula in May (Bogoslovskaya *et al.*, 1982; Bessonov *et al.*, 1990; Ainana *et al.*, 1995; Zelensky *et al.*, 1995), June (Mel'nikov and Bobkov, 1993) and July (Mel'nikov *et al.*, 1998). One group of seven whales was observed off Cape Netten, Chukotka Peninsula, on 26 July 1991 travelling north, and a group of seven was seen there on 27 September travelling east (Mel'nikov and Bobkov, 1994). Farther northwest, near Cape Schmidt, single animals were observed on 5 August and 1 September by the crew of the Russian ice-breaker *Krasin*. Bowhead whales were present throughout the summer of 1994 along the southeastern Chukotka Peninsula (127 sightings in June, 59 in July, 5 in August, and 6 in September; Ainana *et al.*, 1995) and the easternmost portion of the peninsula (21 sightings in June and 39 in August; Zelensky *et al.*, 1995). On 10 and 11 August 1995, four groups of bowhead whales, with 5-10 per group, were seen off the southern tip of the Chukotka Peninsula, moving west into the Gulf of Anadyr (Mel'nikov *et al.*, 1998). Moore *et al.* (1995) suggested that bowhead whales seen in the Chukchi Sea in early October could have migrated from the Beaufort Sea three weeks earlier, as whales seen in the Alaskan Beaufort Sea in August and early September were often swimming west (Moore *et al.*, 1989b). There appears to be an increase in summer sightings in the Bering and Chukchi Seas, perhaps as a function of increased survey effort but possibly also representative of increased range expansion as the population abundance increases.

EVIDENCE FROM VARIOUS METHODS USED TO INVESTIGATE STOCK IDENTITY

Geographic distribution and abundance

Commonly, information on where animals have been sighted or harvested has been important in discussions of stocks differentiation. The five stocks of bowhead whales were originally delimited essentially from information on their distribution, and the stocks were named according to the

principal areas in which they were found. Much of the original data on distribution come from records of whaling effort (e.g. Scammon, 1874; Bockstoce and Botkin, 1983) whereas current distribution is recorded from aerial observations (e.g. Moore and Clarke, 1991; Rugh *et al.*, 1994), vessels (e.g. Miller *et al.*, 1986), acoustics (e.g. Moore *et al.*, 1989a), shore (e.g. Rugh and Cabbage, 1980), ice-based sites (e.g. George *et al.*, 1995), satellite tags (e.g. Mate *et al.*, 2000) or reidentifying individuals (see section below). Apparent gaps in distribution between areas of relatively high sighting rates have been attributed to stock separation (Perrin, 2001). The reasons for these gaps sometimes appear obvious (e.g. when there are barriers such as land masses), but there are less obvious features (such as ocean fronts) that may also be effective (Perrin, 2001).

Stocks may be differentiated if abundance changes in one stock relative to another. The reverse of this is also true in that abundances rising proportionally in two areas might indicate a common stock. This argument has been used to show that the B-C-B stock of bowhead whales should not be separated into a Bering/Chukchi population and a Beaufort Sea population (see section on B-C-B stock).

Genetics

Genetics has recently become an important tool for the discrimination of whale stocks. Punt *et al.* (2000) used North Pacific minke whale (*Balaenoptera acutorostrata*) allele frequency data to evaluate the relative probabilities of alternative stock structures. Baker *et al.* (1998) examined Southern Hemisphere humpback whale (*Megaptera novaeangliae*) stocks through mitochondrial DNA variation and maternal gene flow. Richard *et al.* (1996) used multiple molecular genetic analyses to study patterns of kinship in groups of sperm whales (*Physeter macrocephalus*). The practicality of assessing gray whale (*Eschrichtius robustus*) management units was explored using mitochondrial DNA and was found to have good potential for providing unambiguous answers (Ramakrishnan and Taylor, 2001).

There have been only a few genetic studies that examined the relationships among bowhead whale stocks or putative sub-stocks. Previous genetic studies conducted by Rooney *et al.* (1999; 2001) focused primarily on investigating the extent of potential bottleneck effects on genetic variability in the B-C-B stock. Some preliminary work has been done on the degree of genetic differentiation between the B-C-B stock and the Okhotsk Sea stock (LeDuc *et al.*, 1998) as well as between the B-C-B and the Hudson Bay and Davis Strait stocks (Maiers *et al.*, 2001). Rosenbaum *et al.* (2001), proposed further research to evaluate bowhead whale genetic diversity and population structure through historical and extant samples such as the DNA extractions done from bowhead skulls at an archaeological site on the Chukotka Peninsula (Kellar and Brownell, 2001). The findings of some of these studies are summarised below, and potential avenues for investigating stock structure within the western Arctic are also discussed.

Analyses of mitochondrial DNA polymorphism

Rooney (1998) analysed the first 455 nucleotides of the mitochondrial DNA (mtDNA) control region from 99 bowhead whales taken from the B-C-B stock, and Rooney *et al.* (2001) analysed patterns of genetic variability among these whales. The samples were taken from the northern coast of Alaska, with the exception of six that were from whales landed on St Lawrence Island in the Bering Sea. The primary conclusion of this research was that there was no genetic bottleneck in the B-C-B stock and that the level of

genetic variability has remained relatively high (nucleotide diversity = 1.63%) in spite of the depletion of the population before the 1900s. The population reached its lowest abundance around 1914, when commercial whaling ceased; at that time there were probably 1,000-3,000 bowhead whales (Woodby and Botkin, 1993). However, the mtDNA data indicate that the effective population size had remained large despite the extensive reduction in total population numbers (Rooney *et al.*, 2001). These researchers were further interested in determining the time to the most recent common ancestor of mtDNA haplotypes in the B-C-B stock. By using phylogenetic and coalescent approaches, further analyses revealed that this population had undergone a size expansion initiated approximately 267,000 years before the present (Rooney *et al.*, 2001). These results suggest that the formation of the M'Clintock Channel sea-ice plug roughly 8,500 years ago did not influence the signature of historical population size change in the mtDNA sequence data (Rooney *et al.*, 2001). Analyses of mtDNA control region sequence data indicate that the Hudson Bay stock is more closely related to the B-C-B stock than to the Davis Strait stock (Maiers *et al.*, 2001). This confirms the suggestion of Rooney (1998) and Rooney *et al.* (1999) that the Hudson Bay and B-C-B stocks were a part of a larger stock until relatively recent times, which is consistent with the idea that only recently the M'Clintock Channel sea-ice plug served as a barrier to gene flow between these two stocks (Dyke *et al.*, 1996; Rooney *et al.*, 1999).

To investigate the possibility that the B-C-B stock might be further sub-divided, the pattern of polymorphism in the mtDNA control region sequences was compared between the six samples from St Lawrence Island (in the Bering Sea) and 93 samples from sites in northern Alaska where the whales presumably were migrating to the Beaufort Sea (Rooney, 1998; Rooney *et al.*, 2001). No differences were found. The average number of nucleotide substitutions per site between these groups (D_{xy} ; Nei, 1987, equations 10.20 and 10.24) was 0.01744 ± 0.00214 , while the net number of nucleotide substitutions per site between groups (D_a ; Nei, 1987, equations 10.21 and 10.23) was -0.00017 ± 0.00237 ; there were no fixed differences between these groups. The sample size from St Lawrence Island was small, and more samples are needed to increase the power of this test. However, it is not known whether whales taken at St Lawrence Island were part of the northward migration through the Bering Strait and into the Beaufort Sea or whether they represent whales that remain year round in the Bering Sea. It would be more definitive if samples were collected from whales in the Bering Sea in July or August, but this effort has been limited by poor access and the scarcity of these whales. A similar comparison was made between whales in the B-C-B and Okhotsk Seas using mtDNA data, revealing small but significant differences (LeDuc *et al.*, 1998).

Analyses of microsatellite marker polymorphism

Rooney *et al.* (1999) investigated the patterns of microsatellite DNA polymorphism in the B-C-B stock from 108 bowhead whales, six of which came from St Lawrence Island. As with the analysis of mitochondrial DNA polymorphism, these researchers found no evidence of any recent genetic bottlenecks. In this study, five out of 15 polymorphic loci showed evidence of heterozygote deficiency. However, Hardy-Weinberg equilibrium could not be rejected at a table-wide level based on analyses using Fisher's exact test. The observed heterozygote deficiencies at four of the five loci are apparently the result of high

frequencies (0.089, 0.206, 0.348 and 0.539) of null alleles. Similar to the mtDNA studies of Rooney *et al.* (2001), further analyses of the microsatellite marker polymorphism data indicated bowhead whales had a period of historical population growth. As mentioned earlier, Maiers *et al.* (2001) found that the B-C-B and Hudson Bay stocks are more closely related to each other than either is to the Davis Strait stock based on studies of microsatellite polymorphism patterns. This may have resulted from two genetically distinct stocks, one from the west and one from the east, immigrating into the eastern Arctic after the last glaciation and subsequently mixing (Maiers *et al.*, 2001).

When data from Rooney *et al.* (1999) were used to compare the St Lawrence Island whales to the remaining B-C-B whales, no evidence of genetic differentiation could be found ($0.05 < p < 0.1$). This result was obtained by using an exact test (probability test) of population differentiation (Raymond and Rousset, 1995; Goudet *et al.*, 1996), specifically the genic test of population differentiation. Exact tests of population differentiation are reported to be accurate and unbiased in the case of small sample size or low-frequency alleles (Raymond and Rousset, 1995; Goudet *et al.*, 1996). However, such results should be used with caution because a larger sample size might reveal different patterns of genetic polymorphism, which could in turn influence tests of genetic differentiation.

While no evidence of stock substructuring was found in the comparison between bowhead whales landed at St Lawrence Island and whales landed along the north coast of Alaska, the summer feeding destination of the whales collected from St Lawrence in the spring is unknown. As with the analysis of mitochondrial DNA polymorphism, this compromises the interpretation of these results. And as mentioned in the previous section, a more appropriate comparison would be between whales that remain associated with the Chukotka Peninsula in the summer and those that migrate along the north coast of Alaska, past Pt Barrow, into the Beaufort Sea. A sufficient sample is already available for the latter (108 animals examined by Rooney *et al.*, 1999); however, it is very difficult to collect samples from whales that undoubtedly stay in the Bering or Chukchi Seas in the summer. Sampling of these whales will need to be made through biopsies from live whales rather than relying on a subsistence harvest or opportunistic strandings.

Ongoing studies of genetic diversity and population structure in the bowhead whale can be evaluated through an expanded database that includes samples from all regions where bowhead whales are currently found as well as from museums where baleen or bone samples may be archived. For example, Rosenbaum *et al.* (2001) reported that DNA has been extracted from tissue over 1,000 years old (a bone from the Viking era in Norway and baleen from excavations of a Thule Inuit whaling village on Somerset Island); such data may be useful for examining historical patterns of population structure. Currently studies are underway to learn more about genetic identity of the Okhotsk Sea stock (e.g. LeDuc *et al.*, 1998) and the eastern Arctic stocks (e.g. Maiers *et al.*, 2001). Previously, LeDuc *et al.* (1998) compared patterns of microsatellite polymorphism in the Okhotsk Sea and B-C-B stocks and found small differences, similar to their study on mtDNA polymorphism patterns.

Morphology and morphometrics

Morphological differences between putative stocks may provide evidence of low genetic dispersal, but these differences might be effected by environmental factors, so differences in habitat or geographic distribution should be

examined before making conclusions about stock separation (Perrin, 2001). Morphological comparisons among various whale stocks have used various body proportions (including length), baleen, throat grooves, skeleton, internal organs and pigmentation (Perrin, 2001). No comparative studies of morphology and morphometrics have been conducted yet among the five bowhead whale stocks. Within-stock variability has been mentioned for nearly all of the stocks though insufficient data have been gathered to confirm these differences. For the Spitsbergen stock, whalers described how a group of whales would arrive out of the east during heavy ice years to summer along the southern coast of Spitsbergen, then return east as the ice retreated (Zorgdrager, 1720; summarised in Eschricht and Reinhardt, 1866). These whales were said to look and behave differently from the other Spitsbergen whales. Establishing any genetic or morphological variations between these groups is now virtually impossible given how rare sightings are. Similar references to 'small whales' or different 'races' were made by whalers operating in the Okhotsk Sea (e.g. poggy: Scammon, 1874) and in Davis Strait (e.g. middle-icers, rock-nosers, Pond's Bay fish: Brown, 1868). A possible morphological variant of the B-C-B stock (the *ingutuk*) has been described as smaller, paler and possessing denser bones than other bowhead whales (Braham *et al.*, 1980; Fetter and Everitt, 1981); however, Jarrell (1981) showed that *ingutuks* are yearling bowhead whales and are not genetically distinct from other bowhead whales, a finding confirmed by phylogenetic analyses based on morphometric data and mtDNA polymorphism (A. Rooney, R. Tarpley and J.C. George, unpubl. data).

Individual identification

There are several relatively simple approaches to stock identity using reidentification of individual whales. When a whale is found with an identifiable harpoon head or other marker used on whales in a different stock, then it is clear that the whale travelled between stock boundaries. Aerial photography allows for reidentification of individual whales which could, in the same way as harpoon markers, show movements of whales between stock areas.

Tags and other marks

Identifiable markers, such as parts of harpoons or discovery tags, provide insights on longevity or movements of individual whales. Ivory or stone harpoon heads, not used by Eskimos for over a century, were found in five recently harvested whales. If these represent some of the last primitive harpoons ever used, and if they struck very young whales, then this evidence indicates that bowhead whales may live > 50yrs (Philo *et al.*, 1993), > 75yrs (George *et al.*, 1995) or > 100yrs (George *et al.*, 1999). Such longevity has also been indicated via eye lens aspartic acid racemisation (George *et al.*, 1999). Commercial whalers reported incidents in which 'unsuccessfully harpooned' whales from one stock (Davis Strait or Spitsbergen) were later killed or found dead in the waters inhabited by the other stock (Eschricht and Reinhardt, 1866; Reeves *et al.*, 1983). Also, some exchange between the North Atlantic and the B-C-B stock has been documented. Bockstoce and Burns (1993) described two incidents in which whaling irons used in the western North Atlantic fishery were later found in whales taken in the Chukchi Sea, and Tomilin (1957) reviewed at least four reports, some as far back as 1643, of European-made harpoons found in bowhead whales in the Bering or Chukchi Seas.

A USSR discovery tag found in a bowhead whale that had been marked in October 1981 off Chukotka was recovered when the whale was taken off Wainwright, Alaska, in May 1983 (Dronenburg *et al.*, 1984).

In 1992, 12 whales were tagged off the Mackenzie Delta in the Canadian Beaufort Sea with Argos satellite-monitored radio tags (Krutzikowsky and Mate, 2000; Mate *et al.*, 2000). Although only one whale was successfully tracked out of the Beaufort Sea, it documented the autumn migration across the Chukchi Sea to Wrangel Island and south through the Chukchi Sea, a migration that had been inferred through sighting data (Moore and Reeves, 1993).

In 2001, five bowhead whales were instrumented with satellite transmitters in northwestern Disko Bay, West Greenland (Heide-Jorgensen *et al.*, 2001). Two of the whales travelled west on different routes across Baffin Bay toward Lancaster Sound, northern Canada, in 9-10 days. This confirms that bowhead whales on both sides of Baffin Bay are from the same stock.

Photo-identification

Aerial photography has proved to be a viable technique for identifying individual bowhead whales (Rugh *et al.*, 1992). Most images have been collected during the whales' spring migration past Pt Barrow (Rugh, 1990) and in the summer in the Beaufort Sea (Miller *et al.*, 1992); a few have been taken in the Bering Sea in winter (NMFS, unpubl. data) and in the Canadian Arctic (Finley, 1990). As more images become available from other areas, comparisons may be made that could establish movements of whales between stocks, if these movements do occur. It would be especially interesting to collect photographs of bowhead whales in the summer in the Chukchi and Bering Seas for the possibility that the same whales may have been seen in the Beaufort Sea during other summers.

Acoustics

If whale stocks have been isolated for a long time, their call types may change. For example, blue whale (*Balaenoptera musculus*) calls recorded in the Northeast Pacific are quite distinct from calls recorded in the western Pacific, and both show characteristic differences from southern blue whale calls (e.g. Stafford *et al.*, 1999).

To date, comparison of the limited recordings available has not resulted in positive attributions of call differences among bowhead stocks. Call types have been compared between bowhead whales migrating past Pt Barrow in the spring and whales in the Beaufort Sea during summer and autumn, and comparisons have been made between bowhead whales in the Davis Strait and the B-C-B (Würsig and Clark, 1993). Calls recorded from whales migrating past Pt Barrow were 85% simple-calls and 15% complex-calls, while those recorded near whales socialising in the Beaufort Sea during late summer and autumn were 52% simple-calls and 48% complex-calls. These differences are likely due to differences in sampling methods (ice-based continuous recordings vs 1-2 hour recordings from expendable sonobuoys) and primary behaviours (i.e. migrating vs socialising) in each locale. Differences in call characteristics as well as call proportions were found between recordings of western Arctic and Davis Strait bowhead whales (Würsig and Clark, 1993). In general, calls recorded near socialising whales in Isabella Bay were most often the complex-type, and these pulsed-tonal calls were often two to four times longer in duration than similar calls recorded from the B-C-B stock. Again, differences in recording circumstances probably contribute to the variability in call proportions. To

make call-type comparisons reliable, environmental, temporal, behavioural parameters and sampling methods must be considered and standardised to the extent possible.

Passive acoustics has proven itself a reliable tool to monitor the timing, and sometimes the spatial distribution, of migrating bowhead whales. Acoustic detection methods have augmented the spring visual census of bowhead whales off Pt Barrow since 1984 (Clark *et al.*, 1996; Clark and Ellison, 2000). Passive acoustic location based on arrival-time differences on a sparse array of three to five hydrophones deployed from 1.5-4.5km along the ice edge has provided detailed information on the variability of bowhead distribution offshore the counting stations, both within and among years. This information is fundamental to improving estimates of stock abundance (Zeh *et al.*, 1993). In autumn 1986 and 1987, acoustic monitoring augmented sightings from aerial surveys to determine migration timing past Barter Island and Barrow, respectively (Moore *et al.*, 1989a). Three periods of peak calling activity were recognised over the course of each season, with the temporal pattern described by calling rates generally agreeing with those from aerial survey sighting rates.

Pollutant burden

Pollutant levels in tissue samples represent a potential source of information for investigating stock structure (e.g. Fujise *et al.*, 1997), assuming that individuals from distinct stocks display different levels of contaminants. This technique has the advantage over some of the other stock identification methods in that samples can be collected by biopsy from live animals (Perrin, 2001). Unfortunately, data only exist for animals that pass Pt Barrow during the spring migration. However, stock identification studies using information on pollutant levels presume that such levels will change imperceptibly through time for the respective areas. If such changes are substantial or if pollutant levels fluctuate moderately over the short term, then the reliability of studies based on pollutant levels would be called into question.

Parasites and predators

The possibility that distinct stocks of whales will harbour different parasites or different levels of infestation of the same parasites has been suggested as a useful tool for stock discrimination (e.g. Balbuena *et al.*, 1995). Such information has been used in studies of other cetaceans, such as the southern minke whale, *Balaenoptera bonaerensis* (Bushuev, 1990), sperm whales, *Physeter macrocephalus* (Dailey and Vogelbein, 1991) and pilot whales, *Globicephala melas* (Balbuena *et al.*, 1995). Virtually all information concerning bowhead whale parasite burden comes from studies of the B-C-B area, as this is the only regularly exploited stock with access to samples demonstrating parasite profiles. As yet, there are no data from animals from other stocks or geographic locales, so comparative analyses are not yet possible.

Whales in different areas may be differentially impacted by predators, as indicated by scarring (Perrin, 2001). For example, Bryde's whales (*Balaenoptera edeni* and *B. brydei*) off South Africa have differences in scarring depending on whether the whales inhabit primarily offshore or coastal areas (Best, 1977), and sperm whale populations have been differentiated based on environmental marks, including scars caused by killer whales (Dufault and Whitehead, 1993). Bowhead whales can reach great ages (George *et al.*, 1999) and accumulate many scars (Rugh *et*

al., 1992). Bowhead whales that tend to explore deep into the ice pack are more vulnerable to having ice-caused scarring than bowhead whales that spend most of their time near the ice front or in open water. The reverse may be true for scarring caused by killer whales, in that bowhead whales are more vulnerable to killer whale attacks when they are away from sea ice. Bowhead whales in the western Arctic do not appear to have as many scars from killer whale bites as do those from the eastern Arctic (George *et al.*, 1994; Finley, 2001), but this is clearly insufficient information upon which to base stock differentiation.

Feeding ecology

Differences in feeding ecology may also provide a basis for differentiating between stocks. For instance, two morphologically distinct forms of Bryde's whale off South Africa have consistent dietary differences (Best, 1977). However, gut contents are a very transient index and may be easily affected by ecological factors, whereas isotope ratios in hard tissues, parasites and tooth ultrastructure reflect characteristics over much of the lifetime of an individual (Perrin, 2001). In bowhead whales, $\delta^{13}\text{C}$ techniques have been used to establish tracer 'signatures' in zooplankton from various seas to indicate the respective feeding areas of bowhead whales across a chronological record of as much as 20 years stored in their baleen (Schell and Saupe, 1993). However, if whales that migrate to the Beaufort Sea for the summer do a preponderance of their feeding in the Bering and Chukchi Seas in autumn and winter (as presented by Schell and Saupe, 1993), it will be difficult to discriminate them from whales that reside year-round in the Bering and Chukchi Seas.

Fatty acid analysis, tracing signals from the prey to lipid deposits in a whale, may become a powerful tool in describing the feeding ecology of bowhead whales through a better understanding of their physiology, biochemistry and anatomy (Castellini, 2000).

Biological features

Differences in biological parameters or factors such as conception dates can provide valuable information on stock identity; for example, minke whales off Japan have two foetal cohorts per year, indicating a separation in breeding seasons of two stocks (Kato, 1992). However, the mating period for bowhead whales is not well defined. Apparent sexual activity has been observed in most months of the year (as reviewed in Koski *et al.*, 1993). Although the calving period may extend across half of the year, it seems that most calving occurs from April to early June. Therefore, most conceptions must occur approximately one gestation period (i.e. 13–14 months) earlier (Nerini *et al.*, 1984; Koski *et al.*, 1993), from March to May. Foetus sizes indicate that most conceptions occur during late winter or spring, and there is no evidence of delayed implantations (Koski *et al.*, 1993). This would mean conceptions occur during the spring migration, which provides a distinct possibility that bowhead whales who share a wintering area have opportunities to mate with animals that feed (spend the summer) in various geographic regions.

Other means that may potentially be used for discriminating stocks, such as differences in reproductive rates or age and sex structures (Perrin, 2001), will probably not help discriminate bowhead stocks. There is a very low probability that sufficient sample sizes will be collected for any stock other than the B-C-B stock.

CONCLUSIONS

The most effective way to examine questions of stock identity is to consider results from a suite of genetic and non-genetic techniques (e.g. Donovan, 1991; Perrin, 2001). The discovery of genetic differences between the Hudson Bay and Davis Straits stocks with no land barrier between them, provides a reason to investigate whether a similar separation occurs within the B-C-B management stock. To examine this question, one or more of the following approaches should be attempted: (1) genetic analysis of bowhead whales in the Bering Sea or Chukchi Sea in summer should be compared with samples collected from animals migrating past Pt Barrow; (2) multi-year aerial or vessel surveys, augmented by acoustic detection of calling whales, should be carried out along the Russian coast of the Chukchi Sea and north of Pt Barrow during the spring migration and during the summer feeding season to detect the consistency of whale occurrence; (3) satellite tagging of animals should be carried out in late spring in the Bering Sea to determine if whales seen there still migrate to the Beaufort Sea; (4) aerial photography should be attempted to capture images of bowhead whales summering in the Bering and Chukchi Seas for comparison to images collected from Pt Barrow during the spring migration and images from the summer in the Beaufort Sea; (5) acoustic recordings should be made to determine if there are differences in call characteristics, or proportions, that can be attributed to stocks in different areas; and (6) tissue analysis should be conducted to differentiate pollutant, parasitic or isotope levels.

At this time, the recognition of a single B-C-B stock is the most appropriate interpretation of the available data. In the many reviews of this issue undertaken by the IWC Scientific Committee, it has always concluded that a single-stock designation was appropriate based on evidence from a number of techniques as listed below.

- (1) Very few bowhead whales are seen in the Bering or Chukchi Seas in the summer or early autumn, at a time when bowhead whales are common in the Beaufort Sea; however, bowhead occurrence seasonally increases in each of these areas at a time best explained as a migration of one stock from the Bering to the Beaufort Seas and back.
- (2) There may have been an increase in summer sightings in the Chukchi and Bering Seas over the past several decades. This increase is probably due to the increase in abundance of the B-C-B stock. Such an increase would not be discerned if there were separate, small stocks.
- (3) The highly labile nature of the bowhead migration (affected by sea ice, food availability and potentially by anthropogenic perturbations) allows for whale occurrence in areas other than the expected migratory routes. Some whales might migrate east in the spring and return west well before the typical autumn migration; some whales might not migrate east of the Chukchi Sea in some years; and some whales might not migrate out of the Bering Sea.
- (4) Virtually all of the whales harvested by subsistence hunters on St Lawrence Island are taken in the winter or spring, a time when whales are probably migrating to or from the Beaufort Sea.

In conclusion, the available evidence (mostly through geographic distribution) indicates that there are currently five stocks of bowhead whales: the Spitzbergen, Davis Strait, Hudson Bay, Okhotsk and B-C-B stocks. Although

there appears to be some degree of geographical and genetic differentiation between these stocks, there are also many indications that these whales can and have intermingled across the Arctic.

ACKNOWLEDGEMENTS

This paper was much improved by comments from Tom Albert, Craig George, Todd O'Hara and Robert Suydam (Department of Wildlife Management, North Slope Borough, Barrow, Alaska); Robyn Angliss (National Marine Mammal Laboratory, Alaska Fisheries Science Center, NMFS, NOAA, Seattle, Washington); Robert Brownell, Jr. and Barbara Taylor (Southwest Fisheries Science Center, NMFS, NOAA, La Jolla, California); Geoff Givens (Dept. of Statistics, Colorado State University, Fort Collins, Colorado); Judy Zeh (Statistics, University of Washington, Seattle, Washington); and two anonymous reviewers. Their efforts in reviewing this case study were much appreciated.

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Date received: 8 October 2001.

Date accepted: 18 December 2002.