The enigmatic whale: the North Atlantic humpback

Tim D. Smith[1] and Daniel G.Pike[2]

[1]*World Whaling Project, 1774 Sterling Drive, Redding CA 96003, USA*
[2]*1210 Ski Club Road, North Bay, Ontario, P1B 8E5, Canada*

ABSTRACT

We know more about the North Atlantic humpback whale (*Megaptera novaeangliae*) than we do for virtually any other cetacean, yet attempts to use this information to describe the status of the populations in this ocean basin have not proven satisfactory. The North Atlantic humpback has been the subject of extensive research over the past few decades, resulting in a substantial amount of knowledge about what has proven to be a species with a very complex life history and population structure. While several population models have been developed to integrate the available information, the data overall are not well described by any of the models. This has left considerable uncertainty about population status, and has raised questions about the interpretation of some of the data. We describe 7 specific areas where puzzling or ambiguous observations have been made; these require closer attention if population status is to be determined. These areas raise several fundamental questions, including: How many breeding populations are there? How much do the populations mix on the feeding grounds? How has the distribution of animals on both feeding and breeding grounds changed? We identify additional research needed to address the 7 areas and these questions in particular, so that population status might be determined.

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INTRODUCTION

"Round about the accredited and orderly facts of every science there ever floats a sort of dust cloud of exceptional observations . . . which it always proves more easy to ignore than to attend to . . .. Anyone will renovate his science who will steadily look after the irregular phenomena, and when science is renewed, its new formulas often have more of the voice of the exceptions in them than of what were supposed to be the rules.

The art of being wise is the art of knowing what to overlook."

William James

Over the past half century humpback whales (*Megaptera novaeangliae*) in the North Atlantic have been increasing in numbers in most areas as evidenced by the results of sighting surveys and of studies using photographic and genetic methods of identifying and reidentifying animals, here referred to as reidentification methods. These studies have resulted in these being among the best known cetacean populations in the world. But while much is known, a recent study by the Scientific Committee of the International Whaling Commission (IWC) has shown that we do not yet have a coherent overall understanding of the population dynamics and biology of humpbacks in the North Atlantic (IWC 2003). Developing an understanding of the status of humpbacks in the North Atlantic is important to address management considerations that arise in the context of individual nations as well as in the broader context of the IWC, the North Atlantic Marine Mammal Commission (NAMMCO), the United Nation's International Union for the Conservation of Nature, and the Convention on International Trade in Endangered Flora and Fauna (Klinowska, 1991). Although formally declared endangered under the US Endangered

Species Act, that declaration along with those for several other species of great whales was made globally and without formally developing and applying criteria. The blanket declaration of endangered status globally without specific criteria makes reconsideration of the present day appropriateness of that designation important, especially in light of the apparent increases in numbers of this species. Population status of cetaceans, although often treated simply in terms of present abundance relative to pre whaling abundance, is more appropriately treated as a question of historical ecology (Holm *et al.* 2001). In addition to past and present abundance of individual breeding populations, in the case of humpback whales other forms of population structure, range and distribution are important to understand, both in the present and where possible in the past. In many ways determining the status of humpbacks in the North Atlantic in a way that will allow useful management advice requires such broader considerations.

In light of this importance, the North Atlantic Marine Mammal Commission's Scientific Committee invited us to prepare a summary of recent and needed studies of the North Atlantic humpback relevant to determining status. Although we have written within the context of a volume where many other papers describe what is known about this species, we have briefly outlined the basic understanding of humpbacks in the North Atlantic especially as is relevant to understanding the basic issues that have arisen in the attempted assessment. Additional details are given where relevant below.

In this ocean, the humpback whale ranges from the equator to the Arctic pack ice (Winn and Reichley 1985). Winter calving and mating occurs in low latitudes, in recent times, primarily on offshore banks and off insular coasts on the Atlantic margins of the West Indies (Winn *et al.* 1975, Whitehead 1982, Smith *et al.* 1999). Historically humpbacks were caught in the winter primarily further south through the Windward Islands (Winn *et al.* 1975, Mitchell and Reeves 1983) and near the Cape Verde Islands in the eastern North Atlantic (Braham 1984). In spring, North Atlantic humpbacks migrate to several high latitude feeding grounds, which they occupy during the summer and fall (Smith *et al.* 1999). Feeding grounds are located in the Gulf of Maine, off the eastern Canadian maritime provinces (Canada), along West Greenland, around Iceland (including Jan Mayen), and to the north of Norway.

Humpback whaling reduced abundances to low levels throughout the North Atlantic during the late 19th and early 20th centuries (Braham 1984, Mitchell and Reeves 1983, Winn and Reichley 1985). Aboriginal whaling for humpbacks continued in West Greenland until 1985, and continues at low levels on Bequia in the Windward Islands (IWC 1994).

The reduction in harvests in the 20th century led to an increase in population size at least in the western North Atlantic. Photographic capture recapture data provide the longest time series of estimates of abundance for this component of the humpback population. These data suggest a steady increase of roughly 3% per year from 1979 to 1993 (Stevick *et al.* 2003). In addition, data on relative and absolute abundance are also available for several of the feeding grounds in the North Atlantic (*e.g.* Clapham *et al.* 2003, Larsen and Hammond 2004, Øien 2009, Pike *et al.* 2009, Paxton *et al.* 2009). Further, genetic mark recapture data have been used to estimate the proportion of the animals off Iceland and Norway that breed in the West Indies (IWC, 2002, 2003). We address the question of research priorities using the advice of William James quoted above. We describe "exceptional observations" in 7 specific areas that have proven puzzling or ambiguous, that is, enigmatic, relative to the status of North Atlantic humpback whales. Then we attempt to use the rigor of the results of recent population modeling to pragmatically balance the tendency towards ignoring the "dust cloud of exceptional observations" and the need for "knowing what to overlook" for each of these 7 enigmas. We use this analysis to suggest directions for future research.

First enigma:
Breeding population structure

While the evidence for the existence of 2 breeding populations is clear, 3 "exceptional observations" that have not been completely accounted for raise the question of the existence of a third breeding group. First, data were collected from catches in a fishery that occurred around

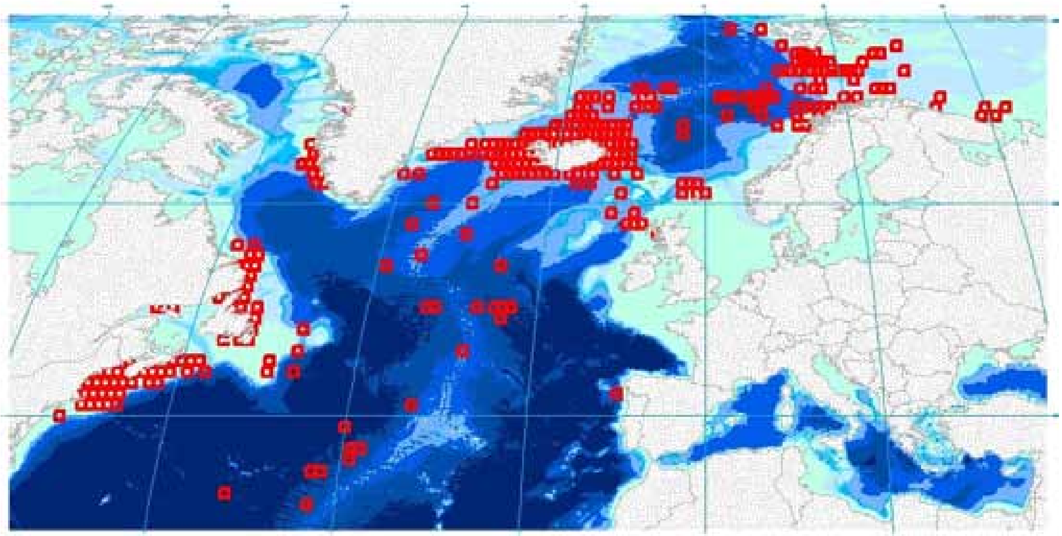

Figure 1. *The location of those 1 degree squares of latitude and longitude where humpback whales were reported during July and August in 1 or more sets of sightings data collected aboard whaling, research and whale watching vessels. Whalers included mid 20th century baleen whalers (Sigurjønsson and Gunnlaugsson 1990) and mid 19th century sperm whalers (Reeves et al. 2004). Research vessels included late 20th and early 21st century fishery surveys and directed cetacean sighting surveys (Paxton et al. 2009, Pike et al. 2009). Whale watching vessel data was primarily from the Gulf of Maine (Peter Stevick personal communication). Search effort and efficiency varied greatly among the data sets, so only presence and absence are shown in order to describe broad scale spatial distribution patterns.*

the beginning of the 20th century from February to March off Finmark, Norway (Ingebrigtsen 1929). Included in the catches were females with very small and very large, nearly full term, fetuses. The latter females would have had to travel roughly 7,000 km to give birth in either the Cape Verde Islands or the Caribbean breeding grounds in a few weeks based on the present breeding season. This would require sustained swimming at speeds approaching 10 km/hr for about 30 days. While sustained movements of this nature are not impossible, these observations raise the possibility of calving further north. Further, singing whales have been detected acoustically in the southern Norwegian Sea in the winter (IWC 2002). This is earlier than the post-breeding season singing reported by Clark and Clapham (2004), and although there could be other explanations as those authors suggest for whales singing away from breeding grounds, such winter activity is consistent with there being breeding in that area. In addition, humpback whales are regularly sighted throughout the winter off Iceland, particularly on the capelin fishing grounds (Gisli Víkingsson, Marine Research Institute, Reykjavik, Iceland, pers. comm.). While none of these observations are definitive about the existence of such a population, they suggest the possibility of there being more than 2 breeding populations in the North Atlantic.

Second enigma:
Feeding season distribution

One uncertainty about feeding grounds is that many sightings of whales have been made in summer months outside the 5 feeding grounds defined in the IWC assessment model, even though at least in the western grounds Stevick *et al.* (2006) noted from movements of identified whales site fidelity at much smaller spatial scales than the feeding grounds themselves. The broad scale distribution patterns of the feeding grounds are relatively well defined by the areas with and without recorded sightings (Fig. 1), although some of the areas without recorded sightings are undoubtedly due to limited sighting spatial coverage. On the other hand, some of these sightings where searching effort cannot be measured in comparable terms revealed aspects of the distribution that have not previously been clear to us. Whales in the 3 western feeding grounds identified in the IWC assessment model (Gulf of Maine, Eastern Canada and Western Greenland) have relatively compact and coastal distributions, although there are discontinuities between 3 areas of aggregation in Eastern Canada. The 2 feeding grounds in the eastern North Atlantic used in the model (Iceland and Norway) are also apparent in Figure 1, although sightings around Iceland and in the northern Norwegian Sea and the Barents Sea occurred over much larger spatial scales than in the west.

Humpback whales have been sighted in July and August in several areas outside these 5 primary areas of concentration. For example, sightings of humpbacks in July and August have been made west of the Mid Atlantic Ridge from north of roughly 35° N and west and east of the Mid Atlantic Ridge north of roughly 50° N, and northwest and northeast of Scotland. While some of the outlying sightings were made by 19th century sperm whalers, others including some on the mid Atlantic Ridge were the result of recent research surveys in offshore areas (Paxton *et al.* 2009, Sigurjónsson *et al.* 1991). The apparent discreteness of these areas may be reflective of distribution patterns before the intense whaling. It is unclear if any of these latter areas themselves constitute separate maternally directed feeding areas, but it is possible that humpbacks may have different behavior in the eastern North Atlantic. For example, Stevick *et al.* (2006) noted that whales in the east exhibited longer distance movements over short time periods, and they associated these patterns with differences in the spatial scale of variability of prey. They raised the question of whether discrete maternally directed feeding grounds occur in the east as they have been shown to in the west. This possibility would be consistent with the more diffuse distribution patterns seen in Figure 1.

It is unclear the extent to which the 2 known breeding populations mix on the 5 feeding grounds. Whales using the Cape Verde Islands breeding ground have been matched to whales using the Iceland feeding ground (Jann *et al.* 2003), although small sample sizes leave open the possibility that they use other feeding grounds as well. Whales using the Caribbean breeding ground use all 5 identified feeding grounds. Genetic data suggest that only a small proportion of whales on the eastern North Atlantic feeding grounds are part of the Caribbean breeding population. This conflicts with the low estimate of the numbers of whales using the only other known breeding ground around the Cape Verde Islands (see 5th enigma). However, those estimated proportions are thought to have greater uncertainty than reflected in their estimated coefficients of variation because of relatively low sample sizes and unrepresentative sampling. For example, the rate for Iceland is based on data collected primarily in the west and south of that region, and may not be representative of whales to the east and north. Further, of course, these estimates are based on data from the past decade or 2 and the nature of mixing prior to extensive whaling may have been quite different then. If the mixing patterns were different historically, the allocation of historical feeding ground catches to population would have been different than assumed in the IWC model.

Third enigma:
Breeding season distribution

Humpback whale migration between the summer and winter grounds is known to follow a broadly diffuse pattern across the central North Atlantic (Clapham and Mattila 1990, Reeves *et al.* 2004). However, it is possible that not all humpbacks migrate to the 2 known breeding grounds in any year, and if so, they would not be accounted for in the population models used. As previously mentioned, humpback whales occur off eastern and northern Iceland year round and are often associated with capelin schools there (Gisli Víkingsson, pers. comm.). Further, songs of presumably mature whales have been detected acoustically in the southern Norwegian Sea throughout the winter months (IWC 2002). Although the latter may eventually migrate to known breeding grounds, as Straley (1990) showed for humpbacks off southeast Alaska, the migratory behavior of these whales in the North Atlantic is unknown. Further, Swingle *et al.* (1993) noted that some juveniles winter off the southeastern US, and these have been shown to be from the western Atlantic feeding grounds and presumably the western breeding ground (Barco *et al.* 2002). The age and sex structure of these whales is poorly known, however.

Relative to the 2 known breeding grounds, the distribution of whales within the Cape Verde Islands is not known and within the Caribbean is apparently different now from what it was in the 19th century. The present day distribution of humpbacks within the Cape Verde Islands is known exclusively from sampling in the 3 easternmost islands (Jann *et al.* 2003). Historically, the 19th century American whalers worked mostly around the eastern 3 of the more northern islands (Reeves *et al.* 2002), with observations available from the island of Sal in both time periods. Thus the extent of both the historic and present distribution within this breeding ground is poorly known, which leaves substantial uncertainties about breeding population size.

The present day distribution of humpbacks in the Caribbean is mostly centered in the northern West Indies. Although humpbacks are known from the Windward Islands, including a remnant fishery on the island of Bequia, recent acoustic and sightings surveys (Swartz *et al.* 2003) have suggested very low abundance in this region. In contrast, most American 19th century whaling occurred in the Windward Islands (Reeves *et al.* 2001). These 2 areas do not appear to host separate breeding populations because reidentification studies have demonstrated movement of animals between them (IWC 2003), although the frequency of such movement is not known. Various hypotheses have been suggested as to the cause of this apparent shift in distribution as the population has recovered, but there is little evidence for any of them (Reeves *et al.* 2001).

Fourth enigma:
Feeding ground abundance

Recent abundance estimates in the North Atlantic from various sources are summarized in Table 1. The estimates are divided into 2 periods: 1988-1995, corresponding roughly to the estimate from the YoNAH which was carried out 1992-1993; and 1996-2005. Mark recapture-based estimates of numbers of animals on feeding grounds have proven difficult to obtain, and are available only for West Greenland (Larsen and Hammond 2004) and the Gulf of Maine (Clapham *et al.* 2003). Sightings based estimates are available for all feeding grounds except Canada, and for the Gulf of Maine, West Greenland and Norway these have ranged from 900 to 1,500 animals. In contrast, the estimates for the Iceland feeding ground based on aerial and shipboard sighting surveys have been much larger, albeit with large sampling errors. Paxton *et al.* (2009) provide estimates based on simultaneous shipboard and aerial surveys around Iceland of 10,521 (95% CI 3,716–24,636) in 1995 and 14,662 (95% CI 9,403–29,877) in 2001. This high density of humpback whales has also been confirmed by Norwegian surveys to the north and east of Iceland (Øien 2009).The 1995 estimate for this feeding ground alone is nearly as large as that for the entire North Atlantic basin from the YoNAH project (Stevick *et al.* 2003). The total of all available feeding ground estimates for the first period is 12,743 (95% CI 4,688–25,527), which is similar to the YoNAH estimate. The estimate for the later period is even higher, at 17,774 (95% CI 12,061–32,597). However neither of the total survey estimates included an estimate for the Canadian feeding ground, which is thought to number more than 2,500 animals (IWC 2002). In addition all the survey estimates are considered to be negatively biased because of uncorrected availability and perception biases. This suggests that there is a considerable discrepancy between the estimates from surveys and that from the YoNAH project. It also suggests that the great majority of humpback whales, over 80% of the total survey estimates for both periods, feed around Iceland.

The ocean basin estimate from YoNAH is thought to be negatively biased by the presence of individuals feeding in the Icelandic and Norwegian grounds that go to the un sampled eastern breeding grounds (Stevick *et al.* 2003). This problem may have been exacerbated by the fact that the area off eastern Iceland, where large numbers of humpbacks were counted in both the 1995 and 2001 NASS (Paxton *et al.* 2009, Pike *et al.* 2009), was very poorly sampled in the YoNAH project (Smith *et al.* 1999). If a large proportion of animals from this area go to the eastern breeding ground or possibly another as yet undiscovered breeding ground (see below), the magnitude of the negative bias of the YoNAH ocean basin estimate might be greater than previously thought.

Table 1. Abundance estimates for humpback whales in the North Atlantic from 2 periods: 1–1988 to 1995; 2–1996 to 2005. An alternative total for Period 1 from YoNAH is also shown. Confidence intervals for the total survey estimates were estimated using the bootstrap distribution from the Iceland In+Offshore estimate (Charles Paxton, RUWPA, University of St Andrews, UK, pers. Comm.) and assuming log normal distributions for the other estimates, using a parametric bootstrap procedure and the 2.5 and 97.5 percentiles of 1,000 bootstrap replicates.

Area	Period	Year	*N*	cv	95% CI		Comments	Reference
					L	U		
Gulf of Maine	1	1992 1993	652	0.29			Mark recapture estimate.	Clapham *et al.* (2003)
Iceland In+Offshore	1	1995	10,521		3,716	24,636	Ship survey, spatial analysis. Not corrected for perception or availability biases.	Paxton *et al.* (2009)
Iceland Inshore	1	1995	1,674	0.45	656	4,269	Aerial survey. Not corrected for perception or availability biases.	Pike *et al.* (2009)
Norway	1	1995	1,210	0.26	725	2,021	Ship survey. Not corrected for perception or availability biases.	Øien (2009)
West Green-land	1	1988 1993	360	0.07			Mark recapture using fluke markings. Confidence intervals calculated assuming a log normal distribution.	Larsen and Hammond (2004)
Total Period 1	**1**		**12,743**		**4,688**	**25,527**	**Total of survey estimates 1988 to 1995.**	
Total Period 1	**1**		**11,570**		**10,290**	**13,390**	**Mark recapture, whole ocean basin.**	**Stevick *et al.* (2003)**
Gulf of Maine			902	0.41			Aerial and ship surveys. Partially corrected for perception bias.	Clapham *et al.* (2003)
Iceland In+Offshore	2	2001	14,662		9,403	29,877	Ship survey, spatial analysis. Not corrected for perception or availability biases.	Paxton *et al.* (2009)
Iceland Inshore	2	2001	4,928	0.46	1,926	12,611	Aerial survey. Not corrected for availability bias.	Pike *et al.* (2009)
Norway	2	1996 2001	934	0.35	479	1,819	Ship survey. Not corrected for perception or availability biases.	Øien (2009)
West Green-land	2	2005	1,246	0.56	448	3,468	Aerial survey. Not corrected for perception or availability biases. Confidence intervals calculated assuming a log normal distribution.	Heide-Jørgensen *et al.* (MS 2006)
Total Period 2	**2**		**17,744**		**12,061**	**32,597**	**Total of survey estimates 1996 to 2005.**	

Fifth enigma:
Breeding population abundances

The abundance of the western breeding population has been estimated from mark recapture analyses over the period 1979-1993 (Stevick *et al.* 2003). The series of estimates for the western population is consistent over time, showing a steady rate of increase of 3.5% per year over the period with an abundance of 10,752 (cv 0.068) in 1993. Only a single point estimate is available for the eastern population (Punt *et al.* 2006), and the present day abundance there is thought to be in the neighborhood of only 100 animals. This 3 order of magnitude difference is vastly greater than the difference in historic catches from these 2 regions (Smith and Reeves 2003), suggesting different levels of either depletion or of recovery. In addition these estimates are difficult to reconcile with the estimated proportions of the 2 breeding populations on the feeding grounds. For example, it was estimated that 40% of the Icelandic and 87% of the Norwegian feeding areas breed outside of the western breeding area, presumably in the eastern grounds (although these proportions themselves are uncertain, see above). Applying these percentages to the feeding ground abundance estimates for the later period in Table 1 gives a total of 6,677 animals breeding outside of the Western ground. This suggests that either a) the abundance in the Eastern breeding ground has been severely underestimated, or b) that there is a third breeding area with a considerably larger number of animals than found at the Cape Verde Islands.

Sixth enigma:
Rates of increase

The rates of increase in numbers of whales have been estimated for the western breeding population and for several of the feeding grounds. These estimates have been based on life history modeling (Barlow and Clapham 1997), abundance estimates from long term re identification studies (Stevick *et al.* 2003, Larsen and Hammond 2004) and relative abundance estimates from fishery encounter rates and aerial surveys, and are summarized in Table 2. The rates range from 0 for West Greenland to levels over 11% per year in Iceland. However, recent results from West Greenland suggest possible increases there as well (Heide-Jørgensen *et al.* (MS) 2006). While a range of rates of increase in different population components is to be expected, the higher values from Iceland are at the upper end of the range of biological plausibility (Clapham *et al.* 2001). In particular, sightings by Icelandic whalers working to the west of Iceland increased between 1970 to 1988 by roughly 11.6% per year (Sigurjónsson and Gunnlaugsson 1990), while sightings during aerial surveys conducted all around Iceland increased from 1986 to 2001 by 10.8% (Pike *et al.* 2009). Therefore similar rates of increase have been estimated for 2 different time periods using different datasets and methodologies. Although these high rates of increase in sightings may reflect actual population growth, it is also possible that they are due to some complex changes in humpback distribution resulting in net immigration to the Icelandic feeding area. However, Icelandic ship and aerial surveys since 1986 have covered all or most of the summer range of the species around Iceland, so if immigration is contributing to the observed rates of increase from these surveys, animals must be coming in from other feeding areas. Given that the Icelandic summering group is so much larger than any other known summering group, it is difficult to see where such immigration could be coming from.

The high observed rate of increase around Iceland also raises questions about the putative stock structure, in which most whales feeding around Iceland are thought to breed in the Western area. In addition, whales on the Gulf of Maine feeding ground, which also winter in the Western ground, increased at a rate of 6.5% per year between 1979 and 1991 (Barlow and Clapham 1997). Therefore a relatively high rate of increase should also be observed in the Western breeding area, since a large proportion of these whales would originate in Iceland and the Gulf of Maine. However, the observed rate of increase in the Western breeding ground between 1979 and 1993 was only 3.2% per year (Stevick *et al.* 2003). Therefore it seems likely that a large proportion of the population summering at Iceland must overwinter outside of the Western breeding ground.

Table 2. Rates of increase observed on humpback whale breeding and feeding grounds in the North Atlantic, from published sources.

Area	Period	Rate	Variance	Source
Gulf of Maine	1979-1991	1.065	SE=0.012	Barlow and Clapham (1997)
Iceland	1970-1988	1.112	SE=0.02	Sigurjønsson and Gunnlaugsson (1990)
Iceland	1986-2001	1.108	cv=0.25	Pike *et al.* (2009)
Greenland	1988-1993	No trend.		Larsen and Hammond (2004)
Western Breeding Ground	1979-1993	1.032	SE=0.0052	Stevick *et al.* (2003)

Seventh enigma:
Pre-whaling abundance

The "notional upper limit" on pre-whaling abundance (Holt *et al.* 2004) is the sum of the historical removals (29,000) and modern abundance of the 2 breeding populations (10,752+99, from Table 2 of Punt *et al.* 2006), or roughly 40,000 animals. This is an upper bound on pre-whaling abundance assuming 0 population rate of increase, and is only a fraction of an estimate of pre whaling abundance of 240,000 based on MtDNA variability (Roman and Palumbi 2003). The difference between the total feeding ground abundance (17,744 from Table 1, without Canada) and the total of the 2 breeding ground estimates would suggest a higher notional upper limit, for example, 47,000 (=29,000+17,744). However, this just demonstrates that there is little possibility of reconciling the difference between the catch history based and the genetic based estimates of whale abundance before whaling.

For example, the meaning of the notional upper limit has been misinterpreted. Contrary to Palumbi and Roman's (2007) interpretation of one of us (TDS), the total removals of 29,000 are not "consistent with a population of 40,000." Rather, that latter value is an upper bound based on pre whaling population size. On the other hand, Clapham and Link (2007) suggest from the estimated level of historical removals that the pre whaling population size was "probably not greatly larger than current abundance..." The basis for this suggestion is not given, but it implies that the population is near carrying capacity, for which there is no evidence.

Similarly, there are erroneous and speculative arguments about the catch history. For example, Palumbi and Roman (2007) suggest incorrectly that the estimated removals (Smith and Reeves 2003) allowed for a 2% struck and lost rate; in fact, the actual rates used varied among the fisheries and were larger than that for most fisheries as specified in that paper. Further, they suggest that the 2 estimates of historic population size might be reconciled if the struck and lost rate were 50% and if, further, 50% of the catches were not accounted for. Whether such values would suffice to reconcile the 2 estimates is moot because there is absolutely no basis either given or available for such speculative values.

On the other hand, the MtDNA variability base estimate is based on adjusting an estimate of the "long term effective female population size" of North Atlantic humpbacks, obtained from genetic variability to account from other components of the population. There are a number of yet untested assumptions in this method, and there has been extensive speculation on the impossibility of such large numbers of whales occupying the North Atlantic. For example, Clapham and Link (2007) despair of reconciling the 2 estimates of carrying capacity, arguing (somewhat circularly) that "given the constraints of carrying capacity and suitable habitat, it is very difficult to imagine a quarter million humpback whales (together with large pre-exploitation populations of other species) in the North Atlantic at any time in prehistory."

This difference is an enigma that may or may not be due to "bad science rushed into print," as 1 reviewer suggested. But rather than resorting to speculations about what is and is not possible, there is a need, as Palumbi and Roman (2007) concluded, to focus on "the validity of assumption sets for both types of data and analytical approaches."

Interactions among the enigmas

The 7 enigmas described above interact with one another in complex ways (Table 3), making it difficult to identify the most important issues. In this table, the nature of each enigma as developed above is summarized in the diagonal boxes, while their interactions are identified in the off diagonal boxes and described below.

Table 3. Seven enigmas about North Atlantic humpback whales, showing the basic conflict in the diagonal boxes and the main interactions among the enigmas in the above diagonal boxes.

	1. Breeding Population Structure	2. Feeding Season Distribution	3. Breeding Season Distribution	4. Feeding Ground Abundance	5. Breeding Population Abundance	6. Rates of Increase	7. Pre Whaling Abundance
1. Breeding Population Structure	More than 2 populations suggested		Location of 3rd breeding population unknown	Breeding ground proportions unknown	Spatial boundaries & movements poorly known	Difficult to interpret abundance or density trends	Single population assumed
2. Feeding Season Distribution		Changes over time and whales outside the grounds		Highly clustered and shifting spatial distribution difficult to sample	Mixing of 2 populations on some feeding grounds		
3. Breeding Season Distribution			Non migrating whales known		Non migrating whales bias reidentification estimates.	.Rates on some feeding grounds exceed breeding grounds	
4. Feeding Ground Abundance				Total of feeding grounds exceeds total of breeding grounds.	Total of feeding grounds exceeds total of breeding grounds.		
5. Breeding Population Abundance					CVI and WI estimates differ by factor of 100.	Differential recovery among populations.	
6. Rates of Increase						Rates approach biological implausibility	MtDNA estimates imply pre whaling declines in abundance
7. Pre Whaling Abundance							MtDNA estimate exceeds notional upper limit.

Considering the first enigma, breeding population structure (first row of Table 3), the possibility of there being more than the 2 breeding populations interacts with 5 of the remaining enigmas. First, whales are known from other areas during at least part of the breeding season, for example the southern Norwegian Sea, but the information is incomplete. Second, the proportional distribution of populations on the feeding grounds is not known, particularly for the eastern grounds. Thirdly, estimating both abundance and rates of increase of such putative populations is of course not possible without better information on distribution patterns. Finally, this enigma interacts with the MtDNA variability abundance estimate because such estimates would be biased by not including such "ghost" populations (Clapham and Link 2007).

Considering the second enigma, feeding season distribution, changes over time and the existence of whales outside the nominal feeding grounds may have induced biases in abundance estimates because of the areas sampled. For example the western Atlantic abundance estimates were based on near shore sampling in Canada even though humpbacks are known to occur in offshore waters at least in some years (Smith *et al.* 1999). Further, this enigma interacts with breeding population abundance through estimates of differential use of the feeding grounds by the 2 populations.

Considering the third enigma, breeding season distribution, the possible existence of whales that do not migrate to either of the 2 known breeding grounds obviously interacts with the first enigma as discussed above. Further, it interacts with the fifth enigma, breeding population abundance, especially in possibly inducing biases in estimates of abundance. Finally, it interacts with the sixth enigma, rates of increase, in that rates of increase observed on some feeding grounds apparently greatly exceed that observed on the western breeding ground, even though these feeding grounds are thought to account for a large proportion of the whales that use that breeding ground.

Table 4. Implications of the catch-based population model and needed research in terms of the 7 enigmas about North Atlantic humpback whales.

Enigma	Implications of Catch-based Population Model	Research Needs
1. Breeding Population Structure	Model with 3 breeding populations plausible, but did not improve model fit.	Improved sampling for population structure in ENA. Improved acoustic and satellite telemetry for winter distribution in ENA.
2. Feeding Season Distribution	Inconsistency between mixing proportion and CVI abundance.	Improved estimates of mixing rates. Determine significance of whales outside known feeding grounds.
3. Breeding Season Distribution		Improve knowledge of within CVI spatial distribution. Improve knowledge of within WI movements. Improved knowledge of age & sex structure of animals outside breeding grounds.
4. Feeding Ground Abundance	Icelandic abundance estimates inconsistent with total of WI and CVI breeding population estimates. No estimate of Canadian abundance.	Improve abundance estimation sampling to better account or extreme spatial aggregation. Estimate abundance in Canadian area.
5. Breeding Population Abundance	CVI abundance estimate has low sample size and poor spatial coverage. WI abundance increases not fitted by model.	Improve CVI abundance estimate. Improve WI abundance estimates by using new sampling and by matching to NAHWC photographic catalog.
6. Rates of Increase	Iceland abundance increases not fitted by model. Allowing changing carrying capacity improved model fit slightly.	Examine spatial distribution of ENA catches and sightings for long term distribution changes. Examine long term environmental changes.
7. Pre-Whaling Abundance	Catch based model estimate less than 10% of MtDNA variability based estimate. Using upper bounds on catch history improved model fit slightly.	Test MtDNA variability abundance estimation methodology. Complete sampling uncertainty of catch history.

Considering the fourth enigma, feeding ground abundance, the total numbers observed on those feeding grounds that have been surveyed are high relative to the numbers estimated for the entire North Atlantic from YoNAH, even though the survey estimates are negatively biased from several sources. This interacts with the second enigma to the extent that the estimates themselves may be biased by spatial clustering, with the fourth enigma, breeding ground abundance, for obvious reasons, and also with the sixth enigma, rates of increase, to the degree there may be systematic biases over time.

Considering the fifth enigma, breeding population size, the magnitude of the difference between the 2 known populations interacts with the first, second and third enigmas, as discussed above, and with the sixth enigma, rates of increase. While different rates of increase are to be expected, depending on population status, the large difference in abundance implies very different rates of increase.

Considering the sixth and seventh enigmas, the rates of increase interacts with all of the enigmas except perhaps feeding season distribution, as discussed above. It also interacts with the seventh enigma, pre-whaling abundance, in that in order for the notional upper limit and the MtDNA variability estimate to both be correct there would have been a rapid decline in abundance prior to whaling.

Using assessment modeling to evaluate research direction

In the face of these interacting enigmas, the present status and historical distribution of the North Atlantic humpback whale is uncertain. The enigmas individually suggest various types of needed research, but the interactions among the enigmas make it difficult to identify with confidence any single key important next research task. Something is wrong in our understanding, and merely repeating what has been done before is unlikely to reveal what that is.

In the face of this uncertainty, it is useful to systematically consider the implications of recent population modeling. As mentioned above, the IWC Scientific Committee's attempt to complete a "comprehensive assessment" of the status of humpbacks in the North Atlantic was unsuccessful (IWC 2003). The Committee had attempted to use a complex population model to combine historical whaling levels, present abundance estimates, and data on rates of increase and feeding to breeding ground mixing to estimate the likely pre whaling abundance in the 17th century. However, it was unable to find combinations of model assumptions and data that were consistent.

Punt *et al.* (2006) extended the Committee's approach by examining the influence of several of the enigmas described above, and especially the effect of making alternate assumptions about those enigmas. They examined the fit of a set of density dependent age and sex structured population models, which accounted for the multiple feeding and breeding grounds, to the available information on catches, abundance, population rates of increase and spatial structure (however Punt *et al.* (2006) did not have access to some of the abundance estimates for Iceland, Norway and Greenland in Table 1). Models were fit to the available data assuming different density dependence mechanisms, including alternate functional forms of dependence of vital rates on feeding ground density, depensatory changes in vital rates at low density, and the possible changes over time in carrying capacity. The available data were inconsistent with any form of the model when 2 particular pieces of information were used simultaneously. These were the estimated number of whales in the eastern breeding ground and the estimated proportion of animals in the eastern feeding grounds that used the western breeding ground, the feeding breeding mixing proportion. Three of the eighteen model variations, those using either but not both the estimated mixing proportion and the estimated CVI abundance, fit substantially better than the other 15.

Using an estimate of the feeding breeding mixing proportion but no estimate of the eastern population abundance, the best model variant had constant carrying capacity, no depensation, and no differences in density dependence among feeding grounds. Not using the mixing proportions but using a photographic reidentification estimate of abundance in the Cape Verde Islands as the size of the eastern breeding population, 2 model variants fit similarly well. Both were similar to the above described model, but 1 of the 2 models had constant carrying capacity while the other implied an increasing carrying capacity. For all 3 of these models, the pre whaling abundance levels were similar for the 2 breeding populations, ranging from 17,151 to 22,647 for the western population and from 3,152 to 5,510 for the eastern population. However, the current population sizes relative to those historic levels were very different, ranging over the 3 models from 42 to 62% and 5 to 95% for the western and eastern populations, respectively. Preliminary explorations of a 3 breeding population model allowed the mixing proportion and the CVI abundance estimate to both be used, but this model was not pursued because it also did not fit the increasing WI abundance estimates.

Despite their differences and this lack of fit, however, the 3 models have similar estimates of pre whaling abundance, from 22,000 and 26,000 animals. Although the 3 models described above fit substantially better than any other model considered, the actual fit to the abundance information was not very good. Considering the 7 enigmas in turn, the results of Punt *et al.* (2006) suggest some specific research tasks (Table 4). Also in this table some other research tasks are identified pertaining to aspects of the populations that are not addressed by the assessment model but that are nonetheless important for a complete understanding of the past and present condition of this population.

First, relative to breeding population structure, Punt *et al.* (2006) described as promising a preliminary attempt to resolve the inconsistency between the mixing rate estimate and the CVI abundance estimate using a 3 population model. Further information is required before such modeling can be usefully pursed. One research need is for additional reidentification sampling and acoustic and satellite telemetry sampling to determine if such a third population exists. However, such information is unlikely in itself to allow population status to be determined because the 3 population model did not improve the fit to the increasing WI abundance estimates.

Second, relative to the feeding season distribution, the inconsistency between the breeding feeding mixing proportion and the CVI abundance estimate suggests a need for collection of better data on mixing rates. This will require collection of samples for genetic analysis from areas where they have not been collected before, especially off eastern Iceland and the CVI. In addition there are a number of areas where humpbacks have been encountered in the feeding season outside the 5 regions considered in the modeling (Fig. 1). Exploratory or opportunistic surveys should be carried out in these areas to determine their significance as possible feeding areas and, if whales are found, to collect samples for genetic analysis and reidentification studies.

Third, relative to breeding season distribution, although the population model did not distinguish distribution within grounds, it is apparent that a major sampling weakness is the spatial coverage of the CVI breeding area. This is known historically to be substantially larger than the area recently sampled, but few modern observations over this larger area are available. Similarly, more information is needed on movements within the WI breeding ground. As well, determination of the relative age and sex composition of animals outside the known breeding grounds during the breeding season, for example in the Icelandic feeding area, would be valuable, for example to determine if mature females are present. Again this could be achieved through reconnaissance surveys and the collection of biopsies for genetic and reidentification studies.

Fourth, relative to feeding ground abundance, the estimates for the Iceland area are inconsistent with the total of the WI and CVI breeding population estimates. Although the sighting surveys for that region have been conducted using standard line transect methods, application of these methods to highly clustered populations results in estimates with relatively high variance. More precise estimates from this area, in which a large proportion of the North Atlantic population apparently feed, would be desirable. This could be achieved by increasing survey effort in areas of humpback whale concentration and possibly also by the application of model based estimation procedures incorporating more covariates than those used by Paxton *et al.* (2009). Alternatively re-identification methods could be used. On a broader scale, an estimate for the Canadian area would help bound the population model to a much greater degree, improving overall performance. The results of reidentification studies on the western breeding ground and in the Gulf Maine (Clapham 2005) may provide improved estimates of abundance, although the proposed estimate does not rely on sampling other feeding grounds. Similarly, the Trans North Atlantic Sightings Survey planned for summer 2007 includes Canadian and USA participation and should provide improved estimates for this area.

Fifth, relative to breeding population abundance, the estimate for CVI needs to be improved in terms of sample sizes and spatial coverage. Further, the WI abundance series was not well fitted by the model, and additional information could be obtained by matching newer photographic samples to the long standing North Atlantic Humpback Whale Catalog (NAHWC). As outlined above the estimate for the WI breeding area seems low compared to the sum of the feeding ground estimates. In the future efforts should be made to ensure that all feeding areas are adequately sampled in reidentification studies, particularly the area around Iceland as this is the most numerous feeding concentration.

Sixth, the Iceland abundance increases were not well fitted by the model, and further examination of long term changes in distribution patterns using the catch history and sightings would be valuable.

Finally, the pre-whaling abundance estimates from the model are, as expected, less than the notional upper limit, in this case being roughly 60% as large. This estimate is only about 10% of the MtDNA variability based estimate. This large a difference suggests further research is needed. One is to improve the sampling and test the assumptions in the MtDNA methodology. Further, because the sensitivity analysis using upper bounds on the estimated catches improved the model fit somewhat (Punt *et al.*, 2006), estimates of sampling uncertainty for the catch history would be useful in allowing specification of a more rigorous sensitivity analysis.

What to do next?

As is apparent in Table 4, there are several research tasks that could be undertaken but none that in and of themselves shows promise of resolving the uncertainty about the status of humpbacks in the North Atlantic. Some tasks are straightforward repetition of what has been done previously, while others are substantially new and likely difficult both methodologically and logistically. An important question is which tasks are most likely to advance our understanding of the status of the North Atlantic humpback whale.

One approach that has been undertaken already is a partial repeat of the earlier "Years of the North Atlantic Humpback" (Smith *et al.* 1999). Dubbed "More Years of the North Atlantic Humpback" (Clapham *et al.* (MS) 2005), this study was designed to address US concerns about the status of humpbacks in the western North Atlantic. It involved repeating the West Indies genetic sampling in 2 successive years, while sampling in the feeding season was restricted to the Gulf of Maine. From analyses of the genetic samples, which were collected in 2003 and 2004, it is expected that a new abundance estimate for the western North Atlantic breeding population will be obtained, extending the time series of estimates.

A second approach just getting underway is to improve the catch history, filling in some residual uncertainties and completing estimates of the sampling uncertainty (Reeves and Smith 2007). Further work also just underway is focusing on improving the sampling basis for the MtDNA variability based pre whaling abundance estimates and testing key assumptions (Steven Palumbi pers. comm.).

In addition, work has continued on photographic and genetic sampling humpbacks in CVI, although with previously used platforms and methods (Wenzel *et al.* 2006). This will improve both photographic and genetic sample sizes, and will help resolving feeding ground mixing proportions. However, it is unlikely to address the logistical constraints which will continue to limit spatial coverage of that area. Wider spatial coverage in this area would be extremely valuable.

Further, surveys off Eastern Canada, West Greenland, Iceland, the Faroes and Norway are planned for 2007 under the Trans North Atlantic Sightings Survey programme (Desportes and Pike (MS) 2006). Improved estimation techniques for humpback whales, taking into account their known geographical distribution and tendency to form large and disjunct clusters, will be implemented as well as opportunistic collection of biopsy and photographic samples.

One area where additional work would be fruitful is completing analyses and cross linking of existing data sets. Experience with the YoNAH project is that the complete analyses of such large and complex datasets requires much longer than the data collection. For example, major aspects of that project have been published as recently as 2006 (Stevick *et al.* 2006), more than a decade after completion of the field work. Re-identification data especially require extensive laboratory analyses and increase in value by being linked with other reidentification datasets. Thus other re identification data sets, especially in the Eastern North Atlantic, should be analyzed and also linked into previously collected data sets.

One important possibility that the ongoing studies do not address is that of a third breeding population. As Punt *et al.* (2006) note, several tantalizing winter observations of whales around Iceland and in the southern Norwegian Sea suggest that there could be a population utilizing the area between Iceland and Norway. Unlike for most other humpback populations, a population restricted to this region would not, of course, have access to tropical calving areas.

This raises the more general possibility that humpbacks may behave quite differently in the eastern than in the western North Atlantic, and hence the latter may not be a good model for the former. For example, Reeves *et al.* (2004) identified central North Atlantic sightings during the feeding season just west along the Mid Atlantic Ridge (Fig. 1), far from known feeding grounds. That figure also suggests that humpback have substantially broader spatial distribution patterns in the east than in the west. This is consistent with Stevick *et al.*'s (2006) description of differences in movement patterns in the 2 regions, and suggests that the applicability of the fundamental understanding of humpback whales population biology that has been developed from studies in the western North Atlantic be tested for humpbacks in the east.

Finally, research to test for the existence of a third breeding population would have a higher likelihood of resolving major uncertainties about the status of North Atlantic humpbacks than any of the other research tasks in Table 3 that are not already being pursued. If this possibility could be ruled out, for example, the range of uncertainties would be substantially reduced. At the same time, such research would provide information on the rates at which whales from the populations mix on the feeding grounds. Although such an undertaking would be difficult and would require substantial resources, it would address an important question about the status of humpbacks in the North Atlantic.

Related to the question of population status as used in the context of management is the role of humpbacks in the North Atlantic ecosystems that they are part of. This is addressed indirectly in the modeling context in Punt *et al.* (2006) in their testing if changes in carrying capacity helped explain population status, and somewhat more generally here in our concern about changes in spatial distributions within feeding and breeding grounds. These questions require the expansion of the scope of cetacean studies to include other aspects of the ecosystem (Smith *et al.* 1996, Clapham and Link 2007). Because human impact in this ocean has been extensive the historical signals are likely strong, and it is important that all relevant historical sources of data be explored if we are to detect those signals. This will be important if we are to understand the present status and the potential for recovery of North Atlantic humpbacks, as well as the several other species of large whales that have been depleted by whaling.

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