ICES CM 2005/ Session R/ Marine Mammals: Monitoring Techniques, Abundance Estimation, and Interactions with Fisheries

Distribution, abundance and trends in abundance of fin and humpback whales in the North Atlantic

D.G. Pike, Th. Gunnlaugsson, N. Øien, G. Desportes, G.A. Víkingsson, C.G.M. Paxton and D. Bloch.

ABSTRACT

The North Atlantic Sightings Surveys (NASS) are a series of international cetacean line transect surveys, including participation from the Faroe Islands, Iceland, Norway and Spain, that have been conducted in 1987, 1989, 1995 and 2001. The NASS have covered a very large area of the central and eastern North Atlantic, from East Greenland east to coastal Norway, and from Svalbard south to the Iberian peninsula. The surveys used ships and aircraft as survey platforms. Target species were minke, fin and pilot whales, but all species encountered were registered. Here we present estimates of abundance for fin and humpback whales from the Northeast and Central portions of the survey area. The estimates are negatively biased because of whales diving during the passage of the survey platform and whales being missed by observers, but these and other potential biases are likely small for these species. Fin whales occurred in highest densities in Denmark Strait west of Iceland, while humpback whales were most abundant in shelf waters east and west of Iceland. The abundance of fin whales increased in the survey area over the period, with the greatest increase observed in the waters west of Iceland. There were 29,900 (cv 0.11) fin whales in the area in 2001. There has been a great increase in the abundance of humpback whales around Iceland, but not in other areas. Aerial surveys conducted in Icelandic coastal waters indicate an annual rate of increase of 15% in this area. There were 14,900 (cv 0.26) humpback whales in the entire survey area in 2001. The observed trends are consistent with increases in abundance following the cessation of whaling in this area, but the magnitudes of the observed increases, taken at face value, are greater than expected.. For humpback whales in particular, our recent estimates are substantially higher than some estimates of pre-whaling abundance. Other factors, including differential harvesting of sub-stocks, changes in carrying capacity, immigration from other areas, the near extirpation of some other cetacean species, and operational factors in the surveys themselves, may be involved.

Keywords: fin whale, humpback whale, abundance, distribution, trends, North Atlantic, whaling.

Contact author: Daniel G. Pike, North Atlantic Marine Mammal Commission, Polar Environmental Centre, N-9296 Tromsø, Norway. Tel.:: +47 77750177 Fax: +47 77750181 email: Daniel.pike@nammco.no.

Please do not cite without the permission of the contact author.

INTRODUCTION

Krebs (2001) defined ecology as "…the scientific study of the interactions that determine the distribution and abundance of organisms." Essentially ecologists are interested in where plants and animals occur, how many occur there, and why. Thus the study of distribution and abundance, be it by census, survey or experimental mark-recapture study, is central to ecology and a necessary starting point for the elucidation of underlying ecological relationships. On a practical level, periodic estimates of absolute or relative abundance are required for virtually all systems of harvest management. In addition, an historical record of distribution and abundance can be used to predict the effects of environmental change, such as through human induced global warming.

Among mammals, few groups have undergone such dramatic changes in abundance over the past 200 years as the large cetaceans. Most of these changes can be attributed directly to the effects of human harvesting, and (in some cases) population recovery after harvesting ceased or was reduced to sustainable levels. For the relatively fast-moving rorquals, including fin (*Balaenoptera physalus*) and humpback (*Megaptera novaengliae*) whales, the "modern" period of whaling is most relevant, after the invention of the steam ship and explosive harpoon in the late 1800's made it feasible to catch them. In this period, which lasted into the 1970's, virtually every population of large whales was severely overexploited, in some cases reducing populations to very low levels (Tønnessen and Johnsen 1982, Martin 1990). In the North Atlantic, most harvesting of humpback whales ceased in 1966 when the International Whaling Commission (IWC) imposed a moratorium on all but aboriginal hunting for the species. Takes of fin whales ceased in most areas in 1986 when the IWC implemented a general moratorium on all commercial whaling, although a small fin whale hunt continues off West Greenland. Both species were seriously depleted in most areas of the North Atlantic by about 1920.

Dedicated surveys to enumerate cetaceans are a relatively new phenomenon. Prior to the 1970's most management related data collection was fishery-based, consisting of catch rates and sighting records from whaling stations and expeditions, and biological data from killed animals. By the 1980's it was widely recognised that this was inadequate, mainly because the relationship between catch, hunting effort and the number of whales in the sea was not straightforward. Moreover, catch-per-unit-effort data was becoming less available as fewer countries engaged in whaling, The uncertainties inherent in utilizing these data for stock management, combined with decline of whaling as an industry due to falling catches and the imposition of the moratorium in 1986, provided an impetus to find other sources of information on the distribution and abundance of cetaceans. Reliable and robust field and analytical methodologies for cetacean surveys were developed primarily in the 1980's (Hiby and Hammond 1989, Smith and Donovan 2006).

North Atlantic Sightings Surveys (NASS) are a series of internationally co-ordinated cetacean surveys that have been conducted in 1987, 1989, 1995 and 2001. The earliest surveys (1987 and 1989) were the largest, involving the participation of 5 countries: the Faroes, Greenland, Iceland, Norway and Spain (see Fig. 1). By 1995, Spain and Greenland were no longer participating and the survey area was consequently smaller. After 1995, Norway began surveying a portion of their area annually on a 6 year rotation. Therefore, by 2001, only 2 countries, the Faroes and Iceland, participated fully in NASS.

The target species of the surveys have been fin whales (Iceland and Spain), minke whales (*Balaenoptera acutorostrata*) (Iceland, Norway, Greenland, the Faroes), sei whales (*B. borealis*) (Iceland 1989) and pilot whales (*Globicephala melas*) (the Faroes). However sightings of all species are recorded. The choice of target species influences the temporal and spatial extent of the surveys, and to some extent the survey methods used. Ships have been used in most areas, however the coastal areas of Iceland and Greenland have been covered by plane.

The NASS are perhaps the largest-scale wildlife surveys ever attempted, covering a maximum area of around 2 million square nautical miles, about the same size as Western Europe, and involving as many as 15 ships, 3 aircraft and 100 observers in a single survey. The distance covered by ships and planes while surveying has been as high as 40,000 nautical miles, a distance equivalent to about twice around the world. As many as 5,000 whales have been seen in a single survey.

Large whales are slow growing, long-lived animals. Populations grow relatively slowly compared to many other mammal species. The NASS have occurred over a time period of 17 years, which provides a realistic opportunity for detecting changes in abundance over time. Both fin (IWC 1992, NAMMCO 2000, 2001, 2004) and humpback (IWC 2001) whales have been severely overexploited in most parts of the North Atlantic over the past century. Therefore, we might expect to see some recovery of the stocks on a decadal scale since the cessation of whaling in most areas. In this paper, we will use the time series from the NASS to determine if there have been changes in abundance of these 2 species, and will discuss the ecological significance of the observed trends or lack thereof.

The life history of humpback whales in the North Atlantic is fairly well described (summarized by Punt *et al.* 2005). Two main breeding areas are known, in the Caribbean and around the Cape Verde Islands off North Africa. The latter breeding population is thought to be much smaller than the former. Breeding takes place in the winter. During the spring, humpback whales migrate to discrete high-latitude feeding areas, which they occupy during the summer and fall. However small numbers of animals may remain in high latitude areas throughout the year. The areas covered by the NASS constitute the Icelandic and Norwegian summer feeding areas. Animals from these areas apparently use both breeding areas, in differing proportions.

Fin whales follow the migratory pattern of most species of baleen whales in that they summer in high latitudes and winter (and breed) in low. However the summer and winter areas are not nearly so well defined as for humpback whales. Four stocks of fin whales have been recognized in the NASS survey area, based largely on limited genetic, morphometric and tag return data and historical patterns of depletion (see Fig. 2). However the stock structure of fin whales remains most uncertain in the North Atlantic and other areas.

Previous abundance estimates for fin whales are available from all areas for the 1987 and 1989 surveys (Buckland *et al.* 1992a,b, Christensen *et al.* 1990, Sanpera and Jover 1989), and as yet unpublished estimates are available for the later surveys (Borchers *et al.* 1997, Gunnlaugsson *et al.* 2002, Øien 2003, 2004). Estimates for humpback whales from the Norwegian (Christensen *et al.* 1992, Øien 2003, 2004) and some Icelandic/Faroese (Pike *et al.* 2002, 2006, Paxton *et al.* 2006) surveys have also been produced. However to date regional trends in abundance for these 2 species have not been examined in detail. This is complicated by the fact that the coverage and stratification of particularly the Icelandic and Faroese surveys has changed in every survey. In addition, previous analyses have used differing data selection and analytical options, which will affect the estimates to an unknown degree and confound the interpretation of trends. Here we use post-stratification and standardized data selection and analytical options to present regional estimates of roughly equivalent areas over time.

MATERIALS AND METHODS

Field methodology

Field methodologies for the NASS and associated Norwegian surveys have been fully described elsewhere (Desportes *et al.* 1996, Donovan and Gunnlaugsson 1989, Gunnlaugsson *et al.* 2002, Joyce *et al.* 1990, 1992, Lens 1991, Lens *et al.* 1989, Øritsland *et al.* 1989, Øien 1991,1996, Pike and Víkingsson 2002, Sanpera and Jover 1989, Sigurjónsson and Gunnlaugsson 1989, Sigurjónsson *et al.* 1991, Sigurjónsson *et al.* 1996a,b). In addition to the NASS we also use estimates from an Icelandic aerial survey conducted in 1986 (Gunnlaugsson *et al.* 1988) and a Norwegian shipboard survey conducted in 1988 (Øien 1990). We will not go into field methodology here but will report how the methodology has evolved since the first NASS.

Aerial surveys
Aerial surveys have been conducted in coastal areas of Iceland (1986, 1987, 1995 and 2001), Greenland (1987) and Norway (1987). Here we use only the Icelandic surveys. The target species of the aerial surveys has been the minke whale, but sightings of all species are recorded. The first survey conducted in 1986 used conventional line transect methodology. Subsequent surveys used cue counting methods (Hiby and Hammond 1989) for minke whales, but the data were recorded in such a way that conventional line transect estimates could be derived. Fully independent observer platforms were partially implemented in the 1987 survey and fully implemented in the 2001 survey, which allows estimates from the latter survey to be corrected for bias due to visible animals being missed by the observers. The design and stratification of the Icelandic survey has been identical since 1987, but the achieved coverage has varied due to weather conditions and logistical factors (Fig 3). Generally speaking the greatest coverage was achieved in 1995, and the least in 1987.

Ship surveys
Ship surveys have been conducted in the offshore waters of Iceland, inshore and offshore waters of the Faroes and Norway, and offshore waters of Spain (1987 and 1989 only). Here we exclude estimates from the Spanish surveys. The 1987 survey used single platforms only. In 1989 double platforms were used onboard Norwegian vessels, in 1995 onboard Norwegian and Faroese vessels, and in 2001 onboard all vessels. The design and stratification of the surveys has varied, especially in the Icelandic and Faroese areas (Fig 1). The 1989 Icelandic survey was conducted about 2 weeks later and extended farther south than all other surveys. Northern areas were not covered in 1989. Stratification of the Norwegian survey area has been stable since 1989.

After 1995, Norway began a system of “mosaic” surveys wherein only a portion of the survey area was covered in any one year, and the entire area was covered over the course of 6 years (Øien 2004). The first coverage under this system was completed from 1996 to 2001. For the purpose of maintaining compatibility to the other areas that were surveyed in 2001, we apply the 1996-2001 series to the year 2001, while understanding that any trends dependent on the latter series must be interpreted with caution.

Analytical methods
Data from the Icelandic and Faroese surveys were re-analyzed using standardized methods, while we rely on previous estimates from the Norwegian sector, which were analyzed in a similar way (Christensen *et al.* 1992, Øien 2003, 2004).

Data treatment
All cetacean sightings registered as definite, or most likely, fin or humpback whales were included in this analysis, while the more uncertain categories (large baleen whales, large whales etc) were excluded. In the case of surveys conducted with double platforms, sightings from both platforms were used, excluding duplicate sightings. All sightings and effort conducted at Beaufort sea states (BSS) greater than 5 were excluded. When group size was given as a range, the midpoint of the range (rounded up) was used.

Post-stratification
The objective of post-stratification was to produce estimates for regions which were roughly equivalent in shape and size across surveys. The surveys were originally stratified according to the expected density of the target species, but the stratification schemes were changed as experience was gained. Hence equivalent areas across surveys cannot be produced by simple

combinations of the original blocks.

Since the surveys were designed such that effort varied across blocks, it would be inappropriate to post-stratify across the original block boundaries as this would result in spatial variation in effort within post-blocks. Therefore we post-stratified only within the original blocks. These post-blocks were then combined into "regions" that were roughly equivalent in size across surveys (Fig. 4 and 5) and tailored to the putative stock relationships for the 2 species. For fin whales, the following regions were defined: WEST, corresponding to the area of Icelandic fin whale harvesting in the past century; EGI, corresponding to the East Greenland-Iceland stock area for fin whales (Donovan 1991); NORWAY, corresponding to the kernel area surveyed off Norway in all surveys (Øien and Bøthun 2005); and TOTAL, which is the total for the Icelandic, Faroese and Norwegian survey areas. For humpback whales, the regions were as follows: COASTAL, the Icelandic shelf area, also corresponding to the aerial survey block; ICELAND, corresponding to the Icelandic and Faroese survey areas covered by ship; NORWAY, corresponding to the Norwegian kernel area defined above; and TOTAL as defined above.

Analysis

Density and abundance were estimated using stratified line transect methods (Buckland *et al.* 2001) using the DISTANCE 4.1 (Thomas *et al.* 2001) software package. The perpendicular distance data were truncated such that 10% of the greatest distances were discarded. Unlike in some previous treatments of these data (Buckland *et al*. 1992, Borchers *et al.* 1997), smearing and binning of perpendicular distance intervals were not used.

The Hazard Rate and Half Normal models for the detection function $f(x)$ were initially considered, and the final model was chosen by minimisation of Akaike's information criterion (AIC) (Buckland *et al.* 2001). Covariates were considered for inclusion in the model to improve precision and reduce bias. Covariates were assumed to affect the scale rather than the shape of the detection function, and were incorporated into the detection function through the scale parameter in the key function (Thomas *et al.* 2001). Covariates were retained only if the resultant AIC value was lower than that for the model without the covariate. The following covariates were considered: BSS, as recorded and in 2 and 3 level classifications; vessel identity; weather code and sightability. For the 1989 survey, when 3 research vessels and 2 whalers participated in the survey, vessel type was also considered.

If pod size did not vary significantly between survey blocks, a single mean pod size for the survey year was used to estimate density. Otherwise pod size was stratified by survey block. To determine if there was size bias in pod detectability, ln(s) (pod size) was regressed against the estimated detection probability. If this regression was significant at the $P<0.15$ level, the detection of groups was considered to be size biased and the estimate of mean group size was adjusted using this regression.

Regional estimates were derived by summing the estimates for the appropriate post-blocks. The variance estimates for each post-block are not independent as they contain common components of variance for the estimation of effective strip width (*esw*) and group size. The variances of regional estimates were calculated by summing the variances for those components that were calculated independently for each post-block (encounter rate) and incorporating the additional variance for *esw* and group size using the Delta method (Buckland *et al.* 2001).

Regional and total rates of increase were calculated using log-linear regression, and confidence intervals for the rates of increase were estimated using a parametric bootstrapping procedure.

RESULTS

Fin whales

Distribution

Fin whales occurred throughout the survey area, but were most heavily concentrated off the continental shelf of Iceland (Fig. 6). There were very few seen in the aerial surveys (Fig. 3). They occurred in highest densities in Denmark Strait in the WEST region. They also occurred in moderate densities the middle Norwegian Sea, and in later surveys to the south and west of Svalbard. The distribution of fin whales changed little from year to year, except that there was a clear tendency towards a broadening of the distribution area in Denmark Strait. In the 1987 and 1989 surveys, fin whales were concentrated at the west side of the Strait near the East Greenland ice edge. By 1995 and especially 2001, they were distributed throughout Denmark Strait. In addition, there was a marked increase in the occurrence of fin whales in the northern Norwegian sector in later surveys, especially to the south and west of Svalbard. The southward extension of the survey area in 1989 revealed that fin whales also occur in this area, but there appeared to be a hiatus in distribution between the southern and northern areas.

Regional and total abundance estimates

Because the 1987 and 1989 surveys did not achieve the spatial coverage of later surveys, we combined them for the purpose of estimating abundance in the EGI and TOTAL regions (Fig. 4). The resulting estimates were applied to the year 1988.

Fin whale abundance increased rapidly and significantly in the WEST region but not in the other regions (Table 1, Fig. 8). The small increases noted in the EGI and TOTAL regions are largely a result of the increase in WEST. It is apparent that the increase in the WEST region accounts for nearly all the increase in the EGI and TOTAL areas. Highest abundance was observed in 2001 when there were nearly 30,000 (cv 0.11) in the area.

Humpback whales

Distribution

In the Icelandic/Faroese sector, most sightings of humpback whales were made in the COASTAL region, which was covered by aerial surveys in most years (Fig. 3 and 5). In later surveys and especially 2001, humpback whales occurred with increasing frequency outside of the COASTAL region, primarily along the East Greenland ice edge and to the North of Iceland. Rather few humpback whales were seen around the Faroes and in the southern area surveyed only in 1989. Distribution in the Norwegian sector varied over the course of the surveys. In 1989 and the 1996-2001 series, most humpback whales were seen in the far western Norwegian Sea and around Bear Island, whereas in 1995 their distribution was more tightly centred around Bear Island.

Regional and total abundance estimates

Humpback whale sightings in the 1986 and 1987 aerial surveys of the COASTAL region were too few to provide an estimate. We therefore used encounter rate (n/L) as an indicator of relative abundance to assess trends in the Region. Encounter rate increased rapidly and significantly in the region, at a mean rate of 15% per year (Fig. 8). Total abundance in the COASTAL region, corrected for bias due to animals missed by observers but not that due to diving animals, was 4,928 (cv 0.463) in 2001 (Pike *et al.* 2006).

Abundance also increased rapidly in the ICELAND region, especially between 1987 and 1995. The mean rate of increase for the period was 16.6%. Abundance did not increase nearly so rapidly in the NORWAY region (2%). The rate of increase for the TOTAL area was 12.9% per year, and virtually all of this increase can be attributed to the ICELAND region, including COASTAL.

DISCUSSION AND CONCLUSIONS

Potential biases

The estimates presented here are potentially biased both because of visible whales being missed by the observers (perception bias) and whales that are diving while the ship or plane passes (availability bias). For ship surveys we would not expect these biases to be serious for these species. Both humpback and fin whales are large and under most circumstances have a visible blow, and are not easily missed if they are nearby. Their mean diving times are relatively short, and long dives are relatively rare, so it is unlikely that they would remain underwater during the passage of a slow-moving ship. However, these biases, if present, would lead to abundance being underestimated by an unknown degree.

The surveys did not cover the entire summer range of fin whales in particularly the EGI stock area. The southward extension of the 1989 NASS revealed that fin whales do occur to the south of the area normally surveyed. Therefore the estimates for the EGI stock area must be considered to be negatively biased.

Some of the regions varied in size from survey to survey, which would affect estimates of abundance. For fin whales, the WEST region varied little in size, and the NORWAY region did not vary in size. Even though the EGI TOTAL areas were larger in 1987-1989 and 1995 than in 2001, the estimates for 2001 were largest. For humpback whales, the defined regions captured virtually the entire distribution range for all estimates, so bias due to size variation is probably nonsignificant.

Distribution

Humpback whales

Humpback whales have a tendency to concentrate in coastal shelf areas in many areas of the world (Martin *et al.* 1990). This would seem to be the case in the central and northeastern North Atlantic where highest densities were seen on the Icelandic shelf and in the relatively shallow waters (< 1000 m) of the western Barents Sea around Bear Island. However some animals were seen in the deeper waters of the central Norwegian Sea, particularly in 1989 and the 1996-2001 series. The expansion in the summer range of humpback whales around Iceland observed over the course of the survey series would seem to parallel the increase in numbers, rather than being a shift in distribution.

Fin whales

The most marked change in the distribution of fin whales in the survey area occurred in the WEST region. In the early surveys fin whales tended to be concentrated along the East Greenland ice edge. By 1995 and especially 2001, they were spread much more evenly throughout the region. However this coincided with a substantial increase in fin whale numbers in the region, and may be seen as a range expansion rather than a distribution shift.

Trends in abundance

Humpback whales

There has been a substantial and significant increase in the abundance of the Icelandic feeding stock, as indicated by the increases in encounter rate in the aerial surveys in the COASTAL region, and the increases in the shipboard estimates in the ICELAND region. These increases in abundance imply an annual rate of population increase of about 15-16%, which is probably beyond the realm of biological plausibility due to natural increase alone for this species (Clapham *et al.* 2001). However it is possible that humpback whales may be emigrating to Icelandic waters from other areas, possibly from the Atlantic Canada summering area for which valid estimates of abundance and trends are not available. Similarly high apparent rates of increase have been observed for this species in the Antarctic (Matsuoku *et al.* MS 2004).

Additional evidence from other sources also suggests that the humpback whale feeding stock around Iceland has been increasing rapidly. Sigurjónsson and Gunnlaugsson (1990) used an index based on systematic sightings records from whaling vessels kept between 1970 and 1988 to derive an annual rate of increase of 11.6% for humpback whales off western Iceland. Sightings of humpback whales were absent or quite rare at the beginning of this period. Sighting rates of humpback whales have also increased in other ship surveys conducted around Iceland between 1987 and 2003 (Gunnlaugsson *et al.* 2006).

In contrast to the Icelandic area, there is little evidence of any trend in the abundance of humpback whales off Norway.

Modern whaling began in Norwegian and Icelandic waters in the late 1800's and continued in its first phase until banned in 1904 (Norway) and 1915 (Iceland) (Tønnessen and Johnsen 1982). By this time stocks of blue, fin and humpback whales had been reduced in both areas to the point where whaling was barely profitable. In this period, about 3,000 humpback whales were estimated taken around Iceland, mainly from land stations on the east and west coasts (Sigurjónsson and Gunnlaugsson 1990). Around 1,500 were taken off Norway (Ingebrightsen 1929). Prior to this considerable whaling had occurred on possible breeding grounds (Mitchell and Reeves 1983), and unknown, but presumably small numbers of humpbacks were taken in earlier centuries in Icelandic coastal waters. Whaling continued for humpbacks in other areas of the North Atlantic, but catches in Iceland and Norway have been very low since 1915 (7 and *ca.* 50 animals respectively). It seems likely that humpback whale numbers were reduced to very low levels in both areas by 1915, since they would certainly have been taken in later whaling operations had they been present (Ingebrigtsen 1929, Sigurjónsson and Gunnlaugsson 1990). Humpback whales were fully protected in 1966, but some very limited native subsistence harvesting has occurred since that time off West Greenland (until 1985) and at Bequia in the Caribbean.

Given the historical level of catch, it seems likely that the feeding stock off Norway is fully recovered and of similar size now as it was at the beginning of the first phase of whaling. The status of the Icelandic feeding stock is less clear. Given that a catch of about 3,000 animals apparently severely reduced humpback whale abundance around Iceland, and that the present abundance estimate from 1995 and 2001 surveys is in the order of 11-14 thousand animals, it seems likely that the feeding stock around Iceland has recovered from overexploitation and may in fact be above its historical abundance level in this area. Punt *et al.* (2005) carried out a modelling exercise to try to reconcile historical catches with present and past estimates of abundance and rates of increase in the North Atlantic. They noted that none of their model formulations could mimic the high apparent rate of increase (from Sigurjónsson and Gunnlaugsson 1990) and high abundance (based on an earlier, lower estimate from NASS-95) around Iceland. The inclusion of the abundance estimates and rates of increase presented here would certainly not have improved the situation. Therefore we conclude that the present stock size around Iceland may be greater than it was at the onset of modern whaling.

Fin whales

There has been a substantial and significant increase in the numbers of fin whales in the WEST region, corresponding to an annual rate of increase of about 10%. The increases in the EGI and TOTAL regions are largely due to the increases in WEST. In contrast the NORWAY region shows little evidence of any trend over the period.

The history of Icelandic and Norwegian whaling for fin whales is similar to that for humpback whales, but catches of fin whales were much larger. At Iceland approximately 11,000 fin whales were taken in the first period of whaling which lasted from 1883-1915 (NAMMCO 2000). Whaling was conducted from both the east and west coasts but most were probably taken from the west coast. By 1915 it was evident that the fin whale stock around Iceland was severely depleted. A second period of whaling began off the west coast in 1929 and persisted until 1989, during which a total of about 9,000 fin whales were taken.

About 10,500 fin whales were taken off the North Norwegian coast during the period 1868-1904 (Rørvik and Jonsgård 1981). In the later part of this period it became necessary to search further offshore, often as far as Bear Island, to find whales as the coastal area became depleted (Christensen *et al.* 1992). Subsequently whaling stations were built at Bear Island and Spitzbergen, and conducted by pelagic operations in other areas. Whaling from Norwegian land stations resumed in 1918 and fin whale catches continued until about 1972, taking a total of 9,920 animals (Bloch 2005).

Since 1989, fin whale catching has all but ceased in the North Atlantic, with catches limited to a few each year off West Greenland.

The assessment of fin whale stocks in the North Atlantic is complicated by uncertainty about stock structure. The Scientific Committee of NAMMCO has recently (NAMMCO 2000, 2001, 2004) conducted assessments of mainly the putative East Greenland-Iceland stock. In these assessments the most current information on historical catches, abundance and biological parameters is used in a model to attempt to replicate past population trends, and to forecast future abundance under various catch regimes. Under most simulations the stock was forecast to have been approaching its carrying capacity by about 2000. However the modelling efforts fail to reconcile all sources of data, and in particular cannot explain why a catch of about 11,000 fin whales over more than 30 years should have reduced the population to a low level, if it was as large then as it is today. One explanation may be that there is population sub-structure within the EGI stock area, and that local areas within range of the shore stations were depleted. This would seem to be supported by the observation that the stock seemed to have rebounded by the 1930's when whaling around Iceland resumed. Models incorporating inshore and offshore "substocks" that mix slowly have been more successful in fitting the apparent historical trends in the abundance of whales around Iceland (NAMMCO 2004). An alternative explanation, that has not been formally assessed, is that the population now is higher than it was at the onset of modern whaling; *ie.* that carrying capacity has increased or stock distribution has changed.

Formal assessments of the Norwegian fin whale populations have not yet been carried out by the NAMMCO Scientific Committee. However a cursory look at the catch data compared to the present population size raises some questions. Clearly fin whales must have been more abundant in this area in the past, as the present population size of under 2000 animals could not have supported the historical catches. Yet there is no evidence that the abundance of fin whales is increasing rapidly in this area, as we might expect for a recovering population and as is observed around Iceland.

Ecological implications

Clearly the abundance of both humpback and fin whales in the North Atlantic has changed dramatically over the past 130 years, and much of this change can be ascribed to human intervention through whaling. But that populations continue to change rapidly is somewhat surprising, particularly for humpback whales for which whaling has occurred only at very low levels in this area for the past 50 years. There are several possible explanations for the observed changes, discussed in detail below.

Survey bias

For survey bias to have been a factor in the trends seen in the NASS series, the magnitude and/or direction of these biases would have to have changed over the course of the surveys. While we have no evidence for this, one might expect that the earlier surveys were less efficient than later ones, as the observers and cruise leaders gained experience and became more proficient at their tasks. Also, platform heights and the number of observers on duty have tended to increase over the course of the surveys. However we would then expect to see positive trends in most or all species, and this is not the case (Gunnlaugsson *et al.* 2006). Moreover, given the trends seen in particularly humpback whale abundance around Iceland, survey efficiency would have to have increased by over an order of magnitude if this factor alone were operant.

Recovery after whaling

North Atlantic populations of both fin and humpback whales were severely reduced by whaling in the early 20th century. It is therefore not unexpected that populations should be recovering after the cessation of whaling. However the observed pattern of population growth indicates that this may not be the only factor responsible.

For humpback whales, the size and continued growth of the population around Iceland seems incompatible with past catches and the size of the North Atlantic population as a whole (Punt *et al.* 2005). The stock around Iceland appears to be growing at a rate that is not possible through internal growth alone for this species (Clapham *et al.* 2001), indicating that whales may be emigrating in from other areas. The situation is less extreme for Icelandic fin whales: still, population recovery should be nearly complete by now if the EGI stock is a single unit. The apparent growth of the EGI stock in the WEST region alone has been about 10,000 animals since 1987; this exceeds the total catch of fin whales in the area from 1929-1989.

In contrast, the stock of humpback whales around Norway appears to have recovered to something approaching its original size. The stock of fin whales is much smaller than one might expect given historical harvests. However it must be borne in mind that fin whaling continued along the Norwegian coast up until 1972, and it is possible that the stock might have been reduced to a low level. Future assessments planned by the NAMMCO Scientific Committee will address this issue.

Stock structure

The issue of uncertain stock structure is mainly relevant to fin whales. The depletion of local sub-stocks within the EGI stock area, followed by their relatively rapid recovery through both internal growth and mixing, might explain the trends seen in the Icelandic catch-effort series. Further work on this issue is planned by both the NAMMCO and IWC Scientific Committees.

Immigration from other areas

This applies mainly to the case of humpback whales around Iceland, where the apparent growth rate of the population is too large to be a result of internal population dynamics (Clapham *et al.* 2001). However the maximum population growth rate of 11% is well within the confidence interval of the growth rate calculated from the NASS. If immigration is occurring, it follows that the area must be able to support more animals than it did historically (see below).

Change in carrying capacity

Carrying capacity (K) is nearly impossible to measure directly. We must assume that a population is at carrying capacity if it has not been harvested or has fully recovered from past harvesting. Changes in carrying capacity could to some extent explain the trends observed especially around Iceland, where there is some evidence that the sizes of present populations of both humpback and fin whales exceed those of the pre-whaling populations. The North Atlantic is certainly not a "pristine" ecosystem, and it is not unreasonable to expect that the carrying capacity for many species has changed due to human intervention over the past 1-200 years. For example, populations of large predatory fish have been heavily targeted by fisheries, and have been reduced in many parts of the world to 10% or less of their original size (Myers and Worm 2003). The diet of both humpback and fin whales is dominated by small pelagic fish and macrozooplankton (Martin *et al.* 1990), which are also the prey of predatory fish. Therefore these large cetaceans are competitors with predatory fish. It is therefore easy to advance an argument that the decline of predatory fish has lead to a higher carrying capacity for recovering whale stocks. Unfortunately there is little information on the long-term trends of pelagic fish and macrozooplankton in the North Atlantic, so this appealing "ecological story" is difficult to confirm or falsify. It is also the case that populations of other cetaceans, such as right (*Eubalaena glacialis*), bowhead (*Balaena mysticetus*) and blue (*B. musculus*) whales have been even more heavily impacted by past whaling activities than have fin and humpback whales, and populations do not seem to have recovered to nearly the same extent as have those of fin and humpback whales. As these species are, to some extent at least, ecological competitors, the selective removal of some may have lead to ecological opportunities for the others.

ACKNOWLEDGEMENTS

We thank all those involved in the planning, conduct and analysis of the NASS and other surveys, and to the National Research Institutes that funded them.

REFERENCES

Bloch, D. 2005. Norwegian coastal and pelagic whaling, 1917-1986. SC/13/FW/4 for the NAMMCO Scientific Committee.

Borchers, D.L. and Burt, M.L. 1997. Sei and fin whale abundance in the North Atlantic, estimated from NASS-95 shipboard survey data. NAMMCO SC/5/AE/1.

Buckland, S.T., Bloch, D., Cattanach, K.L., Gunnlaugsson, Th. 1993a. Fin whale abundance in the North Atlantic, estimated from Icelandic and Faroese NASS-87 and NASS-89 data. *Rep. int. Whal. Commn* 42:645-651.

Buckland, S.T., Cattanach, K.L. and Lens, S. 1992b. Fin whale abundance in the Eastern North Atlantic, estimated from Spanish NASS-89 data. *Rep. int. Whal. Commn* 42:457-460.

Christensen, I., Haug, T. and Øien, N. 1990. Seasonal distribution, exploitation and present abundance of stocks of large baleen whales (Mysticeti) and sperm whales (*Physeter macrocephalus*) in Norwegian and adjacent waters. *ICES J. Mar. Sci.* 49:341-355.

Clapham, P., Robbins, J., Brown, M., Wade, P. and Findlay, K. 2001. Report of the Scientific Committee. Annex G. Report of the Sub-Committee on the Comprehensive Assessment of Whale Stocks – In-depth Assessments. Appendix 5. A note on plausible rates of population growth in humpback whales. *J. Cetacean Res. Manage. (Suppl.)* 3:196-7.

Clapham, P., Robbins, J., Brown, M., Wade, P. and Findlay, K. 2001. Report of the Scientific Committee. Annex G. Report of the Sub-Committee on the Comprehensive Assessment of Whale Stocks – In-depth Assessments. Appendix 5. A note on plausible rates of population growth in humpback whales. *J. Cetacean Res. Manage. (Suppl.)* 3:196-7.

Desportes, G., Bloch, D. Allali, P., Barbraud, C., Egholm, J., Joensen, M., Leroy, B., Mougeot, F., Mouritsen, R., Reinert, A., and Sequeira, M. 1996. NASS-95, preliminary report of the Faroese cruise. SC/4/16 for the NAMMCO Scientific Committee.

Donovan, G.P. 1991. A review of IWC stock boundaries. In: Hoelzel, A.R. (ed.) *Genetic ecology of whales and dolphins*. *Rep. int. Whal. Commn* (Special Issue 13):39-68.

Donovan, G.P. and Gunnlaugsson, Th. 1989. North Atlantic Sightings Survey 1987: Report of the aerial survey off Iceland. *Rep. int. Whal. Commn* 39:437-441.

Gunnlaugsson, Th., Halldórsson, S.D., Ólafsdóttir, D. and Víkingsson, G.A. NASS 2001 Icelandic shipboard survey report. SC/10/AE/10 for the NAMMCO Scientific Committee.

Gunnlaugsson, Th., Sigurjónsson, J. and Donovan, G.P. 1988. Aerial survey of cetaceans in the coastal waters of Iceland, June-July 1986. *Rep. int. Whal. Commn* 38:489-500.

Gunnlaugsson, Th., Víkingsson, G.A. and Pike, D.G. 2005. Comparison of sighting rates from NASS and other dedicated cetacean vessel effort around Iceland during 1982 to 2003. *NAMMCO Sci. Publ.* 6:pp-pp.

Gunnlaugsson, Th., Víkingsson, G.A. and Pike, D.G. 2006. Comparison of sighting rates from NASS and other dedicated cetacean vessel effort around Iceland during 1982 to 2003. *NAMMCO Sci. Publ.* 7:xxx-xxx.

Hiby, A.R. and Hammond, P.S. 1989. Survey techniques for estimating abundance of cetaceans. *Rep. int. Whal. Commn* (Special Issue 11):47-80.

Ingebrigtsen, A. 1929. Whales caught in the North Atlantic and other seas. *Rapports et Proces-Verbaux des Reunions. Conseil International pour l'Exploration de la Mer* 56:1-26.

[IWC] International Whaling Commission. 1992. Report of the comprehensive assessment special meeting on North Atlantic fin whales. *Rep. int. Whal. Comm.* 42:595-606.

Joyce, G.G., Desportes, G. and Bloch, D. 1990. The Faroese NASS-89 Sightings Cruise. SC/42/O11 for IWC Scientific Committee.

Krebs, C. J. 2001. Ecology: the experimental analysis of distribution and abundance. 5th edition. Benjamin Cummings, Montréal.

Lens, S. 1991. North Atlantic Sightings Survey 1989: Report of the Spanish cruise. *Rep. int. Whal. Commn* 41:539-544-

Lens, S., Quiroga, H. and Gil de Sola, L. 1989. Report of the cruise undertaken by Spain as part of the North Atlantic Sightings Survey, 1987. *Rep. int. Whal. Commn* 39:423-425.

Martin, A. R. [ed.] 1990. *Whales and Dolphins.* Salamander Books Ltd. 192 pp

Matsuoka, K., Hakamada, T., Murase, H. and Nishiwaki, S. (MS) 2004. Current abundance estimates of humpback and fin whales in the Antarctic Areas IIIE, IV, V and VIW (35 °E-145 °W). SC/56/SH11 for the IWC Scientific Committee.

Mitchell E, Reeves RR. 1983. Catch history, abundance and present status of Northwest Atlantic humpback whales. *Rep. int. Whal Commn* Special Issue 5:153-212

Myers, R.A. and Worm, B. 2003. Rapid worldwide depletion of predatory fish communities. *Nature* 423:280-283.

[NAMMCO] North Atlantic Marine Mammal Commission. 2000. Report of the Working Group on North Atlantic Fin Whales. In: NAMMCO, *Annual Report 1999*, 189-211.

[NAMMCO] North Atlantic Marine Mammal Commission. 2001. Report of the Working Group on North Atlantic Fin Whales. In: NAMMCO, *Annual Report 2000*, 275-294.

[NAMMCO] North Atlantic Marine Mammal Commission. 2004. Report of the Working Group on Minke and Fin Whales. In: NAMMCO, *Annual Report 2003*, 196-229.

Øien, N. 1990. Sightings surveys in the northeast Atlantic in July 1988: distribution and abundance of cetaceans. *Rep. int. Whal. Commn* 40:499-511.

Øien, N. 1996. Cruise and data report from the Norwegian sighting survey (NILS-95). SC/48/NA3 for the IWC Scientific Committee.

Øien, N. 2003. Distribution and abundance of large whales in the Northeast Atlantic, 1995. SC/11/MF/10 for the NAMMCO Scientific Committee.

Øien, N. 2004. Distribution and abundance of large whales in the northeast Atlantic, based on data from partial coverages 1996-2001. SC/12/20 for the NAMMCO Scientific Committee.

Øien, N. and Bøthun, G. 2005. Trends in local abundance of large whales in the Northeast Atlantic, based on Norwegian surveys 1987-2004. SC/57/O11 for the IWC Scientific Committee.

Øritsland, T., Øien, N., Calambokidis, J., Christensen, I., Cubbage, J.C., Hartvedt, S., Jensen, P.M., Joyce, G.G., Tellnes, K. and Troutman, B.L. 1989. Norwegian whale sightings surveys in the North Atlantic, 1987. *Rep. int. Whal. Commn* 39:411-415.

Paxton, C.G.M., Burt, M.L. and Hedley, S.L. 2006. Others Using environmental covariates to estimate the density of humpback whales with application to the 1995 and 2001 NASS aerial and shipboard surveys. *NAMMCO Sci. Publ.* 7:xx-xx.

Pike, D.G. and Víkingsson, G.A. 2002. The NASS-2001 Icelandic aerial survey: Introduction and evaluation. SC/10/AE/12 for the NAMMCO Scientific Committee.

Pike, D.G., Gunnlaugsson, T, and Víkingsson, G.A. 2002a. Estimates of humpback whale (*Megaptera noveangliae*) abundance in the North Atlantic, from NASS-95 shipboard survey data. Paper SC/54/H10 presented to the Scientific Committee of the International Whaling Commission, May 2002

Pike. D.G.. Paxton, C.G.M., Gunnlaugsson, Th. and Vikingsson, G.A. 2006. Trends in the distribution and abundance of cetaceans from aerial surveys in Icelandic coastal waters, 1986 – 2001. *NAMMCO Sci. Publ.* 7:xx-xx.

Rørvik, C.J. and Jonsgård, Å. 1981. Review of the balaenopterids in the North Atlantic Ocean. FAO Fisheries Series (5) (Mammals in the Seas):269-286.

Sanpera, C. and Jover, L. 1989. Density estimate of fin whales in the North Atlantic from NASS-87 Spanish crise data. *Rep. int. Whal. Commn* 39:427-429.

Sanpera, C. and Jover, L. 1989. Density estimate of fin whales in the North Atlantic from NASS-87 Spanish cruise data. *Rep. int. Whal. Commn* 39:427-429.

Sigurjónsson, J. and Gunnlaugsson, Th. 1990. Recent trends in abundance of blue (*Balaenoptera musculus*) and humpback whales (*Megaptera novaengliae*) off west and southwest Iceland, with a note on occurrence of other cetacean species. *Rep. Int. Whal. Commn* 40:537-551.

Sigurjónsson, J., Gunnlaugsson, Th., Víkingsson, G. and Guðmundsson, H. 1996a. North Atlantic Sightings Survey 1995 (NASS-95): Aerial survey in coastal Icelandic waters July 1995. SC/4/17 for the NAMMCO Scientific Committee.

Sigurjónsson, J., Gunnlaugsson. Th. And Payne, M. 1989. NASS-87: Shipboard sightings surveys in Icelandic and adjacent waters Jun-July 1987. *Rep. Int. Whal. Commn* 39: 395-409.

Sigurjónsson, J., Gunnlaugsson. Th., Ensor, P. Newcomer, M. and Víkingsson, G. 1991. North Atlantic Sightings Survey 1989 (NASS-89): Shipboard surveys in Icelandic and adjacent waters July-August 1989. *Rep. Int. Whal. Commn* 41: 559-572.

Sigurjónsson, J., Víkingsson, G., Gunnlaugsson, Th., and Halldórsson, S.D. 1996b. North Atlantic Sightings Survey 1995 (NASS-95): Shipboard surveys in Icelandic and adjacent waters June- July 1995. Preliminary cruise report. SC/4/17 for the NAMMCO Scientific Committee.

Tønnessen, J.N. and Johnsen, A.O. 1982. *The History of Modern Whaling.* C. Hurst and Company, London

LIST OF TABLES

LIST OF FIGURES

HUMPBACK WHALES

YEAR	REGION	N	CV	L	R	COMMENTS
1986	COASTAL	0.0036	0.36	0.0018	0.0071	N is encounter rate.
1995	COASTAL	0.0141	0.31	0.0077	0.0257	N is encounter rate.
2001	COASTAL	0.0291	0.22	0.0191	0.0444	N is encounter rate.
GROWTH RATE		0.15		0.09	0.25	
1987	ICELAND	1,722	0.25	1,061	2,795	
1995	ICELAND	11,060	0.33	4,470	27,362	
2001	ICELAND	13,965	0.27	7,993	24,397	
GROWTH RATE		0.17		0.10	0.24	
1988	NORWAY	768	0.37	325	1,814	Øien and Bøthun (2005)
1989	NORWAY	427	0.70	110	1,661	Øien and Bøthun (2005)
1995	NORWAY	953	0.97	137	6,638	Øien and Bøthun (2005)
1998	NORWAY	628	0.69	155	2,541	Øien and Bøthun (2005)
GROWTH RATE		0.02		-0.41	0.43	
1987	TOTAL	2,848	0.19	1,957	4,144	Includes total from Norwegian sector in 1988 (Øien 1990)
1995	TOTAL	12,270	0.30	6,872	21,909	Norwegian – Øien (2003)
2001	TOTAL	14,899	0.26	9,103	24,387	Norwegian – Øien (2004)
GROWTH RATE		0.12		0.07	0.17	

FIN WHALES

1987	WEST	3,607	0.18	2,537	5,132	
1989	WEST	6,006	0.25	3,468	10,401	
1995	WEST	13,726	0.23	8,667	21,740	
2001	WEST	14,021	0.18	9,550	20,586	
GROWTH RATE		0.10		0.06	0.15	
1988	EGI	15,237	0.22	9,990	23,239	Includes components of 1987 and 1989 surveys.
1995	EGI	20,262	0.21	13,464	30,492	Norwegian – Øien (2003)
2001	EGI	23,676	0.13	18,024	31,101	
GROWTH RATE		0.03		0.00	0.09	
1988	NOR	1,242	0.38	512	3,009	Øien and Bøthun (2005)
1989	NOR	1,106	0.43	464	2,637	Øien and Bøthun (2005)
1995	NOR	1,806	0.51	576	5,668	Øien and Bøthun (2005)
1998	NOR	1,723	1.09	201	14,734	Øien and Bøthun (2005)
GROWTH RATE		0.05		-0.45	0.24	
1988	TOTAL	17,482	0.19	11,981	25,508	Includes components of 1987 and 1989 surveys.
1995	TOTAL	26,343	0.17	18,754	37,004	Norwegian – Øien (2003)
2001	TOTAL	29,891	0.11	24,040	37,167	Norwegian – Øien (2004)
GROWTH RATE		0.04		0.01	0.08	

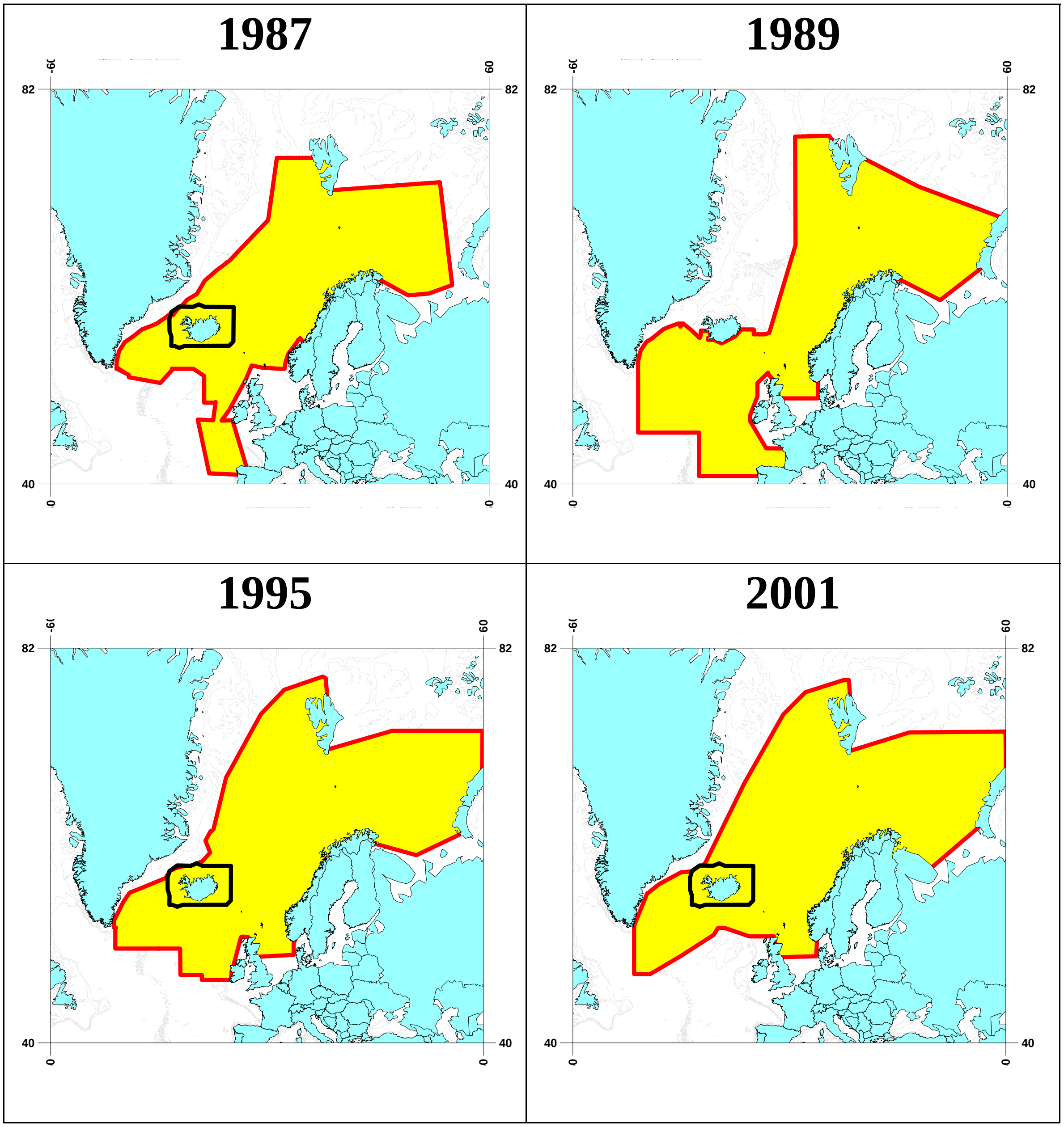


Fig. 1

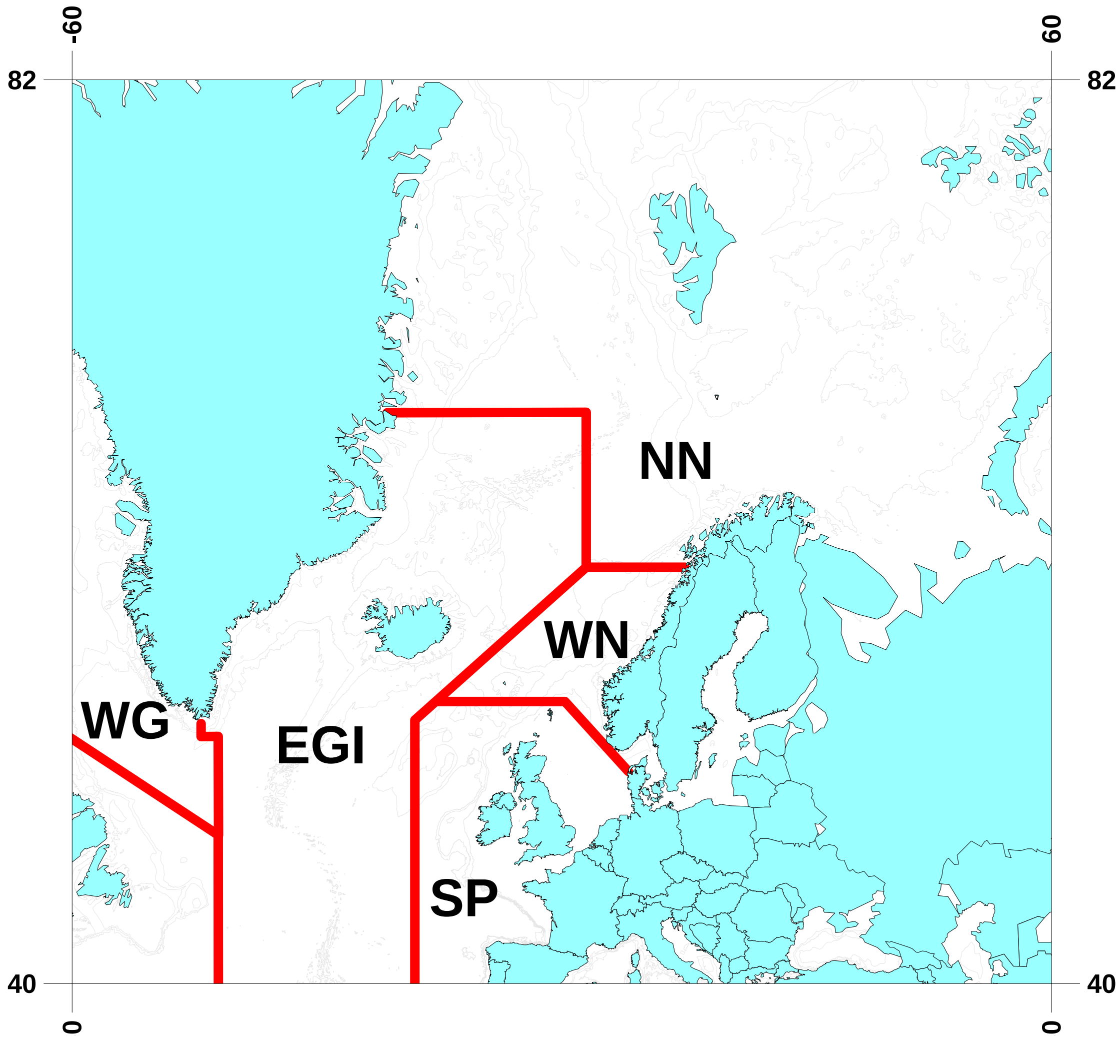


Fig. 2

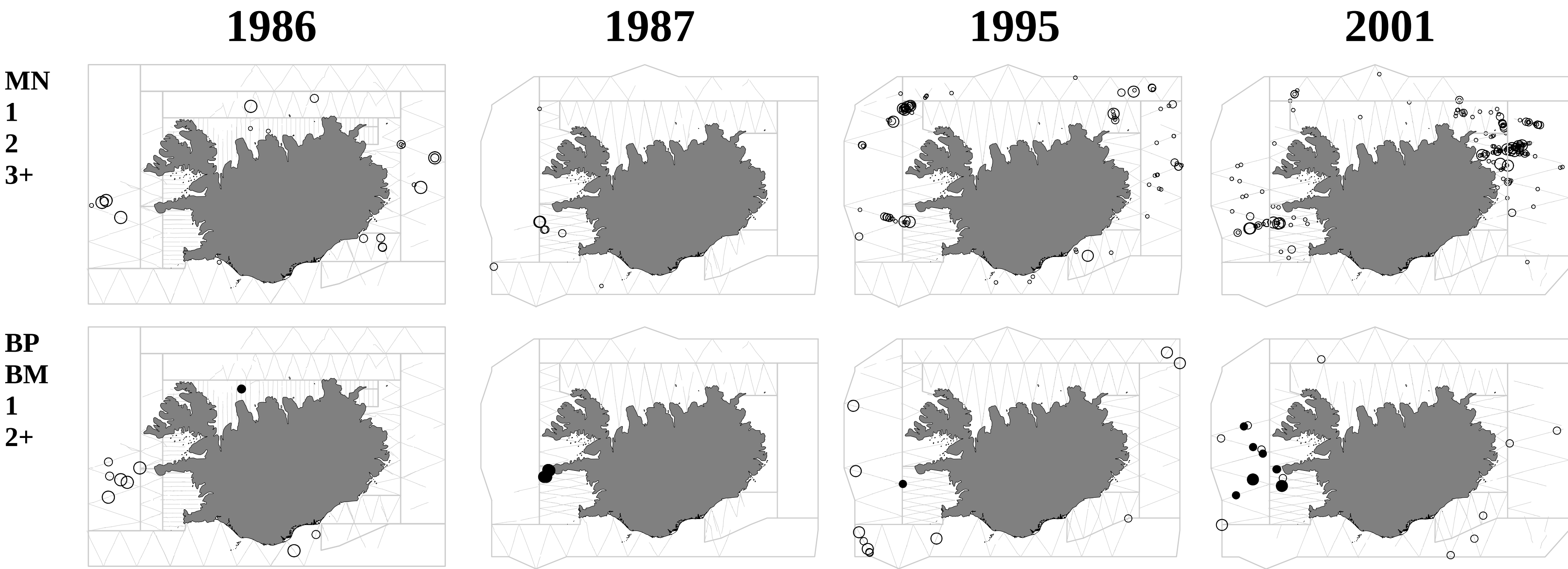
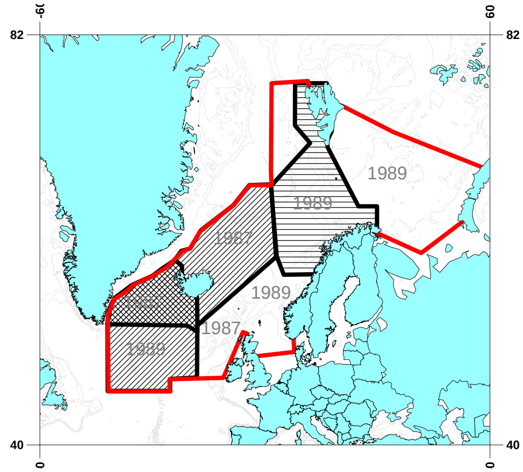
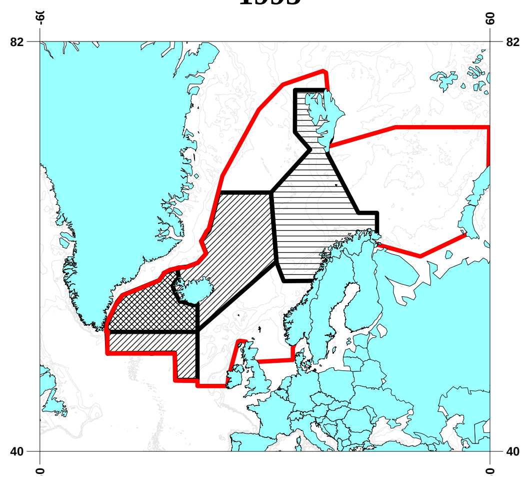


Fig. 3

1987-1989



1995



2001

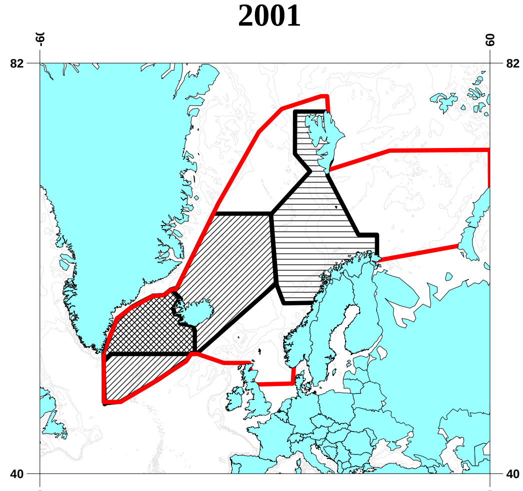


Fig. 4

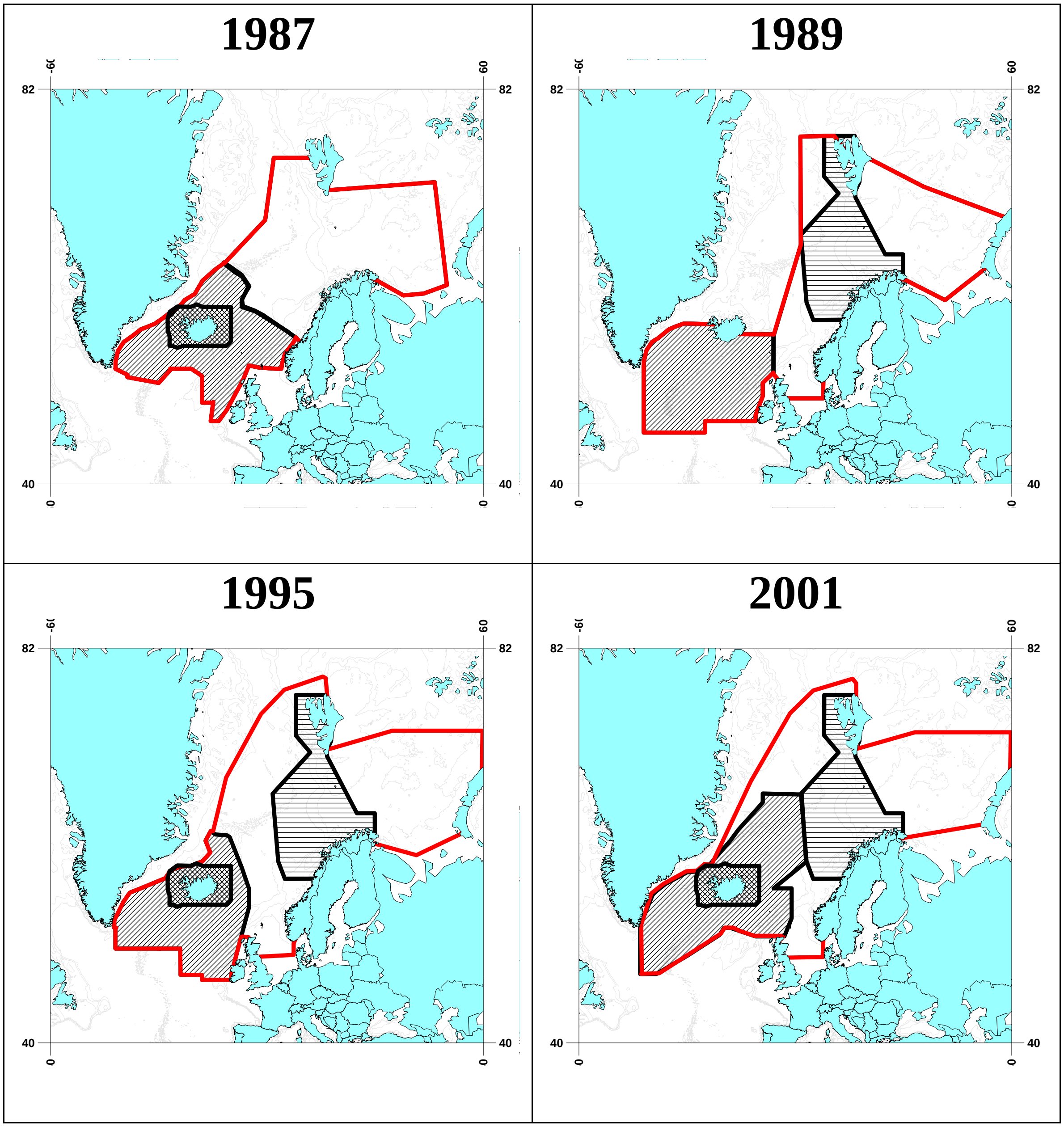


Fig. 5

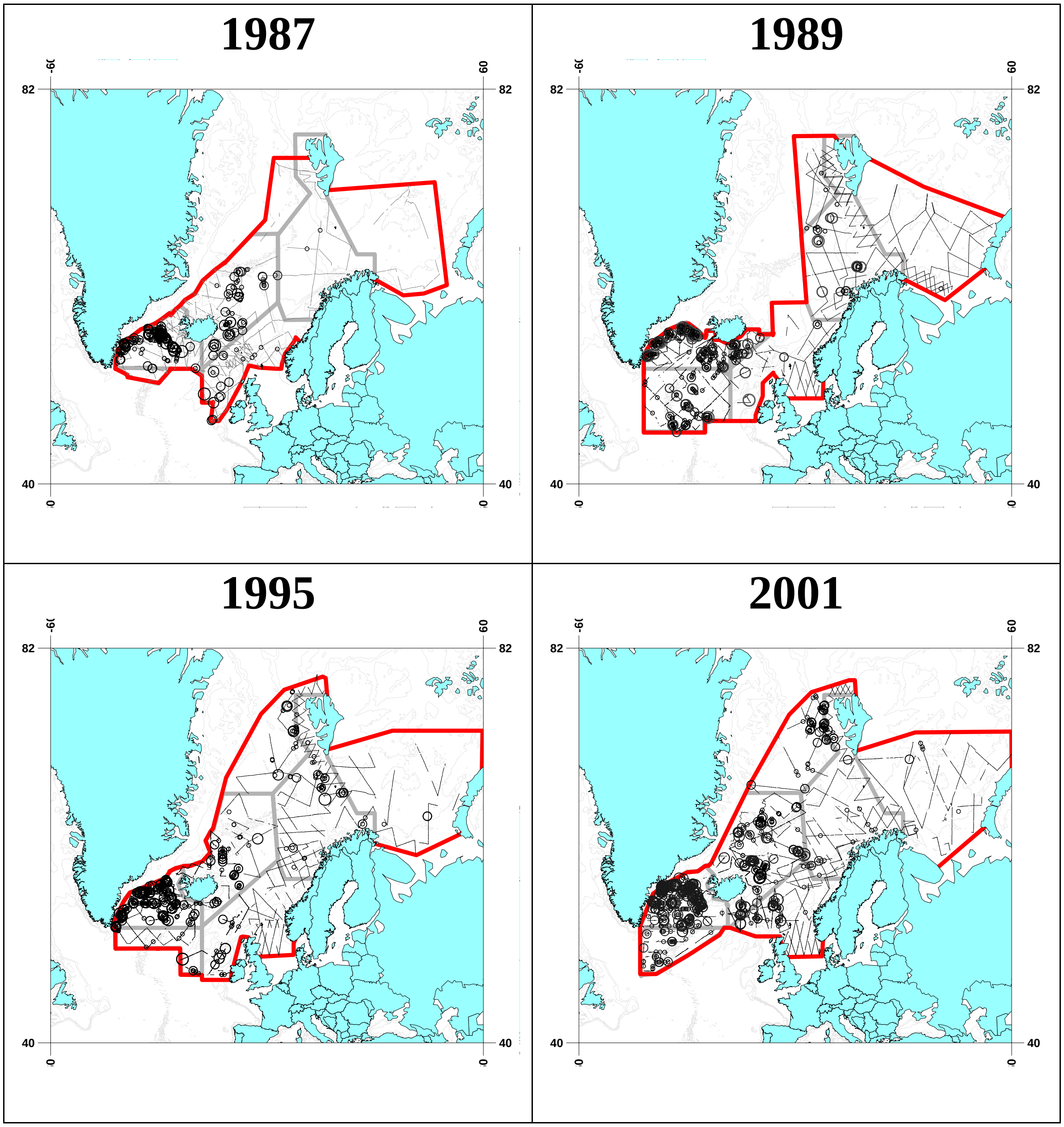


Fig. 6

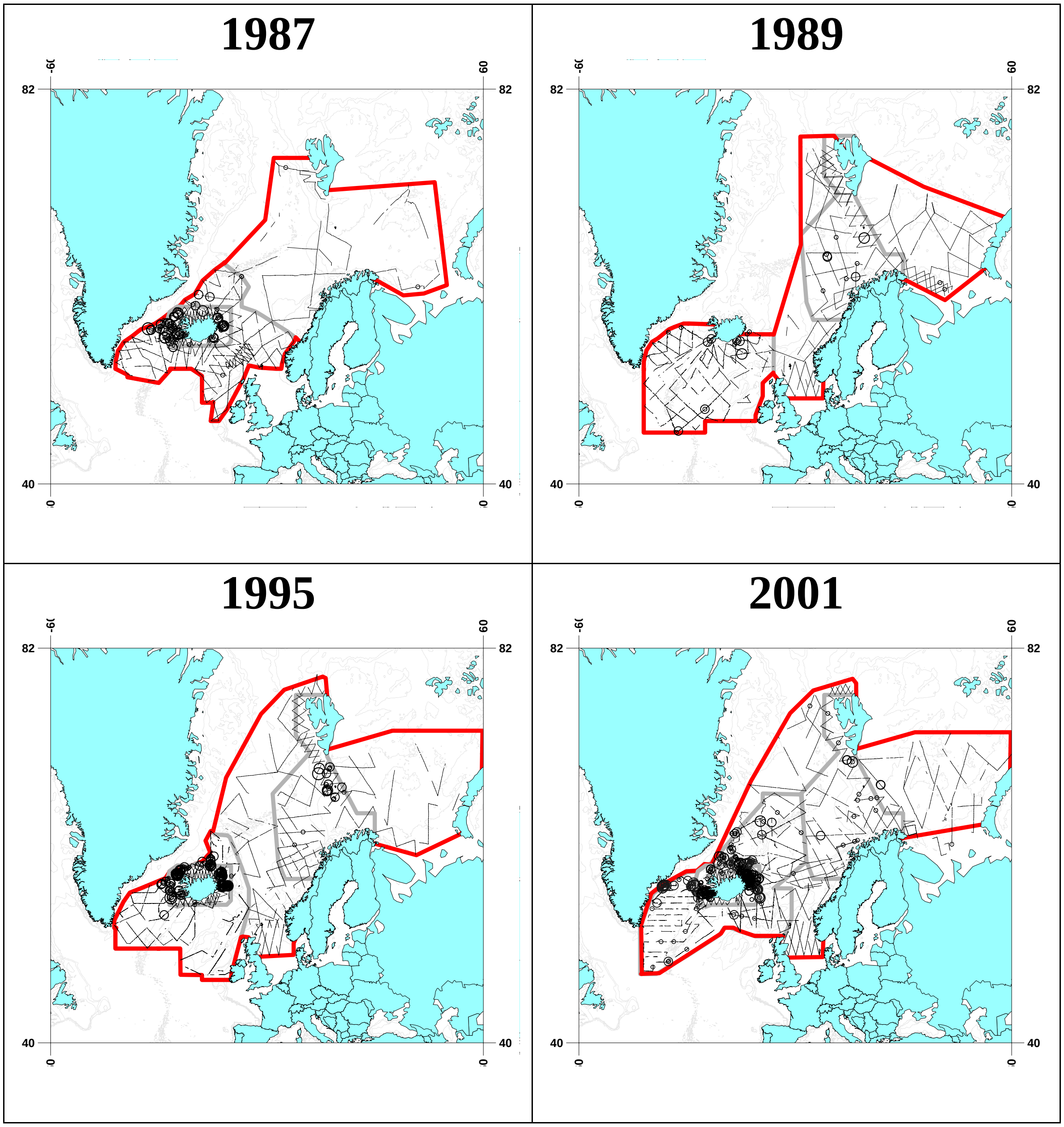


Fig. 7

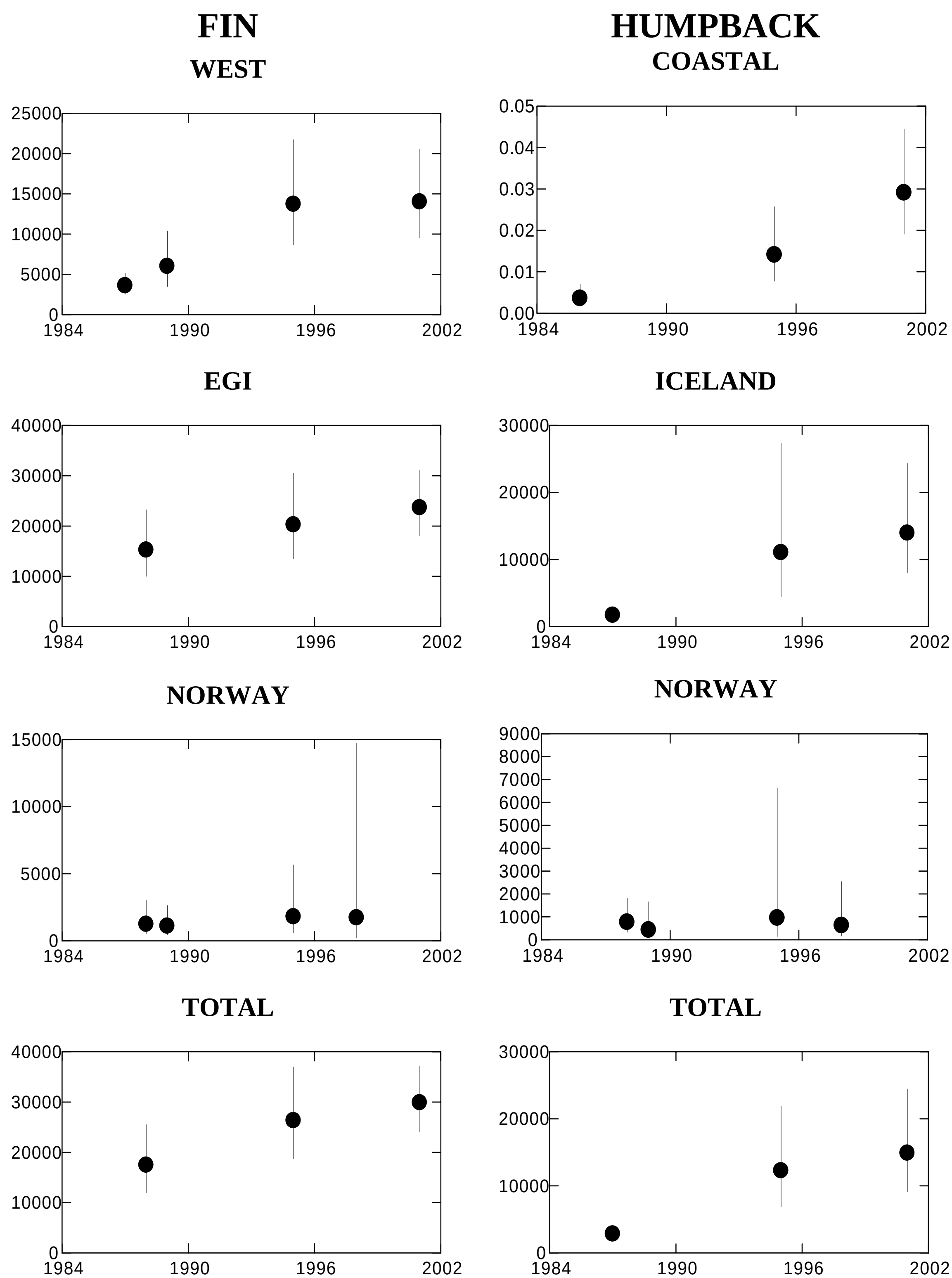

FIN
HUMPBACK
WEST
COASTAL
EGI
ICELAND
NORWAY
NORWAY
TOTAL
TOTAL
1984
1990
1996
2002
0
5000
10000
15000
20000
25000
30000
40000
0.00
0.01
0.02
0.03
0.04
0.05
1000
2000
3000
4000
5000
6000
7000
8000
9000

Fig. 8