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Estimation of Food Consumption by Cetaceans in Icelandic and Adjacent Waters

by

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ABSTRACT

This paper reports on estimation of consumption by cetaceans on fish, cephalopods and planktonic crustacea in Icelandic and adjacent waters. The estimates are based on (i) abundance estimates from recent sighting surveys (NASS-87 and NASS-89); (ii) seasonal variation in abundance estimated by sightings and/or catch data from whaling vessels; and consumption rates, calculated from the estimated biomass of cetaceans in the area throughout the year. The total food consumption was estimated as 4.6M metric tons in a smaller area defined as Icelandic and adjacent waters, and 6.2M tons in the larger area north of 60°N. Fin whales (*Balaenoptera physalus*) were the largest consumers in the area, followed by pilot whales (*Globicephala melas*), minke (*B. acutorostrata*) and Northern bottlenose whales (*Hyperoodon ampullatus*). According to our calculations crustaceans comprise around 50% of the total consumption, whereas finfish and cephalopods comprise about 25% each. The principal prey species ...

INTRODUCTION

The ecological role of cetaceans and particularly their alleged interactions with fisheries is often debated by layman and scientists. A number of studies have in recent years addressed this question, particularly with respect to the drastic changes that took place in the Southern Ocean subsequent to the collapse of most of the stocks of large baleen whales in the area during this century (e.g. Laws, 1977 , 1985; Hinga, 1979). Several studies have examined at the situation in other ocean areas, such as off the eastern coast of North America, where cetaceans have been investigated with respect to their role in the ecosytem (e.g. Scott *et al.*, 1983; Overholtz *et al.*, 1991). These studies have been centered around the question of total biomass of cetaceans and the estimated predation. In this context a series of studies have dealt with theoretical aspects of cetacean bioenergetics and food requirements (Sergeant, 1969; Kawamura, 1974; Brodie, 1975; Mitchell, 1975; Lockyer, 1981, 1987a, 1987b; Lavigne *et al.*, 1986; Innes, Lavigne *et al.*, 1987; Víkingsson *et al.*, 1988; Víkingsson, 1990, 1995, 1996; Ichii and Kato, 1991), which have formed an important basis for further calculations of cetacean predation. Recent studies conducted by several scientists in Norway have further developed this work as a part of an extensive research into the role of marine mammals in Norwegian waters (e.g. Markussen *et al.*, 1992; Folkow and Blix, 1992).

Recently, studies have been initiated by the Marine Research Institue (MRI), Reykjavík with the overall aim to elucidate the question of the role of cetaceans in Icelandic and adjacent waters in a broad multi-species context. While the long-term aim of the research programme is to answer questions related to the future dynamic relationships between the different species, it became soon evident that very limited knowledge on the current consumption of whales in these waters was available, and in fact no attempts had been made earlier to estimate this. This was partly due to various problems in judging the food selection and energy requirements of the different species of whales, but even more so because of lack of data on absolute abundance of each species and seasonal variations thereof, and lack of direct observations on cetacean feeding. In 1987 and 1989, the MRI undertook extensive whale sightings surveys in Icelandic and adjacent waters as a part of joint international efforts (North Atlantic Sightings surveys, NASS-87 and NASS-89) of several North Atlantic nations (see Sigurjónsson *et al.*, 1989; Sigurjónsson *et al.*, 1991). The survey results have greatly improved our knowledge on abundance of the many species of whales that frequent high latitude North Atlantic waters during the summer season.

This paper reports on some calculations made on the available data related to abundance and feeding of whales in Icelandic and adjacent waters, and makes an attempt to estimate the total amount of food consumed by cetaceans in the area. It is intended to be a basis for later and more in-depth analysis of the situation and a guidance for planning further research into this subject.

The paper makes use of the abundance estimates derived from the NASS-surveys, sightings data obtained from whaling vessels west and southwest of Iceland during the period 1979-1985 (for estimation of relative seasonality in abundance), and catch data for large whales caught off Iceland 1948-1989 and minke whales (*Balaenoptera acutorostrata*) in the period 1973-1985, respectively. Furthermore, we base our analysis on our observations of food selection, but have to a large degree to rely upon published records of food selection of cetaceans in other ocean areas. Finally, our analysis is based on published formulae for the relationship between marine mammal ingestion rates and body weight, mainly calculated from Icelandic catch data.

ESTIMATES OF WHALE ABUNDANCE

Most of the Icelandic NASS-survey data have been analysed according to accepted methodology (see Hiby and Hammond, 1989) developed in recent years by several investigators. This applies to the data on fin, *B. physalus* (Gunnlaugsson and Sigurjónsson, 1990; Buckland *et al.*, 1992; IWC, 1992), sei *B. borealis* (Cattanach *et al.*, 1993; IWC, 1993), minke (IWC, 1991,1992) and pilot whales, *Globicephala melas* (Buckland *et al.*, 1993) obtained in 1987 and 1989. Estimates for blue (*B. musculus*), humpback (*Megaptera novaeangliae*), sperm (*Physeter macrocephalus*), Northern bottlenose (*Hyperoodon ampullatus*), and killer whales (*Orcinus orca*) from the NASS-87 survey were presented in Gunnlaugsson and Sigurjónsson (1990). The present paper makes further uses of the NASS-87 data and applies corrections for diving Northern bottlenose and sperm whales as suggested by Gunnlaugsson and Sigurjónsson (1990). It further makes rough calculations on abundance of dolphin species and harbour porpoises (*Phocoena phocoena*) observed in 1987, but not analysed before, and on blue and sperm whales for the NASS-89 survey, based on data published in Sigurjónsson *et al.* (1989 and 1991).

Although the survey design and the survey blocks already analysed for the purpose of abundance estimation are not strictly the same as would suit our study on whale predation in Icelandic waters (continental shelf or 200 EEZ around Iceland), we have tried to choose the relevant survey blocks for our purposes. Firstly, we consider the waters roughly north of 60°N, surveyed by Iceland in 1987 (blocks 1, 2, 3, 4, 5, 6, 7, 8, 9 and 10 in Fig. 1a and the corresponding areas shown in Fig. 1b) and 1989 (blocks 1, 2, 3, 8 and 9 in Fig. 2a and the corresponding areas in Fig. 2b), i.e. the Irminger Sea, the waters north and northeast of Iceland towards Jan Mayen and the Iceland Basin approximately midway towards the Faroe Islands. Secondly, we consider the same areas, but leaving out blocks 4 and 5 (corresponding to 94 and 95) for the purposes of evaluating the proper "Icelandic and adjacent waters" area.

The reader is referred to the above papers on details of the abundance estimation procedure in general. However, it should be mentioned that the correction factors of 2.11 and 9.07 applied for sperm and Northern bottlenose whale sightings data, respectively, were arrived at according method suggested by Gunnlaugsson and Sigurjónsson (1990), on the assumption that the first has a mean dive-time interval of 10mins (see Lockyer, 1977) and the latter of 33.1mins (see Benjaminsen and Christensen, 1979). Blue whale and sperm whale estimates for 1989 were made using the same approach and same perpendicular distances as in 1987. The blue, fin, and sei estimates were derived from the 1989 surveys, because of more coverage and/or more appropriate timing of the survey in that year for these species. Block 8 from 1987 was, however, added to the 1989 estimates, due to lack of coverage in the northernmost areas in the latter. The minke whale estimate was derived from 1987 data (since aerial survey was not conducted in 1989). The same applies to humpbacks, but due to survey timing. For the two species with estimates given in both years in Table 1 (sperm and n. bottlenose), the average of both years was used.

For calculating abundance of dolphins, we assumed conservatively that perpendicular distance, w, was equal to 0.4 n.mile (in $N = n*s*A/L/4w$, where N is abundance in survey block, n is no. of sightings, s is school size, A is survey area, L is track length). No stratification for school sizes were made and the estimates should only be taken as rough approximations subject for further analysis. Two species were considered, white-beaked dolphin (*Lagenorhynchus albirostris*) and Atlantic white-sided dolphin (*L. acutus*), while the large number of unidentified dolphins are likely to be mainly the former species. Similarly, estimates on the harbour porpoise should be regarded with caution, since in our rough calculations we applied Øien's (1992) correction factor for $g(0)=0.7$ obtained from Norwegian surveys, and Bjørge's *et al.* (1991) estimated effective strip width of 0.221 n.mile.

The abundance estimates used in the calculations below are given in Table 1. The surveys were conducted during 24 June-28 July 1987 and 10 July-13 August 1989 (with main effort in the latter half of the period), respectively. In the bimonthly estimations of abundance for the highly migratory species (see next section), the survey estimates usually refer to July indices when 1987 estimates are considered and late July-early August for 1989. Although associated coefficients of variation or confidence intervals of the abundance estimates are available for most published data on the species dealt with here, no such parameters were produced during the preparation of this paper for species not analysed before. However, the number of sightings behind each estimate are given in Table 1.

ABUNDANCE INDICES AND SEASONAL MIGRATION

In order to take into account the effects of seasonal migration of some of the whale species that occur in Icelandic and adjacent waters, available indices of abundance were explored. For all large whale species, the within-seasonal catch distribution at the single land station operating off the western and southwestern coasts of Iceland was analysed for the months May-October 1948-1985. Although the catches clearly demonstrate seasonal variation in abundance of the species concerned, i.e. blue, fin, sei and sperm whales (only 6 humpbacks were caught during this operation in the 1950's), the within-season effort behind the catch throughout the seasons was not available. Instead, use was made of sightings records kept onboard the whaling vessels in operation during the period 1979-1985 (see detailed description of the data in Sigurjónsson and Gunnlaugsson, 1990).

The sighting records used comprise exact locations, dates and other detailed information on each sighting event, including species identification and estimated group sizes. The data used includes June-September with some observations made in May and October, but with very small and sporadic effort in these two months, which thus are mostly left out (see below). As a crude approach to correct for different level of sightings effort in the years 1979-1985, the actual days in operation for each vessel were calculated. Further, the operation time was corrected for seasonal variation in daylight hours by bimonthly mean number of hours from sunrise to sunset as reported for Reykjavík. The combined sightings per effective operation time (SEOP) for the 1979-1985 seasons are shown for blue, fin, sei, humpback and sperm whales in Figs 3-7. Although the migratory pattern of these species may be somewhat different in other areas around Iceland than demonstrated by the sigthings records west and southwest of Iceland, we assume that this approach reflects the general situation, at least with respect to the length of the season.

Since the SEOP series only gives relative abundance during the months June-September, the remaining part of the year was estimated as follows. For the blue whale and sperm whales, the off-season value was set at 10% of peak abundance in summer and the values for the bimonthly periods before and after the study season were adjusted according to the shape of the seasonal curve. The same was done for fin whales, except that the September level (9.3% of peak abundance in the latter half of June) was used as the off-season abundance index. For humpbacks the late-May value was also used and 10% as off-season level. For all these species, historical catch records (see e.g. Risting, 1922) and recent incidental sightings around Iceland (MRI, unpubl. data) indicate significant, though low, abundance off Iceland during off-season months, but the level is not known. With respect to sei whales, we assume absence of that species during winter months. The SEOP for sei whales was equal to nil until late June, but an assumed mirror-reflected level was chosen in the fall, assuming similar migration pattern during spring and fall.

When examining the seasonal sightings curves for minke whales west and southwest of Iceland, it became evident that this would only partly reflect the real situation for Iceland, since catch records show that minke whales were caught as early as March and as late as November (Sigurjónsson, 1982). Therefore, an uncorrected catch series for one of the most active minke whaler in operation in the 1970's, was used to indicate relative seasonal abundance. This vessel operated north of Iceland, but although it may to some extent be out of phase with the peak abundance in other areas, it is likely to reflect the length of the season. The data are shown in Fig. 8. Only the years 1973 (the first year of available minke whale catch records, see Sigurjónsson, 1982) to 1980 were included, since the period after that is seriously biassed due to restrictions set by catch limits in later years. The off-season level was set at 10% of peak abundance, i.e. for the months late November to early March.

Generally, the medium sized and small odontocete whales are not regarded as highly north-south migratory as the above species. The observations onboard the whaling vessels of the medium sized species (killer, pilot and Northern bottlenose whales) are probably less reliable due to lack of economic interest in these species (see Sigurjónsson and Gunnlaugsson, 1990), and evidently almost no recording of the smaller dolphins and porpoises have been practiced. Therefore the sightings data for these species is not suitable for the present purpose and we simply assume that the whales occur all year round in our large study area. One exception is the Northern bottlenose whale, where published seasonal catch curve (Benjaminsen, 1972; Benjaminsen and Christensen, 1979) shows a marked peak in June, the bulk of the catches being taken in the area east and northeast of Iceland towards the Jan Mayen Island or the same area as had far the greatest abundance in the 1987 survey (ca 75%). Since Norwegian regulations for catches of small whales, including this species (Jonsgård, 1977), set limitations on catch operations in July, only the catch curve (substracted by hand) until and including June is used here (Fig. 9) to reflect the seasonality off Iceland. The right hand side of the catch curve is a mirror reflection (by regression) of the left hand side. Again, the winter abundance was set at 10% of the peak June level.

As said above the abundance estimates were linked to the seasonal curves in Figs 3-9 in accordance with the timing of the surveys. If the peak of the relative index is much out of phase with the reference period for the survey estimate, this will seriously affect the estimate of the total biomass, but does not, however, necessarily cause a bias in that estimate. The peak for blue whales coincided with the survey period, while this was somewhat out of phase although not seriously for fin, minke and humpback whales, but more severely so for sperm whales. However, for sei whales, the two were badly out of phase. Although the survey estimate was obtained mainly in the latter half of July and first half of August 1989, i.e. rather late in the season, the reference point from the sightings data during this time of the season was less than 20% of the peak in late September. This resulted in considerable scaling-up of the bimonthly estimates in the latter part of the season. As mentioned above, the relative index for Northern bottlenose whale was seriously biassed in July. Therefore, the June value was used as reference point for the survey estimate based on the survey conducted during late June-July 1987.

FOOD COMPOSITION

As many cetacean species appear to be opportunistic in food selection varying prey both in time and space, all available information from Icelandic and adjacent waters was used in the assessment of food composition. These are, however, rather limited for most species. In cases where no local material was available, data from other localities throughout the North Atlantic was used. Even for the species most extensively studies (e.g. the recently harvested fin, sei and minke whales), the data is far from complete with respect to time and space.

Table 2 gives the estimated food composition expressed by three main groups of prey species, finfish, cephalopods and crustaceans, with the main source of information indicated. Below, further outline of the rationale behind the broad categorization of food preferences is given by species:

Blue whale: We assume here that blue whales feed exclusively on euphausiids since the species is globally known for being pure plankton feeder (e.g. Yochem and Leatherwood, 1985; Christensen *et al.* 1992).

Fin whale: In our calculations, we assume that 3% of the food is composed of fish and 97% of planktonic euphausiids. This is based on observations of fin whales landed at the Hvalfjordur whaling station, Southwest Iceland, during 1967-1989, where 1609 whales were examined. Of these, 96% of the whales had krill only, 0.7% capelin only, 0.1% sandeel only, 0.8% some fishbones or -flesh and 2.5% a mixture of krill and fish remains. Of the fish, we estimate that capelin comprises some 2.4% and other species of fish (mainly juveniles) like blue whiting (*Micromesistius poutassou* (Risso) comprise less than 1%. Of 159 stomach samples examined during the 1979-1989 seasons and containing krill, 99.4% had *Meganyctiphanes norvegica* but only one *Thysanoessa longicaudata*.

ESTIMATION OF CONSUMPTION

As the abundance estimates for the whale stocks off Iceland are not stratified by age or length classes, calculations of consumption rates are based on mean weights, calculated from data on weight- or length distributions of direct or indirect catches off Iceland. For fin and sei whales, weight/length equations based on Icelandic data were used (Víkingsson *et al.*, 1988), but for other large whales the equations of Lockyer (1976) were applied to the Icelandic length distributions. Mean weights of harbour porpoises and white-beaked dolphins were derived from incidental catches off Iceland (MRI, unpubl. data) but information on other species of small and medium sized cetaceans was obtained from the litterature (see Table 3). The mean weight of Northern bottlenose whales was calculated from the weight of blubber and meat (Benjaminsen and Christensen, 1979), assuming that these constituted 69% of the total body weight as in killer whales (Christensen, 1982). The average weight values were adjusted for sexual size differences and uneven sex ratio as observed in the catch of this species off Iceland (Benjaminsen, 1972).

Ingestion rates were calculated by two methods:
A) From information on actual feeding rates of cetaceans in captivity (Sergeant, 1969), the formula modified by Innes *et al.* (1986) and Armstrong and Siegfried (1991) was used:

$$I=0.42M_t^{0.67}$$

where I is the ingestion rate (kg/day) and M is body mass in kgs. As the underlying data was based on fish consumption, the value 1.3 kcal/g was used for conversion into energy units (Steimle and Terranova, 1985).

B) Calculations of energy requirements based on assumptions regarding the relationship between some physiological parameters and body weight as done by Overholtz *et al.* (1991). Assuming an assimilation rate of 80% and an activity coefficient of 1.5 (Overholtz *et al*, 1991; Hinga, 1979) the daily ration is given by:

$$DR=206.25M_i^{0.783}$$

where DR=daily active ration (kcal/day) and M=body weight in kgs.

For the highly migratory baleen whales the large seasonal variation in feeding intensity has to be taken into account. Although very little information exists on the winter-distribution and biology of most North Atlantic rorqual species, energetic studies on the summer feeding grounds (Lockyer, 1987a, 1987b; Víkingsson, 1990, 1995), as well as feeding studies from the Southern Hemisphere (summarized in Lockyer, 1981), indicate that these species obtain most of their yearly energy needs during the approximately 4 month summer period of intense feeding at high latitudes. According to Lockyer (1981) around 83% of the annual energy intake in Southern Hemisphere Balaenopterids is ingested during the summer season, corresponding to approximately ten times higher feeding rates during the summer than in winter. Based on this assumption, calculations on mean daily feeding rates during a 120 days summer period were made for the baleen whales by the equation:

$$SI=2.525I,$$

where SI is the summer ingestion rate and I is the mean annual ingestion rate. In the absence of data on seasonal fattening in odontocetes no attempt was made to allow for possible increased summer feeding rates of these species, although judging from the migratory behaviour of some species this does not seem unlikely.

Although no biological investigations have been conducted on the small proportion of the migratory whale species spending the winter months in Icelandic waters, the MRI often receives information from fishermen on whales feeding on the fishing grounds off Iceland throughout the year, particularly humpback whales. For these overwintering baleen whales, the average annual ingestion rates were used during winter on the assumption that these were feeding at relatively high level during winter despite a period of intense feeding in the summer season. By rejecting this hypothesis and taking these animals as feeding at a lower winter rate (10% of summer rate), the total consumption of baleen whales a estimated in this study should be reduced by 5-10%.

The calculated daily food consumption by the two methods is given in Table 4. The conversion factors 0.93 kcal/g for crustaceans (Lockyer, 1987a) and 1.3 kcal/g for fish and cephalopods (Steimle and Terranova, 1985) were used for calculations of ingested biomass. The results of the estimation of total consumption of finfish, cephalopods and crustacea (mainly krill) by species of whales are given Tables 5 and 6. Fig. 10 shows the general pattern of proportions of food type consumed by the different whale species according to this study for method A in Icelandic and adjacent waters. The total food consumption of all cetacean species is around 6.2M and 4.6M metric tons north of 60°N and in Icelandic and adjacent waters, respectively, according to method A. The corresponding figures for method B are slightly higher or 6.6 and 4.8M metric tons, respectively. The four largest consumers in the area north of 60°N are in the right order fin, pilot, minke and Northern bottlenose whales, while the last two mentioned species shift place in Icelandic and adjacent waters. The annual food consumption of fin whales is by far the most important, comprising around 2M metric tons for the larger area and around 1.5M metric tons for Icelandic and adjacent waters, respectively. This equals about 1/3 of the biomass consumed by cetaceans in these areas according to our calculations.

The crustaceans consumed are all taken by the baleen whales and comprise around 50% of the total consumption in the larger area, but 43.4% in the smaller area according to method A. Method B gives somewhat higher proportion of crustaceans consumed or 57% and 51.5% for the larger and smaller area, respectively.

According to method A, finfish and cephalopods are consumed in nearly equal quantities or about 1/4 of the total food consumed in both areas, but the fish comprises around 22% for method B in both areas, while cephalopods comprise 21.4% of the consumption in the large area north of 60°N, but 26.3% in Icelandic and adjacent waters. Although the cephalopods are taken by several odontocete species, the bulk of the total is taken by only two species, the pilot and Northern bottlenose whale, or between 45 and 52% each of the total cephalopods consumed, depending on which method and area is considered.

Finfish is consumed on the other hand by most species of whales and amounts to around 1.4-1.5M metric tons for the area north of 60°N and 1.1-1.2M metric tons for Icelandic and adjacent waters. The estimated amount according to method A for the Icelandic and adjacent seas is shown in Fig. 11. The most important fish eaters around Iceland according to the present calculations (method A) are minke whales (16.4% of fish consumed), white-sided dolphins (15.3%), pilot (14.5%), killer (11.5%) and humpback whales (10.9%).

DISCUSSION

Although the two methods for calculating the average daily feeding rates give similar results for the total consumption of all populations (Table 5), they differ considerably in the extremes of the size range

(Table 4) and thus with regard to the proportional contribution of the different species to the total consumption. The calculations by method A (Table 4) appear to be in better agreement with feeding rates of small cetaceans in captivity (Sergeant, 1969), as well as with studies on seasonal fattening rates and quantities of stomach content in large whales (Kawamura, 1974; Oshumi, 1979; Lockyer, 1981, 1987a, 1987b; Bushuev, 1986; Víkingsson, 1990, 1996).

Mean weights calculated from the length distribution of the catch of fin and sei whales are probably somewhat overestimated because of the IWC (International Whaling Commission) regulations on minimum size limits and probable size selection by whalers. This may, however, be balanced by increased metabolic rate (Kleiber, 1975; Lavigne *et al.*, 1986) of growing individuals and possible segregation (IWC, 1986) with older animals migrating farther polewards resulting in positively skewed age distribution around Iceland. The calculations by Markussen *et al.* (1992) on consumption of minke whales off Norway, gave approximately 20% lower mean consumption rates than the present results for that species. The present results on total consumption of fin, sei and blue whales are around 20% lower than calculations based on a 120 day mean feeding period for the whole population at high feeding rates (Lockyer, 1981), and assuming two times Kleiber's (1975) basal metaboloc rates as ordinarily assumed for mammals in general (Innes *et al.*, 1987).

It has become evident from this study how critical the results are with respect to bias of different nature during the many phases of calculations and to the assumptions that have to be made to come to a conclusion. Particularly critical are of course the estimates of abundance for all species and it needs be emphasized that some of these require further study. This applies specifically to all the odontocete species, although the estimates for killer and pilot whales are probably the best ones that can be obtained based on the available data. The great variations in group sizes of many of the odontocetes is of concern when, because they result in wide confidence intervals of the abundance estimates (e.g. in pilot whales), which we have not considered here. The corrections applied here for animals missed on the track-line when surveys are conducted (i.e. for Northern bottlenose whale, sperm whale and harbour porpoise) also need further elaboration. And finally, it needs to be kept in mind which species are the target species for the survey in question, when using sightings survey data.

Another factor of importance is the seasonal variation in abundance. Although we believe our approach to some extent solves this problem, more information on migration behaviour is needed and from different parts of the study area. Whether all age and sex groups behave the same could also be of importance in further calculations. Winter abundance is very little known, but would be useful to look further into, both with respect to feeding activities and what portion of the stock overwinters. Recent studies on fin whales off Icelenad have indicated a somewhat longer feeding season than assumed here, especially for younger animals (Víkingsson, 1995). This could further be addressed with respect to humpback whales, that often occur on the winter capelin (*Mallotus villosus*) grounds in the deep waters off Iceland. But in general, the continuation of ongoing studies into the energetics and feeding rates of different whale species is needed. Also there is a strong need for a more extensive data base of actual observations of the food composition by each species, including studies of temporal and spatial variation. Here the problem is not serious for species like the blue whale, which in all oceans appears to feed exclusively on planktonic crustacea, or pilot whale, where extensive studies in the Faroe Islands (Desportes and Mouritsen, 1988) have given a reliable basis for calculations. But for other species like minke and fin whales, which appear to be highly opportunistic in food selection in the Northern Hemisphere (see e.g. Mitchell, 1975; Jonsgård, 1966; Horwood, 1990; Sigurjónsson, 1995) and eating both different fish species and euphausiids (off Iceland mainly *Meganyctiphanes norvegica*), the situation is more difficult. Our observations for fin and sei whales show that these species almost exclusively feed on crustacea during the summer season west and southwest of Iceland, while at least fin whales are well known fish eaters off the Canadian coast. The energy content of the food (which may vay seasonally and between years) is obviously also very critical in all calculations based on energy requirements. The trophic levels, at which the animals seek their energy resource is of major importance regarding the potential impact on the ecosystem.

The present analysis of consumption in whales, dolphins and porpoises in the area between Greenland, Iceland, Jan Mayen and the Faroe Islands is thus just one step towards a better understanding of the role of cetaceans in the marine ecosystem in these waters. The results show, however, that the amount of food consumed is substantial, while the implications of that conclusion require further study. Some initial exploration of the potential dynamic relationships between some of the fish resources in this area and three baleen whale species,feeding partly on fish, is given in Stefánsson *et al.* (*1996*).

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Table 1. Abundance estimates of cetaceans by survey blocks based on sightings surveys in in Icelandic and adjacent waters in 1987 and 1989

see further note 11) below and text

Species	Area	Blocks	Year	Date	Abundan	n	Notes
Blue	N of 50°N	2,3,5,8,9	1989	10.7.-13.8.	937	33	1
	N of 60°N	2,3,8,9	1989	10.7-13.8.	878	32	1
	Iceland	2,3,8,9	1989	10.7-13.8.	878	32	1
Fin	N of 50°N	All	1987/89	24.6.-13.8.	15614		2
	N of 60°N	8,9,20,36,88,93,94,95	1989	10.7-13.8.	8289	276	3
	Iceland	8,9,20,36,88,93	1989	10.7-13.8.	6105	205	3
Sei	N of 50°N	All	1989	10.7.-13.8.	10412	108	4
	N of 60°N	36,88,93,94,95+8 (in 1987)	1989	10.7-13.8.	1662	30	4
	Iceland	36,88,93+8 (in 1987)	1989	10.7-13.8.	375	7	4
Minke	N of 50°N	All	1987/89	24.6.-13.8.	27150		5
	N of 60°N	aerial87+2,3,4,6,8,9+Norw	1987	24.6.-28.7.	20005		5
	Iceland	aerial87+2,6(part),8 (part)	1987	24.6.-28.7.	10098		5
Humpback	N of 50°N	1,2,3,6,8,9,10+5,6	1987/89	24.6.-13.8.	2131	78	6
	N of 60°N	1,2,3,6,8,9,10	1987	24.6.-28.7.	1796	74	8
	Iceland	1,2,3,6,8,9,10	1987	24.6.-28.7.	1796	74	8
Sperm	N of 60°N	2,3,6,8,9	1987	24.6.-28.7.	2262	75	7
	Iceland	2,3,4,5,6,8,9	1987	24.6.-28.7.	1435	51	7
	N of 50°N	2,3,4,5,6,7,8,9	1989	10.7.-13.8.	9645	122	1
	N of 60°N	2,3,8,9	1989	10.7.-13.8.	2456	54	1
	Iceland	2,3,8	1989	10.7.-13.8.	1163	27	1
Northern	N of 60°N	3,4,5,6,8,9	1987	24.6.-28.7.	44304	85	1
bottlenose	Iceland	3,6,8,9	1987	24.6.-28.7.	41625	80	1
Pilot	N of 60°N	1,2,36,88,93,94,95	1987	24.6.-28.7.	53211	46	9
	Iceland	1,2,36,88,93	1987	24.6.-28.7.	34824	35	9
	N of 60°N	36,88,93,94,95	1989	10.7.-13.8.	99254	38	9
	Iceland	36,88,93	1989	10.7.-13.8.	80867	27	9
Killer	N of 60°N	2,3,5,6,8,9	1987	24.6.-28.7.	5508	21	8
	Iceland	2,3,6,8,9	1987	24.6.-28.7.	5013	20	8
White beaked	N of 60°N	1,2,3,4,5,6,8,9,10	1987	24.6.-28.7.	13420	78	10
dolphin	Iceland	1,2,3,6,8,9,10	1987	24.6.-28.7.	12341	72	10
White sided	N of 60°N	3,4,5,6,8	1987	24.6.-28.7.	38682	93	10
dolphin	Iceland	3,6,8	1987	24.6.-28.7.	37622	89	10
Unident.	N of 60°N	1,2,3,4,5,6,8,9	1987	24.6.-28.7.	36701	118	10
dolphins	Iceland	1,2,3,6,8,9	1987	24.6.-28.7.	26672	86	10
Harbour	N of 60°N	1,2,4,5,6,9,10	1987	24.6.-28.7.	28514	47	10
porpoise	Iceland	1,2,6,9,10	1987	24.6.-28.7.	26843	45	10

Notes and sources:

1) estimate based on data from Sigurjónsson et al. (1991), same methods as in Gunnlaugsson and Sigurjónsson (1990)
2) IWC (1992a)
3) Buckland, Cattanach & Gunnlaugsson (1992)
4) Cattanch, Sigurjónsson, Buckland and Gunnlaugsson (1992)
5) IWC (1992b); Buckland, Cattanach, Gunnlaugsson and Zeh (1992)
6) estimate for 1987 from Gunnlaugsson and Sigurjónsson (1990); for 1989 based on Sigurjónsson et al. (1991) with same methods as above
7) estimate from Gunnlaugsson and Sigurjónsson (1990), but corrected for diving animals; group size and distribution of sightings based on Sigurjónsson et al. (1989)
8) estimate from Gunnlaugsson and Sigurjónsson (1990)
9) Buckland, Cattanach, Gunnlaugsson, Bloch, Lens and Sigurjónsson (1992)
10) Based on data in Sigurjónsson et al. (1989).
11) *Iceland* refers to Iceland and adjacent seas, see further text

Table 2. Assumed food composition (per cent) by prey groups and species of whales

Species	Fish	Cephalop.	Crustace.	Source
Blue			100	Hjort & Ruud, 1929; Tomilin, 1967
Fin	3		97	MRI*
Sei	2		98	MRI*
Minke	59		41	Sigurjónsson & Galan, 1991
Humpback	60		40	Mitchell, 1975
Sperm	76	24		Martin, 1986
Northern bottlenose	5	95		Benjaminsen & Christensen, 1979
Pilot	20	80		Desportes & Mouritsen, 1988
Killer	100			MRI*
Atlantic white s. dolphin	95	5		Evans, 1980; Tomilin, 1967
White beaked dolphin	95	5		MRI*; Evans, 1980; Tomilin, 1967
Harbour porpoise	95	5		MRI*; Evans, 1980; Tomilin, 1967

*MRI: Unpublished information from the Marine Research Institute, Reykjavik, Iceland

Table 3. Estimated mean weight of cetaceans used in this study

Species	Weight (kgs)	Source
Blue	69235	**Lockyer, 1976
Fin	42279	**Vikingsson et.al., 1988
Sei	19919	**Vikingsson et.al., 1988
minke	5251	**Lockyer, 1976
Humpback	31782	**Lockyer, 1976
Sperm	34322	**Lockyer, 1976
Northern bottlenose	5418	Benjaminsen & Christensen, 1979; Benjaminsen, 1972; Christensen, 1982
Pilot	789	Bloch & Lockyer, 1989
Killer	2350	Christensen, 1982
Atlantic white s. dolphin	190	Watson, 1981
White beaked dolphin	225	MRI unpubl. data
Harbour porpoise	39	MRI unpubl. data

* Calculated from catch data by weight/length formula

Table 4. Estimated energy consumption (Kcal*1000/day) by whale species based on two different methods A and B (see text)

Species	Mean A	Mean B	Summer A	Summer B
Blue	955,4	1271,5	2421,3	3211,8
Fin	686,6	864,2	1734,4	2183
Sei	414,7	479,4	1047,5	1211
minke	169,7	168,8	428,7	426,4
Humpback	567,1	691,1	1432,1	1745,7
Sperm	597,1	734		
Northern bottlenose	173,3	173		
Pilot	47,7	38,3		
Killer	99	89,9		
Unspecified dolphin	19,5	13,5		
Atlantic white s. dolphin	18,4	12,5		
White beaked dolphin	20,6	14,3		
Harbour porpoise	6,4	3,6		

Table 5. Consumption by species (tons) north of 60°N and around Iceland by method A (see text).

Species	North of 60°N				Iceland			
Prey gr.	Fish	Cephalop.	Crustac.	Total	Fish	Cephalop.	Crustac.	Total
Blue			226531	226531			226531	226531
Fin	40332		1822913	1863245	29706		1342609	1372315
Sei	7906		521525	529431	1784		122185	123969
Minke	400379		388923	789302	198551		192870	391421
Humpback	131986		122998	254984	131986		122998	254984
Sperm	105519	33322		138841	58104	18349		76453
N-Bottlenose	36523	693941		730464	34315	651980		686295
Pilot	204193	816772		1020965	179567	718266		897833
Killer	153101			153101	139342			139342
White-b. dolphin	73738	3881		77619	67810	3569		71378
White s. dolphin	189845	9992		199837	184643	9718		194361
Unident. dolphins	190891	10047		200938	138728	7301		146029
Harbour porpoise	48676	2562		51237	45823	2412		48235
Total	1583089	1570517	3082890	6236496	1210358	1411595	2007193	4629146

Table 6. Consumption by species(tons)north of 60°N and around Iceland by method B (see text).

Species	North of 60°N				Iceland			
Prey gr.	Fish	Cephalop.	Crustac.	Total	Fish	Cephalop.	Crustac.	Total
Blue whale			301483	301483			301483	301483
Fin	50765		2294411	2345176	37389		1689875	1727264
Sei	9140		626049	635189	2062		141257	143319
Minke	391240		380046	771286	197488		191837	389325
Humpback	160883		149927	310810	160883		149927	310810
Sperm	129712	40962		170674	71427	22556		93983
N-Bottlenose	36460	692740		729200	34255	650851		685106
Pilot	163954	655815		819769	144180	576721		720901
Killer	139028			139028	126534			126534
White-b. dolphin	51187	2694		53881	47072	2477		49549
White s. dolphin	128971	6788		135759	125437	6602		132039
Unident. dolphins	132155	6956		139111	96042	5055		101097
Harbour porpoise	27380	1441		28821	25775	1357		27132
	1420876	1407396	3751916	6580187	1068544	1265619	2474379	4808542

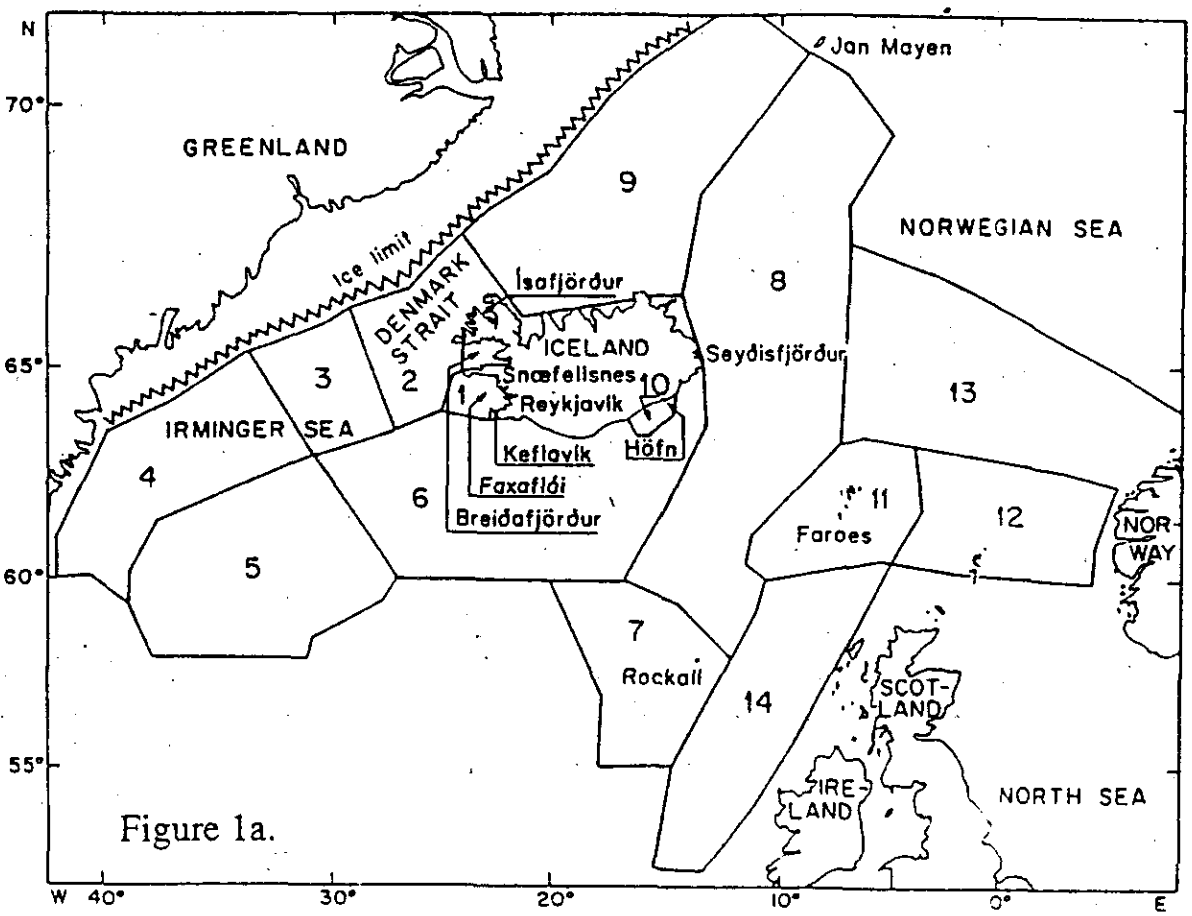

Figure 1a.

Fig. 1. Division of survey areas into geographical blocks covered by the three Icelandic sightings vessels during 24 June through 28 July 1987 and one Faroese vessel during June-August 1987, with location names mentioned in text.

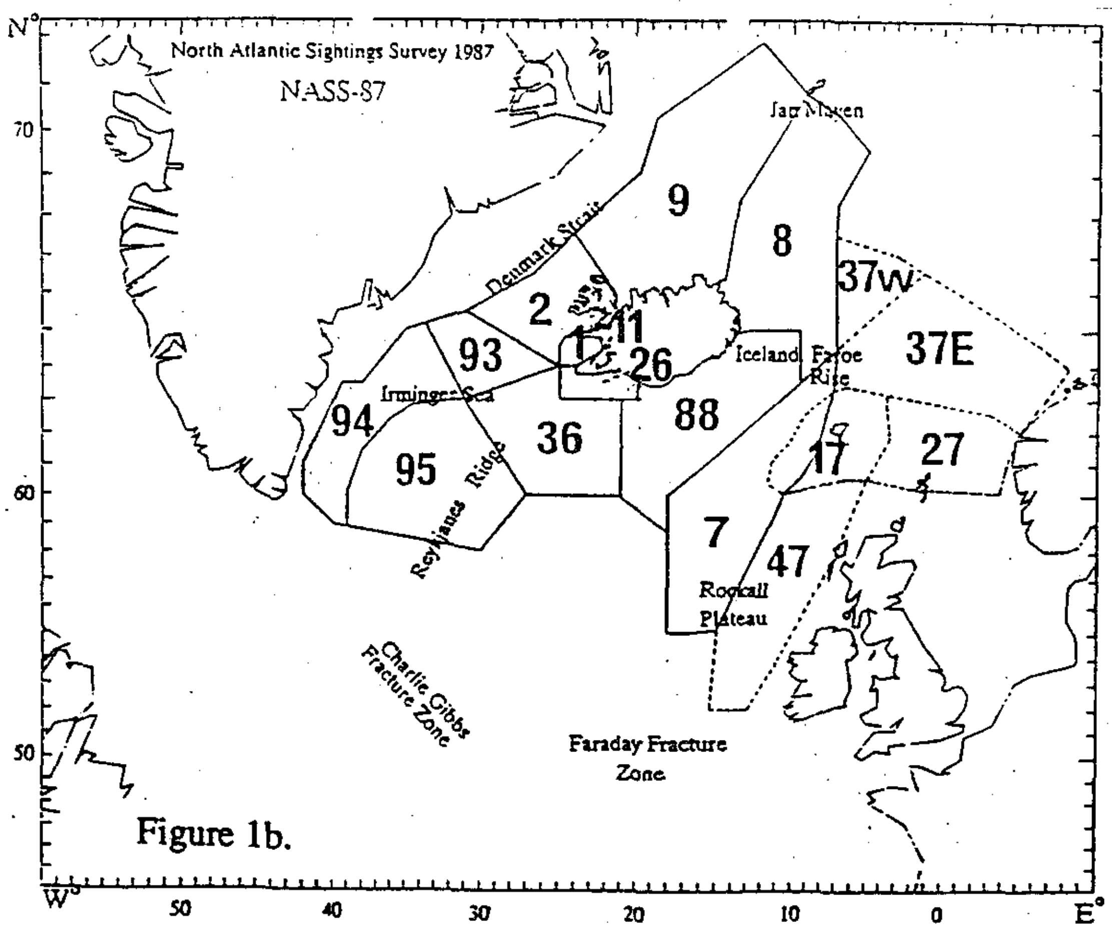

Figure 1b.

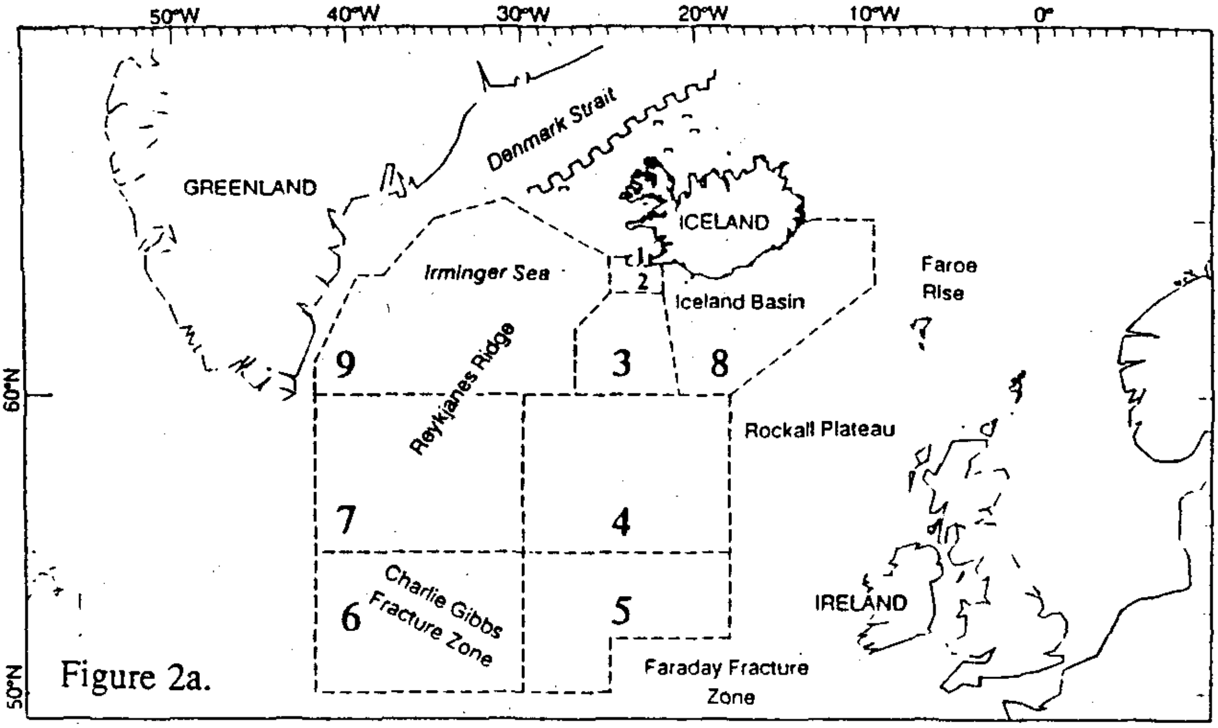

Figure 2a.

. Division of survey areas into geographical blocks covered by the four Icelandic NASS-89 survey vessels during 10 July through 14 Aug 1989, with location names mentioned in text. Ice edge between Iceland and Greenland shown.

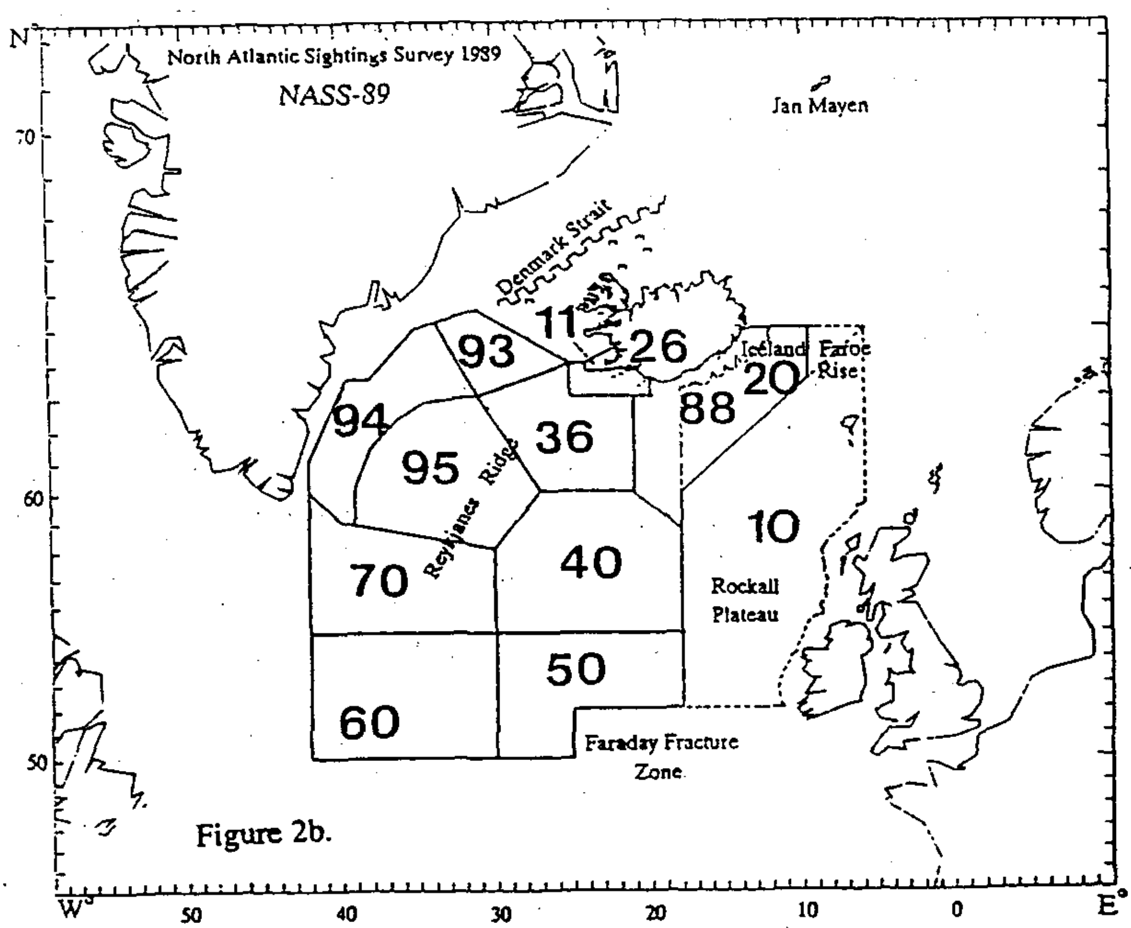

Figure 2b.

Fig. 3. Blue whale sightings (no. of animals per effective operation time) west and southwest of Iceland, June-September 1979-1985, and assumed relative abundance during October-May (see text).

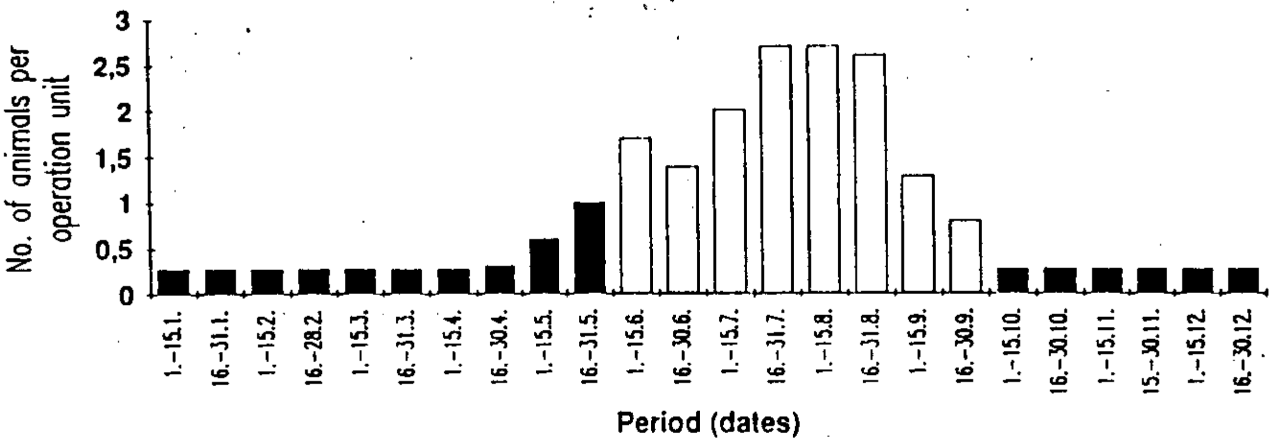

Fig. 4. Fin whale sightings west and southwest of Iceland, May-September 1979-1985, and assumed relative abundance during October-May (see text)

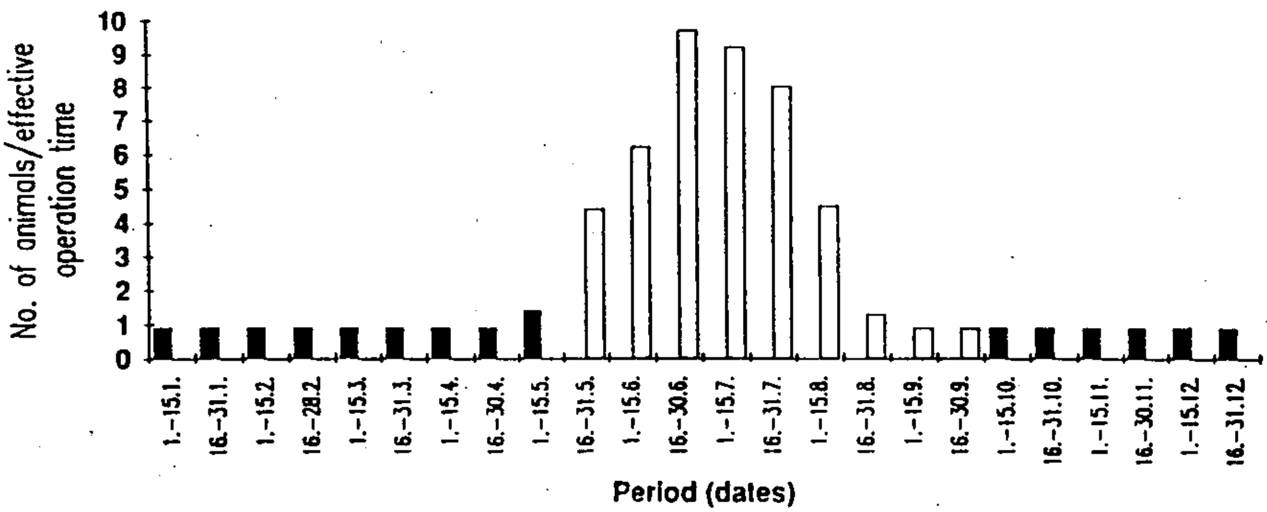

Fig. 5. Sei whale sightings west and southwest of Iceland, June-September 1979-1985, and assumed relative abundance during October-May (see text)

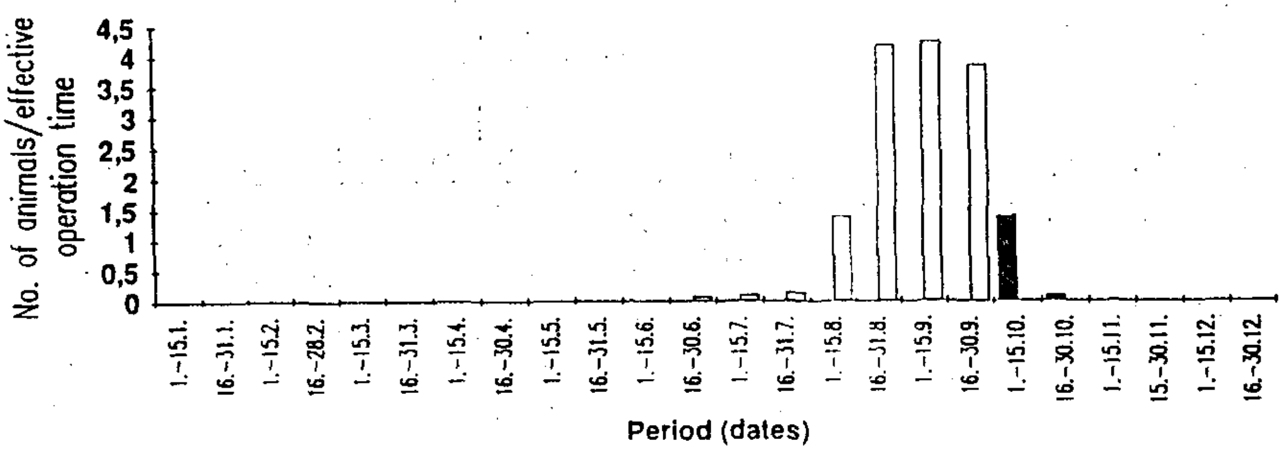

Fig. 6. Humpback whale sightings west and southwest of Iceland, late May-September 1979-1985, and assumed relative abundance during October-early May (see text)

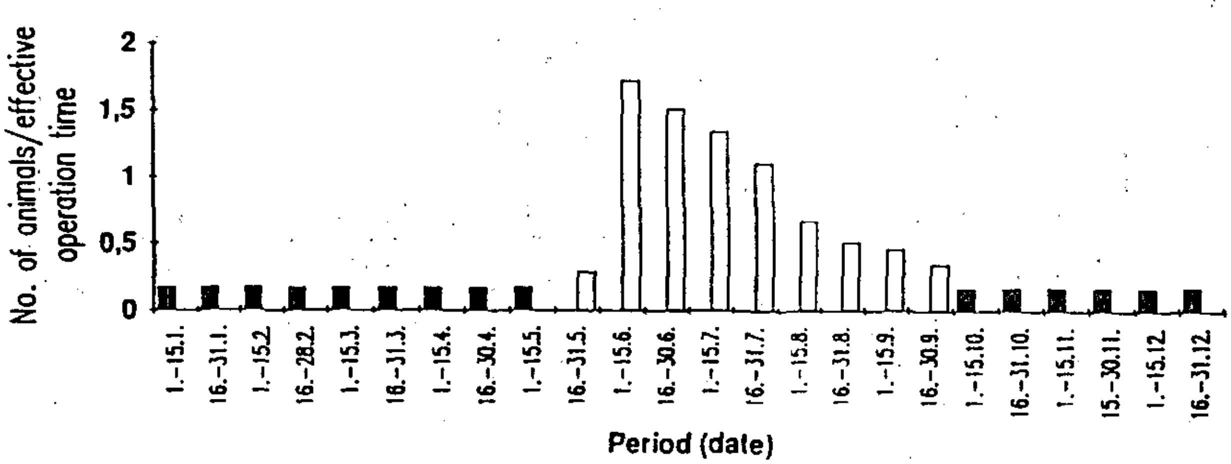

Fig 7. Sperm whale sightings west and southwest of Iceland, June-September 1979-1985, and assumed relative abundance during October-May (see text)

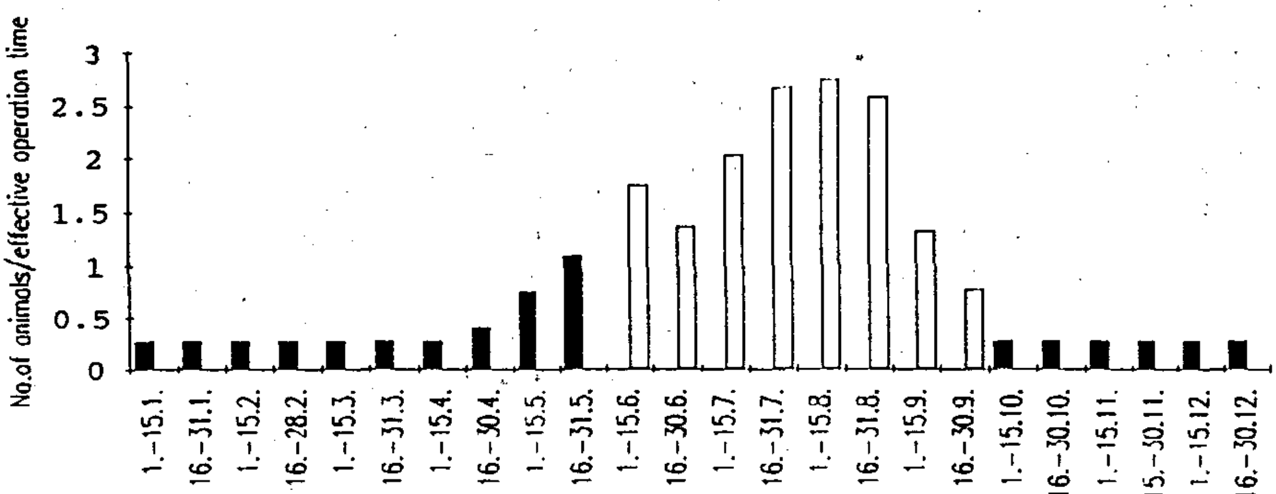

Fig. 8. Minke whales caught by m/v Njörður of Iceland, late March-early November 1973-1980 by period, and assumed relative abundance (scaled) during the months late November-early March

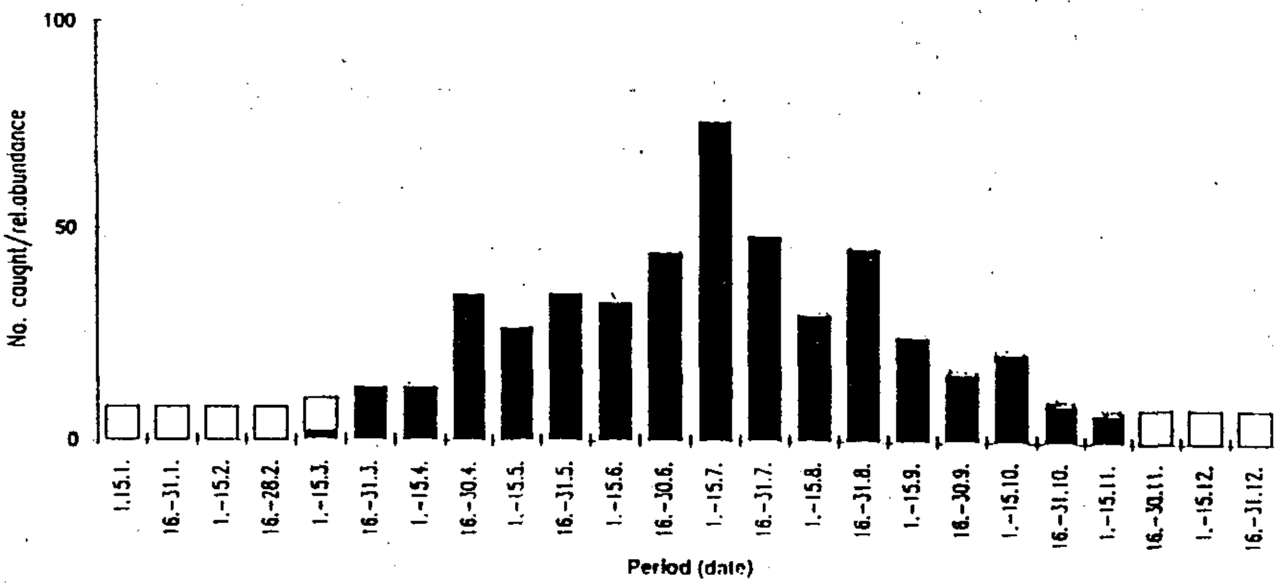

Fig. 9. Bimonthly catches of Northern bottlenose whale off Iceland by Norway during late March-June 1938-1969, and assumed relative abundance (scaled) during July-early March

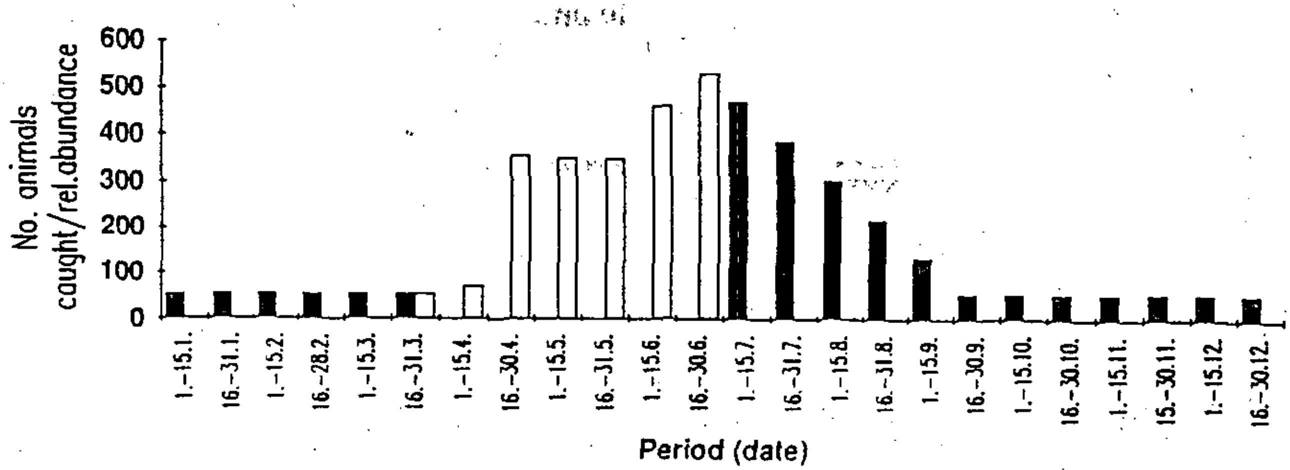

Fig. 10. Estimated amount of prey consumed (in tons) by cetacean species in Icelandic and adjacent waters

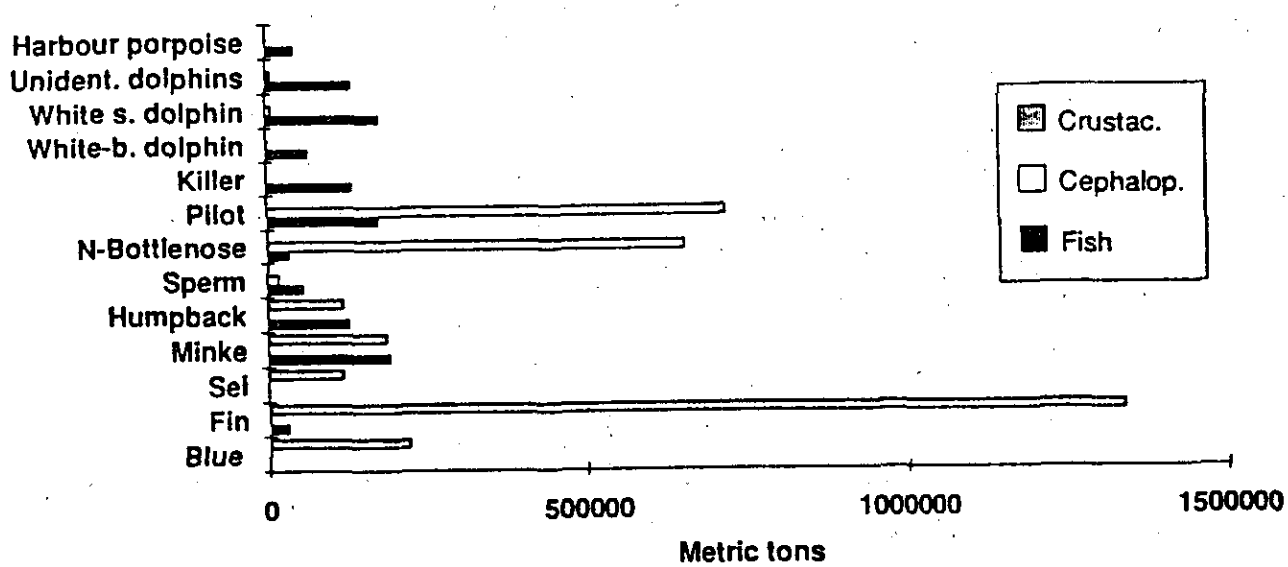

Fig. 11. Estimated amount of finfish (in tons) consumed by cetaceans in Icelandic and adjacent waters