J. Northw. Atl. Fish. Sci., Vol. 22: 271–287

Seasonal Abundance of and Estimated Food Consumption by Cetaceans in Icelandic and Adjacent Waters

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Abstract

The consumption of fish, cephalopods and planktonic crustaceans by cetaceans in Icelandic and adjacent waters was estimated. The estimates were based on (i) abundance estimates from recent sighting surveys (NASS-87,89,95); (ii) seasonal variation in abundance estimated from sightings and/or catch data from whaling vessels; and (iii) consumption rates calculated from the estimated biomass of cetaceans in the area throughout the year. A large number of assumptions had to be made, and these calculations were mainly intended to give an idea of the possible magnitude of consumption as well as to be a guidance for further research in this field. The total food consumption was estimated as 6.3 million tons in a smaller area defined as Icelandic and adjacent waters, and 8.8 million tons in the larger area north of 60°N. Considering total consumption, fin whales (*Balaenoptera physalus*) and minke whales (*B. acutorostrata*) were the largest consumers in the area, followed by long-finned pilot whales (*Globicephala melas*) and northern bottlenose whales (*Hyperoodon ampullatus*). Crustaceans comprise around 50% of the total consumption within the study area while finfish and cephalopods comprised 27% and 22%, respectively, in the large area. Minke whales were the largest consumers of finfish, consuming more than 1 million tons of fish in Icelandic and adjacent waters.

Key words: feeding, food, Iceland area, whales

Introduction

The ecological role of cetaceans, particularly their potential interactions with fisheries is often debated by laymen and scientists. In recent years a number of studies have addressed this question, particularly with respect to the drastic changes that took place in the Southern Ocean subsequent to the collapse of most large baleen whale stocks during this century (e.g. Laws, 1977, 1985; Hinga, 1979). Several studies have examined 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.*, MS 1983; Overholtz *et al.*, 1991; Kenney *et al.*, 1997). These studies have been centered around the question of total biomass of cetaceans and their estimated predation. A series of studies have dealt with theoretical aspects of cetacean bioenergetics and food requirements (Sergeant, 1969; Kawamura, 1974; Brodie, 1975; Mitchell, 1975; Lockyer, 1981a, 1987a, 1987b; Lavigne *et al.*, 1986; Innes *et al.*, 1987; Víkingsson *et al.*, 1988; Víkingsson, 1990, 1995, 1997; Ichii and Kato, 1991), which have formed an important basis for further calculations of cetacean predation. Recent studies in Norway have further developed this work as a part of extensive research into the role of marine mammals in Norwegian waters (e.g. Markussen *et al.*, 1992; Folkow and Blix, 1992; Haug *et al.*, 1996; Nordøy *et al.*, 1995).

Recently, studies have been initiated by the Marine Research Institute (MRI), Reykjavík, with the aim of understanding the ecological role of cetaceans in Icelandic and adjacent waters within a broad multi-species context. While the long-term aim of the research program is to make predictions concerning the dynamic relationship between the different species, it soon became evident that very limited knowledge on the current consumption by whales in these waters was available. This was partly due to various difficulties in estimating the food selection and energy requirements of the different species of whales, but mainly because of the absence of data on absolute and seasonal abundance of each species. In 1987, 1989 and 1995 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, NASS-89 and NASS-95) of several North Atlantic nations (see Sigurjónsson *et al.*, 1989; Sigurjónsson *et al.*, 1991; Sigurjónsson *et al.*, MS 1996). The results of these surveys have greatly improved our knowledge on abundance of the many species of whales that frequent high latitude North Atlantic waters during the summer season.

In this paper estimates of cetacean prey consumption in Icelandic and adjacent waters are reported. These results are mainly intended to serve as a basis for more in-depth analysis, and as a guide for planning future research. Our results were derived from abundance estimates based on the NASS surveys, supplemented by sightings data on seasonal occurrence from whaling vessels west and southwest of Iceland during 1979–85 and Icelandic catch data for large whales (1948–89) and minke whales *(Balaenoptera acutorostrata)* (1973–85). Estimated consumption rates for each species were based on published relationships of ingestion rates and body weight, with the latter calculated from Icelandic catch data whenever possible. Finally, estimates of consumption of specific prey were based on our observations of food selection where possible, but to a large degree upon published records of food selection by cetaceans in other ocean areas.

Material and Methods

Estimates of whale abundance

The NASS surveys were conducted during 24 June–28 July 1987, 10 July–13 August 1989 (with main effort in the latter half of the period) and 22 June–4 August 1995, respectively. 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 naut. miles 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 the years 1987, 1989 and 1995 (Fig. 1), i.e. the Irminger Sea, the waters north and northeast of Iceland towards Jan Mayen and the Iceland Basin towards the Faroe Islands. Secondly, we consider the same areas, but leaving out the southwestern part of the Irminger Sea for the purposes of evaluating the proper "Icelandic and adjacent waters" area (Fig. 1).

For most species we used abundance estimates for the relevant survey blocks, directly or indirectly, from published sources or manuscripts based on the NASS surveys (see Table 1), calculated according to accepted line-transect methodology (see Hiby and Hammond, 1989) as follows:

- fin whale (*Balaenoptera physalus*) – Borchers and Burt, MS 1997; NAMMCO, 1997
- sei whale (*B. borealis*) – Cattanach *et al.* (1993); IWC (1993)
- minke whale – Borchers *et al.*, MS 1997; NAMMCO, 1997
- long-finned pilot whale (*Globicephala melas*) – Buckland *et al.* ,1993
- blue whale (*Balaenoptera musculus*) – Sigurjónsson *et al.*, 1991
- humpback whale (*Megaptera novaeangliae*) – Gunnlaugsson and Sigurjónsson, 1990
- sperm whale (*Physeter macrocephalus*) – Gunnlaugsson and Sigurjónsson, 1990, Sigurjónsson *et al.*, 1991
- northern bottlenose whale (*Hyperoodon ampullatus*) – Sigurjónsson *et al.*, 1991
- killer whale (*Orcinus orca*) – Gunnlaugsson and Sigurjónsson, 1990.

In addition we calculated new or revised estimates for several species. The published estimates for sperm whales were corrected for diving behaviour using factors of 2.11 and 9.07, respectively. These corrections were done according to the method of Gunnlaugsson and Sigurjónsson (1990), assuming mean dive times of 10 min for sperm whales (Lockyer, 1977) and 33.1 min for northern bottlenose whales (Benjaminsen and Christensen, 1979). Blue and sperm whale abundance for 1989 was calculated from data published in Sigurjónsson *et al.* (1989, 1991) using the 1987 pependicular distance data (Gunnlaugsson and Sigurjónsson, 1990). For the 1989 estimates of blue and sei whales, data from 1987 for one survey block which was not surveyed in 1989 were added, assuming similar distribution of these species in 1987 and 1989.

We also estimated approximate abundance of white-beaked dolphin (*Lagenorhynchus albirostris*), Atlantic white-sided dolphin (*L. acutus*), unidentified dolphins and harbour porpoise (*Phocoena phocoena*) from the NASS-87 survey data by:

$$N = n * s * A / (L * 2W)$$

where N is abundance in a survey block, n is the number of schools sighted, s is mean school size,

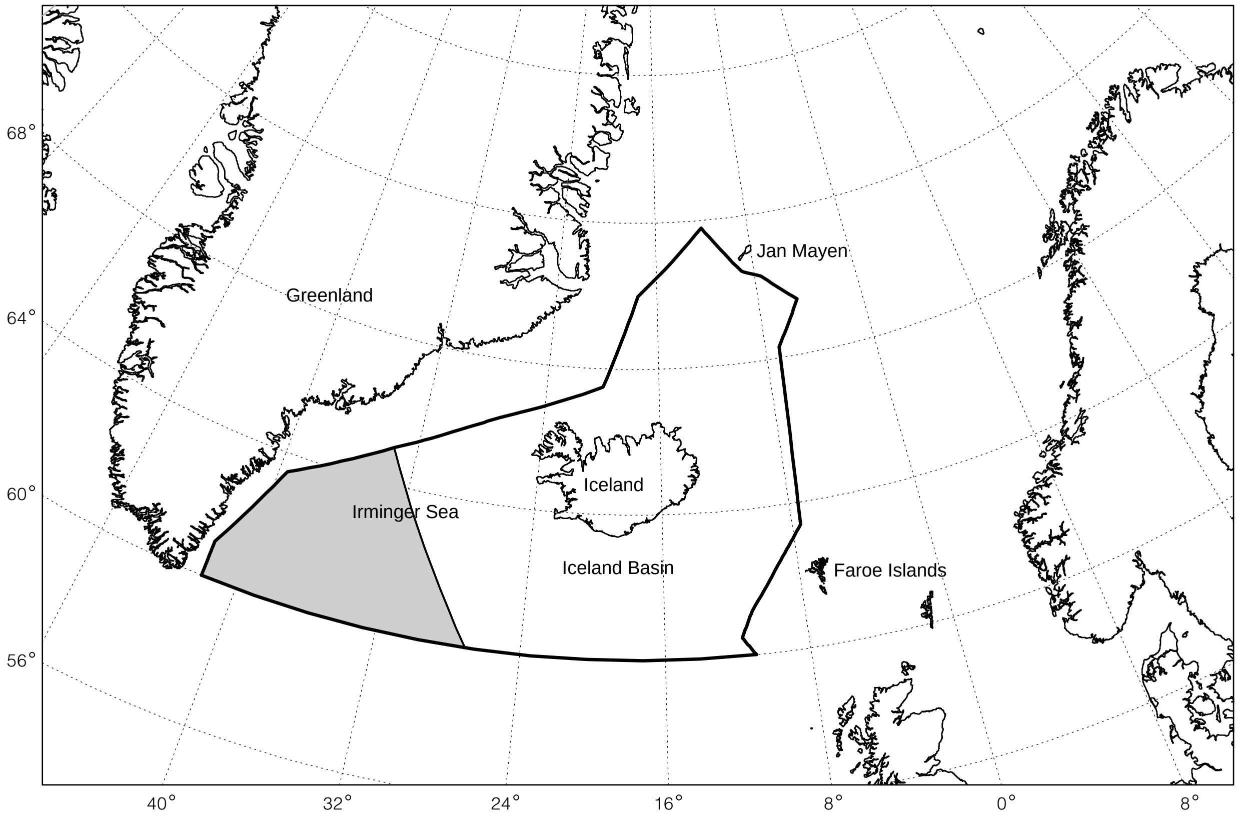

Fig. 1. Area of the NASS surveys, used in the analysis. The shaded area indicates difference between the two areas, "Iceland and adjacent waters" and larger "north of 60°N" includes the former plus the shaded area.

A is the area of the block, *L* is the length of the survey track, and *w* is the effective search half-width. For dolphins, *w* was assumed to be 0.8 naut. miles, which is probably in the upper range for these species. No stratification for school sizes were made and the estimates should only be taken as rough approximations subject for further analysis. For harbour porpoise we used *w* = 0.1105 naut. miles (Bjørge and Øien, 1995) and a correction factor for *g* (0) of 0.7 (Øien, MS 1992). Associated statistical measures of variability are available for the published abundance estimates. However, since estimating statistical confidence intervals around our preliminary consumption estimates was beyond the scope of our present analysis, we did not compute variances for any of our new or revised estimates, and have not included any estimates of variance in this paper. The species identification of dolphins varied greatly between survey vessels. The largest number of sightings of unidentified dolphins were made in the northern part of the survey area, and are thus likely to be *L. albirostris*, judging from the known distribution of the two dolphin species occurring regularly in Icelandic waters.

For several species, we then had abundance estimates for both 1987 and 1989 to use in our consumption estimates, while estimates from NASS-95 were only available for fin and minke whales at the time of writing of this paper. Thus, for blue and sei whales we used the 1989 data (with one survey block from 1987 added) because of more extensive coverage and/or more appropriate timing of that survey. For fin and minke whales the most recent estimate (1995) was used, with the aerial survey component in 1995 contributing significantly to the latter estimate. The 1987 data were used for humpback whales, dolphins and porpoises due to more appropriate timing of the survey than in 1989. Finally, for sperm, long-finned pilot and northern bottlenose whales the average of 1987 and 1989 were used.

Seasonal patterns of abundance

Large whales are known to be highly migratory, so their abundance within a given area may vary greatly on a seasonal basis. However, our abundance estimates pertain only to relatively short time during summer – July 1987 or late July-early August

TABLE 1. Abundance estimates of cetaceans based on the NASS sightings surveys conducted in 1987 and 1989 and 1995, respectively. "Iceland" refers to "Iceland and adjacent waters" (see text). *n*: number of sightings. *n* is missing for minke whales as the estimate is mainly based on aerial survey (cue counting).

Species	Area	Year	Abundance	*n*	Note
Blue whale	N of 60°N	1989	878	32	1
	Iceland	1989	878	32	1
Fin whale	N of 60°N	1995	17 427	300	2
	Iceland	1995	9867	171	2
Sei whale	N of 60°N	1989	1662	30	3
	Iceland	1989	375	7	3
Minke whale	N of 60°N	1995	65 956		4
	Iceland	1995	62 507		4
Humpback whale	N of 60°N	1987	1 796	74	5
	Iceland	1987	1 796	74	5
Sperm whale	N of 60°N	1987	2 262	75	6
	Iceland	1987	1 435	51	6
N of 60°N	1989	2456	54	1	
	Iceland	1989	1 163	27	1
Northern Bottlenose whale	N of 60°N	1987	44 304	85	1
	Iceland	1987	41 625	80	1
Long-finned pilot whale	N of 60°N	1987	53 211	46	7
	Iceland	1987	34 824	35	7
	N of 60°N	1989	164 679	45	7
	Iceland	1989	80 867	27	7
Killer whale	N of 60°N	1987	5 508	21	5
	Iceland	1987	5 013	20	5
White-beaked dolphin	N of 60°N	1987	13 420	78	8
	Iceland	1987	12341	72	8
White-sided dolphin	N of 60°N	1987	38 682	93	8
	Iceland	1987	37 622	89	8
Unidentified dolphin	N of 60°N	1987	36 701	118	8
	Iceland	1987	26 672	86	8
Harbour porpoise	N of 60°N	1987	28 514	47	8
	Iceland	1987	26 843	45	8

[1] Estimate based on data from Sigurjónsson *et al*., 1991, same methods as in Gunnlaugsson and Sigurjónsson (1990).
[2] Borchers and Burt, MS 1997; NAMMCO, 1997.
[3] Cattanach *et al*., 1993.
[4] Borchers *et al.*, MS 1997; NAMMCO, 1997.
[5] Estimate from Gunnlaugsson and Sigurjónsson, 1990.
[6] Estimate from Gunnlaugsson and Sigurjónsson, 1990, but corrected for diving animals; group size and distribution of sightings based on Sigurjónsson *et al.*, 1989.
[7] Buckland *et al.*, 1993.
[8] Based on data in Sigurjónsson *et al.*, 1989; assumptions on track-width (see text).

1989. We therefore used sighting records kept onboard operating whaling vessels during 1979–85 to estimate the seasonal pattern of relative abundance. The sighting records included date, location, species identification, estimated group size, and other detailed information for each sighting event (see detailed description of the data in Sigurjónsson and Gunnlaugsson, 1990). The records were primarily from June through September, with sporadic observations in May and October. The number of individuals sighted of each species was tallied within half-month intervals. These totals were then corrected for varying levels of search effort using the actual days of operation for each vessel and the mean time from sunrise to sunset (at Reykjavík) within each interval. We termed the resulting index (see Fig. 2) sightings per effective operation time (SEOP).

For most of the large whales, 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. Relative abundance outside the months of June through September was estimated as follows. For blue whales (Fig. 2a) and sperm whales (Fig. 2e), the off season value was arbitrarily set at 10% of peak summer abundance and the values for the periods before and after the study season were adjusted according to the shape of the seasonal curve. This was done by linear regression to determine the slope of the curve during spring. For fin whales (Fig. 2b) the September level (9.3% of peak abundance in the latter half of June) was used as the off season abundance index, and abundance in the first half of May was assumed to be similar to that in late September. For humpbacks (Fig. 2d) the late-May SEOP value was included and 10% used as off season level. Sei whales (Fig. 2c) were assumed to be absent during the winter months as no records of sightings of this species in Icelandic waters during winter are available. The SEOP for sei whales was equal to nil until late June, but an assumed mirror-reflected level was chosen in the autumn.

The seasonal sightings curve for minke whales west and southwest of Iceland only partly reflects 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 whalers in operation in the 1970s was used to indicate relative seasonal abundance (Fig. 2f). This vessel operated north of Iceland but although its catch distribution may, to some extent, be out of phase with the peak abundance of minke whales in other areas it is likely to reflect the length of the season. Only the years 1978 (the first year of available minke whale catch records) to 1980 were included, since the period after that is seriously biased due to restrictions set by catch limits in later years. The off season level was arbitrarily assumed to be 10% of peak abundance.

The observations onboard the whaling vessels of the medium-sized species (killer, pilot and northern bottlenose whales) are probably less reliable than for large whales due to lack of economic interest in these species (see Sigurjónsson and Gunnlaugsson, 1990) and almost no sightings of the smaller dolphins and porpoises were recorded. Therefore, the sightings data for these species were not considered suitable for the present purpose and we simply assumed, based on sporadic evidence (MRI, unpubl. data) that they occur year-round in our study area. One exception is the northern bottlenose whale, where seasonal catches (Benjaminsen, 1972; Benjaminsen and Christensen, 1979) show 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. This same area had by far the greatest abundance in the 1987 survey (approx. 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 through June was used here (see Fig. 2g, based on Benjaminsen, 1972) to estimate the seasonality off Iceland. For the period July–September we assumed a steady decline from the late June level to the assumed winter abundance of 10%, starting in late September.

The absolute abundance estimates were then linked to the seasonal relative abundance curves. The absolute abundance value from the NASS data was assigned to the appropriate half-month-interval, and then abundance estimates for all other intervals were calculated in proportion to the relative abundance indices. The one exception was the northern bottlenose whale, where the July relative abundance index was assumed because of the bias in the catch data. The absolute abundance estimate for that species was assigned to the late June interval.

Prey

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. This is, 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 studied (e.g. the recently harvested fin, sei and minke whales), the data are far from complete with respect to time and space. Therefore, due to lack of more detailed information on prey species, we classified the prey into three

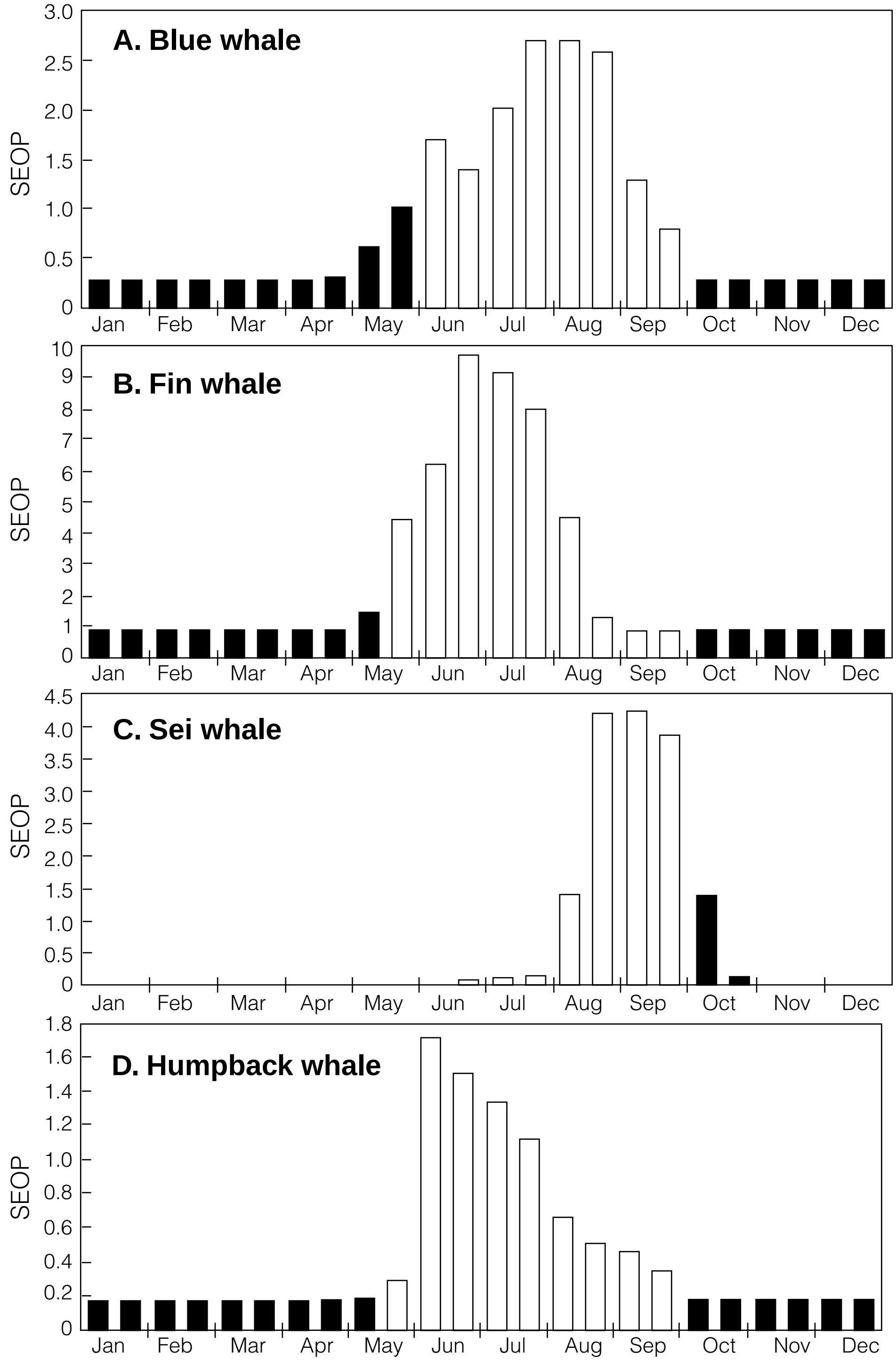

Fig. 2. Relative seasonal abundance of baleen whales (a–d, f), sperm whales (e) and northern bottlenose whales (g) in Icelandic waters. a–e are based on sightings data from whaling vessels while f–g are based on catch data. White bars are calculated directly from the data, black bars indicate assumed winter distribution. The unit SEOP (Sightings per effective operation time) does not necessarily indicate the relative abundance of the different species.

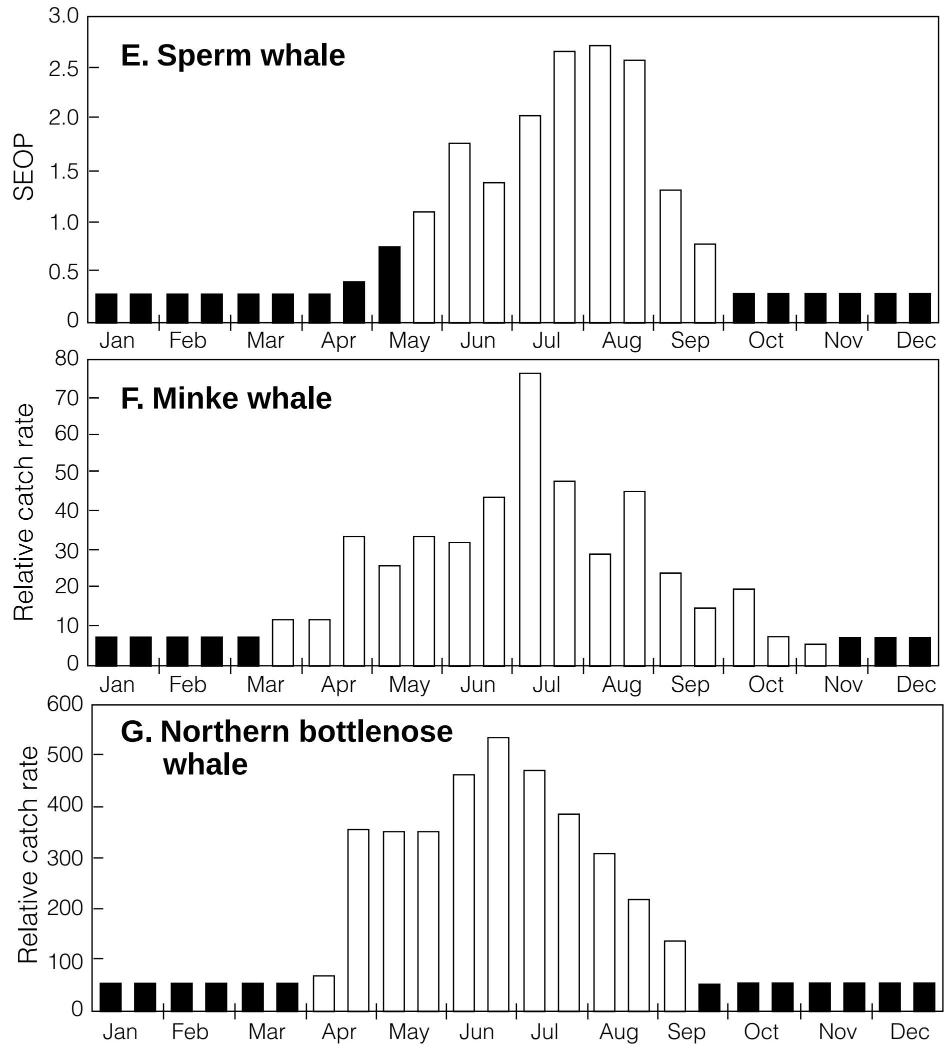

Fig. 2. (Continued). Relative seasonal abundance of baleen whales (a–d, f), sperm whales (e) and northern bottlenose whales (g) in Icelandic waters. a–e are based on sightings data from whaling vessels while f–g are based on catch data. White bars are calculated directly from the data, black bars indicate assumed winter distribution. The unit SEOP (Sightings per effective operation time) does not necessarily indicate the relative abundance of the different species.

groups, crustaceans, cephalopods and finfish (see Table 2).

Estimation of consumption

As the abundance estimates for the whale stocks off Iceland were not stratified by age or length classes, calculations of consumption rates were based on mean weights. For fin and sei whales, weight/length equations based on Icelandic catch 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 literature (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).

TABLE 2. Assumed food composition (% weight) of cetaceans in Icelandic and adjacent waters.

Species	Fish	Cephalopoda	Crustacea	Source
Blue whale			100	Hjort and Ruud, 1929; Tomilin, 1967
Fin whale	3		97	MRI*
Sei whale	2		98	MRI*
Minke whale	59		41	Sigurjónsson and Galan, 1991
Humpback whale	60		40	Mitchell, 1973
Sperm whale	76	24		Martin and Clarke, 1986
Northern Bottlenose whale	5	95		Benjaminsen and Christensen, 1979
Pilot whale	20	80		Desportes and Mouritsen, 1993; Sigurjónsson *et al.*, 1993
Killer whale	100			MRI*
White-sided dolphin	95	5		Evans, 1980; Tomilin, 1967; Katona *et al.*, 1978, Sergeant *et al.*, 1980
White-beaked dolphin	95	5		MRI*; Evans, 1980; Tomilin, 1967
Harbour porpoise	95	5		MRI*; Evans, 1980; Tomilin, 1967 Víkingsson and Sigurjónsson, MS 1996

* Unpublished information from the Marine Research Institute, Reykjavík, Iceland.

TABLE 3. Estimated mean weight (kg) of cetaceans used in this study.

Species	Weight	Source
Blue whale	69 235	* Lockyer, 1976
Fin whale	42 279	* Víkingsson *et al.*, 1988
Sei whale	19 919	* Víkingsson *et al.*, 1988
Minke whale	5 251	* Lockyer, 1976
Humpback whale	31 782	* Lockyer, 1976
Sperm whale	34 322	* Lockyer, 1976
Northern Bottlenose whale	5 418	Benjaminsen and Christensen, 1979; Benjaminsen, 1972; Christensen, 1982
Pilot whale	789	Bloch and Lockyer, MS 1989
Killer whale	2 350	Christensen, 1982
White-sided 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.

The average weight values were adjusted for sexual size difference and uneven sex ratio as observed in the catch of this species off Iceland (Benjaminsen, 1972).

Ingestion rates were calculated by two methods:

a) calculations based 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:

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

where I is the ingestion rate (kg/day) and M is body weight in kg. As the underlying data were based on fish consumption, the value l.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 physiological parameters and body weight. Using Lockyer's (1981b) "near-basal metabolic rate" and 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:

$$D = 206.25\ M^{0.783}$$

where D is the daily active ration (kcal/day) and M is the body weight in kg.

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 rorquals, 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, 1981a), 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 (1981a) 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 the 120 days summer period (mid-May to mid-September) and during winter (mid-September-mid May) were made for the baleen whales by the following equations:

$$S = 2.53D$$
$$W = 0.235D$$

where S and W are the summer and winter ingestion rates, respectively, and D is the mean ingestion rate on an annual basis. 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.

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 in the absence of data on seasonal variation in energy content of prey species. To calculate the annual consumption of each species we multiplied abundance by daily ration and the number of days for each half-month, and then summed all the half-month periods of the year.

Results

The abundance estimates used in the calculations are given in Table 1, separately for the two areas "Iceland and adjacent waters" and "north of 60°N".

Data on diet of cetaceans in Icelandic waters were available for fin, sei, minke, sperm and long-finned pilot whales, white-beaked dolphins and harbour porpoises, while extrapolations from other areas within the North Atlantic had to be made for other species (Table 2). Most of the Icelandic data are unpublished.

For the fin whale we assumed that 3% of the food was composed of fish and 97% of planktonic euphausiids. This was based on observations of fin whales landed, during June–September 1967–89, at the Hvalfjörður whaling station, Southwest Iceland. Of 1 609 whales examined, 96% had krill only in their stomachs, 0.7% capelin (*Mallotus villosus*) only, 0.1% sandeel (Ammodytidae) only, 0.8% some fish remains and 2.5% a mixture of krill and fish remains. Of the fish, it was estimated that capelin comprised some 2.4% and other species of fish (mainly juveniles) like blue whiting (*Micromesistius poutassou*) comprised less than 1%. Of 159 stomach samples examined during the 1979–89 seasons and containing krill, 99.4% had *Meganyctiphanes norvegica* but only one *Thysanoessa longicaudata*.

Of 247 sei whales caught during 1967–88 and analysed for stomach contents, 243 (98%) had eaten planktonic crustaceans, two had eaten sandeels and one each lumpfish and capelin, respectively.

A limited sample of 58 minke whales was examined during 1977–90 (Sigurjónsson and Galan, 1991). Based on these observations 59% of the food is taken to be fish and 41% krill. No stomach samples are available from humpback whales in Icelandic waters, but Canadian studies indicate a ratio of 60:40 fish:krill diet (Mitchell, 1973), which may be in accordance with the very often reported occurrence of humpback whales at the capelin grounds around the coast of Iceland and behavioural observations (MRI, unpubl. data).

Visual observations of killer whales in Icelandic waters indicate that herring is their main food in Icelandic waters (Sigurjónsson *et al.*, 1988; MRI, unpubl. information). Although killer whales have occasionally been observed chasing seals and seabirds off Iceland (Karl Gunnarsson, MRI, Iceland, pers. comm.) a 100% fish diet was assumed for the present analysis (Table 2). While limited examinations on stomach contents of white-beaked dolphins by-caught in Icelandic waters indicated almost total dominance of fish in the diet, we here assume that 5% of the food of both dolphin species is cephalopods in accordance with studies elsewhere in the North Atlantic (Tomilin, 1967; Katona *et al.*, 1978; Evans, 1980; Sergeant *et al.*, 1980).

The estimated mean weights of cetaceans in Icelandic and adjacent waters ranged from 39 kg for the harbour porpoise to nearly 70 tons for the blue whale (Table 3).

The calculated daily food consumption by the two methods, A and B, is given in Table 4. The results of the estimation of annual consumption of finfish, cephalopods and crustacea (mainly krill) by species of whales are given in Tables 5 and 6. Figure 3 shows the general pattern of proportions of food type consumed by the different whale species according to this study for method A in the larger area, north of 60°N. The total food consumption of all cetacean species is around 8.8 million tons and 6.3 million 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 9.2 and 6.5 million tons, respectively. The four largest consumers in the area north of 60°N placed in descending order were: fin, minke, pilot and northern bottlenose whales. These four species accounted for around 80% of the total cetacean consumption in the larger area. Fin and minke whales alone consumed 4.8 million tons or 55% of the total. Within the smaller area, 'Iceland and adjacent waters', minke whales were the greatest consumers, followed by fin whales and then pilot and northern bottlenose whales. Here, minke whales alone were responsible for 33% of the total cetacean consumption (2.1 million tons), while the four species together consumed similar proportion of the total as in the larger area (Table 5).

Crustaceans were consumed by all of the baleen whales and comprised around 51% of the total consumption in the larger area, but 46.5% in the smaller area according to method A. Method B gives somewhat higher proportion of crustaceans consumed; 58% and 52% of the larger and smaller areas, respectively.

According to these calculations, finfish comprised 24–27% (depending on methods A–B) of the cetacean food within the larger area. The proportion of fish was somewhat higher, 29–32% in the more nearshore waters of the smaller area, where total consumption of fish was around 2 million tons. Although cephalopods were taken by several odontocete species, the majority were consumed by pilot and northern bottlenose whales, accounting for between 36 and 60% each of the total cephalopods consumed, depending on which method and area was considered. Together these two species consumed 97% of the total consumption of cephalopods.

On the other hand, finfish were consumed by most species of whales and amounted to 2.2–2.4 million tons for the area north of 60°N and 1.9–2.0 million tons for Icelandic and adjacent waters. The estimated amount determined by method A for the Icelandic and adjacent seas is shown in Fig. 4. According to the present calculations (method A) minke whales were, by far, the most important fish eaters around Iceland, consuming around 1 million tons of fish in Icelandic and adjacent waters, corresponding to 52% of the total fish consumption by cetaceans in the area. White-sided dolphins, long-finned pilot whales, killer whales and humpback whales each consumed 6–9% of the total cetacean fish consumption in the small area (Tables 5–6). Unidentified dolphins and white-beaked dolphins together consumed more fish than white-sided dolphins, so taken together dolphins were the second greatest fish consumers in the area, accounting for 19% and 14% of the total fish consumtion in the smaller area according to methods A and B, respectively.

TABLE 4. Estimated energy consumption (thousands of Kcal/day) by whale species and season based on two different methods A and B (see text).

Species	Mean A	Mean B	Summer A	Summer B	Winter A	Winter B
Blue whale	955.4	1271.5	2421.3	3211.8	222.5	301.4
Fin whale	686.6	864.2	1734.4	2183.0	162.7	204.8
Sei whale	414.7	479.4	1047.5	1211.0	98.3	113.6
Minke whale	169.7	168.8	428.7	426.4	40.2	40.0
Humpback whale	567.1	691.1	1432.1	1745.7	134.6	163.8
Sperm whale	597.1	734.0				
Northern Bottlenose whale	173.3	173.0				
Pilot whale	47.7	38.3				
Killer whale	99.0	89.9				
Unidentified dolphin	19.5	13.5				
White-sided 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 Fish	North of 60°N Cephalopoda	North of 60°N Crustacea	North of 60°N Total	Iceland Fish	Iceland Cephalopoda	Iceland Crustacea	Iceland Total
Blue whale			206 364	206 364			206 364	206 364
Fin whale	56 598		2 558 085	2 614 683	32 045		1 448 363	1 480 408
Sei whale	7 895		540 797	548 692	1 781		122 021	123 802
Minke whale	1 113 847		1 081 977	2 195 824	1 055 602		1 025 398	2 081 000
Humpback whale	118 889		110 792	229 681	118 889		110 792	229 681
Sperm whale	105 519	33 322		138 841	58 104	18 349		76 453
Northern Bottlenose whale	36 523	693 941		730 464	34 315	651 980		686 295
Pilot whale	291 813	1 167 253		1 459 067	154 943	619 771		774 714
Killer whale	153 101			153 101	139 342			139 342
White-beaked dolphin	73 738	3 881		77 619	67 810	3 569		71 378
White-sided dolphin	189 845	9 992		199 837	184 643	9 718		194 361
Unidentified dolphins	190 891	10 047		200 938	138 728	7 301		146 029
Harbour porpoise	48 676	2 562		51 237	45 823	2 412		48 235
Total	2 387 336	1 920 998	4 498 015	8 806 349	2 032 024	1 313 100	2 912 938	6 258 062

Discussion

Although the two methods for calculating the average daily feeding rates give similar results for the total consumption of all populations (Tables 5–6), they differ considerably in the extremes of the size range of species (Table 4) and thus with regard to the proportional contribution of the different

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

	North of 60°N				Iceland			
Species	Fish	Cephalopoda	Crustacea	Total	Fish	Cephalopoda	Crustacea	Total
Blue whale			274 791	274 791			274 791	274 791
Fin whale	71 238		3 219 738	3 290 976	40 334		1 822 985	1 863 319
Sei whale	9 128		625 208	634 336	2 060		141 067	143 127
Minke whale	1 107 894		1 076 193	2 184 087	1 049 959		1 019 917	2 069 876
Humpback whale	144 914		135 046	279 960	144 914		135 046	279 960
Sperm whale	129 712	40 962		170 674	71 427	22 556		93 983
Northern Bottlefish whale	36 460	692 740		729 200	34 255	650 851		685 106
Pilot whale	234 307	937 229		1 171 536	124 409	497 636		622 045
Killer whale	139 028			139 028	126 534			126 534
White-beaked dolphin	51 187	2 694		53 881	47 072	2 477		49 549
White-sided dolphin	128 971	6 788		135 759	125 437	6 602		132 039
Unidentified dolphins	132 155	6 956		139 111	96 042	5 055		101 097
Harbour porpoise	27 380	1 441		28 821	25 775	1 357		27 132
Total	2 212 375	1 688 809	5 330 976	9 232 160	1 888 218	1 186 534	3 393 806	6 468 558

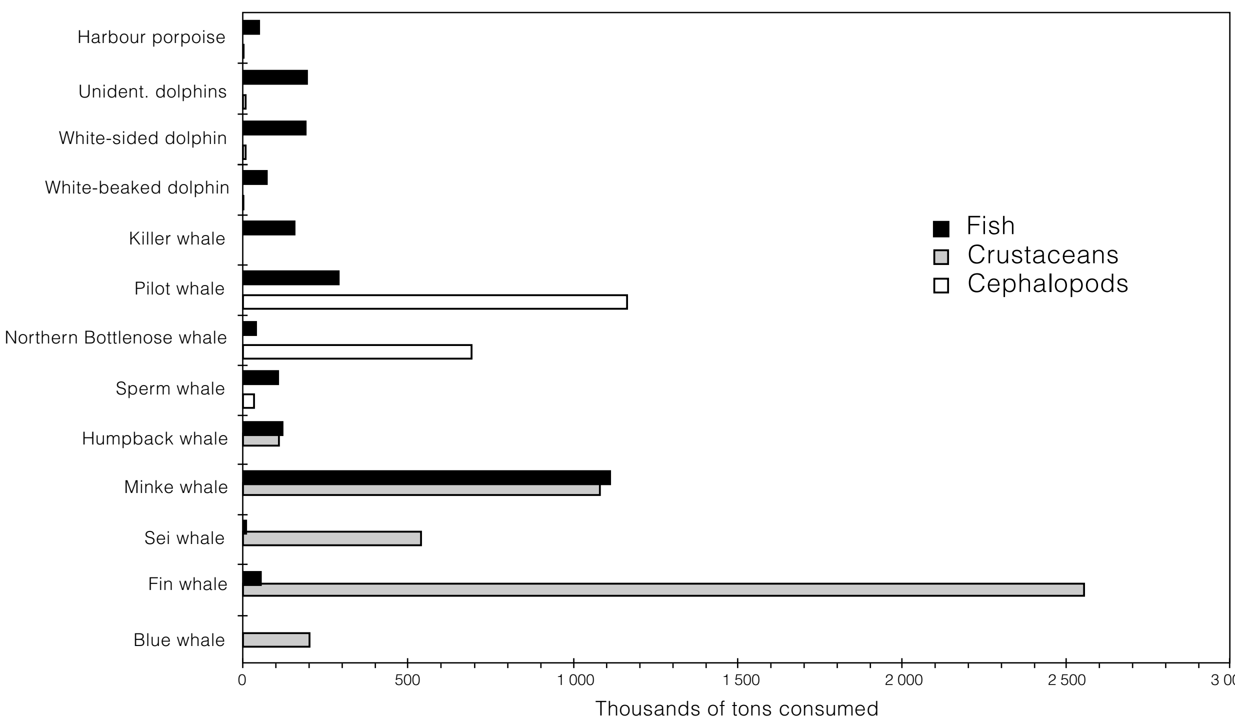

Fig. 3. Estimated consumption (thousands of tons) of crustaceans, cephalopods and finfish by cetaceans in the larger survey area north of 60°N.

species to the total consumption. As the underlying data for method A are based on measurements of small and medium sized cetaceans in captivity (Sergeant, 1969), we consider that method more reliable for those species. However, the summer ingestion rates obtained by method A also appear to be in better agreement with studies on seasonal fattening rates and quantities of stomach content in large whales (Kawamura, 1974; Lockyer, 1981a, 1987a, 1987b; Víkingsson, 1995, 1997).

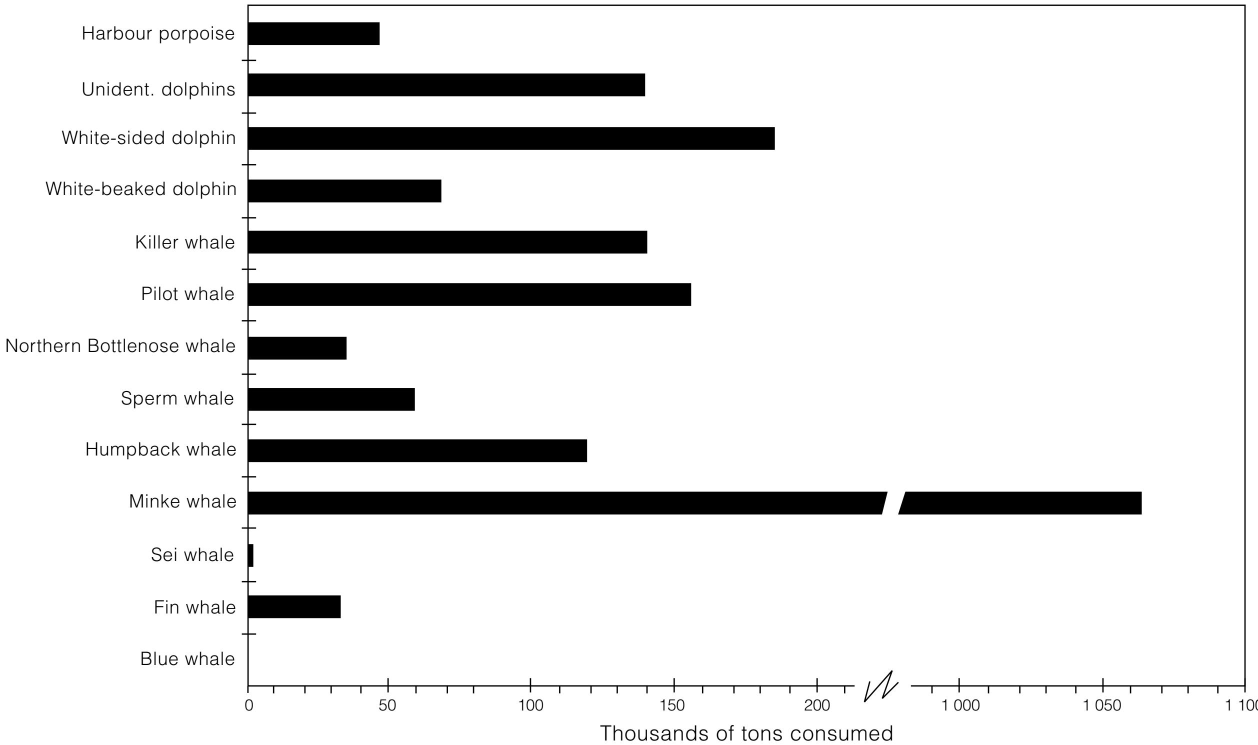

Fig. 4. Estimated consumption (thousands of tons) of finfish by cetaceans in the smaller survey area "Iceland and adjacent waters".

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 for individual minke whales than the present results. However, the present results on total consumption of fin, sei and blue whales are around 20% lower than simple calculations based on the assumptions that the whole populations (the peaks of the migration curves) stay in the area for 120 days, but are absent the rest of the year and either i) feed at the summer rates (35g/kg body weight) given by Lockyer (1981a) or ii) one assumes two times Kleiber's (1975) basal metabolic rates as often done for mammals in general (Innes *et al*., 1987).

It has become evident from this study how sensitive the results are to the various input parameters and assumptions required to reach a conclusion. Particularly critical are 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 that can be obtained based on the available data. The great variations in group sizes of many of the odontocetes is of concern since 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 the surveys were 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 are the target species for the various surveys, when using sightings survey data. The NASS surveys were designed primarily for abundance estimation of large baleen whales and the provisional estimates for the smaller species are therefore likely to be biased downward. This may apply especially to the harbour porpoise, where specially designed surveys (Borchers *et al*., 1995;

Hammond *et al.*, 1995; Palka, 1995; Polacheck, 1995) are needed for proper abundance estimation.

Another factor of importance is the seasonal variation in abundance. Although we believe our approach to some extent solves this problem, more information is needed on migratory behaviour and geographical variation within the study area. The linking between the absolute abundance estimates and the relative indices of seasonal abundance is a potential source of bias. 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 period for blue whales coincided with the survey period, while this was somewhat out of phase, although not seriously, for fin, minke and humpback whales. It was more severely out of phase for sperm whales and 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 seasonal sei whale sightings data suggest that abundance was less than 20% of the peak in late September, resulting in considerable scaling-up of the half-monthly estimates in the latter part of the season. As mentioned above, the relative index for northern bottlenose whale was seriously biased in July.

Whether all age and sex groups behave the same way, could also be of importance in further calculations. Winter abundance is poorly known, but would be useful to look into further, both with respect to feeding activities and what portion of the stock overwinters. Recent studies on fin whales off Iceland 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 grounds in the deep waters off Iceland. In general, the continuation of ongoing studies into the energetics and feeding rates of different whale species is needed.

There is a strong need for a more extensive data base of actual observations of food composition by each species, including studies of temporal and spatial variation. In the present study the bias is not serious for species like the blue whale, which appears to feed almost exclusively on planktonic crustacea in all oceans (Yochem and Leatherwood, 1985), or the long-finned pilot whale, where extensive studies in the Faroe Islands (Desportes and Mouritsen, 1993) 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; Haug *et al*., 1996) and eat 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 feed almost exclusively on crustacea during the summer season west and southwest of Iceland, while at least off the Canadian coast, fin whales are well known fish eaters. The large fish consumption by minke whales in Icelandic and adjacent waters and the coastal distribution of the species (NAMMCO, 1997), overlapping to a large extent with the most important fishing grounds off Iceland, may lead to conflicts with fisheries and calls for further studies into the feeding ecology of minke whales in the area.

The energy content of the food, which may vary 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 still another important factor with respect to the potential impact on the ecosystem.

The present analysis of consumption by 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 total biomass consumed is substantial, or more than three times the total landings of the Icelandic fishing fleet. The implications of this requires 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*. (1997).

Acknowledgements

Sincere thanks are extended to our colleagues at the MRI. Thorvaldur Gunnlaugsson is thanked for useful suggestions and advice regarding the abundance estimates, Droplaug Ólafsdóttir for useful suggestions and help with the figures and Inga

F. Egilsdóttir for assistance in the preparation of the manuscript. Two anonymous reviewers are thanked for very useful suggestions.

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