Northwest Atlantic Fisheries Organization

Serial No. N2621 NAFO SCR Doc. 95/99

SCIENTIFIC COUNCIL MEETING - SEPTEMBER 1995
Symposium - The Role of Marine Mammals in the Ecosystem

On Dynamic Interactions Between Some Fish Resources and Cetaceans off Iceland Based on a Simulation Model

by

Gunnar Stefánsson, Jóhann Sigurjónsson and Gísli Víkingsson

Marine Research Institute, P. O. Box 1390
Skúlagata 4, 121 Reykjavík, Iceland

ABSTRACT

In Icelandic and adjacent waters 12 species of cetaceans are regarded as common or number at least in several thousands. Based on available estimates of the total food consumption of the cetaceans in the area, this paper explores potential interactions between three piscivorous baleen whale species off Iceland and the relevant fish resources that constitute their principal prey. The three species of whales are fin whale (*Balaenoptera physalus*), the largest cetacean consumer in this area, feeding mainly on *krill (Meganyctiphanes norvegica)* but also preying on some fish species like capelin (*Mallotus villosus*); minke whale (*Balaenoptera acutorostrata*), taking krill as well as a variety of fish, including capelin and gadoids (e.g. cod, *Gadus morhua*); and humpback whale (*Megaptera novaeangliae*) assumed to be feeding mainly on capelin.

The study is based on a variety of assumptions regarding stock sizes, food preference, potential rates of increase and harvesting strategies, where a single-species model developed for investigating the effects of different utilization policies of the Icelandic cod stock and this combined with a crude multispecies model are used to study the potential impacts on capelin and cod stocks by various developments of the whale stocks under consideration. A Pella-Tomlinson like model is used to describe the whale stocks. In the multispecies model, the population and fisheries dynamics for shrimp (*Pandalus borealis*) and capelin (both important food items for cod) are modeled using simple models. Thus, only aggregates such as total, recruiting or adult numbers or biomass are considered as opposed to the fully age-class based cod model.

The results indicate that both minke and humpback whales may have significant direct impact on the status of the capelin stock. The effects of fin whale predation on the capelin stock seems less significant unless such consumption occurs outside the sampled area, which is quite possible. The impact of the three baleen whale species on the development of the cod stock is uncertain, but may be considerable.

INTRODUCTION

In recent years increased importance has been attached to the role of species interactions in decisions on harvesting methods for individual marine species or complexes. This is reflected e.g. in recent multispecies-directed work in the North Sea (Anon., 1994), Boreal systems in general (Anon., 1991) and also specifically in the Barents Sea (Bogstad *et al.*, 1995), and Iceland waters (Pálsson and Stefánsson, 1995, Stefánsson *et al.*, 1995a-b).

Multispecies biological, assessment and harvesting models Icelandic waters, have put emphasis on the cod-capelin interaction (Magnússon and Pálsson, 1989 and 1991, Anon. 1995a-d and Pálsson and Stefánsson, 1995). Recent work on biological management advice and economic considerations has also incorporated the cod-shrimp interaction (Stefánsson *et al.* 1994a-b). Such considerations implied that a harvesting strategy for cod taking 25% of the fishable (i.e. 4+) biomass (possibly with a minimum catch level) would be beneficial in the medium term, even accounting for the predicted decrease in capelin and shrimp catches, possible density-dependence in cod growth, cod cannibalism and uncertainty in assessments, model assumptions and predictions. In particular it was found that the overwhelmingly important economic consideration was the rebuilding of the cod stock and catches. Based on these considerations, this harvesting strategy for cod was adopted by the Icelandic government in 1995.

These previous works on effects of harvesting strategies for fish stocks in Icelandic waters have not included the possible effects of other predators in the system, such as marine mammals. This is best done in such a fashion as to include most of these factors in a single model. If each predator is only considered separately, then the total effect on prey catches cannot be determined since such a prediction will completely depend on the remaining mortality in the system: Even if a predator consumes huge amounts of juvenile prey, this will not result in major increases in catches of older prey, if the amount consumed is minor compared to other prey.

For this reason, this paper incorporates predation on cod, capelin and shrimp by whales and cod into a single model. The model is conceptually simple and in particular it does not incorporate such features as areal differences in overlap except through the estimation of consumption rates. The principle used throughout has been to take a commonly used population model for each species and incorporate that in the overall framework, rather than to take a uniform and symmetric model. This sacrifices some of the mathematical elegance of e.g. MSVPA (Anon. 1995d) but allows each population model to contain recognizable parameters commonly used for that species.

The paper compares various possible scenarios on how much the apex predators may consume cod and capelin and how this may affect catches through changes in population abundance or cod mean weight at age.

METHODS

A simulation model is used to investigate the possible variations in the combined population dynamics of apex predators, cod, capelin and shrimp. The principles are simply to use a regular age-based prediction model for the cod and simpler common models for other species. Each component is added in a fairly transparent fashion, so that it can be switched on or off for sensitivity evaluation.

Population dynamics

The model dynamics of the various populations will be described in the order implied by the trophic level.

Whale population dynamics

Minke whale: The population is assumed to change in accordance with the Pella-Tomlinson model, as described e.g. in Magnússon and Stefánsson (1988). The basic model described the population numbers in year t+1 based with the equation:

$$P_{t+1} = (P_t - C_t)S + (1-S)\left\{1 + A\left[1 - \left(\frac{P_{t-T}}{K}\right)^z\right]\right\}P_{t-T},$$

where the parameters A, z and survival, S=exp(-M), control the dynamics along with the age at maturation, T, taken as 5 years here. The natural mortality rate will simply be taken as M=0.05 throughout this paper, as has been commonly used in other studies. The parameters A and z can be cast in terms of the maximum sustainable yield rate (MSYR) and the corresponding population size, i.e. the maximum sustainable yield level (MSYL):

$$MSYL = \left(\frac{1}{z+1}\right)^{1/z},$$

and

$$MSYR = \left(\frac{1-S}{S}\right)\left(\frac{z}{z+1}\right)A.$$

Thus the dynamics of the minke whale population will be determined by the values of MSYR and MSYL. In the base case, MSYL will be taken to be 0.6 (conventional value for baleen whales, see Allen, 1980) and thus z=1.38. MSYR will be taken at 5% in base runs, but in stochastic runs MSYR will be considered in the range from 0 to 10%.

Humpback and fin whale

The dynamics of the humpback and fin whale are taken to be exactly the same as for the minke whale, with different values of some of the population-size parameters. In addition to those listed below, there are indications that the current and historical increase in the humpback stock size can be of the order of 10% (Katona and Beard, 1990, Mitchell, 1975). As there has not been any whaling operation aimed at humpback whales for several decades, this stock should be well above MSYL and hence MSYR should be no less than the observed 10% increase. For this reason, it is of interest to investigate the effect of assuming MSYR=10% in addition to other alternatives.

Cod population dynamics

Stefánsson *et al.* (1994b) considered only cod of age 3 and older. In this model, recruitment was taken to occur according to the Ricker model, but modified to account for potential cannibalism or competition by immature juveniles. In order to accommodate predation on pre-recruits, the age range has been extended down to age 1 (i.e. January 1 of the year after the year of birth).

Initial stock size and recruitment

The initial stock size and recruitment up to and including the 1994 yearclass are determined from catches at age in numbers, survey and CPUE data as described in Anon. (1995b), with uncertainty attached as described in Stefánsson *et al.* (1994b).

Natural mortality and recruitment of cod

Stefánsson *et al.* (1994b) described the stock-recruitment relationship with a function of the form initially developed by Pope and Woolner (1981) and similar to the one used by Bogstad *et al.* (1993). The functional form is given by

$$R = \alpha S e^{-S/K} e^{-cJ},$$

where R denotes 3-year old recruits, S spawning stock biomass and J the biomass of immature cod available as cannibals at the time of birth of the yearclass in question. For *J*, an index of the biomass of 2+ cod was taken as a measure of potential cannibals. In Stefánsson and Steinarsson (1993) it is shown that there is a good relationship between the indices of abundance from the 0-group survey in August and the 1-group survey in March of the following year. There are also indications that there is a poorer relationship between the abundance of 1-group in March and 2-group in March of the following year. There is, however, a very good relationship between the 2-group survey index and the 3-group recruitment estimate from VPA (Stefánsson, 1992).

Bogstad *et al.* (1993) also found that the possible cannibalism seemed mainly to occur by immatures after the 0-group survey. The above further indicates that this mortality is most likely to occur in the 1-group stage and not thereafter.

In all, this indicates that a plausible model of the recruitment process is to generate 1-group stock abundances by :

$$N_1 = \alpha' S e^{-S/K},$$

and to reduce these according to natural mortality due to cannibalism on the 1-group by:

$$N_2 = N_1 e^{-M_{1,1}} e^{-cJ}.$$

Here, the revised constant, α', is increased from α in order to account for natural mortality other than cannibalism during the 1- and 2-group stage. $M_{1,1}$ is used to denote this natural mortality at the 1-group stage and similarly $M_{2,1}$ denotes the base natural mortality at the 2-group stage. Both numbers are set at 0.2 in the base simulations, as is the base natural mortality on all older age groups.

For all age groups of cod, the natural mortality is also connected to the possible predation by apex predators. Thus, the total natural mortality is written as :

$$M_a = M_{a,1} + \sum_{pred} M_{a,2}^{pred} .$$

The mortality, $M_{a,2}^{pred}$, generated by each predator is produced in the model by taking a base induced mortality and scaling it with the relative size of the apex predator population in the present year to the reference period. Thus a doubling in predator population size will double the natural mortality inflicted by the predator. The other side of the coin is that a doubling of the cod stock will double the estimated consumption of cod by the predators.

Although some odontocete cetaceans have been found to eat cod in Icelandic waters (Sigurjónsson and Víkingsson, 1996), these are not included in the present model. Thus, only minke whales are included as direct predators of cod.

In addition to the above dynamics, Steinarsson and Stefánsson (1991) found relationships between the abundance of capelin and the mean weight at age of cod. Thus, a reduction in the biomass of capelin, from fishing or predation, is likely to have an effect on the harvest of cod through a reduction in the mean weight at age. This effect is regularly included in assessments (Anon. 1995b), has been included in other medium-term predictions and the effect will be included here in order to verify the potential indirect effect of capelin predation on the cod harvest.

Capelin population dynamics

Apart from natural mortality, the same dynamics are used for capelin as in Stefánsson *et al.* (1994b). The model is a simplistic description of the capelin stock, generated as random 1-group recruits in year t-1, entering the fishery as 2-group in fall of year t to spawn and die at age 3 in year t+1.

Capelin recruitment

As in Stefánsson *et al.* (1994b), capelin recruitment is taken to be cyclic (with an unknown period in stochastic simulations) to simulate the stock crashes observed in the past decades (Vilhjálmsson, 1994). The actual level of recruitment is based on the average value on 1. August, derived from acoustic measurement (Vilhjálmsson, 1994) and base level consumption estimates by the various predators. Thus one obtains a recruitment biomass level along with a biomass level at the start of the fishery. All predation is assumed to take place between these two time points.

Capelin natural mortality

Stefánsson *et al.* (1994b) assumed natural mortality for capelin to occur during a 12-month period before recruitment to the fishery. Natural mortality during the fishing season has been estimated to have been on average 0.035 per month (Vilhjálmsson, 1994) for recent years. Stefánsson *et al.* (1994b) simply scaled this value according to changes in the size of the spawning stock biomass of cod and applied the scaled value to the prerecruit period. This is equivalent to assuming that cod is the overwhelming cause of natural mortality for capelin. Natural mortality and weight-at-age have been found to roughly cancel during the winter months when the fishery takes place (Vilhjálmsson, 1994) and therefore this natural mortality is omitted from the computations.

The present paper changes this assumption and replaces it with a model where the capelin natural mortality is composed of a component for each of the predators, cod, minke whale, fin whale and humpback whale, respectively.

In order to complete the formulation of capelin natural mortality, the relative magnitude of the different contributing factors needs to be defined. The approach taken here is to take the log-ratio of the recruitment to the initial biomass as an estimate of the total pre-recruit natural mortality and to separate this into components according to the point estimate of consumption by each predator. Deviations from this approach can then be considered as alternative models.

Shrimp population dynamics

The shrimp population dynamics are taken unmodified from Stefánsson *et al.* (1994a and b). Notably, consumption of shrimp by apex predators is ignored in the simulations presented.

RELATING AVAILABLE NUMERICAL DATA TO THE MODEL

Consumption

Assumptions regarding the amount and type of food taken by each of the whales species involved are based on Sigurjónsson and Víkingsson's (1996) estimates of consumption by area and species. The basic inputs in their calculations are estimates of absolute abundance (based on systematic sightings surveys), estimated migratory cycle for each species, average weight of individual whales, estimated energy requirement per individual and the food consumption as found by direct sampling or by other means. Based on these findings, the capelin consumption of the humpbacks, fin and minke whales and the cod consumption of the minke whales is as outlined below.

Humpback whale: During the winter capelin fishery deep north of Iceland, humpback whales are frequently reported around fishing vessels taking capelin (Sigurjónsson and Gunnlaugsson, 1990). Also, the humpback whale is frequently sighted close to the capelin concentrations off the northwestern clockwise to the eastern coasts of Iceland during the summer season, e.g. during the 1995 sightings surveys (June-August), where major concentrations occurred in this area (MRI unpublished information). The northerly areas are juvenile grounds for capelin, but the adult capelin also occupies this area during the spawning migration from Jan Mayen to the southern coast of Iceland (Vilhjálmsson, 1994). In absence of stomach samples and in light of these observations and observations from other areas, Sigurjónsson and Víkingsson (1996) assumed that 60% of the humpback diet around Iceland is capelin and the remaining 40% planktonic krill. This gave an annual consumption of capelin around 153,000 tonnes, which is the value we apply here.

Minke whale: Two alternative estimates of the capelin consumption by minke whales are used, i.e. one that only refers to the Icelandic coastal waters within the continental slope and amounts to 108,424 tonnes; and the other, amounting to 218,636 tonnes, that also covers the waters along the East Greenland coast and the area towards the Jan Mayen Island, i.e. the main area of the Icelandic capelin stock. The latter will be used as the base case since it this is based on a more extensive description of the areal distribution of the two species.

The minke whale is apparently the only one of the species of whales here considered that consumes significant amounts of cod. Approximately 6.1% (by frequency) of the animals sampled in the coastal waters around Iceland was large teleost fish species (Sigurjónsson and Galan, 1990). Since cod is far the largest stock of large teleosts occupying the shelf areas around Iceland, the following calculations will be based on the assumption that this all equals the cod consumption of the minke whale. Taking only the shelf area, 6.1% of Sigurjónsson and Víkingsson's (1996) estimate of 391,421 tonnes gives approximately 23,877 tonnes.

The effect of this on the cod stock and fishery will depend on what age groups of cod the minke whale is assumed to prefer. The base-case assumption used here is that the minke whale has a uniform selection pattern for cod age 1 and older. The actual scaling multiplier is set so that the amount consumed by the minke whale in the model in 1994 is close to the estimated value.

There is considerable uncertainty surrounding this consumption estimate and in base-case stochastic simulations it will be assumed that the actual consumption of cod by minke whales is between zero and twice the measured number.

Fin whale: The total consumption of capelin by fin whales in the main capelin area as defined above is some 47,000 tonnes annually, assuming Sigurjónsson and Víkingsson's (1996) estimate of 2.5% of the fin whale diet consists of capelin. That figure will be used as a base-case assumption in this modeling exercise. However, as discussed by Sigurjónsson and Víkingsson (1996), the sampling in Iceland took place west and southwest of Iceland, where euphausiid crustaceans are abundant and during only part of the year. Since fin whales often take fish as an important second prey choice in other North Atlantic areas (Sigurjónsson, 1995) and as main prey in others (capelin comprised 80-90% of the diet in Newfoundland, Mitchell, 1975), one alternative and perhaps not unrealistic hypothesis that some 30% of the fin whale diet consists of capelin will be considered here. This would correspond to an annual consumption of about 560,000 tonnes of capelin.

Cod: The cod stock is a considerable capelin predator (Pálsson, 1983) and typical estimates of the consumption of capelin by cod in specific months have been in a range which may correspond to an annual consumption in the range 0.5-1.0 million tonnes (Magnússon and Pálsson, 1989). It is not clear how this consumption should be separated into capelin prerecruits, the fishable stock and dying post-spawners. For the base model, a value of 500 thousand tonnes will be used for the consumption of prerecruit capelin by cod.

Using the base-case numbers, the above indicates that the total consumption of capelin by the modeled predators may have been about 920 thousand tonnes per annum in recent years. Since the average capelin adult biomass in fall during 1983-1993 was estimated at around 1.4 million tonnes (Vilhjálmsson, 1994), this implies that the total biomass before the consumption by predators in the model may have been about 2.3 million tonnes, implying a natural mortality of about 0.042 per month. This natural mortality can then be separated into mortality induced by the various predators by using the relative consumption by each one. The results are given in Table 1.

Table 1. Consumption of capelin by modeled predators in base-case and alternative models along with corresponding induced natural mortality.

Predator species	Base-case consumption	Induced mortality	Alternative cons.
Minke	218 636t	0.010	108 424 t
Fin	46 581t	0.002	558 974t
Humpback	152 990t	0.007	
Cod	500 000t	0.023	1 000 000t
Total	918 207t	0.042	

It should be noted that this particular approximation to the real world lumps several processes into one. In particular, the consumption is converted to natural mortality in a fashion which is equivalent to assuming that the consumption of capelin by its predators occurs in fall, just before the start of the fishing season, but after the main capelin growth period. Furthermore, the modeling approach of scaling natural mortality with the size of the predator stock will of course imply that a doubling of the predator stock doubles the natural mortality (but not consumption) of the prey, and a doubling of the prey stock size doubles the consumption by each predator.

Population dynamics parameters

The parameters controlling the base-case population dynamics of the apex predators are given in Table 2.

Table 2. Input parameter values in base-case. Also given are bounds (L=Lower, C=Center, U=Upper) for stochastic simulations.

	A	T	z	MSY L %	MSYR%			K	N88		Depletion		
					L	C	U		n	CV	L	C	U
Minke	1.38	5	2.39	60	0	5	10	40000	28000	.15	.4	.7	1
Fin	1.38	8	2.39	60	0	5	10	22306	15614	.27	.4	.7	1
Humpback	1.38	4	2.39	60	0	5	10	2566	1796	.18	.4	.7	1

Bounds and CVs are given for some of the parameters. For stochastic simulations, the bounds are used by assuming a uniform distribution of the associated parameter, and the CV is used in a lognormal distribution. In this table, K is determined from the initial (approx. 1988, see Sigurjónsson and Víkingsson, 1996) stock size along with the depletion level. Thus, bounds on the depletion level imply bounds on the maximum stock size.

The initial state of the stock (before 1988) in the model is set constant (as in the N88-columns) so that the recruitment function can be initiated with the time lag according to the age at maturity (T), starting in 1988.

Harvesting strategies

The catch control law for capelin is to attempt to leave 400 thousand tonnes for spawning.

The adopted catch control law for cod is to catch 25% of the biomass of cod of age 4 and older.

The modeled catch control law for shrimp is to harvest the sustainable yield.

RESULTS

Initial simulations and sensitivity analyses

Four scenarios with respect to the consumption of capelin and cod by whales are considered for the purpose of initial analyses:

Predation by apex predators		**Cod consumption**	
		Included	Omitted
Capelin consumption	Included	A (Base-case model)	B
	Omitted	C	D

Scenario A includes all the various apex predation components, described above as the "base case", whereas scenario D mimics the analyses in Stefánsson *et al.* (1994) albeit with slight modifications in parameter values *in lieu* of Anon. (1995b) and Anon. (1995c).

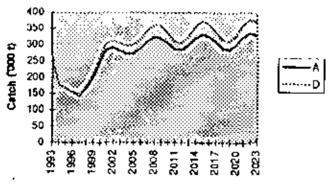
Deviations B-D from the base-case model A are implemented simply by omitting completely the corresponding facet of the model. Thus, when consumption of capelin by apex predators is omitted, this leads to a revision of recruitment and allocation of all prerecruit natural mortality to cod only.

In addition to these simulations, further deviations were considered:

- E: As in base-case simulation, except fin whales consume some 570 thousand tonnes of capelin
- F: As in base-case simulation, except cod consume 1 million tonnes of prerecruit capelin.
- G: More accurate knowledge on the depletion level.
- H: More accurate abundance data.
- I: More accurate estimates of MSYR (0.04-0.06 in place of 0-0.1).
- J: Exact knowledge of apex stomach content data on capelin (CV on inflicted M set to 0.01 in place of 0.25).
- K: Exact knowledge of minke stomach content data on cod (fixed at 6.1% rather than uniform from 0 to 12%).
- L: Less consumption of capelin by minke whales.
- M: Increased MSYR to 10% for humpback whales.
- N: Minke whale selection pattern for cod bent towards older fish.

The simulation can be conducted as a deterministic simulation where the model is computed forward in time without stochasticity and all variables are simply set to their expected value. Results regarding cod catches from two such simulations are shown in Fig 1 which depicts the trend in yield in the two particularly interesting cases, A and D. This figure contrasts the expected catches when the whales are included at base-case levels with the expected catches when the apex predators are completely omitted from the model.

Fig. 1. Trends in cod catches in scenarios A (base case) and D.

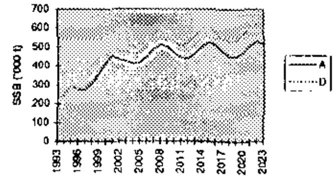


Similar results for the spawning stock biomass (SSB) are shown in Fig. 2.

It is seen that the curves are at lower levels in scenario A, which is reasonable given that the minke whale is assumed to consume some 23 thousand tonnes of cod per annum and that the minke whale stock is expected to increase during the forthcoming decades since it is currently below carrying capacity (K).

The implication of this is that a prediction made while omitting the apex predators will be too optimistic, so that if (D) is used as a model but (A) is closer to reality, then the long-term utilization of the cod stock will result in lower catches than predicted.

Fig. 2. Trends in SSB of cod in scenarios A (base case) and D.



In particular, the evaluations in Stefánsson *et al.* (1994b), which were used as a basis for the choice of a management procedure for cod, may indicate long-term catches of cod which are about 35 thousand tonnes (about 10%) too high. Naturally this follows from the increased total mortality on the cod stock, which leads to an "equilibrium" at a lower stock size and lower productivity than in D.

This particular effect is illustrated in Fig. 3. The "equilibrium" cod catch as a function of cod biomass is computed by projecting the system forward using a fixed fishing mortality for cod and computing an average at the end of the time period (there is no true fixed equilibrium due to the cycles in the capelin stock). The catch control law for cod is also shown (straight line), as is the predicted path from the 1993 level towards "equilibrium".

Fig. 3. Catch control law for cod (solid, straight), "equilibrium" curve and projected trajectory (thin) under scenario D.

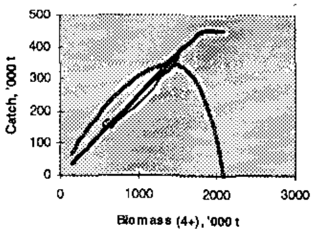
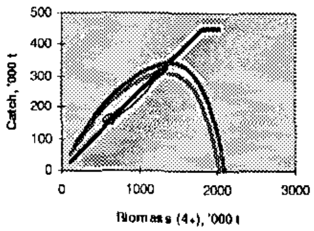


Fig. 4 also shows the "equilibrium" curve for scenario A. It is seen how the catch control law intersects the "equilibrium" curve at a lower catch and stock level in scenario A than in D. It is clearly seen from the above, how predictions based on a model excluding the whale stocks may lead to a bias in the expected catch levels.

Fig. 4. Catch control law for cod (solid, straight), A (low) and D (high) "equilibrium" curves and projected (thin) trajectory under D.



The extent of the bias depends on the assumptions of the model. Some of these assumptions are based on detailed knowledge whereas others have considerable uncertainty attached to them. Thus, alternative scenarios can be argued, which will increase the difference between the "equilibrium" curves or make them closer. This is a basic problem which is inherent in making deterministic projections without taking uncertainty into account.

Alternatively, the simulation can be conducted in a stochastic fashion by selecting a set of random values from the distributions assigned to each uncertain variable. The stochastic simulations are conducted by running 300 such simulations.

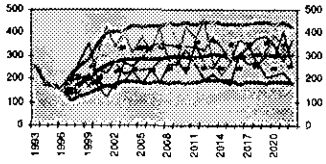
Although it would be possible to encompass all the uncertainty and variation listed in the various scenarios into one stochastic simulation, some of these variations can better be considered completely alternative models and this is done in what follows.

Some of the more important output values are contrasted in the table below, where final (years 2016-2023) average values are compared:

	Cod biomass		Cod catch		Capelin catch		Notes
	Average	std. dev.	Average	std. dev.	Average	std. dev.	
A	1255	213	309	52	645	153	Base case
B	1383	150	339	35	614	151	No predation on cod
C	1274	212	313	50	674	154	No apex predation on capelin
D	1403	139	344	30	646	150	No apex predation
E	1240	224	305	53	610	171	Increase consumption by fin of capelin
F	1245	197	307	48	604	173	Increase consumption by cod on capelin
G	1266	184	312	43	649	153	More accurate info on depletion
H	1256	213	309	51	640	155	More accurate survey data
I	1227	220	302	55	637	152	More accurate info on MSYR
J	1250	221	308	53	645	144	No error in apex capelin stomach data
K	1251	202	308	47	645	142	No error in minke cod stomach data
L	1249	221	308	52	653	158	Reduced capelin consumption by minke
M	1254	220	309	53	638	156	Increased MSYR by humpback
N	1271	202	313	49	643	158	Move minke sel. pattern to older cod

It is seen that the major factor affecting the result on cod yield is the predation by minke on cod (A vs. B). It is also seen that assuming increased consumption of capelin by fin whale or cod (A vs. E or A vs. F) has the effect of decreasing the predicted capelin catch. The range from 0 to maximum fin whale consumption (B vs. E) corresponds to a drop from 675 to 610 thousand tonnes capelin catch.

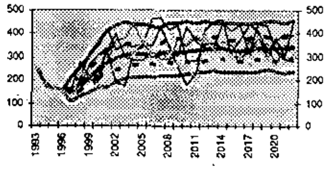
Fig. 5. Scenario A (base case) trend in cod catch. All apex predation set at base levels.



An important additional concern is the effect of the uncertainty in the whale stocks on the variance in predictions. It is seen that the variability in apex predation is reflected as an increase in the standard error of cod yield from about 30 to about 50 or by about 60%. The CV in cod yield changes from below 10% to some 15%.

This effect is depicted in Figs 5 and 6 which summarize the probability distribution of future catches in terms of 5%, 25%, 50%, 75% and 95% percentiles along with 5 sample trajectories. It is seen that the median catch is lower in Fig. 5, and although the upper bound is the same, the lower bound is lower, reflecting the increased variance in the results due to the uncertainty in the whale consumption.

Fig. 6. Scenario D (no apex predators) trend in cod catch. Apex predators completely omitted.



As for capelin, it is seen that the sort of variation encountered when considering the whale stocks is a change in expected capelin yield from about 675 to some 600 thousand tonnes. Similarly, the standard deviation can be expected to increase by some 10% in the high consumption case for fin whales.

The variation and uncertainty described above can be considered from several viewpoints. One issue is clearly the effect of different assumptions concerning the whales on future levels of fish catches and this is e.g. reflected directly in comparisons between the averages obtained in scenarios A and D. This can therefore be thought of as a sensitivity test: How does the future cod catch change as a function of the consumption by minke whales etc.

Another issue is how the uncertainty in the whale parameters is reflected as increased uncertainty in future prediction of fish catches. This is reflected in how the standard error in predictions changes as a result of changes in standard errors of whale parameters. This issue can be thought of as a question of what knowledge is important in order to reduce prediction variability.

In terms of the state of knowledge and importance of knowledge, it is seen that knowledge of the depletion level and of whether or not the minke whales consumes cod are the main factors affecting the variability in the medium-term prediction of cod yield.

CONCLUSIONS AND DISCUSSION

Available data on the behavior and consumption of cetaceans off Iceland indicate that these animals include cod and capelin as a part of their diet (Sigurjónsson and Víkingsson, 1996). The present study has shown how this consumption can affect the results of predictions of future yields from the two fish stocks.

The point estimate of the effect of marine mammals on cod catches is a reduction by 35 thousand tonnes, or about 10% and similar results are obtained for the capelin catches. There is considerable uncertainty associated with these numbers, however. The major components of this uncertainty are the potential increase in the whale stocks from their current size, and the diet of these predators.

The uncertainty in the marine mammal parameters are seen to have a considerable effect towards increasing the uncertainty in future catch predictions for the fish catches. Thus, not only are future catches expected to become lower than if marine mammals are not included in the model, but the level of these catches also becomes more uncertain.

REFERENCES

Allen, K. R. 1980. *Conservation and management of whales.* Washington Sea Grant, Seattle, 110 pp.

Anon. 1991. Report of the ICES Multispecies Assessment Working Group. ICES C.M. 1991/Assess. <Boreal meeting>

Anon. 1994. Report of the ICES Multispecies Assessment Working Group. ICES C.M. 1994/Assess.

Anon. 1995a. Nytjastofnar sjávar og umhverfisþættir 1995. Aflahorfur fiskveiðiárið 1995/1996 (State of marine stocks and environmental conditions in Icelandic waters 1993, prospects for te quota year 1993/94), mimeo, Marine Research Institute, Reykjavík.

Anon. 1995b. Report of the North-Western Working Group. ICES, C.M. 1995/Assess.

Anon. 1995c. The ICES Advisory Committee on Fishery Management (ACFM). Management advice for 1996.

Anon. 1995d. Report of the ICES Multispecies Assessment Working Group. ICES C.M. 1995/Assess.

Bogstad, B., G. Lilly, S. Mehl, Ó. K. Pálsson, and G. Stefánsson. 1993. Cannibalism and year-class strength in Atlantic cod (Gadus morhua) in Arcto-boreal ecosystems Barents sea, Iceland and eastern Newfoundland. ICES symposium on cod and climate change No. 43

Bogstad, B., K. H. Hauge and O. Ultang. 1995. A multispecies model for fish a marine mammals in the Barents Sea. This symposium.

Katona, S.K. and J.A. Beard. 1990. Population size, migrations and substock structure of the humpback whale (*Megaptera novaeangliae*) in the western North Atlantic Ocean. *Rep. int. Whal. Commn* (special issue 12): 295-305.

Magnússon, K.G. and G. Stefánsson. 1988. A feedback strategy to regulate catches from a whale stock. *Rep. Int. Whal. Commn* (special issue 11): 171

Magnússon, K. G. and Ó. K. Pálsson. 1989. Trophic ecological relationships of Icelandic cod. Rapp. P.-v. Réun. Cons. int. Explor. Mer. 188:206-224.

Magnússon, K. G. and Ó. K. Pálsson. 1991. Predator-prey interactions of cod and capelin in Icelandic waters. ICES Mar. Sci. Symp., 193: 153-170.

Mitchell, E. 1975. Trophic relationships and competition for food in Northwest Atlantic whales. Proc. Can. Soc. Zool. Ann. Meet.: 123-33.

Pálsson, Ó. K. 1983. The feeding habits of demersal fish species in Icelandic waters. Rit Fiskideildar, 7(1): 1-60.

Pálsson, Ó. K. 1994. A review of the tropic interactions of cod stocks in the North Atlantic. Pp. 553-575 *in* J. Jakobsson *et al.* Cod and Climate Change. *ICES mar. Sci. Symp. 198*, 693 pp.

Pálsson, Ó. K. and G. Stefánsson. (eds.) 1995. Bormicon - a boreal migration and consumption model. MRI technical report.

Pope, J. and L. Woolner, 1981. A simple investigation into the effects of predation on recruitment to some North Sea fish stocks. ICES. C.M. 1981/G:14.

Sigurjónsson, J. 1995. On the life history and autecology of North Atlantic rorquals. Pp. 425-441 *in* A. Schytte-Blix, L. Wallöe and Ö. Ulltang (eds.) *Whales, seals, fish and man*, Elsevier Science B.V.

Sigurjónsson, J. and A. Galan. 1990. Information on stomach contents of minke whales in Icelandic waters. Paper SC/42/NHMi28 submitted to the Scientific Committee of the IWC, 1990 (unpubl.), 6 pp.

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

Sigurjónsson, J. and G. A Víkingsson. 1996. Estimation of food consumption by cetaceans in Icelandic and adjacent waters. Published in this volume.

Stefánsson, G. 1992. Notes on the stock-dynamics and assessments of the Icelandic cod. ICES C.M. 1992/G:71.

Stefánsson, G., U. Skúladóttir, and G. Pétursson. 1994a. Yhe use of a stock production type model in evaluating the offshore (Pandalus borealis) stock of North Icelandic waters, including the predation of northern shrimp by cod. ICES C.M. 1994/K:.

Stefánsson, G., F. M. Baldursson, Á. Daníelsson and K. Thorarinsson. 1994b. Utilisation of the Icelandic cod stock in a multispecies context. ICES. C. M. 1994/T:43

Stefánsson, G. and B. Æ Steinarsson. 1993. Um nýliðun þorsks ?Ægir. (in Icelandic).

Steinarsson, B. Æ. and G. Stefánsson, 1991. An attempt to explain cod growth variability. ICES C.M. 1991/G:42.

Vilhjálmsson, H. 1994. The Icelandic capelin stock-Capelin, *Mallotus villosus* (Muller) in the Iceland-Greenland-Jan Mayen area. *Rit Fiskideildar XIII*(1): 1-281.