

On the potential impact of harbour seal predation on the cod population in the eastern North Sea

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Abstract

Increasing Scandinavian harbour seal populations during the last decades coincide in time with the collapse of the cod fishery. Assumptions of a causal relationship have led to claims favouring re-introduction of seal hunting. Proposals for ‘adaptive management’ often assume that decimating seal populations will automatically favour the fishery. This argument presupposes seal predation to be sufficiently large to have a measurable impact on the fish population. The potential magnitude of the cod-seal interaction was analysed using data on harbour seal abundance, feeding habits and compiled information on cod life history and cod landing statistics. A size-structured life history matrix for the cod population was applied and the size-specific prey preferences of harbour seals were taken into account. Estimated seal predation was small compared to both the landings by the fishery, and to minimum estimates of the total cod population. Furthermore, since the size classes of cod targeted by seals have low reproductive values, the impact of seal predation on cod production will be further reduced. Our analyses suggest harbour seals have a negligible impact on the cod fishery.

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1. Introduction

Marine mammals changed status from constituting an important resource during the 18th and 19th centuries, to being considered as competitors to human fisheries in the 20th century (Clark, 1946). As a result, considerable efforts were put into long-term state-funded bounty programs, which led to the collapse of many local seal populations in Europe during the first half of the 20th century (Reijnders, 1994, 1995; Kokko et al., 1997; Harding and Härkönen, 1999). By 1970 only 5% of Baltic grey seals (*Halichoerus grypus*), 5%

of the Baltic ringed seals (*Phoca hispida*), and about 10% of the Kattegat-Skagerrak harbour seal (*Phoca vitulina*) populations remained compared to estimated pristine levels (Heide-Jørgensen and Härkönen, 1988; Harding and Härkönen, 1999). However, by the second half of the 20th century, public opinion concerning marine mammals changed, which led to complete protection of the seals in most European countries. As a result, the seal populations began to recover.

Today, the debate about the seals as competitors to the fishery has been rekindled. National authorities recommend ‘adaptive management’ of wildlife populations and advocate that conflicts between commercial interests and wildlife should be solved with hunting instead of economic compensation (Anonymous, 2002).

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Such ‘adaptive management plans’ may suggest that seal populations should be reduced to enhance fisheries. However, it is not clear under what circumstances seals could have measurable effects on fish populations (Harwood and Croxall, 1988; Mohn and Bowen, 1996; Fu et al., 2001). We argue that the expected efficiency of management regimes must be evaluated before implementation. In the following, we focus on the seal-fishery conflict in the Kattegat-Skagerrak, where increasing harbour seal populations coincide in time with the collapse of the cod (*Gadus morhua*) fishery.

As a result of the bounty campaign, the harbour seal population in the entire Kattegat-Skagerrak decreased from about 18,000 in the early 20th century to about 1500 in the late 1960s (Heide-Jørgensen and Härkönen, 1988). After protective measures had been implemented the population increased by about 12% per year over the period 1979–1987 (Heide-Jørgensen and Härkönen, 1988). The exponential increase was interrupted twice by Phocine Distemper Virus (PDV) epidemics, which caused mass mortalities of up to 70% of local populations in 1988 and 2002 (Dietz et al., 1989; Harding et al., 2002, 2003; Härkönen et al., 2002, 2006; Jensen et al., 2002). Immediately after the die-offs the harbour seal population resumed exponential growth and was estimated to number 11,700 individuals in 2004 (Härkönen et al., 1999, 2002, 2006).

The cod population in the Skagerrak and Kattegat was exposed to heavy fishing pressure during the latter half of the 20th century, resulting in severe depletion (Cook, 2002). In spite of major reductions in allowable harvests (Fiskeriverket, 1994–2004; data available at www.fiskeriverket.se), the population has not recovered. Although ICES has recommended a closure of the cod fishery in the North Atlantic area for the last three years (Fletcher, 2003), this has been ignored. A central question is how large an impact the growing harbour seal population has on the recovery of the cod population? The extreme stochastic variation in fish population recruitment and the complex marine food web makes modelling of cause-effect relationships in marine environments extremely difficult. Detailed, multi-species models will not necessarily produce meaningful results (Levin et al., 1997; Bundy, 2001). Similar to documented problems in meteorological forecasting, small variations in parameter values and assumptions have large effects, and thus complex model predictions only tend to be valid over very narrow time-frames.

We adopt a straightforward approach to illustrate the potential impact of harbour seal predation on the cod

fishery. First, we compare the cod biomass removed by the fishery and by seal predation. Statistics of the annual registered harvest of cod over the last 30 years are compared with the maximum possible cod biomass removed by seals during the same time period. Since the effect of predation and harvest on the cod population also depends on the age composition of removed cod, we also develop an age structured model approach. Thirdly, by implementing a stochastic population model for cod proposed by Bjørnstad et al. (1999), we illustrate how variability in cod recruitment could influence the relative importance of seal predation and fishery. Although we do not attempt to describe the true development in the complicated cod population dynamics, we do think that the multiple approaches we take provide realistic scenarios describing the relative importance of harbour seal predation in the recovery of the cod population as compared to the fishery.

2. Material and methods

The dynamics of the cod population were modelled under different human harvesting regimes, and levels of seal predation. Thus we need: (1) a population model for the cod, (2) a range of realistic human harvests, (3) size structure of the human catches, (4) the size and growth rate of the harbour seal population, (5) the overall consumption by seals, including prey size composition, (6) predation efficiency. Each of these aspects is treated below.

2.1. Population model for cod

The cod population was simulated using a Leslie matrix (Leslie, 1945, 1948). Fertility (F) and survival (P) are given for each age class of cod.

$$A = \begin{pmatrix} F_1 & F_2 & \dots & F_{a-1} & F_a \\ P_1 & 0 & \dots & 0 & 0 \\ 0 & P_2 & \dots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \dots & P_{a-1} & 0 \end{pmatrix} \quad (1)$$

The population development of cod is calculated as the population projection matrix (A) multiplied at time t by the population vector (v_t). The resulting age structured vector gives the population at the time $t+1$, etc. While studies on stock size and recruitment are available for the Baltic cod population (e.g. Solari et al., 1997; Cardinale and Arhthenius, 2000; MacKenzie et al., 2002), such basic data are scarce for cod at the Swedish

west coast. Therefore, studies from the nearby Norwegian Skagerrak coast (Bjørnstad et al., 1999; Stenseth et al., 1999) were used to parameterise the matrix model. Data from the Northwest Atlantic cod (NAFO zone 2J3KL) were also used in a few cases when supported by preliminary results from the Skagerrak area (Hutchings, 1999). Annual survival was set to 0.42 for individuals at age 1, 0.60 at age 2, 0.64 at age 3 and 0.51 for ages 4 to 10. The lower survival at the higher ages is due to higher costs associated with reproduction (Hutchings, 1999).

We followed established cod models that have density dependent stochastic survival for the recruitment of the first age class (e.g. Bjørnstad et al., 1999; Brooks, 2002):

$$Y_t = X_{t-1} e^{c+\beta \log X_{t-1}} e^{\gamma \log Y_{t-1}} \quad (2)$$

where Y_t (the number of individuals that survive to become one-year-old fish larvae) depends on the number of hatched eggs in the previous year (X_{t-1}) and how these young individuals survived the first year. The underlying, density-independent first-year survival is represented by the term e^c (where c is a constant <0). This density-independent survival is reduced by density dependence estimated as the population size of 0-year olds (X_{t-1}) multiplied by a constant β (<0). Further, survival up to age 1 is also reduced by cannibalism by the 1-y olds (Y_{t-1}) multiplied by a constant γ (<0) (Bjørnstad et al., 1999). The values of these constants were altered slightly from the values of Bjørnstad et al. (1999) to give a response to fishing pressure similar to the one observed in empirical data from our study region. (Without this alteration, the cod population would have such a high rate of increase that even the highest of historical fishery catches would pass unnoticed, which obviously is unrealistic.) The parameters used in Eq. (1) had mean values: $c = -0.58$, $\beta = -0.314$ and $\gamma = -0.09$, with variances of 20% for c and γ and 8% for β . Cod fecundity was calculated using:

$$m_x = \left(0.48 \left(\frac{w_x + 0.37}{1.45} \right) + 0.12 \right) * 10^6 \quad (3)$$

where m_x is the mean number of eggs produced by a female breeding at age x and w_x is the mean weight of females at the same age (Hutchings, 1999). The average weight in each age class was estimated using data from the Canadian east coast (NAFO fishing zone 2J3KL) (Lilly, 1997), which was similar to preliminary data for the Swedish West Coast from ICES (www.ices.dk, info@ices.dk). The proportions of mature individuals were estimated from empirical data from the Swedish

west coast (ICES: www.ices.dk, info@ices.dk). The initial cod population size was chosen such that it could easily withstand a lower fishing pressure, but responded to heavy fishing pressure (see below). All models were implemented in MATLAB (*The MathWorks, Inc, Version 6.5*).

2.2. Harvesting regimes

We explored the dynamics of the cod population for a range of different harvesting regimes. Values were chosen to mimic actual catches in the area during different periods. Each simulation of the model used a fixed harvesting quota throughout the 20-y simulation period. We used the quotas 70,000, 50,000, 40,000, 30,000 and 20,000 metric tons y^{-1} . 70,000 t represents the maximum level of catches (reflecting the average catches during 1976–1985), whereas 50,000 t reflects the total average catch during 1970–2001, 40,000 t is the average catches during 1986–2001, 30,000 t the minimum reported catch during 1970–2001. Data on the total catches of cod in the Skagerrak and Kattegat for 1973–2001 (Fig. 1) were based on official reports (ICES, 2002).

2.3. Size structure of human catches

The fishery was assumed to target age classes 3–10 with an age distribution similar to the age structure of the total population at each given time, thus including cod longer than about 35 cm in the catches (Martinez-Gamendia, 1998). To test the impact of size selection of human fishery, we studied how the population would respond if the cod harvest was directed towards the following age groups; 2–10, 3–10, 4–10, 5–10 or 3–8.

2.4. Harbour seal population

The harbour seal population growth was calculated using a deterministic Leslie matrix model that simulated the actual population growth during 1970–2001 (Heide-Jørgensen et al., 1992; Härkönen et al., 2002), with a population of about 2000 individuals at the beginning of the period. The population increased by 1.12 each year (survival 0.86 for age classes 1–4, 0.96 for classes 5–37 and fertility 0.45 for age classes 5–37). We simulated two scenarios: In the first, the population was reduced by 60% after 15 y (simulating the consequence of epizootics). In the second, the seal population was allowed to grow unhindered for the full 20-y period. Due to exponential growth, projections of these two models differ significantly. When the seal population is

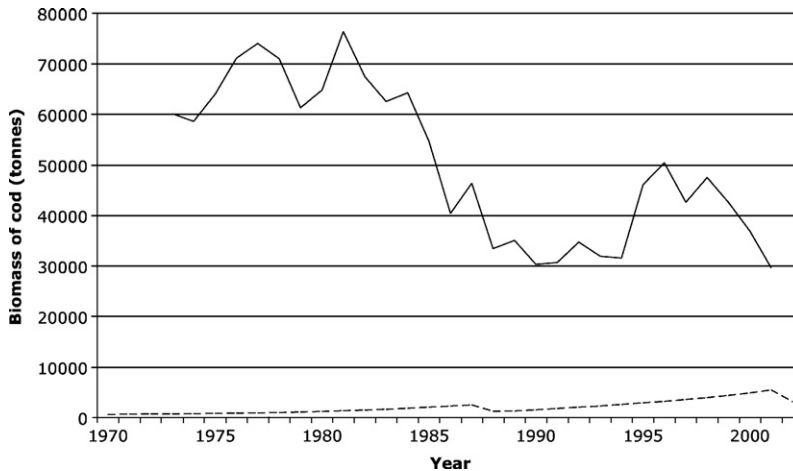


Fig. 1. Comparison between the biomass of reported landings of cod (black line) and the theoretical maximum consumption by harbour seals (dashed line). N.b. the comparison exaggerates relative consumption by harbour seals.

exposed to epizootics it reaches about 10,000 seals after 20 y, compared with 20,000 seals after 20 y in the model with unlimited growth. The true population size in 2005 was about 14,400 (Härkönen et al., 2006).

2.5. Cod consumption by seals

An average harbour seal consumes about 4 kg of fish a day (from 1.6 kg for pups, 3.4 kg in juvenile females, 3.8 in juvenile males, 5.5 in adult males to a maximum of 5.7 kg for adult females; Bjørge et al., 2002). The amount of cod in the diet was determined from the recovery of otoliths from harbour seal scats and the reconstruction of diet composition using otolith size - fish length/weight relationships (Härkönen, 1987; Härkönen unpubl.). From the diet reconstructions, cod

is estimated to represent approximately 17% of the diet by weight (Härkönen and Heide-Jørgensen, 1991; Berg et al., 2002). This represents about 287 kg cod $\text{ind}^{-1} \text{y}^{-1}$. In the model, we assumed that young seals (1–4 y) consumed 252 kg cod, while older seals (5+y) consumed 326 kg cod $\text{ind}^{-1} \text{y}^{-1}$.

The size of cod consumed by harbour seal was determined from previous work in the area (Härkönen, 1987; Härkönen unpubl. data) (Fig. 2). Harbour seals feed mainly on fish 10–30 cm long (Fig. 2). Therefore, mortality caused by harbour seal predation was only added to cod of ages 1–3, since they are usually within this length span (Martínez-Gamendia, 1998; Dutil et al., 1999). Twenty percent of the total seal-related mortality was assumed to target cod, 20% at age 1 and 40% at ages 2 and 3, respectively, as based on weight

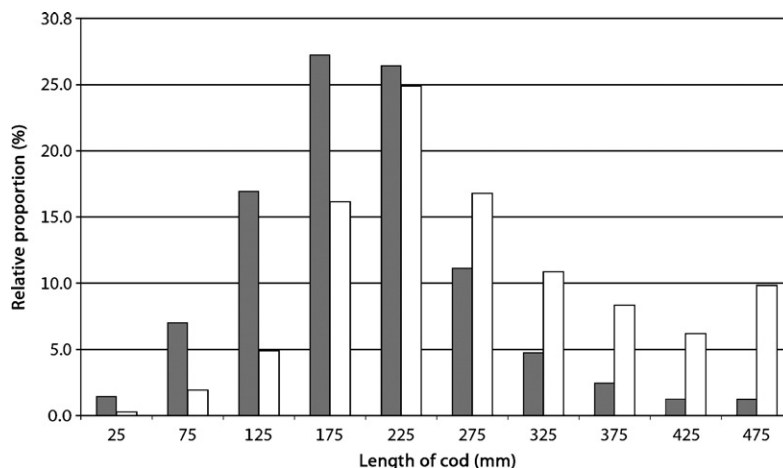


Fig. 2. The relative distribution of cod body length in the prey caught by harbour seal. The grey bars represent the frequency of the specific length class, while a white bar represents the frequency in weight of the total feeding mass. N=484 (Data from Härkönen unpubl.).

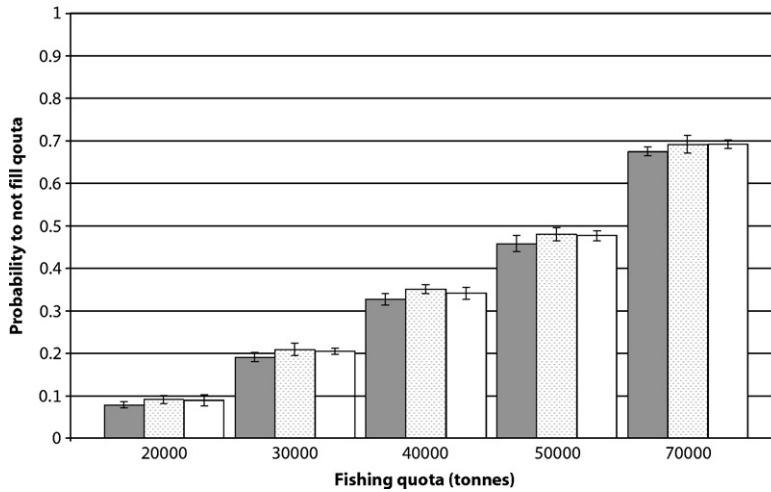


Fig. 3. The probability of not reaching full fishery quotas every year during a 20-y simulation period (y-axis) is given for some different levels of annual human catches (x-axis). Dark grey bars represent the scenario where no seal predation is included in the model. The light grey bars give the risk not to fill quotas when seal predation is added and the seals are exposed to epizootics. White bars illustrate the risk when the seal population grows exponentially for 20 years. Each bar gives the average value of 10,000 simulations.

proportions. So for each year the total amount of cod taken by seals is calculated as the number of seals times the average cod consumption (287 kg). Out of this mass, 20% was taken from cod of class 1 and 40% from each of the classes 2 and 3.

2.6. Predation efficiency

The predation is calculated with a type III functional response, described as

$$P = \frac{kV^2}{D^2 + V^2} \quad (4)$$

where the number of prey caught by predator (P) is estimated from, maximum consumption per predator (k), prey population size (V), and the half-saturation constant (D) (Gotelli, 1998). The half saturation point determines the response of the predator to low prey abundance. A high half saturation point gives a less efficient predator. The half saturation point is the size of the prey population (numbers of prey) where the efficiency of the predator is reduced by half. In the models to follow, the half saturation point is set to a value representing two times the theoretical maximum consumption of cod by the seal population during that year.

The cod population model was run for 20-year periods using different harvesting regimes and seal predation scenarios. Because the cod model is highly stochastic, the mean cod population size after a 20-year

simulation was not used as a test parameter in comparing different scenarios. Instead, we estimated the probability that there was enough cod for the fisheries to fill >95% of their quotas during all years in a 20-y time series. Each combination of parameters was simulated for 10,000 twenty-year periods. The result of each individual run was either 1 (there is not enough cod for the fisheries to fill their quota in all 20 years) or 0 (the quota is filled during all 20 years in the period). The total average gives the probability for not filling the quota (Fig. 3). For each of the five different fishery quotas, three different seal scenarios were explored: (1) without harbour seals, (2) with a harbour seal population exposed to an epizootic every 15th year, and (3) with an exponentially growing harbour seal population.

3. Results

A comparison between fishery landings statistics and theoretical maximum cod consumption by seals (without adjusting estimated seal predation to the declining availability of cod at low cod population sizes) shows the gross scale of cod biomass removal since 1970 (Fig. 1). However, the simple comparison fails to consider the age structure of the harvested cod. We therefore parameterised an age-structured cod model and translated harvested biomass into numbers of individuals at different ages. In the following all results refer to this age-structured approach. Despite high stochasticity, the model clearly demonstrates that higher fishing quotas gradually increase the risk for declines in the cod

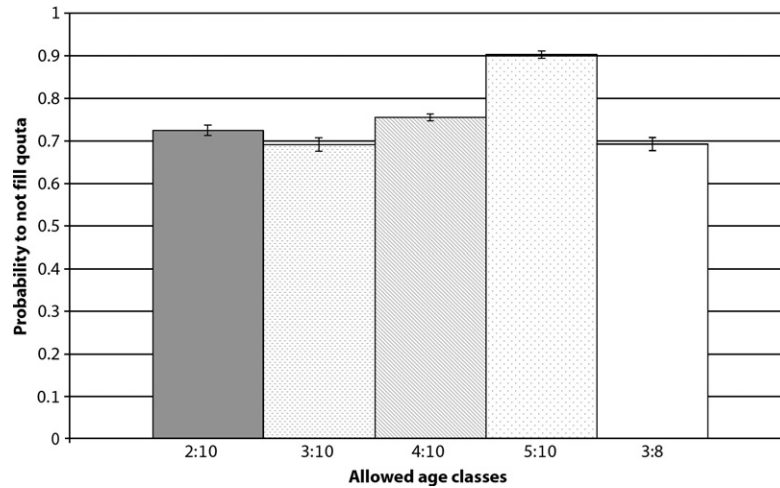


Fig. 4. The probability of the fishery not filling the quota every year during a 20-y period depends on the age composition of the catches. The simulated age compositions of the harvest were: 2–10 y, 3–10 y, 4–10 y, 5–10 y and 3–8 y. In all five scenarios shown here the fishing quota was set to 70,000 metric tons.

population (Fig. 3). The probability of not filling the fishing quota increases from about 10% at a harvest of 20,000 t, to 70% at harvest of 70,000 t in the model simulations. When taking harbour seal predation into account, the risk for declines in the model cod population is slightly elevated, but not significantly in any model projection (Fig. 3). In all five harvesting regimes, the risk of not reaching the harvesting quota is increased by 2% in the presence of seals. Since this difference is independent of the size of the human harvest (Fig. 3), it is likely to be an effect of stochasticity and not a direct influence of seals on the cod population.

The simulations that included periodic mass mortality of harbour seals did not produce significantly different results. Due to stochasticity, the simulations including mass mortality (with fewer seals) even incidentally affected the fishery more than the scenario with a seal population with exponential growth. The differences among the different scenarios are in general extremely small and the model must be run a vast number of times to be able to detect such minor differences.

The impacts of the size selective fishery and of size selective seal predation on the cod population were also examined. The modelling presented above was repeated, but assumed that the harvest targeted different age classes (i.e. keeping the cod catch biomass constant only varying the age and number of individuals in the catch). We used the scenario with a quota of 70,000 t. The 70% risk of not filling the quota with the present age structure of the fishery (3–10-y-old cod), increased further using other age-structure combinations. Decreasing

the minimum size from 3-y olds to include all ages between 2 and 10 increased the risk above 70%. However, increasing the target age classes to ≥ 4 -year-olds would be detrimental. A fishing regime targeting age classes 5 to 10 leads to a substantial risk of 90% for a non-sustainable fishery (Fig. 4). Since older individuals have a vast reproductive capacity, we tried a hypothetical scenario where the oldest fish could be protected. However, as a consequence of the size-number trade-off, harvesting age classes 3–8 did not improve cod population performance compared to the present age structure taken by the fishery.

4. Discussion

The magnitude of seal-fishery interactions was investigated in terms of relative influence on cod population dynamics. A comparison of the cod biomass removed by the fishery with the maximum theoretical biomass that could be consumed by seals shows that fishery removals exceed seal predation removals by several orders of magnitude (over 80 times, Fig. 1). This comparison assumed that cod remained as a fixed proportion in the seal diet. However, this is unlikely. Instead we would expect that the proportion of cod in the diet would decline as the cod abundance declines.

We also developed a size-structured stochastic model for the cod and allowed seal predation to vary with cod availability. The addition of seal predation to different fishery catch levels had only a very slight impact on modelled commercial fisheries catches. The slight effect resulted from stochastic changes in the cod population

rather than as an effect of a particular harvesting scheme or level of seal predation. Overall, the difference in cod population size, with or without harbour seals, is so small that it would be impossible to detect in nature.

4.1. Size composition of the cod population

Small cod have a lower reproductive value than larger individuals. The removal of a small individual will have a lower impact on future population growth than removal of an individual with high reproductive value (Caswell, 2001). On the other hand, very large numbers of individuals would be required to fill fishery quotas with small cod only. Investigating this balance, we simulated different age structures of cod in the harvest and estimated the risk for population declines large enough that the fisheries would not be able to fill their quota. The present fishery (of cod >35 cm: about 3–10 y) was found to be less harmful to future population growth than a fishery including either larger (4–10 or 5–10 y) or smaller minimum sizes (2–10 y) would be.

Earlier studies on harbour seals (Härkönen and Heide-Jørgensen, 1991) also suggested that seals have a small impact on cod populations. Fu et al. (2001) found that grey seals could have contributed to the slow recovery after the collapse of cod in the eastern Scotian Shelf in Canada, although they assumed seal predation to be independent of cod population size, which seems unrealistic. However, grey seals consume more fish per individual and the grey seal population on the eastern Scotian Shelf is about 5 times larger than the North East Atlantic stock of harbour seals (Mohn and Bowen, 1996), and could therefore have a larger impact on the cod stock.

4.2. Model assumptions

There are three main assumptions in the present study: (1) panmixia of the cod population, (2) the assumed function of the predation response, (3) and the exclusion of other ecosystem interactions.

The cod population was treated as a single panmictic unit, while in reality there are many local populations along the Skagerrak coast and in the North Sea, which affects the dynamics of the total coastal population (Knutsen et al., 2004). Taking this into account would make the impact of seals on cod even more difficult to detect globally while it could be more significant at specific locations, with small local cod stocks. The current model can be transformed into a metapopulation model in order to account for this.

The second assumption concerns the predation response and efficiency of the harbour seal. The harbour seal in the region feeds on more than 30 species of which six contribute substantially to the diet (Härkönen and Heide-Jørgensen, 1991). Large local and seasonal variation in prey composition and switches between main prey species show that the harbour seal is opportunistic (Härkönen and Heide-Jørgensen, 1991; Hall et al., 1998; Wilson et al., 2002). Thus it is well motivated to assume that the harbour seal has a type III predator response (with no or very low predation at low prey population) and a high half saturation point (low efficiency at low prey population sizes), although the exact position of the half saturation point was chosen arbitrarily and could be different. However, since the seal predation is so small compared to the fisheries and the stochastic variation, the impact of a more exact half saturation point on the model outcome would be swamped, and would not affect the conclusion of the present study.

We have not considered ecosystem interactions, and as previously mentioned, cod is only one of more than 30 species in the diet of harbour seals (Härkönen and Heide-Jørgensen, 1991), of which at least six species have a significant role in the diet. Food web dynamics can influence the impact of harbour seals on the cod population indirectly in a variety of ways. For example, harbour seals could even indirectly enhance cod survival by feeding on cod competitors and predators.

5. Summary

We have analysed effects of harbour seal predation on a rather small cod population exposed to heavy human harvest. The impact from harbour seal predation was found to be negligible, despite the fact that we used minimum estimates of human harvest, and exaggerated seal predation. It seems safe to conclude that the negative effects harbour seals have on the fisheries are limited to local damage of nets and other equipment. The predation pressure from harbour seals is too small to affect the cod population growth rate, and independent stochastic factors together with human harvest have a much larger influence.

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