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Assessing the potential impact of salmon fisheries management on the conservation status of harbour seals (*Phoca vitulina*) in north-east Scotland

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Abstract

Conservation efforts are often constrained by uncertainty over the factors driving declines in marine mammal populations. In Scotland, there is concern over the potential impact of unrecorded shooting of seals, particularly where this occurs near Special Areas of Conservation. Here, we show that the abundance of harbour seals *Phoca vitulina* in the Moray Firth, north-east Scotland, declined by 2–5% per annum between 1993 and 2004. Records from local salmon fisheries and aquaculture sites indicated that 66–327 harbour seals were shot each year between 1994 and 2002. Matrix models and estimates of potential biological removal indicate that this level of shooting is sufficient to explain observed declines. Nevertheless, uncertainty over the number and identity of seals shot means that other factors such as changes in food availability may be contributing. Recent conservation measures markedly reduced the recorded levels of shooting in 2003 and 2004. In 2005, a coordinated management plan was developed to protect salmon fisheries interests while minimizing impacts on local seal populations. Comprehensive monitoring of future population trends and improved regulation of culls are now required to provide more robust assessments of the impact of human persecution on harbour seal populations in the Moray Firth and in other parts of the UK.

Introduction

Uncertainty over the factors driving population change often constrain conservation efforts to protect declining marine mammals (Springer *et al*., 2003; McMahon *et al*., 2005). Some marine predators are exposed to levels of exploitation or by-catch that threaten population viability (Heinsohn *et al*., 2004; Lewison *et al*., 2004), but for many populations the relative influence of predation, exploitation and changes in food availability on conservation status is unknown.

Concern over the impact of seals on UK fisheries led to widespread culls over the last century (Bonner, 1989). Attention has focused on rapidly increasing grey seal *Halichoerus grypus* populations, but harbour seals *Phoca vitulina* are also culled locally where they interact with coastal salmon fisheries (Rae, 1968). Under the 1970 Conservation of Seals Act, shooting of either species is licensed during their respective breeding seasons (Bonner, 1989). At other times, seals can be legally shot, and there is no requirement to report animals killed. Hence statutory information on the number of UK seals shot each year is unavailable.

Continued increases in UK grey seal populations indicate that exploitation and persecution do not pose a major threat (Hammond, 2001). In contrast, the status of UK harbour seals is less clear, and it is not known whether current levels of shooting affect population viability. Studies across Europe and North America indicate that harbour seal populations show marked regional variations in population trends. Populations that were dramatically reduced by the 1988 phocine distemper virus (PDV) outbreak recovered rapidly, before a subsequent outbreak of PDV in 2002 (Härkönen *et al*., 2006). In contrast, other populations have shown marked reductions in abundance over similar time periods (Thompson, Van Parijs & Kovacs, 2001; Bowen *et al*., 2003; Small, Pendleton & Pitcher, 2003).

Over 85% of UK harbour seals are found in Scotland (Sea Mammal Research Unit, unpubl. data), where concern over their impact on salmon fisheries has been greatest. Mortality during 1988 and 2002 PDV outbreaks appeared to be low for these populations (Härkönen *et al*., 2006), but published information on recent trends in abundance is available for only one local area (Thompson *et al*., 2001). The Moray Firth supports a population of *c*. 1600 harbour seals, the largest on the east coast of Scotland. Here, interannual changes in food availability have influenced diet, behaviour (Thompson *et al*., 1996*b*) and various measures of individual condition (Thompson, Corpe &

Reid, 1998*a*), highlighting the possibility that changes in resource availability have influenced population dynamics. At the same time, there is evidence that substantial numbers of seals in this area have been shot to reduce interactions with salmonid fisheries. However, the unregulated nature of these actions has constrained efforts to estimate the impact that they may have on the dynamics of this population.

In response to the EU Habitats and Birds Directive (Baxter, 2001), the UK has designated 11 Special Areas of Conservation (SACs) to protect harbour seal populations, including the Dornoch Firth within the Moray Firth. Many seal SACs are also in the vicinity of commercial fisheries and aquaculture sites. Consequently, the effective management of SACs and local fisheries interactions requires a better understanding of recent seal population trends, and the potential impact of human exploitation on their conservation status. We examine recent trends of harbour seals in the inner Moray Firth using an 18-year time series of annual surveys. We also use estimates of seals shot by salmon fisheries and fish farms, matrix population models and sustainability indices to assess the possible role of exploitation in recent changes in abundance.

Methods

Study area

Moray Firth harbour seals are found breeding on scattered sandbanks within three estuaries: the Beauly, Cromarty and Dornoch Firths (Thompson *et al*., 1996*a*; Fig. 1). The Dornoch Firth has been designated as a SAC for harbour seals and Loch Fleet, <10 km to the north, has also been used for breeding in recent years. Non-breeding seals are also found at the mouth of the Inverness Firth. Smaller groups of harbour seals occur along the outer coasts of the Moray Firth (Fig. 1). The nearest major breeding sites are found in Orkney, 130 km to the north, and the Tay estuary, 325 km to the south. Previous radio-tracking (e.g. Thompson *et al*., 1998*b*) and marking (Härkönen & Harding, 2001) studies on this and other harbour seal populations indicate that exchange between breeding areas this far apart is rare.

Inner Moray Firth haul-out sites were grouped on the basis of geographic distance between sites. The Dornoch Firth and Loch Fleet formed one group in the north, with those in the Cromarty, Beauly and Inverness Firths forming a southern group (Fig. 1). Within each group, sites were all <25 km of each other, whereas the minimum distance between groups was 40 km. Quantitative estimates of interchange within and between these two groups of sites are not available, but earlier studies found no movement of marked individuals between these two groups in summer (Thompson *et al*., 1996*a*). This should therefore provide an ecologically appropriate method for sub-dividing the population during the summer breeding season and moult. From a management perspective, it allows comparison of abundance trends within a northern group that approximates to the Dornoch Firth SAC, and a southern group that includes the other main breeding units within the inner Moray Firth.

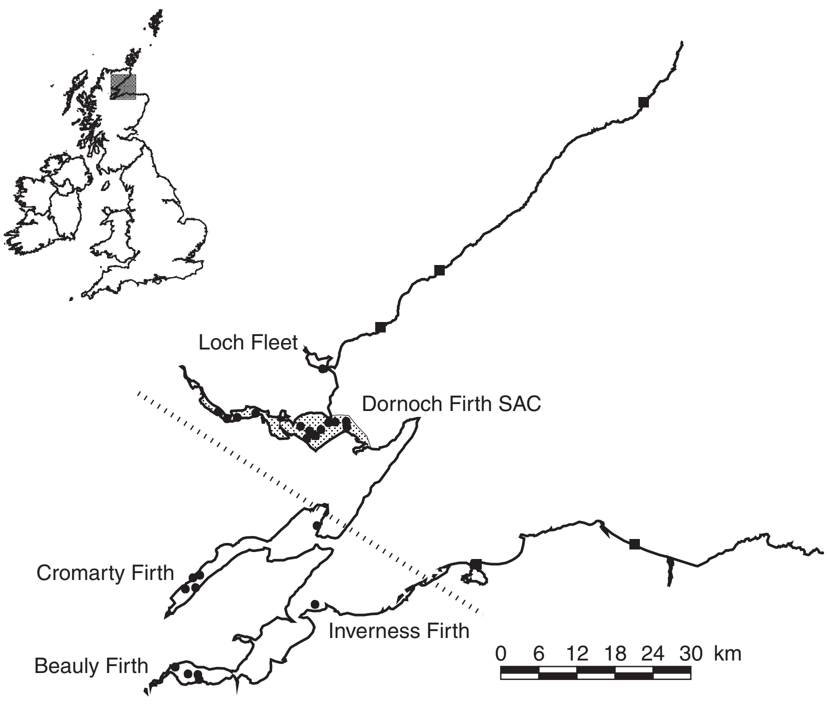

Figure 1 A map of Moray Firth showing the location of haul-out sites in the main inner firth study area (●), and the location of other haul-out sites along the outer Moray Firth coast (■). The dashed line separates haul-out sites in the northern and southern areas, with the former including the Dornoch Firth SAC (shaded). SAC, Special Areas of Conservation.

Abundance trends

Between 1987 and 2004, abundance trends in the inner Moray Firth were estimated from annual land-based counts during both the pupping season (15 June–15 July) and the moult (1–31 August). Each year, seals were counted from shore at distances of 0.5–4.0 km using a 30×70 telescope. Counts were all ± 2 h of low tide, in good visibility, following methodology described in Thompson *et al.* (1997*b*). We assume that there is no interannual variability in the frequency with which individual seals haul out during each of these survey periods, and that mean values for the two to five repeat counts made during each survey period therefore provide a suitable index of abundance [see Thompson *et al.* (2001) for a further discussion on this point]. During the pupping season, pups of the year were excluded from this estimate. During the moult, all animals were counted. Linear regression analysis was used to estimate the significance of trends and rates of change. Analyses were carried out using SYSTAT.

In August 1997 and 2002, helicopter surveys were also carried out along the entire Moray Firth coast as part of national monitoring of UK harbour seals by the NERC Sea Mammal Research Unit (Hammond, 2001). These data provided information on the relative importance of sites within the more intensively studied inner Moray Firth.

Estimates of seals shot

For the period 1994–2004 estimates of the number of seals shot were made available to J. R. A. B. following a request from the Spey District Fishery Board to all licensed salmon fisheries and aquaculture sites in the Moray Firth region. In some years, a bounty scheme was operated in parts of the Moray Firth, resulting in more accurate counts and carcass identification. Data were grouped into numbers of harbour, grey and unidentified seals shot annually.

We used these data to provide three different estimates of the number of harbour seals killed in each year. First, our most probable estimate assumed that the proportion of grey seals to harbour seals in the unidentified sample was the same as that in the sample of seals identified to species. Second, our maximum estimate assumed that all unidentified seals were harbour seals. Finally, our minimum estimate assumed that all unidentified seals were grey seals.

Assessing the impact of culling on population trends

We assessed the potential impact of culling on population trends using two methods. First, we used Leslie matrix models (Leslie, 1945; Caswell, 1989) to explore historical and future population trends under different culling regimes, and second, we used the concept of potential biological removal (PBR; Wade, 1998).

The only comprehensive life-history data for European harbour seals result from analyses of seals that died in the Kattegat and Skaggerak during the 1988 PDV epizootic (Harkonen & Heide-Jorgensen, 1990; Heide-Jorgensen & Harkonen, 1992). Using these data, we constructed a stage-specific model for six life stages (Fig. 2). The ages of seals in each stage class, together with their respective fertility and survival probabilities, are presented in Table 1. A population projection matrix [Eqn. (1)] was produced for a fixed stage duration two-sex model, taking account of the probability of survival in each stage (P_i), the per capita fertility of stage i (F_i) and the probability of moving into the next stage (G_i), where $\sigma_i = P$ (survival of an individual in stage i) and $\gamma_i = P$ (growth from i to $i+1$/survival). Thus, $G_i = \sigma_i \gamma_I$ and $P_i = \sigma_i(1-\gamma_i)$. Stage durations were calculated using

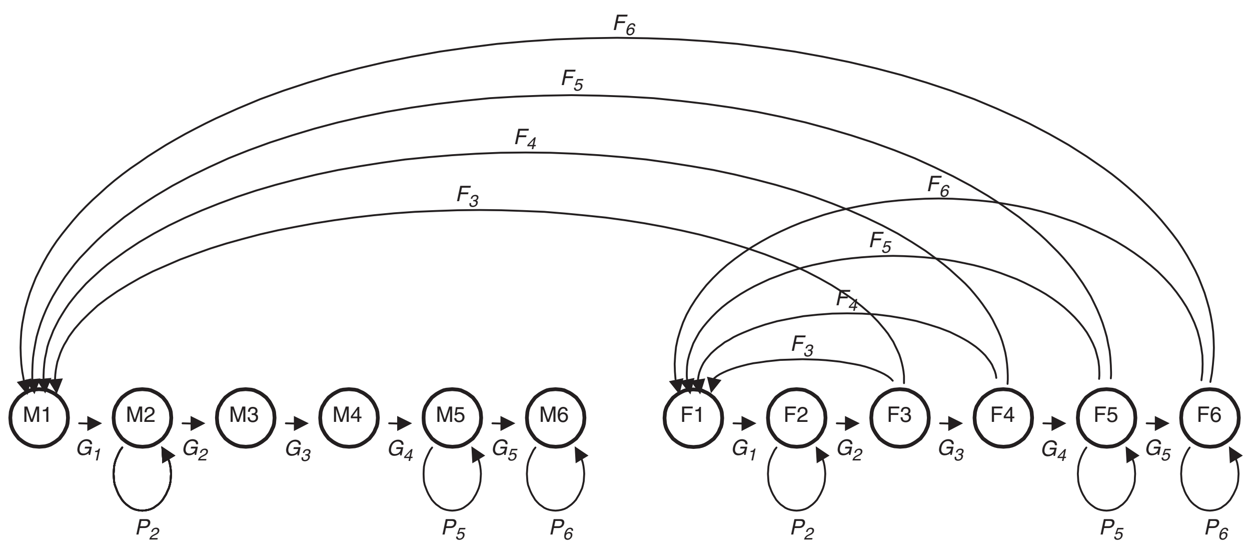

Figure 2 Life-cycle graph for the stage-classified two sex harbour seal *Phoca vitulina* model. M1–M6 and F1–F6 represent the six stage classes for males and females, respectively. The values for F_i represent the per capita fertility of stage class i, G_i the probability of survival in each stage and P_i the probability of growing into the next stage.

methods given by Caswell (1989):

$$A = \begin{pmatrix} P_1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & F_3 & F_4 & F_5 & F_6 \\ G_1 & P_2 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & G_2 & P_3 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & G_3 & P_4 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & G_4 & P_5 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & G_5 & P_6 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & P_1 & 0 & F_3 & F_4 & F_5 & F_6 \\ 0 & 0 & 0 & 0 & 0 & 0 & G_1 & P_2 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & G_2 & P_3 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & G_3 & P_4 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & G_4 & P_5 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & G_5 & P_6 \end{pmatrix} \quad (1)$$

Using the life-history data from Table 1, the following population projection matrix (A) was calculated as the basis for modelling projections:

$$A = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.17 & 0.33 & 0.48 & 0.35 \\ 0.75 & 0.63 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.28 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.91 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.91 & 0.9 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.01 & 0.91 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.17 & 0.33 & 0.48 & 0.35 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0.75 & 0.63 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.28 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.91 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.95 & 0.92 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.03 & 0.95 \end{pmatrix}$$

We assumed that starting populations had a stable distribution, estimated by projecting the population matrix for 100 years. Initial population size was estimated by integrating data on the mean number of seals counted during 1990 with telemetric data on the probability that seals were ashore during the survey period (Thompson *et al.*, 1997*b*). Mean counts for each year were also corrected using telemetric data for comparison with the models' projections of total abundance. Initially, the projected growth rate between 1990 and 2004 was examined using the population projection matrix A. We then assessed the impact of culling different numbers of seals on population growth. Two culling scenarios were investigated to explore historical trends. The first allowed for interannual variation by drawing a random number between the minimum and the maximum estimate of seals shot in that year (see Results). The second was based on consistent levels of removal across the whole time period. The number shot in each year was randomly drawn from within the overall range of annual estimates for the number of seals shot. Within this scenario, shooting was simulated at three different levels: (1) a *conservative* level set to vary randomly between the lowest minimum estimate and the highest minimum estimate of seals shot; (2) a more *extreme* level with shooting set to vary randomly between the lowest maximum and highest maximum estimates of seals shot; and (3) a broad, and more *uncertain*, simulation with the estimate set to vary between the lowest minimum and highest maximum of seals shot. Each simulation was repeated for 1000 iterations. Finally, we modelled potential future population trends given the annual removal of 60 individuals, the maximum allowed by the Scottish Executive under a recent management plan for Moray Firth seals (Butler, 2005). In all simulations, the numbers removed from each stage class were assumed to be directly proportional to the number of seals present in that class. Model simulations were carried out using MATLAB 6.1 (The MathWorks Inc.).

Table 1 Age class and sex-specific per capita fertility and survival probabilities (after Harkonen & Heide-Jorgensen, 1990; Heide-Jorgensen & Harkonen, 1992)

Age class (years)	0	1–3	4	5	6–26	27–37
Stage	1	2	3	4	5	6
Females	0	0	0.17	0.33	0.48	0.35
	0.75	0	0	0	0	0
	0	0.91	0	0	0	0
	0	0	0.91	0	0	0
	0	0	0	0.95	0	0
	0	0	0	0	0.95	0.95
Males	0	0	0.17	0.33	0.48	0.35
	0.75	0	0	0	0	0
	0	0.91	0	0	0	0
	0	0	0.91	0	0	0
	0	0	0	0.91	0	0
	0	0	0	0	0.91	0.91

Per capita fertility (F_i) is given across the row for each sex and stage, and probabilities of survival (P_i) are given on the sub-diagonal.

PBR has increasingly been used to assess marine mammal–fisheries interactions (Read & Wade, 2000; Marsh *et al.*, 2004), and simulations indicate that it is the most robust and precautionary of sustainability indices currently used by conservation managers (Milner-Gulland & Akcakaya, 2001). Estimates of PBR [Eqn. (2)] are based on a knowledge of population size and maximum rates of increase, and provide estimates of levels of human-caused mortality that might lead to population declines:

$$\mathrm{PBR} = n_{\mathrm{MIN}} \times R_{\mathrm{MAX}} \times F_R/2 \quad (2)$$

where n_{MIN} is a minimum population estimate (usually the lower 20th percentile of the distribution of the population estimate), R_{MAX} is the maximum rate of increase of the population (typically set at 0.12 for pinnipeds; Wade, 1998) and F_{R} is a correction factor that is usually set to 1 unless populations are particularly at risk. Thus, the PBR is designed to ensure that there is a low probability that a particular population will decline. We used data on the abundance of Moray Firth seals (Thompson *et al.*, 1997*b*) to estimate the PBR for this population, and compared this with estimates of the number of seals that had been shot in the area.

Results

Abundance trends

Between 1989 and 1993 there was a significant increase in the mean number of seals hauled out in the inner Moray Firth (Fig. 3). This trend was apparent during both the pupping season (least-squares linear regression: $F_{1,3} = 25.3$, $r^2 = 0.89$, $P < 0.05$) and the moult ($F_{1,3} = 17.01$, $r^2 = 0.85$, $P < 0.05$), representing rates of increase of 0.075 and 0.11, respectively. However, counts made between 1993 and 2004 indicate that there has since been a significant decline in the mean number of seals hauled out during both the pupping season ($F_{1,10} = 13.84$, $r^2 = 0.58$, $P < 0.01$) and the moult ($F_{1,9} = 31.69$, $r^2 = 0.77$, $P < 0.001$). Over the period 1993 and 2004, these counts declined at rates of −0.024 and −0.043 in the pupping season and moult, respectively.

A closer inspection of counts from different sub-regions within the inner Moray Firth suggests that much of the recent decline in abundance has been driven by changes occurring within the Dornoch Firth (Fig. 4). Here, the decreasing trend in abundance between 1993 and 2004 remained significant for counts made in both the pupping season ($F_{1,10} = 14.78$, $r^2 = 0.60$, $P < 0.01$) and the moult ($F_{1,9} = 32.84$, $r^2 = 0.78$, $P < 0.01$). Estimated rates of decline in this area were −0.04 (pupping) and −0.07 (moult). In contrast, there was no significant trend in the counts made in the southern area over this period (pupping season: $F_{1,10} = 3.62$, $r^2 = 0.27$, $P = 0.09$; moult: $F_{1,10} = 0.77$, $r^2 = 0.07$, $P = 0.4$).

In 1997 and 2004, aerial surveys of the outer Moray Firth recorded groups of moulting harbour seals on northern and southern coasts. At this time of year, our inner Moray Firth study area contained an estimated 79% of Moray Firth seals in 1997 and 69% of seals in 2002 (Table 2).

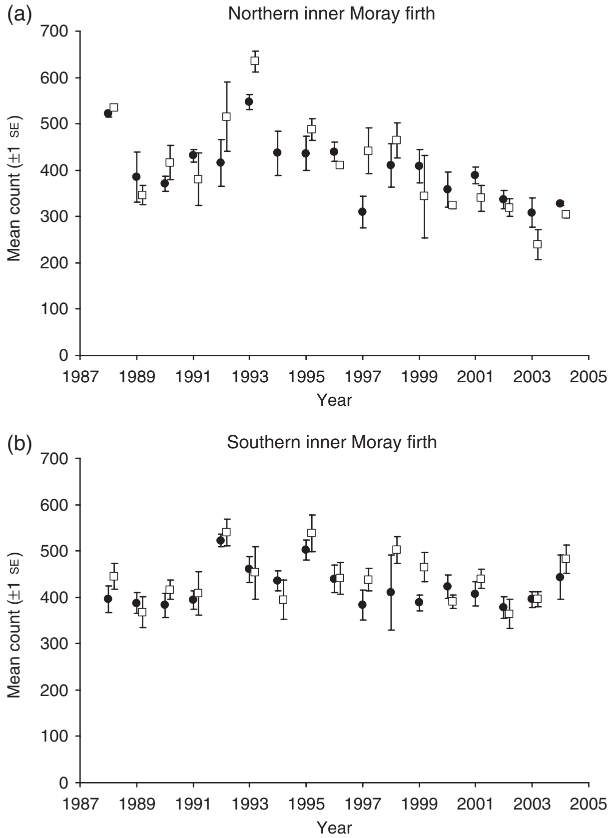

Figure 4 Mean counts (±1 SE) of the number of seals hauled out in each of the two sub-areas within the inner Moray Firth: (a) the Dornoch Firth and Loch Fleet in the northern part of the inner Moray Firth and (b) the Beauly, Cromarty and Inverness Firths in the southern part of the study area. Both time series include mean counts for both the pupping season (●) and the moult (□).

Estimates of seals shot

Estimates of the total number of seals shot each year ranged from 255 to 425 during 1994–2002, but fell to 56 in 2003 and 65 in 2004 (Table 3). The proportion of shot seals that were identified varied considerably from year to year, with the minimum estimate of the annual number of harbour seals shot between 1994 and 2002 varying from 66 to 192. Our most probable estimate of the number of harbour seals shot in 1994–2002 ranged between 124 and 231 (mean = 160, SD = 35), and the maximum estimate ranged between 161 and 327 (mean = 213, SD = 57).

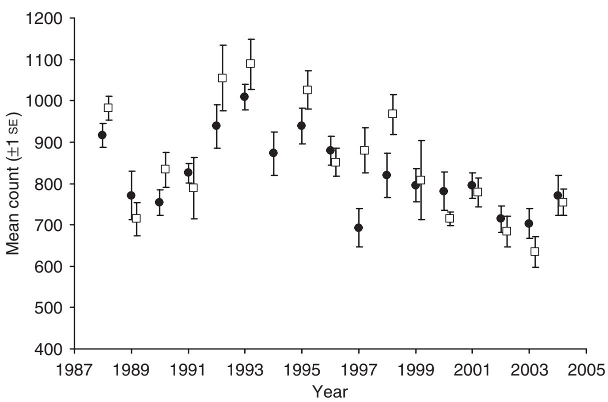

Figure 3 Mean counts (±1 SE) of the number of seals hauled out in the inner Moray Firth study area during the pupping season (●15 June–15 July) and the moult (□1–31 August).

Assessing the impact of culling on population trends

Model projections for population growth, together with corrected observed counts, are shown in Fig. 5. Between 1990 and 1993, the average growth rates are similar (predicted $\lambda = 1.1049$; observed = 1.0705). However, between 1993 and 2004, the population declined with a λ of 0.9703.

Figure 6a shows the projection using year-specific estimates of the number of seals shot, but observed and predicted growth rates were more comparable when the number of seals shot each year was drawn from the full range of estimates (Fig. 6b). The conservative estimate of cull levels (varying between the upper and lower estimates for the minimum number of seals shot) gave a λ of 1.0487 post-1993. The more extreme cull levels, which varied between the upper and lower bounds for maximum estimates of seals shot, gave a λ of 0.9422. The more uncertain cull levels, between the lowest minimum and highest maximum estimates, gave a λ of 1.0006. Simulating the culling of 60 seals, as permitted under the Scottish Executive management plan, resulted in a predicted λ of 1.07 during 2005–2009 (Fig. 7).

The estimated PBR for 1993, when a peak of 1653 harbour seals were recorded in the inner Moray Firth, was 79 individuals. Given that wider scale aerial surveys indicated that this core study area contained 69–79% of the Moray Firth population, the PBR for the whole population is *c*. 100–114. The most recent abundance estimate was 1265 in 2004, when the PBR for the inner Moray Firth was estimated to be 59, and that for the whole Moray Firth was 75–86.

Table 2 Haul-out counts in the main inner firth study area (see Fig. 1) in relation to abundance within the whole Moray Firth area

	1997			2002		
	AU	SMRU	Mean	AU	SMRU	Mean
Inner Firth sites						
Inverness Firth	202 (3)	234	209	82 (4)	110	87
Beauly Firth	163 (3)	219	177	175 (4)	66	153
Cromarty Firth	65 (3)	95	72	108 (4)	42	94
Dornoch Firth	407 (2)	593	469	265 (2)	220	250
Loch Fleet	35 (2)	27	32	55 (2)	62	57
Outer Moray Firth sites						
Findhorn	–	46	46	–	144	144
Loch Fleet to Dunbeath	–	214	214	–	145	145
Total			1219			930
% of animals in Inner Firths			79%			69%

Data are from those years when land-based counts were made by Aberdeen University (AU) and complete surveys were also conducted by the Sea Mammal Research Unit (SMRU). Where more than one count was made at each site during the survey area, the mean value is presented, with the sample size in parentheses.

Discussion

Abundance trends

Moray Firth harbour seals suffered relatively low mortality during the 1988 PDV outbreak (Härkönen *et al*., 2006). Our data show that, like other European populations, numbers initially increased. However, abundance in the Moray Firth peaked in 1993 and subsequently declined at around 2–5% per annum (Fig. 3). This post-1993 decline was driven largely by changes in the northern part of the study area, which includes the Dornoch Firth SAC (Fig. 4). Here, the decline was estimated to be 4–7% per annum, in marked contrast to studies of harbour seal populations outside Scotland. In the southern North Sea (Reijnders *et al*., 1997; Thompson, Lonergan & Duck, 2005) and the Kattegat and Skaggerak (Reijnders *et al*., 1997; Harkonen, Harding & Heide-Jorgensen, 2002), seal abundance increased steadily until the 2002 PDV outbreak led to mortality of up to 66% of these regional populations (Härkönen *et al*., 2006).

Observed declines in the inner Moray Firth could result from emigration or local changes in fecundity and survival. Harbour seals are also found at sites along the outer coasts of the Moray Firth, and earlier radio-tracking studies have shown that individuals breeding within the inner Moray Firth occasionally use these alternative sites during longer foraging trips (Thompson *et al*., 1996*a*). However, surveys of the outer Moray Firth coast were made in 1997 and 2002

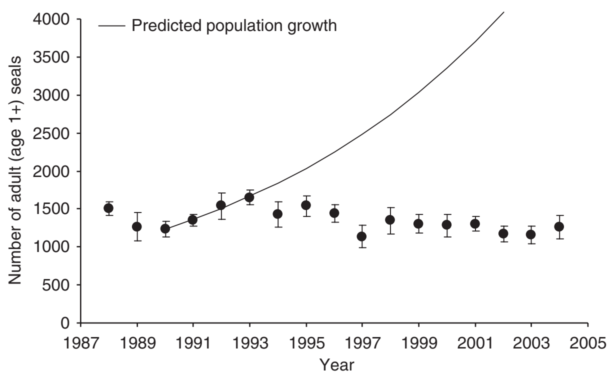

Figure 5 Predicted population growth 1990–2004 using population projection matrix *A* (solid line), together with estimates of the abundance of age 1+ adults (±95% confidence interval) based upon observed pupping season haul-out counts (●).

Table 3 Annual reported numbers of harbour *Phoca vitulina*, grey *Halichoerus grypus* and unidentified seals shot in the Moray Firth, 1994–2004, and derived most probable and maximum estimates of harbour seals removed

	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004
Grey seals	102	99	98	94	104	161	131	88	56	22	25
Harbour seals	101	100	97	89	106	192	128	66	92	24	28
Unidentified	72	72	72	72	72	72	103	261	149	10	12
Total	275	271	267	255	282	425	362	415	297	56	65
Most probable estimate of harbour seals	136	136	132	124	142	231	178	177	184	29	34
Maximum estimate of harbour seals	173	172	169	161	178	264	231	327	241	34	40

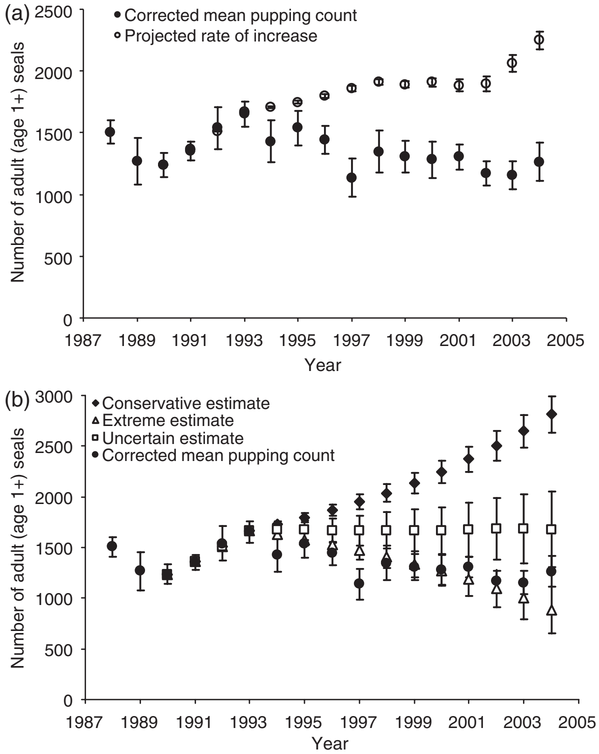

Figure 6 Predicted population growth 1990–2004 following 1000 simulations using (a) interannual variation in numbers shot (the number is drawn randomly from between the minimum and maximum estimate for each year) and (b) the number of seals shot being drawn randomly from a conservative (124–231 individuals), extreme (161–327 individuals) and uncertain (124–327 individuals) estimate. In each figure estimated adult (age 1+) abundance is shown ±95% confidence interval (●).

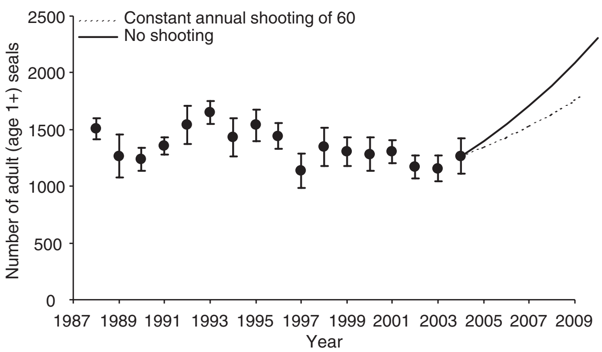

Figure 7 Predicted population growth post-2004 with a constant removal of 60 individuals and no removal. Estimated adult (age 1+) abundance 1988–2004 is shown ±95% confidence interval (●).

(Table 2), and the 145–214 seals counted in this area are insufficient to account for differences between observed and predicted abundance (Fig. 5). Previous studies have produced no evidence for long-distance movements of adult harbour seals between different breeding areas (Thompson & Goodman, 1997; Thompson *et al.*, 1998*b*; Härkönen & Harding, 2001), and it seems unlikely that the decline in abundance in the Moray Firth is due to dispersal of animals outside the entire region. Nevertheless, it remains possible that differences in trends between northern and southern parts of the study area (Fig. 4) could result from dispersal of seals from haul-out sites in the northern area to those in the south rather than local differences in fecundity and survival.

Effects of shooting on population status

Estimates of the total number of seals shot exceeded 300 in some years. Determining how many were harbour seals is problematic, as seals were not always identified to species, and the reliability of species identifications is unknown. Nevertheless, between 1994 and 2002, our most probable estimate of the number of harbour seals shot always exceeded our maximum PBR estimate of 114. Even the minimum estimate exceeded this value in 2 years, raising the possibility that much of the observed decline since 1993 could be due to shooting. If so, shooting levels in 1988–1993 may have been lower, because this was a period of population growth, but there are no complete shooting records before 1994 to corroborate this.

Differences in trends in the southern and northern parts of our study area may reflect spatial variations in the levels of shooting. However, while shooting was known to be carried out by all Moray Firth fisheries, the records of seals shot are insufficiently detailed to allow comparisons between areas. Furthermore, seals were often shot outside the breeding season when there is greater interchange between sites (Thompson *et al.*, 1996*a*). Consequently, seals from the Dornoch Firth SAC may have been shot while visiting more southern sites, highlighting the need to manage the Moray Firth as a single population unit when considering seal–fishery interactions.

The potential impact of removing seals was further explored using matrix models. Similar approaches have previously been used to assess the impact of both persecution and harvesting (Heinsohn *et al.*, 2004; Whitfield *et al.*, 2004; Hunter & Caswell, 2005). Here, we chose to use a simple stage-based model, as the limited life-history and demographic data from this population precluded use of more complex models. Even then, our models required the use of life-history data obtained from other populations. We also assumed that our starting population had a stable age structure. While this is unlikely, no data exist on the age- or sex-structure of this or any other harbour seal population. Despite these caveats, the model provided a good reflection of initial population recovery following the 1988 PDV outbreak (Fig. 5).

Using year-specific estimates of the number of seals shot (Table 3), projected population sizes remained higher than observed values during the period 1994–2004 (Fig. 6a). The best reflection of observed trends was obtained by randomly drawing values that lay between the minimum and maximum of our extreme estimate for the number of harbour seals shot. Uncertainties over species identification and accuracy of reporting prevent firm conclusions being drawn about the impact of culling on this population. There may be observation errors involving underestimation of the total number shot, or incorrect species classification. If most unidentified seals were harbour seals, our most extreme simulations illustrate that shooting alone would be sufficient to explain the decline. Alternatively, if shooting records accurately reflect the numbers shot, then these losses appear insufficient to explain the observed decline in harbour seal abundance, and fishery management may be only one contributory factor to recent declines. Previous work has shown that reductions in winter food availability and quality affected individual health and behaviour in this population (Thompson *et al.*, 1997*a*, 1998*a*). These short-term effects could have subsequently influenced process error through temporal variations in fecundity, survival or dispersal. Other fisheries activities, such as by-catch in salmon nets, could also have contributed to variations in survival.

In future, more complex state-space models (e.g. Bjornstad *et al.*, 1999; De Valpine & Hastings, 2002) could be used to investigate process and observation error in more detail. In the meantime, simpler modelling frameworks and the use of sustainability indices such as PBR indicate that conservation managers should not necessarily wait for the development of more complex models before taking precautionary action. Consequently, while it was not possible to accurately determine the relative influence of these different driving forces on this population, the Scottish Executive introduced a Conservation Order limiting the shooting of Moray Firth harbour and grey seals. The order was introduced in 2002, and its effects are reflected in the reduction in the number of seals shot in 2003 and 2004. Subsequently, a management plan has also been introduced by salmon fisheries and other stakeholders to protect fisheries while also minimizing impacts on local seal populations (Butler, 2005). In response to this plan, and based on precautionary estimates of PBR, the Scottish Executive allowed the shooting of 60 harbour seals in 2005. If recent declines are primarily the result of shooting, model predictions indicate that the population should slowly recover over the next 5–10 years. Given the assumptions underlying our models, particularly those concerning the age structure of both the population and the culled sample, these predictions of future growth should be treated with caution. Comprehensive monitoring of future population trends, and the species-, age- and sex-structure of culls, now need to be integrated into more complex models to improve assessments of the impact of human exploitation on harbour seal populations.

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