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# Do 'rogue' seals exist? Implications for seal conservation in the UK

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## Abstract

The management of conflict between people and large carnivores frequently focuses on the selective removal of the so-called 'problem' or 'rogue' animals. However, the existence of such individuals has rarely been examined. Recent management of seal–salmon fishery conflict in Scotland follows this approach, and under the Moray Firth Seal Management Plan the lethal removal of perceived problem individuals is permitted in salmon rivers. However, the efficacy of this strategy depends on (1) the existence of river-specialist individuals; (2) these individuals having a greater per capita impact on salmon fisheries than individuals in the general population. Using data collected in three rivers from March 2005 to February 2008, we show using photo-identification that a small fraction of the population ($\leq$ 1%) comprises individual seals that specialize in using rivers. This behaviour was more pronounced for grey seals *Halichoerus grypus* than harbour seals *Phoca vitulina*, and a greater proportion of individual harbour seals were seen only once during the study. A higher percentage of digestive tract samples collected from seals in rivers tested positive for salmon and trout DNA compared with seal scats collected at coastal sites, although the sample size was small. These results indicate that targeting individual seals present in rivers is more likely to remove those individuals consuming salmon, and have a larger per seal benefit to salmon compared with targeting seals hauled out in estuaries. This lends rare scientific support to the established management paradigm of problem-individual removal.

## Introduction

Conflicts between humans and wild carnivores occur primarily due to competition over a shared resource, usually either livestock or game (Graham, Beckerman & Thirgood, 2005). Management of predator–prey systems is particularly complex where the species involved are economically or socially valuable and/or are protected under law (Thirgood *et al*., 2000; Graham *et al*., 2005). There is considerable debate over the impact of predation by pinnipeds (seals and sea lions) on populations of, and fisheries for, both Atlantic (*Salmo* spp.) and Pacific (*Oncorhynchus* spp.) salmonids, many of which are endangered or in decline (Fraker & Mate, 1999; Middlemas, Armstrong & Thompson, 2003). Pinnipeds and salmon are protected under US, UK and European legislation, resulting in potentially conflicting requirements for government agencies to conserve and manage both pinniped predators and their salmonid prey, particularly where protected populations of predators and prey coincide spatially (Fraker & Mate, 1999; Butler *et al*., 2008). Managers must therefore attempt to find a compromise between the competing legal requirements for the conservation and management of seal and salmon populations and their associated economic activities, primarily salmon fisheries and eco-tourism.

Goodrich & Buskirk (1995) argued against population control as a general management practise for the conservation of endangered species. They proposed, instead, a decision pathway to help determine when control may be effective or necessary, for example when a problem is caused by a few individual predators. The selective removal (either lethal or non-lethal, by translocation) of 'problem' or 'rogue' individuals has become a paradigm in the management of large carnivores that kill domestic (Linnell *et al*., 1999) or wild prey species (David *et al*., 2003). However, the underlying assumption that only a small proportion of the individuals in the predator population are responsible, either by specializing in feeding in certain areas or on certain prey species, has rarely been tested (Linnell *et al*., 1999). Understanding whether this is the case is key to evaluating the potential efficacy of this management action (Ormerod, 2002).

Historically, management of seal–salmon interactions in Scotland has focused on killing seals at coastal haul-out sites in the vicinity of rivers with fisheries for Atlantic salmon *Salmo salar* and sea trout *Salmo trutta* (Thompson *et al*., 2007). There are concerns over how effective this approach is at targeting those seals that actually eat salmon (Matejusová *et al*., 2008) and over the negative impact this may have had on local seal populations (Thompson *et al*., 2007). Recent management has therefore focused on targeting problem individuals in rivers on the basis that, in the absence of scientific data, seals present in rivers and river mouths are most likely to be those preying on salmon as, at sea, salmon are generally a rare species and are therefore probably not available to most individual seals (Butler *et al*., 2008).

According to Linnell *et al*.'s (1999) conceptual framework, seals in rivers may be considered to be type 1 problem individuals, which occur when only some individuals in a predator population have the prey in question within their home range. It follows that any seal 'in the wrong place', in this case a river, would be defined as a problem individual (Linnell *et al.,* 1999). However, this framework excludes the possibility that in this situation there might still be behavioural differences between individuals in the extent to which they specialize in feeding in certain areas or on certain prey species. Should such differences exist, then the definition of a problem individual as any individual in the wrong place might require refinement.

The benefits of managing seals in rivers will be determined by a number of factors, including the degree of river use by individual seals. Although only a limited number of studies have examined river use by seals in Scotland, it appears that the number of seals seen in Scottish rivers at any one time is generally low (Williamson, 1988; Carter *et al*., 2001; Middlemas *et al*., 2006). However, it is not known whether this is due to a small number of individuals repeatedly visiting rivers or simply a larger sector of the population using these areas more occasionally. If only a small number of seals use rivers then removing them to alleviate any direct impacts on fisheries is theoretically practicable, and potentially acceptable from a management and seal conservation perspective. Focusing on managing seals in rivers to provide protection for salmonid stocks also requires that seals in rivers prey on salmonids to a greater extent than seals in estuaries. Once the potential benefits to the fishery of managing seals in rivers have been determined, they can then be weighed against the costs of alternative options, both in financial, ecological and welfare terms.

It is possible to use photo-identification to identify individual seals on the basis of their pelage pattern (Harrison *et al*., 2006; Mackey *et al*., 2008; Thompson & Wheeler, 2008). Using this technique, we aimed to determine whether or not specific individual seals were repeatedly using rivers and to determine the frequency and pattern of occurrence of seals in rivers. In addition we compared the occurrence of salmon and trout DNA in seal diet samples collected in rivers and estuaries to test the assumption that seals present in rivers eat more salmonids than those present in estuaries.

# Methods

## Study area

The study was carried out from March 2005 to February 2008 in the Rivers Conon, Kyle of Sutherland and Ness, north-east Scotland (Fig. 1). All three rivers support important Atlantic salmon stocks and fisheries and drain into the Moray Firth, which contains special areas of conservation for Atlantic salmon and harbour seals *Phoca vitulina* designated under the EU Habitats Directive. Management of seals and salmon in the Moray Firth region is coordinated

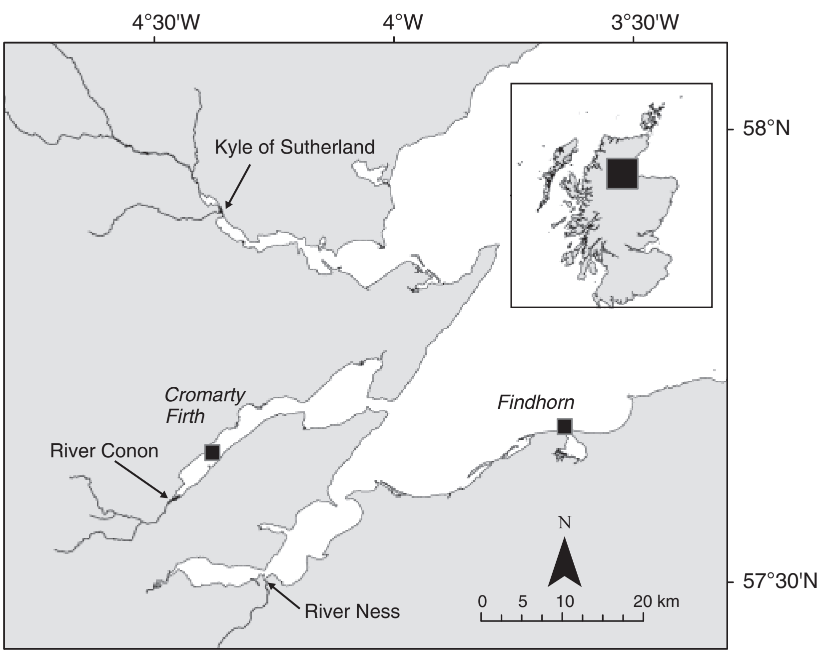


**Figure 1** The Moray Firth, Scotland, showing the transect locations on the surveyed rivers and the coastal haul-out sites in the Cromarty Firth and Findhorn Bay.

under the Moray Firth Seal Management Plan (Butler *et al.*, 2008).

## River surveys

Seals were counted from the river bank over standard transects within 3 h of high tide (Fig. 1). As seals are sighted most frequently in rod fisheries closest to the river mouth (Butler *et al.*, 2011), transects were chosen to be mainly within the normal tidal limits of each river, with the lower boundary set as close to the mouth of each river as possible. The length of river surveyed was *c*. 1.5, 2.25 and 4.25 km for the Rivers Conon, Kyle of Sutherland and Ness, respectively (generally taking around 1.5, 1.25 and 2.5 h to complete). At least four surveys were carried out on each of the three rivers each month, apart from on the River Conon in December 2005 and the Kyle of Sutherland in September 2006 when only three surveys were carried out. An index of seal abundance was derived by calculating a 3-month rolling average of the number of seals sighted per survey. Given the variation in survey lengths between rivers, the seasonal patterns seen in each river are appropriate for comparison rather than the precise number of seals sighted.

## Photo-identification

Seals observed in rivers during the course of surveys, and opportunistically, were photographed [using a Canon EOS 20D digital camera (Canon Inc., Tokyo, Japan) with a 600 mm lens and 1.4 converter, a Konica-Minolta Dynax 7D digital camera (Konica Minolta Inc., Tokyo, Japan) with a 600 mm lens and 1.4 converter or a Canon XM2 digital video camcorder]. Images were matched manually and graded on a scale of 1 (best) to 4 (worst) based on image quality and pelage 'discernibility' (the presence of unique pelage markings suitable for recognizing an individual). Matches and grades were confirmed independently by two observers and only images graded 1 or 2, for both criteria, were considered of sufficient quality to identify individual seals. Only one capture (i.e. photograph) of each individual was counted per day.

## Collection of digestive tract samples and DNA analysis

Digestive tract samples from harbour and grey seals *Halichoerus grypus* were collected from seals shot ($n = 8$) and live-captured ($n = 1$) in rivers from 2005 to 2008. Seals were shot by District Salmon Fishery Boards under the UK's Conservation of Seals Act 1970 to protect fisheries and licensed through the Moray Firth Seal Management Plan. Whenever possible, carcasses were retrieved and sampled within 24 h of death. The stomach and intestines were removed from each carcass, sealed in individual polythene bags and stored intact at −20 °C. They were later thawed and their contents removed using sterile equipment. Stomach contents were mixed thoroughly and one to three subsamples from each were stored at −70 °C for subsequent DNA extraction. The same procedure was followed for the intestine contents. One harbour seal was live-captured using nets in the Kyle of Sutherland. The seal was anaesthetized with an intravenous injection of Zoletil (Virbac Laboratories, Carros, France) and a faecal sample obtained by faecal lavage. The faecal sample was stored at −70 °C before DNA extraction. Seal capture was permitted under licence issued by the Home Office. All procedures were carried out in accordance with the Animals (Scientific Procedures) Act 1986.

The presence or absence of DNA from salmon and trout in the samples was determined using the qPCR techniques described in Matejusová *et al.* (2008). In order to compare occurrence of salmonids in the diet of seals in rivers with those in the Moray Firth, the presence of salmon and trout DNA in seal digestive tract samples ($n = 9$) collected in rivers was compared with DNA extracted from seal scat samples ($n = 182$) collected at haul-out sites in the Cromarty Firth and Findhorn Bay during 2003 and 2005 (Matejusová *et al.*, 2008).

## Data analysis

Both left- and right-side images of the head were not known for every individual identified, therefore all analyses were carried out using left- and right-side images separately. Kolmogorov–Smirnov tests were used to test for differences in the frequency distributions of captures per individual, and time between first and last capture, between the different rivers and species. Kruskal–Wallis and Wilcoxon's tests were used to test for differences between the median number of captures per individual, and days between first and last capture, for the three rivers and two species, respectively.

Resighting data were grouped into quarterly periods and mark-recapture estimates produced, assuming that a closed population of seals was using the surveyed areas during a given period. The duration of each sampling period (3 months) was considered sufficiently short to assume that mortality was negligible and that there was no permanent immigration or emigration during each period. Although satellite telemetry has shown that both grey and harbour seals in Scotland do travel long distances occasionally, individual harbour seals generally show a relatively high degree of site fidelity, particularly over a short period of time (Cunningham *et al.*, 2009) and in the majority of trips to sea, individual grey seals returned to the same haul-out site from which they departed (McConnell *et al.*, 1999; Matthiopoulos *et al.*, 2004). Abundance estimates were produced with the CAPTURE function of MARK (White & Burnham, 1999) using the jackknife estimator, which allowed for variation in capture probabilities among individuals.

In order to determine the proportion of the Moray Firth population using the surveyed areas, the size of Moray Firth population was estimated for each species. For harbour seals, the Moray Firth population was estimated from coastal breeding season haul-out counts in 2006 corrected for seals that were in the water (Thompson *et al.*, 1997). For grey seals, the Moray Firth population was estimated from coastal haul-out counts in August 2005 corrected for seals

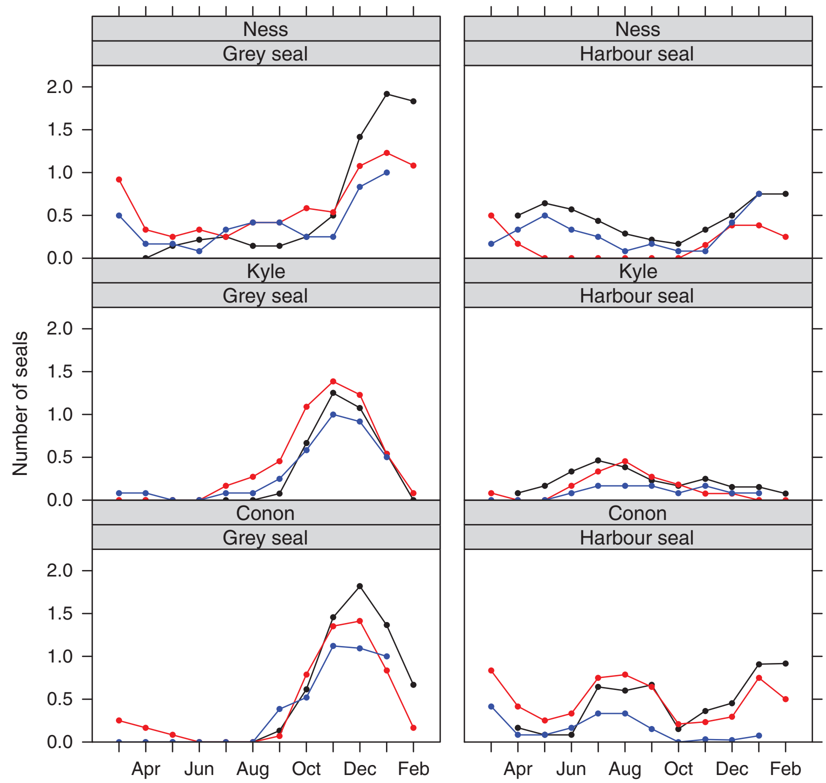


**Figure 2** The 3-month rolling average number of seals sighted per survey for the Rivers Conon, Kyle of Sutherland and Ness in the Moray Firth, March 2005–February 2008. Left side panels: grey seals *Halichoerus grypus*; right side panels: harbour seals *Phoca vitulina*. Black line: March 2005–February 2006; red line: March 2006–February 2007; blue line: March 2007-February 2008.

that were in the water (NERC, 2010). For each species, the proportion of the local population using the surveyed areas in rivers was calculated by dividing the quarterly abundance estimates for each survey area by the estimated Moray Firth population. Upper limits to the proportion were estimated by dividing the abundance estimates' upper confidence limits by the Moray Firth population estimate's lower confidence limit. Lower limits to the proportion were estimated by dividing the abundance estimates' lower confidence limits by the Moray Firth population estimate's upper confidence limit.

The difference between prey species (salmon vs. trout) and sampling location (river vs. coast) in the probability of a positive DNA test was compared using generalized linear models with a binomial error distribution. The significance of variables was assessed from the change in deviance caused by removing or adding that term to the selected model, assuming a $\chi^2$-distribution.

# Results

## Temporal patterns of river use

There was considerable temporal variation in the number of seals present in all three rivers during the study (Fig. 2). Both species of seal, harbour and grey, were observed in all rivers. Grey seal abundance fluctuated intra-annually in a similar way in all three rivers, being most abundant between November and February and either absent or present in much lower numbers throughout the rest of the year. During this winter period grey seals were more prevalent than harbour seals. This pattern was also consistent between years for all rivers. There was less consistency in harbour seal abundance fluctuation between rivers and, to a lesser extent, within rivers between years, although some patterns were still apparent. Like grey seal abundance, harbour seal abundance increased during the winter between December and March in the Conon and Ness. The Conon and Kyle of Sutherland showed an additional increase in harbour seal abundance during the summer, in July or August.

## Photo-identification

Photographs taken were of sufficient quality and resolution to distinguish individual pelage markings for a large proportion of the total number of capture occasions for both harbour and grey seals in all three rivers (Table 1).

Only a small number of individuals of both species appeared to be using rivers. Using left-side images we identified 25 (23 using right-side images) individual harbour seals and 18 (19) individual grey seals in all three surveyed areas out of a total of 97 (86) and 149 (147) identifiable captures of harbour and grey seals, respectively. In addition to harbour and grey seals, in August 2005, one hooded seal *Cystophora cristata* was sighted in the River Conon and in December 2005, one ringed seal *Phoca hispida* was sighted in the Kyle of Sutherland.

There were no significant differences between the rivers in the frequency distributions (Kolmogorov–Smirnov test, all $P>0.05$) and the median number of captures per individual

**Table 1** The number of captures and individual seals identified on the basis of left- and right-side images for the Rivers Conon, Kyle of Sutherland and Ness, March 2005–February 2008

| | Conon | | Kyle | | Ness | | Total | |
|---|---|---|---|---|---|---|---|---|
| | Left | Right | Left | Right | Left | Right | Left | Right |
| Harbour seals | | | | | | | | |
| Total no. of captures | 57 | 40 | 16 | 15 | 43 | 42 | 116 | 97 |
| % (no.) of unidentifiable captures | 18 (10) | 8 (3) | 38 (6) | 27 (4) | 7 (3) | 10 (4) | 16 (19) | 11 (11) |
| % (no.) of identifiable captures | 82 (47) | 92 (37) | 62 (10) | 73 (11) | 93 (40) | 90 (38) | 84 (97) | 89 (86) |
| No. of individuals identified | 8 | 8 | 7 | 8 | 10 | 7 | 25 | 23 |
| Grey seals | | | | | | | | |
| Total no. of captures | 46 | 43 | 34 | 36 | 92 | 98 | 172 | 177 |
| % (no.) of unidentifiable captures | 2 (1) | 0 (0) | 29 (10) | 31 (11) | 13 (12) | 19 (19) | 13 (23) | 17 (30) |
| % (no.) of identifiable captures | 98 (45) | 100 (43) | 71 (24) | 69 (25) | 87 (80) | 81 (79) | 87 (149) | 83 (147) |
| No. of individuals identified | 4 | 5 | 6 | 6 | 8 | 8 | 18 | 19 |
| No. of days observation | 210 | | 149 | | 179 | | 538 | |

(Kruskal–Wallis test, all $P > 0.05$) within each species. Data from the three rivers were therefore combined to examine the differences between the two species. Individual grey seals were re-sighted more often than individual harbour seals, for both left- and right-side images (median number of captures per individual seal: harbour seals = 2, grey seals = 7; Wilcoxon's test: left-side: $W = 353.5$, $P = 0.001$; right-side: $W = 316.5$, $P = 0.011$). In addition, the frequency distribution of captures per individual seal was significantly different between the two species, with more harbour seals being seen only once or twice compared with grey seals (Fig. 3, Kolmogorov–Smirnov test: left-side: $D = 0.547$, $P = 0.004$; right-side: $D = 0.606$, $P = 0.001$).

As there were, again, no significant differences between the rivers in the frequency distributions and the median number of days between the first and last capture for individuals of either species ($P > 0.05$ for all comparisons; Kolmogorov–Smirnov and Kruskal–Wallis tests), the data from the three rivers were combined to test for differences between the two species (Fig. 4). The frequency distributions of time between the first and last capture of individual seals were found to be significantly different between the two species (Fig. 4, Kolmogorov–Smirnov test: left-side: $D = 0.57$, $P = 0.002$; right-side: $D = 0.44$, $P = 0.036$). In addition there was a significantly longer period of time between the first and last sightings of individual grey seals than harbour seals (Wilcoxon's test: left-side: $W = 363.5$, $P < 0.001$; right-side: $W = 301$, $P = 0.034$), with the majority of grey seals being seen in $> 2$ years (over 730 days between first and last sighting) and the majority of harbour seals seen in only one.

## Abundance estimates

Although the number of captures, for each survey area and species, in any given quarter was generally low, in 30 cases there were enough captures and recaptures to allow an abundance estimate to be calculated (Table 2). The estimated number of harbour and grey seals using the surveyed areas calculated using mark-recapture methods was low for all rivers ($< 16$ animals), confirming that only a small number of individuals of both species appeared to be using rivers (Table 2). The proportion of the Moray Firth harbour seal population estimated to be using the surveyed areas was low: $\leq 1.1\%$ (Table 2; Fig. 5), and not exceeding 3.4% at the upper limit (Fig. 5). Similarly, the proportion of the Moray Firth grey seal population estimated to be using the surveyed areas was low: $\leq 0.5\%$ (Table 2; Fig. 6), and not exceeding 2.5% at the upper limit (Fig. 6).

## DNA analysis

A total of nine digestive tract samples collected from seals in rivers were analysed for the presence of Atlantic salmon and trout DNA (Table 3). A higher percentage of samples collected in rivers tested positive for both salmon (22.2%) and trout (44.4%) DNA than those collected at coastal sites (Table 3; salmon: 6.6%; trout: 7.7%). There was no difference between prey species (salmon vs. trout) in the probability of a positive test ($\chi^2 = 0.57$, d.f. = 1, $P = 0.45$), however, significantly more samples tested positive for salmon or trout DNA in rivers than at coastal sites ($\chi^2 = 8.39$, d.f. = 1, $P = 0.004$).

# Discussion

The effectiveness of removing problem individuals as a management strategy in reducing predation is dependant on the occurrence of problem individuals, and the underlying assumption that only a small proportion of the individuals in the predator population are responsible for most predation on a certain prey species, either by specializing in feeding in certain areas or on that prey species. This study found that, for grey seals in particular, a small number of individuals, constituting only a small proportion of the local population, appeared to specialize in using the surveyed areas in three rivers. In addition, salmon and trout DNA were detected in a greater percentage of seal diet samples collected in rivers than at coastal sites, although the data were limited. This suggests that there are problem individuals, who are more likely to consume salmonids than

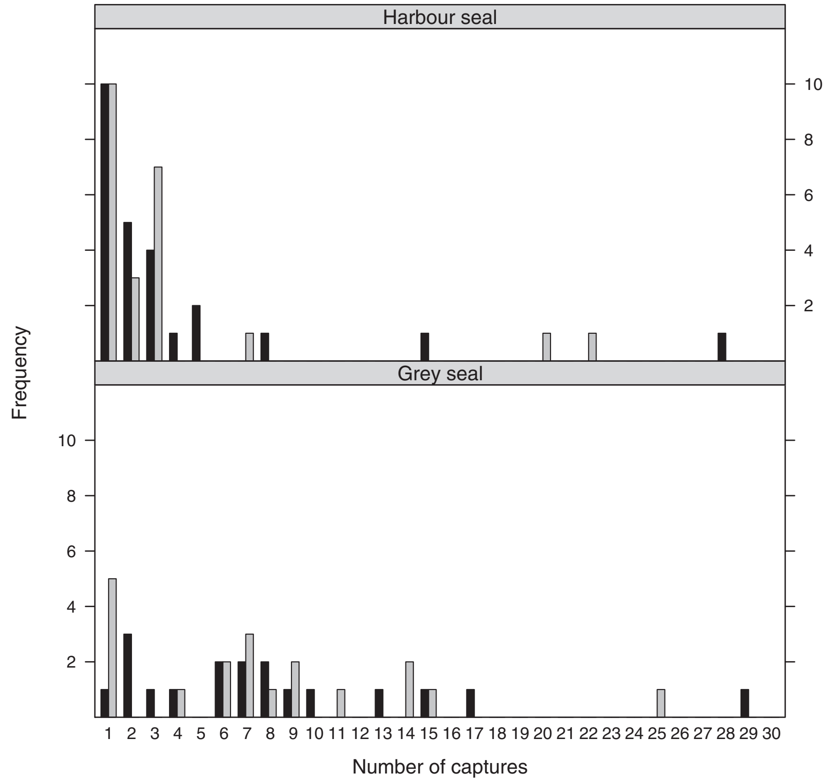


**Figure 3** Sighting frequencies of individual harbour seals *Phoca vitulina* and grey seals *Halichoerus grypus* identified using left (black bars) and right (grey bars) side images in all three study rivers, March 2005–February 2008.

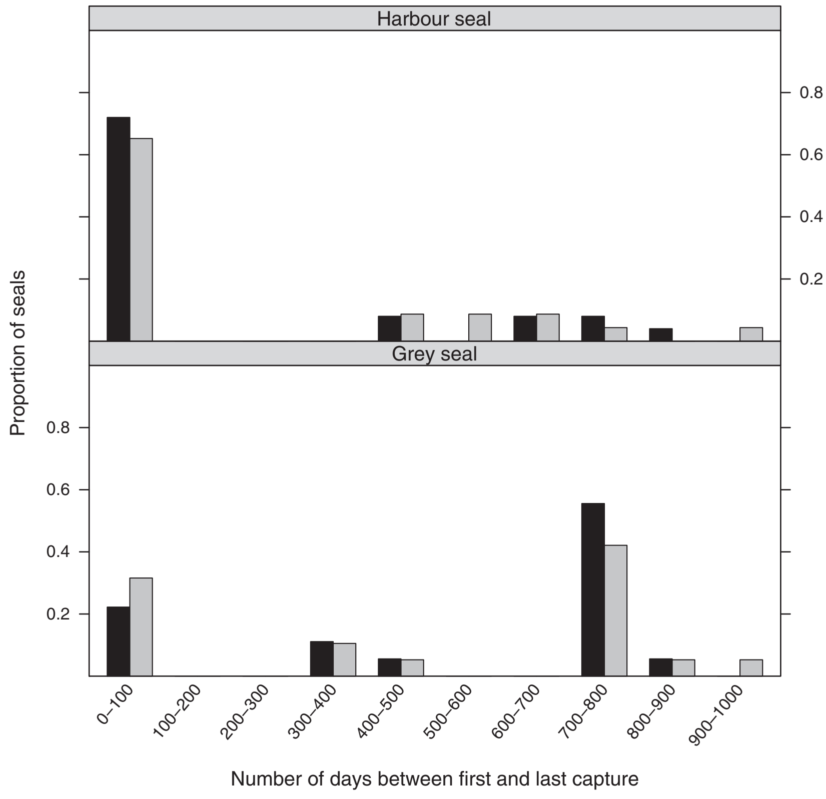


**Figure 4** Variation in the time between the first and last capture of individual grey seals *Halichoerus grypus* and harbour seals *Phoca vitulina* expressed as a proportion of the total number of seals seen, March 2005–February 2008. Top panel: harbour seals; bottom panel: grey seals. Left-side images: black bars; right-side images: grey bars.

**Table 2** Estimated number of grey seals *Halichoerus grypus* and harbour seals *Phoca vitulina* and proportion of the Moray Firth population using the Rivers Conon, Kyle of Sutherland and Ness for specified quarters

| | | Abundance estimate (95% confidence limits) | | Proportion of M. F. population (%) | |
|---|---|---|---|---|---|
| River | Year/quarter | Left side | Right side | Left side | Right side |
| Grey seals | | | | | |
| Conon | 2005/October–December | 4 (4–10) | 4 (4–10) | 0.1 | 0.1 |
| Conon | 2006/October–December | 4 (4–4) | 5 (5–12) | 0.1 | 0.1 |
| Conon | 2007/October–December | 3 (3–3) | 5 (5–12) | 0.1 | 0.1 |
| Kyle | 2005/October–December | 6 (6–13) | 6 (5–62) | 0.2 | 0.2 |
| Kyle | 2006/October–December | 3 (3–3) | 3 (3–3) | 0.1 | 0.1 |
| Kyle | 2007/October–December | 6 (5–14) | 4 (4–21) | 0.2 | 0.1 |
| Ness | 2005/October–December | 6 (5–14) | 6 (5–14) | 0.2 | 0.2 |
| Ness | 2006/January–March | 8 (8–15) | 7 (7–7) | 0.2 | 0.2 |
| Ness | 2006/October–December | – | 4 (4–21) | – | 0.1 |
| Ness | 2007/January–March | 16 (9–39) | 4 (4–21) | 0.5 | 0.1 |
| Ness | 2008/January–March | 4 (4–10) | 6 (5–13) | 0.1 | 0.2 |
| Harbour seals | | | | | |
| Conon | 2005/July–September | 4 (4–11) | – | 0.4 | – |
| Conon | 2005/October–December | – | 12 (6–32) | – | 1.1 |
| Conon | 2006/January–March | 4 (4–11) | 4 (4–11) | 0.4 | 0.4 |
| Conon | 2006/July–September | 4 (4–10) | 7 (4–18) | 0.4 | 0.6 |
| Ness | 2005/April–June | 5 (5–12) | – | 0.5 | – |
| Ness | 2006/January–March | 5 (5–11) | 5 (5–11) | 0.5 | 0.5 |

Abundance estimates were calculated using mark-recapture of individually photographed seals. Estimates are given for left- and right-side images separately and were calculated using the jack knife estimator in programme CAPTURE. For each species, the Moray Firth (M. F.) population was estimated using haul-out counts corrected for seals that were still in the water.

those in the general population, providing empirical support for the management paradigm of problem-individual removal (Linnell *et al.*, 1999).

For both harbour and grey seals, the estimated number of individuals using the surveyed areas was small suggesting that, irrespective of individual behaviour, control of seals in rivers may be feasible because it incurs only minimal costs for seal conservation, while benefitting fishery management (Goodrich & Buskirk, 1995). Although previous studies observed only a small number of seals in rivers at any one time (Williamson, 1988; Carter *et al.*, 2001; Middlemas *et al.*, 2006), the number of individuals using rivers has not previously been quantified. For both grey and harbour seals, the number of individuals that used rivers represented only a small proportion of the local population, which is consistent with studies of harbour seals and sea lions in North America (Fraker & Mate, 1999; Wright *et al.*, 2007). Unlike some previous Scottish studies, we found that grey seals were more prevalent than harbour seals in rivers during the winter (Williamson, 1988; Carter *et al.*, 2001). The winter peak in seal abundance in rivers is coincident with the grey seal moult, and similarly the summer peak in seal abundance in rivers is coincident with the harbour seal breeding season and moult. At these times, the proximity to key breeding and moulting haul-out sites for each species may influence the observed patterns of in-river seal abundance.

The majority of individual grey seals and about a third of individual harbour seals (78/68% vs. 28/35%, Fig. 4) were seen in two or more years of the study supporting the idea that they specialized in using rivers. Although at a population level, grey and harbour seals are often thought of as generalist predators, it does not necessarily follow that all individual seals are the same (Harwood, 1990). In many cases, populations of generalists can be made up of individuals with a narrower, more specialized diet than the whole population. Previous radio-telemetry studies have shown that individual harbour seals repeatedly return to the same foraging locations at sea (Bjorge *et al.*, 1995; Tollit *et al.*, 1998) and this would seem to be paralleled in the use of rivers by grey and some harbour seals. The diet choice of such individuals is often a reflection of the prey that are available in those areas (Holbrook & Schmitt, 1992), and it is not possible to distinguish preference for a particular foraging location from preference for a particular prey species.

A number of individual grey and harbour seals, however, were seen only once during the study suggesting that they may not have been specialist river-users (6/26% vs. 40/43%, Fig. 3). In contrast to grey seals, the majority of harbour seals in this study were seen only once or twice and in only 1 year. During the course of the study, six harbour seals but only one grey seal were shot in two of the study rivers under the auspices of the Moray Firth Seal Management Plan. The difference in the occurrence of river specialists between the two species could therefore potentially be due to the differing number of individuals of each species removed. However, in the third river, no individuals of either species were killed and, for both species, all the statistical tests carried out indicated that there were no significant differences between rivers. This suggests that the lethal removal of these few

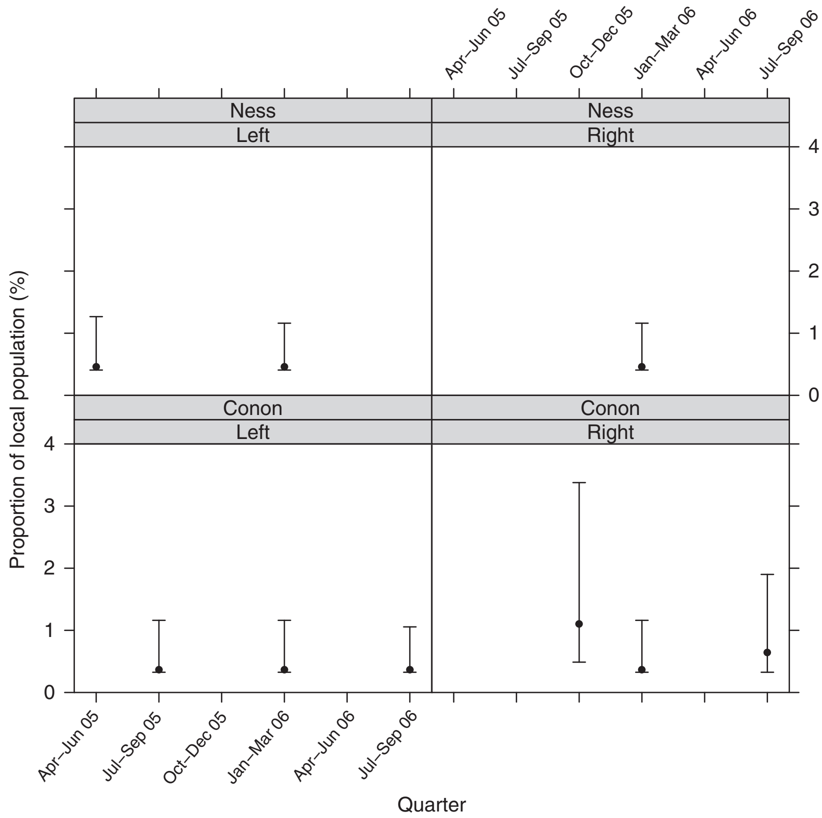


**Figure 5** Proportion of Moray Firth harbour seal population using the Rivers Conon and Ness during specified quarters. Abundance estimates of the number of seals using rivers were calculated using photo-identification techniques and mark-recapture methods. The Moray Firth harbour seal population was estimated using breeding season haul-out counts in 2006 corrected for seals that were still in the water. Mark-recapture estimates were calculated separately for left- and right-side images.

individuals may not have influenced the observed results. An alternative explanation is that, the presence of harbour seals was influenced by the presence of grey seals. Grey seals are the larger of the two species and are therefore likely to out-compete harbour seals in competition for a shared resource (Bowen *et al.*, 2003). This may explain the predominance of grey seals during winter, although it is not clear how this would reduce the number of specialist harbour seals unless the presence of grey seals simply deters individual harbour seals from returning to rivers. In a similar way, cheetahs *Acinonyx jubatus* have been shown to actively avoid lions *Panthera leo* and hyenas *Crocuta crocuta* and the distribution of cheetahs appears to be influenced by this competitor avoidance (Durant, 1998; Durant, 2000).

The greater occurrence of individuals that were seen only once during the study among harbour seals could be a function of the proximity of local haul-out sites and foraging behaviour. In general in the Moray Firth haul-out sites used by grey seals are further from the mouths of rivers than those used by harbour seals (Thompson *et al.*, 1996). In addition, grey seals forage in the open sea typically within 100 km of a haul-out site, although sometimes up to several hundred kilometres offshore, whereas harbour seals normally feed within 60 km of their haul-out site (Thompson *et al.*, 1996). Consequently, harbour seals may simply be more likely to enter rivers by chance than grey seals.

Management based on the selective removal of problem individuals is dependent on being able to define and identify them and having suitable, selective control methods (Linnell *et al.*, 1999). In the Moray Firth, problem individuals have been defined for management purposes as any individuals using rivers (Butler *et al.*, 2008). This definition of a problem individual concurs with Linnell *et al.*'s (1999) conceptual definition of a type 1 problem individual. However, our results suggest that this definition is a simplification, as the extent to which individuals specialized in using rivers clearly differed between individuals. The issues of defining, identifying and selectively controlling problem individuals are interlinked. While our results suggest that problem individuals would be better defined, and therefore identified and controlled, according to the extent of their river-use, this would be impossible to achieve in practice in the absence of detailed photo-identification or equivalent data such as ours. The advantage in defining a problem individual as any individual in a certain area, therefore, is that the difficulty associated with actually identifying problem individuals is avoided. As any form of selective control is preferable to widespread population reduction from both an ecological and a welfare perspective (Linnell *et al.*, 1999; Baker *et al.*, 2008), a pragmatic solution may be to accept that, by defining problem individuals as any individuals in a certain area, a few individuals that rarely use that area will also be removed.

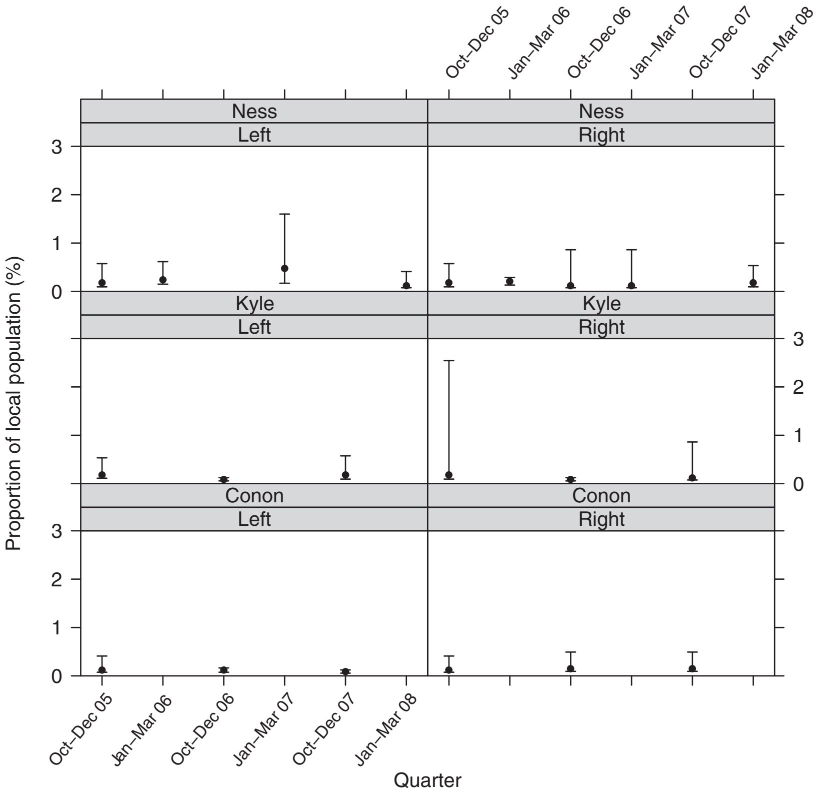


**Figure 6** Proportion of Moray Firth grey seal population using the Rivers Conon, Kyle of Sutherland and Ness during specified quarters. Abundance estimates of the number of seals using rivers were calculated using photo-identification techniques and mark-recapture methods. The Moray Firth grey seal population was estimated using coastal haul-out counts in August 2005 corrected for seals that were still in the water. Mark-recapture estimates were calculated separately for left- and right-side images.

**Table 3** Number of diet samples collected from seals in rivers showing the presence of DNA from Atlantic salmon *Salmo salar* and trout *Salmo trutta* using PCR

| Species | Month | Number of samples | Salmon | Trout |
|---|---|---|---|---|
| Grey | February–March | 2 | 1 | 1 |
| Harbour | February–March | 2 | 1 | 1 |
| | April–September | 5 | 0 | 2 |
| Total (%) | | 9 | 2 (22%) | 4 (44%) |

The average level of use by type 1 problem individuals of certain areas will determine the positive impact, on the target prey species, that will be achieved by removing them. In the current study, as more harbour seals than grey seals were seen only once, controlling grey seals compared with harbour seals may be of greater benefit to salmon conservation and fisheries. Given the recent decline in most of the harbour seal populations around Britain and the greater conservation imperative for this species relative to grey seals (Lonergan *et al.*, 2007) there may be an important distinction to make between the species. Management decisions based on this difference, however, need to be balanced with the fact that harbour seals were more prevalent during the summer and are therefore more likely to be targeting adult salmonids and interfering directly with the fishery than grey seals.

The benefits of different options for managing seals need to be weighed against their costs. Due to the designation of SACs in the Moray Firth, management must provide protection for salmon populations and fisheries without threatening the conservation status of seal populations (Butler *et al.*, 2008). In order to achieve this goal, acceptable levels of removal are calculated (Wade, 1998) and in the case of the Moray Firth these are much lower than historic shooting levels (Thompson *et al.*, 2007). Only a few individual harbour and grey seals have been shown to use rivers suggesting that the maximum limit of seals permitted to be shot annually in rivers is sufficient to provide acceptable protection against interactions with fisheries in these areas. Moreover, the small proportion of the overall population seen in rivers and the existence of 'rogue' individuals indicates that, given that only a small number of seals can be shot, the greatest benefit to fish stocks will be achieved by focusing control on those individuals that use rivers most extensively and have the greatest per capita consumption of salmon and sea trout.

The small number of diet samples collected from seals in rivers, and the collection of the two datasets in different years, present some difficulties in interpretation. In particular, the small sample size makes it difficult to compare adequately between different times of the year or between seal species. Nevertheless, the data presented here support the hypothesis that salmonids are more prevalent in the diet of seals in rivers compared with those hauling out on the coast; 56% of digestive tract samples collected in rivers tested positive for salmon or trout DNA compared with only 13% of scat samples collected at coastal sites (Matejusová *et al.*, 2008). Our diet work suggests that targeting seals present in rivers is more likely to remove those individuals consuming salmonids and have a greater per capita benefit to salmonid fisheries compared with traditional indiscriminate shooting of seals. This is particularly the case when, as we have shown using the photo-identification data, there are individuals that specialize in using rivers. Although the occurrence of salmonids in the diet provides only presence/absence information, rather than a more informative measure of diet, it is possible that, given the small percentage of the population ($\leq 1\%$) that were using rivers, overall seals in rivers may consume fewer salmonids than the wider population as salmonids were still present in samples collected at coastal sites. While this might suggest that it would be more beneficial to focus management actions at the population level, this needs to be balanced against the negative impact this would have on the seal population and related conservation imperatives, and additionally it is possible that some of the samples collected at coastal sites could have come from animals feeding in rivers potentially inflating the prevalence of salmonids in those samples.

In order to be effective, management action should be beneficial to the fishery and/or the fish stock, whether or not lethal or non-lethal strategies are used (Graham *et al.*, 2009). It is difficult to quantify the overall benefit of targeted seal removal for salmonid fisheries and conservation. In this study, the number of both grey and harbour seals in rivers peaked overwinter. Previous studies have found a similar pattern of seal occurrence over winter (Carter *et al.*, 2001; Graham *et al.*, 2009). The peak in seal abundance during the winter, suggests that seals are likely to be targeting emigrating spawned adult salmonids. This would reduce their consumption of adult salmon, and therefore their impact on fish stocks, although a small proportion of the predated emigrants would return to spawn in subsequent years. During the start of the year (late winter/early spring), however, early running salmon will also be entering rivers, coinciding in some rivers with the winter peak of seal numbers. Early running salmon stocks in the UK are currently declining (Youngson, MacLean & Fryer, 2002) and as they are generally small in number are more vulnerable to the impacts of predation (Butler *et al.*, 2006). As a precautionary measure to protect early running stocks management action should focus on those months when these fish enter rivers as recommended by the Moray Firth Seal Management Plan (Butler *et al.*, 2008).

The additional peak in harbour seal abundance during the summer in two out of the three rivers coincides with the movement of adult salmonids into rivers. The relatively large stocks of fish running during the summer in many rivers means that the management of seal predation at that time of the year would probably have little impact on fish stocks except in rivers with very small late-running fish stocks (Butler *et al.*, 2006). The direct impact of seal interference with fisheries, however (as opposed to the indirect impact on fish stocks discussed above), is likely to be greater during the summer than the winter when most fisheries are closed. Therefore the management of seal predation during the summer, which would focus more on harbour seals than grey seals, may still be beneficial, although the actual direct cost to fisheries of seal interference is apparently low, as reported by Moray Firth stakeholders in a recent survey (Butler *et al.*, 2011).

Consideration of problem individual management in human–wildlife conflicts has tended to focus on terrestrial systems, in particular livestock–carnivore conflicts. However, our study demonstrates that the large carnivore discourse about problem individual management is equally relevant to aquatic systems. The study also highlights that Linnell *et al.*'s (1999) simple dichotomous classification of problem individuals can not accommodate the full complexities of predator behaviour. While ideally, managers would have a full understanding of the predator–prey system on which to base their decisions, in many cases a more pragmatic approach based on the best information available is required. Therefore, while the diet data presented here is insufficient to allow robust conclusions to be reached over the collective impact of predation by problem seals in rivers relative those in the wider population, the increasing lack of social acceptance for widespread predator control dictates that control should to be targeted at those individual predators with the greatest per capita impact. In this case, the photo-identification data provide strong evidence that focusing efforts on controlling seals in rivers may provide the best per capita protection for salmon conservation and fisheries, which is vital in a framework where both predator and prey are of conservation concern.

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