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Modelling the impacts of removing seal predation from Atlantic salmon, *Salmo salar*, rivers in Scotland: a tool for targeting conflict resolution

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Abstract Bioenergetics were used to model the potential impacts on adult Atlantic salmon, *Salmo salar* L., stocks and rod fisheries of removing harbour seals, *Phoca vitulina* L., from three rivers of different scales in the Moray Firth, Scotland, viz: the Spey (large), Conon (medium) and Moriston (small). Overall, seals had the greatest impact on the Moriston, where removal of a single animal could increase cumulative catch by 17% during the fishing season. On the Conon and Spey the impacts were negligible, and resulted in increased catches of $<1\%$ annually. On all rivers eliminating seal predation had the greatest impact during the spring due to the smaller size of spring salmon sub-stocks. A generalised model of seal removal illustrated that stocks and catches increased by $>33\%$ in rivers with monthly rod catches ≤ 10 fish, but declined to $<10\%$ for rivers with catches >34 fish. The outputs of the models are qualitative, but provide a management tool for targeting action to resolve seal-salmon fishery conflict. Smaller salmon population units, and spring salmon sub-stocks and fisheries in particular, are most vulnerable to predation. The merit of this approach is discussed regarding the management of Special Areas of Conservation for salmon and seals.

KEYWORDS: Atlantic salmon, fisheries, grey seals, harbour seals, predation, special area of conservation.

Introduction

Managers of Atlantic salmon, *Salmo salar* L., rivers aim to identify actions that protect and increase fish populations to sustain fisheries, while also maintaining adequate adult spawning stocks (e.g. Potter, Maclean, Wyatt & Campbell 2003; Solomon, Mawle & Duncan 2003). In recent years there has been

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concern about the declining abundance of adults returning to rivers across the species' range (Boisclair 2004), driven largely by climatic changes in the marine environment (Friedland, Hansen, Dunkley & Maclean 2000; Jonsson & Jonsson 2004). Predation by marine mammals may also have a role in stock declines, but this impact is not well understood (Anderson 2003; Middlemas, Armstrong & Thompson 2003). However, river managers only have scope to alter factors influencing the abundance of adult salmon within rivers and estuaries.

One of these factors is predation by seals, which are known to consume salmonids in rivers (e.g. Brown & Mate 1983; Fraker & Mate 1999; Carter, Pierce, Hislop, Houseman & Boyle 2001; Middlemas, Barton, Armstrong & Thompson 2006). Such predation fuels the debate over the potential impact of seals on salmonid fisheries (Fraker & Mate 1999; Middlemas *et al.* 2003). The perceived contribution of seals to declines of salmonid populations has led to calls from fisheries stakeholders for seal predation to be controlled, for example by shooting, scaring with acoustic deterrents or capture and relocation (Fraker & Mate 1999; Yurk & Trites 2001). However, the management of marine mammal interactions with fisheries is particularly challenging when both predator and prey populations are protected (Fraker & Mate 1999; Read & Wade 2000). This is the case in Scotland where Atlantic salmon, harbour seals, *Phoca vitulina* L., and grey seals *Halichoerus grypus* Fabricius, are protected by Special Areas of Conservation (SACs) designated under the European Commission Habitats Directive (Council Directive 92.43/EEC).

A prerequisite for managing seal predation on Atlantic salmon in rivers and estuaries is evaluation of the impacts of seals on stocks, and the fisheries reliant upon them. In Scotland, Carter *et al.* (2001) estimated the number of adult salmon consumed by seals annually in the rivers Don and Dee to be an order of magnitude lower than that removed by rod fisheries. However, it has been established that larger rivers contain genetically-distinct population units (sub-stocks) which differ in the timing of their return migration, and hence their seasonal availability to fisheries (e.g. Stewart, Smith & Youngson 2002; Jordan, Cross, Crozier, Ferguson, Galvin, Hurrell, McGinnity, Martin, Moffett, Price, Youngson & Verspoor 2005), and management should be targeted at the scale of such sub-stocks (Youngson, Jordan, Verspoor, McGinnity, Cross & Ferguson 2003). Early-running sub-stocks ('spring' salmon) are currently experiencing a steeper decline in abundance than later-running stocks (Youngson, Maclean & Fryer 2002) and may therefore be more affected by predation than indicated by studies such as Carter *et al.* (2001). Similarly, salmon population units from small rivers, such as those on the west coast of Scotland, may be inherently more susceptible to impacts from exogenous factors such as disease and predation (Butler & Watt 2003).

In this study the potential effects of removing seals present within three rivers of differing scales in the Moray Firth region of Scotland [the Spey (large), Conon (medium) and Moriston (small)] on adult salmon stocks and freshwater rod fisheries were examined. Seasonal variation in predation levels on sub-stocks was also examined, and a generalised model to assess the impacts on stocks and fisheries at different scales was developed. The Moray Firth also provides an example of conflicts between conservation interests, since the Spey and Moriston are European Commission-designated SACs for salmon, and an SAC for harbour seals exists within the region. Against this background the models are presented as a tool to identify situations where removal of seals will have the greatest potential benefit for salmon stocks and fisheries, and management actions can be targeted to resolve conflict.

Materials and methods

Study area

The Moray Firth region is situated in the north-east of Scotland (57°40′ N, 3°30′ W), and contains an SAC designated for harbour seals in the Dornoch Firth (Fig. 1). Because seals from the Dornoch Firth range throughout the Moray Firth (Thompson, McConnell, Tollit, Mackay, Hunter & Racey 1996), they are managed as one population unit for the purposes of the SAC (Butler 2004). The catchment areas of the Rivers Spey and Conon are 2991 km^2 and 1172 km^2, respectively. The River Moriston is a tributary of the Loch Ness/River Ness system, and has a catchment area of 384 km^2 (Fig. 1).

Seal bioenergetics model

The number of salmon consumed by seals was modelled for the Spey, Conon and Moriston using a bioenergetic approach. It was assumed that seals obtained their daily energy requirement solely from returning adult salmon. Seal consumption was calculated as:

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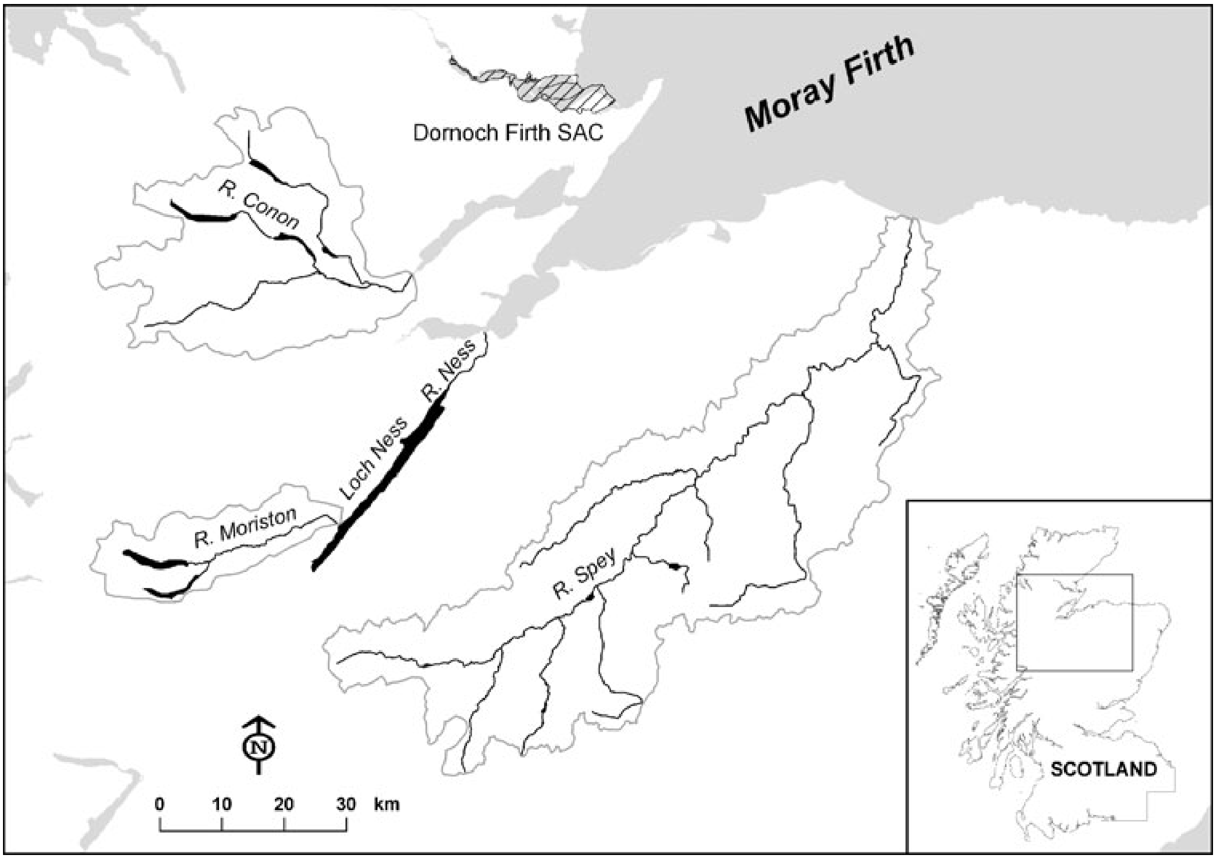

Figure 1. The Moray Firth, showing the locations of the Rivers Spey, Conon and Moriston catchments and the Dornoch Firth Special Area of Conservation for harbour seals.

$$s = \frac{N.C.D}{\varepsilon_c}$$

where s is the number of salmon consumed by seals, N the average number of seals present daily in each river, C the per capita daily energy requirement of a harbour seal (14689 kJ; Olesiuk 1993), D the time period in days and ε_c the average energy content of an individual salmon.

Potential impact on salmon stocks and fisheries

To model the potential impact of removing seals from each river it was assumed that fish released from seal predation were as likely to be captured in freshwater rod fisheries as those from the wider population. It was also assumed that seals were not replaced by conspecifics once they were removed from rivers. Under these assumptions the theoretical cumulative increase in stock size and catch for each river was calculated using the monthly cumulative exploitation rate by rod fisheries:

$$i.stock_j = \frac{\sum_{j=1}^{J} s_j}{\left(\sum_{j=1}^{J} f_j\right) \div E} \times 100$$

where $i.stock_j$ is the percentage increase in cumulative stock or catch at month j, E the exploitation rate, f the number of salmon caught by the fishery, s the number of salmon consumed by seals and J the total number of months in the sample. As stock size is extrapolated from the rod catch, relative changes in the results were directly proportional for both stocks and catches:

$$i.catch_j = \frac{E \times \sum_{j=1}^{J} s_j}{\sum_{j=1}^{J} f_j} \times 100 = \frac{\left(E \times \sum_{j=1}^{J} s_j\right) \div E}{\left(\sum_{j=1}^{J} f_j\right) \div E} \times 100 = i.stock_j$$

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Seal consumption (*s*) for the Spey and Conon was calculated using monthly values for the number of seals present daily in each river based on survey data (Table 1). Williamson (1988) reported that one seal may be resident in Loch Ness annually, and preliminary results from recent studies corroborated this observation (authors' unpublished data). It was therefore assumed that one seal was continually present in the freshwater estuary of the Moriston. Middlemas *et al.* (2006) and recent surveys (authors' unpublished data) showed that the majority of animals present in the three rivers during the rod fishing season are harbour seals. For the purpose of this model it was therefore assumed that all animals in rivers were harbour seals.

The potential effect of removing in-river predation by seals during the rod fishing season for the Spey (February to September), Conon (April to September) and Moriston (January to May) was examined. For the Spey and Conon, monthly catch data were taken for the same periods that the seal survey data were collected (2004 and 1999–2000 respectively). For the Moriston, average monthly catches for the period 2000–2004 was used. The exploitation rate for all rod fisheries over the season was assumed to be 15%, based on contemporary information for the Spey (Butler 2005). River-specific values for the average energy content of an individual salmon were calculated from average monthly weights (kg) of salmon caught in each river during the study periods, and an assumed energy density of 5933 kJ kg^{-1} (average value for *Salmo* species from Murray & Burt 1977). Values of *i* were then calculated for each river using the cumulative monthly rod catch (Fig. 2).

Generalised model

A generalised model was developed to predict the increase in catch and stock (*i*) of different scales

Table 1. Average number of seals observed daily by month in the River Spey in 2004 (from Butler 2005) and the River Conon in 1999–2000 (from Middlemas *et al.* 2006). The monthly presence of seals for the River Moriston was derived from Williamson (1988)

Month	Spey	Conon	Moriston
January	–	–	1.0
February	0.5	–	1.0
March	1.3	–	1.0
April	0.7	0.2	1.0
May	0.3	0	1.0
June	0.3	0.2	–
July	0.1	0.7	–
August	1.2	0.2	–
September	1.1	0	–

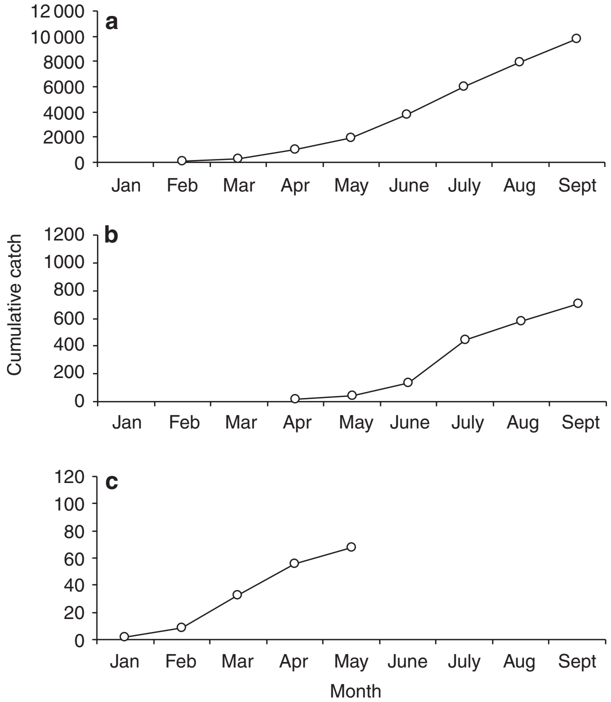

Figure 2. The cumulative monthly rod catch of salmon during the fishing seasons on (a) the River Spey (February to September 2004), (b) River Conon (April to September, averaged for 1999–2000) and (c) River Moriston (January to May, averaged for 2000–2004). Note that the cumulative catch axes differ for each river.

resulting from the removal of one harbour seal from a river for 1 month. The average energy content of a salmon was estimated using the energy density of 5993 kJ kg^{-1} and a weight of 3.42 kg, the average for Scottish rod fisheries in 2004 (Anonymous 2005). The exploitation rate of rod fisheries was again assumed to be 15%. Values of *i* were calculated for a 1-month (30 day) period and for fishery catches of between 5 and 200 salmon.

Results

The potential increase in salmon stocks and catches for the whole fishing season varied among the three rivers according to their size (Fig. 3). The cumulative annual value of *i* was greatest for the Moriston (17%) as the smallest river with an average total rod catch of 68 in 2000–2004, intermediate (0.7%) for the Conon with an average catch of 702 in 1999–2000, and lowest (0.2%) for the Spey, as the largest river with a catch of 9819 in 2004.

The potential cumulative monthly increase in salmon stocks and catches similarly varied with the size of the river. On the smallest river, the Moriston, the value of *i* was greatest (128%) in January, when

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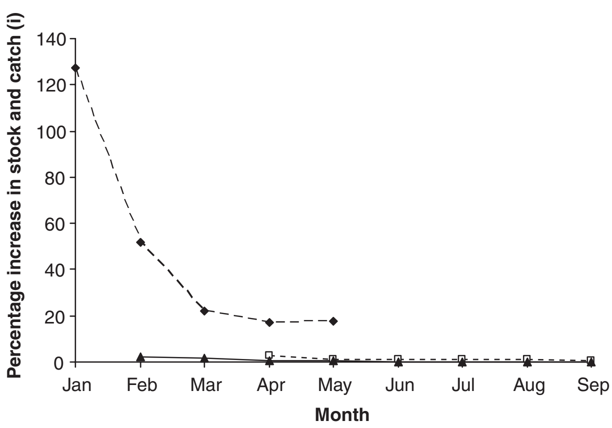

Figure 3. The predicted monthly increase in cumulative stock and rod catch (*i*) for the Rivers Spey (triangles), Conon (squares) and Moriston (diamonds) as a result of removing observed monthly numbers of seals during the rod fishing seasons. See Table 1 for mean daily presence of seals.

spring salmon were at their lowest abundance. As the cumulative catch increased the benefits of removing seal predation decreased, and values of i fell to 17% in May. A similar trend was evident for spring salmon in the Spey, where i in February was 2.3%, falling to $<1\%$ by April. Comparisons were not possible with the Conon in January to March because the fishery starts in April (Fig. 2).

The generalised model showed that the predicted increase in the value of i following the removal of one harbour seal for 1 month declined rapidly as the rod catch increased (Fig. 4). The predicted value of i exceeded 33% for monthly catches ≤ 10 fish, but declined to $<10\%$ for catches >34.

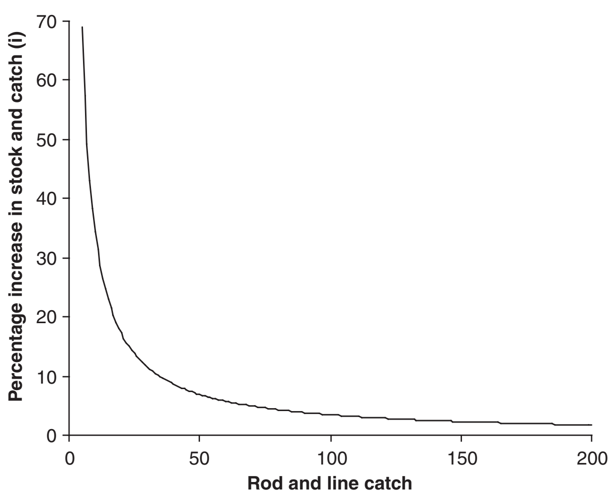

Figure 4. Generalised model of relationships between the monthly rod catch and predicted increase in stock and catch (*i*) resulting from the removal of one harbour seal from a river for 1 month.

Discussion

By modelling the potential effect of harbour seals in terms of their consumption of salmon it is possible to identify those situations where the impact of seal predation on stocks and catches of returning adult salmon may be greatest. The bioenergetics model showed that in large or medium-sized rivers, such as the Spey and Conon, removal of seals may lead to an overall increase of $<1\%$ to the stock and catch during the fishing season. However, for smaller rivers, such as the Moriston, removing a single seal could potentially increase the stock and catch by 17% in January to May. The generalised model also illustrated that the impacts of seal predation were disproportionately greater on smaller stocks of salmon. The removal of one harbour seal resulted in stock and catch increases $>33\%$ for population units yielding monthly catches of $\leqslant 10$ fish, but declined to $<10\%$ for catches of >34 fish.

The potential impact of reducing seal predation is also greatest on all rivers at the start of the year due to the smaller size of spring sub-stocks. This is particularly important since early-running salmon populations are currently experiencing a greater decline in abundance than later-running populations (Youngson *et al.* 2002). For rivers such as the Conon, which do not support spring fisheries in January to March, this effect is of little economic consequence. However, for small rivers such as the Moriston during January and February, removal of seal predation may have a marked impact since the fishery is reliant on a small population of spring salmon, estimated from recent fish counter data upstream from the fishery to be approximately 300 anadromous adults (A. Stephen, personal communication). Large rivers, such as the Spey, are also most affected during this period, but due to the relatively larger size of their spring salmon stocks, the impact is likely to be less.

There are several potential sources of bias associated with the assumptions of the models. Most notably, the impact on the Moriston was derived from an assumed presence of one harbour seal per day. At a population level harbour seals in the Moray Firth are generalist predators which focus on the most abundant prey available (Thompson *et al.* 1996; Middlemas *et al.* 2006). Hence low levels of adult salmon abundance, such as those in the spring on the Moriston, may not attract seals at the assumed level. The predicted impacts on the Moriston, and the results of the generalised model, may therefore be exaggerated. However, individual harbour seals are believed to become specialist predators of salmon in rivers

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(e.g. Yurk & Trites 2001; authors' unpublished data), and it remains feasible that some seals are attracted by apparently low abundances of adult salmon, and could have disproportionately large effects on small population units such as that of the Moriston.

In addition, it was assumed that when present in rivers, seals consumed only adult salmon. However, seals also prey on other species in these and other Scottish rivers (Carter *et al.* 2001; authors' unpublished data), and hence the impacts may have been overestimated. Conversely, several assumptions may have underestimated the potential benefits of removing seals. First, exploitation rates of spring salmon are likely to be higher than 15% (Youngson *et al.* 2002; Butler 2004) in which case the potential benefits of removing seal predation in January to May may have been underestimated. Secondly, it was assumed that all salmon caught by seals were eaten entirely. However, seals often eat only part of the fish (e.g. Rae & Shearer 1965), and may therefore require larger numbers than predicted to satisfy their bioenergetic requirements. Thirdly, it is not known to what degree seals prey upon spawned, emigrating adult salmon (kelts) in November to May and juvenile smolts in April to June in river mouths. Although predation of kelts and smolts will reduce consumption of adult salmon, it may still impact on subsequent returns of adults, and hence fisheries, as a proportion of these predated emigrants would have returned to the river. Finally, all seals present in rivers were assumed to be harbour seals. However, grey seals have been observed in the Spey, Conon and Ness (Butler 2004; authors' unpublished data) and due to their larger size they have a greater per capita daily energy requirement than harbour seals (23150 kJ day^{-1}; Hammond, Hall & Prime 1994).

The models also do not take account of indirect impacts of seals on stocks and fisheries. First, the presence of seals in rivers and estuaries may alter fish behaviour, reducing rod catches and therefore the economic viability of these fisheries. Secondly, salmon may be injured by seal attack (e.g. Thompson & Mackay 1999), but die subsequently of secondary effects. However, at present the extent of such factors are difficult to quantify.

The results should therefore only be considered as qualitative indications of the impacts of removing seal predation, rather than quantitative predictions. Furthermore, the models do not consider the effects of predation on stock–recruitment relationships underlying salmon population dynamics. Irrespective, they are helpful in demonstrating that the scale of salmon population units is important in determining the potential impact of seal predation, and hence identifying situations where actions to mitigate seal–salmon fishery conflict should be targeted. The results suggest that relieving predation pressure may have the greatest impact on spring salmon sub-stocks and fisheries, and particularly for rivers such as the Moriston, where smaller populations of spring salmon exist.

These models are therefore useful for managing protected populations of salmon and seals, such as those in the Spey, Moriston and Dornoch Firth SACs. While seal predation potentially has deleterious effects on spring salmon sub-stocks in the Spey and Moriston SACs, indiscriminate shooting of seals by fishery managers may also have significantly reduced the Moray Firth harbour seal population, and hence the conservation status of the Dornoch Firth SAC (Butler 2004; Thompson, Mackey, Barton, Duck & Butler in press). The models could be used to identify spatial and temporal bottlenecks where seal predation control can be undertaken, which minimises impacts on the conservation status of seal populations, but maximises benefits for salmon SACs, stocks and fisheries. This targeted approach is currently being piloted within the Moray Firth (Butler 2004), and is advocated in the management of similar marine mammal conservation issues elsewhere (Wade 1998; Read & Wade 2000). The tool could also be applied to the management of other depleted and/or inherently small salmon stocks, such as those on the west coast of Scotland, and in particular for other salmon and seal SACs.

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