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Authors: Harris, Catriona M., Calladine, John R., Wernham, Chris V., and Park, Kirsty J.

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REVIEW ARTICLE

Impacts of piscivorous birds on salmonid populations and game fisheries in Scotland: a review

Catriona M. Harris, John R. Calladine, Chris V. Wernham & Kirsty J. Park

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The Scottish populations of salmonids are important both ecologically and economically. Game fisheries for Atlantic salmon *Salmo salar*, sea trout *Salmo trutta trutta* and brown trout *Salmo trutta fari* are all highly acclaimed and generate substantial levels of income for Scotland, but many populations are in decline and efforts are being made to ensure the future sustainability of these species. These declines have led to a focus on the impact of piscivorous bird predation on fish populations. The purpose of our review was to assess the evidence for population-level impacts on salmonid populations, and/or economic impacts on Scottish game fisheries of predation by the four primary UK freshwater piscivorous bird species: cormorant *Phalacrocorax carbo*, goosander *Mergus merganser*, red-breasted merganser *Mergus serrator* and grey heron *Ardea cinerea*. There is evidence that these birds can, in some situations, remove large numbers of fish from stocked and natural fisheries. However, a lack of information on fish population levels, the numbers and species composition of feeding birds, and robust calculations of fish consumption has hampered the conversion of the results of the existing studies into useful quantitative measures of impact. As a consequence, few studies have demonstrated any reductions in numbers of breeding fish or fish productivity due to predation by piscivorous birds, or direct economic loss to fisheries in Scotland. We support a previous recommendation for a reiterative procedure of modelling, experimentation and remodelling to assess the impacts of piscivorous birds on fisheries. Wide-scale studies of the movements of piscivorous birds, their feeding locations in relation to river characteristics, and the factors that make fish particularly vulnerable to predation are seen as important areas for future research.

Key words: cormorant, economic losses, goosander, heron, predation, red-breasted merganser, salmon, trout

Catriona M. Harris, Centre for Conservation Science, School of Biological & Environmental Sciences, University of Stirling, and Centre for Research into Ecological and Environmental Modelling, University of St Andrews, UK - e-mail: catriona@mcs.st-and.ac.uk

John R. Calladine & Chris V. Wernham, BTO Scotland, School of Biological & Environmental Sciences, University of Stirling, UK - e-mail addresses: john.calladine@bto.org (J.R. Calladine); chris.wernham@bto.org (C.V. Wernham)
Kirsty J. Park, Centre for Conservation Science, School of Biological & Environmental Sciences, University of Stirling, UK - e-mail: k.j.park@stir.ac.uk

Corresponding author: Catriona M. Harris

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The future sustainability of Scottish freshwater salmonid fisheries, game fisheries in particular, is being threatened by a number of contributing factors. The factors that receive most attention, however, are often those that provoke emotive responses rather than those that necessarily have the greatest impact (Duffy 1995, Butler et al. 2006). Predation of salmonids by birds and mammals is one such factor: the conflict that has arisen as a consequence of competition between humans and predators has become increasingly controversial as fish populations have declined and predator populations have increased (Kirby et al. 1996, Carss 2003). Such conflict often results in calls for predator reduction but in the absence of evidence of predator impact, the efficacy of such management remains unknown (Marquiss & Carss 1994b, Butler et al. 2006). In this review, we aim to summarise the evidence for population-level and economic impacts of the four piscivorous bird species great cormorant *Phalacrocorax carbo*, grey heron *Ardea cinerea*, goosander *Mergus merganser* and red-breasted merganser *Mergus serrator* on salmonid populations and game fisheries in Scotland. Other factors that potentially impact upon salmonid stocks are also reviewed briefly.

Reviewing process

We conducted literature searches that encompassed published (peer-reviewed), 'grey' and web-based literature. Published material was identified initially using the ISI Web of Knowledge database (up to the year end of 2006). Other published material and 'grey' literature was identified by carrying out web searches using the Google search engine and from the reference sections of papers and reports already obtained. Literature covered in this review focuses on piscivorous birds and salmonid populations in Scotland, but studies investigating bird-salmonid/fishery interactions elsewhere were included in the discussion section where the issue of 'impacts' on fish populations from piscivorous birds was addressed specifically. We also conducted a small number of one-to-one consultations and workshops with key stakeholder groups (see the Acknowledgements), in order to assess research needs and identify further sources of unpublished data that might not have been found as a result of the literature search.

The level of critical evaluation to which a piece of 'evidence' can be subjected necessarily depends on the amount of supporting information that is provided. In the context of the reviewing for our study, full critical scientific appraisal was only possible where (at the very least) data were presented together with full details of the methodology used to collect and analyse them. Reports are generally not formally peer-reviewed, although some will have undergone internal review from the source organisation, or in some cases, there may have been a more formal external review process. For this review, we occasionally used unpublished data, and this has been made clear in the text. The full details of the data collection and analytical methods were not always available for these data.

What does impact of predation mean?

Any factor such as food availability, space for breeding or predation can be considered limiting (i.e. having a population-level impact) if it prevents a population from increasing or causes it to decline (Newton 1998). The impact of predation on prey species depends largely on whether and how predators respond to changes in prey density (Begon et al. 1990). They can respond by changing individual predation rates (the functional response) or their density (the numerical response; Solomon 1949). Predation mortality may be wholly or partially offset by improved survival of the remaining individuals, i.e. the predation may be compensated for via reduced mortality from other factors. This is thought to be the case for young salmonids in their first year of life (Armstrong 1997, Milner et al. 2003). For predation to have an impact at the population level, it must represent additive mortality (Begon et al. 1990). For example, it is thought that mortality of salmon at sea is largely density-independent (e.g. Milner et al. 2003), and if this is the case, predation on smolts (juvenile salmon physiologically adapted for the migration from fresh water to salt water) leaving to enter the marine environment may inflict additive mortality and reduce the size of the returning population.

Regardless of whether piscivorous birds exert population-level impacts on prey populations, they may inflict an economic impact on fisheries through competition with humans. There is only a direct economic cost if predators remove fish that would otherwise have been available for anglers, and that would have been caught. The economic impact of predation, therefore, does not necessarily equate to the number of individual prey taken by a predator. Predators may also exert economic impacts indirectly, without necessarily reducing population abundance. For example, when anglers perceive that there are fewer fish to catch, this can lead to a reduction in the number of anglers purchasing permits. For systems involving piscivorous birds and fisheries, the nature of the impacts may differ slightly between natural and stocked systems, and consist of:

- reductions in the number of fish reaching maturity and/or returning to the river;
- changes in fish behaviour reducing catchability;
- reductions in the number of fish available to anglers;
- reductions in the number of permits sold to anglers;
- reductions in the value of fish due to damage;
- costs of fishery protection measures;
- reductions in the breeding success of the fish population.

Status of Scotland's freshwater fisheries

Most freshwater sport fishing in Scotland has traditionally revolved around the game species that form the focus of this review: Atlantic salmon *Salmo salar*, sea trout *Salmo trutta trutta* and brown trout *Salmo trutta fari*. More recently, important sport fisheries have developed for other species such as rainbow trout *Oncorhynchus mykiss*, grayling *Thymallus thymallus* and coarse fish such as pike *Esox lucius*.

Information on numbers of salmon and sea trout caught by rod and line throughout Scotland each year is collated by the Fisheries Research Services, alongside the numbers caught by the netting industry (e.g. Fisheries Research Services 2006c). The catch statistics for the rod and line industry are believed to represent a suitable index of fish abundance, although there is no record of changes in angling effort over time (Youngson et al. 2002). For salmon, figures on abundance are broken down into seasonal components: spring salmon, summer salmon and grilse (salmon that have returned to fresh water after one winter at sea). In an effort to conserve stocks, anglers have increased the numbers of salmon and sea trout that are released again immediately after having been caught. These releases have been monitored since 1994. The term 'total rod catch' refers to the annual numbers of fish retained by the rod and line industry plus those caught and released.

Salmon fishing is the most highly acclaimed and economically important of Scotland's fisheries. However, whilst total rod catches of all salmon have remained relatively stable since 1950, there has been a long-term decline in the total rod catch of spring salmon (Fisheries Research Services 2006c), thought to be due, predominantly, to a decrease in survival at sea (Fisheries Research Services 2006a,c). It has been suggested that the decline over the last 50 years in fishing effort by the netting industry has partially compensated for the effect of declines in the survival of salmon at sea (e.g. Fisheries Research Services 2006c). Any such compensatory effect is now believed to be almost completely utilised, however, and if survival in the marine environment continues to decline, an increasing number of spawning populations are likely to be at risk (Fisheries Research Services 2006c). There has been relatively little research to investigate the threats facing salmonids in the marine environment, in part due to the difficulty of conducting such studies. Existing data indicate a positive linear correlation between numbers going to sea and numbers returning (see Milner et al. 2003 for review). Current management efforts are therefore focussed on populations within the freshwater environment with the objective of maximising the number that survive to go to sea.

As with salmon, net fisheries of sea trout have also declined, with the numbers of fish caught reflecting the decrease in effort (Fisheries Research Services 2006c). Although not so marked as the net fisheries, there has also been a decrease in rod catches of sea trout, with historically low levels of sea trout being caught by the rod and line fisheries in 2003, 2004 and 2005 (Fisheries Research Services 2006c). These trends also vary across Scotland, with the east coast fisheries showing little change, but west coast fisheries showing a marked decrease in the numbers caught (Fisheries Research Services 2006c).

The fishery for brown trout in Scotland is popular with anglers in both rivers and lochs (stillwater fisheries) and generates millions of pounds in revenue in some regions (e.g. Central Scotland and the Highlands; Radford et al. 2004). In areas where demand is high, for example in Loch Leven, both brown and rainbow trout are stocked to maintain angling levels. The rainbow trout is a non-native species in Scotland, but is being stocked increasingly in lochs and ponds for angling purposes, and rainbow trout fisheries have become an important economic and recreational resource in Scotland (Fisheries Research Services 2003, 2004). Of the total farmed rainbow trout production in 2005, 11.7% was supplied to fisheries for the purpose of restocking angling waters (Fisheries Research Services 2006b).

Together, all the freshwater fisheries within Scotland comprise an important component of the Scottish economy but are threatened by uncertainty surrounding the future productivity and economic viability of fish stocks. The economic importance of freshwater sport fisheries in Scotland is substantial, particularly in many rural areas. For example, in 2003, the total expenditure by anglers within the River Spey catchment was £11.8 million, 92% of which was due to salmon and sea trout anglers (Riddington et al. 2004). In 2004, the entire Scottish angling industry was estimated to generate £113 million in output, with salmon and sea trout angling accounting for £73 million of this total (Radford et al. 2004). The industry was shown to support around 2,800 jobs and generate nearly £50 million in wages and self-employment income to Scottish households.

Population estimates and trends of piscivorous birds

There has not been a recent review of the population sizes or population trends in Scotland of the five piscivorous bird species considered here (population estimates of shag *Phalacrocorax aristotelis* are also presented). We have assembled estimates using the highest quality data available to us to assess the status of these species within Scotland relative to European populations, and, in particular, recent trends (Table 1). Several of the population estimates have a number of caveats attached, in many cases because they have been produced using more recent trend information to extrapolate from older population estimates, some of which were derived from surveys not designed specifically for the species in question. In some cases, there has never been a survey that is comprehensive enough to allow a population estimate to be produced with any confidence (e.g. there has never been a specific survey of all breeding red-breasted mergansers in Scotland or Britain). A fuller consideration of the caveats associated with these population figures is provided in Park et al. (2005). The figures demonstrate that while the existing data suggest that several of the species have favourable conservation status at the UK and European level (e.g. the sawbills and grey heron), both great cormorant and shag are of medium conservation concern in the UK, and the shag has a population that is concentrated within Europe (see Table 1). Regardless of their present conservation listings, and often increasing populations in the early part of the period under consideration (post-1960), the populations of some species have shown evidence of decline in more recent years; i.e. breeding cormorant populations in northern Scotland and possibly Scottish wintering numbers, breeding shags, wintering and possibly breeding red-breasted mergansers, wintering goosanders and some local reports of declines in breeding birds.

Impact of piscivorous birds on game fisheries in Scotland

Cormorants

The literature on the great cormorant (subsequently referred to as 'cormorant') does not generally distinguish between the two races that are known to occur in England and Wales, but not in Scotland (Carss 2003). Most of the literature refers to cormorant, but it is possible that misidentification of shags may have occurred in some studies encompassing coastal regions.

The perceived level of impact of cormorant predation in Britain has increased in recent years and

Table 1. Most recent estimates of the population size in Scotland, trends since 1960, and population status within Europe for the five piscivorous bird species covered by the current review. Superscribed numbers refer to the main sources of reference which are listed below the table itself. The populations include breeding (Bre) and wintering (Win) birds. For full details of derivation of estimates see Park et al. (2005).

Species	Pop.	Most recent population estimate	Year of estimate	Caveats for population size	Trend since 1960	Caveats for trends	% of European breeding population[a]	BOCC listing[b]	SPEC status[c]	EU Wild Birds Directive Annex[d]	Notes
Great cormorant	Bre	3,626 apparently occupied nests[1]	1998-2002	Some underestimate due to asynchronous breeding and breeding abstinence	Decline 1960s - late 1980s;[1] increasing or stable late 1980s - 2004 in most regions except northern Scotland[1,2]	Trends from national censuses supported by annual sample monitoring	*P. c. carbo* 7.8% All races 1.4%	Amber	Non-SPEC	NOT LISTED	
	Win	ca 4,250 individuals[3,4]	1985/86 updated to 2005/06[e]	Comprehensive survey in 1985/86 (4,549 individuals) extrapolated to 2005/06 from smoothed WeBS indices	General increase 1986/87 - 1992/93, followed by decline to 2005/06e		Wintering population comprises mostly Scottish breeding or bred birds.[5]				
Shag	Bre	21,487 apparently occupied nests[1]	1998-2002	Some underestimate due to asynchronous breeding (20-40%) and breeding abstinence	Increase 1960s - late 1980s;[1] decrease late 1980s - 2004 in most regions except southwestern Scotland (increase 1994-2004)[1,2]	Trends from national censuses supported by annual sample monitoring	*P. a. aristotelis* 29.4-32.6% All races 25.9%	Amber	SPEC 4	ANNEX I	
	Win	Unknown		Winter numbers probably comparable with those present during the breeding season[5]	Unknown	Winter numbers not monitored directly	Wintering population probably mostly Scottish breeding or bred birds.[5]				
Red-breasted merganser	Bre	3,600 individuals[6]	1988-1991	From general atlassing work. No specific representative survey information	Increase 1960s - early 1980s;[7] stable (possible decline) early 1980s - early 1990s[6,8]	As for population size	1.6-3.1%	Green	Non-SPEC	ANNEX II-2	
	Win	ca 3,800 individuals[4,9,10]	1994/95-1998/99 updated to 2005/06[e]	Estimated for 1994/95-1998/99 by assuming that an average of 51% of wintering birds in Britain winter in Scotland (5,020 individuals) and extrapolated to 2005/06 from smoothed WeBS indices	Increase 1974/75 - 1986/87;[9] subsequent decline to 2005/06.[4,10]		Scottish breeding birds augmented by birds from Iceland, Greenland and northern Europe in winter[5]				

Goosander	Bre	ca 1,800 pairs[6,8]	1987-1991 updated to 2006[f]	Sample survey of rivers and general atlas work (1987-1991: ca 1,500 pairs) extrapolated to 2006 from UK WBS/WBBS trend	Increase, though not constant, 1960-2002;[8,3,13] some local declines reported[11]	As for population size	4.0-6.7%	Green	Non-SPEC	ANNEX II-2
	Win	ca 4,600 individuals[4,9,10]	1994/95-1998/99 updated to 2005/06[e]	Estimated for 1994/95-1998/99 by assuming average of 40% of wintering birds in Britain winter in Scotland (6,440 individuals) and extrapolated to 2005/06 from smoothed WeBS indices	General increase 1960s - late 1980s;[9] subsequent decline to 2005/06[4,10]		Net movement of birds out of Scotland for the winter[5]			
Grey heron	Bre	4,359 (95% confidence limits 3,539-5,300) active nests[12]	2002	Underestimate (by <15%)?	Increase, though not constant, 1960-2006[g,12]		2.2-2.7%	Green	Non-SPEC	NOT LISTED
	Win	Unknown		Not monitored outside the breeding season	Unknown	As for population size	Scottish breeding and bred birds probably augmented by migrants from northern Europe in winter[5]			

Notes

[a] Based on information provided by Mitchell et al. (2004) for cormorant and shag, and BirdLife International/European Bird Census Council (2000) for red-breasted merganser, goosander and grey heron. In cases where the Scottish contribution was not separated from the UK contribution as a whole for the European estimate, the European estimate from which the proportion here is derived may include an estimated contribution from Scotland that differs from that given in this table.

[b] Birds of Conservation Concern listing (Gregory et al. 2002): 'Red List' are species that are 'Globally Threatened' according to the IUCN, those whose population size or range has declined rapidly in recent years, those whose population has declined historically and not shown a substantial recovery. 'Amber List' are species with unfavourable conservation status in Europe (see note b), those whose population size or range has declined moderately in recent years, those whose population has declined historically but made a substantial recent recovery, rare breeders, and those with internationally important or localised populations. 'Green List' are species that fulfil none of the above criteria.

[c] European conservation status listing (BirdLife International/European Bird Census Council 2000 B: 'SPEC 3' are species whose global populations are not concentrated in Europe but have Unfavourable Conservation Status within Europe ('Endangered', 'Vulnerable', 'Rare', 'Declining', 'Localised' or 'Insufficiently Known' categories). 'SPEC 4' are species whose populations are concentrated in Europe (> 50% global population or range in Europe) but have 'Favourable Conservation Status' ('Secure' category). 'Non-SPEC' are species not of conservation concern in Europe.

[d] See http://europa.eu.int/comm./environment/nature/nature_conservation/focus_wild_birds/species_birds_directive. 'Annex I' are species in danger of extinction, species vulnerable to specific changes in habitat, species considered rare because of small populations or restricted local distribution, and other species requiring particular attention for reasons of the specific nature of habitat. 'Annex II' are species that, owing to their population level, distribution and reproductive rate, may be hunted throughout the European Community ('Annex II-1') or in specific Member States ('Annex II-2').

[e] Updated from estimates provided by Park et al. (2005) using updated smoothed trend information from the BTO/WWT/RSPB/JNCC Wetland Bird Survey (G. Austin, pers. comm.).

[f] Updated from estimates provided by Park et al. (2005) using updated smoothed trend information from the BTO Waterways Bird Survey (WBS)/Waterways Breeding Bird Survey (WBBS; J. Marchant & A. Joys, pers. comm.). Assumes that the Scottish trend since 1991 is similar to that for the UK for which there is equivocal evidence.

[g] Updated from estimates provided by Park et al. (2005) using updated information from the BTO Heronries Census (J. Marchant, pers. comm.).

References: 1 - Mitchell et al. 2004, 2 - Mavor et al. 2006, 3 - Rehfisch et al. 1999, 4 - BTO/WWT/RSPB/JNCC Wetland Bird Survey, WeBS (mostly BTO unpubl. data), 5 - Wernham et al. 2002, 6 - Gibbons et al. 1993, 7 - Thom 1986, 8 - Armitage et al. 1997, 9 - Lack 1986, 10 - Kershaw & Cranswick 2003, 11 - Marquiss et al. 1998, 12 - BTO Heronries Census (unpubl. data), 13 - BTO Waterways Bird Survey (WBS)/Waterways Breeding Bird Survey (WBBS); unpubl. data and Baillie et al. 2007.

calls for population regulation have become more frequent (e.g. Kirby et al. 1996), so much that in England and Wales in September 2004, the decision was taken to licence the killing of an increased number of birds (see http://www.naturalengland.org.uk/conservation/wildlife-management-licensing/docs/proposals-strategy.pdf). The main conflict between cormorants and freshwater fisheries in Europe, as a whole, occurs during the winter months, when there are large numbers of cormorants roosting inland (Carss 2003). During the winter period, the main concerns within Scotland relate to cormorants removing large numbers of wild and stocked trout from important stillwater fisheries, such as Loch Leven, and large numbers of young salmonids (particularly large parr and smolts) from rivers (McIntosh 1978, Carss et al. 1997b). There is also concern about cormorants wounding fish, which may reduce their survival and alter their behaviour, so that they become harder for anglers to catch (e.g. Russell et al. 1996).

Most Scottish studies reviewed here consist of observational data either relating to bird numbers and foraging behaviour or dietary data obtained from pellets, regurgitates or stomach samples from shot birds (Table 2). Whilst these studies can be combined with daily food intake (DFI) estimates to calculate consumption (e.g. Carss & Ekins 2002, Wilson et al. 2003), researchers have used a variety of different methods to derive DFI, so that it is hard to make meaningful comparisons between studies (Carss et al. 1997a, Gremillet et al. 2003). In addition, few studies have sufficient fish population data with which to estimate the proportion of fish being removed. In order to demonstrate the scale of any population-level impacts, however, the degree to which the predation is additive to other sources of mortality is required (Armstrong et al. 1998). Some studies have suggested that cormorant predation on salmon in rivers is low and that, of the salmon that are removed, small smolts or pre-smolt parr are preferentially selected (Carss & Marquiss 1997, 1998; but see Armstrong & Stewart 1996, Carss & Marquiss 1999b, Middlemas & Armstrong 2002 for a discussion of the methodology used to distinguish parr and smolt). The stage of the fish taken by predators is important in relation to the likely impact of predation. Thus, whilst mortality in young fish (pre-smolt) is considered to be density dependent, when they become smolts and leave the river system for the sea, it may be largely density independent (e.g. Milner et al. 2003).

The highest quality data relating to a Scottish fishery are for the trout fishery at Loch Leven (e.g. Carss & Marquiss 1992, 1994, Carss et al. 1997b, Wright 2003, Stewart et al. 2005). Since 1983, Loch Leven has been stocked with brown trout (and since 1993 also with rainbow trout), and recent work has indicated that the numbers of brown (both stocked and wild) and rainbow trout removed by cormorants are substantial (Stewart et al. 2005). The diet of cormorants shot under licence at Loch Leven was assessed and used to estimate the likely loss of trout to cormorants roosting on the loch. The model estimated that 80,803 (95% Cl: 41,617-128,248) brown and 5,213 (95% Cl: 830-12,454) rainbow trout were taken by cormorants over a seven-month period (Stewart et al. 2005). The population of brown trout with >260 mm fork length (i.e. sufficiently large to contribute directly to the fishery) in Loch Leven in 1998 was estimated to be 157,000 using a mark-recapture method and 48,000 using sonar and netting (Wright 2003); the reason for the two estimates being so markedly different is not discussed in any depth. A comparison between the estimated number of brown trout (>260 mm fork length) taken by cormorants, and the size of the brown trout population suggested that cormorants were removing 30% (95% Cl: 16-49%) of the stock over the study period using mark-recapture estimates, and 98% (95% CI: 53-159%) of the stock using sonar and netting population estimates (Stewart et al. 2005). The latter, very high estimate in particular reflects the high degree of uncertainty in the estimation of the fish population size. For rainbow trout, the proportion of fish removed by cormorants was 31% (CI: 5-73%) over the study period (Stewart et al. 2005). The study also found a significant positive relationship between stocking levels of yearling brown trout and numbers of cormorants counted the following winter over a 17-year period. There appear to be different patterns of prey selection in juvenile and adult birds, and between the sexes, such that adult males fed almost exclusively on trout whereas juvenile females fed mainly on small shoaling fish (sticklebacks *Gasterosteus aculeatus* and perch fry *Perca fluviatilis*; Stewart et al. 2005). In economic terms, cormorant consumption was estimated to be removing 40% of the rainbow trout fishery catch, whereas for brown trout, cormorants removed almost 16 times the fishery catch (Stewart et al. 2005). The degree to which this predation may be compensated for by decreases in other sources of mortality is unknown although the authors

Table 2. Summary of methods used to estimate consumption by piscivorous birds (see also Carss et al. 1997a): Studies reviewed for this paper have been given as examples of where particular techniques have been used. Superscribed numbers refer to the main sources of reference which are listed below the table itself.

Methods	Advantages	Assumptions	Possible biases	Limitations
Estimation of dietary composition				
Stomach contents of shot birds & regurgitates[1-19]	• Stomachs contain fresh material • Bias related to digestion is lower than for pellet analysis • Can be related to sex, age & health of bird	• Shot birds are representative of population • Regurgitates represent complete sample of food intake	• Influence of bird behaviour on vulnerability of being shot • Digestion of food prior to returning to regurgitation • Nestling regurgitates may not be representative of adult diet	• Generally small sample sizes • Spatial & temporal scale often limited
Pellets[14,20,21]	• Relatively cheap • Can obtain large samples • Minimal disturbance to birds	• Contents reflect diet over the previous 24 hours • Pellets collected from roosting site assumed to come from particular foraging sites	• Underrepresentation of fish with easily digestible hard parts • Inaccuracies in fish size estimation	
Feeding observations[6,15,2]	• Minimal disturbance to birds • Can obtain large samples • Can gather data over large temporal &spatial scales	• All prey are brought to the surface	• Prey items of birds close to observer easier to identify & may not be the same as those of distant birds • Observer error in estimation of prey size	• Extent of swallowing fish underwater unknown • Cannot be used to calculate DFI; unknown whether a bird has fed to satiation during observation period
Estimation of Daily Food Requirement (DFR)				
Requirements of captive birds[2,23]	• Detailed individual measurements • Can manipulate diet & conditions	• Captive bird diet, environmental conditions & energy budgets representative of wild birds	• Flying & swimming components of energy budget not included in calculations • Birds fed dead fish - no active foraging	• Extrapolation to wild birds limited by assumptions
Daily energy expenditure (DEE) based on basal metabolic rate (BMR) & time-budgets[2,4,18,19,20]	• Relatively easy & cheap to collect data on time-budgets through focal sampling & direct observation	• BMR often predicted from allometric relationship with body mass • DEE assumed to be 3 x BMR		• Few empirical BMR data available for birds > 1000 g; BMR extrapolated from small birds • Energy costs unknown for many activities • Time-budgets should be season specific
Doubly-labelled water experiments[2,23]	• More direct measurement of energy expenditure than other methods	• Assumes captive birds behave naturally when released in wild for measurements	• Extrapolation to other species based on body size only, not activity levels	• Expensive • Small sample sizes
Estimation of bird population size				
Counts at roosting sites[16,18,20]	• Annual trends in bird numbers can be detected	• All birds at roosting site feed exclusively at fishery of interest		• Requires monthly/seasonal abundance data for comparison with fish presence, particularly migrating salmonids
Counts on river / stillwater[4,6,7,9,10,22]	• More fishery site-specific than counts at roosting sites	• Counts carried out at time of day when greatest numbers of birds are using river/ Stillwater • All birds on river/stillwater feed there exclusively		• Difficult to cover entire river/large stillwater • Requires monthly/seasonal abundance data for comparison with fish presence, particularly migrating salmonids

References: 1 - Feltham 1990, 2 - Marquiss et al. 1991, 3 - Feltham & MacLean 1996, 4 - Marquiss et al. 1998, 5 - Carss & Marquiss 1999b, 6 - Feltham et al. 1999, 7 - J. Bulter (unpubl. data), 8 - Carss & Marquiss 1996, 9 - McIntosh 1978, 10 - Kennedy & Greer 1988, 11 - Davies & Feltham 1994, 12 - Davies & Feltham 1996, 13 - Carss & Marquiss 1997, 14 - Collis et al. 2001, 15 - Collis et al. 2002, 16 - Carss & Marquiss 1992, 17 - Carss & Marquiss 1994, 18 - Stewart et al. 2005, 19 - Derby & Lovvorn 1997, 20 - Noordhuis et al. 1997, 21 - Keller 1998, 22 - Lekuona & Campos 1997, 23 - Feltham 1995.

conclude that there is currently no evidence for compensation, and that the potential for competition between cormorants and this fishery at this site is therefore high (Stewart et al. 2005).

The predation by piscivorous birds of fish stocked for the purposes of angling is often viewed as a direct economic loss to the fishery concerned. Whilst it is not known to what extent cormorant predation actually reduces the number of fish available to anglers, the perception that there are fewer fish to catch can lead to a reduction in the number of anglers purchasing permits (DEFRA Technical Advice Note 2004, Carss 2003). There are no reported examples of this in Scotland, however, during a conflict resolution workshop held in the Lea Valley in southeastern England, many anglers stated that they had stopped fishing the Lea because of low catch rates and the increase in cormorant numbers. These claims were reflected in the declines in fishing permits (Carss 2003). For example, in 1992/93 (over a period of nine months) approximately 23,000 anglers purchased a day ticket, 600 season tickets were sold and club membership at this time numbered around 6,500. In contrast, the forecast for the 12 months to December 2002 expected to see (at the time of reporting) season and club membership dropping by approximately 54% and day membership decreasing by >70%. This has had knock-on effects for fishing tackle shops across northeastern London, many of which have reportedly closed (Carss 2003).

In summary, there have been few quantitative studies undertaken that have actually demonstrated reductions in population size or productivity as a result of cormorant predation in Scotland. The recent study at Loch Leven indicated that large numbers of fish were removed by cormorants. However, it also highlighted some of the problems that exist in quantifying the scale of the impact on fish stocks and fishery economics, in part due to the uncertainties over fish population sizes.

Sawbill ducks

In Scotland, sawbill ducks (i.e. goosanders and red-breasted merganser) are predominantly perceived as a problem on rivers, where they are thought to consume substantial proportions of salmonid stocks, in particular salmonid smolts (e.g. Marquiss et al. 1991,1998). The majority of studies of sawbill predation carried out in Scottish rivers have been dietary and/or observational, but they are not, however, all independent studies as many relate to dietary information collected from the same individual shot birds (e.g. Marquiss & Carss 1998, Carss & Marquiss 1999a). Doubly-labelled water and respirometry experiments have been carried out on captive birds (Feltham 1995), which have improved estimates of consumption, but some of the assumptions associated with the doubly-labelled water method (see Table 2) and with the comparison of consumption with fish populations are either untested or have been shown to be violated to some degree (see Carss & Marquiss 1998 for details).

For both sawbill ducks, diet is varied, but there are consistent patterns in all the Scottish dietary data sets that are important to consider when gauging potential impact on any given river: diet is less diverse and contains a greater proportion of salmon in northern rivers as compared to southern rivers; and larger numbers of salmon are consumed in early winter, March and April compared to all other times of the year (Marquiss & Carss 1998). Most early studies assumed that birds were feeding on 'average-sized' smolts, leading to calculations of sawbills removing up to 35% of salmon production (e.g. Shearer et al. 1987). Since then, however, some studies have indicated that the birds preferentially take parr and small smolts and this has implications for the extent to which any losses can be considered additive and the overall impact of predation on these fish populations, depending on the point at which population regulation switches from density-dependent to density-independent (e.g. Feltham 1990, Marquiss et al. 1998).

By measuring the metabolic rates of nine captive goosanders released onto two Scottish rivers, and using data from previous dietary studies, daily consumption of salmon was estimated and numbers of fish removed was calculated (Feltham 1995). Annual predation of smolts by goosanders was estimated to have been 3-16% of the annual smolt production for one river in eastern Scotland (Feltham 1995). This assumes, however, that captive birds behave as wild birds upon release, the validity of which has been questioned (Carss & Marquiss 1998). A recent quantitative study on the Spey catchment in Scotland attempted to estimate the impact that salmon smolt removal by sawbills has on the number of returning adults and therefore, the number of fish available to anglers (J. Butler, unpubl. data). The minimum loss of salmon to sawbill ducks was calculated as 18,582 smolts between February-April 2003, equating to 3-5% of the smolt run, a loss of 335 salmon to the rod fishery and up to £569,500 of lost revenue to the local economy. This value assumes each rod-caught salmon is worth £1700 to the local economy, which was calculated using the figure derived for total expenditure on the rod fishery for salmon and sea trout on the Spey in 2003 (Riddington et al. 2004), divided by the rod catch for the same year. It is believed that these values represent underestimates, because the study focussed on the impact of predation on the spring salmon stock, so it did not include the losses of large parr and sea trout smolts from the calculations, or losses outside of the period February-April (J. Butler, unpubl. data). Caution is required, however, in assessing the economic impact of changes in fish populations. Specifically, Riddington et al. (2004) highlight the non-linear nature of economic returns from fish such that "a doubling of the returning salmon stock will not result in a doubling of the economic impact of salmon angling" and that "the causal chain between salmon stocks and output, income and employment is complicated and is not linear".

There may be differences in the proportions of salmon in the diet of sawbills on different rivers, and so any economic impact is also likely to vary between rivers. Salmon was predominant in the stomachs of sawbills from the three northern-most rivers in one study in Scotland, but in the other nine rivers, trout, eel *Anguilla anguilla* or minnow *Phoxinus phoxinus* were the main dietary constituents (Marquiss & Carss 1998). These results could reflect differences in river characteristics or the relative ratios of salmon to sawbill populations on the different rivers, and further work is required in order to clarify the reasons for the observed dietary variation.

In summary, there is some evidence that sawbill ducks may have population-level impacts on salmon fisheries in some Scottish rivers, but the extent of any impact has not been quantified. Estimates of impact are likely to vary between studies, however, and all of the studies undertaken to date have necessarily incorporated assumptions, some of which have been proven to be violated to a greater or lesser degree.

Grey herons

Herons have been reported less often as a threat to Scottish fisheries than cormorants and sawbills, and their perceived impact has generally been reported for the fish farming industry (Carss 1993, Quick et al. 2004, Park et al. 2005). However, a questionnaire survey indicated that anglers do perceive herons to be a problem throughout Britain, largely in rivers but also in still waters in northwestern and south-eastern England (Carss & Marquiss 1996). To our knowledge, there have been no assessments of grey heron impact on river or stillwater fisheries in Scotland, or in Britain as a whole (see also Hughes et al. 1999).

Other factors affecting Scottish game fisheries

Few of the Scottish studies reviewed here have considered how predation by piscivorous birds compares to other sources of mortality, and the lack of quantitative studies on piscivorous bird predation makes any quantitative comparisons with other mortality factors impossible at present. Below, we discuss briefly other factors thought to be affecting the Scottish salmonid fishery, despite evidence not always existing for the Scottish situation.

Other predators

Aside from piscivorous birds, the main predators of salmonids in freshwater in Scotland are seals, mustelids, piscivorous fish and humans. In Scotland, there are two species of seal, the grey seal *Halichoerus grypus* and the common seal *Phoca vitulina*. Most individuals of both species spend all their time at sea, feeding exclusively on marine fish species, although some also feed on estuaries and up rivers, where they are perceived to be removing commercially important salmonids and impacting on salmonid populations (e.g. Last 2000, Butler et al. 2006). The main studies of predation by seals have been largely observational and dietary (e.g. Boyle et al. 1990, Pierce et al. 1991, Greenstreet et al. 1993, Carter et al. 2001). One of the problems encountered when carrying out dietary studies of seals is the high digestibility of salmonid otoliths, which may lead to under-representation of salmon in diet analysis (Pierce et al. 1991 and references therein). It is thought that seals in the UK are unlikely to be responsible for the long-term declines in salmon abundance (SCOS 2005), although modelling work has indicated that the removal of seals from small rivers at the start of a year is likely to have a positive impact on salmon populations, particularly on the spring salmon stocks, which are in decline and at low population levels in some rivers (SCOS 2005, Butler et al. 2006). Otters *Lutra lutra* and mink *Mustela vison* are both found in riparian habitats in Scotland and have been reported to feed on salmonids, but due to the population status of both these species in

Scotland (in particular, otters), it is not thought that either are currently having a large impact on populations (Carss et al. 1990, Cunningham et al. 2002). Predation on juvenile salmonids by fish such as pike, eels or larger salmonids may be substantial (McIntosh 1978, Henderson & Letcher 2003, Hyvarinen & Vehanen 2004), and there have been some attempts by managers of salmonid fish to control populations of piscivorous fish, such as pike (Morrison 1988). McIntosh (1978) suggested that such predation on juvenile salmonids is compensatory mortality, however, and in fact may reduce density-dependent competition within a fish population.

Habitat degradation

Water quality, quantity and the physical structure of water courses are all important components of salmonid habitat, many of which have been altered over time through anthropogenic activities (e.g. Gilvear et al. 2002). In Scotland, one of the main pollutants of concern is contamination of rivers from the fish farming industry (e.g. Hennessey et al. 1996, Jacobs et al. 2002). Climate change may affect conditions such as temperature within both freshwater and marine ecosystems, (e.g. Friedland 1998, Swansburg et al. 2002, Stefansson et al. 2003), and both river and sea surface temperature have been shown to be related to the growth and survival of salmonids (Friedland et al. 2000, Swansburg et al. 2002). There are many hydro-electric dam constructions on rivers in Scotland, and although there are no studies that report the impact of these on salmonid populations in Scotland, there are a number of other studies from Europe and North America that show that they block the upstream movement of migratory fish such as salmonids, thereby obstructing their return to their spawning grounds (e.g. Levin & Tolimieri 2001, Koed et al. 2002). They also invariably alter flow regimes and change the nature of the habitat available downstream of the dam (Dauble et al. 2003). In addition to this, dams create bottlenecks, where fish are delayed in their migrations and become more vulnerable to predation (eg. Collis et al. 2002 and references therein, Koed et al. 2002, Mathers et al. 2002).

Survival at sea

Poor survival in the marine environment is considered to be one of the main factors contributing to the declining numbers of returning salmonids in Scotland (e.g. Fisheries Research Services 2006a). However, survival at sea is very difficult to quantify directly because of the huge complexity of the marine environment. Food availability in the sea is of great importance to survival, as the marine stage in the life cycle of a salmonid is the main growth stage. Evidence to date suggests that long-term changes in prey availability are linked to changes in the climate and sea-surface temperatures, and this has resulted in a decline in the abundance of salmon, a trend which is likely to continue with predicted temperature changes in the future (Beaugrand & Reid 2003).

Aquaculture

In 2005, approximately 900,000 fish were reported as having escaped from fish farms in Scotland (Fisheries Research Service 2006b), and as a result of continuing escapes, there is concern that farmed fish may compromise the genetic integrity of wild stocks. Evidence from a river system in Ireland suggests that both farmed and hybrid salmon progeny can survive to the smolt stage, survive at sea and even return to their river of origin (McGinnity et al. 1997). Although farmed salmon progeny have a lower chance of survival to the smolt stage, they grow faster than hybrid and wild salmon and competitively displace wild fish from preferred habitat (McGinnity et al. 1997). Therefore, the survival of farmed and hybrid progeny is likely to be threatening wild salmon genetic integrity, and levels of adaptation and fitness to some extent (e.g. Fleming et al. 2000). Fish farming has also been linked with an increase in reports of sea-lice on wild salmonids (SEERAD 2001a,b, Butler 2002).

Discussion

The controversy surrounding the impact of the four piscivorous birds on fisheries covered by this review is not an issue confined to Scotland, or to the game fishing industry. This particularly applies to cormorants because of their widespread distribution. For example, in a recent report on cormorant-fisheries conflicts across Europe, Carss (2003) reported that the highest proportion of fish species recorded in conflicts involving cormorants were cyprinids followed by salmonids, perch/pike and a number of fish species associated with coastal aquaculture. Looking specifically at game species, we found case studies from Europe and North America that report that the estimated proportion of salmonids removed by cormorants from rivers can be high in some cases (e.g. Kennedy & Greer 1988, Lekuona & Campos 1997, Collis et al. 2001, 2002, Koed et al. 2006). It should be noted that much of the literature from North America, including some of the afore-mentioned studies, relates to the double-crested cormorant *Phalacrocorax auritus*, and Pacific salmonid species; therefore, we have limited our discussion of these studies. Although relevant studies exist from other geographical locations and for closely-related species, focussing the review on the situation in Scotland has highlighted the difficulties associated with assessing the impact of piscivorous birds on fish populations and fisheries in general and the following 'take-home' messages can be applied to more than just the Scottish situation.

Most of the relevant studies on the impacts of piscivorous birds on salmonid fisheries have been based on observational and/or dietary data, and the conversion of these data into useful quantitative measures of impact has often been hampered by a lack of information on fish populations and reliable consumption calculations. This does not necessarily mean that there are no impacts, but rather that the difficulties of measuring the key parameters of fish populations and bird predation have not allowed the scale of any impact to be assessed rigorously. Marquiss et al. (1991) reviewed a number of experimental sawbill duck removal studies that were carried out in Canada but concluded that in all cases, experimental design was sufficiently flawed to prevent impact assessment. Experiments in which birds are excluded from sites through netting or removal, and where the outcome (e.g. fish population size) can be measured and compared to similar sites with no manipulation, are the best way to demonstrate impact (Marquiss & Carss 1994a). Steinmetz et al. (2003) carried out such an experiment in the USA and showed that the presence of belted kingfisher *Ceryle alcyon* and great blue herons *Ardea herodias* altered both fish abundance and size distribution. Unfortunately, these types of experiments are most often only practical on fish cages or small areas of stocked stillwaters, so may be of limited relevance to larger, more complex systems.

Other than those reviewed in Marquiss et al. (1991), we found only one other study that attempted to quantify the effect of removal on populations of piscivorous birds (Marquiss 1998). Long-term bird survey data from the Rivers Dee and North Esk in Scotland were used to assess the effectiveness of bird removal (Marquiss 1998). In three out of four cases, shooting reduced the subsequent numbers of sawbill ducks on a stretch of river, but the reduction in numbers was always much less than the number of birds shot (e.g. 16 fewer birds resulting from 49 birds being shot), indicating that areas with artificially low bird densities become more attractive (Marquiss 1998). Whilst shooting in this context is designed to scare birds away for periods when fish are most vulnerable to predation, rather than to reduce population densities, it does demonstrate that the scale of reduction in numbers of birds at a site was influenced by the time of year that shooting took place and the overall intensity of shooting (Marquiss 1998). Besides this example, there are few studies that have shown that the removal of predators (either by scaring or killing) actually reduces bird abundance or increases fish yields (Draulans 1987, Russell et al. 1996). Studies, such as those described above, generally assume the 'surplus-yield calculation', whereby it is believed that removing the top predator from a system results in more fish becoming available to the fishery (Yodzis 2001). The reality is unlikely to be this straightforward, due to the complexity of the relevant ecosystems and their underlying food webs (Yodzis 2001).

In a previous review of the impacts of piscivorous birds on fisheries, Wires et al. (2003) stress the need for reliable diet assessment for predatory birds, combined with daily food intake estimates, improved information on the biology and demography of each predatory bird species, spatial and temporal abundance and distribution information for the relevant fish populations and an understanding of fish population dynamics. Marquiss & Carss (1994a,b) also emphasised the importance of experimental manipulations in demonstrating 'cause and effect' but acknowledged the difficulty of carrying out such experiments on rivers or large stillwater fisheries. Expanding on this recommendation, Marquiss et al. (1998) suggested a combination of modelling and experimentation, i.e. 'model-field experiment-remodel', due to the limitations associated with each in isolation. For the development of testable models, however, a number of parameters relating to both bird and fish biology are required and these are listed in Marquiss et al. (1998). We fully support these previous recommendations.

Following our review of the literature, and discussions with stakeholders, we have identified the need for a Scotland-wide survey of piscivorous birds to be carried out along important salmonid rivers, designed carefully to encompass the important seasons of the year when impacts are believed to be greatest and to cover all important salmonid rivers (Park et al. 2005). This work should be combined with research to establish the relationships between bird numbers and distribution and the characteristics of individual river sections. To get closer to assessing the likelihood of impact in this complex system, a review of existing demographic data for fish populations in Scotland is needed, given the quality of existing empirical data and sensitivities of such models to the many parameters involved. In addition, a review of the data on numbers of fish-eating birds (available from applications for licences to control them) would be valuable, to assess their utility for demonstrating spatial and seasonal variation in bird numbers, and hence for informing the design of Scotland-wide river surveys.

In conclusion, piscivorous birds are perceived to impact on fisheries in a number of ways that are all interrelated: economically, ecologically and behaviourally (Kirby et al. 1996, 1997, DEFRA Technical Advice Note 2004). They have the potential to compete directly with anglers for the same species and sizes of fish, reduce recruitment by taking smaller fish, damage fish that are then not marketable and are more prone to disease, and make fish less catchable through stress and behavioural changes. Piscivorous birds also have the potential to impact on fisheries indirectly by influencing the perceptions of anglers as to the 'quality' of a fishery, leading to loss of permit sales. However, research is required before many of these putative impacts can be quantified or demonstrated at the population level.

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