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IAN DAVIDSON

SENIOR TECHNICAL ADVISOR SALMONIDS

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Incorporating natural variability in biological reference points and population dynamics into management of Atlantic salmon (*Salmo salar* L.) stocks returning to home waters

Jonathan White[1]*, Niall Ó Maoiléidigh[2], Paddy Gargan[3], Elvira de Eyto[2], Gerald Chaput[4], Willie Roche[3], Phil McGinnity[5], Walter W. Crozier[6], Paddy Boylan[7], Dennis Doherty[8], Kealan O'Higgins[3], Brian Kennedy[9], Ian Lawler[10], David Lyons[11], and Ferdia Marnell[12]

[1]*Marine Institute, Oranmore, Co. Galway, Ireland*
[2]*Marine Institute, Newport, Co. Mayo, Ireland*
[3]*Inland Fisheries Ireland, Dublin, Ireland*
[4]*Fisheries and Oceans, Moncton, NB, Canada E1C 9B6*
[5]*School of Biological, Earth and Environmental Sciences, University College Cork, Cork, Ireland*
[6]*Agri-Food and Biosciences Institute, Newforge Lane, Belfast BT9 5PX, Northern Ireland*
[7]*The Loughs Agency, Derry–Londonderry BT47 2AB, Northern Ireland*
[8]*Electricity Supply Board, Castlebanks, Ardnacrusha, Co. Clare, Ireland*
[9]*Environmental Protection Agency, Castlebar, Co. Mayo, Ireland*
[10]*Bord Iascaigh Mhara, Dun Laoghaire, Co. Dublin, Ireland*
[11]*National Parks and Wildlife Service, Galway, Ireland*
[12]*National Parks and Wildlife Service, Dublin, Ireland*

**Corresponding author: tel: + 353 91 387 361; fax: + 353 91 387 201; e-mail: jonathan.white@marine.ie.*

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Following advice from the International Council for the Exploration of the Seas and North Atlantic Salmon Conservation Organization, Irish salmon stocks have been managed on a river-by-river basis since 2007 with biological reference points (BRPs) based on maximum sustainable yield (MSY). A method for estimating BRPs at the river scale and the associated variability arising from observed variability in population structures and fecundities is presented here. Calculations of BRPs (referred to as conservation limits, CLs) were updated and their natural variability was included. Angling logbooks provided new river-specific weight data to give sea age and fecundity ranges, and improved estimates of river-wetted areas, to account for available nursery habitat for juveniles and river-specific carrying capacities, were introduced. To transport BRPs, Bayesian stock–recruitment analysis was re-run with an updated list of monitored rivers and smolt ages. Results were converted to salmon numbers per river in Monte Carlo simulations incorporating the variability in sea ages and fecundities. Minimum sample size rules were implemented to reduce sampling error effects. Results showed that average total CL increased by 7%, average one sea-winter (1SW) CL decreased by 5% and average multi-sea-winter (MSW) CL increased by 157%. Differences were attributed to increases in wetted areas, MSW proportions, and changes in both 1SW and MSW fecundities. While some changes were large, we believe that these updated CLs provide more accurate estimates and with associated confidence limits they are more robust, river-specific, and readily incorporated into stock assessments. As a significant improvement on their predecessors, they represent a major development for the conservation and management of salmon stocks. Additionally, the approach described is portable across stocks and has the potential to be implemented in other jurisdictions to improve the management of Atlantic salmon. Finally, this method of incorporating variation has application for the development of BRPs and management of other species.

Keywords: Bayesian hierarchical stock and recruitment analyses, biological reference points, conservation limits, natural variability, risk assessment, salmon.

Introduction

Atlantic salmon (*Salmo salar*) populations have been declining throughout its range in the North Atlantic since the mid-1980s (Chaput, 2012; ICES, 2013a) and as a valuable resource and species listed in Annex II of the EU Habitats Directive [92/43/EEC], their conservation is mandated in European countries. Providing scientifically robust management advice for Atlantic salmon is challenging owing to the extensive population structuring of the species to individual rivers throughout its range, there being more than 2000 such rivers in the North Atlantic. In addition, fisheries take place on most of these populations in individual rivers and fisheries managers have sought advice on appropriate spawner reference points for these individual river populations with the objective of establishing sustainable fisheries. Management of salmon stocks is best conducted in home waters, at the river level (NASCO, 1998, 2006; ICES, 2013a), and the stated management objective of the North Atlantic Salmon Conservation Organization (NASCO) is to maintain stocks above conservation limits (CLs) by management targets. For a fishery to take place, there needs to be a high probability that the numbers remaining after a fishery meet the CL. This requires the establishment of river-specific biological reference points (BRPs), along with estimates of the number of returning fish to advise on the availability of a harvestable surplus over the required CL. Faced with this challenge, science has endeavoured to utilize diverse and generally incomplete information on abundance, demographics, and population dynamics.

The International Council for the Exploration of the Seas (ICES) have recommended the use of BRPs to manage fish stocks in accordance with principles of the precautionary approach framework (ICES, 1996), including consideration of scientific uncertainty and risk management (Cadrin and Pastoors, 2008), and NASCO also recommends the use of the Precautionary Principle (FAO, 1995, 1996). CLs for North Atlantic salmon are considered to be synonymous with a limit reference point and the default choice has been to establish the CL at the level of spawning stock that will achieve long-term, average maximum sustainable yield (S_{MSY}; NASCO, 1998; ICES, 2013a). Typically, the reference points are derived from stock–recruitment (S–R) analysis and implemented as a limit reference point with the objective that there be a very low probability (<5%) of the spawning escapement after fisheries being less than the CL (ICES, 1996).

The MSY approach is intended to make the best use of ecosystem productivity (ICES, 2012) and has traditionally been used as a fixed, point measurement (ICES, 2013a, b). Cadrin and Pastoors (2008) noted that 'the role of F_{MSY} (fishing mortality that produces the maximum sustainable yield) as a limit reference point in a dynamic system is a considerable shift from the traditional view of S_{MSY} as an objective, estimated using methods that assume equilibrium'. River and marine ecosystems are dynamic, changing temporally and spatially owing to biotic, abiotic, and anthropogenic factors. For Atlantic salmon, this will have consequences on the spawning potential for a population, freshwater and marine productivity and carrying capacities, and ultimately the stock and recruitment potential. If S_{MSY} is to be used as a limit reference point in a dynamic system, incorporating the variability of that dynamic system into the BRP is essential. The approach taken in this study was to estimate river-specific CLs, incorporating the uncertainty around estimates of MSY, the ratio of one sea-winter (1SW) to multi-sea-winter (MSW) fish and their respective fecundities, for each of the 140 rivers being managed as salmon fisheries in Ireland (Standing Scientific Committee on Salmon, 2015).

Relatively few rivers have historical long-term time-series from which to derive S–R parameters, Prévost *et al.* (2003) developed a Bayesian hierarchical stock–recruit analysis (BHSRA) and analysed a set of 13 monitored rivers covering the range of northeastern Atlantic salmon. They used latitude (a proxy for productivity associated with climate among other factors) and riverine wetted area (accounting for river carrying capacity) as covariates to characterize variations in abundance and recruitment rates of Atlantic salmon in Europe and to transfer reference points among studied populations to data-poor situations in non-monitored rivers. Subsequently, Ó Maoiléidigh *et al.* (2004) applied this approach to provide stock status and catch advice for Irish salmon stocks with CLs summed from the river level and applied at a regional scale. Transported BRPs were implemented as point estimates, with ratios of 1SW to MSW fixed by river, fecundity estimates of 1SW and MSW fixed nationally, and wetted area estimates made through ground-truthed GIS (McGinnity *et al.*, 2003). Following the closure of the Irish marine salmon fishery in 2006, CLs have been used at the river scale to provide annual catch advice (Standing Scientific Committee, 2006, 2007, 2008, 2009, 2010, 2011).

Since 2001, new data have become available through the introduction of a mandatory carcass tagging and logbook scheme for all salmon fishing (commercial and recreational). Since 2000, estimates of abundance of salmon in rivers have been improved through the installation and operation of 26 fish counters in various rivers. More accurate ground-truthing of freshwater habitat (McGinnity *et al.*, 2012) has provided improved estimates of wetted areas of Irish salmon rivers. Finally, fecundity to weight relationships from several salmon populations have been analysed and associations described (de Eyto *et al.*, 2015).

While variability around management objectives has been incorporated into assessments of mixed-stocks of Baltic resident Atlantic salmon (Michielsens *et al.*, 2008; ICES, 2013b) and examined for Pacific salmonids [sockeye salmon (*Oncorhynchus nerka*), Holt and Peterman (2008)], stock assessments that incorporate uncertainty around CLs are not commonly the case. The analyses presented here represent a further development in incorporating uncertainty into the development of BRPs at the river scale. The study provides an example of how diverse and incomplete information on demographics is used to develop stock and recruitment time-series, how innovative hierarchical Bayesian models are used to analyse data from multiple stock and recruitment datasets and develop transferrable parameters of interest that incorporates data-rich, data-poor, and unstudied populations in a consistent framework, and finally how the parameters of interest with uncertainties are incorporated into the development of management reference points in currencies (fish) for managing fisheries and other anthropogenic impacts on Atlantic salmon. This new approach uses distributions rather than fixed point descriptors of key variables and incorporates the uncertainties to provide updated river-specific CL estimates and importantly, their associated uncertainty. To deal with small sample sizes from some rivers, the approach included a set of minimum sample size rules to ensure that, in such situations, realistic parameter distributions were used. The compilation of these new data and the development of the modelling approach provide a more robust framework for CL estimation and the subsequent provision of catch advice. Atlantic salmon is used as the case study to demonstrate the approach for a highly complex species population and management structure. This presents a further step forward from theoretical to practical incorporation of natural variability in fish populations into stock assessments and ultimately catch advice for sustainable fisheries.

Material and methods

The inference and prediction processes for developing reference points for populations of Atlantic salmon from Ireland are presented in Figure 1. To undertake stock–recruitment analyses and establish river-specific CLs, river-specific estimates of salmon fecundity and sea age ratios of 1SW : MSW salmon are needed.

Biological characteristics and reconstruction of spawner and recruitment series

River-specific biological characteristics, including sea age composition and fecundity, and time-series of spawners and recruits were reconstructed using data from Irish rivers.

River-specific data on salmon weights were available from the database of reported angling catch weights (National Wild Salmon and Sea Trout Carcass Tagging and Logbook Scheme) from 6 years, 2006–2011, a period before the implementation of the CLs used in stock assessment and management. The data, a total of 174 795 observations, consisted of individual weights of rod-caught salmon by river and date of capture. A total of 169 991 observations with complete information were used in the following analyses.

The first analysis consisted of estimating the river-specific sea age composition in Irish rivers. Nicieza *et al.* (1991) reported on the bimodality of salmon fork length corresponding to sea age groups and Bacon *et al.* (2009) reported efficiencies of >97.9 and $>95.8\%$ in assigning 1SW and two sea-winter ages, respectively, based on weight. We chose to separate the adult age classes using catch weight. On the basis of expert opinion and the analysis by Quinn *et al.* (2006), salmon weights were divided into two groups, split at 4 kg as an initial division of 1SW and MSW age classes. Median weights and associated standard deviations of the two sea age groups were used to parameterize normal frequency distributions [after Burgman *et al.* (1993) and Latto (1992)] of the weights of the 1SW and MSW components of each river stock (for example in Figure 2, the Blackwater river in Kerry). Median values of the observed weight ranges were used as the average as they proved the best estimate of the most likely 1SW and MSW weights in the data owing to the initial data split at 4 kg [consistent with de Eyto *et al.* (2015)].

The bimodal frequency weight distributions of the weight data in the database of river-specific angling reports were used to apportion the returns of salmon to the monitored rivers and to define the sea age composition for all sampled rivers into their sea age components (Figure 1). Weights were used to define age class in general preference to date of catch owing to variability in run timing across salmon rivers. This variability may or may not be prevalent, however, by tending to age classification based on weight, the

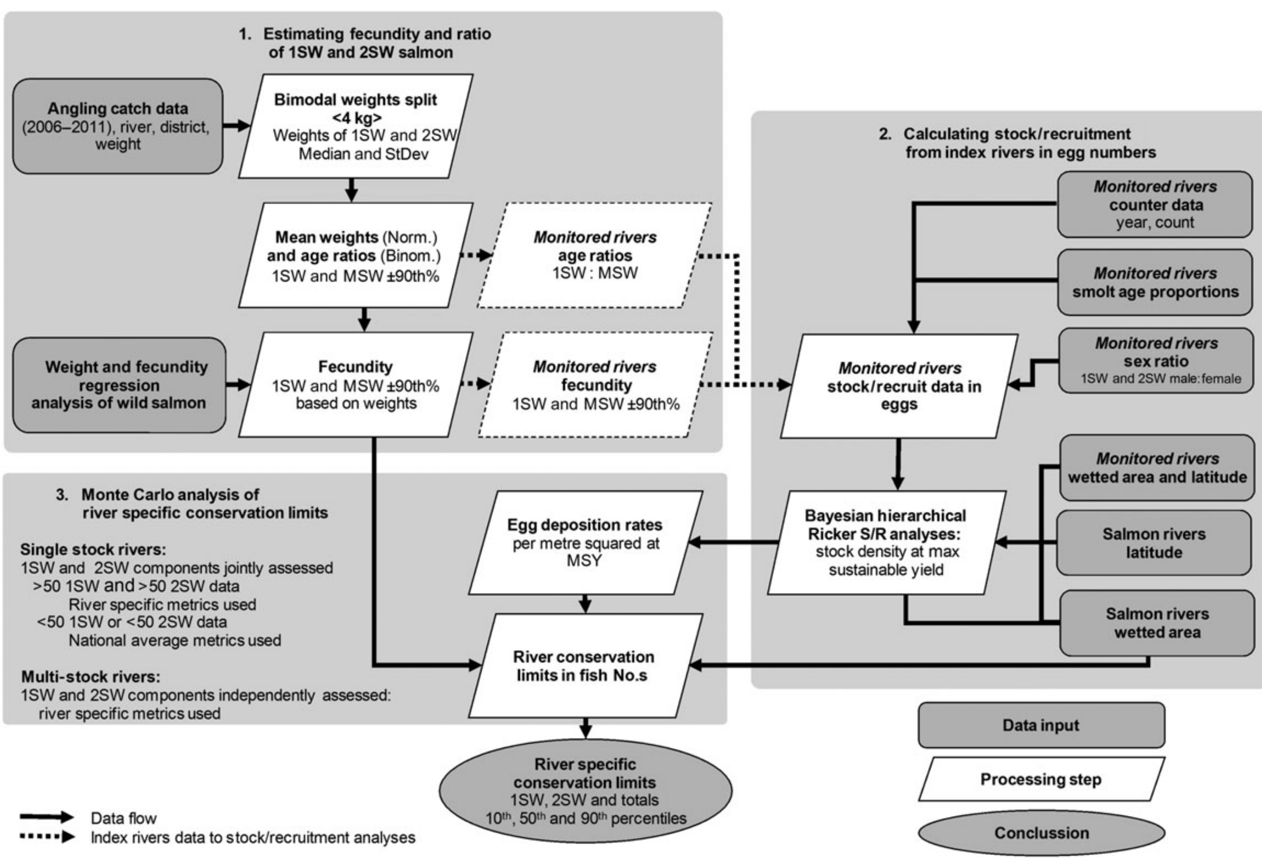

Figure 1. Schematic overview of the process of estimating river-specific CLs.

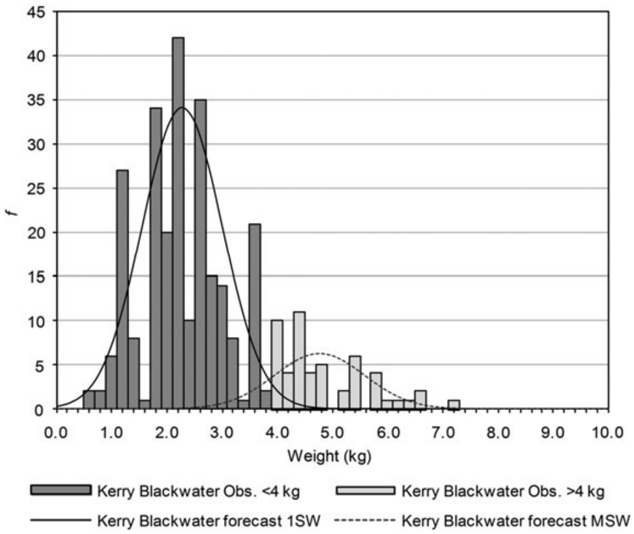

Figure 2. Observed and forecast weight frequency distributions of 1SW and MSW fish in the Blackwater river, Kerry.

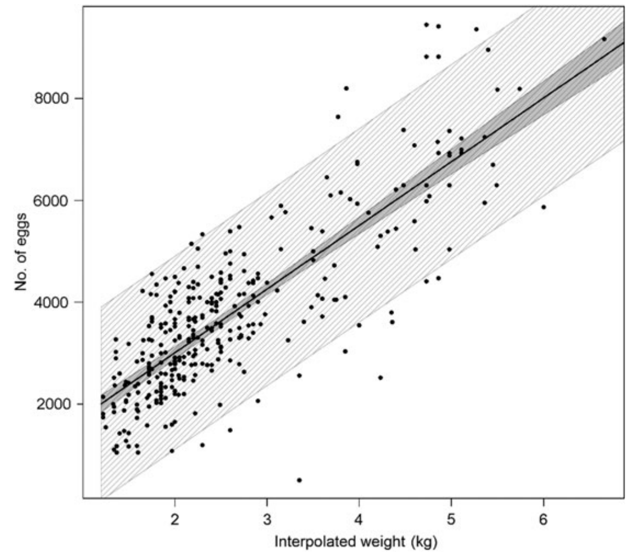

Figure 3. Salmon weights to the number of stripped eggs for 336 Irish wild salmon stripped between 1992 and 2011. Centre line is the least-squares linear regression following Equation (1); the dark grey area is the 95% confidence interval; the light grey area is the 95% prediction interval; $r^2 = 0.266$.

dates of catch become superfluous. Traditionally, the early run of salmon or "spring salmon" in Ireland occurs before May 31st in a distinct run (evidenced from catches and counters) and is known to comprise the earlier returning and larger multi-sea-winter fish. While some multi-sea-winter fish return to all rivers, there are only a small number of true "spring salmon" rivers. In instances where greater than 20% of the catch on a river occurred before May 31st, the number of fish recorded before this period was used to define the MSW proportion of the age structure on the river. This was considered as an appropriate cut-off based on empirical evidence and expert judgement, and represents a considerable contribution from MSW fish to the overall egg deposition of the population and a sizeable proportion of the catch to separate spring returning MSW salmon from summer returning 1SW salmon. There were 16 of 140 rivers where the cut-off was applied. In instances where fewer than 50 measurements for either weight class were available, national average values were applied (Supplementary Appendix S1).

Repeat spawners are known to occur but in small proportions (Ó Maoileidigh *et al.*, 2002; ICES, 2010; Klemetsen *et al.*, 2003) and while they are not incorporated as a specific class in these analyses, their fecundity and probability of occurrence is encapsulated in the MSW age class. In a small number of instances where recent, detailed, investigations of weights or 1SW : MSW ratios had been conducted in specific rivers, these data were used rather than those derived from catch statistics as they were viewed as being more accurate (instances recorded in Supplementary Appendix S1).

Fecundities of 1SW and MSW salmon, in eggs per fish and their 10th and 90th percentiles, were estimated using the normal distribution of mean weight estimates and the corresponding $\pm 90^{\text{th}}$ percentiles, and the weight to fecundity relationship for salmon from Irish rivers described by de Eyto *et al.* (2015) [Equation 1]. The fecundity data of de Eyto *et al.* (2015) were collected from 336 adult wild salmon sampled between 1992 and 2011 (Figure 3).

$$\text{Eggs} = 505.56 + 1250.83 \times \text{weight (kg)}. \qquad (1)$$

The stock and recruitment time-series analysed by Ó Maoiléidigh *et al.* (2004) were updated using revised freshwater habitat areas (McGinnity *et al.*, 2012), updated information on abundance of recruits and spawners, and updated sea age composition, and fecundity data. The abundance data are from annual counts of salmon moving up stream through fish counters or traps. The numbers of returning salmon and the spawning population were converted into egg equivalents using the proportions at sea age (1SW or MSW), the average fecundity of each age class based on river catch weight records in the catch statistics for the two sea age classes, and proportion of female in each sea age class. Sex ratios as reported by Ó Maoiléidigh *et al.* (2004), for 1SW at 0.6 : 0.4 and MSW at 0.85 : 0.15 females to males, respectively, were retained as there was no significant change in the available information from monitored stocks for this parameter compared with that used previously and no new systematic studies to allow variation in this parameter to be included. On the basis of age of returning spawners and smolt age proportions specific to each river (Table 1), the brood year for each age class of spawners was assigned (Potter *et al.*, 2004). Recruits and spawners were expressed in units of total eggs. Reconstructed time-series were available for 22 rivers ranging from 51°N to 55°N latitude (Table 1). The number of observations per river ranged from 3 (the Kerry Blackwater and the Casla) to 26 (Burrishoole) with 20 having 5 or more, 17 having 8 or more, and 15 having 10 or more years of observations.

The river-specific details of the sample sizes in the catch logbook data, the applied sample sizes following the application rules, and the resulting age composition ratios of 1SW to MSW, weight ranges, applied fecundities, and their 10th and 90th percentile are listed in Supplementary Appendix S1.

Hierarchical Bayesian model to estimate reference points

The hierarchical Bayesian model described in Prévost *et al.* (2003) was used in this analysis, in which a Ricker stock and recruitment function was assumed (Ricker, 1954, 1975). Non-informative priors, as described in Prévost *et al.* (2003) and Ó Maoiléidigh *et al.* (2004), were assumed. Fitting was done using Monte Carlo Markov Chain in Gibbs sampling with the software OpenBUGS

Table 1. Stock–recruitment monitored rivers, latitudes, wetted areas, number of observations, and smolt age composition (arranged according to latitude).

River	Country	Latitude (dec °N)	Wetted area (ha)	Number of years of S–R observations	Smolt age composition[a]		
					1 year	2 years	3 years
Frome	UK (England)	50.50	87.642	20	0.95	0.05	0.00
Tamar	UK (England)	50.58	292.566	13	0.07	0.92	0.01
Bandon	Ireland	51.74	136.041	4	0.05	0.86	0.08
Curraune	Ireland	51.84	20.162	4	0.05	0.86	0.08
Blackwater (Lismore)	Ireland	51.91	888.253	4	0.05	0.86	0.08
Blackwater (Kerry)	Ireland	51.91	27.611	3	0.05	0.86	0.08
Feale	Ireland	52.34	211.806	4	0.05	0.86	0.08
Slaney	Ireland	52.60	321.927	4	0.14	0.79	0.07
Dee	UK (England)	53.00	617.000	15	NA[b]	NA[b]	NA[b]
Liffey	Ireland	53.20	233.782	4	0.05	0.86	0.08
Casla	Ireland	53.34	17.621	3	0.05	0.86	0.08
Screebe	Ireland	53.44	6.192	6	0.05	0.86	0.08
Erriff	Ireland	53.67	54.040	21	0.02	0.85	0.14
Dee	Ireland	53.84	94.684	3	0.05	0.86	0.08
Burrishoole	Ireland	53.99	12.767	26	0.14	0.85	0.01
Ballysadare	Ireland	54.12	214.721	3	0.05	0.86	0.08
Lune	UK (England)	54.50	423.000	18	NA[b]	NA[b]	NA[b]
Eany	Ireland	54.71	45.746	3	0.05	0.86	0.08
Bush	UK (North Ireland)	55.00	84.550	21	0.30	0.70	0.01
Faughan[c]	UK (North Ireland)	55.00	88.238	11	–	–	–
Mourne[c]	UK (North Ireland)	55.00	1036.056	13	–	–	–
North Esk	UK (Scotland)	57.00	210.000	16	NA[b]	NA[b]	NA[b]

[a]Smolt age proportions as advised by river managers/biologists from *ad hoc* electrofishing and scale reading.
[b]Smolt ages were not available, and spawner–recruit data were provided precalculated in the number of eggs.
[c]No update of data was available for the rivers Faughen or Mourne on that of Prèvost *et al.* (2003).

(Lunn *et al.*, 2009). Convergence was achieved with 66 000 iterations of three chains. Leaving the first 22 000 as burn-in gave 132 000 implemented iterations and was checked using Gelman–Rubin diagnostic (Gelman and Rubin, 1992) and the multivariate analogue of Brooks and Gelman (1998) for assessing convergence of multiple parameters simultaneously.

The reference point chosen was "S_{opt}", the egg deposition corresponding to MSY (Prévost *et al.*, 2003). This value is considered equivalent to a limit reference point and a CL as used in other jurisdictions (ICES, 2012).

River-specific CLs

The posterior distribution for the CL of a new river without stock and recruitment data was derived from the BHSR model. The CLs are expressed in units of eggs per m^2 of river habitat area. The egg deposition rates are converted to total eggs by raising to the wetted area of a river and converting into adult fish equivalents (number of 1SW and MSW fish) using the river-specific proportions of 1SW and MSW sea age groups, and 1SW and MSW salmon fecundities.

For this study, the relationship reported in Ó Maoiléidigh *et al.* (2004) was further developed through Monte Carlo simulations in Equation (2), by introducing variability at the 10th and 90th percentiles around the estimate of median ratios of 1SW to MSW fish, median fecundities of 1SW and MSW fish, and the posterior BHSRA transport model median BRP egg deposition rates [after Prévost *et al.* (2003)]. This translates MSY in the number of eggs per metre squared into MSY in numbers of adult salmon per metre squared while also providing the variability around the estimates.

$$S_{MSY_{fish,j,i}} = \frac{(S_{MSY_{eggs,j,i}} \times Hab_j)}{(P1SW_{j,i} \times P1SWFem_{j,i} \times Fec1SW_{j,i} + PMSW_{j,i} \times PMSWFem_{j,i} \times FecMSW_{j,i})}, \quad (2)$$

where

(i) $S_{MSY_{fish,j,i}}$ = spawners for MSW in terms of fish for river j and simulation i,

(ii) $S_{MSY_{eggs,j,i}}$ = CL in units of eggs per m^2 for river j and simulation i, from the BHSR model,

(iii) Hab_j = habitat area (m^2) for river j,

(iv) $P1SW_{j,i}$ = proportion of adult salmon that are 1SW sea age for river j in simulation i,

(v) $P1SWFem_{j,i}$ = proportion of female in the adult salmon of 1SW sea age for river j in simulation i,

(vi) $Fec1SWFem_{j,i}$ = fecundity in terms of eggs per female adult salmon of 1SW sea age for river j in simulation i, and

(vii) $PMSW_{j,i}$, $PMSWFem_{j,i}$, and $FecMSW_{j,i}$, are, respectively, proportion of adults that are MSW sea age, proportion of female in the MSW adult sea age group, and fecundity of female adult MSW salmon for river j and simulation i.

Uncertainties in the biological characteristics for each river and in the CL per river were incorporated by Monte Carlo simulations according to Equation (2). Triangular distributions were implemented for the proportions of 1SW and MSW fish, their fecundities (based on variations in mean weight by sea age), and the river MSY in the number of eggs. The triangular distributions were characterized with median values set as mid-points, and 10th and 90th percentiles as minimum and maximum values, respectively. The Monte Carlo simulations were run in Oracle Crystal Ball (risk assessment software add-in for Microsoft Excel™ from Oracle™). Triangular Monte Carlo distributions were applied to accommodate asymmetry in the egg deposition rates and subsequently calculated distributions (Ó Maoiléidigh *et al.*, 2004; Forseth *et al.*, 2013). A total of 75 000 Monte Carlo iterations were run to describe the posterior distributions of the CLs in terms of fish for each river.

Analysis of changes in input data that result in changes in CLs

Multiple linear regressions were used to quantify the relative consequences of the changes in input data, sea ages, fecundities, and wetted areas, on revised CLs, the effect in terms of differences between the original and the revised CLs.

Results

Salmon count data from reference rivers provide a range of S–R scenarios (Table 1), which were incorporated into the hierarchical structuring for transfer to non-monitored rivers, using latitude and wetted area as co-variates. Ricker S–R plots of monitored rivers (Figure 4)

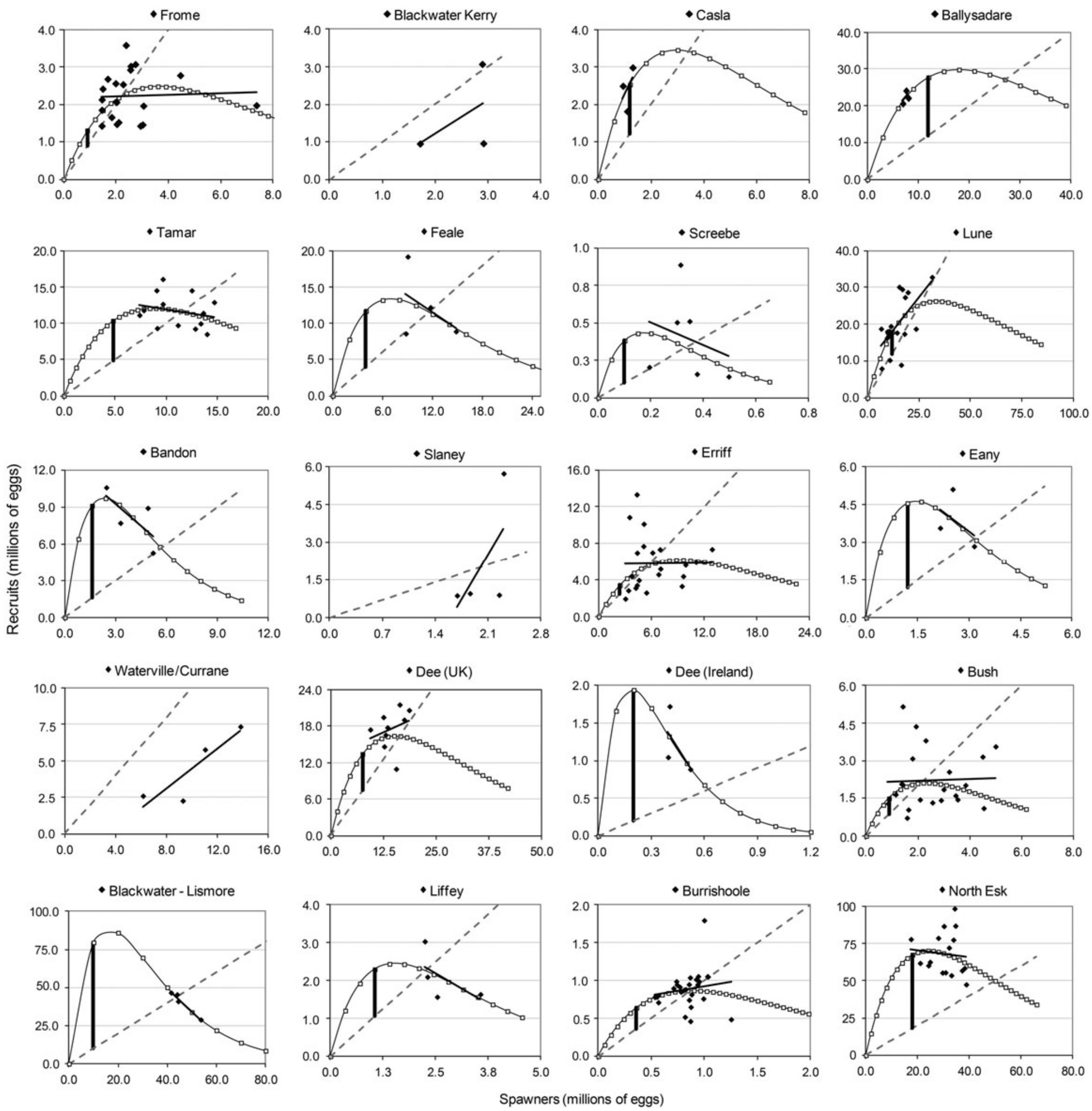

Figure 4. Stock–recruitment series of the monitored rivers used in BHSRA and transportation of BRPs. Filled points = S–R data points; lines with open points = Ricker curves; dashed diagonal lines = 1 in 1 replacement; solid vertical lines = surplus at MSY; solid horizontal/diagonal lines = linear regressions of S–R data points. Ricker curves are not detailed for the Blackwater—Kerry, Slaney, and Waterville/Currane as data did not lead to prediction of asymptotes. Details for the rivers Faughan and Mourne are not given as no update from Prévost *et al.* (2003) was available.

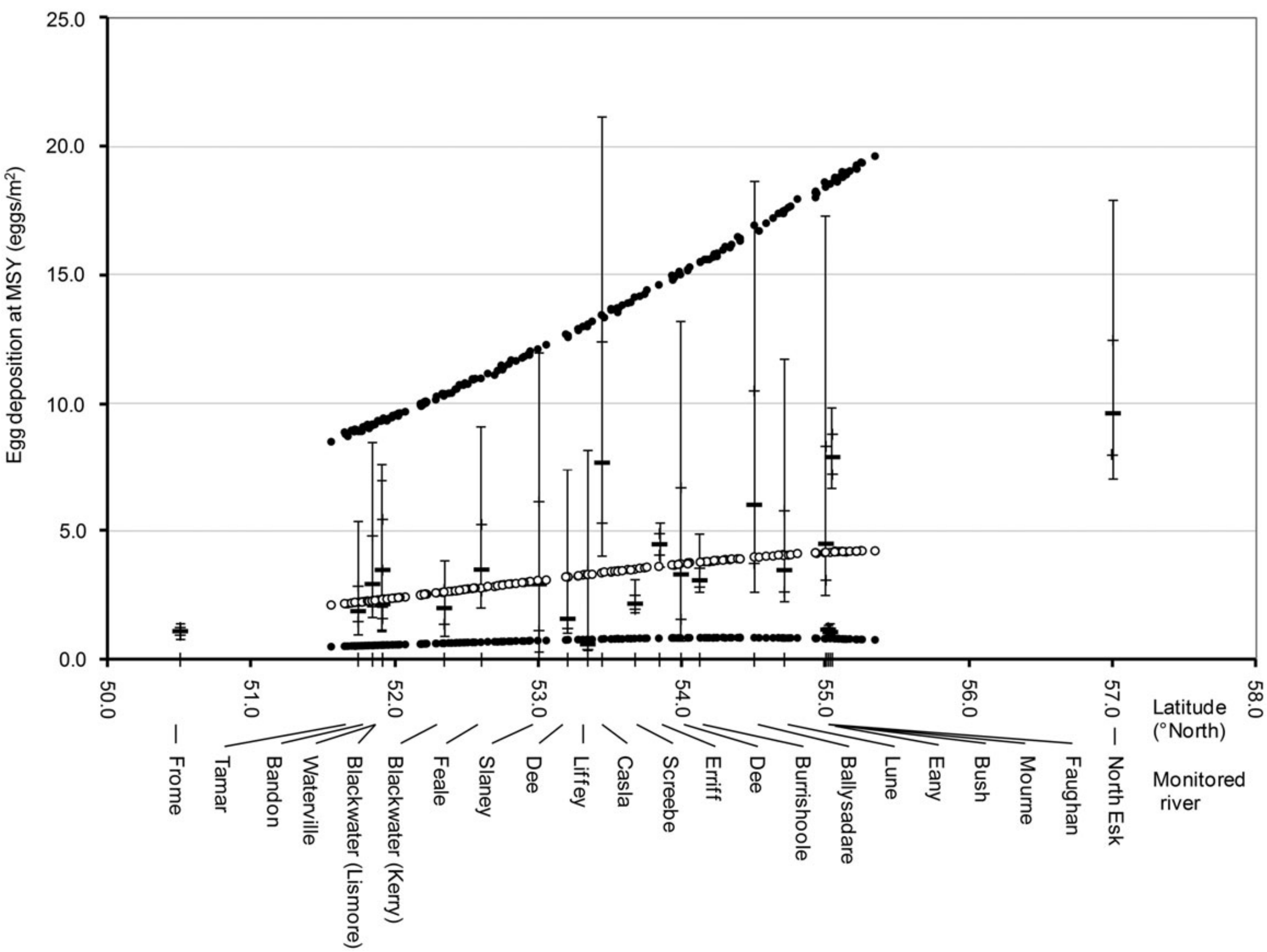

Figure 5. Egg deposition at MSY through BHSRA for monitored rivers (as indicated) and transported to other Irish salmon rivers. Open circles are median transported egg deposition rates at MSY of non-monitored rivers, and filled circles are their 90th percentiles. Error bars are 90th percentiles of the monitored rivers with interquartile ranges and medians.

demonstrate a range of spawner—recruit dynamics. While the data from the Kerry Blackwater, the Slaney, and the Currane were individually uninformative of the stock and recruitment dynamics, they were kept in the hierarchical analyses as observations provide information on variability in the S–R relationship within and among rivers.

Ricker S–R models of all rivers excluding the three rivers mentioned above suggest compensatory and in several cases overcompensation of the stock and recruitment series (Figure 4). Analyses with the updated list of monitored rivers, stock–recruitment time-series, and wetted areas showed a relationship between egg deposition rates and latitude similar to that shown by Prévost *et al.* (2003). Recruitment (in eggs per m^2) in monitored rivers increased with northerly progression (Figure 5), showing that salmon populations in rivers produce higher recruitment with increasing latitude. For the monitored rivers, the positive skew in S_{MSY} and recruitment at MSY (R_{MSY}) distributions are evident (Figures 5 and 6). Such positive skews are commonly found in distributions of organisms exhibiting spatial clumping (Elliot, 1977).

When these relationships were transferred to non-monitored rivers by the BHSRA using the covariates of wetted area and latitude, the values of egg deposition at MSY showed a similar increase with latitude and increasing positive skew in their distributions, covering similar ranges to the monitored rivers (Figure 5).

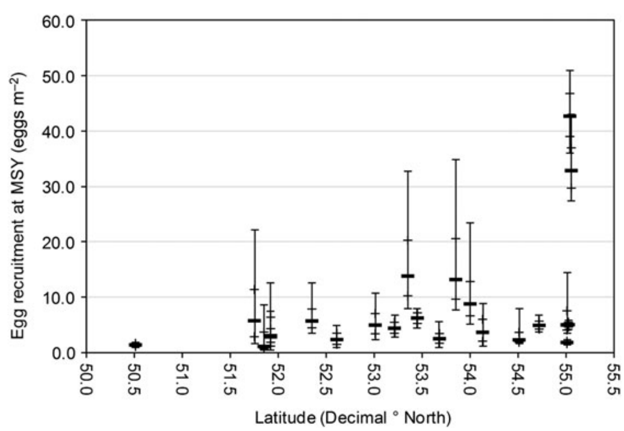

Figure 6. Egg recruitments at MSY from monitored rivers through BHSRA (medians, interquartile ranges, and 90th percentiles).

The Monte Carlo construction of river-specific CLs enabled the uncertainties in the input data to be incorporated and for the resulting CLs to have associated uncertainty ranges. These uncertainties can be carried forward into stock assessments and included in determining attainment of CLs. Calculated CLs (Supplementary

Appendix S2) display positively skewed distributions, which are evident when comparing the 10th and 90th percentiles, medians, and means of the estimate.

Differences between the CLs applied to national catch advice before 2012 and those calculated here varied widely. Of the 139 age-specific 1SW CLs, the values increased for 31 rivers and decreased in 107 rivers (Figure 7). Almost all (137 of 139) of the MSW CLs increased. For combined sea age CLs, the values increased for 53 rivers (Figure 7).

For all but three rivers, 1SW CLs are greater than their MSW counterparts. This may be expected in Ireland where most stocks are grilse (1SW) dominated. The three exceptions are the Slaney (Wexford), the Lackagh, and the Leannan (Letterkenny). For the Slaney, the 1SW : MSW ratio was set based on independent age analyses (Inland Fisheries Ireland, unpublished data). For the Lackagh and Leannan, the split was made based on the date of capture as the two rivers are known to have strong spring runs of MSW fish.

The effect on CL estimates from using updated biological variables and wetted areas was discernible (Supplementary Appendix S2). For 1SW CLs, most changes [accounting for 130 (94%) of rivers] were within ±50% of the pre-2012 CLs and 100 rivers (72%) within ±20% of their previous values (Figure 7). Similarly, 130 (94%) newly calculated total CLs were within ±50% of their pre-2012 values and 109 (79%) within ±20% of their original values. Changes were greater for the MSW CL components, where 13 (9%) exhibited changes within ±50% of their MSW CLs, 38 (28%) increased by up to 100% on their pre-2012 counterparts, and 100 (72%) showed increases of over 100%. This may be expected considering the age structure of populations in the original study, with most fixed at 92.5% 1SW and 7.5% MSW, and sea age fecundities fixed for all at 3400 eggs per 1SW salmon and 8000 per MSW salmon.

For 1SW, MSW, and total CLs, the change in wetted areas had an extremely significant effect (Table 2). For 1SW CLs, changes in the fecundity of the age group also had an extremely significant effect, whereas for the MSW CLs, the proportional change of the age group had a significant effect. For the total CL, the changes in fecundities of both age groups had significant effects on CLs.

Post-2012 1SW CLs were strongly correlated with the pre-2012 values (Figure 8; $p < 0.001$; r^2 of 0.85). While they are in general slightly greater for smaller stocks and lower for larger stocks, the 90% uncertainty interval for the regression line included unity. Paired *t*-test of log-transformed pre- and post-2012 1SW CLs

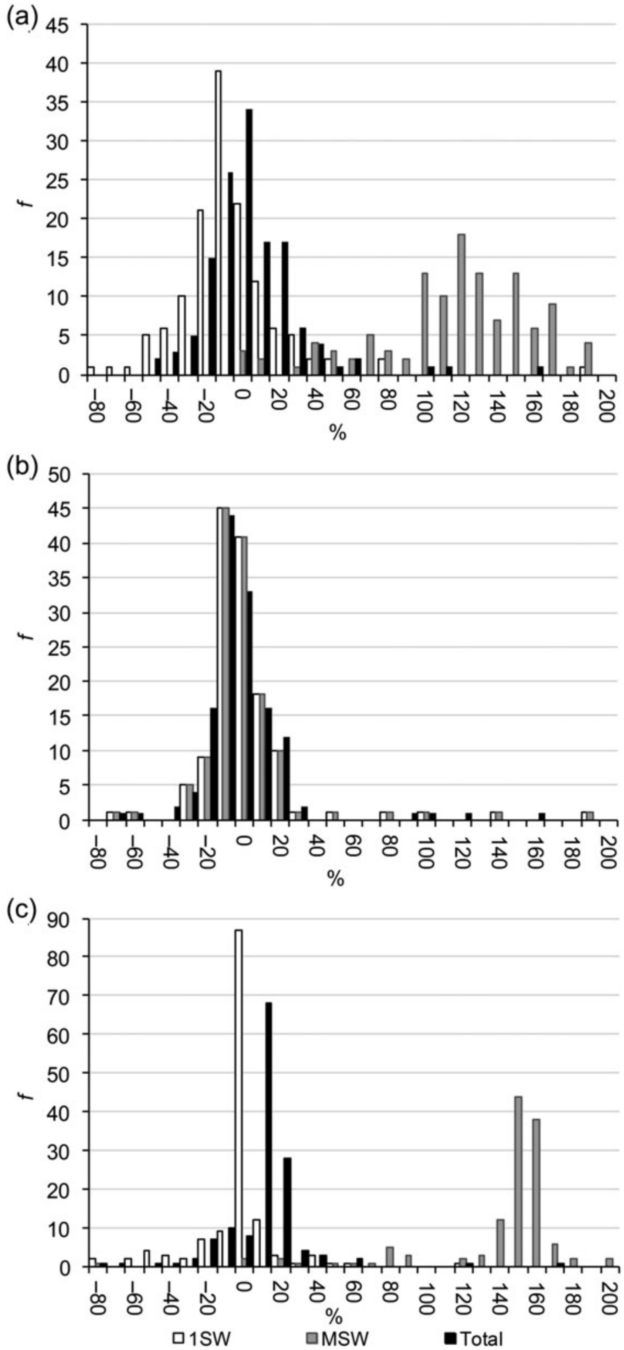

Figure 7. Differences between pre- and post-2012 CLs expressed as percentage difference from pre-2012 values (a) and percentage contributions of updated wetted areas (b) and biology (c) for 1SW, MSW, and total CLs.

Table 2. Multiple linear regression estimates of the effects, standard errors, *t*-values, and significances of changing the values of variables in Equation (1), from their pre-2012 values to their post-2012 values (Supplementary Appendix S2) on CL values (136 degrees of freedom in each case).

CL	Variable	Estimate	Std. error	*t*-value	Pr(>|*t*|)
1SW	(Intercept)	−0.135	0.050	−2.708	0.008**
	1SW age prop.	−0.132	0.233	−0.567	0.572
	1SW fecundity	−0.992	0.265	−3.752	<0.001***
	Wetted area	0.954	0.023	40.898	<0.001***
MSW	(Intercept)	2.282	0.786	2.903	0.004**
	MSW age prop.	0.136	0.043	3.179	0.002**
	MSW fecundity	4.404	3.410	1.291	0.199
	Wetted area	2.486	0.073	34.033	<0.001***
Total	(Intercept)	−0.798	0.291	−2.741	0.007**
	1SW age prop.	−119.502	103.720	−1.152	0.251
	MSW age prop.	−9.652	8.412	−1.147	0.253
	1SW fecundity	−0.830	0.361	−2.300	0.023*
	MSW fecundity	−3.520	1.339	−2.629	0.010**
	Wetted area	1.076	0.025	42.852	<0.001***

*Significant at $p < 0.05$.
**Significant at $p < 0.01$.
***Significant at $p < 0.001$.

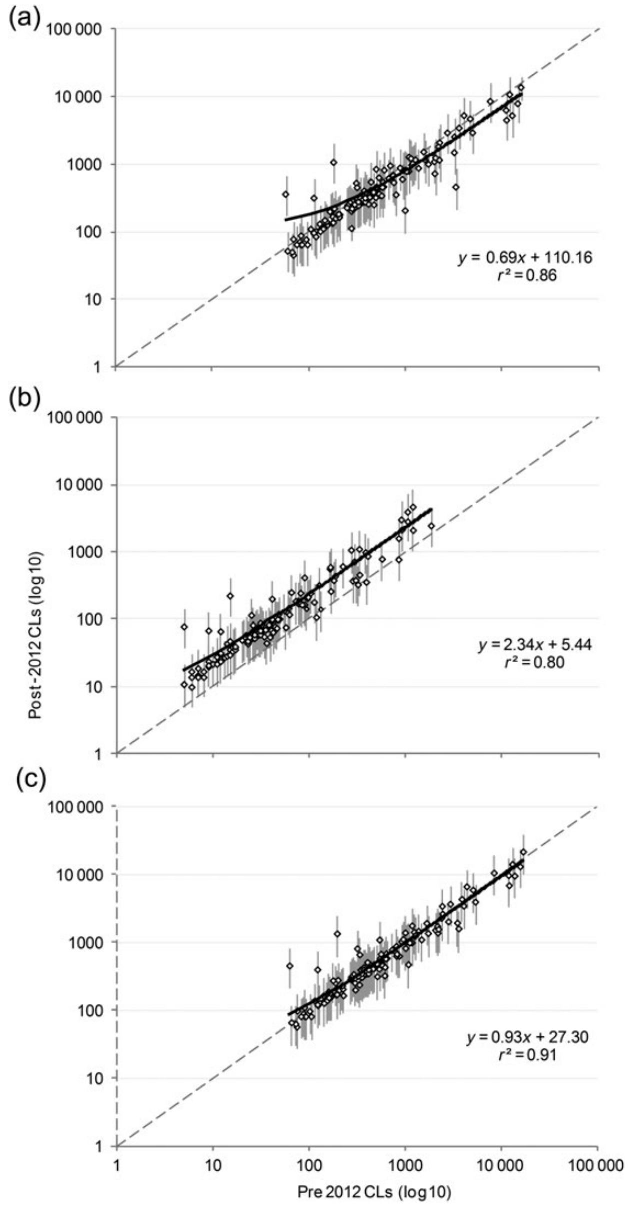

Figure 8. Post-2012 CLs plotted against their pre-2012 counterparts for (a) 1SW, (b) MSW, and (c) total CLs. Dashed diagonal lines show a 1 : 1 linear gradient. Errors on the post-2012 CLs are 90th percentiles. Solid lines are linear regressions; regression equations and r^2 values shown.

showed that their averages were extremely significantly different ($t = 4.127$; $p < 0.001$, d.f. = 137), with new CLs lower than their pre-2012 counterparts. Conversely, the post-2012 MSW CLs were greater than their pre-2012 counterparts. As with the 1SW CLs, there is a statistically significant regression ($p < 0.001$; $r^2 = 0.79$) although in terms of absolute values, the CLs were statistically significantly different (paired *t*-test on log-transformed values; $t = 24.77$; $p < 0.001$, d.f. = 137). Regression between the two sets of total CLs was significant ($p > 0.001$) with a slope of 0.93 in 1, close to 1 in 1, $r^2 = 0.91$, and their averages, however, were not significantly different (paired *t*-test on log-transformed values; $t = 0.286$; $p > 0.05$, d.f. = 137). Ranges of variability around the original reference points (pre-2012) were not calculated and while the ranges around some of the CLs detailed here are wide, they are within what may be considered expected ecological and biological ranges, and incorporate the values of pre-2012 CLs.

Discussion

Harwood (2000) discussed the interplay of the terms 'risk', 'uncertainty', 'probability of loss', 'hazard', and 'threat', and the perception that 'risk' is synonymous with them all, but that often when using it we are implying 'uncertainty' around estimated outcomes. Conservation biology is primarily concerned with avoiding undesirable outcomes in an uncertain world, which is also the aim of fisheries stock assessments. By including an assessment of uncertainty with management advice, the probability of failure or success [the 'probable risk' following Harwood (2000)] of not achieving a management target that is tolerable to managers, science advisors, and the general populous can be chosen.

In light of the downward trends in marine survival of Atlantic salmon (ICES, 2015) it is important to continue to review S–R data and relationships, sea age structures, and fecundities, if the declines in returns are to be understood and possibly mitigated against. While revising CLs does not change the realized population dynamics or result in more fish back to rivers, the use of the revised CLs should account for the current productive capacity of the stocks and be more appropriate for management whose purpose is ultimately conservation of the stocks for the long-term benefit of users. Age-specific CLs have been calculated as it is also important to enable separate management of spring and summer components of the returning stocks and monitor their numbers at MSY.

The S–R data in this study from the 22 monitored rivers cover a wide range of years, productivity ranges, population, and river sizes and latitudes (Figure 3). Latitude and wetted area operated as covariates for transporting the MSY point to non-monitored rivers in the BHSR model as they were shown to be proxies for available habitat and associated population size and productivity (Parent and Rivot, 2011). Information on these parameters is also widely available with little standardization required between catchments or jurisdictions. A refinement using the area of accessible riffle habitat and water temperature (minimum, maximum, or degree days) might provide more accurate estimates; however, these data are not readily available or standardized for all rivers.

Plots of stock and recruitment relationships shown in Figure 4 are based on individual fits and the Ricker S–R curves are drawn using the point estimates of the parameter values, and are not the fits from the BHSRA model. While the lack of points in the lower parts of the relationships may be a concern for individual assessments, the hierarchical power of the BHSRA transfers information among the relationships making for robust estimates of the S_{MSY} points. In addition, the BHSRA incorporates variability and this can be transported and incorporated into estimates for other rivers. With more points in the lower reaches of the S–R time-series, the errors may have been reduced; however, the data, being observations, are robust and the error ranges accommodate the uncertainty. Ó Maoiléidigh *et al.* (2004) stated that the wide range of BRP posterior distributions illustrates the uncertainty that managers are faced with and that application of a precautionary approach in providing catch advice is important to afford adequate protection to stocks. This remains the case, and while uncertainties in ecological models are generally inherent to our incomplete knowledge and true ecological variability (Parent and Rivot, 2011), assessments can be improved by the inclusion of measurable uncertainty from implicit sources (Harwood, 2000).

Measurements of variables provide us with estimates of their true values and their associated ranges, which in ecology will always

Table 3. Annual percentage of rivers achieving CLs (proportion of CL achieved >1.00 = recommended open for harvest fishing; between 1.00 and 0.65, recommended open for catch and release, <0.65 = recommend fishery is closed) and the numbers of stocks changing categories between years.

	Proportion of CLs achieved					Improving				Disimproving			
Year	>1.00 (%)	1.00 : 0.65 (%)	<0.65 (%)	No. of stocks	Year and change	Closed to C&R	C&R to catch	Closed to catch	Total	Catch to C&R	C&R to closed	Catch to closed	Total
2007	33	14	53	138									
2008	40	14	46	139	**2007–2008**	6	5	4	**15**	0	0	0	**0**
2009	39	12	49	139	**2008–2009**	0	3	0	**3**	2	2	1	**5**
2010	41	11	48	138	**2009–2010**	1	5	1	**7**	4	2	0	**6**
2011	42	12	47	137	**2010–2011**	2	4	0	**6**	3	0	0	**3**
2012	42	10	48	138	**2011–2012**	0	5	1	**6**	4	1	1	**6**
2013	41	8	51	140	**2012–2013**	1	4	1	**6**	5	5	1	**11**
2014	44	5	51	140	**2013–2014**	1	6	0	7	1	0	0	**1**

Horizontal line following 2012 highlights the cut between the use of old and new CLs.

contain extreme values. Variability in our estimates can be attributed to the natural range of the variable (including random and systematic errors) and survey errors where measurements are incorrectly taken or transcribed. In some instances, natural variability and survey errors can be clearly separated, for example extremely small or large records that fall outside possible ranges, though in many instances this will not be the case. The catch data used here derive from mandatory individual angler logbooks associated with a carcass tagging scheme. To reduce errors associated with recording catch date, location, fish weights, or their units, and in their digitization the removal of the top and bottom 10% of estimates, through implementation of 10^{th} and 90^{th} percentiles as minimum and maximum values, respectively, reduced their potential influence in the stochastic CL estimation. The restraint of variability is an important consideration, as ranges can be inflated through stochastic process calculations and can lead to large uncertainties. While extreme values have low likelihoods, they tend to be uninformative in management situations and Clark *et al.* (2001) stated that the information content of a forecast is inversely proportional to its uncertainty with a wide confidence envelope indicating low information content. Therefore, ecosystem forecasts that are going to be of use need to include measured and calculated uncertainty while ensuring that the forecast also reports a useful degree of information.

To ensure a precautionary approach in setting salmon total allowable catch (TAC) and or quotas, BRPs need to be applied about their probabilities, as they are still estimates. Annual TACs are calculated by subtracting the CLs presented here (Supplementary Appendix S2) from the estimated number of returning salmon in a stochastic framework. CL ranges are set as triangular distributions with 10^{th} and 90^{th} percentiles applied as minimum and maximum values, respectively and the 50^{th} percentile as the most likely value, so their information content is retained (Clark *et al.*, 2001). The variability in returning salmon numbers is also incorporated giving TAC management advice with a range of probabilities of CLs being met (Standing Scientific Committee, 2006, 2007, 2008, 2009, 2010, 2011). Management of salmon stocks in Ireland specifically requires objective stock assessments implementing an MSY approach following ICES and NASCO advice to maximize probability of attaining CLs.

In Ireland, the use of these CLs allows managers to set fishery rules which are relatively unambiguous, understandable, and practical to administer. Where a stock is exceeding CL, no harvest fishery is allowed. If the stock is below CL but exceeding 65%, managers

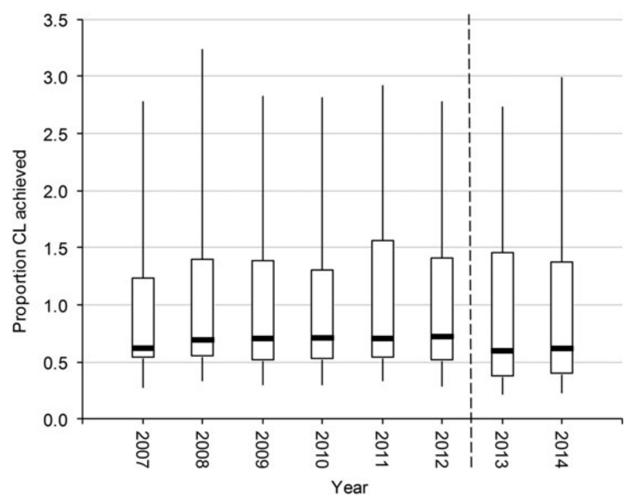

Figure 9. Annual ranges in proportions of CLs achieved (whiskers represent 2.5^{th} and 97.5^{th}; boxes represent 25^{th} and 75^{th} and midline 50^{th} percentiles). Vertical dashed line represents the cut between the use of old and new CLs.

allow a catch and release angling fishery to proceed. Finally, if the stock is below 65% of the CL, all fisheries are closed. Accompanying the advice secondary information would include the shortfall below the CL of rivers not attaining the management target and would give course to advise on how to best manage the stock towards recovery. This system is facilitated by having the vast majority of fisheries operating within a river or estuary where it is more likely that the stocks will be from a single population (Potter and Ó Maoiléidigh, 2006). Since the introduction of updated CLs, the percentage of salmon rivers open for fishing has shown no notable change (Table 3) although the number of stocks that may be seen as having disimproved (changed to a more conservative fishing category) based on advice is 11, and while this is the largest number of changes seen since the new CLs were introduced in 2013, this is not an extreme change. This suggests a degree of consistency in the catch advice process between years. It also illustrates that despite the closure of a significant coastal fishery for salmon, it is likely that an increase in numbers of fish owing to the absence of this fishery is being offset by continued declines in marine survival for many stocks (ICES, 2015). Likewise, the range in the proportions of CLs achieved in each year (Figure 9) shows that the variability did not appear to change markedly following their introduction.

Continued review and improvement in stock assessment techniques, applications, and forecasts will provide more information on the rates of population decline and recovery. The continued use of new data as they become available is also essential if we are to improve our ability to manage these resources under changing circumstances and to ensure the long-term survival of the more fragile Atlantic salmon stocks.

The work described here represents a major development in the management and conservation of wild Atlantic salmon. The application of these new river-specific CLs along with their associated variability represents significant progress in ongoing efforts to improve salmon and other fish stock assessments.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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