

The identification and characterisation of small salmon populations to support their conservation and management.



Report No: 674

Authors: **Nigel Milner¹ & Carlos Garcia de Leaniz²**

Author Affiliation: ¹Bangor University & APEM ²Swansea University

About Natural Resources Wales

Natural Resources Wales' purpose is to pursue sustainable management of natural resources. This means looking after air, land, water, wildlife, plants and soil to improve Wales' well-being, and provide a better future for everyone.

Evidence at Natural Resources Wales

Natural Resources Wales is an evidence-based organisation. We seek to ensure that our strategy, decisions, operations and advice to Welsh Government and others are underpinned by sound and quality-assured evidence. We recognise that it is critically important to have a good understanding of our changing environment.

We will realise this vision by:

- Maintaining and developing the technical specialist skills of our staff;
- Securing our data and information;
- Having a well resourced proactive programme of evidence work;
- Continuing to review and add to our evidence to ensure it is fit for the challenges facing us; and
- Communicating our evidence in an open and transparent way.

This Evidence Report series serves as a record of work carried out or commissioned by Natural Resources Wales. It also helps us to share and promote use of our evidence by others and develop future collaborations. However, the views and recommendations presented in this report are not necessarily those of NRW and should, therefore, not be attributed to NRW.

Report series: NRW Evidence Report
Report number: 674
Publication date: 22 March 2023
Contractor: Nigel Milner & Carlos Garcia de Leaniz
Contract Manager: Peter Gough and Ben Wilson (2022)
Title: The identification and characterisation of small salmon populations to support their conservation and management
Author(s): Nigel Milner & Carlos Garcia de Leaniz
Technical Editor: Ben Wilson
Quality assurance: Tier 3 Richard Cardwell, David Letellier
Peer Reviewer(s): Ben Wilson, Ian Davidson, David Mee, Josie Jackson and Peter Gough
Approved By: Ben Wilson
Restrictions: None

Distribution List (core)

NRW Library, Bangor	2
National Library of Wales	1
British Library	1
Welsh Government Library	1
Scottish Natural Heritage Library	1
Natural England Library (Electronic Only)	1

Recommended citation for this volume:

Milner, N. & Garcia de Leaniz, C. 2023. The identification and characterisation of small salmon populations to support their conservation and management. NRW Evidence Report No: 674

Table of Contents

About Natural Resources Wales.....	2
Evidence at Natural Resources Wales.....	2
Distribution List (core).....	3
Recommended citation for this volume:.....	3
Table of Content	4
List of Figures	6
List of Tables	9
Crynodeb Gweithredol	10
Executive summary	11
1 Background and Aim	12
2 What is a small population?.....	16
2.1 Demographic consideration (3R's).....	22
2.2 Genetic considerations.....	25
3 How can small populations and population declines be identified?	26
3.1 Demographic indicators	26
3.2 Genetic indicators	27
3.3 How useful and reliable are genetic estimates of population size?.....	28
3.4 The effect of metapopulations	30
4 Are there intervention points for managing small populations?	32
4.1 Conservation Limits & Management targets	32
4.2 Critical Values based on Effective population size.....	34
4.3 Conservation status based on the IUCN Red List approach	36
4.4 Application to Salmonids	38
5 Can small populations rebound without intervention?.....	40
5.1 Vulnerability and recovery of small populations	40
5.2 Lessons from invasive salmonids	41
5.3 Management interventions for critically small populations.	41
6 How can population size and conservation status be monitored?	42

6.1	Outline of a monitoring plan and IUCN Assessment of Atlantic salmon and sea trout in Wales	42
7	Conclusions & Recommendations	46
8	References	48
9	Appendices	57
9.1	Data Archive Appendix	66

List of Figures

- | | | |
|----------|---|----|
| Figure 1 | Temporal trend (1990-2021) in the median % conservation limit compliance for 22 salmon rivers in Wales and Holt prediction forecast for the next 20 years. The blue line represents the point forecast and the envelopes the 80% (dark grey) and 95% (light grey) prediction intervals. The results suggest that salmon may become extirpated from 50% of Welsh rivers by 2034, although the uncertainty is high | 12 |
| Figure 2 | Predicted trends in % CL compliance for Welsh salmon rivers over the next 20 years based on Holt prediction forecasts for the period 1990-2021. The blue line represents the mean value, the light blue envelope the 95 CI, and the dotted line the extinction threshold (CL = 0). Only 7 rivers (highlighted in green) are predicted to lie above the extinction threshold by 2040 and only three rivers (Nevern, Wye and Cleddau) display non-declining trends. If conditions continue as they are now, most salmon populations in Welsh rivers (highlighted in red) may become extirpated within two decades. Note that negative CL values (Y-axis) are not possible, these are shown simply to depict the extent of the predicted declines. | 13 |
| Figure 3 | The interplay between genetic variation, demographics and the environment determines the fitness, and thus the extinction risk, of salmon populations. | 15 |
| Figure 4 | Relationship between catchment size (wetted area, hectares) and (a) annual egg deposition when stock is at the Conservation Limit (CL, million eggs) and (b) average annual number of spawners (No.) over the period 1994 to 2015 in 22 Welsh rivers. Large catchments can sustain larger salmon populations. Note log scales on axes. | 17 |
| Figure 5 | Relationship between catchment size (wetted area, hectares) and (a) annual egg deposition when stock is at the Conservation Limit (CL, million eggs) and (b) average annual number of spawners (No.) over the period 1994 to 2015 in 22 Welsh rivers. Large catchments can sustain larger salmon populations. Note log scales on axes. | 18 |

Figure 6	Recent levels of egg deposition (eggs/m ²) during 2017-2021 indicates that current salmon productivity in Wales is low because most rivers are producing too few eggs (<2 eggs/m ²), well below their conservation limit	20
Figure 7	Relationship between river size (wetted area, hectares) and proportion of salmon returning annually as 1SW spawners to the main Welsh salmon rivers averaged for the period 2000 to 2021. The envelope represents the 95% confidence interval. Note the log scale for the x-axis.	21
Figure 8	The concepts of resistance and resilience that underpin the response of natural populations to stressors (adapted from Ford 1999). Scenario (a) is an easily disrupted system with low resistance but high resilience, the population will simply move to a new equivalent state in response to a stressor and will stop moving once the stressor is removed (i.e there are no carry over effects). Scenario (b) has high resilience and high resistance, the population will bounce back to its original state once the stressor is removed. Scenario (c) has low resilience and low resistance, the population is easily disrupted and will not return to its original state even when the stressor is removed. Scenario (d) has high resistance that makes it more difficult to disrupt, but as in (c), it has low resilience, it will not return to its original state even when the stressor is removed. The danger for small populations is to be in (c), the least desirable state	23
Figure 9	Relationship between the mean spawner abundance of salmon (an index of population size) on log scale and the coefficient of variation (standard deviation*100/mean) in rivers of Northwest England and Wales during 1994-2015.	24
Figure 10	The two ways in which habitat loss can affect the stock-recruitment relationships and reduce productivity: (a) through a reduction in the area available to fish (loss of habitat quantity), for example caused by barriers, and (b) through the loss of habitat quality, for example due to pollution or reduced flows.	27
Figure 11	Patterns of gene flow in an Atlantic salmon meta-population showing broad concordance between results from (a) physical tagging and (b) variation at	31

microsatellite DNA loci. The size of the circles is proportional to N_e , the size of the arrows is proportional to the proportion of fish migrating between rivers, and the numbers represent the proportion of migrants between rivers (from Consuegra et al 2005b). Note that the micro-tagging data refers to the recapture of stocked hatchery fish.

- Figure 12 Expected changes in the effective size of a four-river metapopulation of Atlantic salmon, when the N_e of each subpopulation increases or decreases by up to $\pm 20\%$. The simulation shows that the size of one of the subpopulations (River Ason, dashed line) has a disproportionate large effect on the size of the metapopulation (from Kuparinen et al., 2010). 31
- Figure 13 Example of a stock recruitment curve for the River Tawe, showing the influence of adult spawners on smolt numbers (recruits) (red line) and density-dependent egg to smolt survival (blue line). The black lines show spawners and recruits at the Conservation Limit (equivalent to 704 spawners). The right hand panel is a diagram of the region within which an Allee effect might lie: it is indicative only. The vertical arrow illustrates the point at which recruits will be zero even though some spawners return to the river. 34

List of Tables

Table 1	Comparison of the mean number of spawners per year in the main salmon rivers of Wales during 1994-2015 and during 2017-2021. There were 21 rivers in the later period because data was missing for the Taff & Ely system.	19
Table 2	Estimates of effective population size (N_e) of 111 Atlantic salmon populations across the species' range (Garcia de Leaniz, 2021).	35
Table 3	Annual effective population size (N_e) for the River Taff, with and without hatchery returns estimated using two different methods (LD and TMP). a) Linkage Disequilibrium method (LD) b) Temporal method (TMP) comparing 2010 vs 2011, and 2010 vs 2012	36

Crynodeb Gweithredol

Mae'r eog dan fygythiad yng Nghymru ac yn y rhan fwyaf o'r dyfroedd lle mae'n byw. Nawr, yn fwy nag erioed o'r blaen, mae ar reolwyr angen canllawiau clir ar sut i adnabod poblogaethau sy'n lleihau, a chyngor ymarferol ar beth i'w wneud pan fydd poblogaethau'n mynd yn ddifrifol isel.

Rydym wedi adolygu'r llenyddiaeth ac wedi darparu canllawiau ymarferol ar sut i [ddiffinio poblogaethau bach](#) a nodi poblogaethau sy'n lleihau gan ddefnyddio ystyriaethau demograffig a genetig, pan fo poblogaethau wedi'u hynysu a phan fo cysylltiad rhyngddynt fel rhan o fetaboblogaethau mwy. Aethom ati i nodi a oes poblogaeth sy'n ddifrifol fach [ar hyn o bryd yng Nghymru](#), a gwerthuso defnyddioldeb defnyddio amcangyfrifon genetig o faint poblogaethau i nodi achosion lle ceir gostyngiad difrifol.

Archwiliwyd gwahanol fathau o bwytiau ymyrraeth i reoli poblogaethau bach ac yn ystyriwyd rhinweddau gwahanol fathau o derfynau cadwraeth, gan gynnwys y posibilrwydd y gallai poblogaethau adfer heb ymyrraeth ddynol o feintiau bach iawn pan fydd ffactorau cyfyngol yn cael eu dileu neu eu lleihau.

Rydym yn gwahaniaethu rhwng poblogaethau naturiol fach, a geir yn nodweddiadol mewn dalgylchoedd arfordirol bach, a phoblogaethau sy'n dirywio sydd wedi mynd yn llai o ganlyniad i effeithiau amrywiol.

Mae ein dadansoddiad yn dangos bod y rhan fwyaf o boblogaethau'r eogiaid yng Nghymru wedi bod yn dirywio dros y ddau ddegawd diwethaf a'u bod yn is na'r terfyn cadwraeth ar hyn o bryd. Mae rhagolygon yn awgrymu y gallai eogiaid ddiflannu o lawer o afonydd Cymru o fewn y degawdau nesaf, er bod lefel yr ansicrwydd yn uchel a bod rhai poblogaethau'n parhau'n sefydlog. Mae newid yn yr hinsawdd yn debygol o fod yn gyfrifol am y gostyngiad a welwyd mewn goroesiad morol sy'n effeithio ar y rhan fwyaf o boblogaethau, ond mae effeithiau lleol mewn dŵr croyw hefyd yn bwysig fel y gwelir yn yr amrywiad yn nhueddiadau toreithrwydd y poblogaethau cyfagos.

Er nad oes trothwy sefydlog yn bodoli lle mae adferiad yn amhosibl, po hiraf y bydd poblogaethau o dan y terfyn cadwraeth, y lleiaf tebygol ydyw y bydd adferiad. Yn seiliedig ar y data genetig a demograffig sydd ar gael, rydym yn mentro amcangyfrif bod yn rhaid ystyried fod poblogaethau eogiaid yn "ddifrifol fach" pan fydd llai na ~400 o oedolion yn dychwelyd bob blwyddyn ar gyfartaledd, a fydd yn arwain yn fras at lai nag 20 o eogiaid benyw sy'n silio bob blwyddyn. Terfynau tyngedfennol yw'r rhain, nid targedau rheoli, a dylid eu diwygio wrth i ragor o ddata ddod ar gael.

Yn olaf, rydym yn amlinellu cynllun ar gyfer asesu statws cadwraeth eogiaid a siwin (brithyllod môr) yng Nghymru ac yn cynnig rhai argymhellion i lywio cynllun gweithredu. Mae asesiad yn arddull yr IUCN sy'n cynnwys metrigau dosbarthiad, presenoldeb, toreithrwydd, amrywiadau ym maint poblogaethau, a data genetig (amrywiaeth a maint poblogaethau effeithiol) yn cynnig y rhagolygon gorau ar gyfer monitro statws cadwraeth eogiaid a siwin yng Nghymru yn effeithiol.

Yn gyffredinol, roedd y poblogaethau lleiaf o eogiaid yng Nghymru i'w gweld yn y dalgylchoedd lleiaf, ac fel y rhagwelwyd ar sail ddamcaniaethol, roeddent yn naturiol yn fwy amrywiol o flwyddyn i flwyddyn na'r rhai mwy. Mae hyn yn pwysleisio manteision cysylltedd mewn gwaith adfer ac ychwanegu at faint ac ansawdd y cynefin sydd ar gael i'r rhywogaeth. Gall cael poblogaethau mawr gerllaw helpu poblogaeth sy'n dirywio i gryfhau ac adfer oherwydd dynameg metaboblogaethau ac ailgytrefu naturiol ond rhaid nodi a dileu ffactorau cyfyngol a chyfyngiadau amgylcheddol (gan gynnwys pysgota).

Executive summary

Atlantic salmon (*Salmo salar*) is under threat in Wales and throughout most of its range. Now more than ever managers need clear guidance on how to identify declining populations, and practical advice on what to do when populations become critically low.

We reviewed the literature and provide practical guidance on how to define small populations and to identify declining populations using both demographic and genetic considerations, when populations are isolated and when they are connected as part of larger metapopulations. We addressed whether there are critically small population sizes currently in Wales, and evaluated the utility of using genetic estimates of population size to identify bottlenecks.

We examined different types of intervention points to manage small populations and considered the merits of different types of conservation limits, including the possibility that populations may rebound without human intervention and recover from very small population sizes when limiting factors are removed or reduced.

We distinguish between naturally small populations, typically found in small coastal catchments, and declining populations that have become smaller through various impacts

Our analysis indicates that most Atlantic salmon populations in Wales have been declining for the last two decades and are currently below the conservation limit. Forecasts suggest that salmon may become extirpated from many Welsh rivers within the next few decades, although uncertainty is high and a few populations remain stable. Climate change is likely responsible for the observed decrease in marine survival that is affecting most populations, but local impacts in freshwater are also important as evidenced by the variation in abundance trends of neighbouring populations.

Although no fixed threshold exists below which recovery is impossible, the further populations are below the conservation limit and the longer they remain there the less likely recovery will be. Based on the available genetic and demographic data, we tentatively estimate that salmon populations must be considered “critically small” when on average less than ~400 adults return every year which will roughly translate to less than 20 female spawning per year. These are critical limits, not management targets, and should be revised as more data becomes available.

Finally, we outline a plan for assessing the conservation status of Atlantic salmon and sea trout in Wales and provide some recommendations to inform a plan of action. An IUCN-type assessment that incorporates metrics of distribution, occupancy, abundance, population

size fluctuations, and genetic data (diversity and effective population size) offers the best prospects for effective monitoring of the conservation status of Atlantic salmon and sea trout in Wales.

The smallest salmon populations in Wales were generally found in the smallest catchments, and as predicted from theory, were intrinsically more variable from year to year than the larger ones. This serves to emphasize the benefits of restoring connectivity and augmenting the quantity and quality of habitat available to the species. Having large neighbouring populations may help declining populations bounce back and recover due to metapopulation dynamics and natural recolonization but limiting factors and environmental constraints (including fishing) must be identified and removed.

1 Background and Aim

Atlantic salmon stocks on the great majority of rivers in Wales (and England) are currently well below Conservation Limits (CL). Egg deposition levels in Welsh rivers were at a historical ~20+ year low during 2021, with half of the rivers being at 20% of their Conservation Limits (**Figure 1**), with many populations predicted to become extirpated within the next two decades.

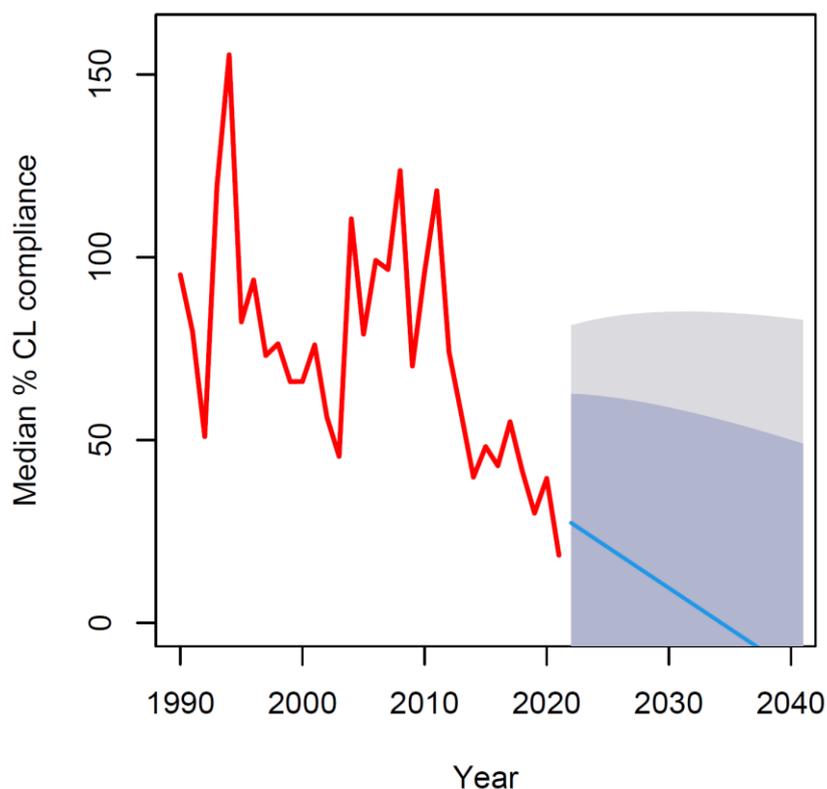


Figure 1. Temporal trend (1990-2021) in the median % conservation limit compliance for 22 salmon rivers in Wales and Holt prediction forecast for the next 20 years. The blue line represents the point forecast and the envelopes the 80% (dark grey) and 95% (light grey) prediction intervals. The results suggest that salmon may become extirpated from 50% of Welsh rivers by 2034, although the uncertainty is high .

The fall in recruitment appears to have been driven primarily by poor survival at sea and is evident not just in Wales, but also across the species' range (April et al., 2021; WGNAS, 2022). Many stocks display synchrony in their declines, suggesting they are responding to some common factors (Olmos et al., 2020). The underlying mechanisms for such steep decline are not fully understood but likely involve many stressors, including disrupted nutrient pathways and food chains, but also unreported, and unregulated bycatches at sea (Chaput, 2012; Dadswell et al., 2022; Gillson et al., 2022). Whatever the reasons, the fact is that many Welsh salmon populations have now become very small, compromising their long term survival and bringing them dangerously close to extinction (**Figure 2**)

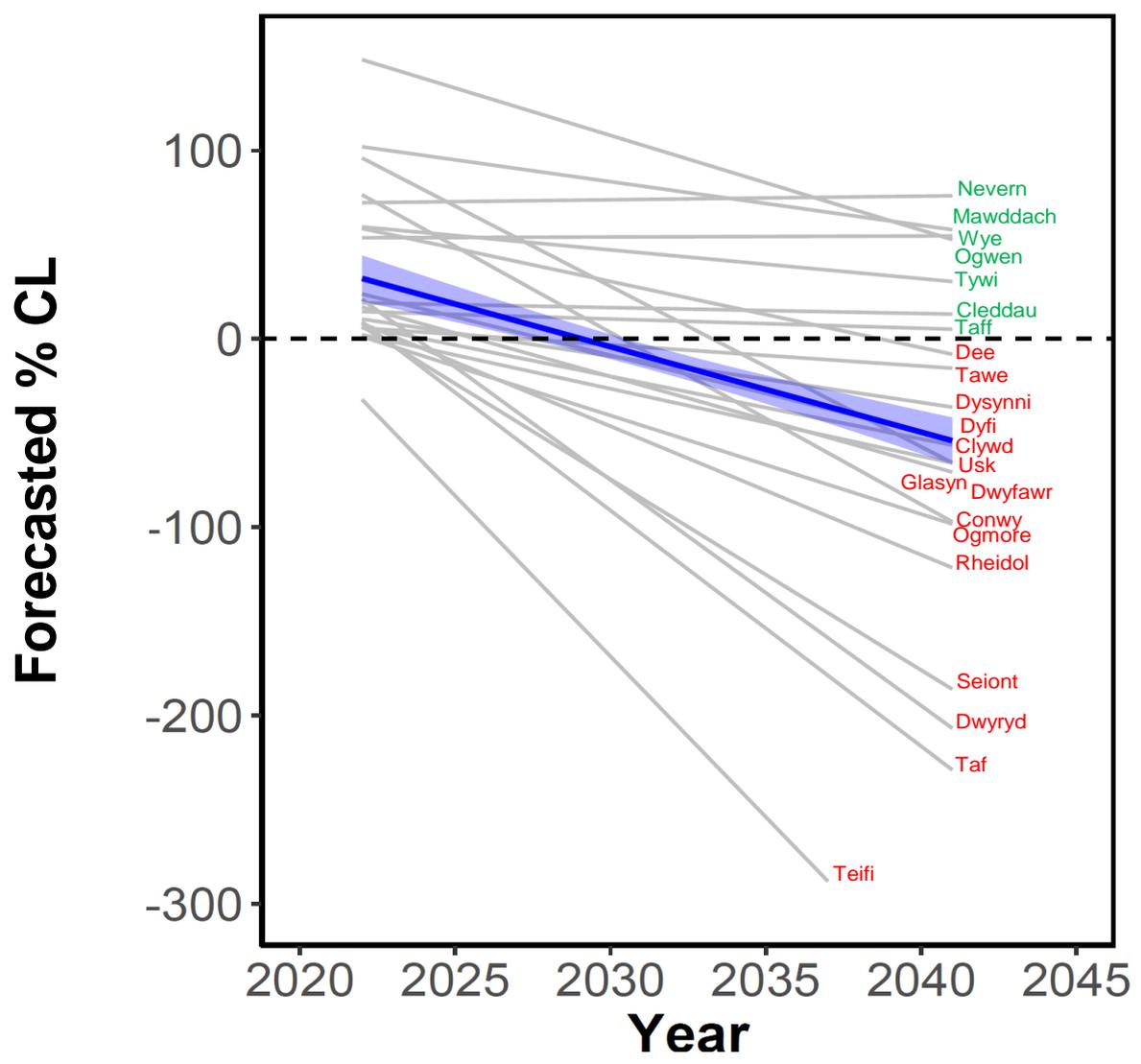


Figure 2. Predicted trends in % CL compliance for Welsh salmon rivers over the next 20 years based on Holt prediction forecasts for the period 1990-2021. The blue line represents the mean value, the light blue envelope the 95 CI, and the dotted line the extinction threshold (CL = 0). Only 7 rivers (highlighted in green) are predicted to lie above the extinction threshold by 2040 and only three rivers (Nevern, Wye and Cleddau) display non-declining trends. If conditions continue as they are now, most salmon populations in Welsh rivers (highlighted in red) may become extirpated within two decades. Note that negative CL values (Y-axis) are not possible, these are shown simply to depict the extent of the predicted declines.

Low juvenile abundance is apparent in many Welsh rivers, and a widespread fry recruitment crash was observed in 2016 (Cefas/EA/NRW, 2017). It is thought that the decrease in juvenile numbers may have been linked not just to poor marine survival and a general decline in spawner numbers, but also to extreme environmental conditions in freshwater. The 2016 recruitment crash coincided with extreme winter weather conditions, leading to speculation that unusually warm temperatures and high flows adversely affected salmon spawning success (and to a lesser extent trout) across Wales (Bewes et al., 2019a; Gregory et al., 2020). The impact of such extreme environmental events on salmon stocks – particularly stocks already at low levels – is of great concern because their frequency is expected to increase with climate change (Kendon et al., 2022). Further to the 2016 crash, and similar extreme events (e.g. 2007), the overall standing stocks of juveniles has been decreasing since about 2015, whereas previously it had been fairly stable (Bewes et al., 2019b). The start of the decline appears to differ between rivers, which may point to the operation of local factors in freshwater, but the implication is that the former comparative stability of juvenile abundance has changed. This may indicate that the buffering to parr abundance offered by early stage compensatory mortality (Milner et al., 2003) may have reduced and is now insufficient to compensate for current very low levels of spawning escapement and egg deposition.

To help address poor recruitment, and to increase spawning escapement, NRW have implemented mandatory catch-and-release (C&R) byelaws for salmon in all net and rod fisheries in Wales. Such measures may help stocks re-generate and build resilience, but if external conditions remain as in recent years recovery may, at best, be very slow or not be enough. Should conditions deteriorate, recruitment will most likely fall even further and further protection measures may be necessary. Ultimately recovery time will be determined by future environmental conditions, the natural resilience of stocks and our ability to address all tractable sources of mortality.

The poor status of salmon stocks has prompted interest in how salmon populations perform at very low abundance levels, and on how one might be able to identify those populations most at risk, based on (1) population size or other demographic metrics, and (2) genetic variation. From a practical perspective, the aim is to identify intervention points (*'red flags'*) and management actions according to a *'traffic light rating system'*.

Genetic and demographic processes (i.e. the suite of life history traits, including stage-specific survival, growth, maturation and breeding success) interact to influence the risk of population extinction at low population sizes (Lande, 1988; 1993; Lande and Orzack, 1988), with demographic parameters usually being of more immediate importance than genetic ones in determining the risk of extinction. However, both demography and population genetics need to be evaluated. Such a demographic and genetic assessment may help to identify potential intervention points, inform the adoption of management responses, and determine the needs for future monitoring. Both processes act on populations against the template of the fishes' habitat, which determines carrying capacity, and stochastic pressures on populations that tend to perturb stocks and drive selection, adaptation, and ultimately population resilience and extinction risk (**Figure 3**).

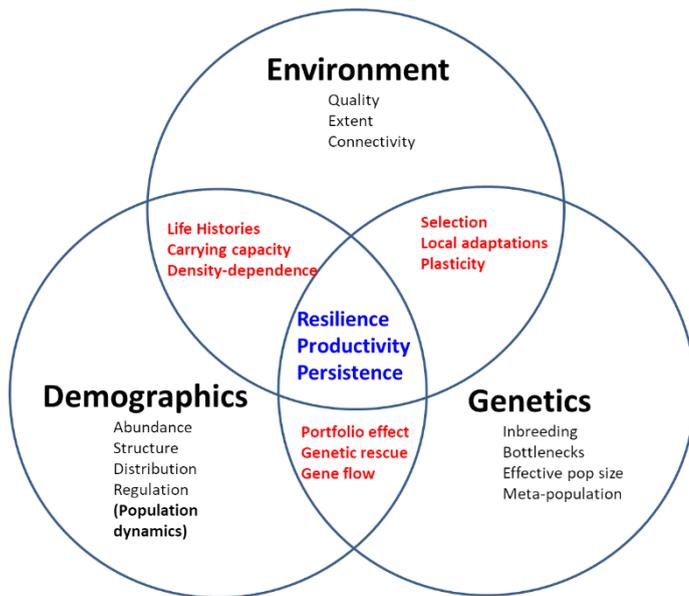


Figure 3. The interplay between genetic variation, demographics and the environment determines the fitness, and thus the extinction risk, of salmon populations.

NRW has identified the need to explore the consequences of low salmon abundance for stock dynamics and genetics, and to identify possible intervention points and management responses that might be considered to prevent populations sliding into an extinction vortex. From a management perspective, some of the most pressing questions are listed below.

(i) Demographics: stock recruitment and stock dynamics

Given that stock recruitment relationships (SR) are used for setting Conservation Limits for Atlantic salmon - as recommended by ICES (ICES, 1995) and NASCO (NASCO, 2009), is it possible to identify and quantify an increasing risk of population extinction as spawner abundance declines? Specifically NRW raised the following questions:

Does stock-recruitment theory help us from a pragmatic and management perspective?

Is there literature and/or precedent in any Atlantic salmon population in which this has been explored to determine management actions and, if so, with what result?

Do we know if any management agency is currently considering this with an eye to management implementation?

(ii) Genetics: variability, adaptations, resilience

What size does a discrete Atlantic salmon stock have to be in order to conserve critical stock characteristics in order to maintain stock viability, preserve key adaptations and restore resilience?

What is a “safe” stock level?

(iii) Management Issues

How equipped are we with evidence to describe and quantify stock “fragility” or health?

Does the concept of “effective population size” help?

What monitoring should be devised and implemented to inform a stock descriptor that reflects:

- Population viability
- Risk of extinction
- Intervention options
- Scope to improve (and at what point this is lost)
- Management options to trigger improvement

To this end, NRW organised a one-day workshop at the Cynrig hatchery on 10th January 2018 to consider the above issues in relation to the persistence of **small salmon populations**. The workshop was commissioned by Peter Gough and attended by David Mee, John Taylor, and Ian Davidson (NRW), Nigel Milner (APEM) and Carlos Garcia de Leaniz (Swansea University). The main focus was on Atlantic salmon because the recent declines for this species have been particularly severe and populations are more at risk, but the same issues probably apply to sea trout and are also briefly considered in this report.

This report was formally commissioned to summarise the proceedings of that workshop and to provide NRW with recommendations. Additional inputs were subsequently provided by Ben Wilson and Josie Jackson (NRW), and Sonia Consuegra (Swansea University). We present first the conceptual background and some examples of the demographics and population dynamics of Atlantic salmon in Wales and then review some genetic traits of small populations. We finish with some recommendations for managing and monitoring small populations.

2 What is a small population?

There is no formal demographic definition of a ‘small population’ size, but salmon (and trout) populations may be considered ‘small’ if they are smaller than neighbouring populations, or if they are smaller than they should (or used to) be. Hence populations can become small through two very different mechanisms

1. **The population is *intrinsically small*** due to the small size and natural carrying capacity of the catchment. When Conservation Limits (expressed as either egg deposition or total number of returning spawners) are scaled to catchment size, two findings become evident: (a) larger rivers typically sustain larger populations and (b) many of the 22 principal salmon rivers in Wales are intrinsically small (**Figure 4**).

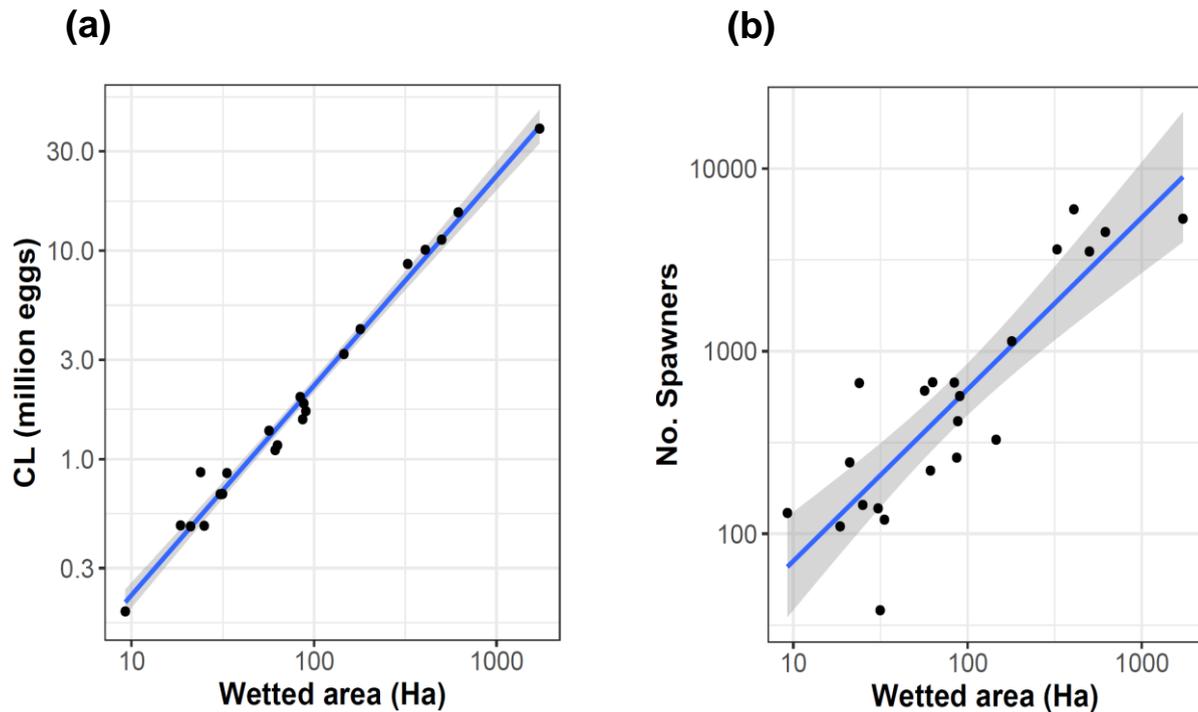


Figure 4. Relationship between catchment size (wetted area, hectares) and (a) annual egg deposition when stock is at the Conservation Limit (CL, million eggs) and (b) average annual number of spawners (No.) over the period 1994 to 2015 in 22 Welsh rivers. Large catchments can sustain larger salmon populations. Note log scales on axes.

2. **The population has become *functionally* small because it has declined as a consequence of some impacts**, that have reduced its breeding size below its natural carrying capacity. This is also evident in Wales, where the rate of decline differs markedly between populations (**Figures 2,5**), presumably because they have been impacted in different ways, with different intensity, or simply because they differ in resilience to absorb impacts (see below). Such impacts might arise through environmental or other pressures acting on recruitment and spawner abundance.

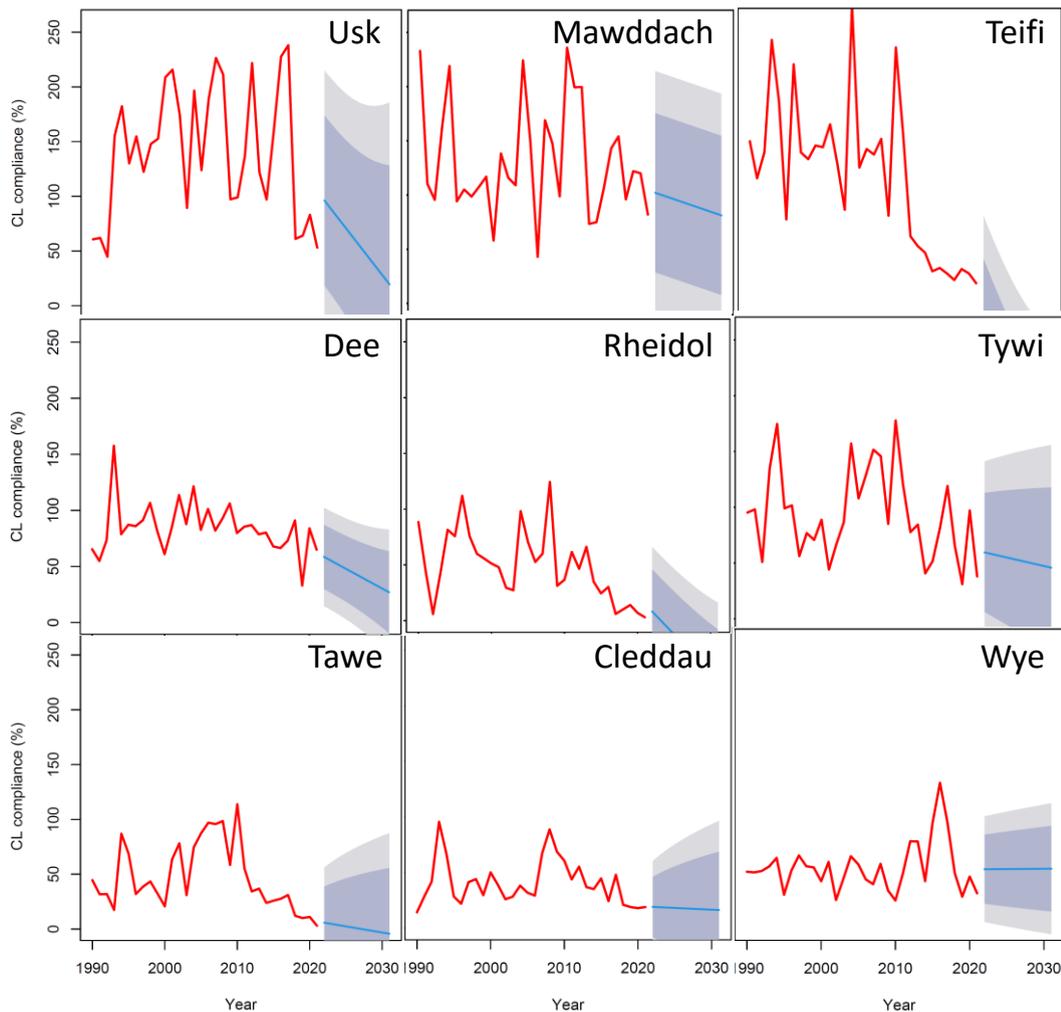


Figure 5. Temporal trend in % CL compliance (1990-2021) of nine representative salmon populations in Wales and Holt prediction forecasts for the next 10 years. The blue line represents the point forecasts and the envelopes the 80% (dark grey) and 95% (light grey) prediction intervals. None of the rivers are predicted to achieve the Conservation Limit (%CL = 100) but the slope of the decline varies significantly between rivers, being particularly steep in the rivers Usk, Teifi and Rheidol. Salmon may become extirpated (%CL= 0) from most Welsh rivers within two decades.

From a management perspective, these two situations (*intrinsically small vs. functionally small*) present different problems that may call for different courses of action. A functionally small population that has become small because of one or more impacts requires management measures to resolve the problem, if tractable, whereas an intrinsically (naturally) small population is simply part of the diversity of population sizes and requires no action other than protection against deterioration. However, at the present time, all Welsh rivers have depleted or severely depleted salmon populations (**Figures 2 & 5**) including both (a) intrinsically small populations inhabiting small catchments and (b) functionally small populations that were originally much larger in size.

The rivers in **Figure 2** cover a range of catchments designated as Principal Salmon Rivers, but the lower end is truncated by the reporting scheme, which excludes rivers with very low

reported catches (and thus not considered 'principal salmon rivers'). The exception is the Gwyrfai, a small river in North Wales (although an SAC, designated for salmon) with annual salmon catches in single figures, sometimes zero. This was omitted from analysis, because of the unreliability of the catch data and other missing variables. There are many smaller rivers in Wales with very small salmon populations although some sustain significant sea trout rod fisheries. We restricted our analysis to rivers that routinely report salmon catches, the data for these rivers are summarised in Appendix A1.

Analysis of the size of the adult breeding populations (No. of anadromous spawners, S) over the last three decades indicates that populations are getting substantially smaller (**Table 1**). For example, until 2015 half of the rivers in Wales sustained breeding adult populations in excess of 500 individuals, but these accounted for only 38% over the last 5 years. An increase in the number of small populations ($S < 200$) is also evident, having increased from 6 to 11.

Table 1. Comparison of the mean number of spawners per year in the main salmon rivers of Wales during 1994-2015 and during 2017-2021. There were 21 rivers in the later period because data was missing for the Taff & Ely system.

Mean No. of spawners/year (S, range)	Period			
	1994-2015	(%)	2017-2021	(%)
<50	1	4.50	3	14.3
51-200	5	22.7	8	38.1
201-500	5	22.7	2	9.50
>500	11	50.0	8	38.1

Inspection of recent levels of egg deposition (scaled by catchment size) indicate a markedly right-skewed distribution (skewness = 2.16; **Figure 6**). This occurs when the modal (i.e. the most common) egg deposition (0.3 eggs/m²) is lower than the median (0.8 eggs/m²), which is in turn less than the mean (1.2 eggs/m²).

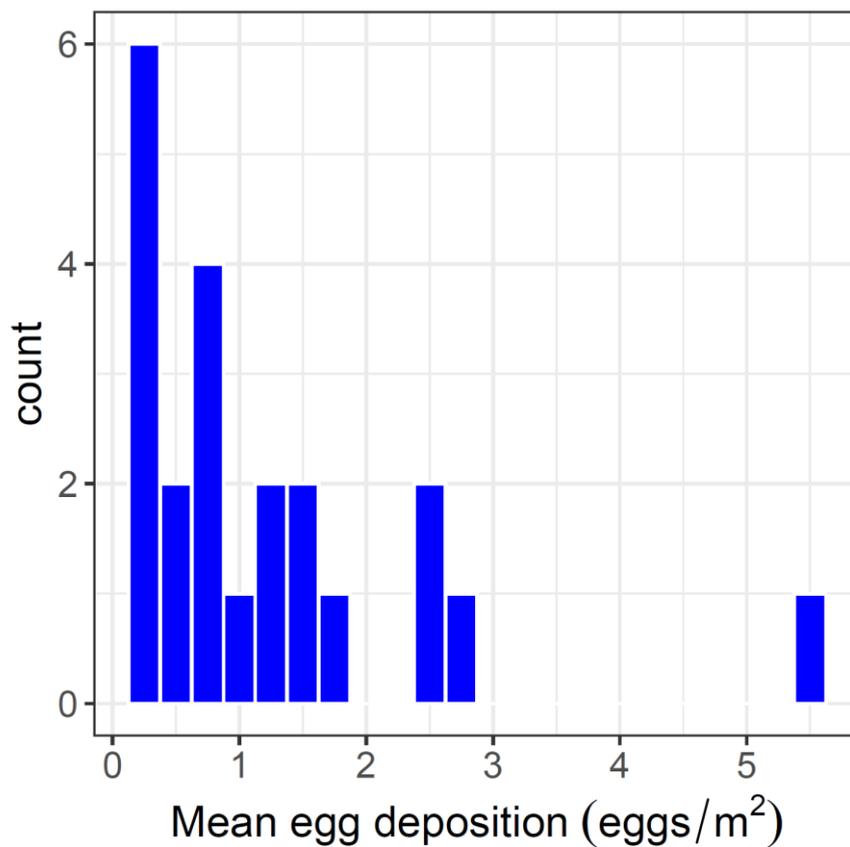


Figure 6. Recent levels of egg deposition (eggs/m²) during 2017-2021 indicates that current salmon productivity in Wales is low because most rivers are producing too few eggs (<2 eggs/m²), well below their conservation limit.

A noteworthy feature of many naturally small salmon populations (i.e. those that inhabit small rivers) is that they typically have a higher proportion of 1SW spawners (grilse) than those found in large rivers (**Figure 7**).

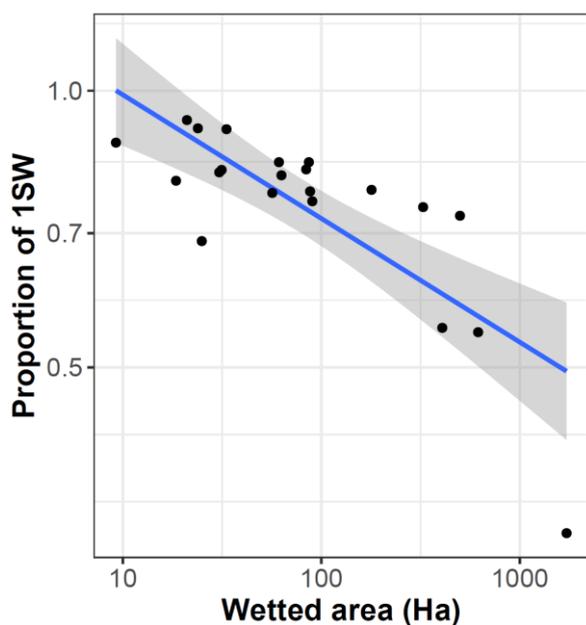


Figure 7. Relationship between river size (wetter area, hectares) and proportion of salmon returning annually as 1SW spawners to the main Welsh salmon rivers averaged for the period 2000 to 2021. The envelope represents the 95% confidence interval. Note the log scale for the x-axis.

The reasons why 1SW (grilse) appear to be more common in small rivers and MSW in large rivers are probably related to their different body size and life history strategies. Grilse are typically smaller than MSW and enter rivers after June, closer to the spawning season, in contrast to MSW which are larger and tend to enter rivers earlier in the season. Small rivers tend to have lower river discharges and are more prone to extended low flow periods which may select against a large body size and an early river entry. MSW have more energy reserves than 1SW fish and may be able to enter rivers earlier (in the spring) and survive without feeding until the autumn, a strategy that may only be possible in large rivers with sufficient discharge during the dry summer months.

The associations between river size, timing of return and salmon age and body size are important for conservation. First, a wider, more even distribution of sea ages is expected on first principles to reduce variance in annual abundance. Second, return rates (a proxy for marine survival) of 1SW and MSW salmon have changed differently over recent decades (WGNAS, 2022), possibly due to different mortality at sea reflecting salmon migrations, habitat, feeding opportunity and maturation timing. MSW salmon (being larger and more likely to be females), produce disproportionately more eggs, hence changes in total spawners may not directly translate into changes in total egg deposition when 1SW/MSW ratios change. Thus, trends and variance in population size of small rivers might be expected to be different from large rivers due to the higher prevalence of 1SW salmon in small rivers.

Recent analysis of Welsh rivers (unpublished) has shown that an upturn in MSW return rates (post-2000) has damped to some extent the recent decline in total egg deposition in large rivers, compared to small ones (although MSW return rates have declined again over the last 5 years). From a demographic perspective, shifting proportions of 1SW vs MSW fish having different body sizes and sex ratios can greatly affect the reproductive potential, and hence the abundance, fitness and resilience of stocks, although the implications for small populations are not clear. It must also be noted that conservation limits are based on the level of egg deposition - and thus on the number of females that survive to spawn - rather than on the total number of returning adults.

Given that small salmon populations can result from two different mechanisms, some questions arise that are important for management and conservation:

1. does small size *per se* compromise population persistence, stability and resilience regardless of how its small size arose? or
2. are functionally small populations worse off than intrinsically small ones?, and
3. at what population size might bottleneck effects occur?

2.1 Demographic consideration (3R's)

In conservation planning, it has been stressed the need to consider the 3R's, namely **Resiliency**, **Redundancy**, and **Representation** (Tear et al., 2005; Wolf et al., 2015).

Resiliency refers to the ability to recover from disturbance. It is affected by the abundance, spatial distribution, and productivity of a population.

Redundancy refers to the distribution of the population across the landscape and the extent to which there is a safety margin to cope with catastrophic events; it is affected by the abundance and spatial distribution of the population.

Representation refers to the range of variation found in a population or species; it ensures that the adaptive capabilities and evolutionary potential of the species are conserved; it is affected by its spatial distribution, abundance and diversity.

Stability, resilience and persistence are emergent properties of a population dependent upon its intrinsic growth rate (r), which is in turn determined by life history traits, survival, fertility and age at first reproduction and repeat spawning schedule. To be able to evaluate the consequences of small size it is helpful to establish what these properties mean, and how might they be measured, although their definitions are still somewhat loose.

Stability has been defined as the ability of a perturbed population to return to its pre-impact state, and *resilience* as the capacity to absorb impacts and not be re-set to an alternative lower state (Fraser, 2014). However, *resilience* has also been defined as the ability of a population to recover after a catastrophic disturbance and can be considered one of the two components of *stability* (Vincenzi, 2014; Vincenzi et al., 2014):

“The ability of a population to persist in the face of severe disturbances has often been considered as a measure of **stability**, which can be further differentiated into **resilience** and **resistance**. **Resilience** of a population [analogous with Holling’s (1996) ‘engineering resilience’] is the degree to which a population is able to recover from disturbance without major persistent changes in structure, as well as the time to return to equilibrium or steady state in population size, age and size structure (Gunderson, 2000). On the other hand, **resistance** is often defined as the amount of disturbance a system can absorb without undergoing a fundamental change (Grimm & Wissel, 1997).” (references in Vincenzi et al (2014).

These concepts are represented graphically in **Figure 8**, adapted from Ford (1999), where we show the response of natural populations to stressors under different scenarios (a-d) of resistance (friction) and resilience (recovery).

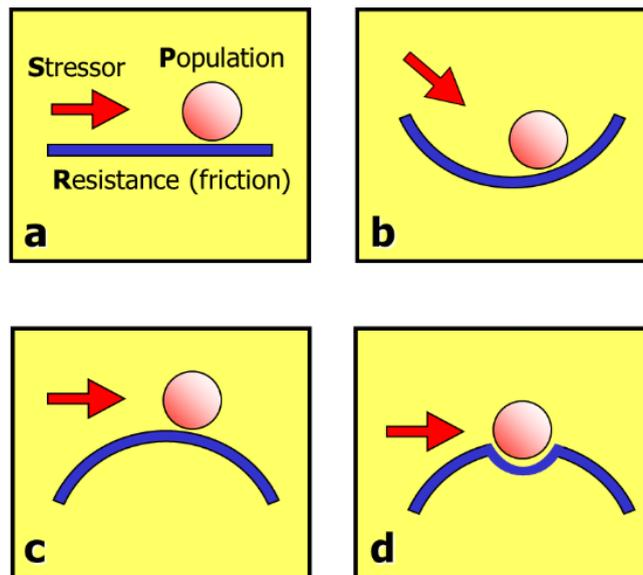


Figure 8. The concepts of *resistance* and *resilience* that underpin the response of natural populations to stressors (adapted from Ford 1999). Scenario (a) is an easily disrupted system with low resistance but high resilience, the population will simply move to a new equivalent state in response to a stressor and will stop moving once the stressor is removed (i.e there are no carry over effects). Scenario (b) has high resilience and high resistance, the population will bounce back to its original state once the stressor is removed. Scenario (c) has low resilience and low resistance, the population is easily disrupted and will not return to its original state even when the stressor is removed. Scenario (d) has high resistance that makes it more difficult to disrupt, but as in (c), it has low resilience, it will not return to its original state even when the stressor is removed. The danger for small populations is to be in (c), the least desirable state.

Small populations are intrinsically more variable from year to year than large ones

It can be proposed from first principles that small populations will be more variable than large ones because they have a lower intrinsic growth rate (Gotelli, 2008). Large populations may be more stable because they are more genetically diverse, occupy a wider spatial distribution (Einum et al., 2003) allowing them to reduce the risk of local extinctions across different habitats, and consist of more age classes (Vincenzi et al., 2014) which will buffer them against environmental change. Small populations, on the other hand, are more likely to have a simplified age structure and this will reduce the population buffering that would have been afforded by the port-folio effect (Moore et al., 2010; Schindler et al., 2010).

Spawner abundance data for salmon for Northwest England and Wales show that small populations tend to vary more (as evidenced by their larger coefficient of variation) than large ones (**Figure 9**).

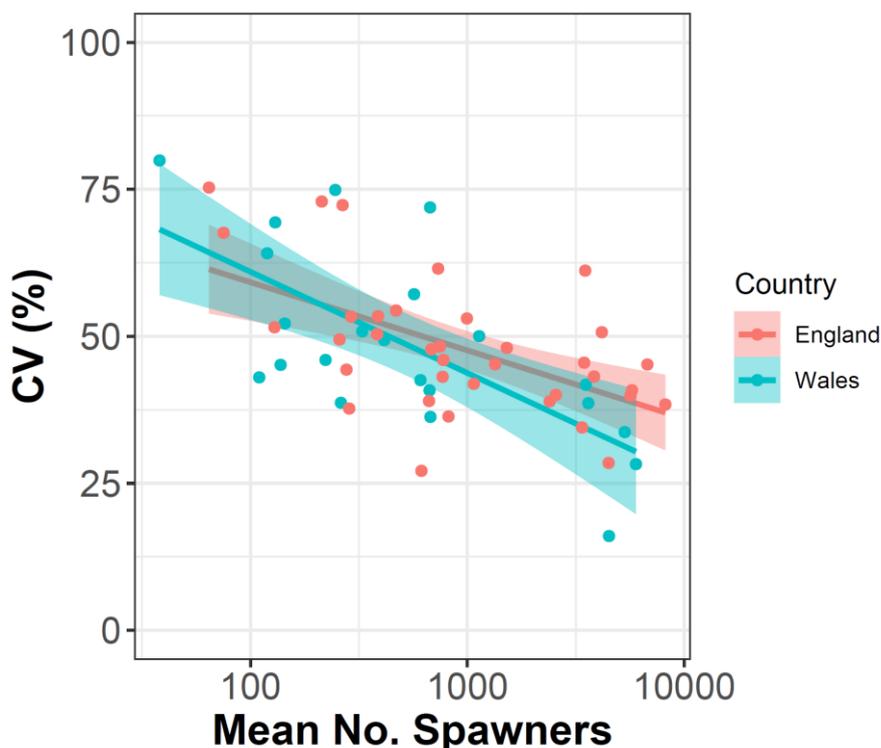


Figure 9. Relationship between the mean spawner abundance of salmon (an index of population size) on log scale and the coefficient of variation (standard deviation*100/mean) in rivers of Northwest England and Wales during 1994-2015.

These simple plots show that small populations are more variable than larger ones, but tell us nothing about the causal mechanisms or the consequences. The relationships shown in the above figures may result from a combination of intrinsically small population sizes and various impacts that have reduced the abundance of these populations below carrying capacity.

The dynamics of sea trout differ somewhat from those of salmon because of their life histories. Based on their much higher level of iteroparity (multiple spawning), sea trout populations would be expected to be inherently more stable than salmon, and the data show this to be the case. Comparisons across 23 Welsh rivers during 2008-2016 indicate that the coefficient of variation in egg deposition was significantly lower for sea trout than it was for salmon ($p = 0.016$). This is despite size selection and reporting biases likely being more acute and variable in sea trout than in salmon, because the former usually comprises varying proportions of small young (whitling/finnock) fish less likely to be declared in angling catches. Moreover, the incidence of whitling/finnock in the rod catch appears to vary considerably with marine environmental conditions, possibly through plasticity in timing of first maturity (Milner et al., 2017). Total rod catch data alone do not fully characterise population status of sea trout or salmon, because of the way that different sea age groups (representing different life history tactics) emerge in response to changing environments. Therefore, partitioning of the catch into runs and sea age components is needed to better describe populations responses.

2.2 Genetic considerations

From a genetics perspective, small populations are those that have an increased risk of losing genetic variation that may compromise their capacity to adapt to future environmental change.

Although studies on the effects of low genetic variation in natural salmonid populations are still few, they tend to reinforce the importance of maintaining genetic variation within populations as a primary goal of conservation and management. Maintenance of genetic diversity will be particularly important for fitness in heterogeneous and fluctuating environments. In small populations the main diversifying force is genetic drift, not adaptation. Thus, for natural selection to operate at maximum efficiency, salmon populations need to be maintained above a certain size, though determining such minimum viable population size is not easy. Small salmon populations can still maintain relatively high levels of genetic diversity despite evidence of recurrent bottlenecks (Consuegra et al., 2005b).

Four general problems can lead to loss of fitness in small salmon populations (Garcia de Leaniz et al., 2007a; Garcia de Leaniz et al., 2007b):

(a) *genotype shifts*. These may happen when the genotype, and likely the phenotype, shift outside an adaptive peak due to random genetic drift or outbreeding depression that might result from the deliberate (stocking) or accidental (farm escapes) introduction of maladapted individuals. Genotype shifts may also occur through the selective exploitation of particular phenotypic traits having a genetic component. For example, fisheries may target individuals of a particular size (Consuegra et al., 2005a), that enter the fishery at particular times (Hindar et al., 2007) or that behave in particular ways (Klefoth et al., 2017). If these make them more likely to be caught by fishers, changes in genetic structure may ensue.

(b) *Loss of genetic diversity (population bottlenecks)*. Demographic bottlenecks may result in loss of genetic diversity, for example due to overexploitation or introduction of novel parasites and diseases. These may result in inbreeding depression causing salmon populations to become more vulnerable to environmental change, curtailing their capacity to adapt, and increasing their risk of extinction.

(c) *Loss of habitat quality* may lead to phenotypic mismatch, if the environment is pushed beyond the species' habitat requirements, or more typically, beyond the population's adaptive zone.

(d) *Rapid environmental change* may result in maladaptation if changes in the environment are simply too rapid, making it impossible for local phenotypes to adjust.

When salmon populations are very small, genetic drift may cause weakly selected genes to start behaving like neutral genes, and natural selection to become less effective. This is one of the reasons why small inbred populations, and those subjected to recurring bottlenecks, are particularly at risk of losing genetic variation due to random loss or fixation of alleles (Garcia de Leaniz et al., 2007b). In such situations, the influence of genetic drift outweighs the effects of natural selection, further restricting the capacity of populations to adapt. This is particularly important for small populations of salmonids, because studies have shown

that they fluctuate much more than larger ones (Einum et al., 2003), as shown also for Wales (**Figure 9**).

3 How can small populations and population declines be identified?

Given the increased risk of extinction faced by small populations, it might be useful to examine what criteria could be used to detect population declines, and to identify those populations already at risk for being too small.

3.1 Demographic indicators

Empirical evidence from vertebrate populations that became extinct indicates that the size of the populations, the rate of decline, and the extent of year to year variability can be used as tell-tales of impending extinctions (Fagan & Holmes, 2006). In general, the results indicate that smaller populations, those that oscillate the most, and suffer the steepest declines are the ones most likely to become extinct.

Although little demographic information exists on salmonid declines, population stability and demographic resilience are also thought to be good indicators of population viability, and thus of extinction risks, in salmon (Dodson et al., 1998; Einum et al., 2003). However, other considerations, like the level of biocomplexity (Michener et al., 2001) resulting from the interaction of discrete spawning populations with local characteristics (Ford, 2004; Garcia de Leaniz et al., 2007a; Garcia de Leaniz et al., 2007b) can buffer against environmental and anthropogenic change (Hilborn et al., 2003; Schindler et al., 2010) and reduce the risk of extinctions.

In Wales no relationship was found between population size (estimated as the number of eggs deposited at the CL) and the extent of population decline (estimated as % loss in egg deposition in relation to the CL in recent years, 2017-2021). The extensive variation observed in population declines (**Figure 2**) appears to be driven mainly by common responses to climate stressors, both in the marine and freshwater environments, and by river-specific factors, rather than by population size *per se*.

However, an explicit partitioning of factors contributing to salmon population declines in Wales requires more rigorous statistical modelling than was possible within the timescale of this study.

Habitat losses can reduce carrying capacity in two different ways: (1) by reducing the **quantity** of the habitat available to spawners and juveniles and/or (2) by reducing the **quality** of such habitat. Both result in a decrease in productivity (**Figure 10**).

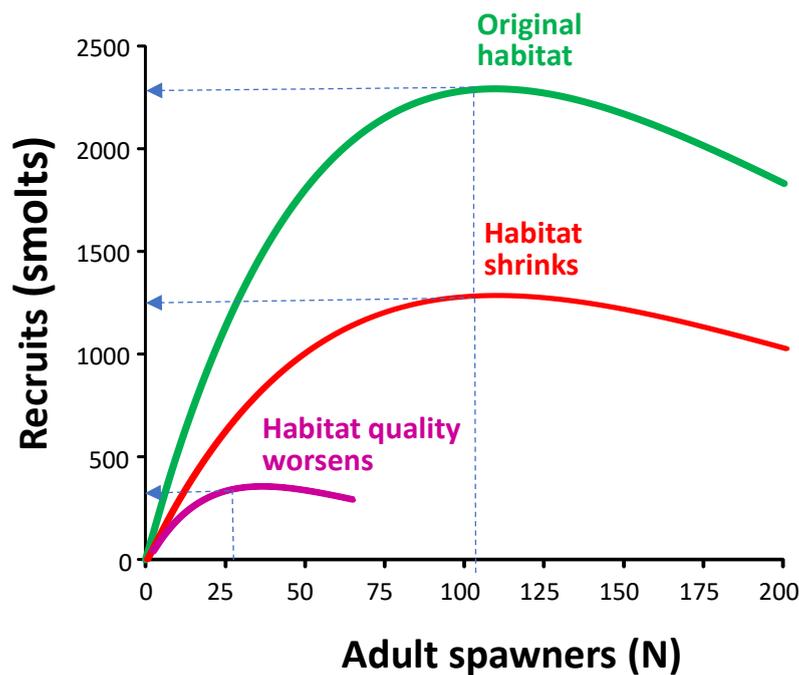


Figure 10. The two ways in which habitat loss can affect the stock-recruitment relationships and reduce productivity: (a) through a reduction in the area available to fish (loss of habitat quantity), for example caused by barriers, and (b) through the loss of habitat quality, for example due to pollution or reduced flows.

Habitat fragmentation often accompanies progressive environmental degradation and can lead to multiple smaller populations (Zastavniouk et al., 2017). Fragmentation will typically make the resulting subpopulations smaller, and hence more vulnerable. Loss of connectivity can therefore be used as an early warning of impending population declines. However, it has also been suggested that fragmentation can result in multiple, diversifying selection pressures and local adaptations and that these could increase overall metapopulation genetic diversity, provided enough gene flow is maintained between subpopulations (Fraser et al., 2014).

3.2 Genetic indicators

Loss of genetic variation can be assessed by measuring changes in heterozygosity and allelic diversity. After a bottleneck, rare alleles are lost and this tends to result in a temporary excess of heterozygosity, as rare alleles only make a small contribution to overall heterozygosity (Consuegra & Nielsen, 2007). Thus, testing for heterozygosity excess (in relation to allelic richness) can be used to detect recent population bottlenecks in salmonids (Consuegra et al., 2005b). In the longer term, loss of heterozygosity and allelic diversity are also to be expected.

However, it must be noted that many salmon populations are fairly small (i.e., census size, $N_c < 400$; effective population size, $N_e < 100$; Tables 1 & 2) and must have lost much genetic variation due to genetic drift (Bentsen, 1994; Adkison, 1995) and that the

relationship between genetic variation and fitness in salmonids is a complex one (Wang et al., 2002a; Wang et al., 2002b). For example, high levels of adaptive variation can be found even among surprisingly small populations (Koskinen et al., 2002; Quinn et al., 2001; Quinn, 1999; Quinn et al., 1998). Genetic diversity, at least with respect to neutral markers, does not always reflect well the size of Atlantic salmon populations (Consuegra et al., 2005b), and as with other species, the relation between genetic diversity and extinction risk is typically weak (Jamieson & Allendorf, 2012). Whole genome sequencing and novel SNP chips can help overcome some of these shortcomings, and can offer greater insights into the relationship between genetic variation and population fitness.

Hutchings et al. (2012) have suggested that incorporating genetic parameters could serve as 'red flags' of impaired population recovery (**Table A2**), as loss of genetic diversity is expected to slow down recovery. In general, it can be predicted that the faster the loss of genetic variation, the more endangered the population will be, and also the longer it will take for populations to recover. Therefore, obtaining temporal measures of genetic variation are useful not only for ascertaining conservation status, but also for monitoring recovery (Hutchings et al., 2012). In this sense, the use of 'genetic scorecards' can prove useful, as used recently in Scotland ([Scotland in world first for genetic diversity | NatureScot](#)). Here expert opinion is used to assess whether observed demographic declines are likely to result in loss of genetic diversity, and whether the impacts of hybridisation (as it might occur due to stocking with hatchery fish) and restrictions to regeneration/turnover are likely to impede evolutionary change.

3.3 How useful and reliable are genetic estimates of population size?

The amount of genetic diversity harboured by a population, and hence its capacity to adapt, depends on the number of fish that reproduce successfully (the effective population size), not on the actual (census) size of the population (N_c), which simply reflects the number available to reproduce.

Loss of genetic variation is a function of effective population size and the elapsed time in generations (Allendorf et al., 1997; Consuegra & Nielsen 2007). Therefore, reductions in effective population size provide a more relevant measure of changes in conservation status, and of extinction risk, than demographic parameters such as changes in rod catches or juvenile densities (Allendorf et al 1997; Consuegra & Nielsen 2007). Methods for population viability analysis use mostly demographic parameters (such as population size, population growth and stability), but effective population size has been shown to be a better surrogate criterion for extinction risk, as it is a function of genetic variability which provides a direct measure of adaptive potential. The assumption is that populations that already have low genetic variability, or lose genetic variability rapidly, will also lose the ability to adapt to future conditions, and thus have a greater probability of becoming extinct.

The effective population size can be calculated over a generation (N_e), or over a reproductive cycle (N_b), termed the effective number of breeders. The effective number of breeders represents the number of spawners that pass on their genes to their next generation, i.e. those that spawn successfully and contribute to the genetic variation of the

next cohort. N_e is more affected by the loss of genetic diversity and can be used to infer the demographic history of the population, whereas N_b is typically more useful for monitoring population size (Ferchaud et al., 2016), though both are related by G (the mean generation time) through the expression $N_e = N_b \times G$ (Waples, 2002).

Populations that have grown from a few founder individuals, or that experience strong reductions in abundance (bottlenecks), are particularly susceptible to genetic drift and this will be reflected in a reduced effective population size (Consuegra & Nielsen 2007; Primack, 2012). Evidence suggests that long-term effective population size may exceed short-term (contemporary) effective population size by 2-10 times (Fraser et al., 2007)

Results from 10 Atlantic salmon populations in Canada sampled over 5 consecutive years indicate that both N_e and N_b are positively related to census size (N_c), and show that N_b can be used for tracking changes in abundance of Atlantic salmon (Ferchaud et al., 2016). However the ratio N_b/N_c was found to be very variable, both among populations (37%) and among years (19%) which calls for caution. This point was emphasized in a recent meta-analysis of N_b/N_c ratios in salmonids that found that, unlike for Chinook salmon and brook trout where census size could be estimated from N_b (and vice versa), for Atlantic salmon the variability around N_b/N_c ratios may simply be too high to allow for confident predictions of population size based on genetic estimates (Yates et al., 2017). In brown trout, in contrast, estimates of N_e/N_c ratios were found to be relatively narrow, ranging between 0.16 and 0.28 (Serbezov et al., 2012a; Serbezov et al., 2012b).

Factors that may bias the estimation of N_e in practical terms have been reviewed in Gilbey & Bacon (2017) and include inadequate linking of N_e and N_c , undetected underlying population structure (for example metapopulations – see below), overlapping generations, presence of sexually mature parr, and iteroparity (Ruzzante et al., 2016; Waples et al., 2014). Uncertainty and errors in estimating N_e/N_c ratios in natural salmonid populations can span two orders of magnitude (Palstra & Fraser, 2012). Apart from various limitations and assumptions made by different estimation methods (reviewed in Luikart et al., 2010 and Gilbey & Bacon, 2017), one reason for this uncertainty is that it is notoriously difficult to get an accurate census of the number of salmon or trout in a stream (N_c). As John Shepherd once remarked, '*counting fish is like counting trees, except they are invisible and they keep moving*' (cited in Hilborn, 2002). Salmonid census size has been approximated variously from catch data (corrected for exploitation and reporting rates, and survival), from counts at fish traps or counters, or from juvenile densities extrapolated from comparatively few sampling sites. None of these methods are particularly reliable for large streams, or take into account the contribution of mature male parr, and with the possible exception of a few reference streams with good monitoring data (e.g. Gironck Burn in Scotland, River Dee in Wales), they rarely provide accurate estimates of census size necessary to properly calibrate N_e/N_c ratios (Gilbey & Bacon, 2017).

Without calibration, extrapolation from census size to effective population size (and vice versa) is difficult, particularly in the case of Atlantic salmon due to iteroparity, overlapping generations, the contribution of mature male parr, and the existence of gene flow between adjacent populations. Mature male parr will tend to augment genetic variation and increase N_e (Saura et al., 2008; Consuegra et al., 2005b) but will also shorten mean generation time and bias sex ratios in favour of males, which might decrease N_e . As the abundance of mature parr is seldom included in estimates of census size (N_c), derived N_b/N_c ratios are likely to be overestimated (i.e. they are in reality lower than they appear to be – Perrier et

al., 2016) although some authors have found these to be unaffected (Saura et al., 2008). Another source of bias may be introduced by the presence of hatchery fish. Repeated stocking was found to reduce N_b/N_c ratios in Atlantic salmon, most likely due to reduced reproductive success of hatchery-reared fish compared to wild fish (Perrier et al., 2016). The above results indicate that the use of genetic estimates of effective population size (N_e or N_b) as a tool for conservation and management of salmonids needs to be ground truthed and calibrated for different systems, a point that has been reiterated by various authors (Ferchaud et al., 2016; Gilbey & Bacon, 2017; Palstra & Fraser, 2012). The need for caution is particularly important for small populations (precisely those in greater need for conservation) because these tend to have particularly low N_e/N_c ratios, often less than 0.1 (Palstra & Ruzzante, 2008; Harris et al., 2017), and genetic estimates of population size are more variable and less reliable in small populations than in large ones (Bernos et al., 2016). In the absence of better information, an N_e/N_c ratio of 0.1-0.2 may be assumed (Frankham et al., 2014) a range that encompasses the empirical N_e/N_c ratio of 0.11-0.14 found for several species, including salmonids (Palstra & Fraser, 2012). If so, this would mean that a salmon population of 500-1,000 individuals (census size) would be the minimum necessary to prevent loss of genetic variation and fitness through inbreeding depression in the short term. However, even a ratio of 0.10 may be too high for Atlantic salmon if the contribution of mature male parr is high and not taken into account, or if there are meta-populations maintained by substantial gene flow.

3.4 The effect of metapopulations

Estimates of effective population size, census size, as well as extinction risks, are much affected by whether populations are isolated (i.e. can be considered closed systems) or are instead connected to other neighbouring populations by the exchange of migrants. Common practice in salmon management is to consider most populations to comprise discrete stocks at a catchment level, whilst acknowledging that some "straying" between stocks does occur. Evidence suggests that many salmonid populations, including brown trout and Atlantic salmon are rarely isolated, but rather exchange migrants to form meta-populations (Hindar et al., 2004; Palstra et al., 2007; Consuegra et al., 2005b; Fraser et al., 2007; Kuparinen et al., 2010; Harris et al., 2017). The exchange of migrants is typically asymmetric with some rivers acting as sources and others as sinks (Kuparinen et al., 2010; Consuegra et al., 2005b; Horreo et al., 2011) as seen in **Figure 11**.

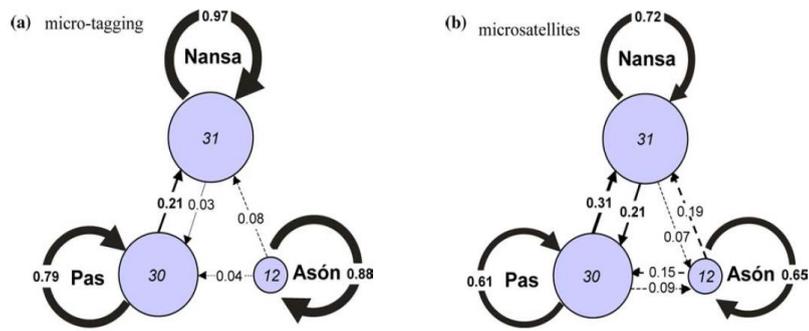


Figure 11. Patterns of gene flow in an Atlantic salmon meta-population showing broad concordance between results from (a) physical tagging and (b) variation at microsatellite DNA loci. The size of the circles is proportional to N_e , the size of the arrows is proportional to the proportion of fish migrating between rivers, and the numbers represent the proportion of migrants between rivers (from Consuegra et al 2005b). Note that the micro-tagging data refers to the recapture of stocked hatchery fish.

Crucially, the effective size of the metapopulation ($meta-N_e$) is lower than the sum of the individual N_e , and may depend on the size of the smallest subpopulation (Consuegra et al., 2005b; Horreo et al., 2011; Kuparinen et al., 2010), as seen in **Figure 12**.

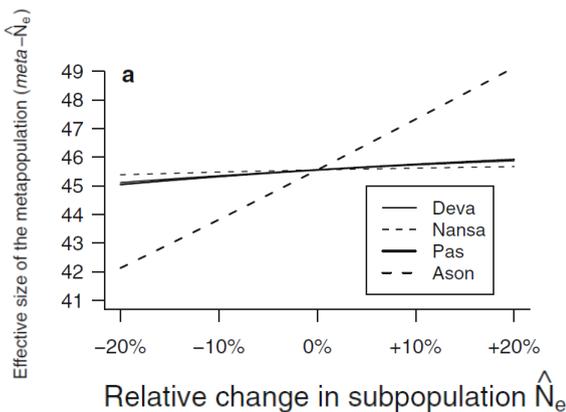


Figure 22. Expected changes in the effective size of a four-river metapopulation of Atlantic salmon, when the N_e of each subpopulation increases or decreases by up to $\pm 20\%$. The simulation shows that the size of one of the subpopulations (River Ason, dashed line) has a disproportionate large effect on the size of the metapopulation (from Kuparinen et al., 2010).

In a similar study in Spain, Horreo et al. (2011) noted that N_e estimates were 2-4 times *smaller* when one considered a large (regional) metapopulation (range = 56-132) than when one considered the additive sizes of each subpopulation in isolation (range = 179-271).

A study of 10 neighbouring Atlantic salmon populations in Norway showed that they were structured as a “source–sink” metapopulation, with catches dominated by one large population that acted as a source of migrants into the smaller nine populations (Hindar et al., 2004). As in Spain, the total effective population size of the metapopulation was critically dependent on the effective population size of this single population. Thus, metapopulation structure has consequences for overall genetic variation that needs to be taken into account when calculating effective population size. In particular, the viability of small populations may be highly dependent on having large neighbouring populations as the ‘source’ of their

genetic variation. Although the headline concern may be for the well being of small populations, the failure of large source populations may be a greater issue (as a herald of decline in the wider metapopulation).

A meta-analysis across taxa has suggested that minimum viable population sizes for some species may not need to be as high as previously thought because even modest levels of gene flow can increase genetic variation and help small populations to adapt (Wood et al., 2016).

Among anadromous salmonids, metapopulations are likely to occur when (a) populations inhabit discrete habitats, (2) there is a degree of asynchrony, and (3) there is dispersal between sub-populations (Schtickzelle and Quinn, 2007). These conditions are likely met in the case of Atlantic salmon and sea trout in Wales, although it has not formally been tested (but see Marburger, 2011).

4 Are there intervention points for managing small populations?

The idea that there may be a critical population size below which recovery is impossible (i.e. a minimum viable population size) is appealing for its simplicity (Nunney & Campbell, 1993) but if there is one, it has been notoriously difficult to determine for salmonids. Nonetheless, salmon managers will often want to know if there is a reference point in order to decide whether, and when, to intervene (intervention points).

4.1 Conservation Limits & Management targets

The Salmon Conservation Limit (CL) is a threshold Biological Reference Point (BRP) that defines a spawning stock level below which further reductions would increase the risk of population collapse. The CL was established in the mid-1990s as a Biological Reference Point for salmon conservation purposes (Chaput, 2006), but its origins lie in the regulation of stock fisheries (Potter et al., 2003). CL marks the spawning stock size at which surplus recruitment of juvenile fish is Maximised in terms of harvest by the fisheries (termed 'Maximum Sustainable Yield' or 'Maximum Gain').

As a stock decreases below CL there are still surplus recruits present and able to support recovery, but just not as many as at the CL. Reduction in spawning stock down towards CL from a stock initially above CL has the advantage of increasing surplus recruits. As spawners reduce from the CL, surplus recruits decrease. However, although such a stock is less resilient and stable than at the CL, it still has the capacity to recover and many stocks evidently have done from well below their conservation limit (Mawle & Milner, 2003). Therefore, while stocks are more vulnerable to additional pressures below the CL,

the risk of collapse progressively increases as spawner abundance decreases. The CL does not mark a sudden “no-recovery” position below which a stock is unsustainable but, in broad terms, equates to a point where, from the shape of the stock-recruitment relationship (its steepness rising from the origin), the risk of “no recovery” and extinction increases rapidly.

The use of CL as a biological reference point is an essential part of the Precautionary Approach recommended by NASCO and adopted by signatories to the NASCO Convention (NASCO CNL(98)46). In NASCO guidelines for Stock Rebuilding Programmes (SRP) (NASCO CNL(04)55), it is recognised that levels below the CL can occur by chance as well as systematically due to the effect of multiple pressures reducing stock size as well as non-linear responses affecting the stock-recruitment relationship. It also recognises the options of setting interim CLs or agreed recovery rates, but what these might be is left open. For this reason NASCO and ICES recommend that managers do not aim for the CL but for a value **above the CL**, termed the Management Target (MT).

The Management Target (MT) is the spawning stock level that managers should aim for to ensure that the Conservation Limit (CL) is met 80% of the time on the long run, therefore reducing the risk of bottlenecks (NRW, 2018). Setting the Management Target involves calculating the standard deviation (SD) of recent observed annual egg deposition (and applying a correction factor (0.842) that represents the 20 percentile of the standard normal distribution, as follows: $MT = CL + 0.842 * SD$

One problem with the use of CL is that, as with most reference points, it is based on models, rather than on empirical data. Nevertheless, the idea of a genuine critical threshold of low spawner abundance (much lower than CL) appears to have some credibility, and might represent an example of the Allee effect, by which recruitment ceases at low spawner abundance (Courchamp et al., 2008). The Allee effect (if one exists for salmon, and that has not yet been unequivocally demonstrated) can be seen as an important breakdown of the general tenet of the stock-recruitment assessment, namely that survival is high at low spawner abundance due to reduced density-dependent mortality at low egg and fry densities, thereby increasing population growth rate (**Figure 13**).

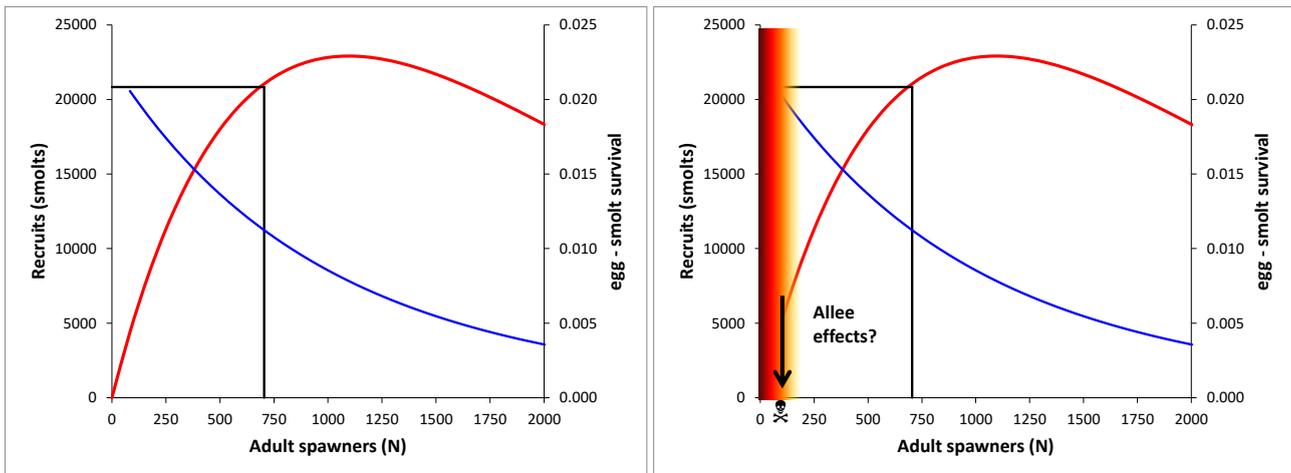


Figure 13. Example of a stock recruitment curve for the River Tawe, showing the influence of adult spawners on smolt numbers (recruits) (red line) and density-dependent egg to smolt survival (blue line). The black lines show spawners and recruits at the Conservation Limit (equivalent to 704 spawners). The right hand panel is a diagram of the region within which an Allee effect might lie: it is indicative only. The vertical arrow illustrates the point at which recruits will be zero even though some spawners return to the river.

With an Allee effect, density dependent loss would occur at low spawner abundance, leading to reduced population growth and eventual extinction. In practice, the process leading to extinction is more likely to occur from a failure to spawn successfully than from a reduction in survival. Intuitively, and due to homing and dispersal, as a spawning stock decreases to a very low level the probability of salmon spawners finding mates in a large catchment would appear to be greatly diminished. Chadwick (1982) proposed that a minimal viable population in a Canadian river required 80 spawner pairs (or 160 adults). However, this is probably dependent upon catchment size, the distribution of spawners, and the amount of spawning and rearing habitats.

4.2 Critical Values based on Effective population size

Bearing in mind the caution required in using effective population size estimates (see above), it is possible that they can be used to establish critical population thresholds to inform salmon conservation (Consuegra & Nielsen, 2007). To achieve this, periodic genetic screening of selected populations will be necessary, although this would not be needed every year.

Based on simulations and some empirical data Franklin and Soulé introduced the “50/500” rule, which posits that a minimum effective population size of 50 is required to prevent inbreeding depression in the short term and a minimum of $N_e = 500$ is required to prevent genetic drift and avoid extinction in the long term (Franklin, 1980; Soulé, 1980). Although the rule remains controversial, it is one of the most important guiding principles in conservation (Jamieson and Allendorf, 2012). It has recently been revised upwards to 100/1000, as recent studies have shown that an effective population size (N_e) of only 50

individuals may be insufficient to prevent inbreeding depression and that $N_e = 500$ is also too low for retaining long-term evolutionary potential (Frankham et al., 2014).

Estimates of contemporary effective population size (N_e or N_b) for Atlantic salmon populations can be very variable, ranging from just 12 fish in some endangered Spanish populations to in excess of 8,000 in some rivers on Russia (**Table 2**). In general, the more northerly (and presumably less impacted) populations are those that tend to have the largest effective population sizes.

Estimates of effective population size (N_e) can be used to determine conservation limits that are independent of habitat availability or carrying capacity. In Quebec a minimum threshold of $N_e = 95$ has been proposed for Atlantic salmon (Perrier et al., 2016), which is not far from the theoretical minimum of $N_e = 100$ proposed by Frankham et al. (2014) to prevent inbreeding depression in the short term. If so, many Atlantic populations, particularly the most southerly ones (**Table 2**) would fall below such a minimum.

Table 2. Estimates of effective population size (N_e) of 111 Atlantic salmon populations across the species' range (Garcia de Leaniz, 2021).

Location	No. rivers	N_e			Reference
		Min	Max	Mean	
Labrador & NF	20	443	1,697	1,067	Palstra et al. (2007)
Russia	26	26	8,318	888	Ozerov et al. (2012)
Quebec	10	196	2,167	984	Ferchaud et al. (2016)
Quebec	9	217	1,723	686	Perrier et al. (2016)
France	34	48	1,289	304	Perrier et al. (2013)
Wales (R. Taff)	1	158	225	191	Consuegra and Garcia de Leaniz (2013)
Nivelle (France)	1	67	213	113	
Asturias (Spain)	5	37	96	60	Horreo et al. (2011)
Cantabria (Spain)	4	12	31	25	Consuegra et al. (2005)
Galicia (Spain)	1	20	23	22	Saura et al. (2008)
Bidasoa (Spain)	1	10	20	~15	Morán and Saura (2020)

Data from Wales is very limited, but based on 14 microsatellites, Consuegra & Garcia de Leaniz (2013) estimated an N_e for Atlantic salmon in the River Taff of 158-225 (mean = 191). This may avoid inbreeding depression in the short term, but is well below the 1,000 recommended to avoid genetic drift and to maintain long-term evolutionary potential. Interestingly, N_e estimates for the River Taff were not affected by the presence of c. 10% of hatchery-reared fish in the runs (**Table 3**), and were statistically undistinguishable from those that only considered wild fish. This suggests that stocking had not helped to increase the effective population size of this population.

Table 3. Annual effective population size (N_e) for the River Taff, with and without hatchery returns estimated using two different methods (LD and TMP).

a) Linkage Disequilibrium method (LD)

	2010		2011		2012	
	<i>With hatchery fish</i>	<i>Excluding hatchery fish</i>	<i>With hatchery fish</i>	<i>Excluding hatchery fish</i>	<i>With hatchery fish</i>	<i>Excluding hatchery fish</i>
Ne-LD	158	159	225	223	184	171
95% CI	82-391	78-468	183-284	180-282	139-455	127-246

b) Temporal method (TMP) comparing 2010 vs 2011, and 2010 vs 2012

	2010-2011	2010-2011	2010-2012	2010-2012
	<i>With hatchery fish</i>	<i>Excluding hatchery fish</i>	<i>With hatchery fish</i>	<i>Excluding hatchery fish</i>
Ne-TMP	221	195	108	104
95% CI	151-303	133-266	70-233	71-142

Salmon counter data (Vaki counts) for the river Taff (effectively a Returning Stock Estimate, RSE) indicates an average annual return of 725 adult salmon during 2010-2014, decreasing to just 215 during 2017-2021. Using the 2010-2014 data, this suggests an N_e/N_c ratio of ~0.25 which is within the 0.11-0.28 range found for other salmonids (Palstra & Fraser, 2012; Serbezov et al., 2012a; Serbezov et al., 2012b).

Estimates of N_e for sea trout in Wales ranged from 698 for the River Tawe to 1,131 for the R. Teifi (Marburger, 2011), which reflect the larger catchment size and higher sea trout abundance of the latter.

Tentatively, and based on the results from the River Taff ($N_e/N_c = 0.25$), it is proposed that Welsh salmon populations may be considered “critically small” when they have a census size (N_c) < 400, an effective population size (N_e) < 100 and (using a mean generation time of $G = 2.5$ yrs. to factor in the contribution of mature male parr) an effective number of breeders (N_b) < 40, which will roughly translate to less than 20 female spawners per year. These are critical genetic limits, not management targets, and should be revised as more data becomes available.

4.3 Conservation status based on the IUCN Red List approach

Possibly the best way to ascertain whether there is a need to intervene is first to determine the conservation status of the populations of Atlantic salmon and sea trout under investigation. This can be achieved using the IUCN Red List, which can be considered the ‘gold standard’ for conservation. This has the advantage that the assessment is benchmarked against a set of tried and tested criteria that are audited independently from

the assessment process, thus reducing bias. The IUCN Red List classifies species into several categories, three of which conform the threatened group, defined as follows (IUCN Species Survival Commission, 2000):

CRITICALLY ENDANGERED (CR). A taxon is Critically Endangered when the best available evidence indicates that it meets any of the criteria A to E for Critically Endangered (see below), and it is therefore considered to be facing an **extremely high risk of extinction** in the wild.

ENDANGERED (EN). A taxon is Endangered when the best available evidence indicates that it meets any of the criteria A to E for Endangered (see below), and it is therefore considered to be facing a **very high risk of extinction** in the wild.

VULNERABLE (VU). A taxon is Vulnerable when the best available evidence indicates that it meets any of the criteria A to E for Vulnerable (see below), and it is therefore considered to be facing a **high risk of extinction** in the wild.

The **five criteria** (A-E) used to evaluate if a taxon belongs in an IUCN Red List Threatened Category are the following (**Table A3**).

- A. Population size reduction measured over the longer of 10 years or 3 generations
- B. Geographic range in the form of either extent of occurrence and/or area of occupancy
- C. Small population size and decline
- D. Very small or restricted population
- E. Quantitative Analysis of the probability of extinction in the wild

In the case of criterion A (population size reductions) these are based on observed, estimated, inferred or suspected reductions based on (and specifying) any of the following data:

- (a) direct observation
- (b) an index of abundance appropriate to the taxon
- (c) a decline in area of occupancy, extent of occurrence and/or quality of habitat
- (d) actual or potential levels of exploitation
- (e) effects of introduced taxa, hybridization, pathogens, pollutants, competitors or parasites.

In the case of criterion C that sets thresholds for minimum population size, this was recently found to be too low and may require doubling (Frankham, 2014 – see above).

A full IUCN assessment of conservation status and risk of extinction is a laborious process, but a simplified, rapid assessment can be done to flag those populations most at risk where a full assessment may be warranted. Specialized software is available for such a rapid assessment (<http://www.ramas.com/rapidlist>), using data on population size, trends, and geographic distribution to assign threat status to one of the following three categories:

1. Likely Threatened: Likely to be in one of the IUCN Red List categories of Critically Endangered (CR), Endangered (EN), or Vulnerable (VU)

2. Likely Not Threatened: Likely to be in the IUCN Red List categories of Least Concern (LC) or Near Threatened (NT);
3. Likely Data Deficient: Likely to be in the IUCN category of Data Deficient (DD).

One advantage of this approach is that parameter uncertainty can be incorporated into the assessment, so it is possible to determine what gaps in knowledge are crucial and which ones are not.

4.4 Application to Salmonids

Allendorf et al (1997) combined genetic and demographic data to estimate extinction risks and prioritize populations for conservation in Pacific salmon based on five criteria (**Table A4**): (1) population viability analysis (PVA), (2) estimates of effective population size per generation, (3) total population size per generation, (4) rate of population decline, and (5) catastrophes (Appendix Table A1). Populations with a high risk of extinction were deemed to be those with a 50% extinction risk within the next five years according to results of the PVA, those that had an N_e less than 50 or a total population size (N_c) less than 250, and/or those which had suffered a precipitous decline of an order of magnitude within one generation.

The authors stressed that those populations historically present but without enough data to carry out an assessment should be regarded as of *special concern* and data should urgently be obtained on run size or some proxy for population strength, basic demographic parameters such as proportions that spawn at each age or adult survival between spawning, as well as genetic data and measures of genetic diversity.

In Spain, García de Leániz et al. (2001) assessed the conservation status of 7 Atlantic salmon populations using IUCN criteria of effective population size, abundance, declines and fluctuations, and recent catastrophes and concluded that three populations were functionally extinct, two were endangered, and two were critically endangered. In a more recent assessment of the same populations, Barquín et al., (2012) concluded that, from the perspective of Natura 2000, the conservation status of these populations was clearly inadequate.

IUCN criteria were also used to produce a global assessment of the extinction risk to populations of sockeye salmon (*Oncorhynchus nerka*) across North America (Rand et al., 2012) (Table A4). The authors generally adhered to the Red List terminology but to avoid confusion they used 'population' to refer to genetically distinct groups and used "demes" for "groups" that were ecologically but not genetically isolated within populations (i.e. subpopulations). To group populations for assessment they used *Evolutionary Significant Units* (ESUs), as defined by U.S. ESA (Endangered Species Act) and [*Designatable Units* (DU), as defined by the Canadian Species at Risk Act (SARA) of June 2003 (Green et al., 2005). The authors used the Red List A2 criterion (rather than the A1 criterion) because population reductions or its causes may not have ceased, may not be fully understood, or may not be reversible, a situation which is probably common to many salmonid populations. They applied B1 and B2 criteria at the species level (including both extent of occurrence and

area of occupancy). For the population assessment, they considered B2a,b(v) criterion, based on area of occupancy, severe fragmentation or the number of extant locations, and the rate of change in the number of mature individuals. In cases where there had been substantial declines in freshwater habitat quality for populations, they evaluated status against Red List B2b(iii) criterion. They assessed status based on absolute adult abundance using the thresholds for the Red List D criterion. For all three of these criteria (A, B, and D), they used escapement as the measure of population abundance, as this was deemed to be more directly related to the number of mature individuals than catches. They did not consider Red List C and E criteria, which involves projecting habitat conditions and population responses. As per IUCN guidelines, the criterion/criteria that returned the greatest risk of extinction was used to characterise conservation status.

Another example of the application of IUCN criteria to the assessment of salmonids is the study of population persistence of Chinook salmon in Puget Sound (Ruckelshaus et al., 2004). Here the authors used the rapid, simplified procedure outlined above to decide whether a full assessment was warranted.

In Canada, the Committee on the Status of Endangered Wildlife (COSEWIC) http://www.registrelepsararegistry.gc.ca/sar/assessment/default_e.cfm has used slightly modified IUCN criteria to assess the conservation status of Atlantic salmon (**Table A6**). In their assessment, COSEWIC uses genetic data to determine Demographically Functional Units (called designatable units, DUs). These tend to be at the watershed scale, but population subdivision may occur within watersheds. Atlantic salmon are thought to spawn in c. 700 rivers in Canada, but COSEWIC guidelines state that “a population or group of populations may be recognized as a DU if it has attributes that make it “discrete” and evolutionarily “significant” relative to other populations”. Evidence of discreteness can include “inherited traits (e.g. morphology, life history, behaviour) and/or neutral genetic markers (e.g. allozymes, DNA microsatellites...)” as well as large disjunctions between populations, and occupation of different eco-geographic regions. To determine the units of assessment (COSEWIC, 2018; COSEWIC, 2010) used results from landscape genetics based on 13 microsatellites and the screening of 2,775 anadromous (adults) from 51 rivers that helped to delineate different regions (Dionne et al., 2008) and to assess the possibility of genetic rescue from outside populations (based on gene flow). Additional data from Newfoundland and Labrador were also used (Adams, 2007).

The Canadian range of this species was subdivided into 16 designatable units (DUs) based on genetic data and broad patterns in life history variation, environmental variables, and geographic separation (**Table A5**).

http://www.sararegistry.gc.ca/document/default_e.cfm?documentID=2258

At the last assessment (COSEWIC, 2010) considered there were 16 Atlantic salmon DUs in Canada, one of which was DATA DEFICIENT, four were NOT AT RISK, one was THREATENED, four were of SPECIAL CONCERN, five were ENDANGERED, and one was EXTINCT (**Table A6**; note that the Critically Endangered category is not used).

In the US, salmonid populations are also classified into ESUs for conservation status assessments based on genetic, ecological, and life-history characteristics (Gustafson et al., 2007; Fay et al., 2006). Genetic data includes not just microsatellites but also allozyme data.

5 Can small populations rebound without intervention?

Unquestionably, the loss of salmon populations from individual rivers should be avoided, but the history of salmon in the British Isles and elsewhere has examples of populations that recover from very low population size or even from complete eradication, once the constraining factors are lifted (Mawle & Milner, 2003). This arises mainly through natural recolonization, with partial support from stocking programmes in some cases (Cross et al., 2007) or with none (Ikediashi et al., 2012). It must be remembered that many salmon populations became extinct during the Last Glacial Maximum (~18,000 years BP) and were subsequently recolonised from glacial refugia through straying when the ice retreated (Consuegra et al., 2002).

5.1 Vulnerability and recovery of small populations

The mechanisms that underly recovery from population declines (or even extirpation) in salmonids are not well understood, but natural straying from other rivers, which is a natural colonising process in anadromous salmonids (Quinn, 1993), appears to be of paramount importance. The effectiveness of this process and speed of recovery will depend on the source and suitability of straying spawners, as well as the removal of previously limiting factors. Adjacent source populations may constitute metapopulations, *sensu* Schtickzelle et al. (2007) which comprise groups of rivers that display a degree of asynchrony coupled with the appropriate similarities in environment that promote relevant adapted genotypes.

It seems obvious that a formerly large population that has been reduced to a small one through environmental pressures would be more vulnerable to further perturbations, because the consequent greater demographic stochasticity (**Figure 9**) would likely increase the extinction risk in the face of heightened environmental stochasticity. It is argued above that this is not a sudden threshold at the CL. Although evidence for Allee effects is very scant in salmonids, it has been demonstrated for coho salmon (Chen et al., 2002). Allee effects may be more widespread, but may be difficult to detect due to data constraints and low statistical power (Myers et al., 1995), and would require further investigation.

As Hutchings (2013) has pointed out “*the longer a population remains at low abundance, the more likely it is that the environment around it will change in ways that are unfavourable to recovery [and] it is this “temporal tyranny” of small population size that is most likely to produce an emergent Allee effect.*”

Two mechanisms that may enable small populations to recover without intervention are **evolutionary rescue** and **genetic rescue** (Carlson et al. 2014). *Evolutionary rescue* refers to the genetic adaptation that allows populations to recover from environmentally-induced demographic crashes that would otherwise have caused extinction (Carlson et al., 2014). *Genetic rescue* refers to the increase in absolute fitness that occurs in small inbred populations when there is an influx of genetic variation from immigrants from other

populations. Although there is limited evidence for evolutionary rescue in salmonids (Johannesson et al., 2011), genetic rescue may account for the surprising persistence of very small salmon populations inhabiting marginal habitats, provided they are connected by gene flow (see **Figure 11**), which could lead to a full recovery if environmental impacts are addressed. Therefore, the best chances for depressed populations to recover may lie in being connected to larger, more healthy neighbouring populations.

5.2 Lessons from invasive salmonids

The spread of salmonids in the Southern Hemisphere, where they have often become invasive (Garcia de Leaniz et al., 2010), is perhaps the best proof that salmon and trout can thrive and expand from very small population sizes, provided the habitat is appropriate.

5.3 Management interventions for critically small populations.

The above account shows that from a population dynamics perspective, beyond the qualitative mechanism of the (poorly understood) Allee effect, there is no reported evidence to support a fixed biological reference point marking a declining population's point of no return.

Extirpation risks progressively increase below the CL and management practice to reverse decline should identify the extent and causes and act accordingly. As populations decrease to very low levels (as they are in some Welsh rivers), potential interventions fall into five broad categories:

- 1) Restore habitat and environmental quality to allow natural breeding and juvenile rearing to occur unimpeded to produce good quality smolts at the maximum carrying capacity of the catchment. NB smolt size is a crucial determinant of later survival (Russell et al., 2012, Gregory et al., 2020). This should be an ongoing activity whatever the conservation status of the populations.
- 2) Maximise natural connectivity to allow adults access to spawning habitat and facilitate smolt migration to sea. NB this refers only to man-made barriers.
- 3) Protect the spawning stock from any additional sources of mortality, beyond the normal, natural mortality experienced throughout the life-cycle.
- 4) Support by artificial rearing. This is advised against without a thorough, critical investigation of the causes of decline and the likely outcomes. This is not the place to reprise the debate on stocking, although it can always be revisited with new information and under new circumstances.
- 5) Gene-banking. This can be used as a last resort conservation measure (e.g. O'Reilly & Doyle, 2007), but the long term aims need to be set against the reality of whatever

has brought a population to near extinction. The obvious context is of long term global climate change that could render the North Atlantic and freshwater environments unsuitable to support natural salmon populations.

Provisional examination of trends and synchrony amongst Welsh salmon and sea trout populations suggest that (i) there are definite climate signals (of decline) across all rivers, but (ii) there are also river-specific signals that point to local factors which are likely amenable to resolution by effective management. This course of action is what gives hope for the currently depleted stocks: but it is urgent.

6 How can population size and conservation status be monitored?

There is a need to know how many distinct salmon and trout conservation units exist in Wales, where they are, what their conservation status is, and how they are connected. It is also important to know whether salmon originating from some rivers contribute more to the populations (and to the fisheries) than others. One would probably also want to know what the genetic diversity and effective population sizes are, and whether there is evidence of population expansion (as one would predict from habitat improvements) or contraction (as one might expect from increasing mortality at sea or in freshwater). A more efficient monitoring of the conservation status of salmon and trout will require combining various pieces of information to make the best possible use of all the resources and data available.

6.1 Outline of a monitoring plan and IUCN Assessment of Atlantic salmon and sea trout in Wales

Although rod catch data provides essential information on the trends of salmon and trout fisheries (Bunt & House, 1991) - and have the added merit of being available for most rivers over relatively long periods, such data can have important shortcomings as indicators of stock abundance and need to be interpreted with caution, particularly if no information is available on fishing effort.

Rod catches alone may not adequately reflect the size of salmon populations, particularly if these are small, because rod catches depend on fishing effort and vulnerability to capture, both influenced by environment, especially river flow and temperature. When fish populations decline they may be more vulnerable to fishing, resulting in 'hyperstability' and giving an 'illusion of plenty' (Dassow et al., 2020; Erisman et al., 2011; Tsuboi et al., 2021). Critically, fisheries may also be affected by Allee effects (Dulvy et al., 2003; Sadovy, 2001), whereby the probability of catching salmon or trout may be higher when abundance is low than when abundance is high, which may grossly underestimate extinction risks (Berec & Mrkvička, 2013; Rougier et al., 2012). Except on rivers where there are means of enumerating numbers of returning fish directly – e.g. through the operation of validated counters or traps, the relationship between salmonid rod catch and abundance is typically unknown, and will likely vary from year to year, and also from river to river (Youngson et al., 2002). Rod catch may be affected by fishing effort, catch and release, river conditions, run

timing, and variation in angler's fishing success, among many other factors (Mills et al., 1986; Milner et al., 2001).

A statistical assessment of the salmon and sea trout rod catches in the rivers Afan, Neath and Tawe indicates that catch is highly variable so that it may take many years to detect a genuine decline against such noisy background (**Figure A1**). Hence, although rod catches may be of paramount importance to anglers, on their own they will typically afford low statistical power to detect recent population declines in all but the most drastic of cases (Garcia de Leaniz et al., 2015).

We note, however, that rod catches lie at the core of processes used to assess the status of salmon and sea trout stocks against CLs – including in Wales and England and that in rivers where there is counter data, rod catches and salmon counts are often significantly correlated (Cefas/EA/NRW 2022), giving some confidence in their use. In addition, synchronies between catch data from numerous rivers suggest that rod catches reflect, to some degree, common patterns. Moreover, rod catches are the primary metric of fishery performance and as such need to be measured as accurately and consistently as possible. Options now exist to incorporate into analysis models of the effects of river flow and temperature, both factors that strongly influence fishing effort, and fish availability and catchability. Such approaches, coupled with better reporting systems, could significantly enhance the value of catch data for fisheries and population monitoring purposes. Catch records in England and Wales also include other information such as fishing effort, the size and timing of the runs, and environmental factors influencing fish availability, accessibility, catchability and fishing efficiency, which are used to refine the interpretation of catch data and aid in modelling exploitation rates and derive population size and egg deposition estimates with greater confidence.

Most data sources used to assess salmon stocks suffer from some shortcomings, not just rod catches. For example, estimates of juvenile salmonid abundance conducted by electrofishing are also prone to various errors and biases. Salmonid 'density' is not a particularly good metric as it is scale-dependent and depends greatly on catchability (e.g. vulnerability to fishing gear). In this context, one pressing challenge is to compile and standardize all electrofishing data, and to make it available in a suitable form (online database, meta-data) to support an evidence-based approach to salmonid monitoring and conservation. A recent review of the NRW salmonid monitoring programme has greatly increased the potential value of juvenile data to derive estimates of standing stocks (Bewes et al 2019b) but further work is needed to resolve some important details of stream carrying capacity and absolute stock sizes.

Monitoring could perhaps also take into account other parameters, such as the spatial distribution of individuals, the extent of habitat occupancy (habitat saturation) and the degree of genetic variation (more of this below). Habitat models such as Habscore (Barnard et al., 1995) can make use of habitat quality data to explain some of the spatial variance in juvenile abundance. One would need to incorporate measures of habitat quality and stream connectivity, determine how many sampling points are needed, how often they should be sampled and how intensively. It may be that for many cases 'presence/absence' models (P/A) may work just as well and be considerable cheaper than more costly semi-quantitative surveys.

Robust methods are also needed to enable managers to assess to what extent habitat improvements are having a positive effect on fish populations, and to determine what statistical power is needed to detect such improvements against an inherently noisy background (i.e. absence of evidence is not evidence of absence).

Compared to capture-based methods, genetic methods have the advantage that they can provide an assessment of the abundance and conservation status of populations which are independent of catches, or effort. They necessitate, however, that populations are sampled without bias, and that representative samples are available for analysis - ideally comprising several year classes (Schwartz et al., 2007). They rely on the assumption that genetic diversity will tend to increase with population size, and that rare alleles are more likely to be persist in large populations than in small ones (Moran, 2002; Carvalho & Pitcher, 2012). In the context of a monitoring plan, genetic methods may allow the detection of:

Reductions in effective population size (N_e), as we have seen, this metric can provide a more relevant measure of changes in conservation status, and of extinction risks, than changes in rod catches or juvenile densities (Consuegra & Nielsen, 2007)

Reductions in genetic diversity (genetic bottlenecks). As population size declines, neutral genetic diversity should also decrease; analysis of allele frequency data, hence, can be used to infer recent population bottlenecks that can help to inform management and could help establish intervention points (Piry et al., 2000).

Straying and movements of salmon and sea trout between rivers. Molecular markers are good surrogates for physical tags to infer salmonid movements (**Figure 11**); they also provide valuable additional information. Most salmon and sea trout populations are not completely isolated, and genetic data can allow the estimation of gene flow. This information can be used to identify the existence of meta-populations consisting of 'sources' and 'sinks' (Schtickezele & Quinn, 1993; Vanhaecke et al., 2012; Consuegra et al., 2005b). Because gene flow in salmonids is often asymmetrical, fish from some rivers may have a disproportionate effect on the global meta-population structure and conservation of some key populations may be more critical than others (Kuparinen et al., 2010) These need to be identified because, as we have shown above, they will respond very differently to population declines.

Results from electrofishing surveys (available for all major Welsh rivers) could be combined to provide a meaningful baseline of relative salmon and trout abundance against which to compare any future impacts (Bewes et al., 2019b). For some Welsh Rivers, for example the River Afan at Green Park Weir, there are also counter data on the number of salmon and trout passing through a fish-pass (Golding, 2014). This information could also be used to construct baseline values, and may afford some form of calibration of rod catches, and also of electrofishing surveys. Similar trapping/counting facilities also exist in other nearby rivers (e.g. R. Teifi, R. Tawe, R. Taff) and the River Dee in North Wales (the longest duration index river in England and Wales), and information gathered from these rivers could be statistically combined to reduce uncertainty and maximize monitoring power. Developments in data mining (Elith et al., 2008) and use of Bayesian belief networks (Marcot, 2012) could then be used to combine very heterogeneous sources of data (electrofishing surveys, genetic data, rod catches, fish counters, movement data) to reduce uncertainty and develop more efficient monitoring plans.

Other approaches (e.g. Hutchings et al., 2012 or the IUCN assessment) are likely to rely also on catch data to some extent as indices of abundance for individual river stocks.

IUCN Assessment of the conservation status of Atlantic salmon and sea trout

There is merit in assessing the conservation status of Atlantic salmon and sea trout across Wales using the IUCN methodology, as shown in the examples given above. This would be an invaluable tool to secure the best possible protection to the species and to draw public attention in the form of a colour-coded Salmon Atlas depicting the conservation status of every salmon and sea-trout river in Wales. Both WWF (2001) and the NASCO Salmon Rivers Database (<https://nasco.int/rivers-database/>) provide some information for Atlantic salmon but both are too coarse for detailed conservation planning.

With the help of local fish biologists, such an exercise would help to identify the main threats to salmon and trout and to evaluate the merits of different recovery actions; this would represent a turning point in the conservation of salmon in Wales. Some of the questions that need to be addressed include:

- (1) What are the current appropriate IUCN categories of risk for Atlantic salmon and sea trout in Wales?
- (2) What do healthy populations have in common? Where are they?
- (3) What about the threatened ones?
- (4) What recovery actions are being used?
- (5) Which ones work best or are likely to work best and under which conditions?

Strategy and some sampling considerations

To address the questions above and carry out such an assessment one could begin with individual catchments as a reasonable first approximation to conservation units. For this, one would use the NRW databases that hold the location and basic information on adult and juvenile population sizes and composition in each of the major salmon and sea trout rivers in Wales. The nine steps of the proposed assessment would be as follows:

1. Check existing salmon and sea trout river database for errors and omissions
2. Expand, if needed, the current database
3. Adapt IUCN criteria for use on salmon and sea trout populations based on measures of abundance, distribution, rate of change and effective population size
4. Pilot trial the score system and assess robustness and repeatability using the rapid, simplified IUCN assessment
5. Compile data on required metrics for each population
6. Determine suitable units of assessment
7. Carry out evidence-based assessment
8. Submit to IUCN for auditing
9. Produce report and global map

Yates et al. (2017) have compared the cost of obtaining estimates of census size in brook trout (derived from physical mark and recapture of adults at spawning time) with genetic estimates of N_b based on 10-15 microsatellite markers, and came up with very similar costs for a range of sample sizes. This may not hold true for Atlantic salmon because mark and recapture is unlikely to be an option at spawning time and fish typically spawn in larger

systems than brook trout which can make census size estimates substantially more expensive than estimates of effective population size. In addition, genetic analysis provides additional information that are important for conservation on their own right, including measures of genetic diversity and evidence of bottlenecks (Consuegra et al., 2005b).

From a cost-effective and practical point of view, for genetic characterisation, it may be better and easier to sample juveniles than adults. Juveniles have the added advantage that one can be fairly confident they have originated from the river system that is being sampled, and fin clips for genetic analysis can easily be obtained from current electro-fishing surveys. The drawback is that ensuring that samples are random is more challenging and one runs the risk of simply sampling families due to limited dispersal. To ensure a random representative sampling, it has been recommended to sample at least 100 juveniles per river system, distributed in five or more spatially-structured samples each contributing no more than 20 juveniles each (Perrier et al., 2016; Ferchaud, et al., 2016). This appears readily achievable within NRW's current spatial/temporal electrofishing framework and would probably involve little additional sampling effort, only the additional analytical costs.

7 Conclusions and Recommendations

- Atlantic salmon and sea trout in Wales are declining at unprecedented fast rates and predictive modelling indicates that many populations may be threatened with extinction within the next few decades if current conditions remain.
- However, there are few examples in Wales of permanently lost salmon and sea-trout populations, and several formerly depleted stocks have recovered from very low levels. Salmon populations may recover from complete extirpation if limiting factors and environmental constraints (including fishing) are removed, and if neighbouring populations remain healthy, due to metapopulation dynamics and natural recolonization.
- Evidence for a threshold population size (Allee effect) is limited, but there are few data sets to test this, so the statistical power may simply be too low.
- It is possible that Welsh rivers represent one or more metapopulations, which may confer some collective resilience. However, that is contingent on climate driven factors, acting in marine and freshwater habitats, not over-riding any collective resilience.
- There is a need to understand how and why populations contract, and whether they do these evenly or unevenly, or in combination. Partial synchrony indicates that salmon and sea trout are responding to a mixture of common (e.g. climate-driven) and local catchment-specific pressures.
- There is also a need to understand how small populations recover, and whether recovery is more likely to happen between populations within a metapopulation,

perhaps depending on dispersal and source-sink dynamics which may affect effective reproductive rates.

- Data from rod catches, and to some extent also from juvenile surveys, are inherently noisy, particularly for small populations, and simulations indicate that many years may be required to detect declines of salmon and trout, which may limit their value as red flags for triggering immediate action. Statistical modelling of adult and juvenile life stages with environmental covariates, and including their reciprocal influences through life cycle models offers a more robust and informative use of the monitoring data.
- A combination of demographic and genetic methods is recommended to assess population declines and decide on intervention points in exploited salmonid populations, particularly at very low levels.
- An IUCN-type assessment of the conservation status that incorporates metrics of distribution, occupancy, abundance, population size fluctuations, and genetic data (diversity and effective population size) offers the best prospects for effective monitoring of Atlantic salmon and sea trout in Wales.

8 References

- Adams, B. K. (2007). Migratory strategies of Atlantic salmon (*Salmo salar*) of Newfoundland and Labrador. P. 170: Dalhousie University.
- Adkison, M. D. (1995). Population differentiation in Pacific salmon: local adaptation genetic drift, or the environment? *Canadian Journal of Fisheries and Aquatic Sciences* **52**, 2762-2777.
- Allendorf, F.W., Bayles, D., Bottom, D.L., Currens, K.P., Frissell, C.A., Hankin, D., Lichatowich, J.A., Nehlsen, W., Trotter, P.C., Williams, T.H. (1997). Prioritizing Pacific salmon stocks for conservation. *Conservation Biology* **11**, 140-152.
- Anon (2018). Assessment of Salmon Stocks and fisheries in England and Wales. Standing Report on Methods, Approaches and wider Stock Conservation and Management Considerations. Cardiff: NRW.
- April, J., Bardarson, H., Ahlbeck-Bergendahl, I., Bolstad, G.H., Breau, C., Buoro, M., Camara, K., Chaput, G., Cooper, A., Dauphin, G. (2021). ICES. 2021. Working Group on North Atlantic Salmon (WGNAS).
- Bacles, C.F., Bouchard, C., Lange, F., Manicki, A., Tentelier, C., Lepais, O. (2018). Estimating the effective number of breeders from single parr samples for conservation monitoring of wild populations of Atlantic salmon *Salmo salar*. *Journal of Fish Biology* **92**, 699-726.
- Barnard, S.J., Wyatt, R.J. and Milner, N.J. (1995). The development of habitat models for stream salmonids, and their application to fisheries management. *Bull.Fr.Pêche Piscic.* **337/338/339**, 375-35.
- Barquín, J., Ondiviela, B., Recio, M., Alvarez-Cabria, M., Penas, F. J., Fernandez, D., Gómez, A., Álvarez, C. & Juanes, J. A. (2012). Assessing the conservation status of alder-ash alluvial forest and Atlantic salmon in the Natura 2000 river network of Cantabria, Northern Spain. In *River Conservation and Management* (Boon, P. J. & Raven, P. J., eds.), pp. 191-208: John Wiley & Sons.
- Bentsen, H. B. (1994). Genetic effects of selection on polygenic traits with examples from Atlantic salmon, *Salmo salar* L. *Aquaculture Research* **25**, 89-102.
- Berec, L. & Mrkvička, T. (2013). Neglecting uncertainty behind Allee effect estimation may generate false predictions of population extinction risk. *Oikos* **122**, 845-856.
- Bernos, T. A. & Fraser, D. J. (2016). Spatiotemporal relationship between adult census size and genetic population size across a wide population size gradient. *Molecular Ecology* **25**, 4472-4487.
- Bewes, V., Davey, A., Gregory, S. (2019a). Investigations into the extent and causes of recruitment failure of salmon and trout in Wales in 2016, NRW Evidence Report pp. 134
- Bewes, V., Davey, A., Green, A., Milner, N. (2019b). Evaluation of approaches to catchment-scale monitoring of fish, NRW Report
- Bunt, D. A. & House, R. (1991). Use of rod catch effort data to monitor migratory salmonids in Wales. In *Catch effort sampling strategies: their application in freshwater fisheries management* (Cowx, I. G., ed.), pp. 15-32. Oxford: Fishing News Books, Blackwell Science.

- Carlson, S. M., Cunningham, C. J. & Westley, P. A. (2014). Evolutionary rescue in a changing world. *Trends in Ecology & Evolution* **29**, 521-530.
- Carvalho, G. R. & Pitcher, T. J. (2012). *Molecular Genetics in Fisheries*: Springer Science & Business Media.
- Cefas/EA/NRW (2017). Salmon Stocks and Fisheries in England and Wales in 2016, pp. 88.
- Cefas/EA/NRW (2022). Salmon Stocks and Fisheries in England and Wales in 2021, p53.
- Chadwick, E. M. P. (1982). Stock-recruitment relationship for Atlantic salmon (*Salmo salar*) in Newfoundland rivers. *Canadian Journal of Fisheries and Aquatic Sciences* **39**, 1496-1501.
- Chaput, G. (2006). Definition and application of conservation requirements for the management of Atlantic salmon (*Salmo salar*) fisheries in eastern Canada. Fisheries and Oceans Canada, Science Report.
- Chaput, G. (2012). Overview of the status of Atlantic salmon (*Salmo salar*) in the North Atlantic and trends in marine mortality. *ICES Journal of Marine Science* **69**, 1538-1548.
- Chen, D. G., Irvine, J. R. & Cass, A. J. (2002). Incorporating Allee effects in fish stock–recruitment models and applications for determining reference points. *Canadian Journal of Fisheries and Aquatic Sciences* **59**, 242-249.
- Coblentz, B. E. (1990). Exotic organisms: a dilemma for conservation biology. *Conservation Biology* **4**, 261-265.
- Consuegra, S., García de Leániz, C., Serdio, A., González Morales, M., Straus, L., Knox, D., Verspoor, E. (2002). Mitochondrial DNA variation in Pleistocene and modern Atlantic salmon from the Iberian glacial refugium. *Molecular Ecology* **11**, 2037-2048.
- Consuegra, S. & Garcia de Leaniz, C. (2013). The contribution of hatchery fish to the salmon run in the River Taff (2010-2012 returns). Report to Natural Resources Wales., p. 9: Natural Resources Wales.
- Consuegra, S. & Nielsen, E. E. (2007). Population Size Reductions. In *The Atlantic Salmon: Genetics, Conservation and Management* (Verspoor, E., Stradmeyer, L. & Nielsen, J., eds.), pp. 243-275. Oxford Blackwell.
- Consuegra, S., Garcia de Leaniz, C., Serdio, A. & Verspoor, E. (2005a). Selective exploitation of early running fish may induce genetic and phenotypic changes in Atlantic salmon. *Journal of Fish Biology* **67**, 129-145.
- Consuegra, S., Verspoor, E., Knox, D. & Garcia de Leaniz, C. (2005b). Asymmetric gene flow and the evolutionary maintenance of genetic diversity in small, peripheral Atlantic salmon populations. *Conservation Genetics* **6**, 823–842.
- COSEWIC (2010). COSEWIC assessment and status report on the Atlantic salmon *Salmo salar* in Canada. P. xvii + 136 Ottawa: Committee on the Status of Endangered Wildlife in Canada.
- COSEWIC (2018). Appendix F5. Guidelines for recognizing designatable units. COSEWIC Operations and Procedures Manual. . Ottawa: Committee on the Status of Endangered Wildlife in Canada.
- Courchamp, F., Berec, L. & Gascoigne, J. (2008). *Allee Effects in Ecology and Conservation*: Oxford University Press.
- Cross, T.F., McGinnitty, P., Coughlan, J., Dillane, E., Ferguson, A., Lojonene, M-L., Milner, N., O'reilly, P and Vasemägi, A. (2007) In: Eds, Verspoor, E, Stradmeyer, L., and Nielsen, J. The Atlantic Salmon. Genetics, Conservation and Management. Blackwell Publishing, Oxford. 325-356
- Dadswell, M., Spares, A., Reader, J., McLean, M., McDermott, T., Samways, K., Lilly, J. (2022). The decline and impending collapse of the atlantic salmon (*Salmo salar*)

- population in the north atlantic ocean: a review of possible causes. *Reviews in Fisheries Science & Aquaculture* **30**, 215-258.
- Dassow, C.J., Ross, A.J., Jensen, O.P., Sass, G.G., van Poorten, B.T., Solomon, C.T., Jones, S.E. (2020). Experimental demonstration of catch hyperstability from habitat aggregation, not effort sorting, in a recreational fishery. *Canadian Journal of Fisheries and Aquatic Sciences* **77**, 762-769.
- Dionne, M., Caron, F., Dodson, J. J. & Bernatchez, L. (2008). Landscape genetics and hierarchical genetic structure in Atlantic salmon: the interaction of gene flow and local adaptation. *Molecular Ecology* **17**, 2382-2396.
- Dodson, J. J., Gibson, R. J., Cunjak, R. A., Friedland, K. D., Garcia de Leaniz, C., Gross, M. R., Newbury, R., Nielsen, J. L., Power, M. E. & Roy, S. (1998). Elements in the development of conservation plans for Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* **55**, 312-323.
- Dulvy, N.K., Sadovy, Y., Reynolds, J.D. (2003). Extinction vulnerability in marine populations. *Fish and Fisheries* **4**, 25-64.
- Einum, S., Fleming, I. A., Côté, I. M. & Reynolds, J. D. (2003). Population stability in salmon species: effects of population size and female reproductive allocation. *Journal of Animal Ecology* **72**, 811-821.
- Elith, J., Leathwick, J. R. & Hastie, T. (2008). A working guide to boosted regression trees. *Journal of Animal Ecology* **77**, 802-813.
- Erismann, B.E., Allen, L.G., Claisse, J.T., Pondella, D.J., Miller, E.F., Murray, J.H. (2011). The illusion of plenty: hyperstability masks collapses in two recreational fisheries that target fish spawning aggregations. *Canadian Journal of Fisheries and Aquatic Sciences* **68**, 1705-1716.
- Fagan, W.F., Holmes, E. (2006). Quantifying the extinction vortex. *Ecology Letters* **9**, 51-60.
- Fay, C., Bartron, M., Craig, S., Hecht, A., Pruden, J., Saunders, R., Sheehan, T. & Trial, J. (2006). Status Review for Anadromous Atlantic Salmon (*Salmo salar*) in the United States. P. 294: National Marine Fisheries Service and U.S. Fish and Wildlife Service.
- Ferchaud, A. L., Perrier, C., April, J., Hernandez, C., Dionne, M. & Bernatchez, L. (2016). Making sense of the relationships between N_e , N_b and N_c towards defining conservation thresholds in Atlantic salmon (*Salmo salar*). *Heredity* **117**, 268.
- Ford, A. (1999). *Modeling the Environment: an Introduction to System Dynamics Models of Environmental Systems*. Island Press.
- Ford, M.J. (2004). Conservation units and preserving diversity. In: Hendry, A.P., Stearns, S.C. (Eds.), *Evolution Illuminated: salmon and their relatives*. Oxford University Press, New York, pp. 338-357.
- Frankham, R., Bradshaw, C. J. A. & Brook, B. W. (2014). Genetics in conservation management: revised recommendations for the 50/500 rules, Red List criteria and population viability analyses. *Biological Conservation* **170**, 56-63.
- Franklin, I. R. (1980). Evolutionary change in small populations. In *Conservation Biology: An Evolutionary- Ecological Perspective* (Soulé, M. E. & Wilcox, B. A., eds.), pp. 135-140. Sunderland, Mass.: Sinauer Associates.
- Fraser, D. J. (2014). Evolutionary hypotheses for a constraint to life-history resilience in depleted *Salmo salar* populations. *Journal of Fish Biology* **85**, 119-131.
- Fraser, D. J., Debes, P. V., Bernatchez, L. & Hutchings, J. A. (2014). Population size, habitat fragmentation, and the nature of adaptive variation in a stream fish. *Proceedings of the Royal Society of London B: Biological Sciences* **281**, 20140370.

- Fraser, D. J., Hansen, M. M., Østergaard, S., Tessier, N., Legault, M. & Bernatchez, L. (2007). Comparative estimation of effective population sizes and temporal gene flow in two contrasting population systems. *Molecular Ecology* **16**, 3866-3889.
- García de Leaniz, C. (2021). Conservation of the Atlantic salmon in the river Bidasoa. Report to Gobierno de Navarra, pp. 31.
- García de Leaniz, C., Börger, L., Bull, J. & Consuegra, S. (2015). Expert Assessment of TLSB's monitoring proposal for Atlantic salmon and sea trout, as set out in the Adaptive Environmental Management Plan (AEMP). P. 18. Swansea Swansea University, College of Science Department of BioSciences.
- García de Leaniz, C., Fleming, I. A., Einum, S., Verspoor, E., Consuegra, S., Jordan, W. C., Aubin-Horth, N., Lajus, D. L., Villanueva, B. & Ferguson, A. (2007b). Local Adaptation. In *The Atlantic salmon: genetics, conservation and management* (Verspoor, E., Stradmeyer, L. & Nielsen, J. L., eds.), pp. 200-240. Oxford: Blackwell.
- García de Leaniz, C., Fleming, I., Einum, S., Verspoor, E., Jordan, W., Consuegra, S., Aubin-Horth, N., Lajus, D., Letcher, B. & Youngson, A. (2007a). A critical review of adaptive genetic variation in Atlantic salmon: implications for conservation. *Biological Reviews* **82**, 173-211.
- García de Leaniz, C., Gajardo, G. & Consuegra, S. (2010). From best to pest: changing perspectives on the impact of exotic salmonids in the Southern Hemisphere. *Systematics and Biodiversity* **8**, 447-459.
- García de Leaniz, C., Serdio, A. & Consuegra, S. (2001). Situación actual del salmón Atlántico en Cantabria. Actas de las III Jornadas sobre el Salmón Atlántico en la Península Ibérica In *El Salmón, Joya de Nuestros Ríos* (García de Leaniz, C., Serdio, A. & Consuegra, S., eds.), pp. 55-81. Santander: Consejería de Ganadería, Agricultura y Pesca.
- Gilbey, J. & Bacon, P. J. (2017). Using genetic approaches to estimate population sizes of salmon in Scotland. P. 14: Scottish Marine and Freshwater Science
- Gillson, J.P., Bašić, T., Davison, P.I., Riley, W.D., Talks, L., Walker, A.M., Russell, I.C. (2022). A review of marine stressors impacting Atlantic salmon *Salmo salar*, with an assessment of the major threats to English stocks. *Reviews in Fish Biology and Fisheries* **32**, 879-919.
- Golding, F. M. (2014). Monitoring Atlantic salmon and brown trout migrations through the use of a video camera at Green Park Weir (River Afan, Port Talbot) Swansea: Swansea University.
- Gotelli, N. J. (2008). *A Primer of Ecology*. Sunderland, Massachusetts: Sinauer Associates Inc. .
- Green, D. M. (2005). Designatable units for status assessment of endangered species. *Conservation Biology* **19**, 1813-1820.
- Gregory, S.D., Bewes, V.E., Davey, A.J., Roberts, D.E., Gough, P., Davidson, I.C. (2020). Environmental conditions modify density-dependent salmonid recruitment: Insights into the 2016 recruitment crash in Wales. *Freshwater Biology* **65**, 2135-2153.
- Gustafson, R. G., Waples, R. S., Myers, J. M., Weitkamp, L. A., Bryant, G. J., Johnson, O. W. & Hard, J. J. (2007). Pacific salmon extinctions: quantifying lost and remaining diversity. *Conservation Biology* **21**, 1009-1020.
- Harris, L. N., Palstra, F. P., Bajno, R., Gallagher, C. P., Howland, K. L., Taylor, E. B. & Reist, J. D. (2017). Assessing conservation risks to populations of an anadromous Arctic salmonid, the northern Dolly Varden (*Salvelinus malma malma*), via estimates of effective and census population sizes and approximate Bayesian computation. *Conservation Genetics* **18**, 393-410.

- Hilborn, R. (2002). The dark side of reference points. *Bulletin of Marine Science* **70**, 403-408.
- Hilborn, R., Quinn, T. P., Schindler, D. E. & Rogers, D. E. (2003). Biocomplexity and fisheries sustainability. *Proceedings of the National Academy of Sciences* **100**, 6564-6568.
- Hindar, K., García de Leániz, C., Koljonen, M. L., Tufto, J. & Youngson, A. F. (2007). Fisheries Exploitation. In *The Atlantic salmon: genetics, conservation and management* (Verspoor, E., Stradmeyer, L. & Nielsen, J. L., eds.), pp. 299-324. Oxford: Blackwell.
- Hindar, K., Tufto, J., Sættem, L. M. & Balstad, T. (2004). Conservation of genetic variation in harvested salmon populations. *ICES Journal of Marine Science* **61**, 1389-1397.
- Holling, C.S. (1996). Engineering resilience versus ecological resilience. In *Engineering within Ecological Constraints* (Shulze, P.C. ed), National Academy of Engineering, Washington D.C. (USA), pp. 32.
- Horreo, J. L., Machado-Schiaffino, G., Griffiths, A. M., Bright, D., Stevens, J. R. & Garcia-Vazquez, E. (2011). Atlantic salmon at risk: apparent rapid declines in effective population size in southern European populations. *Transactions of the American Fisheries Society* **140**, 605-610.
- Hutchings, J. A. (2013). Renaissance of a caveat: Allee effects in marine fish. *ICES Journal of Marine Science* **71**, 2152-2157.
- Hutchings, J. A., Butchart, S. H., Collen, B., Schwartz, M. K. & Waples, R. S. (2012). Red flags: correlates of impaired species recovery. *Trends in Ecology & Evolution* **27**, 542-546.
- ICES (1995). Report of the North Atlantic Salmon Working Group, pp. 191.
- Ikedashi, C., Billington, S. & Stevens, J. (2012). The origins of Atlantic salmon (*Salmo salar* L.) recolonizing the River Mersey in northwest England. *Ecology and Evolution* **2**, 2537-2548.
- IUCN Species Survival Commission (2000). IUCN Red List Categories and Criteria, Version 3.1 pp. 38.
- Jamieson, I. G. & Allendorf, F. W. (2012). How does the 50/500 rule apply to MVPs? *Trends in Ecology and Evolution* **27**, 578-584.
- Johannesson, K., Smolarz, K., Grahn, M. & André, C. (2011). The future of Baltic Sea populations: local extinction or evolutionary rescue? *Ambio* **40**, 179-190.
- Kendon, M., McCarthy, M., Jevrejeva, S., Matthews, A., Sparks, T., Garforth, J., Kennedy, J. (2022). State of the UK Climate 2021. *International Journal of Climatology* **42**, 1-80.
- Klefoth, T., Skov, C., Kuparinen, A. & Arlinghaus, R. (2017). Toward a mechanistic understanding of vulnerability to hook-and-line fishing: Boldness as the basic target of angling-induced selection. *Evolutionary Applications* **10**, 994-1006.
- Koskinen, M. T., Haugen, T. O. & Primmer, C. R. (2002). Contemporary fisherian life-history evolution in small salmonid populations. *Nature* **419**, 826.
- Kuparinen, A., Tufto, J., Consuegra, S., Hindar, K., Merilä, J. & Garcia de Leaniz, C. (2010). Effective size of an Atlantic salmon (*Salmo salar* L.) metapopulation in Northern Spain. *Conservation Genetics* **11**, 1559-1565.
- Lande, R. (1988). Genetics and demography in biological conservation. *Science* **241**, 1455-1460
- Lande, R. (1993). Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *The American Naturalist* **142**, 911-927.

- Lande, R., Orzack, S.H. (1988). Extinction dynamics of age-structured populations in a fluctuating environment. *Proceedings of the National Academy of Sciences* **85**, 7418-7421.
- Luikart, G., Ryman, N., Tallmon, D. A., Schwartz, M. K. & Allendorf, F. W. (2010). Estimation of census and effective population sizes: the increasing usefulness of DNA-based approaches. *Conservation Genetics* **11**, 355-373.
- Marburger, S. (2011). Linking River Connectivity with Genetic Variation of Brown Trout in Wales. Mres thesis, Swansea University, Department of Biosciences, Swansea . 78 p..
- Marcot, B. G. (2012). Metrics for evaluating performance and uncertainty of Bayesian network models. *Ecological Modelling* **230**, 50-62.
- Mawle, G. W. & Milner, N. J. (2003). The return of salmon to cleaner rivers—England and Wales. In *Proceedings of Atlantic Salmon Symposium, Edinburgh, July 2002*. Oxford: Blackwell Science.
- Michener, W. K., Baerwald, T. J., Firth, P., Palmer, M. A., Rosenberger, J. L., Sandlin, E. A. & Zimmerman, H. (2001). Defining and unraveling biocomplexity. *BioScience* **51**, 1018-1023.
- Michener, W.K., Baerwald, T.J., Firth, P., Palmer, M.A., Rosenberger, J.L., Sandlin, E.A., Zimmerman, H. (2001). Defining and unraveling biocomplexity. *BioScience* **51**, 1018-1023.
- Mills, C., Mahon, G. & Piggins, D. (1986). Influence of stock levels, fishing effort and environmental factors on anglers' catches of Atlantic salmon, *Salmo salar* L., and sea trout, *Salmo trutta* L. *Aquaculture Research* **17**, 289-297.
- Milner, N.J., Davidson, I.C., Evan, R., Locke, V. and Wyatt, R.J. (2001). The use of rod catches to estimate salmon runs in England and Wales. In R. Shelton (Ed) *Proceedings of Atlantic Salmon Trust Workshop, Lowestoft, November 2001*. P46-65.
- Milner, N., Potter, E., Roche, W., Tysklind, N., Davidson, I., King, J., Coyne, J., Davies, C., (2017). Variation in sea trout (*Salmo trutta*) abundance and life histories in the Irish Sea, Sea Trout: Science and Management: Proceedings of the 2nd International Sea Trout Symposium. Matador, pp. 96-128.
- Milner, N.J., Elliott, J.M., Armstrong, J.D., Gardiner, R., Welton, J.S., Ladle, M. (2003). The natural control of salmon and trout populations in streams. *Fisheries Research* **62**, 111-125.
- Moore, J.W., McClure, M., Rogers, L.A., Schindler, D.E. (2010). Synchronization and portfolio performance of threatened salmon. *Conservation Letters* **3**, 340-348.
- Moran, P. (2002). Current conservation genetics: building an ecological approach to the synthesis of molecular and quantitative genetic methods. *Ecology of Freshwater Fish* **11**, 30-55.
- Morán, P. & Saura, M. (2020). Estudio de variabilidad genética del salmón del Bidasoa. Universidad de Vigo. Report to Gobierno de Navarra.
- Myers, R. A., Barrowman, N. J., Hutchings, J. A. & Rosenberg, A. A. (1995). Population dynamics of exploited fish stocks at low population levels. *Science* **269**, 1106-1108.
- NASCO (1998) Agreement on Adoption of a Precautionary Approach. NASCO CNL(98)46.
- NASCO (2009). NASCO Guidelines for the Management of Salmon Fisheries. NASCO, pp. 9.
- Nunney, L. & Campbell, K. A. (1993). Assessing minimum viable population size: demography meets population genetics. *Trends in Ecology & Evolution* **8**, 234-239.
- Olmos, M., Payne, M.R., Nevoux, M., Prévost, E., Chaput, G., Du Pontavice, H., Guitton, J., Sheehan, T., Mills, K., Rivot, E. (2020) Spatial synchrony in the response of a long range migratory species (*Salmo salar*) to climate change in the North Atlantic Ocean. *Global Change Biology* **26**, 1319–1337

- O'Reilly, P.O., Doyle, R., 2007. Live gene banking of endangered populations of Atlantic salmon. In: Verspoor, E., Stradmeyer, L., Nielsen, J. (Eds.), *The Atlantic Salmon: Genetics, Conservation and Management*. Blackwell, Oxford, pp. 425-469.
- Ozerov, M. Y., Veselov, A. E., Lumme, J. & Primmer, C. R. (2012). "Riverscape" genetics: river characteristics influence the genetic structure and diversity of anadromous and freshwater Atlantic salmon (*Salmo salar*) populations in northwest Russia. *Canadian Journal of Fisheries and Aquatic Sciences* **69**, 1947-1958.
- Palstra, F. P. & Fraser, D. J. (2012). Effective/census population size ratio estimation: a compendium and appraisal. *Ecology and Evolution* **2**, 2357-2365.
- Palstra, F. P. & Ruzzante, D. E. (2008). Genetic estimates of contemporary effective population size: what can they tell us about the importance of genetic stochasticity for wild population persistence? *Molecular Ecology* **17**, 3428-3447.
- Palstra, F. P., O'Connell, M. F. & Ruzzante, D. E. (2007). Population structure and gene flow reversals in Atlantic salmon (*Salmo salar*) over contemporary and long-term temporal scales: effects of population size and life history. *Molecular Ecology* **16**, 4504-4522.
- Perrier, C., April, J., Cote, G., Bernatchez, L. & Dionne, M. (2016). Effective number of breeders in relation to census size as management tools for Atlantic salmon conservation in a context of stocked populations. *Conservation Genetics* **17**, 31-44.
- Perrier, C., Guyomard, R., Bagliniere, J. L., Nikolic, N. & Evanno, G. (2013). Changes in the genetic structure of Atlantic salmon populations over four decades reveal substantial impacts of stocking and potential resiliency. *Ecology and Evolution* **3**, 2334-2349.
- Piry, S., Luikart, G. & Cornuet, J. M. (2000). BOTTLENECK: A program for detecting recent effective population size reductions from allele data frequencies.
- Potter, E.C.E., Maclean, J.C., Wyatt, R.J. & Campbell, R.N.B. (2003). Managing the exploitation of migratory salmonids. *Fisheries Research* **62**, 127-142.
- Primack, R. B. (2012). *A Primer of Conservation Biology*. Sunderland, Massachusetts: Sinauer Associates.
- Quinn, T. P. (1993). A review of homing and straying of wild and hatchery-produced salmon. *Fisheries Research* **18**, 29-44.
- Quinn, T. P. (1999). Revisiting the stock concept in Pacific salmon: insights from Alaska and New Zealand.
- Quinn, T. P., Kinnison, M. T. & Unwin, M. J. (2001). Evolution of chinook salmon (*Oncorhynchus tshawytscha*) populations in New Zealand: pattern, rate, and process. In *Microevolution Rate, Pattern, Process*, pp. 493-513: Springer.
- Quinn, T., Graynoth, E., Wood, C. & Foote, C. (1998). Genotypic and phenotypic divergence of sockeye salmon in New Zealand from their ancestral British Columbia populations. *Transactions of the American Fisheries Society* **127**, 517-534.
- Rand, P. S., Goslin, M., Gross, M. R., Irvine, J. R., Augerot, X., McHugh, P. A. & Bugaev, V. F. (2012). Global assessment of extinction risk to populations of sockeye salmon *Oncorhynchus nerka*. *PloS One* **7**, e34065.
- Rougier, T., Lambert, P., Drouineau, H., Girardin, M., Castelnaud, G., Carry, L., Aprahamian, M., Rivot, E. & Rochard, E. (2012). Collapse of allis shad, *Alosa alosa*, in the Gironde system (southwest France): environmental change, fishing mortality, or Allee effect? *ICES Journal of Marine Science: Journal du Conseil* **69**, 1802-1811.
- Ruckelshaus, M., McElhany, P., McClure, M. & Heppell, S. (2004). Chinook salmon in Puget Sound: Effects of spatially correlated catastrophes on persistence. In *Species Conservation and Management: Case Studies* (Akçakaya, H. R., Burgman, M. A.,

- Kindvall, O., Wood, C. C., Sjogren-Gulve, P., Hatfield, J. S. & McCarthy, M. A., eds.), pp. 208-218. New York: Oxford University Press.
- Russell, I.C., Aprahamian, M.W., Barry, J., Davidson, I.C., Fiske, P., Ibbotson, A.T., Kennedy, R.J., Maclean, J.C., Moore, A., Otero, J. (2012). The influence of the freshwater environment and the biological characteristics of Atlantic salmon smolts on their subsequent marine survival. *ICES Journal of Marine Science* **69**, 1563-1573.
- Ruzzante, D. E., McCracken, G. R., Parmelee, S., Hill, K., Corrigan, A., MacMillan, J. & Walde, S. J. (2016). Effective number of breeders, effective population size and their relationship with census size in an iteroparous species, *Salvelinus fontinalis*. *Proceedings of the Royal Society B* **283**, 20152601.
- Sadovy, Y. (2001). The threat of fishing to highly fecund fishes. *Journal of Fish Biology* **59**, 90-108.
- Saura, M., Caballero, A., Caballero, P. & Moran, P. (2008). Impact of precocious male parr on the effective size of a wild population of Atlantic salmon. *Freshwater Biology* **53**, 2375-2384.
- Schindler, D. E., Hilborn, R., Chasco, B., Boatright, C. P., Quinn, T. P., Rogers, L. A. & Webster, M. S. (2010). Population diversity and the portfolio effect in an exploited species. *Nature* **465**, 609-612.
- Schtickzelle, N. & Quinn, T. P. (2007). A metapopulation perspective for salmon and other anadromous fish. *Fish and Fisheries* **8**, 297-341.
- Schwartz, M. K., Luikart, G. & Waples, R. S. (2007). Genetic monitoring as a promising tool for conservation and management. *Trends in Ecology & Evolution* **22**, 25-33.
- Serbezov, D., Jorde, P. E., Bernatchez, L., Olsen, E. M. & Vøllestad, L. A. (2012a). Life history and demographic determinants of effective/census size ratios as exemplified by brown trout (*Salmo trutta*). *Evolutionary Applications* **5**, 607-618.
- Serbezov, D., Jorde, P. E., Bernatchez, L., Olsen, E. M. & Vøllestad, L. A. (2012b). Short-term genetic changes: evaluating effective population size estimates in a comprehensively described brown trout (*Salmo trutta*) population. *Genetics*. 111.136580.
- Soulé, M. E. (1980). Thresholds for survival: maintaining fitness and evolutionary potential. In *Conservation Biology: An Evolutionary--Ecological Perspective* (Soulé, M. E. & Wilcox, B. A., eds.), pp. 151-169. Sunderland, Mass.: Sinauer Associates.
- Tear, T. H., Kareiva, P., Angermeier, P. L., Comer, P., Czech, B., Kautz, R., Landon, L., Mehlman, D., Murphy, K. & Ruckelshaus, M. (2005). How much is enough? The recurrent problem of setting measurable objectives in conservation. *BioScience* **55**, 835-849.
- Tsuboi, J.-i., Morita, K., Sahashi, G., Kuroki, M., Baba, S., Arlinghaus, R. (2021). Species-specific vulnerability to angling and its size-selectivity in sympatric stream salmonids. *Canadian Journal of Fisheries and Aquatic Sciences* **78**, 1470-1478.
- Vanhaecke, D., Garcia de Leaniz, C., Gajardo, G., Thomas, C. J. & Consuegra, S. (2012). Metapopulation dynamics of a diadromous galaxiid fish and potential effects of salmonid aquaculture. *Freshwater Biology* **57**, 1241-1252.
- Vincenzi, S. (2014). Extinction risk and eco-evolutionary dynamics in a variable environment with increasing frequency of extreme events. *Journal of The Royal Society Interface*. **11**, 20140441.
- Vincenzi, S., Crivelli, A. J., Satterthwaite, W. H. & Mangel, M. (2014). Eco-evolutionary dynamics induced by massive mortality events. *Journal of Fish Biology* **85**, 8-30.
- Wang, S., Hard, J. J. & Utter, F. (2002a). Genetic variation and fitness in salmonids. *Conservation Genetics* **3**, 321-333.

- Wang, S., Hard, J. J. & Utter, F. (2002b). Salmonid inbreeding: a review. *Reviews in Fish Biology and Fisheries* **11**, 301-319.
- Waples, R. S. (2002). Definition and estimation of effective population size in the conservation of endangered species. In *Population viability analysis* (Beissinger, S. R. & McCullough, D. R., eds.), pp. 147-168: University of Chicago Press.
- Waples, R. S., Antao, T. & Luikart, G. (2014). Effects of overlapping generations on linkage disequilibrium estimates of effective population size. *Genetics*. 114.164822.
- WGNAS, 2022. Working Group on North Atlantic Salmon (WGNAS), pp. 11.
- Wolf, S., Hartl, B., Carroll, C., Neel, M. C. & Greenwald, D. N. (2015). Beyond PVA: Why Recovery under the Endangered Species Act Is More than Population Viability. *BioScience* **65**, 200-207.
- Wood, J.L., Yates, M.C., Fraser, D.J. (2016). Are heritability and selection related to population size in nature? Meta-analysis and conservation implications. *Evolutionary Applications* **9**, 640-657.
- WWF (2001). The status of wild Atlantic salmon: A river by river assessment.
- Yates, M. C., Bernos, T. A. & Fraser, D. J. (2017). A critical assessment of estimating census population size from genetic population size (or vice versa) in three fishes. *Evolutionary Applications* **10**, 935-945.
- Youngson, A. F., MacLean, J. C. & Fryer, R. J. (2002). Rod catch trends for early-running MSW salmon in Scottish rivers (1952-1997): divergence among stock components. *ICES Journal of Marine Science* **59**, 836-849.
- Zastavniouk, C., Weir, L. K. & Fraser, D. J. (2017). The evolutionary consequences of habitat fragmentation: Body morphology and coloration differentiation among brook trout populations of varying size. *Ecology and Evolution* **7**, 6850-6862.

9 Appendices

Table A1. English and Welsh salmon river size and basic population data.

River	riv.ref	Country	Location	Wetted area (hectare)	Eggs CL.100m ²	Eggs at CL (m)	Rod catch 1994-2015 meaN	Spawners 1994-2015 mean	Spawners 1994-2021 CV	Spawners 2017-2021 mean	Eggs 2017-2021 (m) mean	Propn 1SW spawners 2017 2021	Propn 1SW eggs 2017-2021 mean	Eggs 2017-2021 % of CL	Eggs 2021 % of CL
Dwryrd	57	Wales	Mid	9.24	201.38	0.186	15.3	130.1	69.38	54.4	0.141	0.878	0.790	75.526	21
Seiont	60	Wales	North	21.05	226.11	0.476	29.1	246.1	74.90	65.0	0.166	0.929	0.893	34.956	4
Glaslyn	58	Wales	Mid	25.01	191.49	0.479	25.9	143.9	52.18	59.6	0.210	0.686	0.604	43.837	18
NeVERN	53	Wales	Mid	18.55	259.36	0.481	33.4	109.8	43.02	77.2	0.239	0.798	0.716	49.579	13
Rheidol	52	Wales	Mid	30.63	222.03	0.680	31.6	137.8	45.15	20.8	0.055	0.815	0.700	8.105	3
Dysynni	55	Wales	Mid	31.49	216.27	0.681	4.6	38.1	79.91	36.2	0.063	0.820	0.753	9.283	11
Dwrfawr	59	Wales	Mid	33.31	257.59	0.858	15.0	119.5	64.12	44.8	0.099	0.908	0.872	11.510	13
Ogwen	61	Wales	North	23.90	362.29	0.866	80.4	669.5	40.82	545.1	1.301	0.910	0.854	150.272	69
Ogmore	46	Wales	South	61.21	180.45	1.105	58.4	222.0	45.99	67.7	0.193	0.836	0.737	17.464	4
Conwy	62	Wales	North	63.01	185.06	1.166	165.6	675.9	36.30	540.4	1.595	0.809	0.694	136.787	33
Mawddach	56	Wales	Mid	56.66	241.86	1.370	120.6	607.8	42.55	499.0	1.573	0.774	0.667	114.781	82
Cleddau	50	Wales	South	86.61	179.42	1.554	52.0	261.3	38.70	162.7	0.387	0.836	0.733	24.928	19
Taf	49	Wales	South	90.12	188.59	1.700	83.1	568.0	57.16	274.6	0.627	0.758	0.706	36.889	14
Tawe	47	Wales	South	87.85	210.85	1.852	116.9	413.9	49.37	106.9	0.248	0.777	0.740	13.390	3
Chwyd	63	Wales	North	83.92	237.06	1.989	79.0	673.4	71.93	158.4	0.416	0.821	0.711	20.920	7
Taff.Ely	45	Wales	South	145.72	219.19	3.194	34.9	327.7	50.84	N	0.410	NA	NA	12.827	12
Dyfi	54	Wales	Mid	179.13	234.90	4.208	132.5	1134.1	50.03	604.1	1.714	0.780	0.649	40.746	22
Teifi	51	Wales	Mid	325.92	265.34	8.648	540.2	3611.9	38.63	925.0	2.242	0.747	0.690	25.922	19
Usk	44	Wales	South	407.09	248.35	10.110	720.2	5990.9	28.27	2670.4	10.062	0.552	0.359	99.521	53
Tywi	48	Wales	South	500.07	226.04	11.303	508.7	3518.3	41.77	3277.3	7.916	0.731	0.662	70.030	38
Dee	64	Wales	North	617.04	247.92	15.297	583.7	4499.8	16.04	2934.4	10.602	0.546	0.329	69.308	65
Wye	43	Wales	South	1721.04	224.09	38.567	819.0	5318.3	33.72	4637.3	19.600	0.330	0.153	50.819	32
Coquet	1	England	NA	143.76	218.22	3.137	637.0	2557.3	40.05	NA	NA	NA	NA	NA	NA
Tyne	2	England	NA	541.60	207.74	11.251	2869.8	8187.3	38.41	NA	NA	NA	NA	NA	NA
Wear	3	England	NA	232.42	249.64	5.802	757.1	3496.1	61.18	NA	NA	NA	NA	NA	NA
Tees	4	England	NA	620.05	240.30	14.900	101.9	733.2	61.52	NA	NA	NA	NA	NA	NA
Esk.Yorks	5	England	NA	85.66	236.10	2.022	91.0	469.5	54.39	NA	NA	NA	NA	NA	NA
Test	6	England	NA	138.21	246.34	3.405	211.8	775.4	45.97	NA	NA	NA	NA	NA	NA
Itchen	7	England	NA	69.45	234.19	1.626	173.5	387.4	53.42	NA	NA	NA	NA	NA	NA
Avon.Hants	8	England	NA	369.28	175.35	6.475	84.3	1071.0	41.93	NA	NA	NA	NA	NA	NA
Frome	11	England	NA	87.64	170.90	1.498	85.3	818.8	36.37	NA	NA	NA	NA	NA	NA
Eve	13	England	NA	281.99	253.24	7.141	431.5	6760.1	45.21	NA	NA	NA	NA	NA	NA
Teign	14	England	NA	98.45	250.69	2.468	116.0	1342.8	45.27	NA	NA	NA	NA	NA	NA
Dart	15	England	NA	136.68	217.96	2.979	95.3	683.0	47.80	NA	NA	NA	NA	NA	NA
Avon.Devon	16	England	NA	34.63	201.77	0.699	36.4	285.3	37.72	NA	NA	NA	NA	NA	NA
Plym	19	England	NA	29.43	188.37	0.554	19.3	75.2	67.61	NA	NA	NA	NA	NA	NA
Tavy	20	England	NA	68.50	200.58	1.374	72.7	383.8	50.37	NA	NA	NA	NA	NA	NA
Tamar	21	England	NA	292.57	395.19	11.562	268.0	4481.0	28.47	NA	NA	NA	NA	NA	NA
Lynher	22	England	NA	29.18	233.43	0.681	64.1	291.3	53.34	NA	NA	NA	NA	NA	NA
Fowey	23	England	NA	41.50	207.44	0.861	151.9	614.1	27.13	NA	NA	NA	NA	NA	NA
Camel	24	England	NA	55.70	176.31	0.982	280.3	665.7	39.00	NA	NA	NA	NA	NA	NA
Taw	25	England	NA	273.91	210.89	5.777	239.0	3837.4	43.16	NA	NA	NA	NA	NA	NA
Torridge	26	England	NA	198.31	206.59	4.097	71.7	995.4	53.04	NA	NA	NA	NA	NA	NA
Lyn	27	England	NA	27.06	359.12	0.972	124.4	769.5	43.12	NA	NA	NA	NA	NA	NA
Severn	28	England	NA	898.07	143.13	12.854	327.0	4170.2	50.70	NA	NA	NA	NA	NA	NA
Ribble	29	England	NA	351.07	202.20	7.099	814.8	2397.3	38.93	NA	NA	NA	NA	NA	NA
Wyre	30	England	NA	66.78	73.11	0.488	11.3	64.4	75.30	NA	NA	NA	NA	NA	NA
Lune	31	England	NA	422.73	236.72	10.007	1037.0	5651.7	39.91	NA	NA	NA	NA	NA	NA
Kent	32	England	NA	68.13	223.41	1.522	417.2	1521.5	48.04	NA	NA	NA	NA	NA	NA
Leven	33	England	NA	45.84	182.05	0.835	50.6	257.4	49.46	NA	NA	NA	NA	NA	NA
Duddon	35	England	NA	25.67	120.99	0.311	42.4	266.0	72.32	NA	NA	NA	NA	NA	NA
Esk	36	England	NA	20.48	180.75	0.370	65.4	213.2	72.93	NA	NA	NA	NA	NA	NA
Irt	37	England	NA	34.85	197.55	0.688	98.4	277.1	44.34	NA	NA	NA	NA	NA	NA
Ehen	38	England	NA	40.84	229.94	0.939	275.5	746.9	48.29	NA	NA	NA	NA	NA	NA
Calder	39	England	NA	12.61	260.69	0.329	41.7	129.1	51.54	NA	NA	NA	NA	NA	NA
Derwent	40	England	NA	212.85	184.82	3.934	891.5	3456.1	45.52	NA	NA	NA	NA	NA	NA
Eden	41	England	NA	687.53	199.99	13.750	1358.0	5740.0	40.83	NA	NA	NA	NA	NA	NA
Esk.Border	42	England	NA	305.63	255.05	7.795	723.0	3380.5	34.50	NA	NA	NA	NA	NA	NA

Table A2. Correlates and red flags that can be used for population monitoring and to assess species recovery (from Hutchings et al., 2012).

Correlate	Red flag	Postulated influence on recovery
Magnitude of reduction in abundance or distribution	Numerical or distributional declines in excess of 50% ^a	Greater reductions are associated with slower recovery
Rate of decline in abundance or distribution	Numerical or distributional declines >30% during the greater of three generations or 10 years ^b	Faster rates of decline are associated with slower rates of recovery
Temporal trajectory of decline in abundance or distribution ^c	Large concavity in the shape of trajectories of abundance or distribution	Shift in trajectory; rate of recovery declines as trajectories in abundance or distribution shift from highly convex to highly concave shapes
Life history traits ^d	Advanced age at maturity; large size at maturity; long generation time; slow individual growth rate (ectotherms); low fecundity (excluding teleost fish); low dispersal ability	Trait combinations that reduce r will retard recovery; reduced among-population variation might reduce recovery rate (reduced portfolio effect) ^e
Allee effect (depensation, positive density dependence)	Reductions in r with declining abundance	Populations that fall below the threshold at which Allee effects are expressed will have slower, more uncertain recovery
Variance in r	Increases in the variance of r , particularly when associated with population decline	The greater the variance in r , the greater the uncertainty in the trajectory of recovery
Interspecific interactions	Increases in the relative abundance of negatively interacting species (e.g., predators, competitors, parasites, pathogens); decreases in the relative abundance of positively interacting species (e.g., prey, mutualists)	The greater the proportional change in abundances of interacting species, the slower the recovery
Threats	Increases in number and magnitude of threats, particularly those with high irreversibility	Intense threats (or combinations of threats) and highly irreversible threats will impair recovery
Evolutionary responses to anthropogenic threats	Genetic changes in fitness-related traits; loss of genetic diversity within and between populations; reversibility of selection responses	The greater the selection response, and the greater the loss of genetic variability, the slower the recovery
Conservation action	Lack of effective implementation of conservation interventions within one species generation of a species qualifying for elevated conservation concern	The sooner remedial action is taken, the greater the rate and probability of recovery

Table A3. Summary of the 5 IUCN criteria (A-E) used to assign a taxon to a threatened category (<http://www.iucnredlist.org/technical-documents/assessment-process>).

A. Population size reduction. Population reduction (measured over the longer of 10 years or 3 generations) based on any of A1 to A4			
	Critically Endangered	Endangered	Vulnerable
A1	≥ 90%	≥ 70%	≥ 50%
A2, A3 & A4	≥ 80%	≥ 50%	≥ 30%
A1 Population reduction observed, estimated, inferred, or suspected in the past where the causes of the reduction are clearly reversible AND understood AND have ceased.	} based on any of the following:	(a) direct observation [except A3]	
A2 Population reduction observed, estimated, inferred, or suspected in the past where the causes of reduction may not have ceased OR may not be understood OR may not be reversible.		(b) an index of abundance appropriate to the taxon	
A3 Population reduction projected, inferred or suspected to be met in the future (up to a maximum of 100 years) [(a) cannot be used for A3].		(c) a decline in area of occupancy (AOO), extent of occurrence (EOO) and/or habitat quality	
A4 An observed, estimated, inferred, projected or suspected population reduction where the time period must include both the past and the future (up to a max. of 100 years in future), and where the causes of reduction may not have ceased OR may not be understood OR may not be reversible.		(d) actual or potential levels of exploitation	
		(e) effects of introduced taxa, hybridization, pathogens, pollutants, competitors or parasites.	
B. Geographic range in the form of either B1 (extent of occurrence) AND/OR B2 (area of occupancy)			
	Critically Endangered	Endangered	Vulnerable
B1. Extent of occurrence (EOO)	< 100 km ²	< 5,000 km ²	< 20,000 km ²
B2. Area of occupancy (AOO)	< 10 km ²	< 500 km ²	< 2,000 km ²
AND at least 2 of the following 3 conditions:			
(a) Severely fragmented OR Number of locations	= 1	≤ 5	≤ 10
(b) Continuing decline observed, estimated, inferred or projected in any of: (I) extent of occurrence; (II) area of occupancy; (III) area, extent and/or quality of habitat; (IV) number of locations or subpopulations; (V) number of mature individuals			
(c) Extreme fluctuations in any of: (I) extent of occurrence; (II) area of occupancy; (III) number of locations or subpopulations; (IV) number of mature individuals			
C. Small population size and decline			
	Critically Endangered	Endangered	Vulnerable
Number of mature individuals	< 250	< 2,500	< 10,000
AND at least one of C1 or C2			
C1. An observed, estimated or projected continuing decline of at least (up to a max. of 100 years in future):	25% in 3 years or 1 generation (whichever is longer)	20% in 5 years or 2 generations (whichever is longer)	10% in 10 years or 3 generations (whichever is longer)
C2. An observed, estimated, projected or inferred continuing decline AND at least 1 of the following 3 conditions:			
(a) (I) Number of mature individuals in each subpopulation	≤ 50	≤ 250	≤ 1,000
(II) % of mature individuals in one subpopulation =	90–100%	95–100%	100%
(b) Extreme fluctuations in the number of mature individuals			
D. Very small or restricted population			
	Critically Endangered	Endangered	Vulnerable
D. Number of mature individuals	< 50	< 250	D1. < 1,000
D2. Only applies to the VU category Restricted area of occupancy or number of locations with a plausible future threat that could drive the taxon to CR or EX in a very short time.	-	-	D2. typically: AOO < 20 km ² or number of locations ≤ 5
E. Quantitative Analysis			
	Critically Endangered	Endangered	Vulnerable
Indicating the probability of extinction in the wild to be:	≥ 50% in 10 years or 3 generations, whichever is longer (100 years max.)	≥ 20% in 20 years or 5 generations, whichever is longer (100 years max.)	≥ 10% in 100 years

Table A4. IUCN criteria used to categorise conservation status of sockeye salmon in North America (from Rand et al., 2012).

Criterion	Threshold by category		
	CR	EN	VU
A2. Percent decline over last 3 generations (12 years)	80	50	30
B1. Extent of occurrence (km ²)	100	5,000	20,000
B2. Area of occupancy (km ²)	10	500	2,000
B2a. Severely fragmented, or number of locations ^a	1	< = 5	< = 10
B2b(iii). Continuing decline in area, extent and/or quality of habitat B2b(v). Continuing decline in number of mature individuals			
D. Absolute abundance	50	500	1,000

^aNumber of sockeye juvenile nursery lakes and distinct spawning regions within a population.

Quantitative criteria used in the study to determine extinction risk. CR = Critically Endangered, EN = Endangered, VU = Vulnerable.

doi:10.1371/journal.pone.0034065.t001

Table A5. Criteria used for assessing the risk of extinction in Pacific salmon (from Allendorf et al., 1997).

Risk of extinction criteria	Risk of extinction			
	Very high	High	Moderate	Special concern ^b
Probability of extinction using population viability analysis	50% within 5 years -or- any TWO of the following criteria	20% within 20 years -or- ONE very high risk criterion -or- any TWO of	5% within 100 years -or- ONE high risk criterion -or-	Historically present, believed or known to still exist but no current data ACTION Build data set from which risk level can be established
Effective population size per generation	N _e = 50 or less	N _e < 500	Not applicable	Run size or population strength estimate
Total population size per generation	N = 250 or less	N < 2500	Not applicable	Demographic data such as: —proportion that spawn at each age —adult survival between spawnings
Population decline	Precipitous decline	Chronic decline or depression	Decline apparent or probable	Genetic data
Catastrophe, rate and effect	Order of magnitude decline within one generation	Smaller but significant decline	Not applicable, stocks rate at least high risk	

^aBased on responses to risk criteria, level of risk can be determined. For example, if a population has a probability of extinction of 50% within 5 years based on PVA, it has a very high risk of extinction. If PVA is not available, then surrogate criteria are used. For example, if N is 250 or less and population decline is precipitous (the population meets two of the three surrogate criteria), the population is in the very high risk category. Example using Winchuck River fall chinook is provided in Table 2.

^bPopulations for which there are insufficient data to apply the risk of extinction criteria are considered of special concern. Action should be taken to obtain the necessary data, as described in this column.

Table A6. Example of a Technical Summary used to carry out the conservation assessment of one Atlantic salmon DU (DU14) in Canada (from COSEWIC 2010).

TECHNICAL SUMMARY - Nova Scotia Southern Upland population (DU14)

Salmo salar
 Atlantic Salmon
 Nova Scotia Southern Upland population

Saumon atlantique
 Population des hautes terres du sud de la
 Nouvelle-Écosse

Range of Occurrence in Canada: Nova Scotia / Atlantic Ocean

Demographic Information

Generation time (average age of parents in the population)	4 yrs
Estimated percent decline in total number of mature individuals from 1993 to 2007 (3 generations)	61
[Projected or suspected] percent [reduction or increase] in total number of mature individuals over the next [10 or 5 years, or 3 or 2 generations].	Unknown
[Observed, estimated, inferred, or suspected] percent [reduction or increase] in total number of mature individuals over any [10 or 5 years, or 3 or 2 generations] period, over a time period including both the past and the future.	N/A
Are the causes of the decline clearly reversible?	No
Are the causes of the decline understood?	No
Have the causes of the decline ceased?	No
Observed trend in number of populations	Declining
Are there extreme fluctuations in number of mature individuals?	No
Are there extreme fluctuations in number of populations?	No

Extent and Area Information

Estimated extent of occurrence	>20,000 km ²
Observed trend in extent of occurrence	Declining
Are there extreme fluctuations in extent of occurrence?	No
Index of area of occupancy (IAO)	4280 km ²
Observed trend in area of occupancy	Declining
Are there extreme fluctuations in area of occupancy?	No
Is the total population severely fragmented?	No
Number of current locations	31 known rivers
Trend in number of locations	Declining
Are there extreme fluctuations in number of locations?	No
Trend in [area and/or quality] of habitat	Declining

Number of Mature Individuals (in each population)

Population	N Mature Individuals
Only 4 of the 31 rivers included in estimate.	1,427(2008)
Total	1,427(2008)

Quantitative Analysis

--	--

Threats (actual or imminent, to populations or habitats)

Acidification, habitat loss, recreational fishing, poorly understood changes in marine ecosystems resulting in reduced survival during the marine phase of the life history, ecological and genetic interactions with escaped domestic Atlantic Salmon.

Table A6 (Cont)

Rescue Effect (immigration from an outside source)

Status of outside population(s)? Nearby Nova Scotia and New Brunswick populations appear to be declining.	
Is immigration known?	No
Would immigrants be adapted to survive in Canada?	Unknown
Is there sufficient habitat for immigrants in Canada?	No
Is rescue from outside populations likely?	No

Current Status

COSEWIC: Endangered (Nov 2010)

Status and Reasons for Designation

Status: Endangered	Alpha-numeric code: A2bce; C1
Reasons for designation: This species requires rivers or streams that are generally clear, cool and well-oxygenated for reproduction and the first few years of rearing, but undertakes lengthy feeding migrations in the North Atlantic Ocean as older juveniles and adults. This population breeds in rivers from northeastern mainland Nova Scotia, along the Atlantic coast and into the Bay of Fundy as far as Cape Split. Small (one-sea-winter) and large (multi-sea-winter) fish have both declined over the last 3 generations by approximately 59% and 74%, respectively, for a net decline of all mature individuals of about 61%. Moreover, these declines represent continuations of greater declines extending far into the past. During the past century, spawning occurred in 63 rivers, but a recent (2008) survey detected juveniles in only 20 of 51 rivers examined. There is no likelihood of rescue, as neighbouring regions harbour severely depleted, genetically dissimilar populations. The population has historically suffered from dams that have impeded spawning migrations and flooded spawning and rearing habitats, and other human influences, such as pollution and logging, that have reduced or degraded freshwater habitats. Acidification of freshwater habitats brought about by acidic precipitation is a major, ongoing threat, as is poor marine survival related to substantial but incompletely understood changes in marine ecosystems. There are a few salmon farms in this area that could lead to negative effects of interbreeding or ecological interactions with escaped domestic salmon.	

Applicability of Criteria

Criterion A (Decline in Total Number of Mature Individuals): Meets Endangered A2b,c,e with a decline of 61% in the number of mature individuals over the last 3 generations (12 years), in part due to a decline in the quality of the habitat due to acid precipitation. Breeding has ceased in half of the rivers since the 1980s.
Criterion B (Small Distribution Range and Decline or Fluctuation): Not applicable.
Criterion C (Small and Declining Number of Mature Individuals): Meets Endangered C1. The number of mature individuals in 2008 was 1427 in 4 rivers thought to include the majority of the population, and therefore is thought to be well below 2500. The population is declining, with a 2-generation decline of ~40%.
Criterion D (Very Small Population or Restricted Distribution): Not applicable.
Criterion E (Quantitative Analysis): Not applicable.

Table A7. Characteristics used to delineate 16 Atlantic salmon conservation units (DU's) in Canada (COSEWIC 2011).

Table 1. Summary of DU characteristics.						
DU	Adjacent DUs	Salmon/Quebec Fishing Areas	Genetic Variation	Phenotypic Variation	Geographic	Ecological/Habitat
1 - Nunavik	2	Q11	Limited gene flow with other DUs based on neutral markers Verspoor (2005), Dionne <i>et al.</i> (2008), Fontaine <i>et al.</i> (1997).	Evidence of local migratory routes.	Disjunct from the rest of the species distribution (~650 km of coastline).	At the northern extreme of the species' range in Canada, Arctic-like conditions.
2 - Labrador	1,3,6,7	SFA 1.2, 14b and 6 rivers from Q9	Minimal evidence of sub-structuring in southern portion of DU, data deficient in northern portion. Some evidence Lake Melville may be distinct King <i>et al.</i> (2001), Adams (2007), Dionne <i>et al.</i> (2008).	Higher incidence of MSW fish. Smolt primarily age 4+ (Chaput <i>et al.</i> 2006a).	Separated from insular Newfoundland by the Strait of Belle Isle.	Arctic and subarctic conditions in much of the DU. Anadromous Arctic char and brook trout abundant in many watersheds.
3 - Northeast Newfoundland	2,4,6	SFA 3-8	'European-type' mtDNA genotypes present in this area. Low levels of gene flow with other DUs based on neutral genetic markers. Some evidence of within-DU sub-structure King <i>et al.</i> 2000, Verspoor (2005), Adams (2007), Palstra <i>et al.</i> (2007).	Primarily grilse populations. Smolt predominantly age 4 (Chaput <i>et al.</i> 2006a). Highest incidence of repeat spawners in Canadian range. Substantial non-anadromous population components.	All rivers flow directly into open Northeast Atlantic and the Grand Banks.	Relatively low natural pH 6.1-6.5. Low gradient rivers.
4 - South Newfoundland	3,5	SFA 9-12	Evidence of within-DU sub-structuring, but no geographic pattern. Low levels of gene flow with other DUs based on neutral markers Verspoor (2005), Adams (2007), Palstra <i>et al.</i> (2007).	Some rivers have early run timing, and median smolt age of 3 years (Chaput <i>et al.</i> 2006a). Substantial non-anadromous population components.	Rivers empty into a region influenced by the Gulf Stream versus the Labrador Current.	Relatively low pH water usually < 5.5. Some areas are high gradient systems. Milder climate relative to northern portions of insular Newfoundland.

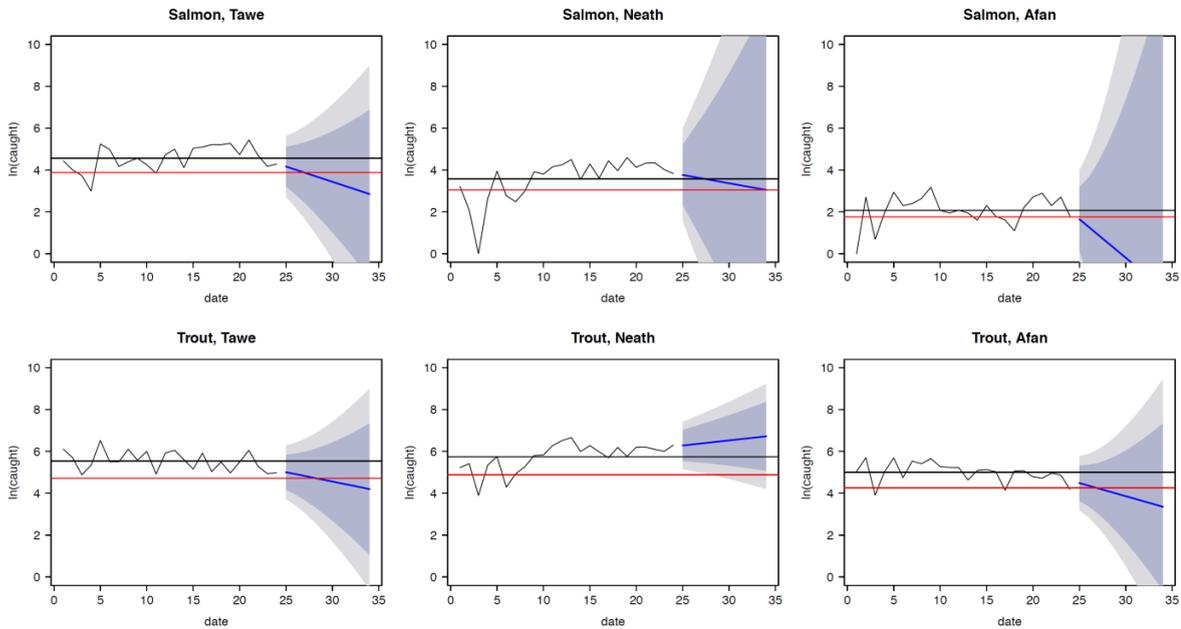
Table A7 (cont.)

DU	Adjacent DUs	Salmon/Quebec Fishing Areas	Genetic Variation	Phenotypic Variation	Geographic	Ecological/Habitat
5 - Southwest Newfoundland	4,6	SFA 13	Evidence of higher rates of gene flow within this DU than among adjacent DUs and within other DUs (Verspoor (2005), Palstra <i>et al.</i> (2007)).	Earliest ages of smoltification on the Island. Only DU on insular Newfoundland with a substantial MSW component (Chaput <i>et al.</i> 2006a).	Rivers empty in the Cabot Strait and Gulf of St. Lawrence. Close proximity to southern DUs (e.g., DU 13).	Many low gradient streams, limited lacustrine habitat.
6 - Northwest Newfoundland	2,5,7	SFA 14a	Data deficient.	Small MSW component (Chaput <i>et al.</i> 2006a).	Rivers flow into the Strait of Belle Isle.	Lacustrine habitat abundant.
7 - Quebec Eastern North Shore	2,6,8,9	Part of Q8 and Q9	Neutral markers suggest higher gene flow within this region than among adjacent DUs. Data suggest western border with DU 8 may be ambiguous. Dionne <i>et al.</i> (2008).	Characterized by populations with high proportions of 1SW salmon (Chaput <i>et al.</i> 2006a).	No clear geographic boundary with DU 8 or DU 2, but separated from other DUs by Gulf of St. Lawrence	Rivers with lower temperature regimes than DU 8
8 - Quebec Western North Shore	7,9,10	Part of Q7 and Q8	Neutral markers suggest within DU gene flow is higher than among adjacent DUs. Some evidence of transitional areas on borders. Dionne <i>et al.</i> (2008)	Highest proportion of MSW salmon by a significant margin relative to the other DUs of the North Shore (Chaput <i>et al.</i> 2006a).	No clear geographic boundary with DU 7 or DU 10, but separated from other DUs by Gulf of St. Lawrence.	Higher gradient rivers than nearby DUs (Dionne <i>et al.</i> 2008).
9 - Anticosti Island	7,8,10,12,13	Q10	Neutral markers suggest gene flow within this DU may be variable. Low levels of distinction among some rivers, but clearly divergent from mainland Dionne <i>et al.</i> (2008).	Higher proportion of 1SW salmon than many nearby DUs (Chaput <i>et al.</i> 2006a).	Distinct island system in the Gulf of St. Lawrence.	Lower gradient rivers (Dionne <i>et al.</i> 2008).
10 - Inner St. Lawrence	8,11,12	Q4,5,6	Neutral markers suggest divergence from adjacent DUs (Dionne <i>et al.</i> (2008)).	Lower mean age at smoltification than nearby DUs (Chaput <i>et al.</i> 2006a).	NA	Freshwater habitat is also the warmest along the Quebec North Shore.
11- Lake Ontario	10	FMZ 20	Data deficient	Likely potamodromous with the possibility of some anadromous populations. Had the youngest smolt ages in Canadian range.	Inland lake system	Unknown
12 - Gaspé-Southern Gulf of St. Lawrence	9,10,13	Q1,2,3 and SFA 15,16,17,18	Data deficient, but some evidence of divergence at eastern (Dionne <i>et al.</i> 2008) and western edges (P. O'Reilly pers. comm.)	Variable life histories across the DU, but no clear geographic pattern (Chaput <i>et al.</i> 2006a).	Encompasses entire southern Gulf of St. Lawrence and PEI.	Variable across the DU. PEI is a distinct island system. Miramichi River is the dominant system.

Table A7 (cont.)

DU	Adjacent DUs	Salmon/Quebec Fishing Areas	Genetic Variation	Phenotypic Variation	Geographic	Ecological/Habitat
13 - Eastern Cape Breton	12,14	SFA 19	Absence of mitochondrial haplotype observed in DU 14. Verspoor <i>et al.</i> (2005).	Variable life histories across the DU. Some evidence of western and eastern geographic pattern (Chaput <i>et al.</i> 2006a).	Island system. Many of the DU rivers flow into the open Atlantic Ocean. Large inland lake system.	Higher gradient rivers than nearby DUs.
14 - Nova Scotia Southern Upland	13,15	SFA 20, 21	Allozyme, mitochondrial, and microsatellite data suggest divergence among DUs 14,15,16. Verspoor (2005), Verspoor <i>et al.</i> (2005), O'Reilly, pers. com.	Lower proportions of MSW fish than their northern neighbours. Southerly populations in DU 14 also have some of the youngest smolt ages reported in Canada (Chaput <i>et al.</i> 2006a).	Rivers flow into Western North Atlantic Ocean	Many rivers in DU 14 have freshwater habitat with relatively low pH.
15 - Inner Bay of Fundy	14,16	Portions of SFA 22 and 23	Allozyme, mitochondrial, and microsatellite data suggest divergence among DUs 14,15,16. Verspoor (2005), Verspoor <i>et al.</i> (2005), O'Reilly, pers. com.	Unique migratory behaviour.	Confined to the inner Bay of Fundy.	Unique Bay of Fundy tidal system.
16 - Outer Bay of Fundy	15	Portion of SFA 23	Allozyme, mitochondrial, and microsatellite data suggest divergence among DUs 14,15,16. Verspoor (2005), Verspoor <i>et al.</i> (2005), O'Reilly, pers. com.	DU 16 has a higher proportion of MSW salmon migrating to the North Atlantic than DU 15 (Chaput <i>et al.</i> 2006a). Several systems with unusual run timing.		

Figure A1.



Holt-Winters 10 year forecasting of rod catches based on historic records (1993- 2014) for salmon and sea trout in the rivers Tawe, Neath and Afan. Black line shows mean catch, red line shows 15% reduction in mean catch, blue line shows most likely forecast, mid-blue ribbon shows 80% prediction intervals, and light grey-blue ribbon shows 95% prediction intervals (from Garcia de Leaniz et al., 2015).

9.1 Data Archive Appendix

No data outputs were produced as part of this project.

© Natural Resources Wales

All rights reserved. This document may be reproduced with prior permission of Natural Resources Wales.

Further copies of this report are available from library@cyfoethnaturiolcymru.gov.uk