



HAL
open science

Population dynamics analysis of sea trout populations around the Celtic and Irish Seas

Niklas Tysklind, Nigel Milner, Gary R. Carvalho

► **To cite this version:**

Niklas Tysklind, Nigel Milner, Gary R. Carvalho. Population dynamics analysis of sea trout populations around the Celtic and Irish Seas. [Research Report] Bangor University. 2015, pp.1-56. hal-03772786

HAL Id: hal-03772786

<https://hal.inrae.fr/hal-03772786v1>

Submitted on 8 Sep 2022

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Population dynamics analysis of sea trout populations around the Celtic and Irish Seas:



Niklas Tysklind

Team Leader « Ecological Genetics and Genomics »

INRA - UMR 0745 ECOFOG "Ecologie des Forêts de Guyane" / "Ecology of Guiana Forests"

Campus agronomique, Avenue de France

BP 709 - 97387 KOUROU Cedex

FRENCH GUIANA, FRANCE

Phone: +594 (0)59432-9279

Email: niklas.tysklind@ecofog.gf

Nigel Milner

Associate Senior Fisheries Biologist

APEM Limited, C/O School of Biological Sciences, Bangor University,

Brambell Building, Deiniol Road, Bangor, Gwynedd

Wales, UK, LL57 2UW

Tel: (01248) 388664

Email: n.milner@apemltd.co.uk

Gary R. Carvalho

Professor of Molecular Ecology

Molecular Ecology and Fisheries Genetics Laboratory,

School of Biological Sciences, Bangor University,

Bangor, Gwynedd, Wales, UK, LL57 2DG

Phone: 01248 382100

Email: g.r.carvalho@bangor.ac.uk



Ireland's EU Structural Funds
Programmes 2007 - 2013
Co-funded by the Irish Government
and the European Union



1. Introduction:

The Celtic Sea Trout Project (CSTP), a large international collaborative project, funded by Interreg IVA, but set up with AST support, has produced a large data set on sea trout stocks and population characteristics that is unique in its spatial scale, covering 99 rivers draining into the Celtic and Irish Seas. It is also vast in the number of sea trout included in the study (over 20,000 individuals), and the nature of data collected, including rod fishery catch size distribution data, environmental data, trout population genetic spatial structure, elementary microchemistry of scales and otoliths, unveiling of marine migratory patterns, and ageing and ascertainment of individual life history strategies. The latter were reconstructed from the banding patterns recorded on fish scales, where phases of summer and winter growth and fresh water and marine environment growth are recognisable by the density of circuli on the scales (Figure 1).

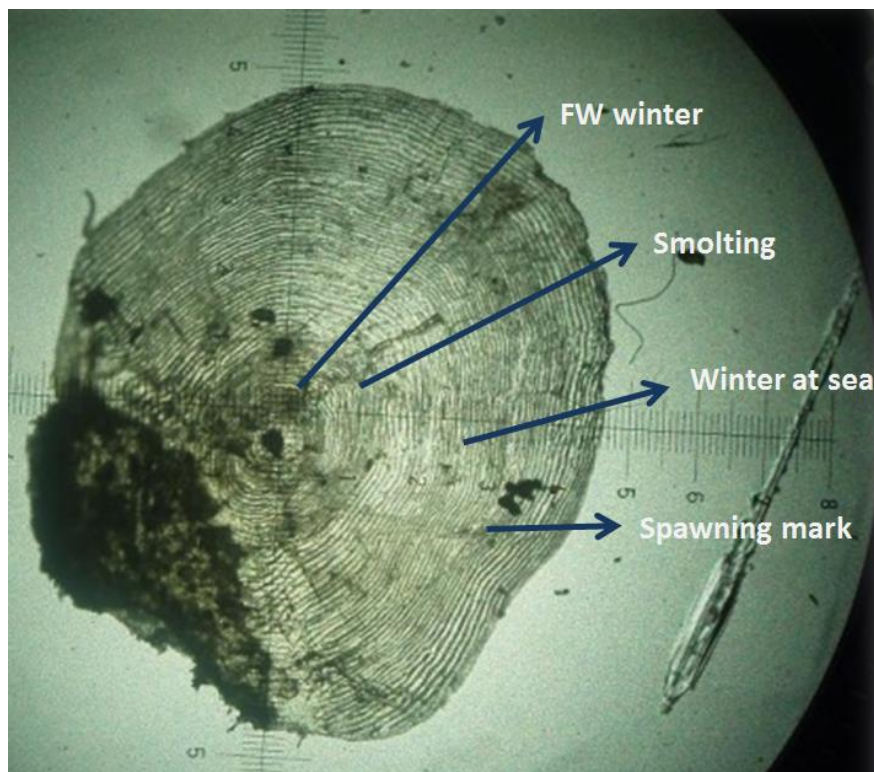


Figure 1: Sea trout scale viewed under the microscope showing the patterning in circuli typical of fresh water and marine phases of its life history

Once the individual life history strategies are known, one can evaluate the population consequences, in terms of dynamics, of the individual choice in life history strategies. One of the aims of the CSTP is to develop life history based population dynamics models to better understand the biology of sea trout, and its variance among populations around the Celtic and Irish Seas, which could have practical applications to fisheries management and conservation of this valuable wildlife resource. Key life history traits include age- or stage-specific survivorship, somatic growth, maturation rate, and fecundity, population genetic structuring and connectivity, which control population recruitment, rates of population growth and age structure and thus ultimately fisheries attributes of catch size and composition. The applications of these models, if they prove practicable with the available information, include estimating the effects of variables,

such as environmental characteristics, genetic traits, and fishing regulations and conservation policies, which are likely to alter population dynamics parameters.

Using the data collected during the CSTP, the aim of this report is to analyse the variance among rivers in population demographic dynamic parameters of the the anadromous contingent (sea trout) of some of the trout populations studied by the CSTP. When modelling population demographics, it is important to choose the variable with the largest influence on the demography (Caswell 2001). For many organisms, age is a critical variable determining onset of reproduction, fecundity and senescence. For others, size or developmental stage are more critical in determining fecundity or survival. In sea trout both stage (parr age, number of full years at sea, and number of years as a spawner) and size are critical in determining reproduction onset, fecundity and mortality, more so than age *per se*. Hence a stage based model was employed. Stage models allow individuals remaining in a stage for more than one year (i.e. a parr spending 2 years in fresh water), or jumping stages (e.g. a whitling which returns before spending a winter at sea, can spawn without going through a sea winter phase). Such flexibility allows modelling the complexity in life history patterns found in sea trout previous to reproduction onset, and preserves the variance among populations in the length of time from fry to first reproduction. The increase in fecundity as sea trout age is captured by having several spawning classes as stages, as many as the oldest fish encountered in a population, which behave as an age model, i.e. individuals have to proceed to the next stage and cannot jump stages.

Matrix projection models were developed using stage specific approaches with stages defined by the recreated life history based on the scale reading, viz: number of years in freshwater (FW), number of full years at sea as maiden fish (sea winter stage: SW; .0+,.1+,.2+), number of full years at indeterminate stage (IM, as for SW), number of years as spawner (SM n , where n = the number of previous spawning events), and dead (D). The analysis was based on those individuals for whom age, life history, and fecundity could be estimated. The age and life history were estimated from scales collected at the time of capture. The scale reading methodology is described on the CSTP report, but in summary, life history events were inferred from the number of winter and spawning marks encountered on the scales (Figure 1). Fresh water winter marks can normally readily be distinguished from sea winter and spawning marks. However, the distinction between the latter two can sometimes be ambiguous: scale erosion may be limited, or only present on the shoulders of the scales. There is discrepancy among expert sea trout scale readers on the interpretation of these scale features, and there are several observed life events that could explain such incomplete erosion including erosion at sea, partial migration to estuary, migration to river without spawning, and actual spawning. Aiming to manage such ambiguity, marks of uncertain origin (sea winter/spawning) were classified as indeterminate marks (IM). For population dynamics, IM marks could be considered as sea winters, thus not spawning, or as partial spawners in which a fraction of the individuals recorded as IMs are true spawners. The following analysis considers IMs as non-spawning, but it is possible to do a parallel analysis where IM are given a reduced fecundity compared to SM 1 (i.e. a percentage equal to that of the proportion of IM believed to be true spawners).

2. Materials and Methods:

2.1. Data description, variable management:

The initial dataset contained 20,902 individuals for which there was a maximum of 116 variables, although many of them were only collected for subsets of individuals (i.e. sex data only collected for some adult sea trout). The variables river and marine zone were given a specific geographical order: starting from the west of Ireland, around the Irish Sea, and finishing in the south east of Wales (Figure 2). All sea trout collected from the three rivers in the Isle of Man were combined into a single composite sample (IOM). The sequence of months from January to December was specified for the variable Month. All missing data was set to NA.

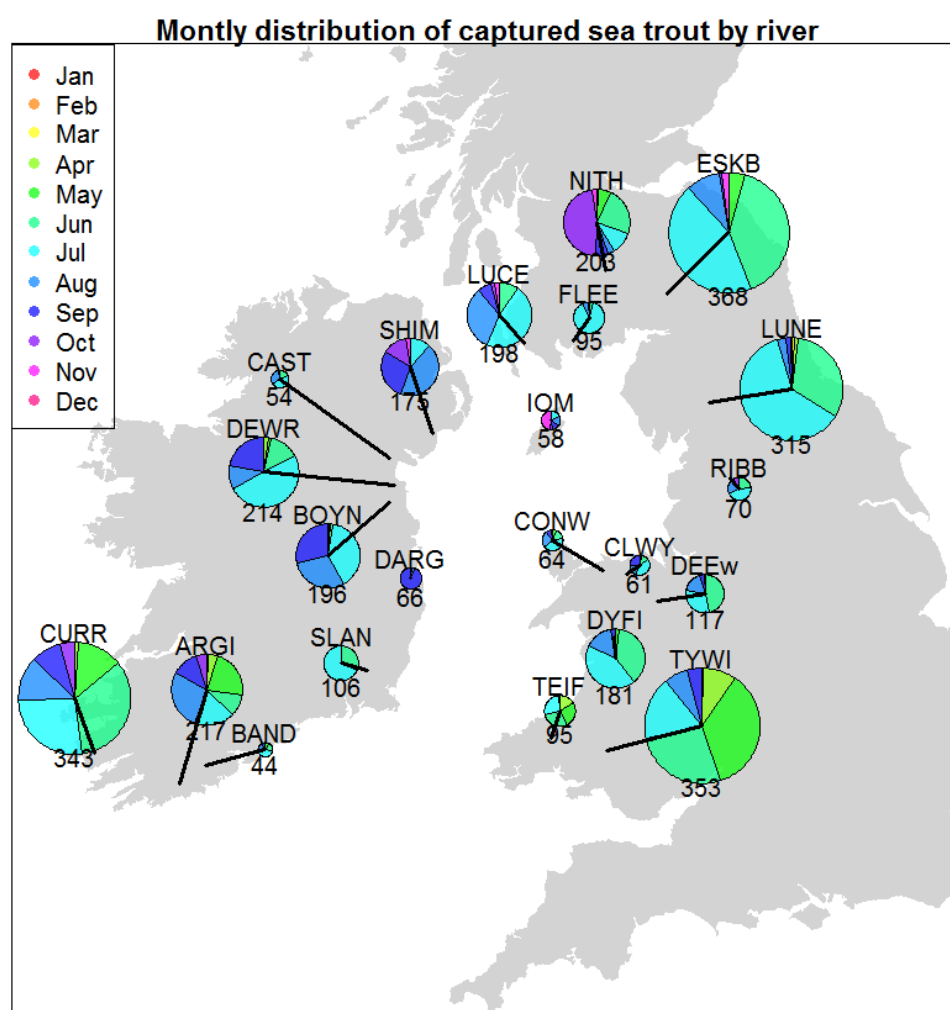


Figure 2: Monthly distribution of captured sea trout by river. Monthly proportions are depicted as pie charts coloured by month. River codes are indicated above pies, while sample size numbers are below pies.

2.2. Data checking:

Sea trout weight and length measurements were collected fresh, thawed, or both fresh and thawed. The individuals with both fresh and thawed measurements were used to inspect the effects of freezing and thawing on the weight and length measurements (N=1295 for weight; N=1603 for length). For some of these individuals the relationships between fresh and thawed measurement was very skewed and are most likely due to data input errors (Figure 3). These

outliers were removed by creating an index (fresh/thawed) for each individual, assigning a standard score (z-score) to each index, and removing individuals with standard scores over 2 and below -2.

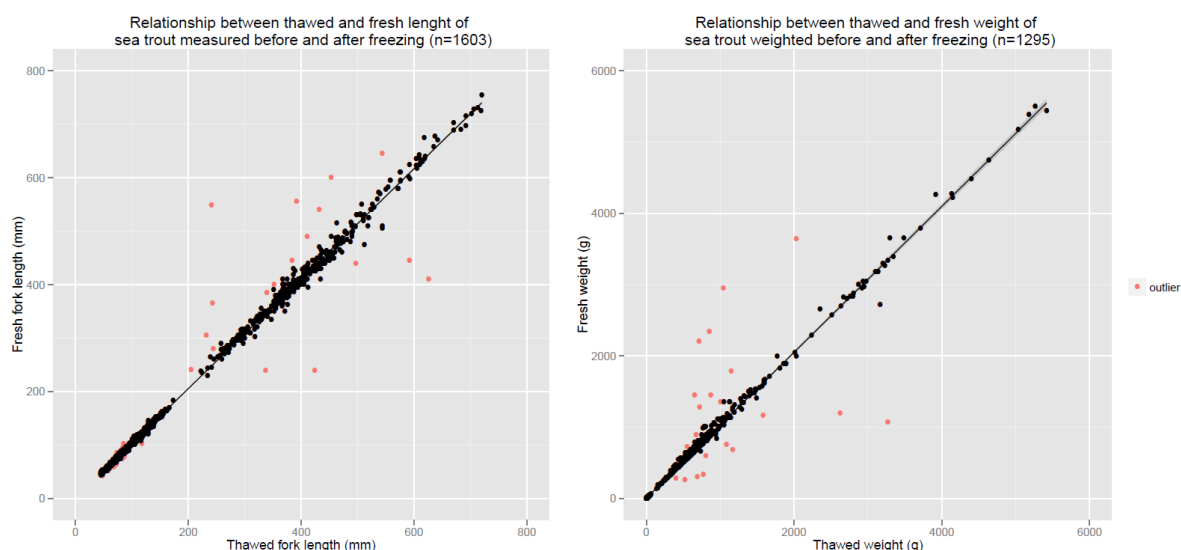


Figure 3: Relationship between thawed and fresh length and weight of sea trout

Models predicting fresh measurements from thawed measurements were constructed from the remaining individuals and used to estimate fresh measurements for all individuals with only thawed measurements (N=2699 for weight; N=2405 for length):

$$W_{estimated}(g) = 2.526 + 1.032 * W_{thawed}(g)$$

$$L_{estimated}(mm) = -0.2195 + 1.0294 * L_{thawed}(mm)$$

The relationship between length and weight of adult sea trout (N=9753) was also studied to check for input errors. Some individuals had no data for either length or weight (N=2772) or had unlikely lengths for an adult (< 50 mm; N=3) and were thus not included for evaluation of the weight-length relationship. k-factors were calculated for all remaining individuals (N=6979).

$$k = \frac{W * 100000}{L^3}$$

Each k-factors was assigned a z-score, and only individuals with z-score between -1 and 1.8 were considered to be realistic (N=6839; Figure 4; 140 individuals removed). The standard values of -2 and 2 were not considered to be stringent enough, as many obvious entry errors remained when using two standard deviations. The difference in upper and lower cutting values is due a more

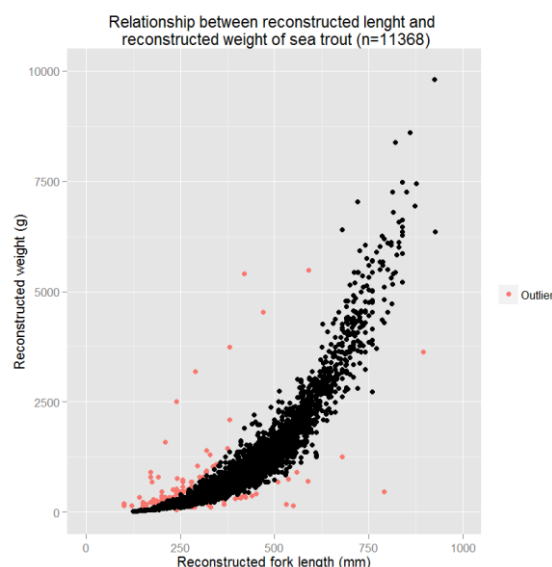


Figure 4: Relationship between reconstructed length and reconstructed weight of sea trout

stringent cutting needed at the bottom of the distribution. The trimmed dataset was used for all analysis involving weight or length.

Of the individuals included in the trimmed adult dataset, 4965 had ageing data. However, ages derived from scale readings were sometimes flagged as unreliable (e.g. mismatch between scales, patterns too unclear, or very unlikely age for size), and individuals with clearly unreliable ages were excluded from the adult aged dataset (N=4710; 255 individuals removed).

2.3. Life history reconstruction:

The CSTP population genetic analysis, based on 18 independent microsatellite loci, revealed that sea trout from different rivers around the Celtic and Irish Seas are all independent populations exchanging few migrants among themselves, therefore, the returning adults from each river were analysed independently as separate populations. The life history of each individual was reconstructed based on the year of capture and the ageing formula. For example, a 2.1+3SM+ sea trout is captured in 2012 on its way up to its spawning grounds. Based on the ageing formula, said sea trout was born in 2006, it stayed in fresh water during the summer of 2007, it smolted and spent a summer and winter at sea in 2008, and then spawned in 2009, 2010, and 2011. As all individuals were caught on their way up to spawning grounds, they were all assumed to contribute to the eggs produced on the year of capture (i.e. 2012) and then die before the next spawning season (i.e. 2013). Such an assumption may exaggerate the number of eggs produced each year, as some individuals may not reach the spawning grounds. However, the alternative, assuming that all captured fish die and do not contribute to the next spawning event, creates an even more unrealistic effect where: 1) all individuals returning for the first time (whitling) do not contribute to the next spawning event; and 2) undermines the importance of repeat spawners, as the increase in fecundity associated with their larger size in their latest effort to reach the spawning grounds is not accounted for. Furthermore, the individuals caught are only a sample of the population, which should be representative of the remainder of the population. Thus, assuming successful reproduction for caught individuals should resemble the fate of the remainder of the population. Similarly, assuming that all caught individuals die after the next spawning event may seem drastic, as obviously some individuals will return the following year as repeat spawners. Nevertheless, assuming all caught individuals die, allows the between-spawning events survival rate to be estimated effectively from the frequency of repeat spawners in the dataset (those individuals that are known to have survived to a certain age).

2.4. Construction of population specific individual size at age somatic growth model:

The fecundity of females is dependent on their size (length or weight), and thus, the lifetime egg contribution of a female to a population will be dependent on its size each time it spawned.

Von Bertalanffy models, such as:

$$L_t = L_\infty [1 - e^{-K(t-t_0)}]$$

were constructed based on the distribution of the total age / length relationship. The length at age relationship varies among rivers and regions, and thus, to avoid losing important river specific growth traits that may influence the dynamics of the population, river specific models

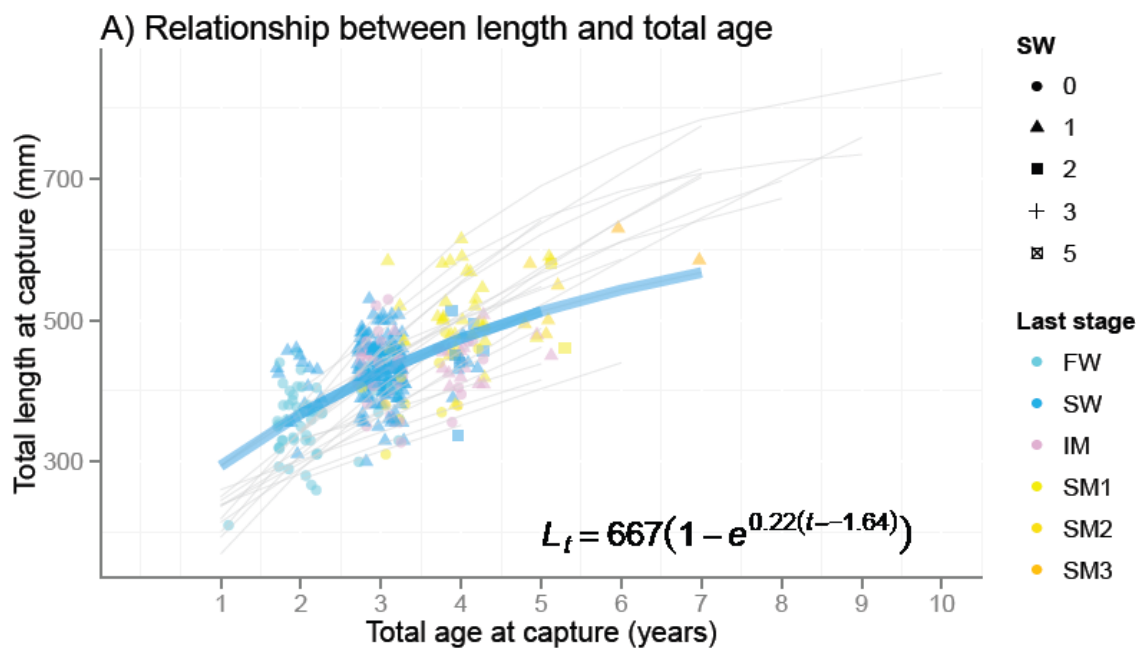


Figure 5: Relationship between length and total age for the River ESKB

were constructed for each river. Variance among life strategies can be observed on the length at age graphs if the different combinations of sea winters and spawning marks are highlighted (Figure 5). In the example from the river ESKB, sea trout returning in their third year of life (total age=2) are larger when they've spent a winter at sea (triangles) than the ones who have only gone out at sea for a few summer months (circles); while at total age 4, individuals who have already spawned (yellow) are larger than those who haven't spawned (blue). The variance among life strategies has an important effect on the relationship of length at age, but creating independent somatic growth models for each life strategy (n=87) would be unpractical. Instead, river specific somatic growth models combined with individual correction were employed. The individual difference between fitted and real values at capture was used to calculate an individual percentage of divergence from the somatic growth model. It was assumed that if a sea trout was 12% larger than predicted on the year of capture, then that sea trout would have been 12% larger throughout its life. These somatic growth models were then used to reconstruct the length of individuals in previous years until age 1.

2.5. Effect of sex on the data:

The effect of sex on size at age was examined through analysis of covariance (ANCOVA) to evaluate if different somatic growth models were needed for each sex.

2.6. Estimation of fecundity:

The length to egg production relationship estimated in the fecundity chapter of the CSTP report was employed to calculate individual fecundity.

$$Fecundity = 2.1023 * L - 2.3029$$

The fecundity relationship was constructed based on 55 individual females captured on several marine zones of the Irish and Celtic Seas. The individual reconstructed lengths were only

translated into fertilities if a spawning mark (SM) was identified for that individual on that year (Table 1). The final population recreated life history table is a stacked list of the recreated annual life history events for every individual (Table 1), with estimated back calculated lengths and associated fecundities, which allows estimating the number of individuals spawning and the eggs produced every year based on our sample.

Table 1: Extract of the recreated life history table for five individuals from the River CURR. The first individual, I-CURR-10-037, was captured in 2010 as a 3.1IM+ returning to spawn for the first time with a length of 57cm. The first six records on the table refer to such individual, and indicate the stage, back calculated length and associated fecundity in 2010 (the first time the individual was about to spawn), the projected final state of dead in 2011. Individual I-CURR-10-039 was captured as a 3.0+4SM+ in 2010, hence it has 5 years where this individual spawned, the 4 previous to capture and the one it was captured on (2010 = SM5).

Id	Year	Stage	Total age (years)	Length (mm)	Fecundity
I-CURR-10-037	2006	FW	0	211	0
I-CURR-10-037	2007	FW	1	306	0
I-CURR-10-037	2008	FW	2	397	0
I-CURR-10-037	2009	IM	3	485	0
I-CURR-10-037	2010	SM1	4	570	3096
I-CURR-10-037	2011	dead	5	651	0
I-CURR-10-038	2007	FW	0	184	0
I-CURR-10-038	2008	FW	1	268	0
I-CURR-10-038	2009	IM	2	348	0
I-CURR-10-038	2010	SM1	3	425	1670
I-CURR-10-038	2011	dead	4	499	0
I-CURR-10-039	2003	FW	0	186	0
I-CURR-10-039	2004	FW	1	270	0
I-CURR-10-039	2005	FW	2	350	0
I-CURR-10-039	2006	SM1	3	428	1695
I-CURR-10-039	2007	SM2	4	503	2377
I-CURR-10-039	2008	SM3	5	574	3147
I-CURR-10-039	2009	SM4	6	644	3996
I-CURR-10-039	2010	SM5	7	710	4912
I-CURR-10-039	2011	dead	8	774	0
I-CURR-10-040	2007	FW	0	204	0
I-CURR-10-040	2008	FW	1	296	0
I-CURR-10-040	2009	IM	2	385	0
I-CURR-10-040	2010	SM1	3	470	2064
I-CURR-10-040	2011	dead	4	552	0
I-CURR-10-043	2004	FW	0	185	0
I-CURR-10-043	2005	FW	1	268	0
I-CURR-10-043	2006	FW	2	348	0
I-CURR-10-043	2007	IM	3	426	0
I-CURR-10-043	2008	SM1	4	500	2349
I-CURR-10-043	2009	SM2	5	571	3111
I-CURR-10-043	2010	SM3	6	640	3949

2.7. Construction of population specific transition matrices:

Construction of the transition matrices and analysis of the population demographics was done with the analysis package *popbio* (Stubben & Milligan 2007) for R (R Development Core Team 2014). Transition (Table 2) and fecundity (Table 3) matrices were constructed based on the recreated life histories using *popbio*. Each matrix values is estimated based on the proportion of individuals in stage *a* (indicated along the top of the matrix) entering stage *b* (indicated on the left of the matrix) recorded on the recreated life history tables. Thus transition values indicates the probability of an individual being in one stage going to another, while fecundity values indicate the numbers of new recruits generated on average by every individual in a particular stage.

Table 2: Transition matrix from the River ESKB without mortality modifiers

§T	FW	SW	IM	SM1	SM2	SM3	SM4	dead
FW	0.500	0	0	0	0	0	0	0
SW	0.352	0.029	0	0	0	0	0	0
IM	0.061	0.077	0.082	0	0	0	0	0
SM1	0.087	0.894	0.918	0	0	0	0	0
SM2	0	0	0	0.148	0	0	0	0
SM3	0	0	0	0	0.179	0	0	0
SM4	0	0	0	0	0	0.200	0	0
dead	0	0	0	0.852	0.821	0.800	1.000	0

Table 3: Fecundity matrix form the River ESKB without egg mortality modifiers

§F	FW	SW	IM	SM1	SM2	SM3	SM4	dead
FW	0	0	0	1663	2242	2573	3546	0
SW	0	0	0	0	0	0	0	0
IM	0	0	0	0	0	0	0	0
SM1	0	0	0	0	0	0	0	0
SM2	0	0	0	0	0	0	0	0
SM3	0	0	0	0	0	0	0	0
SM4	0	0	0	0	0	0	0	0
dead	0	0	0	0	0	0	0	0

Mortality cannot be estimated for all stages before first return of sea trout (FW, SW, IM) from the data available here, and thus a mortality modifier needs to be applied to the transition matrix. A standard annual mortality of 0.7 in fresh water and 0.95 at sea was applied to transition matrices of all rivers. Individuals which have returned to fresh water more than once can be used to estimate survival from one spawning event to another (i.e. transition rate from SM1 to SM2 based on all individuals who survived to SM2 compared to those present in SM1). The difference in the number of individuals who survived to SM2 compared to those present in SM1, can be obtained by adding an extra final stage (dead) to all individual life histories. Such final stage has no transition rates to any other stages. A modifier of 0.01 was applied to the fecundity matrix transition values to simulate the probability of egg survival to FW stage (1%). Such approach

produces a matrix ready for demographic analysis through matrix projection using *popbio* (Table 4).

Table 4: Combined transition and fecundity matrix for the river ESKB with mortality modifiers

	FW	SW	IM	SM1	SM2	SM3	SM4	dead
FW	0.150	0.000	0.000	16.594	22.189	25.273	35.455	0.000
SW	0.106	0.001	0.000	0.000	0.000	0.000	0.000	0.000
IM	0.018	0.004	0.004	0.000	0.000	0.000	0.000	0.000
SM1	0.026	0.045	0.046	0.000	0.000	0.000	0.000	0.000
SM2	0.000	0.000	0.000	0.148	0.000	0.000	0.000	0.000
SM3	0.000	0.000	0.000	0.000	0.179	0.000	0.000	0.000
SM4	0.000	0.000	0.000	0.000	0.000	0.200	0.000	0.000
dead	0.700	0.950	0.950	0.852	0.821	0.800	1.000	0.000

2.8. An introduction to measures of population growth

Many models of population growth are described for organisms (Gotelli 2008) and all are approximations of reality, as no model can really aim to explain the biology of a population exactly.

A basic outline of a differential equation is that that over a year the population size (N) changes by a combination of annual birth rate (b) and death rate (d), such that $dN/dt = (b - d)N$. Let $(b - d) = r$, r being a constant called the instantaneous rate of increase or intrinsic rate of increase, then $dN/dt = rN$. This is normally written as $N_t = N_0 e^{rt}$, where t = time. If $r = 0$ the population will remain constant, if $r > 0$ it will increase to infinity, if $r < 0$ it will decline to extinction. For discrete time steps, $N_{t+1} = N_t + rN_t$, which rearranged gives $N_{t+1} = N_t(1 + r)$.

Let $\lambda = (1 + r)$, the population rate of increase, then $N_{t+1} = \lambda N_t$.

λ is a positive dimensionless (because it is a ratio) number that measures the proportional change in population size from one time step to the next (frequently measured in years). Thus, to find the population size in the following year (N_{t+1}) from that of the current year (N_t), simply multiply N_t by λ . It can be seen that if $\lambda = 1.0$ the population remains constant, if $\lambda < 1.0$ it will decrease and if $\lambda > 1.0$ the population will increase. For completeness, note that λ and r are related by $e^r = \lambda$.

A further important variable of population dynamics is R_0 , the net reproductive rate, which can be interpreted as the mean number of female offspring by which a female will be replaced by the end of its life. Its units are number of offspring and intuitively if $R_0 = 1.0$ there is no population growth, because it exactly replaced itself, if $R_0 < 1.0$ the population decreases, and if $R_0 > 1.0$ then it increases. R_0 is positively related to λ , ($\lambda^{Gen.T} = R_0$, where *Gen.T* is generation time), but they are intrinsically different: λ indicates the population growth per year, while R_0 the population growth per generation. R_0 , and λ are often used as indices of population “fitness”, the ability of the population to recover from perturbations and in turn related to population features of stability and resilience (Caswell 2001).

2.9. Population demographics modelling:

Among the results of the matrix projection analysis, some of the most valuable information obtainable are the age-specific survival and the likelihood of reaching and staying in each stage. These parameters are tabulated in the *fundamental matrix*, which was calculated from the projection matrix.

Eigen analysis of the transition matrices was used to estimate several population parameters:

- the **population growth rate** (λ), which is the dominant eigenvalue of the population transition matrix, and the **net reproductive rate**, (R_0). Two sources of uncertainty around λ values were evaluated: that due to which individuals are included in the estimation and that due to the number of individuals included in the estimation. 1) The variance in the life history of individuals included the modelling of population dynamics could have an effect on the estimated values of λ , hence 95% confidence intervals around values of λ were constructed based on bootstraps ($n=1000$) of the individual transitions included in the transition matrix (i.e. to evaluate the impact of not including all sampled transitions in each population). The number of transitions to be sampled was set to equal the number of transitions available for the population being analysed. 2) There was strong variance in the number of individuals per population, thus, to evaluate the effect of the variance among rivers in the number of individuals on the estimated λ , a second bootstrapping exercise ($n=1000$) was undertaken where the number of transitions resampled was fixed to 200, approximately 40 individuals with an average 5 transitions through their life time.
- The **generation time**, which can be interpreted as either the time needed for the population to increase by a factor of R_0 , or the mean age of the parents of the offspring produced by a cohort over its life time.
- The **stable stage distribution**, which is the right eigenvector associated with λ , indicates the proportion of each stage in a population at equilibrium.
- The **stage specific reproductive value**, which is the left eigenvector associated with λ , indicates the potential reproductive contribution (mean number of offspring to be produced in its remaining lifetime) of an individual in a particular class.
- The **damping ratio** (ρ), which describes the relationship between the dominant eigenvalue (λ_1), and the second largest eigenvalue (λ_2) as $\rho = \lambda_1/|\lambda_2|$, and can be interpreted as the rate of convergence to the stable stage distribution. The larger λ_1 is compared to λ_2 (i.e. the higher the ρ value), the more rapid the convergence to stable stage distribution will be.
- Different life stage transitions have varying influences on population growth rate (λ), it may thus be interesting to know the impact on λ of augmenting each transition parameter (A_{ij}). Analysis of the **sensitivities of λ** to additive perturbations of transition parameters (A_{ij} = survival, growth, and fecundity transitions) allows evaluation of the relative importance of each transition (A_{ij}) and how sensitive they are to additive perturbations.
- The **elasticity of λ** measures the proportionality of the response of λ to proportional perturbations of transition parameters (A_{ij}). In other words, how tied is the response of λ to perturbations of a transition parameter (A_{ij}). It can also be interpreted as the

transition's (A_{ij}) contribution to λ , as elasticities always add up to one. The elasticities of λ to transition parameters can be added by columns or rows to know the elasticity of λ to a particular stage. To evaluate the dependence of a population on the most basic life history strategy (FW \rightarrow SM1 \rightarrow FW, i.e. a 2.0+ whitling returning to spawn for the first time), the elasticities of the FW to FW, FW to SM1, and SM1 to FW were added up (E_{minLH}). The remainder up to 1 was considered as the dependence of the population on alternative life histories (E_{altLH}), or as a measure of the complexity of life histories contributing to λ . To evaluate the elasticity of λ in each population to particular life history strategies of sea trout, we calculated the *elasticity of λ to the fresh water phase*; the *elasticity of λ to whitling* (the elasticities to the FW to SM1 transition); the *elasticity of λ to the sea winter phase* (sum of elasticities of λ to transitions involving SW and IM as start or final stage); the *elasticity for first time spawners* (elasticity of SM1 fecundity) and the *elasticity of λ to repeat spawners* (sum of elasticities of all repeat spawners). These five elasticities add to 1 as they include all transitions in the projection matrix. The relative importance of the summed elasticities of λ to perturbations in the whitling, sea winter phase, and repeat spawners is illustrated on ternary plots (triangular plots). Ternary plots allow depicting on a two dimensional space the contributions of three variables, each on one axis from 0 to 100%. The positioning of each dot (representing the sea trout population of a river) is determined by the percentage of summed elasticities of λ of each phase and can be understood as the relative contribution of whitling, sea winter phase, and repeat spawners to population growth rate. The plots have been focused on the range of values encountered in this study ($E_{Whitling}$ = 30-100%, $E_{SeaWinter}$ =0-70%, $E_{RepSpawn}$ = 0-70%). For the among river comparative analysis, population-specific traits such as population growth rate (λ), generation time, and damping ratio (ρ) were overlaid to understand the relationship between the frequency of alternative life strategies and population dynamics.

3. Results:

The cleaned up dataset (N=4710) included individuals from 42 rivers and marine zones for which there were estimates of age, life history and somatic growth. However, the distribution of individuals among locations was heterogeneous (). Among the sea trout captured in rivers (N=3755), there were 87 different life history patterns (Table X), although the three most common life histories (2.0+, 2.1+, and 2.0+1M) were found in 2338 individuals (62.3% of river caught sea trout).

Although the provenance of marine caught trout could be inferred through genetic and microchemistry assignment to river of origin, the marine samples were not included in the population dynamics assessment due to the uncertainty of whether they would remain at sea or spawn the following spawning season. Thus only sea trout caught within rivers were employed in the population dynamics assessment. Of the 25 rivers, 22 had at least 40 individuals sampled. Such a low number of individuals may not be enough to sample all the possible life history patterns that exist in a population, but should provide an indication of which type of life history strategy (sea winters, whitling, repeat spawners) dominate the population. To provide guidance on the confidence of the population dynamic modelling exercise, the samples sizes are indicated on the river specific summary plates.

The total age and age after year of smolting (sea age), was heterogeneous among rivers (Figure 6). For some rivers, like the BAND and CAST, the oldest fish only had a maximum sea age of two years, while in other rivers like the CURR and TYWI there was a great diversity of life histories including individuals with sea ages up to 8 years.

Table 5: Samples sizes by rivers and Marine zones

River	N	Marine Zone	N
CURR	346	MZ04	32
ARGI	223	MZ05	105
BAND	44	MZ06	167
SLAN	126	MZ07	64
DARG	66	MZ08	74
BOYN	205	MZ09	69
DEWR	217	MZ10	107
CAST	54	MZ11	18
SHIM	181	MZ12	114
IOM	59	MZ13	28
LUCE	205	MZ14	33
FLEE	95	MZ15	7
NITH	204	MZ16	15
ESKB	378	MZ18	5
EHEN	20	MZ23	33
LUNE	319	MZ29	14
RIBB	72	MZ30	44
DEEW	117		
CLWY	65		
CONW	64		
DYFI	236		
TEIF	103		
TYWI	357		
LOUG	1		
TAWE	32		

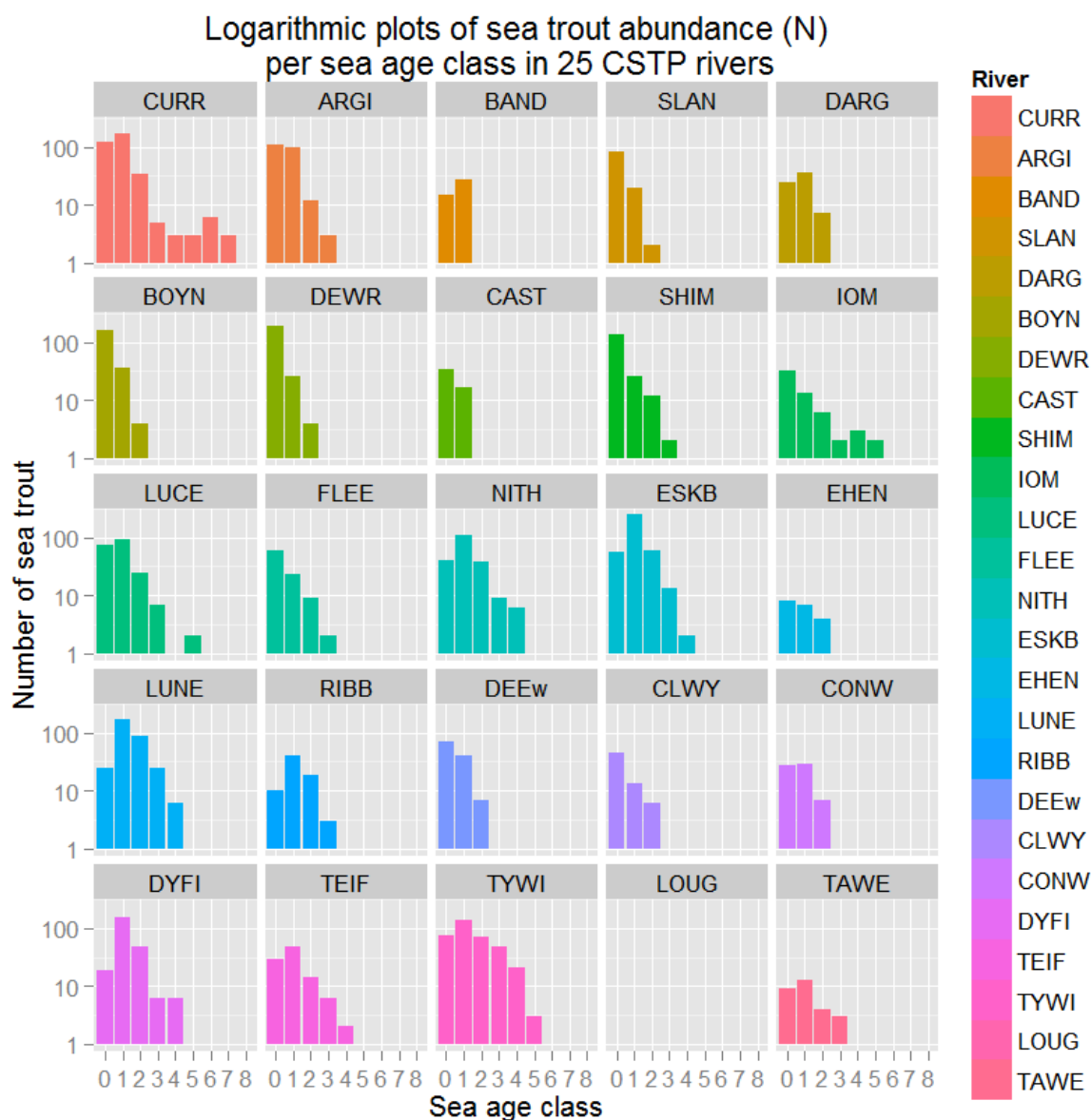


Figure 6: Logarithmic plots of sea trout abundance (N) per sea age class in 25 CSTP rivers

3.1. Effect of sex on the data:

Of the individuals captured in fresh water rivers, there were 1697 females, and 598 males (Table 6). The remainder were of indeterminate sex or not examined. Analysis of the slopes of the overall relationship of length and weight at age indicated that the slopes are not significantly different for females and males (ANCOVA: $p(L)=0.078$; $p(W)=0.829$; Figure 7). However, variance in sex proportion by month and by river can have confounding effects on relationship of size at age (Figure 8; Figure 9).

Table 6: Number of females, males, and non-sexed sea trout

Female	Male	Indeterminate	NotExamined
1692	598	726	734

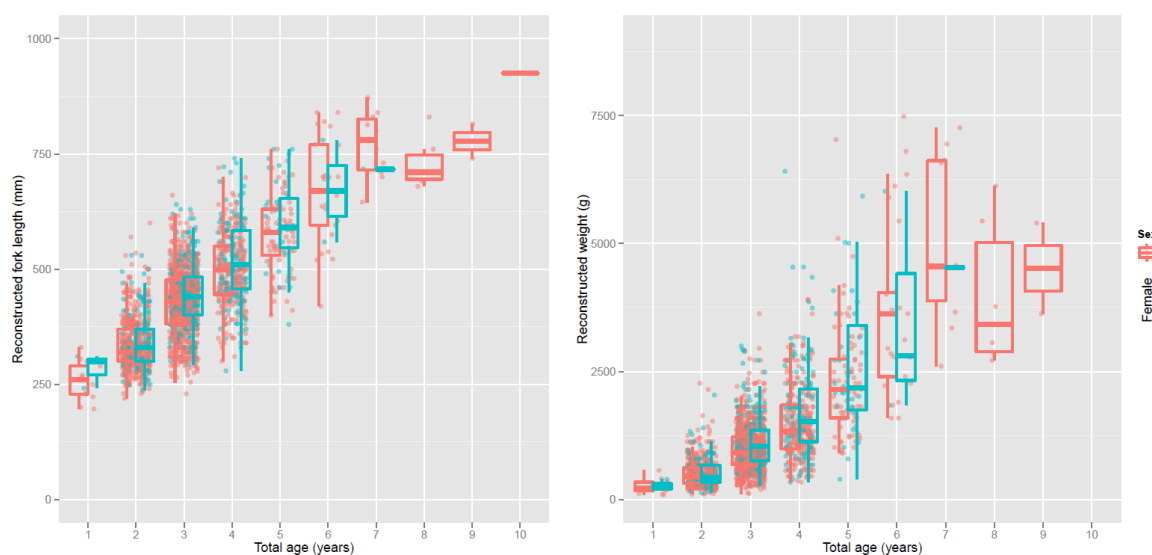


Figure 7: Reconstructed length and weight by age class for male and female sea trout

Only females, and their fecundity, are normally modelled in population dynamics studies as the spermatozooids of males are unlikely to be a limiting factor in the production of offspring. Females represented 73.9% of all sexed individuals, and in all our samples, females represented over 50% of the sexed individuals (Table 7). A possible approach would be to model the population dynamics exclusively with the sexed females. However, as there are no significant differences in length at age between sexes, the male proportion of the population can be assumed to be representative of the variance in size classes, size at age relationship, and life histories of the female proportion of the population. Hence, to augment the sample size of the individuals included in the population modelling, all individuals (females, males, and unsexed) will be considered as reproductive females.

Such assumption will augment the number of females used in the modelling, but as the sampling has not included every individual in the population, males and unsexed individuals can be considered representative of unsampled females. Furthermore, the absolute number of individual females used in the modelling does not affect the outcome of the modelling, although the more individuals that are included in it the more realistic the estimates of the transition and fecundity terms.

Table 7: Sample size and proportion of females by river

River	N	%Fem
CURR	345	69.2
ARGI	221	80.3
BAND	44	85.7
SLAN	106	82.8
DARG	66	82.1
BOYN	204	69
DEWR	217	100
CAST	54	79.4
SHIM	177	88.9
IOM	59	91.7
LUCE	204	73.2
FLEE	95	53.3
NITH	199	89.6
ESKB	378	66.8
EHEN	20	60
LUNE	318	71.3
RIBB	72	65.1
DEEW	117	65.7
CLWY	64	67.4
CONW	64	77.1
DYFI	236	79.3
TEIF	102	61.6
TYWI	356	67.5
LOUG	1	100
TAWC	31	61.9



Figure 8: Proportion of females (red) and males (blue) by sea age among sea trout by river. Indeterminate and not examined sea trout are in grey.

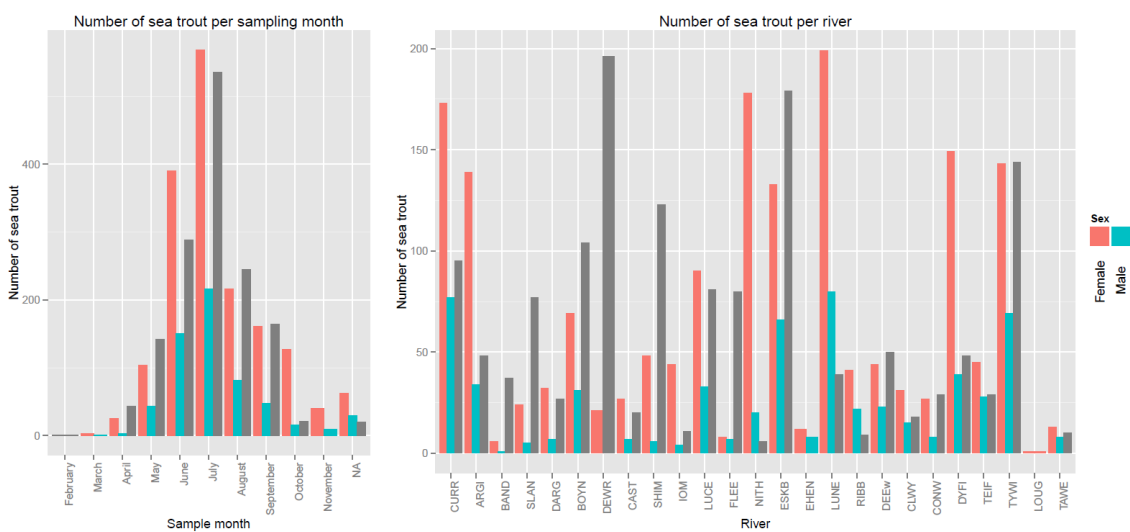


Figure 9: Number of female (red) and male (blue) sea trout by sampling month and by river. Indeterminate and not examined individuals are in grey.

3.2. Recreation of life history:

Size at age of sea trout varied considerably among rivers, which resulted in a diverse range of somatic growth models (Figure 10). Trout from rivers in south Wales had the fastest somatic growth rates, while those in the north east of Ireland grew at the slowest rates.

	River	Lin _f	K	t ₀
1	CURR	2163.465	0.039	-2.084
2	ARGI	1300.875	0.059	-2.382
3	BAND	371.625	1.489	0.481
4	SLAN	713.801	0.096	-3.047
5	DARG	1373.885	0.062	-2.048
6	BOYN	1106.296	0.051	-4.289
7	DEWR	1275.143	0.043	-3.830
8	CAST	733.923	0.104	-3.762
9	SHIM	2963.568	0.028	-1.654
10	IOM	840.864	0.275	0.109
11	LUCE	893.931	0.182	-0.340
12	FLEE	1185.795	0.125	-0.231
13	NITH	1449.801	0.079	-1.399
14	ESKB	667.201	0.220	-1.639
15	EHEN	841.084	0.190	-0.452
16	LUNE	765.081	0.253	-0.330
17	RIBB	648.805	0.366	-0.073
18	DEEW	1283.557	0.126	-0.479
19	CLWY	536.851	0.905	0.886
20	CONW	769.076	0.191	-1.521
21	DYFI	2075.772	0.050	-2.280
22	TEIF	754.531	0.428	0.491
23	TYWI	892.770	0.311	0.229
24	LOUG	1000.115	0.169	-0.541
25	TAW	2099.471	0.052	-2.410

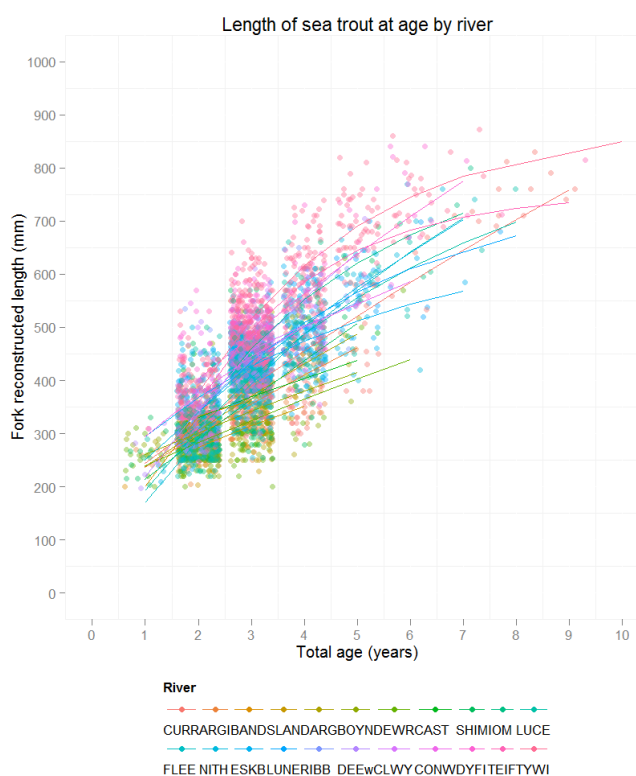


Figure 10: Length at age relationship for sea trout for all rivers and estimates of von Bertalanffy model parameters by river

These river-specific somatic growth models are based exclusively on returning sea trout, which in some rivers included some very rare 1.0+ aged trout captured late in the year (October, November). These unusual fish skewed the somatic growth models so that reconstructed lengths at age 1 seemed unrealistic. However, such bias does not affect the reconstructed fecundity as the vast majority of sea trout do not reproduce until at least 2 years of age. As stated in the methods, the data collected here do not allow the estimation of egg, FW, SW and IM mortality, and thus, identical values were imposed on all populations. The imposed values may not be necessarily close to reality, but by being equal, they allow comparison among rivers of the impact of the sea trout contingent on each rivers trout population. The survival from one spawning event to the next was obtained from the frequency of repeat spawners present in each river dataset. The estimated survival estimated from this method varied widely among rivers (Figure 11). For most rivers, survival between spawning events is relatively low (<0.3) and individuals with more than SM₃ mark are very rare (Figure 10). However, for a few rivers like the CURR, IOM, LUCE, FLEE, DYFY, TEIF and TYWI, once a sea trout had survived from SM₁ to SM₂, stage specific survival increased (up to 0.8 for SM₄ to SM₅ at the CURR and IOM) before decreasing to zero.



Figure 11: Stage specific survival of returning adult sea trout by river

3.3. Population dynamics:

Transition matrices were constructed for all rivers with at least 40 individuals (n=22). Results of the Eigen analysis of the transition matrix of each river are illustrated in river specific plates. Although there are commonalities, sea trout populations from rivers draining into the Celtic and Irish Seas were heterogeneous and followed different population dynamics patterns (Table 8).

Table 8: Population dynamics summary statistics by river.

N = number of individuals; λ = population growth rate; $NetRepRate$ = net reproductive rate; $GenTime$ = generation time; $DampR$ (ρ) = damping ratio; $E.FW$ = elasticity of λ to fresh water phase; $E.Whitling$ = elasticity of λ to whitling; $E.SeaWinter$ = elasticity of λ to the sea winter phase; $E.FirstSpawn$ = elasticity of λ to first spawning event; $E.RepSpawn$ = elasticity of λ to repeat spawners.

	River	N	Lambda	NetRepRate	GenTime	DampR	E.FW	E.Whitling	E.SeaWinter	E.FirstSpawn	E.RepSpawn
1	CURR	345	1.180	1.707	3.225	1.824	0.058	0.315	0.034	0.222	0.370
2	ARGI	221	1.163	1.451	2.460	1.724	0.062	0.403	0.019	0.325	0.191
3	BAND	44	0.996	0.991	2.277	1.375	0.064	0.410	0.058	0.410	0.058
4	SLAN	106	1.094	1.231	2.308	1.409	0.075	0.433	0.006	0.386	0.100
5	DARG	66	1.204	1.596	2.519	2.398	0.073	0.393	0.023	0.301	0.211
6	BOYN	204	1.113	1.265	2.191	1.185	0.075	0.455	0.009	0.456	0.006
7	DEWR	217	1.110	1.268	2.276	1.223	0.072	0.440	0.006	0.414	0.068
8	CAST	54	1.200	1.525	2.313	1.272	0.063	0.431	0.016	0.397	0.093
9	SHIM	177	1.183	1.479	2.330	1.320	0.066	0.432	0.008	0.393	0.101
10	IOM	59	1.537	3.700	3.043	1.514	0.040	0.360	0.012	0.241	0.347
11	LUCE	204	1.171	1.540	2.732	1.723	0.057	0.359	0.039	0.276	0.270
12	FLEE	95	1.243	1.788	2.673	1.475	0.052	0.383	0.015	0.295	0.255
13	NITH	204	1.106	1.329	2.824	2.204	0.057	0.322	0.077	0.234	0.310
14	ESKB	378	0.909	0.778	2.638	2.543	0.074	0.303	0.143	0.291	0.189
15	LUNE	318	0.952	0.860	3.033	2.180	0.061	0.242	0.170	0.186	0.341
16	RIBB	72	0.970	0.920	2.746	2.699	0.063	0.293	0.140	0.246	0.259
17	DEEW	117	1.352	2.030	2.349	1.379	0.052	0.427	0.017	0.374	0.130
18	CLWY	64	1.340	1.949	2.279	1.316	0.056	0.440	0.013	0.403	0.088
19	CONW	64	1.262	1.768	2.445	1.617	0.054	0.401	0.037	0.348	0.161
20	DYFI	236	1.001	1.002	2.951	2.211	0.059	0.265	0.149	0.230	0.297
21	TEIF	102	1.379	2.526	2.885	1.650	0.045	0.356	0.038	0.258	0.303
22	TYWI	356	1.512	3.532	3.051	2.037	0.040	0.338	0.038	0.209	0.376

3.3.1. Population growth rate:

Population growth rate (λ) ranged from slightly negative values in rivers on the North East of the Irish Sea ($\lambda_{ESKB} = 0.909, \lambda_{LUNE} = 0.952, \lambda_{RIBB} = 0.970$) to strongly positive values for most rivers in Wales ($\lambda_{DEEW} = 1.352, \lambda_{TEIF} = 1.379, \lambda_{TYWI} = 1.512$). The strongest population growth rate was found in the Isle of Man ($\lambda_{IOM} = 1.537$). The IOM was a composite sample of three Manx rivers ($N_{SULB} = 1; N_{GLSS} = 2; N_{NEB} = 54$), where long lived repeat spawners (i.e. 2.0+4SM+) were particularly prevalent, leading to the strong population growth rate.

Estimations of λ , and all subsequent analysis were performed on sea trout populations from rivers with at least 40 individuals. To evaluate the effect of the number of individuals per sample on the estimated λ , bootstraps ($n=1000$) of 200 transitions (approximately 40 individuals) were drawn from every dataset. For most rivers, at smaller sampling rates (i.e. 40 individuals) the 95%CI become quite large (~ 0.5), however the estimated values from whole samples are centred among the bootstrapped values, indicating that values collected from smaller samples would be similar to these estimated from whole samples (Figure 12).

There is one notable exception, the river ESKB, for which the value estimated from the whole sample was at the edge of the 95%CI. The ESKB was the largest sample in terms of size ($n=378$), and had the lowest population growth rate ($\lambda_{ESKB} = 0.909$); however, subsamples of the transitions led to even lower λ values (mean $\lambda_{ESKB''} = 0.717$), indicating that a few transitions present in the real dataset have critical importance in maintaining λ around 1.

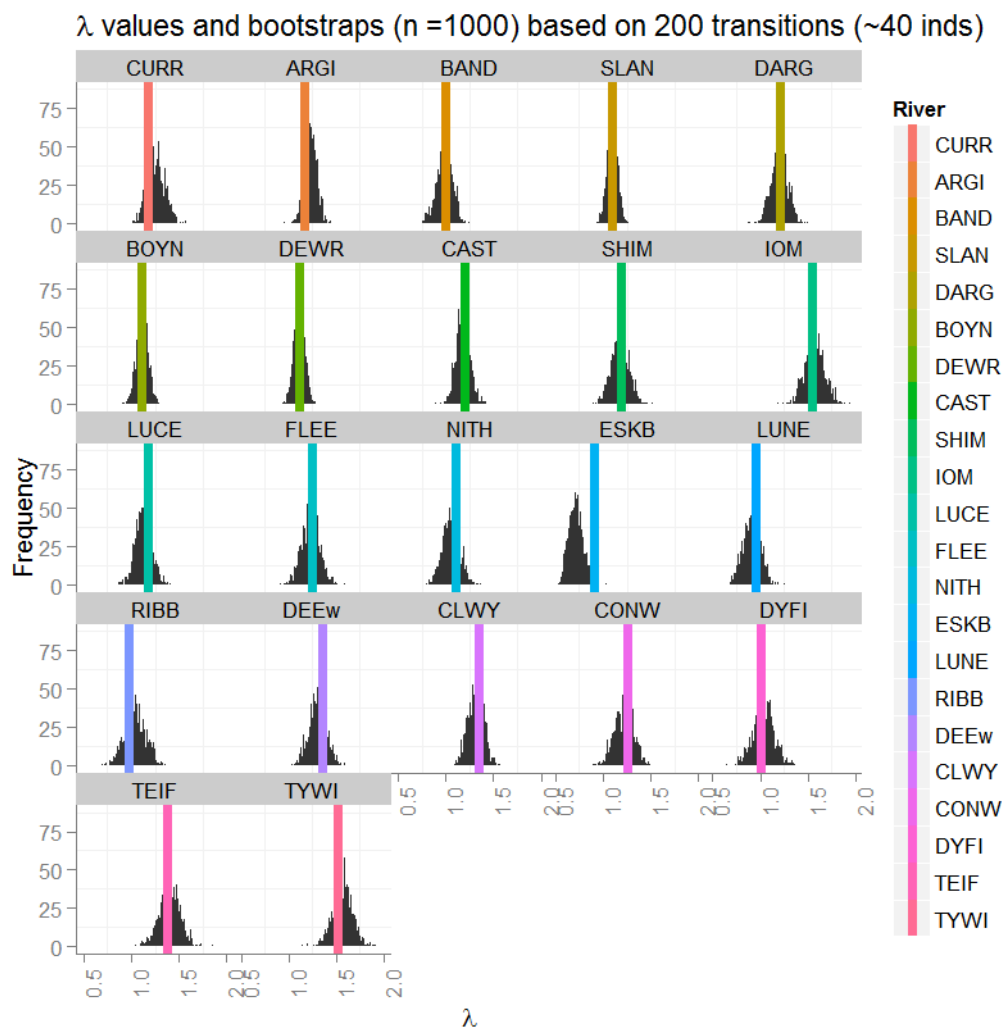


Figure 12: Population specific λ values and bootstraps (n=1000) based on 200 transitions (~40 inds)

3.3.2. Generation time:

Generation time varied from 2.19 years for sea trout from the BOYN, which showed the highest elasticity of λ to whitling (0.459), to 3.23 years for those from the CURR (Table 8), characterised by high frequency of repeat spawners and highest elasticity of λ to repeat spawners (0.259). The variance in generation time highlights the time required by the population to grow by a factor of R_0 ($R_{0\text{BOYN}} = 1.27$; $R_{0\text{CURR}} = 1.71$). It can also be understood as the average age of the parents of a cohort.

3.3.3. Stable stage distribution:

Stable stage distributions are the constant proportions of each stage in a population at equilibrium. Stable stage distributions for sea trout populations from all rivers were strongly dominated by the FW stage, which always composed over half of the stable stage population (Table 9; Figure 13). SM1 were the next most common stage in all Irish rivers (except the CURR), the IOM, and the LUCE, FLEE, DEEW, CLWY and CONW in Great Britain. Conversely SW was the second most common stage in the NITH, ESKB, LUNE, RIBB, DYFI, TEIF, and TYWI. The stable stage distribution allows the identification of which rivers are more likely to be dominated by SW, whitling, or repeat spawners.

Table 9: River-specific stable stage distributions of 22 sea trout populations around the Celtic and Irish Seas.

River	FW	SW	IM	SM1	SM2	SM3	SM4	SM5	SM6	SM7	SM8	SM9	SM10
1 CURR	0.556	0.004	0.030	0.026	0.004	0.001	0.001	0.000	0.000	0.000	0.000		
2 ARGJ	0.539	0.001	0.024	0.045	0.008	0.001	0.000						
3 BAND	0.485	0.015	0.035	0.037	0.003								
4 SLAN	0.529	0.003	0.006	0.059	0.005								
5 DARG	0.564	0.008	0.015	0.032	0.008	0.000							
6 BOYN	0.533	0.003	0.011	0.056	0.000								
7 DEWR	0.531	0.004	0.005	0.061	0.001	0.000							
8 CAST	0.551	0.003	0.019	0.048	0.002	0.001							
9 SHIM	0.549	0.006	0.008	0.054	0.002	0.000	0.000						
10 IOM	0.615	0.014	0.007	0.039	0.006	0.002	0.001	0.000					
11 LUCE	0.543	0.025	0.014	0.030	0.004	0.001	0.000	0.000	0.000				
12 FLEE	0.557	0.021	0.004	0.045	0.004	0.001	0.000	0.000					
13 NITH	0.525	0.037	0.016	0.020	0.005	0.001	0.000						
14 ESKB	0.469	0.055	0.010	0.017	0.003	0.001	0.000						
15 LUNE	0.480	0.048	0.019	0.013	0.005	0.001	0.000	0.000	0.000				
16 RIBB	0.484	0.039	0.026	0.016	0.004	0.001							
17 DEEW	0.580	0.013	0.011	0.044	0.004	0.000							
18 CLWY	0.581	0.008	0.011	0.046	0.003								
19 CONW	0.560	0.027	0.011	0.033	0.004	0.000	0.000						
20 DYFI	0.496	0.051	0.014	0.013	0.002	0.001	0.000	0.000					
21 TEIF	0.586	0.025	0.014	0.026	0.005	0.001	0.000	0.000	0.000	0.000			
22 TYWI	0.611	0.033	0.006	0.022	0.006	0.002	0.001	0.000	0.000	0.000	0.000		



Figure 13: Stable stage distribution of sea trout populations from 22 rivers around the Irish and Celtic Seas

3.3.4. Stage specific reproductive value:

The variance in somatic growth rates among sea trout from different rivers was translated into variance in individual egg production at stage (Figure 14). For example, the egg production of sea trout at SM2 in the river TYWI (n=3409 eggs) is three times that of SM2 sea trout from the river BAND (n=1105 eggs) (Table 10). The maximum number of eggs is achieved at the SM8 stage for trout in the TYWI (N=8567 eggs)(Table 10). The stage specific reproductive values, which indicates the remaining potential life-time reproductive contribution of an individual in a particular class, also increases initially with older stages, however, as stage specific survival reduces and individuals in the oldest stages become rarer, the stage specific reproductive value for the later stages diminishes (Figure 14).

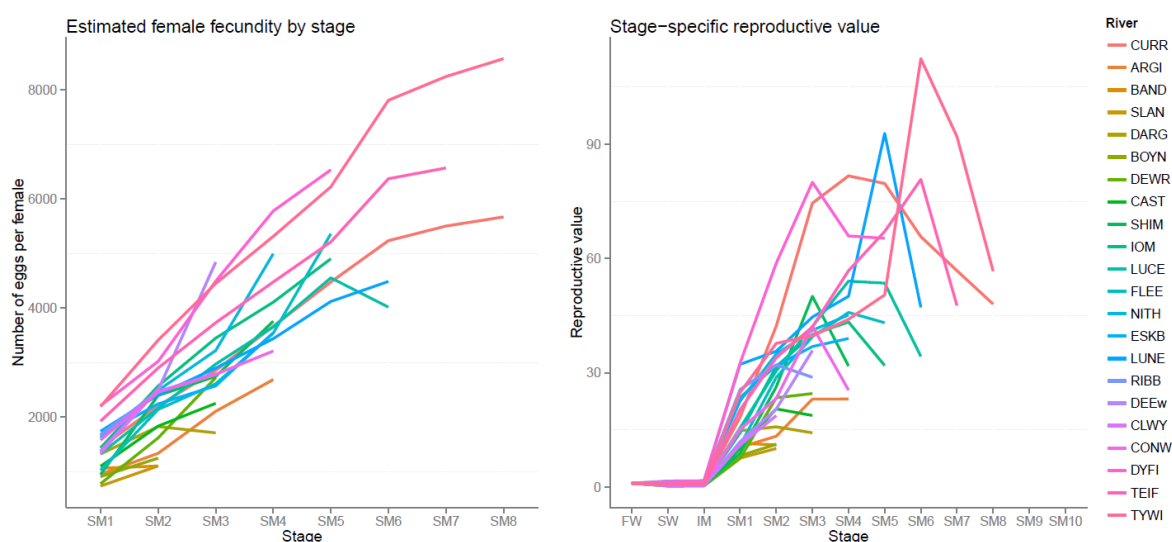


Figure 14: Number of eggs per female and stage specific reproductive value by river

Table 10: Reconstructed average number of eggs per female by stage and river

River	FW	SW	IM	SM1	SM2	SM3	SM4	SM5	SM6	SM7	SM8
1 CURR				1442.316	2207.186	2856.136	3664.250	4475.500	5233.000	5500.750	5668.000
2 ARGJ				953.860	1337.047	2106.000	2688.000				
3 BAND				1063.568	1105.000						
4 SLAN				737.491	1105.900						
5 DARG				1324.545	1827.211	1712.000					
6 BOYN				910.240	1248.000						
7 DEWR				780.046	1619.200	2723.000					
8 CAST				1099.963	1835.667	2253.000					
9 SHIM				949.051	2397.429	2746.000	3757.000				
10 IOM				1436.203	2570.286	3447.625	4105.600	4901.500			
11 LUCE				1326.500	2164.758	2971.182	3652.750	4552.500	4015.000		
12 FLEE				1024.653	2140.545	2610.750	3539.000	5359.000			
13 NITH				1623.583	2489.451	3220.706	4994.200				
14 ESKB				1662.881	2242.304	2572.700	3545.500				
15 LUNE				1741.258	2407.703	2898.308	3437.143	4119.000	4486.000		
16 RIBB				1678.958	2470.167	2794.250					
17 DEEW				1378.641	2494.077	4840.000					
18 CLWY				1343.766	2511.400						
19 CONW				1580.859	2462.556	2784.000	3211.000				
20 DYFI				2210.572	3021.024	4490.067	5776.875	6531.000			
21 TEIF				1927.696	2900.115	3729.273	4476.250	5210.000	6368.000	6565.000	
22 TYWI				2194.466	3409.082	4448.812	5311.833	6219.875	7805.000	8240.000	8567.000

Although juveniles may not reproduce while they are juveniles, they have the potential to grow to the spawning stages and reproduce, and thus every stage has a reproductive value (Figure 14;

Table 11). For the BAND the maximum stage specific reproductive value was at SM1. For the SLAN, DARG, BOYN, CAST, RIBB, and CLWY the maximum stage specific reproductive value was reached at SM2 despite the occurrence of SM3 in some of these rivers. SM3 gave the maximum stage specific reproductive value for DEWR, SHIM, DEEW, CONW, and DYFI. Maximum stage specific reproductive value was reached at SM4 for the two rivers in south west of Ireland (CURR and ARG1) and rivers draining in the north east of the Irish Sea (IOM, LUCE, FLEE, NITH, and ESKB); at SM5 in the LUNE and at SM6 for the two rivers in south Wales (TEIF and TYWI). Late maximum stage specific reproductive value was not related with low reproductive value at early stages, as sea trout from rivers in south west of Ireland, north east of the Irish Sea or south Wales had comparatively high stage specific reproductive values at early stages (SM1 and SM2).

Table 11: Stage specific reproductive value, the mean number of offspring to be produced in its remaining lifetime, by river and the stage at maximal reproductive value (StageMax).

River	FW	SW	IM	SM1	SM2	SM3	SM4	SM5	SM6	SM7	SM8	StageMax
1 CURR	1.000	0.717	0.726	18.339	42.239	74.515	81.666	79.670	65.711	56.773	48.019	SM4
2 ARG1	1.000	0.448	0.427	10.429	13.336	23.066	23.104	0.000				SM4
3 BAND	1.000	0.574	0.545	11.439	11.095	0.000						SM1
4 SLAN	1.000	0.348	0.348	7.611	10.106	0.000						SM2
5 DARG	1.000	0.555	0.614	14.780	15.799	14.220	0.000					SM2
6 BOYN	1.000	0.251	0.341	8.225	11.209	0.000						SM2
7 DEWR	1.000	0.339	0.304	7.515	23.431	24.534	0.000					SM3
8 CAST	1.000	0.421	0.396	10.115	20.510	18.773	0.000					SM2
9 SHIM	1.000	0.275	0.314	8.902	26.310	50.057	31.758	0.000				SM3
10 IOM	1.000	0.431	0.463	14.223	31.606	40.038	43.306	31.888	0.000			SM4
11 LUCE	1.000	0.599	0.650	15.537	30.481	42.149	54.036	53.510	34.283	0.000		SM4
12 FLEE	1.000	0.383	0.439	10.923	28.759	39.436	45.818	43.116	0.000			SM4
13 NITH	1.000	0.889	0.987	22.574	34.910	41.135	45.161	0.000				SM4
14 ESKB	1.000	1.161	1.190	23.483	31.898	36.867	38.989	0.000				SM4
15 LUNE	1.000	1.560	1.639	32.195	35.635	44.622	50.058	92.830	47.144	0.000		SM5
16 RIBB	1.000	1.189	1.270	25.574	32.066	28.807	0.000					SM2
17 DEEW	1.000	0.420	0.440	11.883	20.489	35.806	0.000					SM3
18 CLWY	1.000	0.365	0.415	11.119	18.739	0.000						SM2
19 CONW	1.000	0.575	0.598	15.110	23.222	42.204	25.437	0.000				SM3
20 DYFI	1.000	1.387	1.599	32.542	58.746	79.996	65.890	65.272	0.000			SM3
21 TEIF	1.000	0.642	0.705	20.256	33.934	42.030	56.792	67.069	80.730	47.619	0.000	SM6
22 TYWI	1.000	0.729	0.820	24.812	37.722	39.693	44.018	50.424	112.421	91.954	56.652	SM6

3.3.5. Fundamental matrix:

The likelihoods that an individual from a particular stage will reach another are given in the fundamental matrix. Values along the diagonal must be at least 1, as any individual already in a stage

must at least exist for one iteration at that stage. The values read by columns indicate the likelihood and mean time spent by individuals from that stage in all other stages. For example, in the fundamental matrix of ESKB in Figure 15, an individual in fresh water stays on average in the fresh water stage for 1.176 iterations, such a value above

C) Fundamental matrix

Stage	FW	SW	IM	SM1	SM2	SM3	SM4	dead
FW	1.176	0	0	0	0	0	0	0
SW	0.124	1.001	0	0	0	0	0	0
IM	0.022	0.004	1.004	0	0	0	0	0
SM1	0.037	0.045	0.046	1	0	0	0	0
SM2	0.006	0.007	0.007	0.148	1	0	0	0
SM3	0.001	0.001	0.001	0.026	0.179	1	0	0
SM4	0	0	0	0.005	0.036	0.2	1	0
dead	1	1	1	1	1	1	1	1

Figure 15: Fundamental matrix of sea trout population of the river ESKB

C) Fundamental matrix

Stage	FW	SW	IM	SM1	SM2	SM3	SM4	SM5	SM6	SM7	SM8	dead
FW	1.214	0	0	0	0	0	0	0	0	0	0	0
SW	0.01	1.002	0	0	0	0	0	0	0	0	0	0
IM	0.077	0.002	1.003	0	0	0	0	0	0	0	0	0
SM1	0.067	0.046	0.047	1	0	0	0	0	0	0	0	0
SM2	0.011	0.008	0.008	0.171	1	0	0	0	0	0	0	0
SM3	0.004	0.003	0.003	0.064	0.373	1	0	0	0	0	0	0
SM4	0.003	0.002	0.002	0.046	0.271	0.727	1	0	0	0	0	0
SM5	0.002	0.002	0.002	0.035	0.203	0.545	0.75	1	0	0	0	0
SM6	0.002	0.001	0.001	0.026	0.153	0.409	0.562	0.75	1	0	0	0
SM7	0.001	0.001	0.001	0.012	0.068	0.182	0.25	0.333	0.444	1	0	0
SM8	0	0	0	0.003	0.017	0.045	0.062	0.083	0.111	0.25	1	0
dead	1	1	1	1	1	1	1	1	1	1	1	1

Figure 16: Fundamental matrix of sea trout population of the river CURR

1 reflects the likelihood that some individuals remain in the fresh water stage. Although most individuals alive have stayed in fresh water for two years, the fundamental value doesn't reach two iterations due to the mortality exerted in fresh water (0.7 per year). Other individuals in the FW stage grow into other stages: the same individual in FW will remain in the sea winter stage for an average of 0.124 iterations, in indeterminate mark stage for 0.022 iterations, and as first spawner 0.037 iterations, highlighting the low likelihood that an individual in the FW stage will reach the spawning stages. Once an individual has reached the first spawning stage (SM1), it is relatively likely that it will return for at least another season (SM2 0.148 iterations), but the likelihood of returning a third (SM3) or fourth (SM4) reduces (0.026 and 0.005 respectively). Conversely, for the river CURR (Figure 16) the likelihood of a whitling returning a second time is still low (0.171), but successive likelihoods for SM2 to SM3, SM3 to SM4, SM4 to SM5 increase (0.373, 0.727, 0.75 respectively) before decreasing for SM6 to SM7, and SM7 to SM8 (0.444, 0.250 respectively, Figure 16).

FW retention fundamental values were similar across all rivers (Figure 17). The likelihood of FW individuals returning as SM1 was, however, different among rivers: rivers along the east coast of Ireland (SLAN, BOYN, DEWR, CAST, and SHIM), had particularly high likelihoods of returning as SM1 (~0.14), while the opposite was true for ESKB, NITH, RIBB, and TYWI (~0.04), which were far more likely to go through a sea winter phase (*i.e.* to remain at sea as maidens: SW/IM) (Figure 17).

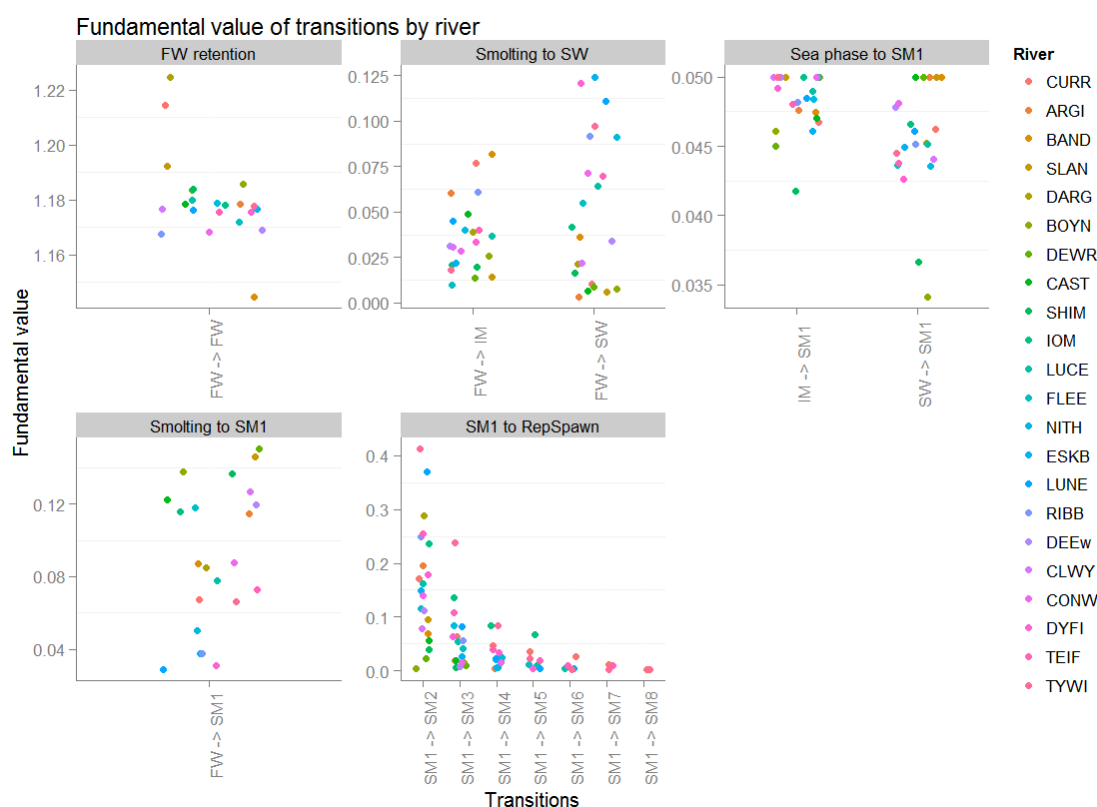


Figure 17: Comparison of fundamental value of transitions among rivers grouped by transition type (retention in freshwater, smolting to sea winter stage, freshwater to first reproduction, sea winter to first reproduction, and first reproduction to repeat spawner)

3.3.6. Sensitivity analysis:

The values of the sensitivity matrix (S_{ij}) for each transition (A_{ij}) can be interpreted as the increase in λ ($\Delta\lambda$) associated with an additive increase (ΔA_{ij}) for that transition:

$$\Delta\lambda = S_{ij} * \Delta A_{ij}$$

For example, if the survival of SM1 to SM2 on the river ESKB were to increase from 0.148 to 0.248 ($\Delta A_{ij} = 0.1$), the population growth rate would increase from $\lambda_{ESKB} = 0.909$ to $\lambda_{ESKB'} = 0.960$ ($\lambda' = \lambda + \Delta\lambda$; where $\Delta\lambda = 0.508 * 0.1$). Sensitivities can be calculated for all possible transition parameters, for example from FW to SM8. However, the utility of sensitivities for transitions other than non-zero transitions is questionable, so here we highlight only those transitions which are found in the population. Trout populations from all rivers were similar in that additive perturbations to the FW to SM1 transition had the largest impact on λ (Figure 18), while additive perturbations to fertilities have relatively little impact. Therefore, in general enhancing or blocking the productions of SM1 will have the greatest impact in terms of sea trout population control, while increases in individual fecundity have negligible impact. In other words, early post-smolt survival is likely more influential on population growth rate than individual marine somatic growth rate. The sensitivity of λ to the FW to SM1 transition was particularly high for some rivers, namely CURR, NITH, ESKB, LUNE, RIBB, DYFI, CONW, TEIF, and TYWI, indicating that the sea trout populations from these rivers would respond very positively to environmental management practices protecting the transition from FW to SM1. These rivers were also characterised by low fundamental values for the FW to SM1 transition, indicating the low likelihood of a FW to return as a SM1 without spending at least a winter at sea. The trout populations from four rivers, the DEWR, SHIM, LUCE, and FLEE, were characterised by relatively low sensitivities to the FW to SM1 transition (<5) while the SM1 to SM2 transition had relatively high sensitivities (>1). For these populations,

protection of whitling may not be enough to insure positive population growth rates, and they would benefit the most of protection of young repeat spawners, if increased population growth is desired.

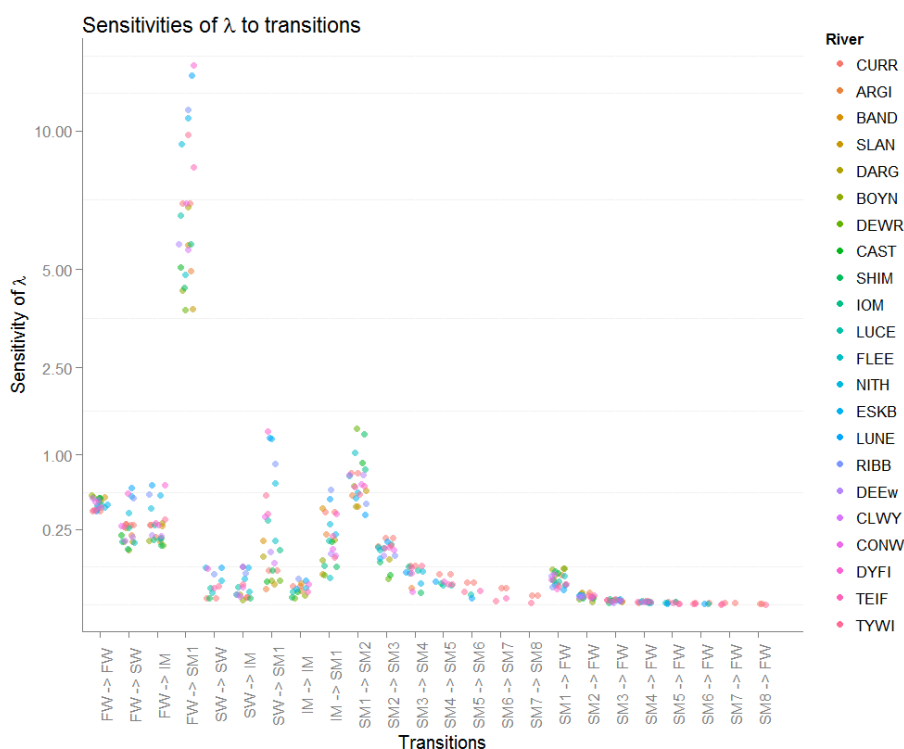


Figure 18: Sensitivities of λ to transitions by river

3.3.7. Elasticity analysis:

Complementary to the fundamental values and the sensitivity of λ to transition perturbations, the elasticity of λ to transition perturbations measures the *proportionality* of the change in λ to a change in a transition value. High elasticity of λ to a certain transition A_{ij} suggests high proportionality between $\Delta\lambda$ and ΔA_{ij} . The elasticities of a transition matrix always add up to one, so they represent the transition's relative importance to λ . Elasticities can be added by rows, columns, or groups of transitions, to estimate the relative importance of such groups. If examined by rows, elasticities highlight the importance of transitions entering a stage, while if examined by columns, elasticities reveal the importance of transitions leaving a stage. For example, FW are, by far, the most important source of SM1 (whitling life history pattern as opposed to .1+ and .2+ maidens), while the most important contribution of SM1 is its fecundity rather than the production of repeat spawners. For all rivers it can be observed that the elasticities of λ to transitions FW to FW, FW to SM1, and SM1 fecundity, contribute over 0.5 to λ , highlighting the importance of whittling for maintaining the all populations of sea trout (Table 12). These transitions (FW \rightarrow FW, FW \rightarrow SM1, and SM1 \rightarrow FW; i.e. a 2.0+ whitling returning to spawn for the first time) compose the shortest life history strategy an individual can take to contribute to the next generation, which is defined here as the *minimum life history* (minLH). The dependency of a population on the minimum life history strategy was calculated by adding the elasticity of λ to the FW to FW, FW to SM1, and SM1 to FW transitions (*E.minLH*). Such dependency varied widely among sea trout populations from different rivers: in some rivers, such as the BAND, SLAN, BOYN, DEWR, CAST, SHIM, and CLWY, the combined elasticities of λ to the minimum life history (*E.minLH*) added up to close to 0.9, showcasing the dependence of these populations on a very short life cycle with little diversity of life strategies. In the BOYN, this value added up to 0.99, indicating no role of alternative strategies in the dynamics of the population. The sum of the elasticities of all other transitions not included in the minLH, can be interpreted as the dependency on alternative life histories (*E.altLH*), such as those with sea winters (SW and IM) and repeat spawners (SM2, SM3...). The elasticities of alternative life strategies summed to around 0.4 in sea trout populations in the CURR, NITH, LUNE, RIBB, DYFI, and TYWI highlighting the importance to population growth rate of the diversity of life strategies found in these rivers. Alternative life strategies can play an important role in the stability of a population, as populations highly dependent on the minimum life history could be strongly affected by stochastic events preventing spawning one year.

Table 12: Elasticities of λ to the minimum life history strategy (E.MinLH) and to alternative life history strategies (E.AltLH) by river

River	E.MinLH	E.AltLH
1 CURR	0.595	0.405
2 ARGJ	0.790	0.210
3 BAND	0.884	0.116
4 SLAN	0.895	0.105
5 DARG	0.766	0.234
6 BOYN	0.986	0.014
7 DEWR	0.926	0.074
8 CAST	0.892	0.108
9 SHIM	0.891	0.109
10 IOM	0.641	0.359
11 LUCE	0.691	0.309
12 FLEE	0.730	0.270
13 NITH	0.614	0.386
14 ESKB	0.669	0.331
15 LUNE	0.488	0.512
16 RIBB	0.601	0.399
17 DEEw	0.853	0.147
18 CLWY	0.899	0.101
19 CONW	0.802	0.198
20 DYFI	0.554	0.446
21 TEIF	0.660	0.340
22 TYWI	0.586	0.414

Elasticities of λ to fresh water, whitling, sea winters, first time spawners, and repeat spawner phases were calculated (Table 8). Low estimated population λ was associated with higher

elasticities of λ to the sea winter phase (Figure 19), indicating that populations where sea winters are a common life history stage (such as ESKB, LUNE, RIBB, and DYFI) had slower population growth rates and that the increased fecundity gained during sea winters does not compensate for the delay in first spawning.

Summed elasticities of λ to adult strategy and λ

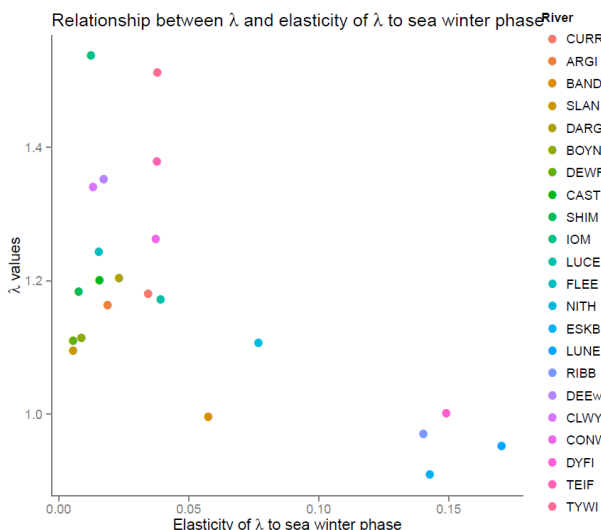
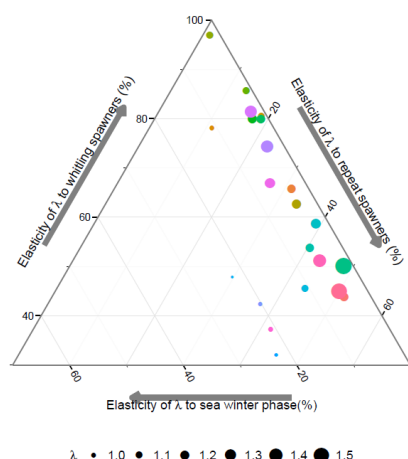


Figure 19: Summed elasticities of λ to different phases of the adult life history strategy and relationship between λ and elasticity of λ to sea winter phase

Longer generation times were associated with high elasticities of λ to repeat spawners (Figure 20), showing the impact of repeat spawners on the time needed to increase the population size by a factor of R_0 .

Summed elasticities of λ to adult strategy and generation time

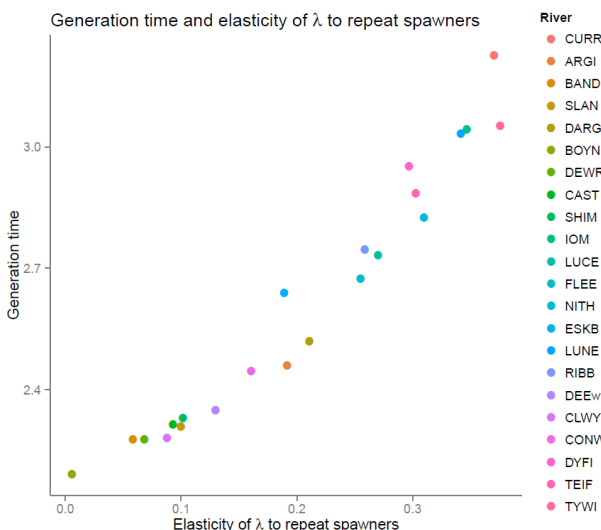
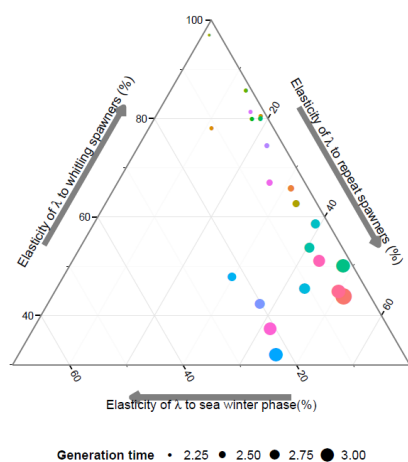


Figure 20: Summed elasticities of λ to different phases of adult life history strategy and relationship between λ and elasticity of λ to repeat spawners

Higher damping ratios were associated with high elasticity of λ to sea winters (Figure 21), illustrating how the distribution of reproductive effort across many stages, such as the inclusion of sea winters, improves the population capacity of converge to stable stage distribution.

Summed elasticities of λ to adult strategy and damping ratio

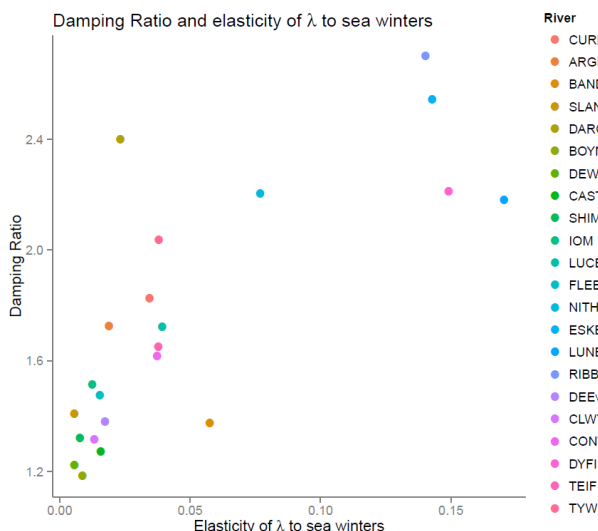
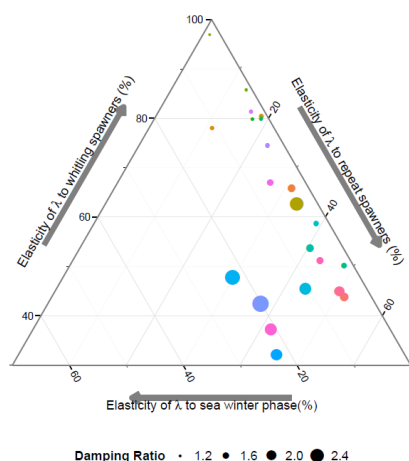


Figure 21: Summed elasticities of λ to different phases of adult life history strategy and relationship between λ and elasticity of λ to sea winters

3.3.8. River specific sea trout population dynamics analysis summary plates:

The outcomes of the population dynamics analysis of the sea trout population of each of 22 rivers have been summarized into plates. The abbreviated name of the river and the number of individuals (n) for which there was age, life history and length and weight is indicated.

A) Relationship between total length (mm) and total age (years) for all individuals collected for the river. The number of sea winters recorded for each individual is indicated by the shape of the point: circles of whiting returns, triangles for 1 sea winter, squares for 2 sea winters, and so on; The colour of the last stage before capture recorded for each individual is indicated by the colour of the point: cyan for fresh water (FW), blue for sea winter (SW), pink for indeterminate marks (IM), and a gradient from yellow to red for increasing number of spawning marks (SM); The von Bertalanffy model best describing the data is written in the form of an equation, $L_t = L_\infty [1 - e^{-K(t-t_0)}]$, where L_t is the estimated length, L_∞ is the asymptotic length at which growth is zero, K is Brody's growth coefficient (the rate at which the asymptote is approached), and t_0 is a scaling factor of no biological significance. The trajectory of the model from the river under study is depicted as a line on the plot in the river specific colour (River Legend). The trajectories of the other 21 rivers analysed are depicted as thin grey lines for comparison among all studied rivers.

B) The transition and fecundity values estimated from the recreated life histories are indicated in the transition matrix, which are the probability of an individual in one stage (columns) moving to another stage (rows).

C) The fundamental matrix indicates the likelihood of an individual from a particular stage (columns) reaching another stage (rows) during their lifetime. The values have been colour coded for ease of interpretation from low (light blue) to high (dark blue).

D) The sensitivities of λ to additive perturbations of the transition matrix are indicated in the Sensitivities matrix. Sensitivities can be calculated for all transitions in a matrix, however, some transitions are not found in populations (e.g. FW to SM4) and do not make sense in most cases,

these values have been indicated in grey. Transitions found in the population are in black font, and the values have been colour coded for ease of interpretation from low (light blue) to high (dark blue).

E) The elasticities of λ to proportional perturbations of the transition matrix are indicated in the sensitivity matrix. The values have been colour coded for ease of interpretation from low (light blue) to high (dark blue).

F) Stable stage distribution. The relative proportions of each stage (colour coded) on the stable stage distribution of a population at equilibrium.

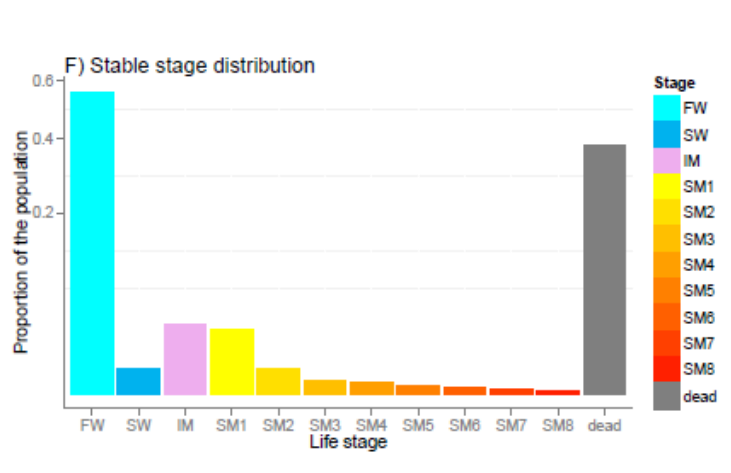
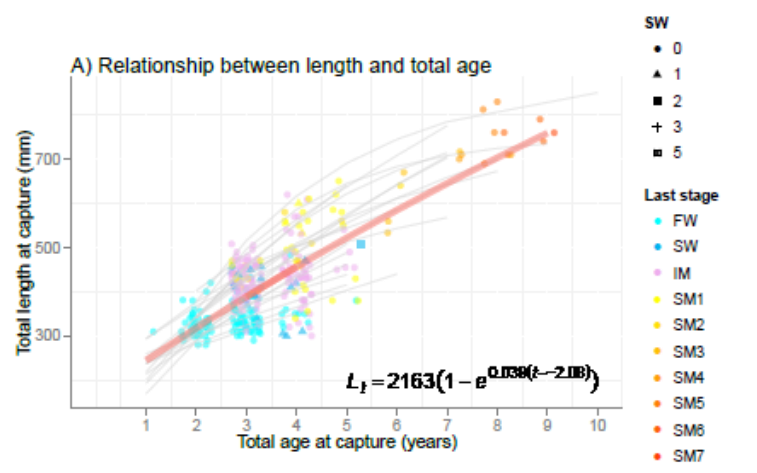
G) Evolution of stage-specific reproductive value (mean number of offspring to be produced in its remaining lifetime) with stage for river under study (thick line in river specific colour). The evolution of stage-specific reproductive values of 21 other rivers is also plotted for comparison with other rivers.

H) The river specific sea trout population growth rate (λ) is indicated with a thick line in the river specific colour (River colour legend). The λ values of 1,000 bootstraps of the data and of the same size as the data (i.e. 345 individuals in the CURR) are plotted as a black histogram. 95%CI of estimated λ values are indicated as black dotted lines. The λ values of the other 21 rivers analysed are also plotted for comparison of the river under study with other rivers.

I) Ternary plot of the summed elasticities of λ of each of the phases in differing life history strategies (sea winters, whitling, and repeat spawners). The river under study is depicted by a larger circle of the river-specific colour (River colour legend). The other 21 rivers have also been plotted for comparison among rivers. The positioning of each dot is determined by the percentage of summed elasticities of λ of each phase and can be understood as the relative contribution of sea winter phase, whitling, and repeat spawners to population growth rate. The plots have been focused on the range of values encountered in this study ($E.whitling=30-100\%$, $E.winter=0-80\%$, $E.RepSpawn=0-80\%$).

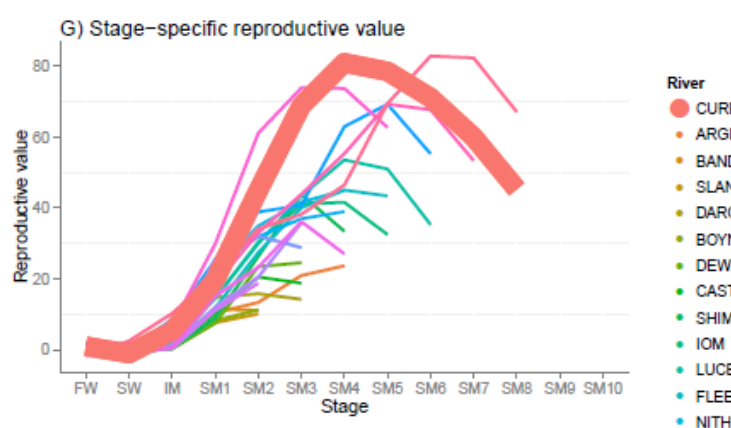
River Currane:

Summary statistics of population dynamics analysis of sea trout from the River CURR (n=345)



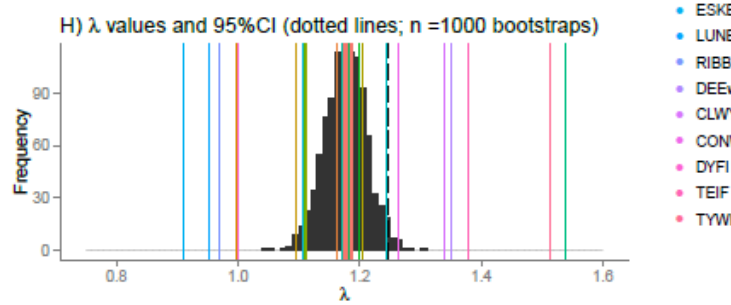
B) Transition matrix

Stage	FW	SW	IM	SM1	SM2	SM3	SM4	SM5	SM6	SM7	SM8	dead
FW	0.178	0	0	14.423	22.072	28.561	36.842	44.755	52.33	55.008	56.88	0
SW	0.009	0.002	0	0	0	0	0	0	0	0	0	0
IM	0.063	0.002	0.003	0	0	0	0	0	0	0	0	0
SM1	0.052	0.046	0.047	0	0	0	0	0	0	0	0	0
SM2	0	0	0	0.171	0	0	0	0	0	0	0	0
SM3	0	0	0	0	0.373	0	0	0	0	0	0	0
SM4	0	0	0	0	0	0.727	0	0	0	0	0	0
SM5	0	0	0	0	0	0	0.75	0	0	0	0	0
SM6	0	0	0	0	0	0	0	0.75	0	0	0	0
SM7	0	0	0	0	0	0	0	0	0.444	0	0	0
SM8	0	0	0	0	0	0	0	0	0	0.25	0	0
dead	0.7	0.95	0.95	0.829	0.627	0.273	0.25	0.25	0.556	0.75	1	0



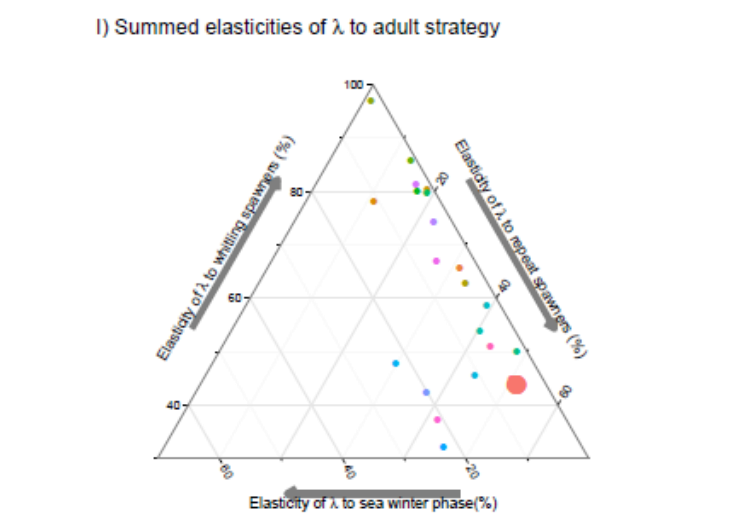
C) Fundamental matrix

Stage	FW	SW	IM	SM1	SM2	SM3	SM4	SM5	SM6	SM7	SM8	dead
FW	1.214	0	0	0	0	0	0	0	0	0	0	0
SW	0.01	1.002	0	0	0	0	0	0	0	0	0	0
IM	0.077	0.002	1.003	0	0	0	0	0	0	0	0	0
SM1	0.067	0.046	0.047	1	0	0	0	0	0	0	0	0
SM2	0.011	0.008	0.008	0.171	1	0	0	0	0	0	0	0
SM3	0.004	0.003	0.003	0.064	0.373	1	0	0	0	0	0	0
SM4	0.003	0.002	0.002	0.046	0.271	0.727	1	0	0	0	0	0
SM5	0.002	0.002	0.002	0.035	0.203	0.545	0.75	1	0	0	0	0
SM6	0.002	0.001	0.001	0.026	0.163	0.409	0.562	0.75	1	0	0	0
SM7	0.001	0.001	0.001	0.012	0.068	0.182	0.25	0.333	0.444	1	0	0
SM8	0	0	0	0.003	0.017	0.045	0.062	0.083	0.111	0.25	1	0
dead	1	1	1	1	1	1	1	1	1	1	1	1



D) Sensitivities of λ to perturbations of the transition matrix

Stage	FW	SW	IM	SM1	SM2	SM3	SM4	SM5	SM6	SM7	SM8	dead
FW	0.391	0.003	0.021	0.018	0.003	0.001	0.001	0	0	0	0	0.266
SW	0.28	0.002	0.015	0.013	0.002	0.001	0	0	0	0	0	0.191
IM	0.284	0.002	0.015	0.013	0.002	0.001	0	0	0	0	0	0.193
SM1	7.171	0.052	0.384	0.333	0.048	0.015	0.009	0.006	0.004	0.001	0	4.872
SM2	16.515	0.12	0.884	0.766	0.111	0.035	0.022	0.014	0.009	0.003	0.001	11.222
SM3	29.135	0.212	1.56	1.351	0.196	0.062	0.038	0.024	0.015	0.006	0.001	19.798
SM4	31.931	0.233	1.71	1.481	0.215	0.088	0.042	0.027	0.017	0.006	0.001	21.697
SM5	31.151	0.227	1.688	1.445	0.209	0.066	0.041	0.026	0.016	0.006	0.001	21.167
SM6	25.893	0.187	1.378	1.192	0.173	0.055	0.034	0.021	0.014	0.005	0.001	17.458
SM7	22.198	0.162	1.189	1.029	0.149	0.047	0.029	0.018	0.012	0.004	0.001	15.084
SM8	18.778	0.137	1.005	0.871	0.126	0.04	0.025	0.016	0.01	0.004	0.001	12.758
dead	0	0	0	0	0	0	0	0	0	0	0	0

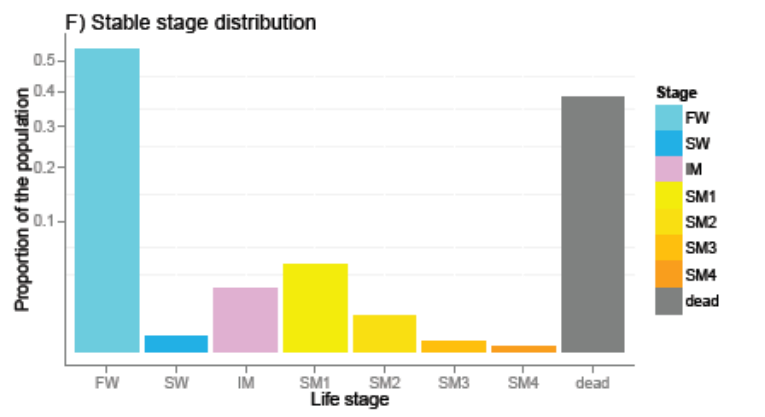
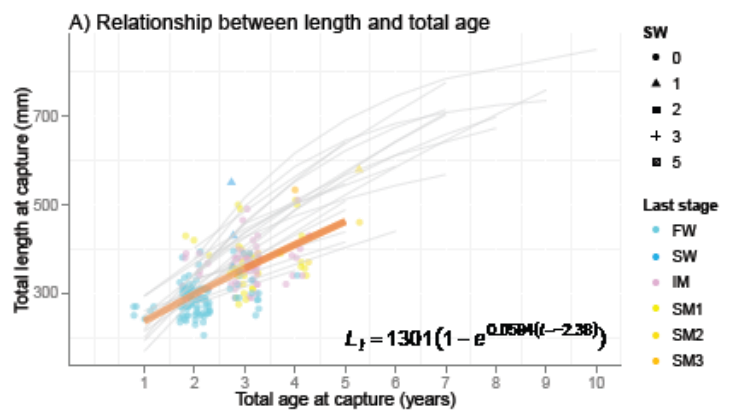


E) Elasticities of λ to perturbations of the transition matrix

Stage	FW	SW	IM	SM1	SM2	SM3	SM4	SM5	SM6	SM7	SM8	dead
FW	0.058	0	0	0.222	0.049	0.02	0.016	0.012	0.009	0.004	0.001	0
SW	0.002	0	0	0	0	0	0	0	0	0	0	0
IM	0.015	0	0	0	0	0	0	0	0	0	0	0
SM1	0.315	0.002	0.015	0	0	0	0	0	0	0	0	0
SM2	0	0	0	0.111	0	0	0	0	0	0	0	0
SM3	0	0	0	0	0.082	0	0	0	0	0	0	0
SM4	0	0	0	0	0	0.042	0	0	0	0	0	0
SM5	0	0	0	0	0	0	0.026	0	0	0	0	0
SM6	0	0	0	0	0	0	0	0.014	0	0	0	0
SM7	0	0	0	0	0	0	0	0	0.004	0	0	0
SM8	0	0	0	0	0	0	0	0	0	0.001	0	0
dead	0	0	0	0	0	0	0	0	0	0	0	0

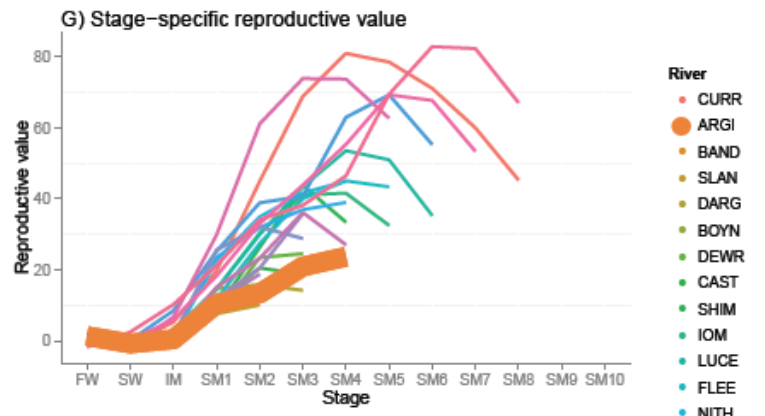
River Argideen:

Summary statistics of population dynamics analysis of sea trout from the River ARG (n=221)



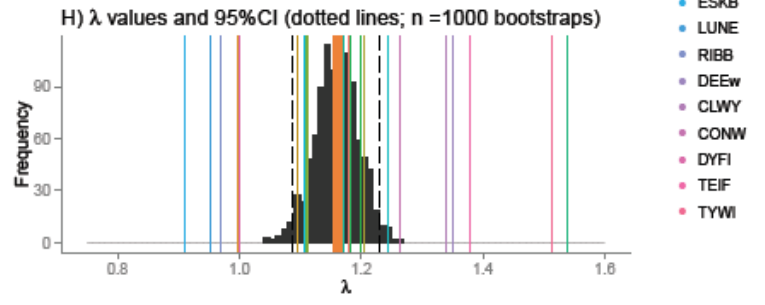
B) Transition matrix

Stage	FW	SW	IM	SM1	SM2	SM3	SM4	dead
FW	0.151	0	0	9.539	13.37	21.06	28.88	0
SW	0.003	0	0	0	0	0	0	0
IM	0.051	0	0.003	0	0	0	0	0
SM1	0.095	0.05	0.048	0	0	0	0	0
SM2	0	0	0	0.195	0	0	0	0
SM3	0	0	0	0	0.093	0	0	0
SM4	0	0	0	0	0	0.25	0	0
dead	0.7	0.95	0.95	0.805	0.907	0.75	1	0



C) Fundamental matrix

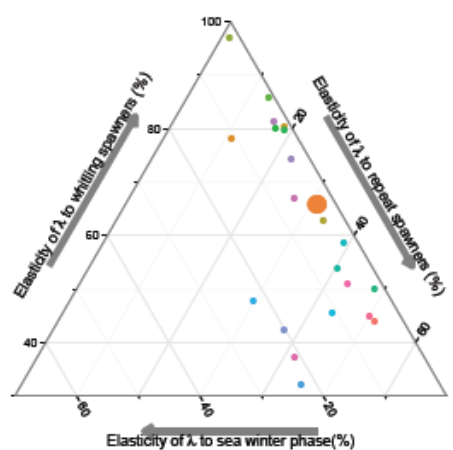
Stage	FW	SW	IM	SM1	SM2	SM3	SM4	dead
FW	1.178	0	0	0	0	0	0	0
SW	0.003	1	0	0	0	0	0	0
IM	0.06	0	1.003	0	0	0	0	0
SM1	0.115	0.05	0.048	1	0	0	0	0
SM2	0.022	0.01	0.009	0.195	1	0	0	0
SM3	0.002	0.001	0.001	0.018	0.093	1	0	0
SM4	0.001	0	0	0.005	0.023	0.25	1	0
dead	1	1	1	1	1	1	1	1



D) Sensitivities of λ to perturbations of the transition matrix

Stage	FW	SW	IM	SM1	SM2	SM3	SM4	dead
FW	0.475	0.001	0.021	0.04	0.007	0.001	0	0.337
SW	0.213	0	0.009	0.018	0.003	0	0	0.151
IM	0.203	0	0.009	0.017	0.003	0	0	0.144
SM1	4.949	0.011	0.218	0.413	0.089	0.006	0.001	3.509
SM2	6.329	0.015	0.279	0.528	0.088	0.007	0.002	4.488
SM3	10.947	0.025	0.482	0.913	0.153	0.012	0.003	7.762
SM4	10.985	0.025	0.483	0.915	0.153	0.012	0.003	7.775
dead	0	0	0	0	0	0	0	0

I) Summed elasticities of λ to adult strategy

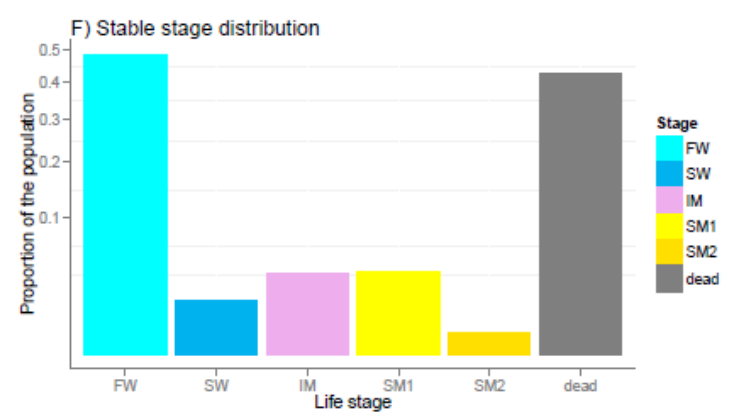
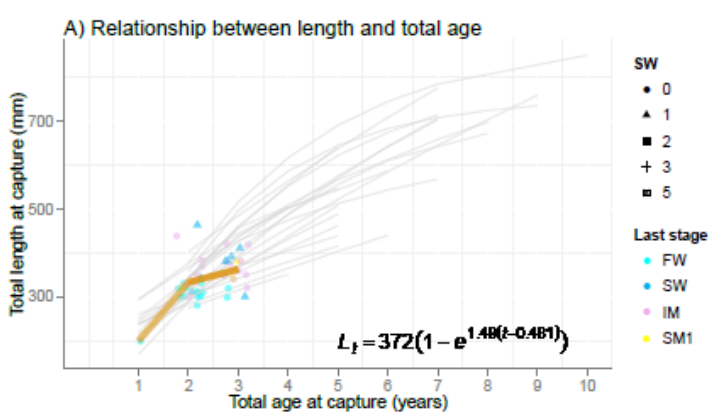


E) Elasticities of λ to perturbations of the transition matrix

Stage	FW	SW	IM	SM1	SM2	SM3	SM4	dead
FW	0.082	0	0	0.325	0.076	0.01	0.003	0
SW	0	0	0	0	0	0	0	0
IM	0.009	0	0	0	0	0	0	0
SM1	0.403	0	0.009	0	0	0	0	0
SM2	0	0	0	0.088	0	0	0	0
SM3	0	0	0	0	0.012	0	0	0
SM4	0	0	0	0	0	0.003	0	0
dead	0	0	0	0	0	0	0	0

River Bandon:

Summary statistics of population dynamics analysis of sea trout from the River BAND (n=44)



B) Transition matrix

Stage	FW	SW	IM	SM1	SM2	dead
FW	0.126	0	0	10.636	11.05	0
SW	0.032	0	0	0	0	0
IM	0.071	0	0.003	0	0	0
SM1	0.071	0.05	0.047	0	0	0
SM2	0	0	0	0.068	0	0
dead	0.7	0.95	0.95	0.932	1	0

C) Fundamental matrix

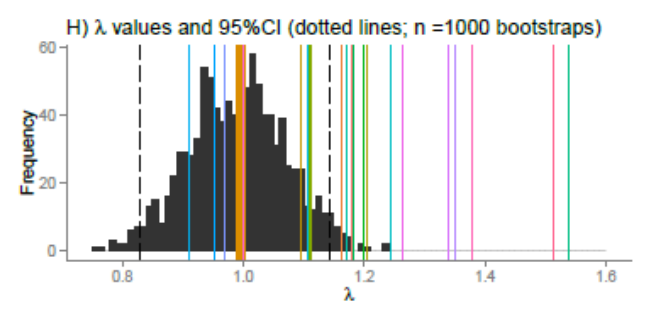
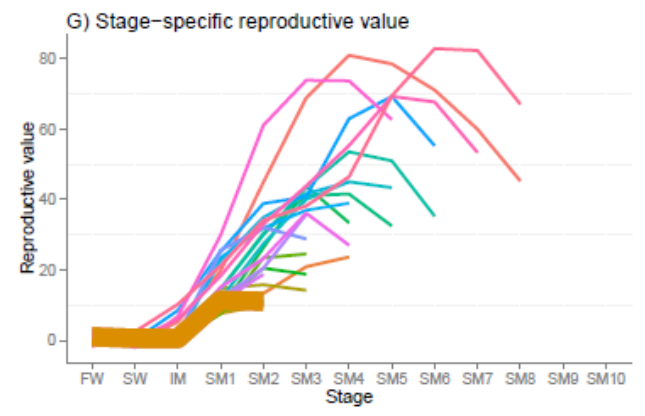
Stage	FW	SW	IM	SM1	SM2	dead
FW	1.145	0	0	0	0	0
SW	0.036	1	0	0	0	0
IM	0.082	0	1.003	0	0	0
SM1	0.087	0.05	0.047	1	0	0
SM2	0.006	0.003	0.003	0.068	1	0
dead	1	1	1	1	1	1

D) Sensitivities of λ to perturbations of the transition matrix

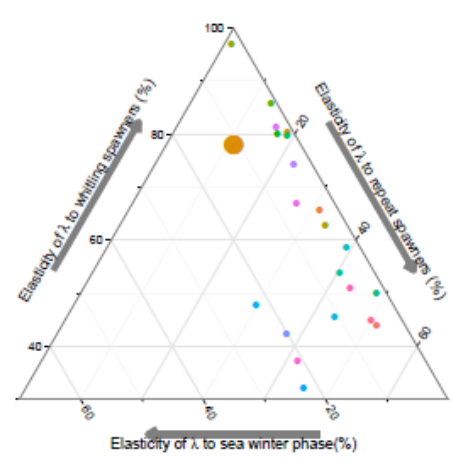
Stage	FW	SW	IM	SM1	SM2	dead
FW	0.503	0.016	0.036	0.038	0.003	0.442
SW	0.289	0.009	0.021	0.022	0.002	0.254
IM	0.274	0.009	0.02	0.021	0.001	0.241
SM1	5.753	0.182	0.411	0.439	0.03	5.051
SM2	5.58	0.177	0.399	0.426	0.029	4.899
dead	0	0	0	0	0	0

E) Elasticities of λ to perturbations of the transition matrix

Stage	FW	SW	IM	SM1	SM2	dead
FW	0.064	0	0	0.41	0.029	0
SW	0.009	0	0	0	0	0
IM	0.02	0	0	0	0	0
SM1	0.41	0.009	0.02	0	0	0
SM2	0	0	0	0.029	0	0
dead	0	0	0	0	0	0

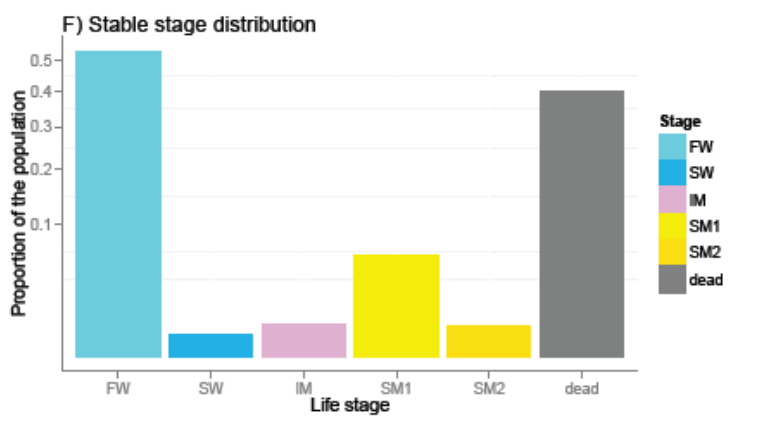
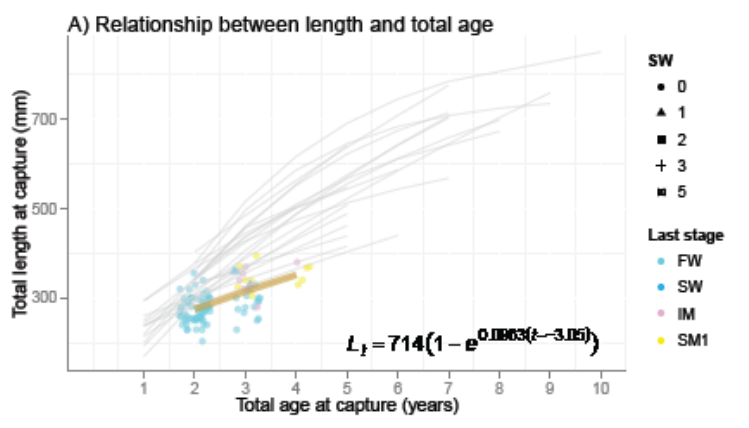


I) Summed elasticities of λ to adult strategy



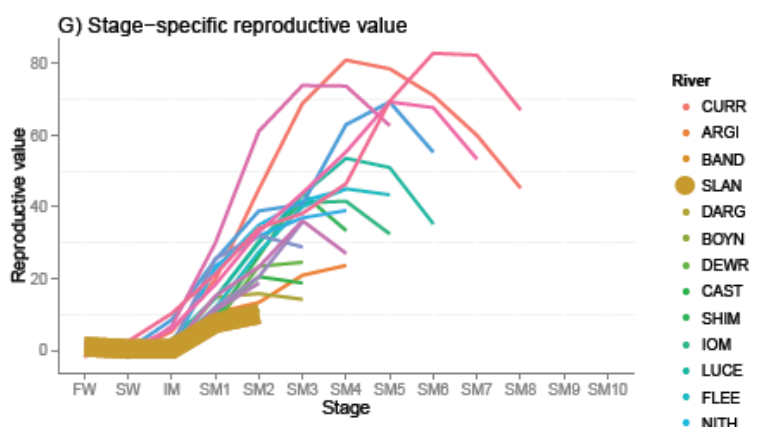
River Slaney:

Summary statistics of population dynamics analysis of sea trout from the River SLAN (n=106)



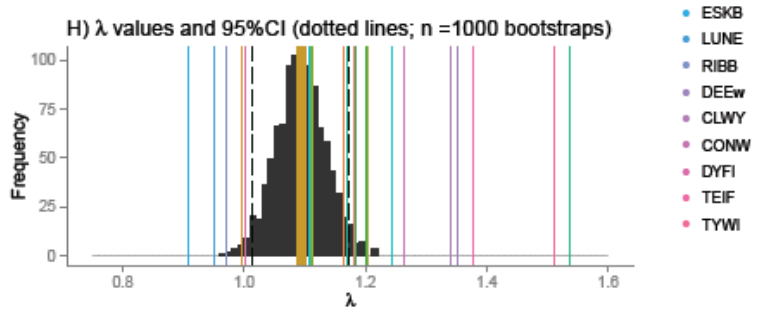
B) Transition matrix

Stage	FW	SW	IM	SM1	SM2	dead
FW	0.161	0	0	7.375	11.059	0
SW	0.005	0	0	0	0	0
IM	0.012	0	0	0	0	0
SM1	0.122	0.05	0.05	0	0	0
SM2	0	0	0	0.094	0	0
dead	0.7	0.95	0.95	0.906	1	0



C) Fundamental matrix

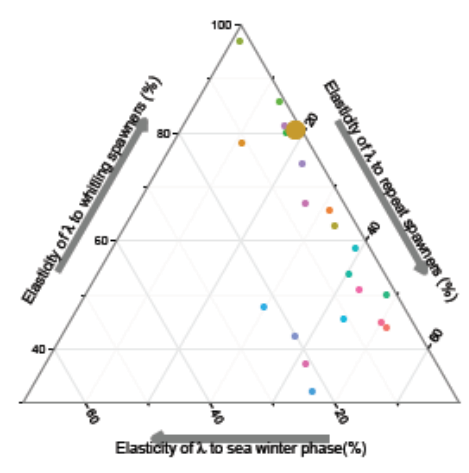
Stage	FW	SW	IM	SM1	SM2	dead
FW	1.192	0	0	0	0	0
SW	0.006	1	0	0	0	0
IM	0.014	0	1	0	0	0
SM1	0.146	0.05	0.05	1	0	0
SM2	0.014	0.005	0.005	0.094	1	0
dead	1	1	1	1	1	1



D) Sensitivities of λ to perturbations of the transition matrix

Stage	FW	SW	IM	SM1	SM2	dead
FW	0.511	0.002	0.006	0.057	0.005	0.386
SW	0.178	0.001	0.002	0.02	0.002	0.134
IM	0.178	0.001	0.002	0.02	0.002	0.134
SM1	3.891	0.019	0.042	0.436	0.038	2.937
SM2	5.167	0.025	0.056	0.579	0.05	3.9
dead	0	0	0	0	0	0

I) Summed elasticities of λ to adult strategy

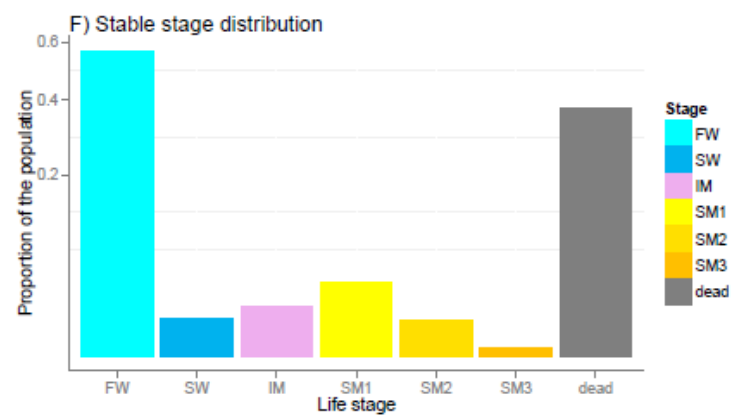
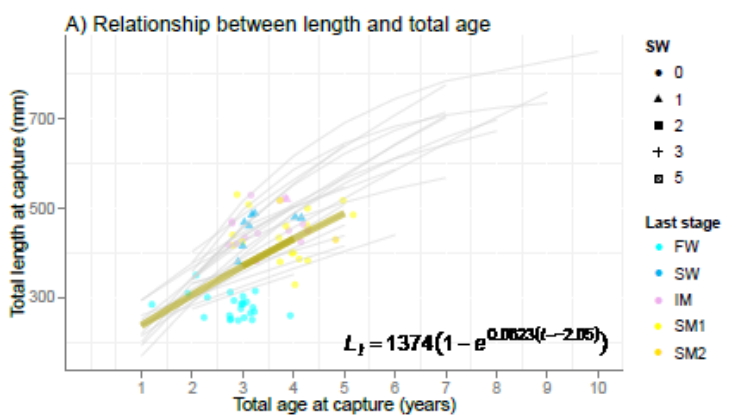


E) Elasticities of λ to perturbations of the transition matrix

Stage	FW	SW	IM	SM1	SM2	dead
FW	0.075	0	0	0.386	0.05	0
SW	0.001	0	0	0	0	0
IM	0.002	0	0	0	0	0
SM1	0.433	0.001	0.002	0	0	0
SM2	0	0	0	0.05	0	0
dead	0	0	0	0	0	0

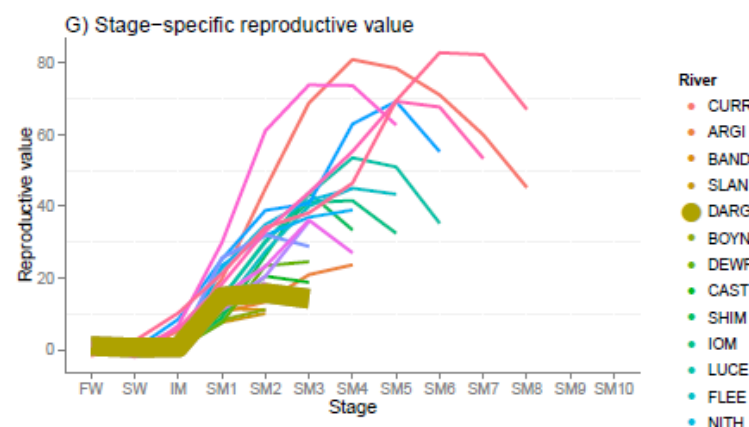
River Dargle:

Summary statistics of population dynamics analysis of sea trout from the River DARG (n=66)



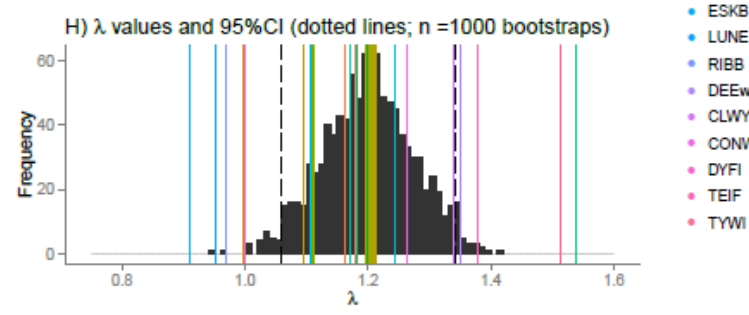
B) Transition matrix

Stage	FW	SW	IM	SM1	SM2	SM3	dead
FW	0.184	0	0	13.245	18.272	17.12	0
SW	0.018	0	0	0	0	0	0
IM	0.032	0.005	0	0	0	0	0
SM1	0.067	0.045	0.05	0	0	0	0
SM2	0	0	0	0.288	0	0	0
SM3	0	0	0	0	0.053	0	0
dead	0.7	0.95	0.95	0.712	0.947	1	0



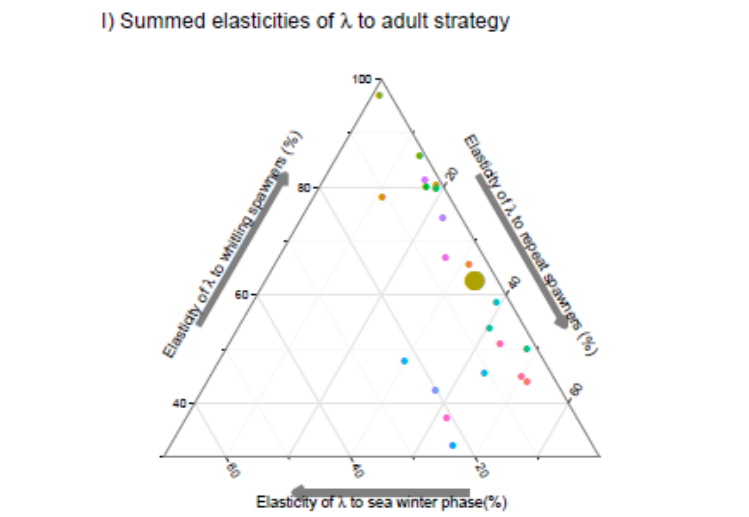
C) Fundamental matrix

Stage	FW	SW	IM	SM1	SM2	SM3	dead
FW	1.225	0	0	0	0	0	0
SW	0.022	1	0	0	0	0	0
IM	0.039	0.005	1	0	0	0	0
SM1	0.085	0.045	0.05	1	0	0	0
SM2	0.024	0.013	0.014	0.288	1	0	0
SM3	0.001	0.001	0.001	0.015	0.053	1	0
dead	1	1	1	1	1	1	1



D) Sensitivities of λ to perturbations of the transition matrix

Stage	FW	SW	IM	SM1	SM2	SM3	dead
FW	0.477	0.007	0.013	0.027	0.007	0	0.314
SW	0.285	0.004	0.007	0.015	0.004	0	0.174
IM	0.293	0.004	0.008	0.017	0.004	0	0.193
SM1	7.048	0.103	0.186	0.404	0.097	0.004	4.645
SM2	7.534	0.11	0.199	0.432	0.103	0.005	4.965
SM3	6.781	0.099	0.179	0.389	0.093	0.004	4.469
dead	0	0	0	0	0	0	0

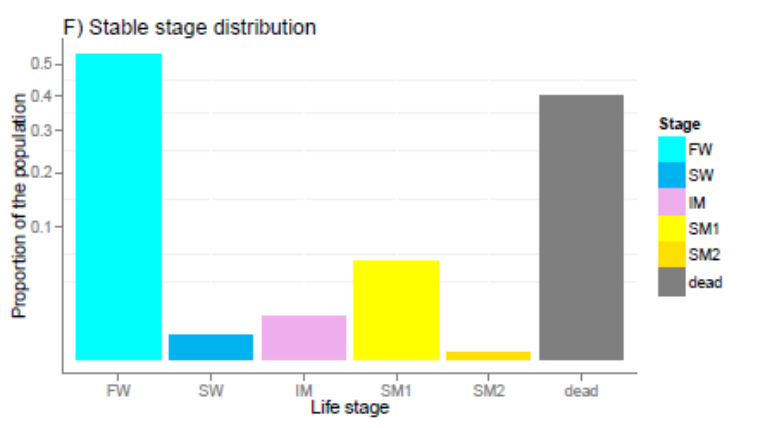
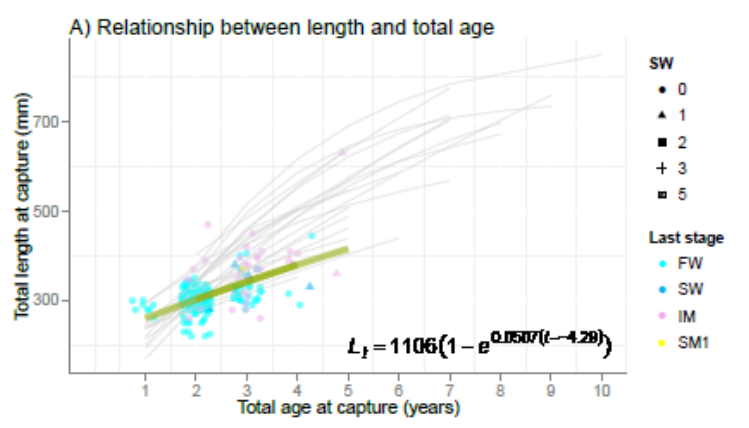


E) Elasticities of λ to perturbations of the transition matrix

Stage	FW	SW	IM	SM1	SM2	SM3	dead
FW	0.073	0	0	0.301	0.099	0.004	0
SW	0.004	0	0	0	0	0	0
IM	0.008	0	0	0	0	0	0
SM1	0.393	0.004	0.008	0	0	0	0
SM2	0	0	0	0.103	0	0	0
SM3	0	0	0	0	0.004	0	0
dead	0	0	0	0	0	0	0

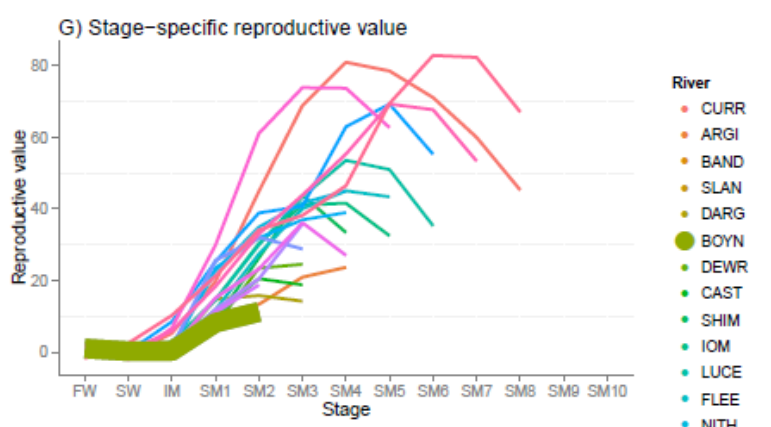
River Boyne:

Summary statistics of population dynamics analysis of sea trout from the River BOYN (n=204)



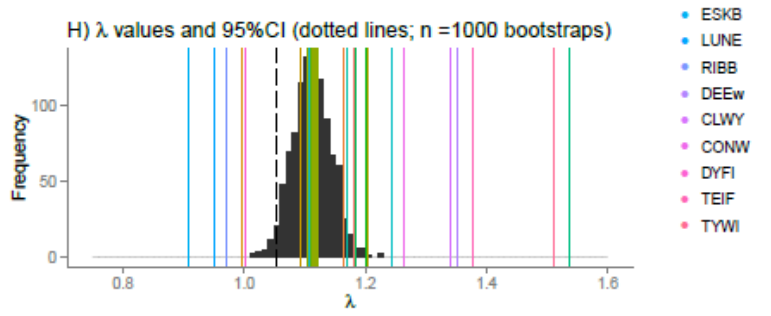
B) Transition matrix

Stage	FW	SW	IM	SM1	SM2	dead
FW	0.157	0	0	9.102	12.48	0
SW	0.008	0	0	0	0	0
IM	0.022	0.017	0.004	0	0	0
SM1	0.115	0.033	0.046	0	0	0
SM2	0	0	0	0.005	0	0
dead	0.7	0.95	0.95	0.995	1	0



C) Fundamental matrix

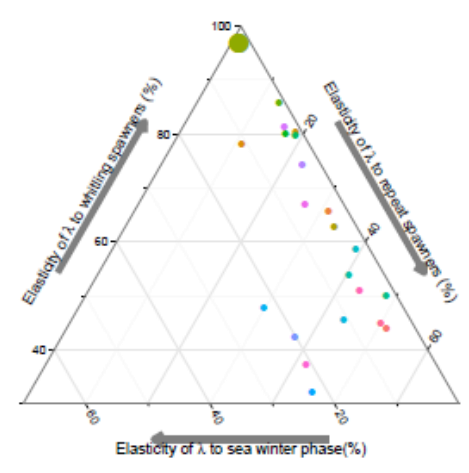
Stage	FW	SW	IM	SM1	SM2	dead
FW	1.186	0	0	0	0	0
SW	0.007	1	0	0	0	0
IM	0.028	0.017	1.004	0	0	0
SM1	0.138	0.034	0.046	1	0	0
SM2	0.001	0	0	0.005	1	0
dead	1	1	1	1	1	1



D) Sensitivities of λ to perturbations of the transition matrix

Stage	FW	SW	IM	SM1	SM2	dead
FW	0.534	0.003	0.011	0.056	0	0.397
SW	0.134	0.001	0.003	0.014	0	0.1
IM	0.182	0.001	0.004	0.019	0	0.135
SM1	4.392	0.025	0.087	0.459	0.002	3.269
SM2	5.988	0.034	0.118	0.625	0.003	4.455
dead	0	0	0	0	0	0

I) Summed elasticities of λ to adult strategy

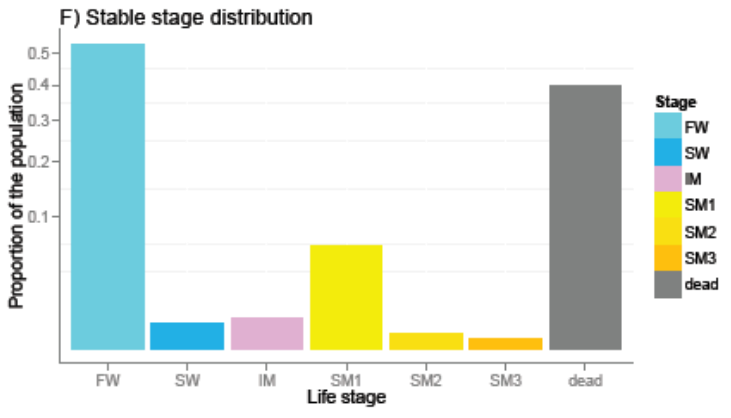
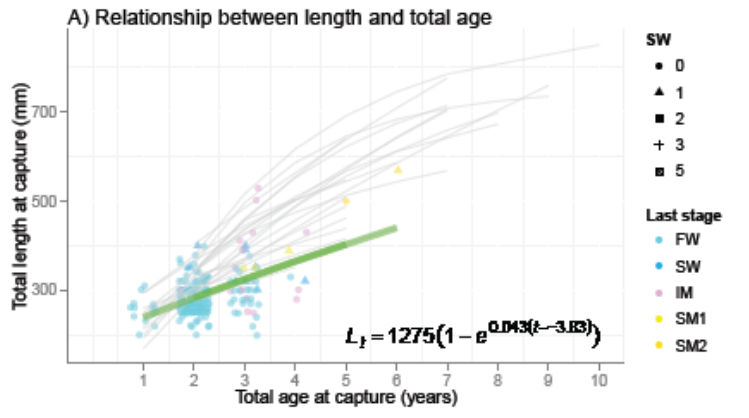


E) Elasticities of λ to perturbations of the transition matrix

Stage	FW	SW	IM	SM1	SM2	dead
FW	0.075	0	0	0.456	0.003	0
SW	0.001	0	0	0	0	0
IM	0.004	0	0	0	0	0
SM1	0.455	0.001	0.004	0	0	0
SM2	0	0	0	0.003	0	0
dead	0	0	0	0	0	0

River Dee White River:

Summary statistics of population dynamics analysis of sea trout from the River DEWR (n=217)



B) Transition matrix

Stage	FW	SW	IM	SM1	SM2	SM3	dead
FW	0.155	0	0	7.8	16.192	27.23	0
SW	0.007	0	0	0	0	0	0
IM	0.011	0	0.005	0	0	0	0
SM1	0.126	0.05	0.045	0	0	0	0
SM2	0	0	0	0.023	0	0	0
SM3	0	0	0	0	0.4	0	0
dead	0.7	0.95	0.95	0.977	0.6	1	0

C) Fundamental matrix

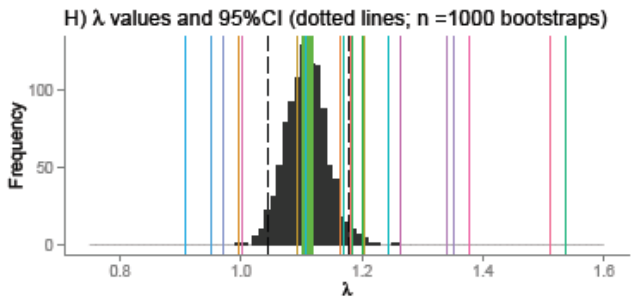
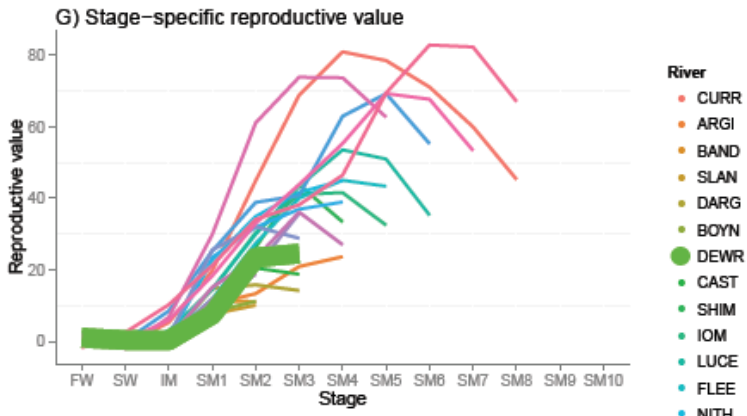
Stage	FW	SW	IM	SM1	SM2	SM3	dead
FW	1.183	0	0	0	0	0	0
SW	0.009	1	0	0	0	0	0
IM	0.014	0	1.005	0	0	0	0
SM1	0.15	0.05	0.045	1	0	0	0
SM2	0.003	0.001	0.001	0.023	1	0	0
SM3	0.001	0	0	0.009	0.4	1	0
dead	1	1	1	1	1	1	1

D) Sensitivities of λ to perturbations of the transition matrix

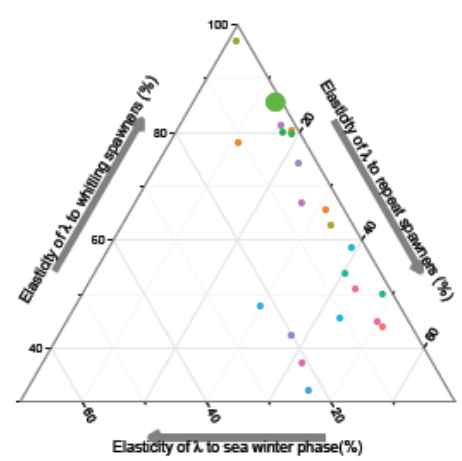
Stage	FW	SW	IM	SM1	SM2	SM3	dead
FW	0.515	0.003	0.005	0.059	0.001	0	0.385
SW	0.174	0.001	0.002	0.02	0	0	0.13
IM	0.157	0.001	0.002	0.018	0	0	0.117
SM1	3.889	0.028	0.04	0.443	0.009	0.003	2.894
SM2	12.063	0.08	0.124	1.381	0.029	0.01	9.023
SM3	12.631	0.084	0.13	1.446	0.03	0.011	9.448
dead	0	0	0	0	0	0	0

E) Elasticities of λ to perturbations of the transition matrix

Stage	FW	SW	IM	SM1	SM2	SM3	dead
FW	0.072	0	0	0.414	0.018	0.011	0
SW	0.001	0	0	0	0	0	0
IM	0.002	0	0	0	0	0	0
SM1	0.44	0.001	0.002	0	0	0	0
SM2	0	0	0	0.029	0	0	0
SM3	0	0	0	0	0.011	0	0
dead	0	0	0	0	0	0	0

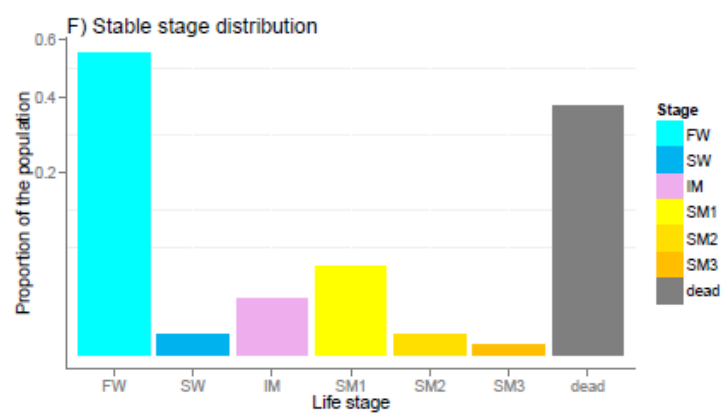
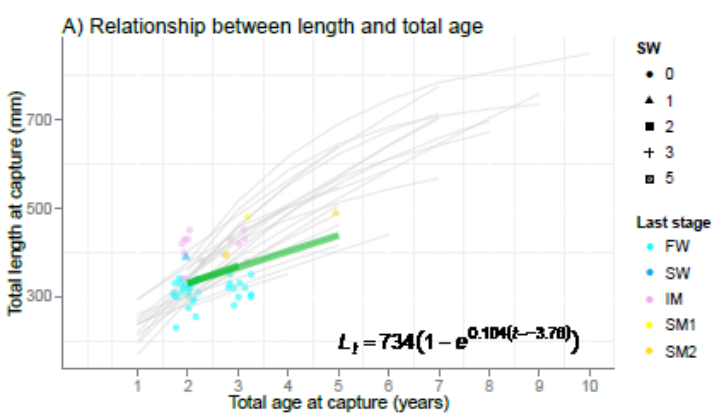


I) Summed elasticities of λ to adult strategy



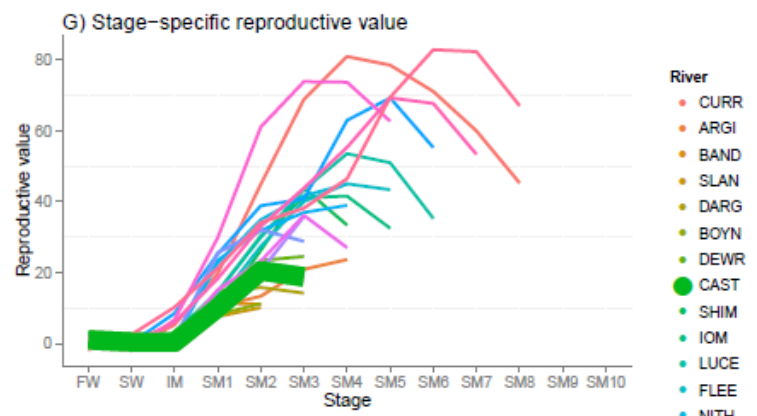
River Castlerock

Summary statistics of population dynamics analysis of sea trout from the River CAST (n=54)



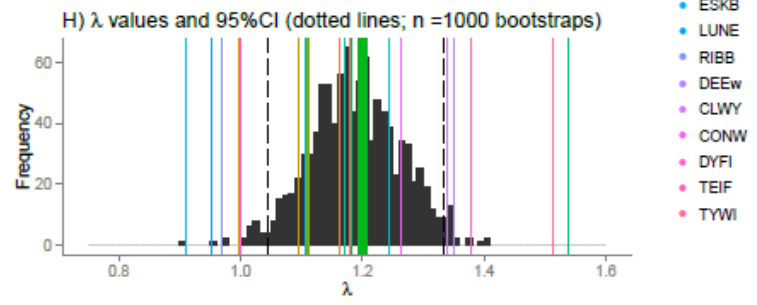
B) Transition matrix

Stage	FW	SW	IM	SM1	SM2	SM3	dead
FW	0.151	0	0	11	18.357	22.53	0
SW	0.006	0	0	0	0	0	0
IM	0.041	0	0.003	0	0	0	0
SM1	0.102	0.05	0.047	0	0	0	0
SM2	0	0	0	0.056	0	0	0
SM3	0	0	0	0	0.333	0	0
dead	0.7	0.95	0.95	0.944	0.667	1	0



C) Fundamental matrix

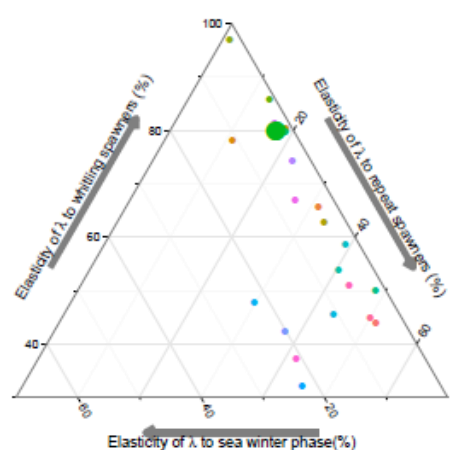
Stage	FW	SW	IM	SM1	SM2	SM3	dead
FW	1.178	0	0	0	0	0	0
SW	0.006	1	0	0	0	0	0
IM	0.049	0	1.003	0	0	0	0
SM1	0.123	0.05	0.047	1	0	0	0
SM2	0.007	0.003	0.003	0.056	1	0	0
SM3	0.002	0.001	0.001	0.019	0.333	1	0
dead	1	1	1	1	1	1	1



D) Sensitivities of λ to perturbations of the transition matrix

Stage	FW	SW	IM	SM1	SM2	SM3	dead
FW	0.502	0.002	0.017	0.043	0.002	0.001	0.344
SW	0.212	0.001	0.007	0.018	0.001	0	0.145
IM	0.199	0.001	0.007	0.017	0.001	0	0.136
SM1	5.077	0.023	0.175	0.439	0.02	0.006	3.479
SM2	10.295	0.047	0.355	0.889	0.041	0.011	7.055
SM3	9.423	0.043	0.325	0.814	0.038	0.01	6.458
dead	0	0	0	0	0	0	0

I) Summed elasticities of λ to adult strategy

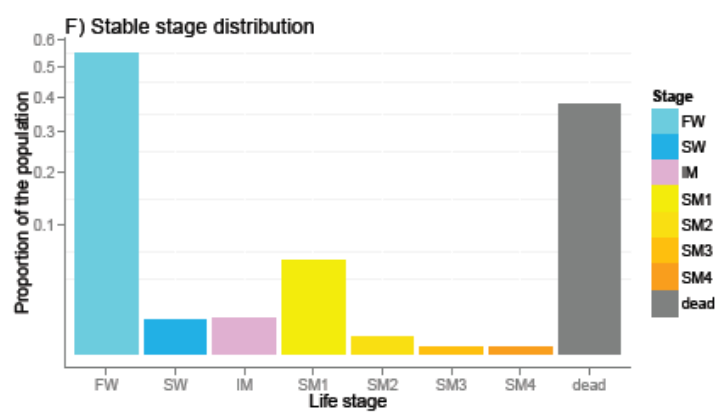
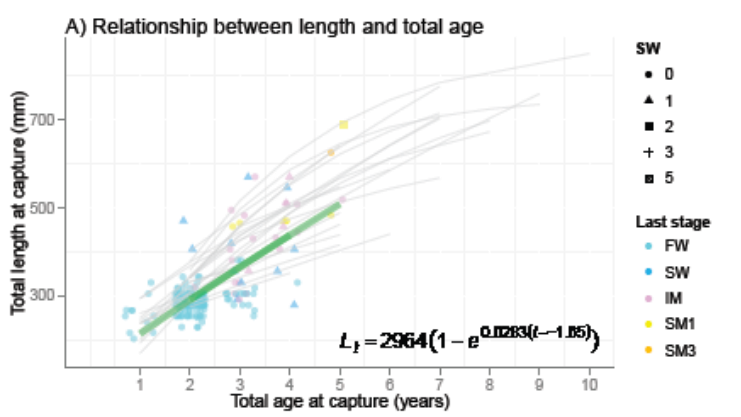


E) Elasticities of λ to perturbations of the transition matrix

Stage	FW	SW	IM	SM1	SM2	SM3	dead
FW	0.063	0	0	0.397	0.031	0.01	0
SW	0.001	0	0	0	0	0	0
IM	0.007	0	0	0	0	0	0
SM1	0.431	0.001	0.007	0	0	0	0
SM2	0	0	0	0.041	0	0	0
SM3	0	0	0	0	0.01	0	0
dead	0	0	0	0	0	0	0

River Shimna:

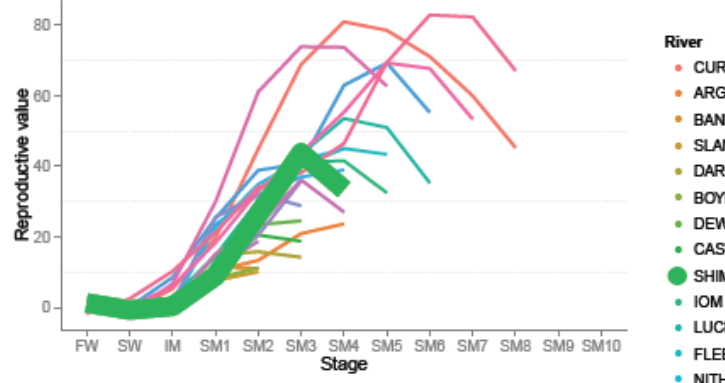
Summary statistics of population dynamics analysis of sea trout from the River SHIM (n=177)



B) Transition matrix

Stage	FW	SW	IM	SM1	SM2	SM3	SM4	dead
FW	0.155	0	0	9.491	23.974	27.46	37.57	0
SW	0.014	0.003	0	0	0	0	0	0
IM	0.016	0.011	0.009	0	0	0	0	0
SM1	0.114	0.036	0.041	0	0	0	0	0
SM2	0	0	0	0.04	0	0	0	0
SM3	0	0	0	0	0.143	0	0	0
SM4	0	0	0	0	0	1	0	0
dead	0.7	0.95	0.95	0.96	0.857	0	1	0

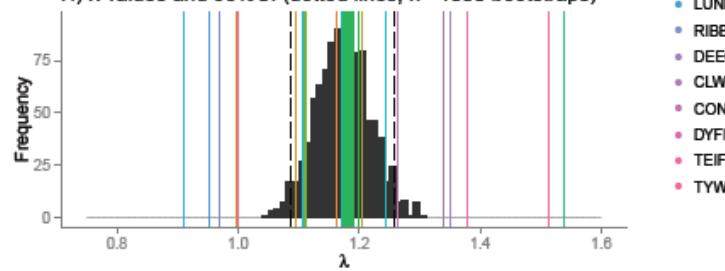
G) Stage-specific reproductive value



C) Fundamental matrix

Stage	FW	SW	IM	SM1	SM2	SM3	SM4	dead
FW	1.184	0	0	0	0	0	0	0
SW	0.016	1.003	0	0	0	0	0	0
IM	0.02	0.011	1.009	0	0	0	0	0
SM1	0.137	0.037	0.042	1	0	0	0	0
SM2	0.005	0.001	0.002	0.04	1	0	0	0
SM3	0.001	0	0	0.006	0.143	1	0	0
SM4	0.001	0	0	0.006	0.143	1	1	0
dead	1	1	1	1	1	1	1	1

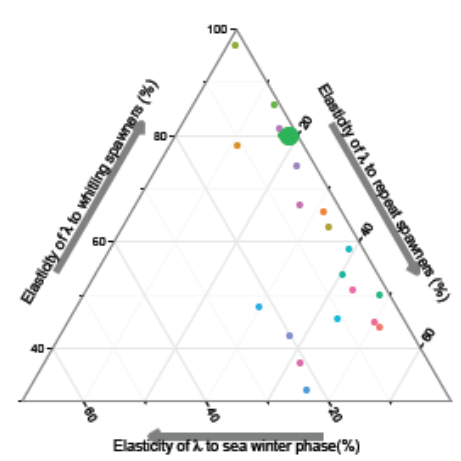
H) λ values and 95%CI (dotted lines; n=1000 bootstraps)



D) Sensitivities of λ to perturbations of the transition matrix

Stage	FW	SW	IM	SM1	SM2	SM3	SM4	dead
FW	0.502	0.006	0.007	0.049	0.002	0	0	0.348
SW	0.138	0.002	0.002	0.013	0	0	0	0.096
IM	0.157	0.002	0.002	0.015	0.001	0	0	0.109
SM1	4.468	0.053	0.063	0.436	0.015	0.002	0.001	3.102
SM2	13.205	0.155	0.185	1.289	0.043	0.005	0.004	9.168
SM3	25.123	0.296	0.353	2.452	0.082	0.01	0.008	17.443
SM4	15.939	0.188	0.224	1.555	0.052	0.006	0.005	11.066
dead	0	0	0	0	0	0	0	0

I) Summed elasticities of λ to adult strategy

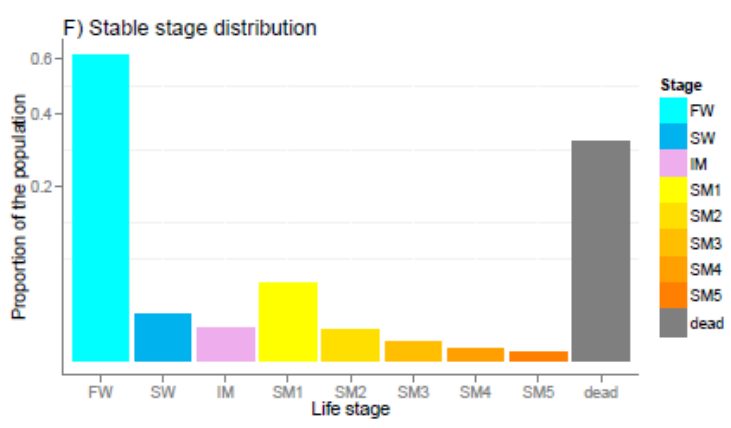
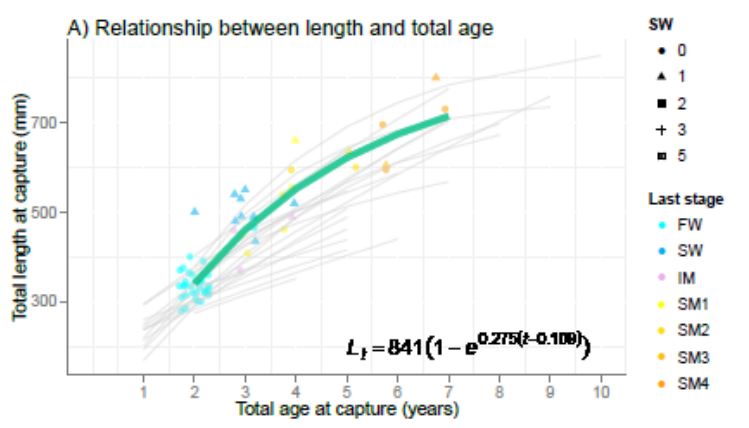


E) Elasticities of λ to perturbations of the transition matrix

Stage	FW	SW	IM	SM1	SM2	SM3	SM4	dead
FW	0.066	0	0	0.393	0.033	0.005	0.005	0
SW	0.002	0	0	0	0	0	0	0
IM	0.002	0	0	0	0	0	0	0
SM1	0.432	0.002	0.002	0	0	0	0	0
SM2	0	0	0	0.043	0	0	0	0
SM3	0	0	0	0	0.01	0	0	0
SM4	0	0	0	0	0	0.005	0	0
dead	0	0	0	0	0	0	0	0

River of Isle of Man (combined):

Summary statistics of population dynamics analysis of sea trout from the River IOM (n=59)



B) Transition matrix

Stage	FW	SW	IM	SM1	SM2	SM3	SM4	SM5	dead
FW	0.151	0	0	14.362	25.703	34.476	41.056	49.015	0
SW	0.035	0	0	0	0	0	0	0	0
IM	0.018	0.004	0	0	0	0	0	0	0
SM1	0.096	0.046	0.05	0	0	0	0	0	0
SM2	0	0	0	0.237	0	0	0	0	0
SM3	0	0	0	0	0.571	0	0	0	0
SM4	0	0	0	0	0	0.625	0	0	0
SM5	0	0	0	0	0	0	0.8	0	0
dead	0.7	0.95	0.95	0.763	0.429	0.375	0.2	1	0

C) Fundamental matrix

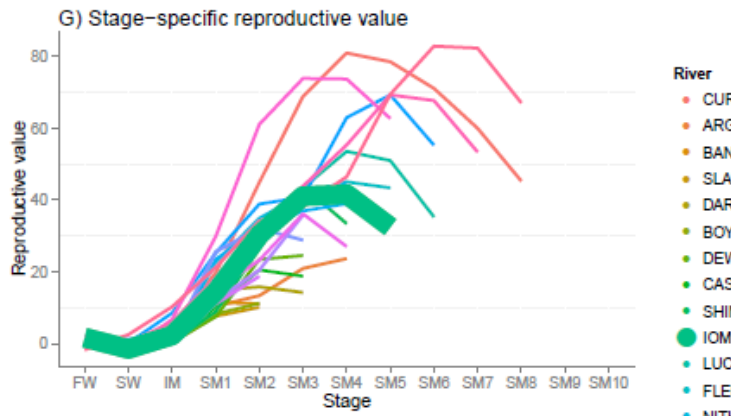
Stage	FW	SW	IM	SM1	SM2	SM3	SM4	SM5	dead
FW	1.178	0	0	0	0	0	0	0	0
SW	0.042	1	0	0	0	0	0	0	0
IM	0.021	0.004	1	0	0	0	0	0	0
SM1	0.116	0.047	0.05	1	0	0	0	0	0
SM2	0.027	0.011	0.012	0.237	1	0	0	0	0
SM3	0.016	0.006	0.007	0.136	0.571	1	0	0	0
SM4	0.01	0.004	0.004	0.085	0.357	0.625	1	0	0
SM5	0.008	0.003	0.003	0.068	0.286	0.5	0.8	1	0
dead	1	1	1	1	1	1	1	1	1

D) Sensitivities of λ to perturbations of the transition matrix

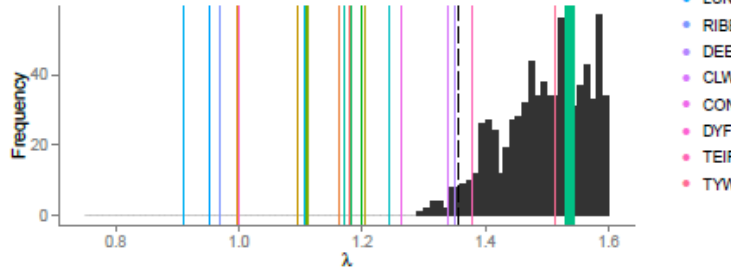
Stage	FW	SW	IM	SM1	SM2	SM3	SM4	SM5	dead
FW	0.406	0.009	0.005	0.026	0.004	0.001	0.001	0	0.208
SW	0.175	0.004	0.002	0.011	0.002	0.001	0	0	0.09
IM	0.188	0.004	0.002	0.012	0.002	0.001	0	0	0.096
SM1	5.781	0.133	0.067	0.366	0.057	0.021	0.009	0.004	2.962
SM2	12.846	0.295	0.148	0.814	0.126	0.047	0.019	0.01	6.583
SM3	16.273	0.374	0.188	1.032	0.159	0.059	0.024	0.013	8.34
SM4	17.601	0.404	0.203	1.116	0.172	0.064	0.026	0.014	9.02
SM5	12.96	0.298	0.149	0.822	0.127	0.047	0.019	0.01	6.642
dead	0	0	0	0	0	0	0	0	0

E) Elasticities of λ to perturbations of the transition matrix

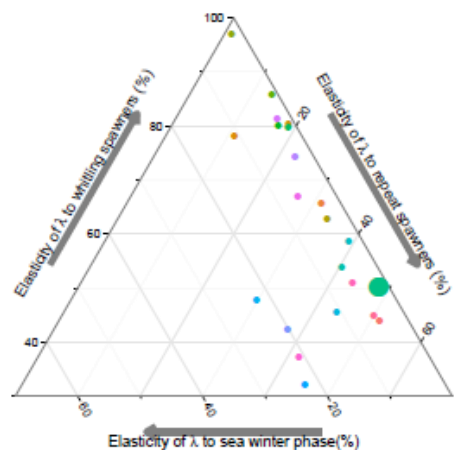
Stage	FW	SW	IM	SM1	SM2	SM3	SM4	SM5	dead
FW	0.04	0	0	0.241	0.067	0.033	0.016	0.01	0
SW	0.004	0	0	0	0	0	0	0	0
IM	0.002	0	0	0	0	0	0	0	0
SM1	0.36	0.004	0.002	0	0	0	0	0	0
SM2	0	0	0	0.126	0	0	0	0	0
SM3	0	0	0	0	0.059	0	0	0	0
SM4	0	0	0	0	0	0.026	0	0	0
SM5	0	0	0	0	0	0	0.01	0	0
dead	0	0	0	0	0	0	0	0	0



H) λ values and 95%CI (dotted lines; n=1000 bootstraps)

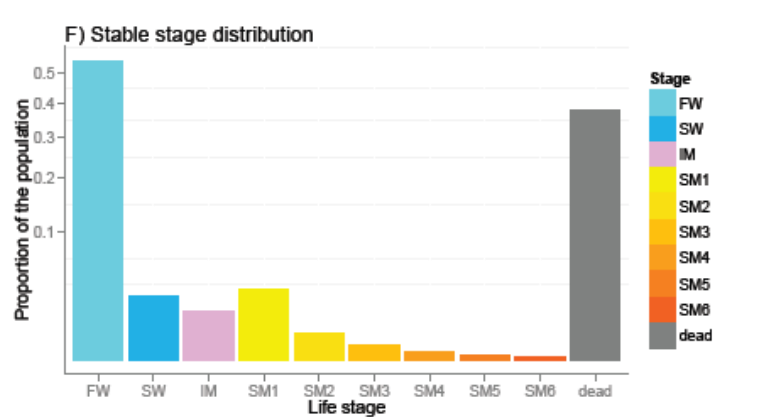
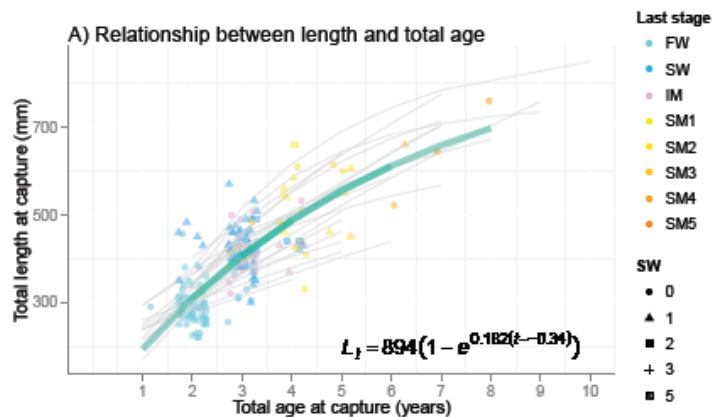


I) Summed elasticities of λ to adult strategy



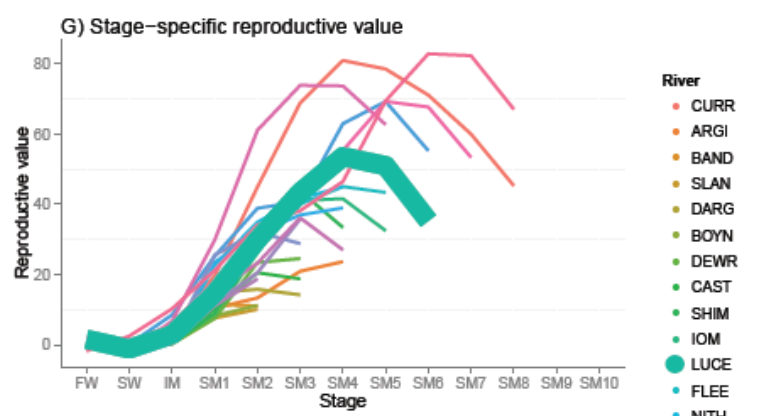
River Luce:

Summary statistics of population dynamics analysis of sea trout from the River LUCE (n=204)



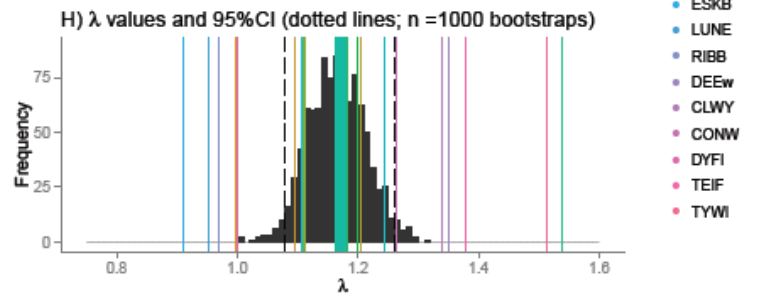
B) Transition matrix

Stage	FW	SW	IM	SM1	SM2	SM3	SM4	SM5	SM6	dead
FW	0.153	0	0	13.285	21.648	29.712	36.528	45.525	40.15	0
SW	0.054	0.003	0	0	0	0	0	0	0	0
IM	0.031	0.003	0.001	0	0	0	0	0	0	0
SM1	0.062	0.045	0.049	0	0	0	0	0	0	0
SM2	0	0	0	0.162	0	0	0	0	0	0
SM3	0	0	0	0	0.333	0	0	0	0	0
SM4	0	0	0	0	0	0.384	0	0	0	0
SM5	0	0	0	0	0	0	0.5	0	0	0
SM6	0	0	0	0	0	0	0	0.5	0	0
dead	0.7	0.95	0.95	0.838	0.867	0.836	0.5	0.5	1	0



C) Fundamental matrix

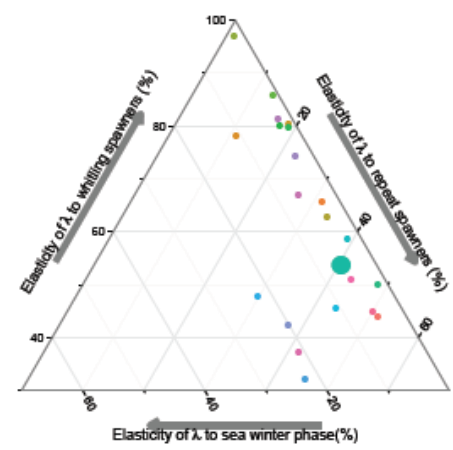
Stage	FW	SW	IM	SM1	SM2	SM3	SM4	SM5	SM6	dead
FW	1.18	0	0	0	0	0	0	0	0	0
SW	0.084	1.003	0	0	0	0	0	0	0	0
IM	0.037	0.003	1.001	0	0	0	0	0	0	0
SM1	0.078	0.045	0.049	1	0	0	0	0	0	0
SM2	0.013	0.007	0.008	0.162	1	0	0	0	0	0
SM3	0.004	0.002	0.003	0.054	0.333	1	0	0	0	0
SM4	0.002	0.001	0.001	0.02	0.121	0.384	1	0	0	0
SM5	0.001	0	0	0.01	0.081	0.182	0.5	1	0	0
SM6	0	0	0	0.005	0.03	0.091	0.25	0.5	1	0
dead	1	1	1	1	1	1	1	1	1	1



D) Sensitivities of λ to perturbations of the transition matrix

Stage	FW	SW	IM	SM1	SM2	SM3	SM4	SM5	SM6	dead
FW	0.435	0.02	0.012	0.024	0.003	0.001	0	0	0	0.306
SW	0.26	0.012	0.007	0.015	0.002	0.001	0	0	0	0.183
IM	0.283	0.013	0.008	0.016	0.002	0.001	0	0	0	0.199
SM1	6.755	3.313	0.18	0.378	0.052	0.015	0.005	0.002	0.001	4.75
SM2	13.252	6.615	0.353	0.742	0.102	0.029	0.009	0.004	0.002	9.318
SM3	18.324	9.158	0.489	1.026	0.142	0.04	0.013	0.005	0.002	12.885
SM4	23.492	11.746	0.628	1.315	0.182	0.052	0.016	0.007	0.003	16.519
SM5	23.264	11.632	0.62	1.302	0.18	0.051	0.016	0.007	0.003	16.358
SM6	14.905	7.452	0.397	0.834	0.115	0.033	0.01	0.004	0.002	10.481
dead	0	0	0	0	0	0	0	0	0	0

I) Summed elasticities of λ to adult strategy

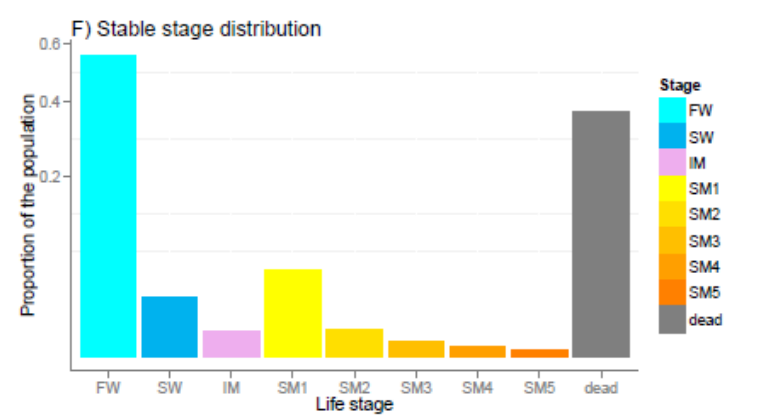
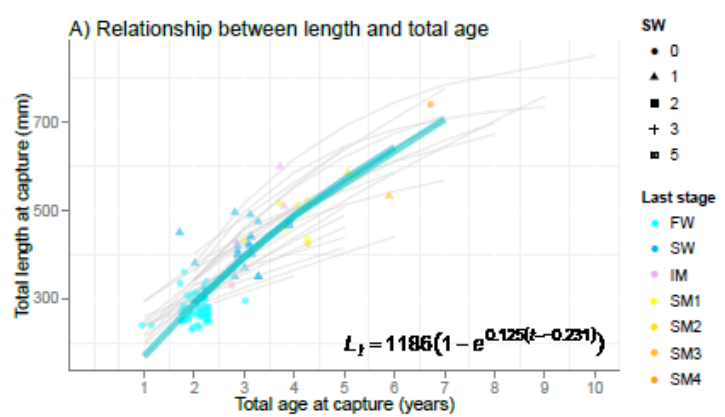


E) Elasticities of λ to perturbations of the transition matrix

Stage	FW	SW	IM	SM1	SM2	SM3	SM4	SM5	SM6	dead
FW	0.057	0	0	0.278	0.062	0.024	0.009	0.005	0.002	0
SW	0.012	0	0	0	0	0	0	0	0	0
IM	0.008	0	0	0	0	0	0	0	0	0
SM1	0.359	0.012	0.008	0	0	0	0	0	0	0
SM2	0	0	0	0.102	0	0	0	0	0	0
SM3	0	0	0	0	0.04	0	0	0	0	0
SM4	0	0	0	0	0	0.016	0	0	0	0
SM5	0	0	0	0	0	0	0.007	0	0	0
SM6	0	0	0	0	0	0	0	0.002	0	0
dead	0	0	0	0	0	0	0	0	0	0

River Fleet:

Summary statistics of population dynamics analysis of sea trout from the River FLEE (n=95)



B) Transition matrix

Stage	FW	SW	IM	SM1	SM2	SM3	SM4	SM5	dead
FW	0.147	0	0	10.247	21.405	26.108	35.39	53.59	0
SW	0.047	0.002	0	0	0	0	0	0	0
IM	0.008	0.005	0	0	0	0	0	0	0
SM1	0.098	0.043	0.05	0	0	0	0	0	0
SM2	0	0	0	0.116	0	0	0	0	0
SM3	0	0	0	0	0.364	0	0	0	0
SM4	0	0	0	0	0	0.5	0	0	0
SM5	0	0	0	0	0	0	0.5	0	0
dead	0.7	0.95	0.95	0.884	0.636	0.5	0.5	1	0

C) Fundamental matrix

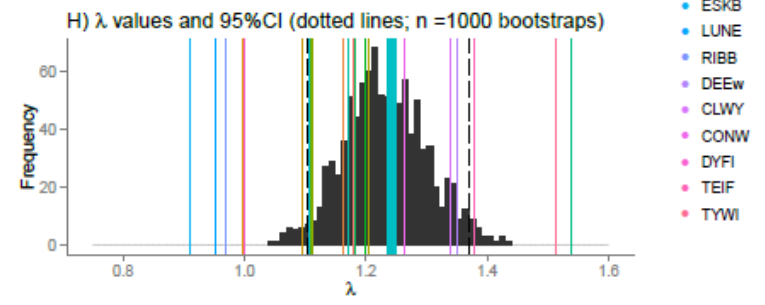
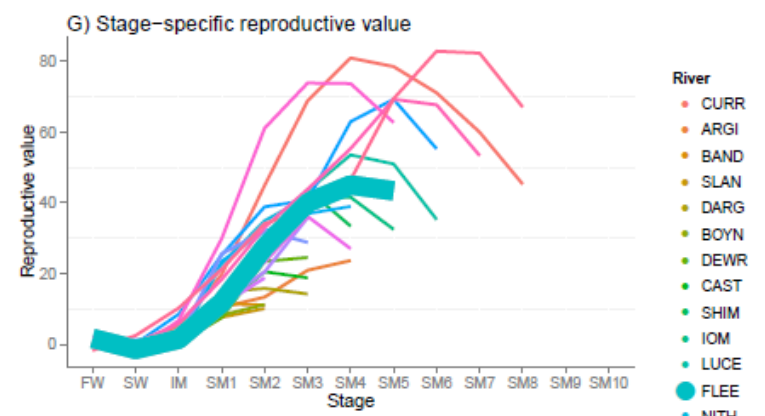
Stage	FW	SW	IM	SM1	SM2	SM3	SM4	SM5	dead
FW	1.172	0	0	0	0	0	0	0	0
SW	0.055	1.002	0	0	0	0	0	0	0
IM	0.01	0.005	1	0	0	0	0	0	0
SM1	0.118	0.044	0.05	1	0	0	0	0	0
SM2	0.014	0.005	0.006	0.116	1	0	0	0	0
SM3	0.005	0.002	0.002	0.042	0.364	1	0	0	0
SM4	0.002	0.001	0.001	0.021	0.182	0.5	1	0	0
SM5	0.001	0	0.001	0.011	0.091	0.25	0.5	1	0
dead	1	1	1	1	1	1	1	1	1

D) Sensitivities of λ to perturbations of the transition matrix

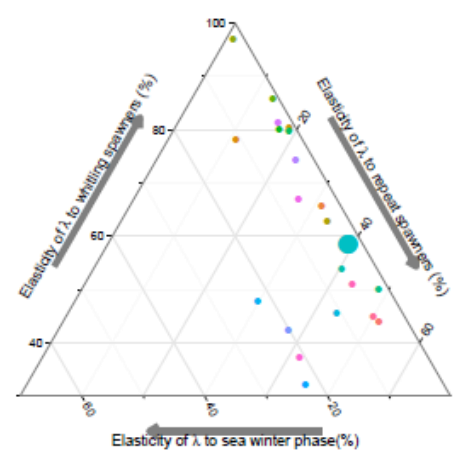
Stage	FW	SW	IM	SM1	SM2	SM3	SM4	SM5	dead
FW	0.443	0.017	0.003	0.036	0.003	0.001	0	0	0.292
SW	0.17	0.006	0.001	0.014	0.001	0	0	0	0.112
IM	0.195	0.007	0.001	0.016	0.001	0	0	0	0.128
SM1	4.837	0.182	0.032	0.391	0.036	0.011	0.004	0.002	3.192
SM2	12.735	0.48	0.085	1.028	0.096	0.028	0.011	0.005	8.404
SM3	17.483	0.658	0.116	1.41	0.131	0.038	0.015	0.006	11.523
SM4	20.289	0.765	0.135	1.638	0.153	0.045	0.018	0.007	13.388
SM5	19.092	0.719	0.127	1.541	0.144	0.042	0.017	0.007	12.599
dead	0	0	0	0	0	0	0	0	0

E) Elasticities of λ to perturbations of the transition matrix

Stage	FW	SW	IM	SM1	SM2	SM3	SM4	SM5	dead
FW	0.052	0	0	0.295	0.057	0.02	0.011	0.007	0
SW	0.006	0	0	0	0	0	0	0	0
IM	0.001	0	0	0	0	0	0	0	0
SM1	0.383	0.006	0.001	0	0	0	0	0	0
SM2	0	0	0	0.098	0	0	0	0	0
SM3	0	0	0	0	0.038	0	0	0	0
SM4	0	0	0	0	0	0.018	0	0	0
SM5	0	0	0	0	0	0	0.007	0	0
dead	0	0	0	0	0	0	0	0	0

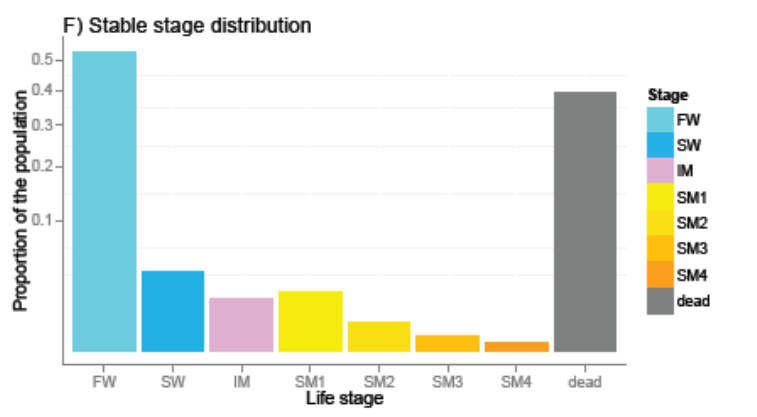
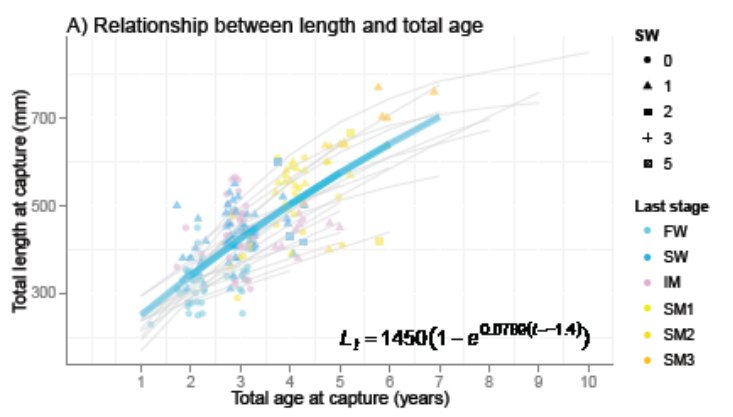


I) Summed elasticities of λ to adult strategy



River Nith:

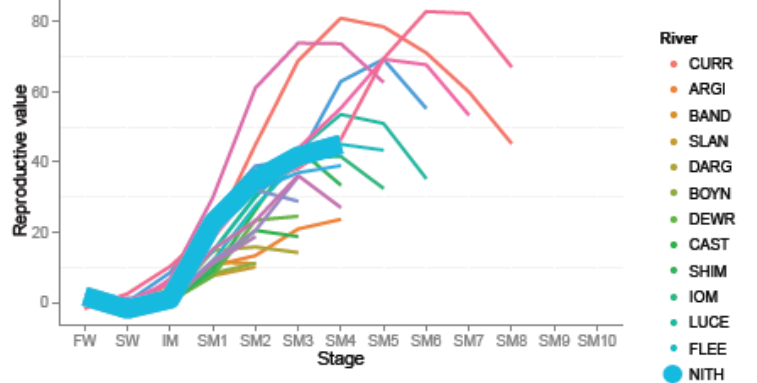
Summary statistics of population dynamics analysis of sea trout from the River NITH (n=204)



B) Transition matrix

Stage	FW	SW	IM	SM1	SM2	SM3	SM4	dead
FW	0.152	0	0	16.236	24.895	32.207	49.942	0
SW	0.077	0.002	0	0	0	0	0	0
IM	0.033	0.005	0.002	0	0	0	0	0
SM1	0.038	0.043	0.048	0	0	0	0	0
SM2	0	0	0	0.25	0	0	0	0
SM3	0	0	0	0	0.333	0	0	0
SM4	0	0	0	0	0	0.294	0	0
dead	0.7	0.95	0.95	0.75	0.867	0.706	1	0

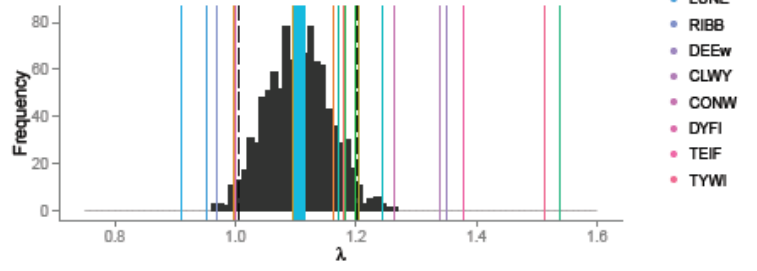
G) Stage-specific reproductive value



C) Fundamental matrix

Stage	FW	SW	IM	SM1	SM2	SM3	SM4	dead
FW	1.179	0	0	0	0	0	0	0
SW	0.091	1.002	0	0	0	0	0	0
IM	0.04	0.005	1.002	0	0	0	0	0
SM1	0.05	0.044	0.048	1	0	0	0	0
SM2	0.013	0.011	0.012	0.25	1	0	0	0
SM3	0.004	0.004	0.004	0.083	0.333	1	0	0
SM4	0.001	0.001	0.001	0.025	0.098	0.294	1	0
dead	1	1	1	1	1	1	1	1

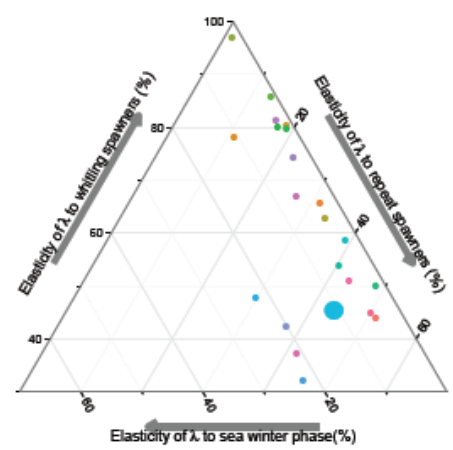
H) λ values and 95%CI (dotted lines; n = 1000 bootstraps)



D) Sensitivities of λ to perturbations of the transition matrix

Stage	FW	SW	IM	SM1	SM2	SM3	SM4	dead
FW	0.418	0.029	0.013	0.016	0.004	0.001	0	0.314
SW	0.371	0.026	0.011	0.014	0.003	0.001	0	0.279
IM	0.412	0.029	0.013	0.016	0.004	0.001	0	0.31
SM1	9.426	0.858	0.288	0.36	0.081	0.025	0.007	7.094
SM2	14.577	1.017	0.445	0.557	0.126	0.038	0.01	10.97
SM3	17.176	1.198	0.525	0.656	0.148	0.045	0.012	12.926
SM4	18.857	1.316	0.576	0.721	0.163	0.049	0.013	14.192
dead	0	0	0	0	0	0	0	0

I) Summed elasticities of λ to adult strategy

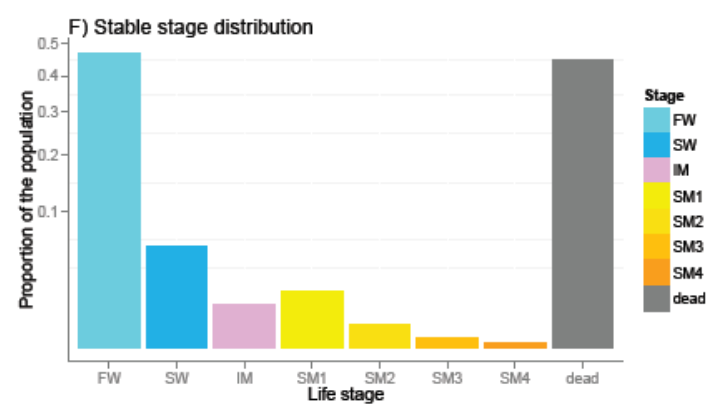
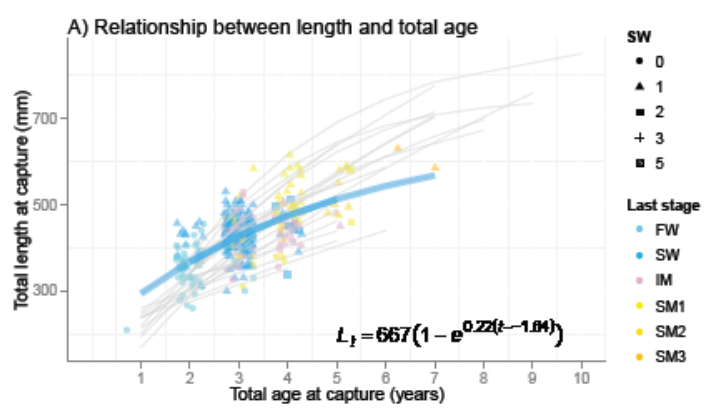


E) Elasticities of λ to perturbations of the transition matrix

Stage	FW	SW	IM	SM1	SM2	SM3	SM4	dead
FW	0.057	0	0	0.234	0.081	0.032	0.013	0
SW	0.026	0	0	0	0	0	0	0
IM	0.012	0	0	0	0	0	0	0
SM1	0.322	0.026	0.013	0	0	0	0	0
SM2	0	0	0	0.126	0	0	0	0
SM3	0	0	0	0	0.045	0	0	0
SM4	0	0	0	0	0	0.013	0	0
dead	0	0	0	0	0	0	0	0

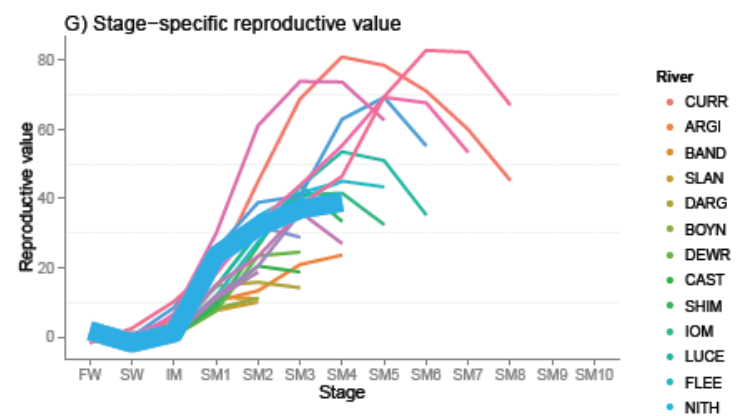
River Border Esk:

Summary statistics of population dynamics analysis of sea trout from the River ESKB (n=378)



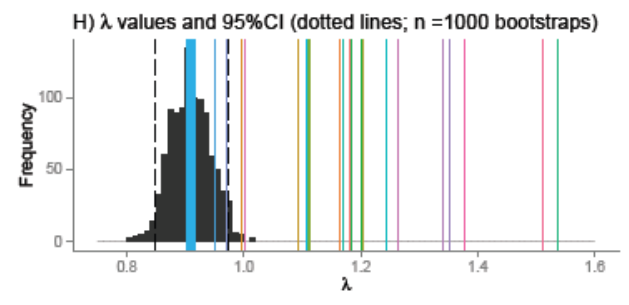
B) Transition matrix

Stage	FW	SW	IM	SM1	SM2	SM3	SM4	dead
FW	0.15	0	0	16.629	22.423	25.727	35.455	0
SW	0.106	0.001	0	0	0	0	0	0
IM	0.018	0.004	0.004	0	0	0	0	0
SM1	0.026	0.045	0.046	0	0	0	0	0
SM2	0	0	0	0.148	0	0	0	0
SM3	0	0	0	0	0.179	0	0	0
SM4	0	0	0	0	0	0.2	0	0
dead	0.7	0.95	0.95	0.852	0.821	0.8	1	0



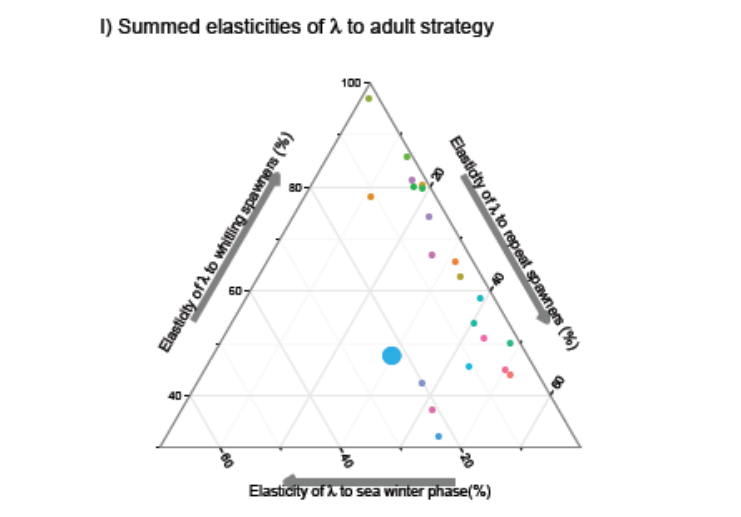
C) Fundamental matrix

Stage	FW	SW	IM	SM1	SM2	SM3	SM4	dead
FW	1.176	0	0	0	0	0	0	0
SW	0.124	1.001	0	0	0	0	0	0
IM	0.022	0.004	1.004	0	0	0	0	0
SM1	0.037	0.045	0.046	1	0	0	0	0
SM2	0.006	0.007	0.007	0.148	1	0	0	0
SM3	0.001	0.001	0.001	0.026	0.179	1	0	0
SM4	0	0	0	0.005	0.038	0.2	1	0
dead	1	1	1	1	1	1	1	1



D) Sensitivities of λ to perturbations of the transition matrix

Stage	FW	SW	IM	SM1	SM2	SM3	SM4	dead
FW	0.448	0.052	0.009	0.016	0.003	0.001	0	0.427
SW	0.521	0.081	0.011	0.019	0.003	0.001	0	0.498
IM	0.534	0.062	0.011	0.019	0.003	0.001	0	0.508
SM1	10.525	1.224	0.217	0.374	0.061	0.012	0.003	10.027
SM2	14.297	1.682	0.295	0.508	0.083	0.016	0.004	13.619
SM3	16.524	1.921	0.341	0.588	0.098	0.019	0.004	15.741
SM4	17.475	2.032	0.381	0.621	0.101	0.02	0.004	16.647
dead	0	0	0	0	0	0	0	0

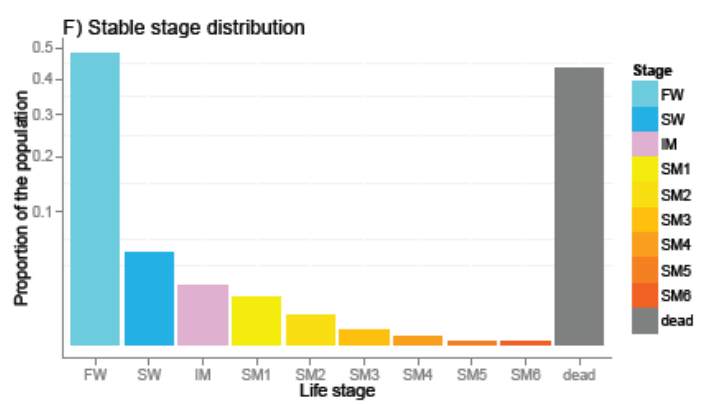
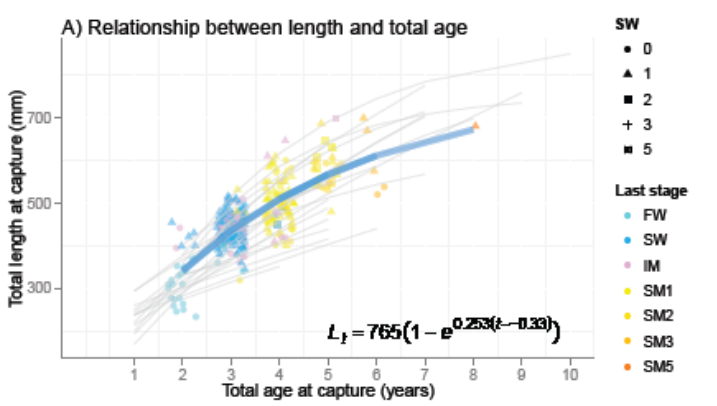


E) Elasticities of λ to perturbations of the transition matrix

Stage	FW	SW	IM	SM1	SM2	SM3	SM4	dead
FW	0.074	0	0	0.291	0.064	0.014	0.004	0
SW	0.06	0	0	0	0	0	0	0
IM	0.011	0	0	0	0	0	0	0
SM1	0.303	0.06	0.011	0	0	0	0	0
SM2	0	0	0	0.083	0	0	0	0
SM3	0	0	0	0	0.019	0	0	0
SM4	0	0	0	0	0	0.004	0	0
dead	0	0	0	0	0	0	0	0

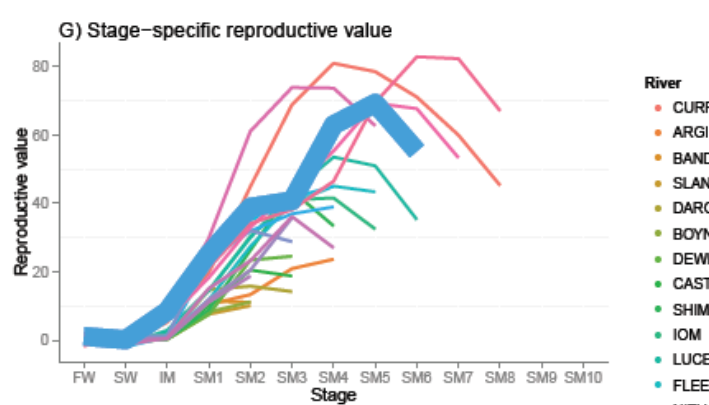
River Lune:

Summary statistics of population dynamics analysis of sea trout from the River LUNE (n=318)



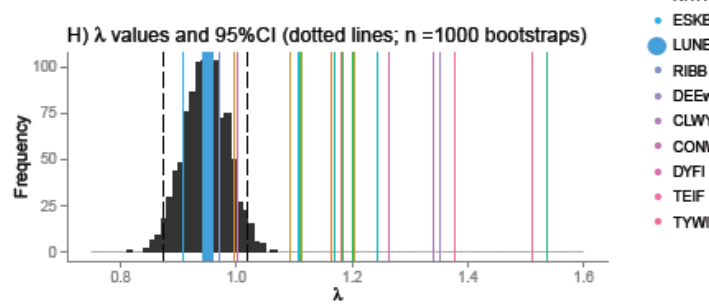
B) Transition matrix

Stage	FW	SW	IM	SM1	SM2	SM3	SM4	SM5	SM6	dead
FW	0.15	0	0	17.413	24.077	28.983	34.371	41.19	44.86	0
SW	0.094	0.002	0	0	0	0	0	0	0	0
IM	0.038	0.002	0.002	0	0	0	0	0	0	0
SM1	0.018	0.046	0.048	0	0	0	0	0	0	0
SM2	0	0	0	0.371	0	0	0	0	0	0
SM3	0	0	0	0	0.22	0	0	0	0	0
SM4	0	0	0	0	0	0.269	0	0	0	0
SM5	0	0	0	0	0	0	0.143	0	0	0
SM6	0	0	0	0	0	0	0	1	0	0
dead	0.7	0.95	0.95	0.629	0.78	0.731	0.857	0	1	0



C) Fundamental matrix

Stage	FW	SW	IM	SM1	SM2	SM3	SM4	SM5	SM6	dead
FW	1.176	0	0	0	0	0	0	0	0	0
SW	0.111	1.002	0	0	0	0	0	0	0	0
IM	0.045	0.002	1.002	0	0	0	0	0	0	0
SM1	0.029	0.046	0.048	1	0	0	0	0	0	0
SM2	0.011	0.017	0.018	0.371	1	0	0	0	0	0
SM3	0.002	0.004	0.004	0.082	0.22	1	0	0	0	0
SM4	0.001	0.001	0.001	0.022	0.059	0.269	1	0	0	0
SM5	0	0	0	0.003	0.008	0.038	0.143	1	0	0
SM6	0	0	0	0.003	0.008	0.038	0.143	1	1	0
dead	1	1	1	1	1	1	1	1	1	1



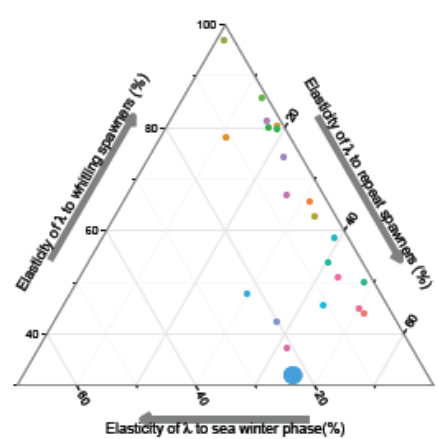
D) Sensitivities of λ to perturbations of the transition matrix

Stage	FW	SW	IM	SM1	SM2	SM3	SM4	SM5	SM6	dead
FW	0.388	0.038	0.016	0.01	0.004	0.001	0	0	0	0.35
SW	0.605	0.06	0.024	0.016	0.006	0.001	0	0	0	0.548
IM	0.636	0.063	0.025	0.017	0.006	0.002	0	0	0	0.574
SM1	12.481	1.236	0.499	0.327	0.127	0.029	0.008	0.001	0.001	11.266
SM2	13.815	1.368	0.553	0.362	0.141	0.033	0.009	0.001	0.001	12.469
SM3	17.298	1.713	0.892	0.453	0.177	0.041	0.012	0.002	0.002	15.814
SM4	19.406	1.921	0.777	0.508	0.198	0.046	0.013	0.002	0.002	17.516
SM5	35.987	3.563	1.44	0.942	0.367	0.085	0.024	0.004	0.004	32.483
SM6	18.276	1.809	0.731	0.478	0.187	0.043	0.012	0.002	0.002	16.496
dead	0	0	0	0	0	0	0	0	0	0

E) Elasticities of λ to perturbations of the transition matrix

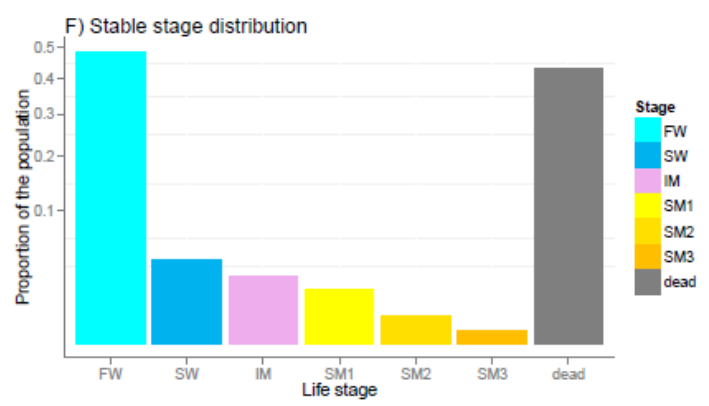
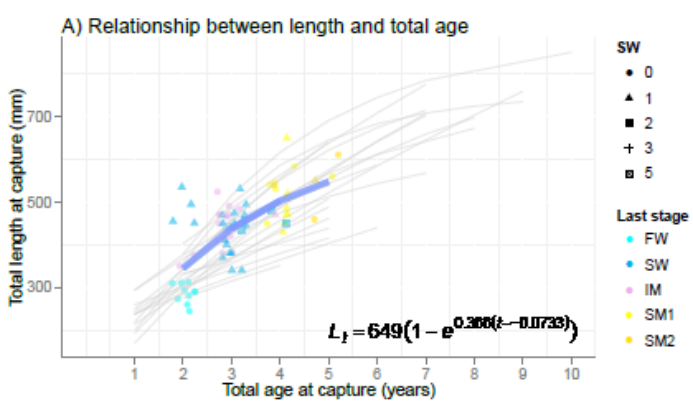
Stage	FW	SW	IM	SM1	SM2	SM3	SM4	SM5	SM6	dead
FW	0.061	0	0	0.188	0.1	0.028	0.009	0.002	0.002	0
SW	0.06	0	0	0	0	0	0	0	0	0
IM	0.025	0	0	0	0	0	0	0	0	0
SM1	0.242	0.06	0.025	0	0	0	0	0	0	0
SM2	0	0	0	0.141	0	0	0	0	0	0
SM3	0	0	0	0	0.041	0	0	0	0	0
SM4	0	0	0	0	0	0.013	0	0	0	0
SM5	0	0	0	0	0	0	0.004	0	0	0
SM6	0	0	0	0	0	0	0	0.002	0	0
dead	0	0	0	0	0	0	0	0	0	0

I) Summed elasticities of λ to adult strategy



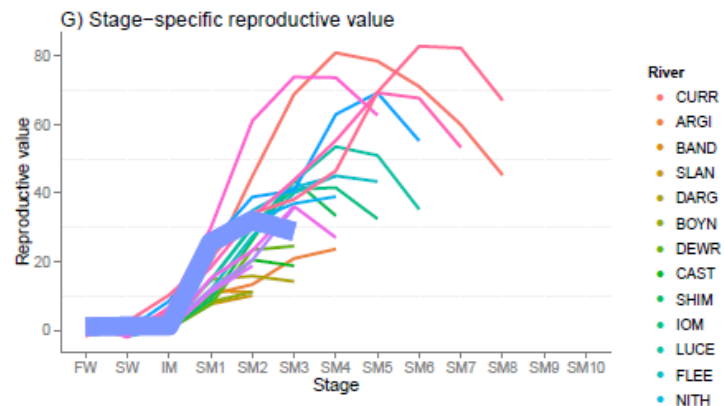
River Ribble:

Summary statistics of population dynamics analysis of sea trout from the River RIBB (n=72)



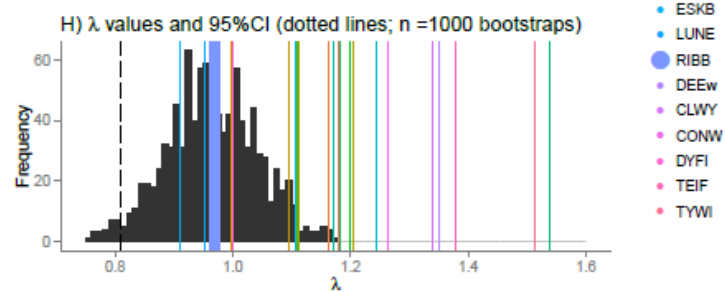
B) Transition matrix

Stage	FW	SW	IM	SM1	SM2	SM3	dead
FW	0.143	0	0	16.79	24.702	27.942	0
SW	0.078	0.004	0	0	0	0	0
IM	0.052	0.001	0.002	0	0	0	0
SM1	0.026	0.045	0.048	0	0	0	0
SM2	0	0	0	0.25	0	0	0
SM3	0	0	0	0	0.222	0	0
dead	0.7	0.95	0.95	0.75	0.778	1	0



C) Fundamental matrix

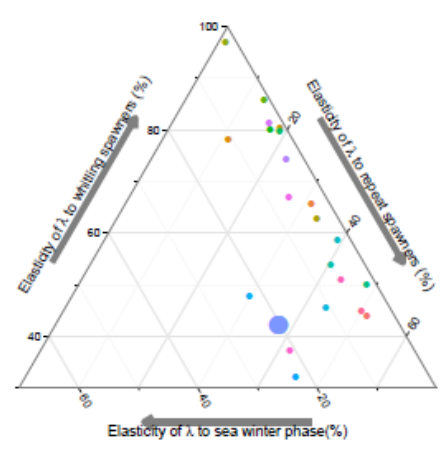
Stage	FW	SW	IM	SM1	SM2	SM3	dead
FW	1.168	0	0	0	0	0	0
SW	0.092	1.004	0	0	0	0	0
IM	0.061	0.001	1.002	0	0	0	0
SM1	0.038	0.045	0.048	1	0	0	0
SM2	0.009	0.011	0.012	0.25	1	0	0
SM3	0.002	0.003	0.003	0.056	0.222	1	0
dead	1	1	1	1	1	1	1



D) Sensitivities of λ to perturbations of the transition matrix

Stage	FW	SW	IM	SM1	SM2	SM3	dead
FW	0.426	0.034	0.023	0.014	0.004	0.001	0.378
SW	0.506	0.041	0.027	0.017	0.004	0.001	0.46
IM	0.541	0.044	0.029	0.018	0.005	0.001	0.48
SM1	10.887	0.882	0.588	0.383	0.093	0.021	9.674
SM2	13.651	1.108	0.737	0.455	0.117	0.027	12.129
SM3	12.263	0.993	0.662	0.409	0.105	0.024	10.897
dead	0	0	0	0	0	0	0

I) Summed elasticities of λ to adult strategy

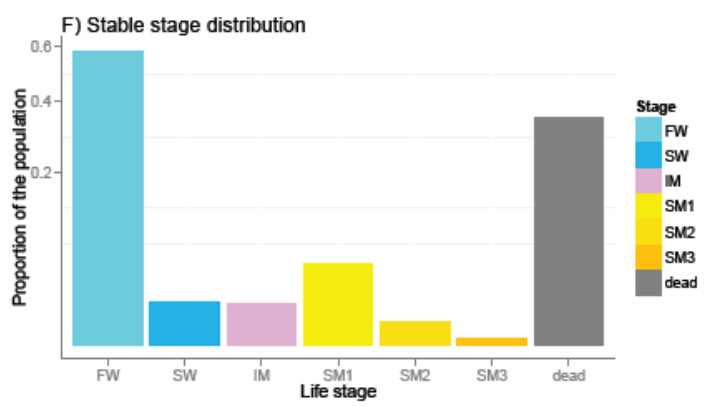
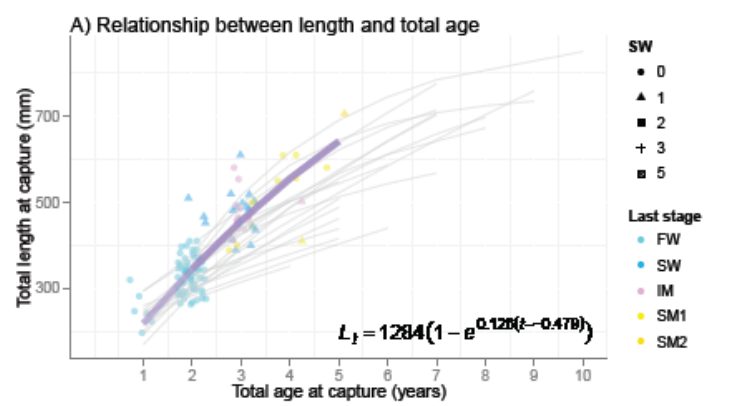


E) Elasticities of λ to perturbations of the transition matrix

Stage	FW	SW	IM	SM1	SM2	SM3	dead
FW	0.083	0	0	0.246	0.093	0.024	0
SW	0.041	0	0	0	0	0	0
IM	0.029	0	0	0	0	0	0
SM1	0.293	0.041	0.029	0	0	0	0
SM2	0	0	0	0.117	0	0	0
SM3	0	0	0	0	0.024	0	0
dead	0	0	0	0	0	0	0

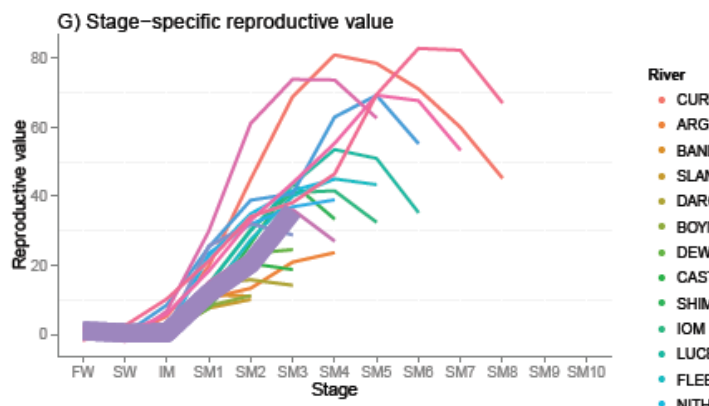
River Dee (Wales):

Summary statistics of population dynamics analysis of sea trout from the River DEEw (n=117)



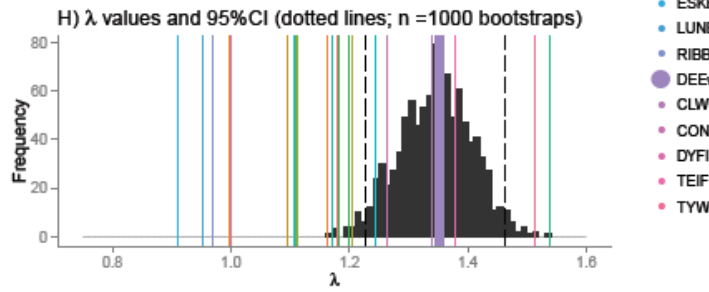
B) Transition matrix

Stage	FW	SW	IM	SM1	SM2	SM3	dead
FW	0.145	0	0	13.788	24.941	48.4	0
SW	0.029	0	0	0	0	0	0
IM	0.027	0.002	0	0	0	0	0
SM1	0.1	0.048	0.05	0	0	0	0
SM2	0	0	0	0.111	0	0	0
SM3	0	0	0	0	0.077	0	0
dead	0.7	0.95	0.95	0.889	0.923	1	0



C) Fundamental matrix

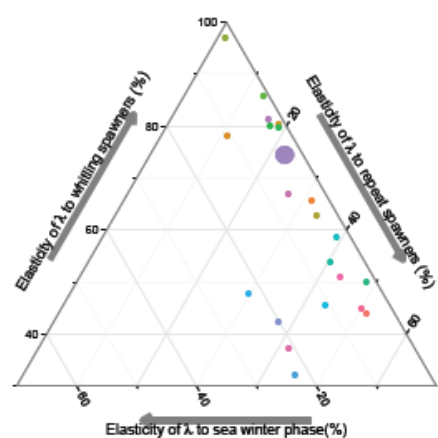
Stage	FW	SW	IM	SM1	SM2	SM3	dead
FW	1.189	0	0	0	0	0	0
SW	0.034	1	0	0	0	0	0
IM	0.031	0.002	1	0	0	0	0
SM1	0.12	0.048	0.05	1	0	0	0
SM2	0.013	0.005	0.006	0.111	1	0	0
SM3	0.001	0	0	0.009	0.077	1	0
dead	1	1	1	1	1	1	1



D) Sensitivities of λ to perturbations of the transition matrix

Stage	FW	SW	IM	SM1	SM2	SM3	dead
FW	0.488	0.011	0.01	0.037	0.003	0	0.293
SW	0.205	0.004	0.004	0.015	0.001	0	0.123
IM	0.214	0.005	0.004	0.016	0.001	0	0.129
SM1	5.797	0.125	0.114	0.436	0.036	0.002	3.483
SM2	9.995	0.216	0.197	0.751	0.062	0.004	6.005
SM3	17.488	0.377	0.344	1.313	0.108	0.006	10.494
dead	0	0	0	0	0	0	0

I) Summed elasticities of λ to adult strategy

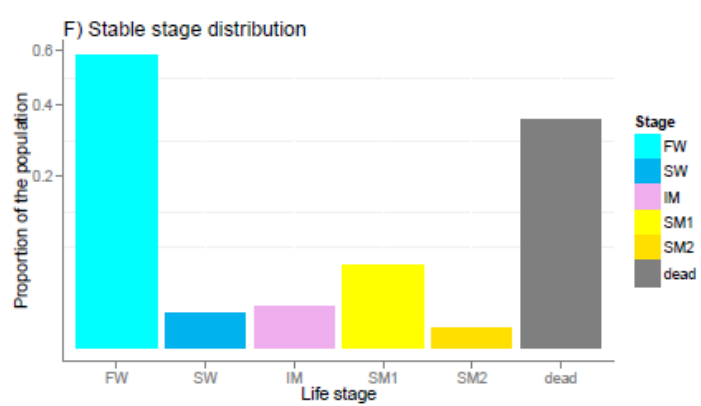
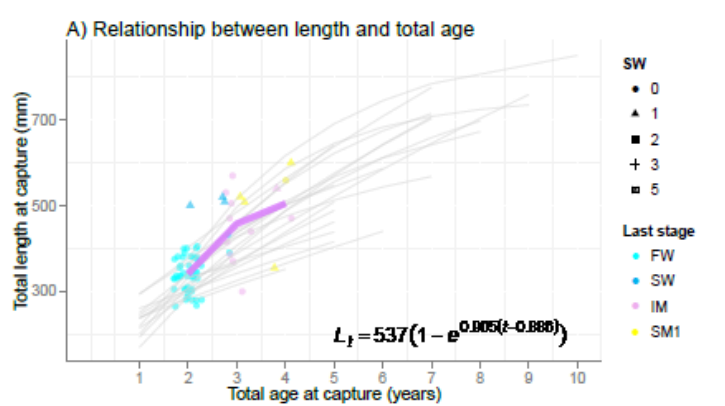


E) Elasticities of λ to perturbations of the transition matrix

Stage	FW	SW	IM	SM1	SM2	SM3	dead
FW	0.052	0	0	0.374	0.056	0.006	0
SW	0.004	0	0	0	0	0	0
IM	0.004	0	0	0	0	0	0
SM1	0.427	0.004	0.004	0	0	0	0
SM2	0	0	0	0.062	0	0	0
SM3	0	0	0	0	0.006	0	0
dead	0	0	0	0	0	0	0

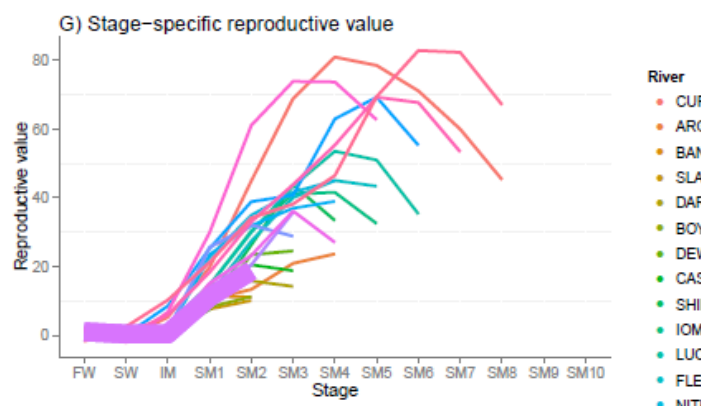
River Clwyd:

Summary statistics of population dynamics analysis of sea trout from the River CLWY (n=64)



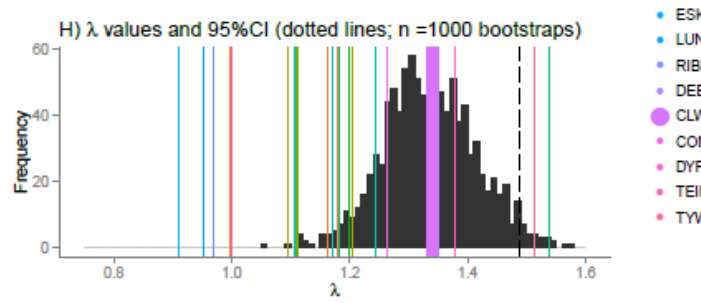
B) Transition matrix

Stage	FW	SW	IM	SM1	SM2	dead
FW	0.15	0	0	13.438	25.114	0
SW	0.019	0	0	0	0	0
IM	0.028	0.008	0	0	0	0
SM1	0.105	0.044	0.05	0	0	0
SM2	0	0	0	0.078	0	0
dead	0.7	0.95	0.95	0.922	1	0



C) Fundamental matrix

Stage	FW	SW	IM	SM1	SM2	dead
FW	1.178	0	0	0	0	0
SW	0.022	1	0	0	0	0
IM	0.03	0.008	1	0	0	0
SM1	0.127	0.044	0.05	1	0	0
SM2	0.01	0.003	0.004	0.078	1	0
dead	1	1	1	1	1	1



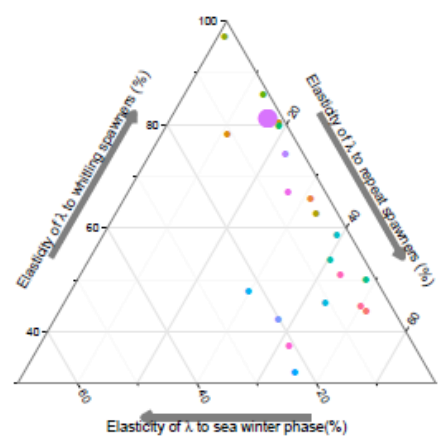
D) Sensitivities of λ to perturbations of the transition matrix

Stage	FW	SW	IM	SM1	SM2	dead
FW	0.503	0.007	0.01	0.04	0.002	0.304
SW	0.184	0.003	0.004	0.015	0.001	0.111
IM	0.209	0.003	0.004	0.017	0.001	0.126
SM1	5.592	0.078	0.108	0.447	0.026	3.379
SM2	9.424	0.132	0.182	0.753	0.044	5.695
dead	0	0	0	0	0	0

I) Summed elasticities of λ to adult strategy

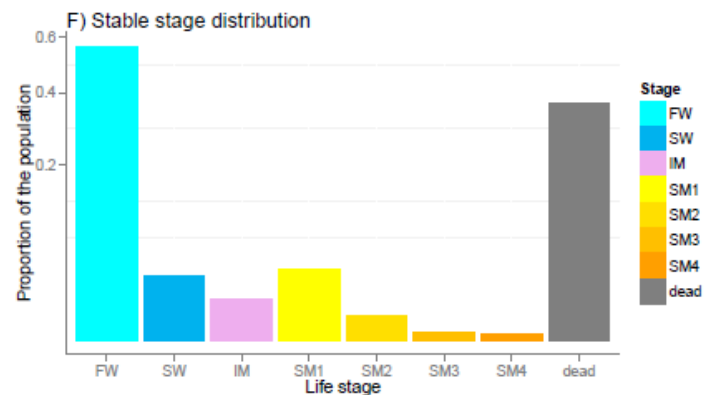
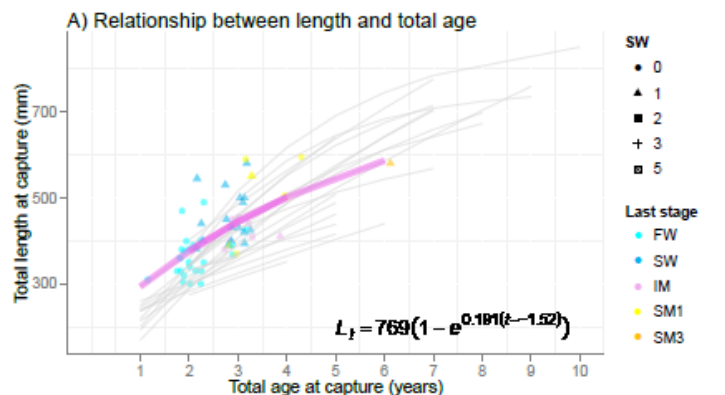
E) Elasticities of λ to perturbations of the transition matrix

Stage	FW	SW	IM	SM1	SM2	dead
FW	0.058	0	0	0.403	0.044	0
SW	0.003	0	0	0	0	0
IM	0.004	0	0	0	0	0
SM1	0.44	0.003	0.004	0	0	0
SM2	0	0	0	0.044	0	0
dead	0	0	0	0	0	0



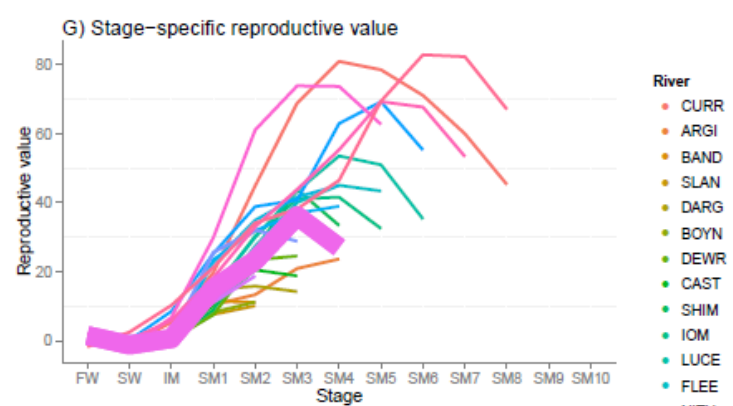
River Conwy:

Summary statistics of population dynamics analysis of sea trout from the River CONW (n=64)



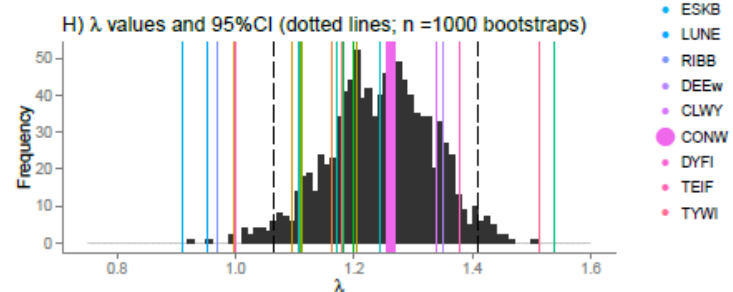
B) Transition matrix

Stage	FW	SW	IM	SM1	SM2	SM3	SM4	dead
FW	0.144	0	0	15.809	24.626	27.84	32.11	0
SW	0.061	0	0	0	0	0	0	0
IM	0.024	0.002	0	0	0	0	0	0
SM1	0.071	0.048	0.05	0	0	0	0	0
SM2	0	0	0	0.141	0	0	0	0
SM3	0	0	0	0	0.111	0	0	0
SM4	0	0	0	0	0	1	0	0
dead	0.7	0.95	0.95	0.859	0.889	0	1	0



C) Fundamental matrix

Stage	FW	SW	IM	SM1	SM2	SM3	SM4	dead
FW	1.168	0	0	0	0	0	0	0
SW	0.071	1	0	0	0	0	0	0
IM	0.029	0.002	1	0	0	0	0	0
SM1	0.087	0.048	0.05	1	0	0	0	0
SM2	0.012	0.007	0.007	0.141	1	0	0	0
SM3	0.001	0.001	0.001	0.016	0.111	1	0	0
SM4	0.001	0.001	0.001	0.016	0.111	1	1	0
dead	1	1	1	1	1	1	1	1



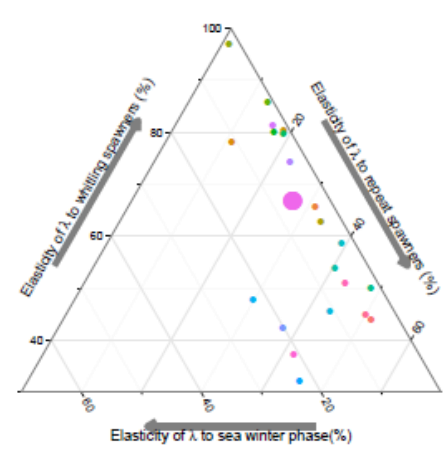
D) Sensitivities of λ to perturbations of the transition matrix

Stage	FW	SW	IM	SM1	SM2	SM3	SM4	dead
FW	0.473	0.023	0.009	0.028	0.003	0	0	0.308
SW	0.272	0.013	0.005	0.016	0.002	0	0	0.177
IM	0.283	0.014	0.005	0.017	0.002	0	0	0.184
SM1	7.151	0.345	0.139	0.419	0.047	0.004	0.003	4.651
SM2	10.991	0.531	0.213	0.644	0.072	0.006	0.005	7.148
SM3	19.974	0.965	0.387	1.171	0.13	0.011	0.009	12.99
SM4	12.038	0.581	0.234	0.706	0.079	0.007	0.005	7.829
dead	0	0	0	0	0	0	0	0

I) Summed elasticities of λ to adult strategy

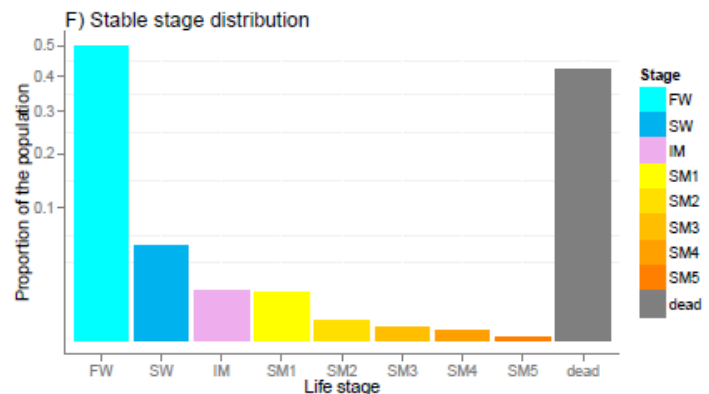
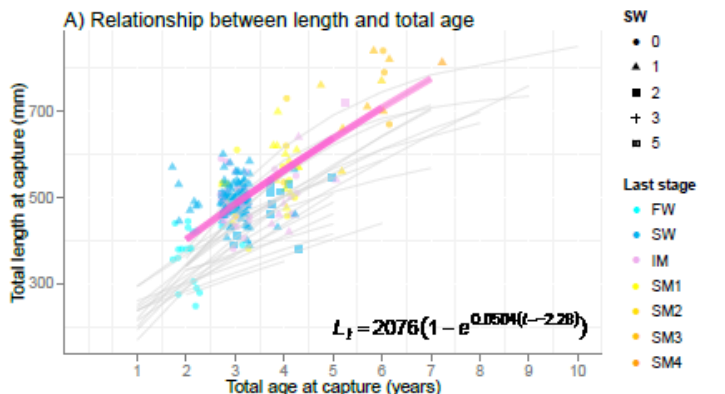
E) Elasticities of λ to perturbations of the transition matrix

Stage	FW	SW	IM	SM1	SM2	SM3	SM4	dead
FW	0.054	0	0	0.348	0.06	0.006	0.005	0
SW	0.013	0	0	0	0	0	0	0
IM	0.005	0	0	0	0	0	0	0
SM1	0.401	0.013	0.005	0	0	0	0	0
SM2	0	0	0	0.072	0	0	0	0
SM3	0	0	0	0	0.011	0	0	0
SM4	0	0	0	0	0	0.005	0	0
dead	0	0	0	0	0	0	0	0



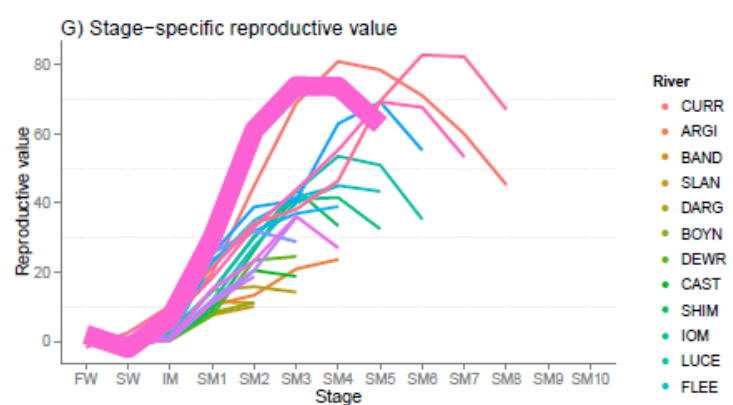
River Dyfi:

Summary statistics of population dynamics analysis of sea trout from the River DYFI (n=236)



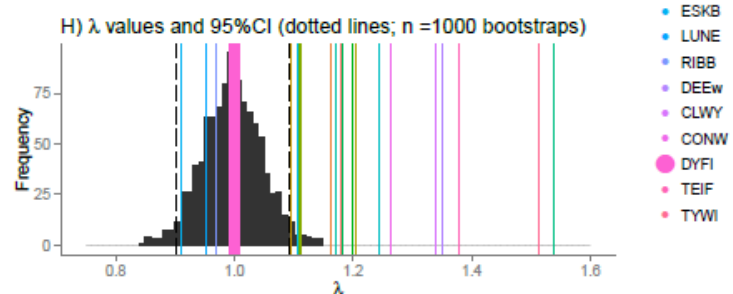
B) Transition matrix

Stage	FW	SW	IM	SM1	SM2	SM3	SM4	SM5	dead
FW	0.149	0	0	22.106	30.21	44.901	57.769	65.31	0
SW	0.102	0.004	0	0	0	0	0	0	0
IM	0.028	0.003	0.001	0	0	0	0	0	0
SM1	0.02	0.042	0.049	0	0	0	0	0	0
SM2	0	0	0	0.178	0	0	0	0	0
SM3	0	0	0	0	0.357	0	0	0	0
SM4	0	0	0	0	0	0.533	0	0	0
SM5	0	0	0	0	0	0	0.125	0	0
dead	0.7	0.95	0.95	0.822	0.643	0.487	0.875	1	0



C) Fundamental matrix

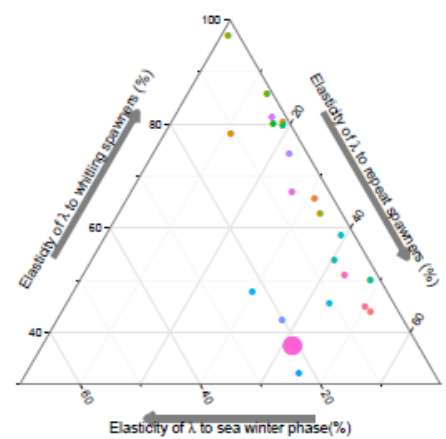
Stage	FW	SW	IM	SM1	SM2	SM3	SM4	SM5	dead
FW	1.178	0	0	0	0	0	0	0	0
SW	0.121	1.004	0	0	0	0	0	0	0
IM	0.033	0.003	1.001	0	0	0	0	0	0
SM1	0.031	0.043	0.049	1	0	0	0	0	0
SM2	0.005	0.008	0.009	0.178	1	0	0	0	0
SM3	0.002	0.003	0.003	0.064	0.357	1	0	0	0
SM4	0.001	0.001	0.002	0.034	0.19	0.533	1	0	0
SM5	0	0	0	0.004	0.024	0.087	0.125	1	0
dead	1	1	1	1	1	1	1	1	1



D) Sensitivities of λ to perturbations of the transition matrix

Stage	FW	SW	IM	SM1	SM2	SM3	SM4	SM5	dead
FW	0.398	0.041	0.011	0.01	0.002	0.001	0	0	0.339
SW	0.553	0.057	0.016	0.014	0.003	0.001	0	0	0.47
IM	0.637	0.065	0.018	0.017	0.003	0.001	0.001	0	0.542
SM1	12.966	1.329	0.389	0.339	0.06	0.022	0.011	0.001	11.022
SM2	23.407	2.399	0.668	0.612	0.109	0.039	0.021	0.003	19.897
SM3	31.874	3.267	0.907	0.833	0.148	0.053	0.028	0.004	27.094
SM4	26.253	2.691	0.747	0.688	0.122	0.044	0.023	0.003	22.317
SM5	26.007	2.666	0.74	0.68	0.121	0.043	0.023	0.003	22.108
dead	0	0	0	0	0	0	0	0	0

I) Summed elasticities of λ to adult strategy

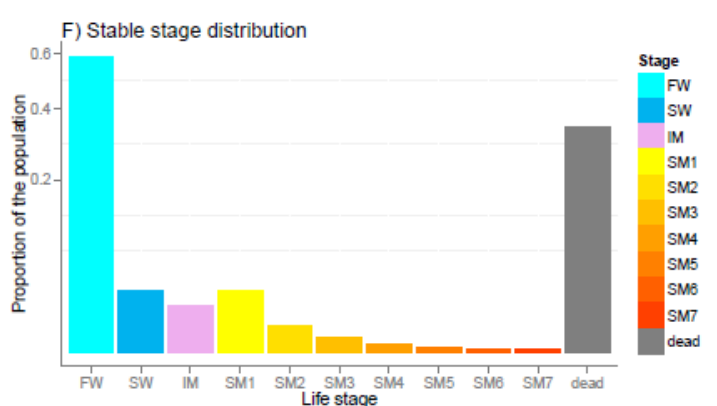
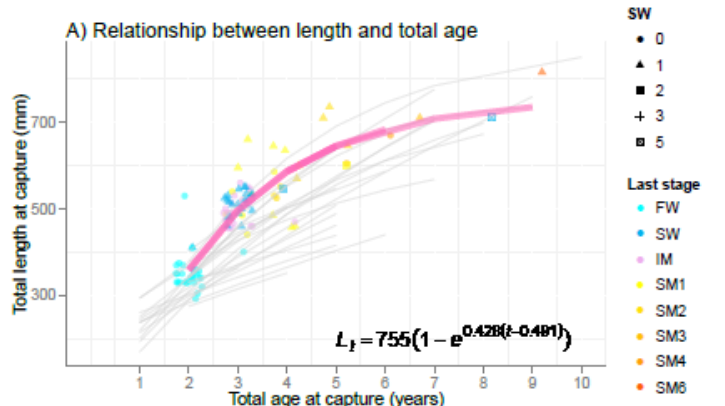


E) Elasticities of λ to perturbations of the transition matrix

Stage	FW	SW	IM	SM1	SM2	SM3	SM4	SM5	dead
FW	0.059	0	0	0.23	0.056	0.03	0.02	0.003	0
SW	0.056	0	0	0	0	0	0	0	0
IM	0.018	0	0	0	0	0	0	0	0
SM1	0.285	0.058	0.018	0	0	0	0	0	0
SM2	0	0	0	0.109	0	0	0	0	0
SM3	0	0	0	0	0.053	0	0	0	0
SM4	0	0	0	0	0	0.023	0	0	0
SM5	0	0	0	0	0	0	0.003	0	0
dead	0	0	0	0	0	0	0	0	0

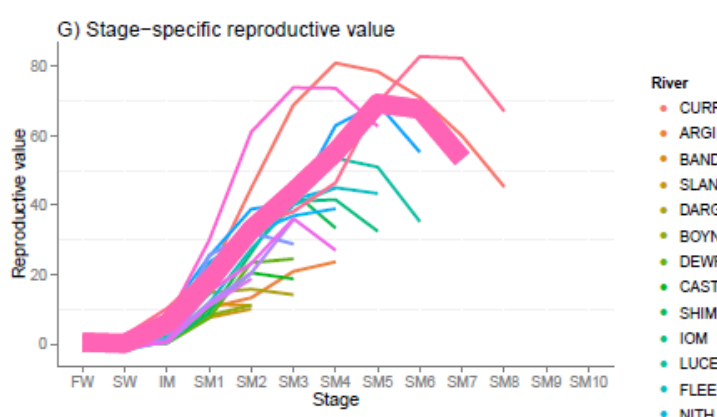
River Teifi:

Summary statistics of population dynamics analysis of sea trout from the River TEIF (n=102)



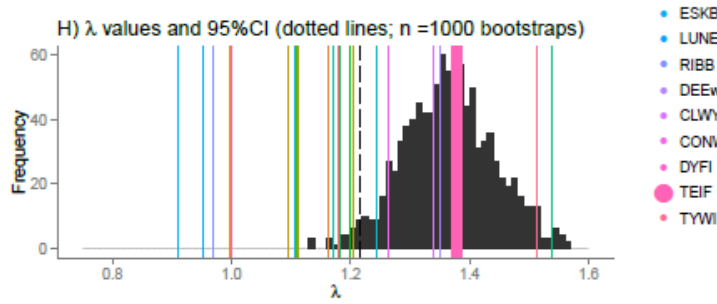
B) Transition matrix

Stage	FW	SW	IM	SM1	SM2	SM3	SM4	SM5	SM6	SM7	dead
FW	0.149	0	0	19.277	29.001	37.293	44.763	52.1	63.68	65.65	0
SW	0.059	0.007	0	0	0	0	0	0	0	0	0
IM	0.034	0	0.002	0	0	0	0	0	0	0	0
SM1	0.058	0.043	0.048	0	0	0	0	0	0	0	0
SM2	0	0	0	0.255	0	0	0	0	0	0	0
SM3	0	0	0	0	0.423	0	0	0	0	0	0
SM4	0	0	0	0	0	0.364	0	0	0	0	0
SM5	0	0	0	0	0	0	0.5	0	0	0	0
SM6	0	0	0	0	0	0	0	0.5	0	0	0
SM7	0	0	0	0	0	0	0	0	1	0	0
dead	0.7	0.95	0.95	0.745	0.577	0.636	0.5	0.5	0	1	0



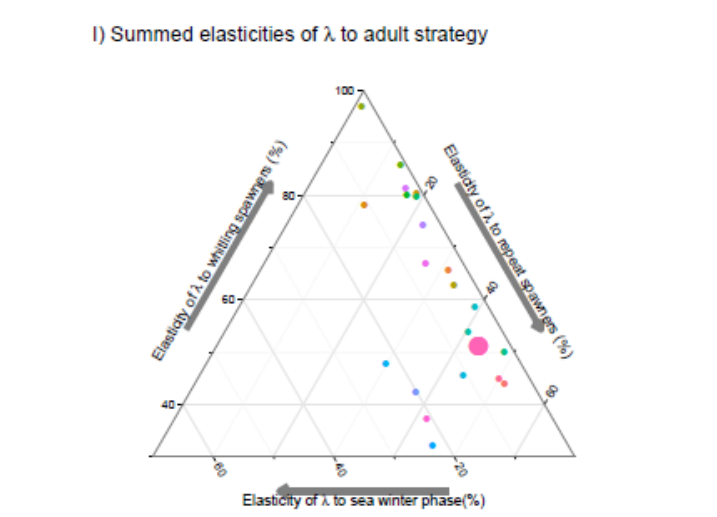
C) Fundamental matrix

Stage	FW	SW	IM	SM1	SM2	SM3	SM4	SM5	SM6	SM7	dead
FW	1.175	0	0	0	0	0	0	0	0	0	0
SW	0.07	1.007	0	0	0	0	0	0	0	0	0
IM	0.04	0	1.002	0	0	0	0	0	0	0	0
SM1	0.073	0.044	0.048	1	0	0	0	0	0	0	0
SM2	0.019	0.011	0.012	0.255	1	0	0	0	0	0	0
SM3	0.008	0.005	0.005	0.108	0.423	1	0	0	0	0	0
SM4	0.003	0.002	0.002	0.039	0.154	0.364	1	0	0	0	0
SM5	0.001	0.001	0.001	0.02	0.077	0.182	0.5	1	0	0	0
SM6	0.001	0	0	0.01	0.038	0.091	0.25	0.5	1	0	0
SM7	0.001	0	0	0.01	0.038	0.091	0.25	0.5	1	1	0
dead	1	1	1	1	1	1	1	1	1	1	1



D) Sensitivities of λ to perturbations of the transition matrix

Stage	FW	SW	IM	SM1	SM2	SM3	SM4	SM5	SM6	SM7	dead
FW	0.42	0.018	0.01	0.018	0.003	0.001	0	0	0	0	0.245
SW	0.27	0.012	0.007	0.012	0.002	0.001	0	0	0	0	0.157
IM	0.296	0.013	0.007	0.013	0.002	0.001	0	0	0	0	0.173
SM1	8.506	0.366	0.21	0.374	0.069	0.021	0.006	0.002	0.001	0.001	4.96
SM2	14.249	0.614	0.352	0.627	0.116	0.036	0.009	0.003	0.001	0.001	8.31
SM3	17.649	0.76	0.436	0.777	0.144	0.044	0.012	0.004	0.002	0.001	10.292
SM4	23.848	1.027	0.589	1.05	0.194	0.06	0.016	0.006	0.002	0.001	13.907
SM5	28.164	1.213	0.695	1.24	0.229	0.07	0.019	0.007	0.002	0.002	16.424
SM6	33.9	1.46	0.837	1.492	0.276	0.085	0.022	0.008	0.003	0.002	19.789
SM7	19.996	0.861	0.494	0.88	0.163	0.05	0.013	0.005	0.002	0.001	11.661
dead	0	0	0	0	0	0	0	0	0	0	0

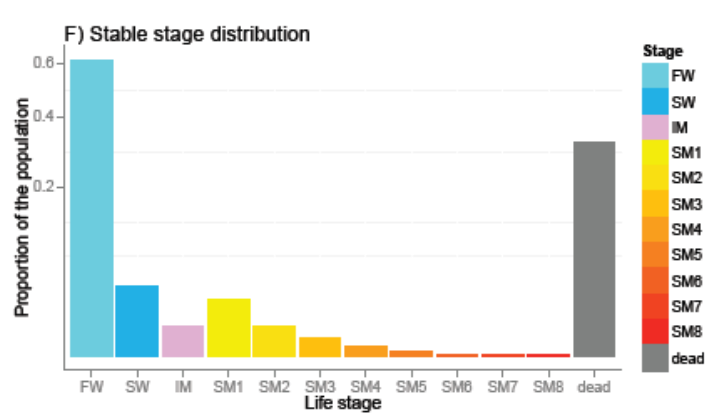
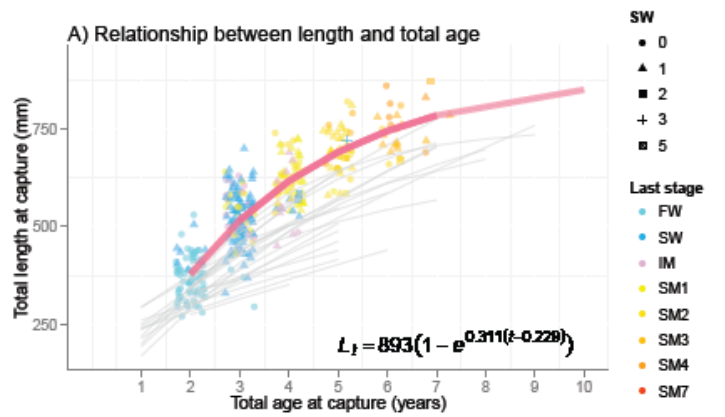


E) Elasticities of λ to perturbations of the transition matrix

Stage	FW	SW	IM	SM1	SM2	SM3	SM4	SM5	SM6	SM7	dead
FW	0.045	0	0	0.258	0.072	0.028	0.009	0.004	0.002	0.001	0
SW	0.012	0	0	0	0	0	0	0	0	0	0
IM	0.007	0	0	0	0	0	0	0	0	0	0
SM1	0.356	0.012	0.007	0	0	0	0	0	0	0	0
SM2	0	0	0	0.116	0	0	0	0	0	0	0
SM3	0	0	0	0	0.044	0	0	0	0	0	0
SM4	0	0	0	0	0	0.016	0	0	0	0	0
SM5	0	0	0	0	0	0	0.007	0	0	0	0
SM6	0	0	0	0	0	0	0	0.003	0	0	0
SM7	0	0	0	0	0	0	0	0	0.001	0	0
dead	0	0	0	0	0	0	0	0	0	0	0

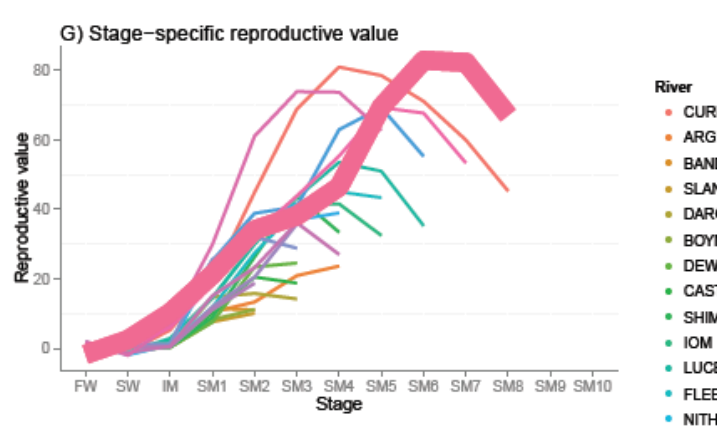
River Tywi:

Summary statistics of population dynamics analysis of sea trout from the River TYWI (n=356)



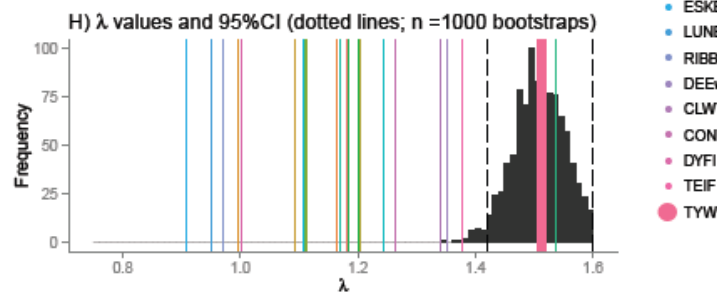
B) Transition matrix

Stage	FW	SW	IM	SM1	SM2	SM3	SM4	SM5	SM6	SM7	SM8	dead
FW	0.151	0	0	21.945	34.091	44.488	53.118	62.199	78.05	82.4	85.67	0
SW	0.082	0.003	0	0	0	0	0	0	0	0	0	0
IM	0.015	0.003	0	0	0	0	0	0	0	0	0	0
SM1	0.052	0.044	0.05	0	0	0	0	0	0	0	0	0
SM2	0	0	0	0.413	0	0	0	0	0	0	0	0
SM3	0	0	0	0	0.578	0	0	0	0	0	0	0
SM4	0	0	0	0	0	0.353	0	0	0	0	0	0
SM5	0	0	0	0	0	0	0.267	0	0	0	0	0
SM6	0	0	0	0	0	0	0	0.125	0	0	0	0
SM7	0	0	0	0	0	0	0	0	0.1	0	0	0
SM8	0	0	0	0	0	0	0	0	0	0.1	0	0
dead	0.7	0.95	0.95	0.587	0.422	0.647	0.733	0.875	0	0	1	0



C) Fundamental matrix

Stage	FW	SW	IM	SM1	SM2	SM3	SM4	SM5	SM6	SM7	SM8	dead
FW	1.178	0	0	0	0	0	0	0	0	0	0	0
SW	0.097	1.003	0	0	0	0	0	0	0	0	0	0
IM	0.018	0.003	1	0	0	0	0	0	0	0	0	0
SM1	0.068	0.045	0.05	1	0	0	0	0	0	0	0	0
SM2	0.027	0.018	0.021	0.413	1	0	0	0	0	0	0	0
SM3	0.016	0.011	0.012	0.239	0.578	1	0	0	0	0	0	0
SM4	0.006	0.004	0.004	0.084	0.204	0.353	1	0	0	0	0	0
SM5	0.001	0.001	0.001	0.022	0.054	0.094	0.267	1	0	0	0	0
SM6	0	0	0	0.003	0.007	0.012	0.033	0.125	1	0	0	0
SM7	0	0	0	0.003	0.007	0.012	0.033	0.125	1	1	0	0
SM8	0	0	0	0.003	0.007	0.012	0.033	0.125	1	1	1	0
dead	1	1	1	1	1	1	1	1	1	1	1	1



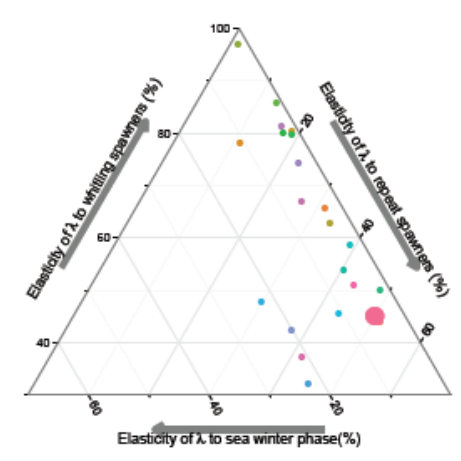
D) Sensitivities of λ to perturbations of the transition matrix

Stage	FW	SW	IM	SM1	SM2	SM3	SM4	SM5	SM6	SM7	SM8	dead
FW	0.397	0.022	0.004	0.014	0.004	0.002	0	0	0	0	0	0.207
SW	0.289	0.018	0.003	0.01	0.003	0.001	0	0	0	0	0	0.151
IM	0.325	0.018	0.003	0.012	0.003	0.001	0	0	0	0	0	0.17
SM1	9.84	0.535	0.099	0.357	0.097	0.037	0.009	0.002	0	0	0	5.14
SM2	14.959	0.814	0.151	0.543	0.148	0.057	0.013	0.002	0	0	0	7.815
SM3	15.741	0.857	0.159	0.571	0.158	0.08	0.014	0.002	0	0	0	8.223
SM4	17.456	0.95	0.176	0.633	0.173	0.088	0.015	0.003	0	0	0	9.119
SM5	19.997	1.088	0.201	0.726	0.198	0.076	0.018	0.003	0	0	0	10.446
SM6	44.583	2.426	0.449	1.618	0.442	0.189	0.039	0.007	0.001	0	0	23.29
SM7	36.486	1.984	0.367	1.323	0.361	0.138	0.032	0.006	0	0	0	19.05
SM8	22.467	1.223	0.226	0.815	0.223	0.085	0.02	0.004	0	0	0	11.737
dead	0	0	0	0	0	0	0	0	0	0	0	0

I) Summed elasticities of λ to adult strategy

E) Elasticities of λ to perturbations of the transition matrix

Stage	FW	SW	IM	SM1	SM2	SM3	SM4	SM5	SM6	SM7	SM8	dead
FW	0.04	0	0	0.209	0.089	0.044	0.012	0.003	0	0	0	0
SW	0.018	0	0	0	0	0	0	0	0	0	0	0
IM	0.003	0	0	0	0	0	0	0	0	0	0	0
SM1	0.338	0.018	0.003	0	0	0	0	0	0	0	0	0
SM2	0	0	0	0.148	0	0	0	0	0	0	0	0
SM3	0	0	0	0	0.08	0	0	0	0	0	0	0
SM4	0	0	0	0	0	0.015	0	0	0	0	0	0
SM5	0	0	0	0	0	0	0.003	0	0	0	0	0
SM6	0	0	0	0	0	0	0	0.001	0	0	0	0
SM7	0	0	0	0	0	0	0	0	0.001	0	0	0
SM8	0	0	0	0	0	0	0	0	0	0.001	0	0
dead	0	0	0	0	0	0	0	0	0	0	0	0



4. Discussion:

It is important to recognise that a number of caveats limit the power of the population dynamics analysis of the current dataset: the variance in sampling efforts among rivers (from 44 in the BAND to 378 in the ESKB) may have led to variance in the certainty of estimated population parameters, and thus interpretation of these parameters from low confidence populations must be done with caution. The average life history of returning sea trout varies strongly over the months, where older sea trout return earlier in the year than whitling. If sampling in certain rivers is biased to early or late months, then the estimated population parameters will not be representative of the whole population inhabiting the river. For example, the BOYN has a rather high proportion of August and September caught individuals (Figure 2), which are frequently whitling, and shows the highest dependence on the minimum life history strategy (2.0+). If the sampling is biased because there was no sampling in earlier months, rather than a true biological feature (no sea trout returning in earlier months), then the high dependence on the minimum life history (2.0+) would be a spurious result. However, other rivers in the area (DARG, DEWR, CAST and SHIM) also have high proportions of late returning fish, and are characterised by relatively high dependency on such short life history strategy, giving weight to a regional tendency of sea trout populations towards simplified life history strategies.

The survival transitions for repeat spawners (e.g. SM₂ -> SM₃, SM₃ -> SM₄...) were estimated based on the transitions reported in the whole data available for each river (i.e. combining all sampling years together). Hence, these transition estimates assume that populations are at stable stage distribution, which is unlikely to be true. For rivers with large sample sizes, future analysis should evaluate the temporal stability of the estimated parameters to assess the confidence on the estimated values.

The fecundity of each individual sea trout was not empirically known, and thus it was estimated based on individual length using a relationship based on 55 sampled individuals (CSTP Report) collected from marine zones between July and October. With the data available, it was not possible to produce river specific fecundity relationships, which may have an important impact on population dynamics. If possible, an evaluation of the variance of river specific fecundity values would improve the estimates of population dynamics parameters.

As indicated in the introduction, sometimes post-smolting winter marks are indeterminate in that some erosion of the scale is present but not enough to clearly state a return of the individual to fresh water to spawn. These winter marks were recorded as indeterminate marks (IM), and were modelled identically as sea winters (SW), i.e. they had no fecundity values associated with them. Without further information on the true nature of these IMs, it is difficult to judge on the impact on the model of inclusion of IMs as spawners. First spawners are by far the highest contributors to the next generation and thus if all IMs are spawners, they would have a significant impact on the estimated parameters. If data were collected that would allow estimating the number of true spawners among the IM, then that proportion could be easily included in the matrix model by multiplying that proportion by the SM₁ fecundity. Such evaluation could have important effect on rivers with a relatively high proportion of IMs, such as the rivers in the south west of Ireland, England, and mid Wales.

The matrix population models were constructed solely on returning individuals on their way back to their spawning grounds, and hence no river specific empirical information on the life cycle before first reproduction (fresh water survival and sea winter survival) was available. This means that the inter-river variance in those parameters has not been captured by the current sampling effort. Identical standardised parameters for the unsampled transition values (fresh water mortality =0.7, brown trout spawning=0, and sea winter mortality=0.95) were employed for all rivers, so all variance in estimated λ values is due to variance in inter-river post-first reproduction survival and fecundity. Hence, the absolute λ values cannot be interpreted as true population growth rate values, as among river variance in the unsampled transitions is likely to have major impacts on λ , but as the relative effects of the variance in post-first reproduction life-history on the population dynamics of trout populations. The available data allows us to estimate that, unless balanced by the unsampled transitions, the ESKB has a lower population growth rate than the TYWI, and that such difference may be explained by the relatively high frequency of individuals experiencing one or two winters at sea before first reproduction combined with a relatively low frequency of repeat spawners in the ESKB compared to the TYWI, a river whose sea trout population is characterised by high elasticity of λ to repeat spawners.

The current model also ignores the contribution of brown trout spawning to the population dynamics of trout on the studied rivers, as no empirical contemporary data was available on: 1) the river specific proportion of the population remaining as brown trout, 2) the somatic growth rate of such brown trout, and 3) the relationship between somatic size and fecundity for brown trout females. These parameters are likely to have major effects on the population dynamics of trout. If empirical data were available for all rivers, then a more complex version of the matrix models employed here as suggested by Ffister & Wang (2005) could be envisaged (Figure 22), where the two alternative life strategies (brown trout and sea trout) are included in the matrix, each with their own survival, growth, and fecundity transition values. However, parameterising such a model would require an extensive sampling of the fresh water phase of all rivers targeted.

$$\begin{bmatrix} s_{L,1}(1 - g_{L,1})p_{LL,1} & s_{H,1}(1 - g_{H,1})p_{HL,1} & F_{LL,2} & F_{HL,2} & F_{LL,3} & F_{HL,3} \\ s_{L,1}(1 - g_{L,1})p_{LH,1} & s_{H,1}(1 - g_{H,1})p_{HH,1} & F_{LH,2} & F_{HH,2} & F_{LH,3} & F_{HH,3} \\ s_{L,1}g_{L,1}p_{LL,1} & s_{H,1}g_{H,1}p_{HL,1} & s_{L,2}(1 - g_{L,2})p_{LL,2} & s_{H,2}(1 - g_{H,2})p_{HL,2} & 0 & 0 \\ s_{L,1}g_{L,1}p_{LH,1} & s_{H,1}g_{H,1}p_{HH,1} & s_{L,2}(1 - g_{L,2})p_{LH,2} & s_{H,2}(1 - g_{H,2})p_{HH,2} & 0 & 0 \\ 0 & 0 & s_{L,2}g_{L,2}p_{LL,2} & s_{H,2}g_{H,2}p_{HL,2} & s_{L,3}p_{LL,3} & s_{H,3}p_{HL,3} \\ 0 & 0 & s_{L,2}g_{L,2}p_{LH,2} & s_{H,2}g_{H,2}p_{HH,2} & s_{L,3}p_{LH,3} & s_{H,3}p_{HH,3} \end{bmatrix}$$

Figure 22: Example of matrix model with two alternative life strategies (H and L): S indicates survival; g indicates growth; p the probability of changing from one strategy to the other; and F indicates the fecundity towards each strategy. Reproduced from (Pfister)

Future work on the current dataset and results should aim to estimate the importance of environmental variables and population genetic structure on explaining the different population dynamic patterns encountered here. The relative importance of environmental variables such as fresh water productivity, temperature, river size, marine food availability, predation, fishing pressure, and population genetic structure on the elasticities of λ to certain transitions of life history patterns should be explored. Associations between environmental or genetic patterns and life history strategies would allow modelling the potential impact of changes on those

patters on the population dynamics parameters of sea trout populations around the Celtic and Irish Seas.

The current models could be improved through integrated projection models (IPMs), in which several sources of data (e.g. scale reading data to estimate life history, fisheries data to estimate census size, mark-recapture data to estimate survival, and published data to estimate unsampled transitions) can be incorporated into a single model (Ellner & Rees 2006; Abadi *et al.* 2010; Schaub & Abadi 2011; Metcalf *et al.* 2013). All sources of uncertainty due to process variability and sampling error can also be included through state-space models (Buckland *et al.* 2004; Petris & Petrone 2011), and thus confidence on parameter estimate can be evaluated as well. The IPMpack (Metcalf *et al.* 2013) offers the possibility of constructing IPMs based on continuous demographic variables, such as weight, and allows the inclusion of complex life cycles and independent covariates, such as environment or genetic population membership. Future work on the dataset presented here should aim to produce IPMs where the different sources of data are incorporated and the uncertainty in each of the estimated parameters is reported.

5. Bibliography

Abadi F, Gimenez O, Arlettaz R, Schaub M (2010) An assesment of integrated population models: bias, accuracy, and violation of the assumption of independence, *Ecology*, **91**, 7-14.

Buckland ST, Newman KB, Thomas L, Koesters NB (2004) State-space models for the dynamics of wild animal populations, *Ecological modelling*, **171**, 157-175.

Caswell H (2001) *Matrix Population Models: construction, analysis and interpretation*, 2nd edition, USA: Sinauer.

Ellner SP, Rees M (2006) Integral projection models for species with complex demography, *The American Naturalist*, **167**, 410-428.

Gotelli NJ (2008) *A primer of Ecology*, W. H. Freeman.

Metcalf CJE, McMahon S, Salguero-Gomez R, Jongejans E (2013) IMPpack: an R package for integral projection models, *Methods in Ecology and Evolution*, **4**, 195-200.

Petris G, Petrone S (2011) State space models in R, *Journal of statistical software*, **41**.

Pfister CA, Wang M (2005) Beyond size: matrix projection models for populations where size is an incomplete descriptor, *Ecology*, **86**, 2673-2683.

R Development Core Team (2014) *R: a language and environment for statistical computing.*, URL: <http://www.R-project.org> edition, Vienna, Austria: R Foundation for Statistical Computing, Available: <http://www.R-project.org>.

Schaub M, Abadi F (2011) Integrated population models: a novel analysis framework for deeper insights into population dynamics, *Journal of Ornithology*, **152**, S227-S237.

Stubben C, Milligan B (2007) Estimating and analyzing Demographic Models using the popbio package in R, *Journal of Statistical Software*, **22**, 1-23.

6. List of Figures and Tables

Figure 1: Sea trout scale viewed under the microscope showing the patterning in circuli typical of fresh water and marine phases of its life history	2
Figure 2: Monthly distribution of captured sea trout by river. Monthly proportions are depicted as pie charts coloured by month. River codes are indicated above pies, while sample size numbers are below pies.	4
Figure 3: Relationship between thawed and fresh length and weight of sea trout	5
Figure 4: Relationship between reconstructed length and reconstructed weight of sea trout	5
Figure 5: Relationship between length and total age for the River ESKB	7
Figure 6: Logarithmic plots of sea trout abundance (N) per sea age class in 25 CSTP rivers	14
Figure 7: Reconstructed length and weight by age class for male and female sea trout.....	15
Figure 8: Proportion of females (red) and males (blue) by sea age among sea trout by river. Indeterminate and not examined sea trout are in grey.....	16
Figure 9: Number of female (red) and male (blue) sea trout by sampling month and by river. Indeterminate and not examined individuals are in grey.	16
Figure 10: Length at age relationship for sea trout for all rivers and estimates of von Bertalanffy model parameters by river	17
Figure 11: Stage specific survival of returning adult sea trout by river.....	18
Figure 12: Population specific λ values and bootstraps (n=1000) based on 200 transitions (~40 inds)	20
Figure 13: Stable stage distribution of sea trout populations from 22 rivers around the Irish and Celtic Seas.....	21
Figure 14: Number of eggs per female and stage specific reproductive value by river	22
Figure 15: Fundamental matrix of sea trout population of the river ESKB	23
Figure 16: Fundamental matrix of sea trout population of the river CURR.....	23
Figure 17: Comparison of fundamental value of transitions among rivers grouped by transition type (retention in freshwater, smolting to sea winter stage, freshwater to first reproduction, sea winter to first reproduction, and first reproduction to repeat spawner)	24
Figure 18: Sensitivities of λ to transitions by river.....	25
Figure 19: Summed elasticities of λ to different phases of the adult life history strategy and relationship between λ and elasticity of λ to sea winter phase.....	27
Figure 20: Summed elasticities of λ to different phases of adult life history strategy and relationship between λ and elasticity of λ to repeat spawners	27
Figure 21: Summed elasticities of λ to different phases of adult life history strategy and relationship between λ and elasticity of λ to sea winters	28
Figure 22: Example of matrix model with two alternative life strategies (H and L): S indicates survival; g indicates growth; p the probability of changing from one strategy to the other; and F indicates the fecundity towards each strategy. Reproduced from (Pfiste	53
Table 1: Extract of the recreated life history table for five individuals from the River CURR.....	8
Table 2: Transition matrix from the River ESKB without mortality modifiers	9
Table 3: Fecundity matrix from the River ESKB without egg mortality modifiers	9

Table 4: Combined transition and fecundity matrix for the river ESKB with mortality modifiers..... 10

Table 5: Samples sizes by rivers and Marine zones.....13

Table 6: Number of females, males, and non-sexed sea trout..... 14

Table 7: Sample size and proportion of females by river.....15

Table 8: Population dynamics summary statistics by river..... 19

Table 9: River-specific stable stage distributions of 22 sea trout populations around the Celtic and Irish Seas.....21

Table 10: Reconstructed average number of eggs per female by stage and river..... 22

Table 11: Stage specific reproductive value, the mean number of offspring to be produced in its remaining lifetime, by river and the stage at maximal reproductive value (StageMax). 23

Table 12: Elasticities of λ to the minimum life history strategy (E.MinLH) and to alternative life history strategies (E.AltLH) by river..... 26