

Modelling the salmon life-cycle: the marine and river-return phases.

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WILLIAM S.C. GURNEY^{*1,2}, BACON P.J.², MACLEAN J.C.²,
SMITH G.² AND YOUNGSON A.F.²

¹*Department of Statistics and Modelling Science, University of Strathclyde,
GLASGOW G1 1XH, Scotland*

²*F.R.S. Marine Laboratory, ABERDEEN, Scotland.*

*Corresponding author

1. The observational context

1.1. Observations the model must encompass

1. Grilse (one sea-winter fish) coexist with multi sea-winter (MSW) fish over a wide range of habitats.
2. Early maturity is known to be heritable in farmed fish and so return after one sea-winter ('grilsing') in the wild must be presumed heritable.
3. Grilse return to their home catchment May → September, while MSW fish return January → September (Fig. 8a). Individuals returning early in 'their' run are associated with high altitude habitats. Late returners are associated with low altitude habitats.
4. The distribution of returners over the grilse run is remarkably stable over the period 1967-2003. The distribution of MSW returners is also quite stable, with the exception of a strong peak in late February which is present pre-1983 and absent thereafter (Fig. 8a).
5. Early, middle and late returning grilse exhibit long-run average growth performance which is consistent over the run, as do MSW fish. The long-run average growth performance of all MSW fish is worse than that of grilse. (Fig. 8b and Table 1)
6. Returning males of a given sea age, river age and run-time are *slightly* larger than returning females of the same group. (Fig. 8b).
7. Grilse are systematically less abundant (relative to MSW fish) in upland habitats (Fig. 1b and 7b, red line) but are numerically dominant in lowland habitats (Fig. 7b, blue line).
8. Spawning MSW fish are roughly 60% female in all habitats. Spawning grilse are increasingly male biased as altitude rises – over 80% of Girnock grilse are male (Fig. 1d), as are early runners in the N. Esk (Fig. 7d, red line), whereas late running grilse in the N. Esk have recently been almost 50% male (Fig. 7d green line).
9. Fertilised ova have a 1:1 sex ratio. Genetic marker studies on coho smolts suggest that in-river survival is sex-independent (implying that the mechanism for observed sex ratio deviations must lie in differential sea survival).
10. Sea-survivals calculated for N. Esk fish on the basis of an arbitrary division of outgoing smolts between those destined to return as grilse and multi-sea-winter fish (Fig. 9) show a post-1980 downward trend for both grilse and MSW fish.
11. The overall survivals thus calculated for grilse and MSW fish differ by only a factor of 2, implying that *either* the mortality rate for MSW fish is around 70% of that for grilse *or* grilse and MSW fish from a given cohort undergo the same risks while both are at sea, implying an MSW mortality rate during their extended sea-life $\approx 25\%$ of that for grilse.
12. Individual fecundity of spawning females in the Baddoch and Girnock rises faster than the cube of their length. Ova mass $\propto L^{4.3}$ (Fig. 3).
13. There is very strong density dependence between spawning and the following autumn's fry census, which leads to a spawning stock fry recruitment relation (fig. 2d) explaining 62% of the observed variance in fry abundance.
14. Parr mortality rates in the river seem only weakly influenced by changes in the physical and biotic environment (survival of about 0.5/year seems a workable rule of thumb in the Girnock). However, there have been climate-associated changes in riverine growth rates which have altered exposure to the apparently constant mortality risk (Fig. 2c).
15. In addition to ongoing mortality at sea, emigrating smolts suffer significant losses from aggregating predators, and the returning spawners suffer from losses to predators and fishers in the coastal/estuarine setting and to sport fishermen in the river.

1.2. Questions arising from a preliminary data analysis

A number of questions arise from the synthesis presented in in section 1.1) above:

1. Much of the synthesis in this document is predicated on an assumption that observation 3 can be interpreted as implying that for both male and female grilse and male and female MSW, proportion of run duration at return maps one to one onto distance of spawning from estuary. For high altitude habitats we have independent confirmation from Girnock data. Is there any count in/count out data for a lowland (high grilse abundance) sub-catchment.
2. Is the apparent post-1980 loss of the very early (end Feb.) run of N.Esk MSW fish (observation 4) real or an effort artifact ? If it's real, what can we conclude from it.
3. The trends in the Fixed Engine fishery seem very different from those observed in the N&C fishery, the Logie counter and in the Girnock. We hypothesise that this is due to strong within-year changes in FE effort (serious fishing doesn't start until April !). We need to confirm this.
4. There is good accord between comparable observations in the Girnock and the N. Esk N&C fishery, but discord between these observations and the trend (or rather lack of it) observed at the Logie counter. If the Logie counter is OK, why do we not see the serious decline in high altitude spawners seen at the Girnock ? If the Logie counter is 'wrong', can we identify the source of the year dependent (!) error and allow for it ?
5. Differences in spawner sex ratio (observation 8) seem attributable to differences in sea-survival (observation 9). This makes the sea survivals deduced for N.Esk fish (observation 11) crucial. Since grilse and MSW smolts are hard to tell apart without genetic identifiers, how secure are the one and two sea-winter survival values ? Could the analysis be repeated for males and females of each persuasion assuming that outgoing smolts have a 1:1 sex ratio ?
6. The competition mechanisms underlying the stock-fry-recruitment relation are critical to population stability. If they occur before ova deposition then the size-fecundity relation (observation 12) should depend on spawner density. Although the coincidence between the 07 data for the Baddoch and Girnock argues against this class of mechanism it seems prudent to look at more years in one or both places if this is possible.
7. If the key density dependence is not occurring pre ova deposition, then our remaining choices are 1) at deposition, 2) between deposition and hatch, 3) between hatch and emergence and 4) between emergence and the autumn fry survey. The later in the life history the critical mechanism operates, the more spatial mixing and hence competition between the between the offspring of different mothers will there be. More data is clearly needed to examine these possibilities.
8. Optimality calculations require a knowledge of female and male fecundity as a function of length. We have egg mass data for Girnock/Baddoch females but this data has few grilse, so the mass of data is concentrated above 65cm. It would be good to have data from a midland/lowland site where grilse are more abundant, both to fill in the gap and to see if the functional relationship between (F) and L is structually the same as that for high altitude habitats.
9. The ratio of grilse and MSW mortality rates while at sea seem likely to be central to any optimality calculations. It thus seems very important to resolve the systematic uncertainty which currently surrounds the determination of this relativity for N. Esk fish.

1.3. The Girnock dataset

1.3.1. Adult trap data

Fig. 1 shows smoothed time series of yearly totals of adults caught in the Girnock trap immediately before spawning between 1967 to 2004. In frame a) we see that the total numbers of MSW spawners has fallen from around 120 in 1970 to about 30 in 2000. Frame b) shows that during the same period the ratio of grilse to MSW fish rose from about 0.2 to over 0.8, indicating that the number of grilse has remain essentially constant over the period.

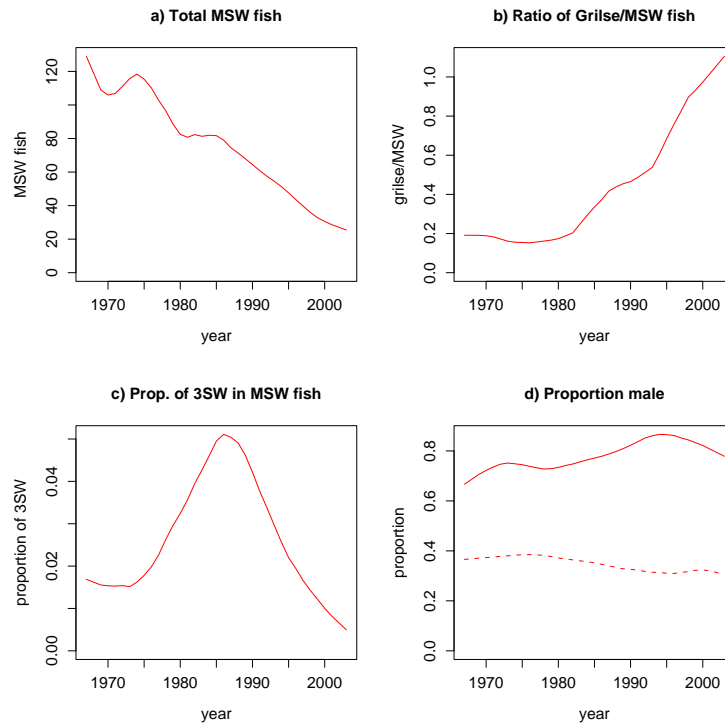


Figure 1: Smoothed time-series from the Girnock adult trap data. All frames show time-series from the Girnock adult trap smoothed using the R routine 'supsmu' with default settings. Frame a) shows the number of multi-sea-winter (2SW+3SW) individuals trapped during the year. Frame b) shows the ratio of grilse and MSW fish. Frame c) shows the proportion of 3SW fish in the MSW fish. Frame d) shows the proportion of males among the grilse (solid) and MSW (dotted) fish.

As we see in frame c) the returning MSW fish were always predominantly 2SW individuals (only 3% or so were 3SW) However, while prior to 1985 the proportion of 3SW individuals increased (indicating a relatively slower decline in 3SW numbers compared to 2SW), since that time the proportion of 3SW individuals has fallen steadily to below 0.5%.

Frame d) shows that the sex ratio of returning grilse and MSW fish remains constant over the 40 year period, but differs very substantially between the two groups. MSW fish are 40% male (and thus 60% female) while grilse are over 70% male (and thus less than 30% female).

1.3.2. Fry and smolt production data

Fig. 2 shows an unsmoothed timeseries of total spawning females at the Girnock from 1967-2000 (frame a), and partial timeseries of fry population (from electrofishing surveys) and seagoing emigrants (from the Little Mill smolt trap). Smolt production is less variable than spawner numbers so their must be some density dependence. The proportion of early runners increases between 1970 ($\approx 50\%$) and 2000 ($\geq 75\%$); indicating a decadal trend in age at smolting.

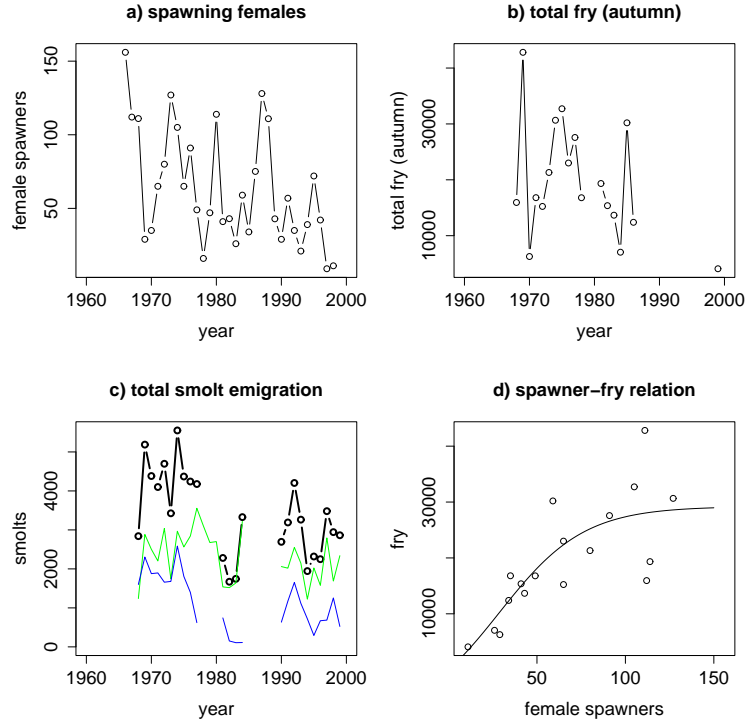


Figure 2: Girnock fry and smolt production 1966-2000 . a) shows total female spawners against year. b) shows total fry population inferred from the autumn electrofishing survey, against year. c) shows sea-going emigrants counted at the Little Mill trap against year. Black line with points shows total emigrants, green line shows early runners (river age ≤ 2.5 years), blue line shows late runners (river age > 2.5 years). d) shows the relationship between female spawner numbers and the resulting fry populations observed the following autumn. Points denote observations and the line denotes a displaced logistic (equation 1) fitted to the data ($R^2 = 0.62$) with parameters $F_0 = 8862$, $F_{max} = 29212$, and $A_h = 24$.

Fry populations show considerable variability (perhaps as a product of variations in the sampling protocol) but no long-term trend. This suggests that some at least of the density dependence may be occurring between spawner return and the fry census the following autumn. To investigate this we plot fry populations against the number of female spawners producing them and see a surprisingly tight, saturating, relationship.

$$F^y = \frac{\gamma^y F_0 F_{max}}{F_0 + \gamma^y F_{max}} \quad \text{where} \quad \gamma^y = \left(1 - \exp \left[-\frac{A_h y^{-1}}{A_h} \right] \right), \quad (1)$$

We fit this relationship with a displaced logistic (equation 1); obtaining a coefficient of determination (R^2) of 62%.

1.3.3. Female fecundity data

Fig. 3a shows that fecundity rises with length considerably faster than L^3 . This is confirmed by Fig. 3b, which shows that the Girnock and Baddoch fecundities plotted against L^3 are quite well represented by straight lines which intersect the length-cubed axis at values equivalent to $360 < L < 460$ mm.

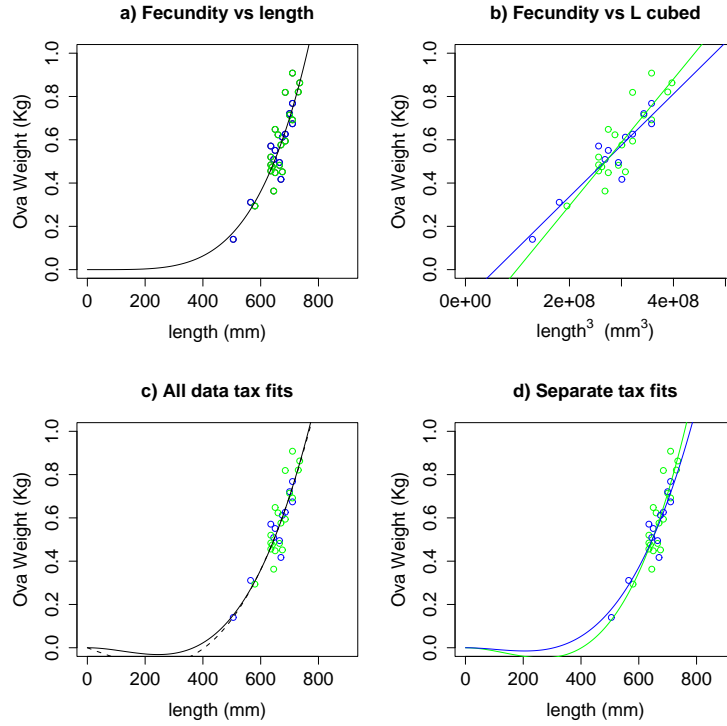


Figure 3: Individual fecundity (ova mass) of 2007 Girnock and Baddoch maiden females. Green points show ova mass of Girnock maiden fish, blue points show ova mass of Baddoch maiden fish. In a) the whole dataset is fitted ($R^2 = 0.79$) with $O = \beta L^p$ with best fit parameters $\beta = 4.15 \times 10^{-13}$, $p = 4.30$. In b) the data is plotted against L^3 and the lines show separate regressions for the Baddoch (blue, $R^2 = 0.86$, slope = $2.37 \pm 0.31 \times 10^{-9}$) and the Girnock (green, $R^2 = 0.74$, slope = $2.93 \pm 0.42 \times 10^{-9}$). c) shows whole data set fits using $O = \beta L^3 - \tau L^2$ (solid, $R^2 = 0.79$, $\beta = 4.29 \times 10^{-9}$, $\tau = 1.58 \times 10^{-6}$) and $O = \beta L^3 - \tau' L$ (dashed, $R^2 = 0.78$, $\beta = 3.06 \times 10^{-9}$, $\tau' = 5.02 \times 10^{-4}$). d) shows separate fits of $O = \beta L^3 - \tau L^2$ to the Girnock data (green, $R^2 = 0.85$, $\beta = 4.88 \times 10^{-9}$, $\tau = 1.96 \times 10^{-6}$.) and the Baddoch data (blue, $R^2 = 0.95$, $\beta = 3.51 \times 10^{-9}$, $\tau = 1.08 \times 10^{-6}$)

If we assume that individuals reach the estuary with reserves (R), expend an amount M on basal maintenance during residence in the river, and an amount T on physical ascent of the river, then it seems reasonable to postulate that the expenditure on spawning, O , will be

$$O = R - M - T. \quad (2)$$

If we now assume that R and M are both proportional to weight, which is in turn proportional to L^3 , then we see that we can write

$$O = \beta L^3 - T(L). \quad (3)$$

The simplest account of the ‘tax’, T , would suppose that it is proportional to the drag on a swimming fish, which we would expect to be proportional to the wetted surface area, i.e. L^2 . If the bigger fish are more efficient swimmers than small ones, then T might increase with L more slowly. In Fig. 3c we show fits to the whole dataset with both these models. We see they provide almost indistinguishably good fits, with pronounced differences only in the region around $L \approx 450\text{mm}$ where we have no data. However, we note that both models predict a minimum length for ascent followed by spawning, of around 400mm.

In Fig. 3d we fit the L^2 tax model to the Girnock and Baddoch data individually. Both fits are good ($R^2 > 85\%$), with that for the Baddoch being particularly close ($R^2 = 95\%$). Although the fits for the two data subsets are hard to distinguish in the region where the data is concentrated, the Girnock fit suggests a noticeably higher minimum length for ascent (420mm) than that for the Baddoch ($\approx 360\text{mm}$).

1.4. The North Esk data

1.4.1. Human consumption fishery: monthly data 1950-2006

Fig. 4 shows smoothed time series of aged catches in the N. Esk net and coble fishery and the N.E. coastal fixed engine fishery. In both cases the grilse and MSW runs have been divided into three groups (early, middle and late) on the assumption that early runners in both categories are associated with upland habitats (like the Girnock) while later runners are aiming for more lowland waters.

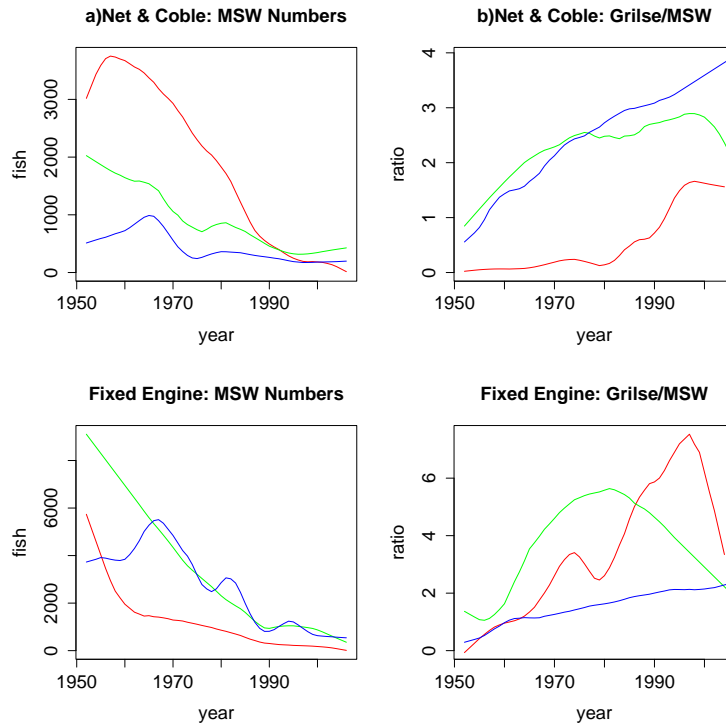


Figure 4: Smoothed time-series from the N. Esk fishery . All frames show time-series from the fishery data smoothed using the R routine ‘supsmu’ with default settings. Frames a) and b) show data from the Net and coble fishery, frames c) and d) show data from the fixed engine fishery. For both grilse and MSW fish the run has been divided into three parts – denoted early (red), middle (green) and late (blue). For grilse these runs are December → June, July, and August → November respectively, while for MSW fish the equivalent periods are December → April, May and June, and July → November. Frames a) and c) show the number of multi-sea-winter (2SW+3SW) individuals caught in the period. Frames b) and d) show the ratio of grilse and MSW fish caught in the equivalent portion of the relevant run.

The total MSW catch (frames a and c) will form an accurate index of returner numbers if and only if the effort expended in the fishery is constant. However, we note reasonable correspondence between the changes in the Net and Coble (N&C) catch of early runners (which fell by about a factor of 10 between 1970 and 2000) and changes in the number of spawners in the Girnock over the same period. We also note that while the N&C catches of early run MSW fish have dropped dramatically, the catches of middle and late run MSW fish have changed rather less over the period.

In accord with the Girnock data, the ratio of (relatively) early run grilse to early MSW fish in the N&C catches, suggest that high altitude waters will have populations comprising mostly MSW fish. The proportion of Grilse in N&C catches from lower altitude populations suggest that these are dominated by grilse rather than MSW fish.

The Fixed Engine (FE) catches show a similar pattern of decline in MSW fish, but the decline in early run fish is initially sharper than that in later runners, with the overall decline being much the same for all three components of the run. A possible explanation is that these changes principally reflect changes in effort, and the reduction in winter fishing effort occurred before that for the spring and summer fishing. This might also explain the otherwise surprising increase over the period in the proportion of grilse among early runners.

1.4.2. Sport fishery: monthly data 1950-2006

Fig. 5 shows smoothed time-series of Rod fishery catches in the N. Esk between 1950 and 2006 and up-river traffic through the Logie counter between 1980 and 2006.

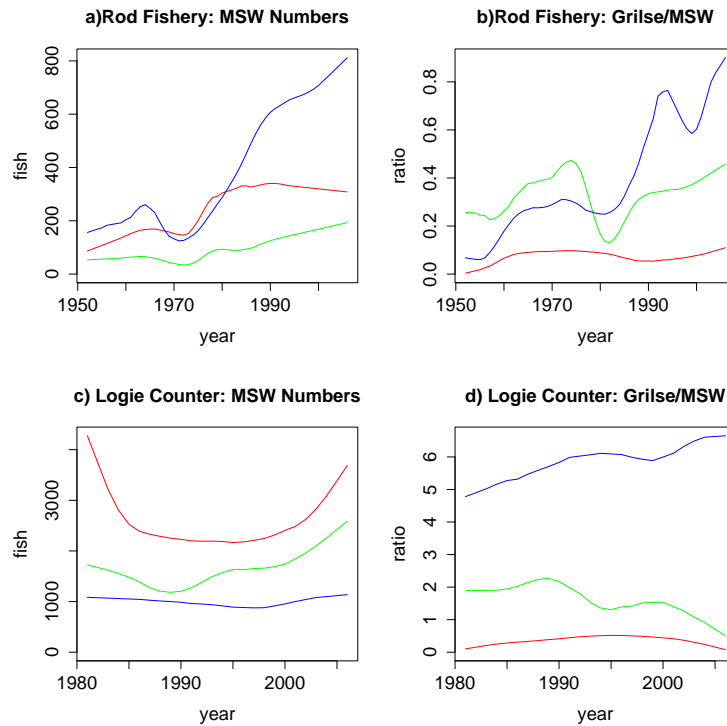


Figure 5: Smoothed time-series from the N. Esk rod and counter catches . All frames show time-series smoothed using the R routine ‘supsmu’ with default settings. Frames a) and b) show data from the rod fishery, frames c) and d) show data from the Logie fish counter, For both grilse and MSW fish the run has been divided into three parts – denoted early (red), middle (green) and late (blue). For grilse these run December → June, July, and August → November respectively, while for MSW fish the equivalent periods are December → April, May and Jun, and July → November. Frames a) and b) show the number of multi-sea-winter (2SW+3SW) individuals caught in the period. Frames b) and d) show the ratio of grilse and MSW fish caught in the equivalent portion of the relevant run.

The Logie counter numbers suggest that the number of fish escaping the human consumption

fishery have been relatively constant over the three decades since 1980; that the early run component above may MSW fish and few grilse, while the late run component is dominated by grilse.

The rod catches are harder to interpret in terms of 'demes' because we are not sure when or how the fish waiting in the river are exposed to the fishery. If they are only exposed when 'moving briskly from estuary to a waiting area' then the partition is presumably pretty much as for the human consumption fishery. This is what is assumed in frames a) and b) of this figure, which then implies that late runners have yielded both more MSW catches and more grilse catches in recent years. *I suggest that this interpretation is probably flawed, and that we might be better assuming that exposure is maximal when waiting so we should try to split the rod catches up by beat altitude.*

1.4.3. Demographic changes 1980-2006

In Fig. 6 we show the changes in pre-fishery abundance and spawner numbers over the period 1980-2006.

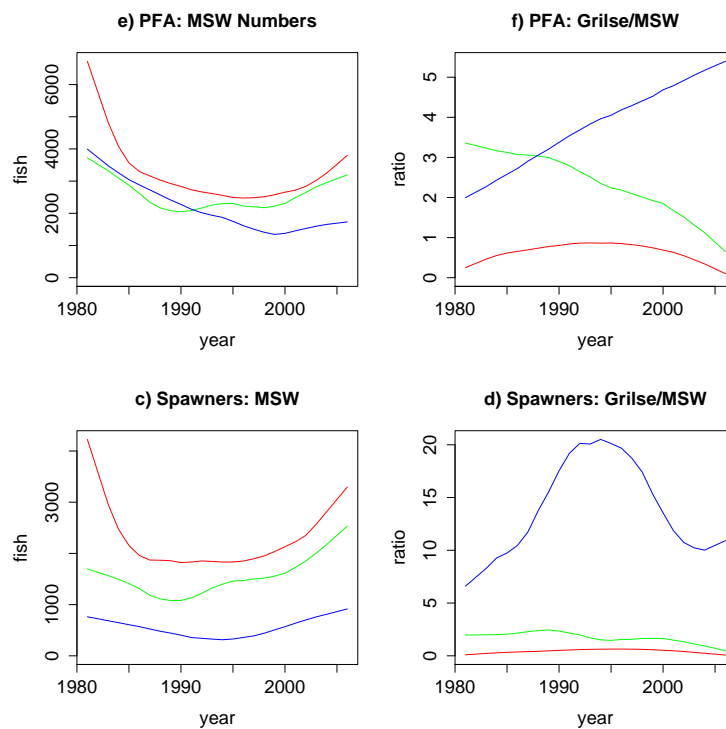


Figure 6: Smoothed time-series of *N. Esk* demography . All frames show time-series smoothed using the R routine 'supsmu' with default settings. Frames a) and b) show pre-fishery abundance. Frames c) and d) show the spawner numbers. For both grilse and MSW fish the run has been divided into three parts – denoted early (red), middle (green) and late (blue). For grilse these run December → June, July, and August → November respectively, while for MSW fish the equivalent periods are December → April, May and Jun, and July → November. Frames a) and b) show the number of multi-sea-winter (2SW+3SW) individuals in the period. Frames c) and d) show the ratio of grilse and MSW fish in the equivalent portion of the relevant run.

The pre-fishery abundance is calculated by adding the total N&C catch and an appropriate

proportion of the FE catch to the Logie counter traffic. We see that the relative stationarity of the Logie counter numbers combined with a dramatic fall in human fishery extraction, implies that the PFA of all run components has fallen (albeit by less than a factor of 2) over the three decades. There is some evidence of a rise post 2000 (in response to the catch and release policy instituted in the late 1990s ?).

Given the relative constancy of the Logie traffic and the relative modesty of the rod catches we are unsurprised that the spawner numbers show relatively weak variation, albeit with clear evidence of an increases due to the post 1995 catch and release policy.

1.4.4. Age and sex of returning fish; weekly data 1960-2006

Fig. 7 shows smoothed time series of aged catches in the N. Esk net and coble fishery. Both the grilse and MSW runs have been divided into three (early, middle and late) on the assumption that early runners in both categories are associated with upland habitats (like the Girnock) while later runners are aiming for more lowland waters.

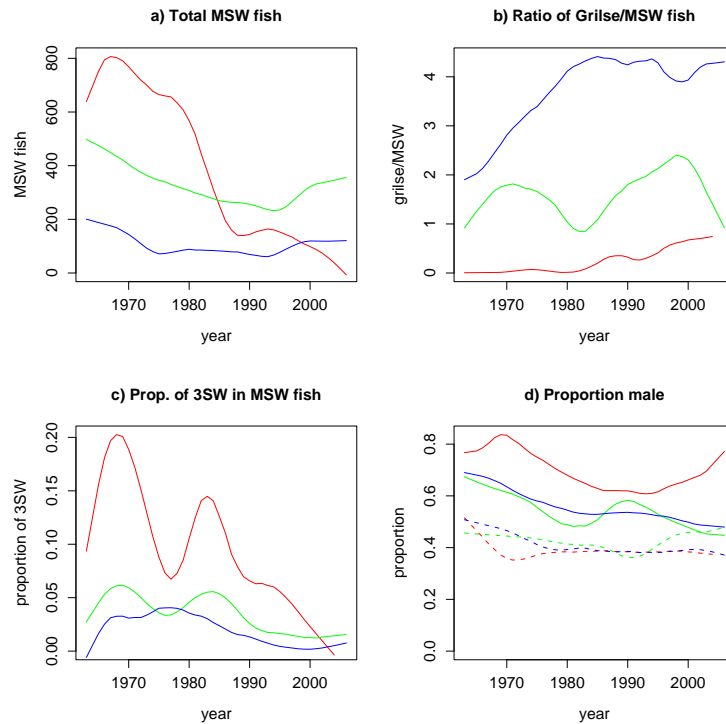


Figure 7: Decadal trends in run composition. All frames show time-series from the aged component of the net and coble fishery catch data smoothed using the R routine ‘supsmu’ with default settings. For both grilse and MSW fish the run has been divided into three (roughly) equal parts – denoted early (red), middle (green) and late (blue). For grilse these span weeks 19-24, 25-30, and 31-36 respectively, while for MSW fish the equivalent periods are weeks 7-16, 17-26 and 27-36. Frame a) shows the number of multi-sea-winter (2SW+3SW) individuals caught in the period. Frame b) shows the ratio of grilse and MSW fish caught in the equivalent portion of the relevant run. Frame c) shows the proportion of 3SW fish in the relevant group of MSW fish. Frame d) shows the proportion of males among the grilse (solid) and MSW (dotted) fish from the relevant period.

The total MSW catch (frame a) will form an accurate index of returner numbers if and only if the effort expended in the fishery is constant. However, we note an extremely good correspondence between the behaviour of the catch of early runners (which fell by about a factor of 4 between 1970 and 2000) and changes in the number of spawners in the Girnock over the same period. We also note that while the catches of early run MSW fish have dropped dramatically, the catches of middle and late run MSW fish have remained almost unchanged over the period. This might be taken to indicate that the numbers of MSW spawners in the parts of the catchment in which these individuals return have likewise remained almost constant.

The remaining frames of Fig. 7 display ratios and are thus not so dependent on constancy of effort between years, although they are of course subject to uncertainties in sex and age determination, and (in the case of the grilse to MSW ratio) to systematic changes in the distribution of effort within year.

In frame b) we see very close correspondence between the properties of the early running component of the N.Esk population and the Girnock population. The ratio of grilse to MSW fish is always less than 1; ranging from about 0.2 in 1970 to something approaching 1 in 2000. For the later running N. Esk populations, the grilse/MSW ratio increases with ‘lateness’ (and thus, by implication with decreasing altitude). Middle running individuals (middle altitude populations ?) have perhaps 60% grilse and 40% MSW returners, while low altitude populations (late runners) have perhaps 80% grilse and 20% MSW.

In frame c) we see both similarities and differences between Girnock and early run N.Esk characteristics. N.Esk early running MSW fish are around 20% 3SW compared to about 4% in the Girnock. However, both show the same rapid decadal decline, reaching very low levels indeed by 2000. Both the lower altitude N.Esk groups show decadal declines in MSW numbers, but these are much less marked than that in the high altitude group.

The sex ratios shown for the high altitude group in Fig. 7d again show almost exact correspondence with the equivalent Girnock results (40% male for the MSW fish, 70% male for the grilse). The results for the other groups show that all MSW groups are about 40% male, while the predominance of males among the grilse, which is always lower than that for the high-altitude group, decreases with time; reaching almost 1:1 (50% male) by 2000.

1.4.5. Decadal average return time and size

In Fig. 8b we show the mean sizes of returners to the N.Esk in given weeks, pooled over period from 1967-2003. We see that returning males and females are very much the same size, with males from equivalent parts of the run, about 2-5cm longer than equivalent females. Returning individuals get larger as each run proceeds, and it is instructive to calculate the long-run average von Bertalanffy growth rate which would produce the observed size outcome (Table 1). From this we see that late returners in a given run exhibit the same overall average

Table 1: Average von Bertalanffy growth rates for N. Esk females, assuming $L_\infty = 120\text{cm}$

Run	age days	Len cm	γ %/d
Grilse - early	400	55.6	0.134
Grilse - mid	430	58.1	0.134
Grilse - late	463	61.2	0.135
Salmon - early	673	70.3	0.118
Salmon - mid	739	74.3	0.119
Salmon - late	806	80.6	0.127

growth rate as early returners Growth rates are noticeably different for grilse and MSW fish, but (perhaps surprisingly) the values for MSW fish are lower than those for grilse. The details of these results are sensitive to the value chosen for L_∞ but the overall pattern is not.

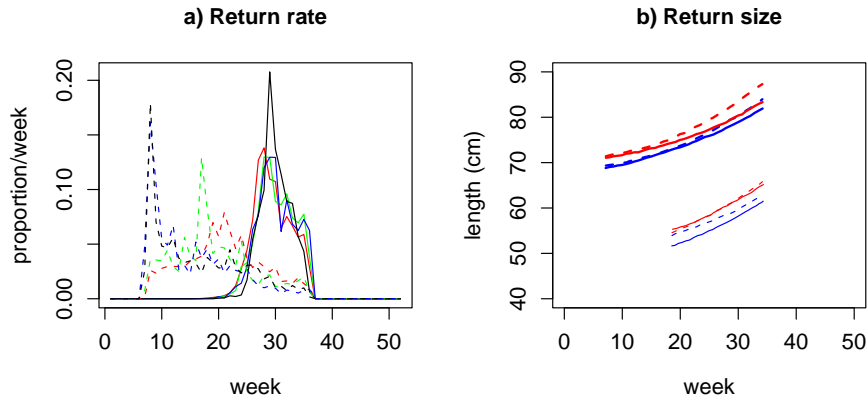


Figure 8: The characteristics of salmon returning to the N. Esk. a) Distribution of returns over the run. All curves show proportion of the year's run arriving in a given week. The solid lines show the grilse run and the dotted lines the MSW run. Red lines show the decade 1993-2002, green lines 1983-1992, blue lines 1973-1982, black lines 1963-1972. b) Mean length of returners – 1967-2003. Red lines show males, blue lines show females. Heavy lines show MSW, light lines show grilse. Solid lines show river age 1 at smolting, dotted lines show river age 3 at smolting.

Fig. 8a shows decadal average catch rate patterns for scale-aged fish in the N.Esk net and coble fishery. Under an assumption of constancy of effort within a year, this gives the temporal pattern of rate of return to the estuary. It is clear, however, that return of MSW fish is already well under way by the time the fishery opens in February and that grilse are still returning when it closes.

We note that the distribution of observed return for grilse is very consistent over all four decades. However, the pattern of return for MSW fish shows consistency for the two decades up to 1983 and for the two after that time, but pre- 1983, nearly 25% of the run arrived in a compact burst around week 9, whereas after 1983 this initial burst of MSW fish is conspicuously absent.

1.4.6. Sea survival

In Fig. 9 we show survivals from smolt to return, calculated for fish from the N. Esk. The most interesting feature of these results is that the sea survival for MSW fish is about half that for grilse – *but note that this comes with a very serious health warning since the absence of genetic observations implies that assignment of outgoing smolts to salmon/grilse return is essentially arbitrary !!*. Grilse returning mid-run spend about 430 days at sea whereas MSW fish returning mid-run spend about 740 days at sea. Thus a survival of 2% for grilse corresponds to a daily mortality rate of 0.0091, whereas a survival of 1% for MSW fish corresponds to a daily mortality rate of 0.0062. A corollary of this finding is that *if* we assumed that grilse and MSW fish suffered the same daily mortality rate until the grilse returned, then the daily mortality rate suffered by the MSW fish during the 310 extra days they remain at sea would

have to be 0.0022/day. The most plausible conclusion is that grilse and MSW fish are exposed to different mortality risks throughout their sojourn at sea.

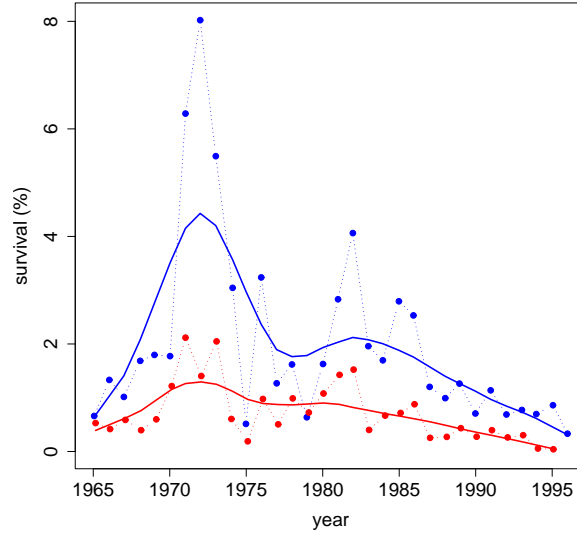


Figure 9: *Calculated sea-survival for N. Esk fish 1965-1995. Blue dots show yearly calculated values for 1SW fish (grilse) and the heavy blue line shows a smoothed version of this time-series produced by the R routine ‘supsmu’ with default settings. The red dots show yearly calculated survivals for MSW fish with the heavy red line showing a smooth of the same data.*

2. Optimality considerations

2.1. Size at return - maximising fitness

We consider a female of sea-age a and length L , which expects to spawn at sea-age a_s and whose ‘expected’ sea-mortality and von Bertalanffy growth rates are m and γ respectively. If she returns to the river now, she will have reserves $R = \beta L^3$, which must be spent on ascending the river, surviving until sea-age a_s and producing eggs each requiring w_e units of reserves.

Guided by Fig. 3 we assume that the costs of river ascent are proportional to L^2 with constant of proportionality τ . If daily maintenance costs while she is in the river amount to a fraction μ of her initial weight, then the reserves available for spawning will be

$$R_s(a, L) = \beta L^3 [1 - \mu(a_s - a)] - \tau L^2. \quad (4)$$

If, during her wait in the river, she has a probability S_e of avoiding being caught by the various fisheries (‘exploited’) then her ‘expected fecundity’ is

$$\hat{F}(a, L) = S_e \frac{R_s(a, L)}{w_e} = S_e \frac{\beta L^3 [1 - \mu(a_s - a)] - \tau L^2}{w_e}. \quad (5)$$

To estimate the fitness of an individual who returns at length L and sea-age a to spawn at sea-age a_s , we define the probability of an egg hatching, and hatched egg surviving to the autumn fry survey and the probability of a fry surviving to smolt as S_h , S_f and S_p respectively.

Hence, given that the survival at sea to age a is e^{-ma} , we see that the fitness of an individual who returns at length L and sea-age a to spawn at sea-age a_s is

$$f(a, L) = S_h S_f S_p e^{-ma} \widehat{F}(a, L) = \frac{S_e S_h S_f S_p}{w_e} e^{-ma} R_s(a, L) \quad (6)$$

We know that egg-size (and hence w_e) increases with the size of the mother (L) but it doesn't seem too fanciful to expect that egg hatch probability would increase with egg size (and hence with L). As a convenient simplification, we shall assert that these two effects operate in exact proportion, so that their ratio is independent of maternal length and age.

Less tentatively we shall also assume that fry and parr survival are also independent of maternal length and age, so that

$$\psi \equiv \frac{S_h S_f S_p}{w_e} \quad (7)$$

is independent of both the female's length and return age. We note in passing that fry survival (S_f) is strongly dependent on the deposited ova density, thus implying a similar density dependence of ψ .

These simplifications allow us to write the fitness of a female returning at length L and age a to spawn at age a_s as

$$f(a, L) = \psi S_e e^{-ma} [\beta L^3 (1 - \mu[a_s - a]) - \tau L^2.] \quad (8)$$

where ψ is independent of both L and a .

From this expression we notice that there is a minimum length $L_m \equiv \tau/\beta$ below which the female cannot ascend the river and have any resource left to reproduce. In terms of this quantity, we can re-express the fitness as

$$f(a, L) = \psi \beta S_e e^{-ma} [L^3 (1 - \mu[a_s - a]) - L_m L^2.] \quad (9)$$

To facilitate an analytic treatment of this problem, we shall further assume that S_e is independent of length (L) and age (a). The first of these assumptions is probably defensible, while the second is more debatable, since effort in both the human consumption and sport fisheries is known to be highly dependent on time of year.

In the special case of very small in-river maintenance cost rate ($\mu \rightarrow 0$) the fitness becomes

$$f(a, L) = \Phi e^{-ma} L^2 [L - L_m] \quad \text{where} \quad \Phi \equiv \psi \beta S_e. \quad (10)$$

To find the optimum return point for this case we differentiate equation (10) with respect to age, remembering that L is a function of age with $dL/da = \gamma(L_\infty - L)$, yielding

$$\frac{df}{da} = \Phi e^{-ma} [3L^2 - 2L_m L] \gamma [L_\infty - L] - \Phi m e^{-ma} [L^3 - L_m L^2] \quad (11)$$

and then look for values of L which make $df/da = 0$, which requires them to be a solution of a quadratic equation, which after algebraic manipulation becomes

$$AL^2 - BL + C = 0 \quad (12)$$

where

$$A \equiv \frac{m}{\gamma} + 3 \quad B \equiv \left(\frac{m}{\gamma} + 2 \right) L_m + 3L_\infty \quad C \equiv 2L_m L_\infty \quad (13)$$

This clearly shows that the fitness function can have only two turning points, one a maximum and the other a minimum. Since we know from equation (10) that f is positive only for $L > L_m$, it is clear that the minimum will be in the range $0 \rightarrow L_m$, with the maximum having $L > L_m$.

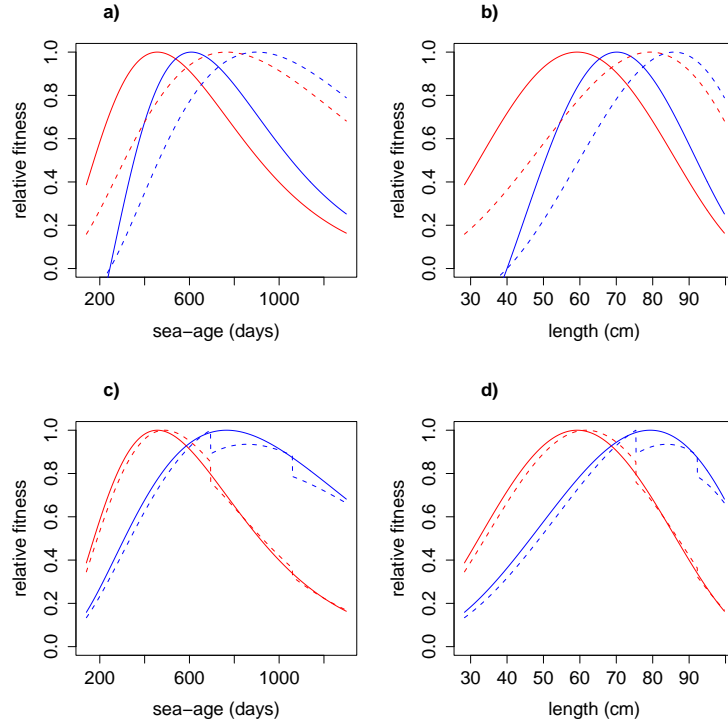


Figure 10: Relative fitness (f/f_{max}) as a function of age and length. Frames a) and c) show the ratio of fitness calculated from equation (10) with $\gamma = 0.0013/\text{day}$ and $L_\infty = 120\text{cm}$ to the maximum fitness with the same parameters as a function of age. Frames b) and d) show the same results as a function of length. Frames a) and b) show calculations with zero river maintenance and $L_m = 0$ (red) and $L_m = 40\text{cm}$ (blue). The solid lines show sea-mortality $m = 0.004/\text{day}$ (solid) and $m = 0.002/\text{day}$ (dotted). Frames c) and d) show calculations with $L_m = 0$, river maintenance $\mu = 0/\text{day}$ (solid) and $\mu = 0.0003/\text{day}$ (dotted). The red lines show results with $m = 0.004/\text{day}$ and the blue line results with $m = 0.002/\text{day}$.

It is useful to note that if we know the optimum return length L_{opt} then we can use equation (13) to infer the equivalent value of the ratio m/γ , namely

$$\frac{m}{\gamma} = \frac{(3L_{opt} - 2L_m)(L_\infty - L_{opt})}{L_{opt}(L_{opt} - L_m)}. \quad (14)$$

In Fig. 10 we show a set of fitness against length and age plots calculated from equation (10) assuming that Φ is a constant. We note that this amounts to ignoring possible (maternal) length and time dependence of exploitation (S_e) and, more seriously, systematic differences in hatch and fry survival between grilse and MSW salmon.

The top two figures illustrate the predicted behaviour when waiting in the river is cost free ($\mu = 0$). When there is no tax on river ascent (red curves) all sizes of returner have positive fitness and increasing sea mortality rate makes the optimum return occur younger and smaller. Introducing an ascent tax makes it impossible for individuals to return at lengths lower than L_m and increases the optimal return age and size for any given sea mortality.

Introducing an ascent tax ($\mu > 0$) and assuming that the appropriate value of a_s is the number following the nominal return age a , produces almost no change in the position for fish who would return as grilse (Fig. 10c and d red curves) but changes the result for fish who

would return as MSW fish with no ascent cost – who now optimally return as Grilse soon as possible before spawning.

My conclusions from this analysis are

1. There is no way that the fitness curve can have two maxima, so there is no way that these considerations can explain simultaneous occurrence of grilse and MSW salmon
2. If we assume that high altitude habitats would have higher values of τ than low altitude ones then considerations like these could explain the change between majority grilse return at low altitude and majority salmon return at high. However, since they cannot explain simultaneous salmon/grilse return we are left trying to explain the minor partner as ‘mistakes’ from neighbouring habitat.
3. For a given return group the higher altitude = higher tax = later return hypothesis has a very serious flaw. MSW salmon return later to lower habitats not to higher ones.
4. I think this analysis tells us first and foremost that salmon and grilse must be in some sense distinct organisms. That is their innate behavioural and energetic parameters must be different enough to override the partial optimality arguments set out above.
5. This argument is supported by the fact that grilse and salmon clearly do different things when at sea. However, we know that they can interbreed and that they can (apparently) spawn in the same habitat. Hence we must conclude that there is a stable polymorphism between the two.
6. Such stable polymorphisms can only be maintained by appropriately configured competition. It is possible, but implausible, that such competition happens at sea, so the most plausible assumption would be that the key lies in competition in the river.
7. We know that there is strong density dependence between ova deposition and the fry survey, but it is not clear whether grilse offspring are different enough from salmon offspring for this to be the engine which maintains the polymorphism. An alternative set of possibilities exists during the ascent and spawning phase when fish might compete for low energy resting spaces and during spawning when overcutting and consequent ova damage might be a risk which could be minimised by physical separation of spawning areas.

3. Some strategic lifecycle models

3.1. A general single-locus two-allele structure with random mating

In this section we construct some (relatively) simple strategic models of the salmon lifecycle. In the previous section, we argued that grilse and MSW salmon must be in some sense ‘different organisms’, notwithstanding that they interbreed readily. To try to represent this relationship while formulating a model which has some chance of yielding to analytic investigation we shall assume that salmon are diploid organisms in which the grilse/MSW differentiation is determined at a single locus on which there are two alleles \mathcal{G} and \mathcal{M} . We shall assume that the \mathcal{M} allele is dominant, so that only homozygote \mathcal{G} individuals are functional grilse. For compactness we refer to $\mathcal{G}\mathcal{G}$, $\mathcal{G}\mathcal{M}$ and $\mathcal{M}\mathcal{M}$ individuals as g , x and m respectively and use G_y , X_y and M_y to denote their respective numbers at spawning time in year y .

We know that the sex-ratio of returning sub-groups can differ substantially from 1:1, and that these differences vary between habitats, so we denote the sex ratio of returning g , x and m individuals by σ_g , σ_x and σ_m respectively. The numbers of g , x and m females spawning in year y are then given by

$$\mathcal{F}_y^g = (1 - \sigma_g)G_y, \quad \mathcal{F}_y^x = (1 - \sigma_x)X_y, \quad \mathcal{F}_y^m = (1 - \sigma_m)M_y. \quad (15)$$

and the numbers of males by

$$\mathcal{M}_y^g = \sigma_g G_y, \quad \mathcal{M}_y^x = \sigma_x X_y, \quad \mathcal{M}_y^m = \sigma_m M_y. \quad (16)$$

We denote the number of ova deposited by type $a \in [g, x, m]$ females in year y by E_y^a , and the probability that in year y an egg from a type a female is fertilised by a type $b \in [g, x, m]$ male by P_y^{ab} . The respective numbers of offspring of types g , x and m in year y are then

$$O_y^g = E_y^g \left[\frac{P_y^{gx}}{2} + P_y^{gg} \right] + E_y^x \left[\frac{P_y^{xg}}{2} + \frac{P_y^{xx}}{4} \right] \quad (17)$$

$$O_y^x = \frac{E_y^x}{2} + E_y^g \left[P_y^{gm} + \frac{P_y^{gx}}{2} \right] + E_y^m \left[P_y^{mg} + \frac{P_y^{mx}}{2} \right] \quad (18)$$

$$O_y^m = E_y^m \left[\frac{P_y^{mx}}{2} + P_y^{mm} \right] + E_y^x \left[\frac{P_y^{xm}}{2} + \frac{P_y^{xx}}{4} \right] \quad (19)$$

To define the fertilisation probabilities P_y^{ab} we assume that any egg from whatever source is fertilised with equal probability by sperm from any of the males in the system. We denote the fecundity ratio of grilse and multi-seawinter males by ρ , define

$$T_y^m = \rho \mathcal{M}_y^g + \mathcal{M}_y^x + \mathcal{M}_y^m \quad (20)$$

as the number of ‘two sea-winter equivalent’ males spawning in the system, and then write

$$P_y^{ag} = \frac{\rho \mathcal{M}_y^g}{T_y^m}, \quad P_y^{ax} = \frac{\mathcal{M}_y^x}{T_y^m}, \quad P_y^{am} = \frac{\mathcal{M}_y^m}{T_y^m}, \quad a \in [g, x, m]. \quad (21)$$

In this case, equations (17) to (19) become

$$O_y^g = \frac{E_y^g}{T_y^m} \left[\rho \mathcal{M}_y^g + \frac{\mathcal{M}_y^x}{2} \right] + \frac{E_y^x}{T_y^m} \left[\frac{\rho \mathcal{M}_y^g}{2} + \frac{\mathcal{M}_y^x}{4} \right] \quad (22)$$

$$O_y^x = \frac{E_y^x}{2} + \frac{E_y^g}{T_y^m} \left[\mathcal{M}_y^m + \frac{\mathcal{M}_y^x}{2} \right] + \frac{E_y^m}{T_y^m} \left[\rho \mathcal{M}_y^g + \frac{\mathcal{M}_y^x}{2} \right] \quad (23)$$

$$O_y^m = \frac{E_y^m}{T_y^m} \left[\frac{\mathcal{M}_y^x}{2} + \mathcal{M}_y^m \right] + \frac{E_y^x}{T_y^m} \left[\frac{\mathcal{M}_y^m}{2} + \frac{\mathcal{M}_y^x}{4} \right] \quad (24)$$

In the interests of simplicity, we shall assume that all parr smolt in the spring of their second year of life (hatch being in year 0). We write the survival from fry to smolt as S_R , the survival from smolt to grilse as S_G and the survival from smolt to two-sea-winter returner as S_M . Under the further simplifying assumption that all g individuals return to spawn after a single winter at sea, and that all x and m individuals spawn after two winters at sea, the population dynamics are described by

$$G_{y+4} = S_R S_G O_y^g \quad X_{y+5} = S_R S_M O_y^x \quad M_{y+5} = S_R S_M O_y^m. \quad (25)$$

3.2. The independent spawning territories model

This model variant assumes that female grilse only spawn in ‘grilse territory’ which can produce a maximum of f fry per year and requires h spawners to fill it, while multi-winter females only spawn in ‘salmon territory’ which produces a maximum of F fry per year and requires H spawners to fill it. Writing the spawner-fry stock recruitment relation in Michaelis-Menton form, we see that the number of fry spawned by g , x and m mothers respectively is

$$E_y^g = \frac{f \mathcal{F}_y^g}{\mathcal{F}_y^g + h}, \quad E_y^x = \frac{F \mathcal{F}_y^x}{\mathcal{F}_y^x + \mathcal{F}_y^m + H}, \quad E_y^m = \frac{F \mathcal{F}_y^m}{\mathcal{F}_y^x + \mathcal{F}_y^m + H}. \quad (26)$$

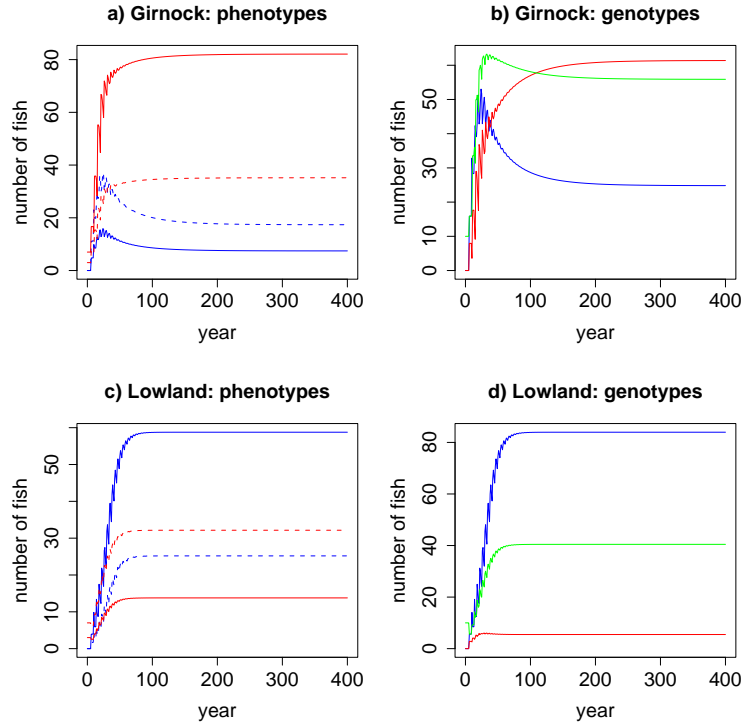


Figure 11: *The independent spawning territories model, with $S_R = 0.3$, $S_G = 0.04$, $S_M = 0.02$ and $\rho = 0.33$, settling to a stable polymorphic equilibrium. a) and b) show a Girnock-type situation with $F = 28000$, $H = 30$, $f = 2000$, $h = 6$, $\sigma_g = 0.7$, and $\sigma_m = 0.3$. c) and d) show a hypothetical lowland situation with $F = 5000$, $H = 5$, $f = 25000$, $h = 75$, $\sigma_g = 0.3$ and $\sigma_m = 0.7$. In a) and c) blue lines show grilse and red lines show two sea-winter fish, with solid lines for females and dashed lines for males. In b) and d) blue and red show numbers of GG and MM homozygotes while green shows the number of GM heterozygotes.*

The model defined by equations (15), (16), (20), (22) to (25), and (26) is very easy to simulate, and two typical examples are shown in Fig. 11. One example is chosen to represent an upland (Girnock) situation, with most territory suitable for MSW females, a small amount of Grilse female territory, and returner sex-ratio (presumably mediated by differential sea-survival) male-biased for the grilse and female biased for the MSW fish. The other simulation represents an essentially inverted configuration which might represent a lowland habitat where the majority of returners are Grilse.

In both cases the simulation settles quickly (< 30 years) to a polymorphic equilibrium in which a significant fraction of the population are heterozygotes. In the ‘Girnock’ case the great majority of spawning females are MSW fish with a fair representation of male grilse but few females. In the ‘Lowland’ case the vast majority of spawning females are grilse with a modest representation of MSW females most of who are heterozygotes.

3.3. The general competition model

Models which seek to predict a stable polymorphism must incorporate competitive asymmetry between phenotypes. The female territories model variant assumed that grilse females (and their offspring) compete only with other grilse females (and their offspring) while MSW females

compete only with other MSW females and that the sum of the maximum production for the two phenotypes constitutes the maximum production of the deme. In this variant we assume that if large populations of either grilse or MSW females are in sole possession of the deme then either can exploit its whole productive potential. When both are present then each produces a characteristic reduction in the productivity of the other.

To implement this picture of reproduction, we retain all elements of the independent territories model except that we replace equations (26) with:

$$E_y^g = \frac{F\mathcal{F}_y^g}{\mathcal{F}_y^g + \eta_{mg}(\mathcal{F}_y^x + \mathcal{F}_y^m) + h}. \quad (27)$$

$$E_y^x = \frac{F\mathcal{F}_y^x}{\eta_{gm}\mathcal{F}_y^g + \mathcal{F}_y^x + \mathcal{F}_y^m + H}, \quad E_y^m = \frac{F\mathcal{F}_y^m}{\eta_{gm}\mathcal{F}_y^g + \mathcal{F}_y^x + \mathcal{F}_y^m + H}. \quad (28)$$

In Fig. 12 we show two simulations of the general competition model with parameter values intended to mimic the ‘Girnock’ and ‘Lowland’ scenarios illustrated in Fig. 11. We again see that in both cases the system settles to a stable polymorphic equilibrium. However although

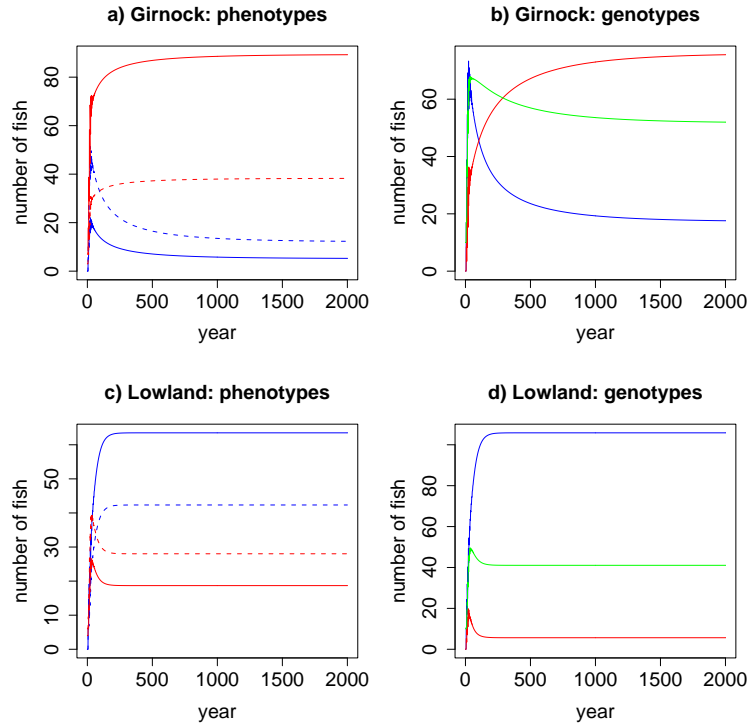


Figure 12: *The general competition model, with $F = 30000$, $H = 30$, $h = 90$, $S_R = 0.3$, $S_G = 0.04$, $S_M = 0.02$ and $\rho = 0.33$, settling to a stable polymorphic equilibrium.* a) and b) show a Girnock-type situation with $\eta_{gm} = 0.5$, $\eta_{mg} = 1.3$, $\sigma_g = 0.7$, and $\sigma_m = 0.3$. c) and d) show a hypothetical lowland situation with $\eta_{gm} = 1.2$, $\eta_{mg} = 0.2$, $\sigma_g = 0.4$ and $\sigma_m = 0.6$. In a) and c) blue lines show grilse and red lines show two sea-winter fish, with solid lines for females and dashed lines for males. In b) and d) blue and red show numbers of GG and MM homozygotes while green shows the number of GM heterozygotes.

in the ‘Lowland case’ this is attained in much the same timescale as the individual territories

model, the transient in the ‘Girnock’ case is rather different. While the phenotype numbers get quite close to their equilibria over the first 500 years or so, the next 1550 years are occupied in a progressive change of the MSW fish from mainly heterozygotes to a majority of homozygotes.

3.4. Simulations of trend and noise in sea survival

In this section we look at the effect of a) noisy sea-survival and b) a decadal downward trend in survival for both salmon and grilse. Taking the survival ‘indices’ calculated for the N. Esk as a guide we look at both the female territories and the general competition model variants in a generally ‘Girnock-like’ configuration, with sea survival which decreases by about a factor of two over three decades and which is subject to noise, taking a log-normal form with coefficient of variation of 50%.

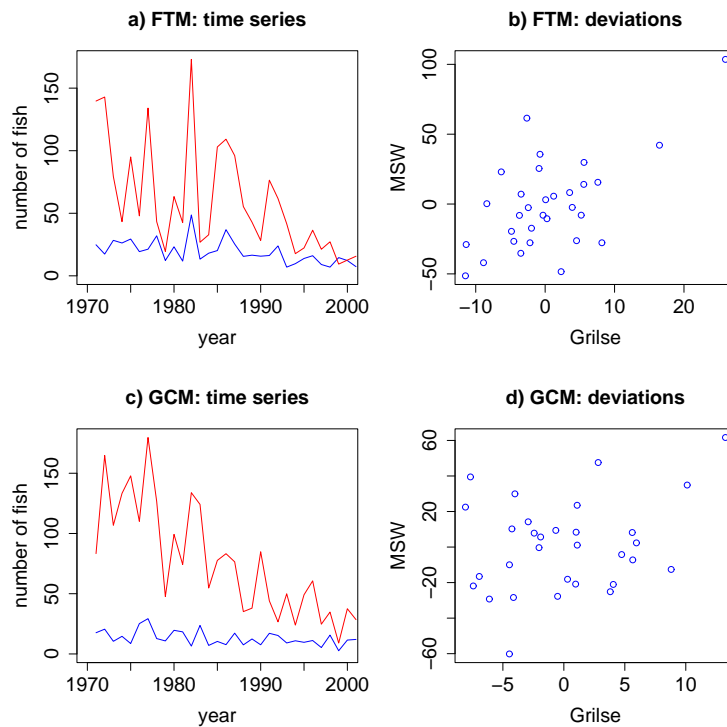


Figure 13: *The two strategic model variants subject to 30-year trends in S_G from 0.04 to 0.02 and S_M from 0.02 to 0.007, together with uncorrelated log-normal noise in both with $c.v.=0.5$. All simulations have ‘Girnock-like’ parameters with $\sigma_g = 0.7$, $\sigma_m = \sigma_x = 0.3$, $\rho = 0.33$ and $S_R = 0.3$. a) and b) show the female territories model with $F = 28000$, $f = 2000$, $H = 30$, $h = 6$. c) and d) show the general competition model with $F = 30000$, $H = 30$, $h = 90$, $\eta_{gm} = 0.5$, $\eta_{mg} = 1.3$. a) and c) show time series of MSW (red) and Grilse (blue). b) and d) show deviations of each time-series from a smoothed trend, plotted against each other.*

The results of simulations with both model variants are shown in Fig. 13. We see that in both cases the long-run time series are very reminiscent of those observed in the Girnock. The MSW fish decline more than the Grilse in both cases with the FCM output shown Grilse numbers declining slightly and GCM output showing almost no discernable change in Grilse

numbers. The residual plots (RH frames) show very little correlation between MSW and Grilse variation – unsurprising in view of the fact that the values of S_g and S_M are uncorrelated.

3.5. Stationary states – non-interbreeding populations

In the limit that ova deposited by grilse females are fertilised with probability one by grilse males and ova deposited by MSW females are fertilised with probability one by MSW males, then equations (17) to (19) become

$$O_y^g = E_y^g \quad O_y^m = E_y^m \quad O_y^x = 0. \quad (29)$$

In this case the stationary states are rather straightforward to determine.

3.5.1. Female territories model

For the female territories model the steady states are $X^* = 0$ and

$$G^* = S_R S_G f - h' \quad M^* = S_R S_M F - H'. \quad (30)$$

where, for compactness, we have defined

$$H' \equiv \frac{H}{1 - \sigma_m} \quad h' \equiv \frac{h}{1 - \sigma_g}, \quad (31)$$

3.5.2. General competition model

For the general competition model the equivalent expressions are rather more cumbersome and, in addition to H' and h' (equation 31) we also define

$$\eta'_{mg} \equiv \eta_{mg} \left(\frac{1 - \sigma_m}{1 - \sigma_g} \right) \quad \eta'_{gm} \equiv \eta_{gm} \left(\frac{1 - \sigma_g}{1 - \sigma_m} \right) \quad (32)$$

and

$$Y_g \equiv F S_R S_G - h' \quad Y_m \equiv F S_R S_M - H, \quad (33)$$

in terms of which the grilse and MSW stationary states are

$$G^* = \frac{Y_g - \eta'_{mg} Y_m}{1 - \eta'_{mg} \eta'_{gm}} \quad M^* = \frac{Y_m - \eta'_{gm} Y_g}{1 - \eta'_{mg} \eta'_{gm}} \quad (34)$$

3.6. Stationary states – random mating populations

In the case of random mating (simulated above) the key to progress in calculating the steady state is to recognise that at equilibrium the number of next generation fry to which a given fry makes a 50% genetic contribution, which we denote by W_a^* , $a \in [g, x, m]$, is exactly two. We use E_T^* to denote the total number of fry produced by the population at equilibrium, e_a^* to denote the equilibrium number of fry produced by a mother of type a , and p_a^* to denote the equilibrium probability that an offspring is fathered by any *given* type a individual. In terms of these quantities, writing the river survival as S_R and the sea survival as S_S , we have

$$W_a^* = S_R S_S [(1 - \sigma_a) e_a^* + \sigma_a E_T^* p_a^*] = 2 \quad a \in [g, x, m] \quad (35)$$

where, under the assumption that $S_S = S_G$ for grilse and $S_S = S_M$ for all multi-sea-winter fish,

$$S_S = \begin{cases} S_G & a = g \\ S_M & a = x \text{ or } a = m \end{cases} \quad (36)$$

3.6.1. Female territories model

For the female territories model variant we shall assume that $\sigma_x = \sigma_m$ so that

$$e_g^* = \frac{f}{(1 - \sigma_g)G^* + h} \quad \text{and} \quad e_x^* = e_m^* = \frac{F}{(1 - \sigma_m)(M^* + X^*) + H}. \quad (37)$$

In addition to h' and H' defined in equation (31) we now define parameter groups

$$\psi_g \equiv \frac{2}{S_R S_G (F + f)} \quad \psi_m \equiv \psi_g \frac{S_G}{S_M} \quad \phi \equiv \frac{f}{F + f} \quad \xi \equiv \frac{\rho \sigma_g}{\sigma_m}. \quad (38)$$

In terms of these parameter groups, and writing $K^* = X^* + M^*$ to represent the total number of MSW fish at equilibrium, the versions of equation (35) for $a = g$ and $a = m$ become

$$\psi_g = \frac{\phi}{G^* + h'} + \left(\frac{\xi}{\xi G^* + K^*} \right) \left(\frac{\phi G^*}{G^* + h'} + \frac{(1 - \phi)K^*}{K^* + H'} \right) \quad (39)$$

$$\psi_g - \frac{\phi}{G^* + h'} = \xi \left(\psi_m - \frac{1 - \phi}{K^* + H'} \right) \quad (40)$$

Equation (40) gives a relationship between the number of functional grilse G^* and the number of function MSW fish, $K^* = X^* + M^*$. In principle, we can solve this expression of K^* , substitute the result back into equation (39) and thus obtain an equation with a single unknown, G^* . The result of this procedure is essentially a cubic in G^* , thus demonstrating that the system can have up to three steady states. However, the coefficients of the cubic are so cumbersome, and the expressions for its roots so un-illuminating, that there is little to be gained thereby. However, we know that the root we require must be positive, so we can relatively easily find it numerically. Once we have a value for the stationary number of homozygote grilse (G^*), we can use equation (40) to obtain the stationary value of the total number of functional multi-sea-winter fish ($X^* + M^*$). To calculate the split between homozygote M's and heterozygotes, we return to the basic model definition (equations 25 and 24) to show that, if we define $K^* = X^* + M^*$ to represent the total number of multi-sea-winter fish at equilibrium, then the equilibrium number of heterozygotes (X^*) is the solution of

$$Q(K^* - X^*) = \left(K^* - \frac{X^*}{2} \right)^2 \quad (41)$$

where

$$Q \equiv \left(\frac{\psi_m}{2(1 - \phi)} \right) (K^* + H') (\xi G^* + K^*) \quad (42)$$

In Fig. 14 we show the results of a short analytic investigation of the female territories model. The top left frame (a) shows what happens when Girnock selected strains (grilse tend to be male and MSW to be female) occupy terrain with different proportions of grilse habitat. As the terrain gets less and less favourable for MSW fish the number of such fish decreases and a steadily greater proportion of them are heterozygotes. Interestingly the maximum grilse population occurs when the terrain is 'only' 70% grilse habitat, because the large number of grilse males can't add to the number of grilse born by grilse mothers but can produce grilse by mating with heterozygote MSW females. The top right frame shows a parallel investigation for 'Lowland' type individuals (MSW fish tend to be male and grilse tend to be female). and the results are not very different from those in a) except that even when the terrain is 100% female grilse territory, the MSW fish can keep going by the heterozygote MSW males mating grilse females.

In the lower two frames we look at the effects of changing the sex ratio of the dominant partner (grilse in frame c and MSW in frame d). The most surprising result is in frame d) where we see that making the type unfavoured by the terrain (MSW) wholly male reduces the population of the dominant partner (grilse) by over 50%.

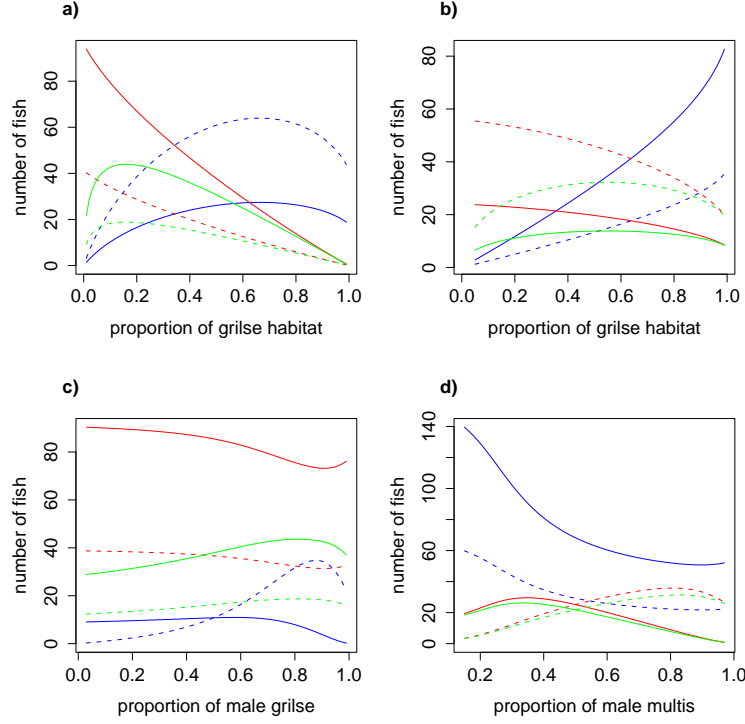


Figure 14: An analytic investigation of the female territories model . In all frames solid lines show females and dotted lines show males, blue lines show grilse, red lines show total MSW fish and green lines show heterozygote MSW fish. a) and c) show a Girnock type situation with varying proportion of grilse habitat in a) and varying grilse male proportion in c). b) and d) show a Lowland type situation with proportion of grilse habitat varying in b) and MSW male proportion varying in d). In all frames $S_R = 0.3$, $S_M = 0.02$, $S_G = 0.04$, $F/H = 1000$, $f/h = 333$, $\sigma_x = \sigma_m$ and the total fry production ($F + f$) is 30000 per annum. In a) $\sigma_g = 0.7$ and $\sigma_m = 0.3$. In b) $\sigma_m = 0.7$ and $\sigma_g = 0.3$. In c) $F = 27000$ and $\sigma_m = 0.7$. In d) $F = 6000$ and $\sigma_g = 0.3$.

3.6.2. General competition model

For the general competition model variant we shall assume that $\sigma_x = \sigma_m$ so that

$$e_g^* = \frac{F}{(1 - \sigma_g)G^* + \eta_{mg}(1 - \sigma_m)(X^* + M^*) + h} \quad (43)$$

and

$$e_x^* = e_m^* = \frac{F}{\eta_{gm}(1 - \sigma_g)G^* + (1 - \sigma_m)(M^* + X^*) + H}. \quad (44)$$

In addition to h' and H' defined in equation (31) and η'_{gm} and η'_{mg} defined in equation (32) we now define parameter groups

$$\psi_g \equiv \frac{2}{S_R S_G F} \quad \psi_m \equiv \psi_g \frac{S_G}{S_M} \quad \xi \equiv \frac{\rho \sigma_g}{\sigma_m} \quad (45)$$

In terms of these parameter groups, and writing $K^* = X^* + M^*$ to represent the total

number of MSW fish at equilibrium, the versions of equation (35) for $a = g$ and $a = m$ become

$$\psi_g = \frac{1}{G^* + \eta'_{mg}K^* + h'} + \left(\frac{\xi}{\xi G^* + K^*} \right) \left(\frac{G^*}{G^* + \eta'_{mg}K^* + h'} + \frac{K^*}{\eta'_{gm}G^* + K^* + H'} \right) \quad (46)$$

$$\psi_g - \frac{1}{G^* + \eta'_{mg}K^* + h'} = \xi \left(\psi_m - \frac{1}{\eta'_{gm}G^* + K^* + H'} \right) \quad (47)$$

From these equations we note that the steady state value for this system is a function of the seven parameter groups defined in equations (45), (32) and (31). We use them in much the same way as their equivalents for the female territories model. Equation (47) yields a quadratic which we can solve for K^* in terms of G^* , which makes equation (46) into an equation in one-unknown (G^*) which we can solve numerically. The results of a typical investigation are shown in Fig. 15.

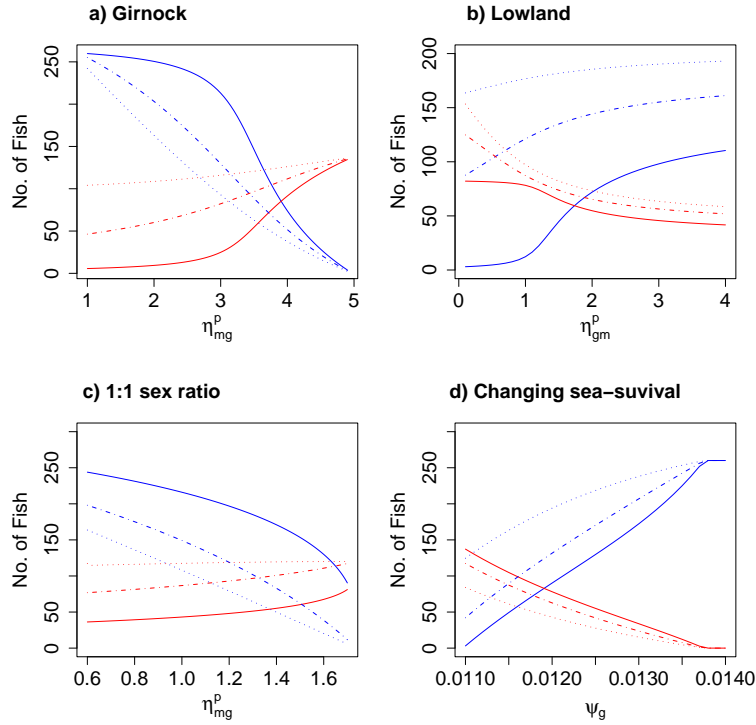


Figure 15: An analytic investigation of the general competition model . All frames have $\psi_g = 0.00555$, $\psi_m = 0.0111$. Blue lines show total grilse and red lines show total MSW fish. a) shows a Girnock type situation with $h' = 100$, $H' = 42.8$, $\xi = 0.77$, $\eta'_{gm} = 0.33$ (solid), 0.2 (dashed), 0.0 (dotted), and η'_{mg} varying. b) shows a Lowland type situation with $h' = 42.8$, $H' = 100$, $\xi = 0.14$, $\eta'_{mg} = 2$ (solid), 0.7 (dashed), 0.1 (dotted), and η'_{gm} varying. c) shows a situation with 1:1 sex ratio, $h' = H' = 60$, $\xi = 0.33$, $\eta'_{gm} = 0.75$ (solid), 0.5 (dashed), 0.25 (dotted) and η'_{mg} varying. d) shows the result of decreasing sea-survival with Girnock-type parameters (solid) and $\eta'_{mg} = 4$ (dotted) and 3 (dashed).

This figure shows many similarities between this model and the female territories model, although the fact that the females of the two phenotypes compete directly means that coexistence is not now guaranteed, and occurs only with well defined parameter ranges. Making

due allowance for that we can see that reducing the competitive advantage of the grilse always reduces grilse numbers and allows the MSW numbers to increase.

4. Conclusions

4.1. Coexistence of Grilse and Multi-sea-winter salmon

The demographic analyses in section 1 make it plain that in the Scottish context:

- Grilse and MSW salmon coexist over a wide range of habitats.
- The characteristics of this coexistence change on a relatively small spatial scale, with run-time, ratio of grilse/MSW spawners and spawner sex ratio all altering significantly from one part of a single catchment to another.

In view of its ubiquity, it seems more plausible that Grilse/MSW coexistence is a long-term phenomenon rather than that it is a transient accident. This supposition is supported by the fact that, at a whole catchment scale such relationships have lasted over 200 years (Summers, PhD Thesis 1992). If this is so, the long-run fitness of the two return strategies *must* be exactly equal. This cannot occur unless the fitness of both players is under dynamic control – that is unless some competitive process sets both the relative and absolute fitness of both players. In short, the fecundity or survival of grilse and MSW salmon must respond to the abundance of both in such a way as to regulate the long-run average fitness of both strategies at exactly 2 surviving genetic contributions per individual.

The characteristics of the coexisting populations vary not only between rivers but between sub-catchments within a river. This clearly demonstrates that the competitive processes which regulate fitness must operate at the level of sub-catchment populations. It is not logically impossible for such sub-catchment specific competition to happen while the fish are at sea, nor are there any observations of salmon at sea which can be interpreted as ruling out the required population segregation. However, it is very hard to construct even remotely plausible models of the details of this process. By contrast conceptual models of competitive processes occurring between the return of putative spawners to the river and emigration of their offspring to sea are very hard to construct without such segregation being a natural property.

We thus conclude that Grilse/MSW coexistence must be maintained by asymmetric competitive processes occurring at the subcatchment level within the river. Potential competitive mechanisms include

- Competition between individuals for low energy resting sites during river ascent.
- Competition between spawners for good quality nest sites
- Density effects on hatch success, for example by overcutting and egg damage after ova deposition, or by competition for oxygen in oxygen depleted groundwater
- Competition between alevins for food, refuge or oxygen
- Competition between fry for food or refuge (from inimical currents, high temperatures or predation)
- Competition between parr for food or refuge (from inimical currents, high temperatures or predation).

4.2. Salmon and Grilse: Choice vs genetics

Grilse and MSW salmon interbreed and the timing of adult maturation (and hence river return) is known to be (at least partly) heritable in farmed fish. Hence there are two groups of potential explanations of salmon population dynamics. One envisages return after one or two sea winters as alternative strategies which might be employed by any individual (i.e.

phenotypic plasticity), the other envisages a genetic differentiation which confers (almost) complete propensity to employ one or the other strategy.

The absence of reliable markers to identify ‘grilse’ smolts makes accurate determination of sea-mortality rates for fish returning to the Girnock extremely problematic. However, it is clear that the rate for individuals who return as grilse is very different from that for those who return as MSW fish. Although this could be explained by behavioural differences such as risk taking, it tends to suggest that the two groups of animals are simply in different places in the ocean. Since they leave from and return to the same estuary, the individual ‘choice’ group of explanations would require that choice to be made before the emigrants have been long at sea. We have expended considerable effort on trying to construct models in which the choice is made according to early growth success in the sea, but have entirely failed to formulate any model which cannot be immediately falsified. Hence the ‘choice’ group of explanations seems to require that choice to be made before going to sea.

We know that the strongest density dependence observed in the Girnock occurs somewhere between return to the river and the observation of catchable fry the following autumn. We have formulated two models which assume that the Grilse/MSW differentiation to be a genetic polymorphism governed by a single locus with two alleles and maintained by asymmetry in the stock-recruitment relation which caricatures the density dependence occurring between spawner return and fry observation. Both these models predict coexistence between grilse and MSW salmon over a wide range of parameters. They also demonstrate how changes in competition asymmetry can lead to changes in the population composition of exactly the kind inferred from the N. Esk fishery data.

4.3. The way forward

4.3.1. Theoretical investigation – coexistence in a single deme

Although the simple strategic models we have so far investigated have a number of very encouraging properties, it is still possible that the grilse/MSW polymorphism has a significant behavioural component in addition to the genetic element necessary to explain the observed heritability. It would seem sensible to examine a number of strategic models still based around a stock-fry-recruitment paradigm but postulating a wholly behavioural polymorphism, to assess whether this group of explanations can be falsified wholesale, or whether they must remain in play.

The present strategic models say nothing about within-year determination of sea-return-time, nor about how this might vary from deme to deme. This needs to be the subject of a separate investigation.

The mechanisms which underly the observed stock-recruitment relation are as yet completely unclear. Until this is remedied the possibility of management level, as opposed to strategic, modelling on waters other than the Girnock will be infeasible due to lack of empirical data. The primary attack on this problem will be observational (see below) but it seems probable that a subsidiary theoretical investigation using strategic models of candidate mechanisms may pay dividends by falsifying plausible but inappropriate candidates more cheaply than by observational approaches and by highlighting cost-effective discriminatory observations.

4.3.2. Theoretical investigation – deme to deme interactions

A key element in building a catchment level salmon population model is understanding how individuals who are optimised to operate in one deme’s zone fare when trying to breed in another. A related version of the same question, which views the demes as a continuum rather than as discrete, is how far from their home physical, biotic and genetic environment can individuals stray before their fitness is seriously compromised.

A completely systematic attack on this group of problems, seems likely to await a resolution of the mechanistic underpinnings of the key competitive interactions which govern grilse/MSW

coexistence. Since this may be some way off it seems plausible that modelling studies using the strategic mechanistic candidate models for the stock recruitment process may form a useful foundation on which progress may be made.

4.3.3. *Observation and experiment*

Although demonstrations that ‘density dependence’ occurs in the early stages of salmon life are not uncommon, observations which might elucidate the underlying mechanisms are few. In addition, observations which might provide a basis for falsifying models which postulate pre-ova-deposition mechanisms, such as competition for low-energy resting sites during river ascent, are almost entirely lacking. To make definitive progress in understanding salmon population dynamics FFL needs to compile an exhaustive inventory of putative mechanistic explanations for the stock–fry–recruitment relation, investigate the use of existing data to falsify these candidates, and finally devise, evaluate and implement observational programmes to yield data to determine the plausibility of the remainder.

4.3.4. *Management-facing models*

Notwithstanding the necessity of conducting further fundamental observational and theoretical science aimed at improving our understanding of the control mechanisms determining the success of, and interaction between, individual demes within a catchment, it is feasible to construct models incorporating best current knowledge, which may be of assistance to managers. The most plausible attack on this problem recognises that many important aspects of the salmon life-cycle co-vary with distance up a large river – a vague metric for which altitude is often a convenient (but potentially misleading) substitute. If we define a deme as those individuals breeding within a fixed distance (say 5km) of a given point then key heritable (i.e. selectable) attributes of the deme would be

- The date of ‘estuary return’
- The ratio of grilse to MSW spawners
- The sex-ratio of both groups of spawners

and the selective forces shaping these characteristics would come from

- The local physical and biotic environment to which it is adapted
- Sea-mortality both natural and exploitation
- The total exploitation risk (coastal, estuary and rod fisheries) to which it is exposed.

Direct observation of changes in genetic composition would require measurements at selectable loci such as MEP-2, while definition of prevalent genetic mixing rates would require observations at neutral loci (micro-satellites).

We note that, of the selective forces acting on the population, the only ones which can be managed selectively in respect of a specific deme are the timing, location and intensity of coastal and riverine fisheries. Managers have already taken some direct actions in this regard, such as buying out the N.Esk coastal nets, rod catch and release policies and so on. We believe that it should be possible to use the strategic models developed thus far both to make preliminary judgements of the efficacy of such actions as have been taken and to design related actions more finely modulated to the properties of individual demes.

The initial questions which such a programme might ask are

- Which N.Esk demes would we expect to have reacted most strongly (weakly) to current management action ?
- How would the impact of a Girnock-style egg planting programme compare with that of changes in exploitation timing or intensity

- What type and quantity of data would be needed to characterise the response of key demes to management action.

The construction of these models would necessarily ignore deme-deme interactions whose elucidation awaits the observational and theoretical programme outlined above. None the less we believe that the outcomes of such a modelling programme would give better insight into the impact of proposed management actions than current ‘whole catchment’ approaches.