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A dynamic state modelling approach to partial migration in brown trout

Master's thesis in Biology

Supervisor: Irja Ida Ratikainen

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The last two years have flown by, and it seems almost surreal that my master project is now coming to an end. Through this project, I have learned a lot about science, modelling, brown trout and not the least myself. It has been a big part of my life for the last years, and I am exceedingly grateful for all the wonderful people who have supported me along the way.

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ABSTRACT

Partial migration, the phenomenon of both resident and migratory individuals in the same population, is commonly observed all over the animal kingdom. The mechanisms behind partial migration can be complex, involving both genetic, developmental and environmental factors. Previous studies have found that brown trout (*Salmo trutta*) populations have different migratory proportions depending on the environment, while strategy distributions within the populations seem to be largely controlled by the individuals' states. There is, however, contradicting support for which traits that are most important and in what direction the states drive the individuals in their choice of becoming migrant or resident. In this thesis, I aimed to illuminate the role of state-dependency in migratory behaviour, and how it can interact with environmental characteristics to create differences in migratory tendencies. I used a dynamic state model to investigate how the states body mass, body length and body condition affect the optimal decisions of smoltification and migration through the course of a year in the life of a female juvenile brown trout. My model demonstrated that identical individuals in the same environment might end up with different strategies due to stochastic food acquisition. Migratory tendencies changed when altering initial states and environmental parameters such as migratory costs and difference in food availability between the river and the feeding areas.

SAMANDRAG

Partiell migrasjon, fenomenet der ein populasjon har både individ som migrerer og individ som let vere, er observert i store delar av dyreriket. Mekanismane bak kan vere komplekse, og kan inkludere både genetikk og miljø som medverkande faktorar. Tidlegare studiar har funne at andelen som migrerer i populasjonar av aure (*Salmo trutta*) varierer utifrå miljøet, medan skilnadar innad ein populasjon er i stor grad kontrollert av den kroppslege tilstanden til individa. Det er dertimot motstridande funn om kva for trekk som har størst påverknad og i kva retning dei påverkar individa i valet om å migrere eller bli verande. I denne masteroppgåva hadde eg som mål å kaste lys over rolla som kroppsleg tilstand spelar i migrasjonsåtferden til aure, og korleis det i samspel med miljøforhold skapar ulike tendensar til å migrere. Eg har nytta ein dynamisk tilstandbasert modell (*dynamic state model*) for å undersøke korleis kropps- masse, kroppslengde og kroppskondisjon påverkar kva som er dei optimale smoltifiserings- og migrasjonsavgjerdene ein umoden hofisk kan ta i laupet av eit år. Modellen min demonstrerte at identiske individ i same miljø kan ende opp med ulike strategiar grunna stokastisitet i mat- tilgjenge. Tilbøyelegheita for å migrere er ulik for individ som startar året i ulike tilstandar, og endrar seg med miljøforhold som migrasjonskostnad og skilnaden i mattilgjenge mellom elv og sjø.

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1 INTRODUCTION

Nature offers a wide range of habitats that differ in safety and food availability. Safe habitats have lower mortality due to less predation or less parasitism, while habitats with high food availability have the benefit of lowering the chance of starvation and increasing growth. Larger size can then lead to higher survival (Skov et al., 2011) and higher reproductive success (Jonsson, 1985; L’Abee-Lund and Hindar, 1990). If a habitat is both productive and safe, this would be the ultimate choice, but often organisms encounter several habitats that vary in their safety and food availability. Depending on the organism’s benefit of safety versus food, there is a trade-off in the decision on where to allocate one’s time. Organisms can then optimize their fitness by choosing the habitat where reproductive output is maximized and mortality over growth is minimized (Werner, 1986). This balance can vary over time. It can for example be different during breeding and non-breeding seasons. The most well-known examples of migration between habitats are perhaps annual flights of birds to-and-fro breeding grounds and salmonid fishes migrating to the sea for feeding and returning rivers to spawn (Dingle, 2014).

A migratory strategy often comes with costs and risks. The travelling itself can be energy consuming (Jonsson and Jonsson, 2006) as well as increasing one’s exposure for predators (Elliott, 1993). An individual in one habitat also has no way of (certainly) assessing the environmental conditions in the other habitat before travelling there. For it to be optimal for an individual to migrate away from the breeding ground to a more productive feeding area, these costs need to be outweighed by enough increased growth and subsequently higher reproductive success and adult survival. Many factors impact this balance. It can be dependent on the organism’s own states (e.g., sex, age, size, body condition) and the environmental conditions in both habitats and on the migratory route between them.

Migratory strategies can vary between species and populations, and even within a population (Chapman et al., 2011). When both migratory and resident individuals are present in the same population, this is referred to as partial migration (Lack, 1943). Chapman et al. (2011) suggests that, except for extreme cases where the habitats are inhabitable at switching times, many migratory populations are actually partially migratory. Partial migration has been observed in a wide range of animal taxa, such as mammals (Ball et al., 2001), amphibians (Grayson and Wilbur, 2009), invertebrates (Hansson and Hylander, 2008), and especially in a range of birds (Hegemann et al., 2019 and references therein) and fish species (Chapman et al., 2012 and references therein).

For a life history trait like migration to stay polymorphic in a population, the fitness of the two strategies (migrant and resident) could vary either dependent on 1) population characteristics, such as frequency (proportion of individuals with each strategy; Lundberg, 2013) or density (number of individuals within each strategy; Leenheer et al., 2017), or 2) individual characteristics such as the above-mentioned sex, age, size and body condition. Either of these can act on their own, but they are not mutually exclusive and can act in combination, e.g. population characteristics can affect food availability which again affects size and condition of individuals. The strategies of individuals could also either be fixed (genetically decided) or plastic (environmentally induced). With partial migration so widely distributed in nature, it follows that the mechanisms behind it can also greatly vary, but while theory has focused on partial migration as an evolutionary game between fixed strategies within a population, conditional state-dependent strategies has received more empirical support (Chapman et al., 2011).

1.1 Migration in brown trout (*Salmo trutta*)

Salmonids is a group of fish species that have a range of migratory patterns, from full migratory through partial migratory and all the way to full residency, as they spawn in their natal brooks but can migrate towards the sea or other larger water bodies to feed (Dodson et al., 2013). To be able to migrate to more saline habitats, such as the estuary or the sea, salmonids must go through smoltification, a physiological process where one of the main results is the ability to osmoregulate (McCormick and Saunders, 1987). In addition to resource allocation to smoltification, migration can also have a cost of travelling, delayed maturation and higher risks of predation and diseases (Jonsson and Jonsson, 1993).

The feeding areas are usually more productive (Gross et al., 1988), but less safe (Elliott, 1993), so migrating out to sea usually results in lower survival, but a larger mean body size than their resident counterparts. For brown trout, a large size can then mean less predation (Dieperink et al., 2001; Hyvärinen and Vehanen, 2004) and higher probability of surviving several reproductive events (Cucherousset et al., 2005). For salmonid females, the reproductive fitness is also strongly dependent on their size (Jonsson and Jonsson, 1993). Due to higher food availability and consequently larger body size, migrating females may produce many times over the egg number that residential individuals produce (Jonsson, 1985).

Brown trout is a species that can have different strategies in separate populations (Lemopoulos et al., 2018) or different strategies within the same populations (Cucherousset et al., 2005). There is variation in the tactics among migrating individuals, both in how far they migrate and the duration of their feeding migration (Cucherousset et al., 2005), but there is a tendency for surviving individuals to partly choose the same tactics next time they migrate (Eldøy et al., 2019).

When looking at what determines the migratory decisions in partially migratory populations of brown trout and other salmonids, Dodson et al. (2013) concluded that genes play a crucial role in the alternative migratory strategies in salmonids, but that body size and body condition are also major influences on individuals' decision to migrate. For brown trout there are some candidate genes for the migratory tendencies (Lemopoulos et al., 2018), but genetic differences are usually between populations with different migratory tendencies and not between strategies within a sympatric population (Ferguson et al., 2017). The brown trout's decision to smoltify and migrate has been shown to be plastic, and environmentally induced by high population density and low food availability (Olsson et al., 2006; Jones et al., 2015). Näslund et al. (2017) on the other hand found low food availability to reduce smoltification. The plasticity in strategy, means that resident individuals can get migratory offspring, and can sometimes contribute substantially to the migratory part of the population (Duval et al., 2021).

While there is general agreement that the individual's states, such as size and body condition, can impact the choice of residency versus migration, which role they play is more debatable and empirical findings can be contradicting (Ferguson et al., 2019). Within brown trout populations, migrants have been found to be both smaller (Winter et al., 2016) and larger (Acolas et al., 2012) than residents. Migrants have also been found to have both higher body mass (Olsson et al., 2006) or lower body mass (Winter et al., 2016), and lower body condition (Boel et al., 2014) and higher growth rate (Acolas et al., 2012) than residents. Within the same population, Jonsson (1985) found that fast and slow growers became migrants (but at different times) but that intermediate growers stayed resident. The sex-dependent fitness-benefit of size is well-acknowledged as an important contributor to sex-difference in migratory strategies in brown trout (e.g. Jonsson and Jonsson, 1993; Ferguson et al., 2019), and similar states may

drive males and females towards different strategies (Cucherousset et al., 2005).

Variation in migratory tendencies across populations have been explained by environmental differences changing the trade-off between the strategies. Two main hypotheses are that the benefit of migration should decrease with increasing migratory costs (such as longer distance or higher altitude; (Bohlin et al., 2001)) and increasing river food availability (Olsson et al., 2006).

1.2 Research question and aims

In this thesis, I aimed to illuminate the role of state-dependent behaviour in brown trout migratory choices within a population. I use a dynamic state modelling approach (Clark and Mangel, 2000; Houston and McNamara, 1999) to answer the following questions:

- 1) *How does the individual female brown trout's states predict the optimal migratory tactics throughout different stochastic environments on the migratory journey?*
- 2) *How does the interplay between stochastic environments and individual states work to create patterns in migratory tactics of females on a population level?*

I further wished to explore how an optimized plastic strategy compares to fixed strategies, and how different environmental characteristics, such as migratory costs and food availability, contribute to differences between populations.

2 METHODS

I use a dynamic state model (Houston and McNamara, 1999; Clark and Mangel, 2000) to look at the optimal state-dependent migratory strategies through a year in the life of a female juvenile brown trout. Each time step in my model represents one week, and allows the individual to make decisions about both smoltification and migration. All modelling has been done in Julia (Bezanson et al., 2017).

2.1 Model set-up

In my model, an individual has three internal states: body mass (g), length (cm) and smolt status (0-1), as well as geographical position along a river-estuary-sea migratory route. Within each time step, an individual can make two decisions: to smoltify or not (Figure 1a) and to move (upstream, downstream or stay; Figure 1b). The optimal decisions are the combinations of these two choices that will give the individual fish the highest expected fitness.

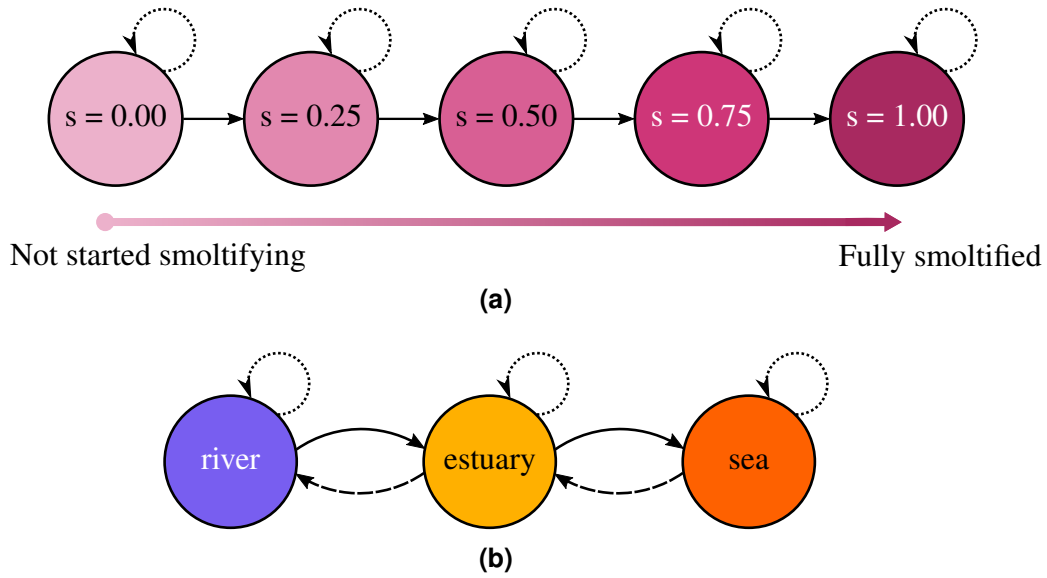


Figure 1. Possible decisions for a) smoltification at each possible smolt status s and b) migration at each possible geographic location. Solid lines (—) indicate smoltifying or downstream migration, dotted (·····) indicate no change, and dashed (- - -) indicate upstream migration.

2.1.1 Internal states

The model looks at the fitness and optimal decisions of individuals with a body mass from 0.0 to 250.0 g, and body length between 10.0 to 30.0 cm (see Table 1). Body mass is increased by food acquirement, and decreased by metabolism and additional costs of smoltification and migration. If an individual dies, its body mass is set to 0.0 g. Length is increased passively as a function of body condition, and never decreases.

Body condition is a function of the two states above, body mass m and body length l . I use Fulton's condition factor K , a common measure of body condition in fish (Nash et al., 2006), given by the formula in Eq. (1) and visually depicted in Fig. 2.

$$K = \frac{m \text{ (g)}}{(l \text{ (cm)})^3} \cdot 100 \quad (1)$$

Table 1. Parameters used in the model.

Parameter	Explanation
h	Habitat. Possible values are {river, estuary, sea}. Simulations start off individuals in river.
m	Body mass, with $m_{min} = 0.0$ g and $m_{max} = 250.0$ g. Optimization calculated with increments of 2.5 g.
l	Body length, with $l_{min} = 10.0$ cm and $l_{max} = 30.0$ cm. Optimization calculated with increments of 0.25 cm. If $l \geq l_{pisc} = 20.0$ cm, the fish is considered piscivorous and acquires 33% more food.
s	Smolt status, with $s_{min} = 0.0$ (representing not smoltified) and $s_{max} = 1.0$ (representing fully smoltified), and increments of 0.25. Minimum smolt status for surviving in the three habitats are $s_{river} = 0.0$, $s_{estuary} = 0.75$ and $s_{sea} = 1.0$.
t	Week (time step), with $t_{min} = 1$ and $t_{max} = 52$. Winter (non-growing season) lasts for $1 \leq t \leq t_{winterend} = 12$, with growing season lasting the remaining time steps.
K	Body condition, a function of body mass and body length, see Eq. (1). Used in thresholds for growth (occurs with $K \geq K_{growth} = 0.8$) and starvation (possible for $K \leq K_{starve1} = 0.7$, certain for $K \leq K_{starve2} = 0.3$). In the final time step, $K > K_{starve1}$ is required to survive.
F	Fitness, using length-dependent fecundity as proxy, see Eq. (9).
d_s	Smoltification decision. Possible are values {0, 1}
d_{mig}	Migration decision. Possible values are {-1, 0, 1}
c_s	Cost of smoltifying ($d_s = 1$), given as percent of body mass m . Baseline value = 4.0.
c_{mig}	Cost of migrating ($d_{mig} \neq 0$), given as percent of body mass m . Baseline value = 10.0. $c_{mig} = \{8.0, 9.0, 11.0, 12.0\}$ also examined.
c_{met}	Weekly cost of metabolism, given as percent of body mass m . Baseline value = 5.0. $c_{met} = \{3.5, 4.25, 5.75, 6.5\}$ also examined.
p_h	Weekly predation rate in habitat h . $p_{river} = 0.0084$, $p_{estuary} = 0.0258$ and $p_{sea} = 0.0174$. There is a negatively linear dependence on body length l , as described in Eq. (5). If downstream migration occurs ($d_{mig} = 1$) in a time step, this value is multiplied by $p_{mig} = 5.0$. Model variations include p_{mig} in {1.0, 3.0, 7.0, 9.0}.
b	Habitat food factor, adjusting the food amount for each habitat: $b_{river} = b^0 = 1$, $b_{estuary} = b^1 = b$, $b_{sea} = b^2$. Baseline value: 1.35. Model variations include b in {1.25, 1.30, 1.40, 1.45}.
q	Food quantity factor, $q_{high} = 1.0$, $q_{average} = 0.65$, and $q_{low} = 0.30$.
u_t	Food seasonality factor, with baseline values $u_{winter} = 0.5$ when $t \leq t_{winterend}$, and $u_{summer} = 1.0$ when $t > t_{winterend}$.
v	Food stochasticity, adjusting the probability of <i>not</i> getting $q_{average}$: $P(q_{average}) = 1 - v$, while $P(q_{high}) = P(q_{low}) = v/2$. Baseline value is $v = 0.75$. Model variations include v in {0.0, 0.375, 1.0}.
a	Constant adjusting slope of growth function, see Eq. (2). Baseline value = 4.0. $a = \{2.0, 3.0, 5.0, 6.0\}$ also examined.

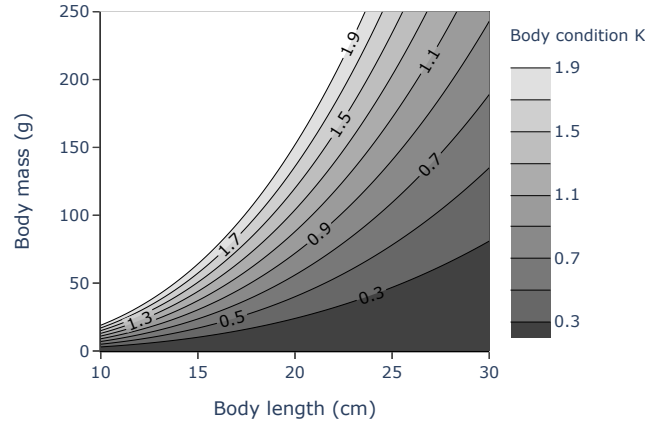


Figure 2. Visual depiction of body condition index K as a function of body mass and body length, given in eq. 1.

In my model, K is used in several thresholds. This includes the threshold for surviving a time step, the threshold for growth during a time step and the threshold for surviving at the end of the period (Table 1).

Smolt status is the third internal state, and represents how far an individual has come in the process of smoltification. It spans from 0 (not started smoltifying) to 1 (fully smoltified). Though this in reality is a continuous process, it is discretized with a step size of 0.25 to make it tangible in the model. An individual can only advance one smoltification step at each time step, so a minimum of four weeks are needed to fully smoltify – matching the 1-2 months long time period that is observed that salmonids use for the parr-smolt transition in nature (McCormick and Saunders, 1987). In my model, I assume smoltification to be an irreversible process. This is a simplification that fits what is generally seen in nature, but there are cases where salmonid individuals that remain in freshwater after smoltifying, desmoltify and regain a parr-like appearance and low salinity tolerance (McCormick and Saunders, 1987).

Growth

Growth occurs passively when the body condition index K is over a certain threshold (Table 1). I assume that individuals with high body condition increase in length faster than those with lower, so body length is increased as in the following equations:

$$rg = \begin{cases} a \cdot \frac{K - K_{\text{growth}}}{K_{\text{growth}}}, & \text{if } K \geq K_{\text{growth}} \\ 0, & \text{if } K < K_{\text{growth}} \end{cases} \quad (2)$$

$$l_{\text{new}} = l_{\text{old}}(1 + rg\%) \quad (3)$$

where rg is relative growth in percent of body length l , a is a constant to scale growth and $K_{\text{growth}} = 0.8$ as given in Table 1. When body length l increases, correspondingly K decreases (Eq.(1)). With the baseline value of $a = 4.0$, it follows from Eqs. (2) and (3) that the new body condition (after growth) still is above K_{growth} and increases with the old body condition (Fig. 3b). In other words, the higher body condition the individual has before growth, the higher body condition it will still have afterwards while also having a larger increase in body length.

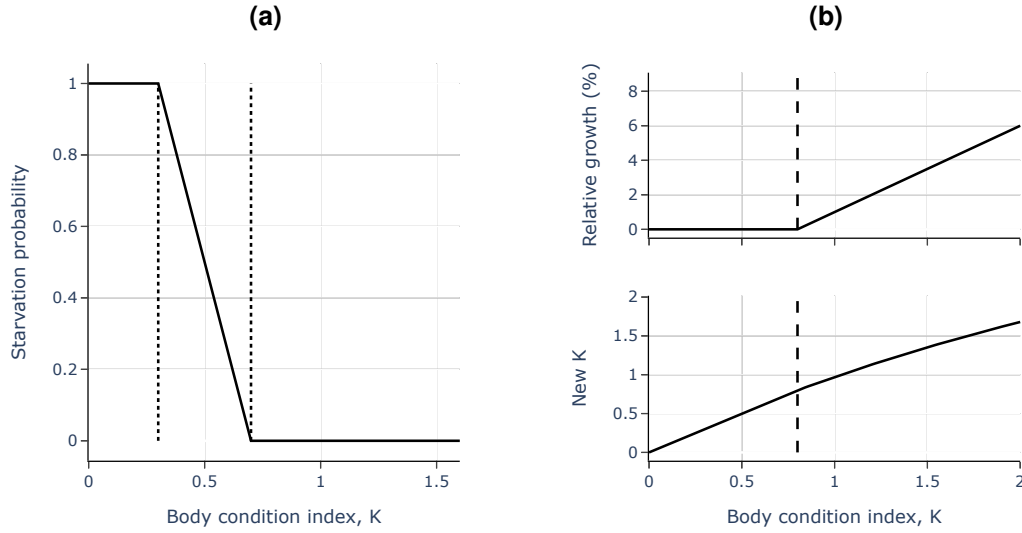


Figure 3. (a) Starvation as a function of K. Under $K = 0.3$ everyone dies of starvation, and over $K = 0.7$ no-one does. (b) Relative growth and subsequently new body condition index as functions of body condition index K (Eqs. (2) and (3), respectively) after acquiring food. Dashed line (---) indicated growth threshold.

2.1.2 Habitats

Habitats differ in predation rates p , food availability b and requirements for smolt status s (Table 1). The river is the safest place to be (less predation) and has no requirements for smolt status, but has the lowest food availability. The sea and estuary are more risky (higher predation), but have also more food. To survive at sea, the fish has to be fully smoltified. In my model, the estuary is between the river and the sea when it comes to food quantity and smolt status requirements, but has the highest predation rates.

If an individual moves to a habitat while they have lower smolt status than the habitat requires, it immediately dies. Because of the certain death this never occurs for optimally behaving individuals, but serves the purpose of forcing them to smoltify before migrating. This is a simplification, as in the real world a small fraction of the anadromous individuals may migrate before they have undergone the smoltification process and survive, assuming they are able to stay in areas with low salinity before smoltification (del Villar-Guerra et al., 2019).

Predation

Mortality rates in brown trout can be quite high, a lot due to predation. Elliott (1993) looked at mortality rates in females in Black Browse Beck in England. The mortality at sea was constant over several years, with a mean of $0.25\% \text{ day}^{-1}$, while the rates in the freshwater varied more between years and within a year. The second summer in fresh water it was found to be $0.12\% \text{ day}^{-1}$, and was the latest estimate that did not include time spent at estuary or sea. I base the predation rates in my model on these values, turning them into probabilities of predation each time step (week) by the following equation:

$$P(\text{predation weekly}) = 1 - (1 - P(\text{predation daily}))^7 \quad (4)$$

From the above estimates, Eq. 4 gives a weekly predation rate at 0.0084 and 0.0174 for the river and sea, respectively. Thorstad et al. (2012) found that the estuary was the part of the

migratory journey with the highest mortality for Atlantic salmon (*Salmo salar*) smolt. Without a real life quantification of estuary mortality compared to sea mortality for brown trout, I therefore set the predation in estuary to be equal to the sum of the river and sea predation rates (0.0258), and can be interpreted as both riverine and marine predators are present in the estuary.

Predation has been found to be higher for small fish than larger fish in both brown trout (Dieperink et al., 2001) and other migratory fish (Skov et al., 2011). This is implemented in my model as predation rate having a negative linear relationship with body length l (Fig. 4). I set the empirical predation rates for each habitat (p_h) to be the predation rate at body length $l = 15.0$ cm. Since most predation happens right after migration (Dieperink et al., 2001), I multiply predation rate by $p_{mig} = 5.0$ if downstream migration occurs ($d_{mig} = 1$) in a time step.

Putting all this together, the predation rate can be described as follows:

$$\text{Pred}(l, h, d_{mig}) = \begin{cases} (1 - 0.5 \cdot \frac{l-15\text{cm}}{15\text{cm}}) \cdot p_h, & \text{if } d_{mig} \neq 1 \\ (1 - 0.5 \cdot \frac{l-15\text{cm}}{15\text{cm}}) \cdot p_h \cdot p_{mig}, & \text{if } d_{mig} = 1 \end{cases} \quad (5)$$

The outcome of predation is fitness is equal to zero.

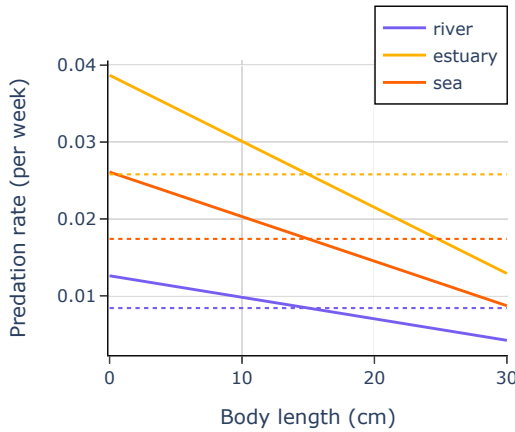


Figure 4. Predation rates in different habitats as a function body length. Based on estimates from (Elliott, 1993), indicated by dashed (---) lines.

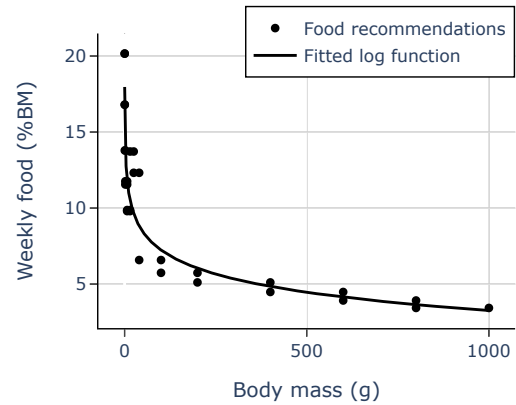


Figure 5. Recommended feeding for optimal growth according to guidelines from AllerAqua and the fitted logarithmic function (Eq. (6)).

Food

If a fish avoids predation, the next stochastic event within a time step is food acquisition. The different outcomes are different food quantities q , and the possible values are q_{high} , $q_{average}$ and q_{low} (Table 1). Probabilities of different food quantities are determined by the parameter food stochasticity v , as described in Table 1. Both Jones et al. (2015) and Näslund et al. (2017) fed hatchery brown trout with two different food quantities, high and low, and found (contrary) effects on smoltification tendencies. They based high rations on recommended feeding for optimal growth and set low rations to be equal to 30% of the high ration. I use the same scheme in my model, adding the "average" quantity to be the mean of the high and low quantities.

The baseline food amount is based on the recommended feeding for optimal growth in fresh water from the website of Aller Aqua (<https://www.aller-aqua.com/species/cold-freshwater->

species/brown-trout). The recommended food amount is dependent on body mass, temperature and type of feed, and is given as kg food per 100 kg fish. To simplify, I have chosen one temperature (8 °C, a temperature where a lot of brown trout downstream migration happen in a Norwegian river (Hembre et al., 2001)) to use as basis, and to fit with my model I have multiplied the food amount by 7 to convert from daily to weekly feeding. I call this value "food percentage" (fp in Eq. (6)) as kg food per 100 kg fish is more generally mass in food as a percentage of body mass. The percentage decreases as fish get bigger, and this is implemented in the model by fitting a decreasing logarithmic function (see Fig. 5). Using the Julia package CurveFit.jl (Jabardo, 2014), the best fit was found (see Eq. 6) to be:

$$fp(m) = 15.19 - 1.73 \cdot \ln(m) \quad (6)$$

The food amount is then calculated back to grams by multiplying body mass m and the food percentage fp. It is subsequently multiplied by a habitat factor b_h , the seasonality factor u_t , and the stochastic quantity factor q .

As the body length increases, the probability of brown trouts being piscivorous is observed to increase (Kahilainen and Lehtonen, 2003; Jensen et al., 2012b). Effect of length depends on the habitat and the community (L'Abée-Lund et al., 1992; Jensen et al., 2008; Sánchez-Hernández et al., 2017; Sánchez-Hernández, 2020), and various threshold lengths has been reported, such as minimum lengths for piscivory at 13 - 20 cm (L'Abée-Lund et al., 1992; Naesje et al., 1998; Jonsson et al., 1999; Kahilainen and Lehtonen, 2003; Rikardsen and Amundsen, 2005; Jensen et al., 2012b; Sánchez-Hernández et al., 2017), and lengths for diet switch at 20 - 54 cm (Naesje et al., 1998; Kahilainen and Lehtonen, 2001, 2003; Jensen et al., 2012b; Sánchez-Hernández et al., 2017). I have simplified this in my model to a switch to piscivorous diet at $l_{pisc} = 20.0$ cm. For a brown trout, a piscivorous diet allows for 33% more efficient conversion of energy into growth, than a diet consisting of invertebrates (Elliott and Hurley, 2000). This is implemented in the model as food amount being multiplied by 1.33 if the fish is above the piscivore threshold.

Putting all this together, the food amount (fa) an individual gets depends on many factors and can be described as follows:

$$fa(m, h, t, q, l) = \begin{cases} fp(m) \cdot b_h \cdot u_t \cdot q, & \text{if } l < l_{pisc} \\ fp(m) \cdot b_h \cdot u_t \cdot q \cdot 1.33, & \text{if } l \geq l_{pisc} \end{cases} \quad (7)$$

2.1.3 The year

In the model, the complex seasonality of the year is highly simplified, and the year is divided into two sections – winter (non-growing) and summer (growing) season. Winter lasts the first 12 weeks of the model, and during this time it is not possible to smoltify or migrate, as very few brown trout individuals migrate when temperatures are very low (Hembre et al., 2001). Stochasticity of predation, food acquisition and starvation still occurs, but food amounts are reduced (multiplied by food seasonality factor $u_{winter} = 0.5$) compared to the rest of the year ($u_{summer} = 1.0$). The remaining 40 weeks makes up the growing season, during which the model allows the fish to make decisions about smoltification and migration. Low temperature can compromise the osmoregulation of brown trout (Thomsen et al., 2007), and it is often observed in nature that anadromous individuals overwinter in fresh or brackish water (Jensen et al., 2015, 2018). At the end of the final time step (week 52), survival at sea is set to 0 to force the fish in my model to migrate to estuary or river to overwinter.

2.2 Optimization (backward iteration)

At each time step three stochastic events can take place: predation, food acquisition and starvation – each with their own probability functions dependent on a different combination states. All in all, for every combination of smoltification and migratory decisions, there are seven possible outcomes (new states and new fitness) in a time step. Following the standard dynamic state variable approach, the outcomes for each decision combination are summarized with the expectation value for fitness, $E(F)$, given in the following equation

$$E(F) = \sum_{i=1}^n F_i \cdot P(F_i), \quad (8)$$

where n is the number of outcomes, F_i the fitness for outcome i and $P(f_i)$ the corresponding probability. This makes the decisions comparable, and the combination of smoltification and migratory decision with the highest expectation value for fitness, is set to be optimal.

The most efficient way to calculate this for all time steps, is to go backwards in time, so the procedure is to start at the final time step (as at this point it is known how states translate to fitness), and work backwards to the initial time step.

The result from the backward iteration is three five-dimensional arrays: one for optimal smoltification decisions d_s , one for optimal migratory decisions d_{mig} and one for expected fitness. The five dimensions are due to these values all being functions of time, habitat, smolt status, body mass and body length.

2.2.1 Fitness

As a proxy for future reproductive success, terminal fitness (fitness at the final time step) is set by the length-dependent fecundity function in Eq. (9), based on findings from L’Abée-Lund and Hindar (1990).

$$F(l) = 10^{-0.746+2.42 \cdot \log_{10}(l)}, \quad (9)$$

where F is fecundity and l is body length of the fish. The fecundity function is depicted in Fig. 6.

To survive in the final time step and get fitness above 0, K must be higher than $K_{starve1} = 0.7$. The terminal fitness at sea is set to 0, so that in my model individuals migrating to sea must return at least to the estuary to overwinter. For all other time steps than the last, fitness is the expected terminal fitness (see Eq. (8)).

Expected (terminal) fitness in the other time steps, assumes that the individual behaves optimally in all the subsequent time steps. It is therefore based on the calculated new states for the subsequent time step, and as body mass and body length are continuous, interpolation between the closest values is used to calculate the expected fitness.

The expected fitness is calculated for each possible decision, or rather combination of smoltification and migration decisions. The optimal decision combination is set to be the one with the highest expectation value for fitness. If two choices give equal fitness (with six significant digits to avoid differences due to handling of float numbers in Julia), the most passive decision (i.e. not doing something opposed to doing something) is preferred.

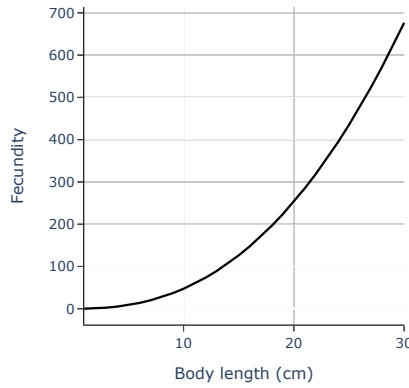


Figure 6. Fecundity F as function of body length l , based on estimates from (L’Abée-Lund and Hindar, 1990).

2.3 Simulation (forward iterations)

All my simulations start at time step $t = 1$, habitat = river and smolt status $s = 0$. Note that $t = 1$ does not mean first week of a calendar year, but rather the first week of winter. I start my baseline simulations with body mass and body length values that are within the range of what a realistic two years old brown trout parr would be, with body mass $m = 25.0$ g and body length $l = 13.0$ cm (Raikova-Petrova et al., 2018), and consequently body condition index $K = 1.14$. The baseline optimization model is also explored for other values for initial states. At two years or older is a typical age for brown trout to migrate, but there does not seem to be any strict lower or upper age limits – it can vary a lot within a population (Jensen et al., 2012a) and mean smolt age varies with latitude (Jonsson and L’Abée-Lund, 1993) and stream size Jonsson et al. (2001). Age is not included in my model, and the results can be interpreted for any brown trout of the relevant body mass and body length.

I run 10 000 simulations for all sets of parameters, and use the Julia-package DataFrames.jl (Kamiński et al., 2022) to track which states the individuals are in and which decisions they make.

2.4 Alternative models

2.4.1 Fixed strategies

To compare fitness of strategies from optimal decision-making and fixed strategies, I run alternative optimization models where the fish only gain any fitness if they in the final time step meet certain criteria related to smolt status s or habitat h . The three alternative models include $s = 0$, $s \geq s_{\text{estuary}} = 0.75$ and $h = \text{estuary}$, forcing individuals to either stay resident, smoltify or migrate, respectively. Note that even when forcing them to smoltify and/or migrate, they still optimize *when* to make the decisions.

2.4.2 Exploring parameter ranges

In my model, I used both parameter values that have been well quantified in literature and those who have weak or missing empirical quantification. Some values are hard to find a real-world quantification of, as they represent more than one aspect, such as the “metabolism” parameter accounting for every energy expenditure or mass loss other than that of smoltification and migration. It should also be noted that in the real world, decisions should be optimized for

a lifetime and not just a year. Costs of one-time events such as smoltification, might have to deviate from the true cost to make sense within the scope of a year.

In the case parameter values without a well-founded empirically based quantitative background, I have chosen baseline values that make a relevant model, i.e. one that cause partial migration to occur. To explore how these parameters affect the main outcome of the model (final strategy distributions), I run alternative optimization models and simulations for a range of relevant values for some of these parameters.

The results of doing this for environmental parameters such as migration cost c_{mig} , travel-induced predation increase p_{mig} , habitat food factor b and food stochasticity v , can investigate how the migratory tendencies change for populations adapted to environments with different characteristics. I also do this for some of the other parameters (metabolism c_{met} and the growth scaling constant a). The distributions of the latter parameters are not included in the main results, but can instead be found in Appendix A.3.

3 RESULTS

3.1 Base result

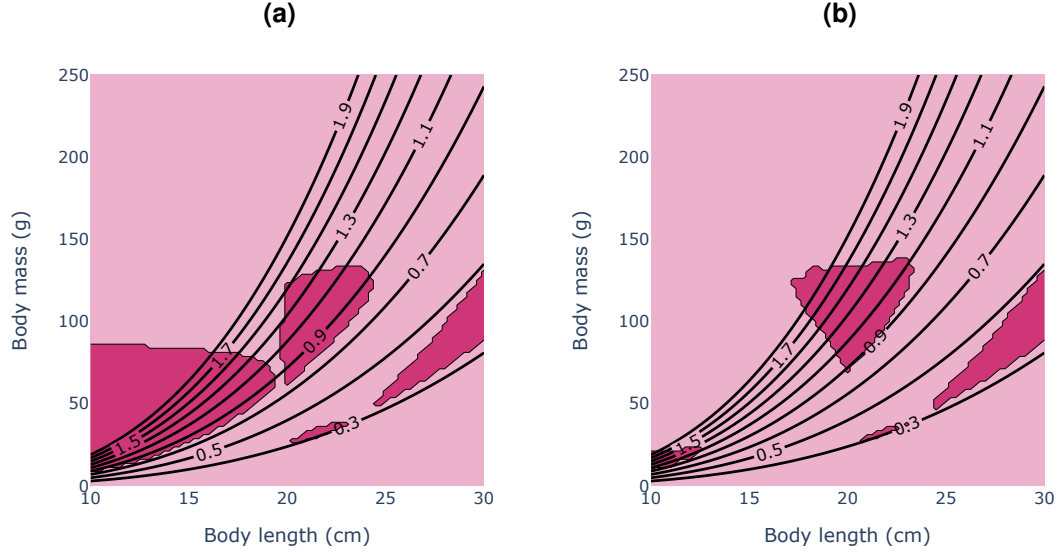


Figure 7. Optimal smoltification for an individual in river that has not smolt status $s = 0$ at time steps **a)** $t = 15$ and **b)** $t = 30$. Light pink (■) means *not* smoltify ($d_s = 0$), hot pink (■) means smoltify ($d_s = 1$). Black lines indicate body condition index K .

3.1.1 Optimization

The optimal decision changes with states and over time. Fig. 7 illustrates this and shows the optimal decisions for smoltification for individuals that are in the river and have not started smoltifying yet (i.e. the option to go to stay with smolt status $s = 0$ or increase to $s = 0.25$), at time step 15 and 30. At time step 15, the majority of combinations that gives smoltification as the best option, has a body condition index above 0.8. Smoltification is also optimal for longer individuals with body condition index below 0.5. There is a break in the pattern at the piscivore threshold for body length $l_{pisc} = 20.0$ cm. At time step 30, the number of combinations where it is beneficial to smoltify has shrunk compared to time step 15, but we see there are both combinations where the optimal decision has changed to smoltification and where it has changed away from smoltification.

3.1.2 Simulations

Initial parameter values are set to be within the range of what a two-year-old parr to be. The baseline values for starting states are body mass $m = 25.0$ g and body length $l = 13.0$ cm, and consequently body condition index $K = 1.14$. All individuals that migrate at least to the estuary are labelled migrants, and all who stay in the river after winter ends are labelled residents. As everyone starts off at the same parameter values, the different outcomes and consequently strategies, come from achieving differing states through the stochastic events.

After running 10 000 simulations, the final distributions (Fig. 8a) showed that 54.4% died, 18.8% were surviving residents and 26.8% were surviving migrants. Including individuals that died, 34.4% chose a resident strategy, 55.3% chose a migrant strategy, while the remaining 10.3% died during winter before they had the chance to make any decisions (Fig. 8b).

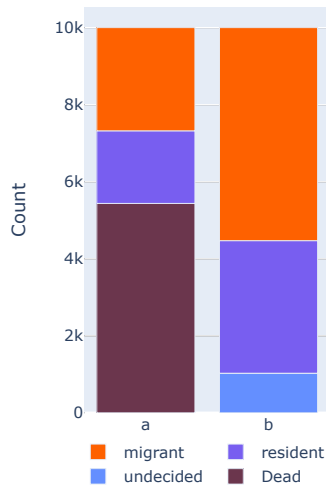


Figure 8. Final distribution for **a)** strategies (living individuals) and mortality, and **b)** strategies of both living and dead individuals.

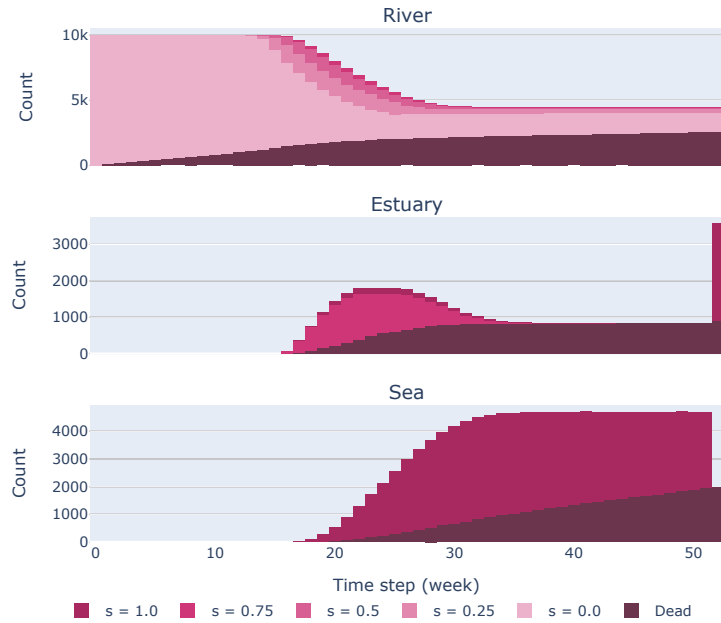


Figure 9. Distribution of mortality and smolt status in the three habitats through the 52 weeks for 10 000 simulations.

From Fig. 9, it is evident that almost all (except five) individuals who smoltify enough to tolerate the salinity in the estuary, move to the estuary, and all who smoltify enough to tolerate sea migrate to the sea. We also see that most individuals that start the smoltification process, either smoltifies enough to migrate or dies, but in the final time step there are still a part of the river residents that have smolt status $s > 0$.

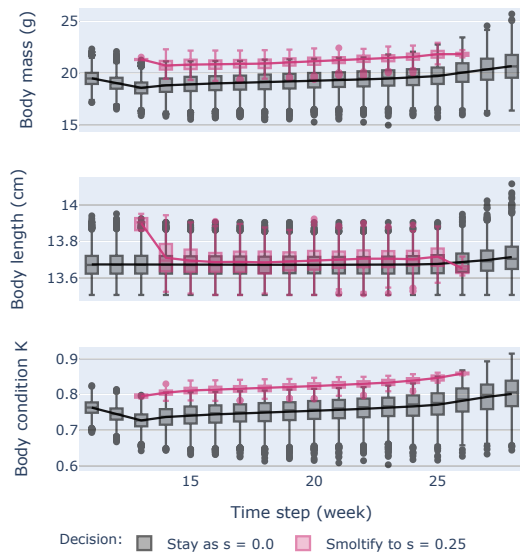


Figure 10. States of individuals that have the opportunity to decide to advance from $s = 0$ to $s = 0.25$, coloured by decision.

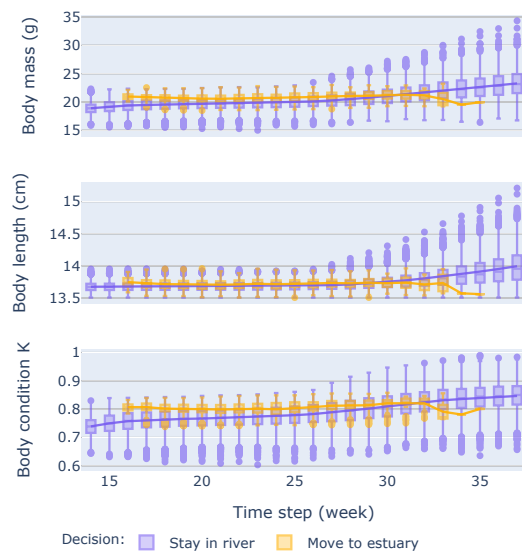


Figure 11. States of individuals that can decide to stay or move from river to estuary, coloured by decision.

Who smoltifies and becomes migrant?

As it is the first step towards becoming a migrant, the first smoltification step is an interesting decision to look closer at. Looking at the states of the individuals that take the first smoltification step (Fig. 10), they tend to have higher body condition and body mass, but there is also some overlap – so the combination of body mass and body length is important. This is also the case for the subsequent decisions to smoltify further (see figures in Appendix A.1). The first week after winter is the first time step they start to smoltify, and no-one takes the first step after time step 26.

Comparing those who stay resident (not accounting for smolt status) with those who decide to migrate (Fig. 11), there seem to be much overlap in both body mass, body length and body condition index. There is also change over time, with migrants being on the higher side of these values (especially body condition index) at early in the season, and the last migrants on the lower side.

What happens to individuals with different strategies?

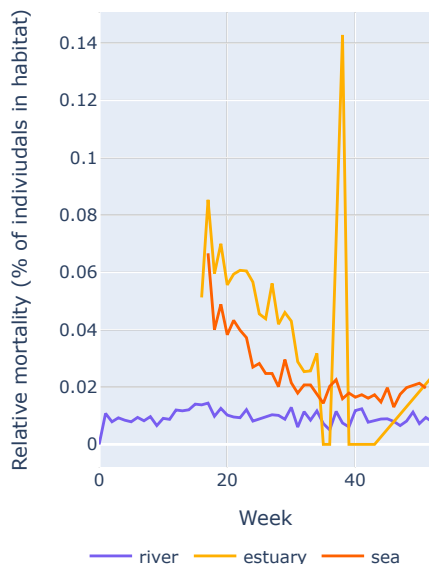


Figure 12. Relative mortality in each habitat at each time step.

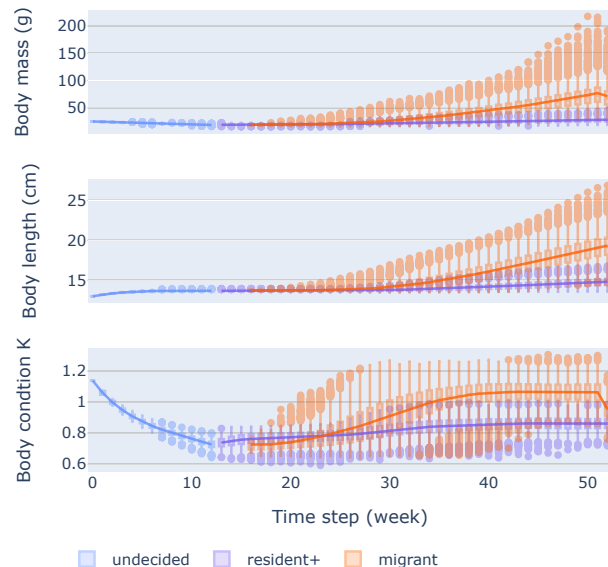


Figure 13. States of living individuals through time, coloured by strategy.

Individuals at sea and estuary experience a higher mortality than individuals in the river (Fig. 12).

During the winter phase, individuals reduce body condition (Fig. 13), and there is little growth in either body mass or body length. As the opportunity to smoltify and migrate opens up, migrants increase their growth more than residents.

Final states for the individuals can be seen in Fig. 14. Surviving residents reached a mean body length of 14.8 cm, meaning they grew 1.8 cm in a year. Surviving migrants reached a mean body length of 19.3 cm, meaning they grew 6.3 cm in a year. Fitness is higher for migrants than residents, both when including ($F_m = 114.7$ vs $F_r = 67.13$) and excluding ($F_m = 236.8$ vs $F_r = 122.6$) dead individuals.

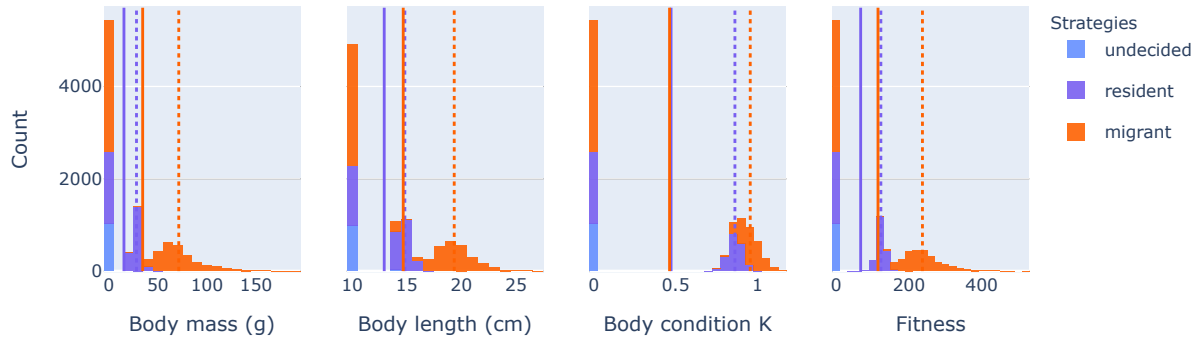


Figure 14. Final states and fitness for 10 000 forward iterations, coloured by strategy. Individuals who died before growing season started, are labelled "undecided" as they never had the option to choose strategy. Dotted lines (.....) indicate strategy mean for survivors, solid lines (—) indicate mean for all individuals within strategy.

Effect of initial states

The migratory proportion decreased with initial body length (Fig. 15a), and increased with initial body condition index (Fig. 15b).

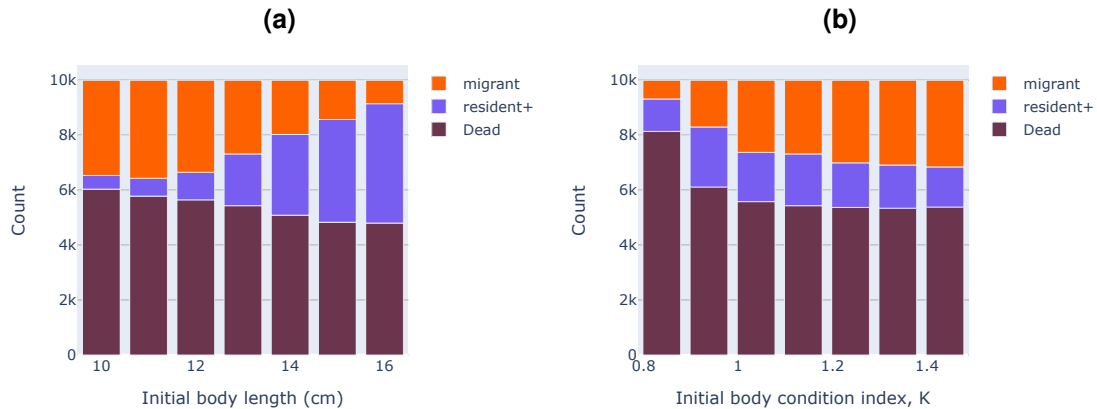


Figure 15. Final strategy distributions for a range of (a) initial body lengths, and (b) initial body condition index K. When initial body length is varied, mass is adjusted so that K stays constant, and vice versa when varying K.

3.2 Optimal vs fixed strategies

Requiring individuals to not smoltify to gain fitness, led them to not migrate at all (expected as migrating before smoltifying leads to certain death in my model). I refer to these individuals as "fixed residents". Requiring the individuals to end up with a smolt status $s \leq 0.75$ (= "fixed smoltification"), increased the proportion of migrants, but some remained resident. A full migratory population (except for those who died early), was achieved by requiring individuals to end up in the estuary (= "fixed migrants"). Compared to optimal strategies (baseline result), fixed residency gave fewer deaths, while fixed smoltification and fixed migration resulted in higher mortalities (Fig. 16a).

Fixed migrants had slightly higher mean fitness ($F_m = 87.63$) than individuals following optimal strategies ($F_o = 86.53$), but also higher variance (std) ($\sigma_m = 123.9$ vs $\sigma_o = 105.5$) due to increased probability of dying. The fixed smoltification strategy resulted in lower mean fitness ($F_s = 85.18$) and higher variance ($\sigma_s = 109.8$), while fixed residents had both the lowest mean fitness ($F_r = 81.58$) and variance ($\sigma_r = 65.63$).

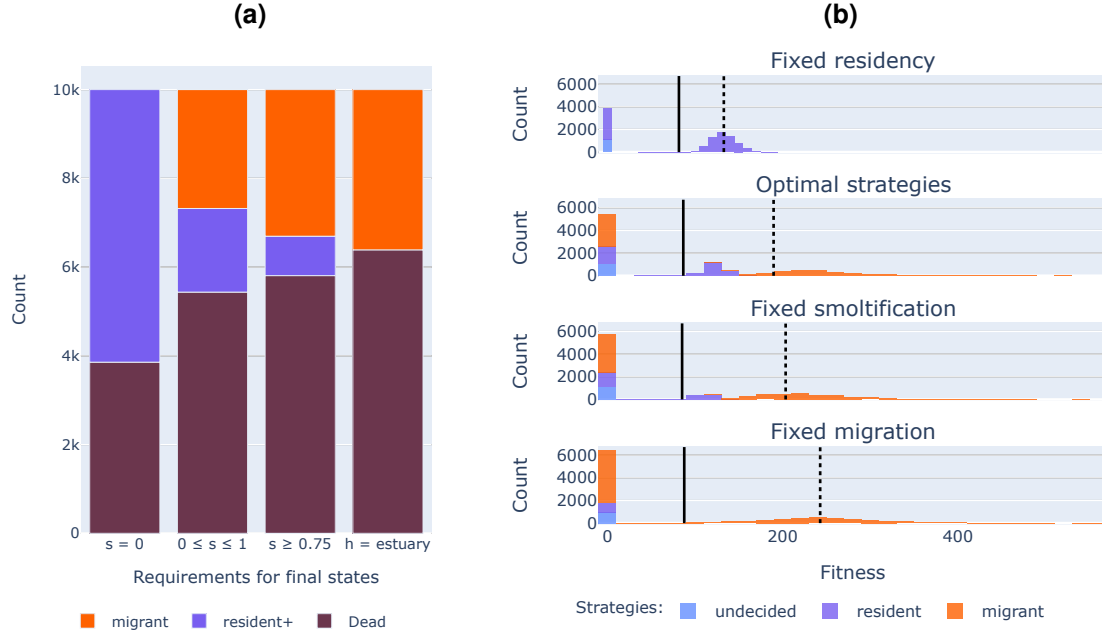


Figure 16. Results from fixed strategies. **a)** Final strategy distributions. **b)** Final fitness distributions, with solid lines (—) indicating mean fitness for all individuals, and dotted lines (·····) indicating mean fitness for survivors.

3.3 Alternative models

Effect of migration costs and migration-induced predation

As migration cost c_{mig} increases, a smaller proportion of the individuals migrates (Fig. 17). The same is true for the migration-induced predation factor p_{mig} (Fig. 18).

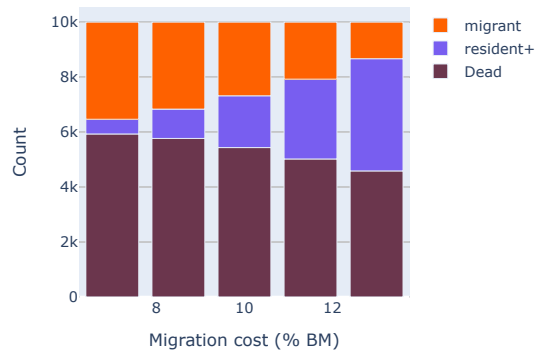


Figure 17. Final distributions at different values for the parameter migration cost c_{mig} .

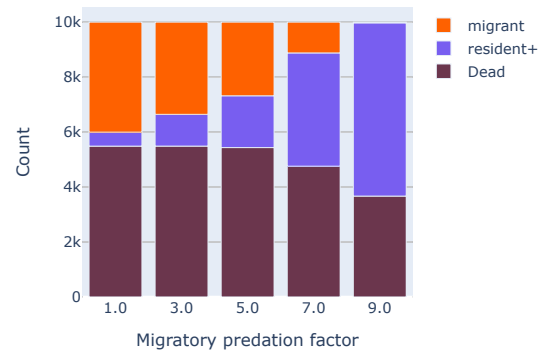


Figure 18. Final distributions at different values for the migration-induced predation factor p_{mig} .

Effect of habitat food factor and food stochasticity

A change in the habitat food factor b , alter food availability at estuary and sea, while keeping it constant in the river (see Table 1). A value of $b = 1.20$ leads to full residency, and increasing b leads to higher migratory proportions all the way to almost full migration (Fig. 19).

By default, when there is no stochasticity in food ($v = 0$) all individuals end up in the same states, and consequently with the same strategy (which here is to become migrant). Fig. 20 shows that partial migration occurs at the other levels of food stochasticity v . Interestingly, both half the baseline stochasticity ($v = 0.375$) and full stochasticity ($v = 1.0$: always food quantity q_{high} or q_{low} , never $q_{average}$) have smaller proportions of migrants than the baseline value ($v = 0.75$).

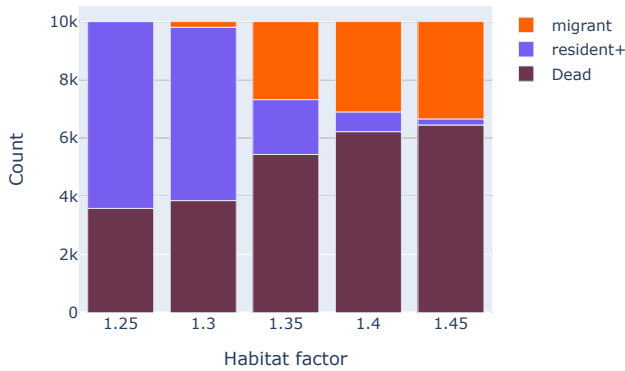


Figure 19. Final distributions at different values for the habitat-dependent food factor b .

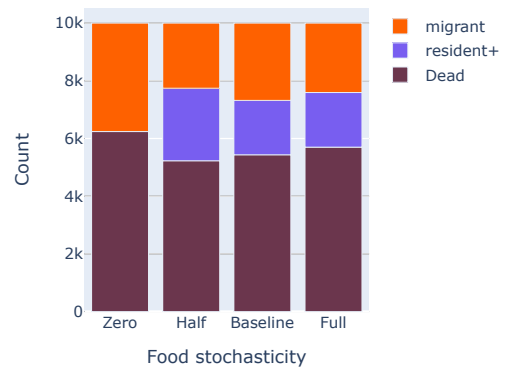


Figure 20. Final distributions at different values for food stochasticity v .

4 DISCUSSION

4.1 Base result

Different combinations of states can have different optimal decisions, and the same combination of states can have different optimal decisions at different time steps. Stochasticity in food acquisition can cause enough variation in states that variation in strategies may arise within a population.

The outcome of the model gives a realistic proportion of individuals dying (Elliott, 1993; Dieperink et al., 2001) but compared to the real-world, a slightly low mean increase in body length is observed for both residents (Raikova-Petrova et al., 2018) and migrants (Davidsen et al., 2021) in my model. Proportion of migratory individuals is by default realistic, since anything between full residency to almost full anadromy is found in nature. It has been a deliberate choice to keep the migratory proportion close to half the population when developing the baseline model, as this enabled me to explore more what increases and decreases the migratory proportion than a very high baseline migratory proportion. On one side, that half of the individuals becomes migrants might be low compared to females in nature (Jonsson et al., 2001), while on the other side it might be rather high that half of the individuals should become migrants in just *one* year considering the range of smolt ages observed within a population (Jensen et al., 2012a).

In my simulations, it is only individuals that have a high body condition that smoltify and migrates. These individuals also generally have higher body mass, but not particularly different length than those who do not smoltify and migrate (Fig. 10). It is also increasing initial body condition and body mass that led to higher migration rates (Fig. 15b), not increasing body length and body mass in the way that body condition remains unchanged (Fig. 15a). This agrees with Acolas et al. (2012) that concluded that specific growth rate (a body mass based unit) was a better predictor than body length.

The results from the optimization suggest that small individuals in good condition and large individuals in bad condition should smoltify, while intermediate individuals should stay. This dualism fits well with what is observed in nature (Jonsson, 1985; Forseth et al., 1999). It is however, not seen in the simulations, as no resident individual ever reached the relevant lengths for "bad condition"-smoltification to occur within in the year that is modelled, even in the simulations with the highest initial body length ($l = 17$ cm). As it is now, the highest initial body length $l = 17$ cm led to a few migrant individuals reaching a final length of 30 cm. In nature, smolts from the same population vary in both age and size (Jensen et al., 2012a), and between populations the mean smolt length can vary from 10.7 cm to 25.2 cm (Jonsson and L'Abée-Lund, 1993). It could therefore be interesting to increase the body length limit l_{max} (and m_{max}) of the model to allow for individuals to grow larger size and test out how state-dependence plays out for individuals that start-off larger than 17 cm.

Starting individuals with different length (but same body condition index K), revealed that smaller individuals more often migrated than larger individuals. This might be because shorter individuals have a higher fitness benefit from the increased food availability and consequently growth, and that the growth benefit is not outweighed by size-dependent predation.

Starting individuals off with different body condition (but same length), revealed that individuals in better condition migrate more. They can afford the (energetic) costs of smoltification and migration.

Since migrants had a higher mean fitness than residents in the baseline model, and fixed migrants did on average even better (though with higher variance) than optimal strategies, it

seems that in my model system, an individual migrate if it can and stay resident if it must. This disagrees with the perception that migrants are individuals who cannot reach an energetic threshold to remain in river (Ferguson et al., 2019), but might be understood if accounting for sex. Cucherousset et al. (2005) found that while the fastest growing males stayed resident, the fastest growing females migrated to sea.

Since migratory proportion increased with body condition, and not length, migration seems to be mostly limited by individuals avoiding starvation by not taking the costs of smoltification and migration, rather than avoiding predation at sea. Probability of starvation increases rapidly as K go below $K_{starve1} = 0.7$, and probability of dying is higher for all $K \leq 0.64$ than for the model's highest possible probability of dying by predation in the model (0.15 for a 10 cm long individual when migrating to estuary). All in all, predation caused around 90% of the mortality in my baseline model, while starvation caused the remaining 10%. This may be an unrealistic high proportion dying from starvation. Even though there is theoretical support for starvation to be a major cause of mortality during times of low food availability such as winter, the empirical support is not large (Hurst, 2007). Many fish implement physiological mechanisms to extract energy from their fat reserves and protein tissues to survive, when facing food deprivation (Bar, 2014).

4.2 Optimal vs fixed strategies

Compared to individuals choosing optimal strategies, fixed migrants had higher fitness variance and higher probability of death, but a slightly higher mean fitness. It should here be noted that within the fixed smoltification and fixed migration strategies, opposed to fixed residents who always have to make the same decision, the timing of decisions are still optimized. The closeness of the mean fitness of optimal strategies vs fixed migration (with optimal timing), raises question about the fitness benefit of having plastic strategy rather than a fixed rule of thumb. But the variance in fitness may lead to it being a less beneficial strategy over time.

My model optimizes the arithmetic mean fitness across individuals, but when comparing fitness between different strategies (Fig. 16), one should also account for the effect of fitness variation and not just fitness mean. In a stochastic environment, the arithmetic mean for small populations will vary across generations. As survival and reproduction fluctuates and are multiplicative processes, an appropriate long-term fitness measure will be the geometric mean fitness across years rather than just the arithmetic mean fitness (Roff, 2002). Geometric mean fitness is very sensitive to low values, especially zero, and as a migratory strategy has larger fitness variation and especially higher probability for not surviving ($F = 0$), the strategy's long term fitness is reduced more than that of the resident counterpart. Therefore, under the same conditions as in the model, we might expect to see less migration in nature.

Fixed smoltification resulted in an increased proportion of migratory fish, but not all individuals migrated. This highlights that smoltification and migration, though generally coinciding, are two separate decision processes. In nature, individuals that go through smoltification may end up desmoltifying if they do not migrate to a more saline habitat (McCormick and Saunders, 1987).

Individuals with the fixed smoltification and fixed migration strategies, made the decisions to smoltify and migrate earlier than in the baseline model (see figures in Appendix A.2). This was expected as it lowers the fitness of doing nothing in a timestep, due the additional costs of smoltifying and migration must be taken at some point anyway. This may relate to observed differences between species. Unlike brown trout, the sister species Atlantic salmon most of-

ten form populations where migration is obligatory for females (Jonsson and Jonsson, 2011). Comparing Atlantic salmon smolt and brown trout smolt from the same river, Atlantic salmon smolts migrated at younger age, earlier in the season, at smaller sizes and lower body condition (Jensen et al., 2012a; Davidsen et al., 2021).

Creating a fixed migratory strategy by requiring individuals to end up in the estuary, is a short-cut to forcing migration as it does not allow for individuals to return all the way to the river in the year they first migrate. This is justified by all migrants ending the year in estuary (meaning none of the migrants returning to the river to overwinter) in my baseline model, but this does not necessitate the same would be optimal for fixed migrants, as the latter includes individuals that would not have migrated if not required.

4.3 Alternative models

As migration costs or migratory predation risk increased, a smaller proportion of the individuals migrated (Figs. 17 & 18). In the real world, these aspects may both be caused by longer rivers, as distance increases energetic costs (Bohlin et al., 2001; Jonsson and Jonsson, 2006) as well as predation (Thorstad et al., 2012). As longer rivers also mean more time spent travelling (Stewart et al., 2006), energetic migratory cost might also represent less time spent feeding. Finally, migration costs are not just affected by distance, but also more varying aspects such as temperature (Enders et al., 2005) and water flow (Jonsson and Jonsson, 2002).

As expected, as the food availability habitat at estuary and sea increased, the migratory proportion got larger (Fig. 19). Individuals are only expected to migrate to sea when there is increased food availability compared to freshwater (Gross et al., 1988). The food availabilities stay constant in my model all year, but in nature there may be seasonal variation in prey abundance and different seasonal cycles in freshwater (Kreivi et al., 1999) and sea (Rikardsen et al., 2006), so the food availability ratio between the habitats may change during the year. Food availabilities also rely not just on prey abundance, but also on competition and population density (Olsson et al., 2006). When population characteristics such as density and strategy frequency come into play, the system becomes more complex: food availability is no longer stable or seasonal, but depends on other individuals (state-dependent) behaviour. Social structure may also play a role in food availability and food stability in brown trout (Sloman et al., 2000). Different parameter values for food availability and food stochasticity may therefore represent both variation between habitats, but also variation between individuals within habitats.

4.4 Further work

The effect of body length both in my model and in the real world, could be dependent on the predator community that the fish experience. In my model, I use a linear relationship (Eq. (5)) and this might be differentiating between small and large individuals too little to see a benefit of waiting until a larger size to migrate. This could perhaps change if using a length-dependent predation function with a more sigmoid shape, similar to what was found by Skov et al. (2011). Predator communities may change rapidly due anthropogenic changes (Koed et al., 2006), so it can be beneficial to understand how different predator communities affect migratory strategies. This could be investigated by testing how different shaped predation functions affect the outcome of the model, including trying out different shapes in different habitats as the predator communities may vary along the migratory journey, and possible mismatch between optimization and simulations.

To make the model more realistic, a next step could be to add seasonality details such as a varying temperature and water flow. As a poikilotherm, the energetic costs of the brown

trout are dependent on the environmental temperature, and migration at temperatures above the optimal temperatures can be costly (Enders et al., 2005). Water flow has also been shown to be very important to when brown trout migrates (Jonsson and Jonsson, 2002), as it affects both the energetic cost and predation risk of the migratory journey. Adding these environmental states that changes with the season, a dynamic state model will also give a valuable insight to the timing of migration - and not just answer *who* migrates, but give a more realistic prediction of *who* migrates *when*.

Another natural extension of the model is to use a fitness function that represents the male fitness, and see how it compares to the outcomes from the model based on the female fitness function, under the same assumptions.

4.5 Conclusion

I have investigated how state can explain female migratory strategies in a partially migratory population, and how the environmental parameters can change the migratory tendencies across populations. I demonstrated that stochasticity in food acquisition can cause enough variation in states that variation in strategies may arise within a population, and that the migratory proportion increased when migratory costs decreased and food availability at estuary and sea increased compared to in the river.

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A APPENDICES

A.1 States before decisions

Smoltification

States before the first smoltification step can be seen in Fig. 10. The rest can be seen below.

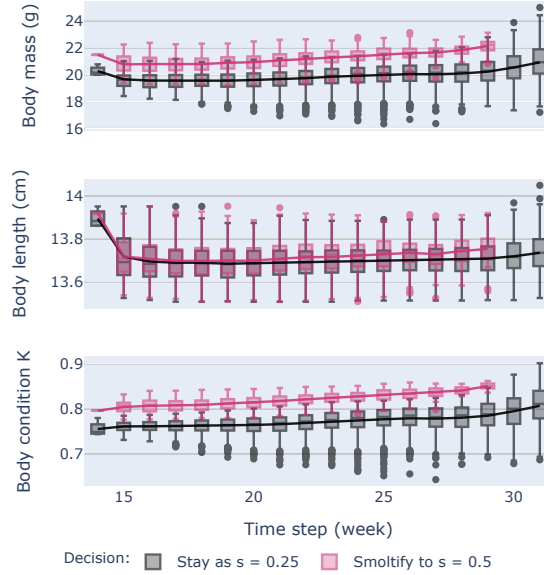


Figure 21. States of individuals that have the opportunity to decide to advance from $s = 0.25$ to $s = 0.50$, coloured by decision.

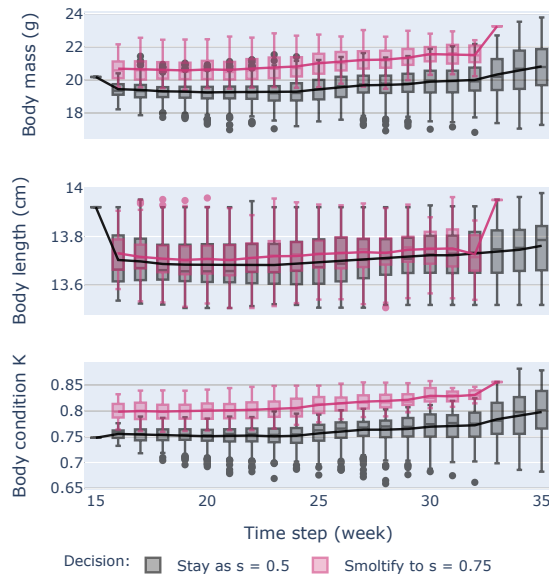


Figure 22. States of individuals that have the opportunity to decide to advance from $s = 0.50$ to $s = 0.75$, coloured by decision.

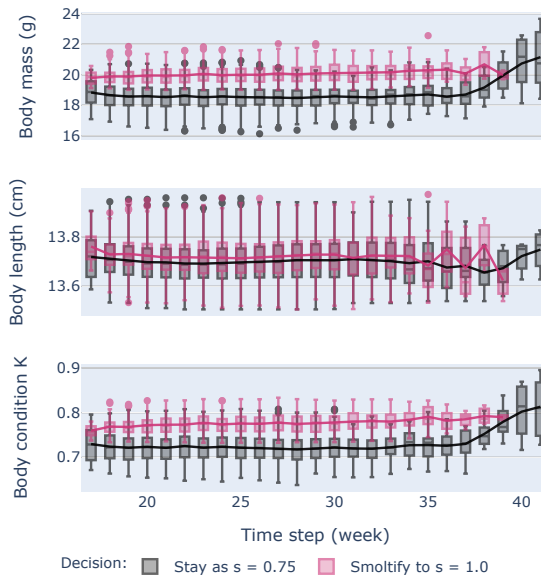


Figure 23. States of individuals that have the opportunity to decide to advance from $s = 0.75$ to $s = 1.00$, coloured by decision.

Migration

States before the first migration step (river-estuary) can be seen in Fig. 11. The second step (estuary-sea) can be seen below.

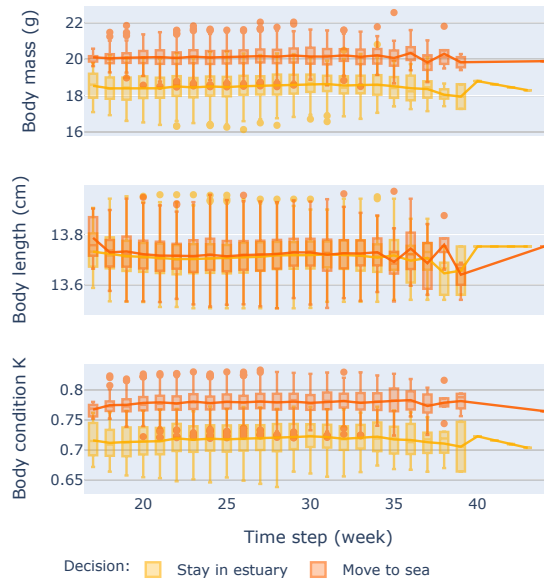


Figure 24. States of individuals that have can decide to move from estuary to sea, coloured by decision.

A.2 Timelines for fixed strategies

Fig. 25 shows timelines from simulations of the alternative optimization models where the fish only gain any fitness if they in the final time step meet certain criteria related to smolt status s or habitat h . The three alternative models include $s = 0$ ("fixed residents"), $s \geq s_{\text{estuary}} = 0.75$ ("fixed smoltification") and $h = \text{river}$ ("fixed migrants"). Timeline for baseline model with optimal strategies is also included for comparisons (Fig. 25b).

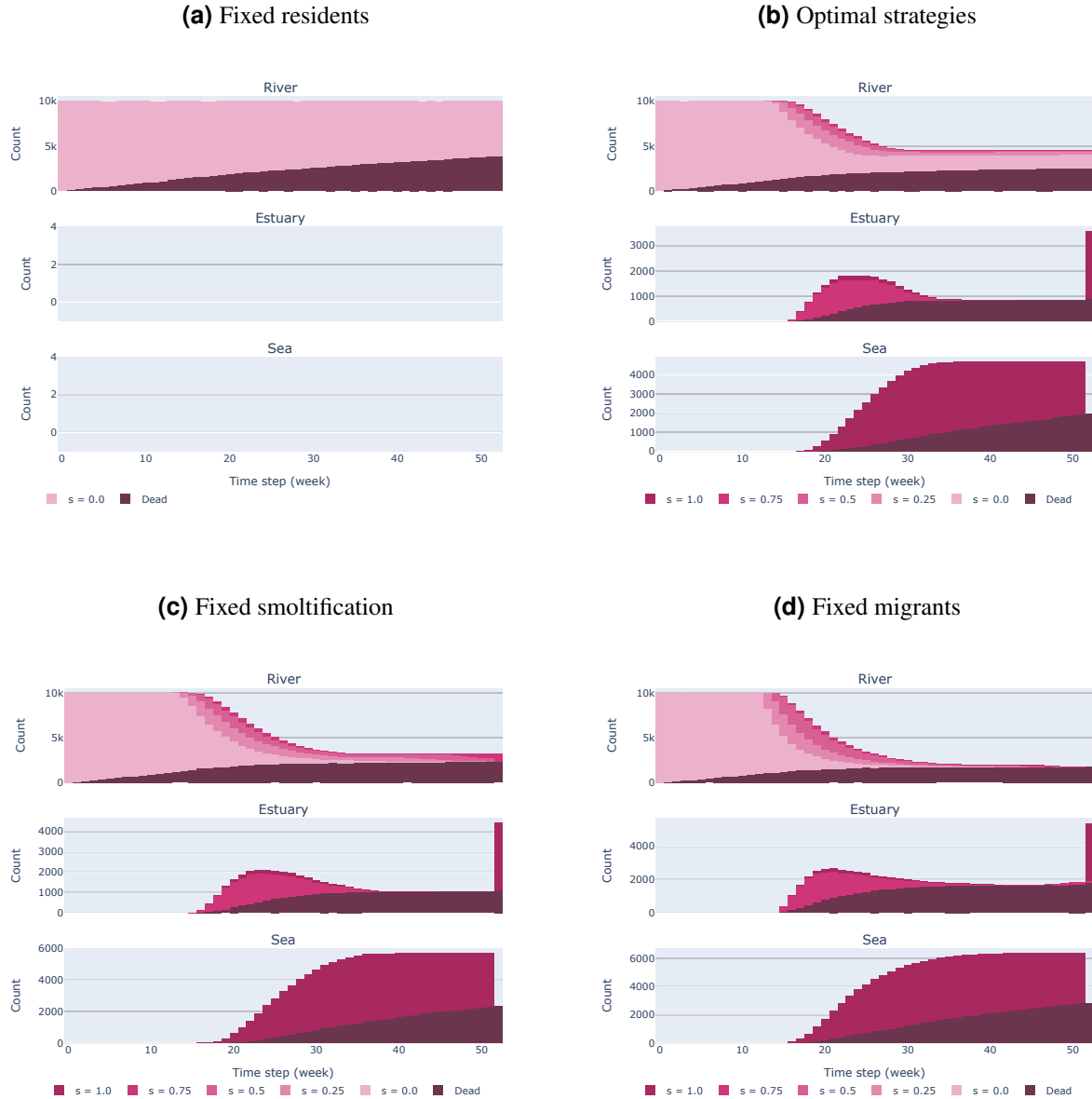


Figure 25. Distribution of mortality and smolt status in the three habitats through the 52 weeks for 10 000 simulations for the baseline model with optimal decisions and for models with different fixed strategies.

A.3 Final distributions for extra parameter exploration

Effect of metabolism

As metabolism c_{met} increased, a smaller proportion of the individuals migrated (Fig. 26). At high values of c_{met} almost all individuals died.

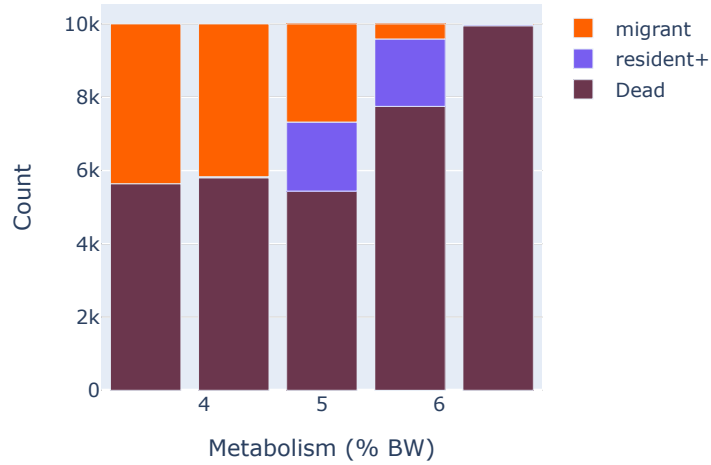


Figure 26. Final distributions at different values for the parameter metabolism c_{met} .

Effect of growth scaling constant

As the value of a increased, a larger proportion of the individuals migrated, but this increase levels off after the baseline value $a = 4.0$ (Fig. 27).

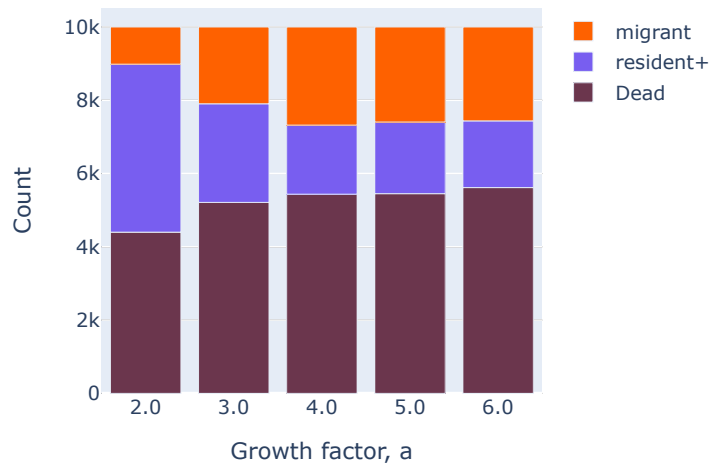


Figure 27. Final distributions at different values for the growth scaling constant a .

