A qualitative model of the salmon life cycle in the context of river rehabilitation

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Abstract

A qualitative model was developed in Garp3 to capture and formalise knowledge about river rehabilitation and the management of an Atlantic salmon population. The model integrates information about the ecology of the salmon life cycle, the environmental factors that may limit the survival of key life stages and links with human activities such as agriculture, habitat rehabilitation and fishing. The overall aim of the model was to explore the effects of rehabilitation in the context of a complete life cycle scenario. The scenarios and simulations produced were able to explore these processes in the context of a complete life cycle, but at this scale the simulations were time consuming. Therefore, in addition to these scenarios a series of smaller demonstrator scenarios were developed that succinctly explored individual concepts within the system.

Introduction

River rehabilitation projects often target economically valuable and/or threatened fish species (e.g. Atlantic salmon, *Salmo salar* L.). Conservation of these species is often based around quantitative life-cycle models (e.g. Faivre *et al.* 1997, Aprahamian, Wyatt & Shields 2006) that examine the recruitment of individuals to each consecutive life stage to either identify the factors that impinge on the size of the population, or to set targets for conservation (Hendry *et al.* 2007, Milner *et al.* 2000). Hence, planning of rehabilitation activities often focus on the key human activities that impact on different life stages of the fish populations/community (Cowx & Welcome 1998). As such, models that are able to integrate concepts in ecology, river rehabilitation and socio-economic elements, could be useful for knowledge communication of the requirements for rehabilitation and the potential outcomes of measures. However, quantitative information concerning the effects of rehabilitation measures is often incomplete and difficult to predict (Cowx & Gerdeaux 2004, Cowx & Van Zyll de Jong 2004).

Computer-based Artificial-Intelligence (AI) approaches have been promoted for use in conceptualising and integrating qualitative and incomplete information in ecology and natural resource management (Rykiel 1989). Qualitative Reasoning (QR) modelling is an example of an AI approach that has been promoted for use in modelling ecological systems. (Salles & Bredeweg 2006 and Salles *et al.* 2006a,b) because much ecological knowledge is incomplete, uncertain, qualitative and fuzzy, expressed verbally and diagrammatically, making analytical or numerical solutions difficult or impossible to achieve (Rykiel 1989). For example, QR modelling has been previously used to examine the functioning of Atlantic salmon redds (spawning “nests”) to model the factors and processes that control mortality at this critical life stage for recruitment success (Guerrin & Dumas 2001a, b). In addition, Tetzlaff *et al.* (2008) highlighted the need for transferable tools in catchment based hydrological modelling that conceptualize system behaviour by integrating theoretical perspectives and empirical studies.

The model developed here followed the compositional modelling approach (Bredeweg *et al.* 2008, Falkenhainer & Forbus 1991) using the Garp3 software. The ultimate aim was to simulate the whole life cycle scenario by considering each individual life stage in the salmon life history and the influence of human activities on the particular river/habitats they occupy. A compositional approach to scenario building was also used in the modelling process to test specific model fragments and to act as final scenarios within the model to demonstrate specific concepts.

Life Cycle Concepts

Salmon life history

Atlantic salmon exhibits an anadromous life history. The fundamentals of anadromy are that spawning and early development occurs within freshwater habitats whilst adult growth occurs in the marine environment (Figure 1). Returning adult salmon migrate to the upper reaches of their natal rivers to spawn, cutting redds (nests) in coarse gravel substrate to provide protection and adequate flow through of clean water and oxygen to the fertilised eggs. Eggs and early larval stages occupy these interstitial habitats until they develop to juveniles and emerge from the gravels to occupy riffle/pool habitats. After two to four years in fresh water, maturing juvenile salmon undergo physiological changes, which allow them to tolerate saline water and prompts their migration, as smolts, to sea. Given this, the model considers four key stages in the life history of the salmon in rivers: within-gravel phase (eggs); juvenile phase; smolt phase and adult phase (Mills 1989, Crisp 1993, Crisp 2000).

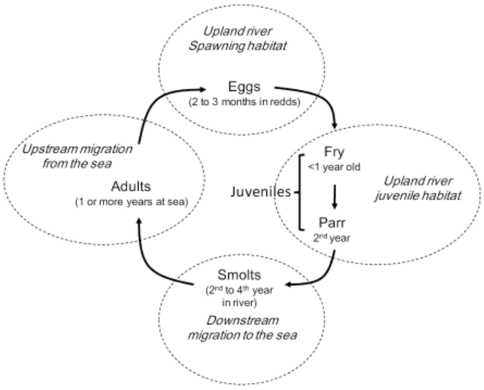

Figure 1 A schematic representation of the key life stages, behaviours and habitats involved in the life cycle of the Atlantic salmon.

Life stages

The key concepts within the life cycle are the different life stages and their survival from one life stage to the next. Therefore, survival is the fundamental process represented by the system. In this context each stage is considered to be an independent (sub) population within the model. This allowed simple model fragments to be developed that apply to all life stages. The basic model fragments "Population" describe that populations are entities that are characterised by the quantities *Recruitment* and *Survival* (Figure 2). This representation allows the modelling of the survival process within a life stage, denoting the numbers that start in the life stage (*Recruitment*) and the numbers that survive to the next life stage (*Survival*). In all cases, both these quantities were represented using the same quantity space (QS): {Zero, Low, Medium, High, Max}. The implementation of ordinal quantity spaces for the number of individuals in each life stage gave a semi-quantitative aspect to the model enabling greater levels of understanding and interpretation of behaviours. The values chosen were designed to be easily understood and give information pertaining to the population/conservation status of the life stage/population as a whole.

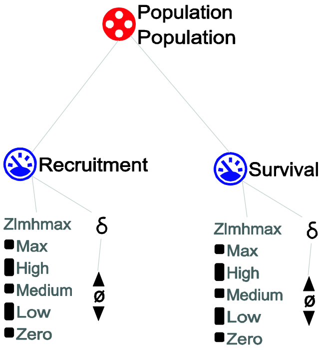

Figure 2 Model fragment "Population" describing the *Population* entity and qualities of *Recruitment* and *Survival*. Each quantity has a QS of {zero, low, medium, high, max}. Each quantity also has a derivative quantity space, denoted by δ; increasing (▲), steady (ø) or decreasing (▼).

Survival and recruitment

Within the salmon life history, the transition of individuals from one life stage to the next (hereafter termed recruitment) is governed by a combination of processes relating to growth, survival and maturation. The number of individuals of each life stage in a salmon population decreases from eggs through the juvenile and sub-adult stages to adults due to factors influencing mortality (e.g. predation, food availability, habitat quality, individual viability and exploitation) (Mills 1989, Crisp 1993, Crisp 2000). In general, fish life histories are typified by adult populations that deposit large numbers of eggs, which are subject to very high mortality in early life stages. Indeed reported values of survival from egg to smolt are around 2-4% (Aprahamian *et al.* 2006).

Most models used to assess the status of salmon populations use life-history models to determine the numbers of spawning adults required to maintain the population given the impact of mortality on different life stages (Aprahamian *et al.* 2006, Milner *et al.* 2000). This is enabled by the relatively distinct life stages and because they either occupy relatively distinct habitats or undergo specific migrations that are themselves potentially characterised by discrete sources/causes of mortality. This model implements this in a qualitative manner.

Although *Recruitment* and *Survival* for all life stages have the same quantity space representation, and hence qualitative equality, this does not necessarily represent quantitative equality. In the case of recruitment quantitative equality is assumed given the instantaneous transition from *Survival* of life stage n to the *Recruitment* to life stage n+1. Within a life stage there is only qualitative equality between *Recruitment* and *Survival* given that due to mortality the number surviving a life stage is always much less than the number at the start of the life stage. However, the qualitative equality of the quantity spaces within a life stage is used to represent the concept that, even though the actual number of individuals in a life stage may be far less than the numbers in the preceding life stage, the numbers in that succeeding life stage can still be considered high or low for that life stage. Therefore, this QS model, in which quantitative and qualitative equality between the QS depended on the concept, was implemented to give some semi-quantitative information without potentially increasing complexity in a model that had inherent complexity due to the number of life stages considered.

Whilst recruitment, mortality and survival are inherently linked (for example successful recruitment to the next life stage is defined by survival through a life stage), the use of sub-populations for each life stage necessitated the isolation of survival and recruitment within the representation. Therefore, recruitment was represented as the process linking one life stage to the next (Figure 3).

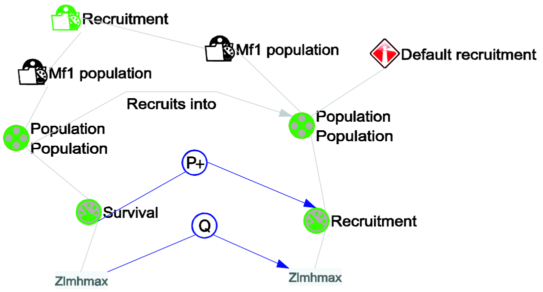

Figure 3 Model fragment “Default recruitment” describing the general recruitment relationship between life stages. In this representation each life stage is modelled as an individual population.

In general this was represented as a simple correspondence (Q) and positive proportionality (P+) between the *Survival* in life stage n to the *Recruitment* in life stage n+1. This survival/recruitment relationship between life stages was represented in different ways depending on the life stages and scenarios being considered. This was implemented using related model fragments, made independent using assumption labels related to the *Population* entity. The assumption “*Default recruitment*” implemented the strict correspondence (Q) and positive proportionality (P+) between the *Survival* in life stage n to the *Recruitment* in life stage n+1 (Figure 3). The assumption “*Spawning recruitment*” implemented a less strict interpretation of this relationship just using a proportionality P+ [*Recruitment* egg, *Survival* adult], zero-zero/max-max value correspondences (V) between their quantity spaces and an equality statement determining that the *Recruitment* of eggs must be greater than or equal to the *Survival* of adults. This denoted the possibility that adults have a high fecundity that may give the potential for the spawning event to regenerate a population and result in a relatively higher number of individuals than the initial number of adults present.

Factors limiting survival

The representation of the within life stage survival modelled the concept that the numbers surviving a life stage is determined by a combination of the starting size of the population (*Recruitment*) and the level of mortality during the life stage. Given the purpose of the model was to represent the effects of human activities on salmon populations, and the fact that human activities generally act through impacts of the habitat (or water) quality within a river, then the number potentially surviving a life stage can be limited by both the level of recruitment and the quality of the habitat they inhabit (Mills 1989, Crisp 1993, Crisp 2000). This representation contains concepts that are similar to the context of carrying capacity in ecological systems. As such the representation considers three basic situations. Firstly, the number recruited is less than the habitat quality and the population is below that which the habitat could support and hence the number surviving is limited by the number recruited (carrying capacity exceeds recruitment) (Figure 4). Secondly, the number recruited exceeds the habitat quality and the numbers surviving is limited by the higher mortality induced by low habitat quality and hence the population is limited by the habitat available (recruitment exceeds carrying capacity). Thirdly, the number recruited and the habitat quality are in balance and the number surviving is limited by both and no increase in recruitment or habitat quality would improve the numbers surviving (system is in balance with carrying capacity). This was modelled using a conceptual quantity, *Potential*, which is a combination of the *Recruitment* and the *Habitat quality*. These two limiting factors act through the *Potential*, which can be viewed as the maximum size limit of the *Survival* in any situation. This was implemented in the model using complex value correspondences (Q) and proportionalities (P+) between the controlling variables and the *Potential* (where the controlling quantity, either *Recruitment* or *Habitat quality*, was the quantity with the lesser magnitude). This necessitated three model fragments where 1) *Habitat quality* > *Recruitment*, 2) *Habitat quality* < *Recruitment*, and 3) *Habitat quality* = *Recruitment*.

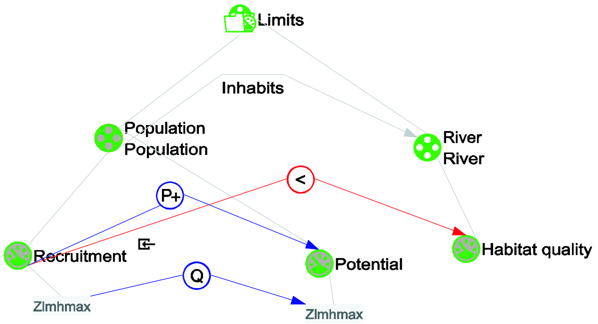

Figure 4 Model fragment “Recruitment limiting” describing the information used to define the value of *Potential* when *Recruitment* < *Habitat quality*.

Recruitment and mortality

The *Survival* is limited by the *Potential* and changes in response to being >, < or = to the *Potential*. The regulation in the *Survival* (due to an imbalance with *Potential*) conceptually results from changes in the balance of the level of recruitment and the mortality/survival rates. In situations where the numbers surviving is less than the potential the numbers surviving can increase due to the effect of recruitment exceeding that of mortality. Conversely, when the *Survival* is greater than the *Potential* the *Survival* decreases due to the effects of higher mortality exceeding the effects of recruitment. To minimise complexity in the model, the net effect of this was modelled as a single abstract quantity, the *Difference* (with QS {extreme min, minus, zero, plus, extreme plus}), which itself was derived as a calculus (Figure 5):

$$\mathit{Difference} = \mathit{Potential} - \mathit{Survival}$$

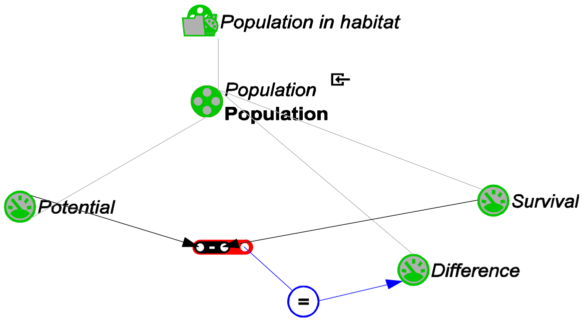

Figure 5 Model fragments “Population difference” that describe the calculation of the *Difference* value which controls the *Survival* of a life stage in relation to the *Potential*.

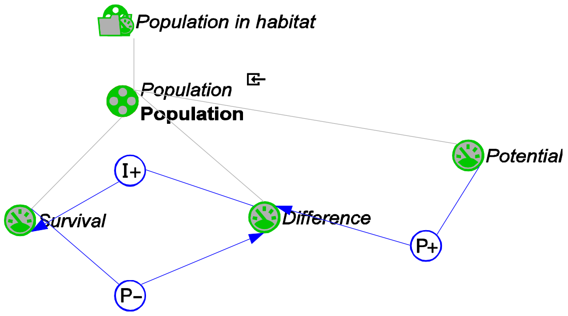

Figure 6 Model fragments “Difference regulates Survival” that describe the relationship I+ [*Survival*, *Difference*] which causes the *Survival* value to increase or decrease towards becoming equal to the *Potential*.

The effect of *Difference* on *Survival* is then modelled as a dependency I+ [*Survival*, *Difference*] (Figure 6). Feedbacks in the calculus are also modelled as P+ [*Difference*, *Potential*] and P- [*Difference*, *Survival*] to determine how the value of *Difference* changes with dynamic behaviours in *Potential* (from the behaviour of *Recruitment* and *Habitat quality*) and *Survival* (caused by the dependency from *Difference*).

Habitat Quality and Human Activities

Catchment concepts

Rivers can be seen as a habitat that integrates a number of physical processes that occur within the catchment of a river (e.g. catchment drainage) and, as such, the quality of a river can be integrated from the quality of these catchment characteristics/processes (e.g. Tetzlaff *et al.* 2007). This is a paradigm within fisheries management that recognises the effects of human activities, such as forestry, agriculture and urbanisation on the quality of the riverine environment (Collares-Pereira & Cowx 2004, Cowx & Welcomme 1998, Cowx 1994). This link is represented in the model by the conceptual chain of reasoning that human activities in a catchment can impact on natural catchment processes; these then impact on some specific quality of the catchment that reduces the integrity of the catchment. This reduced integrity then has an impact on the quality of a specific habitat within a river. This simple conceptual chain, linking both specific factors and conceptual quantities (e.g. catchment integrity) allowed a common approach to modelling different human activities and their effects on different habitats and life stages.

Human influences over habitat

Within the model, humans and human activities were modelled using the notion of “Agent” fragments, which in Garp3 model information about elements of the model which are defined as “external impact”. This gave an explicit representation of humans as agents having an effect on the river/salmon life cycle that was external to the fundamental ecological system being modelled. The chain of reasoning from human agents to catchment integrity through to river habitat quality was modelled using two main groups of model fragments. Firstly, each individual human activity was modelled in a specific Agent model fragment that represented the link between the intensity of the human activity, the quality of the specific catchment characteristic and the catchment’s integrity. Secondly, a general static fragment described the link between the catchment integrity and the river’s habitat quality (Figure 7).

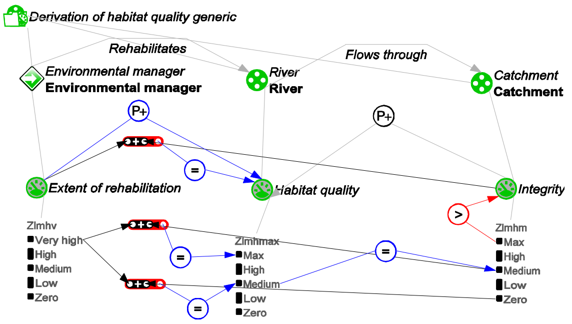

Figure 7 Model fragment “Derivation of habitat quality - generic” describing determination of the magnitude and derivative of *Habitat quality* based on the values and behaviour of catchment *Integrity* and the *Extent of rehabilitation* undertaken by an agent *Environmental manager*.

In each situation the Habitat quality was determined as a calculus between the catchment integrity and the extent of rehabilitation undertaken by an environmental manager (Agent). These model fragments represented the concepts that if catchment integrity was max (the highest value in the QS, equivalent to zero human impacts) then habitat quality was max and that when integrity was less than max then habitat quality could be improved by rehabilitation. Specific calculus statements were made to determine that whilst rehabilitation adds to habitat quality the total effect of rehabilitation may be limited to improving habitat quality through only one quantity space interval.

Modelling issues and solutions

Control of the *Potential*

Whilst the control of *Potential* using directed correspondences and proportionalities (Q and P+ [*Potential*, *Habitat quality*] or Q and P+ [*Potential*, *Number recruited*]) is a simple and successful representation of the system when *Habitat quality* and *Number recruited* are unequal (e.g. Figure 4), difficulties were observed when *Habitat quality* was equal to *Number recruited*. This was especially the case when these two controlling factors had differing derivative behaviours (the values were moving in opposite directions). Essentially, these were dynamic situations where at some point both *Potential* was limited by both *Habitat quality* and *Recruitment* and either one or both of these controlling variables was changing so that one of the variables then became the single controlling factor, e.g. *Potential* switches from being determined by the recruitment to being determined by the habitat quality. In this situation, reasoning produced behaviour paths that terminated in states when the reasoning engine had insufficient information to make suitable influence resolution or the next state would be inconsistent and contain conflicting information. This related to reasoning paths that required *Potential* to change derivative and/or value in an inconsistent way, needing to switch derivative behaviour without first attaining a steady derivative (a behaviour which is terminated by Garp3 as being inconsistent with logical reasoning). To continue representing the system using P+ proportionalities and determining quantity values using directed correspondences a suite of 9 model fragments was developed to control reasoning in situations when *Habitat quality* was equal to *Number recruited*. These 9 fragments (summarised in Table 1) were implemented to consider all 9 possible conditions considering the derivative behaviours of *Habitat quality* and *Recruitment*. In each of these model fragments the consequences for the derivative of *Potential* was determined, together with which factor controlled the value of *Potential* through a directed correspondence (Q). The exclusion of P+ proportionalities and the explicit statement of the resulting behaviour of *Potential* when *Habitat quality* equalled *Recruitment* simplified the reasoning to give the explicitly desired consistent and logical behaviours for further, more complicated, scenarios.

Table 1 Definitions of correspondences (Q) and derivatives (δ) used to define the conditions and consequences in the 9 model fragments used to define *Potential* (P) in the different conditions for the combination of derivatives for *Habitat quality* (Hq) and *Recruitment* (R) when those two quantities are equal.

	Recruitment (R)			
Habitat quality (Hq)	Derivative conditions	δ+	δø	δ-
	δ+	Q [P, R]; Q [P, Hq] P δ+	Q [P, R] P δø	Q [P, R] P δø
	δø	Q [P, Hq] P δø	Q [P, R]; Q [P, Hq] P δø	Q [P, R] P δø
	δ-	Q [P, Hq] P δø	Q [P, Hq] P δø	Q [P, R]; Q [P, Hq] P δ-

Derivative behaviour of *Difference*

Interrogation of the behaviour paths and dependency diagrams generated by Garp3 during the model development indicated inconsistent behaviour relating to the derivatives (δ) of *Difference* when both *Recruitment* and *Habitat quality* resulted in a dynamic behaviour of *Potential*. In particular the inconsistent behaviours were caused in situations when either:

Potential > *Survival* (i.e. *Difference* is plus), δ *Potential* is plus and is bigger than δ *Survival*, which is also plus (due to I+ from *Difference*) OR
Potential < *Survival* (i.e. *Difference* is minus), δ *Potential* is minus and is less than δ *Survival*, which is also minus (due to I+ from *Difference*).

In these situations the result is that *Difference* is either 1) plus and increasing or 2) minus and decreasing. The behaviour paths in this situation become inconsistent in a situation where the derivative of *Potential* becomes steady. In this state the configurations of model fragments indicate that in:

Situation (1) *Difference* should be plus and decreasing (as the difference between *Potential* and *Survival* is now getting smaller because the value of *Potential* is steady and the value of *Survival* is increasing due to the I+ from *Difference*), and in;

Situation (2) *Difference* should be minus and increasing.

In both cases this is an inconsistent behaviour as logically the derivative of *Difference* must pass through a zero derivative (δØ) to move from increase (δ+) to decrease (δ-) or vice versa. These inconsistent behaviours relate to problems in modelling simplistic qualitative calculus of the form:

$$\textit{Potential} - \textit{Survival} = \textit{Difference}$$

Potential and *Survival* have dynamic behaviours, especially as in this case where the relationship I+ [*Survival*, *Difference*] gives complex derivative behaviours to both *Difference* and *Survival*. Current modelling in Garp3 only allows modelling with primary derivative information, although to model this calculus behaviour requires information concerning secondary derivatives to produce consistent transitions for the primary derivative of *Difference*. One solution to this problem was to model the quantity space of *Difference* using extreme point values (extreme minus and extreme plus) and then restrict the model simulation to allow the value of *Difference* to change derivative only in the point values rather than in intervals. For example, in situation (1) this allows the value of *Difference* to go from Plus (δ+) to extreme plus (δØ) and then to extreme plus (δ-) to complete a consistent change in derivative behaviour. This modelling approach can be seen as a fix in a situation where information about secondary derivative behaviour is explicitly required.

Scenarios and behaviours

Simple concept scenarios

The compositional modelling approach used by Garp3 allows for scenarios to be built with different levels of complexity exploring either a specific component of the system in question (hereafter referred to as "concept scenarios") or the system as a whole (the full life cycle in this model). The use of many diverse concept scenarios provides a basis both for building and testing model fragments during the model building process and for exploring important concepts and behaviours within sub-components of the system once the total model is implemented. The use of such an approach, providing "building blocks" that go towards explaining the overall life cycle scenarios, is almost certainly an important step in educational settings to aid interpretation of such a large system that may at first seem complicated and daunting to explore.

The concept scenarios were controlled using exogenous derivative behaviours which can be assigned to any quantity in Garp3 (Bredeweg *et al.* 2007). These exogenous controls (indicated by "*!*" next to the quantity under exogenous control in the scenario diagrams (see Figure 8)) can be used to trigger simulations and behaviours in isolated components of the system or to trigger simulations for scenarios considering the whole life cycle.

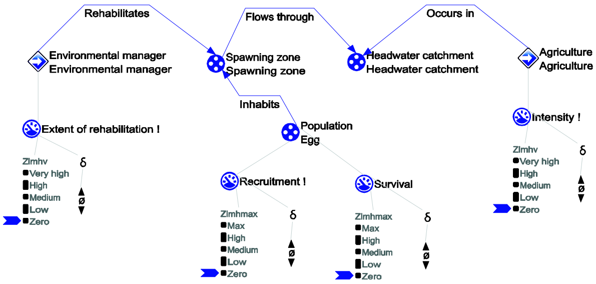

Figure 8 An example concept scenario considering the effect of degradation of spawning habitats due to agriculture on a recovering egg population. Exogenous controls (*!*) are applied to *Recruitment*, *Intensity* and *Extent of rehabilitation* to generate behaviours during a simulation.

Although the concept scenarios only considered a small component of the overall system, the simulations and behaviours they could produce were still large (essentially related to the number of quantities considered and the range of values in their QS). This is due to the potential for the reasoning engine to consider all possible orderings of potential changes in the values of dynamic quantities and produce different behaviour paths accordingly. To reduce this potential complexity the "fastest path heuristic" option in the Garp3 simulation settings was used. Essentially this option allows the reasoning engine to consider that "if a quantity can change value in the next step it will" and as such all quantities that can change value do so in the same reasoning step instead of the engine considering all possible sequences and ordering of quantity value changes. As such, although this option may remove some potential behaviour, it produces simulations of a smaller more manageable size that retain the key behaviours of interest.

Example concept scenario

An example concept scenario detailing the effect of agricultural impacts on the quality of spawning habitat is shown in Figures 8 to 11. This scenario is designed to explore the effects agricultural practises can have on sedimentation processes in a catchment and the amount of fine sediments that enter an upland river reducing its suitability as a spawning habitat (Soulsby *et al*. 2007, Crisp 2000, Crisp 1993, Mills 1989). The outputs of the simulation include the initial scenario (Figure 8) and exogenous controls, the causal model (available for each state transition, Figure 9) behind the behaviour/simulation (Figure 10) and the value history of states and behaviour paths (Figure 11). In the scenario described here, a single egg population inhabits a spawning habitat that occurs within a catchment. Initial value and exogenous behaviour statements are made to determine that the extent of rehabilitation is zero and unchanging, the egg population has zero recruitment (although it is increasing through an exogenous control), zero survival and that the intensity of agriculture in the catchment is initially zero but increasing through an exogenous behaviour. This scenario represents a system with an initially pristine habitat but without a population of eggs (Figure 8).

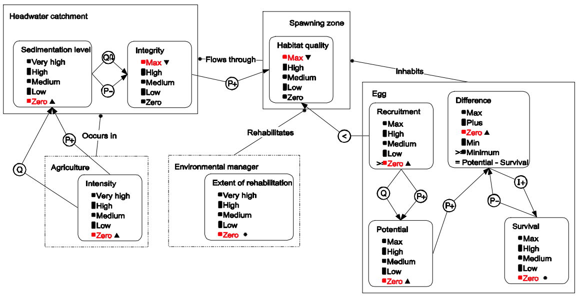

Figure 9 Example causal model indicating both the current state and what is causing the system to change. In this example the exogenous increase in *Intensity* of agriculture (zero ▲), is propagating through the system (P+) causing increase in *Sedimentation level* in the *Headwater catchment* and decreases in *Integrity* and *Habitat quality* (both Max ▼).

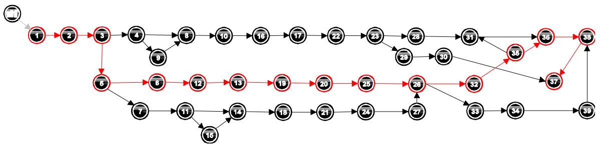

Figure 10 Simulation behaviour paths for the concept scenario (Figure 8). The full simulation for the scenario generated a total of 39 states and one end state, state [37] (a behaviour path [1 → 2 → 3 → 5 → 6 → 12 → 13 → 19 → 20 → 25 → 26 → 32 → 35 → 36 → 38 → 37] is highlighted).

The exogenous behaviour of recruitment represents the creation and establishment of a population although this is happening at the same time as the intensity of agriculture increases causing an impact on the quality of the spawning habitat. The simulation identified a behaviour comprising 39 states and one possible end state (state 37) with a number of possible behaviour paths to the end state (Figure 10). In this case all behaviours include an initial increase in the survival of eggs (due to the increase in *Potential* caused by its link to the increase in *Recruitment*) followed by a period of decline (due to the switch in the potential when it becomes controlled by the declining *Habitat quality*) and then a final state of zero *Survival* when *Habitat quality* becomes zero (Figure 11). In this simulation the different behaviour paths are caused by the potentially different rates in the exogenous derivatives of *Recruitment* and *Habitat quality* and the possibility of *Survival* reaching the low or high interval before the switch in the population behaviour.

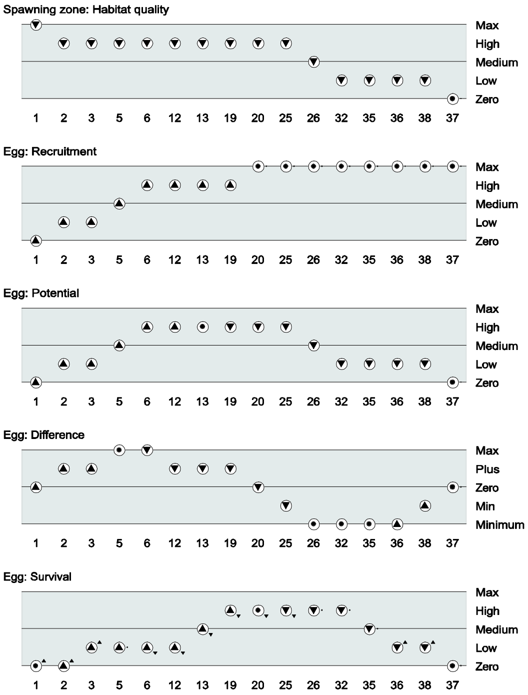

Figure 11 Value history for the behaviour path for the simulation (Figure 10) of a concept scenario (Figure 8).

Life cycle scenarios

The overall aim of this model was to implement scenarios that integrated all the concepts explored in the simple concept demonstrators into single life cycle models that explored human impacts at the whole population level and the link to basic socio-economic elements linked to the system (e.g. costs of rehabilitation). An example of such a scenario is given in Figure 12, which considers the re-establishment of salmon population that previously became extinct, a common situation in systems that have been heavily impacted by agricultural and industrial activities. In this scenario salmon are reintroduced through stocking and the impacts of high intensity agriculture in the catchment surrounding the spawning habitats of the river is rehabilitated. The scenario considers the consequences of these actions for the salmon population.

Unfortunately, the amount of logical reasoning processing required to run a full simulation successfully for such a complex model often took a long time on a desktop PC. The amount of time to obtain simulations from these life cycle scenarios ranged from a couple of hours to a couple of days depending on the contents. This was despite the use of the fastest path heuristic and successfully simulated life cycle scenarios often not generating a huge number of states (for example the simulation above only generated 136 states). This long processing time limited the use and development of this type of cyclical scenario.

Discussion

Design of Quantity spaces – semi-quantitative models

The model presented here aimed to capture and formalise domain knowledge concerning the salmon life cycle and river rehabilitation for use to enhance education about sustainability issues. As such it was developed from knowledge that has been obtained from both qualitative and quantitative sources. For such a model to be easily understood and interpreted within the Garp3 software this qualitative and quantitative information was fused into information concerning quantities and quantity spaces that inherently became semi-quantitative with QS for the main entities and quantities that are ordinal in nature and reflect some key values in the system. This approach is used in QR models to aid their interpretation beyond the basic qualitative concepts of zero; > or < zero; <, > or = and increasing, decreasing or steady. This is achieved using QS with a number of interval and point values that reflect key values and thresholds within the system of study. Whilst this approach is common and fairly straightforward in physical systems, it is less common and less easy to implement for ecological models. For example the ecological models published using Garp3 (e.g. Salles *et al.* 2006a,b, Salles & Bredeweg 2006) have tended to concentrate on exploring and modelling the processes and have used a simple {zero, plus, max} QS to represent the number of individuals in a population. In such systems the interest is generally in whether the population is present/absent or at its maximum and how it is behaving. Further development of QS to include differentiation in the abundance of a population using some key values (e.g. low, medium, high) has had limited use in ecological modelling. In the five state QS used by Salles & Bredeweg (2006) to represent population abundance in a model to explore succession processes in Cerrado vegetation, the max point value in a QS was used as a landmark and related to the concept of carrying capacity. Whereas, in this model carrying capacity was not represented as a fixed point in the QS but could occur at any value at which the *Number surviving* was in balance with the *Potential*. Hence it can be considered that the max point in the QS only reflects the carrying capacity of pristine habitats.

The use of detailed QS has potential to allow for quicker and easier interpretation of a simulation through interrogation of the value history alone, whereas simple QS requires close interrogation of the equation history, something that may be harder for inexperienced learners to comprehend. However, the use of detailed QS does make modelling and model reasoning more complicated, resulting in more complex simulations and larger behaviour paths to represent the semi-quantitative knowledge. The choice of QS used here {zero, low, medium, high, max} only reflects four states of interest; that of zero, low, high and max. The medium point merely reflects an instantaneous transition from low to high. As such it has no real interpretation value to the model in itself. However, the medium point is very important for model development and was fundamental in the implementation of calculus and value correspondences. The difficulties identified in the model implementation together with the solutions used, highlight that determination of QS and model complexity is a fundamental issue in qualitative modelling in ecology.

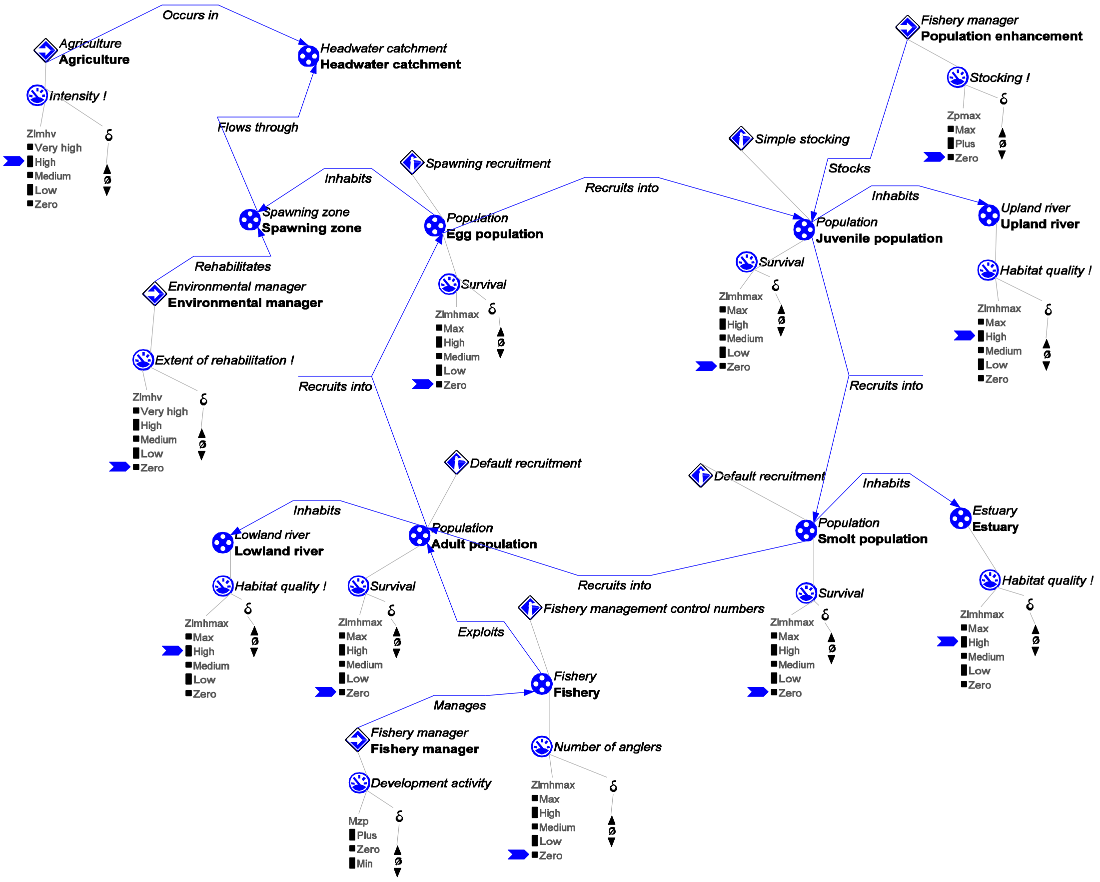

Figure 12 An example of a life cycle scenario detailing the sequence of life stages in the salmon life history that are included in the model and their relationship with specific river habitats and human activities (agents). Scenarios contain details of the entities involved, their structural relations (configurations), the starting values of some of their associated quantities (blue arrows) and modelling assumptions that apply to entities (e.g. Default recruitment). The scenario may also contain exogenous controls (*!*) over some of the quantities. In this scenario the initial values of population size (*Survival* quantity) is set to zero.

Modelling solutions

During model implementation a number of solutions were required to control ambiguity and inconsistency. In some cases these resulted from the choice of the QS used, and the logical conditions and consequences under which processes were modelled. The model fragments used to make these solutions included these approaches:

- a suite of model fragments that fully describe and limit possible behaviours through limiting consequences to conditions;
- a model fragment that removes a possible behaviour.

Examples of the first are found in the model fragments that specify the behaviour of *Potential* when it is switching from being controlled by either *Habitat quality* or *Recruitment* to the other. These model fragments make logical statements about the outcomes of situations and thus ensure behaviours in given situations. Examples of the second are two of the model fragments that control the derivative behaviour of *Difference*. The two model fragments make logical statements that when the *Difference* value is minus or plus then the derivative value cannot be stable. This acts to restrict the reversing of the *Difference* derivative to the extreme point values. This was used to overcome the current limitations in Garp3 for modelling information regarding second order derivatives.

Ideally, such solutions should be, either not required or, kept to a minimum and only act in the same way modelling assumptions are currently used. However, as highlighted by Salles *et al.* (2006), ambiguities and inconsistencies will arise in QR modelling in ecology due to the use of incomplete knowledge. Knowledge representation is likely to be even more incomplete when modelling up scales from models concerning fundamental small scale processes to large scale models that represent abstracted versions of fundamental concepts. For example, the model here does not include the whole suite of biological processes that act to control population size (e.g. Salles & Bredeweg 2006, Salles *et al.* 2006) but represents an abstract version designed to capture the key ideas. In these cases it is likely that such studies will deliberately model incomplete knowledge and thus create ambiguities and inconsistencies that need technical modelling solutions to overcome them. Fundamentally, the choice between the level of complexity used and the use of technical fixes to control ambiguities and inconsistencies must depend on the objectives and final use/users of the model, i.e. what level of causal explanation for behaviours is required by the end user and what knowledge the modeller is attempting to formalise and communicate.

Complexity

The concept scenarios developed here showed that for even simple scenarios complex and variable behaviours could be generated, including when the fastest path heuristic and some modelling assumptions and behaviour limiting model fragments were used. The majority of this complexity was because the modelling approach allows some flexibility in the rate of changes for the *Survival* in each life stage relative to the rate of changes in the *Potential* that is generated by the exogenous behaviours of rehabilitation activities, and their effect on habitat quality. This level of ambiguity for one life stage was multiplied when multiple life stages were considered. The life cycle scenarios became very complex and resulted in large and time consuming simulations, even when only a single human activity was active on a single life stage.

Complex models are to a great extent necessary for large and complicated systems. It is likely that such models necessitate a large number of entities and quantities to convey the required information and concepts. It is also likely that the questions asked of such a model will require complex scenarios with a multitude of active interacting entities, or exogenous factors acting on simulations (Bredeweg *et al*. 2007). Furthermore, additional complexity can be introduced by the use of large quantity spaces that may be used to convey semi-quantitative information to aid interpretation or describe critical points. Therefore, QR models can easily become complex. Given this it is likely that modellers will be interested in controlling complexity when dealing with large systems. Developing model components (such as the solutions used here) and processes (such as fastest path heuristic) will allow modellers to control the levels of complexity in the model, which may allow them to generate relatively simple simulations from complex scenarios, i.e. isolating only the key behaviours whilst still retaining all the elements of the system.

Given the current processing requirements of the life cycle scenarios, the use and exploration of such complex cyclical reasoning scenarios is still limited, especially in an educational setting where time may be critical. However, the results obtained here are positive and indicate there is great potential in such cyclical models, especially when the larger scenarios can be associated with smaller concept demonstrators, which allow the larger scenario to be broken down into more manageable components. In addition to this, software and hardware developments allow for faster reasoning and simulation resolution and thus make these sorts of complex models more manageable in the future.

Conclusions

The salmon life-cycle model was easily able to explore scenarios related to single or pairs of life stages. These small concept scenarios are useful to allow model users to explore and understand fundamental parts of the overall system without having to isolate information contained in models simulating the whole system. The complexity of the system limited the exploration of scenarios considering the whole life cycle. Additional complexity resulted from ambiguity and inconsistency in the abstract representation of some of the concepts. These ambiguities and inconsistencies were controlled using a number of modelling solutions. These solutions, together with developing diverse concept scenarios and using some of the newer simulation options in Garp3, provide a basis for modellers begin to handle complexity in large models.

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