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# Atlantic salmon dynamics in the Foyle catchment (Ireland), a bayesian approach

Guillaume Dauphin

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**ATLANTIC SALMON DYNAMICS IN THE FOYLE  
CATCHMENT (IRELAND),  
A BAYESIAN APPROACH**

**BY**

**GUILLAUME DAUPHIN**

**THIS THESIS IS SUBMITTED IN FULFILMENT OF THE REQUIREMENTS FOR THE  
DEGREE OF DOCTOR OF PHILOSOPHY**

**DEPARTMENT OF ENVIRONMENTAL AND EVOLUTIONARY BIOLOGY,  
FACULTY OF BIOMEDICAL & LIFE SCIENCES.**



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*of*  
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## ABSTRACT

Population dynamics is the study of the abundance of a species at different life stages of a species, the interactions between these life stages and sometimes the interactions with other species. Stage-structured modelling is a popular approach for population dynamics studies. This approach examines populations based on their ecology and allows the incorporation of complex dynamic processes. Model outputs are sensitive to the parameter values. It then becomes crucial to accommodate and quantify parameter uncertainty. This is of particular importance when the population of interest is exploited and the risk of over-exploitation or extinction needs to be assessed.

When studying real world examples of populations exploited by fisheries, several additional problems often arise such as: multiple and heterogeneous sources of information (e.g. datasets collected at different spatial and temporal scales), missing observations, life stages of interest not directly observable. The Bayesian framework allows all of these issues to be handled within the general framework. Thus has proven its particular value in studying the dynamics of exploited populations. Indeed, unknown quantities have associated probability distributions reflecting their uncertainty. Dealing with variations in the interactions/processes between life stages or limited and indirect ecological data is also facilitated by Bayesian modelling.

In this study, I examined a large Atlantic salmon population located in the Foyle catchment (Ireland). This population has been exploited for several centuries and particularly during the 20<sup>th</sup> century. This study focused on the period from 1959 to present for which most monitoring data is available from the Loughs Agency (formerly the Foyle Fisheries Commission). The Loughs Agency is responsible for the management of the salmon population. The aim of the agency is “to manage [the] fisheries towards maximum sustainable exploitation for commercial and recreational purposes”. In order to do so, it is important to understand the regulatory mechanisms occurring in the population in order to (i) estimate the number of fish returning to river, i.e. pre-fishery abundances (PFAs), and (ii) to derive standard reference points for assessing the population status with regards to its sustainable exploitation.

To this end, a state-space model is implemented within a Bayesian framework. A life stage and spatially structured dynamic model describes the lifecycle of the Main components of Atlantic salmon in the Foyle catchment. Several empirical datasets related to the abundances of the stages at different scales of space and time, over a period of 50 years are brought together. Observations and process errors are taken into account ultimately allowing PFAs to be estimated. A retrospective analysis was also carried out providing insights on the historical status of the population and its exploitation.

Geo unit specific abundances of the different states and their associated uncertainty are estimated. The main state of interest is the pre-fishery abundance (PFA), during the time-series considered (1959-2008) the salmon population reached its apex in the mid 1960's. This was followed by a steep decrease until the mid 1970's. From then to present, the population followed a slow declining trend with a slight recovery in the mid 1980's. This decline is shown to be mostly due to a decline of the 0+ juvenile to returning adult survival which is accentuated some years by some overfishing.

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Finally, as Billy D. says, keep the salmon blues alive!

## Declaration

I hereby declare that the work on this thesis has not been submitted for another degree. It is entirely my own composition and that research described herein was carried out by me unless otherwise stated or acknowledged.

Guillaume Dauphin

## Chapter 1:

# Fisheries and Atlantic salmon

Fisheries management requires ecological and environmental knowledge about the species exploited. This knowledge is used to provide information on the dynamics and the abundances of the species of interest, specifically to determine appropriate rates of exploitation. Many exploited fish populations have complex life histories such as diadromous species (e.g. salmonids (Salmonidae), eels (Anguillidae), and sturgeons (Acipenseridae)). Thus complex models will be necessary to take account of the highly complex life-histories of these species. In general, increasingly complex models require more parameters to describe the variability occurring within the population (e.g. where individuals of a same population do not mature simultaneously or are not exploited at the same time). More parameters require more data to provide reasonable estimates of these parameters.

The ideal situation to build a model describing the dynamics of a complex life cycle species would be to have information regarding the abundance and the transition rates for each life stage however, in most cases, data are available only for one or two life stages. In this study, I utilise different methods to deal with partial information on the lifecycle of an exploited species of high conservation value with a complex lifecycle (Atlantic salmon, *Salmo salar* L.) in order to provide abundance estimates and population management advice.

In this chapter, I describe the general context of applied fisheries management for Atlantic salmon. I then describe the Foyle catchment and its Atlantic salmon fishery, studied in this thesis. The Atlantic salmon lifecycle as well as the data available for the Foyle population are also described.

## 1.1. Fisheries management

Three types of management strategy are available to fisheries managers to manage exploitation rates or fish population (Blankenship and Leber, 1995): 1) artificial stock enhancement, 2) habitat manipulation (e.g. increasing available habitat, etc.), and 3) to use traditional exploitation limitation tools (e.g. quotas and bag limits, seasonal closure).

The applicability of stock enhancement as a management technique is still in question (Hilborn, 1998) as it has been relatively unsuccessful in the past (Molony *et al.*, 2003) mainly because of lack of knowledge of the conditions required for effective stocking. Indeed, to be efficient, accurate information on the habitat suitability at the site where the species will be introduced is needed. Even used with all the data requirements met, many risks such as an increase of intra-specific competition and loss of genetic diversity have been associated with stock enhancement management strategies.

Habitat manipulation or restoration in contrast, attempts to improve or enhance environmental conditions for the exploited species; for salmon, this has been largely carried out mainly in freshwaters in order to increase juvenile production (NASCO, 2001).

The most used tool is fisheries regulation since it seems to be the easiest way to control the number of fish caught, through the number of fishing licences given each year, the fishing season duration, the type of gear used, etc. However, to provide efficient exploitation regulations, the managers need scientific information about the abundance before the fisheries take effect (pre-fishery abundance) and reference values of stock or exploitation rate necessary to observe a long-term sustainable population.

Once a model of the population dynamics has been designed and judged close enough to reality. The managers can decide which reference points they want to use.

### 1.1.1 *Precautionary approach and management*

#### 1.1.1.1 Food and Agriculture Organization (FAO) statement

As defined by the FAO (1997), the precautionary approach to fisheries management states that scientists should:



- “provide stock conservation limits and management targets for all rivers stocks”
- “provide advice on the risks of not achieving objectives [...] by considering uncertainty in the current state of stocks [...] in biological reference points related to specific management objectives”
- “provide catch options, or alternative management advice, for fisheries managed by the North Atlantic Salmon Conservation Organisation (NASCO)”

This conceptual approach has led to the definition of biological reference points (BRPs)

### 1.1.1.2 Definition of Biological Reference Points (BRPs)

Fisheries management principles are summarized by Olver *et al.* (2005): 1) The long-term sustainability of native fish stocks should be maintained; 2) habitat of these stocks should be preserved; 3) the native biological community should not be modified; 4) the harvest should not exceed the regeneration rate of the population; and 5) spawning aggregations should not be directly exploited.

BRPs are quantities describing a population's state, calculated at a specific life history stage. Under the precautionary approach, the distinction between limit reference points (LRPs) and the target reference points (TRPs) is fundamental. LRPs are critical threshold values that should never be crossed (Mace, 1994), whereas TRPs are desired states of the population from a management perspective which are estimated on the basis of optimising criteria such as the level of stock that will achieve long-term maximum sustainable yield (MSY, Caddy and McGarvey, 1996) to fisheries. The International Council for the Exploration of the Sea has accepted since 1997 (ICES, 1997) that both LRPs and TRPs should be used as standard management parameters for exploited populations. LRPs set boundaries that should not be crossed while TRPs are values to aim for in sustainable fisheries. Following NASCO recommendations, the terms “conservation limits” and “management targets” will be used for LRPs and TRPs respectively as these terms indicate that management should be associated by sustainability.

In order to be consistent with the precautionary approach, reference points should be expressed using spawning biomass levels ( $B^{\text{lim}}$ ) and fishing mortality rate limits ( $F^{\text{lim}}$ ) (ICES, 1997). Rosenberg *et al.* (1994) describe the advantages and disadvantages of applying  $F^{\text{lim}}$  and  $B^{\text{lim}}$ .

Conservation limits can be specified as a maximum fishing mortality rate or a minimum biomass level for the stock. Using fishing mortality to set the conservation limit present the advantage of being directly related to the fishing activity and can therefore be controlled directly. There is a theoretical and empirical basis for selecting maximum fishing mortality levels (ICES, 1997). There are several economic advantages in using  $F^{\text{lim}}$ , a fishery near the  $F^{\text{lim}}$  will not have to close but rather substantially reduce its catches. Also, setting a maximum fishing mortality can protect the stock from depletion due to over-fishing in the long-term (Rosenberg and Restrepo, 1996). This allows reducing the socio-economic impact of fishery closure. In addition, the data and life history information required from the stock is relatively low. However there are some disadvantages to using maximum fishing mortality rates. For instance, the fishing mortality based definition may not be appropriate at all biomass levels (e.g. stock rebuilding might not be possible when stock was overfished in the past). Fishing mortality rate does not account for environmental condition change or changes of life history characteristics and requires to be modified when these occur (Rosenberg and Restrepo, 1996). Also there are no explicit stock-recruitment considerations (King, 1995), which means that avoiding recruitment failure is not guaranteed.

When conservation limits are set based on minimum biomass level, this level sets a standard for rebuilding stocks. Using minimum biomass level can also allow the stock to be protected during long periods of poor environmental conditions (i.e. under undesirable conditions the minimum stock level provides a buffer by ensuring the survival of a proportion of the stock for an eventual recovery when environmental conditions improve). In addition, the concept of minimal spawning escapement is easily understood by the different groups involved in salmon management (Potter, 2001). But as for the fishing mortality rate, there are disadvantages to using minimum biomass level as a management tool. Setting these reference points is difficult and requires a high level of good quality data (Rosenberg and Restrepo, 1996) as short time-series of stock-recruitment data can lack of contrast in spawner abundance or environmental conditions. Another issue occurs when the minimum biomass level is treated as a fixed value, which can lead to highly variable catches and severe socio-economic impacts (Hilborn, 2001).

Reference points based on either  $B^{\text{lim}}$  or  $F^{\text{lim}}$  are dependent on the stock-recruitment relationship produced by the models used to describe the population dynamics. These population models and associated data are both subject to uncertainties that need to be

accounted for in order to measure the risk of reaching the reference points and achieving the management strategies.

### **1.1.2 Sources of uncertainty**

In this thesis, I use probabilistic modelling which focus on linking models to available datasets. A model is always a partial and simplified representation of the reality. It looks at unobservable variables and unknown parameters of a given population of interest by using available datasets related to observable quantities. Several papers review the different types of uncertainty and how crucial it is to account for them when building models (Chatfield, 1995; Draper *et al.*, 1987; Francis and Shotton, 1997; Hodges, 1987; Regan *et al.*, 2002; Rosenberg and Restrepo, 1994). The quantification of the various sources of uncertainty has been of particular interest in recent years in order to develop harvest or fishery-management strategies (Frederik and Peterman, 1995; McAllister *et al.*, 1999; Smith *et al.*, 1993), to measure risk associated to these strategies (Francis and Shotton, 1997; Ludwig *et al.*, 1993; Richards and Maguire, 1998) and, fishery stock assessment (Hilborn *et al.*, 1993; Punt and Hilborn, 1997; Schnute and Richards, 2001).

When dealing with fisheries the main sources of uncertainty are: 1) natural variability in distribution, abundance and productivity of fish populations, 2) observation error (i.e. imperfect information), 3) model error, 4) communication problems between the different stakeholders (scientists, managers), 5) unclear management objectives and 6) implementation error (i.e. the difference between a management goal and its actual realization) (Harwood and Stokes, 2003; Peterman, 2004). All these sources (if they are not taken in account) are likely to create biases in applications related to the management of the fish population.

In this study, population dynamics is the main focus and therefore (4), (5) and (6) which correspond to management issues are not addressed. (3) is very complicated to address in complex model as it involves looking at models considering the combination of the different model hypotheses. This becomes a vast task as the number of parameters increase and is associated with important computational problems: running all the possible models would be too time consuming. Therefore, in this study I mainly focus on (1) and (2) which are also called *process uncertainty* and *observation uncertainty* respectively.

### 1.1.2.1 Measurement or observation uncertainty

This type of uncertainty represents the limits of the information available in the datasets and has principally two components: 1) the *measurement error*, which is a consequence of the way in which observations are taken (e.g. the choice of sampling strategy, or errors in data collection). Indeed, the conditions of observation are often very difficult to control and sampling techniques may require indirect observation protocols which multiply the sources of uncertainty (Solow, 1998). 2) the *estimation (or inference) error*, which is the inaccuracy and imprecision introduced by the method of statistical inference used to estimate system parameters from observations.

### 1.1.2.2 Process uncertainty

Process uncertainty represents stochasticity, which is a component that can't be ignored in models used in biology and in particular in ecology. The process uncertainty is the probabilistic component of a model, it includes all the effects that are not explicitly expressed in cause and effect relationship represented in the model. When dealing with populations, process uncertainty can be split in two components: environmental stochasticity and demographic stochasticity. Both are often treated together (Harwood and Stokes, 2003). The *environmental stochasticity* represents the environmental factors, which can vary for unknown reasons during the study and affect individuals (or groups of them) in the same way. This variability cannot be avoided when the studies take place in the wild; it is impossible to be able to measure and incorporate in the model all the environmental factors that influence the population studied (and thus the parameters surveyed). The *demographic stochasticity* represents at a population level, the stochastic behaviour of each individuals of this population. It can be modelled in two ways: 1) by considering the inter-individual variability of the vital parameters (i.e. survival, fecundity; Clark, 2003; Fox and Kendall, 2002) or 2) by considering that all individuals have the same vital parameters but have a random behaviour conditionally on these parameters. In this situation, when the size of the population increases, the part of the process uncertainty due to the demographic stochasticity becomes generally negligible in comparison to the environmental variability.

## 1.2. Dealing with uncertainty using a Bayesian approach

Since the end of the 1980's (Dixon and Ellison, 1996), the use of Bayesian inference has expanded rapidly in ecological research and environmental decision making in various field such as: dynamics of single species (Barrowman *et al.*, 2003; Calder *et al.*, 2003; Clark *et al.*, 1999; Clark *et al.*, 2003a; O'Hara *et al.*, 2002; Schnute and Kronlund, 1996; Walters & Ludwig, 1994; Wintle *et al.*, 2003), dynamics of interacting species (Clark *et al.*, 2003b; Frigessi *et al.*, 2005) and multispecies community ecology (Fleishman *et al.*, 2003; Peterson *et al.*, 2003; Shen *et al.*, 2003). Several papers have described the importance of Bayesian inference in ecology (Clark, 2005; Ellison, 2004) and more generally as a tool to deal with uncertainty (Chatfield, 1995) or more specifically in a framework for decision making in natural resource management (Dorazio and Johnson, 2003).

Bayesian inference has become popular in population dynamics because it allows uncertainty to be accounted for directly in the results of the analysis by probability distribution functions associated with the unobservable state variables and unknown parameters. It provides a unique, coherent and rigorous framework which allows incorporation of: (1) results from previous analysis probability distribution function thus allowing an update of the existing knowledge (Weeks and Berkeley, 2000), (2) data from other populations when data are lacking for the population of interest (Myers and Mertz, 1998), (3) expert knowledge (Malakoff, 1999). Finally, recent advances in computer technology, the development of numerical methods (Markov chain Monte Carlo) (Chen *et al.*, 2000; Clark, 2006; Gilks *et al.*, 1996) and the development of more user-friendly software package (WinBUGS, Thomas *et al.*, 1992; BayesX, Lang *et al.*, 2002; FirstBayes, O'Hagan, 1996), Bayesian analysis are less difficult to apply.

Most Bayesian models for diadromous species such as Atlantic salmon focus on the freshwater phase of the life history and therefore ignore the sea fisheries and their management (Mäntyniemi and Romakkaniemi, 2002; Power and Power, 1994; Rivot and Prévost, 2002; Wyatt, 2002). However, several recent studies have been looking at a more comprehensive approach, looking at the full life cycle (Michielsens *et al.*, 2008; Rivot *et al.*, 2004). Theoretical aspects of these models will be discussed in section 1.4 and 1.5.

## 1.3. A case study: Atlantic salmon in the Foyle catchment (Ireland)

### 1.3.1 *Biology*

Atlantic salmon (*Salmo salar* L.)<sup>1</sup> is a fish which belongs to the class Actinopterygii and the family Salmonidae, which includes whitefish (Coregoninae), graylings (Thymallinae) and charrs, Pacific salmon and trout, (Salmoninae).

Salmon occur on both sides of the Atlantic Ocean and are found in rivers flowing in the western seaboard of Europe from northern Portugal to the White Sea, in the British Isles, Iceland and Greenland. On the Eastern seaboard of North America, they are found from approximately 40°N northwards to northern Québec. As a result of anthropomorphic activities (e.g. salmon commercial farming), salmon have expanded their natural range to a more global distribution (McKinell *et al.*, 1997; McKinnell and Thompson, 1997; Ward, 1994).

The Atlantic salmon is euryhaline (i.e. can tolerate a wide range of salt concentrations and can live in both fresh and salt-water) which allows it to have an anadromous life history. The juvenile stage is spent in freshwater with the later stages usually in the marine environment. After several years spent in rivers, salmon move downstream as smolts to travel to the sea where they will spend several months to several years in the ocean before returning to freshwater to spawn.

The complex life cycle of Atlantic salmon (Figure 1.1) has been extensively studied (Crisp, 2000; Klemetsen, 2003; Mills, 1971). Spawning takes place in the winter. The female selects a place with clean flowing water and gravel of suitable size (spawning area). She then digs a cavity where eggs are laid to be fertilised by the male. The female then covers the eggs with gravel creating a mound called a redd. Each female generally produces one redd (Crisp, 2000; Hay, 1987). After incubation, the young fish which is called an alevin hatches with a yolk sac attached to it. As the yolk sac is utilised, the alevin emerges from the gravel and starts to feed, disperse and defend territories. Once dark marks appear on its flank, the fish is then called a parr. During this stage the juveniles inhabit riffle areas

<sup>1</sup> from now on, when no species is indicated the word “salmon” will refer to Atlantic salmon (*Salmo salar*)

(nursery habitat). The reproduction, embryonic development and the juvenile stages correspond to critical stages where density-independent environmental factors and density dependent regulation mechanisms occur (Elliott, 2001; Jonsson *et al.*, 1998; Milner *et al.*, 2003). After spending one to six years in the river depending on water temperature and food availability (Gibson, 1993), the parr undergoes several morphological (e.g. body silvering, parr marks disappear) and physiological (increased salinity tolerance, olfactory sensitivity ...) transformations, which allow it to travel to open sea (McCormick *et al.*, 1998). Elliot (2001) and Friedland (2003) emphasize that this transition phase between freshwater and the sea (i.e. in estuaries and coastal areas) is one of the major bottlenecks occurring in the life cycle. During their downstream migration to the open sea, the young salmon are called smolts. They will then spend one year or more at sea before returning to freshwater to spawn (Hansen and Jacobsen, 2000). Several marine feeding areas are known: Iceland, western Greenland and the Faroe Islands north of Scotland. If a fish has spent one year in the sea, it is called a one-sea-winter fish or grilse; if more than one winter has been spent at sea, the fish is known as a multi-sea-winter fish. Their marine survival is dependent on environmental fluctuations. The precise mechanisms of which are still unknown (Friedland, 1998; Hansen and Quinn, 1998) and predation which decreases as the salmon grows (Potter and Crozier, 2000). In most cases, salmon will return to the streams into which they hatched. This behaviour is called homing. Some proportion of the males never travel to sea but instead become sexually mature in the rivers and can take part in the spawning with female adult salmon. These fish are described as precocious male parr (Crisp, 2000). However salmon returning from the sea have experienced better growth opportunities due to greater food availability at sea compared to freshwater (Hawkins, 2000; McCormick *et al.*, 1998). After spawning, a small proportion of fish survive and go back to the sea. These fish are called kelts. The post-spawning survival is generally low but can reach 17.5 % in certain populations (Hutchings and Jones, 1998). In the Foyle catchment, the post-spawning survival is estimated around 7% (Elson and Tuomi, 1975). For this reason salmon have been considered as semelparous in the Foyle area.

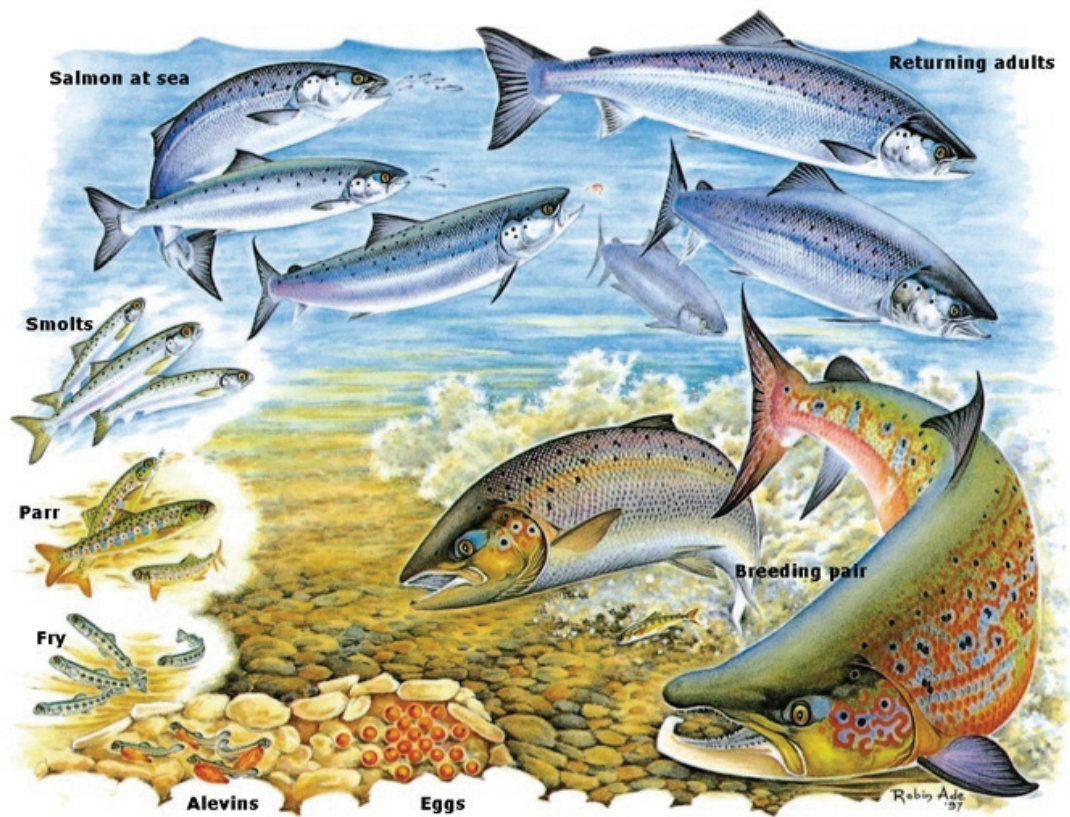


Figure 1.1: Atlantic salmon lifecycle. © Robin Ade and Atlantic Salmon Trust.

### 1.3.2 Conservation status of wild Atlantic salmon

For various reasons, salmon populations are important for humans. They are of economic importance for the commercial and recreational fisheries. In most of the river systems in North America and Europe, salmon populations have declined or disappeared (Parrish, 1998). The reasons for this decline are due to human activities such as significant river modification (e.g. from the 19<sup>th</sup> century, construction of dams) which can cut salmon off from reproduction areas, degradation of the aquatic habitat quality, and overfishing (Armstrong *et al.*, 1998; Parrish, 1998). The salmon's presence in rivers is evidence of good water quality and also has symbolic value. People enjoy seeing salmon feeding in the river or jumping waterfalls.

### 1.3.3 Foyle catchment description and data available

#### 1.3.3.1 Geography

The Foyle catchment is located in the North West of the island of Ireland and is approximately 4,500 km<sup>2</sup>. Located on the border of the Republic of Ireland and Northern Ireland, the catchment is under the jurisdictions of a governmental cross-border



organisation: the Loughs Agency of the Foyle Carlingford and Irish Lights Commission.

For the purposes of this study, the catchment is divided into five geographical (“geo units, Figure 1.2) based on the locations of fish counting devices in the catchment. Four geo units correspond to the wetted area above the fish counter structures and are named after the main stream which goes through them (Faughan, Finn, Mourne and Roe). The last geo unit, named “Foyle” is composed of the wetted area of the remaining parts of the Foyle catchment but not including the Culdaff River and the area north of the Faughan units. These two areas were not included in the Foyle unit since they are known for having a very small population of salmon and are less well monitored than the rest of the system.

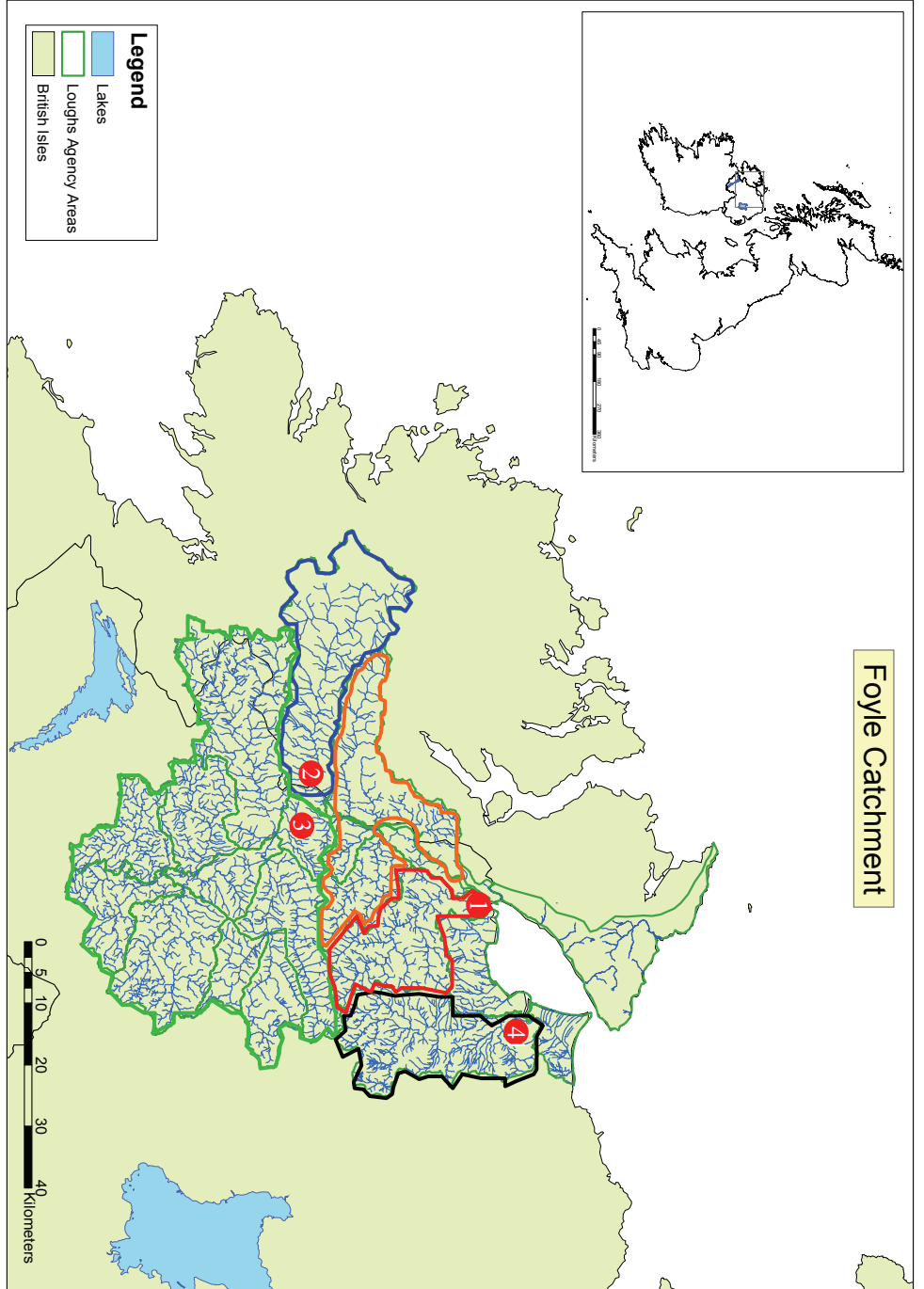


Figure 1.2: Map of the Foyle catchment with the different geo units location in red (Faughan), blue (Finn), green (Mourne), black (Roe) and orange (Foyle) and, the counters location, 1) Faughan, 2) Finn, 3) Mourne and 4) Roe.

### 1.3.3.2 Salmon biology in the Foyle catchment

Most Atlantic salmon return to their natal stream to spawn (i.e. homing) (Hansen *et al.*, 1993; Westerberg, 1982), therefore the gene flow between the various tributaries of a river is relatively low. This leads over a longtime-scale to the development of genetically different subpopulations. Conservation of genetic diversity is increasingly recommended in fisheries management because it is regarded as local adaptation to a particular local habitat. In order to improve the management regime, a genetic assessment of the Foyle salmon population was carried out in 2003, looking at the variability of six microsatellites loci known to detect stock differences (Booth, 2003). The study postulated the presence of two distinct genetically differentiated groups (metapopulations) within the Foyle system; a western group comprising of the River Finn and River Derg and their respective tributaries, and an eastern group comprising of the rest of the Foyle Rivers. In 2008 (Ensing and Crozier), this vision was refined showing the existence of at least three clear higher level populations within the Foyle system. Ensing and Crozier (2008) show that the Foyle salmon stock conforms to a member-vagrant evolutionary model (i.e. the genetic structure of the populations are maintained by areas that limit the dispersal and advection of eggs and early lifestage). This member-vagrant evolutionary model predicts that population structure evolves as a result of natural selection that favours precise homing of sexually mature adults of the same gene pool to spawn in appropriate spawning areas. This process results in strong genetic structuring in populations with locally adapted gene pools as a result of reproductive isolation where the basic level of genetic differentiation appears in a spatial scale within a 5-20 kilometres range (Booth, 2003; Ensing and Crozier, 2008). It should also be noted that the genetics of the fish caught by the commercial fisheries have been studied in 1999, 2001 and 2003 (2000 and 2002 samples are currently being examined). For these three years it appears that one or two rivers stocks are mainly exploited by this fishery. Thus, in 1999 the main contribution was from the R. Derg and Cloughfin R. and in 2001 and 2003, the main contributor was the R. Finn.

### 1.3.3.3 Data available

During the last fifty years, the Foyle Fisheries Commission and subsequently the Loughs Agency have collected a large amount of data related to salmon abundance and habitat.

*a. Commercial and recreational catches*

One of the longest the time-series of data is the commercial and recreational catches. Since 1952, the number of salmon caught by the different fisheries has been recorded. The two main commercial fisheries use drift and draft nets.

The drift nets are gill nets (Mills, 1989), which are laid out near the water surface in the sea lough. These nets can be used in a range of 12 miles from the North coast. Each year, up to 139 drift licences were issued and split into three categories: 1) sea licences, allowing fishing exclusively in the open sea within a 12 miles range of the mouth of Lough Foyle, 2) lough licences, allowing fishing exclusively in the sea lough and 3) sea and lough licences allowing fishing in both sea and lough. Two types of drift nets are used: those used at sea are 1500 metres long with a depth of 45 meshes and a mesh size of 63 millimetres while the nets used in the lough are similar except that their length is 900 meters. At the beginning of the time-series, fishing was allowed 24 hours a day, 4 days a week from the 31<sup>st</sup> of May until the 31<sup>st</sup> of August. Several regulation changes led to a consistent decrease of the authorised fishing season. Nowadays, the netting season is limited to the 15<sup>th</sup> June to 31<sup>st</sup> August, Monday to Thursday from 6:00 am to 6:00 pm.

The draft nets are seine nets, which are used in the main river Foyle and the River Roe at defined netting stations. In contrast to drift nets which are immobile, the operation of draft nets is an active capture technique. One fisherman holds one hand of the net, and then a boat leaves from the bank and goes downstream to create a loop. The other end of the net is given to another fisherman. The two fishermen then pull out the net. The draft netting season is identical to the drift nets except they can be used 24 hours a day as tides and water flow limit fishing opportunities. Fishermen using drift and draft nets licences are required to report their catches to the Loughs Agency.

In addition, the Foyle Fisheries Commission (precursor of the Loughs Agency) had its own draft net fisheries in the main River Foyle and the River Roe (3 sites: Prehen, Rosses Bay and mouth of the Roe). One supplementary licence was also issued to use fixed engines (similar to a box trap) annually in the lough. The Foyle Fisheries Commission also ran a stake netting fishery which was similar to fixed engine but was temporary between 1952 and 1988. Stake nets were made of a barrier net stretched at right angles to the shoreline leading to a box trap where the salmon were caught. Between 1964 and 1990, bag nets

where used in the estuary, they were similar to stake nets, the only difference being that they were permanently fixed.

Anglers are also required to report their catches but it seems like reported angling catches are very low in particular at the beginning of the time-series until a carcass-tag system was implemented in 2001, rod catches before this data are thus likely to be minimum values.

#### *b. Counter structures*

Four resistivity counters (Fewings, 1994) provide data on the number of adult salmon returning from sea to rivers from 2001 to 2006. They are located at the downstream end of four geo units (Faughan, Finn, Mourne and the Roe, Figure 1.2). They detect upstream and downstream movements of any fish with a body length greater than 45 cm. This detection threshold is lower than the minimum size of a returning adult Atlantic salmon in the Foyle system. Brown trout (*Salmo trutta* L.) could potentially be counted however, calibration work on the counters have shown that the number of fish other than salmon that might be included in the counts is negligible relative to the number of salmon (Loughs Agency, personal communication). Subtracting total downstream movements from total upstream movements provides the total number of salmon which returned for a given year. Three of the counting structures (Faughan, Finn and Roe) effectively count all fish moving upstream or downstream of the counting structure. The remaining counter is located at the downstream end of the Mourne unit and only counts an unknown proportion of returning salmon. This proportion is dependent on the weather conditions as when the river is high, fish can move upstream without passing through the counting structure.

#### *c. Redd counts*

From 1952 until the present, the Foyle Fisheries Commission (and subsequently the Loughs Agency) has counted redds annually during and immediately following, the spawning period in approximately 260 zones which correspond to 14 main rivers and tributaries within the catchment (depending on the year, up to 33% of the total wetted area of a geo unit can be surveyed to count redds). Even if the accuracy of counting is dependent on environmental conditions (e.g. when high flow, the poor visibility prevent easy counting) it is still a good method in long-term population monitoring (Elson and Tuomi, 1975; Isaak *et al.*, 2003).

#### *d. Electrofishing*

For salmon, the main population bottleneck occurs during the juvenile life stage (Gibson, 1993). This stage is therefore important to monitor. Juvenile salmon populations have been intensively studied in various ways: growth rate (Arneklev *et al.*, 2006; Jenkins *et al.*, 1999), behaviour (Imre and Boisclair, 2004; Imre *et al.*, 2004), habitat requirement (Armstrong *et al.*, 2003; Gibson, 2002; Heggenes and Cunjack, 1999), and population regulation (Egglisshaw and Shackley, 1985).

Following the technique described by Crozier and Kennedy (1994), Loughs Agency field staff have been collecting 0+ juvenile index of abundance every year since 1998. The index is the number of 0+ juvenile salmon caught during 5 minutes of continuous sampling at a given site. Between 77 and 476 sites were sampled every year between July and September, covering the whole catchment. The different quality of habitat for 0+ juveniles was evaluated qualitatively by different covariates: percentage of the different types of substrate of the riverbed (bedrock, boulder, cobble, gravel, fines, sand and mud), width and length of the site sampled, flow speed and flow level, and vegetation overhang.

#### 1.3.3.4 Management history within the Foyle catchment

The Loughs Agency is a statutory cross-border body, which is responsible for the management, conservation, protection, improvement and development of the inland fisheries of the Foyle and Carlingford areas. Its long term aim is to manage the salmon fisheries towards maximum sustainable exploitation for commercial and recreational purposes (Loughs Agency corporate plan 2005/2007).

Over the last fifty years, the commercial fisheries season has been modified by regulations initiated by the Foyle Fisheries Commission and subsequently the Loughs Agency. Until 1961, the Foyle Fisheries Commission, was delivering unlimited fishing licences to whomever could pay and has ensured that sanctuary areas were not fished. In 1961, the number of licences was reduced and limited to a certain number each year, additionally one person could only be granted one licence (Hadoke, 1972). The fisheries season duration was reduced over time (see section 1.3.3.3a). Also, in 1963 installation of powered winches on the fishing boats led to a catch increase in the following years (Figure 1.3).

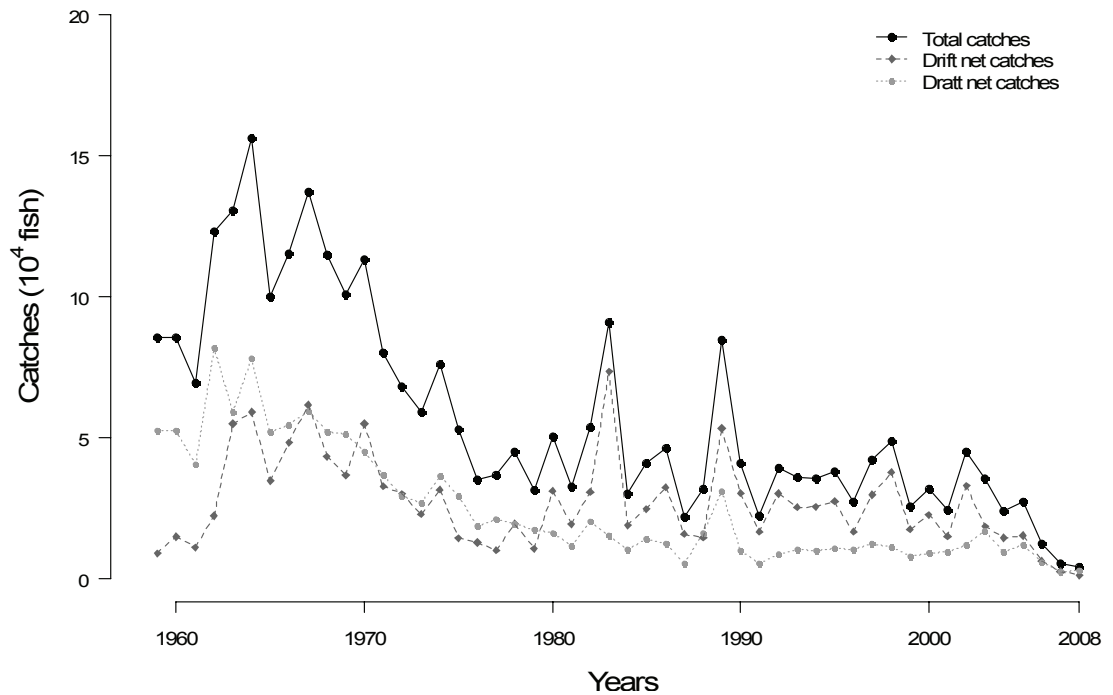


Figure 1.3: Total commercial fisheries, drift nets and draft nets salmon catches between 1959 and 2008.

Following Elson and Tuomi's report (1975) a real-time management regime was set up. This regime has been refined over the years and is now as follows: the fishery is expected to meet in-season population abundances at the Mourne counter (Figure 1.2). The first target must be reached two weeks after the start of the fishing season (30<sup>th</sup> June) when more than 2600 salmon must have passed the counter structure. If the target is not achieved, depending on the water flow as measured at a local Department of the Environment gauging station, the commercial and recreational fisheries will be closed for either 24 or 48 hours. In the same way if a target of 4200 fish is not achieved by the 10<sup>th</sup> July, the fisheries may be closed for 24 or 48 hours. However, whatever the status of the abundance target, the fisheries can only be closed for a maximum of 48 hours during one season. In contrast, if more than 8000 salmon have passed the Mourne counter by the 24<sup>th</sup> July, the commercial fishing season will be extended by 96 hours. Finally, if less than 7000 salmon have passed the Mourne counter by the 20<sup>th</sup> September, the recreational fishery season will be curtailed by 10 days.

The conservation limit estimate of 8000 salmon was calculated from the amount of nursery habitat available upstream of the Mourne counter and an estimated juvenile carrying capacity. Several works (Armstrong *et al.*, 2003; Bult *et al.*, 1999; Crozier and Kennedy, 1991) have highlighted the importance of in-stream habitat and the relationships between

its three main components (holding, spawning and nursery habitat) on the productivity of the rivers. On this basis and using the data collected during habitat surveys, the management targets were improved and calculated according to three identified nursery habitat grades from one to three (the lower the number the better the quality of habitat) to which was associated an egg deposition target (Table 1.1).

*Table 1.1: Egg deposition targets for each grade of nursery habitat*

Grade 1	10 eggs.m <sup>-2</sup>
Grade 2	5 eggs.m <sup>-2</sup>
Grade 3	2.5 eggs.m <sup>-2</sup>

Data from the Loughs Agency hatchery indicates that the average fecundity of Foyle salmon is about 2500 eggs per female and that the sex ratio is 60:40 (female:male) (Loughs Agency, unpublished data) . Using this information and the total area of nursery above the Mourne counter, a target egg deposition of 9.7 millions eggs is obtained. This corresponds to a conservation limit of approximately 6500 salmon. Taking account of angling, poaching and natural predation, the previous spawning target is increased by 25% which gives a management target of 8000 adult salmon above the Mourne counter.

Since its introduction, this spawning target has always been achieved except in 2001 (only 6250 adults counted). However, there are some problems with this management regime; as it appears (Loughs Agency, 2003), that there is some annual variation in the timing of salmon returns. Some salmon from some rivers move into the lough at different times inside or outside of the fishing season, therefore there may be differential exploitation rates on different river stocks (Ensing and Crozier, 2008). The actual system uses the number of salmon moving upstream of the Mourne counter as a proxy of the whole population and thus misses these more subtle variations.

Between 1953 and 1977 several rivers of the catchment were stocked with eggs and fry in the Foyle catchment in order to improve the productivity of the population. The highest number of eggs planted in suitable gravel for egg development was 1 200 000 in 1956. About half of the eggs or fry planted every year came from salmon from the Foyle system, the other half came from hatcheries located on other Irish rivers. It is very difficult to measure how the eggs coming from Foyle salmon have affected the population and the number of returning adults but concerning eggs and fry coming from other rivers, a recent genetic report on the salmon population in the Foyle area (Booth, 2004), suggests that there



is no genetic evidence of these populations in the actual Foyle salmon. In other words, the eggs and fry stocked and originating from other rivers than the Foyle river did not manage to return as adults and spawn, or contribute to future generations.

## 1.4. Bayesian modelling framework

In this section I describe the basics of Bayesian theory in order to introduce the methodology used in chapters 2, 3 and 4. This description will be kept minimal as many textbooks describe extensively Bayesian theory (Berger, 1985; Bernardo and Smith, 1994) or methodology (Congdon, 2001; Lee, 1997), general Bayesian treatments (Carlin and Louis, 2000; Gelman *et al.*, 2004) or specific applications to ecology (Clark and Gelfand, 2006; Clark, 2007).

### 1.4.1 *Frequentist vs. Bayesian statistics*

- 1) Two formal frameworks exist to do statistical inference from observed data (i.e. frequentist and Bayesian framework).
- 2) The conceptual differences, advantages and drawbacks of each frameworks have been largely and extensively discussed (Berger, 1985).
- 3) In this study, I decided to use the Bayesian framework for practical reasons since this framework is more convenient when working on complex models such as the ones presented in the following chapters (Clark, 2007).

Conceptual aspects of Bayesian theory have been extensively reviewed (Bernardo and Smith, 1994; Box and Tiao, 1992; Gelman *et al.*, 1993). In the past the use of Bayesian analysis was discouraged because of the high level of numerical integration needed, however some recently developed computer intensive sampling methods have made this easier (Albert and Chib, 1996; Gilks *et al.*, 1993; Heath, 1997).

### 1.4.2 *Bayes' theorem*

Probability statements about a vector of unknown quantities (e.g. model parameters)  $\theta$ , given a vector of observed data  $y$ , require a model providing a joint probability distribution for  $\theta$  and  $y$ . This joint probability or density distribution  $p(\theta, y)$  is the product of two probability distributions which combine *a priori* knowledge about the parameters  $p(\theta)$

(also known as the prior distribution) and the sampling distribution (or data distribution)  $p(y|\theta)$ .

$$(1.1) p(\theta, y) = p(\theta) \cdot p(y|\theta)$$

The posterior distribution  $p(\theta|y)$  of the parameter  $\theta$  given the observation  $y$  is obtained by using Equation 1.1 :

$$(1.2) p(\theta|y) = \frac{p(\theta, y)}{p(y)} = \frac{p(\theta) \cdot p(y|\theta)}{p(y)}$$

Where

$$(1.3) p(y) = \int p(\theta) \cdot p(y|\theta) d\theta$$

$p(y)$  is a normalisation factor which is not dependent on  $\theta$  and with fixed  $y$  can be considered as constant. Therefore Equation (1.2) is often written in its unnormalized form:

$$(1.4) p(\theta|y) \propto p(\theta) \cdot p(y|\theta)$$

In some cases inference about an unknown observable  $\tilde{y}$  is required (e.g. missing values, predictions). The unknown observable  $\tilde{y}$  is easily estimated conditionally on the observed data  $y$ .

$$(1.5) p(\tilde{y}|y) = \int p(\tilde{y}|\theta) \cdot p(\theta|y) d\theta$$

These few equations summarise the technical core of Bayesian inference about unknown quantities of a given model conditionally on observed data.

### **1.4.3 Prior distributions**

Being able to choose prior distributions allows the incorporation of the current level of knowledge about any variable. Using non-informative prior distributions, allow inferences to be made only based on the information yielded into the data. Construction of reference non-informative prior distributions can be done formally (Kass and Wasserman, 1996; Gelman, 2004, 2006), but Bayesian inference also allows the incorporation of prior

knowledge (e.g. expert knowledge) on a given variable by using informative prior distributions (Hilborn and Lierman, 1998, Bernier *et al.*, 2000; Gelman *et al.*, 2003).

## 1.5. Hierarchical modelling and state-space models

### 1.5.1 Hierarchical modelling

Hierarchical Bayesian models (HBMs, Congdon, 2001; Gelman *et al.*, 2004) describe the heterogeneity across different spatial (e.g. different habitats) or temporal units (e.g. different years of a time-series). Formally this is done by supposing that the vector of parameters  $\theta$  is a random quantity sampled from a prior distribution  $p(\theta|\lambda)$  with  $\lambda$  is a vector of hyper parameters. For instance, if  $y_i$  is an observed abundance of juvenile salmon in a geographical unit  $i$ ,  $\theta_i$  would be the true abundance of juvenile salmon in geographical unit  $i$ . In this context,  $\lambda$  could be a parameter controlling spatial variation across geographical units. If  $\lambda$  is known, equation 1.2 becomes

$$(1.6) p(\theta|y, \lambda) = \frac{p(y, \theta|\lambda)}{p(y|\lambda)} = \frac{p(y|\theta) \cdot p(\theta|\lambda)}{p(y|\lambda)}$$

However in most cases  $\lambda$  will not be known and a hyperprior distribution  $p(\lambda)$  will be required.

$$(1.7) p(\theta, \lambda|y) = \frac{p(y|\theta) \cdot p(\theta|\lambda) \cdot p(\lambda)}{p(y)} = \frac{\int p(y|\theta) \cdot p(\theta|\lambda) \cdot p(\lambda) d\lambda}{\int p(y|\theta) \cdot p(\theta|\lambda) \cdot p(\lambda) d\theta d\lambda}$$

### 1.5.2 State space models

Bayesian state-space models are specific hierarchical models which are made of a dynamic (or process) component which is composed of unobserved variables and an observation component which is composed of observed variables and is a function of the dynamic component.

This can be summarized in two equations (Calder *et al.*, 2003; Carlin *et al.*, 1992). The first one called the process equation summarizes the links between the different states of the model.

$$(1.8) X_t = F(X_{t-1}, \theta_1, \varepsilon_t)$$

Where the function  $F$  accounts for all the equations describing the dynamics of the system studied (e.g. survival, density dependence, etc. for population dynamics) and reflects the dependence of the different hidden states at a given time on the hidden states at another time conditional on the transition parameters  $\theta_1$  and a stochastic component  $\varepsilon_t$ . The second equation is called the observation equation:

$$(1.9) y_t = G(X_t, \theta_2, \omega_t)$$

where the function  $G$  describes the link between the observed datasets  $y_t$  and the hidden states  $X_t$  conditional on the observation model parameters  $\theta_2$  and the stochastic component of the observation models  $\omega_t$ . The Bayesian statistical inference calculates the joint posterior probability density functions (pdf) of all the model parameters  $\theta = (\theta_1, \theta_2)$  and the hidden states series  $X$  conditionally on the observations series  $y$ .

$$(1.10) p(\theta, X|y) \propto p(\theta) \cdot p(X|\theta) \cdot p(y|X, \theta)$$

A basic state space model is described in Figure 1.4.

### **1.5.3 Bayesian inference for complex model in practice**

Markov chain Monte Carlo (MCMC) methods are today the most popular computing tools in Bayesian practice. This is due to their ability to enable inference for joint posterior distributions of very high dimension. This is done by reducing the high-dimensional problem by treating recursively a sequence of lower dimensional (often one dimensional) problems. MCMC methods do not provide a closed form of the posterior distribution (equation 1.2 or 1.7) but a sample of values from this distribution. If the sample is large enough, the histogram of the sampled values is a good approximation to this distribution. Other computation techniques such as sequential importance sampling (SIS) can be used. The basic SIS algorithm is the weighted bootstrap of Smith and Gelfand (1992): first a joint prior distribution on the parameters and initial states is defined. Based on this prior, a large number of initial parameters and state vectors are generated; each pair of parameter and state parameter vectors is called a “particle”. Each particle is then stochastically projected to the first time period using the state process distribution. The particle density

then provides an estimate of the predicted state distribution. The filtered state distribution is estimated by using the observation process distribution to calculate a likelihood weight and take a weighted resample from the particles. This process is then repeated for subsequent time periods, first using the state process distribution to project forward to the next time period and then “correcting” the resulting predicted state distribution using the weighted resample, with weights calculated according to the observation process. This distribution yields estimates of the filtered state and parameter density at each time point. The parameter density at the final time point is an estimate of posterior parameter density given all the data. This technique is not necessarily more efficient than MCMC (see comparison between MCMC and SIS in Newman *et al.*, 2009)

All the models presented in this study were implemented using WinBUGS. This software performs MCMC simulations using principally a generalised Gibbs sampling algorithm (Spiegelhalter *et al.*, 2003).

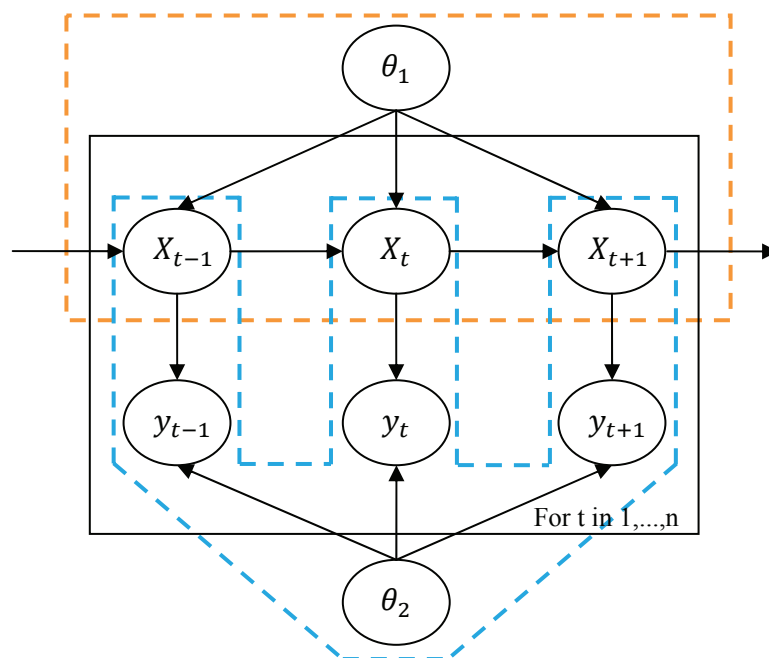


Figure 1.4: Graphical representation of a simple state-space model. The dashed orange frame represents the process model. The dashed blue frame represents the observation models.  $X_t$  is a vector of hidden states during year  $t$ . The transition from  $X_t$  to  $X_{t+1}$  is conditioned by the parameters  $\theta_1$  and forms the process equation.  $y_t$  is a vector of observations depending on one or several hidden states during year  $t$ . These observations are conditioned by  $\theta_2$ , the vector of parameters of the different observation models. The relation between  $X_t$  and  $y_t$  corresponds to the observation equation.

## **Chapter 2:**

# **Estimating 0+ juvenile production from 5 minutes electric fishing abundance indices**

## **2.1. General introduction**

Fish population research and management is usually based on a quantitative assessment of their abundance. In this the chapter, focus is brought on the abundance of juvenile salmon spending their first summer in the river (0+ juvenile salmon). In salmon populations, this stage is of primary interest since the transition from eggs to 0+ juveniles is a major bottleneck (Elliot, 2001; Milner et al., 2003). In addition the 0+ juvenile stage is the earliest and often the only development stage than can be used by managers prior to fisheries and independently from fisheries. The most widely used technique to obtain 0+ juvenile abundances at a site is a combination of electric fishing and a removal sampling technique (Bohlin et al., 1990).

In this chapter a hierarchical Bayesian calibration model (HBM) relating a timed sampling technique to 0+ salmon juvenile densities is proposed. HBM enables an improvement of single site estimates by "borrowing strength" between sites through a transfer of information from sites with informative data to data-poor sites. It also allows rescue estimates for sites with missing data and can make predictions for sites with no observed data. Using posterior distributions of the parameters estimated from this calibration exercise, another HBM model was designed to produce average 0+ juvenile densities for large geographical units ("geo units") based on local site 0+ juvenile densities estimated from the large number of 0+ juvenile index of abundance collected between 1998 and 2008 in the whole Foyle catchment by the Loughs Agency field crews. The average 0+ juvenile densities obtained from this model are then introduced into the full life-cycle state-space

model as pseudo-observations. Using total wetted area of the nursery habitat available in each geo unit, a 0+ juvenile production can be calculated.

## **2.2. Building a relationship between 0+ juvenile densities and 5 minutes electric fishing abundance indices**

This section (2.2) has been published as a scientific paper in *Fisheries Management and Ecology* (Dauphin et al., 2009). The WinBUGS code corresponding to this model can be found in Annex 1.

### **2.2.1 Introduction**

Animal population ecology studies often require population abundance estimates. A wide range of both sampling and statistical techniques have been developed to enable population size to be determined (Williams *et al.*, 2002; Royle and Dorazio, 2006). For stream dwelling salmonid fish populations, a two-stage sampling scheme is often used. A set of sites is first selected within a river network and then the fish are sampled within each site. A combination of electric fishing and a removal sampling technique is the most commonly used method for assessing fish population size at a site (Bohlin *et al.*, 1990). Statistical modelling approaches have been proposed and refined in order to improve estimates of population size from removal sampling data (Bohlin *et al.*, 1990; Mäntyniemi *et al.*, 2005). More recently, the joint treatment of multi-site data sets has been developed within a hierarchical Bayesian modelling (HBM) framework (Wyatt, 2002; Dorazio *et al.*, 2005; Rivot *et al.*, 2008). HBM enables an improvement of single site estimates by "borrowing strength" between sites through a transfer of information from sites with informative data to data-poor sites. It also allows the rescue of estimates for sites with missing data and can make predictions for sites with no observed data.

Removal sampling by electric fishing is time and manpower consuming, making it difficult to utilise on a large number of sites. Several authors have proposed less demanding methods in order to increase the number of sites covered with the same human resources input (Lobón-Cerviá and Utrilla, 1993; Winstone, 1993; Crozier and Kennedy, 1994; Kruse *et al.*, 1998; Prévost and Nihouarn 1999; Bateman *et al.*, 2005). These rapid assessment techniques also use electric fishing but are faster, as they only require a single timed sample for each site. They essentially provide relative abundance measures. To be

used for absolute population abundance estimation, they need to be first inter-calibrated with another method of population size estimation, such as successive removal sampling.

Usually this inter-calibration is done in two steps. First, point estimates of fish abundance are derived from the more classical and resource demanding method. Then, standard statistical techniques are applied to regress the (point estimate of) fish abundance against the index of abundance (IA) obtained by the rapid assessment technique (Lobón-Cerviá and Utrilla, 1993; Winstone, 1993; Crozier and Kennedy, 1994; Kruse *et al.*, 1998; Prévost and Nihouarn 1999; Bateman *et al.*, 2005). With the aim of estimating the absolute abundance from an IA, such an approach is not wholly satisfactory. The uncertainty around the estimation of the absolute abundance estimates is usually ignored. A better approach would be to include the uncertainty of the abundance estimates when utilising the IA alone in order to quantify the confidence that can be put in the abundance estimates.

As a solution to this problem and to improve the inter-calibration, a model using a HBM framework is utilised here to inter-calibrate a classical abundance estimation method (using successive removal) with a rapid assessment technique. The underlying principle of the model is that the data collected using each technique ultimately derives from the same unknown quantity of interest, i.e. the fish density. In addition the assumption of exchangeability between the study sites, after conditioning on covariates measured at the site level when suitable is made. Probability of capture (i.e. catchability) and fish density are allowed to vary between sites and they are assumed to be drawn from a common prior probability distribution governed by some unknown parameters and covariates if any. Besides the known advantages of the HBM (see above), this approach allows the estimate of the absolute abundance from abundance index data alone while accounting for all the sources of uncertainty. Here this approach is applied to a data set collected for young of the year juveniles of salmon on the River Faughan, Northern Ireland.

## **2.2.2 Material and methods**

### **2.2.2.1 Sampling and data collection procedures**

Twenty one sites were sampled using both successive removal and rapid abundance index methods during the summers of 2006 (11 sites between the 15<sup>th</sup> of July and the 10<sup>th</sup> of August) and 2007 (10 sites between the 20<sup>th</sup> and 31<sup>st</sup> of July) in the River Faughan, a sub-catchment of the Foyle, Northern Ireland. Sites were chosen in order to reflect the diversity



of the juvenile salmon production areas both in terms of geographical location and of nursery habitat types, using the Department of Agriculture for Northern Ireland (DANI) classification (Table 2.1) as a guide to habitat quality.

Table 2.1: Nursery habitat classification, following the Department of Agriculture for Northern Ireland (DANI) classification.

Habitat	DANI Grade	Characteristics
Good	Grade 1	- 0.5-8 % Gradient - Stable cobble / boulder substrate $\geq 70$ % bed cover - Providing adequate cover
	Grade 2	Marginally outside Grade 1 on one count only
Poor	Grade 3	Well outside Grade 1 on one or more counts
	Grade 4	Absent, deep, channelised, silty, etc.

Prior to sampling, stop nets were installed upstream and downstream to prevent fish movement into or out of the study site. Length and width of the site were measured (Table 2.2). As recommended by Bohlin *et al.* (1989) all sites had an area larger than 50 m<sup>2</sup>. Two types of electric fishing sampling were conducted on every site by two operatives. To provide an IA, a single timed electric fishing sample of 5 minutes was carried out using the protocol inspired of Crozier and Kennedy (1994): two operatives starting fishing continuously in an upstream direction for 5 minutes using a single anode backpack electrofishing apparatus within the area delimited by the stop nets but avoiding the 5 meters stretches adjacent to the upstream and the downstream nets. This was done to avoid any artificially denser areas caused by the movement of the disturbed fish. The time spent handling the fish caught was discounted so that the 5 minutes correspond to actual fishing only (Crisp and Crisp, 2006).

Thirty minutes after the five minutes electric fishing, three (occasionally four) successive removal samplings (passes) were conducted at the same site (Table 2.2). During these passes, the goal was to capture as many fish as possible while moving from the downstream end to the upstream of the site and therefore no time limit was imposed to complete one pass. The thirty minutes allow the juveniles to recover their positions in the stream (Crozier and Kennedy, 1994). The removal samples covered the sites from the downstream nets to the upstream nets and were conducted systematically to cover the whole area of the site with no time limit.

Both sampling methods were conducted with a single anode, backpack electric fishing apparatus (24V DC input, 240 V, 100W, 50Hz pulsed DC output). One operative fished with the anode and the other operative collected fish with a single hand net. The same two operatives conducted all the electric fishing for all the sites. Salmon and brown trout, *Salmo trutta* L. juveniles were identified according to standard morphological criteria (Maitland, 2004). Distinction between 0+ and 1+ juveniles was based on the fork length of the fish, as the distribution of this variable for a given site was bimodal with very little overlap. Only 0+ juvenile salmon are considered further in the analysis.

Table 2.2: Site characteristics: nursery habitat quality ( $H$ ), area of the site ( $S$ ) and average width of the site ( $W$ ), index of abundances ( $A$ ) and removal samples ( $C1$ ,  $C2$ ,  $C3$ ,  $C4$ ) of the 21 sites used in this study.

Site ( $i$ )	$H_i$	$S_i$ (m <sup>2</sup> )	$W_i$ (m)	$A_i$	Removal samples			
					$C_{i,1}$	$C_{i,2}$	$C_{i,3}$	$C_{i,4}$
1	Good	382	9.65	17	50	38	20	-
2	Poor	135	7.4	6	21	13	11	-
3	Good	133	8.6	10	18	6	7	9
4	Good	172	9.15	13	32	28	17	11
5	Good	134	5.35	28	104	54	55	36
6	Good	108	5.9	13	27	21	18	11
7	Poor	112	3.15	0	1	1	0	-
8	Good	120	5.65	2	5	2	1	2
9	Good	105	5.05	27	62	36	27	17
10	Poor	86	3.6	12	11	7	4	-
11	Poor	72	4.2	25	53	38	29	13
12	Poor	202	5.35	6	8	5	1	-
13	Poor	90	3.6	6	17	2	2	2
14	Poor	173	4.05	3	4	2	2	-
15	Poor	142	3.3	2	3	1	1	-
16	Poor	74	3.95	0	1	1	1	-
17	Poor	61	3.5	6	7	3	1	-
18	Good	82	3.8	32	39	30	31	19
19	Good	78	3.1	18	54	26	20	15
20	Good	93	3.05	16	48	24	6	-
21	Poor	67	3.4	23	52	22	8	-

### 2.2.2.2 Modelling

Henceforth unknown quantities which are constant across sites (i.e. model parameters) will be denoted by Greek lower case letters and observable quantities by capital Roman letters. Intermediate unknown quantities varying between sites and depending upon parameters (i.e. latent variables) will be denoted by lower case Roman letters. The notation  $a|b \sim f(b)$  means the random variable  $a$  (whether unknown or observable) conditional on  $b$ , is distributed according to the probability distribution function (pdf)  $f$ .

#### *a. Relating density to the IA*

For every site  $i = 1, 2, \dots, 21$ , a 5 minute IA ( $A_i$ ) was obtained first. Assuming that the fish were distributed randomly within the sampled site, count data could be modelled as resulting from a Poisson distribution.

$$(2.1) \quad A_i | l_i \sim \text{Poisson}(l_i)$$

The parameter  $l_i$  depends essentially on the fish density in the site sampled, the area swept during the five minutes of electric fishing and the probability of capture of a fish present in the area swept. The standardisation of the electric fishing protocol (see above) for the 5 minutes abundance index aimed at reducing the variability of the area swept and the probability of capture between sites. Ideally, it would be null and the  $l_i$  parameter would then be a deterministic (monotonously increasing) function of the density  $d_i$ . However, some variability in the area swept and the probability of capture is expected between the sites due to variation in the physical characteristics of the sites (depth, substrate, water velocity, etc.) or in the way the electric fishing protocol was actually applied. In addition, the 0+ parr are most probably not randomly distributed but tend to be clustered in favourable micro-habitats (Baglinière and Arribé-Moutounet, 1985). All these phenomena are potential sources of variability which lead to the overdispersion of the abundance index relative to a Poisson distribution. Therefore we modelled the abundance index according to a Negative Binomial distribution, i.e. the overdispersed alternative to the Poisson distribution:

$$(2.2) \quad A_i | a_i, \varphi \sim \text{Negative Binomial}(a_i, \varphi)$$

$a_i$  and  $\varphi$  are the shape and inverse scale parameters, respectively. The mean of this distribution is  $l_i = a_i / \varphi$ . It is deterministically linked to the density  $d_i$ :

$$(2.3) \quad l_i = \kappa \cdot d_i^\eta$$

$\kappa$  is the factor of proportionality between the IA and the density  $d_i$ ;  $\eta$  is a power coefficient applied to the density  $d_i$  to take into account the possibility of a non linear relationship between the 5 minute IA and the density. This possibility is introduced because it is expected the operatives fail to capture a proportion of the fish effected by the electric field and this proportion could increase with fish density. The parsimonious hypothesis of a constant scale  $\varphi$  over the sites leads to a variance of  $A_i | \kappa, d_i$  proportional to its mean  $l_i$ .

### b. Relating density to multiple removal samples

After removing the fish from the initial 5 minute sample, the number of fish remaining was:

$$(2.4) \quad n_{i,1} = n_i^{tot} - I_i$$

Where  $n_i^{tot}$  is the number of fish present in site  $i$  before any electric fishing operation started. The number of fish caught during the first removal sample  $C_{i,1}$  is assumed to follow a binomial distribution.

$$(2.5a) \quad C_{i,1} | n_{i,1}, p_{i,1} \sim \text{Binomial}(n_{i,1}, p_{i,1})$$

where  $p_{i,j}$  is the capture probability at site  $i$  for the  $j^{\text{th}}$  pass . The number of fish remaining in the site after the first removal is:

$$(2.6a) \quad n_{i,2} = n_{i,1} - C_{i,1}$$

Catch and number of fish remaining for the following removals are derived in the same way.

$$(2.5b) \quad C_{i,2} | n_{i,2}, p_{i,2} \sim \text{Binomial}(n_{i,2}, p_{i,2})$$

$$(2.5c) \quad C_{i,3} | n_{i,3}, p_{i,3} \sim \text{Binomial}(n_{i,3}, p_{i,3})$$

$$(2.5d) \quad C_{i,4} | n_{i,4}, p_{i,4} \sim \text{Binomial}(n_{i,4}, p_{i,4})$$

$$(2.6b) \quad n_{i,3} = n_{i,2} - C_{i,2}$$

$$(2.6c) \quad n_{i,4} = n_{i,3} - C_{i,3}$$

Several studies (e.g. Bohlin and Cowx, 1990; Riley *et al.*, 1993; Peterson *et al.*, 2004; Rosenberger and Dunham, 2005) have shown that the probability of capture tends to systematically decrease over successive passes. This feature was incorporated in the model by assuming that, in the logit scale, the probability of capture decreased by an unknown amount  $\varepsilon$  between two consecutive passes:

$$(2.7) \quad \text{Logit}(p_{i,j}) = \text{Logit}(p_{i,j-1}) - \varepsilon \quad j = 2, \dots, 4 \text{ and } \varepsilon > 0$$

The number of fish  $n_i^{\text{tot}}$  present at site  $i$  before any electric fishing operation is dependent on the density. It is assumed to issue from a Poisson distribution with parameter  $m_i$ .

$$(2.8) \quad n_i^{\text{tot}} | m_i \sim \text{Poisson}(m_i)$$

The parameter  $m_i$  is in turn calculated from the fish density  $d_i$  and the area of the site  $S_i$ :

$$(2.9) \quad m_i = d_i \cdot S_i$$

*c. Hierarchical structure on the probability of capture for the removal sampling  $p_{i,1}$ , and the fish density  $d_i$*

The probability of capture  $p_{i,1}$  can vary with the width  $W_i$  of the river at site  $i$  (Kennedy and Strange 1981). Conditionally on  $W_i$ , the sampling sites are assumed to be exchangeable with regard to the probability of capture, i.e. the  $p_{i,1}$  are potentially different but apart from  $W_i$  we have no clue about the causes of their variation. They are thus modelled as drawn from a common non informative probability distribution which parameters depend on  $W_i$ .

$$(2.10) \quad \text{Logit}(p_{i,1}) | \alpha, \beta, W_i \sim \text{Normal}(\mu_i, \sigma)$$

$$(2.11) \quad \mu_i = \alpha + \beta \cdot W_i$$

Density may depend on the nursery habitat quality for young of the year salmon. The quality of nursery habitat was assessed following the DANI classification. However due to the low numbers of sites, DANI category 1 (the best quality) and 2 and 3 and 4 (the poorest quality) were pooled. The new categories correspond to ‘good’ nursery habitat (DANI 1 & 2) ( $H_i = 1$ ) and ‘poor’ nursery habitat (DANI 3 & 4) ( $H_i = 2$ ). Conditionally on the habitat

category  $H_i$ , the sites are assumed to be exchangeable with regard to the fish density.  $d_i$  is assumed to follow a Gamma distribution.

$$(2.12) \quad d_i | b_i, \psi \sim \text{Gamma}(b_i, \psi)$$

$$(2.13) \quad b_i = \gamma \cdot \rho^{(H_i-1)}$$

The mean density in the habitat category 1 is  $\delta = \gamma/\psi$ . The mean fish density in the habitat category 2 is  $\rho \times \delta$ . The scale parameter  $\psi$  is assumed to be constant across sites.

The structure of conditional dependency of the relations (2.1-2.13) can be graphically summarised in a Directed Acyclic Graph (DAG) (Figure 2.1).

### 2.2.2.1 Prior distributions

In order to obtain posterior inferences primarily reflecting the information brought by the data, little-informative and independent prior distributions were assigned to the model parameters. The classical choice for scale parameters of an inverse-Gamma distribution with small values of the shape and inverse scale was adopted here. A *Gamma*(0.01,0.01) prior was assigned to  $1/\kappa$ ,  $1/\eta$ ,  $1/\rho$ ,  $1/\sigma^2$ ,  $\phi$ , and  $\psi$ . A ‘flat’ Normal prior distribution with 0 mean and 1000 variance was attributed to  $\alpha$ ,  $\beta$  and  $\varepsilon$ , but restricting this density to positive values in the last case. A *Gamma*(1,0.01) distribution, used as a proper distribution approximating a uniform distribution, was assigned to  $\delta$ .

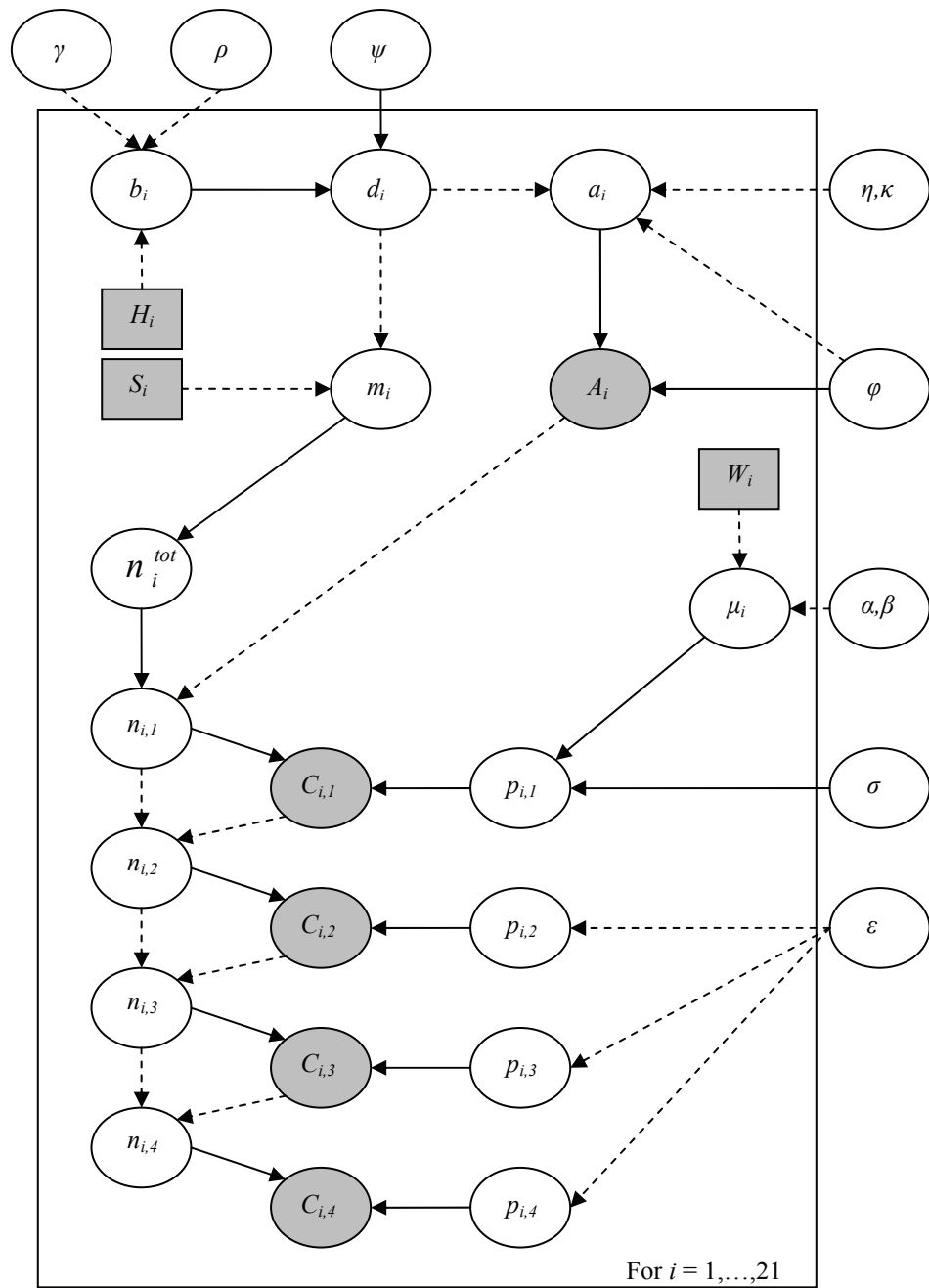


Figure 2.1: Directed Acyclic Graph (DAG) of the model used to estimate densities of the sites studied. Ellipses represent random variables. Squares represent fixed quantities, covariates in our case. All observed quantities are greyed. Arrows represent the parent-child dependencies between the different nodes: single arrows represent probabilistic relationship between the parent(s) and child nodes, dashed arrows indicate deterministic relationship. The frame represents a repetition of structure over sites. Nodes outside the frame are unknown parameters constant across sites.

### 2.2.2.2 Model checking

The model was checked for the adequacy of its fit to the data and its plausibility for its main purpose, i.e. evaluating fish densities based on either abundance indices or removal

sampling. The posterior predictive data replication technique proposed by Gelman *et al.* (2004) was used first to derive the posterior predictive distribution of the observables, for the same sites for which observations are available. It was then used to compare model derived posterior predictions with empirical observations. Under the premise that the model adequately represents the process which has given rise to the observed data, the observed data should be consistent under their posterior predictive distribution.  $Y_i$  being an observable variable at the sampling unit  $i$ , with  $Yrep_i$  its replicate, i.e. data that could have been observed assuming the model is adequate. The posterior predictive distribution of  $Yrep_i$  is:

$$(2.14) p(Yrep_i|Y, X) = \int p(Yrep_i|\theta) \cdot p(\theta|Y, X) \cdot d\theta$$

where  $\theta$  is the set of parameters ( $\alpha, \beta, \varepsilon, \gamma, \kappa, \eta, \rho, \sigma, \varphi, \psi$ ),  $Y$  is the set of observed data ( $A, C1, C2, C3, C4$ ),  $X$  is the set of covariates ( $S, W, H$ ) and  $p(Yrep|\theta)$  is the probability model previously presented (eq. 2.1 to 2.13). To compare observed and replicated data,  $DY_i = Y_i - Yrep_i$  was computed. Under the model assumptions, the expectation of the distribution of the  $DY_i$  is by definition 0. Because the fish density is the variable of main interest in the model, patterns of distribution of  $DY_i$  vs fish density  $d_i$  were examined. Following the "binned residuals" approach proposed by Gelman *et al.* (2004, p.170) for discrete data,  $DY_i$  was averaged for the sites  $i$  in three classes of fish density. The bounds of the three classes of fish densities  $d$  (class 1:  $0 < d < 0.4$ ; class 2:  $0.4 < d < 1.4$ ; class 3:  $d > 1.4$ ,  $d$  being expressed in fish.m<sup>-2</sup>) were chosen in order to have roughly balanced numbers of sites per class. This was used to check for systematic discrepancy between the model and the empirical data as a function of fish density. The distributions of the averaged  $DY_i$  are easier to interpret than the individual distribution of their  $DY_i$  component. Indeed the  $DY_i$  distributions are discrete and often not symmetric. Averaging has the effect of forcing symmetry of the distributions around their 0 expectation. This technique was applied to the observables  $A, C1, C2$  and  $C3$  (the fourth removal was conducted at less than half of the sites and thus was not considered further).

In order to assess the plausibility of the model in its main objective, estimating fish density by either method (removal sampling or single timed sampling), the consistency of the two methods in the density estimates they provide was evaluated. For every site  $i$ , the 5 minute rapid assessment index and population removal estimations are considered independently



as if they were two distinct sites but with exactly the same characteristics (*i.e.* fish population, physical habitat features, etc.). Densities are then estimated for these two fake sites with the rest of the dataset remaining unchanged. The new dataset is then composed of  $n+1$  sites:  $n-1$  sites have data from both methods (*i.e.* 5 minute rapid assessment index and population removal estimations) and two sites have data from only one method (either 5 minutes rapid assessment index or successive removal catches). Estimated densities of the two fake sites ( $d.A_i$ ,  $d.removal_i$ ) with data from only one method were compared (see next paragraph for an explanation of the method for estimating density based on one type of data only). The probability that the difference of the two estimates,  $Dd_i = d.A_i - d.removal_i$ , is higher than zero,  $P(Dd_i > 0 | X, Y)$  was calculated. This technique was applied successively to the 21 sites. The empirical distribution of these probabilities was compared to a reference uniform distribution on the  $[0, 1]$  interval through a quantile-quantile (q-q) plot (Figure 2.4).

### 2.2.2.3 Estimation of juvenile density from abundance indices alone

The fish density at any site where only the 5 minute rapid assessment index is collected can be estimated. This is achieved by extending the current data set with the additional IA observed data and considering the corresponding removal catch data that are missing. Relying on the standard assumptions that the missing data are "missing at random" (MAR), they can be considered as any other unknown in the model and therefore their posterior distribution can be computed by standard Markov chain Monte Carlo (MCMC) sampling technique. From a sample drawn from the joint posterior distribution of all the unknowns, *i.e.* model parameters, latent variables and missing data, it is straightforward to look marginally at the posterior distribution of the fish density for sites with IA observations only. This integrates the joint posterior distribution of all the unknowns over the parameters, the latent variables except the fish densities of interest, and the missing data. It is important to note that for this approach to be founded, the MAR condition must be verified. Assuming that both the sites with both types of data and the sites with IA observations only, are picked at random (conditionally on the habitat category, the river width and the site area covariates) within a common set of sites this ensures that the MAR condition is verified. Simpler assumptions than the latter can also meet the MAR condition (but see Gelman *et al.* (2004) for more precision about the Bayesian treatment of missing data and Rivot *et al.* (Appendix A, 2008) for a discussion in the case of electric fishing

data in which it is shown that the data missing process is ignorable when collecting electric fishing data).

For illustration, densities of 10 fake sites corresponding to 5 fixed abundance indices levels (5, 15, 25, 35, 45) across the two habitat categories were estimated. Densities of the fake sites with good habitat and densities of the fake sites with poor habitat were then compared.

#### 2.2.2.4 Posterior computations

For every analysis presented, the joint distribution of all the unknowns (i.e. parameters, latent variables, observables in the case of missing data or for data replication) conditionally on all the observed data was approximated using MCMC sampling (Gelman *et al.*, 2004). All computations were carried out with the OpenBUGS<sup>®</sup> software (version 3.0.3; Thomas *et al.*, 2006; Spiegelhalter *et al.*, 2003) and the Lattice and Coda packages of R (version 2.7.0, [www.r-project.com](http://www.r-project.com)). Gelman-Rubin (Brooks and Gelman, 1998) diagnostics as implemented by OpenBUGS<sup>®</sup> was used to test the convergence of the MCMC sampling on the model parameters. Three chains with contrasting starting points were used. The Gelman-Rubin statistic indicated good mixing of the MCMC chains was obtained after  $10^6$  iterations. An additional sample of 10 000 values ( $10^6$  iterations, but retaining 1 iteration every 100, thinning was chosen based on the autocorrelation of the parameters' chains) from a single chain was then used to approximate the joint posterior distribution of all the unknowns.

### 2.2.3 Results

#### 2.2.3.1 Posterior estimations of model unknowns

0+ salmon juvenile density varies widely across sites: estimates (posterior means of the  $d_i$ ) range from 0.043 to 3.67 0+ salmon.m<sup>-2</sup> (Figure 2.2). The uncertainty around estimates (as shown by the 90% posterior credibility intervals) tends to increase with the density. However, relative to the estimated density, the uncertainty tends to be reduced: the posterior CV's of the  $d_i$ 's shows a decreasing trend from 0.59 at 0.069 fish.m<sup>-2</sup> to 0.21 at 2.31 fish.m<sup>-2</sup>. The posterior probability that the habitat quality influences the mean density across sites, i.e.  $P(\rho < 1 | X, Y)$ , is greater than 95%. On average, poor habitat sites have

their density almost reduced by half, relative to good habitat sites ( $\rho$  posterior mean is 0.53; Table 2.3).

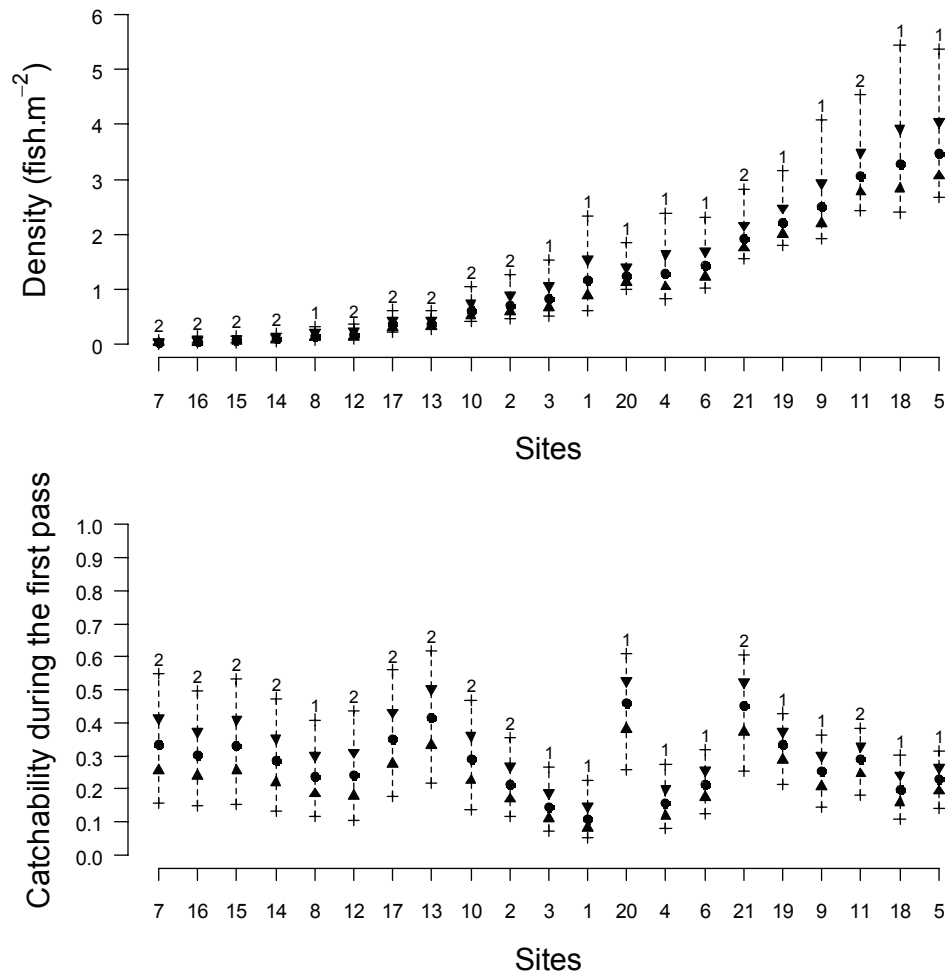


Figure 2.2: Summary of the posterior distributions of the catchability at the first pass ( $p_{i,1}$ ) and the 0+ salmon density ( $d_i$ ) for the 21 sites studied. Median ( $\bullet$ ), 25% and 75% percentiles ( $\blacktriangle$  and  $\blacktriangledown$ ), and 5% and 95% percentiles (+). Numbers above the 95 percentiles correspond to the habitat grade of the site (1: good, 2: poor).

The  $\epsilon$  parameter accounting for the decrease in catchability over successive passes shows *a posteriori* a clear mode at 0.17 and low probabilities in the neighbourhood of 0 (Table 2.3). The catchability during the removal sampling experiments (Figure 2.2) varies widely across sites: estimates (posterior mean of  $p_{i,j}$ ) range from 0.120 to 0.450 (grand mean = 0.250) for the first pass, 0.105 to 0.410 for the second, and 0.091 to 0.373 for the third. It decreases with increasing width of the sampled sites:  $P(\beta < 0 \mid X, Y)$  is above 97.5% (Table 2.3). The catchability estimates show no systematic pattern of association with the fish density (Figure 2.2), but their uncertainty tends to decrease with density. Indeed more fish

are caught with increasing density and in binomial experiments the posterior precision of probability estimates depends primarily on the number of draws.

Table 2.3: Summary statistics of the marginal posterior distributions of the model parameters.

	mean	sd	2.5%	25%	median	75%	97.5%
$\alpha$	-1.03	0.30	-1.69	-1.19	-0.99	-0.82	-0.54
$\beta$	-0.21	0.08	-0.37	-0.26	-0.20	-0.15	-0.05
$\delta$	2.61	0.84	1.47	2.04	2.46	2.99	4.69
$\varepsilon$	0.17	0.07	0.03	0.12	0.17	0.22	0.31
$\varphi$	37.70	45.76	1.66	7.69	19.28	48.16	169.80
$\gamma$	1.35	0.42	0.68	1.05	1.30	1.58	2.30
$\kappa$	12.78	1.64	9.30	11.82	12.88	13.90	15.66
$\eta$	0.68	0.07	0.55	0.63	0.68	0.72	0.82
$\psi$	0.56	0.22	0.21	0.40	0.53	0.68	1.08
$\rho$	0.53	0.16	0.28	0.41	0.51	0.62	0.91
$\sigma^2$	0.23	0.19	0.01	0.10	0.18	0.30	0.71

There is a positive relationship between the IAs and the 0+ salmon densities (Figure 2.3). The  $\kappa$  parameter is fairly precisely estimated ( $CV = 12.8\%$ ; Table 2.3). The abundance index tends to increase slower than proportionally with the density:  $P(\eta < 1 \mid X, Y)$  is greater than 97.5% (Table 2.3). The inverse scale parameter  $\varphi$  is on average very high (Table 2.3) but it is poorly estimated and low values cannot be excluded *a posteriori*. The overdispersion of the IA distribution relative to a simple Poisson distribution would be rather weak but it cannot be ruled out that it is significant.

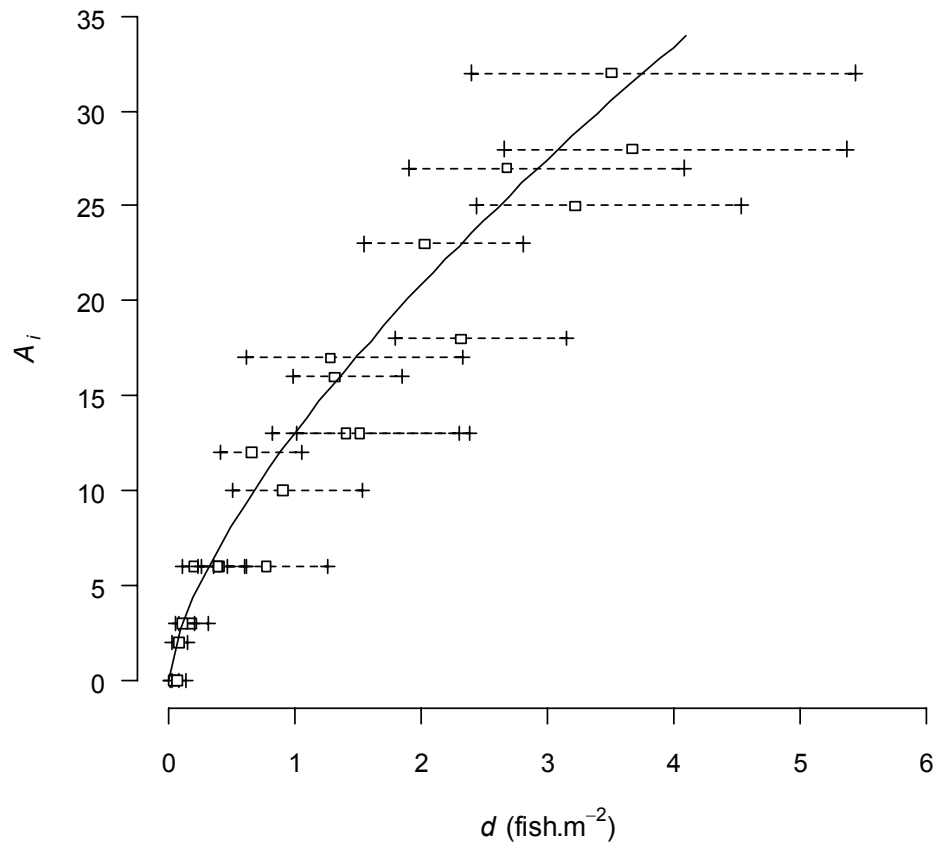


Figure 2.3: 5 minutes index of abundance vs posterior distribution summary of 0+ salmon density ( $d_i$ ) (mean: □, 5% and 95% percentile: +). The curve (plain line) represents the relationship between the density and the mean abundance index for the posterior median of the parameters  $\kappa$  and  $\eta$  (see text).

### 2.2.3.2 Posterior model checking

The comparison of replicated data with observations did not reveal any significant discrepancy (Table 2.4). The density estimates appear consistent whatever the electric fishing method used. The empirical distribution of the probability of the difference of the two estimates to be greater than zero ( $P(D.d > 0 \mid X, Y)$ ) is close to a [0,1] uniform probability distribution (Figure 2.4). There is however a slight tendency for the  $P(D.d > 0 \mid X, Y)$  values to be more concentrated around 0.5 than the reference uniform distribution. This may be due to the fact that the comparison is made for two density estimates which tend to be more uncertain than the others as they are based only on part of the data (IA or removal catch) used for the others (IA and removal catch).

Table 2.4: Summary of the model posterior check based on data replication. Mean differences ( $DY$ ,  $Y$  being an observable, see text) between observed and replicated data and associated probabilities are presented for 3 density classes (class 1:  $0 < d_i < 0.4$ ; class 2:  $0.4 < d_i < 1.4$ ; class 3:  $d_i > 1.4$ ).

	class 1		class 2		class 3	
	mean $DY$	$P(DY < 0)$	mean $DY$	$P(DY < 0)$	mean $DY$	$P(DY < 0)$
5 min IA	-0.527	0.701	-0.409	0.740	-0.849	0.600
C1	0.633	0.335	1.153	0.243	0.065	0.312
C2	-0.239	0.865	0.071	0.695	-2.778	0.500
C3	-0.437	0.451	-0.994	0.864	1.674	0.768

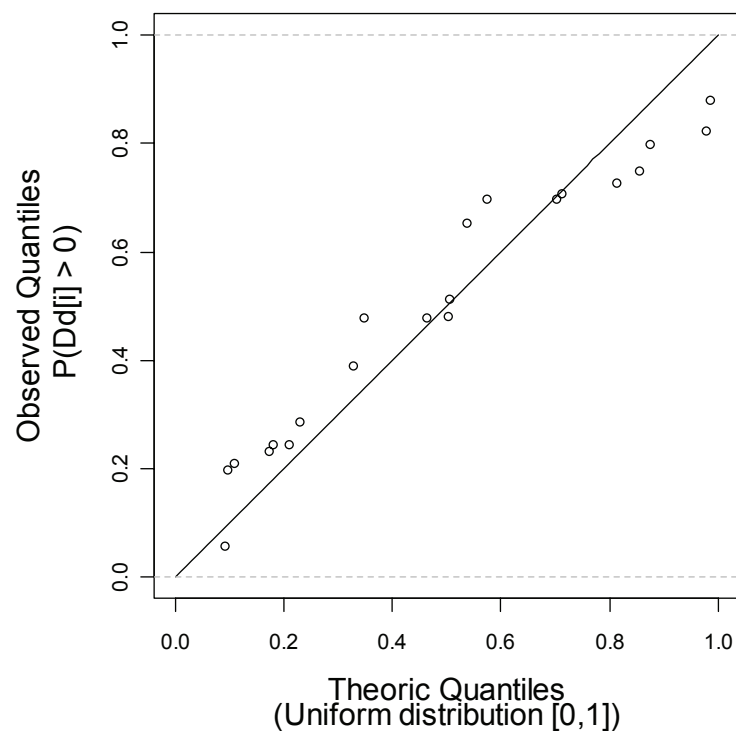


Figure 2.4: Q-q plot of the posterior probability  $P(D.d > 0 | X, Y)$ .  $D.d$  is the difference, calculated for every site, between the two density estimates derived from successive removal data alone and the abundance index data alone (see text). The empirical cumulative distribution of  $P(D.d > 0 | X, Y)$  (dots) is plotted against a reference uniform distribution on the  $[0, 1]$  interval (plain line).

### 2.2.3.3 Estimation of juvenile density from abundance indices alone

Density estimates based on IA data are notably less precise than those which assimilate the additional information brought by removal sampling data (Figure 2.5). The uncertainty, as measured by the width of the 90% *a posteriori* probability interval, increases with the IA value. This partly reflects our initial modelling hypothesis that the IA variability increases

with the density. However, the posterior CV of the densities tends to decrease with the IA value (from 0.64 at 5 fish.5min<sup>-1</sup> to 0.36 at 45 fish.5min<sup>-1</sup>). Little difference was found in the density estimates when comparing good and poor habitat for the same IA value (Figure 2.5). This reflects the overwhelming influence of the IA vs the habitat category in estimating the density. A difference of 10 in the IA almost ensures that the underlying densities are different, although the degree of certainty decreases with increasing IA. The posterior probability that the densities are different between sites of good habitat with an IA of 5 and an IA of 15 is 98% whereas it is 85% when comparing sites with IA of 35 and 45. The same pattern is observed for poor habitat.

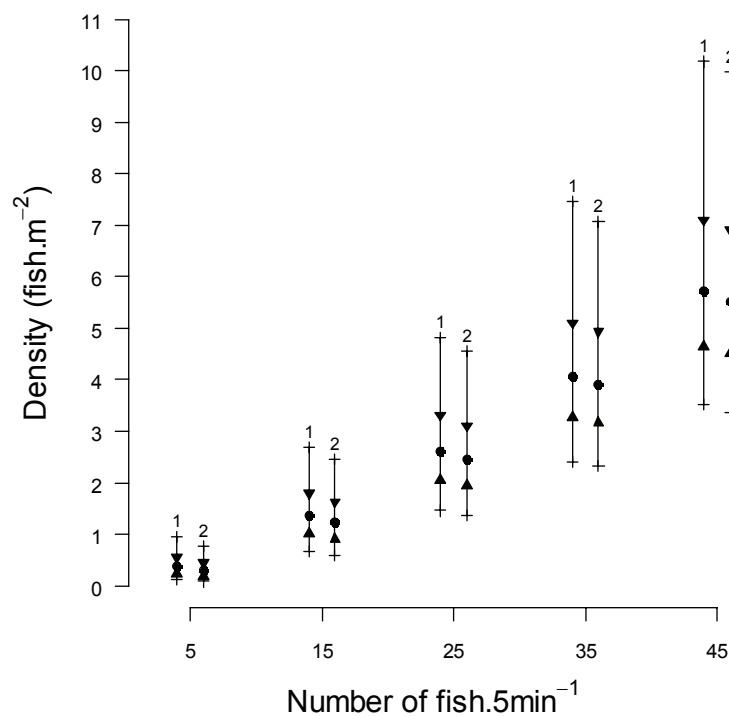


Figure 2.5: Posterior estimates of 0+ juvenile salmon density from index of abundance (IA<sub>i</sub>) data alone. Median (●), 25% and 75% percentiles (▲ and ▼), and 5% and 95% percentile (+). Numbers above the 95 percentiles correspond to the habitat grade (1: good, 2: poor).

## 2.2.4 Discussion

The model and the data presented show a clear and positive relationship between an abundance index collected by a single timed electric fishing technique and the underlying 0+ salmon juvenile density. The posterior checks revealed no major discrepancy between the model assumptions and the observed data, while showing consistency in the density appraisal provided by the timed electric method and the classical successive removal

method. All the effects introduced in the model presented in this paper (*i.e.* density vs habitat, catchability vs river width, power function in the  $A$  vs density link) were justified in *a posteriori* model assessment. The posterior probability that the associated parameters ( $\rho$ ,  $\beta$ ,  $\eta$ ) were greater or lower than the reference value corresponding to an absence of effect were all very low.

Several publications have already addressed the issue of inter-calibrating single timed electric fishing sampling with the classical multiple pass removal method (Lobón-Cerviá and Utrilla, 1993; Winstone 1993; Crozier and Kennedy, 1994; Kruse *et al.*, 1998; Prévost and Nihouarn, 1999; Bateman *et al.*, 2005). In the original approach adopted here the removal catches and the IA are assumed to be both random variables and both dependant on a common unknown density. Other approaches generally use regression techniques of the density against an IA, where the density had been estimated previously from multiple removal catch (or mark-recapture) data. For density estimation based on the IA alone, such approaches are not satisfactory because the unknown density is replaced by a point estimate. A potentially significant part of the uncertainty inherent to the density estimation is thus ignored, resulting in over-precise estimates.

The posterior inferences made in this model rely primarily on the removal catch data. Only these data allow derivation of absolute estimates of the fish density. The absolute density estimates in turn allows the estimate of the proportionality parameter  $\kappa$  and the power coefficient  $\eta$  of the relationship between fish density and the (relative) IA. The posterior knowledge gained on  $\kappa$  and  $\eta$  is key for estimating the (absolute) fish density when only IA data are available. Here the parameter  $\kappa$  is precisely estimated mostly because of significant variation in the 0+ salmon density over the set of 21 sites (Figure 2.2).

The Bayesian paradigm for statistical inference and its implementation by means of MCMC sampling techniques makes the estimation of density from IA observation alone, straightforward, while ensuring the major sources of uncertainty are accounted for. For this approach to be valid, the MAR condition must be verified for the "missing" removal catch data. Although it can be assumed that this is true in many cases (Gelman *et al.*, 2004; Rivot *et al.*, 2008), the verification of the MAR condition must be scrutinised on a case specific basis.



Here, the density estimates obtained from IA data alone are fairly imprecise. This reflects both the variability of the IA observations for a given density and the uncertainty about the density estimates for the sites where the two types of data were collected. The hierarchical setting of our model helps to improve the precision of the density estimates by "borrowing strength" between sites (Rivot *et al.* 2008). Despite this transfer of information between sites, the density estimates remained relatively imprecise in many instances. The precision of these estimates depends mainly on the removal catch data. Indeed, the comparison of estimates between both electric fishing techniques (i.e. single timed and successive removal techniques), undertaken as a posterior check of our model, shows that the estimates from removal catch data are significantly more precise than those derived from the IA data. The main cause for the poor precision of the density estimates is a rather low catchability, always below 0.5 (mean of the posterior pdfs). In addition, it decreases over successive passes. A low catchability means that a smaller proportion of the total population on the site is captured. Therefore there is less certainty about the actual number of fish on the site. The low catchability might be explained by the utilisation of a single dip net during the successive removal samples, leading the operatives to miss fish, and the small size of the 0+ salmon at the time of sampling (average size is 52.65 mm) (Peterson *et al.* 2004). For further inter-calibration work, the removal catch data should be collected using a protocol aimed at maximizing fish catchability. This can be done by increasing the number of people catching the juveniles and by using different types of nets. Whatever the improvement that could be obtained in terms of precision, estimates of 0+ salmon density from IA data shall remain more uncertain than those derived from well conducted experiments of successive removals. Despite this, IAs allow the estimate of 0+ salmon density and the differentiation of contrasted levels of fish density, while being much less resource intensive than successive removal sampling.

When resources for fish population surveys are limited or when a broad spatial coverage is of primary importance, trading off a loss of local precision against increasing the number of sampling sites is inevitable. This is typically the case when surveys are carried out for providing management advice on large river systems. Covering a large number of sites with a single timed electric fishing technique is an attractive option, but it has to be assessed on a case specific basis given the sampling design used and the precision of the estimates derived from the IA. The Bayesian modelling approach presented here is thus a valuable tool which has the dual merit of allowing estimation of density from single pass electric fishing data alone while fairly assessing the associated uncertainty.

## 2.3. Estimating average 0+ juvenile densities for several geographical unit

The WinBUGS code corresponding to this model can be found in Annex 1.

### 2.3.1 Data available

5 minutes electric fishing in the Foyle catchment started in 1998 for the Faughan, the Finn, the Roe and the Foyle unit. In 1999, sites from the Mourne unit were incorporated. Since then more sites in all geo units were sampled and added to the existing list of sites. Over the years, there was some confusion in the attribution of grade for poor nursery habitat (grade 3 and 4 following the DANI classification). Therefore I chose to keep only sites for which a reliable assessment of the nursery habitat quality was available. Thus depending of the year, between 6 and 216 sites were available to estimate average 0+ salmon densities (Table 2.5).

Table 2.5: Number of grade 1 (grade 1+ grade 2 according to DANI's classification) sites electrofished every year in every geo units ( $N_{t,i}$ ).

	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008
Faughan	6	21	13	16	18	17	24	26	24	27	28
Finn	28	46	18	23	7	24	29	14	26	48	49
Mourne	–	27	32	106	137	148	149	144	155	216	131
Roe	18	53	31	37	30	36	42	43	57	59	54
Foyle	10	13	18	27	23	25	29	29	35	34	38

### 2.3.2 Modelling

#### 2.3.2.1 Adding information from the calibration model

To estimate the average 0+ salmon densities per year we need to use some parameters from the calibration however we do not want these parameters to be affected by the observations ( $A_{t,i,n}$ , the index of abundance at the  $n^{\text{th}}$  site, in the  $i^{\text{th}}$  geo unit and, in the  $t^{\text{th}}$  year) used to estimate the average densities per geo unit per year. Therefore, the distributions of these

parameters are “cut” from the model so they are not updated by the new observations. These parameters are identified by the superscript “cut”

### 2.3.2.2 Model description

The model estimating the average densities of 0+ per year and per geo unit borrow a great part of the calibration model’s structure. Three indices are used:  $t$  corresponds to the year (1998 to 2008),  $i$  corresponds to the geo unit (Faughan, Finn, Mourne, Roe, and Foyle) and,  $n$  correspond to the site number. Each year, in each geo unit,  $N_{t,i}$  sites are electrofished for 5 minutes providing an index of abundance  $A_{t,i,n}$  for each site. The index of abundance  $A_{t,i,n}$  are modelled as resulting from a Negative Binomial distribution (see section 2.2.2.2 above for a more detailed description).

$$(2.14) \quad A_{t,i,n} | a_{t,i,n}, \varphi^{cut} \sim \text{Negative Binomial}(a_{t,i,n}, \varphi^{cut})$$

The index of abundance can equivalently be modelled as resulting from a Poisson distribution for which its parameter  $l_{t,i,n}$  follows a Gamma distribution:

$$(2.15) \quad A_{t,i,n} | l_{t,i,n} \sim \text{Poisson}(l_{t,i,n})$$

$$(2.16) \quad l_{t,i,n} \sim \text{Gamma}(a_{t,i,n}, \varphi^{cut})$$

The mean of the  $A_{t,i,n}$  distribution is

$$(2.17) \quad l_{t,i,n} = a_{t,i,n} / \varphi^{cut}$$

Where  $l_{t,i,n}$  is deterministically linked to the site’s 0+ density

$$(2.18) \quad l_{t,i,n} = \kappa^{cut} \cdot (d_{t,i,n})^{\eta^{cut}}$$

Where  $\kappa^{cut}$  is the proportion factor between the index of abundance  $A_{t,i,n}$  and the density  $d_{t,i,n}$  and  $\eta^{cut}$  is the power coefficient applied to the density to account for possible non-linear relationship between  $A_{t,i,n}$  and  $d_{t,i,n}$  respectively. Both parameters are extracted from the calibration model.

The site density  $d_{t,i,n}$  is assumed to follow a Gamma distribution

$$(2.19) \quad d_{t,i,n} \mid \alpha_{t,i}^d, \beta_{t,i}^d \sim \text{Gamma}(\alpha_{t,i}^d, \beta_{t,i}^d)$$

Where

$$(2.20a) \quad \alpha_{t,i}^d = d_{t,i}^\mu \cdot \beta_{t,i}^d$$

And

$$(2.20b) \quad \beta_{t,i}^d = \frac{d_{t,i}^\mu}{(CV_i^d \times d_{t,i}^\mu)^2}$$

Usually, for a Gamma distribution  $\theta \sim \Gamma(\alpha, \beta)$ , the parameters can be expressed as:  $\alpha = \text{var}(\theta) \cdot \beta^2$  and  $\beta = \frac{\alpha}{E(\theta)}$ . In equations 2.20a and b, the parameters  $\alpha_{t,i}^d$  and  $\beta_{t,i}^d$  were re-parameterised in function of  $d_{t,i}^\mu$  and  $CV_i^d$ .  $d_{t,i}^\mu$  is the average density of geo unit  $i$  during year  $t$ . All the  $d_{t,i}^\mu$  were assumed to be independent between geo units as there was no systematic correlation in the average index of abundance per geo unit ( $\text{mean}(A_{t,i,n})$ ); The correlation between the different series of  $\text{mean}(A_{t,i,n})$  varied between 0.109 and 0.774. The  $d_{t,i}^\mu$  were also assumed to be independent between years as the autocorrelation of the series of means ( $A_{t,i,n}$ ) for each geo unit was in most case weak (Faughan: 0.300, Finn: 0.191, Mourne: 0.472, Roe: 0.225, and Foyle: 0.623) (Figure 2.6).

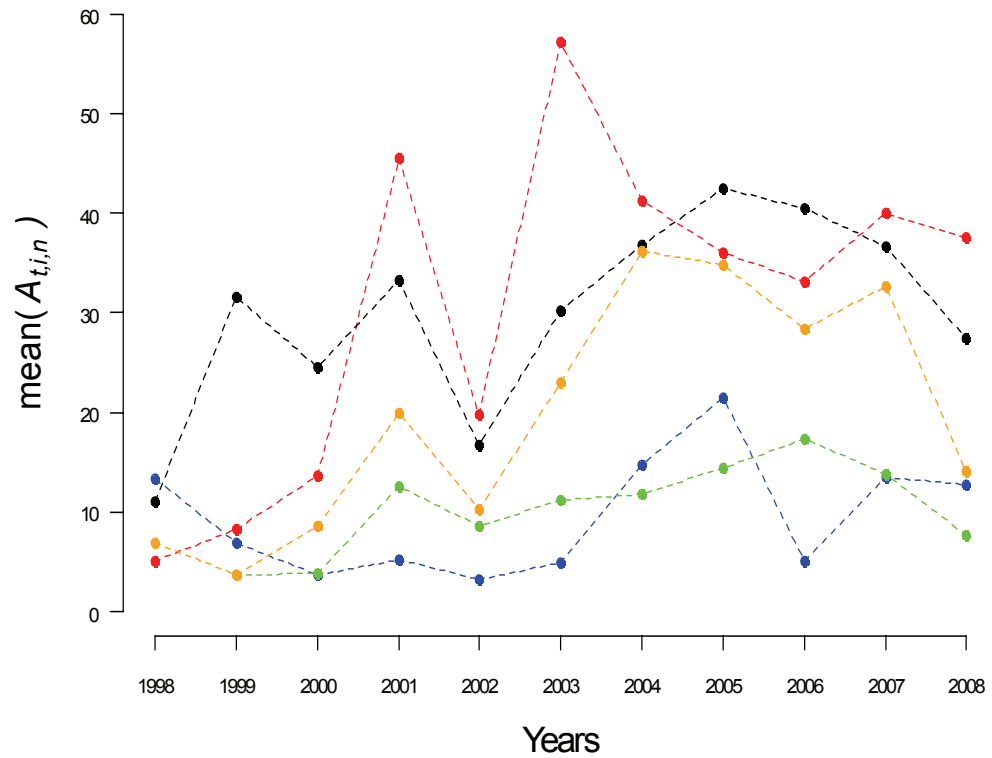


Figure 2.6: Average 5 minutes index of abundance ( $\text{mean}(A_{t,i,n})$ ) between 1998 and 2008; in red, blue, green, black and orange the Faughan, the Finn, the Mourne, the Roe and the Foyle.

$CV_i^d$  are the coefficients of variation (standard deviation / mean) of the average density for geo unit  $i$ . The  $CV^d$  of a given geo unit is assumed to be independent of the other  $CV^d$  however for parsimony it was assumed that the  $CV^d$  of a given geo unit remains constant across years. Parameterisation using  $CV^d$ s was decided after looking through the different other parameter such as standard deviation, variance and scale. Coefficient of variation was the parameter varying the less according to the average index of abundance (Figure 2.7) and had no systematic trends such as the systematic increase of variance or standard deviation along with the increase of the average index of abundance.

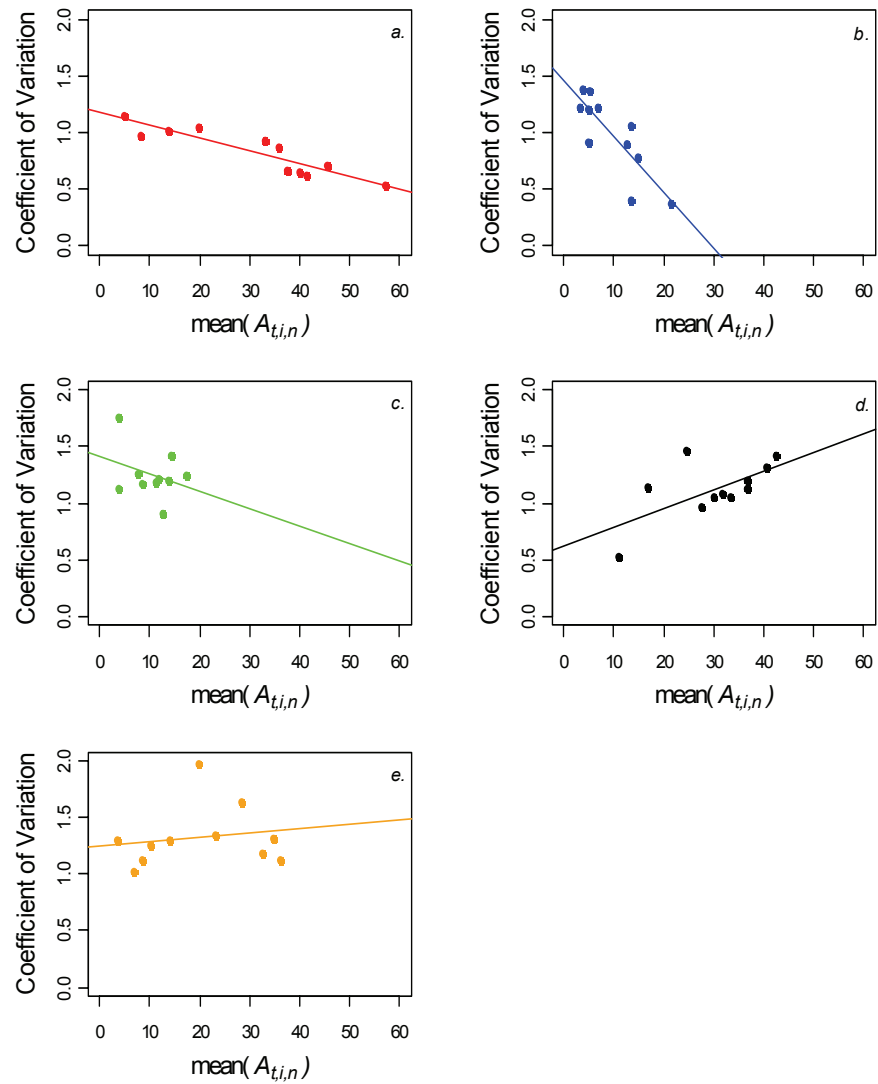


Figure 2.7: Coefficient of variation of the 5 minutes index of abundance vs average 5 minutes index of abundance ( $\text{mean}(A_{t,i,n})$ ) between 1998 and 2008 for each geo unit a) the faughan, b) the Finn, c) the Mourne, d) the Roe and e) the Foyle.

The structure of conditional dependency of relations (2.14) to (2.20) can be graphically summarised in a Directed Acyclic Graph (DAG) (Figure 2.8).

### 2.3.2.3 Prior distribution

To ensure best use of the calibration model (Dauphin *et al.*, 2009) the parameters linking the index of abundance  $A_{t,i,n}$  and the site densities  $d_{t,i,n}$ ,  $\eta^{cut}$ ,  $\kappa^{cut}$  and  $\varphi^{cut}$  were drawn from the posterior distribution of  $\eta$ ,  $\kappa$  and  $\varphi$  respectively. In order to obtain posterior inferences primarily reflecting the information brought by the data, little-informative and independent prior distributions were assigned to the remaining model parameters. A  $\text{Gamma}(1, 0.001)$  distribution, used as an appropriate distribution approximating a

uniform distribution, was assigned to  $d^{d\mu}$ . The coefficients of variation of the densities,  $CV_i^d$ , were given a  $Gamma(0.001,0.001)$  distribution

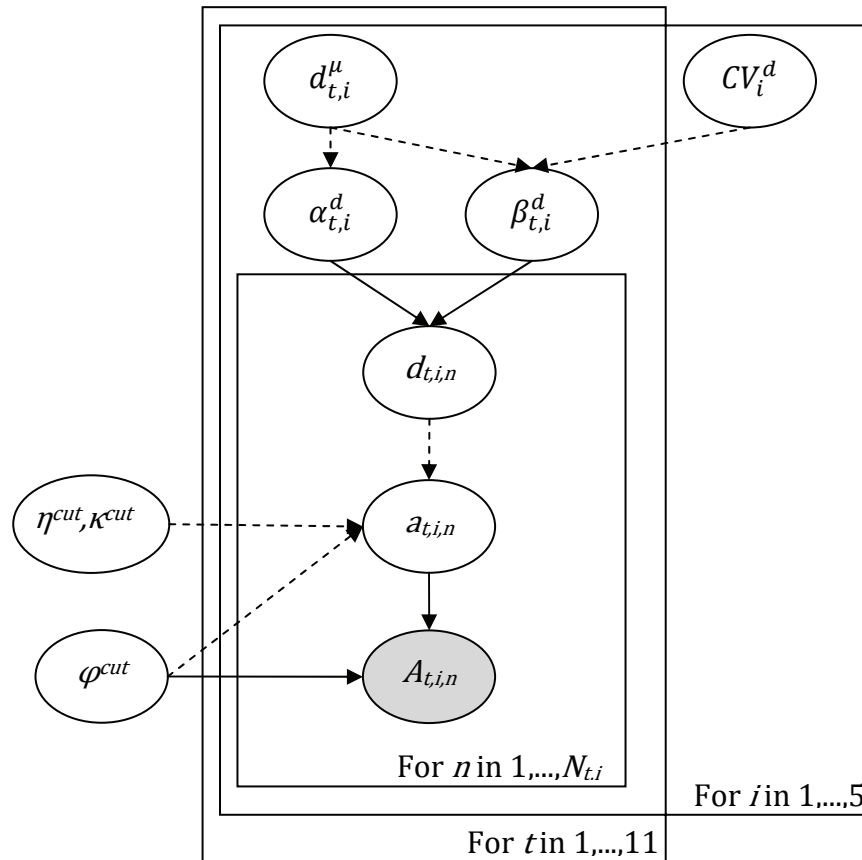


Figure 2.8: Directed acyclic graph (DAG) of the model used to estimate average 0+ salmon densities for each year and each geo unit. Ellipses represent random variables. All observed quantities are greyed. Arrows represent the parent-child dependencies between the different nodes: single arrows represent probabilistic relationship between the parent(s) and child nodes, dashed arrows indicate deterministic relationship. The frame represents a repetition of structure over sites ( $n$ ), geo units ( $i$ ) and years ( $t$ ). Nodes outside the frame are unknown parameters constant across sites.

### 2.3.2.4 Posterior computations

For every analysis presented, the joint distribution of all the unknowns (i.e. parameters, latent variables, observables in the case of missing data or for data replication) conditionally on all the observed data was approximated using MCMC sampling (Gelman *et al.*, 2003). All computations were carried out with the OpenBUGS® software (version 3.0.3; Thomas *et al.*, 2006; Spiegelhalter *et al.*, 2003) and the Lattice and Coda packages of R (version 2.7.0, [www.r-project.com](http://www.r-project.com)). Gelman-Rubin (Brooks and Gelman, 1998) diagnostics as implemented by OpenBUGS® was used to test the convergence of the MCMC sampling on the model parameters. Three chains with contrasting starting points

were used. The Gelman-Rubin statistic indicated good mixing of the MCMC chains was obtained after  $10^6$  iterations. An additional sample of 10 000 values ( $10^6$  iterations, but retaining 1 iteration every 100) from a single chain was then used to approximate the joint posterior distribution of all the unknowns.

### 2.3.2.5 Model checking

Following the approach proposed by Gelman *et al.* (1996), the compatibility between the assumed model and the data was checked by means of posterior predictive assessment techniques. These techniques extend classical goodness-of-fit test in the Bayesian setting by averaging over the posterior distribution of unknown quantities of the model. The  $\chi^2$  discrepancy was used as a discrepancy measure to assess *a posteriori* the consistency between the model and the index of abundance data (Gelman *et al.*, 2004).

$$(2.21) \chi^2(A|l) = \sum_{t,i,n} \frac{(A_{t,i,n} - E(A_{t,i,n}|l_{t,i,n}))^2}{Var(A_{t,i,n}|l_{t,i,n})} = \sum_{t,i,n} \frac{(A_{t,i,n} - l_{t,i,n})^2}{l_{t,i,n}}$$

We compared the realized discrepancies  $\chi^2(A,l)$  computed with the observed values of  $A_{t,i,n}$ , with a posterior predicted  $\chi^2$  discrepancy denoted  $\chi^2(A^{rep},l)$  and computed from posterior replications of the observed data only: the  $A_{t,i,n}^{rep}$  were drawn from the distribution  $A_{t,i,n}^{rep}|l_{t,i,n} \sim Poisson(l_{t,i,n})$  and the  $l_{t,i,n}$  from their posterior distribution. The use of posterior predictive replications aims at checking the adequacy between the data and the assumptions made in our model that provide  $l_{t,i,n}$  estimates.

The  $\chi^2$  discrepancies (equation 2.21) were calculated over all the  $(t,i,n)$  electrofishing sites and for all the  $(t,i,n)$  electrofishing sites within each geo unit  $i$  in order to check for inconsistencies for any particular geo unit. Bayesian  $p$ -values, i.e. the posterior probability that  $\chi^2(A^{rep}|l) \geq \chi^2(A|l)$ , were used to identify inconsistencies between the model and the index of abundance data. A  $p$ -value close to 0.5 indicates consistency, whereas extreme values (lower than 0.05 or higher than 0.95) will provide warnings of inconsistencies between the model and the data. The  $p$ -values are easily obtained by means of MCMC sampling. Gelman *et al.* (1996) and Marshall and Spiegelhalter (2007) provide more details about posterior predictive model checking and associated computational issues.



### 2.3.3 Results

#### 2.3.3.1 Posterior estimations of model unknowns

The variables of interest in this model are the average densities per geo unit  $\mu_{t,i}^d$  and the average densities' coefficients of variation  $CV_i^d$ . Other variables such as site densities  $d_{t,i,n}$  were only checked for consistency as they were expected to give similar posterior distributions than the ones obtain from index of abundance only in Dauphin *et al.* (2009).  $\eta^{cut}$ ,  $\kappa^{cut}$  and  $\varphi^{cut}$  were not considered since they are not updated by the additional data and their posterior distributions are therefore exactly the same than the ones estimated in the calibration model.

The average densities per geo unit and per year are estimated with high levels of uncertainty with coefficients of variation ranging from 35.6% to 188% (Figure 2.9). However, higher values of coefficients of variation (> 90%) for these variables occurred in years when less than fifteen grade 1 sites were electrofished in the geo units. With a mean of the posterior distributions of 6.56, 7.03 and 4.97 0+ juveniles.m<sup>-2</sup>, the Faughan, the Roe and the Foyle units have on average considerably higher average density than the Finn and the Mourne units (1.26 and 1.41 0+ juveniles.m<sup>-2</sup>, respectively).

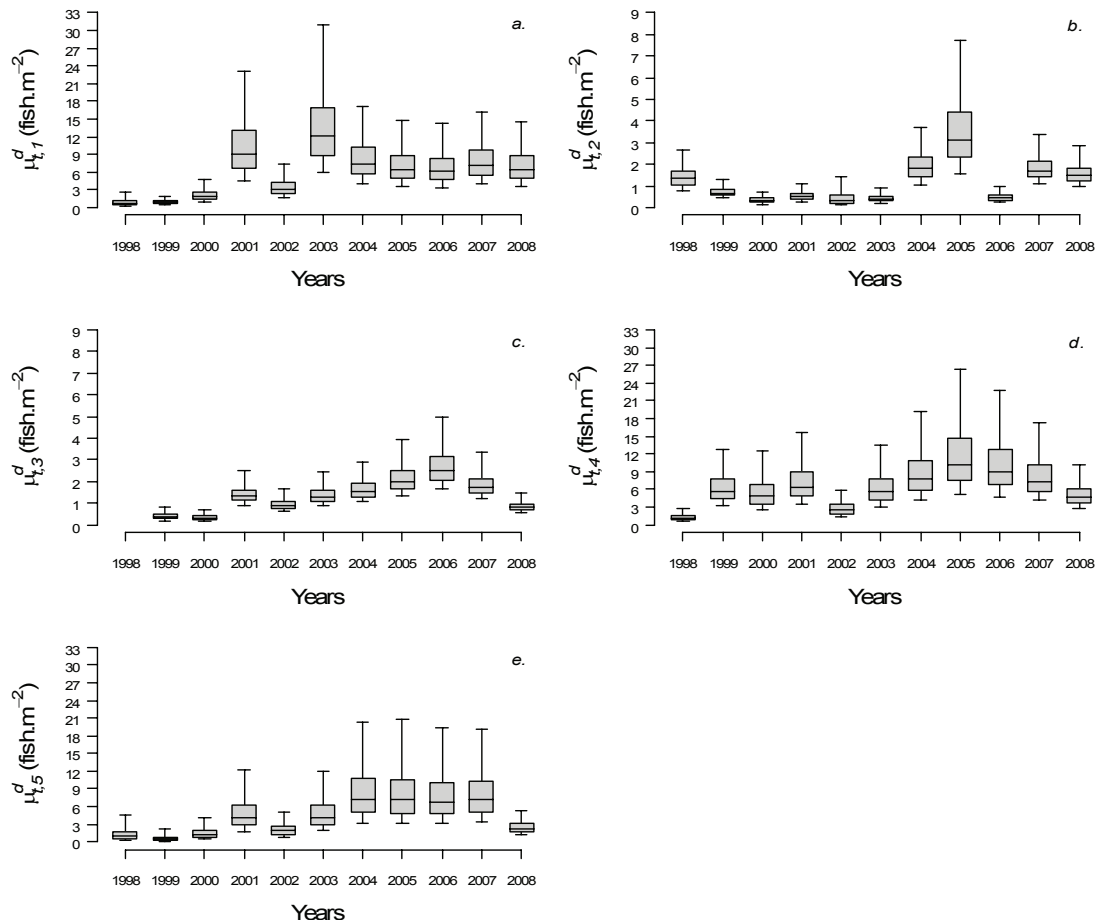


Figure 2.9: Summary of the posterior distribution of the average 0+ juvenile densities  $d^{\mu}$  for a) the Faughan, b) the Finn, c) the Mourne, d) the Roe and e) the Foyle. Boxes indicate 25<sup>th</sup> percentile, median and 75<sup>th</sup> percentile, whiskers indicate 5<sup>th</sup> and 95<sup>th</sup> percentiles.

The average densities' coefficients of variation variable  $CV_i^d$  are very well estimated (Figure 2.10) with posterior coefficients of variations ranging from 6.5 to 8.6 %. All  $CV_i^d$  were higher than 100%. The different geo units can be split into 3 groups with significantly different  $CV_i^d$ . The mean of the posterior distribution of  $CV_i^d$  for the Faughan and the Finn units was 129%, for the Mourne and the Roe units it was 158% and for the Foyle unit, the mean of the posterior distribution was 195%.

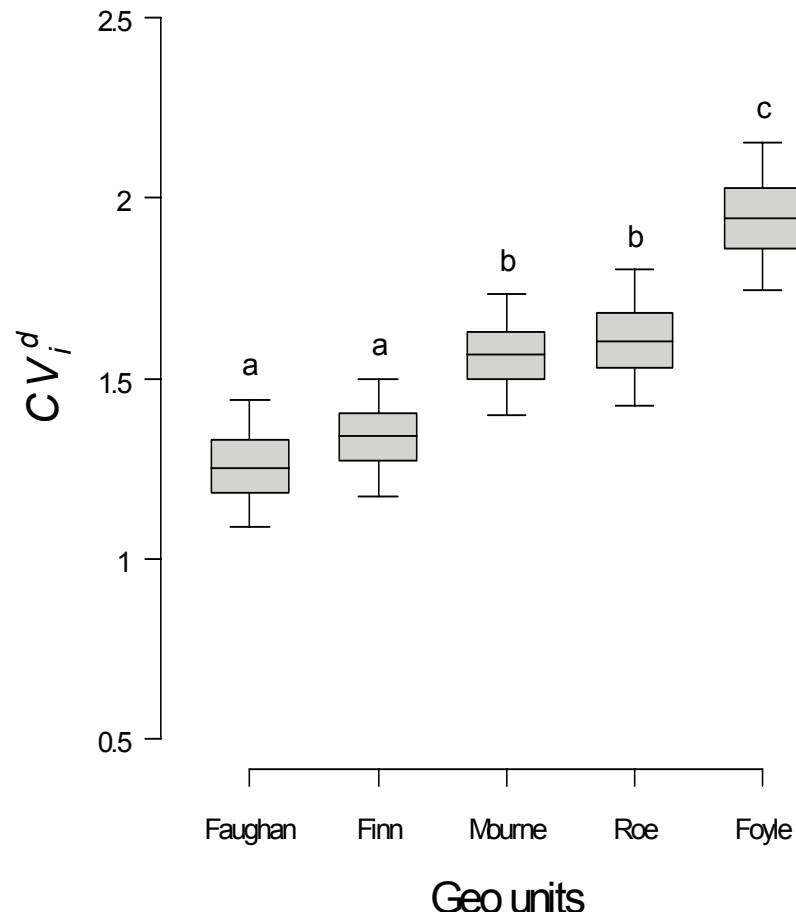


Figure 2.10: Summary of the posterior distribution of the average 0+ juvenile densities' coefficients of variation  $CV_i^d$  for the 5 geo units. Boxes indicate 25<sup>th</sup> percentile, median and 75<sup>th</sup> percentile, whiskers indicate 5<sup>th</sup> and 95<sup>th</sup> percentiles. Letters above whiskers indicate significantly different groups.

### 2.3.3.2 Posterior model checking

The  $\chi^2$  discrepancies statistics do not reveal any significant inconsistencies between our model and the data (Table 2.6). All the  $p$ -values are reasonably close to 0.50 when considering geo units one by one or all together.

Table 2.6: Posterior model checking: Bayesian  $p$ -values of chi-square statistics  $\chi^2(A^{rep}|l) \geq \chi^2(A|l)$  based on data replication technique (see text).

		$p$ -value
$P(\chi^2(A^{rep} l) \geq \chi^2(A l))$	All geo units	0.480
	Faughan	0.593
	Finn	0.504
	Mourne	0.406
	Roe	0.554
	Foyle	0.343

### 2.3.4 Discussion

The model proposed in this section allows estimating local site densities of 0+ salmon juveniles using posterior distribution of parameters estimated in a calibration model (see section 2.2). These densities were then brought together to estimate yearly average densities for each geo unit of the catchment. The posterior checks carried out did not reveal any significant discrepancy between the model and the observed data.

Yearly average density per geo unit  $d_{t,i}^{\mu}$  were fairly imprecise reflecting the vague local densities estimated only from the index of abundance  $A_{t,i,n}$ , nevertheless some patterns emerged and differences appeared among geo units. Thus, The Faughan, the Roe and the Foyle geo units showed some unusually high 0+ densities with average posterior distribution means above 5 fish.m<sup>-2</sup>, in some cases even reaching 10 fish.m<sup>-2</sup>. Such densities have never been recorded in this area (Crozier and Kennedy, 1994) or anywhere else. The maximum density found in the literature was around 7 0+ juveniles per square meter (Niemelä *et al.*, 2005). These particularly high values are mainly explained by the fact that in these geo units, many  $A_{t,i,n}$  are above 50 (See annex 1 for complete data set) and since the calibration relationship is monotonically increasing, there are no mathematical constraints to preventing such high densities even if they have no biological reality. Obtaining these high densities is due to the assumption that the calibration relationship is the same for each geo units and each crew performing the single timed electrofishing every year. This is an important assumption that needs to be made since almost no data on how the crews' technique differs is available. The  $d_{t,i}^{\mu}$  estimated for the Finn and the Mourne are significantly smaller than the one estimated for the 3 others geo units. The high  $A_{t,i,n}$  in these 3 geo units and therefore the differences in mean 0+ juvenile densities across geo units could be explained by several reasons: 1) the habitat quality in these 3 geo units is on average higher than in the other 2 geo units (for an equivalent grade, the food production is better and/or more shelters are available), 2) the different crews collecting for the  $A_{t,i,n}$  do not have the same efficiency in their sampling. This can be due to slight differences in the sampling protocol.

Both hypotheses could be responsible for the density differences encountered: The Faughan and the Roe units are located in an area which is known to have important agricultural activity which can lead to higher river productivity (Loughs Agency, personal communication). Also two of the three geo units with higher  $d_{t,i}^{\mu}$  (the Faughan and the

Roe) and consequently higher  $A_{t,i,n}$  are sampled by the same crew. The remaining geo unit with high  $d_{t,i}^{\mu}$  is sampled for its majority by the crew sampling the Faughan and the Roe units.

The average 0+ juvenile densities' coefficients of variation  $CV_t^d$  were all very precisely estimated at high values (all posterior means above 100%). Such high values indicate a high variability in site densities caused by high variability in the  $A_{t,i,n}$ . Such variability can be explained by several possibilities: 1) Sampling occurs in geo units which have large wetted area. It is likely that variability in good quality nursery habitat occurs across these geo units; 2) every year the sampling is carried out during a 2-3 months period during the summer. Sampling conditions may change over years and within a season (e.g. water discharge, conductivity, etc.) and lead to varying efficiency while sampling; 3) within each geographical sampling can be carried out by several crews (as mentioned above), crews might not have the same efficiency leading to additional variability in the  $A_{t,i,n}$ . It is difficult to measure how much each of these hypotheses contribute to the general variability of the 0+ juvenile densities. The differences among  $A_{t,i,n}$  for sites ranked as good in terms of nursery habitat can range from 0 to 301 in the same geo unit the same year (e.g. Roe unit in 2005 see annex 1).

Future modelling could be improved by having some calibration exercise performed by each crew. If the parameters linking the index of abundance to the density differs between crews, then the different set of parameters should be used to estimate the  $\mu_{t,i}^d$  according to the crew that collected the index of abundance.

## **Chapter 3:**

# **Is it worth counting redds to assess Atlantic salmon spawning escapement?**

This chapter has been submitted as a scientific article in *Fisheries Research* and is currently under review. The WinBUGS code corresponding to this model can be found in Annex 2.

### **3.1. Introduction**

Redd counts are widely used as an indicator of spawner population size for salmonids (Hay, 1987; Emlen, 1995; Rieman and Myers, 1997; Rieman and Allendorf, 2001; Isaak *et al.*, 2003; Al-Chokhaky *et al.*, 2005; Gallagher and Gallagher, 2005). One of the advantages of redd counting is its relatively low cost. With limited resources it is possible to monitor different rivers of a large catchment over long periods of time. Therefore long time-series redd count data are frequently available for salmonid populations (ICES, 1995; Thurow, 2000; Crozier *et al.*, 2003). Redd counts are often criticised because they lack assessment of their associated uncertainty while several authors have documented that sampling error is common in redd counts (Rieman and McIntyre, 1996; Bonneau and LaBar, 1997; Dunham *et al.*, 2001). A number of factors may affect a redd census such as redd age, redd size, redd density, physical characteristics of the redd location (substrate color, amount of flow, etc.), vegetation cover, year to year climatic variation (storm/flood events), and observer experience. Even though, redd counts are often significantly correlated to the spawner abundances (Beland, 1996; Dunham *et al.*, 2001; Gallagher and Gallagher, 2005).

More accurate measures of spawner abundances can be obtained by means of fish counters. Resistivity or infra-red devices provide abundance data for upstream migrating adults returning from the sea (Dunkley and Shearer, 1982; Shardlow and Hyatt, 2004). Counts are usually automated and allow counting migrating fish over the whole year. There are some uncertainties associated to these counts especially during flood events for resistivity counters (Dunkley and Shearer, 1982; Hendry *et al.*, 2007) or at high adult densities for infrared counters (Shardlow and Hyatt, 2004). Since this is a relatively new technology, available fish counter datasets are usually limited in time. Until they become more common and extensively used, it is important to find other sources of information to quantify adult abundance.

When redd counts and fish counters data are simultaneously available, it may be possible to build a calibration relationship between the two datasets. This calibration can then be used to derive spawner estimates and assess their associated uncertainty when only redd counts data are available. With this aim, a generic Bayesian hierarchical model is developed here. The proposed methodological approach is illustrated using an Atlantic salmon (*Salmo salar* L.) data set from three tributaries of the Foyle river system, Ireland. Redd counts and fish counter data were gathered simultaneously over a short period of time (2001 to 2006) and redd count data only were collected over an earlier and much longer period (1959 to 2000).

## 3.2. Material and Methods

### 3.2.1 Study site

The Foyle River basin drains a 4500 km<sup>2</sup> catchment on the North coast of Ireland (55°00' N; 07°20' W). The Foyle supports a large population of Atlantic salmon with commercial catches reaching more than 80 000 fish in the mid 1960's. The catchment also supports Arctic charr (*Salvelinus alpinus* L.), brown trout (*Salmo trutta* L.), European eel (*Anguilla Anguilla* L.), Lampreys (*Petromyzon marinus* L., *Lampetra fluviatilis* L. and *Lampetra planeri* Bloch) and three spined stickleback (*Gasterosteus aculeatus* L.) (Loughs agency, 2009a,b,c).

### **3.2.2 Field data collection**

Atlantic salmon redds have been consistently counted in the Foyle catchment from 1959 to 2006, except for the Faughan and the Roe sub-catchments in 1997. In addition, the wetted area of river surveyed for redd counts is also available since 2001. Fish counters provide adult abundances for three tributaries of the Foyle River basin (Faughan, Finn and Roe rivers) from 2001 to 2006 (Table 3.1).

#### **3.2.2.1 Redd counts**

During reproduction, which occurs usually during winter (November to February), female salmon dig a hole in the gravel where she lays her eggs. After egg deposition and fertilisation, she covers the eggs with gravel to complete the nest (redd). The gravel recently moved and cleaned are visible from the bank of the river and thus redds can be counted. During spawning time, Loughs Agency Fishery Officers aim to survey annually 460km of river channel. Depending on environmental conditions, some areas are visited one or several times during the spawning season. Training in salmon redd identification is provided by experienced Fishery Officers.



Table 3.1: Data for the Faughan, the Finn and the Roe, years 2001 to 2006: counts of returning adults (*A*), rod catches upstream of each counters (*N*), proportion of the wetted area surveyed (*P*) and redd counts (*R*). Dash (—) indicates missing data.

	Year	<i>A</i>	<i>N</i>	<i>P</i>	<i>R</i>
Faughan	2001	1518	656	—	233
	2002	4288	597	—	673
	2003	3097	335	0.33	441
	2004	2855	464	0.33	501
	2005	4245	822	0.33	766
	2006	3625	501	0.03	35
Finn	2001	3311	1162	0.17	137
	2002	5768	2263	0.16	234
	2003	6461	590	0.16	101
	2004	3771	627	—	149
	2005	8571	1118	0.24	343
	2006	5748	752	0.06	94
Roe	2001	3265	267	—	186
	2002	5459	408	0.31	630
	2003	4086	158	0.32	672
	2004	1922	357	0.08	43
	2005	2917	309	0.32	844
	2006	5375	444	0.32	428

### 3.2.2.2 Fish counters

Three Logie Aquantic 2100c resistivity counters (Fewings, 1994) were used to quantify the number of adult salmon returning from the sea from 2001 to 2006. They are located at the downstream end of the Faughan, Finn, and Roe rivers. During the period of time considered, the fish counters provided uninterrupted counts. Important flood events occurred in 2007 and 2008 leading to inconsistent counts. These years are therefore, not included in this study. The total river width is covered in order to count all upstream and downstream movements of any fish with a body length greater than 45 cm passing the fish counter. This detection threshold is lower than the minimum size of a returning adult Atlantic salmon in the Foyle system and well above the average size of returning sea trout which is the only species that could also move across the fish counter. Validation of the fish counters is undertaken by two ways; firstly pseudo-graphical signals are collected and

examined for the characteristic fish signal, secondly, video footage of fish passing the counting station is related to the signals generated by the counter and counts either accepted or rejected on that basis. Total annual fish counts from January to December of a given year are obtained by subtracting total downstream movements from total upstream movements (Table 1). Some downstream movements may correspond to kelts (adults migrating downstream after spawning) while the upstream movements may include the small number of sea trout bigger than 45cm (Elson and Tuomi, 1975). These errors are considered minor relative to the number of adult salmon returns. Given the methodological focus of the present paper, they are ignored in the following. These potential errors are incidental with regard to the modelling approach presented thereafter. It would apply equally well to more refined measures of adults returns.

### 3.2.3 Modelling

Henceforth unobservable quantities will be denoted by Greek lower case letters and observable quantities by capital Roman letters. The notation  $a|b \sim f(b)$  means the random variable  $a$  (whether unobservable or observable) conditionally on  $b$  is distributed according to the probability distribution function (pdf)  $f$ . Unobservable quantities are necessarily unknown but observable quantities may be unknown as well if not observed (missing data). In our case, adult counts are observable quantities but they have been observed only for the last 6 years of the time series (2001-2006).

#### 3.2.3.1 The relationship between spawners and redd counts

Each redd count is identified by two indices:  $t = 1, \dots, 48$  for years 1959 to 2006 and  $i = 1, 2, 3$  for the three rivers equipped with a fish counter. The number of redds counted  $R_{t,i}$  in year  $t$  upstream from the counter  $i$  is assumed to be drawn from a Negative Binomial distribution (Muhlfeld *et al.*, 2006) which is written as a Poisson distribution with its rate parameter  $\lambda_{t,i}$  following a Gamma distribution (Mangel, 2006, p. 103-112):

$$(3.1) \quad R_{t,i} | \lambda_{t,i} \sim \text{Poisson}(\lambda_{t,i})$$

$\lambda_{t,i}$  depends on the number of spawners,  $S_{t,i}$ , a spawner:red ratio  $\kappa_{t,i}$ , and the proportion of wetted area of the catchment unit that has been surveyed for redd counting  $P_{t,i}$ .

$$(3.2) \quad \lambda_{t,i} = S_{t,i} \cdot \kappa_{t,i} \cdot P_{t,i}$$

The spawners are the adults which manage to reach the spawning grounds. Thus,  $S_{t,i}$  is obtained from the adult returns  $A_{t,i}$ , and the rod catches upstream from the counters  $C_{t,i}$ .

$$(3.3) \quad S_{t,i} = A_{t,i} - N_{t,i}$$

For the years 2001 to 2006, the fish counters are assumed to provide an exact count of the number of returning adults, *i.e.*  $A_{t,i}$ . For the years prior to 2001, these data are missing (section 3.2.6).

### 3.2.3.2 Hierarchical structure for the spawner:red ratio $\kappa$

The quantity  $\kappa_{t,i}$  is the yearly average spawner:red ratio. Two embedded levels of variation can affect this ratio: between rivers and between years within rivers. Differences between rivers in the nature of the bottom substrate, the channel morphology, the occurrence of aquatic weeds and hydrological characteristics (including water clarity) can modify the ability to visually detect redds (Table 3.1). River specific characteristics of the salmon spawners (*e.g.* size, sex ratio) can also result in a between river effect on the spawner:red ratio. Yearly variation of the characteristics of the spawners, of the environmental conditions affecting redd detection and of the observers experience and practices during redd counting can influence the number of redds counted each year (Peterson and Metcalfe, 1981; Crisp and Carling, 1989). The spawner:red ratio  $\kappa_{t,i}$  is assumed to be drawn from a Gamma distribution with river specific shape  $\alpha_i$  and inverse scale  $\beta_i$  parameters.

$$(3.4) \quad \kappa_{t,i} | \alpha_i, \beta_i \sim \text{Gamma}(\alpha_i, \beta_i)$$

The river specific  $\alpha_i$  and  $\beta_i$  parameters account for the between rivers effects while the random variations conditional on these parameters account for the within rivers yearly variations.  $\alpha_i$  and  $\beta_i$  can be expressed according to the corresponding mean  $\mu_i^\kappa$  and precision  $\tau^\kappa$ :

$$(3.5) \quad \alpha_i = (\mu_i^\kappa)^2 \cdot \tau^\kappa$$

$$(3.6) \quad \beta_i = \mu_i^\kappa \cdot \tau^\kappa$$

The mean  $\mu_i^\kappa$  is assumed to be river specific while the precision  $\tau^\kappa$  does not vary across rivers. The latter hypothesis is a parsimonious approach because precision (*i.e.* inverse of the variance) parameters are difficult to estimate from small numbers of observations. In our case, only the last six years were available for each river to estimate each river specific precision parameter.

### 3.2.3.3 Hierarchical structure for the number of returning adults

It was assumed that the number of adults returning to the Faughan, the Finn and the Roe were drawn from river-specific Log-Normal distributions:

$$(3.7) \quad A_{t,i} | \mu_i^S, \tau_i^S \sim \text{LogNormal}(\mu_i^S, \tau_i^S)$$

where  $\mu_i^S$  and  $\tau_i^S$  are the mean and the precision of the underlying normal distribution. The Log-Normal distribution was chosen as it is the standard for modelling random variations of population abundance when little is known about the causal mechanisms (Halley and Inchausti, 2002). As for  $\kappa_{i,t}$ , the mean parameter is assumed to vary across rivers. In addition, the precision parameter is also allowed to vary, as early model trials showed poorer estimation of spawner abundances with this parameter remaining constant across rivers.

### 3.2.3.4 Taking into account the area surveyed for redd counts

The area surveyed for redd counting was not available every year and for every river. In order to account for this source of uncertainty in the relationship between the adult counts and the redd counts, the variations of this proportion were explicitly modelled. Whether observed or not (*i.e.* missing data), it is assumed the logit of the proportion of wetted area surveyed was drawn from a common normal probability distribution:

$$(3.8) \quad \text{Logit}(P_{t,i}) | \mu^P, \tau^P \sim \text{Normal}(\mu^P, \tau^P)$$

where  $\mu^P$  and  $\tau^P$  are the mean and the precision of the underlying normal distribution. No between river variation was introduced in the absence of evidence of any river specific factors influencing the proportion of wetted area surveyed for redd counting. This was

confirmed in early trials of the model incorporating such variations and not providing better estimates.

### 3.2.4 Bayesian inference and posterior computations

The structure of conditional dependency of the model's relations (Equations 3.1-3.8) can be graphically summarised in a Directed Acyclic Graph (DAG) (Figure 3.1). The Bayesian treatment of this model for deriving posterior probability distribution of all the unknown quantities requires that a prior probability distribution is assigned to each of the free parameters of the model, *i.e.* those not conditioned by any quantity in the DAG. Weakly-informative and independent prior PDFs were used (Table 3.2) in order to ensure that our posterior inferences would primarily reflect the information brought by the observed data.

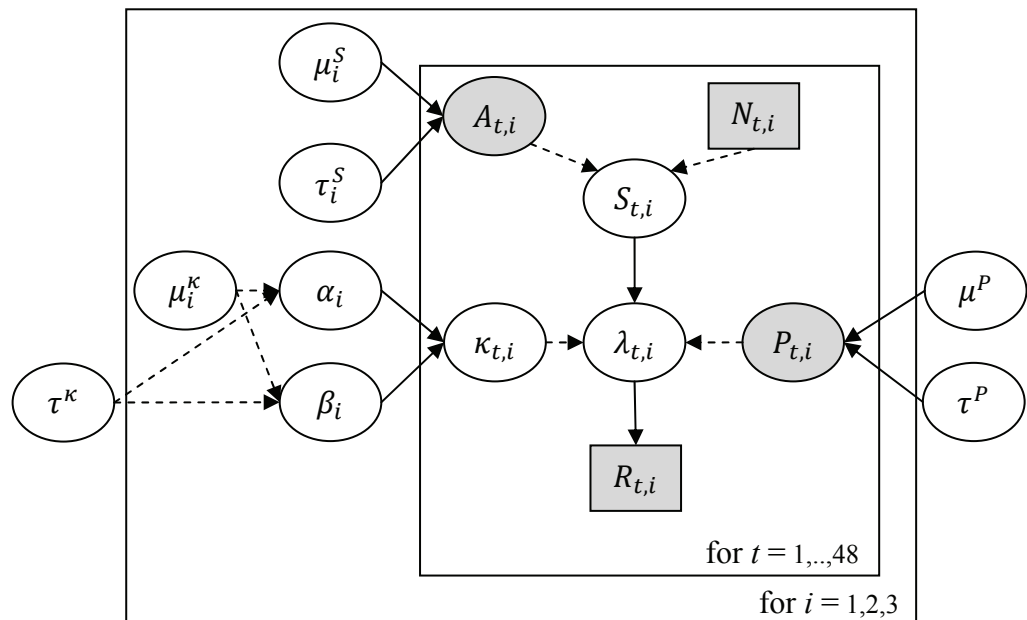


Figure 3.1: Directed Acyclic Graph (DAG) of the model relating the returning adults to the redd counts. All observable quantities are greyed. Arrows represent the conditional dependencies between nodes: solid arrows for probabilistic dependency, broken arrow for deterministic dependency. The frames represent a repetition of structure over units.

The joint posterior distribution of all the model unknowns (*i.e.* unobservable quantities and observables in case of missing data) was approximated using Markov chain Monte Carlo (MCMC) sampling (Gelman *et al.*, 2003). All computations were carried out with the OpenBUGS<sup>®</sup> software (version 3.0.3; Thomas *et al.*, 2006; Spiegelhalter *et al.*, 2007) and the Lattice and Coda packages of R (version 2.5.1, [www.r-project.org](http://www.r-project.org)). We used the Gelman-Rubin (Brooks and Gelman, 1998) diagnostics as implemented by OpenBUGS<sup>®</sup> to

test the convergence of the MCMC sampling on the model parameters. Three chains with contrasted starting points were run. The Gelman-Rubin statistic indicated good mixing of the MCMC chains was obtained after  $10^6$  iterations. An additional sample of 10 000 values ( $10^6$  iterations, but retaining 1 iteration every 100) from a single chain was then used to approximate posterior distributions.

Table 3.2: Prior distribution of the parameters ( $i=1,2,3$ ;  $\varepsilon = 0.001$ ).

Parameter	Distribution
$\mu^P$	$\sim \text{Beta}(1, 1)$
$\tau^P$	$\sim \text{Gamma}(\varepsilon, \varepsilon)$
$\mu_i^K$	$\sim \text{Gamma}(1, \varepsilon)$
$\tau^K$	$\sim \text{Gamma}(\varepsilon, \varepsilon)$
$\mu_i^S$	$\sim \text{Unif}(0, 5.10^5)$
$\tau_i^S$	$\sim \text{Gamma}(\varepsilon, \varepsilon)$

### 3.2.5 Posterior model checking

Following the approach proposed by Gelman *et al.* (1996), the compatibility between the assumed model and the data was checked by means of posterior predictive assessment techniques. These techniques extend classical goodness-of-fit tests in the Bayesian setting by averaging over the posterior distribution of unknown quantities of the model. We used the omnibus  $\chi^2$  statistic as a discrepancy measure to assess *a posteriori* the consistency between the model and the data (Gelman *et al.*, 2003).

$$(3.9) \quad \chi^2(R, \lambda) = \sum_{t,i} \frac{(R_{t,i} - E(R_{t,i} | \lambda_{t,i}))^2}{\text{Var}(R_{t,i} | \lambda_{t,i})} = \sum_{t,i} \frac{(R_{t,i} - \lambda_{t,i})^2}{\lambda_{t,i}}$$

With  $X$  being any observable quantity and  $\theta$  the set of unknown parameters controlling the pdf of  $X$ .

The realized discrepancies  $\chi^2(R, \lambda)$  computed with the observed values of  $R_{t,i}$ , were compared to two posterior predicted  $\chi^2$  discrepancies denoted  $\chi^2(R^{rep1}, \lambda)$  and  $\chi^2(R^{rep2}, \lambda)$ .  $\chi^2(R^{rep1}, \lambda)$  was computed from posterior replications of the observed data only: the  $R_{t,i}^{rep1}$  were drawn from the distribution  $R_{t,i}^{rep1} | \lambda_{t,i} \sim \text{Poisson}(\lambda_{t,i})$  and the  $\lambda_{t,i}$  from their posterior distribution.  $\chi^2(R^{rep2}, \lambda^{rep})$  was computed from posterior replications

of both the observed  $R_{t,i}$  and the  $\lambda_{t,i}$  the  $R_{t,i}^{rep2}$  were drawn from the distribution  $R_{t,i}^{rep2} | \lambda_{t,i}^{rep} \sim Poisson(\lambda_{t,i}^{rep})$  and the  $\lambda_{t,i}^{rep}$  from their posterior predictive distribution. The use of posterior predictive replications at two different levels of our hierarchical model aims at checking the adequacy between the data and the assumptions made in our model at these two levels.

The  $\chi^2$  discrepancies (equation 3.9) were calculated over all the  $(t,i)$  observation units and for all the  $(t,i)$  observations units within each river  $i$  in order to check for inconsistencies for any particular river. Bayesian  $p$ -values, i.e. the posterior probability that  $\chi^2(R^{rep1}, \lambda) \geq \chi^2(R, \lambda)$  or  $\chi^2(R^{rep2}, \lambda^{rep}) \geq \chi^2(R, \lambda)$ , were used to identify inconsistencies between the model and the redd counts data. A  $p$ -value close to 0.5 indicates consistency, whereas extreme values (lower than 0.05 or higher than 0.95) will provide warnings. The  $p$ -values are easily obtained by means of MCMC sampling. Gelman *et al.* (1996) and Marshall and Spiegelhalter (2007) provide more details about posterior predictive model checking and associated computational issues.

### 3.2.6 Estimating adult returns from redd counts alone

From 1959 to 2000, the data available are restricted to the redd counts. The corresponding area surveyed and returning adult data are missing. Relying on the standard assumption that the missing data are "missing at random" (Gelman *et al.*, 2003), they can be considered as any other unknown in the model. Their posterior distribution conditionally on all the observed data (*i.e.* redd counts from 1959 to 2006 and adult counts and area surveyed from 2001 to 2006; Table 3.1) can be computed by standard MCMC sampling techniques. In addition, a relative measure of spawners abundance  $\delta_{t,i}$  was calculated for each river  $i$  and year  $t$  as the ratio of the absolute abundance of this given  $(t,i)$  unit to the average adult abundance for the river  $i$ .

$$(3.10) \delta_{t,i} = \frac{S_{t,i}}{\frac{1}{48} \cdot \sum_{t=1959}^{t=2006} S_{t,i}}$$

This relative abundance measure was calculated with the aim of comparing the precision of absolute vs. relative abundance estimates derived from the same redd count data.

In order to evaluate the potential value of having fully observed the covariate  $P_{t,i}$ , fake observations of the proportion of wetted area surveyed  $P_{t,i}^{fake}$  were generated by a random draw in the posterior predictive distribution of the  $P_{t,i}$  for years when redd counts are the only data available (1959 to 2000). The posterior inferences of spawner abundances  $S_{t,i}^{fake}$  were then derived as if the  $P_{t,i}^{fake}$  were true available data.

### 3.3. Results

The  $\chi^2$  discrepancy statistics do not reveal any significant inconsistencies between our model and the data (Table 3.4). All the  $p$ -values ranged between 0.21 and 0.62 for any level of replication. The free parameters of the model, prior to posterior distribution comparison (Table 3.2 and Table 3.3) reveal a significant updating as a result of the information brought by the observed data. The posterior mean of the  $\mu^p$  parameter corresponds to an average proportion of wetted area surveyed of 21.4%. Posterior mean values of the unknown proportions of wetted area surveyed range from 0.18% to 0.40%. The spawner:red ratio is different across rivers. It is, on average, higher for the Faughan compared to the Roe ( $P(\mu^k_1 \geq \mu^k_3) = 0.88$ ) which is higher than the Finn ( $P(\mu^k_3 \geq \mu^k_2) = 0.92$ ). When all data are available, the  $\kappa_{t,i}$  are estimated with low uncertainty (posterior distributions CVs ranging from 0.035 to 0.155; Figure 3.2). When the proportion of the wetted area surveyed is missing, the uncertainty of the estimates dramatically increases (CVs ranging from 0.298 to 0.549).

Table 3.3: Posterior model checking: Bayesian  $p$ -values of chi-square statistics  $\chi^2(R^{rep1}, \lambda) \geq \chi^2(R, \lambda)$ ,  $\chi^2(R^{rep2}, \lambda^{rep}) \geq \chi^2(R, \lambda)$  or  $\chi^2(A^{rep}, \mu^S, \tau^S) \geq \chi^2(A, \mu^S, \tau^S)$  based on data replication technique (see text).

		$p$ value
$P(\chi^2(R^{rep1}, \lambda) \geq \chi^2(R, \lambda))$	All units	0.507
	Faughan	0.506
	Finn	0.503
	Roe	0.500
$P(\chi^2(R^{rep2}, \lambda^{rep}) \geq \chi^2(R, \lambda))$	All units	0.508
	Faughan	0.510
	Finn	0.502
	Roe	0.500



Table 3.4: Summary statistics of the marginal posterior distributions of the models parameters.

	mean	sd	2.5%	25%	median	75%	97.5%
$\mu^P$	0.214	0.038	0.147	0.188	0.211	0.236	0.297
$\tau^P$	1.365	0.496	0.579	1.007	1.303	1.654	2.464
$\mu_1^K$	0.615	0.095	0.441	0.552	0.611	0.671	0.816
$\mu_2^K$	0.333	0.076	0.203	0.282	0.327	0.376	0.501
$\mu_3^K$	0.478	0.089	0.315	0.418	0.473	0.531	0.670
$\tau^K$	28.35	13.69	8.023	18.44	26.18	36.12	60.81
$\mu_1^S$	3612	467	2787	3289	3580	3904	4620
$\mu_2^S$	6872	811	5511	6297	6791	7351	8708
$\mu_3^S$	5924	799	4604	5375	5837	6391	7739
$\tau_1^S$	4.282	2.226	1.561	2.735	3.764	5.275	10.05
$\tau_2^S$	9.788	4.461	3.684	6.559	8.956	12.08	20.88
$\tau_3^S$	4.660	1.946	1.956	3.300	4.332	5.643	9.387

The absolute number of spawners estimated *a posteriori* between 1959 and 2000 from the redd counts only are very uncertain, with posterior CVs ranging from 0.35 to 0.56 (year 1997 is excluded for the Faughan and the Roe river since no redd counts were available for this year) (Figure 3.3). The pattern of variation over the time series shows a peak of abundance in the 1960 for the river Faughan and the river Roe but is relatively flat for the Finn.

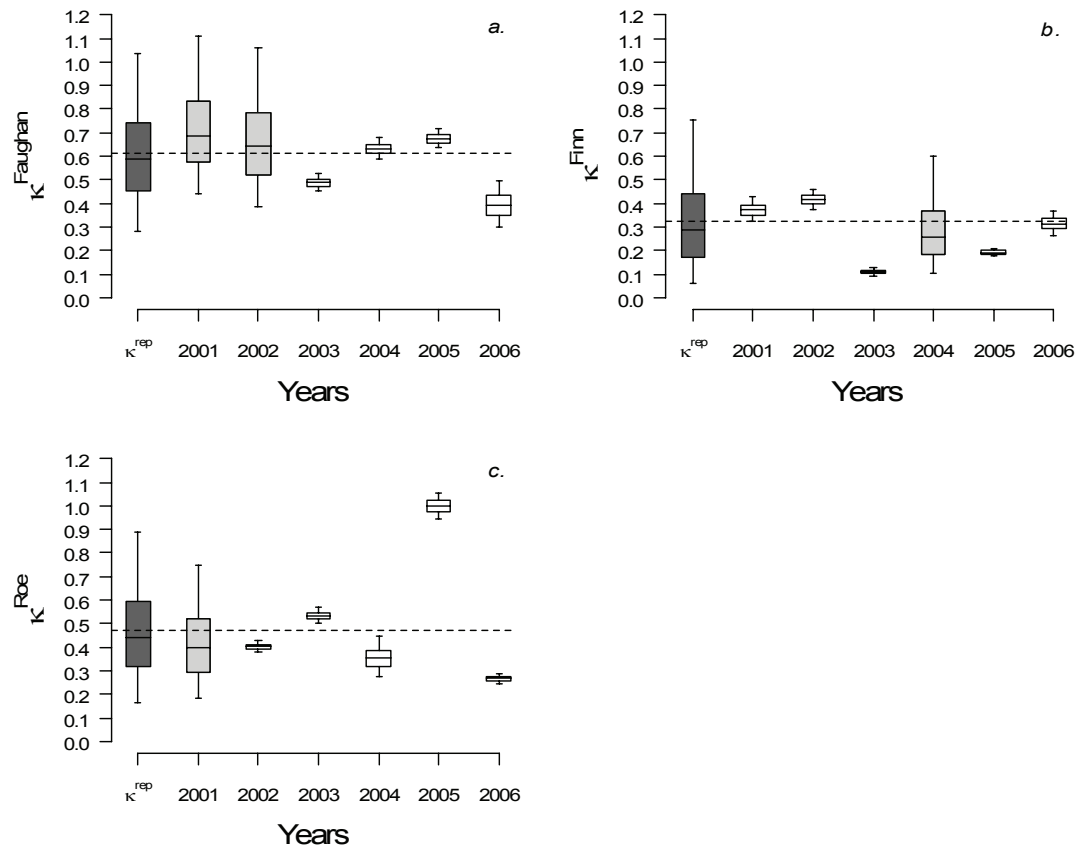


Figure 3.2: Posterior distributions of the yearly spawner:red ratios for each units ( $\kappa_{t,i}$ ) for the years 2001 to 2006. Light grey boxes indicate years for which the proportion of the surveyed area was not available. Dark grey boxes indicate the posterior predictive distribution ( $\kappa^{rep}$ ) summarize the knowledge about the same spawner:red ratio when both adult counts and proportion of the surveyed area data are missing. The line in the middle of the box indicates the median, the boxes indicates the 25<sup>th</sup> and 75<sup>th</sup> percentiles and the whiskers indicate the 2.5<sup>th</sup> and 97.5<sup>th</sup> percentiles. Dashed lines indicate the mean of the posterior distribution of the associated  $\mu^{\kappa}_i$  (Equations 3.5 and 3.6)

Compared to absolute abundance, the relative abundance measure provides slightly, but systematically, more precise estimates (lower CVs; Figure 3.4). The incorporation of fake observations of the proportion of wetted area surveyed  $P_{t,i}^{fake}$  significantly improves the precision of abundances estimates for the Faughan and the Roe, but the improvement is only marginal for the Finn.

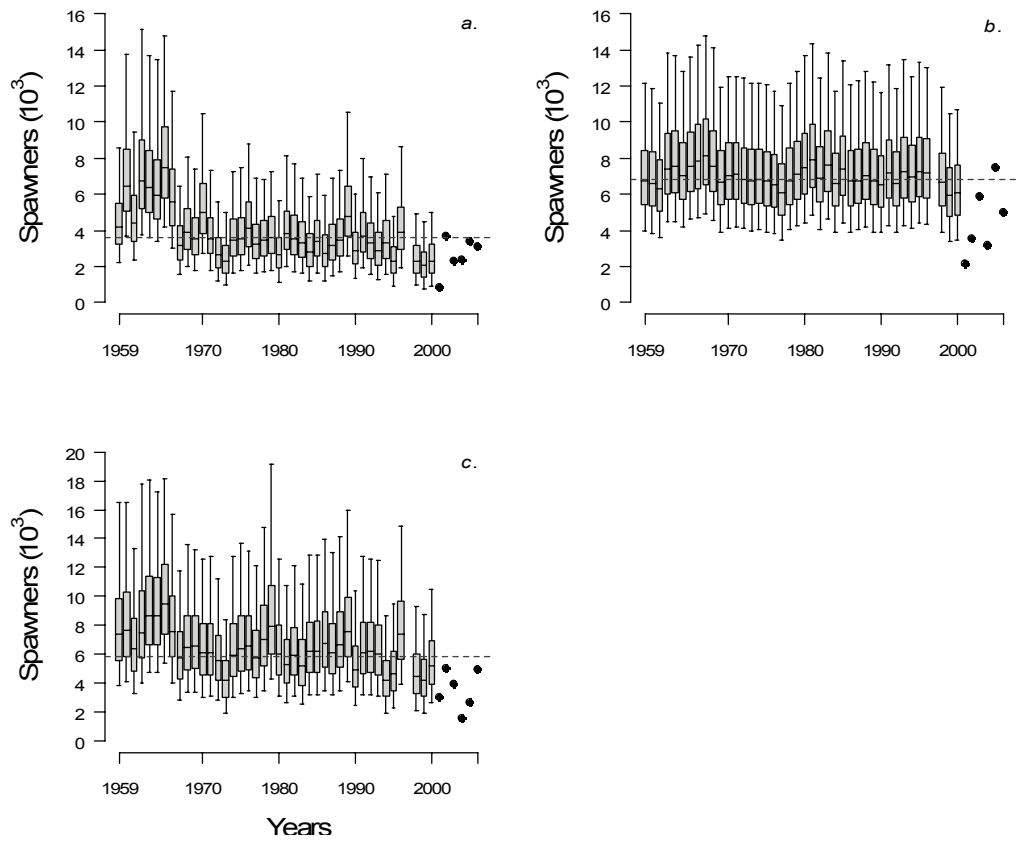


Figure 3.3: Posterior distributions of the spawners abundance from 1959 to 2006 for a) the Faughan, b) the Finn, and c) the Roe. The year 1997 for the Faughan and Roe have been removed as the red counts were missing. The line in the middle of the boxes indicates the median, the box indicates the 25<sup>th</sup> and 75<sup>th</sup> percentiles and the whiskers indicate the 2.5<sup>th</sup> and 97.5<sup>th</sup> percentiles. The dashed lines indicate the mean spawners abundance over the time series.

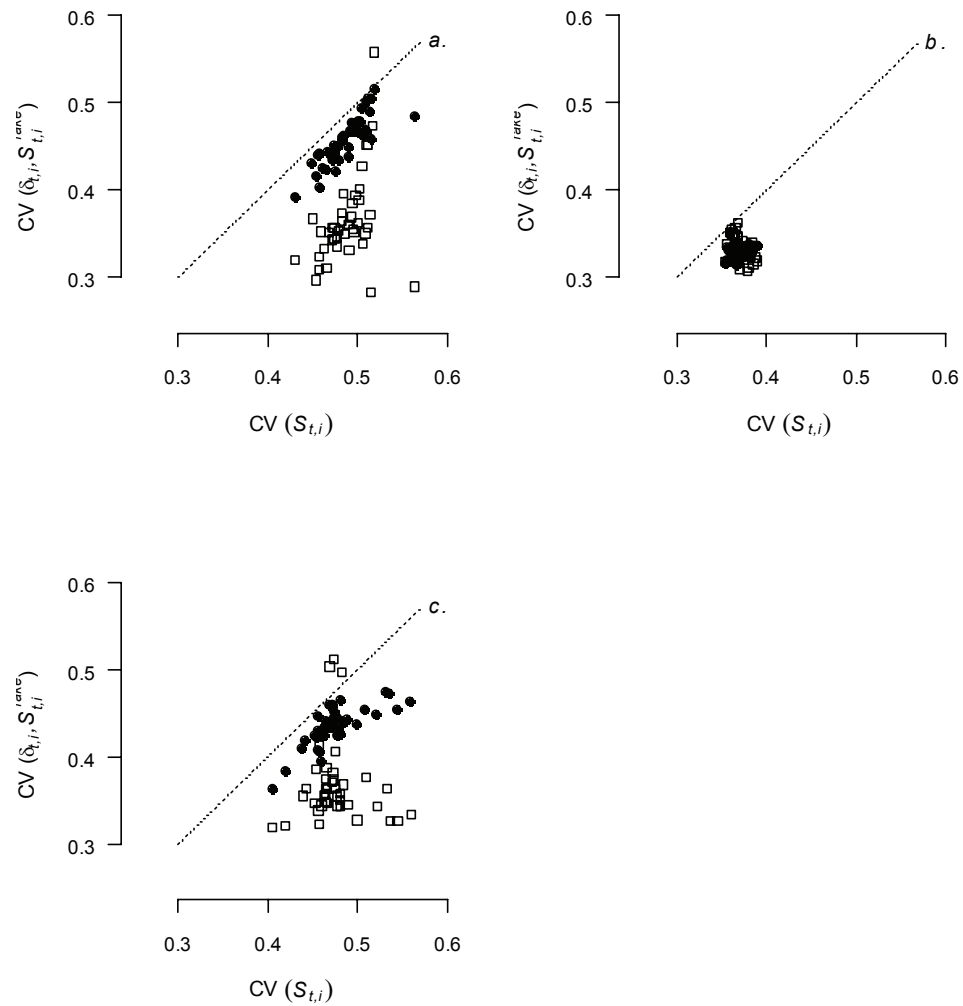


Figure 3.4: Coefficient of variation (CV) of the spawner abundance  $S_{t,i}$  against the associate CV of the relative abundance  $\delta_{t,i}$  ( $\bullet$ ) and the CV of spawner abundance obtained with the incorporation of fake proportions of surveyed wetted area data  $S_{t,i}^{fake}$  ( $\square$ ) from 1959 to 2000 for a) the Faughan, b) the Finn, and c) the Roe. The year 1997 for the Faughan and Roe has been removed as the red counts were missing. The dotted line represents the one-to-one line.

### 3.4. Discussion

The model proposed in this study relates salmon spawner abundance and the number of redds counted in the field. Its structure is generic and could be applied to other redd counts and spawner abundance data sets, at least for salmonids. The posterior checks did not reveal any discrepancy between the model and the observed data in our case. Provided that some spawner abundance and redd counts have been jointly observed for some years, the model can be used to estimate spawner abundance from redd count data alone and assess the associated uncertainty. In this study counts of fish from the fish counters are assumed to accurately reflect the spawning escapement. Any discrepancies between the actual fish counter counts and the real spawning escapement are included within the spawner:red

ratio parameters  $\kappa_{t,i}$ . The magnitude and variation in these uncertainties could be incorporated into further studies.

In the present study, the posterior estimates of absolute spawner abundance derived from redd counts data alone are very uncertain. This results from the cumulative effect of three main sources of uncertainty: the between year variability of the  $\kappa_{t,i}$  coefficient (Figure 3.2), the lack of observation and the inter-annual variation of the  $P_{t,i}$  covariates and the posterior uncertainty about the mean and precision parameters  $\mu_i^K$ ,  $\tau^K$ ,  $\mu^P$  and  $\tau^P$  (Table 3.4). Some of these sources of uncertainty have already been identified and taken into account separately by some authors (Dunham *et al.*, 2001; Gallagher and Gallagher, 2005; Muhlfeld *et al.*, 2006). The modelling approach proposed here is original, in that they are considered jointly in a single and consistent (hierarchical) framework. The approach could easily be extended by introducing observed covariates explaining part of the random variations in the  $\kappa_{t,i}$  and the  $P_{t,i}$ .

Looking at a relative index of abundance essentially amounts to removal of the posterior uncertainty about the mean parameters  $\mu_i^K$  and  $\mu^P$ . The precision of the posterior estimates is somewhat improved, but the other main sources of uncertainty remain. A much more significant improvement could be obtained if the proportion of wetted area surveyed ( $P_{t,i}$ ) was known every year. When the fake  $P_{t,i}^{fake}$  data were used, the CVs of the posterior distributions of the abundance were notably reduced for the Faughan and the Roe River (Figure 3.4).

It is concluded from this exercise that redd counts can be a valuable source of information for monitoring spawning abundance of salmonids and should not be dismissed *a priori*. The generic modelling presented herein allows estimating spawner abundance from redd count data alone and to assess the associated uncertainty. This assessment is essential as the uncertainty of the abundance estimates may be large. Ancillary data informing the redd counting process (*e.g.* the proportion of wetted area surveyed) can make a great difference in improving the precision of the abundance estimates.

## **Chapter 4:**

# **A life stage state-space model for Atlantic salmon population dynamics in the Foyle catchment.**

This chapter is written as a manuscript to be submitted in *Fish and Fisheries* or *Ecological Monographs*. The WinBUGS code corresponding to this model can be found in Annex 3.

## **4.1. Introduction**

Population dynamics is the study of the abundance at different life stages of a species, the interactions between these life stages and sometimes the interactions with other species (Hilborn and Mangel, 1997; Walters and Martell, 2004). Stage-structured modelling is a popular approach for population dynamics studies (Tuljapurkar and Caswell, 1997; Caswell, 2001). This approach examines populations based on their ecology and allows the incorporation of complex dynamic processes. Model outputs are sensitive to the parameter values. It then becomes crucial to accommodate and quantify parameter uncertainty. This is of particular importance when the population of interest is exploited and the risk of over-exploitation or to extinction needs to be assessed (Ludwig *et al.* 1993; Francis and Shotton, 1997; Hilborn and Mangel, 1997, Schnute and Richards, 2001).

When studying real world case studies of population exploited by fisheries, several additional problems often arise such as: multiple and heterogeneous sources of information (e.g. datasets collected at different spatial and temporal scales and with different spatial and temporal coverage), missing observations, life stages of interest not directly observable. The Bayesian framework allows dealing naturally with all these issues. It has proven its particular value in studying the dynamics of exploited populations (Ellison, 1996; Hilborn, 1997; Punt and Hilborn, 1997; Wade, 2000, 2001). Indeed, unknown

quantities have associated probability distributions reflecting their uncertainty. Dealing with variations in the interactions/processes between life stages (Clark, 2003; Clark *et al.*, 2003) or limited and indirect ecological data (Legendre, 1993) is also facilitated by Bayesian modelling.

Bayesian state-space models have become a common tool to deal with diverse datasets and uncertainties related to observation or process errors (Clark and Bjørnstad, 2004; Rivot *et al.*, 2004; Michielsens *et al.*, 2008). A state-space model is composed of two equations (Carlin *et al.*, 1992; Calder *et al.*, 2003). The first one is called the process equation:

$$(4.1) X_t = F(X_{t-1}, \theta_1, \varepsilon_t)$$

where the function  $F$  accounts for all the equations describing the dynamics of the system studied (survival, density dependence, etc. for population dynamics) and reflects the dependence of the different hidden states at a given time on the hidden states at another earlier time conditionally on the transition parameters  $\theta_1$  and a stochastic component  $\varepsilon_t$ . The second equation is called the observation equation:

$$(4.2) y_t = G(X_t, \theta_2, \omega_t)$$

where the function  $G$  describes the link between the observed datasets  $y_t$  and the hidden states  $X_t$  conditionally on the observation model parameters  $\theta_2$  and the stochastic component of the observation models  $\omega_t$ . The Bayesian statistical inference calculates the joint posterior probability density functions (pdf) of all the model parameters  $\theta = (\theta_1, \theta_2)$  and the hidden states series  $X^n$  conditionally on the observations series  $y^n$ .

$$(4.3) p(\theta, X^n | y^n) \propto p(\theta) \cdot p(X^n | \theta) \cdot p(y^n | X^n, \theta)$$

A basic state space model is described in Figure 4.1.

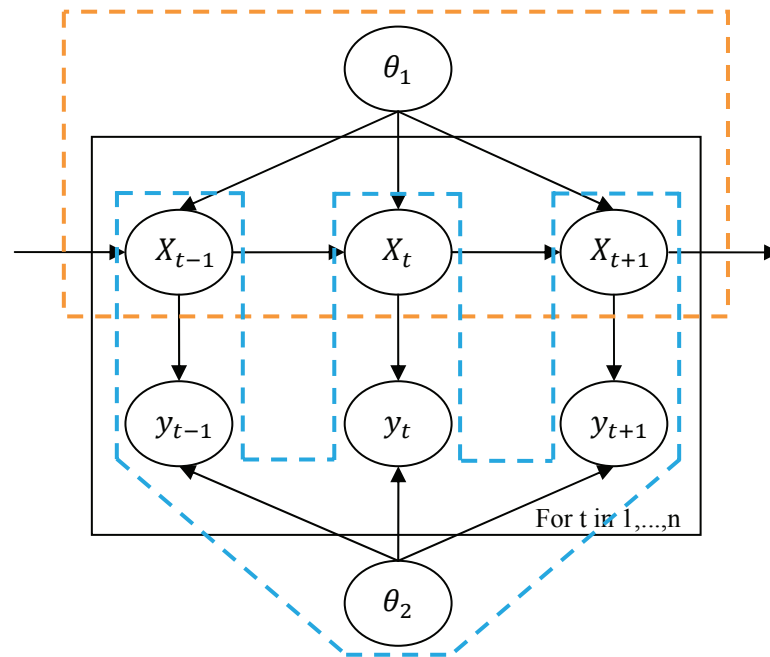


Figure 4.1: Graphical representation of a simple state-space model. The dashed orange frame represents the process model. The dashed blue frame represents the observation models  $X_t$  is a vector of hidden states during year  $t$ . The transition from  $X_t$  to  $X_{t+1}$  is conditioned by the parameters  $\theta_1$  and forms the process equation.  $y_t$  is a vector of observations of one or several hidden states during year  $t$ . These observations are conditioned by  $\theta_2$ , the vector of parameters of the different observation models. The relation between  $X_t$  and  $y_t$  corresponds to the observation equation.

In this study, I examined a large Atlantic salmon population located in the Foyle catchment (Ireland). This population has been exploited for several centuries and particularly during the 20<sup>th</sup> century. This study focused on the period from 1959 to present for which most monitoring data is available from the Loughs Agency (formerly the Foyle Fisheries Commission). The Loughs Agency is responsible for the management of the salmon population. The aim of the agency is “to manage [the] fisheries towards maximum sustainable exploitation for commercial and recreational purposes” (Loughs Agency, 2005). In order to do so, it is important to understand the regulatory mechanisms occurring in the population in order to (i) estimate the number of fish returning to river prior to homewater exploitation, i.e. pre-fishery abundances (PFAs), and (ii) to derive standard reference points (ICES, 1993) for assessing the population status with regards to its sustainable exploitation.

To this end, a state-space model is implemented within a Bayesian framework. A life stage and spatially structured dynamic model describes the lifecycle of the main components of Atlantic salmon in the Foyle catchment. Several empirical datasets related to the abundances of the stages at different scales of space and time, over a period of 50 years are



brought together. Observations and process errors are taken into account ultimately allowing PFAs to be estimated. A retrospective analysis is also carried out providing insights on the historical status of the population and its exploitation.

## **4.2. Material and methods**

### **4.2.1 Data**

The different datasets available provide information on the salmon population abundance at different stages during its lifecycle. Freshwater juvenile abundances are quantified by means of an index of abundance of young of the year (0+) fish. Information on the abundance of adults returning from the sea is obtained through the various fisheries occurring in the sea lough (drift net fisheries) and at the mouth of large rivers in the Foyle system (draft nets fisheries). The abundance of adults returning to the spawning grounds is assessed using fish counters and redd (spawning nests) counts.

#### **4.2.1.1 Geographical structure**

The catchment was divided in five geographical units (“geo units”) (Figure 1.2) to take in account the spatial structure of the population while coping with constraints imposed by the structure of the data collection scheme. Four geo units correspond to the wetted area above fish counter structures and are named after the main stream which flows through them (Faughan, Finn, Mourne and Roe). The last geo unit, named “Foyle” is composed of the wetted area of the remaining parts of the Foyle catchment but excluding the Culdaff River and the area north of the Faughan geo unit (Figure 4.2). These two areas do not hold any significant population of salmon.

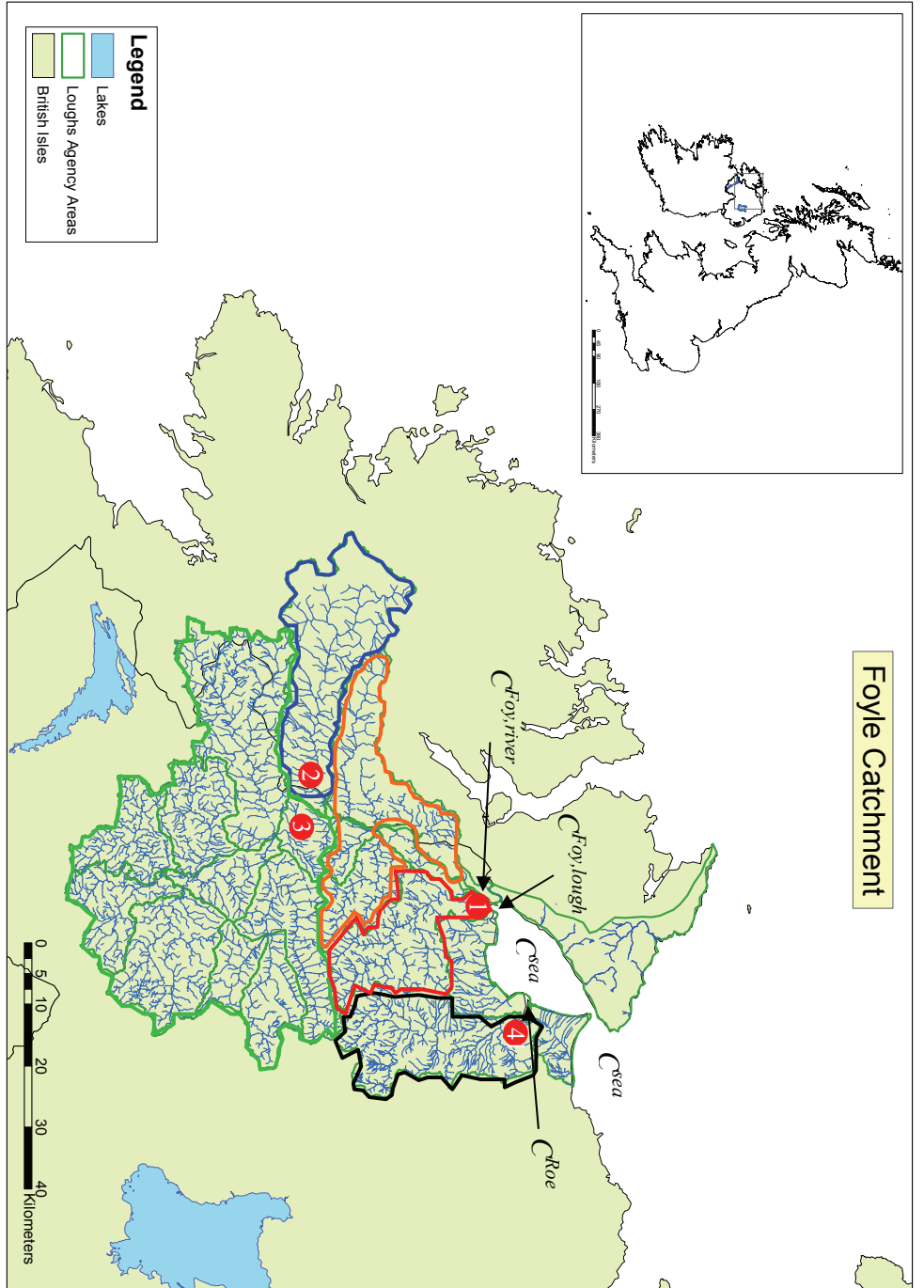


Figure 4.2: Map of the Foyle catchment with the location of the main commercial fisheries as named in Table 4.1, the units location in red, blue, green, black and orange for the Faughan, the Finn, the Mourne, the Roe and the Foyle respectively and, the counters location, 1) Faughan, 2) Finn, 3) Mourne and 4) Roe.

#### 4.2.1.1 Commercial fisheries data

Various commercial fisheries were conducted in the Foyle catchment between 1959 and 2008. The two main types of gears used were drift nets, which are gill nets deployed close to the surface in the sea lough and up to 12 miles out from the North coast and draft nets, which are seine nets deployed in the main river Foyle and the river Roe. Each year, up to 139 drift net licences were issued and split in three categories, 1) sea licences, allowing to fish exclusively in the open sea within a 12 miles range of the mouth of lough Foyle, 2) lough licences, allowing fishing exclusively in the sea lough and 3) sea and lough licences allowing to fish in both sea and lough. The drift and draft nets fishing season extended from the 1<sup>st</sup> of May to the 31<sup>st</sup> of August in 1959 and was consistently reduced over years to a fishing season extending from the 15<sup>th</sup> June to the 31<sup>st</sup> August in 2008. One supplementary licence was also issued to use fixed engines annually in the lough.

In addition, the Foyle Fisheries Commission (now the Loughs Agency) had its own draft nets fisheries in the main River Foyle and the river Roe (Foyle Fisheries: Culmore, Prehen, Roe and Rosses bay, Table 4.1). The Foyle Fisheries Commission also ran a stake netting fishery which were similar to fixed engine but were temporary. Time-series and location of these fisheries are described in Table 4.1 and Figure 4.2 and 4.3

*Table 4.1: Summary of the commercial fisheries catch in Lough Foyle and how the 5 geo units are affected by them.*

Model notation	Data source	Length of the time-series	Geo units affected
$C_{t,tot}^{d,s}$	Drift nets (sea only)	1959 to 2006	All geo units
$C_{t,tot}^{d,s+l}$	Drift nets (sea + lough)	1959 to 2006	
$C_{t,tot}^{d,l}$	Drift nets (lough only)	1959 to 2008	
$C_{t,tot}^f$	Fixed engines	1963 to 1990	
$C_{t,tot}^{Foy,lough}$	Draft nets (Foyle, Faughan)	1959 to 2008	Faughan, Finn,
	Foyle Fisheries (Rosses bay)	1959 to 1980	Mourne and Foyle
$C_{t,tot}^{Foy,river}$	Foyle Fisheries (Culmore)	1959 to 1988	Finn, Mourne
	Foyle Fisheries (Prehen)	1959 to 1970	and Foyle
$C_t^{Roe}$	Draft nets (Roe)	1959 to 2004	Roe only
	Foyle Fisheries (Roe)	1959 to 1972	

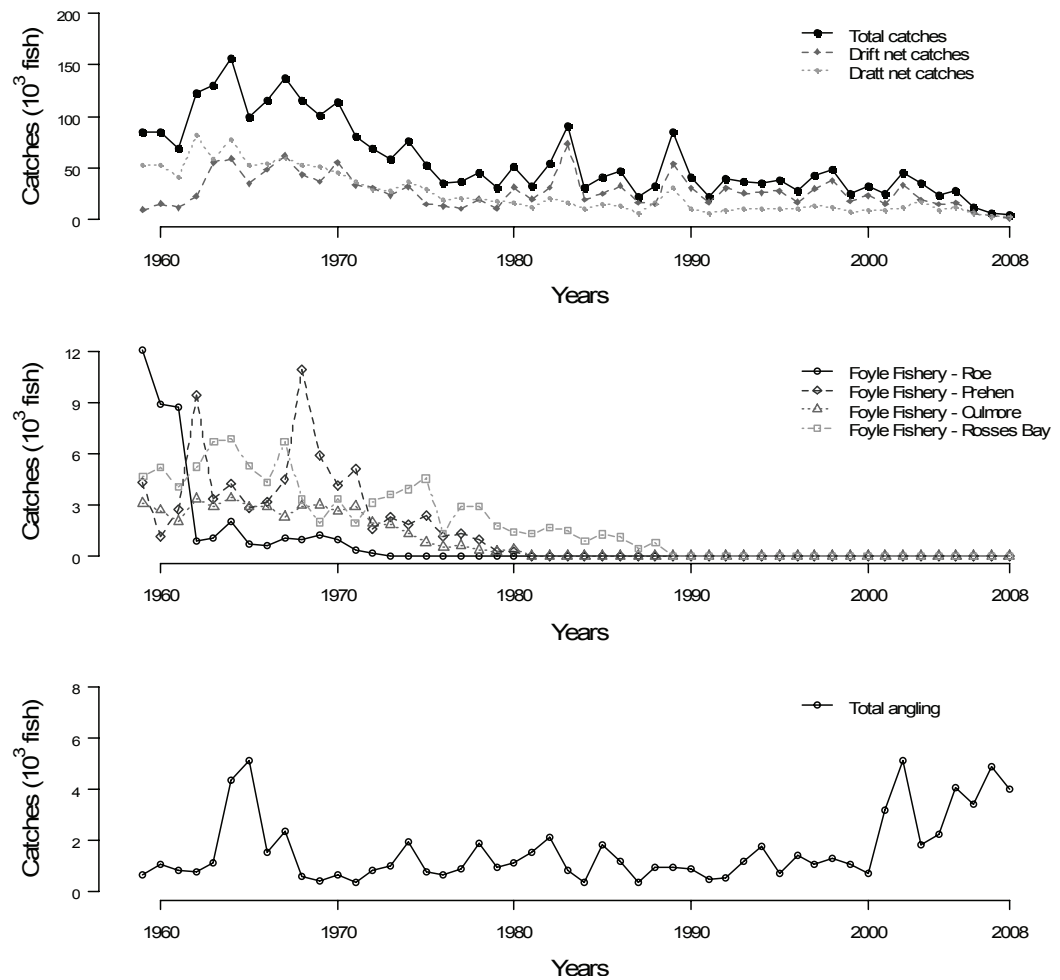


Figure 4.3: Detailed time series of the different fisheries occurring in the Foyle catchment.

#### 4.2.1.2 Fish counter data

Resistivity counters (Fewings, 1994) provided data on the number of adult salmon returning from the sea to the Foyle catchment from 2001 to 2006. They are located at the downstream end of four main branches of the the Foyle system, i.e. the Faughan, the Finn, the Mourne and the Roe in order to determine the number of adult salmon migrating into these geo units (Figure 4.2). Three counters (on the Faughan, Finn and Roe) effectively count all fish passing the counters locations, thus allowing total fish counts. The Mourne counter only offers partial counts. All counters detect upstream and downstream movements of any fish with a body length greater than 45 cm. This detection threshold is lower than the minimum size of a returning adult salmon in the Foyle system. Given the location of the counters and their size threshold for detection, the number of fish other than salmon that might be included in the counts is considered negligible relative to the number of salmon. Subtracting total downstream movements from total upstream movements provides the total number of salmon which returned in a geo unit for a given year.

### 4.2.1.3 Redd counts

From 1959 to present, the Loughs Agency has annually counted redds during and immediately following the spawning period in approximately 260 zones which correspond to 14 main rivers and tributaries within the catchment. Depending on the year, up to 33% of the total wetted area of a geographical unit was walked to count redds. Despite the fact that the accuracy of counting is dependent of environmental conditions (e.g. when high flow, the poor visibility reduces the reliability of the counting) it is a valuable and widely used method for long-term salmonids population monitoring (Elson and Tuomi, 1975; Isaak *et al.*, 2003). In 1997, weather conditions did not allow redd counting in the Faughan and the Roe.

### 4.2.1.4 0+ Juvenile index of abundance

Following the technique described by Crozier and Kennedy (1994), the Loughs Agency field staff have been collecting 0+ juvenile index of abundance every year since 1998. The index is the number of 0+ juvenile salmon caught during a 5 minutes electrofishing sampling at a given site. Between 77 and 476 sites were sampled every year between July and September, covering the whole catchment. The quality of the habitat for 0+ juveniles was evaluated as good or poor following the DANI's recommendations (see Table 2.1). The total wetted area of nursery habitat wetted  $W_i$  measured in  $m^2$  of good nursery habitat equivalent is calculated for each geo unit as  $W_i = W_i^{G1} + W_i^{G2}/\rho$ , where  $W_i^{G1}$  and  $W_i^{G2}$  are the wetted areas of good and poor habitat available in each geo unit (Table 4.2) and  $1/\rho$  is the ratio between average 0+ densities in good habitats and average densities in poor habitats (see chapter 2, section 2.2.2).

Table 4.2: Wetted areas of good and poor nursery habitat available in each geo unit ( $W_i^{G1}$  and  $W_i^{G2}$ ), the total wetted area of nursery habitat available ( $W_i^{tot}$ ) and the total nursery habitat wetted area in good nursery habitat equivalent ( $W_i$ ).

Geo unit	$W_i^{G1}(m^2)$	$W_i^{G2}(m^2)$	$W_i^{tot}(m^2)$	$W_i(m^2)$
Faughan	266992	158793	425785	343778
Finn	1157446	174863	1332309	1242003
Mourne	3613113	1188973	4802086	4188052
Roe	342450	595285	937735	630305
Foyle	313346	564840	878186	586479

## 4.2.2 Modelling

The approach proposed by Craigmile *et al.* (2009) for building complex models was followed. Thus, the different observation models were developed first and their model fit assessed independently. The first versions of the dynamic model were adjusted using point estimators of the hidden states (i.e. ignoring the observation error). The observation models were then added one after another to a basic dynamic model and the model fit was assessed every time something new was incorporated (adding a new observation process or making changes in the dynamic model).

Assumptions about the processes linking the different life stages are described in section 4.2.2.1 in order to present the modelling of the salmon lifecycle. Observation models are described in the second section. They were linked either directly to the dynamic model (e.g. counters data, redds data) or, if the structure of the model is too complex (e.g. 0+ juvenile densities), the likelihoods contribution of these models are calculated independently from the dynamic model and then approximated and integrated using the pseudo-observations technique (Mäntyniemi, 2005; Michielsens *et al.*, 2008).

### 4.2.2.1 Exploitation and populations dynamics model

#### a. 0+ juvenile to adult survival

The returning adult abundance prior to homewater fisheries (pre-fishery abundance)  $PFA_{t,i}$  is assumed to follow a log-normal distribution, with mean  $\mu_{t,i}^{PFA}$  and variance  $\sigma^{PFA}$ .

$$(4.4) \text{Log}(PFA_{t,i}) = \mu_{t,i}^{PFA} + \varepsilon_{t,i} \text{ and } \varepsilon_{t,i} \sim \text{Normal}(0, \sigma^{PFA})$$

Where

$$(4.5) \mu_{t,i}^{PFA} = \text{Log}(p^J \cdot J_{t-3,i} + (1 - p^J) \cdot J_{t-4,i}) + \text{Log}(s_{t,i}^J)$$

$\mu_{t,i}^{PFA}$  is the average  $\text{Log}(PFA)$  for each geo unit each year, it depends on the juvenile abundances three and four years earlier. Juveniles  $J_{t,i}$  are assumed to complete their lifecycle and return as adults mainly in 3 or 4 years. The proportions of juveniles returning as adults after 3 or 4 years are  $p^J$  and  $1 - p^J$  respectively. Based on status reports from the

Loughs Agency (1953 to 1963) this assumption takes into account more than 95% of the possible life histories occurring in the Foyle catchment.  $s_{t,i}^J$  is the mean survival from 0+ juveniles to returning adults for the year  $t$  and the geo unit  $i$ .  $\varepsilon_{t,i}$  is the residual effect ( $\varepsilon_{t,i} = PFA_{t,i} - \mu_{t,i}^{PFA}$ ) and accounts for additional variations that are not explicitly described in the 0+ juveniles to returning adults survival model.

$s_{t,i}^J$  is the result of combined annual variations which are common to salmon from all geo units (this reflects the assumption that salmon from each geo unit of the Foyle catchment spend their time at sea in the same areas, ) and geo unit variations (during the freshwater life stages, from 0+ juveniles to smolts) which are common to all years. The survival is not bounded between 0 and 1 to reflect the fact that some fish from other geo units can return in another geo unit than the one they were originating from. This means that theoretically (if all the juveniles of a geo units returns as adults in the geo units they originate from and if some adults originating from other geo units return in this geo units) the “survival”  $s_{t,i}^J$  can be higher than 1.

$$(4.6) \text{Log}(s_{t,i}^J) = \gamma_t + v_i$$

$v_i$  accounts for the variation across geo units. It follows a normal distribution centered on 0 with a variance  $\sigma^v$ .  $\gamma_t$  is the average across geo unit annual survival effect. The  $\gamma_t$  are autocorrelated in order to reflect the environmental changes leading to variation are likely to be dependent on the environmental conditions of the previous year. They are assumed to vary according to a normal distribution centered on  $\gamma_{t-1}$  with a random residual variation  $\eta_t$  (Box *et al.*, 1996; Chatfield, 1996).

$$(4.7) \gamma_1 | \gamma_0, \sigma^v \sim \text{Normal}(\gamma_0, \sigma^v)$$

And for  $t > 1$

$$(4.8) \gamma_t = \gamma_{t-1} + \eta_t \quad \text{and} \quad (4.9) \eta_t | \sigma^v \sim \text{Normal}(0, \sigma^v)$$

#### b. Commercial fisheries

The adults escaping from the commercial fisheries are calculated by subtracting the number of fish caught by commercial fisheries  $C_{t,i}^{com}$  from the  $PFA_{t,i}$

$$(4.10) A_{t,i} = PFA_{t,i} - C_{t,i}^{com}$$

All the fisheries do not affect geo units in the same way and the fisheries capture are dependent on where fisheries are operating (Figure 4.2 and Table 4.1).

$$(4.11a) C_{t,1}^{com} = C_{t,1}^{sea} + C_{t,1}^{Foy,lough} \quad \text{for the Faughan unit}$$

$$(4.11b) C_{t,2}^{com} = C_{t,2}^{sea} + C_{t,2}^{Foy,lough} + C_{t,1}^{Foy,river} \quad \text{for the Finn unit}$$

$$(4.11c) C_{t,3}^{com} = C_{t,3}^{sea} + C_{t,3}^{Foy,lough} + C_{t,2}^{Foy,river} \quad \text{for the Mourne unit}$$

$$(4.11d) C_{t,4}^{com} = C_{t,4}^{sea} + C_t^{Roe} \quad \text{for the Roe unit}$$

$$(4.11e) C_{t,5}^{com} = C_{t,5}^{sea} + C_{t,4}^{Foy,lough} + C_{t,3}^{Foy,river} \quad \text{for the Foyle unit}$$

The different types of fisheries only provide data on total catches cumulated over the various geo units concerned. Therefore, it is assumed that all geo units affected by one specific fishery will have the same exploitation rate as the other geo units affected by this fishery. Since the geo unit origin of the adult salmon caught by the various fisheries is not available, this is the most parsimonious choice. In other words, catches for one geo unit are calculated proportionally to the abundance before the Foyle fisheries exploitation  $PFA_{t,i}$

$$(e.g. for the Finn:  $C_{t,fin}^{Foy,river} = \frac{PFA_{t,2}}{PFA_{t,2}+PFA_{t,3}+PFA_{t,5}} \cdot C_{t,tot}^{Foy,river}$ ).$$

Licence holders who can fish outside of the lough can catch salmon originating from rivers outside of the Foyle catchment (Ensing and Crozier, 2008).  $C_{t,tot}^{sea}$  corresponds to the total number of fish caught by drift nets and fixed engines every year. The drift nets sea only licence holders have an unknown probability  $p_1^F$  of capturing adult salmon from the Foyle system. The probability of catching a fish from rivers of the Foyle catchment for the drift nets sea and lough licence holder  $p_2^F$  is assumed to be higher than the probability of sea only licence holder  $p_1^F$  since they spend on average less time fishing outside of the lough. Finally, it was assumed that all fish caught by lough-only licence holders originated from the Foyle catchment.

$$(4.12) C_{t,tot}^{sea} = p_1^F \cdot C_{t,tot}^{d,s} + p_2^F \cdot C_{t,tot}^{d+l} + C_{t,tot}^{d,l} + C_{t,tot}^f$$

### c. Spawner abundances and density dependence



Spawner abundances  $S_{t,i}$  are calculated by subtracting the rod catches  $C_{t,i}^{rod}$  from the adult abundances

$$(4.13) S_{t,i} = A_{t,i} - C_{t,i}^{rod}$$

Spawners are related to the 0+ juvenile densities of the following year with a Beverton and Holt density dependence relationship (Beverton and Holt, 1957). This density dependence relationship was retained following Walters and Martell (2004) recommendation to use it for salmonid juveniles.

The 0+ juvenile densities  $d_{t+1,i}^{\mu}$  are assumed to follow a Log Normal distribution with mean and standard deviation parameters  $\mu_i^d$  and  $\sigma^d$  respectively.

$$(4.14) d_{t+1,i}^{\mu} | \mu_i^d, \sigma^d \sim \text{LogNormal}(\mu_i^d, \sigma^d)$$

Where

$$(4.15) \mu_i^d = \text{Log} \left( \frac{S_{t,i}^{sqm}}{\alpha^d + \beta_i^d \cdot S_{t,i}^{sqm}} \right)$$

and

$$(4.16) S_{t,i}^{sqm} = S_{t,i} / W_i$$

$S_{t,i}^{sqm}$  is the number of spawners per square meter of good nursery habitat equivalent (Table 4.2).  $W_i$  is the total nursery habitat wetted area in good nursery habitat equivalent calculated for each geo unit (see section 4.2.1.4).  $\alpha^d$  is inversely related to the slope of the Beverton and Holt relationship close to the origin  $a^d$  and is assumed to be the same for all geo units:  $\alpha^d = 1/a^d$ . Alternative hypothesis of considering geo unit specific  $a^d$  was tested but did not show any significant differences between geo units, therefore the parsimonious choice of a single  $a^d$  for all geo units was retained.  $a^d$  is the average maximum number of 0+ juveniles that one spawner can produce.  $\beta_i^d$  is inversely related to the average maximum 0+ juvenile density  $d_i^{max}$  for each geographical unit:  $\beta_i^d = 1/d_i^{max}$ . The  $d_i^{max}$  are assumed to be drawn from a log-normal distribution with common mean and standard deviation parameters  $\mu^{dmax}$  and  $\sigma^{dmax}$  respectively.

$$(4.17) d_i^{max} | \mu^{dmax}, \sigma^{dmax} \sim \text{LogNormal}(\mu^{dmax}, \sigma^{dmax})$$

0+ juvenile abundances for each unit  $J_{t+1,i}$  are then calculated from the density estimates and the total wetted area in good nursery habitat equivalent.

$$(4.18) J_{t+1,i} = d_{t+1,i}^{\mu} \cdot W_i$$

#### 4.2.2.2 Observation models

##### a. Adult observations

For the Faughan, the Finn and the Roe, counters are assumed to count all salmon movements and therefore provide exact adult abundances. For the Mourne unit the proportion of salmon counted  $p^N$  is unknown and potentially variable according to the year. The fish counted by the counter on the Mourne are assumed to follow a Log normal distribution whose mean parameter is the Log of a mean proportion of the adult escaping from the fisheries.

$$(4.19) N_{t,3} | \mu_{t,3}^N, \sigma^N \sim \text{LogNormal}(\mu_{t,3}^N, \sigma^N) \text{ and } (4.20) \mu_{t,3}^N = \text{Log}(p^N \cdot A_{t,3})$$

##### b. Spawner observations

The same model as the one described in chapter 3 was used to relate salmon spawners to redd counts. However, two modifications were made in order to include redd counts from the Mourne and Foyle units. Redd counts are assumed to be related to the spawner abundance through a Poisson distribution as follow:

$$(4.21) R_{t,i} | \lambda_{t,i}^R \sim \text{Poisson}(\lambda_{t,i}^R)$$

$$(4.22) \lambda_{t,i}^R = S_{t,i} \cdot P_{t,i}^R \cdot \kappa_{t,i}$$

$\kappa_{t,i}$  is the yearly average number of redds counted per spawner. It is assumed in this model that all  $\kappa_{t,i}$  are drawn from the same pdf as early trials for differences across geo units did not reveal any significant geo unit effect.

$$(4.23) \kappa_{t,i} | \alpha^{\kappa}, \beta^{\kappa} \sim \text{Gamma}(\alpha^{\kappa}, \beta^{\kappa})$$

$$(4.24) \alpha^{\kappa} = \mu^{\kappa} \cdot \beta^{\kappa}$$

Where  $\mu^\kappa$  is the mean value of  $\kappa_{t,i}$ .  $P_{t,i}^R$  is the proportion of the wetted area surveyed for redd counting. The logit of  $P_{t,i}^R$  is assumed to follow a Normal distribution:

$$(4.25) \text{Logit}(P_{t,i}^R) | \mu_i^P, \sigma^P \sim \text{Normal}(\mu_i^P, \sigma^P)$$

Where  $\mu_i^P$  is the average (logit) proportion of the total wetted area. Following early trials of the models it was chosen to arrange geo units into two groups, the first one composed of the Faughan and the Roe units ( $\mu_1^P = \mu_4^P$ ) and the second one composed of the Finn, the Mourne and the Foyle units ( $\mu_2^P = \mu_3^P = \mu_5^P$ ). This distinction was made because the Faughan and Roe are surveyed more intensively than the other geo units. This could be due to their closer location to the headquarters of the Loughs Agency.

### c. Juvenile observations

The posterior distributions of the average 0+ juvenile densities derived from the model described in chapter 2 were included in the dynamic model. The observation model providing the density estimates cannot be incorporated directly in the process model for practical reason: the time required to make inferences via MCMC methods would be too long. Therefore, a simplified model that allows making approximately the same inferences about the process model than the inference that would be made with the complex observation model was used. To do so, the pseudo-observations technique is implemented. A pseudo-observation is a numerical value which, when given the right conditional prior, provides a likelihood functions for a given variable Y that is similar to the posterior distribution of Y obtained from a complex observation model (Mäntyniemi, 2005; Michielsens *et al.*, 2008). This can be achieved easily by utilising well known conjugate distributions (Table 2.1 Table 4.3): a Normal model produces a likelihood function for the mean parameter that is proportional to a Normal pdf; a Poisson model yields a Gamma-shaped likelihood function for the rate parameter; and a beta-shaped likelihood function is generated by a Binomial model (Gelman *et al.*, 2004).

In the dynamic model describing the life cycle of salmon in the Foyle catchment, average densities  $d_{t+1,i}^\mu$  are conditioned by the number of spawners  $S_{t,i}$  who entered the geo unit the precedent year, density dependence parameters  $\Theta_i$  which are peculiar to each geo unit and some parameters common to all geo units and years  $\Phi$  (see equations 4.4-4.25). The posterior distributions of  $d_i^\mu$  obtained from the observation model fitted Log Normal

distributions and conjugate Normal distributions were applied to the median of the associated pseudo-observation. For the sake of illustration a DAG was designed to show how the pseudo-observations are integrated in the dynamic model (Figure 4.4).

Table 4.3: Overview of how different pdfs obtained from observation models can be incorporated within subsequent dynamic models by using conjugate pdfs and corresponding pseudo-observations.  $\mu$ : posterior mean;  $m$ : posterior median;  $\sigma^2$  posterior variance;  $CV$ : posterior coefficient of variation;  $a$ : posterior lower bound;  $b$ : posterior higher bound.

Posterior pdf for $\mu_i^d$	Pseudo-observation within the life-cycle model
$d_i^\mu \sim \text{Normal}(\mu, \sigma^2)$	$\mu \sim \text{Normal}(d_i^\mu, \sigma^2)$
$d_i^\mu \sim \text{LogNormal}(m, CV)$	$\log(m) \sim \text{Normal}(\log(d_i^\mu), \log(CV^2 + 1))$
$d_i^\mu \sim \text{Gamma}(\mu, CV)$	$1/CV^2 \sim \text{Poisson}(d_i^\mu / (\mu \cdot CV^2))$
$d_i^\mu \sim \text{Beta}(\mu, CV)I(a, b)$	$\frac{b - \mu}{b - a} \cdot \left(\frac{\mu - a}{CV \cdot \mu}\right)^2 - \frac{\mu - a}{b - a} \sim \text{Binomial}\left(\frac{(b - \mu) \cdot (\mu - a)}{(CV \cdot \mu)^2} - 1, \frac{d_i^\mu - a}{b - a}\right)$

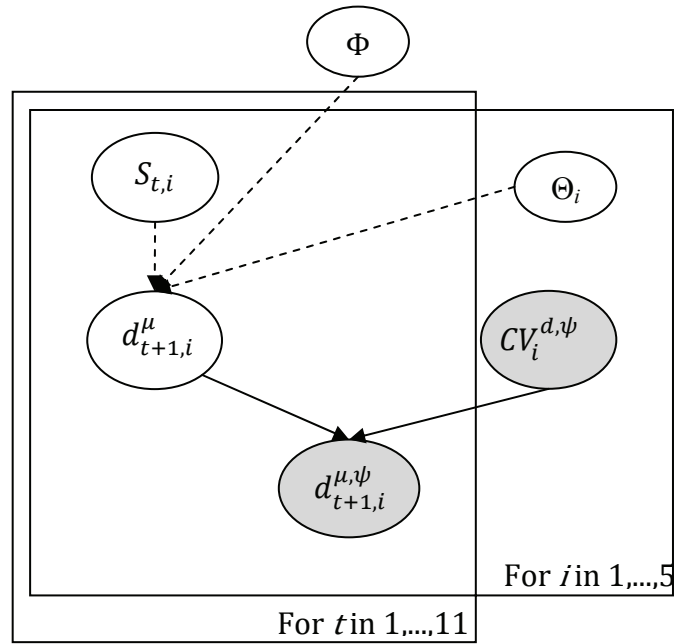
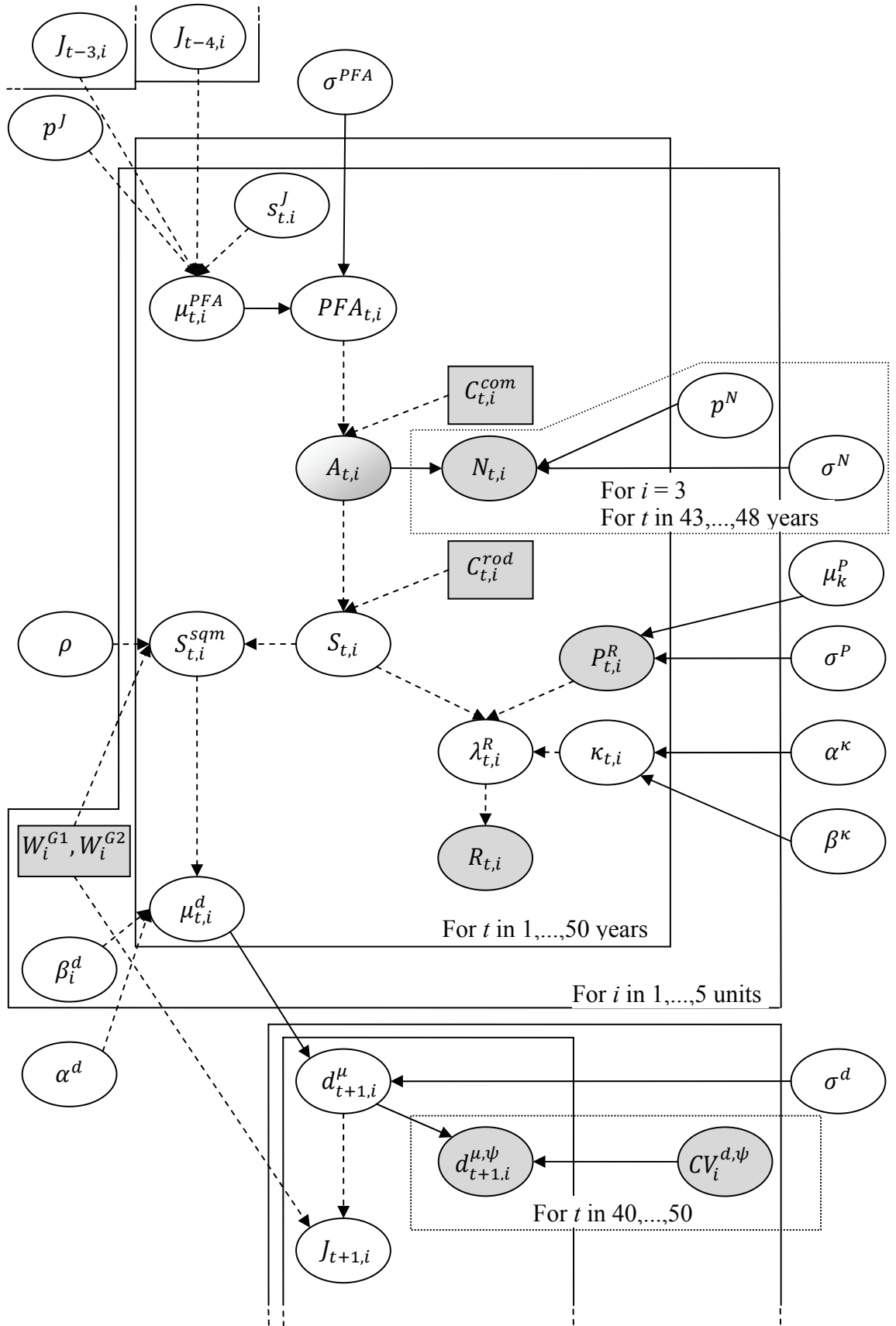


Figure 4.4: Directed acyclic graph (DAG) representing how average 0+juvenile densities are integrated to the full life cycle model as pseudo-observations.  $d_{t+1,i}^{\mu,\psi}$  and  $CV_i^{d,\psi}$  are greyed as they are considered as pseudo-observed. Arrows represent the parent-child dependencies between the different nodes: single arrows represent probabilistic relationship between the parent(s) and child nodes, dashed arrows indicate deterministic relationship. The frame represents a repetition of structure over geo units ( $i$ ) and years ( $t$ ). See text for the meaning of  $\Theta_i$  and  $\Phi$ .

### 4.2.2.3 A summary: Directed Acyclic Graph (DAG)

The dynamic model and the observation models (equations 4.4-4.25) can be brought together in a DAG (Figure 4.5).

*Figure 4.5 (next page): Simplified Directed Acyclic Graph (DAG) of the state-space model described in equations 4.1 to 4.22. Ellipses represent random variables. Squares represent fixed quantities, covariates in our case. All observable quantities are greyed. Arrows represent the parent-child dependencies between the different nodes: plain arrows represent probabilistic relationship between the parent(s) and child quantities, dashed arrows indicate deterministic relationship. A frame represents a repetition of structure over years or geo units. Quantities outside the frame are unknown parameters constant across sites. Note: (i) for the survival from 0+ juvenile to returning  $s_{t,i}^J$ , the year, geo units and residuals effects were not represented. (ii)  $A_{t,i}$  are observed for the Faughan, Finn and Roe units ( $i = \{1,2,4\}$ ) between 2001 and 2006 ( $t = \{43, \dots, 48\}$ ).*



#### 4.2.2.4 Priors

Most of the parameters described in section 4.2.2.1 and 4.2.2.2 were given weakly informative priors (Gelman, *in press*), to reflect the lack of knowledge on these parameters (Table 4.4). However, for some parameters, information is available and worth incorporating. This was the case for the slope of the density dependence relationship  $a^d$  and the probability of capturing fish originating from the Foyle rivers when using sea and sea and lough drift net fisheries.

Based on the literature, I calculated a maximum value of how many juveniles could be produced by one spawner ( $a^d$ ) using the sex ratio from the Foyle catchment (Elson and Tuomi, 1975), fecundity of adults (Moffett *et al*, 2006) and survival from eggs to swim-up fry (Crozier and Kennedy, 1995) of Atlantic salmon from the river Bush. The Bush is a river geographically close to the Foyle catchment which benefits from a more detailed monitoring of its salmon population. The value obtained was 1843 0+ juveniles per spawner. As the survival between the swimup fry stage (February-March) and the moment the 0+ juveniles are sampled (July-August) is not taken into account,  $a^d$  was given a triangular distribution between 0 and 1843 with a higher probability of low values to reflect the belief that the higher values of this parameters are not likely to occur.

Table 4.4: Summary of non-informative priors of the model.

Parameters	Distribution
$\sigma^{PFA}$	$\sim$ Uniform (0,10)
$p^J$	$\sim$ Beta (2,2)
$\gamma_0$	$\sim$ Normal (0,0.001)
$\sigma^Y$	$\sim$ Uniform (0,10)
$\sigma^v$	$\sim$ Uniform (0,10)
$\sigma^d$	$\sim$ Uniform (0,10)
$Log(\mu^{dmax})$	$\sim$ Uniform (-5,5)
$\sigma^{dmax}$	$\sim$ Uniform (0,10)
$\sigma^N$	$\sim$ Uniform (0,10)
$p_3^N$	$\sim$ Beta (1,1)
$\mu^\kappa$	$\sim$ Gamma (0,0.001)
$\sigma^\kappa$	$\sim$ Uniform (0,10)
$\mu_k^P$	$\sim$ Beta (1,1)
$\sigma^P$	$\sim$ Uniform (0,10)

Ensing and Crozier (2008) found that at least 15 % of the salmon caught by sea-only drift net licence fishermen originate from rivers outside of the Foyle catchment. This information was incorporated into the prior distribution by attributing to  $p_1^C$  a weakly informative Beta distribution, rescaled to lie between 0 and 0.85 reflecting the assumption that extreme values (i.e. no salmon or 85% came from the Foyle system) are not likely to occur. In the same way we incorporated our assumption that the proportion of fish originating from the Foyle catchment caught by the sea and lough licence holders was always higher than  $p_1^C$  by attributing to  $p_2^C$  a non informative Beta distribution rescaled to lie between  $p_1^C$  and 1. Information on the origin of salmon caught in the drift net fisheries was available for only one year. For that reason the parsimonious assumption that these probabilities were constant over the time-series was made.

Equations 4.4 and 4.5 assume that the PFA of a given year is calculated conditionally on the juvenile production  $J$ , three and four years earlier. As a consequence, the first four years of the model need to be initialised (no data or estimates of  $J$  are available for these years). The juvenile production  $J$  between 1955 and 1958 (the years involved in the calculation of the PFAs for the four first year of the model) are calculated based on equations 4.14 to 4.18. The spawners  $S_{t,i}$  for these years were given weakly informative priors in the form of a uniform distribution covering a wide range of spawner abundances corresponding to posterior distributions of spawner abundances encountered in early versions of the state-space model presented in this chapter. These priors were little sensitive to the upper limit of the spawners abundance range since the shape of the Beverton and Holt relationship has a maximum 0+ juvenile density ceiling.

### **4.2.3 Parameters of management interest**

Using the density dependent relationship presented above (Equation 4.15) reference points (\*) corresponding to maximum sustainable yield (MSY) such as exploitation rate  $h^*$  and spawner abundance  $S^*$  can be calculated.  $S^*$  is the international standard for conservation limits chosen by the North Atlantic Salmon Conservation Organisation (NASCO) (ICES, 1993). Schnute and Kronlund (2002) give an extensive description of how these reference points are obtained. When the stock-recruitment relationship is stationary over time the reference points are also stationary. In this study, the 0+ juvenile to returning adult survival is non-stationary (i.e. dynamic, varying every year) which leads to non-stationary (i.e. dynamic, varying every year) reference points. The reference points  $h_{t,i}^*$  and  $S_{t,i}^*$  need to be



re-calculated each year  $t$  and are directly related to  $a^d$ ,  $d_i^{max}$  and  $s_{t,i}^J$  based on Schnute and Kronlund (2002) calculations.

$$(4.26) h_{t,i}^* = 1 - \sqrt{\frac{1}{a_{t,i}^{PFA}}}$$

where  $a_{t,i}^{PFA} = a^d \cdot (p^J \cdot s_{t+4,i}^J + (1 - p^J) \cdot s_{t+5,i}^J)$

$a_{t,i}^{PFA}$  is the slope of the Beverton and Holt relationship recalculated to provide a spawner to spawner relationship, which is obtained by calculating the average number of 0+ juveniles surviving in each cohort (3 years or 4 years life histories).

$$(4.27) S_{t,i}^* = \frac{h_{t,i}^* \cdot d_i^{max} \cdot a^d}{(1 - h_{t,i}^*)}$$

The equations 4.26 and 4.27 provide the reference points for the cohort of adults which will return 4 and 5 years after the adults spawned.  $h_{t,i}^*$  and  $S_{t,i}^*$  refer to the year of spawning corresponding to a cohort. The reference points are re-calculated to provide annual “reference points”  $h'_{t,i}$  and  $S'_{t,i}$  for the adults returning any given year, which are the result of two cohorts produced from spawners 4 and 5 years earlier can be calculated. First the theoretical number of returning adults  $R'_{t,i}$  is calculated.

$$(4.28) R'_{t,i} = (p^J \cdot BH(S_{t-4,i}^*) + (1 - p^J) \cdot BH(S_{t-5,i}^*)) \cdot s_{t,i}^J \cdot W_i$$

$$\text{Where } BH(S_{t,i}) = \frac{S_{t,i}}{\alpha^d + \beta_i^d \cdot S_{t,i}}$$

In a similar way, if both cohorts are exploited with a reference exploitation rate  $h^*$  the new “reference” capture will be:

$$(4.29) C'_{t,i} = (h_{t-4,i}^* \cdot p^J \cdot BH(S_{t-4,i}^*) + h_{t-5,i}^* \cdot (1 - p^J) \cdot BH(S_{t-5,i}^*)) \cdot s_{t,i}^J \cdot W_i$$

The new reference exploitation rate  $h'_{t,i}$  is calculated from  $h'_{t,i} = C'_{t,i}/R'_{t,i}$  and the new conservation limit  $S'_{t,i}$  is obtained from  $S'_{t,i} = R'_{t,i} - C'_{t,i}$ .

#### 4.2.4 Inter-generation replacement ratio (IGRR)

The IGRRs look at the ability of a given life stage cohort to replace the same life stage cohort that produced it. This approach is largely described by Rago (2001). More specifically, I look at the spawners of a given year compared to the combined cohort of spawners that produced them 4 and 5 years before (see Equation 4.5). To look at the impact of fisheries I calculate two IGRRs: the first one before exploitation ( $\Phi^{PFA}$ ) and the second one after exploitation ( $\Phi^S$ ).

$$(4.30a) \quad \Phi^{PFA} = \frac{PFA_{t,i}}{p^J \cdot S_{t-4,i} + (1 - p^J) \cdot S_{t-5,i}}$$

$$(4.30b) \quad \Phi^S = \frac{S_{t,i}}{p^J \cdot S_{t-4,i} + (1 - p^J) \cdot S_{t-5,i}}$$

An IGRR equal to 1 indicates that the population is stable (i.e. one spawner produces one spawner). An IGRR under 1 indicates that the population is declining (i.e. one spawner produces less than one spawner). Finally, an IGRR higher than 1 shows that the population is growing (e.g. one spawner produces more than one spawner).

#### 4.2.5 Bayesian inference and posterior computation

The joint posterior distribution of all the model unknowns (i.e. unobservable quantities and observables in case of missing data) was approximated using MCMC sampling (Gelman *et al.*, 2003). All computations were carried out with the OpenBUGS<sup>®</sup> software (version 3.0.3; Thomas *et al.*, 2006; Spiegelhalter *et al.*, 2007) and the Lattice and Coda packages of R (version 2.5.1, [www.r-project.com](http://www.r-project.com)). We used the Gelman-Rubin (Brooks & Gelman, 1998) diagnostics as implemented by OpenBUGS<sup>®</sup> to test the convergence of the MCMC sampling on the model parameters. Three chains with contrasted starting points were used. The Gelman-Rubin statistic indicated good mixing of the MCMC chains was obtained after  $4 \cdot 10^6$  iterations. An additional sample of 10 000 values ( $4 \cdot 10^6$  iterations, but retaining 1 iteration every 400) from a single chain was then used to approximate posterior distributions. In addition, the stationarity of the mean and dispersion of the MCMC chains was checked using OpenBUGS build-in tools.

### 4.2.6 Posterior checking

Following the approach proposed by Gelman *et al.* (1996), the compatibility between the assumed model and the data was checked by means of posterior predictive assessment techniques. These techniques extend classical goodness-of-fit test in the Bayesian setting by averaging over the posterior distribution of unknown quantities of the model. The observation models were checked as they were built (see chapter 2, sections 2.2.2.2 and 2.3.6.3; chapter 3, section 3.2.4). Following Craigmile's approach (2009), observation models and changes about the process model were added progressively, checking the results progressively. Various checks included checking the overall coherence of the life stage estimates and the modelling hypothesis such as the sequential independence of the residuals, the independence of several series of residuals and verified that these series of residuals were centred on 0.

### 4.2.7 Predictions

PFA's for 2009 and 2010 were estimated from the constructed model. Predictions were made only for 2 years; this corresponds to the years for which the cohorts of 0+ juveniles that will produce the returning adults of the predicted year are available. The prediction of 0+ juvenile production is very uncertain and leads to significant increase of the uncertainty of the estimations to a point where they cannot be used for any management purpose.

## 4.3. Results

### 4.3.1 Observation models

#### 4.3.1.1 Spawner observations

Apart from the Mourne counter variance parameter  $\sigma^N$  which is poorly estimated (coefficient of variation = 74.8%), all the other parameters of the observation model relating redd counts to spawner abundances are accurately estimated with coefficients of variation ranging from 9.6 % to 13.1% (Table 4.5). Over all the prior distributions were significantly updated. The probability of counting adults returning in the river at the Mourne unit counter is low. On average slightly more than a third of the total fish are

counted for this geo unit ( $p_3^N = 0.344$ ). A bit less than one redd is counted for every two spawners ( $\mu^\kappa = 0.403$ ) (Table 4.5).

Table 4.5: Summary statistics of the marginal posterior distributions of the main observation model parameters.

Parameters	mean	sd	2.5%	25%	median	75%	97.5%
$\sigma^N$	0.115	0.086	0.025	0.055	0.092	0.151	0.337
$p_3^N$	0.344	0.045	0.270	0.312	0.339	0.371	0.441
$\mu^\kappa$	0.403	0.029	0.349	0.383	0.402	0.422	0.465
$\sigma^\kappa$	2.903	0.278	2.399	2.710	2.889	3.084	3.482
$\mu_1^P$	0.245	0.027	0.198	0.227	0.244	0.263	0.302
$\mu_2^P$	0.123	0.013	0.101	0.114	0.123	0.131	0.150
$\sigma^P$	0.536	0.043	0.458	0.506	0.533	0.564	0.625

#### 4.3.1.2 Juvenile observations

In a great majority of cases, the comparison of prior and posterior distributions of the average 0+ salmon densities  $d_{t,i}^\mu$  shows a significant updating of the pseudo-likelihood distribution as a result of the information brought by the different datasets (other than the juvenile survey data) and the structure of the dynamic model (Figure 4.5). The mean of the marginal posterior distribution of  $d_{t,i}^\mu$  and the probability of obtaining 0+ juvenile densities higher than 7 fish.m<sup>-2</sup>, which is the maximum density of wild juvenile salmonids described in the literature (Niemelä *et al.*, 2005), are both considerably reduced (Figure 4.6).

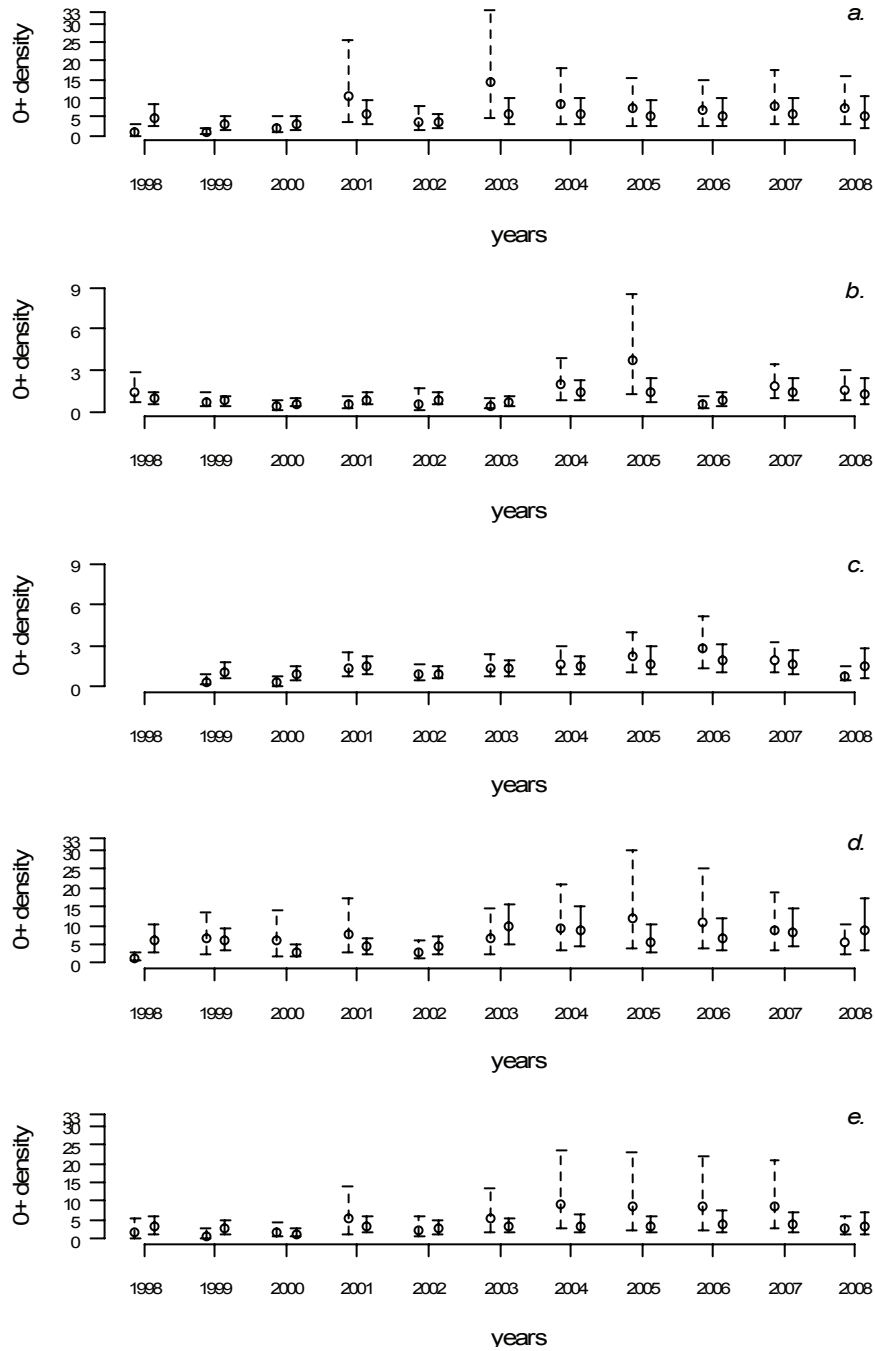


Figure 4.6: Pseudo prior and marginal posterior distribution of the average 0+ salmon densities  $d_{t,i}^{\mu}$  for a) the Faughan, b) the Finn, c) the Mourne, d) the Roe and e) the Foyle geo unit. Pseudo prior 2.5<sup>th</sup> and 97.5<sup>th</sup> percentiles ranges are represented with a dashed line and the posterior distribution with a plain line. The circle indicates the mean of the distribution.

### 4.3.2 Exploitation and populations dynamic model

#### 4.3.2.1 Spawner to 0+ juvenile density-dependent relationship

The parameters of the Beverton and Holt density dependent relationship are estimated with a variable level of certainty. The average maximum number of 0+ juveniles that one

spawner can produce,  $a^d$ , is estimated close to the maximum range of its prior distribution with a CV of 10.4%. The different  $d_i^{max}$  are estimated less precisely (CVs ranging between 18.2% and 36.6%) and significant differences were found between geo units. Two of them are very low (the Finn and the Mourne), two are intermediate (the Faughan and the Foyle) and one is very high (the Roe). The parameters of the distribution from which the  $d^{max}$  is drawn:  $\mu^{dmax}$  and  $\sigma^{dmax}$  are poorly estimated with CVs of 141% and 59.5% respectively. Finally, the variance associated to the Beverton and Holt relationship is small and well estimated (CV=17.7%, Table 4.6). Density dependence relationships drawn from the mean of the posterior distributions of the relevant parameters are represented in Figure 4.7. The residual errors ( $d_{t+1,i}^\mu - \mu_i^d$ ) series were evenly distributed around 0 and did not show any autocorrelation nor correlation between geo units.

Table 4.6: Summary statistics of the marginal posterior distributions of the main dynamic model parameters.

Parameters	mean	sd	2.5%	25%	median	75%	97.5%
$\sigma^{PFA}$	0.165	0.045	0.072	0.136	0.165	0.195	0.253
$p^J$	0.517	0.098	0.319	0.452	0.519	0.584	0.703
$p_1^C$	0.614	0.122	0.364	0.523	0.626	0.716	0.803
$p_2^C$	0.881	0.029	0.831	0.859	0.878	0.903	0.940
$\gamma_0$	-4.614	0.429	-5.458	-4.896	-4.613	-4.336	-3.765
$\sigma^V$	0.340	0.060	0.234	0.298	0.337	0.377	0.472
$v_1$	0.017	0.17	-0.320	-0.097	0.017	0.129	0.355
$v_2$	1.0.14	0.149	0.727	0.912	1.015	1.113	1.311
$v_3$	0.904	0.158	0.591	0.798	0.905	1.013	1.215
$v_4$	-0.842	0.162	-1.144	0.954	0.850	0.734	-0.509
$v_5$	-1.092	0.178	-1.443	-1.212	-1.094	-0.971	-0.746
$\sigma^v$	1.546	1.002	0.619	0.955	1.262	1.784	4.444
$\sigma^d$	0.339	0.060	0.221	0.300	0.339	0.379	0.456
$a^d$	1561	161.75	1196	1461	1585	1688	1801
$\mu^{dmax}$	5.530	7.815	0.743	2.614	3.906	5.982	19.302
$d_1^{max}$	6.138	1.649	3.675	5.000	5.932	6.989	9.956
$d_2^{max}$	1.248	0.236	0.855	1.080	1.225	1.388	1.788
$d_3^{max}$	1.511	0.275	1.042	1.317	1.488	1.678	2.126
$d_4^{max}$	13.385	4.144	7.094	10.340	12.705	15.740	23.330
$d_5^{max}$	7.192	2.614	3.583	5.361	6.704	8.498	13.570
$\sigma^{dmax}$	1.608	0.957	0.644	1.012	1.338	1.882	4.188

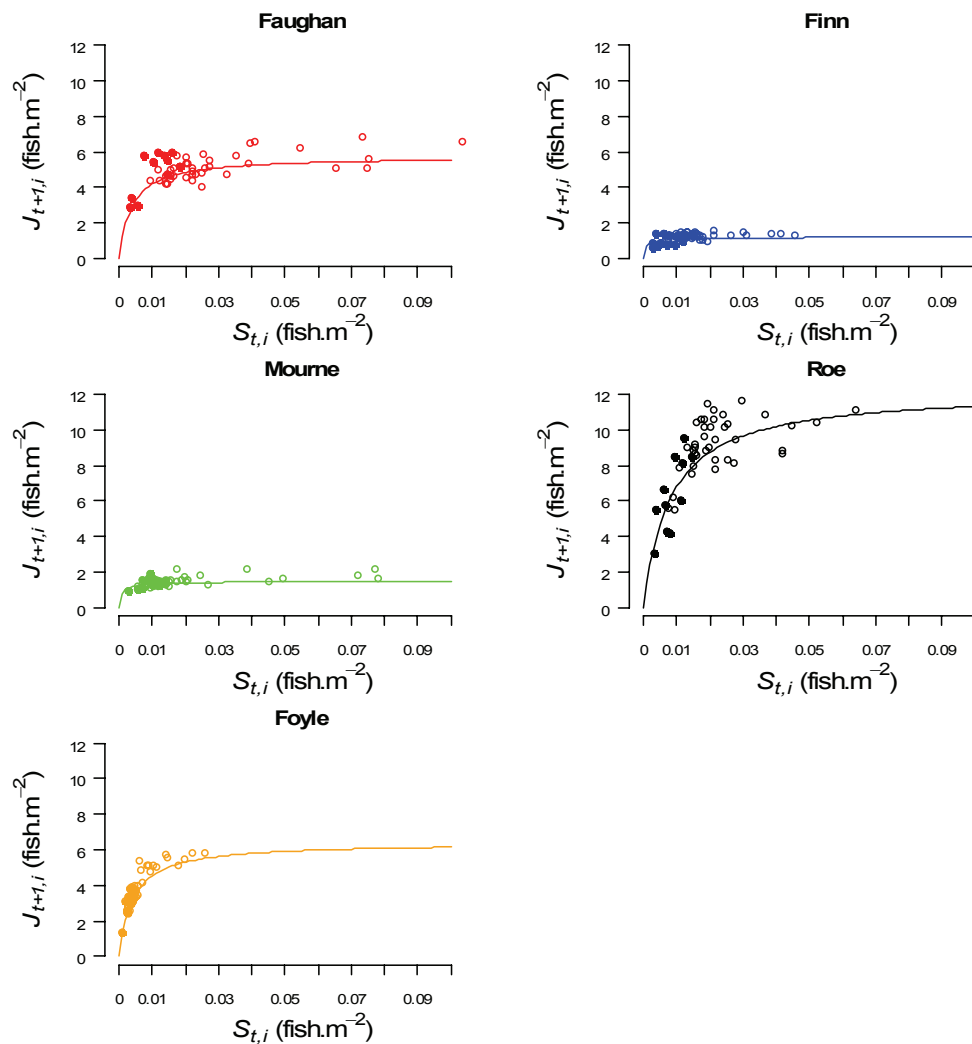


Figure 4.7: Density dependence relationship between spawners ( $\text{fish.m}^{-2}$ ) and 0+ juvenile densities for each geographical unit represented with means of the posterior distribution of the parameters concerned. Plain dots represent year for which electric fishing data are available, empty dots represent years without electric fishing data represented with means of the posterior distribution of the unknown values.

#### 4.3.2.2 0+ juvenile to returning adult survival

The year effects are well estimated with standard deviations of the marginal posterior distributions ranging between 0.149 and 0.258. The smaller standard deviations are found during the 6 years when all datasets were available (fisheries catches, adults counts, redd counts and juvenile index of abundance). Year effects for the 2 predicted years (2009 and 2010) show an increased standard deviation (0.429 and 0.555 respectively). Figure 4.8a helps to visualise how (log) survival evolves over the time-series. Survival from 0+ juveniles to returning adults reached a peak in the middle of the 1960's which was followed by a steep decline until the middle of the 1970's. After a slight recovery until the beginning of the 1980's, the survival has been slowly decreasing, reaching an historic minimum in 1999.

The geo unit effects  $\nu_i$  on the 0+ juvenile to returning adult survival are significantly different (Figure 4.8b). This, leads to higher 0+ juvenile to returning adult survival in the Finn and the Mourne units, lower 0+ juvenile to returning adult survival in the Roe and the Foyle units and intermediate survival in the Faughan unit.

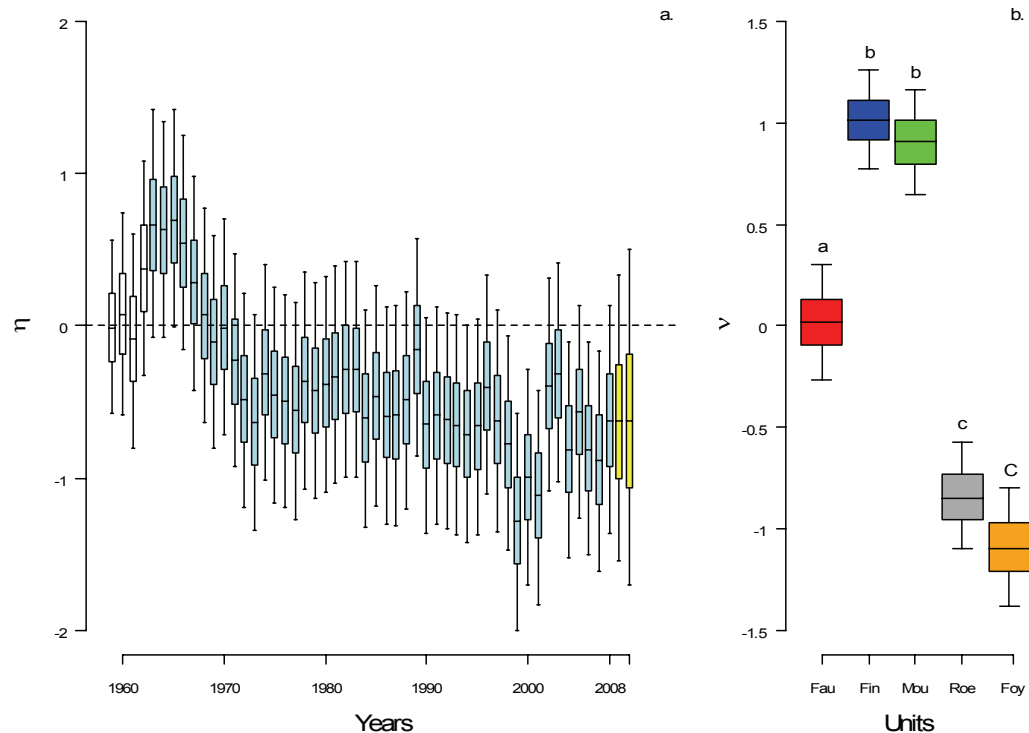


Figure 4.8: Marginal posterior distribution of a) year effect  $\eta_t$ , white boxplot indicate years depending of the initialisations parameters, light blue boxplots correspond to the period 1963 to 2008, yellow boxplots correspond to predictions for years coming and b) geo unit effect  $\nu_i$ , letters above boxplots indicate groups significantly different one to another. The line in the middle of the boxes indicates the median, the box indicates the 25<sup>th</sup> and 75<sup>th</sup> percentiles and the whiskers indicate the 2.5<sup>th</sup> and 97.5<sup>th</sup> percentiles.

Based on the year and geo unit effects, yearly 0+ juvenile to returning adult survival  $s_{t,i}^J$  is calculated and represented with the residual effect  $\varepsilon_{t,i}$  (Equation 4.4 and 4.6, Figure 4.9). The residuals series  $\varepsilon_{t,i}$  do not show any (1<sup>st</sup> order) autocorrelation within geo units and are correlated among geo units. All geo units have the same pattern across the time-series which is governed by the year effect  $\eta_t$ . The differences in 0+ juvenile to returning adult survival across geo units reflect the geo unit effects (Figure 4.9).

The proportion of 0+ juveniles completing their full life-cycle in 3 or 4 years are reasonably well estimated (CV=19%). They are approximately equal: 0.517 for  $p^J$  and 0.483 for  $(1 - p^J)$ .



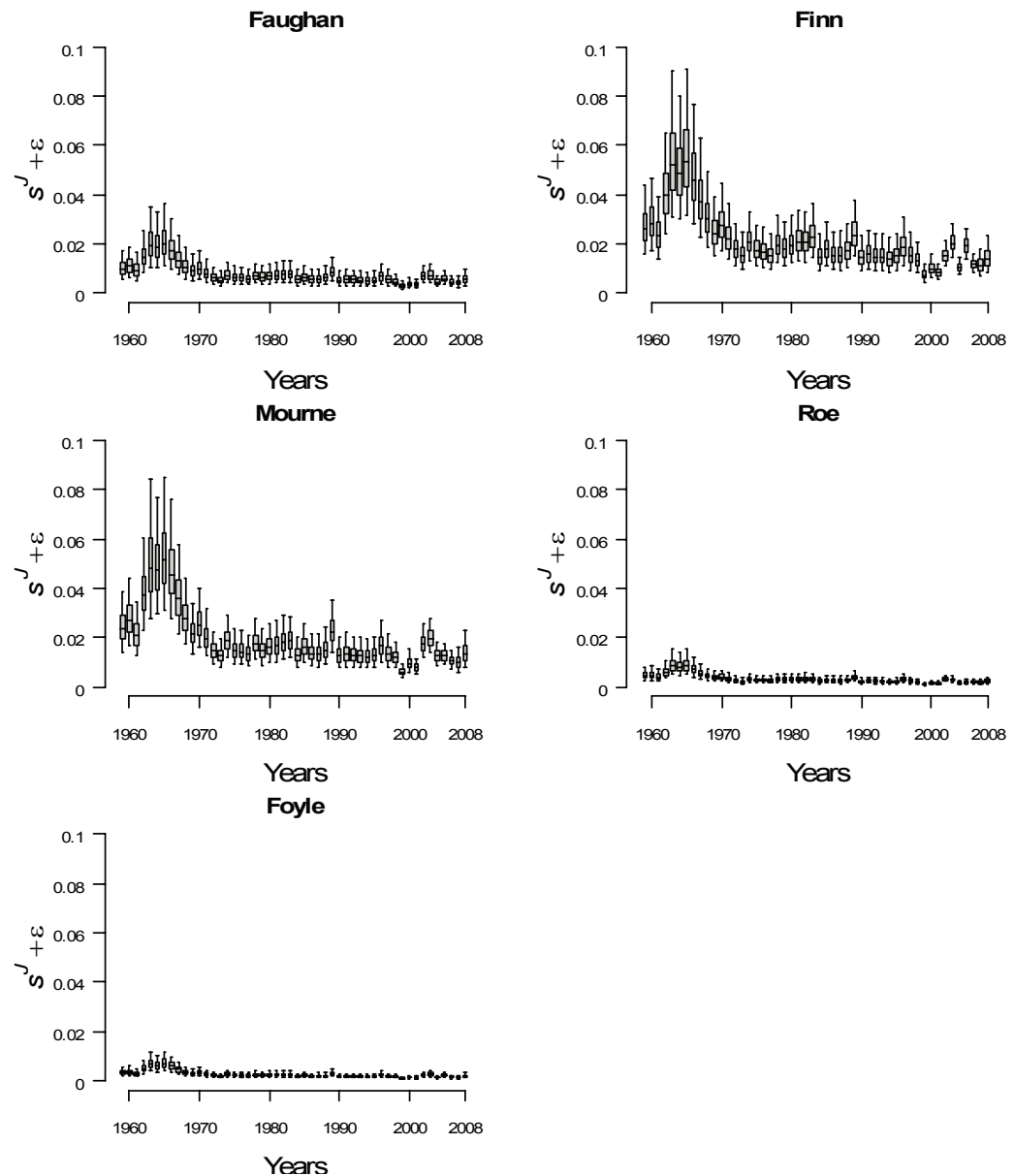


Figure 4.9:  $0+$  juvenile to returning adult survival  $s_{t,i}^J$  time-series with the associated residual effect  $\varepsilon_{t,i}$  for each geographical unit of the Foyle catchment. The line in the middle of the boxes indicates the median, the box indicates the 25<sup>th</sup> and 75<sup>th</sup> percentiles and the whiskers indicate the 2.5<sup>th</sup> and 97.5<sup>th</sup> percentiles.

#### 4.3.2.3 Pre Fishery abundances (PFAs)

PFAs are estimated between 1959 and 2010. The estimations for 2009 and 2010 are predictions. The PFAs are fairly well estimated between 1959 and 2008 with CVs ranging between 5.5% and 38.6%. When all datasets are available for a given year, the estimations noticeably improve (Figure 4.10). PFAs predictions for 2009 and 2010 are much more uncertain with CVs of 48.7 % and 65.6% respectively.

The trend found in the PFAs estimates is similar to the one found for the  $0+$  juvenile to returning adult survival. There is a peak of abundance in the middle of the 1960's with

adult abundances (mean of marginal posterior distribution) around the 400 000 fish mark during four years. Following this peak, there is a steep decline up to the middle of the 1970's when abundances are estimated around the 100 000 fish mark. Since then, there is a slight decreasing trend leading to the lowest abundance in 1999 (just a bit more than 50 000 returning adults).

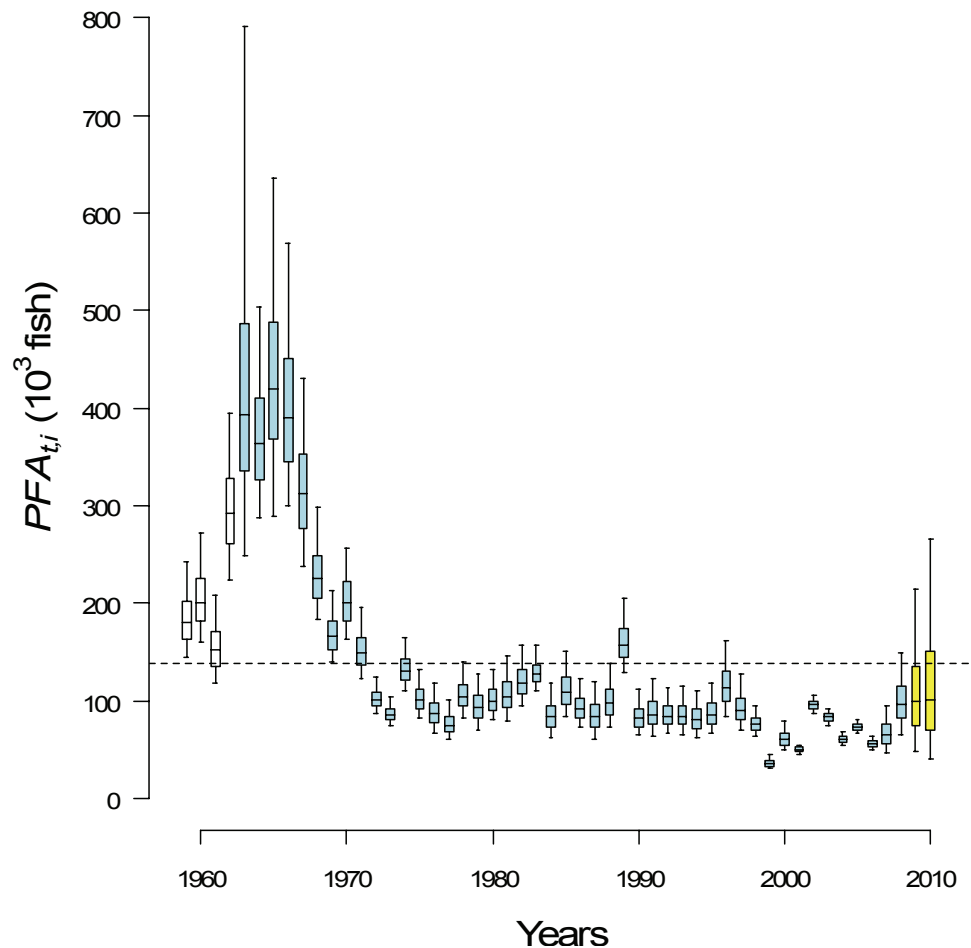


Figure 4.10: Total PFA for the Foyle catchment. The dashed line corresponds to the average PFA over the time-series. White boxplot indicate years depending of the initialisations parameters, light blue boxplots correspond to the period 1963 to 2008, yellow boxplots correspond to predictions for years coming. The line in the middle of the boxes indicates the median, the box indicates the 25<sup>th</sup> and 75<sup>th</sup> percentiles and the whiskers indicate the 2.5<sup>th</sup> and 97.5<sup>th</sup> percentiles.

#### 4.3.2.4 Exploitation rates and conservation limits

The total commercial fisheries exploitation rates (including angling catches) in the 5 geo units are quite variable across the time-series. Means of the marginal posterior distribution of  $h$  range from 0.066 to 0.712 (Figure 4.11). All geo units display the same pattern of exploitation rates across the time-series except for the Roe which lacks the peak of exploitation rates at the beginning of the 1970's. Overall the Roe unit has lower exploitation rates which could be explained by its location (Figure 4.2): salmon returning

to the Roe geo units do not have to go through the lough, “avoiding” in this way many drift nets. For all geo units, the exploitation rates decline steeply during the last 8 years of the time series. This occurs after a peak of exploitation at the turn of the century.

References points  $h'$  (equation 4.28 and 4.29) can be very variable across geo units. In the Finn and the Mourne units,  $h'$  are very high, ranging between 0.734 and 0.882 (marginal posterior distribution mean) over the whole time series. The Faughan geo unit also has a high  $h'$  but shows much more variation in the time series with  $h'$  ranging from 0.561 to 0.816. The last two geo units have significantly lower  $h'$  than the other geo units,  $h'$  in these geo units ranging between 0.238 and 0.717. Overall, there is a more or less pronounced declining trend for the  $h'$  in all geo units.

The probability of exploiting the population at a higher exploitation rate than  $h'$  ( $p_{t,i}^h = P(h_{t,i} \geq h'_{t,i})$ ) is represented at Figure 4.11. The Finn and the Mourne units have  $p_{t,i}^h$  equal to 0 in most of the years except in 1999 when this probability rises around 0.3. The Faughan unit presents the same pattern but between 1998 and 2001 the population was most probably exploited above  $h'$  ( $p_{t,i}^h > 0.8$ ). In the Roe unit, higher  $p_{t,i}^h$  becomes more frequent especially in the second half of the time-series. Finally, in the Foyle unit, high  $p_{t,i}^h$  occur more frequently and during the whole time-series.

The number of spawners ( $S$ ) reaches its maximum in each geo unit during the mid 1960's and follows a steep decrease until the mid 1970's. Then the number of spawner is fairly constant until the end of the 1990's. The reduced number of spawners can be associated with the high levels of exploitation observed during this period. Following this period, there is an increase in the observed number of spawners especially during the last two years (2006 and 2007, Figure 4.12).

The conservation limits  $S'$  decrease steadily between 1964 and 2009 by about 50% on average: 5200 spawners in 1964 to 2300 spawners in 2009 for the Faughan unit; 8500 spawners in 1964 to 4700 spawners in 2009 for the Finn unit; 31500 spawners in 1964 to 17500 spawners in 2009 for the Mourne unit; 9000 spawners in 1964 to 5000 spawners in 2009 for the Roe unit; 6300 spawners in 1964 to 3500 spawners in 2009 for the Foyle unit.

The patterns observed in the probability of having a number of spawners smaller than the conservation limit  $S'$  ( $p_{t,i}^S = P(S_{t,i} \leq S'_{t,i})$ ) are very different across geo units (Figure

4.13). The Finn and the Mourne units have very low probability ( $< 0.2$  on average) of not reaching their conservation limits during most of the time series. However, this probability increases in the mid 1970's and at the end of the 1990's. The Faughan and the Roe units have higher chances to be under the conservation limits ( $p_{t,i}^S$  around 0.4 on average). Finally, in the Foyle unit it is very unlikely that the conservation limit has been reached during most of the years considered. During the last years of the time series, the probability  $p_{t,i}^S$  decreases and is under 0.4 in all geo units except for the Foyle unit.

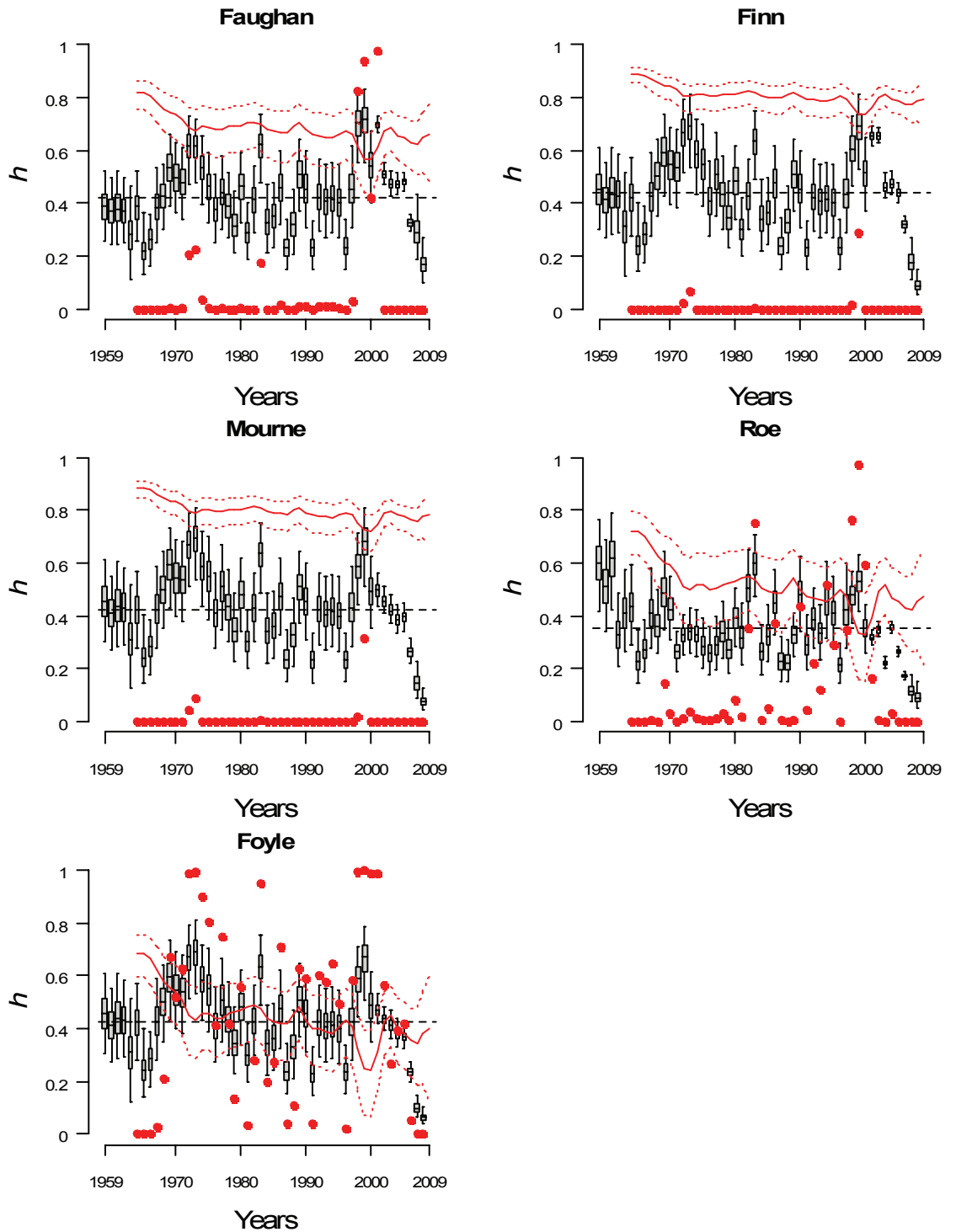


Figure 4.11: Marginal posterior distribution of the exploitation rates  $h_{t,i}$  for the different geo units. The line in the middle of the boxes indicates the median, the box indicates the 25<sup>th</sup> and 75<sup>th</sup> percentiles and the whiskers indicate the 2.5<sup>th</sup> and 97.5<sup>th</sup> percentiles. Plain and dashed red line indicate the median, 2.5<sup>th</sup> and 97.5<sup>th</sup> percentiles of the marginal posterior distribution of the reference exploitation rate  $h'_{t,i}$ . Red dots indicate the probability of exploiting the population at a higher exploitation rate than the reference exploitation rate  $h'$  ( $p_{t,i}^h$ ).

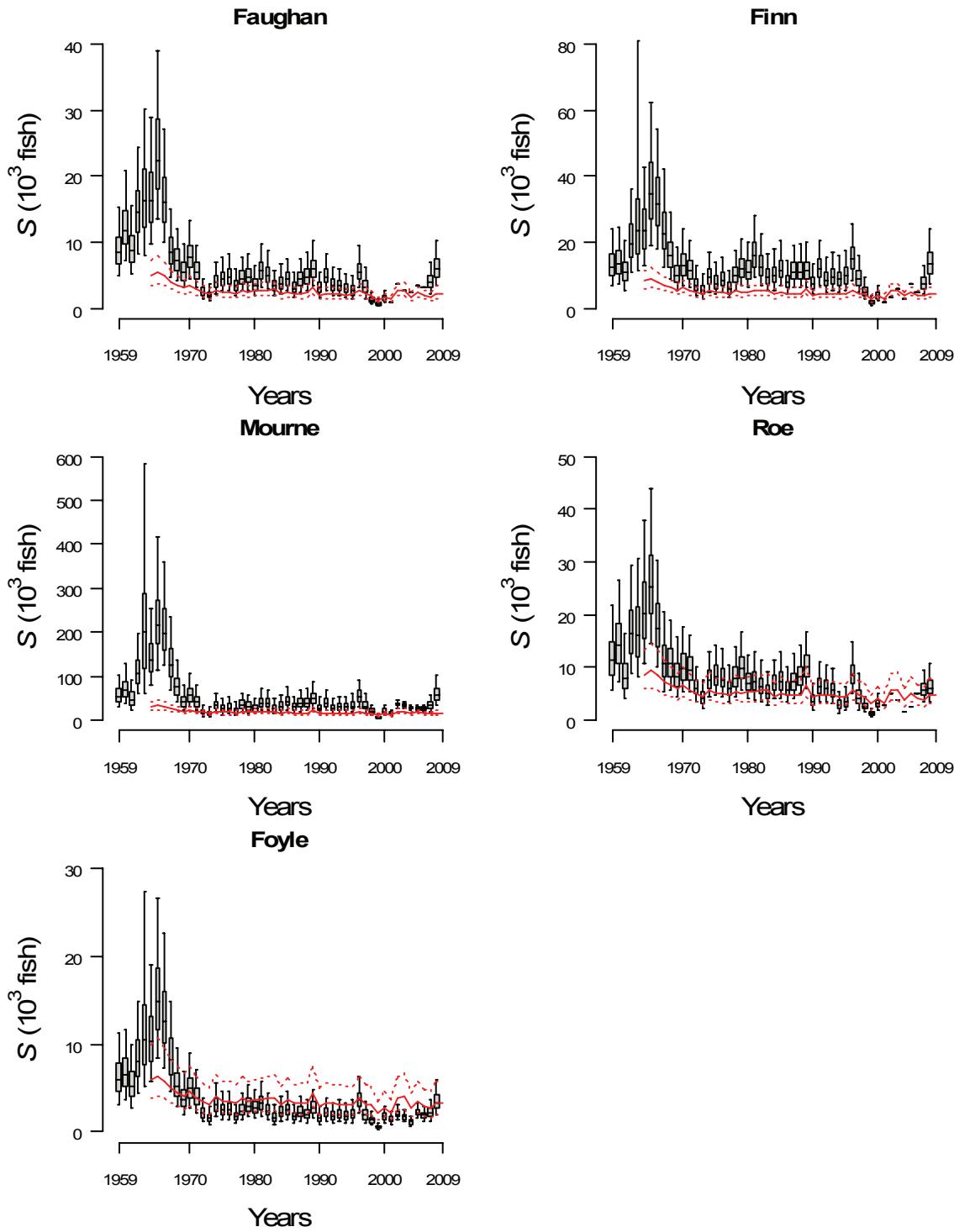


Figure 4.12: Marginal posterior distribution of the spawners  $S_{t,i}$  for the different geo units. The line in the middle of the boxes indicates the median, the box indicates the 25<sup>th</sup> and 75<sup>th</sup> percentiles and the whiskers indicate the 2.5<sup>th</sup> and 97.5<sup>th</sup> percentiles. Plain and dashed red line indicate the median, 2.5<sup>th</sup> and 97.5<sup>th</sup> percentiles of the marginal posterior distribution of the conservation limit  $S'_{t,i}$ .

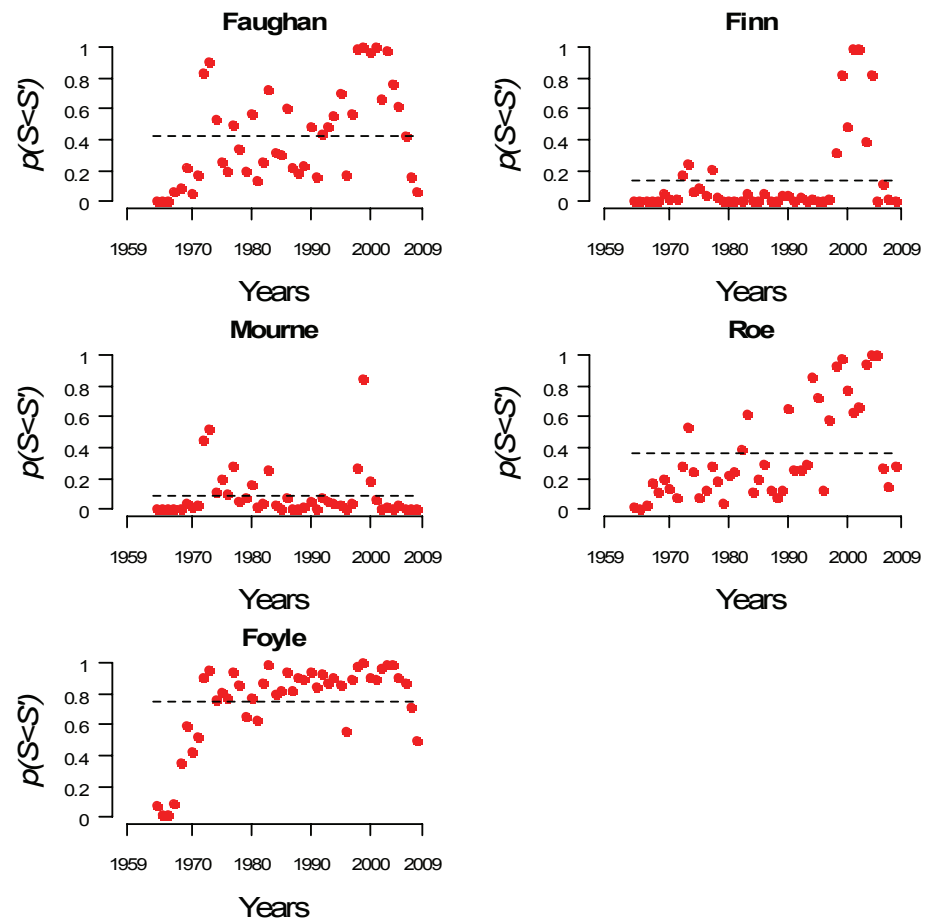


Figure 4.13: Evolution between 1964 and 2008 of the probability that the number of spawners returning in each geo unit of the Foyle catchment is not sufficient to reach their conservation limit  $S'_i$  ( $p_{t,i}^S$ ). Dashed lines indicate the average  $p_{t,i}^S$ .

#### 4.3.2.5 Inter-generation replacement rate (IGRR)

The inter-generation replacement rates (IGRRs) are calculated before and after exploitation ( $\Phi^{PFA}$  and  $\Phi^S$ , Equations 4.30a and 4.30b). IGRRs are only calculated between 1963 and 2008 because for the first four years of the time series (1959 to 1962) there are no information about the cohorts which produced the spawners of these years (Figure 4.14 and Figure 4.15). For a convenient reading, the IGRRs are expressed in a logarithmic scale. Positive values indicate an IGRR higher than 1 and negative values indicate IGRRs smaller than 1.

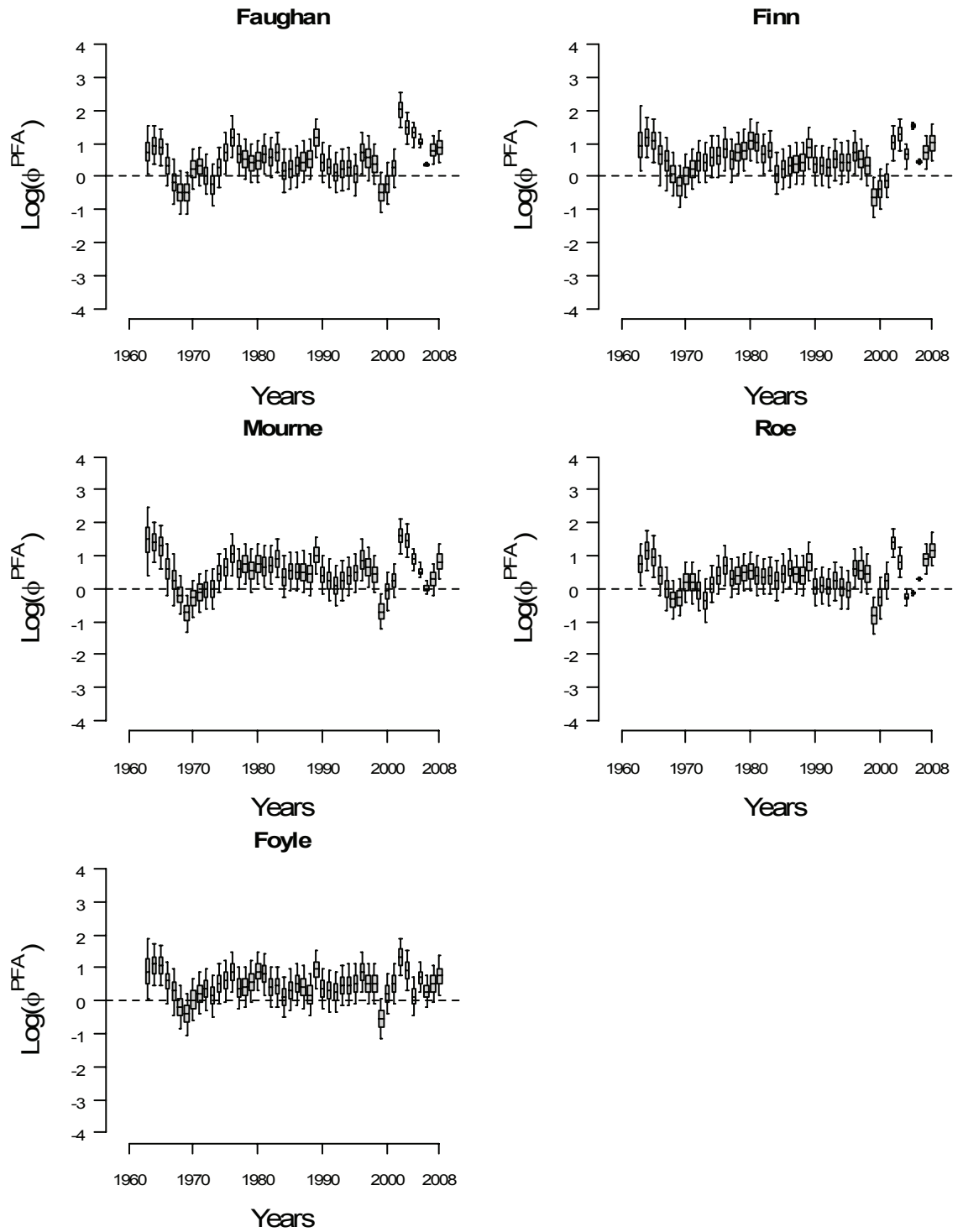


Figure 4.14: Marginal posterior distribution of the pre fishery IGRR in log scale ( $\text{Log}(\Phi^{PFA})$ ). The line in the middle of the boxes indicates the median, the box indicates the 25<sup>th</sup> and 75<sup>th</sup> percentiles and the whiskers indicate the 2.5<sup>th</sup> and 97.5<sup>th</sup> percentiles.



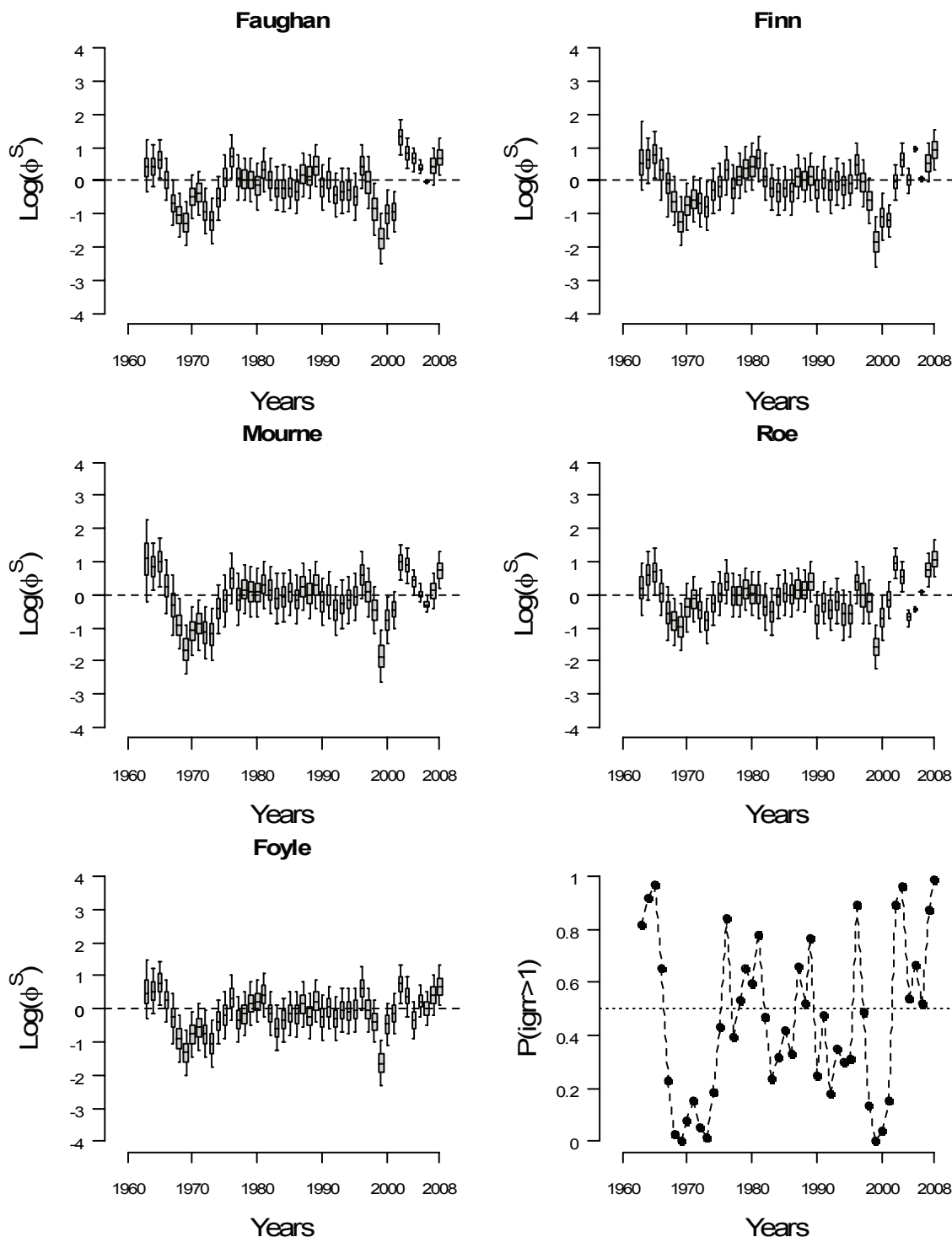


Figure 4.15: Marginal posterior distribution of the post fishery IGRR in log scale ( $\text{Log}(\Phi^S)$ ). The line in the middle of the boxes indicates the median, the box indicates the 25<sup>th</sup> and 75<sup>th</sup> percentiles and the whiskers indicate the 2.5<sup>th</sup> and 97.5<sup>th</sup> percentiles. Bottom right panel shows the averaged probability that the IGRR value will be higher than 1 for all geo units considered together ( $P(\sum_{i=1}^5 \Phi_{t,i}^S / i \geq 1)$ ).

Overall, the  $\Phi^{PFA}$  values are higher than 1, indicating that, in most cases, prior to the commercial fisheries the number of returning adults is sufficient to replace the spawners they originate from. However, in two occasions (at the end of the 1960's and the 1990's) the  $\Phi^{PFA}$  values were smaller than 1. The values calculated after commercial fisheries

exploitation ( $\Phi^S$ , Figure 4.15) show very different results compared with  $\Phi^{PFA}$  values. IGRRs lower than 1 are quite frequent and the average probability across geo units of obtaining an IGRR higher than 1 ( $P(\Phi^S \geq 1)$ ) is under 50% in more than half of the years of the time-series (Figure 4.15, bottom right panel). In most of these cases the mean value of  $\Phi^S$  is just under 1. On two occasions, the  $\Phi^S$  are significantly under 1 for a extended period of time for all geo units. This occurs the first time between 1967 and 1973 when the mean of the marginal posterior distribution of  $\Phi^S$  fluctuates between 0.21 and 0.94. Then, between 1998 and 2001 it fluctuates between 0.18 and 0.93. The first period with  $\Phi^S$  values smaller than 1 occur after a period of very high abundances (Figure 4.10) the second period of low  $\Phi^S$  occurs when adult abundances are much lower. Finally, during most of the last years (2002 to 2008),  $\Phi^S$  has been higher than 1.

## 4.4. Discussion

The state-space model proposed here mimics the lifecycle of Atlantic salmon in the Foyle catchment and provides abundance estimates of three life stages (0+ juveniles, returning adults/PFAs, spawners). The full Bayesian framework allows having direct access to the uncertainties of all the unknown variables of the model. This model allows most of the information available on this population across several and heterogeneous datasets and different spatial and temporal scales to be summarized. Similar work has been recently carried out (Rivot *et al.*, 2004; Michielsens *et al.*, 2008) however this study is the first one providing such a long time-series and allows a retrospective on the history of the population and its fishery. In addition, in comparison to other studies in which data were collected for a “scientific” purpose, all the datasets used in this study are collected by a government agency which is principally interested in the management of salmon population. This study and the associated modelling exercise allow a critical review of the value of the information contained in the various datasets used.

### 4.4.1 Modeling or dealing with limitations and constraints

A model is always a functional and simplified version of what is happening in the real world; it allows both incorporating the knowledge available and testing hypotheses of interest for the modeler. In addition the model allows bringing different datasets together in order to evaluate the status of a population and how it has or will change. For exploited populations the output of the model can also be advice on the management strategies

(Roqueplo, 1997; Bernier *et al.*, 2000). The modelling exercise is very much dependent on the data available, since in order to validate or not a model or not its outputs have to be compared to some observed data (Hiborn and Mangel, 1997). As a consequence, the data available will constrain the range of possible hypotheses to test.

#### 4.4.1.1 Transition parameters

The first transition between life stages that is looked at is the one linking the 0+ juveniles to the returning adults. Due to the lack of data concerning the various life histories of the salmon in the Foyle catchment, all the possible life histories were not explicitly represented in the model. Instead, it was assumed that the returning adults resulted from two different cohorts of 0+ juveniles, 3 or 4 years earlier in a unknown proportion  $p^J$ . Limiting the provenance of adults to only 2 cohorts was based on the data available from status reports indicating that fish caught between 1953 and 1966 were predominantly 3 years old grilse (>90% of total fish sampled, (Foyle Fisheries, 1953, 1955, 1956, 1958, 1959, 1962, 1963, 1966). In addition, in 2001, 100 fish from the drift net fisheries were aged and 55% of them were 3 years old grilse and 29% were 4 years old fish (grilse and 2 sea winter fish). Both cohorts of juveniles are estimated to be on average equally contributing to a cohort of returning adults ( $p^J = 0.517$ , Table 4.6). Any (year  $\times$  geo unit) variation in the life histories will then be captured by all the other effects introduced in the link of 0+ juveniles to returning adults (i.e. year, geo unit and residual effects).

The survival from the 0+ juvenile stage to the returning adult stage is estimated for each cohort of adults taking in account annual and spatial sources of variability (Equation 4.6, Figure 4.8). Across geo units, the survival reaches a peak in the mid 1960's and is followed by a steep decline until the middle of the 1970's. After a slight recovery until the beginning of the 1980's, the survival has been slowly decreasing (Figure 4.9). Since this is the survival before exploitation, it indicates a change during the freshwater phase or the marine phase or both. Whatever these changes are, it seems like the conditions in rivers or/and at sea did not return to where they were since then. These high survivals observed during the mid 1960's could correspond to a stable previous level or to a period of time corresponding to extraordinary and exceptionally favourable conditions for salmon. Several authors have found correlations between salmon abundances and various environmental covariates such as the winter North Atlantic oscillation index (Boylan and Adams, 2006; Dickson and Turell, 2000; Jonsson and Jonsson, 2004) or water temperature (Jonsson and Jonsson, 2004b) but the biological mechanisms are not yet fully understood.

In the transition between the spawners of a given year and the 0+ juveniles the following year, it was assumed that the underlying mechanisms are stable over the time series as opposed to the non stationarity of the transition between 0+ juveniles and returning adults. This choice is mostly imposed by the lack of long time series related to the 0+ juvenile life stage. Except for the last 11 years (1998 to 2008) for which 0+ juvenile data are available, it is not possible to make the distinctions between the changes in the two transitions (0+ juvenile to returning adult and spawner to 0+ juvenile). Therefore, any annual change occurring in these transitions can be captured by the year effects  $\eta_t$  (Figure 4.8).

In this study, only the Beverton and Holt density dependence relationship is considered; other relationships could have been used (e.g. Ricker, “hockey stick”). However, considering the variability observed around the theoretical curve it is unlikely that changing the shape of the density dependence relation will lead to major changes in the outputs of the model (Myers *et al.*, 1995).

#### **4.4.2 Outputs of the model for management advice**

The main outputs of this model for management purpose are the time series of PFA, of exploitation rates and of reference points  $h'_{t,i}$  and  $S'_{t,i}$ . They allow a retrospective analysis of the status of salmon population from the 5 geo units of the Foyle.

Historical abundances are generally estimated with fair levels of uncertainty (Figure 4.10). This uncertainty is considerably reduced during the 6 years when counter data are available. When no counter data are available it is interesting to notice that there is no significant differences in the uncertainty of the PFA between years during which 0+ juvenile index abundance are available and years in which they are not. This indicates that the 0+ juvenile index of abundance does not contain much useful information. As shown in Figure 4.6, there is a clear update of the pseudo-likelihood, issuing from the 0+ juvenile observation model, for each geo unit (Figure 4.6). One of the reasons for this is the high uncertainty (coefficients of variation up to 194% for some years) of the average 0+ juvenile density estimates. High uncertainty is mainly due to the calibration model that estimates 0+ juvenile densities from the timed index of abundance (Dauphin *et al.*, 2009). This calibration exercise could be improved (see discussion in Dauphin *et al.*, 2009) in order to make better use of the information contained in the 0+juvenile index of abundance which are costly to collect.

The proportion of salmon originating from the Foyle caught by the drift nets at sea ( $p_1^C$ ) is estimated with a high uncertainty (Table 4.6). This indicates that the Foyle fishery potentially impacts significantly other salmon stocks. The potential (year  $\times$  geo unit) variations in  $p_1^C$  and  $p_2^C$  are captured by the various effects affecting the returning adults  $PFA_{t,i}$ .

The same pattern of evolution over time can be observed for  $h'$  and for the conservation limits  $S'$ . The reference points consistently decrease over the time-series. This is much more evident for the conservation limit which is reduced on average by about 50 % over the 50 years of the time-series. This pattern is driven by the decrease of the 0+ juvenile to returning adult survival.

The comparison of exploitation rates to the reference exploitation rates in each geo unit shows that in the Faughan, the Finn and the Mourne units, the exploitation rate has been under the reference exploitation rate  $h'$  during most of the years. The two other geo units (Roe and Foyle) have lower  $h'$  and have been exploited very often above this reference level. The only consistent decrease in the exploitation rates  $h$  appear in the last 10 years of the time series in all geo units. This is mainly due the buying out of many drift and draft net licences over the last years (less than 20 drift nets and less than 20 draft nets remain active in 2008 from a maximum of 139 drift nets and 524 draft nets).

The comparison of the number of spawners to the international standard reference point  $S'$  (conservation limit recommended by the North Atlantic Salmon Conservation Organisation) shows that there are some differences across the geo units of the Foyle catchment. All geo units show at some stage a high probability of not reaching their conservation limits, but three out of five geo units (Faughan, Roe and Foyle units) show on average higher probability of having less spawners than the required conservation limit.

The IGRR pre-fishery  $\Phi^{PFA}$ , is above 1 during most of the time series for all geo units. However  $\Phi^{PFA}$  is smaller than 1 at the end of the 1970's and the end of the 1990's (Figure 4.14). Figure 4.11 and Figure 4.15 show that overall the time series for most of the geo units, the populations are exploited under the equilibrium exploitation rate  $h'_{t,i}$  but the IGRR  $\Phi^S$  is more often under the replacement value than above it. Combined with the strong decline in the 0+ juvenile to returning adult survival, this leads to the slow decline of the number of returning adults (Figure 4.9, Figure 4.10). However it can be noted that

during the last seven years, some very high  $\Phi^S$  have occurred in certain geo units ( $\Phi^S > 2$  in 2002 in the Faughan and the Mourne unit). This indicates an increase of the population size which is partly resulting from the significative decrease in the exploitation rates during the last decade.

These results provide the main outcomes of this study regarding the management of the salmon population. When considering the reference points associated to MSY, it appears that, the situation is contrasted when the geo units are considered one by one. For instance, the Foyle unit, which is less productive than the others (i.e.  $h'$  is on average much lower than on the other geo units), has consistently suffered of overexploitation. Indeed, the conservation limits were seldom achieved (Figure 4.13) and the exploitation rates were often exceeding their corresponding reference level (Figure 4.11). At the other extreme, the most productive geo units, the Finn and the Mourne, have occasionally suffered from over exploitation (Figure 4.11). The Roe and the Faughan were in an intermediate situation. But overall, the salmon (meta)population of the Foyle catchment is driven by its two more productive and largest components, the Finn and the Mourne, and therefore it appears that the population has globally not been overexploited during most of the period of time studied. This occurred in a context where the 0+ juvenile to returning adult survival and the associated reference points are consistently decreasing. It implies that the survival decrease is mainly responsible for the global population decline (Figure 4.10). The IGGRs before and after exploitation show that the fisheries have accentuated this phenomenon by sometimes preventing the population replacement. Replacement could have taken place if the exploitation had been more moderate but the population decline would have only been slowed down.

### **4.4.3 Beyond the case study**

Over the last few years, Bayesian state-space modelling has become more and more popular in fisheries science (Punt and Hilborn 1997; Schnute and Richards, 2001). Using this framework, this study is similar to other works such as Rivot *et al.* (2004) and Michielsens *et al.* (2008). It provides useful insights for managers together with a better understanding and assessment of the population of interest. In addition, the work presented here provides reference points for several spatial units of the catchment studied which are estimated and updated every year with their associated uncertainties.

Such an approach is usually time consuming because every population has its own characteristics and knowledge of the different datasets and how they were collected is crucial to guaranty the coherence of the final model. The implementation of such model consists in improvements by trial and error and constant checking for consistency of results. It allows making the best use of all datasets available for a given study and summarizing the information they contain with regards to the quantities of interest. This is done in a formal, unique, rigorous and coherent framework which weights the information brought by the different sources of information used. Moreover information from other systems/population can be incorporated through hierarchical models or informative priors.

Bayesian state space modelling shows yet again its ability to deal with complex models such as the one presented in this chapter. However, at the moment the implementation of this approach such models is facing numerical calculation problems to conduct the Bayesian inference. For instance running this model on WinBUGs required four and half days of calculation on a 64-bits computer.

## **Chapter 5:**

### **General discussion**

#### **5.1. Objectives**

The main objective of this work lies in proposing a way to integrate multiple datasets collected for different purposes (e.g. management, fisheries, science) in order to retrace and understand the different events that have affected the Atlantic salmon population of the Foyle catchment as well as produce new reference points. This objective was completed by building a state space model describing the lifecycle of salmon in the Foyle catchment which was divided into five geographical units. This spatial division was a major step forward, as it is now possible to estimate reference points for each geographical unit. The incorporation of two datasets was accomplished by building two hierarchical models. The first (chapter 2) provides a generic way to relate an index of abundance to densities and the second (chapter 3) allows the estimation of adult abundances based on redd counts.

Bayesian modelling provides a formal and coherent framework to integrate multiple sources of information to deal with uncertainty which is of particular interest for population dynamics and management purpose (Germano,1999; Hilborn, 1997, Michielsens *et al.*, 2008; Rivot *et al.*, 2004; Wade, 2000). The outputs of Bayesian state space inferences are joint posterior distributions of all unknown variables but also the marginal distribution of each unknown individually. In population dynamics and for management purposes, this is of particular interest for the variables corresponding to the abundance of the population at a given life stage and to reference points, and for the population assessments resulting from the comparison of the two.



## 5.2. Population dynamics in the Foyle catchment

### 5.2.1 Main results

In chapter 2 and 3, two observation models which allow inference on unobservable states of the dynamic model are presented. Both models can also be seen in a larger context of enhancing the value of datasets.

The first observation model looks at 0+ juvenile index of abundance (IA) available for up to 11 years and 384 local sites widely spread throughout the catchment. Since no formal relationship was established between the 5 minute IA and the actual densities of 0+ juvenile on site was available for the Foyle catchment, data were collected during two summers in order to unravel this relationship. The modelling exercise reported in chapter 2 showed evidence of different densities depending on habitat quality (good or poor based on DANI classification). More importantly, it provides the methodology to convert an index of abundance into a density estimator with its associated uncertainty. The approach used is generic and can be transferred to similar situations: for any fish index of abundance collected with electric fishing, but also more generally for any relation between relative indexes of abundance to absolute measure of abundance.

The parameters of the relationship described in chapter 2 were then used to calculate retrospectively local 0+ juvenile densities for each site sampled during the last 11 years. Local densities were then incorporated in a basic hierarchical model in order to provide averaged larger scale (geo units) 0+ juvenile densities. The large scale densities estimates for all the time-series of two geo units (Finn and Mourne) and the first 5 years of the time series of another geo unit (Foyle) showed densities consistent with those found in the literature.

The second observation model relates the abundances of adults returning in rivers to redd counts. This model also looks at enhancing the value of several datasets. A six years time-series providing accurate adult salmon counts *via* fish counter is available for three geo units and related to redd counts of the associated geo unit. A simple hierarchical model accounting for potential differences across geo units was built to estimate the parameters of this relationship. This allows enhancing the value of two datasets in two different ways. Firstly, this relationship is “exported” to the Mourne unit where only partial adult counts

are available. Thanks to the hierarchical structure and the redd counts available for the Mourne unit, the probability of counting an adult and the adult abundances for this geo unit can be estimated. Secondly, using the parameters from this relationship and the redd counts time-series it is possible to estimate the historical abundance of adult salmon returning in rivers. Estimates are uncertain but provide valuable quality quantitative information. The model also allows estimating the average probability of counting adults returning in the Mourne unit. This proportion is likely to be highly variable depending on the water flow at the Mourne counter location during salmon run period. However, no systematic information is available on the water conditions during the different summers of the time series. Therefore, the parsimonious hypothesis of an average proportion allowed to vary according to a log-normal error was retained.

The observation models are then incorporated into a full life cycle model structured in several life stages (chapter 4). The life stages are chosen according to the available datasets and transitions between these life stages are designed according to data available and to well-known relationships described in the literature (e.g. density dependence). Furthermore, a spatial structure is incorporated in the model by dividing the catchment into five geo units. This structure also corresponds approximately to the genetic structure found in the catchment (Booth, 2003; Ensing and Crozier, 2008). Because of the hierarchical structure, geo units can share some of their properties with the others or not. This spatial division of the Foyle catchment is a significant step forward in terms of management as it allows providing conservation limits for each geo units, in comparison to the single conservation limit used at the moment. It also allows having a refined and contrasted vision of the status of the different geo units (e.g. some geo units, such as the Foyle, are more exploited than others). It also shows that when exploiting a mixture of populations, some can be overexploited when the others are not. In terms of management, this implies deciding on which population the exploitation regulations should be adjusted on. In addition, the survival from 0+ juveniles to returning adults is assumed to be non stationary (Walters, 1987; Friedland, 1993; Walters and Kronlund, 2001). Several significant differences across geo units are underlined especially showing higher productivity for the Finn and the Mourne units (measured *via* the  $h'$ ).

Geo unit specific abundances of the different states and their associated uncertainty are estimated. The main state of interest is the pre-fishery abundance (PFA), during the time-series considered (1959-2008) the salmon population reached its apex in the mid 1960's. This was followed by a steep decrease until the mid 1970's. From then to present, the

population followed a slow declining trend with a slight recovery in the mid 1980's. In chapter 4, this decline is shown to be mostly due to a decline of the 0+ juvenile to returning adult survival which is accentuated some years by some overfishing.

### **5.2.2 Perspectives and improvements**

A model is always a simplification of the reality and the models presented in this study are no exception to this rule. Most of these simplifications in these models are due to constraints imposed by data availability (e.g. spatial structure) or to the lack of knowledge about the biological processes occurring in the system (e.g. no consideration of the detailed life-histories). Several aspects of the Foyle Atlantic salmon population dynamics model could be improved with the use of datasets already available or by collection of some additional information. Here, several possible improvements are proposed.

Density estimates of at least two geo units (Fauhan and Roe) were surprisingly high, and sometimes with doubtful reality. This is mainly due to the fact that the calibration relationship is assumed to be the same across all geo units and for each crew performing the electric fishing. At the time of the study, no data was available to identify differences in calibration relationship across geo units or crews. Therefore, the parsimonious choice of a calibration relation constant over all sites was made. Notable differences were identified in terms of IA with some crew managing to capture more than three hundreds 0+ juvenile in 5 minutes. Such numbers can be achieved either if the site fished is very productive or if the crew is very effective in fishing. The fact that the geo units with the highest IA/density are sampled by the same crew reinforce the idea that there might be difference among the different crews and therefore the question linked to consistency of sample collection across the crews should be addressed. In order to clarify this situation, it is suggest that a calibration should be carried out for the different crews collecting the 0+ juvenile IA in the Foyle catchment.

In this study, it is assumed that angling catches are known and accurate even for the period before 2001 when reporting of angling was not compulsory. It would be very simple to incorporate a simple relationship between returning adults and rod catches that would be calibrated during the period 2001 to present (i.e. the period during which angling returns are assumed to be accurate) and used to estimate true angling catches in the past. However, it should be kept in mind that rod catches are significantly smaller than the commercial catches especially at the beginning of the time series.

No distinction is made between the survival of juvenile salmon in freshwater and survival at sea. This is mainly due to the lack of data regarding the intermediate life stage (i.e. smolt). A smolt trap has been used since 2004 at the Faughan counter site. Capture-mark-recapture and lengths of captured smolts are available and could be used to calculate a freshwater survival and sea survival (Juttila *et al.*, 2006; Kalio-Nyberg *et al.*, 2004) for this particular geo unit as well as refine abundance estimates. However, collecting information related to smolt abundance requires a lot of time and manpower which can be difficult to have consistently in a management organization such as the Loughs Agency. Therefore, focus should be put on improving the methodology related to the electrofishing index of abundance and redd counts.

Another refinement would be to incorporate a measure of the fisheries effort. For the last 10 years fishermen (drift and draft nets) have been asked to report in log-books their fishing time for each day of the fishing season. For years before 1998, the information available is less accurate and the only information available are the weekly catches for each licences. Moreover a preliminary assessment of the data available showed some discrepancies between the paper log-books and the official total figures used by the agencies. Therefore, clarification and data mining will be required to incorporate this information. This information would allow looking at the relationship between effort and exploitation rates and providing advice to managers regarding to the regulation of the exploitation rates

Finally, in this study it is assumed, that all salmon return in their rivers at the same time of the year and that they are all subject to the same exploitation rate. This is a significant simplification and it might be worth considering different timing of adult returns in each geo units and their interaction with the timing of the fisheries. For instance, the Finn is known to have a proportion of adults returning during spring (Loughs Agency, *unpublished data*). Such differences in timing can lead to geo units being more or less exploited than other. Implementing these differences could be accomplished using the detailed data from counters (daily counts are available) in order to take in account the fact that some fish return outside of the commercial fishing season and are therefore not exposed to the same exploitation rate (they can still be fished by anglers). For instance, in the Finn the adults returning in spring will not be affected by the commercial fisheries.

The potential improvements presented above are all based on datasets already available (however some datasets need some important clarifications). It could also be envisaged to use one of the main principles of Bayesian analysis: the possibility of incorporating information directly via the prior distributions. For instance, information on 0+ to smolt survival available from other salmon rivers could be incorporated to decompose the 0+ juvenile to returning adult into freshwater and marine survival.

Finally and more generally, the approach followed in this study is generic and could be adapted and used in similar case studies. Several Atlantic salmon rivers such as the Nivelle (France, Dumas and Prouzet, 2003), the Bush (Northern Ireland, Kennedy and Crozier, 1993, 1995), the Lærdalselva and Imsa (Norway, Crozier *et al.*, 2003) or the Miramichi (Canada, Chaput *et al.*, 2001) possess large datasets which could be used in a similar way.

### **5.2.3 Management**

The models presented in this study represent significant progress for the understanding and the management of the salmon population in the Foyle catchment. The different biological hypotheses and spatial structure considered to perform the analysis allow making the best use of the data available and estimate population abundance and their associated uncertainties for this population that were never available before. As a result of the Bayesian framework, all variables are estimated with their associated uncertainty. Based on these estimates it is possible to calculate the exploitation rates and the spawner abundances during the time-series. Based on the density dependence relationship and the annual 0+ juvenile to returning adult survivals, the annual reference points as recommended by the NASCO and the population replacement rates for each geographical unit are calculated. It is then possible to see that during most of the time series the overall Foyle salmon (meta)population is very likely to have been exploited under the reference exploitation rate. Some differences are noticeable among the geo units especially for the Foyle which seems to have been suffering more of the fisheries exploitation. Even though the population follows a consistent decline since the mid 1960's which indicates that the main driver for this decline is the declining 0+juvenile to returning adult survival. The model presented here allows short term predictions to be made which can be used to adjust management regulation on a yearly basis.

# Annex 1: WinBUGS code: Electric fishing calibration model and estimation of average 0+juvenile densities in grade 1 site in the five geo units from 1998 to 2008.

## # Model

```
# Electofishing calibration model based on Crozier & Kennedy method
# Estimate density using fully quantitative electrofishing and 5min index of abundance
# Sites located in the Faughan sub-catchment
# Summer 2006 for sites 1:11
# Summer 2007 for sites 12 to 21

model
{
  # parameter of the catchability
  alpha ~ dnorm(0,0.001)
  beta ~ dnorm(0,0.001)

  #scale parameters
  T.AW ~ dgamma(0.01,0.01)
  phi ~ dgamma(0.01,0.01)#I(0.00001,)
  psi ~ dgamma(0.01,0.01)
  delta ~ dgamma(1,0.01)

  #shape paarameters
  inv.kappa ~ dgamma(0.01,0.01)
  kappa <- 1/ inv.kappa
  inv.eta ~ dgamma(0.01,0.01)
  eta <- 1/inv.eta
  inv.rho ~ dgamma(0.01,0.01)
  rho <- 1/inv.rho

  # density parameters
  gamma <- delta * psi
  b[1] <- gamma
  b[2] <- gamma * rho
  dmoy[1] <- b[1] /psi
  dmoy[2] <- b[2] /psi
  epsilon ~ dnorm(0,0.001)I(0,)
  ratio.d <- dmoy[1]/dmoy[2]

  for (i in 1:I){
    # hierarchical structure of the density
    d[i] ~ dgamma(b[H[i]], psi)
    vard[i] <- b[H[i]] / (psi * psi)
    sdd[i] <- sqrt(vard[i])

    # lambda parameter for N[i] : surface * density
    m[i] <- S[i]*d[i]

    # 5min IA is expected to be proportional to the density
    # IA.5min follows a negative binomial distribution which is equivalent to a surdispersed poisson distribution
    # the scale parameter is fixed (variance proportional to the mean)
    # to take in account the fact that the IA seems to reach a maximum for high densities we incorporate 'd[i] ^ a'
    # the proportionality relation between IA.5min and d is modified by the width of the site
```

```

# aw is the average width of the site based on up and down stream measurement
a[i]<-kappa * pow(d[i],eta) * phi
l[i] ~ dgamma(a[i],phi)|(0.01,)
varIA[i] <- a[i] / (phi * phi)
sdIA[i] <- sqrt(varIA[i])
IA[i] ~ dpois(l[i])
# The fish present on the site (N[i]) are expected to be distributed following a poisson distribution
c.N[i]<-10*S[i]
N_tot[i] ~ dpois(m[i])|(,c.N[i])

# parameters for length effect on catchability (catchability =cst over passes)
mu[i] <- alpha + beta * (W[i]-mean(W))
w.theta[i] ~ dnorm(mu[i],T.AW)
logit(p[i,1]) <-w.theta[i]

# The catchability after the first pass decrease by a factor epsilon after each extra pass
for (k in 2:4){
  logit(p[i,k]) <- logit(p[i,k-1]) -epsilon
}
N1[i]<-N[i] - IA[i]
C1[i]~dbin(p[i,1],N1[i])
N2[i]<-N1[i] - C1[i]
C2[i]~dbin( p[i,2],N2[i])
N3[i]<-N2[i] - C2[i]
C3[i]~dbin( p[i,3],N3[i])
N4[i]<-N3[i] - C3[i]
C4[i]~dbin( p[i,4],N4[i])
}

# Estimation of average density in grade 1 sites for each geo units from 1998 to 2008

#The probability density distribution of the parameters of the calibration model are extracted to be used to estimate densities
in all the sites sampled over the years
kappa.cut <- cut(kappa)
eta.cut<- cut(eta)
phi.cut <- cut(phi)

for(i in 1:5){
  CV[i] ~dgamma(0.001, 0.001)
}
# Faughan
for (t in 1:11){
  mu.d.unit[t,1] ~dgamma(1,0.01)
  var.fau[t] <-b.fau[t]/(psi.fau[t]*psi.fau[t])
  sd.d.unit[t,1]<-sqrt(var.fau[t])
  psi.fau[t] <- mu.d.unit[t,1] / ( (CV[1] *mu.d.unit[t,1]) *(CV[1] *mu.d.unit[t,1]) )
  b.fau[t] <- mu.d.unit[t,1]*psi.fau[t]
  sdIA.Fau[t]<- sd(IA.fau.tot[1:N.IA[1,t],t])

  for (n in 1:N.IA[1,t]){
    d.fau[n,t]~dgamma(b.fau[t], psi.fau[t])|(0.001,)
    a.fau[n,t]<-kappa.cut * pow(d.fau[n,t],eta.cut) * phi.cut
    l.fau[n,t] ~ dgamma(a.fau[n,t],phi.cut)|(0.01,)
    varIA.fau[n,t] <- a.fau[n,t] / (phi.cut * phi.cut)
    sdIA.fau[n,t] <- sqrt(varIA.fau[n,t])
    IA.fau.tot[n,t] ~ dpois(l.fau[n,t])
  }
}
# Finn
for (t in 1:11){
  mu.d.unit[t,2] ~dgamma(1,0.01)
  var.fin[t] <-b.fin[t]/(psi.fin[t]*psi.fin[t])
  sd.d.unit[t,2]<-sqrt(var.fin[t])
  psi.fin[t] <- mu.d.unit[t,2] / ( (CV[2] *mu.d.unit[t,2]) *(CV[2] *mu.d.unit[t,2]) )
  b.fin[t] <- mu.d.unit[t,2]*psi.fin[t]
  sdIA.Fin[t]<- sd(IA.fin.tot[1:N.IA[2,t],t])

  for (n in 1:N.IA[2,t]){
    d.fin[n,t]~dgamma(b.fin[t], psi.fin[t])|(0.001,)
    a.fin[n,t]<-kappa.cut * pow(d.fin[n,t],eta.cut) * phi.cut
    l.fin[n,t] ~ dgamma(a.fin[n,t],phi.cut)|(0.01,)
    varIA.fin[n,t] <- a.fin[n,t] / (phi.cut * phi.cut)
    sdIA.fin[n,t] <- sqrt(varIA.fin[n,t])
    IA.fin.tot[n,t] ~ dpois(l.fin[n,t])
  }
}
}

```

```

# Mourné
for (t in 2:11){
  mu.d.unit[t,3] ~dgamma(1,0.01)
  var.mou[t] <-b.mou[t]/(psi.mou[t]*psi.mou[t])
  sd.d.unit[t,3]<-sqrt(var.mou[t])
  psi.mou[t] <- mu.d.unit[t,3] / ( (CV[3] *mu.d.unit[t,3]) *(CV[3] *mu.d.unit[t,3]) )
  b.mou[t] <- mu.d.unit[t,3]* psi.mou[t]
  sdIA.Mou[t]<- sd(IA.mou.tot[1:N.IA[3,t],t])

  for (n in 1:N.IA[3,t]){
    d.mou[n,t]~dgamma(b.mou[t], psi.mou[t])l(0.001,)
    a.mou[n,t]~kappa.cut * pow(d.mou[n,t],eta.cut) * phi.cut
    l.mou[n,t] ~ dgamma(a.mou[n,t],phi.cut)l(0.01,)
    varIA.mou[n,t] <- a.mou[n,t] / (phi.cut * phi.cut)
    sdIA.mou[n,t] <- sqrt(varIA.mou[n,t])
    IA.mou.tot[n,t] ~ dpois(l.mou[n,t])
  }
}
#Roe
for (t in 1:11){
  mu.d.unit[t,4] ~dgamma(1,0.01)
  var.roe[t] <-b.roe[t]/(psi.roe[t]*psi.roe[t])
  sd.d.unit[t,4]<-sqrt(var.roe[t])
  psi.roe[t] <- mu.d.unit[t,4] / ( (CV[4] *mu.d.unit[t,4]) *(CV[4] *mu.d.unit[t,4]) )
  b.roe[t] <- mu.d.unit[t,4]*psi.roe[t]
  sdIA.Roe[t]<- sd(IA.roe.tot[1:N.IA[4,t],t])

  for (n in 1:N.IA[4,t]){
    d.roe[n,t]~dgamma(b.roe[t], psi.roe[t])l(0.001,)
    a.roe[n,t]~kappa.cut * pow(d.roe[n,t],eta.cut) * phi.cut
    l.roe[n,t] ~ dgamma(a.roe[n,t],phi.cut)l(0.01,)
    varIA.roe[n,t] <- a.roe[n,t] / (phi.cut * phi.cut)
    sdIA.roe[n,t] <- sqrt(varIA.roe[n,t])
    IA.roe.tot[n,t] ~ dpois(l.roe[n,t])
  }
}
# Foyle
for (t in 1:11){
  mu.d.unit[t,5] ~dgamma(1,0.01)
  var.foy[t] <-b.foy[t]/(psi.foy[t]*psi.foy[t])
  sd.d.unit[t,5]<-sqrt(var.foy[t])
  psi.foy[t] <- mu.d.unit[t,5] / ( (CV[5] *mu.d.unit[t,5]) *(CV[5] *mu.d.unit[t,5]) )
  b.foy[t] <- mu.d.unit[t,5]*psi.foy[t]
  sdIA.Foy[t]<- sd(IA.foy.tot[1:N.IA[5,t],t])

  for (n in 1:N.IA[5,t]){
    d.foy[n,t]~dgamma(b.foy[t], psi.foy[t])l(0.001,)
    a.foy[n,t]~kappa.cut * pow(d.foy[n,t],eta.cut) * phi.cut
    l.foy[n,t] ~ dgamma(a.foy[n,t],phi.cut)l(0.01,)
    varIA.foy[n,t] <- a.foy[n,t] / (phi.cut * phi.cut)
    sdIA.foy[n,t] <- sqrt(varIA.foy[n,t])
    IA.foy.tot[n,t] ~ dpois(l.foy[n,t])
  }
}
}
}

```

## #data

```

list(
  l = 21,
  # Surface in m2 for each 21 sites of the calibration
  S = c(382,135,133,172,134,108,112,120,105,86,72,202,90,173,142,74,61,82,78,93,67),

  # group 2: nursery grade 1+2; group1: nursery grade 3+4
  H=c(1,2,1,1,1,1,2,1,1,2,2,2,2,2,2,2,1,1,1,2),

  #IA number of 0+ salmon caught in the 5min sample first 11 were done in 2006 the last 10 in 2007
  IA = c(17,6,10,13,28,13,0,3,27,12,25,6,6,3,2,0,6,32,18,16,23),

  #Width of each site
  W = c(9.65,7.4,8.6,9.15,5.35,5.9,3.15,5.65,5.05,3.6,4.2,5.35,3.6,4.05,3.30,3.95,3.5,3.8,3.1,3.05,3.4),
  #Number of 0+ salmon caught in the first non timed pass
  C1 = c(50,21,18,32,104,27,1,5,62,11,53,8,17,4,3,1,7,39,54,48,52),

  #Number of 0+ salmon caught in the second non timed pass
  C2 = c(38,13,6,28,54,21,1,2,36,7,38,5,2,2,1,1,3,30,26,24,22),

```



#Number of 0+ salmon caught in the third non timed pass  
 C3 = c(20,11,7,17,55,18,0,1,27,4,29,1,2,2,1,1,1,31,20,6,8),

#Number of 0+ salmon caught in the fourth non timed pass  
 C4 = c(NA,NA,9,11,36,11,NA,2,17,NA,13,NA,2,NA,NA,NA,NA,19,15,NA,NA),

#Number of sites with a nursery grade 1 sampled every year in each geo units  
 #lines correspond to geo units (Faughan, finn, mourne, roe, foyle) and rows years (1998 to 2008)  
 N.IA=structure(.Data=c(  
 6,21,13,16,18,17,24,26,24,27,28,  
 ... (see table below for full data set)  
 ),,.Dim=c(5,11)),

Geo unit	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008
Faughan	6	21	13	16	18	17	24	26	24	27	28
Finn	28	46	18	23	7	24	29	14	26	48	49
Mourne	0	27	32	106	137	148	149	144	155	216	131
Roe	18	53	31	37	30	36	42	43	57	59	54
Foyle	10	13	18	27	23	25	29	29	35	34	38

# These are all the electrofishing sites for the 5 unit: Faughan, Finn,  
 # Mourne, Roe and Foyle. the columns indicate the year: 1998->2006

IA.fau.tot=structure(.Data=c(  
 0,18,3,101,63,74,91,79,57,75,64,  
 ... (see table below for full data set)  
 ),,.Dim=c(28,11)),

	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008
0	18	3	101	63	74	91	79	57	75	64	
13	34	3	50	74	60	54	81	79	79	56	
8	5	49	30	13	85	66	120	27	51	6	
0	2	2	32	10	14	37	20	6	6	6	
9	8	10	20	10	71	12	22	3	5	70	
0	1	27	64	24	55	31	72	36	0	60	
NA	0	27	88	19	40	16	7	0	75	44	
NA	17	17	94	13	13	58	21	64	0	40	
NA	16	4	85	33	20	33	63	48	65	33	
NA	12	8	18	36	0	65	36	36	46	64	
NA	1	11	15	4	108	55	15	34	45	47	
NA	8	1	41	0	84	41	15	62	51	33	
NA	7	15	14	0	86	46	50	17	61	50	
NA	4	NA	1	10	64	73	58	10	29	40	
NA	2	NA	47	10	58	69	50	28	28	48	
NA	0	NA	28	3	74	54	34	102	64	42	
NA	8	NA	NA	8	67	48	3	14	47	41	
NA	8	NA	NA	26	NA	62	0	48	29	5	
NA	7	NA	NA	NA	NA	0	0	13	46	21	
NA	3	NA	NA	NA	NA	0	50	13	34	97	
NA	13	NA	NA	NA	NA	32	33	2	75	27	
NA	NA	NA	NA	NA	NA	7	0	0	49	27	
NA	NA	NA	NA	NA	NA	0	13	0	7	15	
NA	NA	NA	NA	NA	NA	40	0	97	41	22	
NA	NA	NA	NA	NA	NA	NA	0	NA	5	6	
NA	NA	NA	NA	NA	NA	NA	57	NA	5	0	
NA	NA	NA	NA	NA	NA	NA	NA	NA	64	10	
NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	79	

IA.fin.tot=structure(.Data=c(  
 17,0,5,21,0,0,18,24,12,2,31,  
 ... (see table below for full data set)  
 ),,.Dim=c(49,11)),

	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008
17	0	5	21	0	0	18	24	12	2	31	
8	0	0	2	1	0	22	21	9	8	45	
0	0	1	0	10	0	10	37	18	32	16	
15	0	0	0	2	0	20	19	13	31	4	
18	3	0	0	8	0	19	9	4	40	7	
12	6	1	7	2	5	5	15	0	0	15	
15	5	0	1	0	6	0	30	0	32	9	
10	4	0	2	NA	9	7	31	0	19	22	
10	0	2	3	NA	10	3	25	3	29	0	
8	0	0	3	NA	5	10	14	0	15	22	
7	0	18	4	NA	3	10	20	0	36	15	
13	4	3	5	NA	7	11	14	9	0	31	
12	8	12	6	NA	19	21	20	0	2	8	

25	7	4	0	NA	0	26	25	0	0	15
17	5	4	11	NA	8	22	NA	1	1	4
16	1	11	25	NA	3	11	NA	6	2	6
12	5	3	14	NA	5	35	NA	0	32	0
12	29	2	15	NA	5	29	NA	0	40	26
11	9	NA	0	NA	6	43	NA	0	0	16
21	19	NA	0	NA	8	3	NA	14	15	44
7	12	NA	2	NA	7	2	NA	12	2	23
21	0	NA	0	NA	9	0	NA	8	0	6
21	6	NA	0	NA	2	0	NA	5	6	16
13	6	NA	NA	NA	1	0	NA	0	0	8
16	0	NA	NA	NA	NA	17	NA	0	11	0
8	0	NA	NA	NA	NA	32	NA	17	0	6
NA	0	NA	NA	NA	NA	17	NA	NA	0	0
NA	0	NA	NA	NA	NA	13	NA	NA	6	0
NA	15	NA	NA	NA	NA	18	NA	NA	21	6
NA	6	NA	NA	NA	NA	NA	NA	NA	30	11
NA	10	NA	NA	NA	NA	NA	NA	NA	21	13
NA	31	NA	NA	NA	NA	NA	NA	NA	14	0
NA	15	NA	NA	NA	NA	NA	NA	NA	2	0
NA	26	NA	NA	NA	NA	NA	NA	NA	21	19
NA	10	NA	NA	NA	NA	NA	NA	NA	3	35
NA	13	NA	NA	NA	NA	NA	NA	NA	3	27
NA	0	NA	NA	NA	NA	NA	NA	NA	0	4
NA	0	NA	NA	NA	NA	NA	NA	NA	0	4
NA	0	NA	NA	NA	NA	NA	NA	NA	10	16
NA	1	NA	NA	NA	NA	NA	NA	NA	42	10
NA	1	NA	NA	NA	NA	NA	NA	NA	40	0
NA	30	NA	NA	NA	NA	NA	NA	NA	38	18
NA	10	NA	NA	NA	NA	NA	NA	NA	0	4
NA	13	NA	NA	NA	NA	NA	NA	NA	0	4
NA	7	NA	NA	NA	NA	NA	NA	NA	19	20
NA	3	NA	NA	NA	NA	NA	NA	NA	20	5
NA	NA	NA	NA	NA	NA	NA	NA	NA	3	0
NA	NA	NA	NA	NA	NA	NA	NA	NA	2	20
NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	14

IA.mou.tot=structure(.Data=c(
NA,0,4,2,0,10,75,1,2,0,0,
... (see table below for full data set)
),.Dim=c(216,11)),

1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008
NA	0	4	2	0	10	75	1	2	0	0
NA	0	1	11	30	0	35	0	0	0	4
NA	2	0	0	33	0	42	51	0	10	1
NA	12	0	0	0	0	11	26	26	0	5
NA	16	0	18	0	0	14	53	32	49	15
NA	13	5	28	0	26	12	0	63	13	14
NA	18	0	0	3	3	0	0	0	48	0
NA	21	0	0	2	0	31	0	0	0	0
NA	7	0	0	1	0	10	0	0	0	0
NA	2	0	0	3	0	0	0	0	0	0
NA	0	0	0	11	0	18	0	0	0	0
NA	0	5	16	24	15	25	14	0	0	0
NA	0	5	20	8	24	30	5	0	0	0
NA	0	14	9	9	24	16	4	22	6	5
NA	0	11	7	0	29	6	2	8	11	2
NA	0	6	8	0	4	18	14	2	7	0
NA	0	12	6	5	18	6	7	16	31	9
NA	0	2	4	0	25	5	3	21	22	8
NA	10	4	33	17	13	4	0	9	21	5
NA	0	2	35	18	25	2	11	0	1	16
NA	0	4	39	9	22	7	3	1	5	1
NA	0	5	19	10	21	0	18	4	3	2
NA	0	14	5	23	30	4	12	27	1	12
NA	0	7	30	7	9	0	8	27	0	30
NA	0	10	10	14	25	2	13	37	5	28
NA	0	5	34	8	12	0	6	10	3	13
NA	0	0	22	7	12	1	2	24	28	9
NA	NA	2	17	13	15	8	10	34	10	6
NA	NA	0	6	10	32	2	13	38	6	1
NA	NA	0	35	10	15	3	13	32	6	1
NA	NA	0	19	12	18	2	42	32	22	1
NA	NA	4	9	26	60	4	0	5	14	5
NA	NA	NA	13	11	31	0	0	7	4	1
NA	NA	NA	10	20	27	0	0	60	8	0

NA	NA	NA	6	23	89	0	9	42	15	0
NA	NA	NA	17	4	44	0	20	30	0	12
NA	NA	NA	32	3	15	8	13	2	3	0
NA	NA	NA	41	20	10	12	11	0	8	4
NA	NA	NA	38	0	7	23	3	11	19	10
NA	NA	NA	18	0	2	28	0	2	12	0
NA	NA	NA	12	23	13	58	0	16	4	15
NA	NA	NA	22	41	6	67	12	20	37	0
NA	NA	NA	17	12	8	6	2	12	17	0
NA	NA	NA	9	0	4	18	0	3	15	14
NA	NA	NA	6	0	4	30	0	7	25	15
NA	NA	NA	37	17	2	24	0	29	31	6
NA	NA	NA	9	5	6	24	0	69	30	12
NA	NA	NA	0	7	0	23	52	21	27	16
NA	NA	NA	4	1	0	29	16	18	32	12
NA	NA	NA	0	7	0	2	7	70	17	0
NA	NA	NA	0	2	0	0	0	16	20	0
NA	NA	NA	2	31	3	7	37	6	12	9
NA	NA	NA	12	9	2	1	55	2	13	35
NA	NA	NA	5	18	4	4	88	1	28	0
NA	NA	NA	6	3	5	0	62	0	36	4
NA	NA	NA	11	21	3	7	67	5	6	4
NA	NA	NA	24	5	7	3	31	22	4	4
NA	NA	NA	11	29	19	2	16	40	0	3
NA	NA	NA	7	39	13	3	18	7	5	14
NA	NA	NA	16	53	7	0	14	32	0	13
NA	NA	NA	0	19	5	0	0	22	0	18
NA	NA	NA	0	11	1	0	25	36	18	10
NA	NA	NA	0	21	14	0	5	38	0	6
NA	NA	NA	0	18	18	0	122	1	15	9
NA	NA	NA	1	0	3	0	0	0	54	3
NA	NA	NA	0	2	7	0	0	5	2	2
NA	NA	NA	0	0	3	0	0	1	58	2
NA	NA	NA	6	0	4	0	0	1	38	4
NA	NA	NA	0	3	6	0	0	3	27	1
NA	NA	NA	0	2	1	0	0	3	16	3
NA	NA	NA	0	0	5	0	0	4	17	8
NA	NA	NA	46	0	1	0	0	7	17	18
NA	NA	NA	4	0	0	0	0	23	18	0
NA	NA	NA	5	1	2	0	2	6	14	0
NA	NA	NA	13	1	7	17	7	6	0	0
NA	NA	NA	0	0	0	1	12	12	0	0
NA	NA	NA	2	3	14	13	33	11	1	0
NA	NA	NA	0	23	18	22	0	3	4	0
NA	NA	NA	0	2	6	36	25	6	7	0
NA	NA	NA	1	30	10	13	30	13	6	0
NA	NA	NA	18	20	29	24	15	10	2	0
NA	NA	NA	9	19	40	32	19	4	5	0
NA	NA	NA	20	20	32	36	12	3	17	0
NA	NA	NA	12	9	38	24	0	3	13	0
NA	NA	NA	13	13	6	1	0	1	15	0
NA	NA	NA	30	0	39	17	1	14	22	28
NA	NA	NA	3	0	32	31	0	6	10	21
NA	NA	NA	27	0	45	26	1	2	50	26
NA	NA	NA	22	0	38	1	2	1	29	6
NA	NA	NA	16	0	18	0	18	1	75	35
NA	NA	NA	14	0	21	0	56	0	4	29
NA	NA	NA	3	0	12	0	29	0	0	7
NA	NA	NA	7	0	25	18	32	0	2	5
NA	NA	NA	17	1	10	27	94	0	5	30
NA	NA	NA	13	1	11	38	30	4	3	38
NA	NA	NA	11	1	0	1	0	3	5	21
NA	NA	NA	24	0	3	0	2	25	6	12
NA	NA	NA	21	0	18	0	2	29	57	17
NA	NA	NA	12	0	27	0	24	34	4	21
NA	NA	NA	5	0	0	0	0	18	9	27
NA	NA	NA	9	0	0	0	0	34	0	30
NA	NA	NA	15	4	0	0	26	65	0	32
NA	NA	NA	9	7	0	0	39	52	0	38
NA	NA	NA	2	22	3	0	19	37	4	0
NA	NA	NA	6	5	13	11	1	29	5	4
NA	NA	NA	16	7	2	13	8	43	1	0
NA	NA	NA	NA	13	0	18	44	24	0	0
NA	NA	NA	NA	22	0	15	41	35	0	0
NA	NA	NA	NA	21	0	22	33	106	0	2
NA	NA	NA	NA	9	0	19	33	55	0	0
NA	NA	NA	NA	12	8	0	24	82	4	1
NA	NA	NA	NA	10	0	11	4	107	3	0
NA	NA	NA	NA	7	6	10	0	74	0	0

NA	NA	NA	NA	5	6	0	0	52	2	0
NA	NA	NA	NA	7	4	20	42	67	7	0
NA	NA	NA	NA	2	0	8	39	45	0	8
NA	NA	NA	NA	0	0	36	57	43	0	8
NA	NA	NA	NA	2	0	17	7	0	0	11
NA	NA	NA	NA	2	0	13	0	0	0	18
NA	NA	NA	NA	3	10	25	4	23	0	7
NA	NA	NA	NA	19	10	36	23	10	1	5
NA	NA	NA	NA	2	8	25	0	0	6	5
NA	NA	NA	NA	0	19	36	3	39	2	8
NA	NA	NA	NA	1	6	67	2	7	24	12
NA	NA	NA	NA	3	8	46	2	5	7	2
NA	NA	NA	NA	0	10	21	3	24	17	0
NA	NA	NA	NA	0	6	5	3	1	10	0
NA	NA	NA	NA	0	10	0	26	4	8	0
NA	NA	NA	NA	4	32	27	16	36	41	2
NA	NA	NA	NA	4	8	5	19	28	35	13
NA	NA	NA	NA	9	8	16	14	63	38	3
NA	NA	NA	NA	4	24	0	14	27	30	NA
NA	NA	NA	NA	5	14	8	8	34	42	NA
NA	NA	NA	NA	5	6	5	8	15	104	NA
NA	NA	NA	NA	6	4	0	17	16	29	NA
NA	NA	NA	NA	7	15	20	12	0	47	NA
NA	NA	NA	NA	13	6	20	4	7	29	NA
NA	NA	NA	NA	NA	7	21	4	2	15	NA
NA	NA	NA	NA	NA	8	18	0	3	19	NA
NA	NA	NA	NA	NA	2	7	1	3	15	NA
NA	NA	NA	NA	NA	4	0	0	1	3	NA
NA	NA	NA	NA	NA	4	29	1	0	1	NA
NA	NA	NA	NA	NA	2	0	3	1	1	NA
NA	NA	NA	NA	NA	4	31	2	4	0	NA
NA	NA	NA	NA	NA	0	0	NA	0	32	NA
NA	NA	NA	NA	NA	2	15	NA	0	20	NA
NA	NA	NA	NA	NA	1	11	NA	0	59	NA
NA	NA	NA	NA	NA	1	1	NA	2	0	NA
NA	NA	NA	NA	NA	NA	13	NA	3	69	NA
NA	NA	NA	NA	NA	NA	NA	NA	4	25	NA
NA	NA	NA	NA	NA	NA	NA	NA	0	9	NA
NA	NA	NA	NA	NA	NA	NA	NA	0	31	NA
NA	NA	NA	NA	NA	NA	NA	NA	1	14	NA
NA	NA	NA	NA	NA	NA	NA	NA	0	17	NA
NA	NA	NA	NA	NA	NA	NA	NA	2	26	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	9	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	2	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	5	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	2	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	5	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	9	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	13	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	33	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	2	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	67	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	12	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	45	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	12	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	10	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	3	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	30	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	3	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	0	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	0	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	2	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	0	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	32	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	35	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	32	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	14	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	42	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	43	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	38	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	7	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	13	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	39	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	5	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	23	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	0	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	5	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	0	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	8	NA

NA	NA	NA	NA	NA	NA	NA	NA	NA	5	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	10	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	0	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	4	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	11	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	0	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	7	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	2	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	6	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	5	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	4	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	9	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	7	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	12	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	0	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	14	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	3	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	18	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	4	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	1	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	0	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	1	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	5	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	7	NA

IA.roe.tot=structure(.Data=c(11,9,0,130,12,23,142,155,107,178,53,  
 ... (see table below for full data set)  
 ),..Dim=c(59,11)),

1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008
11	9	0	130	12	23	142	155	107	178	53
18	27	11	11	31	65	22	19	22	27	103
17	22	38	1	59	85	24	13	30	90	22
15	6	34	111	88	54	51	92	194	50	34
13	4	49	8	10	21	10	3	244	56	50
8	5	42	30	14	52	80	301	37	72	56
11	4	63	69	2	17	47	14	27	89	51
15	21	41	36	14	9	32	30	45	55	43
2	4	29	16	26	54	97	21	59	92	35
21	5	0	21	14	16	55	21	57	52	34
7	23	6	43	8	29	35	32	38	56	29
4	16	15	5	31	0	166	96	36	68	18
7	14	18	27	22	107	53	27	20	19	34
8	12	185	39	23	68	78	67	3	6	33
18	17	81	36	29	62	82	174	0	0	26
16	13	16	6	17	15	144	23	2	25	13
2	25	24	98	23	0	49	26	22	58	1
7	0	10	83	0	10	55	57	94	27	0
NA	7	11	27	8	32	0	145	31	0	18
NA	22	27	96	0	4	0	80	6	17	61
NA	29	19	52	0	3	115	97	0	0	16
NA	2	6	25	0	6	26	63	6	0	6
NA	6	1	11	0	3	0	4	0	36	0
NA	66	19	0	31	4	4	0	8	21	0
NA	43	1	4	4	9	0	25	34	0	0
NA	91	6	63	17	8	0	2	33	0	0
NA	51	2	74	4	40	0	0	0	3	0
NA	44	1	20	0	0	48	0	3	0	0
NA	109	5	21	5	9	55	83	0	0	35
NA	57	1	51	8	22	17	32	0	0	14
NA	43	1	12	NA	6	18	19	0	0	27
NA	32	NA	4	NA	14	5	0	0	0	17
NA	20	NA	0	NA	119	8	25	93	50	1
NA	33	NA	0	NA	6	0	0	109	9	2
NA	29	NA	0	NA	76	4	0	5	59	0
NA	6	NA	0	NA	37	1	0	49	33	0
NA	44	NA	0	NA	NA	0	0	0	8	0
NA	37	NA	NA	NA	NA	0	0	1	0	71
NA	44	NA	NA	NA	NA	0	40	0	4	4
NA	74	NA	NA	NA	NA	12	39	0	0	29
NA	29	NA	NA	NA	NA	9	1	29	0	39
NA	48	NA	NA	NA	NA	0	0	1	0	42
NA	114	NA	NA	NA	NA	NA	0	109	39	0
NA	11	NA	NA	NA	NA	NA	NA	49	7	27
NA	22	NA	NA	NA	NA	NA	NA	1	0	45
NA	26	NA	NA	NA	NA	NA	NA	40	173	63
NA	8	NA	NA	NA	NA	NA	NA	110	27	41

NA	21	NA	NA	NA	NA	NA	NA	40	2	28
NA	32	NA	NA	NA	NA	NA	NA	161	52	13
NA	12	NA	NA	NA	NA	NA	NA	141	110	38
NA	194	NA	NA	NA	NA	NA	NA	17	87	119
NA	11	NA	NA	NA	NA	NA	NA	6	82	27
NA	33	NA	NA	NA	NA	NA	NA	41	15	0
NA	NA	NA	NA	NA	NA	NA	NA	20	77	67
NA	NA	NA	NA	NA	NA	NA	NA	13	38	NA
NA	NA	NA	NA	NA	NA	NA	NA	118	56	NA
NA	NA	NA	NA	NA	NA	NA	NA	0	102	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	0	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	38	NA

```
IA.foy.tot=structure(.Data=c(
4,0,7,69,0,11,0,0,169,95,26,
... (see table below for full data set)
),.Dim=c(38,11))
)
```

1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008
4	0	7	69	0	11	0	0	169	95	26
18	0	0	46	24	9	0	6	94	109	29
6	0	20	164	24	48	0	122	100	125	55
0	15	8	74	33	1	0	74	56	94	69
15	7	30	21	40	86	10	144	10	45	51
17	5	19	54	4	88	93	74	2	40	12
3	6	24	3	27	0	136	98	0	16	9
3	7	2	0	49	64	49	92	1	22	20
0	7	19	0	0	69	102	38	167	26	21
3	0	7	0	0	54	103	31	39	101	15
NA	0	10	2	0	1	64	26	33	48	26
NA	0	0	0	0	2	56	11	17	50	0
NA	0	1	3	0	0	32	3	0	31	0
NA	NA	0	0	18	0	9	0	0	0	34
NA	NA	0	8	4	7	48	0	3	0	25
NA	NA	0	0	4	1	8	16	49	38	35
NA	NA	4	5	4	24	81	0	110	82	45
NA	NA	3	1	4	18	39	0	62	87	28
NA	NA	NA	4	8	1	0	0	24	53	0
NA	NA	NA	3	21	0	0	0	3	0	0
NA	NA	NA	0	0	0	0	0	2	0	2
NA	NA	NA	0	0	0	56	0	0	0	6
NA	NA	NA	0	0	0	0	0	0	20	0
NA	NA	NA	0	NA	0	0	0	16	0	0
NA	NA	NA	0	NA	0	17	0	6	2	1
NA	NA	NA	0	NA	NA	3	4	30	1	15
NA	NA	NA	0	NA	NA	0	96	0	0	0
NA	NA	NA	NA	NA	NA	0	0	0	6	4
NA	NA	NA	NA	NA	NA	0	0	0	0	1
NA	NA	NA	NA	NA	NA	NA	NA	0	3	0
NA	NA	NA	NA	NA	NA	NA	NA	0	10	0
NA	NA	NA	NA	NA	NA	NA	NA	0	0	0
NA	NA	NA	NA	NA	NA	NA	NA	0	4	2
NA	NA	NA	NA	NA	NA	NA	NA	0	0	6
NA	NA	NA	NA	NA	NA	NA	NA	0	NA	0
NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0
NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0
NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0

## #Initialisation of the Gibbs sampler (1 chain)

```
list(
```

```
# d is estimated in number of fish / m2
```

```
delta=1.8,
inv.rho=1.81,
psi = 0.79,
epsilon=0.18,
```

```
alpha = -0.7,
beta = -0.17,
inv.kappa= 0.078,
phi=16,
T.AW=6.2,
```

inv.eta = 1.5,  
 # inits for density at the 21 calibration sites  
 d = c(0.43,0.57,0.54,0.75,2.68,1.18,0.03,0.13,1.91,0.5,2.65,0.13,0.35,0.08,0.06,0.16,1.65,2.43,2.12,1.11,1.68),

l = c(18,7,11,14,29,14,1,3,28,13,26,7,7,4,3,1,7,33,19,17,24),

w.theta = c(-2.157,-1.215,-1.533,-0.9548,-0.5708,-0.568,-0.2705,-1.46,-0.1652,-0.3609,-0.7165,-0.7745,0.1161,0.8448,0.4773,-1.217,-0.4425,-1.49,-0.421,0.2168,0.1112),

# inits for population abundance at the 21 calibration sites  
 N = c(180,62,59,119,335,110,4,16,194,40,180,26,32,14,9,12,100,200,164,103,112),

# inits for captures during the 4<sup>th</sup> pass at the calibration sites  
 C4 = c(3,3,NA,NA,NA,NA,0,NA,NA,0,NA,0,NA,0,0,0,0,NA,NA,2,3),

CV=c(1,1,1,1,1),

# inits for average year density in each geo units-> rows: years ; columns: geo units  
 mu.d.unit=structure(.Data=c(0.344, 0.854, NA, 0.731, 0.469, ... (see table below for full data set) ),.Dim=c(11,5)),

Faughan	Finn	Mourne	Roe	Foyle
0.344	0.854	NA	0.731	0.469
0.551	0.453	0.244	1.593	0.260
0.818	0.270	0.283	1.241	0.540
2.186	0.357	0.758	1.611	0.930
1.089	0.253	0.537	0.934	0.605
2.648	0.361	0.679	1.506	1.133
2.015	0.880	0.693	1.693	1.674
1.755	1.248	0.789	1.871	1.565
1.638	0.343	0.939	1.817	1.279
1.5	0.5	0.9	2	2
1.5	0.5	0.9	2	2

# inits for faughan sites densities, column: years  
 d.fau=structure(.Data=c(0.002,1.245,0.396,3.744,2.770,3.070,3.503,3.201,2.598,3.096,2.798, ... (see table below for full data set) ),.Dim=c(28,11)),

1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008
0.002	1.245	0.396	3.744	2.770	3.070	3.503	3.201	2.598	3.096	2.798
1.011	1.868	0.396	2.390	3.070	2.685	2.510	3.252	3.201	3.201	2.569
0.741	0.549	2.359	1.725	1.011	3.354	2.854	4.180	1.612	2.420	0.617
0.002	0.306	0.306	1.797	0.855	1.060	1.972	1.331	0.617	0.617	0.617
0.799	0.741	0.855	1.331	0.855	2.990	0.961	1.415	0.396	0.549	2.963
0.002	0.196	1.612	2.798	1.496	2.540	1.761	3.017	1.938	0.002	2.685
NA	0.002	1.612	3.429	1.288	2.072	1.154	0.681	0.002	3.096	2.202
NA	1.200	1.200	3.577	1.011	1.011	2.627	1.373	2.798	0.002	2.072
NA	1.154	0.476	3.354	1.833	1.331	1.833	2.770	2.328	2.826	1.833
NA	0.961	0.741	1.245	1.938	0.002	2.826	1.938	1.938	2.266	2.798
NA	0.196	0.909	1.108	0.476	3.908	2.540	1.108	1.868	2.234	2.297
NA	0.741	0.196	2.105	0.002	3.329	2.105	1.108	2.742	2.420	1.833
NA	0.681	1.108	1.060	0.002	3.379	2.266	2.390	1.200	2.713	2.390
NA	0.476	NA	0.196	0.855	2.798	3.043	2.627	0.855	1.688	2.072
NA	0.306	NA	2.297	0.855	2.627	2.936	2.390	1.650	1.650	2.328
NA	0.002	NA	1.650	0.396	3.070	2.510	1.868	3.768	2.798	2.138
NA	0.741	NA	NA	0.741	2.881	2.328	0.396	1.060	2.297	2.105
NA	0.741	NA	NA	1.574	NA	2.742	0.002	2.328	1.688	0.549
NA	0.681	NA	NA	NA	NA	0.002	0.002	1.011	2.266	1.373
NA	0.396	NA	NA	NA	NA	0.002	2.390	1.011	1.868	3.649
NA	1.011	NA	NA	NA	NA	1.797	1.833	0.306	3.096	1.612
NA	NA	NA	NA	NA	NA	0.681	0.002	0.002	2.359	1.612
NA	NA	NA	NA	NA	NA	0.002	1.011	0.002	0.681	1.108
NA	NA	NA	NA	NA	NA	2.072	0.002	3.649	2.105	1.415
NA	NA	NA	NA	NA	NA	NA	0.002	NA	0.549	0.617
NA	NA	NA	NA	NA	NA	NA	2.598	NA	0.549	0.002
NA	NA	NA	NA	NA	NA	NA	NA	NA	2.798	0.855
NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	3.201

l.fau=structure(.Data=c(1,18,3,101,63,74,91,79,57,75,64, ... (see table below for full data set) ),.Dim=c(28,11)),

1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008
1	18	3	101	63	74	91	79	57	75	64
13	34	3	50	74	60	54	81	79	79	56
8	5	49	30	13	85	66	120	27	51	6
1	2	2	32	10	14	37	20	6	6	6
9	8	10	20	10	71	12	22	3	5	70
1	1	27	64	24	55	31	72	36	1	60
NA	1	27	88	19	40	16	7	1	75	44
NA	17	17	94	13	13	58	21	64	1	40
NA	16	4	85	33	20	33	63	48	65	33
NA	12	8	18	36	1	65	36	36	46	64
NA	1	11	15	4	108	55	15	34	45	47
NA	8	1	41	1	84	41	15	62	51	33
NA	7	15	14	1	86	46	50	17	61	50
NA	4	NA	1	10	64	73	58	10	29	40
NA	2	NA	47	10	58	69	50	28	28	48
NA	1	NA	28	3	74	54	34	102	64	42
NA	8	NA	NA	8	67	48	3	14	47	41
NA	8	NA	NA	26	NA	62	1	48	29	5
NA	7	NA	NA	NA	NA	1	1	13	46	21
NA	3	NA	NA	NA	NA	1	50	13	34	97
NA	13	NA	NA	NA	NA	32	33	2	75	27
NA	NA	NA	NA	NA	NA	7	1	1	49	27
NA	NA	NA	NA	NA	NA	1	13	1	7	15
NA	NA	NA	NA	NA	NA	40	1	97	41	22
NA	NA	NA	NA	NA	NA	NA	1	NA	5	6
NA	NA	NA	NA	NA	NA	NA	57	NA	5	1
NA	NA	NA	NA	NA	NA	NA	NA	NA	64	10
NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	79

# inits for finn sites densities, column: years

```
d.fin=structure(.Data=c(
1.200,0.002,0.549,1.373,0.002,0.002,1.245,1.496,0.961,0.306,1.761,
... (see table below for full data set)
),.Dim=c(49,11)),
```

1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008
1.200	0.002	0.549	1.373	0.002	0.002	1.245	1.496	0.961	0.306	1.761
0.741	0.002	0.002	0.306	0.196	0.002	1.415	1.373	0.799	0.741	2.234
0.002	0.002	0.196	0.002	0.855	0.002	0.855	1.972	1.245	1.797	1.154
1.108	0.002	0.002	0.002	0.306	0.002	1.331	1.288	1.011	1.761	0.476
1.245	0.396	0.002	0.002	0.741	0.002	1.288	0.799	0.476	2.072	0.681
0.961	0.617	0.196	0.681	0.306	0.549	0.549	1.108	0.002	0.002	1.108
0.396	0.549	0.002	0.196	0.002	0.617	0.002	1.725	0.002	1.797	0.799
1.108	0.476	0.002	0.306	NA	0.799	0.681	1.761	0.002	1.288	1.415
0.855	0.002	0.306	0.396	NA	0.855	0.396	1.535	0.396	1.688	0.002
0.855	0.002	0.002	0.396	NA	0.549	0.855	1.060	0.002	1.108	1.415
0.741	0.002	1.245	0.476	NA	0.396	0.855	1.331	0.002	1.938	1.108
0.855	0.476	0.396	0.549	NA	0.681	0.909	1.060	0.799	0.002	1.761
0.681	0.741	0.961	0.617	NA	1.288	1.373	1.331	0.002	0.306	0.741
1.011	0.681	0.476	0.002	NA	0.002	1.574	1.535	0.002	0.002	1.108
0.961	0.549	0.476	0.909	NA	0.741	1.415	NA	0.196	0.196	0.476
1.245	0.196	0.909	1.535	NA	0.396	0.909	NA	0.617	0.306	0.617
0.961	0.549	0.396	1.060	NA	0.549	1.903	NA	0.002	1.797	0.002
0.909	1.688	0.306	1.108	NA	0.549	1.688	NA	0.002	2.072	1.574
1.535	0.799	NA	0.002	NA	0.617	2.170	NA	0.002	0.002	1.154
1.200	1.288	NA	0.002	NA	0.741	0.396	NA	1.060	1.108	2.202
1.154	0.961	NA	0.306	NA	0.681	0.306	NA	0.961	0.306	1.455
0.961	0.002	NA	0.002	NA	0.799	0.002	NA	0.741	0.002	0.617
0.961	0.617	NA	0.002	NA	0.306	0.002	NA	0.549	0.617	1.154
0.909	0.617	NA	NA	NA	0.196	0.002	NA	0.002	0.002	0.741
1.373	0.002	NA	NA	NA	NA	1.200	NA	0.002	0.909	0.002
0.681	0.002	NA	NA	NA	NA	1.797	NA	1.200	0.002	0.617
1.373	0.002	NA	NA	NA	NA	1.200	NA	NA	0.002	0.002
1.373	0.002	NA	NA	NA	NA	1.011	NA	NA	0.617	0.002
1.011	1.108	NA	NA	NA	NA	1.245	NA	NA	1.373	0.617
1.154	0.617	NA	NA	NA	NA	NA	NA	NA	1.725	0.909
0.741	0.855	NA	NA	NA	NA	NA	NA	NA	1.373	1.011
0.855	1.761	NA	NA	NA	NA	NA	NA	NA	1.060	0.002
NA	1.108	NA	NA	NA	NA	NA	NA	NA	0.306	0.002
NA	1.574	NA	NA	NA	NA	NA	NA	NA	1.373	1.288
NA	0.855	NA	NA	NA	NA	NA	NA	NA	0.396	1.903
NA	1.011	NA	NA	NA	NA	NA	NA	NA	0.396	1.612
NA	0.002	NA	NA	NA	NA	NA	NA	NA	0.002	0.476
NA	0.002	NA	NA	NA	NA	NA	NA	NA	0.002	0.476
NA	0.002	NA	NA	NA	NA	NA	NA	NA	0.855	1.154
NA	0.196	NA	NA	NA	NA	NA	NA	NA	2.138	0.855
NA	0.196	NA	NA	NA	NA	NA	NA	NA	2.072	0.002



NA	1.725	NA	NA	NA	NA	NA	NA	NA	2.006	1.245
NA	0.855	NA	NA	NA	NA	NA	NA	NA	0.002	0.476
NA	1.011	NA	NA	NA	NA	NA	NA	NA	0.002	0.476
NA	0.681	NA	NA	NA	NA	NA	NA	NA	1.288	1.331
NA	0.396	NA	NA	NA	NA	NA	NA	NA	1.331	0.549
NA	NA	NA	NA	NA	NA	NA	NA	NA	0.396	0.002
NA	NA	NA	NA	NA	NA	NA	NA	NA	0.306	1.331
NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	1.060

```
l.fin=structure(.Data=c(
17,1,5,21,1,1,18,24,12,2,31,
... (see table below for full data set)
),..Dim=c(49,11)),
```

1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008
17	1	5	21	1	1	18	24	12	2	31
8	1	1	2	1	1	22	21	9	8	45
1	1	1	1	10	1	10	37	18	32	16
15	1	1	1	2	1	20	19	13	31	4
18	3	1	1	8	1	19	9	4	40	7
12	6	1	7	2	5	5	15	1	1	15
3	5	1	1	1	6	1	30	1	32	9
15	4	1	2	NA	9	7	31	1	19	22
10	1	2	3	NA	10	3	25	3	29	1
10	1	1	3	NA	5	10	14	1	15	22
8	1	18	4	NA	3	10	20	1	36	15
10	4	3	5	NA	7	11	14	9	1	31
7	8	12	6	NA	19	21	20	1	2	8
13	7	4	1	NA	1	26	25	1	1	15
12	5	4	11	NA	8	22	NA	1	1	4
18	1	11	25	NA	3	11	NA	6	2	6
12	5	3	14	NA	5	35	NA	1	32	1
11	29	2	15	NA	5	29	NA	1	40	26
25	9	NA	1	NA	6	43	NA	1	1	16
17	19	NA	1	NA	8	3	NA	14	15	44
16	12	NA	2	NA	7	2	NA	12	2	23
12	1	NA	1	NA	9	1	NA	8	1	6
12	6	NA	1	NA	2	1	NA	5	6	16
11	6	NA	NA	NA	1	1	NA	1	1	8
21	1	NA	NA	NA	NA	17	NA	1	11	1
7	1	NA	NA	NA	NA	32	NA	17	1	6
21	1	NA	NA	NA	NA	17	NA	NA	1	1
21	1	NA	NA	NA	NA	13	NA	NA	6	1
13	15	NA	NA	NA	NA	18	NA	NA	21	6
16	6	NA	NA	NA	NA	NA	NA	NA	30	11
8	10	NA	NA	NA	NA	NA	NA	NA	21	13
10	31	NA	NA	NA	NA	NA	NA	NA	14	1
NA	15	NA	NA	NA	NA	NA	NA	NA	2	1
NA	26	NA	NA	NA	NA	NA	NA	NA	21	19
NA	10	NA	NA	NA	NA	NA	NA	NA	3	35
NA	13	NA	NA	NA	NA	NA	NA	NA	3	27
NA	1	NA	NA	NA	NA	NA	NA	NA	1	4
NA	1	NA	NA	NA	NA	NA	NA	NA	1	4
NA	1	NA	NA	NA	NA	NA	NA	NA	10	16
NA	1	NA	NA	NA	NA	NA	NA	NA	42	10
NA	1	NA	NA	NA	NA	NA	NA	NA	40	1
NA	30	NA	NA	NA	NA	NA	NA	NA	38	18
NA	10	NA	NA	NA	NA	NA	NA	NA	1	4
NA	13	NA	NA	NA	NA	NA	NA	NA	1	4
NA	7	NA	NA	NA	NA	NA	NA	NA	19	20
NA	3	NA	NA	NA	NA	NA	NA	NA	20	5
NA	NA	NA	NA	NA	NA	NA	NA	NA	3	1
NA	NA	NA	NA	NA	NA	NA	NA	NA	2	20
NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	14

```
# inits for finn sites densities, column: years
d.mou=structure(.Data=c(
NA,0.002,0.476,0.306,0.002,0.855,3.096,0.196,0.306,0.002,0.002,
... (see table below for full data set)
),..Dim=c(216,11)),
```

1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008
NA	0.002	0.476	0.306	0.002	0.855	3.096	0.196	0.306	0.002	0.002
NA	0.002	0.196	0.909	1.725	0.002	1.903	0.002	0.002	0.002	0.476
NA	0.306	0.002	0.002	1.833	0.002	2.138	2.420	0.002	0.855	0.196

NA	0.961	0.002	0.002	0.002	0.002	0.909	1.574	1.574	0.002	0.549
NA	1.154	0.002	1.245	0.002	0.002	1.060	2.480	1.797	2.359	1.108
NA	1.011	0.549	1.650	0.002	1.574	0.961	0.002	2.770	1.011	1.060
NA	1.245	0.002	0.002	0.396	0.396	0.002	0.002	0.002	2.328	0.002
NA	1.373	0.002	0.002	0.306	0.002	1.761	0.002	0.002	0.002	0.002
NA	0.681	0.002	0.002	0.196	0.002	0.855	0.002	0.002	0.002	0.002
NA	0.306	0.002	0.002	0.396	0.002	0.002	0.002	0.002	0.002	0.002
NA	0.002	0.002	0.002	0.909	0.002	1.245	0.002	0.002	0.002	0.002
NA	0.002	0.549	1.154	1.496	1.108	1.535	1.060	0.002	0.002	0.002
NA	0.002	0.549	1.331	0.741	1.496	1.725	0.549	0.002	0.002	0.002
NA	0.002	1.060	0.799	0.799	1.496	1.154	0.476	1.415	0.617	0.549
NA	0.002	0.909	0.681	0.002	1.688	0.617	0.306	0.741	0.909	0.306
NA	0.002	0.617	0.741	0.002	0.476	1.245	1.060	0.306	0.681	0.002
NA	0.002	0.961	0.617	0.549	1.245	0.617	0.681	1.154	1.761	0.799
NA	0.002	0.306	0.476	0.002	1.535	0.549	0.396	1.373	1.415	0.741
NA	0.855	0.476	1.833	1.200	1.011	0.476	0.002	0.799	1.373	0.549
NA	0.002	0.306	1.903	1.245	1.535	0.306	0.909	0.002	0.196	1.154
NA	0.002	0.476	2.039	0.799	1.415	0.681	0.396	0.196	0.549	0.196
NA	0.002	0.549	1.288	0.855	1.373	0.002	1.245	0.476	0.396	0.306
NA	0.002	1.060	0.549	1.455	1.725	0.476	0.961	1.612	0.196	0.961
NA	0.002	0.681	1.725	0.681	0.799	0.002	0.741	1.612	0.002	1.725
NA	0.002	0.855	0.855	1.060	1.535	0.306	1.011	1.972	0.549	1.650
NA	0.002	0.549	1.868	0.741	0.961	0.002	0.617	0.855	0.396	1.011
NA	0.002	0.002	1.415	0.681	0.961	0.196	0.306	1.496	1.650	0.799
NA	NA	0.306	1.200	1.011	1.108	0.741	0.855	1.868	0.855	0.617
NA	NA	0.002	0.617	0.855	1.797	0.306	1.011	2.006	0.617	0.196
NA	NA	0.002	1.903	0.855	1.108	0.396	1.011	1.797	0.617	0.196
NA	NA	0.002	1.288	0.961	1.245	0.306	2.138	1.797	1.415	0.196
NA	NA	0.476	0.799	1.574	2.685	0.476	0.002	0.549	1.060	0.549
NA	NA	NA	1.011	0.909	1.761	0.002	0.002	0.681	0.476	0.196
NA	NA	NA	0.855	1.331	1.612	0.002	0.002	2.685	0.741	0.002
NA	NA	NA	0.617	1.455	3.454	0.002	0.799	2.138	1.108	0.002
NA	NA	NA	1.200	0.476	2.202	0.002	1.331	1.725	0.002	0.961
NA	NA	NA	1.797	0.396	1.108	0.741	1.011	0.306	0.396	0.002
NA	NA	NA	2.105	1.331	0.855	0.961	0.909	0.002	0.741	0.476
NA	NA	NA	2.006	0.002	0.681	1.455	0.396	0.909	1.288	0.855
NA	NA	NA	1.245	0.002	0.306	1.650	0.002	0.306	0.961	0.002
NA	NA	NA	0.961	1.455	1.011	2.627	0.002	1.154	0.476	1.108
NA	NA	NA	1.415	2.105	0.617	2.881	0.961	1.331	1.972	0.002
NA	NA	NA	1.200	0.961	0.741	0.617	0.306	0.961	1.200	0.002
NA	NA	NA	0.799	0.002	0.476	1.245	0.002	0.396	1.108	1.060
NA	NA	NA	0.617	0.002	0.476	1.725	0.002	0.681	1.535	1.108
NA	NA	NA	1.972	1.200	0.306	1.496	0.002	1.688	1.761	0.617
NA	NA	NA	0.799	0.549	0.617	1.496	0.002	2.936	1.725	0.961
NA	NA	NA	0.002	0.681	0.002	1.455	2.450	1.373	1.612	1.154
NA	NA	NA	0.476	0.196	0.002	1.688	1.154	1.245	1.797	0.961
NA	NA	NA	0.002	0.681	0.002	0.306	0.681	2.963	1.200	0.002
NA	NA	NA	0.002	0.306	0.002	0.002	0.002	1.154	1.331	0.002
NA	NA	NA	0.306	1.761	0.396	0.681	1.972	0.617	0.961	0.799
NA	NA	NA	0.961	0.799	0.306	0.196	2.540	0.306	1.011	1.903
NA	NA	NA	0.549	1.245	0.476	0.476	3.429	0.196	1.650	0.002
NA	NA	NA	0.617	0.396	0.549	0.002	2.742	0.002	1.938	0.476
NA	NA	NA	0.909	1.373	0.396	0.681	2.881	0.549	0.617	0.476
NA	NA	NA	1.496	0.549	0.681	0.396	1.761	1.415	0.476	0.476
NA	NA	NA	0.909	1.688	1.288	0.306	1.154	2.072	0.002	0.396
NA	NA	NA	0.681	2.039	1.011	0.396	1.245	0.681	0.549	1.060
NA	NA	NA	1.154	2.480	0.681	0.002	1.060	1.797	0.002	1.011
NA	NA	NA	0.002	1.288	0.549	0.002	0.002	1.415	0.002	1.245
NA	NA	NA	0.002	0.909	0.196	0.002	1.535	1.938	1.245	0.855
NA	NA	NA	0.002	1.373	1.060	0.002	0.549	2.006	0.002	0.617
NA	NA	NA	0.002	1.245	1.245	0.002	4.225	0.196	1.108	0.799
NA	NA	NA	0.196	0.002	0.396	0.002	0.002	0.002	2.510	0.396
NA	NA	NA	0.002	0.306	0.681	0.002	0.002	0.549	0.306	0.306
NA	NA	NA	0.002	0.002	0.396	0.002	0.002	0.196	2.627	0.306
NA	NA	NA	0.617	0.002	0.476	0.002	0.002	0.196	2.006	0.476
NA	NA	NA	0.002	0.396	0.617	0.002	0.002	0.396	1.612	0.196
NA	NA	NA	0.002	0.306	0.196	0.002	0.002	0.396	1.154	0.396
NA	NA	NA	0.002	0.002	0.549	0.002	0.002	0.476	1.200	0.741
NA	NA	NA	2.266	0.002	0.196	0.002	0.002	0.681	1.200	1.245
NA	NA	NA	0.476	0.002	0.002	0.002	0.002	1.455	1.245	0.002
NA	NA	NA	0.549	0.196	0.306	0.002	0.306	0.617	1.060	0.002
NA	NA	NA	1.011	0.196	0.681	1.200	0.681	0.617	0.002	0.002
NA	NA	NA	0.002	0.002	0.002	0.196	0.961	0.961	0.002	0.002
NA	NA	NA	0.306	0.396	1.060	1.011	1.833	0.909	0.196	0.002
NA	NA	NA	0.002	1.455	1.245	1.415	0.002	0.396	0.476	0.002
NA	NA	NA	0.002	0.306	0.617	1.938	1.535	0.617	0.681	0.002
NA	NA	NA	0.196	1.725	0.855	1.011	1.725	1.011	0.617	0.002
NA	NA	NA	1.245	1.331	1.688	1.496	1.108	0.855	0.306	0.002
NA	NA	NA	0.799	1.288	2.072	1.797	1.288	0.476	0.549	0.002

NA	NA	NA	1.331	1.331	1.797	1.938	0.961	0.396	1.200	0.002
NA	NA	NA	0.961	0.799	2.006	1.496	0.002	0.396	1.011	0.002
NA	NA	NA	1.011	1.011	0.617	0.196	0.002	0.196	1.108	0.002
NA	NA	NA	1.725	0.002	2.039	1.200	0.196	1.060	1.415	1.650
NA	NA	NA	0.396	0.002	1.797	1.761	0.002	0.617	0.855	1.373
NA	NA	NA	1.612	0.002	2.234	1.574	0.196	0.306	2.390	1.574
NA	NA	NA	1.415	0.002	2.006	0.196	0.306	0.196	1.688	0.617
NA	NA	NA	1.154	0.002	1.245	0.002	1.245	0.196	3.096	1.903
NA	NA	NA	1.060	0.002	1.373	0.002	2.569	0.002	0.476	1.688
NA	NA	NA	0.396	0.002	0.961	0.002	1.688	0.002	0.002	0.681
NA	NA	NA	0.681	0.002	1.535	1.245	1.797	0.002	0.306	0.549
NA	NA	NA	1.200	0.196	0.855	1.612	3.577	0.002	0.549	1.725
NA	NA	NA	1.011	0.196	0.909	2.006	1.725	0.476	0.396	2.006
NA	NA	NA	0.909	0.196	0.002	0.196	0.002	0.396	0.549	1.373
NA	NA	NA	1.496	0.002	0.396	0.002	0.306	1.535	0.617	0.961
NA	NA	NA	1.373	0.002	1.245	0.002	0.306	1.688	2.598	1.200
NA	NA	NA	0.961	0.002	1.612	0.002	1.496	1.868	0.476	1.373
NA	NA	NA	0.549	0.002	0.002	0.002	0.002	1.245	0.799	1.612
NA	NA	NA	0.799	0.002	0.002	0.002	0.002	1.868	0.002	1.725
NA	NA	NA	1.108	0.476	0.002	0.002	1.574	2.826	0.002	1.797
NA	NA	NA	0.799	0.681	0.002	0.002	2.039	2.450	0.002	2.006
NA	NA	NA	0.306	1.415	0.396	0.002	1.288	1.972	0.476	0.002
NA	NA	NA	0.617	0.549	1.011	0.909	0.196	1.688	0.549	0.476
NA	NA	NA	1.154	0.681	0.306	1.011	0.741	2.170	0.196	0.002
NA	NA	NA	NA	1.011	0.002	1.245	2.202	1.496	0.002	0.002
NA	NA	NA	NA	1.415	0.002	1.108	2.105	1.903	0.002	0.002
NA	NA	NA	NA	1.373	0.002	1.415	1.833	3.862	0.002	0.306
NA	NA	NA	NA	0.799	0.002	1.288	1.833	2.540	0.002	0.002
NA	NA	NA	NA	0.961	0.741	0.002	1.496	3.278	0.476	0.196
NA	NA	NA	NA	0.855	0.002	0.909	0.476	3.885	0.396	0.002
NA	NA	NA	NA	0.681	0.617	0.855	0.002	3.070	0.002	0.002
NA	NA	NA	NA	0.549	0.617	0.002	0.002	2.450	0.306	0.002
NA	NA	NA	NA	0.681	0.476	1.331	2.138	2.881	0.681	0.002
NA	NA	NA	NA	0.306	0.002	0.741	2.039	2.234	0.002	0.741
NA	NA	NA	NA	0.002	0.002	1.938	2.598	2.170	0.002	0.741
NA	NA	NA	NA	0.306	0.002	1.200	0.681	0.002	0.002	0.909
NA	NA	NA	NA	0.306	0.002	1.011	0.002	0.002	0.002	1.245
NA	NA	NA	NA	0.396	0.855	1.535	0.476	1.455	0.002	0.681
NA	NA	NA	NA	1.288	0.855	1.938	1.455	0.855	0.196	0.549
NA	NA	NA	NA	0.306	0.741	1.535	0.002	0.002	0.617	0.549
NA	NA	NA	NA	0.002	1.288	1.938	0.396	2.039	0.306	0.741
NA	NA	NA	NA	0.196	0.617	2.881	0.306	0.681	1.496	0.961
NA	NA	NA	NA	0.396	0.741	2.266	0.306	0.549	0.681	0.306
NA	NA	NA	NA	0.002	0.855	1.373	0.396	1.496	1.200	0.002
NA	NA	NA	NA	0.002	0.617	0.549	0.396	0.196	0.855	0.002
NA	NA	NA	NA	0.002	0.855	0.002	1.574	0.476	0.741	0.002
NA	NA	NA	NA	0.476	1.797	1.612	1.154	1.938	2.105	0.306
NA	NA	NA	NA	0.476	0.741	0.549	1.288	1.650	1.903	1.011
NA	NA	NA	NA	0.799	0.741	1.154	1.060	2.770	2.006	0.396
NA	NA	NA	NA	0.476	1.496	0.002	1.060	1.612	1.725	NA
NA	NA	NA	NA	0.549	1.060	0.741	0.741	1.868	2.138	NA
NA	NA	NA	NA	0.549	0.617	0.549	0.741	1.108	3.815	NA
NA	NA	NA	NA	0.617	0.476	0.002	1.200	1.154	1.688	NA
NA	NA	NA	NA	0.681	1.108	1.331	0.961	0.002	2.297	NA
NA	NA	NA	NA	1.011	0.617	1.331	0.476	0.681	1.688	NA
NA	NA	NA	NA	NA	0.681	1.373	0.476	0.306	1.108	NA
NA	NA	NA	NA	NA	0.741	1.245	0.002	0.396	1.288	NA
NA	NA	NA	NA	NA	0.306	0.681	0.196	0.396	1.108	NA
NA	NA	NA	NA	NA	0.476	0.002	0.002	0.196	0.396	NA
NA	NA	NA	NA	NA	0.476	1.688	0.196	0.002	0.196	NA
NA	NA	NA	NA	NA	0.306	0.002	0.396	0.196	0.196	NA
NA	NA	NA	NA	NA	0.476	1.761	0.306	0.476	0.002	NA
NA	NA	NA	NA	NA	0.002	0.002	NA	0.002	1.797	NA
NA	NA	NA	NA	NA	0.306	1.108	NA	0.002	1.331	NA
NA	NA	NA	NA	NA	0.196	0.909	NA	0.002	2.656	NA
NA	NA	NA	NA	NA	0.196	0.196	NA	0.306	0.002	NA
NA	NA	NA	NA	NA	NA	1.011	NA	0.396	2.936	NA
NA	NA	NA	NA	NA	NA	NA	NA	0.476	1.535	NA
NA	NA	NA	NA	NA	NA	NA	NA	0.002	0.799	NA
NA	NA	NA	NA	NA	NA	NA	NA	0.002	1.761	NA
NA	NA	NA	NA	NA	NA	NA	NA	0.196	1.060	NA
NA	NA	NA	NA	NA	NA	NA	NA	0.002	1.200	NA
NA	NA	NA	NA	NA	NA	NA	NA	0.306	1.574	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	0.799	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	0.306	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	0.549	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	0.799	NA

NA	NA	NA	NA	NA	NA	NA	NA	NA	1.011	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	1.833	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	0.306	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	2.881	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	0.961	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	2.234	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	0.961	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	0.855	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	0.396	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	1.725	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	0.396	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	0.002	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	0.002	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	0.306	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	0.002	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	1.797	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	1.903	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	1.797	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	1.060	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	2.138	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	2.170	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	2.006	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	0.681	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	1.011	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	2.039	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	0.549	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	1.455	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	0.002	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	0.549	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	0.002	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	0.741	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	0.549	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	0.855	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	0.002	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	0.476	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	0.909	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	0.002	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	0.681	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	0.306	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	0.617	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	0.549	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	0.476	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	0.799	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	0.681	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	0.961	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	0.002	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	1.060	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	0.396	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	1.245	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	0.476	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	0.196	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	0.002	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	0.196	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	0.549	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	0.681	NA

l.mou=structure(.Data=c(
NA,1,4,2,1,10,75,1,2,1,1,
... (see table below for full data set)
),.Dim=c(216,11)),

1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008
NA	1	4	2	1	10	75	1	2	1	1
NA	1	1	11	30	1	35	1	1	1	4
NA	2	1	1	33	1	42	51	1	10	1
NA	12	1	1	1	1	11	26	26	1	5
NA	16	1	18	1	1	14	53	32	49	15
NA	13	5	28	1	26	12	1	63	13	14
NA	18	1	1	3	3	1	1	1	48	1
NA	21	1	1	2	1	31	1	1	1	1
NA	7	1	1	1	1	10	1	1	1	1
NA	2	1	1	3	1	1	1	1	1	1
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NA	1	5	16	24	15	25	14	1	1	1
NA	1	5	20	8	24	30	5	1	1	1
NA	1	14	9	9	24	16	4	22	6	5

NA	1	11	7	1	29	6	2	8	11	2
NA	1	6	8	1	4	18	14	2	7	1
NA	1	12	6	5	18	6	7	16	31	9
NA	1	2	4	1	25	5	3	21	22	8
NA	10	4	33	17	13	4	1	9	21	5
NA	1	2	35	18	25	2	11	1	1	16
NA	1	4	39	9	22	7	3	1	5	1
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NA	1	14	5	23	30	4	12	27	1	12
NA	1	7	30	7	9	1	8	27	1	30
NA	1	10	10	14	25	2	13	37	5	28
NA	1	5	34	8	12	1	6	10	3	13
NA	1	1	22	7	12	1	2	24	28	9
NA	NA	2	17	13	15	8	10	34	10	6
NA	NA	1	6	10	32	2	13	38	6	1
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NA	NA	1	19	12	18	2	42	32	22	1
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NA	NA	NA	11	1	1	1	1	3	5	21
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NA	NA	NA	NA	5	6	1	1	52	2	1
NA	NA	NA	NA	7	4	20	42	67	7	1
NA	NA	NA	NA	2	1	8	39	45	1	8
NA	NA	NA	NA	1	1	36	57	43	1	8
NA	NA	NA	NA	2	1	17	7	1	1	11
NA	NA	NA	NA	2	1	13	1	1	1	18
NA	NA	NA	NA	3	10	25	4	23	1	7
NA	NA	NA	NA	19	10	36	23	10	1	5
NA	NA	NA	NA	2	8	25	1	1	6	5
NA	NA	NA	NA	1	19	36	3	39	2	8
NA	NA	NA	NA	1	6	67	2	7	24	12
NA	NA	NA	NA	3	8	46	2	5	7	2
NA	NA	NA	NA	1	10	21	3	24	17	1
NA	NA	NA	NA	1	6	5	3	1	10	1
NA	NA	NA	NA	1	10	1	26	4	8	1
NA	NA	NA	NA	4	32	27	16	36	41	2
NA	NA	NA	NA	4	8	5	19	28	35	13
NA	NA	NA	NA	9	8	16	14	63	38	3
NA	NA	NA	NA	4	24	1	14	27	30	NA
NA	NA	NA	NA	5	14	8	8	34	42	NA
NA	NA	NA	NA	5	6	5	8	15	104	NA
NA	NA	NA	NA	6	4	1	17	16	29	NA
NA	NA	NA	NA	7	15	20	12	1	47	NA
NA	NA	NA	NA	13	6	20	4	7	29	NA
NA	NA	NA	NA	NA	7	21	4	2	15	NA
NA	NA	NA	NA	NA	8	18	1	3	19	NA
NA	NA	NA	NA	NA	2	7	1	3	15	NA
NA	NA	NA	NA	NA	4	1	1	1	3	NA
NA	NA	NA	NA	NA	4	29	1	1	1	NA
NA	NA	NA	NA	NA	2	1	3	1	1	NA
NA	NA	NA	NA	NA	4	31	2	4	1	NA
NA	NA	NA	NA	NA	1	1	NA	1	32	NA
NA	NA	NA	NA	NA	2	15	NA	1	20	NA
NA	NA	NA	NA	NA	1	11	NA	1	59	NA
NA	NA	NA	NA	NA	1	1	NA	2	1	NA
NA	NA	NA	NA	NA	NA	13	NA	3	69	NA
NA	NA	NA	NA	NA	NA	NA	NA	4	25	NA
NA	NA	NA	NA	NA	NA	NA	NA	1	9	NA
NA	NA	NA	NA	NA	NA	NA	NA	1	31	NA
NA	NA	NA	NA	NA	NA	NA	NA	1	14	NA
NA	NA	NA	NA	NA	NA	NA	NA	1	17	NA
NA	NA	NA	NA	NA	NA	NA	NA	2	26	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	9	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	2	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	5	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	2	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	5	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	9	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	13	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	33	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	2	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	67	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	12	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	45	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	12	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	10	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	3	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	30	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	3	NA

NA	NA	NA	NA	NA	NA	NA	NA	NA	1	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	1	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	2	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	1	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	32	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	35	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	32	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	14	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	42	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	43	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	38	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	7	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	13	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	39	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	5	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	23	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	1	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	5	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	1	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	8	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	5	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	10	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	1	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	4	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	11	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	1	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	7	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	2	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	6	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	5	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	4	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	9	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	7	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	12	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	1	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	14	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	3	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	18	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	4	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	1	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	1	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	1	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	5	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	7	NA

# inits for roe sites densities, column: years

```
d.roe=structure(.Data=c(
0.681,0.799,0.002,4.399,0.961,1.455,4.655,4.923,3.885,5.377,2.480,
... (see table below for full data set)
),.Dim=c(59,11)),
```

1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008
0.681	0.799	0.002	4.399	0.961	1.455	4.655	4.923	3.885	5.377	2.480
0.909	1.612	0.909	0.909	1.761	2.826	1.415	1.288	1.415	1.612	3.792
1.245	1.415	2.006	0.196	2.656	3.354	1.496	1.011	1.725	3.479	1.415
1.200	0.617	1.868	3.977	3.429	2.510	2.420	3.528	5.681	2.390	1.868
0.909	0.476	2.359	0.741	0.855	1.373	0.855	0.396	6.577	2.569	2.390
1.200	0.549	2.138	1.725	1.060	2.450	3.227	7.521	1.972	3.017	2.569
1.108	0.476	2.770	2.936	0.306	1.200	2.297	1.060	1.612	3.454	2.420
1.011	1.373	2.105	1.938	1.060	0.799	1.797	1.725	2.234	2.540	2.170
0.741	0.476	1.688	1.154	1.574	2.510	3.649	1.373	2.656	3.528	1.903
0.909	0.549	0.002	1.373	1.060	1.154	2.540	1.373	2.598	2.450	1.868
1.200	1.455	0.617	2.170	0.741	1.688	1.903	1.797	2.006	2.569	1.688
0.909	1.154	1.108	0.549	1.761	0.002	5.143	3.625	1.938	2.908	1.245
0.961	1.060	1.245	1.612	1.415	3.885	2.480	1.612	1.331	1.288	1.868
1.200	0.961	5.511	2.039	1.455	2.908	3.175	2.881	0.396	0.617	1.833
1.108	1.200	3.252	1.938	1.688	2.742	3.278	5.300	0.002	0.002	1.574
0.306	1.011	1.154	0.617	1.200	1.108	4.696	1.455	0.306	1.535	1.011
1.373	1.535	1.496	3.673	1.455	0.002	2.359	1.574	1.415	2.627	0.196
0.681	0.002	0.855	3.303	0.002	0.855	2.540	2.598	3.577	1.612	0.002
0.306	0.681	0.909	1.612	0.741	1.797	0.002	4.717	1.761	0.002	1.245
0.476	1.415	1.612	3.625	0.002	0.476	0.002	3.227	0.617	1.200	2.713
0.681	1.688	1.288	2.450	0.002	0.396	4.068	3.649	0.002	0.002	1.154
0.741	0.306	0.617	1.535	0.002	0.617	1.574	2.770	0.617	0.002	0.617
1.245	0.617	0.196	0.909	0.002	0.396	0.002	0.476	0.002	1.938	0.002
1.154	2.854	1.288	0.002	1.761	0.476	0.476	0.002	0.741	1.373	0.002
0.306	2.170	0.196	0.476	0.476	0.799	0.002	1.535	1.868	0.002	0.002

0.396	3.503	0.617	2.770	1.200	0.741	0.002	0.306	1.833	0.002	0.002
0.681	2.420	0.306	3.070	0.476	2.072	0.002	0.002	0.002	0.396	0.002
NA	2.202	0.196	1.331	0.002	0.002	2.328	0.002	0.396	0.002	0.002
NA	3.931	0.549	1.373	0.549	0.799	2.540	3.303	0.002	0.002	1.903
NA	2.598	0.196	2.420	0.741	1.415	1.200	1.797	0.002	0.002	1.060
NA	2.170	0.196	0.961	NA	0.617	1.245	1.288	0.002	0.002	1.612
NA	1.797	NA	0.476	NA	1.060	0.549	0.002	0.002	0.002	1.200
NA	1.331	NA	0.002	NA	4.158	0.741	1.535	3.552	2.390	0.196
NA	1.833	NA	0.002	NA	0.617	0.002	0.002	3.931	0.799	0.306
NA	1.688	NA	0.002	NA	3.123	0.476	0.002	0.549	2.656	0.002
NA	0.617	NA	0.002	NA	1.972	0.196	0.002	2.359	1.833	0.002
NA	2.202	NA	0.002	NA	NA	0.002	0.002	0.002	0.741	0.002
NA	1.972	NA	NA	NA	NA	0.002	0.002	0.196	0.002	2.990
NA	2.202	NA	NA	NA	NA	0.002	2.072	0.002	0.476	0.476
NA	3.070	NA	NA	NA	NA	0.961	2.039	0.002	0.002	1.688
NA	1.688	NA	NA	NA	NA	0.799	0.196	1.688	0.002	2.039
NA	2.328	NA	NA	NA	NA	0.002	0.002	0.196	0.002	2.138
NA	4.046	NA	NA	NA	NA	NA	0.002	3.931	2.039	0.002
NA	0.909	NA	NA	NA	NA	NA	NA	2.359	0.681	1.612
NA	1.415	NA	NA	NA	NA	NA	NA	0.196	0.002	2.234
NA	1.574	NA	NA	NA	NA	NA	NA	2.072	5.280	2.770
NA	0.741	NA	NA	NA	NA	NA	NA	3.954	1.612	2.105
NA	1.373	NA	NA	NA	NA	NA	NA	2.072	0.306	1.650
NA	1.797	NA	NA	NA	NA	NA	NA	5.043	2.450	1.011
NA	0.961	NA	NA	NA	NA	NA	NA	4.634	3.954	2.006
NA	5.681	NA	NA	NA	NA	NA	NA	1.200	3.404	4.158
NA	0.909	NA	NA	NA	NA	NA	NA	0.617	3.278	1.612
NA	1.833	NA	NA	NA	NA	NA	NA	2.105	1.108	0.002
NA	NA	NA	NA	NA	NA	NA	NA	1.331	3.149	2.881
NA	NA	NA	NA	NA	NA	NA	NA	1.011	2.006	NA
NA	NA	NA	NA	NA	NA	NA	NA	4.136	2.569	NA
NA	NA	NA	NA	NA	NA	NA	NA	0.002	3.768	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	0.002	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	2.006	NA

```
l.roe=structure(.Data=c(
7,9,1,130,12,23,142,155,107,178,53,
... (see table below for full data set)
),.Dim=c(59,11)),
```

1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008
7	9	1	130	12	23	142	155	107	178	53
11	27	11	11	31	65	22	19	22	27	103
18	22	38	1	59	85	24	13	30	90	22
17	6	34	111	88	54	51	92	194	50	34
11	4	49	8	10	21	10	3	244	56	50
17	5	42	30	14	52	80	301	37	72	56
15	4	63	69	2	17	47	14	27	89	51
13	21	41	36	14	9	32	30	45	55	43
8	4	29	16	26	54	97	21	59	92	35
11	5	1	21	14	16	55	21	57	52	34
17	23	6	43	8	29	35	32	38	56	29
11	16	15	5	31	1	166	96	36	68	18
12	14	18	27	22	107	53	27	20	19	34
17	12	185	39	23	68	78	67	3	6	33
15	17	81	36	29	62	82	174	1	1	26
2	13	16	6	17	15	144	23	2	25	13
21	25	24	98	23	1	49	26	22	58	1
7	1	10	83	1	10	55	57	94	27	1
2	7	11	27	8	32	1	145	31	1	18
4	22	27	96	1	4	1	80	6	17	61
7	29	19	52	1	3	115	97	1	1	16
8	2	6	25	1	6	26	63	6	1	6
18	6	1	11	1	3	1	4	1	36	1
16	66	19	1	31	4	4	1	8	21	1
2	43	1	4	4	9	1	25	34	1	1
3	91	6	63	17	8	1	2	33	1	1
7	51	2	74	4	40	1	1	1	3	1
NA	44	1	20	1	1	48	1	3	1	1
NA	109	5	21	5	9	55	83	1	1	35
NA	57	1	51	8	22	17	32	1	1	14
NA	43	1	12	NA	6	18	19	1	1	27
NA	32	NA	4	NA	14	5	1	1	1	17
NA	20	NA	1	NA	119	8	25	93	50	1
NA	33	NA	1	NA	6	1	1	109	9	2
NA	29	NA	1	NA	76	4	1	5	59	1
NA	6	NA	1	NA	37	1	1	49	33	1



NA	44	NA	1	NA	NA	1	1	1	8	1
NA	37	NA	NA	NA	NA	1	1	1	1	71
NA	44	NA	NA	NA	NA	1	40	1	4	4
NA	74	NA	NA	NA	NA	12	39	1	1	29
NA	29	NA	NA	NA	NA	9	1	29	1	39
NA	48	NA	NA	NA	NA	1	1	1	1	42
NA	114	NA	NA	NA	NA	NA	1	109	39	1
NA	11	NA	NA	NA	NA	NA	NA	49	7	27
NA	22	NA	NA	NA	NA	NA	NA	1	1	45
NA	26	NA	NA	NA	NA	NA	NA	40	173	63
NA	8	NA	NA	NA	NA	NA	NA	110	27	41
NA	21	NA	NA	NA	NA	NA	NA	40	2	28
NA	32	NA	NA	NA	NA	NA	NA	161	52	13
NA	12	NA	NA	NA	NA	NA	NA	141	110	38
NA	194	NA	NA	NA	NA	NA	NA	17	87	119
NA	11	NA	NA	NA	NA	NA	NA	6	82	27
NA	33	NA	NA	NA	NA	NA	NA	41	15	1
NA	NA	NA	NA	NA	NA	NA	NA	20	77	67
NA	NA	NA	NA	NA	NA	NA	NA	13	38	NA
NA	NA	NA	NA	NA	NA	NA	NA	118	56	NA
NA	NA	NA	NA	NA	NA	NA	NA	1	102	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	1	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	38	NA

# inits for foyle sites densities, column: years

```
d.foy=structure(.Data=c(
0.476,0.002,0.681,2.936,0.002,0.909,0.002,0.002,5.202,3.601,1.574,
... (see table below for full data set)
),.Dim=c(38,11)),
```

1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008
0.476	0.002	0.681	2.936	0.002	0.909	0.002	0.002	5.202	3.601	1.574
0.396	0.002	0.002	2.266	1.496	0.799	0.002	0.617	3.577	3.931	1.688
0.306	0.002	1.331	5.103	1.496	2.328	0.002	4.225	3.721	4.291	2.540
1.245	1.108	0.741	3.070	1.833	0.196	0.002	3.070	2.569	3.577	2.936
0.617	0.681	1.725	1.373	2.072	3.379	0.855	4.696	0.855	2.234	2.420
0.002	0.549	1.288	2.510	0.476	3.429	3.552	3.070	0.306	2.072	0.961
1.108	0.617	1.496	0.396	1.612	0.002	4.528	3.673	0.002	1.154	0.799
1.200	0.681	0.306	0.002	2.359	2.798	2.359	3.528	0.196	1.415	1.331
0.396	0.681	1.288	0.002	0.002	2.936	3.768	2.006	5.163	1.574	1.373
0.396	0.002	0.681	0.002	0.002	2.510	3.792	1.761	2.039	3.744	1.108
0.002	0.002	0.855	0.306	0.002	0.196	2.798	1.574	1.833	2.328	1.574
0.396	0.002	0.002	0.002	0.002	0.306	2.569	0.909	1.200	2.390	0.002
NA	0.002	0.196	0.396	0.002	0.002	1.797	0.396	0.002	1.761	0.002
NA	NA	0.002	0.002	1.245	0.002	0.799	0.002	0.002	0.002	1.868
NA	NA	0.002	0.741	0.476	0.681	2.328	0.002	0.396	0.002	1.535
NA	NA	0.002	0.002	0.476	0.196	0.741	1.154	2.359	2.006	1.903
NA	NA	0.476	0.549	0.476	1.496	3.252	0.002	3.954	3.278	2.234
NA	NA	0.396	0.196	0.476	1.245	2.039	0.002	2.742	3.404	1.650
NA	NA	NA	0.476	0.741	0.196	0.002	0.002	1.496	2.480	0.002
NA	NA	NA	0.396	1.373	0.002	0.002	0.002	0.396	0.002	0.002
NA	NA	NA	0.002	0.002	0.002	0.002	0.002	0.306	0.002	0.306
NA	NA	NA	0.002	0.002	0.002	2.569	0.002	0.002	0.002	0.617
NA	NA	NA	0.002	0.002	0.002	0.002	0.002	0.002	1.331	0.002
NA	NA	NA	0.002	NA	0.002	0.002	0.002	1.154	0.002	0.002
NA	NA	NA	0.002	NA	0.002	1.200	0.002	0.617	0.306	0.196
NA	NA	NA	0.002	NA	NA	0.396	0.476	1.725	0.196	1.108
NA	NA	NA	0.002	NA	NA	0.002	3.625	0.002	0.002	0.002
NA	NA	NA	NA	NA	NA	0.002	0.002	0.002	0.617	0.476
NA	NA	NA	NA	NA	NA	0.002	0.002	0.002	0.002	0.196
NA	NA	NA	NA	NA	NA	NA	NA	0.002	0.396	0.002
NA	NA	NA	NA	NA	NA	NA	NA	0.002	0.855	0.002
NA	NA	NA	NA	NA	NA	NA	NA	0.002	0.002	0.002
NA	NA	NA	NA	NA	NA	NA	NA	0.002	0.476	0.306
NA	NA	NA	NA	NA	NA	NA	NA	0.002	0.002	0.617
NA	NA	NA	NA	NA	NA	NA	NA	0.002	NA	0.002
NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.002
NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.002
NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.002

```
l.foy=structure(.Data=c(
4,1,7,69,1,11,1,1,169,95,26,
... (see table below for full data set)
),.Dim=c(38,11)),
```

1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008
4	1	7	69	1	11	1	1	169	95	26
3	1	1	46	24	9	1	6	94	109	29
2	1	20	164	24	48	1	122	100	125	55
18	15	8	74	33	1	1	74	56	94	69
6	7	30	21	40	86	10	144	10	45	51
1	5	19	54	4	88	93	74	2	40	12
15	6	24	3	27	1	136	98	1	16	9
17	7	2	1	49	64	49	92	1	22	20
3	7	19	1	1	69	102	38	167	26	21
3	1	7	1	1	54	103	31	39	101	15
1	1	10	2	1	1	64	26	33	48	26
3	1	1	1	1	2	56	11	17	50	1
NA	1	1	3	1	1	32	3	1	31	1
NA	NA	1	1	18	1	9	1	1	1	34
NA	NA	1	8	4	7	48	1	3	1	25
NA	NA	1	1	4	1	8	16	49	38	35
NA	NA	4	5	4	24	81	1	110	82	45
NA	NA	3	1	4	18	39	1	62	87	28
NA	NA	NA	4	8	1	1	1	24	53	1
NA	NA	NA	3	21	1	1	1	3	1	1
NA	NA	NA	1	1	1	1	1	2	1	2
NA	NA	NA	1	1	1	56	1	1	1	6
NA	NA	NA	1	1	1	1	1	1	20	1
NA	NA	NA	1	NA	1	1	1	16	1	1
NA	NA	NA	1	NA	1	17	1	6	2	1
NA	NA	NA	1	NA	NA	3	4	30	1	15
NA	NA	NA	1	NA	NA	1	96	1	1	1
NA	NA	NA	NA	NA	NA	1	1	1	6	4
NA	NA	NA	NA	NA	NA	1	1	1	1	1
NA	NA	NA	NA	NA	NA	NA	NA	1	3	1
NA	NA	NA	NA	NA	NA	NA	NA	1	10	1
NA	NA	NA	NA	NA	NA	NA	NA	1	1	1
NA	NA	NA	NA	NA	NA	NA	NA	1	4	2
NA	NA	NA	NA	NA	NA	NA	NA	1	1	6
NA	NA	NA	NA	NA	NA	NA	NA	1	NA	1
NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	1
NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	1
NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	1

)

## Annex 2: WinBUGS code: Model relating redd counts to spawners abundance.

### #Model

#The first part of the model relates redd counts to spawner abundance, the second part of the model provides spawners abundances estimates based on the parameters estimated in the first place and redd counts.

```
model{

tau.p ~dgamma(0.001,0.001)
var.p <- 1 / tau.p

mu.p~dbeta(1,1)|(0.001,)
L.mu.p <- logit(mu.p)

mu.kappa.fau ~ dgamma(1,0.001)
alpha.fau <- mu.kappa.fau * beta.fau
beta.fau <- mu.kappa.fau * tau.kappa

mu.kappa.fin ~ dgamma(1,0.001)
alpha.fin <- mu.kappa.fin * beta.fin
beta.fin <- mu.kappa.fin * tau.kappa

mu.kappa.roe ~ dgamma(1,0.001)
alpha.roe <- mu.kappa.roe * beta.roe
beta.roe <- mu.kappa.roe * tau.kappa

tau.kappa ~ dgamma(0.001,0.001)|(0.001,)
var.kappa <- 1/tau.kappa

for (i in 1:3){
  mu.spawners[i]~dunif(0,500000)
  L.mu.spawners[i]<-log(mu.spawners[i])
  tau.spawners[i]~dgamma(0.001,0.001)
}

for (t in 1:T){
#Faughan unit
  L.p[t,1] ~ dnorm(L.mu.p, tau.p)
  logit(p[t,1]) <- L.p[t,1]

  WA.walked[t,1] <- p[t,1] * WA.total[1]

  Adults[t,1] ~ dlnorm(L.mu.spawners[1],tau.spawners[1])
  Spawners[t,1] <- Adults[t,1] - C.rod.amont.obs[t,1]

  kappa[t,1] ~ dgamma(alpha.fau, beta.fau)|(0.001,)
  lambda.redds[t,1] <- (Adults[t,1] - C.rod.amont.obs[t,1]) * p[t,1] * kappa[t,1]

  Redds[t,1] ~dpois(lambda.redds[t,1])
}
```

**# Finn unit**

```

L.p[t,2] ~ dnorm(L.mu.p, tau.p)
logit(p[t,2]) <- L.p[t,2]

WA.walked[t,2] <- p[t,2] * WA.total[2]

Adults[t,2] ~ dlnorm(L.mu.spawners[2],tau.spawners[2])
Spawners[t,2] <- Adults[t,2] - C.rod.amont.obs[t,2]

kappa[t,2] ~ dgamma(alpha.fin, beta.fin)(0.001,)
lambda.redds[t,2] <- (Adults[t,2] - C.rod.amont.obs[t,2]) * p[t,2] * kappa[t,2]

Redds[t,2] ~dpois(lambda.redds[t,2])

```

**#Roe unit**

```

L.p[t,3] ~ dnorm(L.mu.p, tau.p)
logit(p[t,3]) <- L.p[t,3]

WA.walked[t,3] <- p[t,3] * WA.total[3]

Adults[t,3] ~dlnorm(L.mu.spawners[3],tau.spawners[3])
Spawners[t,3] <- Adults[t,3] - C.rod.amont.obs[t,3]

kappa[t,3] ~ dgamma(alpha.roe, beta.roe)(0.001,)
lambda.redds[t,3] <- (Adults[t,3] - C.rod.amont.obs[t,3]) * p[t,3] * kappa[t,3]

Redds[t,3] ~dpois(lambda.redds[t,3])

```

```

}

```

**# Estimating the number of spawners for each geo units between 1959 to 2000**

```

L.mu.p.cut<-cut(L.mu.p)
tau.p.cut<-cut(tau.p)

for (g in 1:3){
  tau.spawners.cut[g]<-tau.spawners[g]
}

for (y in 1:Y){
#Faughan unit
L.p.old[y,1] ~ dnorm(L.mu.p.cut, tau.p.cut)
logit(p.old[y,1]) <- L.p.old[y,1]

Spawners.old[y,1] ~ dlnorm(L.mu.spawners[1],tau.spawners.cut[1])

kappa.old[y,1] ~ dgamma(alpha.fau.cut, beta.fau.cut)(0.001,)
lambda.redds.old[y,1] <- Spawners.old[y,1] * p.old[y,1] * kappa.old[y,1]

Redds.old[y,1] ~dpois(lambda.redds.old[y,1])

#Finn unit
L.p.old[y,2] ~ dnorm(L.mu.p.cut, tau.p.cut)
logit(p.old[y,2]) <- L.p.old[y,2]

Spawners.old[y,2] ~ dlnorm(L.mu.spawners[2],tau.spawners.cut[2])

kappa.old[y,2] ~ dgamma(alpha.fin.cut, beta.fin.cut)(0.001,)
lambda.redds.old[y,2] <- Spawners.old[y,2] * p.old[y,2] * kappa.old[y,2]

Redds.old[y,2] ~dpois(lambda.redds.old[y,2])

#Roe unit
L.p.old[y,3] ~ dnorm(L.mu.p.cut, tau.p.cut)
logit(p.old[y,3]) <- L.p.old[y,3]

Spawners.old[y,3] ~ dlnorm(L.mu.spawners[3],tau.spawners.cut[3])

kappa.old[y,3] ~ dgamma(alpha.roe.cut, beta.roe.cut)(0.001,)
lambda.redds.old[y,3] <- Spawners.old[y,3] * p.old[y,3] * kappa.old[y,3]

Redds.old[y,3] ~dpois(lambda.redds.old[y,3])
}
}

```

**#data**

```
list(
T=6,
#The counters are assumed to give accurate number of returning adults
# rows=year; columns=geo units
Adults=structure(.Data=c(
1518,3311,3265,
...( see table below for full data set)
),.Dim=c(6,3)),
```

	<b>Faughan</b>	<b>Finn</b>	<b>Roe</b>
<b>2001</b>	1518	3311	3265
<b>2002</b>	4288	5768	5459
<b>2003</b>	3097	6461	4086
<b>2004</b>	2855	3771	1922
<b>2005</b>	4245	8571	2917
<b>2006</b>	3625	5748	5375

```
# Redds for each geo units (Faughan, Finn, Roe, 2001 to 2006)
# rows=year; columns=geo units
Redds= structure(.Data = c(
233,137,186,
... (see table below for full data set)
),.Dim=c(6,3)),
```

	<b>Faughan</b>	<b>Finn</b>	<b>Roe</b>
<b>2001</b>	233	137	186
<b>2002</b>	673	234	630
<b>2003</b>	441	101	672
<b>2004</b>	501	149	43
<b>2005</b>	766	343	844
<b>2006</b>	35	94	428

```
# logit of the proportion of wetted area sampled
# rows=years, columns=geo units
L.p=structure(.Data = c(
NA, -1.58,NA,
... (see table below for full data set)
),.Dim=c(6,3)),
```

	<b>Faughan</b>	<b>Finn</b>	<b>Roe</b>
<b>2001</b>	NA	-1.58	NA
<b>2002</b>	NA	-1.66	-0.7986
<b>2003</b>	-0.7131	-1.66	-0.7532
<b>2004</b>	-0.6991	NA	-2.4387
<b>2005</b>	-0.7016	-1.15	-0.7478
<b>2006</b>	-3.245	-2.75	-0.7272

```
# Total wetted area for each geo unit
WA.total=c(776412,1726922,1292616),
```

```
# Rod catches upstream of the counters
# rows=year; columns=geo units
C.rod.amont.obs=structure(.Data=c(
656,1162,267,
597,2263,408,
335,590,158,
464,627,357,
822,1118,309
501,752,444
),.Dim=c(6,3))
```

	<b>Faughan</b>	<b>Finn</b>	<b>Roe</b>
<b>2001</b>	656	1162	267
<b>2002</b>	597	2263	408
<b>2003</b>	335	590	158
<b>2004</b>	464	627	357
<b>2005</b>	822	1118	309
<b>2006</b>	501	752	444

```
Y=42,
```

```
# Redds for each geo units (Faughan, Finn, Roe, 1959 to 2000)
# rows=year; columns=geo units
Redds.old= structure(.Data = c(
757,456,1204,
... (see table below for full data set)
),.Dim=c(42,3))
)
```

	Faughan	Finn	Roe
1959	757	456	1204
1960	2169	391	1398
1961	853	242	822
1962	2114	896	1328
1963	2039	1041	2082
1964	1823	669	1777
1965	2558	1171	2533
1966	1292	1192	1264
1967	351	1437	526
1968	585	927	775
1969	452	453	823
1970	1164	621	638
1971	513	667	676
1972	156	536	475
1973	90	459	124
1974	362	523	547
1975	468	383	821
1976	630	340	891
1977	356	160	552
1978	427	489	882
1979	479	680	1486
1980	163	872	659
1981	615	1371	435
1982	449	579	650
1983	375	1108	354
1984	203	394	718
1985	411	807	768
1986	188	375	891
1987	329	518	729
1988	410	651	974
1989	1058	452	1426
1990	226	366	298
1991	537	767	706
1992	340	398	698
1993	218	652	648
1994	348	566	126
1995	82	826	241
1996	572	752	1247
1997	NA	552	NA
1998	84	357	169
1999	53	117	136
2000	87	159	383

## #Initialisation of the Gibbs sampler (1 chain)

```
list(
# initial values of the kappa parameter
# rows=year; columns=geo units
kappa = structure(.Data = c(
0.412,0.3872,0.3515,
... (see table below for full data set)
),.Dim = c(6,3)),
```

	Faughan	Finn	Roe
2001	0.412	0.3872	0.3515
2002	1.1	0.3897	0.4135
2003	0.5067	0.1126	0.5193
2004	0.6277	0.2784	0.3077
2005	0.6799	0.1885	0.9592
2006	0.3173	0.2612	0.2819

```
# initial values for the logit of the probability of wetted area sampled 2001 to 2006
# rows=year; columns=geo units
```

```
L.p = structure(.Data = c(
0.877,NA,-1.477,
... (see table below for full data set)
),.Dim = c(6,3)),
```

	Faughan	Finn	Roe
2001	0.877	NA	-1.477
2002	-1.609	NA	NA
2003	NA	NA	NA
2004	NA	-1.576	NA
2005	NA	NA	NA
2006	NA	NA	NA

# initial values for the logit of the probability of wetted area sampled 1959 to 2000  
# rows=year; columns=geo units

```
L.p.old = structure(.Data = c(
-0.7628,-1.029,0.08093,
... (see table below for full data set)
),.Dim = c(42,3)),
```

	Faughan	Finn	Roe
1959	-0.7628	-1.029	0.08093
1960	-0.5703	-0.2061	-0.3784
1961	-1.704	-2.053	-0.268
1962	-0.0627	-2.193	-1.525
1963	-0.364	-0.5275	0.4834
1964	-1.646	-0.6334	0.1491
1965	-0.4492	-1.324	-0.3842
1966	0.3182	-1.081	-1.133
1967	-1.456	-1.013	-1.343
1968	-0.5661	-1.016	-1.349
1969	0.6611	-0.4478	-1.62
1970	-0.2066	-1.651	-1.195
1971	-0.6686	-1.816	-0.1339
1972	-2.92	-1.581	-0.4596
1973	-1.934	-1.264	-2.046
1974	-2.482	0.4432	-1.151
1975	-0.2244	-0.3348	0.0731
1976	-0.8791	-0.4537	-1.358
1977	-1.535	-1.082	-0.6448
1978	-1.373	-1.335	-0.3141
1979	-2.336	-2.277	-0.3458
1980	-1.705	-1.494	-0.3146
1981	-0.4284	0.1983	-1.244
1982	-1.103	-0.9669	-1.511
1983	-1.968	-1.164	-2.213
1984	-1.057	-1.885	-1.71
1985	-1.497	-1.367	-1.599
1986	-2.143	-1.427	-1.289
1987	-2.144	-2.111	-1.101
1988	-1.248	-0.9411	-0.558
1989	-1.739	-0.8295	-0.8767
1990	-1.785	-2.018	-1.569
1991	-2.749	-0.8946	-1.276
1992	-2.652	-2.796	-1.338
1993	-1.947	-2.439	-0.2433
1994	-2.604	-0.8273	-1.947
1995	-2.531	-0.7578	-1.528
1996	-2.518	0.1791	-0.4002
1997	0.938	-1.236	-1.633
1998	-1.817	-0.7198	-1.426
1999	-3.393	-1.429	-1.81
2000	-2.178	-3.118	-1.115

# initial values for the redd counts 1959 to 2000  
# rows=year; columns=geo units

```
Redds.old = structure(.Data = c(
NA,NA,NA,
... (see table below for full data set)
),.Dim = c(42,3)),
```

	Faughan	Finn	Roe
1959	NA	NA	NA
1960	NA	NA	NA
1961	NA	NA	NA
1962	NA	NA	NA
1963	NA	NA	NA
1964	NA	NA	NA
1965	NA	NA	NA

1966	NA	NA	NA
1967	NA	NA	NA
1968	NA	NA	NA
1969	NA	NA	NA
1970	NA	NA	NA
1971	NA	NA	NA
1972	NA	NA	NA
1973	NA	NA	NA
1974	NA	NA	NA
1975	NA	NA	NA
1976	NA	NA	NA
1977	NA	NA	NA
1978	NA	NA	NA
1979	NA	NA	NA
1980	NA	NA	NA
1981	NA	NA	NA
1982	NA	NA	NA
1983	NA	NA	NA
1984	NA	NA	NA
1985	NA	NA	NA
1986	NA	NA	NA
1987	NA	NA	NA
1988	NA	NA	NA
1989	NA	NA	NA
1990	NA	NA	NA
1991	NA	NA	NA
1992	NA	NA	NA
1993	NA	NA	NA
1994	NA	NA	NA
1995	NA	NA	NA
1996	NA	NA	NA
1997	970	NA	171
1998	NA	NA	NA
1999	NA	NA	NA
2000	NA	NA	NA

# initial values for the spawner abundances 1959 to 2000

# rows=year; columns=geo units

```
Spawners.old = structure(.Data = c(
4408,5695,5345,
... (see table below for full data set)
),.Dim = c(42,3)),
```

	Faughan	Finn	Roe
1959	4408	5695	5345
1960	6157	7824	4488
1961	5650	10880	1981
1962	6134	13560	7903
1963	10410	13790	5914
1964	17040	9754	7121
1965	7171	8269	7588
1966	4358	8261	6735
1967	2469	9892	6611
1968	2348	9712	6210
1969	1758	10330	5737
1970	3137	10690	5732
1971	3973	5E+3	3109
1972	3517	7198	3559
1973	2692	11190	4579
1974	6965	11800	3408
1975	1794	13150	3470
1976	2483	3015	8822
1977	3021	8714	6589
1978	2455	5841	6244
1979	7696	19070	5632
1980	2715	11790	3525
1981	2562	5168	4488
1982	2632	5935	5039
1983	6443	13850	5087
1984	1980	9414	5962
1985	2861	11860	7723
1986	2129	6580	8232
1987	3101	10740	6196
1988	3305	7011	6215
1989	10680	6974	6596
1990	1942	9284	5045



<b>1991</b>	14300	9016	5445
<b>1992</b>	8655	12030	3207
<b>1993</b>	3825	15400	5303
<b>1994</b>	6589	4512	4324
<b>1995</b>	2322	7349	3801
<b>1996</b>	7692	6164	9483
<b>1997</b>	5849	8848	3398
<b>1998</b>	1932	4429	3771
<b>1999</b>	3112	13240	5099
<b>2000</b>	2727	9062	4094

---

mu.kappa.fau = 0.633,  
mu.kappa.fin = 0.3761,  
mu.kappa.roe = 0.4847,  
mu.p = 0.2417,  
mu.spawners = c(3402,8872,4457),  
tau.kappa = 14.01,  
tau.p = 1.419,  
tau.spawners = c(  
2.795,5.481,8.363))

## Annex 3: WinBUGS code: Population dynamics model of Atlantic salmon in the Foyle catchment.

### #Model

```
# Full Life Cycle model
# Estimation of hidden states (PFA, Spawners, juvenile production,...)
# Geographic structure, 5 units: 1.Faughan; 2.Finn; 3.Mourne; 4.Roe; 5.foyle
# DATA for years 1959 to 2008 t=1:50
# PREDICTION for years 2009-2010 t=51,52
# DATA available:
# Redds t=1:50
# Commercial catches t=1:50
# Rod catches total t=1:38
# Rod catch/unit t=39:50
# EF t= 40:50 (Use of pseudo observations obtained from the observation model from calibrationwork)
# Counters t=43:48

model
{
#####
# Spawners to redds relationship parameters

sigma.p ~dunif(0,10)
tau.p<-pow( sigma.p,-2)
var.p <- 1 / tau.p

p_N~dbeta(1,1)

# taken from the observation model (cf. calibration)
ratio.d ~dnorm(2.068,2.45)|(0.001,)

mu.p[1]~dbeta(1,1)|(0.01,0.99)
L.mu.p[1] <- logit(mu.p[1])
mu.p[2]~dbeta(1,1)|(0.01,0.99)
L.mu.p[2] <- logit(mu.p[2])

p.diff.mup <- step(mu.p[1] - mu.p[2])

mu.kappa.foyle ~ dgamma(1,0.001)|(0.001,)
alpha.kappa.foyle <- mu.kappa.foyle * beta.kappa

# Only one mean factor of proportionality between the counters and the redds

beta.kappa <- mu.kappa.foyle * tau.kappa

tau.kappa~ dgamma(0.01,0.01)|(0.001,)

#####
# density dependence

sigma.ddlink~dunif(0,10)
tau.ddlink<-pow( sigma.ddlink,-2)

mu_dmax<- exp(L.mu_dmax)
L.mu_dmax ~ dunif(-5,5)
sigma.dmax ~dunif(0,10)
tau.dmax<-pow( sigma.dmax,-2)
```

```

zt~dbeta(1,2)
a_d<-zt *1843

for (i in 1:5) {
  dmax[i] ~dlnorm(L.mu_dmax,tau.dmax)|(.30)
  alpha_d[i]<- 1/a_d
  beta_d[i]<- 1 / dmax[i]
}
#####
# surfaces

for(i in 1:5){
  p.WA[i] <- WA.total[i] / sum(WA.total[])
  # S.grade2[i] <- WA.total[i]-S.grade1[i]
  #total surface in GRade 1 equivalent
  S.G1.tot[i] <- S.grade1[i] + S.grade2[i] / ratio.d
}
#####

# p_J1/p_J2 correspond to the transition rate from smolt to returning
# adults (it also includes mortality).
# Incorporation of a hierarchical structure to pick up any inter-river variation

p_J1 ~ dbeta(2,2)
p_J2 <-1 - p_J1

sigma.PFA ~ dunif(0.02,10)
tau.PFA<-pow( sigma.PFA,-2)

sigma.N~dunif(0,10)
tau.N <-pow( sigma.N,-2)#~dgamma(0.001,0.001)|(.10000) #

for (i in 1:5){
  L.dG1[1,i] ~ dnorm(0,0.001)|(-2.8,2.8)
  log(mu.d[1,i]) <-L.dG1[1,i]
  J[1,i] <- mu.d[1,i]*S.G1.tot[i]
}
# Initialization of the chains, prior on the Spawners (years
# so the RETURNS of the Returns of the 4 first years of the time series
# are restricted by the BH relationship

# parameters of the BH relationship cut from the time series so the 4 "inits" years
# don't affect the time series
for (i in 1:5){
  alpha_d.cut[i] <- alpha_d[i]
  beta_d.cut[i] <- beta_d[i]
}
tau.ddlink.cut<-tau.ddlink

for (t in 1:4){
  #based on min(2.5th) and max(97.5th) percentile obtained from 01-06 model

  S.inits[t,1] ~dunif(0,100000)
  S.inits[t,2] ~dunif(0,220000)
  S.inits[t,3] ~dunif(0,800000)
  S.inits[t,4] ~dunif(0,165000)
  S.inits[t,5] ~dunif(0,180000)

  for (i in 1:5){

    S.sqm.inits[t,i] <- S.inits[t,i] / S.G1.tot[i]

    mu.ddlink.inits[t,i] <- log( S.sqm.inits[t,i] / ( alpha_d.cut[i] + beta_d.cut[i] * S.sqm.inits[t,i] ) )
    L.dG1.inits[t,i] ~ dnorm(mu.ddlink.inits[t,i],tau.ddlink.cut)

    log(mu.d.inits[t,i]) <- L.dG1.inits[t,i]

    J.inits[t,i] <- mu.d.inits[t,i]*S.G1.tot[i]
  }
}

# RETURNS of years 1:3 only depend on the J inits (years before the time series)
for (t in 1:3){
  for (i in 1:5){

```

```

        mu.PFA[t,i] <- log(p_J1*J.inits[t+1,i] + p_J2*J.inits[t,i] ) + year_effect_returns[t]+
unit_effect_fixed_returns[i]
    }
}

# Returns of years 4 depend on the J inits (years before the time series) and
# the first J of the time series
for (i in 1:5){
    mu.PFA[4,i] <- log(p_J1*J[4,i] + p_J2*J.inits[4,i] ) + year_effect_returns[4]+ unit_effect_fixed_returns[i]
}

# PFA of years 5:48 depend on the J of the time series
for (t in 5:52){
    for (i in 1:5){
        mu.PFA[t,i] <- log(p_J1*J[t-3,i] + p_J2*J[t-4,i] ) + year_effect_returns[t]+ unit_effect_fixed_returns[i]
    }
}

# Total juvenile production
for (t in 1:50){
    J.tot[t] <-sum(J[t,])
}

# different effects affecting the returns
sigma_unit_effect~dunif(0,10)
tau_unit_effect<-pow( sigma_unit_effect,-2)
sigma_year_effect~dunif(0,10)
tau_year_effect<-pow( sigma_year_effect,-2)

# mean effect <=> mean survival J 2 ret
mean_effect_returns ~ dnorm(0 , 0.01)
exp_mean_effect_returns <- exp(mean_effect_returns)
# unit effect <=> divergence between units
for (i in 1:5){
    unit_effect_returns[i] ~ dnorm(0 , tau_unit_effect)

    exp_unit_effect_returns[i] <- exp(unit_effect_returns[i])
    unit_effect_fixed_returns[i] <- unit_effect_returns[i] - mean(unit_effect_returns[])
    mean_interaction_effect_returns[i]<-mean( interaction_effect_returns[,i] )
    mean_exp_interaction_effect_returns[i]<-mean(exp_interaction_effect_returns[,i])
}

# year effect <=> divergence between years
# incorporation of rank 1 autocorrelation
# the 1st year is initialized independently
year_effect_returns[1] ~ dnorm(mean_effect_returns , tau_year_effect)
for (t in 2:52){
    year_effect_returns[t] ~ dnorm(year_effect_returns[t-1] , tau_year_effect)
}
for (t in 1:52){
    exp_year_effect_returns[t] <- exp(year_effect_returns[t])
    for(i in 1:5){
# PFA residuals
        interaction_effect_returns[t,i] <- log(PFA[t,i]) - mu.PFA[t,i]
        exp_interaction_effect_returns[t,i] <- exp(interaction_effect_returns[t,i] )
    }
}

#####
# Survival for each cohort of juveniles
for (t in 1:52){
    for (i in 1:5){
        s.J2Ret[t,i] <- exp( year_effect_returns[t]+ unit_effect_fixed_returns[i] )
    }
}

# proportions returns
#proportion of salmon from the foyle stock taken by the drift nets (sea licence)
#genetic report (ensing 2008) tell us that the minimum probability for being from another stock is 0.15%
#therefore the probability of being from the foyle is comprised between 0.15 and 1 for the sea licences
p.temp~dbeta(2,2)
p_f <- (1 - 0.15) * p.temp

#we say that the proportion of fish from the foyle stock is higher for the Lough + sea licences

p_f.temp ~ dbeta(2,2)
p_f2 <- ( (1 - p_f) * p_f.temp ) + p_f

```

```

for (t in 51:52){
  PFA.tot[t] <- sum(PFA[t,])
}

for (t in 1:50){
  PFA.tot[t] <- sum(PFA[t,])
  for (i in 1:5){
    p>Returns[t,i] <- PFA[t,i] / PFA.tot[t]
    p.S[t,i] <- S[t,i] / sum( S[t,] )
  }

  theta.Csea.tot[t]<-(C.sea.tot[t]+C.roe[t]+C.foyle1[t]+C.foyle2[t])/PFA.tot[t]

# Capture at sea affecting all the units
C.sea.tot[t] <- p_f2*Drift.Sea[t] + p_f2*Drift.Sea.Lough[t] + Drift.Lough[t] + Fixed[t]
# Capture affecting the Roe
C.roe[t] <- Draft.roe[t] + FF.Roe[t]
# Capture affecting the Faughan + Finn + Mourne + Rest
C.foyle1[t] <- Draft.foyle[t] + FF.Culmore[t]
# Capture affecting the Finn + Mourne + Rest
C.foyle2[t] <- FF.Rosses[t] + FF.prehen[t]

# Dispatching capture at sea equally in all units
for (i in 1:5){
  C.sea.tot.unit[t,i] <- (PFA[t,i] / sum(PFA[t,])) * C.sea.tot[t]
}
# C.sea.tot.unit[t,5] <-C.sea.tot[t] -sum(C.sea.tot.unit[t,1:4])

# Dispatching capture at sea equally in all units except the Roe
for (i in 1:4){
  C.foyle1.unit[t,i] <- (PFA[t,v.foyle1[i]] / (PFA[t,1]+PFA[t,2]+PFA[t,3]+PFA[t,5])) * C.foyle1[t]
}
# C.foyle1.unit[t,4] <- C.foyle1[t] - sum( C.foyle1.unit[t,1:3])

# Dispatching capture at sea equally in all units except the Roe and the Faughan
for (i in 1:3){
  C.foyle2.unit[t,i] <- (PFA[t,v.foyle2[i]] / (PFA[t,2]+PFA[t,3]+PFA[t,5])) * C.foyle2[t]
}
# Calculation of the total fisheries effort on every unit
theta.Csea[t,1] <- (C.sea.tot.unit[t,1] + C.foyle1.unit[t,1]) / PFA[t,1]
theta.Csea[t,2] <- (C.sea.tot.unit[t,2] + C.foyle1.unit[t,2] + C.foyle2.unit[t,1]) / PFA[t,2]
theta.Csea[t,3] <- (C.sea.tot.unit[t,3] + C.foyle1.unit[t,3] + C.foyle2.unit[t,2]) / PFA[t,3]
theta.Csea[t,4] <- (C.sea.tot.unit[t,4] + C.roe[t]) / PFA[t,4]
theta.Csea[t,5] <- (C.sea.tot.unit[t,5] + C.foyle1.unit[t,4] + C.foyle2.unit[t,3]) / PFA[t,5]
}

# Calculating the total catches for each units including rod catches
for (t in 1:50){
  C.tot[t,1] <- C.sea.tot.unit[t,1] + C.foyle1.unit[t,1] + Crod.unit[t,1]
  C.tot[t,2] <- C.sea.tot.unit[t,2] + C.foyle1.unit[t,2] + C.foyle2.unit[t,1] + Crod.unit[t,2]
  C.tot[t,3] <- C.sea.tot.unit[t,3] + C.foyle1.unit[t,3] + C.foyle2.unit[t,2] + Crod.unit[t,3]
  C.tot[t,4] <- C.sea.tot.unit[t,4] + C.roe[t] + Crod.unit[t,4]
  C.tot[t,5] <- C.sea.tot.unit[t,5] + C.foyle1.unit[t,4] + C.foyle2.unit[t,3] + Crod.unit[t,5]
}
for (t in 1:50){
  for (i in 1:5){
    h[t,i] <- C.tot[t,i] / PFA[t,i]
  }
}

#First loops are for years where no counter information is available
#####
# Faughan
# dynamic link between J and returns
for (t in 1:38) {
  PFA[t,1] ~ dlnorm( mu.PFA[t,1] , tau.PFA)

  A[t,1] <- PFA[t,1] - C.sea.tot.unit[t,1] - C.foyle1.unit[t,1]

  Crod.unit[t,1] <- Crod.tot[t] * (A[t,1]/sum(A[t,]))
  theta.rod[t,1]<- Crod.unit[t,1] / A[t,1]

  S[t,1] <- max(A[t,1],Crod.unit[t,1]) - Crod.unit[t,1]

  L.p[t,1] ~ dnorm(L.mu.p[1], tau.p)l(-4.59,1.5)
  logit(p[t,1]) <- L.p[t,1]
  kappa[t,1] ~ dgamma(alpha.kappa.foyle, beta.kappa)(0.001,)
  lambda.R[t,1] <- S[t,1] * p[t,1] * kappa[t,1]

  R[t,1] ~dpois(lambda.R[t,1])
}

```

```

S.sqm[t,1] <- S[t,1] / S.G1.tot[1]

mu.ddlink[t,1] <- log( S.sqm[t,1] / ( alpha_d[1] + beta_d[1] * S.sqm[t,1] ) )
L.dG1[t+1,1] ~ dnorm(mu.ddlink[t,1],tau.ddlink)

log(mu.d[t+1,1]) <- L.dG1[t+1,1]

J[t+1,1] <- mu.d[t+1,1]*S.G1.tot[1]
}
# Finn
# dynamic link between J and returns
for (t in 1:38) {

  PFA[t,2] ~ dlnorm( mu.PFA[t,2] , tau.PFA)

  A[t,2] <- PFA[t,2] - C.sea.tot.unit[t,2] - C.foyle1.unit[t,2] - C.foyle2.unit[t,1]

  Crod.unit[t,2] <- Crod.tot[t] * (A[t,2]/sum(A[t,]))
  theta.rod[t,2]<- Crod.unit[t,2] / A[t,2]

  S[t,2] <- max(A[t,2],Crod.unit[t,2]) - Crod.unit[t,2]

  L.p[t,2] ~ dnorm(L.mu.p[2], tau.p)|(-4.59,1.5)
  logit(p[t,2]) <- L.p[t,2]

  kappa[t,2] ~ dgamma(alpha.kappa.foyle, beta.kappa)|(0.001,)
  lambda.R[t,2] <- S[t,2] * p[t,2] * kappa[t,2]

  R[t,2] ~dpois(lambda.R[t,2])

  S.sqm[t,2] <- S[t,2] / S.G1.tot[2]

  mu.ddlink[t,2] <- log( S.sqm[t,2] / ( alpha_d[2] + beta_d[2] * S.sqm[t,2] ) )
  L.dG1[t+1,2] ~ dnorm(mu.ddlink[t,2],tau.ddlink)

  log(mu.d[t+1,2]) <- L.dG1[t+1,2]

  J[t+1,2] <- mu.d[t+1,2]*S.G1.tot[2]
}
# Mourne
# dynamic link between J and returns
# for year 39 we have data on the rod catches per unit
for (t in 1:38) {
  Crod.unit[t,3] <- Crod.tot[t] * (A[t,3]/sum(A[t,]))
}
for (t in 1:39) {

  PFA[t,3] ~ dlnorm( mu.PFA[t,3] , tau.PFA)

  A[t,3] <- PFA[t,3] - C.sea.tot.unit[t,3] - C.foyle1.unit[t,3] - C.foyle2.unit[t,2]

  theta.rod[t,3]<- Crod.unit[t,3] / A[t,3]

  S[t,3] <- max(A[t,3],Crod.unit[t,3]) - Crod.unit[t,3]

  L.p[t,3] ~ dnorm(L.mu.p[2], tau.p)|(-4.59,1.5)
  logit(p[t,3]) <- L.p[t,3]

  kappa[t,3] ~ dgamma(alpha.kappa.foyle, beta.kappa)|(0.001,)
  lambda.R[t,3] <- S[t,3] * p[t,3] * kappa[t,3]

  R[t,3] ~dpois(lambda.R[t,3])

  S.sqm[t,3] <- S[t,3] / S.G1.tot[3]

  mu.ddlink[t,3] <- log( S.sqm[t,3] / ( alpha_d[3] + beta_d[3] * S.sqm[t,3] ) )
  L.dG1[t+1,3] ~ dnorm(mu.ddlink[t,3],tau.ddlink)

  log(mu.d[t+1,3]) <- L.dG1[t+1,3]

  J[t+1,3] <- mu.d[t+1,3]*S.G1.tot[3]
}
# Roe
# dynamic link between J and returns
for (t in 1:38) {

  PFA[t,4] ~ dlnorm( mu.PFA[t,4] , tau.PFA)

```

```

A[t,4] <- PFA[t,4] - C.sea.tot.unit[t,4] - C.roe[t]

Crod.unit[t,4] <- Crod.tot[t] * (A[t,4]/sum(A[t,]))
theta.rod[t,4]<- Crod.unit[t,4] / A[t,4]

S[t,4] <- max(A[t,4],Crod.unit[t,4]) - Crod.unit[t,4]

L.p[t,4] ~ dnorm(L.mu.p[1], tau.p)(-4.59,1.5)
logit(p[t,4]) <- L.p[t,4]

kappa[t,4] ~ dgamma(alpha.kappa.foyle, beta.kappa)(0.001,)
lambda.R[t,4] <- S[t,4] * p[t,4] * kappa[t,4]

R[t,4] ~dpois(lambda.R[t,4])

S.sqm[t,4] <- S[t,4] / S.G1.tot[t,4]

mu.ddlink[t,4] <- log( S.sqm[t,4] / ( alpha_d[4] + beta_d[4] * S.sqm[t,4] ) )
L.dG1[t+1,4] ~ dnorm(mu.ddlink[t,4],tau.ddlink)

log(mu.d[t+1,4]) <- L.dG1[t+1,4]

J[t+1,4] <- mu.d[t+1,4]*S.G1.tot[t,4]
}
# foyle
# dynamic link between J and returns
for (t in 1:38) {

  PFA[t,5] ~ dlnorm( mu.PFA[t,5] , tau.PFA)

  A[t,5] <- PFA[t,5] - C.sea.tot.unit[t,5] - C.foyle1.unit[t,4] - C.foyle2.unit[t,3]

  Crod.unit[t,5] <- Crod.tot[t] - sum(Crod.unit[t,1:4])
  theta.rod[t,5]<- Crod.unit[t,5] / A[t,4]

  S[t,5] <- max(A[t,5],Crod.unit[t,5]) - Crod.unit[t,5]
  L.p[t,5] ~ dnorm(L.mu.p[2], tau.p)(-4.59,1.5)
  logit(p[t,5]) <- L.p[t,5]

  kappa[t,5] ~ dgamma(alpha.kappa.foyle, beta.kappa)(0.001,)
  lambda.R[t,5] <- S[t,5] * p[t,5] * kappa[t,5]

  R[t,5] ~dpois(lambda.R[t,5])

  S.sqm[t,5] <- S[t,5] / S.G1.tot[t,5]

  mu.ddlink[t,5] <- log( S.sqm[t,5] / ( alpha_d[5] + beta_d[5] * S.sqm[t,5] ) )
  L.dG1[t+1,5] ~ dnorm(mu.ddlink[t,5],tau.ddlink)

  log(mu.d[t+1,5]) <- L.dG1[t+1,5]

  J[t+1,5] <- mu.d[t+1,5]*S.G1.tot[t,5]
}
#second loops are for years where no counter information is available but with EF data
#####
# Faughan
# dynamic link between J and returns
for (t in 39:42) {

  PFA[t,1] ~ dlnorm( mu.PFA[t,1] , tau.PFA)

  A[t,1] <- PFA[t,1] - C.sea.tot.unit[t,1] - C.foyle1.unit[t,1]

  theta.rod[t,1]<- Crod.unit[t,1] / A[t,1]

  S[t,1] <- max(A[t,1],Crod.unit[t,1]) - Crod.unit[t,1]

  L.p[t,1] ~ dnorm(L.mu.p[1], tau.p)(-4.59,1.5)
  logit(p[t,1]) <- L.p[t,1]

  kappa[t,1] ~ dgamma(alpha.kappa.foyle, beta.kappa)(0.001,)
  lambda.R[t,1] <- S[t,1] * p[t,1] * kappa[t,1]

  R[t,1] ~dpois(lambda.R[t,1])

  S.sqm[t,1] <- S[t,1] / S.G1.tot[t,1]

  mu.ddlink[t,1] <- log( S.sqm[t,1] / ( alpha_d[1] + beta_d[1] * S.sqm[t,1] ) )

```

```

L.dG1[t+1,1] ~ dnorm(mu.ddlink[t,1],tau.ddlink)

log(mu.d[t+1,1]) <- L.dG1[t+1,1]

# Pseudo observations
precision.d.pseudo[t+1,1] <- 1 / log(cv.d.pseudo[t+1,1]*cv.d.pseudo[t+1,1] + 1)
L.mud.pseudo[t+1,1] ~ dnorm(L.dG1[t+1,1] , precision.d.pseudo[t+1,1])
log(mud.pseudo[t+1,1]) <- L.mud.pseudo[t+1,1]

J[t+1,1] <- mu.d[t+1,1]*S.G1.tot[1]
}
# Finn
# dynamic link between J and returns
for (t in 39:42) {

PFA[t,2] ~ dlnorm( mu.PFA[t,2] , tau.PFA)

A[t,2] <- PFA[t,2] - C.sea.tot.unit[t,2] - C.foyle1.unit[t,2] - C.foyle2.unit[t,2]

theta.rod[t,2]<- Crod.unit[t,2] / A[t,2]

S[t,2] <- max(A[t,2],Crod.unit[t,2]) - Crod.unit[t,2]

L.p[t,2] ~ dnorm(L.mu.p[2], tau.p)(-4.59,1.5)
logit(p[t,2]) <- L.p[t,2]
kappa[t,2] ~ dgamma(alpha.kappa.foyle, beta.kappa)(0.001,)
lambda.R[t,2] <- S[t,2] * p[t,2] * kappa[t,2]

R[t,2] ~dpois(lambda.R[t,2])

S.sqm[t,2] <- S[t,2] / S.G1.tot[2]

mu.ddlink[t,2] <- log( S.sqm[t,2] / ( alpha_d[2] + beta_d[2] * S.sqm[t,2] ) )
L.dG1[t+1,2] ~ dnorm(mu.ddlink[t,2],tau.ddlink)

log(mu.d[t+1,2]) <- L.dG1[t+1,2]

# Pseudo observations
precision.d.pseudo[t+1,2] <- 1 / log(cv.d.pseudo[t+1,2]*cv.d.pseudo[t+1,2] + 1)
L.mud.pseudo[t+1,2] ~ dnorm(L.dG1[t+1,2] , precision.d.pseudo[t+1,2])
log(mud.pseudo[t+1,2]) <- L.mud.pseudo[t+1,2]

J[t+1,2] <- mu.d[t+1,2]*S.G1.tot[2]
}
# Mourné
# dynamic link between J and returns
for (t in 40:42) {

PFA[t,3] ~ dlnorm( mu.PFA[t,3] , tau.PFA)

A[t,3] <- PFA[t,3] - C.sea.tot.unit[t,3] - C.foyle1.unit[t,3] - C.foyle2.unit[t,2]

theta.rod[t,3]<- Crod.unit[t,3] / A[t,3]

S[t,3] <- max(A[t,3],Crod.unit[t,3]) - Crod.unit[t,3]

L.p[t,3] ~ dnorm(L.mu.p[2], tau.p)(-4.59,1.5)
logit(p[t,3]) <- L.p[t,3]

kappa[t,3] ~ dgamma(alpha.kappa.foyle, beta.kappa)(0.001,)
lambda.R[t,3] <- S[t,3] * p[t,3] * kappa[t,3]

R[t,3] ~dpois(lambda.R[t,3])

S.sqm[t,3] <- S[t,3] / S.G1.tot[3]

mu.ddlink[t,3] <- log( S.sqm[t,3] / ( alpha_d[3] + beta_d[3] * S.sqm[t,3] ) )

L.dG1[t+1,3] ~ dnorm(mu.ddlink[t,3],tau.ddlink)

log(mu.d[t+1,3]) <- L.dG1[t+1,3]

# Pseudo observations
precision.d.pseudo[t+1,3] <- 1 / log(cv.d.pseudo[t+1,3]*cv.d.pseudo[t+1,3] + 1)
L.mud.pseudo[t+1,3] ~ dnorm(L.dG1[t+1,3] , precision.d.pseudo[t+1,3])
log(mud.pseudo[t+1,3]) <- L.mud.pseudo[t+1,3]

J[t+1,3] <- mu.d[t+1,3]*S.G1.tot[3]
}

```



```

# Roe
# dynamic link between J and returns
for (t in 39:42) {

  PFA[t,4] ~ dlnorm( mu.PFA[t,4] , tau.PFA)

  A[t,4] <- PFA[t,4] - C.sea.tot.unit[t,4] - C.roe[t]

  theta.rod[t,4]<- Crod.unit[t,4] / A[t,4]

  S[t,4] <- max(A[t,4],Crod.unit[t,4]) - Crod.unit[t,4]

  L.p[t,4] ~ dnorm(L.mu.p[1], tau.p)(-4.59,1.5)
  logit(p[t,4]) <- L.p[t,4]

  kappa[t,4] ~ dgamma(alpha.kappa.foyle, beta.kappa)(0.001,)
  lambda.R[t,4] <- S[t,4] * p[t,4] * kappa[t,4]
  R[t,4] ~dpois(lambda.R[t,4])

  S.sqm[t,4] <- S[t,4] / S.G1.tot[4]

  mu.ddlink[t,4] <- log( S.sqm[t,4] / ( alpha_d[4] + beta_d[4] * S.sqm[t,4] ) )
  L.dG1[t+1,4] ~ dnorm(mu.ddlink[t,4],tau.ddlink)

  log(mu.d[t+1,4]) <- L.dG1[t+1,4]

# Pseudo observations
  precision.d.pseudo[t+1,4] <- 1 / log(cv.d.pseudo[t+1,4]*cv.d.pseudo[t+1,4] + 1)
  L.mud.pseudo[t+1,4] ~ dnorm(L.dG1[t+1,4] , precision.d.pseudo[t+1,4])
  log(mud.pseudo[t+1,4]) <- L.mud.pseudo[t+1,4]

  J[t+1,4] <- mu.d[t+1,4]*S.G1.tot[4]
}
# foyle
# dynamic link between J and returns
for (t in 39:42) {

  PFA[t,5] ~ dlnorm( mu.PFA[t,5] , tau.PFA)

  A[t,5] <- PFA[t,5] - C.sea.tot.unit[t,5] - C.foyle1.unit[t,4] - C.foyle2.unit[t,3]

  theta.rod[t,5]<- Crod.unit[t,5] / A[t,4]

  S[t,5] <- max(A[t,5],Crod.unit[t,5]) - Crod.unit[t,5]

  L.p[t,5] ~ dnorm(L.mu.p[2], tau.p)(-4.59,1.5)
  logit(p[t,5]) <- L.p[t,5]

  kappa[t,5] ~ dgamma(alpha.kappa.foyle, beta.kappa)(0.001,)
  lambda.R[t,5] <- S[t,5] * p[t,5] * kappa[t,5]

  R[t,5] ~dpois(lambda.R[t,5])

  S.sqm[t,5] <- S[t,5] / S.G1.tot[5]

  mu.ddlink[t,5] <- log( S.sqm[t,5] / ( alpha_d[5] + beta_d[5] * S.sqm[t,5] ) )
  L.dG1[t+1,5] ~ dnorm(mu.ddlink[t,5],tau.ddlink)

  log(mu.d[t+1,5]) <- L.dG1[t+1,5]

# Pseudo observations
  precision.d.pseudo[t+1,5] <- 1 / log(cv.d.pseudo[t+1,5]*cv.d.pseudo[t+1,5] + 1)
  L.mud.pseudo[t+1,5] ~ dnorm(L.dG1[t+1,5] , precision.d.pseudo[t+1,5])
  log(mud.pseudo[t+1,5]) <- L.mud.pseudo[t+1,5]

  J[t+1,5] <- mu.d[t+1,5]*S.G1.tot[5]
}
# Faughan
# dynamic link between J and returns
for (t in 43:48) {

  PFA[t,1] ~ dlnorm( mu.PFA[t,1] , tau.PFA)
  A[t,1] <- PFA[t,1] - C.sea.tot.unit[t,1] - C.foyle1.unit[t,1]

  N[t,1] ~dnorm( A[t,1],1)C(C.rod.amont.obs[t,1],) #A[t,1]

  theta.rod[t,1]<- C.rod.amont.obs[t,1] / A[t,1]

  S[t,1] <- max(A[t,1],C.rod.amont.obs[t,1]) - C.rod.amont.obs[t,1]

```

```

L.p[t,1] ~ dnorm(L.mu.p[1], tau.p)(-4.59,1.5)
logit(p[t,1]) <- L.p[t,1]

kappa[t,1] ~ dgamma(alpha.kappa.foyle, beta.kappa)(0.001,)
lambda.R[t,1] <- S[t,1] * p[t,1] * kappa[t,1]

R[t,1] ~dpois(lambda.R[t,1])

S.sqm[t,1] <- S[t,1] / S.G1.tot[1]

mu.ddlink[t,1] <- log( S.sqm[t,1] / ( alpha_d[1] + beta_d[1] * S.sqm[t,1] ) )
L.dG1[t+1,1] ~ dnorm(mu.ddlink[t,1],tau.ddlink)

log(mu.d[t+1,1]) <- L.dG1[t+1,1]

# Pseudo observations
precision.d.pseudo[t+1,1] <- 1 / log(cv.d.pseudo[t+1,1]*cv.d.pseudo[t+1,1] + 1)
L.mud.pseudo[t+1,1] ~ dnorm(L.dG1[t+1,1] , precision.d.pseudo[t+1,1])
log(mud.pseudo[t+1,1]) <- L.mud.pseudo[t+1,1]

J[t+1,1] <- mu.d[t+1,1]*S.G1.tot[1]
}
# Finn
# dynamic link between J and returns
for (t in 43:48) {

PFA[t,2] ~ dlnorm( mu.PFA[t,2] , tau.PFA)

A[t,2] <- PFA[t,2] - C.sea.tot.unit[t,2] - C.foyle1.unit[t,2] - C.foyle2.unit[t,1]

N[t,2] ~dnorm( A[t,2],1)C(C.rod.amont.obs[t,2],)
theta.rod[t,2]<- C.rod.amont.obs[t,2] / A[t,2]

S[t,2] <- max(A[t,2],C.rod.amont.obs[t,2]) - C.rod.amont.obs[t,2]

L.p[t,2] ~ dnorm(L.mu.p[2], tau.p)(-4.59,1.5)
logit(p[t,2]) <- L.p[t,2]

kappa[t,2] ~ dgamma(alpha.kappa.foyle, beta.kappa)(0.001,)
lambda.R[t,2] <- S[t,2] * p[t,2] * kappa[t,2]

R[t,2] ~dpois(lambda.R[t,2])

S.sqm[t,2] <- S[t,2] / S.G1.tot[2]

mu.ddlink[t,2] <- log( S.sqm[t,2] / ( alpha_d[2] + beta_d[2] * S.sqm[t,2] ) )
L.dG1[t+1,2] ~ dnorm(mu.ddlink[t,2],tau.ddlink)

log(mu.d[t+1,2]) <- L.dG1[t+1,2]

# Pseudo observations
precision.d.pseudo[t+1,2] <- 1 / log(cv.d.pseudo[t+1,2]*cv.d.pseudo[t+1,2] + 1)
L.mud.pseudo[t+1,2] ~ dnorm(L.dG1[t+1,2] , precision.d.pseudo[t+1,2])
log(mud.pseudo[t+1,2]) <- L.mud.pseudo[t+1,2]

J[t+1,2] <- mu.d[t+1,2]*S.G1.tot[2]
}
# Mourné
# dynamic link between J and returns
for (t in 43:48) {

PFA[t,3] ~ dlnorm( mu.PFA[t,3] , tau.PFA)

A[t,3] <- PFA[t,3] - C.sea.tot.unit[t,3] - C.foyle1.unit[t,3] - C.foyle2.unit[t,2]

L.mu.N[t] <-log( p_N*A[t,3] )

N[t,3] ~dlnorm( L.mu.N[t],tau.N)C(C.rod.amont.obs[t,3],)

theta.rod[t,3]<- C.rod.amont.obs[t,3] / A[t,3]

S[t,3] <- max(A[t,3],C.rod.amont.obs[t,3]) - C.rod.amont.obs[t,3]
L.p[t,3] ~ dnorm(L.mu.p[2], tau.p)(-4.59,1.5)
logit(p[t,3]) <- L.p[t,3]

kappa[t,3] ~ dgamma(alpha.kappa.foyle, beta.kappa)(0.001,)
lambda.R[t,3] <- S[t,3] * p[t,3] * kappa[t,3]

R[t,3] ~dpois(lambda.R[t,3])
}

```

```

S.sqm[t,3] <- S[t,3] / S.G1.tot[3]

mu.ddlink[t,3] <- log( S.sqm[t,3] / ( alpha_d[3] + beta_d[3] * S.sqm[t,3] ) )

L.dG1[t+1,3] ~ dnorm(mu.ddlink[t,3],tau.ddlink)
log(mu.d[t+1,3]) <- L.dG1[t+1,3]
# Pseudo observations
precision.d.pseudo[t+1,3] <- 1 / log(cv.d.pseudo[t+1,3]*cv.d.pseudo[t+1,3] + 1)
L.mud.pseudo[t+1,3] ~ dnorm(L.dG1[t+1,3] , precision.d.pseudo[t+1,3])
log(mud.pseudo[t+1,3]) <- L.mud.pseudo[t+1,3]

J[t+1,3] <- mu.d[t+1,3]*S.G1.tot[3]
}
# Roe
# dynamic link between J and returns
for (t in 43:48) {

PFA[t,4] ~ dlnorm( mu.PFA[t,4] , tau.PFA)

A[t,4] <- PFA[t,4] - C.sea.tot.unit[t,4] - C.roe[t]

N[t,4] ~ dnorm( A[t,4],1)C(C.rod.amont.obs[t,4],)

theta.rod[t,4]<- C.rod.amont.obs[t,4] / A[t,4]

S[t,4] <- max(A[t,4],C.rod.amont.obs[t,4]) - C.rod.amont.obs[t,4]

L.p[t,4] ~ dnorm(L.mu.p[1], tau.p)(-4.59,1.5)
logit(p[t,4]) <- L.p[t,4]

kappa[t,4] ~ dgamma(alpha.kappa.foyle, beta.kappa)(0.001,)
lambda.R[t,4] <- S[t,4] * p[t,4] * kappa[t,4]

R[t,4] ~dpois(lambda.R[t,4])

S.sqm[t,4] <- S[t,4] / S.G1.tot[4]

mu.ddlink[t,4] <- log( S.sqm[t,4] / ( alpha_d[4] + beta_d[4] * S.sqm[t,4] ) )
L.dG1[t+1,4] ~ dnorm(mu.ddlink[t,4],tau.ddlink)

log(mu.d[t+1,4]) <- L.dG1[t+1,4]
# Pseudo observations
precision.d.pseudo[t+1,4] <- 1 / log(cv.d.pseudo[t+1,4]*cv.d.pseudo[t+1,4] + 1)
L.mud.pseudo[t+1,4] ~ dnorm(L.dG1[t+1,4] , precision.d.pseudo[t+1,4])
log(mud.pseudo[t+1,4]) <- L.mud.pseudo[t+1,4]

J[t+1,4] <- mu.d[t+1,4]*S.G1.tot[4]
}
# foyle
# dynamic link between J and returns
for (t in 43:48) {

PFA[t,5] ~ dlnorm( mu.PFA[t,5] , tau.PFA)

A[t,5] <- PFA[t,5] - C.sea.tot.unit[t,5] - C.foyle1.unit[t,4] - C.foyle2.unit[t,3]

theta.rod[t,5]<- C.rod.amont.obs[t,5] / A[t,5]

S[t,5] <- max(A[t,5],C.rod.amont.obs[t,5]) - C.rod.amont.obs[t,5]

L.p[t,5] ~ dnorm(L.mu.p[2], tau.p)(-4.59,1.5)
logit(p[t,5]) <- L.p[t,5]

kappa[t,5] ~ dgamma(alpha.kappa.foyle, beta.kappa)(0.001,)
lambda.R[t,5] <- S[t,5] * p[t,5] * kappa[t,5]

R[t,5] ~dpois(lambda.R[t,5])

S.sqm[t,5] <- S[t,5] / S.G1.tot[5]

mu.ddlink[t,5] <- log( S.sqm[t,5] / ( alpha_d[5] + beta_d[5] * S.sqm[t,5] ) )
L.dG1[t+1,5] ~ dnorm(mu.ddlink[t,5],tau.ddlink)

log(mu.d[t+1,5]) <- L.dG1[t+1,5]

# Pseudo observations
precision.d.pseudo[t+1,5] <- 1 / log(cv.d.pseudo[t+1,5]*cv.d.pseudo[t+1,5] + 1)
L.mud.pseudo[t+1,5] ~ dnorm(L.dG1[t+1,5] , precision.d.pseudo[t+1,5])
log(mud.pseudo[t+1,5]) <- L.mud.pseudo[t+1,5]

```

```

    J[t+1,5] <- mu.d[t+1,5]*S.G1.tot[5]
  }
  # Faughan
  # dynamic link between J and returns
  for (t in 49:49) {

    PFA[t,1] ~ dlnorm( mu.PFA[t,1] , tau.PFA)

    A[t,1] <- PFA[t,1] - C.sea.tot.unit[t,1] - C.foyle1.unit[t,1]

    theta.rod[t,1]<- C.rod.amont.obs[t,1] / A[t,1]

    S[t,1] <- max(A[t,1],C.rod.amont.obs[t,1]) - C.rod.amont.obs[t,1]

    L.p[t,1] ~ dnorm(L.mu.p[1], tau.p)(-4.59,1.5)
    logit(p[t,1]) <- L.p[t,1]

    kappa[t,1] ~ dgamma(alpha.kappa.foyle, beta.kappa)(0.001,)
    lambda.R[t,1] <- S[t,1] * p[t,1] * kappa[t,1]

    R[t,1] ~dpois(lambda.R[t,1])

    S.sqm[t,1] <- S[t,1] / S.G1.tot[1]

    mu.ddlink[t,1] <- log( S.sqm[t,1] / ( alpha_d[1] + beta_d[1] * S.sqm[t,1] ) )
    L.dG1[t+1,1] ~ dnorm(mu.ddlink[t,1],tau.ddlink)

    log(mu.d[t+1,1]) <- L.dG1[t+1,1]

  # Pseudo observations
  precision.d.pseudo[t+1,1] <- 1 / log(cv.d.pseudo[t+1,1]*cv.d.pseudo[t+1,1] + 1)
  L.mud.pseudo[t+1,1] ~ dnorm(L.dG1[t+1,1] , precision.d.pseudo[t+1,1])
  log(mud.pseudo[t+1,1]) <- L.mud.pseudo[t+1,1]

  J[t+1,1] <- mu.d[t+1,1]*S.G1.tot[1]
}
  # Finn
  # dynamic link between J and returns
  for (t in 49:49) {

    PFA[t,2] ~ dlnorm( mu.PFA[t,2] , tau.PFA)

    A[t,2] <- PFA[t,2] - C.sea.tot.unit[t,2] - C.foyle1.unit[t,2] - C.foyle2.unit[t,1]

    theta.rod[t,2]<- C.rod.amont.obs[t,2] / A[t,2]

    S[t,2] <- max(A[t,2],C.rod.amont.obs[t,2]) - C.rod.amont.obs[t,2]

    L.p[t,2] ~ dnorm(L.mu.p[2], tau.p)(-4.59,1.5)
    logit(p[t,2]) <- L.p[t,2]

    kappa[t,2] ~ dgamma(alpha.kappa.foyle, beta.kappa)(0.001,)
    lambda.R[t,2] <- S[t,2] * p[t,2] * kappa[t,2]

    R[t,2] ~dpois(lambda.R[t,2])

    S.sqm[t,2] <- S[t,2] / S.G1.tot[2]

    mu.ddlink[t,2] <- log( S.sqm[t,2] / ( alpha_d[2] + beta_d[2] * S.sqm[t,2] ) )
    L.dG1[t+1,2] ~ dnorm(mu.ddlink[t,2],tau.ddlink)

    log(mu.d[t+1,2]) <- L.dG1[t+1,2]

  # Pseudo observations
  precision.d.pseudo[t+1,2] <- 1 / log(cv.d.pseudo[t+1,2]*cv.d.pseudo[t+1,2] + 1)
  L.mud.pseudo[t+1,2] ~ dnorm(L.dG1[t+1,2] , precision.d.pseudo[t+1,2])
  log(mud.pseudo[t+1,2]) <- L.mud.pseudo[t+1,2]

  J[t+1,2] <- mu.d[t+1,2]*S.G1.tot[2]
}
  # Mourné
  # dynamic link between J and returns
  for (t in 49:49) {

    PFA[t,3] ~ dlnorm( mu.PFA[t,3] , tau.PFA)

    A[t,3] <- PFA[t,3] - C.sea.tot.unit[t,3] - C.foyle1.unit[t,3] - C.foyle2.unit[t,2]

```

```

theta.rod[t,3]<- C.rod.amont.obs[t,3] / A[t,3]

S[t,3] <- max(A[t,3],C.rod.amont.obs[t,3]) - C.rod.amont.obs[t,3]

L.p[t,3] ~ dnorm(L.mu.p[2], tau.p)(-4.59,1.5)
logit(p[t,3]) <- L.p[t,3]

kappa[t,3] ~ dgamma(alpha.kappa.foyle, beta.kappa)(0.001,)
lambda.R[t,3] <- S[t,3] * p[t,3] * kappa[t,3]

R[t,3] ~dpois(lambda.R[t,3])

S.sqm[t,3] <- S[t,3] / S.G1.tot[3]

mu.ddlink[t,3] <- log( S.sqm[t,3] / ( alpha_d[3] + beta_d[3] * S.sqm[t,3] ) )

L.dG1[t+1,3] ~ dnorm(mu.ddlink[t,3],tau.ddlink)

log(mu.d[t+1,3]) <- L.dG1[t+1,3]
# Pseudo observations
precision.d.pseudo[t+1,3] <- 1 / log(cv.d.pseudo[t+1,3]*cv.d.pseudo[t+1,3] + 1)
L.mud.pseudo[t+1,3] ~ dnorm(L.dG1[t+1,3] , precision.d.pseudo[t+1,3])
log(mud.pseudo[t+1,3]) <- L.mud.pseudo[t+1,3]

J[t+1,3] <- mu.d[t+1,3]*S.G1.tot[3]
}
# Roe
# dynamic link between J and returns
for (t in 49:49) {

PFA[t,4] ~ dlnorm( mu.PFA[t,4] , tau.PFA)

A[t,4] <- PFA[t,4] - C.sea.tot.unit[t,4] - C.roe[t]

theta.rod[t,4]<- C.rod.amont.obs[t,4] / A[t,4]

S[t,4] <- max(A[t,4],C.rod.amont.obs[t,4]) - C.rod.amont.obs[t,4]

L.p[t,4] ~ dnorm(L.mu.p[1], tau.p)(-4.59,1.5)
logit(p[t,4]) <- L.p[t,4]

kappa[t,4] ~ dgamma(alpha.kappa.foyle, beta.kappa)(0.001,)
lambda.R[t,4] <- S[t,4] * p[t,4] * kappa[t,4]

R[t,4] ~dpois(lambda.R[t,4])

S.sqm[t,4] <- S[t,4] / S.G1.tot[4]

mu.ddlink[t,4] <- log( S.sqm[t,4] / ( alpha_d[4] + beta_d[4] * S.sqm[t,4] ) )
L.dG1[t+1,4] ~ dnorm(mu.ddlink[t,4],tau.ddlink)

log(mu.d[t+1,4]) <- L.dG1[t+1,4]

# Pseudo observations
precision.d.pseudo[t+1,4] <- 1 / log(cv.d.pseudo[t+1,4]*cv.d.pseudo[t+1,4] + 1)
L.mud.pseudo[t+1,4] ~ dnorm(L.dG1[t+1,4] , precision.d.pseudo[t+1,4])
log(mud.pseudo[t+1,4]) <- L.mud.pseudo[t+1,4]

J[t+1,4] <- mu.d[t+1,4]*S.G1.tot[4]
}
# foyle
# dynamic link between J and returns
for (t in 49:49) {

PFA[t,5] ~ dlnorm( mu.PFA[t,5] , tau.PFA)

A[t,5] <- PFA[t,5] - C.sea.tot.unit[t,5] - C.foyle1.unit[t,4] - C.foyle2.unit[t,3]

theta.rod[t,5]<- C.rod.amont.obs[t,5] / A[t,5]
S[t,5] <- max(A[t,5],C.rod.amont.obs[t,5]) - C.rod.amont.obs[t,5]

L.p[t,5] ~ dnorm(L.mu.p[2], tau.p)(-4.59,1.5)
logit(p[t,5]) <- L.p[t,5]

kappa[t,5] ~ dgamma(alpha.kappa.foyle, beta.kappa)(0.001,)
lambda.R[t,5] <- S[t,5] * p[t,5] * kappa[t,5]

R[t,5] ~dpois(lambda.R[t,5])

```

```

S.sqm[t,5] <- S[t,5] / S.G1.tot[5]

mu.ddlink[t,5] <- log( S.sqm[t,5] / ( alpha_d[5] + beta_d[5] * S.sqm[t,5] ) )
L.dG1[t+1,5] ~ dnorm(mu.ddlink[t,5],tau.ddlink)

log(mu.d[t+1,5]) <- L.dG1[t+1,5]

# Pseudo observations
precision.d.pseudo[t+1,5] <- 1 / log(cv.d.pseudo[t+1,5]*cv.d.pseudo[t+1,5] + 1)
L.mud.pseudo[t+1,5] ~ dnorm(L.dG1[t+1,5] , precision.d.pseudo[t+1,5])
log(mud.pseudo[t+1,5]) <- L.mud.pseudo[t+1,5]

J[t+1,5] <- mu.d[t+1,5]*S.G1.tot[5]
}
# Faughan
# dynamic link between J and returns
# We need to set another set of loops because we dont have pseudo observation for year 51(2009) yet
for (t in 50:50) {

PFA[t,1] ~ dlnorm( mu.PFA[t,1] , tau.PFA)

A[t,1] <- PFA[t,1] - C.sea.tot.unit[t,1] - C.foyle1.unit[t,1]

theta.rod[t,1]<- C.rod.amont.obs[t,1] / A[t,1]

S[t,1] <- max(A[t,1],C.rod.amont.obs[t,1]) - C.rod.amont.obs[t,1]

L.p[t,1] ~ dnorm(L.mu.p[1], tau.p)(-4.59,1.5)
logit(p[t,1]) <- L.p[t,1]

kappa[t,1] ~ dgamma(alpha.kappa.foyle, beta.kappa)(0.001,)
lambda.R[t,1] <- S[t,1] * p[t,1] * kappa[t,1]

R[t,1] ~dpois(lambda.R[t,1])

S.sqm[t,1] <- S[t,1] / S.G1.tot[1]

mu.ddlink[t,1] <- log( S.sqm[t,1] / ( alpha_d[1] + beta_d[1] * S.sqm[t,1] ) )
L.dG1[t+1,1] ~ dnorm(mu.ddlink[t,1],tau.ddlink)

log(mu.d[t+1,1]) <- L.dG1[t+1,1]

J[t+1,1] <- mu.d[t+1,1]*S.G1.tot[1]
}
# Finn
# dynamic link between J and returns
for (t in 50:50) {

PFA[t,2] ~ dlnorm( mu.PFA[t,2] , tau.PFA)

A[t,2] <- PFA[t,2] - C.sea.tot.unit[t,2] - C.foyle1.unit[t,2] - C.foyle2.unit[t,1]

theta.rod[t,2]<- C.rod.amont.obs[t,2] / A[t,2]

S[t,2] <- max(A[t,2],C.rod.amont.obs[t,2]) - C.rod.amont.obs[t,2]

L.p[t,2] ~ dnorm(L.mu.p[2], tau.p)(-4.59,1.5)
logit(p[t,2]) <- L.p[t,2]

kappa[t,2] ~ dgamma(alpha.kappa.foyle, beta.kappa)(0.001,)
lambda.R[t,2] <- S[t,2] * p[t,2] * kappa[t,2]

R[t,2] ~dpois(lambda.R[t,2])

S.sqm[t,2] <- S[t,2] / S.G1.tot[2]

mu.ddlink[t,2] <- log( S.sqm[t,2] / ( alpha_d[2] + beta_d[2] * S.sqm[t,2] ) )
L.dG1[t+1,2] ~ dnorm(mu.ddlink[t,2],tau.ddlink)

log(mu.d[t+1,2]) <- L.dG1[t+1,2]

J[t+1,2] <- mu.d[t+1,2]*S.G1.tot[2]
}
# Mourné
# dynamic link between J and returns
for (t in 50:50) {

PFA[t,3] ~ dlnorm( mu.PFA[t,3] , tau.PFA)

```

```

A[t,3] <- PFA[t,3] - C.sea.tot.unit[t,3] - C.foyle1.unit[t,3] - C.foyle2.unit[t,2]

theta.rod[t,3]<- C.rod.amont.obs[t,3] / A[t,3]

S[t,3] <- max(A[t,3],C.rod.amont.obs[t,3]) - C.rod.amont.obs[t,3]

L.p[t,3] ~ dnorm(L.mu.p[2], tau.p)|(-4.59,1.5)
logit(p[t,3]) <- L.p[t,3]

kappa[t,3] ~ dgamma(alpha.kappa.foyle, beta.kappa)|(0.001,)
lambda.R[t,3] <- S[t,3] * p[t,3] * kappa[t,3]

R[t,3] ~dpois(lambda.R[t,3])

S.sqm[t,3] <- S[t,3] / S.G1.tot[3]

mu.ddlink[t,3] <- log( S.sqm[t,3] / ( alpha_d[3] + beta_d[3] * S.sqm[t,3] ) )

L.dG1[t+1,3] ~ dnorm(mu.ddlink[t,3],tau.ddlink)

log(mu.d[t+1,3]) <- L.dG1[t+1,3]

J[t+1,3] <- mu.d[t+1,3]*S.G1.tot[3]
}
# Roe
# dynamic link between J and returns
for (t in 50:50) {

  PFA[t,4] ~ dlnorm( mu.PFA[t,4] , tau.PFA)
  A[t,4] <- PFA[t,4] - C.sea.tot.unit[t,4] - C.roe[t]
  theta.rod[t,4]<- C.rod.amont.obs[t,4] / A[t,4]

  S[t,4] <- max(A[t,4],C.rod.amont.obs[t,4]) - C.rod.amont.obs[t,4]

  L.p[t,4] ~ dnorm(L.mu.p[1], tau.p)|(-4.59,1.5)
  logit(p[t,4]) <- L.p[t,4]

  kappa[t,4] ~ dgamma(alpha.kappa.foyle, beta.kappa)|(0.001,)
  lambda.R[t,4] <- S[t,4] * p[t,4] * kappa[t,4]

  R[t,4] ~dpois(lambda.R[t,4])

  S.sqm[t,4] <- S[t,4] / S.G1.tot[4]

  mu.ddlink[t,4] <- log( S.sqm[t,4] / ( alpha_d[4] + beta_d[4] * S.sqm[t,4] ) )
  L.dG1[t+1,4] ~ dnorm(mu.ddlink[t,4],tau.ddlink)

  log(mu.d[t+1,4]) <- L.dG1[t+1,4]

  J[t+1,4] <- mu.d[t+1,4]*S.G1.tot[4]
}
# foyle
# dynamic link between J and returns
for (t in 50:50) {

  PFA[t,5] ~ dlnorm( mu.PFA[t,5] , tau.PFA)

  A[t,5] <- PFA[t,5] - C.sea.tot.unit[t,5] - C.foyle1.unit[t,4] - C.foyle2.unit[t,3]

  theta.rod[t,5]<- C.rod.amont.obs[t,5] / A[t,5]

  S[t,5] <- max(A[t,5],C.rod.amont.obs[t,5]) - C.rod.amont.obs[t,5]

  L.p[t,5] ~ dnorm(L.mu.p[2], tau.p)|(-4.59,1.5)
  logit(p[t,5]) <- L.p[t,5]

  kappa[t,5] ~ dgamma(alpha.kappa.foyle, beta.kappa)|(0.001,)
  lambda.R[t,5] <- S[t,5] * p[t,5] * kappa[t,5]

  R[t,5] ~dpois(lambda.R[t,5])

  S.sqm[t,5] <- S[t,5] / S.G1.tot[5]

  mu.ddlink[t,5] <- log( S.sqm[t,5] / ( alpha_d[5] + beta_d[5] * S.sqm[t,5] ) )
  L.dG1[t+1,5] ~ dnorm(mu.ddlink[t,5],tau.ddlink)

  log(mu.d[t+1,5]) <- L.dG1[t+1,5]
}

```

```

        J[t+1,5] <- mu.d[t+1,5]*S.G1.tot[5]
    }
    #####
    # 2 years of predictions only looking at the Returns and Adults

for (t in 51:52) {
  for (i in 1:5){
    PFA[t,i] ~ dlnorm( mu.PFA[t,i] , tau.PFA)
  }
}
}

```

## #data

```

list(
  v.foyle1=c(1,2,3,5),
  v.foyle2=c(2,3,5),
  T=50,

  Drift.Sea=c(
    ... (see table below for full data set)
  ),

  Drift.Sea.Lough=c(
    ... (see table below for full data set)
  ),

  Drift.Lough=c(
    ... (see table below for full data set)
  ),

  Draft.foyle=c(
    ... (see table below for full data set)
  ),

  Draft.roe=c(
    ... (see table below for full data set)
  ),

  Fixed=c(
    ... (see table below for full data set)
  ),

  FF.Roe=c(
    ... (see table below for full data set)
  ),

  FF.Culmore=c(
    ... (see table below for full data set)
  ),
  FF.Rosses=c(
    ... (see table below for full data set)
  ),

  FF.prehen=c(
    ... (see table below for full data set)
  ),

```



	Drift			Draft		Fixed	FF			
	Sea	Sea.Lough	Lough	foyle	roe		Roe	Culmore	Rosses	prehen
1959	521	7995	521	48592	3826	0	12059	3073	4690	4296
1960	1522	11995	1522	48706	3834	0	8954	2671	5201	1082
1961	0	11252	0	37694	2967	0	8767	1991	4050	2726
1962	2677	17064	2677	76688	5418	0	835	3348	5238	9463
1963	6852	41379	6852	52765	6475	2471	1075	2876	6728	3357
1964	6668	45919	6668	70563	7618	2271	2002	3388	6854	4264
1965	6501	21874	6501	48399	3966	1354	660	2853	5260	2842
1966	7512	33337	7512	51583	3268	1447	576	2893	4301	3160
1967	8390	44884	8390	56448	3024	1887	1021	2302	6696	4471
1968	8193	26998	8193	50191	2183	1154	925	2928	3291	10928
1969	7271	22226	7271	47649	3520	843	1199	3003	1961	5916
1970	11310	32486	11310	43310	2031	2080	920	2588	3340	4161
1971	6352	20272	6352	36230	588	486	284	2883	1909	5083
1972	6202	17803	6202	29171	243	1763	149	1930	3115	1530
1973	5239	12587	5239	26660	487	1101	0	1838	3601	2296
1974	7967	15799	7967	35608	1062	949	0	1261	3919	1794
1975	3627	7290	3627	27963	1644	1054	0	789	4533	2321
1976	2982	6983	2982	17573	1229	454	0	517	1277	1102
1977	2615	4989	2615	19920	1223	672	0	598	2863	1300
1978	5081	9450	5081	17795	1688	1800	0	315	2918	936
1979	3024	4697	3024	15362	2001	1110	0	227	1758	243
1980	8089	15140	8089	15248	1190	926	0	390	1422	224
1981	4130	11102	4130	10296	1485	435	0	0	1313	0
1982	5971	18947	5971	17036	3268	943	0	0	1646	0
1983	19880	33760	19880	14237	1244	627	0	0	1490	0
1984	4742	9582	4742	9697	595	78	0	0	863	0
1985	5431	13994	5431	12921	1145	674	0	0	1253	0
1986	4477	23556	4477	11355	1354	282	0	0	1083	0
1987	4781	6400	4781	4883	551	47	0	0	415	0
1988	1121	12502	1121	15358	818	79	0	0	763	0
1989	13202	27037	13202	30612	478	330	0	0	0	0
1990	6261	17921	6261	9188	1011	371	0	0	0	0
1991	2542	11754	2542	4431	1006	0	0	0	0	0
1992	4494	21345	4494	8223	713	0	0	0	0	0
1993	4413	16673	4413	10152	486	0	0	0	0	0
1994	4427	16791	4427	9232	814	0	0	0	0	0
1995	8413	10656	8413	9986	774	0	0	0	0	0
1996	2932	10879	2932	9792	794	0	0	0	0	0
1997	5509	18840	5509	11652	904	0	0	0	0	0
1998	7539	22717	7539	11019	122	0	0	0	0	0
1999	2792	12097	2792	7715	178	0	0	0	0	0
2000	3628	15528	3628	9004	115	0	0	0	0	0
2001	2169	10739	2169	9476	0	0	0	0	0	0
2002	5262	22556	5262	11917	0	0	0	0	0	0
2003	3382	11846	3382	16991	0	0	0	0	0	0
2004	2246	10143	2246	9485	5	0	0	0	0	0
2005	2408	10649	2408	12143	0	0	0	0	0	0
2006	602	5197	602	6031	0	0	0	0	0	0
2007	0	0	2598	2774	0	0	0	0	0	0
2008	0	0	1248	2916	0	0	0	0	0	0
2009	0	0	0	0	0	0	0	0	0	0
2010	0	0	0	0	0	0	0	0	0	0

# counters counts

# row: years, column: geo units

N = structure(.Data = c(

0,0,0,0

... (see table below for full data set)

),.Dim=c(50,4)),

	Faughan	Finn	Mourne	Roe
1959	0	0	0	0
1960	0	0	0	0
1961	0	0	0	0
1962	0	0	0	0
1963	0	0	0	0
1964	0	0	0	0
1965	0	0	0	0
1966	0	0	0	0
1967	0	0	0	0
1968	0	0	0	0
1969	0	0	0	0
1970	0	0	0	0
1971	0	0	0	0
1972	0	0	0	0

1973	0	0	0	0
1974	0	0	0	0
1975	0	0	0	0
1976	0	0	0	0
1977	0	0	0	0
1978	0	0	0	0
1979	0	0	0	0
1980	0	0	0	0
1981	0	0	0	0
1982	0	0	0	0
1983	0	0	0	0
1984	0	0	0	0
1985	0	0	0	0
1986	0	0	0	0
1987	0	0	0	0
1988	0	0	0	0
1989	0	0	0	0
1990	0	0	0	0
1991	0	0	0	0
1992	0	0	0	0
1993	0	0	0	0
1994	0	0	0	0
1995	0	0	0	0
1996	0	0	0	0
1997	0	0	0	0
1998	0	0	0	0
1999	0	0	0	0
2000	0	0	0	0
2001	1518	3311	6250	3265
2002	4288	5768	12991	5459
2003	3097	6461	12129	4086
2004	2855	3771	10270	1922
2005	4245	8571	9397	2917
2006	3625	5748	9352	5375
2007	NA	NA	NA	NA
2008	NA	NA	NA	NA

# Redd counts for each subcatchment

# row: years, column: geo units

R= structure(.Data = c(  
757, 456, 2406, 1204, 179,  
... (see below for full data set)  
,.Dim=c(50,5)),

	Faughan	Finn	Mourne	Roe	Foyle
1959	757	456	2406	1204	179
1960	2169	391	3892	1398	176
1961	853	242	1553	822	136
1962	2114	896	6113	1328	264
1963	2039	1041	6575	2082	539
1964	1823	669	8964	1777	394
1965	2558	1171	15487	2533	922
1966	1292	1192	18372	1264	709
1967	351	1437	12848	526	437
1968	585	927	5167	775	146
1969	452	453	1828	823	109
1970	1164	621	2991	638	178
1971	513	667	2055	676	161
1972	156	536	498	475	109
1973	90	459	482	124	86
1974	362	523	1280	547	253
1975	468	383	797	821	91
1976	630	340	848	891	114
1977	356	160	611	552	111
1978	427	489	1822	882	114
1979	479	680	449	1486	165
1980	163	872	796	659	226
1981	615	1371	811	435	216
1982	449	579	1571	650	113
1983	375	1108	829	354	61
1984	203	394	1062	718	89
1985	411	807	2527	768	88
1986	188	375	1354	891	57
1987	329	518	1355	729	124
1988	410	651	1686	974	32
1989	1058	452	1864	1426	162
1990	226	366	1446	298	45



2002	597	2263	1827	408	22
2003	335	590	748	158	8
2004	464	627	776	357	21
2005	822	1128	1783	309	41
2006	501	752	1664	444	43
2007	1132	814	2382	500	33
2008	861	648	1889	533	67
2009	0	0	0	0	0
2010	0	0	0	0	0

```
C.rod.amont.obs=structure(.Data =c(
0,0,0,0,0,
... (see table below for full data set)
),.Dim=c(52,5)),
```

	Faughan	Finn	Mourne	Roe	Foyle
1959	0	0	0	0	0
1960	0	0	0	0	0
1961	0	0	0	0	0
1962	0	0	0	0	0
1963	0	0	0	0	0
1964	0	0	0	0	0
1965	0	0	0	0	0
1966	0	0	0	0	0
1967	0	0	0	0	0
1968	0	0	0	0	0
1969	0	0	0	0	0
1970	0	0	0	0	0
1971	0	0	0	0	0
1972	0	0	0	0	0
1973	0	0	0	0	0
1974	0	0	0	0	0
1975	0	0	0	0	0
1976	0	0	0	0	0
1977	0	0	0	0	0
1978	0	0	0	0	0
1979	0	0	0	0	0
1980	0	0	0	0	0
1981	0	0	0	0	0
1982	0	0	0	0	0
1983	0	0	0	0	0
1984	0	0	0	0	0
1985	0	0	0	0	0
1986	0	0	0	0	0
1987	0	0	0	0	0
1988	0	0	0	0	0
1989	0	0	0	0	0
1990	0	0	0	0	0
1991	0	0	0	0	0
1992	0	0	0	0	0
1993	0	0	0	0	0
1994	0	0	0	0	0
1995	0	0	0	0	0
1996	0	0	0	0	0
1997	0	0	0	0	0
1998	0	0	0	0	0
1999	0	0	0	0	0
2000	0	0	0	0	0
2001	656	1162	1065	267	18
2002	597	2263	1827	408	22
2003	335	590	748	158	8
2004	464	627	776	357	21
2005	822	1128	1783	309	41
2006	501	752	1664	444	43
2007	1132	814	2382	500	33
2008	861	648	1889	533	67
2009	0	0	0	0	0
2010	0	0	0	0	0

```
#log of the median of the average 0+ density per geo units
# row: years, columns: geo units
```

```
L.mud.pseudo=structure(.Data = c(
NA,NA,NA,NA,NA,
... (see table below for full data set)
),.Dim = c(50,5)),
```

	Faughan	Finn	Mourne	Roe	Foyle
1959	NA	NA	NA	NA	NA
1960	NA	NA	NA	NA	NA
1961	NA	NA	NA	NA	NA
1962	NA	NA	NA	NA	NA
1963	NA	NA	NA	NA	NA
1964	NA	NA	NA	NA	NA
1965	NA	NA	NA	NA	NA
1966	NA	NA	NA	NA	NA
1967	NA	NA	NA	NA	NA
1968	NA	NA	NA	NA	NA
1969	NA	NA	NA	NA	NA
1970	NA	NA	NA	NA	NA
1971	NA	NA	NA	NA	NA
1972	NA	NA	NA	NA	NA
1973	NA	NA	NA	NA	NA
1974	NA	NA	NA	NA	NA
1975	NA	NA	NA	NA	NA
1976	NA	NA	NA	NA	NA
1977	NA	NA	NA	NA	NA
1978	NA	NA	NA	NA	NA
1979	NA	NA	NA	NA	NA
1980	NA	NA	NA	NA	NA
1981	NA	NA	NA	NA	NA
1982	NA	NA	NA	NA	NA
1983	NA	NA	NA	NA	NA
1984	NA	NA	NA	NA	NA
1985	NA	NA	NA	NA	NA
1986	NA	NA	NA	NA	NA
1987	NA	NA	NA	NA	NA
1988	NA	NA	NA	NA	NA
1989	NA	NA	NA	NA	NA
1990	NA	NA	NA	NA	NA
1991	NA	NA	NA	NA	NA
1992	NA	NA	NA	NA	NA
1993	NA	NA	NA	NA	NA
1994	NA	NA	NA	NA	NA
1995	NA	NA	NA	NA	NA
1996	NA	NA	NA	NA	NA
1997	NA	NA	NA	NA	NA
1998	-0.447	0.286	NA	0.166	-0.068
1999	-0.166	-0.394	-1.002	1.736	-0.765
2000	0.632	-1.176	-1.179	1.570	-0.204
2001	2.214	-0.688	0.286	1.862	1.407
2002	1.127	-1.041	-0.111	0.922	0.620
2003	2.489	-0.899	0.260	1.717	1.426
2004	2.009	0.581	0.436	2.051	1.982
2005	1.851	1.139	0.700	2.308	1.960
2006	1.809	-0.790	0.920	2.192	1.922
2007	1.972	0.379	0.564	1.999	1.966
2008	1.874	0.379	-0.238	1.529	0.799

#coefficient of variation of the average 0+ density per geo units  
# row: years, columns: geo units

```
cv.d.pseudo=structure(.Data = c(
NA,NA,NA,NA,NA,
... (see table below for full data set)
),Dim = c(50,5)),
```

	Faughan	Finn	Mourne	Roe	Foyle
1959	NA	NA	NA	NA	NA
1960	NA	NA	NA	NA	NA
1961	NA	NA	NA	NA	NA
1962	NA	NA	NA	NA	NA
1963	NA	NA	NA	NA	NA
1964	NA	NA	NA	NA	NA
1965	NA	NA	NA	NA	NA
1966	NA	NA	NA	NA	NA
1967	NA	NA	NA	NA	NA
1968	NA	NA	NA	NA	NA
1969	NA	NA	NA	NA	NA
1970	NA	NA	NA	NA	NA
1971	NA	NA	NA	NA	NA
1972	NA	NA	NA	NA	NA
1973	NA	NA	NA	NA	NA
1974	NA	NA	NA	NA	NA

1975	NA	NA	NA	NA	NA
1976	NA	NA	NA	NA	NA
1977	NA	NA	NA	NA	NA
1978	NA	NA	NA	NA	NA
1979	NA	NA	NA	NA	NA
1980	NA	NA	NA	NA	NA
1981	NA	NA	NA	NA	NA
1982	NA	NA	NA	NA	NA
1983	NA	NA	NA	NA	NA
1984	NA	NA	NA	NA	NA
1985	NA	NA	NA	NA	NA
1986	NA	NA	NA	NA	NA
1987	NA	NA	NA	NA	NA
1988	NA	NA	NA	NA	NA
1989	NA	NA	NA	NA	NA
1990	NA	NA	NA	NA	NA
1991	NA	NA	NA	NA	NA
1992	NA	NA	NA	NA	NA
1993	NA	NA	NA	NA	NA
1994	NA	NA	NA	NA	NA
1995	NA	NA	NA	NA	NA
1996	NA	NA	NA	NA	NA
1997	NA	NA	NA	NA	NA
1998	1.519	0.433	NA	0.527	1.444
1999	0.492	0.404	0.525	0.559	1.881
2000	0.601	0.587	0.496	0.678	0.894
2001	0.624	0.498	0.367	0.608	0.894
2002	0.561	1.178	0.358	0.555	0.779
2003	0.651	0.493	0.368	0.571	0.815
2004	0.555	0.457	0.371	0.650	0.749
2005	0.557	0.628	0.408	0.747	0.825
2006	0.561	0.481	0.419	0.664	0.813
2007	0.534	0.407	0.371	0.592	0.689
2008	0.518	0.400	0.356	0.505	0.599

# logit of the proportion of wetted area sampled for redd counts  
 # row: years, column= geo units

```
L.p=structure(.Data = c(
  NA,NA,NA,NA,NA,
  ... (see table below for full data set)
),.Dim=c(50,5)),
```

	Faughan	Finn	Mourne	Roe	Foyle
1959	NA	NA	NA	NA	NA
1960	NA	NA	NA	NA	NA
1961	NA	NA	NA	NA	NA
1962	NA	NA	NA	NA	NA
1963	NA	NA	NA	NA	NA
1964	NA	NA	NA	NA	NA
1965	NA	NA	NA	NA	NA
1966	NA	NA	NA	NA	NA
1967	NA	NA	NA	NA	NA
1968	NA	NA	NA	NA	NA
1969	NA	NA	NA	NA	NA
1970	NA	NA	NA	NA	NA
1971	NA	NA	NA	NA	NA
1972	NA	NA	NA	NA	NA
1973	NA	NA	NA	NA	NA
1974	NA	NA	NA	NA	NA
1975	NA	NA	NA	NA	NA
1976	NA	NA	NA	NA	NA
1977	NA	NA	NA	NA	NA
1978	NA	NA	NA	NA	NA
1979	NA	NA	NA	NA	NA
1980	NA	NA	NA	NA	NA
1981	NA	NA	NA	NA	NA
1982	NA	NA	NA	NA	NA
1983	NA	NA	NA	NA	NA
1984	NA	NA	NA	NA	NA
1985	NA	NA	NA	NA	NA
1986	NA	NA	NA	NA	NA
1987	NA	NA	NA	NA	NA
1988	NA	NA	NA	NA	NA
1989	NA	NA	NA	NA	NA
1990	NA	NA	NA	NA	NA
1991	NA	NA	NA	NA	NA

1992	NA	NA	NA	NA	NA
1993	NA	NA	NA	NA	NA
1994	NA	NA	NA	NA	NA
1995	NA	NA	NA	NA	NA
1996	NA	NA	NA	NA	NA
1997	NA	NA	NA	NA	NA
1998	NA	NA	NA	NA	NA
1999	NA	NA	NA	NA	NA
2000	NA	NA	NA	NA	NA
2001	NA	-1.58	NA	NA	NA
2002	NA	-1.66	-1.8804	-0.7986	-1.3859
2003	-0.7131	-1.66	-2.0881	-0.7532	-1.3619
2004	-0.6991	NA	-2.2820	-2.4387	-2.4208
2005	-0.7016	-1.15	-0.8562	-0.7478	-1.3499
2006	-3.425	-2.75	-2.8078	-0.72725	-2.6865
2007	NA	NA	NA	NA	NA
2008	NA	NA	NA	NA	NA

# Surface of grade 1 nursery habitat Based on habitat surveys

S.grade1=c(  
266992,1157446,3613113,342450,313346),

# Surface of grade 2 nursery habitat Based on habitat surveys

S.grade2=c(  
158793,174863,1188973,595285,564840),

# Total wetted area (GIS)

WA.total=c(  
776412,1726922,6240284,1292616,1387720)  
)

## #Initialisation of the Gibbs sampler (1 chain)

list(  
p.temp= 0.7,  
p\_f.temp=0.95,  
tau.kappa=0.1,

#initial values of the kappa parameter

# row=years, column=geo units

kappa = structure(.Data = c(  
0.347,0.1809,0.2491,0.4983,0.2807,  
... (see table below for full data set)  
) ,.Dim = c(50,5)),

	Faughan	Finn	Mourne	Roe	Foyle
1959	0.3478	0.1809	0.2491	0.4983	0.2807
1960	0.396	0.4174	0.4407	0.3034	0.5996
1961	0.1694	0.3791	0.2767	0.6979	0.5988
1962	0.5073	0.3291	0.3859	0.3616	0.2921
1963	0.3894	0.2326	0.4227	0.4392	0.6746
1964	0.7314	0.185	0.3099	0.3656	0.3208
1965	0.29	0.4445	0.3244	0.4719	0.6545
1966	0.2797	0.2621	0.4206	0.4205	0.3552
1967	0.2007	0.3056	0.5157	0.2392	0.4066
1968	0.3183	0.309	0.2794	0.4583	0.4906
1969	0.3631	0.4649	0.5613	0.2881	0.3911
1970	0.4415	0.3749	0.2787	0.2373	0.3155
1971	0.4052	0.4909	0.3248	0.2827	0.3915
1972	0.3677	0.3135	0.1513	0.4915	0.646
1973	0.3154	0.7796	0.4496	0.2212	0.4489
1974	0.3213	0.2851	0.4164	0.3616	0.5687
1975	0.2748	0.6077	0.301	0.3304	0.3431
1976	0.3028	0.3731	0.189	0.5464	0.3939
1977	0.5862	0.1861	0.4124	0.5549	0.5178
1978	0.3055	0.605	0.3495	0.2803	0.4114
1979	0.1555	0.4823	0.1411	0.8077	0.3674
1980	0.1435	0.2518	0.2208	0.431	0.161
1981	0.4787	0.3897	0.2725	0.5427	0.3324
1982	0.4515	0.5721	0.5728	0.5753	0.4386
1983	0.4417	0.5829	0.3094	0.1938	0.2123
1984	0.2224	0.341	0.4509	0.3052	0.4156
1985	0.3991	0.3105	0.1626	0.3847	0.3201
1986	0.2689	0.3274	0.4259	0.3366	0.4165
1987	0.6008	0.552	0.3158	0.2304	0.4727
1988	0.3707	0.3489	0.4107	0.3516	0.4149
1989	0.4774	0.3115	0.3854	0.2697	0.3464
1990	0.6432	1.052	0.4455	0.3756	0.2554
1991	0.2576	0.3736	0.2791	0.4655	0.3923

1992	0.2363	0.493	0.1731	0.1802	0.3701
1993	0.4267	0.5961	0.2871	0.5926	0.3306
1994	0.4865	0.4596	0.4068	0.1583	0.2032
1995	0.2841	0.4102	0.526	0.3728	0.5307
1996	0.4162	0.3855	0.3413	0.5208	0.6725
1997	0.5956	0.4938	0.4479	0.2522	0.4828
1998	0.2742	0.5654	0.3773	0.3266	0.5118
1999	0.3587	0.379	0.2239	0.4729	0.4481
2000	0.2735	0.4602	0.397	0.5507	0.5
2001	0.6749	0.417	0.2725	0.3422	0.5897
2002	0.556	0.4184	0.3902	0.3928	0.4243
2003	0.4931	0.112	0.3197	0.4894	0.4344
2004	0.6161	0.3999	0.4474	0.4279	0.2208
2005	0.6621	0.1897	0.3124	1.037	0.3595
2006	0.318	0.3243	0.3281	0.2641	0.1945
2007	0.2688	0.3975	0.4818	0.6258	0.1438
2008	0.5103	0.2047	0.6639	0.7043	0.5477

L.mu\_dmax = 1.123,

L.dG1 = structure(.Data = c(  
2.236,-0.2376,1.342,2.016,1.107,  
... (see table below for full data set)  
, .Dim = c(51,5)),

	Faughan	Finn	Mourne	Roe	Foyle
1959	2.236	-0.2376	1.342	2.016	1.107
1960	1.644	-0.3655	-0.03926	1.955	0.6161
1961	1.981	0.04026	1.027	1.943	0.6971
1962	1.574	-0.2213	1.598	1.903	1.301
1963	1.249	-0.01214	0.3616	1.919	1.518
1964	0.9523	0.1782	0.5458	1.87	1.076
1965	0.7365	0.09235	0.2554	2.149	0.4729
1966	1.731	-0.8165	0.3727	2.261	0.7924
1967	1.724	-0.2152	0.7259	2.513	0.1256
1968	0.7552	0.07725	0.04047	2.131	0.9828
1969	1.518	0.3333	0.2909	1.701	0.9296
1970	2.011	-0.05549	0.6463	1.314	1.098
1971	1.781	0.4479	0.5677	2.308	1.299
1972	1.637	-0.6596	0.6169	1.532	0.7199
1973	1.598	0.08696	-0.7035	1.682	0.03054
1974	1.884	0.01676	0.1379	1.98	0.4161
1975	1.307	0.3917	0.5288	2.192	0.3916
1976	1.65	0.04349	-0.03165	1.475	1.429
1977	0.8806	0.292	0.04573	1.201	1.016
1978	0.9547	0.3945	-0.2895	1.544	0.1572
1979	1.072	0.926	0.07188	1.814	0.9082
1980	1.603	0.1345	0.001058	2.524	0.4939
1981	1.724	0.2935	-0.07415	2.492	0.8882
1982	0.8566	-0.3489	0.5334	1.787	0.9033
1983	1.016	-0.4489	0.6721	1.882	0.9901
1984	1.734	-0.135	-0.1674	2.347	-0.08436
1985	2.231	0.3969	0.7808	2.36	0.2493
1986	0.9222	-0.1477	0.2906	2.154	0.8263
1987	1.443	-0.3781	-0.03455	1.728	0.1475
1988	1.724	-0.2933	0.4063	1.975	0.1382
1989	0.5295	-0.1841	0.0374	1.996	0.3204
1990	1.017	0.2045	-0.4057	2.039	0.859
1991	0.6655	-0.03377	0.4684	0.6464	0.2986
1992	1.247	0.4182	0.1719	1.685	0.6583
1993	1.271	0.2495	0.9309	2.113	0.4033
1994	1.305	-0.3998	0.1327	0.9221	0.9829
1995	1.11	-0.426	0.7778	1.036	0.5199
1996	1.404	0.1922	0.2115	1.556	0.788
1997	1.049	-0.06659	0.819	1.843	1.615
1998	1.195	-0.2218	0.8908	2.014	0.6352
1999	0.6918	-0.4601	0.006923	1.17	0.4764
2000	1.034	-0.877	0.2332	0.965	-0.4061
2001	1.338	-0.4529	0.5256	1.177	0.5467
2002	0.816	-0.2382	0.3181	1.177	0.87
2003	1.627	-0.4578	0.2171	1.568	0.932
2004	1.793	0.4858	-0.06472	1.514	1.248
2005	1.581	0.3646	-0.3711	1.385	0.5835
2006	1.96	-0.5079	0.9063	1.964	0.9282
2007	1.311	0.6984	1.158	2.316	1.542
2008	1.729	0.3659	0.2359	1.735	1.064
2009	1.227	0.3531	0.2129	1.238	0.5517



```
L.dG1.inits = structure(.Data = c(
-6.925,-7.435,-0.1403,-10.63,-6.651,
1.535,-0.04058,-23.39,1.84,0.7487,
1.9,-0.3225,0.4655,2.02,-3.56,
-1.916,-16.1,-9.439,-25.45,-0.318),
.Dim = c(4,5)),
```

```
L.p = structure(.Data = c(
-1.993,-2.271,-1.365,-1.223,-1.967,
... (see table below for full data set)
), .Dim = c(50,5)),
```

	Faughan	Finn	Mourne	Roe	Foyle
1959	-1.993	-2.271	-1.365	-1.223	-1.967
1960	-1.076	-3.001	-1.644	-1.171	-2.223
1961	-0.7324	-2.416	-2.456	-1.681	-1.991
1962	-1.728	-2.304	-2.838	-0.7931	-2.549
1963	-0.8852	-1.56	-2.358	-0.7212	-1.994
1964	-1.871	-2.033	-1.368	-0.9771	-1.63
1965	-0.8525	-2.649	-2.125	-1.001	-2.31
1966	-0.804	-1.775	-1.92	-1.253	-1.941
1967	-1.401	-1.553	-1.409	-1.862	-2.273
1968	-0.3826	-2.077	-1.343	-2.172	-3.098
1969	-1.501	-2.022	-2.494	-1.466	-2.317
1970	-1.028	-1.968	-2.014	-1.839	-1.805
1971	-1.073	-2.278	-1.905	-1.627	-1.807
1972	-1.076	-0.8447	-1.075	-1.433	-1.87
1973	-2.289	-1.268	-2.065	-1.818	-1.497
1974	-1.409	-1.344	-1.842	-1.523	-1.793
1975	-1.208	-2.525	-2.845	-0.3245	-2.281
1976	-1.164	-2.557	-2.16	-0.9903	-2.116
1977	-1.671	-2.043	-2.197	-1.444	-0.9588
1978	-1.206	-2.419	-1.758	-0.212	-1.388
1979	-0.8677	-2.653	-2.876	-1.471	-2.567
1980	-1.16	-1.457	-2.095	-0.6265	-1.161
1981	-1.011	-1.878	-2.317	-1.66	-1.703
1982	-0.1947	-2.73	-1.938	-0.5039	-2.153
1983	-0.7769	-1.524	-1.667	-0.9171	-1.591
1984	-1.479	-2.305	-1.964	-1.329	-1.927
1985	-1.389	-1.676	-1.008	-1.713	-2.841
1986	-0.9759	-1.508	-2.401	-0.2054	-2.902
1987	-2.071	-2.382	-2.126	-0.9106	-1.964
1988	-2.0	-1.667	-1.937	-0.7903	-2.982
1989	-0.7647	-1.896	-2.186	-0.8388	-1.681
1990	-1.54	-2.118	-1.153	-0.9355	-1.692
1991	-0.6289	-1.271	-1.745	-0.8895	-2.055
1992	-0.577	-2.248	-1.741	-0.02955	-2.088
1993	-1.15	-2.026	-1.264	-1.454	-1.842
1994	-0.9401	-2.043	-1.95	-1.055	-1.548
1995	-2.151	-1.473	-2.186	-1.163	-2.006
1996	-0.887	-1.935	-1.838	-0.5469	-1.889
1997	-0.445	-2.078	-2.354	-0.3519	-2.777
1998	-1.442	-1.573	-2.149	-0.2718	-1.901
1999	-1.614	-2.082	-2.069	-1.092	-2.468
2000	-1.473	-2.652	-1.915	-0.8865	-1.746
2001	-0.5077	NA	-1.659	-1.433	-1.798
2002	-0.749	NA	NA	NA	NA
2003	NA	NA	NA	NA	NA
2004	NA	-2.021	NA	NA	NA
2005	NA	NA	NA	NA	NA
2006	NA	NA	NA	NA	NA
2007	-1.119	-2.775	-1.946	-0.736	-2.468
2008	-1.248	-2.208	-0.9226	-0.3444	-1.444

# initial values for the redd counts

# rows=years, columns=geo units

```
R = structure(.Data = c(
NA, NA, NA, NA, NA,
... (see table below for full data set)
),.Dim = c(50,5)),
```

	Faughan	Finn	Mourne	Roe	Foyle
1959	NA	NA	NA	NA	NA
1960	NA	NA	NA	NA	NA
1961	NA	NA	NA	NA	NA
1962	NA	NA	NA	NA	NA
1963	NA	NA	NA	NA	NA

1964	NA	NA	NA	NA	NA
1965	NA	NA	NA	NA	NA
1966	NA	NA	NA	NA	NA
1967	NA	NA	NA	NA	NA
1968	NA	NA	NA	NA	NA
1969	NA	NA	NA	NA	NA
1970	NA	NA	NA	NA	NA
1971	NA	NA	NA	NA	NA
1972	NA	NA	NA	NA	NA
1973	NA	NA	NA	NA	NA
1974	NA	NA	NA	NA	NA
1975	NA	NA	NA	NA	NA
1976	NA	NA	NA	NA	NA
1977	NA	NA	NA	NA	NA
1978	NA	NA	NA	NA	NA
1979	NA	NA	NA	NA	NA
1980	NA	NA	NA	NA	NA
1981	NA	NA	NA	NA	NA
1982	NA	NA	NA	NA	NA
1983	NA	NA	NA	NA	NA
1984	NA	NA	NA	NA	NA
1985	NA	NA	NA	NA	NA
1986	NA	NA	NA	NA	NA
1987	NA	NA	NA	NA	NA
1988	NA	NA	NA	NA	NA
1989	NA	NA	NA	NA	NA
1990	NA	NA	NA	NA	NA
1991	NA	NA	NA	NA	NA
1992	NA	NA	NA	NA	NA
1993	NA	NA	NA	NA	NA
1994	NA	NA	NA	NA	NA
1995	NA	NA	NA	NA	NA
1996	NA	NA	NA	NA	NA
1997	970	NA	NA	400	NA
1998	NA	NA	NA	NA	NA
1999	NA	NA	NA	NA	NA
2000	NA	NA	NA	NA	NA
2001	NA	NA	NA	NA	NA
2002	NA	NA	NA	NA	NA
2003	NA	NA	NA	NA	NA
2004	NA	NA	NA	NA	NA
2005	NA	NA	NA	NA	NA
2006	NA	NA	NA	NA	NA
2007	NA	NA	NA	NA	NA
2008	NA	NA	NA	NA	NA

# Initial values of the PFA  
# rows=years, column=geo units  
PFA = structure(.Data = c(  
29630,50480,80530,27710,10590,  
... (see table below for full data set)  
), .Dim = c(52,5)),

	Faughan	Finn	Mourne	Roe	Foyle
1959	29630	50480	80530	27710	10590
1960	33490	34940	96710	35140	5031
1961	23020	13720	110700	20960	3561
1962	35620	41500	394200	19560	16050
1963	25570	38500	269400	25900	10240
1964	29540	54080	243100	33330	14190
1965	34250	46670	5.19E+5	26320	17610
1966	18590	38320	426700	19100	20140
1967	14620	45770	214400	24500	20950
1968	7995	53160	169600	23980	11640
1969	16580	19720	1.12E+5	26980	8064
1970	17740	24970	171700	29130	7705
1971	9694	31660	103600	19320	6405
1972	5507	24990	53080	8709	4523
1973	10630	12630	47880	5876	5079
1974	14230	26430	64530	13690	8176
1975	12910	14190	85850	8290	5417
1976	12930	19540	68830	8831	4092
1977	8131	19270	34640	7785	2098
1978	10620	18270	66820	11270	2575
1979	12360	29160	86690	13980	8694
1980	8566	31930	58550	7917	10720
1981	6818	38520	48230	8019	6850

1982	5151	38270	50410	9845	5013
1983	9033	37530	54580	17230	5020
1984	8238	19880	32040	15250	2698
1985	7133	24690	83130	17200	8068
1986	4609	10910	70130	11230	5057
1987	6518	13780	51700	14090	2857
1988	14730	18360	52450	11970	1868
1989	14610	23290	99630	27560	6131
1990	6079	10400	39850	8644	3603
1991	9024	13920	49600	8400	1977
1992	6953	15060	60510	13510	3051
1993	4866	20410	33800	10180	4789
1994	5090	18880	53920	6276	3613
1995	4710	18060	59460	4871	3366
1996	6648	22490	66510	8759	3489
1997	7494	17290	65600	7701	4159
1998	4533	9040	58250	2545	3594
1999	2824	7272	24290	2385	1396
2000	4528	10480	40750	3744	4109
2001	2777	6058	37410	4392	1972
2002	7174	9651	76400	7563	2859
2003	4978	10380	67960	4984	2916
2004	4362	5762	51310	2396	1686
2005	6291	12700	53260	3504	4705
2006	4570	7246	40770	5966	3521
2007	7490	14970	27160	3495	3951
2008	7042	15180	23320	3332	2477
2009	8695	11840	63630	6170	3471
2010	4981	14960	75820	8424	4533

```

dmax = c(
5.51,1.116,1.588,10.41,3.457),

S.inits = structure(.Data = c(
10000,20000,50000,15000,10000,
10000,20000,50000,15000,10000,
10000,20000,50000,15000,10000,
10000,20000,50000,15000,10000
), .Dim = c(4,5)),

p_J1 = 0.5,
mean_effect_returns = -3.805,
mu.kappa.foyle = 0.388,
mu.p = c(
0.2358,0.1215),
p_N = 0.2843,
ratio.d = 4.612,
sigma.dmax = 0.6974,
sigma.ddlink = 0.3648,
sigma.p = 0.522,
sigma.PFA = 0.1436,
sigma_unit_effect = 1.002,
sigma_year_effect = 0.3099,

sigma.N = 0.05,

unit_effect_returns = c(
-0.8561,0.05145,-0.3006,-1.744,-1.794),

year_effect_returns = c(
-3.237,-3.707,-3.47,-3.596,-3.843,
-3.624,-3.827,-3.968,-3.834,-3.913,
-4.079,-4.043,-4.441,-4.908,-5.025,
-4.639,-4.722,-4.511,-4.904,-4.769,
-4.376,-4.384,-4.463,-4.66,-4.671,
-5.001,-4.454,-4.709,-4.9,-4.923,
-4.447,-4.98,-4.903,-4.7,-4.762,
-4.693,-4.922,-4.935,-4.8,-5.156,
-5.695,-5.501,-5.69,-4.709,-4.656,
-5.179,-4.864,-5.037,-5.345,-5.368,
-5.112,-5.304),

zt = 0.9727)

```

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