# Dynamics of the Atlantic salmon (*Salmo salar* L.) population of the River Foyle, Ireland.

by

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A thesis submitted for the degree of Doctor of Philosophy.

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March 2004

# Acknowledgements

I wish to acknowledge the help and support of the Chief Executive, Mr. Derick Anderson, the staff and the Board of the Loughs Agency who provided the majority funding for this study. I also wish to recognise the financial support of the Marine Institute and in particular Dr. Niall O'Maoileidigh. Thanks are also due to the rest of Agency's Scientific Advisors Dr. Walter Crozier, Dr. Philip McGinnity and Dr. Gersham Kennedy for their many helpful comments. I wish also to acknowledge the help and support I received from many people at Glasgow University and in particular my supervisor Dr. Colin Adams. Thanks are also due to Prof. Felicity Huntingford Mirjam Geurts, Sanne de Boer and the staff at the University Field Station.

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# Summary

This study examines the dynamics of the Atlantic salmon (*Salmo* salar L.) population of the Foyle catchment in Ireland, through the analysis of long-term datasets and extensive field data. In Chapter 1 the current conservation status of the salmon is discussed with particular reference to the Foyle. A number of methods used in studying the juvenile and adult life-stages are reviewed.

Chapter 2 considers the interaction between commercial netting and recreational sport angling and the effect of total combined exploitation on an independent measure of population size (redd counts) using a 49 year dataset. While recognising that commercial netting had a relatively small negative impact on recreational sport angling, the evidence suggests that year class strength is the principal modulator of variation in commercial catches, sport angling catches and spawning escapement.

Chapter 3 examines the role of density-dependence in the Foyle salmon population. A Ricker density-dependent model showed that spawning adult population size significantly predicted variation in the resultant filial generation, however, a significant amount of variation (ca. 68%) remained unexplained. Environmental factors were significant in explaining some of the remaining variance and these influences were linked to specific life stages. This finding strongly suggests population bottlenecks in the complex life cycle of this species, during which specific environmental factors may have an impact, that they do not have during other periods. It was concluded that these life stage specific environmental effects are likely to contribute to the stochastic variation in population size resulting from

the application of traditional stock-recruitment models and that the identification and quantification of these effects should allow improved model accuracy.

Chapter 4 investigates the effect of marine climatic conditions in the North Atlantic on the abundance of returning migrant Atlantic salmon, using a 126 year dataset of commercial catches and an index of climate in the northern hemisphere, the North Atlantic Oscillation (NAOI). The NAOI when below 0.151 explained a significant proportion of variation in five year running mean catches of migrant Atlantic salmon returning to the River Foyle. This indicates that a significant proportion of the variance in population size in the past was the result of variability in conditions in the marine environment. However, when the NAOI was above 0.151, this relationship uncoupled. Models of climate change indicate that the NAOI is likely to increase significantly with time. If these models are correct, this study would lead to the conclusion that a decoupling of broad scale climate effects on salmon population size will become the norm. Data presented here suggest two consequences of this: that the value of the NAOI as a predictive tool for forecasting adult salmon population size will be limited; and that the median population size will become lower in the future.

Chapter 5 tests the capacity of local instream and broadscale catchment characteristics to predict 0+ salmon abundance within the Foyle area. Using a combination of local site specific data, from 350 sites chosen for annual electrofishing surveys of 0+ salmonids, and semi-quantitative morphometric information and broadscale catchment characteristics derived from Ordnance and Geological survey maps, two models were constructed. Model 1 used data for all available sites i.e. including those where 0+ salmon were absent, while model 2 used only those sites where salmon were present. Both of these models were

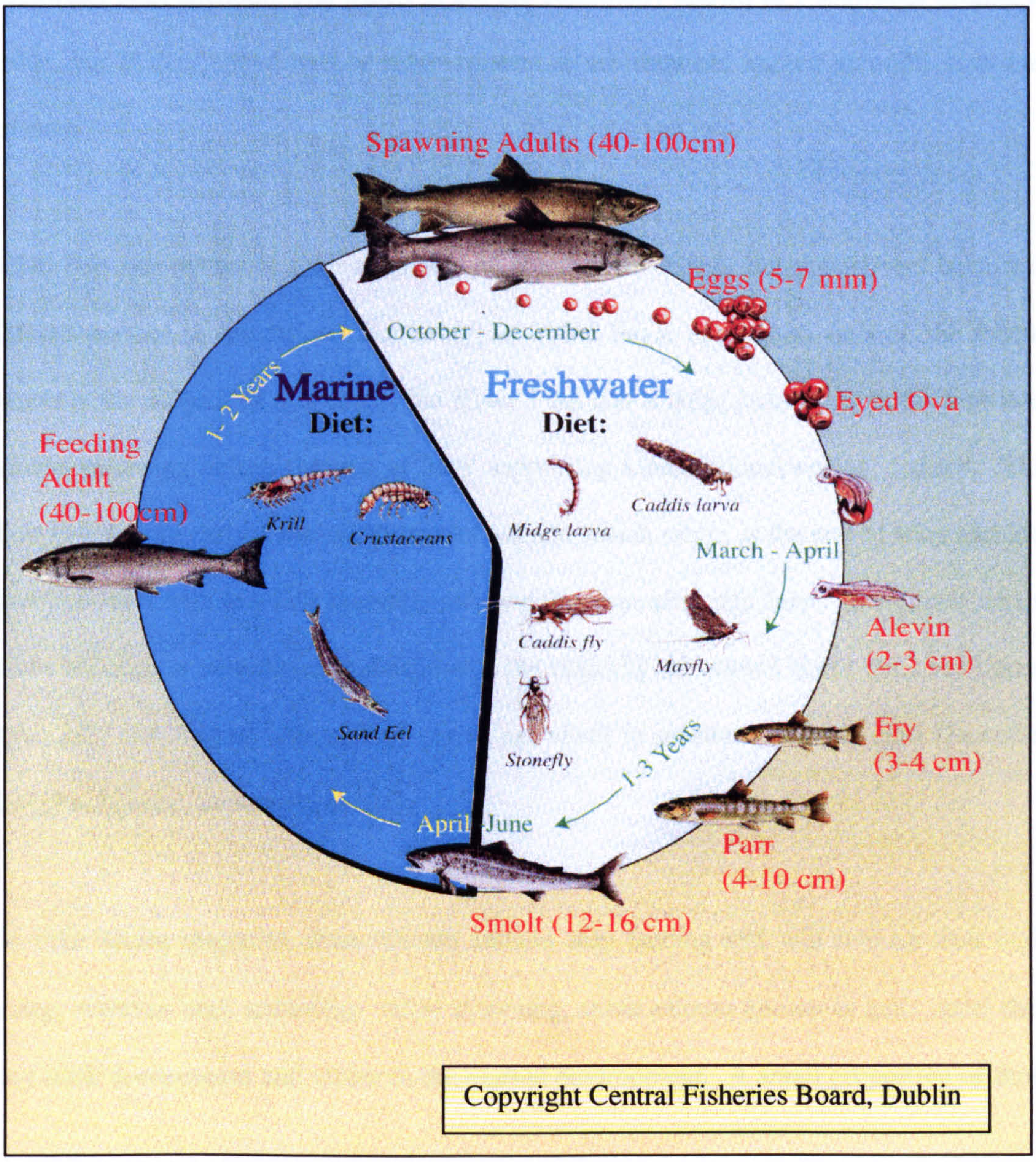
significant predictors of juvenile abundance using site-specific variables. However, both models were improved significantly by the inclusion of wider broadscale catchment characteristics (model 1 $r^2$=30%; model 2 $r^2$=43%). When tested against an independent data set using paired t-tests neither model differed significantly from the actual catch of salmon, although both had relatively high standard error rates (84%±13 and 56%±15.2 respectively). It was concluded that site-specific habitat characteristics were significant predictors of juvenile abundance, but with the inclusion of broadscale catchment characteristics the models predictive power was greatly increased. This chapter also highlighted the potential detrimental impact of increasing urbanisation on the salmon stocks of the Foyle area.

# Chapter 1. General Introduction

## *1.1 Atlantic salmon (Salmo salar L.) Life-cycle*

The Atlantic salmon (*Salmo salar* L.) is an anadromous species of fish whose range extends on both sides of the North Atlantic ocean. Its life cycle is outlined in Figure 1.1 and has been described by various authors (Jones, 1959; Shearer, 1992; Hansen, L.P. & Quinn, T.P., 1998; Klemetsen *et al.,* 2003).

**Figure 1.1** Life cycle of the Atlantic salmon (*Salmo salar* L.)



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The adults spawn in gravel areas of streams and rivers between November and January each year. The females lay eggs in shallow depressions (called redds) which are then fertilised by the male fish and covered by gravel. The eggs remain buried until February/March when they hatch and the alevins migrate through the gravel into the river. The juvenile fish will remain in the river for at least one year, but more usually two in Ireland (Crozier & Kennedy, 1997) before going to sea as smolts. A number of marine feeding areas have been identified, namely the Faroes, Iceland and the west coast of Greenland. The fish will remain at sea for one or more winters. Those that return to freshwater after spending one winter at sea are commonly known as 1 seawinter salmon or grilse, but if they spend two or more winters at sea they are known as multi-seawinter salmon.

Adult fish may return to their natal stream at any time of year but most rivers have well defined periods of migration. For example, in the Foyle catchment, Ireland, the system which is the subject of this study, the River Finn has a large number of multi-seawinter salmon returning before the end of May supporting a recreational spring fishery. This river also has an early 1 sea-winter run of salmon which return at the end of May and into June and July, with few fish generally entering the river after mid July. In contrast, on the River Mourne, a neighbouring catchment, the majority of salmon enter the river during June, July and August with salmon returning, albeit in smaller numbers, until December (Loughs Agency, unpublished data).

On their return migration from the sea salmon stop feeding and will live on their body energy reserves until spawning. After spawning, some salmon known as kelts make their way back downstream and return to the marine environment. A small proportion of these may return to spawn in subsequent years. In Scottish Rivers previous spawners contributed between 5-10% of spawning stock on average, with >95% of these being female (Shearer, 1992).

### *1.2 Conservation Status of Atlantic Salmon*

In much of its range throughout the north Atlantic, the Atlantic salmon has declined, both in terms of catches and actual population size, since the 1960's and early 1970's (Parrish *et al.*, 1998; Jonsson *et al.*, 2003).

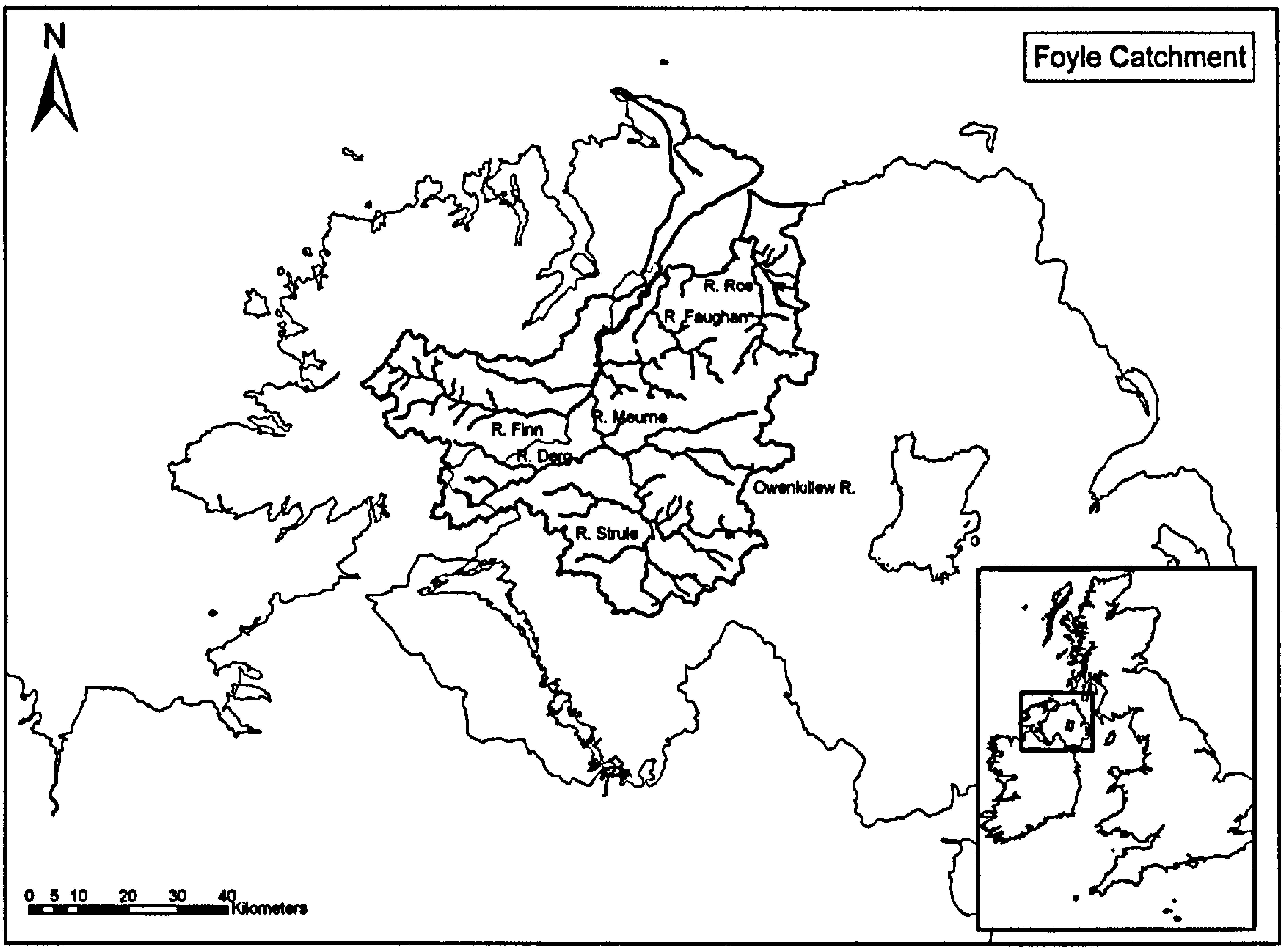
In some parts of its range, such as the Bay of Fundy in Canada, and the Gulf of Maine in the USA, stocks have been listed as endangered (Chase, 2003). Commercial harvesting of salmon has been stopped in many areas of North America as a conservation measure, with the exception of some subsistence catches (O'Connell *et al.*, 1992; Dempson, *et al.*, 2001b) and in some regions sport angling has been closed, or is subject to closure during the normal sport angling season (Dempson, *et al.*, 2001a).

In a European context, commercial fisheries for salmon have been tightly regulated for many years. Despite this however, southern stocks, in contrast to stocks in more northerly latitudes, still appear to be declining (Parrish *et al.*, 1998). In order to protect current strong stocks of salmon the European Union (EU), under the *Directive on the conservation of natural and semi-natural habitats and of wild fauna and flora (92/43 EEC)(Habitats Directive 1992)* (Anon., 1992a), have designated many rivers throughout Europe for extra protection as Special Areas of Conservation (SAC). Within the Foyle system the Rivers Finn, Mourne and Derg have been afforded such designation.

### 1.3 Physical Description of the Foyle System

The Foyle catchment is situated in the north west of the island of Ireland (Figure 1.2) and is approximately 4,500km$^2$ in area. The catchment encompasses two international jurisdictions; those of the Republic of Ireland and Northern Ireland, which is part of the United Kingdom.

**Figure 1.2** Location Map of the Foyle catchment



### 1.4 Salmon Management in the Foyle System

The Loughs Agency is a statutory cross-border body, which aims to provide sustainable social, economic and environmental benefits through the effective conservation, management, promotion and development of the fisheries and marine resources of the Foyle and Carlingford Areas. The Loughs Agency and its predessor the Foyle Fisheries

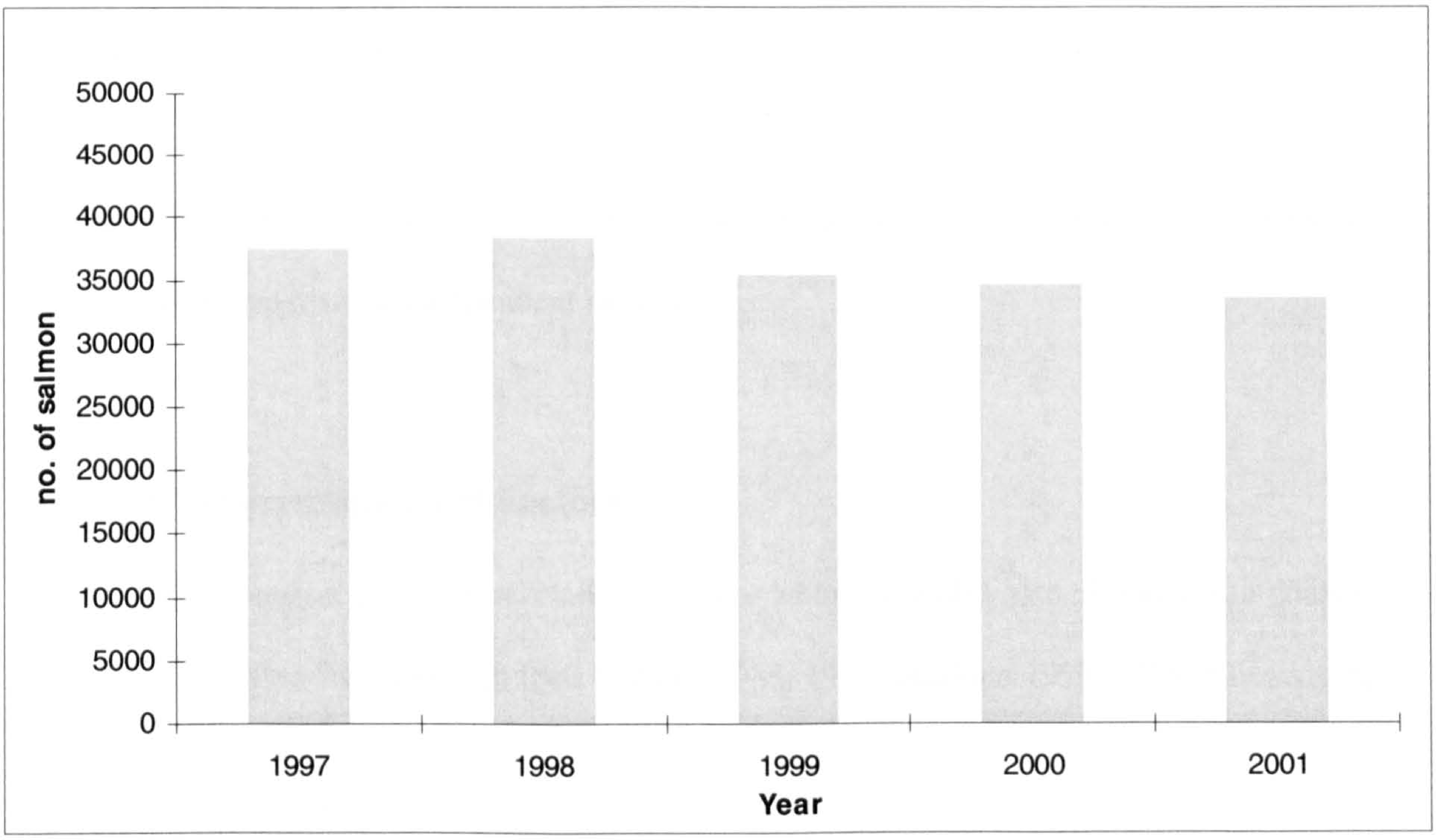
Commission have collated a long data set of catch figures and population estimates. These data indicate that salmon abundance peaked in the late 1960's and subsequently declined until the early to mid 1970's.

As a result of these declines, a report was commissioned (Elson & Tuomi, 1975) which examined the salmon resource of the catchment and made recommendations as to how best manage the stock. Following this report the Foyle Fisheries Commission set up a real time management regime, which, with some refinements, is still in operation. Management of the fishery is predicated on meeting in-season population size targets for the returning migrant population above a control site on the River Mourne at Sion Mills measured using a Logie resistivity 2100C fish counter in-addition to a visual count of salmon crossing the weir outwith the counting channels. The first of these targets is the 30th June, that is, a little over two weeks into the commercial fishing season, which starts on the 15th June. This first target is set at 2,600 returning migrant salmon (or in periods of low water on the next flood). If the target is not achieved, depending on the size of the flood, as measured at a local Department of the Environment gauging station, both commercial fishing and recreational angling will be curtailed by either 24 or 48 hours respectively. Similarly by the 10th July if a target of 4,200 returning migrant salmon has not passed Sion Mills, the fishing may again be closed for either 24 or 48 hours. However, the fishing may only be closed for a maximum of 48 hours in any one season. If by the 24th July the number of salmon above Sion Mills exceeds 8,000, an extension of 96 hours fishing will be granted to commercial netsmen. Finally, if by the 20th September less than 7,000 salmon have crossed the weir at Sion Mills recreational angling will be curtailed by 10 days.

This end of season target of 8,000 salmon is based on the amount of nursery habitat available upstream and its juvenile carrying capacity. Target egg deposition levels are set for three juvenile habitat grades i.e. Grade 1 = 10 eggs $m^{-2}$; Grade 2 = 5 eggs $m^{-2}$ and Grade 3 = 2.5 eggs $m^{-2}$. This combination of habitat quality and quantity assessment equates to approximately 6,500 salmon (male and female) spawning at the end of each season within the catchment. Twenty five percent is added to this figure to allow for sport angling, poaching and natural mortality bringing the final target population size to 8,000. These targets are monitored using data from fish counters and adjusted for a visual assessment of the numbers of fish which cross the weir without passing through the counting channels. The counting site is just above the tidal limit.

Since this management regime's introduction, stocks have increased and there is currently a five-year running average commercial catch of salmon between 30,000-35,000 (Figure 1.3).

**Figure 1.3** Five year running average of commercial salmon catches in the Foyle area 1993-2001.



## *1.5 Population Regulation*

### 1.5.1 General

As with all animals, mechanisms operate to limit the size of individual populations. Alisauskas and Arnold (1994) in a study on American coots (*Fulica americana*) found that a linear relationship explained a high proportion of variance ($r^2=0.54$; $p<0.001$) between an estimate of population size (numbers shot each year) and the number of temporary ponds available for breeding on the prairies the preceeding summer. Models such as these allow predictions of spatial patterns of habitat use and give an insight into mechanisms operating on the population, thus enabling predictions to be made which support population and habitat management. This is particularly important in species of high conservation value or which are exploited.

Many studies have attempted to identify these mechanisms for Atlantic salmon but most of these have been limited by the use of short-term data sets or small sample size. One general aim of this study is to use long-term data sets on population size and exploitation to attempt to identify mechanisms and principal controlling factors influencing population size in the Foyle catchment.

Population regulatory mechanisms are frequently divided into two main types: density-dependent and density-independent factors.

### 1.5.2 Density-Dependent Factors

Density-dependent causes of mortality are those whose mortality rate changes with density e.g. competition for space and food (Elliott, 1985, 1994; Haldane 1953; 1956; Kennedy &

Strange, 1982; Kennedy & Strange, 1986a; Kennedy & Strange, 1986b). Both negative and positive effects of population density on survival have been shown for fish. Chapman (1986) in a review of historical catch records of Pacific salmon species (*Oncorhynchus tshawytscha, O. kisutch, O. nerka, O. keta, O. mykiss*) from the Columbia River in North America, identified reduced aboriginal fishing pressure, around 1800, as the cause of subsequent decreasing runs. The author postulated that this was due to excessive escapement of salmon up river and density-dependent mortality occurring in the freshwater habitat. Heavy fishing pressure after 1850 probably increased runs initially, but led to a sharp subsequent reduction as stocks were over exploited. Ross and Almeida (1986) showed that silver hakes (*Merluccius bilinearis*) were subject to density-dependent control mechanisms, with lower growth rates at high stock densities.

Negative density-dependence may also be known as concurrent (Solomon, 1949), compensatory (Neave, 1953) or regulatory (Nicholson, 1957) and simply means that as a population increases, the probability of individual survival decreases (Elliott, 2001). However, population increases may not always act negatively on a species. For example, among goldfinches (*Carduelis carduelis*), birds in flocks of greater than eight consumed up to 2.3 times more seeds per unit time than singletons, thus increasing their survivorship potential (Glück, 1986).

### 1.5.2 Density-Independent Factors

Density-independent causes of mortality are those exerting a similar effect on mortality, independent of the population density. In general, density-independent factors are mainly thought to be environmental in origin, with events such as drought, temperature, storms etc. being some of the main factors identified. Among Peregrine falcons (*Falco pergrinus*) in Australia, for example, breeding success was negatively related to rainfall with the effect that the total production of the population was lowest in the wettest years, mainly as a result of direct rainfall and runoff flooding nest sites (Olsen & Olsen, 1989).

In reality there is no sharp delineation between density-dependent and density-independent factors. For instance, deaths arising from biological causes, such as disease, parasitism, malnutrition and predation, which may be considered to be initially density-independent will usually become more frequent as density increases. Density-dependent factors can act together or can compensate for each other. For example Jenkins *et al.* (1963), in studying the effects of shooting on Red Grouse (*Lagopus lagopus scoticus*), found that losses at 30% of the post-breeding numbers were entirely compensated for by reduced natural loss, causing no depletion in breeding stocks (Jenkins *et al.*, 1963).

## *1.6 Population Regulation in Salmonids*

### 1.6.1 Population Regulation Processes in the Juvenile Freshwater Phase

There is evidence that density-dependent mortality in the juvenile stages can be a control of population size in salmonids (Ricker, 1954; Kennedy & Strange, 1982; Kennedy & Strange 1986a; Kennedy & Strange 1986b; Egglishaw & Shackley, 1985; Milner, *et al*, 2003; Ruggerone & Rogers, 2003; Dumas & Prouzet, 2003). Gee *et al.* (1978), in a study on the River Wye in Wales, found that maximum smolt production, which they equated to juvenile salmon surviving to 2 years of age, was attained at a fry density of $0.75m^{-2}$ on the 1st of June. Above and below this stocking density, production decreased following a dome-shaped production curve. Gardiner and Shackley (1991), in a study of a six-year data set of salmon fry to their first and second autumns on the Shelligan Burn in Perthshire, Scotland, found that production followed a similar dome shaped Ricker model. However, in a review of the stock-recruitment models of the time, Solomon (1985) suggested that, while Gee *et al.* (1978) were justified in claiming that the curve was indeed dome-shaped, migration could explain differences in the densities of fry in subsequent generations. In contrast, Gardiner and Shackley (1991) suggested on the basis of work carried out by Egglishaw and Shackley (1977) that density related losses in their study were most likely losses of younger parr dying in the stream. Elliott (1994, 1989,1985), showed in his long-term studies on two small streams (Black Brows Beck and Wilfin Beck) in England, that density-dependent mortality is not necessarily always the most significant population regulating effect in salmonid populations. Black Brows Beck (holding a migratory brown trout [*Salmo trutta* L.] population) always had higher juvenile densities than Wilfin Beck (containing resident brown trout) and was regulated by density-dependent survival in the early stages of the life cycle. There was no evidence for this, however, in Wilfin Beck, where simple proportionate survival occurred with fairly constant loss rates. Survival was reduced in both populations by summer droughts and also by spates in Wilfin Beck. Black Brows Beck trout were always larger than those of Wilfin Beck of similar age, mainly due to fry size at the start of the growth season. Variations in water temperature were chiefly responsible for differences in growth between year classes within each population. Food intake was not a limiting factor except in the first winter of the life cycle and for adults over 3 years old in Wilfin Beck. Variation in individual size was inversely density-dependent in Black Brows Beck and decreased with age in Wilfin Beck, these changes being due to natural (stabilising) selection. There was also strong evidence for genotypic differences between the populations.

Results from studies such as these indicate a natural inter-system variation in the relative dominance of density-dependent and density-independent causes of mortality in population size control. This leads to the conclusion that, in order to study the dynamics of individual systems for the purposes of population modelling, an assumption of a generic relationship applied across systems is likely to be inadequate.

### 1.6.2 Population Regulation Processes in the Marine Phase

Density-dependent mortality as a result of competition between Asian Pink salmon (*Oncorhynchus gorbuscha*) and Alaskan sockeye salmon (*O. nerka*) has been shown to occur at sea (Ruggerone *et al.*, 2003). It is not known if density-dependent mortality occurs with Atlantic salmon in the marine phase. As major differences exist between the Pacific and Atlantic species it is impossible to apply conclusions based on Pacific salmon studies to Atlantic salmon. For example, Pacific salmon are the dominant fish species at sea while Atlantic salmon constitutes a very small percentage of the total marine biomass.

What is known, is that mortality in Atlantic salmon, once smolts leave the river, varies depending both on the river location and stock component (Anon., 2003c). Rod catches from the River Spey, Scotland indicate that migrating spring stocks of multi-seawinter salmon are falling (Anon., 1998a). However, numbers of grilse and summer migrating multi-seawinter salmon remain more stable. The mechanisms behind Atlantic salmon survival at sea are not clearly understood. However, North American studies have observed good correlations between sea survival and ocean temperatures and the projected amount of winter habitat available to their stocks of fish at sea (Amiro, 1998).

In many Canadian rivers, juvenile production is thought to be optimal. Despite reductions in the commercial fishing effort and periodic increases in the number of salmon returning to spawn, however, anticipated increases in subsequent recruitment of spawning stock have failed to materialise (Dempson *et al.*, 2001; Amiro, 1998; Ritter, 1997). This trend is also shown by the decline in survival rates of hatchery-released smolts, which are independent of the freshwater habitat. Amiro (1998) suggests that an increase in predator numbers, particularly harp seals (*Phoca groenlandica*), may explain the deficit between actual and expected returns. In a European context, data from the River Bush in N. Ireland indicate that salmon survival at sea outwith direct anthropogenic influences has decreased from an average of 30% pre 1998 (Crozier & Kennedy, 2001) to 10% in 2002 (Crozier *et al.*, 2003d). These declines are also occurring at a time when smolt production from the freshwater phase is decreasing (Kennedy & Crozier, 1991). Changes in the productivity of Pacific salmon species have also been documented and linked to climatic conditions (Peterman *et al.*, 2003) and some studies have developed predictive models to track these changes (Logerwell *et al.*, 2003). Chapter 4 investigates large-scale climatic effects on marine survival and the potential impact of global warming on future trends in salmon abundance in the Foyle system.

With the decline in salmon abundance, attention has tended to focus on the commercial netting sector and in particular on interceptory mixed-stock fisheries, such as those off Greenland, the Faroes, the Northumberland coast of England, Northern Ireland and the Republic of Ireland. In 2002 the Greenland fishery was allocated a total allowable catch of between 20 and 55 tonnes whilst for the long line Faroese fishery no quota was set for 2002 or the 2003 season (Anon., 2003d). In Northern Ireland, within the Fisheries Conservancy Board area, a buy-out scheme for the commercial netsmen was introduced in

2002. The drift net fishery limits off the Republic of Ireland's coast have been reduced from 12 to 6 miles and fishing is only allowed between 6am and 6pm Monday to Thursday (Anon., 1997a). In 1998 the drift nets caught 58% of the total run of fish back to the Irish coast (O'Maoileidigh, pers. comm.). In 2001 carcass tagging was introduced on an all Island of Ireland basis, whereby each individual salmon, whether caught commercially or by sport angling, must carry a tag with a unique identifying number. This has greatly reduced large scale poaching and with the introduction of quotas (Republic of Ireland) to both commercial fisheries and sport angling, further restricts exploitation on stocks.

Within the Foyle system, in line with these restrictions, the commercial fishing season has been reduced from March to September in the 1960's and 1970's to a six-week period during June and July at present. In addition, there are only four days' fishing allowed each week for both the drift and draft nets. The drift nets have also had the permissable fishing hours, reduced to 12 hours per day.

### 1.6.3 2 Population Regulation Processes in the Adult Freshwater Phase

On return to fresh water, the main source of mortality in adult salmon is exploitation. It is estimated that estuarine or in-river draft nets catch approx. 28% to 30% of fish entering the system on the River Erne. This figure is regarded as a national average rate of exploitation for catchments where draft net exploitation occurs in Ireland (O'Maoileidigh, pers. comm.). Angling exploitation can range from 9.7% to 20.6% (Anon., 1992b) for grilse and 35-40% for stocks of Irish multi-seawinter salmon (O'Maoileidigh, pers. comm.). Although, in the Foyle system, sport angling exploitation has reached 50% for grilse (Elson & Tuomi, 1975). As a response to high exploitation levels, the Environment

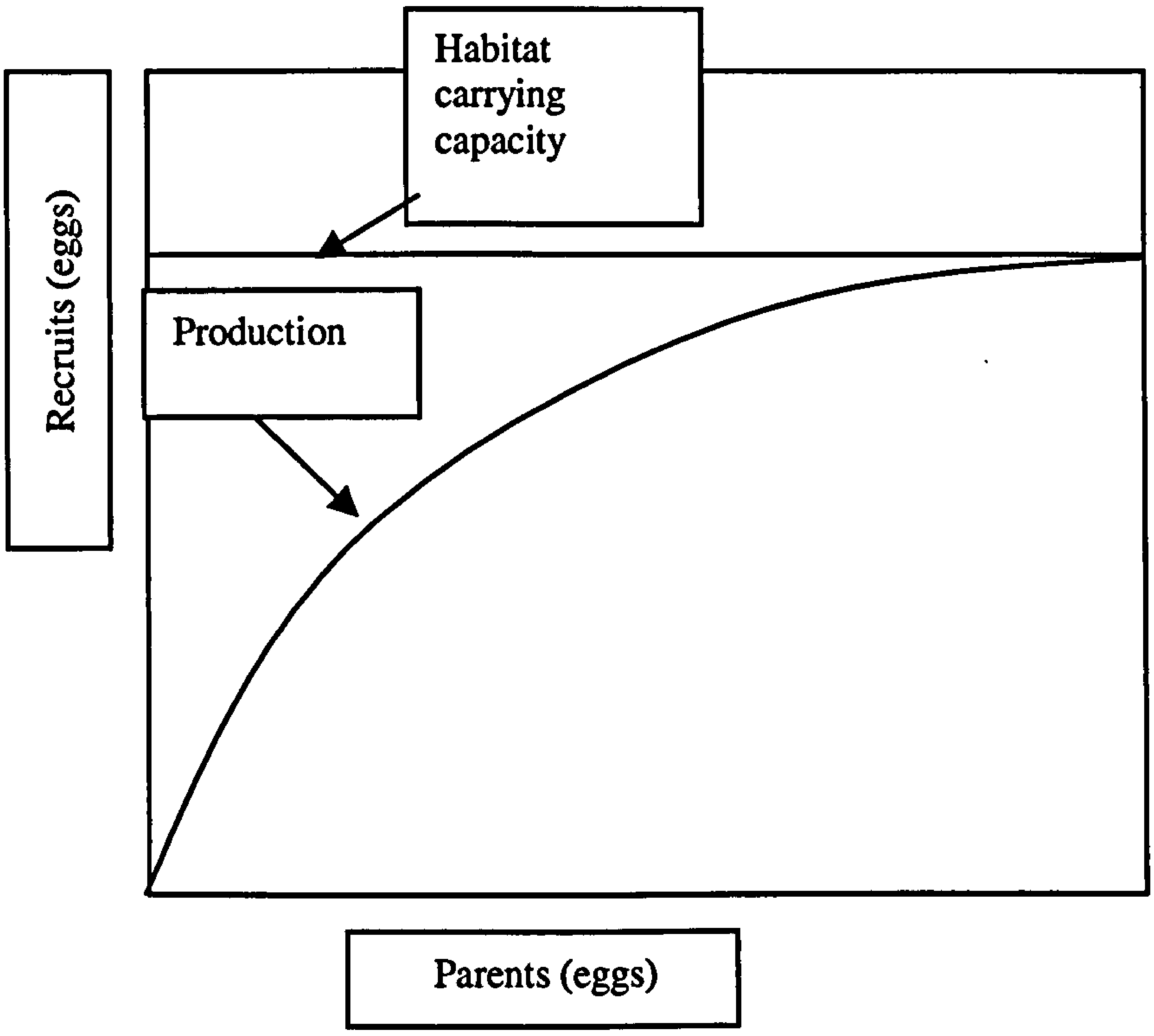
Agency in England and Wales has introduced mandatory catch and release of salmon by anglers before 14th June (Anon., 1999). Many rivers in Scotland, while not having legislation to enforce similar controls, actively encourage anglers to return spring fish (Atlantic Salmon Trust 1998). In the Fisheries Conservancy Board area of jurisdiction in N Ireland, catch and release must be practiced on salmon prior to the 1st June.

In this study (Chapter 2) I attempt to examine the role of competing exploitation methods on population size and also the interaction between these capture methods.

### 1.6.4 Mathematical Models

Several mathematical models have been proposed to describe density-dependence (Ricker, 1954; Beverton and Holt, 1957). When these models are applied to fish populations, they are usually termed stock-recruitment models as they describe the relationship between the number of recruits (*R*) to the population and the parent stock (*S*) of fish. A hypothetical stock-recruitment relationship is outlined in Figure 1.4.

**Figure 1.4** Hypothetical stock-recruitment model.



These models can be used to examine how changes in, for example, fishing mortality, affect yield. For these models to be effective it is necessary to know the production of parent stock over a wide range of recruit numbers. The parent stock can be expressed as numbers of adults, biomass or egg production (Elliott, 1994; Chadwick, 1985; Elson & Tuomi 1975).

A number of stock-recruitment models are shown in Figure 1.5 and their derived equations outlined in Table 1.1. Model 0 shows a population that is increasing without any restriction. While in model 1, as egg density increases, a dome-shaped curve emerges. Thus the initial effect of increasing population size is density-dependence operating in a positive manner. However, as the population reaches maximum return it starts to decline as negative density-dependent effects become dominant. In model 2, the relationship reaches an asymptote as egg density increases (Elliott, 1994), but thereafter remains stable.

**Figure 1.5** Three common stock-recruitment curves: 0=Linear; 1= Ricker (1954); 2=Beverton & Holt (1957).

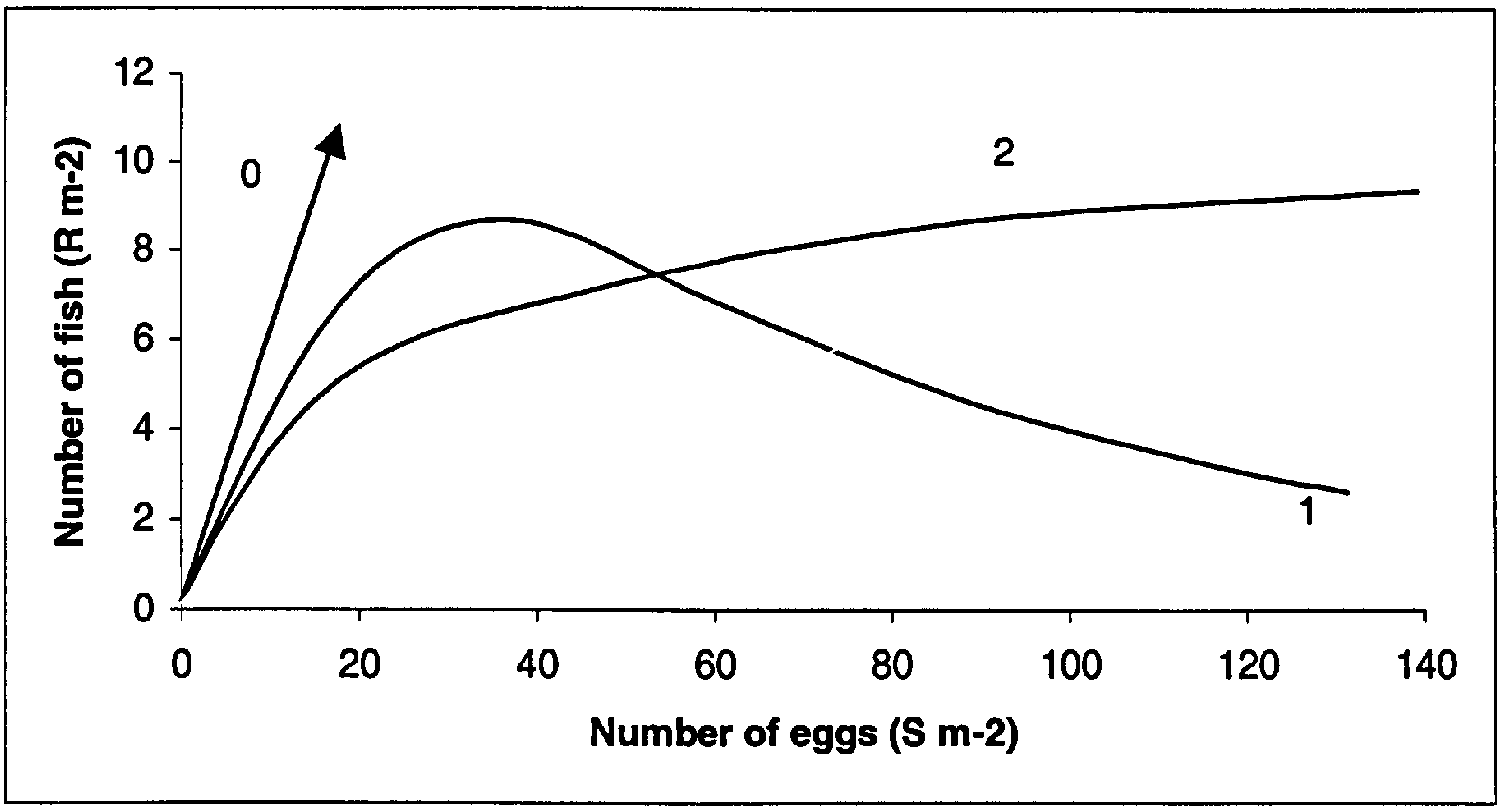


**Table 1.1** Stock-recruitment equations for Beverton & Holt (1957) and Ricker (1954) models where $R$ represents the *recruits* and $S$ the *parental stock.*

| | **Proportionate survival $(R/S)$** | | **Mortality rate [ln $(S/R)$]** | | **Replacement abundance ($S^*$ for $R=S$)** | **Key fisheries references** |
|---|---|---|---|---|---|---|
| **Equation** | **Function** | **Relationship with $S$ (all decreasing monotonic)** | **Function** | **Relationship with $S$ (all increasing monotonic)** | | |
| (1)$R=aS\exp(-bS)$ | $a/\exp(bS)$ | Concave upward | $bS-\ln a$ | Linear | $(\ln a)/b$ | Ricker (1954) |
| (2)$R=aS/(1+bS)$ | $a/(1+bS)$ | Concave upward | $\ln(1+bS)-\ln a$ | Convex upward | $(a-1)/b$ | Beverton & Holt (1957) |

In most studies on salmonids to date, model 1, the Ricker (1954) stock-recruitment model, has been found to be the most applicable. Elliott (1994) found that this model gave the best fit to his data for sea-trout (*Salmo trutta* L.). Elson and Tuomi (1975), Gee *et al.,* (1978), Gardiner and Shackley (1991), Kennedy and Crozier (1993) fitted Ricker curves to their data on Atlantic salmon and many North American studies of Pacific salmon have utilised this model (Ricker, 1954, 1989). Buck and Hay (1984), however, found that a Beverton and Holt curve fitted their population data on Atlantic salmon, with survivor density increasing to an asymptote (curve 2, Figure 1.5) rather than following a dome-shaped curve.

All of these population models incorporate a number of inherent problems. Regression methods for estimating the parameters of these simple stock-recruitment equations generally lead to upward bias in assessments of productivity at low spawning stock sizes, and underestimates of the spawning stock that would produce maximum average surplus for harvest (Hilborn, 1997; Myers, *et al.*, 1995; Myers, *et al.*, 1994). Bias is due to errors-in-variables effects when spawning stock measurement has been inaccurate (Elson & Tuomi, 1975). It can also be difficult to generate data points for an over-abundance of parent stock or egg deposition (Kennedy & Crozier, 1991; Smith & Walters 1981), and therefore it may be difficult to determine if the data set takes the form of a dome-shaped Ricker curve or a flat-topped Beverton and Holt curve. There is also bias in time-series effects when harvest rates have been relatively stable so that recruitment anomalies result in subsequent change in spawning abundance (Walters & Ludwig 1981). There are no satisfactory correction methods for these biases, since they involve fundamental loss of information about average response, especially at low spawning abundance (Myers 1997; Schnute & Kronlund 1996.). Beyond such bias problems, there is also uncertainty as to how to measure the reliability of parameter estimates and define policy prescriptions especially in circumstances where the recruitment relationship may be non-stationary due to persistent directional ecological or environmental changes (Amiro, 1998; Ritter, 1997). As a result of these uncertainties, Walters (1981) recommended that regular probing experiments be carried out on models and that in general results from these types of model be treated with caution.

In this study, Chapter 3 attempts to address the role of density-dependence in determining adult returns and also the potential for environmental factors in influencing these returns, with the use of long term data available for the Foyle system.

## *1.7 Modelling of Juvenile Salmonids*

Density-dependent mortality is known to occur in juvenile salmonids (Elliott, 1994, 1989, 1985; Kennedy & Crozier 1991). This may be as a result of competition for resources and territoriality (Heggenes & Saltveit, 1990; Titus & Mosegaard,1992; Kennedy 1983; Kennedy & Strange 1981; Marshall, 1995). The measurement and classification of instream habitat areas is therefore critical in estimating the potential carrying capacity of streams and thereby deriving data for stock-recruitment relationships. In assessing instream habitat, some studies have used wetted area of the river accessible to fish (Elson & Tuomi, 1975) while others have quantified the available nursery area (Inoue *et al.*, 1997; FHR, 1991). In these latter studies attempts were made to quantify the river area, based on its morphology, and then relate the stock (as determined from electrofishing surveys) of each habitat reach or type to give an overall estimate of productivity. However, these models quantify actual productivity at any given time and make no attempt to predict fish numbers. In dynamic riverine environments, change, whether natural or man-induced, is always occurring, with concomitant effects on fish and other animal assemblages. Therefore, predictive models have been developed in an attempt to monitor and explain these impacts (Wright *et al.*, 1989; Whitehead, 1992; Milner *et al.* 1998). The *River Invertebrate Prediction And Classification System* (RIVPACS), developed by the Institute of Freshwater Ecology, is one such example (Wright *et al.*, 1989; 1996). It encompasses a computer model built from a database holding biological and physical data collected from over 8,000 near pristine sampling sites in England and Wales. Sites were selected to cover as wide a range of environmental variables as possible, with the exclusion of unrepresentative polluted sites. Invertebrates were collected from a wide variety of habitat types at each sampling site and sampling was repeated over different seasons. Samples were collected, sorted and identified to provide species presence/absence, abundance and diversity estimates for each site. The *Biological Monitoring Working Party* (BMWP) score and A*verage Score Per Taxa* (ASPT) were computed for each site as a measure of the richness and diversity of the invertebrate community. Using the TWINSPAN technique (Hill, 1979), RIVPACS invertebrate data were analysed to provide a system for the classification of river sites on the basis of the distribution of invertebrate fauna present. In addition to the invertebrate samples collected, a large number of physico-chemical characteristics were estimated or measured, such as channel width, gradient, flow velocity and substrate type. On the basis of (a) these environmental observations, (b) the observed invertebrate population data and (c) the TWINSPAN classifications, a predictive technique based on multiple discriminant analysis (MDA) was developed. This is used to predict the probability of occurrence of individual taxa, and BMWP and ASPT scores from values of physico-chemical variables alone. At a river site of interest, RIVPACS can be used to predict target values of BMWP, ASPT and the expected composition of invertebrate fauna on the basis of a limited number of observations/measurements of physico-chemical parameters. Comparison of observed and predicted scores using results from the direct sampling of invertebrates at the site and RIVPACS predictions (based on physico-chemical parameters at the site), gives a measure of any loss of biological quality due to environmental stress.

Another model which uses a similar approach to RIVPACS is HABSCORE (Milner *et al.*, 1993). This is a fisheries management model and is designed specifically for salmonids. Direct sampling by electrofishing is conducted at a number of sites, alongside measurements and observations of physical habitat features, such as:

- Conductivity (μS $cm^{-1}$)
- Cover
- Flow type
- Substrate

- Mean width
- Mean depth

These are combined with data from maps, including:

- Gradient (m $km^{-1}$)
- Catchment area ($km^{-2}$)
- Altitude (m OD)
- Distance to mouth (km)

The model is calibrated on the basis of these observed data and can then generate estimates of fish populations from measurements of physical habitat variables alone. As with RIVPACS, a comparison of model predictions with population estimates made by electrofishing may be used to detect anomalies in observed ecological data which may be attributable to impacting factors. The models were produced from a data set of 224 sites on 11 catchments throughout Wales. The sites were screened carefully to avoid any which were subject to identifiable environmental impacts. Models were developed for four categories of salmonid: trout 0+, trout >0+, salmon 0+ and salmon >0+. The predicted densities represent an index of site expectation. This is not to be confused with carrying capacity which may be rarely reached in sites receiving only natural recruitment, because density-independent effects keep the population at lower levels (Milner *et al.*, 1998). The likelihood that many sites used in habitat modelling have population densities below their carrying capacity is one of the principal constraints on the performance of habitat models.

Chapter 5 attempts to build upon existing models by using site specific and broadscale catchment characteristics to investigate their relative importance in determining Atlantic salmon fry numbers within the Foyle system.

# Chapter 2. Competing modes of exploitation and their effects on spawning success in Atlantic salmon (*Salmo salar* L.) in the Foyle Catchment, Ireland

## *2.1 Introduction*

Conflict arising between resource user groups exists in many differing situations around the world today (Quizilbash, 2001). With regard to animal populations, this can be an argument over resource allocation or concerns over the conservation status of the exploited population (Claytor, 2000). Many of these have in the past been pushed to the edge of extinction {blue whale (*Baleanoptera musculus*) (Clark, 1973)} or over it {Great Auk (*Pinguinus (Alca) impennis*); Passenger Pigeon (*Ectopistes migratorius*) (Newton, 1998)} through over-exploitation. It is the balancing of these arguments by managers which science strives to inform.

Amongst the animal species deemed to be of high conservation value and named in statutory instruments requiring protection, the Atlantic salmon (*Salmo* salar L.) is unique in the degree to which it is exploited across its range in Europe. Although designated as a species whose conservation requires the establishment of Special Areas of Conservation (SACs) under the European Union Habitats and Species Directive (Anon., 1992), exploitation through commercial high seas netting, coastal and estuarine netting and sport angling is high. For example, the global harvest of this species in 1999 was ca 2,200 tonnes, the vast majority of this catch being made in North Eastern Atlantic waters (ca 2,000t) (Anon., 2001).

There have been growing efforts to reduce the impact of interceptory commercial fishing on stocks so that individual populations which may be over exploited are protected (Anon., 1996). As well as conflict between exploitation and conservation there is also scope for conflict between the multiple users of a resource. There is a generally accepted belief that commercial interception netting of migrant salmon returning to the natal streams, by trapping, gill or seine netting in coastal waters, estuaries and rivers, reduces the potential for exploitation by riverine sport angling (Johnston, 2002; Anon., 2003b). Based on the presumption that the greatest economic value is derived from sport angling, there has been considerable pressure to close, or at least reduce, commercial fisheries to allow sport angling to flourish (Whitehead, 2003; Anon., 2003). As a result, interception net and trapping fisheries have been reduced considerably over the last 20 years or so (Anon. 2001). However, despite this widely held belief, there is a paucity of data which shows significant benefits deriving for recreational angling from the closure of a commercial fishery (Jensen *et al.* 1999) and what data do exist may not provide a clear cut picture. For example, Bowker *et al.* (1998) found some evidence to suggest that diminished estuarine netting exploitation had a beneficial impact on salmon angling success on the River Usk, England, while with the closure of the marine Norwegian drift net fishery Jensen *et al* (1999) concluded that this contributed to increased catches of grilse and smaller 2 sea-winter salmon in freshwater in Norway. McKinnell & Karlstrom (1999) and Romakkaniemi *et al.* (2003) found some evidence that reduction in commercial exploitation contributed to increased stocks in many Baltic rivers. A buyout of commercial netting stations in Iceland by angling interests was shown to have positive effects on the sport angling catches in the local rivers (Einarsson & Gudbergsson, 2003). In contrast however, Shearer (1992) found that following net closures, rod catches did not necessarily improve on the Aberdeenshire Dee in Scotland.

This chapter examines the potential conflict between the requirements of management for protection of this species and exploitation (commercial net and trap fisheries and recreational angling for sport) in one population, the Foyle system. Within this catchment area there has been long-term monitoring of catches of salmon from all forms of exploitation, in addition to the collection of an exploitation-independent measure of population size.

Specifically two hypotheses are tested:

1. Commercial netting and trapping of Atlantic salmon in the Foyle system significantly impacts upon sport angling, by depressing angling catches.

2. Total exploitation (from all sources) has a significant impact upon the ultimate size of the spawning population.

## *2.2 Materials and Methods*

### 2.2.1 Study Area

The River Foyle system drains ca 4,500km$^2$ of the northwest of the island of Ireland (Figure 1.1), discharging northwards through the Lough Foyle estuary into the northern Atlantic Ocean.

This system supports a significant population of Atlantic salmon for which there is a long history of commercial net and trap fishing and sport angling stretching back over several hundred years (Foyle Fisheries Commission, 1953; Elson and Tuomi, 1975; Foyle

Fisheries Commission, 1996). Total catch in the Foyle area in 1999 was approximately 60 tonnes, representing 11% of the total catch for the island of Ireland (Anon. 2000).

The Loughs Agency of the Foyle, Carlingford and Irish Lights Commission is responsible for the protection, conservation, improvement and development of the salmonid fisheries within the Foyle and Carlingford catchment areas. As part of these responsibilities, the agency and its predecessor the Foyle Fisheries Commission, have collected data on catches and population size on an annual basis since 1952. These data are described below.

### 2.2.2 Exploitation catch data

#### Drift nets

Drift nets are gill nets deployed close to the water surface in the sea lough and up to 12 miles out from the north coast. At present a maximum of 112 licences can be issued annually. In the past, the numbers issued ranged from 39 in 1952 to a peak of 139 in 1962. The nets utilised at sea are 1500 m long, with a depth of 45 meshs and a mesh size of 63 mm knot-to-knot. Those used in the Lough are 900 m long but otherwise of similar dimensions. The drift-netting season currently commences on 15th June and ends on 31st July and nets are fished for four days each week between the hours of 6 am and 6 pm. Licence holders have been required to make annual returns as a condition of the grant of a licence since 1952.

#### Draft Nets

Draft nets are seine nets which are deployed in-river in the main River Foyle and the River Roe at defined netting stations. They are currently used from 15th June to 31st July, for four days each week over the 24-hour period. Tidal movement and water conditions limit their use. On average 50 licences were issued annually over the last 5 years (Wysner, pers. comm.) However, this has fluctuated between a maximum of 524 in 1959 to a minimum of 43 in 1999. There is a statutory requirement for the users of these nets to make catch returns.

### Stake Nets

Stake netting was a commercial fishery run by the Foyle Fisheries Commission between 1952 and 1988. A barrier net stretched at right angles to the shoreline led to a box trap where the salmon were caught. They were fished in the lower River Foyle and the estuary. These were temporary fishing stations, which were installed annually. The Foyle Fisheries Commission collected annual catch records for the duration of this fishery.

### Bag Nets

Bag nets were of a similar construction to the stake nets but were left in place permanently. One licence was issued annually to be fished in the Lough Foyle estuary, although in 1988 an additional licence was issued. Data for these nets are available from 1964 to 1990 when operations ceased. The Foyle Fisheries Commission collected annual catch records for the full period of their use.

### Catch Effort of Commercial Net and Trap Fisheries

The effort employed in all commercial fisheries in the Foyle system has changed over the years. The season is considerably shorter now than previously (currently 15 June to 31 July, cf. March to September in 1952) and the number of hours where fishing is allowed each week has been reduced. There has also been a shift in emphasis between the fisheries, with the closure of some methods of exploitation and a shift in the relative importance of draft and drift net use. Over the years the actual returns from the commercial nets have been good and would appear to tie in with field staff observations (R. Wysner, pers. comm.). For the purposes of analysis presented here no correction has been made for changes in fishing effort as it is the absolute number of fish removed that is most likely to impact upon recreational catches and population size.

### Sport Angling Exploitation Returns

It is a statutory requirement that sport angling licence holders make an annual return of their catch in the Foyle and Carlingford areas. The returns from recreational angling are, in general, low (Small, 1991); this is certainly also true of the Foyle system. Thus, the sport angling catch return cannot be regarded as an accurate measure of total exploitation by recreational anglers. Therefore, to estimate the actual sport angling catches a correction factor was applied to the data (Small, 1991). This correction allowed for the non-reporting of fish caught when anglers made a return and is as follows ((0.3/(percentage return of licences/100))+0.7) this produces a raising factor which is applied to the actual number of fish declared.

## 2.2.3 Salmon population size estimates

### Redd Counts

Since 1952 the Foyle Fisheries Commission (and subsequently the Loughs Agency) field staff have made counts of redds (salmon nests) during and immediately following the salmon spawning period in approximately 260 zones within the catchment annually. This is only a partial count of all redds within the Foyle catchment. The accuracy of counting can be subject to environmental conditions such as high water flows, which can obstruct proper assessment through poor visibility, or flattening of redds making them difficult to see. However, as a method of long-term population monitoring, it is recognised as a useful tool (Elson & Tuomi, 1975; Hay, 1984; Isaak, *et al.*, 2003). Highly accurate data on spawning population size for one year, 1999 showed that counts at these 260 sites represented 11% of the total redds based on the percentage of spawning areas available to fish within the Foyle catchment calculated from instream habitat surveys (Loughs Agency, unpublished data). Thus to estimate the absolute number of redds each year in the Foyle catchment, a correction factor of 9.1 was applied to redd counts from all years. Each redd was taken as representing a single female salmon (Hay, 1987). In order to therefore get an overall population size an additional 40% was added to incorporate the male conponent (Wray, pers. comm.).

### 2.2.4 Analysis

Catches and redd count estimates were assembled by calender year. The data were analysed using the statistical software package SPSS 10.0. Pearson's correlations and linear regressions were used to look for trends in relationships between exploitation and subsequent spawning population size. To avoid Type 1 statistical errors, the acceptable probability when using multiple tests was corrected using a Bonferroni correction. For clarity the corrected probability equivalents are presented here where appropriate.

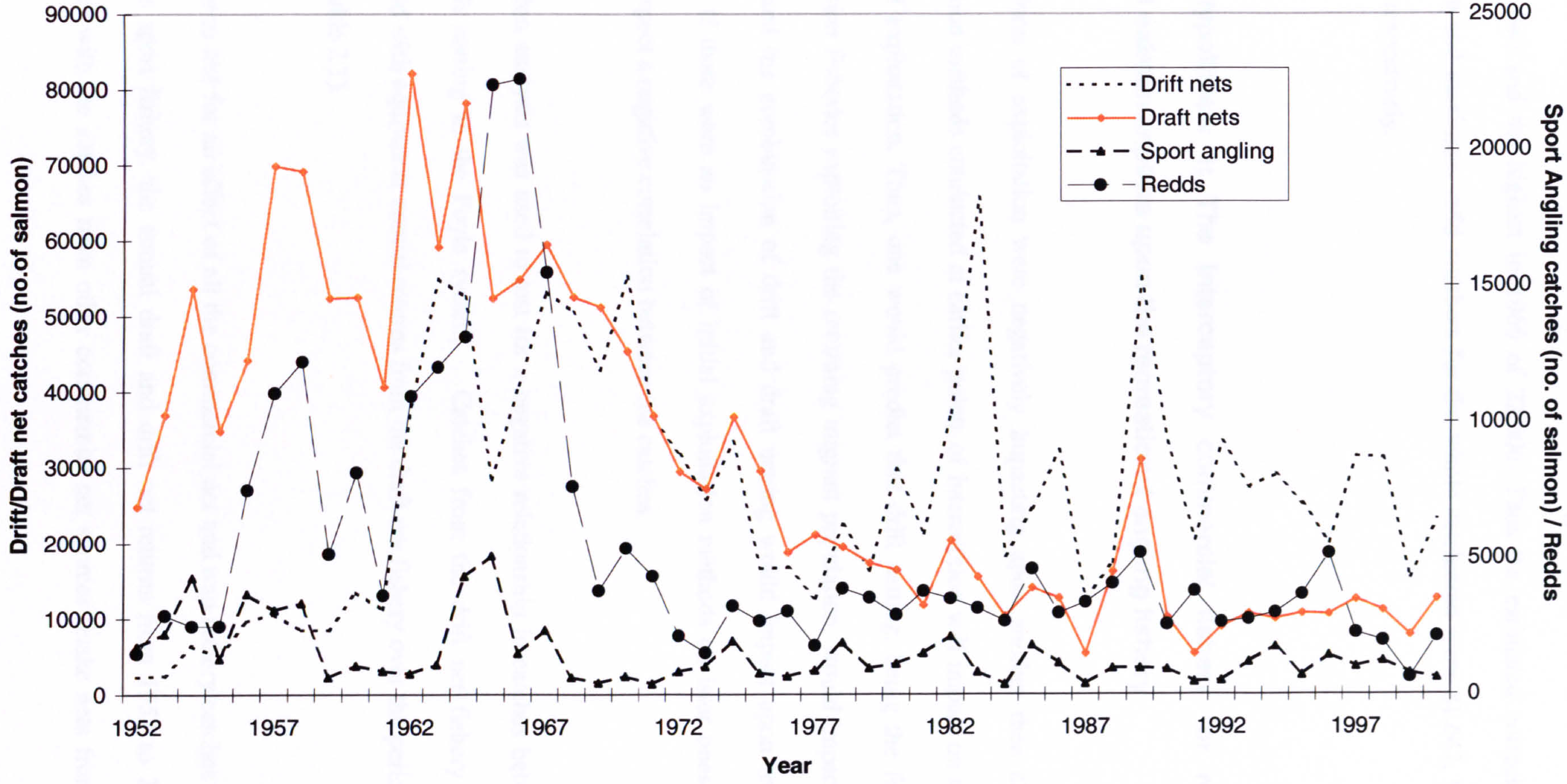
## *2.3 Results*

Analysis of the 49-year dataset showed considerable variation in the yield from the various forms of exploitation.

The 49-year mean catch in the drift nets was 26,753 individual salmon but varied from 2,347 in 1952 to 65,654 in 1983 (Figure 2.1). Reported draft net catches were generally lower than those of drift net catches after the mid 1970's, but the draft nets have a higher overall mean catch of 30,928. The highest reported annual catch was also by draft net,being 82,106 in 1962 while the lowest was 5,434 in 1991. The Foyle Fisheries Commission stake nets operated from 1952 to 1988, during which period they comprised on average 13% of the total commercial netting and trapping catches. The bag nets, which were operated between 1964 and 1990, averaged 1% of the total commercial net and trap catches.

The sport angling fishery reported yield over the 49 year run averaged 1,443 with a range of 379 (1984) to 5,100 (1965).

**Figure 2.1** Drift, Draft net catches, uncorrected Sport Angling catches & uncorrected redd counts in the Foyle area 1952-2000



Actual redd (nest) counts between 1952 and 2000 averaged 5,383 with the lowest count in 1999 of 640 and the highest in 1966 of 22,606. Thus the estimated corrected mean, minimum and maximum redd numbers for the whole catchment were 81,647, 9,607 and 342,858 respectively.

### 2.3.5 Hypothesis 1: The interceptory commercial fishery for returning migrant salmon impacts upon the recreational angling fishery

If one form of exploitation were negatively impacting upon another then clearly the exploitation methods conducted at earlier points of interception will impact on successive forms of exploitation. Thus, one would predict that drift netting, being the first of the interception fisheries exploiting the returning migrant population, would impact on draft netting and the combination of drift and draft netting would impact upon recreational angling. If there were an impact of initial exploitation methods on later ones then one would expect a negative correlation between the catches.

Correlation analysis was used to test for a negative relationship in catches between drift and draft netting in the Foyle system. Catches from the drift net fishery were not correlated with equivalent annual returns from the draft net fishery over the period 1952 to 2000 (Table 2.1).

Similarly to test for an effect of all the commercial net and trap fishery catches combined upon the sport fishery, the annual draft and drift net returns from 1952 to 2000 were combined with the catches from other commercial net sources (stake nets from 1952 to

1988 and bag nets from 1964 to 1990), to produce a measure of the total catches from all commercial fisheries over the 49 year period. These did not predict sport fishery catches (Table 2.1).

When the commercial (drift, draft, stake and bag net fishery catches) were compared individually with the sport fishery catches, no significant correlation relationships with the sport fishery returns were found (Table 2.1).

**Table 2.1** Correlations of commercial fishing catches and corrected sport angling catches..

| | | Drift net catch | Bag net catch | Stake net catch | Draft net catch | Total Commercial catch | Sport Angling catch (corrected) |
|---|---|---|---|---|---|---|---|
| Drift net catch | Pearson Correlation | 1.000 | .410* | .089 | .181 | .596** | -.034 |
| | Sig. (2-tailed) | . | .034 | .602 | .212 | .000 | .815 |
| | N | 49 | 27 | 37 | 49 | 49 | 49 |
| Bag net catch | Pearson Correlation | | 1.000 | .667** | .715** | .684** | -.116 |
| | Sig. (2-tailed) | | . | .000 | .000 | .000 | .565 |
| | N | | 27 | 25 | 27 | 27 | 27 |
| Stake net catch | Pearson Correlation | | | 1.000 | .923** | .775** | -.078 |
| | Sig. (2-tailed) | | | . | .000 | .000 | .648 |
| | N | | | 37 | 37 | 37 | 37 |
| Draft net catch | Pearson Correlation | | | | 1.000 | .895** | -.260 |
| | Sig. (2-tailed) | | | | . | .000 | .071 |
| | N | | | | 49 | 49 | 49 |
| Total Commercial catch | Pearson Correlation | | | | | 1.000 | -.255 |
| | Sig. (2-tailed) | | | | | . | .077 |
| | N | | | | | 49 | 49 |
| Sport Angling catch (corrected) | Pearson Correlation | | | | | | 1.000 |
| | Sig. (2-tailed) | | | | | | . |
| | N | | | | | | 49 |

*. Correlation is significant at the 0.05 level (2-tailed).

**. Correlation is significant at the 0.01 level (2-tailed).

### 2.3.6 Hypothesis 2: Exploitation negatively impacts upon spawning population size

To test the hypothesis that exploitation is having a significant negative impact on that population, a measure of the annual exploitation was derived by combining the catch returns from all fisheries (commercial netting, trapping and sport angling). This was used to test for a relationship with an indicator of breeding population size that was independent of exploitation; the number of redds (nests).

Annual corrected redd counts were significantly but positively correlated with the total annual catch returns of all forms of commercial exploitation combined (Table 2.2). The total annual catch (including the sport fishery) also significantly predicted corrected annual redd counts in a linear regression model ($F_{1,47}$=43.85; $p<0.001$; $r^2$=0.47 - Figure 2.2). Looking at each exploitation method for which there are a full 49 years data, salmon population size, as determined by corrected redd counts, was also significantly and positively correlated with drift netting, draft netting, stake nets, bag nets and total catch (Table 2.2). When corrected using Bonferroni drift netting and bag netting were not significant.

One possible explanation for the significant positive relationships between different exploitation types, and between exploitation and population size, is that years with relatively large returning migrant populations are swamping any negative impacts. To explore this further, the same relationships between exploitation rates with population size were examined, at high and low population levels, separately.

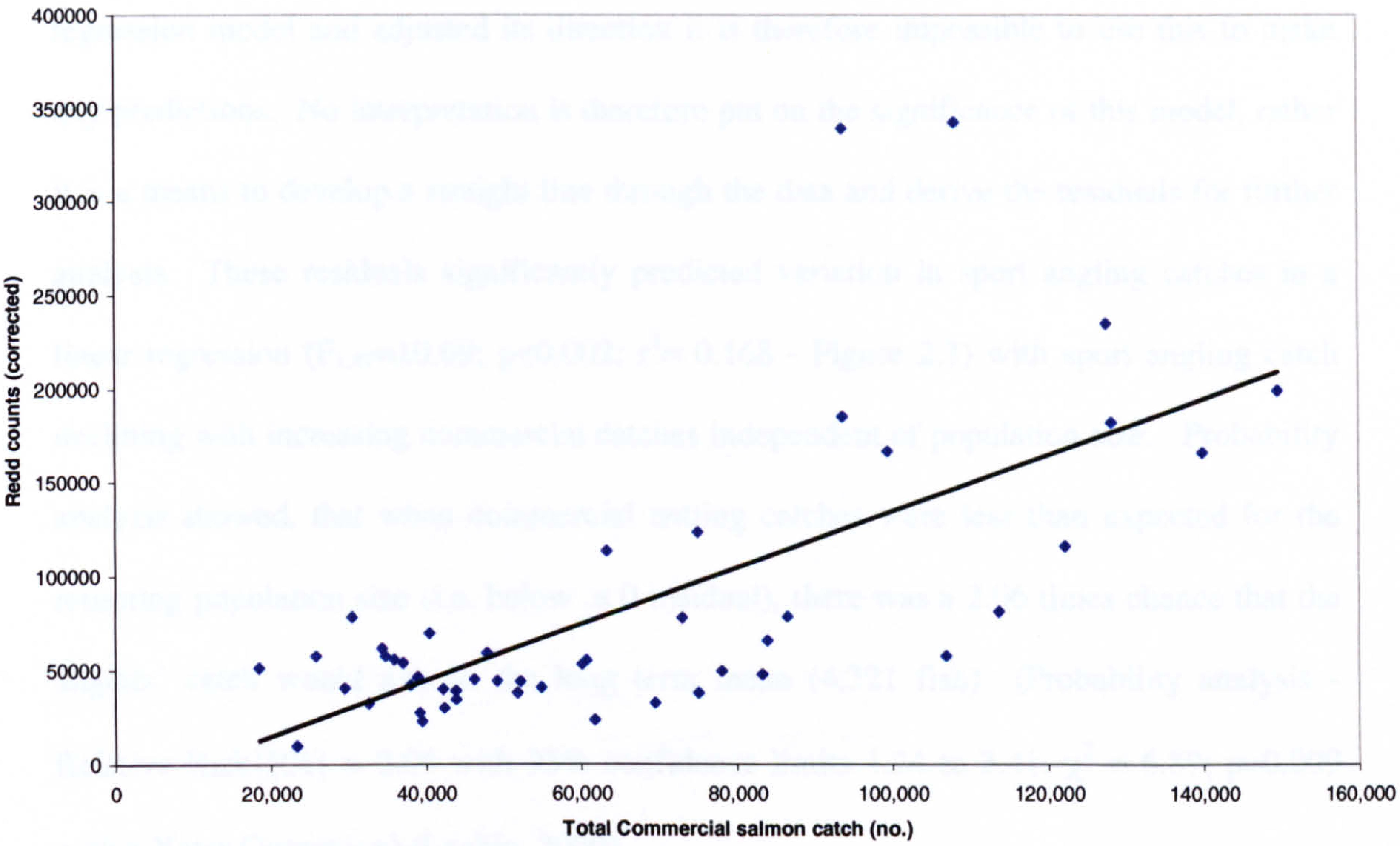
**Table 2.2** Correlations of commercial fishing catches, corrected sport angling catches, corrected total catch, corrected redd counts and corrected total population.

| | | Drift net catch | Bag net catch | Stake net catch | Draft net catch | Total Commercial catch | Sport Angling catch (corrected) | Total catch | Redd counts (corrected) | Total population (corrected) |
|---|---|---|---|---|---|---|---|---|---|---|
| Drift net catch | Pearson Correlation | 1.000 | .410* | .089 | .181 | .596** | -.034 | .605** | .298* | .421** |
| | Sig. (2-tailed) | . | .034 | .602 | .212 | .000 | .815 | .000 | .038 | .003 |
| | N | 49 | 27 | 37 | 49 | 49 | 49 | 49 | 49 | 49 |
| Bag net catch | Pearson Correlation | | 1.000 | .667** | .715** | .684** | -.116 | .677** | .469* | .574** |
| | Sig. (2-tailed) | | . | .000 | .000 | .000 | .565 | .000 | .014 | .002 |
| | N | | 27 | 25 | 27 | 27 | 27 | 27 | 27 | 27 |
| Stake net catch | Pearson Correlation | | | 1.000 | .923** | .775** | -.078 | .769** | .493** | .618** |
| | Sig. (2-tailed) | | | . | .000 | .000 | .648 | .000 | .002 | .000 |
| | N | | | 37 | 37 | 37 | 37 | 37 | 37 | 37 |
| Draft net catch | Pearson Correlation | | | | 1.000 | .895** | -.260 | .889** | .683** | .800** |
| | Sig. (2-tailed) | | | | . | .000 | .071 | .000 | .000 | .000 |
| | N | | | | | 49 | 49 | 49 | 49 | 49 |
| Total Commercial catch | Pearson Correlation | | | | | 1.000 | -.255 | .997** | .678** | .832** |
| | Sig. (2-tailed) | | | | | . | .077 | .000 | .000 | .000 |
| | N | | | | | 49 | 49 | 49 | 49 | 49 |
| Sport Angling catch (corrected) | Pearson Correlation | | | | | | 1.000 | -.173 | .051 | -.020 |
| | Sig. (2-tailed) | | | | | | . | .233 | .728 | .894 |
| | N | | | | | | 49 | 49 | 49 | 49 |
| Total catch (corrected) | Pearson Correlation | | | | | | | 1.000 | .695** | .846** |
| | Sig. (2-tailed) | | | | | | | . | .000 | .000 |
| | N | | | | | | | 49 | 49 | 49 |
| Redd counts (corrected) | Pearson Correlation | | | | | | | | 1.000 | .971** |
| | Sig. (2-tailed) | | | | | | | | . | .000 |
| | N | | | | | | | | 49 | 49 |
| Total population (corrected) | Pearson Correlation | | | | | | | | | 1.000 |
| | Sig. (2-tailed) | | | | | | | | | . |
| | N | | | | | | | | | 49 |

*. Correlation is significant at the 0.05 level (2-tailed).

**. Correlation is significant at the 0.01 level (2-tailed).

**Figure 2.2** Regression of total annual catch of salmon in the Foyle area and corrected redd counts.



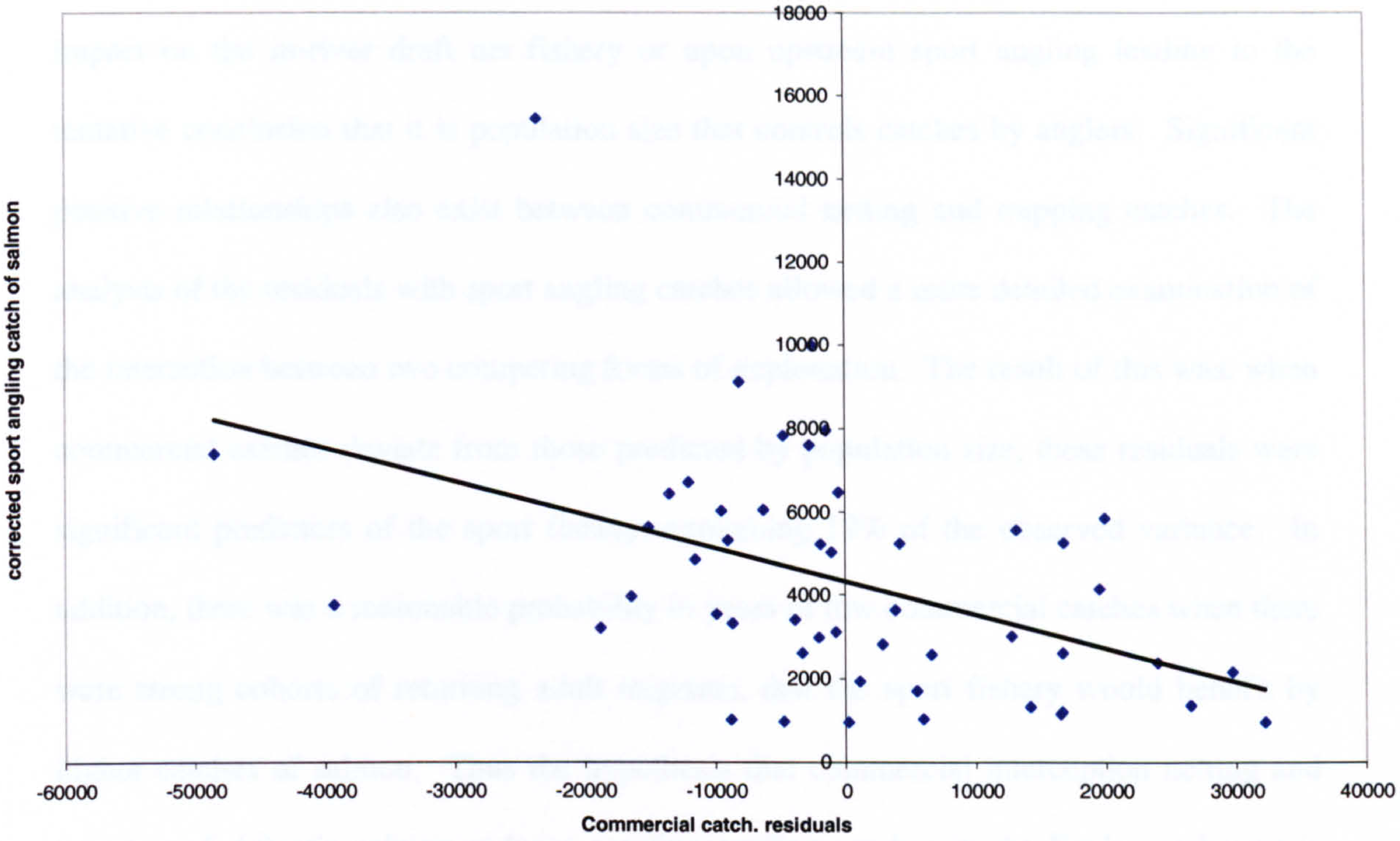
In years when the sport fishing catch returns were below the mean for the period 1952 to 2000, there was no significant correlation between these catches and any of the commercial catches or corrected redd counts. In years when sport-angling catches were high, i.e. exceeding the long-term mean, no significant correlations were found.

When the corrected redd counts were less or greater than the mean of the 49-year period (81,647) there was no significant correlation with total commercial catch or sport angling or all catches combined.

To derive a measure of commercial netting catches which was free from the effects of population size, commercial catch was linearly regressed on total population size and the residuals extracted. As auto-correlation artificially increased the significance of the regression model and adjusted its direction it is therefore impossible to use this to make any predictions. No interpretation is therefore put on the significance of this model, rather it is a means to develop a straight line through the data and derive the residuals for further analysis. These residuals significantly predicted variation in sport angling catches in a linear regression ($F_{1,47}=10.69$; $p<0.002$; $r^2= 0.168$ - Figure 2.3) with sport angling catch declining with increasing commercial catches independent of population size. Probability analysis showed, that when commercial netting catches were less than expected for the returning population size (i.e. below a 0 residual), there was a 2.06 times chance that the anglers' catch would exceed the long term mean (4,321 fish) (Probability analysis - Relative Risk{RR} = 2.06 with 95% confidence limits 1.24 to 3.41: $\chi^2 = 6.89$; p=0.009 with a Yates Correction) (Lachin, 2000).

A similar approach was used to look in greater detail at the impact of total catch (including commercial and sport fishing) on the subsequent spawning population or redd counts. The total catch was regressed against total population size and the residuals extracted. These were then plotted against the redd counts. The relationship was not significant).

**Figure 2.3** Commercial catch residuals regressed on corrected sport angling catch.



## 2.4 Discussion

It is axiomatic that, were there no coastal and tidal water interceptory fisheries for migrant salmon returning to the Foyle catchment, there would be more salmon available for exploitation by sport anglers. As the commercial fisheries intercept the returning population before it becomes available to the sport anglers it is commonly perceived that such an impact does exist and results in depressed angling catches. The availability of high quality data from a very long-term monitoring programme has enabled a pragmatic approach to assessment of the impact of one exploitation method on another. Thus, here the hypothesis was tested that commercial netting and trapping catches in the Foyle system have a significant negative impact upon recreational angling catches. Analysis of the data would suggest that this does not occur in the Foyle area. Data from the drift net fishery, the first interception exploitation of returning migrants, shows no evidence of negative impact on the in-river draft net fishery or upon upstream sport angling leading to the tentative conclusion that it is population size that controls catches by anglers. Significant positive relationships also exist between commercial netting and trapping catches. The analysis of the residuals with sport angling catches allowed a more detailed examination of the interaction between two competing forms of exploitation. The result of this was, when commercial catches deviate from those predicted by population size, these residuals were significant predictors of the sport fishery, explaining 19% of the observed variance. In addition, there was a reasonable probability in years of low commercial catches when there were strong cohorts of returning adult migrants, that the sport fishery would benefit by higher catches of salmon. Thus the hypothesis that commercial interception netting and trapping of Atlantic salmon reduces sporting angling catches in the Foyle catchment is supported by the data. However, this should be qualified, as the amount of variance explained by the commercial netting returns is relatively low leaving 83% of variance unexplained.

The second hypothesis that exploitation from all sources (sport angling and commercial netting and trapping) significantly impact upon the ultimate size of the spawning population, is not supported by the data. As all exploitation of salmon takes place prior to the spawning period in any year, logically, exploitation rates in any one year may be expected to depress the spawning population size. Strong positive correlations between annual exploitation and ultimate spawning population size over a 49 year period superficially suggests that, at the levels of exploitation practiced in this catchment, exploitation does not have a significant impact on spawning population size. Further analysis of the data did not highlight any significant effects. and the most likely explanation for positive correlations between exploitation and spawning escapement is that year class strength is the determining factor.

Other studies have observed that many animal populations can sustain very high levels of exploitation without any apparent adverse impact on overall population size, e.g. Laurian *et al.* (2000) in their work on moose populations in Quebec, Canada found that the species could sustain high levels of exploitation and had a certain adaptability which allowed it to maintain high productivity despite the intensive harvesting. Also, Bosch *et al.* (2000) who looked at the effects of culling on gulls and Frederiksen *et al.* (2001) who examined culling and its impact on cormorants both found that the populations could sustain very high levels of harvesting.

With regard to Foyle salmon one explanation for these findings is that years of high abundance are masking the effects of exploitation in years of lower numbers of returning salmon. To test this years of low sport angling catch and spawning population size (redd counts) were examined. No significant negative relationships were found, this would suggest that even in years of lower abundance, the commercial net fisheries were still not having a negative effect on rod catches and that total exploitation (commercial and sporting) rates were not having a negative effect on subsequent spawning escapement.

Thus it is concluded that in the Foyle catchment, although commercial fishing has been shown to have a significant effect on sport angling catches there still remains 83% of variance unexplained, therefore the year class strength of returning migrants is the principal modulator of variation in the commercial net catches, sport angling catches and escapement, and that this effect over-rides any potential conflicting impacts of one exploitation type on another and of total exploitation on spawning population size. It is unclear how these findings might apply to populations elsewhere. The Foyle system supports a highly abundant population compared with other European Atlantic salmon rivers (five year running average commercial catch between 30,000-35,000 salmon) so it may be able to support multiple exploitation methods that other systems may not. In addition the strong management structure in the Foyle system has resulted in tight control of exploitation in years of low abundance so protecting stocks during these periods. Thus, in the Foyle area, the question regarding cessation of netting may be regarded largely not as a conservation issue, but rather one of resource allocation.

# Chapter 3. Life stage specific, stochastic environmental effects, overlay density-dependent filial cohort strength effects in an Atlantic salmon (*Salmo salar* L.) population from Ireland

## *3.1 Introduction*

All animal populations are subject to controlling mechanisms, which limit their size. However the relative roles of density-dependent and density-independent factors in determining ultimate population size have long been controversial (Elliott, 1985, 1994; Sinclair, 1989; Newton, 1998). It is now widely accepted that for populations to persist over time, at least one negative density dependent mechanism (where the probability of survivorship decreases as population size increases) must operate (Elliott, 2001). In nature, ultimate population size is unlikely to be determined solely by negative density dependent regulatory mechanisms but is most likely to be the result of complex interaction between density dependent and density independent factors (reviews in Newton, 1998; Elliott 2001). Elliott (1994) in long-term studies on trout (*Salmo trutta* L.) showed that both density-dependent and density-independent factors contributed to ultimate population size but their relative effects varied between habitats. Studies such as those by Whittaker (1971) and Newton and Marquiss (1986) have demonstrated that populations may be regulated by density independent factors in stable environments but under less favourable conditions, density independent factors can assume much greater importance.

The evidence from a significant number of studies over a broad range of species is that factors modulating animal population size do not operate at all times over the life-cycle but may act disproportionately at one or more ontogenetic or life-cycle events (Achord *et al.*, 2003; Langeland & Pedersen, 2000). In red grouse (*Lagopus lagopus*) for example, negative density dependance has been shown to occur during autumn when territoriality is at its height (Jenkins, 1963). Similarly in oystercatchers (*Haematopus ostralegus*) density dependent regulation occurred during spring when densities increased during the breeding period (Harris, 1970).

In a review of the literature Sinclair (1989) showed evidence of "population bottlenecks", i.e. life stage specific, negative density-dependent effects, on population size in a number of populations of insects, fish, birds and mammals. Identification of life-stage-specific density independent effects on ultimate population size has received less attention than density dependent factors, possibly because by their nature they are more difficult to detect. However, some studies have shown such effects. In a study of an Australian peregrine falcon (*Falco peregrinus*) population, Olsen & Olsen (1989) demonstrated environmental (flooding) density-independent effects during nesting on egg mortality. In sea-trout (*Salmo trutta*) in Black Brows Beck, Elliott and co-workers (Elliott *et al.* 1997) showed significantly depressed population size as the result of summer droughts and the effect was life-stage dependent while a number of studies have highlighted the potential for exogenous environmental impacts on a number of salmonid species (Einum *et al.*, 2003; Hill *et al.*, 2003; Azumaya & Ishida, 2004).

As a result of the existance of distinct phase shifts in the life cycle and periods during which abundance changes, the Atlantic salmon (*Salmo salar*) is a species with the potential for population bottlenecks (Elliott 1994; 2001).

Here for the Foyle system, Ireland, several long-term datasets on returning migrant Atlantic salmon population size are combined with environmental datasets to test two hypotheses related to the control of ultimate population size. It is postulated that this population is primarily regulated by density dependent factors, but that environmentally induced effects operating at specific life stages, which affect the magnitude of change in population size during population bottlenecks, overlie this effect.

## *3.2 Materials and Methods*

### 3.2.1 Study Area

The River Foyle system drains ca 4,500km$^2$ of the northwest of the island of Ireland (Fig. 1.1), discharging northwards through the Lough Foyle estuary into the northern Atlantic.

This system supports a significant population of Atlantic salmon for which there is a long history of commercial net and trap fishing and sport angling extending back over several hundred years (Foyle Fisheries Commission, 1953; Elson and Tuomi, 1975; Foyle Fisheries Commission, 1996). Total catch in the Foyle area in 2002 was approximately 110 tonnes, representing ca. 11% of the total catch for the island of Ireland (Anon. 2002).

The Loughs Agency of the Foyle, Carlingford and Irish Lights Commission and its predecessor the Foyle Fisheries Commission, have collected data on catches and population size on an annual basis since 1952. These data are described below.

### 3.2.2 Salmon Population Estimation

As the Foyle salmon population is exploited, an estimate of the returning migrant population size has been maintained by the statutory body by combining data on commercial net catches with sport angling catches and the fishery escapement (that portion of the population that remains following exploitation). The origins of a number of elements of these data are described below.

## Commercial Salmon Catches

Four forms of commercial exploitation of returning migrant Atlantic salmon have operated since 1952 on the Foyle system.

Drift nets are gill nets deployed close to the water surface in the Foyle Estuary and in inshore waters up to 12 miles out from the north coast. Drift nets have been in constant operation in the area since 1952.

Draft nets are in-river seine nets which are fished in the main River Foyle and River Roe at defined points. Draft nets have been in constant operation since 1952. There is a statutory requirement for the users of both drift and draft nets to make catch returns.

Stake nets are net traps run as a commercial fishery by the Foyle Fisheries Commission between 1952 and 1988. Annual catch records were collected by the Foyle Fisheries Commission for the duration of this fishery.

Bag Nets are trap nets were of a similar construction to the stake nets but were left in place permanently. Data are available for these from 1964 to 1990, the period spanned by the fishery.

## Catch Effort of Commercial Net Fisheries

The effort employed in these fisheries has changed over the years. The season is considerably shorter now (currently 15th June to 31st July, cf March to September in 1952 the first year of the data set) (Loughs Agency, unpublished data) than previously and the number of hours fished each week has been reduced. There has also been a shift in emphasis between the fisheries, with the closure of some methods of exploitation and a shift in the relative importance of draft and drift net use. The drift nets particularly have become more efficient at catching salmon with increasing mechanisation and the availability of more effective netting materials. Over the years the number of returns of catch data from the commercial nets have been high and catch data appear to broadly tie in with field staff observations (Wysner, pers. comm.). For the purposes of this paper no correction to catch data has been made for effort, as it is the absolute number of fish removed in the fisheries that reflect returning migrant population size.

## Sport Angling Exploitation Returns

Despite it being a statutory requirement that sport angling licence holders make an annual catch return, the number of returns, as a percentage of total licences sold was highly variable between 1952 and 2000. This is typical of previously published studies (Small, 1991). To determine annual catch rate by the recreational fishery a correction factor was used which was calculated using a technique described by Small (1991) to determine a realistic measure of angling catch. This correction allowed for the non-reporting of fish caught when anglers made a return and is as follows ((0.3/(percentage return of licences/100))+0.7) this produces a raising factor which is applied to the actual number of fish declared.

### Spawning Population Estimates – Redd Counts

Since 1952 the Foyle Fisheries Commission (and subsequently the Loughs Agency) field staff have made counts of redds (salmon nests) during and immediately following the salmon spawning period in approximately 260 zones within the catchment annually. This is only a partial count of all redds within the Foyle catchment. The accuracy of counting can be subject to environmental conditions such as high flows, which can obstruct proper counting through poor visibility, or flattening of redds making them difficult to see. However, as a method of long-term population monitoring, it is recognised as a useful tool (Elson & Tuomi, 1975; Hay, 1984; Isaak, *et al.*, 2003). Highly accurate data on spawning population size for one year (1999) showed that counts at these 260 sites represented 11% of the total redds based on the percentage of spawning areas available to fish within the Foyle catchment calculated from instream habitat surveys (unpublished data, Loughs Agency). Thus to estimate the absolute number of redds each year in the Foyle catchment, a correction factor of 9.1 was applied to redd counts from all years. Each redd was taken as representing a single female salmon (Hay, 1987).

## 3.2.3 Population Structure

Scale analysis of 813 migrant adult salmon returning to the Foyle from 1968, 1969 and 1970 showed that the population comprised 93.8% 1-sea-winter salmon (fish that had remained at sea for only one winter) (Anon., 1969; 1970; 1971). The age of metamorphosis from the freshwater to the seawater phase (smolt age) was also determined from these fish. On average over these years 1% left the river at one year old, 92% at two years of age and 7% after three years in fresh water. Scale analysis on a sample of 81 salmon in 1998 (W. Crozier, pers. comm) found that 97.5% were 1-sea-winter and 13% had a smolt age of 1+yrs; 84% had a smolt age of 2+, and 3% of 3+.

For subsequent analysis, all fish were assumed to be 1 sea-winter fish but variation in smolt ages were applied to the data so that the recruits were correctly apportioned to their respective parental year class by the following method. From adult scale analysis the ratio of smolts ages were known for the years 1952 to present (Loughs Agency, unpublished data). This information was used to apportion the recruits of spawning fish to the population in their year of return i.e. fish spawned in 1952 would return as adults in 1955, 1956 or 1957 and were apportioned accordingly.

To compare like-with-like all population data (commercial catch, recreational fisheries and redd counts) were converted to an "egg number equivalent". As fecundity is related to body size, a fecundity of 1,430 eggs $kg^{-1}$ of fish (Shearer 1992) was used. The mean weight of salmon was taken from the commercial fisheries for each year used in the analysis. In addition, as the sex ratio is typically skewed in adult migrant salmon populations, a sex ratio for the population of 60:40 (female to male) (Loughs Agency, unpublished data) was used to adjust egg deposition number for data from the commercial and recreational fisheries.

### 3.2.4 Data Analysis

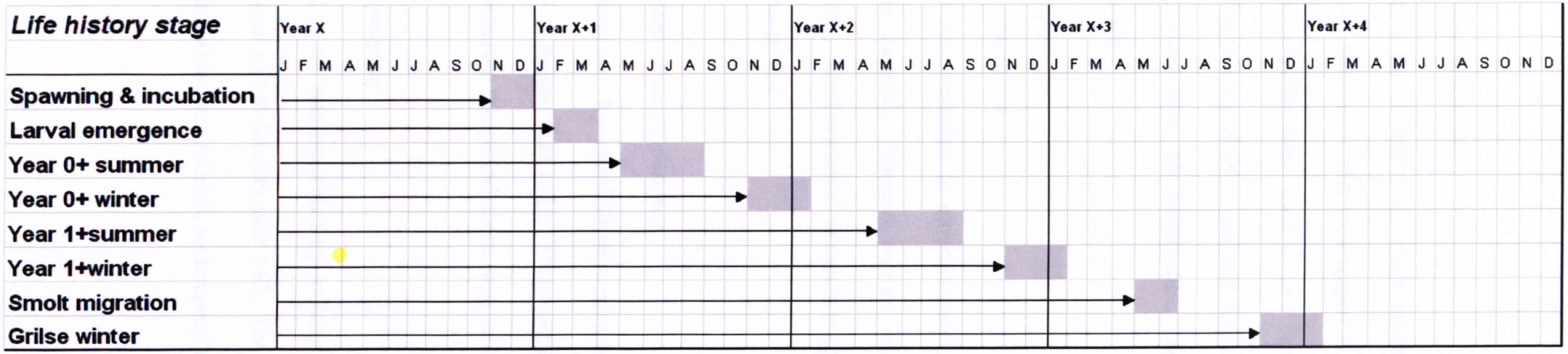
To examine the hypotheses that the Foyle Atlantic salmon population is regulated by density-dependent factors, the relationship between parent and progeny population size, (total egg equivalent derived as above) was examined.

Linear regressions and curvi-linear stock-recruitment models (derived from the literature) were tested to find the model which best explained the variance in recruit population size. To test for additional environmentally influenced modulators of population size, during key life cycle stages (potential population bottlenecks), a number of environmental parameters were used to predict variation in residuals extracted from the stock-recruitment model.

## Life-History Stages

Eight specific life history stages were recognised (Figure 3.1):

**Figure 3.1** Salmon life history stages for one life-cycle.



### *Spawning and egg incubation*

The first stage in the salmon's life cycle examined was from November in year x to January year x+1, when adult fish are engaged in spawning and eggs are developing in the redds. Four variables were used to test for a relationship between environmental conditions during this period (Nov-Jan) and the size of the returning migrant cohort. These were: rainfall, water flow, air temperature, and the North Atlantic Oscillation Index (NAOI) (see below).

### *Larvae/Alevin Emergence*

Subsequent to this, variation in environmental conditions during the period of alevin emergence from the redd; - February year x+1 to March year x+1, was tested for its effect on population size. Environmental variables used were: rainfall, air temperature and water flow, during this period.

### *Fry establishment - Year 0+ Summer*

Following emergence, fry establish territories in the streams during their first summer (May year x+1 to August year x+1). Three variables were tested for significant effects on population size during this period, these were rainfall, air temperature and water flow.

### *Year 0+ Overwintering*

Overwintering of fry was examined by looking for significant effects during the period November in year x+1 to January year x+2. The variables tested for effects on population size during this period were rainfall, air temperature, water flow and the NAOI.

### *Year 1+ Summer survival*

The effects of the environment on one year old parr summer survival, covering the period May year x+2 to August year x+2 were tested using three variables: rainfall, air temperature and water flow.

### *Year 1 + Overwintering*

Overwintering parr during the period November year x+2 to January year x+3, were tested for effects on the overwintering juvenile salmon population size using the environmental variables rainfall, air temperature, water flow and the NAOI

### *Smolt migration*

The smolt migration period May – June year x+3 was tested against the environmental variables rainfall, air temperature and water flow.

### *Marine Survival year x+4*

The NAOI and sea-surface temperature anomalies north of Iceland were tested for significant survival effects during the period when the salmon were in their first winter at sea, November year x+3 to February x+4.

## Environmental Variables

The environmental variables used are explained in greater detail below: –

### *Air Temperature, Local Sea-surface Temperature and Precipitation Data*

This information was obtained from the Meteorological Office in Dublin. These environmental data were collected at Malin Head, Co. Donegal, which is at the entrance to Lough Foyle. Air temperature and precipitation data were available from May 1955 to present, while sea-surface temperature data were available from May 1958. The data used were an average for each month available.

### *Water flow*

These data were derived from a hydrometric station on the Camowen River at Omagh, Co. Tyrone, which is operated by the Department of the Environment for N Ireland. For the analysis an average monthly flow rate was used. The data were available from January 1975 to December 2000.

### *The North Atlantic Oscillation Index (NAOI)*

The NAOI is an atmospheric phenomenon, which is measured as the difference in air pressure between the Azores and Iceland (Hurrell, 1995; Hurrell, 2003; Gillett *et al.*, 2002). The winter index, used in this analysis, is calculated by taking the mean of the index between December and the following March. This Winter NAOI Index then references to the January of that year.

*Winter sea-surface temperature anomalies for Grimsey Island, Iceland*

The period November x+3 to January x+4 was used to examine possible environmental effects of the marine environment. These data were acquired from the British Atmospheric Data Centre (BADC) and are representative of temperature change.

## Analysis

Two statistical approaches were adopted to examine the variation in population size independent of density dependent effects. Three parental-offspring population size models were tested (linear; Beverton & Holt; Ricker) using the software packages SPSS and Statistica. The model which best fitted the data and provided the greatest predictive ability was chosen for further analysis. Environmental variables were then used as independent predictors of residuals derived from this model in regression analysis. However, as it is highly possible that any environmental effect on population variation may not be linear or may show significant threshold effects (see Elliott, 1997), population residuals in years with high for example water flow (upper 30 percentile), low water flow (lower 30 percentile) and intermediate water flow (mid 40 percentile) were compared using ANOVA with a *post hoc* Tukey test pair-wise group comparison. This technique was used with all of the environmental variables. To avoid Type 1 statistical errors, the acceptable probability when using multiple tests was corrected using a Bonferroni correction. For clarity the corrected probability equivalents are presented here where appropriate.

## *3.3 Results*

### 3.3.1 Density Dependent Regulation

Of the three models examined relating parental size to the number of offspring recruited into the population, linear regression explained the lowest amount of variance (17.1%), Beverton and Holt 27.2% and the Ricker model explained most variance at 31.2% (Table 3.1; Figure 3.2a; 3.2b; 3.2c).

**Table 3.1** Comparison of predictive linear; Beverton & Holt and Ricker models.

| **Model** | $r^2$ | **p** | **n** | **F** |
|---|---|---|---|---|
| **Linear** | 0.171 | 0.003 | 43 | 9.88 |

| **Model** | $r^2$ | **n** | **constant** | **parameter** |
|---|---|---|---|---|
| **Beverton & Holt** | 0.272 | 43 | 5.94 | 0.0005 |
| **Ricker** | 0.312 | 43 | 4.385 | 0.00017 |

This model suggests that maximum filial population size resulted from parental egg deposits of around 500,000,000 eggs. Egg deposition in excess of this resulted in a low rate of decline in filial recruitment to the population, deposition rates below optimal filial recruitment declined more rapidly with decreasing egg deposition. Thus, both positive and negative density dependent factors appear to modulate recruitment in this population. To derive a measure of survivorship, i.e. population size independent of parental population, residuals from the Ricker curve were derived. These were then used to examine the role of environmental factors controlling variation in survivorship.

**Figure 3.2a** A linear model fitted to parental population size (egg equivalent *100,000) and filial population size (egg equivalent*100,000).

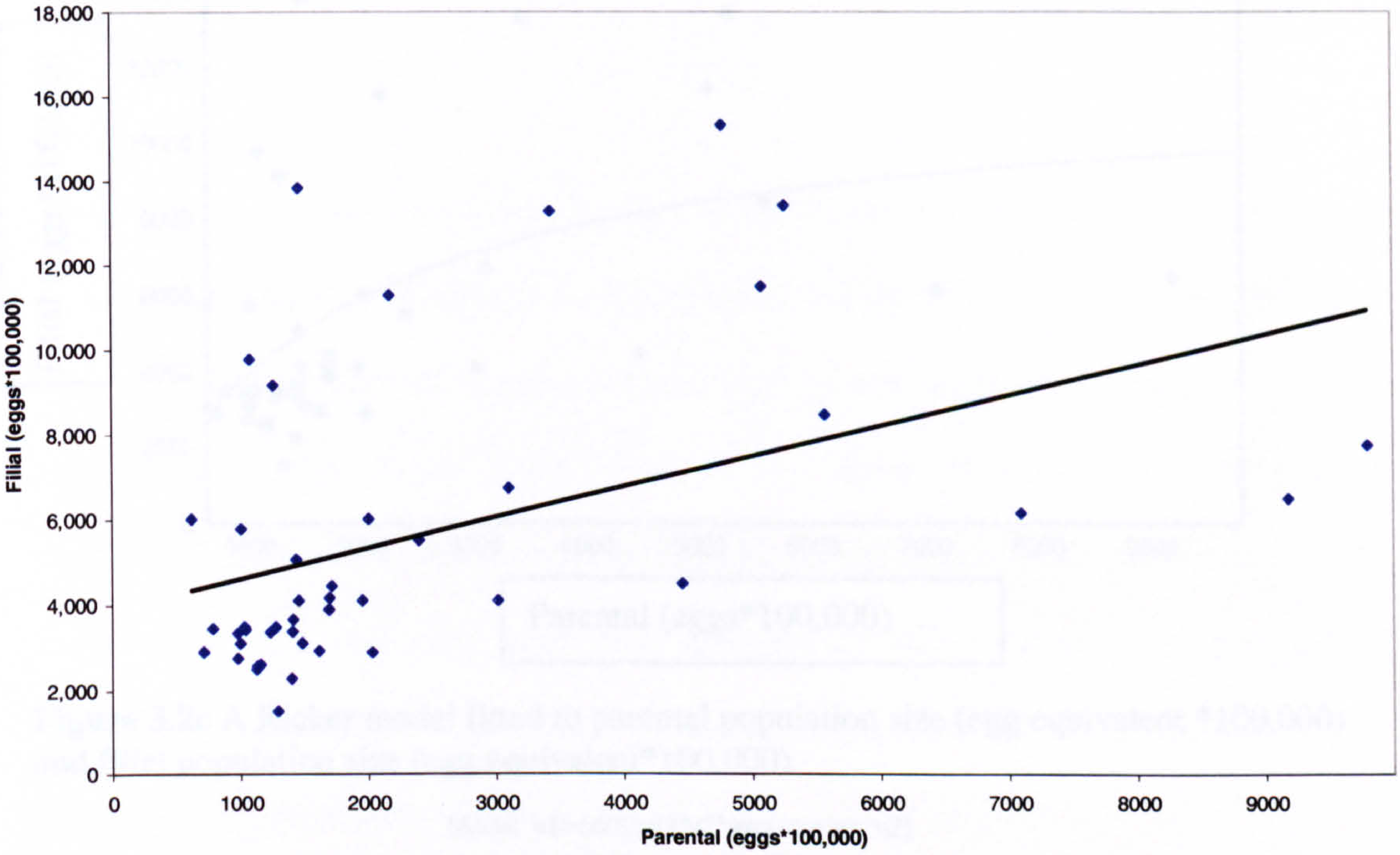


**Figure 3.2b** A Beverton & Holt model fitted to parental population size (egg equivalent *100,000) and filial population size (egg equivalent*100,000).

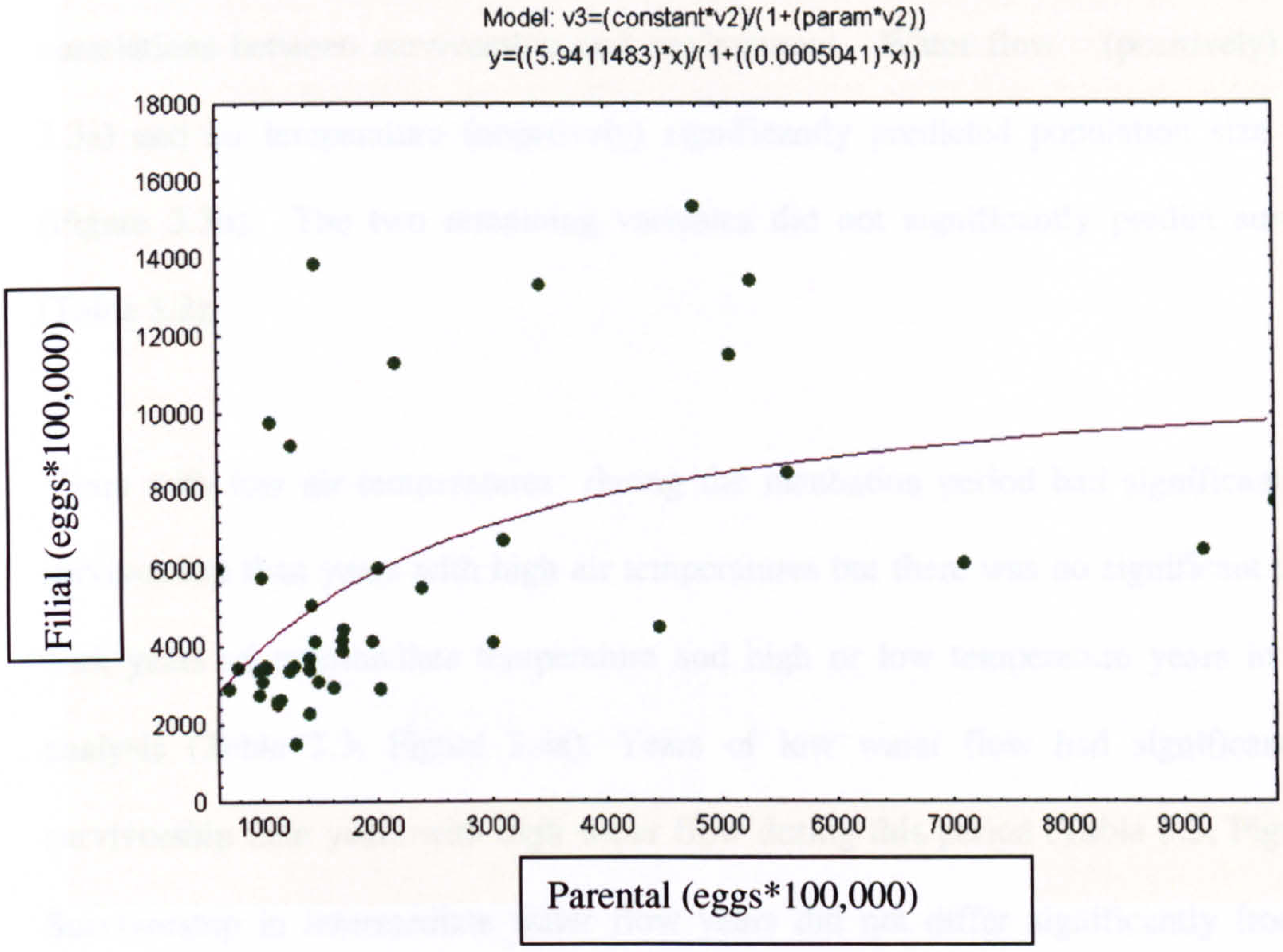
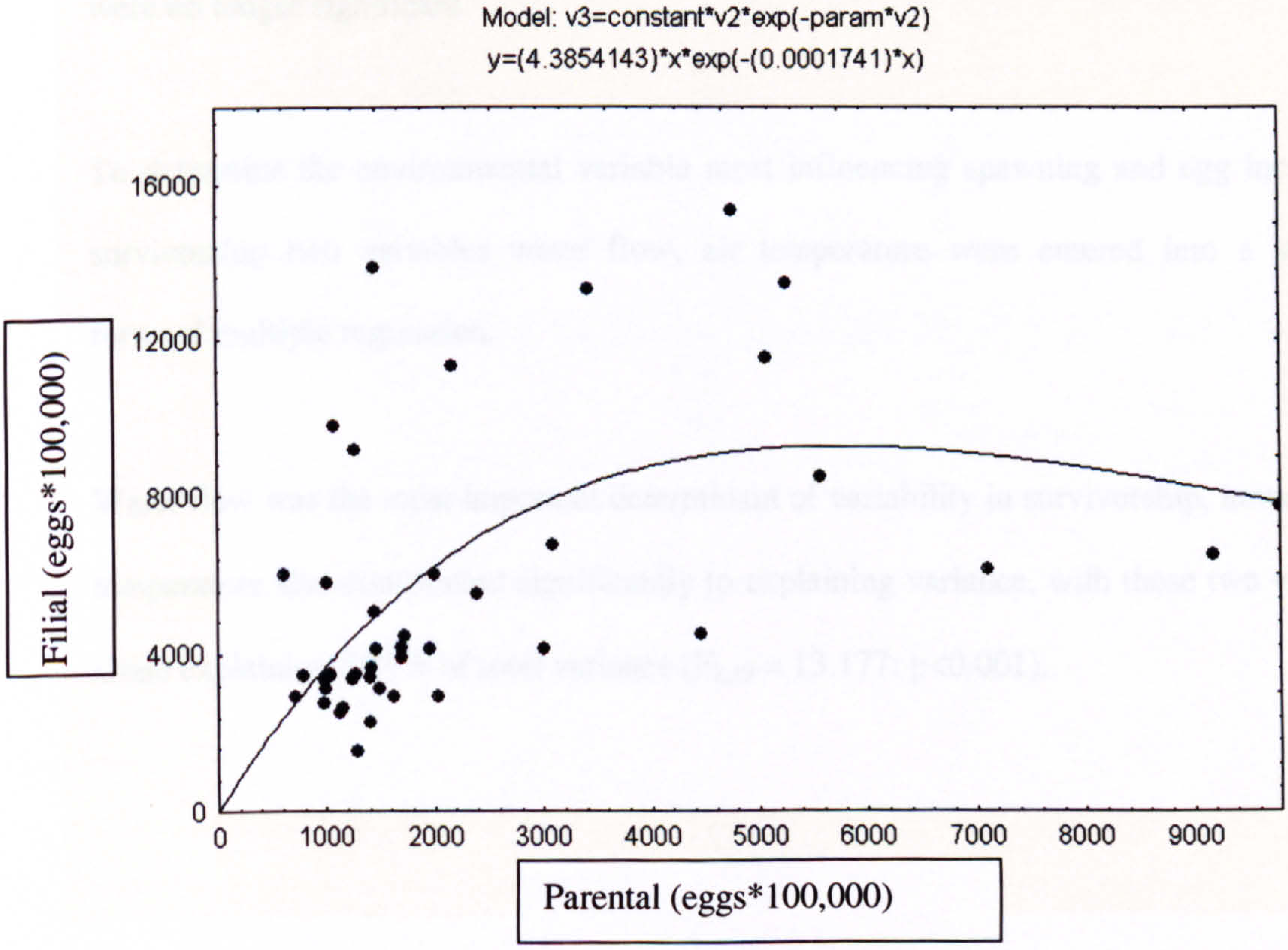


**Figure 3.2c** A Ricker model fitted to parental population size (egg equivalent *100,000) and filial population size (egg equivalent*100,000).



### 3.3.2 Life-stage specific – environmental effects on population size.

Spawning and egg incubation

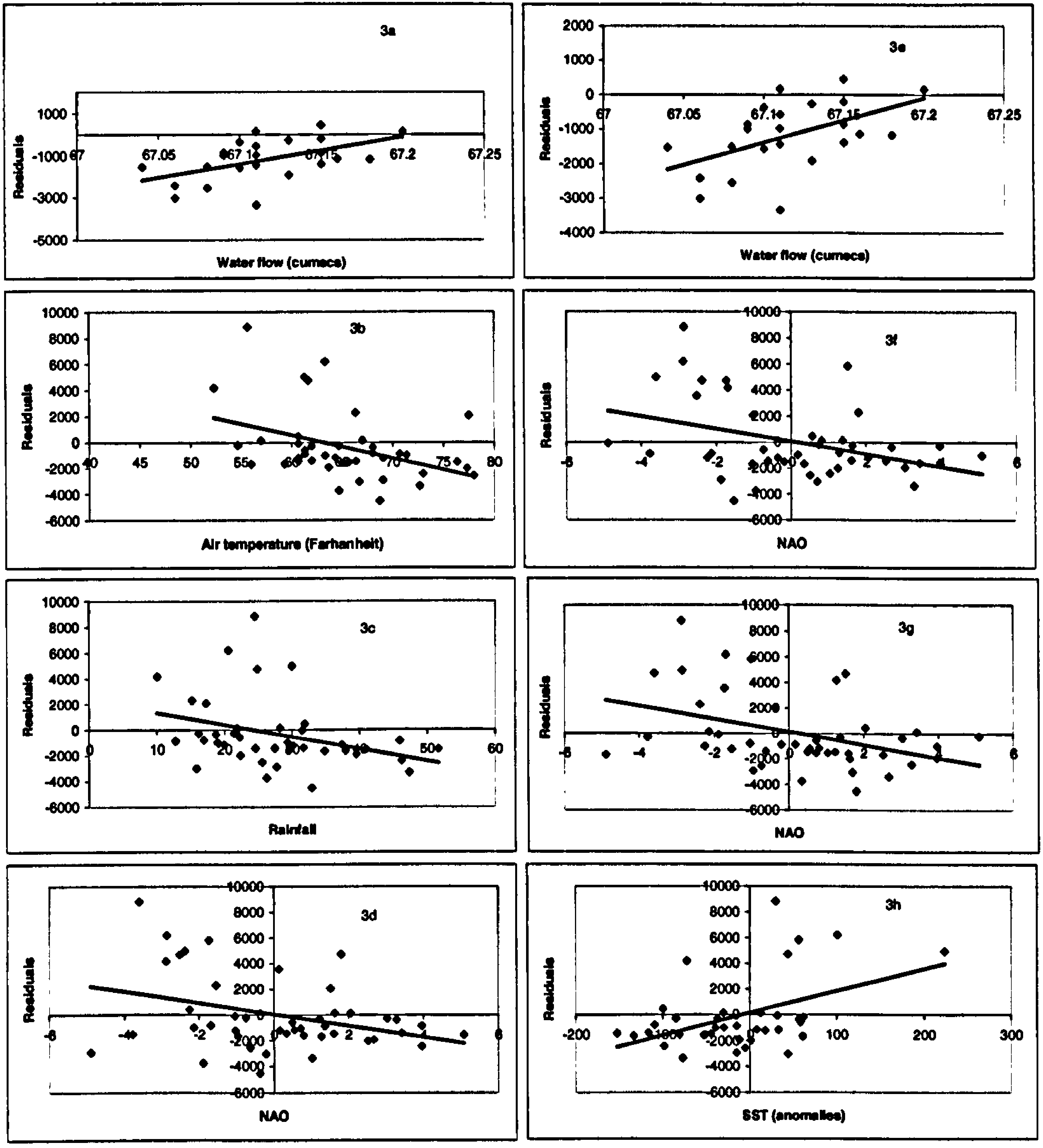
Four variables, air temperature, water flow, rainfall and the NAOI, were used to test for correlations between survivorship and environment. Water flow (positively) (Figure 3.3a) and air temperature (negatively) significantly predicted population size residuals (Figure 3.3b). The two remaining variables did not significantly predict survivorship (Table 3.2).

Years with low air temperatures during the incubation period had significantly higher survivorship than years with high air temperatures but there was no significant difference with years of intermediate temperature and high or low temperature years in ANOVA analysis (Table 3.3; Figure 3.4a). Years of low water flow had significantly lower survivorship than years with high water flow during this period (Table 3.3; Figure 3.4b). Survivorship in intermediate water flow years did not differ significantly from that of either high or low water flow years. However, when corrected using Bonferroni these were no longer significant.

To determine the environmental variable most influencing spawning and egg incubation survivorship two variables water flow, air temperature were entered into a stepwise forward multiple regression.

Water flow was the most important determinant of variability in survivorship, however, air temperature also contributed significantly to explaining variance, with these two variables alone explaining 54.9% of total variance ($F_{2,19} = 13.177$: $p<0.001$).

**Figure 3.3** Regressions of environmental variables during life-stage specific events and population size residuals derived from the Ricker parental-offspring curves. a) water flow during spawning and incubation, $p<0.001$; b) air temperature during spawning and incubation, $p<0.009$; c) rainfall during larval/alevin emergence, $p<0.029$; d) North Atlantic Oscillation during 0+ winter, $p<0.022$; e) water flow during 0+ winter, $p<0.012$; f) North Atlantic Oscillation during 1+ winter, $p<0.011$; g) North Atlantic Oscillation during winter marine feeding, $p<0.008$; h) sea surface temperature anomalies north of Iceland during winter marine feeding, $p<0.002$.



### Larvae/Alevin Emergence

Of the variables tested rainfall, air temperature and water flow in the upper catchment, only rainfall was shown to be significant during this period, however, following correction using Bonferroni this was no longer significant (Table 3.2; Figure 3.3c).

When population size residuals were compared in years with low, intermediate and high flow, the data hinted at an inverse relationship between flow and survival (Table 3.2) although the result was not significant.

The regression of rainfall on survivorship explained 9.3% of the total variance ($F_{1,39} = 5.11$; $p<0.029$).

### Fry establishment - Year 0+ Summer

Three variables (summer rainfall; air temperature and water flow) were regressed on survivorship. None of these were found to be significant predictors of variance or correlated to the population residuals, although water flow during this period was nearly significant (Table 3.2).

ANOVA analysis of years of high, intermediate and low rainfall showed no significant differences in survivorship between these years (Table 3.3).

**Table 3.2** Regression of environmental variables during life-stage specific events and population size residuals derived from the Ricker parental-offspring curves.

| Life stage | Environmental variable | B | F | $r^2$ | p | Bonferroni Correction | N |
|---|---|---|---|---|---|---|---|
| Spawning & incubation of eggs | Rainfall | -8.06 | 0.02 | -0.026 | 0.902 | | 39 |
| | Air temp | -175.74 | 7.54 | 0.14 | 0.009 | sig. at 0.05 | 40 |
| | NAOI | -349.49 | 3.43 | 0.054 | 0.71 | | 43 |
| | Water flow | 18642 | 14.01 | 0.394 | 0.001 | sig. at 0.01 | 20 |
| | | | | | | | |
| Alevin emergence | Rainfall | -93.49 | 5.11 | 0.093 | 0.029 | not sig. | 40 |
| | Air temp | 22.69 | 0.22 | -0.020 | 0.641 | | 40 |
| | Water flow | -4134 | 0.99 | 0.000 | 0.331 | | 21 |
| | | | | | | | |
| 0+ summer | Rainfall | 0.73 | 0.00 | -0.025 | 0.994 | | 41 |
| | Air temp | -15.99 | 0.03 | -0.024 | 0.857 | | 41 |
| | Water flow | 12730 | 3.57 | 0.109 | 0.074 | | 21 |
| | | | | | | | |
| 0+winter | Rainfall | -2.14 | 0.00 | -0.026 | 0.972 | | 40 |
| | Air temp | -67.89 | 0.87 | -0.003 | 0.358 | | 41 |
| | NAOI | -438 | 5.66 | 0.098 | 0.022 | not sig. | 43 |
| | Water flow | 12995 | 7.56 | 0.23 | 0.012 | sig. at 0.05 | 22 |
| | | | | | | | |
| 1+ summer | Rainfall | 66.67 | 0.54 | -0.011 | 0.466 | | 42 |
| | Air temp | -139 | 2.62 | 0.037 | 0.113 | | 42 |
| | Waterflow | 4864 | 0.43 | -0.026 | 0.517 | | 22 |
| | | | | | | | |

**Table 3.2** Regression of environmental variables during life-stage specific events and population size residuals derived from the Ricker parental-offspring curves (continued).

| **Life stage** | **Environmental variable** | **B** | **F** | $r^2$ | **p** | **Bonferroni Correction** | **N** |
|---|---|---|---|---|---|---|---|
| 1+ winter | Rainfall | -94.80 | 2.31 | 0.031 | 0.136 | | 41 |
| | Air temp | -88.74 | 1.58 | 0.014 | 0.216 | | 42 |
| | NAOI | -484.67 | 7.16 | 0.125 | 0.011 | sig. at 0.05 | 43 |
| | Waterflow | 6148 | 1.34 | 0.014 | 0.260 | | 23 |
| | | | | | | | |
| 2+ smolts | Rainfall | 80.53 | 1.08 | 0.002 | 0.305 | | 43 |
| | Air temp | 19.04 | 0.08 | -0.022 | 0.786 | | 43 |
| | Waterflow | -4924 | 0.59 | -0.018 | 0.45 | | 23 |
| | Malin SST | 202 | 0.21 | -0.037 | 0.655 | | 22 |
| | | | | | | | |
| Grilse winter at sea | NAOI | -510 | 7.85 | 0.137 | 0.008 | sig. at 0.05 | 43 |
| | Sea surface temperature | 18.50 | 10.72 | 0.217 | 0.002 | sig. at 0.01 | 35 |

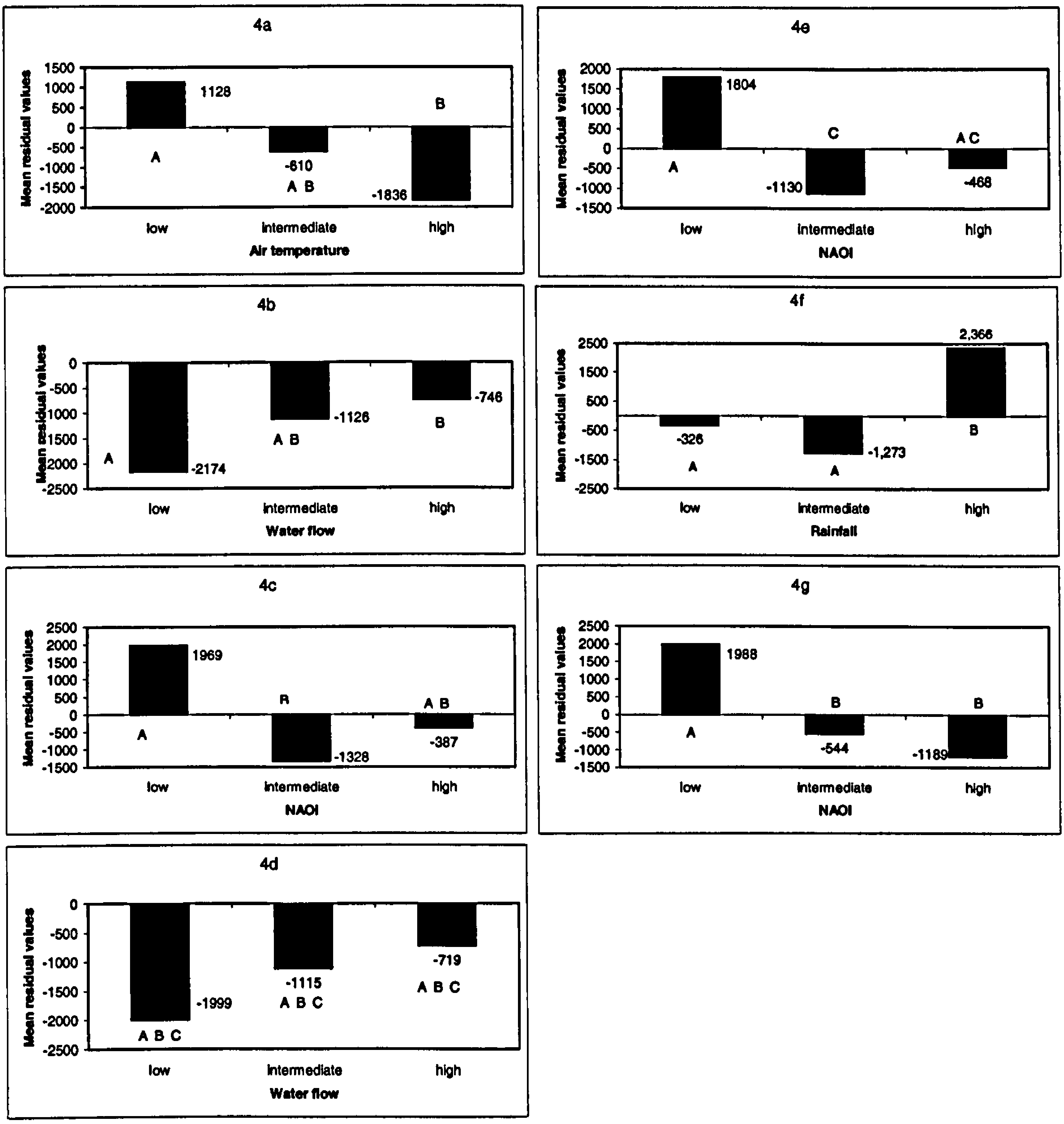
**Table 3.3** ANOVA results of environmental variables during life-stage specific events and population size residuals derived from the Ricker parental-offspring curves.

| | | ANOVA | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | F | df | p | Bonferroni Correction | mean | | |
| **Life stage** | **Environmental variable** | | | | | **low** | **intermediate** | **high** |
| Spawning & incubation of eggs | Rainfall | 0.337 | 2,37 | 0.716 | | -581 | -1.74 | -839 |
| | Air temperature | 4.408 | 2.38 | 0.019 | not sig | 1128 | -610 | -1836 |
| | NAOI | 1.919 | 2,41 | 0.160 | | 1132 | -157 | -1016 |
| | Water flow | 3.878 | 2,18 | 0.04 | not sig. | -2174 | -1126 | -746 |
| Alevin emergence | Rainfall | 2.576 | 2,38 | 0.089 | | 527 | -54 | -1827 |
| | Air temperature | 0.044 | 2,38 | 0.957 | | -520 | -229 | -316 |
| | Water flow | 0.883 | 2,19 | 0.43 | | -1032 | -1043 | -1614 |
| 0+ summer | Rainfall | 0.666 | 2,39 | 0.52 | | -640 | 486 | -512 |
| | Air temperature | 0.257 | 2,39 | 0.774 | | 178 | -579 | -130 |
| | Water flow | 2.874 | 2,19 | 0.081 | | -1355 | -1710 | -613 |
| 0+winter | Rainfall | 0.139 | 2,38 | 0.871 | | -484 | -92 | -609 |
| | Air temperature | 0.319 | 2,39 | 0.729 | | 279 | -319 | -619 |
| | NAOI | 6.197 | 2,41 | 0.004 | sig. at 0.05 | 1969 | -1328 | -887 |
| | Water flow | 3.393 | 2,19 | 0.055 | | -1999 | -1115 | -719 |
| 1+ summer | Rainfall | 0.825 | 2,40 | 0.446 | | -810 | -103 | 667 |
| | Air temperature | 1.865 | 2,40 | 0.168 | | 983 | -158 | -1141 |
| | Waterflow | 0.945 | 2,20 | 0.405 | | -1610 | -1066 | -920 |

**Table 3.3** ANOVA results of environmental variables during life-stage specific events and population size residuals derived from the Ricker parental-offspring curves (continued).

| | | ANOVA | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | **F** | **df** | **p** | **Bonferroni Correction** | **mean** | | |
| **Life stage** | **Environmental variable** | | | | | **low** | **intermediate** | **high** |
| 1+ winter | Rainfall | 1.122 | 2,39 | 0.336 | | 557 | -111 | -1140 |
| | Air temperature | 0.479 | 2,40 | 0.623 | | 218 | 168 | -792 |
| | NAOI | 4.774 | 2,41 | 0.014 | | 1804 | -1129 | -468 |
| | Waterflow | 1.453 | 2,20 | 0.257 | | -1088 | -1516 | -685 |
| 2+ smolts | Rainfall | 7.491 | 2,41 | 0.002 | sig. at 0.05 | -326 | -1273 | 2366 |
| | Air temperature | 1.613 | 2,41 | 0.212 | | -1034 | 67 | 896 |
| | Waterflow | 0.287 | 2,21 | 0.754 | | -905 | -1231 | -1277 |
| | Malin SST | 1.017 | 2,20 | 0.38 | | -1081 | -1403 | -585 |
| Grilse winter at sea | NAOI | 5.293 | 2,41 | 0.009 | sig. at 0.05 | 1988 | -543 | -1188 |
| | Sea surface temperature | 3.127 | 2,33 | 0.057 | | -884 | -575 | 1773 |

**Figure 3.4** Mean residual population size values derived from the Ricker parental-offspring curves for years with high (upper 30 percentile); low (lower 30 percentile) and intermediate (remaining 40 percentile) values for environmental variables during the life-stage specific periods separately for: a) air temperature during spawning and incubation; b) water flow during spawning and incubation; c) North Atlantic Oscillation during 0+ winter; d) water flow during 0+ winter; e) North Atlantic Oscillation during 1+ winter; f) rainfall during smolt migration; g) North Atlantic Oscillation during winter marine feeding. All figures are significant at $p<0.05$ but columns with identical lettering are <u>not</u> significantly different in post-hoc testing. Figures 4a and 4b were not significant after Bonferroni correction.



### Year 0+ Overwintering

Of the four variables examined (rainfall, air temperature, NAOI & water flow) only the NAOI and water flow were found to significantly predict survivorship. The NAOI had an inverse relationship (Figure 3.3d) while water flow was positively correlated with survivorship (Table 3.2; Figure 3.3e). Correcting for multiple tests using Bonferroni however meant that the NAOI was not a significant predictor.

Years with low, intermediate or high values for each of these environmental variables showed significant differences in survivorship for the NAOI (Table 3.3; Figure 3.4c) but not quite significant for water flow, although the data hinted at a positive relationship to higher flow rates in the upper catchment (Table 3.3; Figure 3.4d).

To determine the environmental variable most influencing 0+ winter survivorship, NAOI and water flow were entered into a stepwise forward multiple regression. Water flow was found to be the most important determinant explaining 23% of the total variance ($F_{1,21} = 7.562$; $p<0.012$). NAOI did not add significantly to the model.

### Year 1+ Summer survival

Summer rainfall, air temperature and water flow effects on survival were ascertained using regression and ANOVA. None of these variables were found to have a significant effect.

### Year 1 + overwintering

Of four environmental variables (rainfall, air temperature, NAOI & water flow) examined only the NAOI was found to be significantly inversely related to survivorship (Table 3.2; Figure 3.3f).

Comparing survivorship in years of low, intermediate and high values of the four environmental variables showed that only survivorship in high, intermediate and low NAOI differed significantly (Figure 3.4e). Post-hoc testing showed that survivorship in low NAOI years was significantly higher than that of intermediate years, but not significant from years of high NAOI.

The NAOI explained 12.5% of the total variance ($F_{1,42} = 7.157$; $p<0.011$).

### Smolt migration

Rainfall, air temperature, water flow and the sea surface temperature at Malin Head did not significantly predict survivorship.

However, comparing years with low, intermediate and high values for rainfall using ANOVA showed significant differences in survivorship (Table 3.3 & Figure 3.4f). Post-hoc testing showed that survivorship was higher in years with a high rainfall at this time compared with years of low or intermediate rainfall.

### Marine Feeding - year x+4

The NAOI significantly predicted survivorship (Table 3.2; Figure 3.3g) (inverse relationship), as did the sea surface temperature anomalies north of Iceland (positive relationship) (Figure 3.3h).

Post-hoc testing showed that low NAOI years had significantly higher survivorship than years with intermediate or low NAOI (Figure 3.4g).

To determine which environmental variables (NAOI & SST) best predicted survivorship they were entered into a stepwise forward multiple regression. Sea surface temperature was the most important determinant of variability in population size residuals explaining 21.7% of total variance ($F_{1,34} = 10.718$: $p<0.002$). NAOI did not add significantly to the model.

## 3.4 Discussion

The evidence presented here supports the hypothesis that density-dependent mortality is an important underlying mechanism controlling Atlantic salmon population size in the River Foyle catchment. Modelling the effect of parental population size on the filial population showed a significant relationship, with the Ricker curve providing the best model fit to the data. The domed nature of this curve suggests that negative dependence occurs at high densities. Elliott (1994) showed for brown trout that this model fits data for other salmonid populations while other authors have shown this dome-shaped model fits Atlantic salmon (Chadwick, 1982; 1985a; 1985b; Kennedy & Crozier, 1993;). However, in the study presented here these density-dependent effects only accounted for 31% of the total annual variability in population size. Clearly other factors also influence the population size. Here, a life stage specific approach was adopted to aid the identification of factors modulating the remaining variation in population size. Biologically important critical survivorship periods ("bottlenecks" *sensu* Elliott, 2002) were identified and broad scale environmental data used as predictors of survivorship variance to determine their relative influence on a comprehensive suite of the critical life stage specific events faced by Atlantic salmon during ontogeny. This approach shows clear evidence of environmentally induced population regulating effects at a number of critical life stages.

During the spawning and incubation period, standardised in this study between November and January of the following year, it has been shown that air temperature and water flow are good predictors in explaining residual variation. Higher survivorship is correlated with lower air temperatures and higher water flows in the upper catchment. Approximately 54.9% of survivorship variation was explained at this life stage. It is unclear if these results are linked to the spawning period itself or the incubation period of the eggs. However, it is assumed that water temperature will be a function of air temperature although probably with some time delay. In previous studies it has been shown that a drop in water temperature is required before spawning occurs (Shearer,1992) and it is well recognised that egg incubation is controlled directly by water temperature, higher temperatures leading to faster development and emergence from the redd (Heggeberget, 1988).

On emerging from the redd, the alevin must establish a territory and this period is recognised as a population bottleneck in other salmonid species (Elliott, 1994; Jones *et al.*, 2003). High water during this time, when fish are first exposed to full stream flow conditions, can be particularly important in determining ultimate population size (Elliott, 1994). Consistent with this, it was shown that rainfall explained 9.3% of survivorship variation at this life cycle stage. Although water flow was not significant at this stage, this could be as a result of low sample size as low rainfall predicted higher survivorship.

Previous studies (Elliott, 1994; Elliott, 1997) have linked high periods of mortality to summer when water conditions can have a severe impact on productivity. This may occur through direct mortality or indirectly, for example by affecting growth rates and therefore potential for survival at other crucial periods such as first entrance to the marine phase of the salmonids' life cycle. In the study presented here, there was no direct evidence for environmental control of survivorship during summer periods, although survival in either year 1 (0+) or year 2 (1+) was nearly positively significantly related to water flow.

In contrast, the periods which appear to influence survivorship in the Foyle catchment are more prominent in winter. Survival for both 0+ and 1+ winter periods is strongly linked to the negative phase of the NAOI and in the first winter to increased water flow in the upper catchment. Thus environmental factors accounted for 23% and 12.5% of survivorship during first and second winter periods respectively.

The final critical phase in the freshwater element of the salmons' life-cycle is that of its entrance to the marine environment as smolts. Here it has been shown that high rainfall greatly benefits survivorship during this period but interestingly the worst case scenario appears to be that of intermediate flows, very low flows having a much smaller negative effect. It has been shown previously in other studies that high water flows greatly facilitate movement of these fish downstream (Shearer, 1992; McCormick *et al.*,1998; Byrne *et al.*, 2003) and that low flows may be detrimental to survival. However the impact of these intermediate flows have not been observed previously. One possible explanation for this finding is that in very low flows the fish are less likely to migrate actively downstream while in intermediate water conditions fish will attempt migration and therefore may be more prone to predation.

Survival once the salmon reach the sea is known to be affected by marine conditions and these have been linked previously to the NAOI and also sea surface conditions for North American stocks of salmon (Friedland *et al.*, 1993; 2003a; 2003b). Very little similar information is available for European populations although Martin and Mitchell (1985) linked sea surface temperatures north of Iceland to differing abundances between single and multi-sea winter salmon and Friedland *et al* (1998) linked a thermal habitat index of 10-13°C in the North Sea to survival of Scottish and Norwegian stocks.

The NAOI may influence survival in a number of ways, such as affecting currents, salinity profiles and sea surface temperatures. These conditions may impact on salmon directly, for instance it is known that salmon cease feeding at temperatures below 3°C (Shearer,1992), or indirectly by affecting prey or predator abundance. Sea surface temperature north of Iceland appears to be of particular importance as this variable was found to explain 23% of variance. There may of course be other mechanisms or factors which are linked to these conditions of which little is known at present and which are affecting the abundance of the salmon during this phase of their life-cycle.

The Ricker density-dependent model explained a proportion of the variance in recruitment, however, this is not to state that the mode of operation of environmental factors is completely density-independent. For example, in looking at the effects of water flow on

0+ and 1+ over wintering, higher water flows lead to greater numbers of fish surviving. This is possibly due to the effect of greater areas of habitat being available as a direct result of the increased flow. If so, this implies that these environmental factors are operating in a density-dependent manner as well as having some density-independent effects.

This study highlights the importance of density-dependent regulation as a controlling mechanism for the salmon population in the Foyle area. However, it has been shown that environmental factors also play an important role in determining ultimate returning population size driving life-stage events that may potentially act as population bottlenecks. It is concluded that the life-stage specific environmental effects which are shown to be operating in this population are likely to have similar effects in other salmonid populations, and will contribute to the apparent stochastic variation in population size resulting from the application of traditional stock-recruitment models. The identification and quantification of these effects, from this long-term dataset, should improve the predictive ability of models by enabling the construction of more sophisticated models that combine parent population size and environmental factor variance.

# Chapter 4. The influence of broad scale climatic phenomena on long-term trends in Atlantic salmon population size: an example from the River Foyle, Ireland.

## *4.1 Introduction*

Many animal populations are known to experience large-scale fluctuations in population size e.g. lemmings (*Lemmus lemmus (L.)*) and voles (*Clethrionomys rufocanus*) in Northern Norway (Ekerholm *et al.*, 2001) and red grouse (*Lagopus lagopus*) throughout their range (Jenkins *et al.*, 1963; Newton, 1998). Many of these cycles are related to natural phenomena, operating independently of direct anthropogenic influence, for example, changes in the distribution and abundance of the Pacific sardine (*Sardinops caeruleus*) and northern anchovy (*Engraulis mordax*) have been shown to be related to climate shifts in the north-east Pacific over a 70 year period (Rodríguez-Sánchez *et al.*, 2002).

With regard to Atlantic salmon Martin and Mitchell (1985) showed correlations between sea surface temperatures north of Iceland and the abundance of 1-sea-winter and multi-sea-winter fish returning to the River Dee, Scotland. Increasing sea surface temperatures in the sub-Arctic were associated with larger numbers of adults returning as multi-sea-winter salmon and fewer returning as 1-sea-winter salmon. They also showed that the average weight of 1-sea-winter salmon increased with population size of that group. Friedland *et al.* (2000) also found linkages between survival of salmon and sea-surface temperatures in the North sea area.

Similar linkages have been found for Pacific salmon (McFarlane *et al.*, 2000; Mueter *et al.*, 2002) and North American stocks of Atlantic salmon, where studies have correlated marine survival of Atlantic salmon to winter sea surface temperatures in the Labrador sea (Friedland, 1998; Drinkwater, 2000; Reddin *et al.*, 2004).

Previous studies have shown that the atmospheric phenomenon the North Atlantic Oscillation is also related to stock abundance in Atlantic salmon (Friedland *et al.*, 2003; Beaugrand & Reid, 2003). This index can be used as a proxy for climate variation on a large scale. The North Atlantic Oscillation in winter (NAOI) has been shown to provide a good index of the dominant mode of winter climate variability in the North Atlantic region ranging from central North America to Europe and into much of Northern Asia. It is calculated as a ratio of mean atmospheric pressure in the Azores to that of Iceland between December and the following March. Thus extreme high mean values result from intense low pressure centred over Iceland, corresponding with high pressure centred over the Azores; when this situation is reversed, the corresponding values of the NAOI are low (Hurrell *et al.*, 2003). A high value NAOI is likely to be indicative of higher frequency and more violent winter storms crossing the Atlantic Ocean on a more northerly track. This results in warmer and wetter winters in Europe and in colder and dryer winters in northern Canada and Greenland, while the eastern United States is more likely to experience milder and wetter winter conditions (Hurrell *et al.*, 2003). As a consequence, sea surface winter temperatures over much of the Arctic will generally be colder at a higher NAOI (Dickson & Turrell, 2000; Hurrell *et al.*, 2003). Low NAOI values are likely to indicate fewer and weaker winter storms bringing moist air into the Mediterranean and cold air to northern Europe. However, areas such as Greenland will have milder winter temperatures and as a result, Arctic sea surface temperatures will be generally higher (Hurrell *et al.*, 2003).

The NAOI has previously been shown to correlate with changes in behaviour and abundance of a wide range of natural animal populations, from the timing of migration in birds (Forchhammer *et al.*, 2002), plankton abundance (Reid & Planque, 2000), abundance of squid (*Loligo forbesi*) in Scottish waters (Pierce & Boyle, 2003) to emergence of sea-trout fry from spawning beds (Elliott *et al.*, 2000).

The spatial scale and geographic range over which the NAOI appears is indicative of climate patterns and makes it a potentially powerful predictor of population fluctuations in European Atlantic salmon foraging at sea in winter.

Determining climatic influences on the dynamics of wild populations requires long-term measures of population abundance; such datasets are very rare. However within the Foyle catchment, Ireland, there is a long history of commercial fishing for Atlantic salmon extending back several hundred years (Anon. 1953; Elson & Tuomi, 1975; Anon., 1996). Commercial catch records have been maintained since 1875 with only a short break before and during the First World War (1909 to 1919). These records show periods of abundance and periods when the catches were substantially lower. Many reasons for these changes have been proposed such as Ulcerative Dermal Necrosis (UDN), drainage schemes, pollution and land use change (Elson & Tuomi, 1975; Shearer, 1992; Magee *et al.*, 2003; Waring & Moore, 2004). However, here these records are used as an index of population size, to examine long-term change and the potential effects of climate. Specifically, the hypothesis is tested that the

NAOI can be used to explain variance in the abundance of salmon in the Foyle catchment. In addition, published data from climate change models predicting the effect of global warming on the NAOI are used to make predictions about the possible effects on salmon populations in the future.

### *4.2 Materials and Methods*

Catch data are not absolute measures of population size (Shearer, 1992), but there is evidence that these data do represent a significant relative measure of the dynamic change in returning migrant population size for the Foyle system. Firstly, catch returns apparently accurately reflect actual catches from the commercial fisheries (Wysner, pers. comm.). Secondly, over a 49-year period since 1952, there has been an independent measure of population size. The number of redds (nests) have been monitored annually at 260 sites spread throughout the catchment. Over the period 1952 – 2000, commercial fishery catch was a very good predictor of redd number (Linear regression: $F_{1,47}$= 39.9; $r^2$= 0.45; $p<0.001$). These data strongly support the principal assumption of the study presented here; namely that commercial net catches reflect change in the relative population size of the returning migrant salmon population to the River Foyle.

Data from commercial catch returns are collated by the Loughs Agency of the Foyle, Carlingford and Irish Lights Commission. Prior to 1999, its predecessors the Foyle Fisheries Commission (1952 – 1999) and the Foyle and Bann Systems Ltd. (pre 1952) gathered and collated this information. Overall commercial catch returns dating from 1875 are available on a yearly basis. The commercial catch returns arise from four types of fisheries. Drift nets are gill nets deployed close to the water surface in the lough seawards of Lough Foyle. Draft nets are seine nets, which are deployed in-river in the main River Foyle and the River Roe at defined netting stations. Stake netting was a commercial trap fishery operated by the Foyle Fisheries Commission between 1952 and 1988. Bag nets employed a similar construction to stake nets but were left in place permanently. One licence was issued annually to be fished in the Lough Foyle estuary, although in 1988 an additional licence was issued. Data for these nets are available from 1964 to 1990 when operations ceased. Post 1952 when more detailed records are available, the data show catches of adult salmon peaking during the months June to July. Fish counting stations operating at present indicate that the main run of returning adult salmon occurs during these months with lower numbers of salmon returning in the spring and autumn/winter periods (Loughs Agency, unpublished data).

The catch data used here were not corrected for effort, as prior to 1952 no measure of effort was recorded.

Data on the NAOI are available from 1856 onwards (Hurrell, 1995; Hurrell, *et al.*, 2003). The winter index used in this analysis was calculated by taking the mean of the index between December and the following March. This winter NAOI then references to the January of that year. NAOI varies from year to year, but also exhibits a tendency to remain in one phase for intervals lasting several years. In order to smooth out inter-annual variation and examine periods of abundance, a five-year running average of both the NAOI and commercial catches was used in the analysis.

The data were analysed using the statistical software package SPSS 10.0. Linear and breakpoint regression analyses were used to determine the relationship between the long-term catch data and the NAOI. Relative Risk Analysis was used to determine the probability of catches exceeding a defined threshold (Lachin, 2000)

### *4.3 Results*

The commercial catches of Atlantic salmon in the Foyle system varied significantly between 1875 and 2001 from a maximum of 149,635 to a minimum of 12,500 salmon. Annual mean reported catch was 52,082 +/- 2,541 (mean +/- S.E.). Although there is considerable inter-annual variation evident, some underlying year-on-year trends are apparent (Figure 4.1). A five year running mean showed that catches were high at the end of the 1800s; in the mid 1930s to 1940s; in the 1960s and early 1970s and again in the 1980s and early 1990s (Figure 4.2).

**Figure 4.1** Annual commercial catch of salmon in the Foyle area 1875-2000.

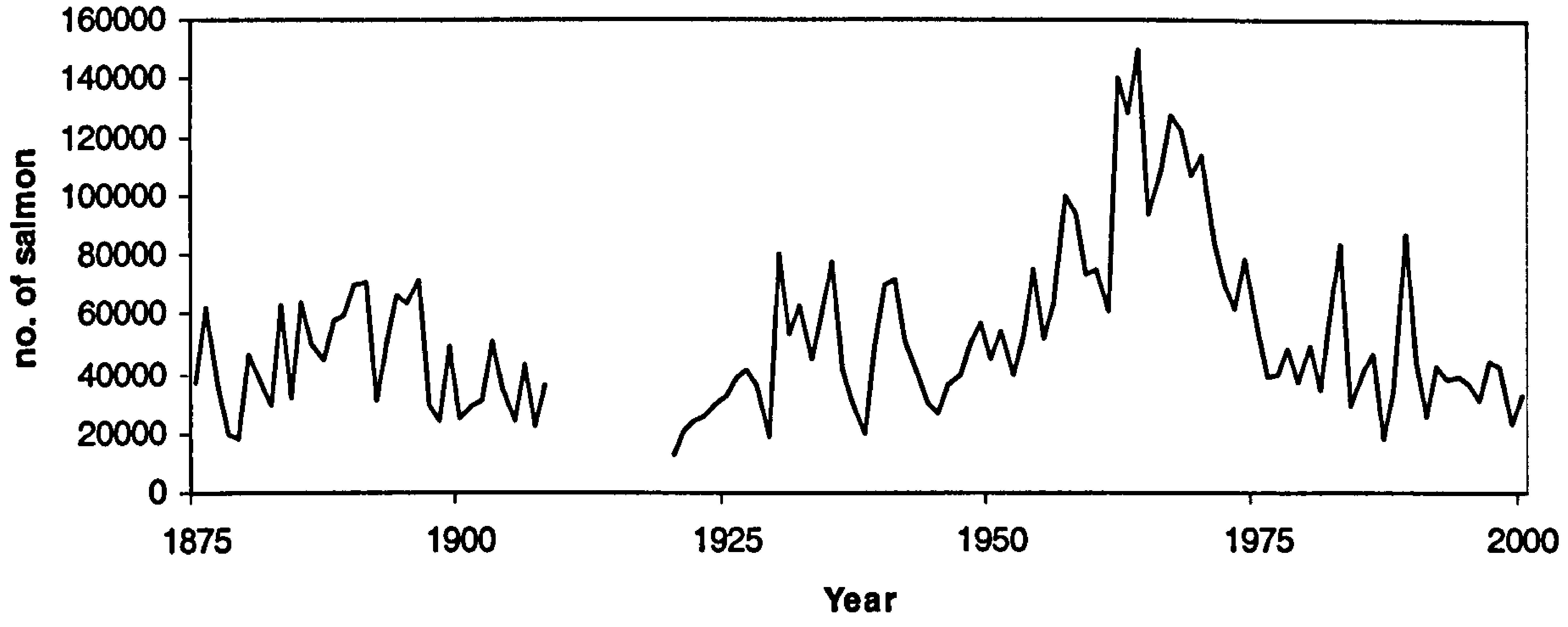
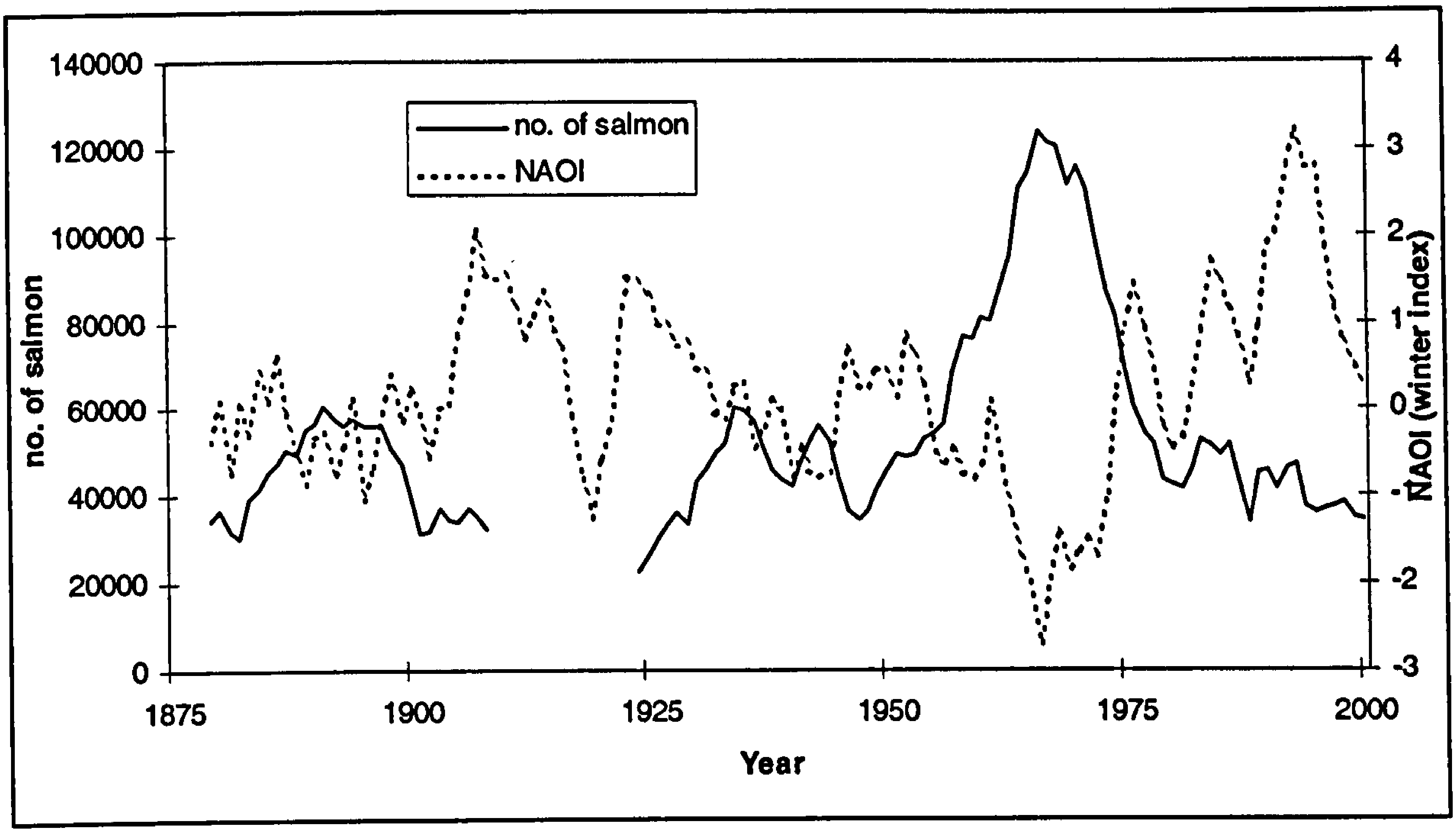
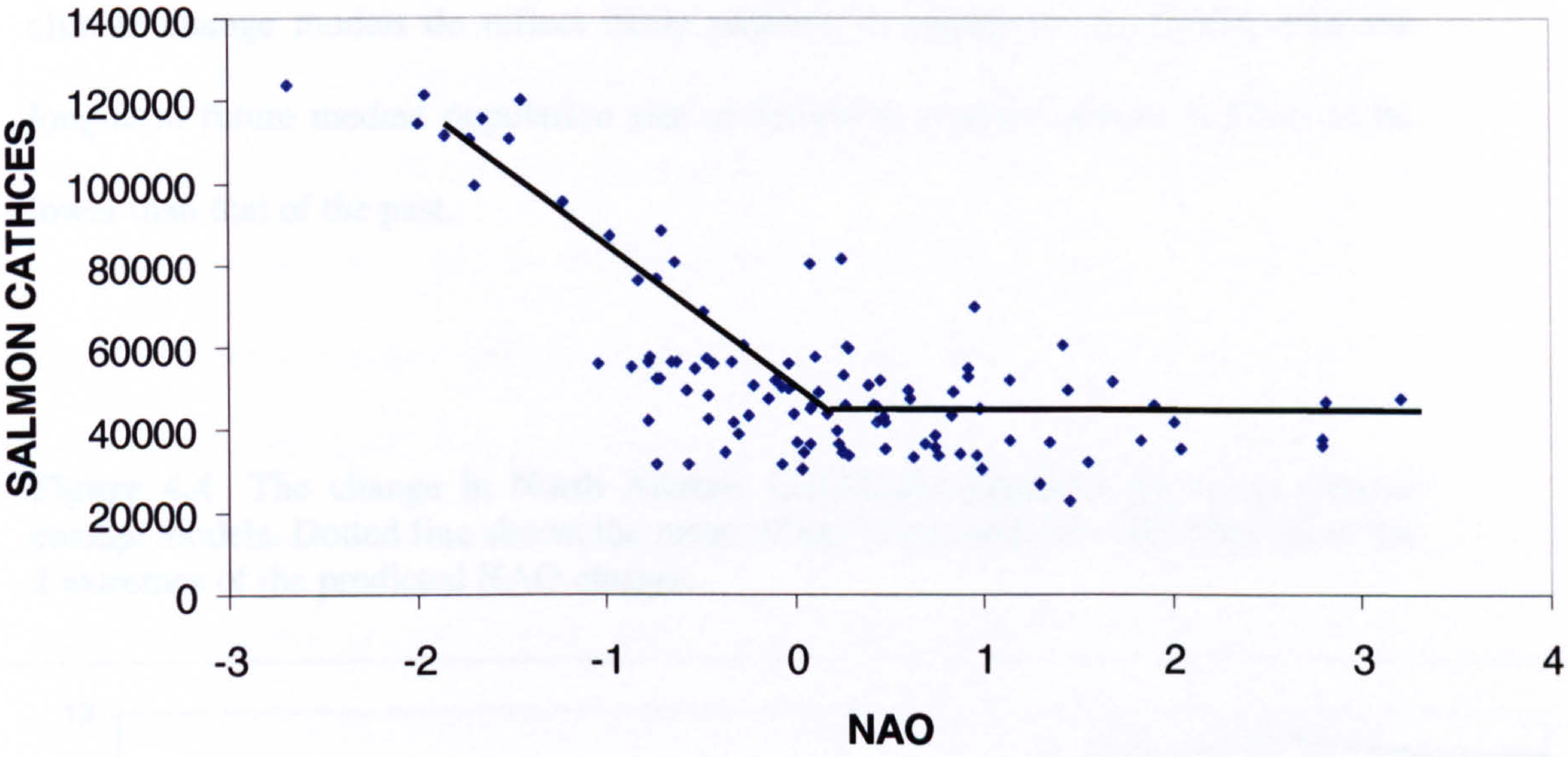


**Figure 4.2** The five year average commercial catches of migrant Atlantic salmon from the Foyle catchment 1875 to 2001 & the five year average NAOI: 1875 – 2000.



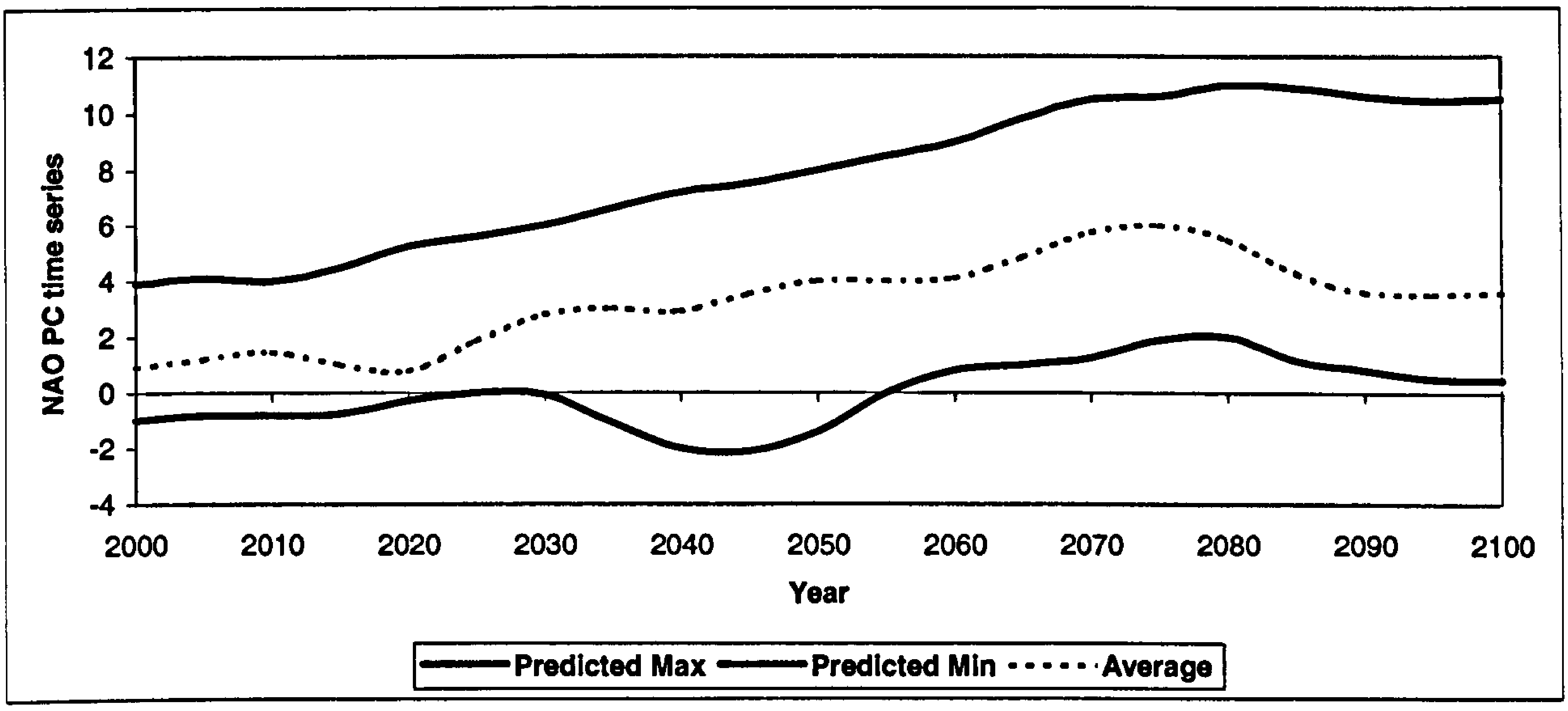
To examine the effect of climatic change on catches, the five-year running mean was regressed on the five year running mean for the NAOI. This showed a highly significant negative relationship ($F_{1,106}$ = 79.07, $r^2$ = 0.43, P<0.001, b = -0.654, intercept = 55,790, test of gradient t = -8.892, P<0.0001). However, there is some evidence that the relationship between NAOI and catch was not constant across the full range of NAOI values. Breakpoint analysis was used to determine the point of any potential change of influence of the NAOI. This analysis suggested a substantial relationship change above a NAOI value of 0.151. Years when the NAOI was above this point showed no significant relationship between the NAOI and catches ($F_{1,50}$ = 1.16; P=0.286; b = -0.15; intercept = 45,661; test of gradient: t= -1.08). However, for years with a NAOI below 0.151, there was a highly significant negative relationship ($F_{1,54}$ = 129.97; $r^2$ = 0.701; P<0.001; b = -0.84; intercept = 41,005.8; test of gradient: t = -11.4; P<0.001) (Fig. 4.3). It was noted that the years of the lowest recorded NAOI (1960's) coincided with the highest catches (Fig. 4.1).

**Figure 4.3** The relationship between the winter NAO and commercial fishery catches of Atlantic salmon returning to the River Foyle over 122 year. Breakpoint analysis shows a uncoupling of a negative relationship about a NAOI of 0.151.



Seven models of the effects of climate change on the NAOI resulting from a 1% per annum compound change in atmospheric carbon dioxide levels have been summarised by Gillett *et al.* (2003) (Figure 4.4). All models predicted an increasing NAOI with time. The mean of the seven models suggests NAOI will increase approximately five fold over the next 75 years. Assuming that the NAOI has a similar response to change over time as does the NAOI for the rest of the year, NAOI values of under 0.151 will become less frequent than in the past, the frequency of occurrence decreasing with time. There is some evidence that this may already be occurring as in only 2 of the last 10 years has the NAOI dropped below 0.151. As a result, data presented here would suggest that the linkage between the NAOI and population size would frequently remain uncoupled in the future. In addition, these data predict a change in the frequency of abundant, returning migrant populations of salmon. Relative Risk Analysis shows that the probability of achieving a catch of salmon greater than the median (47,800 between 1879 and 2001) is 2.34 times lower for a NAOI greater than 0.151 than for a NAOI of less than 0.151 (Relative Risk Analysis: RR=2.34; 95% confidence limits = 1.52-2.34; Yates corrected $P<0.0005$). Thus, assuming that climate change models do reflect likely patterns of change in the NAOI, then the long-term future median population size of returning migrant salmon is likely to be lower than that of the past.

**Figure 4.4** The change in North Atlantic Oscillation predicted by seven climate change models. Dotted line shows the mean of the seven models, solid lines show the 2 extremes of the predicted NAO change.



### *4.4 Discussion*

The population size of adult Atlantic salmon in the Foyle system as indicated by commercial catch returns has been highly variable over the years since 1875, but catches are generally regarded as large when compared with other systems (Shearer, 1992). Within this variation there are general trends of changing abundance linked with variation in the North Atlantic Oscillation. This feature may affect salmonid abundance in several ways. In the freshwater phase, Elliott *et al.* (2000) found that the date of fry emergence over 30 years in a sea trout nursery stream, predicted by an individual based model (Elliott & Hurley, 1998), correlated highly significantly with the NAOI. These authors also found a significant relationship with instream water temperature and suggested that this may be the actual mechanism driving variation in the model. As a measure of the dominant mode of winter climate in the northern hemisphere, the NAOI has also been linked directly to sea temperatures which affect salmon when feeding at sea (Martin & Mitchell, 1985; Reddin *et al.*, 2000; Dickson & Turrell, 2000). Here, a negative relationship is shown between the NAOI and the abundance of migrant salmon returning to the River Foyle in Ireland for indices below 0.151. Above 0.151 this relationship breaks down and at higher values there is no significant relationship between NAOI and catch abundance. The proximate climatic mechanism modulating salmon abundance is unclear, but there are a number of possibilities. Dickson and Turrell (2000) outlined the relationship between ice flux and a positive NAOI, which increased into the 1990s. This potentially affects salinity and water temperature. The NAOI may also indicate changing thermal habitat optima available to salmon through the cooling or warming of either migration routes or feeding areas such as those north of Iceland or off Greenland. Martin and Mitchell

(1985) found evidence to suggest that the abundance of multi-sea-winter salmon returning to the River Dee in Scotland, was linked to an increase in sea-surface temperature in the waters north of Iceland, which has in turn been linked to a decreasing NAOI (Hurrell *et al.,* 2003). This mechanism suggests that a strongly negative NAOI results in an increased quantity or quality of thermal habitat available to Atlantic salmon, resulting from increasing water temperature in these areas. In the northwest Atlantic, a thermal habitat index has been used effectively to predict salmon abundance. This index shows a significant relationship with the NAOI and may therefore be considered a useful tool in determining salmon abundance (Dickson & Turrell 2000; Beaugrand & Reid, 2003). The study presented here indicates that this may not be valid now or in the future.

Although when hindcasting over the last 126 years the NAOI is clearly a significant predictor of returning salmon migrant numbers, it is clear that the value of the NAOI as a forecasting tool to predict population size is highly suspect. Here it is shown that when the NAOI exceeds 0.151, then predictive capacity breaks down. Over the last decade the NAOI has been greater than 0.151 in 8 out of the 10 years. Based on current climate change models, this is a trend that is likely to become more extreme. Thus it is concluded that it is unlikely the NAOI will be a useful tool to forecast Atlantic salmon population abundance and that its inclusion in predictive models should be viewed with caution.

# Chapter 5. Local instream and catchment spatial scale habitat characteristics determine 0+ fry density of Atlantic salmon (*Salmo salar* L.) in the River Foyle.

## *5.1 Introduction*

Temporal variations in population size arise as a result of density-dependent or density-independent factors and the interplay between them (Elliott, 1994; Newton 1999; Harwood *et al.*, 2003). In contrast, spatial variation in density is primarily a function of the habitat in which animals live (Jenkins, 1964; Kennedy & Strange, 1980; Kennedy & Strange, 1982; Elliott, 1994). For a number of species enough is known about the relationship between habitat use and population size to be able to construct predictive models to estimate carrying capacity of a given habitat. For example Alisauskas and Arnold (1994) in a study on American coots (*Fulica americana)* found that a linear relationship explained a high proportion of variance ($r^2$=0.54; p<0.001) between an estimate of population size (numbers shot each year) and the numbers of ponds on the prairies the preceeding summer. Models such as these allow predictions of spatial patterns of habitat use and give an insight into mechanisms operating on the population thus enabling predictions to be made which support population and habitat management. This is particularly important in species of high conservation value or which are exploited. One such species is the Atlantic salmon (*Salmo salar* L.). A number of habitat type, population regression models linking local habitat type and density already exist for stream dwelling salmonids (Binns & Eiserman, 1979; Milner *et al*, 1995, 1998; Grant *et al.*, 1998; Poff & Huryn, 1998).

As some elements of habitat for stream dwelling salmonids, for example water quality, are partly a function of activity higher in the catchment, this study attempts to extend existing models by considering environmental effects at both local and catchment scales. Specifically, it attempts to model effects of the upper catchment on the deviations in density estimated by local habitat type.

### *5.2 Materials and Methods*

Five minute timed electrofishing surveys (Crozier & Kennedy, 1994) were carried out using an Electracatch backpack electrofisher at 307 and 279 sites, during July and August of 2001 and 2002 respectively, throughout the River Foyle catchment, Ireland. This work is part of the Loughs Agency's ongoing development programme and was carried out by field staff. The Agency has a maximum of 350 suitable sites identified, a target of 200 of these are to be fished at a minimum each year. For each site all underyearling (0+) salmon fry and brown trout (*Salmo trutta* L.) were counted. Fish less than 7 cm were counted as 0+. Other fish species such as stoneloach (*Barbulata barbulatus*), roach (*Rutilus rutilus*), eels (*Anguilla anguilla*), encountered were noted as present.

Sites were chosen specifically for their general suitability for juvenile salmonids, i.e. relatively shallow (10-30 cm deep) and relatively coarse substrate. Sixteen measures of in-stream and bankside hydrology and geomorphology were gathered concurrently with the electrofishing data and used in the analysis (Table 5.1). The widest site fished was 33 m with a maximum depth of 30 cm. The greatest maximum depth fished was 120 cm with a site width of 24 m.

**Table 5.1** Local scale site-specific variables collected for each sampling for 350 sites in the Foyle catchment.

| |
|---|
| Width – this was the average width at the site and was measured in metres. |
| Minimum depth – minimum depth of water measured in centimetres. |
| Average depth – average depth of water at the site measured in centimetres. |
| Maximum depth – maximum depth of water measured in centimetres at the site. |
| Flow ($m^{-1}$) – A net float was timed over a 10 m stretch and recorded in seconds. |
| Bankside cover – right hand bank – this was recorded as a percentage for both banks. |
| Bankside cover – left hand bank |
| Over hanging cover – right hand bank – this was recorded for presence or absence. |
| Over hanging cover – left hand bank |
| Percentage bedrock |
| Percentage boulder |
| Percentage cobble |
| Percentage gravel |
| Percentage fines |
| Percentage sand |
| Percentage mud |

For the purposes of analysis, the data sets were combined, and every second site extracted. One set of data was used to construct the model while the second set was used to test its predictive power.

To categorise the broader scale catchment on salmon fry density, data for the catchment upstream of each survey site were extracted from 1:50,000 Discoverer Series OS maps and Geological Survey of N Ireland maps (1:50,000 Drift Edition and 1:250,000 Quarternary Edition). Catchment data collected included (Table 5.2):

**Table 5.2** Catchment scale characteristics calculated from ordnance survey and geological survey maps for each of the 350 sampling sites in the Foyle catchment.

| |
|---|
| Catchment area ($km^2$) |
| Stream order |
| Distance of the site from the stream source (km) |
| Distance of the site from the streams confluence with the main River Foyle (km) |
| Altitude (m) |
| Slope at the site |
| Presence of lake upstream |
| No. of houses per $km^{-2}$ upstream of site |
| Distance to nearest house (km) |
| Distance to nearest farm (km) |
| Percentage of urban areas upstream |
| Percentage area of grassland upstream |
| Percentage area of woodland upstream |
| Percentage area of peat upstream |
| Percentage area of glacial alluvium upstream |
| Percentage area of glacial lacustrine upstream |
| Percentage area of glacial calcareous tufa |
| Percentage area of glacial boulder clay |
| Percentage area of glacial sand and gravel |
| Percentage area of bed rock |
| Percentage area of gneiss |
| Percentage area of felsite |
| Percentage area of diorite |
| Percentage area of sandstone |
| |

### 5.2.1 Catchment Scale Characteristics

#### Catchment area

The catchment area above each sampling site was calculated by determining the river network boundary above the sampling site and calculating catchment area in $km^2$.

#### Stream order

Stream order was derived using the method developed by Horton (1945).

### Distance from source

The distance of the electrofishing site from the upper-most reaches of that arm of the river system.

### Distance from confluence with the River Foyle

This is the distance as measured from the map of the survey site to the streams confluence with the main-stem of the River Foyle.

### Altitude

This was taken by interpolation from height contours on the map either side of the site.

### Stream Gradient

The stream's gradient was derived by measuring the horizontal distance between the nearest two contour lines and dividing this by the change in altitude.

### Presence or absence of a lake upstream

### Number of houses present

This was calculated by counting the individual houses from the map.

### Housing density

A density for the catchment was then derived by dividing the number of houses by the catchment area ($km^2$) above the sampling site.

### Distance to nearest house

The distance to the nearest house from each site was measured in metres.

### Land use

Three categories of landuse: urban; grassland and woodland were defined from the 1:50,000 series 'Discoverer Series' maps. The area of each was measured in $km^2$ for each catchment above each sampling site. These were then converted to percentages of the sub-catchment area and arc-sine transformed before fuller analysis.

### Geology

Seven geological characteristics of the catchment outlined below were also categorised for each site. These were obtained from 'Drift and Quaternary editions of Geological Survey of N Ireland' maps. The areas, in $km^2$, covered by the various deposits were measured on a digitising pad and converted to percentages which were then arc-sine transformed for analysis.

The characteristics used were:

Drift

- *Peat*
- *Glacial alluvium - Waterborne matter deposited by rivers*
- *Glacial lacrustine alluvium - Similar to alluvium only deposited in a lacustrine environment*
- *Glacial calcareous tufa*
- *Glacial boulder clay*
- *Glacial sand and gravel*

Solid

- *Bedrock*
- *Gneiss*
- *Felsite*
- *Diorite*
- *Sandstone*
-
-

### 5.2.2 Analysis

The data was modelled in SPSS V.10 using single and stepwise forward multiple-regressions having 0+ salmon as the dependent variable.

### 5.3 Results

Regressing the catch of 0+ salmon fry from the 5 minute electrofishing samples using all sites including those which had no 0+ salmon present, on local site specific data (Table 5.1) in a forward stepwise multiple regression showed that maximum water depth at the site was the best predictor of 0+ fry number, deeper water having lower 0+ abundance ($F_{1,139}$=4.91; $r^2$=0.027; p=0.028). The model was significantly improved however, by the addition of the width at the site ($F_{2,138}$=4.65; $r^2$=0.05; p=0.011) and the percentage of bedrock present ($F_{3,137}$=4.317; $r^2$=0.066; p<0.006) (Table 5.3).

**Table 5.3** Stepwise regression of local site specific stream characteristics on 0+ salmon numbers for a) all sites (including sites with no 0+ salmon); b) only sites where 0+ salmon were present.

| a) | F | df | $r^2$ | p< |
|---|---|---|---|---|
| Maximum water depth at site (-) | 4.91 | 1,139 | 0.027 | 0.03 |
| Maximum water depth at site (-); Width (+) | 4.65 | 2,138 | 0.050 | 0.01 |
| Maximum water depth at site (-); Width (+); Bedrock (-) | 4.32 | 3,137 | 0.066 | 0.006 |
| b) | | | | |
| Bedrock (-) | 3.844 | 1,98 | 0.028 | 0.053 |
| Bedrock(-); Average water depth (-) | 3.821 | 2,97 | 0.054 | 0.025 |

Increasing river width had a positive effect on numbers of 0+ salmon present but the percentage of bedrock at the site was negatively related to salmon numbers. When only sites with 0+ salmon present were included it was found that the percentage of bedrock and average depth provided the best model ($F_{2,97}$=3.82; $r^2$=0.054; p=0.025), both of these were negatively related to increasing salmon numbers.

Local instream habitat characteristics were highly significant predictors of between site variation in salmon numbers, however the percentage of variation explained was low (6.6% for all sites; 5.4% for sites without 0+ salmon). To test if broader scale catchment characteristics were affecting salmon abundance, wider catchment scale variables (Table 5.2) were used as predictors against 0+ salmon numbers. Firstly, these were examined against all of the available sites including those which did not have 0+ salmon. The percentage of glacial sand and gravel in the catchment above the site was found to be the best predictor ($F_{1,73}$=11.83; $r^2$=0.128; $p<0.001$), the addition of felsite ($F_{2,72}$=9.63; $r^2$=0.189; $p<0.001$) and altitude at the site greatly improved its predictive ability ($F_{3,71}$=8.421; $r^2$=0.231; $p<0.001$) (Table 5.4a). When only sites where salmon were found were included the size of the catchment area above the site was the best predictor ($F_{1,48}$=10.426; $r^2$=0.164; $p<0.002$), the addition of the percentage of sandstone ($F_{2,47}$=7.846; $r^2$=0.218; $p<0.001$) and the distance of the site from the source of the river improved the predictive capacity of the model ($F_{3,46}$=7.045; $r^2$=0.270; $p<0.001$) (Table 5.4b).

**Table 5.4** Stepwise regression of catchment characteristics on 0+ salmon numbers for a) all sites (including sites with no 0+ salmon); b) only sites where 0+ salmon were present.

| a) | F | df | $r^2$ | p< |
|---|---|---|---|---|
| Glacial sand & gravel (+) | 11.83 | 1,73 | 0.128 | 0.001 |
| Glacial sand & gravel (+); Felsite (+) | 9.63 | 2,72 | 0.189 | 0.001 |
| Glacial sand & gravel (+); Felsite (+); Altitude (-) | 8.42 | 3,71 | 0.231 | 0.001 |
| b) | | | | |
| Catchment area (+) | 10.43 | 1,48 | 0.164 | 0.002 |
| Catchment area (+); Sandstone (-) | 7.85 | 2,47 | 0.218 | 0.001 |
| Catchment area (+); Sandstone (-); Distance from mainstem Foyle (-) | 7.05 | 3,46 | 0.27 | 0.001 |

Both of these spatial scales were then combined in a single analysis to determine if catchment features were more important than site specific instream characteristics. It was found that when all the sites (including those with salmon absent) were included glacial sand and gravel, percentage of felsite, altitude, minimum depth of water at the site and stream width provided the best predictive model ($F_{5,69}$=7.347; $r^2$=0.300;

$p<0.001$) (Table 5.5a). Of these, altitude and the minimum depth of water were negatively related while the rest were positive. When the catchment scale characteristics and instream variables were included for only those sites with 0+ salmon present, the best predictors were found to be catchment area above the site, the maximum depth of water found at the site, the number of houses km$^{-2}$ upstream, the amount of urban area upstream, the percentage of boulder clay upstream and the percentage of sandstone in the catchment above the site ($F_{6,43}=7.190$; $r^2=0.431$; $p<0.001$) (Table 5.5b). Maximum depth of water, the amount of urban area upstream and the percentage of sandstone were negatively related to 0+ numbers while the rest of the variables were positive.

**Table 5.5** Stepwise regression of local scale and catchment characteristics combined on 0+ salmon numbers for a) all sites (including sites with no 0+ salmon); b) only sites where 0+ salmon were present.

Equation 1: Y= (Glacial sand/gravel*267.777) + (Felsite*810.421) + (Altitude*-0.0676) + (Minimum water depth at site*-0.300) + (Width at site*0.543) -0.0439

| a) | F | df | $r^2$ | p< |
|---|---|---|---|---|
| Glacial sand & gravel (+) | 11.83 | 1,73 | 0.128 | 0.001 |
| Glacial sand & gravel (+); Felsite (+) | 9.63 | 2,72 | 0.189 | 0.001 |
| Glacial sand & gravel (+); Felsite (+); Altitude (-) | 8.42 | 3,71 | 0.231 | 0.001 |
| Glacial sand & gravel (+); Felsite (+); Altitude (-); Minimum water depth (-) | 7.60 | 4,70 | 0.263 | 0.001 |
| Glacial sand & gravel (+); Felsite (+); Altitude (+); Minimum water depth (-); Stream width (+) | 7.35 | 5,69 | 0.300 | 0.001 |

Equation 2: Y= (Catchment area*0.124) + (Maximum water depth at site*-0.331) + No. houses $km^{-1}$*2.182) + (% urban area upstream*-1197.368) + (Glacial boulder clay*252.548) + (Sandstone*-2099.587) -5.801

| b) | F | df | $r^2$ | p< |
|---|---|---|---|---|
| Catchment area (+) | 10.43 | 1,48 | 0.161 | 0.002 |
| Catchment area (+); Maximum water depth (-) | 8.54 | 2,47 | 0.235 | 0.001 |
| Catchment area (+); Maximum water depth (-); No. houses $km^{-2}$ (+) | 7.31 | 3,46 | 0.279 | 0.001 |
| Catchment area (+); Maximum water depth (-); No. houses $km^{-2}$ (+); Urban area upstream (-) | 6.92 | 4,45 | 0.326 | 0.001 |
| Catchment area (+); Maximum water depth (-); No. houses $km^{-2}$ (+); Urban area upstream (-); Glacial boulder clay (+); | 7.04 | 5,44 | 0.381 | 0.001 |
| Catchment area (+); Maximum water depth (-); No. houses $km^{-2}$ (+); Urban area upstream (-); Glacial boulder clay (+); Sandstone (-) | 7.19 | 6,43 | 0.431 | 0.001 |

In order to test the predictive ability of the combined local and catchment wide characteristics the second data set of electrofishing sites was used. Salmon numbers predicted from the sites not used in model development (equation 1: using all sites) significantly predicted actual numbers caught, although with a low degree of variance explained ($F_{1,80}$=4.849; $r^2$=0.045; p=0,031). Using equation 2 i.e. only those sites where 0+ salmon were present, also significantly predicted the actual numbers of fish caught, although again a very small amount of variance was explained ($F_{1,90}$= 7.51; $r^2$=0.045; p=0.007). In order to investigate this further, paired t-tests were used, it was found that using salmon numbers predicted by equation 1 did not differ significantly from actual number (t=-0.609; 81df; p=0.544). The mean error, the differential between actual and predicted fish being 84% ±13S.E. Similarly, using the model developed for only sites where salmon were detected (equation 2) actual fish numbers did not differ significantly from predicted numbers (t=0.354; 91df; p=0.724). The mean error rate being 56%±15.23 S.E.

## 5.4 Discussion

Local habitat structure is known to influence the density of juvenile salmonids (Kennedy & Strange, 1982, 1986a, 1986b; Elliott, 1994; Kocik & Ferreri, 1998). However, wider catchment characteristics may be important factors in explaining both temporal and spatial salmonid variability (Milner, *et al.* 1998; Pess *et al.*, 2002). The model developed in this study proposes some novel additions to previous models, which are shown to be significant in explaining 0+ salmon numbers. Two variants of the model were developed, variant 1 included local instream and catchment scale characteristics and all of the available sites (including those where 0+ salmon were absent) while the second variant (including local and broadscale characteristics) included only sites at which 0+ salmon were present. It was found that this combination of broader scale catchment characteristics (glacial sand and gravel, felsite and altitude) and instream variables (minimum water depth and river width) explained 30% of the observed variation in variant 1. In this model catchment wide features clearly explained more of the variation in salmon numbers than local instream features. In the second model variant, differing broadscale characteristics were also found to be important (catchment area above the site, the number of houses $km^{-2}$ upstream, the amount of urban area upstream, the percentage of boulder clay upstream and the percentage of sandstone in the catchment) and also different site specific data (maximum depth of water found at the site). This variant of the model as might be expected also explained a higher proportion of the explainable variance ($r^2$=45%)

The relationships in both of these models expose a strong relationship between broadscale catchment wide features and 0+ abundance and are consistent with current understanding of how these underlying physical attributes can influence fish habitat potential. Geology and geomorphic processes dictate the range of morphological characteristics a stream reach can exhibit, thus partially determining the physical and biological characteristics of fish habitat. In model 1 which included all sites, the area upstream of glacial sand and gravel had a positive effect on salmon abundance. Juvenile salmon generally inhabit areas of shallow fast flowing water with a substrate, which is gravel and cobble dominated, in addition, adult salmon require gravel deposits for spawning (Jones, 1956; Shearer, 1992). Therefore it is likely that greater areas of sand and gravel deposits will contribute to providing such suitable habitat. The second variable, felsite, is an igneous rock. Hicks and Hall (2003) found that in the presence of another igneous rock, basalt, production of juvenile salmonids was positively related to its abundance, and they found that streams which flowed through areas of this rock type had generally steeper gradients than those which flowed through sedimentary sandstone rocks and that riffle habitat predominated which is the favoured habitat for juvenile salmonids. Salmon abundance decreased with increasing altitude, higher reaches of streams are generally regarded as being less productive as a result of lower temperatures which are known to adversely affect growth rates and densities of salmonids (Alabaster, and Lloyd, 1987; Elliott *et al.*, 1998). The first of the two local habitat features included was minimum water depth which had a negative effect on salmonid abundance. Symons and Heland (1979) found in laboratory experiments that 0+ salmon preferred depths in the range 6-9cm deep. It is postulated that, as minimum depth at the surveyed site decreased, it was dropping below this preferred range for 0+ fish, and therefore densities decreased as a result. The second and final local habitat feature was river width which was positively related to 0+ abundance. This variable is possibly related to fry dispersal post hatchingas adults tend to spawn in the upper reaches with fry dispersing downstream (Shearer, 1992).

In model variant 2, broader scale catchment characteristics were more important than site specific variables in explaining variation. Larger catchments had a positive influence on salmon abundance, as was found by Milner *et al.* (1995). Interestingly as the number of houses increased salmon numbers also increased although increasing urban areas had a negative affect. This suggests that up to a certain level increasing house numbers may improve productivity, possibly through increase of nutrients but above this threshold they may become detrimental to stocks, with increasing proportions of urban areas in catchments having a negative effect on fish abundance. Sandstone, being a sedimentary rock is the corollary of felsite, and as noted by Hicks and Hall (2003) showed negative relationships between salmonid abundance and increasing presence of of this rock on rivers in north America. They found that rivers which flowed through sandstone were generally low gradient with long reaches of deep slow flowing water, areas such as these are not favourable to 0+ Atlantic salmon production. The only site specific variable which was included in the second model variant was maximum water depth. Kennedy and Strange (1985) also found a negative relationship between increasing water depth and salmonid abundance in their study on streams in N Ireland, with preferred 0+ salmon habitat in water generally less than 20cm in depth.

The results show that there is no significant statistical difference between the actual abundance of salmon and those predicted by the models, but the average deviation between actual and predicted catches was 84 and 56% respectively. Thus the second variant of the model was the more robust of the two. This is to be expected as only sites with 0+ salmon were included. The relatively low predictive capacity and high error rate may in part be attributable to the choice of site. The sites chosen were identified specifically as good quality sites for 0+ salmon and so are likely to be similar within a narrow range of attributes, thus eliminating large variation. The predictive capacity would in all likelihood be improved through the selection of sites which are not as suited to 0+ salmon production.

In summary, it is shown in this study that habitat on two scales, site specific and catchment wide, affects the juvenile density of salmon in the River Foyle catchment. Instream habitat characteristics are shown to be significant predictors of juvenile abundance, but with the inclusion of broader catchment scale characteristics the predictive power of the model is greatly increased. Increasing urbanisation is highlighted as a potential future threat to the salmon of the Foyle area.

# Chapter 6. General Discussion

The Atlantic salmon is in decline in many parts of its range. However, the Foyle population, having declined from a period of high catches in the 1960's and 1970's (Figure 4.1), remains relatively stable at a lower level of production which is still high in comparison with many other systems (Anon., 2001).

In periods when abundance is high, conflicts between users (sport anglers and commercial harvesters) of the resource may diminish. However, during periods of low abundance this is liable to change. These conflicts generally arise out of concern over resource allocation and issues of conservation. Chapter 2 illustrated, using a long-time series of data the impacts of each of the user groups on each other and on successful spawning escapement. A 49 year time series dataset comprising commercial net and trap catches, recreational angling returns and an independent measure of breeding population size for the Atlantic salmon in the Foyle catchment was used to investigate the impact of competing methods of exploitation on each other and the effect of exploitation on population size. Positive correlations between commercial netting and trapping catches over the 49 years of this study did not support the hypothesis that commercial interception fisheries impacted negatively on each other. In order to test the hypothesis that large returning migrant population sizes mask underlying negative relationships between exploitation, or between exploitation and spawning population size, years with smaller than average returns were examined separately. No significant negative correlations between catches from differing forms of exploitation nor between total exploitation and spawning population size were detected in this subset of the data. With regard to sport angling catches it was shown that a reduction in commercial exploitation may result in an increase in the sport fishery catch. However with only 19% variance explained by commercial catches, this effect was weak. Positive correlative relationships between all forms of exploitation combined and an independent measure of spawning population size did not support the hypothesis that exploitation had a significant negative impact upon ultimate spawning population size between 1952 and 2000.

It was concluded that the Atlantic salmon population supported by this catchment is sufficiently large to mask any potential for negative impacts of exploitation on sustainability of stocks. In addition, although there is some small statistically detectable impact from commercial harvesting on the sport fishery, the different modes of commercial exploitation do not significantly impact detrimentally upon each other. Therefore, in the Foyle area, cessation of commercial harvesting should be largely regarded as an issue of resource allocation rather than conservation.

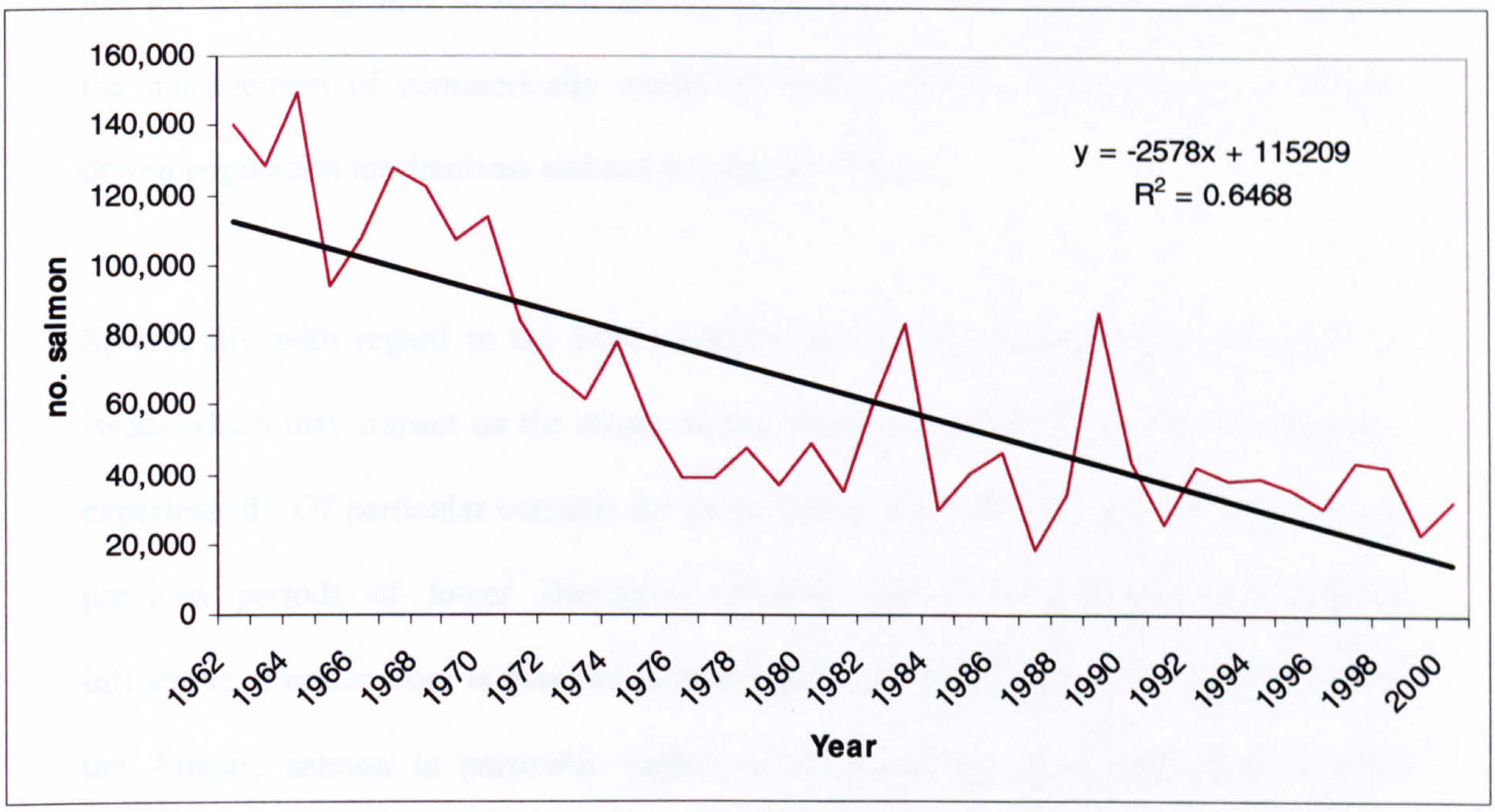
In Chapter 3 using the same long-term data set, the role of density dependent and life-stage specific environmental factors in controlling population size was investigated. A Ricker density-dependent model showed that spawning adult population size significantly explained variation in the resultant filial generation, however a significant amount of variation (ca. 68%) remained unexplained. It was shown that environmental factors were significant in explaining some of the remaining variance and that these influences were linked to specific life stages. This finding strongly suggested population bottlenecks in the complex life cycle of this species, during which, specific environmental effects may have had an impact they did not have during other periods. It was concluded that these life stage specific environmental effects were likely to contribute to the stochastic variation in population size remaining after the application of traditional stock-recruitment models and that the identification and quantification of these effects should allow improved model accuracy.

Chapter 3 highlighted the importance of various environmental parameters on salmon and in Chapter 4 this was investigated further by the testing of the effect of marine climatic conditions in the North Atlantic on the abundance of returning migrant Atlantic salmon, using a 126 year dataset of commercial catches. Catches of salmon from commercial netting stations significantly predicted a measure of population size independent of catches over a 49 year period; hence commercial net catches were assumed to be an adequate measure of relative population size. The North Atlantic Oscillation index in winter (NAOI) provides a generalised measure of climate variability for the northern hemisphere. Between 1875 and 2001, the NAOI explained a significant proportion of variation in five year running mean catches of migrant Atlantic salmon returning to the River Foyle. When the index was below 0.151, the NAOI correlated negatively with salmon catches ($r^2 = 70\%$) indicating that a significant proportion of the variance in population size in the past was the result of variability in conditions in the marine environment. However, when the NAOI was above 0.151, this relationship uncoupled. The probability of catches exceeding the long-term median, was 2.34 times lower in years where the NAOI was above the 0.151 breakpoint than for years when it was below 0.151. The NAOI had exceeded the 0.151 threshold on 8 out of the 10 years prior to 2001. Models of climate change indicate that the NAOI is likely to increase significantly with time. If these models are correct, this study would lead to the conclusion that a decoupling of broad scale climate effects on salmon population size will become the norm. Data presented here suggest two consequences of this: that the value of the NAOI as a predictive tool for forecasting adult salmon population size will be limited; and that the median population size will become lower in the future.

Chapter 5 tested the capacity of local instream and broadscale catchment characteristics to predict 0+ salmon abundance within the Foyle area. Data was collected from 307 and 279 sites for annual electrofishing surveys from 2001 and 2002 respectively of 0+ salmonids and semi-quantitative stream morphometric information. Using a combination of these local site-specific variables and broadscale catchment characteristics derived from Ordnance and Geological survey maps, two models were constructed. Model 1 used data for all available sites i.e. including those where 0+ salmon were absent, while model 2 was developed using only those sites where salmon where present. Both of these models were significant predictors of juvenile abundance using site-specific variables although the variance explained was small. However, both were improved significantly by the inclusion of wider broadscale catchment characteristics (model 1 $r^2$=30%; model 2 $r^2$=43%). When tested against an independent data set using paired t-tests, neither model differed significantly from the actual catch of salmon, although both had relatively high standard error rates (84%±13 and 56%±15.2 respectively). It was concluded that site-specific habitat characteristics were significant predictors of juvenile abundance, but with the inclusion of broadscale catchment characteristics the models' predictive powers were greatly increased.

Although the Foyle population of salmon has declined from the 1960's and 1970's in common with many other systems around the world, if the longer term catches are taken into consideration this period of lower level abundance may just be part of a longer term natural cycle. If the period from the mid 1960's is taken as an example (Figure 6.1) it may be seen that the population appears to be dramatically declining.

**Figure 6.1** Foyle area annual commercial salmon catches 1962-2003 with regression line.



Most of the intensive research work on Atlantic salmon commenced during this period. However, if the longer term picture is looked at (Figure 4.1) it may be seen that the catches during the 1960's coincide with the highest recorded abundance in the long-term dataset and the period we are in now is almost like a background level of abundance. This poses the question if there were similar long-term datasets for other stocks of salmon would they show a similar picture?

Fluctuations such as these have been observed in many different animal populations as previously seen with lemmings, voles (Ekerholm *et al.*, 2001) and red grouse (Jenkins *et al.*, 1963; Newton, 1998). Many of these cycles can be related to natural phenomena, which operate independently of direct anthropogenic influence, as for example changes in the distribution and abundance of the Pacific sardine and northern anchovy (Rodríguez-Sánchez *et al.*, 2002). The results of this study have therefore wider implications than just for the management of salmon and it is hoped that it will contribute to the debate on the management of commerically exploited species and the relative roles of density driven population mechanisms and environmental factors.

Specifically with regard to the Foyle salmon this study has highlighted a number of issues which may impact on the return of the population to the higher levels previously experienced. Of particular concern are those which may not have been an issue during previous periods of lower abundance, namely direct and indirect anthropogenic influences. Further work is required to understand how these influences interact to affect the Atlantic salmon in particular further development on the combination of stock recruitment and environmental models where available data permit. It is hoped that this thesis will form the basis of future study, in particular the development of pre-fishery abundance models which can be linked by genetic analysis to specific stock structures within the Foyle catchment.

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