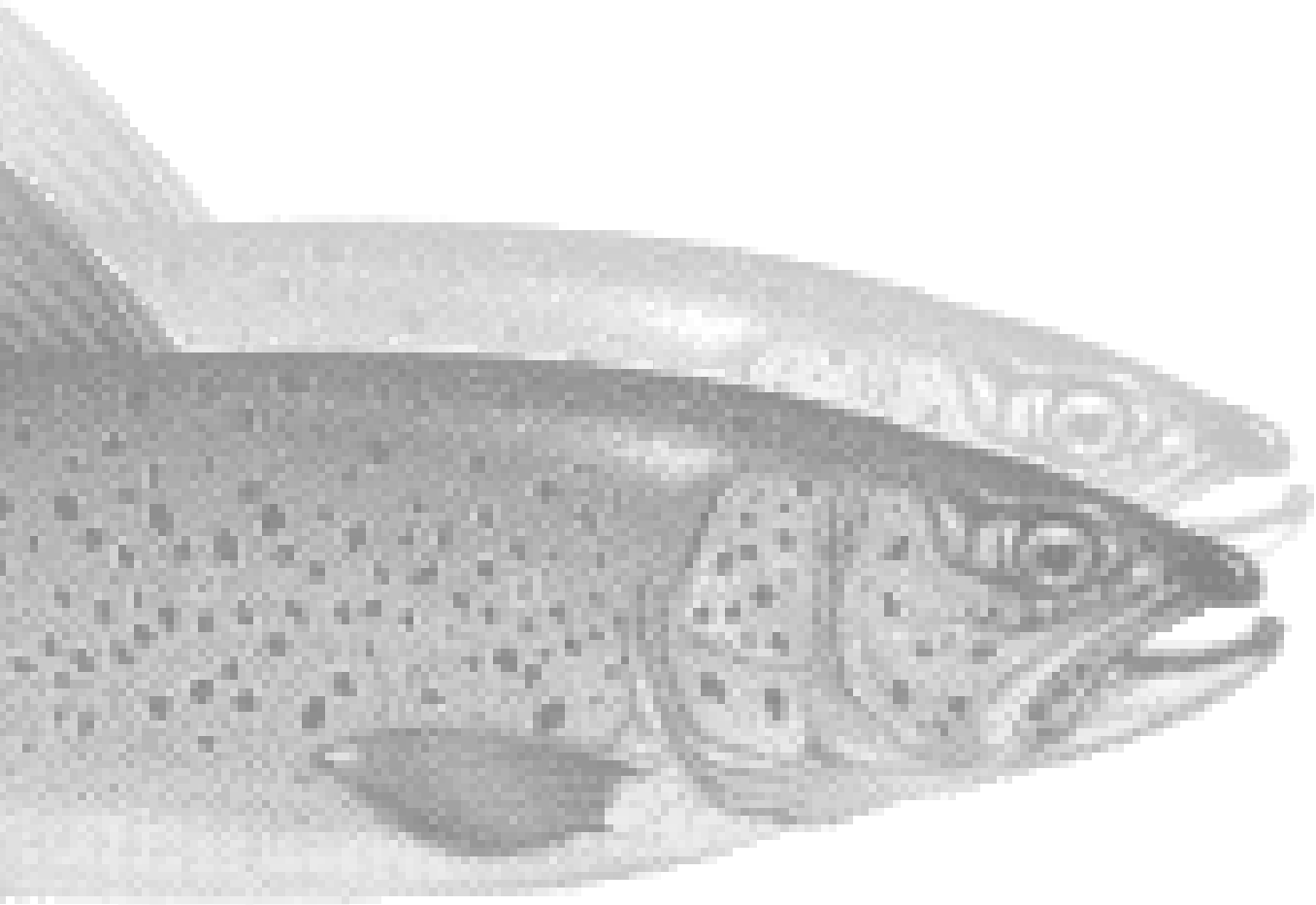


**RESEARCH INTO THE EARLY LIFE HISTORY OF ATLANTIC SALMON
WITH FOCUS ON PRACTICAL IMPLICATIONS FOR
CONSERVATION AND STOCK ENHANCEMENT**



DISSERTATION ZUR ERLANGUNG DES DOKTORGRADES

AXEL BAMBERGER

**RESEARCH INTO THE EARLY LIFE HISTORY OF ATLANTIC SALMON
WITH FOCUS ON PRACTICAL IMPLICATIONS FOR
CONSERVATION AND STOCK ENHANCEMENT**

Dissertation zur Erlangung des Doktorgrades der
Mathematisch-Naturwissenschaftlichen Fakultät
der Christian-Albrechts-Universität zu Kiel

vorgelegt von

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'It is a good morning exercise for a research scientist to discard a pet hypothesis every day before breakfast. It keeps him young.'

Konrad Lorenz (1903 - 1989)

Preface

I acknowledge with gratitude, the help I have received from Prof. Dr. Dietrich Schnack who has supervised my work and has been at hand with valuable editing reference. I greatly appreciate the help as the topic is not a core subject of his working group and reading through several drafts and proposals about a project that was happening on a distant green island must have been tedious.

The funding I received from the Deutscher Akademischer Austauschdienst, the Leibniz-Institut für Meereskunde, and from Dr. Annelise Chapman in the early stages of the project, provided me with a rare opportunity to set up a research project in Cornwall. Continuous travel funding from the Cornwall College Cooperation has kept me going (literately).

I would like to thank the Ecology department of Plymouth University and here especially Dr. Annelise Chapman, Dr Simon Rundle and Prof. Dr Tony Chapman for the interesting discussions and critical comments that put me on the right track at the beginning of the project.

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My sincerest thanks to the late Dikkum Ruscombe-King, his wife Deborah and their son Justin for permission to undertake this work at the Westcountry Trout farm. Without their support and open mindedness towards no-traditional techniques this project would have not been possible.

A very special thanks to Stan Spry from the Wadebridge Anglers, Paul Elliot from the Fowey Fishing Association and Jon Evans from the Camel Fisheries Association who had faith in the German scientist and were prepared to put all their precious salmon eggs into one (experimental) basket. I feel privileged to be the first German that has received Honorary Memberships of the local salmon fishing clubs and the motivating bank-side discussions that this has led to.

Boogie, Dave, Mark and Phil from the Wadebridge boatyard were of invaluable help whilst constructing and setting up the fibreglass monster that is the raceway system, and also for the weeks that we have spent in the cold Cornish rain building the Eco-hatchery, digging out sediment traps and preserving sluice gates with linseed oil. I thank Mr and Mrs Silcocks for allowing me to install the raceway system in their leat.

I have had the advantage -how great I alone can estimate- of my family who have supported me all the way; my parents for their 'constructive pessimisms' (yes, I did finish eventually); Maurissimo and the 'Pest' for the fact that they are more interested in fish than stones, and most of all to Astrid who has never become too tired to listen to salmon stories and Agency problems. Astrid has provided the drive and motivation for this long, long project. However, the list threatens to grow too long and therefore I thank everyone involved in my work for their help and their knowledge.

....so long – Vielen, Vielen Dank!

Executive summary

The widespread decline of anadromous Atlantic salmon (*Salmo salar* L.) populations makes it imperative to research the underlying cause and to develop mitigation measures. One of the most vulnerable phases in the life-cycle of salmon is the fry stage in early spring. Survival rates of juveniles emerging from the gravel of riverbeds are related to the three-dimensional complexity of bottom morphology and hence the variety of microhabitats within the nursery area. However, anthropogenically increased sediment supply due to changes in agricultural land-use reduces complexity, especially the roughness of the streambed.

This study used a series of controlled manipulative field experiments conducted in a purpose built raceway system, to provide quantitative data on the impact of sediment pollution on salmon production in freshwaters. The comparison of in-stream habitat with an increased sediment load and control (i.e. simulated natural) situations revealed that increased sedimentation drastically reduced the salmon fry carrying capacity of a stream. A modest increase in sand bed load (15%) in semi-natural streams reduced the fry density by 50% ten days after stocking with unfed fry. Emigration patterns of fry from sedimented habitat and control habitat were significantly different. Fry from both habitat types showed unusual active upstream migration which compensated for densities exceeding the carrying capacity.

Riverine habitat was optimised on a reach scale to complement the raceway results and to provide a temporary mitigation measure. The in-stream habitat of a mill leat was manipulated to build the first Eco-Hatchery for salmon in the UK based, on results from the raceway and on an extensive literature review. The hatchery achieved high survival rates of salmon juveniles throughout their freshwater life stages. Furthermore, in-stream sediment traps were developed to offer effective protection for key fry nursery habitat from excess sand bed load.

The data provided by the raceway system and the Eco-Hatchery inform riparian management plans. However, addressing sedimentation related issues in salmon rivers is a politically sensitive issue and will take time. Stocking with unfed fry is being used in the interim to temporarily enhance or restore populations. But stocking programmes based on conventional hatchery methodology as a response to declining stocks have frequently failed in both respects. A semi-natural incubator for salmon eggs, the Bamberger-box, was developed to address extremely low survival of newly stocked fry from conventional hatcheries. The new incubator mimics a natural salmon redd and aims in essence to produce wild fish in a hatchery environment. The results of five years field experiments using genetically different broodstock were encouraging. There was a significant increase in the average length and body mass of fry emerging from Bamberger-boxes and the mean eyed-egg-to-fry survival was 93% - greatly exceeding published data for egg-to-fry survival in the wild. Fry from Bamberger-boxes showed a significantly different and more natural rheotactic behaviour, and fewer fry had deformities when compared with fry incubated in conventional hatchery troughs. Seasonal and diurnal emergence patterns from Bamberger-boxes correlated with natural emergence patterns. A potentially crucial advantage of this new semi-natural incubation system was to ensure larvae survival during environmental extremes when all juveniles incubated in conventional hatchery troughs did not survive.

Large-scale commercial incubators based on the same principles as the Bamberger-Box were developed and proved equally effective in producing ecologically viable fry. Low costs of production and operation render the new incubators an economically viable alternative to traditional incubation systems. Exploratory research on the influence of hyporheic invertebrates abundance on fry size at emergence was carried out as a next step in continuously improving semi-natural incubation technology.



Zusammenfassung

Aufgrund der weit verbreiteten Abnahme der Bestände der Wanderform des Atlantischen Lachses, war es eine Notwendigkeit, die Gründe für den Bestandsrückgang zu erforschen und über kurzfristige Rettungsmaßnahmen nachzudenken. Eine der wohl empfindlichsten Phasen im Lebenszyklus des Lachses ist der Fry im Frühjahr. Die Überlebensrate von Larven, die den Schutz des Laichbett verlassen, ist normalerweise mit der dreidimensionalen Komplexität des Flussbettes und der daraus resultierenden Mannigfaltigkeit der Mikrohabitate für die Jungfische positiv korreliert. Die Habitatvielfalt und insbesondere die Mikrorauigkeit des Flussbettes ist allerdings durch anthropogen erhöhte Sedimentzufuhr, die zumeist eine Folge von veränderter landwirtschaftlicher Nutzung ist, bedroht.

Diese Studie liefert erstmals mit Hilfe von kontrolliert-manipulativen Feldversuchen, durchgeführt in speziell angefertigten Strömungsrinnen, quantitative Daten bezüglich der Auswirkungen von erhöhter Sedimentbelastung auf die Lachsproduktion im Süßwasser. Die direkte experimentelle Gegenüberstellung von Habitat mit erhöhten Sedimentablagerungen und Vergleichshabitat verdeutlichte, dass erhöhte Sedimentation die Kapazität eines Flussabschnittes Fry zu beherbergen drastisch reduziert. Eine moderate Erhöhung der Sedimentbelastung in naturnahen, experimentellen Flussabschnitten um 15 %, hatte eine Halbierung der Fryanzahl zehn Tage nach Besatz zur Folge. Das Abwanderungsmuster aus sedimentierten und Vergleichshabitat war signifikant anders geartet. Ein großer Anteil von überzähligen Fry aus beiden Habitattypen die kein Territorium etablieren konnten, wanderte erstaunlicherweise flussaufwärts ab.

Ein weiterer Teil des Projektes hatte als Ziel die Ergebnisse der Strömungsrillen zu untermauern, zu komplimentieren und darüber hinaus eine kurzfristige Lösung für das Problem der zurückgehenden Bestände anzubieten. Basierend auf einer intensiven Literaturrecherche und auf den Ergebnissen aus den Strömungsrinnen wurde ein vollständiger Flussabschnitt optimiert. Um die erste Öko-Fischzucht in Großbritannien für Lachse einzurichten wurde das Nasshabitat eines ausgedienten Mühlengrabens manipuliert. Dadurch konnten hohe Überlebensraten, über alle Lebensabschnitte im Süßwasser hinweg, in dieser neuartigen Fischzucht erzielt werden. Des Weiteren wurden Sedimentfallen entwickelt, die wichtige Laichabschnitte in Flüssen vor hoher Sedimentation gezielt schützen sollten.

Die aus den Strömungsrillen und der Öko-Fischzucht gewonnenen Daten werden benötigt, um langfristige Managementpläne zu erstellen. Es bedarf jedoch Zeit und ist es oft eine politisch sensible Angelegenheit, die eigentlichen Probleme zu beseitigen. In der Zwischenzeit wird deshalb oft auf den Besatz mit ungefütterten Fry zurückgegriffen. Bestände werden so ergänzt oder wieder aufgebaut. Allerdings haben Besatzprogramme, die auf herkömmlicher Fischzuchttechnologie basieren, in beider Hinsicht fortwährend versagt. Um den extrem geringen Überlebensraten von Setzlingen aus konventionellen Fischzuchten entgegenzuwirken, wurde die Bamberger-Box - ein naturnaher Brutkasten für Lachseier - als Alternative entwickelt. Es war das Ziel des neuen Brutkastendesigns ein natürliches Gelege nachzuahmen und, im Prinzip, natürlich-wilde Fische in einer kontrollierten Aufzucht zu erbrüten. Die Ergebnisse von Versuchsreihen, durchgeführt in fünf Jahren mit genetisch unterschiedlichen Brutfischen, belegen einen signifikanten Zuwachs in der durchschnittlichen Länge und dem Gewicht von Fry aus Bamberger-Boxen, im Vergleich zu Fry aus herkömmlichen Brutrinnen. Die durchschnittliche Überlebensrate, von dem Zeitpunkt des Besatzes als Ei im Augenpunktstadium, bis zum Fry, war mit 93 % wesentlich höher als vergleichbare, publizierte Überlebensraten in Flüssen. Fry aus Bamberger-Boxen zeigten natürliches Strömungsverhalten signifikant unterschiedlich im Vergleich zu Fry aus

herkömmlichen Brutrinnen. Weniger Fry aus Bamberger-Boxen hatten offensichtliche Verstümmelungen. Saisonale und Tagesprofile der Abwanderungsraten von Fry aus Bamberger-Boxen korrelierten mit publizierten Daten für natürliche Abwanderungsraten. Ein wichtiger, und potenziell ausschlaggebender, Vorteil der neuen Inkubationsmethodik ist, dass das Überleben der Larven während extrem warmer Klimaperioden sichergestellt werden kann, während die Larven in konventionellen Brutrinnen in vergleichbaren Situationen oftmals sterben.

Auf den gleichen Prinzipien wie die Bamberger-Boxen basierende, kommerzielle, großmaßstäblich Brutkästen wurden entwickelt und stellten sich als ebenso effektiv in der Produktion von ökologisch existenzfähigen Fry heraus. Geringe Produktions- und Betriebskosten qualifizieren die neuen Brutkästen als betriebswirtschaftlich praktikable Alternative zu konventionellen Brutkästen. Sondierungsversuche bezüglich der Relevanz von wirbellosen Tieren, die im hyporheicum des Inkubationsmedium leben, wurden durchgeführt um naturnahe Inkubationstechniken weiter zu verbessern.

Author's declaration

At no time during the registration for the degree of 'Doktorgrades der Mathematisch-Naturwissenschaftlichen Fakultät der Christian-Albrechts-Universität zu Kiel' has the author been registered for any other University award.

The work is original and was solely conducted by the author except where indicated by special reference in the text. The work was has been conducted in accordance with 'best practise' guidelines and regulations of the scientific community.

No part of the dissertation has been submitted for any other degree.

This study was financed with the aid of a studentship from the Deutscher Akademischer Austauschdienst (DAAD), the Leibniz-Institut für Meereskunde an der Universität Kiel, the Cornwall College Cooperation and a personal research fund from Dr Annelise Chapman.

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ITV Regional News (Wednesday 26 March 2002) *on the occasion of the launch of the first salmon 'eco hatchery' in Cornwall, UK*

ITV Nation Evening News (Wednesday 26 March 2002) *on the occasion of the launch of the first salmon 'eco hatchery' in Cornwall, UK*

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1 General introduction

1.1. The current state of the salmon stocks

The Atlantic salmon (*Salmo salar* L.) is a symbol of pristine rivers but also a fish species of major economic importance in the UK and elsewhere in the Northern Hemisphere. Regarded by anglers as the ‘king of fish,’ the salmon's reputation as a sport fish is unmatched. In some areas of the United Kingdom, notably Scotland, Ireland and Cornwall, salmon angling is the main freshwater fishing attraction and forms the basis of a significant local and tourist industry. The economic value one extra rod caught salmon brings each year to a fishery is considerable and was estimated by Postle and Moore (1996) at £5925 (based on 1995 prices).

Over the past two decades the chemical water quality of salmon rivers in the United Kingdom has been gradually improved (Environment Agency 2006), coastal netting has been significantly reduced (Wilkinson 1999), but, at the same time, catches in several salmon fisheries have undergone a steady decline (figure 1).

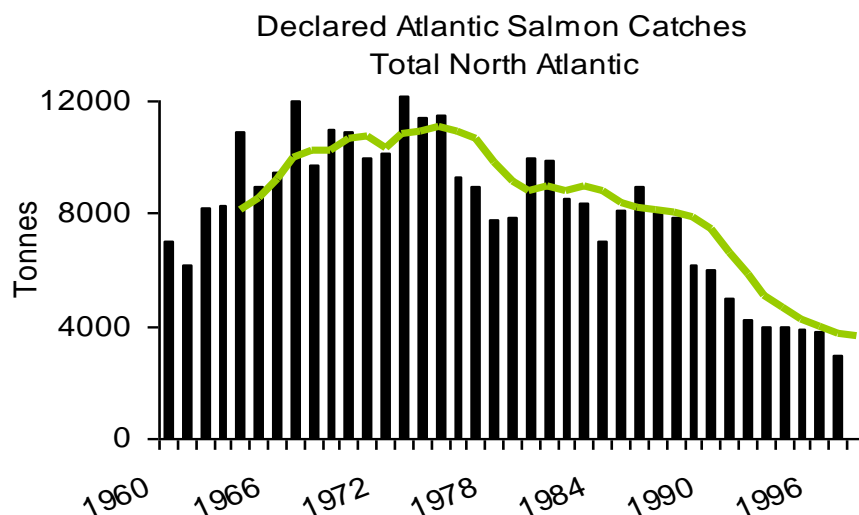


Figure 1: Decline of Atlantic salmon catches for the North Atlantic between 1960 and 1999 (modified after Boisclair (2004))

Over the past 25 years the number of returning salmon has fallen to a fraction of the fish's historic abundance in many regions (Mather et al. 1998, Parrish et al. 1998) and almost all the stocks are now outside the precautionary limits set by the International Committee for the Exploration of the Seas (ICES). Specific reasons for the continued decline are often unclear, but a combination of factors acting synergistically is probably responsible (Parrish et al. 1998):

A major threat to wild salmon populations poses commercial salmon farming, which threatens to erode the gene pool through inter-breeding with escapees, as well as promoting the spread of parasites and diseases (Porter 2003). Other hazards include pollution from industry and agriculture, dams and other man-made obstructions that impede salmon migration, river engineering projects that interfere with habitat and natural ecological processes. Threats to salmon at sea included commercial fishing and reduced food availability due to intensified pelagic fisheries in Arctic regions. Climate change is also increasingly suspected of affecting the salmon at sea. The spring stock component of the salmon population (large multi-sea-winter fish) in particular has reached what has been described as 'crisis level' (Mitchell 1999, WWF 2001, Hansen et al. 2003). The World Wildlife Fund (WWF) has included the Atlantic salmon in a list of ten species under grave threat of extinction. Since the Atlantic salmon is a keystone species of coastal streams, the problem could have far-reaching effects for the ecology of fluvial systems. Immediate remedial action has become crucial as well as publicly demanded (e.g. front page The Times (Nuttall 1998); lead story December issues Salmon and Trout Magazine: (Leventon 1998)).

1.2. Artificial enhancement: temporary mitigation

Generally, the numbers of adult salmon returning from the sea is proportional to the numbers of salmon leaving fresh-water (Jonsson and Jonsson 2004, Niemela et al. 2005) indicating density independent mortality at sea. It follows that the number of juveniles migrating out to the feeding grounds at sea has a direct impact on the numbers of returning adults recruiting into the fishery of a particular river. Stocking the freshwater habitat with

Atlantic salmon juveniles can be a cost effective and time efficient method to enhance the numbers of fish leaving fresh water (Aprahamian et al. 2003). In particular where the aim is to restore populations or mitigate against developments that compromised the freshwater habitat of the species stocking is an valuable tool to increase the number of recruits into a rod-and-line fishery. Stocking can benefit recreational fisheries by increasing the capital value of the fishery (Postle and Moore 1996), anglers may catch more fish, and the numbers of anglers fishing a particular site may increase. Artificial propagation can be implemented to mitigate, restore, enhance and conserve populations within the scope of natural production or it may be to increase the population beyond that which could be supported by the natural carrying capacity of the habitat, in order to increase the harvest. The objective of the former is to facilitate the long-term self-sustaining capacity of the population being managed. The second type of intervention is one for which the limitations of natural production are exceeded in order to expand production and as a consequence to possibly replace a situation of self-sustainability with one which must be artificially maintained. The biological considerations of these two types of intervention are different and for the most part these objectives are mutually exclusive (Aprahamian et al. 2003). A programme that is well suited to harvest augmentation may not conserve natural population structure. If the aim of the stocking exercise is to maximise local abundance temporarily by creating a self-sustaining population in the long term, then it is important to conserve the genetic and phenotypic variability, to ensure that mean individual fitness remains unchanged (Youngson and Verspoor 1998).

1.3. Selection of an appropriate life stage for stocking

Stocking to conserve the natural population structure is a widespread used and legitimate management tool. However, stocking can have irreversible and negative effects on the target population. There is strong pressure to regulate stocking activity and to reduce the risk of damage to the environment and in particular to the recipient population (Welcomme 2001). Costs and benefit calculations, and environmental risk management studies have to be carried out before an informed decision can be made about the most appropriate life stage selected for stocking. A crucial starting point for every stocking programme is the

careful selection of the broodstock. To ensure that the progeny of an augmentation programme is indigenous, and well adapted to their habitat a conservative, precautionary approach based on recent insight in population genetics of Atlantic salmon (e.g. (Stevens et al. 2006, Verspoor et al. 2006a, Verspoor et al. 2006b) has to be taken with regard to broodstock selection. From a genetics point of view it is imperative that the broodstock itself comes from the population selected for enhancement (Youngson et al. 2003). Consequently, fisheries managers have to balance the trade-offs between on one side promoting catch-and-release to enhance the numbers of naturally spawning fish and on the other side removing broodstock from an ailing wild population for a hatchery programme. Once the decision has been taken to implement a hatchery programme a judgment based on economical and biological factors about the live stage selected for stocking has to be made.

Terminology for freshwater development stages of salmon has been standardized with reference to major life changes (Allan and Ritter 1977). A salmon's life starts in winter /early spring as a fertilized egg (figure 2). In the wild eggs are deposited by the female in a depression in the river bed called a redd. During the first stage of development the eggs are referred to as green eggs. This stage commences approximately 24 h after fertilization and water hardening. Whilst it is possible to handle and move eggs within the first six to 24 h hours after water hardening without damaging them (Stead and Lair 2002), the slightest vibration during the green stage can result in high mortalities. The green stage is a stage of rapid cellular differentiation and organogenesis in the developing embryo. After about 245 degree-days (Stead and Lair 2002) when the primordial eyes of the developing embryo are clearly visible by the naked eye the eggs are referred to as eyed up. During the eyed stage major organs have already been formed. The eggs are fairly robust and can be moved without damaging them. They then hatch to an alevin. The alevin receives nourishment mainly from its yolk sac. The short but for the population dynamics critical stage when the fish starts to feed exogenously, is referred to as the fry stage. In the wild the fry would emerge from the gravel during his transition stage, and may disperse from the redd. The fry stage lasts a couple of weeks. The longest lasting juvenile life stage, following fry, where the fish exhibit characteristic bars as dark vertical stripes upon their flanks is called parr.

The transitional development stage, when the young salmon assumes the silvery colour of the adult and gets ready to migrate to the ocean is referred to as the smolt stage.

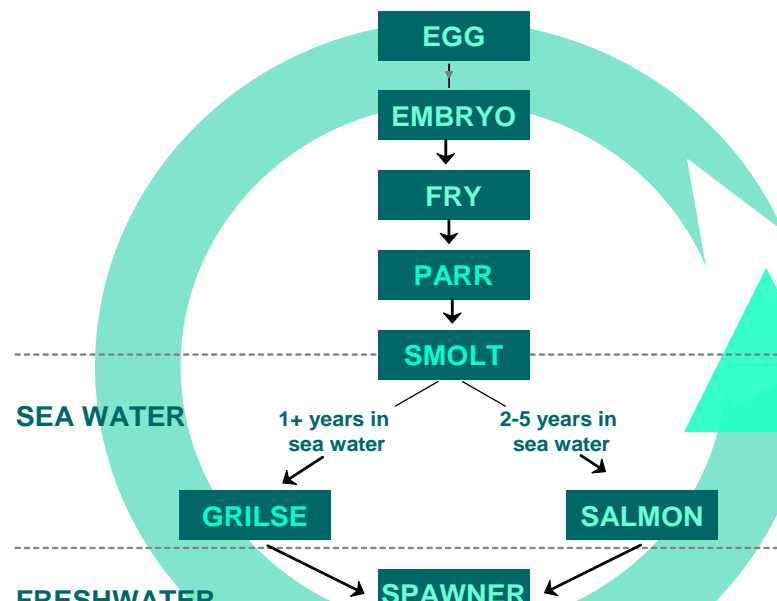


Figure 2: The life cycle of Atlantic salmon with a freshwater and a marine phase (modified after Laird and Needham (1988)).

Only very few augmentation programmes rely on transplanting fertilised eggs immediately after stripping. The short time period when the eggs can be handled without damaging them and the likelihood of adverse environmental conditions coinciding with the time of stripping in winter outweigh the benefits of low production costs and minimal interference with ontogenesis. For the vast majority of augmentation programmes eggs are transferred to a hatchery immediately after fertilisation. Eyed eggs are occasionally planted out into rivers in small, instream incubators like the Vibert Box (Vibert 1949). However, high mortalities in instream incubators can occur mainly due to two phenomena: a) clogging of the substrate interstices by fine particles, which reduces the water flow and the oxygen supply to eggs and alevins, as well as the dispersion of toxic metabolic wastes (review by Chapman (1988)) and b) destruction of artificial redds by the mechanical action of high velocity waters during flood conditions, which levels, scours out or buries the planting

sites (Chapman 1988, Crisp 1993b, 1996). Stocking with unfed fry is an ecological sound and often implemented alternative. It has several advantages compared to stocking with older juveniles: it is the most cost-effective larval stage to produce (Coghlan and Ringler 2004). The revenue costs of producing unfed fry in a hatchery environment are considerably lower than the cost of producing parr or smolts. Aprahamian et al. (2003) estimate hatchery operation cost of £0.04 to produce one unfed fry compared with £0.85 for parr or even £1.70 for smolt. From a biological perspective a more important advantage is that fry do not have to be weaned on an artificial diet before stocking. It has been recognized that feeding fish pellets and keeping them for a prolonged time in a hatchery environment has major negative effects on their performance capacities in the wild, in terms of foraging, movement, migration and predator avoidance (reviewed by Brown and Laland (2003)). Moreover, previous research on survival and growth of fed and unfed Atlantic salmon fry have failed to demonstrate consistent differences in their survival (Letcher and Terrick 2001, Letcher et al. 2004). The use of older juveniles in stocking programmes also has a number of, potential far reaching negative impacts, including bypassing important natural selection events (Einum and Fleming 2001). The key genetic consideration is to minimise artificial selection; the longer the fish are in the hatchery the greater will be the risk (Youngson and Verspoor 1998, Youngson et al. 2003). Stocking unfed fry (for simplicity referred to as fry from here onwards) ensures that juveniles are exposed to natural selection from a very early point in their life history.

1.4. Low survival rates of artificially reared fry

Hatchery supplementation programmes with Atlantic salmon fry are used by fisheries managers worldwide in an attempt to meet the dual goals of conservation and sustainable exploitation of this species (Stickney 1994, Aprahamian et al. 2003, Lorenzen 2005, Saltveit 2006). Increasingly strict regulations in the UK and elsewhere regarding the genotype of the broodstock impose that in most instances fish native to the river system to be stocked must be used for propagation (e.g. Section 30 of the Salmon and Freshwater Fisheries Act 1975). The increasingly difficult logistics of transporting live broodstock are a direct consequence from those recent regulations. Ongoing husbandry to keep the

broodstock alive adds considerably to the production costs of fry. For instance, in Cornwall each year wild salmon have to be caught with rod and line by licensed anglers during the fishing season, individually transported from the bank side to the hatchery and kept in holding tanks for weeks, sometimes months, until the optimum moment of female ripeness (Jon Evans pers. comm.).

Production costs have to be balanced against the survival rate of stocked fry in the wild and indeed more precisely the relative survival success of the 'enhanced' fish compared to the wild stock. On this background it is worrying to note that survival rates are variable and can be extremely low (less than 1% ref). From an operational point of view it is alarming to note that hatchery-reared salmonids typically survive less well in the river than wild reared fish (e.g. (Salo and Bayliff 1958, Foerster 1968, Mead and Woodall 1968, Heggberget et al. 1992, Aprahamian et al. 2003, Letcher et al. 2004) . Letcher et al. (2004) demonstrated that fry allowed to incubate and emerge naturally had higher survival rates than fish stocked as unfed fry. Mortality of newly stocked fry is extremely high during the first couple of days (Henderson and Letcher 2003) indicating that hatchery fry are inferior to naturally produced fry in certain characteristics essential for subsequent survival during a critical time in their life history (Mead and Woodall 1968). To improve post-release survival and hence viability of augmentation programmes attention has to be drawn to produce ecologically viable fry. Stickney (1994) argued that radical changes in fish cultural practices are required, in essence, to rear wild fish in a hatchery environment.

In an attempt to provide a more natural incubation environment, salmon eggs were incubated in a substrate matrix. The technology has been pioneered by the Canadians for Pacific salmon species (Bams and Crabtree 1976, Bams 1985) and subsequently used for incubating Atlantic salmon eggs in Canada (Pepper 1984, O'Flynn et al. 1995) and the Scandinavia (Eriksson et al. 1983, Hansen et al. 1985, Nortvedt 1986, Brannas 1989, Hansen et al. 1990). Similar systems have been used in America (Leon and Bonney 1979, Gray and Cameron 1987) and more recently in the UK (Westcountry Rivers Trust 2000, Environment Agency 2000). Although substrate incubation units were designed in a variety of sizes and filled with different substrates (ranging from natural river gravel to artificial substrates like Intalox Saddles, Biomat and Astro Turf® e.g. (Leon 1982,

O'Flynn et al. 1995)) to different depth (typical 3cm in Japanese style hatcheries and up to 1 m for some Atlantic salmon boxes) most designs share several basic principles: fertilised eggs are stocked into the incubator either green, i.e. within hours after fertilisation or at the eyed stage. The water supply is from below and percolates through the substrate at the top. Alevins develop within the substrate matrix. Emerging fry release themselves from the incubators by working their way to the substrate-water interface and emerging into the supra-gravel water.

There is convincing evidence in the published literature that substrate incubation has a positive effect on fry length and body mass at the time of emergence: O'Flynn et al (1995) found that BIOMAT substrate increased alevin growth in Atlantic salmon, Eriksson and Westlund (1985), Hansen and Torrissen (1985) and Hansen et al. (1985, 1990) all reported higher growth rates for Atlantic salmon alevins or a higher weight of first-feeding fry incubated on Astroturf™ substrate. Brannas (1989) reported that two out of three Atlantic salmon sibling groups grew better in simulated redds compared with conventional hatchery methodology. Peterson and Martinrobichaud (1995) demonstrated experimentally improved yolk utilization efficiencies by Atlantic salmon alevins on gravel substrate due primarily to higher embryonic growth rates at five different incubation temperatures. Leon (1975, 1982) and Leon and Bonney (1979) found that Atlantic salmon fry resulting from incubation in units containing Intalox Saddles were 45% heavier than fry incubated in smooth-based incubators containing no matrix substrate. Astroturf™, Intalox™ Saddles and gravel as incubation substrate had the same positive effect on fry length for five species of Pacific salmon (*Oncorhynchus spp.*)(Leon 1982). Similar results for Pacific salmon species were reported by Bams (1972, 1973, 1974, 1979, 1983, 1984, 1985), Bams and Crabtree (1976) and Bams and Simpson (1977).

Existing deep-substrate incubation units are a step in the right direction to provide a semi-natural incubation environment. They are certainly an improvement over established smooth-bottomed trough incubation systems. However, to achieve the goal of essentially breeding wild fry in a hatchery environment attention has to be drawn to the hydrological conditions within and above the incubation substrate. A need has been

identified by hatchery managers to develop incubators that closely resemble a redd in size and can be used in-situ for bank side incubation.

1.5. Optimum fry stocking densities

Breeding viable fry is the first step of a successful augmentation programme. Artificially reared fry subsequently have to be stocked into a riverine environment that can support them. There is an inherent maximum number of fish that can be supported by a given area of fluvial habitat (Solomon 1985). Thus, the objective for the fisheries manager is to manipulate the numbers of fish through a combination of natural reproduction and artificial stocking to approach carrying capacity. If stocks remain below the carrying capacity then the habitat is perceived to be under-utilised for that species, whereas attempting to increase populations beyond the carrying capacity represents wasted effort (time or money) since higher mortality and/or emigration will occur.

In moderate climates the fry stage is conceded to be a critical stage (or the 'population bottleneck' - (Shuter and Post 1990)) for population abundance and cohort strength (figure 3) where density-dependent processes occur (Einum and Fleming 2000b, Milner et al. 2003). High mortality (up to 95%) has been documented at this key life stage (Gee et al. 1978a, Gee et al. 1978b, DeGraaf and Bain 1986, Bergheim and Hesthagen 1990). To accurately estimate the carrying capacity of a stream section for salmon fry before stocking the question must be raised which factors are responsible for large scale natural mortalities of Atlantic salmon at the sensitive fry stage and whether man-made interventions interfere with the carrying capacity.

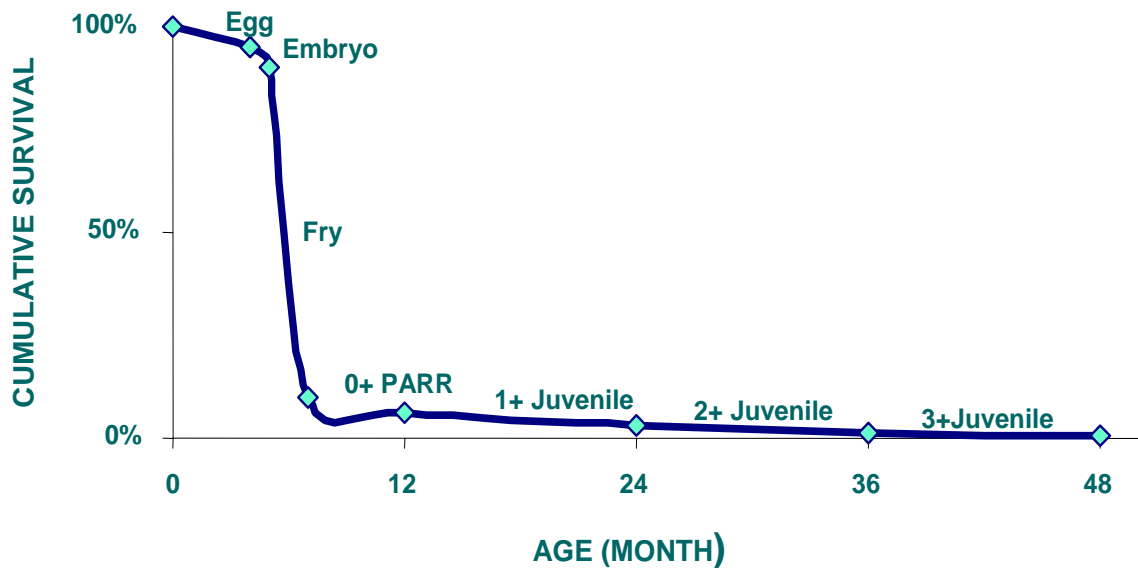


Figure 3: Estimated rates of cumulative survival through successive live stages for Atlantic salmon. Illustrated is the bottleneck of lowest survival at the fry stage. The figure refers to unimpaired rivers without anthropogenic interventions (modified after Symons (1979)).

1.6. Microhabitat is the resource in short supply

High density-dependent mortality of salmon fry is generally attributed to competition associated with initial peak juvenile densities that far exceed the stream carrying capacity (Chapman 1965, Fraser 1969, Kennedy and Crozier 1993). The capacity of a stream to hold salmonid juveniles during the critical first year of their lives is unlikely to be constrained by trophic factors (Gee et al. 1978b, Randall and Chadwick 1986), with the notable exception of very cold, nutrient-poor streams. Rather, fry abundance is largely a function of: (a) the amount of suitable microhabitats; and (b) the aggressive territory formation by juvenile salmonids (Armstrong and Nislow 2006). Territoriality is one principal mechanism for regulating population density in salmonids (e.g. (Gustafson-Greenwood and Moring 1990, Elliot 1994, Johnsson et al. 1999)). Physical and biological site attributes operate by controlling territory size and availability (Chapman 1966, LaVoie and Hubert 1996, Eklöv et al. 1999). A large number of investigations into site attributes, which determine microhabitat preferences of juvenile salmon, have been published, with

often contradictory results (e.g. (Gibson 1978, Hearn 1987, Bugert and Bjornn 1991, Nislow et al. 1998, Valdimarsson and Metcalfe 1998).

However, there is general agreement about the basic demands of juvenile Atlantic salmon and consequently about the factors affecting juvenile salmon mortality:

1. Feeding: Since salmonid juveniles fed mostly on drifting invertebrates, current velocity affects potential prey encounter rates (Bjornn and Chapman 1968, Smith and Li 1983, Nislow et al. 1998) as well as abilities to detect and capture prey items (Hughes and Dill 1990, Hill and Grossman 1993, Nislow et al. 1999, 2000).
2. Sheltering: when fish seek refuges from harsh environmental conditions, instream structure (e.g. rocks, vegetation) reduce energetic expenditure by sheltering individuals from areas of high current velocity (Morantz et al. 1987, Huntingford et al. 1988, Fausch 1993). Conversely, instream cover may negatively influence the reactive field (Eggers 1977, 1982) in which prey items can be detected and may also be associated with areas of reduced food availability (Grant and Kramer 1990).
3. Hiding: Where fish conceal themselves from specific threats. Instream structure, overhead cover (e.g. undercut banks, streamside vegetation, fallen logs, deep water) and turbid, fast flowing riffle sections provide protection from predators (Wilzbach 1985, Shirvell 1990). Moreover, increased visual isolation apparently reduces the agonistic behaviour in juvenile salmonids and thereby increases the holding capacity of a stream area for salmon fry (Kalleberg 1958, Bolliet et al. 2005).

The discussion of several authors over the relative importance of the distinct variables is not surprising, since habitat choice results from a variety of abiotic and biotic factors, which may interact synergistically. Furthermore, habitat requirements alter with: (i) developmental stage of the fish (ii) individual size (iii) season, and (iv) even time of day (Gibson 1966). Therefore, an individual's microhabitat use must be seen as a compromise between conflicting demands of energy intake and survival (Grant and Kramer 1990) - a

compromise that may be extremely context specific. A habitat with a high degree of spatial heterogeneity offers a vast array of low-current-velocity niches and minimises the risk of a short-supply of the resource during any stage of the development. The three-dimensional complexity of a nursery area and - bearing in mind the small size of salmon fry – in particular the complexity of the bottom morphology is often the overriding factor in determining the carrying capacity of spawning burns (McMahon and Hartman 1989, Haury et al. 1995). Thus, a measure for small-scale stream complexity may ultimately allow predictions of appropriate stocking densities for Atlantic salmon fry.

1.7. Effects of sedimentation on microhabitats of fry

In this century, man has had a profound effect on Atlantic salmon populations by fishing and alteration of habitat and water quality. Obviously, artificial interventions, which impact on natural bottlenecks of a population, cause the most direct and permanent alteration for the number of recruits in that population (Sinclair 1989). However, it is the resource which is already naturally in short supply, which is increasingly impaired: an increase in deposited sediment reduces the roughness elements on the streambed (Waters 1995). Sand deposition fills, plugs and buries most of the rough substrate and results in a much smoother stream bottom. Suspended particle matter (the sediment transport in fluvial environments is divided into the categories of suspended load, and bed load: (Miall 1996)) settles down and accumulates in low velocity niches on the stream bed which are essential for the survival of salmonid fry. The problem of increased sediment supply and an altered flow hydrology are wide spread in England and throughout the entire range of salmon distribution. Intensified livestock activity on river banks over the last 30 years, i.e. grazing and drinking, and drainage of marginal wetlands, have exacerbated sediment supply (National Rivers Authority 1996, Woodward and Foster 1997) by erosion runoff and poorer bank stability (figure 4). Sediment supply from agricultural crops such as flax, maize and winter wheat affect the process of sediment supply by means of bare field i.e. exposed soil during the wet winter months (Jackson pers. comm.). Furthermore, modern forestry, urban drain/sewer systems, and urban development contribute to an increased land runoff of sediments.

Most studies on the effects of sediment load, focus on egg-to-fry survival within the stream gravel: siltation of gravel interstices reduces the intra-gravel flows, leading to asphyxiation of eggs or alevins (e.g. (Peterson and Metcalfe 1981, Gustafson-Greenwood and Moring 1991, Berejikian 1995, Malcolm et al. 2003, Malcolm et al. 2004, Greig et al. 2005, Julien and Bergeron 2006, Levasseur et al. 2006). Studies on the effect of deposited sediments on Atlantic salmon fry habitat are scarce in the published literature.

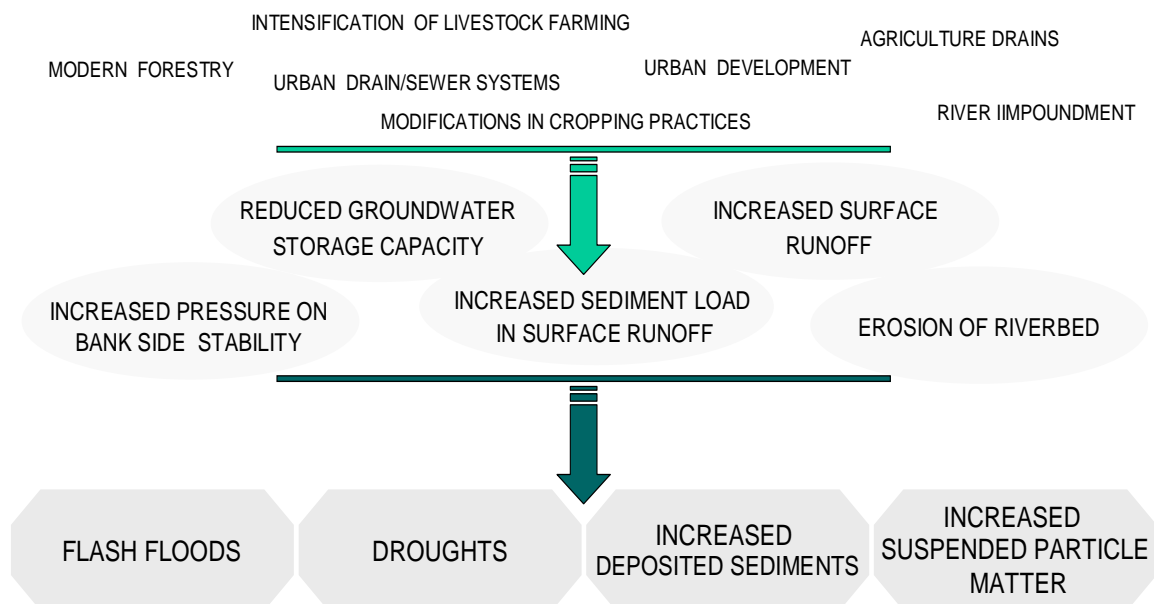


Figure 4: Flowchart illustrating direct and indirect effects of intensified human activities on salmonid habitat.

1.8. Study aims

The aims of this study were two fold: The first aim was to develop semi-natural incubation systems that are capable of producing ecological viable fry on a commercial scale in a hatchery environment. To mimic the conditions a developing alevin would find in a natural redd deep-substrate incubators like the ones used by Bams and Crabtree (1976), Bams and Simpson (1977) or the Environment Agency (2000) were modified to

incorporate a realistic intragravel water flow and a unidirectional surface flow on top of the gravel. During the first year of experimenting the incubators were scaled down to a size not normally used for commercial hatchery operations to enable quick and efficient testing of different prototypes. The most successful incubator design was subsequently benchmark tested against traditional hatchery incubation troughs. Scaled-up versions of this semi-natural design were tested and critically evaluated against biological and economical performance indicators. Test parameters were egg-to-fry survival rates and morphological factors like, body mass, fork length, condition factor, and the number of fish with body deformities. Data of fry emerging from semi-natural incubators were also compared with data available for emergence patterns from natural redds. The behaviour of emerging fry, at a time they would usually stocked into the river, was evaluated in flume tanks.

The second aim of this study was to evaluate the assumed relationship between the degree of sedimentation on the streambed and the carrying capacity of that section for Atlantic salmon fry. The practical execution of the project linked the following interactive approaches (figure 5):

1. A series of controlled manipulative field experiments are conducted in a semi-natural raceway system to investigate the effects of sediment deposits on the carrying capacity of a nursery area for salmon fry. The comparison of carrying capacities in stressed and control (i.e. simulating ‘natural’) situations allows the effects of this non-toxic anthropogenic pollution on survival rates of juvenile Atlantic salmon to be quantified.
2. Based on the experimental results and on an extensive literature review, riverine habitat was be modified on a reach scale (Massimo et al. 2004) to achieve maximum survival rates of salmon juveniles. This concept was used to augment salmon stocks if problems associated with reducing the excessive supply of sediments to salmon streams, necessitate a new, cost-effective and environmentally friendly alternative to conventional hatcheries.

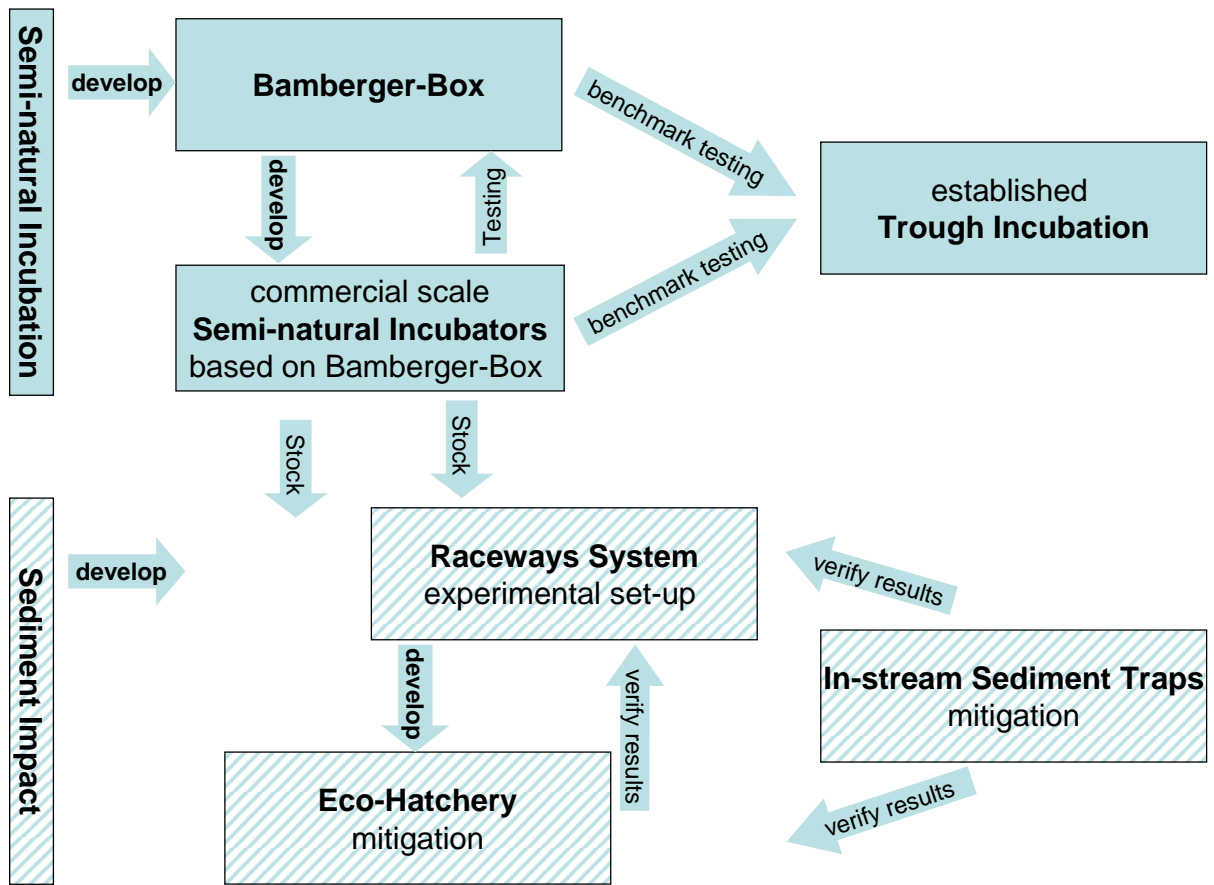


Figure 5: Overall project outline 'Research into the early life history of Atlantic salmon with focus on practical implications for conservation and stock enhancement.'

2 Study area

The study focused on tributaries and headwaters of the River Camel and the River Fowey (figure 6). The Camel and Fowey catchments were chosen for the study because a significant decrease in salmon rod catches has been reported in recent decades along with increased sediment supply into key spawning areas.

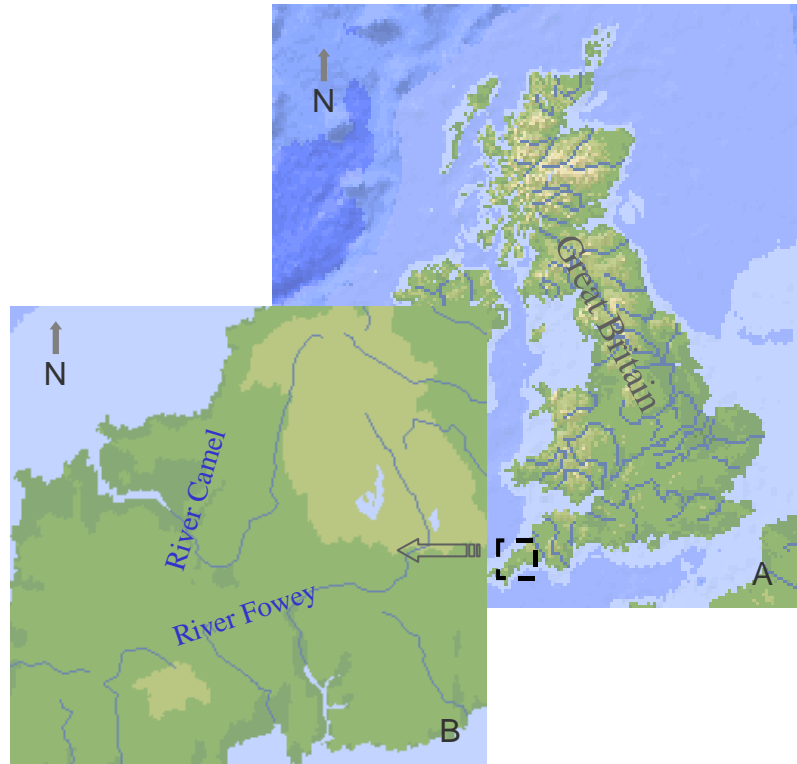


Figure 6: A) General map of Great Britain. B) Map of the study area in Cornwall, UK (not to scale).

2.1. The River Fowey

The River Fowey is the most important salmon and sea trout (*Salmo trutta*) river in south-west England. Its catchment drains the area of south-east Cornwall from the southern slopes of Bodmin moor to the south coast between Gribbin Head to the west and Lantic Bay in the east. Major tributaries are the Trebant Water, the Bedellva Stream, Cardinham Water, the Northwood Brook, Penpoll Creek, the River Lerryn, the River Warleggan, the Withey Brook and the St Neot River. Colliford and Sibleyback reservoirs are situated within the catchment. The total area of the catchment is 169.1 km² (National River Flow Archive Data Retrieval Service 1999b). The catchment is essentially rural in character,

ranging from open, undulating moorland to rolling hills (maximum altitude within catchment: 420 m Ordnance Datum (OD)) intersected by steep sided river valleys. There is no heavy industry, but historically there was extensive mining activity. The catchment is sparsely populated (urban extent (0 - 1): 0.0022) with isolated farmsteads, hamlets, and villages, although there are two larger towns, Lostwithiel and the port of Fowey.

The sources of the River Fowey rise on Bodmin Moor at about 300 metres. The geology of Bodmin Moor is characterised by large granite outcrops which are overlain by Quaternary head deposits. The Bodmin Moor granite pluton belongs to a batholith underlying the whole of the south-west peninsula with a total length of 250 km exposed in a series of six major and several minor plutons (British Geological Survey 1998). Tors and hills of the Bodmin Moor area are formed by resistant granite. River valleys and depressions are underlain by a mixture of detritus derived from the surrounding granite or very often the granite in the depression underwent kaolinisation processes. During these processes the alteration of the plagioclase feldspars to clay minerals changes the rock from a hard stable igneous rock to a soft, friable rock, which is easily eroded. The kaolinisation extends only a few metres down into the granite. The top of the valleys are filled by Quaternary peaty head deposits (ironpan podzolic soils) overlying the kaolinised granite. The peat deposits were laid down in the Late Pleistocene to Early Holocene, when temperatures rose and woodland covered most of Bodmin Moor. The peats are widespread and are usually less than three meters thick with exception of the main River Fowey valley where thickness of 4.3 m was recorded. High annual rainfall (1961 - 90 average rainfall: 1436 mm) and these poor soils result in low grade agricultural land and wet moorland which supports rough grazing and conifer plantations. Moving south, into the middle and low reaches of the Fowey, the granite gives way to Devonian sedimentary rocks (slates, shales and thin limestones), the change being marked by a significant increase in gradient. The gradient of the river begins a steady easing towards the sea (figure 7). The mean slope is 9.15 m/km (National River Flow Archive Data Retrieval Service 1999b).

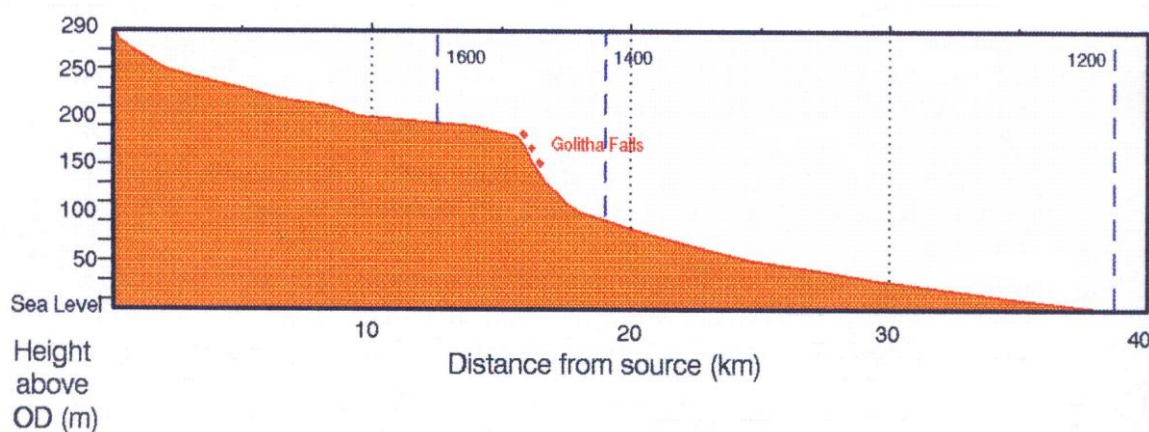


Figure 7: River Fowey profile from Bodmin Moor to the estuary at Fowey (modified from National Rivers Authority (1994)).

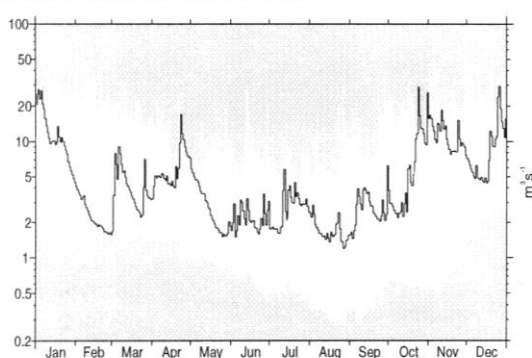
The most widespread soils in the lower catchment are the brown earths, characteristically free draining, readily cultivated, productive soils which, with the mild climate, support a wide range of agriculture. More restricted agriculture occurs on the small pockets of seasonally wet cambic stagnogley soils and alluvial gley soils found in the valleys, the former are poor draining and support stock rearing and woodland, the latter deep, free draining and support dairying and cropping. Mineralisation of the rock through the volcanic activity experienced when Bodmin Moor was forming resulted in pockets of metals such as tin, copper lead and silver. These are located in a series of faults, the trends of which run east -west for tin and copper, and north-south for lead and silver. These have since been commercially mined.

The bedrock underlying the Fowey catchment has been classified as a minor aquifer. It is generally well cemented and has a low intergranular permeability. These rocks have been subject to widespread folding and faulting and it is within associated fractures and fissures that storage and transmission of groundwater occurs. At shallow depths weathering, the accumulation of valley alluvium (as a result of soil creep down valley sides) and other processes enhance groundwater storage and permeability. Locally, modification of the natural low-level water movements has occurred through historic mining activity. Now disused adits and shafts have the ability to hold and move considerable quantities of water. Due to the current unstable nature of internal mine structures this can be in an unpredictable way. The primary groundwater uses are for the provision of river baseflow

and to support numerous small scale potable water supplies. 201 groundwater source abstractions are licensed, and a comparable number of unlicensed domestic supplies are estimated to be present within the catchments (National Rivers Authority 1994). Provision of river baseflow in terms of both quantity and quality is most critical during periods of prolonged dry weather (see figure 8).

Daily Flow Hydrograph

Max. and min. daily mean flows from 1961 to 1998 excluding those for the featured year (1998; mean flow: $5.50 \text{ m}^3 \text{ s}^{-1}$)



Flow Duration Curve

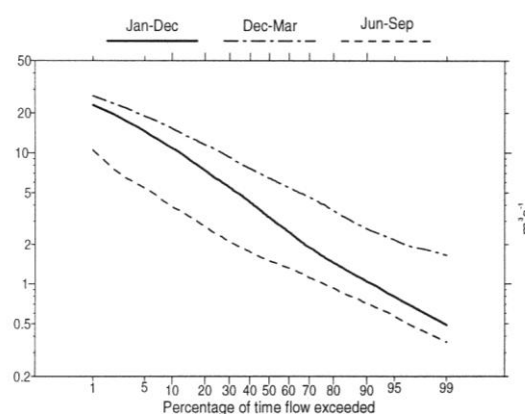


Figure 8: Flow statistics for the River Fowey at Denby (modified after National River Flow Archive Data Retrieval Service (1999b))

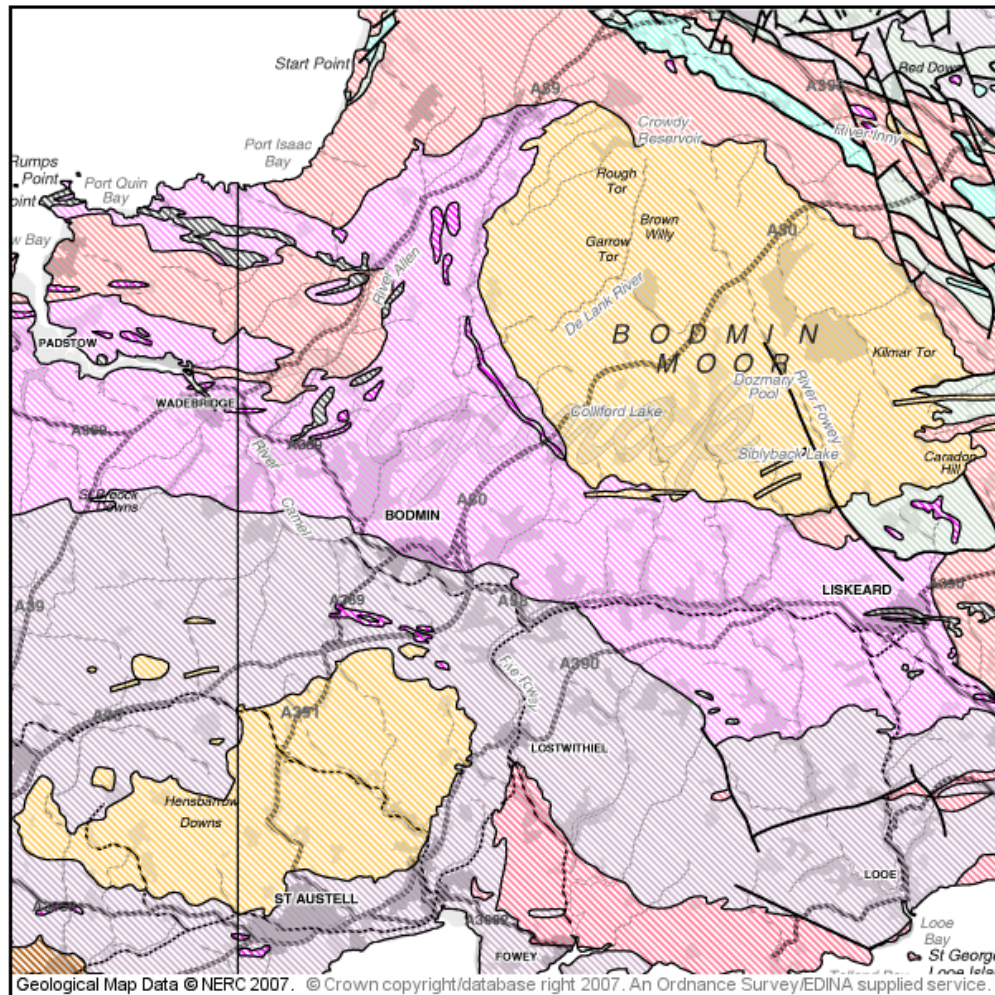
The catchment receives a high average rainfall, with the greatest amount falling on Bodmin Moor. With short tributary networks, the underlying geology and topography the flows in the rivers are characterized by rapid rises and falls in water levels after periods of rainfall (such a characteristic is known as 'flashy'). The effect of Colliford and Siblyback Reservoirs on the Fowey system is to reduce the flood peaks especially in the autumn, extend the period of relatively high flows and increase low flows. Spring tides in the Fowey Estuary typically range from 0.4 m to 5.5 m.

2.2. The River Camel

The River Camel drains at the western coast into the Atlantic. Major tributaries include the River Allen, the Ruthern River, and the De Lank River. The river and its main tributary the Allen supports good runs of salmon and sea trout (National River Flow Archive Data Retrieval Service 1999a). Listed fish species under the EC Habitats and Species Directive, such as shad species, sea lamprey, river lamprey, brook lamprey, bullhead have been identified within the catchment area. It is of international importance for its otters. Rare mosses and liverworts are present in the river and a number of areas of heathland and bog of national importance lie in the headwaters.

The climate is typical of Atlantic Britain with a limited temperature range and high winter rainfall. The catchment is sparsely populated with isolated farmsteads, hamlets, villages and a few small towns. Agriculture land covers approximately 93% of the total area. The majority of the agriculture land, over 74%, is grass reflecting an area largely devoted to livestock farming. Industry within the catchment is primarily associated with agriculture. The wooded valleys of the catchments have been deeply incised. They provide excellent permanent pastureland related to the brown soil which is characteristic for this region. Free-draining, fine loamy soils are mainly developed in areas above 200 m on the margins of Bodmin Moor and on the steeply valley slopes of the rivers Camel and Allen and their tributaries (British Geological Survey 1998). Most of the catchment is underlain by rocks with generally low permeability and porosity which is reflected by a generally flashy river flow response to rainfall and low groundwater storage availability. The geology around the upper Camel and Allen is characterised by Devon slate bedrock of the Trevoise Slate Formation of the Padstow succession (British Geological Survey 1998). The Trevoise Slate Formation describes the Middle Devonian grey slates with an estimated thickness of 3900 m. The formation is built up out of laminated mudstone which is intercalated with silty sediments representing turbidite sequences. The accumulation of the hemipelagic sedimentation occurred during Mid-Devonian time when the marine basin underwent regional subsidence. Deep water anoxigen conditions favoured the pervasive regular lamination of the Trevoise Slate Formation. The valley bed of the Camel River in Bodmin

Moor consist out of fine to coarse grained biotite granite and is covered locally by head deposits (figure 9).



0 4 8 12 16 20 km

- Dartmouth group
- Unnamed igneous intrusion of unknown age (UIIN)
- Gramscatho group
- Unnamed igneous intrusion, carboniferous (UIIC)

Figure 9: Geological map of North Cornwall with reference to sources of sediment to local rivers (modified after Ordnance survey (2008)).

3 Evaluation of a new semi-natural incubation technique for Atlantic salmon fry

3.1. Abstract

The incubation environment had a significant effect on fork length and body mass of Atlantic salmon *Salmo salar* fry at the time of emergence. Fry that were incubated in a new incubator design, that mimics the conditions in a natural redd (the ‘Bamberger-box’), achieved significantly greater length and attained a significantly higher body mass than those reared in conventional hatchery troughs for control. Fewer fry from the ‘Bamberger-boxes’ had visual deformities compared with those from the hatchery troughs. Results were consistent for five consecutive seasons using both wild and domesticated broodstock from genetically different origins. Survival from the eyed embryo stage in the Bamberger-boxes and hatchery troughs was above 93% during normal climatic conditions. However, only larvae reared in Bamberger-boxes survived abnormally high water temperatures during one test season. The results demonstrate that the Bamberger-box is an effective alternative to the conventional incubation technology.

3.2. Introduction

Stocking with hatchery-reared salmonids is a widely used method to enhance populations (Aprahamian et al. 2003, Saltveit 2006). Unfed fry, the development stage when most of the yolk sac is exhausted and the fish undergoes the transition from maternal provisioning to independent foraging, are a primary source of fish for the restoration effort (Fjellheim and Johnsen 2001, Letcher and Terrick 2001). However, hatchery-reared fry suffer from high post-stocking mortality rates (Coghlan and Ringler 2004, Einum and Nislow 2005). Hatchery-reared salmonids survive less well in the river than wild reared fish (Heggberget et al. 1992, Aprahamian et al. 2003, Letcher et al. 2004). The problem of low survival of poorly adapted hatchery stock is universal for augmentation programmes (Huntingford 2004). A possible way to increase survival and promote natural qualities in hatchery-reared fry would be to introduce rearing techniques that approximate natural profiles of incubation.

In the wild salmonids, typically deposit their eggs in excavations in the stream bed and subsequently cover the eggs with gravel. Eleuthero embryos hatch from eggs and live for several weeks within the gravel (Bardonnet and Bagliniere 2000). Surprisingly, the most widely used incubation systems for salmonid eggs do not mimic this undergravel period. Conventional hatchery methodology utilises shallow troughs or egg trays (Stead and Lair 2002) where the eggs are placed on a bare plastic or metal sheet.

In an attempt to provide a more natural incubation environment, eggs were incubated in a substrate matrix. The results were encouraging: most studies found that substrate incubation increased larvae growth thus resulting in a higher body mass of first-feeding Atlantic salmon (*Salmo salar* L.) fry (Leon 1982, Eriksson and Westlund 1983, Hansen and Torrissen 1985, Hansen et al. 1985, Sveier and Raae 1992, Peterson and Martinrobichaud 1995). Similar results for Pacific salmon species (*Oncorhynchus spp.*) were reported by Mead and Woodall (1968), Bams (1972, 1973, 1974, 1979, 1983, 1984, 1985), Bams and Crabtree (1976), and Bams and Simpson (1977).

The semi-natural incubation method evaluated here, the Bamberger-box, is widely used in southwest England for Atlantic salmon augmentation. This new design introduces a river like directional water flow on top of the incubation medium as a further step towards a more natural incubation environment. Whereas most other designs utilise artificial substrate such as Astroturf™ (e.g. (Hansen et al. 1990)), BIOMAT (e.g. (O'Flynn et al. 1995)) or Intalox Saddles (e.g. (Leon 1975)) this incubator utilises natural gravel as incubation medium to ensure a natural interstitial hydrology and invertebrate colonisation. The Bamberger-box is also much smaller than earlier gravel incubator designs, resembling in size a natural redd, which makes the box ideal for bank side use. Experiments were designed to assess the efficacy of the Bamberger-box with conventional hatchery troughs acting as control. Body mass and length variability of swim-up fry were taken as a reliable indicator of incubation efficiency (Pepper and Stansbury 1985). Eyed-embryo-to-fry survival and the number of deformities of emerging fry were compared over five years.

3.3. Methods

The experiments were carried out between 2002 - 2006 at a commercial fish farm (Westcountry Trout, UK (50°40'N, 4°40'W)). Eyed-up Atlantic salmon eggs were obtained from three different hatchery sources. In 2002, the eggs were the progeny of an unknown wild Scottish stock. In 2004 eggs were the progeny of a line of domesticated stock. In 2003, 2005, 2006 experiments were part of a regional salmon enhancement programme and the broodstock was caught with rod-and-line from the River Camel in Cornwall. Fertilization was done in groups of on average five female and male adults aiming at retention of a broad and randomly paired gene distribution for each lot.

3.3.1. Bamberger-box incubation units

The design features of these gravel incubation units evolved between 1998 and 2002. The finalised design is discussed in this article. From the late-eyed stage, experimental incubation took place in a gravel medium that was enclosed within Bamberger-boxes (referred to as B-boxes from here onwards). Four B-boxes were placed outdoors side by side. B-boxes (figure 10) were made of black non-contaminating grade PVC plastic. The inside dimensions of the B-boxes were 45 x 34 x 31 cm. The incubational volume of each B-box was 35.19 dm³ with a gravel depth of 23 cm for incubation. This value compares favourably to the average redd depth found in the natural environment for the size of females used in this experiment (Youngson et al. 2004). An opaque lid with a mesh-covered window allowed light into the B-box whilst excluding predators. The gravel was held 2 cm above the base of the B-box by a false base of 1 mm diameter aluminium mesh. The B-boxes were individually supplied with filtered river water (permanent-medium, upwelling water filter) maintaining a water level approximately 3 cm above the gravel. The water supply pipes were equipped with stopped T-connectors, which were used for introducing dye to test for even intergravel flow pattern after all fry had emerged. Valves controlling the discharge were adjusted to provide a similar intergravel flow in each B-box (4.5 dm³ x min⁻¹). Inside the B-boxes, water was introduced through a perforated feeder pipe which was supplied with water from both ends. The feeder pipes were installed in a wave pattern flat along the sidewall of the Box. Water was drained with a similar pipe

arranged on the opposite sidewall creating a horizontal water flow through the gravel matrix. A second, bigger, supply pipe was installed directly opposite the outflow. This pipe created a surface water flow of $8 \text{ dm}^3 \times \text{min}^{-1}$ and was screened with mesh material to even out the water flow, and to prevent fry swimming up the pipe.

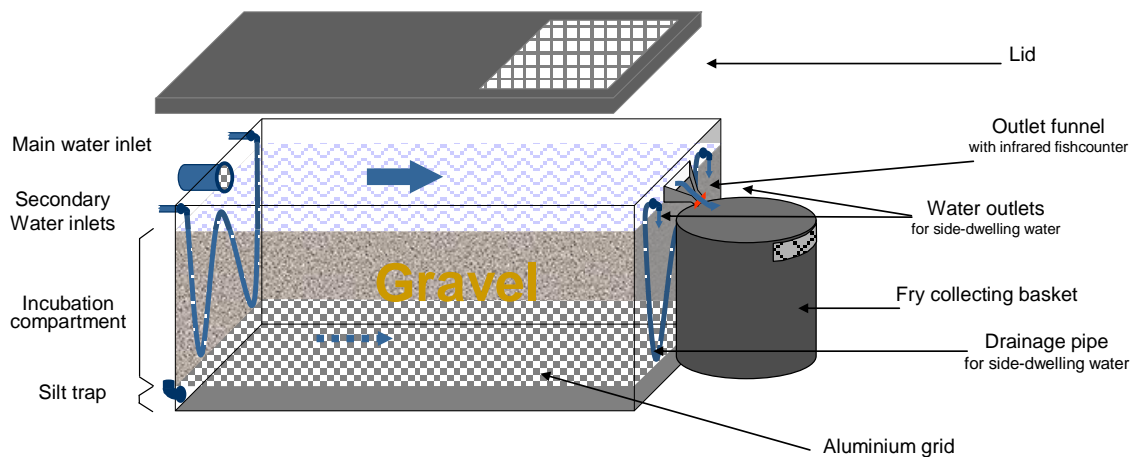


Figure 10: The Bamberger-box uses a horizontal water flow through the incubation gravel and a surface water flow on top of the gravel-filled incubation compartment.

In all B-boxes, a similar gravel composition was used. Egg pockets were established to simulate natural ones (Zimmermann and Lapointe 2005). The surrounding area was filled with a heterogeneous gravel mix (mean gravel particle size 1.67 mm, range < 1 to 42 mm). The gravel was removed from a river where salmon spawned naturally. The ratio of coarse (particle size 16 – 40 mm) to medium/fine gravel (2 - 16 mm) was 7:3 and approximated the ratio found in natural Atlantic salmon redds (Chapman 1988). The gravel contained a mixture of round and sharp-edged stones. Crevice to solid ratios (obtained by pouring the dried gravel into a known volume of water and measuring the increase in volume) ranged from 21% to 29%. The supergravel flow was turbulent ($Re > 4000$).

3.3.2. Physico-chemical water analysis

Interstitial water was sampled continuously at weekly intervals for each B-box and troughs throughout the experiments. Overall, the physico-chemical water characteristics were

similar within replicates and between treatments (Table 1). Conductivity to $1 \mu\text{S cm}^{-1}$, pH (Palintest Micro 500) and dissolved oxygen concentration to 1% or 0.1 mg dm^{-3} (Palintest Waterproof 800) were measured in situ. The water used for incubation was slightly alkaline with a pH range of 7.34 to 7.99. Oxygen levels were generally high with the control troughs recording the highest values. Concentrations of ammonia (indolphenol methodology), nitrite (nitricol methodology), nitrate (nitratest) and phosphates were measured in the laboratory. Air and water temperature to the nearest $0.1 \text{ }^\circ\text{C}$ was continuously recorded (Pasco Xplorer GLX datalogger). The mean water temperature during the incubation period was calculated.

Table 1: Overview of physicochemical water quality parameters pooled for n individual samples taken from Bamberger-boxes and hatchery troughs during five field seasons. Values are means \pm S.D.

Parameter	n	Bamberger-boxes		Hatchery Troughs	
		mean \pm S.D.	range	mean \pm S.D.	range
pH	320	7.67 ± 0.21	7.46 - 8.01	7.56 ± 0.30	7.34 - 7.99
Phosphates (mg l^{-1})	160	0.16 ± 0.04	0.15 - 0.18	0.16 ± 0.07	0.14 - 0.18
Ammonia NH_3 ($\mu\text{g l}^{-1}$)	160	38.8 ± 3.9	12.0 - 44.4	37.8 ± 2.6	29.7 - 42.7
Nitrate NO_3^- ($\mu\text{g l}^{-1}$)	160	1.9 ± 0.4	0.9 - 2.6	1.8 ± 0.3	1.3 - 2.3
Nitrite NO_2^- ($\mu\text{g l}^{-1}$)	160	4.9 ± 0.9	2.1 - 6.7	3.9 ± 0.7	2.1 - 4.9
Oxygen (%)	320	90 ± 6	74 - 97	95 ± 3	89 - 99
Oxygen (mg l^{-1})	320	10.8 ± 0.9	7.9 - 11.9	10.9 ± 0.3	9.6 - 11.9
Conductivity ($\mu\text{S cm}^{-1}$)	320	289 ± 28	161 - 339	279 ± 23	189 - 309
Temperature ($^\circ\text{C}$ cont. logged)		10.9 ± 2.3	8.0 - 16.0	10.8 ± 2.2	7.9 - 16.6

3.3.3. Handling of the eggs and fry

A few days before hatching, at approximately 450 degree days after fertilisation, the eggs were mechanically agitated by gently shaking them and unfertilized eggs were removed. Each B-box received 1000 eggs. The number of eggs was estimated volumetrically using

the Burrows displacement method (described in Leitritz and Lewis (1980)). Control counting showed that the number of eggs was accurate to 3%. The Box outlets were screened with mesh material for 20 days after stocking to prevent immature eleuthero embryos being washed out accidentally. Towards the end of the incubation period, fry emigrated from the Boxes by working their way to the gravel-water interface. The outlets discharged into separate fry-collecting traps.

3.3.4. Control experiment hatchery troughs

Controls were eggs from the same source as those in the B-boxes incubated in four conventional hatchery troughs (as described by Willoughby (1999)). These troughs were 264 cm long, 53 cm wide and 10 cm deep with a water depth of 5 cm. The troughs carried two egg tray (Slotted Aluminium: Aqua Systems Ltd.). Each trough had a separate water supply, which was of the same origin as the water supply for the Boxes. The water flow was UV filtered before it entered the troughs. Each tray was filled with 500 eggs (1000 eggs for each trough) on the same day as the B-boxes were filled with eggs. The trays were removed after all eggs were hatched out. The date of 50% hatching was recorded. During the incubation period, the troughs were covered with plywood sheets to keep the larvae in darkness. Maintenance conformed to standard hatchery procedures (as described by Sedgwick (1995) and elsewhere). Routine included the removal and counting of dead larvae and eggs and the provision of starter feed at a time when most larvae had absorbed their yolk sacs.

3.3.5. Fry measurements

Swim-up fry in the traps were counted and recorded with a tally counter in morning and at peak emerging times additionally in the late afternoon. Body deformities, discolorations, erosion of the fins and fungus infections were visually evaluated and recorded. The scale published by Killeen et al. (1999) was used to judge the state of development of emerging fry and identify prematurely emerged eleuthero embryos. At the first day when a sufficient number of fry (30 individuals per box) had emerged during the night, a sample of 20 fish was taken from each trap and from each hatchery trough. Fry were anaesthetised (2 -

Phenoxy-Ethanol, MERCK-Schuchardt) and body wet mass (M , g) was measured individually to the nearest 0.001 g (Sartorius 2001 MP2). The specimens remained suspended in water to avoid dehydration before the measurements were taken. Individual fork length (L_F , mm, ± 0.1 mm) was measured with callipers. Sampling was repeated after three and six days. In 2002 and 2004 40 randomly selected fish from the treatment and the control group (10 from each trap and trough respectively) were individually dried (70°C for 48h). Dry fish were then separately pooled for treatment and control group and manually ground in a mortar to obtain a homogenous powder before calorimetric analysis (1356 Isoperibol Bomb Calorimeter, Parr Instruments). Four energy measurements were conducted for each pool. The mean of the replicates was calculated and considered as a single value. Two days after emergence had terminated from all B-boxes, the contents of each B-box were inspected for dead eggs and larvae.

3.3.6. Ethical note

All experimental procedures were carried out on the premises of a licensed fish farm and were part of an enhancement programme. Fish samples were terminally anaesthetised before measurements were taken to ensure a minimum of suffering. All remaining fry, which accounts for the vast majority, were released to the river of the broodstock's origin at dusk of the same day (fry from a farmed broodstock were kept in the hatchery). The potential benefit of an increased survival of newly stocked fish due to advances in incubation technology outweighs the harm done by killing a sample for evaluation. An increase in the survival rate of stocked fry of just 2% would translate into over 16000 more fry surviving a critical stage of their life in the South West region of the UK (based on average yearly stocking rate of 800000 fry: J. Ruscombe-King pers. comm.).

3.3.7. Data analysis

Survival rates from eyed ova to fry are reported as yearly means (\pm S.D.) for B-boxes and troughs. Data were arcsine square root -transformed for statistical analysis. The responses were normally distributed (Anderson-Darling (De Muth 2007) test $p < 0.005$). Differences between survival rates in control and experimental group and wild and domesticated

broodstock respectively were tested by two-tailed Student's *t*-test (Sokal and Rohlf 1995). Body mass and fork length were reported for treatments as means (\pm S.D.) for each year. Growth data from B-boxes and troughs, each with four replicates for each season, were analysed using a analysis of variance (ANOVA: (De Muth 2007)) with incubators nested within treatment. ANOVA was used to test for variations between the five test seasons. Differences in the number of deformed fry from B-boxes and troughs were analysed by the Chi-Square test (Sokal and Rohlf 1995). Yates correction for continuity was applied.

3.4. Results

3.4.1. Rearing environment effects on size and deformities of fry

At the time of emigration, fry incubated in B-boxes were longer and heavier than fry incubated in troughs (figures 11, 12) and this difference was significant for all years of the study ($p \leq 0.02$). Overall for five years B-box-fry were on average 12.4% heavier and 3.6% longer than trough-fry (see Tables 2, 3 for F and p values) with a mean fork length of $24.6 \text{ mm} \pm 3.1$ and a mean body mass of $0.162 \text{ g} \pm 0.029$ (Tables 2, 3). Fry incubated in troughs only had a mean fork length of $23.7 \text{ mm} \pm 2.9$ and a mean body mass of $0.142 \text{ g} \pm 0.032$. The lowest mean value for any individual B-box was higher than the highest mean value for any single trough during the same season.

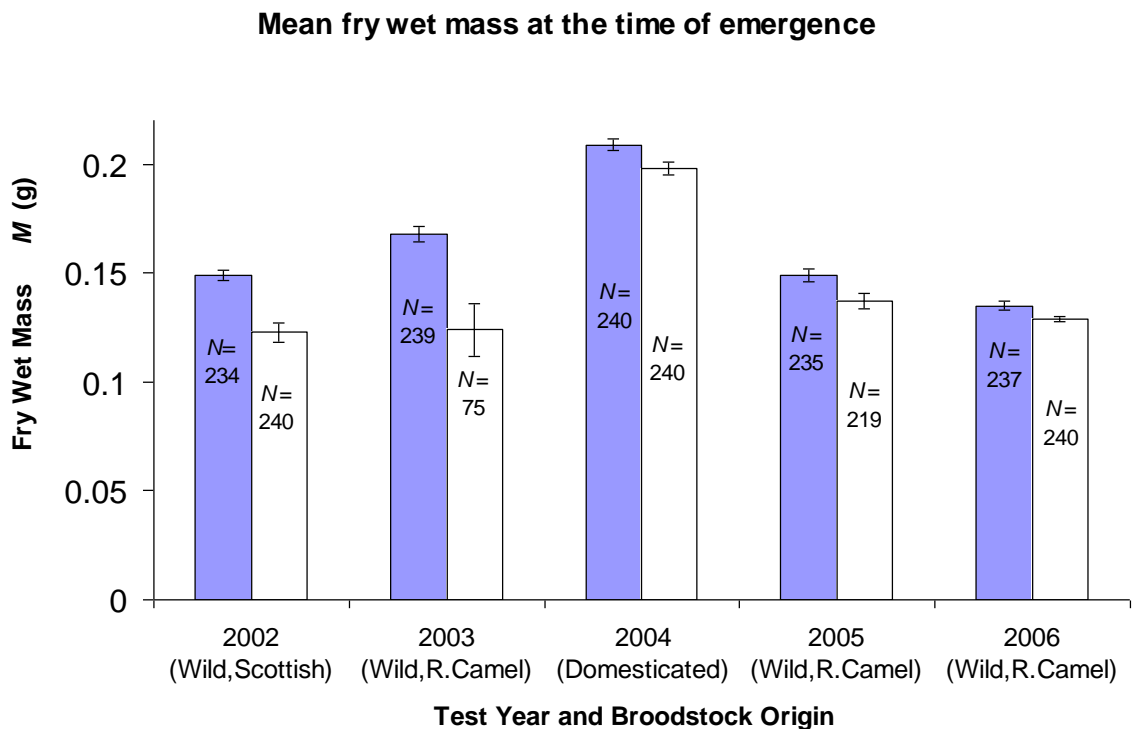


Figure 11: Comparison of mean body wet mass of emergent Atlantic salmon fry incubated in Bamberger-boxes (shaded columns) and hatchery troughs for five field seasons from 2002 to 2006. N gives the number of individual measurements pooled from four replicates for each season. Error bars indicate the standard error SE .

Table 2: Body wet mass $M \pm$ S.D. and range of emergent Atlantic salmon fry incubated in Bamberger-boxes and corresponding body mass of fry incubated in hatchery troughs for five field seasons from 2002 to 2006. F and p values are given for ANOVA-testing across replicates of the same treatment and across treatments. Significant values are highlighted bold.

Year / Parentage	Treatment / N	Wet Mass M (g)		ANOVA (replicates, d.f. = 3)	ANOVA (treatments, d.f. = 1)
		mean \pm S.D.	range		
2002 Wild (Scottish)	Boxes / 234	0.149 \pm 0.019	0.198 – 0.107	$F = 1.72$; $p = 0.16$	$F = 208.27$
	Troughs / 240	0.123 \pm 0.035	0.200 – 0.113	$F = 0.27$; $p = 0.84$	$p < 0.01$
2003 Wild (R. Camel)	Boxes / 239	0.168 \pm 0.029	0.199 – 0.119	$F = 0.83$; $p = 0.48$	$F = 595.45$
	Troughs / 75	0.124 \pm 0.053	0.170 – 0.115	$F = 0.03$; $p = 0.99$	$p < 0.01$
2004 Domesti- cated	Boxes / 240	0.209 \pm 0.020	0.270 – 0.149	$F = 4.35$; $p = 0.01$	$F = 12.10$
	Troughs / 240	0.198 \pm 0.022	0.246 – 0.151	$F = 0.69$; $p = 0.55$	$P = 0.01$
2005 Wild (R. Camel)	Boxes / 235	0.149 \pm 0.023	0.177 – 0.115	$F = 0.62$; $p = 0.61$	$F = 29.43$
	Troughs / 219	0.137 \pm 0.027	0.161 – 0.116	$F = 1.37$; $p = 0.25$	$p < 0.01$
2006 Wild (R. Camel)	Boxes / 237	0.135 \pm 0.016	0.154 – 0.068	$F = 2.04$; $p = 0.11$	$F = 11.21$
	Troughs / 240	0.129 \pm 0.010	0.159 – 0.101	$F = 1.47$; $p = 0.22$	$p = 0.02$

The mean body mass and mean fork length was significantly different between fry from different broodstocks ($p < 0.001$ for body mass and $p < 0.001$ for length). Domesticated parentage used in 2004, produced the heaviest and longest fish. The lowest mean body mass for B-box fry was recorded during 2006 for progeny of wild broodstock taken from the River Camel. The lightest fry from troughs were progeny of Scottish, wild broodstock recorded in 2002.

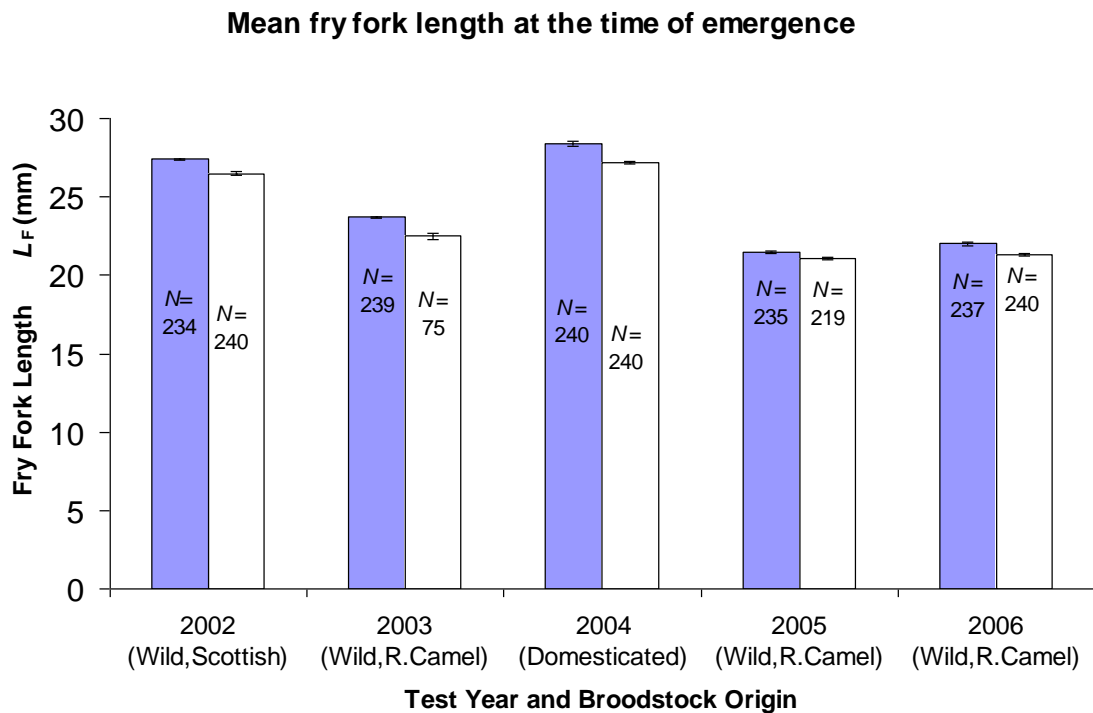


Figure 12: Comparison of mean fork length of emergent Atlantic salmon fry incubated in Bamberger-boxes (shaded columns) and hatchery troughs for five field seasons from 2002 to 2006. *N* gives the number of individual measurements pooled from four replicates for each season. Error bars indicate the standard error *SE*.

Calorimetric measurements were taken during two years. B-box fry sampled during the 2002 tests had a significantly higher energy content ($p = 0.017$) per gram dry body mass (mean $24.99 \text{ kJ g}^{-1} \pm 0.536$) compared to fish from conventional hatchery troughs (mean $22.73 \text{ kJ g}^{-1} \pm 0.327$). For the 2004 test runs the difference in energy content between the B-box-incubated fry (mean $23.73 \text{ kJ g}^{-1} \pm 0.287$) and fry from troughs (mean $23.35 \text{ kJ g}^{-1} \pm 0.135$) was not significant ($p = 0.377$). For both years combined, the overall difference in energy content per gram dry mass between B-box- and trough-incubated fry was 10.6%. The energy content of B-box fry was 9.9% higher when wild broodstock were used and only 1.6% higher for domesticated broodstock.

Table 3: Fork length L_F in mm \pm S.D. and range of emergent Atlantic salmon fry incubated in Bamberger-boxes and corresponding body mass of fry incubated in hatchery troughs for five field seasons from 2002 to 2006. F and p values are given for ANOVA-testing across replicates of the same treatment and across treatments. Significant values are highlighted bold.

Year / Parentage	Treatment / N	Fork Length L_F (mm)		ANOVA (replicates, d.f. = 3)	ANOVA (treatments d.f. = 1)
		mean \pm S.D.	range		
2002 / Wild (Scottish)	Boxes / 234	27.4 \pm 0.5	29.1 – 21.0	$F = 1.68$; $p = 0.17$	$F = 12.46$
	Troughs / 240	26.5 \pm 1.1	29.7 – 22.3	$F = 10.75$; $p < 0.01$	$p = 0.01$
2003 / Wild (R. Camel)	Boxes / 239	23.7 \pm 0.5	25.7 – 22.2	$F = 15.77$; $p < 0.01$	$F = 44.31$
	Troughs / 75	22.5 \pm 0.9	24.3 – 20.0	$F = 1.90$; $p = 0.14$	$p < 0.01$
2004 / Domesti.	Boxes / 240	28.4 \pm 1.1	30.1 – 25.0	$F = 10.17$; $p < 0.01$	$F = 19.68$
	Troughs / 240	27.2 \pm 0.8	30.0 – 25.0	$F = 4.06$; $p = 0.01$	$p < 0.01$
2005 / Wild (R. Camel)	Boxes / 235	21.5 \pm 0.6	23.4 – 19.6	$F = 1.73$; $p = 0.16$	$F = 12.80$
	Troughs / 219	21.1 \pm 0.7	23.5 – 19.2	$F = 2.97$; $p = 0.03$	$p = 0.01$
2006 / Wild (R. Camel)	Boxes / 237	22.0 \pm 0.9	22.8 – 19.6	$F = 3.33$; $p = 0.02$	$F = 39.20$;
	Troughs / 240	21.3 \pm 0.5	23.1 – 19.8	$F = 2.37$; $p = 0.07$	$p < 0.01$

In total 51 deformed specimens were identified over the whole period of the experiments by quick visual inspection while counting fry before release. 35 (2.9%) deformed specimens were found in samples taken from hatchery troughs and 16 (1.3%) deformed fry were sampled from B-boxes. The difference was significant at $p = 0.001$.

3.4.2. Survival rates

Survival from the time of planting at the eyed stage to emergence was high in all B-boxes, usually above 90% (mean, 93.4% \pm 3.0, range 87.9% – 99.0%). Table 4 illustrates that the origin of the broodstock (wild or domesticated Atlantic salmon) had no significant influence on the survival from egg to emerging fry independent of the incubation technique. Eyed-embryo-to-fry survival (referred to as EETF survival from here onwards) in B-boxes was significantly higher ($p = 0.049$) than EETF-survival in troughs (75.5% \pm

38.8; range 0 – 98.1%). Larvae mortality was extremely high in 2003 (> 99%) for fish reared in conventional hatchery troughs. No bacterial or viral pathogens were identified to explain the high mortalities but water temperatures were unusual high for that time of the year peaking at over 16°C. When the 2003 year was excluded from the calculations, similar high survival rates were observed in the troughs (mean 94.3, \pm 1.9, range 90.9 – 98.1). All fry emerging from the B-boxes were in advanced stages of the finfold resorption phases as described by Gorodilov (1996) and Killeen et al. (1999). Few dead larvae were discovered by emptying the boxes after the experiments had finished (nine in total from all boxes combined).

Table 4: Mean percentage eyed-embryo-to-fry survival (\pm S.D) and the range for *n* Bamberger-boxes and hatchery troughs stocked with eyed eggs from wild or domesticated Atlantic salmon broodstock. *t* and *p* values are given for Student *t*-testing across treatments and across broodstock origin. Significant values are highlighted bold.

<i>n</i>	Treatment	Survival (mean % \pm S.D.)	Range (%)	Student <i>t</i> -test (d.f. = 1)
20	Bamberger-boxes (total)	93.4 \pm 3.0	87.9 – 99.0	Bamberger-boxes (total) vs. Hatchery Troughs (total)
20	Hatchery Troughs (total)	75.5 \pm 38.8	0 – 98.1	<i>t</i> (38.0) = 2.03; <i>p</i> = 0.049
16	Hatchery Trough (excluding 2003 data)	94.3 \pm 1.9	90.9 – 98.1	Bamberger-boxes (total) vs. Troughs (excl. 2003)
				<i>t</i> (34.0) = -0.84; <i>p</i> = 0.405
28	Wild Broodstock (Boxes and troughs comb.)	93.8 \pm 2.8	87.9 – 99.0	Wild Broodstock vs. Domesticated
8	Domesticated Broodstock (Boxes and troughs comb.)	94.0 \pm 1.6	90.9 – 96.3	Broodstock
				<i>t</i> (34.0) = -0.08; <i>p</i> = 0.938

3.5. Discussion

3.5.1. Comparison of morphological indices

The substrate incubation system under trial in this study was smaller and operated with a different intragravel hydrology than the majority of earlier incubator designs yet the results support the conclusion of earlier studies. Fry incubated in a substrate matrix have a clear body mass and length advantage at the time of emergence compared to fry incubated in conventional hatchery troughs (e.g. (Leon and Bonney 1979, Brannas 1989, Hansen et al. 1990)). Fry mass was more variable than fry length. Water content of tissues is high and variable for larvae stages hence Heming (1982b) recommended fork length as the more accurate measure of tissue growth during this period. Peterson and Martinrobichaud (1995) measured water content as high as 82% for gravel-incubated alevin before first feeding. The larger overall difference in body mass (12.4%) between B-box- and trough-incubated fry than in length (3.6%) might be attributable to a relative higher water content of gravel incubated fry. An overall relatively small variation in energy content per gram dry body mass reflects more of the variations in length than body mass.

To explain the widely reported increase in body mass and length of first –feeding salmon fry in response to substrate incubation, it has been suggested that larvae incubated on substrate make more efficient use of their endogenous energy reserves for somatic growth (Hansen et al. 1990). The substrate matrix provides support which satisfies the righting response of eleuthero embryos (Mead and Woodall 1968, Hansen et al. 1990). Substrate incubation also reduces stress between times of hatching and emergence by ensuring separation of individual larvae, thus reducing interactions to a natural level. Stress is associated with reallocation of energy away from growth in salmonids (Pickering 1990, McCormick et al. 1998, Weil et al. 2001). The effects of stress should be less pronounced for domesticated fish, as one of the primary goals of domestication has been to achieve maximum growth under hatchery conditions, which include frequent stressors. The mean body mass and length difference of fry progeny of domesticated broodstock in this study was in the mid range for the different broodstocks. This observation suggests no effect of domestication on stress susceptibility during the intergravel phase.

An alternative hypothesis to explain the observed size advantage of B-box-fry is an intake of supplementary exogenous energy by the larvae, facilitated by the availability of suitable prey items in the stream gravel. The results might indicate that invertebrates living in the gravel interstitial are a more suitable energy supply for developing larvae than the commercial starter food offered to hatchery fry before the final yolk sac absorption. The impact of abundance and diversity of the hyporheic meiofauna on larvae growth and fry fitness requires further research.

While fry from B-boxes were consistently larger and heavier than fry from troughs, significant variations in average fork length and mass of fry from different broodstock were observed. Although mean water temperature during the individual incubation periods varied as much as 1.73°C this variation is unlikely to have caused a significant effect on body mass at first feeding (Rungruansak-Torrissen et al. 1998, Bjørnevik et al. 2003). It is likely that genetic differences in egg size between the Camel, Scottish and domesticated broodstock populations caused the difference in phenotypic variability of emerging fry. Thorpe et al. (1984), Hayashizaki et al. (1995), Einum and Fleming (2004), and most recently Moffett et al. (2006) found that larger eggs give rise to larger juveniles and egg size varies considerably among salmon populations (Aulstad and Gjedrem 1973, Beacham and Murray 1993).

Increased length and body mass of B-box-fry might have important advantages for post-stocking survival and ultimately for the effectiveness of stock enhancement programmes. Large juveniles experience higher survival and growth rate (Einum et al. 2002) mostly due to improved feeding (Nislow et al. 1999, 2000) and swimming efficiency (Beamish 1979, Ottaway and Forrest 1983, Heggenes and Traaen 1988, Armstrong 1997) and larger fat reserves (Berg et al. 2001).

3.5.2. Eyed-embryo-to-fry survival

Where the broodstock is taken from a wild population, it is imperative for a new incubation technology that survival rates significantly exceed natural survival. A mean eyed-embryo-to-fry (EETF) survival of 93.4% percent in B-boxes greatly exceeds published data for

egg-to-fry (ETF) survival in the wild (2% to 35%: (MacKenzie and Moring 1988, Pauwels and Haines 1994, Dumas and Marty 2006, Dumas et al. 2007)). EETF survival data from this study are comparable with published ETF survival data as mortality from fertilisation to the eyed stage is generally very low survival in a hatchery environment (e.g. 0.8% (Dumas and Marty 2006)) and was < 1% for the Camel broodstock used in this study (J. Ruscombe-King pers. comm.). High survival rates have been reported for other substrate incubators (Gent and Hunter 2006, Britton et al. 2007).

Overall survival from the eyed stage to emergence was higher in the B-boxes than in the hatchery troughs. This difference resulted from an almost 100% mortality rate in the hatchery troughs during 2003. The high death toll in hatchery troughs during 2003 was most likely caused by unseasonably high temperatures (water temperatures peaking at over 16°C) as most fish died within two days. This hypothesis is consistent with Hanson (1997) and Elliot (1991) who observed a rapid increase in mortality of juvenile salmon as temperatures exceeded a certain limit. No bacterial, viral or fungal pathogens were identified. The temperature during the 2003 incubation period was lower than the upper thermal limit reported by Ojanguren et al. (1999) for a Spanish salmon population, but higher than the tolerable maximum threshold for successful development of the larvae reported for North American and UK stocks (Becker and Neitzel 1985, Bjornn and Reiser 1991, Crisp 1993b). Although the water temperatures during this critical period were identical in the B-boxes and dissolved oxygen levels even slightly lower, survival rates in B-boxes remained unaffected. One likely explanation why larvae died in troughs but survived apparently unharmed in B-boxes, under less favourable physicochemical conditions, is that trough-incubated larvae are more stressed. A high base level for oxygen demand due to interaction with con-species on the bare substrate of the troughs and a constant struggle to maintain the preferred upright position might have caused an oxygen demand higher than the supply. Larvae in B-boxes benefit from the compartmentalisation of space that exists in the gravel matrix. It seems that a further important strength of B-boxes compared with traditional hatchery troughs is to ensure larvae survival during environmental extremes. With the prospect of a changing climate (Stone and Bohannon 2006) associated with an increased likelihood of thermal extremes further increasing stress during incubation (Portner and Knust 2007), the advantage of semi-natural incubation in

this respect will become more and more important. Gravel incubation is an energy-efficient and from a biological point of view superior alternative to setting up cooling systems for traditional hatchery troughs to combat high temperatures.

3.5.3. Effect of gravel-incubation on the number of deformed fry

Deformities are recognized as a recurring problem in fish aquaculture and represent both ethical and economical challenges for the industry (Takle et al. 2005). The overall percentage of fish with visible deformities was very low during this study. This figure is without doubt a gross underestimation of the real number of deformed fish. The economically most significant deformity is that of the 'short-tailed' Atlantic salmon, which shows coalesced, and thus shortened, vertebra (Kvellestad et al. 2000). Salmon fry need to be x-rayed to reliably detect vertebra deformities, which was not carried out during this study. It is likely that the majority of less obvious deformities went unnoticed when fry were rapidly counted to minimize handling damage. However, B-boxes produced fewer deformed fry than troughs. This observation is in agreement with Leon and Bonney (1979), Leon (1982) and Hansen et al. (1985, 1990), who observed yolk sac constrictions on trough-incubated Atlantic salmon embryos. The yolk sac absorption was normal in all studies when embryos were incubated on substrate. The number of deformed fry from traditional hatchery troughs might in reality be much higher than noticeable on quick visual inspection and might contribute significantly to the low stream survival of hatchery reared fry.

4 Large scale semi-natural incubation units: design and evaluation

4.1. Abstract

Extremely high mortality rates of hatchery reared salmonid fry after stocking into a river made it imperative to have a fresh look at substrate incubation techniques as an alternative to traditional hatchery troughs. Four different types of semi-natural incubation units, analogous in utilizing a gravel matrix for incubation and a natural intra- and supra gravel water flow, but differing in size and shape, were developed. The new units required evaluation to establish efficiency of incubation, with existing hatchery troughs acting as control. Trials were carried out in a replicated design during five consecutive years using a range of genetically different Atlantic salmon (*Salmo salar* L.) broodstocks. Comparison at the fry stage showed the substrate incubation units produced significantly larger and heavier fry than the troughs. Semi-natural incubation resulted in a reduction in deformities. Mean eyed-embryo-to-fry (EETF) survival from semi-natural incubators ($89.0\% \pm 4.9$ S.D.) matched EETF survival from hatchery troughs ($94.3\% \pm 3.3$ S.D.) and greatly exceeded published data for egg-to-fry survival in the wild. During a period of unusual high water temperatures all fry died in hatchery troughs whereas fry survived seemingly unaffected in semi-natural incubators. Fry emergence from the semi-natural incubation units on a seasonal and diurnal time scale was similar to emergence patterns reported for wild populations. It was concluded that fry from the new semi-natural units are apt to having an increased survival rate when stocked in to a river. Low costs of production make the new incubators an economically viable alternative to traditional incubation systems.

4.2. Introduction

Hatchery supplementation programmes with unfed Atlantic salmon (*Salmo salar* L.) fry are widely used by fisheries managers worldwide in an attempt to meet the dual goals of conservation and sustainable exploitation of this species (Aprahamian et al. 2003, Lorenzen 2005, Saltveit 2006). Hatchery reared salmon fry, the development stage when most of the yolk sac is exhausted and the larvae starts swimming in the open water are a costly commodity. Restocking programmes in the UK frequently have to rely on anglers donating wild salmon caught by licensed rod and line fishery for broodstock. Against this background it is disappointing to note the poor survival of hatchery-reared salmon fry once stocked (Shackley et al. 1992, Orciari et al. 1994, Coghlan and Ringler 2004). Survival of hatchery reared fish is generally lower than that of equivalent wild fish (Aprahamian et al. 2003). 48% mortality within two days after stocking have been reported (Henderson and Letcher 2003). It appears that in most instances mortality is highest during, and immediately after, release into the wild (Olla et al. 1994, 1998, Einum and Fleming 2000b) indicating problems with the traditional hatchery methodology. Rather than quantifying the success of a hatchery operation in terms of numbers of fish stocked, hatchery managers increasingly need to focus on product quality and survival in the wild (Hallerman 2004). Stickney (1994) argued that radical changes in piscicultural practices are required to rear wild fish in a hatchery environment.

The Bamberger-box (referred to as B-box from here after) is a new semi-natural incubator design, which in addition to providing a natural incubation substrate mimics the hydrology in a natural redd. In contrast to previous substrate incubation units (e.g. (Bams and Simpson 1977, Porter and Meerburg 1977, Environment Agency 2000)) in this new type of semi-natural incubator a constant surface current simulates the river flow on top of the gravel. It has been shown in a comparative study that providing a unidirectional surface flow on top of the incubation medium has a positive effect on the rheotactic behaviour of emerging fry. Fry from B-boxes maintain a positive feeding position in the flow for significantly longer in increasing current velocities than fry which experienced no supra-gravel current during the incubation period. The need to pay attention to interactions between groundwater and surface water when evaluation the quality of salmonid spawning

grounds in the wild was recently highlighted by Grant (2008). The B-boxes are widely used in the southwest of the United Kingdom for Atlantic salmon augmentation purposes but a relatively small carrying capacity of 800 - 1300 salmon eggs limits the range of applications.

This study provides an evaluation of three semi-natural larger incubation systems with conventional hatchery troughs and B-boxes acting as control. Morphological indices, i.e. length, body mass, frequency of deformities, and eyed-embryo-to-fry survival were compared. Temporal emigration patterns from B-boxes were compared with patterns reported for natural redds. The practical and economic implications of using different incubator types for hatchery management were discussed.

4.3. Methods

The experiments were carried out during five consecutive field seasons at a commercial fish farm (Westcountry Trout, Boscastle, UK). From the late-eyed stage on, experimental incubation took place in four different types of substrate incubation units. Control batches were incubated in conventional hatchery troughs.

4.3.1. Tank incubation units

Two black rectangular tanks (200 x 200 cm square and 55 cm deep), manufactured in reinforced concrete, with radius curves at the corners were equipped with a round mesh divider of 45 cm diameter protruding above the water surface to screen the central drain (figure 13). The water supply to each tank was delivered by an elbow pipe from above the surface directed round the side thus creating a circular flow pattern. The flow rate was controlled to about $20 \text{ dm}^3 \text{ min}^{-1}$. Each tank was filled to a depth of 20 cm with stream gravel (see substrate analysis below). Water level was regulated to 7 cm above the gravel surface. Tank incubation units were tested during 2002 and 2005.

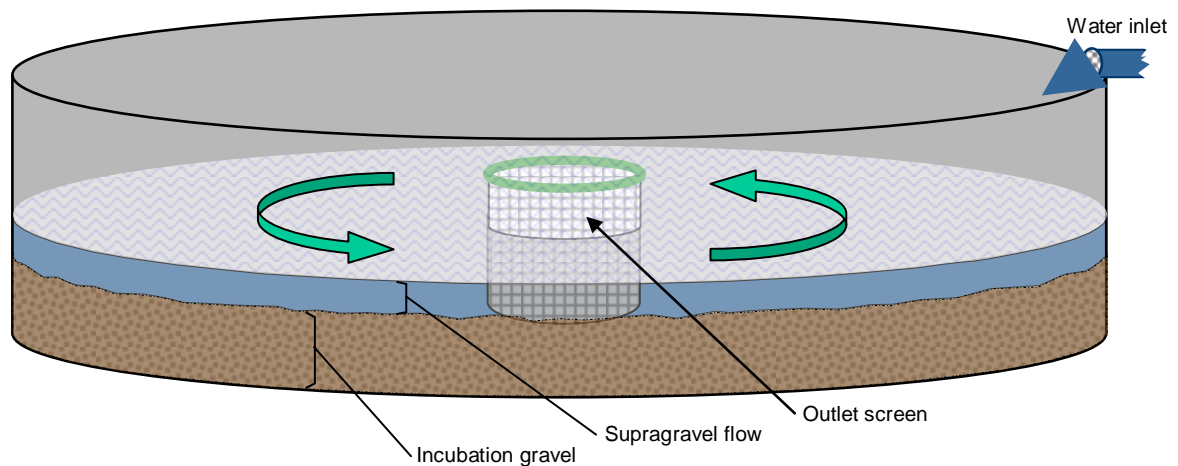


Figure 13: Layout of a tank incubation unit. Depict are the water inlet and outlet and the relative depth of the gravel substratum used for incubation and supra-gravel water. Arrows indicate the direction of water flow.

4.3.2. Raceway incubation units

Two different designs were tested simultaneously during 2003, 2004 and 2006. A standard sheep feed trough (200 cm x 40 cm and 30 cm deep), made of black non-contaminating grade PVC plastic, was equipped with an aluminium outflow funnel at one end (figure 14). On the opposite end a 20 cm long settling area was separated by a wooden board from the rest of the trough which was used for incubation. On top of the wooden board a mesh screen (1 mm mesh diameter) was installed fitting tightly on both sides with the trough. Along the entire length on the base of the incubation area a crushproof plastic hose, reinforced with plastic ribs, was laid in an elongated U-shape. The hose had an inner diameter of 12 mm. Both ends of this hose were connected to the settling area protruding through the dividing board. The incubation area was filled to a depth of 20 cm with stream gravel. The water supply to this type of incubation unit was delivered by an elbow pipe from above the surface into the settling area. The flow rate was controlled to $20 \text{ dm}^3 \text{ min}^{-1}$. The majority of the water ran on top of the incubation gravel towards the outflow. Water level was regulated to 7 cm above the gravel surface. In addition $7 \text{ dm}^3 \text{ min}^{-1}$ freshly oxygenated water percolated through numerous 2 mm holes from the hose into the gravel at the base of the incubation area creating an upwelling interstitial flow.

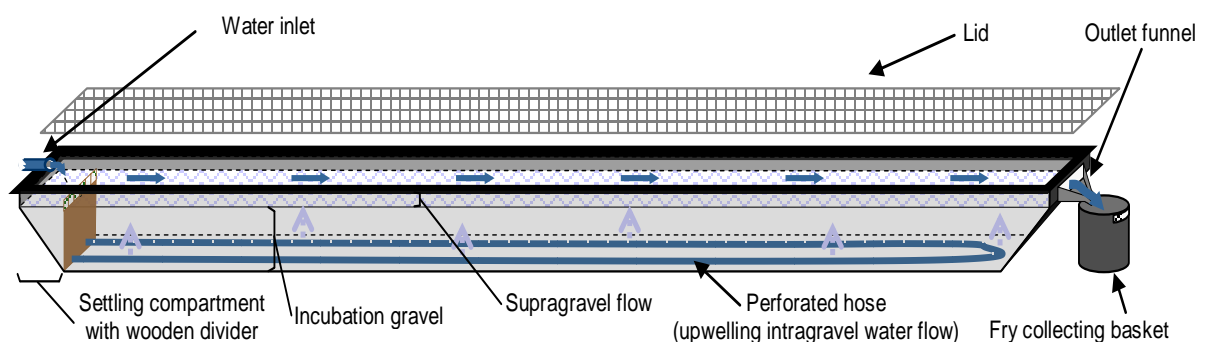


Figure 14: Layout of a plastic raceway incubator. Depict are the water inlet and outlet and the relative depth of the gravel substratum used for incubation and supra-gravel water. Arrows indicate the direction of water flow.

The second raceway design consisted of a standard fingerling tank (Hinshaw 1990) build above ground level, which was divided by concrete blocks into two channels interlinked on both ends (figure 15) each 1100 cm x 47 cm and 40 cm deep. The two channels had a combined outflow at one end. On the other end a wooden board separated a small, 20 cm long, settling area from the area used for incubation. The incubation area was filled to a depth of 20 cm with stream gravel. The water supply was delivered by an elbow pipe from above the surface into the settling area. The flow rate was controlled at $25 \text{ dm}^3 \text{ min}^{-1}$, both sides of the system receiving roughly half the amount of water. Water level was regulated to 7 cm above the gravel surface.

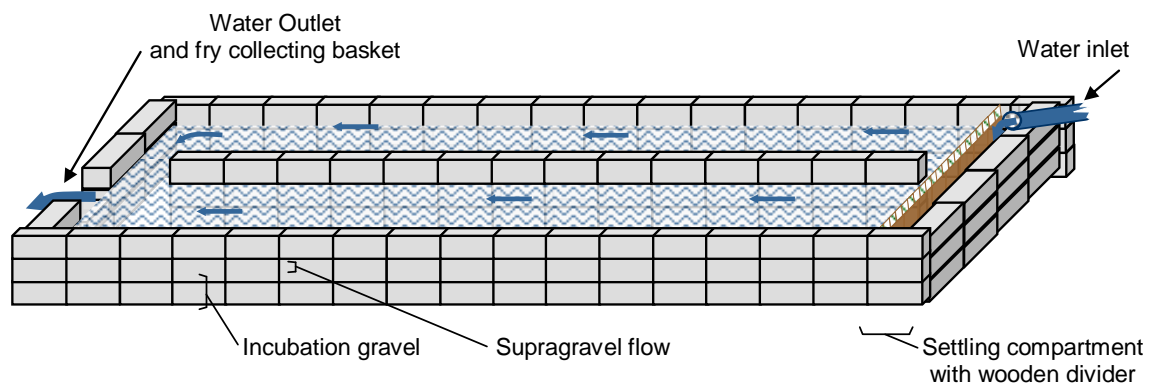


Figure 15: Layout of a raceway incubator modified from a standard trout hatchery raceway. Depict are the water inlet and outlet and the relative depth of the gravel substratum used for incubation and supra-gravel water. Arrows indicate the direction of water flow.

4.3.3. Bamberger-boxes

Four plastic boxes were placed outdoor side by side on a wooden platform. Internal dimensions of all the boxes were 45 x 34 x 31 cm (figure 16). The boxes were filled to 23 cm depth with gravel. The water level on top of the gravel was 2 cm. Along the base of boxes a crushproof plastic hose was laid in a U-shape. The hose had an inner diameter of 12 mm and was perforated with numerous 2 mm holes. Both ends of the hose were connected to a water supply pipe from the outside to provide a roughly similar intergravel flow ($4.5 \text{ dm}^3 \text{ min}^{-1}$). Water percolated in an upwelling pattern through the gravel matrix and exited the box through the outflow on the opposite end. A second, bigger, supply pipe 2.5 cm in inner diameter was installed directly opposite the outflow. This pipe created a

surface water flow of $8 \text{ dm}^3 \text{ min}^{-1}$ and was screened with mesh material to even out the water flow and to prevent larvae swimming up the pipe.

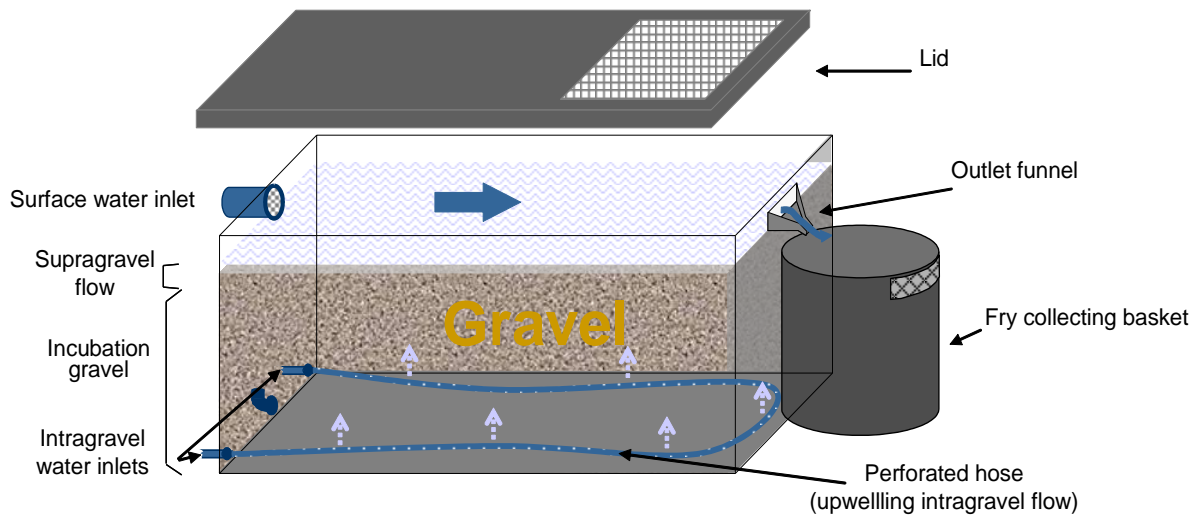


Figure 16: Layout of a Bamberger-box. Depict are the water inlet and outlet and the relative depth of the gravel substratum used for incubation and supra-gravel water. Arrows indicate the direction of water flow.

4.3.4. Hatchery troughs

Experimental controls were conducted in parallel where eggs from the same source as those in the gravel units were incubated in four conventional, hatchery troughs (as described Willoughby (1999) and referred to as troughs from here after). The troughs were 220 cm long, 42 cm wide and 7 cm deep. Each trough carried two rectangular egg-baskets (45 x 45 cm) each. The bases of the baskets were perforated and were about 2 cm above the base of the trough. Each trough had a separate, UV filtered water supply. Water depth was 5 cm. During the incubation period, the troughs were covered with plywood sheets to keep the larvae in darkness. Maintenance conformed to standard hatchery procedures (as described by Sedgwick (1995)) and the routine included the removal and counting of dead larvae and eggs.

4.3.5. Granulometric characterization of the substratum

In all incubation units a similar heterogeneous gravel mix was applied. The respective substrate volume (dm³) for each incubator type is given in Table 5. The gravel was removed from a river where salmon spawn naturally and the mean ratio of coarse gravel (particle size 16 - 40 mm) to medium-fine gravel (2 - 16 mm) of about 7 : 3 (mean 1.67; range < 1 - 42 mm) approximates that found in natural Atlantic salmon redds (Chapman 1988). The gravel contained a mixture of round and sharp-edged stones with many flat surfaces and exposed ridges which aid the fish in retaining their preferred upright position. Crevice to solid ratios (obtained by pouring the dried gravel into a known volume of water and measuring the increase of water) ranged between 21 to 29%. The substratum characteristics of the redds thus created were in conformity with those of natural redds (Bjornn and Reiser 1991, Dumas and Darolles 1999).

Table 5: Number of replicate incubation units, eggs and substrate volume per individual unit for treatments.

Treatment	<i>n</i>	Eggs / unit	Substrate volume (dm ³)	Egg / substrate ratio
B-boxes	20	1000	35	1 : 0.04
Tanks	4	4000	760	1 : 0.19
Raceway 1	3	2000	144	1 : 0.07
Raceway 2	3	6000	12000	1 : 0.5
Troughs	20	1000	n/a	n/a

4.3.6. Physico-chemical water analysis

All substrate incubation units and the control troughs were individually supplied with filtered river water (permanent-medium, upwelling water filter). The surface flow above the gravel in all substrate incubation units was unidirectional and turbulent ($Re > 4000$). Interstitial water was sampled continuously in weekly intervals for each incubation unit

throughout the experiments. Sampling pipes were positioned mid gravel in places where the interstitial water circulation was expected to be lowest. Conductivity to $1 \mu\text{S cm}^{-1}$, pH (Palintest Micro 500) and dissolved oxygen concentration to 1% or 0.1 mg dm^{-3} (Palintest Waterproof 800) were measured in situ. Oxygen levels were highest in the troughs (Table 6). Concentrations of ammonia (indolphenol methodology), nitrite (nitricol methodology), nitrate (nitratest) and phosphates were measured in the laboratory. Air temperature and water temperature were continuously recorded (Pasco Xplore GLT) to the nearest $0.1 \text{ }^\circ\text{C}$. The mean water temperature was calculated for each incubation period.

Table 6: Overview of interstitial water quality parameters. Values are pooled for five field seasons.

Parameter	mean \pm S.D.	range
pH	7.67 ± 0.21	7.46 - 8.01
Phosphates (mg l^{-1})	0.16 ± 0.04	0.15 - 0.18
Ammonia NH_3 ($\mu\text{g l}^{-1}$)	38.8 ± 3.9	12.0 - 44.4
Nitrate NO_3^- ($\mu\text{g l}^{-1}$)	1.9 ± 0.4	0.9 - 2.6
Nitrite NO_2^- ($\mu\text{g l}^{-1}$)	4.9 ± 0.9	2.1 - 6.7
Oxygen (%)	88 ± 8	69 - 97
Oxygen (mg l^{-1})	8.9 ± 1.1	6.4 - 11.9
Conductivity ($\mu\text{S cm}^{-1}$)	289 ± 28	161 - 339
Temperature ($^\circ\text{C}$ cont. logged)	10.9 ± 2.3	8.0 - 17.0

4.3.7. Handling of the eggs and fry

In the first field season (2002) eyed Atlantic salmon eggs were the progeny of an unknown wild Scottish stock. The experiments were repeated in 2003, 2005, 2006 with eyed ova progeny of wild broodstock from the River Camel in southwest England. Fertilization was done in groups of on average five females and same number of male adults aiming at retention of a very broad and randomly paired gene distribution for each lot. In 2004 eyed

ova, progeny of a line of domesticated stock was obtained from Lakeland Smolt Ltd (Furnace, UK).

A few days before hatching, at approximately 450 degree days after fertilisation, the eggs were mechanically agitated by gently shaking them and unfertilized eggs were removed. The number of eggs was estimated volumetrically by the Burrows displacement method (described by Leitritz and Lewis (1980)). Control counting has shown that the number of eggs was accurate within 3%. Eggs were introduced into the substrate incubation units after the units have been running for several weeks allowing for invertebrate colonisation. Eggs were spread evenly over the gravel. The eggs were protected from harmful UV radiation by a lid or black polypropylene netting covering each substrate incubation unit. Surface water flow was reduced initially. Outlets were screened with mesh material for the following 20 days after stocking to prevent immature eleuthero embryos being washed out accidentally. A B-box received 1000 eggs, a tank incubation unit 4000 eggs, the concrete raceway 3000 eggs on each side and the plastic raceway received 2000 eggs. Corresponding egg densities per incubational volume are listed in Table 5. 1000 eggs were incubated for control in each trough. Two baskets within each trough were filled with an equal number of eggs at the same day when the substrate incubators were filled with eggs. The date of 50% hatching was established from counts in the control troughs. The baskets were removed after all eggs were hatched out.

Fully developed fry released themselves from the incubators by working their way to the gravel-water interface and emerging into the supra-gravel water. On B-boxes and raceways the outlets discharged into separate fry-collecting traps. Fry had to be netted from tanks.

4.3.8. Fry measurements

Swim-up fry were counted by hand once a day in the morning. Fin condition, body deformities, discolorations and fungus infections were visually assessed when counting the fry. After recording all fry were retained in one communal glass-fibre tank and usually fry were released into the river where the broodstock came from at dusk of the same day (fry

from a farmed broodstock were kept in the hatchery). When fry started emerging in sufficient numbers from all incubators a sample of 30 fish was taken randomly from each trap and the control troughs. Fry were anaesthetised (2-Phenoxy-Ethanol, MERCK-Schuchardt). Wet body mass (M) was measured individually to the nearest 0.001 g (Sartorius 2001, MP2). The specimens remained suspended in water so as to avoid dehydration before the measurement was taken. Individual fork length (L_F , mm, ± 0.1 mm) was measured with a dial calliper. Sampling was repeated after three days. The relative condition factor (K), as an index of the relationship between fry length and body mass at emigration, was calculated as $10^5 \times \text{mass} \times \text{length}^{-3}$. Two days after emigration had terminated from all incubators, the contents were inspected for remaining larvae and dead eggs. Fry in troughs were counted on the same day. Fish collected alive were counted as being emerged. Dead fry and larvae were excluded from the calculations. The scale published by Killeen et al. (1999) was used to evaluate the state of development of emerging fry throughout the experiment.

4.3.9. Statistical analyses

Body mass and fork length were reported for treatment and control groups as means (\pm S.D.) for each year. Morphological data from B-boxes, raceways, tanks and troughs were subsequently analysed for each year using a two-level nested analysis of variance (ANOVA: (Siegel 1956)) where individual incubation units were nested within treatments. Standard deviation of the means was given for condition factor values. Survival rates for treatment groups from eyed embryo to fry were reported as yearly means (\pm S.D.). Percentage data were arc-sin root transformed for pairwise comparisons of treatments using the student t -test (Siegel 1956). After Bonferroni adjustment for multiple comparisons $p \leq 0.083$ (De Muth 2007) was considered a significant departure from the null hypothesis of equal survival. Daily and hourly frequency distributions for emigration numbers were constructed. Before parametric statistics were used normality was assessed using an Anderson-Darling test (De Muth 2007).

4.4. Results

4.4.1. Rearing environment effects on fry morphology

Fry incubated in substrate incubation units were heavier and longer than fry incubated in troughs for control (figures 17, 18, 19, 20). Although mean fry body mass and length varied within replicates of the same treatment the lowest mean value for any individual substrate incubation unit was higher than the highest mean value for any single trough during the same season (see Table 7 for F and p values). The largest difference in mean length was observed during 2004 comparing trough-incubated and raceway-incubated fry. During that particular year length averaged 27.2 mm and 28.9 mm respectively, for a significant differential of 1.7 mm.

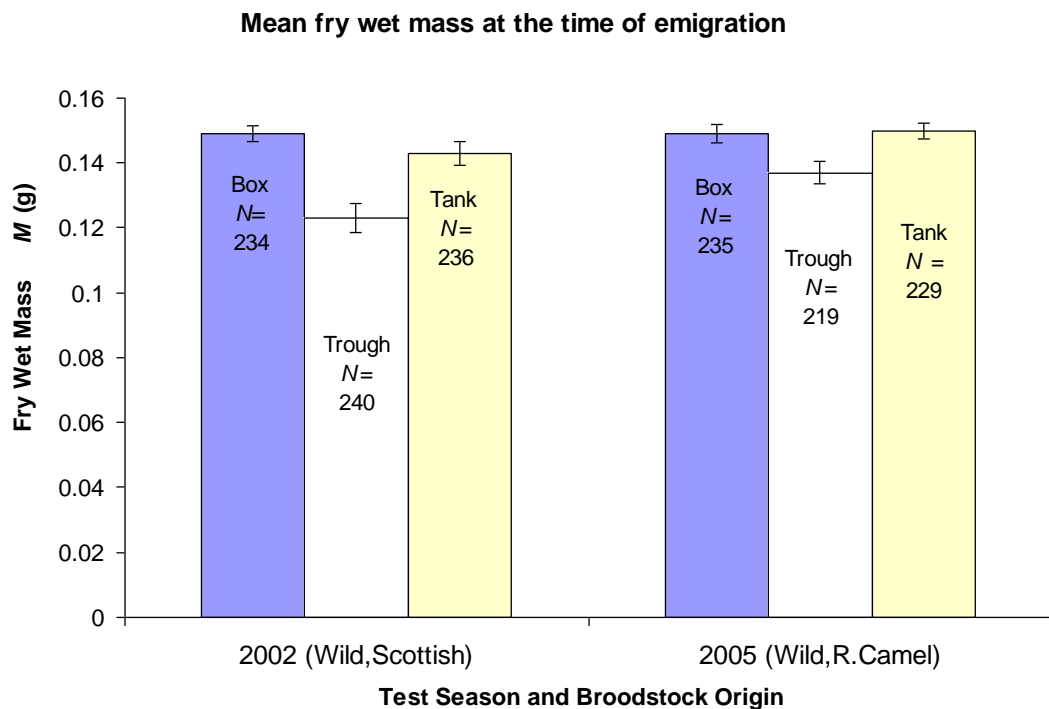


Figure 17: Comparison of mean body mass of emigrating fry incubated in Bamberger-boxes, troughs and tanks for 2002 and 2005. N gives the number of individual measurements pooled from four replicates for each season. Error bars indicate 95% confidence intervals.

Table 7: *P* and *F*-values of pairwise comparisons of treatments on fork length (L_F) and body mass (M) at the time of emigration of fry with individual incubation units nested within treatments. Significant differences are highlighted bold.

		L_F (mm)	M (g)
2002	B-boxes = tanks	$F_{(1, 4)} = 2.89; p = 0.17$	$F_{(1, 4)} = 3.76; p = 0.21$
	B-boxes = tanks > troughs	$F_{(2, 7)} = 7.30; p = \mathbf{0.02}$	$F_{(2, 7)} = 79.45; p < \mathbf{0.01}$
2003	B-boxes = raceways	$F_{(1, 4)} = 0.38; p = 0.57$	$F_{(1, 4)} = 2.73; p = 0.17$
	B-boxes = raceways > troughs	$F_{(2, 7)} = 31.31; p < \mathbf{0.01}$	$F_{(2, 7)} = 399.39; p < \mathbf{0.01}$
2004	B-boxes = raceways	$F_{(1, 4)} = 1.73; p = 0.26$	$F_{(1, 4)} = 3.10; p = 0.15$
	B-boxes = raceways > troughs	$F_{(2, 7)} = 18.95; p < \mathbf{0.01}$	$F_{(2, 7)} = 15.3; p < \mathbf{0.01}$
2005	B-boxes < tanks	$F_{(1, 4)} = 25.91; p = \mathbf{0.01}$	
	B-boxes < tanks > troughs	$F_{(2, 7)} = 24.23; p < \mathbf{0.01}$	
	B-boxes = tanks		$F_{(1, 4)} = 0.04; p = 0.84$
	B-boxes = tanks > troughs		$F_{(2, 7)} = 7.62; p = \mathbf{0.02}$
2006	B-boxes = raceways	$F_{(1, 4)} = 3.43; p = 0.14$	$F_{(1, 4)} = 3.19; p = 0.15$
	B-boxes = raceways > troughs	$F_{(2, 7)} = 34.17; p < \mathbf{0.01}$	$F_{(2, 7)} = 9.77; p = \mathbf{0.01}$

The greatest difference in mean body mass (0.048 g) was recorded during 2003 comparing fry from troughs and fry which emigrated from raceway. The comparison of individual seasons revealed that the heaviest and longest fry emerged during 2004 when domesticated broodstock was used. During that particular year raceways produced the longest fry (28.9 mm \pm 1.3) and troughs the smallest fry (27.2 mm \pm 0.8). The smallest fry overall (21.1 mm \pm 0.7) were the progeny of River Camel broodstock incubated in troughs in 2005. The lightest fry (0.123 g \pm 0.035) were collected in 2002 and came likewise from troughs and were progeny of a wild Scottish broodstock. The condition factor *K* also varied between the years with fry from wild Scottish broodstock recording the lowest values (mean 0.7091 \pm 0.0427). Fry progeny of Camel broodstock consistently had high average condition factor values (1.2088 \pm 0.1043; 1.4584 \pm 0.0409; 1.2914 \pm 0.0377 for 2003, 2005 and 2006 respectively). Domesticated broodstock in 2004 produced fry with a mean condition factor of 0.9318 (\pm 0.0456).

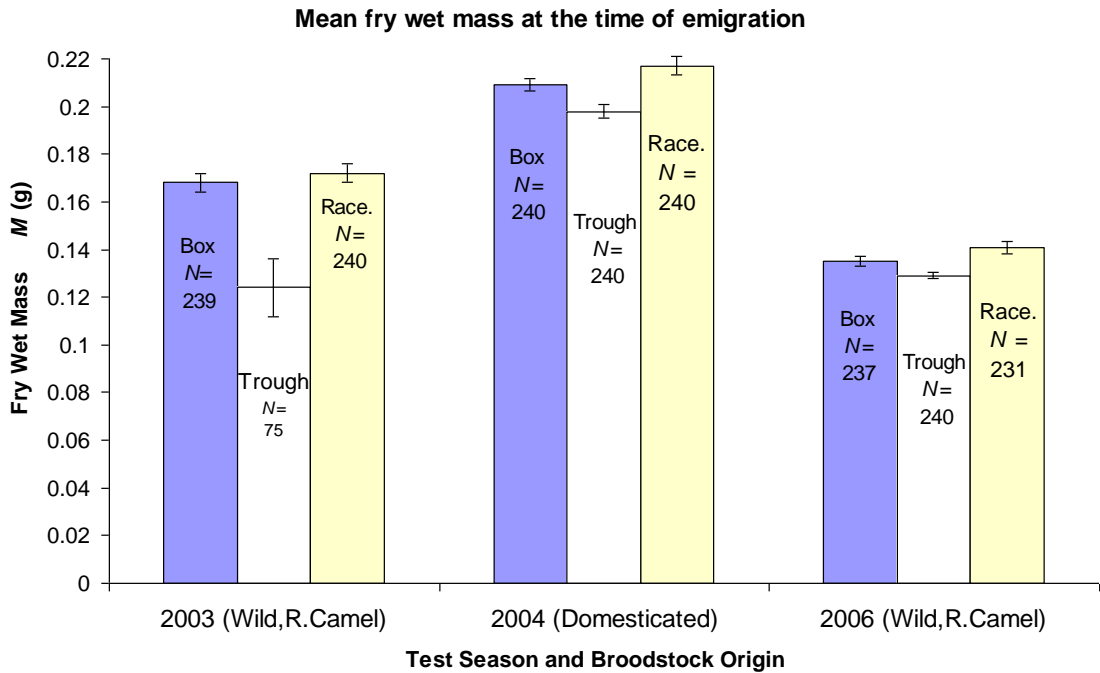


Figure 18: Comparison of mean body mass of emigrating fry incubated in Bamberger-boxes, troughs and raceways for 2003, 2004 and 2006. N gives the number of individual measurements pooled from four replicates for each season. Error bars indicate 95% confidence intervals.

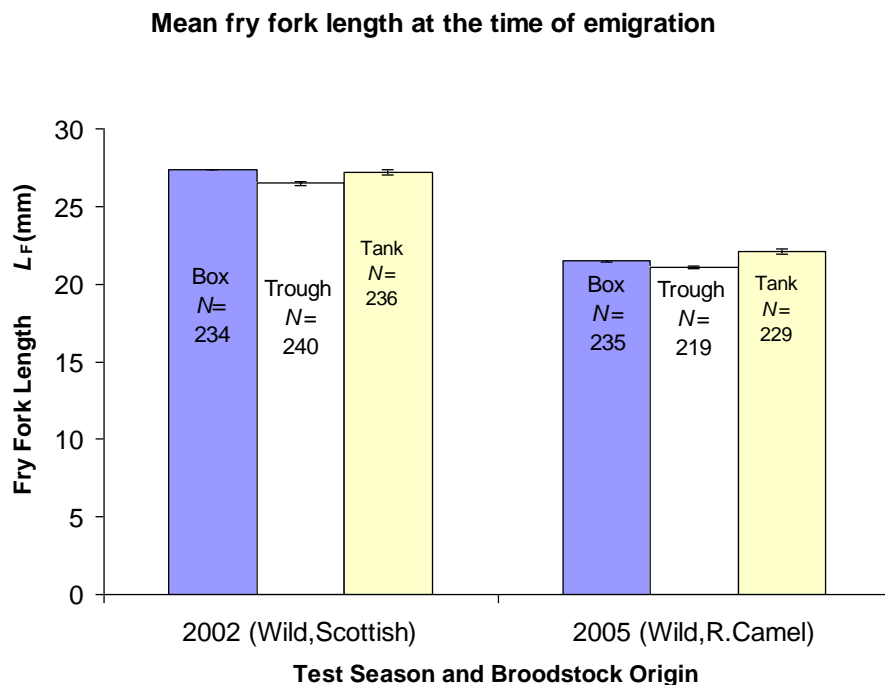


Figure 19: Comparison of mean fork length of emigrating fry incubated in B-boxes, troughs and tanks for 2002 and 2005. N gives the number of individual measurements pooled from four replicates for each season. Error bars indicate 95% confidence intervals

Tanks vs. B-boxes vs. troughs: Differences in fry length and body mass at the time of emigration between tanks and B-boxes were less pronounced and varied between years (figures 17, 19). On average for two years fry from tanks were 0.2 mm (0.73%) longer but 0.005 g (3.5%) lighter than fry from B-boxes (figure 17). The difference in length was statistically significant only for 2005 data. A difference in body mass between B-box- and tank-fry was not statistically significant. The overall difference, averaged for two seasons, in fork length between tank and trough fry was 0.75 mm (3.15%). The difference in fork length was significant for both individual seasons. The difference in body mass between those two incubation techniques was also significant for both seasons with trough fry being overall 0.017 g (11.26%) lighter than tank-fry.

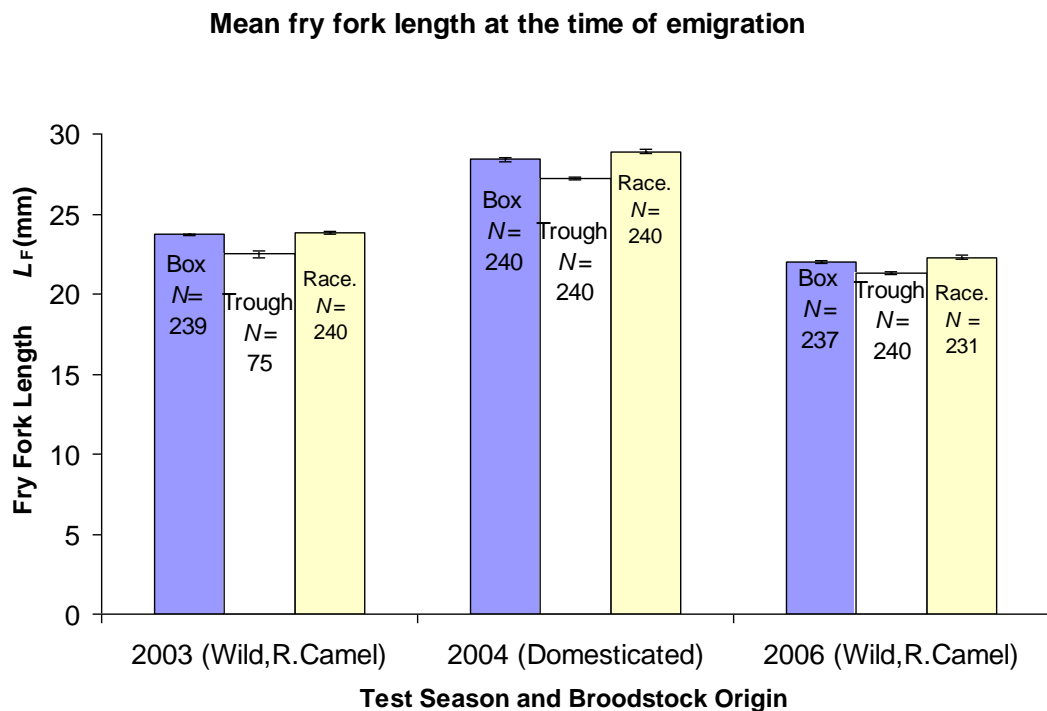


Figure 20: Comparison of mean fork length of emigrating fry incubated in B-boxes, troughs and raceways for 2003, 2004 and 2006. *N* gives the number of individual measurements pooled from four replicates for each season. Error bars indicate 95% confidence intervals.

Raceways vs. B-boxes vs. troughs: On average for three years fry from raceways were longer and heavier than fry from B-boxes and troughs (figures 18, 20). Overall raceway-fry were 1.21% longer than fry from B-boxes and 5.33% longer than fry from troughs. Differences in mean fry length between raceways and B-boxes were not significant but

differences between raceways and troughs were significant for all seasons. Raceway-fry had an overall body mass advantage of 17.52% over trough fry and 3.4% over fry incubated in B-boxes. Differences between fry body mass for individual seasons were not significant when comparing raceways and B-boxes but were significant when comparing raceways and troughs.

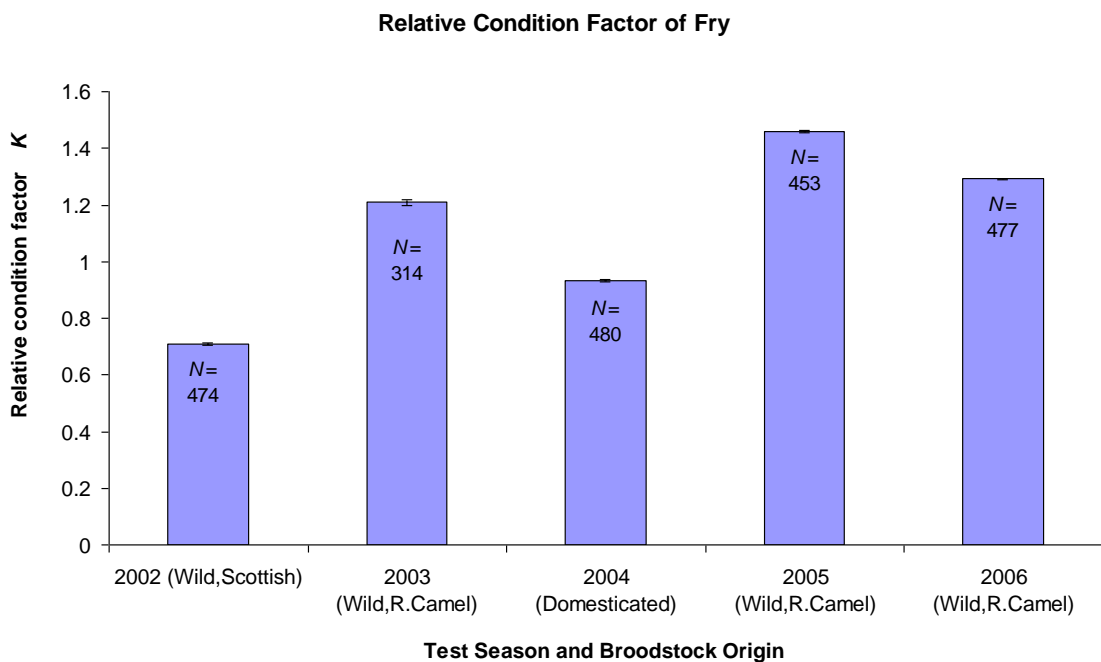


Figure 21: Relative condition factor of emergent fry progeny of five different broodstocks. Error bars indicate 95% confidence intervals of the mean.

Among a total of 68620 fry 60 deformed specimens were recorded over the whole period of the experiments while counting fry before release; 35 came from troughs, 16 from B-boxes, four from raceways and five from tanks. Testing against the expectation of no difference in the number of deformed fry from different incubation techniques revealed a significant difference ($Chi-Sq = 52.88$, d.f. = 3, $p = < 0001$).

4.4.2. Survival rates

Cumulative eyed-embryo-to-fry (EETF) survival rates from the time of planting at the eyed stage to emigration were high in the B-boxes, between 87.9 and 99% (Table 8), with a mean of 93.4% (± 3.0). A mean EETF survival of 85% was recorded for four test runs with tanks. Survival rates varied considerable between replicates (± 8.8) and ranged from 73.3 to 93.5%. The survival rates recorded from six test runs with raceways, independent of the type, were more constant around a mean of 88.5% (± 3.0 ; range 84.5 – 91.5%). Similar high survival rates (for *p* and *t* values see Table 9) were observed in control troughs when 2003 data were excluded from the calculations (mean 94.3%, ± 3.3). Larvae mortality was extremely high during 2003 for fish reared in troughs (< 1% survival). No bacterial or viral pathogens were identified to explain the high mortalities but water temperatures were unusually high for the time of the year peaking at over 16°C. Mean water temperature for the whole incubation period during 2003 was 11.4 °C compared to 9.9, 10.7, 10.5 and 9.8 °C for 2002, 2004, 2005 and 2006 respectively. Survival rates of fish reared in B-boxes and raceways remained similar in 2003 to survival rates recorded in previous and later seasons with cooler water temperatures.

Table 8: Eyed-embryo-to-fry survival for Bamberger-boxes, tank and raceway incubators and hatchery troughs in percentage (mean \pm S.D and range.).

Season	<i>n</i>	Treatment	Survival (% mean \pm S.D.)	Range (%)
2002-2006	20	B-boxes	93.4 \pm 3.0	87.9 – 99.0
2002, 2005	4	Tanks	85.0 \pm 8.8	73.3 – 93.5
2003, 2004, 2006	6	Raceways	88.5 \pm 3.0	84.5 – 91.5
2002-2006	20		75.5 \pm 38.8	0 – 98.1
2002, 2004- 2006	16	Troughs	94.3 \pm 3.3	90.9 – 98.1
2003	4		0	0

Table 9: *P* and *t*-values of pairwise comparisons of treatments on eyed-embryo-to-fry survival after arcsine square root –transformation of percentage data.

	Raceways	Tanks	Troughs
B-boxes	$t(24) = 2.368$ $p = 0.026$	$t(22) = 3.384$ $p = 0.003$	$t(38) = 2.034$ $p = 0.049$
Raceways		$t(8) = 1.398$ $p = 0.199$	$t(24) = 0.813$ $p = 0.423$
Tanks			$t(22) = 0.411$ $p = 0.684$

4.4.3. Emigration pattern for B-box-fry

For most years the exact date of fertilization was not known, hence the date of 50% hatch (estimated from counts in the control troughs) was chosen as the reference point. Fry began to emigrate continuously from the B-boxes on average 37.4 days \pm 3.9 after 50% hatch (Table 10). The emigration period lasted between 12 d and 19 d with a mean of 15.4 d \pm 1. The number of fry emigrating from the B-boxes peaked on average 10 d (\pm 2.5) after emigration started. For the 2004 trials, the only year the exact date of fertilisation was available, the emigration peak was equivalent with 723 degree days incubation after fertilisation. Most emigrating fry were fully developed (R5 – R6 after Killeen et al. (1999)).

Emigration from gravel B-boxes occurred mainly during the night time and activity peaked shortly after dusk (figure 22). Very few fish emigrated during day light. During the two days of emptying traps in intervals of two hours 70% emigration occurred between 22:00 and 1:00.

Table 10: Number of days from 50% hatch to start of fry emigration, duration of the emigration period, numbers of days from the start of the emigration period until its peak and the number of days from the peak to 80% emigration. Data are pooled for four replicate Bamberger-boxes for individual seasons from 2002 to 2006.

Season	<i>n</i>	Emigration start (<i>d</i> after 50% hatch)		Duration of Emigration (<i>d</i>)		Peak of emigration (<i>d</i> after start)	
		mean ± S.D.	range	mean ± S.D.	range	mean ± S.D.	range
2002	3745	37 ± 1	36 - 38	17 ± 1	15 - 19	10 ± 1	9 - 12
2003	3831	42 ± 2	40 - 44	13 ± 1	12 - 14	9 ± 2	7 - 12
2004	3732	35 ± 1	34 - 37	16 ± 1	14 - 17	12 ± 2	10 - 14
2005	3770	33 ± 1	32 - 34	15 ± 1	13 - 17	9 ± 3	5 - 11
2006	3750	40 ± 1	38 - 41	16 ± 1	14 - 17	10 ± 3	7 - 14

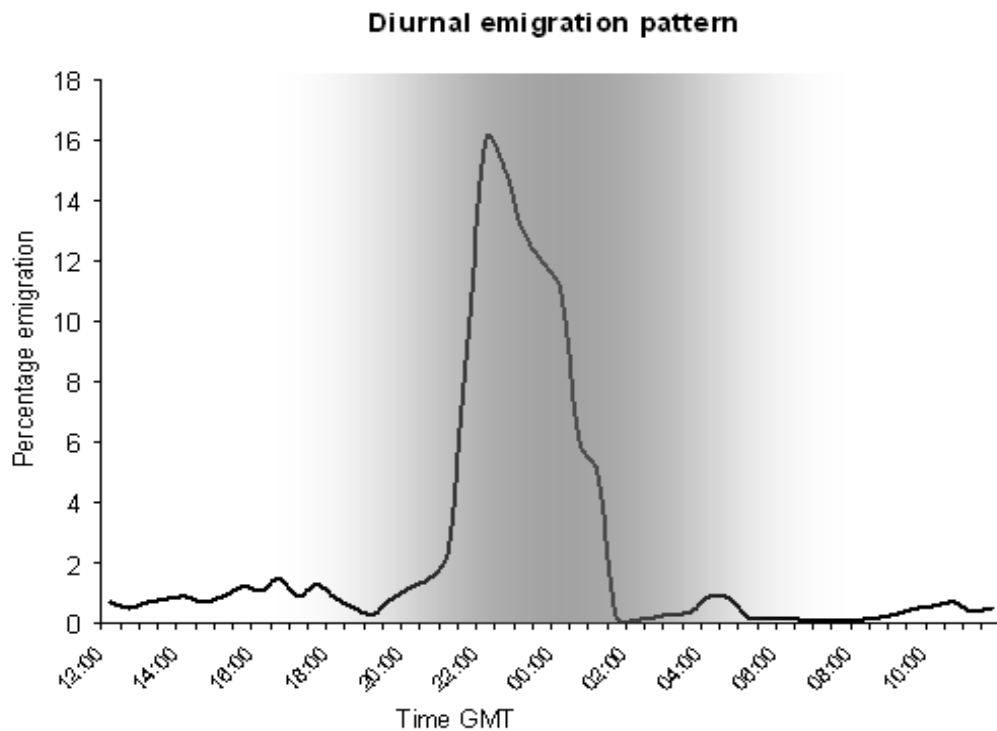


Figure 22: Diurnal profile for fry emigration from Bamberger-boxes during peak emigration. The shaded area indicates night-time. The emigration data are pooled for four Boxes emptied in two-hour intervals for 48 hours.

4.5. Discussion

4.5.1. Rearing environment effects on fry morphology

An important outcome of this study was that all semi-natural incubation systems on trial produced significantly longer and heavier fry than conventional hatchery troughs acting as control. The results of this study were in accordance with numerous authors who reported data for salmonid fry incubated on a variety of substrates (e.g. (Bams 1972, 1973, 1974, Leon 1975, Bams and Crabtree 1976, Bams 1979, Leon and Bonney 1979, Leon 1982, Bams 1983, Eriksson and Westlund 1983, Bams 1984, 1985, Brannas 1989, O'Flynn et al. 1995, Peterson and Martinrobichaud 1995)).

The observation that Camel broodstock always produced the heaviest fry for their body mass irrespective of the incubation technique suggests that the relationship between body mass and length, like egg size (Aulstad and Gjedrem 1973, Beacham and Murray 1993), is a phenotypic variable which is influenced by the genotype rather than by the incubation technique.

The causalities which lead to an increase in body mass and length of first-feeding salmon fry in response to semi-natural incubation are complex and probably interactive: firstly an increased growth rate has been attributed to a lower proportion of vitelline reserves allocated for maintaining body position during incubation. Support of a substrate matrix satisfies the innate righting response of eleuthero embryos and allows the fish to rest. In conventional troughs larvae have to invest more of their energy to maintain an upright position and consequently convert less yolk to body tissue (Hansen et al. 1985). Secondly, with substrate incubation stress is reduced between hatching and emergence by the substratum which separates individual larvae, thus reducing interactions to a natural level. As with other fish (Pickering 1990), a reduction of stress is associated with a higher proportion of energy available for growth in salmonids (Pickering 1990, McCormick et al. 1998, Weil et al. 2001).

An alternative explanation is a supplementary exogenous energy intake by the eleuthero embryos facilitated by the availability of suitable prey items in the stream gravel. There is evidence that larvae start feeding while they still have some yolk reserves (Gustafson-Marjanen and Dowse 1983, Koss and Bromage 1990, Bardonnnet et al. 1993a, Bardonnnet et al. 1993b). The observation that raceways produced slightly larger fry than B-boxes for all test runs might be an indication that larvae feed on hyporheic invertebrates. Raceways had the smallest egg-to-substrate volume ratio during this study hence the amount of potential food items for each individual larva was higher. When conducting laboratory experiments with Atlantic salmon larvae Peterson and Metcalfe (1981) found a similar relationship where gravel depth was positively correlated with mean length and body mass of emerging fry, while stocking density correlated negatively. The role of hyporheic invertebrates as supplementary food for larvae requires further investigations. The effect of different gravel to egg ratios is an interesting factor when comparing substrate incubation systems among each other but in this study it did not mask the benefits of gravel incubation compared to tradition trough incubation. All gravel incubators produced larger and heavier fry than conventional troughs.

Stocking with morphologically superior fry has important advantages: The swimming performance is positively correlated to size (Beamish 1979, Ottaway and Forrest 1983) which in turn decreases the likelihood of catastrophic displacement (Heggenes and Traaen 1988, Einum and Nislow 2005), opens up territories in faster flowing water (Armstrong 1997, Nislow et al. 2000) and enables the larvae to escape predators more effectively. Secondly, while small larvae can ingest only a limited range of small prey, large larvae have a wide food spectrum, from small to large particles. Larger fry are also expected to have larger fat resources than smaller fry (Berg et al. 2001).

4.5.2. Eyed-embryo-to-fry survival

The results of this study demonstrate that semi-natural incubation systems are capable of producing high survival rates of Atlantic salmon fry. Survival from the eyed-embryo stage to fry emigration was always above 85% for all substrate incubation units on trail. Crucially, eyed-embryo-to-fry survival (EETF) in all semi-natural incubation systems was

several times higher than the 2% - 35% ETF survival reported for the majority of salmon streams (MacKenzie and Moring 1988, Pauwels and Haines 1994, Dumas and Marty 2006). Values for EETF survival in a hatchery and ETF survival in the wild can be considered comparable. Although in the wild sometimes considerable mortality occurs during the first weeks after egg deposition (Kennedy and Strange 1981) survival between fertilisation and the eyed stage is generally high in incubation trays (e.g. 99.2% (Dumas and Marty 2006) and was >99% for the Camel broodstock used in this study (J. Ruscombe-King pers. comm.).

In terms of EETF survival the semi-natural incubation units compare favourably with established trough incubation systems. A slightly higher mean EETF survival for hatchery troughs in comparison to substrate incubation during normal climatic conditions was offset by the resilience of semi-natural incubation to high water temperatures. Extremely high larvae mortality in troughs during 2003 was almost certainly linked to a period of unseasonably high temperatures as no bacterial, viral or fungal pathogens were identified and nearly all larvae died within two days. The incident occurred towards the end of the embryo phase when oxygen demand of the now food-searching larvae is highest (Davis 1975). The water temperature was equally high and the dissolved oxygen content even slightly lower in B-boxes and raceways running in parallel to the affected troughs during 2003. However the adverse physico-chemical conditions had no apparent negative effect on the survival numbers in the semi-natural incubation systems. The troughs lack the compartmentalization of space that exists in the gravel environment. Possibly this could mean that conditions in the troughs are more stressful for the alevins. In periods of high temperature this disadvantage may lead to increased mortality. With the prospect of a changing climate (Stone and Bohannon 2006) associated with an increased likelihood of thermal extremes (Portner and Knust 2007) the advantage of semi-natural incubation in this respect will become more important.

4.5.3. Fry emigration patterns from B-boxes

Temporal emigration patterns from B-boxes closely resembled natural emergence patterns both on a seasonal and a diurnal timescale (Gustafson-Marjanen and Dowse 1983, Brannas

1988). The vast majority of fry emigrated synchronously over a short period lasting between three and five days. The peak of emigration each year was highly synchronized between replicate B-boxes. Gustafson-Marjanen and Dowse (1983) and Gustafson-Greenwood and Moring (1991) observed a similar clumped emergence pattern of salmon fry over a period of a few days in the wild. Emergence from B-boxes was also clumped on a diurnal basis with emigration being largely nocturnal. Synchronized nocturnal dispersal among Atlantic salmon fry has been demonstrated both in the laboratory (Brannas 1988, Crisp 1991), and in the wild (Bardonnet et al. 1993a, Bardonnet et al. 1993b, Riley and Moore 2000) and has been attributed to anti-predator tactic (Gustafson-Marjanen and Dowse 1983). Predation is a main source of mortality for artificially reared fry (Henderson and Letcher 2003). It seems plausible that predation from primarily visual predators like birds (Kennedy and Greer 1988) and by fish (Bakshtansky et al. 1983) can be reduced by releasing fish during the dark thus mimicking the timing of natural emergence. However, for practical reasons nearly all artificially reared fish are released during day time. Substrate incubation units offer an advantage in this respect as they can be installed close to the river where the stocking should take place. The units can be modified so that the fry can release themselves directly into the river at night when they are least vulnerable to predation.

Bank side incubation minimises handling and transportation related stressors for the fry. Other factors also need to be taken into account when considering the use of bank-side incubators: in the wild the number of salmon fry emerging on any given night depends on flow rates (Bams 1982, Field-Dodgson 1988, Marty and Beall 1989, Jensen et al. 1991); and on ambient light levels (Field-Dodgson 1988). Artificial incubation units receive a constant amount of filtered water hence there is the possibility that fry release themselves into adverse environmental conditions. The hatchery manager needs to monitor the weather forecast to be able to block the exit for fry to avoid particularly adverse conditions.

4.5.4. Rationale

Substrate incubators have important ecological advantages compared to traditional hatchery troughs but non-biological considerations, such as cost of production and other

economic aspects, come to the fore when the final decisions need to be made. Aprahamian et al. (2003) estimate hatchery operation costs of £0.04 to produce one unfed fry using conventional methodology. The cost to produce a fry using semi-natural incubation systems is of the same order. Set up costs are small for semi-natural incubation systems described in this study. Off-the-shelf equipment can be modified with minimal effort. Labour costs during the incubation period are significantly reduced. An added benefit of setting up incubators so that fish can release themselves into the river is that the sometimes difficult and skill requiring judgement when the larvae enters the free-swimming phase can be omitted. Inexperienced operators or field-based operations without access to expensive equipment benefit from being able to release fish at a time when the fish make optimal use of their endogenous resources. Potential savings in operational costs for planting out unfed fry which account for an estimated £10 - 30 x 1000 eggs⁻¹ depending on the accessibility of the terrain (J. Evans pers. comm.), have to be carefully balanced against the additional costs of setting up incubators in sometimes remote field locations.

The savings on labour and maintenance costs during the incubation period need to be offset against higher costs to clean and store the incubational medium. Semi-natural incubation systems use up several times more space in the hatchery compared to for example vertical-flow Heath incubator trays (Flex-a-Lite Consolidated, Tacoma, Washington).

A strong supra-gravel water flow is considered essential for this type of semi-natural incubation. A stream-like current on top of the gravel used for incubation enable fry to learn appropriate rheotactic behaviour. The water supply for semi-natural incubation systems must be filtered mechanically to reduce the amount of suspended particle matter which might clog the gravel interstices. The amount of filtered water needed for a single unit is substantial and adds to the running costs.

The maximum egg capacity of a particular incubator type depends on the volume of substrate it can take at a maximum depth of about 0.5 m. Applying a deeper gravel depth might impair fry emergence (Crisp 1993a) and creates 'dead spots' with low intergravel water circulation. On the other hand, increasing stocking densities or lowering water exchange rates might have negative consequences on the hyporheic water quality.

The stocking capacity has consequences for application in the field. The small B-boxes and raceways are ideally suited for in-situ incubation on the bank side (Table 11) or for experimental use where a large number of replicates is beneficial. The bigger raceways and the tanks are less suitable for field use as a very large amount of filtered water is required. Furthermore, the large amount of fish incubated at the same time in those incubators makes it necessary to spread fry to different sections of the river which defies the object of setting up an incubator on the bank-side. For hatchery operations the economies of scale are in favour of large raceways and tank incubators particularly in the light that modified standard hatchery equipment can be used.

Table 11: Comparison of practical aspects for the application of four different types of substrate incubation units, the Bamberger-box, raceway incubators type 1 and 2 and tank incubators.

	Bamberger Box	Raceway Type 1	Raceway Type 2	Tank
Construction	PVC Water cistern box	PVC Feed tray	Concrete Trout raceway	GRP Hatchery fry tank
Capacity	800 - 1300 eggs	2000 - 5000 eggs	> 10000 eggs	5000 - 10000 eggs
Application	Experimental and bank site incubation	Bank side incubation, small-scale hatchery operations	Medium and large scale hatchery operations	Hatchery operations
Advantages	Large number of replicates, cheap, easy to transport and set-up, recirculation system possible	Capacity similar to egg density in natural redds, cheap, relatively easy to transport and set-up	Efficient, modified standard hatchery equipment, unidirectional water flow	Efficient, modified standard hatchery equipment
Limitations	Too small for commercial application		Large volume of filtered water needed	Large volume of water, circular water flow, problems identified with removal of fry

5 Importance of the intra-gravel phase for rheotactic development in Atlantic salmon

5.1. Abstract

This study examined the behaviour of newly emerged Atlantic salmon fry (*Salmo salar*) at varying current velocities in a flume tank. Fry which had prior experience of unidirectional current flow on top of the incubation gravel showed significantly different rheotactic behaviour: 75% of fry incubated from the eyed egg stage onwards in semi-natural Bamberger-boxes showed a positive orientation towards the current flow (positive rheotaxis), whereas only 34% of fry from control boxes which lacked a unidirectional water flow above the gravel surface showed positive rheotaxis. The current velocity in flumes had a strong influence on the overall behaviour of fry, with more fry swimming in the open water column at low current speeds and a relatively large number of fry hiding on the flume bed at high current speeds. The behaviour of fry at different current velocities was strongly influenced by their incubation history, with a semi-natural incubation environment and unidirectional water flow above the incubation substratum likely to have a positive impact on fitness and survival of fry after stocking. The findings stress the need for a re-examination of present release programmes using hatchery-reared salmon fry.

5.2. Introduction

Atlantic salmon (*Salmo salar* L.) stocks are in decline throughout most of the historic range of the species (IUCN 2000, Boisclair 2004). Fish culture and stocking are being used to enhance or restore populations (Aprahamian et al. 2003). The majority of artificial propagation programmes are based on releasing unfed fry (Letcher and Terrick 2001) although mortality of hatchery reared fry is higher than co-occurring wild fry of the same species (Salo and Bayliff 1958, Foerster 1968, Mead and Woodall 1968, Letcher et al. 2004). Mortality of newly stocked fry is extremely high during the first couple of days (Henderson and Letcher 2003) indicating that hatchery fry are inferior to naturally produced fry in certain characteristics essential for survival in the wild (Mead and Woodall 1968). To increase post-stocking survival of hatchery-reared fry and retain a 'normal natural' quality in the fish it is imperative to deviate as little as possible from natural development during incubation.

Substrate incubators are an attempt to provide a semi-natural incubation environment. It is well established that incubating salmon fry in a substrate matrix rather than on smooth-bottomed hatchery troughs, has a positive effect on size of emerging fry and the number of fish without deformities (e.g. (Leon and Bonney 1979, Brannas 1989, Hansen et al. 1990)). Although fry size is relevant to survival in the wild (Einum and Fleming 2000a, 2000b), behavioural incompetence of artificially reared fry is still poorly understood and might ultimately explain the high mortality rates of stocked fry. Watters and Meehan (2007) observed that the behavioural plasticity of artificially reared animals is often limited due to a lack of ecologically relevant stimuli during ontogeny. This theory poses the question of what behavioural skills can be learned by the larvae while still under the gravel, relevant to survival during the immediate period after emergence.

The few studies that have focused on larvae behaviour before emergence from the gravel investigated the ability of larvae to learn appropriate responses to predators and prey. It has been demonstrated in the field that larvae are able to start feeding prior to emergence from the gravel (Gustafson-Marjanen and Dowse 1983, Field-Dodgson 1988, Jensen et al. 1991, Zimmerman and Mosegaard 1992, Skoglund and Barlaup 2006). Several laboratory

experiments confirmed that larvae ingest food while having considerable amounts of yolk attached (Twongo and Maccrimmon 1976, Jensen *et al.* 1989, Zimmerman and Mosegaard 1992). Apart from the additional energy intake, feeding during the intragravel phase provides behavioural benefits. Appropriate early experience is essential if individuals are to learn where to eat, what to eat and how to eat and such learning is intimately connected with ontogeny (Paszkowski and Olla 1985, Coughlin 1991).

Courtenay *et al.* (2001) have shown that very young coho salmon, *Oncorhynchus kisutch* Walbaum, can learn the odours of con-specifics to whom they had been exposed immediately after hatching. This learnt recognition was retained for over two months. Conversely Hawkins *et al.* (2004) demonstrated an absence of learning in newly-hatched Atlantic salmon in response to predator odour. The authors explain their results with an absence of opportunities to learn con-specific interactions in the natural river substratum. Access to learning opportunities is an obvious requirement if the animal is to acquire behavioural skills.

Good swimming performance of newly emerged fry is a key prerequisite for survival (Ottaway and Clarke 1981, Nislow *et al.* 2000, Nislow *et al.* 2004a) for a number of reasons. The ability of newly emerged fry to avoid catastrophic displacement during floods is closely linked to swimming performance and appropriate rheotactic behaviour (Ottaway and Clarke 1981). Heland (1978) demonstrated that static swimming behaviour against the current precedes territorial behaviour in brown trout fry (*Salmo trutta* L.). Immediate establishment of a feeding territory adjacent to the river bed is critical for an individual's survival during the critical period shortly after emergence (Armstrong and Nislow 2006). Fry that are unsuccessful in a competitive encounter for a territory frequently die (Gustafson-Marjanen and Dowse 1983, Gustafson-Greenwood and Moring 1990, Bujold *et al.* 2004). Furthermore fry must be able to maintain a positive orientation towards the flow to locate drifting food items (Gibson 1993, Bardonnet and Bagliniere 2000). Positive rheotaxis enables the fish to use their pectoral fins for holding position in typically fast flowing nursery streams with a minimum investment of energy (Bardonnet and Bagliniere 2000). Keeping in mind that starvation is an important factor causing mortality in the first few days after release (Letcher and Terrick 2001) fry with an inappropriate sense of flow may suffer high mortality rates.

In their natural environment are ample opportunities for larvae to learn rheotactic behaviour before they enter the free-swimming stage. During the later stages of development larvae move towards the gravel - surface water interface. The upper hyporheic water flow (the zone beneath the stream bed (Orghidan 1959)) is strongly influenced by the surface water flow (Malcolm et al. 2004). It is also possible that some fry might move up to the riverbed in search of food for a short period and then re-enter the gravel interstices. Such behaviour has been reported to occur prior to emergence (Godin 1982). Some authors even suggested a transitional phase in which Chinook salmon (*Oncorhynchus tshawytscha* Walbaum), brook trout (*Salvelinus fontinalis* Mitchell), and Atlantic salmon larvae repeatedly leave and re-enter the gravel (Heming 1982a, Williams 1988).

The purely upwelling water flow within established substrate incubators is unlike the prevailing water flow in a natural river and does little to promote appropriate rheotactic behaviour in the developing larvae. It is reasonable to argue that the behavioural plasticity of fry from traditional gravel incubation units is compromised in incubators without a unidirectional water flow on top of the incubation medium. The lack of experience of natural conditions may explain the high post-stocking mortality rates.

The aim of this study was to develop and evaluate a semi-natural incubation system that promotes the advantages of established gravel incubators but also provides a unidirectional water flow above the gravel surface. The hypothesis that fry incubated in incubators with a unidirectional water flow above the incubation medium show improved rheotactic behaviour compared to fry that were incubated with upwelling water flow was tested in a flume tank.

5.3. Methods

Three test series were conducted using a range of genetically different broodstocks. In the first field season (2004) eyed ova, progeny of a line of domesticated stock, were obtained from Lakeland Smolt Ltd (Furnace, UK). In 2006 and 2007 eyed ova were obtained from a fish-culture facility at Liskeard, UK (50°26'N, 4°35'W). The broodstock was caught in the wild with rod-and-line from the River Camel in southwest England. Fertilization was done in groups of female and male adults aiming at retention of a very broad and randomly paired gene distribution for each lot. From the late-eyed stage, incubation took place in a gravel medium that was enclosed within Bamberger-boxes. Four identical plastic boxes (figure 23) were placed outdoors and laid side by side on a wooden platform. Inside dimensions of all the boxes were 45 x 34 x 31 cm. Boxes were filled to a depth of 23 cm with natural river gravel. In all boxes a similar gravel composition was used. The substratum characteristics conformed to natural redds (Bjornn and Reiser 1991, Dumas and Darolles 1999). The water depth on top of the gravel was fixed at 4 cm by a water outlet located 2 cm below the box tops. The boxes had an opaque lid with a mesh-covered window (18 x 12 cm) above the outflow to allow in light whilst keeping predators out. Inside the boxes, water was introduced through a feeder pipe which was supplied with water from both ends. Each feeder pipe had diameter of 12 mm and had 1 mm holes drilled in pairs 20 mm apart. The feeder pipes were installed in a wave pattern flat along the sidewall of the box. Water was drained with a similar pipe arranged on the opposite sidewall creating a horizontal water flow through the gravel matrix. The water supply pipes for each box were equipped with valves controlling the discharge to provide a roughly similar inter-gravel flow ($4.5 \text{ dm}^3 \text{ min}^{-1}$). A second, bigger, water supply pipe (inner diameter 2.5 cm) was installed directly opposite the outflow and was screened with mesh material to even out the water flow and to prevent fry swimming up the pipe. In two of the boxes (treatment: figure) this pipe created a medium fast ($Fr \approx 1$) and turbulent ($Re > 4000$) water flow above the gravel surface. The approximate water volume delivered through each pipe was $8 \text{ dm}^3 \text{ min}^{-1}$. Two boxes (control) had the upper supply pipe permanently blocked and only received upwelling water through the gravel.

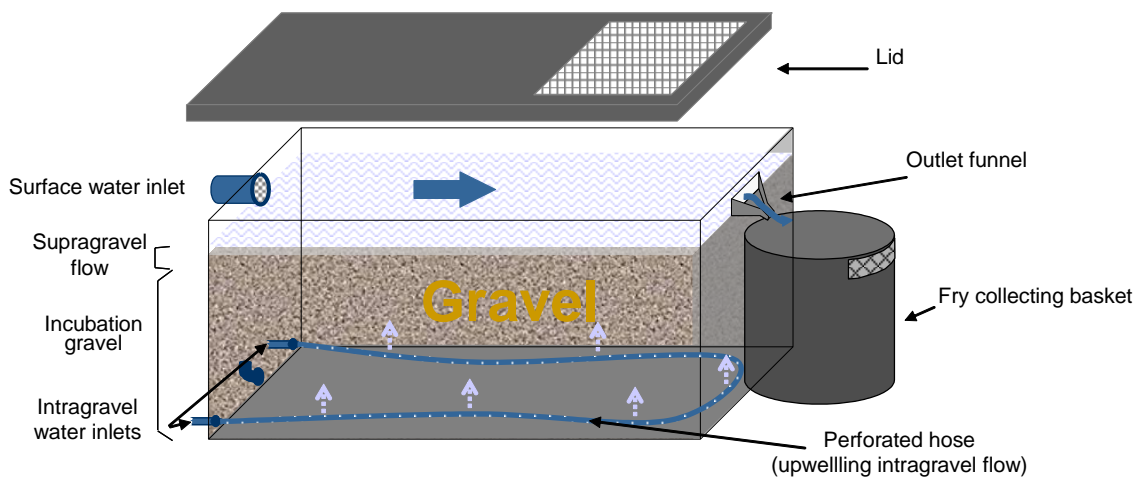


Figure 23: The Bamberger-box (treatment) utilizes a horizontal water flow through the incubation gravel (thin arrows) and a surface water flow on top of the gravel-filled incubation compartment (indicated by the bold arrow).

Interstitial water was sampled at weekly intervals for each box throughout the experiments. Conductivity to $1 \mu\text{S cm}^{-1}$, pH (Palintest Micro 500) and dissolved oxygen concentration to 1% or 0.1 mg dm^{-3} (Palintest Waterproof 800) were measured in situ. Concentrations of ammonia (indolphénol methodology), nitrite (nitricol methodology), nitrate (nitratest) and phosphates were measured in the laboratory. Air and water temperature was continuously recorded (Pasco Xplorer GLX datalogger) with an accuracy of $0.1 \text{ }^\circ\text{C}$.

5.3.1. Handling of the eggs and fry

A few days before hatching, at approximately 450 degree days, the eyed eggs were ‘shocked’, unfertilized eggs removed and the remaining eggs transferred to the prepared boxes. Each box received 1000 eggs. The eggs were protected from UV radiation by the gravel and the box lid covering. The box outlets were screened with mesh material for 20 days after stocking to prevent immature larvae being washed out accidentally. After the initial development period within the gravel matrix, fry emerged from the incubation boxes by working their way to the gravel-water interface and out into the water above the gravel. The outlets discharged into separate fry-collecting traps. Fry in the traps were counted by hand in morning and also in the late afternoon at times of peak emergence. Body deformities, discolorations, erosion of the fins and fungus infections were visually evaluated and recorded. During the peak of emergence, a random sample of 30 fish was

taken from each trap for flume testing. These fry were transported for 45 min in separate containers to Plymouth Marine Laboratory for flume testing on the same day. All surviving fish that were progeny of wild broodstock and that were not used for experiments were returned to their native river after emergence.

5.3.2. Test facilities and protocol

The flume tank was primarily designed for quantifying the impact of biota on aspects of hydro- and sediment dynamics (erosion and deposition), as well as undefined fluxes across the sediment-water interface, thus it was ideal for testing rheotactic behaviour of salmon fry. The flume (figure 24) was constructed of transparent acrylic material with a 0.64 m (outer) and a 0.44 m (inner) diameter, creating a 0.1 m wide annular channel as the experimental arena. It has a continuous bed with a total area of 0.17 m², a working water depth of 0.35 m resulting in a maximum volume of 60 dm³. Water flow is induced by a rotating annular drive cylinder which generates free-stream current velocities, ranging from 0.01 to > 0.5 ms⁻¹. The drive cylinder was rotated with four paddles 0.09 by 0.09 m. The flume was kept at ambient temperature (14.5°C, 13.1°C, 16.3°C for the 2004, 2006 and 2007 test runs respectively) and filled with water extracted from the incubation boxes. The experiments were conducted during daylight.

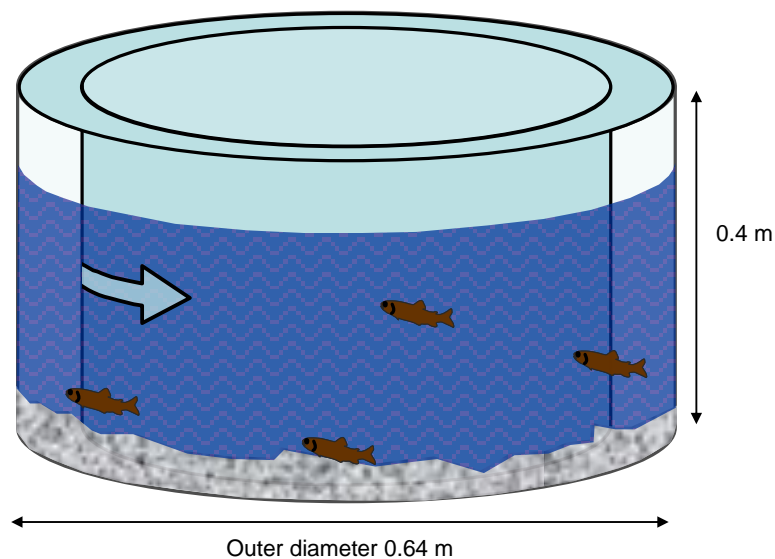


Figure 24: Experimental flume system for studying rheotactic responses of salmon fry. The arrow indicates the current flow direction within the circular flume channel.

A sub-sample of ten randomly selected fry from each box was introduced into the experimental arena when the water was still. The flume drive cylinder speed was then programmed via a portable PC using LabView software in ten step-wise increments every 5 min increasing the depth-averaged current velocity from 0.052 ms^{-1} to 0.482 ms^{-1} and a bed shear stress from 0.031 Nm^{-2} to 1.871 Nm^{-2} . Instantaneous scan sampling (Altmann 1974) was used to estimate activity budgets. The behaviour of all visible fish was censused three times for each current velocity setting at 1.5 min intervals starting at 1 min after each change in velocity. The behaviour of each individual at that instant was recorded. Subjective experimenter bias was reduced by keeping group labels concealed. The results are described in terms of the spatial relationship of fry and flume bed and the relative position of the animal toward the main current flow. A repertoire of four mutually exclusive behavioural patterns was used to define activity:

1. Feeding: defined as using the pectoral fins and boundary layer for holding position towards the current flow (positive rheotaxis) or actively feeding.
2. Swimming: defined as swimming without contact to the substrate or boundary layer.
3. Hiding: defined as concealment on the flume bed and evidently not searching for food items.
4. Undefined: any other behaviour

Four experiments were run every test season using a sub-sample from each incubator. Order effects were avoided by testing each individual fry only once. Fish were kept at densities similar to those that would be experienced in the wild (Grant and Kramer 1990). The experiments were monitored closely to ensure that no injury or unnecessary stress could occur. After flume testing fry were anaesthetised (2-Phenoxy-Ethanol, MERCK-Schuchardt) and body wet mass (M , g) was measured individually to the nearest 0.001 g (Sartorius 2001 MP2). The specimens remained suspended in water to avoid dehydration before the measurements were taken. Individual fork length (L_F , mm, ± 0.1 mm) was measured with callipers (Smiec, Shanghai, precision 0.02 mm). The relative condition factor (K) was calculated as $10^5 \times \text{mass} \times \text{length}^{-3}$. The scale published by (Killeen et al.

1999) was used to evaluate the state of development of emerging fry throughout the experiment.

5.3.3. Statistical analyses

Statistical tests used are described by Sokal and Rohlf (1981) and Zar (1996). The statistical packages MINITAB 15 (Minitab Inc. State College, USA.) and EXCEL VISTA (Microsoft Corp., USA) were used for analysis. Differences in survival between treatment and control group were assessed by two-way analysis of variance (ANOVA) with treatment and years as fixed factors. Body mass, fork length and the relative condition factor are reported as means (\pm S.D., range) for control and treatment. Normality was assessed using a 1-way Kolmogorov-Smirnov test. Variations in morphological indices were tested for by ANOVA, in which individual incubators were nested within treatment.

Frequency data for each category of behavioural patterns were arcsine square root - transformed for statistical analysis. The responses were normally distributed (Anderson-Darling test, AD 2.052; $p < 0.005$) and therefore parametric statistics were used. A variance-ratio test was performed to determine whether the samples of control and treatment fish had shown equal variance in behavioural response. Balanced general linear 3-way ANOVAs were used to test for variations in behavioural patterns across the fixed factors year, current velocity and treatment. If no significant effect of the year (or any interaction of year with one or both of the other factors) was detected, the data for individual years were treated as true replicates for a more powerful balanced 2-way ANOVA with current velocity and treatment as fixed factors. Repeated measures ANOVAs were used to test for variations in behavioural patterns at different sampling intervals.

5.4. Results

This study demonstrated that the incubation environment has a strong impact on the behaviour of Atlantic salmon fry after emergence from the gravel. Fry progeny of the same broodstock, incubated in replicate incubators which only differed in the strength and direction of the water current on top of the incubation medium, showed distinct behavioural differences in experimental flume tanks. No significant difference in the behaviour of fry after one, two and a half or four minutes after the current velocity was experimentally increased was detected. Hence the data from the last observation period, when the fish had time to become accustomed to the new condition, were used for further analysis.

5.4.1. Feeding behaviour

Feeding was the most frequently observed behaviour from fry which were incubated from the eyed egg stage onwards in Bamberger-boxes with a unidirectional water flow above the gravel (treatment: referred to as B-boxes from here onwards) but not fry from the control group (figure 25). This difference was significant (Table 12 provides an overview of relevant *F* and *p* values).

On average, for all experimental current velocities 75% (± 26.99 , range 0 - 100%) of fry from the treatment group established a feeding position, generally behind an obstacle in the substrate, such as a stone or large pebble, from where they started actively catching suspended particles from the drift (Table 12). Fry in feeding position used their pectoral fins and the boundary layer close to the substrate for holding position towards the current flow. Feeding fry were virtually stationary in the current, very close to the bottom or 'anchored' on the bottom with their pectoral fins showing infrequent movements. Only an average of 34% (± 22.54 , range: 0 - 83%) of fry from the control group which were incubated in identical boxes but without water flow above the gravel surface adopted this feeding position.

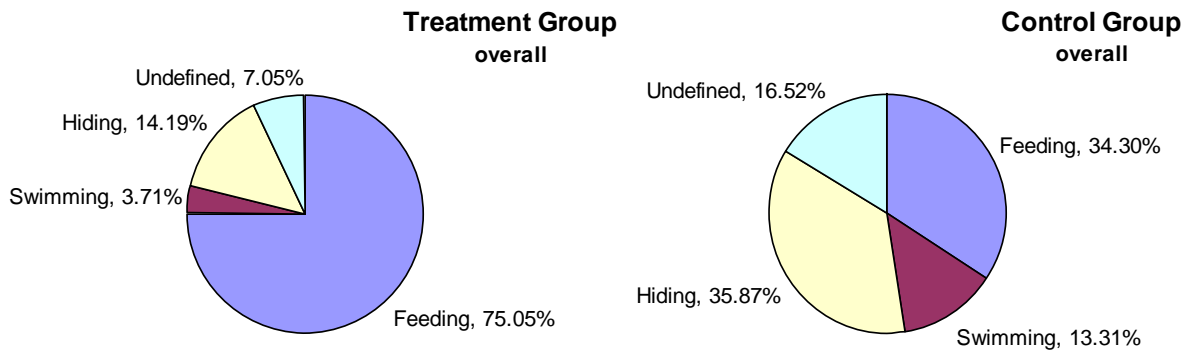


Figure 25: Behavioural response of Atlantic salmon fry in an experimental flume tank subject to different current speeds. The fish response was recorded according to the number of fish visible to the observer performing a particular behaviour (out of four categories). The data are pooled for six individual test runs conducted in 2004, 2006 and 2007. One scan sample was recorded for each of ten increasingly fast current speeds. The pie chart shows the combined data for all current speeds. Treatment and control groups were tested separately.

Table 12: Multivariate analysis of variance of the frequency of occurrence of four categories of behavioural patterns. Interactions that were significant at $p \leq 0.05$ are indicated in bold.

Behaviour	Source of variation	d.f.	<i>F</i>	<i>p</i>
Feeding	Treatment	1	16.30	< 0.001
	Current speed	9	10.79	< 0.001
Swimming	Treatment	1	16.63	< 0.001
	Current speed	9	10.99	< 0.001
	Treatment x Current speed	9	2.79	0.006
Hiding	Treatment	1	67.67	< 0.001
	Current speed	9	12.33	< 0.001
	Year	2	13.04	< 0.001
	Treatment x Year	2	10.45	< 0.001
Hiding + Undefined	Treatment	1	121.30	< 0.001
	Current speed	9	25.72	< 0.001
	Year	2	2.61	0.082

The current velocity in the flume tank had a significant effect on the proportion of fry feeding, both in the treatment and the control group, with most fry feeding at medium current velocities and similar proportions of fry feeding at high and low current velocities (figure 26). Although the fry used for flume testing in 2004, 2006 and 2007 had a significantly different average weight, length and condition factor, the year of testing had no significant effect on the proportion of feeding fish (ANOVA: $F = 2.44$ $p = 0.096$). Interactions between the fixed factors current velocity, treatment and year were not significant.

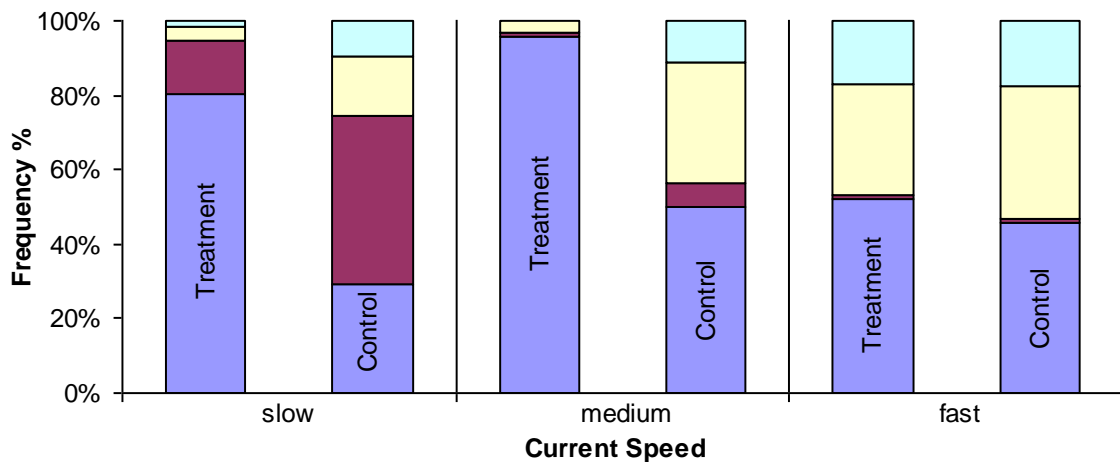


Figure 26: Behavioural response of Atlantic salmon fry in an experimental flume tank subject to different current speeds (slow: 0.052 ms^{-1} – 0.141 ms^{-1} ; medium: 0.170 ms^{-1} – 0.313 ms^{-1} ; fast: 0.357 ms^{-1} – 0.482 ms^{-1}). The fish response was recorded according to the number of fish visible to the observer performing a particular behaviour (■ feeding; ■ swimming; ■ hiding; ■ undefined). The data are pooled for six individual test runs conducted in 2004, 2006 and 2007. One scan sample was recorded for each of ten increasingly fast current speeds. Treatment and control groups were tested separately.

5.4.2. Swimming behaviour

Swimming in the water column was a relatively infrequent behaviour for both the treatment (mean $3\% \pm 9.12$ range 0 - 37%) and the control group (mean $13\% \pm 22.79$, range 0 - 100%) across all experimental current velocities (figure 26). The year of testing

had no significant effect on the proportion of fry swimming in the flume tank without contact to the boundary layer but ANOVA revealed a significant interaction between current velocity in the flume tank and treatment (Table 13). The frequency of swimming behaviour was inversely related to current velocity for treatment and control group (figure 4). The biggest difference between treatment and control group with regard to swimming behaviour was recorded at low current velocities. At low current velocities a large proportion of fry from control boxes (mean 45%, \pm 35.95 range 0 - 100%) were swimming in the water column apparently looking for (and catching) prey items. Those fish often showed no discernible orientation pattern. In comparison, at low current velocities only 14% (\pm 12.29 range 0 - 37%) of fry from the treatment group were swimming. At medium and fast current velocities proportionally less fry from the control group were recorded swimming than at low current velocity (mean 7% \pm 5.26 range 0 - 50% and mean 1% \pm 3.40 range 0 - 33% respectively). At medium and fast current velocities the proportion of swimming fry from the treatment group was very low with a mean of 1% (\pm 2.55, range 0 - 25%). Interactions between observation time and treatment ($F = 1.15$ $p = 0.324$), observation time and current velocity ($F = 0.56$ $p = 0.916$) and observation time, treatment and current velocity ($F = 0.34$ $p = 0.993$) were all insignificant by ANOVA.

Table 13: Mean frequency of occurrence (\pm S.D.) of 'feeding' and 'swimming' behavioural patterns for three current speed categories for the treatment and control group of fry. The depth-averaged current velocity (in ms^{-1}) and the bed shear stress (in Nm^{-2}) are given for ten current speed categories. Values are means \pm S.D.. $N = 6$ for all calculations.

	No.	Veloc. (ms^{-1})	Shear (Nm^{-2})	Feeding %		Swimming %	
				Treatment	Control	Treatment	Control
	Overall all current speeds			75.05 \pm 26.99	34.30 \pm 22.54	3.71 \pm 9.12	13.31 \pm 22.79
Slow	1	0.052	0.031	82.08 \pm 24.31	19.72 \pm 16.75	12.92 \pm 15.53	62.46 \pm 22.38
	2	0.114	0.053	77.50 \pm 22.08	38.89 \pm 22.77	15.83 \pm 12.42	27.78 \pm 27.22
Medium	3	0.170	0.100	92.50 \pm 11.73	57.74 \pm 21.51	4.17 \pm 10.21	14.44 \pm 19.63
	4	0.228	0.184	100.00 \pm 0.00	56.67 \pm 11.55	0.00 \pm 0.00	8.89 \pm 9.81
	5	0.267	0.247	97.92 \pm 5.10	46.11 \pm 20.59	0.00 \pm 0.00	2.78 \pm 6.80
	6	0.313	0.358	91.90 \pm 9.11	39.03 \pm 17.95	0.00 \pm 0.00	0.00 \pm 0.00
Fast	7	0.357	0.433	70.71 \pm 10.59	35.24 \pm 8.97	0.00 \pm 0.00	0.00 \pm 0.00
	8	0.418	0.746	57.74 \pm 12.86	24.86 \pm 8.00	4.17 \pm 10.21	9.72 \pm 15.29
	9	0.462	1.515	45.83 \pm 16.67	18.10 \pm 19.24	0.00 \pm 0.00	3.33 \pm 8.16
	10	0.482	1.871	33.45 \pm 32.73	6.67 \pm 16.33	0.00 \pm 0.00	3.70 \pm 9.07

5.4.3. Hiding behaviour

Overall, for all current velocities, combined hiding was a relatively infrequent observed behavioural category for the treatment group (mean 14% \pm 17.09, range 0 - 67%: figure 26). Fish from the control group showed this behaviour more frequently (mean 36% \pm 24.85, range 0 - 100%). At elevated current velocities (i.e. 0.357 ms⁻¹ – 0.482 ms⁻¹) a proportion of fry from both experimental groups concealed themselves in gaps of the gravel bed at the flume bottom (treatment: 30%, \pm 6.13, range 0 - 67%; control: 35% \pm 16.59, range 0 - 100%). Those fish were unlikely to catch prey items transported by the main current flow and were often observed facing away from the direction of the current flow. Current velocity, treatment and the year when the tests were conducted all had a significant effect on the proportion of fry showing hiding behaviour (Table 14). The interaction of treatment and year with regard to the proportion of hiding fry was also significant. Analysed separately for each year a significant interaction between current velocity and treatment was revealed for 2004 (ANOVA $F = 4.03$ $p = 0.005$), for 2006 (ANOVA $F = 12.56$ $p < 0.001$) and likewise for 2007 data (ANOVA $F = 2.96$ $p = 0.021$). More fry of the control group were hiding at medium water velocities (mean 32% \pm 17.44, range 0 - 80%) than fry from the treatment group (mean 3% \pm 2.80, range 0 - 20%). A similar outcome was recorded for low water velocities with an average of 16% (\pm 11.35, range 0 - 100%) fry from the control group and only an average of 4% (\pm 9.19, range 0 - 25%) of fry from the treatment group hiding within the bottom substratum.

5.4.4. Undefined behaviour

The fourth behavioural category ‘undefined’ was made up by fish showing behaviour patterns that were not clearly accountable to one of the other categories. Most observations for this behavioural group accounted for fish that lost contact with the substrate and were involuntary swept with the current. On average 7% (\pm 13.08, range 0 - 50%) of fry from the treatment group and 17% (\pm 19.17, range 0 - 60%) of the control group were classed as ‘undefined’ (Table 14). The category ‘undefined’ was most frequently observed at high current velocities for both groups (treatment: mean 17% \pm 12.36, range 0 - 50%; control: mean 18% \pm 19.61, range 0 - 60%) and least frequent for

low current velocities (treatment: mean $2\% \pm 4.08$, range 0 - 40%; control: mean $9\% \pm 19.05$, range 0 - 67%). At medium current velocity all fry from the treatment group were attributable to one of the other three behavioural categories but on average $11\% (\pm 18.25, \text{range } 0 - 50\%)$ of fry from the control group had to be classed as ‘undefined’. If the two groups ‘hiding’ and ‘undefined’ were combined for further analysis significant interactions were detected across current velocity and year (ANOVA $F = 1.93$; $p = 0.030$).

Table 14: Mean frequency of occurrence (\pm S.D.) of ‘hiding’ and ‘undefined’ behavioural patterns for three current speed categories for the treatment and control group of fry. The depth-averaged current velocity (in ms^{-1}) and the bed shear stress (in Nm^{-2}) are given for ten current speed categories. Values are means \pm S.D.. $N = 6$ for all calculations.

	No.	Veloc. (ms^{-1})	Shear (Nm^{-2})	Hiding %		Undefined %	
				Treatment	Control	Treatment	Control
Overall all current speeds				14.19 ± 17.09	35.87 ± 24.85	7.05 ± 13.08	16.52 ± 19.17
Slow	1	0.052	0.031	4.17 ± 10.21	13.06 ± 14.92	0.00 ± 0.00	4.76 ± 11.66
	2	0.114	0.053	3.33 ± 8.16	19.44 ± 12.55	3.33 ± 8.16	13.89 ± 26.70
Medium	3	0.170	0.100	3.33 ± 8.16	21.27 ± 22.81	0.00 ± 0.00	6.55 ± 10.69
	4	0.228	0.184	0.00 ± 0.00	31.67 ± 13.12	0.00 ± 0.00	2.78 ± 6.80
	5	0.267	0.247	2.08 ± 5.10	33.33 ± 26.58	0.00 ± 0.00	17.78 ± 18.34
	6	0.313	0.358	8.10 ± 9.11	43.43 ± 22.43	0.00 ± 0.00	17.55 ± 12.33
Fast	7	0.357	0.433	21.19 ± 6.00	40.71 ± 24.87	8.10 ± 12.83	24.05 ± 25.43
	8	0.418	0.746	26.79 ± 1.96	43.33 ± 18.10	11.31 ± 13.25	22.08 ± 20.03
	9	0.462	1.515	36.11 ± 11.39	55.87 ± 25.02	18.06 ± 11.98	22.70 ± 19.27
	10	0.482	1.871	36.83 ± 24.95	56.56 ± 32.25	29.72 ± 19.16	33.07 ± 20.40

5.4.5. Morphological indices

Survival from the time of planting at the eyed stage to emergence was high in all incubators, usually above 90% (mean $91\% \pm 2.70$, range 89% – 97%). No significant difference in survival was detected between years (ANOVA $F = 0.97$, $p = 0.430$) or incubation technique (ANOVA $F = 5.68$, $p = 0.055$). Interactions among factors were not

significant (ANOVA $F = 2.32$, $p = 0.179$). The incubation environment had no apparent effect on morphological indices; body mass, length or condition factor (Table 15).

Table 15: Body wet mass (M in g \pm S.D., range), fork length (L_F in mm \pm S.D., range) and relative condition factor (K) of emergent fry incubated in Bamberger-boxes (treatment) and corresponding body mass of fry incubated in control boxes with upwelling water for three field seasons 2004, 2006 and 2007. $N = 60$ for all groups.

		Wet Mass M (g)		Fork Length L_F (mm)		Relative condition factor K
		mean \pm S.D.	range	mean \pm S.D.	range	
2004	Treatment	0.205 \pm 0.013	0.152 – 0.253	28.1 \pm 1.0	23.9 – 29.5	0.933
	Control	0.201 \pm 0.019	0.150 – 0.269	28.3 \pm 0.9	24.7 – 29.5	0.887
2006	Treatment	0.142 \pm 0.009	0.133 – 0.147	22.3 \pm 0.8	21.9 – 22.9	1.280
	Control	0.138 \pm 0.017	0.068 – 0.144	22.6 \pm 0.5	19.6 – 22.5	1.443
2007	Treatment	0.118 \pm 0.008	0.110 – 0.130	21.9 \pm 0.4	20.0 – 22.2	1.274
	Control	0.121 \pm 0.010	0.107 – 0.139	22.0 \pm 0.7	20.1 – 23.0	1.155

Sampled fry ranged from 19.6 mm to 24.7 mm fork length (L_F) and 0.068 g to 0.269 g body wet mass (M). Mean L_F , M and relative condition factor (K) of fry for the two treatments and three years are shown in Table 15. There were highly significant differences between the three years in L_F (ANOVA $F = 1108$, $p < 0.001$) and M (ANOVA $F = 2067$, $p < 0.001$). The shortest and lightest fry originated from wild Camel broodstock and were sampled during 2007 from the incubation units. The largest and heaviest fry originated from domesticated broodstock and were sampled during 2004. The different types of incubators had no apparent effect on fry length or body mass (length: ANOVA for 2004: $F = 1.326$, $p = 0.252$ for 2006: $F = 3.883$, $p = 0.051$ for 2007: $F = 0.923$, $p = 0.339$; body mass ANOVA for 2004: $F = 1.811$, $p = 0.181$ for 2006: $F = 2.595$, $p = 0.110$ for 2007: $F = 3.293$, $p = 0.072$). The relative condition factor was similar for treatments but varied between fry from different broodstocks (Table 15). Fry progeny of wild broodstock from the River Camel had the highest values in 2006, whereas fry derived from a Scottish broodstock had the lowest relative condition factor. The overall percentage of fish with

visible deformities was low at 0.08%. In total nine deformed specimens were identified by visual inspection over the whole period of the experiments. Two deformed specimens were found in samples taken from B-boxes (treatment) and seven deformed fry were sampled from control boxes. All of the gravel incubated fry seemed to be fit and able to cope with the new environment immediately after release into the flumes for behavioural testing.

5.5. Discussion

5.5.1. Effect of current velocity on behaviour

The behaviour of fry in the flumes was affected by the current velocity and the resultant bed shear stress. At low current velocities ($0.052 \text{ ms}^{-1} - 0.141 \text{ ms}^{-1}$) free swimming in the water column with no discernible orientation pattern was the most frequently observed behavioural pattern for the control group (mean 45%) but not for the treatment group (mean 14%). Fish from the treatment group that had prior experience to a unidirectional current flow were found predominantly feeding directly above the substrate. The results of this study are in agreement with MacCrimmon et al. (1983) who observed a swimming position of hatchery-reared Atlantic salmon juveniles higher off the substrate compared to their wild counterparts. The authors suggested that this behavioural shift accounts for poor survival of planted Atlantic salmon juveniles. Swimming in open water is an inappropriate behaviour for newly emerged Atlantic salmon fry as it leaves the fish open to predation and precludes them from establishing feeding territories on the river bed (Rimmer and Power 1978).

It can be argued that more fry from the control group expressed a non-current oriented movement because they had a weaker sensitivity to flow and to movement of optic cues than fry from the treatment group. Veselov et al. (1998) found that a minimum water velocity of 0.4 ms^{-1} was required to elicit yolk sac fry orienting into the current in a holding tank. Veselov et al. experimented with larvae of a very similar size to the fish used in this study (23 - 26 mm). However their larvae still had not reabsorbed their yolk sacs while all the fish in the present study – at least temporarily - had entered the free-feeding stage. The later development stage might explain why fry in this study, especially fry from the treatment group, were able to react to lower water velocities (Veselov et al. 1998).

At high current velocities ($0.357 \text{ ms}^{-1} - 0.482 \text{ ms}^{-1}$) only very few fry were recorded swimming in the open water. At high current velocities fry avoided the open water and rose above the flume bed only to change their holding position on the substrate. Likewise

Crisp (1991) found that young salmon showed a high rate of instantaneous downstream dispersal at a low velocity (0.075 ms^{-1}) and lower rates of active dispersal at higher velocities (0.25 to 0.70 ms^{-1}). At high current velocities fry used the boundary layer on the flume walls and bed to minimise energy expenditure. The number of fry that lost contact with the boundary layer and were dislocated by the current flow increased proportionately with the current velocity. At high current velocities involuntary displacement makes up most of the uncategorised ‘undefined’ behavioural pattern. This observation is in agreement with Cattaneo et al. (2002) who found that 0+ fish density was strongly and negatively related to the discharge rate during the emergence period, i.e., the higher the discharge during this period, the lower the 0+ fish density. The proportion of fry from the treatment and the control group that were displaced was very similar, indicating that the incubation environment had no significant effect on the velocity threshold of fry. Water velocities at which lotic fish cease to resist the flow and are displaced downstream depend on an array of factors including bed morphology, fish size, development state and water temperature (Brett 1965, Ottaway and Clarke 1981, Ottaway and Forrest 1983, Heggenes and Traaen 1988), which interact synergistically and make absolute values difficult to compare.

5.5.2. Hiding behaviour

Concealment is the classic response reaction from Atlantic salmon juveniles towards a potential threat (Gotceitas et al. 1993). Thus it was not a surprise that a large proportion of fry seek refuge in the gravel matrix when placed in the experimental flumes. Some fish were so successful concealing themselves that the observer was unable to record their behaviour. Consequently the data in this report that include only individuals that were visible to the observer are likely to be biased against hiding behaviour.

It was noted by all observers that fry from the control group were generally less active than fry from the treatment group. This subjective observation was supported by a significantly larger proportion of fish from the control group hiding, especially at low and medium current velocities. One explanation could be that fish from the control group were less hungry than fish from treatment group hence less inclined to search for food (Dill 1977,

Godin and Robert 1989, Gotceitas and Jean-Guy 1991). The surface flow in B-boxes might have resulted in a less efficient use of the yolk reserve due to increased activity leaving fish hungrier at the time of emergence. However, in that case fry from B-boxes would be expected to be smaller and lighter than fry from control boxes as the latter would have more energy available for somatic growth (Wootton 1995, Berg et al. 2001). Fry from the control group would also be expected to be least inclined to take the high risk of swimming in the open water. The data do not support this explanation. Fish from B-boxes had a slightly higher relative condition factor than fry from control boxes (Table 15) and a higher proportion of fry from the control was recorded swimming in the open water of the flumes. An alternative hypothesis to explain the reduced level of activity and larger number of hidden fry from control incubators is that those fry are less accustomed to current flow than fry from B-boxes. It is plausible that fish that have not experienced a directional water flow during incubation find the current flow in the flume tanks an unknown stressor. Those fish lack the learned behavioural plasticity of the treatment group. They may react to the current flow as an unknown stimulus and hide in the gravel bed. However, remaining in the refuge is costly because the gravel matrix provides little opportunity for fitness enhancing activities namely establishing a territory or feeding on drifting invertebrates.

The development status of the fry might partially explain the relatively large number of fry that hide in the gravel bed during the flume experiments. In the wild a transitory period between intergraded and fully pelagic life enables a higher dispersal of salmon fry on spawning grounds of high granularity and increases their chance of avoiding predators (Heard 1991, Salo 1991, Sandercock 1991). When Atlantic salmon larvae begin to disperse from the gravel redds in the spring they do so within the stream bed in low water velocities, and in directions independent of the main flow (Veselov and Shustov 1991). Based on this behaviour it is reasonable to suggest that a large number of fry collected from the incubator traps in the morning were exploring the environment during the night and accidentally ended up in traps. Premature emergence is a phenomenon generally associated with substrate incubation methods compared to wild fry (Bams 1974, Bams and Simpson 1977). Bams (1974) postulates that this behaviour is an artefact due to the lack of opportunity for first emerged fry to re-enter the gravel when trapped. It seems plausible

that those fry try to re-enter the gravel when presented with the opportunity in the flume tanks thus contributing to the hiding behavioural category. The number of hiding fish was strongly affected by the year indicating that factors like temperature, gravel composition or broodstock used for the experiments influenced this behavioural category. Since natural gravel was used for the flume bed a slightly different gravel composition between annual replicates was unavoidable. The ambient temperature and average fry size also varied between annual replicates.

5.5.3. Ontogeny of rheotactic behaviour

Fish which experienced a unidirectional surface flow during incubation showed different rheotactic responses compared to fry from control boxes even though both groups came from the same broodstock. This observation indicates that rheotaxis in salmon fry has both innate and learned components. Fish were able to fine-tune their inherited genetic capabilities by experience in incubators featuring a unidirectional surface flow but not in incubators with solely upwelling water supply.

A variety of pathways have been recognised in which experience shapes behaviour in salmon, including environmental effects on the development of the neuro-endocrine and sensory systems and specific learning effects (Huntingford 2004, Braithwaite 2006). Fry achieve an orientation towards the current flow through vision and by arrays of hydrodynamic sensors located on the surface of the body as superficial neuromasts or embedded in a sub-dermal lateral line (Pavlov 1979, 1986, Montgomery et al. 1997, Montgomery et al. 2002, Montgomery et al. 2003). The development of the locomotor and optomotor response mechanisms is closely connected to development of those sensory organs (Veselov et al. 1998). It has been demonstrated that the sensory and physical capabilities of salmon evolve very quickly during their early life (Skoglund and Barlaup 2006). During ontogeny the greatest changes in the minimum and critical maximum flows to which salmon will respond occur during larvae development (Pavlov 1979), associated with the rapid development of body morphology, locomotor organs, sense organs, and behavioural characteristics. Bahmet (1996) and Veselov (1998) found that the visual sensitivity to movement and tactile sensitivity to water flow of juvenile salmon improved

rapidly as they switch to exogenous feeding and move to the spaces among the gravel on to the bottom of the stream, where they experience a greater effect of water flow. Fast and Stober (1984) observed larvae (*Oncorhynchus spp.*) from hatching through yolk absorption. Their fish demonstrated positive rheotaxis by migrating into the current within the substrate matrix. The present study provides evidence that appropriate rheotactic responses are already shaped during the intragravel phase prior to emergence.

5.5.4. Conclusion and rationale

Inappropriate behaviour of hatchery reared salmon juveniles is widely recognised as a main source of mortality after stocking (see review by Brown and Laland (2003)). Current evidence suggests that a hatchery environment does little to promote behavioural abilities relevant for a survival after planting (Brown and Laland 2003). Indeed, many of the behavioural deficits observed in fish reared in hatcheries appear to be exacerbated by the impoverished hatchery environment (Brown and Laland 2003). On the other hand there are studies illustrating how simple enrichment of the rearing environment affects learning ability, foraging skills, social behaviour, and predator avoidance (Berejikian et al. 2000, Brown et al. 2003). This study demonstrated that environmental enrichment must start very early during ontogeny. Early life history is potentially of crucial importance for the future performance of an individual; the effects of very early events may extend long into the later stages of life (Hepper 2003). Appropriate rheotactic behaviour learned in a semi-natural incubation environment might be the decisive factor when the newly stocked fish struggle for survival during the first few days after stocking. An incubation environment that provides ecological relevant stimuli might turn the balance for successful augmentation programmes.

6 The impact of sedimentary deposits on Atlantic salmon fry habitat: implications for the carrying capacity of a nursery area

6.1. Abstract

Increasing concentrations of deposited sediment in a semi-natural raceway drastically decreased the carrying capacity of the system for Atlantic salmon fry. Final densities ten days after stocking with unfed fry were reduced by 50% compared to reference streams when the sand deposits were increased by only 15%. Emigrating of fry from the semi-natural streams peaked on the first day for reference streams and on day four for streams with experimentally increased sand bed load. A large proportion of fry (48% in stressed streams and 59% in reference streams) migrated out of the system in an upstream direction. The results of the raceway experiments are expected to be an underestimation of the impact that sand deposits have on natural nursery streams due to operational constraints inherent to the semi-natural set up.

6.2. Introduction

One of the most sensitive life stages in Atlantic salmon (*Salmo salar* L.) is the fry stage in early spring (Armstrong and Nislow 2006)). Density-dependent mortality of up to 95% has been documented between the period of emergence of the young fish from the protection of the gravel of riverbeds until the time they establish feeding territories in the river (Gee et al. 1978b, Einum and Nislow 2005). Mortality is generally attributed to competition for microhabitats associated with initial peak juvenile densities that far exceed the stream carrying capacity (Kennedy and Crozier 1993, Armstrong and Nislow 2006).

A habitat with a high degree of spatial heterogeneity offers a vast array of diverse microhabitats (Haury et al. 1995) . There is a general consensus that three-dimensional complexity of a nursery area and, in particular, the complexity of the bed morphology is often the overriding factor in determining productivity of a spawning burn. The resource that is naturally in short supply for salmon fry is increasingly impaired by anthropogenic activity; an increase in sediment deposits fill, plug and bury most of the rough substrate. A much smoother stream bed is the result (Waters 1995). Intensified livestock activity on river banks and drainage of marginal wetlands, have exacerbated sediment supply (National Rivers Authority 1996, Woodward and Foster 1997) through erosion runoff and poorer bank stability. Modern forestry, urban drain systems, drainage maintenance work, forest clearfell and ploughed land also contribute to the sediment bed load (Evans et al. 2006).

Considering that there is significant evidence that increased sediment input through anthropogenic activity is detrimental to fry habitat of Pacific salmon (*Oncorhynchus spp.*) and often ultimately damages adult fish populations (e.g. (Saunders and Smith 1965, Bjornn 1974, 1977, Alexander and Hansen 1983, 1986, Tripp and Poulin 1986, Hillman et al. 1987)), assessments of effects of increased sediments on Atlantic salmon juveniles are scarce. The relatively narrow operational window when fry emerge from redds and the difficulty to sample small fry quantitatively from a river complicates field experiments. One of the few studies investigating destruction of rearing habitat of Atlantic salmon fry due to sand was carried out by McCrimmon (1954) in Ontario County, Canada. Although

his analysis included many factors such as temperature and food, the greatest deleterious effect upon survival of stocked fry was from bed sedimentation; high mortality of the stocked fish occurred as the result of loss of shelter in gravel and riffle spaces with subsequent heavy predation by other fish.

The aim of this study was to use a series of controlled manipulative field experiments to test the hypothesis that increased sand bed load reduces the carrying capacity of a stream section for Atlantic salmon fry. The experimental procedure closely mimicked the standard stocking exercise of hatchery-reared fry and allowed prediction about fry survival in sedimented stream reaches.

6.3. Methods

Experiments were conducted outdoor in simulated stream reaches that allowed Atlantic salmon fry either to become resident or emigrate in response to manipulation of the degree of stream bed sedimentation. The experimental set up and fry incubation procedure were designed to closely match the natural situation, yet providing a controlled environment to test factors independently as well as interactively.

6.3.1. The raceway system

A purpose-build raceway system was embedded in a mill-lead (Dunmere, UK Grid ref. 204417, 67494), which was fed from the River Camel. The rectangular raceway system was constructed of glassfibre-reinforced polyester and was 1100 cm long and 210 cm wide (figure 27).

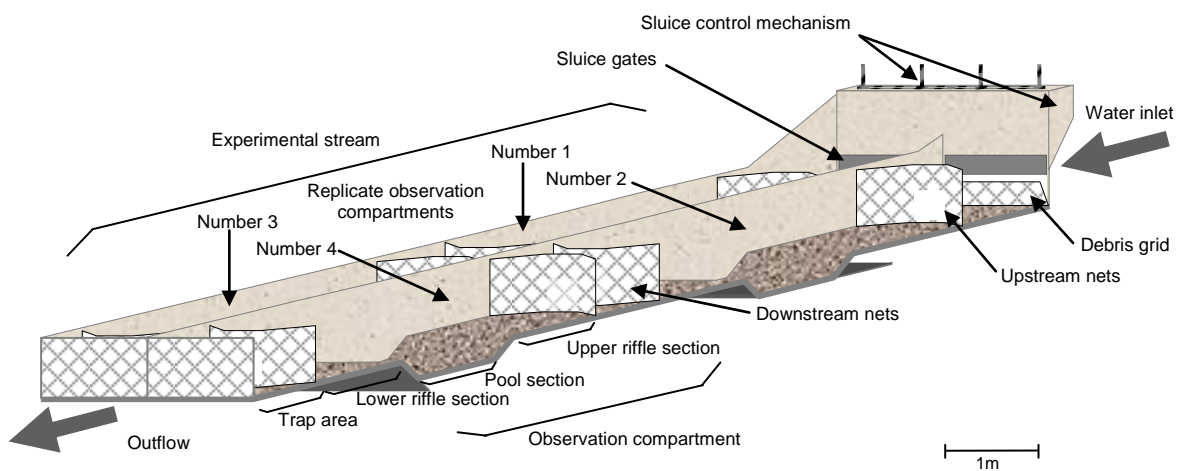


Figure 27: Cut-away view of the experimental raceway system used to assess the impact of bottom sedimentation on fry densities. The nets dividing an experimental stream in two sections during reference experiments were removed for subsequent experiments.

The system was divided longitudinally to create two matching experimental streams. Each stream provided two habitat types: two deeper pool sections were situated between shallow riffle sections. Drift-traps based on modified fyke nets (Hubert 1983) of 0.2 x 1 cm mesh size were installed at both ends of each stream to trap out-migrating salmon fry. Each stream provided 7.6 m² fry habitat in three riffle sections (total area 5.4 m²) and two pool sections (total area 2.2 m²). To double the number of replicate sections for a set of reference experiments additional nets were installed to divide each stream perpendicularly in the middle. Thus each of four experimental stream sections provided 3.3 m² fry habitat in two riffle sections and one pool section.

The experimental streams were initially filled to an average depth of 7 cm with a mixture of gravel and small cobbles providing a substratum with a high 3-dimensional bed complexity. The substratum was taken from an area where salmon are known to spawn naturally and sorted by size and texture, to approximate even bed cover in both experimental streams.

Two automatically operated sluices (controlled by a computer via feedback circuit with a water-level meter) at the upstream end of the raceway system calibrated the discharge at a constant rate of approximately 10 dm³s⁻¹ in both streams throughout the experiments. Water depth was approximately 7 cm in riffle sections and 40 cm in pool sections. Mean water velocity varied between simulated pool (5 cms⁻¹, range 3 - 7 cms⁻¹) and riffle sections (10 cms⁻¹, range 6 - 12 cms⁻¹). Water was run in the channels for at least a month prior to the experiments to permit colonization of a natural invertebrate fauna (Matthaei et al. 1996). Nets of 0.2 x 1 cm mesh size, placed at the inlet downstream from the sluices, evened-out inlet turbulence, and prevented fish from the feeder channel entering the experimental streams. All nets were cleaned on a daily basis. The bed morphology and the hydrodynamic features were broadly similar to natural salmon rearing areas within Cornish rivers.

6.3.2. Fish samples

All fry used for the experiments were progeny of wild brood stock. For 2000 and 2002 eyed salmon ova was supplied by Langass Hatchery, Lochmaddy. For 2003 and 2005, a salmon broodstock was collected from rod catches in the River Camel. Each year, eggs stripped from three individual females (two females for reference experiments) were fertilized with the milt of three anadromous males. Fertilisation dates were a minimum of ten days apart and individual egg batches were reared separately to produce groups of newly emerging fry each year.

A few days before hatching eggs were transferred to semi-natural incubation units. Four B-boxes (figure 28) were placed close to the raceway system and fed with filtered water from the leat. The Boxes closely resembled a natural salmon redd in terms of substratum composition, intra- and supragravel water flow (Chapman 1988). 1000 eggs were introduced into each Box. Fully developed fry released themselves from the incubators by working their way to the gravel-water interface and emerging into the supra-gravel water. The outlets discharged into separate fry-collecting traps. Fry were counted manually once a day in the morning. At the time of peak emigration a sample of 30 fish was taken randomly from each trap for anatomical measurements. Fry were anaesthetised (2-Phenoxy-Ethanol, MERCK-Schuchardt). Wet body mass (M) was measured individually to the nearest 0.001 g (Sartorius 2001 MP2). Individual fork length (L_F , mm, ± 0.1 mm) was measured with a dial calliper. The relative condition factor (K) was calculated as $10^5 \times \text{mass} \times \text{length}^{-3}$. The scale published by Killeen et al. (1999) was used to evaluate the state of development of emerging fry throughout the experiment. The methodology ensured a semi-natural incubation of fry allowing fry to be available when they emerged naturally. It was found that temporal emigration patterns from Boxes closely resembled natural emergence patterns.

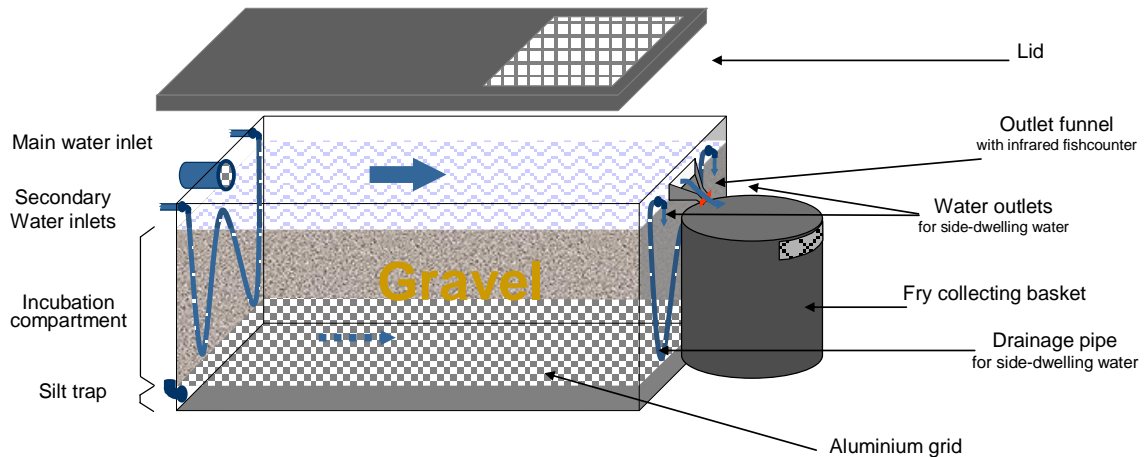


Figure 28: The Bamberger-box uses a horizontal water flow through the incubation gravel and a surface water flow on top of the gravel-filled incubation compartment for a semi-natural incubation of salmon fry.

6.3.3. Experimental procedure

Experiments to assess the carrying capacity of experimental stream sections under reference conditions i.e. with diverse bed morphology were carried out in 2000. For subsequent experiments the sand bed-load was increased on the side of the system, which achieved a higher average carrying capacity during reference experiments (referred to as ‘stressed’ hereafter). Final sand content (ϕ scale 0 - 3 (Krumbein 1941)) was relatively high (approximately 20% by mass). The degree of sand bed-load, corresponded to values observed by the author in Cornish rivers and recorded in other degraded UK rivers (Malcolm et al. 2003). The remaining side was left unchanged (referred to as ‘reference’) and had low sand content (< 8% by mass). Reference and stressed sides were rotated every year.

At the peak of emigration, fry were collected from the incubators at dawn, counted and released immediately into the experimental streams. By stocking the raceway systems with fry emerged the night before the fish were confronted with a situation similar to what they would have to encounter in the wild. Stocking occurred in a uniform manner over a

period of three days. For reference experiments, stream sections on one side of the raceways system received 250 fry each; sections on the opposite side received 150 fry each. The stocking density was reversed for a second test run. Subsequent experiments were conducted in the full-length system. Each experimental stream section was initially stocked with 300 fry equating to a stocking density of 39.47 m^{-2} . On the first day after stocking the fish were denied emigration to allow fry to explore the environment and establish territories without being trapped accidentally. The traps were operated during the second day trapping fish that migrated out of the experimental section. The traps were cleared of fish every day in the morning. Trapped fry were not re-introduced into the observation section. The fish were not fed during the experiments since there was plenty of natural drift food available in the observation sections. After ten days the water flow was stopped temporarily and the fish remaining in the streams were counted and removed. Water and air temperature, turbidity, surface light intensity and water levels were registered continuously throughout the experiment, using fixed sensors and a computer, by means of a purpose written Quick Basic (Microsoft 1999) programme for data storage. Before and after each set of experiments, a sample of water was analyzed for its dissolved oxygen, ammonia, nitrites, nitrates, pH properties. Drifting aquatic invertebrates were sampled every fortnight.

6.3.4. Data analysis

The statistical packages MINITAB 15 (Minitab Inc. State College, USA.) and EXCEL VISTA (Microsoft Corp., USA) were used for analysis. The non-parametric Mann-Whitney *U*-test (Zar 1996) was performed to test the null hypothesis that there was no difference in final fry densities between the two treatments and therefore that the probability distributions are equal. Final densities were ranked on an ordinal scale before analysis. To examine relationships between the different variables, including fry size measures (fork length, wet mass) and density data Pearson's correlation coefficients were used.

6.4. Results

6.4.1. Final fry numbers

Results from test runs conducted in spring 2000 - 2005 in the semi-natural raceway system support the hypothesis that increased sand bed load drastically reduces the carrying capacity of a stream section for Atlantic salmon fry. During two sets of reference experiments carried out in 2000 with a diverse bed morphology when the system was operated with partitioning nets in place the average fry density was 15 m^{-2} ($n = 8$; ± 4 ; range 13 - 19). This value was insignificantly lower than the average final fry density observed when the system was operated with similar bed morphology but at full length (Table 16), i.e. without partitioning nets in place during 2002, 2003 and 2005 (mean 16 m^{-2} ; $n = 9$; ± 3 ; range 11 - 22). However, final fry densities were much lower when the sand bed load was experimentally increased. Average densities dropped to less than half the values recorded for the reference streams and varied between 5 and 11 m^{-2} among replicates (mean 8 m^{-2} , $n = 9$). The difference in carrying capacity for salmon fry among stressed and reference streams was significant (Mann-Whitney, $W = 45.5$; $p < 0.001$).

Table 16: Accumulated counts of fry collected from nets situated upstream and downstream of the two experimental streams. Stressed streams had a higher sediment bedload than reference streams. Three consecutive experiments were carried out each year.

Year	Stressed				Reference			
	No. of trapped fry			Final density (fry / m^2)	No. of trapped fry			Final density (fry / m^2)
	Total	Upstr.	Downstr		Total	Upstr.	Downstr	
2002	143	78	65	9	174	109	65	14
	123	68	55	8	136	77	59	16
	189	69	120	7	58	34	24	18
2003	116	64	52	10	88	55	33	22
	187	87	100	9	128	63	65	14
	152	69	83	6	129	83	46	16
2005	98	42	56	11	104	72	32	18
	186	94	92	9	162	87	75	11
	184	91	93	5	103	55	48	19

During the reference experiments higher initial stocking densities yielded slightly increased final fry densities (Table 17). Stocking with 250 fry per section, i.e. applying a stocking density of 75.76 m^{-2} , resulted in an average final fry density of 17 m^{-2} ($n = 4; \pm 2$; range 13 - 18) whereas stocking with 150 fry per section (stocking density 45.45 m^{-2}) resulted in a lower average density of 14 m^{-2} ($n = 4; \pm 2$; range 12 - 17). This difference was not significant for the small number of replicates in these experiments.

Table 17: Accumulated counts of fry collected from nets situated upstream and downstream of the experimental stream sections during reference experiments carried out in 2000. Four replicate stream sections were tested simultaneously during two consecutive sets of experiments.

Test Run	Section	Stream A		Stream B	
		Number of fry stocked	Final density (fry/m ²)	Number of fry stocked	Final density (fry/m ²)
1	C	250	13	150	17
	D	250	18	150	12
2	C	150	13	250	17
	D	150	14	250	18

6.4.2. Body morphology of fry

Average body length of all sampled fry at the time of emigration from the B-boxes was 24.4 mm (± 1.3 , range 22.5 – 26.5 mm, Table 18). Average body mass was 0.150 g (± 0.021 , range 0.128 – 0.201 g). These values are pooled for all broodstock groups sampled during three seasons. There was no significant correlation between the mass of the fry stocked into the raceway system and the final density of fry in any of the experiments. Likewise, fork length of fry was not significantly related to final densities in reference experiments, reference streams or stressed streams.

On average 18% ($n = 9; \pm 8$; range 5 - 35%) of fry stocked in sections with diverse bed morphology (reference streams) and 29% ($n = 9; \pm 10$; range 15 - 40%) stocked in sections with increased bed load (stressed streams) was neither collected from the traps nor

recaptured from the stream sections after the water flow was stopped. The difference between stressed and reference streams with regard to the amount of missing fry was significant (Mann-Whitney, $W = 108.5$; $p = 0.046$). It is unlikely that a significant amount of fish was simply not detected during the final survey at the end of each experiment. No trend in catch rates, final densities or number of missing fry indicated that residual fry from a previous experiment increased the starting density of a subsequent experiment.

Table 18: Body wet mass M in g, fork length L_F in mm (\pm S.D. and range) and relative condition factor K of newly emergent fry incubated in Bamberger-boxes for subsequent testing in the raceway system.

Year	N	Wet Mass M (g)		Fork Length L_F (mm)		Relative condition factor K
		mean \pm S.D.	range	mean \pm S.D.	range	
2000	60	0.152 \pm 0.051	0.210 - 0.108	26.0 \pm 0.5	26.8 – 25.2	0.865
	60	0.139 \pm 0.035	0.186 - 0.111	24.9 \pm 0.7	25.8 – 22.9	0.900
2002	30	0.152 \pm 0.021	0.183 – 0.127	25.4 \pm 0.5	26.3 – 24.7	0.928
	30	0.144 \pm 0.047	0.194 – 0.112	24.4 \pm 0.7	25.5 – 23.4	0.991
	30	0.131 \pm 0.019	0.163 – 0.113	23.5 \pm 0.6	24.1 – 22.7	1.009
	30	0.143 \pm 0.029	0.200 – 0.110	22.5 \pm 0.8	23.2 – 20.0	1.255
2003	30	0.172 \pm 0.058	0.207 – 0.122	23.6 \pm 0.4	24.6 – 23.0	1.309
	30	0.201 \pm 0.062	0.269 – 0.139	26.5 \pm 0.7	27.4 – 25.7	1.080
2005	30	0.154 \pm 0.022	0.185 – 0.127	24.9 \pm 0.9	26.2 – 24.0	0.998
	30	0.138 \pm 0.025	0.163 – 0.117	23.2 \pm 0.7	24.3 – 22.3	1.105
	30	0.128 \pm 0.057	0.188 - 0.099	23.1 \pm 0.7	24.1 – 22.2	1.038

6.4.3. Emigration pattern

Immediately upon release fry either established a positive rheotactic feeding position or were hiding on the stream bed. Emigration from the artificial streams was predominately nocturnal. The distribution of fry recaptured in traps on a diurnal basis was strongly skewed to the left (figure 29). The quantity of emigrating fry peaked on average on the first day for the reference streams (mean = 1.3 d, $n = 9$; ± 0.5 , range 1-2 d) and on average

on day four for the stressed streams (mean = 3.6 d, $n = 9$; ± 1.0 , range 1 - 4 d). The difference with regard to the day of peak emigration between stressed and reference streams was not significant. The experiments were stopped after ten days when no more than five fry were collected from both traps encompassing a single stream. 85% of emigrants had left the reference streams on average after seven days (± 0.9 , range 5 - 8 d) and 83.7% of emigrants had left the stressed streams after 4 d (± 0.9 , range 1 - 4 d).

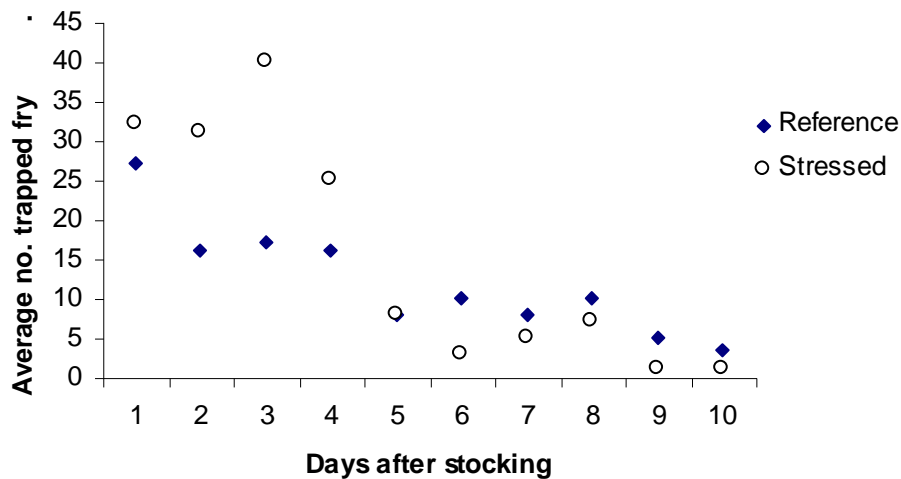


Figure 29: Average number of fry collected from traps confining artificial stream reaches at the upstream and downstream end. Stressed streams had an increased sediment bedload compared to reference streams. Data are pooled for nine test runs. Diamonds represent daily catches in reference streams. Open circles represent catches in stressed streams.

Upstream traps accounted for an average of 48.48% ($n = 9$; ± 6.34 ; range 42.86% - 55.28%, Table 16) of the catches in the stressed streams (figure 30) and 58.92% in reference sections ($n = 9$; ± 6.32 ; range 42.86% - 55.28%; figure 31). The difference between stressed and reference streams with regard to the relative catch numbers in upstream traps was significant (Mann-Whitney, $W = 115.0$; $p = 0.01$).

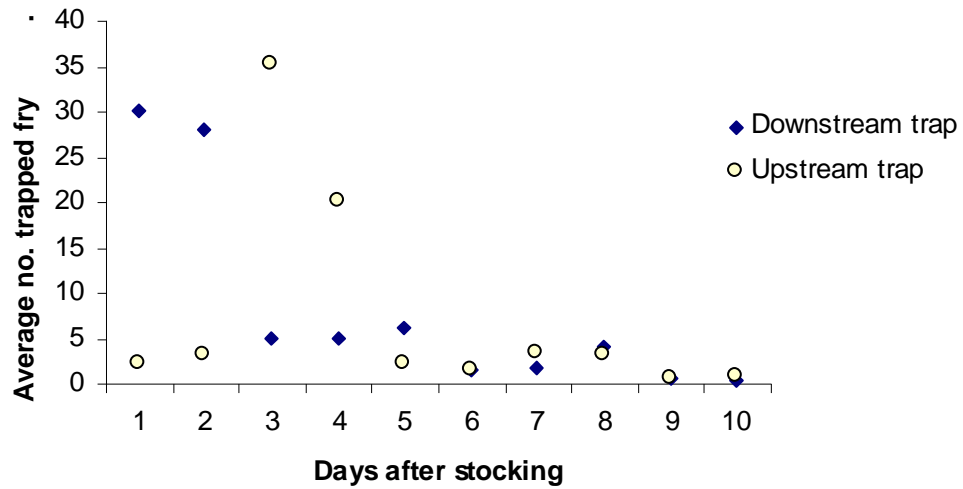


Figure 30: Average number of fry collected from traps situated upstream or downstream of an artificial stream reach with high sediment load. Data are pooled for nine test runs. Diamonds represent daily catches in downstream traps. Open circles represent catches in upstream traps.

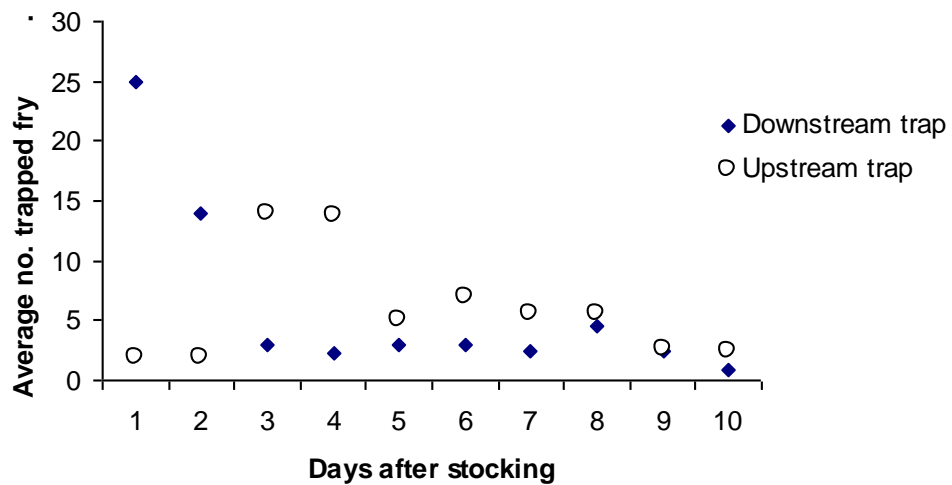


Figure 31: Average number of fry collected from traps situated upstream or downstream of an artificial stream reach with low sediment load. Data are pooled for nine test runs. Diamonds represent daily catches in downstream traps. Open circles represent catches in upstream traps.

The debris nets at the water inlet proved to be efficient in preventing fish from the leat entering the experimental sections. 78 trout fry (*Salmo trutta*), nine eels (*Anguilla anguilla*) and one roach (*Rutilus rutilus*) were found in the debris nets but none of those species were found in the experimental sections.

6.5. Discussion

This study provides clear evidence that increased sand deposition on the stream bed drastically reduces the ability of a nursery area to support Atlantic salmon fry. Average fry densities were reduced to less than half the value recorded for the reference habitat when the sand content was experimentally increased. The results are in agreement with previous studies on juvenile anadromous salmon in the Pacific Northwest of America and inland populations of stream trout that also suggested serious degradation of available physical habitat through sedimentation (Peters 1967, Elwood and Waters 1969, Bjornn 1971, 1974, Bustard and Narver 1975, Barton 1977, Bjornn 1977, Alexander and Hansen 1983, 1986, Tripp and Poulin 1986, Hillman et al. 1987, Suttle et al. 2004, Bolliet et al. 2005).

The sand content in stressed streams (20%) during this experiments was approximately 7% higher than the sand content of the riffle substrate at Atlantic salmon spawning sites reported by Davey and Lapointe (2007) and higher than the median percentage of fines (grain size > 3.2 mm) reported by St-Hilaire et al. (2005) for salmon streams. For Cornish Rivers, where kaolinisation of the granitic bed rock causes surface sand and fine gravel content often to exceed 40% and for low-lying degraded agricultural catchments in other regions (Malcolm et al. 2003) a surface sand content of 20% represents a medium level of impact. Thus these results may be considered as being a realistic representation.

A complex web of proximate mechanisms underlies the detrimental effect that sedimentary deposits have on fry survival. Three important strands can be identified:

- 1) Fry lose energy-efficient feeding stations on the river bed due to increased sand deposits. A feeding position close to a fast current flow is crucial for drift-feeding rheotactic salmonids in order to maximise prey encounter rates. The loss of low-velocity niches adjacent to the stream bed reduces the habitat that fry need for resting and thus energy conservation (Nislow et al. 1999, 2000, Nislow et al. 2004b). Hedger et al. (2005) found that substratum size is more important than velocity in determining habitat use, an observation that underlines the importance of bed roughness in supporting fry at strong current velocities.

- 2) The observation that a significantly larger number of fry were never recaptured from the stressed streams (29%) compared with those of reference streams (18%) could be explained by a greater vulnerability to avian predators in sedimented streams. Fish predators were kept out of the experimental streams with stop nets and the draining of the streams on completion of each experiment allowed for an efficient recapture of fry in the system. Avian predators are the most likely culprits responsible for missing fry. Nislow et al. (2004b) and Elliot (1994) reported that loss rates during the early critical period mostly reflect predation not dispersal. It is well documented that birds prey on juvenile salmonids (Kennedy and Greer 1988). Kingfisher (*Alcedo atthis*) and dipper (*Cinclus cinclus*) were observed in the vicinity of the raceway throughout the experimental time period. Sedimentation fills refugia and leaves salmonid fry exposed to predation (Jenkins 1969). Dionne and Dodson (2002) reported differences in flight reaction in responses to a simulated avian predator of salmon fry on fine sediment. It is reasonable to assume that the relative importance of predation related mortality will increase when fish predators such as brown trout (*Salmo trutta*) and older salmon are present. Henderson and Letcher (2003) reported that 48.6% of fry in their experiments were consumed within the first 2 days after stocking mostly by co-occurring salmonids. In view of this number the 29% loss attributed to predation in stressed streams is likely to be a vast underestimation of the importance of predation in natural streams due to the lack of fish predators in experimental streams.
- 3) Salmon fry are highly territorial (Kalleberg 1958) and defend small (0.1–0.2 m²) territories (Grant et al. 1998). The smoother bed morphology of streams with a high sediment bed load promotes visual contact and interaction between fish resulting in increased territorial competition and stress (Kalleberg 1958, Imre et al. 2002). Furthermore, deposited sediment is often less stable than the original material (Marks and Rutt 1997) and an ever-changing stream bed composed of a moving sand bed load precludes salmon fry from establishing permanent territories (Alexander and Hansen 1986). In support of this hypothesis (Bolliet et al. 2005) attributed a higher rate of emigrating brown trout in their embedded streams reaches to an increase in competition.

6.5.1. Implications of raceway results

The average fry density recorded for reference streams (16 m^{-2}) was much higher than the maximum densities reported by Hedger et al. (2005) or Einum et al. (2006) for natural streams (1.1 m^{-2} and 3.3 m^{-2} respectively). This discrepancy can partly be explained by the fact that the experimental streams provided relatively uniform, optimized fry habitat over the whole width whereas only a proportion of a natural stream provides suitable fry habitat (Hedger et al. 2005). Although several factors intrinsic to the experimental set up facilitated unnaturally high fry densities in reference streams the same factors disproportionately favoured disproportionately high densities in stressed streams:

- 1) A medium-strong constant water flow was applied during the duration of the experiments. In contrast, natural streams are exposed to floods. The period of emergence of the fry from the gravel coincides with the time of natural spring spates which have been reported to reduce fry survival (Ottaway and Clarke 1981, Ottaway and Forrest 1983, Letcher et al. 2004, Tetzlaff et al. 2005). Nislow et al. (2002) stated that reductions in underyearling salmonid abundance after a major flood event were greatest at the study site experiencing greater geomorphic change (bedload movement and sedimentation), even though hydrologic intensity (velocity, shear stress, unit stream power) was greater at a reference site. A combination of factors associated with increased sedimentary deposits might interact synergistically to reduce fry abundance:
- 2) Stable low velocity niches (i.e. instream structures which have a high critical erosion threshold, thereby having a high resistance to mobilisation during flood periods) are covered with sediment (Craig Goch Joint Committee Ecological Investigations 1980) and cannot be used as refuges by the fish during floods. In highly sedimented reaches, the hydraulic dead zone fraction (microhabitats with no water movement (Lancaster and Hildrew 1993) decreases as discharge increases (Kaufmann 1987). This means that physically simple, sedimented reaches become absolutely and relatively more homogeneous as discharge increases during flood events. Decreased channel roughness, results in reduced river bed friction and thereby increased water velocity at the stream bed (Platts et al. 1989). The effective scour depth for a given discharge is

positively correlated to bed load (Montgomery *et al.* 1996a). Increased turbidity caused by re-mobilised materials during floods can result in salmonids visual impairment (Wilzbach *et al.* 1986, Robertson *et al.* 2007). Since station holding is primarily achieved through vision and the lateral senses (Pavlov 1979, 1986), particularly young fry (whose sensitivity to flow and to movement of visual cues is not fully developed (Veselov *et al.* 1998) are apt to be displaced downstream at high turbidity as they are no longer able to keep station visually (Larimore 1975).

- 3) Salmon fry were experimented with in allopatry whereas allopatric populations of Atlantic salmon are extremely rare for natural streams (Heggenes and Borgstrom 1991). Juvenile brown trout (*Salmo trutta*) are common competitors for space (Jones 1975, Egglisshaw and Shackley 1982, Kennedy and Strange 1986). In most encounters, brown trout were found to be dominant, because at an equal size of salmon and trout offspring, young trouts are generally more aggressive (Waters 1983, Glova and Field-Dodgson 1995) and thus competitively superior in acquisition of the resource. In presence of juvenile brown trout Atlantic salmon fry are likely to increase their use of shallow riffle areas and fast flowing sections of nursery stream (Lindroth 1956, Heggenes *et al.* 1990). With increased sediment load, low velocity niches in those fast flowing riffle areas become scarce rendering the habitat energetically unsuitable for salmon fry. With the remaining microhabitats predominately occupied by trout, even a relatively insignificant reduction of the overall microhabitat availability due to human interventions might have serious consequences for salmon populations.

- 4) Fish in stressed streams benefited from a higher food concentration than fish would in natural streams with a similar level of sedimentation. In natural streams increasing concentrations of deposited fine sediment shift invertebrates toward burrowing taxa unavailable as prey for drift-feeding salmon fry (Suttle *et al.* 2004) and generally decrease invertebrate richness (reviewed by (Waters 1995). The experimental streams received a constant drifting food supply from a productive leaf that masked any effect the instream sedimentation had on invertebrate richness. It is plausible to assume that natural streams with similar levels of sedimentation than the stressed streams in these experiments have a lower carrying capacity for salmon fry due to a lower food supply

as Milner et al. (2003) found a positive correlation between food supply and carrying capacity. Firstly, individual territory size decreases in a food-rich environment (Grant and Kramer 1990). Secondly, more microhabitats become energetically efficient with an increased availability of drifting invertebrates, the main food source for salmon fry (Nislow et al. 1998).

6.5.2. Temporal and spatial dispersal pattern

In the river newly emerged salmonid fry try to establish territories within the immediate vicinity of the redd (Crisp 1995, Heland et al. 1995), aggressively defend those territories, form dominance hierarchies and compete intensively for resources (Kalleberg 1958, Heland et al. 1995, Lahti et al. 2001). Fry unsuccessful in a competitive encounter for a territory either die or disperse (Gustafson-Marjanen and Dowse 1983, Gustafson-Greenwood and Moring 1990, Bujold et al. 2004). In the raceway system the large number of fry collected from traps within the first 3 - 4 days can probably be attributed to individuals that were unable to establish a territory within the experimental stream. After the initial migration period numbers of fry emigrating from the system stabilized at a very low level. It can be argued that fish collected from traps following the initial emigration period were displaced by resident fish extending the size of their territory. Gustafson-Greenwood & Moring (1990) observed salmon fry dispersing further as territory size increased with fish size.

Relative catch rates in upstream or downstream nets contradict observations on wild fry dispersal. 68% of fry were found in traps situated upstream of the experimental section in reference streams, a pattern that conflicts with the findings of Bardonnnet et al. (1993b), Einum and Fleming (2000b) and Bujold et al. (2004) who have reported a predominantly passive down-stream drift of newly emerged Atlantic salmon fry. A likely explanation for the high percentage of upstream movement is the lack of predators in the experimental system. The presence of predators often increase downstream movement of fry (Heland et al. 1995). An interesting alternative explanation is that an upstream movement of fry in the system was facilitated by comparatively low current velocities and the three-dimensional complexity of the stream bed. For predominantly drift feeding salmon fry

(Nislow et al. 1998) having first access to the food source would comprise a clear competitive advantage over simultaneously emerged siblings. It is plausible that upstream movement is an active process for fish that were initially successful in establishing a territory whereas competitively inferior fry opt for a passive energy saving downstream drift. The observation that during the first two days movement was predominantly downstream and upstream movement peaked during the third and fourth day is consistent with this hypothesis. The experimental set up did not allow predictions to be made regarding the scale of the upstream movement or if the behaviour persists at higher current velocities. The relative lack of low velocity niches on the stream bed in sedimented experimental streams and consequently the higher energy investment for an upstream movement might explain the significantly lower proportion of fry recovered from upstream traps in stressed streams.

6.5.3. Conclusion and management implications

Even though the average fry density recorded for reference streams is unlikely to be matched even in pristine natural streams the proportional reduction in carrying capacity as a result of sedimentation is likely to be higher in natural streams. For the majority of Atlantic salmon populations a reduction of the carrying capacity of a fry nursery area due to increased sedimentation will subsequently reduce the number of adults (Niemela et al. 2005). In rheotactic salmonids, the short period (a few days) after emergence from the gravel is critically important for individual survival (Armstrong and Nislow 2006). Dispersal from incubation sites to underutilized areas is limited (Gustafson-Marjanen and Dowse 1983, Beall 1994) and in most cases, down stream drift is equivalent to death for juvenile salmon (Symons 1971, Nislow et al. 2004b). The results of this study prove that a moderate exacerbation of fine-sediment delivery and storage in gravel bedded rivers can reduce the carrying capacity of a nursery area for Atlantic salmon by more than 50%. If cohort strength is essentially set by events during the fry stage, this reduction in numbers should alarm fishery managers as it will have serious consequences for the number of returning adult salmon.

7 Pilot experiments

A series of pilot experiments was conducted to improve semi-natural incubation for salmonids further and to verify the detrimental effect of increased sedimentation on fry habitat on a large temporal and spatial scale. The biological and economic benefits of semi-natural incubation systems have been demonstrated in Chapter 3; 4 and 5. New data suggest that simple alteration to gravel incubation systems can further improve efficiency of production. Section 7.1. explores the importance of hyporheic invertebrate abundance (invertebrates that dwell in the region beneath and lateral to a stream bed, where there is mixing of shallow groundwater and surface water: (Orghidan 1959)) on salmon larvae development. The negative effect of sedimentary deposits on the stream bed on the carrying capacity of a stream section for salmon fry was demonstrated in a semi-natural raceway systems (see Chapter 6). Section 7.2. describes a field experiment that was set up to verify the raceways results on a large scale and to help to improve salmon stocks in the short term.

7.1. Impact of hyporheic invertebrate abundance

7.1.1. Introduction and methodology

The observation that Raceways-type incubators produced slightly larger fry than the smaller B-boxes during this study (see Chapter 4) led to the hypothesis that salmonid larvae fed on hyporheic invertebrates while still in the gravel. Raceways had a smaller egg-to-substrate volume ratio (1 : 0.5 dm³ in raceways compared to 1 : 0.04 dm³ in B-boxes: Table 5) hence the amount of potential food items for each individual larva was higher in raceways. This hypothesis is in accordance with Peterson and Metcalfe (1981) who conducted laboratory experiments with Atlantic salmon larvae and found a similar relationship were gravel depth was positively correlated to mean length and weight of emerging fry, but stocking density negatively.

The literature provides evidence that salmon larvae start feeding while they are submerged under gravel and still have some yolk reserves providing a resource buffer (Gustafson-Marjanen and Dowse 1983, Koss and Bromage 1990, Bardonnnet et al. 1993a, Bardonnnet et al. 1993b). Larvae develop crude teeth (Huysseune and Witten 2007, 2008) at early post-hatch stages and have relatively large and well-developed eyes typical for visual predators (Wankowski 1981). Koss and Bromage (1990) found that the highest mean weight was achieved in a hatchery when Atlantic salmon fry were fed prior to final yolk sac absorption.

To test the null hypothesis of hyporheic invertebrate abundance having no measurable effect on Atlantic salmon larvae development a series of pilot experiments was conducted in 2004 at Westcountry Trout hatchery facilities in Boscastle, UK. For four treatment boxes the incubation medium was sterilized with boiling water 24 h before stocking with eyed ova. The water supply for treatment boxes was mechanically filtered throughout the incubation period (Kockney Koi Yamitsu 55W 50Hz UV-filter and Endecotts sieve 0.25 mm). Four control boxes received river water directly from a mature gravel filter. Control boxes were left running for two month to allow for invertebrate colonization before stocking with the same amount of eyed ova as the treatment boxes (figure 32). All eight boxes were identical apart from the described differences. Substrate composition, stocking of boxes with eyed ova, sampling and the general experimental routine were described in detail in Chapter 3 'Evaluation of a new semi-natural incubation technique for Atlantic salmon fry'.

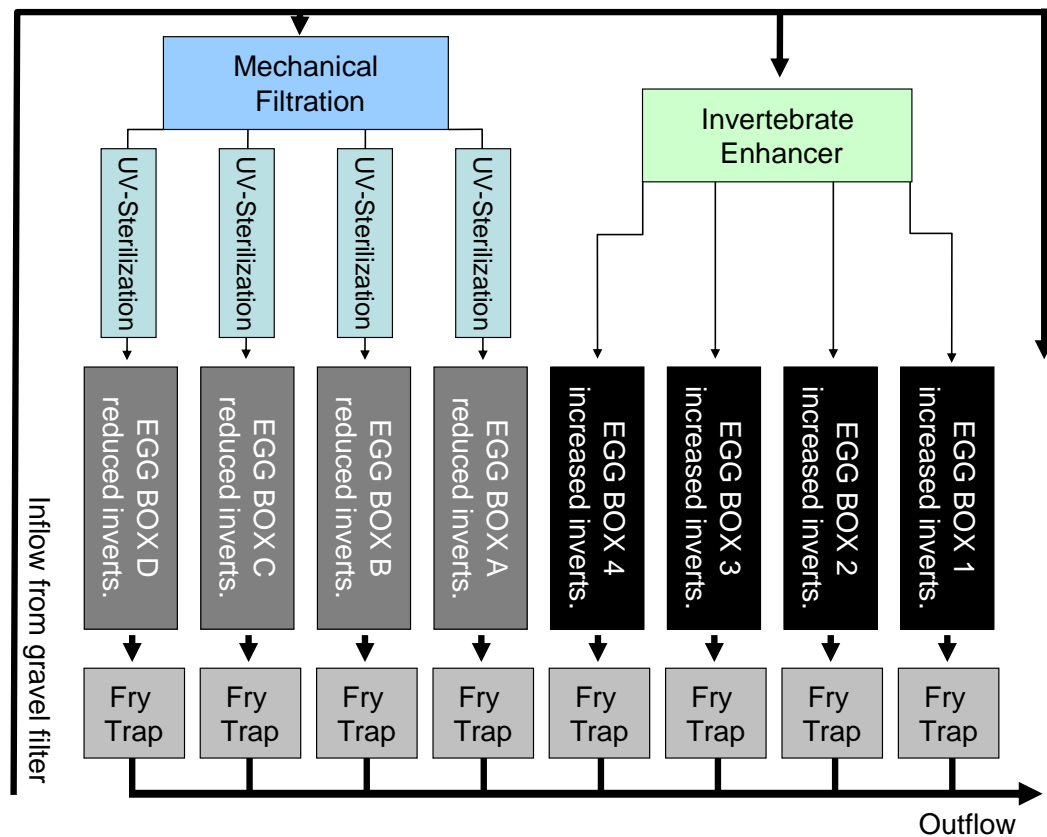


Figure 32: Experimental set up for a pilot experiment to test the influence of reduced hyporheic invertebrate abundance. The water supply was filtered for four treatment boxes to reduce the amount of hyporheic invertebrates.

7.1.2. Results and discussion

The results of the pilot experiments strongly support the hypothesis that salmonid larvae start feeding while still under the protection of the gravel matrix. Emigration pattern differed significantly between treatment boxes which had a reduced invertebrate abundance and control boxes with an unfiltered water supply (figure 33 and figure 34). Fry from treatment boxes emerged on average six days earlier than fry from control boxes indicating that the larvae had used up their yolk reserve earlier. Fry from treatment boxes emigrated over a longer period whereas emigration from the control boxes peaked at one night (24th April). For boxes with reduced invertebrate abundance 80% of the emigration

occurred until the 22nd April. For the other boxes the same figure was reached three days later on the 25th April. Analysis of this distribution indicates a significant departure from normality. The data for boxes with a reduced invertebrate abundance are skewed to the right ($g_1 = 0.72$) and are platykurtic. The data for control boxes with unfiltered water supply are skewed to the left and leptokurtic ($g_1 = -0.54$).

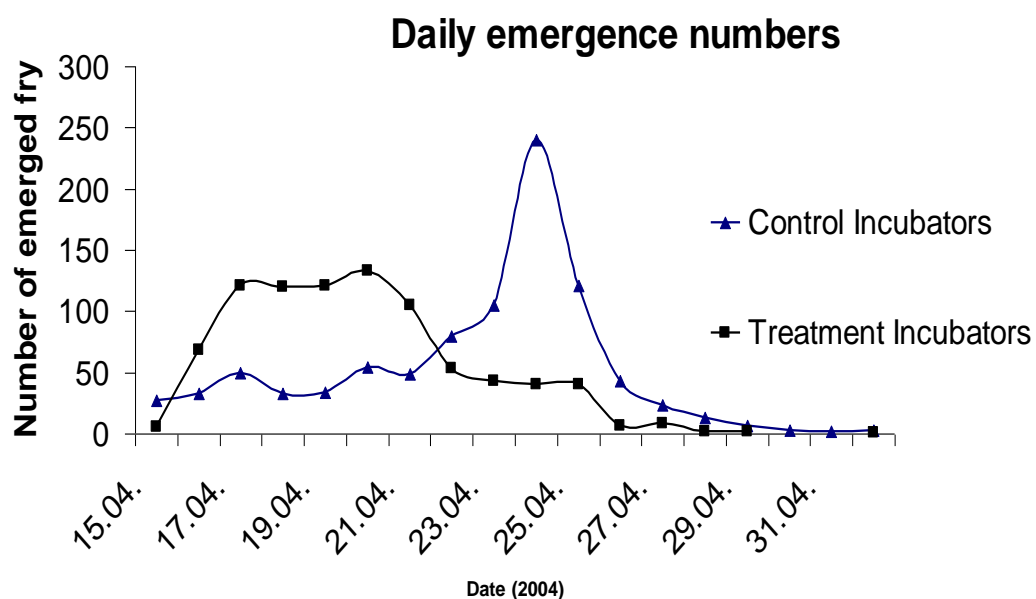


Figure 33: Daily emergence numbers for fry during a pilot experiment to test the influence of hyporheic invertebrate abundance on Atlantic salmon juveniles. Data are pooled for four treatment boxes with a reduced abundance of invertebrates and four standard Bamberger-boxes acting as control.

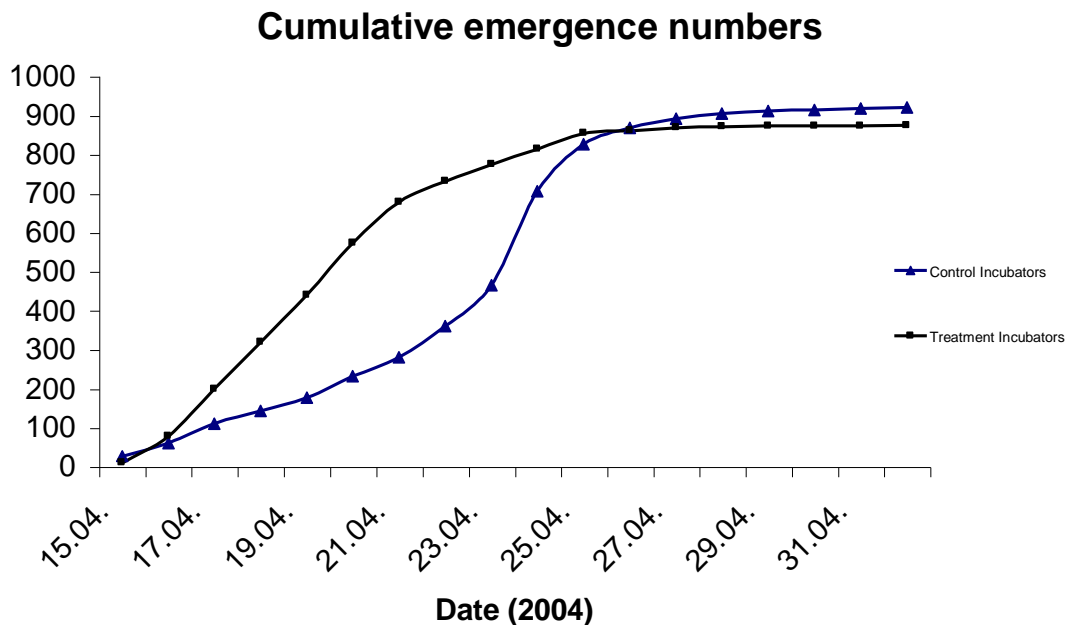


Figure 34: Cumulative emergence numbers for fry during a pilot experiment to test the influence of hyporheic invertebrate abundance on Atlantic salmon juveniles. Data are pooled for four treatment boxes with a reduced abundance of invertebrates and four standard Bamberger-boxes acting as control.

Fry from treatment boxes with a reduced amount of hyporheic invertebrates were on average 4.3% smaller (fork length) and 8.3% lighter than fry from control boxes at the time of emergence. The observed difference in length and weight between treatment and control at emergence was in the same order of magnitude as the difference between standard hatchery troughs and substrate incubators (see Chapter 4). However, the difference was not statistically significant for the small sample number used. Further experiments need to be carried out to confirm the results.

Apart from morphological benefits the availability of suitable prey items in the incubation medium could also provide an important behavioural advantage for the fry. Analogous as it was shown that salmon fry can improve rheotactic behaviour when a suitable stimulus is provided (see Chapter 5 ‘Importance of the intra-gravel phase for rheotactic development in Atlantic salmon’) fry might be able to learn appropriate feeding behaviour when natural prey items are available. It has been reported that upon release, hatchery fish are slow to

start feeding and compared to their wild counterparts, they consume less food, feed on a highly restricted range of food items and are slow to switch between prey items as they vary in abundance (Sosiak et al. 1979). Providing fish with natural occurring prey items during incubation might help to improve post stocking survival as learning allows fishes to improve their foraging efficiency by adjusting their feeding to match changing circumstances (Hughes et al. 1992).

If the results from the pilot experiments can be confirmed and increased abundance of hyporheic invertebrates has indeed a positive effect on the fitness of emerging fry semi-natural incubation technology has the potential of further advance. A system to increase the abundance of hyporheic invertebrates beyond the production potential of the incubation medium itself could be integrated into the water supply to the incubators. For maximum effect this breeding container should provide optimum conditions for the production of hyporheic invertebrates. A high concentration of dissolved oxygen is important as it has been shown that the total abundance (Strommer and Smock 1989, Boulton et al. 1997, Franken et al. 2001), biomass (Strommer and Smock 1989) and taxon richness of hyporheic invertebrates (Boulton et al. 1997, Franken et al. 2001) are positively related to the interstitial oxygen concentration. A large surface area of the incubation medium and a slightly elevated temperature during the incubation period in early spring are also beneficial for the production of hyporheic invertebrates. Figure 35 shows a prototype of a simple but effective invertebrate enhancement system. The water supply leading to the system comes from a mature gravel filter. Fully oxygenated water was introduced from above through diffuser pipes. The black PVC container itself was filled with fine gravel (particle size 2 - 5 mm) and covered with a transparent polycarbonate lid to achieve a greenhouse effect. Dislodged invertebrates were transported by the water current into the semi-natural incubator.

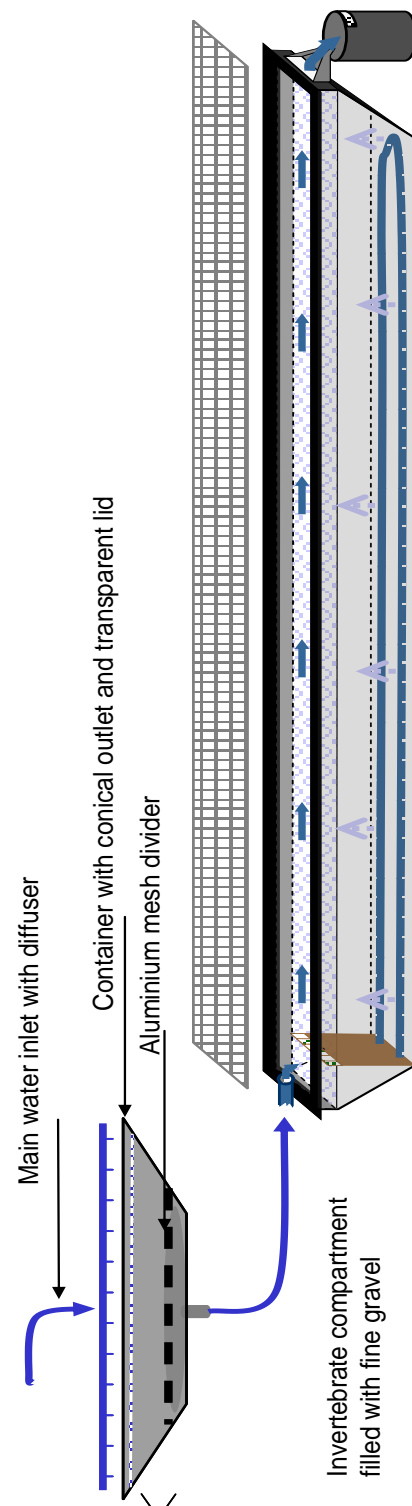


Figure 35: Prototype invertebrate enhancement system. Depict is a breeding container for hyporheic invertebrates that is integrated into the water supply circuit of a semi-natural raceway incubator.

7.2. The Eco-Hatchery

7.2.1. Introduction and methodology

An enclosed branch of a salmon stream was modified to link the findings from the semi-natural raceway system (see Chapter 6 ‘The impact of sedimentary deposits on Atlantic salmon fry habitat: implications for the carrying capacity of a nursery area’) to a natural habitat. Particularly, riverbed morphology, water flow, bank site vegetation, predator and competitor abundance was manipulated to achieve maximum survival of salmon juveniles during the first year and subsequently until smoltation.

Experiments were conducted on a reach scale in a 600 m long, disused, mill leat (Dunmeer Mill: OS Grid ref. 240902, 67966), which was fed by the River Camel (figure 36). The leat was landscaped to produce alternating sections of relatively shallow areas of approximately 20 cm depth (termed riffle) and deeper areas of 52 – 65 cm depth (termed pools) during normal water flow. The study site was low-gradient with natural streambed areas composed of gravel, cobble and boulders on exposed Devon slate bedrock or granite (British Geological Survey 1998), with riffle areas containing 25 - 30% more boulders than deeper regions. The leat-bed was initially cleaned from deposited sediments with a portable water-pump resulting in a ‘low’ substrate embeddedness compared to ‘medium’ in the nearby Camel River (descriptive micro- and macrohabitat categories were used herewith according to the HABSCORE habitat evaluation programme (WCS 2008)). The dominating flow conditions were of the turbulent (shallow) and glide/run (deep) categories. Abundance of biotic cover for > 10 cm salmonids included tree root systems (10%), branches and logs (10%), undercut banks (5%) other submerged cover (5%). Submerged vegetation was largely absent (> 5% cover).

An instream sediment trap (fully discussed in Section 8.2.3.) was excavated at the upstream end of the study site. The basin was constructed by excavating a depression in the leat bed extending from bank side to bank side. To maximise trap efficiency (percent of sediment load deposited), the basins was located where the gradient is relatively flat with minimum turbulence. The basin was designed to trap > 95% of coarse sediments (i.e.

fine and coarse sand: 0.0125 –0.2 cm according to Wentworth (1922)). The effects of spoil removal on the stream's nutrient load were assumed to be negligible because most nutrients are carried in solution and suspension by the water during the periods of basin filling (Hansen et al. 1983).

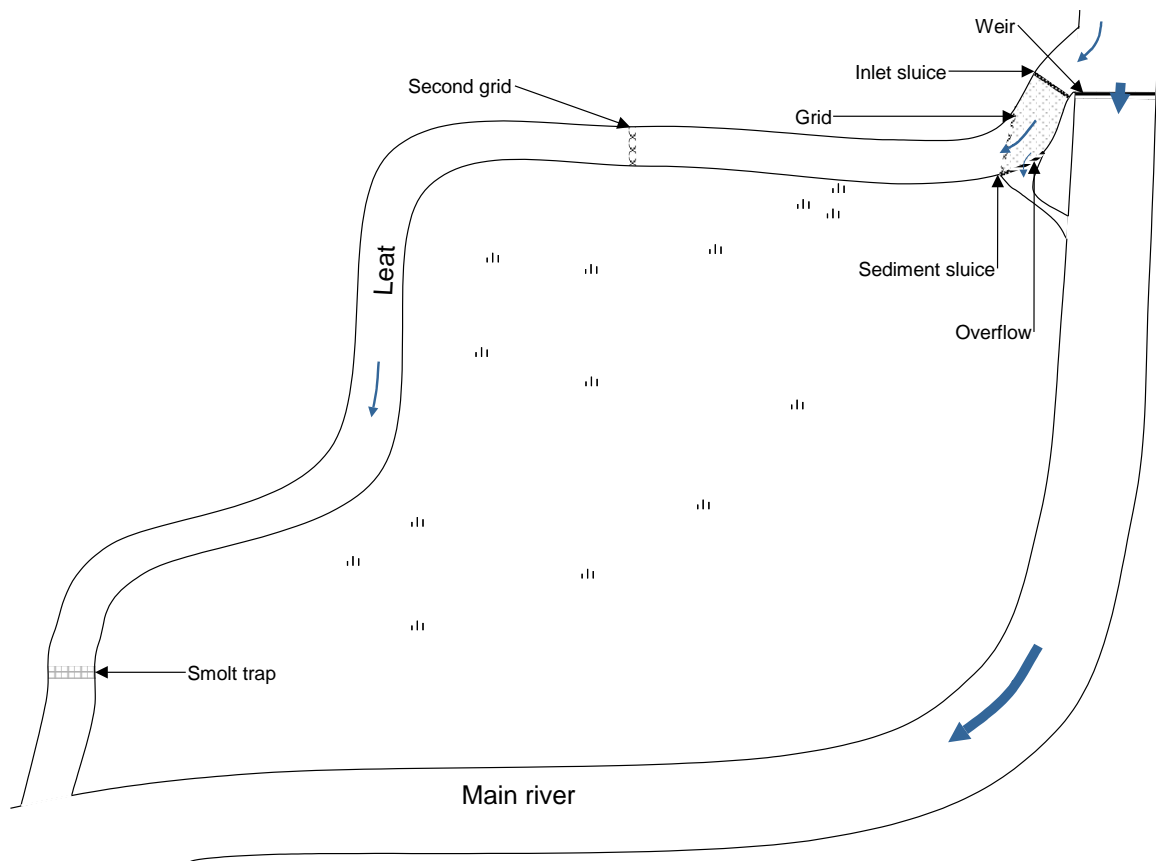


Figure 36: An overview of the leat system used as an 'Eco-Hatchery' (not to scale). The Eco-Hatchery receives the water supply from the River Camel. Sluice gates even out the water flow within the Eco-Hatchery and a sediment trap at the upstream end reduces the sediment bed load.

The water flow to the leat was regulated by sluice gates positioned above the sediment trap. The opening was situated above the ground to further reduce the amount of sediments entering the study site. The sluice gates allowed for complete drainage of the study site to survey the fluvial habitat and count resident fish population. 7 d before stocking with hatchery reared salmon fry the water supply was stopped and the leat was

drained. All resident fish were removed from the study site and transplanted into the nearby River Camel. It was estimated that removal was about 90% efficient for fish < 10 cm body length and 100% efficient for fish > 10 cm. Potential predatory fish species, like brown trout (*Salmo trutta*) or the European eel (*Anguilla anguilla*) were temporally removed from the leat. No effort was made to reduce the amount or restrict the access of avian or mammalian predators. As control surveys have shown, the leat becomes quickly repopulated from the feeder stream with trout and eel of all size classes. Bullhead (*Cottus gobio*) and brook lamprey (*Lampetra planeri*) were present in medium to high densities (graded according to the HABSCORE habitat evaluation programme (WCS 2008)).

In spring 2002 the Eco-Hatchery was stocked with unfed salmon fry for the first time. The fry were descendants of broodstock from the River Camel incubated in Bamberger-boxes (see Chapter 3 ‘Evaluation of a new semi-natural incubation technique for Atlantic salmon fry’ for details on the incubation history and technique). The number of fry stocked ensured an initial saturation of the available habitat with fry. A target density of 12 fry / m² (based on the wetted stream-bed area) was set to exceed the recommended stock density of eyed ova x m⁻² for ‘ideal’ habitat suggested by Egglisshaw and Shackley (1985). The target density was above the densities Gee (1978b), Whalen and LaBar (1994), Heggenes and Borgstrom (1991) and Naissmith (1996) observed as maximum carrying capacities.

The study site was drained annually before stocking with new fry. The number of resident fish was recorded. After counting, all fish were immediately transplanted into the River Camel. The routine of stocking and surveying was repeated in subsequent years.

7.2.2. Results and discussion

Initial results suggest a drastic increase in carrying capacity of the modified habitat for salmon juveniles. The reduction in sediment bed load, constant water flow and initially a reduced abundance of competitors and piscivorous fish resulted in final parr densities six times above the regional average (Simon Toms pers. comm.). Likewise, hatcheries in

British Columbia and Norway had great success in rearing large numbers of fish in semi-natural 'streams'. For example in a 400 m long and 4 m wide side channel, 500000 coho salmon were produced.

The approach to maximise production of juveniles in optimised rearing habitat has several biological and operational advantages:

- Biological engineered in-stream habitat supports a good production of food organisms. Constant water flow, regulated through sluice gates, favours the production of benthic invertebrates which in turn ensure a constant supply of drifting food for salmon juveniles. A rough stream bed provides low velocity niches adjacent to the main current flow and allows for energy efficient feeding for salmon juveniles. Supplementary feeding with artificial food is unnecessary.
- High habitat heterogeneity provides ample hiding places from predators. Fish can learn appropriate predator avoidance reactions in a natural environment.
- The nursery area is protected both from flash floods and drought situations. Since a single flash flood can wipe out a large percentage of 0+ salmon, the design of mill leats having integrated overflows for surplus water eliminates high mortality rates during those events.
- Spatial separation of year classes reduces intraspecific predation and competition.
- The production can be monitored efficiently by draining the water and the effectiveness of habitat alterations can be gauged. The results help to define 'optimal' fry and parr habitat on a large temporal and spatial scale.
- The operational costs for the Eco-Hatchery are very low and maintenance is labour un-intensive compared to a 'traditional' hatchery.
- Incorporating a device at the outflow to trap salmon that are trying to migrate into the hatchery makes broodstock available for future years.
- Abundant or disused leads are readily available in almost any catchment

Disadvantages of the concept are:

- Costs involved in creating the optimised habitat and in construction of inlet sluice gates
- Fish in the Eco-Hatchery are vulnerable, like wild fish of the same river, against chemical pollution.

8 Synopsis and outlook

This project linked the following interactive approaches: 1. Develop semi-natural incubation units for bank-side and hatchery use. Evaluate the performance of the new technology with established hatchery systems as benchmark and morphological indices and behaviour characteristics as a measure of effectiveness. Highlight potential disciplines for further improvement. 2. Evaluate the relationship between the degree of sedimentation on the streambed and the carrying capacity of that stream section for Atlantic salmon fry. Develop short- and long term mitigation techniques and provide verification on a large temporal and spatial scale.

8.1. Semi-natural incubation units

This long-term study provided evidence that semi-natural incubation systems are capable of producing larger and heavier Atlantic salmon fry than established smooth-bottomed hatchery troughs while retaining similarly high egg-to-fry survival rates. It has been demonstrated during this project that scaled-up versions of semi-natural incubation boxes are equally effective in producing morphologically superior fry than small bank-side incubators. Those larger units offer the advantage of scale for commercial hatchery application. The question remains if the measurable morphological advantage of fry produced with this new technique translates into increased stream survival after stocking.

8.1.1. Implications of length and body mass for stream survival

Stocking unfed fry into a river allows hatchery managers to mimic the process of fry emerging from a natural redd. At the time of emergence in the wild, free-swimming juveniles establish territories in the streams. Mortality during this period is exceptionally high. The survival of the individual fish during this early critical period (ECP c. Armstrong and Nislow (2006)), depends on the time of emergence, metabolic rate and

body size (Metcalf and Thorpe 1992, Cutts et al. 1999a, Cutts et al. 1999b). It has been widely observed that larger juveniles enjoy increased survival, competitive ability, swimming performance, growth and overall fitness (Metcalf and Thorpe 1992, Cutts et al. 1999a, Einum and Fleming 2000b, 2004, Hyatt et al. 2005). However, most studies, on fry mortality after emergence, found that selection is more intense on date than on body size at emergence with the early emerging fry having a better chance of establishing a territory (Einum and Fleming 2000b, 2000a). Larger size of post-emergent fry is often attributed to early emergence and a resulting dominance advantage rather than a consequence of larger size at emergence (Metcalf and Thorpe 1992). This interpretation was supported by a laboratory study, where early-stocked fish outgrew late-stocked fish when reared together (Letcher et al. 2004). Gilbey et al. (2005) found in their experiments that larvae length did not influence length, body mass or the condition factor of fish after they started feeding exogenously. Early endogenous growth and later exogenous based growth and developmental status were found to be disconnected. However, it needs to be noted that (Gilbey et al. 2005) conducted their experiments in laboratory tanks in a food rich environment, conditions that can hardly be expected in the wild.

Thus can it be concluded that size at emergence is of minor importance for survival during the ECP? Is early emergence the panacea for fry survival? Certainly not, as early emergence must be seen as a trade off between gaining first access to a feeding territory on one side and an increased predation risk and exposure to adverse environmental conditions (Harwood et al. 2003) on the other side. There is evidence that early emerging fry may be at higher risk from predators than late emergers (Brannas 1995). Survival chances of early-emerging fry may be low relative to late emergers because of the increased likelihood of adverse environmental conditions during early spring. High flow events and cool temperatures are more frequent during winter and early spring (McEwen 2006). Jensen and Johnsen (1999) found in a long term study that high spring floods drastically increase the mortality of Atlantic salmon during the first week of emergence in northern rivers. Low water temperatures, typically for early spring, negatively affect swimming performance of juvenile salmonids thus aggravating the risk of catastrophic displacement for fry. Letcher et al. (2004) found that salmon fry stocked early in the spring, when flows were high and temperatures were low, had significantly lower survival than fry stocked

into the same stream later in the spring, after flows had moderated and temperatures increased. Early-emerging fish grow faster but have a higher risk of mortality because of adverse conditions of the physical environment.

Differences in competitive ability, due to relative time of emergence, obscure intrinsic differences in competitive ability (Cutts et al. 1999a, Johnsson et al. 1999). Letcher et al. (2004) found that larger but later emerging fry keep a size advantage over smaller, but earlier emerging fry when they were reared separately. Competitive superiority in salmonids is generally associated with larger body size (Metcalf 1998, Eium and Fleming 2000b, 2000a). When emerged (or stocked) at the same time, larger fry have an increased competitive ability compared with their smaller rivals and would be expected to occupy the more favourable feeding territories (Kalleberg 1958, Wankowski and Thorpe 1979).

Stocking larger fry has three main advantages:

1. Larger fry are expected to have larger fat resources than smaller fry from the same parentage (Berg et al. 2001). Fat stores are hypothesized to be critical to postemergent survival (Berg et al. 2001) and may lead to a reduced susceptibility to starvation. Fry that were incubated in semi-natural systems maximized their own fitness by most efficient use of endogenous resources and have a clear advantage over fry incubated in smooth-bottomed troughs in that respect.
2. A larger size of fry at the time of stocking decreases the likelihood of catastrophic displacement. Size is positively correlated to swimming performance in salmonids (Beamish 1979, Ottaway and Forrest 1983). Heggenes and Traaen (1988) proved experimentally that the vulnerability to downstream displacement of Atlantic salmon fry, during the critical swim-up stage, decreased with increasing size of fish. Given that the weight difference of fry used by Heggenes and Traaen (1988) was smaller than the difference in weight between treatment and control fry in this study, fry from semi-natural incubators are expected to be less prone to catastrophic displacement than fry from established hatchery systems.
3. Improved swimming performance of larger fry increases the availability of favourable foraging locations (Nislow et al. 2000) thus increasing the carrying

capacity of a stream for fry during the ECP. Suitable habitat appears to be the main limiting factor for fry survival (Nislow et al. 2000) during the first month after stocking, creating a bottleneck of salmon production. If stocking densities exceed carrying capacity at that stage, than mortality of fry, which could not establish a territory, is more likely than dispersal (Einum and Nislow 2005). Swimming performance is critical for fry to establish territories and feed successfully on drifting invertebrates in fast flowing water. The water flow determines which food can be captured efficiently and increases with size of salmon (Nislow et al. 1999) thus opening up more territories in faster flowing water for larger fry (Armstrong 1997). A small difference in fish size may have a noticeable effect on habitat availability. Nislow et al. (2000), using a bioenergetics model, found that a relatively narrow range of current velocities was predicted to yield positive growth rates for first-feeding Atlantic salmon fry particularly under cold water temperatures, characteristic of spring emergence periods. The proportion of the stream suitable for fry is positively related to fish size therefore the carrying capacity of a stream section is expected to be higher for box-fry than for trough fry.

4. While small larvae can ingest only a limited range of small prey, large larvae have a wide food spectrum, from small to large particles.

8.1.2. Implications of length and body mass for on-breeding hatcheries

The transition from maternal provisioning of yolk resources to independence in feeding is not such a critical period for an individual's survival in commercial hatcheries as it is in the wild. Survival rates in a hatchery environment during that period are typically over 90% (J. Ruscombe-King, pers. comm.) compared to < 5% in the wild. However, the timing of when to first present fry starter-feed presents a problem for the hatchery manager: if food is presented too early and is not eaten by the fish it will rot, causing fungal and disease problems; if food is presented too late fish will starve. In smooth based hatchery troughs, it is recommended to provide starter feed to larvae once the yolk sac is reduced to less than 20% (Purser and Forteach, 2003). Needham (1988), recommended regular sampling of larvae to determine the developmental stages and to observe food particles in the gut, a technique that requires considerable experience and is time consuming.

The advantage of substrate-incubation is two fold in that respect. Firstly fish emerge from the gravel and release themselves into the traps at the time when they are ready to start feeding externally. Fish ready to feed can be transferred to fry-tanks, making it easy, even for a relatively inexperienced layman, to administer the right amount of food at the right time. Secondly, substrate incubated fry are likely to have a higher body fat content and are less prone to suffer from starvation (Berg et al. 2001) providing the hatchery manager with a wider operational window.

In commercial hatcheries which produce fry for on-growing to the smolt stage rearing large fry is a key objective. It has been shown that size is the most important factor determining which fish will smolt in the following spring (Strothotte et al. 2005) and which fish will remain in fresh water for at least a further year. Thorpe et al. (1998) argued that the probability of smoltification is increased if a threshold size or growth rate is achieved by a critical time. Large fry and parr frequently grow into 1-year-old smolts (S1) thus occupying freshwater facilities for only one year instead of two (Baglinière et al. 1993, Metcalfe 1998, Thorpe et al. 1998). The implications for the operating costs of a salmon hatchery are evident.

8.2. Sedimentation: Analysing and mitigating

Any effort to produce fry with natural qualities in a hatchery environment will only be rewarded with increased survival of stocked fish (and ultimately an increase in numbers of returning adult salmon) if the new habitat supports an increased number of salmonid fry. This can be the case if the fry hatchery programme has been carried out to stock otherwise productive nursery areas that are underutilized by spawners or suffer from extremely low egg-to-fry survival. Egg deposition can be a limiting factor of salmon production if adult fish access to stream sections has been denied by a variety of man-made obstructions such as weirs, dams, culverts, bridge aprons, water intakes, fords and gravel traps. Egg-to-fry survival in the wild can be a bottleneck of production in situations where siltation of gravel interstices reduces the intra-gravel flows, leading to asphyxiation of eggs or larvae within the gravel (e.g. (Peterson and Metcalfe 1981, Gustafson-Greenwood and Moring 1991)). However, for the majority of rivers in the United Kingdom egg deposition or egg-to-fry survival are not the limiting factors for salmon production (Environment Agency 1998a, 1998b). For most nursery headwaters the availability of suitable fry habitat is the limiting factor. As shown in this study, increased supply of deposited sediments can drastically decrease the carrying capacity of a stream section for salmon fry. In a situation where density-dependent mortality occurs stocking with hatchery-reared fry will only lead to increased competition with wild fry. The overall habitat quality has to be assessed and mitigation measures have to be implemented before stocking.

8.2.1. Synergistic effects of SPM and altered flow hydrographs

The filling of pools and blanketing of structural cover through deposited sediments are two of the most obvious effects of anthropogenic impact on stream fish habitat. Less obvious are increased suspended particle matter (SPM) concentrations during floods, since they are of a short duration. Although both are related to fluvial particulate inputs, different ecological impacts are associated with suspended sediment and sediment deposition. SPM, deriving from a combination of land runoff and erosion of riverbed and banks, drastically raise the turbidity (turbidity is a measure of the quantity of light absorbed or scattered by a sample of water: (Duchrow and Everhart 1971, McCluney 1975)) of a nursery stream after

heavy rainfalls. Moreover, river impoundment, improved field drainage, and the development of arterial drainage networks cause an altered flow hydrograph due to a reduced storage capacity of the catchment: severe droughts are frequent, there are more rapid responses of river flow to rainfall events and higher flood peaks (Robinson 1990, Newson 1997). This situation is exacerbated in the UK as the number of farmland drainage schemes is rising and rainfall is likely to become less frequent, but more intense. The abrupt increases in river discharge (flash floods), reduced water flows (droughts) and muddy waters are hypothesised to exacerbate sedimentation effects on the survival of salmon fry:

1. The period of emergence of the fry from the gravel coincides with the time of natural spring spates which have been reported to reduce fry survival (Craig Goch Joint Committee Ecological Investigations 1980, Ottaway and Clarke 1981, Ottaway and Forrest 1983). When the fry begin to disperse from gravel redds in the spring they are particularly vulnerable to 'wash-out' by high water velocities (Proctor et al. 1980, Ottaway and Forrest 1983, Irvine 1986, Harvey 1987) because of their poor swimming ability and small size. Sudden and drastic changes in current velocity might increase vulnerability to displacement (Liebig et al. 1999). This situation might be exacerbated through a combination of factors associated with increased bed material load: a) stable low velocity niches (i.e. instream structure which has a high critical erosion threshold, thereby having a high resistance to mobilisation during flood periods) are covered with sediment (Craig Goch Joint Committee Ecological Investigations 1980). b) in simple reaches, i.e. highly sedimented reaches, the hydraulic dead zone fraction (microhabitats with no water movement (Lancaster and Hildrew 1993)) decreases as discharge increases (Kaufmann 1987). This means that physically simple, sedimented reaches become absolutely and relatively more homogeneous as discharge increases during flood events. c) decreased channel roughness, results in reduced river bed friction and thereby increased water velocity at the stream bed (Platts *et al.* 1989). The effective scour depth for a given discharge is increased (Montgomery *et al.* 1996b).

2. Sustained low water flow (and consequently a reduction of wetted area) will lead to an overall reduction in habitat availability. In a situation with increased sand bed load large interstitial spaces are mostly clogged with sand, and opportunities for salmon juveniles to extend the period over which they may survive drought by burrowing (Debowski and Beall 1995), would be limited. Fish forced to migrate to pools becoming increasingly vulnerable to predators and very high levels of competition between salmon aggregated in pools have been reported (Armstrong *et al.* 1998). The situation will be aggravated if an increased amount of sand fills a large amount of the pool area in a stream.

3. Increased turbidity associated with suspended sediment can result in salmonids sight impairment (Wilzbach *et al.* 1986). Since station holding is primarily achieved through vision and the lateral senses (Pavlov 1979, 1986), particularly young fry (whose sensitivity to flow and to movement of visual cues is not fully developed: Veselov 1998) are apt to be displaced downstream at high turbidity as they are no longer able to keep station visually. For example, more fish are displaced downstream during the night than during day following the lack of visual orientation (Hoar 1958). Ckeary (1956) and Larimore (1975) noted that turbidity in smallmouth bass streams caused very young fry to be displaced downstream chiefly due to the loss of visual orientation. Since the physical and mechanical properties of water are important for the lateral line sensory system (Wootton 1995), the establishment of new territories by displaced fish might be further aggravated along with a high concentration of suspended particle matter. Juveniles are drifted away from feeding areas essential to early fry stages. They are displaced to areas of the river with high abundance of predators and conspecific competitors and they have to invest energy to re-establish a new territory. In most cases, down stream drift is equivalent to death for juvenile salmon (Symons 1971).

However, in spite of its importance, work on the synergistic effects of non-toxic anthropogenic pollution on fluvial biodiversity is still lacking. Thus, a future aim must be to quantify Atlantic salmon juvenile mortalities in response to the synergistic effects of: a) the degree of sedimentation on the streambed, b) the amount of suspended particle matter

(SPM), and c) the spatial scale of changes in water velocity. Riparian management provides the opportunity to manipulate each component independently (Hansen *et al.* 1983), and therefore the overall effects of all factors need to be tested independently as well as interactively (figure 38).

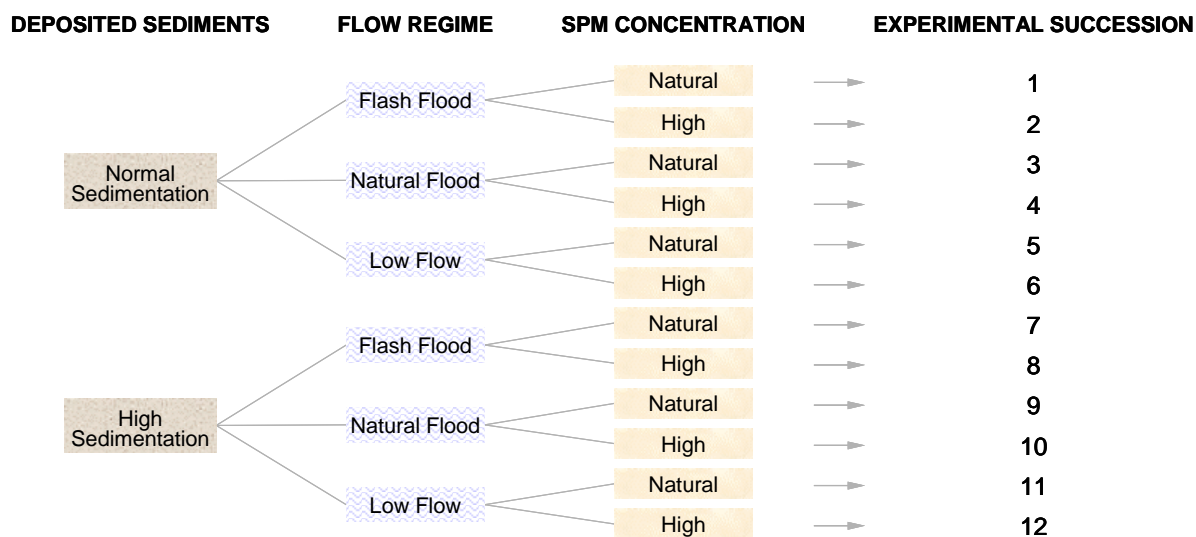


Figure 37: Flowchart illustrating the hierarchy of future raceway experiments to be conducted in allopatry of Atlantic salmon fry to investigate the synergistic effects of sediment deposits, suspended particle matter (SPM), and flow on the carrying capacity of a nursery area for salmon fry.

8.2.2. The impact of interspecific interactions

When examining the question of how susceptible young fish are to man-made interventions, one has to consider the fish as part of a species community: Allopatric populations of Atlantic salmon are extremely rare (Heggenes and Borgstrom 1991) and juvenile anadromous brown trout (*Salmo trutta*) are obvious competitors for space (Jones 1975, Egglshaw and Shackley 1982, Kennedy and Strange 1986, Heggenes and Borgstrom 1991). Early reports suggested that trout dominated salmon, even at the same size (Kalleberg 1958). LeCren (1965, 1973) described experiments where different proportions of Atlantic salmon and brown trout eggs were stocked in enclosed sections of a small Scottish stream. Although no details of methods or results were given, he reported that

mortality of the resulting trout fry was proportional to trout density alone, whereas mortality of salmon fry depended on density of both species. He inferred from this that trout dominated salmon under these conditions. Kennedy and Strange (1986) have shown that interspecific competition between wild populations of brown trout and juvenile Atlantic salmon can affect the survival and growth of individuals of both species. In most encounters, brown trout were found to be dominant, because at an equal size of salmon and trout offspring, young trouts are generally more aggressive (Waters 1983, Glova and Field-Dodgson 1995) and thus competitively superior in acquisition of the resource.

There is no doubt that age-0 brown trout exert considerable behavioural interference on the use of resources by Atlantic salmon, which is likely to increase their use of shallow riffle areas and fast flowing sections of nursery stream (Fahy 1995) when in sympatry with trout (Lindroth 1956, Heggenes *et al.* 1990). Salmon are thought to be better adapted to riffles than trout due to their larger pectoral fins (Jones 1975, Arnold *et al.* 1991) and lower buoyancy (Sosiak 1982). Increased emigration into those sections would not necessarily affect the survival of salmon juveniles adversely in unimpaired rivers, when there is ample suitable habitat. Interactive habitat segregation (Nilsson 1967) may free Atlantic salmon from competitive pressure from dominant brown trout in nursery streams. If the nursery stream incorporate the full range of habitat complexity in which two species evolved, such as riffles and pools, then it is likely that each species will be successful in the proportion that includes its realised niche. In contrast, confining two species to habitat that is too simple allows one species to dominate. With increased sediment load in British rivers, suitable microhabitats are scarce. In such situations, brown trout dominance may reduce the production of Atlantic salmon recruits directly by forcing a great proportion of salmon fry to unsuitable areas. Even a relatively insignificant reduction of the overall microhabitat availability due to human interventions might have serious consequences for salmon populations, since the remaining microhabitats are predominately occupied by brown trout juveniles.

A similar experimental approach to the one described in the Chapter 6 'The impact of sedimentary deposits on Atlantic salmon fry habitat: implications for the carrying capacity of a nursery area' can be used to experimentally investigate the role of biotic interactions

(competition and predation). Additionally, for 'competitor experiments' trout fry will be stocked into the system three days before the normal procedure of stocking with salmon fry will be undertaken. This accounts for the earlier hatching of trout fry in natural streams and allows them to achieve prior residency. Trout fry will be stocked at a density of 20 individuals m^{-2} . For 'predator experiments', one wild brown trout (> 15 cm) will be stocked in each experimental compartment. The trout will be collected from the Dunmere mill leat (figure 39).

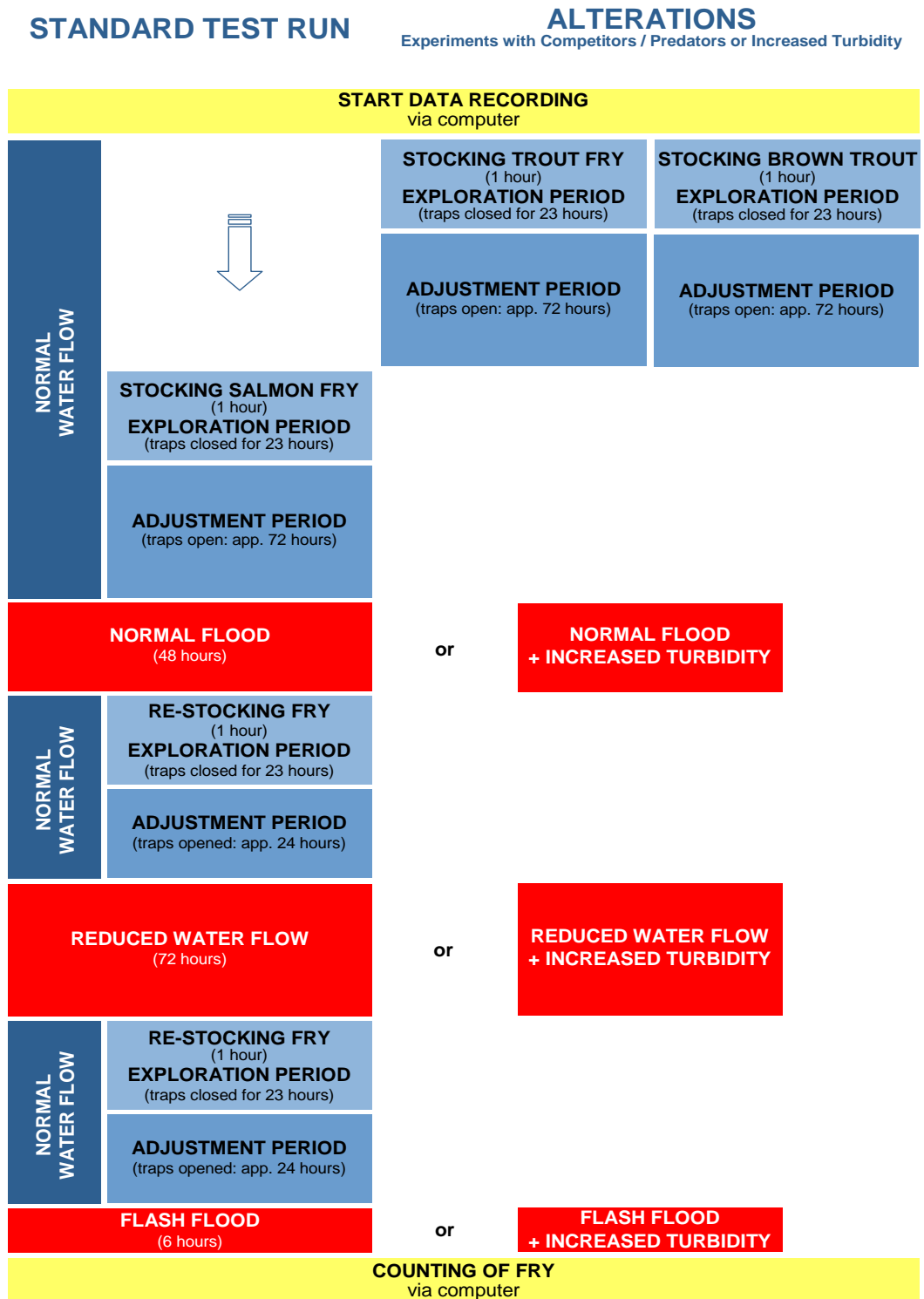


Figure 38: Diagrammatic illustration of a standard test run (in allopatry of salmon fry) and alterations for predator / competitor / turbidity experiments. The experimental procedure of a standard experiment in allopatry of salmon fry, running for 7 d, is depicted on the left side of the diagram. Each of eight distinct experiments, which are illustrated on the right hand side, will be repeated after 14 d.

8.2.3. Instream sediment traps

Stocking programmes are only effective if the new habitat supports an increased amount of fish. Habitat restoration programmes to stop the delivery of excess sediments to the river bed take time and are often politically controversial. To protect important spawning and nursery areas in the short term instream sediment traps (Task Committee on Preparation of Sedimentation Manual 1969) can be employed to trap moving sediments (figure 37). A sediment trap is in effect a depression in the river bed from bank side to bank side designed to slow down the current velocity and aid the deposition of sediments. Deposition of sediment in a basin is a function of the fall velocity of the sediment, the basin length, and the stream discharge per centimetre of basin width. The basin length necessary for trapping the selected particle size, the depth required to halt bed-load movement through the basin (d_1) and the necessary depth for storage (d_2) can be calculated using Vetter's equation:

$$\frac{W}{W_0} = \frac{-V_8 L}{e^q}$$

- where
- W = weight of sediment leaving basin
 - W_0 = weight of sediment entering basin
 - V = fall velocity of sediment particle
 - L = length of basin
 - e = base of natural logs
 - q = stream discharge per cm width of basin

The d_2 basin depth is dependent upon the required sediment storage volume. However, the quantity of moving sand bed-load is difficult to measure (Hubbell 1964, Gomez 1991) and may result in large errors (Garg et al. 1971). Thus, the initial storage volume has to be selected rather arbitrarily and adjusted later if necessary. Observation of the basin for several months gives an indication as to what a more efficient basin depth (in terms of sediment sizes trapped and cleaning frequency) for that stream will be. After each clean-out, the spoil needs to be sloped away from the stream. The trap will be surveyed before and after each clean-out so that the volume of sediment removed can be calculated, hence providing a relative estimation about the total sediment transport of the river.

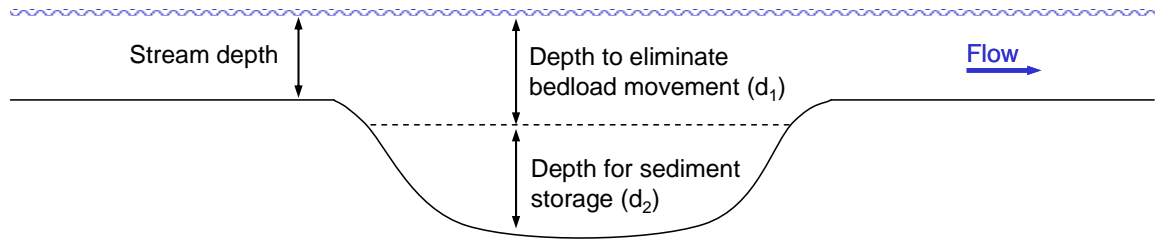


Figure 39: Cross section through an instream sediment trap.

It is known that stream morphology changes considerably with alteration of the sand bed load. To provide a measure of biological, geomorphological and hydrological characteristics, one sections upstream and downstream of the sediment trap needs to be designated for quantitative sampling. Similar sections need to be selected visually based on individual habitat units according to the procedure described by Bovee (1982). Each section covers the range of habitat types available in the stream and has similar inclination (figure 40). To monitor changes in site attributes due to sediment traps, each individual section needs to be surveyed twice a year, before in spring and again in autumn.

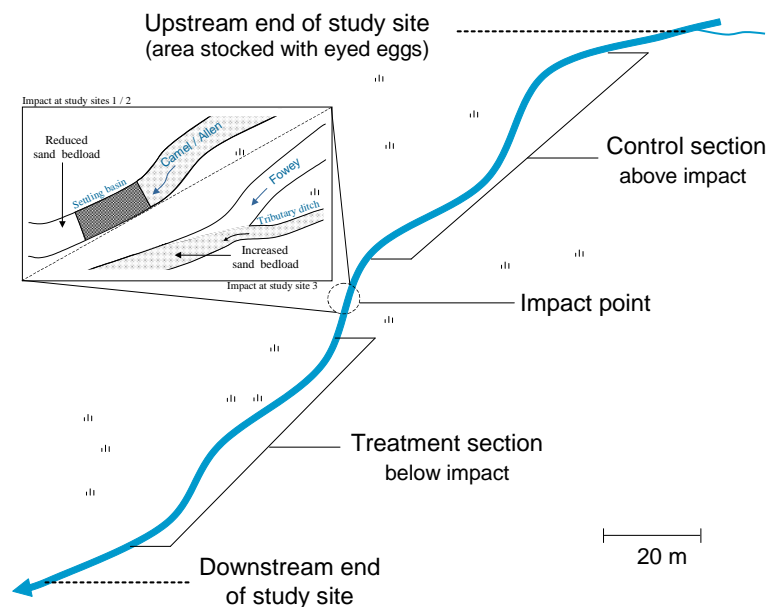


Figure 40: Example of the spatial outline of a monitoring programme to assess the impact of an in-stream sediment trap on physico-chemical and biological characteristics of a stream section.



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10 Schematic project overview

11 Glossary

- abiotic** // adj. inanimate, non-living, not of a biological nature. [a-1 + biotic]
- allopatric** // adj. Biol. occurring in separate geographical areas. [allo- + Greek *patra* 'fatherland']
- anadromous** // adj. (of a fish, e.g. the salmon) that swims up a river from the sea to spawn (opp. catadromous). [Greek *anadromos* (as *ana-*, *dromos* 'running')]
- anthropogenic** // adj. Ecol. originating in human activity.
- biotic** // adj. 1 relating to life or to living things. 2 of biological origin. [French *biotique* or Late Latin *bioticus*, from Greek *biotikos* from *bios* 'life']
- demersal** // adj. (of a fish etc.) being or living near the sea bottom (cf. pelagic). [Latin *demersus*, past part. of *demergere* (as *de-*, *mergere* 'plunge')]
- exogenous** // adj. growing or originating from outside. exogenously adv.
- flume** // n. & v. 1 an artificial channel conveying water etc. for industrial use. v. 1 intr. build flumes. 2 tr. convey down a flume. [Middle English via Old French *flum*, *flun* from Latin *flumen* 'river', from *fluere* 'flow']
- fluvial** // adj. of or found in a river or rivers. [Middle English from Latin *fluvialis*, via *fluvius* 'river' from *fluere* 'flow']
- hatchery** // n. (pl. -ies) a place for hatching eggs, esp. of fish or poultry.
- heterogeneous** // adj. (also disp. heterogenous //) 1 diverse in character. 2 varied in content. heterogeneity // n. heterogeneously adv. heterogeneousness n. [medieval Latin *heterogeneus* from Greek *heterogenes* (as *hetero-*, *genos* 'kind')]
- morphology** // n. the study of the forms of things, esp.: 1 Biol. the study of the forms of organisms. morphological // adj. morphologically // adv. morphologist n. [Greek *morphe* 'form' + -logy]
- pelagic** // adj. (of marine life) belonging to the upper layers of the open sea. [Latin *pelagicus* from Greek *pelagikos* (as *pelagian*)]
- redd** // n. a hollow in a river bed made by a trout or salmon to spawn in. [17th c.: origin unknown]
- rheotaxis** // n. a taxis in response to the stimulus of a current, usually a water current
- riffle** // v. & n. v. N.Amer. a shallow part of a stream where the water flows brokenly.
- riverine** // adj. of or on a river or river bank; riparian.
- salmonid** // adj. & n. adj. of or relating to the family Salmonidae, which includes salmon and trout. n. a fish of this family.
- sediment** // n. & v. n. 1 matter that settles to the bottom of a liquid; dregs. v.tr. (as sedimented adj.) sedimentary // adj. sedimentation // n. [French *sédiment* or Latin *sedimentum* (as *sedile*)]
- smolt** // n. a young salmon migrating to the sea for the first time. [Middle English (originally Scots & northern English): origin unknown: cf. smelt]
- sympathetic** // adj. & n. adj. 1 of, showing, or expressing sympathy. 2 due to sympathy. 3 likeable or capable of evoking sympathy. 4 (of a person) friendly and cooperative. 5

(foll. by to) inclined to favour (a proposal etc.) (was most sympathetic to the idea). 2 the sympathetic system. sympathetically adv. [sympathy, on the pattern of pathetic]

synergy // n. (also synergism //) 1 the interaction or cooperation of two or more drugs, agents, organizations, etc., to produce a new or enhanced effect compared to their separate effects. 2 an instance of this. synergetic // adj. synergic // adj. synergistic // adj. synergistically // adv. [Greek sunergos 'working together' (as syn-, ergon 'work')]

trophic // adj. of or concerned with nutrition (trophic nerves). [Greek trophikos, via trophe 'nourishment' from trepho 'nourish']

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