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Aims and Scope

Nordic Journal of Freshwater Research is a modern version of the Report of the Institute of Freshwater Research, DROTTNINGHOLM. The journal is concerned with all aspects of freshwater research in the northern hemisphere including anadromous and catadromous species. Specific topics covered in the journal include: ecology, ethology, evolution, genetics, limnology, physiology and systematics. The main emphasis of the journal lies both in descriptive and experimental works as well as theoretical models within the field of ecology. Descriptive and monitoring studies will be acceptable if they demonstrate biological principles. Papers describing new techniques, methods and apparatus will also be considered.

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All papers are subject to peer review.

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Proceedings of the

Workshop on the Release of Salmonid Fishes in Norway

June 5-7 2000, Kongsvoll, Norway

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BLOMS I LUND TRYCKERI AB, 2001

Preface

The transplantation of salmonid fishes for stocking purposes in Norway has probably been going on for more than a millennium, with written accounts dating as far back as 900 years. In the 1850's, the construction of the first hatcheries for the cultivation of salmonid fishes ushered in a period of rapid expansion in the number and sizes of releases. As a result, releases of hatchery fish became a principal management practice not only in Norway, but also throughout Scandinavia. For instance, over 90% of salmon in the Baltic Sea are of cultured origin today. The most common reason for such releases is mitigation, particularly to compensate for the impacts of hydropower regulation. Yet, despite many of these release programs having operated for decades, rarely, if ever, have they been evaluated in terms of biological objectives.

In response to this situation, the present workshop was organised to critically examine the current state of release programs in Norway in the light of emerging scientific evidence, and to provide a forum for the interchange of ideas and recent developments. Moreover, by critically examining past and present release programs, the workshop aimed to provide recommendations for future management and research. Researchers from various universities and institutes in Norway, Sweden and Finland, having expertise in the ecology, population dynamics and genetics, behaviour and evolution of salmonid fishes, were invited to Kongsvoll, Norway, 5-7 June 2000, to participate. Representatives from Norwegian hatchery, water-regulatory and management agencies also partook. The workshop was divided into two parts, the first consisting of a series of 15 presentations on a range of issues, including interactions between wild and hatchery fish, life stages at release, habitat limitations, interspecific effects, disease and parasites, and user concerns. In the second part, participants were divided into working groups to discuss one of four themes, cultivation, conservation, habitat and inland fish. In addition, they were asked to address a series of questions, including when is it appropriate to use fish releases, how to measure/evaluate the success of such programs and what directions should future management and research take?

Several conclusions were drawn from the workshop. It was emphasized that the release of hatchery fish poses an ecological and genetic risk to recipient fish populations. At present, stocking is being carried out at too large a scale in Norway, and in Scandinavia as a whole, and often without a thorough prior consideration of the ecological and genetic consequences. From a conservation perspective, the causes of population declines must be first recognized and addressed, e.g. through habitat restoration and/or fishing regulation. If stocking is to be carried out, the management goals should be clearly identified and a critical assessment of the potential benefits and risks undertaken, particularly in terms of the ecological and genetic consequences. Furthermore, a monitoring program needs to be instituted by which to evaluate whether the management goals are being achieved. It was clear from the workshop that few, if any release programs in Norway, past or present, have the data by which to begin adequately doing so. When releases are conducted despite the potential damage they may cause (for politicial and/or economic reasons) they should be carried out so as to minimize the threat to natural biodiversity.

It was felt that the most urgent action needed with respect to hatchery releases was the application of existing knowledge. Guidelines and recommendations based on ecological and genetic considerations have been available for ten years or more, but have been rarely applied. Moreover, management must more clearly define its goals and with researchers, design strategies for evaluating whether these goals are being achieved.

There is also a need to educate local management and the public about the risks associated with hatchery releases, in addition to the potential benefits. It was recognized, that as a general principle, fish releases and habitat manipulations should not be carried out in natural, unperturbed watercourses.

This publication contains papers submitted to the Nordic Journal of Freshwater Research and accepted following peer review by referees from across Europe and North America. A report edited by members of the organising committee, containing a workshop overview, reports from the four working groups (Culturing, Conservation, Habitat and Inland Fish), viewpoints from veterinary, water-regulatory and hatchery groups, and abstracts of all papers presented at the workshop has been published separately (Strand, R., I.A. Fleming and B.O. Johnsen. 2000. Releases of salmonid fishes. Kongsvoll Workshop 2000. NINA Fagrapport 045 [In Norwegian]).

The workshop was hosted by the Norwegian Institute for Nature Research (NINA) and received financial support from the Norwegian Research Council "Effekt" Program, the Norwegian Directorate of Nature Management (DN) and the Norwegian Energy Suppliers Organisation (EnFo). I received considerable help from the other members of the Organising Committee: Steinar Sandøy (DN), Bjørn Ove Johnsen (NINA), Rita Strand (NINA), Gunnbjørn Bremset (DN) and Bengt Finstad (NINA). A special thanks to Rita Strand, who was instrumental in taking charge of the meeting logistics. Teresa Soler at the Institute for Freshwater Research, Drottningholm, did a professional job as technical editor for this volume of the Nordic Journal of Freshwater Research. I would also like to thank the four Work Group Leaders, Nina Jonsson, Linda Laikre, Jan Heggenes and Jan Henning L'Abeé-Lund, for their efforts. Finally, I thank the authors and reviewers for their assistance and cooperation, often in the face of tight deadlines.

Ian A. Fleming

Co-convenor and Editor

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Planting of Salmonid Eggs for Stock Enhancement - a Review of the Most Commonly Used Methods

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Abstract

Successful planting of eggs has been reported from several studies which span a variety of planting techniques and salmonid species. The techniques used generally fall into two groups; 1) eggs incubated in boxes (e.g. Vibert-boxes) that are buried in the river bed or 2) eggs placed freely into a gravel structure, which to some degree imitates a natural redd. Poor results of egg planting have been ascribed to unnatural clustering of eggs, fungus infections, or accumulation of fine particles leading to reduced egg survival. Both newly fertilized eggs (green eggs) and eyed eggs have been used for planting. In contrast to green eggs, eyed eggs are robust and tolerate substantial handling. Eyed eggs also provide a much wider time span for disease control and for the planting of the eggs. These are weighty arguments for using eyed eggs instead of green eggs, although both developmental stages have shown to be viable alternatives. The main advantages of using egg planting over traditional use of hatchery-reared fish are that it is likely to result in fry more closely adapted to the local natural conditions, it reduces the risk of spreading disease, and it is more cost-effective.

Keywords: salmonids, egg planting, egg boxes, artificial redd, egg survival

Introduction

Egg planting for salmonid stock enhancement has a long tradition and includes a variety of methods. One of the obvious reasons for the use of egg planting is that the method requires low investments in labour and maintenance compared to hatchery production of fry. In spite of its common use, evaluation of the different methods of egg planting has been relatively sparse. One reason for this could be that egg planting is largely used in small-scale, local fishery management projects. In many such projects, the success of egg planting has been documented by subsequent observation of fry or later life stages, and no further evaluation has been performed. However, egg planting should be relevant also in large scale projects and we find it surprising that it has not been reviewed previously. The reason for this may partly be attributed to the many different techniques used for both planting eggs and evaluating the success. This constitutes a major source of variation when comparing different studies.

Methods used for egg planting generally fall into two groups; 1) eggs are incubated in boxes that are buried in the stream bed (e.g. Vibert-boxes), or 2) eggs are buried directly into the gravel bed. Here we describe some of the most commonly used methods and if reported, their success in terms of egg survival. Emphasis is placed on factors likely to impact the success of egg planting, i.e. factors affecting survival from planting to emergence of fry.

Methods used to quantify the result of egg planting

Several methods have been used to obtain survival estimates from egg planting. It is important to be aware that the variable methodology may cause considerable variation among results reported from different studies. The most commonly used method is to subsample the eggs during one or several developmental stages. In this way, survival estimates are obtained by calculating the ratio of dead to live embryos, or the ratio of eggs deposited to dead embryos left in the egg plant (e.g. MacDonald 1960, Sægrov 1998, Barlaup et al. 1999). This method may overestimate survival as dead embryos can disappear as a result of gravel movements, predation or disintegration. Accordingly, MacDonald (1960) reported that the loss of dead eggs in redds could cause up to 15% difference between estimated and actual egg survival. Likewise, Rubin (1995) calculated that loss of eggs in experimental boxes caused an overestimation of survival of 2% to the eyed stage, 9.5% up to hatching and 26.3% up to emergence.

Alternatively, fry traps (Phillips and Koski 1969, Porter 1973) can be positioned over the gravel where the eggs are planted to catch emerging fry (Harshbarger and Porter 1979, 1982). Although the method may give good estimates if operating as planned, fry escaping the trap will cause an underestimation of egg survival. Electrofishing of fry may also be used to evaluate egg planting given that there is no natural recruitment in the studied area. However, varying conditions for electrofishing are an obvious source of variation when comparing results from different sites or studies. Novel marking methods now provide an easily applicable, safe, and inexpensive way of marking eyed eggs (Tsukamoto 1995, Radtke and Fey 1996, Moen 1996, 2000). Marking eyed eggs and recapture of later life stages therefore provides an interesting and new method for assessing the success of egg planting. It is unclear whether the marking method used for eyed eggs also is applicable to green eggs, not least given the narrow time frame available prior to stocking when using green eggs (see below).

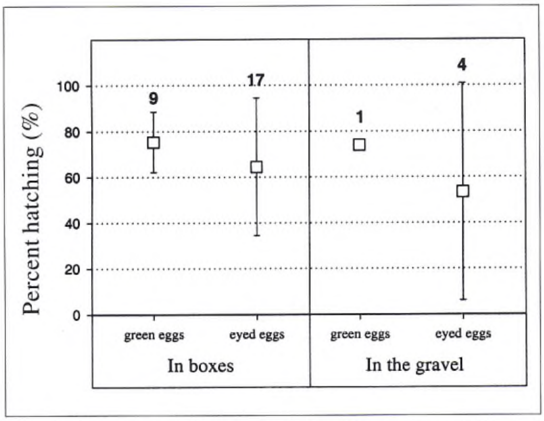

Fig. 1. Summary of reported data from Appendix 1-4 showing percent survival up to hatching (mean±SD) of green- and eyed eggs placed in various types of egg boxes or planted directly into the gravel. Data from studies influenced by unfavourable environmental conditions (low pH etc.) in Appendix 1-4 are omitted.

Planting of green eggs versus eyed eggs

When planting eggs one must adjust the procedure according to the developmental stage of the eggs used. Green eggs can be planted within 24 to 48 hours after stripping, fertilizing and water hardening. After this limited period, green eggs are highly sensitive to movement and planting can not be done without causing unacceptably high mortality. The restricted period for planting is, of course, a drawback for planting green eggs as planting may coincide with high water discharge or other unfavourable conditions that increase the risk of a poor result. Also, if green eggs are planted and subsequently exposed to disturbances (e.g. movements of gravel) this may cause mortality. An advantage with the use of green eggs is that the embryos will develop according to the temperature at the planting site. When using eyed eggs, different temperature between the planting site and the rearing environment may cause an unfavourable time of hatching and emergence. If present, such temperature differences can be a major disadvantage when using eyed eggs.

Table 1. Summary of reported data from Appendix 1-4 on survival to hatching and emergence of salmonid eggs planted in egg boxes or directly into the gravel as green eggs or eyed eggs. For description of the various methods see Appendix 1-4 and text. *N* = Number of reports. Species: 1 = Atlantic salmon (*Salmo salar*); 2 = brown trout (*Salmo trutta*); 3 = rainbow trout (*Oncorhynchus mykiss*); 4 = chum salmon (*Oncorhynchus keta*); 5 = coho salmon (*Oncorhynchus kisutch*); 6 = brook trout (*Salvelinus fontinalis*). Data from studies influenced by unfavourable environmental conditions (low pH etc.) are omitted.

Planting procedure	Developmental stage	Planting aparatus	Hatch (%)					Emergence (%)					Species
			N	mean	min	max	std.	*N*	mean	min	max	std.	
In egg boxes	Green eggs	Plastic/PVC cylinder	1	84				2	96	93	98	1.7	1,2
		Vibert/Whitlock boxes	5	73.6	51	95	17.9						2, 3, 6
		Plastic baskets	3	78.6	70	85	7.8						2,3
	Eyed eggs	Plastic/PVC cylinder	6	69.7	20	91	26.1						1
		Vibert/Whitlock boxes	10	58.4	6	98	32.7						2,3
		Plastic baskets	1	94									1
Directly into gravel	Green eggs	Shovel & standpipe	1	74				1	89				1
		Planting box						1	65.5				5
	Eyed eggs	Shovel & standpipe	4	53.5	6	100	47.4	2	7.5	5	10	3.5	1,2
		Planting box						2	74.5	55	94	27.2	4
		Shovel & cylinder						1	11				4
		Standpipe & waterpump						1	51				4

The regulation of stock enhancement measures including egg planting may involve veterinary screening and documentation of disease status of the broodstock. Veterinary control for diseases may require the extraction and analysis of a series of samples. When using green eggs the results of the veterinary control may not be completed until after the eggs have been planted. If a disease is proven, careful registration of parenthood and localisation of each egg plant are needed if infected eggs are to be removed from the gravel.

Eyed eggs are more robust than green eggs and tolerate substantial handling. Using eyed eggs also allows for a much wider time span for handling the eggs and conducting the egg planting. In contrast to green eggs, disease control may be performed during a period of 3-5 months prior to stocking. The period of exposure to natural mortality will also be several months shorter for eyed eggs than for green eggs. These are weighty arguments for using eyed eggs instead of green eggs for planting. However, there is no persistent difference in egg survival reported between studies using green or eyed eggs (Fig. 1 and Table 1). Likewise, Kelly-Quinn et al. (1993) found no significant differences when comparing survival to hatch for planted eyed- and green eggs of Atlantic salmon (*Salmo salar*). In conclusion, both developmental stages can be considered viable alternatives when planning to plant eggs, but the arguments listed above are in favour of eyed eggs.

Methods where eggs are incubated in holding boxes

Egg incubation boxes are perhaps the most commonly used technique for egg planting in association with stock enhancement or the assessment of egg survival. Vibert (1949) provided the first description of a incubation box, and this device has later been modified to the widely used Whitlock-Vibert box (4.5·6.3 cm, height 1.5 cm, with 0.3·1.2 cm openings). The openings are too small for the eggs to fall through but are large enough for the newly hatched alevins to escape (Whitlock 1978). Before burial into the river bed, the boxes are normally filled with gravel in addition to the eggs. The popularity of the Whitlock-Vibert boxes and other, similar boxes is likely due to a robust and easily operated design, commercial availability and recommendations in the fishery management literature (e.g. Egglishaw et al. 1984, Solomon 1988).

Harris (1973) describes a box made by sealing together sections of perforated, woven plastic sheeting from the material used in hatcheries for making egg troughs. The boxes were cylindrical in shape, 10 cm deep by 7.5 cm diameter with a tight fitting lid. The bottom of the box was filled with a layer of fine gravel, overlaid by coarser gravel, then 200 freshly fertilized eggs were added and the remainder of the box filled with coarser gravel and the lid added. The box was then planted into an excavated pit and positioned so that it would lie about 25 cm below the gravel surface. A similar technique was used by Barlaup et al. (1998) to incubate brown trout (*Salmo trutta*) eggs.

Scrivener (1988) gives a description and evaluation of incubating eggs in perforated plastic cylinders (10·5 cm) to assess survival from fertilized eggs to the alevin stage. The cylinders, referred to as egg capsules, were planted 20 cm into the gravel using a specially designed planting pipe. It was concluded that the technique was simple and inexpensive (average time for filling and bury one egg capsule was 15 min). It was also argued that the technique caused minimal disturbance to the streambed as opposed to most other methods for egg planting. A similar technique for planting 16·7 cm and 10·7 cm PVC eggboxes was used by Rubin (1995) to estimate survival from fertilization to emergence of fry.

The devices presented above (Harris 1973, Scrivener 1988, Rubin 1995) could well be used for egg planting with the aim of increasing recruitment, but the devices would then have to be modified so that the fry can escape from the boxes.

Perforated plastic baskets (35·25 cm, 15 cm deep) filled with gravel were used by Raddum and Fjellheim (1995) to incubate green eggs of Atlantic salmon. Each basket contained six separate clusters of eggs buried in the baskets using plastic tubes (3.5 cm diameter, 6 cm long) which were removed after egg deposition. The baskets were then buried into the streambed so that the eggs were buried at 12-18 cm depth.

Recently Donaghy and Verspoor (2000) developed a new modification of the methods of placing trays and baskets with eggs of Atlantic salmon into the gravel. They used plastic-coated steel weld mesh trays with an aperture of 6 mm, formed into the dimensions 140·140· 8 mm. After plastic coating the resulting aperture is about 4 mm. Once filled with eggs the trays were placed into a plastic coated wire basket with dimensions 150·150·150 mm. Each basket had a capacity of up to 4,000 eggs, around 400 in each tray. An evaluation showed good survival to hatching for both green and eyed eggs (Appendix 1 and 2).

In addition to stock enhancement, egg boxes are also extensively used by researchers to assess egg survival under various environmental conditions (for instance Turnpenny and Williams 1980, Gunn and Keller 1980, Harshbarger and Porter 1982, Kelly-Quinn et al. 1993, Fiss and Carline 1993, Scrivener 1988, Rubin 1995, Ingendahl and Neumann 1996). However, incubation and hatching in egg boxes is artificial compared to the conditions within a natural redd. This has raised the concern that incubation in egg boxes may cause a bias when monitoring egg survival under natural conditions (Harshberger and Porter 1982, Rubin 1995). In this respect, several aspects of the incubation environment have been suggested to lead to differential egg survival in egg boxes and natural redds.

The high number of eggs normally placed in boxes may leave the eggs more clustered than what is found in natural egg pockets. This clustering of eggs has been suggested to make the egg plants more susceptible to fungus infections, which is a well known problem (Harshbarger and

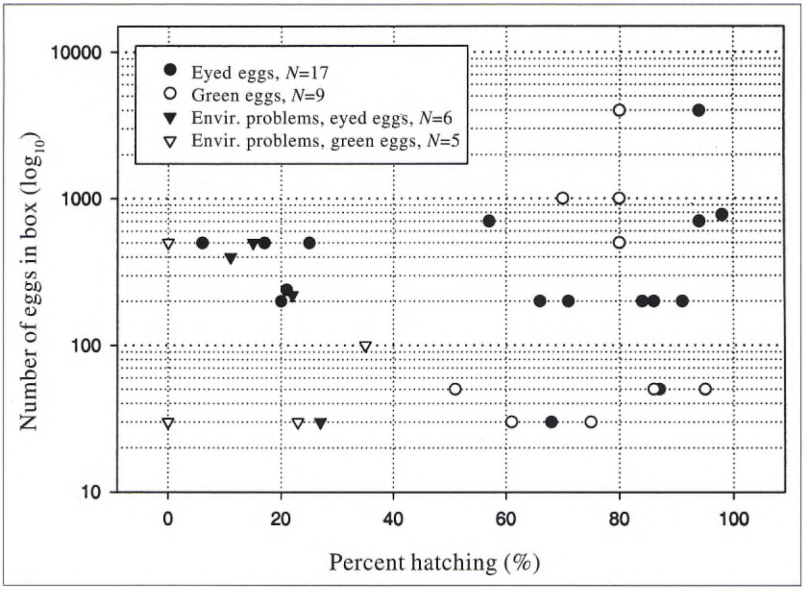

Fig. 2. Number of eggs per box and percent survival up to hatching based on the data given in Appendix 1 and 2. No correlation was found (Spearman Rank, $P>0.05$). Data from studies influenced by various environmental problems were omitted from the correlation.

Porter 1979, Gustafson-Marjanen and Moring 1984, Scrivener 1988). Fungi are likely to increase mortality when natural survival is poor and egg clustering is artificially high (Tabachek et al. 1993). It is also possible that artificial clustering of eggs may increase mortality due to oxygen deficiency, especially in waters with low oxygen content. Scrivener (1988) reported that high egg density and too small holes in egg boxes most likely contributed to the reduced survival of chum salmon (*Oncorhynchus keta*) green eggs. He found that reducing the egg density from 100 to 30 and increasing the size of the holes from 1 mm to 2.5 mm increased survival at all experimental sites. In the reported studies using egg boxes (Appendix 1 and 2), the number of eggs in each box varied between 30 and 4,000. The survival up to hatching was not found to be correlated with the number of eggs per box as shown in Fig. 2. However, various environmental problems as low pH, low DOC, high salinity, siltation and fungi clearly had a negative impact on survival (Fig. 2).

It has also been reported that egg boxes may serve as sediment traps accumulating fine particles. This may cause reduced egg survival because hatching success is negatively affected by intrusion of fine sediments in redds (reviewed by Chapman 1988). Harshbarger and Porter (1979) found strong indications that sedimentation reduced egg survival in both Vibert-boxes and Whitlock-Vibert boxes. In 250 boxes, sediment accumulation averaged 75% of the box volume. This was ascribed to the fact that the boxes impeded water movement and induced sediment deposition in and around the boxes. In a later study, the same authors reported that substrate in the 0.84-4.76 mm particle range constituted 30% of the substrate at sites with Whitlock-Vibert boxes compared to 13% at sites where eggs had been directly placed into the gravel (Harshberger and Porter 1982). The sediment accumulation in egg boxes were suggested as the main reason for the lower survival to emergence (8%) in WV-boxes compared to the survival (29%) obtained when planting eggs directly into the gravel (Harshberger and Porter 1982).

Contrary to this, Garrett and Bennett (1996) found that Whitlock-Vibert boxes did not trap or accumulate fine sediments differently than surrounding gravels, and concluded that the use of these boxes provide representative results in incubation studies.

Although artificial incubation in egg boxes in some instances may lead to negative effects reducing egg survival, the continuous and widespread use of egg boxes is perhaps the best documentation of the suitability and success of the method. Further, data on egg survival reported in the literature also documents that high egg survival is frequently obtained when using egg boxes (Appendix 1 and 2). The low survival experienced in some of the studies reported can be ascribed to unfavourable environmental conditions.

Methods where eggs are inserted freely into the gravel

Several techniques have been used for planting salmonid eggs directly into the stream gravel. Most methods involve planting eggs in what is considered an artificial redd. Care is therefore taken to plant the eggs in areas where salmonids likely spawn and in a gravel construction that is similar to a redd. Consequently, when using these techniques one must rely on knowledge about salmonid spawning biology.

To locate a potential spawning area can be a difficult task because female salmonids are very selective about their redd sites. The chosen redd site largely determines offspring survival and selection of redd site is therefore a critical part of female spawning behaviour. This is illustrated by the fact that female salmonids practise a "test-digging" behaviour, and abandon redds without depositing eggs if low-quality substrate makes conditions unsuitable for spawning (e.g. Burner 1951, Crisp and Carling 1989, Barlaup et al. 1994). In general, redds are placed within given limits of water depth, water velocity and substrate composition which fulfil the criteria for successful embryo survival (e.g. Belding 1934, White 1942, Ottaway et al. 1981, Shirvell and Dungey 1983, Witzel and MacCrimmon 1983, Heggberget et al. 1988).

A salmonid redd is defined as the gravel structure made by the female as she digs a pit, deposits the eggs, and subsequently covers the eggs with gravel (Hobbs 1937, White 1942). Within the redd, the eggs are placed in one or several egg pockets, which are dense clusters of eggs produced by a single spawning act (Hobbs 1937, Jones and Ball 1954). In several studies it has been noted that the egg pocket, which is placed in the deepest part of the redd, often is associated with gravel larger than what is otherwise found in the redd (Hobbs 1937, Burner 1951, Jones and Ball 1954, Barlaup et al. 1994). This has been attributed to the fact that large gravel is likely to be retained in the bottom of the pit during the digging process. Also, as the female digs the pit, fine material is transported downstream. In this way the female modifies the gravel composition in a way that is likely to enhance conditions for egg survival in the completed redd (see reviews by Chapman 1988, Kondolf et al. 1993a).

The fecundity and size of the female likely determines the number of eggs placed in a single egg pocket. Small salmonids like brown trout are not likely to deposit more than a few hundred eggs in an egg pocket, and large sized Atlantic salmon (>5 kg) will normally spawn about 500-1,000 eggs per egg pocket (e.g. Barlaup et al. 1994, Fleming 1996). These numbers should be taken into consideration when planting eggs. Planting unnaturally high numbers of eggs, which may be tempting in order to save labour, will lead to abnormal clustering of eggs that may adversely affect egg survival. Additionally, high densities of eggs may lead to high density-dependent mortality after the fry have emerged from the gravel.

Egg survival is also likely to be affected by the chosen gravel size and the burial depth of the eggs. In natural redds, both factors vary with female size because larger females normally spawn in coarser gravel and bury their eggs deeper than smaller females (e.g. White 1942, Crisp and Carling 1989, Kitano and Shimazaki 1995, Fleming et al. 1997, Steen and Quinn 1999). As a rule of thumb, one can assume that salmonids can spawn in gravels with a median diameter up to about 10% of their body length (Kondolf et al. 1993b). Small-sized salmonids (ca <30 cm) will bury their eggs at about 10 cm whereas larger salmonids will bury their eggs at about 10-30 cm or deeper, reviewed by DeVries, 1997.

The most widely used method for direct planting is by shovel and standpipe. The following description of the method is based on the procedures reported by various workers (Stockley 1954, Sedgwick 1960, Harshbarger and Porter 1982, Gustafson-Marjanen and Moring 1984, Sægrov 1998), as well as the authors' own experience. Upon locating a suitable "spawning site" for egg planting, an artificial redd is excavated using a pointed shovel or similar tools. During digging the material removed is placed on the downstream end of the pit. As during natural spawning, the digging combined with the water current remove the finer particles from the gravel. When the depression is of the wanted depth, the end of a standpipe (diameter ca. 3-15 cm, ca. 100 cm long) is placed into the bottom of the pit. Rocks or relatively coarse gravel is then arranged around the base of the standpipe to mimic the natural environment of the egg pocket. Thereafter the pit is covered with the gravel accumulated when digging the pit. Eggs are then introduced to the redd through the standpipe. In order to help the eggs settle it is recommended that the addition of eggs be followed by a few handfuls of gravel added into the standpipe. The standpipe is then carefully withdrawn from the gravel and the artificial redd is completed. When eggs are deposited it is vital to position a bag net at the downstream end of the redd to catch any eggs that are washed free. The bag net is essential to identify minor problems that result in the loss of eggs and thus allow for subsequent modifications to improve the technique.

In both natural and artificial redds, egg survival will be a function of the interplay between environmental conditions and redd quality. The success of egg planting is therefore highly dependent on site-specific hydrological and gravel conditions (i.e. redd quality). Consequently, field experience with studies of natural redds and knowledge of salmonid spawning biology are advantageous. Given that the method is performed correctly, the deposited eggs will experience much the same environmental conditions as eggs spawned in a natural redd. If optimal conditions are achieved, one may expect a hatching success exceeding 90% (Humpesch 1985). Such high survival has been reported from several studies of egg planting using the shovel and standpipe method (Appendix 3 and 4). These results, which span a variety of different salmonid species and localities, reflect the robustness and applicability of the method.

Modifications of the shovel and standpipe method have been suggested and applied by White (1980), who describes a standpipe used in combination with a centrifugal waterpump. The pump creates water pressure that facilitates driving the probe into the streambed and it will also remove intragravel fines. This method was reported to be 3.5 times faster than planting eggs by excavating an area inside a 60 cm diameter cylinder. The waterpump method resulted in higher eyed egg to fry survival (50.8%) in sockeye salmon (*Oncorhynchus nerka*) than when planting eggs using the 60 cm diameter cylinder (11%). However, both these methods appear to result in a more artificial redd environment than that created using the shovel and standpipe method.

Harrison (1923) describes a box used for burying eggs in gravel. The box has two bottom shutters, which are removed after it has been placed into a dug channel or depression in the gravel bed. The box is then gently withdrawn from the gravel of the artificial redd. The survival from eyed eggs and green eggs to emergence varied from 40% to nearly 100% for Pacific salmon (Appendix 3 and 4).

Concluding remarks

This review has shown that a variety of techniques have been used for successful egg planting, and new methods may also be developed. For any method, the key to success is to provide conditions that promote egg survival. In this respect, knowledge about the spawning biology of the salmonid to be stocked is valuable in identifying the factors likely to govern egg survival, including gravel composition, burial depth, number of eggs per pocket and hydrological conditions. However, both in natural and artificial redds, site specific conditions are expected to result in variation in egg survival.

Several reasons can be found to prefer stock enhancement by use of egg planting over traditional release of hatchery-reared fish. In most cases, egg planting will be more cost-effective than producing hatchery-reared fry. It may also reduce the risk of spreading disease as contagious infections arise in, and are more readily transmitted between, fry than eggs. Further, it is likely that egg planting results in fry more closely adapted to the local natural conditions than hatchery-reared fish. Hatchery-reared fish often diverge from naturally produced fry in size and behaviour due to artificial environmental conditions. It would therefore be of major importance to know the survival of offspring originating from planted eggs compared to that of hatchery-released fry. However, such comparative studies are presently lacking.

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Appendix 1. Reported survival to hatch or emergence of salmonid eggs planted as green eggs in various types of egg boxes. See text for a description of the egg boxes used. In several of the studies, survival is negatively effected by unfavorable environmental factors. Atlantic salmon (*Salmo salar*); brook trout (*Salvelinus fontinalis*); brown trout (*Salmo trutta*); chum salmon (*Oncorhynchus keta*).

Method	Species	No. eggs per box	No. of boxes	Survival to hatch (%)	Survival to emergence (%)	Environmental factors	Reference
Plastic baskets (35·25·15 cm)	Atlantic salmon	400-2400	24	69-91*	-		Raddum and Fjellheim 1995
Plastic baskets (35·25·15 cm)	Atlantic salmon	1000	12	73-98*	-		Raddum and Fjellheim 1995
Plastic-cylinders (8·6 cm)	Brown trout	100	6	0-71	-	Low pH	Barlaup et al. 1998
Plastic cylinders (10·7.5 cm)	Salmonids	500	8	69-99	-		Harris 1973
PVC cylinders (16·7 cm)	Brown trout	200	3		96-98		Rubin 1995
PVC cylinders (10·7 cm)	Brown trout	100	3		93-96		Rubin 1995
Vibert- boxes	Atlantic salmon	500	4	0	0	Siltation and fungi	Harshbarger and Porter 1979
Vibert- boxes	Atlantic salmon	30	5	23	-	Low pH	Kelly-Quinn et al. 1993
Vibert- boxes	Atlantic salmon	30	5	0	-	Low pH	Kelly-Quinn et al. 1993
Vibert- boxes	Atlantic salmon	30	5	75			Kelly-Quinn et al. 1993
Vibert- boxes	Atlantic salmon	30	5	61	-		Kelly-Quinn et al. 1993
Vibert- boxes	Atlantic salmon	30	5	23	-	Low pH	Kelly-Quinn et al. 1993
Plastic baskets (15·15·15 cm)	Atlantic salmon	4000	10	65-98	-		Donaghy and Verspoor 2000
Vibert- boxes	Brook trout	50	8	95	-		Fiss and Carline 1993
Vibert- boxes	Brook trout	50	4	86	-		Fiss and Carline 1993
Vibert- boxes	Brook trout	50	5	51	-		Fiss and Carline 1993
Plastic cylinders (10·5 cm)	Chum salmon	30	20	-	0-47	High salinity	Scrivener 1988
Plastic cylinders (10·5 cm)	Chum salmon	100	26	-	0-99	High salinity	Scrivener 1988
Plastic cylinders (10·5 cm)	Chum salmon	50	37	-	0	High salinity	Scrivener 1988

* survival to eyed eggs

Appendix 2. Reported survival to hatch or emergence of salmonid eggs planted as eyed eggs in various types of egg boxes. See text for a description of the egg boxes used. In several of the studies, survival is negatively effected by unfavourable environmental factors. Atlantic salmon (*Salmo salar*); brown trout (*Salmo trutta*); rainbow trout (*Oncorhynchus mykiss*).

Method	Species	No. eggs per box	No. of boxes	Survival to hatch (%)	Survival to emergence (%)	Environ. factors	Reference
Plastic cylinders (5·7.5 cm)	Brown trout	200	4	16-24	-		Ottaway and Forrest 1983
Plastic cylinders (10·7.5 cm)	Rainbow trout	200	6	84	-		Turnpenny and Williams 1980
Plastic cylinders (10·7.5 cm)	Rainbow trout	200	2	86	-		Turnpenny and Williams 1980
Plastic cylinders (10·7.5 cm)	Rainbow trout	200	3	91	-		Turnpenny and Williams 1980
Plastic cylinders (10·7.5 cm)	Rainbow trout	200	3	71	-		Turnpenny and Williams 1980
Plastic cylinders (10·7.5 cm)	Rainbow trout	200	3	66	-		Turnpenny and Williams 1980
Plastic cylinders (10·7.5 cm)	Rainbow trout	200	3	21	-	Low DOC	Turnpenny and Williams 1980
Vibert-boxes	Atlantic salmon	30	5	27	-	Low pH	Kelly-Quinn et al. 1993
Vibert-boxes	Atlantic salmon	30	5	0	-	Low pH	Kelly-Quinn et al. 1993
Vibert-boxes	Atlantic salmon	30	5	75	-		Kelly-Quinn et al. 1993
Vibert-boxes	Atlantic salmon	30	5	68	-		Kelly-Quinn et al. 1993
Vibert-boxes	Atlantic salmon	30	5	23	-	Low pH	Kelly-Quinn et al. 1993
Plastic baskets (15·15·15cm)	Atlantic salmon	4000	10	89-100	-		Donaghy and Verspoor 2000
Whitlock-Vibert boxes	Brown trout	500	8	15	4	Siltation and fungi	Harshbarger and Porter 1979
Whitlock-Vibert boxes	Brown trout	500	6	6	-		Harshbarger and Porter 1982
Whitlock-Vibert boxes	Brown trout	500	13	17	-		Harshbarger and Porter 1982
Whitlock-Vibert boxes	Brown trout	500	6	25	-		Harshbarger and Porter 1982

Appendix 2. cont.

Method	Species	No. eggs per box	No. of boxes	Survival to hatch (%)	Survival to emergence (%)	Environ. factors	Reference
Whitlock-Vibert boxes	Brown trout		4	-	3		Harshbarger and Porter 1982
Whitlock-Vibert boxes	Brown trout	500	6	-	8		Harshbarger and Porter 1982
Whitlock-Vibert boxes	Brown trout	500	2	-	14		Harshbarger and Porter 1982
Whitlock-Vibert boxes	Rainbow trout	644-966	3	57	-		Gunn and Keller 1980
Whitlock-Vibert boxes	Rainbow trout	966	3	-	13*	Low pH	Gunn and Keller 1980
Whitlock-Vibert boxes	Rainbow trout	644-966	3	57	-		Gunn and Keller 1980
Whitlock-Vibert boxes	Rainbow trout	966	3	-	0	Low pH	Gunn and Keller 1980
Whitlock-Vibert boxes	Rainbow trout	36-70	2	87	-		Gunn and Keller 1980
Whitlock-Vibert boxes	Rainbow trout	775	2	-	61		Gunn and Keller 1980
Whitlock-Vibert boxes	Rainbow trout	327-538	2	11	-	Low pH	Gunn and Keller 1980
Whitlock-Vibert boxes	Rainbow trout	775	2	-	0	Low pH	Gunn and Keller 1980
Whitlock-Vibert boxes	Rainbow trout	644-966	3	94	-		Gunn and Keller 1980
Whitlock-Vibert boxes	Rainbow trout	775	1	98	-		Gunn and Keller 1980

*sac fry survival

Appendix 3. Reported survival to hatch or emergence of salmonid eggs planted directly into the gravelbed as green eggs by use of various techniques. See text for a closer description of the methods used. Atlantic salmon (*Salmo salar*); Coho salmon (*Oncorhynchus kisutch*).

Method	Species	No. eggs per pocket	No. of pockets	Survival to hatch	Survival to emergence (%)	Reference
Shovel & standpipe	Atlantic salmon	1000	22	74*		Barlaup et al. 1999
Shovel & standpipe	Atlantic salmon	1000	9		89	Barlaup et al. 1999
Planting box	Coho salmon	500	5		40-91	Harrison 1923

* survival to eyed eggs

Appendix 4. Reported survival to hatch or emergence of salmonid eggs planted directly into the gravelbed as eyed eggs by use of various techniques. See text for a closer description of the methods used. Atlantic salmon (*Salmo salar*); Brown trout (*Salmo trutta*); sockeye salmon (*Oncorhynchus nerka*).

Method	Species	No. eggs per pocket	No. of pockets	Survival to hatch (%)	Survival to emergence (%)	Reference
Shovel & standpipe	Atlantic salmon	805-938	8	-	3.3-7.2	Gustafson-Marjanen and Moring 1984
Shovel & standpipe	Atlantic salmon	500	18	88		Sægrov 1998
Shovel & standpipe	Atlantic salmon	500	6	100		Sægrov 1998
Shovel & standpipe	Brown trout	5000	6	20	10	Harshbarger and Porter 1979
Shovel & standpipe	Brown trout	500	6	6	-	Harshbarger and Porter 1979
Planting Box	Sockeye salmon	500	3	-	40-70	Harrison 1923
Planting Box	Sockeye salmon	500	4	-	90-97	Harrison 1923
Shovel & cylinder	Sockeye salmon	2000-3000	4	-	11	White 1980
Standpipe and water pump	Sockeye salmon	200-300	40		51	White 1980

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Experiences from Stocking Salmonid Fry and Fingerlings in Norway

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Abstract

Due to anthropogenically induced factors, such as pollution, river regulation, introduction of diseases and parasites and over-fishing, the stocks of Atlantic salmon (*Salmo salar* L.) and anadromous brown trout (*Salmo trutta* L.) have declined considerably in many Norwegian river systems. For decades, extensive stockings of different stages of young fish have been the most common way to mitigate population decline. In spite of this, populations of Atlantic salmon have continued to decline during the last decades, including salmon stocks in rivers subjected to massive stocking. This has focused attention on the validity of large stocking programs. Evaluation of Norwegian large-scale stocking programs indicate that the productive output from stocking in many cases is inferior to that of wild spawners. Additionally, extensive exploitation of eggs from spawning populations for hatchery use may be harmful to fish populations and fisheries. On the other hand, there are examples of stockings outside anadromous habitats that have been successful in terms of producing smolts and returning adults. Endangered or reduced salmonid populations should, if possible, be conserved by mitigating the underlying causes of the decline and eventually by increasing young fish production using different biotope improvement techniques. In addition, there remains a need for supplemental stockings in many Norwegian river systems.

Key words: stocking, salmon, trout, rivers, lakes.

Introduction

Cultivation of anadromous fish, mainly Atlantic salmon (*Salmo salar* L.) and brown trout (*Salmo trutta* L.), has a long tradition in Norway. The first hatcheries were built in the 1850's (Rasch 1852) and some years later the first salmon ladders were constructed (Berg 1986). Initially, fish were stocked as fry. Later, as rearing techniques improved, older stages of fish were produced. The production of fish for stocking also increased, especially due to the growing demand to mitigate negative effects of environmental impacts, such as river regulation and acidification. Additionally, local river-owner organisations and fishing societies began to run hatcheries on a voluntarily basis, with the main objective to increase production and yield. In 1987, 108 hatcheries produced Atlantic salmon and anadromous brown trout for stocking, with a total production of 14.8 million salmon fry, 1.6 million salmon fingerlings, 1.5 million trout fry and about 0.1 million trout fingerlings (Anon. 1987).

The intensity of fish stocking has long been based on intuition and until recently few attempts have been made to evaluate the needs for stocking or alternative methods (Fjellheim et al. 1995). Increasing decline of the Norwegian populations of Atlantic salmon during the last decades, including salmon stocks in rivers subject to massive stocking, has focused attention on the validity of large stocking programs (Fjellheim et al. 1995, Saltveit 1998).

From the beginning of the 1990's, a new and more restrictive stocking policy was introduced in Norway. This led to a reduction in the number of fish stocked. For Atlantic salmon 14.8 million fry were produced in 1987, 5.3 million fry in 1990 and to 2.3 million fry in 1995 (Johnsen et al. 1997a). Based on the new Salmon Act (1992), new guidelines for fish stocking were published by the Directorate for Nature Management in 1998. According to these guidelines all fish stocking is forbidden without special permission.

Atlantic salmon and brown trout are the only anadromous salmonids that are widely distributed in Norway. They are the most important fish species economically and represent the main target species for cultivation. The main goal of this paper is to review and evaluate earlier stocking programs of juvenile salmonids in Norway, and to use this evaluation to make recommendations for future management of anadromous fish.

Norwegian case studies

Table 1 presents a summary of investigations evaluating stocking programs of juvenile anadromous salmonids, excluding smolts (reviewed by Finstad and Jonsson 2001) in Norway. We critically reviewed each report to determine the success of the project. Success was judged on the survival of young fish and the return of spawners. The research programs generally falls into two categories: 1) research programs dealing with long-term investigations of river sections accessible to anadromous salmonids, mainly in regulated rivers and 2) small-scale experiments to increase salmonid production by increasing the productive area for young fish. Both cases may have been accompanied by stream habitat improvements, such as weir construction or substrate improvements. In some cases other native fish species were removed in order to decrease interspecific competition.

On the background of the high number of rivers stocked by salmonids, surprisingly few salmon rivers have been subject to long-term studies with respect to the output of the stocking program. The majority of these are strongly regulated rivers:

River Lærdalselva

The river Lærdalselva was regulated in 1974 (Saltveit and Nielsen, 1987). The discharge in the anadromous section was increased in winter and decreased during summer. In order to mitigate possible negative effects on the salmon stock, the anadromous section was increased from 24 to 40 km by the construction of four fish ladders (Saltveit 1989), and a large stocking program was initiated on this new stretch. During 1974-1994, approximately 8 million young Atlantic salmon were stocked (Saltveit 1998). The parental stocks consisted of local adults. A strong, significant correlation ($P<0.001$, $r^2=0.98$) was found between the age-0 Atlantic salmon stocked and the corresponding density of age-0 salmon on the new stretch. This indicated that stocking was important for the production of Atlantic salmon smolts in the enlarged anadromous section (Saltveit 1993). However, in spite of the great effort made to increase salmon production in the river, catches of adult salmon have declined in this river. According to Saltveit (1998) there is no apparent reason why the stocking did not lead to higher catches in the river. The lack of relationships between stocking and catches may be explained partly by events in the sea. Saltveit (1998) highlighted that positive effects from stocking can only be achieved if natural reproduction in the river is below carrying capacity. He also stressed that only a surplus of spawners should be used for production of stocked fish. If not, removal of spawners might have negative effects on the salmon stock, as the natural reproduction is depleted.

River Aurlandselva

During the 1970's, the River Aurlandselva, western Norway, was heavily regulated. Before the regulation, this river hosted one of the largest populations of anadromous sea trout in Norway. The discharge of the river was reduced both summer and winter, and the summer temperature was markedly reduced because of hypolimnetic drain from the mountain reservoirs used to maintain a minimum discharge. After regulation, the Atlan-

Table 1. A review of investigations aiming to evaluate stocking of Atlantic salmon and brown trout fry and fingerlings in Norway.

Locality	Habitat	Year(s)	Background for stocking	Fish species	Stocked stage(s)
Kjaglielva/ Sandvikselva (Akershus)	Non-anadromous river	1967-1974	Experimental	Atlantic salmon	Fry
Lærdalselva (Sogn og Fjordane)	Anadromous river	1974-1995	River Regulation	Atlantic salmon	Fry, fingerlings
Langelatbekken and Tverrelva (Troms)	Non-anadromous river	1975-1977	Experimental	Atlantic salmon	Fry
Aurlandselva (Sogn og Fjordane)	Anadromous river	1979 - 1999	River Regulation	brown trout, Atlantic salmon	Presmolt, smolt
Imsa (Rogaland)	Non-anadromous river	1980-1982	Experimental	Atlantic salmon	Fingerlings
Drammenselva (Buskerud)	Non-anadromous river	1983-1987	*G. salaris* rehabilitation	Atlantic salmon	Fingerlings
Litjvasselva/ Vefsna (Nordland)	Non-anadromous river	1985-1989	Sea ranching/ *G. salaris* rehabilitation	Atlantic salmon	Fry
Suldalslågen (Rogaland)	Anadromous river, tributaries, Lake Suldalsvatn	1985-1996	River Regulation	Atlantic salmon	Fry, fingerlings
Nedre Mosvasstjern/ Vefsna (Nordland)	Non-anadromous lake	1986-1994	Sea ranching/ *G. salaris* rehabilitation	Atlantic salmon	Fry
Øvre Mosvasstjern/ Vefsna (Nordland)	Non-anadromous lake	1986-1994	Sea ranching/ *G. salaris* rehabilitation	Atlantic salmon	Fry
Klubbvasselva (Nordland)	Non-anadromous?	1987-1996	Sea ranching/ *G. salaris* rehabilitation	Atlantic salmon	Fry
Hoenselva/ Drammens-vassdraget (Buskerud)	Non-anadromous river	1987	Sea ranching, *G. salaris* in main river	Atlantic salmon	Fry, fingerlings, 1+
Djupdalsbekken (Sør Trøndelag)	Non-anadromous river	1987	Comparison between pond-reared and hatchery-reared fish	Atlantic salmon	Fingerlings

Table 1. cont.

Survival of young fish	Return of spawners	Comments	Author(s)
High - very high	—	Data for survival from fry to fingerlings, 1 year old and 2 year old fish.	Rosseland (1975)
High	Low	Enlargement of anadromous stretch; High stocking intensity did not result in higher catches.	Saltveit (1993) Saltveit (1996) Saltveit (1998)
Normal - high	—		Heggberget and Hesthagen (1981)
Low	Low	High numbers of the brown trout smolt did not smoltify and became stationary.	Sægrov et al. (2000)
Low	Low		Hansen (1987)
Very high	High		Hansen (1991)
Normal - very high	High	Fertilization, reduction of trout population; Low inter- and intraspecific competition gave best results.	Johnsen et al. (1991)
Normal	Low	Smolts from wild salmon significantly larger; Sea-run of wild smolts earlier; Mortality of stocked fish higher in the sea.	Saltveit (1993), Saltveit (1996), Saltveit (1997), Saltveit (1998)
Very low - very high	High	Low inter- and intraspecific competition gave best results.	Johnsen et al. (1997b)
Very low - very high	High	Low inter- and intraspecific competition gave best results.	Johnsen et al. (1997b)
No response - normal	High	Improved growth after fertilization.	Johnsen et al. (1997a)
Normal survival during first summer	—	Surroundings of deciduous forest and cultivated land gave better survival than coniferous forest.	Lillehammer et al. (1990)
+++	—	No significant differences between the two groups; No data later than 15 days after release.	Koksvik and Haug (1998)

Table 1. cont.

Locality	Habitat	Year (s)	Background for stocking	Fish species	Stocked stage (s)
Årdalselva (Rogaland)	Anadromous river	1950's-1987	River Regulation	Atlantic salmon, brown trout	Fry
Årdalselva (Rogaland)	Anadromous river	1988-1994	River Regulation	Atlantic salmon, brown trout	Fry, fingerlings
Suldalslågen (Rogaland)	Side-channels in main anadromous river	1990-1996	River Regulation	Atlantic salmon	Fry, fingerlings
Vosso/Bolstadelv (Hordaland)	Anadromous river	1990-1998	River Regulation, acidification	Atlantic salmon	Fingerlings
Teigdalselva (Hordaland)	Anadromous river	1991-1993	River regulation	brown trout	Fingerlings
Stjørdalsvassdraget/ Dalåa (Nord Trøndelag)	Anadromous river	1993-1995	River Regulation	Atlantic salmon	Fry, fingerlings
Teigdalselva/ Vossovassdraget (Hordaland)	Anadromous river	1996-1997	River Regulation, acidification	brown trout	Fingerlings
Tovdalselva (Vest-Agder)	Non-anadromous river	1997 -	Rehabilitation	Atlantic salmon	Fingerlings
Mandalselva (Vest-Agder)	Non-anadromous river	1997 -	Rehabilitation	Atlantic salmon	Fingerlings

Survival of young fish (%):

	Fry - smolt	Fingerling - smolt
Very high	> 5	> 50
High	2 - 5	20 - 50
Normal	1 - 2	10 - 20
Low	0.2 - 1	2 - 10
Very low	0.1 - 0.2	1 - 2
No response	0	0

Survival of spawners:

High = Justifiable on basis of removed number of spawners

Low = Not justifiable on basis of removed number of spawners

— = No response or data missing

Table 1. cont.

Survival of young fish	Return of spawners	Comments	Author(s)
—	Low		Gravem et al. (1994)
+++	—	Proportion of wild to stocked fish uncertain.	Gravem et al. (1994)
Normal	Low	Fingerlings survived better than fry; Mortality of stocked fish higher in the sea.	Pethon et al. (1998)
Low	Very low	Liming; Natural population drastically reduced High proportion of escaped farmed fish.	Fjellheim et al. (1994), Barlaup et al. 1999
Very low	Low	Stocking densities above carrying capacity.	Fjellheim et al. (1994)
+++	—	Delayed smolt-run compared to main river.	Arnekleiv (1996)
Low	Low	Weirs; Substrate improvement; Liming; Wild fish survived better than stocked fish.	Fjellheim et al. (1998a)
Normal	—	Liming.	Hindar and Johnsen (1999)
Very low - normal	—	Liming.	Hindar and Johnsen (1999)

tic salmon population was reduced to 10% of its pre-regulation size and was considered close to extinction. The brown trout population was reduced similarly to 40% of its original size (Sægrov et al. 2000). A large number of sea trout and a smaller number of juvenile Atlantic salmon have yearly been stocked in the river since 1979. A large number of the brown trout stocked as presmolts in the river Aurlandselva failed to smoltify. This resulted in high densities of large-sized stocked fish in the river. Many of these fish were damaged morphologically and were in poor condition. According to Sægrov et al. (2000), stocked trout contributed to 10-15% of the brown trout population, in spite of the large numbers stocked. During the last years, several attempts were made to improve the quality and survival of young fish, including construction of weirs, increased quality of the stocked fish and reduced numbers of stocked fish (Sægrov et al. 2000).

River Suldalslågen

The river Suldalslågen, south-western Norway, was exposed to two hydropower developments in the period 1965 to 1980 (Anon. 1994). Water is now transferred from the main river to the sea, resulting in reduced flow, altered temperature and in periods of low flow, detrimental inputs of acidic water from tributaries (Kaasa et al. 1998). Suldalslågen has been stocked with Atlantic salmon since 1982. During the first years, fish were stocked as smolts and later as fry and fingerlings. After 1990, stocked fish were mainly summer-fed 0+, between 6 and 11 cm long, and marked by clipping of the adipose fin. The fish were stocked in the main river, in side-channels, in Lake Suldalsvatn and in tributaries (Saltveit 1995, 1998, Pethon et al. 1998). Age 0+ stocked salmon were of an equivalent size to the 1+ and some of the 2+ wild fish. The stockings did not seem to affect the density or growth of the wild juveniles, even if the number of stocked fish was high. During winter, a reduction in density of wild, young-of-the-year was observed, while no decline in density was observed among the stocked fish (Saltveit 1995,1998). However, the following spring and summer, the decline in density of stocked fish was higher ($P<0.05$) than that of wild juveniles of the same size, due to either higher mortality or migration as younger smolts. In the period 1993-1997, approximately 50% of the salmon smolts leaving the river Suldalslågen were stocked (Saltveit 1998). In spite of this, 5-10% of the spawners returning to the river were of stocked origin (Saltveit 1997, 1998). Atlantic salmon stocked in the river Suldalslågen showed different life-history characteristics than the wild fish. The smolts were smaller in size and the smolt-run occurred at an earlier age and later in the season than that of the wild fish. The size of the spawning population of the river Suldalslågen has declined since 1990 and is now far below the carrying capacity of the river (Saltveit 1997, Sægrov et al. 1998, Saltveit and Sægrov pers. comm., Sægrov et al. 2001). In spite of most of the adult fish deriving from natural production, broodstock fish continue to be taken from the low number of returnees leaving ever fewer fish for natural reproduction. On this basis, Saltveit (1997, 1998) advised the stocking program in river Suldalslågen to be discontinued.

River Teigdalselva

The river Teigdalselva, a tributary to the larger river Vosso, western Norway, was regulated in 1969. Water was directed to a hydropower station outside the catchment area (Fjellheim et al.1994), resulting in strongly reduced discharge in the river. Due to alarming decreases in fisheries for anadromous salmonids, a stocking programme started in 1990. The first two years, approximately 70,000 Atlantic salmon fingerlings and 1+ originating from the river Vosso were stocked. Nearly all of these died before reaching the smolt stage. Between 1992 and 1995, 45,000-75,000 brown trout fingerlings of anadromous origin were stocked yearly. Most of these were marked by clipping the adipose fin. An evaluation of the trout-stocking programme concluded that the stocking density was unnaturally high (Fjellheim et al. 1994, 1995). The stocked trout densities were initially many times higher than that of the wild fish. During the first winter, mortality of stocked trout was very high, leaving a smaller population of stocked than wild fish the following spring. In order to fulfil the needs of the stocking programme, between 30 and 36% of the population of mature females was removed for broodstock. Fjellheim et al. (1995) concluded that the stocking programme should be reduced or stopped. They also recommended that more effort should be made to improve fish habitat, especially by constructing deeper pools, because drought and unfavourable conditions during winter were key bottlenecks for the survival of young fish. The stocking programme in the river Teigdalselva was stopped in 1996. Four weir basins have since been built in suitable parts of the river. Additional habitat improvements were made by placing coarse substrate in a locality with uniform bottom substrate. These habitat adjustments proved to be successful. The carrying capacity of wild trout in the riffles close to the weir basins was generally increased. A study of two weir basins showed a considerable increase in population density of 1+ and older fish (Fjellheim et al. 1998a). One of the basins (150 m long), hosted 1,100 trout and nearly 500 salmon in 1997, the other (100 m long) hosted more than 900 trout. The weir basins constructed in the river Teigdalselva proved to also play an important role in segregating young-of-the-year from larger fish, with latter being mainly found in the pools (Fjellheim et al. 1998b). This likely reduced intercohort aggression (Kalleberg 1958) and was probably the main factor explaining overall increased fish densities.

River Tovdalselva

In the middle of the 1990's, the salmon population of the river Tovdalselva in southernmost Norway was classified as extinct due to acidification (Lien et al. 1996). Liming of the river started in October 1996, and in September 1997, 6,750 fingerlings (average weight 2.8 g, average length 65 mm) were released in a limited reach of the river. In august 1998, the population of salmon parr in this reach was estimated at 1,800 1+ with an average size of 144.5 mm, and an estimated survival of 27% from the previous year (Hindar and Johnsen 1999). One year later no salmon parr were found, indicating that most had emigrated as two-year-old smolts.

Stocking outside anadromous habitats

Stocking of juvenile anadromous salmonids in lakes and streams outside their natural habitat has a long tradition in Norway. In the period 1954-1963, a total of 41,100 salmon fry were released in 10 different fishless ponds and lakes in the Snøfjord watercourse of the county of Finnmark (Berg 1969). Berg concluded that about 2/3 of the stocked fry survived to the smolt stage and that 0.9% of the migrating smolts were recaptured as adult salmon. He also reviewed results from earlier stockings of salmon fry in Norwegian lakes and concluded that salmon survival was high, and growth very good in fishless lakes. In lakes with brown trout, stocking of salmon fry was also found to be successful. In some of the lakes, the salmon smolted and migrated, while in other lakes fish remained resident.

The first systematic attempts to estimate salmon smolt production from successive fry stockings in rivers in Norway were reported by Rosseland (1975) from the River Kjaglielv, a tributary to the River Sandvikselv, close to Oslo. Since the beginning of the sixties, the river has been stocked annually with 1.7 unfed fry m^{-2}. Based on annual electrofishing during 1967-1973, mean survival was estimated to be 45.5% from unfed fry to 1-summer old fish, 25.9% from fry to 2-summer old fish and 14.4%. from fry to 3-summer old fish. Assuming a stocking density of 2 unfed fry m^{-2}, Rosseland (1975) concluded that the river Kjaglielv could produce one salmon smolt 3-4 m^{-2}. There are, however no report on the effects of these stockings in form of adults returning to the main river. Heggberget and Hesthagen (1981) calculated densities of age 1+ salmon to be 38 and 62 fish 100 m^{-2}, one and two years after introduction to two small streams in northern Norway, respectively, while densities of cohabiting brown trout were 17 and 28 fish 100 m^{-2}, respectively. The density of age 2 salmon was 10 fish 100 m^{-2}. Despite a brown trout standing stock of 77-89% of the total biomass, Atlantic salmon were able to establish suitable territories in the streams.

Another example of successful stocking in an area where there was no natural run of salmon comes from the river Drammenselva (Hansen 1991). In September 1983, 14,000 salmon fingerlings of the local stock were released in the river, which already contained populations of resident brown trout, whitefish, minnow, roach, pike and perch. All fish stocked had their adipose fin clipped. In total, the estimated return to the river was 320 salmon, which was 2.3% of the number of 0+ released. Based on the marine exploitation rate of the stock, the total production of adult fish in this experiment was estimated to be 914 fish (6.5% of the number released) weighing about 6,300 kg. This equals a production of 0.45 kg per 0+ released. The experiment was repeated in 1986 when 50,000 fingerlings were stocked in the same area. In 1989 and 1990, a total of about 350 adult fish from this group were recorded in the river. There was a high proportion of grilse returning in 1990, indicating that a relatively high proportion left the river as 3+ smolts.

An example of unsuccessful stocking of Atlantic salmon in lakes was reported by Hansen (1987). A release of 16,740 Atlantic salmon fingerlings in lake Storevatnet in the river Imsa system resulted in a downstream migration of 580 smolts. Most of the smolts were two years of age, but there was also a significant proportion of one-year-old smolts. Growth of the lake-reared smolts was excellent, but they migrated downstream over a much longer period than naturally produced smolts, which descended mainly in May. In total, 0.7% of the Carlin-tagged lake-reared smolts were recaptured as adults compared with 15.4% of the naturally produced smolts. It was suggested that the low survival of lake reared smolts in this case was mainly due to an extended migration time (Hansen 1987).

During the last decades, several studies aiming to use rivers and lakes outside the natural habitat for sea ranching of Atlantic salmon were conducted in tributaries to the River Vefsna. Since 1983, unfed Atlantic salmon fry were stocked annually into the river Litjvasselva and during the period 1985-89, the mean density of salmon parr (>0+) was 17,000-54,100 m^{-2}, indicating that the stockings were successful (Johnsen et al. 1991). In another tributary, the river Klubbvasselva, 30,000 unfed fry (2 fry m^{-2}) were released annually during 1984-92, resulting in a mean density of salmon parr (>0+) of 21-44 100 m^{-2} during 1987-93. Survival from fry to smolt, based on captures in a smolt trap, varied between 0.21% for fry released in 1988 to 1.17% for fry released in 1987. A total of 1,065 migrating smolts were Carlin-tagged in the years 1988-91 and approximately 2% were recaptured (Johnsen et al. 1997b). In two fishless oligotrophic/ultraoligotrophic high mountain lakes in Vefsna, stocking of unfed fry gave decreasing survival rates and growth with time. While the first release (1983) in one of the lakes resulted in an estimated minimum survival of 6.7% to smolt, the survival varied between 0.15 and 0.62% for fry released in the same lake in the period 1986-91. For both lakes combined, the survival of fry released during 1987-90 when conditions had "stabilised" varied between 0.66 and 1.0%, with an average of 0.85%. A total of 5,429 smolts caught in traps were Carlin-tagged and 25 (0.5%) were recaptured (Johnsen et al. 1997a).

Discussion

The studies presented in Table 1 lack uniformity of design, and it is therefore difficult to make precise comparisons. A disadvantage of several of the investigations is that they were short-term, lacked of knowledge of natural variation, and failed to measure success in terms of returning spawners. Investigations of large-scale Norwegian stocking programs within the natural anadromous habitat generally indicate that natural breeding is superior to extensive stocking programs, as indicated by the results from the rivers Suldalslågen and Teigdalselva (Fjellheim et al.1995, Saltveit, 1997, 1998). The examples from the rivers Lærdalselva and Tovdalselva illustrate that stocking fry in habitats with low densities of resident fish may increase the production of juvenile fish. Similar conclusions regarding stocking success of salmonids have also been found outside Norway. Generally stocking success in anadromous sections is low, with regards to brown trout (Kelly-Quinn and Bracken 1989, Berg and Jorgensen 1991, Hansen et al. 1995) and Atlantic salmon (Verspoor and Garcia de Leaniz 1997, Crozier et al. 1997, Mowbray and Locke 1998). An example of successful stocking of Atlantic salmon in lacustrine nursery habitats is given by Pepper et al. (1992).

The most successful cases listed in Table 1 deal with attempts to increase Atlantic salmon production using nursery areas outside the natural anadromous stretch, both in lentic and lotic waters. The examples show that stocking of fry outside anadromous habitats leads to establishment of young salmon even when the environmental conditions are unfavourable and interspecific competition may be intense. Survival to the smolt stage was highest when the fry were released in localities with no other fish. Several investigations in other countries have dealt with stockings in non-anadromous rivers (MacCrimmon 1954, Mills 1964, Egglishaw and Shackley 1980, Kennedy and Strange 1980, Cote and Pomerlau 1985, Kennedy and Strange 1986a, b, Whalen and LaBar 1998, Jokikokko 1999). The results from these investigations show that stocking of salmon fry in non-anadromous rivers may be successful even when the fry is stocked in rivers with populations of brown trout, brook trout, rainbow trout or other species. They further indicate that fry quality, fry feeding stage, stocking density, stocking time, stocking place and local fish populations are important factors that may influence the survival of the fry. Harris (1978) and Pedley and Jones (1978) concluded that stocking of fry in lakes may result in high survival and good growth to the smolt stage especially when the fry are stocked in fishless lakes. The main problem with stocking in lakes is that smolts may have problems with the migration from the lake (Munro 1965, Frantsi et al. 1972, Harris 1973, Hansen 1987).

In rivers where the production of young fish in the anadromous habitats is threatened for some reason it may be wise to catch brood fish and stock the offspring in localities outside anadromous habitats. This may also be a strategy in rivers threatened by invasion of farmed fish. To secure the stock, it may be necessary to keep it in a living gene bank. Offspring from these fish may be released in rivers and lakes outside anadromous habitats and serve as an "reservoir" against the invasion of farmed fish. This may also be a strategy to secure the stock in rivers threatened by pollution or parasites. In the rivers Vefsna and Drammenselva the production of young fish in the anadromous stretches was strongly impacted by infection of *Gyrodactylus salaris*. These examples illustrate the importance of stocking outside the natural salmon habitat as a means of conserving of fish stocks.

The Norwegian examples of stockings in anadromous habitats indicate that this seldom contributes to increased fishery. The example from the river Lærdalselva shows that stocking of presmolts above the natural anadromous stretch, in combination with establishment of fish ladders, was a successful strategy for increasing the production of juvenile salmon. However, no positive effect on the catches of adult fish from these stocking activities was found. This was also the case in the river Suldalslågen, where very few stocked Atlantic salmon return as adults (Saltveit 1995, 1998). These examples illustrate the situation in regulated rivers where limiting factors are complex and to a large extent not known. On the other hand, limiting factors are better known in acidified watersheds and rivers infected by parasites. The example from the river Drammenselva, which is infected by *G. salaris*, showed that stocking of fingerlings outside natural salmon habitats could be extremely profitable. In such cases, stocking may contribute to increased fishery if there is a surplus of brood fish and the fish are stocked outside anadromous sections.

Salmonids reared in hatcheries will experience an environment that is very different from natural conditions. The fish are raised from egg to fry in non-natural substrate and hydrophysical surroundings. The temperature, light and feeding conditions are different and densities are many thousand times higher than in rivers. This results in phenotypic divergence that may have severe implications for the competitive and survival abilities of hatchery fish (Cooney and Brodeur 1996, Einum and Fleming 2001). Already Miller (1952) concluded that even the shortest exposure of a stock of fish to hatchery environment had a definite, but unknown effect which reduced survival after release from the protective environment. Smith (1961) stated that behavioural patterns in particular may be altered by even a short exposure to an artificial environment. Fenderson et al. (1968) suggested that high levels of aggressiveness may contribute to mortalities of hatchery-reared salmon planted in streams, caused by loss of feeding time, excessive use of energy, and increased exposure to predation. According to Dickson and MacCrimmon (1982) behavioural modifications occurring in juvenile wild Atlantic salmon when hatched and reared under prevailing hatchery conditions are of particular ecological significance when these fish are released into streams. The changes are so distinctive that the fish behave as a different species in their environmental demands and during interactions with wild Atlantic salmon and brook trout.

In rivers, one should expect an optimum density or biomass of salmonids close to the carrying capacity (Fjellheim et al. 1995, Sægrov et al. 2001, Saltveit and Sægrov pers. comm.). Any attempt to increase densities above carrying capacity without the introduction of other remedial measures will fail. A general policy regarding fish stocking is to stock fish in terms of appropriate numbers. We will additionally highlight stocking in terms of biomass; a theme that has been neglected surprisingly in many stocking programs in Norway. Hatcheries often provide excellent conditions for fish growth. Elevated temperatures and good feeding conditions result in 0+ fish that are larger than their wild counterparts. The brown trout stocking programme in the river Teigdalselva illustrates the consequences of this. In 1992, at the time of stocking, the mean size of the stocked fingerlings was 6.4±0.6 cm, while that of the natural fry was 3.0±0.2 cm. Assuming a condition factor of 1.0, the stocked fish had a body weight nearly 10 times more than that of the wild 0+. Using data from Fjellheim et al. (1994, 1995), the initial biomass of stocked 0+ was 430 g 100 m^{-2}, which is equivalent to the biomass of 1,580 wild 0+ 100 m^{-2}. A similar case is found in the river Suldalslågen (Saltveit 1995, 1996). At the time of stocking, 0+ Atlantic salmon fingerlings were between 8 and 9 cm long, while the wild 0+ was less than 4 cm. Stocked fish biomass was thus equivalent to the biomass of approximately 1,300 wild 0+ 100 m^{-2}.

Populations of salmonids in a stream may be space limited (as a function of body size, Grant and Kramer 1990) or food-limited (Mundie and Mounce 1978, Henderson et al. 1991, Marschall and Crowder 1995). Because individual consumption rate increases with size (Elliott 1975), density of fish supported by a particular food resource will also depend on body size. A high stocking density of large fish will negatively influence the supply of food animals (Marschall and Crowder 1995). It is therefore vital to understand the interplay of size and numbers in stream salmonid populations, of how available resources might support different numbers of different sized individuals and how different sized individuals impact resources available to other individuals (Marschall and Crowder 1995).

A size difference between wild and stocked fingerlings will also disrupt the natural demographic size distribution in the population. Normally, different year-classes of salmonids are ecologically segregated according to their size. The smallest fish are mostly found in shallow slow-flowing parts of riffles, while larger fish occupy deeper riffle areas and pools (Raddum et al. 1989, Bremset and Berg 1997, 1999, Fjellheim et al. 1998b, Heggenes et al. 1999, Bremset and Heggenes 2001, Einum and Fleming 2001). Shortly after stocking, the stocked fingerlings will experience problems competing with similarly-sized fish (Bachman 1984) and will end up occupying the same niche as the wild 0+, which will be inferior due to their smaller size (Fjellheim et al. 1995). In cases were size-differences are large, encounters between stocked and wild 0+ brown trout may result in cannibalism (Fjellheim et al. 1994). Today it is generally accepted that habitat improvements are the best method of increasing densities of salmonid stocks in running waters where salmon and trout densities have been reduced due to environmental impact. Examples include liming of acidified rivers (Norrgren et al. 1993, Larsen and Hesthagen 1995, Lacroix 1992, 1996, Clayton et al. 1998), minimum discharge in regulated rivers, construction of weirs (Heggberget 1984), increasing spawning habitats by introducing gravel (Harby and Arnekleiv 1994, Avery1996, House 1996, Scruton et al. 1997) and increasing productive area by constructing side channels (Pethon et al.1998) or fish ladders (Saltveit 1989). Habitat improvements may be accompanied by stocking programs to speed up recolonisation or, if fish are extinct, selection of an appropriate genetic strain. Additionally, salmonid production may be increased by stocking fry or fingerlings in suitable areas in the non-anadromous section and in this manner contribute both to conservation of the stock and to an increased fishery. Such stocking should only be allowed if there is an excess of spawners, or if fry of the local strain are available from a living gene bank. In the worst case, extensive removal of spawners may be harmful to fish population and fisheries.

A better way to conserve endangered or reduced salmonid populations is to mitigate the underlying cause of the decline and eventually increase young fish production by different mitigation techniques. This implies that limiting factors are known. Before considering fish stocking, the localities should be recognised according to three different categories:

1) Fish population densities are normal, i.e. no population decline as seen from long-term records. No stocking is recommended.

2) Fish populations are extinct. The cause of the extinction needs to be identified and if possible, rectified. We recommend stocking as a method of restoring extinct populations. This provides a better opportunity to control the genetic and ecological qualities of the fish. Stocking also allows for quicker recolonisation of the entire anadromous section of the watershed. In cases of poor availability of suitable parental fish, one may want to allow colonisation by natural straying from nearby rivers. In Norway acidification is a common problem that has led to strongly reduced populations (Hesthagen and Hansen 1991). Many of the affected rivers are now subject to liming, and the water quality is again acceptable for fish. Such rivers may be colonised by stocking programs, by mature fish migrating from the sea (escaped farmed fish or strays) or by a combination of these means. *G. salaris* is another cause of strong declines in salmon populations in Norwegian rivers. In many rivers the parasite has been exterminated by rotenone treatment. Re-establishment of the salmon population in these rivers has been faster in rivers with a stocking programme than in rivers with no stocking (Johnsen et al. 1999).

3) Fish population density is sub-optimal, i.e. it is lower than expected based on long-term records or compared to similar rivers. Sub-optimal densities are unfortunately the normal situation in many Norwegian rivers. The reasons for this are numerous: stream regulation, canalisation, eutrophication, acidification, other sources of pollution, invasion of farmed fish, parasites, over fishing, and/or abnormally high mortality at sea. In most cases, it is not recommended to increase densities of fry and fingerlings in the main river at the expense of natural spawners. Instead, the underlying causes should be clarified and if possible corrected. Regulated rivers may never again support the same population size, because the carrying capacity has changed. Fish populations in regulated rivers will probably, without interference, adapt to the new situation, which may be improved using other management strategies. We approve of the use of nursery areas in running and lentic waters outside the anadromous section as a method of strengthening fish populations and fisheries. In addition to stocking of fry and fingerlings, egg planting should be considered as a method in non-anadromous sections (Barlaup and Moen 2001). In this way the fry will be exposed to a natural physical, chemical and biological environment from the egg stage and on, resulting in selection as close to natural as possible.

There is still need for supplemental stockings in many Norwegian river systems. Most studies in Norway conclude that the quality of the stocked fish needs to be improved. Solving this problem is a challenge to scientists and nature managers. There is a strong need for refinement of stocking methods: time, suitable localities, stocking density, life cycle stage. We still lack information to be able to answer questions of the type: Should fingerlings be released early in the summer as small individuals just slightly affected by hatchery life or is it wise to let them grow bigger in the hatchery for later stocking in the autumn or even the next spring?

The escapement of farmed fish will not stop in the nearest future. This may lead to an invasion of farmed fish in many Norwegian rivers which in turn for some rivers probably will impoverish the local stock. We need to assess if stocking of the local stock or a closely related stock can be used to counteract this influence of farmed fish. We also need more knowledge if stocking in supplemental nursery areas outside the anadromous section is a method to conserve local stocks threatened by invasion of farmed fish.

In rivers with reduced densities of salmonids, the potential spawning habitat may not be fully used. In cases of suboptimal densities we need to know if it is advisable to move spawners or naturally hatched fry from areas of surplus densities to low-density areas in order to get a more even distribution of young fish. We also need more information of the ecological consequences of moving fish within the river system and if this may lead to a better exploitation of the river.

We also need more information the effects of biotope adjustments, like weir building, substrate improvement, establishment of riverbank vegetation, etc on stocked fish and how such measures affects the competitive ability of the stocked fish.

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Factors Influencing the Yield of Smolt Releases in Norway

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Abstract

Hatchery-reared smolt, chiefly Atlantic salmon, but also brown trout and Arctic charr, are released annually in Norwegian watercourses mainly to compensate for habitat losses due to impoundment of streams for hydropower purposes. A "good smolt" for this objective is a fish with a strong tendency to migrate to sea, and good chance of survival to adulthood and returning to the site of release. Survival rates of the released smolts are low and approximately half of that of wild smolts. The reduced survival rate may be due to adaptation to artificial rearing conditions, and poor handling, transport and release procedures. Release experiments show that the time and site of release, age and size of the released fish, water quality, sexual maturity and sea water acclimatization before release affect survival of the released fish, whereas time and site of release affect the homing of the adult fish. The timing of smolting is controlled by light regime and temperature conditions in the hatcheries. Different temperature and light conditions have been tested in hatcheries to control the smolting process. The survival of juvenile salmonids at sea affects the number of returning adults to fresh water. In fresh water, density dependent factors influence the survival-rate, i.e. when density of juveniles exceeds a threshold limit, mortality increases greatly. At sea, however, such density independent factors as e.g. predation, parasites appear most important. This means that mean number of survivors will increase linearly with the number of released smolts. The yield of smolt releases varies between species, rivers, stocks year-classes and age of the smolts released. The yields are higher for 2-year-old smolt than 1-year-old, and higher in Atlantic salmon than brown trout and Arctic charr.

Keywords: smolt, releases, yield, survival, homing.

Introduction

In Norway, hatchery-reared smolts have been released since the 1950's to compensate for habitat loss due to impoundment of streams, but in later years also in experimental sea ranching programmes. Between 200,000 and 500,000 reared smolts have been stocked annually (Jonsson and Fleming 1993), mainly Atlantic salmon (*Salmo salar*) but also brown trout (*Salmo trutta*) and Arctic charr (*Salvelinus alpinus*). The survival-rate of hatchery-reared smolts is low, approximately one half of that of wild salmon smolts (Jonsson et al. 1991). This reduced survival may be due to artificial rearing conditions and/or poor handling and releasing procedures, resulting in decreased smolt quality and reduced performance after release.

Handling and transport may stress anadromous salmonids (e.g. Nikinmaa et al. 1983, Robertson et al. 1987, Barton and Iwama 1991, Wendelaar Bonga 1997, Mommsen 1999, Barton 2000). It is known that «stress-related» cortisol surges in fish can suppress the immunological capacity (Fries 1986, Maule et al. 1989, Schreck et al. 1993) and affect seawater tolerance (Redding and Schreck 1983, Iversen et al. 1998) and migratory activity (Specker and Schreck 1980). It has been hypothesized that handling stress may affect survival rates in the wild

(Schreck et al. 1989) through mortality after release.

Salmonid smolting includes morphological, physiological, biochemical and behavioural changes (Folmar and Dickhoff 1980, Wedemeyer et al. 1980, Hoar 1988, Høgåsen 1998). The smolting process is influenced by photoperiod (Saunders and Henderson 1970, McCormick and Saunders 1987, McCormick et al. 1995) and water temperature (Johnston and Saunders 1981, McCormick et al. 1999, 2000), and the process is partly driven by endogenous rhythms (Eriksson and Lundqvist 1982). Thus, by manipulating the photoperiod, the time of smolting can be shifted (Saunders and Henderson 1970, Clarke 1989). Water temperature is a factor that can accelerate or decelerate the smolting process, and it works in concert with photoperiod (Wedemeyer et al. 1980, Hoar 1988, Høgåsen 1998). A temperature increase accelerates the smoltification, but may also accelerate desmoltification so that the period in which the fish are smolts is considerably shortened at high temperatures (Clarke et al. 1978, Soivio et al. 1988, 1989). In wild populations, the migration will occur during a few weeks in spring, and there will be an annual variation in the timing in each river, as well as variations among rivers at different latitudes, at least partly as a consequence of variation in temperature (Jonsson and Ruud-Hansen 1985) and light condition (Metcalfe et al. 1988).

Atlantic salmon, brown trout and Arctic charr are common salmonids used for stocking in Norway (Jonsson and Fleming 1993). Atlantic salmon live in freshwater as juvenile parr for 1-8 years before transforming to smolts and migrating to the ocean for feeding (Metcalfe and Thorpe 1990). In the ocean, they are free ranging in near-surface waters for 1-4 years before attaining maturity and returning to fresh water for spawning (Jonsson et al. 1991). In some populations the juveniles may mature in fresh water without any prior sea run (Jonsson et al. 1998b).

Arctic charr and brown trout are polymorphic species. The populations in coastal streams often consist of freshwater resident and anadromous individuals (Nordeng 1983, Jonsson 1989, Hindar et al. 1991). The residents stay in freshwater throughout life, whereas the anadromous fish migrate between fresh and salt waters (Jonsson 1985, Dellefors and Faremo 1988). The juveniles stay in fresh water for 1-7 years before smolting and migration in fjords and coastal waters for feeding (L'Abée-Lund et al. 1989). After 1.5-3 months at sea, the post smolts return to fresh water for spawning and/or wintering (Jonsson 1985, 1989, Finstad and Heggberget 1993, 1995). Often, both species remain in fresh water during the winter, because their ionic regulation is impaired at low sea temperatures (Finstad et al. 1989, Finstad and Heggberget 1993, 1995). The sea trout mature sexually after 1 to 4 sea sojourns and about one third of the spawners breed again in later years (Jonsson and L'Abée-Lund 1993).

Scientific experiments have been performed to produce "good smolt", i.e. a fish with a strong tendency to migration to sea, high survival to adulthood and high return rate to the site of release. The experiments have been focused on smolt size and age at release, temperature and light condition in hatchery to control the smoltification process, seawater acclimatization before release, site and time of release, and release techniques. In the present paper, we summarize information on factors influencing survival and homing of hatchery-reared Atlantic salmon, brown trout and Arctic charr, and then we review information on yields of smolt releases.

Intensive production in hatchery - releases of presmolts and smolts

Intensive production of smolts in hatcheries is a method where eggs from the parent fish (preferably a local stock) is hatched and fed by dry pellets in a hatchery. In Norway the fish is partly reared in heated water in order to decrease the time to smolting by one or more years. Selection pressures in hatcheries differ from those in natural rivers. In hatcheries, juveniles are aggressive especially when reared at low densities. To suppress the aggressive behaviour, density is usually high so that juveniles give up territories and start swimming in shoals, unlike the situation in a river where the juveniles are territorial and form dominance hierarchies (Einum and Fleming 2001). Hatchery smolts do not learn to find natural foods and avoid predators. On the other hand, they are more exposed to bacterial, viral or fungal diseases and often develop fin erosion due to the fin-nipping. The use of natural light and temperature conditions will lead to production of smolts ready to be released in spring (Iversen et al. 1999). Lack of such control, which is seen in some hatcheries, leads shifts the time of smolting. When releasing such fish in spring, they have poor survival and growth after release (Finstad and Iversen 1995).

Density regulation

The survival of juvenile salmonids at sea affects the number of returning adults to freshwater. In freshwater, density dependent factors such as food and space appear important for survival of wild juvenile Atlantic salmon and brown trout (Elliott 1994, Jonsson et al. 1998a), and there is a carrying capacity limiting the population size. When density exceeds this threshold limit, mortality increases greatly. Release of salmonid fry or parr in freshwater will therefore only enhance the stock when the recruitment rate is below the carrying capacity. The released fish may either be inferior or die, or they may compete with wild fish and increase their mortality (Sægrov et al. 2001).

At sea, density independent mortality factors appear to dominate (Jonsson et al. 1998a). This means that the mean number of survivors will increase linearly with the number of released smolts. Most probably, factors related to the climate influence the survival the smolt (Friedland et al. 1998a, b). The effect of climatic variation is similar whether few or many smolts enter seawater. In Atlantic salmon, the number of adults returning to the spawning river, increased rectilinearly with annual smolt number (Jonsson et al. 1998a). The higher the average smolt output, the higher the average number of returning spawners. This indicates that the population density is far below the carrying capacity for Atlantic salmon in the North Atlantic, and higher numbers of smolts released will increase the number of returning adults proportionally, given even smolt quality.

Time of release

Marine survival of smolts has been intensively studied in relation to time of transfer from freshwater to seawater (Lundqvist et al. 1986, Jonsson et al. 1998a). The time of release appears to be very important for survival and homing of adults.

The main smolt run in wild Atlantic salmon, sea trout and Arctic charr usually occurs during a short period (1 month or less) in spring (Österdahl 1969, Jonsson and Ruud-Hansen 1985, Jonsson et al. 1990, Bohlin et al. 1993, Finstad and Heggberget 1993, 1995). This period appears to reflect local environmental conditions such as photoperiod, temperature, waterflow etc. (Jonsson 1991, Heggberget et al. 1993, Hvidsten et al. 1998). To test the effect of release time on survival, seawater adapted Atlantic salmon smolts were released monthly from January through December in the estuary of the River Imsa, south-western Norway, and in seawater 4 km from the river mouth (Hansen and Jonsson 1989a). Based on tag returns, the survival appeared high for 1-year-old smolt released in the spring, at the same time as natural smolts left the river and decreased through summer to a minimum in autumn and winter. The recapture-rate of smolt released in May and June were 11 and 13%, in August approximately 4% and in September to January between 0.5-1%. In February and March the recaptures increased to approximately 4 and 7%, respectivley. Furthermore, Staurnes et al. (1993b) tested the survival and status of 2-year-old Atlantic salmon smolts released from middle of April to late June in the River Ingdalselva, Mid-Norway. They found that the return rate of adults were highest for smolt released during a period from late April to mid-May (1.4-1.6%), which coincided with the time of the highest seawater tolerance of the smolts. The recaptures from late

May to late June were between 0.3-0.7%.

Juvenile Atlantic salmon released as one-summer old parr and reared to smolts in a lake, migrated to sea over a much longer time period than naturally produced smolts (Hansen 1987). The main downstream migration of naturally produced smolts took place in May, whereas the lake reared fish descended in large numbers during the whole summer. The survival of these fish was low (0.7%) compared to naturally produced smolts (15.4%) from the same river, which may be due to their irregular time of migration.

In Baltic salmon (*Salmo salar*), experiments with delayed release (retained in sea water pens outside the river mouth for one to four months before release) have demonstrated that these fish had a higher survival than those released in the spring (Eriksson and Eriksson 1985, Eriksson 1988). Similarly for brown trout, delayed release for 4 to 8 weeks showed that the fish survived better than corresponding groups released in spring (Jonsson et al. 1994c). The positive effect of delayed release on survival may be caused by the enhanced growth during the sea retention period. Large fish are less vulnerable to predation than smaller ones (Dill 1983).

The time of release will also affect homing in salmonids. Atlantic salmon smolts and seawater acclimated post-smolts were released montly through a year (Hansen and Jonsson 1991b). Groups released in winter (February-March) strayed more (80%) and entered rivers farther away than fish released during the rest of the year (April-September: 25-30%).

Site of release

Site of release of juveniles influences the survival and homing of the adults. Hatchery-reared fish released as smolts return as mature fish to the area of release, whether this is a river, estuary or at sea (Hansen et al. 1989c, Hansen et al. 1993, Jonsson et al. 1995). Homing with high precision to the river of release depends on juvenile experience with the river (Hansen and Jonsson 1994, Hvidsten et al. 1994, Jonsson et al. 1994a) i.e. the young must be released in the river.

Survival of hatchery-reared smolts, expressed as recapture rate, differs among release sites. In the River Surna coastal releases resulted in 111% higher total recapture rates than river releases (Gunnerød et al. 1988). Similar results were found in experiments performed in Iceland (Jonasson 1996).

Smolts often experience heavy predation in the estuary on their smolt migration. In the River Opløy, groups of hatchery-reared salmon smolts towed in net pens through the fjord from the estuary before release experienced a lower predation rate (0.9%) and higher recapture rate (3.3%) than smolts released in the river (predation 6.75%, 1.25% recapture) (Strand et al. 1996). Smolts released close to the river mouth survived better than smolts released higher up in the river (Hansen 1980, Hansen and Lea 1982, Staurnes et al. 1996). For instance, recapture rate of adults released as smolts in the upper part of the River Glomma, eastern Norway, was 0.8%, whereas recaptures from releases in the lower part of the River Glomma and in the River Ågårdselva (a tributary in the lower part of the River Glomma) were 3.8% and 2.5%, respectively (Hansen 1980). Releases in the upper part of rivers may delay the outward migration of smolts and reduce their survival (jfr. release time). Smolts released in the River Imsa, 1 km above the mouth, and in two lakes (3 km and 11 km) upstream of the mouth, showed that the downstream migration speed is dependent on release site (Hansen et al. 1984). Fifty per cent of the smolts released 1 km upstream were recaptured at the river mouth after 9 hours, whereas those released 3 and 11 km above were delayed for several days.

Site of release is important for successful homing in salmonids. In brown trout, hatchery-reared smolts released in fjords showed a decreased tendency to enter rivers than those released at river mouths (Jonsson et al. 1995). These results parallel findings from experiments with Atlantic salmon, indicating that learning during the outward smolt migration is critical for successful location of the home river during the return migration to fresh water. This appears to be a general feature of anadromous salmonids.

ERRATA

The errors in this number of Nordic J. Freshw. Res. are due to the incompatibilities between the software programs used when editing and when printing. We regret this deeply.

The arrows in Fig. 3. on page 132 should be as presented to the right.

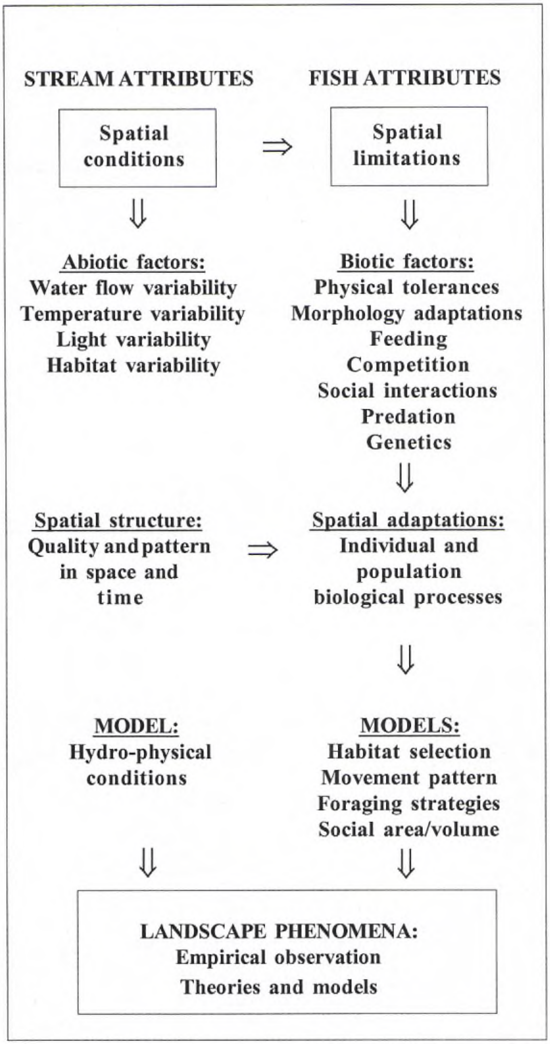

Fig. 3. Conceptual model for the fish habitat selection process. All processes may be scale dependent and variable in space and time.

Errors in symbols:

Page	column	line	written	should read
59	1	15	c^2	χ^2
59	2	20	c^2	χ^2
62	1	42,45	c^2	χ^2
80	2	30,38	c^2	χ^2
82	2	31,35,44	c^2	χ^2
83	1	5,7,9	c^2	χ^2

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Structure of the Crustacean Plankton in some Lakes in Northern Sweden when Influenced by Char Predation

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Abstract

Structuring effects of char on the coexisting zooplankton prey populations might have been expected when important environmental changes occurred in two districts in Northern Sweden. It is the resilience of the Daphnia galeata populations that is elucidated by the results of the present study.

The vertical distribution of D.galeata, with adult females in the upper strata in the daytime, has remained virtually the same in the lakes and lake reservoir in the Vålå district over nearly 50 years of changing lake ecology. This indicates the importance of the warmest possible water in the trade-off between the rate of development of eggs/embryos in the brood sacs and the reduced risk of predators in deeper water.

Resilience is also illustrated by the establishment of a D.galeata population in spite of intense predation by char in a shallow lake where the shelter possibilities were limited and not very much used. It is indicated that the establishment of this population was favoured by an abundance of alternative char food.

The pattern of patchiness in the lakes is mapped out. Patchiness in the microdistribution of D.galeata occurred at both low and high char densities and suggests swarming, but no actual swarming behaviour on the part of D.galeata is conclusively revealed in this material.

The material gave rise to the hypothesis that the microdistribution and depth distribution of Eubosmina longispina was influenced more by invertebrate predators than by fish in the districts studied.

The full version of this paper is published as a webpaper in http://www.fiskeriverket.se/publikationer/Finfo 2001:3.

Survival of brown trout released as smolt in rivers or fjords varies. For instance, survival of smolts released in the River Akerselva, southeastern Norway, and in the fjord outside the river (Oslofjorden) was highest when the fish was released in the river (Jonsson et al. 1995). In total, 20% of the fish were recaptured when released in the river and 12% and 17% when released in the inner and outer part of the fjord, respectively. However, survival of trout released as smolts in the River Drammen and in the Drammmen fjord were nearly the same (Jonsson et al. 1994c). The results of the trout-releases differed from experiments with Atlantic salmon in the same area, where the survival rates were higher when the fish were released at sea than in rivers and fjords (see references above). One reason may be that the habitats occupied at sea by the species differ. Atlantic salmon move rapidly through coastal waters into feeding areas in the high seas, whereas brown trout spend their entire sea-sojourn in fjords and coastal waters. Trout releases at sea may therefore have little effect on mortality, as they still spend the summer in the same habitat, not moving through like the Atlantic salmon.

Releases of hatchery-reared smolts into large shoals of migrating wild smolts appear to increase the survival to adulthood of the hatchery fish (Hvidsten and Johnsen 1993). Hansen and Jonsson (1985) argued that schooling behaviour in descending smolts might give protection against predators, as they also found that wild smolts joined the schools of hatchery fish during day time. Without dense schools of hatchery fish, wild fish moved downstream only at night.

The migratory behaviour of the fish is influenced by heredity. When sea ranched brown trout from populations naturally spawning upstream or downstream of a lake were released at the mouth of Imsa, a marked difference behaviour was observed (Jonsson et al. 1994d). The 2-year-old hatchery-reared progeny of outlet spawners from the Lake Tyrifjorden moved against the water current and ascended the river, whereas the inlet river fish from the same lake tended to migrate with the water current out to sea. This differential response to water current in juveniles appears to be due to inherited differences between the populations. Thus, inlet but not outlet spawning inland populations of brown trout is suitable for sea ranching purposes. There appears to be no problem that the population has been freshwater resident for several thousand years.

Size and age

In the hatchery, parr are reared under accelerated development regimes, producing large and young smolts. The size and age of the smolts influence the rate of descent in hatchery-reared fish. From wild Atlantic salmon and brown trout populations it is known that older and larger smolt migrate to sea before younger and smaller ones (Österdahl 1969, Jonsson et al. 1990, Bohlin et al. 1993, 1996). To test this in hatchery-reared fish, 1- and 2-years-old Atlantic salmon smolts were released in the River Imsa during middle of May (Hansen and Jonsson 1985). Most smolts descended during the first 12 h after release. Two-year old smolts descended faster and in a higher proportion, than 1-year-old smolt. Small 1-year-old smolt descended faster than larger 1-year-olds, whereas large 2-year-old smolt descended faster than smaller ones (Hansen and Jonsson 1985). Thus, the large 2-year-olds might be in the most advanced smolting stage, whereas several of the largest 1-year-old males might prepare for sexual maturation. In 2-year-old hatchery-reared brown trout Ugedal et al. (1998) found that the migration tendency increased with increasing fish size at release.

Older smolt survived better than younger ones. Releases of 1- and 2-year-old smolts of the same body size in the River Rana, Norway, showed higher recapture rates as grilse from the oldest smolt group (Hansen and Lea 1982). The recaptures were 56% of the 2-year-old smolts and 25% of the 1-year-olds. Similar results were found for brown trout. Recapture rates of brown trout smolts from 11 trout populations varied between 3-52% in 2-years-olds and between 1-8% in 1-year-olds (Jonsson et al. 1994b). Larger and older fish generally have better osmoregulatory capacity in seawater than smaller fish (e.g. Heifetz et al. 1989, Finstad and Ugedal 1998), due to their larger body volume relative to surface area (Parry 1960, Wagner et al. 1969). Moreover, the larger 2-year-old smolts may be less vulnerable to predation than their smaller and younger conspecifics (Dill 1983).

Sexual maturation

Thorpe (1987) suggests that the smolt migration is a response to adversity in the nursery stream. This view is based on findings indicating that high fat content of salmon parr leads to sexual maturation and residency (Rowe et al. 1991). This is the case in anadromous brown trout and Arctic charr, but to a lesser extent in Atlantic salmon (Jonsson 1985, Hansen et al. 1989d).

Within populations, the proportion of parr attaining sexual maturity is partly inherited, and consequently it differs between population and species (Fleming 1998). For instance, in the large River Alta, northern Norway, 2% of the parr males mature sexually before seaward migration (Heggberget 1989), whereas in small salmon rivers nearly all males may mature sexually before smolting (Ritter et al. 1986). In the small River Imsa, 14% of the downstream migrating smolt, exhibited enlarged gonads indicative of prior parr maturation (Jonsson et al. 1998b). In other anadromous salmonids, the proportion of mature parr that migrate may be smaller than that observed in Atlantic salmon. In Arctic charr, Nordeng (1983) observed a reduced smolting rate among mature parr. Also in brown trout, most mature parr seems to remature and become freshwater residents rather than smolting and migrating to sea (Jonsson 1985, Dellefors and Faremo 1988).

The migratory tendency also differs among species. In 2-year old hatchery-reared brown trout and Atlantic salmon smolts released in the River Halselva, northern Norway, 4% of the released brown trout and 74% of the Atlantic salmon smolts migrated downstream (Ugedal et al. 1998). This corresponds well with differences in life histories between these two species. Similarly, releases of hatchery-reared brown trout from several stocks in the River Akerselva showed that 23-53% of the various trout populations became migratory after release (Jonsson et al. 1995), i.e. a large proportion of the brown trout became freshwater resident after release in freshwater. It is an open question how the proportion of migratory trout may be increased.

Under the accelerated development regimes in hatcheries it is common to find high proportion of 1-and 2-year-old males maturing as parr (Leyzerovich 1973, Hansen et al. 1989d). In the following spring, after maturation, these males undergo morphological changes similar to those in immature smolting fish, and are treated as ready for release as emigrants, or ready for transfer to seawater farms. However, in Atlantic salmon parr, maturity appears to often inhibit downstream migration, although it does not prevent it completely (Hansen et al. 1989d). In release experiments with Atlantic salmon in the River Imsa immature Atlantic salmon migrated sooner and in significantly higher proportions than did previously mature males. Furthermore, at Lussa, Scotland, 5.6 and 5.9% of the smolting fish released in two separate years remained resident at the release site throughout the summer, and 91.8 and 93.4% of these matured in the autumn of release (Hansen et al. 1989d). Thus, mature male salmon parr which prepare for rematuration the subsequent autumn may become resident whereas those which rest from gonadal development during the previous year may smolt and migrate to sea.

It has been speculated that lowering the steroid level may decrease the frequency of rematuring fish. This may be done by (1) increased metabolism during the first winter after maturity or (2) stripping the fish and thereby mechanically decreasing the hormonal level. This hypothesis was tested by Berglund et al. (1991). They reared mature male parr in water with winter temperatures 4-9 °C above the ambient. This increased the degree of testicular resorption in previously mature male Atlantic salmon parr. Mature male parr maintained at a temperature of 9 °C over the ambient for 5 months showed an increase in hypoosmoregulatory ability when challenged in seawater at the time of smoltification whereas parr kept at elevated temperatures for various 2-month periods from January to April failed to show this improvement. Furthermore, previously mature males kept at an elevated winter water temperature for either 2 or 5 months showed a lower incidence of sexual maturation, and consequently a higher mean growth rate, after one summer in sea pens. A river release experiment showed that rearing previously mature males at 4-7 °C above the ambient water temperature from December to April increased the number of downstream migrating fish to a level similar to that of immature smolts (Berglund et al. 1991). However, water heating is expensive, and although the method works, it may not come into common use because of the economic costs involved. As a less costly alternative, the mature gonads of the parr males can be stripped in the autumn. This reduce residency and increases the frequency of smolting fish (Hansen et al. 1989d).

Water quality

Atlantic salmon are more sensitive to acid water than other naturally occurring salmonids in Scandinavia (Rosseland and Skogheim 1984, Exley and Phillips 1988), and the smolts are especially sensitive (Staurnes et al. 1993a, Kroglund and Staurnes 1999).

Experiments with hatchery-reared Atlantic salmon smolt in Norway show that short term exposure to acid water before release impairs osmoregulation, seawater tolerance and marine survival (Staurnes et al. 1996, Finstad et al. 1999). Even concentrations as low as 10-20 mg l^{-1} inorganic aluminium may reduce gill Na^+-, K^+ - ATP-ase activity and therefore reduce seawater tolerance of smolts. Smolts exposed to acid water in rivers will suffer from osmoregulatory failure and high mortality after entering the sea. Simple physiological tests will reveal whether smolts used for stocking will survive in seawater or not. A better understanding of the causes for mortality in acid water is important if one would predict effects of changes in water quality (Rosseland and Staurnes 1994).

In Norway, limestone has been used to improve water quality in hatcheries since the 1920s, and liming is most frequently employed for amelioration of acidified waters (Exley and Phillips 1988). Liming of water in hatcheries is difficult because of the fact that there must be no disruption of the water supply and that the water quality must be optimal, especially in the smoltification period. Several treatments have been used such as crushed lime, limestone, shellsand, limeslurry, seawater and silica (Staurnes et al. 1998). Following liming, the pH is raised instantaneously, but Al, the other toxic component in most lakes acidified by acid rain, can maintain its toxic action over a period of time. In mixing zones between acid Al rich water and non-acidified water, Al detoxifies slowly and can increase its toxicity for a short time (Kroglund et al. 2000 and references therein). In water treatments of this kind it is therefore very important that the residence time between water treatment and the rearing tanks is long enough in order to avoid the unstable forms of aluminium (Staurnes et al. 1998).

Another aspect is rearing of smolts in high densities that may affect the quality of fish (Söderberg et al. 1993, Banks 1994). As a generally rule, densities up to 40 kg fish m^{-3} is recommended for smolt production. However, at such densities, operating accidents quickly can lead to oxygen debt in the tanks and eventually lead to fish mortality. Banks (1994) reared four broods of spring chinook salmon (*Oncorhynchus tshawytscha*) in raceways in a year-round coldwater hatchery at three densities and at three levels of water inflow. During hatchery rearing, increased density and decreased water flow were related to increased fingerling mortality from bacterial kidney disease (*Renibacterium salmoninarum*). The physiological performance was also suppressed in this group at release. However, increased raceway water flow seemed to increase adult contribution.

Discharge

Water discharge or variables correlated with discharge such as current velocity or the turbidity of the water, may also influence survival of released smolts. Releases of hatchery-reared smolts at high water discharge during the normal migratory period have increased the smolt survival in the River Gaula and Surna (Hvidsten and Hansen 1988). This has also been observed in rivers in Maine, USA (Hosmer et al. 1979). Thus, if possible, the fish should be released during periods of high water discharge. Presently, it is not known why high water discharges are preferable, but one might hypothesise that this is caused by decreased exposure to predators. A high flow rate increases the speed of outward migration fish in the river and possible in the fjord (Jonsson 1991). Turbid water due to high flow or water levels may shelter the fish from predation.

Seawater acclimatization

Seawater acclimatization may speed up the ability of the smolts to regulate the ionic concentration of their body fluid before release and increase seawater tolerance (Staurnes and Finstad 2000). However, seawater acclimatization of Atlantic salmon smolts seems to have little or no effect on the survival and the lack of effect on salmon may be due to their greater degree of salinity tolerance that develops during smolting (McCormick 1994). Smolts acclimated to brackish and salt water for 2 weeks and longer were released outside the River Imsa (Hansen and Jonsson 1986). There were no significant differences in survival (recapture rate) between smolts kept in brackish or salt water for 2 weeks compared with the control groups. However, the recapture rate of smolts kept 4 weeks or longer in brackish or salt water decreased significantly compared with the control groups. Moreover, monthly releases of seawater acclimated smolts and post-smolts at Ims indicated that sea survival was highest for those released in May, at the same time as the wild smolt migrated to sea. Sea survival decreased rapidly for those released after being retained in sea pens for more than 1 month after smolting (Hansen and Jonsson 1989a). Thus for this species, there appears to be a survival window which is open in spring but starts to close after approximately one month (McCormick et al. 1998). When moving to sea in winter, the survival is very low.

In brown trout and Arctic charr, however, seawater acclimatization appears to increase the survival at sea (Jonsson et al. 1994a, Staurnes and Finstad 2000). Jonsson et al. (1994a) found that smolts retained 4 and 8 weeks in seawater before release had higher total recapture rates than controls. As mentioned earlier this might be an effect of increased body size. The fish stay in the same coastal area until return to fresh water, and when entering later may escape some predation. The effects of delays on the survival of the Atlantic salmon may be different because this species moves long distances and arrives later at the feeding and winter areas at sea. This is, however, a little investigated area, and our contention is not currently supported by experimental results.

Physical training

The effects of exercise training on teleost fish have proven to be positive for survival and growth (Davison 1997). One might hypothesize that exercise would improve the performance of sea ranched fish because of the positive effects measured in hatcheries (Jørgensen and Jobling 1993). Training increases aerobic potentials in red and white muscles and improves heart performance. Oxygen-carrying capacity of the blood is increased, allowing more blood to be directed towards the gut. Exercise, however, did not appear to lead to improvement of the osmoregulatory capacity of fish undergoing parr-smolt transformation, and so far it has not indicated improved return rates of hatchery-reared fish (Skilbrei and Holm 1998). The only observed effect was that unexercised parr strayed more as adults than did exercised fish.

Handling, transport and use of anaesthesia

Handling, transport and use of anaesthesia are known to stress salmonid smolts before release (Soivio et al. 1977, Barton et al. 1980, Pickering et al. 1982, Iwama et al. 1997), and reduce their survival. It has also been shown that Atlantic salmon smolts are more responsive to stress than parr and that development differences are more important than seasonal changes (Carey and McCormick 1998). Hansen and Jonsson (1988) studied the effect of handling and transport on the survival of 1- and 2-year-old Atlantic salmon smolts. They found that dip-netting and transport by truck reduced the survival (counted as return rates) of 1- but not 2-year-old smolts. In 1-year-old smolt, the survival after dip-netting was 1.6% compared to 3.3% in the control groups. Adding an additional transport stress lasting 4 h gave similar results. The corresponding values were 1.8% and 7.7%. However, handling and chlorobutanol anaesthesia immediately before release reduced the survival of both smolt ages: the survival rate of stressed 2-year-old smolts was 0.3% (control group 2.3%) compared to 2.6% for 1-year-olds (control group 7.7%).

It has been shown that even 48 hours after transport the plasma-cortisol level of the fish had not returned to the resting level, which prior to transport (Finstad and Iversen 1997). With chinook salmon (*Oncorhynchus tshawytscha*) parr the plasma-cortisol level was found to peak 3.5 hours after dip netting, whereupon it returned to normal values after approximately 12 hours (Robertson et al. 1987). Other experiments have shown longer or shorter "recovery" periods (Carmichael 1984). It has been shown earlier that when under stress the fish will acquire osmoregulatory problems both in fresh water and sea water (Eddy 1981, Redding and Schreck 1983, Finstad and Iversen 1997). Optimal release methods using recovery tanks, brackish water and anaesthethics such as methomidate have a more moderate stress response and better recaptures (Iversen et al. 1998, Strand and Finstad 2000). Use of improved releasing methods could lead to a more efficient line from production of smolts to recaptures of adult fish in rivers and at sea. Acclimatization of fish before release, after handling and transport, increases the number and size at recapture in brown trout (Jonssonn et al. 1999). Increased recapture rate was also found in Atlantic salmon given a week rest after transport as compared with fish released directly into the River Alta (Strand and Finstad 2000).

Seasonal return pattern

Seasonal return patterns of salmonids are partly under genetic control (Ricker 1972, Bams 1976, Saunders 1981, Hansen and Jonsson 1991a). Atlantic salmon in small rivers usually have only late autumn runs, probably because of low water flow during most summers (Jonsson et al. 1990). Early summer runs are usually found in large rivers, often with lakes and pools providing refuges for adult fish during dry summers (Saunders 1981). Hansen and Jonsson (1991b) released hatchery-reared smolts, originating from a population known to return as adults to the home stream early in the season, and smolt from a population known to return to the home river late in the autumn. Both stocks were released at the mouth of the River Imsa. Adults from the early homing stock return to coastal Norway earlier than adults from the late returning stock. This indicates that the two stocks are not genetically identical in migratory timing. To secure successful homing and upstream migration of adults, it is preferable to rear the smolts from broodstocks captured in the river where the smolts will be released.

Marine survival of hatchery-reared Atlantic salmon populations appear to differ with respect to post-smolt growth (Friedland et al. 1996). Releases of smolts from the Penobscot and Connecticut stocks, in North America, exhibited different return rates for one-sea-winter and two-sea-winter salmon, with the Penobscot stock being higher. The results suggest that post-smolt growth may influence age at maturity and survival patterns for Atlantic salmon stocks.

Stock reducing factors - predation and parasites

Smolts and post-smolts are subjected to heavy mortality in rivers, estuaries and fjords due to predation by different animals. Important predators are fish such as burbot (*Lota lota*) and pike (*Esox lucius*) in freshwater and Atlantic cod (*Gadhus morhua*), saithe (*Pollachius virens*) and pollack (*Pollachius pollachius*) at sea (Hvidsten and Møkkelgjerd 1987, Hvidsten and Lund 1988, Jepsen et al. 1998) and birds such as gulls (*Larus sp.*), cormorants (*Phalacrocorax carbo*) and mergansers (*Mergus merganser*) (Reitan et al. 1987, Kålås et al. 1993, Dieperink 1994, Lekuona and Campos 1997). There may be major differences between localities regarding types and numbers of predators. In the estuaries of the rivers Orkla and Surna, Atlantic cod ate 20-25% of the downstream migrating hatchery-reared salmon smolts during the first week after release. The predation from saithe was estimated at 12.5% (Hvidsten and Møkkelgjerd 1987, Hvidsten and Lund 1988). Bird predation appeared important in the estuary of the River Opløy and greater than that from fish (Strand et al. 1992, 1993). In total, 2.5% of the smolts were eaten by gulls and 0.1-0.7% were eaten by cod. Predation of downstream migrating salmonid smolts (50 radio-tagged salmon and 24 trout) as in Lake Tange, a 12 km long, shallow reservoir, showed that the most important predator was pike, 56% of the observed mortality (Jepsen et al. 1998). Avian predators were assumed to be responsible for 31% of the observed mortality. Another study by Lyse et al. (1998) showed that schooling of sea trout post-smolts acted as a defence against predators in the littoral zone where trout could avoid fast swimming predators such as fish and seals and attacks from gulls. As pointed out by Järvi (1989; 1990) and Handeland et al. (1996), the increase in mortality rate of Atlantic salmon smolts when entering the estuary did not induce any lethal stress, but in conjunction with predator-stress there was a synergistic effect, leading to an increase in the mortality. Normally smolts shoal when exposed to predators, but when in the same situation added physiological stress, they shoal to a much lesser extent and are more vulnerable for predation.

Salmon lice (*Lepeophtheirus salmonis*) are known to infest salmonids, create physiological disturbances and finally lead to death of these species (Bjørn & Finstad 1997, Pike and Wadsworth 1999, Finstad et al. 1999, Bjørn et al. 2000, Finstad et al. 2000b). Releases of salmon lice protected Atlantic salmon and sea trout smolts (chemical bath treatment - up to 16 weeks protection against salmon lice) in areas with heavy fish farming activity have resulted in higher recaptures (0.90%) compared to unprotected fish (0.03%) (Finstad et al. 1999).

Recaptures

In Norway, hydropower regulation has led to increasing numbers of hatcheries producing Atlantic salmon and sea trout smolts since the early 1950's in order to compensate for the lower production of salmonids in regulated rivers. Atlantic salmon, sea trout and Arctic charr have also been released for sea ranching in Norwegian rivers (Table 1).

Due to differences in production strategies in the hatcheries leading to a various smolt quality it is difficult to generalize a conclusion from these results. For Atlantic salmon recaptures have varied between 0-19%, but more commonly recaptures have been in the range of 0.5 to 2.5%. Releases of sea trout have given recaptures up to 53%, but more commonly these releases have had an average recapture of 10-15% (Jonsson et al. 1994b, 1995, Finstad and Ugedal 1998). Releases of Arctic charr have given recaptures up to 46% with an average recapture at 10-15% (Finstad and Heggberget 1993, 1995).

Yield of smolt releases

The yield of smolts released varies between rivers, stocks, years, age of smolts released and species. At the mouth of the River Imsa 12 different stocks of 1- and 2-year-old Atlantic salmon smolts were released during 1981-1984 (Hansen and Jonsson 1989b). The 2-year-olds gave a higher yield of adult salmon than 1-year-old smolts. In the releases at Ims, the total yield of the 2-year-old smolts varied between 125 and 1,050 kg per 1,000 smolts released. Fourteen of 21 groups released gave total yields higher than 250 kg per 1,000 smolts released, and were higher than the economic break-even yield. The total yield of 1-year-old smolts varied between 25 and 1,260 kg

Table 1. Releases of smolts of Atlantic salmon (A.s.), sea trout (S.t.) and Arctic charr (A.c.) in Norwegian rivers during 1959-1999. Years of release, numbers of fish released, recapture rate and references are given.

River	Species	Years of release	Numbers released	Recapture rate (%)	References
Akerselva	A.s.	1985	1,928	9.0-19.1	Hansen and Jonsson 1990
		1987	2,905	7.1-8.9	
Altaelva	A.s.	1978-90	33,646	0.6	Hvidsten et al. 1994
Altaelva	A.s.	1986-90	51,098	0.00-2.1	Saksgård et al. 1992
Altaelva	A.s.	1995-99	44,613	0.02-1.1	Strand and Finstad 2000
Audna/Lygna	A.s.	1986-92	36,817	2.8-5.0	Hansen et al. 1997
Drammenselva	A.s.	1984-86	6,865	1.5-3.9	Hansen 1990
Drammenselva	A.s.	1990- 94	27,458	0.2-4.1	Hansen et al. 1996
Eira	A.s.	1959-80		0.85-1.6	Møkkelgjerd and Jensen 1987
Eira	A.s.	1987-90	44,381	0.07-0.8	Jakobsen et al. 1992
Eira	A.s.	1992-99	5,982	0.0-0.3	Saksgård et al. 1999
Figgjo	A.s.	1965-94	35,911	0.3-13.0	Hansen and Friedland 1994
Gaula	A.s.	1978-90	19,399	4.3	Hvidsten et al. 1994
Gaula	A.s.	1980-88	17,331	2.6-7.6	Hansen 1993
Glomma	A.s.	1963-71	16,860	0.8-3.8	Hansen 1980
Imsa	A.s.	1981	34,032	0.2-11.6	Hansen and Jonsson 1986
Ingdalselva	A.s.	1986	10,784	0.3-1.6	Staurnes et al. 1993b
Mandalselva	A.s.	1968-69	1,999	4.5	Hansen 1982
Mandalselva	A.s.	1996-97	8,000		Johnsen et al. 1999
Nidelva	A.s.	1980-88	17,722	0.1-7.4	Hansen 1993
Opløyelva	A.s.	1989-96	158,567	0.03-6.4	Strand et al. 1996
Orkla	A.s.	1978-90	25,696	2.7	Hvidsten et al. 1994
Rana	A.s.	1970-74	18,592	0.0-5.6	Hansen and Lea 1982
Suldalslågen	A.s.	1996-99	75,000	0.0-0.3	Finstad et al. 2000a
Surna	A.s.	1973- 83	36,388	1.2-6.5	Gunnerød et al. 1988
Tovdalselva	A.s.	1996-97	8,000	-	Johnsen et al. 1999
Vefsna	A.s.	1992-95	58,310	0.0-3.4	Johnsen and Jensen 1997
Vefsna*	A.s.	1987-95	10,512	0.0-9.3	Johnsen and Jensen 1997
Vefsna	A.s.	1966-89	13,066	0.4-6.0	Johnsen and Jensen 1997
Åna-Sira	A.s	1969	1,000	0.0	Hansen 1982
Aurlandselva	S.t	1990-92	24,000	0.7-1.4	Jensen et al. 1993
Imsa	S.t	1983-89	23,050	1.1-52.5	Jonsson et al 1994b
Halselva	S.t.	1997-98	7,000	4.6-17.8	Finstad and Ugedal 1998
Halselva	A.c.	1988-93	70,798	1.2-46	Finstad and Heggberget 1993, 1995

*tagged with smolts

per 1,000 released smolts, and only in 3 of 8 releases the yields exceeded the economical break-even of 200 kg per 1,000 smolts released. Of the 1-years-olds the River Figga salmon (1- and 2-sea-winter fish) gave highest estimated yield, whereas of the 2-years-olds, the River Årøy (a multi-sea-winter-fish) was highest. Furthermore, releases of 1- and 2-year-old salmon smolt in the River Akerselva, eastern Norway, gave yields per 1,000 smolt released between 77.5 and 138.4 kg (Hansen and Jonsson 1990). According to the authors these figures are gross underestimates when taking tagging and handling mortality and non-reported tags into consideration.

To be profitable, the recapture rate of Atlantic salmon should be 10% or more, according to analysis by Moksness et al. (1998). They based their estimations on the use of 2-year-old smolts. Higher yields of 2- than 1-year-old smolts have been reported by e.g. Hansen and Lea (1982). In the River Rana, northern Norway, yields of 2-year-old smolts were 302 kg per 1,000 released smolts (Hansen and Lea 1982). The corresponding value for 1-year-old smolts was 197 kg. Higher yields of 2-year-old smolt may be partly due to the larger size of the 2-year-old than 1-year-olds. But even between smolt groups with the same body size, the 2-year-olds survive better than the 1-year olds (Hansen and Lea 1982).

The yields of smolts releases also differ among stocks and rivers. This may be partly due to the proportion of one- and multi-sea-winter salmon returning to the rivers (Jonsson et al. 1991). In large rivers the proportion of multi-sea winter salmon are higher than in small rivers. The mortality rate has been higher for multi-sea-winter than one-sea-winter salmon, because they stay for a longer time at sea before returning to freshwater as sexual mature fish. In addition, the marine harvest has been higher for multi-sea-winter than for one-sea-winter. For instance, the long-line fishery in the Norwegian Sea has mainly caught salmon during their second and third winter at sea (Hansen and Jonsson 1989b). This fishing is now almost closed.

Estimated yields of released brown trout smolts were higher for 2- than 1-year-old fish, although the recapture rates varied between years of release and stocks (Jonsson et al. 1994b). Estimated yields of 11 stocks released ranged from 2 to 20 kg per 1,000 released 1-year-old fish and between 11 and 250 kg per 1,000 released 2-year-old fish. Of 1-year-old fish the Emån stock gave the highest yield and of 2-year-olds the Emån (anadromous population) and Tunhovd (originally freshwater resident) stocks were at the top of the list (240 and 250 kg, respectively). In all cases, yields were lower than the economic break-even yield. Most of the fish were recaptured the year of release (89% of 2-year-olds and 76% of 1-year-olds), so the size of the fish was small.

In Arctic charr, present releases of 1- and 2-year-old smolts for commercial sea ranching purposes will not be economically profitable (Moksness et al. 1998). When 1-year-old smolts were released, the yield was positive when the cost of juveniles was lower than 0.5 US$ per fish and the recapture rate higher than 20%. With a cost of 1.04 US$ per juvenile charr, only a recapture rate above 40% will give positive yields. When 300 g fish were released, the economic break even point equalled a recapture rate of 30%.

Conclusion

Releases of salmonid fry and smolts in freshwater will only enhance stocks when recruitment rate is below the carrying capacity of the river. At sea, density independent mortality factors appear and the mean number of returning fish will increase with the number of the released smolts.

Use of natural light and temperature conditions are essential for producing a smolt that can be released at the natural smolt migration time for the actual river. Normal migration time reflects local environmental conditions and deviation between optimal smolting time of the reared fish and the natural migration time of wild smolts of the river lead to lower yield. This may be caused both by lower survival and growth rate, but also larger straying rate. Learning during outward migration is critical for successful homing.

Larger and older smolts generally have better return rates than younger and smaller ones. However, it is common to find a higher proportion of males maturing under accelerated development regimes in hatcheries than in the wild populations. In Atlantic salmon, maturity appears to inhibit downstream migration although it does not prevent it completely.

Release during high water discharge seems to give increased survival of released smolts. Atlantic salmon are more sensitive to acid water than other naturally occurring salmonids in Scandinavia and the smolt stage is generally the most sensitive stage.

Seawater acclimatization of Atlantic salmon smolts seems to have no effect on recapture rate. However, in sea trout and Arctic charr, seawater acclimatization appears to increase the survival in sea.

Transport and handling stress reduces survival after release of smolts. However, new release methods using recovery tanks, brackish water and anaesthetics have shown to greatly reduce these negative effects.

Smolts and postsmolts are subjected to heavy mortality in rivers, estuaries and fjord systems due to predation of both fish and birds. Salmon lice may cause mortality in post smolts. Recent experiments with release of salmon lice protected salmon and sea trout smolts have given better recapture rates compared to unprotected fish.

Recaptures of Atlantic salmon varies between 0-19%, but more commonly rates are 0.5-2.5%. Releases of sea trout have given recaptures up to 53%, but 10-15% are more common. Arctic charr recaptures up to 46% are found while rates of 10-15% are more common. The yield of smolt releases varies between species, rivers, stocks year-classes and age of the smolts released. The yields are higher for 2-year-old smolt than 1-year-old smolts, and higher in Atlantic salmon than brown trout and Arctic charr.

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Implications of Stocking: Ecological Interactions Between Wild and Released Salmonids

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Abstract

The common management practice of introducing artificially produced fish into wild populations has raised concerns among fishery biologists. In part, these concerns arise from the observation that hatchery-produced fish commonly differ from wild fish in ways that may influence ecological interactions between them. In this review, we use a meta-analytical approach to provide quantitative tests for such differences and show that the hatchery rearing of salmonids results in increased pre-adult aggression, decreased response to predators, and decreased survival. Changes in growth rates are common, but less consistent. Changes in other fitness-related traits such as migration, feeding, habitat use and morphology also occur. Based on the presented evidence we conclude that differences between hatchery-reared and wild fish may have negative implications for the success of stocking programs. A number of studies reporting population responses to stocking support this, suggesting that the performance of hatchery fish and their interactions with wild fish is of such a character that many of the current stocking practices may be detrimental to the recipient population.

Keywords: hatchery releases, competition, predation, survival, growth.

Introduction

Deliberate releases of artificially produced fish into wild populations have recently caused concern among fishery biologists (e.g. Hindar et al. 1991, Saunders 1991, Waples 1991, Thomas and Mathisen 1993, Ryman et al. 1995, Youngson and Verspoor 1998). Although such releases are often implemented to compensate for reduced production caused by human induced habitat degradation, a range of potential ecological problems may be associated with this practice. First, stocking of large numbers of fish into a limited habitat will inevitably affect population density, at least initially. Thus, any density-dependent characteristics of the environment or of the fish itself are potentially affected (cf. Elliott 1989, 1990). This numerical effect of stocking could, for example, include changes in the frequency of competitive interactions, levels of food availability, or a functional response of predators, and hence influence growth and survival of the wild fish. Theoretical considerations suggest that this may cause hatchery releases to increase temporal variability of population strength (Fagen and Smoker 1989). Second, hatchery fish may differ genetically and/or phenotypically from wild fish. Such differences may affect how stocked and wild fish interact, and thus cause effects of stocking beyond those due to pure density-dependence.

Here we review the literature dealing with such effects in salmonids, summarising what is known about differences between hatchery- and wild-reared fish, and the implications these differences have for ecological interactions between the two types of fish. Literature data are used to examine whether the predicted effects of differences between the two types of fish have been observed in the wild. We also identify areas where research is needed to increase our knowledge about ecological interactions between hatchery and wild fish, and to establish better management practices.

Why do hatchery and wild fish differ?

Fish reared in hatchery facilities may differ from their wild conspecifics for three reasons. First, fish are highly phenotypically plastic and therefore their phenotypes may be shaped considerably by the rearing environment (e.g. Wootton 1994, Pakkasmaa 2000). The traditional way of rearing fish in hatcheries (i.e. high densities in flow-through tanks) shows little or no resemblance to natural rearing. In fact, most environmental characteristics that may influence fish development differ. This includes feeding regimes, density, substrate, exposure to predators, and interactions with conspecifics. It is not surprising that such differences can have substantial impacts on the resulting fish phenotype.

The second reason why hatchery fish may differ from wild fish is that the intensity and direction of selection differs between the two environments. Perhaps most importantly, survival during egg and juvenile stages is substantially higher in the hatchery environment than in the wild (reviewed by Jonsson and Fleming 1993). This means that genotypes that potentially are eradicated in the wild, by predation or starvation, are artificially brought through the vulnerable period of selection during early juvenile stages (Elliott 1989, Einum and Fleming 2000a, b). In theory, hatchery fish could also experience altered selection pressures. For example, the high juvenile density and abundance of food may select for behavioural and physiological traits that are disadvantageous in nature. The importance of such altered selection is unknown, but the intensity of selection may be limited due to the low levels of mortality. However, this may not necessarily be so, if traits such as body size attained in the hatchery are tightly linked to survival after release, a period of intense mortality among hatchery fish. Such genetic changes due to relaxed and/or altered selection are likely to accumulate in stocks being cultured over multiple generations (e.g., when brood stock is consistently chosen from adults originating from hatchery produced smolts). Multi-generation hatchery stocks are thus likely to differ more from wild fish than first generation stocks where most of the changes are likely to be of environmental origin.

The third reason why hatchery fish may differ from wild fish is the use of non-native fish for stocking. Such procedures may introduce novel, genetically based characters into the wild population and break up co-adapted gene complexes that may lead to outbreeding depression (e.g. Gharrett and Smoker 1991). Fortunately, the potential importance of local adaptations is being increasingly acknowledged (reviewed by Ricker 1972, Taylor 1991), and the practice of releasing non-native fish has therefore decreased in frequency.

Intentional artificial selection may also generate genetic change in hatchery populations, as has occurred with commercially farmed fish (Einum and Fleming 1997, Fleming and Einum 1997). However, such selection is rarely performed in any systematic way in non-commercial hatcheries. Thus, studies reporting differences caused by such selection have been omitted in this review.

Studies of differences between hatchery and wild fish take three forms. (1) The most common form simply documents the existence of differences and speculates about their origins. More detailed studies attempt to identify (2) the environmental and/or (3) genetic origins of the differences. The first form of study usually compares fish hatched and reared in the hatchery with fish from the wild, and while the differences observed likely have an environmental component, additional effects due to genetic differences may ex-

Table 1. Differences in pre-adult aggression and response to predators between wild and hatchery populations of salmonids. Pos = hatchery population more aggressive, Neg = hatchery population less aggressive/ lower response to predators, 0 = no significant difference. E = predominantly environmental, G = predominantly genetic, E > G = likely predominantly environmental.

Trait	Origin of effect	Form of effect	Fish	Species	Reference
Aggression	E	Pos	Native	Coho salmon	Rhodes and Quinn 1998
	E > G	Pos	Non-native	Atlantic salmon	Fenderson et al. 1968[1]
	E > G	Pos	Non-native	Cutthroat trout	Mesa 1991
	G	Neg	Non-native	Atlantic salmon	Norman 1987
	G	Pos	Non-native	Brook trout	Moyle 1969[2]
	G	0	Native	Brown trout	Johnsson et al. 1996[3]
	G	Pos	Non-native	Coho salmon	Swain and Riddell 1990[4]
	G	Pos/Neg*	Native	Rainbow trout	Berejikian et al. 1996[5]
	G	0	Non-native	Masu salmon	Reinhardt in press[6]
Predation	E	Neg	Native	Brown trout	Dellefors and Johnsson 1995[6]
	G	Neg	Native	Brown trout	Johnsson et al. 1996[2]
	G	Neg	Non-native	Rainbow trout	Johnsson and Abrahams 1991[2]
	G	Neg	Native	Rainbow trout	Berejikian 1995[7]
	G	Neg	Native	Brown trout	Fernö and Järvi 1998[2, 8]

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*Direction depended on age.

Comments regarding usage of data in meta-analysis:

[1] *P*-value was calculated from data.

[2] *P*-value, given as < 0.05 or just "statistically significant", was set to 0.05.

[3] *P*-value, given as > 0.6, was set to 0.61.

[4] Separate statistics were given for each of seven days of observations. Each of the *P*-values (range 0.9 - 0.001) was treated as independent.

[5] Separate statistics were given for each of three juvenile ages. These *P*-values were treated as independent.

[6] No statistics or raw data were available for inclusion of study.

[7] Separate statistics were given for two different test-environments. The two *P*-values were treated as independent.

[8] *P*-value for difference in "fleeing" was used.

ist. Tests for environmental effects compare fish, of a common origin, reared in a hatchery with those reared in the wild. By contrast, tests for genetic effects compare hatchery and wild fish reared from eggs in a common environment.

Because tests of differences are usually conducted under artificial hatchery conditions, their value for predicting effects of interactions in the wild may be somewhat limited. This may be particularly problematic if genotype/phenotype by environment interactions exist, whereby the relative expression of traits between the two types of fish differs among environments. Some studies try to control for such interactions by conducting tests under differing environments (e.g., hatchery and wild), yet most studies do not. Any lack of correspondence between hatchery tests and data from the wild, therefore, may be partly attributable to this problem.

Which characters differ?

Ecological interactions among fish are an outcome of their behavioural traits. Thus, knowledge about behavioural differences between hatchery and wild populations is vital to understanding the potential impact from released fish. A substantial body of data that tests for such differences exists. These studies suggest that hatchery fish differ from wild fish in levels of aggression and predator avoidance behaviour (Table 1). In most studies, the effect of artificial rearing appears to result in an increase in levels of aggression (5 out of 9 studies). If we combine the probability values from the separate significance tests of the independent data sets (a meta-analytical approach described in Sokal and Rohlf (1981), p. 779; data handling described in footnotes to Table 1) these support the hypothesis that hatchery fish exhibit increased levels of aggression relative to wild fish ($c^2 = 85.75$, df = 30, $P < 0.001$).

Only in one study were the offspring from the wild population more aggressive than those from the hatchery population, and in this case, the hatchery population was of non-native origin (Norman 1987). Thus, population-specific levels of aggression rather than effects of hatchery-rearing may be responsible for the result (e.g. Taylor 1988, Swain and Holtby 1989, Einum and Fleming 1997). Finally, in one study the direction of the difference depended on the age of the fish, with wild fish being more aggressive at emergence, and hatchery fish being more aggressive after 105 days of rearing (Berejikian et al. 1996). In the three studies where the origin of the difference was predominantly environmental, hatchery fish were consistently more aggressive than wild fish. The less consistent results appear in those studies where the difference was genetic. There has been some debate as to whether artificial selection in fish causes an increase or a decrease in levels of aggression. Both theoretical and empirical studies suggest that the direction of selection during artificial rearing may depend on the environment (Doyle and Talbot 1986, Ruzzante and Doyle 1991). Although these studies have focused on situations where there is intentional selection for rapid juvenile growth, and thus may not be directly applicable to most hatcheries producing fish for stocking of wild populations, they suggest that a correlated increase in aggression only will result if food is limited. Thus, if the environment to which fish are exposed differs among hatchery stocks this may influence the direction of evolutionary divergence of social behaviour away from that of wild fish. Nevertheless, increased aggression may evolve as a correlated response to selection for rapid growth, if such selection occurs (cf. Johnsson et al. 1996). Furthermore, evidence from guppies suggests that levels of aggression may be negatively correlated with predation rates (Endler 1995). Thus, if hatchery populations are less exposed to predators, phenotypic or genetic correlations may cause increased aggression as well. Tightly controlled experiments are needed to further elucidate the causal relations between feeding, growth, body size, aggression and dominance under various selective regimes.

Hatchery populations do differ from wild fish in levels of anti-predator behaviour (combined probabilites $c^2 = 37.63$, df = 10, $P < 0.001$). The lack of exposure to predators in hatchery populations appears to result in a reduced response to predation risk, both as an environmental effect and as a response to relaxed selection in hatchery populations (Table 1).

One intriguing feature of anadromous salmonids is their long distance migrations to feeding and breeding areas. As well as being energetically costly, such migrations potentially increase predation risk. Selection is therefore expected to mould patterns of movement to optimise fitness. It is therefore worrying that migration patterns of hatchery-reared fish often differ from those of wild fish (Table 2). For example, hatchery fish are observed to differ from wild fish in their timing of migration, which may influence both their susceptibility to predation and their energetic costs (i.e. due to different temperature and flow regimes). If this effect on timing of migration also influences breeding time, offspring survival may be compromised due to inappropriate emergence timing from nests (Einum and Fleming 2000b).

Hatchery populations may also differ from wild populations in feeding behaviour and habitat use (Table 3). However, results regarding such effects are more equivocal, potentially reflecting a time

Table 2. Movement patterns of pre-adults from hatchery populations of salmonids. E = predominantly environmental, G = predominantly genetic, E + G = both environmental and genetic effects potentially important, E > G = likely predominantly environmental, G > E = likely predominantly genetic.

Origin of effect	Observations	Fish Origin	Species	Reference
E	Stay longer in sea.	Native	Arctic char	Finstad and Heggberget 1993
E	Extended period of smolting.	Native	Atlantic salmon	Hansen 1987
E	Differences in timing of recapture of hatchery and wild fish in coastal net fishery.	Native	Atlantic salmon	Potter and Russell 1994
E	Use same oceanic areas as wild fish.	Native	Atlantic salmon	Hansen and Jonsson 1991, Hansen 1988
E	Similar oceanic migration patterns.	Native	Atlantic salmon	Jonsson et al. 1990
E	Wild fry resided in estuary longer than hatchery fish.	Native	Chinook salmon	Levings et al. 1986
E + G	Juveniles enter estuary earlier than natural produced fry. Long-term change in mean date of entry of adult fish after hatchery program initiated.	Native	Chum salmon	Lannan 1980
E + G	Earlier returns of adult fish to rivers in stocked streams.	Non-native	Coho salmon	Nickelson et al. 1986
E > G	Move more within stream.	Non-native	Brown trout	Bachman 1984
G	Low stamina during swim trials.	Non-native	Brook trout	Green 1964
G	Juveniles stay higher in water column.	Non-native	Brook trout	Moyle 1969
G	Juveniles tamer, surface oriented and lower stamina during swim tests.	Non-native	Brook trout	Vincent 1960
G	Juveniles stay higher in water column.	Non-native	Masu salmon	Reinhardt in press
G > E	Distance transferred from natal stream negatively related to recovery rate for hatchery reared fish.	Non-native	Coho salmon	Reisenbichler 1988

Table 3. Pre-adult feeding, habitat use and morphology of hatchery populations compared to wild fish. E = predominantly environmental, G = predominantly genetic, E + G = both environmental and genetic effects potentially important, E > G = likely predominantly environmental, G > E = likely predominantly genetic.

Trait	Origin of effect	Observations	Fish Origin	Species	Reference
Feeding	E	Different diet.	Native	Atlantic salmon	Reiriz et al. 1998
	E	Lower total consumption and feeding efficiency of live prey.	Native	Brown trout	Sundström and Johnsson in press
	E > G	Reduced feeding and diet width.	Native and non-native	Atlantic salmon	Sosiak et al. 1979
	E > G	Low feeding rate.	Non-native	Atlantic salmon	Fenderson et al. 1968
	E > G	Different diet initially, similar later.	Native and non-native	Brown trout	L'Abée-Lund and Langeland 1995
	E > G	Reduced feeding.	Non-native	Brown trout	Bachman 1984
	E > G	Different diet initially, similar later.	Non-native	Brown trout	Johnsen and Ugedal 1986, 1989, 1990
	G	Similar diet.	Non-native	Brook trout	Lachance and Magnan 1990a
Habitat use	E > G	No difference in habitat.	Non-native	Brown trout	Greenberg 1992
	E > G	Different habitat.	Non-native	Cutthroat trout	Mesa 1991
	G	Similar habitat.	Non-native	Brook trout	Lachance and Magnan 1990a
	G > E	Non-native use different habitat in lake.	Native and non-native	Brown trout	Hesthagen et al. 1995
Morphology	E	Different from wild.	Native	Atlantic salmon	Fleming et al. 1994
	E + G	Increased smolt and adult body size.	Native	Brown trout and Atlantic salmon	Petersson et al. 1996
	E + G	Hatchery populations more similar to each other than to wild populations.	Native and non-native	Coho salmon	Hjort and Schreck 1982
	E > G	Different from wild.	Non-native	Coho salmon	Taylor 1986
	G	Different from wild.	Native	Brown trout	Petersson and Järvi 1995
	G, E + G	Hatchery reared wild and hatchery population differed least. These differed substantially from wild reared wild population.	Non-native	Coho salmon	Swain et al. 1991

lag in adjustment to feeding on natural prey. Released fish may initially behave inappropriately after being introduced into a novel environment, but with time may acclimate to the local environment. For example, L'Abée-Lund and Langeland (1995) found that the diet of released brown trout initially differed from that of wild trout, but within the first summer the released fish adopted a similar diet (see also Johnsen and Ugedal 1986, 1989, 1990).

Hatchery populations may also differ morphologically from wild fish (Table 3). Salmonid populations exhibit differences in morphological traits, and these differences have been suggested to result from local adaptations to environmental conditions (e.g. Riddell and Leggett 1981, Riddell et al. 1981). Furthermore, morphological traits are important determinants of breeding success (Fleming and Petersson 2001). Thus, any deviation in morphology from the local population may be expected to result in decreased fitness.

How successful are hatchery fish in the wild?

If hatchery fish differ from wild fish in so many respects, how successful are the released fish likely to be in the wild? Assuming that the wild populations have undergone natural selection for ten thousand years (since end of the last ice age) to become adapted to the local environment (Ricker 1972, Taylor 1991), one would predict that these changes in fitness-related traits are a potential problem for released fish, and may influence their ability to survive and reproduce (see also Fleming and Petersson 2001). Their performance in the wild should therefore be expected to be inferior to that of wild fish, a pattern that is commonly observed (Table 4). In four of eight studies wild fish outgrew released hatchery fish, whereas the opposite was observed in two studies. Thus, although growth rates usually differ among hatchery and wild fish, the direction of this difference is not consistent (combined probabilites $c^2 = 4.07$, df = 12, $P > 0.99$). In contrast, hatchery fish consistently experienced reduced survival compared to wild fish (15 of 16 studies, combined probabilites $c^2 = 109.15$, df = 18, $P < 0.001$). Thus, the success of hatchery-produced fish after release appears to be constrained by phenotypic divergence from their wild conspecifics. This is not surprising given the potential importance of local differences among wild salmonid populations in fitness-related traits and the evidence we have presented concerning the effects of hatchery environments on development and selection.

How do naturally produced fish respond to released fish?

Given our knowledge about the performance of hatchery-reared fish in the wild, can we predict how stocking may influence the natural productivity of salmonid populations? How will ecological interactions with hatchery fish impact wild fish? For instance, if the fish we release into a river are more aggressive than the native fish, chances are that naturally produced fish are displaced from their territories during competitive interactions (Table 5). Such effects may be modified due to competitive asymmetries caused by prior residency or differences in body size (cf. Johnsson et al. 1999, Cutts et al. 1999).

One intriguing question arises from the observation that even though hatchery-reared fish appear to be more aggressive than wild fish, and thus should be able to displace them in territorial contests, they suffer higher mortality in the wild. Obviously, social hierarchies are not the only determinants of mortality rates in salmonids. Other factors such as response to predators and metabolic rate relative to food availability (i.e. vulnerability to starvation) may contribute substantially to mortality rates. One might speculate that hatchery fish are to some degree able to displace naturally produced fish, but that they are unable to cope with the high cost associated with this behaviour in terms of risk of starvation or predation. If so, net fish production may actually decrease as a result of stocking (cf. Fleming et al. 2000).

An additional number of potential effects can cause releases to have detrimental effects on wild fish. For example, released fish may influence the

Table 4. Pre-adult growth and survival of hatchery populations in the wild. E = predominantly environmental, G = predominantly genetic, E > G = likely predominantly environmental. Neg = hatchery fish inferior performance, Pos = hatchery fish superior performance, 0 = no observable difference.

Trait	Origin of effect	Form of effect	Fish origin	Species	Reference
Growth	E	Neg	Native	Arctic char	Finstad and Heggberget 1993
	E	0	Native	Atlantic salmo	Jonsson et al. 1991[1]
	E	Pos	Native	Coho salmon	Irvine and Bailey 1992[2]
	E > G	Neg	Non-native	Brown trout	Hesthagen et al. 1999
	E > G	Neg	Non-native	Cutthroat trout	Miller 1952[3]
	E > G	Neg	Non-native	Cutthroat trout	Miller 1953[3]
	G	Pos	Native	Atlantic salmon	Kallio-Nyberg and Koljonen 1997
	G	*	Native	Rainbow trout	Reisenbichler and McIntyre 1977[4]
Survival	E	Neg	Native	Arctic char	Finstad and Heggberget 1993
	E	Neg	Native	Atlantic salmon	Hansen 1987[5]
	E	Neg	Native	Atlantic salmon	Jonsson et al. 1991
	E	Neg	Native	Chinook salmon	Unwin 1997[3]
	E	Neg	Native	Rainbow trout	Reisenbichler and McIntyre 1977[4]
	E > G	Neg	Non-native	Brown & Rainbow trout	Weiss and Schmutz 1999[3]
	E > G	Neg	Non-native	Brown trout	Kelly-Quinn and Bracken 1989[3]
	E > G	Neg	Non-native	Brown trout	Skaala et al. 1996[3]
	E > G	Neg	Non-native	Cutthroat trout	Miller 1953[3]
	E > G	Neg	Non-native	Cutthroat trout	Miller 1952[3]
	G	Neg	Non-native	Atlantic salmon	De Leaniz et al. 1989
	G	Neg	Non native	Brook trout	Flick and Webster 1964[6]
	G	Neg	Non-native	Brook trout	Lachance and Magnan 1990b[1]
	G	Neg	Non-native	Brook trout	Vincent 1960
	G	Neg	Non-native	Brook trout	Fraser 1981[7]
	G	**	Native & non-native	Brown trout	L'Abée-Lund and Langeland 1995[3]

*Hatchery/wild hybrids outgrew pure populations.
**Wild population intermediate survival of two hatchery populations.

Comments regarding usage of data in meta-analysis:
[1] *P*-value was calculated from Table 3.
[2] *P*-value was calculated from length data in Table 3.
[3] No statistics or raw data were available for inclusion of study.
[4] *P*-value was calculated from Table 4, comparing pure hatchery strain with pure wild strain.
[5] *P*-value was calculated from data.
[6] *P*-value was calculated from Table 2.
[7] *P*-value was calculated from Table 4.

timing of migration of wild fish. Hansen and Jonsson (1985) suggested that wild smolts were attracted to shoals of released smolts and join them when migrating downstream. Furthermore, releasing fish may influence interspecific hybridisation rates. Jansson and Öst (1997) suggested that this was the reason for the high levels of hybridisation between Atlantic salmon and brown trout observed in the River Dalälven, Sweden (41.5% hybrid parr). This may be of particular concern when species are extended beyond their natural range, where pre-zygotic isolation mechanisms against hybridisation with indigenous species may be absent (Leary et al. 1995). Releases of hatchery fish can also attract predators (including humans), and thus may cause the inten-

Table 5. Effects of stocking on wild populations.

Performance	Observation	Fish origin	Species	Reference
Productivity	Densities similar in stocked and unstocked sections of stream.	Non-native	Brown trout	Kelly-Quinn and Bracken 1989
	Spawning among hatchery reared and hybridisation with native population demonstrated. Survival rates of 0+ three times higher in native than in hybrids.	Non-native	Brown trout	Skaala et al. 1996
	Movement of resident trout higher out of stocked sections. Total population size unaffected by stocking.	Non-native	Brown & Rainbow trout	Weiss and Schmutz 1999
	No increase in total population size. Reduced natural production.	Native	Chinook salmon	Unwin and Glova 1997
	10-fold reduction in wild spawner densities, suggested to be result of hatchery selection for early spawning and displacement of wild fish.	Native & non-native	Coho salmon	Flagg et al. 1995
	Total number of juveniles higher in stocked streams than unstocked one summer after stocking. Wild juveniles less abundant in stocked than unstocked areas. Similar numbers returned to spawn in stocked and unstocked, but lower density of resulting juveniles in stocked streams.	Non-native	Coho salmon	Nickelson et al. 1986
	After stop of stocking, large increases in natural production of rainbow and brown trout. Stocking in previously unstocked stream caused reduced production of wild brown trout.	Native*	Rainbow & Brown trout	Vincent 1987
	Stocking of high rates of rainbow (8-10 times wild density), but not lower rates, caused reduced survival of wild rainbow and cutthroat trout.	Non-native	Rainbow & Cutthroat trout	Petrosky and Bjornn 1988
Growth	Residence time and growth in estuary unaffected by presence of hatchery fish.	Native	Chinook salmon	Levings et al. 1986
	Growth of resident brown trout unaffected. Resident rainbow reduced growth in stocked sections.	Non-native	Brown & Rainbow trout	Weiss and Schmutz 1999
Hybridisation	Massive stocking of hatchery reared fish force salmon and trout to common spawning grounds, causing hybridization. 41.5 % hybrid parr in restored river section.	Native & non-native	Brown trout & Atlantic salmon	Jansson and Öst 1997
Migration	Wild smolt attracted to shoals of released smolt and join them when migrating downstream.	Native	Atlantic salmon	Hansen and Jonsson 1985
	Long-term change in mean date of entry of adult fish after hatchery program initiated.	Native	Chum salmon	Lannan 1980
Predation	Numerical response of spiny dogfish to stream mouth at time of hatchery release of smolt.	Native	Coho & Chinook salmon	Beamish et al. 1992
	Squawfish aggregate to feed on hatchery-released juvenile salmonids.	Native	Pacific salmon	Collis et al. 1995

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* Both brown and rainbow trout were historically non-native species in this system, but have now established self sustaining populations.

sity of predation on naturally produced fish to increase (Beamish et al. 1992, Collis et al. 1995).

While little is known about the level of early maturation as parr among hatchery-reared fish, it is likely that the high growth rates that they experienced in the hatchery will increase the potential for early maturation following release. If so, this will alter patterns of sexual selection in wild populations and may ultimately affect the adaptive landscape, leading to evolutionary responses in the recipient population (reviewed in Fleming 1998).

The effects that released hatchery fish can impose on naturally produced fish should make us cautious toward implementing stocking programs to compensate for habitat degradation and to increase fisheries. Indeed, under certain scenarios, theoretical models suggest that long-term stocking may lead to extinction of the native population (Evans and Willox 1991, Byrne et al. 1992). Existing empirical studies clearly show that fish density in stocked streams may not show the desired positive response to releases (Table 5). In fact, in some cases a negative trend in population density has been associated with releases. Perhaps the best evidence for such an effect comes from a controlled study where populations of coho salmon were monitored for five years in 15 stocked and 15 unstocked streams (Nickelson et al. 1986). Stocked streams had higher densities of juveniles after stocking, but the number of adults returning to the two types of streams did not differ. Furthermore, spawning success of released fish was reduced, causing a lower density of juveniles in the stocked streams than in the unstocked ones one generation later.

Conclusions

The performance of hatchery fish and their interactions with wild fish appear to be of such a character as to suggest that many of the current stocking practices may be detrimental to the recipient populations. The present synthesis should incite caution in our attempts to mitigate negative effects of habitat degradation by releasing hatchery-produced fish. Although the reports published, and thus referred to here, may be biased towards negative effects of stocking, the potential for negative effects must nevertheless be acknowledged and dealt with.

A critical question we might ask ourselves is whether something can be done to avoid negative ecological effects of stocking? The answer to this question is yes and no. Better broodstock collection and mating protocols, more-natural rearing conditions, wild-fish-friendly release strategies and more focus on local broodstocks can improve the quality of hatchery fish released and reduce their impacts on wild fish. Behavioural deficits arise due to phenotypic responses to the radically unnatural abiotic and biotic environment of hatcheries, and will initially be environmental in origin but over generations of rearing will also involve genetic responses. Generally, hatcheries are psychosensory-deprived environments for fish (Olla et al. 1998). Adding complexity and enriching the environment is a common method for improving the well-being of captive animals (e.g., mammals, reptiles and birds) and may have application to hatchery populations of salmonids. Such an approach could reduce environmentally induced differences between cultured and wild fish, and increase post-release survival by decreasing stress, reducing domestication and acclimating fish more appropriately for their future environments (Berejikian et al. 2000). This could be done by adding habitat complexity, altering water-flow velocities, supplementing diets with natural live foods and reducing rearing densities to produce fish more wild-like in appearance and with natural behaviours and survival (Flagg and Nash 1999). For example, increasing habitat complexity has been shown to aid in the development of appropriate body camouflage colouration and increase behavioural fitness (Maynard et al. 1995). Similarly, anti-predator conditioning can improve post-release survival, as predator recognition and avoidance behaviour in juvenile salmonids improves in fish exposed to predators (Potter 1977, Olla and Davis 1989, Berejikian 1995) or odours from injured conspecifics (Brown and Smith 1998, Berejikian et al. 1999).

The development of release strategies that minimise negative ecological effects of hatchery fish on wild fish could also be a significant improvement. Released juveniles should be within the size range of wild juveniles, if not of a similar size distribution. The greatest risk of releasing large hatchery fish is that they may out-compete wild fish, endangering the natural production of the population. Releases of hatchery fish should also complement the natural spatial and temporal patterns of abundance of wild fish in the population. That is, the number of fish released should not exceed the carrying capacity of the environment, which varies spatially within the river and through time.

Thus improvement in the way hatchery fish are reared and released can lead to significant strides towards reducing their negative ecological impacts on wild fish. However, as Waples (1999) points out, it is a myth to believe that these changes will make the problems disappear altogether. This is because (1) environmental and genetic changes to fish in hatcheries cannot be avoided entirely; and (2) many of the risks are negatively correlated, so efforts to reduce one risk simultaneously increases another. Clearly we need to, first and foremost, be cautious in our use of hatcheries, particularly when releases are to be used in supplementing wild populations. We need to better understand how to culture fish for release (i.e. phenotypic responses to culture and effects of domestication, and how to minimise them) and how to release these fish to minimise/eliminate potentially detrimental impacts on wild populations while contributing to an overall increase in productivity.

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The Ability of Released, Hatchery Salmonids to Breed and Contribute to the Natural Productivity of Wild Populations

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Abstract

The success and implications of hatchery release programmes are intimately tied to the reproductive capabilities of the hatchery fish in the wild. Moreover, reproductive interactions are important in understanding the ecological and genetic threats that hatchery fish may pose to wild populations. Reproductive success is a key to self-sustainability, shaping natural and sexual selection, and influencing the genetic diversity of populations. In this paper, we review the determinants of breeding success in natural populations and the implications of parental traits and decisions for offspring survival and success. We then address how rearing and release programmes affect the reproductive traits and performance of fish. A review of such programmes reveals that in the few cases where adequate assessments have been made released fish frequently fail to attain self-sustainability and/or contribute significantly to populations. Clearly, new approaches based on sound scientific research are needed and these need to be tailored specifically to the management objectives.

Keywords: hatchery, salmonids, natural productivity, breeding success, spawning.

Introduction

Deliberate releases of salmonid fishes appear to take two main forms: (1) *fisheries releases* to increase population size for fisheries; and (2) *conservation releases* to save populations at risk of extinction or re-establish native populations that have been eradicated. Fisheries releases are the most common and in Norway, are most often undertaken for mitigation purposes, i.e. to compensate for the impacts of habitat alteration/degradation such as hydropower regulation (Finstad and Jonsson 2001, Fjellheim and Johnsen 2001, Vøllestad and Hesthagen 2001). An unfortunate consequence of this approach is that it can become acceptable to sacrifice the productivity of natural populations as long as the hatchery releases compensate for the loss to the fisheries. Little consideration is given to habitat or other improvements. This approach is also problematic because hatchery fish are often stocked on top of the natural production, which has become constrained by habitat loss (i.e. reduced natural carrying capacity), thus inducing potentially deleterious competition between the wild and released fish (reviewed in Einum and Fleming 2001, Sægrov et al. 2001). Only recently have we begun to fully appreciate that the long-term sustainability of salmonids requires conservation of natural populations and their habitats.

Conservation releases are often undertaken to save populations that are likely to perish due to demographic factors (e.g., small population size). Such releases aim to use native fish as broodstock to give the population a boost (supportive breeding) and in theory, are to be considered a temporary solution until the factors responsible for the population decline are identified and alleviated. Conservation releases may also be undertaken to re-introduce/re-establish populations that have been eradicated (e.g., because of acid rain or the parasite *Gyrodactulus salaris*). Once the cause of the extinction has been rectified, fish are re-introduced either from the population's gene bank or from neighbouring populations inhabiting similar environmental conditions, i.e. having adaptations likely to aid in establishment.

One of the main premises/goals upon which many of the above concepts of fish releases are built upon is that they can provide a positive long-term benefit to natural populations. Yet, there appears to have been little or no attempt to find out whether this goal is achieved, and this is not a problem restricted to Norway, but a universal problem (cf. Waples et al. in press). Thus, the role of fish releases in the conservation of wild salmon populations is intimately linked to understanding the dynamics of breeding and ultimately, reproductive success between wild and hatchery released salmon. The aim of the paper is to review the determinates of breeding success and its close link with offspring success (reproductive success) in salmonid fishes, particularly Atlantic salmon (*Salmo salar*) and brown trout (*S. trutta*). Then we examine the close relation between reproductive success and the desired goals of release programs, and how they may affect the reproductive traits and performance of fish. Finally, we provide an analysis of release programs where direct and indirect information·about the reproductive success of released salmonids and their potential effect on natural productivity exist.

Demographic and genetic consequences of breeding success

Breeding success is the outcome of competition among individuals to maximise the number of embryos surviving until independence (i.e. yolk absorption in salmonids) within the constraints imposed by the opposite sex (e.g., number of mates, mate choice) and the environment. Because of its link via offspring survival to individual reproductive success (a measure of fitness), it plays an important role in shaping the demographic and genetic structures of populations (cf. Vehrencamp and Bradbury 1984).

From the population perspective, the most obvious implication of variation in breeding success is its effects on annual recruitment and thus natural production. However, natural breeding also generates intense selection upon both male and female salmon that shapes life history strategies and thus the demographic structure of populations. Evidence from a series of semi-natural breeding experiments with Atlantic salmon (Fleming et al.1996, 1997) indicate that breeding alone can generate a coefficient of variation in female success of 102% (range 71-131%) and in male success of 151% (range 60-268%). Thus, the variance in breeding success is often considerably larger than the mean success, with some individuals being highly successful while others are unsuccessful (range in female success: 0-4,644; male success: 0-11,188 embryos parented). This generates intense natural and sexual selection on male and female salmonids targeting traits such as body, hooked snout, kype, dorsal hump, caudal peduncle, and adipose fin size (van den Berghe and Gross 1989, Järvi 1990, Fleming and Gross 1994, Quinn and Foote 1994, Petersson et al.1999). It also affects life history traits, including survival, egg production, age at maturity and the evolution of alternative reproductive tactics (e.g., sneaking versus fighting), and subsequently the demographic features of the population such as sex ratio and age structure (reviewed in Fleming 1998). Any program to conserve salmonid populations, therefore, must take account of the variation in breeding success, particularly when hatchery release programmes are being considered.

Variability in breeding success of individuals also affects the genetic structure of populations in subsequent generations, both directly through selection as described above and indirectly through its affects on a population's effective size. The effective size of a population (N_e) is an important parameter determining the amount of genetic variability that can be maintained, particularly when the population is small (e.g., Martinez et al. 2000). It is defined as the size of an ideal population that would lose genetic variation at the same rate as a given real population (Lande and Barrowclough 1987). The loss of genetic variability influences the population's probability of long-term survival because genetic variation is requisite for evolutionary adaptation in changing environments. Things that affect N_e include variability in population size through time, skewed sex ratios and variability among individuals in breeding success (Lande and Barrowclough 1987, Nunney 1991). Variability in breeding success in salmonids can reduce the breeding effective size to 48-76% of the number of adults on the spawning grounds (Fleming 1994, cf. Nunney and Elam 1994).

Populations will often go extinct due to demographic problems (stochastic and/or deterministic) before loss of genetic variability can become a problem (Lande 1988). Thus demography will often be a more pressing conservation problem than genetics, though genetic diversity will remain important in maintaining the potential for adaptive evolution. Two forms of variability will affect the demography of populations at small sizes, demographic (e.g., sex ratio, age-structure) and environmental (e.g., weather, food supply, competitors, parasites). They are generally overlapping categories to describe different forms of variation that influence the demography (i.e. survival and reproduction) of a population. Environmental variability is considered to pose a greater threat to population survival (Lande 1988, 1993, Caughley 1994). Analyses by Leigh (1981) and Goodman (1987) suggest that environmental variability will usually dominate other forms of variability in populations larger than 20-100 individuals. In most real situations we are likely to have environmental variability first driving populations to low levels and demographic and genetic variability then putting on the finishing touches. The central message is that risk of extinction increases with decreasing population size and will be affected by variation in breeding success.

A final aspect where breeding success plays a critical role is in understanding the potential for gene flow. In the present context, such gene flow will frequently be one-way from cultured to native fish, though some supplementation programs will obtain a fraction of their broodstock from the wild each generation. If interbreeding is successful, the resultant gene flow may lead to the loss of genetic variability among populations, an important component of genetic variation in salmonid species and their evolutionary potential (e.g., Ståhl 1987, Allendorf and Leary 1988, Waples 1991, Hansen and Loeschcke 1994). At the within-population level, however, the effects may be negative or positive. Interbreeding may disrupt local adaptations and break up coadapted gene complexes (i.e. combinations of genetic traits that have evolved over a long period to work complementarily) resulting in a reduction in fitness known as outbreeding depression (Templeton 1986). By contrast, it may simultaneously increase genetic variability, thereby reducing the accumulation of recessive deleterious mutations in populations suffering from inbreeding depression, and increasing within-population evolutionary potential. Despite such potential positive effects, Hindar et al. (1991) in a review of intentional (e.g., transplants) and unintentional introductions of salmon (e.g., salmon farm escapes, straying of hatchery releases) found that the effects were frequently negative (see also Gharrett and Smoker 1991).

What determines breeding success?

Mating success is one of the most important factors determining breeding success. If an individual were not able to achieve matings, its reproductive output would be zero, whatever qualities the individual has in other respects. But, an ability to achieve matings does not necessarily translate into breeding success (e.g., due to low gamete viability or poor embryo survival). Breeding success in salmonid fishes will be determined by a variety of factors, such as body size, timing, egg production, competitive ability, attractiveness, and embryo viability. The theoretical underpinnings to understanding investments in these various traits assume that different life history components are causally related and increases in allocation to one component, for example reproduction, will be at the expense of allocation to other components, such as growth and survivorship (Williams 1966, Gadgil and Bossert 1970). However, such trade-offs may be masked in the wild because of individual variation in the ability to acquire resources, with individuals having better acquisition abilities being able to devote more energy into a wide array of traits (Reznick et al. 2000). In this section we aim to review some important elements of breeding success and how they are interrelated.

Age and size at maturity

Age and size are coupled in most fish species, with older individuals being generally larger than younger ones. In organisms having indeterminate growth, such as fish, the relation between growth and reproduction is potentially very important because size and fecundity are often positively related. In terms of lifetime reproductive potential, early-breeding individuals may maintain a higher cumulative reproductive output until a certain age; after which late-breeding individuals may have a higher cumulative potential (cf. Ford and Seigel 1994). This reflects the decreased growth often associated with increased reproductive investment that reduces future fecundity (cf. Williams 1966). Also, maturing at young age provides a demographic benefit in terms of decreasing generation times in expanding populations, while delaying breeding incurs an accumulated risk of dying (e.g., due to diseases, parasites, predators or senescence)(Bell 1980). Thus, the optimal size-to-age at maturity depends on growth and mortality rates, which vary with environment (Charlesworth 1980). Therefore, organisms in spatially or temporally changing environments frequently show adaptive phenotypic plasticity for this trait (Schlichting and Pigliucci 1998).

Early experimental work by Alm (1959) showed that a dome-shaped norm of reaction for size-to-age at maturity is common in fishes, with size at maturity being smaller for both fast- and slow-growing individuals than for more intermediate-growing fish. Using computer simulations, Perrin and Rubin (1990) showed that such a dome-shaped norm of reaction is optimal when assuming a finite life span and a negative relationship between production and survival rates. This latter assumption is supported by empirical data (e.g. Beverton and Holt 1959, Jensen 1985), as well as by physiological and demographic arguments (e.g. Sibly and Calow 1986). Age and size at which to mature are then among the principal components of the reproductive strategy (i.e. a genetically based life history or behaviour programme affecting an organism's allocation to reproductive effort among alternative phenotypes or tactics; Gross 1984, 1996) of a salmonid species.

Considerable variability in these traits exists among and within species, and also among and within populations of a species, including salmonid fishes (e.g., Alm 1959, Jonsson 1985, Groot and Margolis 1991, Hutchings and Jones 1998). In addition to the effects of abiotic conditions, this variability in salmonid fishes is influenced strongly by reproductive success as affected by the breeding environment (reviewed in Fleming 1998), and by the costs of reproduction (e.g., survival; Hutchings 1994). One of the most striking examples of this occurs within Atlantic salmon and brown trout, where some males mature during their freshwater stage as parr while others mature after an oceanic migration. The mature male parr may be less than a hundredth the weight, and about a third the age of ocean-migratory (anadromous) males (Fleming 1998). These two male phenotypes appear to coexist as a result of the combined effects of frequency- and status-dependent selection during breeding (Gross 1984, 1996, Bohlin et al.1986, 1990, Hutchings and Myers 1994), where the relative success gained from using a particular tactic (anadromy versus parr maturity) will be influenced by an individual's competitive ability ("state") and the tactic used by others in the population.

Intrasexual competition

In most salmonid species, competition among individuals of the same sex for breeding resources is intense. Moreover, because males and females fight over different resources, access to females and spawning sites respectively, the intensity of intrasexual competition differs between the sexes. The operational sex ratio (OSR, i.e. the number of sexually active males to that of sexually active females on the spawning ground) is a good predictor of contest competition for mates and to some extent mate choice. However, it will not necessarily be a good predictor of the prevalence or intensity of other mechanisms of sexual selection, such as sperm competition, infanticide or coercion (see Kvarnemo and Ahnesjö 1996). In salmonids, the OSR is highly male biased in most cases (e.g., Quinn et al. 1996). Even though the sex ratio of returning adults in some cases may be female biased (Fleming 1998), the OSR (i.e. the sex ratio on the spawning grounds) is likely to be male biased. This is a consequence of (1) asynchronous spawning by females and the male ability to spawn rapid and repeatedly; for example, female Atlantic salmon may be active on the spawning ground for 7-10 days, while males may remain so for about a month (Webb and Hawkins 1989, Fleming et al.1996, 1997; see also Blanchfield and Ridgway 1997), and (2) the presence of early maturing male parr. It is not uncommon in salmonids to observe ten or more males, including mature parr, competing for access to a single female (Keenleyside and Dupuis 1988, Evans 1994; personal observations of wild Atlantic salmon).

Evidence from coho salmon (*Oncorhynchus kisutch*) suggests that male breeding competition can generate a 52-fold increase in the opportunity for selection (Fleming and Gross 1994). Such intense selection has likely been responsible for the evolution of elaborate secondary sexual characteristics (i.e. developed for accessing breeding resources, including mates and spawning sites), such as elongated jaws and canine-like breeding teeth, dorsal humps, bright breeding colouration and skin thickening (Schroder 1982, Järvi 1990, Fleming and Gross 1994, Quinn and Foote 1994, Petersson et al. 1999). Moreover, the studies above indicate that males are more intensively selected than females. For example, Fleming and Gross (1994) found the intensity of selection due to breeding competition to be nine times greater in male than female coho, suggesting that this was responsible for the sexual dimorphism in the expression of secondary sexual characters. Such sexual dimorphism is common in salmonid fishes.

This is not to suggest that breeding competition among females is weak, but rather less intense than that among males. While breeding sites in many rivers may appear non-limiting, females do show strong preferences for particular sites, often clumping nests in such areas (Heggberget et al. 1988, Blanchfield and Ridgway 1997, Essington et al. 1998). Competition over breeding sites can result in delays in breeding, female displacement and nest destruction by superimposition (e.g., Schroder 1981, van den Berghe and Gross 1989, Fleming 1996, Petersson and Järvi 1997, McPhee and Quinn 1998, Essington et al. 2000). Fleming and Gross (1994) found that female breeding competition generated a 6-fold increase in the opportunity for selection among female coho salmon (see also van den Berghe and Gross 1989). Thus intrasexual competition in both sexes will be important in determining breeding success, and ultimately the demographic and genetic structure of salmonid populations.

Mate choice

Empirical and theoretical data pinpoint what most biologists intuitively know, that female mate choice is much more common than male mate choice (reviewed in Andersson 1994). In salmonid fishes, females appear to express mate choice through delays in breeding (Schroder 1981, Foote and Larkin 1988, Foote 1989, de Gaudemar et al. 2000) and aggression, sometimes directing a large proportion of their aggressive activity towards males (e.g., Keenleyside and Dupuis 1988, Fleming et al. 1997, Petersson and Järvi 1997). The choice criteria of female salmonids are still relatively unstudied, with the exception of experiments by Petersson et al. (1999) and de Gaudemar et al. (2000) showing female choice of males with relatively large adipose fins in brown trout and large body size in Atlantic salmon, respectively. It is unlikely that female salmonids gain direct, material benefits from such mate choice (e.g., territories, food, parental care), although they may gain genetic benefits for their offspring (e.g. 'good genes' or 'runaway' coevolution; see Andersson 1994), safety from disruption and injury during spawning, reduced risk of infection and assurance of fertilisation (see Reynolds and Gross 1990). Recent evidence suggests males may also affect egg swelling immediately following fertilisation, which may be a special case of 'male contribution' (Pakkasmaa 2000, cf. Seppä 1999), though its significance remains unclear and unstudied. The extent of female choice in salmonids, however, appears to be constrained or circumvented by male-male competition, because dominant males can monopolise access to females (Jones 1959, Järvi 1990, Fleming et al.1996, 1997, Petersson et al.1999). Female incitation of male-male competition, however, may be viewed as a means of 'passive' choice (cf. Cox and Leboeuf 1977), though its role in salmonid fishes is unstudied. The costs of the female choice in terms of energy, predation risk and aggression from males may often outweigh its benefits for salmonid fishes and as a result it is unlikely to play a dominant role in the mating system.

Mate choice by male salmonids is probably even less well studied than that of females. Males may show choice either for absolute female size because of its direct relation with female quality (e.g., fecundity, egg size and parental care ability; Sargent et al.1986) or for similar-sized females because of the male's ability to obtain and control mates (Foote 1988). It is common for the number of males associated with a spawning female to increase with her size (Hanson and Smith 1967, Campbell 1977, Jonsson and Hindar 1982, Sargent et al.1986). Asynchronous spawning by females in some circumstances, however, may constrain male mating options.

One possible outcome of the combination of mate choice and intrasexual competition is assortative mating, where males and females in a population mate more frequently with a phenotype (in a broad sense) similar to their own than expected from random. Assortative mating may arise when individuals of both sexes actively choose a mate of a similar phenotype (Burley 1983). The rapid phenotypic and genetic divergence of Icelandic Arctic char may be an example of this (cf. Gíslason et al.1999). Alternatively, assortative mating may arise when all individuals of one sex have the same preference, but only some of them are able to achieve it (Burley 1983). For example, if all females prefer large males and all males prefer larger, more fecund females, then only the larger males are able to gain access to the preferred females. The smaller males and females, as a result, will be forced to mate with each other (cf. Petersson 1990). This pattern is most likely operating in Dolly Varden (Maekawa et al.1993) and Japanese charr (Maekawa et al.1994). Several other studies also report positive size-assortative mating in salmonids (Hanson and Smith 1967, Schroder 1981, Jonssson and Hindar 1982, Foote 1988). It has also been suggested that negative assortative mating based on major histocompatability complex (MHC) genes may be important in salmonids, though this remains untested (Grahn et al. 1998). Assortative mating is likely to be a common pattern in salmonid fishes.

The link between adult reproductive traits and offspring success

Most of the factors contributing to embryo survival and early juvenile survival are linked to the female, as she chooses the spawning time and site, constructs the redd and deposits the nutrient-rich eggs. In Atlantic salmon, the survival of eggs in the nests not destroyed during incubation (e.g., by scouring and nest superimposition, see below) may be as high as 74-91% until hatching (Shearer 1961, MacKenzie and Moring 1988). When the eggs hatch, the small juveniles still have a considerable amount of nutrients and energy stored in the yolk-sac as a result of maternal provisioning (Einum and Fleming 1999, Berg et al. in press). Once the yolk sac is absorbed, the juveniles emerge from the gravel into the open water. Loss rates during the first weeks thereafter are very high, with 68-88% mortality during the first 17-28 days (Einum and Fleming 2000a,b). Similar patterns have been observed in brown trout, where about 80% of fry rarely feed after emergence, quickly lose weight and drift downstream during night and die (Elliott 1986; see also Héland 1980a, b). Incubation and early juvenile life are thus periods of intense selection (Elliott 1994, Einum and Fleming 2000a,b).

Spawning Time – A female's spawning time will dictate the thermal regime her embryos experience during development and to a large extent, their hatching and emergence time from the gravel as fry (e.g., Crisp 1981, Jensen et al.1991). Peak spawning times between the earliest and latest breeding populations of a salmonid species may range by several months (Groot and Margolis 1991, Fleming 1996). The timing among populations correlates with water temperature during incubation (Heggberget 1988), likely to ensure optimal timing of hatching and initial feeding for the offspring (Brannon 1987, Heggberget 1988, Quinn et al. 2000). Other factors such as water-flow regime during egg incubation or limited access to the breeding grounds due to river freeze-up might also be important (Fleming 1996).

Within populations, spawning may extend over many weeks (e.g., Fleming and Gross 1989, Tallman and Healey 1994, Fleming 1996, Blanchfield and Ridgway 1997), and may be temporally segregated between upper and lower reaches of the river, particularly in large systems where environmental conditions differ (Burger et al. 1985, Webb and McLay 1996). In addition to within-river variability in environmental conditions, intraspecific breeding competition may be an important factor affecting spawning times (Schroder 1981, Fleming and Gross 1993, Elliott 1994, Petersson and Järvi 1997). For the offspring, spawning time will affect emergence time, with early emerging fry having an advantage in establishing territories, and beginning to feed and grow before late emergers (Fausch and White 1986, Chandler and Bjornn 1988, Brännäs 1995). Metcalfe and Thorpe (1992) showed that Atlantic salmon emerging first were dominant, grew faster and smolted a year earlier than later emerging conspecifics. Moreover, Einum and Fleming (2000a) identified directional selection for early emergence in Atlantic salmon due to differential survival and influences on body size. The advantages of early offspring emergence and ready access to highest-quality nest sites, however, must be traded off against susceptibility to nest destruction by digging activity of later-breeding females and probability of unfavourable environmental conditions early in the spring during emergence. These trade-offs may generate adaptive variation in spawning time within populations and result in the evolution of adaptive temporal variation in life history traits ("adaptation-by-time", Hendry et al.1999).

Spawning Site – Female choice of spawning site will dictate the environment her embryos and subsequently, her emerging offspring will experience as fry. Poor quality nests, having high concentrations of fine sediment/sand and thus poor permeabilities and low intragravel dissolved oxygen will severely reduce embryo survival (reviewed in Chapman 1988). Location will also be critical to the emerging fry, which initially remain in the nest's vicinity due to their poor swimming ability and negative buoyancy. Thus, females unable to choose and/or fight for a good site will expose her offspring to potentially harsh environmental conditions and thus high mortality immediately after emergence. For example, proximity of the spawning site to suitable nursery habitat, particularly downstream (Elson 1962, Gibson 1993), may be important as fry slowly disperse. Egg burial depth will be important in decreasing the probability of egg destruction by scour during spates and by nest superimposition by later spawning females (e.g., Crisp 1989, van den Berghe and Gross 1989, Steen and Quinn 1999). While deeply buried embryos could suffer from inadequate water flow, evidence from chum salmon (*O. keta*) suggests this is not necessarily the case possibly because larger females, which dig deeper nests, do so in faster water than small females (Peterson and Quinn 1996). In general, egg burial depth increases with female size (reviewed in DeVries 1997), suggesting that it is selectively advantageous.

Egg size – How a female partitions her resources available for egg production has important fitness consequences affecting the number of surviving offspring she can expect. Large eggs give rise to larger juveniles than smaller ones (e.g., Fowler 1972, Gall 1974, Pitman 1979, Thorpe et al.1984), which in turn may afford faster juvenile growth (Bagenal 1969), higher status (Wankowski and Thorpe 1979), reduced susceptibility to starvation (Hutchings 1991), predation (Parker 1971) and parasites (Boyce 1974), or in other words, better offspring survival. However, large egg size appears to be at the cost of reduced egg number (fecundity)(Svärdson 1949, Fleming and Gross 1990, Quinn and Bloomberg 1992, Jonsson et al.1996). Theory suggests that natural selection should maximise a female's fitness returns per unit of resource invested in egg production. This will be accomplished by dividing that investment into eggs of optimal size (Smith and Fretwell 1974, Parker and Begon 1986, Roff 1992). Thus, for a given amount of resources for egg production, egg number should vary in response to selection upon egg size. Einum and Fleming (2000b) tested this by manipulating egg size in Atlantic salmon and showed that the joint effect of egg size on egg number and offspring survival resulted in stabilising phenotypic selection for an optimal size. A size that closely matched the mean egg size in the population, but was below that that maximised offspring survival. The results indicated that egg size had evolved largely in response to selection on maternal rather than offspring fitness.

In another study, Einum and Fleming (1999) found distinct reaction norms in the performance of juvenile brown trout from small and large eggs, with growth and survival being similar in high quality environments but becoming increasingly divergent in poorer environments. The existence of such reaction norms indicates that the optimal egg size varies across gradients of environmental quality, and this has likely shaped the evolution of egg size. This may help explain why the eggs of individual females are fairly uniformed in salmonid fishes (Fleming and Ng 1987, Fleming et al.1996), while among females and across population eggs may differ more than twofold in weight (Beacham and Murray 1993, Fleming 1998). Like fecundity, egg size typically increases with female size, such that larger females forgo more eggs to have larger eggs for their body size than do small females. This suggests that the optimal egg size likely varies in relation to abiotic and biotic factors as affected by female size. For example, because larger females deposit more eggs on average in their nests than smaller females (Fleming 1996), sibling competition at emergence is likely to be more intense and hence select for a larger optimal egg size (cf. Parker and Begon 1986). Alternatively, female size may influence the quality of incubation habitat her eggs experience (van den Berghe and Gross 1989; modelled by Hendry et al. in press). Small females, which are often less competitive than larger females, may be forced to use sub-optimal substrate, having high proportions of fine sediment, limited intragravel water movement and low levels of dissolved oxygen. Such sub-optimal incubation substrate may select against large eggs, because of their higher metabolic demands and less efficient surface-to-volume ratio for acquiring oxygen (van den Berghe and Gross 1989). Quinn et al. (1995) found a positive association between egg size and substrate size in sockeye salmon (*Oncorhynchus nerka*), suggesting adaptation in response to spawning site quality. Furthermore, under conditions of intense nest competition, some large females may also be displaced into poor nesting environments and thus incur lower success than smaller females (Holtby and Healey 1986), which over time should select for a smaller average egg size within the population.

What is known about the reproductive patterns of released fish?

As evident from the previous discussion, the evolution and dynamics of the breeding system of salmonid fishes is complex, having important consequences for the demographic and genetic structure of populations. The release of hatchery fish will almost certainly affect this structure and understanding the reproductive patterns of the released fish will be important in predicting their effect on the population's natural productivity.

The reproductive traits of released fish will reflect the stock's genetic origin, rearing history (domestication effects) and form of rearing (environmental effects). The term 'domestication' has been applied differently, though all agree that it involves animals being 'farmed by' man in a human-imposed environment. This process inevitably results in evolutionary changes due to intentional and unintentional artificial selection by humans and random genetic effects (e.g., bottlenecks, founder effects). A conservative viewpoint holds that domestication should be defined as involving certain irreversible changes of the animal exposed to the new environment as a result of an active selection procedure by man (cf. Hemmer 1990). From this point of view, there are very few 'true' domestic fishes in the world, though the carp (*Cyprinus carpio*), which has been intentionally selected for over 2000 years (Ling 1977), would likely qualify. A more liberal viewpoint holds that domestication involves all forms of evolutionary change due to artificial rearing, not just those due to intentional selection. The use of the term 'domesticated' for hatchery-reared fish has a long history, and was, for example, used in the 1950's (see e.g., Wood et al. 1957). For practical reasons we concur with this traditional use of the term.

Most studies examining the reproductive traits of released fish have thus far been laboratory studies, in a broad sense; i.e. comparisons of the behaviour of wild and domesticated fish in controlled environments such as aquaria, stream channels or small enclosed areas of rivers. In addition, most studies have compared wild and multi-generation hatchery fish, often of differing genetic origins, thus making it difficult to separate genetic from environmental effects. This, however, is not surprising given the scale at which these experiments must be conducted, and the fact that for most hatchery stocks their founding wild population has been altered by large-scale introgression from hatchery fish. Nevertheless, in this section we will attempt to address the environmental and genetic (domestication and non-native origin) effects of hatchery rearing on the reproductive traits of released fish.

Age and size at maturity

Typically, hatchery-rearing leads to rapid growth of fish due to *ad libitum* food availability, which can affect the age and size at maturity. Early (i.e. precocial) maturity among male salmonids is well known to be positively related to growth (e.g., Alm 1959, Saunders et al.1982, Gross 1996). Thus, releases of parr that have experienced rapid growth in hatcheries may affect mating dynamics in wild populations by dramatically increasing the number of mature male parr. Rapid juvenile growth can also result in low age-at-smolting (e.g., Metcalfe et al.1989, Økland et al.1993) and subsequently, age-at-maturity. Moreover, the proportion of fish returning as grilse (one-sea-winter) is positively correlated with the size of smolts released (Chadwick 1988, Chadwick and Clayton 1990, Crozier and Kennedy 1993). A decrease in the age- and thus, size-at-maturity is a pattern observed in hatchery-supplemented populations of Atlantic salmon (e.g., Christensen and Larsson 1979, Sharov and Zubchencko 1993). In addition to environmental effects due to growth rate, there are indications that such responses may also reflect domestication selection in hatchery populations (Kallio-Nyberg and Koljonen 1997, also Fleming and Gross 1989). The effects of domestication on size-at-maturity, however, may not be straight forward as evidenced by the apparent lack of effect on Atlantic salmon and positive effect on brown trout of the Älvkarleby hatchery, Sweden (Petersson et al. 1996).

Homing

Generally, the homing precision of returning hatchery adults released as freshwater juveniles or as smolts in rivers is much higher than that for fish escaping or being released at marine sites, without any connection with a river (Hansen and Jonsson 1994, Hansen and Quinn 1998). Smolts and post-smolts escaping or released from a marine site return to the area in the sea from which they escaped/were released, but because of a lack of home-river imprinting, the sexually mature fish will enter several rivers in that area to spawn late in the season (Sutterlin et al. 1982, Gunnerød et al.1988, Hansen et al. 1989). For example, experiments in the Baltic in the early 1980s demonstrated that transporting smolts to sea pens and delaying their release a few months dramatically improved survival, however, it also significantly increased their rate of straying (Anon. 1997). Similarly, hatchery Atlantic salmon released as smolts at a river mouth return there as adults at a similar time as wild fish, but ascend the river later apparently due to a lack of juvenile experience with the river (Jonsson et al.1990, 1991; cf. McKinnell et al.1994, Petersson and Järvi 1993). Also, the timing of release of smolts and post-smolts can affect straying, with those released during winter straying more and farther away than fish released during the rest of the year (Hansen and Jonsson 1991). As a rule of thumb, fish released at the wrong time and at the wrong site stray more, i.e. have worse homing behaviour, than those released at more appropriate (natural) times and sites (reviewed by Quinn 1993).

Spawning time and location

If hatchery fish differ from wild fish in location or timing of spawning the implications for offspring survival can be critical (see above). In a study of coho salmon (*O. kisutch*) in Oregon, Nickelson et al. (1986) found that hatchery fish returned and spawned earlier than the native wild fish, and concluded that this was largely responsible for the failure to rebuild populations in streams stocked with presmolt hatchery fish. Spawning time has a high heritability in salmonid fishes (Siitonen and Gall 1989, Silverstein 1993, Gharrett and Smoker 1993, Quinn et al. 2000) and evidence suggests that unintentional hatchery selection for early spawners can alter it (Ayerst 1977, Leider et al.1984, Flagg et al. 1995, Petersson and Järvi 1993). There are also indications that hatchery rearing can affect the choice of spawning location. Not only do fish having experienced only the lower reaches of the river (as normally is the case for released hatchery-reared fish) hesitate to ascend to the upper parts where the spawning grounds lie, they also wander more within the river than wild fish (Jonsson et al. 1990, 1994). An interesting potential outcome of altered choice of spawning time and location is increased interspecific hybridisation due to a break down of spatial and/or temporal isolation between species (Leary et al. 1995, Jansson and Öst 1997).

Fecundity and egg size

The relaxation (or perhaps even removal) of sexual and natural selection, and the artificial nature of the hatchery breeding process will likely favour those individuals that allocate their available resources to gonads instead of elaborate secondary characteristics or energy-demanding spawning activities (Fleming and Gross 1989). However, the few studies that have tested this hypothesis have been indirect (i.e. comparative or time series analyses; Table 1). To examine whether a general pattern exists among these studies we used a meta-analytical approach. Such an analysis combines the separate significance tests from the different data sets that test the same scientific (but not statistical) hypothesis. Each independent test reports a probability value for the particular outcome, assuming the null hypothesis to be correct. From the studies listed in the Table 1, we extracted probability values relevant for the trait concerned (i.e. total egg biomass). These probability values were combined according to Sokal and Rohlf (1995) to create an overall test of significance. The meta-analysis identified weak support, at best, for increased gonad allocation with hatchery rearing ($c^2 = 20.81$, df = 12, $P = 0.054$). Such effects may be small and masked by other trade-offs and factors, such as body condition, and thus carefully designed investigations may be needed to reveal differences.

There are indications that hatchery-rearing may affect female allocation (size-adjusted) to egg size (6 of 8 studies, Table 1), however, the pattern appears inconsistent (meta-analysis: $c^2 = 13.78$, df = 16, $P = 0.62$). Fleming and Gross (1990) hypothesized that the elimination of the constraint of gravel quality that eggs experience in nature (van den Berghe and Gross 1989, Quinn et al. 1995) will favour larger eggs in hatcheries because of survival and growth advantages. In addition, if incubation temperatures in hatcheries are higher than in nature this may also select for

Table 1. Differences in egg production traits between wild and hatchery populations of salmonids. Effect: whether the trait expression in the hatchery fish differs from that in wild fish and in what direction. Origin of Effect: G + E = genetic and environmental, E = predominantly environmental, G = predominantly genetic, G > E = genetic effects suspected to be greater, E > G = environmental effects suspected to be greater.

Trait	Effect	Origin of Effect	Origin of Hatchery Fish	Length of Propagation	Species	Reference
Total Egg Biomass	Increase*	G + E	Native	4-83 years	Coho salmon	Fleming and Gross 1989
	Increase	G + E	Non-native	15 years	Coho salmon	Fleming and Gross 1992
	Not different	G + E	Native	25+ years	Brown trout	Petersson and Järvi 1993
	Not different	G > E	Native	25 years	Atlantic salmon	Petersson et al. 1996
	Not different	G > E	Native	25 years	Brown trout	Petersson et al. 1996
	Not different	E	Native	First generation	Atlantic salmon	Jonsson et al. 1996
Egg Size	Increase	G + E	Native	4-83 years	Coho salmon	Fleming and Gross 1990
	Increase	G + E	Non-native	15 years	Coho salmon	Fleming and Gross 1992
	Not different	G + E	Native	4-83 years	Coho salmon	Beacham and Murray 1993
	Not different	G + E	Native	25+ years	Brown trout	Petersson and Järvi 1993
	Increase	G > E	Native	25 years	Brown trout	Petersson et al. 1996
	Increase	G > E	Native	25 years	Atlantic salmon	Petersson et al. 1996
	Decrease	E	Native	First generation	Atlantic salmon	Jonsson et al. 1996
	Decrease	E	Native	First generation	Atlantic salmon	Fleming et al. 1997

* Not significant at $P = 0.082$

larger eggs because of reduced efficiency of conversion of yolk to body tissue (Heming 1982) and increased maintenance costs associated with increased water temperature (Hamor and Garside 1977). Thus, hatchery populations exposed to selection over generations may be expected to show increased egg sizes. Support for this, however, has been inconclusive and based on comparative and time-series analyses that do not fully control for other potential factors (e.g., gene flow, environment, phylogeny; Fleming and Gross 1990, Petersson et al. 1996; Beacham and Murray 1993, Petersson and Järvi 1993). By contrast, more controlled studies examining single generation (environmental) effects of hatchery rearing indicate a decrease in egg size (Jonsson et al. 1996, Fleming et al. 1997). It has been proposed on theoretical grounds that egg size should be sensitive to juvenile growth and survival (Sibly and Calow 1986, Winemiller and Rose 1993), and its expression phenotypically plastic in spatially and temporally varying environments (Perrin 1988). This appears to be the case among at least some salmonids, where egg size is negatively associated with early maternal growth (Thorpe et al. 1984, Jonsson et al. 1996, Morita et al. 1999, Tamate and Maekawa 2000). Such a phenotypically plastic response may also over time select for reduced egg size, if competition among newly emerged fry is reduced relative to that experienced in nature. While there are clear indications that hatchery rearing affects egg size, the direction of response, particularly the long-term evolutionary response remains less clear. The important point here, however, is that any alteration in egg size is likely to have important implications for the success of hatchery releases (cf. Einum and Fleming 2000b).

Breeding morphology

Morphology affects an individual's performance, and thereby its fitness (Arnold 1983). Fish morphology is under conflicting selection pressures (e.g. Riddell and Leggett 1981, Fleming and Gross 1989, Swain and Holtby 1989), and there are clear relationships between form and function (Robinson and Wilson 1996), so that body shape affects swimming performance (e.g., Skúlason et al. 1989). The hatchery environment exposes the fish to new developmental and evolutionary forces that may not only effect juvenile (reviewed in Einum and Fleming 2001), but also adult phenotypes. Hatchery adults appear to show reduced expressions of morphological characters important during breeding, such as secondary sexual characters (Fleming and Gross 1989, 1994, Petersson and Järvi 1993, Hard et al. 2000). Both environmental and genetic (domestication) factors appear responsible for these changes (Fleming et al. 1994). Such reduced expressions of secondary sexual characters can have negative consequences for natural breeding success (see below).

Breeding behaviour

Like morphology, the breeding behaviour of hatchery fish is predicted to be influenced by environmental effects and the relaxation, removal and/or alteration of natural and sexual selection. Experimental studies under semi-natural conditions indicate that these effects become evident primarily when hatchery fish breed sympatrically with, and face competition from wild fish (Fleming and Gross 1992, 1993, Fleming et al. 1996, 1997, Berejikian et al. 1997, Petersson and Järvi 1997). For hatchery females in competition with wild females, indicators of inferior competitive ability include delays in the onset of breeding (Fleming and Gross 1993), fewer nests (meta-analysis: $c^2 = 24.66$, df = 10, $P = 0.006$, Table 2) and greater retention of unspawned eggs (Fleming and Gross 1993, Fleming et al. 1996). This often occurs despite similar levels of overt aggression by hatchery and wild females ($c^2 = 5.64$, df = 12, $P = 0.93$, Table 2; but see Petersson and Järvi 1997). Hatchery females also appear more likely to have their eggs fertilised by several secondary males (most likely parr) than wild females, suggesting either poorer defence against, and/or a greater willingness to have secondary males present (Thompson et al. 1999). Ultimately, the breeding success of hatchery fish is frequently inferior to that of wild females ($c^2 = 19.97$, df = 6, $P = 0.003$, Table 2).

The breeding behaviour of males appears more strongly affected by hatchery rearing than that of females, reflecting the greater intensity of selection on male competitive ability during this period. Hatchery males tend to be less aggressive (meta-analysis: $c^2 = 24.54$, df = 12, $P = 0.017$) and less active courting females (meta-analysis: $c^2 = 60.38$, df = 12, $P < 0.001$), and ultimately achieve fewer spawnings than wild males (meta-analysis: $c^2 = 48.59$, df = 10, $P < 0.001$; Table 1). Across the studies reported in Tables 2 and 3, hatchery males suffer more from inferior breeding performance than hatchery females. This pattern also appears to carry over into the wild, where gene flow between cultured and wild salmonids is sex biased, principally involving wild males mating with cultured females (Fleming et al. 2000). The presence of male parr of cultured origin, however, could change this substantially (Fleming, unpublished data).

In most studies, environmental and genetic factors affecting the breeding behaviour of hatchery fish cannot be definitively separated. Fleming et al. (1997) in a study controlling for the genetic background of the fish, however, revealed that the environmental effects of hatchery-rearing up to smolting could be significant. They found differences in the breeding performance of hatchery and wild male, but not female Atlantic salmon. While having similar levels of aggression, hatchery males were involved in more prolonged aggressive encounters and incurred greater wounding and mortality than wild males. Furthermore, hatchery males were less able to monopolise spawnings and obtained an estimated 51% the breeding success of wild males. In another study, Fleming and Gross (1994) were able to experimentally quantify the intensity of natural and sexual selection on different male and female morphological traits, as well as behavioural differences between multi-generation hatchery and wild coho salmon. They revealed direct (i.e. independent) selection on body size, the secondary sexual trait hooked snout (significantly larger in wild than hatchery males), and hatchery-wild behavioural differences associated with breeding success. Such information provides a basis for predictions about effects of relaxed or altered selective pressures in hatcheries.

Breeding success and the contribution to natural productivity

Clearly, an array of changes in behavioural, life history and morphological traits associated with reproduction occur in culture environments and these may have important implications for the ability of released fish to contribute to natural productivity. The success of release programs must lie in their ability to allow fish to bypass the high mortality of early life in the wild (see above) and then to survive, breed and produce offspring that ***contribute*** to natural production in the wild (Waples et al. in press). The word "contribute" is important here, for it means that the released fish should not take away from the production of the wild population, if it still exists. Our aim in this section thus is to review the literature for evidence regarding the contribution of released salmonids to natural productivity.

The best examples of successful contribution come from the release of salmonids to re-establish extirpated populations (i.e. driven to extinction) once the cause(s) of extinction have been remedied or to introduce fish into areas formerly inaccessible to natural colonisation due to an obvious physical barrier (Ricker 1972, Withler 1982). Success appears to reflect the presence of an open or unsaturated niche, i.e. the absence of competition from local con- and/or heterospecifics. Such programs should be short term, aiming to establish populations rapidly and then once founded, allow natural selection to shape the population to its local environment. Continued releases are only likely to hindered proper establishment, i.e. adaptation to local conditions. This may be particularly problematic if the habitat has been altered in ways that require the fish to re-adapt (e.g., following hydropower development). What is unclear about such releases is whether they are any better in the long term than natural colonisation through straying from nearby populations, if the possibility exists. This, however, has never been addressed and unfortunately in our current environment, may be nearly impossible to examine because the vast

Table 2. Female reproductive behaviour of hatchery relative to wild salmonids. Effect: whether the trait expression in the hatchery fish differs from that in wild fish and in what direction. Origin of Effect: G + E = genetic and environmental, E = predominantly environmental, G = predominantly genetic, G > E = genetic effects suspected to be greater, E > G = environmental effects suspected to be greater.

Trait	Effect	Origin of Effect	Origin of Hatchery Fish	Length of Propagation	Species	Reference
Overt Aggression	Not different	G + E	Non-Native	15 years	Coho salmon	Fleming and Gross 1992
	Not different	G + E	Non-Native	15-16 years	Coho salmon	Fleming and Gross 1993
	Not different	G + E	Non-Native*	20 years	Atlantic salmon	Fleming et al. 1996
	Not different	E > G	Non-Native*	First generation	Coho salmon	Berejikian et al. 1997
	Not different	E	Native	First generation	Atlantic salmon	Fleming et al. 1997
	Less	G + E	Native	26-27 years	Brown Trout	Petersson and Järvi 1997
Number of Nests	Not different	G + E	Non-native	15 years	Coho salmon	Fleming and Gross 1992
	Not different	G + E	Non-native	15-16 years	Coho salmon	Fleming and Gross 1993
	Fewer	G + E	Non-native*	20 years	Atlantic salmon	Fleming et al. 1996
	Fewer	E > G	Non-Native*	First generation	Coho salmon	Berejikian et al. 1997
	Not different	E	Native	First generation	Atlantic salmon	Fleming et al. 1997
Breeding Success	Lower	G + E	Non-native	15-16 years	Coho salmon	Fleming and Gross 1993
	Lower	G + E	Non-native*	20 years	Atlantic salmon	Fleming et al. 1996
	Not different	E	Native	First generation	Atlantic salmon	Fleming et al. 1997
	Lower	G + E	Non-native*	23 years	Atlantic salmon	Fleming et al. 2000

* Fish were captively reared to maturity

Table 3. Male reproductive behaviour of hatchery relative to wild salmonids. Effect: whether the trait expression in the hatchery fish differs from that in wild fish and in what direction. Origin of Effect: G + E = genetic and environmental, E = predominantly environmental, G = predominantly genetic, G > E = genetic effects suspected to be greater, E > G = environmental effects suspected to be greater.

Trait	Effect	Origin of Effect	Origin of Hatchery Fish	Length of Propagation	Species	Reference
Overt Aggression	Less	G + E	Non-native	15 years	Coho salmon	Fleming and Gross 1992
	Less	G + E	Non-native	15-16 years	Coho salmon	Fleming and Gross 1993
	Less	G + E	Non-native*	20 years	Atlantic salmon	Fleming et al. 1996
	Not different	E > G	Non-native*	First generation	Coho salmon	Berejikian et al. 1997
	Not different	E	Native	First generation	Atlantic salmon	Fleming et al. 1997
	Not different	G + E	Native	26-27 years	Brown trout	Petersson and Järvi 1997
Courting	Less	G + E	Non-native	15 years	Coho salmon	Fleming and Gross 1992
	Less	G + E	Non-native	15-16 years	Coho salmon	Fleming and Gross 1993
	Less	G + E	Non-native*	20 years	Atlantic salmon	Fleming et al. 1996
	Less	E > G	Non-native*	First generation	Coho salmon	Berejikian et al. 1997
	Not different	E	Native	First generation	Atlantic salmon	Fleming et al. 1997
	Less	G + E	Native	26-27 years	Brown Trout	Petersson and Järvi 1997
Number of Spawnings	Fewer	G + E	Non-native	15-16 years	Coho salmon	Fleming and Gross 1993
	Fewer	G + E	Non-native*	20 years	Atlantic salmon	Fleming et al. 1996
	Fewer	E > G	Non-native*	First generation	Coho salmon	Berejikian et al. 1997
	Not different	E	Native	First generation	Atlantic salmon	Fleming et al. 1997
	Fewer	G + E	Native	26-27 years	Brown Trout	Petersson and Järvi 1997

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* Fish were captively reared to maturity

majority of strays are domesticated fish (farm escapees and hatchery strays).

Other examples of successful contributions from released salmonids are rare, if not non-existent. The most common form of release program is aimed at the supplementation of wild populations, i.e. the intentional integration of hatchery and natural production, with the goal of improving the status of an existing natural population (Finstad et al. 2000, Fjellheim and Johnsen 2001, Vøllestad and Hesthagen 2001, Waples et al. in press). Such integration, however, entails significant ecological and genetic risks to the wild population (e.g., Hindar et al. 1991, Waples 1991, Youngson and Verspoor 1998, Einum and Fleming 2001), as well as potential benefits. Yet, despite the vast majority of release programs involving supplementation and its importance as a management strategy, astonishingly little has been done in Norway and other countries to evaluate its effectiveness to meet its principal objective/goal.

The evidence that does exist is generally qualitative and indirect, based on genetic studies of introgression and ecological studies of correlates of breeding success or semi-natural experiments (Table 4). While genetic studies often provide quantitative estimates of introgression, they provide little information regarding the actual relative contribution of the released to wild fish to the natural production. For example, frequently the levels of introgression observed are the result of large-scale releases over many years. By this process, introgression must almost be inevitable. However, what is striking from our somewhat limited review of the literature is that 45% (14 of 31) of the investigations reported little or no evidence of introgression (Table 4). Thus, despite large-scale releases in many of these cases, the supplementation programs must be deemed failures. In ***none*** of the studies reporting significant introgression, is there information on whether the release program resulted in improved natural production of the population. Moreover, these genetic studies provide little clue as to the underlying determinants of introgression (e.g., relative lifetime reproductive success) or lack there of. At a broad scale, however, Utter (2000) noted a pattern of greater resistance to introgression among anadromous than among comparable freshwater populations, suggesting that more complex adaptations associated with an anadromous life history may be responsible (cf. Hansen et al. 2000).

All the ecological evidence points to diminished lifetime reproductive success and abilities of hatchery-released salmonids to contribute to natural productivity (Table 4). These studies identify critical life history episodes, particularly breeding, juvenile emergence and first year life, as key determinants of introgression (see also McGinnity et al. 1997, Fleming et al. 2000, review by Einum and Fleming, 2001). They also identify not only the directions of gene flow, but more importantly the causes for sex biases and general predictive models as to when and how such biases arise. Quantitative experimental evidence indicates that among anadromous adults, gene flow into wild populations occurs mainly via hatchery females because of the intense competition that hatchery males face from wild males (Fleming and Gross 1993, Fleming et al. 1996, 1997, 2000). However, where males have the opportunity to mature early as parr or as resident fish, such males may make significant genetic contributions to the population (Hansen et al. 2000). This likely results from their large size at release, which can influence both the propensity to mature early (e.g., Alm 1959, Thorpe 1986) and competitive ability (Jones 1959, Thomaz et al. 1997) relative to that of wild fish. The most complete evidence on relative lifetime reproductive performance of hatchery fish comes from two natural experiments that suggest that released fish have approximately a tenth the ability of wild fish to contribute to natural productivity (Table 4; see also Fleming et al. 2000). Neither study, however, examined whether the contribution of the released fish actually added to, or simply replaced the natural productivity of the wild fish. Addressing this latter issue is extremely important, but difficult, requiring an experimental design that incorporates manipulations (i.e. adding hatchery fish) and controls (i.e. excluding hatchery fish) on both spatial and temporal scales. Such experiments are expensive, long term and require management vision to address this vitally important question on the contribution of released fish to natural productivity.

In probably the most thorough attempt to date to examine the ability of supplementation programs to contribute to natural productivity, Waples et al. (in press) reviewed 19 such programs developed for Pacific salmon. Of those, nine populations showed an increase or had remained stable in size since the start of supplementation, while the remainder (10) had declined. They also found that supplemented and unsupplemented (control) populations showed similar trends in four of the six possible comparisons, while the supplemented population outperformed the control in one case and the reverse occurred in the other. Moreover, for two programs it was possible to compare the populations' status before and after supplementation had ended, and both remained "at risk". It thus seems clear that the supplementation of depressed natural populations using hatchery fish seldom achieves the objective of increased natural production (cf. Steward and Bjorn 1990). Predicting the outcome of a release must be considered a highly complex, and as yet unresolved problem, involving ecological and genetic factors.

Conclusions

The current review indicates that understanding breeding dynamics and reproductive success are critical to predicting effects of various conservation and supplementation programs, through their effects on the demographically and genetically effective population size, and gene flow. The value of reproductive performance in hatchery fish depends on the management goal. If the goal is to re-establish or rebuild wild populations for conservation purposes (i.e. conservation releases), current hatchery practices appear to result in competitively and reproductively inferior fish that limit their effectiveness. Long-term application of such releases will moreover inhibit local adaptation and thus natural productivity. On the other hand, if the goal is to supplement wild populations to increase fisheries (i.e. fisheries releases) while reducing impacts on the wild populations, such reproductive inferiority could be advantageous, limiting the negative effects of introgression. However, the threats of ecological interference and altered selection regimes associated with the introduction of hatchery fish remain. Moreover, reproductive isolation is likely to remain incomplete and even limited introgressive hybridisation may pose a concern, particularly when the scale of hatchery introductions is significantly greater than that of natural production. Clearly, the appropriate and effective use of hatcheries will be a balancing act.

Poorly managed hatchery programs can alter or even destroy biological diversity of species/populations. This does not mean, however, that we should give up on the hatchery concept as a management tool, particularly for populations facing high short-term risk of extinction. Rather, hatcheries need to be modified to minimise the detrimental effects of hatchery rearing on fish phenotypes and genotypes, including morphological and behavioural traits, and thus increase the potential for successful enhancement. We must also recognise an inherent conflict that exists in the way hatcheries currently function, to both conserve threatened wild populations and to enhance fisheries (cf. Fleming 1994). The use of hatcheries for the enhancement of fisheries will often directly threaten the existence of wild populations, particularly those in need of conservation, through direct and indirect genetic effects (reviewed by Hindar et al.1991, Waples 1991). Finally, we must recognise that release programs are not a solution to conservation problems, but rather should be thought of as a short-term aid for wild populations at risk. Conservation will only be successful if causes of decline in wild populations are remedied.

The biggest gap in our knowledge is understanding the performance of hatchery-produced fish and their progeny in the natural environment. Can release programs, particularly those designed for conservation, provide a net long-term benefit to natural populations? Moreover, when do we implement such programs, and then how do we best manage them to achieve this? Ideally, evaluations of supplementation programs should be conducted over a number of generations to

Table 4. Evidence of the ability of salmonid supplementation programs to contribute to the natural productivity of populations.

Type of Evidence	Frequency of release	Origin of Hatchery fish	Life stage at release	Species
Significant Interbreeding/Contribution to Natural Productivity				
Genetic	Repeated	Non-local	—	Brown trout
	Repeated (1968-83)	Non-local	Eyed eggs, 0+ fry, 1+ parr	Brown trout
	Repeated	Non-local	—	Brown trout
	Repeated (6-20 years)	Non-local	0+ fry, adults	Brown trout
	Repeated	Non-local	—	Brown trout
	Repeated (20+ years)	Non-local	0+ fry	Brown trout
	Repeated	Non-local	—	Brown trout
	Repeated	Non-local	—	Brown trout
	Repeated (1944-74)	Non-local	—	Brown trout
	Repeated (1970-92)	Non-local	Eggs, fry	Brown trout
	Repeated (test over 2 years)	Non-local	—	Brown trout
	Repeated	Non-local	—	Brown trout
	Repeated (1980-1992)	Non-local	0-2+, smolts	Brown trout
	Repeated	Non-local	Primarily smolts	Chinook salmon
	Repeated	Non-local	—	Cutthroat trout
	Repeated	Non-local	—	Rainbow trout
	Repeated (1938-95)	Non-local	Fingerlings, yearlings	Rainbow trout
Strongly Diminished or No Interbreeding/Contribution to Nautral Productivity				
Experimental	Single (1989)	Non-local	Adults	Brown trout
	Repeated (1976-79)	Non-local, but same drainage	Smolts	Steelhead trout
Genetic	Repeated (1950-76)	Non-local	Fry	Atlantic salmon
	Single (1990)	Non-local	0+ parr	Atlantic salmon
	Repeated (6-20 years)	Non-local	0+ fry, adults	Brown trout
	Repeated (20 years)	Non-local	0+	Brown trout
	Repeated	Non-local	0-2+	Brown trout
	Repeated (20+ years)	Non-local	0+ fry	Brown trout
	Repeated (1980-1992)	Non-local	0-2+, smolts	Brown trout
	Repeated	Non-local	—	Brown trout
	Repeated (1966-89)	Non-local	Eyed eggs, 0+, adults	Brown trout
	Repeated	Non-local	—	Brown trout
	Repeated (1980-90's)	Non-local	0-2+, smolts	Brown trout
	Repeated	Non-local	—	Chinook salmon
	Repeated (1, 2, 4 years)	Non-local	Eyed eggs	Chum salmon

Table 4. cont.

Observation	Reference
Significant Interbreeding/Contribution to Natural Productivity	
Genetic admixture of native and hatchery fish (Sweden)	Ryman 1981
Natural-spawning hatchery fish 42% genetic contribution to 0+ juveniles; excessive heterozygosity (N. Ireland)	Taggart and Ferguson 1986
Introgression common (France)	Barbat-Leterrier et al. 1989
Introgression rates up to 80% in some areas (France)	Guyomard 1989
Replacement of 2 natural river populations and near elimination of another (Spain)	Garcia-Marin et al.1991
Strong introgression in 2 lake populations (Spain)	Martínez et al. 1993
Introgression rates of ca. 75% (Greece)	Apostolidis et al. 1996, 1997
Introgression rates of 30-70% at 4 of 6 stocked localities (Italy)	Giuffra et al. 1996
Natural breeding and some introgression, but positive assortative mating common (Switzerland)	Largiadèr and Scholl 1996
2-55% introgression (Spain)	Cagigas et al. 1999
10% introgression within 2 years (Spain)	Garcia-Marin et al.1999
Introgression as high as 77% (France)	Berrebi et al. 2000
Up to 46% introgression with resident fish (Denmark)	Hansen et al. 2000
Genetic homogenisation in areas of intense hatchery culture (USA Pacific Northwest)	Utter et al. 1989
Extensive introgression between subspecies in the (USA Pacific Northwest)	Gyllensten et al. 1985
5 of 8 populations are interior-coastal hybrid swarms (Western USA)	Williams et al. 1996
Lower river pure, upper river a hybrid swarm (Oregon, USA)	Williams et al. 1997
Strongly Diminished or No Interbreeding/Contribution to Nautral Productivity	
Despite more hatchery than wild spawners, only 16-19% genetic contribution to 0+ juveniles; survival 3 times lower for hatchery-wild hybrids than wild fish to age 2+ (Norway)	Skaala et al. 1996
Success from breeding to 0+ juveniles 75-79% that of wild fish; lifetime reproductive success 11-13% that of wild fish (WA, USA)	Chilcote et al.1986, Leider et al.1990, Campton et al. 1991
Despite large releases of anadromous fish, landlocked salmon not detectably altered (Norway)	Vuorinen and Berg 1989
No indication of genetic contribution among adult fish (Spain)	Moran et al. 1994
Introgression rates as low as 0% in some areas (France)	Guyomard 1989
No evident genetic contribution (Spain)	Moran et al. 1991
Intensive stocking with little or no evidence of genetic contribution (Denmark)	Hansen et al.1993, Hansen and Loeschcke 1994
No detectable genetic influence in several rivers (Spain)	Martínez et al. 1993
Introgression low among anadromous fish (Denmark)	Hansen et al. 1995, 2000
Introgression rates of < 10% in 2 of 6 stocked localiteis (Italy)	Giuffra et al. 1996
Reproduced and interbred, but contribution diminished over time (France)	Poteaux et al. 1998
Extensive stocking had limited genetic impact (Spain)	Garcia-Marin et al. 1999
Little or no introgression (Denmark)	Hansen et al., in press
No evidence that strays had homogenised genetic characteristics of wild population (Snake R., USA)	Marshall et al. 2000
Despite millions of released fish, genetic contribution small and disappearing (Russia)	Altukhov and Salmenkhova 1987, 1990

Table 4. cont.

Type of Evidence	Frequency of release	Origin of Hatchery fish	Life stage at release	Species
Strongly Diminished or No Interbreeding/Contribution to Nautral Productivity				
Genetic	Repeated	Non-local	—	Rainbow trout
Ecological (Indirect)	Repeated (1982-88)	Local	Smolts	Atlantic salmon
	Single	Local	Smolts	Atlantic salmon
	Repeated (1991-93)	Local	Smolts	Brown trout
	Repeated (1980-82)	Non-local	Pre-smolts	Coho salmon
	Repeated (1988-89)	Non-local	Smolts	Coho salmon
	Repeated (decades)	Non-local	Smolts	Steelhead trout

permit distinguishing ecological and genetic effects of fish culture, and to evaluate the effectiveness of natural selection to restore fitness in natural populations of mixed hatchery-wild ancestry (cf. Waples et al. in press). Releases of hatchery fish can be a valuable management tool in our attempts to conserve wild salmon populations, yet considerable risks exist.

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Table 4. cont.

Observation	Reference
Strongly Diminished or No Interbreeding/Contribution to Nautral Productivity	
No detectable introgression (ID, USA)	Wishard et al. 1984
14% of females and 37% of males appeared not to have spawned (Norway)	Jonsson et al. 1990
Females similar, and males 51% the breeding success of wild fish (Norway)	Fleming et al. 1997
Males lower mating success (Sweden)	Petersson and Järvi 1999
Densities of juvenile offspring lower in stocked than unstocked streams (OR, USA)	Nickelson et al. 1986
Males 62% and females 82% the breeding success of wild fish (BC, Canada)	Fleming and Gross 1993
Population productivity and proportion of hatchery fish among natural spawners negatively related (OR, USA)	Chilcote 1997 cited in Waples 1999

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Estimating Carrying Capacity and Presmolt Production of Atlantic Salmon (*Salmo salar*) and Anadromous Brown Trout (*Salmo trutta*) in West Norwegian Rivers

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Abstract

Density estimates of presmolt Atlantic salmon and brown trout were obtained by electrofishing in late autumn in eleven rivers in western Norway during 1991 to 1999. Total presmolt density varied from 4 to 34 presmolt 100 m^{-2}, and decreased significantly with the natural logarithm of annual discharge (linear regression, R^2=0.84, P<0.001, N=11). Overall mean presmolt density and biomass were 15.8 and 282 g 100 m^{-2}. The results indicate that factors associated with high discharge constrain smolt production in some of these rivers. This may occur particularly during early summer when high water velocity may restrict the area of available habitat within rivers. Atlantic salmon presmolts outnumbered brown trout presmolts in the warm rivers, while there was a shift towards dominance of brown trout in the coldest rivers. The presmolt-discharge relation may provide a simple method to check if smolt production in a river differs from expected carrying capacity.

Keywords: carrying capacity, rivers, salmonids, presmolts, density.

Introduction

Knowledge about the carrying capacity for smolt production in rivers is crucial in order to measure changes in production and species composition due to different kinds of human impacts, such as river regulation, pollution, stocking and habitat changes. Published data on production of Atlantic salmon (*Salmo salar*) smolts in Norway are limited to two rivers. The methods used are either smolt traps (Jonsson et al 1998a), or mark-recapture (Hvidsten 1993). These methods are rather expensive and thus results are limited to a few rivers, providing little predictive power for estimating smolt production or for identifying carrying capacity in other rivers. For effective management, cost effective and robust methods for estimating smolt production are important. The abundance of young, stream-living Atlantic salmon and brown trout is regulated by density-dependent biotic factors (competition, predation), and density-independent abiotic factors (Gibson 1993, Elliott 1994). Important abiotic factors include flow and temperature, both of which influence habitat availability and fish behaviour (Heggenes and Saltveit 1990, Bremset and Heggenes 2001). Most Norwegian rivers, which are accessible for anadromous fish, host populations of both Atlantic salmon and brown trout. The presence of Atlantic salmon may be restricted more by low temperatures (Jensen and Johnsen 1999), low pH and high concentrations of aluminium (Hesthagen and Hansen 1991) than that of brown trout.

The relative abundance of juvenile Atlantic salmon and brown trout in rivers is also affected through stocking programs, predominantly of juvenile Atlantic salmon. During the last 20 years the survival of Norwegian stocks of Atlantic salmon has decreased in the sea, presumably due to low sea temperatures (Friedland et al. 1998), and in some areas also from the impact of heavy infestations of salmon lice (Holst and Jakobsen 1999). Consequently, the production of Atlantic salmon smolts may be influenced directly by poor water quality or indirectly by low numbers of spawners (Jonsson et al. 1998b). Depending on bottlenecks for recruitment, several types and combinations of actions can be taken, including limiting the catches of adult fish or stocking of juveniles. However, for action to be taken one should know both the minimum numbers of spawners needed to ensure sufficient recruitment (Jonsson et al. 1998b) and the carrying capacity for recruits. So far, there is limited information on both aspects.

Among rivers in western Norway, there is great variation with respect to flow and temperature, particularly during spring and early summer. Most of the coastal rivers in the west are characterised by relatively low discharge and rather early warming in spring. As one moves into fjords, the rivers are increasingly characterised by high flow and low temperatures during spring and early summer due to melting water from catchments at high altitudes. According to habitat studies, current speed and water depth are important determinants of the habitat use of Atlantic salmon and brown trout in rivers (Bremset and Heggenes 2001). When the discharge is high, water speed and depth restrict the area with profitable habitats for young fish (Heggenes and Saltveit 1990). These differences in physical conditions among rivers could, therefore, be reflected in differences in smolt production. The aim of the present study was to test the hypothesis that densities of Atlantic salmon and brown trout presmolts are related to discharge.

Methods and material

Study rivers

The investigated rivers were situated in western Norway. The county of Sogn and Fjordane was represented by the rivers Oldenelva, Eidselva, Nausta, Lona and Flåmselva, the county of Hordaland by Vosso, Botnaelva, Granvinelva, Oselva and Etneelva, and the county of Rogaland by Håelva (Table 1, Fig. 1). The rivers were chosen to avoid those clearly affected by acid precipitation and heavy transport of silt from glaciers. Rivers where recruitment was expected to be constrained by the number of adult spawners were also avoided, as were rivers containing stocked fish during summer/autumn that would be smolts the next spring. Records of discharge in nine rivers were obtained from the Norwegian Watercourse and Energy Directorate (NVE), and the discharges in two other rivers, Lona and Granvin, were calculated from run-off maps and precipitation records (NVE).

All the rivers have rather short stretches accessible for anadromous fish, ranging from 2.2 km to 28.0 km. Catchment areas vary from 24 to 1,070 km^2, and mean annual discharges vary from 1.7 to 95.9 m^{3}s^{-1} (Table 1). The actual watercourses span most of the variation in western Norwegian rivers, from small, warm coastal rivers to cold inland rivers of varying size (small to large). For example, the river Vosso is the second largest watercourse in western Norway. In five of the watercourses, there are lakes within reach of anadromous fish (Table 1), and these lakes might be nursery areas for anadromous brown trout (Jonsson 1985), but to a lesser extent for Atlantic salmon (own unpublished results). Mean temperatures during June vary from 5.9 °C in the coldest river to 15.2 °C in the warmest. In some of the warm rivers, the temperature rises rapidly through April as indicated by relatively high average temperatures already in May (Table 2).

Presmolt estimates

Presmolts are here defined as fish of a certain age and minimum length in the autumn, which

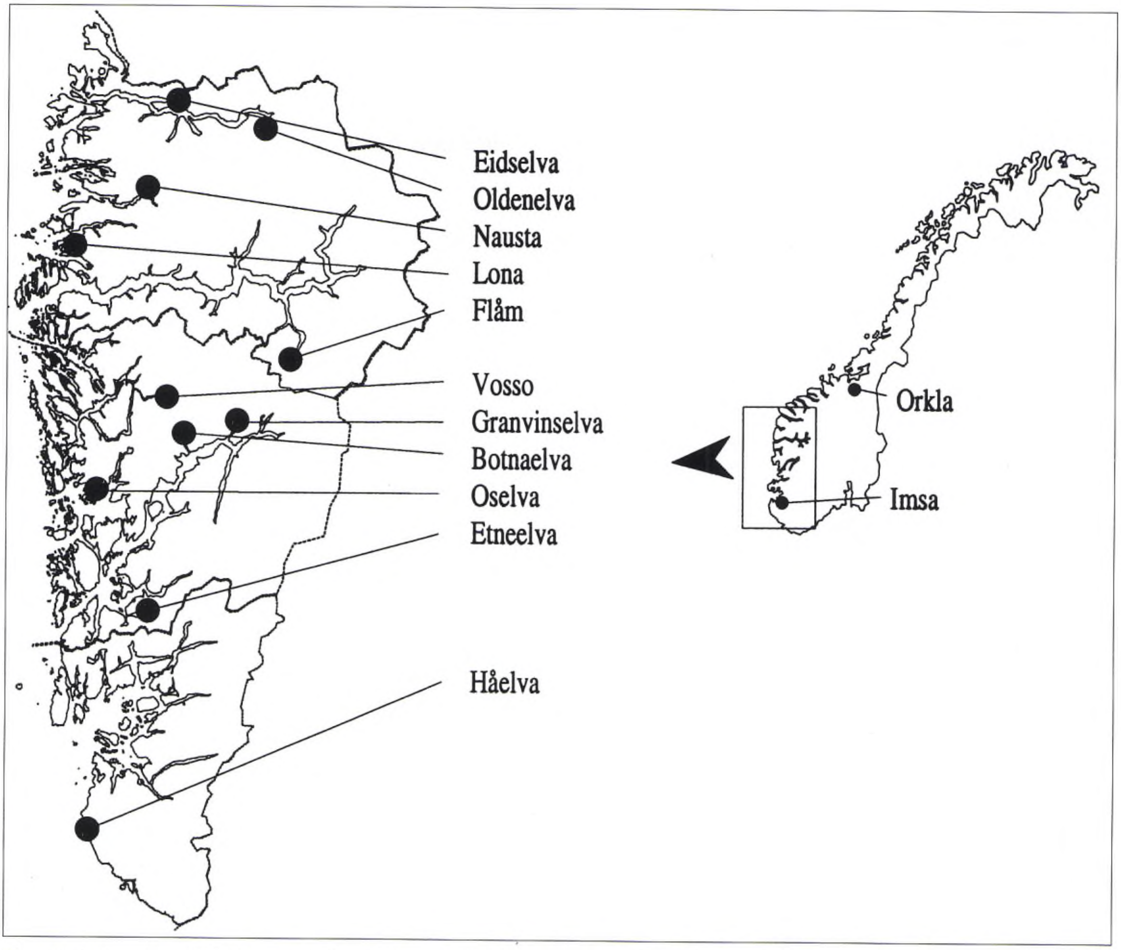

Fig. 1. Map showing the counties of Sogn & Fjordane, Hordaland and Rogaland in western Norway, and location of the eleven rivers indicated.

are likely to become smolts the following spring. The lower length limit for presmolts of different age groups was set according to reported smolt lengths of Atlantic salmon (Økland et al.1993) and brown trout (L'Abée-Lund et al. 1989). For both species, these limits were set to >90 mm for 0+, >100 mm for 1+, >110 mm for 2+ and >120 mm for 3+ and older fish. For brown trout, an upper limit of 160 mm was set due to the possibility that larger fish would remain resident rather than become anadromous.

Presmolt density was estimated using standard electrofishing procedures (Bohlin et al. 1989). In each river, fish were sampled from a minimum of three sites, each having an area of 100 m². The electrofishing was carried out during October-December at temperatures normally below 8 °C. Length and weight were measured on all fish captured, sex and gonadal stage were determined, and they were aged using otholits and/or scales. In most cases, the discharge at the time of electrofishing was below 30% of the annual mean discharge in the largest rivers, and below 50% of that in the smallest rivers. Usually more than 80% of the total river area was covered with water when electrofishing (Sægrov et al. 1998). The sites

Table 1. The rivers in western Norway investigated during 1991 to 1999 with catchment area of each river, passable river length for anadromous fish, year of investigation, number of sites electrofished, discharge as yearly mean, and through May-July as mean and percent of yearly mean. Presmolt densities are given for Atlantic salmon (As), brown trout (bt) and both species combined with 95% confidence interval. Density of Atlantic salmon presmolts is also given as percent of total density. Fish biomass is given as total weight of fish captured and biomass of presmolts. * indicate rivers where lakes are used as nursery areas for anadromous brown trout.

River	Catchm. area (km^2)	Asc. river stretch (km)	Year	No. of sites	Mean discharge (m^3 s^{-1})			Presmolt density (*N* 100 m^{-2})				Fish biomass (g 100 m^{-2})		
					Annual	May-July	% of year	As	bt	Combined ±95% c.i.	As %	Total	Pre-smolt	% pre-smolt
Olden	222	2.7	1995	4	17.5	26.5	151	3.3	4.9	8.1 ± 1.5	40.7	448	130	29.0
			1996	4	14.4	18.9	131	8.1	14.0	21.2 ± 5.0	38.2	892	384	43.0
			1998	4	14.6	23.4	160	4.3	7.6	11.0 ± 1.7	39.1	515	206	40.0
			1999	4	12.0	24.7	206	2.9	12.2	15.1 ± 4..7	19.2	570	211	37.0
Eid*	422	12.0	1995	8	27.1	43.3	160	2.9	1.7	4.4 ± 2.3	65.9	189	82	43.4
			1996	5		21.4		5.4	4.4	9.8 ± 1.1	55.1	353	189	53.5
Nausta	273	12.4	1995	10	22.5	36.8	164	6.1	7.6	13.8 ± 1.7	44.2	406	273	67.2
			1996	10	11.4	16.0	140	10.2	10.0	20.1 ± 2.6	50.7	497	309	62.2
Lona	24	7.0	1995	4	1.7	0.9	53	2.0	31.4	33.3 ± 3.6	6.0	1188	617	51.9
			1996	4	1.7	0.9	53	1.9	32.4	34.1 ± 3.0	5.6	979	575	58.7
Flåm	277	4.8	1993	9	16.7	41.0	246	3.7	5.6	9.3 ± 1.4	39.8	327	137	41.9
			1994	9	19.2	44.2	230	5.8	3.9	9.8 ± 1.2	59.2	345	142	41.2
			1996	5	13.4	30.4	227	2.2	9.4	11.5 ± 0.9	19.1	467	249	53.3
			1998	5	15.1	33.4	221	5.3	8.3	13.6 ± 1.0	39.0	706	314	44.5

Table 1. cont.

Vosso*	1070	10.0	1991	6	69.2	100.3	145	4.7	1.3	6.0 ± 0.4	78.3	262	88	33.4
			1992	14	95.9	195.2	204	6.4	1.0	7.3 ± 2.7	87.7	321	106	33.0
			1993	12	73.9	184.5	250	3.9	0.5	4.4 ± 0.7	88.6	229	67	29.3
			1996	8	44.9	72.2	161	9.0	0.7	9.7 ± 3.5	92.8	289	152	52.6
			1997	9		164.5		7.8	0.4	8.2 ± 4.1	95.1	262	122	46.6
Os*	113	9.0	1991	6	5.6	3.3	59	23.7	3.8	27.4 ± 2.7	86.5	631	520	82.4
			1993	6	3.5	2.3	66	17.9	4.5	22.3 ± 2.0	80.3	581	448	77.1
			1994	6	4.6	4.7	102	16.1	3.6	19.8 ± 2.7	81.3	473	387	81.8
			1995	6	5.3	4.5	85	12.5	5.0	17.4 ± 2.9	71.8	565	425	75.2
			1996	6	3.3	3.0	91	11.8	4.1	15.3 ± 4.7	77.1	320	273	85.3
			1997	6		1.6		15.4	4.6	19.5 ± 5.0	80.0	478	250	52.3
			1998	6	5.3	3.0	57	13.8	4.2	17.7 ± 1.7	78.0	422	330	78.2
Botnaelv	27	2.2	1999	6	2.1	3.9	186	0.0	29.8	29.8 ± 2.6	0.0	1316	607	46.1
Granvin*	179	8.5	1991	5	4.6	7.3	159	13.6	3.4	17.0 ± 0.9	80.0	538	289	53.7
			1993	4	4.6	7.3	159	17.8	5.4	23.1 ± 1.2	77.1	562	371	66.0
Etne*	252	13.0	1991	5	15.6	13.4	86	5.2	0.9	6.2 ± 1.2	83.9	161	112	69.6
			1995	3	17.6	23.6	134	13.9	3.8	17.2 ± 1.3	80.8	404	304	75.2
			1997	9	15.6	15.3	98	8.2	2.9	10.7 ± 2.3	76.6	169	127	75.1
Håelva	159	28.0	1999	11	7.1	4.8	67	22.9	3.5	26.2 ± 6.1	87.4	653	468	71.7

for electrofishing were chosen to cover representative habitats. However, areas with sand and deep pools were avoided because of limitations of the method in these habitats. At most sites, the riverbed was cobbles and stones, and included both riffles and calmer areas with water depth from 5 to 80 cm. The habitats fished did not differ systematically with regards to water velocity, substrate and depth among rivers.

The fish were sampled during 1991-1999, and from 6.7 sites on average in each river. From nine of the rivers there are records from two or more years, in the remaining two rivers there are records from one year only. Presmolt density was estimated as a mean for all sites in each river in one year, producing a total of 33 estimates. A total of 14,366 parr were sampled, 8,896 (61.9%) Atlantic salmon and 5,470 (38.1%) brown trout. Of these, 3,022 were presmolts, of which 1,798 (59.5%) were Atlantic salmon and 1,224 (40.5%) were brown trout. Both species were present in ten of the rivers, while one river contained only brown trout.

Results

In six of the ten rivers where both species were present, Atlantic salmon presmolts outnumbered brown trout presmolts all years. In three rivers, brown trout outnumbered Atlantic salmon presmolts all years, and in the remaining two rivers, the presmolt dominance shifted between the two species in successive years. The highest presmolt densities were found in the river with only brown trout (Botnaelva), and in the river where brown trout presmolts outnumbered Atlantic salmon presmolts (Lona) (Table 1).

The combined densities of Atlantic salmon and

Table 2. Mean temperatures in May, June and July of the year that presmolt length (mm) and age (years), were determined for Atlantic salmon (As) and brown trout (bt) captured in eleven rivers in western Norway during late autumn.* indicates that the temperatures were recorded in 2000, and fishing was carried out in the autumn of 1999.

		Mean temperature, °C			Estimated smolt length±SD (*N*)		Estimated smolt age±SD	
River	Year	May	June	July	Atlantic salmon	brown trout	As	bt
Olden	1999	9.4	11.2	11.2	109.5±11.5 (11)	115.7±11.0 (47)	2.3±0,7	2.2±0.5
Eid	1996	5.0	6.5	9.7	120.0±11.6 (31)	120.8±14.2 (31)	3.1±0.8	2.1±0.3
Nausta	1996				115.8±13.9 (96)	125.5±15.6 (92)	2.5±0.7	2.3±0.5
Lona	1996				113.0±22.2 (6)	121.7±14.8 (124)	2.7±1.6	2.5±0.7
Flåm	1998	5.2	6.9	9.2	124.4±6.3 (31)	125.2±12.5 (49)	3.9±0.8	3.3±0.6
Vosso	1996	6.0	10.3	14.5	123.7±11.5 (54)	124.2±21.0 (5)	3.2±0.9	2.6±0.6
Os	1996	8.6	13.5	14.4	121.6±14.1 (73)	123.6±17.1 (27)	2.1±0.3	2.1±0.4
Botnaelv	1999	5.4*	6.2*	9.2*	-	126.7±13.6 (172)	-	3.3±0.7
Granvin	1999				122.8±13.1 (46)	133.0±14.5 (9)	3.0±0.7	2.9±0.6
Etne	1997	7.0	12.0	16.8	122.7±14.8 (47)	121.8±18.1 (13)	2.6±0.6	2.1±0.3
Håelva	1999	12.8	15.2	17.6	125.1±23.3 (216)	108.2±26.2 (28)	1.7±0.4	1.2±0.4

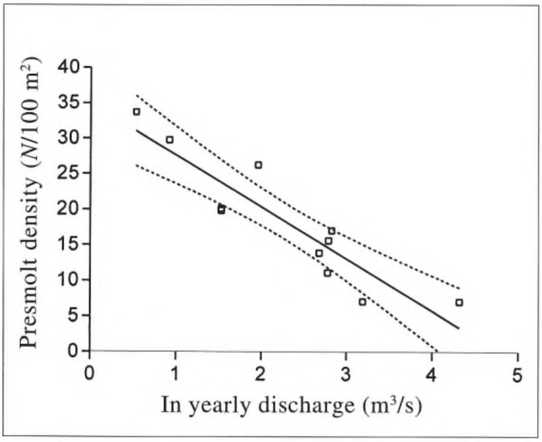

Fig. 2. Annual mean density of Atlantic salmon and brown trout presmolts in eleven rivers in western Norway in relation to the natural logarithm of annual water discharge. The linear regression is given with 95% confidence interval.

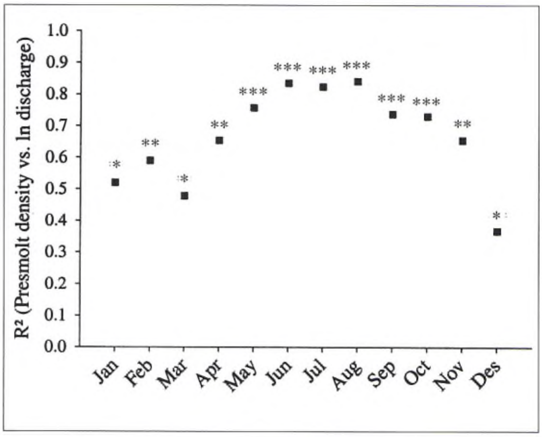

Fig. 3. R^2 of the linear regressions of mean presmolt density vs. ln mean monthly discharge in eleven rivers in western Norway. Significance levels are indicated for each month: $^*P<0.05$; $^{**}P<0.01$; $^{***}P<0.001$.

brown trout presmolts ranged among rivers and years from 4.4 to 34.1 presmolts 100 m^{-2} (Table 1), with an overall average (± SD) of 15.8 (± 8.1) 100 m^{-2}. Average Atlantic salmon and brown trout presmolt densities were 9.1 and 7.1 per 100 m^{-2}. Because the density of presmolts in one year may be affected by the density the previous year and are therefore not necessarily independent, presmolt densities were averaged over all years to obtain a single presmolt density for each river. The average presmolt density was significantly correlated to mean annual discharge ($y_1=34.91-7.29\ \ln(x_1)$, $R^2=0.84$, $P<0.001$, $N=11$, Fig. 2). The average presmolt density was also significantly correlated to discharge in every month of the year, but the relation showed the best fit during the summer months; June, July and August (Fig. 3).

Mean fish biomass (± SD) in the eleven rivers was 501 g (± 271) 100 m^{-2}, ranging from 161 g to 1,316 g 100 m^{-2}. Average presmolt biomass was 282 g (±157) 100 m^{-2}, and made up 56% of total parr biomass. In rivers where the fish grow slowly and consequently had a high smolt age, the presmolts made up less of the total parr biomass than in rivers with lower smolt age (Tables 1 and 2). In the warmest river, presmolts made up as much as 85% of the total parr biomass, while presmolts made up only 29% of total parr biomass in the coldest river.

In some of the rivers, low temperature in spring and summer may be related to a high discharge, but it not possible with this dataset to test if and possibly how presmolt density is affected by temperature or a possible combination of temperature and discharge (Table 2 and 3). The datasets from the rivers Botnaelva and Håelva may illustrate that the combined effect of discharge and temperature in spring-early summer is not clearcut. Both rivers had discharges of 4.8 m^3 s^{-1} during May-July, but the average temperature during May-July was highly different with 6.9 °C and 15.2 °C, respectively (Table 2). In the autumn of 1999, the presmolt densities were estimated at 29.8 and 26.2 100 m^{-2} in Botnaelva and Håelva, respectively (Table 1). Average presmolt age of brown trout was 3.3 and 1.2 years, while presmolt lengths were 126.7 mm and 108.2 mm, respectively in the two rivers (Table 2).

Mean temperatures in spring and early summer varied considerably among the studied rivers, from 3.1 to 12.8 °C in May, and from 9.2 to 17.6 °C in July (Table 2). In accordance with a high variation in temperatures among rivers, the estimated mean presmolt age varied from 1.2 years to 3.7 years for brown trout, and from 1.7 to 4.8 years for Atlantic salmon (Table 2).

An important question is whether the relation between presmolt densities and discharge is indicative of actual smolt production. If that is the case, the carrying capacity for smolt production can be predicted from discharge data. To validate the model, we compared a series of actual and estimated smolt densities, with predicted presmolt densities for two rivers, the Imsa and Orkla. In the river Imsa, the number of descending Atlantic salmon smolts has been recorded in a smolt trap each year since 1975. During 1975 to 1993 the production of Atlantic salmon smolts varied from 4 to 31 ind. 100 m^{-2} (Jonsson et al. 1998a). Jonsson et al. (1998a) estimated brown trout to comprise 10% of all past smolts, thus on average there are 17.2 smolts 100 m^{-2}. When using the equation for y_1 above, and an annual discharge of 5.1 m^3 s^{-1}, the presmolt estimate was 23.1 smolts 100 m^{-2}, and thereby 34% higher than the average smolt density. The average smolt density in river Imsa is significantly less than predicted from equation y_1 and the 95% confidence limits (Fig. 2), but still within the range of variation in smolt density (Jonsson et al. 1998a). In the river Orkla, smolt production has been estimated annually by mark-recapture since 1983 (Hvidsten 1993). Average smolt density during 1983 to 1991 (including 10% of brown trout; Hvidsten 1993), was estimated at 7.6 100 m^{-2}. The average yearly discharge was 41 m^3 s^{-1}, and the presmolt estimate from equation y_1 is 7.8 100 m^{-2}, which is nearly similar to the average smolt estimate.

Discussion

This investigation identified a significant negative relation between density of presmolts and discharge. While discharge itself may not be the determining factor, other factors such as river size and water velocity, which are related to discharge, may be important determinants. For example, in small rivers a greater proportion of the river is likely to contain suitable habitats than in larger rivers, where large sections may have high water velocity. The variation in presmolt density among rivers may well be a consequence of the correlated effects of water velocity, which may restrict the availability of suitable habitats for young fish at high discharges (Heggenes and Saltveit 1990, Bremset and Heggenes 2001). When flow is moderate or low, the total bredth of the riverbed may offer good feeding opportunities. The summer appears to be a particularly important period because discharge and temperature differ more among rivers in western Norway than during winter (Sægrov et al. 1998). This annual pattern of discharge and temperature is related to climate and topography, and the pattern may well be different in other geographic regions.

The regression line of presmolt density on discharge was rather steep in the discharge interval from 1 to 20 m^3 s^{-1}, at discharges above this the line levelled off. Obviously, the presmolt density in larger rivers would not increase to a maximum if discharge was reduced to very low levels, but it not unlikely that each river has an optimum discharge when the area with preferred habitats is maximised.

Estimates of presmolt densities in the autumn are not directly comparable with estimates of the smolt production the next spring because there will be some mortality during winter (Hvidsten 1993). It is not known if the mortality rate differs among rivers, years and species. Coastal rivers commonly have higher discharges during winter than inland rivers in western Norway due to the mild coastal climate. In the lowland areas, most winter precipitation is in the form of rain, whereas the catchments of inland rivers receive more of their winter precipitation as snow. This difference in climatic conditions could possibly affect winter mortality. However, if winter mortality is similar in the investigated rivers, the established relation between presmolt density in the autumn and mean water discharge may provide an index of smolt production and carrying capacity for rivers in western Norway. The actual smolt production in the small river Imsa (Jonsson et al. 1998a) was higher than in the larger river Orkla (Hvidsten 1993). Although not directly comparable with the smolt estimates, we also found higher presmolt densities in the small rivers than in the larger rivers.

The estimated presmolt age varied considerably among rivers and between the two species, but there was little variation in estimated smolt length among rivers and species. Lower temperature limit for growth is about 4 °C for brown trout (Elliott 1994) and 6-7 °C for Atlantic salmon (Jensen and Johnsen 1986). In the investigated rivers in western Norway, brown trout will experience temperatures above their lower limit for growth from April in the warmest rivers, and from May in most others. The lower limit for growth of Atlantic salmon is reached during May in some rivers, and not until late June in the coldest. The higher growth rate of brown trout compared that of Atlantic salmon may be explained by the former's longer growing season and ability to grow at lower temperatures. In addition, brown trout spawn earlier than Atlantic salmon, and consequently their offspring emerge earlier from the gravel in many rivers. In the present study, we have focused on the total density of presmolts, under the assumption that parr of the two species compete for available resources. Brown trout presmolts outnumbered Atlantic salmon presmolts in some rivers and years, and the reason may well be that brown trout benefit from their physiological ability to survive at lower temperatures than Atlantic salmon at swim-up (Jensen and Johnsen 1999). Thus, the dominance relation between the two species might vary in relation to variation in spring temperatures.

The presmolt biomass in the eleven rivers in this study averaged 282 g 100 m^{-2}, and made up 56% of the total parr biomass of 501 g 100 m^{-2}. One can assume little or no growth during winter, and the average biomass of parr should thereby be 219 g 100 m^{-2} after the smolt run the next spring. In the warm river Håelva and the cold river Botnaelva, presmolts made up 72% and 46% of the total fish biomass, respectively. The total presmolt biomass, however, was similar in the two rivers, with 568 g 100 m^{-2} of predominantly Atlantic salmon in the river Håelva, and 607 g 100 m^{-2} of only brown trout presmolts in river Botnaelva. These rivers are of similar size, but highly different with respect to spring temperatures, and the results indicate that the relation between spring temperatures and smolt production is not straightforward. Bremset and Berg (1997) found 2.5 times higher density of parr in pools compared to riffle areas in the same rivers. In two of the pools, fish biomass was estimated at 690 and 1,200 g 100 m^{-2} compared with 160 to 370 g 100m^{-2} in riffle areas. The pools were deep, with back-waters and generally low flow, and had a larger waterbody masses than riffles, which could explain the differences in fish density.

The fish and presmolt biomass found in the eleven rivers in the present study are within the range reported from other rivers. The actual densities of smolts in the small river Imsa and estimates of smolt production in the larger river Orkla, show the same trend according to discharge as the presmolt model. Thus, the relation may have applicability to the management of stocks of Atlantic salmon and anadromous brown trout, at least within the region studied, providing estimates of the status of such populations relative to their expected carrying capacities.

In situations where stockings of fish are being considered, it will be valuable to know the carrying capacity of the river and the current status of the wild population relative to this. If total presmolt densities are below carrying capacity, one should identify the reason or reasons. A check-list of possible bottlenecks could include the number of spawners and reproductive potential of both Atlantic salmon and brown trout, water temperatures and water quality. Until the major bottleneck(s) are identified, stocking of fish should be avoided because stocking itself may have adverse effects on the wild stocks (see other papers in this volume).

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Stocking Atlantic Salmon (*Salmo salar* L.) and Brown Trout (*Salmo trutta* L.) in Rivers: Diet Selectivity and the Effects on the Macroinvertebrate Community

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Abstract

This paper reviews the literature on diet selectivity and the effects of fish predation on the invertebrate community in streams. Further we give examples from Scandinavian investigations and stocking programs aiming to give a state of the art of knowledge on how fish stocking can influence and structure invertebrate communities in running water. Several studies have shown weak or no effects of fish predation, whereas others have shown strong cascading effects. Benthic-feeding fish have greater impact on benthic prey than drift-feeding fish like Atlantic salmon and brown trout. Predator impacts seem to be less apparent when prey replenishment rates are high. Terrestrial prey in the drift may reduce the impact on lower trophic levels. Several Scandinavian studies conducted on stocked fish and their nutrition indicate that stocking of anadromous fish probably has little effect on abundance and biomass of invertebrates, particularly if the river stretch already has juvenile fish of the same species. There is a need for laboratory and comparative field studies and experiments aimed at testing specific hypotheses related to predator-prey interactions in running water.

Key words: Atlantic salmon, brown trout, stocking, predator-prey, interactions, macroinvertebrates, poulation dynamics.

Introduction

Predation is known to exert an important influence over aquatic communities, and can affect the biological community both directly and indirectly (Kerfoot and Sih 1987). A direct effect can be a reduction in prey abundance and biomass. Indirect effects can include behavioural alterations in prey activity and distribution. The role of predation by fish and invertebrates in the population dynamics of their prey and in structuring benthic communities in running water has received much attention, but still there seems to be little consensus regarding this aspect (Cooper and Walde 1990, Allan 1995, Dahl 1998a). Stocking of fish in running water represents a possible impact on the invertebrate community through grazing. Stocking of anadromous fish in Norway is performed for different reasons (Vøllestad and Hesthagen 2001). The most common is to compensate for lost recruitment due to hydropower regulation. Stocking also associated with the restoration of brown trout (*Salmo trutta* L.) and Atlantic salmon (*Salmo salar* L.) populations after liming of acidified lakes and rivers (Fjellheim and Johnsen 2001). Put-and-take releases are carried out in some cases, as well as stocking by local fishing organisations aiming to increase fish yield. The physical and chemical environments that damage fish populations will also affect the community of invertebrates. Therefore, compensation of fish recruitment by releasing fish does not improve the damaged habitat either for fish or invertebrates. It is important to realize this when evaluating biological interactions after fish stocking. After hydropower regulation for instance, it will be difficult to discriminate between the effects of regulation and effects from fish predation on the invertebrates.

In fishless systems, invertebrate predators control the lower levels in the ecosystems, while fish are the driving force in systems with fish. The different biotic interactions caused either by invertebrate or fish predation, give rise to quite different species communities (Stenson et al. 1993). Due to this, introduction of fish into fishless habitats will have a major impact on the invertebrate community. Predation may reduce the density of dominant benthic species and allow for the possibility of increased densities of less competitive species. There may also be a difference in the effects of salmonid predation on invertebrates depending on whether the fish are stocked to enhance recruitment of an already existing population, or stocking is done to introduce a new species into a river stretch. For instance, Atlantic salmon have been stocked in river stretches not previously accessible to anadromous fish. Thus, we will expect the three levels of stocking to have different influence on the macroinvertebrate community: i) stocking of no-fish systems, ii) increased fish density where species already exists and iii) introducing a new fish species into a watershed or river stretch.

In Norway, very few studies have been carried out to investigate the interaction between stocking of fish and invertebrates in running water. Investigations performed in other countries show varying results. As examples, Allan (1982), Flecker and Allan (1984), Culp (1986) and Reice (1991) found no effect of fish predation on invertebrates in running water, while Gilliam et al. (1989), Power (1990), Bechara et al. (1992), Dudgeon (1993) and Dahl (1998a) recorded reduction of several invertebrate taxa as well as changes in the community structure.

In this review we will focus on predation effects from fish on invertebrates primarily in running water. One important aim will be to compare studies on the invertebrate community in streams with and without fish to evaluate the structuring effect from fish on the river fauna. Further, we will discriminate between drift-feeding fish (salmonids) and benthic-feeding fish. Our hypothesis is that fish with different feeding patterns have different structuring effects on the invertebrate species composition.

Fish-macroinvertebrate interactions in running water

Foraging theories – foraging strategies for Atlantic salmon and brown trout

In their stream-dwelling parr stage, the food choice of both salmon and trout is strongly liable to food availability (Egglishaw 1967). This variation in feeding may be due to differences in habitats in, and between different rivers, and the availability of feeding particles.

In this way, the foundation for an opportunistic foraging behaviour is laid, regulated by the presence and behaviour of prey and the ability of fish to utilize different kinds of prey (Cada et al. 1987, Nielsen 1992). This grazing strategy was also shown by Keely and Grant (1996), while other research suggests that fish are selective in their choice of food (Allen 1940, Maitland 1965, Metz 1974, Ringler 1979, Williams 1990).

The choices of food are affected by availability and size of prey (Allan 1978), the prey's digestibility (Elliot 1967, Wootton 1990) and the predator‘s experience (Werner et al. 1981). According to optimal foraging theory, the predator at all times will choose the most profitable prey providing it occurs in sufficiently large quantities (Charnov 1976). If the density of the prey decreases, the diet will be supplemented by less profitable prey. According to theory, the diet will never be determined by the least profitable prey. Consequently, it is presumed that the predator tries to maximize the net intake ratio per time unit. It will therefore be profitable to feed on prey having high densities and energy content, and minimal consumption time in terms of catching and "treating" the prey. This means that the chance of salmon or trout seriously impacting rare species by predation is small.

Many investigations show, however, that fish often deviate from optimal grazing behaviour (Bannon and Ringler 1986). In the stomach of juvenile salmon one often finds most of the available kinds of prey in the environment (Elliot 1967, 1970, Allan 1981, Sagar and Glova 1995, Kjelsaas 1995, Tønset 1996, Johnsen et al. 1997). This type of opportunistic grazing behaviour is presumed to be common when the density of prey is low or preferable prey items are difficult to find (Bannon and Ringler 1986, Frankievicz et al. 1993). The fact that the fish graze on most available kinds of prey is sub-optimal according to optimal foraging theory. But periodically grazing on a wide spectrum of prey, enhances the fish's ability to respond to quick changes in the environment with respect to the occurrence of different prey (Ringler 1979). A strategy maximizing the number of consumed prey and not the energy intake might be optimal under certain circumstances (Frankievicz et al. 1993). This can occur when the energy cost of sustaining position in the current is so high that the costs of grazing on bigger and smaller animals stay the same (Wankowski and Thorpe 1979, Frankievicz et al. 1993). In areas where the costs of keeping the position are lower, for example in pools and slow-flowing parts of the river, it is likely that salmon have an energy maximizing strategy (Frankievicz et al. 1993, Tønset 1996). This may result in different grazing effects from juvenile fish on the benthic invertebrates in pools than in riffles.

Juvenile salmon and trout have the possibility of grazing both on benthic invertebrates and drifting fauna. However, during the summer, drifting invertebrates in the water are the main food source (Bachman 1984, Stradmeyer and Thorpe 1987, Keely and Grant 1995). Drift-feeding fish like Atlantic salmon and brown trout might therefore have a different effect on invertebrates than typically benthic-feeding fish such as bullhead and burbot.

Several studies show that benthic feeding fish species may have a direct negative effect on both invertebrate biomass, diversity of species and invertebrate activity (Anderson et al. 1986, Dahl 1998a, Koksvik 1998). However, drifting fauna is produced in neighbouring stretches of the river and will often have a composition much like the bottom fauna (Brittain and Eikeland 1988, Tønset 1996). Furthermore, the drift will contain a varying degree of terrestrial animals. Since drift is a product of the mixture of invertebrates, it is likely that predation from fish influencing the invertebrates also will have an indirect influence on drifting fauna.

Most studies on juvenile salmon and trout's choice of habitat and food have been carried out during summer. Rivers are, however, extremely time-space variable, and summer studies do not give a sufficient basis for evaluating grazing effects of salmon and trout on the invertebrates taken as a whole. During the warmer periods of the year the parr keeps its position above, but close to substrate in river stretches with riffles, while spreading throughout pools (Bremset 1999). In the colder periods, however, the parr takes cover in the substrate (Gibson 1978, Cunjak 1988, Heggenes and Saltveit 1990, Bremset and Berg 1999). Juvenile salmon and trout stay in the same areas of the river both summer and winter (Morantz et al. 1987, Heggenes et al. 1993). In addition to a cryptic way of living, recent research indicates that the fish also have a distinct change of behaviour between day and night at low temperatures during the winter. These studies show that the fish reappears from its daytime hiding places and may stay active all night. This change in behaviour occurs when the water temperature falls below 8-10°C, and is regulated by light (Fraser et al. 1993, Heggenes et al. 1993). Simultaneously, physiological changes in the fish's retinae occur, enhancing its vision (Allen et al. 1982) and the possibility to catch a prey in the dark. This type of behaviour in cold rivers may cause salmon and trout to shift from being primarily drift-feeders to benthic-feeders, as has been demonstrated for salmon in subarctic rivers (Bergersen 1989, Amundsen et al. 1999, Gabler and Amundsen 1999, Amundsen et al. 2000). Benthic feeding by salmon and trout appear to be particularly important in winter and in subarctic rivers in autumn when drift rates appear to be low (Brittain and Eikeland 1988). The grazing effects on the macroinvertebrates might therefore be different in the cold season compared to the warm season. However, at lower temperatures the need for food will decrease together with basal needs, although recent laboratory study has demonstrated that young salmon are able to grow at near-freezing temperatures (Koskela et al. 1997). In rivers, the young-of-the-year of wild Atlantic salmon come out of the gravel to start feeding at ca. 8°C (Jensen et al. 1991), and minimum temperature of 8°C is recommended for the initial feeding (Refstie 1979). Brown trout, however, seems able to grow and utilize food at somewhat lower temperatures than salmon. We suspect, therefore, that juvenile fish of both species have a low grazing pressure on forage animals throughout the cold season, making the impacts of fish predation on macroinvertebrates during the summer season the most important. Benthic diversity and densities, drift rates, feeding by salmonids and the grazing effects on invertebrates during the winter have not been the subject of much investigation, however.

Direct effects of predation - impacts on benthic stocks, species diversity and biomass

Predation affects the biological community directly and indirectly (Kerfoot and Sih 1987). A direct effect is a reduction in prey abundance and/or biomass. There have been many studies on the predatory effect of fish on invertebrate communities in running water and the results are highly variable. Several surveys show only minor or no effect on density and species composition of invertebrates after fish predation (Allan 1982, Flecker and Allan 1984, Culp 1986, Reice 1991), while others have shown stronger effects with the reduction of at least some invertebrate taxa and a change in community structure (Flecker 1984, Gilliam et al. 1989, Power 1990, Bechara et al. 1992, Dudgeon 1993, Dahl 1998a).

Allan (1982) reduced the trout density in a creek to 10-25% of its original level, but found no changes in the density of invertebrates or drift as a result of reduced fish density. He pointed out, however, that the variation in the invertebrate samples was very large. Allan proposed that invertebrate communities in running water are adapted to fish predation and that the invertebrates are less sensitive to changes in fish density and predation pressure.

Straskraba (1965) reported that an amphipod that was common in a headwater stream, became very scarce within a 100 m stretch, coincident with a high weir and the occurrence of large numbers of brown trout. In contrast, neither Jacobi (1979) nor Reice and Edwards (1986) found any changes in invertebrate abundances during comparison of sections above and below waterfalls in North American trout streams. Examining 30 stream sites in southern Ontario, Canada, Bowlby and Rolff (1986) demonstrated that sites with piscivorous fish exhibited a lower biomass of non-piscivorous fish but higher biomass and abundance of benthic invertebrates, indicating a top-down effect from fish predators.

As pointed out by Allan (1995) such comparisons and field experiments lack replication and thus unmeasured factors may be responsible for observed differences. Usually it is difficult to resolve this satisfactorily. On the other hand, the well known problem of getting statistically good data from benthic samples in rivers can mask real differences in benthic densities caused by fish predation. Therefore, experimental manipulation of one or another population can be a valuable alternative or supplement to natural comparisons.

Laboratory and field experiments manipulating the abundance of fish and invertebrates have been designed to test the influence of fish predation on invertebrate stocks. Several such experiments in the 1980's using enclosures, have shown minor effects on invertebrate communities (Flecker and Allan 1984, Culp 1986, Reice 1991, Reice and Edwards 1986). By contrast, Schofield et al. (1988) observed a significant reduction in density of the trichopteran *Plectrocnemia conspersa,* in less than 8 days in enclosures with large trout. Williams and Feltmate (1992) called attention to several factors limiting the universal validity of these conclusions: the use of small fish and/or low density in the surveys, which often were carried out over a short period of time, spatial (cages) scales were small and only prey density and drift rates were considered in detail. Other poulation parameters, such as growth, life cycle and niche segregation, were not studied. Recent surveys which also have included other population parameters and the influence of several factors combined, have shown that predation may have an effect on invertebrate communities in several different ways in different habitats (Hart 1992, Power 1992, Dudgeon 1993, Gilinsky 1984, Crowl et al. 1997, Tikkanen 1995).

The reason for the ambiguous results in different predation experiments is also discussed in several papers, pointing at methodical differences which may influence interactions between predator and prey (e.g., size of enclosure, use of different mesh sizes in enclosures and sampling equipment, different densities of predatory fish; Cooper and Walde 1990, Sih and Wooster 1994, Englund and Olsson 1996, Cooper and Walde 1990, Pecarsky et al. 1997). Furthermore, it has been shown that the grazing effect may vary strongly among different predator fish species used in the experiments. In contrast to drift-feeding fish like salmon and trout, Dahl (1998a) and Dahl and Greenberg (1996) showed great differences in the effect of predation from benthic-feeding fish, such as bullhead (*Cottus* spp.), on invertebrate communities. They found that trout had only a minor impact on invertebrate densities, affecting only one taxon in their field experiment. From their review of predation studies, Cooper and Walde (1990) concluded that predator impacts are less apparent when prey replenishment rates are high. Palmer et al. (1996) maintained that the influence of predation and competition on the structure of invertebrate communities in running water is strongest when transfer and drift ratios of invertebrates are low, while the influence is weaker when the emigration/immigration rates in the river system are high. Habitat complexity and spatial refuges in running water also contribute greatly to the survival of prey (Reice 1983, Gilinsky 1984, Thorpe 1986, Fuller and Rand 1990). In river pools, especially in those situations where refuges are scant, predation effects have been most apparent (Power 1992). Thus, the effects of salmonid grazing on invertebrate communities vary among localities and according to time, space and heterogeneity of the environment.

However, predation effects extend far beyond a simple depression of number or biomass of invertebrates. Predation risk may force prey to restrict their foraging to certain times or places, perhaps resulting in less growth or reduced fecundity, or influence life cycles and drift behaviour.

Indirect effects of predation - changes in behaviour, drift and niche segregation

In addition to direct effects, a reduction in density of certain invertebrate species exposed to fish predation can be caused by behavioural changes in the form of evasive reactions and increased prey drift. Several studies have shown that the presence of predatory fish can lead prey, such as *Bäetis* (Ephemeroptera) and *Gammarus* to change foraging strategy, anti-predatory behaviour, and increase prey drift (Peckarsky and Dodson 1980, Peckarsky 1985, Douglas et al. 1994, Forrester 1994, Sih and Wooster 1994, Wooster and Sih 1995, Tikkanen 1995).

Tikkanen (1995) showed in laboratory trials that large mayfly nymphs (*Bäetis*) change their diurnal variation in drift rate in the presence of fish, while small nymphs change their use of micro habitat. He found no behavioural change in the mayfly *Heptagenia* in the presence of fish. This may be explained by the fact that *Heptagenia* species have a very efficient anti-predatory behaviour traits, including a flattened body and cryptic way of living, while the *Bäetis* are more apt to drift and seek fish free microhabitats during foraging. The nocturnal periodicity of downstream drift may be explained as an adaptation to fish predation. Numerous laboratory studies of drift show that nocturnal periodicity is retained in a predator-free environment (e.g. Elliot 1968, Allan 1978). Flecker (1992) demonstrated that drift was aperiodic or diurnal in streams lacking drift-feeding fish, a finding also reported by Turcotte and Harper (1982).

Other studies also show that several invertebrates change their location and foraging behaviour in the presence of predatory fish, and that the heterogeneity in the substrate may have a major impact on this kind of prey response

(Crowder 1982, Feltmate and Williams 1989, 1991, Power 1990, Bechara et al.1992, 1993). Brusven and Rose (1981) found that predation by benthic-feeding sculpins on species of mayflies, stoneflies and caddisflies varied at different substrate types, and that the invertebrates to a greater extent avoided predation by changing habitat use and living in interstitial spaces where possible. In enclosure experiments with the objective of studying the predatory effect of rainbow trout on stoneflies, Sih (1987) showed that the presence of rainbow trout reduced the stonefly activity. Feltmate and Williams (1991) reported that the presence of rainbow trout reduced density, individual size and condition (weight/head-width ratio) of fully-grown stonefly larvae. Cooper (1984) found that adult waterbugs (Gerridae) occupied all areas of stream pools when trout were absent, but only the margins of pools containing trout. In autumn, female gerrids from trout pools weighed less than their counterparts, suggesting that lost feeding opportunity translated into reduced growth. Although direct salmonid predation does not seem to reduce many invertebrate stocks to a great extent in running water, many investigations show that salmonid predators influence the behavior and history of invertebrates, and may influence community structure and interactions in river ecosystems (see also McIntosh and Townsend 1996, Crowl et al. 1997).

Selective predation by drift-feeding salmonids - phenotypic effects and prey size

Juvenile salmon and trout are positively rheotaxic and typically, territorial (Kalleberg 1958) "sit and wait" predators in running water (O'Brien et al. 1990), but may have different grazing strategies in pools and slow-flowing river stretches (Tønset 1996, Bremset 1999). The visual characteristics of the prey are important for the predator's selection of prey. Size, contrast, motion, shape and colour are examples of such characteristics, although size is considered the main factor when it comes to selection (Metz 1974, Ringler 1979, Frankiewicz et al. 1993). Diet selectivity in salmonid fishes has often been studied by comparing the invertebrates found in stomach samples with those found in drift samples. Prey which seem to be caught in larger portions than what is actually available in the surroundings, are most frequently large or are found in the surface drift (terrestrial organisms) (Allan 1981). There are, however, many examples of selective grazing of prey that are not necessarily large, but that are easily accessible, for example small mayfly larvae and chironomids (Johnsen et al. 1991, Koksvik and Haug 1998, Næsje et al. 1998). Several investigations indicate size-selective grazing by different size groups of fish (Bannon and Ringler 1986, Brodeur 1991, Johnsen et al. 1991, Kjelsaas 1995). The maximum prey size will be limited by the size of the fish's mouth, while the prey's minimum size will be limited by the fish's gill raker spacing. Prey size seems to be a major criterion in the selection of prey as fish choose bigger prey according to availability (Ware 1972, Wankowsky 1979, Newman and Waters 1984, Brodeur 1991). Allometric studies of diet in stream-dwelling salmonids have documented an increase in prey size with body size (Rose 1986, Keely and Grant 1996), perhaps because they become increasingly size selective as they grow larger (Grant and Noakes 1986, Keely and Grant 1996). Several Norwegian studies also show such selective grazing by different age groups of salmon and trout (Johnsen et al 1991, Kjelsaas 1995, Næsje et al. 1998). How such selection of prey size effects invertebrate communities in running water seems, however, to be a subject of little research.

In contrast, the literature dealing with the effects of size-selective predation by fish in lakes are numerous (cf. Langeland 1982, Jensen 1988). In lake Langvatn, central Norway, Langeland (1982) reported a change in the composition of zooplankton as a consequence of fish predation. Species that are sensitive to fish predation are often very abundant when fish are scarce or missing, as occurs in some areas of the southern parts of Norway and Sweden due to acidification (Zaret 1980, Erikson et al. 1980, Henrikson and Oscarson

1985, Raddum et al. 1986). In such locations, the number of large free-living invertebrate species, such as waterbugs and phantom midges, has increased and they have become the new top predators. When fish is stocked in such environments, the process is reversed and invertebrates that are highly exposed to fish predation, are consumed, resulting in a major change in the invertebrate community (cf. Stenson and Svensson 1995, Raddum et al. 1986).

Experiences from Scandinavian research and fish stocking programs

Examples of investigations aiming to study effects of fish stocking on invertebrate communities

Many investigations on foraging of stocked fish have been carried out (Johnsen and Ugedal 1985, 1986, 1988, 1989, 1990, Koksvik and Haug 1998), but we have few examples of Nordic investigations with the purpose of studying interactions between salmon, trout and invertebrates in running water. In Sweden, a few enclosure experiments have been carried out in streams (Dahl 1998a, Dahl and Greenberg 1998, Englund and Olsson 1996). Dahl and Greenberg (1998) made a theoretical analysis of the influence of grazing of benthivorous and drift-feeding fish on invertebrate communities in running water and concluded that benthic-feeding fish, in most cases, will have a major negative effect on the invertebrate communities, while trout will have a minor influence. This was explained by the fact that trout are a less efficient invertebrate feeder and do not graze in the substrate, and the fact that surface drift with terrestrial origin makes up a major nutritional source for trout in the summer season. Dahl (1998a) studied this aspect by carrying out field experiments in two streams in the southern part of Sweden. He found that bullheads (*Cottus gobio*) reduced the density of seven invertebrate taxa (*Gammarus pulex*, species of mayflies, stoneflies, caddisflies and black fly larvae), while trout reduced the density of only one mayfly species (*Bäetis rhodani*). This was partly due to the fact that 80% of the prey consumed by brown trout were terrestrial animals, whereas bullhead only consumed benthic prey. However, in a different study, Dahl (1998b) showed that trout had an influence on both the density and drift rates of *Gammarus pulex, Bäetis rhodani* and *Ephemrella ignita* mayfly larvae. In this study, the three species were the dominant prey consumed by brown trout, while the contribution of terrestrial animals was small. Dahl concluded that different fish species will have different influences on invertebrate communities, and that terrestrial animal availability in the drift markedly affects the impact of trout predation on benthic prey. Therefore, in rivers stocked with drift-feeders, terrestrial prey may reduce the impact on lower trophic levels, and such effects should be most pronounced in summer when the availability of terrestrial animals in streams are high. At other times of the year, one would expect the impact of driftfeeders on benthic prey to be higher. Several studies also indicate that terrestrial animals drifting in the surface water compose a larger proportion of the diet of juvenile trout than that of salmon (Kelly-Quinn and Bracken 1990, Tønset 1996). It is therefore possible that juvenile salmon may have a greater influence on invertebrate communities in running water than juvenile trout.

Studies that may indirectly show effects of fish stocking on invertebrate communities

The diet of wild and stocked juvenile salmon and trout

Many studies show that both hatchery-reared salmon and trout start feeding relatively quickly after release, and they seem to utilize the same food items as wild fish, regardless of type of habitat they were planted in (Johnsen and Ugedal 1985, 1986,1988, 1989, 1990, Koksvik and Haug 1998). After a while, hatchery fish seem to utilize their new habitat in the same way wild fish do (Johnsen and Hesthagen 1990, Johnsen and Ugedal 1990, Koksvik and Haug 1998, LAbée-Lund et al. 1994). In a project on stocked brown trout, Johnsen and Ugedal (1990) performed several studies of feeding choice by wild and reared fish stocked in different locations at different times of the year. Research on both young-of-the-year and yearling brown trout of hatchery origin showed that after a week 77-90% of the hatchery fish had fed on natural food (Johnsen and Ugedal 1985, 1998). In a comparative study on feeding by hatchery and wild brown trout (age 1+) in a stream, they found that the hatchery fish were able to adapt faster to natural food in spring and summer than in autumn. A week after release, the hatchery fish had established the same index of stomach fullness as wild fish in May, and all captured hatchery fish had fed on natural food. In October, only 56% of the hatchery fish had started to feed after a week and their index of fullness was lower than that of wild fish. These studies however, have not looked into the availability of invertebrates in the stream and how stocked and wild trout possibly have influenced the invertebrate communities. Koksvik and Haug (1998) studied both the availability of invertebrates in a stream and the foraging of two groups of Atlantic salmon fingerlings, one with a traditional hatchery background and the other reared on live zooplankton in a lake. One day after release, 92% of fish with lake background had started to feed on river fauna compared to 51% of the hatchery fish. Eight and 15 days after release the two groups had very similar fractions of fish with stomach content, and the diet of both fish categories was quite similar. Compared to the density and abundance of taxa in the benthic samples, they found that both groups of fish had a strong preference for chironomids, caddisflies and blackflies. Mayflies and stoneflies were eaten approximately in accordance with their occurrence in the bottom fauna, while oligochaetes were rarely selected. Again, the study did not look into whether the stocked fish's grazing had any effect on the invertebrate composition.

Fish stocking and invertebrate studies

In the Teigdal river, significant amounts of sea trout were stocked during 1990-1995. In the first two years, both salmon and sea trout smolts were planted, while the last three years, marked sea trout fry were stocked to follow the population development. The stocking ended in 1995, when it turned out that recruitment was not the problem. Fish density was limited by physical conditions, i.e. the carrying capacity in the watercourse (Fjellheim et al.1994, 1995, 1998). Investigations of invertebrates during 1991-1999 have shown that the species composition of invertebrates both before, during and after fish stocking did not change qualitatively (Raddum and Fjellheim 1996, Raddum et al. 1992).

The Førland channel in River Suldalslågen is part of an artificial channel where investigations on salmon and invertebrates have been carried out for several years. Here, co-variation occurs between high juvenile density and low invertebrate density in some locations in riffles. The study concluded that the invertebrate density at one location was influenced by fish predation (Lillehammer et al. 1995). At this location, there could be up to 4-6 times as many salmon fry and up to 13 times higher predation pressure on chironomids than at a different location further downstream. The fish in this system preyed primarily upon animals in the range of 2-5 mm, and only as an exception, animals greater than 8 mm (Prestø 1994), which may explain the low portion of chironomids and small stonefly larva at this location (Lillehammer et al. 1995).

In a research program on Atlantic salmon production, fry were planted into rivers not naturally populated by salmon (Rivers Litjvasselva and Klubbvasselva in the Vefsna river course, northern Norway). The main objective was to study the possibility of smolt production from stockings in non-anadromous river sections (Johnsen et al. 1991, 1997). At the same time, invertebrate samples and stomach samples of juvenile salmon were taken. In the River Litjvasselva, 50,000 salmon fry were stocked yearly in the period of 1985-1989, which gave an average density of 17-54 juvenile salmon 100 m^{-2}. The utilization of invertebrates in relation to occurence, expressed by Ivlev's electivity index (Ivlev 1961), showed a positive selection of mayfly larvae and to some extent chironomids by all age groups of fish, and a negative selection of stonefly larvae and to some extent caddisfly larvae. A fertilization experiment in 1988/89 led to a significant increase in the biomass of chronomids, mayflies and stoneflies in particular, and a large increase in the food uptake and growth of juvenile salmon. However, there was only a slight change in the selection of feeding organisms by the fish. High invertebrate densities resulted in juvenile salmon foraging on fewer invertebrate groups. The study does not, however, provide data by which the significance of predation effects on the invertebrate community can be evaluated. A similar study in the river Klubbvasselva (Johnsen et al. 1997), also showed diet selectivity of different salmon age groups before and during a fertilization experiment, but none of these data indicate to what extent fish stocking effects the invertebrates.

Also in River Dalåa, a brown trout stream in the Stjørdalselv watercourse, central Norway, stocking of young-of-the-year Atlantic salmon was done in the period 1993-1999. Stocking resulted in a density of 1-2 juvenile salmon m^{-2} (Arnekleiv 1996), followed by distinct changes in both number and diversity of species of invertebrates (Arnekleiv et al. own data). Stockings were, however, performed in connection with river regulation, and a major reduction in water flow had occurred, and biotope improvements had been carried out. It is, therefore, hard to say to what extent fish stocking has contributed to the changes in the invertebrates.

After hydropower development and stocking of brown trout in the River Aurlandselva, western Norway, total invertebrate density increased in the river. The bottom fauna was dominated by chironomids and the mayfly *B. rhodani,* which are important food organisms for juvenile brown trout (Raddum and Fjellheim 1994, Jensen et al. 1994).

Limed watercourses – effects on invertebrates after fish stocking

In limed watercourses, such as Flekke-Guddal, Ydnesdal, Vikedal, Ogna and Audna in southern Norway, the density of salmon and sea trout has increased due to stocking and increased natural recruitment.

Observations of invertebrates in these waterways have shown that the species number of invertebrates has simultaneously increased (Fjellheim and Raddum 1992, 1995, Raddum and Bjerknes in press). Increased fish density has, therefore, not hindered recolonization of predation-sensitive invertebrates like snails and mayflies. These animal groups make up a significant portion of the stomach content of fish, and spread rapidly within waterways, such as in Audna, after liming. The number of taxa of benthic animals containing species with known critical limits to acidity (e.g. Trichoptera, Ephemeroptera, Plecoptera, Turbellaria, Hirudinea and Gastropoda) increased continouosly in the limed section of River Audna. Until 1999, a total of 17 sensitive species were recorded. In the unlimed reference stations a slight response was seen during the first years after liming. Since 1991, no additional sensitive taxa beyond the 7 recorded species have been found. It is uncertain what the density of these invertebrates would have been without fish stocking, but the fish do not seem to have limited the growth of acid-sensitive species after liming. In the case of mayflies, their food basis and habitat demands are probably the limiting factor. Predation appears to be of secondary significance in limiting their density.

Field investigations in rivers and streams aiming to quantify the effect of fish predation on invertebrates are difficult. As mentioned earlier, this is probably due to both insufficient methods and the fact that juvenile salmonids mainly eat drift organisms and feed to a lesser degree on animals living in the substrate. The drift frequency varies from species to species, but rarely exceeds 1-2% of the existing number in the benthos per time (Brittain and Eikeland 1988). This means that only a small part of the fauna is exposed to salmonid predation at any time, and the substrate heterogenity in stony streams creates spatial and temporal variations in refugia that stabilize predator/prey models (Begon et al. 1990) and are probably of great dynamic significance in food webs.

Rotenone treatments

In Norway, several salmon rivers have been treated with rotenone in an effort to get rid of the salmon parasite *Gyrodactylus salaris*. Fish stocked after rotenone treatment experience very good growth (Johnsen et al. 1991, Andersen pers. comm.). Most benthic insects are found to recolonize treated river stretches quickly, and in the absence of fish, they exist in considerable numbers (Arnekleiv 1997, Arnekleiv and Bongard 1990, Arnekleiv et al. 1997, 2001). In the River Lærdal, western Norway, there are no indications that the fish managed to change the composition of invertebrate species after stocking and natural recruitment (Gladsø and Raddum 2000, Gladsø pers. comm.). When several age groups are added in subsequent years after rotenone treatment, growth decreases (Johnsen et al. 1991). It is not obvious whether this is caused by predation on desirable food sources (i.e. exploitive competition) or increased interactive competition between individuals when fish density increases.

The rivers Rauma, Isa and Glutra were treated with rotenone in the autumn of 1993, and invertebrate investigations were carried out before, during and after treatment (Arnekleiv et al. 1997). The rotenone treatment caused a temporary, 16-74% reduction in the densities of invertebrates immediately after treatment. The reduction in the number of stoneflies, caddisflies and blackfly larvae were most distinct, while partly mayflies (*Ephemerella aurivilli* in particular), watermites and chironomids better survived the treatment. The invertebrates quickly recovered, and within one year about the same amounts of, and proportions of most invertebrate groups and species were observed as prior to the treatment. The fish stock (Atlantic salmon and brown trout) rebuilt itself relatively quickly (2-3 years) through natural recruitment and stocking. Moreover, there were no indications that the amount or species composition of invertebrates decreased as a result of increased fish grazing. However, an analysis of quantitative invertebrate data is still lacking, and finding causal connections for variations in non-replicated field data is always difficult. Surveys of invertebrates in connection with rotenone treatment of several salmon rivers (Arnekleiv 1997, Arnekleiv and Bongard 1990, Arnekleiv et al.1997, 2001) also showed a fast invertebrate recolonization with great variation in numbers and species composition. However, no significant reduction in the amount of invertebrates was found as the juvenile salmonid stocks rebuilt.

Johnsen et al. (1997) reports that fish growth increased after experimental fertilization of the River Klubbvasselva, northern Norway. No increase in the density of bottom invertebrates was found in June after the fertilization program started, but a considerable increase was observed in October. The composition of the diet of the salmon parr did not change extensively after fertilization and while fertilization did not provide an increase in salmon parr density, it did appear to improve fish growth. This indicates that the amount and quality of available food in running water affects fish growth as expected. Data on the food-web dynamics and effects of grazing from the salmon parr population are lacking, however.

Concluding remarks

Based on the examples given, we may conclude that there is little evidence to show that stocking of salmonid fish in running water in Norway has had significant effect on invertebrate density, biomass or species composition. However, very few investigations have been carried out with the intention of specifically studying interactions between hatchery fish and invertebrate fauna. Field studies, usually with different objectives, have shed a little light on the relations between fish predation and invertebrate communities. In most of the examples given, river regulation, liming or rotenone treatment all introduce an influence on the ecosystem which is very difficult to separate from other factors influencing the dynamics between prey and predator.

As seen from the literature, salmonids seem to affect only rather large or otherwise vulnerable, predator-sensitive prey, while benthic feeders (Cottidae, Cyprinidae) have more widespread effects on abundance and biomass of prey (Table 1).

Table 1. Direct effects of fish predation on invertebrates based on field observations and field experiments. Decreasing effect from left to right column.

Significant effects of fish predation on invertebrates are recorded on:	Reduction in number of taxa / abundance in experiments	Selecive grazing	Minor or no detectable effect
Amphipods in running water (Straskraba 1965). Other predation sensitive taxa like corixidae, coleopterans, phantom midge etc. are susceptible to fish predation. Stocking of fish after liming acidic lakes has reduced such animals considerably (Zaret 1980, Erikson et al. 1980, Henrikson & Oscarson 1985, Raddum et al. 1986). In an artificial channel Lillehammer et al. (1995) found co-variation between high fish density and low invertebrate density in some locations. Significant reduction of invertebrates is caused by bottom feeding fish like sculpins (Dahl 1998, Dahl and Greenberg 1996).	In enclosure experiments the invertebrate community or special taxa, are reduced by fish predation (Schofield et al. 1988). In such experiments the pray organisms are isolated from the natural dynamics. Cooper et al. (1990), Sih & Wooster (1994) and Englund & Olsson (1996) discussed the interaction between pray and predator in enclosures experiments. They found that the methods used had a relatively large influence on the results. Such experiments are therefore not suitable for studding predation effects in natural environments. Thorpe (1986) pointed out that the predation varies greatly depending on time, space and heterogeneity of the habitat. Somewhat stronger effects with at least some reduction of some taxa have also been reported (Flecker 1984, Gilliam et al. 1989, Power 1990, Bechara et al. 1992, Dudgeon 1993 and Dahl 1998a, b).	Different size groups of salmonids have selective grazing on drifting invertebrates. Larger fish choose larger pray. Selective grazing might reduce species sensitive to predation. Generally it is difficult to point at significant effects on the invertebrate community in running water (Johnsen et al. 1991, Kjelsaas 1995, Koksvik & Haug 1998, Næsje et al. 1998, Hellen 1995). Although salmonid predation does not seem to reduce significantly invertebrate stocks in running water, such predation may, however, influence on the community structure and species interactions in the ecosystem (McIntosh & Townsend 1996, Crowl et al. 1997). Grazing effect might be different depending on temperature and drift activity (Brittain & Eikeland 1988).	Allan 1982 stressed that invertebrates in running water are adapted to fish predation and less sensitive to changes in fish density. Jacobi (1979) and Reice and Edwards (1986) found no predation effect when comparing stream streches with and without fish. Flecker & Allan (1984), Culp (1986) and Reice (1983) found also minor effects on invertebrates exposed to fish predation. Stocking of fish in limed rivers seems not to reduce recovery of sensitive species. Increased density and recruitment of fish is accompanied with increased density of invertebrates (Fjellheim & Raddum 1992, Raddum & Bjerknes 2000). Either elimination of fish or stocking of fish in connection with rotenone treatments have changed number of taxa or abundance of invertebrates significantly in treated rivers (Arnekleiv 1997, Arnekleiv et al. 1997, 2001, Gladsø 2000, Gladsø & Raddum 2000).

Table 2. Indirect effects on invertebrates caused by fish predation

Changes in habitat use	Changes in drift patterns
Gerridae occupy all areas in absence of trout (Cooper 1984). Activity of sonefly nymphs depressed by rainbow trout (Sih, 1987).	*Bäetis* and *Gammarus* change their drift pattern depending on presence of predator fish (Peckarsky & Dodson 1980, Perckarsky 1985, Douglas et al. 1994, Forrester 1994, Sih & Wooster 1994, Wooster & Sih 1995 and Tikkanen 1995). In predator-free environment nocturnal periodicity in drift is retained (Elliot 1968, Allan 1978) or became aperiodic (Turcotte and Harper 1982).

Drift-feeding fish performs size selective grazing on invertebrates and they can also influence the drift pattern of some invertebrate taxa (Table 2). Many features of the morphology, physiology and behaviour of invertebrates seem to be designed for defence against fish and invertebrate predators, indicating that predation is a powerful selective force in running water (cf. Jeffries and Lawton 1984, Peckarsky et al. 1997). However, a structuring effect of this feeding pattern on the invertebrate populations is difficult to detect and is far from those found in lakes on zooplankton. Fluctuations in discharge and drift rates, substrate heterogenity and temporal variations are examples of factors that may limit predator (i.e. salmonid) impacts on macrozoobenthos in running water. Predator impacts are less apparent, or masked when prey replenishment rates due to drift are high (Cooper and Walde 1990, Allan 1995). However, nocturnal feeding in cold rivers, and a habitat shift to more benthic feeding by salmonids in winter and in subarctic rivers, may affect prey populations and give temporal variations in predator effects on the macroinvertebrates. Bottom feeding fish is much more effective grazers and have a large influence on the invertebrate community. The reason for the different structuring effect of drift- and benthic-feeding fish might be:

- Drift-feeding fish eat invertebrates that expose themselves to fish through the drift pattern (mainly invertebrate behaviour determined).
- Benthic-feeding fish are active searching for invertebrates on/in the river substrate (manly fish feeding activity determined).

In fish-less systems, stocking of salmonids may produce cascading effects on the biota by supressing the invertebrate predators. Such ecosystems can be very specialized, mostly controlled by invertebrate top predators which are usually very sensitive to fish predation and consequently stocking of fish will force a major structuring effect in such ecosystems. Stocking Atlantic salmon in river stretches without recruitment of salmon will probably have low effect if the stretches already have trout since both species have more or less the same structuring effect on the invertebrate community. However, it is important to evaluate the invertebrate fauna before stocking, since special invertebrate communities can have developed.

How different species and sizes of stocked fish affect invertebrate communities in running water through grazing and competition seems to be largely unknown, or at least a matter of controversy. Moreover, there seems to be particular need for increased knowledge about how hatchery fish may affect biomass, diversity of species and structure of invertebrate communities in running water. Studies of top-down effects and food-web research in Nordic streams needs to be more focused, and we feel that experimental studies are necessary to distinguish cause and effect. Also, one should consider the stocking of anadromous fish in non-anadromous river stretches, and the question how this may effect the diversity of species.

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Competitive Interactions in Young Atlantic Salmon (*Salmo salar* L.) and Brown Trout (*Salmo trutta* L.) in Lotic Environments

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Abstract

Young Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) are ecologically similar in most respects. Considerable interspecific niche similarities, e.g. in feeding, habitat use and behaviour, are indicative of potentially severe interspecific competition. Trout are generally more aggressive and have a higher freshwater growth than salmon, and at the juvenile stage trout are recognised to be a superior competitor dominating salmon of similar body size. In order to minimise interspecific competition, sympatric species can be spatially segregated. On the macro scale, juvenile salmon are predominantly found in the faster-flowing habitats such as riffles and runs, while brown trout tend to favour slower flowing habitats such as pools and flats. On a smaller spatial scale, young salmon are often found at longer distances from the riverbank than young trout, and seem to use the mid-river areas to a greater extent than trout. Moreover, young trout are less attached to the riverbed than similar-aged salmon. This interspecific difference in habitat use could be the result of competition for profitable feeding positions. On the micro scale, juvenile trout occupy microhabitats with lower water velocities than salmon juveniles. Juveniles of both species are segregated both along the horizontal and the vertical axis, with the younger specimen closest to the riverbank and riverbed. This three-dimensional habitat segregation is probably due to that subordinate fish are excluded from the most profitable feeding areas by higher ranked individuals, and are restricted to areas of less profitability in terms of food availability and predation risk.

Keywords: competition, behaviour, habitat, niche, young salmonids

Introduction

Population regulation is the central dynamical question in ecology, and underlies most other ecological problems. An important mechanism in population regulation is competition, in particular for food and space. All organisms are adapted to a particular spatial niche or habitat, or a limited number of habitats. Interspecific differences in morphological adaptations, and selective segregation, and thus habitat preferences, can be viewed as mechanisms for reducing competition between sympatric species. Dietary, spatial and temporal segregation are the three major axes for resource partitioning in stream ecosystems (Schoener 1974, Wootton 1990, Allan 1995). Among these, spatial segregation may be considered the most important (Schoener 1974). Typically, many stream-dwelling animals are trophic generalists (Hynes 1970, Cummins 1973), with corresponding large dietary overlaps among species, which in turn increases the importance of spatial segregation in lotic environments.

Both abiotic and biotic factors are important for the distribution and abundance of organisms (Flecker 1984, Feminella and Resh 1990, Hemphill

1991). The importance of abiotic habitat factors are affected by morphological, physiological and behavioural tolerances and may determine the habitat use of a species largely independent of other species. However, biotic interactions such as competition and predation may modify such responses (Connell 1975, Toft 1985). Abiotic and biotic factors affect organisms in several complex ways that interact with each other (Greenberg 1994). Furthermore, the environmental factors might vary in relative importance in space and time, and with ontogenetic development. In fisheries management identification of limiting habitat factors is of great importance.

Young Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) are ecologically similar in most respects (Allen 1969, Gibson 1988). Both feed mainly on drifting invertebrates (Waters 1969, Bachman 1984, Gibson 1993), and may coexist in the same lotic environment with considerable spatial niche overlaps (Heggenes and Saltveit 1990), and are territorial in shallow, fast-flowing river areas (e.g. Keenleyside 1962, Elliott 1990, Titus 1990, Grant 1997). Considerable interspecific niche similarities, e.g. in feeding, habitat use and behaviour, are indicative of potentially severe interspecific competition. Competition occurs in two separate ways (Wootton 1990); direct (interference competition) or indirect competition for a resource (exploitative competition). Direct competition is less common than indirect competition, and agonistic behaviour by juvenile salmon and trout is not frequently observed (e.g. Gibson 1993, Heggenes et al. 1993, Bremset and Berg 1997, Bremset 2000).

The distribution and abundance of young salmon and trout vary a lot within as well as among rivers. Competitive interactions are important in this respect. The highest potential number of salmon and trout in shallow, faster river reaches may be governed by the highest potential number of territories (cf. Le Cren 1965, Allen 1969). Territorial space may be a result of agonistic behaviour and interference competition (e.g. visual isolation; Kalleberg 1958, Keeley and Grant 1995), or be a surrogate for competition for a vital resource, such as food or shelter available in that space (e.g. Marschall and Crowder 1995), and the need for territorial space is therefore flexible. Territory size also depends on ontogenetic development (Elliott 1994). In deep, slow-flowing areas, however, where juvenile salmonids do not hold territories (Gibson 1973, Wankowski and Thorpe 1979, Elliott 1990, Nakano and Furukawa-Tanaka 1994, Bremset and Berg 1997), fish may hold positions in all parts of the water column and in the vicinity of several other fish without showing agonistic behaviour (Gibson 1973, Nakano and Furukawa-Tanaka 1994, Nakano 1995, Bremset and Berg 1997).

The objective of this paper is to review the literature on the competitive interactions in juvenile Atlantic salmon and brown trout living in lotic environments, with special emphasis on their behavioural, spatial and temporal segregation into different niches.

Dominance, aggression and social organisation

Dominance and social status are factors of significant importance for juvenile salmonids. Jenkins (1969) found that size and prior residence, but not sex, were important in determining dominance by juvenile brown trout. Generally, larger fish dominate smaller ones (Jenkins 1969, Bohlin 1977, Bachman 1984, Gibson 1993), and resident fish seem to have an 'owner's advantage' over introduced fish (Bohlin 1977). However, body size is not always the determining factor for dominance status (Metcalfe 1986), as dominance also might be a function of high aggressiveness (Huntingford et al. 1990). In a laboratory study of Atlantic salmon juveniles, dominant individuals exhibited more agonistic behaviour than subordinates (Keenleyside and Yamamoto 1962).

Aggressiveness in young salmon and trout is related to both abiotic and biotic factors. Water temperature and photointensity are ambient factor that affect the aggressiveness of juvenile salmonids, as this behaviour appears to be reduced at lower water temperatures in both species (Fraser et al. 1993, Heggenes et al. 1993), concomitant with the behavioural shift to nocturnal activity and risk-avoidance daytime sheltering that occur in both species with the onset of winter (e.g. Fraser et al. 1993, Heggenes et al. 1993, Whalen and Parrish 1999, Bremset 2000, Heggenes and Dokk own data). Atlantic salmon and brown trout also exhibit less aggressive behaviour in slow water flows (Gibson 1993, Bremset and Berg 1997), which permits habitat-dependent shifts in social strategies, from territoriality to dominance hierarchies (see below). Aggression is also closely related to food availability and feeding (Slaney and Northcote 1974, Wankowski and Thorpe 1979, Metcalfe and Huntingford 1986, Metcalfe et al. 1988). Gibson (1988) suggested that the level of aggression declines when food is abundant, as indicated from a study in the Matamek River, where young Atlantic salmon and brook trout (*Salvelinus fontinalis*) were foraging in large numbers on invertebrates trapped in foam at the water surface (Gibson 1973). Aggressive and thus dominant individuals have preferential access to food (Fausch 1984, Metcalfe et al. 1990, 1992), hence dominant fish may achieve the highest specific growth rate (Fausch 1984, Nakano 1995).

The social organisation of juvenile salmonids seems to be governed by several abiotic and biotic factors like habitat, temperature, food and social interactions (Wankowski and Thorpe 1979, Gibson 1988). At low densities the most common social organisation is territoriality, where each specimen defends a certain area areas (e.g. Keenleyside 1962, Elliott 1990, Titus 1990, Grant 1997). At high densities young salmonids may form dominance-related hierarchies or shoals (Elliott 1990, Nakano 1995, Bremset and Berg 1997). In such established interspecific hierarchies, dominant individuals usually keep positions which give maximum potential energy gain, whereas a hierarchy of subordinate fish keep positions with successive declining profitability (Fausch 1984). However, the benefit of being dominant can be reduced at very high rewards, and the hierarchic pattern may break up (Alanärä and Brännäs 1997).

Interspecific competition

Brown trout is considered an aggressive salmonid species (Lindroth 1955, Le Cren 1973, Karlström 1977). Young brown trout are recognised to be a superior competitor dominating Atlantic salmon of similar or slightly larger body size (e.g. Lindroth 1955, Kalleberg 1958, Karlström 1977, Kennedy and Strange 1986b, Gibson 1993). This competitive advantage might be a function of higher aggression by young brown trout (Kalleberg 1958, Allen 1969), because aggressive specimens tend to dominate less aggressive individuals (Allen 1969). Aggressive, and thus dominant individuals can to some extent monopolise the most profitable feeding areas (Adams et al. 1998), and will consequently obtain a higher growth rate compared with subordinates. Growth is normally better in brown trout compared with Atlantic salmon in the river phase, which is partly due to earlier emergence and feeding in the spring by trout fry (Allen 1969). This may also be caused by selection of more energetically profitable positions, as Atlantic salmon even in the near-absence of competition show slower growth in faster stream habitats (Heggenes 1991). Differences in growth manifest themselves quickly and the size disparity increases over time (Cutts et al. 1998).

The higher competitive ability and dominance of trout does not necessarily lead to a numerical dominance of this salmonid in rivers and streams. In a survey of 13 Scandinavian rivers inhabited by anadromous salmon and trout, Karlström (1977) found a numerical dominance by juvenile Atlantic salmon over brown trout in the main stem in all rivers. In the tributaries, however, only brown trout were recorded. Similarly to the findings of Karlström (1977), Egglishaw and Shackley (1977) found four times more juvenile Atlantic salmon compared to brown trout in a Scottish stream. Salmon, probably by their morphometric adaptations and behaviour in fast water, have the competitive advantage in high gradient riffle areas in which brown trout are not so well adapted (Kennedy and Strange 1982). Karlström (1977) proposed that salmon juveniles can find suitable territories across the entire river section, whereas young trout only find suitable territories along the riverbanks. Habitat selection and competition appear to be important in salmon and trout. Few young salmon in the tributaries was suggested to result from that large, mature salmon, in contrast to smaller trout, probably were unable to ascend these areas due to very small water flows, i.e. interspecific differences in morphological or behavioural tolerances.

Field studies have given evidence for that salmonid carrying capacities are higher in lotic habitats with more than one salmonid species present (Kennedy and Strange 1980, Gibson and Haedrich 1988, Gibson et al. 1993), indicating that the different salmonid species to some extent utilise different resources. After introducing salmon to trout rivers, Kennedy and Strange (1980) and Gibson and Haedrich (1988) found that total salmonid biomass did not increase in slower and deeper types of habitat, where trout were numerically dominant, suggesting that interspecific competition in these areas was less severe on trout than in the riffle habitats.

Intraspecific competition

Intraspecific competition occurs at two different levels: within and among cohorts (Bohlin 1977). Generally, aggressive attacks occur most frequently between fish of equal size (Symons 1968), implying that intracohort competition is more severe than intercohort competition. Conspecifics of similar size and age are competitors with respect to both food and space, and the large excess of deposited eggs in most salmonid rivers and streams entail a large mortality during the early life stages (Le Cren 1961, 1965). Territorial salmonids need more space as they grow (Elliott 1990, Grant 1993), and as a result some fish are excluded from feeding areas and vanish. Self-thinning is a intraspecific regulatory mechanism that have attained increased attention the recent years, and several field studies have indicated that this mechanism is very important with respect to juvenile salmonid production (e.g. Grant 1993, Armstrong 1997, Dunham and Vinyard 1997).

In addition to the interspecific habitat segregation of salmon and trout, the different cohorts of juvenile salmonids can be spatially segregated, which is documented both under experimental (Vehanen et al. 1999) and field conditions (Bremset and Berg 1999; cf. Fig. 1 and Fig. 2). Several studies have shown that underyearlings of Atlantic salmon and brown trout are found closer to the riverbank than older conspecifics (e.g. McCrimmon 1954, Egglishaw and Shackley 1985, Gibson et al. 1993, Bremset and Berg 1999), and that underyearlings prefer microhabitats with less water depth than yearlings and older parr (e.g. Karlström 1977, Greenberg et al. 1996, Mäki-Petays et al. 1997, Bremset and Berg 1999). This relative distribution could be related to both competitive interactions and predation risk. In deeper water, small fish face greater competitive and predatory pressure by larger fish (Power 1987, Schlosser 1987, Power et al. 1990, Gibson et al. 1993). Among salmonids dominance in intraspecific competition is bestowed on individuals of greatest body size (Newman 1956, Jenkins 1969, Bassett 1978, Bachman 1984), and subordinate fish can often be excluded from the most profitable feeding areas by higher ranked individuals (Fausch 1984), and are restricted to areas that are less profitable in terms of food availability and predation risk (Fausch and White 1986, Hughes and Dill 1990, Hughes 1998). Larger fish are vulnerable for avian predators in shallow areas nearby the riverbanks (Peterson 1982, Gibson et al. 1993, Godin 1997), and seem to avoid these areas (Bremset and Berg 1999).

Corresponding to the horizontal segregation of juvenile salmonids, there is also evidence for a vertical segregation of species and cohorts. In Canadian rivers, Gibson (1993) and Gibson et al. (1993) found vertical segregation of young Atlantic salmon in pools, with underyearlings holding positions closer to the substratum than older individuals. A similar but more pronounced vertical segregation of the different cohorts of pooldwelling Atlantic salmon and brown trout were found in Norwegian rivers (Fig. 2; Bremset and Berg 1999). These observations provide additional evidence for that spatial segregation is an important mechanism for decreasing direct competition for resources, and that size-dependent habitat

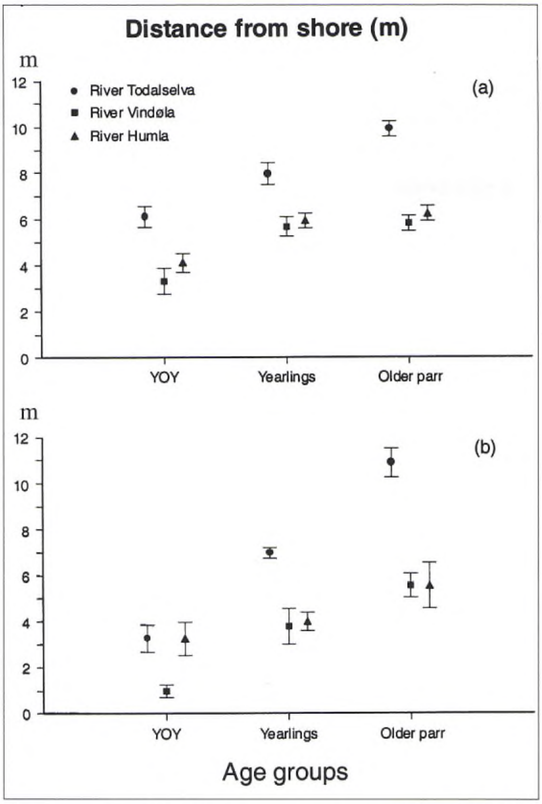

Fig. 1. Age-specific distance from the riverbank kept by (a) salmon and (b) trout holding positions in pools in the Rivers Todalselva, Vindøla and Humla. Vertical bars indicate SE. YOY: Young-of-the-year (underyearlings). From Bremset and Berg (1999).

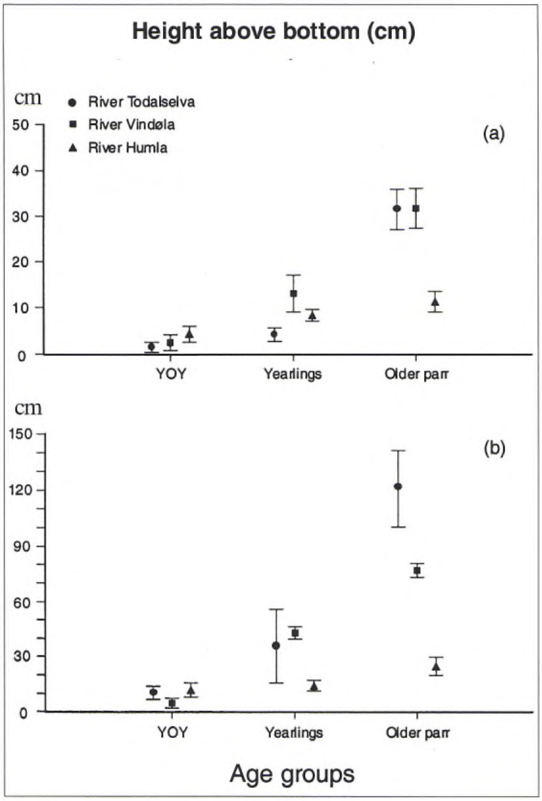

Fig. 2. Age-specific height above bottom kept by (a) salmon and (b) trout holding positions in pools in the Rivers Todalselva, Vindøla and Humla. Vertical bars indicate SE. Note the difference in scales. YOY = underyearlings. From Bremset and Berg (1999).

use in young salmonids probably is a trade-off between predation risk, feeding opportunities and social interactions (Hughes 1998, Bremset and Berg 1999).

Interactions between different cohorts of salmonids have been recognised to have large importance within Pacific salmon of the genus *Oncorhynchus*, and there are also evidence for that year-class dynamics is important for European salmonids like Atlantic salmon. Survival and growth of underyearlings of salmon is reduced by the presence of older conspecifics (e.g. Kennedy and Strange 1980, 1982, Egglishaw and Shackley 1985). Kennedy and Strange (1980) reported that salmon fry survival was reduced by half in the presence of older salmon in Scotland streams. Similarly, Buck and Hay (1984) reported and inverse correlation between the survival of salmon underyearlings and density of salmon yearlings in the River Dee. In two Canadian rivers, Symons and Heland (1978) observed that salmon yearlings actively reduced the numbers of underyearlings in the deeper habitats by chasing them, and occasionally by catching and eating them.

Intraspecific or intercohort competition has shown to have large impact on survival, habitat use, growth and behaviour of juvenile trout. Intercohort predation and competition is believed to regulate survival of trout fry (Burnet 1959, McFadden 1969), and several adaptations have presumably evolved in order to reduce the impact of intercohort interactions (Bohlin 1977). Larger brown trout dominate smaller, and consequently tend to restrict smaller trout to sub-optimal habitat areas (Jenkins 1969, Bohlin 1977, Bachman 1984, Heggenes 1988b). Bohlin (1977) found that trout yearlings in a small Swedish stream excluded underyearlings from territories they both found suitable. Studies on brown trout have demonstrated that subordinate individuals, that are forced to use suboptimal feeding stations, can form a roving subpopulation of fish trying to forage in available places, until the fish are driven away by resident trout (Bachman 1984). Dominant individuals of brown trout also seem to have a considerable impact on the foraging strategy and growth of subordinates (Metcalfe 1986).

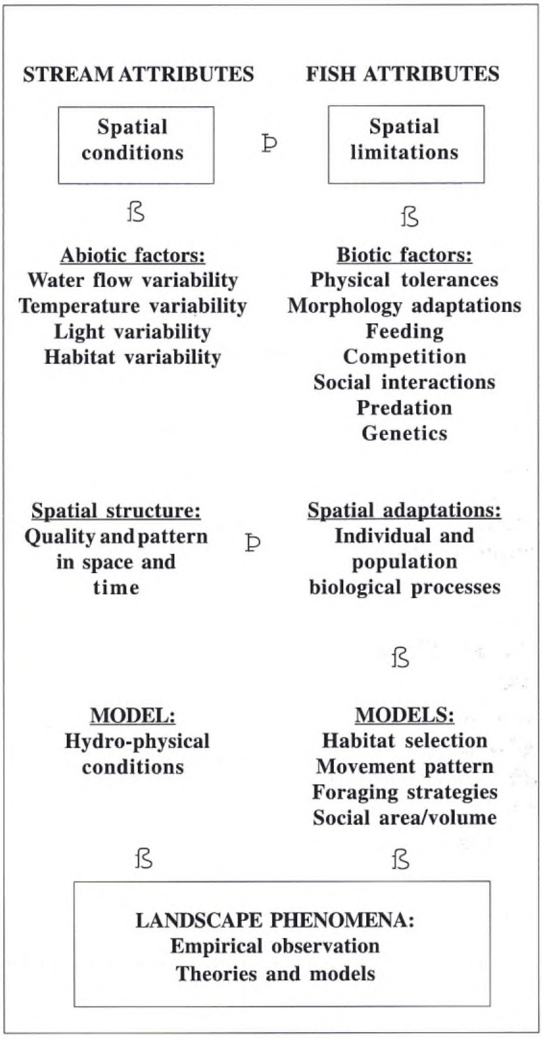

Fig. 3. Conceptual model for the fish habitat selection process. All processes may be scale dependent and variable in space and time.

The habitat dimension

The general term habitat might refer to different spatial scales. It is appropriate to subdivide the term into macrohabitat, mesohabitat and microhabitat. Macrohabitat is a term used for describing the general type of place in which an animal lives, and applies to a scale larger than the animal's normal daily range (Kramer et al. 1997), typically spatial scales of 10^1 meters (Frissell et al. 1986, Allan 1995) or often more in stream habitat studies. Habitat observations coupled with data on geomorphology, hydrology and climate, on a scale of stream reaches or subcatchments, may be referred to as macrohabitat descriptions (e.g. Stanford 1996, Cunjak and Therrien 1998). Studies quantifying physical characteristics of stream areas (habitat types) within a fish' normal daily range, i.e. patches from a few to tens of m^2, may be referred to as mesohabitat (Heggenes et al. 1999). Microhabitat is a term used for describing small spaces inside mesohabitats, and within the normal daily range of the animal of interest (Kramer et al. 1997). Microhabitat usually refers to spatial scales of 10^{-1} meters (Frissell et al. 1986, Allan 1995). Microhabitat studies in salmon and trout focus on quantifying physical characteristics in one or a number of stream points (i.e. at the snout position of the individual fish) with additional information in the immediate vicinity of the fish (i.e. patches up to some cm^2).

Habitat use and habitat selection

Habitat selection in young Atlantic salmon and brown trout is affected by a number of factors, and may therefore be both variable and flexible (Fig. 3; see review in Heggenes et al. 1999). On the landscape level, spatial variation such as availability and distribution of different habitats (e.g. Kocik and Ferreri 1998), and temporal variation such as frequency and amplitude of water flow (e.g. Heggenes 1996), water temperatures (Elliott et al. 1998), and light (Fraser et al. 1993, Heggenes et al. 1993, Bremset 2000), influence physiology, behaviour, and habitat selection in salmon and trout. On the population level, population structure such as size, density and competitors (see below) modify behaviours and thereby habitat use. On the individual level, the prevailing view is that choice of holding position (microhabitat) is determined by optimal foraging theory; i.e. net energy intake is maximised (e.g. Bachman 1984).

In lotic environments, where drift-feeding is the main foraging strategy (Wankowski and Thorpe 1979, Bachman 1984), competition for space may substitute for direct competition for food and reduced risk (Chapman 1966). Food intake is more important in summer (Metcalfe et al. 1999), while reduced risk appear to be more important in winter (Heggenes et al. 1993, Bremset 2000, Heggenes and Dokk own data). The principal foraging strategy for salmon and trout in summer may be described as an energy intake-maximising sit-and-wait strategy, because the cost curve with increased water velocity is rather flat, while the drift availability peaks due to reduced capture success at higher water velocities (e.g. Hill and Grossman 1993). In winter, however, young salmon and trout adopt a cost-minimising strategy by switching to a nocturnal activity pattern (Heggenes et al. 1993, Fraser et al. 1995, Bremset 2000), resulting in a lower predation risk at the cost of a lower food capture efficiency (Metcalfe et al. 1999). The temporal variations in daily activity patterns are concequently suggested to be the result of at complex trade-off between growth and survival, which takes account of diel fluctuations in food availability, food capture efficiency and predation risk (Metcalfe et al. 1999).

Habitat segregation

A principal mechanism for reducing competition for space, is habitat segregation, either through competitive interactions, or selective segregation. Albeit ecologically similar with overlapping niches, Atlantic salmon and brown trout may segregate in their use of, and preferences for riverine habitats (for details, see reviews in Gibson 1993 and Heggenes et al. 1999). On the macro scale, i.e. at the level of entire watersheds or parts of watersheds, there are relatively large differences in the distribution and abundance of salmon and trout. Although the rivers and streams occupied by Atlantic salmon are diverse across the species' range (Elliott et al. 1998), salmon have the highest abundances in the main stems of large rivers, whereas trout are predominantly found in the tributaries of large river systems or in small streams, where salmon are found in small numbers or not at all (Berg 1964, Karlström 1977). Moreover, in larger river systems, anadromous trout are found mainly in the lower parts (García de Jalón et al. 1996), whereas salmon are as frequent in the upper reaches of the anadromous parts of the river system. This phenomenon could be explained in terms of species-specific responses to the changes in river morphology from the nromally high-gradient, faster-flowing upper reaches to the low-gradient slower-flowing lower reaches (see Vannote et al. 1980).

On a somewhat smaller scale, i.e. at the level of mesohabitats (see above), several field studies have documented that Atlantic salmon living in sympatry with brown trout predominantly are found in faster-flowing habitats, often in combination with coarse substrates such as riffles (e.g. Kennedy and Strange 1986b, Heggenes and Saltveit 1990, Peake et al. 1997, Prenda et al. 1997), while brown trout tend to favour slower flowing habitats (e.g. Maitland 1965, Jones 1975, Baglinière and Champigneulle 1982, Gibson 1988). Young salmon have been found at longer distances from the riverbank than young trout (Heggberget 1991, Bremset and Berg 1999), and salmon are recognised as using the mid-river areas to a greater extent than trout (Lindroth 1955). In a comprehensive study of habitat use of sympatric salmon and trout juveniles in the Stjørdalselva River, trout were generally found in shallower microhabitats than salmon (Fig. 4). Salmon may respond to increased water velocities in a stream reach or river stretch by increased use, for example if vegetation is removed (e.g. Roussel et al.

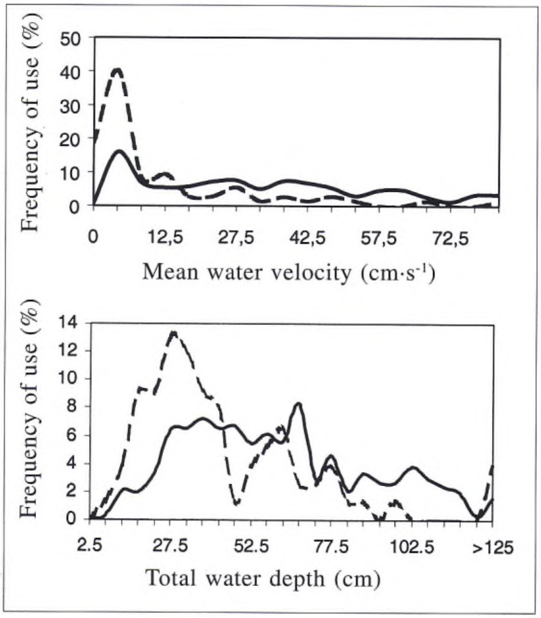

Fig. 4. Mean water velocity and depth use by sympatric young Atlantic salmon (solid line; $N = 290$) and brown trout (darted line; $N = 76$) in the Stjørdalselva River, central Norway.

1998). However, both species are to some extent flexible in their use of habitat, depending on competition and other environmental conditions both as alevins (e.g. Heland et al. 1995) and older juveniles (see below). This pattern of segregation may be modified in a number of ways and is certainly not universal.

In some field studies (Saunders and Gee 1964, Jones 1975, Bremset and Berg 1997), Atlantic salmon parr have been reported to use slower flowing stream sections such as pools as frequently as riffles. This realised habitat use may be restricted to a narrower range through interspecific competition with brown trout. In the absence of or at low abundances of brown trout (e.g. in Canada and northern Norway), young Atlantic salmon expand their effective habitat to include relatively slow-deep areas like estuarine and lacustrine habitats, pools and ponds (Chadwick and Green 1985, Pepper et al. 1985, Cunjak 1992, Halvorsen and Jørgensen 1996, O'Connell and Dempson 1996, Erkinaro et al. 1998). This may be more common than previously thought. Use of lacustrine habitat is reported also for sympatric Atlantic salmon and brown trout in temperate Europe (e.g. Pedley and Jones 1978, Matthews et al. 1997). We speculate if different environments over time may favour local adaptations also with respect to selective segregation. Peake et al. (1997) reported slightly higher stamina in currents for wild salmon from river environments compared to fish from lacustrine habitats.

The acknowledged importance of higher water velocities in the distribution of Atlantic salmon in sympatry with brown trout, may be the combined expression of innate selective segregation and adaptation (larger pectoral fins; see below), and of interference competition with the more aggressive brown trout. These habitat segregation patterns are also modified by the presence of predators (e.g. Huntingford et al. 1988, Bardonnet and Heland 1994), and by abiotic factors. Most important of the latter are changing water flow that change available habitat, temperatures that induce behavioural changes and habitat switches, and light that induce night and day changes in habitat use (e.g. Roussel and Bardonnet 1999; see Heggenes et al. 1999 for review).

Several authors have proposed that river areas of particular water depths are more suitable as habitats for young Atlantic salmon and brown trout. Baglinière and Champigneulle (1982), Kennedy and Strange (1982) and Egglishaw and Shackley (1985) found that salmon tended to concentrate in intermediate depths (15-40 cm). However, other studies indicate water depth to be of little importance in habitat selection by Atlantic salmon. DeGraaf and Bain (1986) found water depth to be unimportant for habitat use by Atlantic salmon juveniles. Similarly, Bremset and Berg (1997) found no clear preferences for certain water depths by young salmon and trout in deep pools (cf. Fig. 5). For brown trout in particular, fish tend to select deeper areas with increasing size. Greenberg et al. (1996) found that small- and medium-sized trout preferred water depths < 90 cm, with the smallest individuals preferring the shallower areas. Larger brown trout seem to have strong preference for deeper areas (> 60 cm; Heggenes 1996), and based on a model he suggested that water depths over a relatively wide range (20-80 cm) were suitable for both salmon and trout.

In studies of microhabitat use by young salmonids, most of the attention has been directed to water depth, water velocity, river bed substrate and cover, all of which are considered to be important physical habitat variables for salmonids in streams (Lindroth 1955, Karlström 1977, Gibson 1978, Rimmer et al. 1984, Heggenes 1989). There are some discrepancies as to which of these variables are the most important. Bohlin (1977), Kennedy and Strange (1982) and Heggenes (1988a) rated water depth as the most important variable for habitat use of brown trout juveniles, whereas Baldes and Vincent (1969) and Shirvell and Dungey (1983) focused on water velocity, and Gatz et al. (1987) and Lewis (1969) emphasised the importance of substrate and cover, respectively (for further review, see Heggenes 1990). These inconsistencies among studies could be a function of physical habitat complexity and availability or the result of differences in study design and limitations in spatial scale.

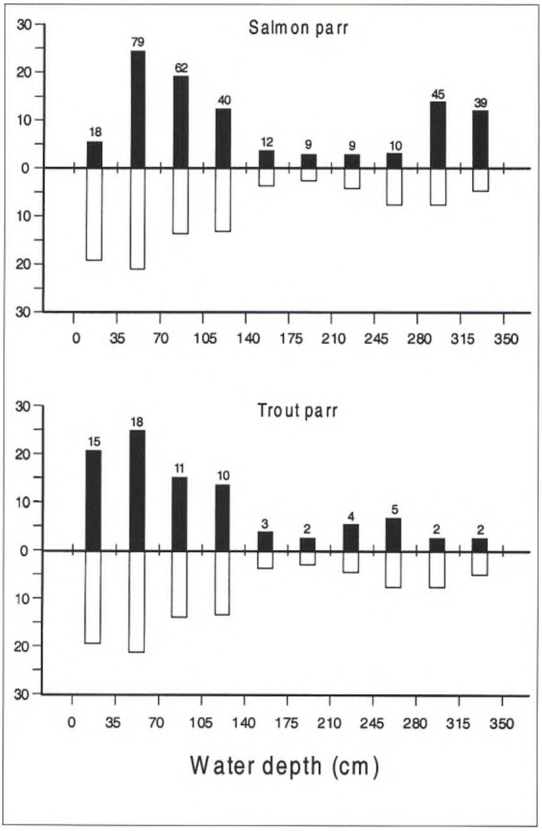

Fig. 5. Comparison of microhabitats used by (a) salmon and (b) trout parr (■) and their availability (□) with respect to water depth in three pools. The number of fish observations at each depth interval is indicated above the bars (from Bremset and Berg 1999).

The niche dimension

Fish species living in sympatry are always segregated in the sense that they never have a complete overlap in their use of resources (Nilsson 1967, Wootton 1990). Allen (1969) observed that young brown trout were less attached to the riverbed than Atlantic salmon, and related this to differences in the feeding biology of the two species. The higher occurrence of trout parr compared with salmon parr recorded in the upper part of the water column in the deep pools of three Norwegian rivers is probably the outcome of interspecific competition for profitable feeding positions (Fig. 2; Bremset and Berg 1999, Bremset 2000).

Morphological adaptations

Juvenile salmon are well adapted to high water velocities, because of their large pectoral fins and hydrofoil shape that helps them maintain their position in the water current (Jones 1975). As a consequence, salmon juveniles are more capable of using a wider range of water velocity (micro)habitats than trout juveniles (Jones 1975) and better hold stations in fast water (Peake et al. 1997). This morphological adaptation is probably the reason why salmon parr have shown to be numerically dominant in faster flowing areas in a large number of Scandinavian rivers where the two species coexist (above).

Food and feeding

In running waters drift is the main source of food for fish (Waters 1969, Wankowski and Thorpe

1979, Bachman 1984). Because drifting fauna on a regular basis is more accessible, the fish generally feed on drifting fauna in preference of bottom fauna (Waters 1972, Stradmeyer and Thorpe 1987). Food availability in terms of drifting invertebrates is dependent on several spatial and temporal factors, such as substratum (Collier and Wakelin 1992), water velocity (Hynes 1970) and time of day or season (Metcalfe et al. 1999). The drift rate increases to some extent with water velocity in the lower range (e.g. Wankowski and Thorpe 1979, Smith and Li 1983, Metcalfe 1986, Nislow et al. 1998), and the water velocity increases almost logarithmically from the river bed to the water surface in river channels (Hynes 1970, Allan 1995).

Drifting invertebrates in the water surface and upper part of the water column are generally larger than invertebrates drifting in the lower parts of the water column (Waters 1969). As a consequence, trout parr, i.e. dominant fish, keep positions high in the water column where the availability of drifting invertebrates is greatest (cf. Allen 1969, Bremset and Berg 1999, Bremset 2000). The subordinate fish, i.e. salmon as a group, are restricted to less profitable feeding areas closer to the riverbed, and subject to aggression from trout, also reducing food intake and growth. This is corroborated by experimental studies showing no effect of the presence of salmon on brown trout growth, while salmon growth is reduced in the presence of brown trout (Jobling et al. 1998).

Innate selective differences

To the extent that habitat segregation in salmon and trout are not affected by competitive interactions, it may be a result of selective segregation. If salmon show a stronger preference for higher water velocities, this would explain the commonly observed distribution pattern with salmon in the faster flowing (mid-)stream sections (above). Allen's (1969) observation that salmon tend to hold position closer to the riverbed, might be a result of selection for faster mean water column flows. Experimental studies indicate innate selective differences between salmon and trout, and at a very early state, i.e. what appear to be genetically fixed differences. Gaudin et al. (1995) observed post-emergent fry of brown trout to hold station and feed more actively in the water column, and to be more aggressive, than salmon, which were strongly substrate bound, in a laboratory flume at low water velocities.

Ecological release

Reduced niche breadth and displacement from habitat optima for Atlantic salmon or trout when in sympatry, as compared to allopatry, indicate competition. The few studies reported on young Atlantic salmon in allopatry, indicate that salmon are restricted to a narrower habitat in sympatry with brown trout. Salmon may use a wider depth range in the absence of brown trout (Lindroth 1955, Heggenes 1991), and occupy more slow-flowing areas (Karlstrøm 1977, Kennedy and Strange 1986a, b, Heggenes 1991). Kennedy and Strange (1986a, b) compared habitat use by young salmon in a small stream first when in natural sympatry with brown trout. After removing brown trout in a closed section of the stream, young salmon expanded their habitat use to include also more deep stream habitat, even in preference to the shallow areas. In streams with high densities of other pool-dwelling species in addition to brown trout, density of salmon parr appear to be reduced in slow water and pools (Keenleyside 1962, Elson 1975, Baglinière and Arribe-Moutounet 1985, Baglinière and Champigneulle 1986). Thus, the reported use of large, deep pools by salmon in streams (e.g. Bremset and Berg 1997) and lacustrine habitats (e.g. Erkinaro et al. 1998) may be flexible and sensitive to the presence and abundance of potential predators and competitors.

The terms pool and riffles appear to be somewhat imprecise when quantifying habitat optima for salmon. Physical characteristics of the pools are likely to be important. Bremset and Berg (1997) studied pools with relatively high water velocities and coarse substrates. In a small Norwegian stream stocked with an allopatric cohort of young Atlantic salmon, the fish deserted slow pools with fine substrates, even in a cafeteria situation (Heggenes 1991). This is also consistent with experimental studies (Crisp and Hurley 1991). Although subtle innate selective differences exist, habitat use by young Atlantic salmon in the presence of brown trout and other potential competitors and predators, appears to be restricted to a narrower range, indicating interference competition. Habitat segregation in sympatric salmon and trout is the combined expression of competition and selective segregation.

As may be expected because of more aggressive behaviours conferring a competitive advantage, habitat use by brown trout is less affected by the presence or absence of salmon. However, as salmon is better adapted to tolerate higher water velocities, they appear to have a competitive advantage over trout in fast stream sections. In the absence of salmon, trout may expand their use of fast-flowing habitats (Karlström 1977). Baglinière and Arribe-Moutounet (1985) attributed the occasional occurrence of young brown trout in deep water in a French river, to competition with young salmon present in the fast-flowing shallow river reaches. A similar pattern of expanded habitat use by young trout may, however, also be caused by reduced intraspecific interference competition with larger trout.

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Stocking of Freshwater Fish in Norway: Management Goals and Effects

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Abstract

In Norway, freshwater fish have been transported between localities for stocking purposes for at least 1000 years. Consequently, a large number of extant populations derive from such stockings. Even today, stocking of fish such as brown trout, *Salmo trutta*, is the main fish management action in freshwater. Unfortunately, there is not available any comprehensive summary statistic of the fish stocking activity. Further, very few studies have quantified the effect of stocking on the target species, or on non-target species. In this paper we discuss the reasons for stocking freshwater fish, and how such stocking may influence wild conspecifics and other taxa. Stocking is often performed without a well-defined management goal, and thus it has been difficult to evaluate its success. When management goals are formulated, they are usually qualitative rather than quantitative. In the future it is important to formulate precise management goals to allow for testing if the goal is met. Further, it is important to collate and analyse data on stockings performed to date, and identify positive and negative effects on target and non-target taxa.

Keywords: stocking, effect size, brown trout, freshwater fish, management, restoration, yield enhancement.

Introduction

Stocking, transfer and introduction of freshwater fish are commonly used to enhance recreational catches, mitigate the loss or reduction of stocks and to create new fisheries (Cowx 1998). The word stocking is often used to imply the repeated release of fish into an ecosystem from an external location (Welcomme 1998). However, we will refer to the word stocking as all kinds of transfers and introductions of fish. Stocking of fish has a long tradition in Europe, probably dating back to the Roman period (Welcomme 1998).

Large parts of Norway have a depauperate fish fauna due to its glacial history and its geography (Økland and Økland 1999). Unsurpassable waterfalls prevented fish from penetrating inland to large areas. The present occurrence of fish in these areas is thus largely due to human introductions. In Norway, the history of freshwater fish stockings dates back to around the year 1100, when written accounts mention the transport of brown trout, *Salmo trutta*, into Lake Rausjøen at 712 m above sea level. In those days the person who stocked a lake probably also acquired exclusive fishing rights (Bleken Ruud 1967, Berg 1986). Since that time, stocking has been the most important fish management activity in Norwegian freshwaters. In 1852, a small book written by Halvor Heyerdal Rasch started a period of massive fish introductions and transfers. Rasch (1852) mentioned a large number of freshwater fish species which he found suitable for stocking, e.g. Atlantic salmon *Salmo salar*, brown trout, Arctic char *Salvelinus alpinus*, whitefish *Coregonus lavaretus*, vendace *C. albula*, grayling *Thy-*

mallus thymallus, smelt *Osmerus eperlanus*, pikeperch *Stizostedion lucioperca*, perch *Perca fluviatilis* and bream *Abramis brama*. Since then one of the main activities of the fisheries managers has been to initiate and oversee stocking programs (Bleken Ruud 1967, Berg 1986).

One of the most important activities prior to stocking is the identification of biological bottlenecks. Without such knowledge no management activity should be started. In general, density-dependent mechanisms regulate population growth rate and biomass in most ecosystems (Begon et al. 1990). In systems exposed to human interference, total productivity is often reduced. In regulated lakes and rivers, availability of suitable habitats and food is reduced leading to a reduced carrying capacity (Gore and Pettsw 1989, Thornton et al. 1990). Recruitment may be impeded if access to spawning areas is denied or restricted. It is also necessary to understand how different species interact in a system, in order to predict effects of stocking on non-target taxa.

There is not available any comprehensive summary of the stocking practice in inland waters of Norway. Some statistics from recent stockings are available for different counties or districts (Hesthagen and Østborg 1999), but the quality is often questionable. Stockings that were carried out some decades ago are even less well documented. In the eastern part of Norway, it is estimated that brown trout were stocked into at least 1,400 localities (Eie 1999). Today, brown trout is the most commonly stocked species in freshwater (Anon. 1991), whereas species such as Arctic char and grayling are rarely used. Thus, we will focus on brown trout and only occasionally refer to other fish species for specific examples. Our main aim is to examine the stocking of non-anadromous freshwater fishes in Norway.

Norwegian legislation today and tomorrow

In Norway, a new law on "salmonid and other freshwater fish etc." was introduced in 1992. §§9 and 10 are especially pertinent to the subject of fish stockings. §9 states: "it is forbidden to introduce anadromous salmonids, freshwater fish, or their egg and fry, into watercourses, fjords or sea areas". Further §10 states that no one must start fish cultivation without prior consent from the Department of the Environment. However, both paragraphs states that it is possible to obtain such consent through application. During recent discussions of this law, it has been maintained that the law only regulates the stockings performed by private and state organisations, but not by court decisions. The latter involves freshwater fish stockings that are carried out to compensate for the loss of fish production due to hydropower regulation.

Following this new law, local management organisations started a planning process whereby stocking practice was included into a number of regional plans. Stocking without an approved plan would then not be allowed. This planning process has not yet been completed. There seems to be two main components to this planning process. First, a number of "cultivation zones" are recognised which usually encompass separate watercourses. According to these, no fish should be transported between these zones, mainly to reduce the probability of transferring parasites and other pathogens (see Skår, this volume). Secondly, it is advocated that local populations should be used in the stocking programs to maintain the integrity of local populations, based on the assumption that local populations are adapted to their environment and thus have evolved specific locally-adapted traits (Hindar et al. 1991, Taylor 1991). However, plans rarely involve the use of locally adapted populations in the stocking programs, but rather populations from nearby areas (Hesthagen and Østborg 1999). The decision to use such populations is usually based on an evaluation of the costs and difficulties of maintaining large numbers of separate populations in hatcheries.

What are the management goals?

The goals of stocking practices vary considerably. In order to study or quantify the success of a stocking exercise, a management goal has to be unequivocally stated. But before such a goal can be formulated, it is necessary to clearly state the reasons for doing the stocking. In Norway, the reason for stocking freshwater fish can be divided into four categories, and examples of each of these will be given.

Yield restoration or compensation

Stockings are often performed to compensate for a human disturbance to the environment that has reduced fish production. In Norway, the most common reason for such a stocking practise is hydropower development. In recent years more than four million salmonid fish have been stocked to compensate for losses due to such activities (Anon. 1991), of which about half involve brown trout (L'Abée-Lund 1991). The aim of these stockings is usually to compensate for lost fishing opportunities by maintaining or increaseing recreational yield. However, this goal is rarely quantified.

Stocking has also been used to recreate a fishery after losses due to pollution. In Norway, acidification is one of the major environmental problems (Henriksen et al. 1988, Henriksen et al. 1989). This has led to a strong reduction or extinction of fish populations due to recruitment failure (Hesthagen et al. 1999b). After restoring water quality through liming, lakes are usually stocked to increase fish production, or in the case of extinction, to reintroduce fish.

Yield enhancement

Yield enhancement is performed to increase catches in a more or less intact ecosystem. This is attempted by increasing recruitment or by introducing new species. The reasons for enhancing yield vary considerably. In some cases, fishers are not satisfied with their catch and local fishery associations or landowner organisations introduce hatchery-reared fish to increase yields. More than 1 million brown trout are probably stocked annually by such organisations (L'Abée-Lund 1991). In Oppland County alone, it is estimated that brown trout have been stocked in more than 1,000 lakes and rivers. These stockings are largely carried out by private organisations and until recently, no management plan was necessary (Anon. 1991).

Other examples of yield enhancement practises include "put-and-take" stocking, where large harvestable-sized or smaller fish are released into lakes or rivers where natural recruitment is impossible (Hesthagen et al. 1989, Skurdal et al. 1989). In Norway, classical "put-and-take" fisheries are relatively rare. Recently, cyprinid fishes such as carp, *Cyprinus carpio*, and tench, *Tinca tinca*, have been introduced illegally to a number of small lakes and ponds in eastern Norway to produce an exclusive "catch and release" fishery (Johansen 1995).

Conservation

In certain instances, fish populations experiencing significant reductions in recruitment and population size are deemed to be in need of aid. Particular attention is given to populations considered of special interest. For example, the landlocked Atlantic salmon, *Salmo salar*, population of Lake Byglandsfjord have for some years existed solely as a hatchery population due to acidification of the lake (Hesthagen et al. 1999b). Landlocked populations of Atlantic salmon are rare in Norway: one population is extinct (River Nidelva), one is in need of restoration (Lake Byglandsfjord), and the remaining one is assumed to be relatively healthy (River Namsen) (Berg 1985; Hesthagen et al. 1999b). We, however, found few examples from Norway where conservation has been the principal reason for stocking.

Bio-manipulation

The term bio-manipulation was coined following discussions on the use of top-down effects to manipulate food webs (Benndorf et al. 1984; McQueen et al. 1989). By stocking top-predators it is possible to manipulate lower trophic levels in order to improve water quality or change population structure of the target fish population. The presence of a predator may change the prey population structure directly (predation) or indirectly (induced behavioural changes in the prey fish population).

In Norway, introductions of new piscivorous species, such as pikeperch, has been used to reduce the density of roach, *Rutilus rutilus*, and reverse eutrophication in lakes (Brabrand and Faafeng 1993). Pikeperch induce a strong change in habitat use by the roach leading to reduced predation on large zooplankton (mainly *Daphnia*), thereby increasing the feeding rate on phytoplankton and reducing their biomass. Experiments have also been performed on the use of piscivorous brown trout to reduce the density or change the behaviour (i.e. habitat use) of Arctic char in order to increase individual growth rates and thus size (Damsgård and Langeland 1994). These experiments are based on the assumption that strong intra-specific interaction (i.e. competition) constrain Arctic char growth. Similar results may be obtained by introducing large cannibalistic char (Damsgård and Ugedal 1997). Such bio-manipulations are recognised as experimental at present, and will therefore not be discussed any further.

What are the effects of stocking?

It is only possible to formulate management goals when reasoning based on sound biological principles is used. Only then, is it possible to test if the goals are met (i.e. the effect size). Adaptive management is the ability to design management actions such that it is possible to, within the management process, learn from mistakes so that corrections can be made (Ham and Pearsons 2000). If management actions are designed as experiments, using controls and replicates, it is possible to quantify effects using standard statistical methods. However, as emphasised by Ham and Pearsons (2000), a good monitoring strategy used to evaluate an effect is essential for high quality feedback to be given to the management community. Standard population abundance monitoring may not provide data that are sensitive enough to detect negative impacts of a management action. One of the main reasons for this is the strong temporal variation in most ecological systems. To learn anything from a management action, it is necessary to introduce strong effects that are certain to lead to changes in population structure or growth rate (Walters and Holling 1990). Minor experiments are not favoured because they erode average performance without significantly improving learning rates.

When clearly stated management goals are formulated, based on biologically sound reasoning, it is possible to develop studies that can test if, and to what degree the goals are met. Below we examine examples from different kinds of broadly defined management goals. It will become evident that most stockings are performed without a well-defined management goal.

Yield restoration or compensation

In a large number of locations in Norway, fish (mainly brown trout) are stocked to compensate for loss in fish production due to hydropower development. The main test for success of such a stocking program has usually been to quantify the number or percent of fish of hatchery origin in the total catch. The proportion of stocked fish in the yield from such systems may vary from 0 to almost 100% (Aass 1991). However, the proportion of stocked fish in the catch is a poor measure of success. Recent studies have therefore focused on the total harvest (yield) in the population. In some cases, stocked fish do not contribute significantly to total production, as occurred in the sub-alpine reservoirs Vinstervatna and Tesse (Hesthagen et al. 1995b, Hesthagen et al. 1999a). The Vinstervatna reservoir had been stocked with hatchery-reared brown trout for a number of years; however, these trout grew more slowly and had a shorter life span than the native trout. Consequently, the stocking program did not increase brown trout production significantly and was terminated (Hesthagen et al. 1999a). A similar result was obtained in the regulated River Teigdal, where the hatchery-reared fish suffered higher mortality and grew slower than their wild conspecifics (Fjellheim et al. 1995). Stocking cannot compensate for reduced production, if the loss is due to a reduction in available suitable habitat, or reduced primary and secondary production, as is often the case in regulated rivers.

Yield enhancement

A yield enhancement program is based on the assumption that the carrying capacity in the system has not been met, and that no or weak density-dependent effects are present. This may occur when natural recruitment is low or reduced, as for example when hydropower regulation results in the destruction of spawning possibilities (reduced habitat, impeded migration). However, the primary and secondary production is often reduced simultaneously, due to increased amplitude in seasonal water level variation in such lakes (up to 140 m!). In Lake Aursjoen, Skjåk, a good fishery has been maintained due to stocking, and stocked fish commonly constitute 70-75% of the total catch (Hesthagen et al. 1995a). In contrast to this, in Lake Aursjøen, Lesja, catches of naturally produced brown trout declined with increasing numbers of stocked trout (Haugen 1998), probably due to increased intraspecific competition. In Lake Silsetvatn, it was found that introduced brown trout replaced wild brown trout without increasing the total population size (Aass and Wold 1999). In an evaluation of 49 stocking programs for brown trout in regulated lakes in Telemark, it was suggested that stocking should be stopped in 12 lakes and strongly reduced in 18 localities (Solhøi 1999). The reason for this was that stocking invariably led to a fish population of reduced quality (reduced growth rate and small fish size), probably due to increased intraspecific competition after stocking.

It is usually assumed that stocked (i.e. hatchery-reared) fish behave like their wild conspecifics. However, this is often not the case, as discussed by Einum and Fleming 2001. Moreover, if the fish used for stocking are genetically different from their wild conspecifics, genetic changes in the wild population may be the result. Where genetic effects on performance traits have been documented, they always appear to be negative in comparison with the unaffected populations (Hindar et al. 1991).

Conservation

We have no examples from Norway to show that this strategy has been used successfully. For a stocking program to be successful as a conservation tool it is necessary to document that the genetic integrity of the population is maintained. Hatchery programs may lead to reductions in genetic variability in the hatchery population, as well as to strong genetic drift (Ryman 1991, Ryman and Laikre 1991). It is not clear if the hatchery program for the landlocked Atlantic salmon in Lake Byglandsfjord has been successful, since no study of the genetic integrity of the populations has been performed.

Bio-manipulation

We have a few examples where bio-manipulation has been used successfully (Brabrand and Faafeng 1993), but the impact of such experiments have often been different from that predicted. Information on ecosystem functioning is at present not detailed enough to give good and precise predictions about the outcome of bio-manipulation programs. Stocking of large piscivorous brown trout or Arctic char has been advocated as an efficient tool for increasing growth rate in Arctic char populations dominated by small fish (Damsgård 1993, Damsgård and Langeland 1994), but its success will depend on lake morphometry and different ecosystem processes.

Efforts to increase stocking effectiveness

Much effort has been put into increasing the number of stocked fish that are recovered, often without testing if this in any way influences overall success. We refer to this as the "engineering" approach to biology, and this effort includes studies of rearing techniques, naturalisation of the fish before stocking and stocking techniques (timing, methods, etc.). Such studies are of vital interest for designing optimal stocking programs, once a management goal has been formulated.

A number of studies focus on the effects of rearing techniques (Hesthagen and Johnsen

1989a, Johnsen and Hesthagen 1990, Johnsen and Ugedal 1990), or timing of stocking (time of season, size of fish) (Hesthagen and Johnsen 1989b, Hesthagen and Johnsen 1992, Näslund 1998) on survival. It has been found that brown trout which are pre-stocked in ponds before release into lakes survive better than brown trout released directly into lakes (Hesthagen and Johnsen 1989a). If the brown trout are stocked into small streams, however, no effect of a previous pond experience is evident (Johnsen and Ugedal 1990). It is often found that the recapture rate of brown trout released in lakes increases with the initial fish length (Hesthagen and Johnsen 1992). A recent Swedish study found the opposite result for brown trout stocked in small streams (Näslund 1998). It is evident that different regulating mechanisms are important in streams and lakes.

Another factor of importance is stocking density. Hesthagen and Johnsen (1992) stocked four small lakes with brown trout at different densities (67-450 fish ha^{-1}). Individual growth was inversely correlated with density, but total production increased with density. Lake Tesse has been stocked annually with brown trout since ca 1950 (Hesthagen 1997). The number of stocked fish increased during 1980-86, but this did not lead to increased yield. Rather, fish size decreased probably due to reduced growth rate as a consequence of increased intraspecific competition.

The spatial distribution of stocking can also influence fish performance. L'Abée-Lund and Langeland (1995) compared recapture rates of brown trout stocked either as one batch (spot-planted) or distributed evenly along the shoreline (scatter-planted) in Lake Våvatn. The overall recapture rate of scatter-planted brown trout was higher than that of spot-planted trout. On the other hand, Jokikokko (1999) found no significant differences in the performance of spot-planted or scatter-planted brown trout in a small Finnish river. The same result was found by Johnsen (1990, 1994) who compared the recapture rate and growth of brown trout spot-planted and scatter-planted in a number of streams and lakes. Thus, the results seem to depend on locality type and probably also stocking density and time.

How to quantify effects?

Most studies focus on the yield of stocked fish, e.g. kg ha^{-1} or percentage of hatchery-reared fish in the total catch. However, this is not an acceptable measure of success if density-dependent mechanisms are present. Introducing more fish into such a system may lead to negative impacts on the wild conspecifics, usually in the form of reduced growth or increased mortality (Berg and Jørgensen 1991, Weiss and Schmutz 1999). Therefore the benefit of stocked fish may be measured by the presence of these stocked fish in excess of the number of wild fish of that size predicted from previous studies (Millard and MacCrimmon 1971). Even when a "positive" effect of the stocking has been documented in such a way, genetic changes may have long-term negative effects (Hindar et al. 1991, Hansen and Loeschcke 1994). Another reason for genetic change, albeit less well documented, is the effect of introducing large numbers of fish where progeny of one or a few families may dominate (Ryman and Laikre 1991). Both effects may lead to changes in gene frequencies and possibly also to a breakdown of local adaptations (Skaala et al. 1996; Laikre 1999).

We know of few, if any, stocking programs in Norway which have formulated management goals for non-target species or for ecosystem functioning (exceptions are bio-manipulation experiments). Stocked fish may harm non-target taxa through various ecological mechanisms, including competition, predation, behavioural anomalies, and pathogenic interactions (Pearsons and Hopley 1999). Stocking of fish in small ponds has been regarded as a threat to invertebrates and amphibians (Dolmen 1993). Stocking may influence ecosystem characteristics such as species richness and productivity. In order to study such effects, a thorough consideration of all non-target taxa and all relevant ecosystem levels is necessary.

The most common experimental design used to quantify the effect of stocking is longitudinal studies, with a pre- and post-treatment study period. Usually such studies include a short pre-treatment period and a relatively longer post-treatment period, depending on the generation length of the target taxa. The problem with such a study design is the difficulty of removing temporal environmental variability. In order to remove such bias a study has to be of relatively long duration, usually well past that of most project funds. The reason for this is the low statistical power of such tests. Ham and Pearsons (2000) evaluated the ability to detect the response of native salmonids to hatchery supplementation in eight Yakima River populations. High inter-annual variation in abundance estimates (CV of 25-95%) prevented detection of impacts.

Inter-annual variability is a problem when trying to infer cause and effect. The study design in itself reduces the probability of making general conclusions. Every major change in management policy is a perturbation experiment with a highly uncertain outcome, no matter how clever the design (Walters and Holling 1990). One main reason for this is that a management action does not change a system from one state to another, rather they induce transient responses that may be quite complex. There are a number of statistical techniques for analysing such time series, and for removing temporal and large-scale trends. Jassby and Powell (1990) advocates the use of principal component analysis and residual analysis to remove multidimensional trends. Another option is to use Bayesian statistical inference, where the results from the analysis may be presented as the probability of a unique event (e.g. the probability that population biomass has increased by 10% after stocking) (Reckhow 1990). However, the central questions in large-scale, unreplicated experiments have two main components: 1) is the difference between pre-treatment and post-treatment periods non-random; and 2) did the treatment cause the difference (Carpenter 1990).

There are statistical methods for analysing the outcomes of a number of single non-replicated studies. For a number of studies that are relatively comparable, effects can be summarised and analysed using meta-analysis (Rosenthal 1991; Arnqvist and Wooster 1995). The meta-analysis tests for consistency among outcomes of different studies, determines the magnitude (basically the amount of variance explained) and significance of the effects they measure, and uses standardised estimates of effect size. Meta-analysis also provides a stringent way of evaluating heterogeneity in the data set (Hedges and Olkin 1985). If no statistically significant heterogeneity exists, there is no reason to search for explanatory factors. Significant heterogeneity justifies a systematic search for variables that may account for different effects among studies.

The optimal study design, however, is the replicated and controlled study. By designing studies with an adequate number of replicates and controls it is possible to infer cause and effect, and also to quantify effect sizes with high precision. Such studies have rarely, if ever, been done on the effect of stocking. One reason is probably the difficulty of obtaining the necessary number of localities for doing the experiments, and also the probability of obtaining the necessary long term funding. There is, however, no doubt that the highest learning rate from a management perspective can be obtained from such a study design.

Concluding remarks

Fish stocking is still the main management action in freshwater in Norway, and in some communities this practise is an integral part of a social and cultural heritage. Thus, a large number of stockings may not have a biological purpose other than that it is assumed to increase the number of harvestable-sized fish in a lake or river. Since no biological goal has been explicitly formulated it is thus impossible to test the effectiveness.

We will now discuss how stocking practices should be organised in the future. We will base this discussion on useful papers by Cowx (1994) and Pearsons and Hopley (1999), focussing on how stocking exercises should be carried out to minimise the risk and maximise the potential benefit. To perform an ecological risk assessment of a fish-stocking program, the following five main tasks have to be performed (Pearsons and Hopley 1999): 1) determine non-target taxa objectives; 2) determine spatio-temporal overlap of target and non-target taxa; 3) determine existence of strong ecological interactions; 4) determine ecological risk; and 5) determine scientific uncertainty. These five tasks are best accomplished collaboratively by gathering scientist, managers and policy makers who will then systematically work through a risk template worksheet. Such a program is clearly only possible with larger stocking programs. Cowx (1994) focuses on a number of issues: 1) setting an objective; 2) assessing the status of the existing population; 3) documenting if the population is experiencing density-dependent regulation; 4) evaluating if other management strategies are possible; and 5) developing a stocking strategy. After implementing a stocking program, a post-stocking evaluation is always necessary. Based on our knowledge of fish stocking in Norwegian fresh water, almost no project has been through any of these planning steps. Many projects fail on step one, namely on defining an objective or goal. And, as pointed out by Kondolf (2000), general goals must be translated into specific measurable objectives to evaluate the performance of the project and to gain insights for the design of future projects.

We conclude that most fish stocking programs in Norway are not founded on well-based reasoning and a well-defined goal, and therefore, are difficult to evaluate. Further, we suggest that many stockings in Norwegian lakes and rivers with relatively healthy native populations are unnecessary and probably also harmful. A large-scale evaluation of the Norwegian stocking exercise should, however, be undertaken using available statistical tools. We propose that three different types of enquiry should be undertaken: 1) collect and analyse all available stocking data and analyse the material using meta-analysis; 2) analyse available long-term studies and use different kinds of time-series analysis to evaluate long-term and treatment effects; and 3) design and perform controlled and replicated experiments where the effect of stocking on wild populations of target and non-target taxa are tested.

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Guide to authors

General editorial practice

Submit the manuscript in triplicate.

All manuscripts submitted are considered for publication on the understanding that they have not been published, submitted, or accepted for publication elsewhere.

Manuscripts are submitted to reviewers for evaluation of their significance and soundness. Authors will generally be notified of acceptance, rejection, or need for revision within three months.

Decisions of the editors are final.

Manuscripts are edited to improve communication between the author and the readers.

Authors will receive one set of first proofs.

Authors are recommended to keep their papers short.

Fifty reprints are supplied free of charge. An additional number may be ordered at cost. Price list and order forms for reprints are sent with proofs.

Manuscripts

Language

Manuscripts should be in English. Linguistic usage should be correct. Write in a clear style. Avoid extensive reviews in the Introduction and Discussion. Cite only essential sources of a theory or opinion.

Title

The title should be brief and contain words useful for indexing and information retrieval.

Abstract

The abstract should succinctly mirror the content and emphasis of the paper in about 175 words. Like the title, the abstract enables readers to determine the paper's content and decide whether or not they need to read the entire article.

Keywords

Five keywords should be given for indexing and information retrieval.

Text

The first page should contain only the title and author's name and address. Begin the text on page two. The manuscript should be type-written, double-spaced with wide margins and on one side only of good quality paper. Word processor generated manuscripts should be in upper and lower case letters of typewriter quality font. Manuscripts printed by 7 x 9 or 9 x 9 dot matrix printers will not be accepted for publication or review. Underlinings in the text should be avoided. After re-submission please enclose a diskette containing the final version of the manuscript in any DOS-wordprocessing program.

Illustrations

Submit each diagram, graph, map or photograph in one original and three copies. All illustrations should bear author's name. Tables and legends of illustrations should be written on separate sheets. Do not incorporate the legend in the figure itself. Tables and illustrations should be comprehensible without reference to the text.

Colour plates may be included at the author's expense.

Plan your illustrations for the smallest size possible. Figures, letters, and other symbols on illustrations should be drawn so large that they will be at least 1.5 mm high in the final print.

Units

Use SI units as far as possible.

Nomenclature

Binomial Latin names should be underlined and used in accordance with International Rules of Nomenclature.

References

In the list of references the following usage should be conformed to:

Journal

Svärdson, G. 1976. Interspecific population dominance in fish communities of Scandinavian lakes. - Rep. Inst. Freshw. Res., Drottningholm 55: 144-171.

Book

Krebs, J.R. and N.B. Davies. 1991. Behavioural ecology. An evolutionary approach. Third edition. - Blackwell Scientific Publications, Oxford. 482 p.

Chapter

Krebs, J.R. and R.H. McCleery. 1984. Optimization in behavioural ecology. p. 91-121. - In: Krebs, J.R. and N.B. Davies (eds.) Behavioural ecology. An evolutionary approach. Second edition. Blackwell Scientific Publications, Oxford.

In the text references are given:

Svärdson (1976) or, at the end of a sentence (Svärdson 1976).

Titles of journals should be abbreviated according to the World List of Scientific Periodicals. If in doubt, give the title in full.

Do not refer to unpublished material.

Acknowledgments

Keep them short.

Symbols and Abbreviations

The following symbols and abbreviations, as well as others approved for the Systeme International d'Unités (SI), are used in this journal without definition. Any others must be defined in the text at first mention, as well as in the captions or footnotes of tables and in fiugres or figure captions. A variable divided with another variable should be noted as the following example L per min is L min^{-1}.

Time

A colon should be used as the separator between hour and minute and between minute and second. The symbols "h", "min", and "s" are not used, since they are the symbols for hour, minute, and second in the sense of duration or the length of time. Thus "12 h 30 min" expresses a measured time of twelve hours and thirty minutes duration whereas 12:30 refers to the time of day.

Prefixes

giga	(10^9)	G
mega	(10^6)	M
kilo	(10^3)	k
milli	(10^{-3})	m
micro	(10^{-6})	µ
nano	(10^{-9})	n
pico	(10^{-12})	p

Time and Temperature

day	d
degrees Celsius	°C
hour (spell out for diel time)	h
kelvin	K
minute	min
second	s

Spell out year, month, and week.

In Table and Fig.:

year	yr
month	mo
week	wk

Weights and Measures

centimeter	cm
gram	g
kilogram	kg
kilometer	km
liter (exception to SI)	L
meter	m

Spell out hectare and tonne.

Mathematics and Statistics

all standard mathematical signs, symbols, and abbreviations	
base of natural logarithm	*e*
common test statistics (*F, t,* etc.)	
correlation or regression coefficient (multiple)	*R*
correlation or regression coefficient (simple)	*r*
degree (angular)	°
degrees of freedom	df
expected value	*E*
intercept	α
logarithm (specify base)	log
minute (angular)	'
not significant	NS
percent	%
probability	*P*
probability of type I error (false rejection of null hypothesis)	$P\alpha$

probability of type II error (false acceptance of null hypothesis)	$P\beta$
radian	rad
sample size	N
second (angular)	″
standard deviation	SD
standard error	SE
variance	V or var

Physics and Chemistry

all atomic symbols	
alternating current	AC
ampere	A
becquerel	Bq
candela	cd
chemical acronyms listed in Webster's dictionaries (DDT, EDTA, etc.)	
coulomb	C
dextro	D
direct current	DC
electron volt	eV
equivalent	eq
farad	F
gray	Gy
hertz	Hz
hydrogen ion activity (negative log of)	pH
joule	J
levo	L
lumen	lm
lux	lx
molar	M
mole	mol
newton	N
normal	N
ohm	Ω
ortho	*o*
para	*p*
pascal	Pa
per mille (per thousand)	‰
siemens	S
tesla	T
trishydroxymethylaminomethane	tris
volt	V
watt	W
weber	Wb

General (some are restricted)

compass directions (maps and coordinates):	east	E
	north	N
	south	S
	west	W
et alii		et al.
et cetera		etc.
filial generation		F
for example		e.g.,
international unit		IU
months (tables, figures): first three letters (Feb, Jun, etc.)		
ploidy		n
sex (tables, figures, hybrid crosses):	female	♀
	male	♂
that is		i.e.,

Word List

The spelling of the following words is frequently inconsisten in submitted manuscripts. We prefer that authors adhere to the Journal's house style for these commonly used terms:

age-class (n.)
age-group (n.)
aquaculture (n.)
Arctic char (n.)
brackish water (n.)
brackish-water (adj.)
chi-square (n., adj.)
cold water (n.)
cold-water (adj.)
deep sea (n.)
deep-sea (adj.)
deep water (n.)
deepwater (adj.)
freshwater (n., adj.)
fresh water (n.)
groundwater (n., adj.)
hard water (n.)
hardwater (adj.)
headwater (n., adj.)
lake water (n., adj.)
meltwater (n., adj.)
open water (n.)
open-water (adj.)
percent (n.)
salt water (n.)
saltwater (adj.)
sea-run (adj.)
seawater (n., adj.)
shallow water (n.)
shallow-water (adj.)
short term (n.)
size-class (n.)
snowmelt (n.)
soft water (n.)
softwater (adj.)
tidewater (n., adj.)
t-test (n., adj.)
warm water (n.)
warmwater (adj.)
year-class (n.)
young-of-the-year (n., adj.)

CONTENTS

Proceedings of the
Workshop on the Release of Salmonid Fishes in Norway
June 5-7 2000, Kongsvoll, Norway