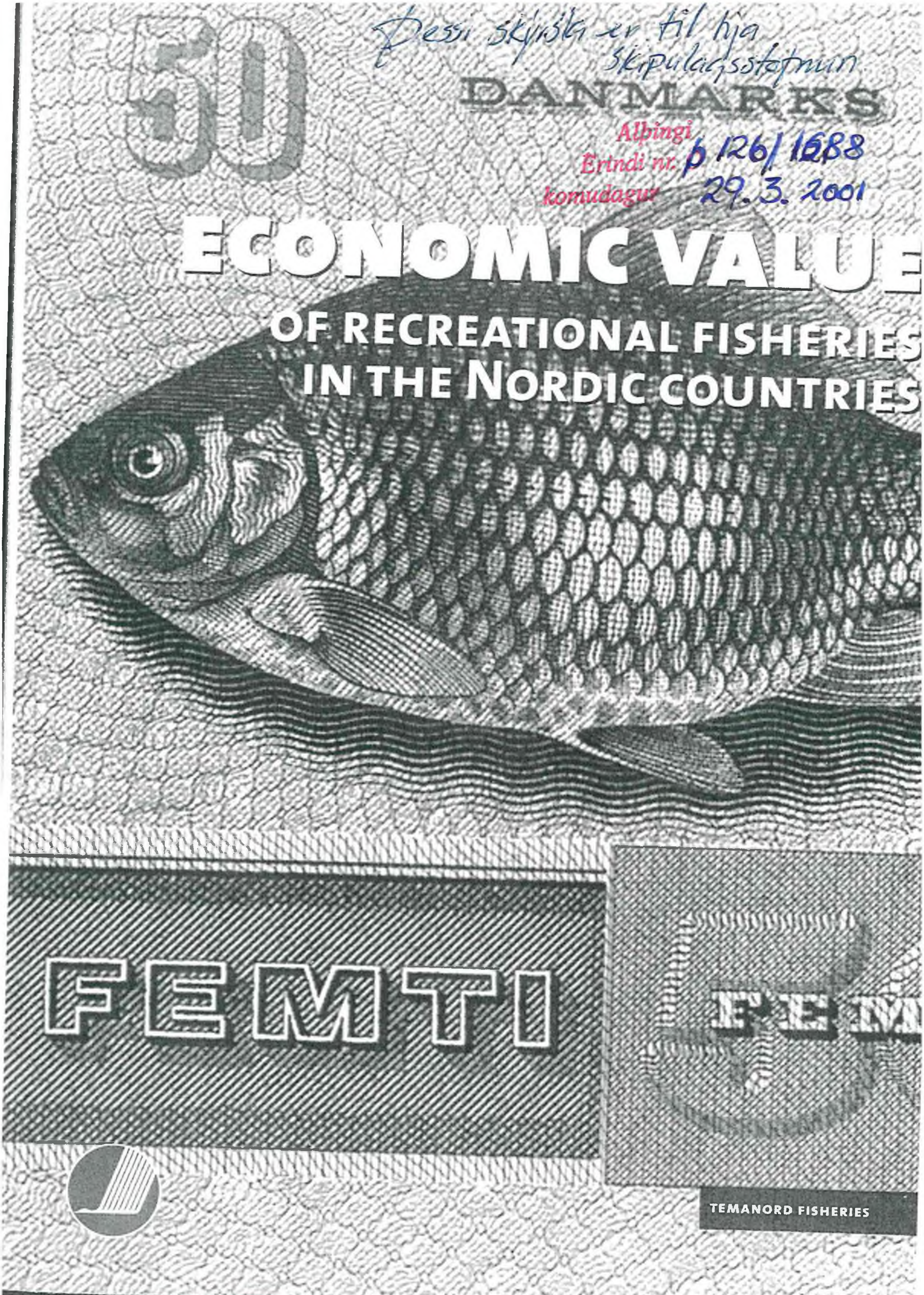
Þessi skýrsla er til hjá Skipulagsstofnun

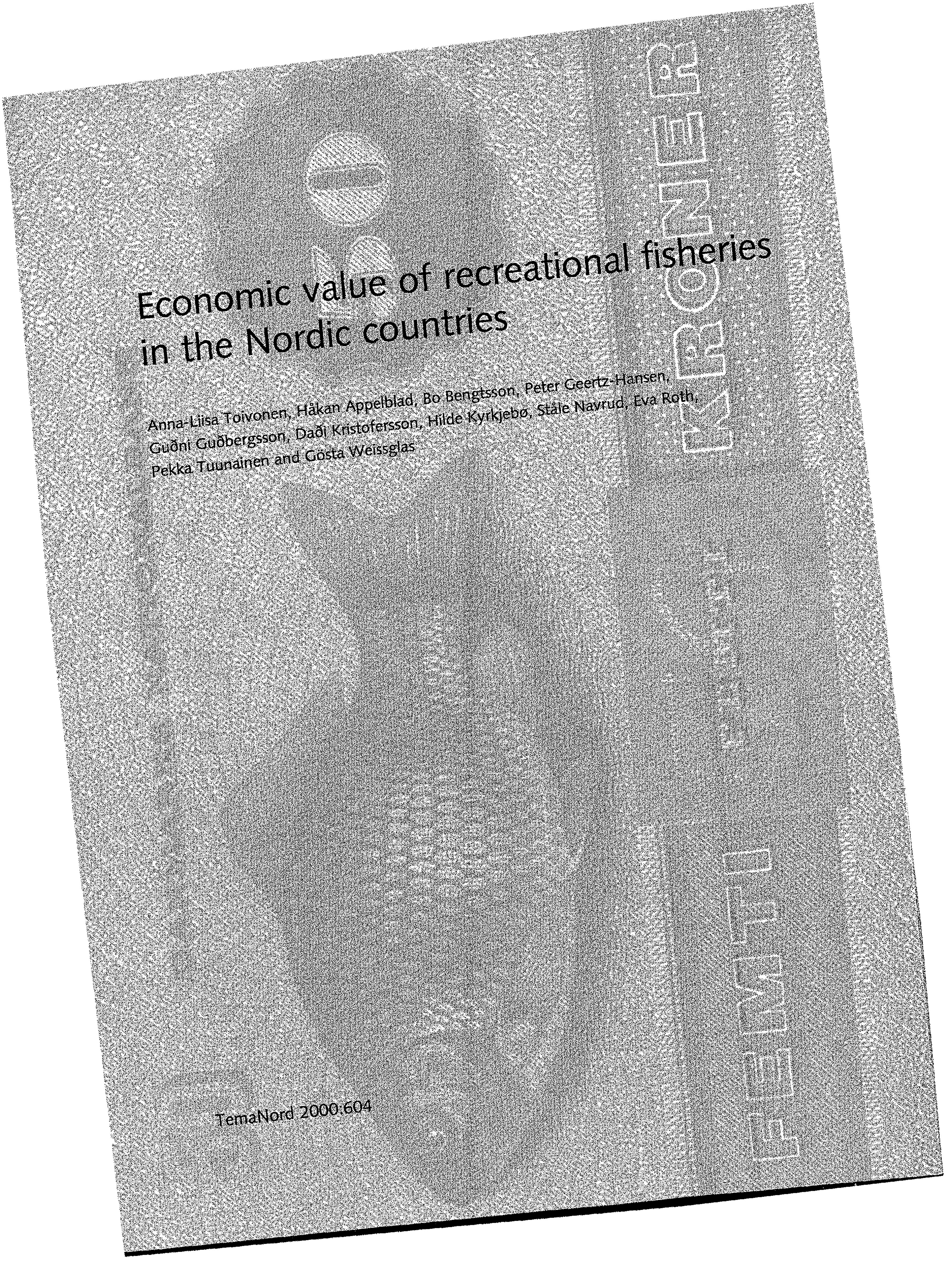
Alþingi
Erindi nr. Þ 126/1688
komudagur 29.3.2001

ECONOMIC VALUE
OF RECREATIONAL FISHERIES IN THE NORDIC COUNTRIES



TEMANORD FISHERIES

ECONOMIC VALUE OF RECREATIONAL FISHERIES IN THE NORDIC COUNTRIES



Economic value of recreational fisheries in the Nordic countries

Anna-Liisa Toivonen, Håkan Appelblad, Bo Bengtsson, Peter Geertz-Hansen,
Guðni Guðbergsson, Daði Kristofersson, Hilde Kyrkjebø, Ståle Navrud, Eva Roth,
Pekka Tuunainen and Gösta Weissglas

TemaNord 2000:604

Economic value of recreational fisheries in the Nordic countries
TemaNord 2000:604

ISBN 92-893-0551-7
ISSN 0908-6692
Cover printed with approval from the National Bank of Denmark
Print: Ekspressen Tryk & Kopicenter
Copies: 600
Printed on paper approved by the Nordic Environmental Labelling.
This publication may be purchased from any of the agents listed on the last page.

Nordic Council of Ministers
Store Strandstræde 18
DK-1255 København K
Phone (+45) 3396 02 00
Fax (+45) 3396 02 02

Nordic Council
P.O.box 3043
DK-1021 København K
Phone (+45) 3396 04 00
Fax (+45) 3311 18 70

Homepage: www.norden.org

Nordic fishery co-operation

The first Nordic Fisheries Conference was established in 1949. Since then, a comprehensive co-operation has been established involving politicians, management, scientists, trades and industries and other interest groups. The fishery sectors of the Nordic countries have numerous features in common. Fishery co-operation within the Nordic area involves co-operation, financed by the Council of Ministers, on issues and problems of broad interest in the Nordic countries. The steady flow of knowledge and information characterising Nordic fishery co-operation thus becomes a vital tool in ensuring a balanced development of fisheries. The motive of co-operation is thus to contribute to a sustainable and rational use of the living, marine resources.

The Nordic Council of Ministers

was established in 1971. It submits proposals on cooperation between the governments of the five Nordic countries to the Nordic Council, implements the Council's recommendations and reports on results, while directing the work carried out in the targeted areas. The Prime Ministers of the five Nordic countries assume overall responsibility for the cooperation measures, which are co-ordinated by the ministers for cooperation and the Nordic Cooperation committee. The composition of the Council of Ministers varies, depending on the nature of the issue to be treated.

The Nordic Council

was formed in 1952 to promote cooperation between the parliaments and governments of Denmark, Iceland, Norway and Sweden. Finland joined in 1955. At the sessions held by the Council, representatives from the Faroe Islands and Greenland form part of the Danish delegation, while Åland is represented on the Finnish delegation. The Council consists of 87 elected members – all of whom are members of parliament. The Nordic Council takes initiatives, acts in a consultative capacity and monitors co-operation measures. The Council operates via its institutions: the Plenary Assembly, the Presidium and standing committees.

Contents

Abstract

Both the total expenditure used for recreational fishing and the market value of the catch have previously often been used as measures of the economic value of recreational fisheries. However, these are both incorrect measures of the social benefits that freshwater fish stocks provide. In this study, we aim at providing a correct estimate of the annual, total economic value (TEV) of recreational fisheries and the non-use value that the overall population (both fishermen and non-fishermen) attach to preserving the existence of the current Nordic fish stocks and the possibility of passing on this existence to future generations.

A questionnaire using the Contingent Valuation (CV) method was used to measure TEV by estimating the willingness-to-pay (WTP) for recreational fisheries and the preservation of fish stocks. The survey included questions concerning: attitudes towards the environment and outdoor recreation; which category of recreational fishermen they belonged to; recreational fishing activities and preferences; fishing expenditures; WTP for three scenarios of new recreational fisheries; WTP for a fish stock preservation scenario; and socio-economic variables. The same CV mail survey was conducted simultaneously in all five Nordic countries: Denmark, Finland, Iceland, Norway and Sweden. National population registers were used as sampling frames. The sample size was 25 000 Nordic citizens between ages 18 and 69. After three contacts the final response rate was 45.8 %.

Results show that "occasional anglers" form the largest category of recreational fishermen in all Nordic countries; except Sweden where this category is not used. In Sweden the largest category (81 %) is sports fishermen i.e. those who only use rod and line. The selected age group (18-69) spends over 77 million fishing days annually in the Nordic countries, and on average 14 fishing days per recreational fisherman. Recreational fishing on the coast is the preferred style in Norway, Denmark and Sweden, while Icelanders and Finns prefer rivers and lakes, respectively.

The annual economic values of recreational fisheries (use value), expressed as the WTP of recreational fishermen for their fishing experience over and above their actual expenditures during the last 12 months, are (expressed as a percentage of actual expenditures): Denmark 48 %, Finland 41 %, Iceland 30 %, Norway 55 % and Sweden 38 %. TEV expressed as a percentage of the actual expenditures of recreational fishermen are: Denmark 415 %, Finland 79 %, Iceland 100 %, Norway 95 % and Sweden 92 %. These results clearly show the importance of including the WTP of both recreational fishermen and non-users of fish stocks when calculating the economic value of recreational fisheries and fish stocks. The results can be used in cost-benefit analyses (CBAs) of alternative uses of water flow, projects effecting water flow and CBAs of measures to restore and protect recreational fisheries and fish stocks. They can also be used to calculate compensation payment after pollution accidents affecting fish stocks, and as inputs in models for optimal fisheries management. Results on expenditures by fishermen can be used in models to calculate the local economic impact of tourism based recreational fishing.

Key words: recreational fisheries, economic valuation, contingent valuation, Nordic countries

Sammanfattning

Såväl fritidsfiskets totala utgifter som fiskfångstens marknadsvärde har tidigare ofta använts som mått på det ekonomiska värdet av fritidsfisket. Dessa måttstockar är dock båda inadekvata om avsikten är att mäta den sociala nytta som fritidsfisket och fiskfaunan kan erbjuda. I denna studie är syftet att presentera en korrekt beräkning av det årliga totala ekonomiska värdet (TEV, total economic value) av fritidsfisket samt det icke-användarvärde som hela befolkningen (både fiskare och icke-fiskare) tillerkänner ett bevarande av den nuvarande nordiska fiskfaunan och av möjligheten att bevara dess existens för kommande generationer.

Ett frågeformulär, där Contingent Valuation (CV) -metoden tillämpas, används i studien för att mäta TEV genom att skatta betalningsviljan (WTP, willingness-to-pay) för fritidsfisket och bevarandet av fiskfaunan. Undersökningen inkluderar frågor som berör attityder till naturmiljö och friluftsliv, vilken kategori av fritidsfiskare man tillhör, fritidsfiskeaktivitet och preferenser, utgifter för fisket, WTP för tre scenarier med nya fisken, WTP för bevarande av nuvarande fiskfauna samt socioekonomiska variabler. Enkätundersökningen genomfördes i de nordiska länderna, Danmark, Finland, Island, Norge och Sverige, samtidigt och med samma metodik. Vid urvalsförfarandet användes de nationella befolkningsregistren. Urvalet uppgick till sammanlagt 25 000 nordiska medborgare i åldersintervallet 18 till 69 år. Efter tre kontakter blev den slutgiltiga svarsfrekvensen 45.8 %.

Resultaten visar att tillfälliga fiskare, occasional angler, är den största kategorin av fritidsfiskare inom Norden (om man undantar Sverige, där denna benämning inte använts). I Sverige utgörs den största gruppen av sportfiskare, dvs. de som bara fiskar med handredskap (81 %). Den utvalda åldersgruppen (18-69) genererar sammantaget 77 miljoner fiskedagar årligen i Norden. I genomsnitt blir detta 14 fiskedagar per fritidsfiskare. Kustfiske sätts i första rummet av fiskare i Norge, Danmark och Sverige. Islänningar prefererar fiske i åar och älvar, medan finska fritidsfiskare helst fiskar i sjöar.

Det årliga ekonomiska värdet av fritidsfisket (användarvärdet) uttryckt som fritidsfiskarnas WTP för sitt eget befintliga fiske, utöver vad de årligen betalar är (uttryckt som procent av de faktiska utgifterna) för Danmark 48 %, Finland 41 %, Island 30 %, Norge 55 % och för Sverige 38 %. TEV uttryckt som procent av de faktiska utgifterna för fritidsfiske är för Danmark 415 %, Finland 79 %, Island 100 %, Norge 95 % och Sverige 92 %. Dessa resultat visar tydligt vikten av att inkludera WTP både för fritidsfiskare och för icke-användare av fiskfaunan när man kalkylerar fritidsfiskets och fiskfaunans ekonomiska värde.

Resultaten kan användas i kostnads-intäkts analyser (CBA, cost-benefit analysis) av alternativa nyttjanden av vattendrag och projekt som påverkar vattendrag, och för åtgärder som syftar till att restaurera, skydda och bevara fritidsfiske och fiskfauna. De kan också användas för uträkning av ekonomisk kompensation vid sådan miljöförstöring som påverkar fiskfaunan, och som ingångsvärden i modeller för förvaltnings-optimering. Resultaten avseende fritidsfiskarnas befintliga utgifter kan användas i kalkylmodeller över lokalekonomiska effekter av ett turistbaserat fritidsfiske.

Key words: fritidsfiske, ekonomisk värdering, contingent valuation, nordiska länder

Tiivistelmä

Vapaa-ajankalastukseen käytettyjä kustannuksia sekä saaliin arvoa on aikaisemmin usein käytetty mittaamaan vapaa-ajankalastuksen taloudellista arvoa. Nämä ovat kuitenkin kummatkin vääriä mittareita niistä yhteiskunnallisista hyödyistä, joita saadaan kalavaroista. Tämä raportti pyrkii esittämään taloustieteellisesti kestävin perustein lasketut estimaatit vapaa-ajankalastuksen vuosittaisesta kokonaisarvosta (total economic value, TEV) sekä siitä olemassaoloarvosta, jonka koko väestö, kalastavat ja kalastamattomat, asettavat vapaa-ajankalastukselle ja nykyisten kalakantojen säilyttämiselle sekä mahdollisuudelle niiden säilyttämisestä edelleen tuleville sukupolville.

Vapaa-ajankalastuksen taloudellista arvoa mitattiin ehdollisen arvottamisen menetelmään (contingent valuation, CV) perustuvalla kyselylomakkeella arvioimalla maksuhalukkuutta (willingness-to-pay, WTP) vapaa-ajankalastuksesta ja kalakantojen säilyttämisestä. Kysymysten aiheita olivat asenteet luontoon, ympäristöön ja vapaa-aikaan, mihin kalastaryhmään vastaajat tunsivat kuuluvansa, vapaa-ajankalastustottumukset ja -mieltymykset, kalastuskustannukset, maksuhalukkuus kolmesta vapaa-ajankalastusskenaariosta, maksuhalukkuus kalakantojen säilyttämisskenaariosta sekä yhteiskunnallis-taloudelliset taustatiedot. Kyselytutkimus toteutettiin samanlaisena ja samaan aikaan kaikissa viidessä Pohjoismaassa, Islannissa, Norjassa, Ruotsissa, Suomessa ja Tanskassa. Väestörekistereitä käytettiin otantakehikkoina. Otoskoko oli 25 000 pohjoismaista, 18-69 -vuotiasta kansalaista. Lopullinen vastausprosentti oli 45,8 kolmen kontaktin jälkeen.

Tulokset osoittavat, että "satunnaiset onkijat" ovat suurin vapaa-ajankalastajaryhmä muualla paitsi Ruotsissa, missä heidät lasketaan urheilukalastajiin. Kyselyssä mukana ollut ikäryhmä viettää yhteensä 77 miljoonaa kalastuspäivää ja keskimäärin 14 kalastuspäivää harrastajaa kohti vuosittain. Norjalaiset, tanskalaiset ja ruotsalaiset kalastavat mieluiten rannikolla, Islantilaiset pitävät eniten jokikalastuksesta ja suomalaiset haluavat kalastaa järvellä.

Vapaa-ajankalastajien vuosittainen ylimääräinen maksuhalukkuus viimeisen 12 kuukauden kalastuksesta jo maksettujen kulujen lisäksi prosentteina maksetuista kuluista oli Islannissa 30 %, Norjassa 55 %, Ruotsissa 38 %, Suomessa 41 % ja Tanskassa 48 %. Koko väestön, sekä kalastavien että kalastamattomien, maksuhalukkuus kalakantojen nykytilan ja vapaa-ajankalastuksen nykyisen tason säilyttämisestä prosentteina vapaa-ajankalastajien maksamista todellisista kustannuksista oli Islannissa 100 %, Norjassa 95 %, Ruotsissa 92 %, Suomessa 79 % ja Tanskassa 415 %. Tulokset osoittavat, että vapaa-ajankalastuksen ja kalakantojen taloudellista arvoa laskettaessa kyselytutkimuksen avulla, otokseen on tärkeää ottaa sekä kalastajia että kalastusta harrastamattomia. Tuloksia voidaan käyttää vesialueiden vaihtoehtoisten käyttötarkoitusten ja vesialueisiin vaikuttavien hankkeiden sekä vapaa-ajankalastuksen ja kalakantojen entisöinti- ja suojeluhankkeiden kustannus-hyötyanalyyseihin (cost-benefit analysis, CBA). Tuloksia voidaan käyttää myös kalakantoihin vaikuttaneiden ympäristövahinkojen korvauslaskelmiin sekä kalastuksen hoidon optimaaliseen mallintamiseen. Tietoja kalastajien maksamista kustannuksista voidaan käyttää turismipohjaisen kalastusmatkailun paikallisten taloudellisten vaikutusten mallintamiseen.

Asiasanat: vapaa-ajankalastus, taloudellinen arvottaminen, maksuhalukkuuskysely, Pohjoismaat

List of tables

Þessi skýrsla er til hjá
Skipulagsstofnun.

TILTAKSPLAN
MOT
RØMMING

Nasjonal tiltaksplan
mot
rømming

Mars 2000

Forord

Nasjonal tiltaksplan mot rømming er resultatet av rømmingsutvalgets arbeid siden oppnevnelsen i mars 1999.

Tiltaksplanen er basert på en betydelig informasjonsmengde som – etter utvalgets mening – samlet sett gir et nyansert og riktig bilde av denne problemstillingen ved milleniumsskiftet.

Det har vært et mål at forslagene til tiltak skal komme som logiske slutninger basert på den informasjon som er presentert først i tiltaksplanen.

Utvalget ønsker at flest mulig, både de som er innenfor og de som sitter mer på sidelinjen i norsk oppdrettsnæring, skal diskutere innholdet i planen og ta lærdom av dette. Utvalget ber samtidig om at eventuelle feil, unøyaktigheter eller forslag til forbedringer meldes tilbake til utvalgets leder innen utgangen av april 2000. Tidlig i mai vil utvalget diskutere de innspill som måtte komme og eventuelt ta disse inn i den endelige tiltaksplanen, som vil foreligge i løpet av mai. Derfor legges denne tiltaksplanen fram som et foreløpig dokument.

Utvalget vil takke alle som, på forskjellige måter, har bidratt med sin erfaring og kunnskap til utarbeidelsen av **Nasjonal tiltaksplan mot rømming.**

20. mars 2000

Håvard Vannebo
Norske fiskeoppdretteres forening
utvalgets leder

Axel R. Anfinsen
Fiskeridirektoratet

Svein Arne Aas
Norges forsikringsforbund

Harald Lura
Fylkesmannen i Rogaland, MVA

Egil Postmyr
Direktoratet for naturforvaltning

Roger Sørensen
Fiskeridirektoratet, Nordland

Olav Halsne
Norske fiskeoppdretteres forening

NASJONAL TILTAKSPLAN MOT RØMMING - SAMMENDRAG

Innholdsfortegnelse

Side

1. Innledning

Norske fiskeoppdretteres forening (NFF) tok i skriv av 25.5.98 (skrivet følger vedlagt i kapittel 13.1) et initiativ overfor Fiskeridepartementet (FD) og Miljøverndepartementet (MD) for å få organisert et samarbeid om en nasjonal tiltaksplan mot rømming. Det ble holdt et innledende møte høsten 1998 mellom NFF, FD og MD. På møtet var det enighet om at det ville være ønskelig at næringen selv ved NFF utarbeidet en nasjonal tiltaksplan mot rømming. Det ble også enighet om at det ville være hensiktsmessig at forvaltningen bidrar til dette arbeidet.

Det ble videre enighet om at arbeidet med å utarbeide en slik tiltaksplan bør organiseres gjennom en mindre arbeidsgruppe med deltakelse fra både direktorats- og regionalt nivå. NFF skulle lede og organisere arbeidet. Følgende personer ble oppnevnt:

Håvard Vannebo	NFF (leder)	Svein Arne Aas	Forsikringsforbundet
Olav Halsne	NFF	Roger Sørensen	F.dir. Region Nordland
Harald Lura	MVA i Rogaland	Axel R. Anfinsen	F.dir.
Egil Postmyr	Direktoratet for naturforvaltning (DN)		

Fiskeridepartementet signaliserte at de ønsket å vurdere et forslag fra arbeidsgruppen for tiltaksplan mot rømming i forbindelse med utarbeidelsen av sin sektorvise miljøhandlingsplan. Derfor ble det utarbeidet en foreløpig rapport - kalt delrapport - om fremdrift og status. Delrapporten ble oversendt Fiskeridepartementet, Miljøverndepartementet og Norske fiskeoppdretteres forening i august 1999.

2. Sammendrag

Kapittel 1. Innledning

Norske fiskeoppdretteres forening tok i mai 1998 et initiativ overfor Fiskeridepartementet og Miljøverndepartementet for å få organisert et samarbeid om en nasjonal tiltaksplan mot rømming. Arbeidet med å utarbeide denne tiltaksplanen mot rømming er organisert gjennom en mindre arbeidsgruppe med deltakelse fra både direktorats- og regionalt nivå. NFF har ledet og organisert arbeidet.

Kapittel 2. Sammendrag

Her er gitt er sammendrag av utvalgets tiltaksplan.

Kapittel 3. Mandat

Styret i NFF oppnevnte utvalget i sak 27/99. Det ble forutsatt at utvalget utarbeidet sitt eget mandat innenfor de rammer som var gitt. Mandatet er gjengitt på side 9.

Kapittel 4. Utvalgets målsetninger

Utvalget har lagt følgende målsetninger til grunn for sitt arbeid:

- Legge grunnlaget for et systematisk og planmessig arbeid for å redusere omfanget av rømming ved å:
    1. lage en god oversikt over rømmingsomfang og årsaker til rømming
    2. foreslå tiltak mot rømming
    3. skape en bred forståelse i forvaltning og næring om alvoret i rømming
    4. påpeke forskningsbehov

Kapittel 5. Produksjon av oppdrettslaks

Oppdrett av laks har pågått i en menneskealder. I denne tiden har det vært en rivende utvikling på nesten alle felt. Produksjonstiden er kraftig redusert og er idag 18 - 32 mnd. Sjøfasen er ansett som den mest risikofylte med hensyn til rømming. Arbeidsoperasjonene som utføres, slik som notskift, avlusing, håving, lasting, lossing og sortering, kan være kritiske i forhold til rømming.

Kapittel 6. Rømming - omfang og årsak

Utvalget har benyttet følgende seks kilder til å estimere omfang og årsaker til rømming av laks fra norske oppdrettsanlegg:

1. Fiskeridirektoratets statistikker over innrapportert rømming fra oppdretterne. Den ene er basert på rapportert rømming fra oppdretter til Fiskeridirektoratets regionkontorer straks rømmingen er oppdaget. Den andre er basert på Fiskeridirektoratets årlige statistikkundersøkelse
2. Direktoratet for naturforvaltnings statistikker fra overvåkningsfisket av rømt oppdrettslaks (Utarbeidet av Stiftelsen for naturforskning, NINA).
3. Forsikringsselskapenes statistikk over innmeldte skader som inkluderer rømming.
4. Undersøkelse om årsakssammenheng for rømming fra oppdrettsanlegg, Rogaland fiskeoppdretterlag / Vestnorsk havbrukslag, desember 1998
5. Rapport fra MARINTEK: «Omfang av og årsaker til rømming. ...», februar 1997
6. Informasjon gitt av ressurspersoner i utvalgets møter

I forhold til produksjonen synes rømmingsomfanget de siste årene å være relativt stabilt, noe i overkant av de miljømål som er satt for rømming. Registreringen tyder på en viss underrapportering og utvalget antar et en del av det som er oppgitt som uspesifisert svinn er rømming.

Årsaker til rømming som går igjen er:

- Skader forårsaket av uvær
- Skader forårsaket av propell
- Skader forårsaket av påkjørsel
- Skader forårsaket av drivgods
- Svikt i driftsrutiner
- Teknisk svikt i settefiskanlegg
- Predatorskader

I oppgaven fra forsikringsselskapene fremgår det at månedene juni, oktober, november og desember er spesielle «rømmingsmåneder» og at antall fisk som rømmer ved hver skade de siste årene har økt.

Kapittel 7. Tidligere foreslåtte tiltak mot rømming

Publikasjoner som tar for seg rømmingsproblemet, og som utvalget har benyttet er:

1. MARINTEK: «Omfang av og årsaker til rømming. Tiltak for å redusere rømming som ikke skyldes havari og skade», februar 1997
2. Rogaland Fiskeoppdretterlag / Vestnorsk Havbrukslag. «Rømming frå oppdrettsanlegg. Årsakssammenheng og forslag til tiltak», desember 1998
3. Villaksutvalgets innstilling NOU 1999:9: «Til laks åt alle kan ingen gjera», februar 1999.
4. Miljømål for norsk havbruk, 1999-1, mai 1999.

Kapittel 8. Spørreundersøkelse vdr. rømming fra settefisk anlegg

Oppmerksomheten mot rømming har tradisjonelt vært konsentrert om sjøfasen. Overvåkingsfiske indikerer at en betydelig del av den fisken, som kontrolleres, må ha rømt på smolt- eller postsmoltstadiet. For å få en bedre oversikt over rømmingssituasjonen ved settefiskanlegg anbefaler utvalget at det foretas en spørreundersøkelse blant settefiskprodusentene.

Kapittel 9. Utvalgets vurdering

Rømming fra oppdrettsanlegg er av myndighetene ansett for å være den mest alvorlige negative effekt av fiskeoppdrett. Rømt fisk kan bidra til sykdomssmitte, og der er betydelig engstelse for effekten av den genetiske innblanding av oppdrettsfisk i de ville bestandene.

Følgende miljømål er satt for rømming:

R-1: Langsiktig overordnet mål	**R-2: Resultatmål på kort sikt** (innen utgangen av 2000)
Omfanget av rømt fisk fra oppdrettsanlegg skal ikke representere noen trussel for opprettholdelsen av norske villaksstammer	Antall rømt fisk fra oppdrettsanlegg skal ikke overstige 400 000 per år

Fiskeoppdrettsnæringen må, som annen næring, ha hovedansvaret for at virksomheten skjer innen forsvarlige rammer. Det må således være næringen som har hovedansvaret for å få kontroll med rømmingen. Myndighetenes oppgave må være å stille vilkår, følge opp om vilkårene blir innfridde og medvirke til etablering av den nødvendige infrastruktur for utvikling av en bærekraftig fiskeoppdrettsnæring.

Årsaker til rømming som går igjen synes å være akutte episoder, av sporadisk karakter, hvor tap av fisk kan være betydelig. Etterhvert er det blitt rettet mer oppmerksomhet mot det som blir kalt smårømming, dryppørmming e.l. Dette er - for den enkelte episode - episoder med små rømmingstall, men dersom dette er rømming av kronisk karakter, kan summen av rømlinger bli betydelig. Flere ting kan tyde på at den kroniske rømming i sum kan være omfattende. Resultatet av DNs overvåkingsfiske tyder på en diffus rømming, uten bakgrunn i store enkelt uhell. Det kan reises spørsmål om de akutte episodene, ofte med dramatisk karakter, skygger for de kroniske episodene.

Utvalget mener at en har mangelfull kunnskap om rømming. Registrering av rømming bør forbedres til å gi bedre oversikt om rømmingsomfang og -årsaker. I tillegg kommer at det er lagt for liten vekt på å utvikle det merdteknologiske miljø, noe som har forsinket en forbedring av teknologien. I langt større grad enn det som er tilfelle i dag, må en sørge for å lære av sine feil.

Enten rømmingen er omfattende eller beskjeden, innebærer den tap for oppdretter. Men utfra rene bedriftsøkonomiske betraktninger er det andre tapsposter som er mer alvorlig for oppdretteren, hvilket understreker betydningen av at kampen mot rømming opprioriteres av næringen om en skal lykkes.

Utvalgets tilnærming for utarbeidelse av tiltaksplanen er å konsentrer seg om de viktigste årsakene til rømming. Konsentrasjon om innsatsen til de viktigste årsakene til rømming skal bidra til å sikre en planmessig og systematisk tilnærming til problemet. Etter beste skjønn har utvalget valgt å prioritere følgende fem årsaker som - utfra dagens kunnskap - anses for å være de viktigste rømmingsårsaker:

- **Svikt i driftsrutiner ved anlegg**
    - Håndteringsskader
    - Driftsuhell
    - Mangelfull overvåking og vedlikehold
    - Overgroing av not
    - Gnagskader
- **Teknisk svikt av anlegg**
    - Miljøkreftene på lokaliteten overstiger anleggets tåleevne
    - Konstruksjonsfeil av anlegget eller deler av anlegget
    - Tretthetsbrudd på konstruksjonen
    - Feil bruk av anlegget eller dets komponenter
- **Båttrafikk ved anlegget**
    - Påkjørsel
    - Propellskader på not
- **Teknisk svikt i settefiskanlegg**
    - Manglende sikring av avløp
    - Fundamenteringssvikt
- **Mangelfull kunnskap**
    - Mangelfull utvikling av merdteknologien
    - Mangelfull kunnskap om årsaker til rømming
    - Mangelfull FoU-innsats

En prioritering av tiltakene fordrer også en prioritering av innsatsen mot rømming fra de som har ansvar for å få kontroll med rømmingen, det vil si først og fremst fiskeoppdrettsnæringen, men også myndighetene. Ved en reell prioritering vil en stå overfor en rekke dilemmaer. Dersom utgangen av dilemmaene blir at innsatsen mot rømming ikke blir styrket, da har man ikke prioritert kampen mot rømming. Dette gjelder alle parter. Dersom myndighetene ikke vil påta seg sin del av ansvaret, vil det influere på andre parters innsats mot rømming. En opprioritering av innsatsen mot rømming vil også være et utrykk for holdninger som ikke aksepterer rømming. Dersom holdningene til rømming er avslappet, mangler en av de viktigste forutsetningene for å kunne få kontroll med den.

Kapittel 10. Utvalgets forslag til prioriterte tiltak

Utvalgets forslag til tiltak på de prioriterte områdene er omtalt i kapittel 10 fra side 31. Hovedtrekkene er skissert nedenfor.

Tiltak mot rømming som følge av svikt i driftsrutiner ved anlegg

Dette omfatter forhold som håndteringsskader, driftsuhell, mangelfull overvåking/ vedlikehold, overgroing av not og gnagskader. Dette er rømming som er forårsaket av svikt i driftsrutiner ved anlegg, og er et uttrykk på mangelfulle styringssystemer hos selskapet. Utvalget foreslår at oppdrettsselskapene skal etablere kvalitetssystemer med prioritert målsetning om å eliminere rømming. Kvalitetssystemene må ligge på nivå med sertifiserte kvalitetssystemer. I tillegg må myndighetene snarest innføre krav om internkontroll med hjemmel i blant annet fiskeoppdrettsloven, og bygge opp den nødvendige kompetanse for et IK-basert tilsyn.

Tiltak mot rømming som følge av teknisk svikt av anlegg

Dette er rømming som skyldes skade på anlegget eller deler av anlegget på grunn av for stor belastning eller feil bruk, og omfatter forhold som at miljøkreftene på lokaliteten overstiger anleggets tåleevne, konstruksjonsfeil av anlegget eller deler av anlegget, tretthetsbrudd på konstruksjonen og feil bruk av anlegget eller dets komponenter. Utvalget foreslår at TYGUT[1] settes i verk så snart som mulig. Fordi ordningen i utgangspunktet kan anses som et teknisk handelshinder i henhold til EØS-avtalen vil den - med henvisning til relevante unntaksbestemmelser - måtte godkjennes av EØS. Det vil derfor fortsatt gå noe tid før ordningen kan tre i kraft. Dette burde være et ekstra incitament til de ansvarlige myndigheter om å sette fortgang i arbeidet med å få ordningen vedtatt.

På grunn av at det fortsatt vil gå noe tid før TYGUT vil være operativ, anbefaler utvalget at regjeringen fatter prinsippvedtak om at ordningen skal innføres, og at en deretter setter i verk de delene av ordningen som ikke krever godkjennelse i EØS.

Tiltak mot rømming som følge av båttrafikk ved anlegget

Dette omfatter forhold som påkjørsel og propellskader på not. Slike skader medfører betydelig rømming. På oppdrag av utvalget har SINTEF fiskeri og havbruk utarbeidet er forundersøkelse[2] angående propellskader og muligheter for propellbeskyttelse.

Utvalget anbefaler at det utarbeides skriftlige prosedyrer for all ferdsel med båt rundt anlegget. Av prosedyrene må det fremgå under hvilke værforhold båtanløp ikke skal foretas. Ved anløp av brønn- og fôringsbåter skal disse ha tegninger av anlegget med fortøyningssystem. Anlegget skal være bemannet ved båtanløp. Ved plassering av fôrstasjoner må risikoen for skade på anlegget ved båtanløp vurderes. Det bør vurderes å installere indikatorer for strømstyrke og -retning på anlegget. I tillegg vil utvalget anbefale at spørsmålet om propellbeskyttelse på båter som ferdes rundt anlegg utredes videre.

Tiltak mot rømming som følge av teknisk svikt i settefiskanlegg

Dette omfatter forhold som manglende sikring av avløp, fundamenteringssvikt og konstruksjonsfeil av oppdrettskar. Tiltak mot rømming fra settefiskanlegg er prioritert fordi overvåkingsfisket viser at en stor del av den fisken som kontrolleres må ha rømt i tidlige livsstadier. Utvalget foreslår at det kreves at settefiskanlegg skal sikres med rist i avløpsledningen, og at det ved anlegget foretas forsvarlige grunnundersøkelser

Tiltak mot rømming som følge av mangelfull kunnskap

Dette omfatter forhold som mangelfull utvikling av merdteknologien, mangelfull kunnskap om årsaker til rømming og mangelfull FoU-innsats. Utvalget foreslår et forskningprogram for flytende oppdrettsanlegg hvor rømmingssikring og kompetanseoppbygging i forhold til TYGUT er sentrale elementer. Videre foreslås at rapporteringsrutinene for rømming legges om, og at det opprettes et rømmingsregister i Fiskeridirektoratet. Dessuten foreslås at følgende forskningsoppgaver gjennomføres: Svinnstudier og studier av årsakssammenheng / oppretting av uhellskommisjon.

Kapittel 11. Andre tiltak for å hindre rømming

Utvalgets prioriterte tiltak er gjengitt i kapittel 10. I kapittel 11 er en rekke andre forslag til tiltak tatt opp.

Begrense biomasse per merd

Utvalget foreslår at fiskerimyndighetene innfører maksimal biomassebegrensning i hver merd, inntil TYGUT og internkontroll er etablert.

---

[1] TYGUT er et godkjenningssystem for flytende fiskeoppdrettsanlegg fremmet av Typegodkjenningsutvalget i februar 1997. Samme sommer sluttet Fiskeridirektøren seg til forslaget og anbefalte overfor Fiskeridepartementet at ordning blir iverksatt.

[2] Rapporten fra SINTEF fiskeri og havbruk følger som vedlegg, se kapittel 13.5

Bedre rutiner for sleping

Utvalget foreslår at det utarbeides et regelverk (med relasjon til rømming) for sleping av merder med fisk

Sikre ventemerder (slaktemerder) mot rømming

Utvalget forslår at det utarbeides forskrifter for bruk av slaktemerder, der ansvarsforholdet for drifting av slike enheter blir definert sterkere. Kontroll av slaktemerder må inngå i fiskeriforvaltningens ordinære kontrollprogram. Slaktemerdene må inngå som et element i slakterienes internkontroll.

Hindre predatorskader

Tiltak som hindrer eller skremmer predatorer som oter og sel fra å gjøre skade på anlegg er ennå lite utprøvd. Dersom oppdrettsanlegg søkes etablert i områder med vesentlige bestander av predatorer, som kan forårsake rømming av fisk, må søknaden vurderes med spesiell fokus på rømmingsrisiko.

Merking

I «Miljømål for norsk havbruk» er det i forbindelse med merking satt opp følgende mål:

R-1: Langsiktig overordnet mål	**R-2: Resultatmål på kort sikt** (innen utgangen av 2000)
Rømt oppdrettsfisk skal kunne identifiseres og spores tilbake til opprinnelsessted	Teknologi for massemerking av fisk skal kartlegges og egnet metode for implementering utprøves

I møte 9.2.00 med representanter fra blant annet DN, Fiskeridirektoratet, Statens dyrehelsetilsyn og NFF, ble den foreløpige utgaven av NINA Oppdragsmelding: 000: 1-00, «Merking av kulturlaks i Norge - en utredning av aktuelle metoder, kostnader og effekter» drøftet. Det ble konkludert med at når endelig rapport foreligger opprettes en arbeidsgruppe på direktoratsnivå for å arbeide videre med problemstillingen.

Utvalget tar til etterretning at problemstillinger med merking skal utredes videre.

Kapittel 12. Andre oppdrag utført av utvalget

Under utvalgets arbeid er det kommet anmodning om å utarbeide forslag til:

1. endring av drifts- og sykdomsforskriftens § 25.2
2. rapporteringsskjema for tilfeller av rømming

1.

Utvalgets forslag til ny ordlyd av drifts- og sykdomsforskriftens § 25.2 fremgår av vedlegg kapittel 13.2. Forslaget bygger på at dykking, videoovervåking eller andre metoder godkjent av Regiondirektøren kan benyttes til erstatning av overvåkingsfiske.

2.

Utvalgets forslag til rapporteringsskjema i tilfelle rømming fremgår av vedlegg kapittel 13.3. Rapporteringen foreslås gjort i to stadier.

1. Umiddelbart etter at rømming er oppdaget.
2. Når merden er tømt og skaden oppgjort.

Kapittel 13. Vedlegg

En oversikt over vedlegg er gitt i kapittel 13.

Kapittel 14. Henvisninger

En oversikt over dokumenter det er henvist til i rapporten er gitt i kapittel 14.

NOU Norges offentlige utredninger **1999: 9**

Til laks åt alle kan ingen gjera?

Om årsaker til nedgangen i de norske villaksbestandene og forslag til strategier og tiltak for å bedre situasjonen

Utredning fra et utvalg oppnevnt ved kongelig resolusjon av 18. juli 1997.
Avgitt til Miljøverndepartementet 12. mars 1999

Statens forvaltningstjeneste
Statens trykning

Oslo 1999

Til Miljøverndepartementet

Utvalget som har hatt i oppdrag å utrede situasjonen for de ville laksebestandene og foreslå nye forvaltningsstrategier og tiltak, legger med dette frem sin innstilling. Utvalget ble oppnevnt ved kongelig resolusjon av 18. juli 1997. Utvalgets mandat er vidtfavnende og omfatter en gjennomgang av alle sider av lakseforvaltningen og det som kan kalles villakspolitikken.

Innstillingen er enstemmig når det ikke er gjort rede for annet.

Mange utenforstående har gjennom ulike bidrag gitt viktige impulser til arbeidet. Utvalget vil takke alle som har bidratt.

En spesiell takk rettes til H. M. Kong Harald som ønsket å delta og deltok på utvalgets statusseminar i Asker, 2. februar 1998. Kongens tilstedeværelse og interesse ga stor inspirasjon i det videre arbeid.

12. februar 1999

Georg Fr. Rieber-Mohn
leder

Arne Eggereide
Axel R. Anfinsen
Inger Eithun
Arne Jørrestol
Bror Jonsson

Marianne Balto Henriksen
Bjørnulf Kristiansen
Else-Beth Stamer Wahl
Jan Henning L'Abée-Lund

Børre Pettersen
Marit Solberg
Øyvind Mårvik
Elise Førde

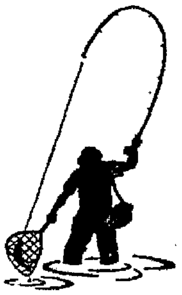
Jostein Skurdal
Øystein Aas
Jon Lenæs

Offentlige publikasjoner

Abonnement, løssalg og pris fåes ved
hendvendelse til:
Akademika AS
Avdeling for offentlige publikasjoner
Postboks 8134 Dep
0033 OSLO
Telefon 22 11 67 70
Telefaks 22 42 05 51
Grønt nummer 800 80 960

Innhold

Vedlegg



REPORT OF THE NORWEGIAN WILD SALMON COMMITTEE (NOU 1999:9)

ENGLISH SUMMARY

The Wild Salmon Committee was appointed by Royal Decree of 18th July 1997 and had 14 members. The background for the Committee's work is the sharp decline in stocks of wild salmon in Norway in recent years.

The Committee was given the following terms of reference:

«The Committee shall review the overall situation for the wild salmon stocks and present proposals for management strategies and action programmes. Issues associated with regulatory measures, watercourse management and salmon farming shall be given particular attention.»

The report reviews:
- the distribution and biology of the salmon (chapter 3).
- the important and complex economic and cultural significance of the salmon through the centuries (chapter 4).
- the current situation for the wild salmon, including possible reasons for the natural fluctuations in salmon stocks and important human activities with a negative impact on the stocks (chapter 5).
- the management of salmon in Norway (chapter 6).
- the management of salmon in various other nations (chapter 7).

The report also contains a presentation of the Committee's assessments and summary of the situation for the wild salmon (chapter 8). It reviews the Committee's proposed measures and strategies, covering both strategic overarching measures and initiatives within areas of special attention (chapter 9). A brief outline of the administrative and economic consequences of the proposals are presented in the last chapter of the report.

From 1978 all fishing other than rod fishing was, with few exceptions, banned in the rivers. Drift net fishing was stopped in 1989 and the fishing was moved back to the fjords and rivers.

Besides being a symbol of Norway's identity and enjoyment of the outdoors, the wild salmon represents a large number of jobs and considerable revenues. The most visible factor is the local economic ripple effects of salmon fishing in the rivers, the annual value of which is at least NOK 400-500 million, equivalent to at least 600 man years. Vigorous wild salmon stocks also have a large value beyond the market price of the fish and fishery. Salmon fishing influences the pattern of settlement. Wild salmon stocks are also the foundation of salmon farming. The willingness of people to pay for the protection of viable salmon stocks is high. Recreational and commercial fishing now take equally large catches each year. Lower prices for salmon and smaller catches have reduced the financial return on fishing for salmon in the sea and river fishing. Angling now accounts for the majority of the actual value added.

Since 1970 Norway has built up the world's largest salmon farming industry. The industry makes a major employer and creator of value along the coast and is one of the country's largest export industries. The production of farmed salmon has grown from a few thousand tonnes in 1980 to 330,000 tonnes in 1997. The export value was nearly NOK 8 billion in 1997.

The salmon is central to Norwegian, Sami and Kven (descendants of Finns living in Northern Norway) culture and settlement. The salmon is also visible in Norway's cultural history, where it figures in various forms of expression ranging from rock carvings, folk tales and legends to paintings, handicrafts and language. In the salmon districts the salmon is a vital part of life and the change of the seasons has a major impact on people's health and enjoyment and quality of life. The salmon is an important basic resource in Sami (Lapp) culture. Salmon fishing is a fine way to enjoy nature. Holders of fishing rights and fishermen's associations take an active part in caring for, restoring and managing salmon habitats.

Chapter 5 Current situation of the salmon

The occurrence of salmon in the North Atlantic varies in long and short cycles. Changes in natural conditions were previously the only reason for the fluctuations, while the influence of human intervention and pollution has grown. The decline in salmon stocks in the 1970s and 1980s was attributed to overfishing, acid rain, intervention in watercourses and the parasite Gyrodactylus salaris.

Natural variations in stocks are also a factor and the complicated interplay of natural and human-created factors makes it difficult to identify the individual loss factors and their respective contribution to the decline.

The decline of the salmon stocks is clearly evident in catch statistics, which peaked in the 1960s and '70s. Since then the catches have diminished and the size composition has also changed. The percentage of small salmon has increased while large salmon have declined. Salmon catches in Norway have fallen from around 2,000 tonnes in 1980 to 630 tonnes in 1997. The situation is further exacerbated by the fact that the data from recent years also include catches of escaped farmed salmon and that a larger share of the catches are now reported and are included in official statistics. Smaller catches are primarily due to a sharp decline in stocks, while more limited fishing is also a factor. Catches in the remaining fisheries have continued to decline despite the fact that fishing with drift nets, fishing of the Faeroes and most of the coastal fishing with bend nets has been banned or scaled back in the '90s. This gives justifiable grounds for concern about the development of spawning stocks.

Nine watercourses have been treated and are under supervision and evaluation for a clean bill of health. The parasite is now found in 19 watercourses. Treatment by rotenone in the largest watercourses and brackish water systems presents practical problems and is anyway far more resource-intensive than the treatment of smaller watercourses.

Fishing has been the major mortality factor for migrating spawning salmon. In the sea, salmon are caught with bag-nets, bend nets and sportfishing. In watercourses, salmon are with few exceptions caught by anglers. River catches vary from one watercourse to the next and from year to year. The International Council for Exploration of the Sea has calculated that the stock complex of small salmon in Northern Europe is within safe biological limits, while multi-sea winter salmon are at a minimum level relative to the need for spawning fish.

The percentage of salmon smolt that migrate from streams and rivers and return from their feeding areas in the sea has declined over the last 15 to 20 years. The major causes of higher mortality in the seawater phase appear to be changes in environmental conditions in the sea and increased salmon lice infection, particularly in the early part of the sea phase. There is also concern about the effect of by-catches in the Norwegian Sea. Continued growth in stocks of Arctic and coastal seal and cormorant could cause greater predation compared with the level of the past 10 years.

There are considerable differences between regions and individual watercourses with respect to the stock situation and the relative importance of loss factors. The situation is the most serious in Western Norway north of Jæren and least serious in Finnmark, Namdalen and Jæren. Most of the major loss factors occur along large parts of the coast between Rogaland and Troms. Finnmark currently has minor problems with physical intervention, fish farming and disease but the impact is increasing there too. In Eastern Norway, old hydropower projects, channelling and industrial development have combined to reduce salmon stocks while Gyrodactylus salaris is to blame in the Drammen and Lier watercourse. Acid rain mainly affects Southern Norway and Western Norway south of Stad.

Chapter 6 Salmon management in Norway

Management on land and in freshwater is mainly based on private property rights and the national state's legitimate right to pass and enforce laws. In Norwegian waters in the sea, landowners have the right to fish with fixed gear. Public access and international negotiation rights otherwise apply.

Several sector authorities and management levels are involved in decisions and actions that affect the salmon. Legislation for the relevant sectors is relatively modern and incorporates environmental considerations. Private management of salmon is also extensive. International salmon management includes bilateral agreements, conventions and recommendations of international organisations.

Environmental authorities have the prime responsibility for managing wild salmon, with the Directorate for Nature Management as the central advisory and executive agency. The county governor has regional responsibility. An advisory system has been established on all levels where decisions about the regulation of fishing and other measures are discussed.

The 1992 Act relating to Salmonids and Fresh-water Fish etc. is an enabling act whose objective is «to ensure that natural stocks of anadromous salmonids, fresh-water fish and their

Several factors are at work simultaneously and can assert themselves with varying force in different combinations in various watercourses, regions and nations. In more than one-third of the salmon watercourses the authorities have declared the salmon to be wiped out, threatened or vulnerable. Smolt production was estimated at around six million in 1985 and includes additional production due to fish ladders and stocking. The major loss factors are acid rain, the parasite Gyrodactylus salaris, hydropower regulation and other physical intervention. The Committee has judged the losses from these factors at 2.6-3-6 million smolt. Since many of these factors act in the same river, the total sum may represent an overestimate. Losses due to escaped farmed salmon appear to have had modest impact but the potential damaging effects could be huge.

The situation for salmon is particularly serious because it involves an interplay of old human-caused loss, natural fluctuations and new threats whose consequences are not yet known. New serious threats such as the escape of farmed salmon and new diseases could have a major negative impact in the years to come without providing an explanation for the current situation of the salmon at the national level. Losses associated with salmon lice is unclear, but it is likely that lice losses has increased in many regions the last years.

Only a major and coordinated effect in many fields can reverse the trends of earlier years to ensure the protection of the genetic diversity of salmon stocks and utilize the natural production capacity in freshwater and the ocean.

A number of salmon-strengthening measures have been implemented without reversing the negative trend. These efforts have not been successful because they have not been comprehensive enough. Many salmon stocks are in danger of dying out or being weakened so that they cannot utilize the production basis in freshwater and in the ocean. Monitoring of salmon stocks is clearly deficient and the same applies to monitoring of environmental conditions and threats such as watercourse intervention, the escape of farmed salmon and salmon lice. All serve to weaken the usefulness of monitoring in ongoing management.

The Committee concludes that the situation for salmon in Norway is very serious and in many areas of the country the crisis is acute. At the same time, it has been demonstrated that there is scope for improvements and changes that can reduce the damage from old causes of loss, remove or reduce the significance of new threat factors and increase the benefits of actions and programs.

Salmon management is a task that cannot be organized and solved by any one sector because it touches on central Norwegian interests such as energy supply, industry, industrial and commercial development and regional policy. The Committee views the fragmented system of management as one of the main problems in salmon management.
Concentrating solely on partial solutions within the framework of such a system is no longer viable and legislative remedies have moreover not been sufficiently invoked to protect the salmon.

Chapter 9 Proposed measures and strategies

The Committee believes it is realistic for the Norwegian stock complex of salmon to recover much of its former vigour. This will lay the basis for a long-term preservation of the species and its diversity predicated on a goal-oriented and effective effort to remove and reduce the threat factors.

It is the opinion of this member that there is not a necessary basis for recommending protection of a number of named watercourses at this time in addition to the watercourses included in the existing protection plans 1-4. When choosing watercourses and giving guidelines for management restrictions also other user interests must be considered. Outside national salmon watercourses where national salmon fjords will not be established, the Committee recommends that protection zones and action zones be approved in accordance with the recommendations of the 1996 Evaluation Committee, pending a more thorough evaluation of the effect of the zones, including an opinion that the zones can be strengthened. The Committee proposes to abolish existing protection zones outside watercourses not proposed as national salmon watercourses.

The Committee proposes the establishment of an «International Salmon Heritage Rivers and Fjords» system to protect the most important salmon watercourses and fjords around the entire North Atlantic~~.~~ Special guidelines, recommendations and provisions for managing and protecting these areas must be developed. The highest priority national watercourses must be included here and they must have a joint monitoring and reporting system binding on the individual countries. Member countries must also take responsibility for implementing measures to remove the threats and strengthen the stocks within their own jurisdiction. NASCO must take responsibility for ensuring monitoring, management, protection and sea catches in accordance with the requirements made of members and the status and development of the international and national salmon watercourses.

Formalized cooperation and stepped up supervision

Public management has grown and become highly fragmented and complicated. The salmon is constantly being subjected to new dangers and threats without any changes being made in management of the wild salmon.

A long-distance migratory species such as the salmon is particularly hard hit because its habitats are governed by different legal regimes. The Committee proposes greater and more binding cooperation between the central sector authorities in issues concerning the salmon.

A separate cooperative forum should be established at the directorate level, with the Directorate for Nature Management, the Norwegian Watercourse and Energy Administration, the Directorate of Fisheries, Norwegian Animal Health Authority, Norwegian Pollution Control Authority and agricultural and transport authorities as major participants. Responsibility for coordination must be vested with the Directorate for Nature Management. There is a need to prioritize inspection and supervisory tasks in important areas.

Knowledge-based management

The critical situation for the wild salmon and the uncertainty about causal factors and effect of measures indicates a need for stepping up research. The Committee believes that greater knowledge is a necessary prerequisite for solving many of the problems affecting salmon. Research must have both a short-term perspective relating to the current threats to wild salmon, and a long-term perspective for increasing knowledge and expertise about salmon. There is also a great need for monitoring statistics that can document the status and development of the salmon stocks.

The Committee recommends that monitoring be carried out on the basis of a long-term overarching programme covering all the life phases and habitats of the salmon.

Watercourse management

Watercourse regulation and other physical intervention represent significant causes of loss in the wild salmon equation. Impact studies and statutory mitigating measures have been carried out for major projects, but not for a long list of smaller projects. Many of the mitigating measures have not had the anticipated effect.

The Committee assumes that there will be no new or further regulation of or intervention in the selected national salmon watercourses. The introduction of a new Water Resources Act containing provisions on edging woodland, extraction of gravel, protection of natural conditions during embankment building etc. and rules for managing protected watercourses will have a positive effect on the salmon. The Committee recommends that a plan be drawn up for modernizing and enhancing the efficiency of mitigating measures in watercourse regulation. The Committee also proposes that the Norwegian Watercourse and Energy Administration and other relevant players including the environmental authorities and landowners initiate a major programme for the restoration of salmon watercourses with funds from the concession fee fund. The Committee also recommends stepped-up supervision and inspection via compliance with concession terms in regulated watercourses.

Measures to combat the escape of farmed salmon

The Committee views the escape of farmed salmon and outbreaks of salmon lice as the most serious environmental problems of the fish farming industry in relation to the wild salmon. The Committee's strategy for reducing the problem of escaped salmon is twofold. Firstly, the Committee proposes via the establishment of national salmon fjords that fish farming be increasingly located outside important wild salmon areas. It furthermore proposes to establish protection and action zones outside the national salmon watercourses in line with the recommendations of the 1996 Evaluation Committee, pending the evaluation and assessment of opportunities to strengthen the expansion of the zones. The Committee proposes the abolishment of provisional protection zones outside salmon watercourses not proposed as national salmon watercourses. Secondly, comprehensive measures to reduce escapes of salmon from fish farms must be initiated.

The Committee proposes and supports a number of measures and regulatory changes, greater supervision and better expertise as a way of contributing to standards and operating routines that reduce escapes of salmon from farms on an overall basis.
Good statistics on the scope and cause of escaped salmon and the continued testing of microtagging of farmed salmon by the authorities are necessary to have good control of the situation and conduct selective fishing for escaped salmon. Stricter enforcement and more active use of coercive sanctions or criminal prosecution are necessary vis-à-vis farms that violate laws and regulations.

The Committee split in two concerning the question of controlling escapes of salmon from fish farms. One half, represented by Arne Eggereide, Elise Førde, Marianne Balto Henriksen, Bror Jonsson, Bjørnulf Kristiansen, Børre Pettersen and Else-Beth Stamer Wahl proposes giving closer consideration to whether the Norwegian Pollution Control Authority should take over responsibility for escapes from fish farms. The other half, represented by Axel R. Anfinsen, Inger Eithun, Arne Jørrestol, Jan Henning L'Abée-Lund, Øyvind Mårvik, Georg Fr. Rieber-Mohn and Marit Solberg believes the recent separation of the fishery authorities' supervisory and industrial policy functions must prove inadequate before such a reorganization can be evaluated.

The gene bank is also an important protective measure for the fish farming industry and the industry should contribute to its operation together with the regulators, holders of fishing rights, and agricultural and environmental authorities. The Committee recommends continued liming of acidified watercourses. More active monitoring of the stocks of the main predator stocks is necessary along with speedier decisions regarding hunting or capture when a biological case for it exists.

The Committee proposes closer follow-up of the possible by-catch problem of postsmolt in the «loophole ocean area» through Norwegian participation in for instance the ICES and NASCO.

Administrative and economical consequences

The Committee was given a short deadline to present its study and has consequently not had the opportunity to review the administrative and economic consequences in detail. The objective of the Committee's proposals is to protect the wild salmon and bring the stocks back to their former strength. The proposals are based on the current organisation of management and the various sector authorities' responsibilities and do not as far as these are concerned advocate any significant changes in the present system. They do, however, point out the need for greater cooperation among the central agencies. The authorities want the various sectors to take increasing responsibility for environmental problems. The sectors must therefore take increasing responsibility for studying and preventing damaging effects on the wild salmon, and finance measures to avert the problems their operations create through appropriate and suitable arrangements. The Committee believes that greater cooperation could potentially yield considerable efficiency gains. There is a need for stronger supervisory and inspection efforts and the increased costs must be charged to those who are inspected.

It will be necessary to strengthen the Directorate for Nature Management, Norwegian Watercourse and Energy Administration, Directorate of Fisheries and Norwegian Animal Health Authority to implement the Committee's proposals regarding national salmon watercourses and fjords, the rewriting of fishing regulations, greater inspection and supervisory functions and improved watercourse and fish farming management.

The Committee proposes strengthening and improving the Norwegian Fishing Fund and examining new funding schemes more closely. The Committee supports the proposal from the fish farming industry to establish a fund financed by an R&D fee on the production of farmed salmon. The Committee recommends that the concession fee fund step up its efforts for wild salmon.

THE ROYAL SOCIETY

doi 10.1098/rspb.2000.1173

Lifetime success and interactions of farm salmon invading a native population

Ian A. Fleming[1*], Kjetil Hindar[1], Ingrid B. Mjølnerød[1]†, Bror Jonsson[2], Torveig Balstad[1] and Anders Lamberg[1]

[1] *Norwegian Institute for Nature Research, Tungasletta 2, N-7485 Trondheim, Norway*
[2] *Norwegian Institute for Nature Research, Dronningensgate 13, PO Box 736, Sentrum, N-0105 Oslo, Norway*

Farm Atlantic salmon escape and invade rivers throughout the North Atlantic annually, which has generated growing concern about their impacts on native salmon populations. A large-scale experiment was therefore undertaken in order to quantify the lifetime success and interactions of farm salmon invading a Norwegian river. Sexually mature farm and native salmon were genetically screened, radio tagged and released into the River Imsa where no other salmon had been allowed to ascend. The farm fishes were competitively and reproductively inferior, achieving less than one-third the breeding success of the native fishes. Moreover, this inferiority was sex biased, being more pronounced in farm males than females, resulting in the principal route of gene flow involving native males mating with farm females. There were also indications of selection against farm genotypes during early survival but not thereafter. However, evidence of resource competition and competitive displacement existed as the productivity of the native population was depressed by more than 30%. Ultimately, the lifetime reproductive success (adult to adult) of the farm fishes was 16% that of the native salmon. Our results indicate that such annual invasions have the potential for impacting on population productivity, disrupting local adaptations and reducing the genetic diversity of wild salmon populations.

Keywords: biological invasion; gene flow; lifetime reproductive success; hybridization; aquaculture; farm salmon

1. INTRODUCTION

The farming of Atlantic salmon (*Salmo salar*) has expanded exponentially from its beginnings in the 1960s to its production today, which dwarfs wild salmon fishery by two orders of magnitude (Anonymous 1999). One consequence is that large numbers of farm fishes escape and enter the rivers of native salmon throughout the North Atlantic (Hansen *et al.* 1991, and references therein; Carr *et al.* 1997; Youngson *et al.* 1997; Fiske & Lund 1999). The impact of such invasions has been the subject of mounting concern (Hansen *et al.* 1991; Hindar *et al.* 1991; Hutchinson 1997; Naylor *et al.* 1998), particularly given a global decline in native salmon populations (Parrish *et al.* 1998; Kellogg 1999).

This concern arises from the potentially deleterious effects of ecological and genetic interactions between farm and native salmon. Farm salmon may compete directly with native salmon for resources such as space, food or mates, alter predation regimes and transfer diseases and parasites (reviewed in Jonsson 1997). Moreover, farm salmon are commonly derived from non-indigenous sources and their genetic make-up has been altered through selective breeding and domestication (Hansen *et al.* 1991, and references therein; Hutchinson 1997, and references therein; Mjølnerød *et al.* 1997; Clifford *et al.* 1998; Norris *et al.* 1999). Interbreeding thus represents an additional threat to native populations (i.e. disruption of local adaptations and genetic homogenization). However, no study to date has quantified the lifetime success (adult to adult) and interactions resulting from farm salmon invading a native population. We therefore undertook a large-scale experiment in order to simulate such an invasion of farm salmon into a Norwegian river and quantify their lifetime success and interactions with native salmon.

2. MATERIAL AND METHODS

(a) *Anadromous adults and breeding success*

The experimental release of farm Atlantic salmon was conducted in the River Imsa, south-western Norway (58°59′ N, 5°58′ E), a small, 1 km long river supporting a small native population of Atlantic salmon (described in Jonsson *et al.* 1998). Adult farm salmon (fifth generation) derived from Norway's national breeding programme (Gjedrem *et al.* 1991) and reared locally were transported to the Norwegian Institute for Nature Research (NINA) station at Ims in September–October 1993 where they were maintained in 4000-l holding tanks. Over 50% of the world's farm Atlantic salmon derive from this programme or its predecessor with the fishes having been used in Australia, Canada, Chile, Ireland, Norway, Scotland and the USA. Native salmon returning to the Imsa were collected during July–October in a fish trap (100 m upstream of the river mouth) that controls the ascent and descent of fishes (Jonsson *et al.* 1998), and held in similar 4000-l tanks.

The fishes were biopsied and screened genetically for the muscle enzyme $MEP\text{-}2^{*}$ during the second half of October (Cross & Ward 1980). Twenty-two farm salmon homozygous for $MEP\text{-}2^{*}$ (${}^{*}125/{}^{*}125$) and 17 native salmon homozygous for $MEP\text{-}2^{*}$ (${}^{*}100/{}^{*}100$) were selected for release. The selection reflected the background gene frequencies of the farm (0.399 ${}^{*}100$ allele and 0.601 ${}^{*}125$ allele) ($n = 207$) and native populations (0.595 ${}^{*}100$ allele and 0.405 ${}^{*}125$ allele, $n = 63$). Natural

---

[*] Author for correspondence (ian.fleming@ninatrd.ninaniku.no).

† Present address: Directorate for Nature Management, Tungasletta 2, N-7485 Trondheim, Norway.

selection acting on *MEP-2** or a linked locus has been suggested (Jordan *et al.* 1997), but does not appear to influence cohorts of the Imsa population significantly (genotype proportions in 18 groups of half-sibs sampled as age 0+ on two occasions following hatching, Fisher's combined probability $p > 0.20$, and genotype proportions of five-year classes sampled as age 1+, 2+ or 3+ smolts, combined $p > 0.90$; age 0+ refers to fishes in the first year of life, age 1+ refers to fishes in the second year, subsequent to winter annulus formation, etc.) (K. Hindar, unpublished data). Moreover, parallel experiments using non-genetically marked fishes have produced similar results to those found in the present release experiment (Fleming *et al.* 1996; Einum & Fleming 1997; Fleming & Einum 1997; present experimental arena study). The selected farm salmon were larger (mean length ± s.d. = 575 ± 34 mm) than the native salmon (545 ± 39 mm) ($F_{1,35} = 6.75$ and $p = 0.014$ and no sex or interaction effects $p > 0.30$) reflecting the natural size difference.

The selected fishes were radio tagged (Økland *et al.* 1996) and released into the Imsa above the fish trap on 4 November 1993. They were subsequently tracked daily until 22 December (excluding 21, 25 and 28 November and 10 December) and then again on 28 December and 2, 6 and 10 January. The locations of all individuals were recorded during each tracking and visual focal observations (2 min) were made of individuals stationed in spawning areas in order to record activity.

An experiment, which involved the release of 12 farm and nine native salmon (randomly selected) into an arena designed to mimic a natural spawning environment ($47\,\mathrm{m}^2$) (described in Fleming *et al.* 1996), was initiated on 5 November in parallel with the river release. The experiment was a smaller-scale version of that carried out earlier by Fleming *et al.* (1996) and was designed to supplement the river release by providing more detailed data about breeding behaviour and success. The arena was monitored $24\,\mathrm{h\,day}^{-1}$ by video until 23 December and spawning activity and nest locations were recorded. This was supplemented with daily manual observations, which included a 20 min scan sample of behaviour. The arena was excavated during 14 and 15 March 1994 and all nests present were recovered and the number of live and dead eggs recorded. The nests were assigned to females using spawning records and cross-checked using egg-size data. The breeding success for females was measured as the total number of live embryos recovered from their nests. Male breeding success was calculated as the number of live embryos recovered from nests that they fertilized and, in cases of multiple-male paternity (9% of spawnings involved both farm and native males), it was calculated following the method of Fleming *et al.* (1996). This method incorporates the order of male precedence at spawning, which is an important determinant of fertilization success in Atlantic salmon (Mjolnerod *et al.* 1998).

All fishes from the experimental arena and those recovered from the river were examined at the end of the spawning season for gamete retention, which was expressed as a percentage of their estimated pre-spawning gamete investment. Females' initial fecundity was estimated from their weight using relations established for Imsa females (Jonsson *et al.* 1996) and for 18 unspawned farm females sampled during the study (fecundity $= 0.0091 \times (\mathrm{weight})^{1.814}$) ($r^2 = 0.644$ and $p < 0.001$). These relationships were also used to estimate the potential egg deposition in the river by the farm and native females. Ten fresh eggs from each of the 18 farm females were also weighed individually in order to compare them with those of Imsa females (Jonsson *et al.* 1996). Males' initial testes weight was estimated from gonadal-somatic indices for Imsa males (Jonsson *et al.* 1991) and for 17 unspawned farm males sampled during the study (mean ± s.d. = 6.08 ± 1.51%).

(b) *Offspring and lifetime reproductive success*

Offspring (age 0+ parr) from the spawnings in the river were sampled by electrofishing the length of the Imsa on 6 and 7 September ($n = 55$) and 18 and 19 October 1994 ($n = 67$). The location of capture was recorded and the fishes were sacrificed, weighed, their lengths measured and stomachs dissected and a sample of muscle was placed in ethanol and another was frozen. Their stomach contents were analysed following the methods of Hindar *et al.* (1988) and Breistein & Nost (1997) and a similarity index was calculated following Schoener (1968).

The origin of the offspring was accurately identified by genetic typing (*MEP-2**) since all spawners had been genetically screened and no spawning had occurred during the previous two years (i.e. few if any mature male parr present) (Jonsson *et al.* 1998). In addition, DNA was extracted from the ethanol-preserved tissue by phenol–chloroform extraction. The mitochondrial ND-1 gene (NADH dehydrogenase 1) was polymerase chain reaction amplified (Cronin *et al.* 1993) and digested with restriction enzymes showing fragment length polymorphism in *Hae*III and *Rsa*I digests (no additional mtDNA heterogeneity was found at two other ND genes).

Juveniles descending the Imsa to the ocean in 1995–1996 were captured in the fish trap, anaesthetized, measured, muscle biopsied, tagged with a unique Carlin tag and released after 24 h recovery. The biopsy of every other fish was analysed for *MEP-2** expression (i.e. 50% of all migrants); no significant differences existed between typed and untyped fish (descent date, length, weight and condition factor) ($p > 0.50$). The production of downstream migrants relative to the estimated total potential egg deposition (described in § 2(a)) was compared to the population's stock-recruitment relationship (Jonsson *et al.* 1998).

Returns of adult offspring were recorded from the coastal and river fisheries (Carlin tag recoveries) and the Imsa fish trap. Fishes recovered at the fish trap were weighed and their lengths measured and tissues sampled. The data for fishes captured in the fishery were less complete, but all individuals could be genetically typed by cross-referencing their Carlin tag identification to the tissue samples taken at the Imsa fish trap during juvenile seaward migration.

(c) *Statistical analysis*

The fishes' growth rate from emergence was adjusted to a common body mass and calculated following Elliott & Hurley (1997). Emergence was estimated based on the mean spawning dates for the farm and native females, daily river temperatures and equations relating temperature to hatching (Crisp 1981) and emergence (Jensen *et al.* 1991).

The predicted effect of t generations of one-way gene flow from farm salmon on the allele frequency q_t of the recipient (native) population was calculated as

$$q_t = (1-m)^t q_0 + [1-(1-m)^t]q_m, \tag{1}$$

where q_0 is the allele frequency of the recipient population before migration and q_m is the allele frequency of the migrants (Hedrick 1983). The equation applies not only to allele frequencies but also approximately to weakly selected quantitative genetic traits having an additive genetic basis (Bulmer 1980).

Table 1. *Comparisons of the native and farm spawners in the River Imsa and the experimental arena (control)*

(Nesting by one farm and one native female and courting by two farm and one native male was never observed for the river data for initiation of nesting/courting (Julian day) and nesting location. Intact carcasses were recovered from six female and five male native salmon and seven female and seven male farm salmon for the river data for gamete retention. One farm female did not spawn for the experimental arena data for egg survival in nests. The breeding success data were adjusted for unequal variances. The data are means ± standard deviations or medians with quartiles in parentheses. The statistics are *t*-tests, ANCOVAs with body weight as a covariate ($p < 0.05$) or Mann–Whitney *U*-tests (Z). $^{*}p < 0.05$, $^{**}p < 0.01$.)

location	females			males		
trait	native	farm	statistic	native	farm	statistic
river						
daily migration (m)	59 ± 24	59 ± 29	$t_{17} = 0.328$	111 ± 44	121 ± 27	$t_{18} = 0.63$
initiation of nesting/courting (Julian day)	331 ± 12	315 ± 6	$t_{15} = 3.87^{**}$	311 ± 2	311 ± 3	$t_{15} = 0.01$
nesting location (metres upstream of fish trap)	316 ± 155	312 ± 219	$t_{15} = 0.42$	—	—	—
females courted/male courting (number of observations)	4.0 (1.0–8.0)	6.0 (2.3–8.3)	$Z = 0.66$	6.0 (3.0–9.0)	2.0 (1.0–2.0)	$Z = 2.15^{*}$
gamete retention (% of initial gametes)	0.8 (0.3–2.5)	1.1 (0.2–2.5)	$Z = 0.08$	30.6 (13.3–75.8)	104.8 (81.2–120.3)	$Z = 2.03^{*}$
experimental arena						
initiation of nesting/courting (Julian day)	324 (311–361)	311 (310–315)	$Z = 1.10$	311 ± 1	311 ± 1	$t_{9} = 0.09$
females courted/males courting (number of observations)	30.0 ± 18.9	15.0 ± 16.3	$t_{8} = 1.36$	29.8 ± 17.9	11.7 ± 7.8	$F_{1,8} = 5.67^{*}$
gamete retention (% of initial gametes)	0.3 (0.1–0.6)	7.7 (0.1–28.5)	$Z = 1.28$	82.4 (54.3–85.1)	104.3 (86.9–107.1)	$Z = 2.01^{*}$
female nests/male spawnings	6.3 ± 1.3	3.8 ± 1.9	$t_{8} = 2.85^{*}$	7.0 ± 5.2	2.2 ± 2.4	$F_{1,8} = 9.88^{*}$
egg survival in nests (%)	82.8 ± 1.9	56.5 ± 15.6	$t_{7} = 2.97^{*}$	—	—	—
breeding success (embryos parented)	1912 ± 182	611 ± 539	$t_{6.5} = 5.46^{**}$	1516 ± 1303	360 ± 554	$F_{1,8} = 7.43^{*}$

Half of the genetic difference between the donor and recipient remains after $t_{0.5} = \ln(0.5)/\ln(1-m)$ generations. The calculations assume that the effects of genetic drift and selection in the recipients are small relative to migration and that the allele frequencies of the migrants remain stable.

All of the proportion/percentage data were arcsine, square-root transformed and the courting and breeding success data were log transformed prior to analysis in order to meet the assumptions of analysis of variance. Data that did not meet the requirements for parametric analysis were analysed using non-parametric tests.

3. RESULTS

(a) *Reproduction*

The farm and native adults had similar migration patterns and nesting locations in the river, though the farm females spawned before the native females (table 1). Courting by both the farm and native males began shortly after release. However, the native males courted females more often than the farm males and retained less of their initial testes unspawned (table 1). Evidence from the experimental arena indicates that the latter correlates inversely with the number of spawnings (Spearman $r = -0.695$ and $p = 0.018$).

The findings from the experimental arena paralleled those from the river. The farm females began spawning before the native females while both male types began courting females almost immediately after release. Moreover, the farm males appeared competitively disadvantaged, courting females less frequently than native males (table 1) and at times showing inappropriate mating behaviour. As a result, they participated in fewer spawnings and retained a larger proportion of their testes unspawned. Ultimately, the farm males attained just 24% of the breeding success of the native males. The farm females also incurred a breeding disadvantage, constructing fewer nests, having lower egg survival and achieving only 32% of the success of the native females. The eggs of the farm females (mean ± s.d. = 804 ± 128 mg) ($n = 18$) were also significantly smaller than those of the native females (896 ± 144 mg) ($n = 104$) ($t_{120} = 2.53$ and $p < 0.05$) (Jonsson *et al.* 1996).

(b) *Early life history*

The proportion of native to farm genotypes among the offspring (age 0+ parr) from spawnings in the river shifted significantly from that of the spawners ($\chi^2 = 37.97$, d.f. = 1 and $p < 0.001$) (figure 1). Most of the fishes were now of pure native origin (65.1%) with farm genetic representation occurring mainly through hybridization with native fishes. The maternal origin, which was identified using the mitochondrial ND-1 gene, revealed that 25 out of the 31 hybrid offspring had a unique farm female haplotype (found in eight farm females), five a common haplotype (found in three farm and six native females) and none a unique native female haplotype (found in two native females; one offspring was not analysable). Thus, most if not all hybrids had farm mothers.

The farm adults had only 19% of the reproductive success of the native fishes up to this stage (i.e. breeding and early survival). Furthermore, based on breeding success in the experimental arena (farm:native 28%), early survival of the farm genotypes was estimated at 70% that of the native genotypes. Thereafter, there was little evidence of differential freshwater survival (parr to smolt, $\chi^2_2 = 1.85$ and $p = 0.397$) (figure 1).

However, there were indications of resource competition as the diets of the farm, native and hybrid offspring were similar, having a mean diet overlap of 82 ± 7% (proportional composition of different food types, ANOVAs controlling for sampling date $p > 0.30$). In addition, the total production of smolts (i.e. oceanic migrants) from the spawnings was 28% below that expected based on the potential egg deposition (48 831) and the stock-recruitment relationship for the River Imsa (Jonsson *et al.* 1998). Moreover, the smolt production by the native females (494 pure native smolts plus 0–17% (based on mtDNA analyses of age 0+ fishes) of the farm × native smolts) was 31–32% below that expected in the absence of farm females. This effect may reflect competitive asymmetries as the native juveniles were smaller at age 0+ (figure 2) (also weight $F_{2,116} = 4.67$ and $p = 0.011$, and controlling for sampling date $p < 0.001$) due to differences in the female spawning dates (table 1) and offspring growth rates ($F_{2,116} = 3.09$ and $p = 0.049$, and controlling for sampling date $p < 0.001$). Native offspring (age 0+ parr) were captured further upstream than their farm and farm × native counterparts ($F_{2,115} = 12.55$ and $p < 0.001$, and independent of sampling date $p = 0.295$ and fish weight $p = 0.143$).

(c) *Seaward migration and return*

Most fishes descended as smolts in the spring with 13% (93 out of 718) descending as parr during the winter of 1995–1996. The proportional compositions of the farm, native and hybrid fishes did not differ between smolts and descending parr ($\chi^2_2 = 0.50$ and $p = 0.778$). There were distinct behavioural and life history differences among the smolts as the farm smolts descended earlier ($F_{2,303} = 70.50$ and $p < 0.001$) (year $F_{1,303} = 127.13$ and $p < 0.001$) and at a younger age ($\chi^2_2 = 41.91$ and $p < 0.001$) (figure 1) than the wild smolts, with the hybrids being intermediate (all pairwise comparisons $p < 0.05$ with Bonferroni adjustment). The hybrid smolts were also longer (figure 2) and heavier than the native smolts ($F_{1,289} = 18.21$ and $p < 0.001$, and controlling for smolt age $p < 0.001$), while the farm smolts weighed less for a given length than their counterparts (figure 2).

There was no significant difference between the offspring types in survival from seaward migration to maturity ($\chi^2_2 = 0.04$ and $p = 0.840$) (figure 1). As a result, the lifetime reproductive success (adult to adult) of the farm salmon was 16% that of the native salmon. All adult recaptures occurred in either the coastal fishery or the River Imsa and no fishes were reported straying into other rivers. There were no significant differences between the offspring types in body size and condition at recapture (figure 2) or in sea age at maturity (22 out of 26 matured after one year at sea) (Mann–Whitney *U*-test, $Z = 0.14$ and $p = 0.929$, with single farm fish excluded). However, the mean age at maturity of the hybrid fishes (mean ± s.d. = 3.4 ± 0.5 years) was less than that of the native fishes (4.2 ± 0.4 years) (Mann–Whitney *U*-test, $Z = 3.11$ and $p = 0.002$) because of differences in their age at smolting and poor survival of native age 1+ smolts (none were recaptured).

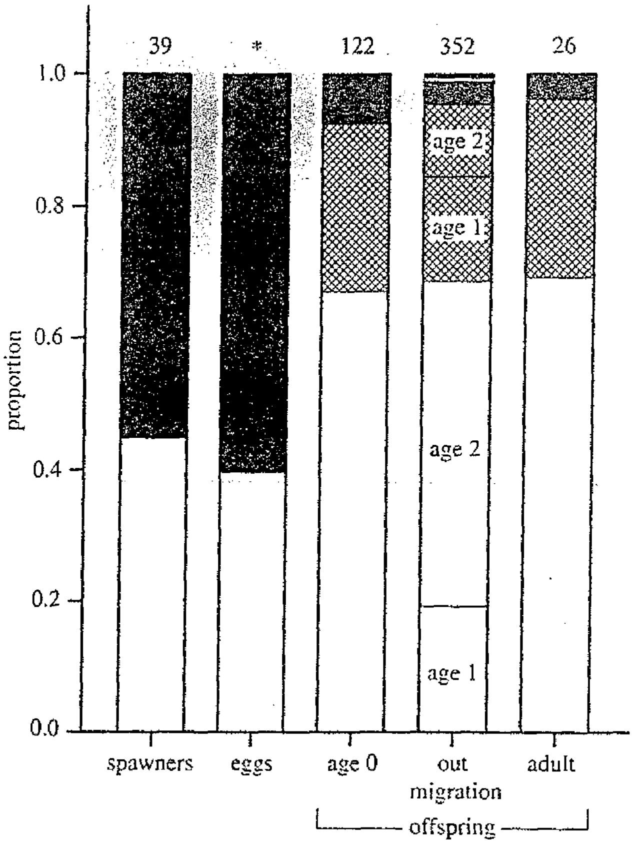


Figure 1. Changes in the proportional constitution of the Atlantic salmon population in the River Imsa following the release of native and farm spawners. The number above each bar represents either the total population size (spawners and adult offspring) or the sample size examined at each life stage (age 0+ and out migration). Two age groups of out migrants existed, age 1+ and 2+ and are stacked on top of each other for each offspring type. The asterisk denotes that the potential egg deposition was 19 443 for the native females and 29 388 for the farm females (see §2). Solid bars, farm offspring; open bars, native offspring; hatched bars, hybrid offspring.

4. DISCUSSION AND CONCLUSIONS

We were able to document, for the first time to our knowledge, the lifetime success of farm salmon invading a natural river and found it to be 16% that of the native fish. Both the results from the river and the parallel experiment in the stream arena indicated that breeding was the major bottleneck impeding the invasion. The farm salmon reared to maturity were competitively and reproductively inferior, achieving less than one-third the breeding success of the native fishes. This may be a general pattern for farm salmon invading native populations (Fleming *et al.* 1996; Clifford *et al.* 1998). The present results also indicated that this inferiority was sex biased, being more pronounced among farm males than females. Few if any of the farm × native offspring recovered from the river were fathered by farm males. Thus, gene flow occurred mainly through native males breeding with

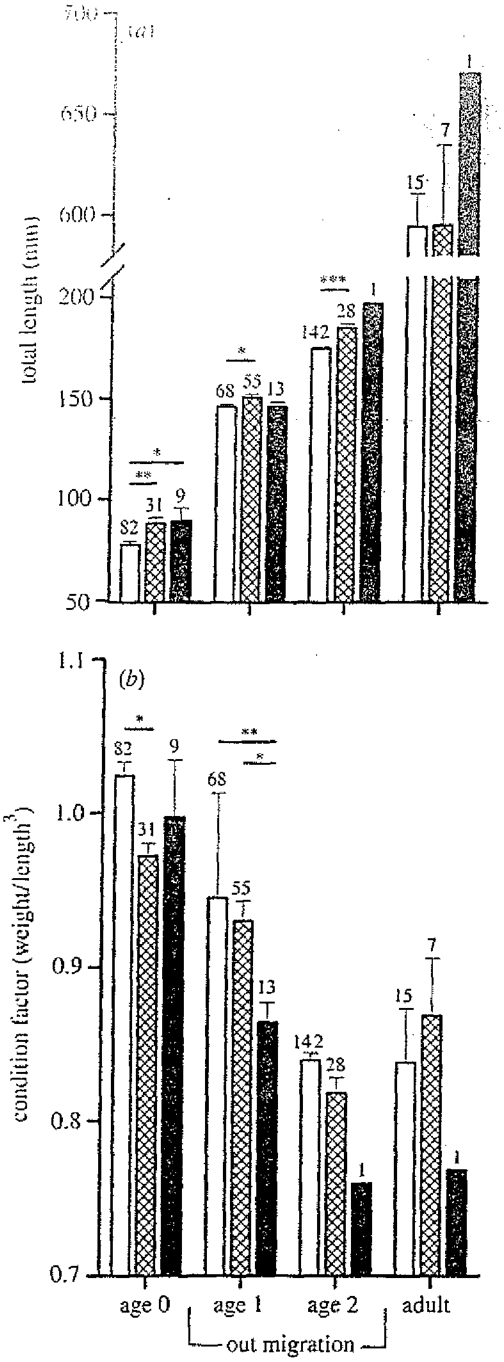


Figure 2. (*a*) Comparison of the mean (+ 1 standard error) body length at various life stages for the native (open bars), farm (solid bars) and hybrid (hatched bars) offspring. (*b*) Comparison of condition factor for the same groups. The sample size is given above each bar. Significant pairwise differences (Tukey test for multiple comparisons) are shown. $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

farm females. This parallels the findings of Fleming *et al.* (1996) where farm males were found to be behaviourally deficient, infrequently attained access to spawning females and exhibited inappropriate mating behaviour.

The lower early survival of the farm genotypes compared to the native genotypes in the river also appeared to constrain invasion, though to a lesser extent than breeding. McGinnity *et al.* (1997) reported a similar degree of differential survival between farm and native genotypes in age 0+ juveniles outplanted as eggs in an Irish river. Both findings may reflect the smaller egg size of farm females, which can affect survival after emergence directly (Einum & Fleming 2000) and differences in their innate behaviour, including predator avoidance (Einum & Fleming 1997; Fleming & Einum 1997). However, the survival differences occurred principally during the earliest life-history stages (see also McGinnity *et al.* 1997), which may prove to be common following the intense natural selection of early life (Einum & Fleming 2000).

The potential for significant resource competition existed as there was considerable overlap in the diets of the native, farm and hybrid offspring (see also Einum & Fleming 1997). Furthermore, there were indications of competitive displacement as the offspring distributions differed despite the native and farm females having had similar nesting locations. This may reflect the faster growth rate and, thus, larger size of the farm and farm × native offspring than the native offspring (see also Einum & Fleming 1997; McGinnity *et al.* 1997). Norwegian farm salmon have undergone selection for rapid growth (Gjedrem *et al.* 1991), which may also explain their greater allocation of resources to length than weight growth (body condition) (figure 2), a pattern consistent with increased growth hormone production (Johnsson *et al.* 1996). Similarly, McGinnity *et al.* (1997) reported competitive displacement; however, in contrast to the present study the native offspring were displaced downstream into a lake by faster-growing and larger farm and hybrid offspring.

Moreover, the present results indicate that the production of seaward migrants was depressed, particularly that by the native females, which was more than 30% below that expected. While stock-recruitment relationships are notoriously variable, this depression was the second largest in 16 years (Jonsson *et al.* 1998) and occurred despite the absence of competition from older salmon cohorts, which should have been favourable for smolt production (Kennedy & Strange 1980; Gibson 1993). Moreover, the environmental conditions did not appear unfavourable because the juvenile growth was good, age at smolting was young (cf. Jonsson *et al.* 1998) and indications from other North-East Atlantic salmon rivers suggested that the broadscale conditions were favourable for smolt production (Anonymous 1999). Alternatively, the depression in smolt production may have reflected fluctuating selection on offspring type, with competition from the farm and hybrid offspring depressing the wild offspring survival during one or more life-history episodes and maladaptation depressing the farm and hybrid offspring at other times (McGinnity *et al.* 1997). While the definitive cause of the depression is unknown, it appears likely that interactions with the farm and hybrid salmon played a role.

There were no indications that the differences in age, size and condition at smolting and timing of descent affected the relative survival to maturity of the different offspring types overall or at least that of the native and hybrid fishes. Thus, the bottlenecks to the invasion by farm salmon occurred principally during breeding and early life history. The poor marine survival of age 1+ wild smolts compared with that of hybrid and age 2+ wild smolts is likely explained by their small size and late migration (cf. Hansen & Quinn 1998).

During the 1990s, escaped farm fishes were estimated to have composed 20–40% of the salmon recorded over large areas of the North Atlantic (Hansen *et al.* 1999) and more than 80% of the salmon in some Norwegian spawning populations (Lund *et al.* 1991; Fiske & Lund 1999). This approaches and exceeds that of our experiment (55%). The gene flow from the farm to native salmon, which occurred during one generation in this experiment, was $m = 0.19$. One-way gene flow of this magnitude is a potent evolutionary force (Hedrick 1983; Barton 1992). The native population will eventually be composed of individuals that have all descended from the migrants and this situation is approached rapidly for selectively neutral loci and/or traits. For $m = 0.19$, the genetic difference between the donor (farm) and recipient (native) population is halved every 3.3 generations, though this will be partly dependent on the fitness of hybrids and backcrosses during subsequent generations. The shorter generation time of the hybrid than native fish observed in the present study would also tend to increase the rate of introgression (Hedrick 1983), though this may not be a general pattern (McGinnity *et al.* 1997). For rates of gene flow reflecting average proportions of escaped salmon in the North Atlantic, the half-life of the difference would be in the order of ten generations. As farm salmon have been shown to differ genetically from their wild origin in allele frequencies, allelic diversity and quantitative traits (Fleming & Einum 1997; Mjolnerod *et al.* 1997; Norris *et al.* 1999), it is clear that escaped farm salmon may have wide-ranging genetic effects on native salmon populations. Such effects are frequently negative (reviewed by Hindar *et al.* 1991) and purging by natural selection will be hindered by the annual, repeated invasions of escaped farm salmon. This genetic impact comes on top of the potential effects of intraspecific interactions on productivity (e.g. smolt production) and calls into question the long-term viability of many salmon populations.

We thank F. Okland, G. Ståhl and the staff of the NINA Research Station, Ims, for invaluable assistance during the study and S. Einum, A. Ferguson, T. Forseth, N. B. Metcalfe, M. S. Ridgway, J. Tufto, O. Ugedal, F. Utter and R. S. Waples for helpful comments. Funding was provided by the Norwegian Research Council and the Norwegian Directorate for Nature Management.

REFERENCES

Anonymous 1999 *Report of the Working Group on North Atlantic Salmon*. Copenhagen, Denmark: International Council for Exploration of the Sea CM 1999/ACFM:14.

Barton, N. H. 1992 On the spread of new gene combinations in the third phase of Wright's shifting balance theory. *Evolution* **46**, 551–557.

Breistein, J. & Nost, T. 1997 Standardization of methods: biomass of freshwater invertebrates. *NINA Oppdragsmelding* **480**, 1–19. (In Norwegian with an English abstract.)

Bulmer, M. G. 1980 *The mathematical theory of quantitative genetics*. Oxford, UK: Clarendon Press.

Carr, J. W., Anderson, J. M., Whoriskey, F. G. & Dilworth, T. 1997 The occurrence and spawning of cultured Atlantic salmon (*Salmo salar*) in a Canadian river. *ICES J. Mar. Sci.* **54**, 1064–1073.

Clifford, S. L., McGinnity, P. & Ferguson, A. 1998 Genetic changes in Atlantic salmon (*Salmo salar*) populations of northwest Irish rivers resulting from escapes of adult farm salmon. *Can. J. Fish Aquat. Sci.* **55**, 358–363.

Crisp, D. T. 1981 A desk study of the relationship between temperature and hatching time for the eggs of five species of salmonid fishes. *Freshw. Biol.* **11**, 361–368.

Cronin, M. A., Spearman, W. J., Wilmot, R., Patton, J. C. & Bickham, J. W. 1993 Mitochondrial-DNA variation in chinook (*Oncorhynchus tshawytscha*) and chum salmon (*O. keta*) detected by restriction enzyme analysis of polymerase chain-reaction (PCR) products. *Can. J. Fish. Aquat. Sci.* **50**, 708–715.

Cross, T. F. & Ward, R. D. 1980 Protein variation and duplicate loci in the Atlantic salmon, *Salmo salar* L. *Genet. Res.* **36**, 147–165.

Einum, S. & Fleming, I. A. 1997 Genetic divergence and interactions in the wild among native, farmed and hybrid Atlantic salmon. *J. Fish Biol.* **50**, 634–651.

Einum, S. & Fleming, I. A. 2000 Highly fecund mothers sacrifice offspring survival to maximize fitness. *Nature* **405**, 565–567.

Elliott, J. M. & Hurley, M. A. 1997 A functional model for maximum growth of Atlantic salmon parr, *Salmo salar*, from two populations in north-west England. *Funct. Ecol.* **11**, 592–603.

Fiske, P. & Lund, R. A. 1999 Escapees of reared salmon in coastal and riverine fisheries in the period 1989–1998. *NINA Oppdragsmelding* **603**, 1–23 (in Norwegian with an English abstract).

Fleming, I. A. & Einum, S. 1997 Experimental tests of genetic divergence of farmed from wild Atlantic salmon due to domestication. *ICES J. Mar. Sci.* **54**, 1051–1063.

Fleming, I. A., Jonsson, B., Gross, M. R. & Lamberg, A. 1996 An experimental study of the reproductive behaviour and success of farmed and wild Atlantic salmon (*Salmo salar*). *J. Appl. Ecol.* **33**, 893–905.

Gibson, R. J. 1993 The Atlantic salmon in fresh water: spawning, rearing and production. *Rev. Fish Biol. Fish.* **3**, 39–73.

Gjedrem, T., Gjoen, H. M. & Gjerde, B. 1991 Genetic origin of Norwegian farmed Atlantic salmon. *Aquaculture* **98**, 41–50.

Hansen, L. P. & Quinn, T. P. 1998 The marine phase of the Atlantic salmon (*Salmo salar*) life cycle, with comparisons to Pacific salmon. *Can. J. Fish. Aquat. Sci.* **55** (Suppl. 1), 104–118.

Hansen, L. P., Håstein, T., Nævdal, G., Saunders, R. L. & Thorpe, J. E. (ed.) 1991 Interactions between cultured and wild Atlantic salmon. *Aquaculture* **98**, 1–324.

Hansen, L. P., Jacobsen, J. A. & Lund, R. A. 1999 The incidence of escaped farmed Atlantic salmon, *Salmo salar* L., in the Faroese fishery and estimates of catches of wild salmon. *ICES J. Mar. Sci.* **56**, 200–206.

Hedrick, P. W. 1983 *Genetics of populations*. Boston, MA: Science Books International.

Hindar, K., Jonsson, B., Andrew, J. H. & Northcote, T. G. 1988 Resource utilization of sympatric and experimentally allopatric cutthroat trout and Dolly Varden charr. *Oecologia* **74**, 481–491.

Hindar, K., Ryman, N. & Utter, F. 1991 Genetic effects of cultured fish on natural fish populations. *Can. J. Fish. Aquat. Sci.* **48**, 945–957.

Hutchinson, P. (ed.) 1997 Interactions between salmon culture and wild stocks of Atlantic salmon: the scientific and management issues. *ICES J. Mar. Sci.* **54**, 963–1225.

Jensen, A. J., Johnsen, B. O. & Saksgård, L. 1991 Temperature requirements in Atlantic salmon (*Salmo salar*), brown trout (*Salmo trutta*), and Arctic charr (*Salvelinus alpinus*) from hatching to initial feeding compared with geographic distribution. *Can. J. Fish. Aquat. Sci.* **46**, 786–789.

Johnsson, J. I., Petersson, E., Jönsson, E., Björnsson, B. Th. & Järvi, T. 1996 Domestication and growth hormone alter antipredator behaviour and growth patterns in juvenile brown trout, *Salmo trutta*. *Can. J. Fish. Aquat. Sci.* **53**, 1546–1554.

[illegible] B. 1997 A review of ecological and behavioural interactions between cultured and wild Atlantic salmon. *ICES J. Mar. Sci.* 54, 1051–1059.

Jonsson, N., Jonsson, B. & Hansen, L. P. 1991 Energetic cost of spawning in male and female Atlantic salmon (*Salmo salar* L.). *J. Fish Biol.* 39, 739–744.

Jonsson, N., Jonsson, B. & Fleming, I. A. 1996 Does early growth cause a phenotypically plastic response in egg production of Atlantic salmon? *Funct. Ecol.* **10**, 89–96.

Jonsson, N., Jonsson, B. & Hansen, L. P. 1998 The relative role of density-dependent and density-independent survival in the life cycle of Atlantic salmon *Salmo salar*. *J. Anim. Ecol.* **67**, 751–762.

Jordan, W. C., Verspoor, E. & Youngson, A. F. 1997 The effect of natural selection on estimates of genetic divergence among populations of Atlantic salmon. *J. Fish Biol.* 51, 546–560.

Kellogg, K. A. 1999 Salmon on the edge. *Trends Ecol. Evol.* 14, 45–46.

Kennedy, G. J. A. & Strange, C. D. 1980 Population changes after two years of salmon (*Salmo salar* L.) stocking in upland trout (*Salmo trutta* L.) streams. *J. Fish Biol.* 17, 577–586.

Lund, R. A., Okland, F. & Hansen, L. P. 1991 Farmed Atlantic salmon (*Salmo salar*) in fisheries and rivers in Norway. *Aquaculture* 98, 143–150.

McGinnity, P., Stone, C., Taggart, J. B., Cooke, D., Cotter, D., Hynes, R., McCamley, C., Cross, T. & Ferguson, A. 1997 Genetic impact of escaped farmed Atlantic salmon (*Salmo salar* L.) on native populations: use of DNA profiling to assess freshwater performance of wild, farmed, and hybrid progeny in a natural river environment. *ICES J. Mar. Sci.* 54, 998–1008.

Mjolnerod, I. B., Refseth, U. H., Karlsen, E., Balstad, T., Jakobsen, K. S. & Hindar, K. 1997 Genetic differences between two wild and one farmed population of Atlantic salmon (*Salmo salar*) revealed by three classes of genetic markers. *Hereditas* 127, 239–248.

Mjolnerod, I. B., Fleming, I. A., Refseth, U. H. & Hindar, K. 1998 Mate and sperm competition during multiple-male spawnings of Atlantic salmon. *Can. J. Zool.* 76, 70–75.

Naylor, R. L., Goldburg, R. J., Mooney, H., Beveridge, M., Clay, J., Folke, C., Kautsky, N., Lubchenco, J., Primavera, J. & Williams, M. 1998 Nature's subsidies to shrimp and salmon farming. *Science* 282, 883–884.

Norris, A. T., Bradley, D. G. & Cunningham, E. P. 1999 Microsatellite genetic variation between and within farmed and wild Atlantic salmon (*Salmo salar*) populations. *Aquaculture* 180, 247–264.

Økland, F., Lamberg, A., Heggberget, T. G., Fleming, I. A. & McKinley, R. S. 1996 Identification of spawning behaviour in Atlantic salmon (*Salmo salar* L.) by radiotelemetry. In *Underwater biotelemetry: Proceedings of the First Conference and Workshop on Fish Telemetry in Europe* (ed. E. Baras & J. C. Philippart), pp. 35–46. Liège, Belgium: University of Liège.

Parrish, D. L., Behnke, R. J., Gephard, S. R., McCormick, S. D. & Reeves, G. H. 1998 Why aren't there more Atlantic salmon (*Salmo salar*)? *Can. J. Fish. Aquat. Sci.* 55(Suppl. 1), 281–287.

Schoener, T. W. 1968 The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. *Ecology* 49, 704–726.

Youngson, A. F., Webb, J. H., MacLean, J. C. & Whyte, B. M. 1997 Frequency of occurrence of reared Atlantic salmon in Scottish salmon fisheries. *ICES J. Mar. Sci.* 54, 1216–1220.

As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.

Journal of
Applied Ecology
1996, 33,
893–905

An experimental study of the reproductive behaviour and success of farmed and wild Atlantic salmon (*Salmo salar*)

I.A. FLEMING, B. JONSSON, M.R. GROSS* and A. LAMBERG

*Norwegian Institute for Nature Research, Tungasletta 2, N-7005 Trondheim, Norway; and *Department of Zoology, University of Toronto, Toronto, Ontario, Canada M5S 1A1*

Summary

1. Escape of cultured organisms into natural ecosystems may threaten wild populations both ecologically and genetically. In the aquaculture industry, farmed Atlantic salmon (*Salmo salar* L.) often escape and enter the spawning grounds of wild salmon. We report experiments to assess the competitive and reproductive abilities of fifth-generation farmed salmon and their potential impacts upon wild salmon.

2. The farmed and wild females had similar levels of competitive behaviour; however, they differed in reproductive behaviour and success. Farmed females displayed less breeding behaviour, constructed fewer nests, retained a greater weight of eggs unspawned, were less efficient at nest covering, incurred more nest destruction, and suffered greater egg mortality than wild females. As a result, farmed females had less than one-third of the reproductive success of wild females.

3. The farmed males were even less successful than the farmed females in competition with the wild fish. They were less aggressive, courted less, partook in fewer spawnings, and achieved only an estimated one to three percentage of the reproductive success of the wild males.

4. The farmed males exhibited inappropriate mating behaviour, that led to poor fertilization success, even in the absence of competition with wild males.

5. Adult farmed fish are thus likely to be relatively unsuccessful in natural environments due to a competitive and reproductive inferiority apparently resulting from domestication.

Key-words: artificial culture, captive breeding, fish farming, aquatic biodiversity, breeding success.

Journal of Applied Ecology (1996) **33**, 893–905

Introduction

Biodiversity is threatened by intentional and unintentional releases of cultured organisms into natural ecosystems (e.g. Allendorf 1983; Hindar, Ryman & Utter 1991; Ledig 1992). Animals derived from cultured populations may have both ecological (e.g. competition, disease introductions) and genetic (e.g. loss of local adaptation, genetic homogenization) impacts on wild populations, but few data are available on how cultured and wild animals interact.

Fishes, particularly salmon, are among the most intensely cultured organisms. Farmed salmon frequently escape in large numbers from aquaculture facilities and at maturity, enter nearby rivers where they may outnumber spawning populations of wild salmon (Gausen & Moen 1991; Webb *et al.* 1991). Farmed salmon are artificially cultured throughout their lives. Eggs are collected from broodstock females, artificially fertilized with sperm from broodstock males and the offspring are reared in freshwater hatcheries for 6 months to 1 year before transfer to marine net pens, where they are reared until harvest. Captive rearing conditions combined with artificial selection, both intentional and unintentional, cause farmed Atlantic salmon to diverge from their wild phenotype through environmental and eventually, evolutionary processes (e.g. Cross & Challanain 1991; Youngson *et al.* 1991; Fleming, Jonsson & Gross 1994). Moreover, farmed salmon are often derived from non-indigenous sources (e.g. Cross & Challanain 1991; Gjedrem, Gjøen & Gjerde 1991). Thus, the escape of farmed salmon, which occurs primarily during the marine phase, raises both ecological and genetic concerns for the existence of wild salmon (reviewed in Hindar *et al.* 1991; Hutchings 1991; Waples 1991).

In nature, female Atlantic salmon compete for oviposition territories within which they may sequentially construct several nests to form a redd, i.e. area of disturbed gravel containing one or more nests (White 1942; Crisp & Carling 1989). Each nest contains a portion of the female's eggs fertilized by one or more males. Construction of the nest, including its structure and gravel composition, will determine embryo survival during incubation (reviewed by Chapman 1988). Thus, female reproductive success is largely determined by territory access, nest quality, egg fertilization and nest survival.

Males do not partake in nest construction, but compete for access to ovipositing females. The complex of female and male courting- and spawning-behaviour is important for successful oviposition and fertilization (Jones 1959). While females are sexually active for only a few days, males may be active for a month or more (Webb & Hawkins 1989). This can result in extreme male biased operational sex ratios (i.e. number of sexually active males relative to sexually active females). Thus, there may be intense male competition, with competitive ability determining male breeding success.

Successful spawning by farmed Atlantic salmon has been documented (Lura & Sægrov 1991; Webb *et al.* 1991, 1993a,b) and evidence of genetic intermixing with wild populations found (Crozier 1993). Evidence suggests, however, that artificial culture impairs natural reproductive success in salmonids reared for searanching purposes (artificially reared in fresh water and free-ranged in the ocean; Jonsson, Jonsson & Hansen 1990; Leider *et al.* 1990; Fleming & Gross 1993). It is thus likely that escaped farmed salmon, which spend a greater proportion of their life in culture, would therefore incur further reduced reproductive success.

Thus, the purpose of our study was to contrast the breeding behaviour of farmed and wild salmon, and determine how farmed salmon interact reproductively with wild salmon. To do this, we quantified the reproductive ability of adult farmed Atlantic salmon in the presence and absence of competition with wild salmon; and also examined the effects of competition with farmed salmon on reproductive behaviour and success of wild salmon.

Materials and methods

STUDY SITE AND EXPERIMENTAL DESIGN

Experiments were conducted in 1990 at the Norsk Institutt for Naturforskning (NINA) Research Station in south-western Norway (58°59′N, 5°58′E). Four outdoor arenas provided circular stream environments that simulate natural breeding conditions (Fig. 1). Each stream had gravel substrate suitable for embryo incubation (mean fredle index of 11·25 ± 3·84 SD; Lotspeich & Everest 1981). Water velocities ranged between 4 and 32 cm s^{-1} (measured 15 cm above the gravel substrate, every meter throughout each stream), encompassing velocities spawning salmon occupy in nature (Heggberget *et al.* 1988). Two floodlights, which could be adjusted by dimmer switches, were directed at each arena to provide dim light for night-time observation ($\bar{x} = 11{\cdot}9 \pm 3{\cdot}6$ lx at water surface; mid-day, December light range: 1500 lx [overcast] to 14 000 lx [direct sun]). A 1 × 1 m grid of strings suspended over the arenas allowed observers to record fish positions and nest locations. Arenas were similar, with no two differing significantly in physical parameters (Scheffé multiple range tests: $P > 0{\cdot}05$).

One experiment examined competition between farmed and wild Atlantic salmon. Arenas 2 and 3 each contained six female and six male farmed, and wild fish (Fig. 1). In a second experiment attempts were made to gather information that could be used to separate effects of intergroup (farmed vs. wild) competition from behavioural differences within groups. Twelve female and 12 male wild fish were placed in Arena 1, and 12 female and 12 male farmed fish in Arena 4.

FISH GROUPS

The farmed Atlantic salmon were fifth-generation fish from the breeding programme at Sunndalsøra, Norway. 'Sunndalsøra strain' salmon are widely cultured both in Norway, where they represent over 80% of farmed salmon in the Norwegian fish farming industry, and in Great Britain. Salmon of the 1987 brood, originally derived from collections of salmon from 18 localities in 1971 (Gjedrem *et al.* 1991), were reared in sea cages at the Riska Fisk farm (59°02′N, 5°49′E) and in August 1990 transported to the NINA Research Station, where they were maintained in a 72 m^2 freshwater pool until the start of experiments (described in Fleming *et al.* 1994).

The wild salmon were collected in a fish trap 100 m above the outlet of the River Imsa during their spawning ascent in the period July–October 1990. The trap was checked daily and fish were transported to the Research Station where they were maintained in a 72 m^2 freshwater pool until the start of experiments.

On 11 November 1990 all experimental fish were lightly anaesthetized with MS-222, length measured (total, fork and postorbital–hypural), weighed and tagged with uniquely marked 3·4 cm diameter disc tags. The farmed females were heavier, but not significantly longer than the wild females (Table 1). The farmed females were also less variable in body size (weight: farmed CV = 19·1%, wild CV = 58·4%; length: farmed CV = 8·5%, wild CV = 16·7%). The farmed males were much heavier and longer than wild

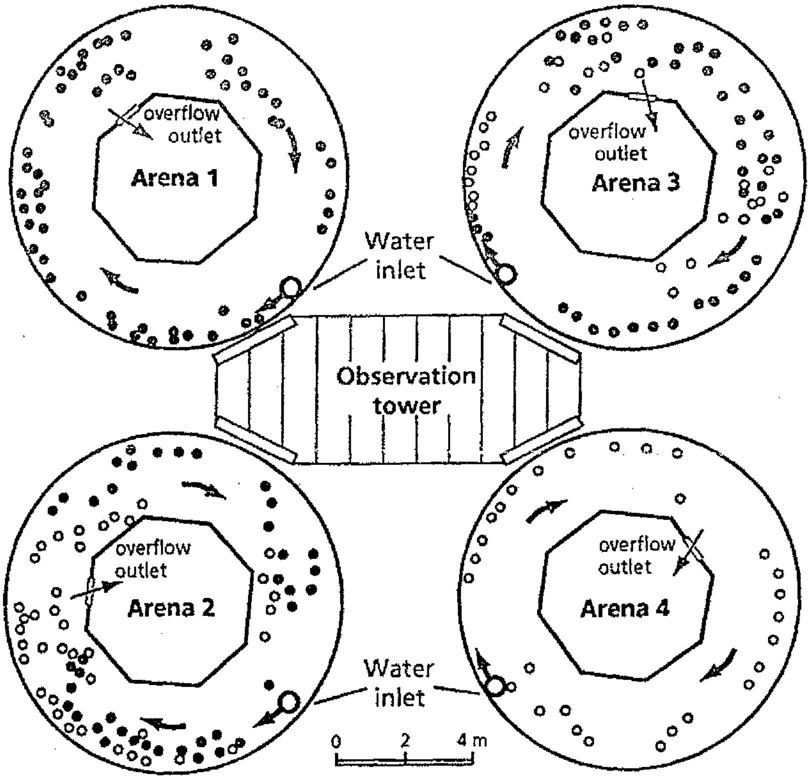


Fig. 1. Experimental arenas used to simulate natural breeding streams. Each circular stream averaged 2·2 m in width, was 21 m in length (measured as circumference at mid stream) and provided 47 m² of spawnable area filled with a 36 cm deep, heterogeneous mixture of gravel. Constantly flowing water from Lake Liavatn at the headwaters of the River Imsa was supplied to each arena and water depth was maintained at 40 cm (arrows indicate direction of water flow). Arenas were observed from a tower, ≈ 3 m above ground. Nests made by farmed (○) and wild females (●) are shown.

Table 1. Mean body weight (total, g) and length (postorbital–hypural, mm), with standard deviation in parentheses, of farmed and wild Atlantic salmon used in the experiments. Statistics are analyses of variance of female and male body size among the four arenas and *t*-tests of differences between populations

								Effect			
								Arena		Population	
Sex	Character	Population	Arena 1	Arena 2	Arena 3	Arena 4	Total	$F_{2,21}$	P	t_{46}	P
Female	Weight	Farmed	– –	3767 (414)	3535 (781)	3742 (818)	3696 (706)	0·20	0·823	2·27	0·030
		Wild	2819 (1902)	2722 (1655)	3063 (1426)	– –	2856 (1669)	0·06	0·939		
	Length	Farmed	– –	559 (18)	563 (38)	547 (61)	554 (47)	0·26	0·776	1·31	0·199
		Wild	526 (96)	519 (93)	536 (83)	– –	527 (88)	0·05	0·951		
Male	Weight	Farmed –	–	4036 (436)	4329 (575)	3835 (995)	4008 (793)	0·77	0·478	11·12	<0·001
		Wild	2000 (429)	2019 (646)	1662 (269)	– –	1920 (466)	1·26	0·305		
	Length	Farmed	– –	579 (21)	587 (26)	567 (50)	575 (39)	0·54	0·592	9·76	<0·001
		Wild	485 (25)	482 (39)	458 (23)	– –	477 (30)	1·87	0·179		

males, but the degree of body size variation was similar (weight: farmed CV = 19·8%, wild CV = 24·2%; length: farmed CV = 6·8%, wild CV = 6·3%). Male and female fish from each source were sorted by body size and distributed such that there were no significant differences among arenas (Table 1).

BEHAVIOURAL OBSERVATIONS

Arenas were monitored continuously, 24 h day^{-1}, beginning the morning of 12 November 1990. Activity within each arena was recorded for 30 min, four to seven times each 24-h period with at least 3 h between successive samples. Fish were identified individually by their tags and all instances of aggressive, submissive, breeding and cruising behaviour were recorded. *Aggressive behaviour* included *chasing* (attack of another fish without reciprocation), *fighting* (reciprocal attacks between two fish) and *agonistic display* (aggressive posturing towards another fish). Three forms of agonistic display were recognized: (i) *lateral display*, which involved presentation of the lateral side, with dorsal and anal fins extended, to an opponent; (ii) *parallel swimming*, where two fish swam side by side for several metres, often with dorsal fins erect; and (iii) *head-down display*, in which the tail was raised, often breaking the water surface, and the head was lowered towards the gravel. *Submissive behaviour* was defined as fleeing from an aggressive opponent. Male breeding behaviour included *courting* (attending a nesting female) and *quivering* (vibrating the body next to a female), while female breeding behaviour included *digging* (a series of body flexures while turned to one side; usually associated with nest construction) and being *courted* (attended by a courting male). The final category of behaviour was *cruising* which was defined as swimming over a large area without chasing or being pursued.

Onset of female breeding was measured as the time from introduction into the arena until the female's first oviposition event, and *duration* as the time from the female's first to last oviposition event. Male *onset* of breeding was measured as the time from introduction into the arena until his first observed courting, and *duration* as time from first to last observed courting.

The frequency with which each individual performed a given behaviour was calculated as the sum of the average number of behavioural acts per 30 min each day divided by the number of days of observation. Observations of general activity were discontinued on 20, 8, 12 and 8 December for fish in Arenas 1, 2, 3 and 4, respectively. These dates coincided with cessation of spawning activity, with the exception of Arena 1 in which one female did not complete spawning until 4 January.

Spawning activity was monitored continuously, 24 h day^{-1}, and focal data on the activity of nesting females and all courting males in spawning aggregations were collected with the aid of video cameras. A theodolite was used to map the location of nests. Focal observations continued until all spawning activity had ceased on 4 January.

CONDITION AT DEATH

Moribund fish were removed from the arenas and inspected for wounds and fungal infection. Wounds and fungus were scored on a scale from 0 to 3 based on increasing body coverage (0 = none; 1 = small, localized [< 10%]; 2 = moderate; 3 = extensive [> 40%]). Gonads were removed and the fish weighed. Total weights of eggs remaining in females were recorded to assess the extent of breeding failure. The heart was removed, frozen and later dried in a desiccating oven at 60°C for 48 h before weighing. Dry heart mass relative to somatic mass was used as a measure of physical condition (Farrell *et al.* 1988; Houlihan *et al.* 1988; Järvi 1990). All adults that survived the breeding season were sacrificed on 13 February 1991 and the above measures recorded. Most spent adults in the wild would have been expected to have left the river and returned to the sea by mid-February (Jonsson *et al.* 1991).

REPRODUCTIVE SUCCESS

Eggs were retrieved from all nests that survived the spawning period (i.e. were not destroyed by females digging subsequent nests). A minimum of 170 degree days since oviposition (days × temperature above 0°C) were used to assess when eggs in each nest could be handled (i.e. 'eyed'; Leitritz 1959), and nests were excavated between 21 February and 6 March 1991. After draining the arenas, the depth of each nest from the gravel surface to the centre of the egg pocket was measured. Then an open-ended rectangular steel box was inserted into the gravel, the egg pocket removed and the eggs separated from the gravel by flushing with water. Both live and dead eggs were counted, and a sample of each was preserved separately in 4% buffered formalin. Three months after preservation, wet weights of 10 live and 10 dead eggs from each sample were measured individually to assess egg size. The gravel surrounding the egg pocket was analysed following Lotspeich & Everest (1981).

Spawning records, which assigned females to nests, were cross-checked using the egg size data. Egg size is a reliable means of confirming maternity because intra-individual variation in egg size is small relative to that among females (coefficient of variation (CV) among females = 11·0%, within female mean CV = 3·4 ± 1·2% SD, $n = 41$ females: I.A. Fleming, unpublished data).

For each female, absolute reproductive success was accurately measured as the total number of live embryos and spawning success was defined as absolute success divided by fecundity. Initial fecundity was estimated for each female from regressions of unspawned females (Imsa wild: fecundity = 3·41 × [total weight]$^{0.896}$; $R^2 = 0{\cdot}79$, $n = 12$, $P < 0{\cdot}001$; Sunndalsøra farmed: fecundity = 0·12 × [total weight]$^{1.341}$; $R^2 = 0{\cdot}98$, $n = 5$, $P < 0{\cdot}001$; B. Jonsson & I.A. Fleming, unpublished data).

The reproductive success of each male was calculated from an estimate of his proportional paternity times the number of live embryos in each nest he spawned at or was suspected to have spawned at. In the latter case, the spawning was missed but the spawning aggregation immediately prior to the spawning had been observed. Sixty-two percentage of all spawnings were observed directly (109 of the 175 nests recovered with live embryos). Male reproductive success was thus analysed both including and excluding indirect observations (38%; see Results). If more than one male partook (13%, 14 of 109 direct observations), or was suspected to have possibly partaken in a spawning (74%, 49 of 66 indirect observations), a male's paternity was estimated from his rank order of nest entry at spawning, or of dominance in the spawning aggregation, respectively. Each successive male entering, or ranked in the dominance hierarchy, was assumed to obtain 50% the success of the male ahead of him. This allocation was made on the basis of results obtained in studies of chum salmon (*Oncorhynchus keta* W.; Schroder 1982), the only salmon species for which such data appear to be available. The overall results were not sensitive to this assumption, because an alternative assumption of equal paternity produced similar estimates of overall male reproductive success, the two estimates being highly correlated ($R^2 = 0{\cdot}998$, $n = 48$, slope $\beta = 0{\cdot}971 \pm 0{\cdot}006$ SE).

STATISTICAL ANALYSES

Heart and body mass, all frequency data, and all measures of male reproductive success were logarithmic transformed to meet the assumptions of analysis of variance. Similarly, all percentage data were arcsine, square-root transformed. Data that did not meet requirements for parametric analysis were analysed by nonparametric Mann–Whitney *U*-tests or Chi-square tests. Individual fish were considered replicates within arenas. Arena effects were examined by comparing replicate arenas 2 and 3. Adjustment for multiple comparisons was carried out using sequential Bonferroni tests (Rice 1989).

Results

BEHAVIOUR

When held in mixed groups, wild and farmed females did not differ in either aggressive or submissive behaviour (Fig. 2). Possible differences in the aggressive behaviours combat (i.e. chasing and fighting; ANOVA $P = 0{\cdot}933$) and display ($P = 0{\cdot}339$) were also examined, but none were found. Aggression was directed equally at farmed and wild female opponents (paired *t*-test, farmed: $t_{11} = 1{\cdot}01$, $P = 0{\cdot}334$; wild: $t_{11} = 1{\cdot}34$, $P = 0{\cdot}208$). Female aggression towards males, however, was directed more often at wild than farmed individuals (farmed females: $t_{11} = 4{\cdot}31$, $P = 0{\cdot}001$; wild females: $t_{11} = 5{\cdot}09$, $P < 0{\cdot}001$), reflecting the higher frequency of courting by wild than farmed males. Farmed females were less active than wild females in cruising and digging, and were courted less often, presumably reflecting their lower levels of digging and associated nesting activity (Fig. 2). Only the frequency of female submissive behaviour differed

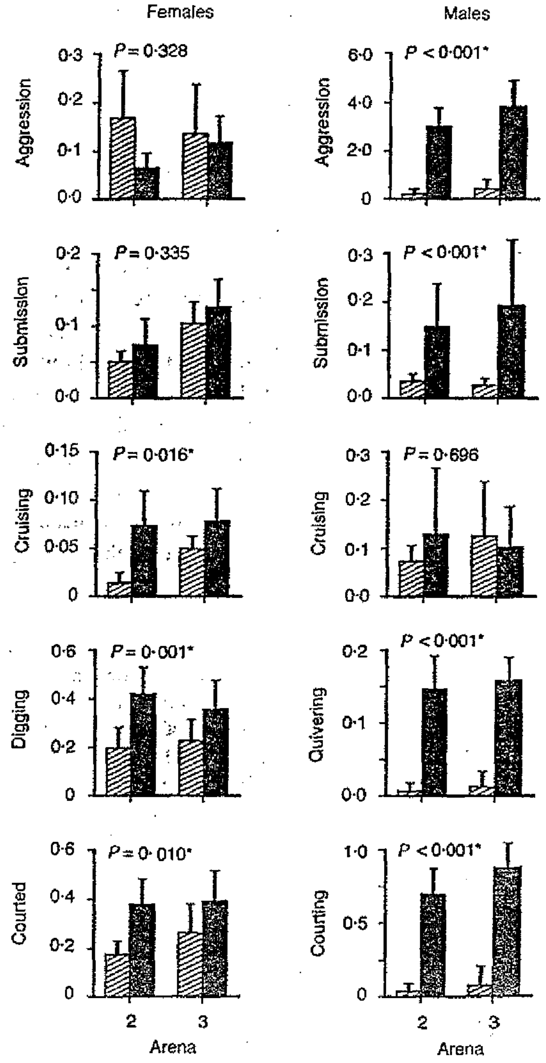


Fig. 2. Frequency of female and male behaviours in farmed and wild salmon in Arenas 2 and 3. Data are means and standard deviations across arenas adjusted for the covariate body size where significant. Probability values are from analyses of variance or covariance testing for behavioural differences between farmed and wild fish. Significant differences adjusted for multiple comparison by sequential Bonferroni tests are indicated (*). Hatched bars = farmed; solid bars = wild.

between Arenas 2 and 3 ($P = 0·008$) and there were no significant fish type-by-arena interactions ($P > 0·05$).

In contrast to farmed females, farmed males were less aggressive, exhibiting less combat ($P < 0·001$) and display behaviour ($P = 0·004$) than wild males (Fig. 2). Male aggression was directed more often at wild than farmed males (paired *t*-test, farmed: $t_{11} = 2·49$, $P = 0·030$; wild: $t_{11} = 5·69$, $P < 0·001$) and wild males exhibited more submissive behaviour. Farmed males exhibited no significant directionality in their aggression towards females ($t_{11} = 1·37$, $P = 0·199$), whereas wild males were more aggressive to wild than farmed females ($t_{11} = 3·81$, $P = 0·003$). There was no difference between wild and farmed males in cruising behaviour, which tends to be associated with searching for mates. Farmed males, however, had difficulty acquiring access to mates, showing less quivering and courting behaviour than wild males (Fig. 2). There were no significant arena effects or fish type-by-arena interactions ($P > 0·05$).

There were only minor differences in behaviours displayed by wild females in mixed groups compared to those together only with other wild fish (Table 2). Similarly, wild males did not alter their aggressive and submissive behaviours in the presence of farmed males, but did increase cruising, courting and quivering behaviour when held in mixed groups, apparently reflecting their superior competitive ability.

Farmed females exhibited a tendency towards reduced aggressiveness, particularly combat behaviour ($P = 0·008$), displayed less digging behaviour, were courted less often and cruised more frequently when wild salmon were absent (Table 2). This may be a reflection of the reduced breeding behaviour displayed by farmed relative to wild males. Behaviour of farmed males in the absence of wild fish differed little from that in their presence (Table 2), though there was a non-significant tendency for farmed males to be more submissive and court less in the presence of wild males.

HEART MASS, WOUNDING AND MORTALITY

Heart mass relative to somatic mass was smaller for farmed than for wild females (ANCOVA $F_{1,42} = 18·68$, $P < 0·001$; allometric coefficient $\beta = 0·42$, $P < 0·001$), but did not differ significantly between farmed and wild males (ANCOVA $F_{1,41} = 2·03$, $P = 0·162$; allometric coefficient $\beta = 0·37$, $P < 0·001$).

In mixed groups, farmed and wild females incurred similar degrees of wounding (Mann–Whitney $U = 84·0$, $P = 0·148$), but farmed females suffered higher mortality (farmed: 42% died before 13 February 1991; wild: 0%; $\chi^2 = 6·32$, d.f. = 1, $P = 0·012$). Body condition of farmed males appeared to deteriorate rapidly as they incurred more wounding (Mann–Whitney $U = 128·0$, $P < 0·001$) and suffered higher mortality than wild males (farmed: 100%; wild: 42%; $\chi^2 = 9·88$, d.f. = 1, $P = 0·002$).

Wounding rates of wild salmon were unaffected by the presence of farmed salmon (females: Mann–Whitney $U = 72·0$, $P = 1·0$; males: $U = 83·5$, $P = 0·381$), as was mortality (females: 0% irrespective of treatment; males: $\chi^2 = 0·75$, d.f. = 1, $P = 0·609$). Similarly, the deterioration of body condition in farmed salmon, particularly males, was unaffected by the presence of wild salmon, as neither wounding (females: Mann–Whitney $U = 78·0$, $P = 0·623$; males: $U = 79·0$, $P = 0·569$) nor mortality (females:

Table 2. Comparison of behaviours of wild and farmed salmon when held as separate groups (Arenas 1 and 4, respectively) with that when they were held in mixed groups (Arenas 2 and 3). *F* statistics and probability values (*P*) are from analyses of variance or covariance (> indicates variable greater in separate than in mixed groups; < indicates the vice versa; = indicates no significant effect at $P < 0·05$; and [*] indicates significant difference adjusted for multiple comparison by sequential Bonferroni tests)

			Wild fish				Farmed fish		
			Separate vs. mixed		Covariate body weight		Separate vs. mixed		Covariate body weight
Variable	Sex		*F*	*P*	*P*		*F*	*P*	*P*
Aggression	F	=	1·39	0·251[a]	<0·001*	≤	5·09	0·035	0·003*
	M	=	4·21	0·050	0·007*	=	1·31	0·265	–
Submission	F	≤	5·30	0·031	–	=	1·60	0·220[a]	–
	M	=	0·71	0·409	0·003*	≤	5·30	0·032	0·084
Cruising	F	=	0·07	0·790	<0·001*	≤	4·93	0·037	–
	M	<	9·68	0·005*	0·017	=	1·46	0·241	–
Digging	F	=	4·04	0·054	<0·001*	<	20·97	<0·001*	0·001*
Courted	F	=	0·77	0·390	<0·001*	<	14·42	0·001*	0·061
Courting	M	=	4·41	0·045	0·061	≤	7·55	0·012	<0·001*
Quivering	M	<	7·42	0·012*	0·031	=	2·24	0·149	–

[a] Arenas 2 and 3 differed significantly ($P < 0·05$).

tably, the information on densities and maximum longevity is limited on its own without knowledge of the above-ground vegetation and management of a site: maximum longevity, of course, also tells us nothing about the fate of the majority of seeds. The authors recognize these and other topics as challenges for future research.

In this electronic era, I was surprised that a book, with an accompanying diskette, was considered to be the most effective way of disseminating a database of this sort. Clearly Cambridge University Press does not consider that we are yet at the stage where such information is made available via the Web, at an appropriate charge of course.

A.R. WATKINSON

Erratum

Fleming, I.A., Jonsson, B., Gross, M.R. & Lamberg, A. (1996) An experimental study of the reproductive behaviour and success of farmed and wild Atlantic salmon. *Journal of Applied Ecology*, **33**, 893–905.

Please replace Fig. 3 on p. 899 with the following figure. The typesetters apologise for the errors in the version first published.

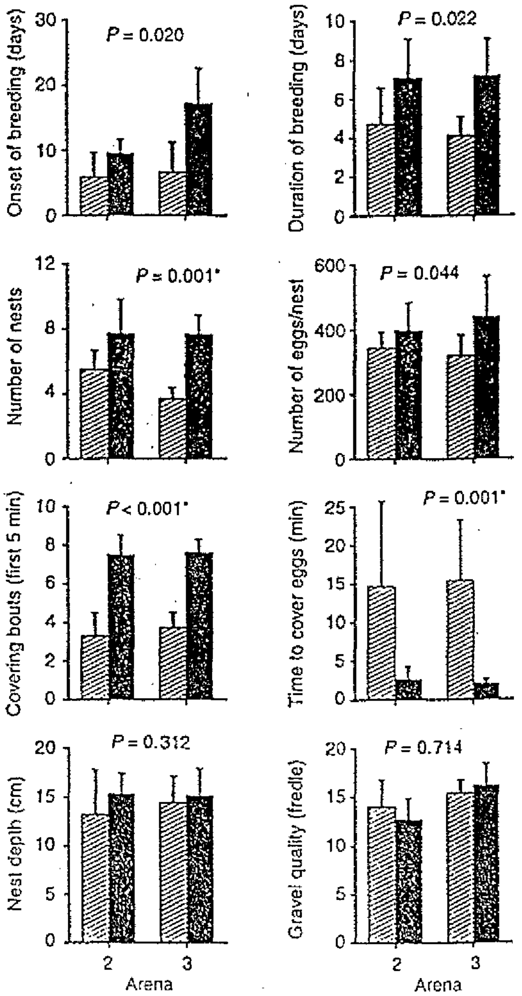


Fig. 3. Nesting characteristics of farmed and wild female salmon in Arenas 2 and 3. Data are means and standard deviations across arenas adjusted for the covariate body size where significant. Probability values are derived from analyses of variance or covariance. Significant differences adjusted for multiple comparisons by sequential Bonferroni tests are indicated (*) Hatched bars = farmed; solid bars = wild.

$\chi^2 = 0{\cdot}75$, d.f. = 1, $P = 0{\cdot}061$; males: $\chi^2 = 0{\cdot}0$, d.f. = 1, $P = 1{\cdot}0$) differed between treatments.

FEMALE NESTING AND REPRODUCTIVE SUCCESS

In mixed groups there was a non-significant tendency for farmed females to begin breeding slightly earlier than wild females (Fig. 3). Farmed females made fewer nests and there was a non-significant trend for farmed females to breed for a slightly shorter period than wild females. The majority of females made all their nests within a single redd, and this did not differ between farmed (58%) and wild females (67%) ($\chi^2 = 0{\cdot}18$, d.f. = 1, $P = 0{\cdot}675$). Although farmed females constructed fewer nests than wild females, the total number of eggs recovered per nest did not differ significantly (Fig. 3). Farmed females seemed to be poorer at nest covering, as they dug less frequently during the first 5 min following oviposition and took longer to cover their eggs. There were, however, no significant differences in the depth of nests or nest gravel quality.

Farmed females retained significantly greater weight of unspawned eggs than wild females (Fig. 4). Nest destruction, resulting from reuse of the nest site by other females, also occurred more often to farmed than wild females (farmed: 11%; wild: 1%; $\chi^2 = 8{\cdot}95$, d.f. = 1, $P = 0{\cdot}003$). Survival of eggs in nests, which included the effects of poor fertilization and mortality, was significantly lower for farmed than wild females. As a consequence of greater egg retention and poorer survival of deposited eggs, the farmed females were less than one-third as successful as wild females at having their eggs survive through incubation (Fig. 4). This resulted in a considerably lower reproductive success for farmed females (ANCOVA $F_{1,19} = 50{\cdot}72$, $P < 0{\cdot}001$; Fig. 5). There were no significant differ-

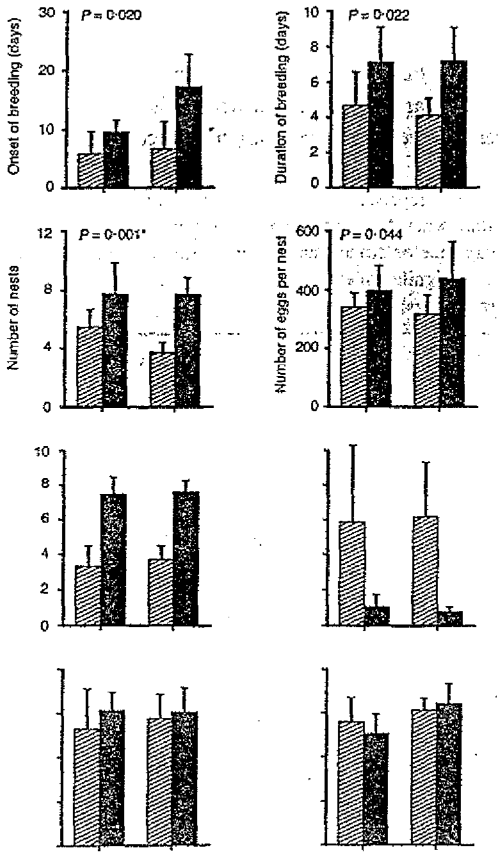


Fig. 3. Nesting characteristics of farmed and wild female salmon in Arenas 2 and 3. Data are means and standard deviations across arenas adjusted for the covariate body size where significant. Probability values are derived from analyses of variance or covariance. Significant differences adjusted for multiple comparison by sequential Bonferroni tests are indicated (*). Hatched bars = farmed; solid bars = wild.

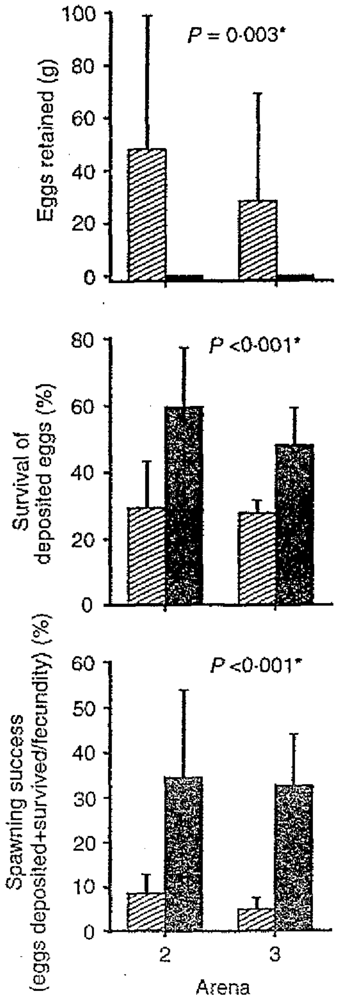


Fig. 4. Breeding success of farmed and wild female salmon in Arenas 2 and 3. Data are means and standard deviations across experiments. Probability values are derived from a Mann–Whitney *U*-test for analysis of eggs retained ($U = 114$, $N = 24$) and from analyses of variance for the other variables. Significant differences adjusted for multiple comparison by sequential Bonferroni tests are indicated (*). Hatched bars = farmed; solid bars = wild.

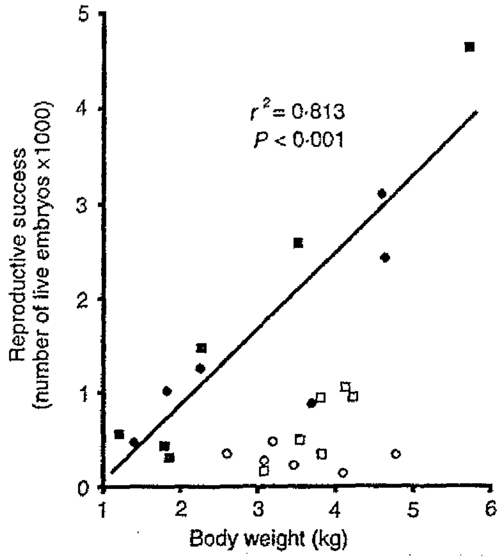


Fig. 5. Reproductive success of farmed (Arena 2 = □, Arena 3 = ○) and wild female salmon (Arena 2 = ■, Arena 3 = ●) in competition. Solid line is the relationship of reproductive success vs. body size for wild females ($y = 0{\cdot}811$*[weight, g] − 743). The relationship was non-significant for farmed females ($R^2 = 0{\cdot}123$, $P = 0{\cdot}262$).

ences between Arenas 2 and 3, and no significant fish type-by-arena interactions ($P > 0{\cdot}05$).

There was little difference in nesting behaviour of wild females irrespective of whether or not farmed salmon were present (Table 3). There were, however, some differences in nest characteristics, as nests were found at greater depths and there was a non-significant trend for females to construct fewer nests when farmed salmon were absent. Egg retention and egg survival in nests were unaffected by the presence of farmed salmon (Table 3). Nest destruction, however, increased when farmed females were absent (i.e. when they were replaced by an equal number of wild females; $\chi^2 = 18{\cdot}89$, d.f. = 1, $P < 0{\cdot}001$) and thus wild females were less reproductively successful (Table 3).

Farmed females showed a non-significant tendency to delay breeding in the absence of wild salmon (Table 3). Duration of breeding, and nest depth and gravel characteristics of farmed females were not influenced by the presence of wild fish. Farmed females made fewer nests in the absence of wild salmon, but more eggs were deposited in each nest (Table 3). Reproductive success of farmed females was dramatically reduced in the absence of wild fish. Egg retention increased and fewer of the eggs spawned survived. In the absence of wild males, only 10% of the nests constructed by farmed females contained eggs with live embryos, while 98% of nests contained live embryos when wild males were present ($\chi^2 = 74{\cdot}93$, d.f. = 1, $P < 0{\cdot}001$). This indicates that many of the ovipositions made by farmed females remained unfertilized when wild males were absent. As a result, the reproductive success of farmed females in the absence

Table 3. Comparison of nesting characteristics and reproductive success of wild and farmed females when held as separate groups (Arenas 1 and 4, respectively) with that when they were held in mixed groups (Arenas 2 and 3). *F* statistics and probability values (*P*) are from analyses of variance or covariance (> indicates variable greater in separate than in mixed groups; < indicates the vice versa; = indicates no significant effect at $P < 0{\cdot}05$; and [*] indicates significant difference adjusted for multiple comparison by sequential Bonferroni tests)

		Wild females				Farmed females		
		Separate vs. mixed		Covariate body weight		Separate vs. mixed		Covariate body weight
Variable		*F*	*P*	*P*		*F*	*P*	*P*
Nesting characteristics								
Onset of breeding	=	0·48	0·495	<0·001*	⩾	6·96	0·017	<0·003*
Duration of breeding	=	0·02	0·874	<0·001*	=	0·83	0·373	–
Number of nests	⩽	7·89	0·011	<0·001*	<	17·01	<0·001*	0·010
Eggs per nest[a]	=	0·05	0·823	<0·001	>	11·51	0·003*	<0·001*
Covering bouts[b]	=	1·47	0·243	–		–	–	–
Time to cover eggs[b]	=	0·04	0·831	–		–	–	–
Nest depth[a]	>	13·64	0·001*	0·027	=	0·33	0·572	–
Gravel quality[a]	=	0·05	0·822[c]	–	=	0·35	0·562	–
Reproductive success								
Eggs retained	=	0·01	0·981	–	>	19·41	<0·001*	–
Survival of deposited eggs[a]	=	1·53	0·230	–	<	92·51	<0·001*	–
Spawning success (eggs deposited + survived/fecundity)	<	15·20	0·001*	0·001*	<	64·15	<0·001*	–
Reproductive success	⩽	7·71	0·011	<0·001*	<	63·48	<0·001*	–

[a] No nests recovered for one wild female in Arena 1 and three farmed females in Arena 4.

[b] No nesting covering data for four wild females in Arena 1 and one wild female in each of Arenas 2 and 3. Nest covering was not analysed for farmed females because insufficient data existed from Arena 4.

[c] Arenas 2 and 3 differed significantly ($P < 0{\cdot}05$) for wild females.

of wild fish was less than one-tenth of what it was in the presence of wild fish.

MALE BREEDING AND REPRODUCTIVE SUCCESS

When held together, farmed and wild males began breeding at about the same time, but the farmed males had a short breeding duration (Fig. 6). This was a consequence of the high mortality of farmed males during the breeding season. Farmed males took part in few spawnings and had lower reproductive success than wild males (ANCOVA, direct + indirect spawning observations: $F_{1,19} = 8{\cdot}67$, $P = 0{\cdot}008$; Fig. 7; ANCOVA, direct observations only: $F_{1,19} = 41{\cdot}52$, $P < 0{\cdot}001$). There were no significant differences between Arenas 2 and 3, and no significant fish type-by-arena interactions ($P > 0{\cdot}05$).

Neither the onset nor the duration of spawning activity by wild males was influenced by farmed salmon (Table 4). Wild males did, however, obtain greater numbers of spawnings and had higher reproductive success with farmed fish present, than when held in groups comprised solely of wild fish.

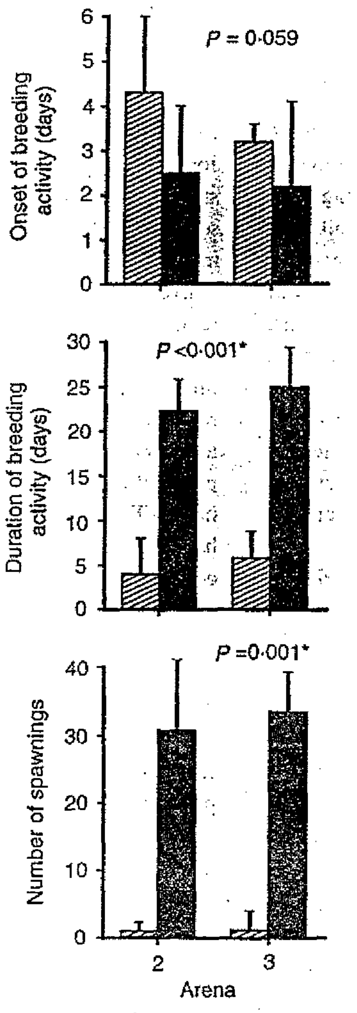


Fig. 6. Breeding activity of farmed and wild male salmon in Arenas 2 and 3. Data are means and standard deviations across experiments adjusted for the covariate body size where significant. Probability values are derived from analyses of variance and covariance. Significant differences adjusted for multiple comparison by sequential Bonferroni tests are indicated (*). Hatched bars = farmed; solid bars = wild.

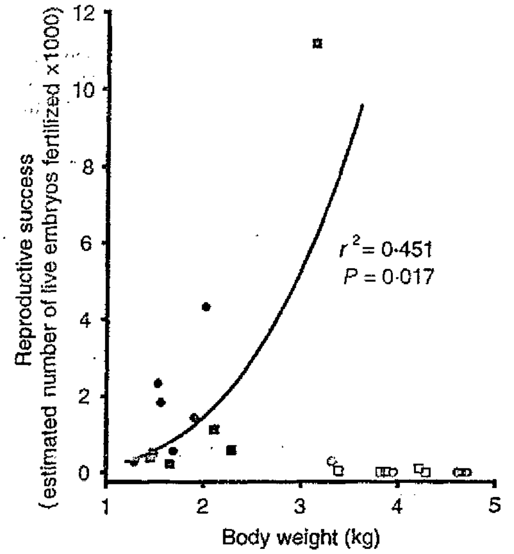


Fig. 7. Reproductive success of farmed (Arena 2 = □, Arena 3 = ○) and wild male salmon (Arena 2 = ■, Arena 3 = ●) in competition. Solid line is the relationship between reproductive success and body size for wild males ($y = 4{\cdot}96 \times [\text{weight}]^{3{\cdot}173}$), which is also significant by Spearman rank correlation ($R_s = 0{\cdot}615$, $P = 0{\cdot}033$). The relationship was non-significant for farmed males ($R^2 = 0{\cdot}180$, $P = 0{\cdot}170$).

Farmed males were not influenced by wild males in their breeding and reproductive success (Table 4). Even in the absence of wild males, farmed males displayed inappropriate reproductive behaviours and only in two of six spawnings did the courting farmed male(s) enter the nest and release sperm when the female oviposited.

Discussion

Farmed fish were competitively and reproductively inferior to wild fish (Figs 2–7). Body size was a key determinant of reproductive success in wild, but not farmed salmon (Figs 5 and 7). The farmed fish, males and females combined, achieved only 11–19% the reproductive success of the wild fish when in competition. Intergroup competition, however, did not reduce the reproductive ability or success of either the farmed or wild salmon (Tables 2–4).

COMPETITIVE AND BREEDING BEHAVIOUR

While there were no evident differences in expression of aggressive behaviour of farmed and wild female Atlantic salmon, farmed males were distinctly less aggressive than wild males. Reduced aggressiveness of cultured relative to wild adult males has also been observed in sea-ranched coho salmon (Fleming & Gross 1992, 1993). This response to domestication

Table 4. Comparison of breeding of wild and farmed males when held as separate groups (Arenas 1 and 4, respectively) with that when they were held in mixed groups (Arenas 2 and 3). F statistics and probability values (P) are from analyses of variance or covariance (> indicates variable is greater in separate than in mixed groups; < indicates the vice versa; = indicates no significant effect at $P < 0{\cdot}05$; and [*] indicates significant difference adjusted for multiple comparison by sequential Bonferroni tests)

		Wild males				Farmed males		
		Separate vs. mixed		Covariate body weight		Separate vs. mixed		Covariate body weight
Variable		F	P	P		F	P	P
Onset of breeding activity[a]	=	3·16	0·090	–	=	0·73	0·405	–
Duration of breeding activity	=	4·07	0·056	–	=	0·85	0·366	–
Number of spawnings	<	8·53	0·008*	0·038	=	0·97	0·336	–
Estimated reproductive success								
Direct spawning observations	<	7·48	0·012*	0·225	=	1·00	0·328	–
Direct + indirect observations	<	8·78	0·007*	0·148	=	0·10	0·754	–

[a] Two farmed males in Arena 2 and one in Arena 3 were never observed expressing breeding behaviour.

may involve both genetic and environmentally induced changes as a consequence of culture. Some species have been shown to rapidly adapt genetically to captivity (Frankham & Loebel 1992) and behavioural traits may be among the first traits to respond (Kohane & Parsons 1988). In salmon culture, where matings are determined artificially, adult aggression would afford no apparent reproductive advantage and directed selection for rapid growth may result in a correlated response for reduced aggressiveness (reviewed in Ruzzante 1994). Thus, a combination of artificial and domestication selection may, in part, contribute to differences in aggressiveness between farmed and wild males.

Reduced aggressiveness is also likely to be environmentally induced and may reflect the rapid deterioration in body condition of the farmed fish, particularly the males, which incurred high mortality, wounding and fungus infection. Sexual maturation in combination with chronic stress typically associated with aquaculture adversely affect the condition of salmonids, particularly males, increasing susceptibility to disease and mortality (Pickering 1993). Observations of escaped farmed salmon having higher incidence of local scale loss than wild salmon in nature (Webb *et al.* 1991) further suggests that the detrimental effects of culture on body condition persist till spawning. Similar observations have been made of sea-ranched salmon, which incur more extensive wounding during the breeding season than wild salmon (Jonsson *et al.* 1990; Fleming & Gross 1993). The increased wounding of farmed males may also be due to their apparent inability, or unwillingness, to avoid physical contact when attacked. This cannot, however, be the full explanation as wounding in farmed males was unaffected by levels of aggression directed at them, which was higher in the presence than absence of wild salmon.

Differences in aggressiveness between farmed and wild males, but not females may reflect differences between the sexes in intensity of competition for breeding resources (cf. Fleming & Gross 1994; Quinn & Foote 1994). Male Atlantic salmon compete overtly for access to spawning females, while females appear to compete more subtly for breeding territories (also Jones 1959; Webb & Hawkins 1989). This pattern is similar to that observed in adult coho salmon, where sea-ranched and wild males, but not females, differed in aggressiveness (Fleming & Gross 1993).

Competitive differences between farmed and wild females were subtle. Reduced breeding behaviour, construction of fewer nests and retention of more eggs unspawned by farmed than wild females may have resulted from competitive inferiority. Altered behaviour patterns caused by domestication and poorer physical condition (relatively small hearts; also Graham & Farrell 1992) of farmed than wild females may have also contributed to the differences. Similarly, a combination of these factors and reduced caudal fin size, the primary fin used in nest construction, due to sea-pen culturing (Fleming *et al.*, in press) may explain the inefficient covering of nests by farmed relative to wild females. Inefficient nest covering probably resulted in greater egg loss, as fewer eggs of farmed females were recovered per nest even though they partitioned their initial fecundity among fewer nests than wild females. Similarly, inefficient nest covering may explain the observation of Lura, Barlaup & Sægrov (1993) that the nests of a farmed female in the River Vosso, Norway, were more variable in volume and contained fewer eggs than those of wild females.

REPRODUCTIVE SUCCESS

There were clear differences between farmed and wild females in reproductive success with farmed females having only between 20 and 40% the reproductive success of wild females. Several factors contributed to these differences. The retention of more eggs unspawned by farmed than wild females in the competitive environment is a pattern that has also been observed between sea-ranched and wild salmonids (Jonsson *et al.* 1990; Fleming & Gross 1993). Farmed females also incurred higher levels of nest destruction than wild females. Nest destruction through nest superimposition may be an important cause of female egg mortality in Atlantic salmon, even in seemingly low density populations (Webb & Hawkins 1989; Lura & Sægrov 1991). Reduced egg survival in nests of farmed relative to wild females might have been related to poorer nest covering and/or poorer egg quality (Srivastava & Brown 1991).

Farmed males, more so than farmed females, were reproductively inferior to wild fish. Lack of any apparent differences in reproductive success in the presence and absence of wild salmon suggests this was not due to competitive inferiority alone. Rather, inappropriate reproductive behaviour and poor condition are important explanations. Farmed males when courting females often failed to enter nests to fertilize the eggs during female oviposition. Inappropriate reproductive behaviour of farmed males may explain Lura & Sægrov's (1991) observation that eggs in several nests spawned by escaped farmed female Atlantic salmon were unfertilized. Farmed males in our experiments were estimated to have attained 1–3% of the reproductive success of wild males. Such loss of breeding fitness is known to occur in other species, even where strict breeding programmes to maintain genetic variability are implemented, due to rapid domestication (Loebel *et al.* 1992; see also Lyles & May 1987). The process of environmental and genetic adaptation, including behavioural and physiological responses to captivity, is likely accelerated in farmed salmon, where breeding is determined artificially.

It is possible that interpopulational differences unrelated to artificial culture may explain the present results; however, this seems unlikely given the magnitude of differences observed. Our experiments were designed to be representative of the intentional or unintentional presence of farmed salmon in Norwegian rivers and thus farmed salmon from the principal breeding programme of farmed salmon in Norway were used. Furthermore, these results agree with other evidence that suggests captive breeding and artificial culture reduce natural reproductive ability of fish (Jonsson *et al.* 1990; Leider *et al.* 1990; Fleming & Gross 1993) and other organisms (Cade 1988; Loebel *et al.* 1992).

IMPLICATIONS

Large numbers of farmed Atlantic salmon escape; minimum estimates suggest they compose 25–48% of salmon on the feeding grounds in the north-east Atlantic Ocean (Hansen, Jacobsen & Lund 1993). Some of these fish enter onto breeding grounds of wild populations where it is not uncommon for them to outnumber wild spawners by as much as 3:1 (Lund, Hansen & Økland 1994; Lura & Økland 1994). Our results suggest that farmed salmonids, artificially reared to maturity, will have an inferior reproductive ability relative to their wild counterparts. The extent of this inferiority is likely to be affected by the proportion of a fish's life, as well as the number of generations in culture (Fleming *et al.* 1994). For instance, the reproductive inferiority shown by sea-ranched salmonids relative to their wild counterparts (Leider *et al.* 1990; Fleming & Gross 1993; Jonsson & Fleming 1993) is less than that shown by farmed salmon in this study. The extent of residency in the natural environment following escape is thus likely to be an important determinant of reproductive ability once on the spawning grounds.

Even when reared to maturity, hybridization is likely to occur between escaped farmed females and wild males as found in the present study. This would result in sex-biased gene flow between cultured and wild fish (also Fleming & Gross 1993). Given the large numbers of farmed salmon escaping and entering spawning grounds of wild populations the potential for gene flow is great. Long-term effects of such gene flow are unclear, as little is known about success of offspring from such spawnings, although in most cases we would expect it to be lower than that of wild offspring due to lack of local adaptation. Evidence of lower fitness in cultured/foreign and hybrid offspring relative to that of native offspring supports this contention (e.g. Reisenbichler & McIntyre 1977; Lachance & Magnan 1990; Leider *et al.* 1990; Philipp 1991; Reisenbichler cited by Emlen 1991; Skaala 1992).

It might be speculated that the productivity of wild populations could be depressed by intrusions of cultured salmon that resulted in ecological interference, including mate and territorial competition. Our results suggest that the effects resulting from intrusions by cultured salmonids will be sex biased, being generated primarily by cultured females, and such effects would be very much dependent on timing of spawning. If farmed salmon spawn prior to, or at the same time as wild salmon, as occurs in parts of south-western Norway (also Lura & Sægrov 1993), ecological disruption to wild populations during breeding may be minimal. Later spawning by farmed females would, however, probably result in destruction of nests of wild females (Lura & Sægrov 1991; Webb *et al.* 1991). Thus, the spawning time of wild relative to farmed salmon would be an important determinant of susceptibility of wild populations to ecological interference.

Our results also have application to captive breeding programmes for conservation and reintroduction of species, e.g. Sacramento River winter-run chinook salmon *Oncorhynchus tshawytscha* (Hedrick & Hedgecock 1994). To increase the success of such programmes, detrimental effects of captive-rearing on an organism's phenotype and genotype, including its behavioural, morphological and physiological traits, must be minimized. This may be accomplished by keeping the number of generations a species needs to be in captivity low and exposing it to naturalistic experiences and selection during this time.

Acknowledgements

We thank A. Braa, L. Korsnes, J. H. Pettersen, I. Uglem and the staff of the NINA Research Station at Ims for their assistance with the experiments, and T. Forseth, K. Hindar and T. Järvi for their comments on the manuscript. Financial support was provided by grants from the Norwegian Fisheries Research Council to Jonsson and Fleming, and the National Science and Engineering Research Council of Canada to M.R. Gross.

References

Allendorf, F.W. (1983) Conservation biology of fishes. *Conservation Biology*, **2**, 145–148.

Cade, T.J. (1988) Using science and technology to re-establish species lost in nature. *Biodiversity* (ed. E. O. Wilson), pp. 279–288. National Academy Press, Washington.

Chapman, D.W. (1988) Critical review of variables used to define effects of fines in redds of large salmonids. *Transactions of the American Fisheries Society*, **117**, 1–21.

Crisp, D.T. & Carling, P.A. (1989) Observations on siting, dimensions and structure of salmonid redds. *Journal of Fish Biology*, **34**, 119–134.

Cross, T.F. & Challanain, D.N. (1991) Genetic characterisation of Atlantic salmon (*Salmo salar*) lines farmed in Ireland. *Aquaculture*, **98**, 209–216.

Crozier, W.W. (1993) Evidence of genetic interaction between escaped farmed salmon and wild Atlantic salmon (*Salmo salar* L.) in a Northern Irish river. *Aquaculture*, **113**, 19–29.

Emlen, J.M. (1991) Heterosis and outbreeding depression: a multi-locus model and an application to salmon production. *Fisheries Research*, **12**, 187–212.

Farrell, A.P., Hammons, A.M., Graham, M.S. & Tibbits, G.F. (1988) Cardiac growth in rainbow trout, *Salmo gairdneri*. *Canadian Journal of Zoology*, **66**, 2368–2373.

Fleming, I.A. & Gross, M.R. (1992) Reproductive behavior of hatchery and wild coho salmon (*Oncorhynchus kisutch*): does it differ? *Aquaculture*, **103**, 101–121.

Fleming, I.A. & Gross, M.R. (1993) Breeding success of hatchery and wild coho salmon (*Oncorhynchus kisutch*) in competition. *Ecological Applications*, **3**, 230–245.

Fleming, I.A. & Gross, M.R. (1994) Breeding competition in a Pacific salmon (coho: *Oncorhynchus kisutch*): measures of natural and sexual selection. *Evolution*, **48**, 637–657.

Fleming, I.A., Jonsson, B. & Gross, M.R. (1994) Phenotypic divergence of sea-ranched, farmed and wild salmon. *Canadian Journal of Fisheries and Aquatic Sciences*, **51**, 2808–2824.

Frankham, R. & Loebel, D.A. (1992) Modeling problems in conservation genetics using captive *Drosophila* populations: rapid genetic adaptation to captivity. *Zoo Biology*, **11**, 333–342.

Gausen, D. & Moen, V. (1991) Large-scale escapes of farmed Atlantic salmon (*Salmo salar*) into Norwegian rivers threaten natural populations. *Canadian Journal of Fisheries and Aquatic Sciences*, **48**, 426–428.

Gjedrem, T., Gjoen, H.M. & Gjerde, B. (1991) Genetic origin of Norwegian farmed Atlantic salmon. *Aquaculture*, **98**, 41–50.

Graham, M.S. & Farrell, A.P. (1992) Environmental influences on cardiovascular variables in rainbow trout. *Oncorhynchus mykiss* (Walbaum). *Journal of Fish Biology*, **41**, 851–858.

Hansen, L.P., Jacobsen, J.A. & Lund, R.A. (1993) High numbers of farmed Atlantic salmon, *Salmo salar*, L., observed in oceanic waters north of the Faroe Islands. *Aquaculture* and *Fisheries Management*, **24**, 777–781.

Hedrick, P.W. & Hedgecock, D. (1994) Effective population size in winter-run chinook salmon. *Conservation Biology*, **8**, 890–892.

Heggberget, T.G., Haukebø, T., Mork, J. & Ståhl, G. (1988) Temporal and spatial segregation of spawning in sympatric populations of Atlantic salmon, *Salmo salar*, L. & brown trout, *Salmo trutta* L. *Journal of Fish Biology*, **33**, 347–357.

Hindar, K., Ryman, N. & Utter, F. (1991) Genetic effects of cultured fish on natural fish populations. *Canadian Journal of Fisheries and Aquatic Sciences*, **48**, 945–957.

Houlihan, D.F., Agnisola, C., Lyndon, A.R., Gray, C. & Hamilton, N.M. (1988) Protein synthesis in a fish heart: responses to increased power output. *Journal of Experimental Biology*, **137**, 565–587.

Hutchings, J.A. (1991) The threat of extinction to native populations experiencing spawning intrusions by cultured Atlantic salmon. *Aquaculture*, **98**, 119–132.

Järvi, T. (1990) The effects of male dominance, secondary sexual characteristics and female mate choice on the mating success of male Atlantic salmon *Salmo salar*. *Ethology*, **84**, 123–132.

Jones, J.W. (1959) *The Salmon*. Collins, London.

Jonsson, B. & Fleming, I.A. (1993) Enhancement of wild salmon populations. *Human Impact on Self-Recruiting Populations* (ed. G. Sundnes), pp. 209–242. Tapir Press, Trondheim.

Jonsson, B., Jonsson, N. & Hansen, L.P. (1990) Does juvenile experience affect migration and spawning of adult Atlantic salmon? *Behavioural Ecology and Sociobiology*, **26**, 225–230.

Jonsson, B., Jonsson, N. & Hansen, L.P. (1991) Differences in life history and migratory behaviour between wild and hatchery-reared Atlantic salmon in nature. *Aquaculture*, **98**, 69–78.

Kohane, M.J. & Parsons, P.A. (1988) Domestication: evolutionary change under stress. *Evolutionary Biology*, **23**, 31–48.

Lachance, S. & Magnan, P. (1990) Performance of domestic, hybrid, and wild strains of brook trout, *Salvelinus fontinalis*, after stocking: the impact of intra- and interspecific competition. *Canadian Journal of Fisheries and Aquatic Sciences*, **47**, 2278–2284.

Ledig, F.T. (1992) Human impacts on genetic diversity in forest ecosystems. *Oikos*, **63**, 87–108.

Leider, S.A., Hulett, P.L., Loch, J.J. & Chilcote, M.W. (1990) Electrophoretic comparison of the reproductive success of naturally spawning transplanted and wild steelhead trout through the returning adult stage. *Aquaculture*, **88**, 239–252.

Leitritz, E. (1959) Trout and salmon culture. *California Department of Fish and Game, Fish Bulletin*, 107, 1–169.

Loebel, D.A., Nurthen, R.K., Frankham, R., Briscoe, D.A. & Craven, D. (1992) Modeling problems in conservation genetics using captive *Drosophila* populations: consequences of equalizing founder representation. *Zoo Biology*, **11**, 319–332.

Lotspeich, F.B. & Everest, F.H. (1981) A new method for reporting and interpreting textural composition of spawning gravel. *United States Department of Agriculture and Forestry Service Research Note PNW-369*. Pacific Nortwest Forest and Range Experimental Station, Corvallis, OR.

Lund, R.A., Hansen, L.P. & Økland, F. (1994) Escaped farmed salmon and geographical zones established for wild fish protection. *NINA Oppdragsmelding, Trondheim*, **303**, 15 pp. [In Norwegian with English Abstract.]

Lura, H., Barlaup, B.T. & Sægrov, H. (1993) Spawning behaviour of a farmed escaped female Atlantic salmon (*Salmo salar*). *Journal of Fish Biology*, **42**, 311–313.

Lura, H. & Økland, F. (1994) Content of synthetic astaxanthin in escaped farmed Atlantic salmon, *Salmo salar*, L., ascending Norwegian rivers. *Fisheries Management and Ecology*, 1, 205–216.

Lura, H. & Sægrov, H. (1991) Documentation of successful spawning of escaped farmed female Atlantic salmon, *Salmo salar*, in Norwegian rivers. *Aquaculture*, **98**, 151–159.

Lura, H. & Sægrov, H. (1993) Timing of spawning in cultured and wild Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) in the River Vosso, Norway. *Ecology of Freshwater Fish*, 2, 167–172.

Lyles, A.M. & May, R.M. (1987) Problems in leaving the ark. *Nature*, **326**, 245–246.

Philipp, D.P. (1991) Genetic implications of introducing Florida largemouth bass, *Micropterus salmoides floridanus*. *Canadian Journal of Fisheries and Aquatic Sciences*, **48** (Suppl. 1), 58–65.

Pickering, A.D. (1993) Endocrine-induced pathology in stressed salmonid fish. *Fisheries Research*, **17**, 35–50.

Quinn, T.P. & Foote, C.J. (1994) The effects of body size and sexual dimorphism on the reproductive behaviour of sockeye salmon, *Oncorhynchus nerka*. *Animal Behavior*, **48**, 751–761.

Reisenbichler, R.R. & McIntyre, J.D. (1977) Genetic differences in growth and survival of juvenile hatchery and wild steelhead trout, *Salmo gairdneri*. *Journal of the Fisheries Research Board of Canada*, **34**, 123–128.

Rice, W.R. (1989) Analyzing tables of statistical tests. *Evolution*, **43**, 223–225.

Ruzzante, D.E. (1994) Domestication effects on aggressive and schooling behavior in fish. *Aquaculture*, **120**, 1–24.

Schroder, S.L. (1982) The influence of intrasexual competition on the distribution of chum salmon in an experimental stream. *Salmon and Trout Migratory Behavior Symposium* (eds E. L. Brannon & E. O. Salo), pp. 275–285. University of Washington Press, Seattle.

Skaala, Ø. (1992) *Genetic variation in brown trout* Salmo trutta, *L. & application of genetic markers in studies on gene flow from cultured populations*. PhD thesis, University of Bergen.

Srivastava, R.K. & Brown, J.A. (1991) The biochemical characteristics and hatching performance of cultured and wild Atlantic salmon (*Salmo salar*) eggs. *Canadian Journal of Zoology*, **69**, 2436–2441.

Waples, R.S. (1991) Genetic interactions between hatchery and wild salmonids: lessons from the Pacific Northwest. *Canadian Journal of Fisheries and Aquatic Sciences*, **48** (Suppl. 1), 124–133.

Webb, J.H. & Hawkins, A.D. (1989) The movements and spawning behaviour of adult salmon in the Girnock Burn, a tributary of the Aberdeenshire Dee (1986) *Scottish Fisheries Research Report*, **40**, 1–42.

Webb, J.H., Hay, D.W., Cunningham, P.D. & Youngson, A.F. (1991) The spawning behaviour of escaped farmed and wild adult Atlantic salmon (*Salmo salar* L.) in a northern Scottish river. *Aquaculture*, **98**, 97–110.

Webb, J.H., McLaren, I.S., Donaghy, M.J. & Youngson, A.F. (1993a) Spawning of farmed Atlantic salmon, *Salmo salar*, L., in the second year after their escape. *Aquaculture and Fisheries Management*, **24**, 557–561.

Webb, J.H., Youngson, A.F., Thompson, C.E., Hay, D.W., Donaghy, M.J. & McLaren, I.S. (1993b) Spawning of escaped farmed Atlantic salmon, *Salmo salar*, L., in western and northern Scottish rivers: egg deposition by females. *Aquaculture and Fisheries Management*, **24**, 663–670.

White, H.C. (1942) Atlantic salmon redds and artificial spawning beds. *Journal of the Fisheries Research Board of Canada*, **6**, 37–44.

Youngson, A.F., Martin, S.A.M., Jordan, W.C. & Verspoor, E. (1991) Genetic protein variation in Atlantic salmon in Scotland: comparison of wild and farmed fish. *Aquaculture*, **98**, 231–242.

Received 16 September 1994; revision received 13 January 1995

ICES Journal of Marine Science, 54: 1051–1063. 1997

Experimental tests of genetic divergence of farmed from wild Atlantic salmon due to domestication

I. A. Fleming and S. Einum

Fleming, I. A. and Einum, S. Experimental tests of genetic divergence of farmed from wild Atlantic salmon due to domestication. – ICES Journal of Marine Science, 54: 1051–1063.

The genetic response of Atlantic salmon to culture is important in predicting the success of these fish in nature and their impacts on wild populations through competition and interbreeding. We compared a seventh-generation strain of farmed Atlantic salmon from Sunndalsora, Norway, with its principal founder population from the wild, the River Namsen. The fish were reared from eggs in a common environment and assessed for the extent of genetic divergence in several fitness-related traits. Morphology had diverged, as farmed juveniles showed more robust bodies and smaller rayed fins than the wild juveniles. Ecologically important aspects of behaviour also differed. Farmed juveniles were more aggressive in a tank environment typical of culture facilities, while wild juveniles dominated in a stream-like environment. Farmed juveniles were also more risk-prone, reappearing from cover sooner after a simulated predator attack. It was not surprising that growth performance was higher in farmed than wild juveniles, as the former had been subjected to intentional selection for this trait. Correlated responses to this selection may also explain the higher rate of smolting and lower rate of male parr maturity in the farmed than the wild salmon. Competition with wild juveniles, however, negatively affected the growth of the farmed juveniles, particularly under semi-natural conditions. Our results indicate that farming of Atlantic salmon generates rapid genetic change, as a result of both intentional and unintentional selection in culture, that alters important fitness-related traits.

Key words: aggression, aquaculture, Atlantic salmon, farmed salmon, growth, maturity, morphology, predation risk, *Salmo salar*, smolting.

I. A. Fleming and S. Einum: Norwegian Institute for Nature Research, Tungasletta 2, N-7005 Trondheim, Norway.

Introduction

Increasingly, it is becoming evident that cultured fish differ from wild fish in important fitness-related traits. These differences arise, in part, from phenotypically plastic responses of the fish to the radically divergent environment of culture facilities relative to nature (e.g. Fenderson *et al.*, 1968; Swain *et al.*, 1991; Fleming *et al.*, 1994, 1997; Olla *et al.*, 1994). Unlike nature, culture facilities provide predator-free, high-density, rapid-growth environments that can affect the morphological, behavioural, and life-historical development of the fish. The differences between cultured and wild fish are also likely to arise for genetic reasons. First, cultured fish are often derived from non-indigenous sources and are thus likely to differ genetically from wild populations (e.g. Philipp, 1991; Youngson *et al.*, 1991). Second, cultured populations are sometimes established using few fish and have small genetically-effective population sizes that can result in random genetic changes (e.g. Allendorf and Phelps, 1980; Ryman and Ståhl, 1980). Finally, the human-engineered breeding patterns and the culture environment imposed on the fish create intentional and unintentional selection that can result in domestication over a few generations (reviewed in Fleming, 1995).

While it has been relatively straightforward to identify phenotypically-plastic responses of fish to culture, identifying genetic responses has been somewhat more difficult, particularly for traits that are likely to have consequences for fitness. Rarely can a cultured population be compared with its founding population from the wild to assess genetic change in fitness-related traits due to culture. Often the integrity of the wild population is compromised subsequent to the initiation of the culturing programme because of large-scale introgression by the cultured fish (e.g. Schramm and Piper, 1995). Yet, knowledge of the genetic responses of fish to culture is important in predicting the success of these fish in nature and their impacts on wild populations through

1054-3139/97/061051+13 $25.00/0/jm970289

competition and interbreeding. Such information is also of value to culture programmes where domestication can be important in improving yields.

The Atlantic salmon (*Salmo salar* L.) is one of the most intensively cultured fishes as a result of a large and economically successful farming industry (Anon., 1996). In 1971, Norway established a national breeding programme for farmed salmon at Sunndalsøra and this programme is now the principal supplier of fish for the Norwegian salmon farming industry. The first generation of fish used in the breeding programme were derived from 41 different rivers and localities (Gjedrem *et al.*, 1991). However, by the fourth generation of selective breeding for characteristics such as increased growth and delayed sea-age at maturity, all four of the brood lines that had been created were dominated by from one to three of the original populations (Gjedrem *et al.*, 1991). It is thus possible to compare fish from some of these brood lines, particularly brood line one, with their principal founder population from the wild.

Our aim in this study was to test for genetic response to domestication in fitness-related traits of farmed Atlantic salmon. Seventh-generation farmed salmon from brood line one of the breeding programme at Sunndalsøra were compared with their principal founder population from the wild, the River Namsen. Both groups were reared in the same way, under similar environmental conditions, and contrasted as juveniles for their morphology, dominance abilities, aggressive and anti-predator behaviour, growth performance in cultured and semi-natural environments, male parr maturity, and smolting.

Materials and methods

The salmon

Eyed eggs (ca. 5000) from eight families of farmed salmon were obtained from the breeding programme at Sunndalsora in 1996 and reared at the Norwegian Institute for Nature Research (NINA) Research Station at Ims (Rogaland, south-west Norway). The eggs represented the seventh generation of the first brood line ("population 1" *sensu* Gjedrem *et al.*, 1991), which had been developed using fish from 18 different localities, including the River Namsen. The River Namsen originally constituted 11% of the brood line; however, by the fourth generation its representation had risen to more than 70% (Gjedrem *et al.*, 1991) and it is unlikely that this trend has stopped (H. M. Gjoen, AKVAFORSK, Institute of Aquaculture Research, Ås, Norway, pers. comm.).

Eyed eggs (ca. 5000) derived from at least six families of wild (confirmed by scale analyses) River Namsen salmon were obtained from the Skorstad rearing station at Fosslandsosen and transported to the NINA Research Station. The River Namsen is a relatively large river (mean annual water discharge: 300 m^3 s^{-1}), located in mid-Norway (64°28′N, 11°30′E). The majority of the salmon in this population mature after 2–3 years in the ocean (Jonsson *et al.*, 1991).

Eggs from the two populations were incubated in Heath vertical stack incubators with a water flow of 4 l min^{-1}. At the onset of feeding, the alevins from the two populations were transferred to separate 2 m^2 tangential-flow tanks. They were given an excess of commercial food pellets (EWOS) using automatic feeders dispensing food at 10-min intervals. On 21 May, 840 fry from each population were randomly chosen and placed in separate 1 m^2 tangential-flow tanks, with the remaining fry from each population (ca. 4000) being reared in the separate 2 m^2 tangential-flow tanks. The former groups were used in all subsequent behavioural and growth experiments, and the latter groups for examining parr maturity and smolting. On 27 June, the fish in the 2 m^2 tanks were transferred to 12 m^2 tangential-flow tanks, where they were reared until smolting, and the fish in the 1 m^2 tanks moved between tanks. The use of several rearing tanks and rotation among tanks was done to reduce possible rearing tank effects.

Morphology

Samples of the farmed (Sunndalsora) and wild (River Namsen) fry were photographed on 13 May 1996 (Table 1). Prior to photographing, each fish was lightly anaesthetized with chlorobutanol and placed left side up on a moistened, light blue carpet that had a millimetre ruler affixed along its lower edge. Anal, dorsal, and caudal fins were teased to an erect position and small pieces of white paper were placed under the anal, dorsal, pectoral, and pelvic fins to increase their visibility. Photographs were taken using a copy stand and Nikon F90x 35-mm camera with a Nikkor 55-mm macro-lens and ring flash set at a fixed distance from the fish.

The photographs were later digitized using a computer graphics tablet, recording body area and spatial co-ordinates of 19 landmarks as described in Fleming *et al.* (1994). From these landmark co-ordinates seven conventional (i.e. anal and dorsal fin heights and bases, pectoral and pelvic fin lengths and snout length) and 21 truss measurements (Winans, 1984) were calculated.

All morphometric measures were natural log-transformed and standardized to mean = 0 and standard deviation = 1. Characters were then size-adjusted and transformed into shape variates by expressing them as residuals from the regression line describing the relation between the character and body size. Centroid size, the sum of squared distances between all pairs of marginal landmark co-ordinates on the body, was used as a multivariate measure of fish body size (Bookstein, 1990).

Table 1. Mean (mm; sample size in parentheses), range, standard deviation, and analysis of variance of fork length for the salmon fry photographed from the Sunndalsøra breeding programme (seventh generation of brood line 1) and their principal founder population, the River Namsen.

	Wild Namsen	Farmed Sunndalsøra	ANOVA	
			F	p
Mean	49.9 (35)	46.6 (37)	20.89	<0.001
Range	39.9–56.8	38.0–52.3		
Standard error	0.6	0.4		

The common within-groups slope for each character was used for size adjustment (Thorpe, 1983; Reist, 1986). There were no significant differences between the populations in slopes for any of the character-body size relations (ANCOVA with sequential Bonferroni adjustment for multiple character comparisons: $p>0.05$).

Aggression

To test for innate differences in aggressiveness among juveniles from the two populations (farmed and wild), groups of four fish from a population were weighed and placed into one of 12 stream tank enclosures 60 × 40 cm. Fish were chosen to avoid differences in mean and variance in weight among replicates and between populations (overall mean=2.42 g, $F_{1,94}=0.611$, $p=0.436$; overall variance=0.373, $F_{1,22}=0.001$, $p=0.972$). Water depth was maintained at 4 cm and water flow at 10 l min^{-1}, and mean water temperature ± s.d. was 16.1°C ± 0.8 (measured daily).

The fish were allowed 2 d to acclimate to the stream tank, during which time they were fed 1 g of food pellets delivered twice daily through a PVC pipe to the water inlet. Then, five 10-min sequences were recorded by video, one each hour for a 5 h period. Between 20 June and 13 July, 12 replicates were conducted with each population. The populations were tested in each of the experimental tanks, controlling for tank effects. Video tapes were analysed for overt aggressive acts directed at other fish.

To determine relative dominance among juveniles of farmed and wild origin we used a methodology similar to that of Einum and Fleming (1997). Six stream channels with v-shaped cross-sections, each consisting of five 20-cm long sections, were used. Food pellets were supplied to the upstream end of each section through a PVC pipe extending from a hole in the blind surrounding each channel. Water depth was maintained at 4 cm and velocity varied between 1.4 and 2.0 cm s^{-1} in the different channels. Mean water temperature ± s.d. throughout the experiment was 10.6°C ± 0.4.

The experiment was carried out between 27 and 31 May 1996. Each fish was weighed (± 0.01 g), measured (fork length ± 0.1 cm), and marked alternately on the left or right pectoral fin with alcian blue dye for recognition. Fish from the two populations were matched in pairs of similar size (t-test for paired samples, weight: $p=0.569$; length: $p=0.801$, $n=30$). Following marking, the pairs were kept separately in 10 × 10 × 40 cm containers for recovery for 2 d. They were then added to the channels and allowed to acclimate for 2 d without food before observations began.

The fish were observed for 1 min every 30 min for a period of 2.5 h, and scored for position and foraging success, both of which correlate well with dominance (Fausch, 1984). During each observation, one point was given for occupying the preferred upstream position, two points for obtaining a food pellet dropped into the current and two points for each unreciprocated attack on the other fish (Metcalfe *et al.*, 1989, 1992; Einum and Fleming, 1997). A fish was determined to be the dominant of the pair whenever its total score after the six observations was three or more points greater than that of its opponent. A difference of less than three points resulted in an unresolved trial.

We also conducted a similar experiment in a tank environment to determine whether dominance might be environmentally dependent. Pairs were matched in weight and length (t-test for paired samples, weight: $p=0.901$; length: $p=0.207$; $n=15$), and marked following the procedure described below. The pairs were then placed in one of five 40 × 30 cm tank enclosures which were surrounded by black plastic to avoid disturbance. The fish were allowed at least 8 h to acclimate to the tank, and then were recorded by video for five 5-min sequences during a 2 h period. Fifteen replicates were conducted during 29–31 July. The video tapes were analysed for the total number of overt aggressive acts by each fish. Water depth and water flow were maintained at 8 cm and 3 l min^{-1}, respectively, and mean water temperature ± s.d. was 16.8°C ± 0.9 throughout the experiment.

Behavioural response to a simulated predator

The responses of farmed and wild juveniles to a simulated predator were tested in 38 × 100 cm sections of four tangential-flow 1 m^2 tanks. The sections were screened off by perforated plastic plates. A hide consisting of a 5 × 7 × 9 cm tunnel with a sealed end provided refuge and was designed to prevent the fish from feeding without leaving it. An automatic feeder released food pellets every 10 min during the acclimation period. Water flow and depth were maintained at 12 l min^{-1} and 30 cm, respectively, and mean water temperature ± s.d. was 16.0°C ± 0.9 throughout the experiments.

A fish was weighed (± 0.01 g) and added to each of the four tanks. We tested two fish from each population simultaneously, and both populations were tested equally many times in the different tanks, controlling for tank effects. The fish from the two populations were matched for weight such that no significant difference existed ($F_{1,56}$=0.001, p=0.973).

After an acclimation period of at least 18 h the fish was exposed to a 60-cm-long fibre glass brown trout (*Salmo trutta* L.) model for 10 s. The model was placed in the part of the tank holding the fish through a hole in the blind surrounding the tank. Simultaneously, the automatic feeder was turned off so that differences in the timing of exposure relative to the feeding interval did not affect the motivation of the fish to come out from the hide. The fish were recorded by video, and the time which had elapsed before the fish first reappeared from the hide was determined. Between 19 June and 8 July 1996, 25 replicates were conducted with each of the two populations.

Growth in hatchery

Two series of experiments were conducted in 0.36 m^2 tangential-flow tanks to compare the growth of the farmed and wild juveniles in the absence and presence of interpopulation competition. The first series of experiments began on 25 June and was conducted at water temperatures of 15, 16, 17, 19, and 21°C. The second series of experiments began on 6 August and involved water temperatures of 12, 14, and 15°C. The standard deviation in temperature (registered daily) within an experiment was always less than 1.0 deg C and usually less than 0.5 deg C. Two pure groups of wild (n=10), one pure group of farmed (n=10), and one mixed group (n=5 wild and 5 farmed) were tested at each temperature within an experimental series.

The fish to be tested at 15, 16, and 17°C, and at 19, and 21°C in the first experimental series and at 12, 14, and 15°C in the second series were acclimated for 3 weeks at 15, 19, and 11°C, respectively. They were then starved for 24 h to ensure stomach evacuation, and groups of 10 individuals were weighed and marked individually using a combination of alcian blue dye and adipose fin clips. Fish were matched for size such that there were no differences in mean initial weight or variance between the populations in the pure groups (p=0.790 for mean and p=0.140 for variance, one-way ANOVA and Levene test) and in the mixed groups (all tanks: p>0.90 for mean and p>0.80 for variance). The fish were then allowed a day to acclimate to the experimental tanks.

Water depth and flow within the tanks were maintained at 30 cm and 3 l min^{-1}, respectively, and black plastic erected around the outside prevented unintentional disturbance. Artificial light provided a light regime of 6 h night and 18 h day. The fish were fed to excess using commercial food pellets (EWOS) for a period of 3 wk before being starved for 24 h and weighed again. Fish dying during the experiment were replaced by fish from the same population and of similar size to avoid density differences among tanks. Specific growth rate (*G*) was calculated as:

$$G=100(\log_e \text{ final weight [g]} - \log_e \text{ initial weight [g]})/(\text{length of experiment [d]}).$$

Performance in a semi-natural environment

To assess growth and mortality under simulated natural conditions two series of experiments were conducted using four outdoor, circular stream environments (described in Fleming *et al.*, 1996). Each stream averaged 2.2 m in width, 21 m in length, and provided 47 m^2 of suitable juvenile habitat. The stream bed was covered with a gravel substratum, and water velocities ranged between 1 and 62 cm s^{-1} (measured 15 cm above the gravel, every 4 m throughout the streams), and depths between 12 and 50 cm. A diverse fauna in and on the gravel provided a constant drift of food for the juveniles.

The first series of experiments was conducted between 28 June and 22 July, and the second series between 29 July and 27 August. Prior to each experimental series, the fish were starved for 24 h. Then, four groups of 120 juveniles consisting of 60 wild and 60 farmed fish were weighed (± 0.01 g), matched for size (comparison between populations within streams: t-tests, p>0.60; Levene test for variance, p>0.10), and individually marked using a combination of alcian blue dye and adipose fin clips. The different groups were then kept separately for recovery in 1 m^2 stream tanks for 24 h before being released into the four stream environments. To examine the effect of predators on growth and survival we added three brown trout (weight 543–790 g) to two of the streams 4 d after the juveniles were released. At the end of the experiments, all streams were drained and surviving fish were identified and weighed. Mean water temperature ± s.d. was 16.0°C ± 0.9 and 18.0°C ± 1.4 throughout the first and second series, respectively.

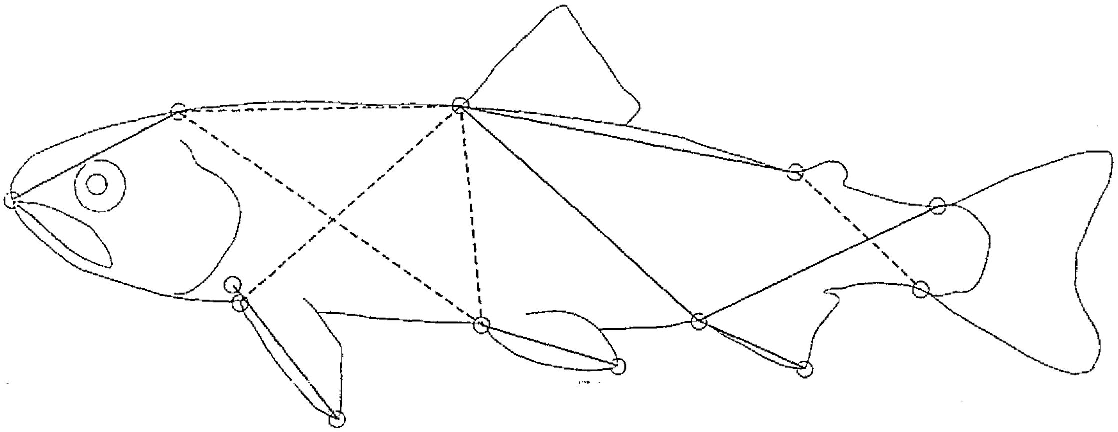


Figure 1. Comparison of the juvenile morphology of Sunndalsora farmed salmon (brood line 1) with their principal founder population, the River Namsen. Characters differing significantly (t-tests adjusted by the sequential Bonferroni method) between the populations are shown by solid (character larger in Namsen salmon) and dashed lines (character larger in Sunndalsora salmon) on the fish outline.

Parr maturity and smolting

On 13 November, a sample of 120 parr from each population was examined for maturity by dissection. During 12–15 May 1997, a further sample of 450 juveniles from each population were weighed, their length measured and smolt status identified by external appearance (Hoar, 1988).

Results

Morphology

In a univariate comparison of morphology, Sunndalsøra farmed salmon (brood line 1) differed significantly from their principal founder population, the River Namsen, in 13 of the 28 traits examined (t-tests with sequential Bonferroni adjustment for multiple comparisons: $p<0.05$; Fig. 1). The farmed fry had deeper bodies, particularly in the anterior trunk region, and thus tended to be more robust and less streamlined than the wild fry. Moreover, they had smaller rayed fins, including dorsal fin width and anal, pelvic, and pectoral fin lengths. Principal components analysis using the correlation matrix of size-adjusted data showed significant differences in component scores across PC1 and PC2, primarily reflecting differences in body shape (Table 2, Fig. 2). Stepwise discriminant function analysis classified the fish to their population origin, based on *a priori* knowledge of the relationship between the populations, with 97% accuracy ($F_{8,63}=35.50$, $p<0.001$).

Aggression

In a tank environment and in the absence of inter-population competition, the Sunndalsøra farmed fish showed a higher mean frequency of overt aggressive acts (mean ± s.e. $=3.45 \pm 0.73$ acts per 5 min) than Namsen fish (1.72 ± 0.45; $F_{1,11}=4.86$, $p=0.048$, controlling for tank effects $F_{11,11}=1.37$, $p=0.305$). Wild salmon, however, were able to dominate farmed salmon during pairwise contests in a stream-like environment (sign test: $Z=2.69$, $n=30$, $p<0.001$). Namsen fish dominated in 21 of the contests and farmed fish in three, with six contests being unresolved.

To determine whether environment influences the outcome of interpopulation competition, pairwise contests similar to the dominance experiments, but conducted in a tank environment, were performed. Under these conditions there was no significant difference in dominance, as expressed by the number of overt

Table 2. Means and t-tests of principal component scores of fry morphology for Sunndalsøra farmed (brood line 1) and River Namsen wild salmon (principal founder population for the farmed salmon). Percentage of variation explained by each component is given in parentheses.

Principal component	Wild Namsen (n=35)	Farmed Sunndalsøra (n=37)	t-test	
			t_{70}	p
PC1 (20.6%)	0.75	−0.71	8.97	<0.001
PC2 (12.1%)	−0.26	0.24	−2.17	0.033
PC3 (11.1%)	−0.13	0.12	−1.04	0.303
PC4 (9.2%)	−0.15	0.14	−1.27	0.209

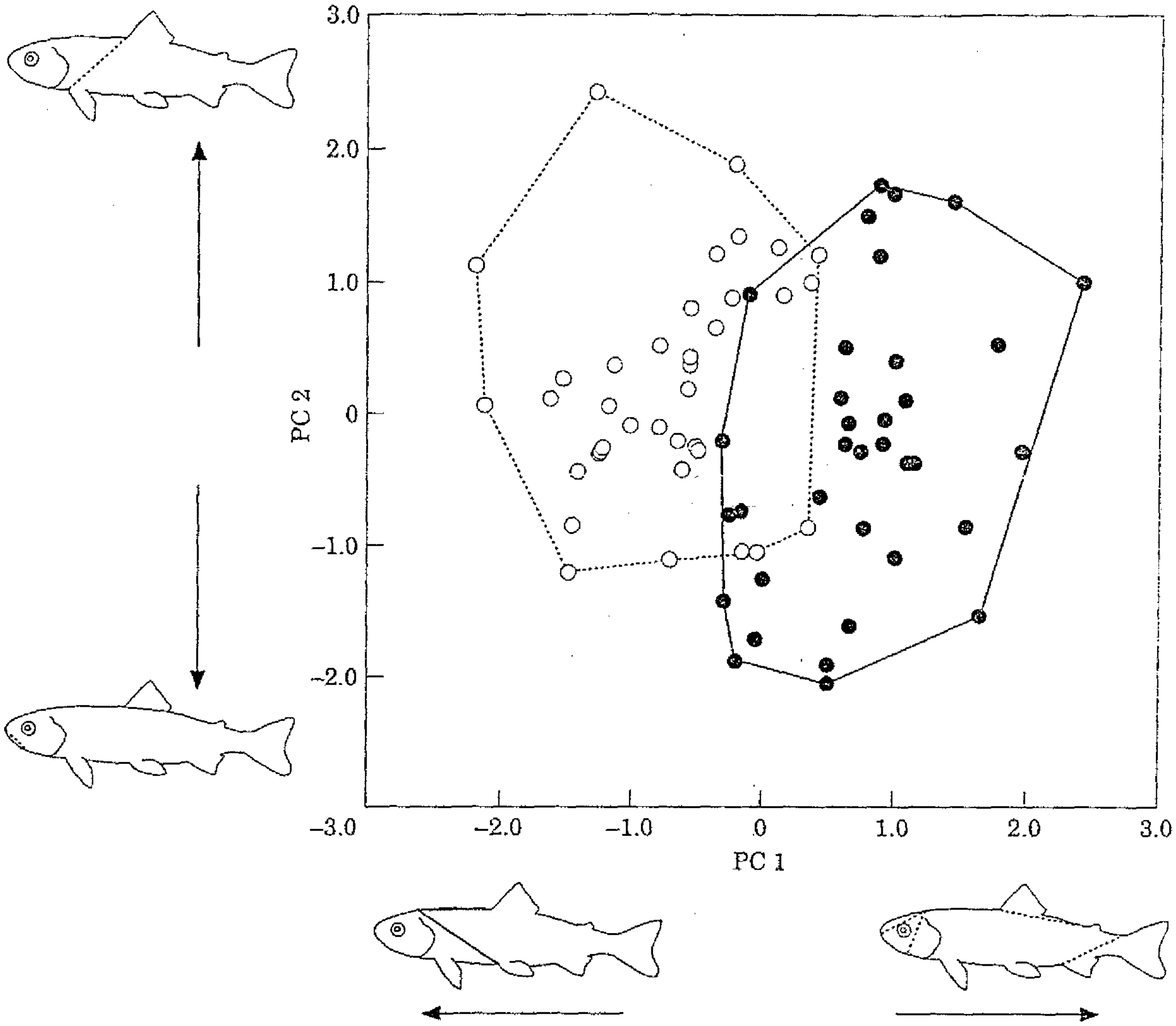


Figure 2. Principal components (PC) analysis of the size-adjusted morphology of Sunndalsora farmed salmon (brood line 1: ○) and their principal founder population, the River Namsen (●). Characters loading highly on each PC are diagrammed on the fish outlines (loadings: solid lines, 0.70–0.80; dotted lines, 0.50–0.69) and arrows indicate direction of correlation.

aggressive acts (sign test based on binomial distribution: $n=15$, $p=0.302$). The farmed fish were more aggressive in 10 of the contests and Namsen fish in the remaining 5.

Behavioural response to a simulated predator

Behaviour of the juvenile salmon when exposed to the trout model was variable. Most fish darted for cover immediately, however, some froze motionless at their feeding station and then swam into the hide some time after the model was removed. Mean time elapsed from onset of exposure until the fish was in the hide was 14.5 s, and did not differ between populations (Mann–Whitney U-test: $Z=0.65$, $n=25$, $p=0.516$). However, time elapsed before first reappearance differed significantly between the two populations ($Z=3.27$, $n=25$, $p=0.001$), as the Namsen fish (mean ± s.e.$=2619 \pm 577$ s) took significantly longer than the farmed fish (731 ± 208 s).

Growth in hatchery

An overall ANOVA of growth rate incorporating population, temperature, presence/absence of interpopulation competition and the respective interaction terms, identified two significant effects. Not surprisingly, temperature had a strong influence on growth rate and affected both populations in a similar way (Fig. 3; $F_{7,266}=5.16$, $p<0.001$). There was also a significant population-by-competition interaction ($F_{1,266}=5.12$, $p=0.024$), suggesting that interpopulation competition affected the populations in different ways. Interpopulation competition resulted in a decline in the growth performance of the farmed salmon (Fig. 4a: $F_{1,102}=5.66$, $p=0.019$, controlling for temperature $p<0.05$), but did not significantly affect the Namsen salmon (Fig. 4b: $F_{1,178}=0.87$, $p=0.353$, controlling for temperature $p<0.05$). As a result, the farmed salmon outgrew the Namsen salmon in pure groups ($F_{1,216}=6.00$, $p=0.015$; controlling for temperature $p<0.05$), but not in the presence of

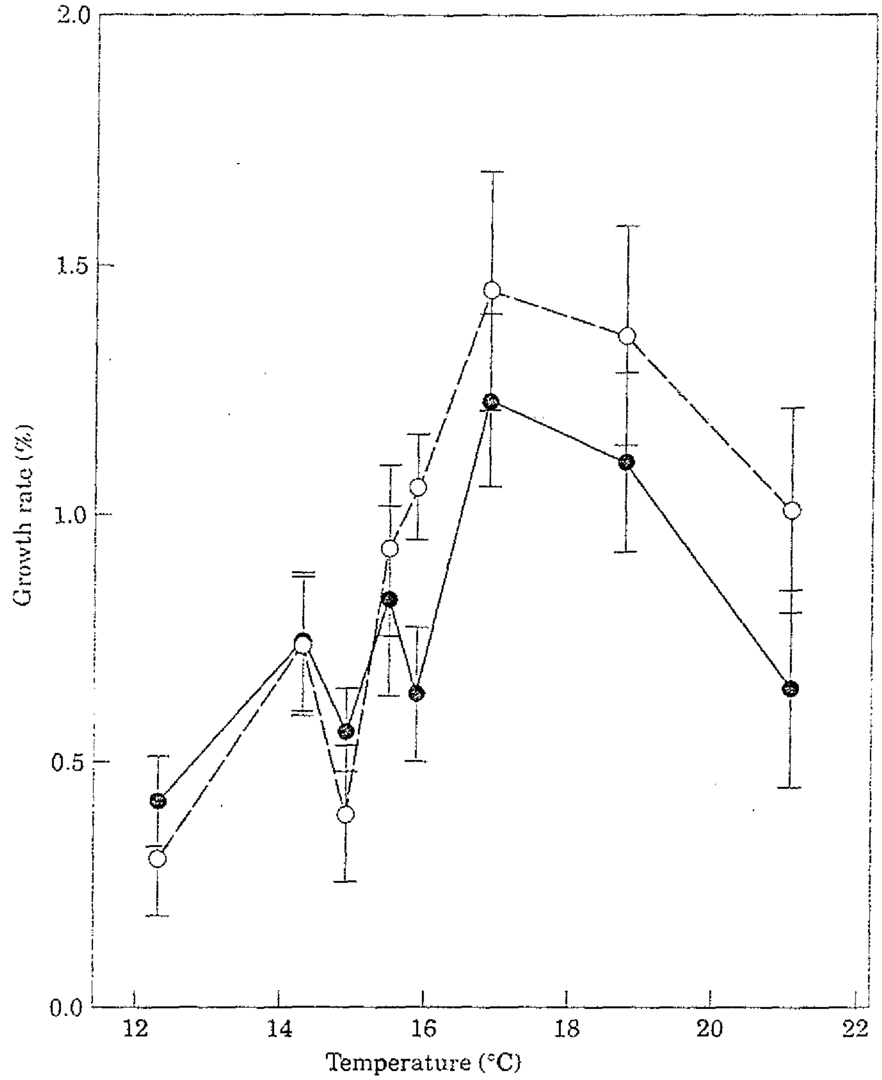


Figure 3. Comparison of the mean specific growth rates (% g g^{-1} day^{-1}) across a range of temperatures of seventh-generation Sunndalsøra farmed parr (brood line 1; ○) with their principal founder population from the River Namsen (●), combining both pure and mixed groups. One standard error is shown.

interpopulation competition (i.e. mixed tanks) ($F_{1,64}$=1.33, p=0.254; controlling for temperature p<0.05).

Performance in a semi-natural environment

The wild Namsen parr outgrew the farmed parr across the experiments in the semi-natural streams (Table 3; $F_{1,803}$=5.80, p=0.016, controlling for stream and experimental series effects p<0.05). The presence of brown trout predators caused a decline in growth rates ($F_{1,803}$=7.25, p=0.007) and there was a tendency for this effect to be greater in the Namsen than in the farmed fish, though the difference was not significant (Table 3; predator–population interaction: $F_{1,803}$=1.27, p=0.259). Predation by brown trout, however, was low or absent, as recovery rates were similar from streams with (89.2%) and without brown trout (89.4%; χ^2<0.01, d.f.=1, p=0.987; one trial excluded due to the accidental loss of some fish when the stream was drained). Nor was there any significant difference in recapture rates of fish from the two populations (Namsen, 89.5%; farmed, 88.6%; χ^2<0.01, d.f.=1, p=0.972).

Parr maturity and smolting

Parr maturity was significantly lower among the Sunndalsøra farmed males (21.6%, n=60) than males from their principal founding population, the River Namsen (44.6%, n=65; χ^2=7.37, d.f.=1, p=0.007). The farmed salmon, however, grew faster and were larger overall after one year in the hatchery than the Namsen salmon (total length: t_{898}=16.61, p<0.001; weight: t_{898}=18.47, p<0.001). This, in part, reflected the bimodal distribution of body sizes in the two groups (Fig. 5), with a higher proportion of the farmed (88.0%, n=450) than Namsen salmon (72.7%, n=450; χ^2=33.81, d.f.=1, p<0.001) being in the upper modal group that smolted. Moreover, the farmed salmon in the upper modal group

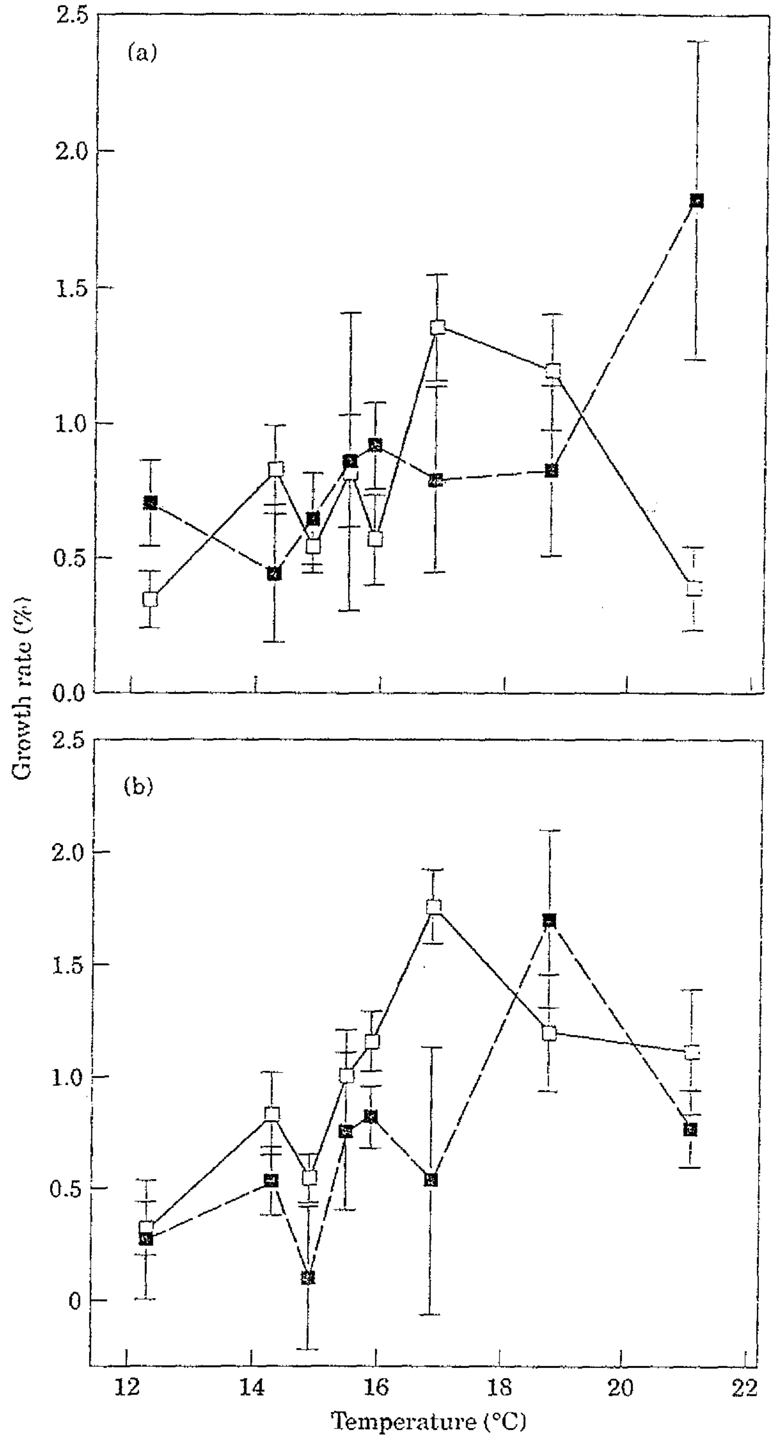


Figure 4. Comparison of the mean specific growth rates (% g g^{-1} d^{-1}) across a range of temperatures for (a) River Namsen and (b) Sunndalsora farmed parr (brood line 1) in the presence (▨) and absence of interpopulation competition (□). One standard error is shown.

were larger than the Namsen salmon (total length: t_{699}= 25.31, $p<0.001$; weight: t_{699}=22.05, $p<0.001$), while the opposite was the case in the lower modal group (total length: t_{197}=2.26, p=0.025; weight: t_{197}=2.73, p=0.007).

Discussion

The farmed salmon had diverged from their wild founder population in several fitness-related traits,

Table 3. Mean specific growth rate (% g g^{-1} d^{-1}) ± s.e. of the farmed and Namsen salmon in semi-natural streams with and without predatory brown trout present.

Population	With predators	Without predators	Overall
Namsen	1.51 ± 0.05	1.69 ± 0.06	1.59 ± 0.04
Farmed	1.47 ± 0.05	1.55 ± 0.06	1.51 ± 0.04

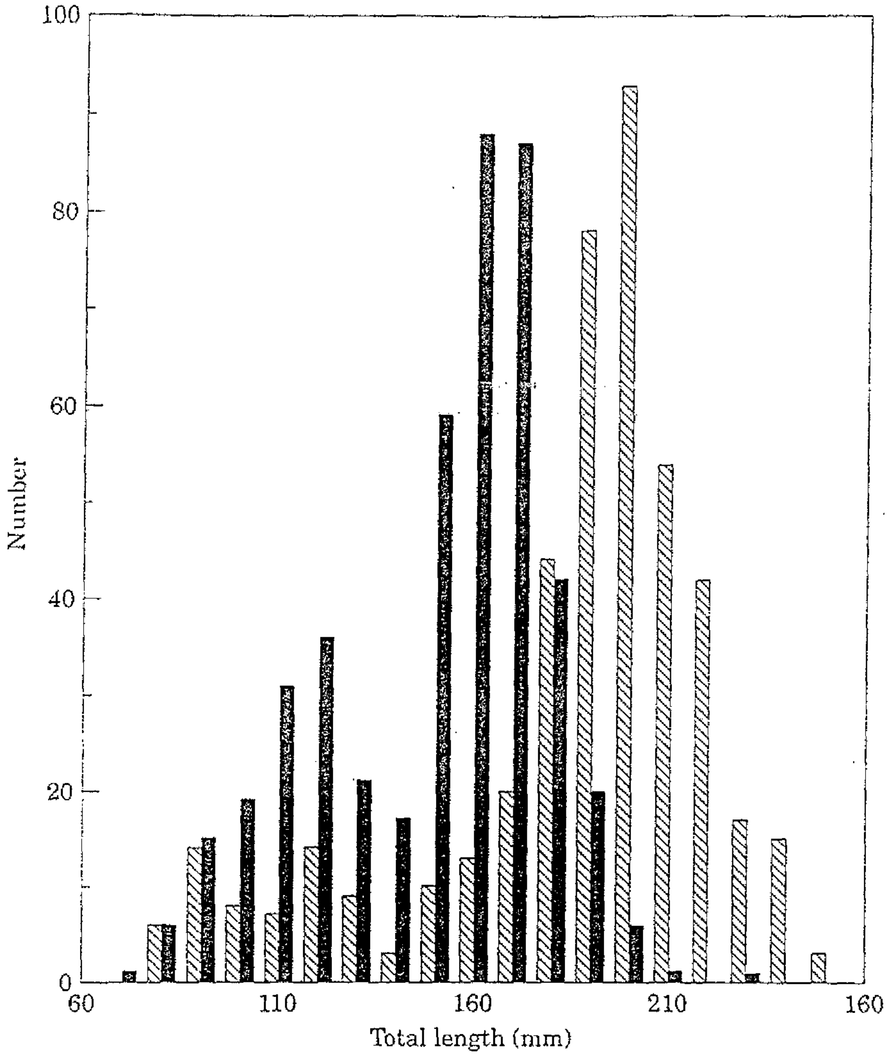


Figure 5. Size distribution of Sunndalsora farmed (▨) and River Namsen salmon (▩) in May 1997, one year after hatching.

including morphology, behaviour, growth, and life history. These differences are likely to be genetic in origin as the fish were reared in the same way, under similar environmental conditions (i.e. in separate tanks housed in a common environment with rotation among tanks). While it is possible that the differences could have arisen due to maternal effects, this seems unlikely. For example, differences in egg size can positively affect early survival, growth, and body size (Bagenal, 1969; Glebe *et al.*, 1979; Kazakov, 1981; Thorpe *et al.*, 1984). To minimize such a possibility, the juvenile fish were matched for size throughout the experiments. Moreover, the differences in size and growth that were observed were contrary to expectation based on maternal differences in egg size (i.e. wild larger than cultured; Jonsson *et al.*, 1996), as farmed outgrew wild salmon. It is also known that pre-fertilization environments can affect meristic traits in fishes (Dentry and Lindsey, 1978; Swain and Lindsey, 1986), however, effects on body shape, if they occur, are unlikely to persist months after emergence (Swain *et al.*, 1991). Thus the changes observed in the farmed salmon appear to reflect micro-evolutionary change that has occurred in culture.

Random genetic processes, such as inbreeding, and/or altered selection could produce such evolutionary responses in farmed salmon. It is unlikely, however, that inbreeding has played a large role, because the breeding programme at Sunndalsøra has maintained pedigrees and avoided mating close relatives (Gjedrem *et al.*, 1991). Moreover, many of the changes observed appear non-random (see below) and are thus inconsistent with predictions based on genetic drift. Rather, our results indicate that intentional and unintentional selection during the seven generations of domestication generated the observed divergence in morphology, behaviour, growth, and life history of the farmed salmon from their wild progenitors.

The morphology of the farmed juveniles had diverged from its ancestral form as represented by the wild salmon from the River Namsen, with the body becoming more robust and rayed fins smaller. This change in body robustness contrasts with studies on juvenile sea-ranched salmon (i.e. artificially bred and reared as juveniles, but free-range as sub-adults in the ocean), where the opposite trend relative to wild fish has been observed and is thought to be principally environmental in origin (Taylor, 1986; Swain *et al.*, 1991; Fleming *et al.*, 1994). The different rearing regimes may be responsible for this. Unlike the sea-ranched fish, the farmed fish are cultured throughout their lives and never exposed to natural selection for swimming performance. Additionally, they have been subjected to directed artificial selection for rapid growth based on body weight (Gjedrem *et al.*, 1988), which probably generated a correlated positive response in body depth (see Gjerde and Schaeffer, 1989). The changes in fin morphology of the farmed salmon do parallel observations from sea-ranched salmon (Taylor, 1986; Swain *et al.*, 1991; Fleming *et al.*, 1994). Moreover, they indicate that seven generations of intense culturing can generate genetic change in such traits. Relaxed selection for swimming performance combined with artificial selection generated by high levels of fin nipping (Abbott and Dill, 1985) and erosion (Bosakowski and Wagner, 1994) are likely to be responsible.

The farmed salmon have also diverged genetically from the wild salmon in ecologically important aspects of behaviour, including aggression, dominance, and predator avoidance. This is not surprising, because behavioural traits are believed to be among the first traits to respond to domestication (Price, 1984). Genetic differences in aggressive behaviour and dominance between cultured and wild fish have been documented previously, but the direction of response has varied. Some studies have recorded higher levels of aggression and/or dominance in cultured fish (Moyle, 1969; Swain and Riddell, 1990; Einum and Fleming, 1997), while others have noted the opposite (Ruzzante and Doyle, 1991; Berejikian *et al.*, 1996). The present study, suggests that the expression of aggression and dominance may be context-dependent (see also Berejikian *et al.*, 1996) and this may explain earlier equivocal results (Ruzzante, 1994). The farmed juveniles were more aggressive and tended to dominate in a tank environment typical of culture facilities, while the wild juveniles dominated in the stream-like environment.

The more risk-prone behaviour of the farmed than wild salmon in the face of potential predation (i.e. emerging from cover sooner following disturbance) appears to be a pattern common to cultured salmonids (Johnsson and Abrahams, 1991; Berejikian, 1995; Johnsson *et al.*, 1996; Einum and Fleming, 1997). It probably reflects a relaxation of selection against predator-vulnerable phenotypes in culture facilities where predators are absent but competition for food remains. The proximate cause of these changes in antipredator behaviour may be increased growth hormone production and thus appetite (Johnsson *et al.*, 1996).

Having been subjected to intentional selection for increased growth, it is also not surprising that the farmed salmon had higher growth performance in the absence of interpopulation competition and were larger at 1 year of age than the wild salmon. While genetic changes in the growth rate of domesticated fish are well documented (Weatherley and Gill, 1987), the form of the genetic response is poorly understood. The present study suggests that the selection implemented at the Sunndalsøra salmon breeding programme increased growth performance at temperatures above 15°C, close to that which is optimal for growth (Elliott and Hurley, in press), but did not alter the optimal temperature (ca. 17°C for both populations; Fig. 3). This may be a common pattern, as fish appear to show more genetic variation in the overall growth performance than in optimal temperature for growth (Conover, 1992; Forseth, 1994; Conover and Schultz, 1995).

Interpopulation competition, however, negatively affected the growth performance of the farmed relative to the wild juveniles both in the hatchery and in the semi-natural streams. This effect was most pronounced in the semi-natural streams where the wild juveniles outgrew the farmed juveniles, reflecting the former's competitive superiority in such an environment. A similar depression in growth performance under natural competitive conditions has been observed in sea-ranched relative to wild steelhead trout (*Salmo gairdneri*) (Reisenbichler and McIntyre, 1977). In contrast, Einum and Fleming (1997) found Sunndalsora farmed salmon to be competitively superior to native salmon from the River Imsa, Norway, and outgrew them both in the hatchery and in the wild. In combination with the present results, this suggests that differing genetic origins of the two populations prior to culturing may have as much to do with the outcome of competition and growth as the effect of culturing itself. This is not surprising as the breeding programme at Sunndalsora not only selected for among individual differences in performance, but also incidentally for among-population differences (Gjedrem *et al.*, 1991).

The higher rate of smolting among the farmed compared with the wild juveniles is likely to be related to the differences in hatchery growth performance between the two groups. Smolting in Atlantic salmon is thought to be determined more than half a year prior to emigration (Thorpe, 1986; Metcalfe *et al.*, 1988) and affected by the state (lipid or weight) and/or rate of change of the state (growth rate) at this time (Thorpe, 1986; Berglund, 1992; Økland *et al.*, 1993; Thorpe *et al.*, in press). Thus, selection for increased growth performance and the desire to produce half-year-old smolts may have generated a correlated response in smolting. Rapid growth and/or condition are also believed to influence male parr maturity (Thorpe, 1986; Hutchings and Myers, 1994;

Thorpe *et al.*, in press). The faster growing farmed fish, however, showed a lower incidence of male parr maturity than the wild fish. This may reflect a correlated response due to the directed selection for delayed sea-age at maturation instituted by the Sunndalsøra breeding programme, although the two traits are believed to be independently heritable (Gjerde, 1984). Alternatively, because maturation involves a change in the allocation of resources from somatic to gonadal development and thus a decrease in growth (Berglund, 1992), directed selection for freshwater growth could necessarily involve selection against male parr maturity.

Our results thus indicate that the farming of Atlantic salmon can generate rapid genetic change in fitness-related traits as a result of domestication due to intentional and unintentional selection. As much of this change appears to be an adaptive response to the culture environment, it can be of value for programmes attempting to improve aquaculture production (e.g. Doyle *et al.*, 1991). This change, however, is a threat to wild populations when these fish escape, and compete and breed with wild salmon. The invasion of escaped farmed salmon into rivers not only increases competition for resources, but also results in the infusion of different genetic traits into wild populations. Many of these traits are likely to be maladaptive for the local environment both because of the non-indigenous origins of the farmed salmon (Einum and Fleming, 1997) and because of the changes that have occurred due to culturing. While natural selection may be able to purge wild populations of such maladaptive traits, its actions are severely hindered by the year-after-year introgression of farmed salmon. The net result is almost certainly a decline in population fitness, as the influence of selection from the culture environment overrides that in the wild.

Acknowledgements

We thank the staff at the NINA Research Station, Ims for assistance throughout the experiments. AKVAGEN at Sunndalsøra kindly provided the farmed salmon eggs. We also thank T. Forseth for valuable discussion and J. H. S. Blaxter, T. Forseth, K. Hindar, and J. E. Thorpe for comments on an earlier version of this manuscript. Financial support was provided by grants from the Norwegian Research Council and the Directorate for Nature Management.

References

Abbott, J. C. and Dill, L. M. 1985. Patterns of aggressive attack in juvenile steelhead trout (*Salmo gairdneri*). Canadian Journal of Fisheries and Aquatic Sciences, 42: 1702–1706.

Allendorf, F. W. and Phelps, S. R. 1980. Loss of genetic variation in a hatchery stock of cutthroat trout. Transactions of the American Fisheries Society, 109: 537–543.

Anon. 1996. State of World Fisheries and Aquaculture. FAO, Rome.

Bagenal, T. B. 1969. Relationship between egg size and fry survival in brown trout, *Salmo trutta* L. Journal of Fish Biology, 1: 349–353.

Berejikian, B. A. 1995. The effects of hatchery and wild ancestry and experience on the relative ability of steelhead trout fry (*Oncorhynchus mykiss*) to avoid a benthic predator. Canadian Journal of Aquatic Sciences, 52: 2476–2482.

Berejikian, B. A., Mathews, S. B., and Quinn, T. P. 1996. Effects of hatchery and wild ancestry and rearing environments on the development of agonistic behavior in steelhead trout (*Oncorhynchus mykiss*) fry. Canadian Journal of Fisheries and Aquatic Sciences, 53: 2004–2014.

Berglund, I. 1992. Growth and early sexual maturation in Baltic salmon (*Salmo salar* L.) parr. Canadian Journal of Zoology, 70: 205–211.

Bookstein, F. L. 1990. Introduction and overview: geometry and biology. *In* Proceedings of the Michigan Morphometrics Workshop, pp. 61–74. Ed. by F. J. Rohlf and F. L. Bookstein. University of Michigan Museum of Zoology Special Publication No. 2. 380 pp.

Bosakowski, T. and Wagner, E. J. 1994. Assessment of fin erosion by comparison of relative fin length of hatchery and wild trout in Utah. Canadian Journal of Fisheries and Aquatic Sciences, 51: 636–641.

Conover, D. O. 1992. Seasonality and the scheduling of life history at different latitudes. Journal of Fish Biology, 41 (Supplement B): 161.178.

Conover, D. O. and Schultz, E. T. 1995. Phenotypic similarity and the evolutionary significance of countergradient variation. Trends in Ecology and Evolution, 10: 248–252.

Dentry, W. and Lindsey, C. C. 1978. Vertebral variation in zebrafish (*Brachydanio rerio*) related to the prefertilization temperature history of their parents. Canadian Journal of Zoology, 56: 280–283.

Doyle, R. W., Shackel, N. L., Basiao, Z., Uraiwan, S., Maricia, T., and Talbot, A. J. 1991. Selective diversification of aquaculture stocks: a proposal for economically sustainable genetic conservation. Canadian Journal of Fisheries and Aquatic Sciences, 48 (Supplement 1): 148–154.

Einum, S. and Fleming, I. A. 1997. Genetic divergence and interactions in the wild among native, farmed and hybrid Atlantic salmon. Journal of Fish Biology, 50: 634–651.

Elliott, J. M. and Hurley, M. A. A functional model for maximum growth of Atlantic salmon parr, *Salmo salar*, from two populations in north-west England. Functional Ecology. (In press.)

Fausch, K. D. 1984. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. Canadian Journal of Zoology, 62: 441–451.

Fenderson, O. C., Everhart, W. H., and Muth, K. M. 1968. Comparative agonistic and feeding behavior of hatchery-reared and wild salmon in aquaria. Journal of the Fisheries Research Board of Canada, 25: 1–14.

Fleming, I. A. 1995. Reproductive success and the genetic threat of cultured fish to wild populations. *In* Protection of aquatic biodiversity. Proceedings of the World Fisheries Congress, Theme 3, pp. 117–135. Ed. by D. P. Philipp, J. M. Epifanio, J. E. Marsden, and J. E. Claussen. Oxford and IBH Publishing, New Delhi, India. 282 pp.

Fleming, I. A., Jonsson, B., and Gross, M. R. 1994. Phenotypic divergence of sea-ranched, farmed, and wild salmon. Canadian Journal of Fisheries and Aquatic Sciences, 51: 2808–2824.

Fleming, I. A., Jonsson, B., Gross, M. R., and Lamberg, A. 1996. An experimental study of the reproductive behaviour and success of farmed and wild Atlantic salmon (*Salmo salar*). Journal of Applied Ecology, 33: 893–905.

Fleming, I. A., Lamberg, A., and Jonsson, B. 1997. Effects of early experience on the reproductive performance of Atlantic salmon. Behavioural Ecology, 8: 470–480.

Forseth, T. 1994. Bioenergetics in ecological and life history studies of fishes. PhD thesis, University of Trondheim, Norway.

Gjedrem, T., Gjerde, B., and Refstie, T. 1988. A review of quantitative genetic research in salmonids at AKVAFORSK. *In* Proceedings of the Second International Conference on Quantitative Genetics, pp. 527–535. Ed. by B. S. Weir, E. J. Eisen, M. M. Goodman, and G. Namkoong. Sinauer, Sunderland.

Gjedrem, T., Gjøen, H. M., and Gjerde, B. 1991. Genetic origin of Norwegian farmed Atlantic salmon. Aquaculture, 98: 41–50.

Gjerde, B. 1984. Response to individual selection for age at sexual maturity in Atlantic salmon. Aquaculture, 38: 229–240.

Gjerde, B. and Schaeffer, L. R. 1989. Body traits in rainbow trout. II. Estimates of heritabilities and of phenotypic and genetic correlations. Aquaculture, 80: 25–44.

Glebe, B. D., Appy, T. D., and Saunders, R. L. 1979. Variation in Atlantic salmon (*Salmo salar*) reproductive traits and their implications in breeding programs. ICES CM 1979/M: 23. 11 pp.

Hoar, W. S. 1988. The physiology of smolting salmonids. *In* Fish physiology. Volume 11B, The physiology of developing fish: viviparity and post hatching, pp. 275–343. Ed. by W. S. Hoar, and D. J. Randall. Academic Press, New York.

Hutchings, J. A. and Myers, R. A. 1994. The evolution of alternative mating strategies in variable environments. Evolutionary Ecology, 8: 256–268.

Johnsson, J. I. and Abrahams, M. V. 1991. Interbreeding with domestic strain increases foraging under threat of predation in juvenile steelhead trout (*Oncorhynchus mykiss*): an experimental study. Canadian Journal of Fisheries and Aquatic Sciences, 48: 243–247.

Johnsson, J. I., Petersson, E., Jönsson, E., Björnsson, B. Th., and Järvi, T. 1996. Domestication and growth hormone alter antipredator behaviour and growth patterns in juvenile brown trout, *Salmo trutta*. Canadian Journal of Fisheries and Aquatic Sciences, 53: 1546–1554.

Jonsson, N., Hansen, L. P., and Jonsson, B. 1991. Variation in age, size and repeat spawning of adult Atlantic salmon in relation to river discharge. Journal of Animal Ecology, 60: 937–947.

Jonsson, N., Jonsson, B., and Fleming, I. A. 1996. Does early growth cause a phenotypically plastic response in egg production of Atlantic salmon? Functional Ecology, 10: 89–96.

Kazakov, R. V. 1981. The effect of the size of Atlantic salmon, *Salmo salar* L., eggs on embryos and alevins. Journal of Fish Biology, 19: 353–360.

Metcalfe, N. B., Huntingford, F. A., and Thorpe, J. E. 1988. Feeding intensity, growth rates, and the establishment of life-history patterns in juvenile Atlantic salmon *Salmo salar*. Journal of Animal Ecology, 57: 463–474.

Metcalfe, N. B., Huntingford, F. A., Graham, W. D., and Thorpe, J. E. 1989. Early social status and the development of life-history strategies in Atlantic salmon. Proceedings of the Royal Society of London, Series B, 236: 7–19.

Metcalfe, N. B., Wright, P. J., and Thorpe, J. E. 1992. Relationships between social status, otolith size at first feeding and subsequent growth in Atlantic salmon (*Salmo salar*). Journal of Animal Ecology, 61: 585–589.

Moyle, P. B. 1969. Comparative behavior of young brook trout of domestic and wild origin. Progressive Fish-Culturist, 31: 51–59.

Økland, F., Jonsson, B., Jensen, A. J., and Hansen, L. P. 1993. Is there a threshold size regulating seaward migration of brown trout and Atlantic salmon? Journal of Fish Biology, 42: 541–550.

Olla, B. L., Davis, M. V., and Ryder, C. H. 1994. Behavioural deficits in hatchery-reared fish: potential effects on survival following release. Aquaculture and Fisheries Management, 25 (Supplement 1): 19–34.

Philipp, D. P. 1991. Genetic implications of introducing Florida largemouth bass, *Micropterus salmoides floridanus*. Canadian Journal of Fisheries and Aquatic Sciences, 48 (Supplement 1): 58–65.

Price, E. O. 1984. Behavioral aspects of animal domestication. Quarterly Review of Biology, 59: 1–32.

Reisenbichler, R. R. and McIntyre, J. D. 1977. Genetic differences in growth and survival of juvenile hatchery and wild steelhead trout, *Salmo gairdneri*. Journal of the Fisheries Research Board of Canada, 34: 123–128.

Reist, J. D. 1986. An empirical evaluation of coefficients used in residual and allometric adjustment of size covariation. Canadian Journal of Zoology, 64: 1363–1368.

Ruzzante, D. E. 1994. Domestication effects on aggressive and schooling behavior in fish. Aquaculture, 120: 1–24.

Ruzzante, D. E. and Doyle, R. W. 1991. Rapid behavioral changes in medaka (*Oryzias latipes*) caused by selection for competitive and noncompetitive growth. Evolution, 45: 1936–1946.

Ryman, N. and Ståhl, G. 1980. Genetic changes in hatchery stocks of brown trout (*Salmo trutta*). Canadian Journal of Fisheries and Aquatic Sciences, 37: 82–87.

Schramm, H. L., Jr. and Piper, R. G. (eds) 1995. Uses and effects of cultured fishes in aquatic ecosystems. American Fisheries Society Symposium, 15, 608 pp.

Swain, D. P. and Lindsey, C. C. 1986. Meristic variation in a clone of the cyprinodont fish *Rivulus marmoratus* related to temperature history of the parents and of the embryos. Canadian Journal of Zoology, 64: 1444–1459.

Swain, D. P. and Riddell, B. E. 1990. Variation in agonistic behavior between newly emerged juveniles from hatchery and wild populations of coho salmon, *Oncorhynchus kisutch*. Canadian Journal of Fisheries and Aquatic Sciences, 47: 566–571.

Swain, D. P., Riddell, B. E., and Murray, C. B. 1991. Morphological differences between hatchery and wild populations of coho salmon (*Oncorhynchus kisutch*): environmental versus genetic origin. Canadian Journal of Fisheries and Aquatic Sciences, 48: 1783–1791.

Taylor, E. B. 1986. Differences in morphology between wild and hatchery populations of juvenile coho salmon. Progressive Fish-culturist, 48: 171–176.

Thorpe, J. E. 1986. Age at first maturity in Atlantic salmon, *Salmo salar*: freshwater period and conflicts with smolting. Canadian Special Publications in Fisheries and Aquatic Sciences, 89: 7–14.

Thorpe, J. E., Miles, M. S., and Keay, D. S. 1984. Developmental rate, fecundity and egg size in Atlantic salmon, *Salmo salar* L. Aquaculture, 43: 289–305.

Thorpe, J. E., Mangel, M., Metcalfe, N. B., and Huntingford, F. A. Modeling the proximate basis of salmonid life history variation, with application to Atlantic salmon, *Salmo salar* L. Evolutionary ecology. (In press.)

Thorpe, R. S. 1983. A review of the numerical methods for recognizing and analysing racial differentiation. *In* Numerical taxonomy, pp. 404–423. Ed. by J. Felsenstein. Springer-Verlag, Berlin.

Weatherley, A. H. and Gill, H. S. 1987. The biology of fish growth. Academic Press, London. 443 pp.

Winans, G. 1984. Multivariate morphometric variability in Pacific salmon: technical demonstration. Canadian Journal of Fisheries and Aquatic Sciences, 41: 1150–1159.

Youngson, A. F., Martin, S. A. M., Jordan, W. C., and Verspoor, E. 1991. Genetic protein variation in Atlantic salmon in Scotland: comparison of wild and farmed fish. Aquaculture, 98: 231–242.

Journal of Fish Biology (1997) **50**, 634–651

Genetic divergence and interactions in the wild among native, farmed and hybrid Atlantic salmon

S. EINUM* AND I. A. FLEMING†

**Norwegian University of Science and Technology, Department of Zoology, N-7055 Dragvoll, Norway and †Norwegian Institute for Nature Research, Tungasletta 2, N-7005 Trondheim, Norway*

(*Received 16 July 1996, Accepted 2 October 1996*)

There is concern that the progeny resulting from the spawnings of escaped farmed Atlantic salmon may compete with and disrupt native salmon populations. This study compared, both in the hatchery and in the wild, fitness-related traits and examined interactions among farmed, native and hybrid 0+ parr derived from controlled crosses and reared under common conditions. The farmed salmon were seventh-generation fish from the principal commercial strain in Norway and native salmon were from the rivers Imsa and Lone, Norway. In the hatchery, farmed salmon were more aggressive than both native populations and tended to dominate them in pairwise contests. Farmed salmon were also more prone to risk, leaving cover sooner after a simulated predator attack, and had higher growth rates than native fish. Interbreeding between farmed and native fish generally resulted in intermediate expression of the above traits. There was, however, evidence of hybrid vigour in Lone/farmed crosses which were able to dominate both pure Lone and farmed parr in pairwise contests. In the wild, observations of habitat use and diet suggested that the populations compete for territory and food, and both farmed fish and hybrids expressed higher growth rates than native fish. Our results suggest that these innate differences in behaviour and growth, that probably are linked closely to fitness, will threaten native populations through competition and disruption of local adaptations.

Key words: aquaculture; domestication; *Salmo salar*; aggression; predation risk; growth.

INTRODUCTION

It is becoming increasingly clear that introduction of cultured fishes may have negative effects on native fish populations (Hindar *et al.*, 1991; Saunders, 1991; Waples, 1991; Heggberget *et al.*, 1993). The Atlantic salmon *Salmo salar* L., is one of the species believed to be threatened by such introductions. Large numbers of farmed salmon escape from aquaculture facilities each year and enter rivers to spawn (Gausen & Moen, 1991; Webb *et al.*, 1993; Lund *et al.*, 1996). In some Norwegian rivers, farmed fish are reported even to outnumber the native fish. Successful breeding of farmed fish (Lura & Sœgrov, 1991; Webb *et al.*, 1993) and the resultant hybridization with native salmon (Crozier, 1993; Fleming *et al.*, 1996) may represent an ecological and genetic threat to native populations.

Interbreeding between farmed and native salmon threatens the local adaptations that appear to be so prevalent among salmonid populations (reviewed by Ricker, 1972; Taylor, 1991). Farmed salmon have been exposed to intended and unintended artificial selection during domestication that can result in evolutionary changes causing them to diverge from their wild conspecifics

---

†Author to whom correspondence should be sent. Tel.: +47 73 58 05 00; fax: +47 73 91 54 33; email: ian.fleming@nina.nina.no.

0022–1112/97/030634+18 $25.00/0/jb960330

(reviewed by Fleming, 1995). Furthermore, the farmed salmon are derived often from non-indigenous individuals (Gjedrem *et al.*, 1991). Thus, competition and interbreeding with locally adapted populations may result in a loss of biological diversity.

Although some differences between cultured and wild fish have been documented (e.g. Swain & Riddell, 1990; Mesa, 1991; Ruzzante & Doyle, 1991; Berejikian, 1995), little is known about the performance of native/farmed hybrids, particularly in the wild. Yet, breeding by farmed salmon in native populations is most likely to produce hybrid offspring because of a sex bias in the reproductive performance of farmed spawners and non-discriminatory mate choice by males (Fleming *et al.*, 1996). In general, there are two possible outcomes of hybridization (reviewed by Leary *et al.*, 1995). If the two parental populations are somewhat inbred, the hybrids may experience an increase in fitness relative to that of the parental populations due to heterosis. Alternatively, hybridization between two reproductively isolated populations may result in a breakdown of local adaptations and/or co-adapted gene complexes and thus entail reduced fitness through outbreeding depression. Hybrids from crosses between native and non-native fish may then express either intermediate or poorer performance than the two parental populations. In fish, outbreeding depression seems to prevail (e.g. Ferguson *et al.*, 1985; Lachance & Magnan, 1990; Philipp & Whitt, 1991), but hybrid vigour has also been reported (e.g. Webster & Flick, 1981; Ferguson *et al.*, 1988). While the outcome will depend in part on genetic differences between the populations (Emlen, 1991), it would be difficult to predict even when the expression of parental traits are known.

Most comparisons of farmed and native salmon have been conducted in a hatchery environment. Although such studies are important to establish genetic differences in certain traits, only tentative inferences can be made about performance of farmed fish in the wild. Knowledge about effects of hybridization and performance of farmed and native/farmed hybrids in the wild is therefore badly needed to assess the effects spawning by escaped farmed salmon has on productivity and viability of native populations.

The purpose of this study was to test for genetically based differences in some fitness-related traits and to compare performance in the wild of juvenile Atlantic salmon of native, farmed and hybrid origin. Native salmon were derived from two Norwegian populations and farmed salmon were from the principal commercial strain used in Norway. Crosses were made and reared in a common environment. The offspring of these crosses were then contrasted for their (1) ability to dominate in pairwise encounters; (2) level of overt aggression; (3) anti-predator behaviour; and (4) growth in a series of controlled experiments. Finally, the survival, growth, diet composition and habitat use of the juveniles in the wild were compared.

MATERIALS AND METHODS

POPULATIONS

Adult salmon from the River Imsa (four females and eight males), the River Lone (four females and eight males) and from a sixth-generation strain of farmed salmon developed at Sunndalsora, Norway (eight females and eight males) were bred to create pure and hybrid offspring. The River Imsa (described in Fleming *et al.*, 1994) is a small river with a 128-km^2 catchment area and is located in south-western Norway (58°59′ N, 5°58′ E) near the city of Stavanger. Most salmon in this population mature after 1 year in the ocean, but there is a significant return of two sea-winter fish. In recent years, some fish have been sea-ranched (i.e. hatchery reared as freshwater juveniles and then released to range freely in the ocean), and currently only first-generation sea-ranched fish are allowed to spawn in the river with the wild salmon. The River Lone is also a small river with a 64-km^2 catchment area and is located in western Norway (60°32′ N, 5°30′ E) near the city of Bergen. Nearly all salmon in this population attain sexual maturity after one winter at sea (Hansen & Jonsson, 1990). The River Lone fish used in the experiments were the offspring of parents that had been sea-ranched at the Norwegian Institute of Nature Research (NINA) Research Station, located by the River Imsa, for the first time. The Sunndalsøra salmon were developed for the Norwegian fish farming industry and have been bred selectively since 1971 to attain certain characters such as increased growth and delayed maturity (Gjedrem *et al.*, 1991). The first generation of fish were derived from 41 different wild salmon populations, including the rivers Imsa and Lone. However, by the fourth generation, all four brood lines were dominated by from one to three populations characterized by fast-growing and late-maturing fish (i.e. not including rivers Imsa and Lone) (Gjedrem *et al.*, 1991). Fish from this selection program now constitute >80% of commercial salmon production in Norway.

CROSSES

The adult salmon were bred artificially at the NINA Research Station to create the following family groups: pure Imsa (1994, n=4; 1995, n=4), pure Lone (1994. n=4). Imsa/farmed hybrids (1994, n=8; 1995, n=4), Lone/farmed hybrids (n=9, 1994) and pure farmed (1994, n=7; 1995, $n \geqslant 8$). In 1995, the 32 family groups of alevins were transferred from egg incubators to 0·36-m^2 tangential-flow tanks at the onset of feeding. They were given an excess of commercial food pellets (Felleskjøpet) using automatic feeders dispensing food at 10-min intervals. Each family group was reduced to 200 randomly chosen individuals and the groups were rotated among the tanks on 19 April. This was done to avoid differences in density-dependent effects on growth and aggressiveness, and to minimize tank effects. On 29 June, 500 parr from each population (i.e. each type of cross) were placed in separate 2-m^2 tangential-flow tanks. They were chosen so that each family group within a population was equally represented. In 1996, the fish from each population were placed in separate 1-m^2 tangential-flow tanks at the onset of feeding and given food as above.

Each fish was used only once throughout the experimental period, being marked on the tail fin with alcian blue dye following use and before being returned to the holding tank.

HATCHERY EXPERIMENTS

Dominance comparisons

To determine relative dominance among native, farmed and hybrid fish, a methodology similar to that of Metcalfe *et al.* (1992) was used. Six stream channels with V-shaped cross-sections, each consisting of five 20-cm long sections, were built of wood and surrounded by black plastic sheets with observation slits. The sections within the channels were separated by perforated plastic plates, and an identical plate between the water inlet and the first section prevented turbulence. Water depth was maintained at 4 cm, and velocity varied between 1·4 and 2·0 cm s^{-1} in the different channels. The V-shaped cross-section was designed to preclude the possibility of two fish beside each other on the bottom of the channel, and thus ease the determination of dominance (see below). Food pellets were supplied through PVC pipes extending from holes in the blind to the upstream end of each channel section. Mean water temperature ± S.D. throughout the experiment was 14·8 ± 0·6° C.

Each fish was anaesthetized lightly with chlorobutanol in cooled water (*c.* 4° C). weighed (±0·01 g), measured (fork length ± 0·1 cm) and marked alternately on left or right pectoral fin with alcian blue dye for recognition. Fish from different populations were derived from rearing groups of similar mean body size and matched in pairs of

TABLE I. Weight (g) and fork length (cm) of fish used in the dominance experiment

Pairs	Weight ± S.D.	*P*	Length ± S.D.	*P*
Imsa	1·57 ± 0·16	0·001	5·13 ± 0·13	<0·001
Farmed	1·52 ± 0·20		5·33 ± 0·20	
Imsa hybrids	1·52 ± 0·23	0·272	5·28 ± 0·22	0·767
Farmed	1·47 ± 0·28		5·28 ± 0·21	
Imsa	1·46 ± 0·18	0·464	5·08 ± 0·17	0·879
Imsa hybrids	1·44 ± 0·18		5·08 ± 0·18	
Lone	1·20 ± 0·15	0·251	4·79 ± 0·16	0·311
Farmed	1·19 ± 0·15		4·80 ± 0·18	
Lone hybrids	1·85 ± 0·34	0·309	5·57 ± 0·30	0·944
Farmed	1·82 ± 0·33		5·56 ± 0·32	
Lone	1·34 ± 0·18	0·358	4·99 ± 0·19	0·116
Lone hybrids	1·32 ± 0·17		4·97 ± 0·19	
Imsa	1·29 ± 0·23	0·690	4·75 ± 0·31	0·802
Lone	1·28 ± 0·27		4·74 ± 0·34	

Differences were tested by two-tailed Wilcoxon matched-pairs signed-ranks test (length) and *t*-test for paired samples (weight). Data presented as mean ± S.D..

similar size. Rearing groups of similar mean body size were chosen to avoid comparing dominant fish from one group and subordinate fish from another (cf. Huntingford *et al.*, 1990). Fish larger than the mean size of their family group, and thus probably dominant within their rearing group, were chosen also. There were no significant differences in the weight and length of the fish used in the pairwise contests between populations, except that between Imsa and farmed fish (Table I). Difficulties in finding rearing groups of Imsa and farmed fish having similar weight–length ratios meant that fish were paired such that the differences in weight and length were intermediate. As a result, Imsa fish were heavier than the farmed fish, but shorter in length.

Following marking, the fish were added to the channels and allowed to acclimatize for 2 days without food before observations began. The fish were observed for 1 min every 20 min for a period of 2 h, and scored for position and foraging success, both of which correlate well with dominance (Fausch, 1984). Preferred position was assumed to be upstream of the other fish because this gave first access to food (Metcalfe *et al.*, 1992). During each observation, one point was given for occupying this position and two points for obtaining a food pellet dropped into the current. Larger weighting was given to obtaining the pellet because dominance appears more highly correlated to feeding than to position (Metcalfe *et al.*, 1989). Two points were also given each time a fish made an unreciprocated attack towards the other, and given four points if the fish contested and won the pellet. A fish was determined to be the dominant of the pair whenever its total score after the seven observations was three or more points greater than that of its opponent. A difference of less than three points resulted in an unresolved trial.

The experiment was carried out between 25 May and 6 June 1995. The results suggested that there may be differences between the two native populations in ability to dominate. Thus, we tested 30 pairs of pure Lone *v.* pure Imsa between 2 and 5 June 1996.

Within-population aggression

To test for innate differences in aggressiveness among populations, groups of eight fish from a population were weighed and placed into one of four stream tanks. Water depth was maintained at 5 cm and water flow was 8 l min^{-1}. Black plastic was erected around the tanks to avoid disturbances. Mean water temperature ± S.D. throughout the experiment was 19·9 ± 1·7° C.

Mean size and degree of variance in size within a replicate may affect social structure, and thus the frequency of aggressive interactions (e.g. Symons, 1968; Frey & Miller,

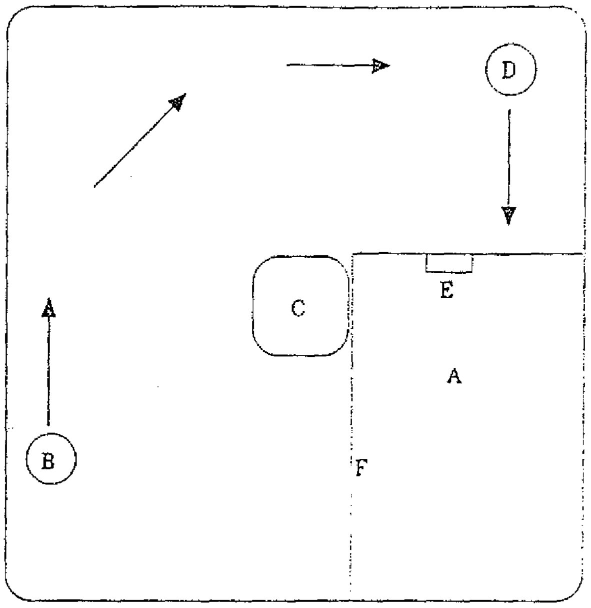


FIG. 1. The 90 × 110-cm section (A) used to test behavioural responses to exposure of a simulated predator. Water inlet (B), water outlet (C), automatic feeder (D), hide (E) and screen (F) are indicated. Water depth was maintained at 30 cm and water flow was 12 l min^{-1} (arrows indicate flow direction).

1972). Therefore, fish were chosen carefully to avoid differences among populations in these parameters (overall mean=5·01 g, $F_{4,315}=0·45$, $P=0·769$; overall variance ± 0·25. $F_{4,35}=0·93$, $P=0·460$).

The fish were allowed 2 days to acclimate to the stream tank, during which time they were fed 1 g of food pellets delivered through a PVC pipe to the water inlet twice daily. Then, five 10-min sequences were recorded by video, one each hour for a 5-h period with the fish being fed once after each sequence. Between 17 July and 10 August eight replicates were conducted with each of the five populations (i.e. Imsa, Imsa/farmed hybrids, Lone, Lone/farmed hybrids and pure farmed). Each population was tested equally many times in each of the experimental tanks, controlling for tank effects.

The video tapes were analysed later for overt aggression. This experimental design gave no opportunity to quantify displays or to identify individuals. thus only the total number of charges, number of chases and duration of chases were recorded. A charge was defined as a 'rapid, direct movement by an aggressor towards another fish and distinguished by rapid acceleration' (*sensu* Kratt & Smith, 1979), while a chase was a 'prolonged approach or charge by aggressor and flight by chased fish from its original station' (*sensu* Swain & Holtby, 1989). If the flight by the chased fish lasted <1 s, the event was registered as a charge.

Behavioural response to a simulated predator

In this experiment, the behavioural responses of pure Imsa, Imsa/farmed hybrid and pure farmed fish to a simulated predator were examined. The fish were tested in 90 × 110-cm sections of five tangential-flow stream tanks (Fig. 1). The sections were screened off by perforated plastic plates. A hide consisting of a 3 × 3 × 7-cm tunnel with a sealed end provided refuge and was designed to prevent the fish from feeding without leaving the hide. An automatic feeder released food pellets every 10 min during the acclimatization period. Black plastic erected around the tank created a blind to prevent unintentional disturbance of the fish. Mean water temperature ± S.D. throughout the experiments was 20·1 ± 1·6° C.

A fish was weighed (± 0·01 g) and added to each of the five tanks. Simultaneously, two fish from two of the populations and one from the third were tested. and each population was tested equally many times in the different tanks. controlling for tank effects. The fish from different populations were matched for weight such that no significant difference existed ($F_{2,75}=0{\cdot}50$, $P=0{\cdot}610$).

After an acclimatization period of at least 18 h, the fish was exposed to a 60-cm long fibreglass brown trout *Salmo trutta* L., model for 10 s. This was done by placing the model into the same part of the tank as the fish, through a hole in the blind. At the same time, the automatic feeder was turned off so that differences in the timing of exposure relative to the feeding interval did not affect the motivation of the fish to come out from the hide. Following exposure, the fish was recorded by video. The first time the fish reappeared from the hide it often remained out for only a few seconds before returning, appearing to be still affected by the exposure. Thus, both the time elapsed before first reappearance, and the time elapsed until the fish had remained out for a total of 1 min was recorded. Between 12 July and 7 August 1995, 26 replicates were conducted with each of the three populations.

Growth in hatchery

On 11 August 1995, 60 fish from each of three populations, Imsa, Imsa/farmed hybrids and farmed fish, were anaesthetized with chlorobutanol, weighed (± 0·01 g) and a passive integrated transponder (PIT) tag, that allowed individual recognition, was implanted into the body cavity. The fish were divided into four mixed groups of 45 individuals containing 15 fish from each of the populations and transferred to separate 1-m^2 tangential-flow tanks having a water depth of 15 cm and a flow of 9 l min^{-1}. There were no differences in mean (overall=6·91 g, $P>0{\cdot}70$ in all cases, one-way ANOVA) nor in variance of initial weight (overall=3·25, $P>0{\cdot}05$ in all cases, Levene test) among the populations in any of the tanks. In addition, nine control groups (three for each population) each consisting of 45 non-tagged individuals of similar size, were placed in tanks identical to those of the mixed groups. Food pellets were dispensed from automatic feeders at 10-min intervals. The group were rotated among the tanks on 1 September to reduce tank effects. Mean water temperature ± S.D. throughout the experiment was 17·9 ± 1·8° C. Fish dying during the experiment were weighed and replaced with fish from the same population of similar size to avoid effects of unequal density.

On 14 September the fish were removed from the tanks and weighed (± 0·01 g). Individual growth was registered in the pit-tagged groups, and fish dying during the experiment were not included in the analysis. Mean growth within each control tank was calculated by adding the summed difference between all dead fish and replacement fish to the total weight by the end of the experiment, subtracting the total initial weight, and then dividing this sum by the number of fish. Specific growth rate (G) was calculated as:

$$G=100(\log_e W_2-\log_e W_1)\,d^{-1}$$

where W_2 and W_1 are final and initial weights respectively in g and d is the length of the experiment in days.

RELEASE EXPERIMENTS

Study area

Release experiments were conducted in 1995 and 1996 in a 70-m section of the Stream Ålabekk (Fig. 2), a tributary to the River Imsa which contains natural populations of salmon, brown trout and eel *Anguilla anguilla* L. The downstream end of the study area was screened off by a 200 × 100-cm steel plate, perforated with 10-mm holes, and attached to a wooden frame. The upstream end of the study area was delimited by a waterfall that prevented extensive upstream dispersion. This waterfall was enlarged artificially in 1996. Important habitat parameters (e.g. Heggenes, 1990) were measured in the middle of the brook at 1-m intervals throughout the study area on 6 August 1995. Mean width and depth of the study site were 191 cm (range 60–310 cm) and 23 cm (range 4–58 cm), respectively. Mean current, measured in the middle of the water

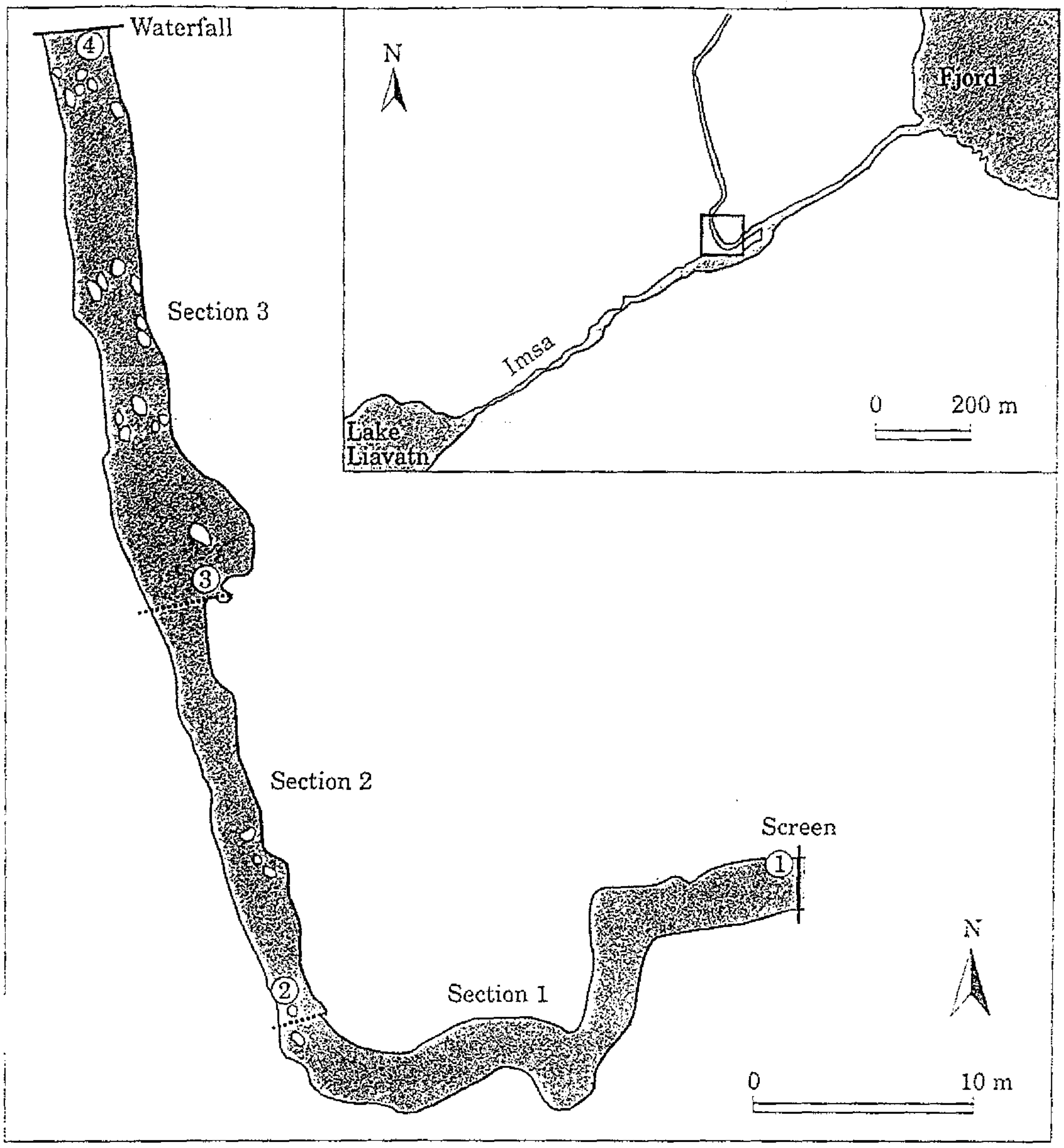


FIG. 2. Location and map of the study area on the Stream Ålabekk, with release localities 1–4 marked.

column using a current reader with a 1·8-cm propeller, was 16 cm s^{-1} (range: 0–98 cm s^{-1}) and the substratum varied from fine sand to gravel and bedrock. Mean water temperature ± S.D. was 19·9 ± 1·8° C in 1995 and 15·5 ± 1·3° C in 1996.

Release and recapturing

In both years, 80 0+ parr from each of the three populations (Imsa, Imsa/farmed hybrids and farmed) were anaesthetized using chlorobutanol and weighed (±0·01 g), matching the populations such that mean weight and variance did not differ significantly (1995, overall mean ± S.D. = 3·37 g ± 0·72; 1996, overall mean ± S.D. = 2·40 g ± 0·45; both years, $P > 0{\cdot}05$). The fish were tagged with PIT tags and divided into four groups, each consisting of 20 individuals from each population, and placed in separate 2-m^2 tangential-flow tanks for recovery. The following day (1995, 10 July; 1996, 4 June), they were released into the stream at four locations (Fig. 2).

The study area was electrofished four times between 10–12 August and again between 13–14 September in 1995, and seven times between 1–5 July and again between 1–5 August in 1996. The site of recapture of each fish was recorded on a map of the stream. To examine distribution, the stream was divided into three sections of approximately

TABLE II. Results from the dominance experiment

Comparisons	*n*	Dominant	Unresolved	Subordinate	*P*
Imsa comparisons					
Farmed *v.* Imsa hybrids	30	12	9	9	0·664
Imsa hybrids *v.* Imsa	29	14	8	7	0·182
Farmed *v.* Imsa	42	30	2	10	0·003*
Lone comparisons					
Lone hybrids *v.* Farmed	25	18	3	4	0·004*
Lone hybrids *v.* Lone	28	17	6	5	0·017*
Farmed *v.* Lone	30	16	5	9	0·230
Native fish comparison					
Lone *v.* Imsa	30	15	6	9	0·308

*Significantly different at the 0·05 level after adjustment by sequential Bonferroni method.
Dominant denotes the number of pairs where the first population mentioned in the comparisons column was assessed as dominant. Differences were tested by Sign test.

similar length (Fig. 2). Section 1 was relatively deep (mean ± S.D. = 35 ± 12 cm) and had low current (3 ± 3 cm s^{-1}). Sections 2 and 3 were shallower (13 ± 8 and 15 ± 7 cm, respectively) and had higher current (27 ± 28 and 22 ± 12 cm s^{-1}, respectively). In addition, in 1995 depth and current in the middle of the water column at the position were measured where the fish was observed first during electrofishing.

Following each electrofishing, the fish were identified by their pit-tag and weighed (± 0·01 g). In 1995, stomach contents of all fish were identified and counted under a stereoscopic dissecting microscope.

STATISTICS

Data that did not meet requirements for parametric analyses, before or following log or square root transformation, were analysed using nonparametric statistics. Multiple comparisons were adjusted for using either the least significant difference (LSD) method associated with ANOVA or sequential Bonferroni tests (Rice, 1989). All statistical analyses were performed with the Statistical Package for the Social Sciences (SPSS version 6.0).

RESULTS

HATCHERY EXPERIMENTS

Dominance comparisons

In 81·8% of the pairs, one fish was assessed as dominant; the remaining pairs were unresolved (i.e. difference in score of less than three points). In three out of seven comparisons, one population had a significantly higher frequency of dominant individuals than the other (Table II). Farmed fish dominated fish from Imsa, with Imsa hybrids being intermediate between the two pure populations. In contrast, Lone hybrids dominated both pure farmed and pure Lone fish. In comparisons between the two pure native populations, Lone fish dominated more contests than Imsa fish; however, the difference was not significant.

To test if differences in size within pairs influenced the outcome of the dominance comparison, pairwise differences in weight and length were compared with differences in score using pooled data. No significant correlation was found

TABLE III. Mean number of charges ± S.E. per 10-min period (eight replicates per population)

Population	Mean ± S.E.	Imsa	Imsa hybrids	Lone	Lone hybrids
Imsa	11·9 ± 2·2	—	—	—	—
Imsa hybrids	10·5 ± 1·6	NS	—	—	—
Lone	11·7 ± 1·6	NS	NS	—	—
Lone hybrids	19·6 ± 3·4	NS	*	NS	—
Farmed	20·8 ± 4·5	*	*	*	NS

*Pairs of populations significantly different at the 0·05 level; NS, no significant difference (one-way LSD multiple range test).

TABLE IV. Mean number of chases per 10-min period and mean duration of each chase in seconds (eight replicates per population)

Population	Number of chases ± S.E.	Duration chase ± S.E.
Imsa	2·2 ± 0·9	10·1 ± 3·8
Imsa hybrids	1·0 ± 0·4	5·5 ± 2·4
Lone	1·1 ± 0·5	5·1 ± 2·2
Lone hybrids	0·9 ± 0·3	4·3 ± 1·6
Farmed	1·8 ± 0·6	8·8 ± 2·8

($n=184$; weight: $r=0{\cdot}05$, $P=0{\cdot}244$; length: $r=0{\cdot}09$, $P=0{\cdot}203$, Spearman rank correlations).

Within-population aggression

The frequency of charges differed significantly among populations ($F_{4,39}=4{\cdot}00$, $P=0{\cdot}015$; controlling for tank effect $F_{3,39}=4{\cdot}45$, $P=0{\cdot}015$), with farmed fish and Lone hybrids having higher frequencies than the other three populations (Table III). In pairwise comparison, farmed fish differed significantly from Lone, Imsa and Imsa hybrid fish, and Lone hybrids differed from Imsa hybrids. There was no significant difference among populations in the frequency of chases ($F_{4,39}=1{\cdot}08$, $P=0{\cdot}393$; tank effect $F_{3,39}=1{\cdot}51$, $P=0{\cdot}240$), nor in the duration of chases ($F_{4,39}=0{\cdot}49$, $P=0{\cdot}743$; tank effect $F_{3,39}=0{\cdot}31$, $P=0{\cdot}816$) (Table IV).

When charges and chases were combined, forming the new variable overt aggression, the Lone hybrids and pure farmed salmon still showed the highest values, and there was a significant difference among populations ($F_{4,39}=3{\cdot}11$, $P=0{\cdot}038$; tank effect $F_{3,39}=4{\cdot}37$, $P=0{\cdot}016$) (Fig. 3). However, no significant pairwise differences existed ($P>0{\cdot}05$, one-way LSD multiple range test). To test if the level of aggressive interactions was affected by the degree of variance in weight within a replicate, variance was compared with frequency of overt aggression using pooled data. No significant correlation was found ($r=-0{\cdot}15$, $n=40$ tanks, $P=0{\cdot}356$, Spearman rank correlation).

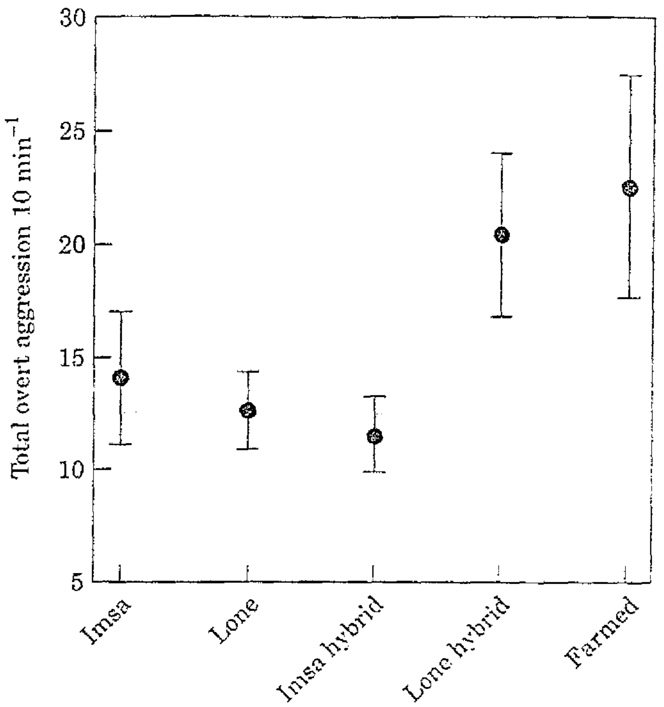


FIG. 3. Mean number of total overt aggression (charges and chases combined) (± S.E.) observed during 10-min periods in groups of eight salmon juveniles from the different populations.

Behavioural response to a simulated predator

Behaviour of the juvenile salmon when exposed to the trout model was variable. Most fish darted for cover immediately, however, some froze motionless at their feeding station and then swam into the hide some time after the model was removed. Mean time elapsed from onset of exposure until the fish was in the hide was 14·9 s, and did not differ among populations ($\chi^2=0{\cdot}89$, d.f.=2, $P=0{\cdot}642$, Kruskall–Wallis one-way ANOVA). Nor did the frequency with which the different populations performed the two behaviours ($\chi^2=0{\cdot}16$, d.f.=2, $P=0{\cdot}921$, Pearson χ^2). Both time elapsed before first reappearance ($\chi^2=11{\cdot}26$, d.f.=2, $P=0{\cdot}004$, Kruskall–Wallis one-way ANOVA) and before the fish had remained out for a total of 1 min ($\chi^2=11{\cdot}67$, d.f.=2, $P=0{\cdot}003$) differed significantly among populations (Fig. 4). Imsa fish took significantly longer than Imsa hybrids and pure farmed fish for both variables ($P<0{\cdot}05$, Mann–Whitney U-tests adjusted for multiple comparisons by sequential Bonferroni tests). There were no significant differences between Imsa hybrids and pure farmed fish in either of the variables (first reappearance: $P=0{\cdot}341$; reappearance for 1 min: $P=0{\cdot}400$). To test if weight affected either of the variables, Spearman correlation coefficients were calculated on pooled data. No correlation was found ($n=78$ fish, first reappearance: $r=0{\cdot}16$, $P=0{\cdot}167$; reappearance for 1 min: $r=0{\cdot}05$, $P=0{\cdot}692$).

Growth in hatchery

A significant difference in growth was found among the populations in the mixed tanks ($F_{2,106}=6{\cdot}53$, $P=0{\cdot}002$; controlling for tank effect $F_{2,106}=10{\cdot}49$, $P<0{\cdot}001$) (Fig. 5). Farmed fish grew faster than both pure Imsa ($F_{1,73}=5{\cdot}60$, $P=0{\cdot}021$, tank effect $F_{2,73}=7{\cdot}32$, $P=0{\cdot}001$) and Imsa hybrids ($F_{1,75}=10{\cdot}53$,

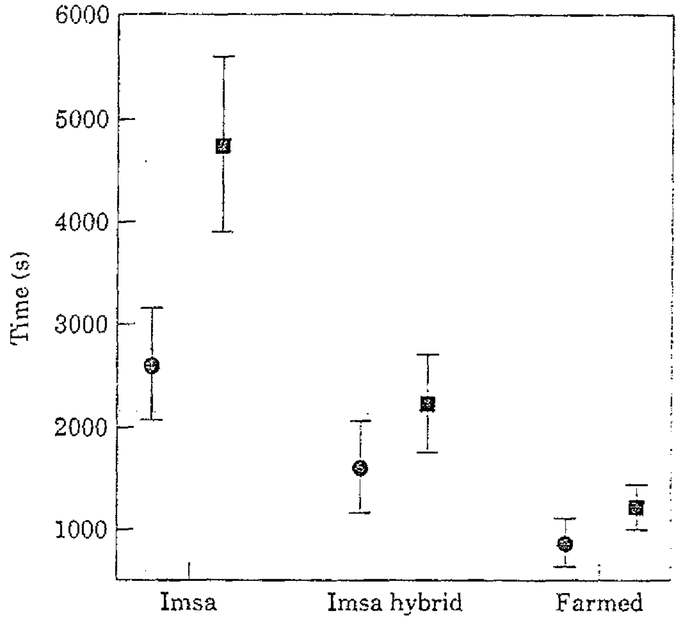


FIG. 4. Time spent by juvenile salmon from the different populations in a hide after exposure to a brown trout model. Data are mean values ± S.E. of time before first reappearance (●) and before remaining out for a total of 1 min (▨).

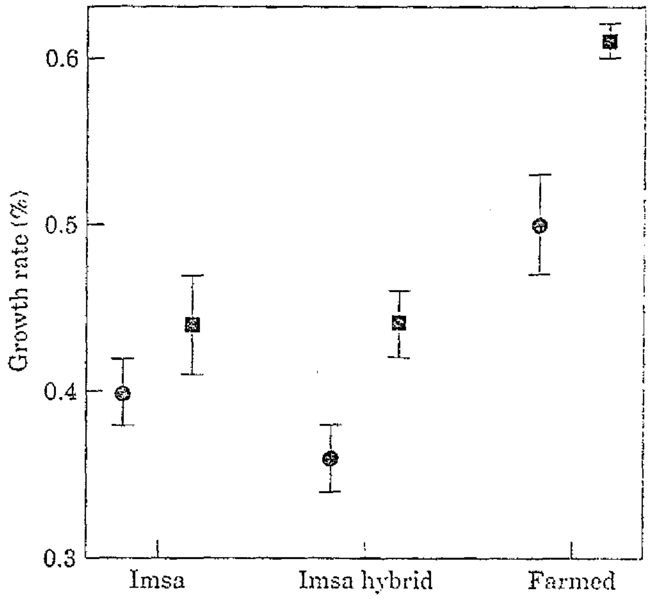


FIG. 5. Growth of salmon from the different populations in the hatchery, expressed as mean specific growth rate (% g g^{-1} day^{-1}) ± S.E. ●, Mixed groups; ▨, control groups.

$P=0{\cdot}002$, tank effect $F_{2,75}=4{\cdot}54$, $P=0{\cdot}014$). There was no significant difference between pure Imsa fish and Imsa hybrids ($F_{1,79}=1{\cdot}68$, $P=0{\cdot}199$, tank effect $F_{2,79}=11{\cdot}38$, $P<0{\cdot}001$). The controls, where only mean growth rate of fish within tanks could be calculated, showed the same tendency (Fig. 5). However, although the differences in mean growth were larger in the controls, they were not significant due to small sample sizes ($\chi^2=5{\cdot}42$, d.f.=2, $P=0{\cdot}067$, Kruskal-Wallis one-way ANOVA).

RELEASE EXPERIMENTS

Recapture rates and growth

Overall recapture rates were 41·7% in 1995 and 63·3% in 1996. Some fish had lost their PIT tags and this made identification impossible in 27% of the cases in 1995 and 3% in 1996. These fish were excluded from further analysis. There were no significant differences in recapture rates among populations in either of the years or when data from the two years were pooled ($P>0{\cdot}05$ in all cases, χ^2 test) (Fig. 6). Distribution in the stream differed between years ($\chi^2=7{\cdot}08$, d.f.$=2$, $P=0{\cdot}029$), but not among populations (1995, $\chi^2=5{\cdot}66$, d.f.$=4$, $P=0{\cdot}226$; 1996, $\chi^2=6{\cdot}33$, d.f.$=4$, $P=0{\cdot}176$) (Fig. 6). A flood made dispersal possible during a short period each year, but repeated electrofishing in a 50-m section above and below the study area indicated low dispersal rates (1995, two hybrids and four farmed; 1996, three Imsa, five hybrids and three farmed).

A significant difference in growth rate was found among the populations when combining data from the two years ($F_{2,220}=5{\cdot}56$, $P=0{\cdot}004$; controlling for year effect $F_{1,220}=42{\cdot}35$, $P<0{\cdot}001$) (Fig. 6). Fish from Imsa had a lower growth rate than both farmed fish ($F_{1,132}=9{\cdot}10$, $P=0{\cdot}003$; year effect $F_{1,132}=104{\cdot}93$, $P<0{\cdot}001$) and hybrids ($F_{1,158}=9{\cdot}15$, $P=0{\cdot}003$: year effect $F_{1,158}=172{\cdot}75$, $P<0{\cdot}001$). There was no significant difference between farmed fish and hybrids ($F_{1,149}=0{\cdot}05$, $P=0{\cdot}882$; year effect $F_{1,149}=145{\cdot}94$, $P<0{\cdot}001$). There was a significant year–population interaction in growth, with farmed fish expressing highest growth rates in 1995 and hybrid fish in 1996 ($F_{2,220}=3{\cdot}19$, $P=0{\cdot}043$).

Habitat use and diet

There were no significant differences among populations in current ($\chi^2=5{\cdot}86$, d.f.$=2$, $P=0{\cdot}053$) or depth ($\chi^2=2{\cdot}86$, d.f.$=2$, $P=0{\cdot}239$) occupied. Farmed fish, however, tended to be found in slower flowing parts of the stream than fish from the two other populations (Fig. 7).

The five most important groups of invertebrates in the stomach samples were: (1) Chironomidae, (2) Trichoptera, (3) surface insects, (4) Plecoptera, and (5) Ephemeroptera (Fig. 8). Together these constituted 91·1% of the total number of prey. There was some variation in diet composition among populations, but no significant differences were observed ($P>0{\cdot}05$ in all prey types, Kruskall–Wallis one-way ANOVA adjusted for multiple comparisons by sequential Bonferroni method).

DISCUSSION

HATCHERY EXPERIMENTS

This study has demonstrated that aggression and response to a predator, two ecologically important aspects of behaviour, differ among farmed and native fish and their hybrids. Farmed fish were more aggressive, having a higher frequency of charges than both populations of native fish studied. Moreover, in pairwise contests, farmed fish dominated River Imsa fish and won more contests with River Lone fish, though the latter difference was not significant. These results may be partly due to the different genetic origins of the populations prior to farming. Similar findings of higher aggressiveness among cultured than wild

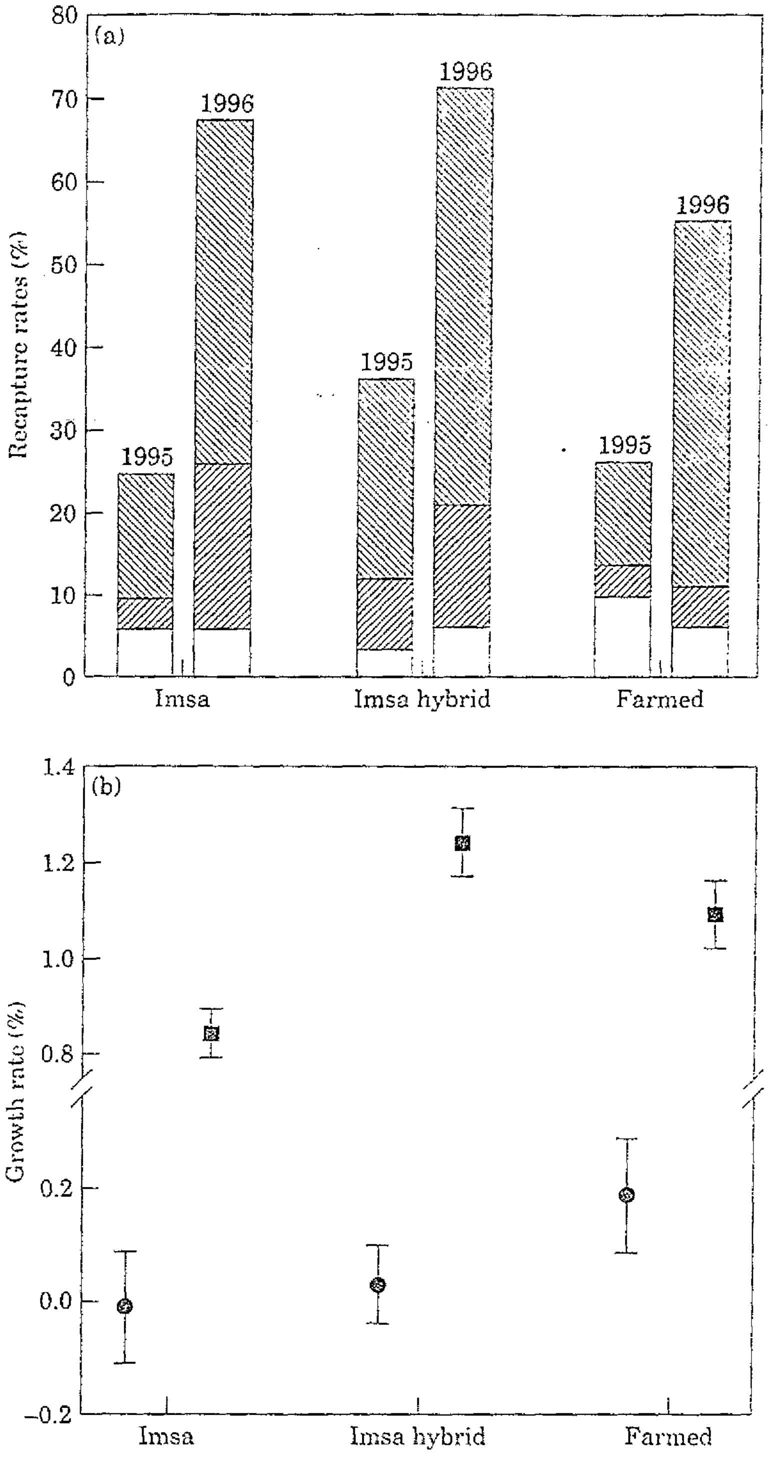


Fig. 6. (a) Recapture rates and distribution (% of released fish) of the different populations released in the Stream Ålabekk in the different years and (b) mean specific growth rates (% g g^{-1} day^{-1}) in 1995 (◉) and 1996 (▣). Error bars denote s.e. ☐, Section 1; ▨, section 2; ▧, section 3.

salmonids, however, have been observed previously (Swain & Riddell, 1990; Mesa, 1991; but see Ruzzante & Doyle, 1991; Ruzzante, 1994).

The effects of hybridization with farmed fish differed between the two native populations. Lone hybrids were not only absolutely more aggressive than Imsa hybrids, but also relatively more aggressive in comparison to their native

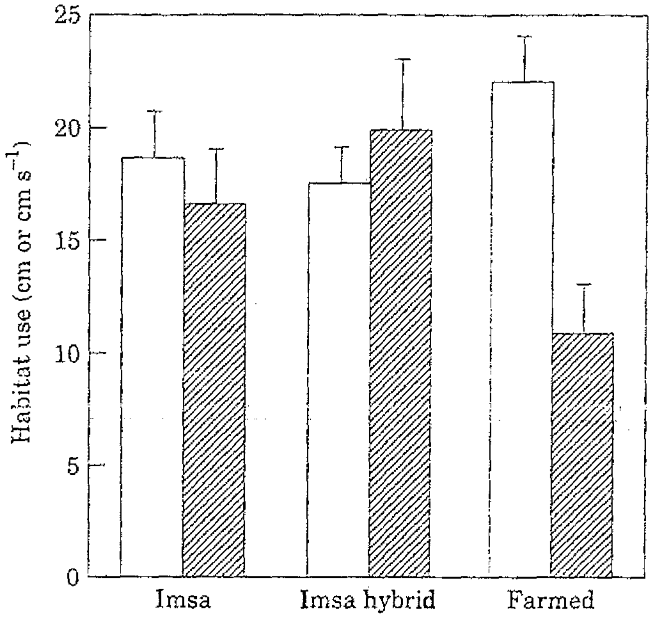


FIG. 7. Mean depth (cm) and current (cm s^{-1}) at the site of recapture of the different populations released in the Stream Ålabekk. Error bars denote S.E. □, Depth; ▨, current.

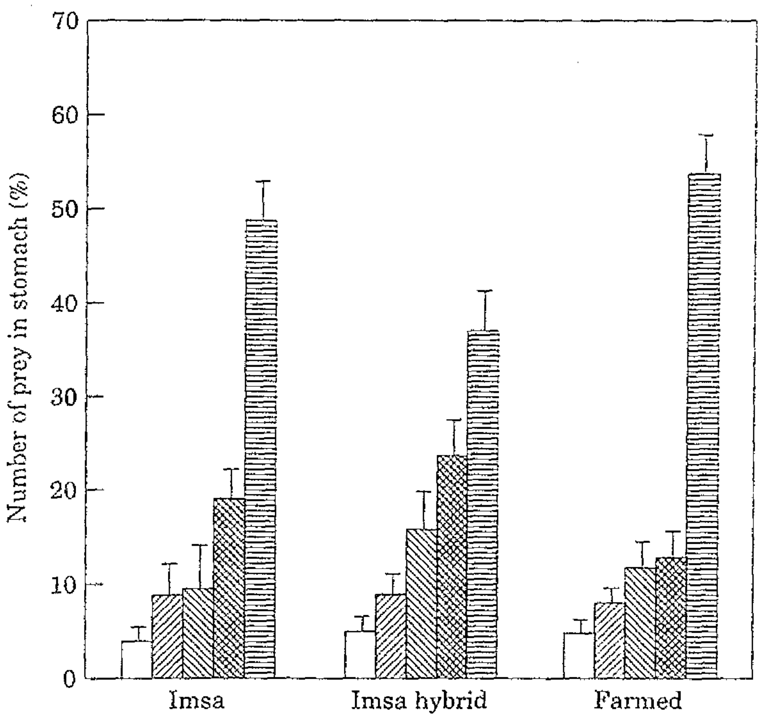


FIG. 8. Mean number of individuals from different prey groups (%) in the stomach samples among the different populations released in the Stream Ålabekk. Errors bars denote S.E. □, Ephemeroptera; ▨, Plecoptera; ▧, surface; ▩, Tricoptera; ▤, Chironomidae.

counterparts. This difference in the effect of hybridization on aggression may be attributable to differences in local adaptations between the populations (e.g. Chapman, 1962; Holm & Fernö, 1986; Rosenau & McPhail, 1987; Swain & Holtby, 1989). However, this seems unlikely because both native populations had similar levels of aggression, and did not differ in pairwise dominance comparisons. Alternatively, there may have been heterosis during hybridization between Lone and farmed salmon, at least for competitive traits.

Farmed fish and hybrids were less responsive to predation risk as both returned from cover following disturbance sooner than native fish (Imsa). This was consistent with earlier findings of Johnsson & Abrahams (1991) and Berejikian (1995) on steelhead trout *Oncorhynchus mykiss* (Walbaum). Our results indicate that this difference was genetic in origin and may have arisen due to artificial selection, as fish in farming facilities experience little or no natural predation, and cautious fish are likely to be less successful at competing for food under such circumstances.

Farmed fish had a higher growth rate than Imsa fish and Imsa hybrids in the hatchery. The higher growth of farmed salmon is probably a consequence of genetic differences in consumption rate, metabolism, assimilation efficiency or a combination of any of these three (see Wootton, 1994). The results from our behavioural experiments suggested that the answer may lie with higher aggressiveness and decreased response to disturbances. However, physiological changes such as increased assimilation and digestive rates or decreased response to stress during artificial rearing as a result of domestication would have the same effect, even in the absence of behavioural differences. Further investigations would be required to obtain a more complete understanding of the underlying mechanisms.

From these results, it seems that the effect of hybridization depends on the trait examined, and perhaps also on the native population in question. However, the general trend was an intermediate performance in the hybrids relative to those of the pure farmed and native populations. Thus, when considering lifetime success in the wild, native/farmed hybrids may be inferior to the locally adapted native fish due to the genetic differences in behaviour and growth, but superior to the pure farmed fish. However, during certain life history stages, farmed and hybrid offspring outcompete wild offspring.

RELEASE EXPERIMENT

Survival in the stream was similar for Imsa, farmed and hybrid parr, as there were no significant differences in recapture rates. Reisenbichler & McIntyre (1977), however, found that wild steelhead trout survived better than cultured and hybrid trout when hatched and reared in the wild. Differences in viability may be most pronounced and easiest to detect at earlier stages (i.e. shortly after emergence) when mortality in juvenile salmonids appears to be highest (Elliott, 1986). After reaching a certain size, differences in survival may not be very apparent, except at times of high stress and predation such as during seaward migration (e.g. Järvi, 1990).

There was no segregation in habitat use or diet among Imsa, farmed and hybrid parr, suggesting that they may compete for territories and food. In spite of this similarity, farmed fish and native/farmed hybrids outgrew the pure native fish. Both behavioural differences observed in the hatchery (i.e. aggression and response to predators) and physiological differences, as discussed above, may be responsible for this. The result may be that native fish are outcompeted and displaced by the farmed fish and the hybrids, because size can be an important determinant of dominance and territory acquisition (e.g. Huntingford *et al.*, 1990).

IMPLICATIONS

Our results have shown that native Atlantic salmon may differ genetically from farmed and native/farmed hybrid salmon in important fitness related traits. Native juveniles were competitively inferior to farmed and hybrid juveniles being less aggressive and more risk sensitive. Furthermore, similarities in habitat use and diet make interpopulational competition likely. Therefore, different growth rates in the wild may be partly an effect of competition, with native fish being dominated by the farmed fish and the hybrids. Irrespective of what causes these differences, non-indigenous origin or artificial selection, the presence of farmed and hybrid juveniles may reduce the production of pure native fish due to increased competition. In addition, although there were no differences in survival among the populations, innate differences in response to predators may lead to decreased survival in the farmed fish and hybrids during other life stages. Consequently, extensive interbreeding with farmed fish may eventually lead to an overall reduction in population size. One might also ask whether farmed fish differ more from some native populations than from others, as our results may suggest. If so, hybridization may be most detrimental in populations which differ highly from the farmed fish (e.g. slow-growing populations with a history of high predation).

We thank J. Backer, T. Husebø and the staff at the NINA Research Station, Ims for assistance with the experiments; B. Jonsson for valuable discussions; M. Einum, H. M. Norman and L. Roksvåg for assistance in the field; and H. M. Norman for technical assistance. Finally, we appreciate the kindness of landowner D. Ims and the comments of T. Forseth on an earlier version of this manuscript. Financial support was provided by a student research grant from the Norwegian University of Science and Technology to SE and grants from the Norwegian Institute for Nature Research and the Directorate for Nature Management to IAF.

References

Berejikian, B. A. (1995). The effects of hatchery and wild ancestry and experience on the relative ability of steelhead trout fry (*Oncorhynchus mykiss*) to avoid a benthic predator. *Canadian Journal of Fisheries and Aquatic Sciences* **52**, 2476–2482.

Chapman, D. W. (1962). Aggressive behavior in juvenile coho salmon as a cause of emigration. *Journal of the Fisheries Research Board of Canada* **19**, 1047–1080.

Crozier, W. W. (1993). Evidence of genetic interaction between escaped farmed salmon and wild Atlantic salmon (*Salmo salar* L.) in a Northern Irish River. *Aquaculture* **113**, 19–29.

Elliott, J. M. (1986). Spatial distribution and behavioural movements of migratory trout *Salmo trutta* in a Lake District stream. *Journal of Animal Ecology* **55**, 907–922.

Emlen, J. M. (1991). Heterosis and outbreeding depression: a multilocus model and an application to salmon production. *Fisheries Research* **12**, 187–212.

Fausch, K. D. (1984). Profitable stream positions for salmonids: relating specific growth rate to net energy gain. *Canadian Journal of Zoology* **62**, 441–451.

Ferguson, M. M., Danzmann, R. G. & Allendorf, F. W. (1985). Developmental divergence among hatchery strains of rainbow trout (*Salmo gairdneri*). part 2. Hybrids. *Canadian Journal of Genetics and Cytology* 27, 298–307.

Ferguson, M. M., Danzmann, R. G. & Allendorf, F. W. (1988). Developmental success of hybrids between two taxa of salmonid fishes with moderate structural gene divergence. *Canadian Journal of Zoology* **66**, 1389–1395.

Fleming, I. A. (1995). Reproductive success and the genetic threat of cultured fish to wild populations. In *Protection of Aquatic Biodiversity, Proceedings of the World Fisheries Congress, Theme 3* (Philipp, D. P., Epifanio, J. M., Marsden, J. E. & Claussen, J. E., eds), pp. 117–135. New Delhi: Oxford & IBH.

Fleming, I. A., Jonsson, B. & Gross, M. R. (1994). Phenotypic divergence of sea-ranched, farmed and wild salmon. *Canadian Journal of Fisheries and Aquatic Sciences* **51**, 2808–2824.

Fleming, I. A., Jonsson, B., Gross, M. R. & Lamberg, A. (1996). An experimental study of the reproductive behaviour and success of farmed and wild Atlantic salmon (*Salmo salar*). *Journal of Applied Ecology* **33**, 893–905.

Frey, D. F. & Miller, R. J. (1972). The establishment of dominance relationships in the blue gourami, *Trichogaster trichopterus* (Pallas). *Behaviour* **42**, 8–62.

Gausen, D. & Moen, V. (1991). Large-scale escapes of farmed Atlantic salmon (*Salmo salar*) into Norwegian rivers threaten natural populations. *Canadian Journal of Fisheries and Aquatic Sciences* **48**, 426–428.

Gjedrem, T., Gjøen, H. M. & Gjerde, B. (1991). Genetic origin of Norwegian farmed Atlantic salmon. *Aquaculture* **98**, 41–50.

Hansen, L. P. & Jonsson, B. (1990). Restocking the River Akerselv, Oslo with Atlantic salmon smolts *Salmo salar* L. of different stocks. *Fauna Norvegica Serie A* **11**, 9–15.

Heggberget, T. G., Johnsen, B. O., Hindar, K., Jonsson, B., Hansen, L. P., Hvidsten, N. A. & Jensen, A. J. (1993). Interactions between wild and cultured Atlantic salmon: a review of the Norwegian experience. *Fisheries Research* **18**, 123–146.

Heggenes, J. (1990). Habitat utilization and preferences in juvenile Atlantic salmon (*Salmo salar*) in streams. *Regulated Rivers: Research and Management* **5**, 341–354.

Hindar, K., Ryman, N. & Utter, F. (1991). Genetic effects of cultured fish on natural fish populations. *Canadian Journal of Fisheries and Aquatic Sciences* **48**, 945–957.

Holm, M. & Fernö, A. (1986). Aggression and growth of Atlantic salmon parr. II. Different populations in pure and mixed groups. *Fiskeridirektoratets Skrifter, Serie Havundersokelser* **18**, 123–129.

Huntingford, F. A., Metcalfe, N. B., Thorpe, J. E., Graham, W. D. & Adams, C. E. (1990). Social dominance and body size in Atlantic salmon parr, *Salmo salar* L. *Journal of Fish Biology* **36**, 877–881.

Järvi, T. (1990). Cumulative acute physiological stress in Atlantic salmon smolts: the effect of osmotic imbalance and the presence of predators. *Aquaculture* **89**, 337–350.

Johnsson, J. I. & Abrahams, M. V. (1991). Inbreeding with domestic strain increases foraging under threat of predation in juvenile steelhead trout (*Oncorhynchus mykiss*): an experimental study. *Canadian Journal of Fisheries and Aquatic Sciences* **48**, 243–247.

Kratt, L. F. & Smith, R. J. F. (1979). Agonistic behaviour of age 0, age I and non-breeding adult Arctic grayling, *Thymallus arcticus* (Pallas). *Journal of Fish Biology* **15**, 389–404.

Lachance, S. & Magnan, P. (1990). Comparative ecology and behavior of domestic, hybrid, and wild strains of brook trout, *Salvelinus fontinalis*, after stocking. *Canadian Journal of Fisheries and Aquatic Sciences* **47**, 2285–2292.

Leary, R. F., Allendorf, F. W. & Sage, G. K. (1995). Hybridization and introgression between introduced and native fish. *American Fisheries Society Symposium* **15**, 91–101.

Lund, R. A., Østborg, G. M. & Hansen, L. P. (1996). Escapes of farmed salmon in marine homewater and in riverine fisheries in the period 1989–1995. NINA *Oppdragsmelding* **411**, 1–16. (In Norwegian, English summary.)

Lura, H. & Sægrov, H. (1991). Documentation of successful spawning of escaped farmed female Atlantic salmon, *Salmo salar*, in Norwegian rivers. *Aquaculture* **98**, 151–159.

Mesa, M. G. (1991). Variation in feeding, aggression, and position choice between hatchery and wild cutthroat trout in an artificial stream. *Transactions of the American Fisheries Society* **120**, 723–727.

Metcalfe, N. B., Huntingford, F. A., Graham, W. D. & Thorpe, J. E. (1989). Early social status and the development of life-history strategies in Atlantic salmon. *Proceedings of the Royal Society of London, Series B* **236**, 7–19.

Metcalfe, N. B., Wright, P. J. & Thorpe, J. E. (1992). Relationships between social status, otolith size at first feeding and subsequent growth in Atlantic salmon (*Salmo salar*). *Journal of Animal Ecology* **61**, 585–589.

Philipp, D. P. & Whitt, G. S. (1991). Survival and growth of northern, Florida, and reciprocal F_1 hybrid largemouth bass in central Illinois. *Transactions of the American Fisheries Society* **120**, 56–64.

Reisenbichler, R. R. & McIntyre, J. D. (1977). Genetic difference in growth and survival of juvenile hatchery and wild steelhead trout, *Salmo gairdneri. Journal of the Fisheries Research Board of Canada* **34**, 123–128.

Rice, W. R. (1989). Analyzing tables of statistical tests. *Evolution* **43**, 223–225.

Ricker, W. E. (1972). Hereditary and environmental factors affecting certain salmonid populations. In *The Stock Concept in Pacific Salmon* (Simon, R. C. & Larkin, P. A., eds), pp. 19–160. Vancouver: MacMillan Lectures in Fisheries, University of British Columbia.

Rosenau, M. L. & McPhail, J. D. (1987). Inherited differences in agonistic behavior between two populations of coho salmon. *Transactions of the American Fisheries Society* **116**, 646–654.

Ruzzante, D. E. (1994). Domestication effects on aggressive and schooling behavior in fish. *Aquaculture* **120**, 1–24.

Ruzzante, D. E. & Doyle, R. W. (1991). Rapid behavioral changes in medaka (*Oryzias latipes*) caused by selection for competitive and noncompetitive growth. *Evolution* **45**, 1936–1946.

Saunders, R. L. (1991). Potential interaction between cultured and wild Atlantic salmon. *Aquaculture* **98**, 51–60.

Swain, D. P. & Holtby, L. B. (1989). Differences in morphology and behavior between juvenile coho salmon (*Oncorhynchus kisutch*) rearing in a lake and in its tributary stream. *Canadian Journal of Fisheries and Aquatic Sciences* **46**, 1406–1414.

Swain, D. P. & Riddell, B. E. (1990). Variation in agonistic behavior between newly emerged juveniles from hatchery and wild populations of coho salmon, *Oncorhynchus kisutch. Canadian Journal of Fisheries and Aquatic Sciences* **47**, 566–571.

Symons, P. E. K. (1968). Increase in aggression and in strength of the social hierarchy among juvenile Atlantic salmon deprived of food. *Journal of the Fisheries Research Board of Canada* **25**, 2387–2401.

Taylor, E. B. (1991). A review of local adaptation in Salmonidae, with particular reference to Pacific and Atlantic salmon. *Aquaculture* **98**, 185–207.

Waples, R. S. (1991). Genetic interactions between hatchery and wild salmonids: lessons from the Pacific Northwest. *Canadian Journal of Fisheries and Aquatic Sciences* **48** (Suppl. 1), 124–133.

Webb, J. H., Youngson, A. F., Thompson, C. E., Hay, D. W., Donaghy, M. J. & McLaren, I. S. (1993). Spawning of escaped farmed Atlantic salmon, *Salmo salar* L., in western and northern Scottish rivers: egg deposition by females. *Aquaculture and Fisheries Management* **24**, 663–670.

Webster, D. A. & Flick, W. A. (1981). Performance of indigenous, exotic, and hybrid strains of brook trout (*Salvelinus fontinalis*) in waters of the Adirondack Mountains, New York. *Canadian Journal of Fisheries and Aquatic Sciences* **38**, 1701–1707.

Wootton, R. J. (1994). *Ecology of Teleost Fishes*, 4th edn. London: Chapman & Hall.