AUREBESTANDEN I TESSEMAGASINET
KONSEKVENSER AV REGULERINGEN

OLA HEGGE OG TRYGVE HESTHAGEN

FYLKESMANNEN I OPPLAND

MILJØVERNAVDELINGEN

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FORORD

Tillatelse til reguleringen av Tesse ble gitt i konsesjon av 3. februar 1941 til A/S Eidefoss og konsesjon av 26. juli 1941 til Glommens og Laagens Brukseierforening (GLB). Til AS Eidefoss og de private eierne i GLB ble reguleringskonsesjonene gitt med en varighet på 50 år. GLB forbereder nå søknad om fornyet konsesjon for reguleringen av Tesse. I søknaden vil GLB søke om å opprettholde reguleringen i samme omfang som tidligere. Med søknaden skal det følge dokumentasjon på reguleringens ettervirkninger. GLB har derfor behov for en vurdering av reguleringens virkning på fiskebestanden i Tesse.

Det foreligger relativt gode opplysninger om fiskeforholdene i Tesse før reguleringen (Hesthagen & Gunnerød 1980), og i 1979 og 1980 ble det gjennomført fiskeundersøkelser av Direktoratet for naturforvaltning (Hesthagen & Gunnerød 1980, 1981). Etter dette har det i perioden fra 1984 og fram til i dag pågått omfattende fiskefaglige undersøkelser i Tesse i regi av Norsk institutt for naturforskning og prosjektet "Bedre bruk av fiskeressursene i regulerte vassdrag i Oppland" hos fylkesmannen i Oppland. Undersøkelsene pågår fortsatt. Formålet med undersøkelsene er å fremskaffe generell kunnskap om virkningen av fiskeutsettinger, men undersøkelsene gir samtidig omfattende kunnskaper om fiskebestanden i Tesse som er verdifulle for forvaltningen av fiskevatnet. Deler av disse undersøkelsene er rapportert tidligere, for andre deler av undersøkelsene foreligger det foreløpig upubliserte manuskript og en del data er ikke rapportert tidligere. For å dekke GLB´s behov for en fiskefaglig vurdering av konsekvensene av Tessereguleringen er kunnskapen fra undersøkelsene i Tesse kort sammenfattet i denne rapporten. De enkelte artikler og upubliserte artikkelmanuskript som rapporten bygger på følger som vedlegg.

Undersøkelsene i Tesse er finansiert av Norsk institutt for naturforskning, NTNF, NAVF og prosjektet "Bedre bruk av fiskeressursene i regulerte vassdrag i Oppland" som finanisieres av vassdragsregulantene i fylket. Gjennom de år undersøkelsene i Tesse har pågått har en rekke personer deltatt i arbeidet. Det rettes en spesiell takk til Vegard Brimi, Børre K. Dervo, Heidi Eriksen, Arne Fjellheim, Leidulf Fløystad og Jostein Skurdal for medvirkning i undersøkelsene.

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INNHOLD

1. SAMMENDRAG

Rapporten gir en sammenfattet vurdering av konsekvensene av reguleringen av Tesse, Lom kommune, Oppland fylke, for aurebestanden i vatnet. Rapporten er skrevet for å tjene som underlagsdokumentasjon ved Glommens og Laagens Brukseierforenings søknad om fornyet konsesjon for reguleringen av Tesse. Rapporten er basert på en rekke fiskeribiologiske undersøkelser i vassdraget. En mer detaljert beskrivelse av enkeltundersøkelsene i form av publiserte artikler og upubliserte manuskript følger som vedlegg til rapporten.

Undersøkelsene viser at aureproduksjonen i Tesse er redusert etter reguleringen, selv om vatnet fortsatt er et bra fiskevatn. Rekrutteringsmulighetene for auren er redusert gjennom avstengning av utløpselva, tørrlegging av gyteplasser i strandsona ved nedtapping vinterstid og overføring av breslamholdig vatn fra Veo til hovedinnløpselva Smådøla. Den mest alvorlige konsekvensen av reguleringen for aureproduksjonen i Tesse er imidlertid at næringsdyrproduksjonen i vatnet er redusert som følge av vannstandsvariasjonene og redusert siktedyp som følge av overføring av breslam fra Veo. Reduksjonen i næringsdyrproduksjonen synes å ha redusert vatnets kapasitet til å produsere aure. Skadene på aureproduksjonen kan derfor ikke kompenseres fullt ut gjennom utsetting av settefisk. Før reguleringen var den årlige avkastningen av aure i Tesse 7.4 kg/ha, mens en etter reguleringen ikke kan forvente å oppnå avkastninger av aure over 2.5 kg/ha pr. år.

2. OMRÅDEBESKRIVELSE

Tesse (853.9 m o.h.) ligger i Lom kommune, Oppland fylke. Vatnet er regulert til kraftformål og reguleringshøyden er 12.4 m. Magasinet rommer 130 mill. m^3. Tesse har et overflateareal på 1 426 ha ved hrv og 937 ha ved lrv. Maksimaldypet er 64 m.

Tessemagasinet har et nedbørfelt på 380 km^2 som gir et midlere årlig tilsig på 230 mill. m^3. Nedbørfeltet drenerer høytliggende områder i Jotunheimen, og etter overføringen av elva Veo, som naturlig drenerte til Sjoavassdraget, er tilsiget blitt sterkt påvirket av breslam, noe som har medført sterkt redusert siktedyp (2 - 7 m). Vanntemperaturen sommerstid ligger normalt mellom 10 og 15 °C.

I strandsona består bunnsubstratet av stein, med unntak av de sørligste og nordligste delene hvor bunnen består av sand. På større dyp består bunnen av gytje.

Aure er eneste fiskeart i Tesse. Fiskeretten tilhører Vårdalen grunneierlag. Det drives et aktivt fiske i vatnet. De fiskeberettigede fisker med garn (35 mm maskevidde) og oter, mens almenheten har adgang til stangfiske og oterfiske fra land ved kjøp av fiskekort.

3. AUREBESTANDEN I TESSE

Fisket på Tesse har lange historiske tradisjoner. Det er gjort funn av garnsøkker som viser at det foregikk et aktivt fiske i vatnet så langt tilbake som i perioden 600 - 1000 e. Kr. Det foreligger gode oversikter over avkastningen i Tesse på 1930 tallet som viser at det tidligere var et usedvanlig produktivt aurevatn. Det ble da årlig fanget ca 9 000 kg (7.4 kg/ha) aure i Tesse (Hesthagen & Gunnerød 1980).

Etter reguleringen har fisket gått sterkt tilbake, selv om Tesse fortsatt må kunne regnes som et godt fiskevatn. Avkastningen har i perioden 1979 - 1992 variert mellom 0.60 - 2.47 kg/ha (x = 1.75 kg/ha). Størrelsen og kvaliteten på fisken er fortsatt god. Middelstørrelsen for fisk i ordinære fangster varierer mellom 267 - 369 g.

Reguleringen av Tesse har medført en sterk reduksjon av aurens rekrutteringsmuligheter. Før reguleringen var uløpselva, Tessa, og hovedinnløpselva, Smådøla, de viktigste gyteelvene for auren i Tesse. I tillegg hadde gyting i strandsona i selve innsjøen stor betydning (Sunde 1942). Etter reguleringen har reguleringsdammen blokkert for vandring mellom utløpselva og magasinet. Overføringen av Veo til Smådøla har medført at Smådøla nå er sterkt tilgrumset av breslam, og det har foregått betydelig graving i de nedre deler av Smådøla, der de viktigste gyteområdene var tidligere. Etter overføringen av Veo er det ikke registrert oppgang av gytefisk i Smådøla (Hesthagen & Gunnerød 1980). En undersøkelse av Hesthagen & Fjellheim (Vedlegg 1) viser også at næringsdyrproduksjonen i Smådøla er betydelig redusert som følge av breslammet fra Veo-overføringen. Nedtappingen av magasinet vinterstid (12.4 m) utelukker strandsonen som mulig gyteområde. Gytemulighetene til auren i Tesse er derfor etter reguleringen begrenset til mindre tilløpsbekker til Tesse. De viktigste er Ilva, Krokåtebekken, Nåvårseterbekken og Silongsbekken.

Vannstandsvariasjonen i kraftverksmagasin medfører som regel betydelige reduksjoner i bunndyrfaunaen i strandsona gjennom tørrlegging og innfrysing av næringsdyr og utvasking av næringsstoff fra bunnen i reguleringssona (Grimås 1962). Dette er åpenbart også tilfelle i Tesse. Marflo og skivesnegl, som var viktige næringsdyr for auren før utbyggingen (Sunde 1932), er ikke lenger påvist i magasinet. Også produksjonen av andre næringsdyr som lever i strandsona må forventes å være betydelig redusert i og med den relativt store reguleringshøyden på 12.4 m. Reduksjonen i næringsproduksjonen i strandsona må forventes å være ytterligere forsterket på grunn av overføringen av Veo. Breslam fra Veo har medført kraftig reduksjon av siktedypet i Tesse fra 8 - 10 m før reguleringen (Huitfeldt-Kaas 1906) til 2 - 7 m i dag avhengig av hvor mye vann som overføres fra Veo. Dette reduserer lysmengdene nedover i vannmassen, og derved primærproduksjonen på dypere vann.

Tapet av marflo og skivesnegl som næringsdyr for auren i Tesse, er forsøkt erstattet ved utsetting av skjoldkreps (*Lepidurus arcticus*) (Per Aass, upubl.). Skjoldkrepsen har vist seg å kunne tolerere betydelig reguleringshøyde, og er i flere reguleringsmagasin et helt avgjørende næringsdyr for aure (Aass 1969). Utsettingen har imidlertid ikke slått til (Hesthagen & Gunnerød 1980). Skjoldkrepsen finnes naturlig i vatn som drenerer til Tesse. Dersom forholdene i Tesse var egnet for skjoldkreps ville den trolig også kolonisert Tesse.

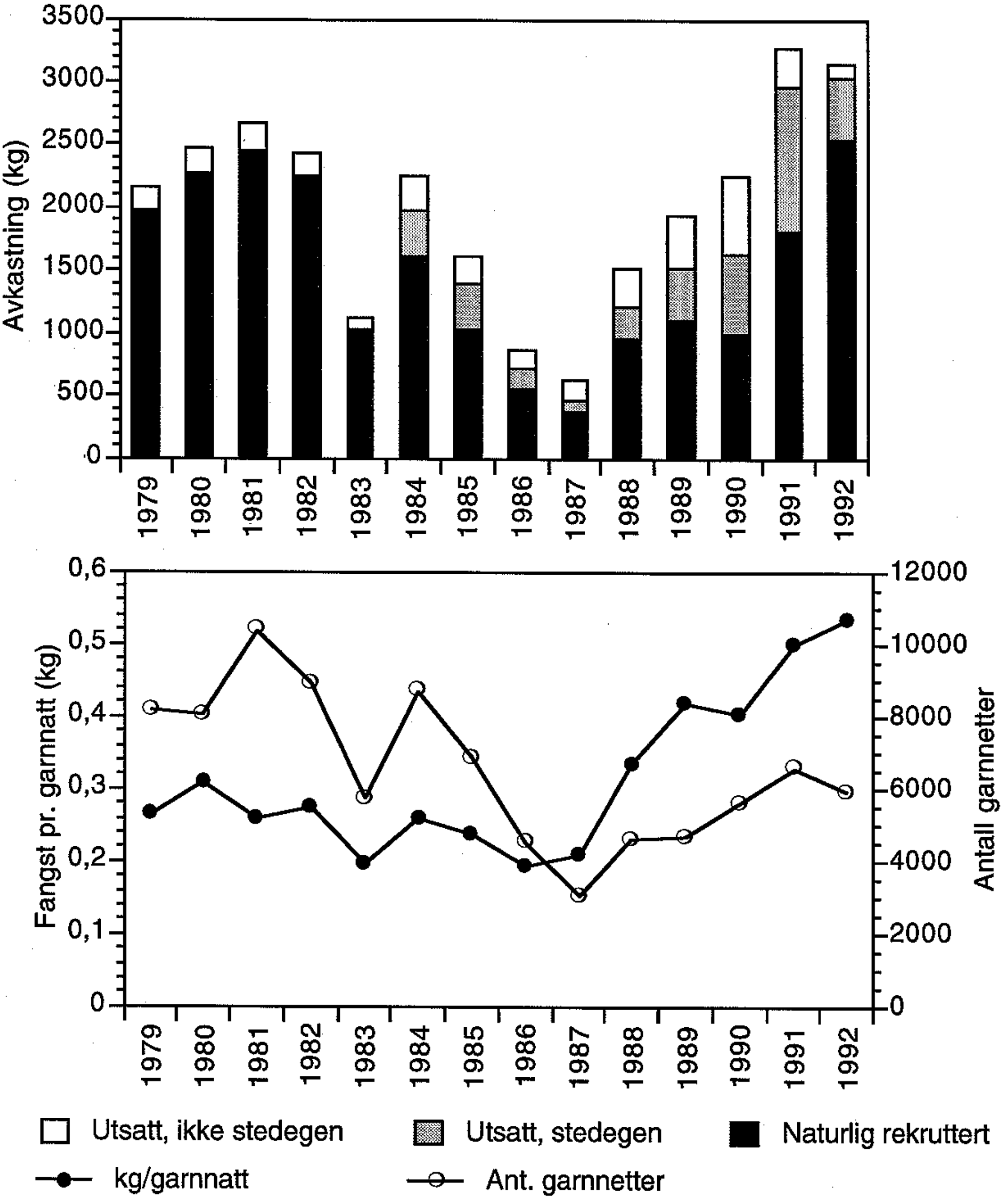
Aure av Tessestammen (både naturlig rekruttert og utsatt) utnytter både strandsona og de frie vannmassene. Små fisk (< 22 cm) oppholder seg nær utelukkende i strandsona (Vedlegg 2 og 3). Dette er et vanlig forhold i mange store dype aurevatn i Norge (Haraldstad & Jonsson 1983, Hegge et al. 1989, Jonsson 1989), og særlig når vatna er regulert (Vedlegg 3). I strandsona lever småfisken tett knyttet til bunnen på grovkornet substrat som gir gode skjulemuligheter og livnærer seg vesentlig av næringsdyr som er tilgjengelig nede ved bunnen, som vanninsekter, linsekreps og gelekreps (Vedlegg 4). Større fisk utnytter i stor grad de frie vannmassene, og ernæringen er dominert av de store planktonkrepsdyrene *Daphnia longispina* og *Bythotrephes longimanus* og av overflateinsekter. I og med at Tesse er en relativt stor og dyp innsjø, utgjør de frie vannmassene en stor del av innsjøens plass- og næringstilbud. Ettersom nær all småfisken oppholder seg i strandsona, blir fisketettheten der relativt stor sammenlignet med fisketettheten i de frie vannmassene. Konkurransen om plass og mat blir derfor hard i strandsona. Dette forsterkes av at bunndyrfaunaen i strandsona er redusert som følge av reguleringen. Nærings- og konkurransesituasjonen for auren synes derfor å være best i de frie vannmassene. Årsaken til at små aure begrenser sin habitatbruk til strandsona, hvor konkurransen om plass og næring synes langt hardere, er trolig at småauren er avhengig av tilgang på skjul som beskyttelse mot predasjon og aggressjon fra større aure. Tilgangen til næring og plass har avgjørende betydning for overlevelsen til småaure (Chapman 1966), og dette medfører derfor en flaskehals i vatnets kapasitet til å produsere aure (se vedlegg 3).

Reduksjoner i aurens rekrutteringsmuligheter kompenseres ofte gjennom utsetting av aure. I Tesse er gjeldende utsettingspålegg 25 000 1-somrige aure av uspesifisert stamme. Det har både vært benyttet settefisk av stedegen stamme og av to fremmede stammer, Tunhovdstammen og Bjornesstammen. Som et ledd i undersøkelsene av tilslaget på fiskeutsettingene i Tesse har en variert utsettingsmengden fra de pålagte 25000 1-somrige settefiskene og helt ned til 0 i noen år (Tabell 1). Settefisken har vært merket, slik at det har vært mulig å skille mellom naturlig rekruttert aure, utsatt stedegen aure og utsatt aure av fremmed stamme. Oppgangen av gytefisk i tilløpsbekkene til Tesse har samtidig vært overvåket ved hjelp av ruser, og disse registreringene har vist at utsatt aure av fremmed stamme ikke har gått opp i gytebekkene for å gyte. En må derfor kunne anta at utsettingen av fremmed fisk i Tesse i liten grad har medført påvirkning av den stedegne aurestammens arveegenskaper. Utsatt fisk av Tessestammen har derimot gått opp i gytebekkene.

Tabell 1. *Antall settefisk av stedegen og ikke stedegen stamme utsatt i Tesse i perioden 1952 - 1992.*

År	Stedegen fisk	Ikke stedegen fisk	
	Antall	Antall	Stamme
1952-79	0	10 000	-
1980	7 800	10 000	Bjornesfjord
1981	8 000	15 000	Tunhovdfjord
1982	9 000	17 000	Tunhovdfjord
1983	12 000	15 000	Bjornesfjord
1984	12 000	15 000	Bjornesfjord
1985	12 000	16 000	Bjornesfjord
1986	12 000	12 000	Tunhovdfjord
1987	10 000	0	-
1988	0	0	-
1989	0	0	-
1990	3320	0	-
1991	14 300	0	-
1992	10 865	0	-

Det har vært betydelig variasjon i avkastningen av aure og i fangst pr. garnnatt i Tesse i undersøkelsesperioden (Figur 1). Variasjonene i fisket synes imidlertid ikke å være positivt korrelert med de store variasjonene i den mengde fisk som årlig ble satt ut i Tesse. Storparten av den utsatte fisk som ble gjennfanget ved ordinært fiske på Tesse ble fanget 3 - 5 år etter utsetting (ikke stedegen settefisk er større enn stedegen settefisk ved utsetting og kommer noe raskere inn i fangstene). Utfra utsettingsmengdene skulle en derfor forvente størst avkastning i perioden 1984 - 1989. Det beste fisket var imidlertid i årene 1980 - 1982, 1991 og 1992, mens fisket var dårligst i 1986 og 1987. De lave avkastningstallene for 1986 og 1987 skyldes delvis lav fiskeinnsats disse årene, men spesiellt sammenlignet med den påfølgende perioden 1988 - 1992 da fangstutbyttet var sterkt økende, forklarer variasjonen i fiskeinnsats på langt nær hele forskjellen i fisket. Det kan derfor synes som om fiskeutsettingene ikke har gitt vesentlig bedring av fisket, snarere tvert om. Avkastningen av naturlig rekruttert fisk avtok sterkt fra perioden 1979 - 1982 og fram til et bunn-nivå i 1987, for deretter å øke fram til 1992. Selv om tendensen i svingningene ikke er entydige for alle år, tyder undersøkelsene på at fiskeutsettingene har hatt negativ innvirkning på produksjonen av naturlig rekruttert fisk, slik at effekten av utsettingene for totalavkastningen i vatnet har vært dårlige. Dette skyldes etter all sannsynlighet tetthetsavhengig konkurranse (Vedlegg 5, se også vedleggene 2, 3 og 4), og tilsier at utsettingsmengden har vært for stor i forhold til vatnets kapasitet til å produsere fisk etter reguleringen. Sikrere viten om utsettingenes effekt på aureproduksjonen vil en imidlertid få når undersøkelsene er fullført i 1996.



Figur 1. *Årlig avkastning, fangst pr. innsats og fangstinnsats ved garnfiske i Tesse i perioden 1979 - 1992.*

Særlig lite hensiktsmessig synes utsettingen av aure av de to ikke stedegne stammene, Bjornesfjordstammen og Tunhovdfjordstammen. Undersøkelser av aurens habitatbruk (Vedlegg 2) har vist at mens aure av Tessestammen oppholder seg i strandsona til den når en størrelse på ca 22 cm for deretter vesentlig å oppholde seg i de frie vannmasser, blir den utsatte fisken av Bjornesstammen og Tunhovdstammen værende i strandsona gjennom hele livet. Ettersom utsatt fisk av stedegen stamme har samme habitatbruk som naturlig rekruttert fisk i Tesse er det rimelig å anta at forskjellene i habitatbruk er genetisk betinget. Større aure er kjent for å undertrykke mindre aure. Utsetting av aurestammer som oppholder seg i strandsona gjennom hele livet vil derfor forsterke konkurransepresset på småauren i strandsona, og må derved forventes å virke negativt inn på småaurens overlevelse og vekst.

Det er foreløpig for tidlig å fastslå hvorvidt utsetting av settefisk kan gi en positiv effekt på avkastningen av aure i Tesse. Det vil kommende års resultater gi bedre informasjon om. Det er imidlertid åpenbart at den pålagte utsettingsmengde på 25 000 1-somrige settefisk er for stor. Ved eventuelle fremtidige fiskeutsettinger i Tesse bør det videre kun benyttes fisk av stedegen stamme, slik at forsterket konkurranse som følge av utsetting av fisk som kun utnytter de begrensede ressursene i strandsona unngås. Bruk av stedegen stamme er også ønskelig utfra hensynet til å bevare den opprinnelige aurestammen i Tesse, som har eksistert i vatnet i minst 1 000 år (trolig mye lengre). For å minimere konkurransepresset fra utsatt fisk på den naturlig rekrutterte auren i Tesse, kan det også være aktuellt å gå over til å bruke 2-årig settefisk, idet 2-årig settefisk (forutsatt stedegen stamme) vil være tilstrekkelig stor til å utnytte de frie vannmasser allerede ved utsetting, og derved i mindre grad medføre økt fisketetthet i strandsona (se vedlegg 3).

Undersøkelsene i Tesse viser at det ikke er mulig å iverksette tiltak som fullt ut kompenserer for reguleringens negative innvirkning på aureproduksjonen i vatnet. Dette fordi reduksjonen i næringsdyrproduksjonen ikke kan kompenseres. Største årlige avkastning av aure i Tessemagasinet i undersøkelsesperioden var 2.47 kg/ha. Det synes ikke realistisk å kunne oppnå betydelig høyere varig avkastning en det, selv ved optimalt valg av utsettingsmengde, settefiskstørrelse og stamme.

4. LITTERATUR

Chapman, D. W. 1966. Food and space as regulators of salmonid populations in streams. Am. Natural., 100: 345 - 347.

Grimås, U. 1962. The effect of increased water level fluctuations upon the bottom fauna in Lake Blåsjøen, Northern Sweden. Rep. Inst. Freshw. Res. Drottningholm, 44: 14 - 41.

Haraldstad, Ø. & Jonsson, B. 1983. Age and sex aggregation in habitat utilization by brown trout in a Norwegian lake. Trans. Am. Fish. Soc. 112: 27 - 37.

Hegge, O., Dervo, B. K., Skurdal, J. & Hessen, D. O. 1989. Habitat utilization by sympatric arctic charr (Salvelinus alpinus (L.)) and brown trout (Salmo trutta L.) in Lake Atnsjø, south-east Norway. Freshwater Biol., 22: 143 - 152.

Hesthagen, T. & Gunnerød 1980. Fisket i Tesse i Lom kommune, Oppland, før og etter regulering. DVF-Reguleringsundersøkelsene, Rapp. nr. 12-1980, 109 s + vedlegg.

Hesthagen, T. & Gunnerød 1981. Fiskeribiologiske undersøkjingar i Tesse, Oppland, i 1980. DVF-Reguleringsundersøkelsene, Rapp. nr. 5-1981, 58 s + vedlegg.

Huitfeldt-Kaas, H. 1906. Planktonundersøgelser i norske vande. Nationaltrykkeriet, Christiania, 199 s.

Jonsson, B. 1989. Life history and habitat use of Norwegian brown trout (Salmo trutta). Freshwater Biol., 21: 71 - 86.

Sunde, S. E. 1932. Regulering av Tessevatn i Lom og Lemonsjø i Vågå. Fiskesekretær for det øst- og sønnenfjelske. Landbruksdep., stensil, 7 s.

Sunde, S. E. 1942. Tessereguleringen og fisket. Overskjønnet 1942. Fiskesekretær for det øst- og sønnenfjelske. Landbruksdep., stensil, 7 s.

Aass, P. 1969. Crustacea, especially *Lepidurus arcticus* Pallas, as brown trout food in Norwegian mountains reservoirs. Rep. INst. Freshw. Res. Drottningholm, 49: 183 - 201.

5. VEDLEGG

VEDLEGG 1: Hesthagen, T. & Fjellheim, A. 1987. Effects of transferring glacier-fed water to a clear-water mountain river on the production and food organisms of brown trout (*Salmo trutta* L.) in southern Norway. Regulated Rivers: Research & Management, 1: 161 - 170.

VEDLEGG 2: Hesthagen, T., Hegge, O., Skurdal, J. & Dervo, B. K. 1993. Difference in habitat utilization of native and non-native brown trout *Salmo trutta*, stocked in a hydroelectric reservoir. (Upublisert manuskript).

VEDLEGG 3: Hegge, O., Hesthagen, T. & Skurdal, J. 1993. Juvenile competitive bottleneck in the production of brown trout in hydroelectric reservoirs due to intraspecific habitat segregation. Regulated Rivers: Research & Management, 8: 41 - 48.

VEDLEGG 4: Hegge, O., Hesthagen, T. & Skurdal, J. 1993. Vertical distribution and substrate preference of brown trout in a littoral zone. Environmental Biology of Fishes, 36: 17 - 24.

VEDLEGG 5: Hesthagen, T. 1993. Response of native brown trout, *Salmo trutta* L., to stockings in a Norwegian reservoir. (Upublisert manuskript).

Vedlegg 1

REGULATED RIVERS: RESEARCH & MANAGEMENT, VOL. 1, 161–170 (1987)

EFFECTS OF TRANSFERRING GLACIER-FED WATER TO A CLEAR-WATER MOUNTAIN RIVER ON THE PRODUCTION AND FOOD ORGANISMS OF BROWN TROUT (*SALMO TRUTTA* L.) IN SOUTHERN NORWAY

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ABSTRACT

The effects of transferring glacier-fed water to a clear-water river on production and food organisms of brown trout (*Salmo trutta* L.) were investigated in a mountain river, in southern Norway. Production in unregulated fluvial habitat was 271·5 g 100 m^{-2} yr^{-1} compared with 103·1 g 100 m^{-2} yr^{-1} in a glacier-fed reach of the river. This difference was due to low fish density and recruitment rate. The growth rate, at least for younger fish (2+ to 4+ age groups), was significantly higher in the regulated reach of the river. The main difference in food composition was the low abundance of crustaceans *Eurycercus lamellatus* and *Gammarus lacustris* in the regulated reach. Trichopterans were the main diet component in both sites.

KEY WORDS Water transfers Turbid water Brown trout Fish production Food organisms

INTRODUCTION

Hydroelectric power development of Norwegian rivers may involve the transfer of highly turbid waters (Rübberdt, 1976; Lillehammer and Saltveit, 1979). Long-term exposure to suspended solids and sediment deposition may impair fish production due to recruitment failure (Stuart, 1953; Campbell, 1954; Herbert and Merkens, 1961) and increased migration (Borgström, 1973; Barton, 1977; Aass, 1979). Behavioural modifications suggest that the fitness of salmonid populations which are exposed to short-term pulses of suspended sediment may be reduced (Berg and Northcote, 1985). Turbid water may also have detrimental effects on the benthic fauna (Rosenberg and Snow, 1975; Armitage, 1984).

This paper discusses the effects of turbid water on food organisms and brown trout production in the river Smådøla in southern Norway, which receives glacier-fed water from the neighbouring river Veo. The river is morphologically similar above and below the transferring site, and it is therefore assumed that any negative effects of the regulation could be studied by comparing data from these two sites.

STUDY AREA

The river Smådøla is situated in Jotunheimen in southern Norway (Figure 1), and the study area is located at an altitude between 1070–1080 m above sea level. The unregulated basin of the river is 93 km^2, and bedrock is largely composed of gabbro. The vegetation cover along the river consists of grass and bushes,

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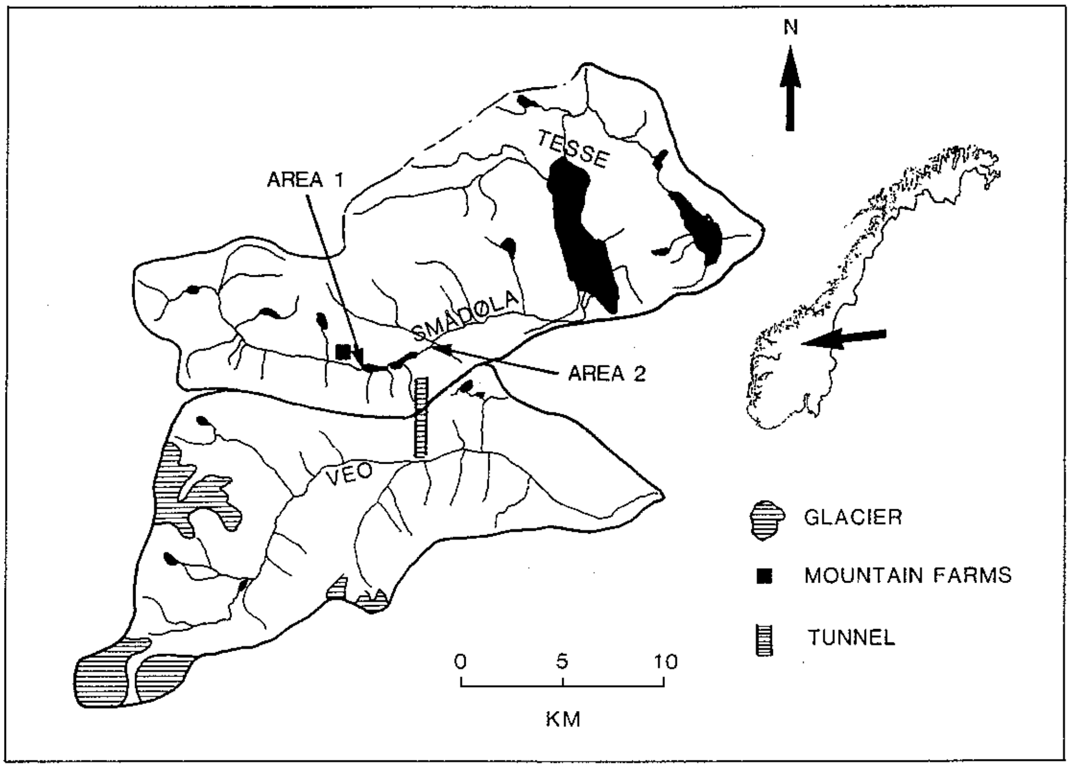

Figure 1. Geographic location and the basin areas of the rivers Smådøla and Veo including that of the lake Tesse reservoir. Areas I and II represent the study area in unregulated and regulated reaches, respectively. (Redrawn from Walseng and Halvorsen, 1986).

while areas of birch are found on valley slopes. The elevated parts of the basin area are bare rock. Only a few small lakes are located in the catchment. A group of small mountain farms are located in the valley (Figure 1), but today only a few cattle graze in this area. The river Smådøla is between 20–50 m wide and has a gentle slope which alternates between shallow fluvial (5–40 cm) and deeper lacustrine habitats (1·0–2·5 m). The river bed on riffle areas consist mainly of large stones (15 to 45 cm diameter) with patches of boulders. Large amounts of sediments have settled on the river bed in the regulated part of the river. Vegetation is relatively scarce in the unaffected part of the river Smådøla, while the green algae *Microspora amoena* (Kuetz) has developed a dense cover in some riffle areas below the transferring site.

The regulation of the river Smådøla began in December 1963. The waterflow from the neighbouring river Veo is carried through a tunnel, which ends on the valley slope about 1200 m above the lake Nedre Smådalsvatn (Figure 1). The river Smådøla flows into Lake Tesse which is used as a reservoir for hydroelectric power production. The river Veo originates in glacial areas (Figure 1), and carries highly turbid water. Seston values in the river have been measured at nearly 100 mg l^{-1}, compared with < 1·0 mg l^{-1} in the unaffected reach of river Smådøla (Blakar, 1976). High amounts of sediment have settled in the lake Nedre Smådalsvatn, which is now nearly filled with clay. The total basin area of the river Veo is 200 km^2, of which 155 km^2 is transferred to the river Smådøla. The tunnel inlet is located at an altitude of 1255 m.

Mean annual discharge in the unregulated river Smådøla is 2·03 $m^3 s^{-1}$, compared with 3·36 $m^3 s^{-1}$ in the river Veo at the tunnel inlet. Based on basin areas and specific run-off data (Table I), the river Veo annually contributes 68·5 per cent of the discharge in the river Smådøla measured at the outlet from the lake Nedre Smådalsvatn. The discharge is high from mid-May to August, with peak levels in June (25 $m^3 s^{-1}$, Figure 2). Winter discharge is low, mostly below 3·0 $m^3 s^{-1}$.

Table I. Specific run off ($l\ s^{-1}\ km^{-2}$) and mean annual discharge for the rivers Veo and Smådøla

River	Basin area (km^{-2})	Run off ($l\ s^{-1}\ km^{-2}$)	Mean annual discharge ($m^3\ s^{-1}$)	($m^3 \times 10^6$)
Veo	155	21·69	3·36	106
Smådøla	93	16·63	2·03	49

Brown trout is the only fish species present in the river Smådøla. The river Veo did not originally contain any fish, but in recent years the river has been stocked and a small population of brown trout is now established.

The climate in this area is typically continental with relatively high summer temperatures and low amounts of rain. Mean annual precipitation at Vågåmo, which is located about 22 km from the Smådalen valley, is 326 mm. The mean air temperature is 11.1°C from May to September.

METHODS

Sampling stations were located about 3 km above the transfer site (Figure 1, Area I), and 500–800 m below this outlet (Figure 1, Area II). Brown trout were collected with bottom gill nets in mid-September 1983, and with an electrofishing apparatus (1600 V, D.C., unloaded) during the same time period in 1984.

The gill nets were 32 m × 1·5 m, and consisted of panels of eight different mesh sizes (bar meshes between 10–45 mm) which were 4 m long. One serie of gill nets consisted of three nets, and the various panels were placed in different combinations in each net (State Pollution Control Authority, 1982). Gill netting was carried out in lacustrine habitats only.

Electrofishing was conducted at ten sites in fluvial habitat, covering 675 m^2 above and 1184 m^2 below the outlet from the river Veo. These sites were located in areas with similar bed gravel (15–45 cm diameter) and water depth (10–30 cm). Density estimates were made by using the removal method and

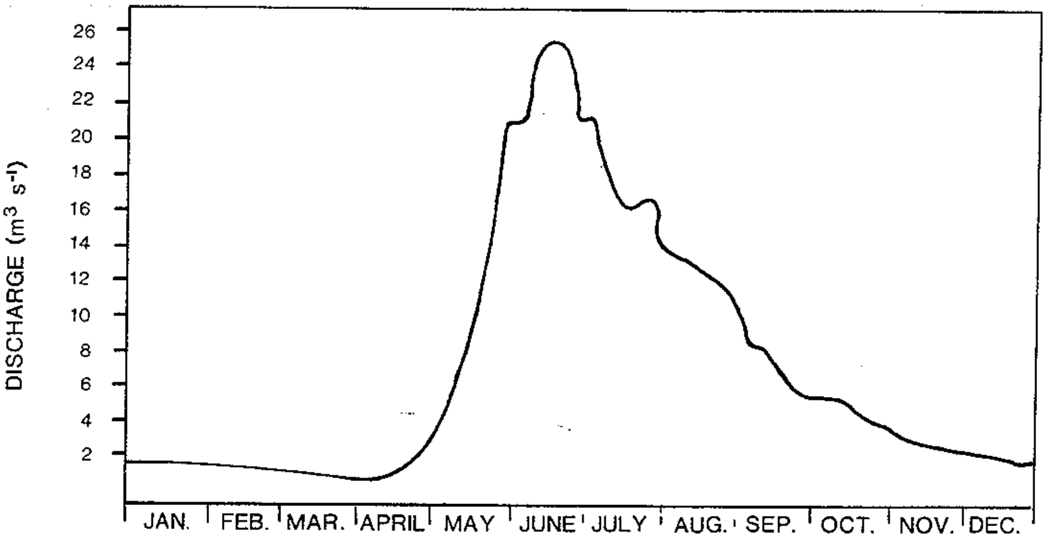

Figure 2. Mean average monthly discharge in the river Smådøla at the inlet of the reservoir Tesse

each site was electrofished twice. Catchability and density estimates were derived from the least-squares regression of cumulative catch (x), on catches in each sampling run (y). Fish density is presented as the mean number of fish 100 m^{-2} based on a common catchability (Bohlin, 1981) which was estimated as 0·57 in both areas. The sampling was carried out at low waterflow (about 4 $m^3 s^{-1}$), when the turbidity level in the regulated reach was also low.

Ages were determined by using both scales and otoliths (Jonsson, 1976). In many cases, trout had not formed their first scale annulus. Most of the collected fish were frozen after sampling, and total length (0·1 cm), weight (1 g) and degree of sexual maturity (Frost and Brown, 1967) were determined later. Mean length and weight-for-age are based on pooled data from both 1983 and 1984, and differences in growth rates were tested by Student t-test (Sokal and Rohlf, 1969). The instantaneous rate of total mortality was estimated from the age-frequency distribution (Ricker, 1975).

Average production for all fluvial stations, was individually analysed for regulated and unregulated reaches of the Smådøla. Calculations for different age groups used the formula $P = G\bar{B}$ where G = instantaneous growth-rate, estimated as the difference between natural logarithm of mean weight of fish in age groups t and $t + 1$; and $\bar{B}$ = arithmetic means of standing stock (density times mean weight) of age groups t and $t + 1$. The density of different age groups was obtained by dividing the mean density for all fluvial stations on the basis of the age-frequency distribution in electrofishing catches.

Stomach contents of trout were sorted according to groups and species. The relative composition in % volume was estimated using the points method of Hynes (1950).

RESULTS

Fish population

Trout density in fluvial habitat estimated from electrofishing data averaged 17.9 fish 100 m^{-2} in the unregulated reach, while the corresponding value in river sections carrying highly turbid water was 5·2 specimens. With one exception, fish densities were higher in all stations in the unregulated river reach (Table II). The gill net catch in lacustrine habitat was twice as high in the unregulated river Smådøla (50 fish) as that in the glacier-fed reach (26 fish).

No difference was found between the age structure of unregulated and regulated reaches $\chi^2 = 0{\cdot}32$; $df = 2$; $P > 0{\cdot}05$), when comparing the number of fish aged ≤ 4+, 5+ and ≥ 6+ caught in gill nets in lacustrine habitat (Figure 3). Very few fish of age ≤ 4+ were caught at these sites. Age structure observed in the fluvial regulated and unregulated reaches of the river differed significantly $\chi^2 = 9{\cdot}31$; $df = 6$; $P < 0{\cdot}05$). This was due to low recruitment (0+ and 1+ age groups) in the regulated area. There were no

Table II. Density of brown trout in unregulated (UR) and regulated (R) fluvial habitats in the river Smådøla

Station	Area (m^2)	Density (100 m^{-2})
UR 1	216	7·3
UR 2	144	20·3
UR 3	135	27·1
UR 4	100	18·3
UR 5	80	25·9
R 1	80	16·8
R 2	300	4·5
R 3	576	3·4
R 4	108	5·7
R 5	120	7·1

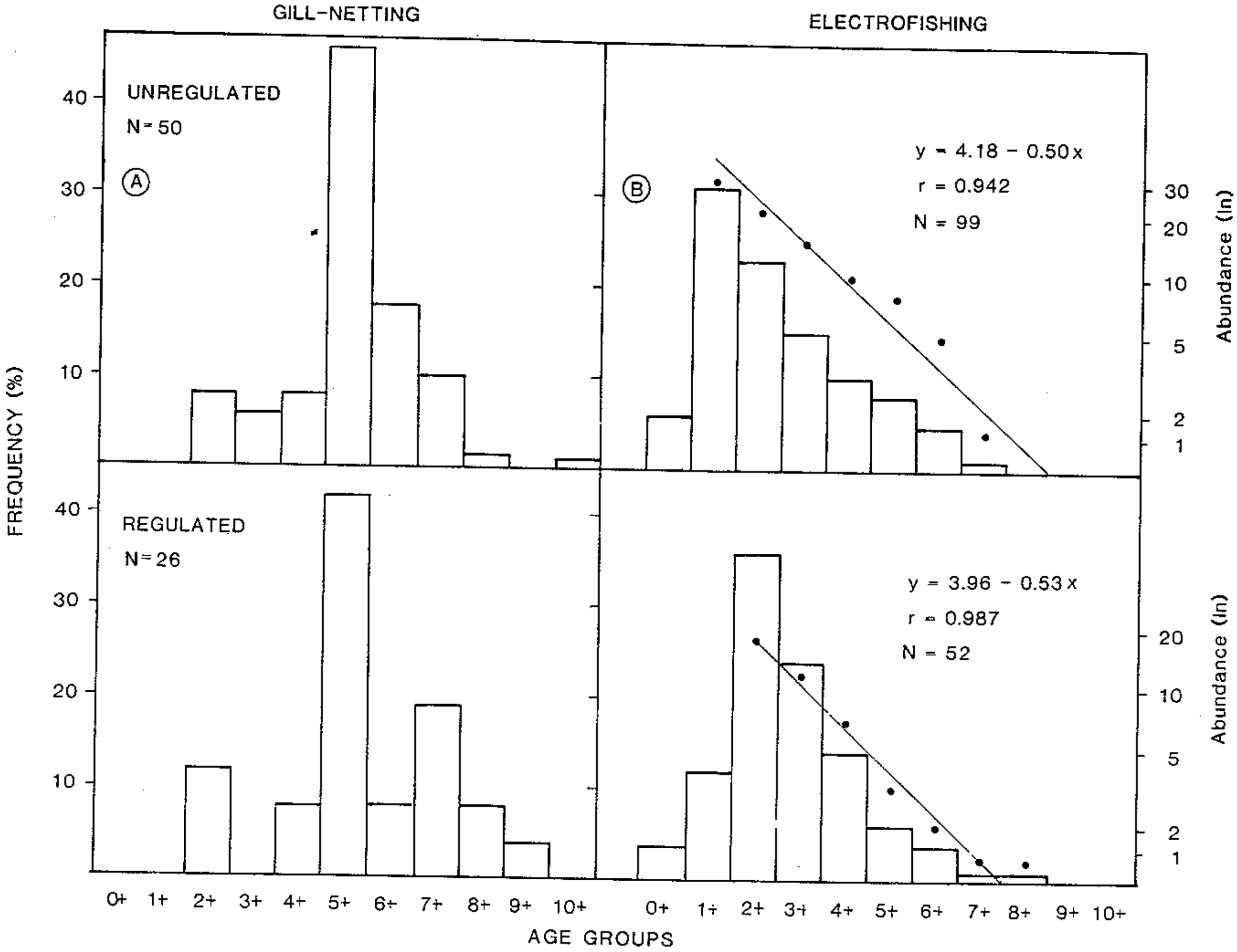

Figure 3. Age–frequency distribution of fish (A) caught by gill nets and (B) caught by electrofishing in the unregulated and regulated reaches of the river Smådøla. (B) also shows the equation between logarithm of number to age versus age: $y = ax + b$, where a is the instantaneous rate of total mortality, r = correlation coefficient, and N = number of fish caught

significant differences in the instantaneous mortality rates, which were 0·50 and 0·53 in these two reaches, respectively (analysis of covariance, $P > 0{\cdot}05$, Figure 3B).

Mean weights of 2+ to 4+ brown trout from the glacier-fed reach were significantly larger than specimens of the same age from the unaffected reach (t-test, $P < 0{\cdot}05$, Table III). However, for fish of age 5+ no significant differences in size were registered. Differences in growth for trout of higher age were inconclusive.

Production in the unregulated fluvial habitat was 271·5 g 100 m^{-2} yr^{-1} for ages 0+ to 7+ (Table IV). The highest production (31 per cent) occurred between the 4+ and 5+ age groups. Mean production estimated for ages 0+ to 8+ on the regulated reach was 103.1 g 100m^{-2} yr^{-1}. Younger age groups constituted a relatively higher fraction of production on the regulated reach of the river Smådøla.

Food organisms

The bulk of ingested food consisted of aquatic insect larvae (Table V). Generally Trichopera larvae were the most important group. Most of the trichopterans eaten belonged to the family Limnephilidae, of which *Potamophylax* sp. dominated. Chironomids also formed an important part of the diet, especially at

Table III. Mean length (x̄l, cm) and weight (x̄W, g) of brown trout caught in the unregulated and regulated reaches of the river Smådøfla in September 1983 and 1984. Standard deviation in parentheses. N = number of fish in each age group

	Unregulated					Regulated				
Age	x̄l	(S.D.)	x̄W	(S.D.)	N	x̄l	(S.D.)	x̄W	(S.D.)	N
0+	3·6	(0·32)	0·5	(0·2)	6	3·6	(0·07)	—	—	2
1+	7·5	(0·56)	4·9	(1·2)	31	7·7	(0·70)	5·0	(1·1)	6
2+	10·0	(1·00)	11·4	(3·1)	27	11·0	(1·24)	14·8	(4·8	21
3+	12·7	(1·47)	23·8	(10·2)	18	13·9	(1·33)	30·9	(9·0)	12
4+	15·3	(0·77)	38·9	(8·6)	14	17·6	(2·12)	65·9	(22·9	9
5+	19·9	(2·32)	90·1	(35·5)	31	19·6	(1·78)	90·1	(26·4)	14
6+	22·2	(1·89)	118·2	(28·2)	14	22·6	(1·22)	130·8	(24·6)	4
7+	23·6	(1·82)	153·4	(36·2)	6	23·0	(0·61)	141·0	(14·6)	6
8+	23·1	—	130·0	—	1	25·2	(2·30	195·5	(40·0)	3
9+						36·5	—	406·00	—	1
10+	29·8	—	256·0	—	1					

the regulated site (43·5 and 35·8 volume per cent in 1983 and 1984, respectively). Cranefly larvae, mayflies and stoneflies were also important food items, at both the regulated and unregulated sites. Terrestrial animals were only a minor constituent of the diet.

The most striking difference between the two localities was demonstrated by the crustaceans. *Eurycercus lamellatus* (O. F. Müller), which formed 16 per cent of the trout food at the unregulated site in 1983 and 1984, was not found in the stomachs of trout from the regulated area. *Gammarus lacustris* (Sars) was also more abundant at the regulated site (12·4 per cent in 1983). A χ^2-test based on observed frequencies of fish stomachs containing crustaceans showed significant differences for *E. lamellatus* in both years ($P < 0{\cdot}001$). *G. lacustris* was eaten with significantly greater frequency at the unregulated lacustrine sites in 1983 ($P < 0{\cdot}05$). This species was an unimportant food item for fish in fluvial habitat (1984) in both reaches.

DISCUSSION

This study documents lower trout production in regulated fluvial habitat influenced by glacier-fed water carrying high turbidities as compared with unregulated areas having clear-water conditions. This difference in production was mainly due to low fish density, through inferior recruitment rate. There was no significant difference in mortality rates for fish caught in these two reaches.

Low recruitment rate below the transfer site of turbid water in the river Smådøla may be due to reduced survival of eggs and alevins. High mortality has been demonstrated in several studies of the young stages of salmonids in water containing high amounts of suspended matter. If silt and mud

Table IV. Production (g 100 m^{-2} yr^{-1}) of brown trout in the unregulated and regulated reaches of the river Smådøla

Age groups	Unregulated	Regulated
0+/1+	31·7	3·6
1+/2+	31·4	16·1
2+/3+	41·4	23·6
3+/4+	33·1	31·6
4+/5+	84·5	11·3
5+/6+	32·0	9·8
6+/7+	17·4	1·5
7+/8+		5·6
Total	271·5	103·1

Table V. Volume % composition of different food items in the diet of trout at the unregulated and regulated reach of the river Smådøla

	Unregulated		Regulated	
Year	1983	1984	1983	1984
Number of fish examined	43	62	24	38
Gastropoda	1·8			
Bivalvia	2·8			
Hydracarina	0·2	1·2		0·6
Crustacea:				
Eurycercus lamellatus (O F Müller)	16·4	16·9		
Gammarus lacustris Sars	12·5	1·9		1·4
Ephemeroptera:				
Baetis rhodani (Pictet)	0·2	4·7		1·4
Baetis sp.			5·9	3·6
Ameletus inopinatus Eaton	0·1			
Siphlonorus sp.		2·5		0·5
Ephemeroptera im.		4·3		
Total Ephemeroptera	0·3	11·5	5·9	5·5
Plecoptera:				
Nemoura cinerea (Retzius)	1·1			6·5
Nemurella picteti (Klapalek)			0·9	
Isoperla sp.	0·3		6·2	
Taeniopteryx nebulosa (L.)		0·7		1·3
Plecoptera l. indet.	0·9	2·8	1·0	0·7
Isoperla obscura im. (Zetterstedt)			0·2	
Plecoptera im.	1·6	3·6		
Total Plecoptera	3·9	7·1	8·3	8·5
Trichoptera:				
Rhyacophila nubila (Zetterstedt)		1·2		5·3
Potamophylax sp.	11·0	5·7	12·6	3·8
Apatania sp.		0·2	1·1	0·7
Limnephilidae indet.	24·2	9·7	8·2	14·8
Trichoptera l. indet.	4·1	5·5	1·4	13·6
Trichoptera p.	1·3	1·5	0·4	0·9
Trichoptera im.	1·4		0·2	3·4
Total Trichoptera	42·0	23·8	23·3	42·5
Chironomidae l.	4·6	21·6	43·5	35·8
Chironomidae p.			0·1	
Simuliidae		0·8	0·6	
Tipulidae	13·1	9·7	16·5	4·1
Coleoptera	0·4	0·4	1·3	
Terrestrial animals	2·2	5·1		1·3

remained in contact with eggs and alevins of brown trout, death occurred quickly (Stuart, 1953). However, young stages could survive adverse conditions for shorter periods of time. Campbell (1954) found high mortality in the eye-egg stage of rainbow trout due to silt deposition, while in a clear-water stream the mortality was low. Similarly, a study carried out by Shelton and Polloch (1962) showed a negative correlation between the amounts of sediment load and survival of chinook salmon. However, hatching experiments and recruitment studies of Atlantic salmon did not reveal any detrimental effects of sedimentation (Andersen and Langeland, 1977). These results may be due to low sedimentation in salmon spawning areas which have high discharge levels.

Some small clear-water tributaries drain into the regulated reach of the river Smådøla. Gill netting outside the outlet of one such stream yielded a relatively high catch, including several mature specimens. This indicates that such refuges of good water quality may be important areas of reproduction of brown trout in turbid rivers.

Pulse dynamics appeared to be important in affecting the initial response of juvenile coho salmon to suspended sediment. An 'alarm' reaction was observed during episodes of sudden increase (Berg and Northcote, 1985). They suggest that in the field the 'alarm' reaction may bring about a displacement away from the sediment source of fish downstream. Thus, lower fish densities in the affected reach of the river Smådøla may be partly due to a high migration rate induced by turbid water. In fact, high catches of relatively small-sized trout in lake Tesse reservoir a few years after regulation (Hesthagen and Gunnerød, 1980) strongly indicate such an effect. Detrimental effects of turbid water were also registered in the catchment area of the river Hallingdalselva in the form of immediate fish kill and a high migration rate (Aass, 1979). In the reservoir Mårvatn, brown trout migrated out of the main basin after an episode of heavy silt deposition load, to areas of less turbid water (Borgström, 1973). A short-term drop in the standing stock of fish just below a highway construction site, was also related to migration to avoid the high levels of suspended solids (Barton, 1977). Ritchie (1972) also believes that fish may move during periods of high turbidities to areas with less turbid water.

Reduced trout density below the transferring site in the river Smådøla may also partly be due to habitat destruction where sedimentation has reduced the complexity of the river bed. Density-dependent mortality is probably the main factor regulating and limiting juvenile trout numbers in streams, and territorial behaviour and the extent of a suitable rearing habitat are important in this respect (Le Cren, 1973; Mortensen, 1977; Elliott, 1984). Saunders and Smith (1965) registered a decrease in brook trout numbers caused by increased silt deposition. They relate the reduction to habitat destruction, because the direct effects of silt deposition on trout was low. High sediment loads in the regulated reach of the river Smådøla have also reduced the depth of pools, which are important habitat for larger fish. In addition, exposure to suspended sediment pulses adversely affects territorial and feeding behaviour by interrupting dominance hierarchies and interfering with the defence of territories (Berg and Northcote, 1985).

Brown trout in age groups 2+ to 4+ grew faster in the regulated turbid water than in the unregulated clear-water reach. This may be an effect of lower population density and less competition for food. Treasurer (1976) relates differences in growth rates of Scottish trout stocks to restricted spawning facilities which may keep the population at a low level, thus placing less limitations on food.

The composition of the diet of trout at both stations was dominated by chironomids and large case-building trichopterans. No quantitative benthic samples were taken in 1983 and 1984. The benthic fauna of the same areas were found to be numerically dominated by chironomids and ephemeropterans in 1975 (Borgström and Saltveit, 1976).

High sediment loads in rivers generally reduce habitat diversity by clogging interstices. This often leads to reduced invertebrate diversity (Armitage, 1984; Cline and Ward, 1984). Non-burrowing species (McClelland and Brusven, 1980; Baekken *et al.*, 1984) and filtering species (Fjellheim and Raddum, 1982) are especially affected. Avoidance of suspended sediments by non-burrowing species is also demonstrated by drift studies (Ciborowski *et al.*, 1977; Rosenberg and Wiens, 1978).

The most common trichopterans in the stomachs of trout were species building cases of stones. The anchoring effect of these stones probably prevents heavy drift from the most sedimented areas.

The most marked difference in the diets of trout from regulated and unregulated parts of the river was the low abundance of crustaceans *E. lamellatus* and *G. lacustris* in the regulated area. This is probably mainly caused by the high load of suspended inorganic matter which results in habitat destruction and shortage of the particulate organic matter, which is the main food of *E. lamellatus* (Smirnov, 1962) and species of *Gammarus* (Anderson and Sedell, 1979; Welton, 1980). Avoidance of sediment laden reservoir releases by *Gammarus* has similarly been demonstrated by Roux (1984). *Gammarus* is an important food organism for brown trout (Lien, 1978), and the drop in abundance in the regulated reach of the river Smådøla has probably contributed to decreased fish production.

The concentration of phosphorus may limit biological production in running water (Harrisman, 1978). Blakar (1976) found considerably higher levels in the river Veo water (maximum 31 μg tot-$P\ l^{-1}$) than in the river Smådøla (maximum 9 μg tot-P 1^{-1}). In Walla Brook, Horton *et al.* (1968) concluded that fish production was limited by lack of a bottom fauna, which in turn had been correlated with a lack of nutrient salts (Horton, 1961). However, it is assumed that any positive effect of this nutrient salt is neutralized by the negative effect of suspended solids and sediment deposition in the river Smådøla. Mean summer temperatures were approximately 1 °C higher in the unregulated part of the river. This may also have influenced production.

This study indicates that the transfer of highly turbid water to a clear-water river had reduced fish production significantly. Fish recruitment is affected, and availability of important food organisms is sharply reduced.

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REFERENCES

Aass, P. 1979. 'Tilslammingen i Hallingdalselva 1966–67. Fisket i Ustedalsfjord og Strandafjord', in Gunnerød, T. B. and Mellquist, P. (Eds), *Vassdragsreguleringers Biologiske Virkninger i Magasiner og Lakseelver*, Symposium, Leangkollen in May 1978. Norges Vassdrags- og elektrisitetsvesen, Oslo. Direktoratet for vilt og ferskvannsfisk, Trondheim, 93–115. (In Norwegian)

Andersen, C. and Langeland, A. 1977. *Reguleringenes innvirkning på bestand og fiske i Målselvvassdraget*, Betenkning til Malangen herredsrett, Sak 15/1971B, Dividalskjønnet. (In Norwegian)

Anderson, N. H. and Sedell, J. R. 1979. 'Detritus processing by macroinvertebrates in stream ecosystems', *Annual Revue of Entomology*, **24**, 351–377.

Armitage, P. D. 1984. 'Environmental changes induced by stream regulation and their effect on lotic macroinvertebrate communities', in Lillehammer, A. and Saltveit, S. J. (Eds), *Regulated Rivers*, University Press, Oslo, 139–165.

Baekken, T., Fjellheim, A., and Larsen, R. 1984. 'Benthic animal production in a weir basin area in western Norway' in Lillehammer, A. and Saltveit, S. J. (Eds), *Regulated Rivers*, University Press, Oslo, 223–232.

Barton, B. A. 1977. 'Short-term effects of highway construction on the limnology of a small stream in southern Ontario', *Freshwater Biology*, **7**, 99–108.

Berg, L. and Northcote, T. G. 1985. 'Changes in territorial, gill-flaring, and feeding behaviour in juvenile coho salmon (*Oncorhynchus kisutch*) following short-term pulses of suspended sediment', *Canadian Journal of Fisheries and Aquatic Sciences*, **42**, 1410–1417.

Blakar, I. 1976. 'Øvre og Nedre Smådalsvatn. En limnologisk undersøkelse med hovedvekt på hydrografi, sommeren 1975', *Laboratorium for ferskvannsøkologi og innlandsfiske, Oslo*, Rapp. **28**, 7–41. (In Norwegian)

Bohlin, T. 1981. 'Methods of estimating total stock, smolt output and survival of salmonids using electrofishing', *Institute of Freshwater Research Drottningholm*, **59**, 5–14.

Borgström, R. 1973. 'The effect of increased water level fluctuation upon the brown trout population of Mårvatn, a Norwegian reservoir', *Norwegian Journal of Zoology*, **21**, 101–112.

Borgström, R. and Saltveit, S. J. 1976. 'Bunndyr og fiskebestander i Øvre og Nedre Smådalsvatn', *Laboratorium for ferskvannsøkologi og innlandsfiske, Oslo*, Rapp. **28**, 77–104. (In Norwegian)

Campbell, H. J. 1954. *The Effect of Silation from Gold Dredging on the Survival of Rainbow Trout and Eyed Eggs in Powder River, Oregon*, Oregon State Game Commission, 3 pp.

Ciborowski, J. J. H., Pointing, P .J., and Corkum, L. D. 1977. 'The effect of current velocity and sediment on the drift of the mayfly *Ephemerella subvaria* McDunnough', *Freshwater Biology*, **7**, 567–572.

Cline, L. D. and Ward, J. V. 1984. 'Biological and physiochemical changes downstream from construction of a subalpine reservoir in Colorado, USA', in Lillehammer, A. and Saltveit, S. J. (Eds), *Regulated Rivers*, University Press, Oslo, 233–243.

Elliott, J. M. 1984. 'Numerical changes and population regulation in young migratory trout, *Salmo trutta* in a Lake District Stream 1966–1983', *Journal of Animal Ecology*, **53**, 327–350.

Fjellheim, A. and Raddum, G. G. 1982. 'Ferskvannsbiologiske undersøkelser i Fåbergstølsdeltaet, Jostedal i Sogn og Fjordane, i forbindelse med planlagt utbygging av Breheimen', *Laboratorium for ferskvannsøkologi og innlandsfiske, Bergen*, Rapp. **49**, 57 pp. (In Norwegian)

Frost, W. E. and Brown, M. E. 1967. *The Trout*, Collins, London, England.

Harrisman, R. 1978. 'Nutrient leaching from fertilized forest watershed in Scotland', *Journal of Applied Ecology*, **15**, 933–942.

Herbert, D. W. M. and Merkens, J. C. 1961. 'The effect of suspended mineral solids on the survival of trout', *Journal of Air and Water Pollution*, **5**, 46–55.

Hesthagen, T. and Gunnerød, T. B. 1980. 'Fisket i Tesse i Lom kommune, Oppland, før og etter regulering', *DVF–Reguleringsundersøkelsene Rapp. nr.* 12–1980, Trondheim, 109 pp. (In Norwegian)

Horton, P. A. 1961. 'The bionomics of brown trout in a Dartmoor stream', *Journal of Animal Ecology*, **30**, 311–338.

Horton, P. A., Bailey, R. G., and Wilsdon, S. I. 1968. 'A comparative study of the bionomics of the Salmonids of three Devon streams', *Archiv für Hydrobiologie*, **65**, 187–204.

Hynes, H. B. N. 1950. 'The food of fresh-water sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*) , with a review of methods used in studies of the food of fishes', *Journal of Animal Ecology*, **19**, 36–58.

Jonsson, B. 1976. 'Comparison of scales and otoliths for age determination in brown trout', *Norwegian Journal of Zoology*, **24**, 285–301.

Le Cren, E. D. 1973. 'The population dynamics of young trout (*Salmo trutta*) in relation to density and territorial behaviour', *Rapports et Proces-Verbaux des Reunions Conseil International pour l'Exploration de la Mer*, **164**, 241–246.

Lien, L. 1978. 'The energy budget of the brown trout population of Øvre Heimdalsvatn', *Holarctic Ecology*, **1**, 279–300.

Lillehammer, A. and Saltveit, S. J. 1979. 'Stream regulation in Norway', in Ward, J. V. and Stanford, J. A. (Eds), *The Ecology of Regulated Streams*, Plenum Press, New York, London, 201–213.

McClelland, W. T. and Brusven, M. A. 1980. 'Effects of sedimentation on the behavior and distribution of rifle insects in a laboratory stream', *Aquatic Insects*, **2**, 161–169.

Mortensen, E. 1977. 'Density-dependent mortality of trout fry (*Salmo trutta* L.) and its relationship to the management of small streams', *Journal of Fish Biology*, **11**, 613–617.

Ricker, W. E. 1975. *Computation and Interpretation of Biological Statistics of Fish Populations*, Bulletin Fisheries Research Board of Canada, Report 191, 382 pp.

Ritchie, J. C. 1972. 'Sediment, fish and fish habitat', *Journal of Soil and Water Conservation*, **27**, 124–125.

Rosenberg, D. M. and Snow N. B. 1975. *Ecological Studies of Aquatic Organisms in the Mackenzie and Porcupine River Drainages in Relation to Sedimentation*, Fisheries and Marine Service, Technical Report No. 547, 86 pp.

Rosenberg, D. M. and Wiens, A. P. 1978. 'Effects of sediment addition on macrobenthic invertebrates in a northern Canadian river', *Water Research*, **12**, 753–763.

Roux, A. L. 1984. 'The impact of emptying and cleaning reservoirs on the physicochemical and biological water quality of the Rhone downstream of the dams', in Lillehammer, A. and Saltveit, S. J. (Eds), *Regulated Rivers*, University Press, Oslo, 61–70.

Rübberdt, S. 1976. *Leirslammets innvirkning på noen laksefisk (Salmonidae) og deres næringsdyr*, Thesis, Norges Landbrukshøgskole, Ås, 64 pp. (In Norwegian).

Saunders, J. W. and Smith, M. W. 1965. 'Changes in a stream population of trout associated with increased silt', *Journal of Fisheries Research Board of Canada*, **22**, 395–404.

Shelton, J. M. and Pollock, R. O. 1962. *Siltation and Egg Survival in Incubation Channels*, United States Bureau of Commercial Fisheries, Columbia Fisheries Program Office, Portland, Oregon, 183–187.

Smirnov, N. N. 1962. '*Eurycerus lamellatus* (O. F. Müller) (Chydoridae, Cladocera): field observation and nutrition', *Hydrobiologia*, **20**, 280–294.

Sokal, R. R. and Rohlf, F. J. 1969. *Biometry*, W. H. Freeman and Company, San Francisco, 776 pp.

State Pollution Control Authority 1982. 'Overvåking av langtransportert forurenset luft og nedbør', *Statlig program for forurensningsovervåking, Statens forurensningstilsyn*, Oslo, Rapp. **64/82**, 176 pp. (In Norwegian)

Stuart, T. A. 1953. 'Spawning migration, reproduction and young stages of loch trout (*Salmo trutta* L.)', Scottish Home Department, Freshwater and Salmon Fisheries Research, **5**, 1–39.

Treasurer, J. W. 1976. 'Age, growth and length–weight relationship of brown trout *Salmo trutta* (L.) in the Loch of Strathbeg, Aberdeenshire', *Journal of Fish Biology*, **8**, 241–253.

Walseng, B. and Halvorsen, G. 1986. 'Flerbruksplan for vassdrag i Gudbrandsdalen, limnologisk oversikt', *Vassdragsforsk*, Oslo, Rapp. **95**, Oslo, 153 pp. (In Norwegian)

Welton, J. S. 1980. 'Dynamics of sediment and organic detritus in a small chalk stream', *Archiv für Hydrobiologie*, **90**, 162–181.

Differences in habitat utilization among native, native stocked and non-native stocked brown trout (Salmo trutta) in a hydroelectric reservoir

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Native and native-stocked brown trout (Salmo trutta) were spatially segregated according to size. Small individuals mainly occurred in epibenthic habitat, while larger individuals were mainly caught in pelagic habitat. In contrast, all size groups of non-native brown trout were largely restricted to epibenthic habitat. Age specific lengths were generally larger for non-native fish than for native stocked trout, which were larger than native fish. However, growth rate (G) between age 3 and 4 was significantly lower for non-native stocked fish than for native and native stocked fish. Differences in body length were mainly due to strain, but also to some extent to habitat. Native and native stocked fish exhibited a significantly higher stomach fullness in pelagic than in epibenthic habitat, with the exception of native stocked fish in August. Epibenthic non-native fish had a significantly higher stomach fullness than native and native stocked fish in July but not in August. Native and native stocked fish fed mainly on surface insects and plantonic crustaceans in both habitats. We hypothesized that the non-native brown trout stocked in Lake Tesse lack a pelagic habitat utilization in the "home lake", and were therefore less adapted to utilize such habitat than populations originating from lakes where pelagic habitat is available.

Habitat use has important implications for fish production, and there is now considerable interest regarding behavior and ecological traits of new or supplementary stocked fish (O'Hara 1986; Wydoski 1986).

Little is known about whether habitat utilization by fish from different stocks will be identical when they are offered identical environmental conditions. There are several examples of differences in food and habitat use between sympatric morphs within salmonid species (e.g., Svärdson 1979; Hindar and Jonsson 1982; Ferguson 1986; Sandlund et al. 1987). In contrast, lake plantings of domestic, hybrid and wild strains of brook trout (Salvelinus fontinalis) and brown trout showed use of space and food resources similar to that of native trout (Fraser 1981; Lachance and Magnan 1990; L'Abee-Lund and Sægrov 1991; L'Abee-Lund et al. 1992). Studies of resource utilization also indicate that an intrinsic preference for space and food exists in several salmonid species (Olson et al. 1988).

Stocking of brown trout (Salmo trutta) is widely carried out to compensate for reduced natural propagation in Norwegian hydroelectric reservoirs. Most supplementary stocking involves fry of non-native stocks raised in large central hatcheries. This species usually occupy shallow littoral areas (Nilsson 1963; Thorpe 1974; Svärdson 1976; Langeland et al. 1991). However, in large deep lakes with small littoral zones, brown trout are also found to exploit pelagic habitats, where they feed on surface insects and crustacean zooplankton (e.g. Klemetsen 1968; Haraldstad and Jonsson 1983; Hegge et al. 1989; Schei and Jonsson 1989; Langeland et al. 1991). Such resource utilization is especially important in hydroelectric reservoirs where the prey fauna in littoral areas is reduced by water level fluctuations (Grimås 1962). In brown trout, there are marked differences in habitat utilization according to size as small and large individuals generally occupy benthic and pelagic habitats, respectively (Haraldstad and Jonsson 1983; Hegge et al. 1989; Jonsson 1989).

The purpose of this study was to test the null-hypotheses that there are no significant differences in feeding habits and use of space between native and non-native brown trout. Lake Tesse, a Norwegian hydroelectric reservoir where allopatric brown trout exploit both epibenthic and pelagic habitat, was chosen for our experiments. Two of the most frequently used hatchery strains in Norway, Tunhovdfjord and Bjornesfjord, were used for the experiment. As a reference we also stocked the lake with offspring from native brown trout stock.

Study area

Lake Tesse is located in southern Norway at an altitude of 853.9 m above sea level. Lake Tesse was first regulated in 1943, and until 1963 the mean annual water amplitude was 7.3 m (range 3.7-11.8 m). In 1963, the glacier-fed River Veo was transferred into Lake Tesse through the River Smådøla (Hesthagen and Fjellheim 1987). The annual water amplitude increased to 12.4 m, of which 0.9 m is dammed. The reservoir covers an area of 937 and 1426 ha at the lowest and highest water levels, respectively. The catchment area of 430 km^2 mainly consists of basic deep rocks such as anortsite and Valdres sparagmite. Lake Tesse was originally a clear water lake, but is now heavily influenced by glacier-fed water from the river Veo. The secchi disc transparency was measured to 4.0 m during the study period in 1989, as opposed to 8-10 m prior to regulation (Huitfeldt-Kaas 1906). A dominant proportion of the basin includes areas with depths between 5-30 m, and the deepest area is 64 m. The pH is near neutral (6.7) and calcium concentration is of 1.4 mg/l.

The spawning grounds for brown trout in the outlet of Lake Tesse were lost due to the construction of a dam. Further, channalization and transfer of glacier-fed water strongly reduced recruitment in the inlet River Smådøla, which was the main spawning river. Brown trout spawn in the lake along the shore at depths between 3-5 m (Simen Bjørgen, personal communication), and these areas now dry out at low water levels during winter. Brown trout also still spawn in several smaller tributaries which drain into the reservoir.

Methods

Juvenile (age 0+) brown trout, originating from both native and non-native stocks (Bjornesfjord and Tunhovdfjord strains), were marked and released in Lake Tesse in the autumn. Non-native fish were raised in circular tanks at Reinsvoll Hatchery about 250 km south of Tesse and fed artificial food. The Bjornesfjord strain has been domesticated since 1966, while the Tunhovdfjord strain originated from wild parents (Stabell et al. 1988). The fertilized eggs of native brown trout from Lake Tesse were placed in a hatchery at Lemonsjøen shortly after fertilization. The unfed fry were released in an earthen pond about 10 km from Lake Tesse in early June, where they fed on natural food items.

During the period from 1980 to 1987, a total of 88000 non-native and 72800 native fish were released in the lake. In addition, 14000 native stocked fish were released in four tributaries. Of the non-native fish in the present study, individuals of age 3+ originated from the Tunhovdfjord strain while those of age 4+ - 6+ were offspring of the Bjornesfjord strain. Non-native fish ranged in mean length at release between 47-60 mm compared to 42-55 mm for native stocked fish. Juvenile (age 0+) native fish caught in the tributaries usually range between 35-45 mm.

The fish were marked by removing the adipose and either left or right pelvic fins of native and non-native individuals, respectively. Fish released in the tributaries were marked by removing the adipose fin only. All non-native brown trout, and those native stocked fish released in 1984-1987 (age 2+ - 5+ at recapture in 1989), were marked. Only 48% of the 5200 native stocked fish released in the reservoir during the period 1980-1983 were marked. Non-native fish were marked prior to transportation from the hatchery.

The number of circuli in the scales can be used to separate naturally produced and stocked brown trout (L'Abee-Lund and Sægrov 1991). We counted the number of first-year circuli on scales from fish of known origin, e.g. those of age 2+ - 5+. Based on the number of first-year circuli (C) of classified stocked and native fish, we performed an unstandardized canonical discriminant function:

$$D = -3.003 + 0.580\ C$$

which grouped 79.1% of native brown trout as native and 71.1% of stocked brown trout as stocked. We used this function to classify fish of age 6+ - 8+ as either native or native stocked.

Prior to stocking in late August/early September, fish from both groups were mixed and placed overnight in a net cage in the reservoir. The fish were released along the shore throughout most of the reservoir except for the northern and southern parts where the littoral bed consists of fine gravel.

The fish were caught with 25 m long benthic and pelagic monofilament nets which were 1.5 m and 6.0 m in vertical dimension, respectively. Eight nets consisted of panels with the following bar mesh sizes: 16.6, 21.0, 21.0, 26.0, 29.0, 35.0, 39.0 and 45 mm. Mesh sizes between 21.0 and 45.0 mm caught brown trout in the 20-38 cm size interval with equal efficiency (Jensen 1977). Benthic nets were set perpendicular to the shore at depth ranging between 0-27 m, while pelagic nets were set at a station about 500 m off shore at depths between 45-55 m. Benthic nets were used during three 24-h periods in July covering depth zones 0-10 m. In August, benthic nets were used during two 24-h periods. Pelagic nets were used during three 24-h periods in July and one 24-h period in August, and these nets were set at depths of 0-6 and 6-12 m. The catch per unit effort (CPUE) is presented as the number of fish caught per 100 m^2 net area during 24 hours of fishing. Tests for the goodness of fit by means of chi-square analyses were done with actual frequencies.

Each fish was examined for marks, and total length (millimetres) and weight (grams) were measured. The fish were aged from scales and otoliths (Jonsson 1976). The scale sample was taken from the left side of the fish just below the lateral line (below the adipose fin). Impressions of 4-6 scales were made in celluloid and read using a microfiche projector. Distances from the focus of the scale to each annulus and to the outer scale margin were measured. Body length at age x (SL_x) was back-calculated according to the Fraser-Lee method (Ricker 1975; Francis 1990):

$$SL_x = \frac{(SL_c - SL_o)\, R_x}{R_c} + SL_o$$

where SL_c is length at capture, SL_o is the fish length when scales first appear, R_x is the distance from the focus of the scale to annulus x, and R_c is scale radii at capture. SL_o can be derived from the intercept of the regression of fish length on scale radius. The relationship between fish length (SL_c, mm) and scale length (R_c, mm) is given by the equation:

$$R_c = 0.38\ SL_c - 3.42,\ R^2 = 0.67,\ P < 0.00001$$

In the present study, any estimate of SL_o is biased because of the lack of individuals smaller than 10 cm in the sample. Therefore we used data from the literature. SL_o for brown trout in Norwegian waters ranges between 35-41 mm (Gunnerød 1966; Jonsson 1976; Jensen and Johnsen 1982). We choose the value 35 mm in our model. The back-calculated length at age 1 is not presented because this value may be biased (cf. Francis 1990).

The back-calculated lengths were further converted to weights from the weight-length relationships by logarithmic transformation of weights (W, g) and total lengths (L, mm) at capture. The relationship between weights and lengths is given by the equation:

$$\ln W = 2.93 \ln L - 4.40,\ R2=0.97,\ P < 0.00001$$

Growth rates for individual fish were then expressed as the instantaneous growth coefficient (G), which was estimated from the formula:

$$G = \log_e W_{t+1} - \log_e W_t$$

where W_{t+1} and W_t = weight at age t+1 and t, respectively.

The start size of non-native fish was larger than for native stocked and native fish. This may affect the growth rate between age 1 and 2. Therefore, we omitted G-value for these two age groups in our analysis.

Fish stomachs were preserved in 70% ethanol for later examination with a binocular microscope. The mean percent composition of each taxonomic category in each stomach was determined from dry weights which were calculated from body lengths according to formulas for different taxonomic categories (Bottrell et al. 1976; Langeland 1982; Hindar et al. 1988; Langeland et al. 1991). The number of different prey items in each stomach was counted except for samples containing a high number of zooplankton, in which case a subsample of a 1/10 or 1/4 was counted.

We used the Schoener (1968) index to measure overlap in diet (D) between different trout strains and fish caught in different habitats:

$$D=1-0.5\sum_{i=1}^{n}(p_i-q_i)$$

where p_i = the weight proportion of food item i in the diet of trout strain 1, and q_i = the weight proportion of food item i in the diet of trout strain 2.

Results

Spatial Distribution

There were no differences in frequencies of native and native stocked brown trout caught in the epibenthic and pelagic zones in either July (X^2=0.26, P >0.05) or August in Lake Tesse (X^2=0.12, P >0.05). The data were therefore pooled (Table 1). There was a significant difference in habitat use between native and native stocked brown trout and non-native brown trout (both the Tunhovd and Bjornesfjord strain). Non-native brown trout were strongly underrepresented in the pelagic habitat (July X^2 = 59.6, P < 0.0001 and August X^2 = 12.9, P < 0.01).

Size and Age Distribution

All size groups of non-native brown trout were mainly restricted to epibenthic habitat (Fig. 1). On the other hand, both native and native stocked fish were spatially segregated according to size. 57-58% of naturally recruited and native individuals < 220 mm occupied epibenthic habitat, while 86-87% of individuals >220 mm occupied the pelagic habitat. A Kolmogorov-Smirnov two sample test showed that the length frequency distributions of fish caught in the epibenthic and pelagic habitats were significantly different (Fig. 1).

Back-calculated lengths of individuals caught in epibenthic and pelagic zones showed that non-native fish were generally significantly larger than individuals of corresponding age of native stocked fish, which were significantly larger than native fish (Table 2, ANOVA, P<0.05). The instantaneous growth rate (G) between age 2 and 3 did not differ significantly between different groups (Fig. 2, ANOVA, P > 0.05). However, between age 3 and 4, the G-value for both native and native stocked fish was significantly higher than for non-native individuals, $F_{2,259}$ = 14.28, P < 0.00001. Between ages 4 and 5 and between age 5 and 6, the G-value for native fish was significantly higher than for native stocked individuals, $F_{2,95}$ = 4.45, P < 0.05 and $F_{2,93}$ = 3.53, P < 0.05, respectively. Comparison of growth rate of non-native fish in age groups $\geq$ 5 was invalidated due to low numbers (n=4).

Fish obtained in the pelagic zone were usually significantly larger than individuals of corresponding age obtained in the epibenthic zone (Table 2). Analysis of covariance showed that the differences in back-calculated length were mainly due to strain but also to some extent to habitat, after having removed the effect of age (Table 3).

Feeding Habits

The diets of all three types of brown trout in epibenthic habitat in July consisted mostly of terrestrial insects and benthic crustaceans, Eurycercus lamellatus and Sida crystalina (Fig. 3). However, non-native trout fed more on Mollusca and other zoobenthos and less on benthic crustaceans than native and native stocked trout. However, the overall difference in diet between native and non-native fish and between native stocked and non-native fish was small as indicated by the high diet overlap (Schoener index equal to 0.85 and 0.87, respectively).

Surface insects were less imporant as food for fish caught in the epibenthic zone in August. At that time, zoobenthos were the dominant food for non-native fish while Bythotrephes longimanus and Daphnia longispina dominated the diet of native and native stocked trout. The difference in diet between native and non-native fish and between native stocked and non-native fish is illustrated by the relatively low diet overlap; Schoener index equal to 0.47 for both categories.

Native and native-stocked fish caught in pelagic nets in July fed mainly on surface insects (70%). Planktonic crustaceans B. longimanus and D. longispina made up the main part of the rest of the diet. In August, surface insects were of less importance as food for trout in offshore regions, and D. longispina was the predominant food item. The diet overlap between native and native stocked trout caught in the pelagic zone was 0.95 in July and 0.89 in August.

In epibenthic and pelagic habitats, the stomach fullness expressed in dry weight of both native and native stocked fish was significantly higher in July than in August (ANOVA, $P < 0.005$, Table 4). There was no seasonal variation in stomach fullness for non-native fish (epibenthic habitat only, ANOVA, $P > 0.05$). Native fish and native stocked fish exhibited a significantly higher stomach fullness in pelagic than in epibenthic habitat in both July (ANOVA, $P < 0.001$) and August ($P < 0.005$). Non-native fish had a significantly higher stomach fullness than native fish in epibenthic habitat, regardless of season (ANOVA, $P < 0.00001$), whereas no such difference was observed in pelagic habitat in July (ANOVA, $P > 0.05$).

Discussion

The habitat use of native and native stocked brown trout differed significantly from that of non-native brown trout in Lake Tesse. Naturally recruited and native stocked trout were both spatially segregated according to size. Small individiuals occurred mainly in the epibenthic habitat while larger individuals dominated in the pelagic habitat. In contrast, the habitat use of all size groups of non-native brown trout was restricted mainly to the epibenthic habitat.

The diet of brown trout in the epibenthic habitat mainly consisted of terrestrial insects and zooplankton. Benthic foods were of little importance. Brown trout caught in the pelagic habitat fed almost exclusively on surface insects and the two planktonic crustaceans B. longimanus and D. longispina. Pelagic trout utilized a broad part of the water column when foraging. Observations in summer of higher stomach fullness of pelagic brown trout compared to those caught in epibenthic habitat, indicate that food access was temporally better in the pelagic habitat. This finding is in accordance with data on the resource base in Lake Tesse, which show low densities of zoobenthos, while the biomass of zooplankton was relatively high compared to other Norwegian lakes (unpubl.

data).

Non-native fish exhibited significantly lower growth rate than either native or native stocked fish between ages 3 and 4. At this age, there was an increase in the number of pelagically caught fish, hence, the habitat switch of native and native stocked fish was manifested in better growth. Differences in growth rate and longevity is not related to the maturity pattern as very few non-native fish were sexually mature compared with native and native stocked brown trout (unpubl. data). The disappearance of older non-native fish is probably only to a small extent related to size selective fishery as brown trout in Lake Tesse is harvested with gill nets of 35 mm mesh size.

Several authors (e.g. Haraldstad and Jonsson 1983; Jonsson and Gravem 1985; Hegge et al. 1989; Jonsson 1989) report that small individuals of brown trout prefer epibenthic habitat despite better food access in pelagic habitats. This is interpreted by a strong need for shelter in small individuals to avoid predation and agonistic encounters with larger individuals (Haraldstad and Jonsson 1983; Hegge et al. 1989). This behavior may cause reduced food intake and growth depression (cf. Brown 1946; Fenderson et al. 1968; Jobling and Reinsnes 1986). Another study conducted in Lake Tesse demonstrated that smaller brown trout were more strongly associated with the bottom than larger fish (Hegge et al. 1993). Accordingly, the most profitable habitat for smaller brown trout seems to be the epibenthic habitat where fish have access to shelter among stones. We suggest that the most profitable habitat for larger individuals In Lake Tesse may be the pelagic zone where food resources are best.

Spatial segregation within population according to size appears to represent an ontogenetic niche shift (cf. Werner and Gilliam 1984). Jonsson et al. (1988) hypothesized that such habitat shift is brought about by size-related differences in competitive abilities. However, in spite of a greater initial length and larger size in all age groups of non-native fish compared with native and native stocked fish, the non-natives remained in the epibenthic zone without exhibiting any apparent niche shift as exhibited by native fish. It is unlikely that the larger non-native brown trout are forced to remain in epibenthic habitat by social interactions with the smaller native brown trout because the outcome of agonistic encounters is primarily a function of size (Bachman 1984).

Differences in habitat use between native and non-native fish in Lake Tesse, could be due to a delayed phenotypic response to new environmental conditions. However, size-related differences between native stocked and non-native stocked fish were small. Behavioral changes (e.g. habitat shift) related to experiences during development cannot be overlooked (Huntingford 1986). Our experimental fish differed in rearing background; non-native fish were hatchery-reared whereas native stocked fish were pond-reared. However, the fact that the diet of hatchery-reared brown trout released in natural waters differs from native fish shortly after release (Johnsen and Ugedal 1989) may indicate any habitat shift several years later is not related to rearing background.

Segregation in resource utilization has been found in phenotypically and ecologically different sympatric populations of salmonids elsewhere (e.g. Svärdson 1979; Hindar and Jonsson 1982; Ferguson 1986; Sandlund et al. 1987). Ferguson (1986) found differences in feeding preference and habitat use of the three sympatric populations of brown trout in Lough Melvin (Ireland), and stated that these differences appear to be genetically controlled. Similarly, native and native stocked Bjornesfjord and Tunhovdfjord brown trout largely utilizated the same habitat and were mainly caught in the epibenthic zone (L'Abee-Lund and Sægrov 1991, L'Abee-Lund et al. 1992).

The existence of genetically determined differences between stocks in characteristics such as behavior, morphology and physiology is well documented in various fish species (e.g. Svärdson 1979; Rosseland and Skogheim 1987; Skúlason et al. 1989; Magurran 1990). These differences may be adaptations to local environmental conditions (Magurran 1990). Such characteristics may influence feeding efficiency (e.g. Kliewer 1970; Schulz and Northcote 1972; Henderson and Northcote 1985; Townsend and Winfield 1985; Lavin and McPhail 1986), and thereby feeding habits and habitat choice. Variation in habitat choice due to species differences in feeding efficiency is well documented (e.g. Werner and Hall 1979; Persson 1987; Ehlinger and Wilson 1988; Hindar et al. 1988). Differences in food choice also seem to exist among populations within a single species, e.g. for brown trout in Lough Melvin which differ in morphometric and meristic characteristics (Cawdery and Ferguson 1988). In addition, differences in head morphology of coexisting Arctic charr (Salvelinus alpinus) in Thingvallavatn (Iceland) appear to be related to differences in feeding habits (Skúlason et al. 1989). Olsson et al. (1988) suggested that resource utilization by stocked fish in Lake Ontario is due to previously evolved morphological and physiological traits.

We hypothesized that the rigid use of space by non-native fish stocked in Lake Tesse may be related to lacking adaptation to pelagic habitat utilization in their "home lakes". In Lake Bjornesfjorden, with a maximum depth of 6 m, there is limited pelagic zone (Tysse and Garnås 1990; L'Abée-Lund and Sægrov 1991). In the regulated Lake Tunhovdfjord, the pelagic zone is mainly occupied by Arctic charr which were introduced about 70 years ago (L'Abée-Lund et al. 1992). Thus, it seems reasonable to hypothesize that brown trout from these two lakes are specially adapted to exploit epibenthic habitats, and are less adapted to utilizing pelagic habitat when stocked in Lake Tesse in the same manner as native brown trout. As there were only small differences in habitat use between native and stocked brown trout of native origin, we suggest that the observed variation between native and non-native brown trout were influenced by genetic differences.

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References

BACHMAN, R.A. 1984. Foraging behavior of free-ranging wild and hatchery brown trout in a stream. Trans. Am. Fish. Soc. 113: 1-32.

BOTTRELL, H.H., A. DUNCAN, Z.M. GLIWICZ, E. GRYGIEREK, A. HERZIG, A. HILLBRICHT-ILKOWSKA, H. KURASAWA, R. LARSSON, AND T. WEGLENSKA. 1976. Review of some problems in zooplankton production studies. Norw. J. Zool. 24: 419-456.

BROWN, M.E. 1946. The growth of brown trout (Salmo trutta Linn.). I. Factors influencing growth of trout fry. J. Exp. Biol. 22: 118-129.

CAWDERY, S.A.H., AND A. FERGUSON. 1988. Origins and differentiation of three sympatric species of trout (Salmo trutta L.) in Lough Melvin. Pol. Arch. Hydrobiol. 35: 267-277.

EHLINGER, T.J., AND D.S. WILSON. 1988. A complex foraging polymorphism in bluegill sunfish. Proc. Nat. Acad. Sci. (USA) 85: 1878-1882.

FENDERSON, O.C., W.H. EVERHART, AND L.M. MUTH. 1968. Comparative agonistic and feeding behaviour of hatchery-reared and wild salmon in aquaria. J. Fish. Res. Board Can. 25: 1-14.

FERGUSON, A. 1986. Lough Melvin, a unique fish community. Roy. Dublin Soc. Occas. Pap. Irish Sci. Tech 1: 1-17.

FRANCIS, R.I.C.C. 1990. Back-calculation of fish length: a critical review. J. Fish Biol. 36: 883-902.

FRASER, J.M. 1981. Comparative survival and growth of planted wild, hybrid, and domestic strains of brook trout (Salvelinus fontinalis) in Ontario lakes. Can. J. Fish. Aquat. Sci. 38: 1672-1684.

GRIMÅS, U. 1962. The effect of increased water level fluctuation upon the bottom fauna in Lake Blåsjøn, northern Sweden. Rep. Inst. Freshwater Res. Drottningholm 44: 14-41.

GUNNERØD, T.B. 1966. Dannelse av annuli i skjellene og tilvekst hos ørret (Salmo trutta L.) i et overbefolket myrvann i det sørlige Norge. Unpublished thesis, Univ. of Oslo, 79 p. (In Norwegian).

HARALDSTAD, Ø., AND B. JONSSON. 1983. Age and sex segregation in habitat utilization by brown trout in a Norwegian lake. Trans. Am. Fish. Soc. 112: 27-37.

HEGGE, O., B.K. DERVO., J. SKURDAL, AND D.O. HESSEN. 1989. Habitat utilization by sympatric arctic charr (Salvelinus alpinus (L.)) and brown trout (Salmo trutta L.) in Lake Atnsjø, south-east Norway. Freshwat. Biol. 22: 143-152.

HEGGE, O., T. HESTHAGEN, AND J. SKURDAL. 1993. Vertical distribution and substrate preference of brown trout in a littoral zone. Environ. Biol. Fish. 36: 17-24.

HENDERSON, M.A. , AND T.G. NORTHCOTE. 1985. Visual prey detection and foraging in sympatric cutthroat trout (Salmo clarki clarki) and Dolly Varden (Salvelinus malma). Can. J. Fish. Aquat. Sci. 42: 785-790.

HESTHAGEN, T., AND A. FJELLHEIM. 1987. Effects of transferring glacier-fed water to a clear-water mountain river on the production and food organisms of brown trout (Salmo trutta L.) in southern Norway. Regulated Rivers: Res. & Mgmt. 1:161-170.

HINDAR, K., AND B. JONSSON. 1982. Habitat and food segregation of dwarf and normal Artic charr (Salvelinus alpinus) from Vangsvatnet Lake, western Norway. Can J. Fish. Aquat. Sci. 39: 1030-1045.

HINDAR, K., B. JONSSON, J.H. ANDREW, AND T.G. NORTHCOTE. 1988. Resource utilization of sympatric and experimentally allopatric cutthroat trout and Dolly Varden charr. Oecologia (Berlin) 74: 481-491.

HUITFELDT-KAAS, H. 1906. Planktonundersøkelser i norske vande. Nationaltrykkeriet, Christiania. (In Norwegian, German summary).

HUNTINGFORD, F.A. 1986. Development of behaviour in fish, p. 47-68 In T.J. Pitcher (ed.) The behaviour of Teleost fishes. Croom Helm, London, Sydney.

JENSEN, A.J., AND B.O. JOHNSEN. 1982. Difficulties in aging Atlantic salmon (Salmo salar) and brown trout (Salmo trutta) from cold rivers due to lack of scales as yearlings. Can. J. Fish. Aquat. Sci. 39: 321-325.

JENSEN, K.W. 1977. On the dynamics and exploitation of the

L'ABÉE-LUND, J.H., AND H. SÆGROV. 1991. Resource use, growth and effects of stocking in alpine brown trout, Salmo trutta L. Aquacult. & Fish. Manage. 22: 519-526.

L'ABÉE-LUND, J.H., H. SÆGROV; AND H. LURA. 1992. Resource partitioning and spatial segregation in native and stocked brown trout; Salmo trutta L., and Arctic charr, Salvelinus alpinus (L.), in a hydroelectric reservoir. Aquacult. & Fish. Manage. 23:623-632.

LACHANCE, S., AND P. MAGNAN. 1990. Comparative ecology and behavoir of domestic, hybrid, and wild strains of brook trout, Salvelinus fontinalis, after stocking. Can. J. Fish. Aquat. Sci. 47: 2285-2292.

LANGELAND, A. 1982. Interactions between zooplankton and fish in a fertilized lake. Holarct. Ecol. 5: 273-310.

LANGELAND, A., J.H. L'ABEE-LUND, B. JONSSON, AND N. JONSSON. 1991. Resource partitioning and niche shift in Arctic charr Salvelinus alpinus and brown trout Salmo trutta. J. Anim. Ecol. 60: 895-912.

LAVIN, P.A., AND J.D. MCPHAIL. 1986. Adaptive divergence of trophic phenotype among freshwater population of the threespine stickleback (Gasterosteus aculeatus). Can. J. Fish. Aquat. Sci. 43: 2455-2463.

MAGURRAN, A.E. 1990. The inheritance and delevopment of anti-predator behaviour. Anim. Behav. 39: 834-842.

NILSSON, N.-A. 1963. Interaction between trout and char in Scandinavia. Trans. Am. Fish. Soc. 92: 276-285.

O'HARA, K. 1986. Fish behaviour and the management of freshwater fisheries, p. 496-521 In T.J. Pitcher (ed.) The behaviour of Teleost fishes. Croom Helm, London, Sydney.

OLSON, R.A., J.D. WINTER, D.C. NETTLES, AND J.M. HAYNES. 1988. Resource partitioning in summer by salmonids in south-central Lake Ontario. Trans. Am. Fish. Soc. 117: 552-559.

PERSSON, L. 1987. Effects of habitat and season on competitive interactions between roach (Rutilus rutilus) and perch (Perca fluviatilis). Oecologia (Berlin) 73: 170-177.

RICKER, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can., Rep. 191. 382 p.

ROSSELAND, B.O., AND O.K. SKOGHEIM. 1987. Difference in sensitivity to acidic soft water among strains of brown trout (Salmo trutta L.). Annls Soc. r. zool. Belg. 117 (suppl. 1):255-264.

SANDLUND, O.T., B. JONSSON, H.J. MALMQUIST, R.GYDEMO, T. LINDEM, S. SKULASON, S.S. SNORRASON, AND P.M. JONASSON. 1987. Habitat use of Arctic charr Salvelinus alpinus in Thingvallavatn, Iceland. Environ. Biol. Fish. 20: 263-274.

SCHEI, T.A., AND B. JONSSON. 1989. Habitat use of lake-feeding, allopatric brown trout in Lake Oppheimsvatnet, Norway, p. 156-168 In E. Brannon and B. Jonsson (ed.) Proc. Sec. Int. Salmonid Migration and Distribution Symp. School of Fisheries, Univ. Wash. Seattle, USA, and Norw. Inst. Nature Res., Trondheim, Norway.

SCHOENER, T. 1968. The Anolis lizards of Bimini: resource partitioning in a complex fauna. Ecology 49: 704-726.

SCHUTZ, D.C., AND T.G. NORTHCOTE. 1972. An experimental study of feeding behaviour and interaction of coastal cutthroat trout (Salmo clarki clarki) and Dolly Varden (Salvelinus malma). J. Fish. Res. Board Can. 29: 555-565.

SKULASON, S., D.L.G. NOAKES, AND S.S. SNORRASON. 1989. Ontogeny of trophic morphology in four sympatric morphs of arctic charr Salvelinus alpinus in Thingvallavatn, Iceland. Biol. J. Linn. Soc. 38: 281-301.

STABELL, F.R., F. HAFSUND, AND J. SKURDAL. 1988. Rognstørrelse og rognantall for stamfisk av ørret Salmo trutta (L.) med ulik alder og avstamning. A/L Settefisk, Reinsvoll, Report 1- 1988. (In Norwegian).

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

SVÄRDSON, G. 1979. Speciation of Scandinavian Coregonus. Rep.

Inst. Freshwater Res. Drottningholm 57: 834-842.

THORPE, J. E. 1974. The movements of brown trout Salmo trutta L. in Loch Leven, Kinross. J. Fish Biol. 6: 153-180.

TOWNSEND, C.R., AND I.J. WINFIELD. 1985. The application of optimal foraging theory to feeding behaviour in fish, p. 67-98 In P. Tytler and P.Calow (ed.) Fish Energetics, New Perspectives, Croom and Helm, London.

TYSSE, Å, AND E. GARNÅS. 1990. Fiskeribiologisk undersøkjing i Langesjøen og Bjornesfjorden, Nore og Uvdal kommune 1989. Fylkesmannen i Buskerud, Miljøvernavd. Rapp. 11-1990. 48 p. (In Norwegian).

WERNER, E.E., AND D.J. HALL. 1979. Foraging efficiency and habitat switching in competing sunfishes. Ecology 60: 256- 264.

WERNER, E.E., AND J. GILLIAM. 1984. The ontogenetic niche and species interactions in size-structured populations. Ann. Rev. Ecol. Syst. 15: 393-425.

WYDOSKI, R.S. 1986. Informational needs to improve stocking as a cold-water fisheries management tool, p. 41-57 In R.H. Stroud (ed.) Fish Culture in Fisheries Management. Proc. Symp. The role of Fish Cult. Fish. Mgmt. at Lake Ozark, Missouri, Am. Fish. Soc., Bethesda, Maryland.

TABLE 1. Catch per unit effort for native (NA) native stocked (NA–S) and non–native stocked (NNA–S) brown trout expressed as catches per 100 m^2 net area during 24 hours fishing in the epibenthic (C_B) and pelagic zone (C_p) in Lake Tesse in July and August 1989. N=total number of fish caught.

Month	Strain	C_B	N	C_p	N
July	NA	3.48	94	1.32	143
	NA–S	2.52	68	0.84	91
	NNA–S	2.48	67	0.07	8
August	NA	9.75	117	6.00	72
	NA–S	7.00	84	4.67	56
	NNA–S	2.08	25	0.08	1

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TABLE 2. Back–calculated growth in length (L2–L7, mm ± standard deviation) for native (NA), native stocked (NA–S) and non–native stocked (NNA–S) brown trout of age 2–7 caught in epibenthic (B) and pelagic (P) habitat in Lake Tesse in 1989. N = number of fish. Data for one NNA–S fish of age 7 is omitted. Within age groups and habitat, mean length followed by different letters (x,y,z) are significantly different ($P<0.05$) and mean length followed by the same letter are not significantly different ($P>0.05$). In cases were NNA–S and NA fish are significantly different, but neither group is different compared with NA–S fish, this latter group is labelled both by x and y.

		Age 2		Age 3				Age 4		
Habitat	Strain	L2	N	L2	L3	N	L2	L3	L4	N
B	NA	$117\pm16_x$	31	$103\pm12_x$	$155\pm18_x$	72	$106\pm12_x$	$148\pm17_x$	$205\pm26_x$	68
B	NA–S	$133\pm15_y$	20	$111\pm10_y$	$166\pm16_y$	72	$115\pm15_y$	$159\pm19_y$	$219\pm22_y$	29
B	NNA–S			$130\pm11_z$	$195\pm18_z$	70	$136\pm10_z$	$183\pm13_z$	$233\pm20_y$	15
P	NA	$121\pm 1_x$	2	$111\pm 9_x$	$172\pm18_x$	16	$109\pm12_x$	$153\pm16_x$	$218\pm20_x$	102
P	NS	$152\pm 9_y$	2	$117\pm 9_{xy}$	$178\pm18_x$	28	$122\pm10_y$	$169\pm16_y$	$238\pm21_y$	45
P	NNA–S			$142\pm13_z$	$219\pm 8_y$	4	$140\pm16_z$	$201\pm29_z$	$242\pm 9_y$	4

			Age 5					Age 6				
Habitat	Strain	L2	L3	L4	L5	N	L2	L3	L4	L5	L6	N
B	NA	$99\pm18_x$	$143\pm28_x$	$192\pm35_x$	$246\pm26_x$	14	$110\pm13_x$	$159\pm22_x$	$218\pm33_x$	$265\pm31_x$	$291\pm22_x$	18
B	NA–S	$124\pm13_y$	$176\pm23_y$	$228\pm28_y$	$272\pm22_y$	11	$130\pm19_y$	$195\pm37_y$	$245\pm37_x$	$284\pm26_x$	$304\pm23_x$	11
B	NNA–S	$143\pm10_y$	$195\pm15_y$	$231\pm15_y$	$277\pm 9_y$	3	$152\pm22_y$	$206\pm23_y$	$254\pm21_x$	$289\pm19_x$	$315\pm12_x$	4
P	NA	$109\pm15_x$	$161\pm23_x$	$214\pm34_x$	$261\pm29_x$	29	$113\pm14_x$	$163\pm20_x$	$222\pm27_x$	$268\pm26_x$	$294\pm20_x$	41
P	NA–S	$123\pm12_y$	$176\pm19_y$	$235\pm22_y$	$277\pm19_y$	42	$124\pm12_y$	$183\pm26_y$	$241\pm28_y$	$278\pm21_x$	$299\pm18_x$	22

				Age 7				
Habitat	strain	L2	L3	L4	L5	L6	L7	N
B	NA	$103\pm20_x$	$151\pm38_x$	$205\pm54_x$	$256\pm46_x$	$278\pm40_x$	$297\pm26_x$	7
B	NA–S	$131\pm8_x$	$188\pm18_y$	$251\pm26_y$	$289\pm19_x$	$305\pm20_x$	$316\pm23_x$	9
P	NA	$109\pm11_x$	$166\pm18_x$	$239\pm25_x$	$279\pm22_x$	$299\pm17_x$	$311\pm14_x$	17
P	NA–S	$133\pm12_y$	$203\pm22_y$	$272\pm15_y$	$303\pm16_y$	$317\pm16_y$	$325\pm15_y$	7

Table 3. Analysis of covariance (back-calculated length at age 2 - 7) of different strains of brown trout caught in epibenthic and pelagic habitat in Lake Tesse in July and August 1989.

		MS	df	F-ratio	P	R^2
L2	Age	50.043	1	0.275	0.600	0.302
	Habitat	1692.095	1	9.284	0.002	
	Strain	32349.390	2	177.484	<0.000	
	Residual	182.266	818			
L3	Age	25.021	1	0.062	0.803	0.338
	Habitat	5397.086	1	13.399	<0.000	
	Strain	78708.225	2	195.404	<0.000	
	Residual	402.798	763			
L4	Age	16179.158	1	22.686	<0.000	0.202
	Habitat	15997.488	1	22.431	<0.000	
	Strain	31442.666	2	44.088	<0.000	
	Residual	713.184	501			
L5	Age	2322.478	1	3.598	0.059	0.136
	Habitat	1851.031	1	2.868	0.092	
	Strain	10412.642	2	16.131	<0.000	
	Residual	645.503	236			
L6	Age	50.142	1	0.113	0.737	0.083
	Habitat	466.889	1	1.056	0.306	
	Strain	2773.102	2	6.275	0.002	
	Residual	441.946	139			
L7	Age	66.477	1	0.181	0.673	0.143
	Habitat	1229.404	1	3.348	0.074	
	Strain	2056.983	1	5.602	0.022	
	Residual	367.184	44			

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TABLE 4. Mean stomach content (mg) measured in dry weight ± standard deviation (x, SD) of native, native stocked and non–native stocked brown trout caught in epibenthic and pelagic gill nets in Lake Tesse in July and August 1989. N=number of stomachs examined.

Category	Epibenthic				Pelagic			
	July		August		July		August	
	x ± SD	N	x ± SD	N	x ± SD	N	x ± SD	N
Native	107 ± 170	94	18 ± 30	117	187 ± 227	143	67 ± 161	50
Native stocked	106 ± 140	68	33 ± 72	84	165 ± 224	91	25 ± 30	37
Non–native stocked	185 ± 213	67	185±213	25	201 ± 180	8	77	1

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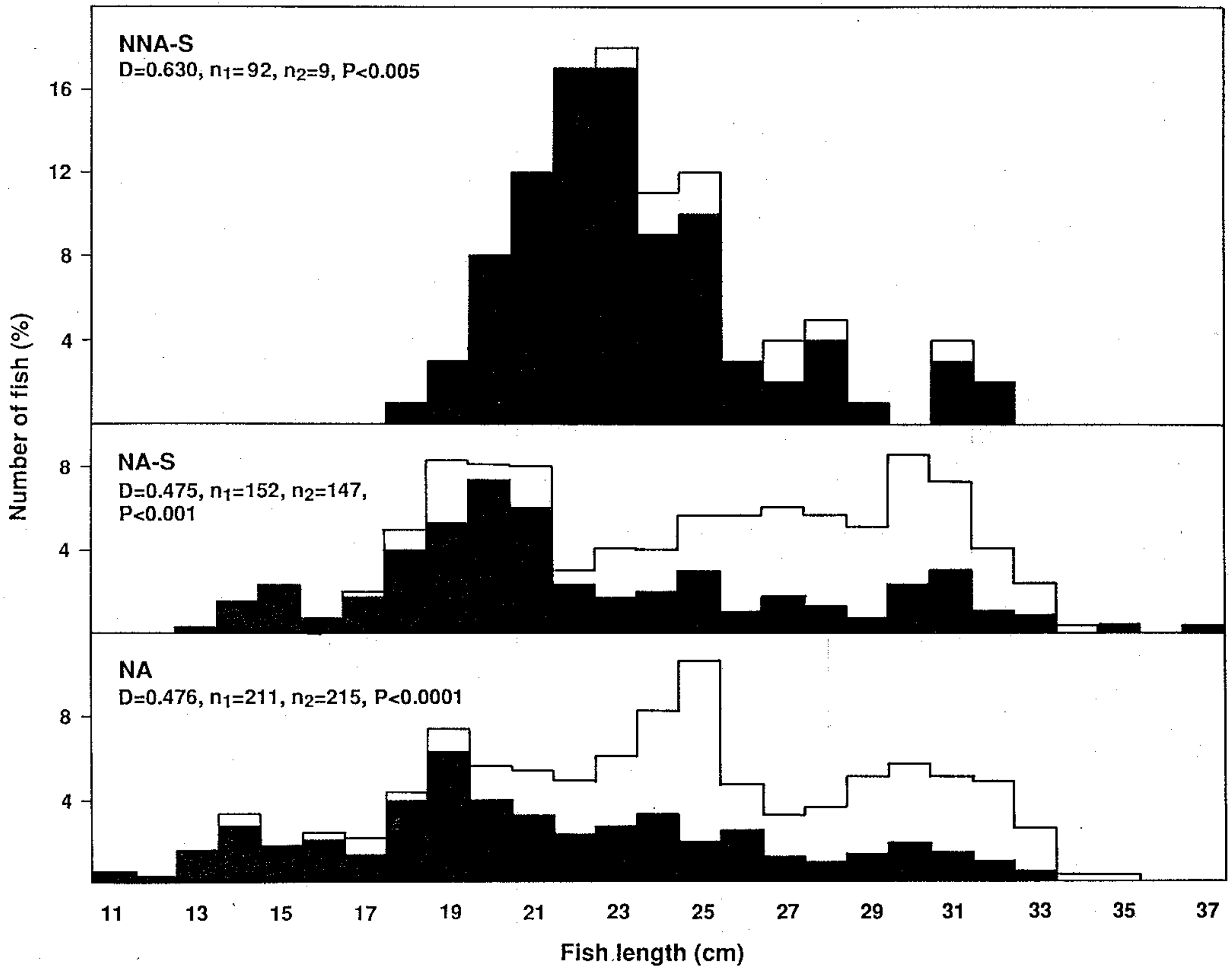
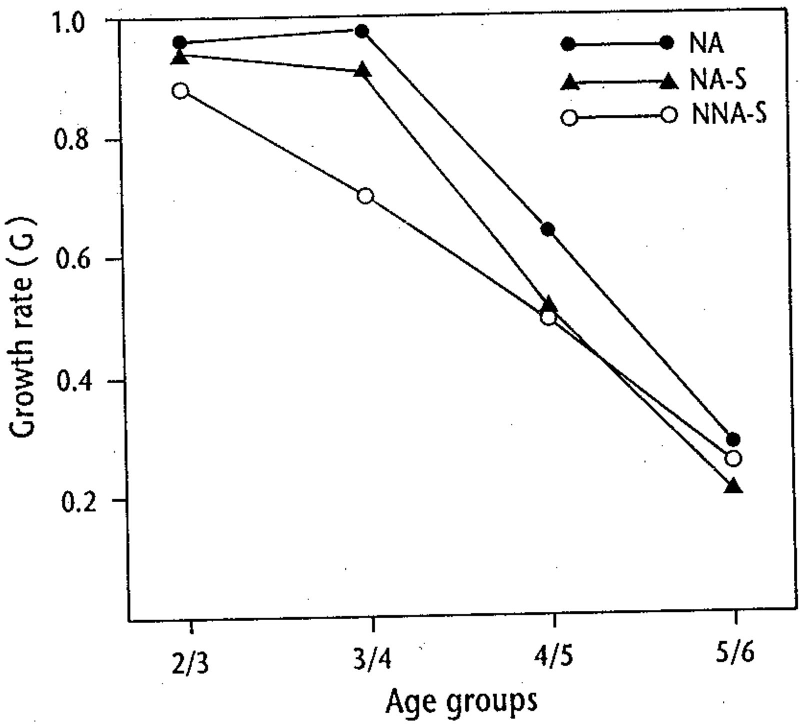
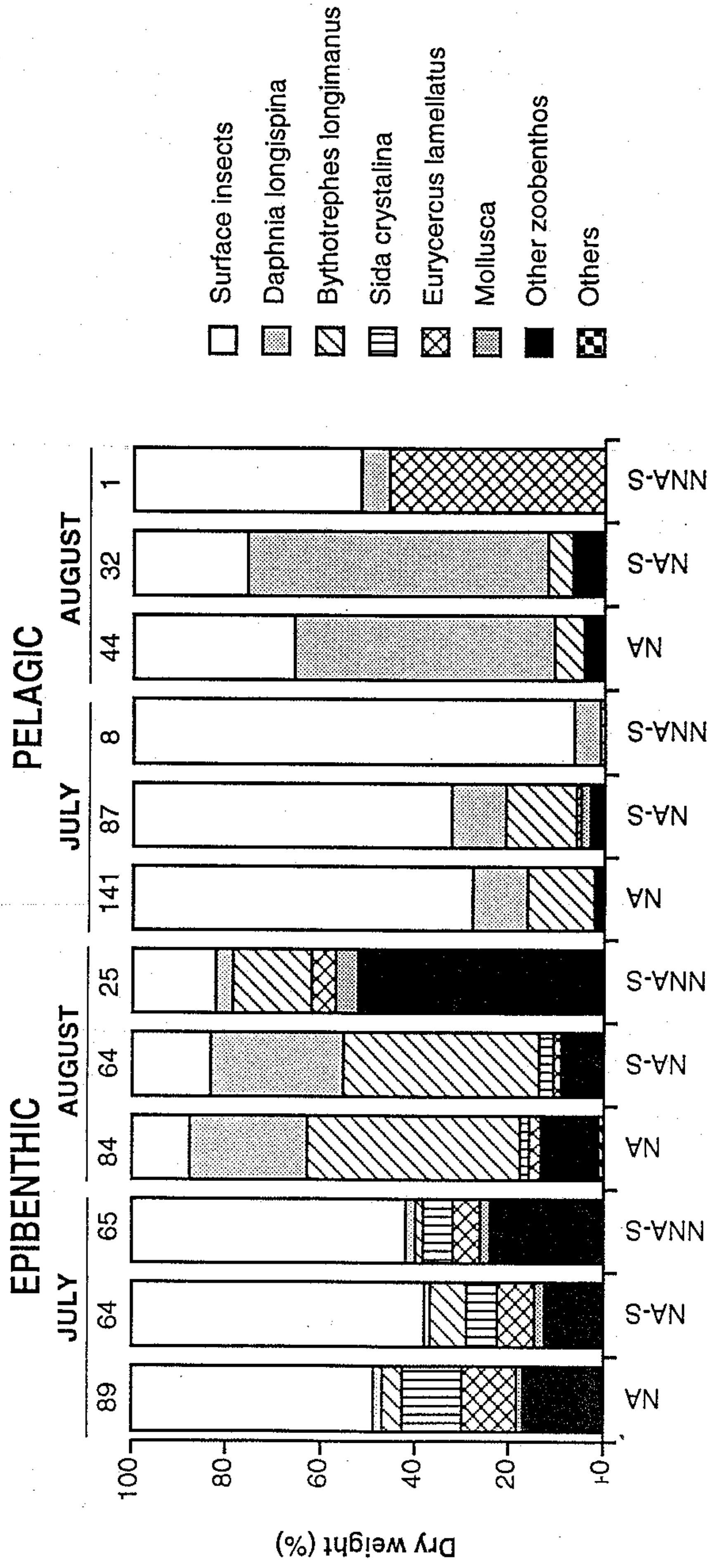
FIG. 1. Length frequency distributions of non-native stocked (NNA-S), native stocked (NA-S) and native (NA) brown trout caught in the epibenthic - (black area) and pelagic (open area) habitat in Lake Tesse in July and August 1989. D=the Kolmogorov-Smirnov two-sample test statistic for difference in length distribution between epibenthic and pelagic catches, n_1 and n_2 = number of fish caught in epibenthic and pelagic nets, respectively. P = level of significance.

FIG. 2. Instantaneous growth rate (G) for native (NA), native stocked (NA-S) and non-native stocked (NNA-S) brown trout of different ages in Lake Tesse.

FIG. 3. Percent composition (dry weight) of major prey items for native (NA), native stocked (NA-S) and non-native stocked (NNA-S) brown trout caught in epibenthic and pelagic habitat in Lake Tesse in July and August 1989. Number of stomachs examined is given above each column.


NNA-S
D=0.630, n_1=92, n_2=9, P<0.005
NA-S
D=0.475, n_1=152, n_2=147, P<0.001
NA
D=0.476, n_1=211, n_2=215, P<0.0001
Number of fish (%)
16
12
8
4
8
4
8
4
11
13
15
17
19
21
23
25
27
29
31
33
35
37
Fish length (cm)


1.0
0.8
0.6
0.4
0.2
Growth rate (G)
2/3
3/4
4/5
5/6
Age groups
NA
NA-S
NNA-S


EPIBENTHIC
PELAGIC
JULY
AUGUST
JULY
AUGUST
89
64
65
84
64
25
141
87
8
44
32
1
NA
NA-S
NNA-S
NA
NA-S
NNA-S
NA
NA-S
NNA-S
NA
NA-S
NNA-S
Dry weight (%)
100
80
60
40
20
0
□ Surface insects
▨ Daphnia longispina
▧ Bythotrephes longimanus
▤ Sida crystalina
▩ Eurycercus lamellatus
▨ Mollusca
■ Other zoobenthos
▦ Others

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JUVENILE COMPETITIVE BOTTLENECK IN THE PRODUCTION OF BROWN TROUT IN HYDROELECTRIC RESERVOIRS DUE TO INTRASPECIFIC HABITAT SEGREGATION

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ABSTRACT

Resource utilization and growth of brown trout were studied in four deep (mean depths 16·2–37·5 m) Norwegian hydroelectric reservoirs by benthic and pelagic gillnet sampling. In all the reservoirs supplementary stockings are carried out. The brown trout were spatially segregated according to size as the habitat use of small individuals (< 180–220 mm) was completely restricted to benthic habitats, whereas larger individuals mainly utilized the upper strata of pelagic waters. It is argued that the pelagic habitat is the more rewarding, and that small-sized brown trout are forced into the less favourable benthic habitat through social interactions with larger specimens. This is supported by an increase in growth of brown trout from their third to fifth year of life, which seems to be related to the shift from benthic to pelagic behaviour. It is also argued that the conditions for small-sized brown trout may be a bottleneck in the capacity to produce brown trout in hydroelectric reservoirs with limited benthic feeding conditions, despite ample access to food in pelagic habitats.

When evaluating the possibility of increasing the yield of brown trout through supplementary stockings, it is therefore important to consider food and growth conditions for all age and size groups of brown trout. In reservoirs with poor benthic feeding conditions it may be necessary to stock with brown trout of sizes that are large enough to utilize pelagic habitat, to avoid the limiting benthic living stage.

KEY WORDS Brown trout Habitat segregation Food Growth Competitive bottleneck

INTRODUCTION

Brown trout commonly prefer shallow benthic habitats, where they feed on benthic prey and surface insects (Nilsson, 1963; Thorpe, 1974; Svärdson, 1976). In hydroelectric reservoirs water level fluctuations imply severe reductions of the bottom fauna in the littoral habitat (Grimås, 1962), whereas the impact on the production of zooplankton is small (Elgmork, 1970). When benthic feeding conditions are reduced by water level fluctuations the brown trout may shift to a more pelagic habitat use where zooplankton offer a profitable feeding refuge (Brabrand and Saltveit, 1988). Such a shift in habitat use may reduce the impact of the regulation on the production of brown trout. However, in many lakes with pelagic living brown trout, the trout are spatially segregated according to size, as only larger individuals use the pelagic habitat whereas smaller specimens remain in benthic habitats (Haraldstad and Jonsson, 1983; Hegge *et al.*, 1989; Jonsson, 1989). If small size groups also remain in benthic habitats in regulated lakes with poor benthic feeding

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conditions, the competition among the smaller individuals may be harsh. This may limit the capacity to raise young brown trout, and the production of brown trout may be seriously affected by the regulation, even if valuable food items are available in pelagic habitats.

In this paper we describe the habitat use and growth of brown trout in four relatively deep reservoirs. The results are discussed with respect to the existence of limitations in the capacity to produce brown trout.

STUDY AREA

The reservoirs are all located in southern central Norway and are all relatively large and deep (Table I). Tesse and Tisleifjorden have high water level amplitudes whereas the water level fluctuations in Helin and Slidrefjorden are smaller.

All the reservoirs are inhabited by brown trout of superb quality, which commonly reach sizes of 300–700 g. In Tesse, brown trout is the only fish species. Besides brown trout, the other lakes are all densely populated by minnow, *Phoxinus phoxinus*, and Tisleifjorden and Slidrefjorden also support perch, *Perca fluviatilis*. In Slidrefjorden there are also some rainbow trout, *Oncorhynchus mykiss*, which have escaped from commercial fish farms in the reservoir. The rainbow trout does not seem to reproduce, and presently has a low abundance.

In Tesse and Helin most of the brown trout leave their nursery brooks and rivers during their first summer. In Tisleifjorden most of the brown trout enter the reservoirs after one or two years in the nursery rivers. This is also the possibility of river spawning brown trout in Slidrefjorden. However, in Slidrefjorden the brown trout also spawn in the lake.

The natural recruitment of brown trout in the reservoirs is negatively influenced by the regulation, and supplementary stockings of brown trout are therefore carried out. The brown trout are stocked at an age of one summer in Tesse and Helin, and at the age of two summers in Tisleifjorden and Slidrefjorden.

METHODS

In all the reservoirs the fish were sampled using series of benthic (1·5 × 25 m) and pelagic (6 × 25 mm) gillnets, all with mesh sizes between 16 and 39 mm. Benthic nets were set in chains from the shore and covered depths down to 25–40 m in the various reservoirs. All mesh sizes were equally represented at all depths covered by the nets. The depth interval covered by the benthic nets varied between reservoirs due to their different depth gradients. In Helin, additional benthic gillnet series were used to strengthen the material of benthic brown trout by setting the nets individually from the shore, as the habitat use of benthic brown trout in the reservoir is mainly restricted to shallow littoral areas. Pelagic nets were set offshore over deep areas (>25 m) in the lakes. The nets were anchored to the bottom by ropes, and set at depth intervals of 0–6 and 6–12 m below the surface.

The catch per unit effort (CPUE) is presented as the number of fish caught per 100 m^2 net area × 12 hours of fishing. In Helin, where the benthic fishing efforts in shallow areas were far higher than in deeper water, the CPUE was first calculated separately for each depth interval and then averaged for all depths to compensate for this difference in effort. The distributions of fish in the lakes were interpreted from the net catches. The

Table I. Morphometrical data for the reservoirs

Reservoir	Altitude (m.a.s.l.)	Water level fluctuation (m)	Surface area (km^2) High water level	Surface area (km^2) Low water level	Depth (m) Maximum	Depth (m) Mean
Tesse	853·90	12·40	14·26	9·37	64·0	23·5
Helin	867·83	2·00	10·90	9·00	87·6	37·5
Tisleifjorden	820·57	11·50	13·70	8·00	37·0	16·2
Slidrefjorden	366·21	3·50	12·50	10·50	76·0	24·0

capture efficiencies of benthic and pelagic gillnets may be different; however no attempt was made to compensate for this.

Fish length was measured to the nearest millimetre from the tip of the snout to the outer lobes of the tail as the tail lay in the natural position (Ricker, 1979). The ageing was based on scales, but was also controlled by reading otoliths. Winter zone and total radius in scales were measured to the nearest 0·1 mm. Back-calculation of length at a certain age was based on direct proportionality between fish length and scale radius (Lea, 1910). Owing to the presence of pronounced Lee phenomena (Lee, 1912), probably caused by high exploitation of the brown trout, the growth is calculated separately for each age group. With the exception of Helin, only naturally recruited fish were used for growth analysis. The stocked trout in Helin were not marked, and could not be distinguished from naturally recruited trout. Thus the estimated first year growth of brown trout in Helin may not be representative for the growth in the reservoirs.

Stomachs were collected and stored on 70% alcohol before examination. Crustaceans were identified to species and other food organisms to order. The volume percentage for each food category was evaluated subjectively. Stomach fullness was evaluated, using a scale from 0 to 5, where 0 represents an empty stomach and 5 a distended stomach.

Length frequency differences between groups were tested using the Kolmogorov-Smirnov two-sample test (Sokal and Rohlf, 1969, pp. 440–445). All statistical tests are based on a 5% significance level.

RESULTS

In all the reservoirs the brown trout were caught in both benthic and pelagic nets (Table II). Benthically caught brown trout occurred at the highest frequencies in shallow areas, down to about 10 m depth, although some trout were caught down to the deepest nets in the chains. In pelagic nets, most of the trout was caught in the upper 6 m depth interval.

The perch dominated the benthic catches in Tisleifjorden, but were only caught in minor numbers in pelagic nets. In Slidrefjorden, a few perch were caught in benthic nets, and a single rainbow trout was caught in pelagic nets.

The length distributions of brown trout caught in pelagic nets was dominated by larger fish compared with those caught in pelagic nets in all the reservoirs (Figure 1). The differences were significant in all the reservoirs. Most of the larger fish were caught in pelagic nets whereas the smallest size groups of brown trout were completely lacking in the pelagic catches. The smallest brown trout caught in pelagic nets varied between the reservoirs from 180 to 220 mm.

The large crustacean zooplankton *Bythotrephes longimanus* and/or *Daphnia longispina* were the most important food for the brown trout in pelagic habitat in all the reservoirs, and with the exception of Helin, these zooplankton species were also the dominant food items in the benthic habitat (Table III). In Helin, benthic prey, mainly aquatic insects, *Eurycercus lamellatus* and *Gammarus lacustris*, were the most important food items in the benthic habitat. Surface insects also made up a considerable part of the stomach content of the brown trout, especially in Helin and Tisleifjorden.

Table II. Catches of brown trout and perch per 100 m^2 gillnet area per 12 hours of fishing in four Norwegian hydroelectric reservoirs

	Brown trout		Perch	
Reservoir	Benthic	Pelagic	Benthic	Pelagic
Tesse	7·43	7·71	—	—
Helin	2·70	0·95	—	—
Tisleifjorden	2·10	1·26	3·75	0·29
Slidrefjorden	1·22	2·86	0·31	0·00

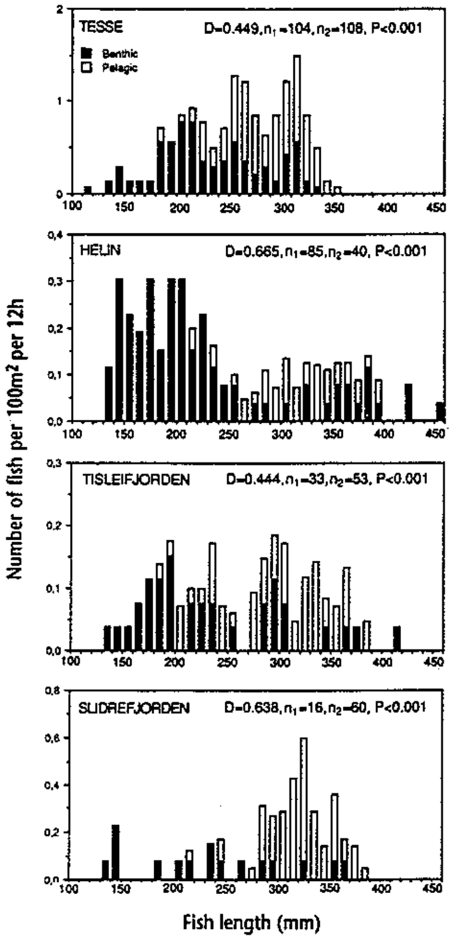

Figure 1. Length frequency distributions of brown trout caught in benthic (■) and pelagic (□) gillnets in four Norwegian hydroelectric reservoirs. D = Kolmogorov-Smirnov two-sample test statistic for difference in length distribution between benthic and pelagic catches, n_1 = number of fish caught in benthic nets, n_2 = number of fish caught in pelagic nets, P = level of significance

Table III. Percentage volume composition of food items of brown trout caught in benthic and pelagic gillnets in four Norwegian hydroelectric reservoirs. B = fish caught in benthic nets, P = fish caught in pelagic nets

	Tesse		Helin		Tisleifjorden		Slidrefjorden	
Food category	B	P	B	P	B	P	B	P
Surface insects	12	17	31	20	39	23	3	2
Aquatic insects	9	4	23	0	9	3	7	0
Daphnia longispina	42	73	6	0	0	0	52	86
Bytothrepes longimanus	30	6	4	76	52	73	20	12
Eurycercus lamellatus	2	0	11	0	0	0	3	0
Gammarus lacustris	0	0	19	0	0	0	0	0
Fish	0	0	0	0	0	0	13	0
Others	5	0	6	4	0	0	2	0
Number of stomachs analysed	76	59	58	38	23	49	15	18

In Helin and Slidrefjorden the stomach fullness of the brown trout caught in pelagic habitat was higher than for those caught in benthic habitat, whereas in Tesse and Tisleifjorden there was no significant differences in stomach fullness of brown trout from benthic and pelagic catches (Table IV).

In all the reservoirs, the brown trout had a moderate growth in the first year of life (32–52 mm). Later the growth was faster, and from their third to fifth year of life the growth increased markedly (Figure 2). After this increase in growth, the brown trout achieved mean yearly length increments of 77–88 mm in their fastest growing years, and individual fish with yearly length increments above 100 mm were recorded. In Helin, this increase in growth only occurred in one part of the brown trout. In the benthic habitat we caught several small specimens, both males and females, that had ceased to grow at a young age and small size. Several of these were mature. This masked the growth increase of the other specimens in the figure where the average growth is presented. However, when we only included fish caught in pelagic nets in the growth analysis, the growth increase is clearly expressed (Figure 3).

DISCUSSION

The importance of zooplankton as food for the brown trout is probably explained by reduced access to benthic food items due to the water level fluctuations in the reservoirs (Brabrand and Saltveit, 1988). Below the draw down limit the benthic fauna is less affected by the regulation, but the feeding conditions for brown

Table IV. Mean stomach fullness for brown trout caught in benthic and pelagic gillnets in four Norwegian hydroelectric reservoirs

	Benthic		Pelagic	
Reservoir	Mean ± SD	*n*	Mean ± SD	*n*
Tesse	1·40 ± 1·12	104	1·43 ± 0·84	67
Helin	1·51 ± 1·21	78	2·05 ± 1·06	40
Tisleifjorden	1·79 ± 1·52	33	1·77 ± 1·03	53
Slidrefjorden	2·06 ± 1·00	16	2·95 ± 1·27	19

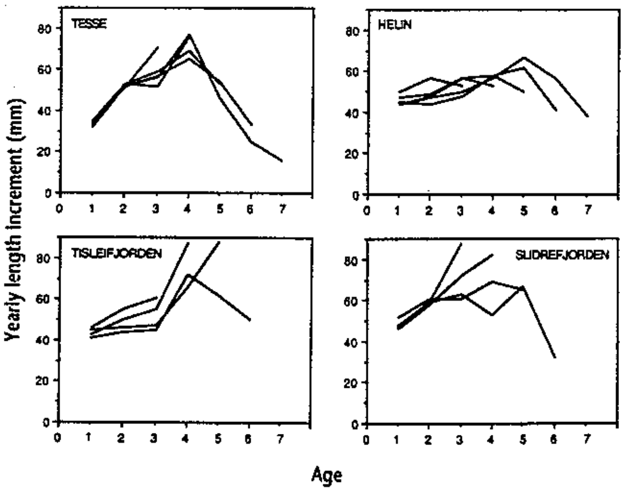

Figure 2. Yearly length increments for different age groups of brown trout caught in benthic and pelagic gillnets in four Norwegian hydroelectric reservoirs

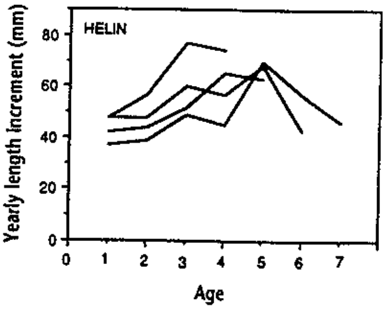

Figure 3. Yearly length increments for different age groups of brown trout caught in pelagic gillnets in Helin

trout at greater depths are usually less favourable due to low densities of valuable prey and also to reduced foraging efficiency as the light intensity is lower (Schutz and Northcote, 1972; Henderson and Northcote, 1985). In Helin, where benthic prey were the most important food in the benthic habitat, the water level fluctuation is only 2 m, and the benthic fauna is probably less affected by the regulation than in the other reservoirs where benthic prey were negligible as food for the trout.

As the trout fed on zooplankton in both benthic and pelagic habitats in three of the reservoirs, we should expect all the fish to be spread over the entire lake areas. Larger size groups of brown trout were distributed in accordance with this expectation in all the reservoirs, but the occurrence of smaller specimens was restricted to shallow benthic habitat. All the reservoirs are relatively deep, with only small shallow areas. Thus when the smaller individuals use only this habitat, the concentration of fish is relatively high, leading to high competition for food and space. In Helin, where the fish fed on benthic prey in the littoral habitat, the shallow areas are especially small and the competition for space especially hard. Corresponding spatial segregation between size groups of brown trout is also reported from several other lakes, and the restricted benthic habitat use of the smaller specimens is explained by a strong urge for shelter to avoid predation and agonistic behaviour from larger individuals (Haraldstad and Jonsson, 1983; Hegge *et al.*, 1989). Brown trout are known to compete aggressively for space and food and their social dominance hierarchy is related to size (Jenkins, 1969; Bachman, 1984). Stress due to aggressive behaviour from larger fish may cause reduced food intake and growth depression in salmonids (Brown, 1946; Fenderson *et al.*, 1968; Jobling and Reinsnes, 1986). Accordingly, small brown trout may feed more profitably in the benthic habitat where the access to shelter is best, despite a better access to food and space in the pelagic habitat. As small specimens of brown trout are dependent on access to food and space in the benthic habitat, the negative impact of the regulation is especially severe for small individuals.

The observed increase in growth occurred at the same age, or one year before this age where the trout shifted from benthic to pelagic habitat, evidently supporting the assumption that pelagic behaviour is the more rewarding. A more detailed study of habitat use of littoral brown trout in Tesse (Hegge *et al.*, in press) indicates that the shift from a true benthic to a true pelagic behaviour occurs gradually. In that study we observed small brown trout in the littoral zone to take a position close to the bottom, whereas trout of increasing size occurred at increasing distance from the bottom and thereby improved their access to valuable zooplankton species. This factor, combined with reduced aggressive behaviour from other fish due to a gradually higher position in the social dominance hierarchy as the trout grows larger, may explain why the increase in growth may take place earlier than the shift to the use of a true pelagic habitat.

The access to food and space are of decisive importance for the survival of young brown trout (Chapman, 1966). As intraspecific competition force small-sized trout into the less favourable benthic habitat where they suffer from limited access to food and space, this may limit the capacity to raise young trout in the reservoirs. This results in sparse populations of trout in larger size classes which experience rich feeding conditions and attain fast growths and good qualities. This situation is clearly documented in Tesse, where a reduction in the stockings of one summer old brown trout from 20 fish/ha to eight fish/ha had no influence on the yield of catchable sized brown trout, despite the fact that the size and quality of the trout was excellent and unchanged all the time (Hesthagen, unpublished data). Similar situations, where competition during juvenile stages reduces recruitment to larger size classes, while the resources for these larger size classes may not be limited, are documented in several fish species and are often referred to as juvenile competitive bottlenecks (Persson, 1986; Werner, 1986; Persson and Greenberg, 1990).

Damming of hydroelectric reservoirs often implies reduced recruitment of brown trout, and the hydroelectric companies are often required to carry out compensatory stockings. As the determination of stocking numbers is usually based on evaluation of the growth and quality of the trout, the number of fish to be stocked may easily be set too high in reservoirs where such juvenile bottlenecks in trout production exist. It is therefore important to consider the food and growth conditions of all size groups when determining stocking numbers.

The size of brown trout used for stocking may be of great importance in reservoirs where such bottlenecks exist. To increase the yield of brown trout it may be necessary to stock with trout of sizes large enough to exploit the pelagic habitat immediately after release, and thereby avoid the limiting conditions in the littoral habitat.

The limited resources in littoral areas may also have implications for the choice of strain of brown trout used for stocking. In Tesse we have documented considerable differences in the habitat use between the native strain and a non-native strain which was earlier used for stocking in the reservoir, and it seems evident that the differences were genetically determined (Hesthagen *et al.*, unpublished data). Although the native trout were spatially segregated according to size as small individuals occurred in the benthic habitat and larger specimens mainly occurred in the pelagic habitat, the habitat use of all size groups of the non-native stock was mainly benthic. This increased competition in the benthic habitat. As competition among small trout in this habitat seems to be the limiting factor for the trout production in Tesse, stocking of brown trout that will grow and stay in benthic habitat throughout their life may suppress the recruitment of native fish and probably reduce than increase the yield of trout. Thus in reservoirs where zooplankton are the main food item for the trout, only strains that also utilize the pelagic habitat should be used for stocking.

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REFERENCES

Bachman, R. A. 1984. 'Foraging behaviour of free-ranging wild and hatchery brown trout in a stream', *Trans. Am. Fish. Soc.*, **113**, 1–32.

Brabrand, Å. and Saltveit, S. J. 1988. 'Feeding behaviour and habitat shift in allopatric and sympatric populations of brown trout (*Salmo trutta* L.): effects of water level fluctuations versus interspecific competition', *Freshwater Ecology and Inland Fishery Lab. (LFI), Report No. 102.* 13 pp.

Brown, M. E. 1946. 'The growth of brown trout (*Salmo trutta* Linn.). I. Factors influencing the growth of trout fry', *J. Exp. Biol.*, **22**, 118–129.

Chapman, D. W. 1966. 'Food and space as regulators of salmonid populations in streams', *Am. Natural.*, **100**, 345–347.

Elgmork, K. 1970. 'Plankton og planktonproduksjon i regulerte innsjøer', *Kraft og Miljø, Norwegian Water Resources and Energy Administration*, **1**, 11–15 (in Norwegian).

Fenderson, O. C., Everhart, W. H., and Muth, L. M. 1968. 'Comparative agonistic and feeding behaviour of hatchery-reared and wild salmon in aquaria', *J. Fish. Res. Board Can.*, **25**, 1–14.

Grimås, U. 1962. 'The effect of increased water level fluctuations upon the bottom fauna in Lake Blåsjøn, Northern Sweden', *Rep. Inst. Freshw. Res. Drottningholm*, **44**, 14–41.

Haraldstad, Ø. and Jonsson, B. 1983. 'Age and sex aggregation in habitat utilization by brown trout in a Norwegian lake', *Trans. Am. Fish. Soc.*, **112**, 27–37.

Hegge, O., Dervo, B. K., Skurdal, J., and Hessen, D. H. 1989. 'Habitat utilization by sympatric arctic charr (*Salvelinus alpinus* (L.)) and brown trout (*Salmo trutta* L.) in Lake Atnsjø, south-east Norway', *Freshwater Biol.*, **22**, 143–152.

Hegge, O., Hesthagen, T., and Skurdal, J. 'Vertical distribution and substrate preference of brown trout in a littorale zone', *Environ. Biol. Fish*, in press.

Henderson, M. A. and Northcote, T. G. 1985. 'Visual prey detection and foraging in sympatric cutthroat trout (*Salmo clarki clarki*) and Dolly Varden (*Salvelinus malma*)', *Can. J. Fisher. Aquat. Sci.*, **42**, 785–790.

Jenkins, T. M. 1969. 'Social structure, position choice and microdistribution of two trout species (*Salmo trutta* and *Salmo gairdneri*) resident in mountain streams', *Anim. Behav. Monogr.*, **2**, 57–123.

Jobling, M. and Reinsnes, T. G. 1986. 'Physiological and social constraints on growth of Arctic charr, *Salvelinus alpinus* L.: an investigation of factors leading to stunting', *J. Fish. Biol.*, **28**, 379–384.

Jonsson, B. 1989. 'Life history and habitat use of Norwegian brown trout (*Salmo trutta*)', *Freshwater Biol.*, **21**, 71–86.

Lea, E. 1910. 'On the methods used in herring investigations', *Publication de Circonstance, Conseil International pour l'Exploràtion de la Mer*, **53**, 7–174.

Lee, R. M. 1912. 'An investigation into the methods of growth determination in fishes', *Publication de Circonstance, Conseil International pour l'Exploràtion de la Mer*, **63**, 1–35.

Nilsson, N. A. 1963. 'Interaction between trout and char in Scandinavia', *Trans. Am. Fish. Soc.*, **92**, 276–285.

Persson, L. 1986. 'Effects of reduced interspecific competition on resource utilization in perch (*Perca fluviatilis*)', *Ecology*, **67**, 355–364.

Persson, L. and Greenberg, L. A. 1990. 'Juvenile competitive bottlenecks: the perch (*Perca fluviatilis*)-roach (*Rutilus rutilus*) interaction', *Ecology*, **71**, 44–56.

Ricker, W. E. 1979. 'Growth rates and models' in Hoar, W. S., Randall, D. J., and Brett, J. R. (Eds), *Fish Physiology*, Vol. 8, Academic Press, New York. pp. 677–743.

Schutz, D. C. and Northcote, T. G. 1972. 'An experimental study of feeding behaviour and interaction of coastal cutthroat (*Salmo clarki clarki*) and Dolly Varden (*Salvelinus malma*)', *J. Fish. Res. Board Can.*, **29**, 555–565.

Sokal, R. R. and Rohlf, F. J. 1969. *Biometry*, Freeman, San Francisco.

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

Thorpe, J. E. 1974. 'The movements of brown trout *Salmo trutta* L. in Loch Leven, Kinross', *J. Fish Biol.*, **6**, 153–180.

Werner, E. E. 1986. 'Species interactions in freshwater fish communities' in Diamond, J. and Case, T. (Eds), *Community Ecology*, Harper and Row, New York. pp. 344–358.

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Vertical distribution and substrate preference of brown trout in a littoral zone

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Synopsis

We studied vertical distribution, substrate preference and food choice of brown trout, *Salmo trutta*, from benthic gillnet catches at four littoral sampling locations in a Norwegian hydroelectric reservoir. The sampling locations had different bottom substrates; at one location the bottom substrate consisted of sand, while at the other three, substrates consisted of stones ranging 2–5 cm, 10–30 cm and 30–150 cm in diameter, respectively. Small-sized (< 160 cm) and intermediate-size (160–269 mm) brown trout were mainly caught close to the bottom (0–0.5 m above). Small-sized brown trout were caught in the highest frequency at the location with substrate consisting of 10–30 cm large stones. Intermediate-sized brown trout were also caught in highest frequency at this location, but were also caught in a high frequency at the location with sandy substrate. In contrast, the catches of large-sized (≥ 270 mm) brown trout did not vary with distance from the bottom or with substrate coarseness. The most important food items for the brown trout were aquatic insects, surface insects, *Eurycercus lamellatus* and crustacean zooplankton, mainly *Daphnia longispina, Bythotrephes longimanus,* and *Holopedium gibberum*. In accordance with the differences in vertical distribution, benthic food was more important to small than to large brown trout. We argue that small brown trout stayed close to the bottom to reduce aggressive behaviour from larger specimens, and that small brown trout were therefore more dependent on benthic food items. We also argue that the observed differences in substrate preference between the size groups of brown trout is explained by variation in access to shelter, visual isolation between individuals and benthic feeding conditions between locations.

Introduction

In a number of lakes, habitat use by small-sized brown trout is restricted to littoral areas, while larger specimens utilize both benthic and pelagic areas (e.g., Haraldstad & Jonsson 1983, Jonsson & Gravem 1985, Hegge et al. 1989, Jonsson 1989). In most larger lakes, the littoral areas are small compared to the whole lake surface, implying that small brown trout are more concentrated than larger specimens, which may be distributed throughout the entire lake area. Small brown trout may therefore experience higher intraspecific competition for space and food than larger trout. The use of littoral areas by brown trout is therefore of particular importance for trout production.

Substrate preference and position choice by brown trout has been studied by several authors in lotic environments (e.g., Bachman 1984, Heggenes 1988, Heggenes & Saltveit 1990), but corresponding knowledge in lenthic waters is scarce. Stream-living salmonids, including brown trout, are known to prefer coarse substrate (Bjornn 1971, Bustard & Narver 1975, Heggenes 1988). Addition of coarse substrate is also observed to increase the densities of stream-living salmonids (Gilbert 1978, Hillman et al. 1987). The documented preference for coarse substrate by brown trout in running water may be a way to save energy by reducing exposed water velocity, as water velocity is known to influence habitat choice by brown trout (Karlstrøm 1977, Kennedy & Strange 1982). The substrate preference of lake-living brown trout is therefore not necessarily identical. However, suitable substrate is also believed to be important as shelter for salmonids (Bjornn 1971, Bustard & Narver 1975). For several fish species in lenthic water, habitat structural complexity is known to provide shelter against predators (Charnov et al. 1976, Savino & Stein 1982), and small fish are often found closely associated with vegetation or structures on the bottom (Mittelbach 1984, Werner & Hall 1988). Because small brown trout have been hypothesised to inhabit littoral areas to find shelter against predators and to avoid social interactions with larger specimens (Haraldstad & Jonsson 1983, Hegge et al. 1989, Jonsson 1989), we would expect small brown trout to prefer coarse bottom substrate and spend much time close to the substrate, while larger specimens are expected to choose substrate and position in the water to maximize food intake.

To test this hypothesis we studied vertical distribution, substrate preference and food choice of brown trout in the littoral zone of Lake Tesse, Norway. The study was carried out by benthic gillnet sampling at four sampling locations with different substrate coarseness.

Study area

Lake Tesse (61°84′ N, 8°57′ E), situated 854 m a.s.l. in central southern Norway, is a subalpine hydroelectric reservoir with a water-level amplitude of 12 m. The reservoir has a surface area of 937 ha and 1426 ha at the lowest and highest water levels, respectively. The lake has a maximum depth of 64 m and a mean depth of 27 m at the highest water level.

In the littoral zone, the bottom substrate consists of boulders and stones, except for the southern and northern parts where the substrate consists of sand. In deeper areas the bottom consists of gyttja. There is no macrophytic vegetation in the lake.

The lake is ice-covered from late November to late May. During summer, surface water temperatures usually remain between 10–15° C. The water is glacier fed, and secchi-depths range from 3.5 to 4 m.

Brown trout is the only fish species in Lake Tesse. Due to reduced natural propagation after impoundment, compensatory stockings of brown trout were carried out until 1987. The length of the brown trout commonly ranges up to 350 mm. Small individuals mainly occupy benthic areas while larger specimens also exploit pelagic habitats (Hesthagen et al. unpublished).

Methods

During 4 sampling periods (11 July, 7 August, 4 September and 1 November, 1990) we caught 318 brown trout using a series of 8 benthic gillnets (1.5 × 25 m) with mesh sizes of 10, 12.5, 16, 2 × 21, 26, 29 and 35 mm, set at four littoral locations. All locations were sampled each period. The nets were set individually from the shore, covering depths from 0.5 m to about 3 m. The locations were selected according to substrate coarseness; one station had bottom substrate consisting of sand, while the other three locations had substrate consisting of stones ranging 2–5 cm, 10–30 cm and 30–150 cm in diameter, respectively. Substrate coarseness was determined in the spring, when the water level was still below the sampling depth. In this way locations with desirable and homogeneous substrates could easily be chosen.

Of the 318 brown trout caught, 304 specimens were naturally propagated or stocked fish originating from wild parents of the native brown trout in Lake Tesse. The remaining 14 brown trout caught during this study were stocked fish from non-native strains. The non-native brown trout stocked in Lake Tesse differ in habitat use from the native brown trout strain (Hesthagen et al. unpublished), and were therefore omitted from this study.

For each fish the distance from the bottom of the net to the capture site was measured, and grouped into three intervals; 0.0–0.5 m, 0.5–1.0 m and 1.0–1.5 m. Total fish length (L) was measured to the nearest 1 mm. Stomachs were collected and stored in 70% alcohol. The stomach contents were identified and counted under a stereoscopic microscope. Crustaceans were identified to species, while other food organisms were grouped into larger food categories. The volume percent for each food category was evaluated subjectively. Stomach fullness was determined subjectively on a scale from 0–5, where 0 represents empty and 5 extended stomachs. The size of the food items was determined as larger or smaller than 15 mm.

The brown trout caught ranged between 83–370 mm in total length (Fig. 1), and were divided into three size-intervals for analysis of the results; small-sized trout ($L < 160$ mm), intermediate-sized trout ($160\,\text{mm} \leq L < 270$ mm) and large-sized trout ($L \geq 270$ mm).

As a measure of food overlap between size groups we calculated niche overlap as the proportional similarity of Schoener (1968):

$$D = 1 - 0.5 \sum |p_i - q_i|,$$

where p_i = volume proportion of food category *i* in size group 1, q_i = volume proportion of food category *i* in size group 2, and *n* is the number of food categories. The index ranges from 0 to 1; where 0 is no overlap and 1 is 100% overlap.

Differences between size groups in distribution of catches according to location and distance from bottom to the site of capture and differences in stomach fullness were tested using X^2-test for independence, and deviation from even distribution of catches according to location and distance from bottom to the site of capture by using X^2-test for goodness of fit. All statistical analyses were based upon 5% significance level.

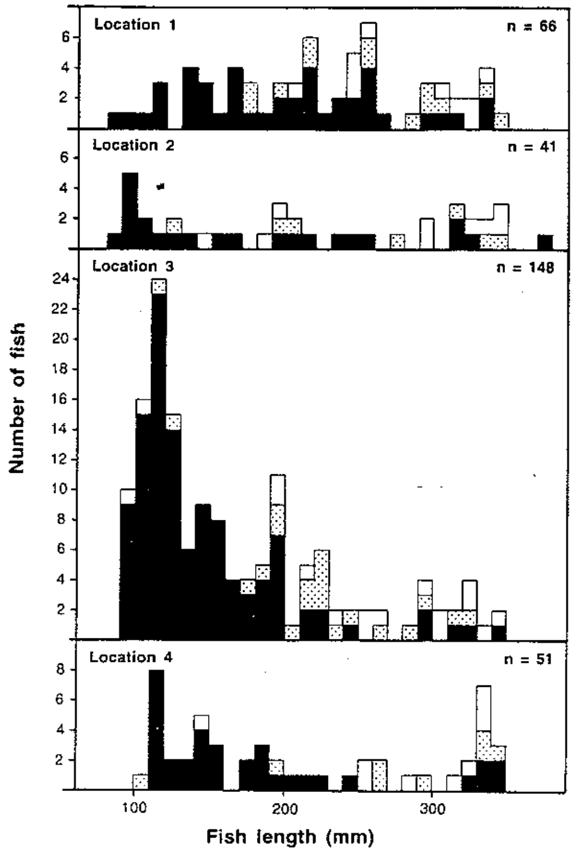

Fig. 1. Length distribution of brown trout caught 0–0.5 m ■, 0.5–1.0 m ▨ and 1.0–1.5 m □ above the bottom at 4 littoral locations in Lake Tesse, 1990.

Results

There were major differences in the distribution of the three size-groups of brown trout both according to station ($X^2 = 39.40$, df = 6, $p < 0.001$) and distance from bottom to the site of capture ($X^2 = 91.58$, df = 4, $p < 0.001$). While large-sized fish were evenly distributed both according to location and distance from the bottom to the site of capture, the two smaller size-groups showed significant preferences according to both location (Fig. 2) and distance from the bottom (Fig. 3). Most small-sized trout were caught at location 3 with 10–30 cm large stones (64%). Also intermediate-sized trout occurred in highest frequency at location 3 (42%), but in July this size-group was also caught in high frequency at location 1, which bottom consisted of

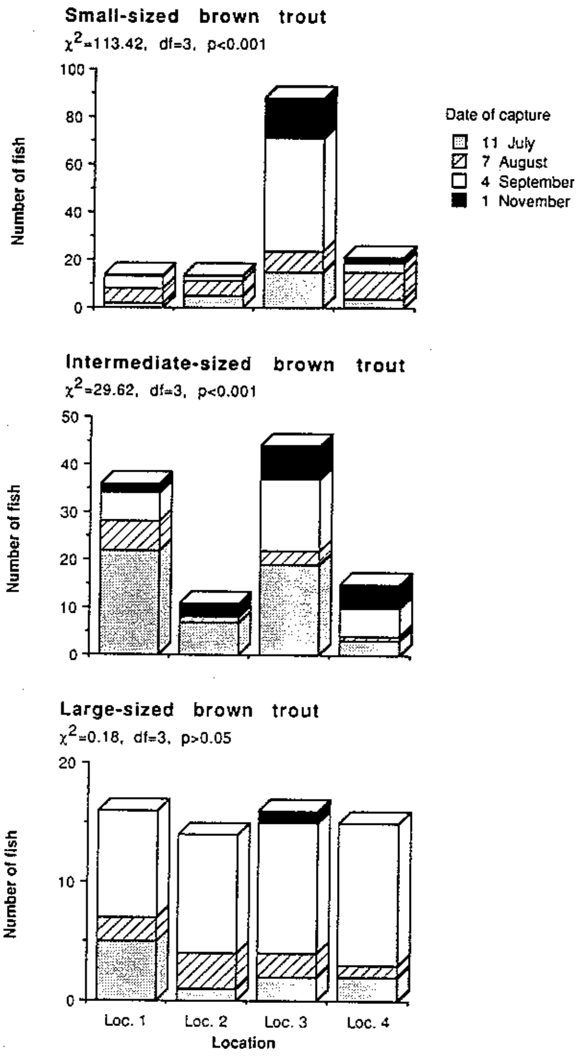

Fig. 2. Distribution according to location and time of capture of the catches of three size-groups of brown trout in the littoral zone of Lake Tesse, 1990. X^2 is the test statistic for deviation from even distribution according to location, df is degree of freedom, p is level of significance.

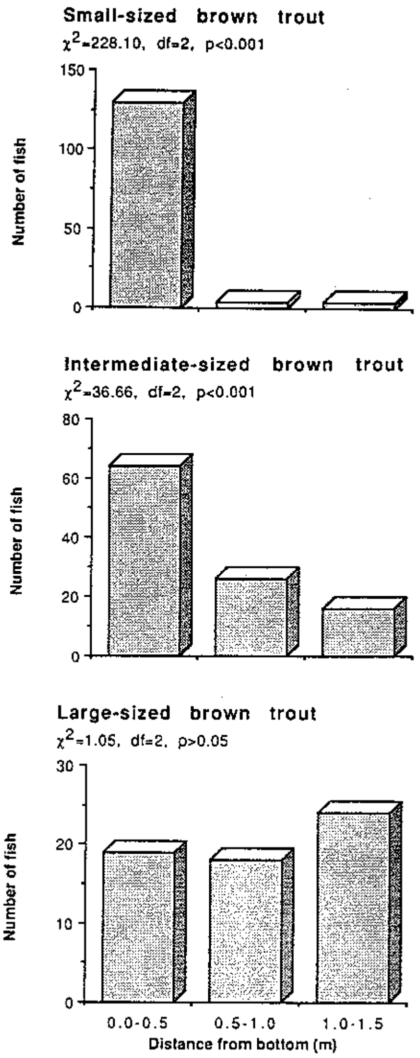

Fig. 3. Distribution according to distance from bottom to the site of capture of the catches of three size-groups of brown trout in the littoral zone of Lake Tesse, 1990. X^2 is the test statistic for deviation from even distribution according to distance from bottom, df is degree of freedom, p is level of significance.

sand. Small- and intermediate-sized trout were most frequently caught close to the bottom (0.0–0.5 m). This tendency was most clearly expressed among the small-sized trout, of which 94% were caught at this height compared to 60% of the intermediate-sized trout.

The trout diet was dominated by aquatic insects, surface insects, *Eurycercus lamellatus* and crustacean zooplankton, of which *Daphnia longispina, Bythotrephes longimanus,* and *Holopedium gibberum* were the dominating species (Table 1). Aquatic insects consisted an important part of the diet of small- (36–46%) and intermediate- (41–47%) sized trout. The importance of surface insects varied considerably between locations, but was generally most important among intermediate- and large-sized trout. Crustacean zooplankton were important as food for all size-groups, but there were major differences between the size-groups in the species selected. *D. longispina* and *B. longimanus* were the most important species for large-sized trout, while they were almost neglegible as food for small-sized trout. The most important plankton species selected by small-sized trout was either *H. gibberum* or *E. lamellatus,* depending on location. The selection of crustacean zooplankton by intermediate-sized trout was somewhat between that of small- and large-sized trout. Intermediate-sized trout also preyed to some extent on molluscs (3–10%), while this food category was neglegible as prey for both small- and large-sized trout except at location 4.

The food items eaten by the trout were mainly small. Only one group of the aquatic insects, cranefly (Tipulidae) larvae, was larger than 15 mm. This food item constituted on average 6% of the food volume eaten by the trout, and was mainly taken by small-sized trout.

The overlap in diet between small- and large-sized trout was low at all locations; the Schoener index ranged from 0.32–0.43. Between small- and intermediate-sized trout and between intermediate- and large-sized trout, the diet overlap was higher; the Schoener index ranged from 0.61–0.79 and from 0.48–0.69, respectively (Table 2).

Mean stomach fullness at the four locations ranged between 2.1–2.8 in small-sized trout, 1.9–2.5 in intermediate-sized trout and 1.8–2.8 in large-sized trout (Table 3). There were no significant variation in stomach fullness between size groups at any location ($X^2 = 5.07 - 15.77$, $df = 10$, $p > 0.05$), nor between locations in any size group ($X^2 = 9.66 - 21.37$, $df = 15$, $p > 0.05$).

Discussion

While small trout showed a strong association with the bottom, larger trout occurred more frequently higher up in the water column. This difference in vertical distribution was also reflected in the food choice. Small trout preyed more on aquatic insects and less on surface insects than larger trout. While the zooplankton species selected by large trout were *B. longimanus* and *D. longispina*, small trout preyed upon *H. gibberum* or the littoral species *E. lamellatus. D. longispina* and especially *B. longimanus* are all large, easily visible species (Flössner 1972) and are usually positively selected by planktivorous brown trout (Nilsson 1965, Klemetsen 1967, Dervo et al. 1991). These normally pelagic species (Flössner 1972) are probably less available to small trout living close to the bottom. *H. gibberum* is usually a less preferred food item for brown trout than *B. longimanus* and *D. longispina* (Klemetsen 1967, Dervo et al. 1991). *H. gibberum* is usually regarded as a pelagic species, but is also commonly found in littoral areas (Flössner 1972), and may even occur benthically (Herr 1917). Thus, it seems reasonable that *H. gibberum* were more

Table 1. Food choice as volume percent of small- (< 160 mm), intermediate- (160–269 mm) and large- (≥ 270 mm) sized brown trout caught at 4 littoral locations in Lake Tesse, 1990.

Food category	Location 1			Location 2			Location 3			Location 4		
	Small	Intermediate	Large	Small	Intermediate	Large	Small	Intermediate	Large	Small	Intermediate	Large
Surface insects	11	21	25	0	3	0	1	13	14	0	0	4
Aquatic insects	36	42	15	46	41	11	45	44	15	44	47	9
Daphnia longispina	0	5	13	0	6	4	0	12	16	0	14	17
Bythotrephes longimanus	0	9	23	0	4	56	0	8	37	0	18	46
Holopedium gibberum	43	7	8	39	24	18	6	4	9	14	2	7
Eurycercus lamellatus	8	5	7	14	13	11	48	14	9	22	2	10
Mollusca	0	5	0	0	8	0	0	3	0	9	10	6
Others	2	6	9	1	1	0	0	2	0	11	7	1
Number of stomachs	9	28	15	9	8	12	77	35	12	14	10	13

Table 2. Food niche overlap as the proportional similarity of Schoener (1968) of small- and intermediate-sized, small- and large-sized and intermediate- and large-sized brown trout caught at 4 littoral locations in Lake Tesse during 1990.

	Loc. 1	Loc. 2	Loc. 3	Loc. 4
Small- and intermediate-sized	0.61	0.79	0.65	0.64
Small- and large-sized	0.43	0.40	0.32	0.33
Intermediate- and large-sized	0.69	0.48	0.60	0.52

available close to the bottom than *B. longimanus* and *D. longispina*. The food segregation between size groups observed in Lake Tesse is in accordance with the findings of Vøllestad & Andersen (1985), who found that small, littoral brown trout feed more on benthic food than did larger littoral specimens.

The prey items eaten by the brown trout in Lake Tesse were mainly small (< 15 mm), and should be easily handled by all the size groups considered in this study (Bannon & Ringler 1986). The only larger food item was the cranefly larvae, which is benthic and mainly eaten by small-sized trout. Thus we would expect that the most favourable prey should be the same for all size groups, if given the same opportunity to exploit the different prey items. This indicates that the observed differences in food choice between the size-groups are enforced by the differences in position choice and not the reverse. Brown trout are known to compete aggressively for food and space, and have a social hierarchy formation related to size (Jenkins 1969, Bachman 1984). Thus, although no significant differences in stomach fullness between size-groups was observed, it is reasonable to assume that large specimens occupy the most rewarding feeding areas. Agonistic behaviour and physiological stress in fish has been shown to reduce food intake and supress growth of subordinate individuals (Fenderson et al. 1968, Li & Brocksen 1977, McIntyre et al. 1979). By taking position close to the bottom, small brown trout are less detectable and thereby probably reduce the rate of agonistic encounters with larger specimens. As the position choice of small trout seems to be restricted by social interactions with larger specimens, their feeding conditions become considerably dependent on the availability of benthic food.

In accordance with their strong association to the bottom, small trout showed pronounced preferences for bottom substrate, while larger specimens that preyed more in open waters showed no such preference. Intermediate- and especially small-sized trout were most abundant at the location with a bottom substratum consisting of stones with diametres of 10–30 cm. Structures on the bottom are known to provide shelter against predators (Charnov et al. 1976, Savino & Stein 1982). In Lake Tesse cannibalism among brown trout seems negligible. However, coarse stones may be of considerable importance as shelter against agonistic encounters with larger individuals. Coarse stones also decrease the probability of aggressive confrontations among small fish staying close to the bottom by offering visual isolation between individuals, and thereby allowing higher densities of fish (Kalleberg 1958, Magnusson 1962). However, small trout showed no preference for the location with the largest stones and boulders, and the intermediate-sized trout exhibited some preference for the station

Table 3. Mean stomach fullness ± SD of small-, intermediate- and large-sized brown trout caught at four littoral locations in Lake Tesse, 1990. Numbers in parentheses are the number of fish analyzed.

	Loc. 1	Loc. 2	Loc. 3	Loc. 4
Small-sized	2.1 ± 1.4 (14)	2.4 ± 1.9 (14)	2.8 ± 1.5 (86)	2.2 ± 2.2 (21)
Intermediate-sized	2.4 ± 1.6 (32)	1.9 ± 1.6 (11)	2.1 ± 1.5 (41)	2.5 ± 1.4 (15)
Large-sized	2.8 ± 1.5 (13)	2.7 ± 1.4 (13)	1.8 ± 1.2 (16)	2.4 ± 1.5 (15)

with a sandy bottom in July, despite that this area was completely open. Thus, visual isolation and access to hiding places does not completely explain the differences in fish abundance between locations.

Despite the far higher fish density, the stomach fullness of small-sized brown trout at the location with substrate consisting of 10–30 cm large stones was as high as at the other locations. Thus it appears that the access to valuable food for small trout was better at this location. The relative importance of the highly preferable prey item *E. lamellatus* was highest at this station. This benthic crustacean is known to feed on periphyton and detritus (Flössner 1972), for which the production is probably low in the unstable sandy substrate. High structural complexity is known to reduce foraging efficiency (e.g. Ware 1973), allowing highly profitable prey to coexist with their predators. Densities of valuable food items are therefore often positively correlated with structural complexity (Macan 1949, Hruška 1961). However, due to increased search and pursuit time, capture return rates generally decline with increasing structural complexity (Ware 1973, Stein & Magnuson 1976) and the feeding rates of a predator may therefore be maximized at an intermediate structural complexity (Crowder & Cooper 1979, 1982). A possible explanation for the low density of small-sized trout at the station with the most coarse stones may therefore be that the structural complexity at this station was too high to provide profitable benthic feeding conditions.

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References cited

Bachman, R.A. 1984. Foraging behaviour of free-ranging wild and hatchery brown trout in a stream. Trans. Amer. Fish. Soc. 113: 1–32.

Bannon, E. & N.H. Ringler. 1986. Optimal prey size for stream resident brown trout (*Salmo trutta*): test of predictive models. Can. J. Zool. 64: 704–713.

Bjornn, T.C. 1971. Trout and salmon movements in two Idaho streams as related to temperature, food, streamflow, cover and population density. Trans. Amer. Fish. Soc. 100: 423–438.

Bustard, D.R. & D.W. Narver. 1975. Aspects of the winter ecology of juvenile coho salmon (*Onchorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). J. Fish. Res. Board. Can. 32: 667–680.

Charnov, E.L., G.H. Orians & K. Hyatt. 1976. Ecological implications of resource depression. Amer. Nat. 110: 247–259.

Crowder, L.B. & W.E. Cooper. 1979. Structural complexity and fish-prey interactions in ponds: a point of view. pp. 2–10. *In:* D.L. Johnson & R.A. Stein (ed.) Response of Fish to Habitat Structure in Standing Water, North Central Div. Amer. Fish. Soc. Special Publ. 6, Bethesda.

Crowder, L.B. & W.E. Cooper. 1982. Habitat structural complexity and the interaction between bluegills and their prey. Ecology 63: 1802–1813.

Dervo, B.K., O. Hegge, D.O. Hessen & J. Skurdal. 1991. Diel food selection of pelagic Arctic charr, *Salvelinus alpinus* (L.), and brown trout, *Salmo trutta* L., in Lake Atnsjø, SE Norway. J. Fish. Biol. 38: 199–209.

Fenderson, O.C., W.H. Everhart & L.M. Muth. 1968. Comparative agonistic and feeding behaviour of hatchery-reared and wild salmon in aquaria. J. Fish. Res. Board. Can. 25: 1–14.

Flössner, D. 1972. Krebstiere, Crustacea, Kiemen- und Blattfüsser, Branchiopoda, Fichläuse, Branchiura. Die Tierwelt Deutchlands 60: 1–501.

Gilbert, J.C. 1978. Large scale experimental salmonid nursery area habitat improvement. Big Tricadie River, New Brunnswick. New Brunnsvick Dep. Nat. Res. Fish. Bull. 23 pp.

Haraldstad, Ø. & B. Jonsson. 1983. Age and sex segregation in habitat utilization by brown trout in a Norwegian lake. Trans. Amer. Fish. Soc. 112: 27–37.

Hegge, O., B.K. Dervo, J. Skurdal & D.O. Hessen. 1989. Habitat utilization by sympatric arctic charr (*Salvelinus alpinus* (L.)) and brown trout (*Salmo trutta* L.) in Lake Atnsjø, south-east Norway. Freshwat. Biol. 22: 143–152.

Heggenes, J. 1988. Substrate preferences of brown trout fry (*Salmo trutta*) in artificial stream channels. Can. J. Fish. Aquat. Sci. 45: 1801–1806.

Heggenes, J. & S.J. Saltveit. 1990. Seasonal and spatial microhabitat selection and segregation in young Atlantic salmon, *Salmo salar* L., and brown trout, *Salmo trutta* L., in a Norwegian river. J. Fish. Biol. 36: 707–720.

Herr, O. 1917. Die Phyllopodenfauna der preussischen Oberlausitz und der benachbarten Gebiete. Abh. naturf. Ges. Görlitz 28: 1–162.

Hillman, T.W., J.S. Griffith & W.S. Platts. 1987. Summer and winter habitat selection by juvenile chinook salmon in a highly sedimented Idaho stream. Trans. Amer. Fish. Soc. 116: 185–195.

Hruška, V. 1961. An attempt at a direct investigation of the influence of the carp stock on the bottom fauna of two ponds. Verh. Intern. Verein. theor. angew. Limnol. 14: 732–736.

Jenkins, T.M. 1969. Social structure, position choice and microdistribution of two trout species (*Salmo trutta* and *Salmo gairdneri*) resident in mountain streams. Anim. Behav. Monogr. 2: 57–123.

Jonsson, B. 1989. Life history and habitat use of Norwegian brown trout (*Salmo trutta*). Freshwater Biol. 21: 71–86.

Jonsson, B. & F.R. Gravem. 1985. Use of space and food by resident and migrant brown trout, *Salmo trutta*. Env. Biol. Fish. 14: 281–293.

Kalleberg, H. 1958. Observations in a stream tank of territoriality and competition in juvenile salmon and trout (*Salmo salar* L. and *S. trutta* L.). Rep. Inst. Freshwat. Res. Drottningholm 39: 55–98.

Karlstrøm, Ø. 1977. Biotopval og besättningstäthet hos lax- och öringungar i svenska vattendrag (Habitat choice and densities of young salmon and trout in Swedish watercourses). Inform. Inst. Freshwat. Res. Drottningholm 6. 72 pp.

Kennedy, G.J.A. & C.D. Strange. 1982. The distribution of salmonids in upland streams in relation to depth and gradient. J. Fish. Biol. 20: 579–591.

Klemetsen, A. 1967. On the feeding habits of the population of brown trout (*Salmo trutta* L.) in Jølstervann, west Norway, with special reference to the utilization of planktonic crustaceans. Nytt. Mag. Zool. 15: 50–67.

Li, H.W. & R.W. Brocksen. 1977. Approaches to the analysis of energetic costs of intraspecific competition for space by rainbow trout (*Salmo gairdneri*). J. Fish. Biol. 11: 329–341.

Macan, T.T. 1949. Survey of a moorland fishpond. J. Anim. Ecol. 18: 169–186.

Magnuson, J.J. 1962. An analysis of aggressive behaviour, growth, and competition for food and space in medaka (*Oryzias latipes* (Pisces, Cyprinodontidae)). Can. J. Zool. 40: 313–363.

McIntyre, D.C., L.M. Healy & M. Saari. 1979. Intraspecific aggression and monoamine levels in rainbow trout (*Salmo gairdneri*) fingerlings. Behav. Neural. Biol. 25: 90–98.

Mittelbach, G.G. 1984. Predation and resource partitioning in two sunfishes (Centrarchidae). Ecology 65: 499–513.

Nilsson, N.A. 1965. Food segregation between salmonid species in North Sweden. Rep. Inst. Freshwat. Res. Drottningholm 46: 58–78.

Savino, J.F. & R.A. Stein. 1982. Predator-prey interaction between largemouth bass and bluegills as mediated by simulated submerged vegetation. Trans. Amer. Fish. Soc. 111: 255–266.

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

Stein, R.A. & J.J. Magnuson. 1976. Behavioural response of crayfish to a fish predator. Ecology 57: 751–761.

Vøllestad, L.A. & R. Andersen. 1985. Resource partitioning of various age groups of brown trout *Salmo trutta* in the littoral zone of Lake Selura, Norway. Arch. Hydrobiol. 105: 177–185.

Ware, D.M. 1973. Risk of epibenthic prey to predation by rainbow trout (*Salmo gairdneri*). J. Fish. Res. Board. Can. 30: 787–797.

Werner, E.E. & D.J. Hall. 1988. Ontogenetic habitat shifts in bluegill: the foraging rate – predation risk trade-off. Ecology 69: 1352–1366.

Response of native brown trout, Salmo trutta L., to stockings in a Norwegian reservoir

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Abstract. The response of stockings on the native population of brown trout, Salmo trutta L., was studied in Lake Tesse, a subalpine Norwegian reservoir. Yield data are available from 1979 to 1988, whereas test fishing was conducted from 1984 to 1988. The number of brown trout (age 0+) released ranged between 14.7 and 18.2 native and non-native fish ha^{-1} yr^{-1} from 1981 to 1986 as opposed to not more than 7.0 non-native fish ha^{-1} yr^{-1} prior to 1980. There was no positive correlation between annual variation in yield and number of fish released. In fact, both yield of native fish and the proportion of native fish in the catches decreased with increasing stocking density. The proportion of native fish in the test fishing catches decreased from 47% in 1984 to 25/30% in 1987/1988. Totally, stocked fish constituted about 70% of the total catch among younger specimens (age 2+ and 3+). Both non-native and native stocked fish were larger at release than natural recruited individuals, and this difference in size at age existed throughout their life span. There was a significant reduction in annual growth of both native and non-native stocked fish of age 2 and 3 during the study period. This study indicate that these supplementary stockings had a negative effect of native trout in terms of both growth and survival, and should therefore be strongly considered.

Introduction

A high fraction of Norwegian lakes are regulated for the porpose of producing hydroelectric power. Brown trout, Salmo trutta L., is in many lakes the only fish species present, and their natural propagation generally become negatively affected due to the regulation. Therefore, supplementary stockings of hatchery fish are usually carried out because it is considered to be necessary to sustain an acceptable sport - or commercial fishery (cf L'Abee-Lund 1986).

The debate of fish stockings concentrated initially on the survival and advisability of releasing hatchery-produced salmonids in natural waters due to their inferior adaptation compared to wild individuals (Miller 1954, 1958; Reimers 1957). Extensive release of brown trout fry in five regulated Swedish lakes showed to be of little use, which was related to intra- and interspecific competition. Several other studies also indicated poor return of hatchery fish in locations supporting well established native populations (Ayles 1975; Sutber, Sealing & Bergersen 1985; Gunn et al. 1987; Hesthagen & Johnsen 1989). These differences have been attributed to aspects such as improper feeding behaviour and low competitive ability (Ersbak & Haase 1983; Bachman 1984) or the origin of the hatchery stock (Aass 1982; Lachance & Magnan 1990).

In later years stockings of brown trout have been addressed to the management and preservation of native population (Elliott 1989). In fact, studies conducted in stream-dwelling salmonids indicate that rebuilding of wild stocks by use of hatchery fish might have a negative effect on wild fish through competition for food and space (Butler 1975; Vincent 1975, 1987; Petrosky & Bjornn 1988; Näslund 1992).

In this paper, we study the response on native brown trout in a Norwegian reservoir which has been subjected to relatively high stocking densities over several years in order to increase the fish yield.

Study area

The study was conducted in Lake Tesse, a subalpine hydroelectric reservoir located at an altitude of 853.9 m in southern central Norway (Fig. 1). The annual water amplitude is 12.4 m, corresponding to a surface area of 937 and 1426 hectare at the lowest and highest water level, respectively. Maximum depth is measured at 64 m. Lake Tesse was first regulated in 1943, and with an addition regulation in 1963. Brown trout is the only fish species present in the system. The inlet and the outlet were originally the two main spawning areas for brown trout in Lake Tesse. However, in connection with the regualtion, channalization was carried out in lower reaches of the inlet river. In addition, glacier-fed water was transferred to the river causing sedimentation on the river bottom (Hesthagen & Fjellheim 1987). Further, spawning areas in the outlet river were distroyed due to the construction of a dam. Native brown trout also spawned in several areas along the shore in the lake at depths between 3-5 m before the regulation (Simen Bjørgen, personal communication). The spawning areas for brown trout in the reservoir is now restricted to small tributaries.

Methods

Supplementary brown trout stockings of unmarked non-native fish in Lake Tesse were conducted from 1952-1979. During the 1970's, the annual release was about 10.000 specimens (7.0 fish ha^{-1}). From 1980 onwards, it was decided to stock Lake Tesse with both native of non-native fish.

Mature fish from Lake Tesse were obtained with gill nets outside River Smådøla in late September each year from 1979 to 1985. The fish were kept in circular tanks at the lake until complete maturity was reached. We generally used three males to fertilize one female. The roe were placed in a hatchery at Lake Lemonsjøen near Lake Tesse shortly after fertilization. The unfed fry were released in an earthen pond about 15 km from Lake Tesse in early June, where they fed on natural food items only. Two strains of non-native fish were raised in circular tanks at A/L Settefisk Hatchery at Reinsvoll and fed artificial food. The Bjornesfjord strain have been domesticated since 1966, while the Tunhovdfjord strain originated from second generation individuals (Stabell, Hafsund & Skurdal 1988).

The fish were batch-marked, and for lake stocked native and non-native fish, we removed the adipose and either the left or right pelvic fin, respectively. Prior to stocking in late August/early September each year, all fish were mixed and placed over-night in a net cage in the reservoir. From 1980 to 1986, between 10.000 and 17.000 non-native and between 5800 and 10.000 fish of native origin were stocked annually, representing between 14.7 and 18.2 fish ha^{-1} (Table 1). In addition, 2000 native fish were released in several tributaries each year.

The fish were released along the shore of the entire reservoir, except for the northern and southern areas where the littoral bed consists of fine gravel. Some of the native stocked fish were marked by removing the adipose fin only, and released into a few streams penetrating into Lake Tesse.

Only 48% of the native stocked fish released in the reservoir during the period 1980-1983 were marked. Based on the number of first-year circuli on scales, we used a discriminant analysis to distinguish between stocked and native fish. This analysis grouped 79.1% of native fish as native and 71.1% of native stocked fish as stocked (Hesthagen, Hegge, Skurdal & Dervo 1993). Fin regeneration of the pelvic fins was considered in 16 specimens of a total of 2360 fish (0.7%) examined for marks, and they were omitted from further analysis.

We conducted monthly test-fishing from June through October each year from 1984 to 1988. Fish were captured with bottom gill nets of 25 m in length and 1.5 in height. Each fleet consisted of 7 nets with mesh sizes ranging between 21-45 mm, which catch brown trout with about equal efficiency in the 20 - 38 cm length interval (Jensen 1977). Each net was set independently from the shore for one night, covering depths between 0-5 m. The gill nets were distributed throughout the entire reservoir so that most stretches were sampled each year.

For each fish, total length and weight was measured to the nearest mm and g, respectively. Ages were obtained from both scales and otoliths (Jonsson 1976). Scales were removed from an area between the front of the adipose and the back of the dorsal fin above the lateral line (Dannevig & Høst 1931). We aged totally 2334 fish, while 10 specimens were disregarded. We made impressions of 5-6 scales on celluloid before they were read and the distance between each annuli measured using a scale projector of 100 times magnification. Back-calculation of growth in length at age was made using the Lea method (Francis 1990).

Results

Yield

The brown trout stock in Lake Tesse is mainly harvested by means of gill of 35 mm mesh size. During the period 1979 to 1988, the annual yield on gill nets ranged between 638.1 and 2673.1 kg (Figure 2). The marked fish became fully expoited from 1985 omwards, however, there was no positive correlation between annual yield and number of fish released. In fact, both yield of native fish and the proportion of native fish in the catches decreased with increasing stocking density. From 1979 to 1982, stocked fish constituted about 8% of fish in the catches as opposed to 39 and 43% in 1986 and 1987, respectively. During the study period there have been som variation in total effort, however, this does not explain the annual variation in yield (unpublished data).

Proportion of native fish in the test fishing catches

The proportion of native brown trout decreased significantly during the study period (linear regression, $P<0.05$, Figure 3). In 1984, natives made up 47% of the total catch compared to 25-30% in 1987 and 1988. Opposite, the fraction of non-native stocked fish in the catches increased highly during the study period, being 22% in 1984 and 47% in 1988.

Age distribution

Brown trout caught during test fishing in Lake Tesse ranged in age between 2+ and 9+ (Figure 4). Any comparison of age distribution between strains are invalided because of gill net selectivity (they differ in size at age) and annual variation in survival (e.g. strong 1983 year-class of non-native stocked fish).

Among younger age groups (e.g. age 2+ and 3+) about 70% originated from stocked brown trout (Fig. 5). The proportion of released fish decreased highly among older individuals. This is probably mainly because stocked fish grew more rapidly than native fish, and were consequently caught at a lower age by commercial fishermen (cf. L'Abee-Lund & Sægrov 1991).

Growth

Attained length was highly related to strain, after having removed the effect of age (ANCOVA, $P<0.0001$, Table 2).

Back-calculated lengths showed that non-native stocked fish of age 2 and 3 were generally significantly larger than individuals of corresponding age of native stocked fish, which were significantly larger than native fish (ANOVA, Table 3). However, for older fish there was generally no difference in lengths between native stocked and non-native stocked fish of the same age, however, both categories were larger than native fish.

Length increment of different cohorts exhibit a reduction in growth for younger fish during the study period, e.g. in age groups 2 and 3 (Figure 6). However, for fish in age group 4 there was in fact an general increase in growth rate during the same period.

Discussion

The present study indicate that the survival and growth of native brown trout in Lake Tesse is affected by supplementary stockings of conspecifics. We suggest therefore that native fish suffer from strong ecological interactions for space and food from stocked individuals in the epibenthic zone. This is thought to occur because (i) native fish were significantly smaller than stocked fish in all age groups and (ii) increased density due to stocking reduced survival of native fish

The competition from stocked fish may be strong already in their first year of life. Native brown trout of Lake Tesse mainly leave their nursery streams in their first year of life (unpublished data). In the lake, it is reasonable to assume that stocked fish outcompete wild individuals for territories because of their larger size (Bachman 1984). If stockings are carried out yearly, and without any apparent differences in survival between wild and stocked fish after the first year, wild fish are successively replaced by cultured ones (Naslund 1992). Comparative data on survival of native and stocked fish are difficult to obtain in Lake Tesse due to few un-exploited year classes.

A study of habitat selection conducted in the littoral zone of Lake Tesse strongly indicate intraspecific competition among brown trout for space (Hegge, Hesthagen & Skurdal 1993a). Smaller individuals showed a strong association to the bottom and a pronounced preference for bottom substratum compared with larger fish. We hypothesize that by taking position close to the bottom, smaller brown trout are less detectable and thereby probably reduce the rate of agonistic encounters with larger specimens.

Differences in habitat utilization among native and non-native stocked brown trout in Lake Tesse is also of importance in evaluating the ecological effects of stockings. We found that native and native stocked fish were both spatially segregated according to size as small (< 220 mm) and large specimens mainly occupy the epibenthic and pelagic zone, respectively (Hesthagen et al. 1993). In contrast, all size groups of non-native trout were largely restricted to epibenthic habitat. In this paper, we argue that the pelagic zone was temporary the most rewarding habitat, but that non-native fish were less adapted to utilize this habitat. Because non-native trout generally lack a habitat shift, there will be a strong intraspecific competition in the littoral zone. Therefore, small brown trout are forced into the less favourable epibenthic habitat through social interactions with large specimens (Hegge, Hesthagen & Skurdal 1993b). We also argue that the conditions for small brown trout is a bottleneck in the capacity of fish production in hydroelectric reservoirs where the bottom fauna is strongly reduced (Grimås 1961).

We found a reduction in growth among both native and non-native stocked brown trout in age groups 2 and 3 during the study period. Although we found a decrease in yield during the same period, does not necessarily means that there was a corresponding decrease in density of fish in younger age groups. The influence of density on fish growth has been documented in brown trout (Jensen 1977; Hesthagen & Johnsen 1992). Therefore, variation in growth rate prove to be a useful parameter when considering changes in fish density. Similar, Keast (1977) found that the abundance of other fish was the primary factor influencing growth in different yellow perch stocks.

The number of young trout in the littoral zone of Lake Tesse might be close to carrying capacity prior to the increase in stocking density. Therefore, any further supplementary stockings does not necessary mean an increase in the standing stock of young fish. In fact as indicated from this study, native trout might became replaced by stocked fish due to their size-related inferior competitive ability. Such cases might cause a decrease in production of wild fish, and eventually also a decrease in total production.

Management implications

We recommended to stop the stockings in lake Tesse for a three-year period (1987-1989 except for 10.000 native stream-stocked fish) in order to evaluate the stockings in terms of fish yield in the reservoir. Further, stockings of non native fish have been stopped due to their lack of using pelagic habitat (cf. Hesthagen et al. 1993). At present, stockings of native fish reared both in hatchery and earthen pond are carried out to evaluate survival, growth and habitat use.

The decline in the the number of native fish during the study period, is not thought to be due to a smaller spawning stock and hence not to reduced recruitment. Spawning migration have been registered in several streams draining Lake Tesse since 1980 (unpublished data). No mature non-native brown trout have been obtained in these streams, indicating no interbreeding between native and introduced non-native brown trout in Lake Tesse water system.

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References

Aass P. (1982) Brown trout stocking in Norway. In: Report of the Symposium on Stock Enhancement in the Management of Freshwater Fisheries, pp. 123-128. EIFAC Technical Paper 42, FAO, Rome.

Ayles G.B. (1975) Influence of the genoptype and the environment on growth and survival of raibow trout (*Salmo gairdneri*) in central Canadian aquaculture lakes. Aquaculture 6, 181-188.

Bachman R.A. (1984) Foraging behavior of free-ranging wild and hatchery brown trout in a stream. Transactions of the American Fisheries Society 113, 1-32.

Butler R.L. (1975) Some thoughts on the effects of stocking hatchery trout on wild trout populations. In: Proceedings of the wild trout management symposium (ed. by W. King), pp. 83-87. Trout Unlimited, Washington, D.C.

Dannevig A. & Høst P. (1931) Sources of error in computing l_1-l_2 etc. from scales taken from different parts of the fish. Coceil International pour l'Exploration de la Mer 6, 64-93.

Elliott, J.M. (1989) Wild brown trout *Salmo trutta*: an important national and international resource. Freshwater Biology 21,1-5.

Ersbak K. & Haase B.L. (1983) Nutritional deprivation after stocking as a possible mechanism leading to mortality in stream-stocked brown trout. North American Journal of Fisheries Management 3, 142-151.

Francis R.I.C.C. (1990) Back-calculation of fish length: a critical review. Journal of Fish Biology 36, 883-902.

Grimås U. (1961) The bottom fauna of natural and impounded lakes in Northern Sweden (Ankarvattnet and Blåsjøn). Report of the Institute of Freshwater Research, Drottningholm 42, 183-237.

Gunn J.M., McMurthry M.J., Bowlby J.N., Casselman J.M. & Liimatainen V.A. (1987) Survival and growth of stocked lake trout in relation to body size, stocking season, lake acidity, and biomass of competitors. Transactions of the American Fisheries Society 116, 618-627.

Hegge O., Hesthagen, T. & Skurdal J. (1993a) Vertical distribution and substrate preference of brown trout (*Salmo trutta* L.) in a littoral zone. Environmental Biology of Fishes 36, 17-24

Hegge O., Hesthagen T. & Skurdal J. (1993b) Juvenile competitive bottleneck in the production of brown trout in hydroelectric reservoirs due to intraspecific habitat segregation. Regulated Rivers: Research & Mangement 8,41-48.

Hesthagen, T.& Fjellheim, A. (1987) Effects of transferring glacier-fed water to a clear-water mountain river on the production and food organisms of brown trout (Salmo trutta) in southern Norway. Regulated Rivers: Research & Management 1, 161-170.

Hesthagen T. & Johnsen B.O. (1992) Effects of fish density and size on survival, growth and production of hatchery-reared brown trout (Salmo trutta L.) in lakes. Fisheries Research 15, 147-156.

Hesthagen T., Hegge, O., Skurdal J. & Dervo B.K. (1993) Differences in habitat utilization among native, native stocked and non-native stocked brown trout (Salmo trutta) in a hydroelectric reservoir (Manuscript).

Jensen K.W. (1977) On the dynamics and exploitation of the population of brown trout, Salmo trutta L., in Lake Øvre Heimdalsvatn, Southern Norway. Institute of Freshwater Research Drottningholm Report 56, 18-69.

Jonsson B. (1976) Comparison of scales and otoliths for age determination in brown trout, Salmo trutta L. Norwegian Journal of Zoology 24, 295-301.

Keast A. (1977) Mechanisms expanding niche width and minimizing intraspecific competition in two centrarchid fishes. In: Evolutionary Biology, volume 10. (ed by M.K.Steere & B. Wallace), pp. 333-395. Plenum Press, New York, USA.

L'Abee-Lund J. H. (1986). Fiskeforsterkningstiltak i norske vassdrag. Ørretens økologi og erfaringer fra kultiveringsarbeid. Miljøvirkninger av vassdrags-regulering, Rapp. Nr. A6. 128 s.

L'Abee-Lund J.H. & Sægrov H. (1991) Resource use, growth and effects of stocking in alpine brown trout, Salmo trutta L. Aquaculture and Fisheries Management 22, 519-526.

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.

Miller R.B. (1954) Comparative survival of wild and hatchery-reared cutthroat trout in a stream. Transcations of the American Fisheries Society 83, 120-130.

Miller R.B. (1958) The role of competition in the mortality of hatchery trout. Journal of the Fisheries Research Board of Canada 15, 27-45.

Näslund I. (1992) Survival and distribution of pond- and hatchery-reared brown trout, Salmo trutta L., released in a Swedish stream. Aquaculture and Fisheries Management 23, 477-488.

Petrosky C.E. & Bjornn T.C. (1988) Response of wild rainbow (Salmo gairdneri) and cutthroat trout (S. clarki) to stocked rainbow trout in fertile and infertile streams. Canadian Journal of Fisheries and Aquatic Sciences 45, 2087-2105.

Reimers N. (1957) Some aspects of the relation between stream foods and trout survival. California Fish and Game 43, 43-69.

Stabell, F.R., Hafsund F. & Skurdal J. (1988) Rognstørrelse og rognantall for stamfisk av ørret Salmo trutta L. med ulik alder og avstamning. A/L Settefisk, Reinsvoll, Report 1-1988. (In Norwegian).

Sutber, R.J., Sealing C. & Bergersen E.P. (1985) Rainbow trout returns from fingerlings plantings in Dillon Reservoir, Colorado, 1975-1979. North American Journal of Fisheries Management 5, 471-474.

Vincent, E.R. (1975) Effect of stocking catchable trout on wild trout populations. In: Proceedings of the wild trout management symposium (ed. by W. King), pp. 88-92. Trout Unlimited, Washington, D.C.

Vincent, E.R. (1987) Effects of stocking catchable-size hatchery rainbow trout on two wild trout species in the

Madison River and O'dell Creek, Montana. Nort American Journal of Fisheries Management 7, 91-109.

Table 1. Density and total number released (N_R) and mean length in mm ± standard deviation (XL ± SD) of juvenil (age 0+) non-native and native brown trout released in Lake Tesse, 1980-1986. In addition, 2000 native fish were released in same tributaries each year during the same period, i.e. totally 14000 specimens.

		Non-native fish				Native fish			
		Density		Fish size		Density		Fish size	
Year	Strain	Ha^{-1}	N_R	XL±SD	N	Ha^{-1}	N_R	XL±SD	N
1980	Bjornesfjord	7.0	10000	47 ± 5	121	4.1	5800	52 ± 8	130
1981	Tunhovdsfjord	10.5	15000	52 ± 4	259	4.2	6000	51 ± 4	130
1982	Tunhovdsfjord	11.9	17000	54 ± 6	115	4.9	7000	55 ± 7	165
1983	Bjornesfjord	10.5	15000	53 ± 5	51	7.0	10000	42 ± 7	149
1984	Bjornesfjord	10.5	15000	52 ± 7	102	7.0	10000	42 ± 4	343
1985	Bjornesfjord	11.2	16000	50 ± 6	107	7.0	10000	47 ± 4	112
1986	Tunhovdsfjord	8.4	12000	60 ± 5	115	7.0	10000	54 ± 4	178

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Table 2. Analysis of covariance (back-calculated length at age 2–5) of brown trout caught in epibenthic habitat in Lake Tesse, 1984–1988.

		MS	df	F–ratio	P	R^2
L2	Age	186740.635	1	747.200	< 0.0001	0.486
	Strain	183657.312	2	734.863	< 0.0001	
	Residual	249.920	2343			
L3	Age	148493.571	1	231.452	< 0.0001	0.296
	Strain	192391.730	2	299.859	< 0.0001	
	Residual	641.573	1981			
L4	Age	49156.779	1	44.352	< 0.0001	0.183
	Strain	99558.069	2	89.827	< 0.0001	
	Residual	1108.337	999			
L5	Age	23626.265	1	15.815	< 0.0001	0.146
	Strain	33786.557	2	22.616	< 0.0001	
	Residual	1493.889	358			

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Table 3. Back-calculated length in mm (L2-L6, ± standard deviation) for native (NA), native stocked (NA-S) and non-native stocked (NNA-S) brown trout caught in epibenthic habitat in Lake Tesse, 1984-1988. N = number of fish. Within age group, mean length followed by different letters (a,b,c) are significantly different ($P<0.05$) wheras mean length followed by the same letter are not significantly different ($P>0.05$). In cases where NNA-S and NA fish are significantly different, but neither group is different compared with NA-S fish, NNA-S group is labelled both by a and c.

Year	Strain	L1	N	L2	N	L3	N	L4	N	L5	N	L6	N
1984	NA	36± 6	162	$88\pm21_a$	162	$154\pm28_a$	143	$229\pm33_a$	88	$284\pm41_a$	38	283±63	9
	NA-S	48± 8	109	$124\pm15_b$	109	$202\pm25_b$	94	$269\pm20_b$	34	314- $_b$	1	-	
	NNA-S	48±10	76	$132\pm18_b$	72	$210\pm26_b$	41	$266\pm20_{bc}$	9	373	1	398	1
1985	NA	36± 9	242	$94\pm17_a$	242	$161\pm27_a$	237	$214\pm39_a$	105	$258\pm54_a$	42	$295\pm58_a$	16
	NA-S	52±10	220	$121\pm18_b$	220	$196\pm27_b$	190	$265\pm29_b$	69	$299\pm21_b$	16	-	
	NNA-S	57±10	163	$145\pm21_c$	163	$215\pm31_c$	55	$265\pm21_b$	22	$294\pm17_{bc}$	7	$329\pm17_a$	3
1986	NA	37± 8	179	$97\pm18_a$	179	$166\pm28_a$	176	$229\pm41_a$	127	$251\pm49_a$	34	$269\pm47_a$	6
	NA-S	52±12	143	$119\pm22_b$	143	$192\pm31_b$	135	$261\pm31_b$	101	$307\pm41_b$	21	$289\pm82_a$	3
	NNA-S	54±10	198	$139\pm22_c$	198	$205\pm27_b$	166	$263\pm41_b$	8	$300\pm62_{bc}$	2	-	
1987	NA	35± 8	90	$87\ 20_a$	90	$143\pm28_a$	84	$199\pm36_a$	67	$243\pm43_a$	37	$264\pm45_a$	15
	NA-S	43± 8	103	$111\pm16_b$	103	$173\pm22_b$	99	$239\pm29_b$	59	$289\pm19_b$	30	$317\pm11_b$	6
	NNA-S	52±10	165	$131\pm18_c$	162	$193\pm26_c$	126	$242\pm31_b$	75	$293\pm52_b$	5	-	
1988	NA	37±21	164	$89\pm20_a$	164	$145\pm30_a$	158	$193\pm43_a$	103	$237\pm47_a$	83	$253\pm39_a$	44
	NA-S	41± 8	118	$103\pm14_b$	118	$165\pm21_b$	104	$228\pm25_b$	58	$280\pm20_b$	24	$314\pm12_a$	2
	NNA-S	51± 9	248	$124\pm16_c$	248	$186\pm24_c$	204	$234\pm25_b$	106	$271\pm21_b$	49	-	

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Figure 1. Lake Tesse with geographic location

Figure 2. Yield in kg ha^{-1} of non-native stocked, native stocked and natural recruited brown trout caught on gill nets of 35 mm mesh size in Lake Tesse, 1979-1988

Figure 3. Proportion of non-native stocked, native stocked and native brown trout in Lake Tesse, 1984-1988. Sample sizes in each year are given on the figure.

Figure 4. Age frequency distribution of native, native stocked and non-native stocked brown trout in Lake Tesse, 1984-1988. N=number of fish. Seven non native fish of age 1+ are not presented in the figure.

Figure 5. Proportion of stocked brown trout (native and non-native fish combined) in different age groups in Lake Tesse, 1984-1988. Sample sizes in each age group are given on the figure.

Figure 6. Annual length increment of native (solid circles) and non-native stocked (open circles) brown trout of different cohorts caught in Lake Tesse, 1984-1988.

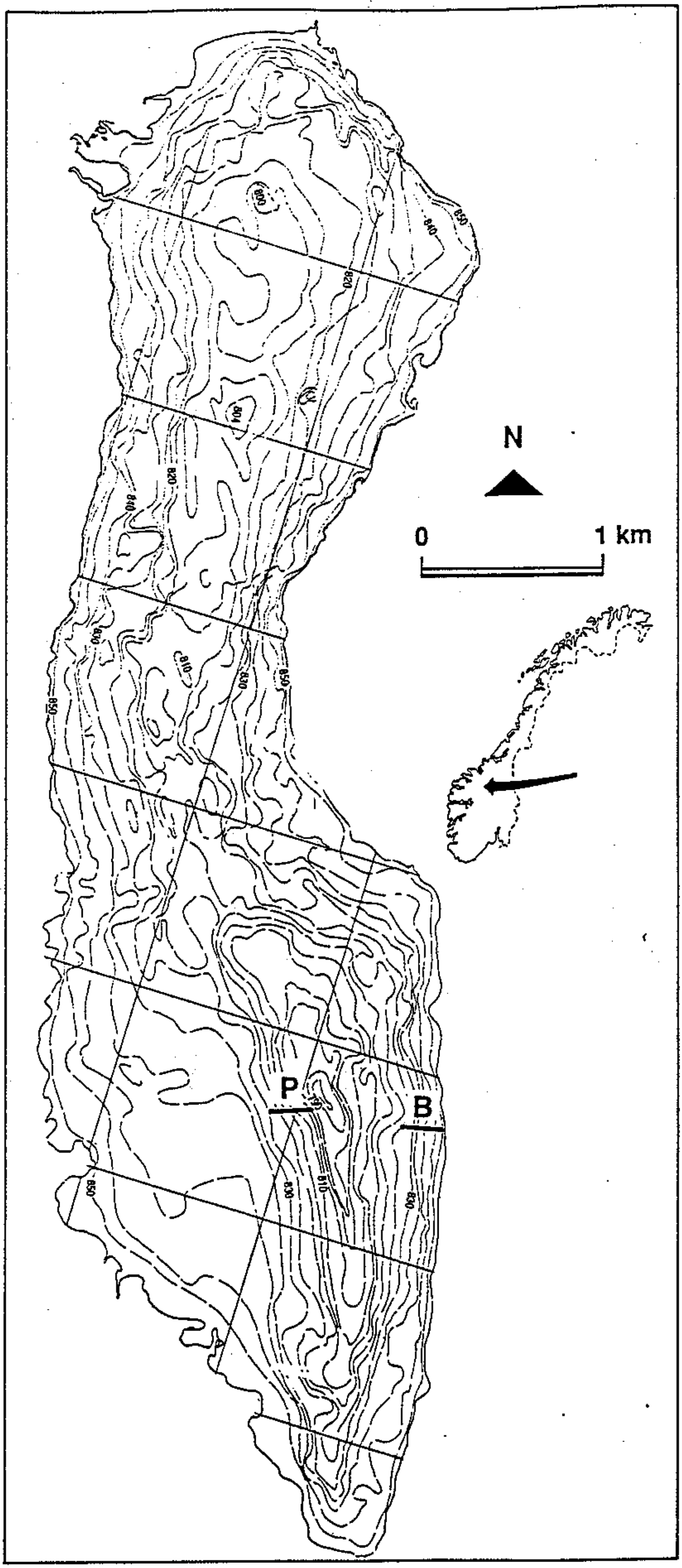

Figure 1

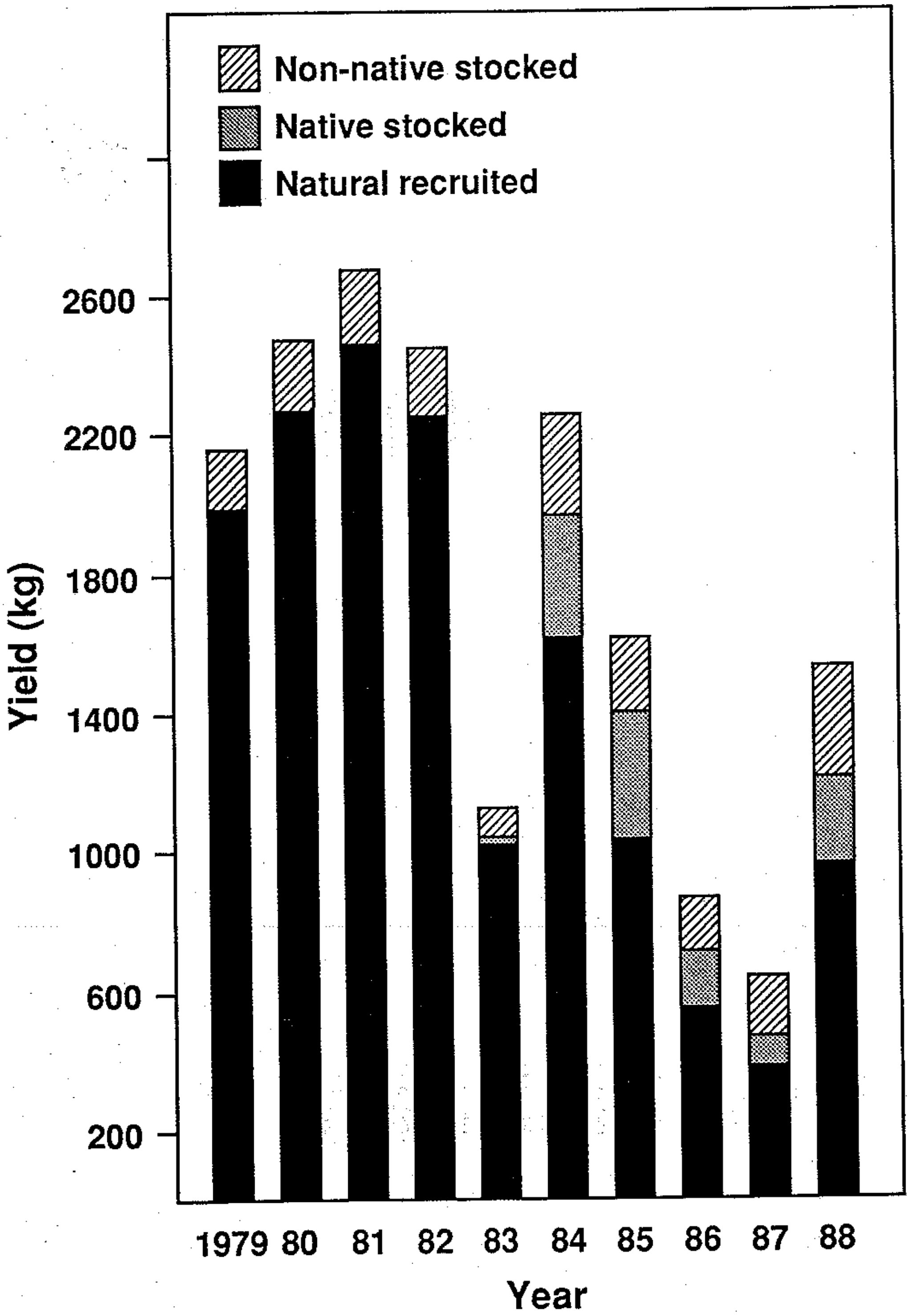
Non-native stocked
Native stocked
Natural recruited
Yield (kg)
2600
2200
1800
1400
1000
600
200
1979
80
81
82
83
84
85
86
87
88
Year

Figure 2

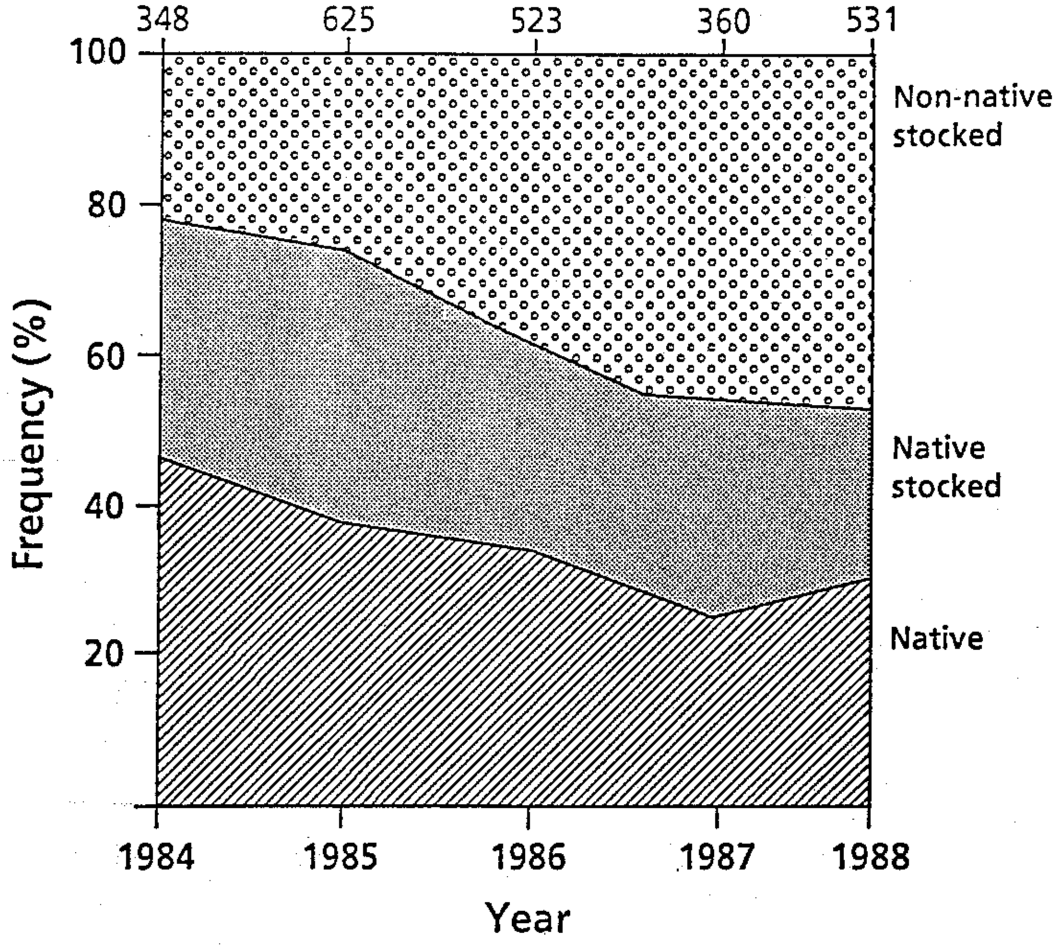
348
625
523
360
531
100
80
60
40
20
Frequency (%)
Non-native stocked
Native stocked
Native
1984
1985
1986
1987
1988
Year

Figure 3

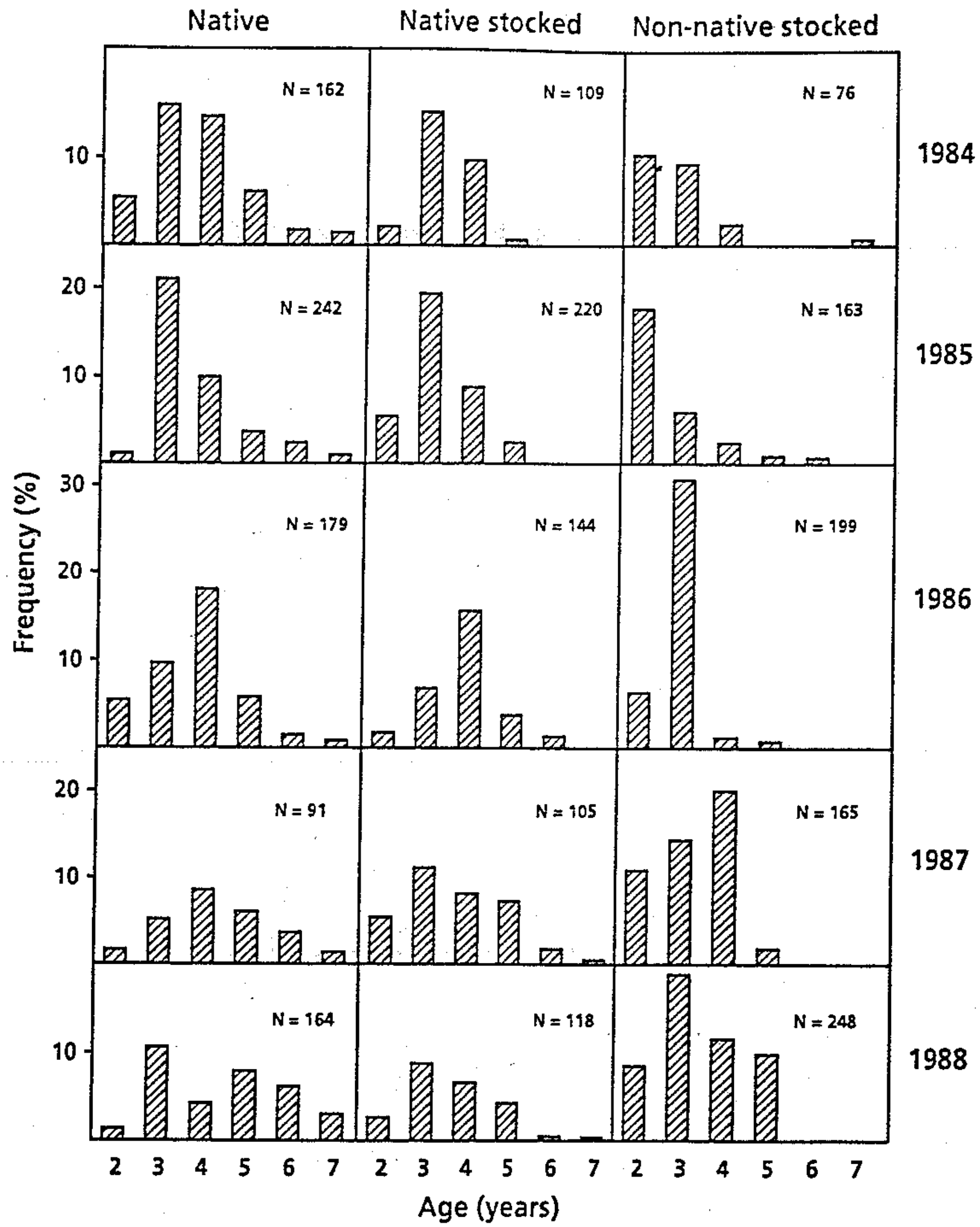
Native
Native stocked
Non-native stocked
Frequency (%)
N = 162
N = 109
N = 76
1984
N = 242
N = 220
N = 163
1985
N = 179
N = 144
N = 199
1986
N = 91
N = 105
N = 165
1987
N = 164
N = 118
N = 248
1988
10
20
10
30
20
10
20
10
10
2 3 4 5 6 7
2 3 4 5 6 7
2 3 4 5 6 7
Age (years)

Figure 4

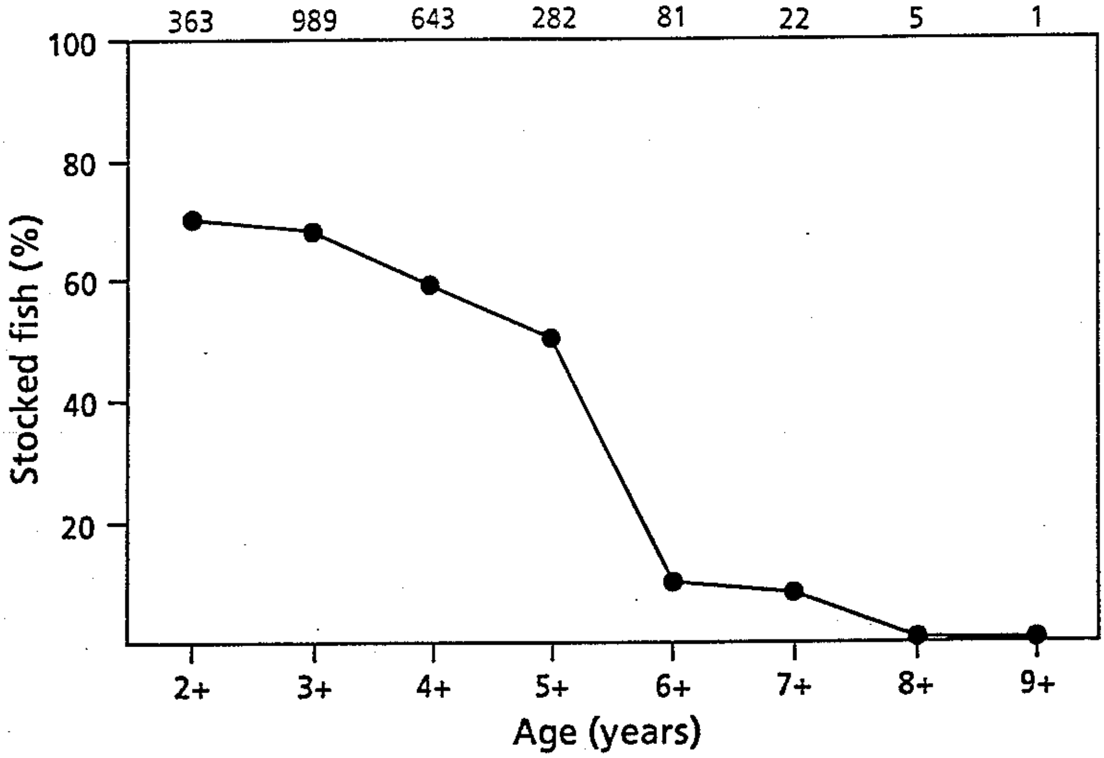
363
989
643
282
81
22
5
1
100
80
60
40
20
Stocked fish (%)
2+
3+
4+
5+
6+
7+
8+
9+
Age (years)

Figure 5

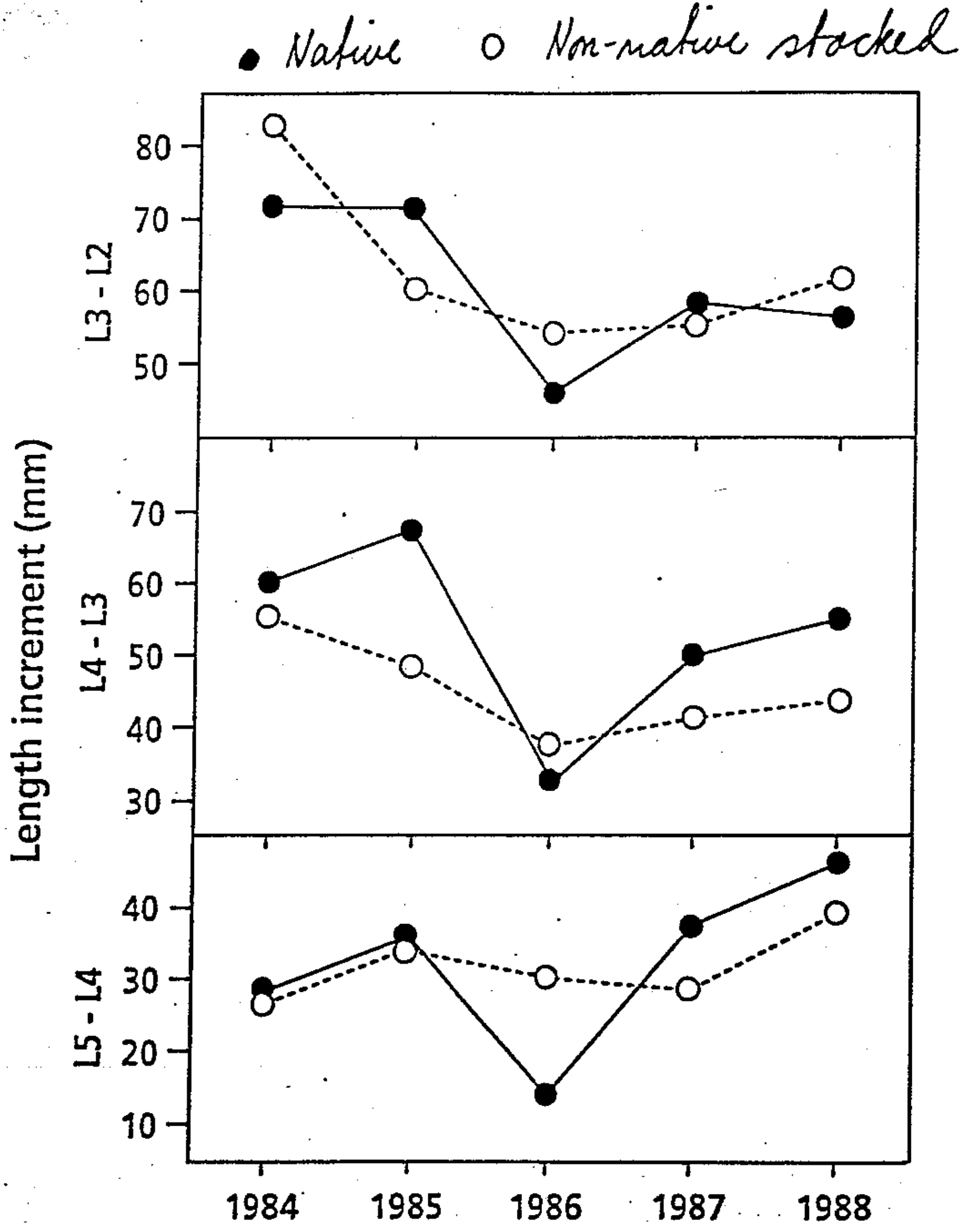
● Native ○ Non-native stocked
Length increment (mm)
L3 - L2
80
70
60
50
L4 - L3
70
60
50
40
30
L5 - L4
40
30
20
10
1984
1985
1986
1987
1988

Figure 6