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I. DEVELOPMENT AND EARLY LIFE HISTORY

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謹呈

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I. DEVELOPMENT AND EARLY LIFE HISTORY

Koji MAEKAWA, *Department of Oral Anatomy, Faculty of Dental Medicine, Hokkaido University, Sapporo 060*

Synopsis

MAEKAWA, Koji (Dep. Oral Anat., Fac. Dent. Med., Hokkaido Univ., Sapporo). 1977. Studies on the variability of the Land-locked miyabe char, *Salvelinus malma miyabei* OSHIMA. I. Development and early life history. Jap. J. Ecol., 27: 91–102.

The early life history of the land-locked miyabe char, *Salvelinus malma miyabei* OSHIMA, was investigated in an inlet stream of Lake Shikaribetsu in central Hokkaido from 1971 to 1974. The ontogenetic process of this species was divided into seven developmental stages according to the ETAP theory of Vasnetzov. A relatively high proportion of drifting terrestrial insects was found in the food of all developmental stages except the alevin in every season of the year. Two developmental stages were found among juvenile fish which migrated into the lake. One stage consisted of smolt and/or presmolt-like fish which were 2 years or more old and varied from 105 to 155 mm in fork length. Migration occurred in June and July. Another stage consisted of relatively younger fish of different age and size classes. They migrated into the lake from July to Novemeber with a peak in October. It was suggested that these fishes were using the lake as a wintering area, since, of all the available water sources, it maintains the highest water temperature during the winter season.

はじめに

オショロコマ，*Salvelinus malma* は北半球の太平洋北部地域に広く分布するサケ科イワナ属のそ河性回遊魚である（McPhail, 1961；1970）．この魚種には降海型と河川残留型の二型が見られ，分布圏の南方ほど後者の出現頻度が高く（McPhail, 1961），南限にあたる北海道では降海型の発見例はきわめて少ない（疋田，1962；石城，1967；前川，1973）．

北海道然別湖には，生活様式も形態もオショロコマの降海型とよく似た陸封型の魚が生息しており，幾人かの研究者により，分類学的側面をも含めて，その特殊性が注目されてきた（大島，1938；青柳，1957；久保，1967；Behnke, 1972；Yoshiyasu, 1973）．しかしながら，これらの研究は本魚種の適応様式を明らかにすることに重点がなかったために，その特殊性の意味を解明することに十分成功したとは言えなかった．

著者は然別湖産イワナの形態および生活史の特徴を，生長と発育の関係から明らかにするために研究を進めてきたが，さしあたり本報告はその第一報としてその発育過程を整理し，河川生活中の稚魚期の移動を中心とした生活様式の諸特徴について報告する．

本論文をまとめるにあたって，多くの有益な批判と原稿の校閲をしていただいた北大農学部森樊須教授，阿部永助教授，同演習林石城謙吉助教授ならびに太田嘉四夫助教授に，さらに種々の便宜をはかっていただいた北大歯学部中根文雄教授，大泰司紀之講師に，心から感謝の意を表したい．また調査中いろいろお教え下さった北海道水産ふ化場長内稔氏および然別湖自然保護管理人阿部佐美雄氏と原稿および図表の作製に協力していただいた北大歯学部寺崎純子氏に深く感謝の意を表する．

材料および方法

調査は1971年４月から1975年３月まで，然別湖とその注入河川のヤンベツ川で行なった．1972年７月までは毎月７～12日間，それ以後は３～11月の間必要に応じて調査を行なった．

1976年10月22日受理

[1] 北海道大学審査学位論文の一部

河川での魚の採集は主に投網（網目8.0mm）・すくい網（同 5.0mm）・釣りにより，湖では網目 10.0mm〜45.0mmの刺し網と釣りによった．ただ，受精直後から卵黄がほぼ¼に吸収された段階までのものは，人工ふ化（北海道鹿追町営）のものを用いた．採集した魚はいずれも，直ちに約10%ホルマリン液に入れ，研究室に持ち帰ったのち測定に供した．

川から湖への稚魚の降下は，1973年3月から8月まではヤンベツ川本流の河口から約 1〜2 km 上流，同年8月から1974年10月までは山田川（後述）の本流との合流点付近で調査した．この場合，ナイロン製の網目 3.0〜5.0 mm のトラップ（Fig. 1）を本流では中心部のみ，山田川では川幅全体が仕切られるように設置した．

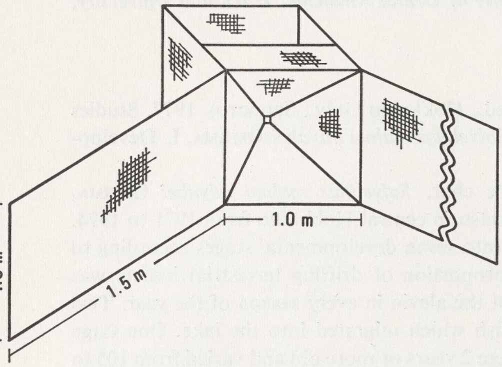

Fig. 1. Diagram of a trap.

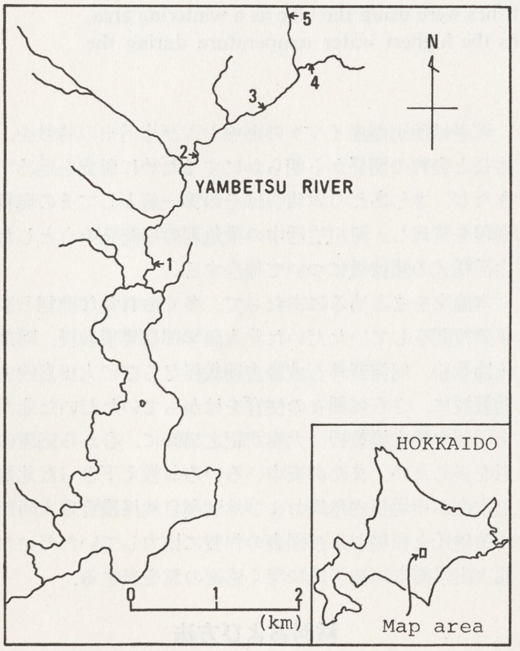

Fig. 2. Location and map of Shikaribetsu Lake and the Yambetsu creek. Shikaribetsu Lake (elevation 800 m) is deep (maximum 101 m). Number shows the stations at which the water temperature was measured.

胃内容物は餌種の個体数の百分率か又は出現頻度で表わした．また年令査定は Grainger (1953), Heiser (1966) により耳石の冬帯数を目安とした．従来日本でのイワナ属の年令査定には，鱗を用いることが多かったが（疋田，1962；久保，1967；石城，未発表2)），その冬帯はきわめて不明瞭であるばかりでなくかなりの誤差がある（Heiser, 1966）．Heiser (1966) は耳石の冬帯の出方が有効であることを報告しており，最近のイワナ属研究者（例えば Armstrong, 1970）もこれに従っているので，今回の調査もこれにならった．

さらに河川の流下昆虫の組成を知るため，25×25 cm のサバネットを3〜10月の間，昼夜4〜6回，各1時間づつ瀬の中央部に仕掛けた．

然別湖とその注入河川の概要

然別湖は大雪山連峰の南端に位置する海抜 800m，周囲 16 km の典型的な高山湖である（Fig. 2）．最高深度 100m を越えるすりばち状の湖で，注入河川は大小4本である．そのうち最大の川はヤンベツ川で，五つの支流をもつ全長約 10 km の渓流である．河口から 2 km 付近までは，可児（1943）の河川形態の分類によれば，典型的な Bb 型で河原がよく発達している．それより上流は源流の 3 km（Aa 型）を除いてほぼ Aa 型あるいは Aa—Bb 型の移行型である．また河口から 8 km 付近に約3〜4 mの落差のある滝があり，これが障壁となって，その上流にはイワナは分布しない．移動を調査した支流山田川は支流中最大のもので，本流とは河口から上流 1.5 km のところで合流している．

流出河川は昭和27年まではトウマベツ川を経て，シカリベツ川，十勝川に連なっていた．しかしその後は北海道電力によるダムによって人工的にせき止められ，湖水はパイプで直接取り出されている．

調査中に採集された魚種はミヤベイワナ *Salvelinus malma miyabei* Oshima，ニジマス *Salmo gairdnerii irideus* (Gibbons)，ウグイ *Trbolodon hakonensis* (Gunther)，エゾウグイ *T. ezoe* (Okada et Ikeda)，ワカサギ *Hypomesus olidus* (Pallas)，フクドジョウ *Barbatula tonitoni* (Dybowsky)，フナの一種 *Carassius sp.*，およびエゾトミヨ *Pungitius pungitius tymensis* (Nikolsky) である．このうち明らかな在来種はイワナのみであり，その他の魚種は昭和30年から50年の間に人

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2) 北海道産イワナ属魚類の形態学的，生態学的研究．北海道大学農学部博士論文．

為的に移殖されたものである．

然別湖産イワナの発育過程の整理

久保（1974）はサケ科サケ属のサクラマス *Oncorhychus masou* の発育をその名称と共に整理し，宇藤（未発表[3)]）は同じくサクラマス稚魚の発育区分を試みている．魚類の発育過程をどのような指標を用いて区分するかは，議論のあるところであるが，ここでは上記の二つの論文を参照しながら，さらにビワ湖のコアユの発育を整理した東（1964，1970）に従って，まず形態的（外観および若干の解剖学的観察）に発育段階を区分した．Fig. 3 に D_2 期までの発育区分の外形を示した．

A期——ふ化直後のもので，大きな卵黄をつけ，パーマークが出現する直前までである．形態的に二つに分ける．

A_1 期—叉長 15.5～17.5mm．約 4.0°C で受精後100日以後．

ふ化直後で大きな卵黄をつけている．開口しているが，顎は上下咬合しない．ふ化直前では背鰭は膜鰭から分離していなかったものがふ化後急速に分離する．すでに尾鰭に相当する部分に不透明な鰭条の原基が出現しているが，その他の鰭条はまだ形成されていない．体表はきわめてうすい黒色色素胞によっておおわれている．

鰓は形成が進み，鰓葉が鰓弓下枝で形成され始める．歯は外見上観察されず，消化管は直線状で胃の部分でわずかに膨大するのみである．

A_2 期—叉長 17.0～20.0mm．約 4.0°C で受精後110日以後．

体表の黒色色素胞は一層その数を増し，体全体に広がる．顎は依然咬合しない．背鰭，臀鰭および胸鰭に不透明な鰭条の原基が出現し急速に一定数に近づく．尾鰭はまだ丸型のままである．

鰓弁は鰓弓下枝から上枝にも広がる．消化管は胃の部分でわずかに屈曲し始める．

B期——卵黄の吸収が進み，パーマークが出現してから卵黄の吸収が完了する直前までである．形態的に二つに分ける．

B_1 期—叉長 20.5～21.7mm．採集された期間，3月初旬～4月初旬．

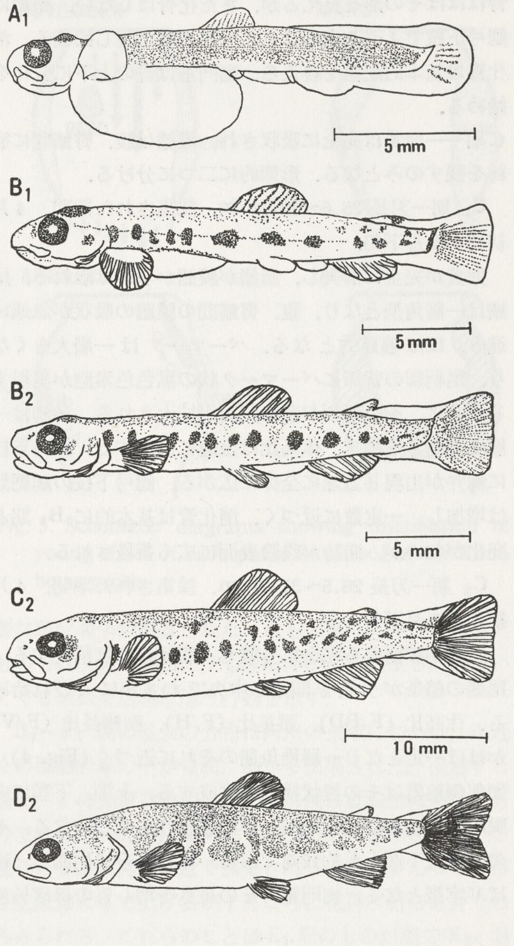

Fig. 3. Developmental aspects from post-hatching to phase D_2 of the Miyabe char. A_1: a larva just after hatching. B_1: a larva just after the appearance of parr marks. B_2: a larva just after the absorption of yolk. C_2: a juvenile after the separation of adipose fin from fin membrane. D_2: a juvenile just after the branching of rays of all fins.

卵黄は急速に吸収されA期の卵黄の¼ほどになると，側線にパーマークが出現する．背鰭，臀鰭，胸鰭，腹鰭の鰭条はすでに一定数に達しており，その高さを増す．脂鰭はまだ分化しないが，その原基周辺に黒色色素胞が出現する．下顎は上顎後縁にほぼ達する．消化管は胃の部分でわずかに屈曲し，その形態を整える．幽門垂が出現するが，肝臓は胃上方に位置する．鰾は食道で連結し，まだガスを満たしていない．鰓弓下枝に二列目の鰓弁が出現する．鰓弓下枝に突起状の鰓耙が出現する．

B_2 期—叉長 21.7～26.2mm．採集された期間，3月下旬～4月中旬．

卵黄は完全に腹腔内にかくれ，胃上方にわずかに残るのみとなる．各鰭はその高さを急速に増す．脂鰭の分化が開始される．尾鰭が丸型から角型へと変化し，上葉，下葉の分化が始まる．消化管はほぼその配置を完了し，胃は B_1 期よりもさらに屈曲し，ほぼU字型となる．椎

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3) サクラマス，*Oncorhychus masou*（Brevoort）仔稚魚の生育と生活様式．北海道大学水産学部修士論文．

骨はほぼその形を整えるが，まだ化骨はしない．鰓耙は鰓弓下枝で４～７本となり，上枝にも出現し始める．消化管は基本的配置を終える．幽門垂は胃の上下に分化を始める．

Ｃ期──卵黄は完全に吸収され，膜鰭は腹，臀鰭間に痕跡を残すのみとなる．形態的に二つに分ける．

C_1 期―叉長 25.6～30.1mm．採集された期間，４月初旬～５月下旬．

卵黄が完全に消失し，脂鰭が膜鰭からほぼ離れる．尾鰭は一層角型となり，腹，臀鰭間の膜鰭の吸収が急速に進み，ほぼ痕跡的となる．パーマークは一層大きくなり，尾柄部の背部にパーマーク状の黒色色素胞が出現すると共に，その配列が乱れ変異が拡大される．各鰭は一層その高さを増す．体高比は急速に低下する．鰓弓下枝に鰓弁が出現し急速に全体に広がる．鰓弓下枝の鰓耙数は増加し，一定数に近づく．消化管は基本的に B_1 期と変化がないが，脂肪が腸管表面に広く蓄積される．

C_2 期―叉長 26.5～37.7mm．採集された期間，４月初旬～５月下旬．

脂鰭が膜鰭から完全に分離し，膜鰭はほぼ消失する．尾鰭の鰭条が分岐を開始し中央でわずかにくびれ始める．体高比（F/BD），頭長比（F/H），胸鰭長比（F/V）がほぼ一定となり一層稚魚期のそれに近づく（Fig. 4）．頭部側線器はその管状構造を完成する．上顎，下顎に肉眼的に透明な歯（円錐歯）が観察されるようになる．その数は上下顎とも約12対である．胃はさらに屈曲し，ほぼＶ字型となる．幽門垂はその長さを増し胃のほぼ½にまで達する．鰾にガスがいっぱいに満たされる．脂肪の蓄積が腸，幽門垂の周辺で顕著となる．

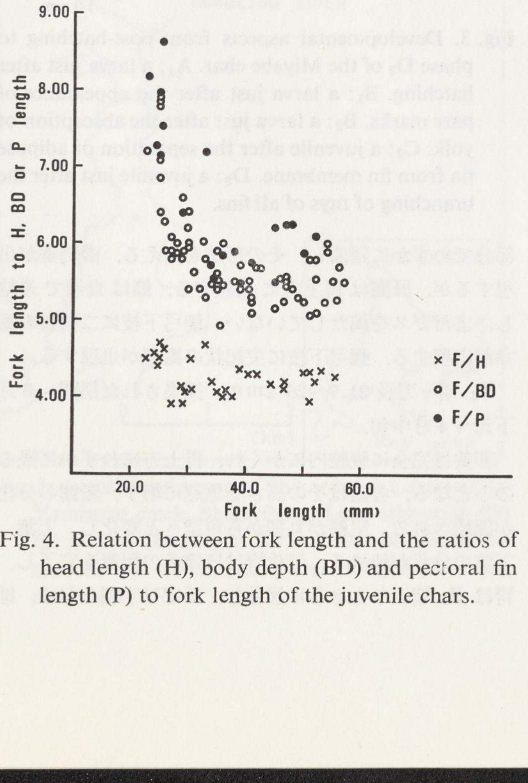


Fig. 4. Relation between fork length and the ratios of head length (H), body depth (BD) and pectoral fin length (P) to fork length of the juvenile chars.

Ｄ期──各鰭の鰭条の分岐が始まり，鱗が出現し全身をおおうと共に白点の原基が出現する．生態的には生息場所等の多様化が目立ってくる．形態的に二つに分ける．

D_1 期―叉長 34.1～50.1mm．採集された期間，４月下旬～８月下旬．

体高比が高まり成魚的形態に近づく．背部の黒色色素胞はさらに数を増し，パーマーク近くにまで分布する．背鰭，胸鰭，臀鰭の鰭条の分岐が始まり，鰭条の展開および収斂が可能となる．尾鰭は一層上下葉に高さを増し，中央部のくびれはさらに深くなる．

D_2 期―叉長 49.0～68.0mm．６月中旬以後年間を通して採集される．

体側背部の黒色色素胞の分布はさらに広がり，パーマークに近接したところにも存在する．各鰭の鰭条は明瞭に分岐し，鰭膜も発達し一層収斂が自由となる．鱗が全体に広がると共に側線器は管器として完成する．鰓耙はその数を増加させ，この期間中に一定の数（23～29）に達すると共にその長さを増す．

Ｅ期──白色斑点が出現しそれが赤色斑点に変化するまでで，生活様式の多様化に伴って，外部形態はさらに変異が拡大される．この時期に降湖型と残留型の識別が容易となる．採集はほぼ年間を通して可能となるため，これ以後はその出現時期を省く．

E_1 期―叉長 53.0～113.0mm．

パーマークとその間にのびた黒色色素胞集団との間隔はさらに接近し，この間に側線を中心にして白色斑点が出現する．肝臓，脾臓は茶色を呈し始め，特に脾臓はさらに黒みを帯びるようになる．

E_2S 期―叉長 85.0～130.0mm．

皮膚表面にうすいグアニン色素が出現する．グアニン色素は顎を含む頭部全体に広がると共に腹部も白色を呈するようになる．パーマークはうすいが，ホルマリン標本では明瞭になる．

E_2R 期―叉長 95.0～105.0mm．

基本的形態は E_1 期と区別しにくいが，生殖腺が明らかに他と区別されるほどに肥大し始める．体高が幾分高く，一見して E_2S 期と区別される．下顎は上顎に達することはない．この時期はほとんどが雄である．いわゆる河川残留型と呼ばれるものである．

E_3S 期―叉長 110mm以上．

体側にちらばった白色斑点が側線付近を中心に赤みを帯びるようになる．色はきわめてうすく，不明瞭な場合もある．湖で採集されたものではグアニン色素は一層強く，パーマークは生体ではほとんど認められず，ホルマ

リン標本ではじめてうすく出る程度である．下顎が急速に前方に伸び，ほぼ上顎先端に達する．生殖腺の発達は悪い．歯は肉眼で認められる程度になるが，相対的には小さなままである．尾鰭のくびれが深くなる．

E_{3R} 期—刃長115.0～175.0mm.

体側表面の赤点は一層赤くなり，体高も高く，さらに残留型の様相を深める．腹面はほぼ年間にわたって顕著に赤い．雌雄とも採集が可能となる．雌では下顎が上顎に達することはないが，雄では成熟に伴って下顎が伸び，上顎先端にほぼ交わる程度になる．歯（犬歯）がよく発達する．

E_{4S} 期

観察されたものは少数であったので体長を示すことはできないが，体高の低い，グアニン色素がきわめて顕著で，尾鰭のきれこみが顕著な個体が現れる．特に尾鰭，背鰭の先端が黒化しており，久保（1974）による mid-smolt と考えられる．その生態はほとんど不明である．

F期——180.0mm以上.

グアニン色素が退色し，赤点がきわめて赤みを増すと共に，体全体が黒みを帯びる．特に雄では下顎が上顎先端を若干越えて屈曲し，著しく黒くなる．歯が犬歯状となり強大となる．

稚魚期の分布

前節で然別湖産イワナの生長をA期からF期に区分したが，ここではそれぞれの発育期のうち主に河川内での生息場所等を整理しておく．

A_1 期から A_2 期は産卵床以外で採集されることはない．しかし B_1 期以後は追いこみ網によって採集が可能となる．Fig. 5 に毎月の追跡調査によって得られた各発育期の生息場所を模式的に示した．3～4月の調査では B_1 期は淵尻付近の岸辺の雪の下で採集された．しかし B_1 期の稚魚が遊泳するのは観察されていないことから，石の下や枯葉の下などで静止していると推定される．胃に食物をみることはなく，栄養はもっぱら卵黄からとっている．4月の調査時には B_1 期と共に B_2 期も混獲される．しかし，B_2 期は岸近くの浅瀬で定位しながら餌をとっているものもあり，胃に食物をみることから（後述），すでに活発に索餌していると考えられる．

4～5月の調査の時には，C_1，C_2 期の稚魚は上流から下流までの浅瀬全体に広がり，群をなしているのが観察された．追いこみ網による採集では D_1 期の稚魚と共に混獲された．しかし C_1 期のものは瀬尻で索餌したり，石の下や枯葉の下で静止しているものもある．一層発育の進んだ C_2，D_1 期の稚魚は浅瀬の瀬頭や枝沢の瀬，一部のものは淵尻などで活発に索餌し，個体間に顕著な順位関係が観察された．最も大きく，生長の進んだものでは浅瀬の瀬頭に少し体を浮かせて定位し，近づいてくる個体を活発に追う行動を示す．

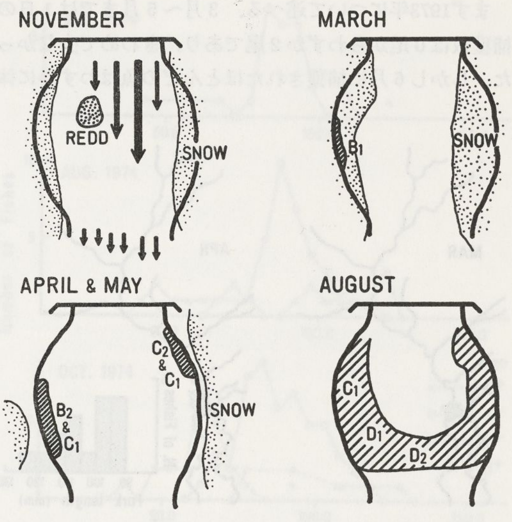


Fig. 5. Schematic diagrams showing distribution of young chars of each phase in a pool of the Yambetsu creek.

D_2～E_1 期の稚魚の分布は河川の全域にわたり，岸近くの浅瀬や草の下から淵，瀬から採集された．後述する通り，この発育期の個体は秋の降湖移動の主体をなすものである．一方 E_{2S} 期のものは Fig. 6 に示されている通り，3月に河口付近で採集されると共に少しづつ分布を上流部にまで広げるが7月ごろには再び河口付近でのみみられる．これらのことは E_1 期のものが湖で E_{2S} 期に変化し，その一部は湖と河の間を往復しながら生活していることを推察させる．これは井上ら（1973）が十勝川上流での河川型オショロコマの分布域の下流部には E_{2S} 期と考えられる個体の分布を観察しているのとよく似た現象を示している．

E_{2R} および E_{3R} 期は E_{2S} 期以後の魚と区別される．特に E_{2R} 期では3～6月ごろまでは本流中流部まで採集可能であるが，ほぼ7月以後は主に最上流部や枝沢でのみ採集される．E_{2R} 期は今回の調査中では9～10月に枝沢で多く採集された．

E_{3S} および E_{4S} 期はほぼ湖中でのみ採集される．久保（1967）は魚群探知機による調査によって，水深10m付近にその群をみた．

降下移動の諸特徴

月別による降下移動と体長，令構成

Fig. 7 に1973および1974年の降下用トラップによって捕獲された月別捕獲数を示す．

まず1973年について述べる．3月～5月までは1日の捕獲数は0尾からわずか2尾であり，きわめて少なかった．しかし6月に捕獲されたほとんどの魚はわずかに体色が銀色を呈し，E_2s 期に相当するものであった．さらにそのうちの1尾（26.5cm）は一面銀白色を呈し（E_4s 期），尾鰭先端が黒い smolt であった，8月下旬の調査では，1日当り最高37尾，平均（4日間）約30尾と，6月に比較してきわめて多数捕獲された．この傾向は9月，10月も続く．9月の調査中，最高は8月同様37尾，平均は約32尾であった．10月は16日から24日までのうち7日間設置されたが，そのうち雨による増水によってトラップが流された日（10月17日および23日）を除けばすべて捕獲された．この5日間の最高捕獲数は1日当り52尾，平均は約31尾であった．なお，この年の初雪は10月19日にあった．11月は24日から27日までの3日間設置中2日にそれぞれ3尾が捕獲された．

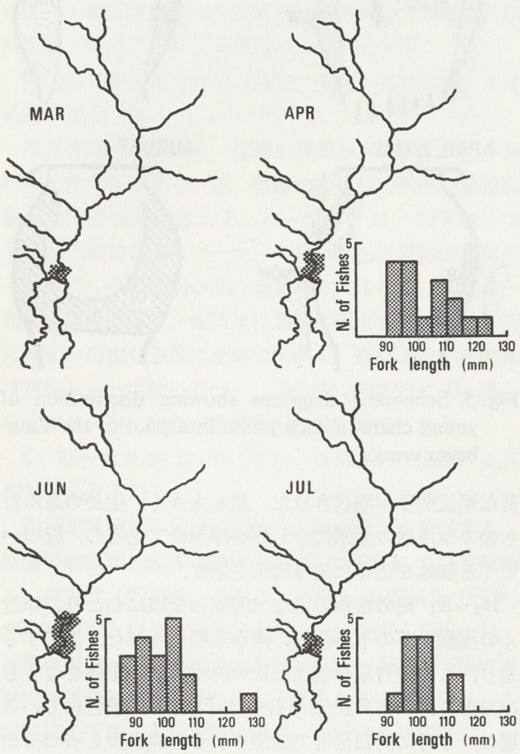


Fig. 6. Monthly distribution of phase E_2s fish in Yambetsu Creek and their fork length frequency.

1974年は前年に比較して，きわ立った変化は，4月～6月までの間にほとんど捕獲されなかった点にある．捕獲は7月に始まった．その1日当り最高捕獲数は20尾，平均は約9尾である．8月には最高捕獲数は1日当り22尾，平均19尾であった．10月には最高捕獲数は1日当り56尾，平均は30尾であった．

このように1973，1974年の両年とも7～8月から10月にかけてきわめて多数の降下移動が観察された．

さて，これらの捕獲された魚の発育段階をみると，ほとんどのものは D_2 期～E_1 期の発育段階のもので，一部 C_2，D_1 および E_2s 期のものが含まれていた．しかし1974年の7月には E_3s 期と考えられる魚が2尾捕獲された．これは1973年6月に捕獲されたものときわめてよく似ている．

次にこれらの捕獲された魚の体長分布を Fig. 8 に示

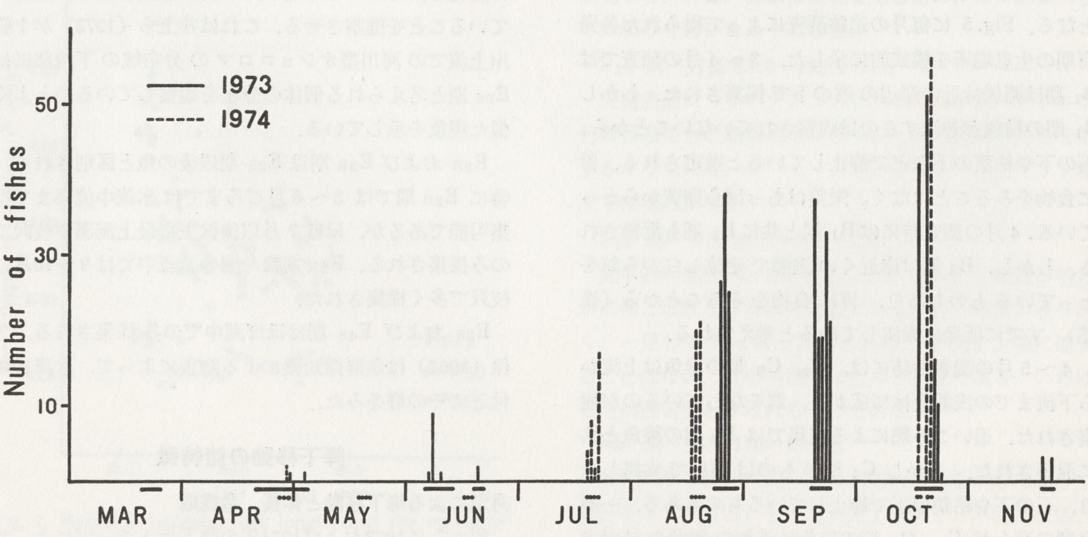


Fig. 7. Seasonal variation of the number of down-migrating chars as determined by a trap set up across the river. Trapping duration for each month is indicated by horizontal lines.

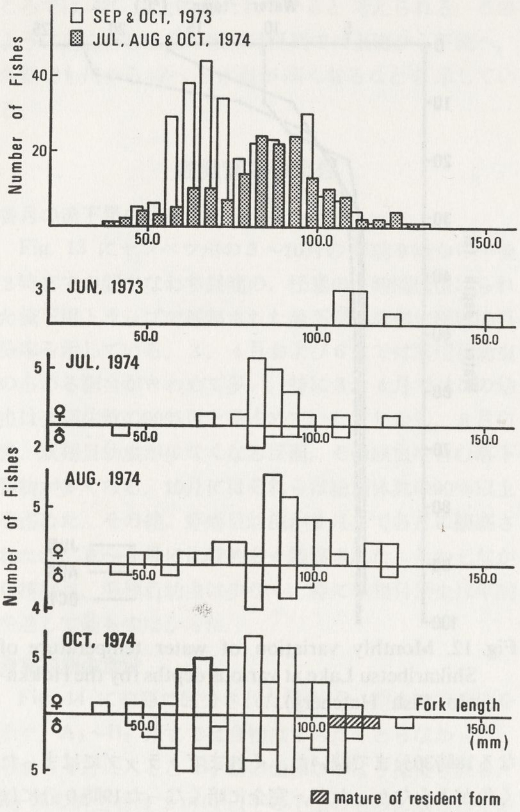


Fig. 8. Size compositions of the total number and the monthly compositions of down-migrating chars captured by the trap, 1973 and 1974.

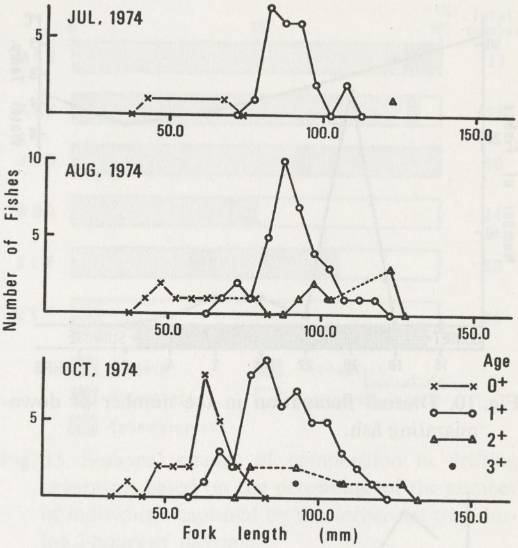


Fig. 9. Age and size composition of the fish captured by the trap.

す．1973年は標本として持ち帰ることができなかったので９月，10月の捕獲数の合計で示した．まず1973年の６月の体長分布をみると，すべて105.0mm以上で平均は116.6mmであり，７月～８月以後に捕獲された魚より明瞭に大きい．なお６月の魚の性比は雌，雄がそれぞれ５：３であった．

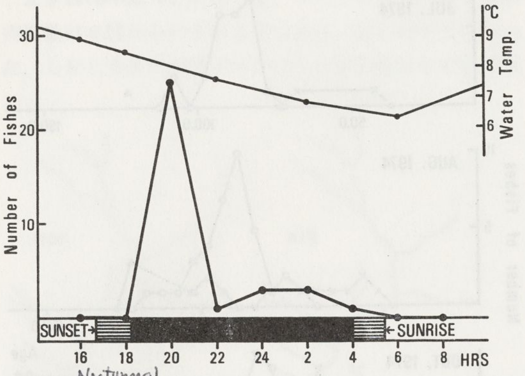
1973年の９月および10月までの体長分布では40.0～135.0mmの範囲まで，65.0～70.0mmと80.0～100.0mm付近に高頻度部分が認められる．1974年は月別，性別および全体の体長分布を示した．体長範囲は35.0～130.0mmで，全体としてみると1973年とほぼ同様65.0mm付近と80.0～100.0mmの間に二つの高頻度部分が不明瞭ながら認められる．ただし1973年の場合には小さい体長分布のグループの方が大きいそれより数が多かったが，1974年には逆であった．これをさらに月別で詳しくみると，７月および８月では雌が雄よりもきわめて多い（７月の性比約４：１，８月の性比約２：１）が，10月では約１：１と雌雄比がほぼ等しくなる．さらに７月～８月では小さな個体が比較的少ないが，10月ではきわめて多くなる．なお，10月にE_{2R}期すなわち残留型が３尾のみ捕獲された．

次に1973年６月および1974年７月～10月に捕獲された魚の令構成をFig. 9に示す．６月に捕獲された魚はほとんどが2^+のものであった．７月～10月までに捕獲された魚の令は0^+～3^+までで，そのうちほとんどが0^+と1^+のものであった．さらに各年令の体長分布のモードはほぼ各月の体長分布の二つの高頻度部分とほぼ一致している．各月の令別体長分布をさらに詳しくみると７月から10月までモードはほとんど変化していない．７月から８月～９月までは体長の生長がきわめて良いのに対し（続報），ここに示された体長分布が変化を示さなかったのは，どの月にも一定の大きさの魚だけが降下することを示唆している．

降湖移動の日周期

1973年の８月，９月，10月にそれぞれ降湖移動の日周期を調べた．そのうち９月の結果をFig. 10に示す．これによれば日中の降湖はほとんど（２年間の調査中1973年６月の１尾のみ）起こらなかった．しかし，うす暗くなる18時ごろ（９月）から暗くなる20時までの間にその日に降下する大半が捕獲された．その後降下魚数は急速に減少し，日の出の４時以後は捕獲数は０になった．このように降下移動は夜間に行なわれることが明らかである．

1972年９月に予備的に行なった落ちこみトラップによる調査の際，降下移動の直前の様相を観察することがで



Nocturnal
Fig. 10. ~~Diurnal~~ fluctuation in the number of downmigrating fish.

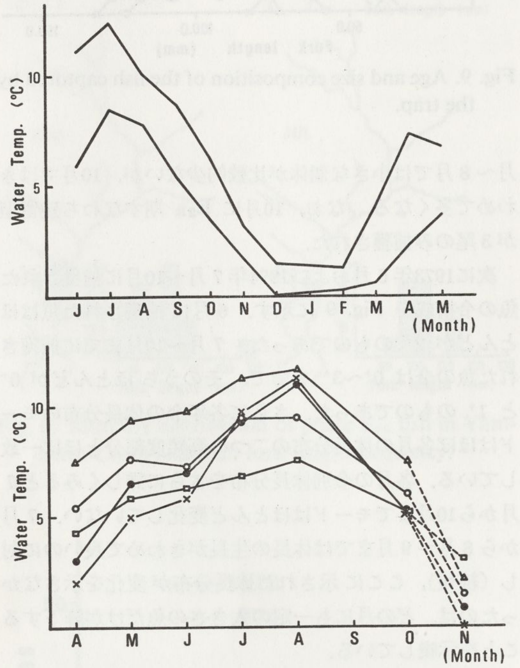


Fig. 11. Seasonal changes of water temperature in the Yambetsu creek. The upper graph shows the highest and the lowest temperature at station 2 in Fig. 2. The lower one shows the temperature at each station. △: st. 1, ○: st. 2, ●: st. 3, □: st. 4, ×: st. 5.

きた4)．すなわち日中活発に索餌していた十数尾の魚は日没後の17時30分ごろからルーズな群れを形成し，まもなくきわめて明瞭な Schooling を始め，淵全体を泳ぎ始めた．この Schooling は日没により肉眼で見えなくなる18時30分まで続いた．それまでトラップにはまったく魚が入らなかったが，完全に暗くなった19時0分にはほぼ50尾が捕獲された．

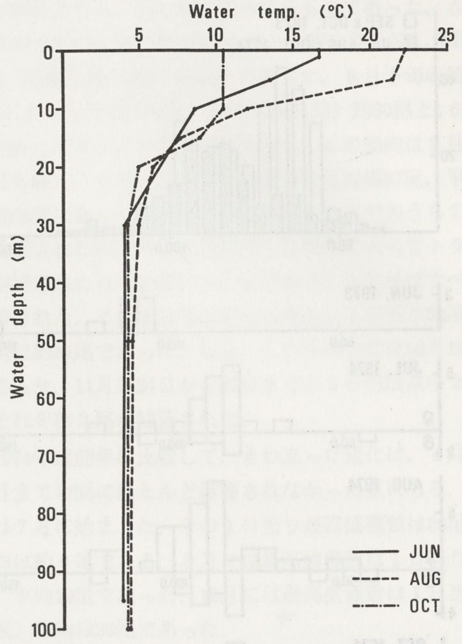


Fig. 12. Monthly variation of water temperature of Shikaribetsu Lake at various depths (by the Hokkaido Fish Hatchery).

河川の水温傾斜

河川の水温傾斜は夏期に下流部で高く上流部で低いのが普通である．しかし冬期ではこれが常に逆になるとは言いがたい（新井，1971)．ここでは秋から冬にかけてのイワナ移動の要因の一つとして，温度の差によるものかどうかを確かめたい．石城2)は道東地方の小河川イチャニ川で各月水温傾斜を調べた．これによれば夏期には上流部から中流部，下流部の順に水温が高くなる．しかし冬期にはこの関係が逆転し，最上流で最も高く，河口部で最も低くなる．北海道大学水産学部の後藤晃氏（私信）によれば，道南地方の諸河川でもこの関係が成り立つという．

次にヤンベツ川の河口より2 km上流地点で年間を通して測定したものおよび4月～11月までの温度傾斜を示す（Fig. 11)．これによれば年間を通して最も高いのは7～8月で，逆に低いのは2月で0°C近くにまで下がる．温度傾斜は夏期は上流部から下流部に順にほぼ高くなり，冬期でも本流では同様の関係が認められた．Fig. 12に示す通り，湖水では10月でも躍層より深いところではきわめて高い温度（4°C以上）に保たれており，実測は欠けているが厚い氷のはる冬期でも，躍層より深いと

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4) 山田川の一部が山田温泉によって作られたため池（淵状）(10×5 m) を通過する際，排出口が1 mの落差になっている．トラップはこの落差部に設置された．

ところでは 4°C 以上に保たれていると考えられる．このように湖を含む水温の傾斜は夏期では上流から下流へ，冬期でも川から湖へと水温が高くなることを示している．

各発育期の食性

各月の流下昆虫組成

Fig. 13 にヤンベツ川の３～10月の午前９時から午後２時までの間すなわち昼間の，任意の２時間仕掛けられた流下用トラップで採集された流下昆虫の個体総数の百分率を示している．３，４月および６月では双翅目幼虫の占める割合がきわめて多い．特に３，４月ではこの幼虫は全個体数の90%以上を占めていた．しかし，８月以後，双翅目幼虫が少なくなる反面，その成虫を含む落下動物が多くなる．10月にはそれらは総個体数の90%以上を占めた．その他，蜉蝣目幼虫が９月まで各月に観察されたが，６～９月に比較的多く観察された．しかしながら積翅目，毛翅目幼虫は少なく，特に毛翅目幼虫は年間を通して最も少なかった．

発育初期の食性

Fig. 14 に前節で区分された稚魚 D_1 期までの食性を示す．A_1～B_1 期までは食物はまったくとらなかった．しかし４月に入ると B_2 期の個体がかなり採集される．B_2 期の餌生物は 2 mm 以下の小型のものに限られており，双翅目幼虫（ユスリカ）がほとんどであった．中には 1 mm以下の蜉蝣目の動物（種は不明）も含まれていた．C_1 期の餌生物も基本的に B_2 期と類似していた．一方，C_2 期になると餌生物の種類が多様化し，蜉蝣目，積翅目，毛翅目と共に落下昆虫（アリ類，カ類，ウンカ類，トビムシ類）が出現する．D_1 期では食物内容はやや単純化するものの，積翅目，蜉蝣目，落下昆虫，中でも後者の量が増加した．D_2 期（９月以降）にはさらに落下昆虫および水生動物の比率が増大し，餌生物も比較的大きくなる．

石城[2)] は発育段階別に河川型オショロコマの食性を調べ,D_1 期(石城による段階Ⅲ～Ⅳ)にはトビケラ等の底層性毛翅目の幼虫が増すことを報告しているが，本調査による食性分析結果は各月の流下昆虫組成にきわめてよく対応している．このように発育段階別の食性はその発育に伴う生息場所の変化に対応していると考えられるが，この河川で特に興味深いのは発育初期から流下昆虫をよく捕食していることで，これは近縁種間の餌生物をめぐる社会関係をみる上で検討に値する．Armstrong（私信）によればアラスカ付近のオショロコマもイチャニ川における石城の場合と同様，他のサケ科魚類の稚魚との社会関係で，すでに C_1 期には底層性餌種の摂食が顕著となる．筆者もアラスカの Juneau の Eagle 河でこの様相を観察している．

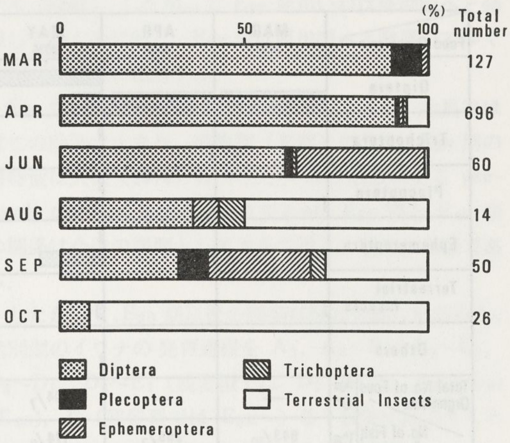

Fig. 13. Seasonal change of composition in drifting organisms based on the percentage of the number of individuals captured by the surber-net trap during 2 hours of daytime.

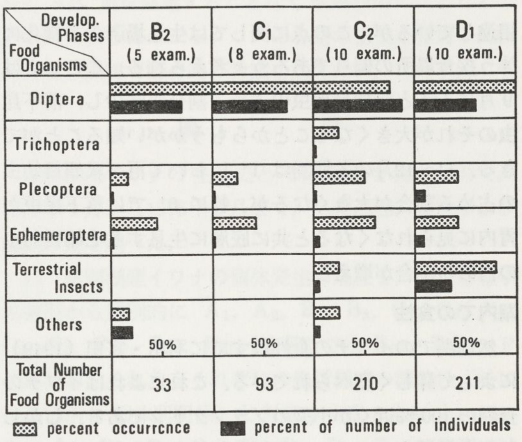

Fig. 14. Composition of food organisms in each phase of the juvenile chars based on the percentage of the occurrence and the number of individuals. The aspect of each phase is shown in Fig. 3.

0^+ および 1^+ 以上の個体の食性

湖に入る前までの各月の食性を Fig. 15 に示す．３～４月の 1^+ 以上の個体における食餌の個体総数の90%以上が双翅目幼虫によって占められていた．特にこの中ではユスリカが主であった．しかし５～６月になると，1^+ 以上においては食物内容が多様化し，その反面双翅目幼虫の占める割合は明瞭に減少した．ただし 0^+ においては双翅目が顕著に優占した．一方，７～８月になると再び双翅目幼虫を食べる傾向が強くなるが落下昆虫も比較的多い．流下昆虫組成と胃内容を比較してみると，若干

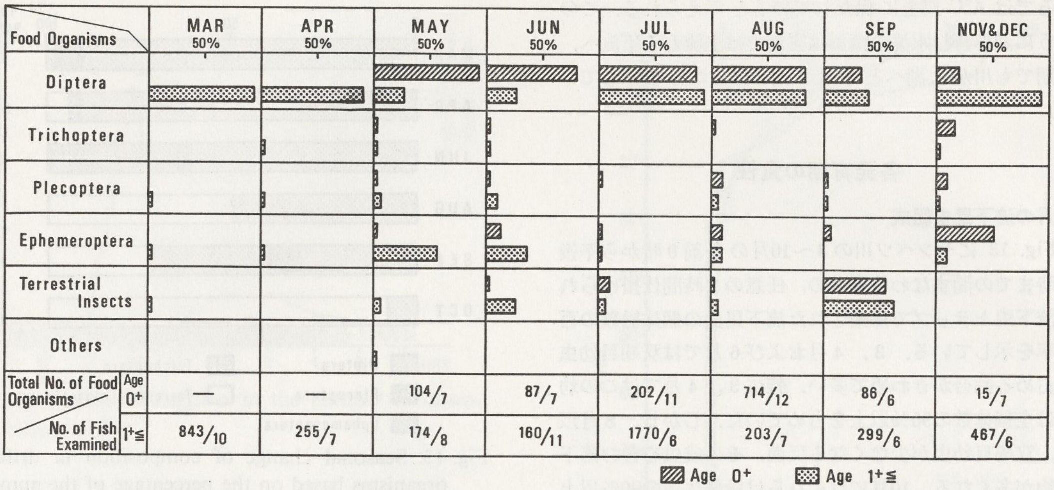

Fig. 15. Monthly composition of food organisms by young fish based on the percentage of the number of individuals.

相違しているが，この点に関しては生息場所の多様化に伴う採食場所の偏りであろうと考えられる．このことは9月に入ると双翅目昆虫の占める割合が減少し，落下昆虫のそれが大きくなることからもうかがい知ることができる．11～12月の冬期間は 1^+ において再び双翅目幼虫の占める割合が大きくなるが，特に 0^+ では落下昆虫が胃内に見られなくなると共に底層に生息する毛翅目幼虫の占める割合が増える．

湖内での食性

然別湖でのイワナの食性はすでに羽田・富田（1949）によって詳しく調べられている．これによればイワナの食物の 100 %近くが小型のプランクトンである．しかしながら最近オショロコマの餌となると考えられるワカサギ等の移殖があるので，今回はそれ以後の食性の変化をみるという目的も含めて調査した．しかし刺し網によって捕獲した標本を用いたので空胃のものが多く，調べた個体数も多くはないので，ただ傾向として述べるにとどめる．Table 1 に7月，10月の空胃のものを除いて，その餌生物の出現頻度を示す．これによれば動物プランクトン（*Bosmina spp.*, *Daphnia cucullata*）が両月にわたって食物の50～70%を占めている．しかし落下昆虫もほぼ同じ割合を占めており，ワカサギも10%以上を占めている．これらから湖内での食性は依然としてプランクトンが主要な餌生物になっていると考えられるが，昆虫や魚類（ワカサギ）に依存する割合の増加をも示している．特に湖内で魚食が始まったのはワカサギ導入後の近年の出来事であると考えられ，注目される．

考察と結論

以上の結果を総合して，Васнецов（1946）の発育段階（ЭТАП）に従って生活の変化に重点をおきながら整理すれば次の通りである．

ふ化直後の A_1 期は，遊泳能力がきわめて弱く，産卵床の中で静止していると考えられる．しかし A_2～B_1 期には大きな卵黄をもちながも鰭の分化が進み，運動力も活発となる．このころまでは外部の餌をとることはない

Table 1. Stomach contents of chars captured in Lake Shikaribetsu shown by percent occurrence in feeding fish.

	July (19 exam.)		October (7 exam.)	
	Incidence of Feeding	percent Occurrence	Incidence of Feeding	Percent Occurrence
Fish	3	15.7	1	14.2
Bosmina	6	31.5	4	57.1
Daphnia	8	42.1	0	0
Insects	12	63.1	4	57.1

が，周囲の石の下や枯葉の下等に移動を開始する．これらのことから A_1 期と A_2～B_1 期は生活上異質な側面を有しており，異なった発育段階に区分するのが妥当であろう．一方，卵黄から栄養をとる A_1 期，A_2～B_1 期に対して，B_2 期では卵黄をもちながらも消化管が基本的に完成し，食物を外部に求めるようになる．特にこの時期は尾鰭の形状の変化（丸型一角型）が伴っており，運動力は一層活発になるであろう．食物もすでに流下昆虫に求めており，このような運動力の増加は必要欠くべからざることと考えられる．C_1 期においてこのような特徴は一層整備される．このように B_2～C_1 期は A_2～B_1 期と明瞭に質的に異なった内容を含んでおり，独立した発育段階であろうと考えられる．

C_1 期は C_2 期と外見上きわめてよく類似しているにもかかわらず，前者は頭長比，体高比および胸鰭長比が最低となると共に，自家栄養から他家栄養への移行という，生態上過渡的で危険な発育期であるとみなされる．しかし C_2 期に入れば運動力はさらに一層増大し，餌生物をめぐる個体間の社会関係が顕著になる．D_1 期ではこの傾向が増大し，分散が種内の社会関係によって促進され，徐々にその生息範囲を拡大する．このように B_2～C_1 期，C_2～D_1 期は種内の個体間の「あり方」という意味で質的に相違していると共に，形態的にも飛躍が認められることから，明瞭に区別される独立した発育段階とすることが妥当である．

一方，D_2 期は鱗が全体に広がると共に側線器などの感覚器官が完成し，鰭条の分岐が一層発達することによって，相対的に大きな淵へと分散を始める．D_1 期までの種内関係が主に 0^+ 令同士の関係にあるとすれば，D_2 期以後は 1^+ 令以上の個体との関係が成立し，社会関係は一層複雑になると言える．このことは E_1 期と共に河川内移動や降湖移動による生息場所の多様化と関係していると考えられる．しかも越冬のためと考えられる降湖移動の集団のほとんどが D_1～E_1 期で占められているのである．久保（1967）はオショロコマが一般的にとる生活史の中で smolt への変態には広い水界での生活が必要であろうと述べているが，この時期の研究はきわめて少ない（Armstrong, 1970；Armstrong & Morton, 1969）．然別湖産イワナに限って言えばこの発育段階は，生息場所の変化やそれに伴う食性等の生態の移行期的な性格をもっていると考えることができる．

区別された E_{2S} 期がどの発育段階に属するか依然として検討の余地を残しているが，完全に湖中生活に入る前の準備の時期と考えられる．しかも一方で，この段階で残留型（E_{2R} 期）が顕著に見分けられるようになる．残留型は発育的には E_1 期の諸特徴を備えたままで成熟する（続報）．したがって E_{2S} 期がいわば降湖型へと発展してゆくのに対し，E_{2R} 期は河川型へと発展してゆくという分岐点に相当する．

E_{3S} 期以後はほぼすべて湖中で生活するが，生長はほぼこの段階で止まり，成熟期（F期）に入る．E_{3S} 期の諸特徴は久保（1974）のサクラマスの観察による pre-smolt の様相にきわめて類似するが，E_{3S} 期と E_{4S} 期の関係は今後の課題としてさらに詳しい研究が必要である．

したがって，E_{2S} 期以後の詳細な検討を残しながらも，然別湖のイワナの発育過程を A_1，A_2～B_1，B_2～C_1，C_2～D_1，D_2～E_1（残留型では D_2～E_{2R}），E_{2S}～E_{3S}（E_{4S}），F（残留型では E_{3R}～）の7段階に区切ることが，現段階で一応可能であると考えられる．

石城[2)] は河川型オショロコマの段階区分に際し，6段階に区分している．石城の段階区分は検討の余地を残しているけれども，注目すべき点は河川型が然別湖でみられる E_{3S} 期を経過することなく成熟段階に入ることである．これらはオショロコマの各型の生長と発育の比較を行なう続報で総合的に考察を加えたい．

摘　要

然別湖産イワナの生活史とその特徴を知る目的で，1971年4月から1975年3月まで，発育過程，食性および降湖移動を調べた．

1）然別湖産イワナの個体発生の過程を，主に形態学的側面から鑑別的に A_1，A_2，B_1，B_2，C_1，C_2，D_1，D_2，E_1，E_{2S}，E_{3S}，E_{4S}（残留型では E_{2R}，E_{3R}），F に区分し，それらをそれぞれの生活様式の諸特性（特に生息場所や個体間関係）と対応させることによって，A_1，A_2～B_1，B_2～C_1，C_2～D_1，D_2～E_1（残留型では D_2～E_{2R}），E_{2S}～E_{3S}（～E_{4S}），F（残留型では E_{3R}）の7段階に区分した．

2）B_2 期から D_1 期までの食性を調べ，発育初期から流下昆虫にきわめて強く依存していることが明らかになった．さらに発育が進むにつれて餌生物の種類が多様化する傾向が認められた．D_2 期以降も基本的に流下昆虫に強く依存する傾向が認められた．

3）湖内で採集されたイワナ（E_{2S}～E_{3S}（E_{4S}）期）の食性は魚類相が多様化している現在でもきわめて高率（50%以上）にプランクトン（*Bosmina, Daphnia*）を捕食しているが，魚類（ワカサギ）を捕食する傾向が強くなっていることが明らかとなった．

4）本イワナの降湖移動を調べた結果，二つの時期に降湖することが明らかになった．一つは E_{2S}～E_{3S} 期の様相を示す6～7月を中心に降湖するグループ，一つは

D_2 期（まれに C_1 期）から E_1 期の様相を示す10月をピークとする大きなグループであった．後者の構成はさらに体長と令から二つのグループに分けられた．一つは体長 6〜7cm（令 0^+），一つは体長 8〜10 cm（令 1^+〜2^+）をモードとするグループであった．

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謹呈

Reprinted from
Japanese Journal of Ichthyology

Vol. 25, No. 1 : 9–18, figs. 1–7. June 26, 1978

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Koji Maekawa

Pyloric caeca = 30

Japanese Journal of Ichthyology
Vol. 25, No. 1 1978

魚 類 学 雑 誌
25巻1号 1978年

Growth and Development of *Salvelinus malma miyabei* Compared with Other Forms of *S. malma*

Koji Maekawa

(Received November 7, 1977)

Abstract Three forms of the Dolly Varden, *Salvelinus malma*, land-locked form (Miyabe char), river-resident form and sea-run form, were examined with special reference to their growth and development. The growth rate of the Miyabe char was closely similar in early stages of growth to that of the river-resident form, but a remarkable difference of body size appeared from two years of age, when the former descended into the lake and grew rapidly thereafter. The Miyabe char attained maturity at a later and more advanced growth stage than the river-resident form. The most striking difference was that a remarkable inflection corresponding to the fork length of the smolt was recognized in the relative growth line of the sea-run form, but the Miyabe char and river-resident form did not show this inflection in the growth line. The Miyabe char, therefore, might have more neotenous body form and size in relation to its precocity than the anadromous one. The process of land-locking and the subsequent evolution of the Miyabe char might be similar to that of kokanee, *Oncorhynchus nerka*, land-locked in lakes.

In a previous paper (Maekawa, 1977a), some divisions in the developmental stages, especially those in the juvenile stage of the Miyabe char, *Salvelinus malma miyabei* Oshima, a land-locked form in Lake Shikaribetsu in Hokkaido, Japan, were made with special reference to the early life history. A comparison of development and growth between the Miyabe char and other forms of the Dolly Varden, *S. malma* (Walbaum), such as the residual and anadromous forms is important. It is necessary to acount for the relationship between them, since land-locked processes or differentiation of the Salmonidae and closely related species have been discussed in relation to their precocity by many previous authors (Ohno, 1938; Ricker, 1938, 1940; Azuma, 1973; Kubo, 1974; Utoh, 1976, 1977). No such reports, however, have been made on the Miyabe char, except for preliminary reports by Kubo (1967) and Kimura (1976).

This paper describes the development and growth of the Miyabe char in comparison with some other prominent forms of the Dolly Varden.

Material and methods

The materials examined in the present investigation were collected from the following districts from 1970 to 1974. The Miyabe char were collected from Lake Shikaribetsu of the Tokachi River system and the Yambetsu and Kohan Rivers, flowing into the lake. The river-resident forms were collected from the upper reaches of the Nuppun-Tomuraushi River of the Tokachi River system, the Tokoro River, and the Nishitappu River of the Ishikari River system. The anadromous forms were collected in Alaska from the Eagle and Switzer Rivers, a lake (name unknown), the sea surrounding Juneau, and the Sea of Okhotsk. The name of each form is abbreviated as follows.

Lake-run form of the Miyabe char: L-form
River-resident form of the Miyabe char: LR-form
River-resident form of the Dolly Varden in the Nuppun-Tomuraushi River: RNu-form
River-resident form of the Dolly Varden in the Nishitappu River: RN-form
River-resident form of the Dolly Varden in the Tokoro River: RT-form
Sea-run form of the Dolly Varden: S-form

All of the Miyabe char from the Kohan River were resident-form, land-locked by a concrete dam. Data on the body length of the Miyabe char from Lake Shikaribetsu was obtained from a report by the Hokkaido Fish Hatchery, to compute the relation between body and fork lengths. It was $y=0.93x+0.03$ (y: body length, x: fork length). The following dimensions of the body were measured: fork length, head length, body depth, pectoral fin length, maxillary length, and eye diameter.

In order to compute the relative size of the body parts of the sea-run form, river-resident forms, and the Miyabe char, specimens collected during summer (June, July, and August) were used, to exclude seasonal variation, except for the LR-form which was collected throughout the seasons. A log-log was made of the fork length on the x axis and body part length on the y axis. When inflections were thought to occur, an equation, $\log y=k \log x+\log b$, of each straight-line was

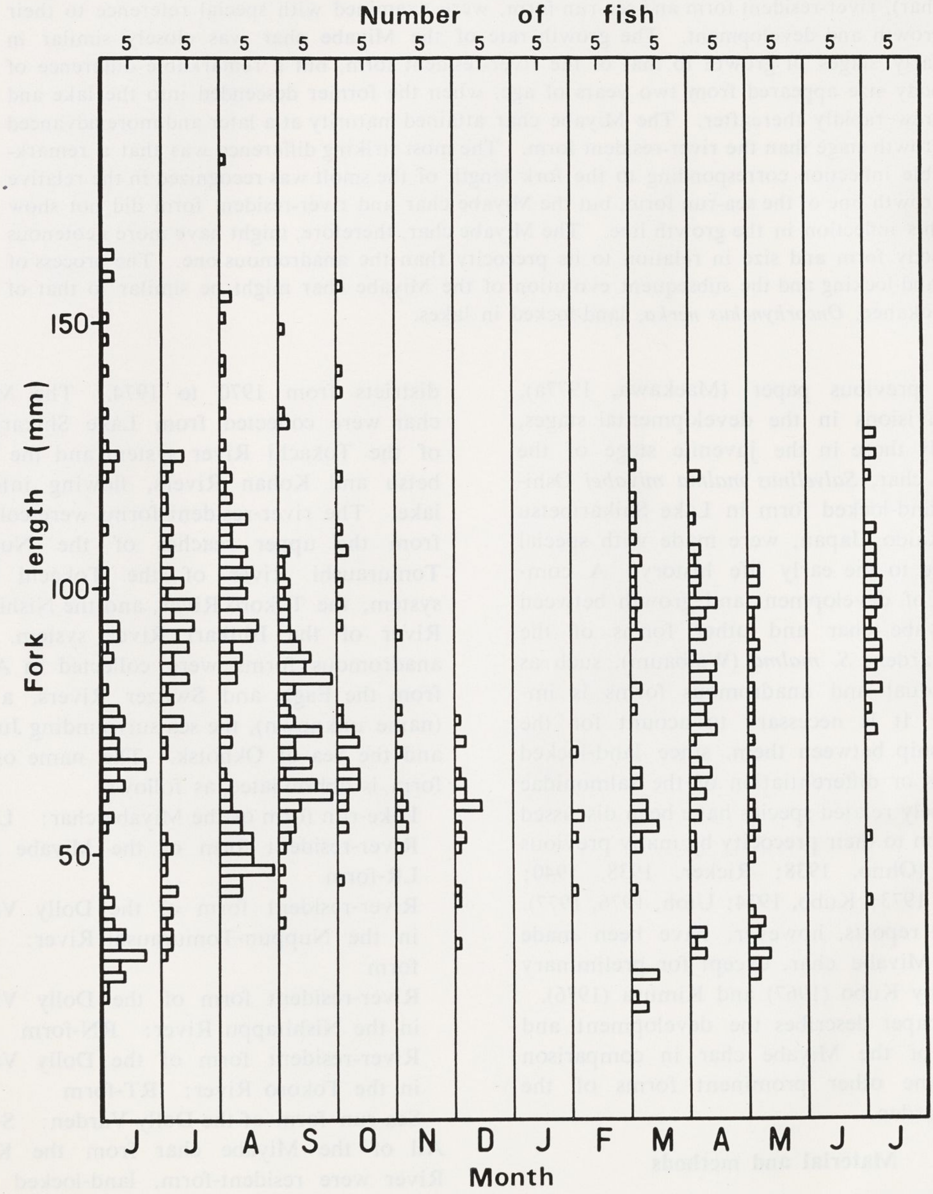

Fig. 1. Monthly length-composition of Miyabe char collected by hand and cast nets at the Yambetsu River in 1971~1972.

computed at the estimated point of the inflection. The statistical significance of the lines was examined (Kondo, 1964) and a possible intersecting point was calculated from the equations.

Otoliths were used for age determination (Grainger, 1953; Heiser, 1966). However, it could not be used for the S-form because they were strongly decalcified from storage in 10% formalin for 1 year or less.

Results

Comparison of growth and body forms of three forms of the Dolly Varden. Comparisons of growth and body forms should be made at the same developmental stage, but there were not sufficient specimens from each locality, except for those from Lake Shikaribetsu, Hokkaido. In considering the developmental stage, the growth aspect of the fork length will be described first in order to compare the S-form, RNu-form, L-form and LR-form.

A) Growth aspect to fork length: The fork length distribution of the Miyabe char collected from the mouth to the middle reaches of the Yambetsu River in 1971～1972 is shown in Fig. 1. The growth trend of individuals of the first year, presumed by the mode and mean of the fork length, showed rapid growth from June (32 mm in fork length in average) to August or September (65 mm in average), and almost no growth occurred after October and during the winter. The larger groups of the fork length distribution in June (Fig. 1) were assemblages of one- and two-year-old individuals, and were assumed to grow to 80～100 mm in fork length in late summer (Maekawa, 1977a).

Histograms (Fig. 2) show the size and age frequency of samples from Lake Shikaribetsu in June, July, August and October. Monthly variation in the age-determined groups of July and October and the mode of the smallest group of fork length indicate that the smallest fish grew rapidly from July to August. Two groups were recognized in the fork length distributions for the two-year-old individuals in October, the smaller one with an average length of 130 mm, which could be fall migrants (Maekawa, 1977a). The histograms of October also indicate that the fork lengths overlapped extensively among individuals older than three years of age.

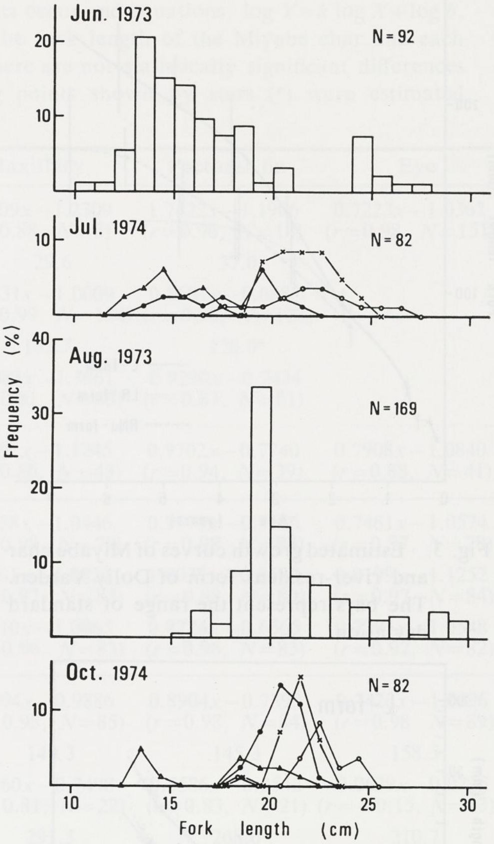

Fig. 2. Monthly length- and age-frequencies of Miyabe char collected by gill nets in Lake Shikaribetsu. Six- and seven-year-old individuals, two samples in July and four in October, 1974, are excluded from the figures shown by age frequency. Symbols indicate as follows: △—△: 2 years old, ●—●: 3 years old, ×—×: 4 years old, ○—○: 5 years old.

Fig. 3 shows the growth curve of the fork length of the L-form, LR-form and RNu-form. The LR-form in a group of fish is differentiated from the Phase E_2 of the developmental stages of the Miyabe char (Maekawa, 1977a). The growth curve of the LR-form was very slack and the size of five-year-old individuals of this type was smaller than that of other forms. The growth curve of the RNu-form could closely resemble that of the L-form in the early stage of growth, since there was no significant difference in

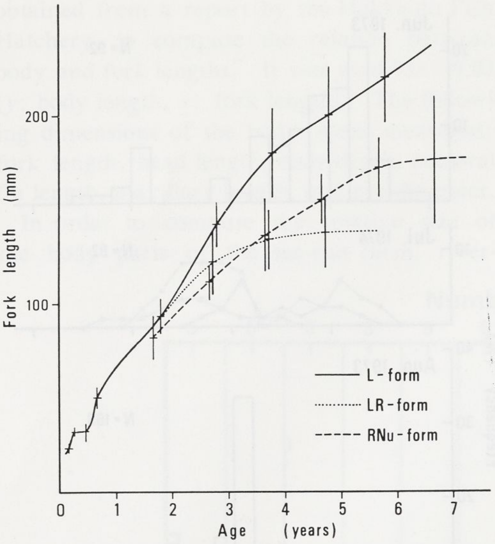

Fig. 3. Estimated growth curves of Miyabe char and river-resident form of Dolly Varden. The bars represent the range of standard deviation.

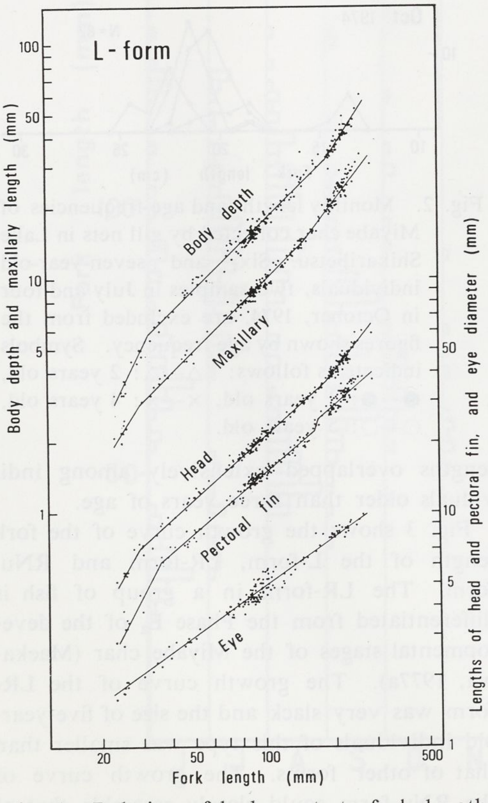

Fig. 4. Relation of body parts to fork length in lake-run form (L-form) of Miyabe char.

the size of one-year-old individuals between the RNu- and L-forms, though the author did not have samples for the first year of life of the RNu-form. The curve of the RNu-form, however, became retarded at the later stages, two years after hatching.

B) Relative growth of body form: The relative growth patterns of the head, body depth, maxillary, pectoral fin and eye to fork length were compared among all forms examined in this study.

The L-form showed two inflections in the relative-growth curves of the head length, body depth, maxillary length, and pectoral fin length but not in the eye diameter (Fig. 4). The first inflection clearly appeared at 29.4～37.0 mm in fork length, and the second at about 130～180 mm. The body, head and maxillary growth ratios showed a remarkable tachyauxesis up to the points of the first inflection, and bradyauxesis between the first and the second, and tachyauxesis again thereafter (Table 1). There is no significant difference in the relative growth coefficient between K_2 and K_3 of the pectoral fin. However, a possible intersecting point of the second inflection of the pectoral fin was estimated from visual observation, not from the equations, since it could be clearly recognized from the line. The inflection of the LR-form was not clear in the growth curve of all the body parts, but individual variation was larger than that of the other forms. This might be due to seasonal or sexual variations.

In the case of the S-form (Fig. 5), however, the relative-growth curves of the dimensions showed more complex patterns, which had clearly two inflections. The possible inflection could have appeared at about 30 mm in fork length as in the L-form, but since only a few samples less than 35 mm in fork length were used, these influections could not be estimated. The growth ratios which showed remarkable bradyauxesis after the first inflections were found in the maxillary, eye and pectoral fin growth. This inflection, however, was somewhat unclear in the body depth and head. Possible intersecting points were observed from about 145.0 to 160.0 mm in fork length. In the eye, the relative growth coefficient of K_2 could be near zero, indicating

Table 1. Fork length at which growth inflection points occur and equations, $\log Y = k \log X + \log b$, of the relative growth curve in body parts to the fork length of the Miyabe char and each form of the Dolly Varden. x denotes $\log X$. There are not statistically significant differences in the coefficients between $*1$. The intersecting points shown by stars (*) were estimated from visual observations.

		Body depth	Head	Maxillary	Pectoral fin	Eye
L-form	K_1	$2.0255x-1.2695$ $(r=0.94,\ N=12)$	$1.5581x-0.8736$ $(r=0.96,\ N=12)$	$1.4709x-1.2309$ $(r=0.88,\ N=8)$	$1.7422x-1.1906$ $(r=0.96,\ N=14)$	$0.7223x-1.0362$ $(r=0.98,\ N=151)$
	1st inflect.	32.1	29.4	29.6	37.0	
	K_2	$0.9869x-0.7426$ $(r=0.98,\ N=132)$	$0.8917x-0.5615$ $(r=0.99,\ N=156)$	$0.9831x-1.0009$ $(r=0.99,\ N=134)$	$0.8607x-0.6887$ $(r=0.98,\ N=123)$	
	2nd inflect.	184.0	182.5	132.7	170.0*	
	K_3	$1.4010x-1.2666$ $(r=0.90,\ N=49)$	$1.1323x-0.8651$ $(r=0.86,\ N=48)$	$1.3083x-1.3661$ $(r=0.81,\ N=65)$	$0.9290x-0.7434$ $(r=0.83,\ N=61)$	
	LR-form	$1.4548x-1.2202$ $(r=0.86,\ N=43)$	$0.8358x-0.4906$ $(r=0.90,\ N=43)$	$1.1491x-1.1245$ $(r=0.86,\ N=43)$	$0.9702x-0.7740$ $(r=0.94,\ N=39)$	$0.7908x-1.0840$ $(r=0.88,\ N=41)$
R-form	RT-form	$1.0964x-0.8273$ $(r=0.99,\ N=85)$	$0.8808x-0.5477$ $(r=0.99,\ N=85)$	$1.0428x-1.0446$ $(r=0.98,\ N=79)$	$0.9379x-0.7646$ $(r=0.98,\ N=83)$	$0.7461x-1.0574$ $(r=0.97,\ N=78)$
	RN-form	$0.9925x-0.7164$ $(r=0.97,\ N=82)$	$0.9561x-0.5964$ $(r=0.99,\ N=81)$	$1.1261x-1.0822$ $(r=0.97,\ N=83)$	$1.0037x-0.8183$ $(r=0.98,\ N=80)$	$0.8199x-1.1252$ $(r=0.97,\ N=84)$
	RNu-form	$1.1442x-0.8823$ $(r=0.98,\ N=83)$	$0.8816x-0.5526$ $(r=0.98,\ N=83)$	$1.1010x-1.0865$ $(r=0.96,\ N=83)$	$0.8224x-0.6565$ $(r=0.96,\ N=83)$	$0.7203x-1.0548$ $(r=0.92,\ N=82)$
S-form	K_1	$1.0369x-0.7893$ $(r=0.98,\ N=91)$	$0.8892x-0.5540^{*1}$ $(r=0.99,\ N=87)$	$0.9994x-0.9886$ $(r=0.98,\ N=85)$	$0.8904x-0.7399$ $(r=0.98,\ N=84)$	$0.7420x-1.0396$ $(r=0.98,\ N=89)$
	1st inflect.	—	—	149.3	145.3	158.5
	K_2	—	$0.8726x-0.5445^{*1}$ $(r=0.90,\ N=21)$	$0.7960x-0.7498$ $(r=0.81,\ N=22)$	$0.5586x-0.3542$ $(r=0.83,\ N=21)$	$-0.0639x-0.0725$ $(r=-0.15,\ N=13)$
	2nd infiect.	225.0*	357.1	291.5	268.0	210.7
	K_3	$1.0946x-0.8106$ $(r=0.95,\ N=26)$	$1.3860x-1.3417$ $(r=0.97,\ N=10)$	$1.6219x-1.9594$ $(r=0.97,\ N=10)$	$1.3477x-1.4811$ $(r=0.96,\ N=10)$	$0.5098x-0.8319$ $(r=0.89,\ N=14)$

no growth between the first and next inflections. The second inflection occurred in all of the body parts examined, when the fish attained 200～350 mm in fork length, and their growth ratios showed tachyauxesis thereafter, though the intersecting points of the body depth were estimated from visual observation, not from the equations. In contrast with these two forms, all of the river-resident forms did not show remarkable inflections in the relative-growth curve of all the body parts examined.

Between k_2 in the L-form and k_1 in the S-form, the relative growth coefficient showed no significant differences in all the body parts examined. No significant differences were recognized in k between the RT-form and RNu-form, but there were significant differences in k of the body parts examined between the RT-form and RN-form ($P < 0.05$). Significant differences also existed between the RN-form and RNu-form in all the body parts examined except the maxillary. Comparing k_2 of the L-form and k of the RNu-form, there was no significant difference in each body part, except for the body depth. However, no difference was recognized in the body depth between L-form and RT- or RN-forms. The most striking difference between the S-form and the other forms was that the S-form has a lower growth ratio in the maxillary, pectoral fin, and eye after the first inflection, and a greater ratio in the maxillary, pectoral fin, and eye after the second inflection.

Fork length, sex ratio, and age at maturity of the Miyabe char. The fork length and age and sex ratios at maturity of both the L- and LR-forms are shown in Fig. 7. All of the L-form were over 180 mm in fork length, but there was no such great length in the

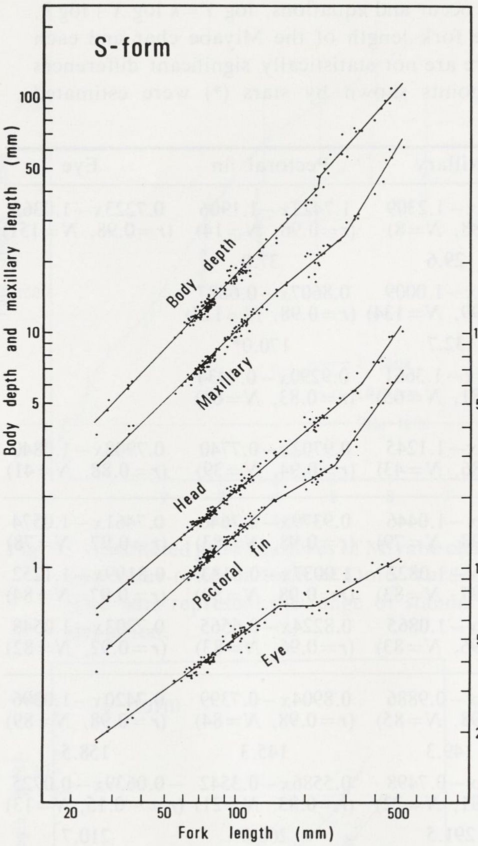

Fig. 5. Relation of body parts to fork length in sea-run form (S-form) of Dolly Varden.

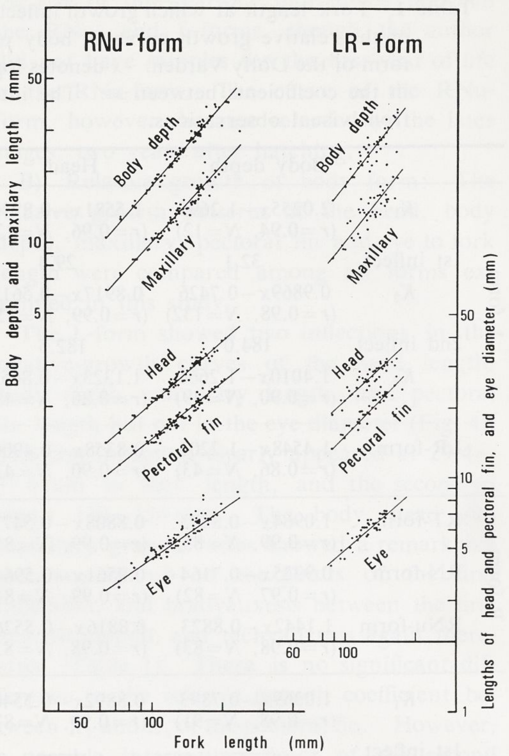

Fig. 6. Relation of body parts to fork length in river-resident form of Miyabe char (LR-form) and river-resident form of Dolly Varden (RNu-form).

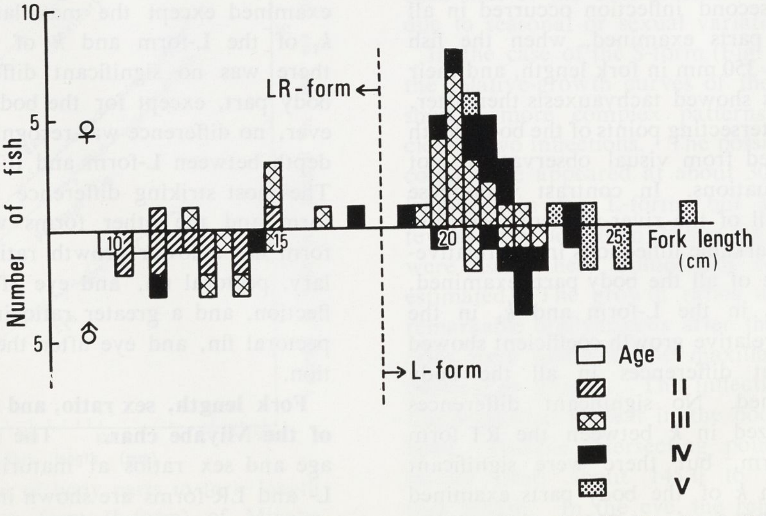

Fig. 7. Size and age compositions of mature Miyabe char collected in the Yambetsu River and the Kohan River.

LR-form. The minimum size of the latter was 95.0 mm in fork length. Therefore, a distinct difference in the fork length at maturity was recognized between the two forms.

The male to female ratio was about 1:2 in the L-form and about 3:1 in the LR-form.

The population sample of the L-form consisted of individuals of age groups of three to five, and those of three (40%) and four (37%) years were predominant. A few samples were seven years old or more with a fork length of 30～35 cm. On the other hand, individuals belonging to the LR-form were younger than those of the L-form, and consisted at age groups of one to four years old, with a mode at two years for male and three years for females.

Discussion

The shape of a fish is modified by different rates of growth, acceleration or retardation and development in various body parts (Hubbs, 1926). In the present study, the growth rate of the Miyabe char (L-form) was similar in the early stage of growth to that of the river-resident form, but the remarkable difference appeared from two years of age, when the former migrated into the lake and grew rapidly thereafter. Heiser (1966), who investigated the age and growth of anadromous Dolly Varden, showed that this char exhibited a slow growth rate before the stage of two or three years of age and a very rapid growth rate after the stage of migration into the sea. Blackett (1968, 1973) and Armstrong and Winslow (1968) studied the fecundity of the resident and anadromous Dolly Varden in southeastern Alaska and reported that the resident char matured sexually a year or more earlier and at a smaller size than did the migratory char (from 5 or 6 years of age). Ishigaki (1969) found that the river-resident form of the Dolly Varden in Hokkaido reached maturity at one year of age, 12 cm in fork length, based on the reading of circuli of scales, but Komiyama (1978), on the basis of the examination of otolith, reported recently that the river-resident form matured from two years of age. The lake-run form of the Miyabe char matured from three years of age at about 180 mm in fork length, while the river-resident form of the Miyabe char matured in one year at 95 mm in fork length. Of the forms of *S. malma* examined, therefore, the greatest retardation of growth and acceleration of maturity were in the river-resident form of the Miyabe char, while in the lake-run form of the Miyabe char muturity was attained at a later and more advanced stage of growth than in the river-resident form of the Dolly Varden, and in the anadromous char in Alaska at the most advanced stage. Therefore, the stage of divergence in the relative body size might be connected with the age of sexual maturity, although the Alaskan forms cannot be compared with Asian races since there is no report on their accurate age of maturity determined by means of otoliths.

Martin (1949) studied the growth rates of many fishes and showed that inflections occurred at the hatching stage, some stages of metamorphosis, ossification, and sexual maturity. He also pointed out that differences in the relative sizes of body parts between fish of the same species were the results of changes in the time of inflections, not in the gradient of the relative growth curves. Many other authors have also investigated growth inflections of fish and have discussed the mechanism of the inflection (cf. Amaoka, 1964). In this study, the relative-growth pattern of each form of the Dolly Varden seemed to be closely similar to that of the brook trout, *S. fontinalis*, from small brooks, from larger bodies of water and of sea-run stocks, which were compared by Wilder (1952). The first inflection observed in the head, body depth, and maxillary occurred at about 30 mm in fork length and corresponded well with the distinguishing point between the phases C_1 and C_2 of development (Maekawa, 1977a). This inflection may probably occur in the growth line in each body part of sea-run form and also river-resident form.

One of the characteristic inflections appeared in the sea-run form between 140 and 160 mm in fork length, though it was not clear in the other forms. The growth ratios showed a remarkable bradyauxesis from this inflection to the next. This may be due to a more rapid growth rate of fork length after the migration into the sea (Heiser, 1966). Therefore, differences in the relative size of body parts between these three forms become clear after this inflection.

Second inflections of some dimensions in the lake-run form of the Miyabe char and the sea-run form of the Dolly Varden occurred in the area of sexual maturity, though they were somewhat unclear in the river-resident form in Hokkaido. From these considerations as mentioned above, it can be concluded that differences in the relative sizes of body parts among the three forms are results of changes in the timing or the number of times of the inflections, as was pointed out by Martin (1949).

Here, it is interesting to note that the inflection of fork length, which appeared at about 150 mm in fork length in the sea-run form, almost coincided with that of smolts (Armstrong, 1970). The author suggested in an earlier paper (1977a) that the Miyabe char might grow to sexual maturity without transformation to a complete smolt, or if they were transformed, such individuals might be very few. The work of Kubo (1967) is very interesting in that smolt transformation did not occur in the Miyabe char when cultured in a pond under usual conditions, but some juveniles transformed into silvery smolts in the third spring of their life when reared under blue light. This occurrence of smolts suggests that the silvery colour of the Miyabe char could be due to a change in the quality of ambient light or by other unknown factors after the fish migrates into the lake during their young stage (Maekawa, 1977a). This change to smolt did not appear or appeared very seldom in the resident form of the Dolly Varden in Hokkaido (Ishigaki, 1969; Maekawa, 1973). Individuals of the Dolly Varden living in lakes dammed artificially change to a silvery body colour, but they retain juvenile characteristics, such as a reduced lower jaw, even in an adult (Maekawa, in preparation). Therefore, it is supposed that most of the Miyabe char, as in the river-resident form of the Dolly Varden, continu~~i~~es to grow without changing to a complete smolt, in contrast with the anadromous form, since the inflection corresponding to the fork length of smolt in the sea-run form does not occur in the relative growth line for the lake-run form of the Miyabe char. As a result, most of the Miyabe char might retain a juvenile body form even as an adult.

The most striking characteristics of the lake-run form of the Miyabe char are, as in the river-resident form, those remarkable parr marks which appear at maturity. A large number of the lake-run and river-resident Miyabe char live to spawn more than twice (Maekawa, in preperation), in contrast with the sea-run form of the Dolly Varden (Armstrong, personal communication). On the other hand, the Miyabe char resembles the anadromous form of the Dolly Varden in some characteristics, i.e. both forms produce river-resident form and have such morphological characteristics as a prolonged lower jaw and relatively large red spots on the body in contrast to the reduced jaw and small red spots of the river-resident form. In other words, the Miyabe char has intermediate characteristics between the anadromous and resident forms of the Dolly Varden and is more precocious and has more neotenous characteristics than the anadromous Dolly Varden. Therefore, the relation between the Miyabe char and the anadromous Dolly Varden might correspond well with that between the land-locked kokanee and the anadromous sockeye, *Oncorhychus nerka* (Ricker, 1938).

Kubo (1967) presumed from ecological and physiological studies that the Miyabe char might be a stock of typical anadromous *Salvelinus malma*. As mentioned above, however, the Miyabe char slightly differs from the anadromous form and/or river-resident form, and differs also in the hemoglobin pattern (Yoshiyasu, 1973) and in the number of gill rakers (Maekawa, 1977b).

It is interesting to note that Ricker (1940) thought that the process of the evolution of the kokanee consisted of two stages of growth: (a) the occurrence of residual or lake-type offspring among the progeny of the anadromous stock; (b) the modification of the progeny of such residuals into the typical kokanee. He postulated that the relation between growth and development in the first stage and natural selection in the second stage played an important role. The process of evolution of the Miyabe char in relation to land-locking mechanism might be similar to that of the kokanee, as described by Ricker.

Acknowledgments

I wish to express my hearty thanks to Prof. Hans Mori, Ass. Prof. Hisashi Abe, and Ass. Prof. Kenkichi Ishigaki of the Faculty of Agriculture of Hokkaido Universiy, for their valuable advice during the course of this work and for the critical reading of the manuscript, and also to Prof. John M. Dean, University of South Carolina, for the critical reading of the manuscript. It is also a pleasure to thank Mr. Robert H. Armstrong of Alaska department of Fish and Game, and the staff of the Hokkaido Fish Hatchery and of the North Pacific Resources Division for the supply of materials. Dr. Toru Nakata provided advice in computer programming. I am greatful to Prof. Fumio Nakane, Mr. Noriyuki Ohtaishi, Mr. Noboru Hachiya, and Miss Junko Tarazaki of the Faculty of Dental Medicine of Hokkaido University for their various assistance. This work is part of a dissertation submitted to the Faculty of the Graduate School of Agriculture, Hokkaido University, in partial fulfillment of the requirements for the degree of doctor of agriculture.

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然別湖産イワナおよびオショロコマの降海型，河川残留型の生長と発育

前川　光司

然別湖産イワナ，オショロコマの降海型と河川残留型の生長と発育を比較した．然別湖産イワナの稚魚期の生長率はオショロコマ河川残留型によく似ているが，前者は湖に降りる 2^+ から生長率がより高まり，その結果両者の体の大きさは顕著に違ってくる．然別湖産イワナはオショロコマ河川残留型よりも一層生長が進んでから性成熟に達する．体各部の相対生長曲線を比較すると，これら三型の最も大きな違いは，オショロコマの降海型にスモルトの尾叉長と一致するところに顕著な変曲点があるが，その他の型ではこれが明瞭でないことである．それ故，然別湖産イワナはオショロコマの降海型よりも幼形的な体形や体の大きさをもっており，これは前者が後者よりも早熟であることと関係していると考えられる．然別湖産イワナの陸封化が kokanee のそれと対応していることを論議した．

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INTERNATIONAL SYMPOSIUM ON ARCTIC CHARR

Winnipeg, Manitoba
May 4-7, 1981

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April 8, 1981

Dr. R. Behnke
Department of Fishery & Wildlife Biology
Colorado State University
FORT COLLINS, Colorado
U.S.A. 85023

Dear Dr. Behnke:

In response to your letter of March 31, 1981 we are pleased to be able to provide private accommodation for you at the home of Mr. and Mrs. Bert Van der Veen. Mr. Van der Veen, an electronics technician at the Freshwater Institute, resides at 619 Avila Avenue, a 10 minute walk from Symposium headquarters.

Should you not have already done so, could you please provide us with your travel itinerary so that we may have someone present to meet you at the airport and take you to Mr. Van der Veen's.

We sincerely hope that you will enjoy your stay in Winnipeg and look forward to meeting you.

Sincerely,

Dennis G Wright

Dennis G. Wright
Accommodations Chairman
International Symposium on Arctic Charr
Department of Fisheries and Oceans
Freshwater Institute
501 University Crescent
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cc: B. Van der Veen

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INTERNATIONAL SYMPOSIUM ON ARCTIC CHARR

PROGRAM

MAY 4 - 8, 1981

UNIVERSITY OF MANITOBA
WINNIPEG, MANITOBA
CANADA

SUNDAY

MAY 3, 1981

1800-2000 REGISTRATION Foyer, University College

MONDAY

MAY 4, 1981

0900-1800 REGISTRATION Foyer, University College

1100-1300 LUNCH, University Centre Cafeteria

1630-1900 FILMS Room 247 University College
NATIONAL FILM BOARD OF CANADA
Fishing at the Stone Weir I
Fishing at the Stone Weir II
Jigging for Lake Trout
At the Winter Sea-Ice Camp I
(These are classic films of traditional Inuit (Eskimo) methods of fishing for charr and lake trout.)

1630-1800 DINNER, University Centre Cafeteria

1900-2000 MEETING OF SECTIONAL CHAIRMAN
Reception Lounge, Freshwater Institute

1930-2200 WINE AND CHEESE PARTY
Seminar Room, Freshwater Institute

MONDAY - FRIDAY

MAY 4-8, 1981

ALL PAPERS PRESENTED IN ROOM 240 UNIVERSITY COLLEGE

POSTER PAPERS

On Display in the Foyer, University College

ROBERT H. ARMSTRONG, UNITED STATES
Migration of anadromous Dolly Varden charr in southeastern Alaska: A manager's nightmare.

ERIC C. GYSELMAN, CANADA
The seasonal movements of anadromous arctic charr at Nauyuk Lake, Northwest Territories, Canada

CHARLOTTE KIPLING, ENGLAND
Age and growth of charr in Windermere

SYMPOSIUM OFFICE: ROOM 232 UNIVERSITY COLLEGE

TUESDAY A.M.

MAY 5, 1981

0730-0900	BREAKFAST, University Centre Cafeteria
0900-1000	REGISTRATION
0900-0930	**OFFICIAL GREETINGS** DR. L. JOHNSON, Symposium Governor DR. H. LAWLER, Regional Director-General, Department of Fisheries and Oceans, Winnipeg DR. R. CAMPBELL, President, University of Manitoba, Winnipeg
	TAXONOMY I Chair: CHARLOTTE KIPLING, ENGLAND
0930-1000	ROBERT J. BEHNKE, UNITED STATES OF AMERICA Organizing the diversity of the arctic charr complex.
1000-1020	LENNART NYMAN, SWEDEN Management of allopatric and sympatric populations of landlocked arctic charr of Scandinavia.
1020-1040	COFFEE
1040-1100	JOHAN HAMMAR, SWEDEN Ecological characters of different combinations of sympatric populations of arctic charr in Sweden.
1100-1120	ANDERS KLEMETSEN, NORWAY The arctic charr speciation problem as seen from Northern Norway.
1120-1140	PETER NILSEN and ANDERS KLEMETSEN, NORWAY Anadromous, resident and landlocked arctic charr of the coast of Finnmark, Northern Norway.
1140-1200	ROLF GYDEMO, SWEDEN Preliminary survey results in the distribution of the arctic charr species complex in Iceland.
1200-1230	GENERAL DISCUSSION
1230-1300	LUNCH, University Centre Cafeteria

TUESDAY P.M.

MAY 5, 1981

TAXONOMY II

Chair: RED CLARKE, CANADA

1400-1420	J. BRIAN DEMPSON, CANADA Identification of anadromous arctic charr stocks in coastal areas of northern Labrador.
1420-1440	PETER MCCART, CANADA Systematics of arctic charr in Beaufort Sea drainages, Mackenzie Delta, Canada to Colville River, Alaska.
1440-1500	TED M. CAVENDER, UNITED STATES OF AMERICA Karyotype of *Salvelinus malma* from the American Northwest.
1500-1520	COFFEE
1520-1540	MINEO SANEYOSHI and SHUNJI IZUTA, JAPAN Nucleolytic enzymes in white-spotted charr.
1540-1600	I. A. CHERESHNEV, U.S.S.R. Sympatric anadromous charrs of East Chukotka.
1600-1630	GENERAL DISCUSSION
1800-2230	RIVER-BOAT CRUISE, BUFFET AND CASH BAR Busses leave University College at 1730

WEDNESDAY A.M.

MAY 6, 1981

0730-0815	BREAKFAST, University Centre Cafeteria

HABITAT AND SPECIES INTERACTIONS

Chair: HIROYA KAWANABE, JAPAN

0830-0850	PETER CRAIG, CANADA Habitat use by arctic charr in Simpson Lagoon, Alaska.
0850-0910	HANS NORDENG, NORWAY Solution of the "Charr Problem" based on charr in Norway.
0910-0930	KJETIL HINDAR and BROR JONSSON, NORWAY Habitat utilization and feeding strategy in arctic charr from Vangsvatnet Lake, Norway.
0930-0950	BROR JONSSON and KJETIL HINDAR, NORWAY Reproductive strategy in arctic charr from Vangsvatnet Lake, Norway.
0950-1010	P. GROTNES, NORWAY Plasticity of population characteristics in arctic charr and the systematics of the arctic charr complex.
1010-1030	COFFEE
1030-1050	P.S. MAITLAND, R. GREER and G.F. FRIEND, SCOTLAND Status and biology of charr in Scotland.
1050-1110	EISHIGE KOMIYAMA, JAPAN Inter-relationships of breeding habits among *Salvelinus malma, S. leucomaenis* and *Oncorhynchus masu* in Hokkaido, Japan.
1110-1130	NOEL C. FRASER and GEOFF POWER, CANADA The interactive segregation of landlocked arctic charr from lake charr and brook charr in northern Quebec, Canada.
1130-1150	TOR G. HEGGBERGET, NORWAY Habitat selection and segregation of parr of arctic charr, brown trout and atlantic salmon in two streams in north Norway.
1150-1220	GENERAL DISCUSSION
1220-1300	LUNCH, University Centre Cafeteria

WEDNESDAY P.M.

MAY 6, 1981

LIFE HISTORY AND BIOENERGETICS

Chair: V. STEINER

1400-1430 EUGENE K. BALON, CANADA
Paedomorphosis in arctic charrs: Ontogenetic explanations of their invading ability and of the coexistence of sympatric forms.

1430-1450 KOJI MAEKAWA, JAPAN
Landlocked process and juvenilization of the Miyabe charr in Shikaribetsu Lake, Japan.

1450-1510 ASMUND WANDSVIK, NORWAY
Blood osmolality in migratory arctic charr kept in seawater during summer and fall.

1510-1530 COFFEE

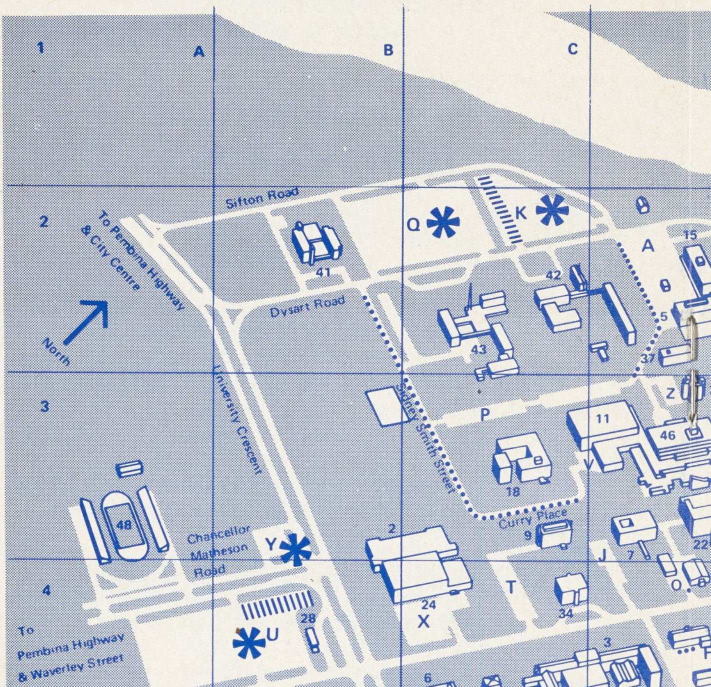
1530-1550 M.A. ALI, MARY ANNE KLYNE and GUDMUNDUR EINARSSON, CANADA
Adaptations ecophysiologiques de la retine chez l'omble chevalier.

1550-1610 WAYNE MACCALLUM and HENRY REGIER, CANADA
The biology and bioenergetics of arctic charr in Charr Lake, N.W.T., Canada.

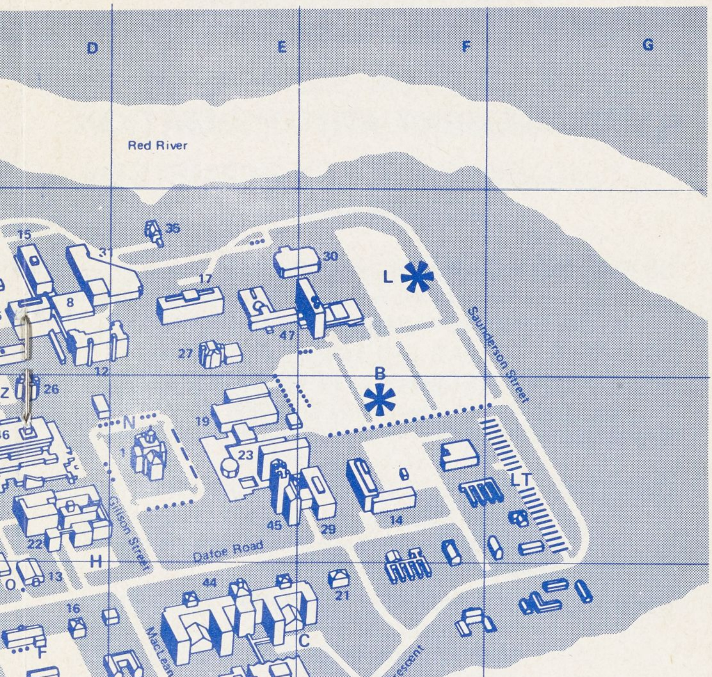
1610-1630 JEAN-DENIS DUTIL, CANADA
Energetic costs associated with the production of gonads in the anadromous arctic charr of Nauyuk Lake, N.W.T., Canada.

1630-1700 GENERAL DISCUSSION

1900-2200 BANQUET AND CASH BAR
University College



25. Freshwater Institute
46. University Centre
47. University College (Great Hall)
24. Frank Kennedy Physical Education Centre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Red River
To King's Park
Fort Richmond

THURSDAY A.M.

MAY 7, 1981

0730-0815 BREAKFAST, University Centre Cafeteria

MANAGEMENT AND UTILIZATION

Chair: ANDERS KLEMETSEN, NORWAY

0830-0900	PER AASS, NORWAY Management and utilization of arctic charr in Norwegian hydroelectric reservoirs.
0900-0920	TOMAS BRENNER, FEDERAL REPUBLIC OF GERMANY The introduction of the arctic charr in Nordrhein Westfalen (Federal Republic of Germany)
0920-0940	MAGNUS FURST and JOHAN HAMMAR, SWEDEN Effect of water level fluctuations on the recruitment of arctic charr.
0940-1000	ROLAND PECHLANER, AUSTRIA Dwarf populations of arctic charr in high-mountain lakes of the Alps resulting from under-exploitation.
1000-1020	JON KIRSTJANSSON, ICELAND The ecology and management of the arctic charr in Lake Myvatin, north Iceland.
1020-1040	COFFEE
1040-1100	R.W. MOSHENKO, R.F. PEET, D.H. DOWLER and L.W. DAHLKE, CANADA The arctic charr sport fishery at Tree River, Northwest Territories, Canada, 1964-78.
1100-1120	ALLAN H. KRISTOFFERSON, D.K. MCGOWAN and G.W. CARDER, CANADA Management of the commercial fishery for anadromous arctic charr in the Cambridge Bay area, N.W.T., Canada.
1120-1140	D.G. IREDALE, CANADA Commercial processing of charr in Canada's eastern Arctic.
1140-1200	JOHN W. JENSEN, NORWAY The selection of arctic charr by nylon gill nets.
1200-1230	GENERAL DISCUSSION
1230-1300	LUNCH, University Centre Cafeteria

THURSDAY P.M.

MAY 7, 1981

PARASITES, AQUACULTURE AND EUTHROPHICATION

Chair: HAROLD WELCH, CANADA

1400-1430 TERRY A. DICK, CANADA
Parasites and arctic charr management — academic curiosity or practical reality?

1430-1450 MARK A. CURTIS, CANADA
Diphyllobothrium spp. and arctic charr: Parasite aquisition and its effects on a lake-resident population.

1450-1510 GEOFF A. BLACK and M.W. LANKESTER, CANADA
Distribution and biology of swim-bladder nematodes in charr.

1510-1530 COFFEE

1530-1550 JURGEN HARTMANN, FEDERAL REPUBLIC OF GERMANY
The charrs of Lake Constance, a lake undergoing cultural eutrophication.

1550-1610 CHRISTIAN P. RUHLE, SWITZERLAND
Charr management in eutrophic Lake Zug, Switzerland.

1610-1630 GORAN MILBRINK and STAFFAN HOLMGREN, SWEDEN
Restoration of arctic charr populations in impounded lakes in Scandinavia by locally applied fertilization.

1630-1650 VOLKER STEINER, AUSTRIA
Experiments towards improved arctic charr culture.

1650-1720 GENERAL DISCUSSION

1900-2100 OPEN LECTURE — L. JOHNSON
Arctic lakes, thermodynamics and ecosystem structure.

FRIDAY A.M.

MAY 8, 1981

0730-0830 BREAKFAST, University Centre Cafeteria

CHARR AND MAN

Chair: PETER MAITLAND, SCOTLAND

0900-0930 LIONEL JOHNSON, CANADA
Charr and man: The philosophy of limited interaction.

0930-0950 CHARLOTTE KIPLING, ENGLAND
Charr fisheries in Windermere during the past four hundred years: Organization and management.

0950-1010 LAWRENCE LEDREW and J. BRIAN DEMPSON, CANADA
Historical development of the arctic charr fishery in northern Labrador.

1010-1030 COFFEE

1030-1050 PETER MAITLAND, SCOTLAND
Charr Watch.

1050-1145 OPEN FORUM

1145-1200 LIONEL JOHNSON, CANADA
Closing remarks by the convenor

1200-1300 LUNCH, University Centre Cafeteria

FRIDAY P.M.
- SATURDAY A.M.

MAY 8-9, 1981

DEPARTURE OF FIELD TRIPS TO:

Experimental Lakes Area

Duck Mountains Field Station

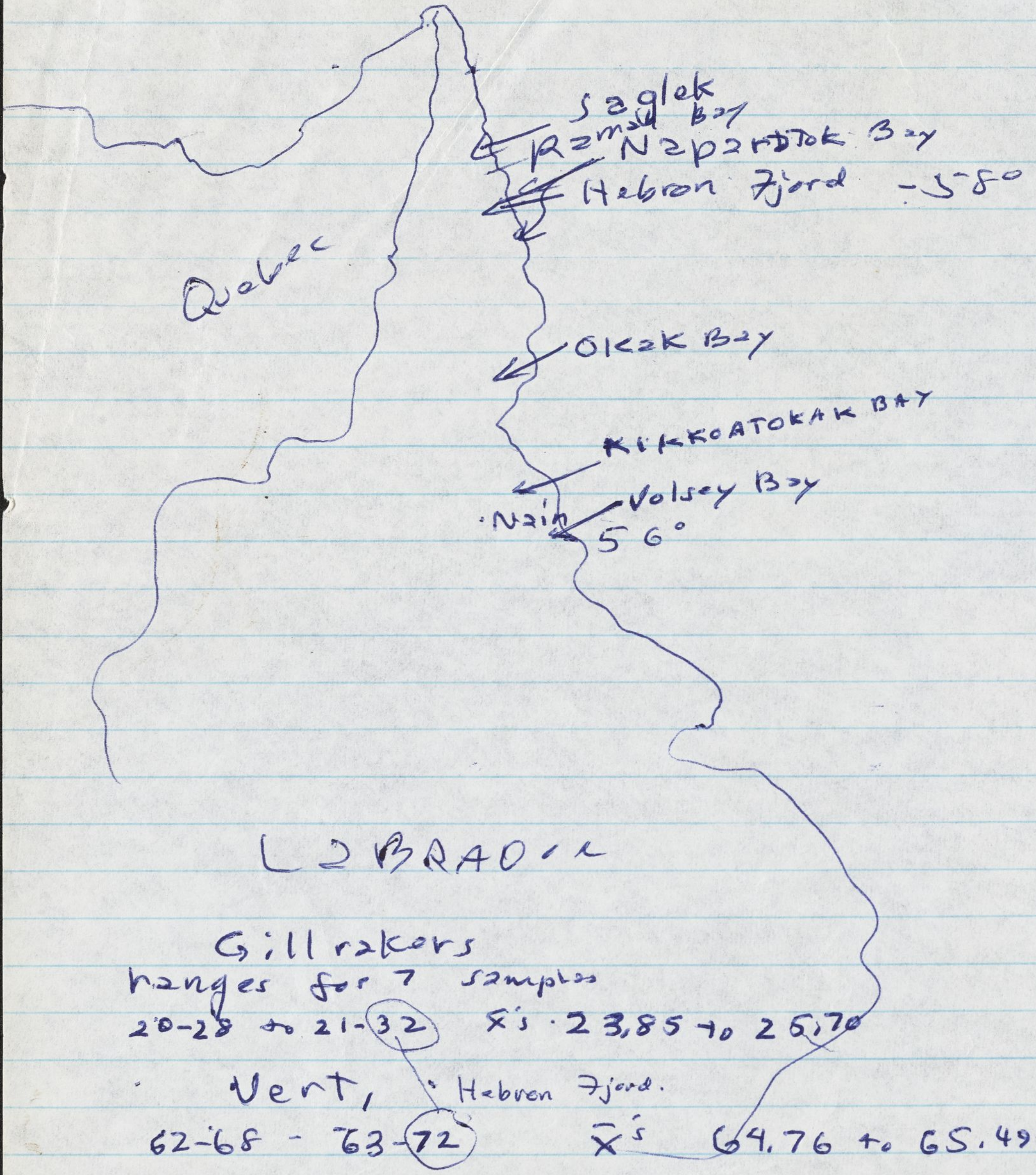
Delta Marsh Field Station

Rockwood Fish Hatchery and
Oak Hammock Marsh

DEPARTURE TIMES AND LOCATION WILL BE ANNOUNCED AND POSTED DURING THE SYMPOSIUM

NOTES

Dempson, J. B. and R. K. Misra. 1983 MS.
Identification of anadromous Arctic charr (*Salvelinus alpinus*) stocks in coastal areas of northern Labrador.
MS. submitted to Can. J. Zool. (Rev. July 83).



Gillrakers
ranges for 7 samples
20-28 to 21-32 $\bar{x}$'s 23,85 to 25,70

Vert, Hebron Fjord.
62-68 - 63-72 $\bar{x}$'s 64.76 to 65.49

- no caeca data

CONTENTS

1. INTRODUCTION

There are numerous opportunities for fish culture operations to make use of low-grade waste heat. Problems arise because fish culturists are secondary users and consequently initial siting and subsequent operations, particularly operating temperatures and shutdown schedules are generally at the convenience of the primary user and are not always ideal for fish rearing (e.g., Gay *et al.* 1976; Tennessee Valley Authority 1977). Solutions to the problems of coupling a low-grade heat source and its operational vagaries with the exacting requirements of a highly efficient intensive fish culture system will have to be addressed before commercial operations can succeed.

Solar energy is an underutilized source of low-grade heat. The objective of the present report is to describe a government of Canada large-scale pilot fish-rearing operation that uses solar energy as a source of low-grade heat. The cyclic nature of the heat source and unscheduled interruptions in the heating of the water are overcome by means of hot water storage tanks, water reuse in the fish tanks and manipulation of the culture procedures.

The system first started operating in 1978. In this report we discuss the detailed results of 6 weeks of operation in early 1980 during the darkest and coldest period of the year.

2. DESCRIPTION OF SYSTEM

2.1 Area

The pilot operation is at the Experimental Fish Hatchery of the Freshwater Institute (Department of Fisheries and Oceans, Canada) located approximately 65 km north of Winnipeg (50^oN, 97^oW) on the Canadian prairies. The hatchery is in an area of mixed grain farms and wooded parkland and there is little topographical relief of any kind in the region. The site is well supplied with groundwater[1] which averages 6 C year around.

A truly continental climate prevails over the Canadian prairies (Hare and Thomas 1974). Winnipeg winters are bitterly cold and summers short but warm (Fig. 1). Heating degree days below 18 C in Winnipeg are 5 966 compared to 3 746 in Toronto and 2 994 in Vancouver. Precipitation is light with moderately

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[1] Artesian wells; TDS 560 mgL^{-1}, Ca, $Mg-HCO_3$ type; pH 7.5-8.0; temperature 6 C.

heavy spring and summer rains and very light falls in winter. Prevailing winds in winter are from the northwest averaging 5.4-6.4 m s^{-1} and in summer and fall from the south averaging 4.6-6.0 m s^{-1}.

Although the climate is extreme, the area receives much bright sunshine, 2 230 hours annually, making it ideal for solar collectors (Fig. 1). Winnipeg receives about 4.5 GJ m^{-2} of radiant energy annually, one of the highest in the country. This compares with 2.9 GJ m^{-2} yr^{-1} on the Canadian Arctic coast, 7.5 GJ m^{-2} yr^{-1} in southern Arizona and 8.4 GJ m^{-2} yr^{-1} on the Sahara. The winter skies are particularly bright; 40-45% of the daylight hours in the coldest months of January and February are bright sunshine compared to 20-30% at Vancouver on the Pacific coast.

2.2 Components

The pilot system consists of a commercial liquid flat-plate solar collector system coupled to a series of 12 modular fish rearing units. The fish rearing units, water blending tank, water storage tank and other mechanical aspects of the solar collector system are housed in a 15.2 x 15.2 m insulated steel building serviced from the main hatchery with electricity and water at a constant 6 ±0.5 C year around. The collector panels are mounted in a steel supporting structure immediately to the south of the building (Fig. 2, Table I).

The building and fish rearing units have been in operation since 1976 and the solar collector system was added in the fall of 1978. After operating through the winter of 1978/79 the collector panels[2] were repaired and modified in the summer of 1979 and the system was put back into operation in September 1979.

2.3 Operation

The solar collector system (Fig. 3) was designed to supply 70 percent of the water heating needs of the rearing building with electrical water heaters as back-up. The water is raised from 6 C to 12 C, a temperature much closer to the optimum for rainbow trout growth. In practice the expectations have been exceeded.

The system operates automatically with manual overrides. The solar loop and process water loop into the heat exchanger begin operating when incoming

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[2] Prototypes when first installed but now in commercial production by Amherst Renewable Energies Ltd., Perth, Ontario.

solar loop temperatures are at least 16 C and also exceed storage tank temperatures by at least 3.5 C. When temperatures reach 40 C in the storage tank, water is dumped to maintain safe temperatures. The blending tank is batch loaded at rearing system operating levels (12 C for this test) by automatic mixing of 6 C and heated ($\geq$ 12 C) process water. The water is delivered to individual rearing units where it can be manually mixed with cold (6 C) water to provide temperature control for individual tanks. Under normal operating conditions (Table 1) the rearing units are supplied with make-up water at a rate of 8.4% continuously.

3. TEST OPERATION

3.1 Methods

3.1.1 Energy Use

The solar array (Fig. 4) is comprised of 48 individual panels connected in a series-parallel arrangement to reduce pressure drop. Each panel (Fig. 5) consists of a number of flattened brass tubes connected in parallel and painted flat black. The panels are double glazed, the inner cover being clear teflon to resist the high temperatures and the outer layer tedlar, a tough abrasion-resistant plastic. The entire solar collector is mounted at a 45° angle to the horizontal. For Winnipeg at a 50° latitude, this is a compromise between winter and summer optimum. The entire array is oriented 10° west of south for maximum heat pickup. In operation, the sun heats the 55% propylene glycol solution which is pumped through the panels from bottom to top. The heated glycol is passed through the tubes of a stainless steel shell and tube heat exchanger and thus transfers heat to the water which passes through the shell of the heat exchanger and hence into the hot water storage tank. Propylene glycol was chosen as the solar loop fluid since it would be less toxic to fish in the event of a leak occurring in the heat exchanger between the solar and hot water streams. Temperatures of the water and glycol entering and leaving the heat exchanger were monitored with copper-constantan thermocouples mounted in thermowells. Outside temperature was measured by a thermocouple mounted in a well-ventilated enclosure. Flows were measured with calibrated pitot tubes and a differential manometer. Total solar radiation was measured by an Eppley thermopile pyranometer mounted in the plane of the collectors at the top center of the array. All sensors were scanned every 15 minutes and recorded on a multipoint datalogger.

Energy usage of the electric pumps was measured by means of elapsed time meters and clamp-on amprobes.

All data were fed to a prewritten computer program which did calculations and produced tables and graphs of energy use,efficiency and coefficient of performance on a daily and weekly basis.

3.1.2 Water Quality

Under normal operating conditions the rearing units receive a continuous supply of make-up water (Table 1). In order to ensure that there were adequate supplies of heated water during this midwinter test the make-up water was only provided 12.2 hours per day. For the rest of the day the rearing units operated on 100% recirculation. A rearing tank temperature of 12 C was maintained by adding 1.2 L min^{-1} of heated 12 C water and 2.6 L min^{-1} of cold 6 C water. The extra heat is provided from the air in the building during recirculation. The normal daily heated water use for the 12 rearing units was 10 520 L (12 units x 1.2 L min^{-1} x 730 min) or 1 full blending tank.

Regular water quality monitoring was carried out to ensure an adequate growing environment for the fish. The rearing units were sampled daily at approximately 9 a.m. for temperature and dissolved oxygen (DO) using a Y.S.I. Model 54 temperature-oxygen meter. The meter was regularly checked using the Winkler method. If DO levels dropped below 5 mg L^{-1}, the measurements were made in 1-2 hour intervals. A 24-hour (or over) continuous measurement of DO was also performed periodically using a Y.S.I. chart recorder. Other chemical parameters were measured twice a week; they included total ammonia nitrogen (NH_4-N), nitrite nitrogen (NO_2-N), nitrate nitrogen (NO_3-N), and pH (Orion meter Model 901). The tanks were also analyzed monthly for soluble reactive phosphorus (SRP) and bicarbonate-carbonate ions (for methods see Stainton et al. 1974).

3.1.3 Fish Production

Four of the 12 tanks were being used for experimental growth studies and only the remaining 8 were used for fish production. The fish production system was designed to produce 1280 commercial-sized (200 g-250 g) rainbow trout a month. At maximum growth rates 9-10 g rainbow trout should reach market size in 4 months. In brief, the system operates as follows: 1280 large fish are removed for market and 1280 9-10 g fish are added to the system, at the end of each month. When the maximum carrying capacity of the tank has been reached the fish are subdivided into additional tanks. At the beginning of the period all 1280 fish are in one tank; after 4 months they occupy 4 tanks. Production is continuous so that at any point in time there are 4 size groups of fish.

Growth during the test run was monitored on a weekly basis. The mean weight of the fish in each group was determined by hand counting 4 lots of 50 fish each and weighing each lot separately. During the course of the experiment fish were fed approximately 150% of rations recommended in published tables (Bardach _et al_. 1974), an amount well in excess of maintenance requirements.

3.2 Results

3.2.1 Energy Use and System Performance

Over the six weeks of the experiment a total of 5 691 kWh of heat was added to the system. Of this total, only 522 kWh was required to be added by supplementary electric heaters, the balance of 5 169 kWh being supplied by the solar panels. Thus 91% of the required heat was supplied by the solar panels.

If all of the other non-heating uses of energy are added and the energy for the 3 extra pumps required by the solar-assisted system is subtracted, the total energy usage for a conventional system would be 6 155 kWh. Thus 5 169/6 155 or 84% of the total energy requirement was supplied by the solar panels. When the extra energy to run the solar pumps is taken into account the total energy used by the present system was 1 750 kWh or a net reduction of 72% when compared to a conventional system.

A comparison of total solar insolation and available solar insolation (Fig. 6A) shows that at a solar insolation of less than about 300 kWh day^{-1} the system does not operate and heat recovery is thus zero. These periods can last as long as four days.

The total solar insolation over the six-week period was 20 722 kWh and the amount available during pump operation was 9 874 kWh. Thus 9 874/20 722 or 47.6% of the total solar insolation occurred while the system was operating.

Storage tank water temperature (Fig. 6B) ranged from 7.0 C at the beginning of the test, gradually increasing to 34.7 C at the end.

Ambient outside daylight temperature (Fig. 6B) ranged from -5.6 C to -25.8 C, the lowest values occurring in the last week of January. Most of the time the value stayed between -10 C and -16 C.

Rearing tank water temperature (Fig. 6B) ranged from 9.2 C at the beginning to 13.7 C at the end of the test. Supplementary electric heat had to be added 7 out of the first 15 days of the test due to insufficient solar input. The total number of hours of supplemental heat during this period was 26.1 h.

Figures 7A and B show respectively solar collector operating efficiency and coefficient of performance as a function of solar insolation. Both efficiency and coefficient of performance increase with increasing solar insolation and drop to 0 at about 300 kWh day^{-1} as expected since the pumps cease operating at this level. Solar collector efficiency or the percent of heat transferred to the water compared to the solar input varied from 0 to 80%. Over the six-week period the total collected was 5 169 kWh compared to a total input of 9 874 kWh. Thus overall efficiency was 5 169/9 874 = 52.3%. Combining this figure with the 47.6% operating/total ratio gives an overall solar utilization factor of 52.3% x 47.5% or 24.9%.

Coefficient of performance or the ratio of the total heat transferred to the water compared to the amount of electrical energy used to run the system, i.e., pumps, supplementary electric heat and lights, varied from 0 to 11.8 with a total overall value of 4.1 over the six-week period.

3.2.2 Water Quality

There was a notable conditioning of the filters during the first 1-2 weeks after beginning of the production experiment (before that, the tanks had been in operation with substantially lower fish densities). This period was characterized by a steady drop of DO values by about 3-4 mg L^{-1} (Fig. 6D). After this initial conditioning period, the overall DO levels remained in a 6-7 mg L^{-1} range. The only exceptions were two tanks with the highest fish densities (up to 58 kg m^{-3}), where DO values would occasionally drop to levels as low as 2.9 - 3.7 mg L^{-1}. This happened only when there was no make-up water added for several hours, or when filters had not been backwashed for a full week. Differences between the individual tanks at sampling times can be seen from standard deviation values in Table II.

NH_4-N showed a trend closely tied to the increasing fish densities and DO as the experiment progressed. An overall buildup to concentrations of 500-1800 μg L^{-1} in low-density tanks and up to 2600-3080 μg L^{-1} in the high-density tanks was an obvious result of increasing fish metabolism as the fish grew. At operating pH values (7.55-8.25) these ammonia concentrations were safe for fish from the toxicity viewpoint (EIFAC 1970). NO_2-N levels remained also in the safe 180-200 μg L^{-1} range (Russo et al. 1976) for most of the experiment. NO_3-N showed a steady buildup during the first 2-3 weeks of conditioning. After this period, values leveled off at the maximum levels of 9-10 mg L^{-1} which suggested a properly functioning nitrifying system, balanced by duration of make-up water addition. SRP values (not shown here) increased from 200 to 800 μg L^{-1} during the experiment as a result of excretion and excess feed.

The production tanks were likely close to their maximum carrying capacity. The high feeding rates, high excretion and heavy loading of the filters resulted in levels of N about twice as high and levels of DO about 1/3 lower than other similar tanks in the hatchery (unpublished data).

After the first month of the test when the fish were divided into new tanks at lower densities (Feb. 21), there was a substantial drop of all N forms and rise in DO levels to initial 9 mg L^{-1} (Fig. 6D).

Figure 8 presents examples of typical diurnal DO distribution in selected tanks. The diurnal DO regime was governed by the duration of make-up water addition, which generally improved it. When make-up was discontinued, there was a gradual decline of DO, presumably due to fish respiration and biochemical oxygen demand. Each feeding was also accompanied by a subsequent DO drop within 10-20 minutes, likely due to increased activity and defecation and their oxygen demand.

3.2.3 Fish Production

The fish grew significantly during the 6 weeks of the test run (Fig. 6C, Table III), although not quite as rapidly as anticipated. The most rapid growth was during the first two weeks of the test and then again after 4 weeks. Mortalities during the tests were insignificant (< 0.3% per month) and could usually be attributed to handling stress.

4. DISCUSSION

Although use of a cheap or free source of heated water offers many advantages to a fish farmer, the location of waste heat sources is not always ideal. Coupling of a water reuse system for the fish tanks with the waste heat source can help solve many difficulties.

Coupling a solar collecting system to fish rearing units decreased energy consumption for raising a projected 432 kg of fish[3] (based on producing 1280, 225 g fish every 4 weeks) from 6 155 kWh to 1 750 kWh in a 6-week period (not including energy cost for food, labor or equipment). At 4¢ per kWh the net saving was approximately $176. The energy cost of running the solar collector system (3 extra electric pumps) was $31 or 17% of the net saving.

In this test run, both the technical and fish production aspects of the system operated efficiently. The maximum densities of fish reached (58 kg m^{-3} and 1.9 kg L^{-1} min) are close to the maximum used for commercial rainbow trout production (Bardach _et_ _al_. 1972).

Water quantity and quality become problems particularly if treatment of water is required before use. In this pilot system, which was designed to produce approximately 3,744 kg yr^{-1}, water reuse has resulted in a 12-fold increase in production from 6.9 kg L^{-1} min annually to 82.1 kg L^{-1} min annually.

Non-scheduled shutdowns of sources of waste heat can have a traumatic effect on fish production. The non-scheduled shutdowns of the solar collectors are buffered by the water reuse system and the water storage system. Without water reuse there would be a complete exchange of cold water in the tanks in less than 35 minutes, which could cause a severe thermal shock, while with water reuse the exchange would take over 11 hours. The blending tank provides 12.2 hours of hot water. If all water was cut off from the outside,the system would operate normally for 3.8 hours.

Cyclical interruptions in heated water such as occurs at night or scheduled interruptions such as for major repairs to the solar collectors for this system, are also ameliorated by reusing water and water storage. When the water in the storage tank is 40 C, the system can operate normally for 8½ days based on using one blending tank of 12 C water per day.

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[3] This does not include the production of the other 4 fish rearing units which use recirculated water. Potential production of all 12 tanks would be 648 kg.

Intensive fish culture operations can benefit substantially by using previously unexploited sources of low-grade heat. Coupling the heat source with water reuse units can, as described above, significantly improve the fish culture potential of such sources.

5. REFERENCES

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6. ACKNOWLEDGMENTS

We would like to acknowledge the assistance of the staff of the Experimental Fish Hatchery, the Graphics Section of the Freshwater Institute and other individuals who participated in the preparation of the manuscript. We would also like to thank Amherst Renewable Energies Ltd. and engineering staff of the Freshwater Institute who were instrumental in the development of the solar collecting system. The Department of Energy, Mines and Resources provided funds for the construction of the solar collectors. This project is funded, in part, by Algas Resources Ltd., Calgary, Canada.

Table I. Characteristics of solar collecting system and fish rearing units at Rockwood Experiment Fish Hatchery.

Number of solar panels	48
Net collecting area	125 m^2
Collector type	Double glazed liquid flat plate collector. (Figure 5).
Supporting structure	Galvanized steel open type structure mounted on concrete piles.
Piping	Solar loop is of copper and stainless steel. Process loop is of stainless steel and plastic.
Solar loop flow	3.2 L s^{-1} of 55% propylene glycol solution.
Hot water storage tank	Fiberglass insulated, 19 130 L operating temperature variable 16 C - 40 C.
Blending tank	Fiberglass insulated 10 520 L operating temperature variable 6 C - 16 C, 12 C for test run.
Fish tanks	12 fiberglass tanks each 1.8 m x 1.8 m x 0.9 m - capacity 1500 L mounted over filter units.
Filter units	12 fiberglass units 1.8 m diameter x 1 m (0.75 m diameter settling chamber in center), granite filter media 0.75 m^3, approximate volume of water 1100 L, mounted beneath fish tanks, backwashed weekly.
Water use per tank	Water flow = 45 L min^{-1}, make up 8.4%, make up flow 3.8 L min^{-1}, water use 65 580 L day^{-1}, (with recirculation 5 509 L day^{-1}) water exchanges 25.2 day^{-1} (with recirculation 2.12 day^{-1}).

Table II. Standard deviations for water quality parameters in individual tanks at various sampling dates.

	Water temperature °C	Dissolved oxygen mg L^{-1}	NH_4-N mg L^{-1}	NO_2-N mg L^{-1}	NO_3-N mg L^{-1}
Mean	0.3	0.8	305	28	1.4
Minimum	0.1	0.4	36	3	0.3
Maximum	1.7	1.5	925	56	3.2

Table III. Fish weight and loading density during 6-week test run.

Test group		Jan. 24	Feb. 21	Feb. 22[4]	Mar. 6
A	Wt (g)	9	19	13	20
	Density (kg m^{-3})	8	16	11	16
B	Wt (g)	42	69	19	25
	Density (kg m^{-3})	35	58	16	21
C	Wt (g)	78	112	69	88
	Density (kg m^{-3})	33	46	29	37
D	Wt (g)	179	208	112	141
	Density (kg m^{-3})	31	47	24	30
				Harvested	

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[4] After one month the large fish were harvested and a new group of small fish added to the system.

G.B. Ayles, K.R. Scott, J. Barica and J.G.I. Lark. E/32

Combination of a solar collector with water recirculation units in a fish culture operation

Figure 1. Monthly mean temperatures and hours of bright sunlight per day for Winnipeg, Canada (Hare and Thomas 1974).

Figure 2. Plan of fish rearing facility showing location of solar panels, blending tank, storage tank and fish rearing tanks.

Figure 3. Schematic of solar collector and fish rearing systems.

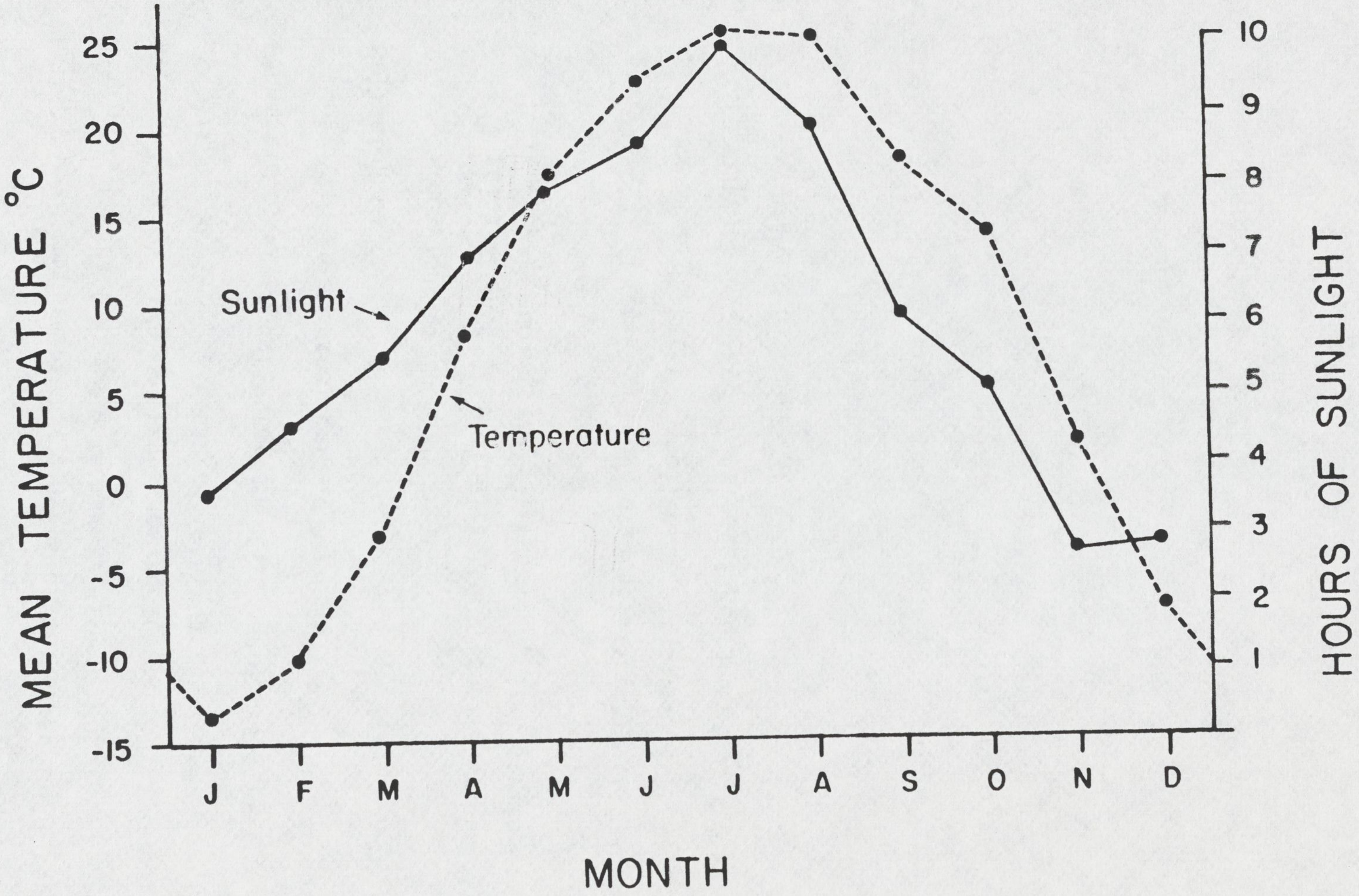
Figure 4. Schematic of solar panel array showing glycol flow and cutaway of collector cores.

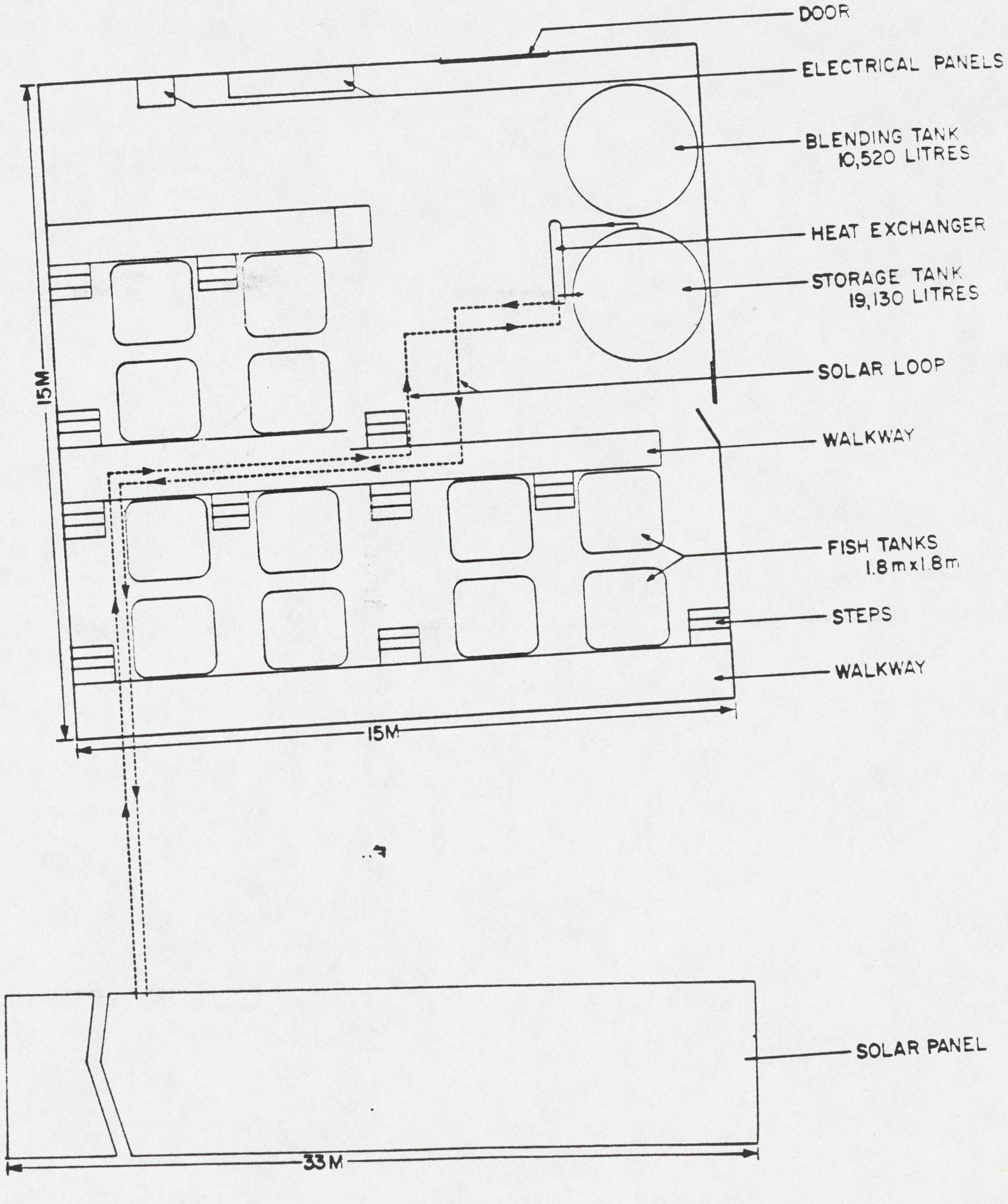
Figure 5. Plan of individual solar panel.

Figure 6. Some physical (6A, 6B), biological (6C), and water quality (6D) parameters (mean values for all rearing units) monitored during test run.

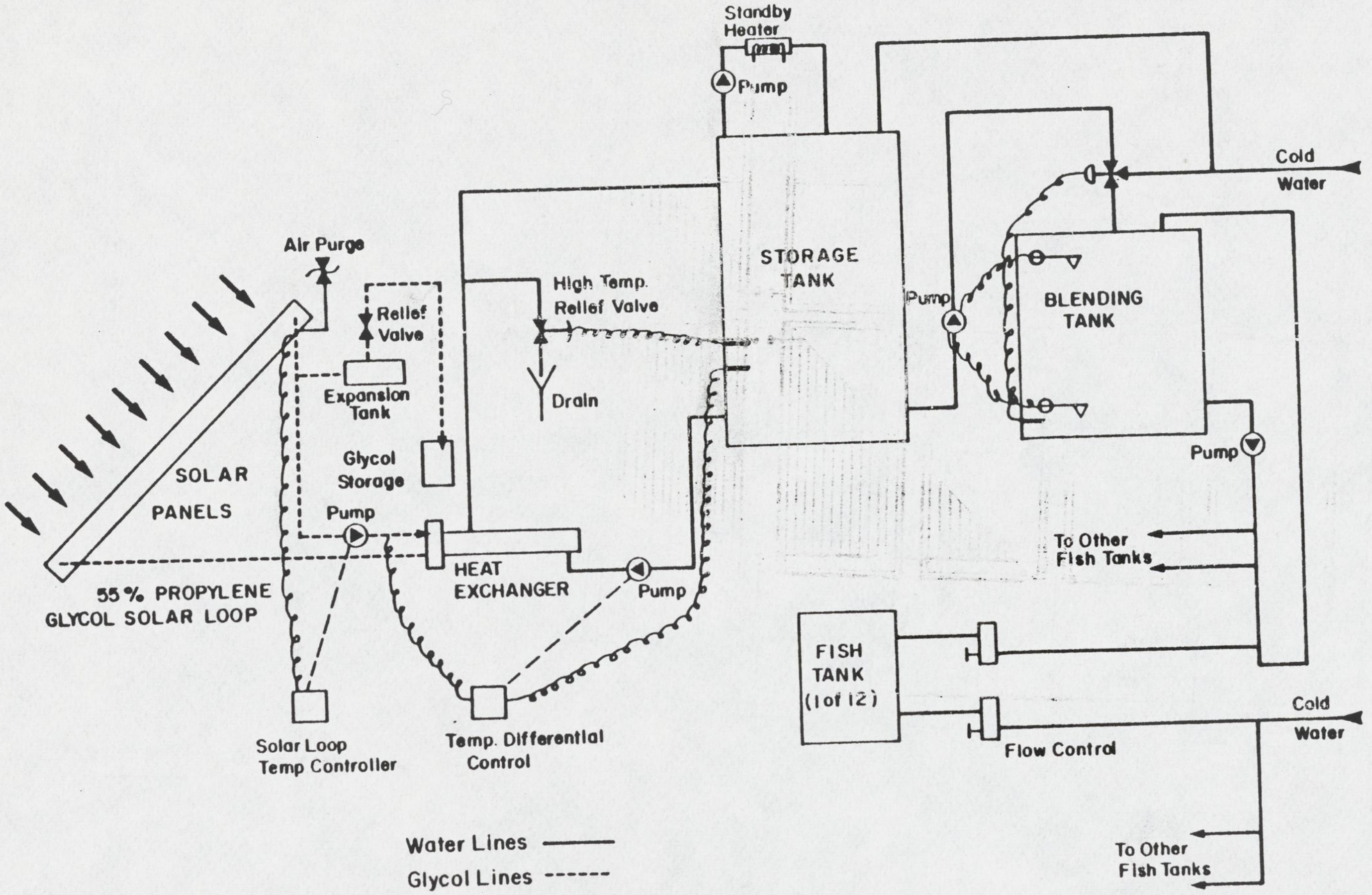
Figure 7. Relationship between daily solar insolation and coefficient performance and operating collector efficiency.

Figure 8. Diurnal DO measurements in selected rearing units. A was low density, B and C high density fish tanks.

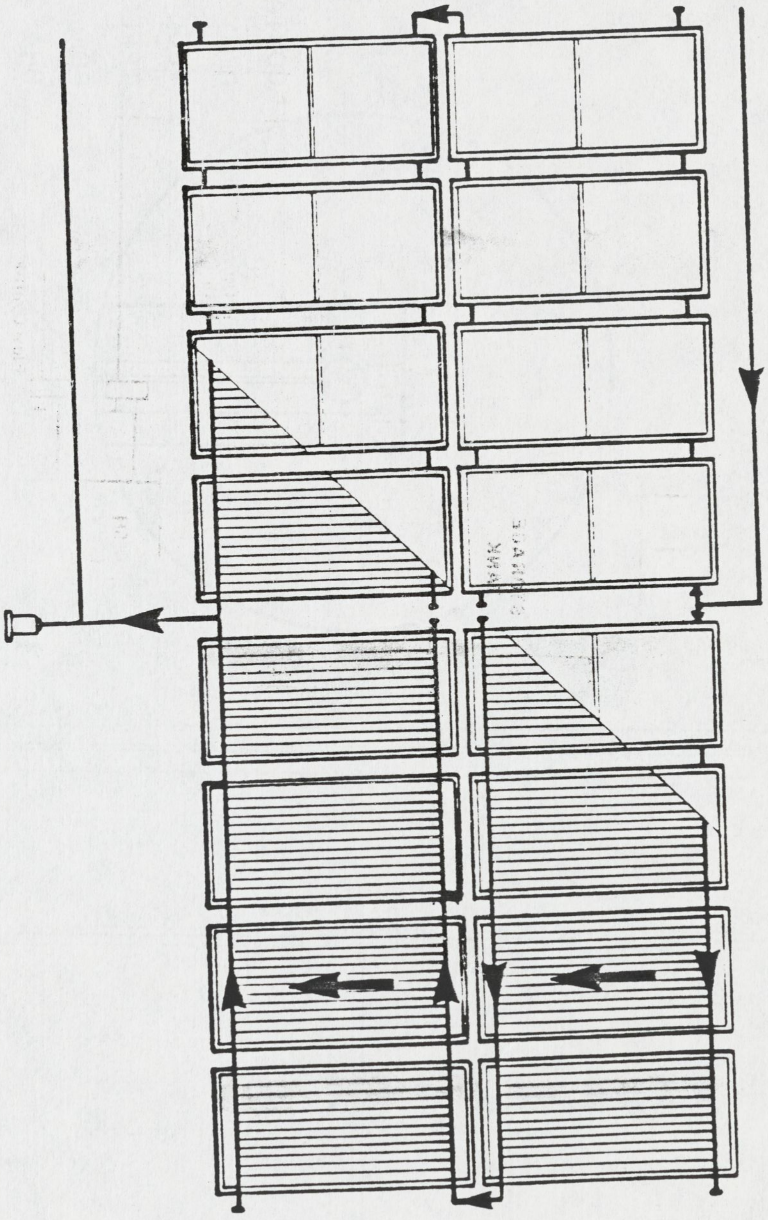

MEAN TEMPERATURE °C
25
20
15
10
5
0
-5
-10
-15
HOURS OF SUNLIGHT
10
9
8
7
6
5
4
3
2
1
Sunlight
Temperature
J
F
M
A
M
J
J
A
S
O
N
D
MONTH

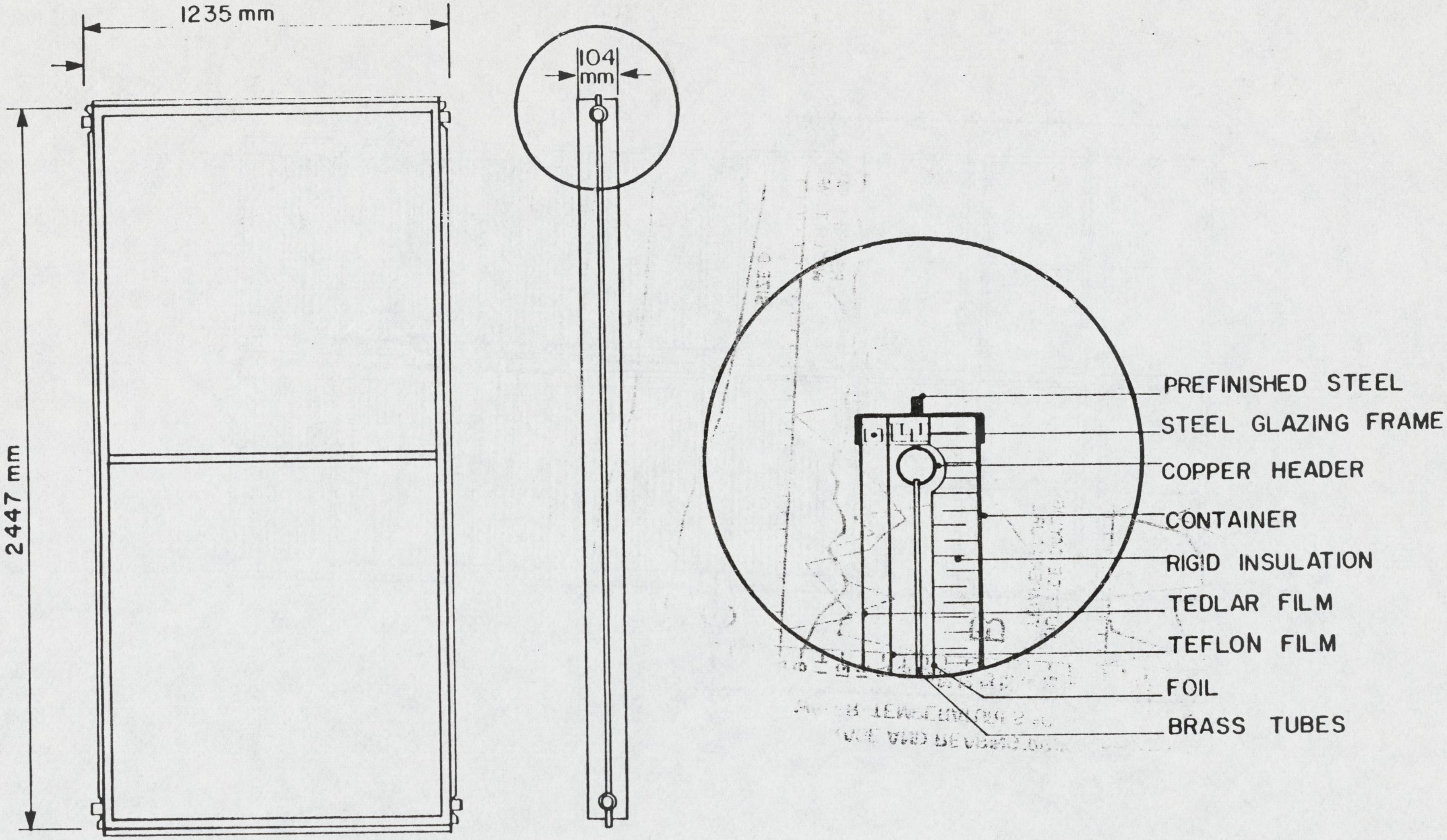


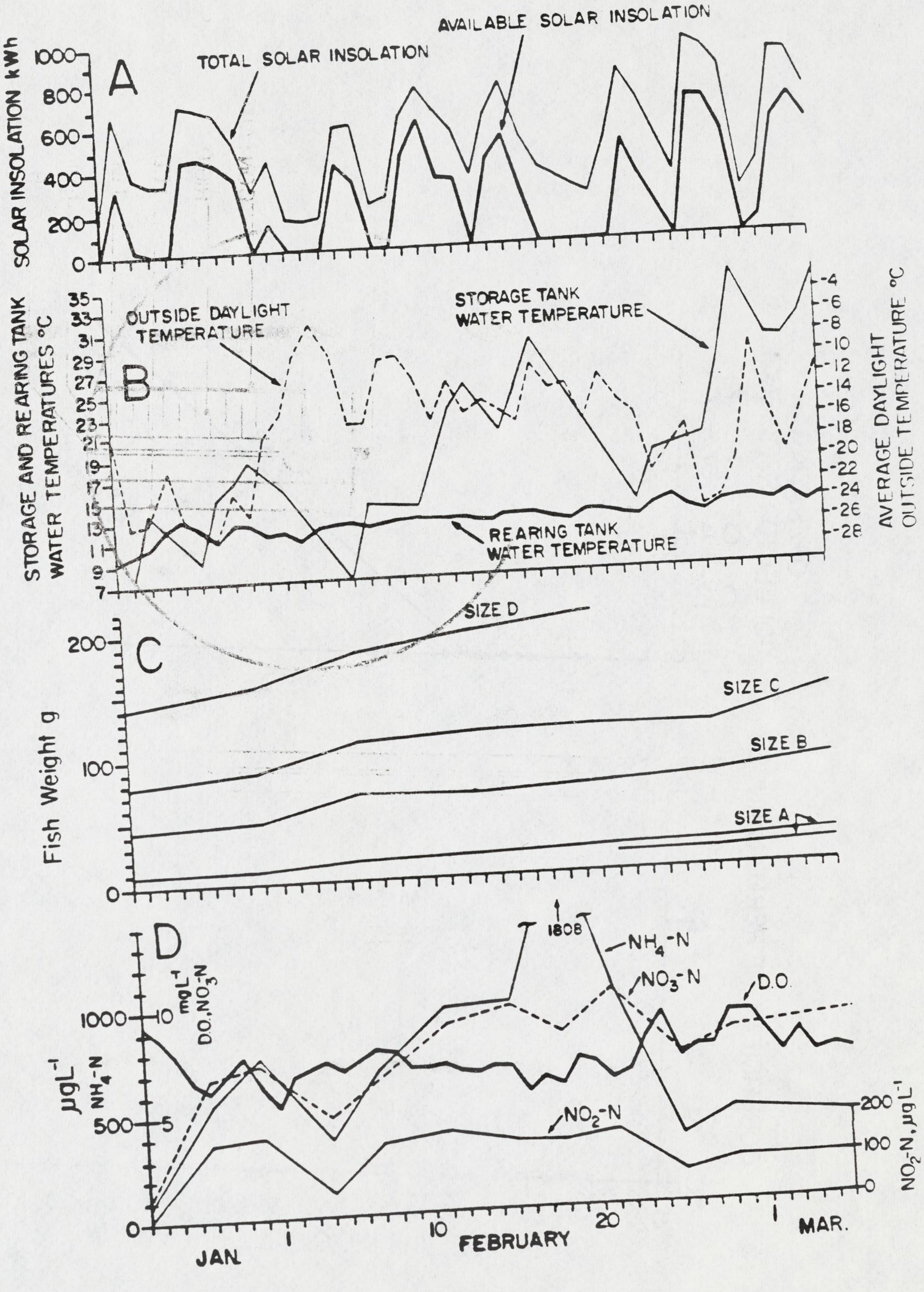
DOOR
ELECTRICAL PANELS
BLENDING TANK 10,520 LITRES
HEAT EXCHANGER
STORAGE TANK 19,130 LITRES
SOLAR LOOP
WALKWAY
FISH TANKS 1.8m x 1.8m
STEPS
WALKWAY
15M
15M
SOLAR PANEL
33M

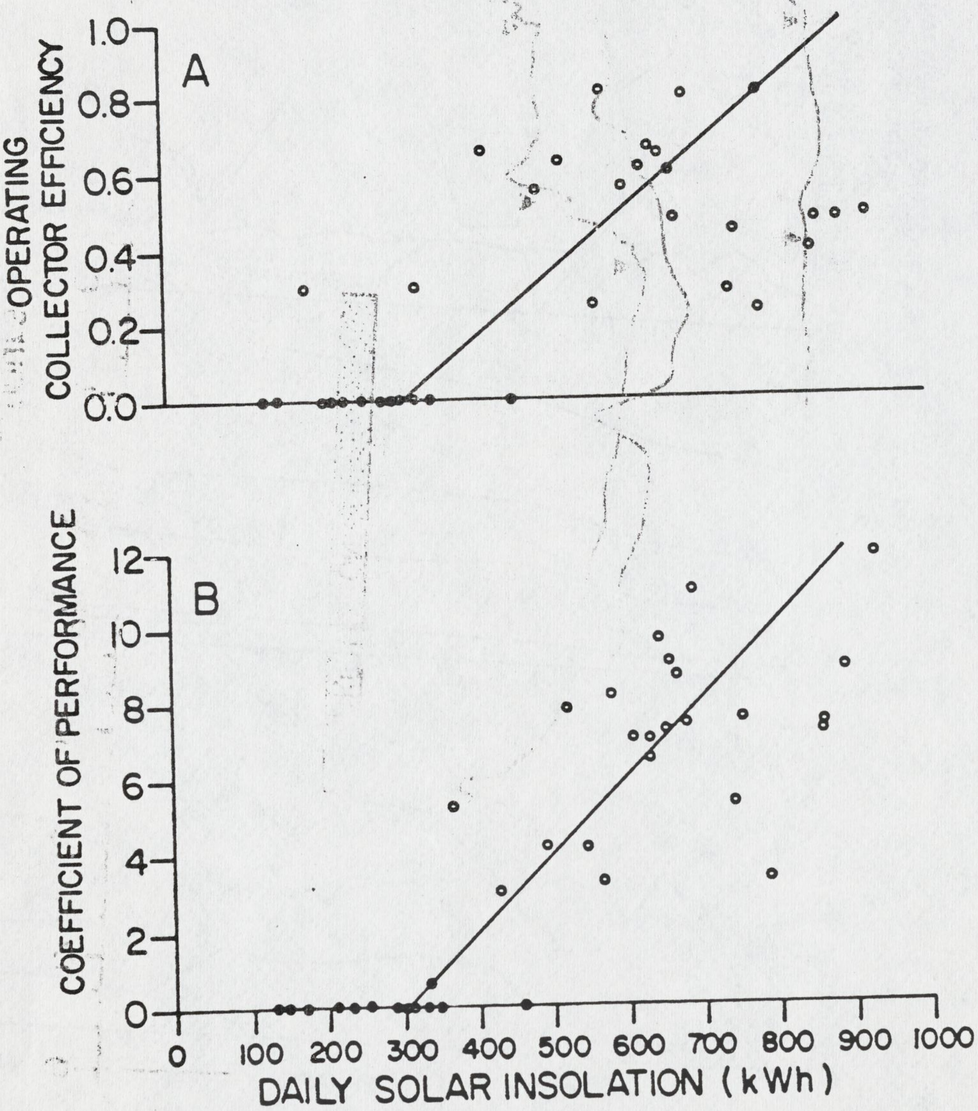


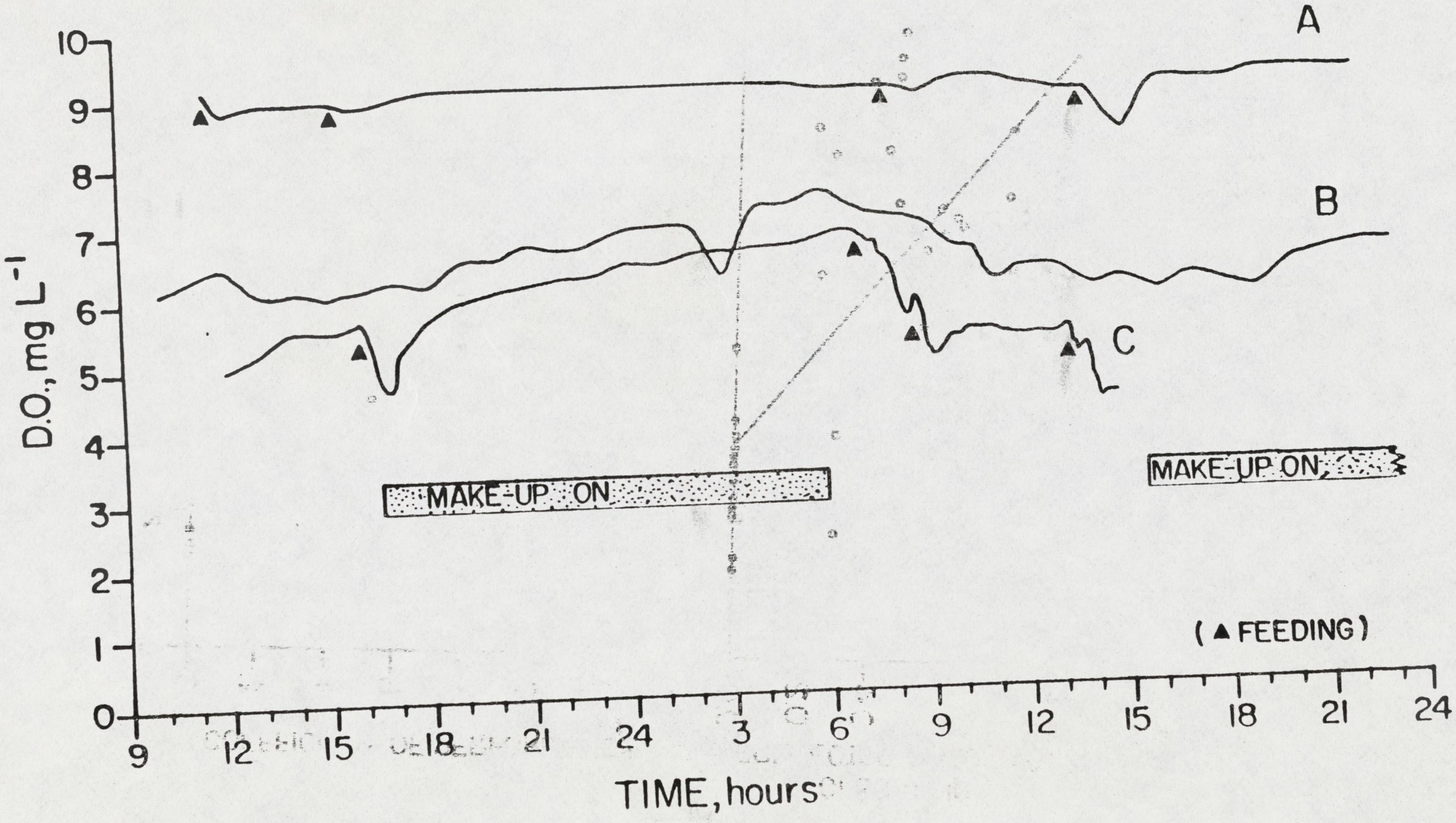
Standby Heater
Pump
STORAGE TANK
Cold Water
Air Purge
Relief Valve
High Temp. Relief Valve
Pump
BLENDING TANK
Expansion Tank
Drain
Glycol Storage
SOLAR PANELS
Pump
Pump
To Other Fish Tanks
Pump
HEAT EXCHANGER
Pump
55% PROPYLENE GLYCOL SOLAR LOOP
FISH TANK (1 of 12)
Cold Water
Solar Loop Temp Controller
Temp. Differential Control
Flow Control
Water Lines
Glycol Lines
To Other Fish Tanks




1235 mm
104 mm
2447 mm
PREFINISHED STEEL
STEEL GLAZING FRAME
COPPER HEADER
CONTAINER
RIGID INSULATION
TEDLAR FILM
TEFLON FILM
FOIL
BRASS TUBES


A
AVAILABLE SOLAR INSOLATION
TOTAL SOLAR INSOLATION
SOLAR INSOLATION kWh
1000
800
600
400
200
0
B
STORAGE AND REARING TANK WATER TEMPERATURES °C
35
33
31
29
27
25
23
21
19
17
15
13
11
9
7
OUTSIDE DAYLIGHT TEMPERATURE
STORAGE TANK WATER TEMPERATURE
REARING TANK WATER TEMPERATURE
AVERAGE DAYLIGHT OUTSIDE TEMPERATURE °C
-4
-6
-8
-10
-12
-14
-16
-18
-20
-22
-24
-26
-28
C
Fish Weight g
200
100
0
SIZE D
SIZE C
SIZE B
SIZE A
D
μgL⁻¹ NH₄-N
mgL⁻¹ D.O., NO₃-N
1000
500
0
10
5
1808
NH₄-N
NO₃-N
D.O.
NO₂-N
NO₂-N, μgL⁻¹
200
100
0
JAN.
1
10
FEBRUARY
20
1
MAR.


A
OPERATING COLLECTOR EFFICIENCY
1.0
0.8
0.6
0.4
0.2
0.0
B
COEFFICIENT OF PERFORMANCE
12
10
8
6
4
2
0
0
100
200
300
400
500
600
700
800
900
1000
DAILY SOLAR INSOLATION (kWh)



A
B
C
D.O., mg L^{-1}
10
9
8
7
6
5
4
3
2
1
0
MAKE-UP ON
MAKE-UP ON
(▲ FEEDING)
9
12
15
18
21
24
3
6
9
12
15
18
21
24
TIME, hours

ORGANIZING THE DIVERSITY OF THE ARCTIC CHARR COMPLEX

Robert J. Behnke
Department of Fishery and Wildlife Biology
Colorado State University
Fort Collins, Colorado

ABSTRACT

The subgenus Salvelinus is divided into the Dolly Varden complex and the Arctic charr complex. S. leucomaenis, S. confluentis, and S. albus are assigned to the Dolly Varden complex. The Arctic charr, S. alpinus, is viewed to be composed of three major groups with origins associated with Europe, Siberia, and the Arctic Ocean in the Chukoskt Sea-Bering Sea region. Except for sympatry between S. malma and S. alpinus, examples of sympatric charr populations almost always involve populations derived from within the geographical area of occurrence and they are very closely related to each other. The origins of most sympatric charr are attributed to divergences during and since the last glacier epoch. Recommendations are given on the preservation and utilization of the diversity present in charrs.

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INTRODUCTION

Questions might be asked concerning the rationale of why I should write another paper on Salvelinus systematics in view of the fact that I so recently gave opinions in a systematic review of the genus (Behnke 1980) published in a large volume of works devoted to charr (Balon 1980). An examination of the works of the various authors in this volume on charrs reveals a range of opinions quite divergent from my position on the evolutionary relationships and classification of the genus. Immediately following my paper, Savvaitova (1980a) discusses how her opinions on charr systematics differ from mine.

Paging through the charr volume, a paper by Leggett (1980) discusses the reproductive behavior of the Dolly Varden charr, S. malma, of Kootenay Lake, British Columbia; but, according to the work of Cavender (1980) in the same volume, the Kootenay Lake charr is the "bull trout," S. confluentus. Cavender (op. cit.) recognized S. imbrius and S. pluvius of Japan as valid species whereas in my paper I considered imbrius as a synonym or subspecies of S. leucomaenis and pluvius as a subspecies of S. malma. Savvaitova (1980b) repeated her stout belief that the Dolly Varden charr, S. malma, should be treated as a synonym of Arctic charr, S. alpinus, but she discussed "alpinoid," "high arctic," and "malmoid" types of charr. Most authors in the charr volume followed the classification given in McPhail and Lindsey (1970) which regarded the common charr in North American waters westward from the Mackenzie River (tributaries to the Beaufort Sea), as S. alpinus, whereas Morrow (1980) and I (Behnke 1980) pointed out that this group of charr is identical to S. malma of the type locality (Kamchatka). Johnson (1980) presented an excellent and comprehensive review on *S. alpinus* but had to admit that he could only arbitrarily draw taxonomic boundaries for the species because of the problems in separating *S. alpinus* from *S. malma*. There is also considerable controversy regarding the spelling; char vs. charr. There is something about the beautiful fish known as char or charr that excites the imagination and emotions.

Thus, on the basis of the divergent opinions found in the most recent and comprehensive compendium on the genus, it is now appropriate that I again try to organize the diversity into a taxonomic scheme and attempt to better define the limits of the subgenus *Salvelinus*, the Arctic charr species complex, and the Arctic charr, *S. alpinus*. Recent literature, color slides, and specimens of the Kamchatkan "stone charr," all kindly sent to me by I. A. Chereshnev, have contributed to my latest "revision." I also borrow heavily from my studies on a group of salmonid fishes, the Pacific basin trouts of the subgenus *Parasalmo*, which are similar in respect to the degree of evolutionary divergence within a comparable era of geological time, relatedness between species, evolution of diverse behavioral and ecological forms, great morphological diversity, and taxonomic problems.

THE SUBGENUS *Salvelinus*

The first step toward a more precise definition of "Arctic charr" is to divide the genus into smaller phylogenetic units. In my last two papers on charr, I recognizec three subgenera; one for the North American lake charr, *S. namaycush*, one for the North American brook charr, *S. fontinalis*, and one for all other members of the genus, but pointed out that the correct position of the Far Eastern "kundscha" charr, *S. leucomaenis*, is in doubt (Behnke 1972, 1980). *S. leucomaenis* has some similarities to *S. namaycush*, but these may be the result of convergent evolution as a predaceous species. Until convincing evidence is forthcoming regarding the phylogenetic branching sequence in the genus leading to *S. leucomaenis*, I will provisionally include the kundscha charr in the subgenus *Salvelinus*.

Thus, based on zoogeographic evidence correlated with degrees of divergence, it appears that an early (Pliocene?) branch of the genus becaue established in North America, eventually giving rise to the two, widely distributed living species, *S. namaycush*, and *S. fontinalis*. The former species specialized as a large lacustrine predator whereas the latter species, in the general absence of other salmonine fishes, evolved a more generalized way of life, utilizing a wide range of environments, more typical of the trouts in the genus *Salmo*. Conveniently ignoring *S. leucomaenis*, the evolutionary divergence in the rest of the genus resulted in two major groups or species complexes--the Arctic charr group and the Dolly Varden group. This split may have occurred during an early Pleistocene glacier period when the common ancestral charr was divided into northern (precursor of the Arctic charr) and southern (precursor of the Dolly Varden group) groups in the Pacific and Arctic ocean drainages.

In view of the contentious nature of my recognition of Arctic charr and Dolly Varden charr not only as separate species but as separate species groups or complexes, the evidence supporting my position must be presented.

Reality of Arctic Charr and Dolly Varden Species Groups

DeLacy and Morton (1943) presented the first conclusive evidence that Dolly Varden charr and Arctic charr are valid species by finding representative populations of the two species occurring sympatrically in Karluk Lake, Alaska where they exhibited sharp differences in life history and taxonomic characters. McPhail (1961) found other Alaskan lakes where the two species were sympatric with no evidence of hybridization and he further strengthened the case for full species recognition between Dolly Varden and Arctic charr. The problem was that all of these examples involved the southern form of North American Dolly Varden which formerly was generally assumed to characterize the taxon *S. malma*.

Consideration of the taxonomic data on Dolly Varden throughout its range reveals a major divergence occurs between northern and southern Dolly Varden that likely was initiated by isolation during a glacier period subsequent to the separation of Dolly Varden and Arctic charr. A relative homogeneous northern Dolly Varden occurs in both Asia and North America. In the Far East, in the northern Okhotsk Sea drainages, Kamchatka, and northward around the Chukotsk Peninsula, the Dolly Varden is typically characterized by 21 to 23 gill rakers, 66 to 68 vertebrae, and 25 to 30 pyloric caeca. This same form of Dolly Varden (which should be recognized as *S. malma malma*, because Kamchatka is the type locality for the name *malma*) occurs in North America, from the Alaska Peninsula (north side) to the Mackenzie River. McPhail (1961) and McPhail and Lindsey (1970) were not aware of the similarities between the Alaskan and Far Eastern northern forms of Dolly Varden and they considered the northern North American form of Dolly Varden as the western Arctic form of *S. alpinus*.

South of the Alaska Peninsula to Oregon, the southern form of North American Dolly Varden occurs and it is differentiated from the northern form by fewer gill rakers and vertebrae (typically 17-18 and 62-64, respectively). In the Far East, the most differentiated southern form of Dolly Varden is found in Honshu Island, Japan and in the Kuril Islands. This extreme form has only 58 to 60 vertebrae, 20 to 25 pyloric caeca, and 16 to 18 gill rakers. This form is commonly recognized as S. pluvius in Japan, but I have pointed out that if the Kuril Islands Dolly Varden is the same taxon then the name should be S. malma curilus. The taxonomic characters of Dolly Varden in Hokkaido and Sakhalin (19-23 gill rakers and 61-63 vertebrae) indicates introgression has occurred between the northern and southern forms in the Far East. There is no evidence of intermediacy between the northern and southern forms of Dolly Varden in North America. All of the above forms that I have identified as Dolly Varden are differentiated from all North Pacific forms of Arctic charr by their general phenotypic appearance (smaller size spots on the body, a more blunt snout) and fewer gill rakers and fewer pyloric caeca. There is no evidence of sympatric occurrence between northern and southern forms of Dolly Varden. The diversity within the species can be arranged into three broadly distributed subspecies--S. malma malma, the northern form in both Asia and North America, S. m. curilus, the southern Asiatic form of Honshu and the Kuril Islands, with probable intergradation between the two subspecies in Hokkaido, Sakhalin and Korea, and the southern North American form, which I have tentatively recognized as S. malma lordi (Behnke 1980).

The validity of full species recognition of S. malma depends on its degree of reproductive isolation where it has come into contact with members of the Arctic charr complex. If Dolly Varden occur sympatrically with Arctic charr over a broad area in Asia and North America, with sympatric populations maintaining their integrity with reproductive isolation, then biologists with a reasonable understanding of evolution and systematics should agree with me that *S. malma* is indeed a "real" species of relatively long (perhaps early Pleistocene) separation from any member of the Arctic charr complex. That is, they are not, as Savvaitova (1980) believed, simply local populations of Arctic charr that happen to be so similar because of convergent evolution since the last glacier period.

In my recent paper (Behnke 1980) I reviewed the records of sympatric occurrence of both the southern and northern forms of North American Dolly Varden with Arctic charr in several lakes in Alaska. Typically, in Alaska, the Dolly Varden is anadromous, overwintering in the lakes and spawning in tributaries (or resident in tributaries) to the lake whereas the Arctic charr is strictly lacustrine (and the more piscivorous species). The most common coexistence is with the form of Arctic charr called the Bristol Bay-Gulf of Alaska form of *S. alpinus* by McPhail (1961), but sympatry also occurs between the northern Dolly Varden and the "eastern Arctic" form of *S. alpinus* in some lakes east of the Mackenzie River mouth. Thus, in North America, there is sympatric occurrence over a broad geographical area between populations of Dolly Varden and Arctic charr and two subspecies of Dolly Varden (northern and southern) and two subspecies of Arctic charr (Bristol Bay-Gulf of Alaska and eastern Arctic) are involved. There is no real evidence of intermediacy or hybridization between Dolly Varden and Arctic charr.

In Asia, there is widespread sympatry between the northern Dolly Varden and Arctic charr. The Asiatic Arctic charr of the Chukotsk Peninsula and Kamchatka is identical to the Gulf of Alaska-Bristol Bay form of Arctic charr of Alaska. It is characterized by large spots, typically 23-26 gill rakers, 40-55 pyloric caeca, and 66-68 vertebrae. Two names have been given for this charr from the Chukotsk area--*S. andraishevi* and *S. taranetzi*.

In Kamchatka, the Arctic charr occurs as lacustrine relict populations in Lake Dalnye and Lake Nachinskoye where it is sympatric with populations of Dolly Varden. In lakes and rivers draining the Chukotsk Peninsula, Arctic charr and Dolly Varden are sympatric, often with both species being anadromous (Chereshnev 1978a, 1978b, 1979). A paper by Volobuyev, et al. (1979) attempted to cast doubt on Chereshnev's conclusions that the Arctic charr and Dolly Varden are two distinct species. The authors examined a series of charr specimens from the Kukekkuyum River, in southern Chukoskt (previously studied by Chereshnev), and attempted to emphasize that intermediate (hybrid) specimens between the large-spotted Arctic charr and small-spotted Dolly Varden occurred in their sample. They did this by emphasizing the overlap in the ranges of numbers of gill rakers and pyloric ceaca that occur between the two species and attributing the overlap to hybridization. If given proper editorial review such a paper should not have been published. Overlap in taxonomic characters between two closely related species is certainly not evidence for hybridization. The appropriate method for the treatment of data from the Kukekkuyum River charr specimens to test the assumption for or against reproductive isolation would be to use a form of multivariate analysis such as a principal components analysis of taxonomic characters from specimens identified as large-spotted specimens and small-spotted specimens. If this were done, I believe 100% separation (or very close to it) would have been obtained between the Arctic charr and Dolly Varden specimens--and complete (or virtually complete) reproductive isolation between them would be the only logical conclusion. Thus, the conclusions drawn by the authors that the two types of Chukoskt charr may be only seasonal races of a single species and should not be recognized as different species (Volobuyev, et al. 1979) borders on the ridiculous, especially in view of the evidence of such widespread sympatric occurrence of Dolly Varden and Arctic charr in Asia and North America.

A problem I must point out, however, concerns the relationships of the north Pacific form of Arctic charr (S. anadraishevi or S. taranetzi). Is it a subspecies of S. alpinus? Where would its branching point be positioned in the phylogeny of Salvelinus? Its large spots are somewhat similar to S. leucomaenis. Is this type of spotting an example of convergent evolution? This form of charr needs much more information on its genetic relationships. Until demonstrated otherwise, however, the large-spotted charr, "S. andriashevi," of the north Pacific drainages of Asia and North America can be considered as part of the S. alpinus "complex."

In relation to phylogenetic affinities to the Dolly Varden or to the Arctic charr complexes, two other Pacific drainage species must be considered--the stone charr, S. albus, of Kamchatka, and the bull trout, S. confluentus, of North America. I discussed the stone charr in my 1980 paper but I did not realize that the description of Salvelinus albus by Glubokovsky (1977) for a charr from the Kamchatkan River basin actually was a description of the stone charr. There is some confusion surrounding the stone charr as I discussed in my 1980 paper. Viktorovsky (1975) discussed various forms of charr from Lake Kronotskoye, Kamachatka, using common names--the white (bely) charr, the longheaded (dlinnogolovy) charr, and the nose or snout (nosaty) charr. Glubokovsky (1977) in naming the "white" charr, *S. albus*, from the Kamchatka River, mentioned it is identical to the white charr of Lake Kronotskoye. Viktorovsky (1978) revised the Lake Kronotskoye charr. He decided the white charr is actually the typical *S. malma*, the nose charr was described as a new subspecies of *malma*, *S. m. schmidti*, and the longheaded charr was described as a new species, *Salvelinus kronocius*. From the descriptions given by Glubokovsky and Viktorovsky and from previous data on the stone charr supplemented by two specimens of *S. albus* sent to me by I. A. Chereshnev, there is no doubt that *S. albus* and *S. kronocius* both represent the stone charr of Kamchatka. Thus *S. kronocius* is a synonym of *S. albus*. Unfortunately, the confusion with the "white"charr of L. Kronotskoye led to the inappropriate name *S. albus*; the stone charr could be called the black charr; the coloration in freshwater specimens is decidedly dark.

As mentioned in my previous paper, I believe the closest relationship of the stone charr is with the North American bull trout, *S. confluentus*. There are some real differences in meristic characters (about what would be expected from two branches of a monophyletic origin that has been separated for more than 100,000 years), but there are basic similarities in the shape of the head and jaws and overall appearance. I believe the bull trout and stone charr represent an early divergence in the Dolly Varden complex.

Associated with the Pacific basin origin of the Dolly Varden complex, I suggest that the relationships of *S. leucomaenis* are also with the Dolly Varden complex. The low values of meristic characters and the karyotype of *S. leucomaenis* (2N = 84-86, identical to *S. malma curilus*) (Viktorovsky 1978) also indicate the closest affinities of *leucomaenis* are to the Dolly Varden complex.

The Arctic Charr Complex

By the process of elimination at the subgeneric and 'complex' levels of discrimination, all the rest of the diversity in the genus can be attributed to the Arctic charr complex. That is, the phylogenetic branching points leading to all of the living forms in the Arctic charr complex should connect to a common ancestor after the separation between the Dolly Varden and Arctic charr complexes.

The key to defining the limits of the species *S. alpinus* concerns the charr of the type locality area ("Swedish Lappland" as given by Linnaeus). Thus, all forms included as *S. alpinus* or in the Arctic charr complex should be more closely related (more recent phylogenetic separation) to Scandinavian *S. alpinus* than they would be to *S. malma* of Kamchatka.

The typical Scandinavian form of *S. alpinus* has about 63-64 vertebrae, 30-50 pyloric caeca and 21-28 gill rakers. This form is distributed in the Kola and Karelian region of the USSR, Finland, northern Sweden, Norway, Great Britain and Ireland. A closely related group, *S. a. salvelinus*, occurs in the Alpine lakes of central Europe. Typically, the central European "normalsaibling" or "wildfangsaibling" has slightly more gill rakers (typically 25-30).

There is an interesting group of Arctic charr that is likely monophyletic in origin but now has a broad and disjunct distribution. These charr have the highest numbers of gillrakers in the genus, from 25 to 35; they are also characterized by about 65 to 70 vertebrae and about 40 to 50 pyloric caeca. They may obtain a weight of 12 kg or more and are typically piscivorous. This type of charr is concentrated in the Taimyr Peninsula region of Siberia and in the Arctic Ocean drainages of North America east of the Mackenzie River (eastern Arctic form of *S. alpinus*). In these regions they occur as anadromous and resident lacustrine populations (resident lacustrine stocks are much more common in Siberia where *S. namaycush* is absent). They occur as disjunct relict populations far inland in Siberia in lakes of the Yenesei, Lena, and Kolyma river basins and in the Baical region (*S. erythrinus*). Headwater transfer from the Kolyma drainage has established this form of charr in lakes of the Okhota River basin, tributary to the Okhotsk Sea (*S. neiva*). They also occur as resident lacustrine populations in lakes west of the Mackenzie basin where they are sympatric with anadromous *S. malma*. I also believe this same form of charr occurs in Lake Coomarsahrn, Ireland (*S. fimbriatus*). The distribution of the Arctic cisco, *Coregonus autumnalis*, exhibits many similarities with this particular group of charr. The Arctic cisco also occurs as relict lacustrine populations in Ireland where it is known as the pollan (Ferguson et al. 1978).

The Taimyr Peninsula is of special interest in regards to sympatry between populations of Arctic charr. I have previously discussed a charr from L. Taimyr (Behnke 1972, 1980) named *S. taimyricus* that has a distinctive morphology. Savvaitova et al. (1980) recorded *S. taimyricus* from Lake Keta and described four sympatric *Salvelinus* populations from Lake I.

Lake Lama. All have meristic characters similar to the generalized anadromous Taimyr charr and most probably all represent minor divergences within this particular "major" divergence in the Arctic charr complex. The life history and ecological differences between the various Taimyr charrs are pronounced. There are anadromous and lacustrine forms and the various lacustrine forms differ in feeding specialization, depth distribution, growth rate and maximum life span.

For a classification of *S. alpinus* best denoting evolutionary relationships among the major divergences making up the species, I could suggest that all of these charr (Taimyr region, eastern Arctic North America, interior Siberia lakes, and Lake Coomarsaharn) be considered as one subspecies (*S. alpinus erythrinus*). The great ecological diversity encompassed in such classification (or any taxonomic arrangement of *S. alpinus* conforming to the international rules of zoological nomenclature), readily reveals the severe limitations of our binomial or trinomial system of nomenclature to accurately describe and classify the enormous diversity manifested in the Arctic charr complex. For proper management of this diversity, the various ecological forms, particularly in sympatry, should be regarded as if they were different species.

One other form of *S. alpinus* that probably deserves subspecific recognition is the group of disjunct lacustrine relicts of northern New England and southern Quebec known as Sunapee, blueback, and red "trout," *S. alpinus oquassa*. This group of charr appear to be an early derivative of the evolutionary line leading to the northern European *S. a. alpinus*. They differ mainly in having fewer gillrakers (18 to 24 vs. 21 to 28). Their distribution appears to be largely the result of exclusion or extermination by S. namaycush. Native populations occurred only where namaycush was absent and they soon disappeared in those lakes where namaycush was introduced.

From a preliminary synthesis of all information, I provisionally recognize three major centers of evolution in the Arctic charr complex (or S. alpinus in the broad sense). A European origin of the north European S. alpinus alpinus. The central European S. a. salvelinus and the eastern North American S. a. oquassa, are probably most closely associated with this group. A Siberian origin for the vast and diverse group that, for purely practical taxonomic purposes, can be recognized as S. a. erythrinus with a multitude of derivative forms such as taimyricus, neiva, drjagini, etc.

The peculiar form of charr with very large spots occurring in Asiatic and North American drainages to the Chukotsk and Bering seas where it is widely synpatric with S. malma, probably evolved in that area. The extremely large spots of this form of Arctic charr may be an example of character displacement that reinforces reproductive isolation with S. malma. This form can provisionally be recognized as S. a. andriashevi, but this taxon should be redescribed because both Dolly Varden charr and Arctic charr occur in Lake Estikhet, the type locality of the taxon. Berg's (1948) description of andriashevi is probably based on a specimen of Dolly Varden.

From what I have been able to determine, examples of sympatry in the Arctic charr complex, are always between members of the same evolutionary group, and are the result of recent divergences initiated during or since the last glacier period. That is, the three major divergences that, for practical purposes of communication, I have classified as S. a. alpinus, *S. a. erythinus*, and *S. a. andriashevi*, do not occur in sympatry with each other. The sympatric populations in Lake Windemere, England, and in many Scandinavian and Karelian lakes are more closely related to other members of the broad and inclusive *S. a. alpinus* than they are to any member of the *S. a. erythrinus* or *S. a. andriashevi* evolutionary lines. This also appears to be true for the numerous sympatric populations in lakes of Taimyr--they are all probably derived from within the *S. a. erythrinus* evolutionary lineage after divergence from the *S. a. alpinus* branch. From a practical point of view and in relation to principles of animal taxonomy, it seems absurd to classify all four of the sympatric populations in Lake Lama as a single subspecies. The most useful taxonomic arrangement of the subgenus *Salvelinus* (for other than evolutionary or systematic purposes) most likely will considerably stray from a strictly cladistic interpretation.

The tiefseesaibling, *S. profundus*, is a striking exception to the rule that sympatric populations (except for *malma* and *alpinus*) have their origins in relatively recent geological time. The degree of differentiation of the tiefseesaibling is extreme in the genus. The uniform, dull coloration, the broad and overhanging snout, the peculiar structure of the gillrakers, the low numbers of gill rakers, vertebrae and pyloric caeca (20-25, 61-63, and about 25-35, respectively) sets off *S. profundus* from any other known form in the genus. I have examined specimens of tiefseesaibling only from the Bodensee but it has been reported from the following Alpine lakes of Central Europe: Neuchatel, Walchensee, Ammersee, Tegernsee, Achensee, Plansee, Attersee, and Traunsee (Berg 1932, Nerseheimer 1937). Brenner (1980) described the tiefssesaibling from the Attersee. Brenner concluded that tiefseesaibling are not a distinct taxon but are only "local forms created in response to different environmental and feeding conditions." Such a statement is pure nonsense to anyone familiar with the range of variability in charr specimens throughout the distribution of the genus. If it were true that sympatric populations of tiefseesaibling evolved independently in each lake inhabited by Salvelinus where suitable conditions were present, then there would be tiefseesaibling throughout the Holarctic region and not only in central European lakes. The rich whitefish (subgenus Coregonus) fauna of the European Alpine lakes, has probably severely restricted the distribution and abundance of tiefseesaibling by competitive exclusion. This would suggest to me that the evolution of the tiefseesaibling occurred before Coregonus invaded the Alpine lakes or it occurred in a contiguous area where Coregonus was absent. In any event, the tiefseesaibling is morphologically very different from any other form of charr. I include it in the Arctic charr complex only on zoogeographical grounds.

DISCUSSION

I believe the charrs in the subgenus Salvelinus like the trouts of the subgenus Parasalmo have undergone rapid morphological and ecological divergence. That is, the morphological or regulatory part of the genome has speciated much more rapidly than the structural or metabolic part of the genome. If this is true then it can be expected that information obtained from the structural genes, typically from electrophoretic studies of proteins, will not be in full accord with the evidence of morphological divergence. As far as is known, all forms in the genus are interfertile when hybridized. This would indicate rather recent origins of all living forms from a common ancestor in relatively recent geological times (perhaps upper Pliocene). To date, comprehensive comparative electrophoretic studies have not been made on diverse forms of charr. A comprehensive study should include data from 25 to 35 gene loci to arrive at comparable genetic relatedness indices such as genetic identity scores. When such research has been done, I suspect that genetic identity scores between the most divergent forms in the genus will be high--on the order of 90 or higher. Unless electrophoretic studies can establish substantial evidence for a discussion of primitive (plesiomorphic) and derived (apmorphic) proteins, and not merely allelic frequency differences, then their contributions to *Salvelinus* systematics will be more-or-less limited to some generalizations on degrees of relatedness but lacking in authoritative cladistic information.

Comprehensive electrophoretic studies should be useful, however, to test my hypothesis concerning the evolutionary reality of the Dolly Varden and Arctic charr complexes and their respective components and to examine the relative affinities of *S. leucomaenis* and *S. profundus*.

In the western North American trouts of the subgenus *Parasalmo*, electrophoretic taxonomic studies on the cutthroat trout (*Salmo clarki*) and rainbow trout (*Salmo gairdneri*) have probably been more intensive than that of any other fish species. However, there is a lack of evidence on primitive and derived genes in these species and no real cladistic interpretation is possible. An overall summation of the electrophoretic data indicates four equally related groups--rainbow trout and three

subspecies

subspecies of cutthroat trout, but the genetic identities are tightly clustered, suggesting all could be considered as subspecies of a single species. The genetic basis governing the striking morphologidal distinctions of the California golden trout (*S. aguabonita*), can not be detected by electrophoresis. Two subspecies of cutthroat trout that have pronounced differences in spotting pattern and ecologies, and are in part sympatric in the upper Snake River drainage, Wyoming, exhibit no electrophoretic differences in the products of 26 gene loci (Loudenslager and Kitchin 1979). Electrophoretic studies of western North American trouts demonstrate close genetic identities, and a distinct lack of concordance in the evolutionary rates of change between the regulatory genome governing morphology and ecological specialization and the structural genome sampled by electrophoresis. I expect the same situation will be found in *Salvelinus*.

The data on *Salvelinus* *karyotypes* indicate the general trend of Robertsonian fusion--going from higher chromosome numbers in primitive form to lower numbers in derived forms. The karyotype of *S. leucomaenis* is given as 2N=84-86 with 100 arms. This same karyotype is found in *S. malma curilus*. *S. malma malma* is listed as 78-80 with 96 arms, and the Far Eastern form intermediate in morphological characters (*S. m. kracheninnikovi*) also has an intermediate karyotype with a diploid number of 82-84 and 98 arms according to Viktorovsky (1978). *S. fontinalis* and *S. namaycush* have diploid numbers of 84 with 100 arms. *S. alpinus* (Sweden) has 80 chromosomes with 100 arms. The stone charr of Kamchatka and the bull trout of North American evidently posses a common karyotype of 2N=78 with 100 arms (Viktorovsky op. cit. and T. Cavender personal communication).

I would not necessarily interpret a smooth progression in karyotype speciation from this data. That is, I don't believe the list of karyotypes can be used as strong evidence that *S. leucomaenis* and all subspecies of *S. malma* were already evolved before *S. malma malma* gave rise to the Arctic charr complex.

In the closely related species and subspecies of western North American trouts, diploid chromosome numbers range from 56 (106 arms) in *S. gilae* and *S. apache* to 68-70 (104 arms) in *S. clarkii clarkii*, but there has been considerable rearrangement of karyotypes in several evolutionary lines. The three major subspecies groups of cutthroat trout follow a Robertsonian fusion pattern of decreasing numbers: 2N=68-70 in *S. c. clarki*, 2N=66 in *S. c. lewisi*, and 2N=64 in *S. c. bouvieri*. In the rainbow trout evolutionary line, the diploid number associated with the most primitive morphological characters and the most primitive distribution pattern is 58. In various populations of the more advanced coastal rainbow trout, modal diploid numbers are 58, 60, 62, and 64. Evidently the evolutionary trend has been that of converting metacentric chromosomes into acrocentric chromosomes with an increase in the diploid number. The most divergent species of *Parasalmo* is the Mexican golden trout, *S. chrysogaster* which has a diploid number of 60. Thus, within a closely related group of trouts of probable relatively recent (perhaps late Pliocene - early Pleistocene) origin from a common ancestor, there is great variation in the karyotypes and the chromosome numbers of 60 and 64 must have been arrived at independently in different evolutionary lines.

Extrapolating the karyotype information from *Parasalmo* to *Salvelinus* suggests that after all of the diverse geographical forms of charr have been karyotyped, the comparative data may not be a decisive factor for determining the position of phylogenetic branching points in *Salvelinus*.

Mednikov, et al. (1980) published an interesting attempt to resolve taxonomic problems in *Salvelinus* by the use of DNA hybridization. I pointed out (Behnke 1980) that DNA hybridization data cannot be trusted because of the noise of experimental error when dealing with groups such as the Arctic charr complex and the Dolly Varden complex. Their evolutionary separation has not had sufficient time to accumulate the amount of genetic differentiation needed to overcome the noise of experimental error.

Thus, despite modern methodology, I doubt that a taxonomic arrangement of charrs will ever be constructed that will be universally accepted and endorsed. This is particularly true because of the conflict between the goals of a phylogenetic (in the strict cladistic sense) classification and the goals of a practical classification useful for fisheries management in relation to degrees of morphological and ecological divergence and sympatric occurrence.

A final point of emphasis concerns the management, preservation, and utilization of the great range of diversity found in diverse groups of charrs. In comparison to other salmonid fishes, most of the distribution of charrs occurs in areas of the world with low human population density and, as yet, relatively lightly impacted by man. In contrast, I estimate that the cutthroat trout species in western North America has lost about 98% of its original distribution (with concommitant loss of genetic diversity) in interior waters during the past 100 years. There can be great ecological and life history differences between local populations of the same subspecies that may be of major significance for management purposes (Hickman and Behnke 1979, Behnke 1981). A long range goal should be to maintain the geographical and ecological diversity still present in Salvelinus, in order that the base of the natural resource (its genetic diversity) be available for utilization.

The natural distribution of the Arctic charr complex, with the exceptions of the European Alpine lakes and some lakes in the interior of Siberia, is largely restricted to within about 100 km of the Arctic coast and associated islands. The Arctic charr is an effective agent to channel the food resources in waters of very low primary productivity into a highly desirable product. There is a great potential to introduce various forms of Arctic charr into suitable new waters and greatly increase the fishery values of these waters. In 1978, I examined specimens of an unknown charr, sent to me from a lake in the Rocky Mountains of Idaho. I identified the specimens as S. alpinus oquassa. Later, it was discovered that charr from Sunapee Lake, New Hampshire, were stocked into a few Idaho lakes in 1925 (the native charr in Sunapee Lake later becaue extinct after S. namaycush was introduced). The Sunapee charr is now known to persist in two lakes in Idaho. These lakes are ultra oligotrophic but the Sunapee charr attain weights of 2 and 3 kg whereas S. fontinalis in these same lakes seldom exceed 100 g. In numerous such lakes in the Rocky Mountains of North America, without suitable spawning inlets to maintain trouts of the genus Salmo, S. fontinalis is often the only fish species but they typically are represented by stunted populations of little fishery value. There must be thousands of similar lacustrine situations in the world where the introduction of members of the Arctic charr complex would greatly improve the fisheries by maximizing salmonid biomass production with their specializations to make efficient use of the pelagic and benthic zones, and produce large size specimens because of their range of food utilization and long life span. Innovative ways to maximize growth and production could be tried such as hybrid combinations and attempts to create sympatric stocks with introductions from diverse parental sources. Consideration of the diversity of the potential niches of the diverse forms of Arctic charr and how the potential niches would be contracted into realized niches in interaction with other species (or other sympatric populations of Arctic charr) offers a wealth of opportunities for theoretical and practical application of fisheries management concepts. I believe the Arctic charr is a fish that will become more widely appreciated, despite its confused taxonomy.

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November 10, 1981

Dr. Robert Behnke
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Dear Bob:

Thanks very much for your recent letter and your earlier one to Bill Valleau regarding tenure. I greatly value your perspective on systematics and evolution.

The Lanao trip is on; I'll leave Maine around December 15. I will also be collecting material from Thailand and Northern Malaysia for suitable outgroup comparisons. A critical morphological evaluation of the specimens I collect is absolutely essential for meaningful interpretation of any inferential genetic data. From my very limited exposure, I fully appreciate the expertise and insights of classical systematists. Time and again, what a good ichthyologist intuitively perceives very rapidly in terms of phylogeny is the conclusion that is arrived at by so-called "critical" electrophoretic analysis. The morphological systematist appreciates the gestalt of a taxon and from experience knows which types of characters are critical and which are of lesser value. I do not pretend to possess such experience. However, I still believe that certain types of characters are more environmentally plastic than others. I find your comments about meristics of sunapee char from Sawtooth Lake particularly enlightening; exactly such demonstrations should be prominently displayed in the literature to counterbalance experimental studies on unrelated taxa which purport opposite findings. It is clear that few systematically general statements can be made regarding relative heritability or environmental plasticity for specific morphological characters.

I agree completely with your (re-) interpretation of S. alpinus genetic similarities. When faced with values of 0.9 or greater, cladistical accuracy is lacking. However, with lower similarities, information content is much higher, and accuracy increases. I completely agree that biochemical systematics is loci dependent. It is clear that some certain classes of enzymes are more informative than others. A recent paper in Genetical Research convincingly demonstrates a significant positive correlation between individual locus heterozygosity and genetic distance. Thus, demonstrable differences at loci with generally low levels of intraspecific variability are more informative cladistically. Esterases are of limited value when used in isolation, particularly if the formal genetics has not been examined. I would hope that Nyman would expand his enzyme arsenal to include additional loci.

Again, thanks for your continued correspondence. I'll keep you posted on the Philippine problem.

Best regards,

Irv Kornfield
Assistant Professor of Zoology

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EUROPEAN INLAND FISHERIES ADVISORY COMMISSION
Eleventh Session

Stavanger, Norway, 28-30 May, 1980

SYMPOSIUM ON NEW DEVELOPMENTS IN THE
UTILIZATION OF HEATED EFFLUENTS AND OF RECIRCULATION
SYSTEMS FOR INTENSIVE AQUACULTURE

EIFAC/80/Symp: E/32

Combination of a Solar Collector with Water Recirculation Units in a Fish Culture Operation

by

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Abstract

Twelve recirculation units comprising fish tanks and individual gravel filters were coupled to a solar collector in a pilot demonstration of the use of low-grade heat for fish culture in northern climates.

The solar system consists of a liquid-type flat-plate solar collector with 125 m^2 of collection area, a 19 130 liter storage tank, a 10 520 liter blending tank, heat exchanger and associated piping, pumps and supporting structure. The system supplants the electrical heat previously used to warm the water from 6 C to 12 C for the rearing units. By manually switching the recirculation systems to 100% from 92% some nights and for up to 2 consecutive days during cloudy periods it was possible to operate without using the electric heat throughout the early winter of 1980 when external temperatures fell below -30 C.

The recirculation units which are essential both to minimize heat requirements and to permit operation during periods without sunlight, consist of 1500 liter fish tanks mounted over 1.0 m deep x 1.8 m diameter filters containing 0.75 m^3 of gravel. Monitoring of chemical parameters showed a high efficiency of metabolite removal, well-balanced oxygen conditions and high nitrification rates, even at loading rates as high as 45-50 g per liter.

Environmental Biology of Fishes Vol. 15, No. 4, pp. 241–242, 1986

Obituary of Vadim Dimitrovitch Vladykov, 1898–1986

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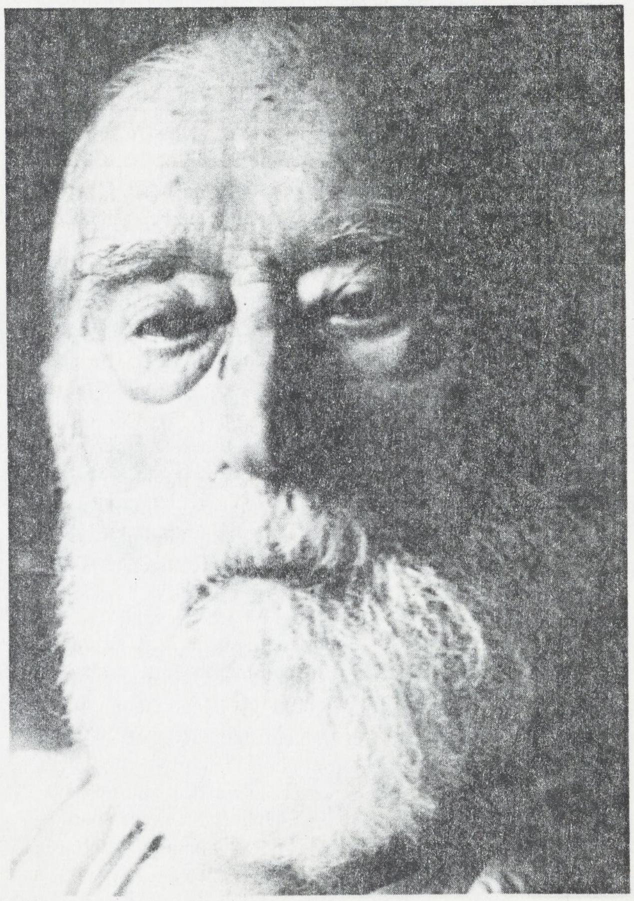
Vadim Dimitrovitch Vladykov died in his retirement apartment on the night of 14 January 1986, after a full and productive life. He was 87 years old. Surviving are his two talented daughters, Nadya Clowes and Kyra Fisher, and four grandchildren. His beloved wife, Nina Formagie, who he married in 1938, predeceased him on the 19th of December 1976.

Dr. Vladykov was born near Kharkov, Ukraine, March 18, 1898 (Gregorian), son of Dimitriy Iv. Vladykov (1863–1955), an archpriest, theologian and missionary of the Russian Orthodox Church. Vadim graduated from the Lycée of Akhtyrka in 1917. He was a student at the University of Kharkov from 1917 to 1918 under Prof. P. Sushkin. He fought in the White Army under generals Vrangel and Deniken, became ill and while convalescing in Crimea, studied the fishes of Kertch Channel (between the Azovsk and Black seas). Following the evacuation of the White Army he surveyed the fishes and herptiles of the Bosporus in Turkey. The collections he made were deposited in the French College of Saint-Georges of Constantinople and in the Natural History Museum of Prague.

In 1921 he became a biology student at the Charles University in Prague, Czechoslovakia and graduated with a RNDr degree (Rerum Naturalium Doctor) in 1925, with a major in zoology and a minor in anthropology. It was there that he began his studies on the fishes of Subcarpathian Russia (then in Czechoslovakia, now part of Ukrainian SSR). This led to his appointment as director of the Ethnographic Museum of Subcarpathian Russia in Uzghorod. These studies were published in Ukrainian in 1926 and in French in 1931 and included several new taxa.

In 1928 he moved to Paris and read agricultural bacteriology and serology at the Institut Pasteur and from 1929 to 1930 studied ichthyology at the Muséum national d'Histoire naturelle under professors L. Roule and J. Pellegrin. He was elected a 'Correspondant of the Museum' and received the gold medal of the Société Centrale d'Agriculture et du Pêche for his work on Subcarpathian fishes.

In September 1930 he arrived in Canada and began to work as an assistant scientist in biology under Dr. A.G. Huntsman for the Biological Board of Canada (which later became the Fish-



Photograph of Vadim D. Vladykov taken in December 1985 by the author.

eries Research Board of Canada). He worked at the biological stations at St. Andrews, N.B., Halifax, N.S. and Toronto, Ontario (where he was reported to cut a dashing figure with his long opera cloak and intriguing accent) up to 1936. Amongst other studies during this period he published a major work on the marine fishes of Hudson Bay and a booklet on the marine fishes of Nova Scotia. In 1936 he became a Canadian citizen.

In 1936 after joining the Maryland Conservation Department he undertook studies of shad and striped bass. He was also a professor of Ichthyology at the University of Maryland at College Park and the Biological Station at Solomons. In 1938 he returned to Canada and joined the Laboratoire de Zoologie at the Université de Montréal as professor of ichthyology. During this period he founded and directed biological stations in the Parc des Laurentides and on Lac St-Louis. Amongst more professional duties he took the Governor General and Her Royal Highness Princess Alice fishing at Grand Lac Jacques Cartier in September 1941. Those knowing Vadim will wonder if he inveigled the Princess into preserving some of her catch for him.

In 1943 Dr. Vladykov organized the 'Service de Biologie' in the Départment de Pêcheries du Québec and was its director from 1943 to 1958. During this period he gave courses in ichthyology every two or three years to students in the Ecole Supérieure des Pêcheries at Ste-Anne-de-la-Pocatière. He undertook studies of the fauna of the estuary of the St. Lawrence River and published an important baseline study on the beluga that is of considerable value today.

In 1958 he left the Département de Pêcheries du Québec and joined the staff of the University of Ottawa as a professor. He remained in this post until his retirement in 1973. He took one year and three month's absence in Iran starting in August 1961, and went on cruises to the Caribbean Sea in 1965, 1966 and 1968 to locate the spawning grounds and study the larvae of the American eel. In Iran he served as a fisheries expert in the Caspian Sea region for FAO. Vadim worked on the sturgeon fisheries important for caviar, but also made significant collections of fishes, many now at the National Museum of Natural Sciences, Ottawa. In Ottawa he taught ichthyology, herpetology, zoogeography, etc. and supervised a number of graduate students.

Prof. Vladykov felt that high quality illustrations were very important in science. He spent considerable time and effort ensuring that the illustrations showed fine detail. George Ben-Tchavtchavadze, a fellow Ukrainian emigrée, worked with Vadim to produce superb photos of larval lampreys, cod tubercles and cod gonads, and P.I. Voevodine made exquisite sepia drawings of skull bones of Pacific salmon (*Oncorhynchus*).

In later years Prof. Vladykov received a number of honours. In 1963 he was elected a Fellow of the Royal Society of Canada. In 1968 a special issue of the 'Věstník Československé společnosti zoologické' was published in honor of his 70th birthday. Following his retirement in 1973 he was appointed professor emeritus at the University of Ottawa and Research Associate at the National Museum of Natural Sciences, National Museums of Canada. In 1975 he was elected an honorary member of the Canadian Society of Zoologists, in November 1976 he received a Doctor of Law, honoris causa degree at Sir Wilfrid Laurier University, Waterloo and in 1978 he received a D.Sc. honoris causa degree from the University of Ottawa.

As a man Vladykov was stocky (about 165 cm) and vigorous. He talked with enthusiasm about his current research or he would look at you piercingly with light blue eyes through his thick glasses (for which he was noted) and strongly criticize your work or that of some noted colleague and then crack a joke. He searched for truth and would not excuse the least error. He marshalled those around him, students, colleagues and family, to help him in his projects, sometimes with scant regard to their priorities and sometimes with diplomacy. His students became fearful of extra work when he approached saying 'You, handsome, strong young man . . .!' But many learned how to carry out research under his tutelage. His views were strongly held and he would disagree with noted figures of his day such as Carl L. Hubbs on lamprey classification and Johannes Schmidt on the location of the spawning grounds for the American eel. His presentations at scientific meetings were salted with humorous comments. He spoke several languages fluently (but all with the famous Vladykov accent). While a dedicated student of taxonomy, he doubted evolution and was a devout member of the Russian Orthodox Church – he was a founding member of the Church of St. Nicholas, a generous contributor to its memorial fund and to the Russian Orthodox seminary in New York.

Despite disputes with colleagues it is accepted that he made major contributions to taxonomy. He was the first one to discover characters enabling identification of larval lampreys, a discovery of great practical importance when sea lampreys invaded the upper Great Lakes and decimated sport and commercial fisheries. Despite imperfect eyesight, he was a keen observer. He was the first to report tubercles on spawning lake charr, a species which had been very well studied. He found differences in velar tentacles which were useful in lamprey taxonomy and was investigating the value of length of the genital papilla in spawning male lampreys up until a short time before his death. As author or co-author (with Prof. E. Kott or students) he described more than one quarter of the world's species of lampreys (10 out of 38), more than any other scientist. While his generic assignments have not been accepted by some of his colleagues, neither have they published refuting evidence. During a career spanning about 63 years he published more than 200 scientific papers.

By the force of his personality, his capacity to question dogma, the keenness of his observation, and his numerous publications Professor Vladykov considerably influenced the development of fish biology in Canada and made his mark in ichthyology worldwide. A dedicated issue of this journal and an anthology in honor of his memory will be published later.

The author is grateful to E.K. Balon, E.W. Burridge, B.W. Coad, C.G. Gruchy, E. Kott, J. McNeill and C. Renaud for information or comments on this obituary.

Japanese Journal of Ichthyology
Vol. 24, No. 1 1977

魚類学雑誌
24巻1号 1977年

謹呈

然別湖産イワナの変異性に関する研究

III. オショロコマ *Salvelinus malma* の地理的変異と然別湖産イワナの形態的特徴

前川光司

Studies on the Variability of the Land-locked Miyabe Char, *Salvelinus malma miyabei*

III. Geographical Variations of the Dolly Varden, *Salvelinus malma*, and Morphological Characters of the Miyabe Char

Koji Maekawa

(Received December 22, 1976)

Geographical variations of some meristic characters of the Dolly Varden, *Salvelinus malma*, which were collected in some districts (Nome, Anchorage, Juneau and Seattle) of North America, Bering Sea, Okhotsk Sea and in some rivers of Hokkaido, were investigated with special reference to the systematics of the Miyabe char, *S. malma miyabei*, in Lake Shikaribetsu in Hokkaido. An obvious "geocline" associated with an increase in the number of vertebrae, gill-rakers, dorsal rays and pored scales of the north American populations was found. Toward the east and toward the uplands, slight increases in the number of vertebrae and pored scale were observed in the land-locked populations of Hokkaido. No significant differences were recognized in the number of anal rays among populations of the Dolly Varden, however, pyloric caeca were slightly fewer in Hokkaido populations than in the others. Meristic characters of the Miyabe char, excepting gill-rakers, were similar to those of Dolly Varden living in Hokkaido. A striking characteristic of the Miyabe char was found in the number of gill-rakers, as well as accessory gill-rakers in the medial surface of the gill arch. Gill-rakers of the Miyabe char were the most numerous among all Dolly Varden investigated. It was discussed that, in relationship to food habitats of the anadromous Dolly Varden, the changes in morphology might be an adaptation to plankton feeding.

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大島 (1938) が北海道然別湖に生息するイワナをミヤベイワナ (*Salvelinus miyabei*) と名づけて以来，幾人かの研究者によって，形態的，生態的，あるいは生理学的な研究が続けられてきた (大島，1938，1961；犬飼・佐藤，1943；稲村・中村，1962；久保，1967；Yoshiyasu, 1973)．しかし形態学的に詳細な研究は少なく，北海道各地に分布するオショロコマ *Salvelinus malma* (Walbaum) との関係も明らかにされていない．

ところで然別湖産イワナの形態的特徴に関する研究は大島 (1938，1961) が18個体の標本をもとに鰓耙数および側線鱗数を調べているし，木村 (1976) および宮地ら (1976) もこのイワナの鰓耙数が多いことを注目している．しかし然別湖産イワナの形態の特殊性を明らかにするためには，オショロコマの形態の地理的変異を検討し，その中から本イワナの位置づけを試みる必要があろう．

北半球に広く分布するオショロコマの地理的変異に関する研究としては，北アメリカで比較的詳細に調べた McPhail (1961) の研究を除けば，Taranets (1937), Schmidt (1950), Andriyashev (1954)の断片的資料があるのみであり，北海道の河川型についても石城(1969)の報告があるのみである．

本論文は北海道産のオショロコマのほか，ベーリング海，オホーツク海および北米の標本を用いてその形態の地理的変異を再検討し，然別湖産イワナの特徴を明らかにすることを目的とした．

材料および方法

河川性および降海性オショロコマの採集は1971年4月から1975年3月までの期間に行なわれた．採集地点および北海道と北米での採集河川名はFig. 1およびTable 1に示す通りである．なおオホーツク海およびベーリング海のオショロコマの標本は北海道区水産研究所，遠洋水産研究所，北海道大学水産学部にそれぞれ保存されていたものを借用した．

然別湖産イワナの標本は，然別湖内の沿岸および湖中央部では刺し網を，注入河川ヤンベツ川では投網および掬網で採集したものを用いた．したがって，これらの標本には沖合型，沿岸型(久保，1967)の両型を含むと考えられる．

採集魚は直ちに約10％ホルマリン液に入れ，研究室に持ち帰って測定を行った．

鰓耙数および幽門垂については実体顕微鏡下で，脊椎骨および背鰭，尻鰭の鰭条はソフテックスで写真撮影した後に数えた．なお脊椎骨の計測では尾部棒状骨は除き，

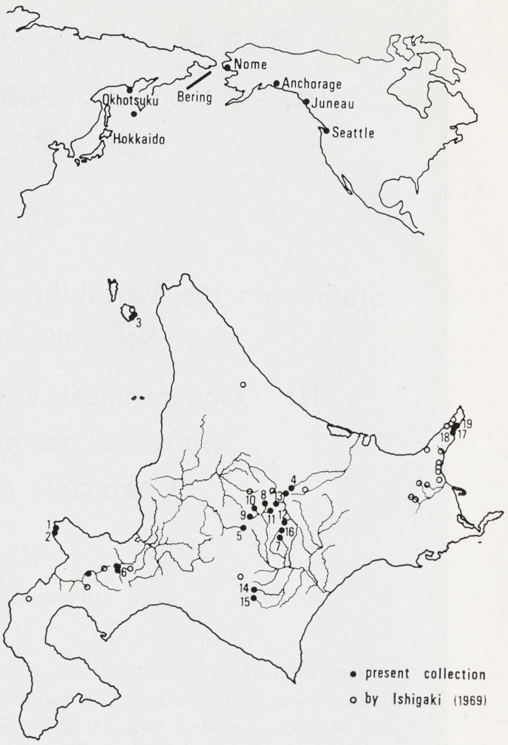

Fig. 1. Areas of capture of the Dolly Varden in Sea of Okhotsk, Bering, and North America (upper), and distribution of the land-locked Dolly Varden and Miyabe char in Hokkaido (lower).

Table 1. Name of rivers and number of specimens of the Dolly Varden and Miyabe char examined in the present study. Figures and tables used in this paper are abbreviated by the number and initial of localities shown in this table.

Name of rivers	Number of specimens	Name of rivers	Number of specimens	Name of rivers	Number of specimens
1. Obukaruishi	11	14. Satsunai	53	A. Anchorage	
2. Notto	6	(by Mr. Komiyama)		Cambell	50
3. A river of Rishiri I.	22	15. Tottabetsu	62	J. Juneau	
4. Tokoro	155	(by Mr. Komiyama)		J(1) Eagle	55
5. Nishitappu	84	16. Shikaribetsu	54	J(2) Switzer	104
6. Lake Bankei	89	17. Shoji	12	J(3) Sheep	13
7. Lake Shikaribetsu		18. Kennebetsu	8	J(4) Gold	13
Yambetsu river	1437	19. Rusa	10	J(5) Sea run form	33
Lake	204	O. Sea of Okhotsk	23	S. Seattle	
Kohan river	27	B. Sea of Bering	18	Skagit	29
8. Nuppun-Tomuraushi	141	N. Nome			
9. Shii-Tokachi	26	N(1) Sun set	58		
10. Tonokarishubetsu	178	N(2) Dry	36		
11. Pon-Tomuraushi	3	N(3) Solomon	17		
12. Nukabira	59	N(4) Penny	12	Total	3121
13. Otofuke	13	N(5) Anvil	6		

鰭条数は前部にある短小な条数を含む全条数を示した．側線有孔鱗は椎骨末端まで数えた．

結　果

1) オショロコマの地理的分布

オショロコマと北極イワナ (*S. alpinus*) の分類学的関係はまだ確定されていない現状にあるので (DeLacy and Morton, 1942; Vladykov, 1954; Walters, 1955; McPhail, 1961; Савваитова, 1961a, 1961b; Berg, 1962; Behnke, 1972)，本報告では一応 McPhail (1961) に従って，オショロコマの地理的分布について概観しておきたい．すなわち，北極イワナは北極海を中心に大西洋まで分布を広げており，然別湖のイワナとの類縁はあるかもしれないけれども，分布上の隔絶その他から，後者はベーリング海以南の太平洋に分布するオショロコマに類縁をもつと考えるのが適当であろう．

McPhail (1961) および McPhail and Lindsey (1970) によれば，アジア側では南限は北朝鮮のヤル川で北はカムチャッカ半島北部の Anadyr 川までである．さらに北アメリカでは南はカリフォルニア州の McCloud 川から北は Mackenzie 水系である．但し，Nome 付近にも分布が認められている (McPhail, 1961)．なお，青柳 (1957) は満州の琿春河で採集したことを報告しているし，Mori (1935) も朝鮮北部の豆満江にオショロコマが生息することに触れている．したがって大陸での南限は朝鮮北部付近であろうと考えられる．

分布南限付近の一つにあたる北海道内の分布は石城 (1969) によって詳しく調査されているが，その他に今回の採集で，新たに次の河川がつけ加えられた．すなわち，利尻島の一河川（無名），知床半島のショウジ川，ケンネベツ川，ルサ川，石狩川水系西達布川，十勝川水系のトムラウシ地方の諸河川および糠平川，音更川，積丹半島オブカルイシ川，尻別川である．その他，日高山系の諸河川（小宮山，未発表）でもオショロコマが採集されている．したがって，北海道でこれまで確認された分布の南限は千走川および日高地方である．北海道のオショロコマは積丹半島および知床半島の諸河川で河口域まで生息しているほかはすべて山地渓流であった．

2) 北海道以外のオショロコマの地理的変異

脊椎骨数　北から南へ連続的に採集された北米産オショロコマの脊椎骨数をみると，Seattle 産から Anchorage 産まですべて 61～67 の範囲にあり，明瞭な差は認められない．モードも 63, 64 のいずれかにあって，地域間に明瞭な差は認めがたい．しかし分布の北限に近い Nome 産では，いずれの河川でもモードが 68, 69 にあり，変異の幅，平均値とも Anchorage 以南よりも明らかに多い（$p<0.05$ で有意）(Fig. 2b)．

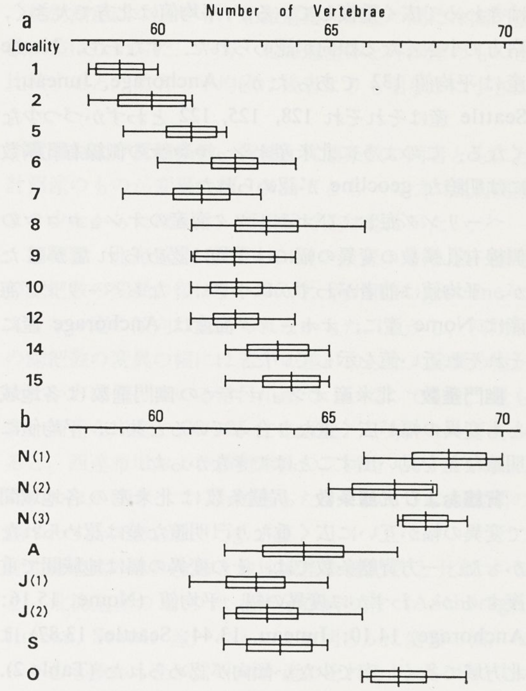

Fig. 2. Geographic variation in number of vertebrae of the Dolly Varden and Miyabe char.

オホーツク海産のオショロコマの脊椎骨数は変異の幅が 66～69，モード 67 であり，Nome 産に近かった．

側線有孔鱗数　北米産オショロコマの側線有孔鱗数についてみると (Fig. 3)，各地域間でそれぞれ変異の幅

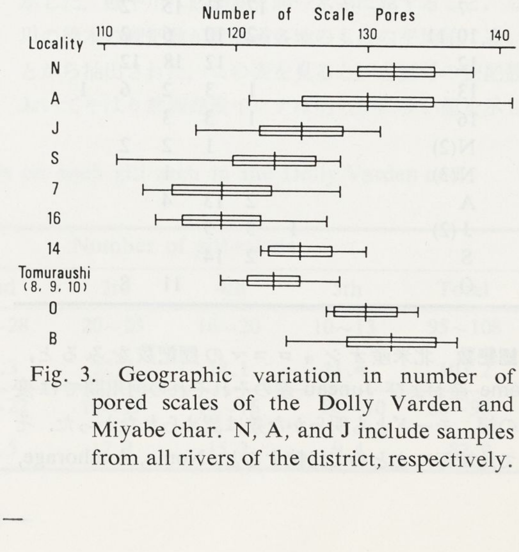

Fig. 3. Geographic variation in number of pored scales of the Dolly Varden and Miyabe char. N, A, and J include samples from all rivers of the district, respectively.

はきわめて広く重複しているが，平均値は北方で大きく，南方で小さくなる傾向が認められた．すなわち，Nome 産は平均値 132 であったが，Anchorage, Juneau, Seattle 産はそれぞれ 128, 125, 122 とわずかづつ少なくなる．このように北米産オショロコマの側線有孔鱗数には明瞭な geocline が認められた．

ベーリング海およびオホーツク海産のオショロコマの側線有孔鱗数の変異の幅には差異は認められなかったが，平均値は前者がわずかに小さい．なおベーリング海産は Nome 産に，オホーツク海産は Anchorage 産にそれぞれ近い値を示していた．

幽門垂数　北米産オショロコマの幽門垂数は各地域とも変異の幅が広く重なり合っていると共に，平均値に明瞭な差を見い出すことはできなかった．

背鰭および尻鰭条数　尻鰭条数は北米産の各地域間で変異の幅が互いに広く重なり，明瞭な差は認められなかった．一方背鰭条数では，その変異の幅は地域間で重複するが，わずかに変異の幅，平均値 (Nome, 15.16; Anchorage, 14.10; Juneau, 13.44; Seattle, 13.87) は北方域で多く，南で少ない傾向が認められた (Table 2).

オホーツク海産の背鰭および尻鰭条数は，Nome 産のそれに近似しており，北米産南方域のものよりも明らかに多かった．

Table 2. Geographic variation in number of dorsal rays of the Dolly Varden *Salvelinus malma* and the Miyabe char, *Salvelinus malma miyabei*.

Locality	Number of dorsal rays							
	11	12	13	14	15	16	17	18
5			1	16	10			
6		1	22	13				
7			17	31	15	2		
8,10,11			2	10	6	2		
12				12	18	12		
13			1	3	2	6	1	
16			1	3	3			
N(2)				1	2	2		
N(3)					1			
A			2	13	4			
J (2)		1	3	5				
S			2	14				
O					11	8		

鰓耙数　北米産オショロコマの鰓耙数をみると，Nome 産および Juneau 産のそれぞれの河川間では変異の幅，モードとも明らかな差は認められなかった．そこで地域毎にまとめて比較すると，Nome, Anchorage, Juneau, Seattle 産のオショロコマの鰓耙数のモードはそれぞれ 21, 18, 17, 16 とわずかに北方域で多く，南方域で少ない傾向が認められた．特に Nome 産と Anchorage 産の間には他地域間 (1～2 本) よりも明らかに大きな差 (3 本) が認められた (Fig. 4b).

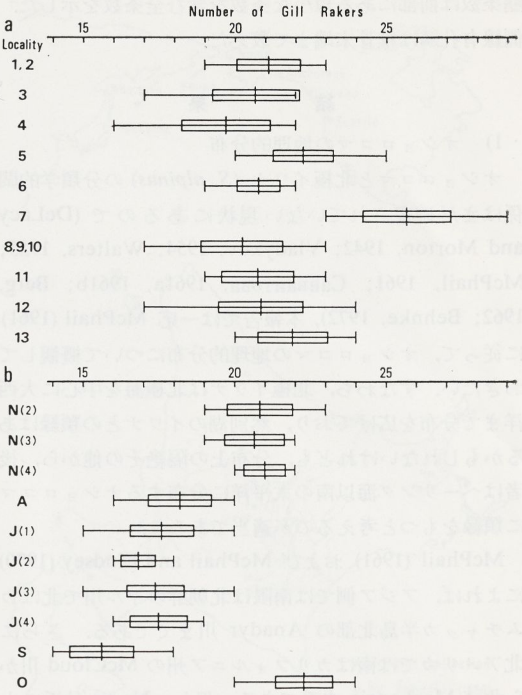

Fig. 4. Geographic variation in number of gill-rakers of the Dolly Varden and Miyabe char.

一方ベーリング海およびオホーツク海産のオショロコマの鰓耙数には明瞭な差は認めがたく，共に Nome 産と変異の幅およびモードともきわめてよく近似していた．このように鰓耙はわずかながら北で多く，南で少ない geocline が認められた．

3) 北海道内のオショロコマの地理的変異

北海道の河川型オショロコマについては石城 (1969) が二，三の形質について地理的変異を調べ，河川間で変異が多いことを述べている．ここでは筆者が採集した河川のうち 13 の河川について述べる．

脊椎骨数　各河川のオショロコマと然別湖産イワナの脊椎骨数を Fig. 2a に示す．

然別湖産を含めて，脊椎骨数の変異の幅は 58～66，モードは 59～64 の間でみられた．この河川間の変異の大きさは北米の河川間の変異よりもきわめて大きかった

が，北海道産を全体としてみれば，Nome 産，オホーツク海産のそれよりも明らかに少なかった．

この形質は北海道内でもきわめて変異に富んでいるが，さらに詳しくみれば次の通りである．すなわち，積丹半島のオブカルイシ川とノット川が最も少なく（変異の幅58～60，モード 59，60），大雪山中央部のトムラウシ地方の諸河川（変異の幅 61～66，モード 62，64），日高山脈の札内川および戸蔦別川（変異の幅 62～65，モード 63，64）と順に多くなる．このように生息域が高くなるに従って変異の幅およびモードがわずかながら多くなる傾向が認められる．石城（1967），前川（1974）の知床半島の河川のオショロコマの脊椎骨数（58～62）と，知床半島の河川と同様，上流から河口付近まで分布しているオブカルイシ川，ノット川を比較すると，より寒冷な地方である前者の方がわずかに多い傾向が認められた．

然別湖産イワナは変異の幅 59～63，モード 61 で，同地方の糠平川（変異の幅 61～66，モード 62）とよく近似しており，北海道内の河川型オショロコマと特に差は認めがたかった．

側線有孔鱗数　調べた 3 河川（札内川，然別川，トムラウシ川）におけるオショロコマの側線有孔鱗数の変異は大幅に重複するが，次のような傾向がみられた．すなわち脊椎骨数と同様に，札内川（平均 125），トムラウシの諸河川（平均 123），然別川（平均 119）の順に平均値は少なくなった（Fig. 3）．

然別湖産は札内川およびトムラウシの両河川より明らかに少なかったが，同一水系で同じ高度（共に 800～900 m）にある然別川のものとは平均値がよく似ていた．

次に北海道全体と外国産のものと比較すると，Seattle，Juneau 産のとよく似た傾向が示されたが，オホーツク，ベーリング海産および Nome 産より明らかに平均値は小さかった．

幽門垂数　幽門垂数は河川間でわずかながら変異の幅，平均値とも差が認められたが，それに一定の傾向を見い出すことはできなかった．

然別湖産についても，北海道産河川型の間には幽門垂数に差はなかった．一方，北海道全体と外国産のものと比較すると，前者の平均値は後者よりも明らかに小さかった．

背鰭および尻鰭条数　背鰭，尻鰭条数の両者ともに万計沼産のものが変異の幅，モードとも一つづつ然別湖産より少なかったほかは，河川間で差は認めがたい．

鰓耙数　北海道内各河川のオショロコマの第一鰓弓の鰓耙数の変異の幅は 16～25 で，河川間に geocline のような一定の傾向は認められなかった．しかし，河川間の鰓耙数の変異の幅には若干の差があった．変異の幅が少ない方に偏っている常呂川産で 16～22 であり，最も多い西達布川産で 20～25 であった．一方，モードをみると，西達布川および積丹半島の二河川（モードは共に 22）のほかはすべて 21 であった．このように河川間の差はわずかであった（Fig. 4a）．

北海道産のもの全体と他地域産の鰓耙数と比較すると，北海道産のものは北米分布域の南（Anchorage，Juneau，Seattle 産）のものより明らかに変異の幅，モードとも多かったが，Nome 産のそれよりモードで 1～2 本少ない傾向が認められた．

一方，然別湖産イワナの鰓耙数の変異の幅およびモードをみると，それぞれ 23～29，26 と多い傾向が認められた．この変異の幅およびモードは北海道内の諸河川の河川型オショロコマの鰓耙数よりそれぞれ下限で 4～7 本，上限で 4～8 本，モードでは 4～5 本多いことを示している．Nome 産やベーリング海産の鰓耙数はそれぞれモード 22～23 であるから，これよりも 3～4 本多いことになる．

次に十勝川水系糠平川産と然別湖産イワナについて，この第 1 ～第 5 鰓弓の鰓耙の数を合せた値を Table 3 に示した．糠平川は然別湖と同一水系に属すること，この川の標本の鰓耙数が北海道各地のものの平均値に近いことから抽出された．この表を見ると，各鰓弓の鰓耙数においてやはり然別湖産イワナは明らかに多い値を示し，

Table 3. Comparison of number of gill-rakers on each gill arch in the Dolly Varden and Miyabe char in Hokkaido.

Locality (Species)		Number of gill-rakers					
	Gill arch	1st	2nd	3rd	4th	5th	Total
Shikaribetsu Lake (Miyabe char)	Range	24～28	24～28	20～23	16～20	10～13	95～108
	Mean	25.7	25.3	22.7	18.1	11.4	103.2
Nukabira River (Dolly Varden)	Range	19～22	18～22	16～19	14～16	80～10	80～90
	Mean	19.9	20.5	17.9	15.2	9.4	82.9

Table 4. Comparison of number of accessory gill-rakers on each gill arch in the Dolly Varden and Miyabe char.

Locality (Species)	Gill arch	Number of accessory gill-rakers			
		1st	2nd	3rd	4th
Shikaribetsu Lake (Miyabe char)	Range	4～12	11～19	14～20	10～13
	Mean	7.5	14.8	16.6	11.4
Nukariba River (Dolly Varden)	Range	0～7	6～13	11～16	8～11
	Mean	3.2	11.0	13.6	9.5

平均値を総計すると 20 本以上の差が認められた．

次に鰓弓の内側で，鰓耙と交互に咬み合う accessory gill-raker の数を調べて Table 4 に示した．この accessory gill-raker も然別湖産が糠平川産よりも各鰓弓で明らかに多かった．

一方，この鰓耙の形態を各地域別に比較してみると，然別湖産イワナは降海型に比べて幾分細く長い傾向が観察された．特に鰓耙数の少ない北米南方型 (McPhail, 1961) の降海型 (Juneau 産) の鰓耙は若干太短くなっていた．

考察

外国産オショロコマの形態のうち，脊椎骨，側線有孔鱗，背鰭々条，鰓耙の数には明らかに一定の変異の傾向が認められた．すなわち北方で多く，南方では少なくなる傾向が現われた．一方，北海道内においても，脊椎骨数，側線有孔鱗数において，北から南へ，又は高地から低地へと明らかな geocline が認められると共に，北海道全体をオホーツク海産やベーリング海産と比較すると，数が少なくなる傾向があった．

しかし，さらに詳しくみれば，北米では脊椎骨数にはアラスカ半島を境として北方型と南方型の二型として現われるのに対し，側線有孔鱗数や鰓耙数ではわずかづつ各地で差が生じ，その結果きわめて明瞭な cline が認められるものであった．

すでに McPhail (1961) は北米産オショロコマについて，アラスカ半島を境として北方型と南方型を認めている．これに従えば，北海道の河川型オショロコマは Nome，ベーリング地方，オホーツク地方に連なる北方型の諸特徴を有していると考えられ，これはオショロコマの分布の拡大経路を地史との関係でみる場合きわめて興味深い．

なお，北海道以外の降海性オショロコマの標本では脊椎骨数の変異が比較的少ないのに対し，北海道の河川残留型では各河川個体群間の脊椎骨数の変異の差が著しいのは互いに地理的に隔離されていることと関係があろう．

魚類の体節的形質における地理的変異は，Hubbs (1922, 1940) を始め多くの研究者によって調べられている (板沢, 1957)．一般的に，体節的形質の数は北で多く，南で少なくなる geocline が認められている．しかしその現われ方はすでに述べたように，すべての体節的あるいは数的形質に現われるわけではない．従来，このような傾向が生じる原因としては発生初期の水温やその他の影響が考えられているが (Ogawa, 1971)，その影響がどの段階で起こるのかは各形質によって異なるとされている．前川 (1977) がすでに述べたように，各形質ができ上る時期はきわめて初期からかなり後期にまでわたっており，影響を受ける時期はそれぞれ異なっていると考えられる．例えば鰓耙の数が揃うのは個体発生後期 (尾叉長約 65.0 mm) になってからである (前川，準備中)．このようにその変異の現われ方は外部の物理的影響と種の発育過程に応じて現われるものと考えられる．

さて然別湖のイワナについて見れば，鰓耙を除く諸形質は，北海道の河川型オショロコマと何ら変るところは認められなかった．すなわち，全体としてみれば南限付近の物理的影響を強く受けているとみることができる．

しかし，北海道産河川型オショロコマの鰓耙数が geocline に従ってわずかに少なくなっているのに対し，然別湖産のイワナのそれは統計的検討の必要もないほど多く，accessory gill-raker の数および長さや太さ等の形質までも若干相違している．大島 (1938, 1961) が，少数例ではあるがこのイワナの鰓耙数を調べ，それが 21～26 と記しているが，大島および他の日本の研究者 (青柳，1957；稲村・中村，1962；宮地ら，1972) もこの点について考察しなかった．最近になって，木村 (1976) および宮地ら (1976) が鰓耙数に注目し始めた．さらに Behnke (1972) はイワナ属の湖沼型を論ずる中に，大島のこの測定値から本イワナを，鰓耙数が 30 以上にも達する北極イワナ *S. alpinus* のレリックであろうと推論

した．

然別湖のイワナのように鰓耙数が明らかに多い例を Behnke (1972) は湖沼に生息するイワナの系統を論ずる際に多数報告している．さらに Taranets (1937) が Okhota 川の上流の湖から報告した *S. neiva* Taranets があり，これは鰓耙数 26～33，脊椎骨 64～66，幽門垂 39～49 で，*S. alpinus* に類似しているが，その後の研究がない．次に最近，McCart (1971) はアラスカ北極海の Sagavanirktok 川の上流の湖で降海型の鰓耙数 (19～27) よりも多い 24～33 の鰓耙数をもつ個体群を報告している．McCart は後者が McPhail (1961) に従って北極イワナの北極海東部型のレリックであることを示唆している．

このように，然別湖のイワナの調べた形態のうち，鰓耙のみが地理的クラインからはずれてきわめて多くなっている．上述した通り，イワナ属は形態的に変異に富むので，この形質が変化して現在にいたったものであるか又はレリックであるかを速断するのは難しい．しかしこの点については，分類上重要な意味をもつので，他の形態の検討や体各部の相対成長を含めてあらためて別稿で論議したい．さて，降海型オショロコマは海洋では魚食性とされているが (Roos, 1959)，一方，然別湖のイワナは古くからプランクトン食者として知られていた（北海道水産試験場，1933; 羽田・富田，1949）．これは然別湖形成以来，本イワナのみが在来種であり，他の魚種が生息していなかったことと関係している．この食性は多くの魚種が移植された現在でもよく保たれている（前川，1977）．普通プランクトン食性の魚類の鰓耙は数が多く，細長くなることはよく知られている事実である（松原ら，1965）．例えばオショロコマと同じサケ科に属するベニザケ *Oncorhynchus nerka* はサケ属の中でもプランクトン食の強い魚種であるが，サケ属の他の魚種よりも数が幾分多くかつ長い鰓耙を持っている (Hikita, 1962)．そして然別湖産イワナの鰓耙は数・形態ともこのベニザケによく似ているのである．さらに Martin and Sandercock (1967) はイワナ属魚類 *S. namaycush* (lake trout) の食性に応じて鰓耙がどのように変異するかを調べ，プランクトン食の傾向の強い個体群の方がそうでない個体群より，数も多く，また長くなることを報告している．したがって，本イワナの餌の選択性の実験的解明という課題を将来に残しながらも，北太平洋に分布するオショロコマに比較すれば，然別湖産イワナはきわめて高率にプランクトンを食べるための適応的構造を有していると考えられる．

謝辞

本研究に対して，常に有益な助言を頂いた北海道大学農学部森樊須教授，ならびに種々有益な助言と原稿の校閲をしていただいた同農学部阿部永助教授，北海道さけ・ますふ化場疋田豊彦博士に深く謝意を表する．また終始御指導して下さった北海道大学農学部石城謙吉助教授は北海道内のオショロコマの分布に関する資料の引用も許された．深く謝意を表する．さらに下記の方々には，研究上の便宜や助言，又採集の援助などを頂いた．北海道大学歯学部口腔解剖学教室　中根文雄教授，　同　大泰司紀之講師，　同　八谷昇氏，　同　寺崎純子氏，Alaska Department of Fish & Game の R.E. Armstrong 氏，北海道大学農学部応用動物学教室　井上聡博士，同大学院小宮山英重氏，同水産学部元教授　岡田篤博士，然別湖自然保護管理人　阿部佐美雄氏，水産庁北海道区水産研究所の方々，ここに記して深く感謝する．なお，本論文は北海道大学農学部学位請求論文の一部である．

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OFFICE MEMO

TO:

Date

FROM: Vasilyeva, E. D. 1981. ~~Lake~~ Lacustrine char,

SUBJECT: S. a., from the Zarubikha River basin. V.I 21(2): J. I. 26-42

REMARKS:

- Kola Pen. - paliya and golets from L. Noskovoye - near Barent Sea - separated spawning char = paliya (bright) golets (dull) - feeding - one sentime - In Aug. terrestrial insects > aquatic mollusca, - age-growth : both small, slow growing - golets 11 yrs, paliya 12 yrs

but max. golets 36 cm 378 mm - max paliya 41 cm 413 mm

golets ♂ N=27	♀ N=28	paliya ♂ N=14	♀ N=1
19-26 (22.8)		22-26	25
23	20-26 (23.1)	(23.7)	24
2			
vt. 59-64	60-66	62-65	62
643 ±.31	61.9	63.4 ±.51	
czeca 36-55 $\binom{44.2}{43.0}$		38-52 (44.5)	

- paliya. longer fins
- longer jaws
- longer head & snout

- but concludes both only variation in single pop. of S. alpinus.

OFFICE MEMO

Borisovets, E. E. 1982. Discriminant analysis of

TO: Date

FROM: diadromous char of genus *Salvelinus* of

the Chukotsk Peninsula, V. I. 22(3):365-373

SUBJECT:

morphol.

REMARKS: 3 characters : 1. least body depth h

2, anal fin height (length) h A

3 width of maxillary (h max).

:551 specimens *malma* & *alpinus* fm 4 rivers & lakes ~~waters~~

99.7% correct ID – i.e. .27% incorrectly classified.

>99%.

S. Kronocius sp. n. longhead charr

to 70 cm

rakers 18-26 (24) branch. 10-15 (12) schmidti (10), vert 63-68 (66)

caeca 24-43

Karyotype	NF	N	m+sm	st+t
S. m m.	48	38-39	9-10	28-30
m. krash	49	41-42	7-8	33-35
m. curil	50	42-43	7-8	34-36
m. schmidti	49	39-41	8-10	29-33
(white?) m. sp.	49	39-40	9-10	29-31
confluentis	51	39	12	27
Kronocius	50	39-41	9-11	32-28
leucom.	50	42-43	7-8	34-36
Hucho taimen	51	42	9	33
Brch. lenok	51	46	5	41

In Kronotskoe L.

- S. m. schmidti -
- White char (S. albus)
- long head S. kronocius
- + S. leucomaenis

→	longhead	Nose	White	river malma	Sea malma	leucomaenis
max l.	70 cm	51	86	40	58	107
	18-26 (22.1)	15-24 (19.1)	17-24 (20.4)	17-25 (21.1)	18-25 (21.5)	12-20 (17.2)
	24-43	23-38		23-41?		11-33

Inst. FW Res. Drottingholm Rep. 59 (1981)

- Results of Int. new fish food organisms into Swedish lakes, M. Fürst - 33-47

- Impacts of Mysis on zooplankton : 64 -

- Feeding Mysis on Macrozooplankton - Kootenay
- will consume copepods after cladocerans depleted

- ~~A~~fertiliz. of reservoirs - reverse oligotrophication

SH 287 D73

Nyman, L., J. Hammar, & R. Gydemo. 1980. The systematics and biology of landlocked populations of Arctic char from northern Europe. Ibid: 128-141.

- lack of intergeneric hybrid sterility

- Ferguson > 60 proteins, 27 loci of Irish char examined no consistant dif. of any - except serum esterase. - Clayton & Ihssen ~~found~~ eye LDH polymorphism in Nottling L. -- S. alpinus complex extreme low level genetic polymorphism .. * might assume could be prone to become extinct due to lack genetic variability - but ecological plasticity belies this.

- Svardson -- reproductive isolation achieved allopatrically in preglacial, interglacial times, w/ subsequent invasion of post glacial river system = this explains the distribution of the 3 species. - fact that many capable of reproductive isolation in small lakes w/ limited diversity is good evidence that ancestral species reached full rank of functional species. - but many instances of introgression.

S. alpinus: Linn. - Swed. Lappland - high altitude lakes above timberline - Probably small headwater lakes

of Tarrejokk R. NW of Kvickjokk, Lapland,
> 800 m " – synonomics given
= "F" char "F tita", 'F-drawf', 'blattjen' –
littoral or benthic, when w/ others; more deep living
benthic fauna = fish, least competitive sp.
most frequent headwater sp. freq. most anodal
esterase allele .9 - 1.0 – typically stunted when
sympatric, but may be large when allopatric
– Range Sweden, Norway, Iceland, Great Britain,
Ireland, perhaps Newfoundland.

S. salvelinus : Type loc. (Artedi) – lake in
Austria near Linz. – *No Austrian specimens used*.
Thus, naming may be premature (No mention
Alp char have 25-30+ rakers).
large, predatory charr, "N" charr – only
char of south. Sweden. L. Vattern, large
lakes. – Sweden, Norway, Great Britain, Ireland,
Iceland. ~ esterase anodal allele .4 - .7 but may
be fixed at 1.0 in small pop. by genetic drift

S. stagnalis
– Fabricius 1780. Greenland.
= "S" char, 'S-Tita', T, drawf – rarely exceeds
30cm; mostly pelagic plankton feeder.
esterase anodal allele .0 - 0.2 fixation at 0

Introgressed populations.
L. B7å sjon : stagnalis (f EST F = .07), salvelinus
(.17 - usually ca. .50) ; L. Yraf; stagnalis (.28), salvelinus (.50)
L. Batsven –, stagnalis (.15) salvelinus (.5)
dumb, wow! S. salvelinus x S. alpinus (both have freq. ca .90) in L. Stora Rösjön.
gene flow between very small!! – but same evidence used above to assess gene flow

~~Nilsson~~ Nyman 81
II

L. Övre Björkvattnet *salvelinus* (.70) *alpinus* (1.0)
(pelagic written above *salvelinus*, littoral above *alpinus*)

L. Bjellojaure: *salvelinus* (.65) *alpinus* (.92)

alpinus x *stagnalis* ? - *stagnalis* freq. altered fm. .15 to .46 in L. Fättjaure (! heavens salve-lit. full of such allelic dif. in spp. w/ no question that completely natural & not due to hybrid influence) - *alpinus* altered from .95 to .61

L. Sitasjaure - *salvelinus* x *stagnalis* x *alpinus*
freq (.25) (.22) (.58)

- "Adds a new dimension to the view of treating all Mendelian polymorphisms as simple population markers" (I'll say! - population markers now become "species markers", Folia Balcanica QL 614 F6 vol 1-2

56-71 Karaman - Radika Trout
Zuckerman* - new isopod in interest

English translation Allerton Press

Nesterov, V.D. and K.A. Savvaitova. 1981. Taxonomic position of migratory chars of the genus Salvelinus (Salmonidae, Salmoniformes) from Chesa Bay of the Barents Sea. Vest. Moskov. Univ. 36 (1): 20-24

- Indiga R. → Chesa Bay.
Sept. 77

Age	3+	4+	5+	6+	7+
cm	37.7	41.5	44.5	48.5	48.6
kg	.6	.9	1.2	1.4	1.4

- Only anad. char in Indiga R. run begins mid June - to late Sept. - start of run largest fish enter - max. size to 58.3 cm - 2.5 kg, max age 7 yrs - most 5-6 yo in run - vs. Kara R. age 10-11.

scales	120-137	(129)
rakers	21-28	(24.3)
caeca	30-46	(37.5)
vert.	62-65	(63)

Behnke (72) suggested Chesha Bay - Kanin Pen char as subsp. only : 18-21 : - Survorov suggest. - relation to Pac. Dolly Varden post glacial warming Pacif immigrants to White Sea = Clupea harengus pallasi maris albi, Lampetra japonica septetrionalis, Osmerus eperlanus dentex. - a polychaete Sculibregma robusta - - "We can assume that Pac. Dolly Varden also penetrated into ~~White~~ Barents Sea. - perhaps char an endemic relict - gillraker no. ambiguous - based on Indiga R - char of of alpinoid type of S. alpinus Sav. & Volobuev - 1978 - Zool. Zhur. 57(1): 1534-44

E. K. Balon, Dept. Zool. Univ Guelph
Guelph Ont. Can. N1G 2W1

reprint. Obit. + Comparative catches and food habits of dolly varden and arctic charrs - - -

- - - wonderful homo Env. Biol Fish. 7 (1).

Bert van der Veen 6/9 Avila

andriashevi – N. Pacific (W. Bering, Gulf Alaska) –
symp. Dolly Varden.
– all symp. w/in subsp. !! 4 in L. Lama.
– symp. spec ?? – Taimyr – glacial – ocean
• Transgressions – isolation – interconnection –

* Obsession taxonomic rectitude! –
w/in sp. subsp. – enormous variability w/
genetic basis – niche special – plasticity
ability coexistence – mgt. utiliz.
implications — ability accumulate biomass
ultra oligotrophic lakes —
natural distrib – mainly 100 km of Arctic Ocean
– tremendous for introd. —
* N. Am. – mysis – ruined salmon O. nerka
fisheries. –

Slides

Sunapee – Rangeley – Candlestick Pond Newt
– tremendous dif. growth, age, size, feeding on
sp. assoc., lake morphom. (vol. food hypolimn.)
large top pred. or dwarf bush – potential wider
realized niche –
~~Nyman~~ Impt. of Limnol. (lake morphometry) – hypolimnion
10° – volume, food, – Sunapee, Rangeley, Candlestick
Sawtooth
* – Loci – 25-30 – fontinalis / namaycush .
— Klemetsen – N. Norway – no correl. w/ Nyman Sweden
Gydemo
Dodson

* Esteraki – homology –
– if S. fontinalis –
J.

Thingvallav
.89 blejks
.74 bjeks
.80 murts
– sq. tail
① odd vert – small spots – bright colors
typ. alpinus – large spots – dull colors

Epidemio Reliability .72

.64 (.9

.64 \ 2-3 studies

symptom..

prob. dietary study — (cannibalism

.43

→ 2-3 yrs 12kiy

V.I. → Jour. Ichthyol. - send   3.N.K. Copeia 1961
Herzen str 6
Mockva. DSP —
Jerry Smith - Parasalmo

S. c. Rio Fuerte 2N = 60 : 104
Mayo, Yaqui, " 64 104
above falls Rio Chico   S. c. 60 104
" Tomachic

find. in Parasalmo 100 + 4 pericent. = 104

* Eschmeyer - S. chrysogaster spec.

S confluentis 2N 78 102 arms
same as longhead - S. kronocoesis

- Spec. Dorofeeva
- gila, apache, golden, cutt + Salv. fr Chereshnev
- Cavender - Morton - received spec. - chondrocranium

ВИКТОРОВСКИЙ, Р. М. 1978.
Механизмы видообразования у
гольцов. (Издательство "Наука", publisher
Москва). Акад. Наук СССР, Дальневосточ-
ный научный центр институт биологии
моря - ; 110 р.
S. malma schmidti - Nose charr
rakers 15-24 (20) caeca 23-37 ; vert. 63-68 (66)

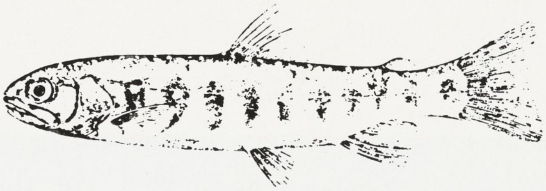
Hindar, K. and B. Jonsson, 1982. Habitat and food segregation of drawf and normal Arctic charr (Salvelinus alpinus) from Vangsvatnet Lake, western Norway. ~~J.C.~~ C. J. F. A. S. 39(7): 1030-1045.

drawf, pale "morph", large, bright colored 'morph'

- both forms - same gillrakers 25.2 (dwarf) 25.5 (normal) not signif. dif.

- Also S. trutta, S. salar - good, detailed data feeding thru year & habitat selection

occurrence Sympatric ~~morphs~~ ~~to~~ depend on niche availability (lake morphometry, species associations) and are local phenomenon.



南限地帯のイワナ

The Southernmost Charrs of the World

安江安宣

岡山大学名誉教授・農学博士

Prof. Emeritus, Dr. Y. Yasue, Okayama University

別冊「フィシング」イワナ・ヤマメ，59〜66頁抜刷
昭和56年5月20日発行

Reprinted from The "Fishing" Special,
Iwana·Yamame (Charrs and Trout), pp. 59-66.

May, 1981. Tokyo

I サケ・マス類の生態地理

伯耆大山、大休峠のブナ天然林

われわれが生をうけている地球という惑星は太陽エネルギーの恩恵をうけ、南北両半球とも赤道をはさんで、寒帯、温帯、熱帯の三気候区に分かれる。それぞれ特有の動植物が繁茂して独特の景観をつくっていることはいうまでもない。この生物相のちがいは気候にもとずくばかりでなく、オーストラリアの有袋類のように地質年代、地理的隔離、大陸移動説などの要因も加わり、特に温帯では洪積世に起こった氷河期の影響を強く受けており、両者相俟ってこの地球は今日みるような華麗多端な衣裳をまとっているわけである。

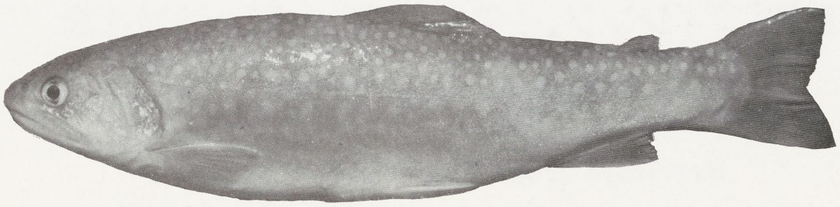
さてわが国の溪流魚の主体を占める淡水魚にはウグイ、アブラハヤなどコイ科のものもいるが、ヤマメ、アマゴ、イワナ、など分類学上ではサケ科にぞくするものが多い。

東亜特産のアユはその特異性から、一科一属一種の独立国家となっているが、もとはれっきとしたサケ科の魚であった。

サケ科魚類は本来北半球の寒帯から温帯北部の海洋にのみ分布しており、いま南半球でみられるマス類はすべて一九世紀になってからの人為的放流である。

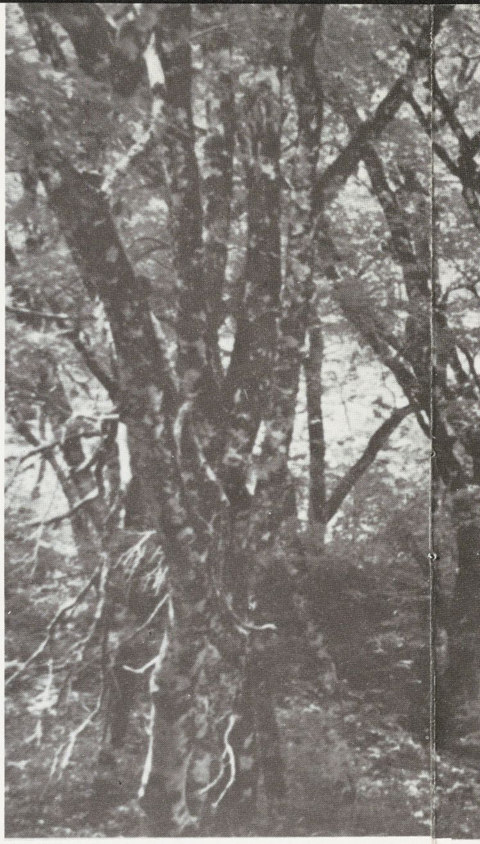
イワナ、ヤマメと生息環境の立地条件が似ている北半球起源の随伴生物をあげると日本では、ブナノキ、ヤグルマソウ(ユキノシタ科)、カワシンジュガイ、川虫ではヒラタカゲロウがある。ヨーロッパではニレの木をあげる学者もいる。南半球ではブナにかわって、常緑広葉樹のナンキョクブナ(ミナミブナ)の森林が山々の中腹をしめ、この地帯では北半球から移殖したマス類がよく育っている。

いままでは巨視的な観点から地球上のサケ・マス類の生息環境の由来を述べたが、ひとつの河川について源流から河口までの流路を考えてみよう。川においてイワナ、ヤマメがすみ分けている事実を名釣り師でもあった文豪幸田露伴の随筆集『潮待ち草』から紹介する。



北陸、石川県手取川(三の宮谷)のイワナ(全長25cm)
Salvelinus leucomaenis f. Pluvius

このことは今日の動物生態学ではすみ分け現象の好例として教科書にも引用されているくらい周知の事実である。しかし明治三九年（一九〇六年）という時点、今日隆盛をきわめている英米の生態学会がまだ発足してもいなかったころ、既に露伴が気づいている点はその自然観照の眼の鋭さにはまったく敬服のほかはない。



II

南限附近のイワナたち

香魚（あゆ）の居るわたりより猶（なお）川上に
至れば、香魚居らざるなりて山鯇（やまめ）
居り、やまめ居るあたりより猶又
川上に至れば、山鯇居らずなりて
嘉魚（いわな）のみ棲むなり

（ふりがなは筆者）

サケ科のなかではイトウ属**Hucho**とならんで、もっとも原始的形態をのこしているといわれるイワナ属**Salvelinus**は主として北半球の寒冷な海洋に生育し、産卵期にはサケと同じく沿岸の河川に溯上する。なかには終生降海しないで内陸の河川や湖沼ですごし、陸封型となって特殊な分化をとげているものが多く、イワナ属の分類の困難さのもととなっている。この世界における地理的分布を示すと第**1**図のように、北極を中心に北緯三四、五度以北の海洋、河川に分布する。図の小黒点は陸封種を意味する。

この分布図から南限のイワナについて探ぐると、北米大陸大西洋沿岸では米国東部アパラチア山脈に広く生息しているカワマス **Salvelinus** （**Baione**） **fontinalis**がもっとも南方種となり、その南限はジョージア州北部（北緯約三四度）とおもわれる。ご承知のようにカワマスはニジマス**Salmo**（**Salmo**）**gardnerii** やブラウントラウト**Salmo**（**Salmo**）**trutta** とともに世界各地へさかんに移殖放流されている。カナダ、ゲルフ大学のマックリモン博士（**H・R・Mac Crimmon,1968～1971**）はこの三種のマス類の各国における放流先を詳しく追跡調査した結果、カワマスだけは放流受入国での成績が著しく劣ることを報告している。

次に北米大陸太平洋沿岸におけるイワナの南限は加州北部カスケード山脈のシャスタ山（**4386m**）南麗のマックロード川**Mc・Cloud River**にいる陸封のブルイワナ（**bull charr**）**Salvelinus confluentus** で、この川はサンフランシスコ湾に注ぐサクラメント川の上流にあたる。その位置は約西経一二二度、北緯四一度一五分になる。

欧亜大陸の西端を占める欧州ではイワナ属の宗家格といえる北極イワナ（アルプスイワナ）**Salvelinus alpinus** が北極海から北大西洋の東岸を南下し、イギリス諸島やアルプス山岳地帯が南限となっている。

標高三、〇〇〇メートルを越すピレネー山脈には氷河が懸っている高山もあるが、イワナの天然分布はなく、現在みられるのは放流ものにすぎない。

因みに欧洲大陸の陸封性イワナの分布南限に近いオーストリアの山岳地帯では琵琶湖の小鮎より小さい成魚で一〇センチ前後の体長しかないコビトイワナ（**dwarfed charr**）が発見されている。それは標高一、二一八メートルの高山湖、デスナー湖に産し、成長がおそく、湖中に発生するユスリ

イワナ属の北半球における分布——第1図

カ幼虫を食餌としているらしい。分類上はコビトイワナは北極イワナに属する。（E. K. Balon & T. Penczak, 1980）

また欧亜大陸の南縁にのぞむインド半島の河川にはサケ科の魚は放流もの以外記録はない。したがって世界の屋根といわれるヒマラヤ山脈の南斜面には土産のイワナ、マス類はおらず、生態的に空白となった山中の溪流には、コイ科の冷水を好むアスラ Schizothorax spp. などが生息する。（M. C. Paint, 1970; 西山, 1976.）ただ西方カラコルム、ヒンズークシ山脈の北斜面では中央アジアのアラル海からアムダリアをへてオキサス川に、ブラウントラウトの一種オキサスマス *Salmo trutta oxianus* が分布する。またカシミール地方では英領時代にブラウントラウトを一八八九年に放流したものが現在よく繁殖して遊漁の対象となっているのは有名である。最近ではネパールにも移殖された。（MacClimmon & Marshall, 1968）

III 本州のイワナの南限

わが国は太平洋の西北隅に位置し、その沿岸はベーリング海峡やオホーツク海から流出する寒流が親潮となって沿岸を洗っている関係上、サケ、マス等の冷水魚が遠く九州あたりまで南下する。広大な太平洋をはさんで、緯度のうえからみて米国とほぼ同位置なので、イワナ類の南限点は米大陸、東亜のそれが奇しくも共に国土内にもつ点で両国は完全に一致する。

さて日本に産するイワナ類だが、この分類はその変異型の多様性から魚類学者により難事とされ、明治以来内外多数の専門家の報告がなされてきた。要するにわが国のイワナ属魚類 *Salvelinus* は北海道と本州にかぎり生息し、四国や九州では陸封型はもちろん、北方からの回遊魚もその姿をみない。東北地方から北と日本海にうかぶ佐渡島では降海性のイワナとなる。なお隠岐島には分布しない。日本全体についてのイワナ属に関する地理的分布図は詳細なものが発表されているので、これを参照してもらう（吉安克彦、釣の友、二二一号、昭和四十四年八月及淡水魚増刊、イワナ特集号、昭和五十五年四月）。

結局日本全体からみると近畿地方以西の山岳地帯を流れる特に紀伊半島と中国地方諸溪流の最奥の源流に、細々と隠遁者のように生息している陸封イワナが、わが国や欧州を含めて欧亜大陸における南限地帯のイワナということになる。

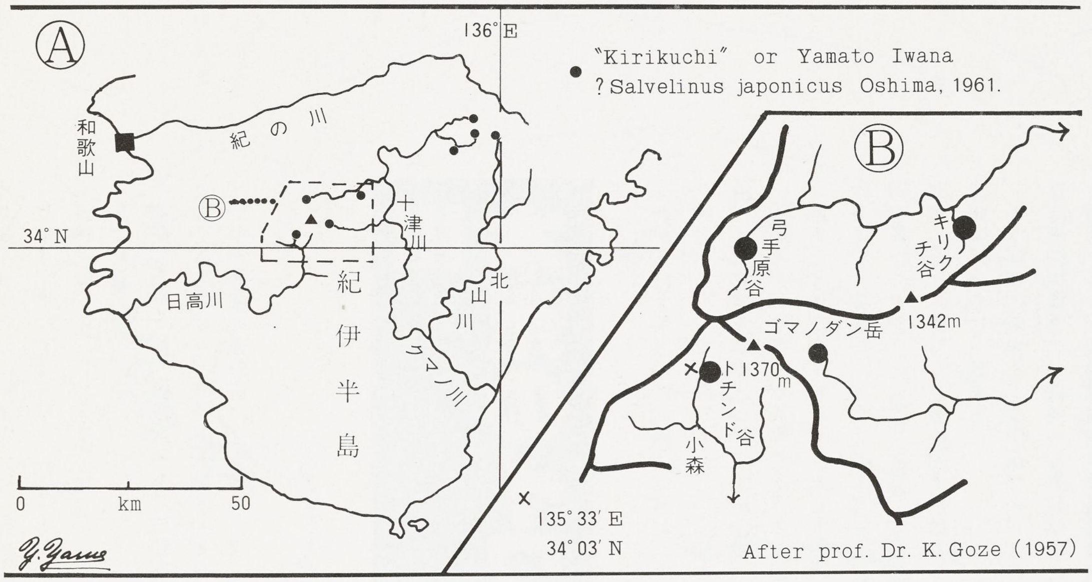
ところで紀伊半島や中国地方にいるイワナを取りあげるにあたり、問題は米国東部アパラチア山脈南端にいるカワマスとの相対的関係だ。カワマスの天然分布をしめす地図はこれまでも数回発表されているが、いずれも世界図的なものばかりで、局地的に適確に生息地点をあらわしたものは筆者には未見、米国東部の地形図から判断するとカワマスの生息地とされる山脈南端はジョージア州の州都アトランタ市より北方で、隣接する北カロライナ州境（カワマスを産す）より南の山岳地域と考えられる。緯度からみると北緯三四度から三五度にあたる。

とすれば緯度のうえではわが国のイワナ類の南限地とほぼ同じ位置にあたる。

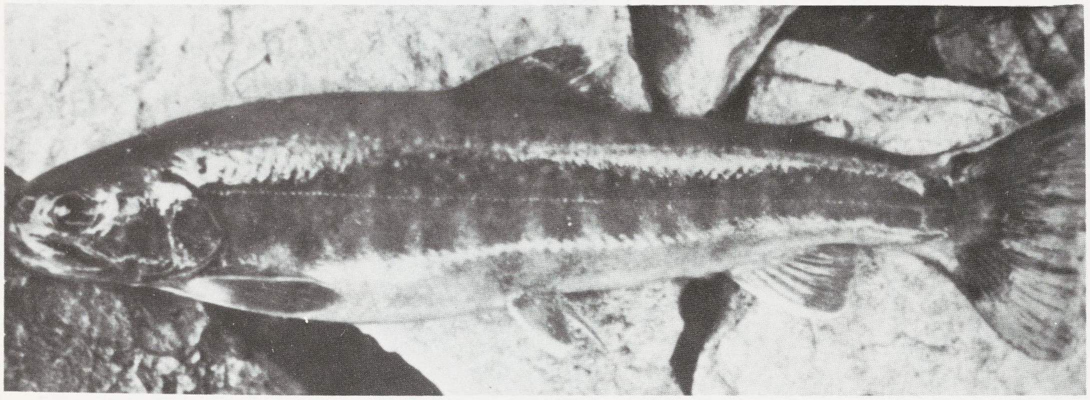
コロラド州立大学のベンケ博士は陸封性サケ・マス類研究の第一線で活躍する専門家だが、昨年世界におけるイワナ属を整理し系統分類に関する有益な総説を発表した。（R. J. Behnke: A systematic review of the genus Salvelinus. 1980）. この論文で彼は日本のイワナはイワナ属のなかでは世界最南限 Southermost distribution of the genus と記している。

IV 紀伊半島のイワナ

世界最南限のイワナ、紀伊半島の〝キリクチ〞の地理的分布——第2図



紀伊半島のイワナ、〝キリクチ（吉安克彦博士、釣の友、221号、1969年より）



紀伊半島でイワナのいるところは奈良県十津川上流、川迫川の大峯山系、山上か岳（一七二〇メートル）周辺の小谷、同じく十津川の支流、川原樋川の源にそびえる護摩の壇岳（一三七〇メートル）周辺の小谷のみであって、不思議に大台が原山（一六九五メートル）には分布をみない。紀伊半島のイワナは、昔から方言でキリクチと呼んでいる。これは眼玉のうしろの方まで、大きく口が裂けているためらしい。

産地は第2図Aで示したように山上が岳頂上直下から急斜面の山腹を南流する神童寺谷、反対に北側を吉野郡天川村洞川へくだる蓮華坂谷、山上川の奥、神童寺谷出合いで南から合流する小壺谷、彌山の八經が岳（一九一五メートル）から発し北流して川迫川に合する彌山川の双門の大滝より上流の部分（ここは県指定永年禁漁区）、神童寺谷とは尾根をはさんで東側にあり、北山川の最源流になる西原谷（移殖放流）。これまでが大峯山系のうち今まで記録のあるイワナの生息地である。

次に護摩の壇岳周辺について述べると（第2図Bを参照）奈良県吉野郡野迫川村にあって、川原樋川が護摩の壇岳の尾根筋から北流する弓手原谷（奈良県天然記念物指定捕獲禁止）、この下流右岸の支谷キリクチ谷、十津川村川津で本流に入る神納川源流地区、

このほか護摩の壇岳西南尾根にかかる日高川の上流、小森谷左岸のトチンド谷（和歌山県日高郡竜神村字小森）。以上がいわゆるキリクチと称する紀伊半島のイワナで従来記録のみられる産地をあげた。因みに釣り場については山本素石氏著「西日本の山釣」（昭和四八年刊）に詳しい。

せんじつめると第2図で明らかなように、今のところ紀伊半島においてイワナの最南限生息地は日高川源流のトチンド谷か、小森谷とは尾根越しに北流する川原樋川上流の弓手原谷（奈良県吉野郡野迫川村）ということになる。念のため国土地理院地形図からトチンド谷出合地点の位置を計測すると、東経一三五度三三分、北緯三四度〇三分であり、弓手原谷は約北緯三四度〇七分となる。これに対し中国地方に生息するイワナの一種ゴギ **Salvelinus leucomaenis imbrius** の南限は山口県都濃郡鹿野町北方の錦川上流（片山・藤岡、一九六五）となっており、緯度にすると北緯三四度一〇分以北に位置する。したがって日本の、いや世界におけるイワナ属 **Genus Salvelinus** の南限地点は若しキリクチが健在であれば、前記のとおり和歌山県日高郡竜神村のトチンド谷に落着く。最近の風説ではこの貴重なイワナも風水害や森林皆伐などのため繁殖が良くないときく。事実なら何らかの保護対策を講ずる要があるのではないか。

V

キリクチの研究

ところで紀伊半島のイワナは近畿地方北部の例えば鈴鹿山脈のイワナ地域から距離的には二〇〇キロ近く南へ隔絶されており、お互いの集団のあいだには遺伝子交換がないものと考えねばならない。またキリクチという独特の方言もあることから、本州中央部にすむ本来のイワナの母集団とはちがった変り者がでてきてもよさそうに思える。

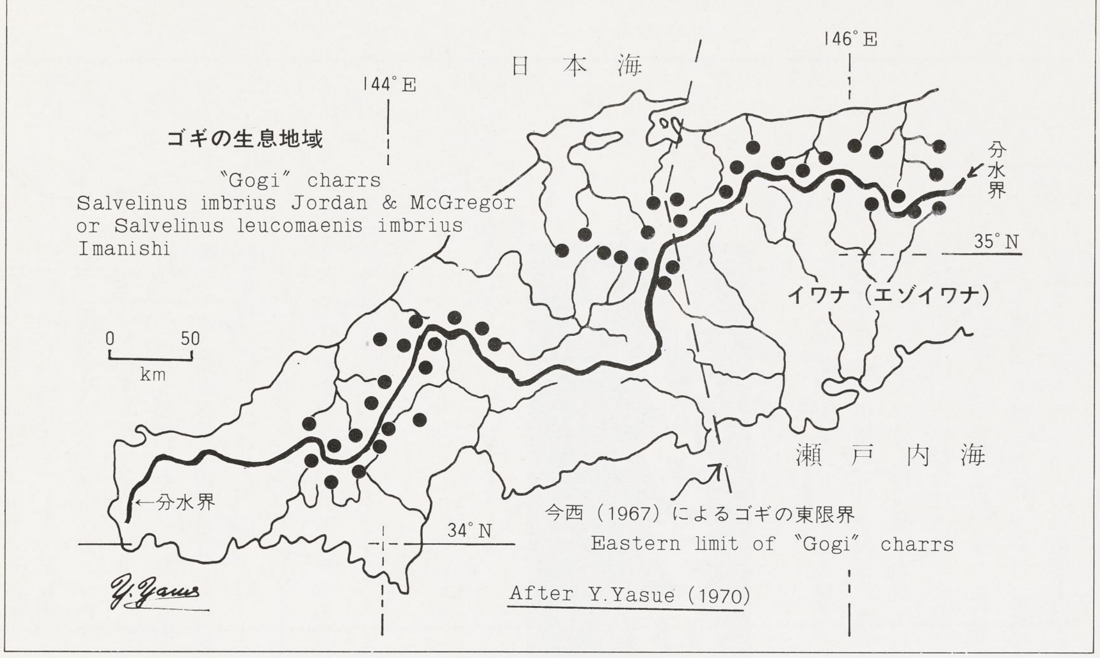
大島正満博士（一九三八）は最初にキリクチの特異性に気づいた黒岩恒氏（一九二六）の慫慂もあり、この溪流魚の側線鱗数の多いこと、鰓耙数の少ない点などに注目した。しかし結局彼は木曽谷や岐阜県の益田川にいるイワナと同系統であるとしてヤマトイワナ **Salvelinus japonicus Oshima, 1961** という新種にキリクチをふくめた。

また吉安克彦博士（一九六九）はキリクチの鱗相は他地域のイワナ類とは異り、鱗の核心部が著しく基部に偏している事実を認めた。

また、キリクチもふくめた各地のイワナについて血液中へモグロビンの電気泳動像を観察し、この研究手段ではアメマス **Salvelinus leucomaenis** とは互いに区別できないという。要するにキリクチは最初黒岩氏（一九二六）が指摘したように総じて表現型についていえば体色が真黒に近く、背上は体色が暗色なので頭から尾部まで全くイワナ特有の白斑を見わけにくい個体が多いのが特色であるらしい。

温血動物では有名なグロージャーの法則がある。それは例えばクマのように北方種ほど体色が白くなり、南方種ほど黒くなる。アマミノクロウサギなどはその好例。冷血脊稚動物の魚類にもこの法則があてはまるのであろうか？生物地理学上からみて特異な立地条件にその生息範囲をもつキリクチと称するイワナに関しては、現在まで学問上、系統的な基礎的研究が殆んどなされていない。このまま幻の魚となって絶滅にむかうようなことにならぬよう念願するばかりである。

中国地方におけるイワナ属(Salvelinus spp.)の分布——第3図



VI 中国地方のゴギについて

与えられた紙数はすでにつきてしまい、本州の西端に位置する中国地方特産のイワナの一種ゴギ **Salvelinus imbrius** (**S. leucomaenis imbrius**）について言及する余地がなくなったが、分布図だけは第3図にしめしておいた。ゴギの現在における南限は先に少しふれたように、山口県錦川源流で北緯三四度一〇分であるから、本州のイワナの南限はゴギではなくて和歌山県日高川上流のトチンド谷のキリクチに落着く。本稿では南限地帯のイワナということなので、ゴギについてはいろいろ面白い問題もかかえているが、今回は割愛する。昨年オランダから出版されてイワナに関する純学術専門の大著バロン編著『イワナ…サケ科魚類のイワナ属』全九二八頁ではカーベンダー、ベンケ両博士はかつて今西錦司博士（一九六七）が主張したように日本のゴギの特異性をみとめて、狭義のいみのイワナ **Salvelinus leucomaenis** とは分類学的には極めて近縁の関係にあるとした。しかし種々の形態的な点を比較すれば、前記のイワナとは別種とする程の違いはないとみている。

頭上にも白斑のある鳥取県三朝町
天神川源流のイワナ、ゴギに近い？
標高750メートル

附記　筆者はこの報文のなかで一部のイワナの生息場所について具体的に地名を明記した。専ら生物地理学の立場から論述したもので、地名抜きでは成りたたない。学者は真実を報告する義務があると信ずるからである。稀少生物に対する自然保護の問題とは次元を異にするが、南限のイワナについても絶滅することのないよう乱獲は勿論つつしまなければならない。

岡山県吉井川源流で出会った　タンブリ（イワナ）・ヒラメ（アマゴ）釣りの村漁師（p. 75）

撮影＝安江安宣

別冊フィッシング　**イワナ・ヤマメ**　釣魚シリーズ①

発行人　松山[illegible]　発行所　産報出版株式会社　1981©
編集人　吉本万里　〒110　東京都台東区東上野4－25－18
企画編集　稲垣智之　振替東京1－58204

Dorofeyeva et. al. 1980 V. I. 5(771-791)

Savvaitova – 3 primitive sp. fontinalis, namaycush, leucomaenis

more derived – S. alpinus complex – w/ 3 forms – alpinoid, high Arctic, malmoid

but convergent evolution, of all types – not phyletic

Glubokovsky 1977, 779 numerical tax, skull bones

Viktorovsky – 75 – *(error – used phenetic methods – phenogram to derive phyletics believed to be cladogram)

→ 2 ancient groups

① Arctic group w/ alpinus & derivatives fontinalis, namaycush

② Pacific group – leucomaenis malma

stone char S. albus

Colo-R. - basin, fishes - 4 - what happened (mil)

E.S.A. — Presence - essentially forever - Psycho lu - but - rather rapid fluctuation human social - few yrs - snail darter.

squaw - gone long way

New enviro - multi-million $ - su - striped bass

humpback - · history - 63 Udall (Gen. study), 64 humpback, squawfish

- belly - 73 ESA

- No continuity - no real competence, low priority

- bonytail - very predictable - conditioned crisis to crisis

- ?

- razorback sucker - Watt - no need change law - but don't let interfere

- 1982 - come up w/ all answers - 50% - possible.

Key 7.5 mil a.f. - L. Powell - if hydrograph arranged

but - 1. 45 mil / 10 yrs. 2. St. water rights

3. Agencies responsible - L. Powell striped bass - if conflict?

impacts? peak power daily 40-40 VVV

- Need Trust Fund - Not FWS - Greyrocks -

- high level - Sec. Int. Congress work out water mgt. plan

- 2 sections

Review Loveladys
cc. - Binns - Hickman

- T shirt Baldes

Loveladys - magnitude of dif
- yr. class
- between polymorphism
mice, fruit flies
time of yr. - temp,
pop. density

— come Fr.
Collins
2nd week ~~Jan~~ 15 July

Ted Cavender S. alpinus specimen
NWT. (Hatchery) 2N=78 98 arms
— Nygren S. alpinus 80 / 100 but
counted 2 fragments
N. Washg. Vikarnola
2N = ~~76~~ 78 96 arms
South. mts. 82 - 98 arms (Cavender)
+ Japan
— J. East / N. Am 82
albus - Kronocius 78 / 102 Cav confs
+ S. confluentus ?
78 - /100

INTERNATIONAL SYMPOSIUM ON ARCTIC CHARR

Winnipeg, Manitoba
May 4-7, 1981

February 3, 1981

Dr. R. Behnke
Dept. of Fishery and Wildlife Biology
Colorado State Univeristy
Fort Collings, Colorado
U.S.A. 80523

Convenor:
L. Johnson

Secretary:
R. Moshenko

Program Chairman:
R. McV. Clarke

Local Organization:
A. Kristofferson

Information:
F. Frittaion

Local Committee:
T. Dick
E. Gyselman
S. Leonhard

Corresponding Member (Newfoundland):
B. Dempson

Dear Dr. Behnke:

We were very pleased to receive the abstract of your paper entitled "Organizing the diversity of the Arctic charr complex" which will lead off the session on Taxonomy. Your paper has been scheduled provisionally for Tuesday, May 5 at 0900-0930.

Please note that 30 minutes is available for your presentation and for any specific questions relating to it. There will be an opportunity for general discussion of yours and related papers later.

We would be most grateful if you would send us the final typed version of your paper by March 31 so that we would be able to discuss any editorial changes with you during the Symposium. We are still investigating the most suitable forum for publishing the proceedings of the Symposium.

We will let you know by the end of February whether we can offer you any assistance with travel and accommodation expenses.

The preliminary program and registration forms will be sent out in mid February.

We are looking forward to your participation in the Symposium.

Yours sincerely,

R. McV. Clarke, Chairman
Program Committee
International Symposium on Arctic Charr
Department of Fisheries and Oceans
Freshwater Institute
501 Univeristy Crescent, Winnipeg
Manitoba CANADA R2T 2N6

INTERNATIONAL SYMPOSIUM ON ARCTIC CHARR

Winnipeg, Manitoba
May 4-7, 1981

March 4, 1981

Robert Behnke
Department of Fish. & Wildlife Biol.
C.S.U. Fort Collins, Co.
U.S.A. 80523
Colorado,

Dear Colleague:

With respect to your request for financial assistance towards the cost of attending the International Symposium on Arctic Charr the Awards Committee is pleased to provide:

$ 450.00

Cheques will be available when you register in person at the time of your arrival for the Symposium.

Yours sincerely,

Lionel Johnson

for C. Austen
Chairman, Finance Committee

CA/dh

Convenor:
L. Johnson

Secretary:
R. Moshenko

Program Chairman:
R. McV. Clarke

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T. Dick
E. Gyselman
S. Leonhard

Corresponding Member
(Newfoundland):
B. Dempson

alpinus – malma
– fluvial – anadromous
– southerly

lacustrine
assoc. anad.
spawning
rearing

predator – non
– kype
non kype

[illegible]

– alpinus

Winnipeg Symp. May 81

– utilization – Europe – vs N. Am.

– Hatchery rearing –

since 1978 – E. Arctic type
anads + lacustrine resident E. Arctic
Labrador anad. –
Norwegian – resident S, a, a,
lacustrine

Mysis – 2n morpho dims
ontogeny – as 2 sp.
– more effective pelagic than R.K. & Sal.
benthic – pelagic – than kokanee
– Campbell – trophy salmo
–

niche not currently utilized – combination part of – ~~R.~~B., Kokanee, lake trout, brook trout.

Morton Herop ~~ters~~
* Forage ~~Fish~~ Species Selection J.R. Sibley & T. Powell, 1980
12 p. – F-053-R-05 / FM

c Evol. - Coregonine. Coregonus - Salvelinus lacustrine compet w ex -

- S, Trutta Alpine lakes -

N. Am. - namaycush -

A erythrinus - Taimyr - 30 lb. +

- Brit. Isle - ex. degree dif loch - loch.

in 10,000 yrs - ~~Sweden~~ Scandanavia -

but - - 21-28 26 33 Coronarisalm

- w/ autumnalis

A coexistence ± environm - influence size

- Sunapee - large - Rangeley - small - Newfundlas Tiny Candlestick R.

- due to dwarf - normal - wildtype Schwartzreiten

A this plasticity - "fits in" - addition to production

Prosopium cylindraceum

Dalia Catostomus catostomus

Perca

fauna

rearrange - replacement

Amur

Coregonus

2 m

Thym. grub

~~autumnalis~~ - lavaretus

Esox

reicherti

Hucho bleekeri

Siberia   T. arcticus   others   E. reichertii

Amur
W. Pacific – Thymallus grubei   C. ussuriensis, chadary   E. lucius
Sakhalin

Hucho bleekeri   no recent radiation.   Dalia   Catostomus
taimen   Prosop. cylindraceum

- Define Arctic charr – Arctic charr complex.
  - Tax arrangement – sympatric pop. ?
  -- Background – yrs. experience -- altho charr-[illegible]
  Artedi – Linnaeus – morphol. interpretation -- very valid ---
  experience what is ancient (>100,000 yrs) what recent last in 10,000 --
  - electroph. – Karyotypes – – West. Trout borrow from
  + raging controversies even on name char vs. charr.

~~Fatherly~~ Advice
– phenetics
– phyletics
– G.I. – electroph.

prim. – der.
plesio – apo   — ex — esterase –

Coregonus – Selander – very sim. electroph
trout – Sweden   G.I. – – NOT species!
rainbow – Kootenay

– redshiner – Brazos R
dan MDH
cool water form

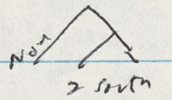
—1

— Percidae - Stizostedion
Perca

Basic Separa

Up. Pliocene - sep. sub genera - Esox
N. Am. americanus
- reicherti
- lucius Pleisto

- Dolly Varden - Bull Str
✓



Coregonus - Amur ussurn
chadary

* groups - mutually exclusive - must have been there ... Iran - Arabia

Cyprinids - Barbus, Varicorhinus, Cyprinion
Cichlids -
obvious - rearrangement, replacement.

— W. Cont. Divide - redband -
inter. cutt, bull trout, above falls

Slides

fine-spotted - yellowstone no dif. at loci
- lake heterogeneity -
dandelion strategy (lngt. implica waste time $, on genetic stock.

Colo. R. Yellowstone coloration

— vast regions, suitable
habitat - unoccupied by
charr (N. Am. fontinalis)

$$\begin{array}{r} .89 \\ 20\overline{)17.8} \\ 160 \\ \hline 180 \end{array}$$

.89

$$\begin{array}{r} 784 \\ .89 \\ \hline 7056 \\ 6272 \\ \hline 69776 \end{array} = \boxed{698}$$

$$\begin{array}{r} .628 \\ .89 \\ \hline 5580 \\ 4960 \\ \hline 6180 \end{array} = \boxed{552}$$

- fanciful beauty - enigma w/ taxonomy

- Sensitive syn. cost doubt on my ~ profundus

+ much resolution needed ex 1980 mono.

- Leggett - - S. malma rep Dolm which is actually S. confluentus

- S. alpinus N. Alaska = S. malma S. e Morrow

Char

Perhaps first admit there will never be a general unanimous agreement on the recognition of species and subsp. genus Salv.

not ~~duplicate~~ repeat my most recent work (B. 1980) but Try to resolve some conflicts

- define Arctic charr - AFS S. alpinus -

- - -

- 72, 80 subgenus Salvelinus

my defin -

empha - Never full aggreement on validity sp. subsp. Arctic charr complex

define Arctic charr S. alpinus

Johnson (80) -

- necessary to erect taxonomy artificial boundaries

major difficulty ay draw line malma - alpinus

- first task clearly - ignore leucomaenis

define the separation betw S. alpinus and S. malma

then assign all see if all ~~no~~ significantly unique to assigned to one or other

'stone charr', 'bull trout',

teifsaecsibliy,

- try not to repeat

-

Similarities - to subgenus Baione - G.S.

technique ^ methods

karyotypes - 25-30 loci

DNA " gene loci G.I >90

level codon

- but sp. recognition

morphol. evol not concordant -

much concordance evol, ecol. types

to evol. dim - degree diffs (G.I.) - specializ. ecol. " competitive - inclusion - exclusion

distribution of lim to 200 exclusivity, coevolution w/ interpreted in light of other fish sp.

Lindsey 64 lake trout lim

- coevolution - bull trout cult. fm non pros S. c. l...

- rare w/ redband isolate

(karyotypes - gene loci not as comprehensive

- sympa. -

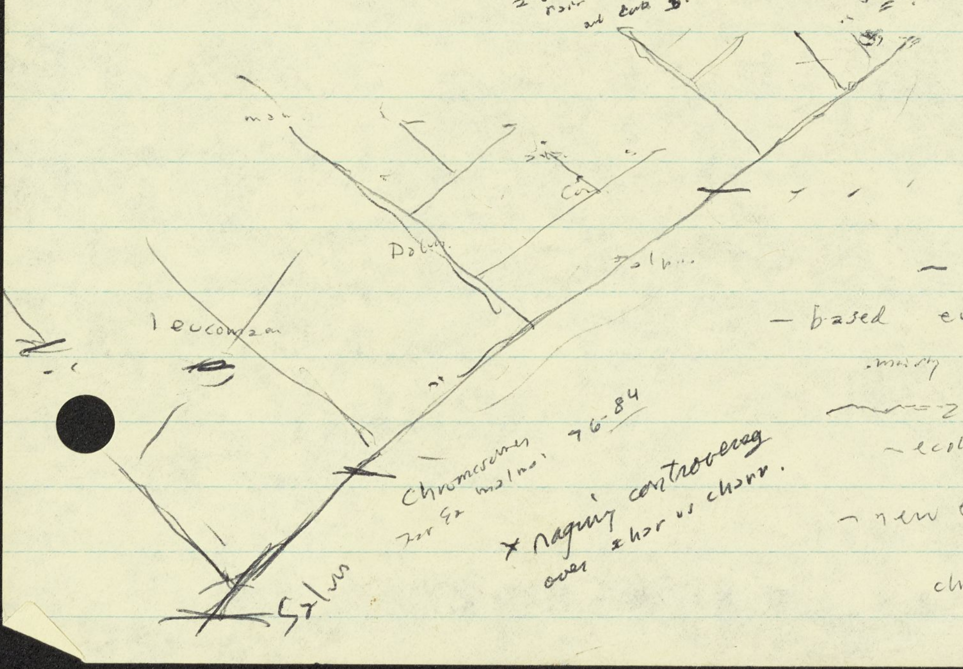
- comments for mgt.

dev as w/ Pars Jor

- whit gr 56 (S. spp) Dolly ... Coastal cutt rainbow

61-70 (S.c.c.)

but ... 2 ... 58-64 ... 64-68 (70) - but not Robertsonian fusion !



Chromosomes 76-84 for Sa malma

* raging controversy over char vs charr.

validity malma

Cheveshaw -

Delacy . Morton 142

- Verification

- based evidence - morphological comparison

. meristic gillrakers, ... vert., ... spots

- zoogeographical evidence

- ecological, life hist. - food, ..., spawn

... predation ...

- new evid. karyotypes.

gene loci - >90% GS 25-30 loci

chromosomes -

- can really take cladistic sense Y.

cutts - coastal

photos - slides

* redband -

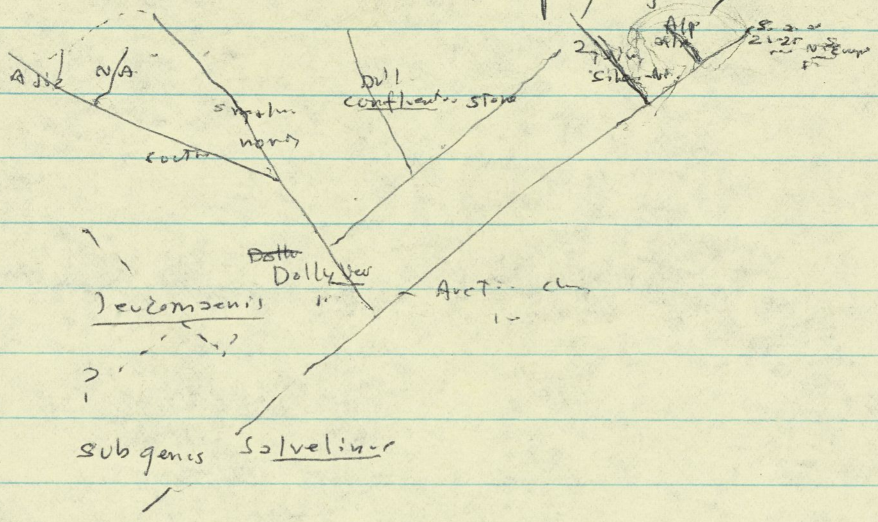
- stone charr

- leucomaenis

- Japanese

- namaycush, fontinalis

- phylogeny



- Why again - review controversy

lively, passionate.
emotions

- common name r/rr - R. Bailey set back 50 yr

- Introd. - basis Tax. - limits binomial.

- Evidence: morphol. - biochem - karyotyp. - DNA h.

- 2) prob based on assumpt. - grad accumul dif

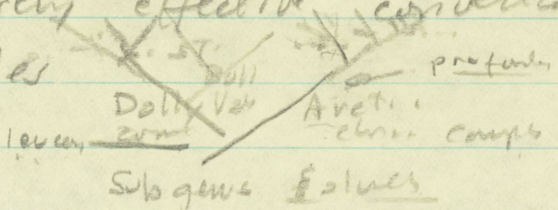
prob. ~~Seud~~ 2 genomes structural - morph —
metabolic regul

time not sufficient - brings in Parasalmo

- Distrib. - very limited. much opportunity introduction

very effective converting lakes oligotrophic - high qual.

Slides



- slides types char

- bull - stone . .

- CVtt - S.R. - Yellowstone 26 loci, no dif

- golden - RB - no dif

karyotypes 68-70-66-64 64

60

58-60-62-64 56

NTIS SFCSI 76-01

Transl. fm. Sci. Lit. 74-75

PB 80-155062

ibid 78-79

PB-278 430T

ibid 76-77

Ex. Fish eating birds and their significance in fish economy

1976 335p. · Moscow 1965 - · USFWS -

NTIS ~~74-75~~

Russian - English Glossary of fishing & related marine terms. 184 p.

TT-73-50005 PC $7,50 Min 2,25

NA

TT-60-21648 | 1960-73 NTIS |

$6,00

Some morphological characters of trout from 14 p.

Lake Mavrovo and the river Radika · USDI

Transl. of Zavod za Ribarstvo za NR Makedonije

Izdanija 1955 · vol 1(5): 135-147 by M. Sidorovski

→ 80 book charr – no symp – little agreement –
– – – – – – disagreements ..
.. name #/#W –
– now Arctic charr – what is it – L. Johnson ..
– .. Now I'll attempt tell you – –
– 3 subgenera – 1 subg.
– 2 complexes – Dolly Varden – Arctic charr
– my views –

– Parasalmo

– Admonition – phenetic vs phyletic G.I. –
– Esterase – – but – Brazos R. dom MDH N. lutrensis
Karyotypes
DNA hybrid. –

– Pract. appl.

– zoogeogr. – open niche – accumul. biomass –
Sawtooth L. .. – plastic ..
* Rangeley – large / dwarf.
* charr – eat Mysis ? – namaycush –
Twin L. Dillon – Ch → kokanee ↓ Tahoe –
Kootenay – shallow → zooplankton
+ interaction – Superior – namaycush –
– distrib. determined by coexistence or elimination
– Mix up Confus tax. – biol.
– evol. special. – rather quick ex. Brazos R.
convergent evol. – anadromous, predaceous.
S. trutta – L. Bjornavatn – Ireland – 3 pop. L. Neagh
– ancient sp.
– Mc. Goreg. clupeaformis
lets stop looking for sp.! – functionally yes, biol. yes
– but – unless every symp. pop – named – polyphyletic sp..
– not good! – – forget obsession – for all fitting to sp.
– C. peled – lavaretus super sp baunti w/ albula

mistake of
Svardson
– biol.
basically
correct
– but Mayr
symp. speciation

– Homo sapiens

– Sympatry – reprod. isol. = species – biol. sp. concept – E. Mayr. 1942 – – – Svardson – biol. v. tax. wrong

Now w/ electrophores. — Sweden, Ireland, brown trout – Maine whitefish – Grt. Lake – .98. .99

G.I. = phenograms not phylo. or cladograms

*biol. mgt. species

25 species

– Salmonid homing behavior – short geol. time ecol. dif. – ecol. sep. – Trajnar & Behnke cutt. r

steelhead rainbow runs

mgr. 25 sp.

← I borrow heavily from Parasalmo – comparable to subgenus Salvelinus time due diversity ecol. forms, plasticity, tax. problems –

- Review evidence electrophor., karyotypes. – more than any other sp. – yet! – My methods same as Peter Artedi – but phenotype – critical smaller much greater part of genome evaluated.

- Also zoogeogr. evidence – distrib. of forms – sp. – when not in isol. – other comp. gr. – ~~ancient~~ advances times of mut. establish. — bull trout – ~~al~~ stone.

N. Am. – As.

rB – cutts

– Salvelinus – 3 subgenera

2 N. Am. ~~tal~~ namaycush fontinalis ——×

- Sal. – 2 complexes Dolly Varden (Pacific) – Arctic char – ?

. N. Pacific 2 ancestors sep. – Plio – Pleisto

- Dolly Varden complex much more complex than rest –

– first – stone & bull – albus (kronocius) – confluen.

N. As

- Dolly Varden – North (S. m. m.) Kamchatk —— McLean

– Southern – Asia – N. Am. Chukotka

curilus – pluvius – lordi

* North – symp. – w 2 curilus alpinus –

South symp. – Alaska –

* first defined malma! Karluk L. 1948 Morton

- S. leucomaenis ? – note large spots – character displ.

– Alpinus – 3 major groups – Centers origin

S. a. a. (Swed. Lappland) → oquassa, salvelinus

– S. a. erythrinus – Baical – Taimyr – Okhesdun – Okhotz – Taimyrus drjaugin neiva – E. Arctic

- book -

- Obvious question
- Why need for ~~another~~ charr symp. -
- 1980 Monogr. - - - - but can we even define Arctic charr
- My paper. 72-80 - - ~~let's~~ page three - -
- Savvaitova rebuttal - Dolly Varden (malma) & Arctic charr = synonym
- (hope to demonstrate to any reasonable person = grasping at straws - -) - × Chereshnev - suppers in Vop. Ikh.
- Reprod. behav. Dolly Varden Kootenay L. (Columb) = confluentus (is bull trout - S.c. part of Arctic charr complex?)
- Cavender imbrius & pluvius - sp. I said
S. leucomaenis subsp. malma - part of complex?
Kundscha or whitex

~~ation~~ Tiefseesaibling - - - vague obscure re/ genetics/ environment
Brenner - only local environment response - Nonsense
is Tiefseesaibling part complex?
- Lionel Johnson's chapter - S. alpinus
~~excellent~~ - - - but malma - alpinus
west. Arctic - S. alpinus = S. m. m
A. Pen McKenzie
*- type ~~spelocality~~ malma.
- Charr vs char ?? even spelling -
fish of exquisite beauty - ~~raise~~ stimulate intense to raise emotions - ~~excites~~ emotion - rejuvenates the spirit & intellect. - - - Vadim Vladykov - Cristoviaque
- - My task organize diversity to define Arctic charr complex & sp. S. alpinus - - -
Need ground rules of game - - As first speaker I invoke old principle of English Common Law - Precedence - - i.e. my rules have more import than yours - -
- First ~~taxonomy~~ prob. classif. - conflicts taxonomy - biology - Intl. Rules - - bi-Trinomial - limits cannot organize properly such diversity.!
- ~~Chars~~ Evidence - rules of - (court + fair hearing) strict adherence prim. (plesiomor) derived - advanced (apomorphic) - - -
Ex. Esterase F S int - - -
not ples - apo - in fact - convergence -
red shiner Brazos R. MDH coolwater type -
- Sp. - 3 sp. monophyletic - - - - great care in speaker or specie! -

Iceland
Jap -
leucomaenis
Iceland
[illegible]

Tax!
4 sp. Kamchatka
leuco
alpinus
alpinus
malma
malma - composite
= w. Arctic
alpinus

Type locality Dolly Varden name
Ssc. R. = bull trout

monophyletic

LDH
mice on Isle Mann
winter
summer

Hokkaido
20-22 lakes
Spathemniken
61-63 wet
71-90 cm,
Miyabi - 25 cm
- only native fish, ? no other malma ?

Salmonid evol

- precocial - specialist
- altricial - generalist

genetics? - dwarf - better adapted
resist cancer

Norway - envir. - temp.?
same parents

— —

═ only locus A, a

- but - dwarfs - Me. → 'normal'
clear
cutoff
- sunapee blueback - Sun
- Sawtooth L.
- Alice L.
- Ramborough -

- Nyman - normal - large most
* competitive - widely dist

Exp. Eveslene - stocked → large
→ dwarf
brook trout
fontinalis

one sp. → ways to use fully env
- cichlids - Quartz Creek
polymorphis - -
↓
- Africa - sp flocks
-

Campbell
- Skreslet
- Sawnson